



# Herbivorous and Carnivorous Animals

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## Chapter 1

# Herbivore



A deer and two fawns feeding on some foliage

**Herbivores** are organisms that eat plants. Herbivory is a form of predation in which an organism principally consumes autotrophs such as plants, algae and photosynthesizing bacteria. More generally, organisms that feed on autotrophs in general are known as **primary consumers**. Comes from the Greek suffix "vora" (Greek -βόρα) meaning "which eat".

By strict interpretation of this definition, many fungi, some bacteria, many animals, some protists and a small number of parasitic plants might be considered herbivores. However, *herbivory* generally refers to animals eating plants. Fungi, bacteria and protists that feed on living plants are usually termed plant pathogens (plant diseases). Microbes that feed on dead plants are saprotrophs. Flowering plants that obtain nutrition from other living plants are usually termed parasitic plants.

### ***Evolution of herbivory***



A fossil *Viburnum lesquereuxii* leaf with evidence of insect herbivory; Dakota Sandstone (Cretaceous) of Ellsworth County, Kansas. Scale bar is 10 mm.

Our understanding of herbivory in geological time comes from three sources: fossilized plants, which may preserve evidence of defence (such as spines), or herbivory-related damage; the observation of plant debris in fossilised animal faeces; and the construction of herbivore mouthparts.

Long thought to be a Mesozoic phenomenon, evidence for herbivory is found almost as soon as fossils which could show it. Within under 20 million years of the first fossils of sporangia and stems towards the close of the Silurian, around 420 million years ago, there is evidence that plants were being consumed by insects. Insects fed on the spores of early Devonian plants, and the Rhynie chert also provides evidence that organisms fed on plants using a "pierce and suck" technique.

Herbivory among terrestrial vertebrates (tetrapods) came much later. 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).

During the ensuing 75 million years, plants evolved a range of more complex organs - from roots to seeds. There is no evidence for these being fed upon until the middle-late Mississippian, 326.4 million years ago. There was a gap of 50 to 100 million years between each organ evolving, and it being fed upon; this may be due to the low levels of oxygen during this period, which may have suppressed evolution. Further than their arthropod status, the identity of these early herbivores is uncertain. Hole feeding and skeletonisation are recorded in the early Permian, with surface fluid feeding evolving by the end of that period.

Arthropods have evolved herbivory in four phases, changing their approach to herbivory in response to changing plant communities.

Another stage of herbivore evolution is characterized by the evolution of tetrapod herbivores, with the first appearance in the fossil record near the Permian-Carboniferous boundary approximately 300 MYA. The earliest evidence of herbivory by tetrapod organisms is seen in fossils of jawbones where dental occlusion (process by which teeth from the upper jaw come in contact with those in the lower jaw) is present. The evolution of dental occlusion lead to a drastic increase in food processing associated with herbivory and provides direct evidence about feeding strategies based on tooth wear patterns. Examination of phylogenetic frameworks reveals that dental occlusion developed independently in several lineages through dental and mandibular morphologies, suggesting that the evolution and radiation of tetrapod herbivores occurred simultaneously within various lineages.

## **Food Chain**



Leaf miners feed on leaf tissue between the epidermal layers, leaving visible trails

Herbivores form an important link in the food chain as they consume plants in order to receive the carbohydrates produced by a plant from photosynthesis. Carnivores in turn consume herbivores for the same reason, while omnivores can obtain their nutrients from either plants or herbivores. Due to an herbivore's ability to survive solely on tough and fibrous plant matter, they are termed the primary consumers in the food cycle(chain). Herbivory, carnivory, and omnivory and call be regarded as special cases of Consumer-Resource Systems.

### ***Predator-prey Theory (herbivore-plant interactions)***

According to the theory of predator-prey interactions, the relationship between herbivores and plants is cyclic. When prey (plants) are numerous their predators (herbivores) increase in numbers, reducing the prey population, which in turn causes predator number to decline. The prey population eventually recovers, starting a new cycle. This suggests that the population of the herbivore fluctuates around the carrying capacity of the food source, in this case the plant.

Several factors play into these fluctuating populations and help stabilize predator-prey dynamics. For example, spatial heterogeneity is maintained, which means there will always be pockets of plants not found by herbivores. This stabilizing dynamic plays an especially important role for specialist herbivores that feed on one species of plant and prevents these specialists from wiping out their food source. Prey defenses also help stabilize predator-prey dynamic. Eating a second prey type helps herbivores' populations

stabilize. Alternating between two or more plant types provides population stability for the herbivore, while the populations of the plants oscillate. This plays an important role for generalist herbivores that eat variety of plants. Keystone herbivores keep vegetation populations in check and allow for a greater diversity of both herbivores and plants. When an invasive herbivore or plant enters the system, the balance is thrown off and the diversity can collapse to a monoton system.

### **Feeding strategies**

Herbivores are limited in their feeding ability by either time or resources. Animals that are time limited, meaning they have a limited amount of time to consume the food they need, use a feeding strategy of grazing and browsing, while those animals that are resource limited, meaning that they are limited in the type of food they eat, use a selective feeding strategy. Grazers/browsers tend to be either very large herbivores that need to consume a lot of food in order to maintain their metabolism, or herbivores that have a very short amount of time to eat as much as possible before reproducing, like many generalist insects. Several theories attempt to explain and quantify the relationship between animals and their food, such as Kleiber's law, Holling's disk equation and Marginal Value Theorem.

Kleiber's law explains the relationship between the size of the animal and the feeding strategy it uses. In essence, it says that larger animals need to eat less food, per unit weight, than smaller animals. Kleiber's law states that the metabolic rate ( $q_0$ ) of an animal is the mass of the animal ( $M$ ) raised to the 3/4th power:

$$q_0 = M^{3/4}$$

Therefore, the mass of the animal increases at a faster rate than the metabolic rate. There are many types of feeding strategies employed by herbivores. Many herbivores do not fall into one specific feeding strategy, but instead employ several strategies and eat a variety of plant parts.

Types of feeding strategies:

| <b>Feeding Strategy</b> | <b>Diet</b>            | <b>Example</b>         |
|-------------------------|------------------------|------------------------|
| Frugivores              | Fruit                  | Ruffed lemurs          |
| Folivores               | Leaves                 | Koalas                 |
| Nectarivores            | Nectar                 | Honey Possum           |
| Granivores              | Seeds                  | Hawaiian Honeycreepers |
| Palynivores             | Pollen                 | Bees                   |
| Mucivores               | Plant fluids, i.e. sap | Aphids                 |
| Xylophages              | Wood                   | Termites               |

Optimal Foraging Theory is a model for predicting animal behavior while looking for food or other resource, such as shelter or water. This model assesses both individual

movement, such as animal behavior while looking for food, and distribution within a habitat, such as dynamics at the population and community level. For example, the model would be used to look at the browsing behavior of a deer while looking for food, as well as that deer's specific location and movement within the forested habitat and its interaction with other deer while in that habitat.

This model can be controversial, where critics say that the theory is circular and untestable. Critics say that the theory uses examples that fit the theory, but that researchers do not use the theory when it does not fit the reality. Other critics point out that animals do not have the ability to assess and maximize their potential gains, therefore the optimal foraging theory is irrelevant and derived to explain trends that do not exist in nature.

Holling's disk equation models the efficiency at which predators consume prey. The model predicts that as the number of prey increases, the amount of time predators spend handling prey also increases and therefore the efficiency of the predator decreases. In 1959, S. Holling proposed an equation to model the rate of return for an optimal diet:  
Rate (R) = Energy gained in foraging (Ef)/(time searching (Ts) + time handling (Th))  
$$R = Ef / (Ts + Th)$$

Where s = cost of search per unit time f = rate of encounter with items, h = handling time, e = energy gained per encounter

In effect, this would indicate that an herbivore in a dense forest would spend more time getting handling (eating) the vegetation because there was so much vegetation around than an herbivore in a sparse forest, who could easily browse through the forest vegetation. Therefore, according to the Holling's disk equation, the herbivore in the sparse forest would be more efficient at eating than the herbivore in the dense forest

Marginal Value Theorem describes the balance between eating all the food in a patch for immediate energy, or moving to a new patch and leaving the plants in the first patch to regenerate for future use. The theory predicts that absent complicating factors, an animal should leave a resource patch when the rate of payoff (amount of food) falls below the average rate of payoff for the entire area. According to this theory, therefore, locus should move to a new patch of food when the patch they are currently feeding on requires more energy to obtain food than an average patch. Within this theory, two subsequent parameters emerge, the Giving Up Density (GUD) and the Giving Up Time (GUT). The Giving Up Density (GUD) quantifies the amount of food that remains in a patch when a forager moves to a new patch. The Giving Up Time (GUT) is used when an animal continuously assesses the patch quality.

## ***Attacks and Counter-Attacks***

### **Plant Defense**

A plant defense is a trait that increases plant fitness when faced with herbivory. This is measured relative to another plant that lacks the defensive trait. Plant defenses increase

survival and/or reproduction (fitness) of plants under pressure of predation from herbivores.

Defense can be divided into two main categories, tolerance and resistance. Tolerance is the ability of a plant to withstand damage without a reduction in fitness. This can occur by diverting herbivory to non-essential plant parts or by rapid regrowth and recovery from herbivory. Resistance refers to the ability of a plant to reduce the amount of damage it receives from an herbivore. This can occur via avoidance in space or time, physical defenses, or chemical defenses. Defenses can either be constitutive, always present in the plant, or induced, produced or translocated by the plant following damage or stress.

Physical, or mechanical, defenses are barriers or structures designed to deter herbivores or reduce intake rates, lowering overall herbivory. thorns such as those found on roses or acacia trees are one example, as are the spines on a cactus. Smaller hairs known as trichomes may cover leaves or stems and are especially effective against invertebrate herbivores. In addition, some plants have waxes or resins that alter their texture, making them difficult to eat. Finally, some plants sequester silica inside their tissues. These are basically small pieces of glass that wear down the teeth of herbivores.

Chemical defenses are secondary metabolites produced by the plant that deter herbivory. There are a wide variety of these in nature and a single plant can have hundreds of different chemical defenses. Chemical defenses can be divided into two main groups, carbon-based defenses and nitrogen-based defenses.

Carbon-based defenses include terpenes and phenolics. Terpenes are derived from 5-carbon isoprene units and comprise essential oils, carotenoids, resins, and latex. They can have a number of functions that disrupt herbivores such as inhibiting adenosine triphosphate (ATP) formation, molting hormones, or the nervous system. Phenolics combine an aromatic carbon ring with a hydroxyl group. There are a number of different phenolics such as lignins, which are found in cell walls and are very indigestible except for specialized microorganisms; tannins, which have a bitter taste and bind to proteins making them indigestible; and furanocoumarins, which produce free radicals disrupting DNA, protein, and lipids, and can cause skin irritation.

Nitrogen-based defenses are synthesized from amino acids and primarily come in the form of alkaloids and cyanogens. Alkaloids include commonly recognized substances such as caffeine, nicotine, and morphine. These compounds are often bitter and can inhibit DNA or RNA synthesis or block nervous system signal transmission. Cyanogens get their name from the cyanide stored within their tissues. This is released when the plant is damaged and inhibits cellular respiration and electron transport.

Plants have also changed features that enhance the probability of attracting natural enemies to herbivores. Some emit semiochemicals, odors that attract natural enemies, while others provide food and housing to maintain the natural enemies' presence (e.g. ants that reduce herbivory). A given plant species often has many types of defensive

mechanisms, mechanical or chemical, constitutive or induced, which additively serve to protect the plant, and allow it to escape from herbivores.

## Herbivore Offense



Aphids are fluid feeders on plant sap.

The myriad of defenses displayed by plants means that their herbivores need a variety of techniques to overcome these defenses and obtain food. These allow herbivores to increase their feeding and use of a host plant. Herbivores have three primary strategies for dealing with plant defenses: choice, herbivore modification, and plant modification.

Feeding choice involves which plants an herbivore chooses to consume. It has been suggested that many herbivores feed on a variety of plants to balance their nutrient uptake and to avoid consuming too much of any one type of defensive chemical. This involves a tradeoff however, between foraging on many plant species to avoid toxins or specializing on one type of plant that can be detoxified.

Herbivore modification is when various adaptations to body or digestive systems of the herbivore allow them to overcome plant defenses. This might include detoxifying secondary metabolites, sequestering toxins unaltered, or avoiding toxins, such as through the production of large amounts of saliva to reduce effectiveness of defenses. Herbivores may also utilize symbionts to evade plant defences. For example, some aphids use bacteria in their gut to provide essential amino acids lacking in their sap diet.

Plant modification occurs when herbivores manipulate their plant prey to increase feeding. For example, some caterpillars roll leaves to reduce the effectiveness of plant defenses activated by sunlight.

## ***The Adaptation Dance***

The back and forth relationship of plant defense and herbivore offense can be seen as a sort of “adaptation dance” in which one partner makes a move and the other counters it. This reciprocal change drives coevolution between many plants and herbivores, resulting in what has been referred to as a “coevolutionary arms race”. The escape and radiation mechanisms for coevolution, presents the idea that adaptations in herbivores and their host plants, has been the driving force behind speciation.

It is important to remember that while much of the interaction of herbivory and plant defense is negative, with one individual reducing the fitness of the other, some is actually beneficial. This beneficial herbivory takes the form of mutualisms in which both partners benefit in some way from the interaction. Seed dispersal by herbivores and pollination are two forms of mutualistic herbivory in which the herbivore receives a food resource and the plant is aided in reproduction.

## ***Impacts of Herbivores***

The impact of herbivory can be seen in many areas ranging from economics to ecological, and sometimes affecting both. For example, environmental degradation from white-tailed deer (*Odocoileus virginianus*) in the U.S. alone has the potential to both change vegetative communities through over-browsing and cost forest restoration projects upwards of \$750 million annually. Agricultural crop damage by the same species totals approximately \$100 million every year. Insect crop damages also contribute largely to annual crop losses in the U.S. Another area in which herbivory greatly affects economics is through the revenue generated by recreational uses of herbivorous organisms, such as hunting and ecotourism. For example, the hunting of herbivorous game species such as white-tailed deer, cottontail rabbits, antelope, and elk in the U.S. contributes greatly to the billion-dollar annually hunting industry. Ecotourism is another major source of revenue, particularly in Africa, where many large mammalian herbivores such as elephants, zebras, and giraffes help to bring in the equivalent of millions of US dollars to various nations annually.

## Chapter 2

# Ruffed Lemur

### Ruffed lemurs



Black-and-white ruffed lemur  
(*Varecia variegata*)

### Scientific classification

|          |                              |
|----------|------------------------------|
| Kingdom: | Animalia                     |
| Phylum:  | Chordata                     |
| Class:   | Mammalia                     |
| Order:   | Primates                     |
| Family:  | Lemuridae                    |
| Genus:   | <i>Varecia</i><br>Gray, 1863 |

### Type species

*Lemur varius*  
É. Geoffroy

(= *Lemur macaco variegatus* Kerr,  
1792)

### Species

*Varecia variegata*

*Varecia rubra*



Distribution of *Varecia* spp.  
red = *V. rubra*; orange = *V. v.*  
*subcincta*;  
green = *V. v. variegata*; blue = *V. v.*  
*editorum*

The **ruffed lemurs** of the genus *Varecia* are strepsirrhine primates and the largest extant lemurs within the family Lemuridae. Like all living lemurs, they are found only on the island of Madagascar. Formerly considered to be a monotypic genus, two species are now recognized: the black-and-white ruffed lemur, with its three subspecies, and the red ruffed lemur.

Ruffed lemurs are diurnal and arboreal quadrupeds, often observed leaping through the upper canopy of the seasonal tropical rainforests in eastern Madagascar. They are also the most frugivorous of the Malagasy lemurs, and they are very sensitive to habitat disturbance. Ruffed lemurs live in multi-male/multi-female groups and have a complex and flexible social structure, described as fission-fusion. They are highly vocal, and have loud, raucous calls.

Ruffed lemurs are seasonal breeders and highly unusual in their reproductive strategy. They are considered an "evolutionary enigma" in that they are the largest of the extant species in Lemuridae, yet exhibit reproductive traits more common in small, nocturnal lemurs, such as short gestation periods (~102 days) and relatively large average litter sizes (~2–3). Ruffed lemurs also build nests for their newborns (the only primates that do so), carry them by mouth, and exhibit an absentee parental system by stashing them while

they forage. Infants are altricial, although they develop relatively quickly, traveling independently in the wild after 70 days and attaining full adult size by six months.

Threatened by habitat loss and hunting, ruffed lemurs are facing extinction in the wild. However, they reproduce readily in captivity, and have been gradually re-introduced into the wild since 1997. Organizations that are involved in ruffed lemur conservation include the Durrell Wildlife Conservation Trust, the Lemur Conservation Foundation (LCF), the Madagascar Fauna Group (MFG), Monkeyland Primate Sanctuary in South Africa, Wildlife Trust, and the Duke Lemur Center (DLC).

### ***Evolutionary history***

No mammalian fossil record exists for Madagascar until recent times. Consequently, little is known about the evolution of ruffed lemurs, let alone the entire order Lemuriformes, which comprises the endemic primate population of the island.

Although there is still much debate about the origins of lemurs on Madagascar, it is generally accepted that a single rafting event, similar to the one that brought New World monkeys to South America, occurred around 50–80 million years ago and allowed ancestral lemurs to cross the Mozambique Channel and colonize the island, which had already split from Africa (while it was joined to the Indian subcontinent), approximately 160 million years ago. The resulting founder effect and either non-existent or inferior competition resulted in speciation as the lemur ancestors radiated out to fill open or insufficiently guarded niches. Today, the endemic primate fauna of Madagascar contains over three-quarters of the extant species of the suborder Strepsirrhini, which had been abundant throughout Laurasia and Africa during the Eocene epoch.

## Taxonomic classification



Color print of the two ruffed lemur species from Alfred Grandidier's *L'Histoire politique, physique et naturelle de Madagascar*. (1892)

The ruffed lemur genus, *Varecia*, is a member of the family Lemnridae. The extinct genus, *Pachylemur* most closely resembled the ruffed lemurs but died out after the arrival of humans. The genus *Varecia* contains two species, red ruffed lemurs and black-and-white ruffed lemurs, the latter having three subspecies.

- **Family Lemnridae**
  - Genus *Eulemur*: true lemurs
  - Genus *Hapalemur*: lesser bamboo lemurs
  - Genus *Lemur*: the ring-tailed lemur

- Genus †*Pachylemur*
- Genus *Prolemur*: the greater bamboo lemur
- **Genus *Varecia***: ruffed lemurs
  - black-and-white ruffed lemur, *Varecia variegata*
    - Variegated black-and-white ruffed lemur, *Varecia variegata variegata*
    - Southern black-and-white ruffed lemur, *Varecia variegata editorum*
    - Northern black-and-white ruffed lemur, *Varecia variegata subcincta*
  - red ruffed lemur, *Varecia rubra*

## Changes in taxonomy

Ruffed lemurs, along with several species of brown lemur were once included in the genus *Lemur*. In 1962, the ruffed lemurs were reassigned to the genus *Varecia*.

The red ruffed lemur and the black-and-white ruffed lemur were formerly recognized as subspecies, *Varecia variegata rubra* and *Varecia variegata variegata* respectively. In 2001 both were elevated to species status, a decision that was later supported by genetic research. Three subspecies of black-and-white ruffed lemur, which had been published decades earlier, were also recognized as *variegata*, *editorum*, and *subcincta*, although studies have not been entirely conclusive.

Subfossil remains of two extinct lemur species were initially classified under the genus *Varecia*. Found at sites in central and southwestern Madagascar, *Varecia insignis* and *V. jullyi* were very similar to modern ruffed lemurs, but more robust and assumed to be more terrestrial, and thus more prone to predation by early human settlers. More recent studies have shown that these extinct species had a diet similar to that of modern ruffed lemurs, and that they were also arboreal in nature. Enough differences were demonstrated to merit a new genus, *Pachylemur*. These close relatives of ruffed lemurs are now named *Pachylemur insignis* and *P. jullyi*.

## ***Anatomy and physiology***



Profile of a typical ruffed lemur overbite

Ruffed lemurs are the largest extant members of the family Lemuridae, with an average head-body length between 43 to 57 cm (17 to 22 in) and a total length from 100 to 120 cm (39 to 47 in), while ranging in weight from 3.1 to 4.1 kg (6.8 to 9.0 lb). The thick, furry tail is longer than the body, averaging 60 and 65 cm (24 and 26 in) in length and is used primarily for balance while moving through the trees. Ruffed lemurs exhibit neither sexual dimorphism nor sexual dichromatism, and females have three pairs of mammary glands.



Foot of a ruffed lemur, showing the toilet-claw on the second toe

Ruffed lemurs are characterized by their long, canine-like muzzle, which includes a significant overbite. The face is mostly black, with furry "ruffs" running from the ears to the neck. Depending on the species, these ruffs are either white (*V. variegata*) or deep reddish (*V. rubra*). Likewise, the coloration of the fluffy fur also varies by species, while the coloration pattern varies by subspecies in the black-and-white ruffed lemur. There are also intermediates in color variation between the two species.

As with all lemurs, the ruffed lemur has special adaptations for grooming, including a toilet-claw on its second toe, and a toothcomb.

### **Locomotion**

Ruffed lemurs are considered arboreal quadrupeds, with the most common type of movement being above-branch quadrupedalism. While in the canopy leaping, vertical clinging, and suspensory behavior, are also common, while bridging, bimanual movement, and bipedalism are infrequently seen. When moving from tree to tree, ruffed

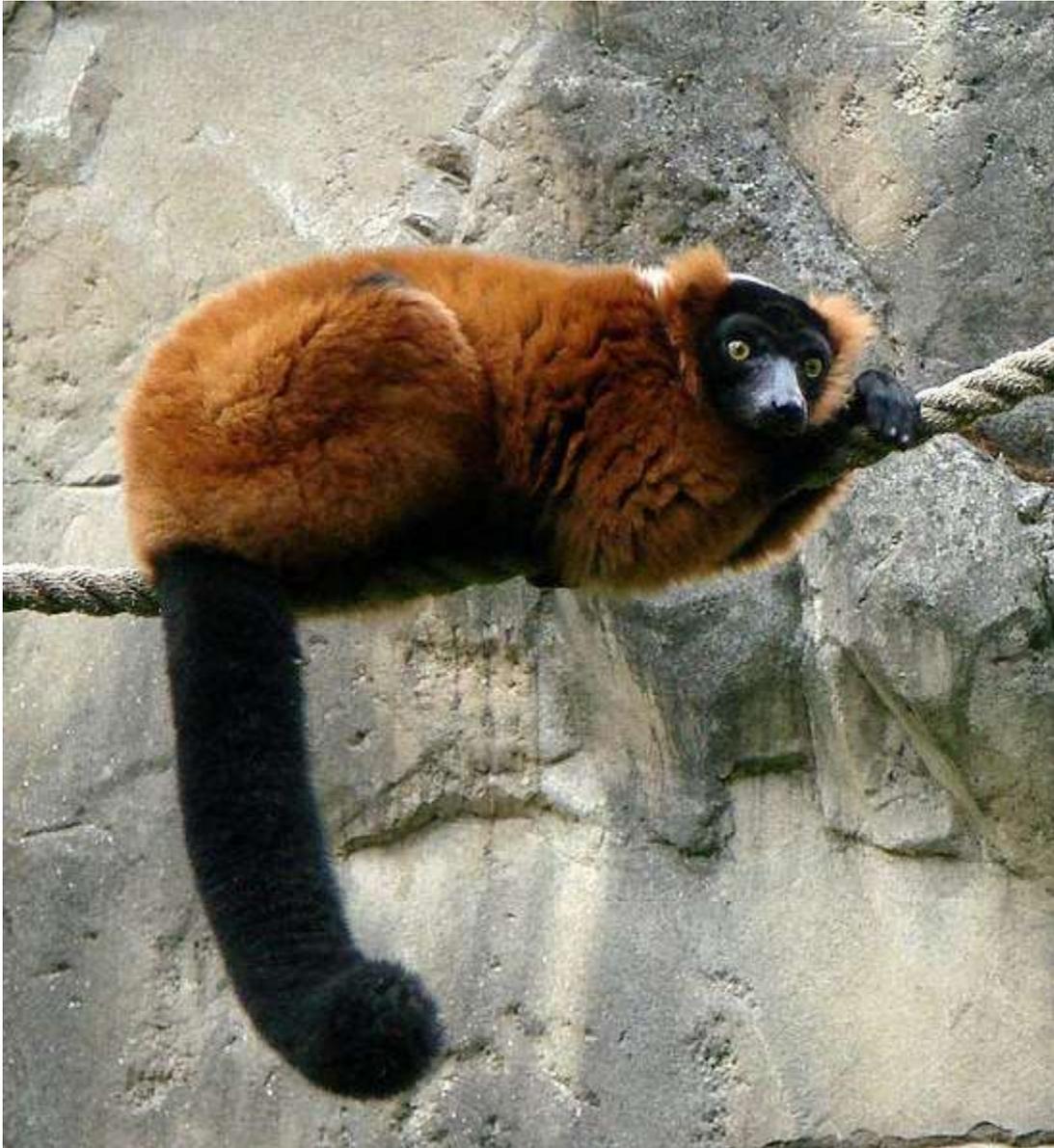
lemurs will look over the shoulder while clinging, launch themselves into the air, and twist mid-air so that their ventral surface lands on the new tree or limb. Suspensory behavior is more common in ruffed lemurs than in other lemur species. When ruffed lemurs come down to the ground, they continue to move quadrupedally, running with bounding hops and the tail held high.

## ***Ecology***

Being highly arboreal and the most frugivorous of the lemurs, they thrive only in primary forest with large fruiting trees, where they spend most of their time in the upper canopy. By spending the majority of their time in the crown of tall forest trees, they are relatively safe from predators such as the fossa.

Ruffed lemurs are active primarily during the day (diurnal), during which time they feed primarily on fruits and nectar, often utilizing suspensory postures while feeding. The seeds of the fruit they eat pass through their digestive tract and are propagated throughout the rainforests in their feces, helping to ensure new plant growth and a healthy forest ecosystem. These lemurs are also significant pollinators of the traveller's tree (*Ravenala madagascariensis*). Without destroying the inflorescence, they lick the nectar from deep inside the flower using their long muzzles and tongues, collecting and transferring pollen on their snouts and fur from plant to plant. This relationship is thought to be a result of co-evolution.

## Geographic range and habitat



red ruffed lemur (*V. rubra*)

Like all lemurs, this genus is found only on the island of Madagascar off the southeastern coast of Africa. Confined to the island's seasonal eastern tropical rainforests, it is uncommon to rare throughout its range, which historically ran from the Masoala Peninsula in the northeast to the Mananara River in the south. Today, the black-and-white ruffed lemur has a much larger range than the red ruffed lemur, although it is very patchy, extending from slightly northwest of Maroantsetra, on Antongil Bay, in the north down the coast to the Mananara River near Vangaindrano in the south. Additionally, a concentrated population of black-and-white ruffed lemurs, of the subspecies *Varecia variegata subcincta*, can also be found on the island reserve of Nosy Mangabe in Antongil Bay. It is suspected that this population was introduced to the island in the

1930s. The red ruffed lemur, on the other hand, has a very restricted range on the Masoala Peninsula.

Historically, the confluence of the Vohimara and Antainambalana Rivers may have been a zone of hybridization between these two species, although no conclusive results have indicated current interbreeding. In general, the Antainambalana River appears to isolate the red ruffed lemurs from the neighboring subspecies of black-and-white ruffed lemur, *V. v. subcincta*. The subspecies *V. v. variegata* can be found further south, and *V. v. editorum* is the southernmost subspecies. The ranges of these two southern subspecies overlap and intermediate forms are reported to exist, although this has not been confirmed.

The rainforests in which these animals live are seasonal, with two primary seasons: the hot, wet season (November through April), and the cool, dry season (May through October). The primary habitat for both species, at any season, is in the crowns of trees, where they spend the majority of their time 15 and 25 m (49 and 82 ft) above ground. With the seasonal availability of resources being similar regardless of location, there is little to no difference in tree usage between species. From September through April, more fruit is available, so females prefer the lianas in the crowns of trees. Both sexes utilize the lower, major branches during the hot, rainy season. The tree crowns are predominantly used from May through August, when young leaves and flowers are in abundance.

### **Sympatric relations**

The following lemur species can be found within the same geographic range as ruffed lemurs:

- Greater dwarf lemur (*Cheirogaleus major*)
- Eastern lesser bamboo lemur (*Haplemur griseus griseus*)
- Weasel sportive lemur (*Lepilemur mustelinus*)
- Diademmed sifaka (*Propithecus diadema*)
- Common brown lemur (*Eulemur fulvus*)
- Red-bellied lemur (*Eulemur rubriventer*)
- Eastern woolly lemur (*Avahi laniger*)
- Indri (*Indri indri*)
- Brown mouse lemur (*Microcebus rufus*)
- Aye-aye (*Daubentonia madagascariensis*)
- White-headed lemur (*Eulemur albifrons*)

Ruffed lemurs either demonstrate feeding dominance or divide resources by using different forest strata. They are dominant over red-bellied lemurs, while eastern lesser bamboo lemurs avoid encountering them all together. White-headed lemurs, on the other hand, utilize the understory and lower canopy, below 15 m (49 ft), while the ruffed lemurs utilize the upper canopy, above 15 m (49 ft). Play has even been observed between infant ruffed lemurs and White-headed Lemurs.

