Animal Physiology

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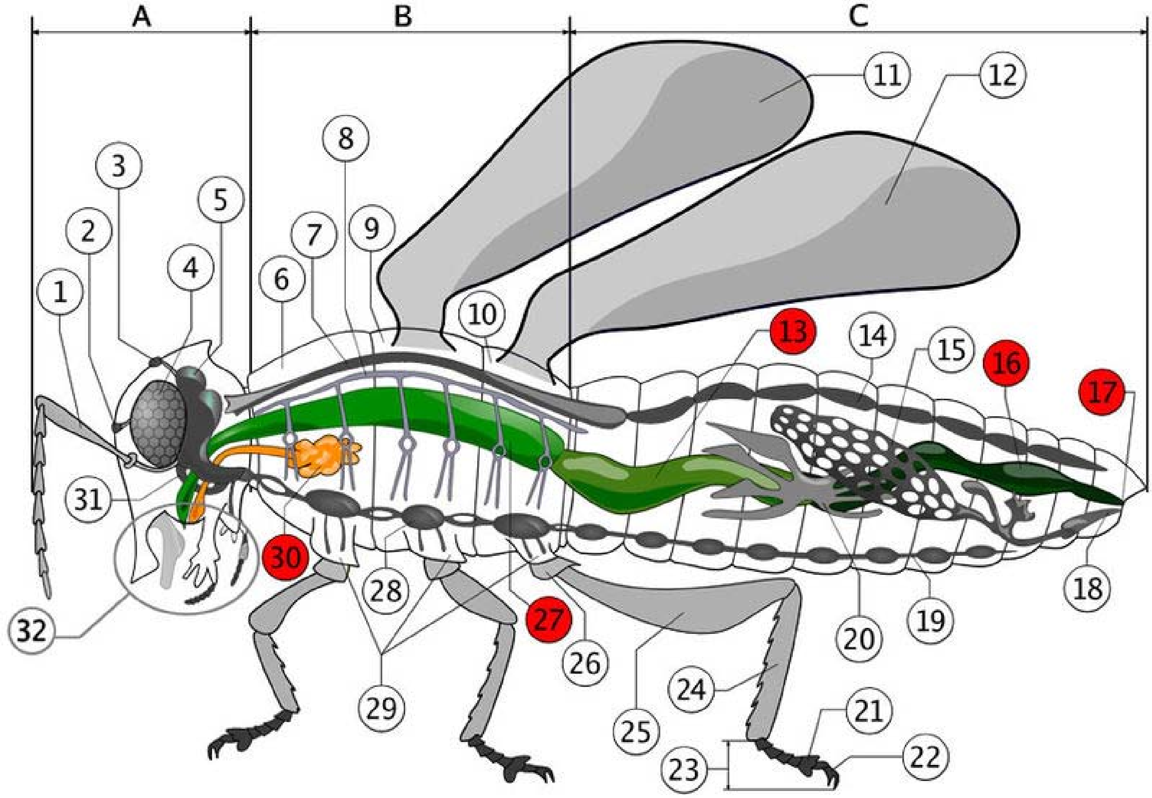
Chapter 1

Insect Physiology

Insect physiology includes the physiology and biochemistry of insect organ systems.

Although diverse, insects are quite similar in overall design, internally and externally. The insect is made up of three main body regions (tagmata), the head, thorax and abdomen. The head comprises six fused segments with compound eyes, ocelli, antennae and mouthparts, which differ according to the insect's particular diet, e.g. grinding, sucking, lapping and chewing. The thorax is made up of three segments the pro, meso and meta thorax, each supporting a pair of legs which may also differ, depending on function, e.g. jumping, digging, swimming and running. Usually the middle and the last segment of the thorax have paired wings. The abdomen generally comprises eleven segments and contains the digestive and reproductive organs (McGavin, 2001). A general overview of the internal structure and physiology of the insect is presented, including digestive, circulatory, respiratory, muscular, endocrine and nervous systems, as well as sensory organs, temperature control, flight and molting.

Digestive System



Insect digestive system

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

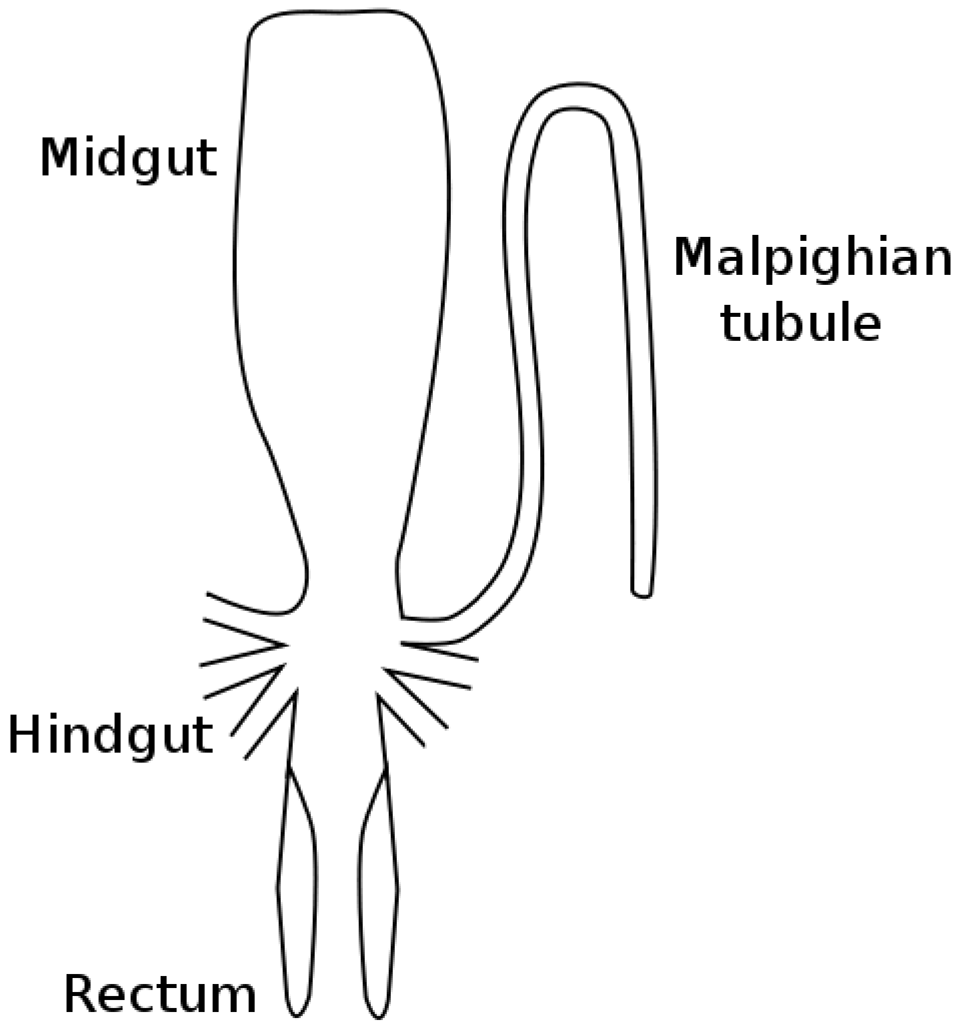
13. mid-gut (stomach)
15. ovary
16. hind-gut (intestine, rectum & anus)
17. anus
27. fore-gut (crop, gizzard)
30. salivary gland

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 (such as proteins, polysaccharides, fats, and nucleic acids) which must be broken down by catabolic reactions into smaller molecules (i.e. amino acids, simple sugars, etc.) before being used by cells of the body for energy, growth, or reproduction. This break-down process is known as digestion.

The insect's digestive system is a closed system, with one long enclosed coiled tube called the alimentary canal which runs lengthwise through the body. The alimentary canal only allows food to enter the mouth, and then gets processed as it travels toward the anus. The insects alimentary canal has specific sections for grinding and food storage, enzyme production and nutrient absorption (McGavin, 2001; Triplehorn & Johnson, 2005). Sphincters control the food and fluid movement between three regions. The three regions include the foregut (stomatodeum)(27,) the midgut (mesenteron)(13), and the hindgut (proctodeum)(16).

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 fore-gut). The salivary glands (30) produce saliva, the salivary ducts lead from the glands to the reservoirs and then forward through the head to an opening called the salivarium behind the hypopharynx; which movements of the mouthparts help mix saliva with food in the buccal cavity. Saliva mixes with food which travels through salivary tubes into the mouth, beginning the process of breaking it down.

The stomatedeum and proctodeum are invaginations of the epidermis and are lined with cuticle (intima). The mesenteron is not lined with cuticle but with rapidly dividing and therefore constantly replaced, epithelial cells (McGavin, 2001; Triplehorn & Johnson, 2005). The cuticle sheds with every moult along with the exoskeleton (Triplehorn & Johnson, 2005). Food is moved down the gut by muscular contractions called peristalsis (Elzinga, 2004).



Stylised diagram of insect digestive tract showing malpighian tubule (Orthopteran type)

1. **Stomatodeum**(foregut): This region stores, grinds and transports food to the next region (Gullan & Cranston, 2005). Included in this are the buccal cavity, the pharynx, the oesophagus, the crop (stores food), and proventriculus or gizzard (grinds food) (Triplehorn & Johnson, 2005). Salivary secretions from the labial glands dilute the ingested food. In mosquitoes (Diptera), which are blood-feeding insects, anticoagulants and blood thinners are also released here.

2. **Mesenteron**(midgut): Digestive enzymes in this region are produced and secreted into the lumen and here nutrients are absorbed into the insect's body. Food is enveloped by this part of the gut as it arrives from the foregut by the peritrophic membrane which is a mucopolysaccharide layer secreted from the midgut's epithelial cells (McGavin, 2001). It

is thought that this membrane prevents food pathogens from contacting the epithelium and attacking the insects' body (McGavin, 2001). It also acts as a filter allowing small molecules through, but preventing large molecules and particles of food from reaching the midgut cells (Gullan & Cranston, 2005). After the large substances are broken down into smaller ones, digestion and consequent nutrient absorption takes place at the surface the epithelium (McGavin, 2001). Microscopic projections from the mid-gut wall, called microvilli, increase surface area and allow for maximum absorption of nutrients.

3. **Proctodeum**(hindgut): This is divided into three sections; the anterior is the ileum, the middle portion, the colon, and the wider, posterior section is the rectum (Gullan & Cranston, 2005). This extends from the pyloric valve which is located between the mid and the hindgut to the anus (Triplehorn & Johnson, 2005). Here absorption of water, salts and other beneficial substances take place before excretion (Gullan & Cranston, 2005). Like other animals, the removal of toxic metabolic waste requires water. However, for very small animals like insects, water conservation is a priority. Because of this, blind-ended ducts called Malpighian tubules come into play (McGavin, 2001). These ducts emerge as evaginations at the anterior end of the hindgut and are the main organs of osmoregulation and excretion (Triplehorn & Johnson, 2005; Gullan & Cranston, 2005). These extract the waste products from the haemolymph, in which all the internal organs are bathed (McGavin, 2001). These tubules continually produce the insect's uric acid, which is transported to the hindgut, where important salts and water are re-absorbed by both the hindgut and rectum. Excrement is then voided as insoluble and non-toxic uric acid granules (McGavin, 2001). Excretion and osmoregulation in insects are not orchestrated by the Malpighian tubules alone, but require a joint function of the ileum and/or rectum (Gullan & Cranston, 2005).

Circulatory System

Insect blood or haemolymph's main function is that of transport and it bathes the insect's body organs. Making up usually less than 25% of an insect's body weight, it transports hormones, nutrients and wastes and has a role in, osmoregulation, temperature control, immunity, storage (water, carbohydrates and fats) and skeletal function. It also plays an essential part in the moulting process (McGavin, 2001; Triplehorn & Johnson, 2005). An additional role of the haemolymph in some orders, can be that of predatory defence. It can contain unpalatable and malodourous chemicals that will act as a deterrent to predators (Gullan & Cranston, 2005).

Haemolymph contains molecules, ions and cells (Gullan & Cranston, 2005). Regulating chemical exchanges between tissues, haemolymph is encased in the insect body cavity or haemocoel (Elzinga, 2004; Gullan & Cranston, 2005). It is transported around the body by combined heart (posterior) and aorta (anterior) pulsations which are located dorsally just under the surface of the body (McGavin, 2001; Gullan & Cranston, 2005; Triplehorn & Johnson, 2005). It differs from vertebrate blood in that it doesn't contain any red blood cells and therefore is without high oxygen carrying capacity, and is more similar to lymph found in vertebrates (Elzinga, 2004; Gullan & Cranston, 2005).

Body fluids enter through one way valved ostia which are openings situated along the length of the combined aorta and heart organ. Pumping of the haemolymph occurs by waves of peristaltic contraction, originating at the body's posterior end, pumping forwards into the dorsal vessel, out via the aorta and then into the head where it flows out into the haemocoel (Elzinga, 2004; Gullan & Cranston, 2005). The haemolymph is circulated to the appendages unidirectionally with the aid of muscular pumps or accessory pulsatile organs which are usually found at the base of the antennae or wings and sometimes in the legs (Gullan & Cranston, 2005). Pumping rate accelerates due to periods of increased activity (Triplehorn & Johnson, 2005). Movement of haemolymph is particularly important for thermoregulation in orders such as Odonata, Lepidoptera, Hymenoptera and Diptera (Gullan & Cranston, 2005).

Respiratory system

Insect respiration is accomplished without lungs using a system of internal tubes and sacs through which gases either diffuse or are actively pumped, delivering oxygen directly to tissues that need oxygen and eliminate carbon dioxide via their cells (Gullan & Cranston, 2005). Since oxygen is delivered directly, the circulatory system is not used to carry oxygen, and is therefore greatly reduced; it has no closed vessels (i.e., no veins or arteries), consisting of little more than a single, perforated dorsal tube which pulses peristaltically, and in doing so helps circulate the hemolymph inside the body cavity.

Air is taken in through spiracles, openings which are positioned laterally in the pleural wall, usually a pair on the anterior margin of the meso and meta thorax, and pairs on each of the eight or less abdominal segments, Numbers of spiracles vary from 1 to 10 pairs (McGavin 2001; Elzinga, 2004; Gullan & Cranston, 2005; Triplehorn & Johnson, 2005). The oxygen passes through the tracheae to the trachioles, and enters the body by the process of diffusion. Carbon dioxide leaves the body by the same process (Triplehorn & Johnson, 2005).

The major tracheae are thickened spirally like a flexible vacuum hose to prevent them from collapsing and often swell into air sacs. Larger insects can augment the flow of air through their tracheal system, with body movement and rhythmic flattening of the tracheal air sacs (Triplehorn & Johnson, 2005). Spiracles are closed and opened by means of valves and can remain partly or completely closed for extended periods in some insects, which minimises water loss (McGavin, 2001; Triplehorn & Johnson, 2005,).

There are many different patterns of gas exchange demonstrated by different groups of insects. Gas exchange patterns in insects can range from continuous, diffusive ventilation, to discontinuous gas exchange.

Terrestrial and a large proportion of aquatic insects perform gaseous exchange as previously mentioned under an open system. Other smaller numbers of aquatic insects have a closed tracheal system, for example, Odonata, Tricoptera, Ephemeroptera, which have tracheal gills and no functional spiracles. Endoparasitic larvae are without spiracles and also operate under a closed system. Here the tracheae separate peripherally, covering the general body surface which results in a cutaneous form of gaseous exchange. This peripheral tracheal division may also lie within the tracheal gills where gaseous exchange may also take place (Gullan & Cranston, 2005).

Muscular system

Many insects are able to lift twenty times their own body weight and may jump distances that are many times greater than their own length. This is not because they are strong but because they are so small. Muscle power is proportional to its cross-sectional area. Because the mass(the insect's body), that is moved is in proportion to its volume and the fact that they also have a better leverage system than we humans do, they can jump remarkable distances. (Elzinga, 2004; Triplehorn & Johnson, 2005).

The muscular system of insects ranges from a few hundred muscles to a few thousand (Triplehorn & Johnson, 2005). Unlike vertebrates that have both smooth and striated muscles, insects have only striated muscles. Muscle cells are amassed into muscle fibres and then into the functional unit, the muscle (Elzinga, 2004). Muscles are attached to the body wall, with attachment fibres running through the cuticle and to the epicuticle, where they can move different parts of the body including appendages such as wings (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005). The muscle fibre has many cells with a plasma membrane and outer sheath or sarcolemma (Gullan & Cranston, 2005). The sarcolemma is invaginated and can make contact with the tracheole carrying oxygen to the muscle fibre. Arranged in sheets or cylindrically, contractile myofibrils run the length of the muscle fibre. Myofibrils comprising a fine actin filament enclosed between a thick pair of myosin filaments slide past each other instigated by nerve impulses (Gullan & Cranston, 2005).

Muscles can be divided into four categories:

1. **Visceral**: these muscles surround the tubes and ducts and produce peristalsis as demonstrated in the digestive system (Elzinga, 2004).
2. **Segmental**: causing telescoping of muscle segments required for moulting, increase in body pressure and locomotion in legless larvae (Elzinga, 2004).
3. **Appendicular**: originating from either the sternum or the tergum and inserted on the coxae these muscles move appendages as one unit. (Elzinga, 2004) These are arranged segmentally and usually in antagonistic pairs (Triplehorn & Johnson, 2005). Appendage parts of some insects, e.g. the galea and the lacinia of the maxillae, only have flexor muscles. Extension of these structures is by haemolymph pressure and cuticle elasticity (Triplehorn & Johnson, 2005).
4. **Flight**: Flight muscles are the most specialised category of muscle and are capable of rapid contractions. Nerve impulses are required to initiate muscle contractions and therefore flight. These muscles are also known as neurogenic or synchronous muscles. This is because there is a one to one correspondence between action potentials and muscle contractions. In insects with higher wing stroke frequencies the muscles contract more frequently than at the rate that the

nerve impulse reaches them and are known as asynchronous muscles (McGavin, 2001; Gullan & Cranston, 2005).

Flight has allowed the insect to disperse, escape from enemies, environmental harm, and colonise new habitats (McGavin, 2001). One of the insect's key adaptations, the mechanics of flight differ from other flying animals because their wings are not modified appendages (McGavin, 2001; Elzinga, 2004). Fully developed and functional wings occur only in adult insects (Gullan & Cranston, 2005). To fly, gravity and drag (air resistance to movement) has to be overcome (Gullan & Cranston, 2005). Most insects fly by beating their wings and to power their flight they have either direct flight muscles attached to the wings, or an indirect system where there is no muscle to wing connection and instead they are attached to a highly flexible box like thorax (Gullan & Cranston, 2005).

Direct flight muscles generate the upward stroke by the contraction of the muscles attached to the base of the wing inside the pivotal point. Outside the pivotal point the downward stroke is generated through contraction of muscles that extend from the sternum to the wing. Indirect flight muscles are attached to the tergum and sternum. Contraction makes the tergum and base of the wing pull down. In turn this movement lever the outer or main part of the wing in strokes upward. Contraction of the second set of muscles, which run from the back to the front of the thorax, powers the downbeat. This deforms the box and lifts the tergum (Gullan & Cranston, 2005).

Endocrine system

Hormones are the chemical substances that are transported in the insect's body fluids (haemolymph) that carry messages away from their point of synthesis to sites that where physiological processes are influenced. These hormones are produced by glandular, neuroglandular and neuronal centres (Gullan & Cranston, 2005). Insects have several organs that produce hormones, controlling reproduction, metamorphosis and moulting (Triplehorn & Johnson, 2005). It has been suggested that a brain hormone is responsible for caste dermination in termites and diapause interruption in some insects (Triplehorn & Johnson, 2005).

Four endocrine centers have been identified:

1. **Neurosecretory cells** in the brain can produce one or more hormones that affect growth, reproduction, homeostasis and metamorphosis (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005).
2. **Corpora cardiaca** are a pair of neuroglandular bodies that are found behind the brain and on either sides of the aorta. These not only produce their own neurohormones but they store and release other neurohormones including PTTH prothoracicotropic hormone (brain hormone), which stimulates the secretory activity of the prothoracic glands, playing an integral role in moulting.
3. **Prothoracic glands** are diffuse, paired glands located at the back of the head or in the thorax. These glands secrete an ecdysteroid called ecdysone, or the moulting

hormone, which initiates the epidermal moulting process (Gullan & Cranston, 2005). Additionally it plays a role in accessory reproductive glands in the female, differentiation of ovarioles and in the process of egg production.

4. **Corpora allata** are small, paired glandular bodies originating from the epithelium located on either side of the foregut. They secrete the juvenile hormone, which regulate reproduction and metamorphosis (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005).

The Nervous System

Insects have a complex nervous system which incorporates a variety of internal physiological information as well as external sensory information (Gullan & Cranston, 2005) Like invertebrates the basic component is the neuron or nerve cell. This is made up of a dendrite with two projections that receive stimuli and an axon, which transmits information to another neuron or organ, like a muscle. As for vertebrates, chemicals (neurotransmitters such as acetylcholine and dopamine) are released at synapses (Gullan & Cranston, 2005).

Central nervous system: An insect's sensory, motor and physiological processes are controlled by the central nervous system along with the endocrine system (Gullan & Cranston, 2005). Being the principal division of the nervous system, it consists of a brain, a ventral nerve cord and a subesophageal ganglion. This is connected to the brain by two nerves, extending around each side of the oesophagus.

The brain has three lobes:

- **Procerebrum,** innervating the compound eyes and the ocelli
- **Deutocerebrum,** innervating the antennae
- **Tritocerebrum,** innervating the foregut and the labrum (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005).

The ventral nerve cord extends from the suboesophageal ganglion posteriorly (Triplehorn & Johnson, 2005). A layer of connective tissue called the neurolemma covers the brain, ganglia, major peripheral nerves and ventral nerve cords.

The head capsule (made up of six fused segments) has six pairs of ganglia. The first three pairs are fused into the brain, while the three following pairs are fused into 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. And some, like the house fly *Musca domestica*, have all the body ganglia fused into a single large thoracic ganglion. The ganglia of the central nervous system act as the coordinating centres with their own specific autonomy where each may coordinate impulses in specified regions of the insect's body (Triplehorn & Johnson, 2005).

Peripheral nervous system: This consists of motor neuron axons that branch out to the muscles from the ganglia of the central nervous system, parts of the sympathetic nervous system and the sensory neurons of the cuticular sense organs that receive chemical, thermal, mechanical or visual stimuli from the insects environment (Gullan & Cranston, 2005). The sympathetic nervous system includes nerves and the ganglia that innervate the gut both posteriorly and anteriorly, some endocrine organs, the spiracles of the tracheal system and the reproductive organs (Gullan & Cranston, 2005).

Sense Organs: Chemical senses include the use of chemoreceptors, related to taste and smell, affecting mating, habitat selection, feeding and parasite-host relationships. Taste is usually located on the mouthparts of the insect but in some insects, such as bees, wasps and ants, taste organs can also be found on the antennae. Taste organs can also be found on the tarsi of moths, butterflies and flies. Olfactory sensilla enable insects to smell and are usually found in the antennae (McGavin, 2001). Chemoreceptor sensitivity related to smell in some substances, is very high and some insects can detect particular odours that are at low concentrations miles from their original source (Triplehorn & Johnson, 2005).

Mechanical senses provide the insect with information that may direct orientation, general movement, flight from enemies, reproduction and feeding and are elicited from the sense organs that are sensitive to mechanical stimuli such as pressure, touch and vibration (Triplehorn & Johnson, 2005). Hairs (setae) on the cuticle are responsible for this as they are sensitive to vibration touch and sound (McGavin, 2001).

Hearing structures or tympanal organs are located on different body parts such as, wings, abdomen, legs and antennae. These can respond to various frequencies ranging from 100 to 240 kHz depending on insect species (Triplehorn & Johnson, 2005). Many of the joints of the insect have tactile setae that register movement. Hair beds and groups of small hair like sensilla, determine proprioreception or information about the position of a limb, and are found on the cuticle at the joints of segments and legs. Pressure on the body wall or strain gauges are detected by the campiniform sensilla and internal stretch receptors sense muscle distension and digestive system stretching (McGavin 2001; Triplehorn & Johnson, 2005,).

The compound eye and the ocelli supply insect vision. The compound eye consists of individual light receptive units called ommatidia. Some ants may have only one or two, however dragonflies may have over 10,000. The more ommatidia the greater the visual acuity. These units have a clear lens system and light sensitive retina cells. By day, the image flying insects receive is made up of a mosaic of specks of differing light intensity from all the different ommatidia. At night or dusk, visual acuity is sacrificed for light sensitivity (McGavin, 2001). The ocelli are unable to form focussed images but are sensitive mainly, to differences in light intensity (Triplehorn & Johnson, 2005). Colour vision occurs in all orders of insects. Generally insects see better at the blue end of the spectrum than at the red end. In some orders sensitivity ranges can include ultraviolet (McGavin, 2001).

A number of insects have temperature and humidity sensors (McGavin, 2001) and insects being small, cool more quickly than larger animals. Insects are generally considered cold-blooded or ectothermic, their body temperature rising and falling with the environment. However, flying insects raise their body temperature through the action of flight, above environmental temperatures (Elzinga, 2004; Triplehorn & Johnson, 2005,).

The body temperature of butterflies and grasshoppers in flight may be 5^{o}C or 10^{o}C above environmental temperature, however moths and bumblebees, insulated by scales and hair, during flight, may raise flight muscle temperature 20–30^{o}C above the environment temperature. Most flying insects have to maintain their flight muscles above a certain temperature to gain power enough to fly. Shivering, or vibrating the wing muscles allow larger insects to actively increase the temperature of their flight muscles, enabling flight (Triplehorn & Johnson, 2005).

Until very recently, no one had ever documented the presence of nociceptors (the cells that detect and transmit sensations of pain) in insects, though recent findings of nociception in larval fruit flies challenges this and raises the possibility that some insects may be capable of feeling pain.

