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Comparative Oral+ENT Biology

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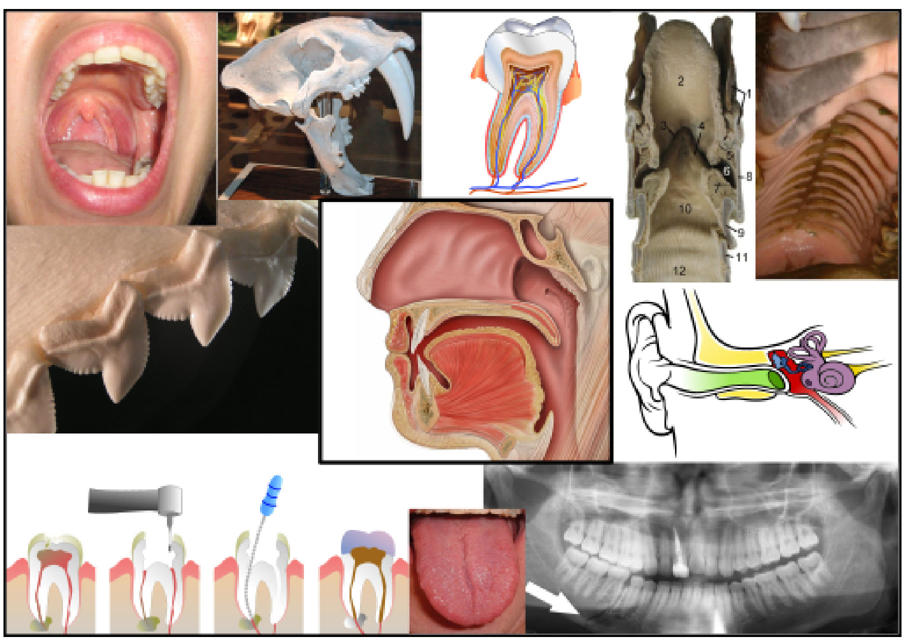
Preface
Comparative Oral+ENT Biology is designed for a semester-long course taken by undergraduate students who are preparing for careers in dentistry, medicine, veterinary, audiology, speech pathology or evolutionary biology. It explores the mouth, ears, nose and throat of humans and animals discussing their evolution, development, function, and some common clinical issues. The text provides a broad background through an integrative and organismal perspective. It crosses the boundaries of disciplines, anatomical regions and professions to present structures and mechanisms within an evolutionary context. This textbook is richly illustrated with images made available at Wikimedia Commons. It contains materials from and links to several sources of Open Education Resources.

Preface to Comparative Oral+ENT Biology



Topics of study in comparative oral+ENT biology.

Welcome to *Comparative Oral+ENT Biology*. We created this textbook to support the multidisciplinary study of the mouth and associated structures. It integrates aspects of evolution, development, ecology, microbiology, structure and function. The main goal is to help college students interested in the subject to build a comprehensive background as a base for their graduate studies.

Building an integrative perspective

This book offers an introduction to the mouth and associated cavities in the head: nose, throat and ears. An integrative view of the subject is developed in a multidisciplinary exploration of the content. Connections between structures, mechanisms and evolution are examined without restraint by the traditional separation between dentistry, otorhynolaryngology, veterinary, evolutionary biology or other related disciplines.

Comparative Oral+ENT Biology is written at a level suitable for college students with the basic background on animal structure, function and diversity that is usually built during the freshman year in the biology major. The book is intended to familiarize the reader with the major aspects of origin, structure, function and clinical relevance of each subject, favoring simplicity over completeness. It explores examples that illustrate the advantages of integrating across fields of knowledge to develop a holistic perspective of the subject. The reader will accrue a multidisciplinary knowledge base that will give context to specific concepts learned in graduate school. This knowledge base will facilitate collaboration with professionals specialized in other fields that are also dedicated to the mouth and associated cavities.

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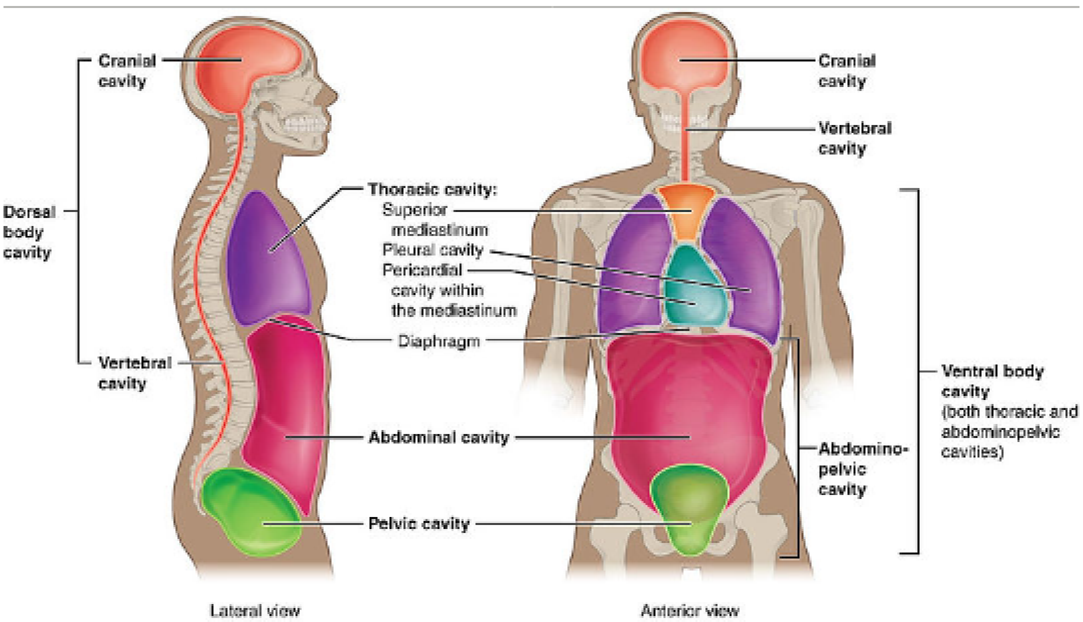
Connected Cephalic Cavities
The mouth, ears, nose and throat are have cavities that are physically interconnected in the head. These structures contain organs that may have very distinct function and yet interact during development, through proximity or action.

The Cavities of the Head

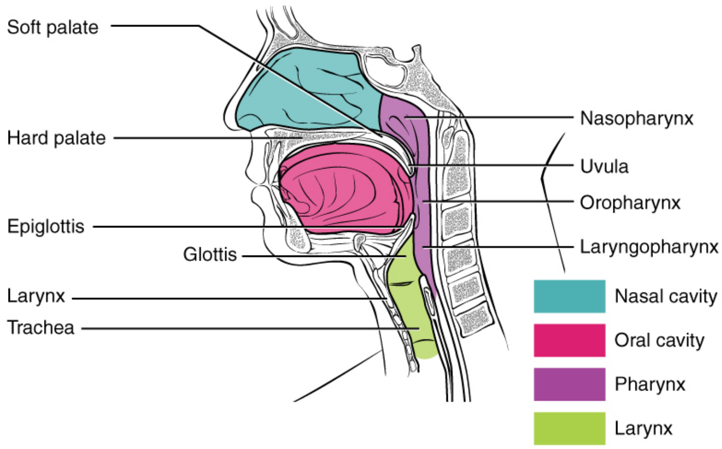
The vertebrate body has several cavities, mostly in the trunk and head. These are well delimited spaces containing fluids or organs. The largest body cavities are found in the trunk. The head contains the cranial cavity housing the brain and the neck contains the vertebral cavity which lodges the spinal cord.



Major cavities of the human body. More details.

Several smaller cavities are also present in the head, however, and these make the subject of this book. The mouth contains the oral cavity. Immediately superior to it, one finds the nasal cavity. Both oral and nasal

cavities connect to the pharynx (throat), which connects to the larynx (voice box) and to the ears. This physical connection between organs reflects evolutionary, developmental or functional interactions between them. It also links them from a clinical perspective, as the connection facilitates the spread of a same malignancy from one region to another.



Major cavities of the facial region of the head and neck. More details.

The mouth is the first portion of the alimentary canal that receives food and saliva. It contains of two spaces, the vestibule (between the teeth and the lips or cheek) and the oral cavity. The mouth, normally moist, is lined with a mucous membrane. The lips mark the transition from mucous membrane to skin, which covers most of the body. After food is processed in the mouth, it is passed into the pharynx, which is a muscular tube that is shared with the respiratory system. Food in the pharynx triggers the swallowing reflex, which is an elaborate behavior involving more than a dozen muscles. Swallowing pushes the food into the esophagus which then transports it down to the stomach.

In addition to its primary role as the beginning of the digestive system, in humans the mouth also plays a significant role in communication. While primary aspects of the voice are produced by focal folds in the larynx.

Muscles in the tongue and lips are also needed to produce the range of sounds included in human language. The voice is also modified through resonance within the nasal cavity and sinuses that are connected to it. The roof of the nasal cavity houses the olfactory epithelium, containing sensory receptors responsible for the sense of smell.

The mouth is also connected to the ears by the auditory (Eustachian) tubes. The ears are essential to hearing and balance. The connection with the mouth allows for the air pressure behind the eardrum the be equalized with that of the external environment but this connection also facilitates the access of germs to the ears, causing middle ear infections.

This book focuses on the mouth and associated cavities of the head, including the ears, nose and throat (ENT) in addition to some smaller spaces. It discusses the anatomy and physiology of these structures in humans but also in animals. The extension to animals is justified because the evolutionary history and diversity of the mouth and ENT can help the students understand the design principles of these structures. Similarly, the book presents some major clinical issues and treatments in animals and humans.

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Origins of the Mouth
The mouth is the entrance of the digestive system. It allows the food to be ingested faster than it could be digested. Most animals have mouths, except sponges and a few species within other groups. The mouth is the first or second structure to be formed during development, through gastrulation.

What is a Mouth?

A mouth is an entrance into a concave, hollow space. In animals, it is the opening through which food enters the body to be processed and digested. The act of bringing a substance into the body through the mouth for digestion is called ingestion.

Human mouth open. More details.

Timing of Digestion and Ingestion

Digestion usually begins after a food item in ingested. In some cases, however, the animal secretes digestive juices onto an external food item and then ingests the food partially digested. As an example, most spiders bite their prey injecting poison to kill it. They have a narrow gut that can only cope with liquid food and spiders have two sets of filters to keep solids out.

[7] They use one of two different systems of external digestion. Some pump digestive enzymes from the midgut into the prey and then suck the liquefied tissues of the prey into the gut, eventually leaving behind the empty husk of the prey. Others grind the prey to pulp using the chelicerae and the bases of the pedipalps, while flooding it with enzymes; in these species, the chelicerae and the bases of the pedipalps form a preoral cavity that holds the food they are processing.

Spider *Cheiracanthium punctorium*, displaying fangs. More details.

Killing the prey without immediately ingesting it prevents potential injury from defensive behaviors. External digestion facilitates ingestion by liquefying the tissues of the prey. Ingestion before digestion, on the other hand, prevents loss of food to competitors and loss of water, digestive juices and small food pieces that could get spread in the environment.

Mouthless Animals

Certain insects lack mouths as adults. Moths in the family Saturniidae, for example, have very short adult lives (< a week). During this time they search for a mate, reproduce and die, but they do not feed. These animals have a normal buccal apparatus as larvae, but during metamorphosis they do not develop a mouth for their adult life.

Mouthless moth *Actias luna* (Saturniidae). More details.

As a more extreme example, marine platyhelmints (flatworms) of the genus *Paracatenula* lack a mouth, pharynx and gut. They live in a symbiosis with intracellular bacteria. Their symbiont-housing cells (bacteriocytes) collectively form the trophosome tissue, which functionally replaces the digestive tract.

Mouthless marine flatworm *Paracatenula* crawling in sediment. The white trophosome contains endosymbiont bacteria while the anterior transparent part of the worm is free of bacteria. More details.

Phylogenetic Origin

Mouths and digestive systems are found in all animal phyla except sponges. The central opening present in most sponges should not be confused with a mouth because it serves as a common exit way for water that enters the sponge throughout its body. Sponges are filtering animals and their cells incorporate nutrients suspended in the water that passes though the animal.