## ***Behavior***

Ruffed lemurs, on average, spend 28% of the day feeding, 53% resting, and 19% traveling, although differences in resting and feeding durations have been observed between males and females, with females resting less and feeding more. They are diurnal; although peak activity occurs during the early morning and late afternoon or evening, resting usually occurs around midday. When resting, ruffed lemurs often sit hunched or upright. They are also frequently seen lying prone over a branch or sunbathing in a supine position with the limbs outstretched. When feeding, they will often hang upside-down by their hind feet, a type of suspensory behavior, which allows them to reach fruits and flowers.

Being highly arboreal, they spend the majority of their time in the high canopy throughout the day. Ruffed lemurs spend the majority of their time between 15 to 20 m (49 to 66 ft) above the forest floor, followed by 20 to 25 metres (66 to 82 ft) up, and are least frequently seen at 10 to 15 metres (33 to 49 ft). During the hot season, they will relocate to the lower canopy to help regulate their body temperature. In the cold season, ruffed lemurs are least active and may dedicate 2% of their resting time to sunbathing in order to warm up.

Long-term field research has shown that range size, group size, social systems, and territorial behavior vary widely, and may be greatly affected by food distribution and quality. It is generally agreed that the ruffed lemur social system is multi-male/multi-female with a fission-fusion society, although some populations of black-and-white ruffed lemur have been reported as monogamous. This social flexibility is suspected to improve survivability despite an inflexible feeding ecology.



Suspensory feeding by a black-and-white ruffed lemur

## Diet

Being the most frugivorous members of the family Lemuridae, consuming an average of 74–90% fruit, ruffed lemurs also consume nectar (4–21%), and supplement the rest of their diet with young leaves (3–6%), mature leaves (1%), flowers (3–6%), and some seeds. Ruffed lemurs have also been reported to come to the ground to eat fungi and exhibit geophagy.

The majority of their diet is made up of relatively few common plant species, with a few species providing more than 50% of the diet. Fig species of the genus *Ficus*, for example, account for 78% of the fruit consumed by red ruffed lemurs on the Masoala Peninsula.

Although plant species and diets vary by location, the most common food plants reported from the field include the following:

- *Canarium*
- *Cryptocarya*
- *Ocotea*
- *Ravensara* (family Lauraceae)
- *Ficus*
- *Eugenia/Syzygium*
- *Grewia*

Fruit trees do not appear to be selected by species, but by availability and accessibility of edible fruit. And despite predominance of a few plant species in the ruffed lemur diet, the remainder of their diet consists of between 80 and 132 other species from 36 plant families.

The availability of food reflects the seasonal nature of the forests in which they live. During the hot season, fruit, flowers, and young leaves are more abundant, whereas the cold, wet season offers more young leaves and flowers. Despite this, the diet changes little between seasons, except that females will consume more high-protein, low-fiber items, such as young leaves and flowers, during pregnancy and lactation in order to offset the energy costs of reproduction. Nectar is only available sporadically, yet constitutes a major food source when the flowers bloom. The nectar of the traveller's palm (*Ravenala madagascariensis*) is a favorite among ruffed lemurs.

## **Social systems**

The social organization of ruffed lemurs is widely variable in both group organization and group composition, although no notable difference can be seen between the two species. Ruffed lemurs are typically described as multi-male groups with a fission-fusion social structure, although this can vary by season and locality.

In a study done at Masoala Peninsula on red ruffed lemurs three levels of organization were identified and defined: communities, core groups, and subgroups. Communities are individuals that affiliated regularly with each other, but rarely with conspecifics outside of the community. Although the entire multi-male/multi-female community lives within a discrete home range, all individuals are never seen in the same location at the same time. Instead, individuals form dispersed social networks, known as core groups, within the community. Core groups are individuals that shared the same core area within a community territory throughout the year. Core groups typically consist of two reproductive females, as well as reproductive males and subadults, ranging in size from two individuals to nine. Females within the groups are cooperative, but male encounters are often agonistic. Subgroups, on the other hand, vary daily in size, composition, and duration, and consist of associated individuals from either the same core group or different core groups, depending on the season. It is from the consistent, daily changes in these subgroups that occur throughout the year, as well as the seasonal formations of core

groups in core areas, that demonstrate the fission-fusion nature of ruffed lemur social structure.



Ruffed lemur sunning position

In another study done at Nosy Mangabe on black-and-white ruffed lemurs a fourth level or organization was defined: affiliates. Affiliates were individuals with more persistent social bonds and more frequent interactions, usually within a core group, but sometimes also between core groups within a subgroup. Adult females typically had many affiliates, whereas adult males rarely interacted with conspecifics, living a more solitary existence.

Past studies have reported other social organizations in ruffed lemurs including monogamous pair bonding. This may have been due to the use of short-term, seasonal

field studies instead of yearlong studies that take into consideration the effects that changing seasons have on ruffed lemur communities. For instance, during the cold, rainy season, which corresponds with the breeding season, interactions between core groups within a community are significantly reduced. During this time small subgroups form consisting of a mature female, a mature male, and sometimes offspring. This can be misinterpreted as monogamous pair bonding.

Ranging behavior can also exhibit seasonal variability. During the hot, wet season, females range widely, either alone or in groups of up to six individuals. In the cool, dry season, smaller core groups stabilize in order to occupy concentrated areas. Therefore, during seasons when fruit is abundant, subgroups are larger while scarcity is met with more solitary behavior. This suggests that although their feeding ecology is inflexible, being tied to widely distributed, patchy, and sometimes scarce fruit, ruffed lemurs instead adapt the social system in order to survive.

In terms of dominance, the ruffed lemur's social structure is not as clear-cut as other lemur societies where female dominance is the norm. Although it is historically reported that "males were subordinate to females," especially with captive and free-ranging ruffed lemur populations demonstrating this, wild populations cannot be definitively labeled as matriarchal due to inter-group variation.

There are also social differences between males and females. Females typically have many affiliates and bond strongly with other females both within and outside their core areas, but do not affiliate with individuals outside the community range, except during mating season. Males, on the other hand, are more solitary, interact with only a couple of conspecifics, have weak social bonds with other males, and rarely associate with others outside their core group. Furthermore, field studies suggest that only females play a role in communal home range defense. Males may scent-mark and remain relatively silent, but otherwise show little involvement during disputes.

Community range or territory size can vary widely, from 16 to 197 ha (0.16 to 2.0 km<sup>2</sup>; 0.062 to 0.76 sq mi) while group size can range from a single pair to 31 individuals. Population density is also noticeably variable. These wide ranges can be attributed to differing levels of protection and degree of environmental degradation, with better protection and a less degraded environment resulting in higher population density and more moderately sized community ranges. (The duration and seasonality of the studies involved may also have contributed to low group size estimates and community ranges. A study at the Betampona Reserve, for instance, observed monogamous pairs with two to five infants maintaining ranges of 16 to 43 ha (0.16 to 0.43 km<sup>2</sup>; 0.062 to 0.17 sq mi).) Core areas at Ambatonikonilahy constituted approximately 10% of the overall community range and showed a close relationship with the location of the largest fruiting trees.

The average daily traveling distance for ruffed lemurs varies between 436 to 2,250 metres (1,430 to 7,380 ft), averaging 1,129 metres (3,704 ft) per day. Activity patterns within the community range vary by gender and season. Males generally stay within a core area all

year, whereas females only confine themselves to a core area during the cold wet season, then expand their range throughout the community range during the hot, rainy season. Females expand their traveling range slightly after giving birth, still staying within the core area, but gradually range further in December when they begin stashing their infants with other community members while they look for food. Females range the furthest later during the hot, rainy season. Both activity level and reproductive activity can be summarized in the following table.

| Season            | Months           | Stage | Seasonal behavior   |   |                      |
|-------------------|------------------|-------|---------------------|---|----------------------|
|                   |                  |       | Reproductive cycle  | Females activity                          | Male activity        |
| hot, rainy season | November – April | early | Infant rearing      | Expanding travel & infant stashing        | Remains in core area |
|                   |                  | late  | Infant rearing      | Expands travel throughout community range | Remains in core area |
| cool, dry season  | May – October    | early | Mating season       | Remains in core area                      | Remains in core area |
|                   |                  | late  | Gestation and birth | Remains in core area & nest building      | Remains in core area |

Although males demonstrate little involvement in territorial disputes between neighboring communities, and ruffed lemur communities lack cohesiveness, females communally defend the community range against females of other communities. These disputes occur mostly during the hot, rainy season, when resources are more abundant and occur near the boundaries of community ranges. Spacing is maintained by scent marking and vocal communication. Ruffed lemurs are known for their loud, raucous calls that are answered by neighboring communities and subgroups within the same community.

During agonistic encounters between communities, chasing, scent-marking, calling, and occasional physical contact can be seen. Other social behaviors appear to vary between wild and captive ruffed lemurs, as illustrated by the following table.

Behavioral differences: captive vs. wild

|                                       | Wild behaviors   | Captive behaviors  |
|---------------------------------------|--|--|
| <b>Aggressive/Agonistic behaviors</b> | <ul style="list-style-type: none"> <li>• attacks</li> <li>• cuffs</li> <li>• grapples</li> <li>• chases</li> </ul> | <ul style="list-style-type: none"> <li>• stare</li> <li>• charge</li> <li>• chase</li> <li>• lunge</li> <li>• cuff</li> <li>• feint-to-cuff</li> <li>• bipedal hop</li> <li>• pounce on</li> </ul> |

### **Submissive behaviors**

- chatter vocalizations
- push down
- bite
- displacement
- head turning/eye aversion
- cowering/flinching
- grimacing
- backing away
- fleeing
- jumping away

### **Affiliate/Affinitive behaviors**

- female greeting behavior (intertwining and scent marking)
- play
- social grooming
- squeal approach / anogenital inspections (males, mating season only)
- group movement
- huddling together with bodily contact
- greeting by sniffing
- play (wrestling, grappling, chasing, fleeing and solitary play)
- social grooming

Some affiliative behaviors are seasonal or gender-specific, such as the male squeal approach and anogenital inspections performed during the mating season. Another example is the female greeting behavior, where two females will use their anogenital scent glands to mark each other's backs, jump over one another, writhe together, and emit squealing vocalizations. This behavior is not seen during the end of the cool, dry season or around gestation. The frequency of other affiliative behaviors can be affected by age. All ruffed lemurs over five months of age allogroom, and, in captivity, subadults participate in play more frequently than adults.

### **Cognitive abilities**

Historically, relatively few studies of learning and cognition have been performed on strepsirrhine primates, including ruffed lemurs. However, a study at the Myakka City Lemur Reserve demonstrated that ruffed lemurs, along with several other members of the family Lemuridae, could understand the outcome of simple arithmetic operations.

## Communication

### Olfactory communication

As with all prosimian primates, olfactory communication is used extensively by ruffed lemurs – scent marking in territorial defense and disputes, as well as female greeting displays. The scents communicate the sex, location, and identity of their owner.

Females predominantly scent mark with their anogenital scent glands, by squatting to rub their anogenital region along horizontal surfaces, such as tree limbs. Males, on the other hand, favor using the glands on their neck, muzzle, and chest, by embracing horizontal and vertical surfaces and rubbing themselves over them. Both sexes will occasionally scent mark in ways characteristic of the opposite sex.

In greeting displays, female ruffed lemurs will leap over one another, scent marking the other individual's back in the process.

### Auditory communication

Ruffed lemurs are highly vocal, with an extensive vocal repertoire with calls being used in multiple contexts. Calls can also vary seasonally. During the hot, rainy season, the loud, raucous calls that are a hallmark of ruffed lemurs allow groups to remain in contact and maintain spacing. These loud calls can be heard up to 1 kilometre (0.6 mi) away.

Ruffed lemurs utilize alarm calls that differentiate between ground and aerial predators. For instance an *abrupt roar* or *huff* alerts the group to an avian predator, and a *pulsed squawk* or *growl-snort* communicates the existence of a mammalian ground predator. When sounding these calls, such as the pulsed squawk, adults direct them at the predator after moving to a safe position. Once the alarm call is sounded by one individual, the resulting chorus can even reach the furthest ranging community members.

In captivity, ruffed lemur vocalizations have been studied and divided into three general groups: high-, medium-, and low-amplitude calls.

|                           | High-amplitude calls   |
|---------------------------|--|
| Call                      | Inferred Function  |
| <b>Roar/shriek chorus</b> | <ul style="list-style-type: none"><li>• Intergroup communication and spacing</li><li>• Intragroup communication (unspecified social functions)</li></ul> |
| <b>Abrupt roar</b>        | <ul style="list-style-type: none"><li>• Signals disturbances</li><li>• Promotes intergroup spacing</li><li>• Avian predator alert</li></ul>              |
| <b>Pulsed squawk</b>      | <ul style="list-style-type: none"><li>• Mammalian predator alert</li><li>• Indicates high arousal</li></ul>  |

- Call group together
- Wail**
- Signals end of disturbance
  - Calls group together
- (*V. variegata* only)
- Bray**
- May serve a mating function (males only)
- Quack**
- May serve a mating function (males only)

The well-known *roar/shriek chorus* is spontaneous, occurring most often during period of high activity, as well as being contagious, involving communal participation including infants three to four months old. *Abrupt roars* are also more common during high activity and aside from alerting group members to the presence of an avian predator, they probably also help maintain contact with individuals outside of visual range or indicate an aggressive/defensive response to a disturbance. In the wild, both of these calls are emitted more during the hot, rainy season due to heightened activity. All high-amplitude calls are delivered with from a "taut" body posture.

| Call   | Medium-amplitude calls  | Inferred Function |
|--|---|-------------------|
| <b>Growl</b>   | <ul style="list-style-type: none"> <li>• Alerts group to low-level disturbance</li> <li>• Announces individual's approach</li> </ul>                                      |                   |
| <b>Growl-snort</b>   | <ul style="list-style-type: none"> <li>• Alerts group to mammalian predator or other startling context</li> </ul>   |                   |
| <b>Chatter</b>   | <ul style="list-style-type: none"> <li>• Signals submission</li> <li>• Signals subordinate status</li> </ul>  |                   |
| <b>Whine</b>   | <ul style="list-style-type: none"> <li>• Behavioral frustration</li> <li>• Signals submission</li> <li>• Signals appeasement during mating season (males only)</li> </ul> |                   |
| <ul style="list-style-type: none"> <li>• <b>sample 1</b></li> <li>• <b>sample 2</b></li> </ul> |   |                   |

Medium-amplitude calls operate over a shorter range or often involve moderately arousing situations, such as frustration or submission. Low-amplitude calls also generally operate over a short range, yet also cover a wider range of aggravation levels.

Whines are highly variable between individual ruffed lemurs. *Cough*, *grumble*, *squeak*, and *squeal* have only been observed and researched in the wild.

## Low-amplitude calls

| Call  | Inferred Function   |
|---|---|
| <b>Grunt</b>  | <ul style="list-style-type: none"><li>• Indicates mild aggravation</li></ul>  |
| <b>Huff</b>   | <ul style="list-style-type: none"><li>• Indicates intense aggravation or high level arousal</li><li>• Aggravation when avian predator is present</li></ul>                |
| <ul style="list-style-type: none"><li>• <b>2 huffs</b></li><li>• <b>3 huffs</b></li></ul>   |   |
| <b>Mew</b>  | <ul style="list-style-type: none"><li>• Contact call between mother and infant</li><li>• Occasionally used for coordination between individuals while traveling</li></ul> |
| <ul style="list-style-type: none"><li>• <b>sample 1</b></li><li>• <b>sample 2</b></li></ul> |   |
| <b>Cough</b>  | <ul style="list-style-type: none"><li>• Aggression between a female and male during mating/birth seasons</li></ul>  |
| <b>Grumble</b>  | <ul style="list-style-type: none"><li>• Advertises the presence of a male to another</li></ul>  |
| <b>Squeak</b>   | <ul style="list-style-type: none"><li>• Infant distress signal</li></ul>  |
| <b>Squeal</b>   | <ul style="list-style-type: none"><li>• Female affiliation</li></ul>  |

The calls of ruffed lemurs vary only slightly between the two species. In fact, in captivity, it has been documented that red ruffed lemurs understand and even join in the alarm calls of black-and-white ruffed lemurs. One minor difference between the vocal repertoires of these two species is in the pulse rate and frequency of the *pulsed squawk*, which is much faster and higher in red ruffed lemurs than in black-and-white ruffed lemurs. The difference in this vocalization is only interspecific, showing no signs of significant sexual dimorphism within each species.

Red ruffed lemurs do not appear to produce a bona fide *wail* vocalization. In black-and-white ruffed lemurs, *pulsed squawks* sometimes slow down as the group calms down, and integrate with the *wail*, creating *pulsed squawk-wail intermediates*. red ruffed lemurs also produce *pulsed squawk-wail intermediate* sounds, but they do not exhibit long, drawn-out *wails* like the black-and-white ruffed lemurs.

## Breeding and reproduction

Contrary to initial reports of monogamy, ruffed lemurs in the wild exhibit seasonal polygamous breeding behavior, with both males and females mating with more than one partner within a single season. Mating is not restricted to just community members, but

also involves members of neighboring communities. Females mate primarily with males with whom they had affiliative relations prior to mating season, although some matings occurred with roaming males from other communities.

Shortly before mating season begins, females exhibit swelling of the sex skin, which reaches its peak around the middle of their 14.8 day estrous cycle. Male sexual physiology also undergoes its own change, with testicular volume increasing during mating season, peaking around the time of breeding. Aggression also increases during the mating season, both between members of the same sex and by females towards the male attempting to mate with her. Females have been observed grappling, cuffing, and biting the male during copulation. Either sex may approach the other when the female is in estrus. Initially they may *roar-shriek* with each other. When a male approaches a female he often lowers his head and squeals, inspecting the female's genitalia by licking or sniffing, scent-marking, and offering a submissive chattering vocalization. When a female approaches a male, she may posture herself for mounting. Mating pairs often copulate many times during the course of a mating bout.

The mating season lasts from May through July, during the cold, rainy season, resulting in birth and peak lactation coinciding with the time that fruit is the most plentiful. The gestation period of ruffed lemurs is the shortest of the family Lemuridae, averaging 102 days (with a range of 90 to 106 days). Gestation in the wild last slightly longer than in captivity, averaging 106 days. Just like the mating season, parturition is also seasonal, synchronized to the end of the cold, dry season and the start of the productive hot, rainy season.

In addition to an abnormally short gestation period, ruffed lemurs share another feature with small, nocturnal lemurs by producing the largest litters of the family Lemuridae. Litters typically include two or three infants, although up to five have been reported. Birth weights in captivity average between 83 to 101.7 g (2.9 to 3.59 oz) and range from 70 to 140 grams (2.5 to 4.9 oz). Ruffed lemur infants are altricial, and are born with their eyes open and a full coat of fur.



Female ruffed lemurs have three pairs of mammary glands for feeding their large litters

Ruffed lemurs are the only known primates to build arboreal nests, used exclusively for birth and for the first week or two of life. Starting three weeks prior to birth, females begin constructing the nest from twigs, branches, leaves, and vines, locating it within her core area and 10 to 25 metres (33 to 82 ft) above ground. The nests have only one apparent entry point, and are shallow and dish-shaped. During the first couple of weeks, the mother is mostly solitary and does not travel far from the nest, spending as much as 70–90% of her time with the newborns (in captivity). In order to find food, she will leave the infants alone in the nest or, after the first couple of weeks, will carry them in her mouth and stash them in concealed locations in the canopy while she forages. Since this early developmental period corresponds with the end of the cold, dry season, which offers the least amount of fruit, energy is conserved for lactation while travel is limited. As the hot, rainy season begins, fruit availability rises, lactation demands rise as well, and females increase their travel distance in search of food.

Unlike other diurnal primates, which usually carry their infants with them, ruffed lemur mothers will stash their young by concealing them in the canopy foliage, leaving them to rest and sit quietly for several hours while she forages and performs other activities. Mothers continue to transport their offspring by mouth, moving them one at a time by grasping the infant's belly crosswise. This form of transport usually stops around 2.5 months of age when the infants become too heavy to carry.

Ruffed lemurs are cooperative breeders, with parental care being shared by all community members. For example, mothers will stash their offspring with other mothers or leave them to be guarded by other community members, including non-breeding individuals of both genders. While the mother is away, community members will not only care for and guard them, but also sound alarm calls if danger is detected or if leaving the infant alone. They will also respond to alarm calls by others. These coordinated vigilance displays further involve communal transmission of the alarm call, with nearby community members repeating the alarm call, potentially summoning the mother back to her offspring. Infant transport by other members of the community has also been recorded. Females have been observed nursing infants of their close relatives, while close kin have adopted rejected infants, acting as foster parents.

Male care for infants has been documented in ruffed lemur societies. During early development, adult males may guard the nests of multiple core group females, as well as help care for the infants that were likely fathered by other males. During the season when females practice infant stashing, males effectively lighten the reproductive burden of up to several mothers by guarding, huddling, grooming, travelling, playing with and feeding the young.

Female ruffed lemurs produce relatively rich milk compared to other lemurs, and consequently, their young develop faster than those of other lemurs. Infants develop rapidly, attaining approximately 70–75% adult weight by the age of four months. They begin climbing and clinging at one month of age, advancing to the point of independently following their mother and group members through the canopy at heights of 50 to 100 metres (160 to 330 ft) by two to three months. Full adult mobility is attained at three to four months of age. Socially, they begin exchanging contact calls with their mother at three weeks, and select their mother as their play partner 75–80% of the time during the first three months. Participation in greeting displays and utilization of more extensive vocalizations commences around four months, while scent marking does not start until six months of age. Infants begin testing solid food starting around 40 days to two months with weaning occurring between four to six months in the wild, although some individuals have continued to nurse until seven to eight months.

Infant mortality is often high among ruffed lemurs, but can also be highly variable. In some seasons, as many as 65% are unable to reach three months of age, possibly due to falls and related injuries, although in some seasons infant mortality is as low as 0%. For those that do survive to adulthood, sexual maturity is attained at 18 to 20 months in females and 32 to 48 months in males. Sexual maturity may take longer to reach in the wild compared to captivity. For females, the inter-birth interval, or time between successive offspring, is typically one year, and in captivity, females can remain reproductively active until the age of 23. The life expectancy for both species of ruffed lemur is estimated at 36 years in captivity, although it is likely to be considerably less in the wild.

## **Conservation status**

In a land where approximately 90% of the original island forest has been destroyed, ruffed lemurs cling to only a small fraction of their original range. Completely dependent upon large fruiting trees, neither species appears to be flexible with its habitat choice, with selective logging resulting in significantly lower population densities. Although they can survive in very disturbed habitats with lower population densities, they are still especially vulnerable to habitat disturbance. Decreased genetic diversity, in tandem with hunting, natural disasters, predation, and disease, can easily wipe out small populations.

The black-and-white ruffed lemur was elevated by the IUCN to Critically Endangered (A2cd) status from Endangered status in 2008. They cite that "the species is believed to have undergone a decline of 80% over a period of 27 years, due primarily to a decline in area and quality of habitat within the known range of the species and due to levels of exploitation." The total area of all known localities in which black-and-white ruffed lemurs exist is estimated at less than 8,000 km<sup>2</sup> (3,100 sq mi), while the total wild population is estimated between 1,000 and 10,000.

The red ruffed lemur was downgraded to Endangered status from Critically Endangered status by the IUCN in 2008. The justification given includes its limited range, its restriction to only the Masoala Peninsula, and its risk from ongoing habitat loss and hunting. This species occupies a range of no more than 4,000 km<sup>2</sup> (1,500 sq mi), while the total wild population is estimated between 29,000 and 52,000 individuals. Red ruffed lemurs are only protected within the boundaries of the Masoala National Park. Historically, this species has been considered more threatened due to its highly restricted range, compared to the widely distributed black-and-white ruffed lemur. However, its protection within the island's largest national park has slightly improved its chances at survival.

There are several organizations involved in ruffed lemur conservation, including the Durrell Wildlife Conservation Trust, the Lemur Conservation Foundation (LCF), the Madagascar Fauna Group (MFG), Monkeyland Primate Sanctuary in South Africa, Wildlife Trust, and the Duke Lemur Center (DLC). To conservation organizations, the ruffed lemurs are considered indicator, umbrella, and flagship species.

## **Threats in the wild**

As with other primates, one of the principal threats to both ruffed lemur species is habitat loss due to slash-and-burn agriculture, logging, and mining. Both species appear to be very sensitive to logging, and are thought to be the most vulnerable of rainforest lemurs. The hardwoods that are favored for construction materials and selectively logged are also preferred by ruffed lemurs for their fruits and potentially affect their travel routes through the canopy. Deforestation, on the other hand, is a result of the need to provide firewood and to support subsistence agriculture and cash crops. For red ruffed lemurs, Slash-and-burn agriculture, known locally as *tavy*, is practiced seasonally on the Masoala peninsula between October and December, and its practice is expanding. Additionally, cattle are

sometimes allowed to free-range over these former agricultural clearings, preventing forest re-growth.

Another principal threat to the survival of ruffed lemurs is hunting. Local human populations still hunt and trap ruffed lemurs with traditional weapons, using them as a source of subsistence. Studies from villages in the Makira Forest have revealed that ruffed lemur meat is not only a desired food, but is being hunted unsustainably. On the Masoala peninsula, the calls of red ruffed lemurs help hunters locate them. On this peninsula, firearms are used in addition to traditional traps, known as *laly*, which involve a 5 metres (16 ft) strip of cleared forest with snares set on the few remaining branches that allow the lemurs to cross. Although hunting is illegal, the laws are generally not enforced and the local inhabitants show little concern about their hunting practices, which occur mostly from May to September. Hunting is the biggest concern in the Masoala peninsula because it is likely to continue, whereas logging and slash-and-burn agriculture could be curtailed. In other regions, hunters can scare away ruffed lemurs from their favorite food sources, even if they are hunting other prey. Lastly, these animals are taken from their natural habitats to display for tourists or are sold as exotic pets.

Frequent cyclones also pose a threat, particularly to concentrated or small populations. In late January 1997, cyclone Gretelle destroyed 80% of the Manombo forest canopy. With their habitat, including most of their food resources, effectively destroyed, the ruffed lemurs of the forest broadened their diet, remaining surprisingly frugivorous. Their body weights dropped and no births were reported for four years, but they managed to stave off starvation. This event demonstrated not only their flexibility in the face of natural disasters, which may highlight the evolutionary reasons behind their reproductive capacity and litter size, but also the threat faced by already stressed populations.

Predation in the wild appears to be very rare for ruffed lemurs, probably because living in the high canopy makes them challenging to catch. Evidence of predation by raptors, such as the Henst's Goshawk (*Accipiter henstii*) suggests it occurs at a low rate. The Fossa (*Cryptoprocta ferox*) could present a potential risk if it found an individual lower in the forest canopy, but no confirmation has been presented to indicate that they prey upon ruffed lemurs. Instead, only re-introduced, captive-bred ruffed lemurs have been killed by Fossa, likely due to their inexperience with predators. Nesting behavior poses the biggest risk of predation, making them susceptible to carnivorous mammals, such as the Ring-tailed Mongoose (*Galidia elegans*) and Brown-tailed Mongoose (*Salanoia concolor*).

### **Captive breeding and reintroductions**

Captive populations of both ruffed lemur species exist in American and European zoos, representing a safeguard against extinction. In the United States, captive breeding is managed by the Species Survival Plan (SSP), a program developed by the Association of Zoos and Aquariums (AZA). Although the populations are very limited in their genetic diversity, these species thrive in captivity, making them an ideal candidate for reintroduction into protected habitat, if it is available. Although reintroduction is seen as a last resort among conservationists, a combination of in situ conservation efforts, such as

legal protection, public education, the spread of sustainable livelihoods, and reforestation offer hope for ruffed lemurs. In the meantime, reintroductions offer conservation research opportunities and allow the limited genetic diversity maintained by the SSP to improve the genetic diversity of dwindling Malagasy ruffed lemur populations.

A captive release first occurred in November 1997, when five black-and-white ruffed lemurs (*Varecia variegata variegata*) born in the United States were returned to Madagascar for release in the Betampona Strict Nature Reserve in eastern Madagascar. Popularly known as the *Carolina Five*, these individuals had lived their entire lives in the Natural Habitat Enclosures at the Duke Lemur Center (DLC). Since then, two more groups totaling 13 captive-born ruffed lemurs have been reintroduced into the same reserve, once in November 1998 and again in January 2001. These latter two groups also received "boot camp training" in the DLC forested free-range enclosures prior to release. So far, the results have shown some success, with 10 surviving longer than one year, 3 individuals integrating into wild groups, and 4 offspring have been born to or sired by released lemurs, all of which were parent-raised. Saraph, a male released with the first group, was reported to be doing well seven years post-release, living in a social group with a wild female and their offspring. Research has been ongoing since the initial release, as illustrated in the 1998 BBC documentary *In the Wild: Operation Lemur with John Cleese*. The research has provided useful information about their adaptation to life in the wild.

## Chapter 3

# Koala



female

VT



male

### Conservation status



Least Concern (IUCN 3.1)

### Scientific classification

Kingdom:    Animalia  
Phylum:    Chordata  
Class:        Mammalia  
Infraclass:  Marsupialia  
Order:        Diprotodontia  
Family:       Phascolarctidae  
Genus:        *Phascolarctos*  
Species:      ***P. cinereus***

### Binomial name

***Phascolarctos cinereus***  
(Goldfuss, 1817)



Koala range  
(brown — native, red — introduced)

The **koala** (*Phascolarctos cinereus*) is an arboreal herbivorous marsupial native to Australia, and the only extant representative of the family Phascolarctidae.