Reproductive System

Most insects have a high reproductive rate. With a short generation time, they evolve faster and can adjust to environmental changes more rapidly than other slower breeding animals (McGavin, 2001). Although there are many forms of reproductive organs in insects, there remains a basic design and function for each reproductive part. These individual parts may vary in shape (gonads), position (accessory gland attachment), and number (testicular and ovarian glands), with different insect groups (Gullan & Cranston, 2005).

Female Reproductive System

The female insect's main reproductive function is to produce eggs, including the egg's protective coating, and to store the male spermatozoa until egg fertilisation is ready. The female reproductive organs include, paired ovaries which empty their eggs (oocytes) via the calyces into lateral oviducts, joining to form the common oviduct. The opening (gonopore) of the common oviduct is concealed in a cavity called the genital chamber and this serves as a copulatory pouch (bursa copulatrix) when mating (Gullan & Cranston, 2005). The external opening to this is the vulva. Often in insects the vulva is narrow and the genital chamber becomes pouch or tube like and is called the vagina. Related to the vagina is a saclike structure, the spermatheca, where spermatozoa are stored ready for egg fertilisation. A secretory gland (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005) nourishes the contained spermatozoa in the vagina.

Egg development is mostly completed by the insect's adult stage and is controlled by hormones that control the initial stages of oogenesis and yolk deposition (Gullan &

Cranston, 2005). Most insects are oviviparous, where the young hatch after the eggs have been laid (Triplehorn & Johnson, 2005).

Insect sexual reproduction starts with sperm entry that stimulates oogenesis, meiosis occurs and the egg moves down the genital tract. Accessory glands of the female secrete an adhesive substance to attach eggs to an object and they also supply material that provides the eggs with a protective coating. Oviposition takes place via the female ovipositor (Elzinga, 2004; Triplehorn & Johnson, 2005).

Male reproductive system

The male's main reproductive function is to produce and store spermatozoa and provide transport to the reproductive tract of the female (Gullan & Cranston, 2005). Sperm development is usually completed by the time the insect reaches adulthood (Triplehorn & Johnson, 2005). The male has two testes, which contain follicles in which the spermatozoa are produced. These open separately into the sperm duct or vas deferens and this stores the sperm (Gullan & Cranston, 2005). The vas deferentia then unite posteriorally to form a central ejaculatory duct, this opens to the outside on an aedeagus or a penis (Triplehorn & Johnson, 2005). Accessory glands secrete fluids that comprise the spermatophore. This becomes a package that surrounds and carries the spermatozoa, forming a sperm-containing capsule (Gullan & Cranston, 2005; Triplehorn & Johnson, 2005,).

Sexual and asexual reproduction Most insects reproduce via sexual reproduction, i.e. the egg is produced by the female, fertilised by the male and oviposited by the female. Eggs are usually deposited in a precise microhabitat on or near the required food (Elzinga, 2004). However, some adult females can reproduce without male input. This is known as parthenogenesis and in the most common type of parthenogenesis the offspring are essentially identical to the mother. This is most often seen in aphids and scale insects (Elzinga, 2004).

Metamorphosis and insect's life cycle

An insect's life-cycle can be divided into three types:

- **Ametabolous,** no metamorphosis, these insects are primitively wingless where the only difference between adult and nymph is size, e.g. Order: Thysanura (Silverfish) (Triplehorn & Johnson, 2005).
- **Hemimetabolous,** or incomplete metamorphosis. The terrestrial young are called nymphs and aquatic young are called naiads. Insect young are usually similar to the adult. Wings appear as buds on the nymphs or early instars. When the last moult is completed the wings expand to the full adult size, e.g. Order: Odonata (Dragonflies).
- **Holometabolus,** or complete metamorphosis. These insects have a different form in their immature and adult stages, have different behaviours and live in different habitats. The immature form is called larvae and remains similar in form but

increases in size. They usually have chewing mouthparts even if the adult form mouth parts suck. At the last larval instar phase the insect forms into a pupa, it doesn't feed and is inactive, and here wing development is initiated, and the adult emerges e.g. Order: Lepidoptera (Butterflies and Moths), (Triplehorn & Johnson, 2005).

Molting

As an insect grows it needs to replace the rigid exoskeleton regularly (McGavin 2001; Triplehorn & Johnson, 2005,). Molting may occur up to three or four times or, in some insects, fifty times or more during its life (McGavin, 2001). A complex process controlled by hormones, it includes the cuticle of the body wall, the cuticular lining of the tracheae, foregut, hindgut and endoskeletal structures (McGavin 2001; Triplehorn & Johnson, 2005).

The stages of molting:

1. **Apolysis**—molting hormones are released into the haemolymph and the old cuticle separates from the underlying epidermal cells. The epidermis increases in size due to mitosis and then the new cuticle is produced. Enzymes secreted by the epidermal cells digest the old endocuticle, not affecting the old sclerotised exocuticle.
2. **Ecdysis**—this begins with the splitting of the old cuticle, usually starting in the midline of the thorax's dorsal side. The rupturing force is mostly from haemolymph pressure that has been forced into thorax by abdominal muscle contractions caused by the insect swallowing air or water. After this the insect wriggles out of the old cuticle.
3. **Sclerotinisation**—after emergence the new cuticle is soft and this a particularly vulnerable time for the insect as its hard protective coating is missing. After an hour or two the exocuticle hardens and darkens. The wings expand by the force of haemolymph into the wing veins (McGavin, 2001; Triplehorn & Johnson, 2005).

Chapter 2

Lactation

Kittens nursing

Lactation of pigs

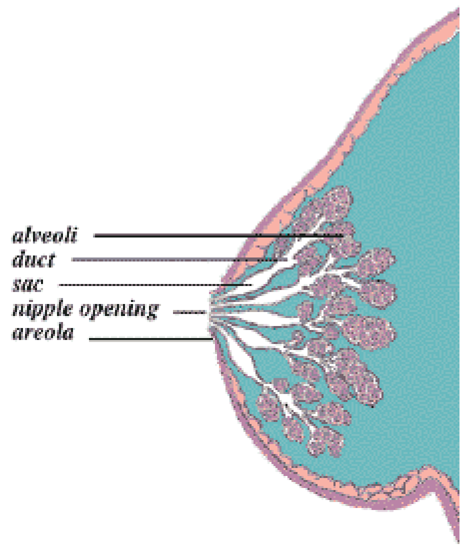
Lactation describes the secretion of milk from the mammary glands and the period of time that a mother lactates to feed her young. The process occurs in all female mammals, however it predates mammals. In humans the process of feeding milk is called breastfeeding or nursing. In most species milk comes out of the mother's nipples; however, the platypus (a non-placental mammal) releases milk through ducts in its abdomen. In only one species of mammal, the Dayak fruit bat, is milk production a normal male function. In some other mammals, the male may produce milk as the result of a hormone imbalance. This phenomenon may also be observed in newborn infants as well (for instance witch's milk).

Galactopoiesis is the maintenance of milk production. This stage requires prolactin (PRL) and oxytocin.

Purpose

The chief function of lactation is to provide nutrition and immune protection to the young after birth. In almost all mammals, lactation induces a period of infertility, which serves to provide the optimal birth spacing for survival of the offspring.

Human lactation



When the baby sucks its mother's breast, a hormone called oxytocin compels the milk to flow from the alveoli, through the ducts (milk canals) into the sacs (milk pools) behind the areola and then into the baby's mouth

Hormonal influences

From the twenty-fourth week of pregnancy (the second and third trimesters), a woman's body produces hormones that stimulate the growth of the milk duct system in the breasts:

- Progesterone—influences the growth in size of alveoli and lobes, high levels of progesterone inhibit lactation before birth. Progesterone levels drop after birth, this triggers the onset of copious milk production.
- Oestrogen—stimulates the milk duct system to grow and differentiate. Like progesterone high levels of oestrogen also inhibit lactation. Oestrogen levels also drop at delivery and remain low for the first several months of breastfeeding. It is recommended that breastfeeding mothers avoid oestrogen-based birth control methods, as a spike in estrogen levels may reduce a mother's milk supply.
- Prolactin—contributes to the increased growth and differentiation of the alveoli, also influences differentiation of ductal structures. High levels of prolactin during pregnancy and breastfeeding also increase insulin resistance, increase growth factor levels (IGF-1) and modify lipid metabolism in preparation for breastfeeding. During lactation prolactin is the main factor maintaining tight junctions of the ductal epithelium and regulating milk production through osmotic balance.

- Growth hormone is structurally very similar to prolactin and contributes to its galactopoietic function.
- ATCH and glucocorticoids have an important lactation inducing function in several animal species. ACTH is thought to contribute as it is structurally similar to prolactin. Glucocorticoids play a complex regulating role in the maintenance of tight junctions.
- TSH is a very important galactopoietic hormone, its levels are naturally increased during pregnancy.
- Oxytocin—contracts the smooth muscle of the uterus during and after birth, and during orgasm(s). After birth, oxytocin contracts the smooth muscle layer of band-like cells surrounding the alveoli to squeeze the newly-produced milk into the duct system. Oxytocin is necessary for the *milk ejection reflex*, or *let-down* to occur.
- Human placental lactogen (HPL)—From the second month of pregnancy, the placenta releases large amounts of HPL. This hormone appears to be instrumental in breast, nipple, and areola growth before birth.
- Follicle stimulating hormone (FSH)
- Luteinizing hormone (LH)

By the fifth or sixth month of pregnancy, the breasts are ready to produce milk. It is also possible to induce lactation without pregnancy.

Lactogenesis I

During the latter part of pregnancy, the woman's breasts enter into the *Lactogenesis I* stage. This is when the breasts make colostrum (see below), a thick, sometimes yellowish fluid. At this stage, high levels of progesterone inhibit most milk production. It is not a medical concern if a pregnant woman leaks any colostrum before her baby's birth, nor is it an indication of future milk production.

Lactogenesis II

At birth, prolactin levels remain high, while the delivery of the placenta results in a sudden drop in progesterone, estrogen, and HPL levels. This abrupt withdrawal of progesterone in the presence of high prolactin levels stimulates the copious milk production of *Lactogenesis II*.

When the breast is stimulated, prolactin levels in the blood rise, peak in about 45 minutes, and return to the pre-breastfeeding state about three hours later. The release of prolactin triggers the cells in the alveoli to make milk. Prolactin also transfers to the breast milk. Some research indicates that prolactin in milk is greater at times of higher milk production, and lower when breasts are fuller, and that the highest levels tend to occur between 2 a.m. and 6 a.m.

Other hormones—notably insulin, thyroxine, and cortisol—are also involved, but their roles are not yet well understood. Although biochemical markers indicate that

Lactogenesis II begins about 30–40 hours after birth, mothers do not typically begin feeling increased breast fullness (the sensation of milk "coming in the breast") until 50–73 hours (2–3 days) after birth.

Colostrum is the first milk a breastfed baby receives. It contains higher amounts of white blood cells and antibodies than mature milk, and is especially high in immunoglobulin A (IgA), which coats the lining of the baby's immature intestines, and helps to prevent pathogens from invading the baby's system. Secretory IgA also helps prevent food allergies. Over the first two weeks after the birth, colostrum production slowly gives way to mature breast milk.

Lactogenesis III

The hormonal endocrine control system drives milk production during pregnancy and the first few days after the birth. When the milk supply is more firmly established, autocrine (or local) control system begins. This stage is called *Lactogenesis III*

During this stage, the more that milk is removed from the breasts, the more the breast will produce milk. Research also suggests that draining the breasts more fully also increases the rate of milk production. Thus the milk supply is strongly influenced by how often the baby feeds and how well it is able to transfer milk from the breast. Low supply can often be traced to:

- not feeding or pumping often enough
- inability of the infant to transfer milk effectively caused by, among other things:
  - jaw or mouth structure deficits
  - poor latching technique
- rare maternal endocrine disorders
- hypoplastic breast tissue
- a metabolic or digestive inability in the infant, making it unable to digest the milk it receives
- inadequate calorie intake or malnutrition of the mother

Milk ejection reflex

The release of the hormone oxytocin leads to the *milk ejection* or *let-down reflex*. Oxytocin stimulates the muscles surrounding the breast to squeeze out the milk. Breastfeeding mothers describe the sensation differently. Some feel a slight tingling, others feel immense amounts of pressure or slight pain/discomfort, and still others do not feel anything different.

The let-down reflex is not always consistent, especially at first. The thought of breastfeeding or the sound of any baby can stimulate this reflex, causing unwanted leakage, or both breasts may give out milk when an infant is feeding from one breast. However, this and other problems often settle after two weeks of feeding. Stress or anxiety can cause difficulties with breastfeeding.

A poor milk ejection reflex can be due to sore or cracked nipples, separation from the infant, a history of breast surgery, or tissue damage from prior breast trauma. If a mother has trouble breastfeeding, different methods of assisting the milk ejection reflex may help. These include feeding in a familiar and comfortable location, massage of the breast or back, or warming the breast with a cloth or shower.

Afterpains

The surge of oxytocin that may also possibly trigger the milk ejection reflex also causes the uterus to contract. During breastfeeding, mothers may feel these contractions as *afterpains*. These may range from period-like cramps to strong labour-like contractions and can be more severe with second and subsequent babies. Some women's breasts also become dry and chapped and even crack open and bleed while breast feeding. Rubbing lanolin on the nipples and areola can help with those problems.

Lactation without pregnancy, induced lactation, relactation

In humans induced lactation and relactation has been observed frequently in primitive cultures and demonstrated with varying success in adoptive mothers. It appears plausible that the possibility of induction of lactation in women (or females of other species) who are not biological mothers does confer an evolutionary advantage especially in groups with high maternal mortality and tight social bonds. The phenomenon has been also observed in most primates, some lemurs and dwarf mongooses.

In humans lactation can be induced by a combination physical and psychological stimulation, by drugs or a combination of those methods.

Also, some couples may use lactation for sexual purposes.

Rare accounts of male lactation (as distinct from galactorrhea) exist in historical medical and anthropological literature, although the phenomenon has not been confirmed by more recent literature.

Evolution

Darwin correctly recognised that mammary glands developed from cutaneous glands and postulated the hypothesis that they evolved from glands in brood pouches of fish where they provided nourishment for eggs. The later aspect of his hypothesis has not been confirmed, but recently the same mechanism has been postulated for early synapsids. Instead the discus fish (Symphysodon aequifasciata) became known for (biparentally) feeding their offspring by epidermal mucus secretion. A closer look reveals that similar to most mammals the secretion of the nourishing fluid may be controlled by prolactin.

Later therapsids such as cynodonts appear to have secreted complex, nutrient-rich milk. This brought them evolutionary advantage by allowing a decline in egg size.

During early evolution of lactation the secretion was through pilosebaceous glands and *mammary hairs* transported the nourishing fluids to the eggs or youngs. Later the development of the *mammary patch* rendered mammary hairs obsolete.

Other well known example of nourishing young with secretions of glands is the crop milk of pigeons. Like in mammals and disc fish this also appears closely related to prolactin. Other birds such as flamingos and penguins are utilizing similar feeding techniques.

Chapter 3

Physiology of Dinosaurs

The **physiology of dinosaurs** has historically been a controversial subject, particularly thermoregulation. Recently, many new lines of evidence have been brought to bear on dinosaur physiology generally, including not only metabolic systems and thermoregulation, but on respiratory and cardiovascular systems as well.

During the early years of dinosaur paleontology, it was widely considered that they were sluggish, cumbersome, and sprawling cold-blooded lizards. However, with the discovery of much more complete skeletons in the western United States, starting in the 1870s, scientists could make more informed interpretations of dinosaur biology and physiology. Edward Drinker Cope, opponent of Othniel Charles Marsh in the Bone Wars, propounded at least some dinosaurs as active and agile, as seen in the painting of two fighting "Laelaps" produced under his direction by Charles R. Knight. In parallel, the development of Darwinian evolution, and the discoveries of *Archaeopteryx* and *Compsognathus*, led Thomas Henry Huxley to propose that dinosaurs were closely related to birds. Despite these considerations, the image of dinosaurs as large reptiles had taken root, and most aspects of their paleobiology were interpreted as being typically reptilian for the first half of the twentieth century. Beginning in the 1960s and with the advent of the Dinosaur Renaissance, views of dinosaurs and the physiology have changed dramatically, including the discovery of feathered dinosaurs in Early Cretaceous age deposits in China, indicating that birds evolved from highly agile maniraptoran dinosaurs.

History of study

Early interpretations of dinosaurs: 1820s to early 1900s

Reconstruction of *Megalosaurus* from 1854, in Crystal Palace, London

The 1897 painting of "*Laelaps*" (now *Dryptosaurus*) by Charles R. Knight.

The study of dinosaurs began in the 1820s in England. Pioneers in the field, such as William Buckland, Gideon Mantell, and Richard Owen, interpreted the first, very fragmentary remains as belonging to large quadrupedal beasts. Their early work can be seen today in the Crystal Palace Dinosaurs, constructed in the 1850s, which present known dinosaurs as elephantine lizard-like reptiles. Despite these reptilian appearances, Owen speculated that dinosaur heart and respiratory systems were more mammal-like than reptile-like.

Changing views and the Dinosaur Renaissance

However, in the late 1960s views began to change, beginning with John Ostrom's work on *Deinonychus* and bird evolution. His student, Bob Bakker, popularized the changing thought in a series of papers beginning with *The superiority of dinosaurs* in 1968. In these publications, he argued strenuously that dinosaurs were warm-blooded and active animals, capable of sustained periods of high activity. In most of his writings Bakker framed his arguments as new evidence leading to a revival of ideas popular the late 19th century, frequently referring to an ongoing *dinosaur renaissance*. He used a variety of anatomical and statistical arguments to defend his case, the methodology of which was fiercely debated among scientists.

These debates sparked interest in new methods for ascertaining the palaeobiology of extinct animals, such as bone histology, which have been successfully applied to determining the growth-rates of many dinosaurs.

Today, it is generally thought that many or perhaps all dinosaurs had higher metabolic rates than living reptiles, but also that the situation is more complex and varied than Bakker originally proposed. For example, while smaller dinosaurs may have been true endotherms, the larger forms could have been inertial homeotherms, or many dinosaurs could have had intermediate metabolic rates.

Feeding and digestion

The earliest dinosaurs were almost certainly predators, and shared several predatory features with their nearest non-dinosaur relatives like *Lagosuchus*, including: relatively large, curved, blade-like teeth in large, wide-opening jaws that closed like scissors; relatively small abdomens, as carnivores do not require large digestive systems. Later dinosaurs regarded as predators sometimes grew much larger, but retain the same set of features. Instead of chewing their food, these predators swallowed it whole.

The feeding habits of ornithomimosaurs and oviraptorosaurs are a mystery: although they evolved from a predatory theropod lineage, they have small jaws and lack the blade-like teeth of typical predators, but there is no evidence of their diet or how they ate and digested it.

Features of other groups of dinosaurs indicate they were vegetarians. These features include:

- Jaws that opened only a little and closed so that all the teeth met at the same time
- Large abdomens that could accommodate large amounts of vegetation and store it for the longer time it takes to digest vegetation
- Guts that likely contained Endosymbiotic micro-organisms that digest cellulose, as no known animal can digest this tough material directly

Sauropods, which were vegetarians, did not chew their food, as their teeth and jaws appear suitable only for stripping leaves off plants. Ornithischians, also vegetarians, show a variety of approaches. The armored ankylosaurs and stegosaurs had small heads and weak jaws and teeth, and are thought to have fed in much the same way as sauropods. The pachycephalosaurs had small heads and weak jaws and teeth, but their lack of large digestive systems suggests a different diet, possibly fruits, seeds, or young shoots, which would have been more nutritious than leaves.

On the other hand ornithopods such as *Hypsilophodon*, *Iguanodon* and various hadrosaurs had horny beaks for snipping off vegetation and jaws and teeth that were well-adapted for chewing. The horned ceratopsians had similar mechanisms.

It has often been suggested that at least some dinosaurs used swallowed stones, known as gastroliths, to aid digestion by grinding their food in muscular gizzards, and that this was a feature they shared with birds. In 2007 Oliver Wings reviewed references to gastroliths in scientific literature and found considerable confusion, starting with the lack of an agreed and objective definition of "gastrolith". He found that swallowed hard stones or grit can assist digestion in birds that mainly feed on grain but may not be essential—and that birds that eat insects in summer and grain in winter usually get rid of the stones and grit in summer. Gastroliths have often been described as important for sauropod dinosaurs, whose diet of vegetation required very thorough digestion, but Wings concluded that this idea was incorrect: gastroliths are found with only a small percentage of sauropod fossils; where they have been found, the amounts are too small and in many cases the stones are too soft to have been effective in grinding food; most of these gastroliths are highly polished, but gastroliths used by modern animals to grind food are roughened by wear and corroded by stomach acids; hence the sauropod gastroliths were probably swallowed accidentally. On the other hand he concluded that gastroliths found with fossils of advanced theropod dinosaurs such as *Sinornithomimus* and *Caudipteryx* resemble those of birds, and that the use of gastroliths for grinding food may have appeared early in the group of dinosaurs from which these dinosaurs and birds both evolved.

Reproductive biology

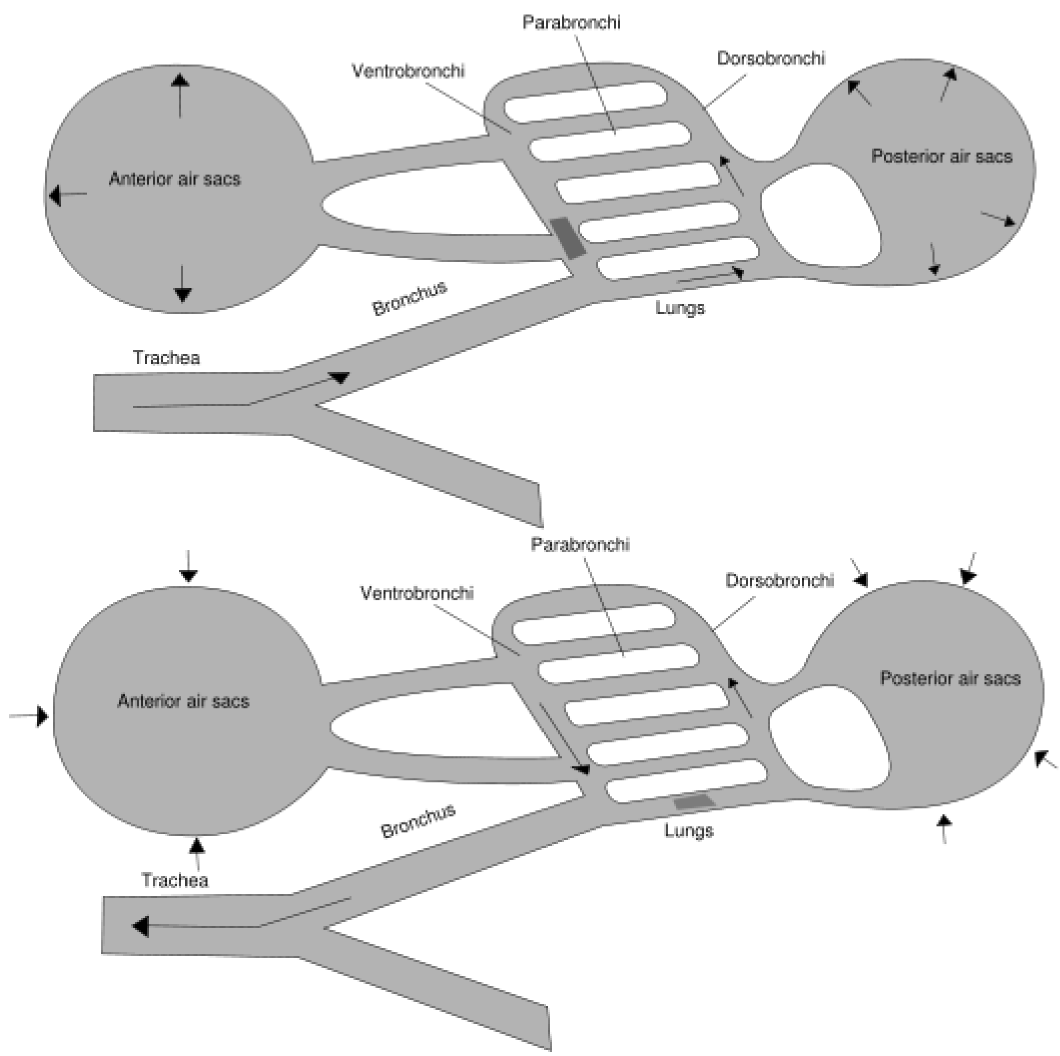
When laying eggs, females of some bird species grow a special type of bone in their limbs between the hard outer bone and the marrow. This medullary bone, which is rich in calcium, is used to make eggshells, and the birds that produced it absorb it when they have finished laying eggs. Medullary bone has been found in fossils of the theropods *Tyrannosaurus* and *Allosaurus* and of the ornithopod *Tenontosaurus*.

Because the line of dinosaurs that includes *Allosaurus* and *Tyrannosaurus* diverged from the line that led to *Tenontosaurus* very early in the evolution of dinosaurs, the presence of medullary bone in both groups suggests that dinosaurs in general produced medullary tissue. On the other hand crocodilians, which are dinosaurs' second closest living relatives after birds, do not produce medullary bone. This tissue may have first appeared in ornithodires, the Triassic archosaur group from which dinosaurs are thought to have evolved.

Medullary bone has been found in specimens of sub-adult size, which suggests that dinosaurs reached sexual maturity before they were fully-grown. Sexual maturity at sub-adult size is also found in reptiles and in medium- to large-sized mammals, but birds and small mammals reach sexual maturity only after they are fully-grown—which happens within their first year. Early sexual maturity is also associated with specific features of animals' life cycles: the young are born relatively well-developed rather than helpless; and the death-rate among adults is high.

Respiratory System

Air sacs



Birds' lungs obtain fresh air during both exhalation and inhalation, because the air sacs do all the "pumping" and the lungs simply absorb oxygen.

From about 1870 onwards scientists have generally agreed that the post-cranial skeletons of many dinosaurs contained many air-filled cavities (postcranial skeletal pneumaticity, especially in the vertebrae. Pneumatization of the skull (such as paranasal sinuses) is found in both synapsids and archosaurs, but postcranial pneumatization is found only in birds, non-avian saurischian dinosaurs, and pterosaurs.