There is no selective ingestion of food by the animal, and no digestive system or digestive juices.

Yellow tube sponge, *Aplysina fistularis*. More details.

Cnidarians (corals, jelly-fish) and ctenophores have mouths and many are predators, using tentacles to capture and ingest their prey. Ctenophorans of the class Nuda lack tentacles. They have large mouths and stiffened cilia that are used as teeth to grip parts of the prey and transport it into the stomach.

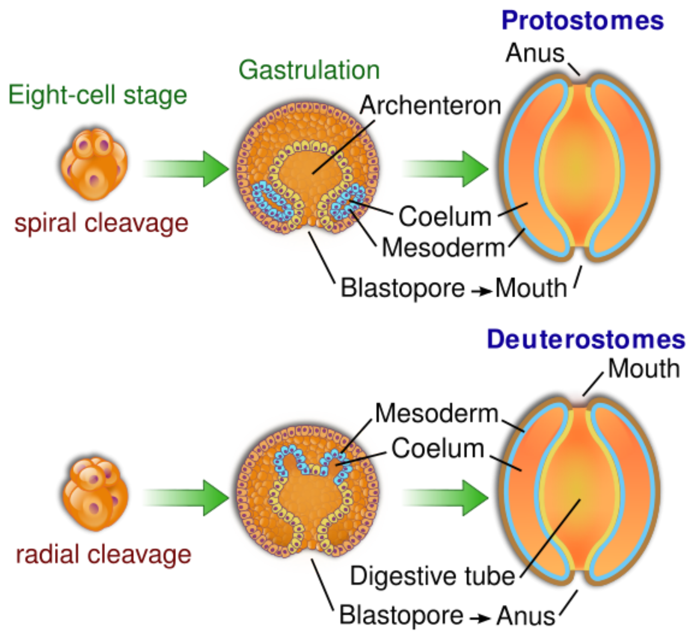
Ctenophores of the family *Beroidae* (class Nuda) are

carnivorous and ingest other ctenophores almost as large as themselves. More details.

Sponges have traditionally been considered the oldest phylum of multicellular animals and ctenophores (comb jellies) have been considered more closely related to cnidarians (corals and jelly-fish). Evidence has been accumulating, however, that ctenophores are the oldest metazoans, followed by sponges and cnidarians. This would include the mouth as a feature of the first major group of metazoans (multicellular animals).

Developmental Origin

The mouth is the first or the second structure in the entire body to have its position determined during development. As the zygote enters cell division, the growing mass of cells eventually forms a sphere with a single layer of cells and a fluid-filled core. At this point the embryo is called a blastula.



After gastrulation, the blastopore gives origin to the mouth in protostome embryos, whereas it originates the anus in deuterostomes embryos. More details.

[link]

Gastrulation occurs when a blastula folds inward, creating and inner tube that later becomes the digestive tube. It also gives origin to the mouth and the anus. The point in which the tissues start folding in is called the blastopore. In protostomes (annelids, mollusks and arthropods), the mouth (stoma) develops from the blastopore. Protostome derives from the Greek word protostoma meaning "first mouth"(πρώτος + στόμα). In deuterostomes (echinoderms and chordates) the order is reversed: the blastopore forms the anus and the mouth forms where the infolding touches the other side of the embryo. Deuterostome means "second mouth" (δεύτερος + στόμα).

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Working with the Mouth+ENT

The structures of the mouth+ENT are the focus of many professions, dealing with biology and health in animals and humans. They are also part of the job in many other professions because these structures are present in some many aspects of our daily lives.

Professions of the Mouth and ENT

The mouth and ENT are not the subject of a single profession. Many professionals with various backgrounds and interests deal with aspects of oral biology. It is important for them not to work in isolation but to learn about all the main aspects of oral biology. Several challenges in oral biology present multidisciplinary problems that take discussion and collaboration among professionals in multiple fields to produce appropriate solutions. Some of the main professions that deal with the mouth are:

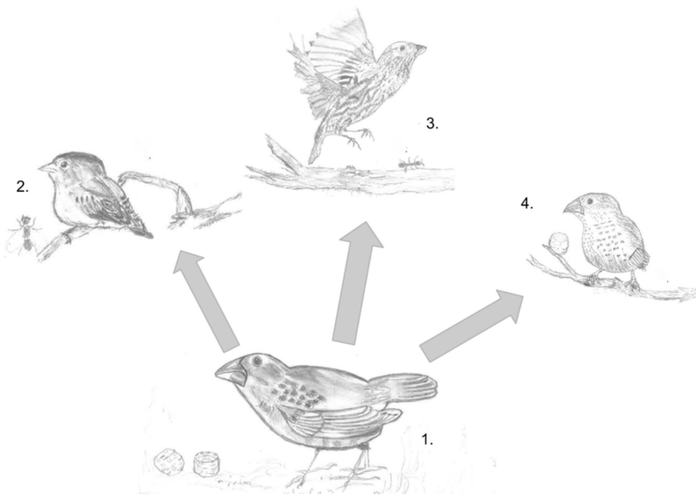
Paleontologist and archeologist, biologist

Paleontologists study life that existed prior to, and sometimes including, the start of the Holocene Epoch (roughly 11,700 years before present). They mostly rely on fossils to determine an organism's evolution and interactions with other organisms and their environments (their paleoecology). Vertebrates have evolved powerful biting which requires highly compact structures for teeth, jaws and other parts of the skull associated with mastication. These structures not only fossilize well but they reveal several aspects of the feeding ecology of the animal. Oral biology therefore makes a disproportionately large part of the material studied in paleontology.

Archeology is the study of human activity through the recovery and analysis of material remains, including human fossils, food remains, the ruins of buildings, and human artifacts—items such as tools, pottery, and jewelry. As described above, remains of jaws and teeth provide rich material for recovery of the human past, including information on age, diet and health condition of the subject.

Fossil remains of Lucy, *Australopithecus afarensis*, from Etiopia, dated 3.2 million years old. More details.

A biologist is a scientist who studies life, specifically organisms and their relationship to their environment. Several branches of biology focus on the mouth. Questions about the evolution of the mouth are answered through comparative analysis, phylogenetic analysis and experimentation. As an example, a series of studies have shown how Darwin's finches (subfamily Geospizinae) have colonized the Galápagos Islands and diversified into various species with different beak morphologies. These endemic species occupy different dietary niches, specializing on different seed sizes and textures that have driven the divergent evolution of their beak morphologies. Other branches of biology conduct most of the non-clinical medical research associated with the mouth. This includes the study of genetic and developmental issues, infections, occupational issues, autoimmune diseases and cancer.



Adaptive radiation of the finch *Geospiza magnirostris* into three other species of finches found on the Galapagos Islands. More details.

Health professionals

Clinical practice and research on heath issues affecting the mouth and ENT is also conducted by various professionals. Dentists deal not only with teeth, but also with gum disease, and issues of the temporomandibular joint. Otorhynolaringologists focus on conditions of the ear, nose, and throat (ENT) and related structures of the head and neck. Both professionals can specialize in maxillofacial surgery.

Dentist treating child.
More details.

Audiologists help treat and prevent hearing loss and balance disorders, and rehabilitate individuals with tinnitus, auditory processing disorders, cochlear implant users and/or hearing aid users. They employ various testing strategies to determine whether someone can hear within the normal range, and if not, which portions of hearing (high, middle, or low frequencies) are affected, to what degree, and where the lesion causing the hearing loss is found (outer ear, middle ear, inner ear, auditory nerve and/or central nervous system).

Audiologist examining the hearing sensitivity of a patient. More details.

Speech pathologists specialize in the evaluation and treatment of communication disorders, cognition, voice disorders, and swallowing disorders. Speech services begin with initial screening for communication and swallowing disorders and continue with assessment and diagnosis, consultation for the provision of advice regarding management, intervention and treatment, and provision counseling and other follow up services for these disorders.

A veterinary will offer most of the services described above but for non-human patients. Veterinary dentistry is a veterinary specialty that offers services in the fields of endodontics, oral and maxillofacial radiology, oral and maxillofacial surgery, oral medicine, orthodontics, pedodontics, periodontics, and prosthodontics. Similar to human dentists, they treat conditions such as jaw fractures, malocclusions, oral cancer, periodontal disease, and stomatitis and other conditions unique to veterinary medicine (e.g. feline odontoclastic resorptive lesions). Some animals have specialist dental workers, such as equine dental technicians who conduct routine work on horses.

Veterinary dentist treating a horse. More details.

Other professions

Many other professions exist that provide direct support to the services described above. And many other professions not directly related to the ones listed above can also have jobs dedicated to the mouth+ENT. These could include, for example, graphical design, marketing or biochemistry. Oral+ENT biology is a subject that permeates our physiology, behavior, culture, and economy, and therefore is naturally present in a great variety of occupations.

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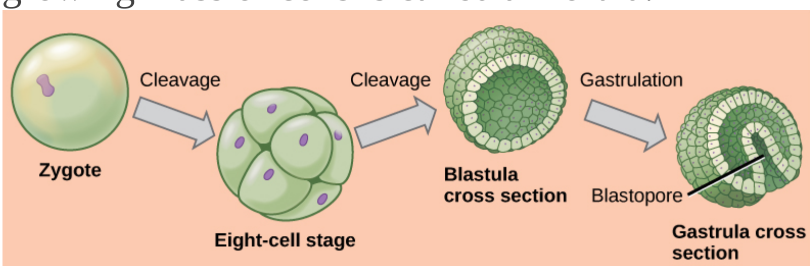
The Origin of the Body Tissues
After fertilization, the zygote starts to divide forming at first a ball of cells called morula. Cell division continues and a hollow inner space is formed, characterizing the stage of blastula. The embryo then folds inwards, creating internal and external layers of cells. This allows for differentiation of ectoderm, mesoderm and endoderm. A second folding of the ectoderm differentiates the tissues that originate the nervous system. Organogenesis follows, producing the basic structure of most body organs early in development.

When fertilization occurs, a zygote is formed. This cell undergoes mitosis repeatedly, increasing the number of cells in a process called cleavage. This growing mass of cells is called a morula.

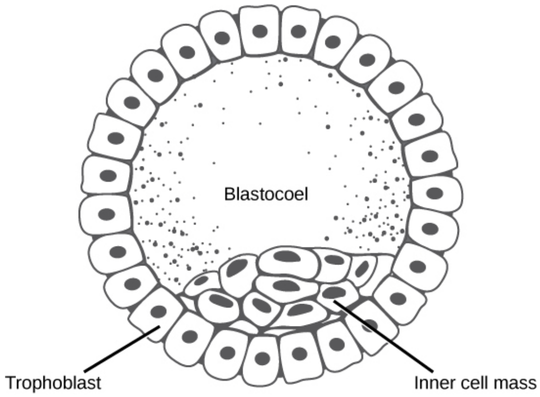


Initial stages of development. More details.

Blastulation

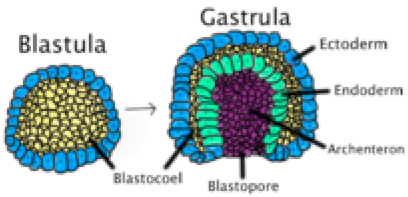
Through cleavage, the cells divide without an increase in mass. One large single-celled zygote divides into multiple smaller cells. After the cleavage has produced over 100 cells, an empty space called blastocoel forms in the center. At this point, the entire structure is called a blastula (in mammals it is called blastocyst). Each cell within the blastula is called a blastomere.

In mammals, this stage is called blastocyst because it has two types of cells. The inner cell mass forms the embryo, whereas the outer layer (called trophoblast) will participate in the formation of the placenta.