The koala is found in coastal regions of eastern and southern Australia, from Adelaide to the southern part of Cape York Peninsula. Populations also extend for considerable distances inland in regions with enough moisture to support suitable woodlands. The koalas of South Australia were largely exterminated during the early part of the 20th century, but the state has since been repopulated with Victorian stock. The koala is not found in Tasmania or Western Australia.

## **Names**

The word *koala* comes from the Dharuk *gula*. Although the vowel /u/ was originally written in the Latin alphabet as "oo" (in spellings such as *coola* or *koolah*), it was changed to "oa" possibly due to an error. The word is erroneously said to mean "doesn't drink".

The scientific name of the koala's genus, *Phascolarctos*, is derived from Greek *phaskolos* "pouch" and *arktos* "bear". Its species name, *cinereus*, is Latin and means "ash-coloured".

Although the koala is not a bear, English-speaking settlers from the late 18th century first called it *koala bear* due to its similarity in appearance to bears. Although taxonomically incorrect, the name *koala bear* is still in use today outside Australia — its use is discouraged because of the inaccuracy in the name. Other descriptive English names based on "bear" have included *monkey bear*, *native bear*, and *tree-bear*.

## Variation



A Southern koala on Kangaroo Island, not native to the island

Although three subspecies have been described, these are arbitrary selections from a cline and are not generally accepted as valid. Following Bergmann's Rule, individuals from the southern cooler climates are larger.

A typical Victorian koala (formerly *P. cinereus victor*) has longer, thicker fur, is a darker, softer grey, often with chocolate-brown highlights on the back and forearms, and has a more prominently light-coloured ventral side and fluffy white ear tufts. Typical and New South Wales koala weights are 12 kg (26 lb) for males and 8.5 kg (19 lb) for females. In tropical and sub-tropical Queensland, however, the koala is smaller (at around 6.5 kg (14 lb) for an average male and just over 5 kg (11 lb) for an average female), a lighter often rather scruffy grey in colour, and has shorter, thinner fur. In Queensland, the koala was previously classified as the subspecies *P. cinereus adustus*, and the intermediate forms in New South Wales as *P. cinereus cinereus*. A fourth variation, though not technically a subspecies, is *Phascolarctos cinereus aurum*, or in English "golden koala", which has a slight golden tinge to the fur as a result of an absence of the melanin pigment that produces albinism in most other mammalian species. The variation from one form to another is continuous and there are substantial differences between individual koalas in any given region such as hair colour. Koalas may also have white fur in rare cases due to a recessive gene.

The origins of the koala are unclear, although almost certainly they descended from terrestrial wombat-like animals. Koala fossils are quite rare, but some have been found in northern Australia dating to 20 million years ago. During this time, the northern half of Australia was rainforest. The koala did not specialise in a diet of eucalyptus until the climate cooled and eucalypt forests grew in the place of rainforests. The fossil record indicates that before 50,000 years ago, giant koalas inhabited the southern regions of Australia. The koala fills the same ecological role as the sloths of South America.

***Physical description***



Female



Koalas have a slow metabolism and sleep for most of the day

The koala is broadly similar in appearance to the wombat (its closest living relative), but has a thicker coat, much larger ears, and longer limbs. The koala has large, sharp claws to assist with climbing tree trunks. Weight varies from about 14 kg (31 lb) for a large southern male, to about 5 kg (11 lb) for a small northern female. The koala's five fingers include two opposable thumbs, providing better gripping ability. The first two fingers are positioned in apposition on the front paws, and the first three fingers for the hind paws. The koala is one of the few mammals (other than primates) that has fingerprints. Koala fingerprints are similar to human fingerprints; even with an electron microscope, it can be quite difficult to distinguish between the two.



A Koala Skeleton

The teeth of the koala are adapted to their herbivorous diet, and are similar to those of other diprotodont marsupials, such as kangaroos and wombats. They have sharp incisors to clip leaves at the front of the mouth, separated from the grinding cheek teeth by a wide diastema. The dental formula for koalas is:

**Dentition**

3.1.1.4

1.0.1.4

The male koala, like many marsupials, has a bifurcated penis. The female has two lateral vaginas and two separate uteri, which is common to all marsupials.



Koalas walk on all four legs when walking on the ground, joey clinging to the back

The brain in the ancestors of the modern koala once filled the whole cranial cavity, but has become drastically reduced in the present species, a degeneration scientists suspect is an adaptation to a diet low in energy. One of the smallest in marsupials with no more than 0.2% of its body weight, about 40% of the cranial cavity is filled with cerebrospinal fluid, while the brain's two cerebral hemispheres are like "a pair of shrivelled walnut halves on top of the brain stem, in contact neither with each other nor the bones of the skull. It is the only animal on Earth with such a strangely reduced brain."

It is generally a silent animal, but males have a very loud advertising call that can be heard from almost a kilometre away during the breeding season. Females glean clues regarding a male's suitability as a mate from these calls, showing a preference for larger males. When under stress, koalas may issue a loud cry, which has been reported as similar to that of a human baby. There is little reliable information about the lifespan of the koala, but in captivity they have been observed to reach the age of 18 years.

***Life cycle***



A young joey, preserved at Port Macquarie Koala Hospital



Baby koala on a mothers back



Baby koala at Currumbin Wildlife Sanctuary

Females reach maturity at 2 to 3 years of age, males at 3 to 4 years. A healthy female koala can produce one young each year for about 12 years. Gestation is 35 days. Twins are very rare; the world's first confirmed identical twin koalas, named "*Euca*" and "*Lyptus*", were born at the University of Queensland in April 1999. Mating normally occurs between December and March, the Southern Hemisphere's summer.

A baby koala is referred to as a joey and is hairless, blind, and earless. At birth the joey, only a quarter of an inch long, crawls into the downward-facing pouch on the mother's belly (which is closed by a drawstring-like muscle that the mother can tighten at will) and attaches itself to one of the two teats.

Young remain hidden in the pouch for about six months, only feeding on milk. During this time they grow ears, eyes, and fur. The joey then begins to explore outside of the pouch. At about this stage it begins to consume small quantities of the mother's "pap" (formerly thought to be excrement, but now thought to come from the mother's cecum) in

order to inoculate its gut with the microbes necessary to digest eucalypt leaves. The joey will remain with its mother for another six months or so, riding on her back, and feeding on both milk and eucalypt leaves until weaning is complete at about 12 months of age. Young females disperse to nearby areas at that time; young males often stay in the mother's home range until they are two or three years old.

### ***Diet and behaviour***



Koala with joey in pouch



Koala dozing during the day

The koala lives almost entirely on eucalypt leaves. This is likely to be an evolutionary adaptation that takes advantage of an otherwise unfilled ecological niche, since eucalypt leaves are low in protein, high in indigestible substances, and contain phenolic and terpene compounds that are toxic to most species. Like wombats and sloths, the koala has a very low metabolic rate for a mammal and rests motionless for about 16 to 18 hours a day, sleeping most of that time. Koalas can be aggressive towards each other, throwing a foreleg around their opponent and biting, though most aggressive behavior is brief squabbles. Handling koalas may cause them stress, and the issue of aggression and stress from handling is a political issue in Australia.

Koalas spend about three of their five active hours eating. Feeding occurs at any time of day, but usually at night. Koalas eat an average of 500 g (18 oz) of eucalypt leaves each day, chewing them with powerful jaws to a very fine paste before swallowing. The liver deactivates the toxic components ready for excretion, and the hind gut (especially the cecum) is greatly enlarged to extract the maximum amount of nutrient from the poor quality diet. Much of this is done through bacterial fermentation: while young are being weaned, the mother passes these essential digestive aids on to her offspring.



A koala eating eucalyptus



Koala in tree, scratching & grooming

The koala will eat the leaves of a wide range of eucalypts, and occasionally even some non-eucalypt species such as *Acacia*, *Leptospermum*, and *Melaleuca*. It has firm preferences for particular varieties of eucalypt and these preferences vary from one region to another: in the south Manna Gum, Blue Gum, and Swamp Gum are favoured; Grey Gum and Tallowwood are important in the north, and the ubiquitous River Red Gum of the isolated seasonal swamps and watercourses that meander across the dry inland plains allows the koala to live in surprisingly arid areas. Many factors determine which of the 680 species of eucalypt trees the koala eats. Among trees of their favourite species, however, the major factor that determines which individual trees the koala chooses is the concentration of a group of phenolic toxins called formylated phloroglucinol compounds. Researches on koalas by keepers at 13 wildlife parks and zoos in New South Wales show that the most preferred group of Eucalyptus foliage had the lowest content of condensed tannins.

## **Conservation status**



A Koala, Victoria, Australia.

The Australian government currently lists the koala as a priority species for conservation status assessment. Government estimates of the national koala population numbers in the hundreds of thousands, although other studies have estimated as few as 80,000 koalas left in the wild. The Australian Koala Foundation estimates there are around 100,000 koalas left in the wild.

As with most native Australian animals, the koala cannot legally be kept as a pet in Australia or anywhere else. The only people who are permitted to keep koalas are wildlife carers and, occasionally, research scientists. These individuals are issued with special permits to care for koalas, but have to return them to the wild when they are either well enough or, in the case of joeys, old enough.

The IUCN lists the species as "Least Concern". The Australian government does not consider the species to be threatened, although the US government has declared the koala a threatened species.

The koala inhabits four Australian states. Under state legislation, the species is listed as:

- Queensland — Common, or "Least Concern Wildlife" throughout the state, except in the South East Queensland bioregion, where it is listed as *vulnerable*.

- New South Wales — listed at a state scale as *vulnerable*, but varying regionally from *secure* to *locally extinct*.
- South Australia — classified as *rare*.
- Victoria — The koala population in Victoria was considered *large and thriving*, according to an article which was last reviewed on 29 October 2007.

The koala was hunted almost to extinction in the early 20th century, largely for its fur. Millions of furs were traded to Europe and the United States, and the population has not fully recovered from such decimations. Extensive cullings occurred in Queensland in 1915, 1917, and again in 1919 when over one million koalas were killed with guns, poisons, and nooses. The public outcry over the cullings was most likely the first wide-scale environmental issue that rallied Australians. Despite the growing movement to protect native species, the poverty brought about by the drought of 1926–28 led to another 600,000 koalas being killed during a one-month open season in August 1927.

Today, habitat loss and the impacts of urbanisation (such as dog attacks and traffic accidents) are the leading threats to the survival of the koala. In recent years, some colonies have been hard hit by disease, especially chlamydia. The koala requires large areas of healthy, connected forest and will travel long distances along tree corridors in search of new territory and mates. The increasing human population of the coastal parts of the continent continues to cut these corridors by agricultural and residential development, forestry, and road-building, marooning koala colonies in decreasing areas of bush. The long term viability of the koala is therefore threatened by genetic weakness. The Australian Koala Foundation is the principal organisation dedicated to the conservation of the koala and its habitat, mapping 40,000 km<sup>2</sup> (15,000 sq mi) of land for koala habitat and claiming strong evidence that wild koala populations are in serious decline throughout the species' natural range. Local councils in growing urban areas with koala populations that have established or are in the process of establishing planning overlays and controls to preserve habitat for koalas include the Victorian councils of City of Ballarat, Macedon Ranges Shire and Glenelg Hopkins Catchment Management Authority as well as the Queensland councils of Moreton Bay Regional Council, Redland Shire Council.

Although the species covers a large area, only 'pieces' of koala habitat remain. Presently, many habitats are lost to weeds, clearance for agriculture, or carved up by developers. Other threats come from logging, poor management, attacks from feral and domestic animals, diseases, and roads.

## ***Pest status***



A koala at Healesville Sanctuary

In contrast to the situation on much of the mainland, where populations are declining, koalas, like many other species, can overrun smaller islands or isolated regions where they have been introduced. On Kangaroo Island in South Australia, koalas introduced some 90 years ago have thrived in the absence of predators and competition. Combined with an inability to migrate to new areas, this has caused the koala populations to become unsustainable and threaten the island's unique ecology. In particular, species of Manna Gum, native to the island, are being stripped by koalas at a rate faster than they can regenerate, endangering local birds and invertebrates that rely on them, and causing the extinction of at least one isolated population of manna. Koala numbers are estimated at over 30,000, with ecologists suggesting that the island can sustain 10,000 at most.

Although culling has been suggested as a means to reduce koala numbers, with the South Australian government seriously considering such in 1996, this has met with fierce opposition both domestically and internationally, and the species remains protected. The popularity of the koala has made the possibility of a cull politically improbable, with any negative perception likely to impact tourism and a government's electability. In place of a cull, sterilization and relocation programs have had only limited success in reducing numbers thus far, and remain expensive. There is evidence that koalas relocated to the mainland have difficulty establishing themselves in the different circumstances. A mooted alternative to the complex sterilization method, wherein the animal must first be captured, are hormonal implants that can be injected via darts.

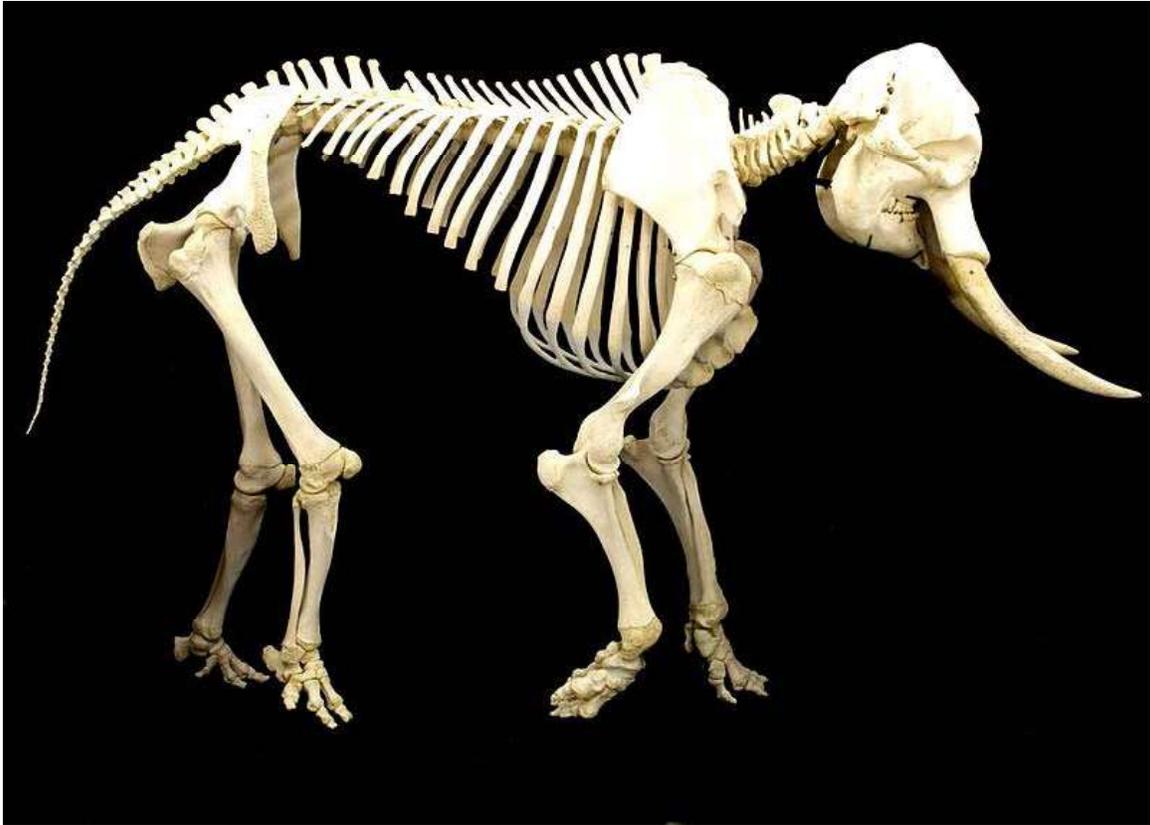
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## Chapter 4

# Elephant



African bush elephant



African elephant skeleton



Asian (*Elephas maximus*) and African (*Loxodonta*) elephants.

**Elephants** are large land mammals in two genera of the family Elephantidae: *Elephas* and *Loxodonta*. Three species of elephant are living today: the African bush elephant, the African forest elephant and the Asian elephant (also known as the Indian elephant). All other species and genera of Elephantidae are extinct, some since the last ice age although dwarf forms of mammoths may have survived as late as 2,000 BCE. Elephants and other Elephantidae were once classified with other thick-skinned animals in a now invalid order, Pachydermata.

Elephants are the largest land animals now living. The elephant's gestation period is 22 months, the longest of any land animal. At birth it is common for an elephant calf to weigh 120 kilograms (260 lb). They typically live for 50 to 70 years, but the oldest recorded elephant lived for 82 years. The largest elephant ever recorded was shot in Angola in 1956. This male weighed about 24,000 lb (11,000 kg), with a shoulder height of 3.96 metres (13.0 ft), a metre (yard) taller than the average male African elephant. The smallest elephants, about the size of a calf or a large pig, were a prehistoric species that lived on the island of Crete during the Pleistocene epoch.

Elephants are a symbol of wisdom in Asian cultures and are famed for their memory and intelligence, where their intelligence level is thought to be equal to that of dolphins and primates. Aristotle once said the elephant was "the beast which passeth all others in wit and mind." The word "elephant" has its origins in the Greek ἑλέφας, meaning "ivory" or "elephant".

According to observations, healthy adult elephants have no natural predators, although lions may take calves or weak individuals. They are, however, threatened by human intrusion and poaching.

## ***Etymology***

**Olifant** and its variations (ex. *oliphant*, *olyphant*) are archaic spellings of *elephant*. Aside from elephants, the word has been used to refer to ivory, elephant tusks, musical horns made of elephant tusks, or a musical instrument resembling such horns.

It appears in Middle English as *olifant* or *olifaunt*, and was borrowed from Medieval French *olifanz*. The French word owes something to both Old High German *olbenta* "camel", and to Latin *elephantus* "elephant", a word of Greek origin. OHG *olbenta* is a word of old Germanic origin; cf. Gothic *ulbandus* also meaning "camel". But the form of the OHG and Gothic words suggests it is also a borrowing, perhaps indeed directly or indirectly from Greek "ἑλέφας" (*elephas*), which in Homer only meant "ivory" but from Herodotus and on the word also referred to the animal. The earliest attested form of the word is the Mycenaean Greek *e-re-pa-to*, written in Linear B syllabic script.

## ***Taxonomy and evolution***



Physical difference between an Asian (left) and African (right) elephant.

The African elephant genus contains two or, arguably, three living species; whereas the Asian elephant species is the only surviving member of the Asian elephant genus, but can be divided into four subspecies. The African and the Asian elephant diverged from a common ancestor some 7.6 million years ago.

### **African elephant**



Elephant crossing a river, Kenya.



African bush (savanna) elephant in Etosha National Park, Namibia.



elephants in the wild

The Elephants of the genus *Loxodonta*, known collectively as African elephants, are currently found in 37 countries in Africa.

African elephants are distinguished from Asian elephants in several ways, the most noticeable being their much larger ears. Also, the African elephant is typically larger than the Asian elephant and has a concave back. In Asian elephants, only males have tusks, but both males and females of African elephants have tusks and are usually less hairy than their Asian cousins.

African elephants have traditionally been classified as a single species comprising two distinct subspecies, namely the savanna elephant (*Loxodonta africana africana*) and the forest elephant (*Loxodonta africana cyclotis*), but recent DNA analysis suggests that these may actually constitute distinct species. This split is not universally accepted by experts. A third species of African elephant has also been proposed.

The authors of an analysis of nuclear DNA extracted from "African savanna elephant, African forest elephant, Asian elephant, the extinct American mastodon, and the woolly mammoth" concluded in 2010 that African savanna and forest elephants are indeed separate species:

We unequivocally establish that the Asian elephant is the sister species to the woolly mammoth. A surprising finding from our study is that the divergence of African savanna and forest elephants—which some have argued to be two populations of the same species—is about as ancient as the divergence of Asian elephants and mammoths. Given their ancient divergence, we conclude that African savanna and forest elephants should be classified as two distinct species.

This reclassification has implications for conservation. If there are two separate species, each will be less abundant (particularly the rarer) and could be more endangered than a more numerous and wide-ranging single species. There is also a potential danger that if the forest elephant is not explicitly listed as an endangered species, poachers and smugglers might be able to evade the law forbidding trade in endangered animals and their products.

The forest elephant and the savanna elephant can hybridize (interbreed), though their preferences for different terrains reduce such opportunities. As the African elephant has only recently been recognized to comprise two separate species, groups of captive elephants have not been comprehensively classified and some could well be hybrids.

Under the new two species classification, *Loxodonta africana* refers specifically to the savanna elephant, the largest of all elephants. It is the largest land animal, with males standing 3.2 metres (10 ft) to 4 metres (13 ft) at the shoulder and weighing 3,500 kilograms (7,700 lb) up to a reported 12,000 kilograms (26,000 lb). The female is smaller, standing about 3 metres (9.8 ft) at the shoulder. Most often, savanna elephants are found in open grasslands, marshes, and lakeshores. They range over much of the savanna zone south of the Sahara.

The other putative species, the forest elephant (*Loxodonta cyclotis*), is usually smaller and rounder, and its tusks thinner and straighter compared with the savanna elephant. The

forest elephant can weigh up to 4,500 kilograms (9,900 lb) and stand about 3 metres (10 ft) tall. Much less is known about these animals than their savanna cousins, because environmental and political obstacles make them difficult to study. Normally, they inhabit the dense African rain forests of central and western Africa, although occasionally they roam the edges of forests, thus overlapping the savanna elephant home ranges and hybridizing. In 1979, Iain Douglas-Hamilton estimated the continental population of African elephants at around 1.3 million animals. This estimate is controversial and is believed to be a gross overestimate,, but it is very widely cited and has become a *de facto* baseline that continues to be incorrectly used to quantify downward population trends in the species. Through the 1980s, *Loxodonta* received worldwide attention due to the dwindling numbers of major populations in East Africa, largely as a result of poaching. According to IUCN's African Elephant Status Report 2007, there are between 470,000 and 690,000 African elephants in the wild. Although this estimate only covers about half of the total elephant range, experts do not believe the true figure to be much higher, as it is unlikely that large populations remain to be discovered. By far, the largest populations are now found in southern and eastern Africa, which together account for the majority of the continental population. According to a recent analysis by IUCN experts, most major populations in eastern and southern Africa are stable or have been steadily increasing since the mid-1990s, at an average rate of 4.5% per year.

Elephant populations in West Africa, on the other hand, are generally small and fragmented, and only account for a small proportion of the continental total. Much uncertainty remains as to the size of the elephant population in central Africa, where the prevalence of forest makes population surveys difficult, but poaching for ivory and bushmeat is believed to be intense through much of the region. South African elephant population more than doubled, rising from 8,000 to over 20,000, in the thirteen years after a 1995 ban on the trade in elephant ivory. The ban on the ivory trade in southern Africa (but not elsewhere) was lifted in February 2008, sparking controversy among environmental groups.

## Asian elephant



A temple elephant in Kerala, India.

The Asian elephant, *Elephas maximus*, is smaller than the African. It has smaller ears, and typically, only the males have large external tusks.

The world population of Asian elephants—also called Indian elephants—is estimated to be around 60,000, about a tenth of the number of African elephants. More precisely, it is estimated that there are between 38,000 and 53,000 wild elephants and between 14,500 and 15,300 domesticated elephants in Asia, with perhaps another 1,000 scattered around zoos in the rest of the world. The Asian elephants' decline has possibly been more gradual than the African and caused primarily by poaching and habitat destruction by human encroachment.



A decorated Indian elephant in Jaipur, India.



Elephant orphanage in Sri Lanka

Several subspecies of *Elephas maximus* have been identified, using morphometric data and molecular markers. *Elephas maximus maximus* (Sri Lankan elephant) is found only on the island of Sri Lanka. It is the largest of the Asians. There are an estimated 3,000–4,500 members of this subspecies left today in the wild, although no accurate census has been carried out recently. Large males can weigh upward to 5,400 kg (12,000 lb) and stand over 3.4 m (11 ft) tall. Sri Lankan males have very large cranial bulges, and both sexes have more areas of depigmentation than other Asians. Typically, their ears, face, trunk, and belly have large concentrations of pink-speckled skin. There is an orphanage for elephants in Pinnawala, Sri Lanka, which plays a large role in protecting the Sri Lankan elephant from extinction.

*Elephas maximus indicus* (Indian elephant) makes up the bulk of the Asian elephant population. Numbering approximately 36,000, these elephants are lighter grey in colour, with depigmentation only on the ears and trunk. Large males will ordinarily weigh only about 5,000 kg (11,000 lb), but are as tall as the Sri Lankan. The mainland Asian can be found in 11 Asian countries, from India to Indonesia. They prefer forested areas and transitional zones, between forests and grasslands, where greater food variety is available.

The Sumatran elephant, *Elephas maximus sumatranus*, found only on Sumatra, is smaller than the Indian elephant. Population estimates for this group range from 2,100 to 3,000 individuals. It is very light grey in colour and has less depigmentation than the other Asians, with pink spots only on the ears. Mature Sumatrans will usually only measure 1.7–2.6 m (5.6–8.5 ft) at the shoulder and weigh less than 3,000 kg (6,600 lb). It is

considerably smaller than its other Asian (and African) cousins and exists only on the island of Sumatra, usually in forested regions and partially wooded habitats.

In 2003, a further subspecies was identified on Borneo. Named the Borneo pygmy elephant, it is smaller and tamer than any other Asian elephants. It also has relatively larger ears, longer tail and straighter tusks.

### ***Physical characteristics***

#### **Trunk**



Trunk of African (left) and Asian (right) elephant.

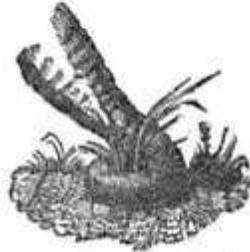




Anterior termination of elephant's trunk (profile).



Anterior extremities of the trunks of male (A) and female elephants (B).



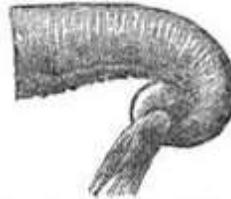
Action of anterior extremity of proboscis in gathering long herbage.



Mode of holding herbage when gathered.



Mode of holding a root till enough is collected for a mouthful.



Curled action, when a powerful grasp and much force is required.

Articulation of elephant trunk.



An elephant can use its trunk for a variety of purposes. This one is wiping its eye.



Eye of an Asian elephant.

The proboscis, or trunk, is a fusion of the nose and upper lip, elongated and specialized to become the elephant's most important and versatile appendage. African elephants are equipped with two fingerlike projections at the tip of their trunk, while Asians have only one. The elephant's trunk is sensitive enough to pick up a single blade of grass, yet strong enough to rip the branches off a tree.

Most herbivores (plant eaters, like the elephant) possess teeth adapted for cutting and tearing off plant materials. However, except for the very young or infirm, elephants always use their trunks to tear up their food and then place it in their mouths. They will graze on grass or reach up into trees to grasp leaves, fruit, or entire branches. If the desired food item is too high up, the elephant will wrap its trunk around the tree or branch and shake its food loose or sometimes simply knock the tree down altogether.

The trunk is also used for drinking. Elephants suck water up into the trunk—up to 14 litres (15 quarts) at a time—and then blow it into their mouths. Elephants also suck up water to spray on their bodies during bathing. On top of this watery coating, the animals will then spray dirt and mud, which dries and acts as a protective sunscreen. When swimming, the trunk makes an excellent snorkel.

This appendage also plays a key role in many social interactions. Familiar elephants will greet each other by entwining their trunks, much like a handshake. They also use them while play-wrestling, caressing during courtship and mother-child interactions, and for dominance displays; a raised trunk can be a warning or threat, while a lowered trunk can be a sign of submission. Elephants can defend themselves very well by flailing their trunks at unwanted intruders or by grasping and flinging them.

An elephant also relies on its trunk for its highly developed sense of smell. By raising the trunk up in the air and swiveling it from side to side, like a periscope, it can determine the location of friends, enemies, and food sources.

Some elephants have been afflicted by floppy trunk syndrome.

## Tusks



Tusks of African and Asian elephants.

The tusks of an elephant are its second upper incisors. Tusks grow continuously; an adult male's tusks grow about 18 cm (7 in) a year. Tusks are used to dig for water, salt, and roots; to debark trees to eat the bark; to dig into baobab trees to get at the pulp inside; and to move trees and branches when clearing a path. In addition, they are used for marking trees to establish territory, and occasionally as weapons.

Like humans who are typically right- or left-handed, elephants are usually right- or left-tusked. The dominant tusk, called the master tusk, is generally shorter and more rounded at the tip from wear. Both male and female African elephants have large tusks that can reach over 3 m (10 ft) in length and weigh over 90 kg (200 lb). In the Asian species, only the males have large tusks. Female Asians have tusks which are very small or absent altogether. Asian males can have tusks as long as the much larger Africans, but they are usually much slimmer and lighter; the heaviest recorded is 39 kg (86 lb). The tusk of both species is mostly made of calcium phosphate in the form of apatite. As a piece of living tissue, it is relatively soft (compared with other minerals such as rock), and the tusk, also known as ivory, is strongly favoured by artists for its carvability. The desire for elephant ivory has been one of the major factors in the reduction of the world's elephant population.