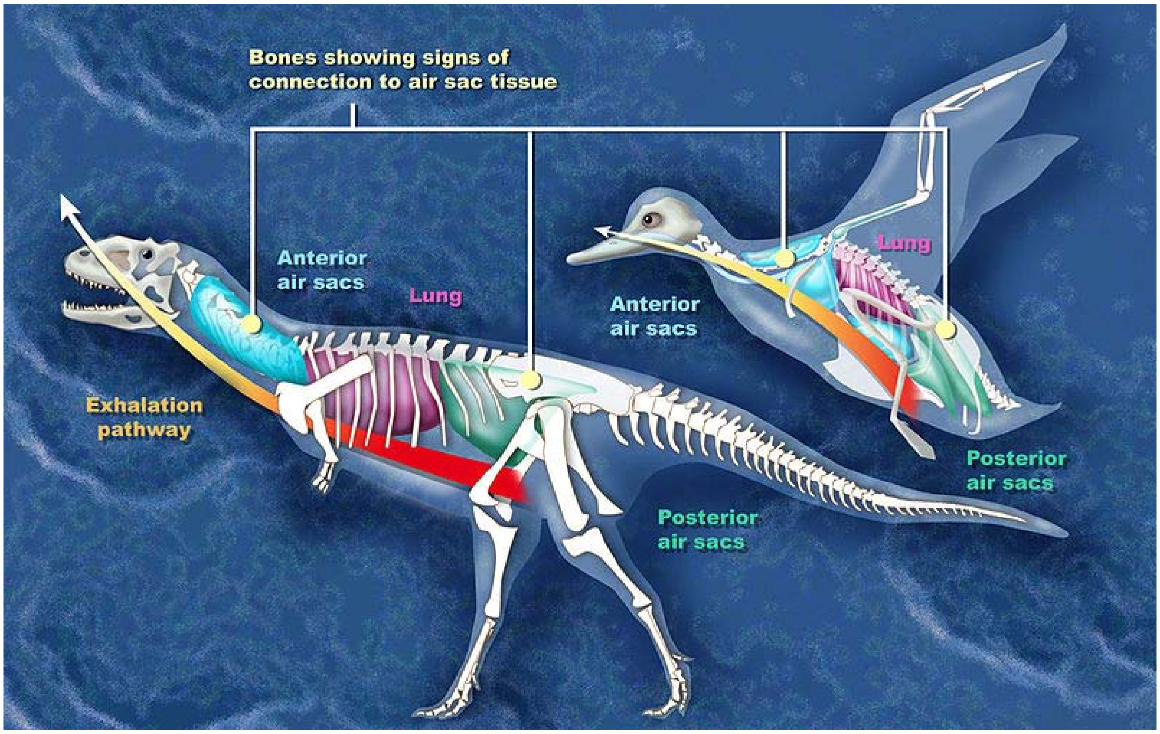
For a long time these cavities were regarded simply as weight-saving devices, but Bakker proposed that they contained air sacs like those that make birds' respiratory systems the most efficient of all animals'.

John Ruben *et al.* (1997, 1999, 2003, 2004) disputed this and suggested that dinosaurs had a "tidal" respiratory system (in and out) powered by a crocodile-like hepatic piston mechanism - muscles attached mainly to the pubis pull the liver backwards, which makes the lungs expand to inhale; when these muscles relax, the lungs return to their previous size and shape, and the animal exhales. They also presented this as a reason for doubting that birds descended from dinosaurs.

Critics have claimed that, without avian air sacs, modest improvements in a few aspects of a modern reptile's circulatory and respiratory systems would enable the reptile to achieve 50% to 70% of the oxygen flow of a mammal of similar size, and that lack of avian air sacs would not prevent the development of endothermy. Very few formal rebuttals have been published in scientific journals of Ruben *et al.*'s claim that dinosaurs could not have had avian-style air sacs; but one points out that the *Sinosauropteryx* fossil on which they based much of their argument was severely flattened and therefore it was impossible to tell whether the liver was the right shape to act as part of a hepatic piston mechanism. Some recent papers simply note without further comment that Ruben *et al.* argued against the presence of air sacs in dinosaurs.

Researchers have presented evidence and arguments for air sacs in sauropods, "prosauropods", coelurosaurs, ceratosaurs, and the theropods *Aerosteon* and *Coelophysis*.

In advanced sauropods ("neosauropods") the vertebrae of the lower back and hip regions show signs of air sacs. In early sauropods only the cervical (neck) vertebrae show these features. If the developmental sequence found in bird embryos is a guide, air sacs actually evolved before the channels in the skeleton that accommodate them in later forms.



Comparison between the air sacs of *Majungasaurus* and a bird

Evidence of air sacs has also been found in theropods. Studies indicate that fossils of coelurosaurs, ceratosaurs, and the theropods *Coelophysis* and *Aerosteon* exhibit evidence of air sacs. *Coelophysis*, from the late Triassic, is one of the earliest dinosaurs whose fossils show evidence of channels for air sacs. *Aerosteon*, a Late Cretaceous allosaur, had the most bird-like air sacs found so far.

Early sauropodomorphs, including the group traditionally called "prosauropods", may also have had air sacs. Although possible pneumatic indentations have been found in *Plateosaurus* and *Thecodontosaurus*, the indentations are very small. One study in 2007 concluded that prosauropods likely had abdominal and cervical air sacs, based on the evidence for them in sister taxa (theropods and sauropods). The study concluded that it was impossible to determine whether prosauropods had a bird-like flow-through lung, but that the air sacs were almost certainly present. A further indication for the presence of air sacs and their use in lung ventilation comes from a reconstruction of the air exchange volume (the volume of air exchanged with each breath) of *Plateosaurus*, which when expressed as a ratio of air volume per body weight at 29 ml/kg is similar to values of geese and other birds, and much higher than typical mammalian values.

So far no evidence of air sacs has been found in ornithischian dinosaurs. But this does not imply that ornithischians could not have had metabolic rates comparable to those of mammals, since mammals also do not have air sacs.

Three explanations have been suggested for the development of air sacs in dinosaurs:

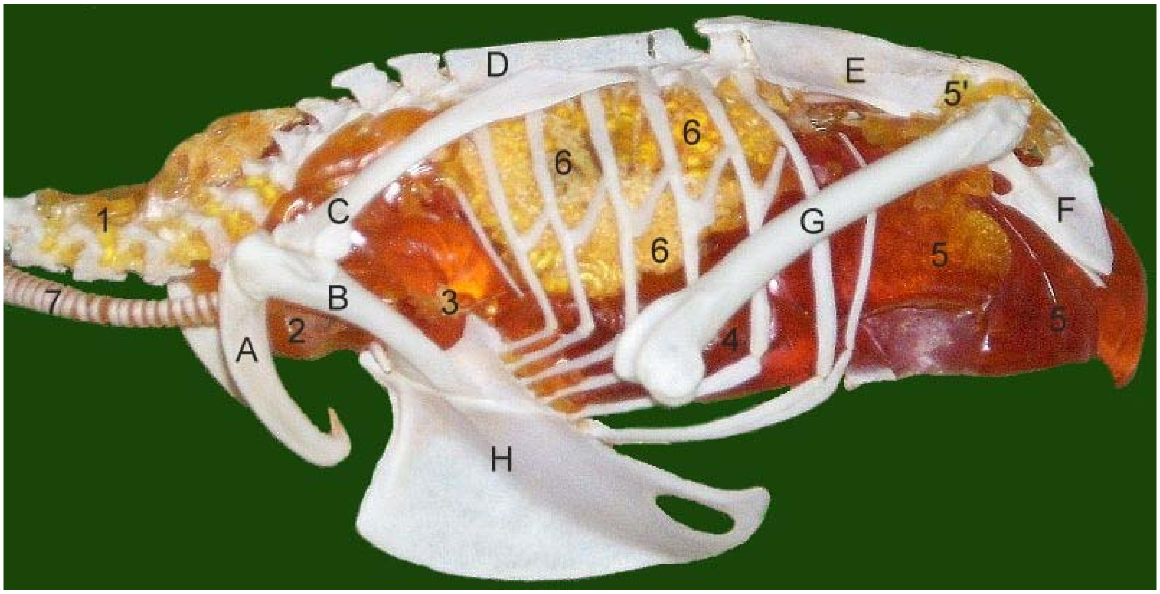
- Increase in respiratory capacity. This is probably the most common hypothesis, and fits well with the idea that many dinosaurs had fairly high metabolic rates.
- Improving balance and maneuvrability by lowering the center of gravity and reducing rotational inertia. However this does not explain the expansion of air sacs in the quadrupedal sauropods.
- As a cooling mechanism. It seems that air sacs and feathers evolved at about the same time in coelurosaurs. If feathers retained heat, their owners would have required a means of dissipating excess heat. This idea is plausible but needs further empirical support.

Calculations of the volumes of various parts of the sauropod *Apatosaurus*' respiratory system support the evidence of bird-like air sacs in sauropods:

- Assuming that *Apatosaurus*, like dinosaurs' nearest surviving relatives crocodilians and birds, did not have a diaphragm, the dead-space volume of a 30-ton specimen would be about 184 liters. This is the total volume of the mouth, trachea and air tubes. If the animal exhales less than this, stale air is not expelled and is sucked back into the lungs on the following inhalation.
- Estimates of its tidal volume – the amount of air moved into or out of the lungs in a single breath – depend on the type of respiratory system the animal had: 904 liters if avian; 225 liters if mammalian; 19 liters if reptilian.

On this basis, *Apatosaurus* could not have had a reptilian respiratory system, as its tidal volume would have been less than its dead-space volume, so that stale air was not expelled but was sucked back into the lungs. Likewise, a mammalian system would only provide to the lungs about 225 − 184 = 41 liters of fresh, oxygenated air on each breath. *Apatosaurus* must therefore have had either a system unknown in the modern world or one like birds', with multiple air sacs and a flow-through lung. Furthermore, an avian system would only need a lung volume of about 600 liters while a mammalian one would have required about 2,950 liters, which would exceed the estimated 1,700 liters of space available in a 30-ton *Apatosaurus'* chest.

Dinosaur respiratory systems with bird-like air sacs may have been capable of sustaining higher activity levels than mammals of similar size and build can sustain. In addition to providing a very efficient supply of oxygen, the rapid airflow would have been an effective cooling mechanism, which is essential for animals that are active but too large to get rid of all the excess heat through their skins.



The uncinate processes are the small white spurs about half-way along the ribs. The rest of this diagram shows the air sacs and other parts of a bird's respiratory system:1 cervical air sac, 2 clavicular air sac, 3 cranial thoracal air sac, 4 caudal thoracal air sac, 5 abdominal air sac (5' diverticulus into pelvic girdle), 6 lung, 7 trachea

Uncinate processes on the ribs

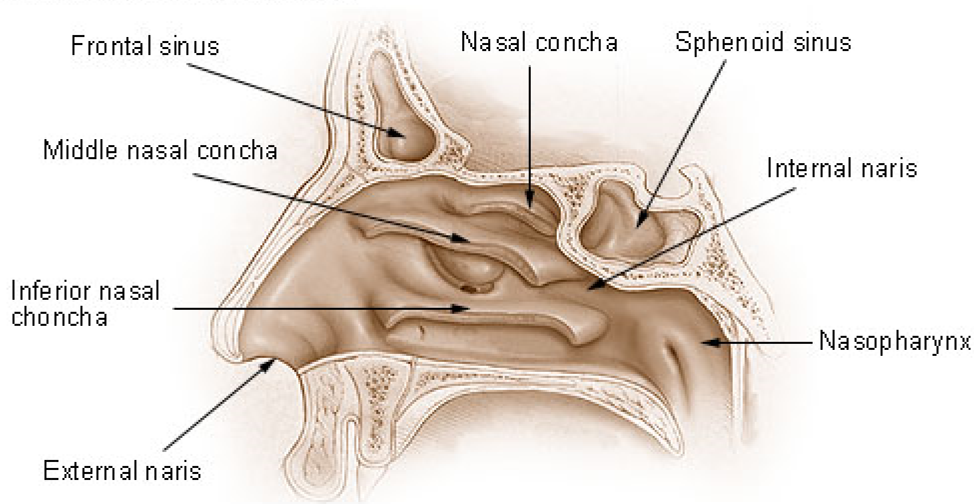
Birds have spurs called "uncinate processes" on the rear edges of their ribs, and these give the chest muscles more leverage when pumping the chest to improve oxygen supply. The size of the uncinate processes is related to the bird's lifestyle and oxygen requirements: they are shortest in walking birds and longest in diving birds, which need to replenish their oxygen reserves quickly when they surface. Non-avian maniraptoran dinosaurs also had these uncinate processes, and they were proportionately as long as in modern diving birds, which indicates that maniraptorans needed a high-capacity oxygen supply.

Plates that may have functioned the same way as uncinate processes have been observed in fossils of the ornithischian dinosaur *Thescelosaurus*, and have been interpreted as evidence of high oxygen consumption and therefore high metabolic rate.

Nasal turbinates

Nasal turbinates (often referred to as "turbinals" or "conchae") are convoluted structures of thin bone in the nasal cavity. In most mammals and birds these are present and lined with mucous membranes that perform two functions. They improve the sense of smell by increasing the area available to absorb airborne chemicals—and they warm and moisten inhaled air, and extract heat and moisture from exhaled air to prevent desiccation of the lungs.

Nose and Nasal Cavities



Human nasal turbinates / conchae are rather simple, but similar in position to those of other mammals.

Ruben *et al.* have argued in several papers that:

- No evidence of nasal turbinates has been found in dinosaurs (the papers focussed on coelurosaurs)
- All the dinosaurs they examined had nasal passages that were too narrow and short to accommodate nasal turbinates.
- Hence dinosaurs could not have sustained the breathing rate required for a mammal-like or bird-like metabolic rate while at rest, because their lungs would have dried out.

However, objections have been raised against this argument:

- Nasal turbinates are absent or very small in some birds (e.g. ratites, Procellariiformes and Falconiformes) and mammals (e.g. whales, anteaters, bats, elephants, and most primates), although these animals are fully endothermic and in some cases very active.
- Other studies conclude that nasal passages of these dinosaurs were long enough and wide enough to accommodate nasal turbinates or similar mechanisms to avoid desiccation of the lungs.
- Nasal turbinates are fragile and seldom found in fossils. In particular none have been found in fossil birds.

Cardiovascular system

The possible heart of "Willo" the thescelosaur (center).

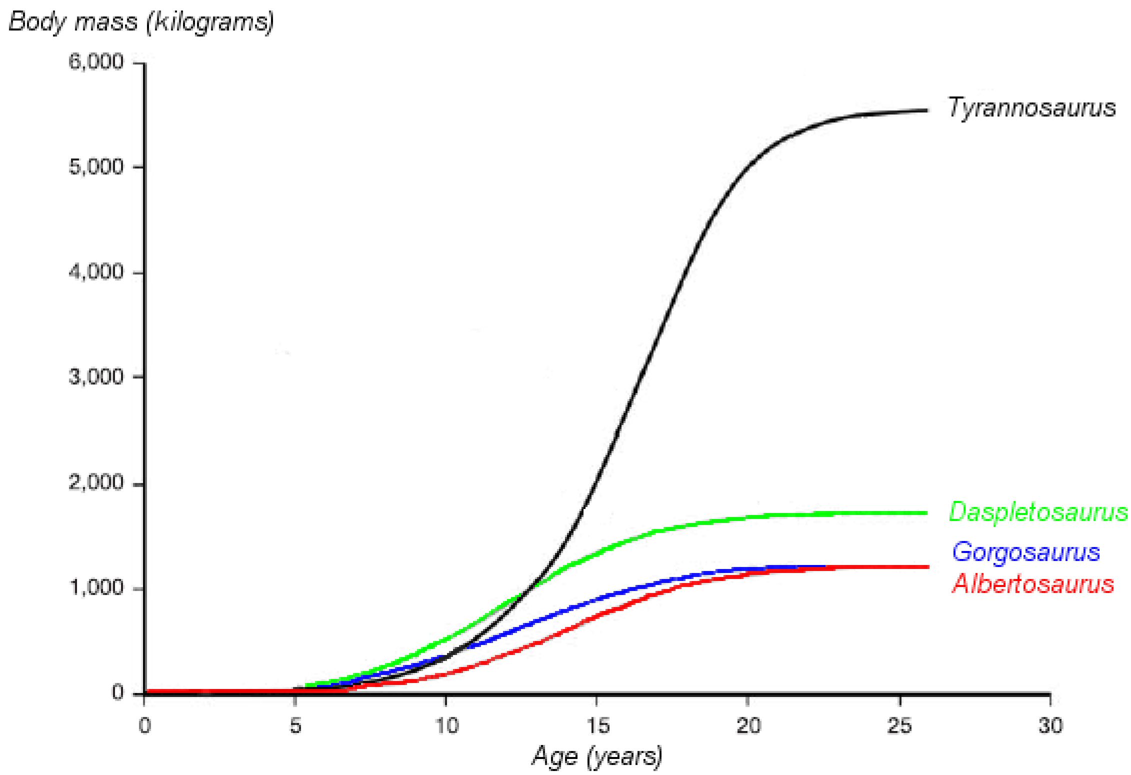
In principle one would expect dinosaurs to have had two-part circulations driven by four-chambered hearts, since many would have needed high blood pressure to deliver blood to their heads, which were high off the ground, but vertebrate lungs can only tolerate fairly low blood pressure. In 2000, a skeleton of *Thescelosaurus*, now on display at the North Carolina Museum of Natural Sciences, was described as including the remnants of a four-chambered heart and an aorta. The authors interpreted the structure of the heart as indicating an elevated metabolic rate for *Thescelosaurus*, not reptilian cold-bloodedness. Their conclusions have been disputed; other researchers published a paper where they assert that the heart is really a concretion of entirely mineral "cement". As they note: the anatomy given for the object is incorrect, for example the alleged "aorta" is narrowest where it meets the "heart" and lacks arteries branching from it; the "heart" partially engulfs one of the ribs and has an internal structure of concentric layers in some places; and another concretion is preserved behind the right leg. The original authors defended their position; they agreed that the chest did contain a type of concretion, but one that had formed around and partially preserved the more muscular portions of the heart and aorta.

Regardless of the object's identity, it may have little relevance to dinosaurs' internal anatomy and metabolic rate. Both modern crocodilians and birds, the closest living relatives of dinosaurs, have four-chambered hearts, although modified in crocodilians, and so dinosaurs probably had them as well. However such hearts are not necessarily tied to metabolic rate.

Growth and lifecycle

No dinosaur egg has been found that is larger than a basketball and embryos of large dinosaurs have been found in relatively small eggs, e.g. Maiasaura. Like mammals, dinosaurs stopped growing when they reached the typical adult size of their species, while mature reptiles continue to grow slowly if they have enough food. Dinosaurs of all sizes grew faster than similarly-sized modern reptiles; but the results of comparisons with similarly-sized "warm-blooded" modern animals depend on their sizes:

Weight (kg)	Comparative growth rate of dinosaurs	Modern animals in this size range
0.22	Slower than marsupials	Rat
1 - 20	Similar to marsupials, slower than precocial birds (those that are born capable of running)	From guinea pig to Andean Condor
100 - 1000	Faster than marsupials, similar to precocial birds, slower than placental mammals	From Red Kangaroo to Polar Bear
1500 – 3500	Similar to most placental mammals	From American Bison to rhinoceros
25000 and over	Very fast, similar to modern whales; but about half that of a scaled-up altricial bird (one that is born helpless) - if one could scale up a bird to 25,000 kilograms (25 LT; 28 ST)	Whales



A graph showing the hypothesized growth curves (body mass versus age) of four tyrannosaurids. *Tyrannosaurus rex* is drawn in black. Based on Erickson et al. 2004.

Tyrannosaurus rex showed a "teenage growth spurt":

- ½ ton at age 10
- very rapid growth to around 2 tons in the mid-teens (about ½ ton per year).
- negligible growth after the second decade.

A 2008 study of one skeleton of the hadrosaur *Hypacrosaurus* concluded that this dinosaur grew even faster, reaching its full size at the age of about 15; the main evidence was the number and spacing of growth rings in its bones. The authors found this consistent with a life-cycle theory that prey species should grow faster than their predators if they lose a lot of juveniles to predators and the local environment provides enough resources for rapid growth.

It appears that individual dinosaurs were rather short-lived, e.g. the oldest (at death) *Tyrannosaurus* found so far was 28 and the oldest sauropod was 38. Predation was probably responsible for the high death rate of very young dinosaurs and sexual competition for the high death rate of sexually mature dinosaurs.

Metabolism

Scientific opinion about the life-style, metabolism and temperature regulation of dinosaurs has varied over time since the discovery of dinosaurs in the mid-19th century. The activity of metabolic enzymes varies with temperature, so temperature control is vital for any organism, whether endothermic or ectothermic. Organisms can be categorized as poikilotherms (poikilo - changing), which are tolerant of internal temperature fluctuations, and homeotherms (homeo - same), which must maintain a constant core temperature. Animals can be further categorized as endotherms, which regulate their temperature internally, and ectotherms, which regulate temperature by the use of external heat sources.

The current consensus view suggests that dinosaur metabolism did not closely match any found in living vertebrates, and, consequently, that they cannot be categorized as either "warm" or "cold-blooded." Rather, they lie somewhere on the spectrum between poikilothermy and homeothermy. Consequently, current research focuses on mechanisms of metabolism and temperature regulation, and the similarities between dinosaurian, avian and mammalian metabolisms.

What the debate is about

"Warm-bloodedness" is a complex and rather ambiguous term, because it includes some or all of:

- **Homeothermy**, i.e. maintaining a fairly constant body temperature. Modern endotherms maintain a variety of temperatures: 28 °C (82 °F) to 30 °C (86 °F) in monotremes and sloths; 33 °C (91 °F) to 36 °C (97 °F) in marsupials; 36 °C (97 °F) to 38 °C (100 °F) in most placentals; and around 41 °C (106 °F) in birds.
- **Tachymetabolism**, i.e. maintaining a high metabolic rate, particularly when at rest. This requires a fairly high and stable body temperature, since: biochemical processes run about half as fast if an animal's temperature drops by 10C°; most enzymes have an optimum operating temperature and their efficiency drops rapidly outside the preferred range.
- **Endothermy**, i.e. the ability to generate heat internally, for example by "burning" fat, rather than via behaviors such as basking or muscular activity. Although endothermy is in principle the most reliable way to maintain a fairly constant temperature, it is expensive, for example modern mammals need 10 to 13 times as much food as modern reptiles.

Large dinosaurs may also have maintained their temperatures by inertial homeothermy, also known as "bulk homeothermy" or "mass homeothermy". In other words, the thermal capacity of such large animals was so high that that it would take two days or more for their temperatures to change significantly, and this would have smoothed out variations caused by daily temperature cycles. This smoothing effect has been observed in large turtles and crocodilians, but *Plateosaurus*, which weighed about 700 kilograms (1,500 lb), may have been the smallest dinosaur in which it would have been effective.

Inertial homeothermy would not have been possible for small species nor for the young of larger species. Vegetation fermenting in the guts of large herbivores can also produce considerable heat, but this method of maintaining a high and stable temperature would not have been possible for carnivores nor for small herbivores or the young of larger herbivores.

Since the internal mechanisms of extinct creatures are unknowable, most discussion focuses on homeothermy and tachymetabolism.

Assessment of metabolic rates is complicated by the distinction between the rates while resting and while active. In all modern reptiles and most mammals and birds the maximum rates during all-out activity are 10 to 20 times higher than minimum rates while at rest. However in a few mammals these rates differ by a factor of 70. Theoretically it would be possible for a land vertebrate to have a reptilian metabolic rate at rest and a bird-like rate while working flat out. However an animal with such a low resting rate would be unable to grow quickly. The huge herbivorous sauropods may have been on the move so constantly in search of food that their energy expenditure would have been much the same irrespective of whether their resting metabolic rates were high or low.

Metabolic options

The main possibilities are that:

- Dinosaurs were cold-blooded, like modern reptiles, except that the large size of many would have stabilized their body temperatures.
- They were warm-blooded, more like modern mammals or birds than modern reptiles.
- They were neither cold-blooded nor warm-blooded in modern terms, but had metabolisms that were different from and some ways intermediate between those of modern cold-blooded and warm-blooded animals.
- They included animals with two or three of these types of metabolism.

Dinosaurs were around for about 150 million years, so it is very likely that different groups evolved different metabolisms and thermoregulatory regimes, and that some developed different physiologies from the first dinosaurs.

If all or some dinosaurs had intermediate metabolisms, they may have had the following features:

- Low resting metabolic rates—which would reduce the amount of food they needed and allow them to use more of that food for growth than do animals with high resting metabolic rates.
- Inertial homeothermy
- The ability to control heat loss by expanding and contracting blood vessels just under the skin, as many modern reptiles do.

- Two-part circulations driven by four-chambered hearts.
- High aerobic capacity, allowing sustained activity.

Robert Reid has suggested that such animals could be regarded as "failed endotherms". He envisaged both dinosaurs and the Triassic ancestors of mammals passing through a stage with these features. Mammals were forced to become smaller as archosaurs came to dominate ecological niches for medium to large animals. Their decreasing size made them more vulnerable to heat loss because it increased their ratios of surface area to mass, and thus forced them to increase internal heat generation and thus become full endotherms. On the other hand dinosaurs became medium to very large animals and thus were able to retain the "intermediate" type of metabolism.

Bone structure

Armand de Ricqlès discovered Haversian canals in dinosaur bones, and argued that they were evidence of endothermy in dinosaurs. These canals are common in "warm-blooded" animals and are associated with fast growth and an active life style because they help to recycle bone to facilitate rapid growth and repair damage caused by stress or injuries. Dense secondary Haversian bone, which is formed during remodeling, is found in many living endotherms as well as dinosaurs, pterosaurs and therapsids. Secondary Haversian canals are correlated with size and age, mechanical stress and nutrient turnover. The presence of secondary Haversian canals suggests comparable bone growth and lifespans in mammals and dinosaurs. Bakker argued that the presence of fibrolamellar bone (produced quickly and having a fibrous, woven appearance) in dinosaur fossils was evidence of endothermy.