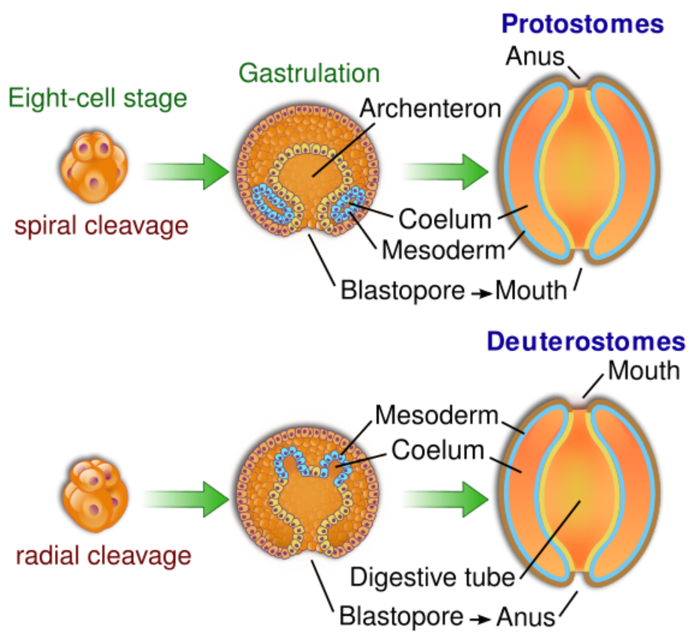
The mammalian blastocyst with two cell groups: the inner cell mass and the trophoblast. More details.

Gastrulation



Gastrulation occurs when a blastula, made up of one layer, folds inward and enlarges to create a gastrula, with 3 layers of cells. More details.

The next stage in embryonic development is the formation of the body plan. The cells in the blastula rearrange themselves spatially to form three layers of cells. This process is called gastrulation. During gastrulation, the blastula folds upon itself through an invagination process. This forms a blastopore that originates the mouth or the anus. By the end of gastrulation, the embryo has three layers of cells: endoderm, mesoderm and ectoderm. Each of these layers is called a germ layer and each germ layer differentiates into different organ systems.

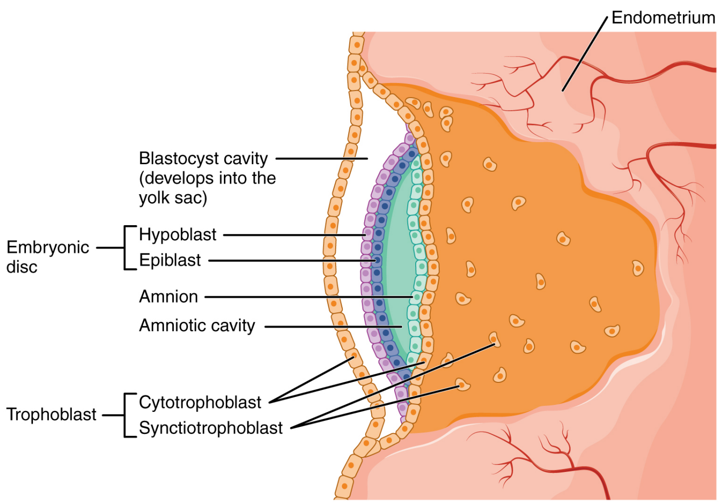


After gastrulation, the blastopore gives origin to the mouth in protostome embryos, whereas it originates the anus in deuterostomes embryos. More details.

In mammals, the process is a bit more complex because the blastocyst is implanted into the wall of the uterus from which it receives nourishment through the developing placenta (Fig. 4). Cells within the blastocyst start to organize into layers. Some grow to form the extra-embryonic membranes

needed to support and protect the growing embryo: the amnion, the yolk sac, the allantois, and the chorion.

At the beginning of the second week, the cells of the inner cell mass form into a two-layered disc of embryonic cells, and a space—the amniotic cavity—opens up between it and the trophoblast. Cells from the upper layer of the disc (the epiblast) extend around the amniotic cavity, creating a membranous sac that forms into the amnion by the end of the second week. The amnion fills with amniotic fluid and eventually grows to surround the embryo. Early in development, amniotic fluid consists almost entirely of a filtrate of maternal plasma, but as the kidneys of the fetus begin to function at approximately the eighth week, they add urine to the volume of amniotic fluid. Floating within the amniotic fluid, the embryo—and later, the fetus—is protected from trauma and rapid temperature changes. It can move freely within the fluid and can prepare for swallowing and breathing out of the uterus.

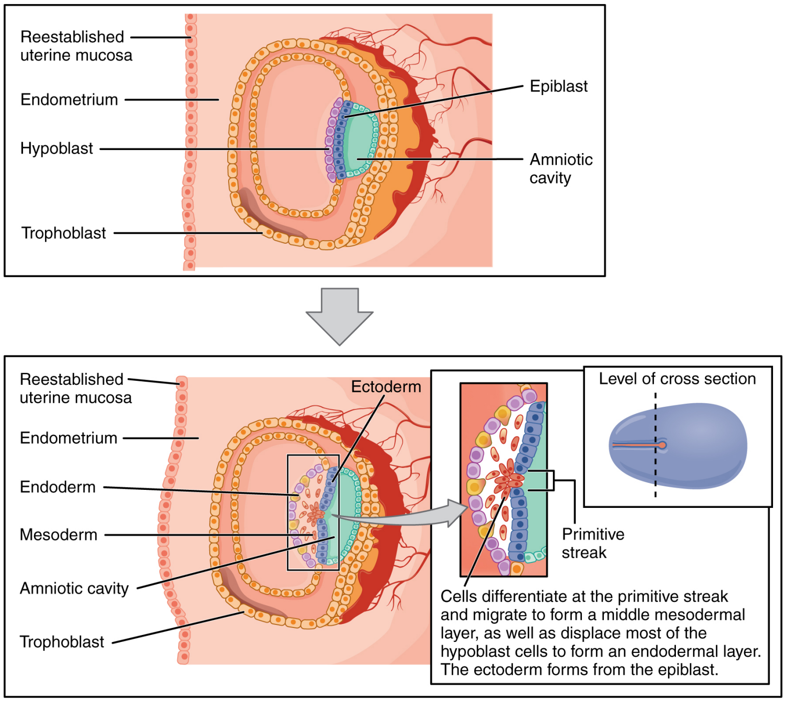


Formation of the embryonic disc leaves spaces on either side that develop into the amniotic cavity and the yolk sac. More details.

On the ventral side of the embryonic disc, opposite the amnion, cells in the lower layer of the embryonic disk (the hypoblast) extend into the blastocyst cavity and form a yolk sac. The yolk sac supplies some nutrients absorbed from the trophoblast and also provides primitive blood circulation to the developing embryo for the second and third week of development. When the placenta takes over nourishing the embryo at approximately week 4, the yolk sac has been greatly reduced in size and its main function is to serve as the source of blood cells and germ cells (cells that will give rise to gametes). During week 3, a finger-like outpocketing of the yolk sac develops into the allantois, a primitive excretory duct of the embryo that will become part of the urinary bladder. Together, the stalks of the yolk sac and allantois establish the outer structure of the umbilical cord.

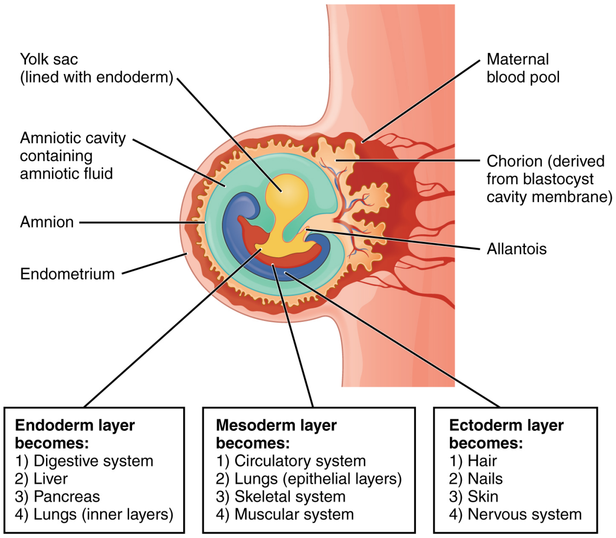
The last of the extra-embryonic membranes is the chorion, which is the one membrane that surrounds all others. The development of the chorion relates to the growth and development of the placenta.

As the third week of development begins, the two-layered disc of cells becomes a three-layered disc through the process of gastrulation, during which the cells transition from totipotency to multipotency. The embryo, which takes the shape of an oval-shaped disc, forms an indentation called the primitive streak along the dorsal surface of the epiblast. A node at the caudal or “tail” end of the primitive streak emits growth factors that direct cells to multiply and migrate. Cells migrate toward and through the primitive streak and then move laterally to create two new layers of cells. The first layer is the endoderm, a sheet of cells that displaces the hypoblast and lies adjacent to the yolk sac. The second layer of cells fills in as the middle layer, or mesoderm. The cells of the epiblast that remain (not having migrated through the primitive streak) become the ectoderm.



Formation of the three primary germ layers occurs during the first 2 weeks of development in humans. The embryo at this stage is only a few millimeters in length. More details.

Each of these germ layers will develop into specific structures in the embryo. Whereas the ectoderm and endoderm form tightly connected epithelial sheets, the mesodermal cells are less organized and exist as a loosely connected cell community. The ectoderm gives rise to cell lineages that differentiate to become the central and peripheral nervous systems, sensory organs, epidermis, hair, and nails. Mesodermal cells ultimately become the skeleton, muscles, connective tissue, heart, blood vessels, and kidneys. The endoderm goes on to form the epithelial lining of the gastrointestinal tract, liver, and pancreas, as well as the lungs.



Following gastrulation, embryonic cells of the ectoderm, mesoderm, and endoderm begin to migrate and differentiate into the cell lineages that will give rise to mature organs and organ systems in the infant. More details.

Neurulation

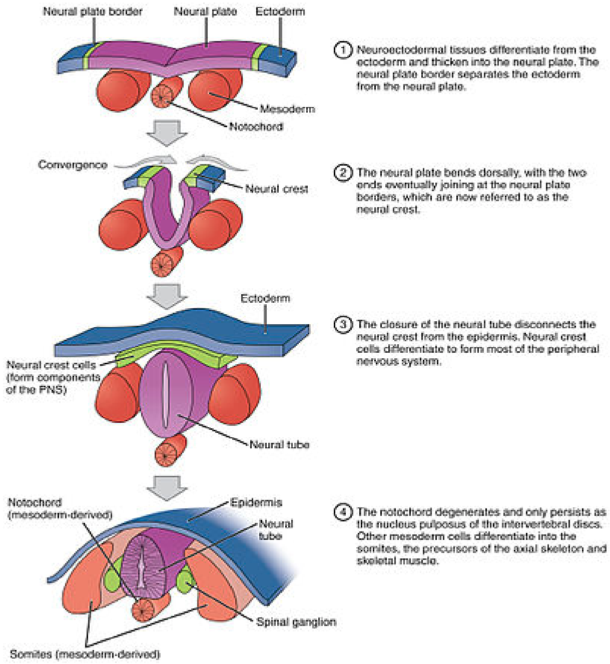
In vertebrates, one of the primary steps during development is the formation of the neural system. The ectoderm forms epithelial cells and tissues, and neuronal tissues. During the formation of the neural system, special signaling molecules called growth factors signal some cells at the edge of the ectoderm to become epidermis cells. The remaining cells in the center form the neural plate. If the signaling by growth factors were disrupted, then the entire ectoderm would differentiate into neural tissue.

In a process called neurulation, the neural plate undergoes a series of cell movements where it rolls up and forms a tube called the neural tube, as

illustrated in Figure. In further development, the neural tube will give rise to the brain and the spinal cord. The process begins when the notochord (formed by mesoderm) induces the formation of the central nervous system (CNS) by signaling the ectoderm germ layer above it to form the thick and flat neural plate. The neural plate folds in upon itself to form the neural tube, which will later differentiate into the spinal cord and the brain, eventually forming the central nervous system.

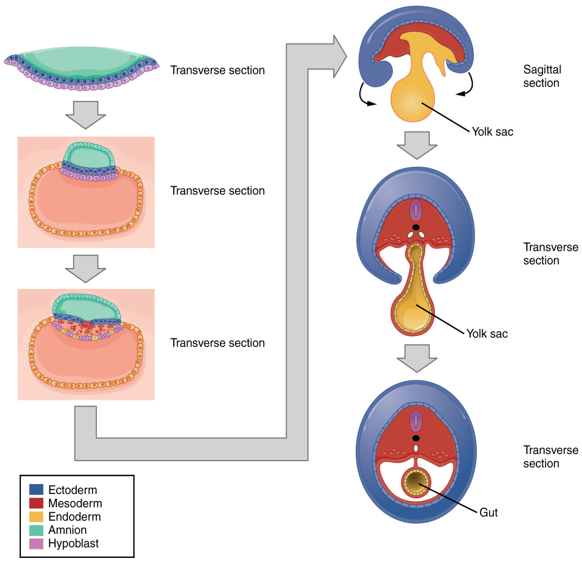
Different portions of the neural tube form by two different processes, called primary and secondary neurulation, in different species.