Some extinct relatives of elephants had tusks in their lower jaws in addition to their upper jaws, such as *Gomphotherium*, or only in their lower jaws, such as *Deinotherium*.

## Teeth

Elephants' teeth are very different from those of most other mammals. Over their lives they usually have 28 teeth. These are:

- The two upper second incisors: these are the tusks.
- The milk precursors of the tusks.
- 12 premolars, 3 in each side of each jaw.
- 12 molars, 3 in each side of each jaw.



Replica of an Asian elephant's molar, showing upper side.

This gives elephants a dental formula of:  $\frac{1.0.3.3}{0.0.3.3}$

Unlike most mammals, which grow baby teeth and then replace them with a permanent set of adult teeth, elephants have cycles of tooth rotation throughout their entire lives. The tusks have milk precursors, which fall out quickly and the adult tusks are in place by one year of age, but the chewing teeth are replaced five or, very rarely, six times in an elephant's lifetime.

Only four chewing teeth (premolars and/or molars), one on each side of each jaw, are in primary use at any given time (or two, as one replaces the other at each location). Adult teeth do not replace milk teeth by emerging from the jaws vertically as human teeth do. Instead, new teeth grow in at the back of the mouth, pushing older teeth toward the front, where the latter break off in pieces until they are gone. In African elephants, the first two sets of chewing teeth (premolars) are in place when an elephant is born. The first chewing tooth on each side in each jaw falls out when the elephant is about two years old. The second set of chewing teeth falls out when the elephant is about six years old. The third set is lost at 13 to 15 years of age, and set four lasts to approximately 28 years of age. The fifth set of chewing teeth (molars) lasts until the elephant is in its early 40s. The sixth (and usually final) set must last the elephant the rest of its life. If an elephant lives to more than 60 years of age, the last set of molars is worn to stumps, and it can no longer feed properly. Moss reports a female elephant in its sixties whose final set of molars were worn smooth and about one-quarter of their original size and who survived "with extra chewing and longer feeding bouts." Abscesses of chewing teeth, as well as of tusks and jaws, are common in elephants, and may lead to premature death.

Tusks in the lower jaw are also second incisors. These grew out large in *Deinotherium* and some mastodons, but in modern elephants they disappear early without erupting.

### Skin



Skin of an African (left) and Asian (right) elephant.



African elephant bathing

Elephants are colloquially called *pachyderms* (from their original scientific classification), which means thick-skinned animals. An elephant's skin is extremely tough around most parts of its body and measures about 2.5 centimetres (1.0 in) thick. However, the skin around the mouth and inside of the ear is considerably thinner. Normally, the skin of an Asian is covered with more hair than its African counterpart. This is most noticeable in the young. Asian calves are usually covered with a thick coat of brownish red fuzz. As they get older, this hair darkens and becomes more sparse, but it will always remain on their heads and tails.

The species of elephants are typically greyish in colour, but the Africans very often appear brown or reddish from wallowing in mud holes of colored soil. Wallowing is an important behaviour in elephant society. Not only is it important for socialization, but the mud acts as a sunscreen, protecting its skin from harsh ultraviolet radiation. Although tough, an elephant's skin is very sensitive. Without regular mud baths to protect it from burning, as well as from insect bites and moisture loss, an elephant's skin would suffer serious damage. After bathing, the elephant will usually use its trunk to blow soil on its body to help dry and bake on its new protective coat. As elephants are limited to smaller and smaller areas, there is less water available, and local herds will often come too close over the right to use these limited resources.

Wallowing also aids the skin in regulating body temperatures. Elephants have difficulty in releasing heat through the skin because, in proportion to their body size, they have very little of it. The ratio of an elephant's mass to the surface area of its skin is many times that of a human. Elephants have even been observed lifting up their legs to expose the soles of their feet, presumably in an effort to expose more skin to the air. Since wild elephants live in very hot climates, they must have other means of getting rid of excess heat.

### **Legs and feet**



Elephant using its feet to crush a watermelon before eating it.

An elephant's legs are roughly shaped like columns or pillars, as they must be to support its bulk. The elephant needs less muscular power to stand because of its straight legs and large padded feet. For this reason, an elephant can stand for very long periods of time without tiring. In fact, African elephants rarely lie down unless they are sick or wounded. Indian elephants, in contrast, lie down frequently.

The feet of an elephant are nearly round. African elephants have three nails on each hind foot, and four on each front foot. Indian elephants have four nails on each hind foot and five on each front foot. Beneath the bones of the foot is a tough, gelatinous material that acts as a cushion or shock absorber. Under the elephant's weight, the foot swells, but it gets smaller when the weight is removed. An elephant can sink deep into mud, but can pull its legs out readily because its feet become smaller when they are lifted.

Elephants swim well, but cannot trot, jump, or gallop. They do have two gaits: a walk and a faster gait that is similar to running.

In walking, the legs act as pendulums, with the hips and shoulders rising and falling while the foot is planted on the ground. With no "aerial phase", the faster gait does not meet all the criteria of running, as elephants always have at least one foot on the ground. However, an elephant moving fast uses its legs much like other running animals, with the hips and shoulders falling and then rising while the feet are on the ground. In this gait, an elephant will have three feet off the ground at one time. As both of the hind feet and both of the front feet are off the ground at the same time, this gait has been likened to the hind legs and the front legs taking turns running. Tests at the Thai Elephant Conservation Centre are reported to show that fast-moving elephants 'run' with their front legs, but 'walk' with their hind legs.

Although they start this "run" at only 8 km/h, elephants have been reported to reach speeds up to 40 km/h (25 mph), all the while using the same gait. In tests at the Thai Elephant Conservation Centre, the fastest elephants reached a top speed of 18 km/h (11 mph). At this speed, most other four-legged creatures are well into a gallop, even accounting for leg length. Spring-like kinetics could explain the difference between the motion of elephants and other animals.

## Ears



Difference between Asian (left) and African (right) elephant ears.

The large flapping ears of an elephant are also very important for temperature regulation. Elephant ears are made of a very thin layer of skin stretched over cartilage and a rich network of blood vessels. On hot days, elephants will flap their ears constantly, creating a slight breeze. This breeze cools the surface blood vessels, and then the cooler blood gets circulated to the rest of the animal's body. The hot blood entering the ears can be cooled as much as 10 °F (6 °C) before returning to the body. Differences in the ear sizes of African and Asian elephants can be explained, in part, by their geographical distribution. Africans originated and stayed near the equator, where it is warmer. Therefore, they have bigger ears. Asians live farther north, in slightly cooler climates, and thus have smaller ears.

The ears are also used in certain displays of aggression and during the males' mating period. If an elephant wants to intimidate a predator or rival, it will spread its ears out wide to make itself look more massive and imposing. During the breeding season, males give off an odor from the musth gland located behind their eyes. Joyce Poole, a well-known elephant researcher, has theorized that the males will fan their ears in an effort to help propel this "elephant cologne" great distances.

### ***Biology and behavior***



The skeleton of a dwarf elephant from the island of Crete. Dwarf elephants were present on some Mediterranean islands until about 10,000 years ago.

### **Evolution**

The earliest known ancestors of modern-day elephants evolved about 60 million years ago. The ancestor of the elephants from 37 million years ago was aquatic and had a similar lifestyle to a hippopotamus.

### **Social behavior**

Elephants live in a structured social order. The social lives of male and female elephants are very different. The females spend their entire lives in tightly knit family groups made up of mothers, daughters, sisters, and aunts. These groups are led by the eldest female, or matriarch. Adult males, on the other hand, live mostly solitary lives.

The social circle of the female elephant does not end with the small family unit. In addition to encountering the local males that live on the fringes of one or more groups, the female's life also involves interaction with other families, clans, and subpopulations. Most immediate family groups range from five to fifteen adults, as well as a number of immature males and females. When a group gets too big, a few of the elder daughters will break off and form their own small group. They remain very aware of which local herds are relatives and which are not.



Elephant footprints (tire tracks for scale)

The life of the adult male is very different. As he gets older, he begins to spend more time at the edge of the herd, gradually going off on his own for hours or days at a time. Eventually, days become weeks, and somewhere around the age of fourteen, the mature male, or bull, sets out from his natal group for good. While males do live primarily solitary lives, they will occasionally form loose associations with other males. These groups are called bachelor herds. The males spend much more time than the females fighting for dominance with each other. Only the most dominant males will be permitted to breed with cycling females. The less dominant ones must wait their turns. It is usually the older bulls, forty to fifty years old, that do most of the breeding.

The dominance battles between males can look very fierce, but typically they inflict very little injury. Most of the bouts are in the form of aggressive displays and bluffs. Ordinarily, the smaller, younger, and less confident animal will back off before any real damage can be done. However, during the breeding season, the battles can get extremely aggressive, and the occasional elephant is injured. During this season, known as musth, a bull will fight with almost any other male it encounters, and it will spend most of its time hovering around the female herds, trying to find a receptive mate.

### **Mating behavior**



Elephant mating behaviour.



Elephant mating behaviour (2)

The mating season is short and females are only able to conceive for a few days each year. She will detach herself from the herd. The scent of the female (cow) elephant in heat (or estrus) attracts the male and she also uses audible signals to attract the male. As the female can usually outrun the male, she does not have to mate with every male that approaches her.

The male initiates the courtship and the female ignores him for several minutes. He then stops and starts again. Elephants display a range of affectionate interactions, such as nuzzling, trunk intertwining, and placing their trunks in each other's mouths (image 2).

In a rarely observed display of his affection, he may drape his trunk outside of his tusks during the ritual (image 1). The interactions may last for 20–30 minutes and do not necessarily result in the male mounting the female, though he may demonstrate arousal during the ritual.

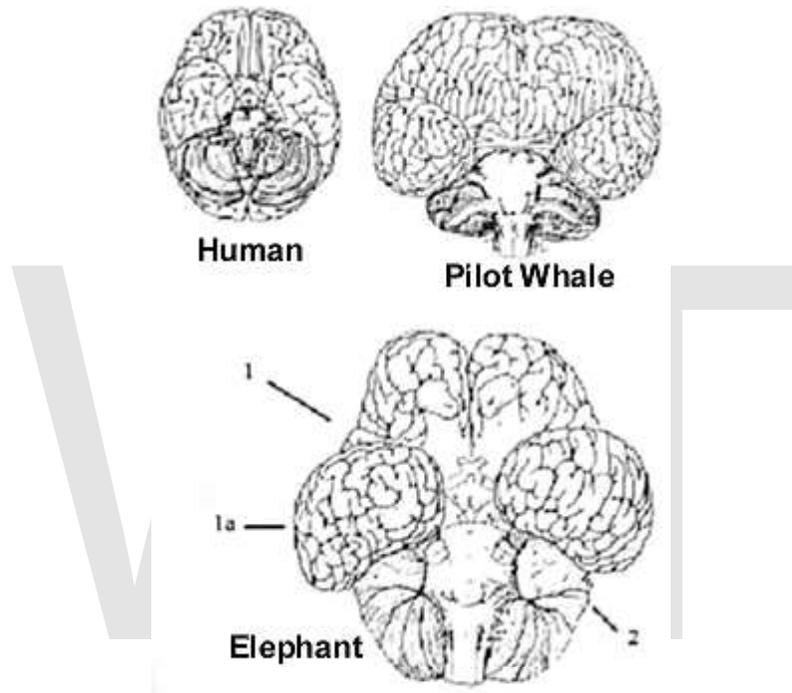
The female elephant is not passive in the ritual and uses the same techniques as the male.

African as well as Asiatic males will engage in same-sex bonding and mounting. The encounters are analogous to heterosexual bouts, one male often extending his trunk along the other's back and pushing forward with his tusks to signify his intention to mount. Unlike heterosexual relations, which are always of a fleeting nature, those between males result in a "companionship", consisting of an older individual and one or two younger,

attendant males. Same-sex relations are common and frequent in both sexes, with Asiatic elephants in captivity devoting roughly 46% of sexual encounters to same-sex activity.

Rogue elephant is a term for a lone, violently aggressive wild elephant. It is a calque of the Sinhala term *hora aliya*. Its introduction to English has been attributed by the Oxford English Dictionary to Sir James Emerson Tennent, but this usage may have been predated by William Sirr.

## Intelligence



Human, pilot whale and elephant brains up to scale. (1)-cerebrum (1a)-temporal lobe and (2)-cerebellum.

With a mass just over 5 kg (11 lb), elephant brains are larger than those of any other land animal. A wide variety of behaviours associated with intelligence have been attributed to elephants, including those associated with grief, making music, art, altruism, allomothering, play, use of tools, compassion and self-awareness. Elephants are believed to rank equally in terms of intelligence with cetaceans and nonhuman primates. The elephant's brain is similar to that of humans in terms of structure and complexity; the elephant brain exhibits a gyral pattern more complex and with more numerous convolutes, or brain folds, than that of humans, primates or carnivores, but less complex than cetaceans. However, the cortex of the elephant brain is "thicker than that of cetaceans" and is believed to have as many cortical neurons (nerve cells) and cortical synapses as that of humans, which exceeds that of cetaceans.

## Senses

Elephants have well innervated trunks, and an exceptional sense of hearing and smell. The hearing receptors reside not only in ears, but also in trunks that are sensitive to vibrations, and most significantly feet, which have special receptors for low frequency sound and are exceptionally well innervated. Elephants communicate by sound over large distances of several kilometers partly through the ground, which is important for their social lives. Elephants are observed listening by putting trunks on the ground and carefully positioning their feet.

The eyesight of elephants is relatively poor.

## Self-awareness

Mirror self recognition is a test of self-awareness and cognition used in animal studies. A mirror was provided and visible marks were made on the elephant. The elephants investigated these marks, which were visible only via the mirror. The tests also included invisible marks to rule out the possibility of their using other senses to detect these marks. This shows that elephants recognize the fact that the image in the mirror is their own self, and such abilities are considered the basis for empathy, altruism and higher social interactions. This ability has also been demonstrated in humans, apes, bottlenose dolphins, and magpies.



A young elephant in Zimbabwe.

## Communication

Elephants make a number of sounds when communicating. Elephants are famous for their trumpet calls, which are made when the animal blows through its nostrils. Trumpeting is usually made during excitement. Its use varies from startlement to a cry of help to rage. Elephants also make rumbling growls when greeting each other. The growl becomes a bellow when the mouth is open and a bellow becomes a moan when prolonged. This can escalate with a roar when threatening another elephant or another animal.

Elephants can communicate over long distances by producing and receiving low-frequency sound (infrasound), a sub-sonic rumbling, which can travel in the air and through the ground much farther than higher frequencies. These calls range in frequency from 15–35 Hz and can be as loud as 117 dB, allowing communication for many kilometres, with a possible maximum range of around 10 km. This sound can be felt by the sensitive skin of an elephant's feet and trunk, which pick up the resonant vibrations much as the flat skin on the head of a drum. To listen attentively, every member of the herd will lift one foreleg from the ground, and face the source of the sound, or often lay its trunk on the ground. The lifting presumably increases the ground contact and sensitivity of the remaining legs. This ability is thought also to aid their navigation by use of external sources of infrasound. Discovery of this new aspect of elephant social communication and perception came with breakthroughs in audio technology, which can pick up frequencies outside the range of the human ear. Pioneering research in elephant infrasound communication was done by Katy Payne, of the Elephant Listening Project, and is detailed in her book *Silent Thunder*. Though this research is still in its infancy, it is helping to solve many mysteries, such as how elephants can find distant potential mates, and how social groups are able to coordinate their movements over extensive range. Joyce Poole has also begun decoding elephant utterances that have been recorded over many years of observation, hoping to create a lexicon based on a systematic catalogue of elephant sounds.

## Diet

Elephants are herbivores, and spend up to 16 hours a day eating plants. Their diets are highly variable, both seasonally and across habitats and regions. Elephants are primarily browsers, feeding on the leaves, bark, and fruits of trees and shrubs, but they may also eat considerable grasses and herbs. As is true for other nonruminant ungulates, elephants only digest approximately 40% of what they eat. They make up for their digestive systems' lack of efficiency in volume. An adult elephant consumes 140–270 kg (300–600 lb) of food a day.

## Reproduction and life cycle

### Elephant calves

Female elephant social life revolves around breeding and raising of the calves. A female will usually be ready to breed around the age of thirteen, when she comes into estrus, a

short phase of receptiveness lasting a couple of days, for the first time. Females announce their estrus with smell signals and special calls.



Female African elephant with calf, in Kenya.

Females prefer bigger, stronger, and, most importantly, older males. Such a reproductive strategy tends to increase their offspring's chances of survival.

After a twenty-two-month pregnancy, the mother gives birth to a calf that weighs about 115 kg (250 lb) and stands over 75 cm (2.5 ft) tall. Elephants have a very long development. As is common with more intelligent species, they are born with fewer survival instincts than many other animals. Instead, they rely on their elders to teach them what they need to know. Today, however, the pressures humans have put on the wild elephant populations, from poaching to habitat destruction, mean that the elderly often die at a younger age, leaving fewer teachers for the young. The consequences of this for the next generation are not known.

A new calf is usually the center of attention for herd members. Adults and most of the other young will gather around the newborn, touching and caressing it with their trunks.

The baby is born nearly blind and at first relies almost completely on its trunk to discover the world around it.

Elephants within a herd are usually related, and all members of the tightly-knit female group participate in the care and protection of the young. After the initial excitement, the mother will usually select several full-time baby-sitters, or "allomothers", from her group. An elephant is considered an allomother when she is not able to have her own calf. The more allomothers, the better the calf's chances of survival. A benefit of being an allomother is she can gain experience or receive assistance when caring for her own calf. According to Cynthia Moss, a well known researcher, these allomothers will help in all aspects of raising the calf. They walk with the young as the herd travels, helping the calves along if they fall or get stuck in the mud. The more allomothers a calf has, the more free time its mother has to feed herself. Providing a calf with nutritious milk means the mother has to eat more nutritious food herself.

### **Effect on the environment**

Elephants can have profound impacts on the ecosystems they occupy, and both positive and negative effects on other species especially with their foraging activities. By pulling down trees to eat leaves, breaking branches, and pulling out roots, they reduce woody cover, creating clearings in forests, converting forests to savannas, and converting savannas to grasslands. These changes tend to benefit grazers at the expense of browsers.

Dung beetles and termites both eat elephant feces. During the dry season, elephants use their tusks to dig into river beds to reach underground sources of water. These holes may then become essential sources of water for other species. Elephants make paths through their environment that are used by other animals. Some of these pathways have apparently been used by several generations of elephants, used by humans and eventually even been converted to roads.

## Chapter 5

# Bee

### Bees



*Osmia ribifloris*

### Scientific classification

Kingdom: Animalia  
Phylum: Arthropoda  
Class: Insecta  
Order: Hymenoptera  
Suborder: Apocrita  
Superfamily: Apoidea  
(unranked): **Anthophila**

### Families

Andrenidae  
Apidae  
Colletidae  
Dasypodidae  
Halictidae  
Megachilidae  
Meganomiidae  
Melittidae  
Stenotritidae

### Synonyms

**Apiformes**

**Bees** are flying insects closely related to wasps and ants, and are known for their role in pollination and for producing honey and beeswax. Bees are a monophyletic lineage within the superfamily **Apoidea**, presently classified by the unranked taxon name **Anthophila**. There are nearly 20,000 known species of bees in seven to nine recognized families, though many are undescribed and the actual number is probably higher. They are found on every continent except Antarctica, in every habitat on the planet that contains insect-pollinated flowering plants.

Bees are adapted for feeding on nectar and pollen, the former primarily as an energy source and the latter primarily for protein and other nutrients. Most pollen is used as food for larvae.

Bees have a long proboscis (a complex "tongue") that enables them to obtain the nectar from flowers. They have antennae almost universally made up of 13 segments in males and 12 in females, as is typical for the superfamily. Bees all have two pairs of wings, the hind pair being the smaller of the two; in a very few species, one sex or caste has relatively short wings that make flight difficult or impossible, but none are wingless.

The smallest bee is *Trigona minima*, a stingless bee whose workers are about 2.1 mm (5/64") long. The largest bee in the world is *Megachile pluto*, a leafcutter bee whose females can attain a length of 39 mm (1.5"). Members of the family Halictidae, or sweat bees, are the most common type of bee in the Northern Hemisphere, though they are small and often mistaken for wasps or flies.

The best-known bee species is the European honey bee, which, as its name suggests, produces honey, as do a few other types of bee. Human management of this species is known as beekeeping or apiculture.

Bees are the favorite meal of *Merops apiaster*, the bee-eater bird. Other common predators are kingbirds, mockingbirds, beewolves, and dragonflies.

## **Pollination**

Bees play an important role in pollinating flowering plants, and are the major type of pollinator in ecosystems that contain flowering plants. Bees either focus on gathering nectar or on gathering pollen depending on demand, especially in social species. Bees gathering nectar may accomplish pollination, but bees that are deliberately gathering pollen are more efficient pollinators. It is estimated that one third of the human food supply depends on insect pollination, most of which is accomplished by bees, especially the domesticated European honey bee. Contract pollination has overtaken the role of honey production for beekeepers in many countries. Monoculture and the massive decline of many bee species (both wild and domesticated) have increasingly caused honey bee keepers to become migratory so that bees can be concentrated in seasonally varying high-demand areas of pollination.



Honey bee (*Apis mellifera*) collecting pollen

Most bees are fuzzy and carry an electrostatic charge, which aids in the adherence of pollen. Female bees periodically stop foraging and groom themselves to pack the pollen into the scopa, which is on the legs in most bees, and on the ventral abdomen on others, and modified into specialized pollen baskets on the legs of honey bees and their relatives. Many bees are opportunistic foragers, and will gather pollen from a variety of plants, while others are oligolectic, gathering pollen from only one or a few types of plant. A small number of plants produce nutritious floral oils rather than pollen, which are gathered and used by oligolectic bees. One small subgroup of stingless bees, called "vulture bees," is specialized to feed on carrion, and these are the only bees that do not use plant products as food. Pollen and nectar are usually combined together to form a "provision mass", which is often soupy, but can be firm. It is formed into various shapes (typically spheroid), and stored in a small chamber (a "cell"), with the egg deposited on the mass. The cell is typically sealed after the egg is laid, and the adult and larva never interact directly (a system called "mass provisioning").

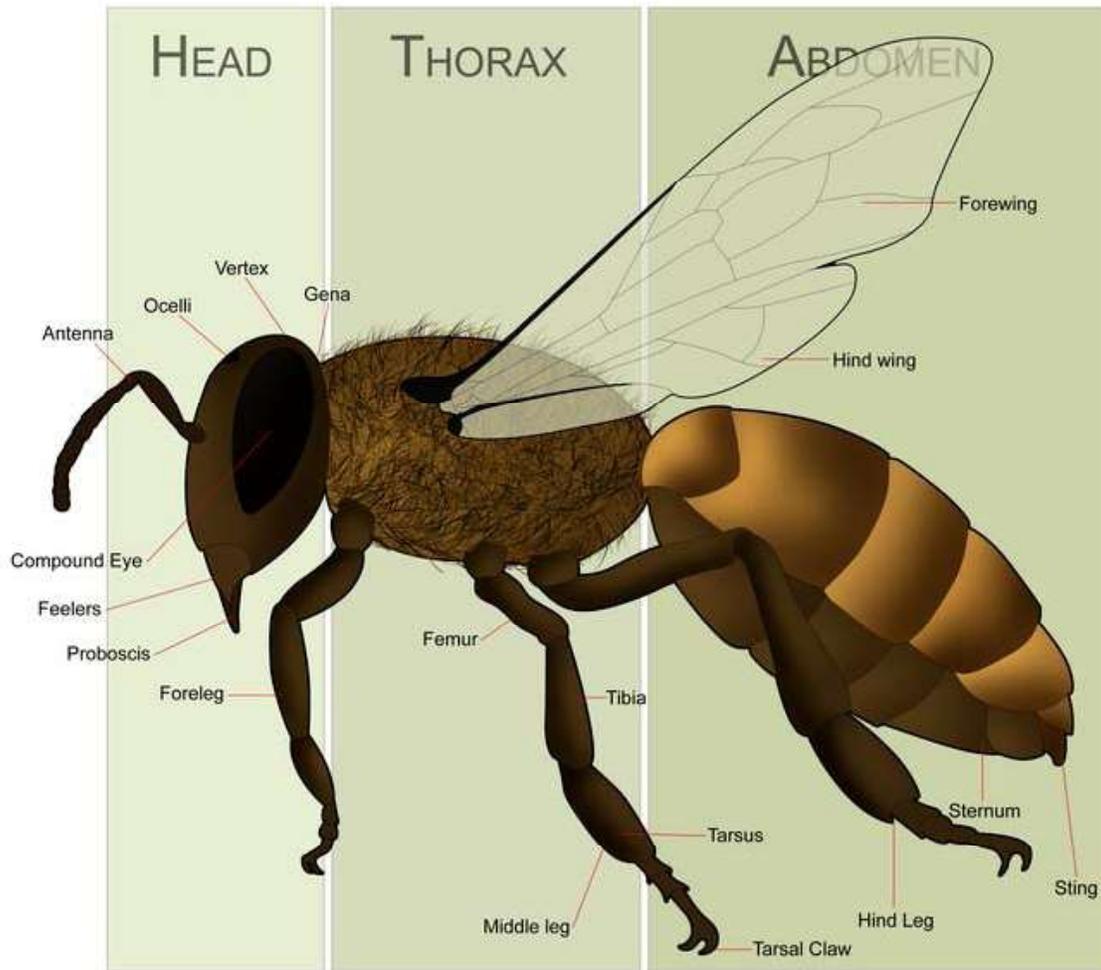
In New Zealand scientists discovered that three genera of native bees have evolved to open flower buds of the native mistletoe *Peraxilla tetrapetala*. The buds cannot open themselves but are visited by birds such as the tui and bellbird which twist the top of the ripe bud. That action releases a mechanism which causes the petals to suddenly spring open, giving access to the nectar and pollen. However, when observing the native bees in

the Canterbury province in the South Island, the scientists were astonished to see the bees biting the top off the buds, then pushing with their legs, occasionally popping open the buds to allow the bees to harvest the nectar and pollen, and therefore aid in the pollination of the mistletoe which is in decline in New Zealand. Nowhere else in the world have bees demonstrated ability to open explosive bird-adapted flowers.

Visiting flowers can be a dangerous occupation. Many assassin bugs and crab spiders hide in flowers to capture unwary bees. Other bees are lost to birds in flight. Insecticides used on blooming plants kill many bees, both by direct poisoning and by contamination of their food supply. A honey bee queen may lay 2000 eggs per day during spring buildup, but she also must lay 1000 to 1500 eggs per day during the foraging season, mostly to replace daily casualties, most of which are workers dying of old age. Among solitary and primitively social bees, however, lifetime reproduction is among the lowest of all insects, as it is common for females of such species to produce fewer than 25 offspring.

The population value of bees depends partly on the individual efficiency of the bees, but also on the population itself. Thus while bumblebees have been found to be about ten times more efficient pollinators on cucurbits, the total efficiency of a colony of honey bees is much greater due to greater numbers. Likewise during early spring orchard blossoms, bumblebee populations are limited to only a few queens, and thus are not significant pollinators of early fruit.

## Pollinator decline



Morphology of a female honey bee

From 1972 to 2006, there was a dramatic reduction in the number of feral honey bees in the US, which are now almost absent. At the same time there was a significant though somewhat gradual decline in the number of colonies maintained by beekeepers. This decline includes the cumulative losses from all factors, such as urbanization, pesticide use, tracheal and *Varroa* mites, and commercial beekeepers' retiring and going out of business. However, in late 2006 and early 2007 the rate of attrition reached new proportions, and the term colony collapse disorder was coined to describe the sudden disappearances. After several years of research and concern, a team of scientists headed by Jerry Bromenshenk published a paper in October 2010 saying that a new DNA-based virus, invertebrate iridescent virus or IIV6, and the fungus *Nosema ceranae* were found in every killed colony the group studied. In their study they found that neither agent alone seemed deadly, but a combination of the virus and *Nosema ceranae* was always 100% fatal. Bromenshenk said it is not yet clear whether one condition weakens the bees enough to be finished off by the second, or whether they somehow compound the other's

destructive power. "They're co-factors, that's all we can say at the moment. They're both present in all these collapsed colonies." Investigations into the phenomenon had occurred amidst great concern over the nature and extent of the losses. In 2009 some reports from the US suggested that 1/3 of the honey bee colonies did not survive the winter, though normal winter losses are known to be around 25%.

Apart from colony collapse disorder, many of the losses outside the US have also been attributed to other causes. Pesticides used to treat seeds, such as Clothianidin and Imidacloprid, have been considered prime suspects. Other species of bees such as mason bees are increasingly cultured and used to meet the agricultural pollination need.

Native pollinators include bumblebees and solitary bees, which often survive in refuges in wild areas away from agricultural spraying, but may still be poisoned in massive spray programs for mosquitoes, gypsy moths, or other insect pests. Although pesticide use remains a concern, the major problem for wild pollinator populations is the loss of the flower-rich habitat on which they depend for food. Throughout the northern hemisphere, the last 70 or so years have seen an intensification of agricultural systems, which has decreased the abundance and diversity of wild flowers.

Legislation such as the UK's Bees Act 1980 is designed to stop the decline of bees.