However as a result of other, mainly later research, bone structure is not considered a reliable indicator of metabolism in dinosaurs, mammals or reptiles:

- Dinosaur bones often contain lines of arrested growth (LAGs), formed by alternating periods of slow and fast growth; in fact many studies count growth rings to estimate the ages of dinosaurs. The formation of growth rings is usually driven by seasonal changes in temperature, and this seasonal influence has sometimes been regarded as a sign of slow metabolism and ectothermy. But growth rings are found in polar bears and in mammals that hibernate. The relationship between LAGs and seasonal growth dependency remains unresolved.

- Fibrolamellar bone is fairly common in young crocodilians and sometimes found in adults.
- Haversian bone has been found in turtles, crocodilians and tortoises, but is often absent in small birds, bats, shrews and rodents.

Nevertheless de Ricqlès persevered with studies of the bone structure of dinosaurs and archosaurs. In mid-2008 he co-authored a paper that examined bone samples from a wide range of archosaurs, including early dinosaurs, and concluded that:

- Even the earliest archosauriformes may have been capable of very fast growth, which suggests they had fairly high metabolic rates. Although drawing conclusions about the earliest archosauriformes from later forms is tricky, because species-specific variations in bone structure and growth rate are very likely, there are research strategies than can minimize the risk that such factors will cause errors in the analysis.
- Archosaurs split into three main groups in the Triassic: ornithodirans, from which dinosaurs evolved, remained committed to rapid growth; crocodilians' ancestors adopted more typical "reptilian" slow growth rates; and most other Triassic archosaurs had intermediate growth rates.

Growth rates

Dinosaurs grew from small eggs to several tons in weight relatively quickly. A natural interpretation of this is that that dinosaurs converted food into body weight very quickly, which requires a fairly fast metabolism both to forage actively and to assimilate the food quickly.Developing bone found in juveniles is distinctly porous, which has been linked to vascularization and bone deposition rate, all suggesting growth rates close to those observed in modern birds.

But a preliminary study of the relationship between adult size, growth rate, and body temperature concluded that larger dinosaurs had higher body temperatures than smaller ones had; *Apatosaurus*, the largest dinosaur in the sample, was estimated to have a body temperature exceeding 41 °C (106 °F), whereas smaller dinosaurs were estimated to have body temperatures around 25 °C (77 °F) – for comparison, normal human body temperature is about 37 °C (99 °F). Based on these estimations, the study concluded that large dinosaurs were inertial homeotherms (their temperatures were stabilized by their sheer bulk) and that dinosaurs were ectothermic (in colloquial terms, "cold-blooded", because they did not generate as much heat as mammals when not moving or digesting food). These results are consistent with the relationship between dinosaurs' sizes and growth rates (described above). Studies of the sauropodomorph *Massospondylus* and early theropod *Syntarsus* (*Megapnosaurus*) reveal growth rates of 3 kg/year and 17 kg/year, respectively, much slower than those estimated of Maiasaura and observed in modern birds.

Oxygen isotope ratios in bone

The ratio of the isotopes ^{16}O and ^{18}O in bone depends on the temperature the bone formed at: the higher the temperature, the more ^{16}O. Barrick and Showers (1999) analyzed the isotope ratios in two theropods that lived in temperate regions with seasonal variation in temperature, *Tyrannosaurus* (USA) and *Giganotosaurus* (Argentina):

- dorsal vertebrae from both dinosaurs showed no sign of seasonal variation, indicating that both maintained a constant core temperature despite seasonal variations in air temperature.

- ribs and leg bones from both dinosaurs showed greater variability in temperature and a lower average temperature as the distance from the vertebrae increased.

Barrick and Showers concluded that both dinosaurs were endothermic but at lower metabolic levels than modern mammals, and that inertial homeothermy was an important part of their temperature regulation as adults. Their similar analysis of some Late Cretaceous ornithischians in 1996 concluded that these animals showed a similar pattern.

However this view has been challenged. The evidence indicates homeothermy, but by itself cannot prove endothermy. Secondly, the production of bone may not have been continuous in areas near the extremities of limbs – in allosaur skeketons lines of arrested growth ("LAGs"; rather like growth rings) are sparse or absent in large limb bones but common in the fingers and toes. While there is no absolute proof that LAGs are temperature-related, they could mark times when the extremities were so cool that the bones ceased to grow. If so, the data about oxygen isotope ratios would be incomplete, especially for times when the extremities were coolest. Oxygen isotope ratios may be an unreliable method of estimating temperatures if it cannot be shown that bone growth was equally continuous in all parts of the animal.

Predator-prey ratios

Bakker argued that:

- cold-blooded predators need much less food than warm-blooded ones, so a given mass of prey can support far more cold-blooded predators than warm-blooded ones.
- the ratio of the total mass of predators to prey in dinosaur communities was much more like that of modern and recent warm-blooded communities than that of recent or fossil cold-blooded communities.
- hence predatory dinosaurs were warm-blooded. And since the earliest dinosaurs (e.g. *Staurikosaurus*, *Herrerasaurus*) were predators, all dinosaurs must have been warm-blooded.

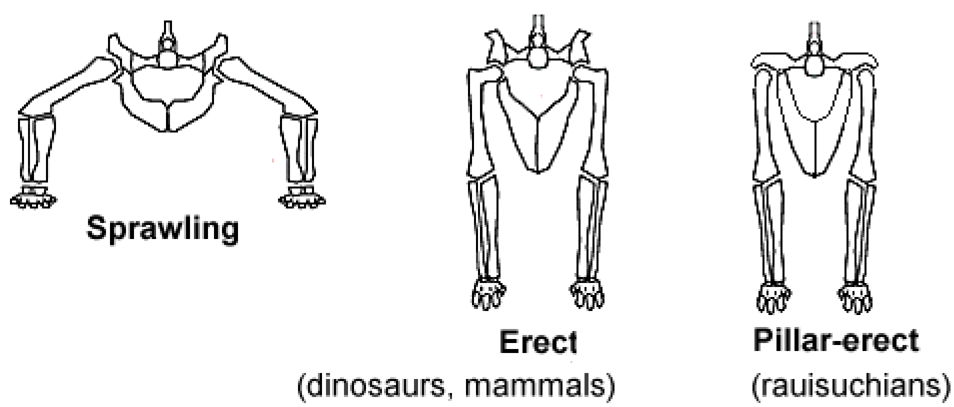
This argument was criticized on several grounds and is no longer taken seriously (the following list of criticisms is far from exhaustive):

- Estimates of dinosaur weights vary widely, and even a small variation can make a large difference to the calculated predator-prey ratio.
- His sample may not have been representative. Bakker obtained his numbers by counting museum specimens, but these have a bias towards rare or especially well-preserved specimens, and do not represent what exists in fossil beds. Even fossil beds may not accurately represent the actual populations, for example smaller and younger animals have less robust bones and are therefore less likely to be preserved.
- There are no published predator-prey ratios for large ectothermic predators, because such predators are very rare and mostly occur only on fairly small

islands. Large ectothermic herbivores are equally rare. So Bakker was forced to compare mammalian predator-prey ratios with those of fish and invertebrate communities, where life expectancies are much shorter and other differences also distort the comparison.

- The concept assumes that predator populations are limited only by the availability of prey. However other factors such as shortage of nesting sites, cannibalism or predation of one predator on another can hold predator populations below the limit imposed by prey biomass, and this would misleadingly reduce the predator-prey ratio. .
- Ecological factors can misleadingly reduce the predator-prey ratio, for example: a predator might prey on only some of the "prey" species present; disease, parasites and starvation might kill some of the prey animals before the predators get a chance to hunt them.
- It is very difficult to state precisely what preys on what. For example the young of herbivores may preyed upon by lizards and snakes while the adults are preyed on by mammals. Conversely the young of many predators live largely on invertrebrates and switch to vertrebrate as they grow.

Posture and gait



Hip joints and limb postures.

Dinosaurs' limbs were erect and held under their bodies, rather than sprawling out to the sides like those of lizards and newts. The evidence for this is the angles of the joint surfaces and the locations of muscle and tendon attachments on the bones. Attempts to represent dinosaurs with sprawling limbs result in creatures with dislocated hips, knees, shoulders and elbows.

Carrier's constraint states that air-breathing vertebrates with two lungs that flex their bodies sideways during locomotion find it difficult to move and breathe at the same time. This severely limits stamina, and forces them to spend more time resting than moving.

Sprawling limbs require sideways flexing during locomotion (except for tortoises and turtles, which are very slow and whose armor keeps their bodies fairly rigid). However, despite Carrier's constraint, sprawling limbs are efficient for creatures that spend most of their time resting on their bellies and only move for a few seconds at a time—because this arrangement minimizes the energy costs of getting up and lying down.

Erect limbs increase the costs of getting up and lying down, but avoid Carrier's constraint. This indicates that dinosaurs were active animals because natural selection would have favored the retention of sprawling limbs if dinosaurs had been sluggish and spent most of their waking time resting. An active lifestyle requires a metabolism that quickly regenerates energy supplies and breaks down waste products which cause fatigue, i.e., it requires a fairly fast metabolism and a considerable degree of homeothermy.

Additionally, an erect posture demands precise balance, the result of a rapidly functioning neuromuscular system. This suggests endothermic metabolism, because an ectothermic animal would be unable to walk or run, and thus to evade predators, when its core temperature was lowered. Other evidence for endothermy includes limb length (many dinosaurs possessed comparatively long limbs) and bipedalism, both found today only in endotherms. Many bipedal dinosaurs possessed gracile leg bones with a short thigh relative to calf length. This is generally an adaptation to frequent sustained running, characteristic of endotherms which, unlike ectotherms, are capable of producing sufficient energy to stave off the onset of anaerobic metabolism in the muscle.

Bakker and Ostrom both pointed out that all dinosaurs had erect hindlimbs and that all quadrupedal dinosaurs except the ceratopsians and ankylosaurs had erect forelimbs; and that among living animals only the endothermic ("warm-blooded") mammals and birds have erect limbs (Ostrom acknowledged that crocodilians' occasional "high walk" was a partial exception). Bakker claimed this was clear evidence of endothermy in dinosaurs, while Ostrom regarded it as persuasive but not conclusive.

A 2009 study supported the hypothesis that endothermy was widespread in at least larger non-avian dinosaurs, and that It was plausibly ancestral for all dinosauriforms, based on the biomechanics of running.

Feathers

Skin impression of the hadrosaur *Edmontosaurus*

There is now no doubt that many theropod dinosaur species had feathers, including *Shuvuuia*, *Sinosauropteryx* and *Dilong* (an early tyrannosaur). These have been interpreted as insulation and therefore evidence of warm-bloodedness.

But impressions of feathers have only been found in coelurosaurs (which includes the ancestors of both birds and tyrannosaurs), so at present feathers give us no information about the metabolisms of the other major dinosaur groups, e.g. coelophysids, ceratosaurs, carnosaurs, sauropods or ornithischians.

In fact the fossilised skin of *Carnotaurus* (an abelisaurid and therefore not a coelurosaur) shows an unfeathered, reptile-like skin with rows of bumps. But an adult *Carnotaurus* weighed about 1 ton, and mammals of this size and larger have either very short hair or naked skins, so perhaps the skin of *Carnotaurus* tells us nothing about whether smaller non-coelurosaurid theropods had feathers.

Skin-impressions of *Pelorosaurus* and other sauropods (dinosaurs with elephantine bodies and long necks) reveal large hexagonal scales, and some sauropods, such as *Saltasaurus*, had bony plates in their skin. The skin of ceratopsians consisted of large polygonal scales, sometimes with scattered circular plates. "Mummified" remains and skin impressions of hadrosaurids reveal pebbly scales. It is unlikely that the ankylosaurids, such as *Euoplocephalus*, had insulation, as most of their surface area was covered in bony knobs and plates. Likewise there is no evidence of insulation in the stegosaurs.

Polar dinosaurs

Dinosaur fossils have been found in regions that were close to the poles at the relevant times, notably in southeastern Australia, Antarctica and the North Slope of Alaska. There is no evidence of major changes in the angle of the Earth's axis, so polar dinosaurs and the rest of these ecosystems would have had to cope with the same extreme variation of day length through the year that occurs at similar latitudes today (up to a full day with no darkness in summer, and a full day with no sunlight in winter).

Studies of fossilized vegetation suggest that the Alaska North Slope had a maximum temperature of 13 °C (55 °F) and a minimum temperature of 2 °C (36 °F) to 8 °C (46 °F) in the last 35 million years of the Cretaceous (slightly cooler than Portland, Oregon but slightly warmer than Calgary, Alberta). Even so, the Alaska North Slope has no fossils of large cold-blooded animals such as lizards and crocodilians, which were common at the same time in Alberta, Montana, and Wyoming. This suggests that at least some non-avian dinosaurs were warm-blooded. It has been proposed that North American polar dinosaurs may have migrated to warmer regions as winter approached, which would allow them to inhabit Alaska during the summers even if they were cold-blooded. But a round trip between there and Montana would probably have used more energy than a cold-blooded land vertebrate produces in a year; in other words the Alaskan dinosaurs would have to be warm-blooded, irrespective of whether they migrated or stayed for the winter. A 2008 paper on dinosaur migration by Phil R. Bell and Eric Snively proposed that most polar dinosaurs, including theropods, sauropods, ankylosaurians, and hypsilophodonts, probably overwintered, although hadrosaurids like *Edmontosaurus* were probably capable of annual 2,600 km (1,600 mile) round trips.

It is more difficult to determine the climate of southeastern Australia when the dinosaur fossil beds were laid down 115 to 105 million years ago, towards the end of the Early Cretaceous: these deposits contain evidence of permafrost, ice wedges, and hummocky ground formed by the movement of subterranean ice, which suggests mean annual temperatures ranged between −6 °C (21.2 °F) and 5 °C (41 °F); oxygen isotope studies of these deposits give a mean annual temperature of 1.5 °C (34.7 °F) to 2.5 °C (36.5 °F). However the diversity of fossil vegetation and the large size of some of fossil trees exceed what is found in such cold environments today, and no-one has explained how such vegetation could have survived in the cold temperatures suggested by the physical indicators – for comparison Fairbanks, Alaska presently has a mean annual temperature of 2.9 °C (37.2 °F). An annual migration from and to southeastern Australia would have been very difficult for fairly small dinosaurs in such as *Leaellynasaura*, a vegetarian about 60 centimetres (2.0 ft) to 90 centimetres (3.0 ft) long, because seaways to the north blocked the passage to warmer latitudes. Bone samples from *Leaellynasaura* and *Timimus*, an ornithomimid about 3.5 metres (11 ft) long and 1.5 metres (4.9 ft) high at the hip, suggested these two dinosaurs had different ways of surviving the cold, dark winters: the *Timimus* sample had lines of arrested growth (LAGs for short; similar to growth rings), and it may have hibernated; but the *Leaellynasaura* sample showed no signs of LAGs, so it may have remained active throughout the winter.

Evidence for behavioral thermoregulation

Some dinosaurs, e.g. *Spinosaurus* and *Ouranosaurus*, had on their backs "sails" supported by spines growing up from the vertebrae. (This was also true, incidentally, for the synapsid *Dimetrodon*.) Such dinosaurs could have used these sails to:

- take in heat by basking with the "sails" at right angles to the sun's rays.
- to lose heat by using the "sails" as radiators while standing in the shade or while facing directly towards or away from the sun.

But these were a very small minority of known dinosaur species. One common interpretation of the plates on stegosaurs' backs is as heat exchangers for thermoregulation, as the plates are filled with blood vessels, which, theoretically, could absorb and dissipate heat.
This might have worked for a stegosaur with large plates, such as *Stegosaurus*, but other stegosaurs, such as *Wuerhosaurus*, *Tuojiangosaurus* and *Kentrosaurus* possessed much smaller plates with a surface area of doubtful value for thermo-regulation. However, the idea of stegosaurian plates as heat exchangers has recently been questioned.

Other evidence

Respiration

Endothermy demands frequent respiration, which can result in water loss. In living birds and mammals, water loss is limited by pulling moisture out of exhaled air with mucous-covered respiratory turbinates, tissue-covered bony sheets in the nasal cavity. Several dinosaurs have olfactory turbinates, used for smell, but none have yet been identified with respiratory turbinates.

Brain size

Because endothermy allows refined neuromuscular control, and because brain matter requires large amounts of energy to sustain, some speculate that increased brain size indicates increased activity and, thus, endothermy. The encephalization quotient (EQ) of dinosaurs, a measure of brain size calculated using brain endocasts, varies on a spectrum from bird-like to reptile-like. Using EQ alone, coelosaurs appear to have been as active as living mammals, while theropods and ornithopods fall somewhere between mammals and reptiles, and other dinosaurs resemble reptiles.

The crocodilian puzzle and early archosaur metabolism

It appears that the earliest dinosaurs had the features that form the basis for arguments for warm-blooded dinosaurs—especially erect limbs. This raises the question "How did dinosaurs become warm-blooded?" The most obvious possible answers are:

- "Their immediate ancestors (archosaurs) were cold-blooded, and dinosaurs began developing warm-bloodedness very early in their evolution." This implies that dinosaurs developed a significant degree of warm-bloodedness in a very short time, possibly less than 20M years. But in mammals' ancestors the evolution of warm-bloodedness seems to have taken much longer, starting with the beginnings of a secondary palate around the beginning of the mid-Permian and going on possibly until the appearance of hair about 164M years ago in the mid Jurassic).
- "Dinosaurs' immediate ancestors (archosaurs) were at least fairly warm-blooded, and dinosaurs evolved further in that direction." This answer raises 2 problems: (**A**) The early evolution of archosaurs is still very poorly understood - large numbers of individuals and species are found from the start of the Triassic but only 2 species are known from the very late Permian (*Archosaurus rossicus* and *Protorosaurus speneri*); (**B**) Crocodilians evolved shortly before dinosaurs and are closely related to them, but are cold-blooded (see below).

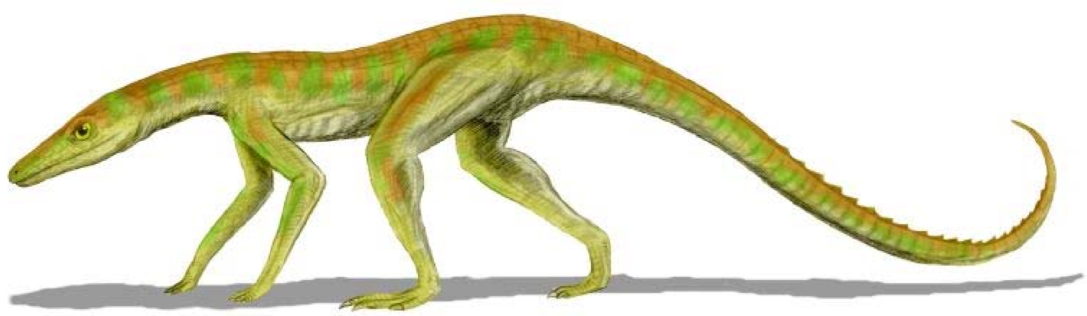
Crocodilians present some puzzles if one regards dinosaurs as active animals with fairly constant body temperatures. Crocodilians evolved shortly before dinosaurs and, second to birds, are dinosaurs' closest living relatives - but modern crocodilians are cold-blooded. This raises some questions:

- If dinosaurs were to a large extent "warm-blooded", when and how fast did warm-bloodedness evolve in their lineage?
- Modern crocodilians are cold-blooded but have several features associated with warm-bloodedness. How did they acquire these features?

Modern crocodilians are cold-blooded but can move with their limbs erect, and have several features normally associated with warm-bloodedness because they improve the animal's oxygen supply:

- 4-chambered hearts. Mammals and birds have four-chambered hearts. Non-crocodilian reptiles have three-chambered hearts, which are less efficient because they allow oxygenated and de-oxygenated blood to mix and therefore send some de-oxygenated blood out to the body instead of to the lungs. Modern crocodilians' hearts are four-chambered, but are smaller relative to body size and run at lower pressure than those of modern mammals and birds. They also have a bypass that makes then functionally three-chambered when under water, conserving oxygen.
- a diaphragm, which aids breathing.
- a secondary palate, which allows the animal to eat and breathe at the same time.
- a hepatic piston mechanism for pumping the lungs. This is different from the lung-pumping mechanisms of mammals and birds but similar to what some researchers claim to have found in some dinosaurs.

So why did natural selection favor these features, which are important for active warm-blooded creatures but of little apparent use to cold-blooded aquatic ambush predators that spend most of their time floating in water or lying on river banks?



Reconstruction of *Terrestrisuchus*, a very slim, leggy Triassic crocodylomorph.

It was suggested in the late 1980s that that crocodilians were originally active, warm-blooded predators and that their archosaur ancestors were warm-blooded. More recently, developmental studies indicate that crocodilian embryos develop fully four-chambered hearts first—then develop the modifications that make their hearts function as three-chambered under water. Using the principle that ontogeny recapitulates phylogeny, the researchers concluded that the original crocodilians had fully 4-chambered hearts and were therefore warm-blooded and that later crocodilians developed the bypass as they reverted to being cold-blooded aquatic ambush predators.

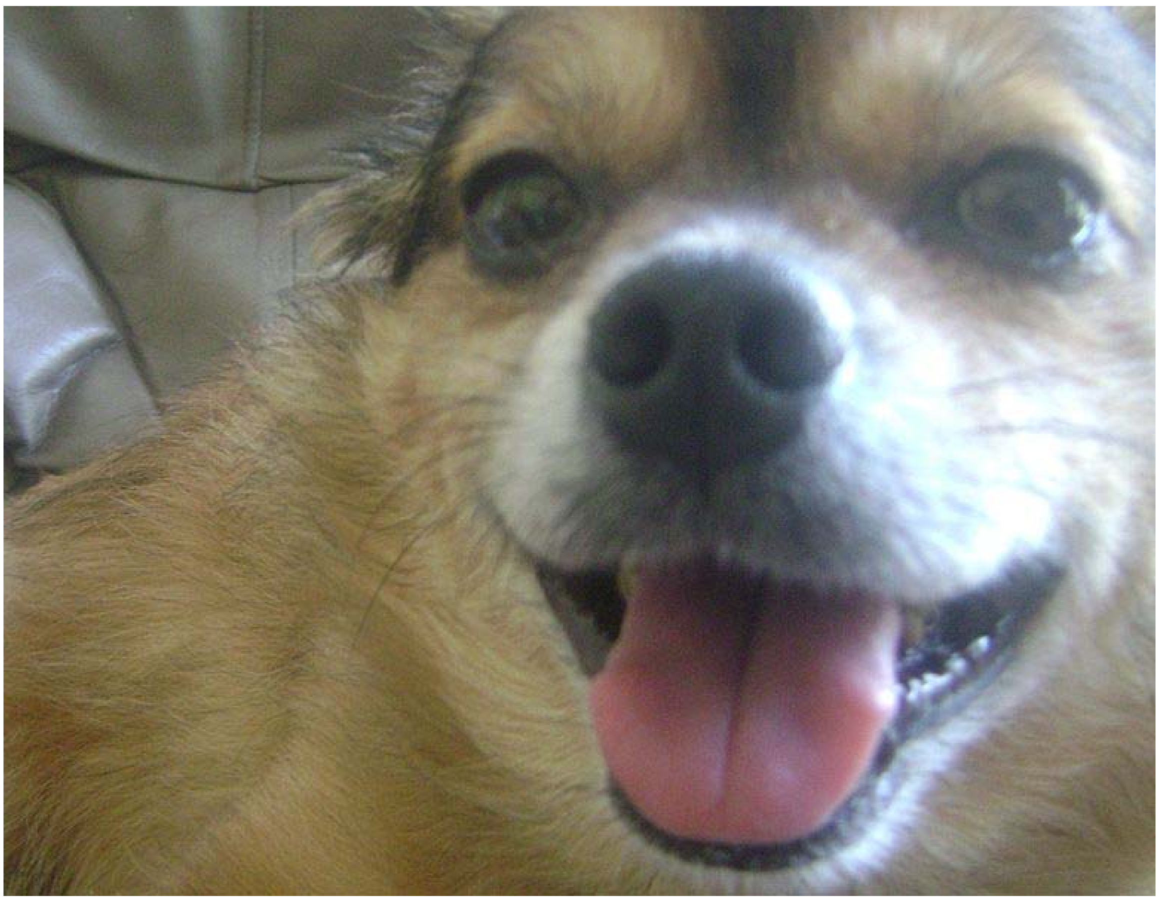
More recent research on archosaur bone structures and their implications for growth rates also suggests that early archosaurs had fairly high metabolic rates and that the Triassic ancestors of crocodilians dropped back to more typically "reptilian" metabolic rates.

If this view is correct, the development of warm-bloodedness in archosaurs (reaching its peak in dinosaurs) and in mammals would have taken more similar amounts of time. It would also be consistent with the fossil evidence:

- The earliest crocodilians, e.g. *Terrestrisuchus*, were slim, leggy terrestrial predators.
- Erect limbs appeared quite early in archosaurs' evolution, and those of rauisuchians are very poorly adapted for any other posture.

Chapter 4

Thermoregulation



A dog panting is an example of thermoregulation.

Thermoregulation is the ability of an organism to keep its body temperature within certain boundaries, even when the surrounding temperature is very different. This process is one aspect of homeostasis: a dynamic state of stability between an animal's internal environment and its *external* environment (the study of such processes in zoology has been called ecophysiology or physiological ecology). If the body is unable to maintain a normal temperature and it increases significantly above normal, a condition known as hyperthermia occurs. This occurs when the body is exposed to constant temperatures of approximately 55° C, any prolonged exposure (longer than a few hours) at this temperature and up to around 70° C death is almost inevitable. The opposite condition, when body temperature decreases below normal levels, is known as hypothermia.