- In **primary neurulation**, the neural plate creases inward until the edges come in contact and fuse. Primary neurulation occurs in response to soluble growth factors secreted by the notochord. Ectodermal cells are induced to form neuroectoderm from a variety of signals.
- In **secondary neurulation**, the tube forms by hollowing out of the interior of a solid precursor. In secondary neurulation, the neural ectoderm and some cells from the endoderm form the medullary cord. The medullary cord condenses, separates and then forms cavities. These cavities then merge to form a single tube. Secondary neurulation occurs in the posterior section of most animals but it is better expressed in birds. Tubes from both primary and secondary neurulation eventually connect.



Transverse sections that show the progression of the neural plate to the neural groove from bottom to top. More details.

The embryo, which begins as a flat sheet of cells, begins to acquire a cylindrical shape through the process of embryonic folding. It folds laterally and again at either end, forming a C-shape with distinct head and tail ends. The embryo envelops a portion of the yolk sac, which protrudes with the umbilical cord from what will become the abdomen. The folding essentially creates a tube, called the primitive gut, that is lined by the endoderm. The amniotic sac, which was sitting on top of the flat embryo, envelops the embryo as it folds.



Embryonic folding converts a flat sheet of cells into a hollow, tube-like structure. More details.

Within the first 8 weeks of gestation, a developing embryo establishes the rudimentary structures of all of its organs and tissues from the ectoderm, mesoderm, and endoderm. This process is called organogenesis.

The mesoderm that lies on either side of the vertebrate neural tube develops into the various connective tissues of the animal body. A spatial pattern of gene expression reorganizes the mesoderm into groups of cells called somites with spaces between them. The somites, illustrated in the figure below will further develop into the ribs, lungs, and segmental (spine) muscle.

Five-week old human embryo with somites along the length of the body. More details.

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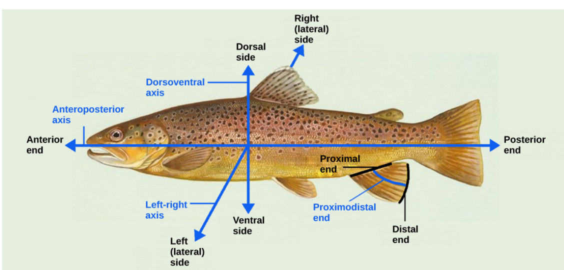
Formation of the Face

The activation of controller genes coordinates the secretion of chemical signals that direct the differentiation of cells. A series of pharyngeal arches forms on each side of the pharynx and provides the precursors to most cranial and facial structures. The hard palate is formed through the early development of its medial anterior portion, followed by growth of the secondary portion from lateral to medial. Incomplete growth or fusion of the secondary portion results in cleft palate.

Vertebrate Axis Formation

Even as the germ layers form, the ball of cells still retains its spherical shape. However, animal bodies have lateral-medial (left-right), dorsal-ventral (back-belly), and anterior-posterior (head-feet) axes, illustrated in the figure below.



Animal bodies have three axes for symmetry. More details.

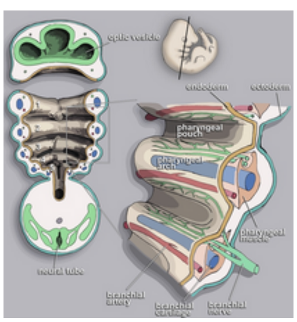
How are these established? Spemann and Mangold took dorsal cells from one embryo and transplanted them into the belly region of another embryo. They found that the transplanted embryo now had two notochords: one at the dorsal site from the original cells and another at the transplanted site. This suggested that the dorsal cells were genetically programmed to form the notochord and define the axis. Since then, researchers have identified

many genes that are responsible for axis formation. Mutations in these genes leads to the loss of symmetry required for organism development.

Animal bodies have externally visible symmetry. However, the internal organs are not symmetric. For example, the heart is on the left side and the liver on the right. The formation of the central left-right axis is an important process during development. This internal asymmetry is established very early during development and involves many genes. Research is still ongoing to fully understand the developmental implications of these genes.

Pharyngeal arches

Unique to the development of vertebrates, a series of pharyngeal arches forms on each side of the pharynx. These arches contain all three embryonic tissues and they are precursors for numerous structures in the developing animal. Each arch contains an artery, a cartilage, a cranial nerve and muscle tissue.



Schematic representation of a frontal section across the pharyngeal arches of a human

embryo, showing the main components of each arch. More details.

The first, most anterior pharyngeal arch gives rise to the lower jaw. The second arch becomes part of the hyoid and most muscles of the facial expression. In fishes, the posterior pharyngeal arches develop into the branchial arches or gill arches that support the gills for respiratory gas exchanges with the medium.

Ventral view of a fish (pike) with the operculums held open to show the gill arches bearing gills. More details.

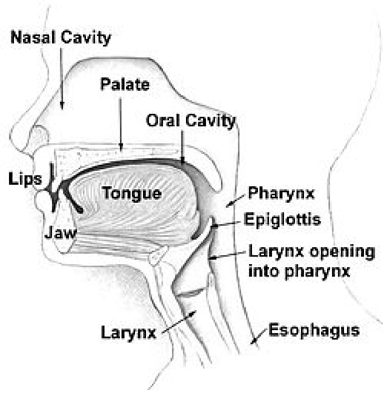
In tetrapods, the anterior arches also develop into components of the ear, larynx, tonsils, and thymus, whereas the posterior arches form the larynx, its muscles and part of the hyoid. The genetic and developmental basis of pharyngeal arch development is well characterized. It has been shown that Hox genes and other developmental genes such as *DLX* are important for patterning the anterior/posterior and dorsal/ventral axes of the branchial arches. Some fish species have a second set of jaws in their throat, known as pharyngeal jaws, which develop using the same genetic pathways involved in oral jaw formation.

In the human embryo, the arches are first seen during the fourth week of development. They appear as a series of outpouchings of mesoderm on both sides of the developing pharynx. The arches are numbered from 1 to 6, with 1 being the arch closest to the head of the embryo, and arch 5 existing only transiently. The vasculature of the pharyngeal arches is also known as the aortic arches.

The development of the pharyngeal arches provides a useful landmark with which to establish the precise stage of embryonic development. Their formation and development corresponds to Carnegie stages 10 to 16 in mammals, and Hamburger-Hamilton stages 14 to 28 in the chicken. Although there are six pharyngeal arches, in humans the fifth arch exists only transiently during embryogenesis.

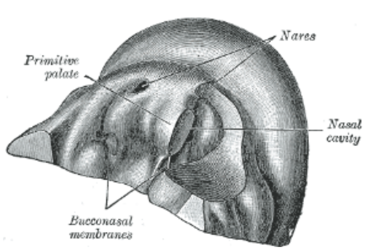
Formation of the palate

The palate is the roof of the mouth and it is exclusive to mammals. It separates the oral cavity from the nasal cavity. A similar structure is found in crocodilians, but, in most other tetrapods, the oral and nasal cavities are not truly separate. The palate is divided into two parts, the anterior bony hard palate, and the posterior fleshy soft palate (or velum).



Sagittal section of the head showing the palate as a physical separation between the oral and nasal cavities. More details.

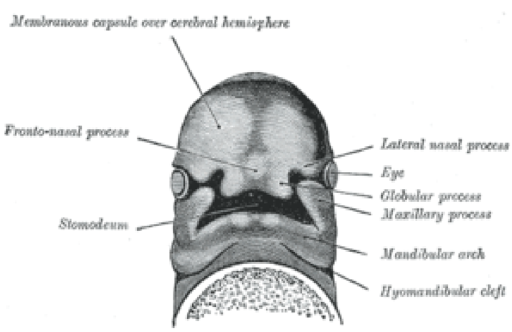
Around the 5th week of human development, the intermaxillary segment arises as a result of fusion of the two medial nasal processes and the frontonasal process within the embryo. The intermaxillary segment give rise to the primary palate. The primary palate will form the premaxillary portion of the maxilla (anterior one-third of the final palate). This small portion is anterior to the incisive foramen and will contain the maxillary incisors.



Primitive

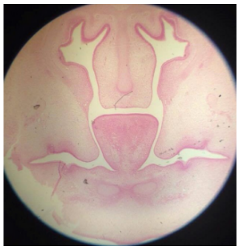
(primary) palate of a human embryo of thirty-seven to thirty-eight days. More details.

The development of the secondary palate commences in the sixth week of human embryological development. It is characterized by the formation of two palatal shelves on the maxillary prominences, the elevation of these shelves to a horizontal position, and then a process of palatal fusion between the horizontal shelves. The shelves will also fuse anteriorly upon the primary palate, with the incisive foramen being the landmark between the primary palate and secondary palate. This forms what is known as the roof of the mouth, or the hard palate.



Formation of the secondary palate in a human embryo about twenty-nine days old. The palatal shelves are yet to form from the maxillary processes. More details.

The formation and development of the secondary palate occurs through signaling molecules SHH, BMP-2, FGF-8 among others. Failure of the secondary palate to develop correctly may result in a cleft palate disorder.

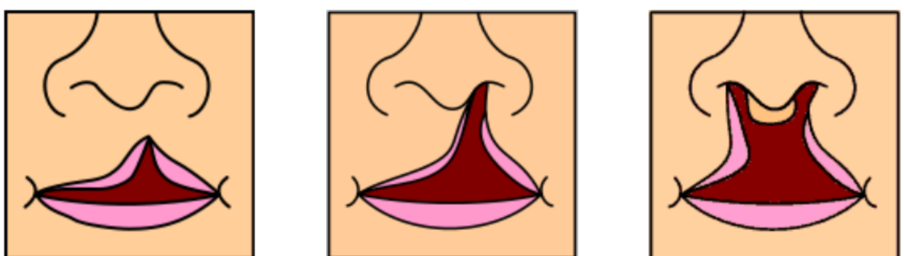


Formation of the secondary palate. The superior central structure is the nasal septum and inferior to it is the tongue. Palatal shelves are developin g on each side of the tongue. They will elevate and fuse to

each other, separating the nasal and oral cavities. More details.

Cleft palate

Cleft lip and cleft palate, also known as orofacial cleft, is a group of conditions that includes cleft lip, cleft palate, and both together. A cleft lip contains an opening in the upper lip that may extend into the nose. The opening may be on one side, both sides, or in the middle.



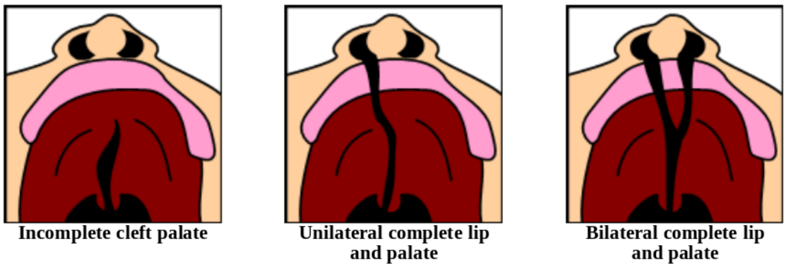
Unilateral incomplete   Unilateral complete   Bilateral complete

Types of cleft lip. More details (left, middle, right).

A cleft palate is when the roof of the mouth contains an opening into the nose. The two plates of the skull that form the hard palate (roof of the mouth) are not completely joined. The soft palate is in these cases cleft as well. In most cases, cleft lip is also present. Cleft palate occurs in about one in 700 live births worldwide.

Cleft palate can occur as complete (soft and hard palate, possibly including a gap in the jaw) or incomplete (a 'hole' in the roof of the mouth, usually as a cleft soft palate). When cleft palate occurs, the uvula is usually split. It occurs due to the failure of fusion of the lateral palatine processes, the nasal septum, and/or the median palatine processes.