## **Evolution**

Bees, like ants, are a specialized form of wasp. The ancestors of bees were wasps in the family Crabronidae, and therefore predators of other insects. The switch from insect prey to pollen may have resulted from the consumption of prey insects which were flower visitors and were partially covered with pollen when they were fed to the wasp larvae. This same evolutionary scenario has also occurred within the vespoid wasps, where the group known as "pollen wasps" also evolved from predatory ancestors. Up until recently, the oldest non-compression bee fossil had been *Cretotrigona prisca* in New Jersey amber and of Cretaceous age, a meliponine. A recently reported bee fossil, of the genus *Melittosphex*, is considered "*an extinct lineage of pollen-collecting Apoidea sister to the modern bees*", and dates from the early Cretaceous (~100 mya). Derived features of its morphology ("apomorphies") place it clearly within the bees, but it retains two unmodified ancestral traits ("plesiomorphies") of the legs (two mid-tibial spurs, and a slender hind basitarsus), indicative of its transitional status.

The earliest animal-pollinated flowers were pollinated by insects such as beetles, so the syndrome of insect pollination was well established before bees first appeared. The novelty is that bees are *specialized* as pollination agents, with behavioral and physical modifications that specifically enhance pollination, and are generally more efficient at the task than any other pollinating insect such as beetles, flies, butterflies and pollen wasps. The appearance of such floral specialists is believed to have driven the adaptive radiation of the angiosperms, and, in turn, the bees themselves.

Among living bee groups, the "short-tongued" bee family Colletidae has traditionally been considered the most "primitive", and sister taxon to the remainder of the bees. In the 21st century, however, some researchers have claimed that the Dasypodidae is the basal group, the short, wasp-like mouthparts of colletids being the result of convergent evolution, rather than indicative of a plesiomorphic condition. This subject is still under debate, and the phylogenetic relationships among bee families are poorly understood.

### ***Eusocial and semisocial bees***



A honey bee swarm

Bees may be solitary or may live in various types of communities. The most advanced of these are eusocial colonies found among the honey bees, bumblebees, and stingless bees.

Sociality, of several different types, is believed to have evolved separately many times within the bees.

In some species, groups of cohabiting females may be sisters, and if there is a division of labor within the group, then they are considered semisocial.

If, in addition to a division of labor, the group consists of a mother and her daughters, then the group is called eusocial. The mother is considered the "queen" and the daughters are "workers". These castes may be purely behavioral alternatives, in which case the system is considered "primitively eusocial" (similar to many paper wasps), and if the castes are morphologically discrete, then the system is "highly eusocial".

There are many more species of primitively eusocial bees than highly eusocial bees, but they have rarely been studied. The biology of most such species is almost completely unknown. The vast majority are in the family Halictidae, or "sweat bees". Colonies are typically small, with a dozen or fewer workers, on average. The only physical difference between queens and workers is average size, if they differ at all. Most species have a single season colony cycle, even in the tropics, and only mated females (future queens, or "gynes") hibernate (called diapause). A few species have long active seasons and attain colony sizes in the hundreds. The orchid bees include a number of primitively eusocial species with similar biology. Certain species of allodapine bees (relatives of carpenter bees) also have primitively eusocial colonies, with unusual levels of interaction between the adult bees and the developing brood. This is "progressive provisioning"; a larva's food is supplied gradually as it develops. This system is also seen in honey bees and some bumblebees.

Highly eusocial bees live in colonies. Each colony has a single queen, many workers and, at certain stages in the colony cycle, drones. When humans provide the nest, it is called a hive. Honey bee hives can contain up to 40,000 bees at their annual peak, which occurs in the spring, but usually have fewer.

## **Bumblebees**

Bumblebees (*Bombus terrestris*, *Bombus pratorum*, et al.) are eusocial in a manner quite similar to the eusocial Vespidae such as hornets. The queen initiates a nest on her own (unlike queens of honey bees and stingless bees which start nests via swarms in the company of a large worker force). Bumblebee colonies typically have from 50 to 200 bees at peak population, which occurs in mid to late summer. Nest architecture is simple, limited by the size of the nest cavity (pre-existing), and colonies are rarely perennial. Bumblebee queens sometimes seek winter safety in honey bee hives, where they are sometimes found dead in the spring by beekeepers, presumably stung to death by the honey bees. It is unknown whether any survive winter in such an environment.

Bumblebees are one of the more important wild pollinators, but have declined significantly in recent decades. In the UK, 2 species have become nationally extinct during the last 75 years while others have been placed on the UK Biodiversity Action

Plan as priority species in recognition of the need for conservation action. In 2006 a new charity, the Bumblebee Conservation Trust, was established in order to coordinate efforts to conserve remaining populations through conservation and education.

### **Stingless bees**

Stingless bees are very diverse in behavior, but all are highly eusocial. They practise mass provisioning, complex nest architecture, and perennial colonies.

### **Honey bees**



A European honey bee extracts nectar from an *Aster* flower

The true honey bees (genus *Apis*) have arguably the most complex social behavior among the bees. The European (or Western) honey bee, *Apis mellifera*, is the best known bee species and one of the best known of all insects.

### **Africanized honey bee**

Africanized bees, also called killer bees, are a hybrid strain of *Apis mellifera* derived from experiments by Warwick Estevam Kerr to cross European and African honey bees.

Several queen bees escaped from his laboratory in South America and have spread throughout the Americas. Africanized honey bees are more defensive than European honey bees.

### ***Solitary and communal bees***

Most other bees, including familiar species of bee such as the Eastern carpenter bee (*Xylocopa virginica*), alfalfa leafcutter bee (*Megachile rotundata*), orchard mason bee (*Osmia lignaria*) and the hornfaced bee (*Osmia cornifrons*) are solitary in the sense that every female is fertile, and typically inhabits a nest she constructs herself. There are no *worker* bees for these species. Solitary bees typically produce neither honey nor beeswax. They are immune from acarine and *Varroa* mites, but have their own unique parasites, pests and diseases.

Solitary bees are important pollinators, and pollen is gathered for provisioning the nest with food for their brood. Often it is mixed with nectar to form a paste-like consistency. Some solitary bees have very advanced types of pollen-carrying structures on their bodies. A very few species of solitary bees are being increasingly cultured for commercial pollination.



A solitary bee, *Anthidium florentinum* (family Megachilidae), visiting *Lantana*

Solitary bees are often oligoleges, in that they only gather pollen from one or a few species/genera of plants (unlike honey bees and bumblebees which are generalists). No known bees are nectar specialists; many oligolectic bees will visit multiple plants for nectar, but there are no bees which visit only one plant for nectar while also gathering pollen from many different sources. Specialist pollinators also include bee species which gather floral oils instead of pollen, and male orchid bees, which gather aromatic compounds from orchids (one of the only cases where male bees are effective pollinators). In a very few cases only one species of bee can effectively pollinate a plant species, and some plants are endangered at least in part because their pollinator is dying off. There is, however, a pronounced tendency for oligolectic bees to be associated with common, widespread plants which are visited by multiple pollinators (e.g., there are some 40 oligoleges associated with creosote bush in the US desert southwest, and a similar pattern is seen in sunflowers, asters, mesquite, etc.)

Solitary bees create nests in hollow reeds or twigs, holes in wood, or, most commonly, in tunnels in the ground. The female typically creates a compartment (a "cell") with an egg and some provisions for the resulting larva, then seals it off. A nest may consist of numerous cells. When the nest is in wood, usually the last (those closer to the entrance) contain eggs that will become males. The adult does not provide care for the brood once the egg is laid, and usually dies after making one or more nests. The males typically emerge first and are ready for mating when the females emerge. Providing nest boxes for solitary bees is increasingly popular for gardeners. Solitary bees are either stingless or very unlikely to sting (only in self defense, if ever).

While solitary females each make individual nests, some species are gregarious, preferring to make nests near others of the same species, giving the appearance to the casual observer that they are social. Large groups of solitary bee nests are called *aggregations*, to distinguish them from colonies.

In some species, multiple females share a common nest, but each makes and provisions her own cells independently. This type of group is called "communal" and is not uncommon. The primary advantage appears to be that a nest entrance is easier to defend from predators and parasites when there are multiple females using that same entrance on a regular basis.

## ***Cleptoparasitic bees***



*Bombus vestalis*, a cuckoo bee parasite of the bumblebee *Bombus terrestris*

Cleptoparasitic bees, commonly called "cuckoo bees" because their behavior is similar to cuckoo birds, occur in several bee families, though the name is technically best applied to the apid subfamily Nomadinae. Females of these bees lack pollen collecting structures (the scopa) and do not construct their own nests. They typically enter the nests of pollen collecting species, and lay their eggs in cells provisioned by the host bee. When the cuckoo bee larva hatches it consumes the host larva's pollen ball, and if the female cleptoparasite has not already done so, kills and eats the host larva. In a few cases where the hosts are social species, the cleptoparasite remains in the host nest and lays many eggs, sometimes even killing the host queen and replacing her.

Many cleptoparasitic bees are closely related to, and resemble, their hosts in looks and size, (i.e., the *Bombus* subgenus *Psithyrus*, which are parasitic bumblebees that infiltrate

nests of species in other subgenera of *Bombus*). This common pattern gave rise to the ecological principle known as "Emery's Rule". Others parasitize bees in different families, like *Townsendiella*, a nomadine apid, one species of which is a cleptoparasite of the dasypodaid genus *Hesperapis*, while the other species in the same genus attack halictid bees.

### **Nocturnal bees**

Four bee families (Andrenidae, Colletidae, Halictidae, and Apidae) contain some species that are crepuscular (these may be either the vespertine or matinal type). These bees have greatly enlarged ocelli, which are extremely sensitive to light and dark, though incapable of forming images. Many are pollinators of flowers that themselves are crepuscular, such as evening primroses, and some live in desert habitats where daytime temperatures are extremely high.

### **Flight**



Bee in mid air flight carrying pollen in pollen basket

In his 1934 French book *Le vol des insectes*, M. Magnan wrote that he and a M. Saint-Lague had applied the equations of air resistance to bumblebees and found that their flight could not be explained by fixed-wing calculations, but that "One shouldn't be surprised that the results of the calculations don't square with reality". This has led to a common misconception that bees "violate aerodynamic theory", but in fact it merely

confirms that bees do not engage in fixed-wing flight, and that their flight is explained by other mechanics, such as those used by helicopters.

In 1996 Charlie Ellington at Cambridge University showed that vortices created by many insects' wings and non-linear effects were a vital source of lift; vortices and non-linear phenomena are notoriously difficult areas of hydrodynamics, which has made for slow progress in theoretical understanding of insect flight.

In 2005, Michael Dickinson and his Caltech colleagues studied honey bee flight with the assistance of high-speed cinematography and a giant robotic mock-up of a bee wing. Their analysis revealed that sufficient lift was generated by "the unconventional combination of short, choppy wing strokes, a rapid rotation of the wing as it flops over and reverses direction, and a very fast wing-beat frequency". Wing-beat frequency normally increases as size decreases, but as the bee's wing beat covers such a small arc, it flaps approximately 230 times per second, faster than a fruitfly (200 times per second) which is 80 times smaller.

### ***Bees and humans***



Bee larvae as food in Java

Bees figure prominently in mythology and have been used by political theorists as a model for human society. Journalist Bee Wilson states that the image of a community of honey bees "occurs from ancient to modern times, in Aristotle and Plato; in Virgil and

Seneca; in Erasmus and Shakespeare; Tolstoy, as well as by social theorists Bernard Mandeville and Karl Marx."

Despite the honey bee's painful sting and the stereotype of insects as pests, bees are generally held in high regard. This is most likely due to their usefulness as pollinators and as producers of honey, their social nature, and their reputation for diligence. Bees are one of the few insects regularly used on advertisements, being used to illustrate honey and foods made with honey (such as Honey Nut Cheerios).

In ancient Egypt, the bee was seen to symbolize the lands of Lower Egypt, with the Pharaoh being referred to as "He of Sedge and Bee" (the sedge representing Upper Egypt).

In North America, yellowjackets and hornets, especially when encountered as flying pests, are often misidentified as bees, despite numerous differences between them.

Although a bee sting can be deadly to those with allergies, virtually all bee species are non-aggressive if undisturbed and many cannot sting at all. Humans are often a greater danger to bees, as bees can be affected or even harmed by encounters with toxic chemicals in the environment.

In Indonesia bee larvae are eaten as a companion to rice, after being mixed with shredded coconut "meat", wrapped in banana leaves, and steamed.

## Chapter 6

# Cattle

### Cattle



A Swiss Braunvieh cow wearing a cowbell

### Conservation status

Domesticated

### Scientific classification

|           |          |
|-----------|----------|
| Kingdom:  | Animalia |
| Phylum:   | Chordata |
| Class:    | Mammalia |
| Subclass: | Theria   |

Infraclass: Eutheria  
Order: Artiodactyla  
Family: Bovidae  
Subfamily: Bovinae  
Genus: *Bos*  
Species: *B. primigenius*  
Subspecies: *B. p. taurus*,  
*B. p. indicus*

#### Binomial name

*Bos primigenius*  
Bojanus, 1827

#### Trinomial name

*Bos primigenius taurus*,  
*Bos primigenius indicus*

#### Synonyms

*Bos taurus*,  
*Bos indicus*

**Cattle** (colloquially **cows**) are the most common type of large domesticated ungulates. They are a prominent modern member of the subfamily Bovinae, are the most widespread species of the genus *Bos*, and are most commonly classified collectively as ***Bos primigenius***. Cattle are raised as livestock for meat (beef and veal), as dairy animals for milk and other dairy products, and as draft animals (pulling carts, plows and the like). Other products include leather and dung for manure or fuel. In some countries, such as India, cattle are sacred. It is estimated that there are 1.3 billion cattle in the world today. In 2009, cattle became the first livestock animal to have its genome mapped.

### **Species of cattle**

Cattle were originally identified as three separate species. These were *Bos taurus*, the European or "taurine" cattle (including similar types from Africa and Asia); *Bos indicus*, the zebu; and the extinct *Bos primigenius*, the aurochs. The aurochs is ancestral to both zebu and taurine cattle. Recently these three have increasingly been grouped as one species, with *Bos primigenius taurus*, *Bos primigenius indicus* and *Bos primigenius primigenius* as the subspecies.



Zubron, a cross between Wisent and cattle.

Complicating the matter is the ability of cattle to interbreed with other closely related species. Hybrid individuals and even breeds exist, not only between taurine cattle and zebu (including the sanga cattle breeds, *Bos taurus africanus*) but also between one or both of these and some other members of the genus *Bos*: yak (called a dzo or "yattle"), banteng and gaur. Hybrids (such as the beefalo breed) can also occur between taurine cattle and either species of bison, which some authors consider to be in the genus *Bos* as well. The hybrid origin of some types may not be obvious – for example, genetic testing of the Dwarf Lulu breed, the only taurine-type cattle in Nepal, found them to be a mix of taurine cattle, zebu and yak. Cattle cannot successfully be hybridized with more distantly related bovines such as water buffalo or African buffalo.

The aurochs originally ranged throughout Europe, North Africa, and much of Asia. In historical times its range became restricted to Europe, and the last known individual died in Masovia, Poland, in about 1627. Breeders have attempted to recreate cattle of similar appearance to aurochs by crossing traditional types of domesticated cattle, creating the Heck cattle breed.

### **Word origin**

*Cattle* did not originate as the term for bovine animals. It was borrowed from Old French *catel*, itself from Latin *caput*, head, and originally meant movable personal property, especially livestock of any kind, as opposed to real property (the land, to also include wild or small free-roaming animals such as chickens, which would be sold as part of the land). The word is closely related to "chattel" (a unit of personal property) and "capital" in the economic sense. The term replaced earlier Old English *feoh* "cattle, property" (cf. German: *Vieh*, Gothic: *faihu*).

The word *cow* came via Anglo-Saxon *cū* (plural *cȳ*), from Common Indo-European *g<sup>w</sup>ōus* (genitive *g<sup>w</sup>ōwes*) = "a bovine animal", compare Persian *Gâv*, Sanskrit *go*, Welsh *buwch*.

In older English sources such as the King James Version of the Bible, "cattle" refers to livestock, as opposed to "deer" which refers to wildlife. "Wild cattle" may refer to feral cattle or to undomesticated species of the genus *Bos*. Today, when used without any other qualifier, the modern meaning of "cattle" is usually restricted to domesticated bovines.

### ***Terminology***



A Hereford bull



Cattle exhibit at Louisiana State Exhibit Museum in Shreveport

In general, the same words are used in different parts of the world but with minor differences in the definitions. The terminology described here contrasts the differences in definition between the United Kingdom and other British influenced parts of world such as Canada, Australia, New Zealand, Ireland, and the United States.

- An *intact* (i.e., not castrated) adult male is called a *bull*. A wild, young, unmarked bull is known as a *micky* in Australia. An unbranded bovine of either sex is called a "maverick" in the USA and Canada.
- An adult female that has had a calf (or two, depending on regional usage) is a *cow*. A young female before she has had a calf of her own and is under three years of age is called a *heifer*. A young female that has had only one calf is occasionally called a *first-calf heifer*.
- Young cattle of both sexes are called *calves* until they are weaned, then *weaners* until they are a year old in some areas; in other areas, particularly with male beef cattle, they may be known as *feeder-calves* or simply *feeders*. After that, they are referred to as *yearlings* or *stirks* if between one and two years of age.
- A castrated male is called a *steer* in the United States; older steers are often called *bullocks* in other parts of the world but in North America this term refers to a young bull. *Piker bullocks* are micky bulls that were caught, castrated and then later lost. In Australia, the term "Japanese ox" is used for grain fed steers in the

weight range of 500 to 650 kg that are destined for the Japanese meat trade. In North America, draft cattle under four years old are called *working steers*. Improper or late castration on a bull results in it becoming a coarse steer known as a *stag* in Australia, Canada and New Zealand. In some countries an incompletely castrated male is known also as a *rig*.

- A castrated male (occasionally a female or in some areas a bull) kept for draft purposes is called an *ox* (plural *oxen*); "ox" may also be used to refer to some carcass products from any adult cattle, such as *ox-hide*, *ox-blood* or *ox-liver*.
- A *springer* is a cow or heifer close to calving.
- In all cattle species, a female that is the twin of a bull usually becomes an infertile partial intersex, and is a *freemartin*.
- *Neat* (horned oxen, from which neatsfoot oil is derived), *beef* (young ox) and *beefing* (young animal fit for slaughtering) are obsolete terms, although *poll*, *pollard* or *polled cattle* are still terms in use for naturally hornless animals, or in some areas also for those that have been disbudded.
- Cattle raised for human consumption are called *beef cattle*. Within the beef cattle industry in parts of the United States, the older term *beef* (plural *beeves*) is still used to refer to an animal of either gender. Some Australian, Canadian, New Zealand and British people use the term *beast*, especially for single animals when the gender is unknown.
- Cattle of certain breeds bred specifically for milk production are called *milking* or *dairy cattle*.; a cow kept to provide milk for one family may be called a *house cow* or *milker*.
- The adjective applying to cattle in general is usually *bovine*. The terms "bull", "cow" and "calf" are also used by extension to denote the gender or age of other large animals, including whales, hippopotamuses, camels, elk and elephants

## Singular terminology issue



A herd of Cattle

*Cattle* can only be used in the plural and not in the singular: it is a plurale tantum. Thus one may refer to "three cattle" or "some cattle", but not "one cattle". There is no universally used singular form in modern English of "cattle", other than the sex- and age-specific terms such as cow, bull, steer and heifer. Historically, "ox" was a non-gender-specific term for adult cattle, but generally this is now used only for draft cattle, especially adult castrated males. The term is also incorporated into the names of other species such as the musk ox and "grunting ox" (yak), and is used in some areas to describe certain cattle products such as ox-hide and ox-tail.



A Brahman calf

"Cow" is in general use as a singular for the collective "cattle", despite the objections by those who insist it to be a female-specific term. Although the phrase "that cow is a bull" is absurd from a lexicographic standpoint, the word "cow" is easy to use when a singular is needed and the sex is unknown or irrelevant - when "there is a cow in the road", for example. Further, any herd of fully mature cattle in or near a pasture is statistically likely to consist mostly of cows, so the term is probably accurate even in the restrictive sense. Other than the few bulls needed for breeding, the vast majority of male cattle are castrated as calves and slaughtered for meat before the age of three years. Thus, in a pastured herd, any calves or herd bulls usually are clearly distinguishable from the cows due to distinctively different sizes and clear anatomical differences. Merriam-Webster, a U.S. dictionary, recognizes the non-sex-specific use of "cow" as an alternate definition, whereas Collins, a UK dictionary, does not.

Colloquially, more general non-specific terms may denote cattle when a singular form is needed. Australian, New Zealand and British farmers use the term "beast" or "cattle beast". "Bovine" is also used in Britain. The term "critter" is common in the western United States and Canada, particularly when referring to young cattle. In some areas of the American South (particularly the Appalachian region), where both dairy and beef cattle are present, an individual animal was once called a "beef critter", though that term is becoming archaic.

## Other terminology

Cattle raised for human consumption are called "beef cattle". Within the beef cattle industry in parts of the United States, the term "beef" (plural "beeves") is still used in its archaic sense to refer to an animal of either gender. Cows of certain breeds that are kept for the milk they give are called "dairy cows" or "milking cows" (formerly "milch cows" – "milch" was pronounced as "milk"). Most young male offspring of dairy cows are sold for veal, and may be referred to as *veal calves*.

The term "dogies" is used to describe orphaned calves in the context of ranch work in the American west, as in "Keep them dogies moving". In some places, a cow kept to provide milk for one family is called a "house cow". Other obsolete terms for cattle include "neat" (this use survives in "neatsfoot oil", extracted from the feet and legs of cattle), and "beefing" (young animal fit for slaughter).

An onomatopoeic term for one of the commonest sounds made by cattle is "moo", and this sound is also called *lowing*. There are a number of other sounds made by cattle, including calves *bawling*, and bulls *bellowing*. The bullroarer makes a sound similar to a territorial call made by bulls.

## Anatomy

Cattle have one stomach with four compartments. They are the rumen, reticulum, omasum, and abomasum, with the rumen being the largest compartment. The reticulum, the smallest compartment, is known as the "honeycomb". Cattle sometimes consume metal objects which are deposited in the reticulum and irritation from the metal objects causes hardware disease. The omasum's main function is to absorb water and nutrients from the digestible feed. The omasum is known as the "many plies". The abomasum is like the human stomach; this is why it is known as the "true stomach".



Dairy farming and the milking of cattle - once performed largely by hand, but now usually replaced by machine – exploits the cow's ruminant biology.

Cattle are ruminants, meaning that they have a digestive system that allows use of otherwise indigestible foods by regurgitating and rechewing them as "cud". The cud is then reswallowed and further digested by specialised microorganisms in the rumen. These microbes are primarily responsible for decomposing cellulose and other carbohydrates into volatile fatty acids that cattle use as their primary metabolic fuel. The microbes inside the rumen are also able to synthesize amino acids from non-protein nitrogenous sources, such as urea and ammonia. As these microbes reproduce in the rumen, older generations die and their carcasses continue on through the digestive tract. These carcasses are then partially digested by the cattle, allowing them to gain a high

quality protein source. These features allow cattle to thrive on grasses and other vegetation.

The gestation period for a cow is nine months. A newborn calf weighs 25 to 45 kilograms (55 to 99 lb). The world record for the heaviest bull was 1,740 kilograms (3,840 lb), a Chianina named Donetto, when he was exhibited at the Arezzo show in 1955. The heaviest steer was eight year old 'Old Ben', a Shorthorn/Hereford cross weighing in at 2,140 kilograms (4,720 lb) in 1910. Steers are generally killed before reaching 750 kilograms (1,650 lb). Breeding stock usually live to about 15 years (occasionally as much as 25 years). The oldest recorded cow, Big Bertha, died at the age of 48 in 1993.

A common misconception about cattle (particularly bulls) is that they are enraged by the color red (something provocative is often said to be "like a red flag to a bull"). This is incorrect, as cattle are red-green color-blind. The myth arose from the use of red capes in the sport of bullfighting; in fact, two different capes are used. The capote is a large, flowing cape that is magenta and yellow. The more famous muleta is the smaller, red cape, used exclusively for the final, fatal segment of the fight. It is not the color of the cape that angers the bull, but rather the movement of the fabric that irritates the bull and incites it to charge.

Although cattle cannot distinguish red from green, they do have two kinds of color receptors in the cone cells in their retinas. Thus they are dichromatic, the same as most other mammals (including dogs, cats, horses and up to ten percent of male humans). They are able to distinguish some colors, particularly blue from yellow, in the same way as most other non-primate land mammals.

### ***Cattle genome***

In the April 24, 2009 edition of the journal *Science*, it was reported that a team of researchers led by the National Institutes of Health and the U.S. Department of Agriculture has mapped the bovine genome. The scientists found that cattle have approximately 22,000 genes, and 80 percent of their genes are shared with humans, and they have approximately 1,000 genes they share with dogs and rodents, but are not found in humans. Using this bovine "HapMap", researchers can track the differences between the breeds that affect the quality of meat and milk yields.

## ***Domestication and husbandry***



Texas Longhorns are a U.S. breed

Cattle occupy a unique role in human history, domesticated since at least the early Neolithic. They are raised for meat (beef cattle), dairy products and hides. They are also used as draft animals and in certain sports. Some consider cattle the oldest form of wealth, and cattle raiding consequently one of the earliest forms of theft.



A hereford being inspected for ticks; cattle are often restrained or confined in Cattle crushes when given medical attention.

Cattle are often raised by allowing herds to graze on the grasses of large tracts of rangeland. Raising cattle in this manner allows the use of land that might be unsuitable for growing crops. The most common interactions with cattle involve daily feeding,

cleaning and milking. Many routine husbandry practices involve ear tagging, dehorning, loading, medical operations, vaccinations and hoof care, as well as training for agricultural shows and preparations. There are also some cultural differences in working with cattle- the cattle husbandry of Fulani men rests on behavioural techniques, whereas in Europe cattle are controlled primarily by physical means like fences. Breeders use cattle husbandry to reduce *M. bovis* infection susceptibility by selective breeding and maintaining herd health to avoid concurrent disease.

Cattle are farmed for beef, veal, dairy, leather and they are less commonly used for conservation grazing, simply to maintain grassland for wildlife – for example, in Epping Forest, England. They are often used in some of the most wild places for livestock. Depending on the breed, cattle can survive on hill grazing, heaths, marshes, moors and semi desert. Modern cows are more commercial than older breeds and, having become more specialized, are less versatile. For this reason many smaller farmers still favor old breeds, like the dairy breed of cattle Jersey.

In Portugal, Spain, Southern France and some Latin American countries, bulls are used in the activity of bullfighting; a similar activity, Jallikattu, is seen in South India; in many other countries this is illegal. Other activities such as bull riding are seen as part of a rodeo, especially in North America. Bull-leaping, a central ritual in Bronze Age Minoan culture, still exists in southwestern France. In modern times, cattle are also entered into agricultural competitions. These competitions can involve live cattle or cattle carcasses in hoof and hook events.

In terms of food intake by humans, consumption of cattle is less efficient than of grain or vegetables with regard to land use, and hence cattle grazing consumes more area than such other agricultural production when raised on grains. Nonetheless, cattle and other forms of domesticated animals can sometimes help to use plant resources in areas not easily amenable to other forms of agriculture.

## ***Economy***



Holstein cattle are the primary dairy breed, bred for high milk production.

Cattle today are the basis of a multi-billion dollar industry worldwide. The international trade in beef for 2000 was over \$30 billion and represented only 23 percent of world beef production. (Clay 2004). The production of milk, which is also made into cheese, butter, yogurt, and other dairy products, is comparable in economic size to beef production and provides an important part of the food supply for many of the world's people. Cattle hides, used for leather to make shoes, couches and clothing, are another widespread product. Cattle remain broadly used as draft animals in many developing countries, such as India.

## ***Environmental impact***



Cattle — especially when kept on enormous feedlots such as this one — have been named as a contributing factor in the rise in greenhouse gas emissions.

A 400-page United Nations report from the Food and Agriculture Organization (FAO) states that cattle farming is "responsible for 18% of greenhouse gases". The production of cattle to feed and clothe humans stresses ecosystems around the world, and is assessed to be one of the top three environmental problems in the world on a local to global scale.

The report, entitled *Livestock's Long Shadow*, also surveys the environmental damage from sheep, chickens, pigs and goats. But in almost every case, the world's 1.5 billion cattle are cited as the greatest adverse impact with respect to climate change as well as species extinction. The report concludes that, unless changes are made, the massive damage reckoned to be due to livestock may more than double by 2050, as demand for meat increases. One of the cited changes suggests that intensification of the livestock industry may be suggested, since intensification leads to less land for a given level of production.

Some microbes respire in the cattle gut by an anaerobic process known as methanogenesis (producing the gas methane). Cattle emit a large volume of methane, 95% of it through eructation or burping, not flatulence. As the carbon in the methane comes from the digestion of vegetation produced by photosynthesis, its release into the air by this process would normally be considered harmless, because there is no net increase in carbon in the atmosphere — it's removed as carbon dioxide from the air by photosynthesis and returned to it as methane. Methane is a more potent greenhouse gas

than carbon dioxide, having a warming effect 23 to 50 times greater, and according to Takahashi and Young "even a small increase in methane concentration in the atmosphere exerts a potentially significant contribution to global warming". Further analysis of the methane gas produced by livestock as a contributor to the increase in greenhouse gases is provided by Weart. Research is underway on methods of reducing this source of methane, by the use of dietary supplements, or treatments to reduce the proportion of methanogenetic microbes, perhaps by vaccination. In 2010, a diet was proposed to reduce the emissions of greenhouse gases by cattle. The diet was conceived by Alexander Hristov of the Pennstate University.