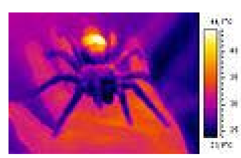
Whereas an organism that *thermoregulates* is one that keeps its core body temperature within certain limits, a **thermoconformer** is subject to changes in body temperature according to changes in the temperature outside of its body. It was not until the introduction of thermometers that any exact data on the temperature of animals could be obtained. It was then found that local differences were present, since heat production and heat loss vary considerably in different parts of the body, although the circulation of the blood tends to bring about a mean temperature of the internal parts. Hence it is important to identify the parts of the body that most closely reflect the temperature of the internal organs. Also, for such results to be comparable, the measurements must be conducted under comparable conditions. The rectum has traditionally been considered to reflect most accurately the temperature of internal parts, or in some cases of sex or species, the vagina, uterus or bladder.

Occasionally the temperature of the urine as it leaves the urethra may be of use. More often the temperature is taken in the mouth, axilla, ear or groin.

Classification of animals by thermal characteristics

Thermoregulation in animals

Ectothermy · Endothermy



Poikilothermy · Heterothermy · Homeothermy (Gigantothermy)

Kleptothermy · Bradymetabolism · Tachymetabolism

Endothermy versus Ectothermy

Organisms can generally be divided into two types of thermoregulators, endotherms and ectotherms. Endotherms create most of their heat via metabolic processes, and are colloquially referred to as warm-blooded. Ectotherms temperature comes mostly from the environment.

Ectotherms

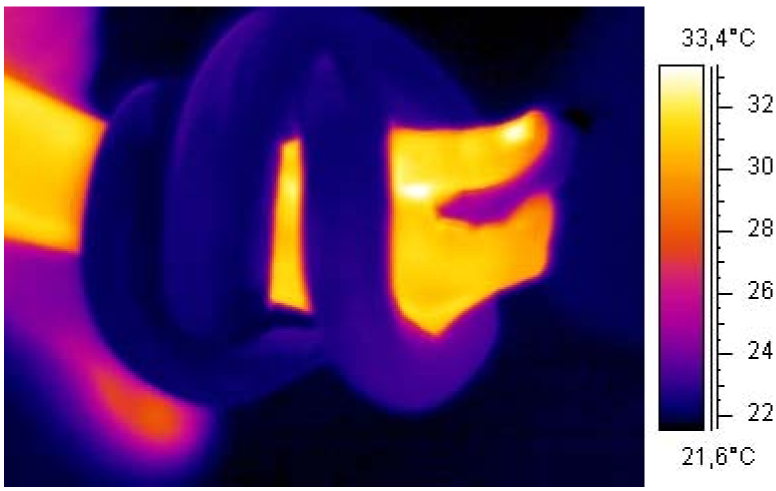
Ectothermic cooling

Seeking shade is one method of cooling. Here Sooty Tern chicks are using a Black-footed Albatross chick for shade.

- Vaporization:
    - Getting wet in a river, lake or sea.
- Convection:
    - Climbing to lower ground from trees, into valleys, burrows, etc.
    - Entering a cold water or air current.
    - Building a nest that allows natural or generated air/water flow for cooling.
- Conduction:
    - Lying on cold ground.
    - Staying wet in a river, lake or sea.
    - Covering in cool mud.
- Radiation:
    - Finding shade.
    - Entering a burrow shaped for radiating heat (Black-box effect).
    - Expanding folds of skin.
    - Exposing wing surfaces.

Ectothermic heating (or minimizing heat loss)

- Convection:
    - Climbing to higher ground up trees, ridges, rocks.
    - Entering a warm water or air current.
    - Building an insulated nest or burrow.
- Conduction:
    - Lie on hot rock.
- Radiation:
    - Lie in sun.
    - Fold skin to reduce exposure.
    - Conceal wing surfaces.
- Insulation
    - Change shape to alter surface/volume ratio
    - Inflate the body



Thermographic image of a snake around an arm

To cope with low temperatures, some fish have developed the ability to remain functional even when the water temperature is below freezing; some use natural antifreeze or antifreeze proteins to resist ice crystal formation in their tissues. Amphibians and reptiles cope with heat loss by evaporative cooling and behavioral adaptations.

Endothermy

An endotherm is an animal that regulates its own body temperature, typically by keeping it a constant level. To regulate body temperature, an organism may need to prevent heat gains in arid environments. Evaporation of water, either across respiratory surfaces or across the skin in those animals possessing sweat glands, helps in cooling body temperature to within the organism's tolerance range. Animals with a body covered by fur have limited ability to sweat, relying heavily on **panting** to increase evaporation of water across the moist surfaces of the lungs and the tongue and mouth. Birds also avoid overheating by **gular fluttering**, flapping the wings near the gular (throat) skin, similar to panting in mammals, since their thin skin has no sweat glands. Down feathers trap warm air acting as excellent insulators just as hair in mammals acts as a good insulator. Mammalian skin is much thicker than that of birds and often has a continuous layer of insulating fat beneath the dermis — in marine mammals such as whales this is called blubber. Dense coats found in desert endotherms also aid in preventing heat gain.

A cold weather strategy is to temporarily decrease metabolic rate, decreasing the temperature difference between the animal and the air and thereby minimizing heat loss. Furthermore, having a lower metabolic rate is less energetically expensive. Many animals survive cold frosty nights through torpor, a short-term temporary drop in body temperature. Organisms when presented with the problem of regulating body temperature have not only behavioural, physiological and structural adaptations, but also a feedback system to trigger these adaptations to regulate temperature accordingly. The main features of this system are *stimulus, receptor, modulator, effector* and then the feedback of the newly adjusted temperature to the *stimulus.* This cyclical process aids in homeostasis.

Homeothermy versus Poikilothermy

Homeothermy and poikilothermy refer to how stable an organism's temperature is. Most endothermic organisms are homeothermic, like mammals. However, animals with facultative endothermy are often pokilothermic, meaning their temperature can vary considerably. Similarly, most fish are ectotherms, as all of their heat comes from the surrounding water. However, most are homeotherms because their temperature is very stable.

Thermoregulation in vertebrates

By numerous observations upon humans and other animals, John Hunter showed that the essential difference between the so-called warm-blooded and cold-blooded animals lies in observed constancy of the temperature of the former, and the observed variability of the temperature of the latter. Almost all birds and mammals have a high temperature almost constant and independent of that of the surrounding air (homeothermy). Almost all other animals display a variation of body temperature, dependent on their surroundings (poikilothermy).

Certain mammals are exceptions to this rule, being warm-blooded during the summer or daytime, but cold-blooded during the winter when they hibernate or at night during sleep. J. O. Wakelin Barratt has demonstrated that under certain pathological conditions, a warm-blooded (homeothermic) animal may become temporarily cold-blooded (poikilothermic). He has shown conclusively that this condition exists in rabbits suffering from rabies during the last period of their life, the rectal temperature being then within a few degrees of the room temperature and varying with it. He explains this condition by the assumption that the nervous mechanism of heat regulation has become paralysed. The respiration and heart-rate being also retarded during this period, the resemblance to the condition of hibernation is considerable. Again, Sutherland Simpson has shown that during deep anaesthesia a warm-blooded animal tends to take the same temperature as that of its environment. He demonstrated that when a monkey is kept deeply anaesthetized with ether and is placed in a cold chamber, its temperature gradually falls, and that when it has reached a sufficiently low point (about 25 °C in the monkey), the employment of an anaesthetic is no longer necessary, the animal then being insensible to pain and incapable of being roused by any form of stimulus; it is, in fact, narcotised by cold, and is in a state of what may be called "artificial hibernation." Once again this is explained by the fact that the heat-regulating mechanism has been interfered with. Similar results have been obtained from experiments on cats.

Brain control

Thermoregulation in both ectotherms and endotherms is controlled mainly by the preoptic area of the anterior hypothalamus. Such homeostatic control is separate from the sensation of temperature.

Thermoregulation in birds and mammals

Kangaroo licking its arms to cool down on a very hot day

In cold environments, birds and mammals employ the following adaptations and strategies to minimize heat loss:

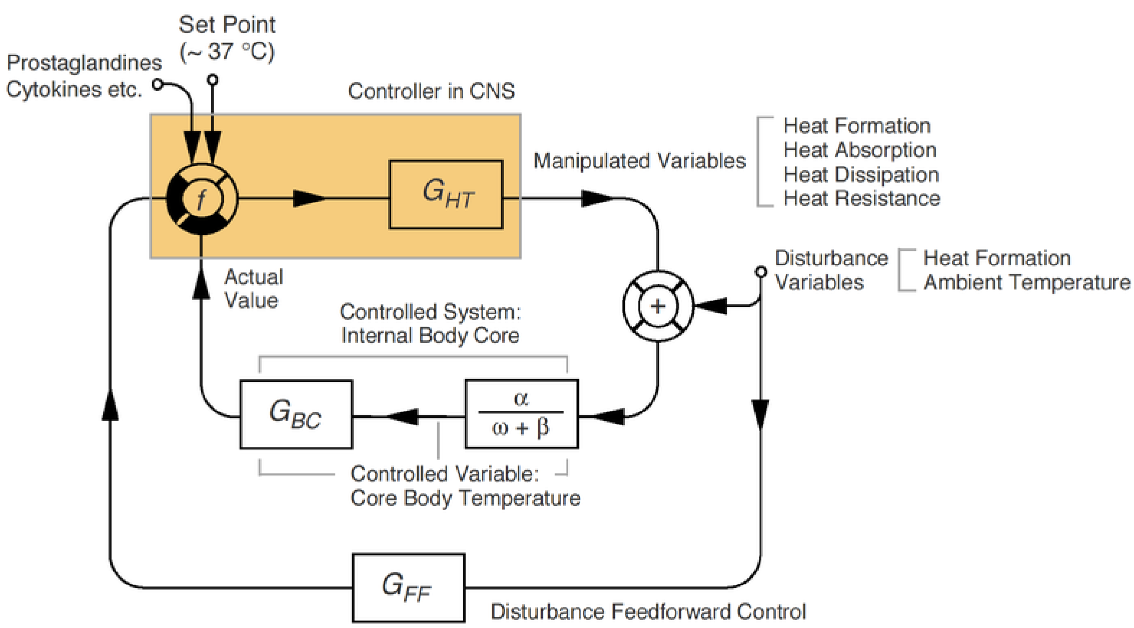
1. using small smooth muscles (erector pili in mammals) which are attached to feather or hair shafts; this non-shivering thermogenesis distorts the surface of the skin as the feather/hair shaft is made more erect (called goose bumps or pimples)
2. increasing body size to more easily maintain core body temperature (warm-blooded animals in cold climates tend to be larger than similar species in warmer climates

3. having the ability to store energy as fat for metabolism
4. have shortened extremities
5. have countercurrent blood flow in extremities - this is where the warm arterial blood travelling to the limb passes the cooler venous blood from the limb and heat is exchanged warming the venous blood and cooling the arterial (e.g. Arctic Wolf or penguins)

In warm environments, birds and mammals employ the following adaptations and strategies to maximize heat loss:

1. behavioural adaptations like living in burrows during the day and being nocturnal
2. evaporative cooling by perspiration and panting
3. storing fat reserves in one place (e.g. camel's hump) to avoid its insulating effect
4. elongated, often vascularized extremities to conduct body heat to the air

Thermoregulation in humans



Simplified information processing structure of human thermoregulation.

As in other mammals, thermoregulation is an important aspect of human homeostasis. Most body heat is generated in the deep organs, especially the liver, brain, and heart, and in contraction of skeletal muscles. Humans have been able to adapt to a great diversity of climates, including hot humid and hot arid. High temperatures pose serious stresses for the human body, placing it in great danger of injury or even death. For humans, adaptation to varying climatic conditions includes both physiological mechanisms as a byproduct of evolution, and the conscious development of cultural adaptations.

There are four avenues of heat loss: convection, conduction, radiation, and evaporation. If skin temperature is greater than that of the surroundings, the body can lose heat by radiation and conduction. But if the temperature of the surroundings is greater than that of the skin, the body actually *gains* heat by radiation and conduction. In such conditions, the only means by which the body can rid itself of heat is by evaporation. So when the surrounding temperature is higher than the skin temperature, anything that prevents adequate evaporation will cause the internal body temperature to rise. During sports activities, evaporation becomes the main avenue of heat loss. Humidity affects thermoregulation by limiting sweat evaporation and thus heat loss.

The skin assists in homeostasis (keeping different aspects of the body constant e.g. temperature). It does this by reacting differently to hot and cold conditions so that the inner body temperature remains more or less constant. Vasodilation and sweating are the primary modes by which humans attempt to lose excess body heat. The brain creates much heat through the countless reactions which occur. Even the process of thought creates heat. The head has a complex system of blood vessels, which keeps the brain from overheating by bringing blood to the thin skin on the head, allowing heat to escape. The effectiveness of these methods is influenced by the character of the climate and the degree to which the individual is acclimatized.

In hot conditions

1. Eccrine sweat glands under the skin secrete sweat (a fluid containing mostly water with some dissolved ions) which travels up the sweat duct, through the sweat pore and onto the surface of the skin. This causes heat loss via evaporative cooling; however, a lot of essential water is lost.
2. The hairs on the skin lie flat, preventing heat from being trapped by the layer of still air between the hairs. This is caused by tiny muscles under the surface of the skin called Arrector pili muscles relaxing so that their attached hair follicles are not erect. These flat hairs increase the flow of air next to the skin increasing heat loss by convection. When environmental temperature is above core body temperature, sweating is the only physiological way for humans to lose heat.
3. Arterioles Vasodilation occurs, this is the process of relaxation of smooth muscle in arteriole walls allowing increased blood flow through the artery. This redirects blood into the superficial capillaries in the skin increasing heat loss by convection and conduction.

Note: Most animals can't sweat efficiently. Cats and dogs have sweat glands only on the pads of their feet. Horses and humans are two of the few animals capable of sweating. Many animals pant rather than sweat because the lungs have a large surface area and are highly vascularised. Air is inhaled, cooling the surface of the lungs and is then exhaled losing heat and some water vapour.

Thermoregulation in hot and humid conditions

In general, humans appear physiologically well adapted to hot dry conditions. However, effective thermoregulation is reduced in hot, humid environments such as the Red Sea and Persian Gulf (where moderately hot summer temperatures are accompanied by unusually high vapor pressures), tropical environments, and deep mines where the atmosphere can be water-saturated. In hot-humid conditions, clothing can impede efficient evaporation. In such environments, it helps to wear light clothing such as cotton, that is pervious to sweat but impervious to radiant heat from the sun. This minimizes the gaining of radiant heat, while allowing as much evaporation to occur as the environment will allow. Clothing such as plastic fabrics that are impermeable to sweat and thus do not facilitate heat loss through evaporation, can actually contribute to heat stress.

In cold conditions

1. Sweat stops being produced.
2. The minute muscles under the surface of the skin called erector pili muscles (attached to an individual hair follicle) contract (piloerection), lifting the hair follicle upright. This makes the hairs stand on end which acts as an insulating layer, trapping heat. This is what also causes goose bumps since humans don't have very much hair and the contracted muscles can easily be seen.
3. Arterioles carrying blood to superficial capillaries under the surface of the skin can shrink (constrict), thereby rerouting blood away from the skin and towards the warmer core of the body. This prevents blood from losing heat to the surroundings and also prevents the core temperature dropping further. This process is called vasoconstriction. It is impossible to prevent all heat loss from the blood, only to reduce it. In extremely cold conditions excessive vasoconstriction leads to numbness and pale skin. Frostbite only occurs when water within the cells begins to freeze, this destroys the cell causing damage.
4. Muscles can also receive messages from the thermo-regulatory center of the brain (the hypothalamus) to cause shivering. This increases heat production as respiration is an exothermic reaction in muscle cells. Shivering is more effective than exercise at producing heat because the animal remains still. This means that less heat is lost to the environment via convection. There are two types of shivering: low intensity and high intensity. During low intensity shivering animals shiver constantly at a low level for months during cold conditions. During high intensity shivering animals shiver violently for a relatively short time. Both processes consume energy although high intensity shivering uses glucose as a fuel source and low intensity tends to use fats. This is a primary reason why animals store up food in the winter.
5. Mitochondria can convert fat directly into heat energy, increasing the temperature of all cells in the body. Brown fat is specialized for this purpose, and is abundant in newborns and animals that hibernate.

The process explained above, in which the skin regulates body temperature is a part of thermoregulation. This is one aspect of homeostasis-the process by which the body regulates itself to keep internal conditions constant.

Diseases and syndromes relating to thermoregulation

- Hypothermia
- Hyperthermia
- Heat stroke
- Raynaud's phenomenon (Raynaud's disease)
- Induced hypothermia
- Erythromelalgia (hyperthermia)

Thermoregulation in plants

Thermogenesis occurs in the flowers of many plants in the Araceae family as well as in cycad cones. In addition, some plants in the Alum family - such as the Eastern Skunk Cabbage, the Philodendron (*Philodendron selloum*), and the Sacred lotus (*Nelumbo nucifera*) are able to thermoregulate themselves, remaining on average 20 °C (36 °F) above air temperature while flowering. Heat is produced by breaking down the starch that was stored in their roots, which requires the consumption of oxygen at a rate approaching that of a flying hummingbird.

One possible explanation for plant thermoregulation is to provide protection against cold temperature. For example, the skunk cabbage is not frost-resistant, yet it begins to grow and flower when there is still snow on the ground. Another theory is that thermogenicity helps attract pollinators, which is borne out by observations that heat production is accompanied by the arrival of beetles or flies.

Behavioural temperature regulation

Animals other than humans regulate and maintain their body temperature with physiological adjustments and behavior. Desert lizards are ectotherms and so unable to metabolically control their temperature but can do this by altering their location. They may do this by in the morning only raising their head from its burrow and then exposing their entire body. By basking in the sun, the lizard absorbs solar heat. It may also absorb heat by conduction from heated rocks that have stored radiant solar energy. To lower their temperature, lizards may seek cooler objects with which to contact, find shade or return to their burrow. They also go to their burrows to avoid cooling when the sun goes down or the temperature falls.

Animals also engage in kleptothermy in which they share or even steal each other's body warmth. In endotherms such as bats and birds (such as the mousebird and emperor penguin) it allows the sharing of body heat (particularly amongst juveniles). This allows the individuals to increase their thermal inertia (as with gigantothermy) and so reduce heat loss. Some ectotherms share burrows of ectotherms. Other animals exploit termite mounds.

Some animals living in cold environments maintain their body temperature by preventing heat loss. Their fur grows more densely to increase the amount of insulation. Some animals are regionally heterothermic and are able to allow their less insulated extremities to cool to temperatures much lower than their core temperature—nearly to 0 °C. This minimizes heat loss through less insulated body parts, like the legs, feet (or hooves), and nose.

An ostrich can keep its body temperature very constant, even though it can be very hot during the day and cold at night.

Hibernation, estivation, and daily torpor

To cope with limited food resources and low temperatures, some mammals hibernate in underground burrows. In order to remain in "stasis" for long periods, these animals must build up brown fat reserves and be capable of slowing all body functions. True hibernators (e.g. groundhogs) keep their body temperature down throughout their hibernation while the core temperature of false hibernators (e.g. bears) varies with them sometimes emerging from their dens for brief periods. Some bats are true hibernators which rely upon a rapid, non-shivering thermogenesis of their brown fat deposit to bring them out of hibernation.

Estivation occurs in summer (like siestas) and allows some mammals to survive periods of high temperature and little water (e.g. turtles burrow in pond mud).

Daily torpor occurs in small endotherms like bats and humming birds which temporarily reduce their high metabolic rates to conserve energy.

Variations in the temperature of human beings and some animals

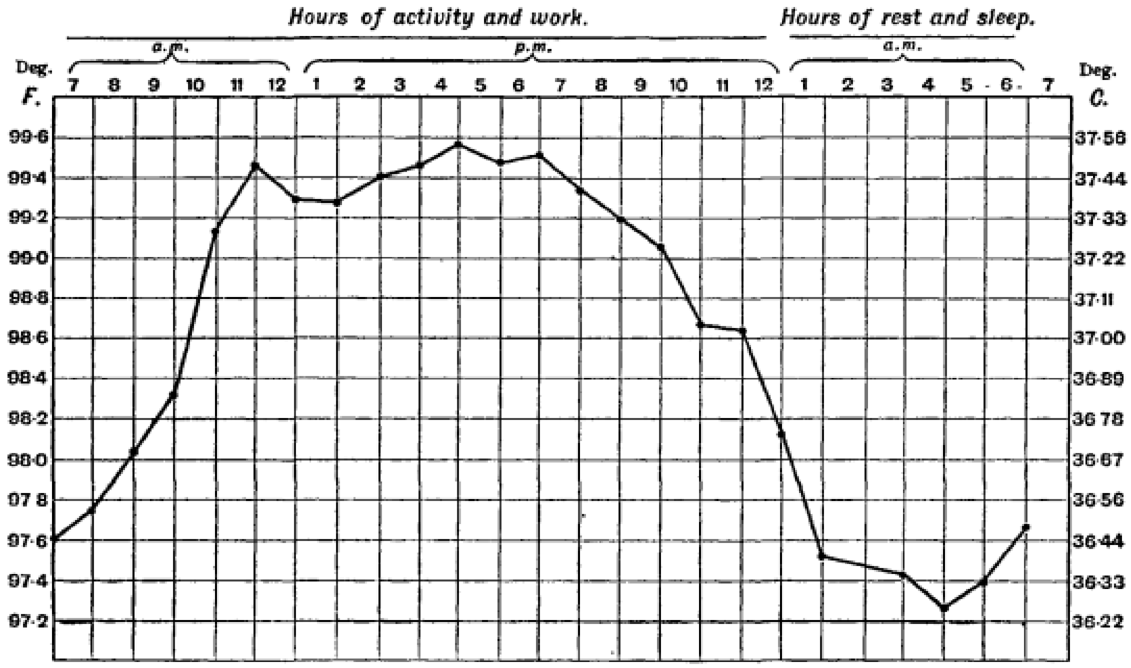


Chart showing diurnal variation in body temperature, ranging from about 37.5 °C from 10 a.m. to 6 p.m., and falling to about 36.3 °C from 2 a.m. to 6 a.m.

Normal human temperature

Previously, average oral temperature for healthy adults had been considered 37.0 °C (98.6 °F), while normal ranges are 36.1 °C (97.0 °F) to 37.8 °C (100.0 °F). In Poland and Russia, the temperature had been measured axillary. 36.6 °C was considered "ideal" temperature in these countries, while normal ranges are 36 °C to 36.9 °C.

Recent studies suggest that the average temperature for healthy adults is 98.2 °F or 36.8 °C (same result in three different studies). Variations (one standard deviation) from three other studies are:

- 36.4 - 37.1 °C (97.5 - 98.8 °F)
- 36.3 - 37.1 °C (97.3 - 98.8 °F) for males, 36.5 - 37.3 °C (97.7 - 99.1 °F) for females
- 36.6 - 37.3 °C (97.9 - 99.1 °F)

Variations from thermometer placement

Temperature varies according to thermometer placement, with rectal temperature being 0.3-0.6 °C (0.5-1 °F) higher than oral temperature, while axillary temperature is 0.3-0.6 °C (0.5-1 °F) lower than oral temperature. The average difference between oral and axillary temperatures of Indian children aged 6–12 was found to be only 0.1 °C (standard deviation 0.2 °C), and the mean difference in Maltese children aged 4–14 between oral and axillary temperature was 0.56 °C, while the mean difference between rectal and axillary temperature for children under 4 years old was 0.38 °C.

Variations associated with development

Of the lower warm-blooded animals, there are some that appear to be cold-blooded at birth. Kittens, rabbits and puppies, if removed from their surroundings shortly after birth, lose their body heat until their temperature has fallen to within a few degrees of that of the surrounding air. But such animals are at birth blind, helpless and in some cases furless. Animals who are born when in a condition of greater development can maintain a fairly constant body temperature. In strong, healthy human infants a day or two old the temperature rises slightly when removed, but in that of weakly, ill-developed children it either remains stationary or falls. The cause of the variable temperature in infants and young immature animals is the imperfect development of the nervous regulating mechanism.

The average temperature falls slightly from infancy to puberty and again from puberty to middle age, but after that stage is passed the temperature begins to rise again, and by about the eightieth year is as high as in infancy.

Variations due to circadian rhythms

In humans, a diurnal variation has been observed dependent on the periods of rest and activity, lowest at 11 p.m. to 3 a.m. and peaking at 10 a.m. to 6 p.m. Monkeys also have a well-marked and regular diurnal variation of body temperature which follows periods of rest and activity, and is not dependent on the incidence of day and night; nocturnal monkeys reach their highest body temperature at night and lowest during the day. Sutherland Simpson and J.J. Galbraith observed that all nocturnal animals and birds - whose periods of rest and activity are naturally reversed through habit and not from outside interference - experience their highest temperature during the natural period of activity (night) and lowest during the period of rest (day). Those diurnal temperatures can be reversed by reversing their daily routine.

The temperature curve of diurnal birds is essentially similar to that of man and other homoeothermal animals, except that the maximum occurs earlier in the afternoon and the minimum earlier in the morning. Also that the curves obtained from rabbits, guinea pigs and dogs were quite similar to those from man. These observations indicate that body temperature is partially regulated by circadian rhythms.

Variations due to women's menstrual cycles

During the follicular phase (which lasts from the first day of menstruation until the day of ovulation), the average basal body temperature in women ranges from 36.45 to 36.7 °C (97.6 to 98.1 °F). Within 24 hours of ovulation, women experience an elevation of 0.15 -

0.45 °C (0.2 - 0.9 °F) due to the increased metabolic rate caused by sharply elevated levels of progesterone. The basal body temperature ranges between 36.7 - 37.3°C (98.1 - 99.2°F) throughout the luteal phase, and drops down to pre-ovulatory levels within a few days of menstruation. Women can chart this phenomenon to determine whether and when they are ovulating, so as to aid conception or contraception.

Variations due to fever

Fever is a regulated elevation of the set point of core temperature in the hypothalamus, caused by circulating pyrogens produced by the immune system. To the subject, a rise in core temperature due to fever may result in feeling cold in an environment where people without fever do not.

Variations due to biofeedback

A group of monks known as the Tummo are known to practice biofeedback meditation techniques that allow them to raise their body temperatures substantially.