These disorders can result in feeding problems, speech problems, hearing problems, and frequent ear infections. Less than half the time the condition is associated with other disorders.



Types of cleft palate. More details (left, middle, right).

The development of the face involves the fusion of elements that grow from each side and meet in the middle. If these tissues fail to meet, a gap appears where the tissues should have joined (fused). This may happen in any single joining site, or simultaneously in several or all of them. The resulting birth defect reflects the locations and severity of individual fusion failures (e.g., from a small lip or palate fissure up to a completely malformed face). More details.

The upper lip is formed earlier than the palate. Formation of the palate is the last step in joining five embryonic facial lobes, and involves the most posterior of them. This process is vulnerable to multiple toxic substances, environmental pollutants, and nutritional imbalance, in addition to being influenced by genetic predisposition.

A cleft lip or palate can be successfully treated with surgery. This is often done in the first few months of life for cleft lip and before eighteen months for cleft palate. Speech therapy and dental care may also be needed. The surgeon approximates the sides of the lips that should have fused and tries to line up the cut with the natural lines in the upper lip to conceal any scar. Stitches are positioned far up the nose to make them less visible. Incomplete cleft provides more tissue for the reconstruction work and tends to result in a more supple and natural-looking upper lip.

A cleft palate can be temporarily covered with a palatal obturator (a prosthetic device made to fit the roof of the mouth covering the gap). It can be corrected by surgery, usually performed between 6 and 12 months. Approximately 20–25% require a single palatal surgery to achieve normal, non-hypernasal speech. Combinations of surgical methods and repeated surgeries are often necessary, however, as the child grows. If the cleft extends into the maxillary alveolar ridge, the gap is usually corrected by filling the gap with bone tissue. The bone tissue can be acquired from the patients own chin, rib or hip.

Cleft palate in animals

Cleft lips and palates are occasionally seen in cattle and dogs, and rarely in goats, sheep, cats, horses, pandas and ferrets. Most commonly, the defect involves the lip, rhinarium, and premaxilla. Clefts of the hard and soft palate are sometimes seen with a cleft lip. Difficulty with nursing is the most common problem associated with clefts, but aspiration pneumonia, regurgitation, and malnutrition are often seen with cleft palate.

Cleft lip in a Boxer. More details.

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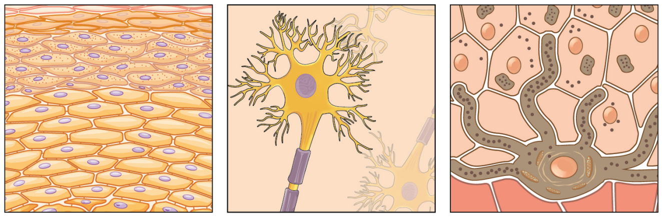
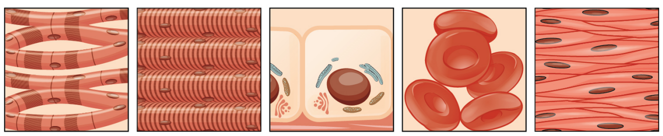
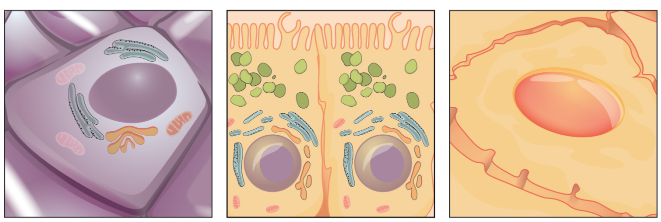
Tissue Types
The three types of embryonic tissue originate the four types of mature tissue. These in turn make up all the organs of the body. One embryonic tissue can form more than one type of mature tissue, whereas a same type of mature tissue can be formed from more than one embryonic tissue.

Embryonic vs. Mature Tissues

The three embryonic tissues form the distinct germ layers from which all the tissues and organs of the human body eventually form. Each germ layer is identified by its relative position: ectoderm (ecto- = “outer”), mesoderm (meso- = “middle”), and endoderm (endo- = “inner”). Figure 1 shows the types of tissues and organs associated with the each of the three germ layers. Note that epithelial tissue originates in all three layers, whereas nervous tissue derives primarily from the ectoderm and muscle tissue from mesoderm.

Four primary body tissues

The tissues of multicellular, complex animals are four primary types: epithelial, connective, muscle, and nervous. Recall that tissues are groups of similar cells group of similar cells carrying out related functions. These tissues combine to form organs—like the skin or kidney—that have specific, specialized functions within the body. Organs are organized into organ systems to perform functions; examples include the circulatory system, which consists of the heart and blood vessels, and the digestive system, consisting of several organs, including the stomach, intestines, liver, and pancreas. Organ systems come together to create an entire organism.

Germ Layer	Gives rise to:
Ectoderm	Epidermis, glands on skin, some cranial bones, pituitary and adrenal medulla, the nervous system, the mouth between cheek and gums, the anus  Skin cells; Neurons; Pigment cell
Mesoderm	Connective tissues proper, bone, cartilage, blood, endothelium of blood vessels, muscle, synovial membranes, serous membranes lining body cavities, kidneys, lining of gonads  Cardiac muscle; Skeletal muscle; Tubule cell of kidney; Red blood cells; Smooth muscle
Endoderm	Lining of airways and digestive system except the mouth and distal part of digestive system (rectum and anal canal); glands (digestive glands, endocrine glands, adrenal cortex)  Lung cell; Thyroid cell; Pancreatic cell

Embryonic origin of tissues and major organs. More details.

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Epithelial Tissue

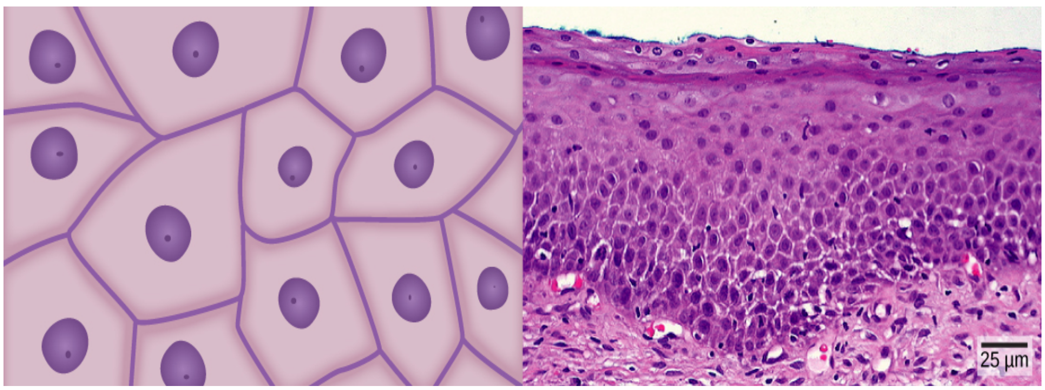
Epithelial tissue forms epithelia (sheets of cells) and glands. The cells are found next to each other and form connections with each other. They are classified by cell shape and number of layers of cells. This type of tissue forms our skin, glands and sheets of tissue that wrap and line hollow organs and ducts.

Epithelial tissues cover the outside of organs and structures in the body and line the lumens of organs in a single layer or multiple layers of cells. The types of epithelia are classified by the shapes of cells present and the number of layers of cells. An epithelium composed of a single layer of cells is called a simple epithelium. It it has multiple layers it is called a stratified epithelium.

Different Types of Epithelial Tissues		
Cell shape	Description	Location
squamous	flat, irregular round shape	simple: lung alveoli, capillaries stratified: skin, mouth, vagina
cuboidal	cube shaped, central nucleus	glands, renal tubules
columnar	tall, narrow, nucleus toward base tall, narrow, nucleus along cell	simple: digestive tract pseudostratified: respiratory tract
transitional	round, simple but appear stratified	urinary bladder

Squamous Epithelia

Squamous epithelial cells are generally round, flat, and have a small, centrally located nucleus. The cell outline is slightly irregular, and cells fit together to form a covering or lining. When the cells are arranged in a single layer (simple epithelia), they facilitate diffusion in tissues, such as the areas of gas exchange in the lungs and the exchange of nutrients and waste at blood capillaries.

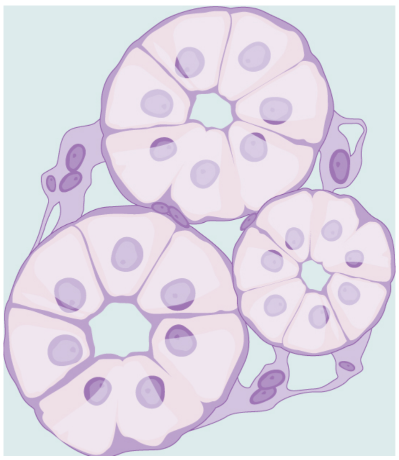


Squamous epithelia cells (a) have a slightly irregular shape, and a small, centrally located nucleus. These cells can be stratified into layers, as in (b) this human cervix specimen. (credit b: modification of work by Ed Uthman; scale-bar data from Matt Russell). More details.

An epithelium is formed by a layer of squamous cells with their membranes joined together. The image in the figure above illustrates squamous epithelial cells arranged in stratified layers, where protection is needed on the body from outside abrasion and damage. This is called a stratified squamous epithelium and occurs in the skin and in tissues lining the mouth and vagina.

Cuboidal Epithelia

Cuboidal epithelial cells are cube-shaped with a single, central nucleus. They are most commonly found in a single layer representing a simple epithelia in glandular tissues throughout the body where they prepare and secrete glandular material. They are also found in the walls of tubules and in the ducts of the kidney and liver.

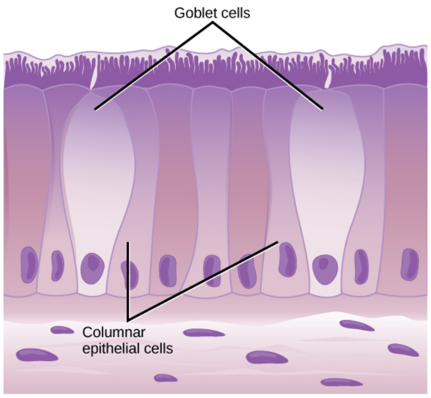


Simple cuboidal epithelial cells line tubules in the mammalian kidney, where they are involved in filtering the blood. More details.

Columnar Epithelia

Columnar epithelial cells are taller than they are wide: they resemble a stack of columns in an epithelial layer, and are most commonly found in a single-layer arrangement. The nuclei of columnar epithelial cells in the digestive tract appear to be lined up at the base of the cells. These cells

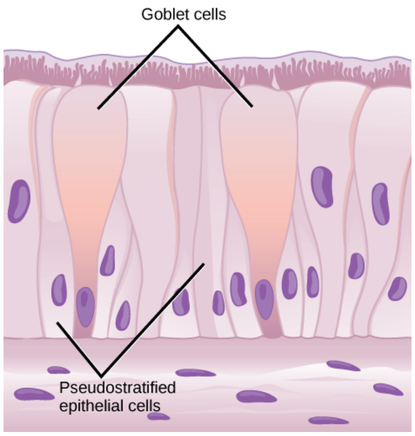
absorb material from the lumen of the digestive tract and prepare it for entry into the body through the circulatory and lymphatic systems.



Simple columnar epithelial cells absorb material from the digestive tract. Goblet cells secret mucous into the digestive tract lumen. More details.

Columnar epithelial cells lining the respiratory tract appear to be stratified. However, each cell is attached to the base membrane of the tissue and, therefore, they are simple tissues. The nuclei are arranged at different levels in the layer of cells, making it appear as though there is more than one layer, as seen in Figure. This is called pseudostratified, columnar epithelia. This cellular covering has cilia at the apical, or free, surface of the cells. The cilia enhance the movement of mucous and trapped particles out of the respiratory tract, helping to protect the system from invasive microorganisms and harmful material that has been breathed into the body. Goblet cells are interspersed in some tissues (such as the lining of the

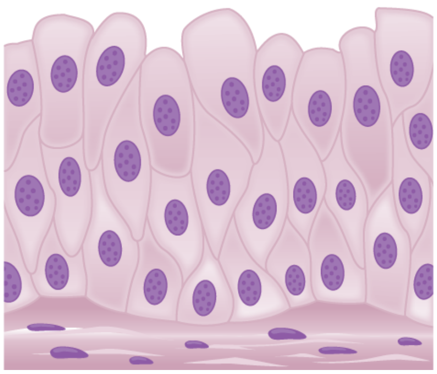
trachea). The goblet cells contain mucous that traps irritants, which in the case of the trachea keep these irritants from getting into the lungs.