Cattle are fed a concentrated high-corn diet which produces rapid weight gain, but this has side effects which include increased acidity in the digestive system. When improperly handled, manure and other byproducts of concentrated agriculture also have environmental consequences.

Grazing by cattle at low intensities can create a favourable environment for native herbs and forbs; however, in most world regions cattle are reducing biodiversity due to overgrazing driven by food demands by an expanding human population.

### ***Health***

Cow urine is commonly used in India for medical purposes. It is distilled and then consumed by patients seeking treatment for a wide variety of illness. At present, there is no conclusive medical evidence that this has any effect.

## Oxen



Draft Zebus in Mumbai, Maharashtra, India

**Oxen** (singular **ox**) are large and heavyset breeds of *Bos taurus* cattle trained as draft animals. Often they are adult, castrated males. Usually an ox is over four years old due to the need for training and to allow it to grow to full size. Oxen are used for plowing, transport, hauling cargo, grain-grinding by trampling or by powering machines, irrigation by powering pumps, and wagon drawing. Oxen were commonly used to skid logs in forests, and sometimes still are, in low-impact select-cut logging. Oxen are most often used in teams of two, paired, for light work such as carting. In the past, teams might have been larger, with some teams exceeding twenty animals when used for logging.

An ox is a mature bovine who has learned to respond appropriately to a teamster's signals. These signals are given by verbal commands or by noise (whip cracks). In North America, the commands are (1) *get up*, (2) *whoa*, (3) *back up*, (4) *gee* (turn right) and (5) *haw* (turn left). U.S. ox trainers favored larger males for their ability to work.



Riding an ox in Hova, Sweden.

Oxen can pull harder and longer than horses. Though not as fast as horses, they are less prone to injury because they are more sure-footed.

Many oxen are used worldwide, especially in developing countries.

Oxen are also used as food products, including their blood, livers, kidneys, hearts, hides, and tails.

## Chapter 7

# Goat

### Domestic Goat



### Conservation status

Domesticated

### Scientific classification

|             |                     |
|-------------|---------------------|
| Kingdom:    | Animalia            |
| Phylum:     | Chordata            |
| Class:      | Mammalia            |
| Order:      | Artiodactyla        |
| Family:     | Bovidae             |
| Subfamily:  | Caprinae            |
| Genus:      | <i>Capra</i>        |
| Species:    | <i>C. aegagrus</i>  |
| Subspecies: | <i>C. a. hircus</i> |

### Trinomial name

*Capra aegagrus hircus*

(Linnaeus, 1758)

### Synonyms

*Capra hircus*

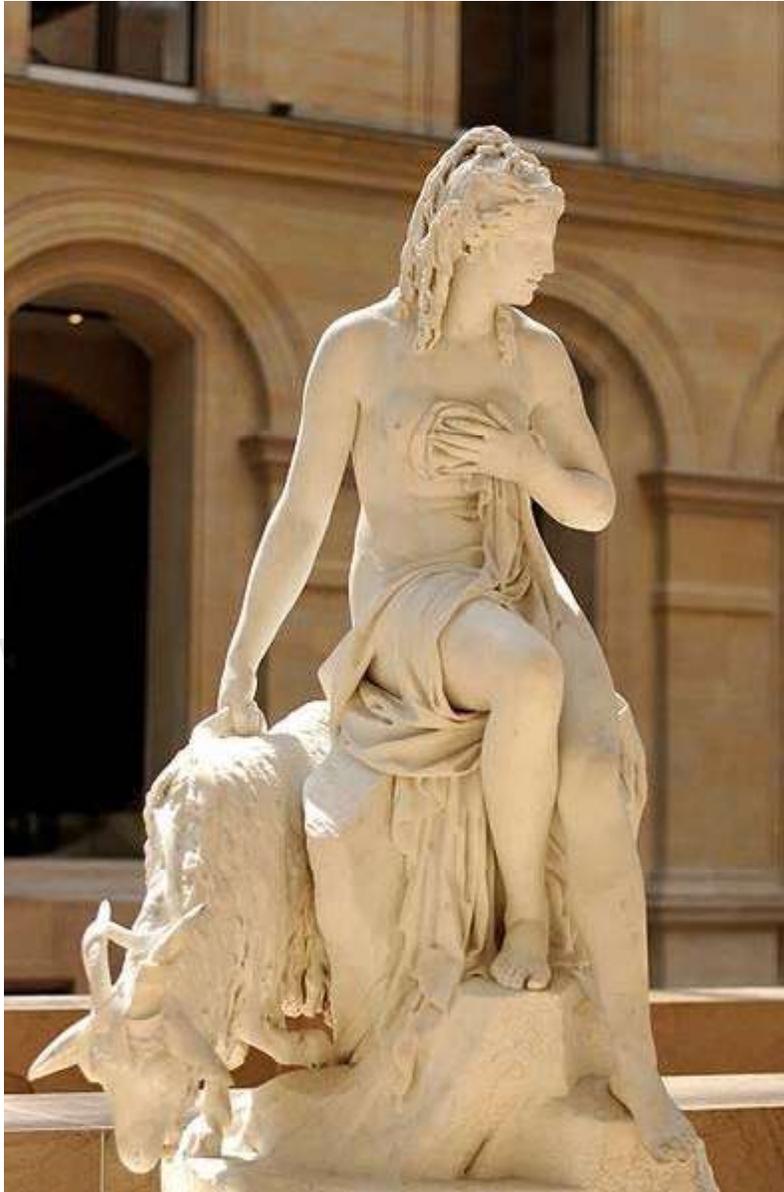
The **domestic goat** (*Capra aegagrus hircus*) is a subspecies of goat domesticated from the wild goat of southwest Asia and Eastern Europe. The goat is a member of the Bovidae family and is closely related to the sheep as both are in the goat-antelope subfamily Caprinae. There are over three hundred distinct breeds of goat.

Goats are one of the oldest domesticated species. Goats have been used for their milk, meat, hair, and skins over much of the world. In the twentieth century they also gained in popularity as pets.

Female goats are referred to as *does* or *nannies*, intact males as *bucks* or *billies*; their offspring are *kids*. Note that many goat breeders prefer the terms "buck" and "doe" to "billy" and "nanny". Castrated males are *wethers*. Goat meat from younger animals is called *kid* or *cabrito*, and from older animals is sometimes called *chevon*, or in some areas "mutton".

### Etymology

The Modern English word *goat* comes from the Old English *gāt* which meant "she-goat", and this in turn derived from Proto-Germanic *\*gaitaz* (cf. Old Norse and Dutch *geit* "goat", German *Geiß* "she-goat", and Gothic *gaitis* "goat"), ultimately from Proto-Indo-European *\*ghaidos* meaning "young goat" (cf. Latin *haedus* "kid"), itself perhaps from a root meaning "jump" (assuming that Old Church Slavonic *zajęci* "hare", Sanskrit *jihīte* "he moves" are related). To refer to the male of the species, Old English used *bucca* (which survives as "buck") until a shift to *he-goat* (and *she-goat*) occurred in the late 12th century. "Nanny goat" originated in the 18th century and "billy goat" in the 19th.



*Amalthée et la chèvre de Jupiter* (Amalthea and Jupiter's goat) Commissioned by the Queen of France in 1787 for the royal dairy at Rambouillet

### **History**

Goats are among the earliest animals domesticated by humans. The most recent genetic analysis confirms the archaeological evidence that the Anatolian Zagros are the likely origin of almost all domestic goats today. Another major genetic source of modern goats is the Bezoar goat, distributed from the mountainous regions of Asia Minor across the Middle East to Sind.

Neolithic farmers began to keep goats for access to milk and meat, primarily, as well as for their dung, which was used as fuel and their bones, hair, and sinew for clothing,

building, and tools. The earliest remnants of domesticated goats dating 10,000 years before present are found in Ganj Dareh in Iran. Goat remains have been found at archaeological sites in Jericho, Choga, Mami, Djeitun and Cayonu, dating the domestication of goats in western Asia at between 8000 and 9000 years ago.

Historically, goat hide has been used for water and wine bottles in both traveling and transporting wine for sale. It has also been used to produce parchment.

### ***Anatomy and health***

Most goats naturally have two horns, of various shapes and sizes depending on the breed. All goats have horns unless they are "polled" meaning they have one parent with a dominant polled gene. There have been incidents of polycerate goats (having as many as eight horns), although this is a genetic rarity thought to be inherited. Their horns are made of living bone surrounded by keratin and other proteins, and are used for defense, dominance, and territoriality.

Goats are ruminants. They have a four-chambered stomach consisting of the rumen, the reticulum, the omasum, and the abomasum. As with other mammal ruminants, they are even-toed ungulates. The females have an udder consisting of two teats, in contrast to cattle, which have four teats.

Goats have horizontal slit-shaped pupils, an adaptation which increases peripheral depth perception. Because goats' irises are usually pale, the pupils are much more visible than in animals with horizontal pupils, but very dark irises, such as cattle, deer, most horses and many sheep.

Both male and female goats have beards, and many types of goat (most commonly dairy goats, dairy-cross boers, and pygmy goats) may have wattles, one dangling from each side of the neck.

Some breeds of sheep and goats look similar, but they can usually be told apart because goat tails are short and point up, whereas sheep tails hang down and are usually longer and bigger – though some (like those of Northern European short-tailed sheep) are short, and longer ones are often docked.

## Reproduction



A 2 month old goat kid in a field of capeweed.

Goats reach puberty between 3 and 15 months of age, depending on breed and nutrition status. Many breeders prefer to postpone breeding until the doe has reached 70% of the adult weight. However, this separation is rarely possible in extensively managed, open range herds.

In temperate climates and among the Swiss breeds, the breeding season commences as the day length shortens, and ends in early spring or before. In equatorial regions, goats are able to breed at any time of the year. Successful breeding in these regions depends more on available forage than on day length. Does of any breed or region come into heat every 21 days for 2 to 48 hours. A doe in heat typically flags (vigorously wags) her tail often, stays near the buck if one is present, becomes more vocal, and may also show a decrease in appetite and milk production for the duration of the heat.

Bucks (intact males) of Swiss and northern breeds come into rut in the fall as with the doe's heat cycles. Bucks of equatorial breeds may show seasonal reduced fertility but, as with the does, are capable of breeding at all times. Rut is characterized by a decrease in appetite and obsessive interest in the does. A buck in rut will display flehmen lip curling and will urinate on his forelegs and face. Sebaceous scent glands at the base of the horns add to the male goat's odor, which is important to make him attractive to the female. Some does will not mate with a buck which has been de-scented.

In addition to natural mating, artificial insemination has gained popularity among goat breeders, as it allows easy access to a wide variety of bloodlines.



Suckling

Gestation length is approximately 150 days. Twins are the usual result, with single and triplet births also common. Less frequent are litters of quadruplet, quintuplet, and even sextuplet kids. Birthing, known as *kidding*, generally occurs uneventfully. Just before kidding, the doe will have a sunken area around the tail and hip, as well as heavy breathing. She may have a worried look, become restless and display great affection for her keeper. The mother often eats the placenta, which gives her much needed nutrients, helps stanch her bleeding, and parallels the behavior of wild herbivores such as deer to reduce the lure of the birth scent for predators.

*Freshening* (coming into milk production) occurs at kidding. Milk production varies with the breed, age, quality, and diet of the doe; dairy goats generally produce between 660 to 1,800 L (1,500 and 4,000 lb) of milk per 305 day lactation. On average, a good quality dairy doe will give at least 6 lb (2.7 l) of milk per day while she is in milk. A first time milker may produce less, or as much as 16 lb (7.3 l), or more of milk in exceptional cases. After the 305 day lactation, the doe will "dry off", typically after she has been bred. Occasionally, goats that have not been bred and are continuously milked will

continue lactation beyond the typical 305 days. Meat, fibre, and pet breeds are not usually milked and simply produce enough for the kids until weaning.

Western European-origin goats without horns (polled) frequently produce intersex offspring. These are generally female animals with male characteristics, and are infertile.

Male lactation is also known to occur in goats.

## **Diet**

Goats are reputed to be willing to eat almost anything, except tin cans and cardboard boxes. While goats will not actually eat inedible material, they are browsing animals, not grazers like cattle and sheep, and (coupled with their natural curiosity) will chew on and taste just about anything resembling plant matter in order to decide whether it is good to eat, including cardboard and paper labels from tin cans. Another possibility is that the goats are curious about the unusual smells of leftover food in discarded cans or boxes.



A domestic goat feeding in a field of capeweed, a weed which is toxic to most stock animals

Aside from sampling many things, goats are quite particular in what they actually consume, preferring to browse on the tips of woody shrubs and trees, as well as the occasional broad-leaved plant. However, it can fairly be said that their plant diet is extremely varied, and includes some species which are otherwise toxic. They will seldom

consume soiled food or contaminated water unless facing starvation. This is one reason goat rearing is most often free ranging, since stall-fed goat rearing involves extensive upkeep and is seldom commercially viable.

Goats prefer to browse on shrubbery and weeds, more like deer than sheep, preferring them to grasses. Nightshade is poisonous; wilted fruit tree leaves can also kill goats. Silage (corn stalks) is not good for goats, but haylage can be used if consumed immediately after opening. Alfalfa is their favorite hay; fescue is the least palatable and least nutritious. Mold in a goat's feed can make it sick and possibly kill it. Goats should not be fed grass showing any signs of mold.

The digestive physiology of a very young kid (like the young of other ruminants) is essentially the same as that of a monogastric animal. Milk digestion begins in the abomasum, the milk having bypassed the rumen via closure of the reticular/esophageal groove during suckling. At birth, the rumen is undeveloped, but as the kid begins to consume solid feed, the rumen soon increases in size and in its capacity to absorb nutrients.

## Behavior



Goats establish a dominance hierarchy in flocks, sometimes through head butting

Goats are extremely curious and intelligent. They are easily trained to pull carts and walk on leads. Ches McCartney, nicknamed "the goat man", toured the United States for over three decades in a wagon pulled by a herd of pet goats. They are also known for escaping their pens. Goats will test fences, either intentionally or simply because they are handy to climb on. If any of the fencing can be spread, pushed over or down, or otherwise be overcome, the goats will escape. Being very intelligent, once a weakness in the fence has been discovered, it will be exploited repeatedly. Goats are very coordinated and can climb and hold their balance in the most precarious places. Goats are also widely known for their ability to climb trees, although the tree generally has to be on somewhat of an angle. The vocalization goats make is called bleating.

Goats have an intensely inquisitive and intelligent nature: they will explore anything new or unfamiliar in their surroundings. They do so primarily with their prehensile upper lip and tongue. This is why they investigate items such as buttons, camera cases or clothing (and many other things besides) by nibbling at them, occasionally even eating them.

When handled as a group, goats tend to display less clumping behavior than sheep, and when grazing undisturbed, tend to spread across the field or range, rather than feed side-by-side as do sheep. When nursing young, goats will leave their kids separated ('lying out') rather than clumped as do sheep. They will generally turn and face an intruder and bucks are more likely to charge or butt at humans than are rams.

## **Diseases**

While goats are generally considered hardy animals and in many situations receive little medical care, they are subject to a number of diseases.

Among the conditions affecting goats are respiratory diseases, including pneumonia, foot rot, internal parasites, pregnancy toxosis and feed toxicity.

Goats can become infected with various viral and bacterial diseases such as foot-and-mouth disease, caprine arthritis encephalitis, caseous lymphadenitis, pinkeye, mastitis, and pseudorabies. They can transmit a number of zoonotic diseases to people, such as tuberculosis, brucellosis, Q-fever, and rabies.

## **Life expectancy**

Life expectancy for goats is between 15 and 18 years. An instance of a goat reaching the age of 24 has been reported.

Several factors can reduce this average expectancy, however; problems during kidding can lower a doe's expected life span to 10 or 11, and stresses of going into rut can lower a buck's expected life span to 8 or 10.

## ***Goats in agriculture***



Goat husbandry is common through the Norte Chico region in Chile, but also produces severe erosion and desertification. Image from upper Limari River

A goat is useful to humans either living or dead, first as a renewable provider of milk, manure, and fiber, and then as meat and hide. Some charities provide goats to impoverished people in poor countries, because goats are easier and cheaper to manage than cattle, and have multiple uses. In addition, goats are used for driving and packing purposes.

For instance, the intestine is used to make "catgut", which is still in use as a material for internal human surgical sutures and strings for musical instruments. The horn of the goat, which signifies wellbeing (Cornucopia), is also used to make spoons.



The Boer goat - in this case a buck - is a widely-kept meat breed.

### Worldwide goat population statistics

According to the FAO, the top producers of goat milk in 2008 were India (4 million metric tons), Bangladesh (2.16 million metric tons) and the Sudan (1.47 metric tons.)

| Country/Region  | Total Animals (millions) | Goat Milk (MT) | Goat Meat (million MT) |
|-----------------|--------------------------|----------------|------------------------|
| <b>World</b>    | -----                    | 15.2           | 4.8                    |
| <b>Africa</b>   | 294.5                    | 3.2            | 1.1                    |
| Nigeria         | 53.8                     | N/A            | 0.26                   |
| Sudan           | 43.1                     | 1.47           | 0.19                   |
| <b>Asia</b>     | 511.3                    | 8.89           | 3.4                    |
| Afghanistan     | 6.38                     | 0.11           | 0.04                   |
| India           | 125.7                    | 4.0            | 0.48                   |
| Bangladesh      | 56.4                     | 2.16           | 0.21                   |
| China           | 149.37                   | 0.26           | 1.83                   |
| Saudi Arabia    | 2.2                      | 0.076          | 0.024                  |
| <b>Americas</b> | 37.3                     | 0.54           | 0.15                   |

|                |       |        |       |
|----------------|-------|--------|-------|
| Mexico         | 8.8   | 0.16   | 0.04  |
| USA            | 3.1   | N/A    | 0.022 |
| <b>Europe</b>  | 17.86 | 2.59   | 0.012 |
| UK             | 0.09  | N/A    | N/A   |
| France         | 1.2   | 0.58   | 0.007 |
| <b>Oceania</b> | 3.42  | 0.0004 | 0.018 |

## Husbandry

Husbandry, or animal care and use, varies from region to region and from culture to culture. The particular housing used for goats depends not only on the intended use of the goat but also on the region of the world where they are raised. Historically, domestic goats were generally kept in herds that wandered on hills or other grazing areas, often tended by goatherds who were frequently children or adolescents, similar to the more widely known shepherd. These methods of herding are still used today.

In some parts of the world, especially Europe and North America, distinct breeds of goat are kept for dairy (milk) and for meat production. As with cattle, only the females give milk. Excess male kids of dairy breeds are typically slaughtered for meat. Both does and bucks of meat breeds may be slaughtered for meat, as well as older animals of any breed. The meat of older bucks (more than 1 year old) is generally considered not desirable for meat for human consumption. Castration at a young age prevents the development of typical buck odor.

Dairy goats are generally pastured in summer and may be stabled during the winter. As dairy does are milked daily, they are generally kept close to the milking shed. Their grazing is typically supplemented with hay and with concentrates. Stabled goats may be kept in stalls similar to horses, or in larger group pens. In the US system, does are generally re-bred annually. In some European commercial dairy systems, the does are bred only twice, and are milked continuously for several years after the second kidding.

Meat goats are more frequently pastured year-round, and may be kept many miles from barns. Angora and other fiber breeds are also kept on pasture or range. Range-kept and pastured goats may be supplemented with hay or concentrates, but this happens most frequently during the winter or dry seasons.

In India, Nepal, and much of Asia, goats are kept largely for milk production, both in commercial and household settings. The goats in this area may be kept closely housed or may be allowed to range for fodder. The Salem Black goat is herded to pasture in fields and along roads during the day but is kept penned at night for safe-keeping.

In Africa and the Mideast, goats are typically run in flocks with sheep. This maximizes the production per acre, as goats and sheep prefer different food plants. Multiple types of goat-raising are found in Ethiopia, where four main types of goat raising have been identified: goats kept pastured in annual crop systems, goats kept in perennial crop

systems, goats kept with cattle, and goats kept in arid areas under pastoral (nomadic) herding systems. In all four systems, however, goats were typically kept in extensive systems, with few purchased inputs. Household goats are traditionally kept in Nigeria. While many goats are allowed to wander the homestead or village, others are kept penned and fed in what is called a 'cut-and-carry' system. This type of husbandry is also used in parts of Latin America. Cut-and-carry, which refers to the practice of cutting down grasses, corn or cane for feed rather than allowing the animal access to the field, is particularly suited for types of feed, such as corn or cane, that are easily destroyed by trampling.

Pet goats may be found in many parts of the world when a family keeps one or more animals for emotional reasons rather than as production animals. It is becoming more common for goats to be kept exclusively as pets in North America and Europe.

## **Meat**

The taste of goat kid meat is similar to that of spring lamb meat; in fact, in the English-speaking islands of the Caribbean, and in some parts of Asia, particularly Pakistan and India, the word "mutton" is used to describe both goat and lamb meat. However, some compare the taste of goat meat to veal or venison, depending on the age and condition of the goat. Its flavor is said to be primarily linked to the presence of 4-methyloctanoic and 4-methylnonanoic acid. It can be prepared in a variety of ways including stewed, baked, grilled, barbecued, minced, canned, fried, curried, or made into sausage. Due to its low fat content, the meat can toughen at high temperatures without additional moisture. One of the most popular goats grown for meat is the South African Boer, introduced into the United States in the early 1990s. The New Zealand Kiko is also considered a meat breed, as is the myotonic or "fainting goat", a breed originating in Tennessee.

## Milk, butter and cheese



A goat being milked on an organic farm.

Goats produce approximately 2% of the world's total annual milk supply. Some goats are bred specifically for milk. If the strong-smelling buck is not separated from the does, his scent will affect the milk.

Doe milk naturally has small, well-emulsified fat globules, which means the cream remains suspended in the milk, instead of rising to the top, as in raw cow milk; therefore, it does not need to be homogenized. Indeed, if the milk is going to be used to make cheese it is recommended that it is not homogenized as this changes the structure of the milk impacting the culture's ability to coagulate the milk and the final quality and yield of cheese.

Dairy goats in their prime, which is generally around the third or fourth lactation cycle, average 6 to 8 pounds (2.7 to 3.6 kg) of milk production daily (roughly 3 to 4 US quarts (2.7 to 3.6 liters)) during a ten-month lactation, producing more just after freshening and gradually dropping in production toward the end of their lactation. The milk generally averages 3.5 percent butterfat. A doe may be expected to reach her heaviest production during her third or fourth lactation.

Doe milk is commonly processed into cheese, butter, ice cream, yoghurt, cajeta and other products. Goat cheese is known as *chèvre* in France, after the French word for "goat". Some varieties include Rocamadour and Montrachet. Goat butter is white because goats produce milk with the yellow beta-carotene converted to a colorless form of vitamin A.

## Nutrition

The American Academy of Pediatrics discourages feeding infants milk derived from goats. An April 2010 case report summarizes their recommendation and presents "a comprehensive review of the consequences associated with this dangerous practice," also stating, "Many infants are exclusively fed unmodified goat's milk as a result of cultural beliefs as well as exposure to false online information. Anecdotal reports have described a host of morbidities associated with that practice, including severe electrolyte abnormalities, metabolic acidosis, megaloblastic anemia, allergic reactions including life-threatening anaphylactic shock, hemolytic uremic syndrome, and infections." Untreated caprine brucellosis results in a 2% case fatality rate. According to the United States Department of Agriculture (USDA), doe milk is not recommended for human infants because it contains "inadequate quantities of iron, folate, vitamins C and D, thiamin, niacin, vitamin B6, and pantothenic acid to meet an infant's nutritional needs" and may cause harm to an infant's kidneys and could cause metabolic damage.

The Department of Health in the United Kingdom has repeatedly released statements stating on various occasions that "Goats' milk is not suitable for babies, and infant formulas and follow-on formulas based on goats' milk protein have not been approved for use in Europe," and "infant milks based on goats' milk protein are not suitable as a source of nutrition for infants."

On the other hand, some farming groups promote the practice. For example Small Farm Today in 2005 claimed beneficial use in invalid and convalescent diets, proposing that glycerol ethers, possibly important in nutrition for nursing infants, are much higher in doe milk than in cow milk. A 1970 book on animal breeding claimed that doe milk differs from cow or human milk by having higher digestibility, distinct alkalinity, higher buffering capacity, and certain therapeutic values in human medicine and nutrition. George Mateljan suggested that doe milk can replace ewe milk or cow milk in diets of those who are allergic to certain mammals' milk. However, like cow milk, doe milk has lactose (sugar), and may cause gastrointestinal problems for individuals with lactose intolerance. In fact, the level of lactose is similar to that of bovine milk.

| Constituent | Doe (Goat) | Cow | Human |
|-------------|------------|-----|-------|
| Fat (g)     | 3.8        | 3.6 | 4.0   |
| Protein (g) | 3.5        | 3.3 | 1.2   |
| Lactose (g) | 4.1        | 4.6 | 6.9   |
| Ash (g)     | 0.8        | 0.7 | 0.2   |

|                         |      |      |      |
|-------------------------|------|------|------|
| <b>Total solids (g)</b> | 12.2 | 12.3 | 12.3 |
| <b>Calories</b>         | 70   | 69   | 68   |

Milk composition analysis, per 100 grams

| <b>Constituents</b>         | <b>unit</b> | <b>Cow</b> | <b>Doe<br/>(Goat)</b> | <b>Ewe<br/>(Sheep)</b> | <b>Water<br/>buffalo</b> |
|-----------------------------|-------------|------------|-----------------------|------------------------|--------------------------|
| Water                       | g           | 87.8       | 88.9                  | 83.0                   | 81.1                     |
| Protein                     | g           | 3.2        | 3.1                   | 5.4                    | 4.5                      |
| Fat                         | g           | 3.9        | 3.5                   | 6.0                    | 8.0                      |
| Carbohydrate                | g           | 4.8        | 4.4                   | 5.1                    | 4.9                      |
| Energy                      | kcal        | 66         | 60                    | 95                     | 110                      |
| Energy                      | kJ          | 275        | 253                   | 396                    | 463                      |
| Sugars (lactose)            | g           | 4.8        | 4.4                   | 5.1                    | 4.9                      |
| Cholesterol                 | mg          | 14         | 10                    | 11                     | 8                        |
| Calcium                     | IU          | 120        | 100                   | 170                    | 195                      |
| Saturated fatty acids       | g           | 2.4        | 2.3                   | 3.8                    | 4.2                      |
| Monounsaturated fatty acids | g           | 1.1        | 0.8                   | 1.5                    | 1.7                      |
| Polyunsaturated fatty acids | g           | 0.1        | 0.1                   | 0.3                    | 0.2                      |

These compositions vary by breed, animal, and point in the lactation period.

## Fiber



An Angora goat



A Cashmere goat

The Angora breed of goats produces long, curling, lustrous locks of mohair. The entire body of the goat is covered with mohair and there are no guard hairs. The locks constantly grow and can be four inches or more in length. Angora crossbreeds, such as the pygora and the nigora, have been created to produce mohair and/or cashgora on a smaller, easier-to-manage animal. The wool is shorn (cut from the body) twice a year, with an average yield of about 10 pounds.

Most goats have softer insulating hairs nearer the skin, and longer guard hairs on the surface. The desirable fiber for the textile industry is the former, and it goes by several names (down, cashmere and pashmina). The coarse guard hairs are of little value as they are too coarse, difficult to spin and difficult to dye. The cashmere goat produces a commercial quantity of cashmere wool, which is one of the most expensive natural fibers commercially produced; cashmere is very fine and soft. The cashmere goat fiber is harvested once a year, yielding around 9 ounces (200 grammes) of down.

In South Asia, cashmere is called "pashmina" (from Persian *pashmina*, "fine wool"). In the 18th and early 19th century, Kashmir (then called Cashmere by the English), had a thriving industry producing shawls from goat down imported from Tibet and Tartary through Ladakh. The shawls were introduced into Western Europe when the General in Chief of the French campaign in Egypt (1799–1802) sent one to Paris. Since these shawls

were produced in the upper Kashmir and Ladakh region, the wool came to be known as "cashmere".

### **Goat breeds**

Goat breeds fall into overlapping, general categories. They are generally distributed in to those used for dairy, fiber, meat, skins, and as companion animals. Some breeds are also particularly noted as pack goats.

### **Showing**



A Nigerian Dwarf milker in show clip. This doe is angular and dairy with a capacious and well supported mammary system.

Goat breeders' clubs frequently hold shows, where goats are judged on traits relating to conformation, udder quality, evidence of high production, longevity, build and muscling (meat goats and pet goats) and fiber production and the fiber itself (fiber goats). People who show their goats usually keep registered stock and the offspring of award-winning

animals command a higher price. Registered goats, in general, are usually higher-priced if for no other reason than that records have been kept proving their ancestry and the production and other data of their sires, dams, and other ancestors. A registered doe is usually less of a gamble than buying a doe at random (as at an auction or sale barn) because of these records and the reputation of the breeder. Children's clubs such as 4-H also allow goats to be shown. Children's shows often include a showmanship class, where the cleanliness and presentation of both the animal and the exhibitor as well as the handler's ability and skill in handling the goat are scored. In a showmanship class, conformation is irrelevant since this is not what is being judged.