Variations due to other factors

In Simpson's & Galbraith's work, the mean temperature of the female was higher than that of the male in all the species examined whose sex had been determined.

Meals sometimes cause a slight elevation, sometimes a slight depression—alcohol seems always to produce a fall. Exercise and variations of external temperature within ordinary limits cause very slight change, as there are many compensating influences at work, which are discussed later. The core temperature of those living in the tropics is within a similar range to those dwelling in the Arctic regions.

Low body temperature increases lifespan

It was long theorised that low body temperature may prolong life. On November 2006, a team of scientists from the Scripps Research Institute reported that transgenic mice which had body temperature 0.3-0.5 C lower than normal mice (due to overexpressing the uncoupling protein 2 in hypocretin neurons (Hcrt-UCP2), which elevated hypothalamic temperature, thus forcing the hypothalamus to lower body temperature) indeed lived longer than normal mice. The lifespan was 12% longer for males and 20% longer for females. Mice were allowed to eat as much as they wanted. The effects of such a genetic change in body temperature on longevity is harder to study in humans. The UCP2 genetic alleles seen in humans so far are associated with obesity

Limits compatible with life

There are limits both of heat and cold that a warm-blooded animal can bear, and other far wider limits that a cold-blooded animal may endure and yet live. The effect of too extreme a cold is to decrease metabolism, and hence to lessen the production of heat.

Both catabolic and anabolic pathways share in this metabolic depression, and, though less energy is used up, still less energy is generated. The effects of this diminished metabolism become telling on the central nervous system first, especially the brain and those parts concerning consciousness; both heart rate and respiration rate decrease; judgment becomes impaired as drowsiness supervenes, becoming steadily deeper until the individual loses consciousness; without medical intervention, death by hypothermia quickly follows. Occasionally, however, convulsions may set in towards the end, and death is caused by asphyxia.

In experiments on cats performed by Sutherland Simpson and Percy T. Herring, the animals were unable to survive when rectal temperature fell below 16°C. At this low temperature respiration became increasingly feeble; heart-impulse usually continued after respiration had ceased, the beats becoming very irregular, apparently ceasing, then beginning again. Death appeared to be mainly due to asphyxia, and the only certain sign that it had taken place was the loss of knee jerks.

Conversely, too high a temperature speeds up the metabolism of different tissues to such a rate that their metabolic capital is soon exhausted. Blood that is too warm produces dyspnea by exhausting the metabolic capital of the respiratory centre; heart rate is increased; the beats then become arrhythmic and eventually cease. The central nervous system is also profoundly affected by hyperthermia and delirium and convulsions may set in. Consciousness may also be lost, propelling the person into a comatose condition. These changes can sometimes also be observed in patients suffering from an acute fever. The lower limit of temperature that humans can endure depends on many factors, but no one can survive a temperature of 45 °C (113 °F) or above for very long. Mammalian muscle becomes rigid with heat rigor at about 50°C, with the sudden rigidity of the whole body rendering life impossible.

H.M. Vernon has done work on the death temperature and paralysis temperature (temperature of heat rigor) of various animals. He found that species of the same class showed very similar temperature values, those from the Amphibia examined being 38.5°C, Fish 39°C, Reptilia 45°C, and various Molluscs 46°C. Also, in the case of Pelagic animals, he showed a relation between death temperature and the quantity of solid constituents of the body. In higher animals, however, his experiments tend to show that there is greater variation in both the chemical and physical characteristics of the protoplasm, and hence greater variation in the extreme temperature compatible with life.

Chapter 5

Poikilotherm and Torpor

Poikilotherm

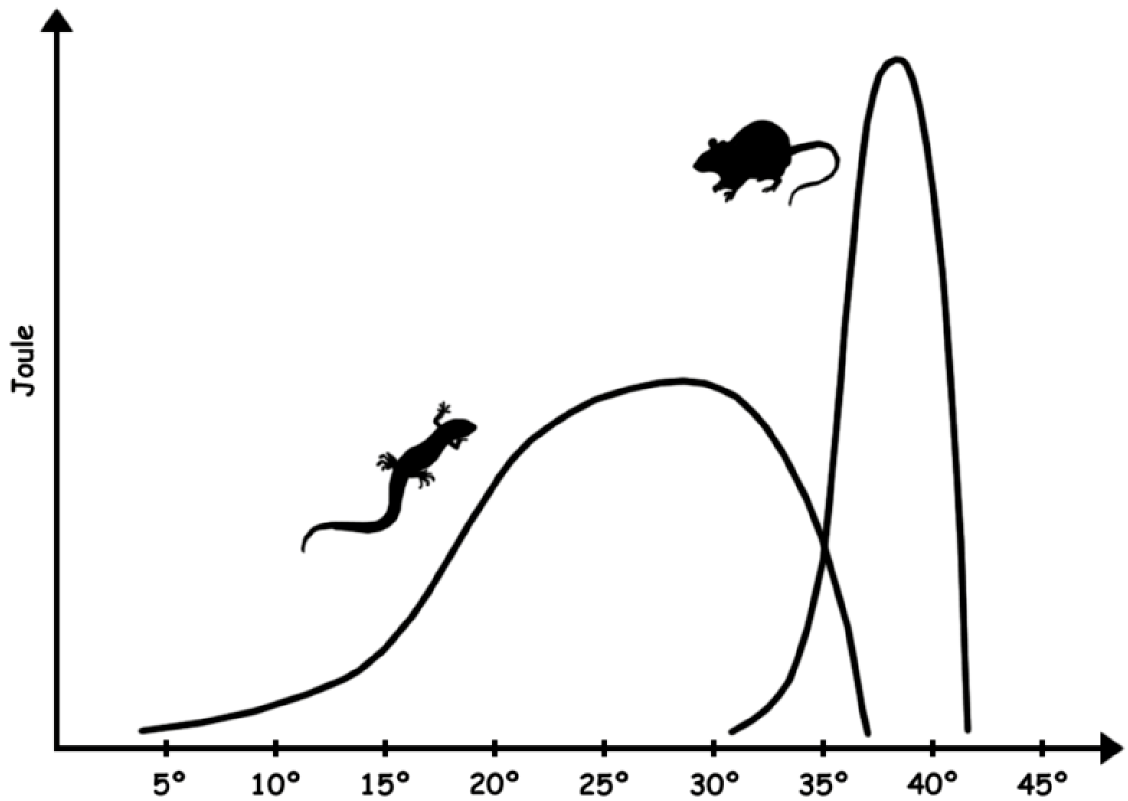
Common frog is a poikilotherm and needs to be able to function over a wide range of body core temperatures.

A **poikilotherm** is a organism whose internal temperature varies considerably. It is the opposite of a homeotherm, organisms which maintain thermal homeostasis. Usually the variation is a consequence of the ambient environmental temperature. Many terrestrial ectotherms are poikilothermic. The term is used as a more exact description of the vernacular "cold-blooded", which can also refer to organisms which are ectothermic (primarily obtain heat from their environment). Poikilothermic animals include types of vertebrate animals, specifically fish, amphibians, and reptiles, as well as a host of invertebrate animals.

Etymology

The term derives from Ancient Greek, *poikilos* (*ποικίλος*), meaning "varied"; and *thermos* (*θερμός*), meaning "heat".

Physiology



Sustained energy output (Joule) of a poikilotherme (a lizard) and a homeotherm (a mouse) as a function of core body temperature. The homeotherm has a much higher output, but can only function over a very narrow range of body temperatures.

For an important chemical reaction, poikilotherms may have four to ten enzyme systems that operate at different temperatures. As a result, poikilotherms often have larger, more complex genomes than homeotherms in the same ecological niche. Frogs are a notable example of this effect.

Because their metabolism is variable and generally below that of homeothermic animals, sustained high-energy activities like powered flight in large animals or maintaining a large brain is generally beyond poikilotherm animals. This favoures e.g. sit-and-wait hunting strategy over chasing prey for larger animals with high movement cost. As they do not use their metabolisms to heat or cool themselves, total energy requirement over time is low. For the same body weight, poikilotherms need half to 1/10 of the energy of homeotherms.

Adaptations in poikilotherms

- Some adaptations are behavioral. Lizards and snakes bask in the sun in the early morning and late evening, and seek shelter around noon.
- Termite mounds are usually oriented in a north-south direction so that they absorb as much heat as possible around dawn and dusk and minimise heat absorption around noon.
- Tuna are able to warm their entire bodies through a heat exchange mechanism called the rete mirabile, which helps keep heat inside the body, and minimises the loss of heat through the gills. They also have their swimming muscles near the center of their bodies instead of near the surface, which minimises heat loss.
- Gigantothermy low ratio of surface area to volume is using a low ratio of surface area to volume minimises heat loss, such as in sea turtles.

Ecological niches

It is comparatively easy for a poikilotherm to accumulate enough energy to reproduce. Poikilotherms in the same ecological niche often have much shorter generations than homeotherms: weeks rather than years.

This difference in energy requirement also means that a given niche of a given ecology can support a greater density of poikilothermic animals as homeothermic animals. This is reflected in e.g. the predator-prey ratio which is usually higher in poikilothermic fauna compared to homeothermic ones. However, in a given niche, homeotherms often drive poikilothermic competitors to extinction because homeotherms can gather food for a greater fraction of each day.

Poikilotherms succeed in some niches, such as islands, or distinct bioregions (such as the small bioregions of the Amazon basin). These often do not have enough food to support a viable breeding population of homeothermic animals. In these niches, poikilotherms such as large lizards, crabs and frogs subplant homeotherms such as birds and mammals.

In medicine

In medicine, loss of normal thermoregulation in humans is referred to as "poikilothermia". This is usually seen with sedative and hypnotic drugs. For example, barbiturates, ethanol, and chloral hydrate may precipitate this effect.

Torpor

Daily torpor, sometimes called **temporary hibernation** is a (usually short-term) state of decreased physiological activity in an animal, usually characterized by a reduced body temperature and rate of metabolism. Animals that go through torpor include birds (notably Cypselomorphae, even tiny hummingbirds) and some mammals such as mice and bats. During the active part of their day, animals that undergo daily torpor maintain normal body temperature and activity levels, but their temperature drops during a portion of the day (usually night) to conserve energy. Torpor is often used to help animals survive during periods of colder temperatures, as it allows the organism to save the amount of energy that would normally be used to maintain a high body temperature.

Torpor may extend for a longer period of time. Some animals such as groundhogs, ground squirrels and jumping mice enter this intensely deep state of hibernation for the duration of the winter. Lungfish switch to the torpor state if their pool dries out; tenrecs switch to the torpor state if food is scarce during the summer in Madagascar. This prolonged and deep torpor during summer months is known as aestivation. Black bears, although often thought of as hibernators, do not truly enter a state of torpor: while their body temperatures lower along with respiration and heartbeat, they do not decrease as significantly as most animals in a state of torpor, and bears are still responsive. Still, there is much debate about this within the scientific community: some feel that black bears are true hibernators that employ a more advanced form of hibernation.

Bats, especially species in temperate regions suffering harsh winters, rely upon torpor to survive. Lowering the body temperature to the ambient temperature allows them to enter torpor for prolonged periods at a lower metabolic cost. Oxygen consumption, heart rate and breathing rates are all lowered significantly meaning less energy is required to survive. Torpor is important in daily cycles to conserve energy as well as prolonged torpor, or hibernation. Pre-hibernation feeding builds up layers of fat which are used as the energy source during torpor. Arousal from torpor in bats is facultative, not obligate, but comes at a high energy cost, meaning awakening must be for a good reason.

Other uses of the word

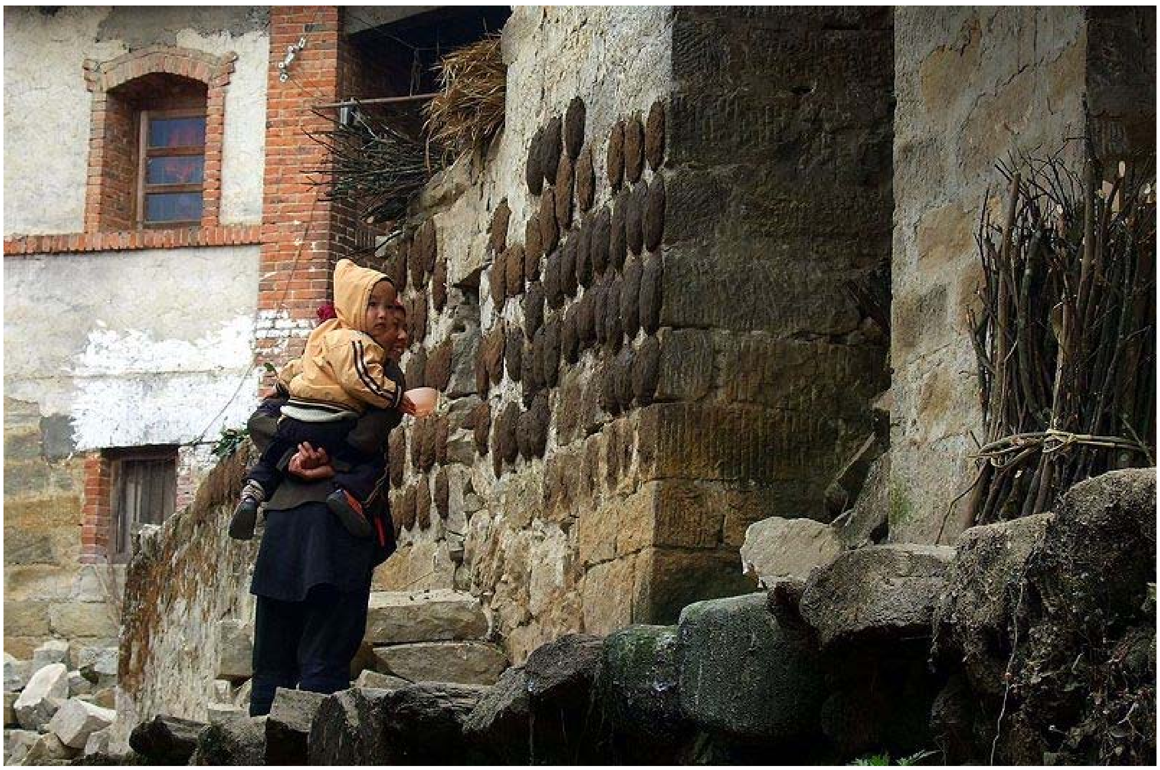
Torpor is alternatively used as a reference to any non-physiological state of inactivity. As an example, recently naturalists have learned that female crocodiles enter a deep torpor without aggression during their short egg laying period.

Chapter 6

Cow Dung

Fresh cow dung

Cow dung being dried for fuel in India.



Water buffalo dung drying on the wall of a house, Yuanyang County, Yunnan

Cow dung is the waste of bovine animal species. These species include domestic cattle ("cows"), bison ("buffalo"), yak and water buffalo. Cow dung is the undigested residue of plant matter which has passed through the animal's gut. The resultant faecal matter is rich in minerals. Colour ranges from greenish to blackish, often darkening in colour soon after exposure to air.

Uses

Cow dung (usually combined with soiled bedding and urine) is often used as manure (agricultural fertilizer). If not recycled into the soil by species such as earthworms and dung beetles, cow dung can dry out and remain on the pasture, creating an area of grazing land which is unpalatable to livestock.

In many parts of the developing world, caked and dried cow dung is used as fuel.

Dung may also be collected and used to produce biogas to generate electricity and heat. The gas is rich in methane and is used in rural areas of India/Pakistan and elsewhere to provide a renewable and stable source of electricity.

Cow dung is also used to line the floor and walls of buildings owing to its insect repellent properties for some types of insects (not flies or dung beetles). In central Africa, Maasai villages have burned cow dung inside to repel mosquitos. In cold places, cow dung is used to line the walls of rustic houses as a cheap thermal insulator.

Cow dung is also an optional ingredient in the manufacture of adobe mud brick housing depending on the availability of materials at hand.

A deposit of cow dung is referred to in American English as a "cow pie", and in British English as a cowpat. Also known as "cow chips" when dry, it is used in the practice of "cow chip throwing" popularized in Beaver, Oklahoma in 1970 . Another game is Cow Chip Bingo.

Ecology

Cow dung provides food for a wide range of animal and fungus species, which break it down and recycle it into the food chain and into the soil.

In areas where cattle (or other mammals with similar dung) are not native, there are often also no native species which can break down their dung, and this can lead to infestations of pests such as flies and parasitic worms. In Australia, dung beetles from elsewhere have been introduced to help recycle the cattle dung back into the soil.

Variants

A *buffalo chip*, also called a *meadow muffin*, is the name for a large, flat, dried piece of dung deposited by the American Bison from the large amount of grass that it eats. Well dried buffalo chips were among the few things that could be collected and burned on the prairie and were used by the Plains Indians, settlers and pioneers, and homesteaders as a source of cooking heat and warmth.

Bison dung is sometimes referred to by the name *nik-nik*. This word is a borrowing from the Sioux language (which probably originally borrowed it from a northern source). In modern Sioux, *nik-nik* can refer to the feces of any bovine, including domestic cattle. It has also come to be used, especially in Lakota, to refer to lies or broken promises (especially by the U.S. government). It probably attained this sense by association with the English term "bullshit".

Chapter 7

Feces

Horse feces

Feces, **faeces**, or **fæces** is a waste product from an animal's digestive tract expelled through the anus (or cloaca) during *defecation*.

Etymology

The word *faeces* is the plural of the Latin word *fæx* meaning "dregs". There is no singular form in the English language, making it a plurale tantum. There are many colloquial terms for feces, of which some are considered profanity (such as *shit*, *crap* and *turd*) while others (such as *poo*, *poop*, *number two*, *dookie* and *doody*) are not. Terms such as *dung*, *scat*, *spoor* and *droppings* are normally used to refer to animal feces.

Stool is a common term normally used in reference to human feces. For example, in medicine to diagnose the presence or absence of a medical condition, a stool sample is sometimes requested for testing purposes. The term "stool" can also be used for that of non-human species.

Ecology

The Cassowary disperses plant seeds via its feces.

Earthworm feces aid in provision of minerals and plant nutrients in an accessible form

After an animal has digested eaten material, the remains of that material are expelled from its body as waste. Though it is lower in energy than the food it came from, feces may still contain a large amount of energy, often 50% of that of the original food. This means that of all food eaten, a significant amount of energy remains for the decomposers of ecosystems. Many organisms feed on feces, from bacteria to fungi to insects such as dung beetles, which can sense odors from long distances. Some may specialize in feces, while others may eat other foods as well. Feces serve not only as a basic food, but also a supplement to the usual diet of some animals. This is known as coprophagia, and occurs in various animal species such as young elephants eating their mother's feces to gain essential gut flora, or by other animals such as dogs, rabbits, and monkeys.

Feces are also important as a signal. Kestrels, for instance, are able to detect the feces of their prey (which reflect ultraviolet), allowing them to identify areas where there are large numbers of voles.

Seeds may also be found in feces. Animals which eat fruit are known as frugivores. The advantage for a plant in having fruit is that animals will eat the fruit and unknowingly disperse the seed in doing so. This mode of seed dispersal is highly successful, as seeds dispersed around the base of a plant are unlikely to succeed and are often subject to heavy predation. Provided the seed can withstand the pathway through the digestive system, it is not only likely to be far away from the parent plant, but is even provided with its own fertilizer.

Organisms which subsist on dead organic matter or *detritus* are known as detritivores, and play an important role in ecosystems by recycling organic matter back into a simpler form which plants and other autotrophs may once again absorb. This cycling of matter is known as the biogeochemical cycle. To maintain nutrients in soil it is therefore important that feces return to the area from which they came, which is not always the case in human society where food may be transported from rural areas to urban populations and then feces disposed of into a river or sea.

Human feces

In humans, defecation may occur (depending on the individual and the circumstances) from once every two or three days to several times a day. Extensive hardening of the feces may cause prolonged interruption in the routine and is called constipation.

Human fecal matter varies significantly in appearance, depending on diet and health. Normally it is semisolid, with a mucus coating. Its brown coloration comes from a combination of bile and bilirubin, which comes from dead red blood cells.

In newborn babies, fecal matter is initially yellow/green after the meconium. This coloration comes from the presence of bile alone. In time, as the body starts expelling bilirubin from dead red blood cells, it acquires its familiar brown appearance, unless the baby is breast feeding, in which case it remains soft, pale yellowish, and not completely malodorous until the baby begins to eat significant amounts of other food.

Throughout the life of an ordinary human, one may experience many types of feces. A "green" stool is from rapid transit of feces through the intestines (or the consumption of certain blue or green food dyes in quantity), and "clay-like" appearance to the feces is the result of a lack of bilirubin.

Bile overload is very rare, and not a health threat. Problems as simple as serious diarrhea can cause blood in one's stool. Black stools caused by blood usually indicate a problem in the intestines (the black is digested blood), whereas red streaks of blood in stool are usually caused by bleeding in the rectum or anus.

Food may sometimes make an appearance in the feces. Common undigested foods found in human feces are seeds, nuts, corn and beans, mainly because of their high dietary fiber content. Beets may turn feces different hues of red. Artificial food coloring in some processed foods such as highly colorful packaged breakfast cereals can also cause unusual feces coloring if eaten in sufficient quantities.

Laboratory examination of feces, usually termed as stool examination or stool test, is done for the sake of diagnosis, for example, to detect presence of parasites such as pinworms and/or their eggs (ova) or to detect disease spreading bacteria.

Personal hygiene

All cultures practice some form of personal cleansing after expelling feces.

- In Western and East Asian society, the use of toilet paper is widespread.
    - Other paper products were also historically used (before the advent of flush toilets).
    - Several companies market toilet tissue or wipes for babies and campers.
    - In some European countries, the use of a bidet for additional cleaning is common.
- In South Asia and Southeast Asia, showers are provided for use in toilets.
- In Islam, washing is prescribed by ritual cleansing with water, of which washing of the anus is part of the ablutions.
- In India, the anus is also washed with water using the left hand. As with all such practices, hand washing after use of the toilet has become a very important public health issue.
- In the United Kingdom, the Indian toilet was adapted as the WC or water closet and widely deployed in England during the reign of Queen Victoria. London was the stage for several instances of food poisoning resulting from workers handling food after using the toilet. Cleansing of the anus was an arbitrary practice left to personal choice and facility available.
- In Ancient Rome, a communal sponge was used, which was then rinsed in a bucket of salt water.
- In Japan, flat sticks were used in ancient times, being replaced by toilet paper as the country became more Westernized. Toilets that include built-in bidets have now become widely popular in private homes; these can be very sophisticated appliances, allowing users to adjust the temperature, direction and force of water jets, and offering warm air to dry the anus and surrounding regions. The toilet automatically flushes when the buttocks leave the seat.

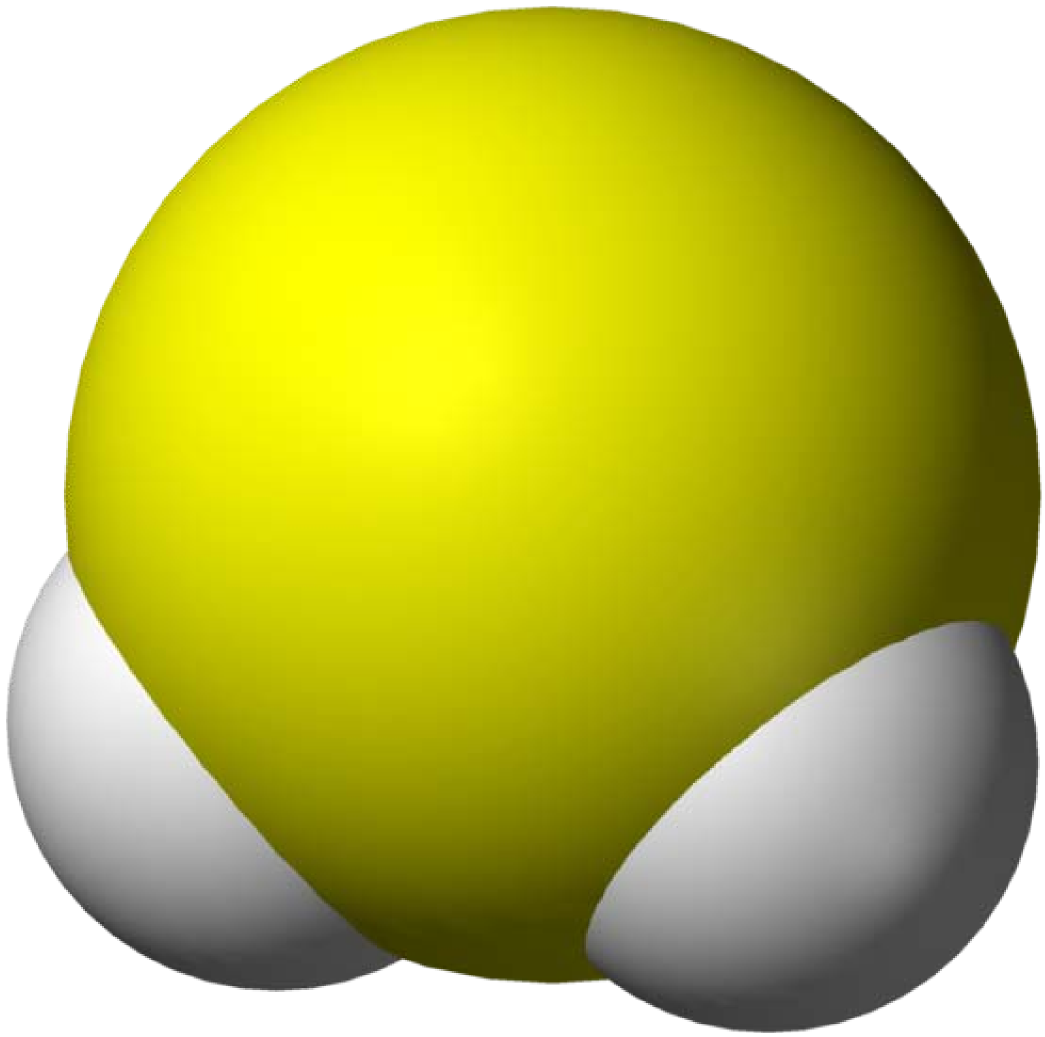
Bristol Stool Scale

Consistency and shape of stools may be classified medically according to the Bristol Stool Scale.