Pseudostratified columnar epithelia line the respiratory tract. They exist in one layer, but the arrangement of nuclei at different levels makes it appear that there is more than one layer. Goblet cells interspersed between the columnar epithelial cells secrete mucous into the respiratory tract. More details.

Transitional Epithelia

Transitional or uroepithelial cells appear only in the urinary system, primarily in the bladder and ureter. These cells are arranged in a stratified layer, but they have the capability of appearing to pile up on top of each other in a relaxed, empty bladder. As the urinary bladder fills, the epithelial layer unfolds and expands to hold the volume of urine introduced into it. As the bladder fills, it expands and the lining becomes thinner. In other words, the tissue transitions from thick to thin.



Transitional epithelia of the urinary bladder undergo changes in thickness depending on how full the bladder is. More details.

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Connective Tissue

In connective tissue, the cells are usually far away from each other, separated by a molecular matrix that they secrete. The matrix is reinforced by protein fibers. The composition of the matrix and fibers is very diverse and this allows connective tissue to form materials as distinct as bone, cartilage, blood and tendons.

Connective tissues are made up of a matrix consisting of living cells and a non-living substance, called the ground substance. The ground substance is made of an organic substance (usually a protein) and an inorganic substance (usually a mineral or water). The principal cell of connective tissues is the fibroblast. This cell makes the fibers found in nearly all of the connective tissues. Fibroblasts are motile, able to carry out mitosis, and can synthesize whichever connective tissue is needed. Macrophages, lymphocytes, and, occasionally, leukocytes can be found in some of the tissues. Some tissues have specialized cells that are not found in the others. The matrix in connective tissues gives the tissue its density. When a connective tissue has a high concentration of cells or fibers, it has proportionally a less dense matrix.

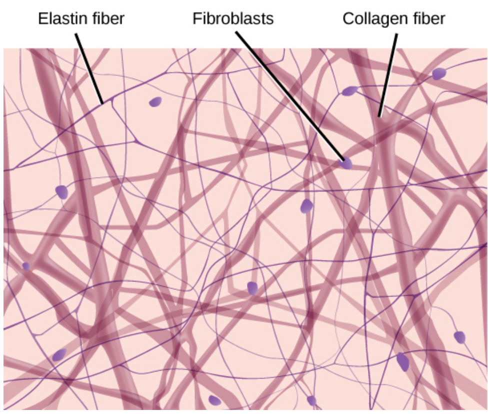
The organic portion or protein fibers found in connective tissues are either collagen, elastic, or reticular fibers. Collagen fibers provide strength to the tissue, preventing it from being torn or separated from the surrounding tissues. Elastic fibers are made of the protein elastin; this fiber can stretch to one and one half of its length and return to its original size and shape. Elastic fibers provide flexibility to the tissues. Reticular fibers are the third type of protein fiber found in connective tissues. This fiber consists of thin strands of collagen that form a network of fibers to support the tissue and other organs to which it is connected.

Connective Tissues

Connective Tissues			
Tissue	Cells	Fibers	Location
loose/areolar	fibroblasts, macrophages, some lymphocytes, some neutrophils	few: collagen, elastic, reticular	around blood vessels; anchors epithelia
dense, fibrous connective tissue	fibroblasts, macrophages,	mostly collagen	irregular: skin regular: tendons, ligaments
cartilage	chondrocytes, chondroblasts	hyaline: few collagen fibrocartilage: large amount of collagen	shark skeleton, fetal bones, human ears, intervertebral discs
bone	osteoblasts, osteocytes, osteoclasts	some: collagen, elastic	vertebrate skeletons
adipose	adipocytes	few	adipose (fat)
blood	red blood cells, white blood cells	none	blood

Loose/Areolar Connective Tissue

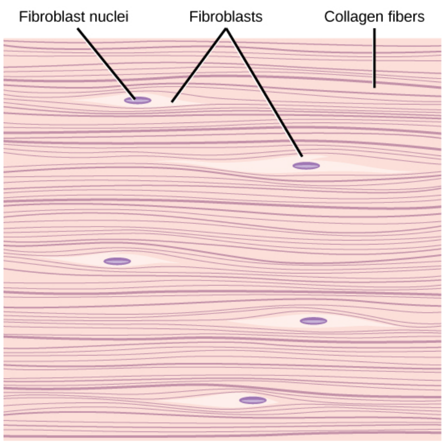
Loose connective tissue, also called areolar connective tissue, has a sampling of all of the components of a connective tissue. Loose connective tissue has some fibroblasts; macrophages are present as well. Collagen fibers are relatively wide and stain a light pink, while elastic fibers are thin and stain dark blue to black. The space between the formed elements of the tissue is filled with the matrix. The material in the connective tissue gives it a loose consistency similar to a cotton ball that has been pulled apart. Loose connective tissue is found around every blood vessel and helps to keep the vessel in place. The tissue is also found around and between most body organs. In summary, areolar tissue is tough, yet flexible, and comprises membranes.



Loose connective tissue is composed of loosely woven collagen and elastic fibers. The fibers and other components of the connective tissue matrix are secreted by fibroblasts. More details.

Fibrous Connective Tissue

Fibrous connective tissues contain large amounts of collagen fibers and few cells or matrix material. The fibers can be arranged irregularly or regularly with the strands lined up in parallel. Irregularly arranged fibrous connective tissues are found in areas of the body where stress occurs from all directions, such as the dermis of the skin. Regular fibrous connective tissue, is found in tendons (which connect muscles to bones) and ligaments (which connect bones to bones).

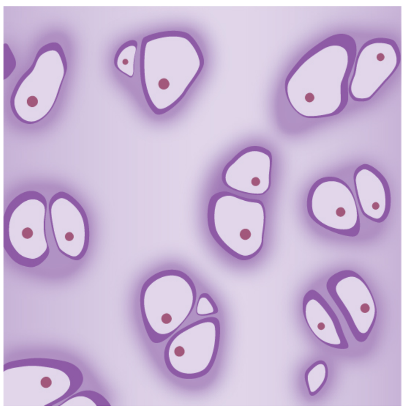


Fibrous connective tissue from the tendon has strands of collagen fibers lined up in parallel. More details.

Cartilage

Cartilage is a connective tissue with a large amount of the matrix and variable amounts of fibers. The cells, called chondrocytes, make the matrix and fibers of the tissue. Chondrocytes are found in spaces within the tissue called lacunae.

A cartilage with few collagen and elastic fibers is hyaline cartilage. The lacunae are randomly scattered throughout the tissue and the matrix takes on a milky or scrubbed appearance with routine histological stains. Sharks have cartilaginous skeletons, as does nearly the entire human skeleton during a specific pre-birth developmental stage. A remnant of this cartilage persists in the outer portion of the human nose. Hyaline cartilage is also found at the ends of long bones, reducing friction and cushioning the articulations of these bones.



Hyaline cartilage consists of a matrix with cells called chondrocytes embedded in it. The chondrocytes exist in cavities in the matrix called lacunae. More details.

Elastic cartilage has a large amount of elastic fibers, giving it tremendous flexibility. The ears of most vertebrate animals contain this cartilage as do portions of the larynx, or voice box. Fibrocartilage contains a large amount of collagen fibers, giving the tissue tremendous strength. Fibrocartilage

comprises the intervertebral discs in vertebrate animals. Hyaline cartilage found in movable joints such as the knee and shoulder becomes damaged as a result of age or trauma. Damaged hyaline cartilage is replaced by fibrocartilage and results in the joints becoming “stiff.”

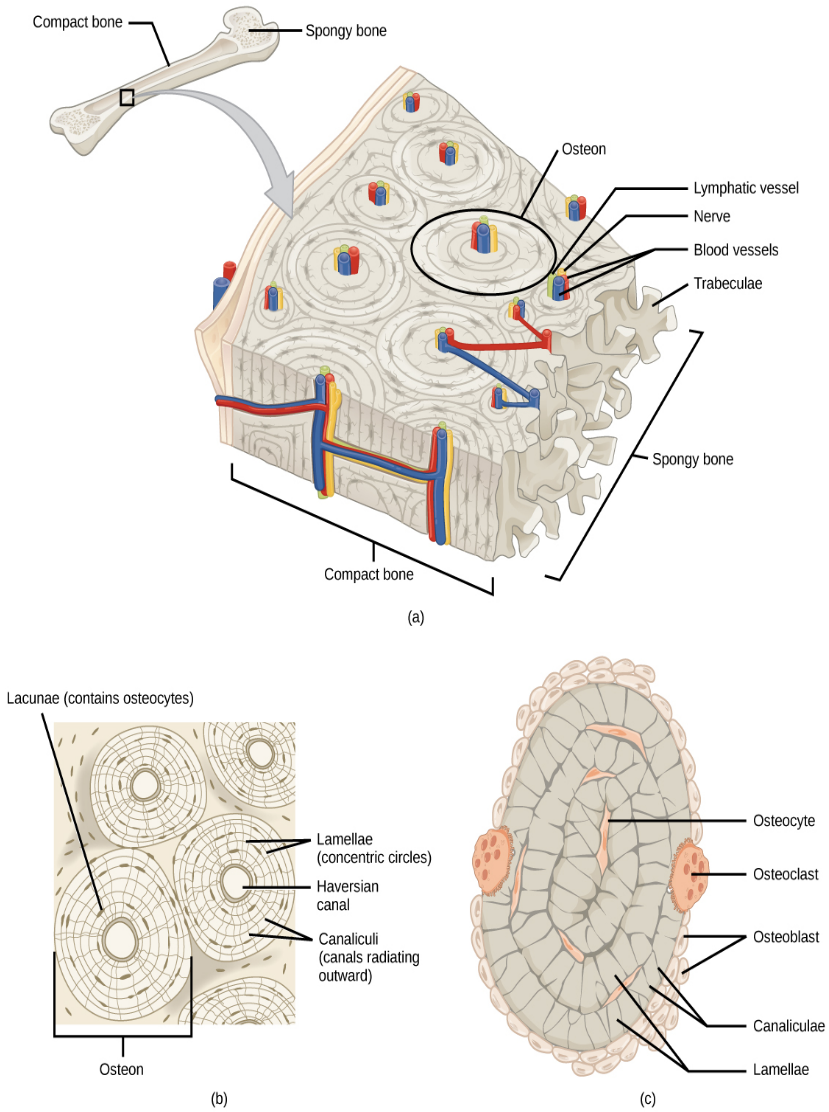
Bone

Bone, or osseous tissue, is a connective tissue that has a large amount of two different types of matrix material. The organic matrix is similar to the matrix material found in other connective tissues, including some amount of collagen and elastic fibers. This gives strength and flexibility to the tissue. The inorganic matrix consists of mineral salts—mostly calcium salts—that give the tissue hardness. Without adequate organic material in the matrix, the tissue breaks; without adequate inorganic material in the matrix, the tissue bends.

There are three types of cells in bone: osteoblasts, osteocytes, and osteoclasts. Osteoblasts are active in making bone for growth and remodeling. Osteoblasts deposit bone material into the matrix and, after the matrix surrounds them, they continue to live, but in a reduced metabolic state as osteocytes. Osteocytes are found in lacunae of the bone. Osteoclasts are active in breaking down bone for bone remodeling, and they provide access to calcium stored in tissues. Osteoclasts are usually found on the surface of the tissue.

Bone can be divided into two types: compact and spongy. Compact bone is found in the shaft (or diaphysis) of a long bone and the surface of the flat bones, while spongy bone is found in the end (or epiphysis) of a long bone. Compact bone is organized into subunits called osteons. A blood vessel and a nerve are found in the center of the structure within the Haversian canal, with radiating circles of lacunae around it known as lamellae. The wavy lines seen between the lacunae are microchannels called canaliculi; they connect the lacunae to aid diffusion between the cells. Spongy bone is made of tiny plates called trabeculae these plates serve as struts to give the spongy bone strength. Over time, these plates can break causing the bone to become less resilient. Bone tissue forms the internal skeleton of vertebrate

animals, providing structure to the animal and points of attachment for tendons.