Various "Dairy Goat Scorecards" (milking does) are systems used for judging shows in the US. The American Dairy Goat Association (ADGA) scorecard for an adult doe includes a point system of a hundred total with major categories that include general appearance, the dairy character of a doe (physical traits that aid and increase milk production), body capacity, and specifically for the mammary system. Young stock and bucks are judged by different scorecards which place more emphasis on the other three categories; general appearance, body capacity, and dairy character.

**The American Goat Society (AGS)** has a similar, but not identical scorecard that is used in their shows. The miniature dairy goats may be judged by either of the two scorecards. The "Angora Goat scorecard" used by the **Colored Angora Goat Breeder's Association CAGBA** (which covers the white and the colored goats) includes evaluation of an animal's fleece color, density, uniformity, fineness, and general body confirmation. Disqualifications include: a deformed mouth, broken down pasterns, deformed feet, crooked legs, abnormalities of testicles, missing testicles, more than 3 inch split in scrotum, and close-set or distorted horns.

**Religion, mythology, and folklore**



The goat Heiðrún consumes the foliage of the tree Læraðr, while her udders produce mead, collected in a pot below (1895) by Lorenz Frølich.



*The Scapegoat* by William Holman Hunt (1854).

According to Norse mythology, the god of thunder, Thor, has a chariot that is pulled by the goats Tanngrisnir and Tanngrjóstr. At night when he sets up camp, Thor eats the meat of the goats, but take care that all bones remain whole. Then he wraps the remains up, and in the morning, the goats always come back to life to pull the chariot. When a farmer's son who is invited to share the meal breaks one of the goats' leg bones to suck the marrow, the animal's leg remains broken in the morning, and the boy is forced to serve Thor as a servant to compensate for the damage.

Possibly related, the Yule Goat is one of the oldest Scandinavian and Northern European Yule and Christmas symbols and traditions. Yule Goat originally denoted the goat that was slaughtered around Yule, but it may also indicate a goat figure made out of straw. It is also used about the custom of going door-to-door singing carols and getting food and drinks in return, often fruit, cakes and sweets. "Going Yule Goat" is similar to the British custom wassailing, both with heathen roots. The Gävle Goat is a giant version of the Yule Goat, erected every year in the Swedish city of Gävle.

The Greek god, Pan, is said to have the upper body of a man and the horns and lower body of a goat. Pan was a very lustful god, nearly all of the myths involving him had to do with him chasing nymphs. He is also credited with creating the pan flute.

The goat is one of the twelve-year cycle of animals which appear in the Chinese zodiac related to the Chinese calendar. Each animal is associated with certain personality traits; those born in a year of the goat are predicted to be shy, introverted, creative, and perfectionist.

Several mythological hybrid creatures are believed to consist of parts of the goat, including the Chimera. The Capricorn sign in the Western zodiac is usually depicted as a goat with a fish's tail. Fauns and satyrs are mythological creatures that are part goat and part human. The mineral bromine is named from the Greek word "brómos," which means "stench of he-goats."

Goats are mentioned many times in the Bible. A goat is considered a "clean" animal by Jewish dietary laws and was slaughtered for an honored guest. It was also acceptable for some kinds of sacrifices. Goat-hair curtains were used in the tent that contained the tabernacle (Exodus 25:4). Its horns can be used instead of sheep's horn to make a shofar. On Yom Kippur, the festival of the Day of Atonement, two goats were chosen and lots were drawn for them. One was sacrificed and the other allowed to escape into the wilderness, symbolically carrying with it the sins of the community. From this comes the word "scapegoat". A leader or king was sometimes compared to a male goat leading the flock. In the New Testament, Jesus told a parable of The Sheep and the Goats. (Gospel of Matthew 25)

Popular Christian folk tradition in Europe associated Satan with imagery of goats. A common superstition in the Middle Ages was that goats whispered lewd sentences in the ears of the saints. The origin of this belief was probably the behavior of the buck in rut, the very epitome of lust. The common medieval depiction of the Devil was that of a goat-like face with horns and small beard (a goatee). The Black Mass, a probably-mythological "Satanic mass," was said to involve a black goat, the form in which Satan supposedly manifested himself for worship.

The goat has had a lingering connection with Satanism and pagan religions, even into modern times. The inverted pentagram, a symbol used in Satanism, is said to be shaped like a goat's head. The "Baphomet of Mendes" refers to a satanic goat-like figure from 19th century occultism.

## **Feral goats**



Feral goat in Aruba

Goats readily revert to the wild (become feral) if given the opportunity. The only domestic animal known to return to feral life as swiftly is the cat. Feral goats have established themselves in many areas: they occur in Australia, New Zealand, Great Britain, the Galapagos and in many other places. When feral goats reach large populations in habitats which are not adapted to them, they may have serious effects, such as removing native scrub, trees and other vegetation. Feral goats are common in Australia. However, in other circumstances they may become a natural component of the habitat.

## Chapter 8

# 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 crocodylians, 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 9

# Crocodylia

### Crocodylians

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:      | <b>Crocodylia</b><br>Owen, 1842 |

### Families

- Gavialidae
- Alligatoridae

- Crocodylidae



Marine and freshwater ranges of crocodylians

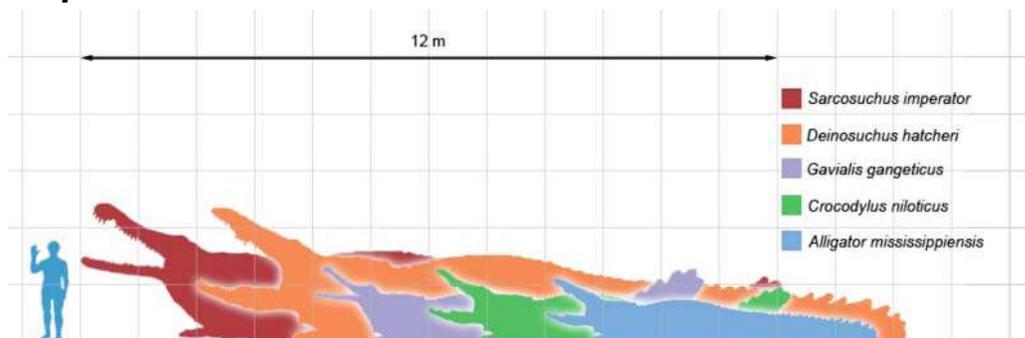
**Crocodylia** (or **Crocodylia**) is an order of large reptiles that appeared about 84 million years ago in the late Cretaceous Period (Campanian stage). They are the closest living relatives of birds, as the two groups are the only known survivors of the Archosauria. Members of the crocodylian total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

The correct vernacular term for this group is "**crocodylians**" 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 (*crocodelilos*, literally "pebble-worm", referring to the texture and shape of the animal). However, the y-spelling is increasingly common, especially in the context of phylogeny-based names in which Crocodylia is limited to the crown group.

### Description



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

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

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

## **Teeth and jaws**

All crocodilians have, like *Homo sapiens* (humans), thecodont dentition (teeth set in bony sockets) but unlike mammals, they replace their teeth throughout life (though not in 'extreme' old-age). Juvenile crocodilians replace teeth with larger ones at a rate as high as 1 new tooth per socket every month. After reaching adult size in a few years, however, tooth replacement rates can slow to two years and even longer. Very old members of some species have been seen in an almost "edentulous" (toothless) state, after teeth have been broken and replacement slowed or ceased. The result of this is that a single crocodile can go through at least 3,000 teeth in its lifetime. Each tooth is hollow, and the new one is growing inside the old. In this way, a new tooth is ready once the old is lost.



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

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

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

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

## Internal organs

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

Like mammals and birds and unlike other reptiles, crocodiles have a four-chambered heart. While the four-chambered heart is traditionally characteristic of endotherms, it is thought that the ectothermic crocodylia have a four-chambered heart because of an endothermic ancestry, originating in the archosaurs or in an earlier predecessor. When crocodylian 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<sub>2</sub> may serve to aid in creating stomach acid to assist in digesting bones from its prey. Their blood has been shown to have strong antibacterial properties.

Crocodylians have lungs with alveoli. They have a unique muscle called the diaphragmaticus that attaches to the liver and viscera and acts as a piston to assist in breathing. The diaphragmaticus is not homologous to the diaphragm of mammals and the proto-diaphragm of tegu lizards. Like other amniotes, crocodylian 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 crocodylians, expiration is mostly passive (involves little muscle contraction) during rest while inspiration always involves muscle contraction. Because many of these ventilatory muscles are used for maneuverability in water, and because the muscles were originally used for locomotion, it is possible that these muscles became ventilatory muscles after they evolved to move air around in the lungs for maneuverability.

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

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

## **Skin and skeleton**

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

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

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

## ***Differences between alligators and crocodiles***



Crocodiles are generally much lighter in color than alligators

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

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

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

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

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

## ***Evolution and classification***

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

## **Extant taxonomy**

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

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

## Taxonomy

- Superorder Crocodylomorpha
  - **Order Crocodylia**
    - 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 10

# 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:      | <b>Chiroptera</b><br>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.

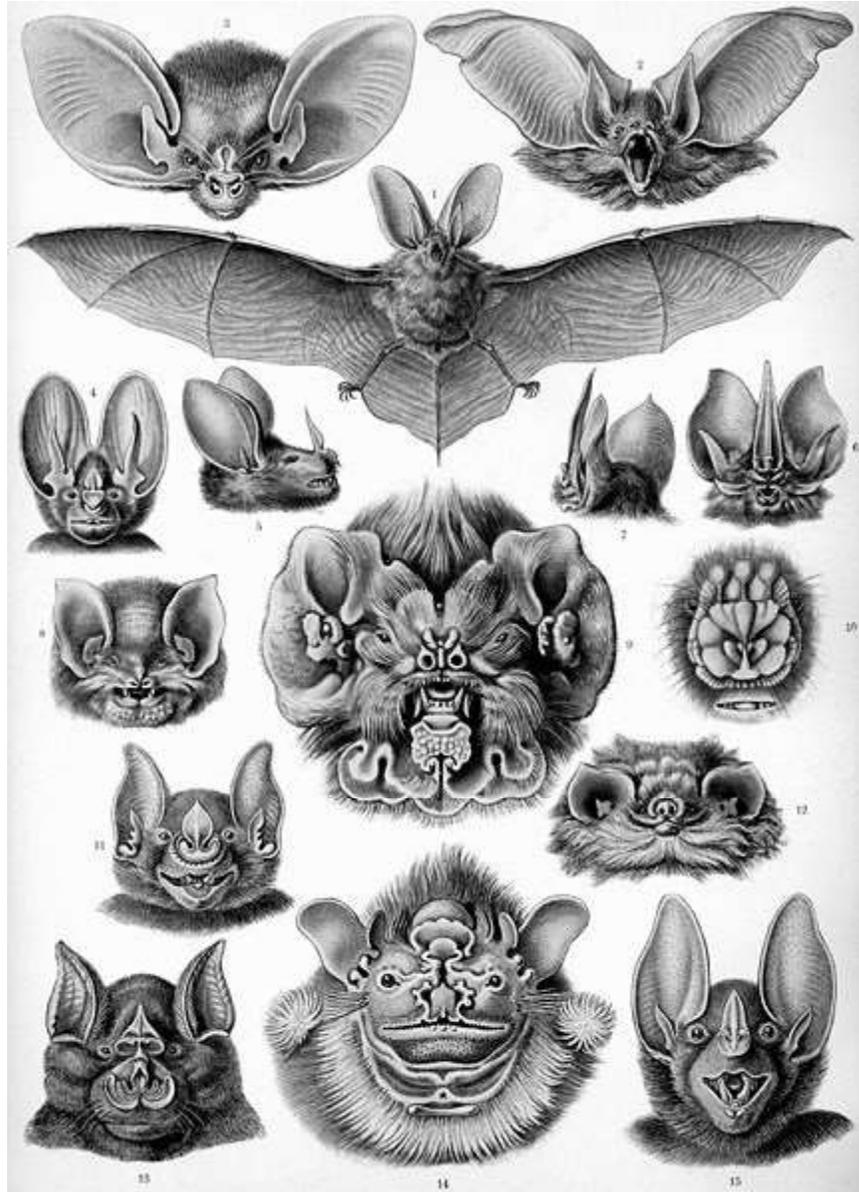
In addition to Yinpterochiroptera and Yangochiroptera, the names Pteropodiformes and Vespertilioniformes have also been proposed for these suborders. Under this new proposed nomenclature, the suborder Pteropodiformes includes all extant bat families more closely related to the genus *Pteropus* than the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

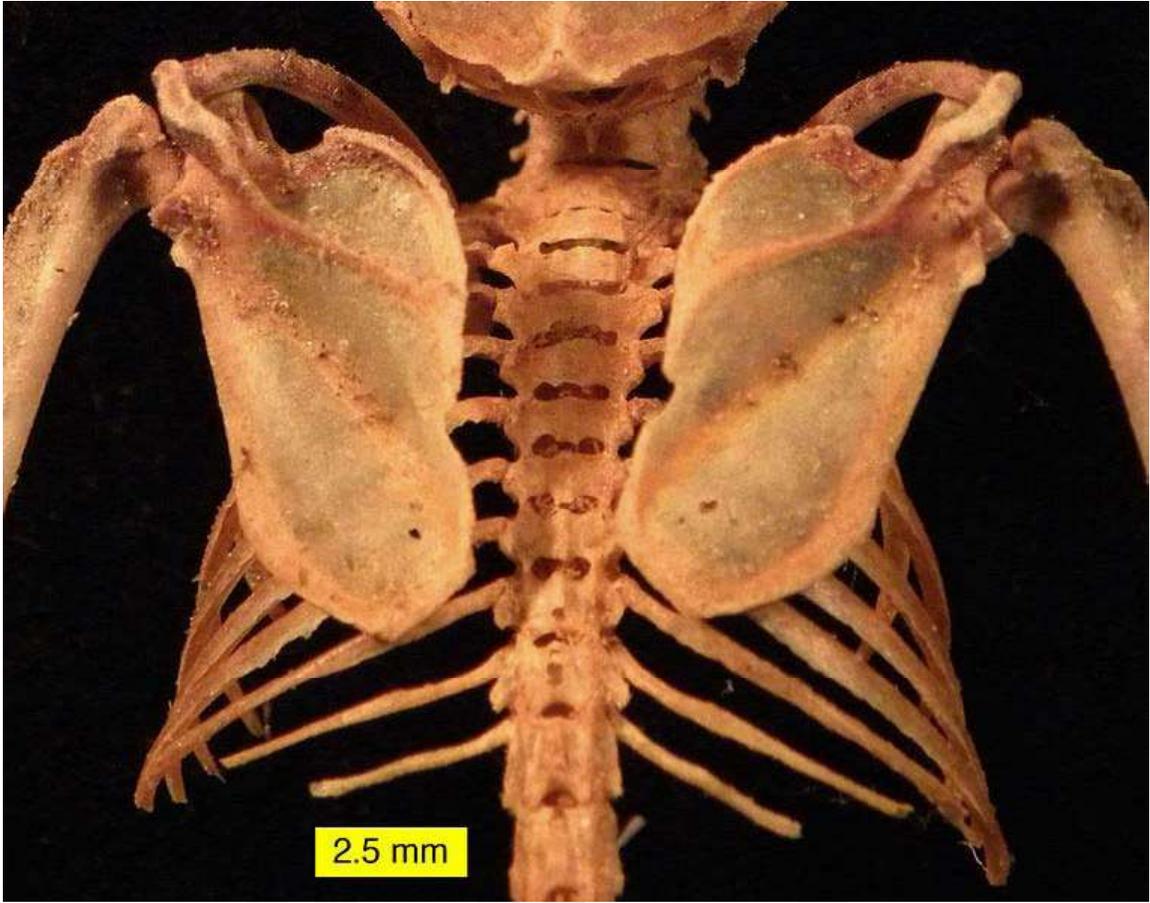
Flight has enabled bats to become one of the most widely distributed groups of mammals. Apart from the Arctic, the Antarctic and a few isolated oceanic islands, bats exist all over the world. Bats are found in almost every habitat available on Earth. Different species select different habitats during different seasons — ranging from seashores 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).



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.

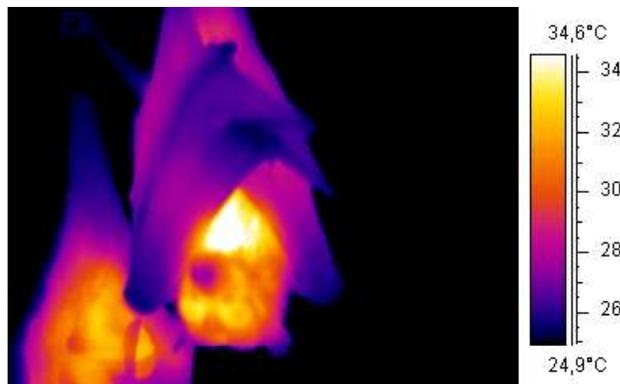
The new Yinpterochiroptera and Yangochiroptera classification of bats that are supported by molecular evidence, suggest two possibilities for the evolution of echolocation. It may have been gained once in a common ancestor of all bats and was then subsequently lost in the Old World fruit bats, only to 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**

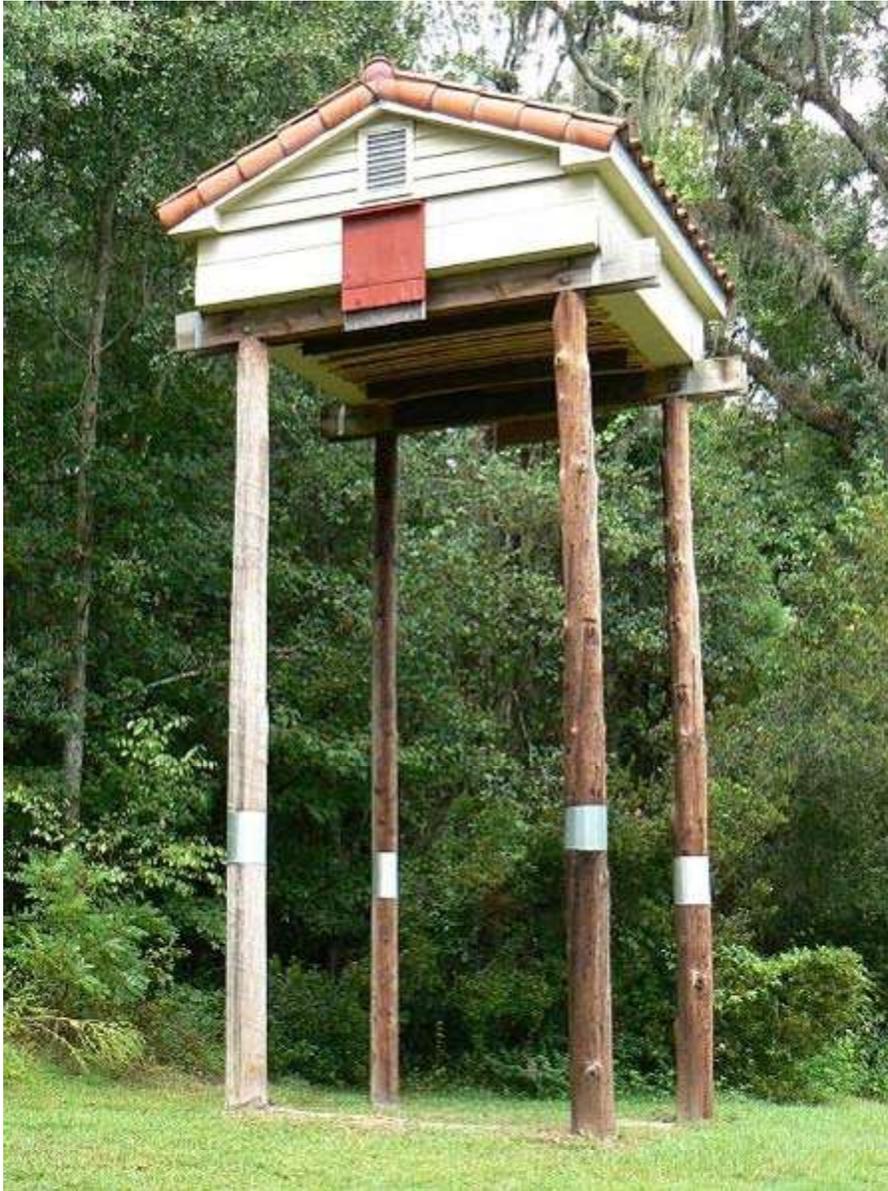
Through conservancy efforts, such as the Organization for Bat Conservation, bats are becoming better understood and people beginning to understand the crucial role bats play in insect control and pollination.

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 O'Neil, 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.

WWT

## Chapter 11

# Snake

### Snakes

Temporal range: 145–0 Ma  
Cretaceous – Recent



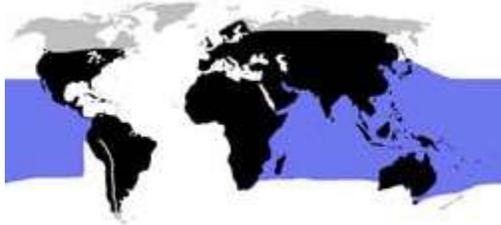
Coast garter snake,  
*Thamnophis elegans terrestris*

### Scientific classification [ e ]

|              |                                    |
|--------------|------------------------------------|
| Kingdom:     | Animalia                           |
| Phylum:      | Chordata                           |
| Class:       | Reptilia                           |
| Order:       | Squamata                           |
| Superfamily: | Varanoidea                         |
| (unranked):  | Pythonomorpha                      |
| Suborder:    | <b>Serpentes</b><br>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 *næddre* was the general word for snake. The other term, *serpent*, is from French, ultimately from Indo-European *\*serp-* (to creep), which also gave Greek *έρπο* (ερω) "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 led 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<br><b>Scolecophidia</b> 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   |

## 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.

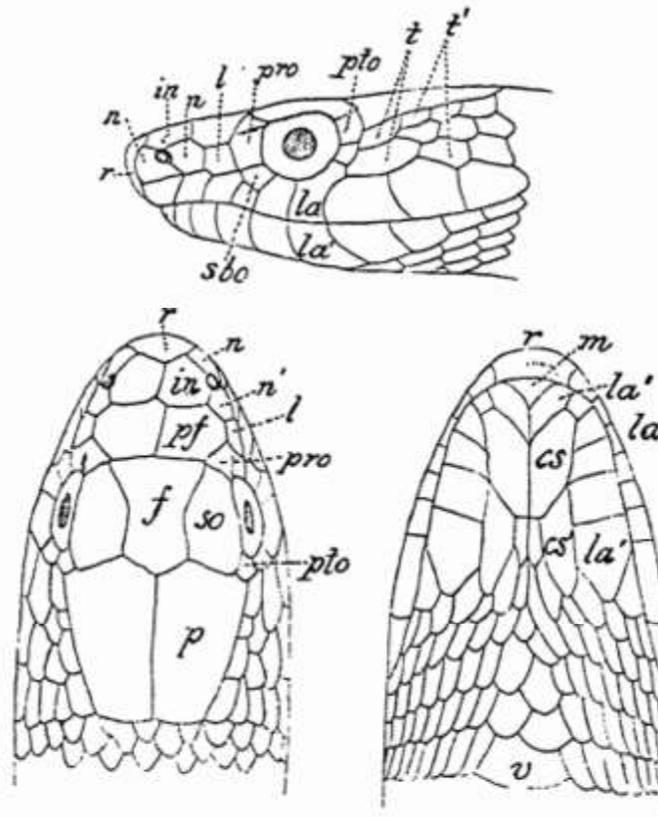


An adult Barbados threadsnake, *Leptotyphlops carlae*, on an American quarter dollar.

## 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.

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

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.

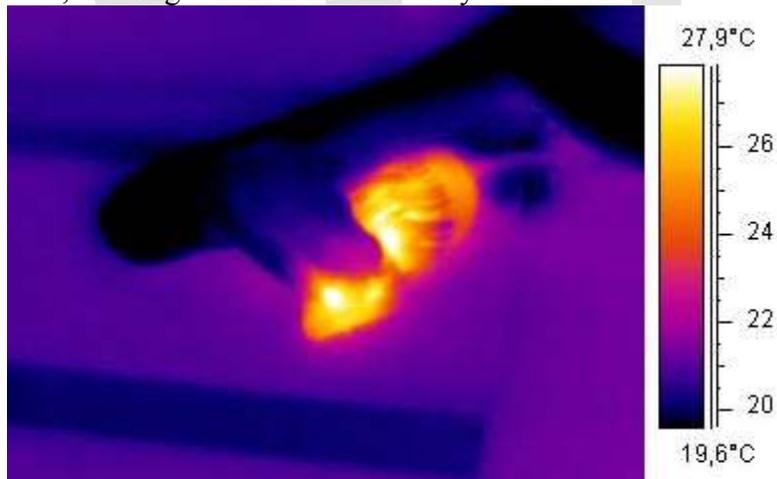
## Perception

### 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  $\frac{1}{3}$  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.

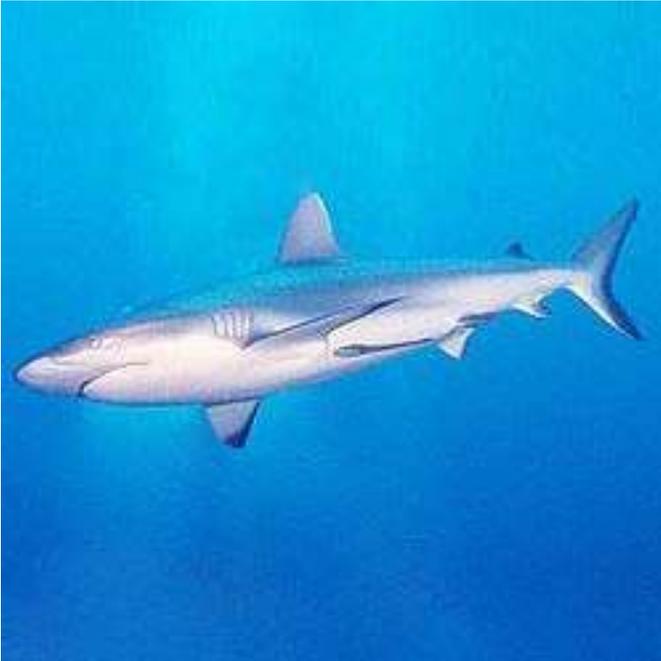
Some species of snake are ovoviviparous and retain the eggs within their bodies until they are almost ready to hatch. Recently, it has been confirmed that several species of snake are fully viviparous, such as the boa constrictor and green anaconda, nourishing their young through a placenta as well as 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 12

# Shark

### Sharks

Temporal range: Silurian–Recent



Grey reef shark (*Carcharhinus amblyrhynchos*)

### Scientific classification

|             |                      |
|-------------|----------------------|
| Kingdom:    | Animalia             |
| Phylum:     | Chordata             |
| Class:      | Chondrichthyes       |
| Subclass:   | Elasmobranchii       |
| Superorder: | <b>Selachimorpha</b> |

### Orders

Carcharhiniformes  
Heterodontiformes

Hexanchiformes  
Lamniformes  
Orectolobiformes  
Pristiophoriformes  
Squaliformes  
Squatiniiformes  
† 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.