Pica, a disorder where non-food items are eaten, can cause unusual stool.

Intestinal parasites and their ova (eggs) can sometimes be visible to the naked eye.

Odor



The molecule hydrogen sulfide contributes to the smell of feces.

The distinctive odor of feces is due to bacterial action. Gut flora produce compounds such as indole, skatole, and thiols (sulfur-containing compounds), as well as the inorganic gas hydrogen sulfide. These are the same compounds that are responsible for the odor of flatulence. Consumption of foods with spices may result in the spices being undigested and adding to the odor of feces. The perceived bad odor of feces has been hypothesized to be a deterrent for humans, as consumption or touching it may result in sickness or infection. Of course, human perception of the odor is a subjective matter; an animal that eats feces may be attracted to its odor.

Pets

Pets can be trained to use litter boxes or wait to be allowed outside and defecate there. Training can be done in several ways, especially dependent on species. An example is crate training for dogs. Several companies market carpet cleaning products aimed at pet owners.

Uses

Human feces may be used as fertilizer in the form of biosolids (treated sewage sludge). The feces of animals are often used as fertilizer. Some animal feces, especially those of camel, bison and cattle, is used as fuel when dried out. Animal dung, besides being used as fuel, is occasionally used as a cement to make adobe mudbrick huts or even in throwing sports such as cow pat throwing or camel dung throwing contests. Kopi Luwak or Civet coffee, is coffee made from coffee berries which have been eaten by and passed through the digestive tract of the Asian Palm Civet (Paradoxurus hermaphroditus).

Dog feces were used in the tanning process of leather during the Victorian era. Collected dog feces were mixed with water to form a substance known as "bate". Enzymes in the dog feces helped to relax the fibrous structure of the hide prior to the final stages of tanning.

Animal feces

Fresh bear scat showing a diet of apples

The feces of animals often have special names. For example:

- **Non-human animals** generally –
    - As bulk material – dung
    - Individually – droppings
- **Cattle** –
    - Bulk material – cow dung
    - Individual droppings – cow pats, meadow muffins etc.
- **Deer** (and formerly other quarry animals) – fewmets.
- **Wild carnivores** – scat.
- **Otter** – spraint.
- **Birds** (individual) – droppings (also include urine as white crystals of uric acid).
- **Seabirds** or **bats** (large accumulations) – guano.
- **Herbivorous insects**, such as caterpillars and leaf beetles – frass.
- **Earthworms**, **lugworms** etc. – worm casts (feces extruded at ground surface).
- **Feces when used as fertilizer** (usually mixed with animal bedding and urine) – manure.

Chapter 8

Kleptothermy, Heterothermy and Ectotherm

Kleptothermy

Neonatal lab rats huddling for warmth.

Kleptothermy is any form of thermoregulation by which an animal shares in the metabolic thermogenesis of another animal. It may or may not be reciprocal, and occurs in both endotherms and ectotherms. Its most common form is huddling.

Huddling

Male Canadian garter snakes huddle around a female after hibernation when mating.

Some species of ectotherms including lizards and snakes, such as boa constrictors and Tiger snakes, increase their effective mass by clustering tightly together. This allows the individuals to increase their thermal inertia (as with gigantothermy) and so reduce heat loss. It is also widespread amongst gregarious endotherms such as bats and birds (such as the mousebird and emperor penguin) where it allows the sharing of body heat (particularly amongst juveniles).

In at least one case this is not reciprocal, and might be accurately described as *heat-stealing*. Some male Canadian red sided garter snakes engage in female mimicry by producing fake pheromones after emerging from hibernation. This causes rival males to cover them in a mistaken attempt to mate, and so transfer heat to them. This allows those males that mimic females to become more quickly revitalized after hibernation (which depends upon raising their body temperature), giving them an advantage in their own attempts to mate.

Habitat sharing

Many ectotherms exploit the heat produced by endotherms by sharing their nests and burrows. For example, mammal burrows are used by geckos and seabird burrows by Australian tiger snakes and New Zealand tuatara Termites create in their mounds high and regulated temperatures and this is exploited by some species of lizards, snakes and crocodiles.

Research has shown such kleptothermy can be advantageous: the Blue-lipped sea krait, when it occupies a burrow of a pair of Wedge-tailed Shearwater incubating their chick, raises its body temperature to 37.5 °C (99.5 °F) compared to 31.7 °C (89.1 °F) when in other habitats. Its body temperature is also more stable. Burrows without birds did not provide this heat being only 28 °C (82 °F).

Heterothermy

Heterothermy (from Greek: *heteros* = "other" *thermē* = "heat.") is a physiological term for animals that exhibit characteristics of both poikilothermy and homeothermy.

Temporal heterothermy

Temporal heterothermy refers to animals that are poikilothermic or homeothermic for a portion of the day, or year. More often than not, it is used as a way to dissociate the fluctuating metabolic rates seen in some small mammals and birds (e.g. bats and hummingbirds), from those of traditional cold blooded animals. In many bat species, body temperature and metabolic rate are elevated only during activity. When at rest, these animals reduce their metabolisms drastically, which results in their body temperature dropping to that of the surrounding environment. This makes them homeothermic when active, and poikilothermic when at rest.

Regional heterothermy

Regional heterothermy describes organisms that are able to maintain different temperature "zones" in different regions of the body. This usually occurs in the limbs, and is made possible through the use of counter-current heat exchangers, such as the rete mirabile found in tuna and certain birds. These exchangers equalise the temperature between hot arterial blood going out to the extremities and cold venous blood coming back, thus reducing heat loss. Penguins and many arctic birds use these exchangers to keep their feet at roughly the same temperature as the surrounding ice. This keeps the birds from getting stuck on an ice sheet. Other animals, like the Leatherback Sea Turtle, use the heat exchangers to gather, and retain heat generated by their muscular flippers. There are even some insects which possess this mechanism, the best-known example being bumblebees, which exhibit counter-current heat exchange at the point of constriction between the mesosoma ("thorax") and metasoma ("abdomen"); heat is retained in the thorax and lost from the abdomen. Using a very similar mechanism, the internal temperature of a honeybee's thorax can exceed 45°C while in flight.

Ectotherm

Pseudemys turtles (shown here basking for warmth) are ectothermic.

An **ectotherm**, from the Greek *εκτός* (*ektós*) "outside" and *θερμός* (*thermós*) "hot", refers to organisms that control body temperature through external means. As a result, organisms are dependent on environmental heat sources and have relatively low metabolic rates. For example, many reptiles regulate their body temperature by basking in the sun. The opposite of ectothermy is endothermy, where heat is primarily generated as a result of internal metabolic processes. Many ectotherms are also poikilotherms, meaning their temperature varies over a wider range than homeotherms.

Ectotherms are animals that warm their bodies by absorbing heat from their surroundings. In most ectotherms, the body temperature fluctuates with changes in the surrounding temperature; these ectotherms are called poikilotherms. The body temperature of snakes, for example, cools in cold weather and warms up in hot weather. Most marine fish and invertebrates, however, live in water that stays the same temperature. Their body temperature, therefore, does not change, and these ectotherms are therefore considered homeotherms.

Adaptations

Certain ectotherm behaviors help regulate body temperature. To warm up, reptiles find sunny places, and stretch out for maximum exposure. If it gets too warm, lizards alternate between sun and shade. Amphibians warm up by moving into the sun or diving into warm water. They cool off by entering the shade. In cold weather, honey bees huddle together to retain heat. Butterflies and moths may orient their wings to maximize exposure to solar radiation in order to build up heat before takeoff. Many flying insects, such as honey bees and bumble bees, also raise their internal temperatures endothermically prior to flight, by contracting their flight muscles without moving their wings.

In addition to behaviors, physiological adaptations help ectotherms regulate temperature. Diving reptiles conserve heat because their blood circulates inward toward the body core during a dive. The skin of bullfrogs secretes more mucus when it is hot, allowing more cooling by evaporation. Many ectotherms exist at a lower temperature during torpor, a state of slowed metabolism. This helps them survive a food shortage. If the food supply increases, they come out of torpor in a few hours.

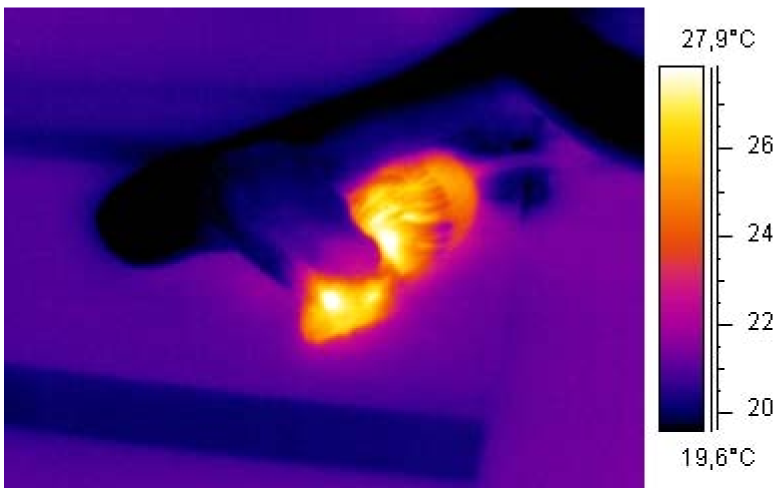
Advantages and Disadvantages

Tropical ectotherms may be particularly vulnerable to climate warming and are experiencing large increases in metabolic rate and will have an increased need for food.

Chapter 9

Warm-Blooded and Blood Type (Non-Human)

Warm-blooded



Thermographic image: a coldblooded snake is eating a warmblooded mouse

The term **warm-blooded** is a colloquial term to describe animal species which have a relatively higher blood temperature, and maintain thermal homeostasis primarily through internal metabolic processes. These are characteristics of mammals and birds.

Both the terms "warm-blooded" and "cold-blooded" have fallen out of favour with scientists because of the vagueness of the terms and an increased understanding of the field. Body temperature types are not discrete categories. Each term may be replaced with one or more variants, see the next section for examples. Body temperature maintenance (thermoregulation) incorporates a wide range of different techniques that result in a body temperature continuum.

Characteristics of warm-bloodedness

Warm-bloodedness generally refers to three separate aspects of thermoregulation.

- Endothermy is the ability of some creatures to control their body temperatures through internal means such as muscle shivering or increasing their metabolism (Greek: *endon* = "within", *thermē* = "heat"). Some writers restrict the meaning of endothermy to mechanisms that directly raise the animal's metabolic rate in order to produce heat. The opposite of endothermy is ectothermy.
- Homeothermy is thermoregulation that maintains a stable internal body temperature regardless of external influence. This temperature is often, though not necessarily, higher than the immediate environment (Greek: *homoios* = "similar", *thermē* = "heat"). The opposite is poikilothermy.
- Tachymetabolism is the kind of thermoregulation used by creatures that maintain a high "resting" metabolism (Greek: *tachys/tachus* = "fast, swift", *metabolēn* = "throw beyond"). Tachymetabolic creatures are, essentially, "on" all the time. Though their resting metabolism is still many times slower than their active metabolism, the difference is often not as large as that seen in bradymetabolic creatures. Tachymetabolic creatures have greater difficulty dealing with a scarcity of food.

Reasons for term falling into disuse

A large proportion of the creatures traditionally called "warm-blooded", such as mammals and birds, fit all three of these categories. However, over the past 30 years, studies in the field of animal thermophysiology have revealed many species belonging to these two groups that do not fit all these criteria. For example, many bats and small birds are poikilothermic and bradymetabolic when they sleep for the night, or day, as the case may be. For these creatures, the term heterothermy was coined.

Further studies on animals that were traditionally assumed to be cold-blooded have shown that most creatures incorporate different variations of the three terms defined above, along with their counterparts (ectothermy, poikilothermy and bradymetabolism), thus creating a broad spectrum of body temperature types. Even some fish have warm-blooded characteristics. Swordfish and some sharks have circulatory mechanisms that keep their brains and eyes above ambient temperatures, and thus increase their ability to detect and react to prey. Tunas and some sharks have similar mechanisms in their muscles, improving their stamina when swimming at high speed.

Blood type (non-human)

Animals and bacteria have cell surface antigens referred to as a **blood type**. Antigens from the human ABO blood group system are also found in apes such as chimpanzees, bonobos and gorillas. Other animal blood sometimes agglutinates (to varying levels of intensity) with human blood group reagents, but the structure of the blood group antigens in animals is not always identical to those typically found in humans. The classification of most animal blood groups therefore uses different blood typing systems to those used for classification of human blood.

Simian blood groups

Two categories of blood groups, human-type and simian-type, have been found in apes and monkeys and can be tested by methods established for grouping human blood.

Rhesus blood group

The Rhesus system is named after the Rhesus monkey, following experiments by Karl Landsteiner and Alexander S. Wiener, which showed that rabbits, when immunised with Rhesus monkey red cells, produce an antibody that also agglutinates the red blood cells of many humans.

Chimpanzee blood group systems

Data on blood groups of chimpanzees, baboons and macaques. Two complex chimpanzee blood group systems, V-A-B-D and R-C-E-F systems, proved to be counterparts of the human MNS and Rh-Hr blood group systems, respectively. Two blood group systems have been defined in Old World monkeys: the Drh system of macaques and the Bp system of baboons, both linked by at least one species shared by either of the blood group systems.

Canine blood groups

Over 13 canine blood groups have been described. Eight DEA (Dog Erythrocyte Antigen) types are recognized as international standards. Of the DEA, DEA 4 and DEA 6 appear on the red blood cell of ~98% of dogs. Dogs with only DEA 4 or DEA 6 can thus serve as blood donors for the majority of the canine population. Any of the DEA may stimulate an immune response in a recipient of a blood transfusion, but reactions to DEA 1.1+ are the most severe.

From DMS Laboratories, Inc : The most important canine blood type is DEA 1.1. **Dogs that are DEA 1.1 positive (33 to 45% of the population) can be considered to be universal recipients** - that is, they can receive blood of any type without expectation of a life-threatening Hemolytic Transfusion Reaction ("HTR"). **Dogs that are DEA 1.1 negative can be considered to be universal donors**. Blood from DEA 1.1 positive dogs should never be transfused into DEA 1.1 negative dogs. If it is the dog's first transfusion the red cells transfused will have a shortened life due to the formation of alloantibodies to the cells themselves and the animal will forever be sensitized to DEA 1.1 blood. If it is a second such transfusion, life-threatening conditions will follow within hours. In addition, these alloantibodies will be present in a female dog's milk (colostrum) and adversely affect the health of DEA 1.1 negative puppies.

Feline blood groups

The commonly recognized system of feline blood designates cats as A, B, or AB. The vast majority of cats in the United States are Type A, but the percentage of Type B cats increases in other countries, such as Australia. Type A and B cats have naturally occurring alloantibodies to the opposite blood type, although the reaction of Type B cats to Type A blood is more severe than vice versa. Based on this, all cats should have a simple blood typing test done to determine their blood type prior to a transfusion or breeding to avoid the haemolytic disease (or neonatal isoerythrolysis).

Equine blood groups

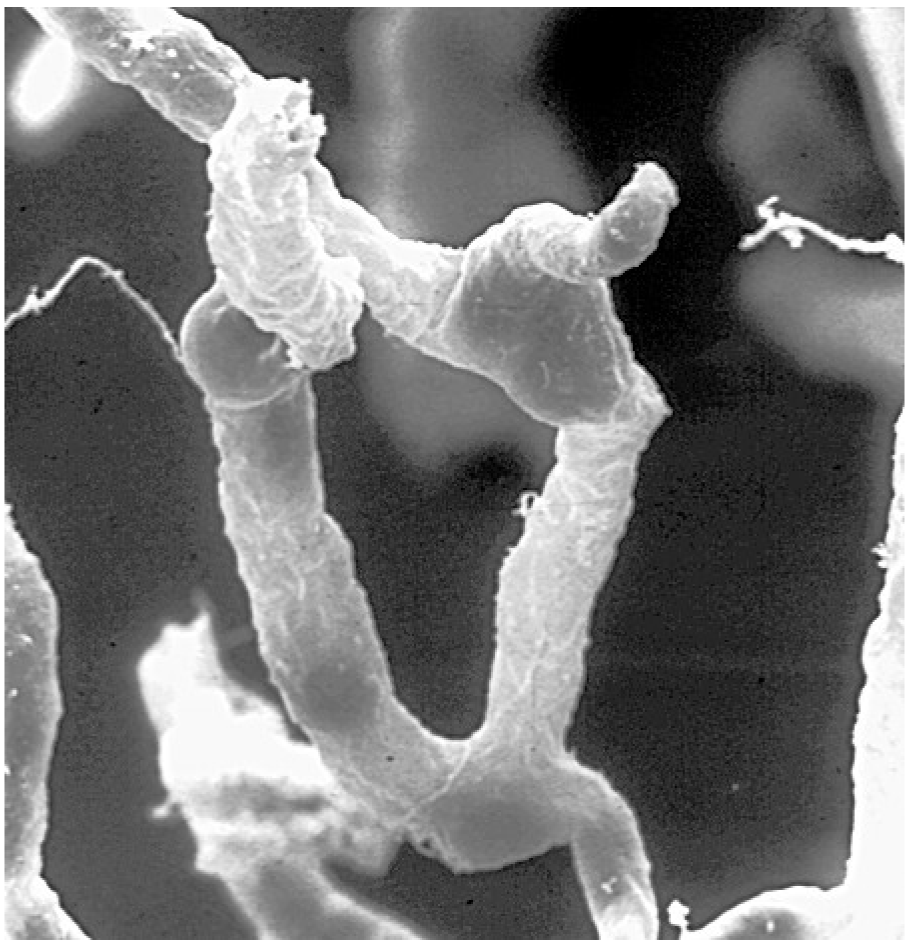
There are eight recognized blood groups in the horse: A, C, D, K, P, Q, T, and U.

Bovine blood groups

The polymorphic systems in cattle include the A, B, C, F, J, L, M, S, and Z polymorphisms.

Chapter 10

Blood-Brain Barrier



Part of a network of capillaries supplying brain cells

The astrocytes type 1 surrounding capillaries in the brain

The **blood–brain barrier** (**BBB**) is a separation of circulating blood and the brain extracellular fluid (BECF) in the central nervous system (CNS). It occurs along all capillaries and consists of tight junctions around the capillaries that do not exist in normal circulation. Endothelial cells restrict the diffusion of microscopic objects (e.g. bacteria) and large or hydrophilic molecules into the cerebrospinal fluid (CSF), while allowing the diffusion of small hydrophobic molecules (O_2, hormones, CO_2). Cells. of the barrier actively transport metabolic products such as glucose across the barrier with specific proteins. This barrier also includes a thick basement membrane and astrocytic endfeet.

History

Paul Ehrlich was a bacteriologist studying staining, a procedure that is used in many microscopic studies to make fine biological structures visible using chemical dyes. When Ehrlich injected some of these dyes (notably the aniline dyes that were then widely-used), the dye would stain all of the organs of some kinds of animals except for their brains. At that time, Ehrlich attributed this lack of staining to the brain's simply not picking up as much of the dye.

However, in a later experiment in 1913, Edwin Goldmann (one of Ehrlich's students) injected the dye into the cerebro-spinal fluids of animals' brains directly. He found that in this case the brains did become dyed, but the rest of the body did not. This clearly demonstrated the existence of some sort of compartmentalization between the two. At that time, it was thought that the blood vessels themselves were responsible for the barrier, since no obvious membrane could be found. The concept of the blood–brain barrier (then termed **hematoencephalic barrier**) was proposed by Lina Stern in 1921. It was not until the introduction of the scanning electron microscope to the medical research fields in the 1960s that the actual membrane could be observed and proven to exist.

Physiology

This "barrier" results from the selectivity of the tight junctions between endothelial cells in CNS vessels that restricts the passage of solutes. At the interface between blood and the brain, endothelial cells are stitched together by these tight junctions, which are composed of smaller subunits, frequently biochemical dimers, that are transmembrane proteins such as occludin, claudins, junctional adhesion molecule (JAM), or ESAM, for example. Each of these transmembrane proteins is anchored into the endothelial cells by another protein complex that includes zo-1 and associated proteins.

The blood–brain barrier is composed of high-density cells restricting passage of substances from the bloodstream much more than endothelial cells in capillaries elsewhere in the body. Astrocyte cell projections called astrocytic feet (also known as "glia limitans") surround the endothelial cells of the BBB, providing biochemical support to those cells. The BBB is distinct from the quite similar blood – cerebrospinal-fluid barrier, which is a function of the choroidal cells of the choroid plexus, and from the blood–retinal barrier, which can be considered a part of the whole realm of such barriers.

Several areas of the human brain are not "behind" the BBB. These include the circumventricular organs. Example of this include: the roof of the 3rd and 4th ventricles; capillaries in the pineal gland on the roof of the diencephalon; and the pineal gland, which secretes the hormone melatonin "directly into the systemic circulation" as this hormone can pass through the blood–brain barrier.

Environment

Originally, experiments in the 1920s showed that the blood–brain barrier (BBB) was still immature in newborns. The reason for this fallacy was a mistake in methodology (the osmotic pressure was too high and the delicate embryonal capillary vessels were partially damaged). It was later shown in experiments with a reduced volume of the injected liquids that the markers under investigation could not pass the BBB. It was reported that those natural substances such as albumin, α-1-fetoprotein or transferrin with elevated plasma concentration in the newborn could not be detected extracellular in the brain. The efflux-transporter P-glycoprotein exists already in the embryonal endothelium.

The measurement of brain uptake of acetamide, antipyrine, benzyl alcohol, butanol, caffeine, cytosine, diphenyl hydantoin, ethanol, ethylene glycol, heroin, mannitol, methanol, phenobarbital, propylene glycol, thiourea, and urea in ether-anesthetized newborn vs. adult rabbits shows that newborn rabbit and adult rat brain endothelia are functionally similar with respect to lipid-mediated permeability. These data confirmed no differences in permeability could be detected between newborn and adult BBB capillaries. No difference in brain uptake of glucose, amino acids, organic acids, purines, nucleosides, or choline was observed between adult and newborn rabbits. These experiments indicate that the newborn BBB has restrictive properties similar to the adult. In contrast to suggestions of an immature barrier in young animals, these studies indicate that a sophisticated, selective BBB is operative at birth.

Pathophysiology

The blood–brain barrier acts very effectively to protect the brain from many common bacterial infections. Thus, infections of the brain are very rare. However, since antibodies and antibiotics are too large to cross the blood–brain barrier, infections of the brain that do occur are often very serious and difficult to treat. However, the blood–brain barrier becomes more permeable during inflammation, meaning that some antibiotics can get across. Viruses easily bypass the blood–brain barrier by attaching themselves to circulating immune cells.

An exception to the bacterial exclusion are the diseases caused by spirochetes, such as Borrelia, which causes Lyme disease, and Treponema pallidum, which causes syphilis. These harmful bacteria seem to breach the blood–brain barrier by physically tunneling through the blood vessel walls.

There are also some biochemical poisons that are made up of large molecules that are too big to pass through the blood–brain barrier. This was especially important in primitive or medieval times when people often ate contaminated food. Neurotoxins such as Botulinum in the food might affect peripheral nerves, but the blood–brain barrier can often prevent such toxins from reaching the central nervous system, where they could cause serious or fatal damage.

Drugs targeting the brain

Overcoming the difficulty of delivering therapeutic agents to specific regions of the brain presents a major challenge to treatment of most brain disorders. In its neuroprotective role, the blood–brain barrier functions to hinder the delivery of many potentially important diagnostic and therapeutic agents to the brain. Therapeutic molecules and genes that might otherwise be effective in diagnosis and therapy do not cross the BBB in adequate amounts.

Mechanisms for drug targeting in the brain involve going either "through" or "behind" the BBB. Modalities for drug delivery through the BBB entail its disruption by osmotic means; biochemically by the use of vasoactive substances such as bradykinin; or even by localized exposure to high-intensity focused ultrasound (HIFU). Other methods used to get through the BBB may entail the use of endogenous transport systems, including carrier-mediated transporters such as glucose and amino acid carriers; receptor-mediated transcytosis for insulin or transferrin; and the blocking of active efflux transporters such as p-glycoprotein. Methods for drug delivery behind the BBB include intracerebral implantation (such as with needles) and convection-enhanced distribution. Mannitol can be used in bypassing the BBB.

Nanoparticles

Nanotechnology may also help in the transfer of drugs across the BBB. Recently, researchers have been trying to build liposomes loaded with nanoparticles to gain access through the BBB. More research is needed to determine which strategies will be most effective and how they can be improved for patients with brain tumors. The potential for using BBB opening to target specific agents to brain tumors has just begun to be explored.

Delivering drugs across the blood–brain barrier is one of the most promising applications of nanotechnology in clinical neuroscience. Nanoparticles could potentially carry out multiple tasks in a predefined sequence, which is very important in the delivery of drugs across the blood–brain barrier.

A significant amount of research in this area has been spent exploring methods of nanoparticle-mediated delivery of antineoplastic drugs to tumors in the central nervous system. For example, radiolabeled polyethylene glycol coated hexadecylcyanoacrylate nanospheres targeted and accumulated in a rat gliosarcoma. However, this method is not yet ready for clinical trials, due to the accumulation of the nanospheres in surrounding healthy tissue.

It should be noted that vascular endothelial cells and associated pericytes are often abnormal in tumors and that the blood–brain barrier may not always be intact in brain tumors. Also, the basement membrane is sometimes incomplete. Other factors, such as astrocytes, may contribute to the resistance of brain tumors to therapy.

Diseases involving the blood–brain barrier

Meningitis

Meningitis is an inflammation of the membranes that surround the brain and spinal cord (these membranes are known as meninges). Meningitis is most commonly caused by infections with various pathogens, examples of which are *Streptococcus pneumoniae* and *Haemophilus influenzae*. When the meninges are inflamed, the blood–brain barrier may be disrupted. This disruption may increase the penetration of various substances (including either toxins or antibiotics) into the brain. Antibiotics used to treat meningitis may aggravate the inflammatory response of the central nervous system by releasing neurotoxins from the cell walls of bacteria-like lipopolysaccharide (LPS) Treatment with third-generation or fourth-generation cephalosporin is usually preferred.