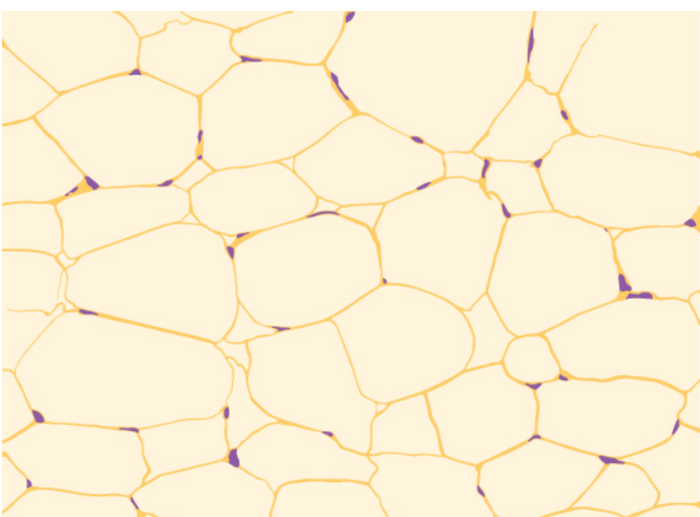


(a) Compact bone is a dense matrix on the outer surface of bone. Spongy bone, inside the compact bone, is porous with web-like trabeculae. (b) Compact bone is organized into rings called osteons. Blood vessels, nerves, and lymphatic vessels are found in the central Haversian canal. Rings of lamellae

surround the Haversian canal. Between the lamellae are cavities called lacunae. Canaliculi are microchannels connecting the lacunae together. (c) Osteoblasts surround the exterior of the bone. Osteoclasts bore tunnels into the bone and osteocytes are found in the lacunae. More details.

Adipose Tissue

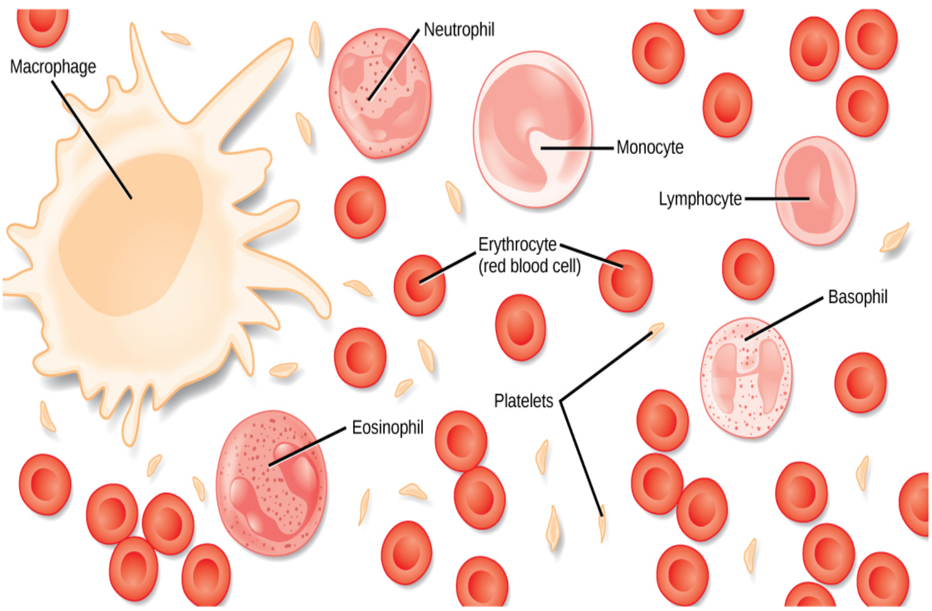
Adipose tissue, or fat tissue, is considered a connective tissue even though it does not have fibroblasts or a real matrix and only has a few fibers. Adipose tissue is made up of cells called adipocytes that collect and store fat in the form of triglycerides, for energy metabolism. Adipose tissues additionally serve as insulation to help maintain body temperatures, allowing animals to be endothermic, and they function as cushioning against damage to body organs. Under a microscope, adipose tissue cells appear empty due to the extraction of fat during the processing of the material for viewing. The thin lines in the image are the cell membranes, and the nuclei are the small, black dots at the edges of the cells.



Adipose is a connective tissue is made up of cells called adipocytes. These cells have small nuclei and a large fat reservoir. More details.

Blood

Blood is considered a connective tissue because it has a matrix, as shown in Figure. The living cell types are red blood cells (RBC), also called erythrocytes, and white blood cells (WBC), also called leukocytes. The fluid portion of whole blood, its matrix, is commonly called plasma.



Blood is a connective tissue that has a fluid matrix, called plasma, and no fibers. Erythrocytes (red blood cells), the predominant cell type, are involved in the transport of oxygen and carbon dioxide. Also present are various leukocytes (white blood cells) involved in immune response. More details.

The cell found in greatest abundance in blood is the erythrocyte. Erythrocytes are counted in millions in a blood sample: the average number of red blood cells in primates is 4.7 to 5.5 million cells per microliter. Erythrocytes are consistently the same size in a species, but vary in size between species. For example, the average diameter of a primate red blood cell is 7.5 µl, a dog is close at 7.0 µl, but a cat's RBC diameter is 5.9 µl. Sheep erythrocytes are even smaller at 4.6 µl. Mammalian erythrocytes lose their nuclei and mitochondria when they are released from the bone marrow where they are made. Fish, amphibian, and avian red blood cells maintain their nuclei and mitochondria throughout the cell's life. The principal job of an erythrocyte is to carry and deliver oxygen to the tissues.

Leukocytes are the predominant white blood cells found in the peripheral blood. Leukocytes are counted in the thousands in the blood with measurements expressed as ranges: primate counts range from 4,800 to 10,800 cells per µl, dogs from 5,600 to 19,200 cells per µl, cats from 8,000 to 25,000 cells per µl, cattle from 4,000 to 12,000 cells per µl, and pigs from 11,000 to 22,000 cells per µl.

Lymphocytes function primarily in the immune response to foreign antigens or material. Different types of lymphocytes make antibodies tailored to the foreign antigens and control the production of those antibodies. Neutrophils are phagocytic cells and they participate in one of the early lines of defense against microbial invaders, aiding in the removal of bacteria that has entered the body. Another leukocyte that is found in the peripheral blood is the monocyte. Monocytes give rise to phagocytic macrophages that clean up dead and damaged cells in the body, whether they are foreign or from the host animal. Two additional leukocytes in the blood are eosinophils and basophils—both help to facilitate the inflammatory response.

The slightly granular material among the cells is a cytoplasmic fragment of a cell in the bone marrow. This is called a platelet or thrombocyte. Platelets participate in the stages leading up to coagulation of the blood to stop bleeding through damaged blood vessels. Blood has a number of functions, but primarily it transports material through the body to bring nutrients to cells and remove waste material from them.

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Muscle Tissue
Muscle tissue can shorten and this ability provides the body with movement. Smooth, skeletal and cardiac muscle differ significantly in morphology and physiology. They are used for different tasks in the body.

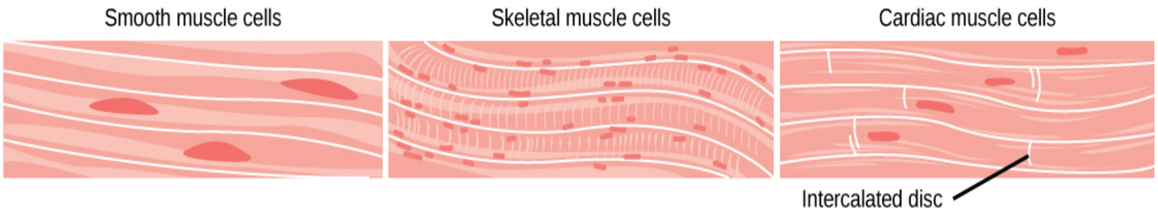
There are three types of muscle in animal bodies: smooth, skeletal, and cardiac. They differ by the presence or absence of striations or bands, the number and location of nuclei, whether they are voluntarily or involuntarily controlled, and their location within the body.

Types of Muscles				
Type of Muscle	Striations	Nuclei	Control	Location
smooth	no	single, in center	involuntary	visceral organs
skeletal	yes	many, at periphery	voluntary	skeletal muscles
cardiac	yes	single, in center	involuntary	heart

Smooth Muscle

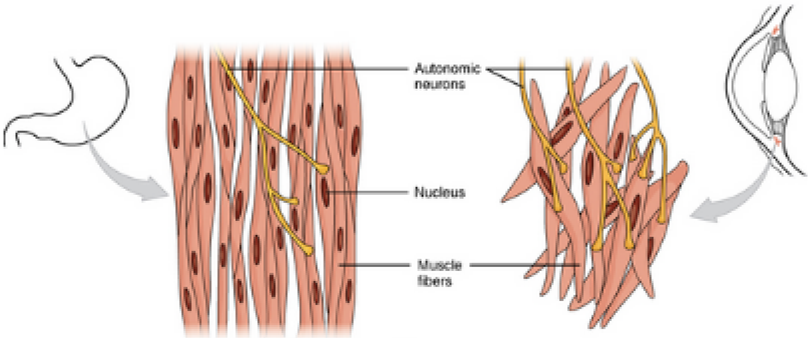
Smooth muscle does not have striations in its cells. It has a single, centrally located nucleus. Constriction of smooth muscle occurs under involuntary, autonomic nervous control and in response to local conditions in the tissues. Smooth muscle tissue is also called non-striated as it lacks the banded appearance of skeletal and cardiac muscle. The walls of blood vessels, the

tubes of the digestive system, and the tubes of the reproductive systems are composed of mostly smooth muscle.

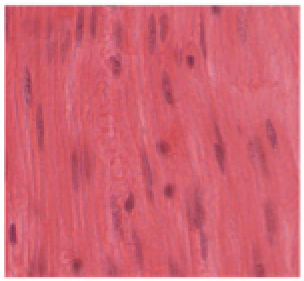


Smooth muscle cells do not have striations, while skeletal muscle cells do. Cardiac muscle cells have striations, but, unlike the multinucleate skeletal cells, they have only one nucleus. Cardiac muscle tissue also has intercalated discs, specialized regions running along the plasma membrane that join adjacent cardiac muscle cells and assist in passing an electrical impulse from cell to cell. More details.

Smooth muscle (so-named because the cells do not have striations) is present in the walls of hollow organs like the urinary bladder, uterus, stomach, intestines, and in the walls of passageways, such as the arteries and veins of the circulatory system, and the tracts of the respiratory, urinary, and reproductive systems. Smooth muscle is also present in the eyes, where it functions to change the size of the iris and alter the shape of the lens; and in the skin where it causes hair to stand erect in response to cold temperature or fear.



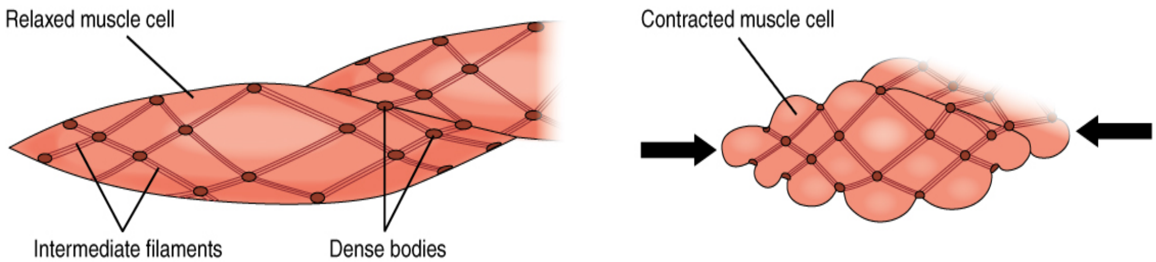
(a)



(b)

Smooth muscle tissue. More details.