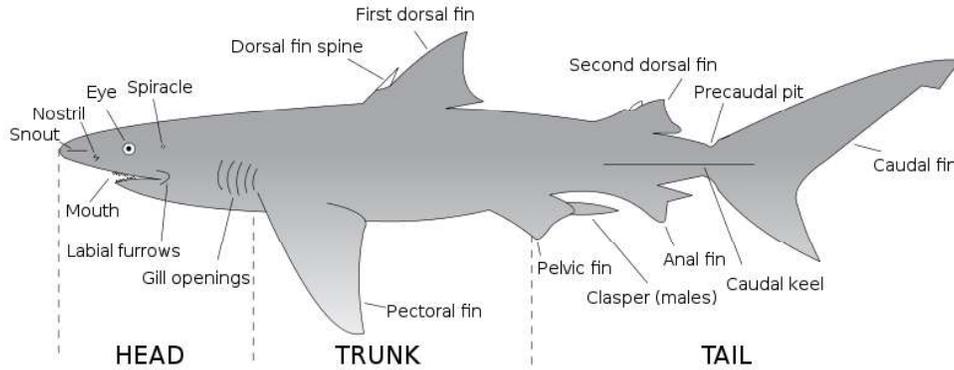
Since that time, sharks have diversified into 440 species, ranging in size from the small dwarf lanternshark, *Etmopterus perryi*, a deep sea species of only 17 centimetres (6.7 in) in length, to the whale shark, *Rhincodon typus*, the largest fish, which reaches approximately 12 metres (39 ft 4 in) 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**

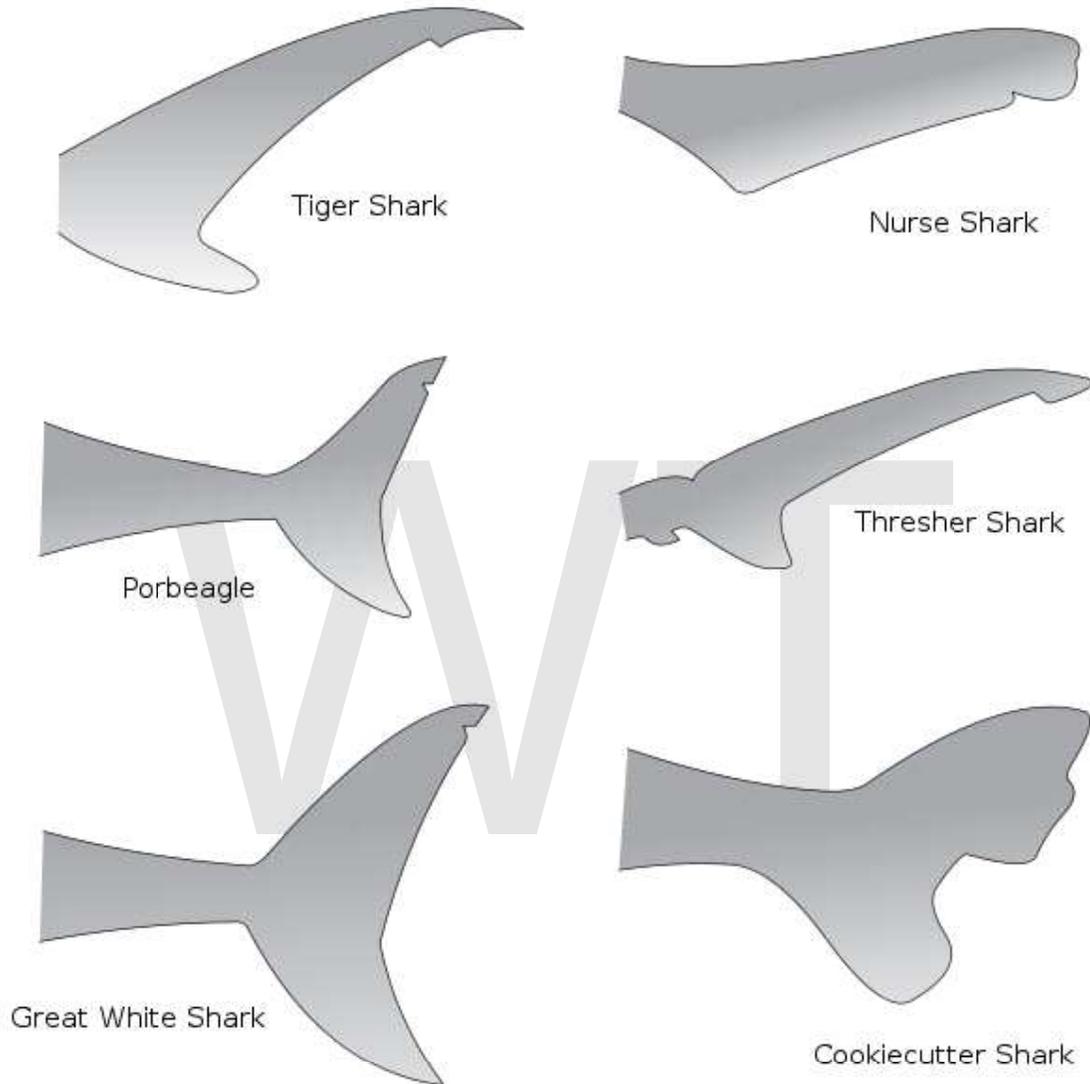
Fin skeletons are elongated and supported with soft and unsegmented rays named ceratotrichia, filaments of elastic protein resembling the horny keratin in hair and feathers. Sharks can only drift away from objects directly in front of them because their fins do not allow them to move in the tail-first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

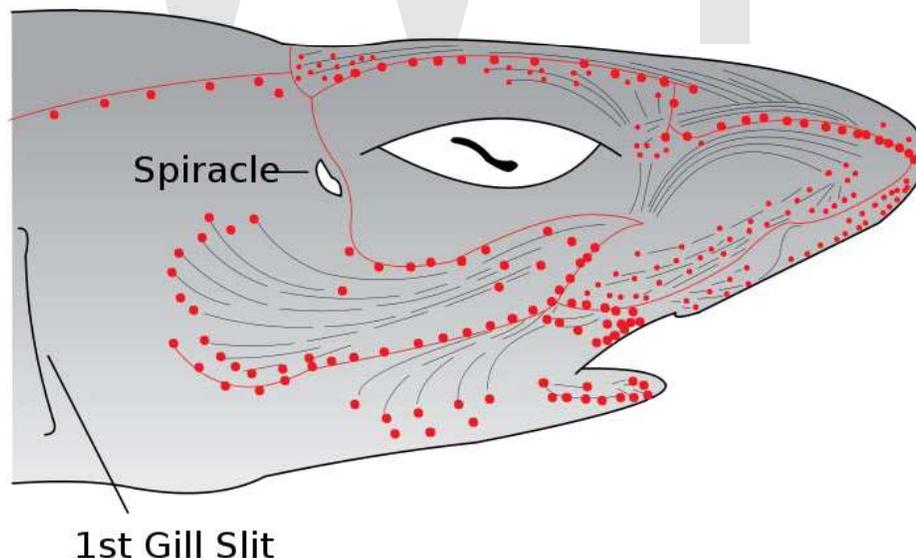
Shark eyes are similar to the eyes of other vertebrates, including similar lenses, corneas and retinas, though their eyesight is well adapted to the marine environment with the help of a tissue called tapetum lucidum. This means that sharks can contract and dilate their pupils, like humans, something 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**

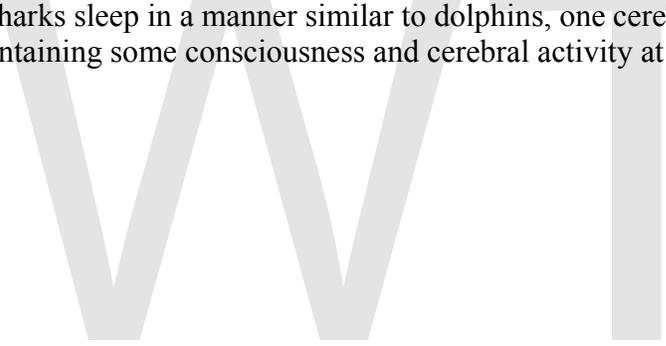
In general, sharks swim ("cruise") at an average speed of 8 kilometres per hour (5.0 mph) but when feeding or attacking, the average shark can reach speeds upwards of 19 kilometres per hour (12 mph). The shortfin mako shark, the fastest shark and one of the fastest fish, can burst at speeds up to 50 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***



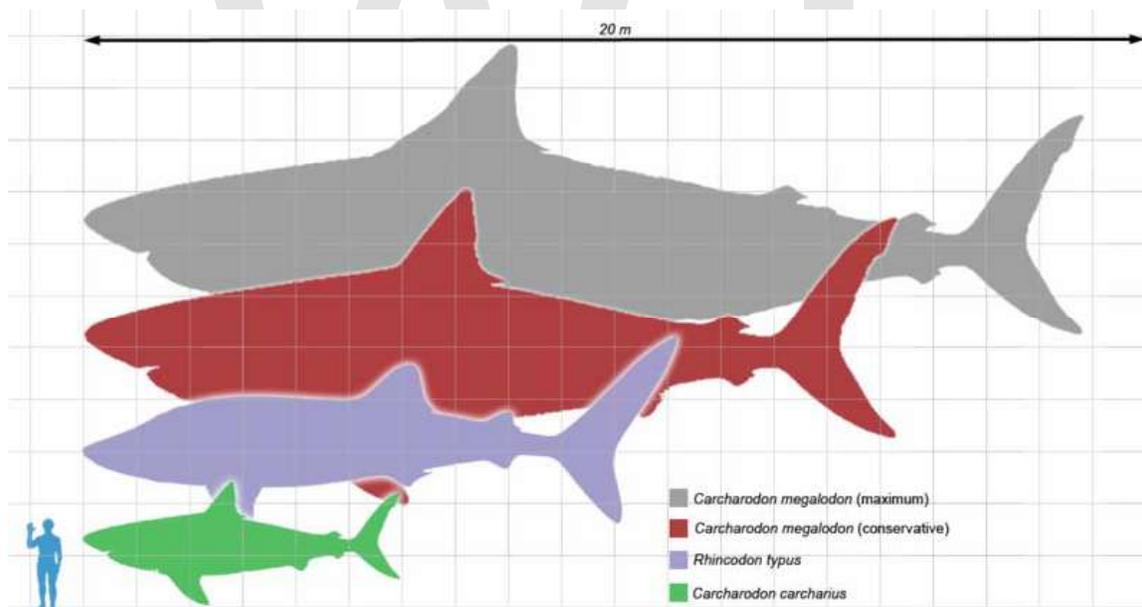
A collection of fossilized shark teeth

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.

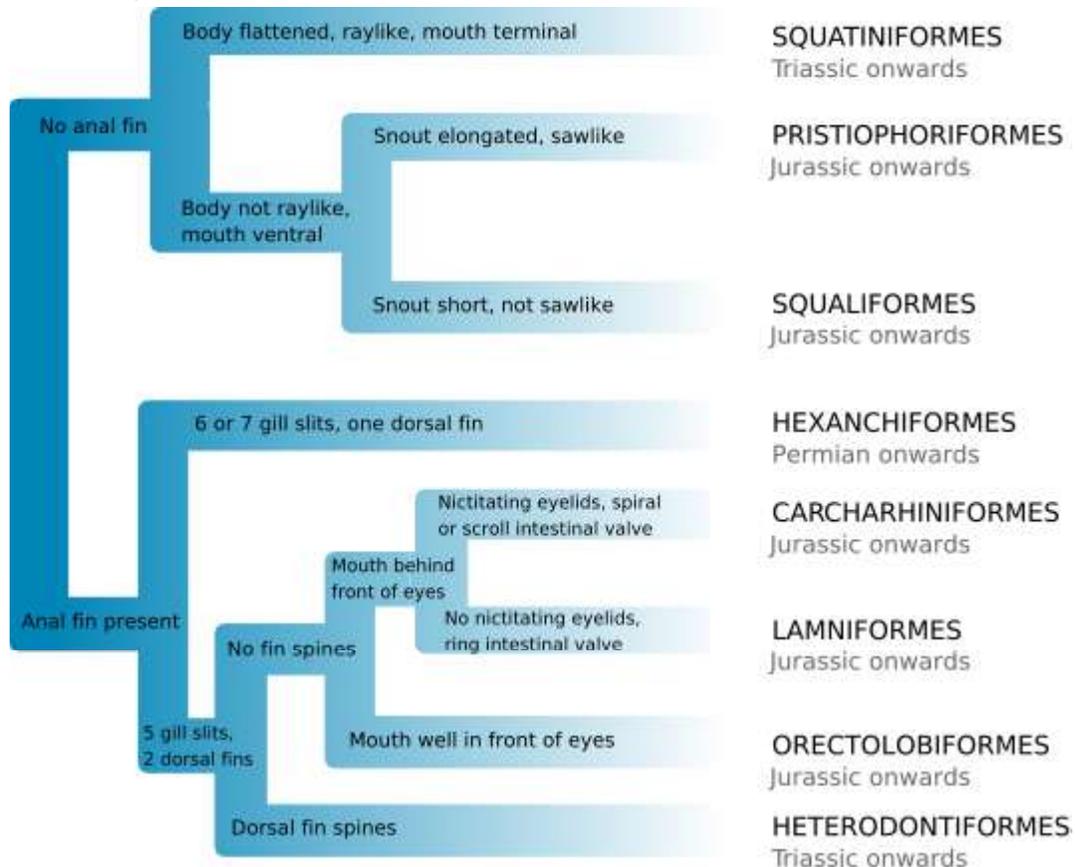


*Megalodon* with the whale shark, great white shark, and a human for scale

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



### Extant Shark Orders

Recognisable external characteristics

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 13

## Insect

### Insects

Temporal range: 396–0 Ma  
Early Devonian – Recent



Clockwise from top left:  
dancefly (*Empis livida*), long-  
nosed weevil (*Rhinotia  
hemistictus*), mole cricket  
(*Grylotalpa 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

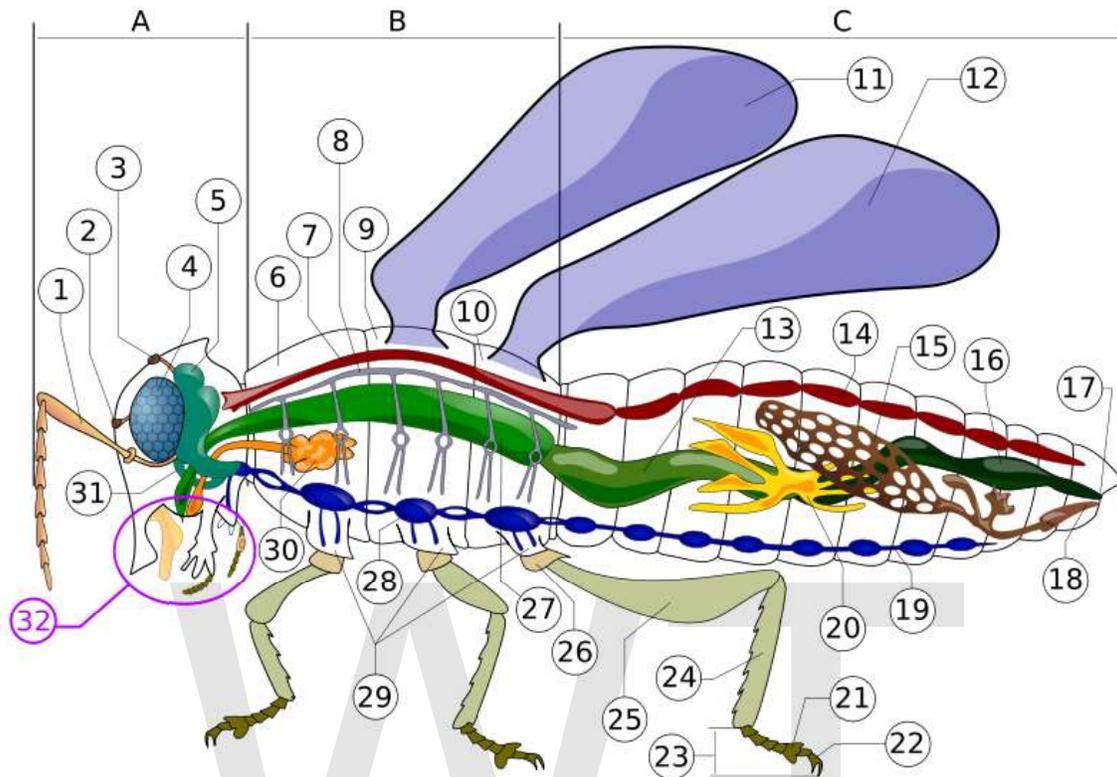
**Insects** (from Latin *insectum*, a calque of Greek ἔντομον [*éntomon*], "cut into sections") are a class within the arthropods that have a chitinous exoskeleton, a three-part body (head, thorax, and abdomen), three pairs of jointed legs, compound eyes, and two antennae. They are among the most diverse 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.

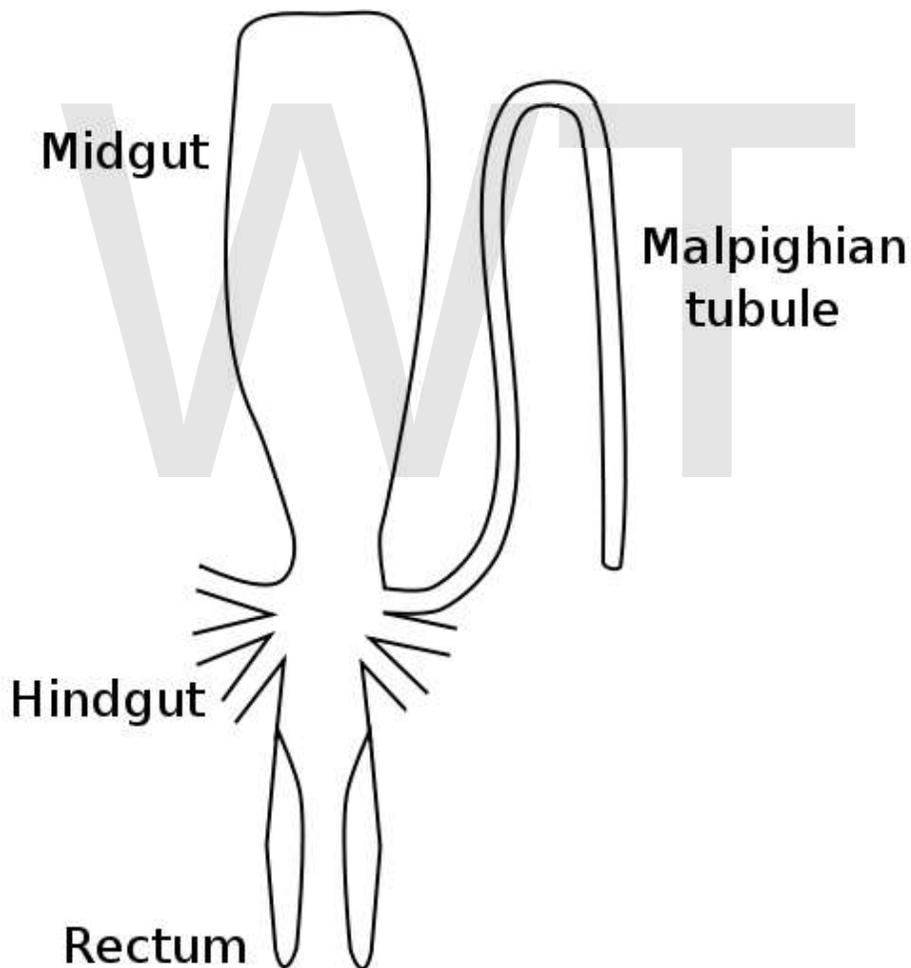
### **Digestive system**

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 lined 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 *Blattella germanica*, 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.

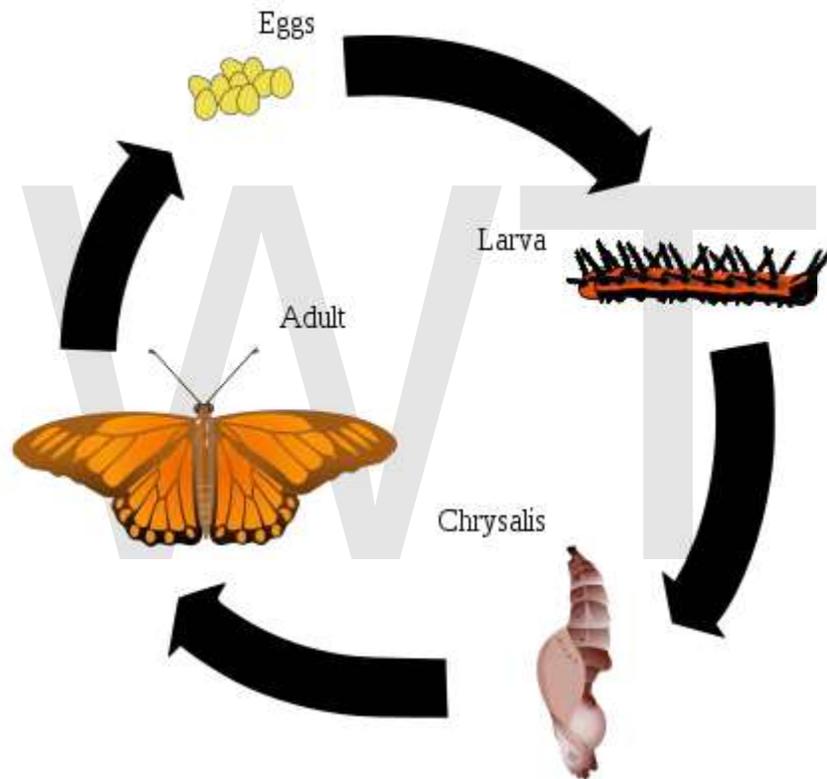
Immature insects that go through incomplete metamorphosis are called nymphs or in the case of dragonflies and damselflies as naiads. Nymphs are similar in form to the adult except for the presence of wings, which are not developed until adulthood. With each molt, nymphs grow larger and become more similar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



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 Hedyliid 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.

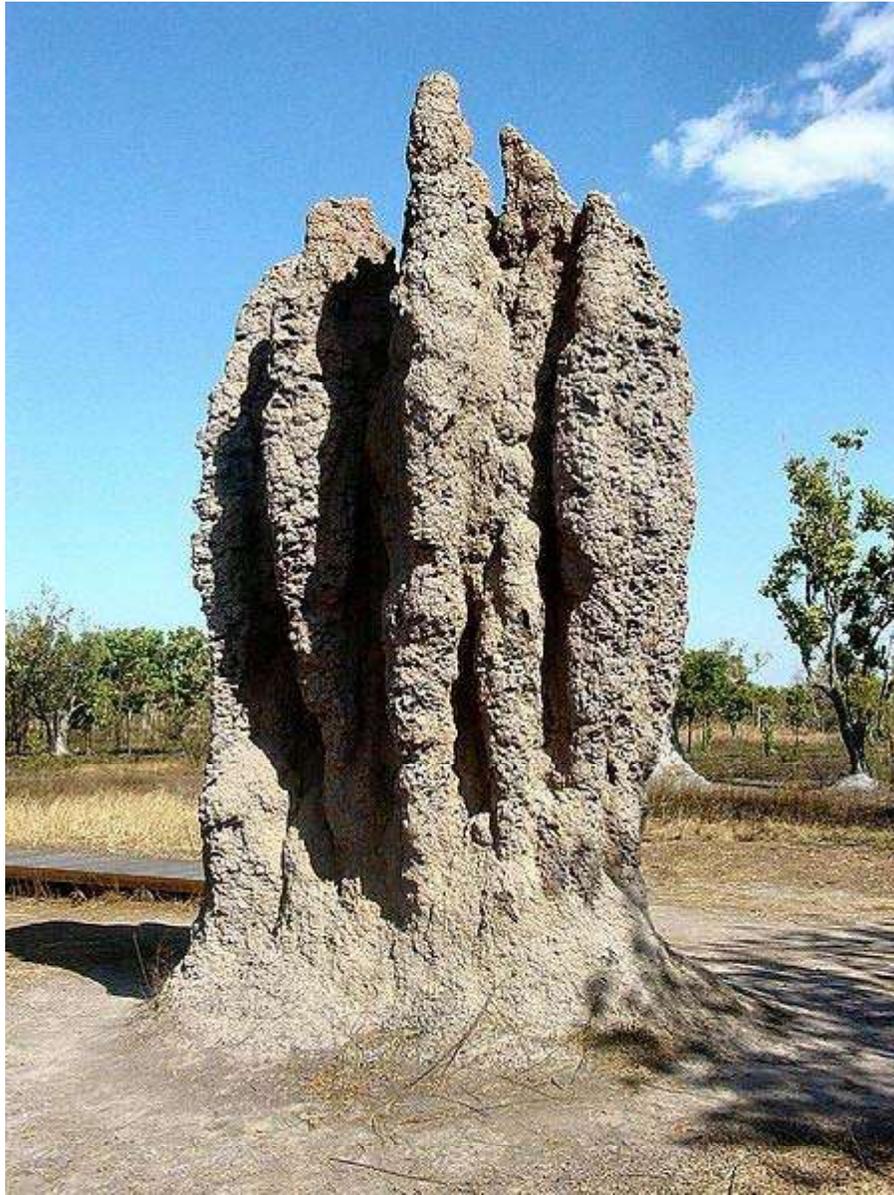
Some species use vibrations for communicating within members of the same species, such as to attract mates as in the songs of the shield bug *Nezara viridula*. Vibrations can

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.

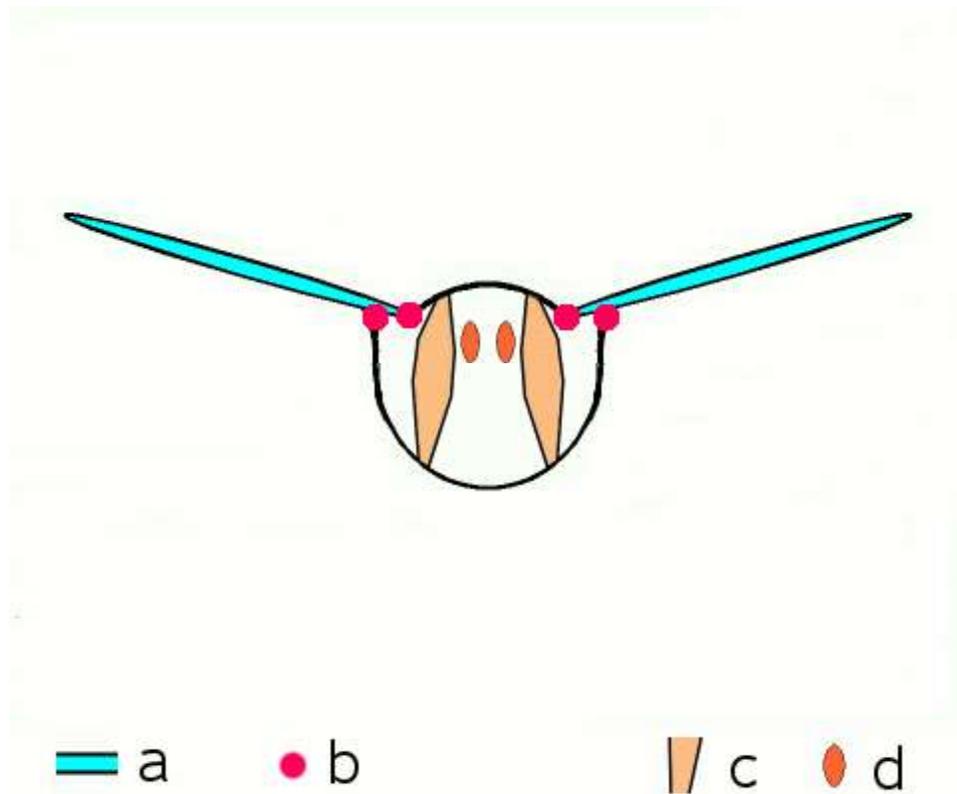
Only insects which live in nests or colonies demonstrate any true capacity for fine-scale spatial orientation or homing. This can allow an insect to return unerringly to a single hole a few millimeters in diameter among thousands of apparently identical holes clustered together, after a trip of up to 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**

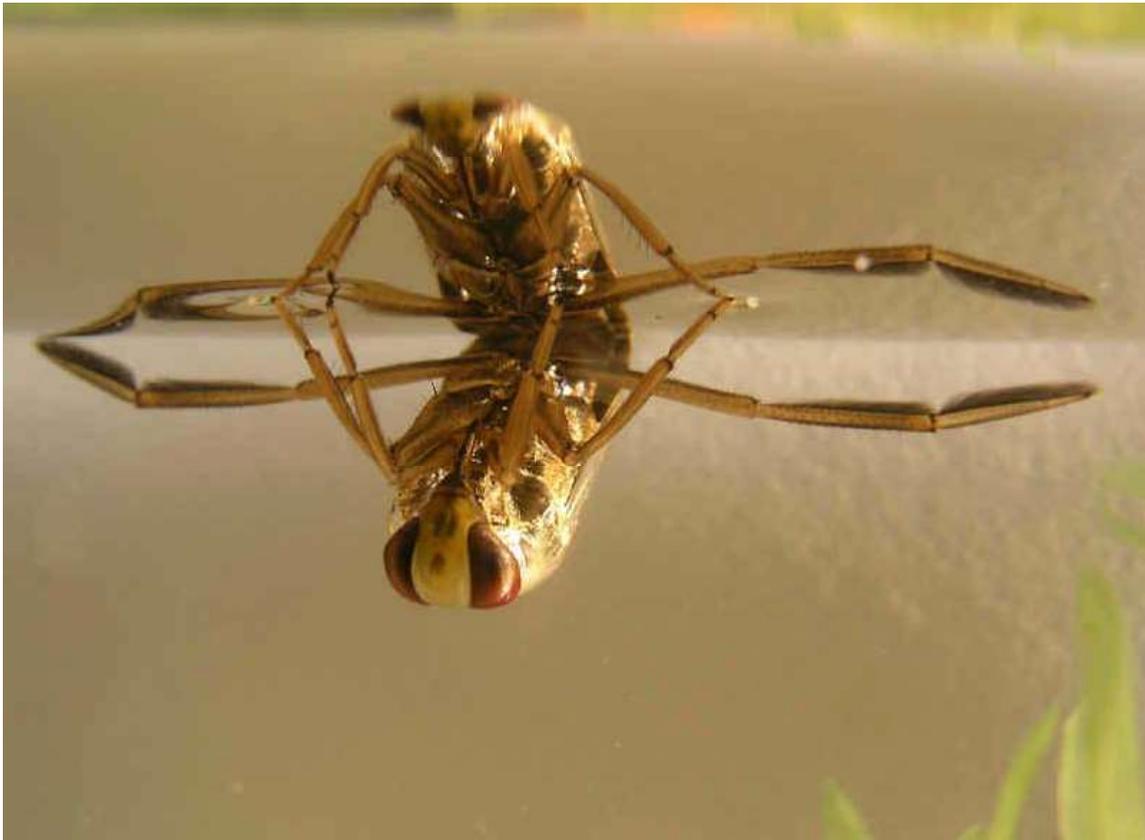
Many adult insects use six legs for walking and have adopted a tripedal gait. The tripedal gait allows for rapid walking while always having a stable stance and has been studied extensively in cockroaches. The legs are used in alternate triangles touching the ground. For the first step, the middle right 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 Hymenoptera 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.