Epilepsy

Epilepsy is a common neurological disease that is characterized by recurrent and sometimes untreatable seizures. Several clinical and experimental data have implicated the failure of blood–brain barrier function in triggering chronic or acute seizures, some studies implicate the interactions between a common blood protein—albumin and astrocytes. These findings have shown that acute seizures are a predictable consequence of disruption of the BBB by either artificial or inflammatory mechanisms. In addition, expression of drug resistance molecules and transporters at the BBB are a significant mechanism of resistance to commonly used anti-epileptic drugs.

Multiple sclerosis (MS)

Multiple sclerosis (MS) is considered to be an auto-immune and neurodegenerative disorder in which the immune system attacks the myelin that protects and electrically insulates the neurons of the central and peripheral nervous systems. Normally, a person's nervous system would be inaccessible to the white blood cells due to the blood–brain barrier. However, it has been shown using Magnetic Resonance Imaging, that when a person is undergoing an MS "attack," the blood–brain barrier has broken down in a section of the brain or spinal cord, allowing white blood cells called T lymphocytes to cross over and attack the myelin. It has sometimes been suggested that, rather than being a disease of the immune system, MS is a disease of the blood–brain barrier. A recent study suggests that the weakening of the blood–brain barrier is a result of a disturbance in the endothelial cells on the inside of the blood vessel, due to which the production of the protein P-glycoprotein is not working well.

There are currently active investigations into treatments for a compromised blood–brain barrier. It is believed that oxidative stress plays an important role into the breakdown of the barrier. Anti-oxidants such as lipoic acid may be able to stabilize a weakening blood–brain barrier.

Neuromyelitis optica

Neuromyelitis optica, also known as Devic's disease, is similar to and is often confused with multiple sclerosis. Among other differences from MS, a different target of the autoimmune response has been identified. Patients with neuromyelitis optica have high levels of antibodies against a protein called aquaporin 4 (a component of the astrocytic foot processes in the blood–brain barrier).

Late-stage neurological trypanosomiasis (Sleeping sickness)

Late-stage neurological trypanosomiasis, or sleeping sickness, is a condition in which trypanosoma protozoa are found in brain tissue. It is not yet known how the parasites infect the brain from the blood, but it is suspected that they cross through the choroid plexus, a circumventricular organ.

Progressive multifocal leukoencephalopathy (PML)

Progressive multifocal leukoencephalopathy (PML) is a demyelinating disease of the central nervous system that is caused by reactivation of a latent papovavirus (the JC polyomavirus) infection, that can cross the BBB. It affects immune-compromised patients and it is usually seen with patients suffering from AIDS.

De Vivo disease

De Vivo disease (also known as GLUT1 deficiency syndrome) is a rare condition caused by inadequate transportation of the sugar, glucose, across the blood–brain barrier, resulting in mental retardation and other neurological problems. Genetic defects in glucose transporter type 1 (GLUT1) appears to be the primary cause of De Vivo disease.

Alzheimer's Disease

Some new evidence indicates that disruption of the blood–brain barrier in Alzheimer's Disease patients allows blood plasma containing amyloid beta (Aβ) to enter the brain where the Aβ adheres preferentially to the surface of astrocytes. These findings have led to the hypotheses that (1) breakdown of the blood–brain barrier allows access of neuron-binding autoantibodies and soluble exogenous Aβ42 to brain neurons and (2) binding of these auto-antibodies to neurons triggers and/or facilitates the internalization and accumulation of cell surface-bound Aβ42 in vulnerable neurons through their natural tendency to clear surface-bound autoantibodies via endocytosis. Eventually the astrocyte is overwhelmed, dies, ruptures, and disintegrates, leaving behind the insoluble Aβ42 plaque. Thus, in some patients, Alzheimer's disease may be caused (or more likely, aggravated) by a breakdown in the blood–brain barrier.

HIV Encephalitis

It is believed that latent HIV can cross the blood–brain barrier inside circulating monocytes in the bloodstream ("Trojan horse theory") within the first 14 days of infection. Once inside, these monocytes become activated and are transformed into macrophages. Activated macrophages release virions into the brain tissue proximate to brain microvessels. These viral particles likely attract the attention of sentinel brain microglia and perivascular macrophages initiating an inflammatory cascade that may cause a series of intracellular signaling in brain microvascular endothelial cells and damage the functional and structural integrity of the BBB. This inflammation is HIV encephalitis (HIVE). Instances of HIVE probably occur throughout the course of AIDS and are a precursor for HIV-associated dementia (HAD). The premier model for studying HIV and HIVE is the simian model.

Chapter 11

Respiration (Physiology)

In physiology, **respiration** (often mistaken with breathing) is defined as the transport of oxygen from the outside air to the cells within tissues, and the transport of carbon dioxide in the opposite direction. This is in contrast to the biochemical definition of respiration, which refers to **cellular respiration**: the metabolic process by which an organism obtains energy by reacting oxygen with glucose to give water, carbon dioxide and ATP (energy). Although physiologic respiration is necessary to sustain cellular respiration and thus life in animals, the processes are distinct: cellular respiration takes place in individual cells of the animal, while physiologic respiration concerns the bulk flow and transport of metabolites between the organism and the external environment.

In unicellular organisms, simple diffusion is sufficient for gas exchange: every cell is constantly bathed in the external environment, with only a short distance for gases to flow across. In contrast, complex multicellular animals such as humans have a much greater distance between the environment and their innermost cells, thus, a respiratory system is needed for effective gas exchange. The respiratory system works in concert with a circulatory system to carry gases to and from the tissues.

In air-breathing vertebrates such as humans, respiration of oxygen includes four stages:

- **Ventilation**, moving of the ambient air into and out of the alveoli of the lungs.
- **Pulmonary gas exchange**, exchange of gases between the alveoli and the pulmonary capillaries.
- **Gas transport**, movement of gases within the pulmonary capillaries through the circulation to the peripheral capillaries in the organs, and then a movement of gases back to the lungs along the same circulatory route.

Organ	Oxygen consumption (ml O_2/min per 100g)
Heart (rest)	8
Heart (heavy exercise)	70
Brain	3
Kidney	5

Skin	0.2
Resting skeletal muscle	1
Contracting skeletal muscle	50

- **Peripheral gas exchange**, exchange of gases between the tissue capillaries and the tissues or organs, impacting the cells composing these and mitochondria within the cells.

Note that ventilation and gas transport require energy to power a mechanical pump (the heart) and the muscles of respiration, mainly the diaphragm. In heavy breathing, energy is also required to power additional respiratory muscles such as the intercostal muscles. The energy requirement for ventilation and gas transport is in contrast to the passive diffusion taking place in the gas exchange steps.

Respiratory behavior is correlated to the cardiovascular behavior to control the gaseous exchange between cells and blood. Both behaviors are intensified by exercise of the body. However, respiratory is highly voluntary compared to cardiovascular activity which is totally involuntary.

Respiratory physiology is the branch of human physiology concerned with respiration.

Classifications of respiration

There are several ways to classify the physiology of respiration:

By species

- Aquatic respiration
- Buccal pumping

By mechanism

- Respiration organ
- Gas exchange
- Arterial blood gas
- Control of respiration
- Apnea

By experiments

- Huff and puff apparatus
- Spirometry
- Selected ion flow tube mass spectrometry
- Bell Jar Model Lung

By disorders

- Sudden Infant Death Syndrome
- Myasthenia gravis
- Asthma
- Drowning
- Choking
- Dyspnea
- Anaphylaxis
- Pneumonia
- Severe acute respiratory syndrome
- Aspiration (medicine) - Pulmonary edema
- Death

By medication

- Asthma medication

Respiration is the process by which oxygen is delivered from the external environment to the cells for cellular exchange. In its proper terminology, it includes the entire process. In terms of visibility, respiration is simply another term for breathing. Respiration includes the inhalation-exhalation process. As unwanted air is expelled from the body during exhalation, the chest 'falls' and a vacuum is created inside the lungs. As new air is then sucked into the body to fill in the vacuum, the chest 'rises'. We call this inhalation. In this process, the unwanted gas expelled is mainly carbon dioxide. This is then replaced during the inhalation breathing phase by the oxygen content within the air inhaled. During this process, via the sacs of the lungs, an exchange of gases first occurs as the blood exchanges carbon dioxide from the body with fresh oxygen. Oxygen attaches to the red blood cells in the blood, and later is diffused from the bloodstream into the intercellular spaces, and eventually diffuses into the cells for use by the cells Therefore, "Respiration" refers to gas exchanged throughout the body with the point of transport of oxygen to the cells for use.

"Cellular Respiration" refers to a specific type of metabolic process that allows an organism to gain energy by breaking down substances.

By intensive care and emergency medicine

- CPR
- Mechanical ventilation
- Intubation
- Iron lung
- Intensive care medicine
- Liquid breathing
- ECMO
- Oxygen toxicity

- Medical ventilator
- Paramedic
- Life support
- General anaesthesia
- Laryngoscope

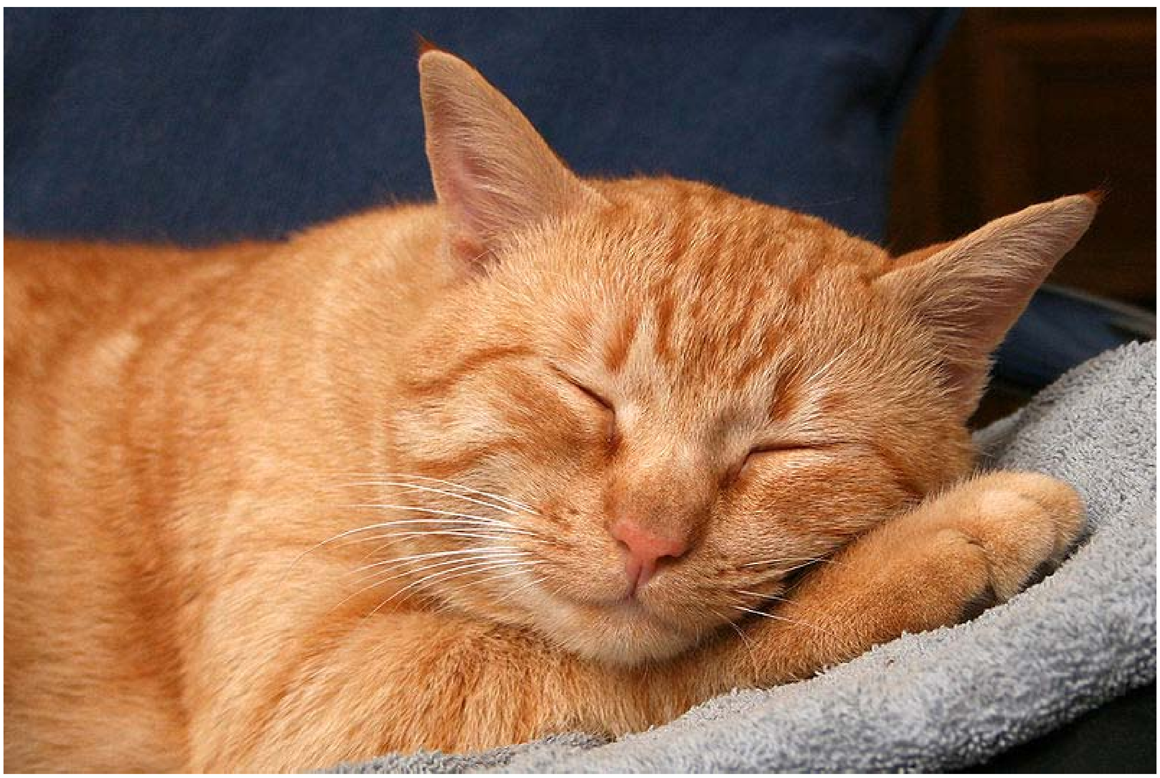
By other medical topics

- Respiratory therapy
- Breathing gases
- Hyperbaric oxygen therapy
- Hypoxia
- Gas embolism
- Decompression sickness
- Barotrauma
- Oxygen toxicity
- Nitrogen narcosis
- Carbon dioxide poisoning
- Carbon monoxide poisoning
- HPNS
- Salt water aspiration syndrome

Chapter 12

Sleep (Non-Human)

Sleep in non-human animals refers to how the behavioral and physiological state of sleep, mainly characterized by reversible unconsciousness, non-responsiveness to external stimuli, and motor passivity, appears in different categories of animals.



A sleeping cat. The upright ears and the body position suggest the cat is experiencing NREM sleep. In REM sleep, the ears would have been tucked in and the skeletal muscles would have been relaxed due to the functional paralysis signifying REM sleep.

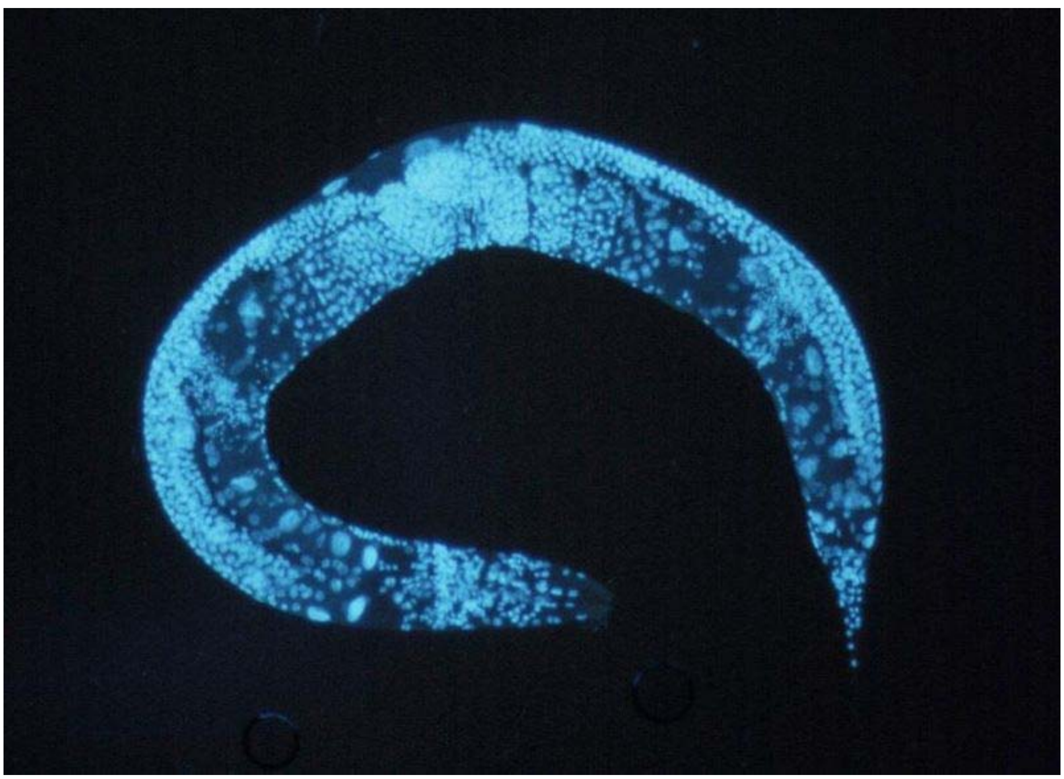
Rats kept from sleeping die within a couple of weeks, but the exact function of sleep is still unknown.

Definition

Sleep can follow a physiological or behavioral definition. In the physiological sense, sleep is a state characterized by reversible unconsciousness, special brainwave patterns, sporadic eye movement, loss of muscle tone (possibly with some exceptions; see below regarding the sleep of birds and of aquatic mammals), and a compensatory increase following deprivation of the state. In the behavioral sense, sleep is characterized by non-responsiveness to external stimuli, the adoption of a typical posture, and the occupation of a sheltered site, all of which is usually repeated on a 24-hour basis. The physiological definition applies well to birds and mammals, but in other animals (whose brain is not as complex), the behavioral definition is more often used. In very simple animals, behavioral definitions of sleep are the only ones possible, and even then the behavioral repertoire of the animal may not be extensive enough to allow distinction between sleep and wakefulness.

Sleep in different species

Sleep in invertebrates



Caenorhabditis elegans is the most primitive organism in which sleep-like states have been observed.

Sleep as a phenomenon appears to have very old evolutionary roots. The nematode *C. elegans* is the most primitive organism in which sleep-like states have been observed.

Here, a *lethargus* phase occurs in short periods preceding each moult, a fact which may indicate that sleep primitively is connected to developmental processes. Raizen *et al.*'s results furthermore suggest that sleep is necessary for changes in the neural system.

The electrophysiological study of sleep in small invertebrates is complicated. However, even such simple animals as fruit flies appear to sleep, and systematic disturbance of that state leads to cognitive disabilities. There are several methods of measuring cognitive functions in fruit flies. A common method is to let the flies choose whether they want to fly through a tunnel that leads to a light source, or through a dark tunnel. Normally, flies are attracted to light. But if sugar is placed in the end of the dark tunnel, and something the flies dislike is placed in the end of the light tunnel, the flies will eventually learn to fly towards darkness rather than light. Flies deprived of sleep require a longer time to learn this and also forget it more quickly. If an arthropod is experimentally kept awake longer than it is used to, then its coming rest period will be prolonged. In cockroaches that rest period is characterized by the antennae being folded down and by a decreased sensitivity to external stimuli. Sleep has been described in crayfish, too, characterized by passivity and increased thresholds for sensory stimuli as well as changes in the EEG pattern, markedly differing from the patterns found in crayfish when they are awake.

Sleep in fish and reptiles

Sleep in fish is not extensively studied. Some species that always live in shoals or that swim continuously (because of a need for ram ventilation of the gills, for example) are suspected never to sleep. There is also doubt about certain blind species that live in caves. Other fishes seem to sleep, however. For example, zebrafish, tilapia, tench, brown bullhead, and swell shark become motionless and unresponsive at night (or by day, in the case of the swell shark); Spanish hogfish and blue-headed wrasse can even be lifted by hand all the way to the surface without evoking a response. A 1961 observational study of approximately 200 species in European public aquaria reported many cases of apparent sleep. On the other hand, sleep patterns are easily disrupted and may even disappear during periods of migration, spawning, and parental care.

Sleeping African Dwarf Fischers chameleon: *Kinyongia tavetanum*, previously known as *Bradypodion tavetanum*.

A Komodo dragon sleeping.

Reptiles have been subjected to electrophysiological studies of sleep. That is to say that electrical activity in the brain has been registered when the animals have been asleep. However, the EEG pattern in reptilian sleep differs from what is seen in mammals and other higher animals. In reptiles, sleep time increases following sleep deprivation, and stronger stimuli are needed to awaken the animals when they have been deprived of sleep as compared to when they have slept normally. This suggests that the sleep which follows deprivation is compensatorily deeper.

Sleep in birds

A sleeping Cockatiel

There are significant similarities between sleep in birds and sleep in mammals, which is one of the reasons for the idea that sleep in higher animals with its division into REM and NREM sleep has evolved together with warm-bloodedness. Birds compensate for sleep loss in a manner similar to mammals, by deeper or more intense SWS (slow-wave sleep).

Birds have both REM and NREM sleep, and the EEG patterns of both have similarities to those of mammals. Different birds sleep different amounts, but the associations seen in mammals between sleep and variables such as body mass, brain mass, relative brain mass, basal metabolism and other factors (see below) are not found in birds. The only clear explanatory factor for the variations in sleep amounts for birds of different species is that birds who sleep in environments where they are exposed to predators have less deep sleep than birds sleeping in more protected environments.

A flamingo with at least one cerebral hemisphere awake

A peculiarity that birds share with aquatic mammals, and possibly also with certain species of lizards (opinions differ about that last point), is the ability for unihemispheric sleep. That is the ability to sleep with one cerebral hemisphere at a time, while the other hemisphere is awake. When only one hemisphere is sleeping, only the contralateral eye will be shut; that is, when the right hemisphere is asleep the left eye will be shut, and vice versa. The distribution of sleep between the two hemispheres and the amount of unihemispheric sleep are determined both by which part of the brain has been the most active during the previous period of wake—that part will sleep the deepest—and it is also determined by the risk of attacks from predators. Ducks near the perimeter of the flock are likely to be the ones that first will detect predator attacks. These ducks have significantly more unihemispheric sleep than those who sleep in the middle of the flock, and they react to threatening stimuli seen by the open eye.

Opinions partly differ about sleep in migratory birds. The controversy is mainly about whether they can sleep while flying or not. Theoretically, certain types of sleep could be possible while flying, but technical difficulties preclude the recording of brain activity in birds while they are flying.

Sleep in mammals

Flying foxes, asleep

Sleep duration

Different animals sleep different amounts. Some animals, such as bats, sleep 18–20 hours per day, while others, including giraffes, sleep only 3–4 hours per day. There can be big differences even between closely related animals. There can also be differences between laboratory and field studies: for example, researchers in 1983 reported that captive sloths slept nearly 16 hours a day, but in 2008, when miniature neurophysiological recorders were developed that could be affixed to wild animals, sloths in nature were found to sleep only 9.6 hours a day.

Sleeping polar bears

As for birds, the main rule for mammals (with certain exceptions, see below) is that they have two essentially different stages of sleep: REM and NREM sleep (see above). An animal's feeding habits are associated with its sleep length. The daily need for sleep is highest in carnivores, lower in omnivores and lowest in herbivores. Humans do not sleep unusually much or unusually little compared to other animals, but we sleep less than many other omnivores. Many herbivores, like Ruminantia (such as cattle), spend much of their wake time in a state of drowsiness, which perhaps could partly explain their relatively low need for sleep. In herbivores, a direct correlation is apparent between body mass and sleep length; big animals sleep more than smaller ones. This correlation is thought to explain about 25% of the difference in sleep amount between different animals. Also, the length of a particular sleep cycle is associated with the size of the animal; on average, bigger animals will have sleep cycles of longer durations than smaller animals. Sleep amount is also coupled to factors like basal metabolism, brain mass and relative brain mass.

Mammals born with well-developed regulatory systems, such as the horse and giraffe, tend to have less REM sleep than the species which are less developed at birth, such as cats and rats. This appears to echo the greater need for REM sleep among newborns than among adults in most mammal species.

Sleep in monotremes

Since monotremes, egg-laying mammals, are considered to represent one of the evolutionarily oldest groups of mammals, they have been subject to special interest in the study of mammalian sleep. As early studies of these animals could not find clear evidence for REM sleep, it was initially assumed that such sleep did not exist in monotremes but developed after the monotremes left the rest of the mammals and became a separate, distinct group. However, EEG registrations of the brain stem in monotremes show a firing pattern that is quite similar to the patterns seen in REM sleep in higher mammals. In fact, the largest amount of REM sleep known in any animal is found in the platypus.

Sleep in aquatic mammals

Northern Sea Lion pup with adult female and male, the largest of the eared seals. Habitat: the northern Pacific

Among others, seals and whales belong to the aquatic mammals. Seals are grouped in earless seals and eared seals, which have solved the problem of sleeping in water differently. Eared seals, like whales, show unihemispheric sleep. The sleeping half of the brain does not awaken when they surface to breathe. When one half of a seal's brain shows slow-wave sleep, the flippers and whiskers on its opposite side are immobile.

While in the water, these seals have almost no REM sleep and may go a week or two without it. As soon as they move onto land they switch to bilateral REM sleep and NREM sleep comparable to land mammals, surprising researchers with their lack of "recovery sleep" after missing so much REM.

Cape Fur Seal, asleep in a zoo

Earless seals sleep bihemispherically like most mammals, under water, hanging at the water surface or on land. They hold their breath while sleeping under water, and wake up regularly to surface and breathe. They can also hang with their nostrils above water and in that position have REM sleep, but they do not have REM sleep underwater.

REM sleep has been observed in the pilot whale, a species of dolphin. Whales do not seem to have REM sleep, nor do they seem to have any problems because of this. One reason REM sleep might be difficult in marine settings is the fact that REM sleep causes muscular atony; that is to say, a functional paralysis of skeletal muscles that can be difficult to combine with the need to breathe regularly.

Unihemispheric sleep

Unihemispheric sleep refers to sleeping with only a single cerebral hemisphere. The phenomenon has been observed in birds and aquatic mammals, as well as in several reptilian species (the latter being disputed: many reptiles behave in a way which could be construed as unihemispheric sleeping, but EEG studies have given contradictory results). Reasons for the development of unihemispheric sleep are likely that it enables the sleeping animal to receive stimuli, threats, for instance, from its environment, and that it enables the animal to fly or periodically surface to breathe when immersed in water. Only NREM sleep exists unihemispherically, and there seems to exist a continuum in unihemispheric sleep regarding the differences in the hemispheres: in animals exhibiting unihemispheric sleep, conditions range from one hemisphere being in deep sleep with the other hemisphere being awake to one hemisphere sleeping lightly with the other hemisphere being awake. If one hemisphere is selectively deprived of sleep in an animal exhibiting unihemispheric sleep (one hemisphere is allowed to sleep freely but the other is awoken whenever it falls asleep), the amount of deep sleep will selectively increase in the hemisphere that was deprived of sleep when both hemispheres are allowed to sleep freely.

The neurobiological background for unihemispheric sleep is still unclear. In experiments on cats, where the connection between the left and the right halves of the brain stem is severed, the brain hemispheres show a desynchronized EEG where the two hemispheres can sleep independently of each other. In these cats, the state where one hemisphere slept NREM and the other was awake, as well as one hemisphere sleeping NREM with the other state sleeping REM were observed. Interestingly, the cats were never seen to sleep REM sleep with one hemisphere while the other hemisphere was awake. This is in accordance with the fact that REM sleep, as far as is currently known, does not occur unihemispherically.

Sleep in hibernating animals

Animals that hibernate are in a state of torpor, differing from sleep. Hibernation markedly reduces the need for sleep, but does not remove it. Hibernating animals end their hibernation a couple of times during the winter so that they can sleep.