Smooth muscle fibers are spindle-shaped (wide in the middle and tapered at both ends, somewhat like a football) and have a single nucleus; they range from about 30 to 200 μm (thousands of times shorter than skeletal muscle fibers), and they produce their own connective tissue, endomysium. Although they do not have striations and sarcomeres, smooth muscle fibers do have actin and myosin contractile proteins, and thick and thin filaments. These thin filaments are anchored by dense bodies. A dense body is analogous to the Z-discs of skeletal and cardiac muscle fibers and is fastened to the sarcolemma. When the thin filaments slide past the thick filaments, they pull on the dense bodies, structures tethered to the sarcolemma, which then pull on the intermediate filaments networks throughout the sarcoplasm. This arrangement causes the entire muscle fiber to contract in a manner whereby the ends are pulled toward the center, causing the midsection to bulge in a corkscrew motion.

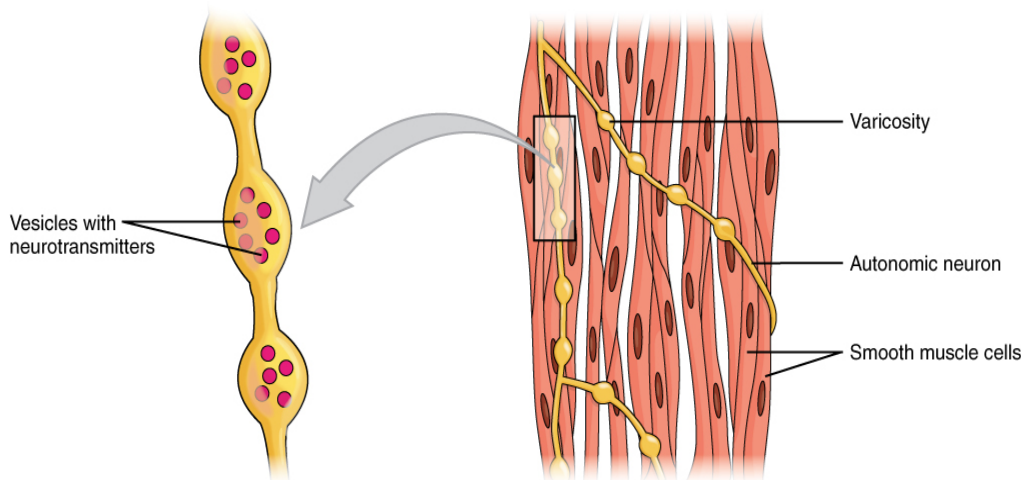


Contraction mechanism in smooth muscle. More details.

Because most smooth muscles must function for long periods without rest, their power output is relatively low, but contractions can continue without using large amounts of energy. Some smooth muscle can also maintain contractions even as Ca++ is removed and myosin kinase is inactivated/dephosphorylated. This can happen as a subset of cross-bridges between myosin heads and actin, called latch-bridges, keep the thick and thin filaments linked together for a prolonged period, and without the need for ATP. This allows for the maintaining of muscle "tone" in smooth muscle that lines arterioles and other visceral organs with very little energy expenditure.

Smooth muscle is not under voluntary control; thus, it is called involuntary muscle. The triggers for smooth muscle contraction include hormones, neural stimulation by the ANS, and local factors. In certain locations, such as the walls of visceral organs, stretching the muscle can trigger its contraction (the stress-relaxation response).

Axons of neurons in the ANS do not form the highly organized NMJs with smooth muscle, as seen between motor neurons and skeletal muscle fibers. Instead, there is a series of neurotransmitter-filled bulges called varicosities as an axon courses through smooth muscle, loosely forming motor units (Figure). A varicosity releases neurotransmitters into the synaptic cleft. Also, visceral muscle in the walls of the hollow organs (except the heart) contains pacesetter cells. A pacesetter cell can spontaneously trigger action potentials and contractions in the muscle.



Neural stimulation of smooth muscles through varicosities. More details.

Smooth muscle is organized in two ways: as single-unit smooth muscle, which is much more common; and as multiunit smooth muscle. The two types have different locations in the body and have different characteristics. Single-unit muscle has its muscle fibers joined by gap junctions so that the muscle contracts as a single unit. This type of smooth muscle is found in the walls of all visceral organs except the heart (which has cardiac muscle in its walls), and so it is commonly called visceral muscle. Because the muscle fibers are not constrained by the organization and stretchability limits of sarcomeres, visceral smooth muscle has a stress-relaxation response. This means that as the muscle of a hollow organ is stretched when it fills, the mechanical stress of the stretching will trigger contraction, but this is immediately followed by relaxation so that the organ does not empty its contents prematurely. This is important for hollow organs, such as the stomach or urinary bladder, which continuously expand as they fill. The smooth muscle around these organs also can maintain a muscle tone when the organ empties and shrinks, a feature that prevents “flabbiness” in the empty organ. In general, visceral smooth muscle produces slow, steady contractions that allow substances, such as food in the digestive tract, to move through the body.

Multiunit smooth muscle cells rarely possess gap junctions, and thus are not electrically coupled. As a result, contraction does not spread from one cell to the next, but is instead confined to the cell that was originally stimulated. Stimuli for multiunit smooth muscles come from autonomic nerves or hormones but not from stretching. This type of tissue is found around large blood vessels, in the respiratory airways, and in the eyes.

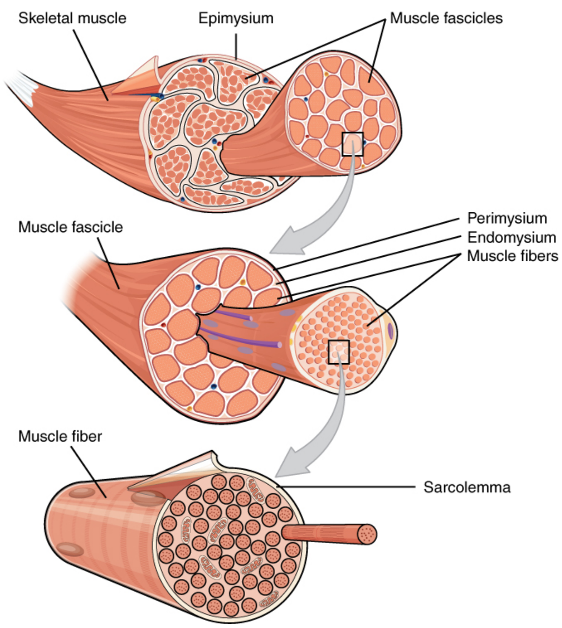
Skeletal Muscle

Skeletal muscle has striations across its cells caused by the arrangement of the contractile proteins actin and myosin. These muscle cells are relatively long and have multiple nuclei along the edge of the cell. Skeletal muscle is under voluntary, somatic nervous system control and is found in the muscles that move bones.

The best-known feature of skeletal muscle is its ability to contract and cause movement. Skeletal muscles act not only to produce movement but also to stop movement, such as resisting gravity to maintain posture. Small, constant adjustments of the skeletal muscles are needed to hold a body upright or balanced in any position. Muscles also prevent excess movement of the bones and joints, maintaining skeletal stability and preventing skeletal structure damage or deformation. Joints can become misaligned or dislocated entirely by pulling on the associated bones; muscles work to keep joints stable. Skeletal muscles are located throughout the body at the openings of internal tracts to control the movement of various substances. These muscles allow functions, such as swallowing, urination, and defecation, to be under voluntary control. Skeletal muscles also protect internal organs (particularly abdominal and pelvic organs) by acting as an external barrier or shield to external trauma and by supporting the weight of the organs.

Skeletal muscles contribute to the maintenance of homeostasis in the body by generating heat. Muscle contraction requires energy, and when ATP is broken down, heat is produced. This heat is very noticeable during exercise, when sustained muscle movement causes body temperature to rise, and in cases of extreme cold, when shivering produces random skeletal muscle contractions to generate heat.

Each skeletal muscle is an organ that consists of various integrated tissues. These tissues include the skeletal muscle fibers, blood vessels, nerve fibers, and connective tissue. Each skeletal muscle has three layers of connective tissue (called "mysia") that enclose it and provide structure to the muscle as a whole, and also compartmentalize the muscle fibers within the muscle. Each muscle is wrapped in a sheath of dense, irregular connective tissue called the epimysium, which allows a muscle to contract and move powerfully while maintaining its structural integrity. The epimysium also separates muscle from other tissues and organs in the area, allowing the muscle to move independently.



The three layers of connective tissue in the framework of skeletal muscles. More details.

Inside each skeletal muscle, muscle fibers are organized into individual bundles, each called a fascicle, by a middle layer of connective tissue called the perimysium. This fascicular organization is common in muscles of the

limbs; it allows the nervous system to trigger a specific movement of a muscle by activating a subset of muscle fibers within a bundle, or fascicle of the muscle. Inside each fascicle, each muscle fiber is encased in a thin connective tissue layer of collagen and reticular fibers called the endomysium. The endomysium contains the extracellular fluid and nutrients to support the muscle fiber. These nutrients are supplied via blood to the muscle tissue.

In skeletal muscles that work with tendons to pull on bones, the collagen in the three tissue layers (the mysia) intertwines with the collagen of a tendon. At the other end of the tendon, it fuses with the periosteum coating the bone. The tension created by contraction of the muscle fibers is then transferred though the mysia, to the tendon, and then to the periosteum to pull on the bone for movement of the skeleton. In other places, the mysia may fuse with a broad, tendon-like sheet called an aponeurosis, or to fascia, the connective tissue between skin and bones. The broad sheet of connective tissue in the lower back that the latissimus dorsi muscles (the "lats") fuse into is an example of an aponeurosis.

Every skeletal muscle is also richly supplied by blood vessels for nourishment, oxygen delivery, and waste removal. In addition, every muscle fiber in a skeletal muscle is supplied by the axon branch of a somatic motor neuron, which signals the fiber to contract. Unlike cardiac and smooth muscle, the only way to functionally contract a skeletal muscle is through signaling from the nervous system.

Cardiac Muscle

Cardiac muscle is found only in the heart. Like skeletal muscle, it has cross striations in its cells, but cardiac muscle has a single, centrally located nucleus. Cardiac muscle is not under voluntary control but can be influenced by the autonomic nervous system to speed up or slow down. An added feature to cardiac muscle cells is a line than extends along the end of the cell as it abuts the next cardiac cell in the row. This line is called an intercalated disc: it assists in passing electrical impulse efficiently from one cell to the next and maintains the strong connection between neighboring cardiac cells.

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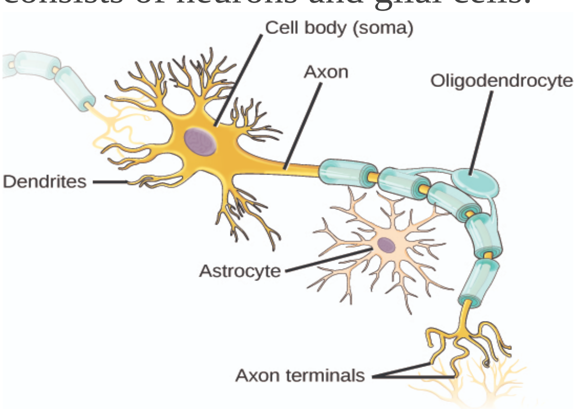
Nervous Tissue
Neurons can transmit signals at great speeds and long distances. The stimulus is electrical along the length of the cell and chemical between cells. Neurons are surrounded, nourished and protected by glial cells, which are much smaller but present in larger number than neurons. There are several types of glial cells, varying in function an position in the nervous system.

Nervous tissues are made of cells specialized to receive and transmit electrical impulses from specific areas of the body and to send them to specific locations in the body. The main cell of the nervous system is the neuron. The large structure with a central nucleus is the cell body of the neuron. Projections from the cell body are either dendrites specialized in receiving input or a single axon specialized in transmitting impulses. Some glial cells are also shown. Astrocytes regulate the chemical environment of the nerve cell, and oligodendrocytes insulate the axon so the electrical nerve impulse is transferred more efficiently. Other glial cells that are not shown support the nutritional and waste requirements of the neuron. Some of the glial cells are phagocytic and remove debris or damaged cells from the tissue. A nerve consists of neurons and glial cells.



A neuron and two glial cells.
More details.

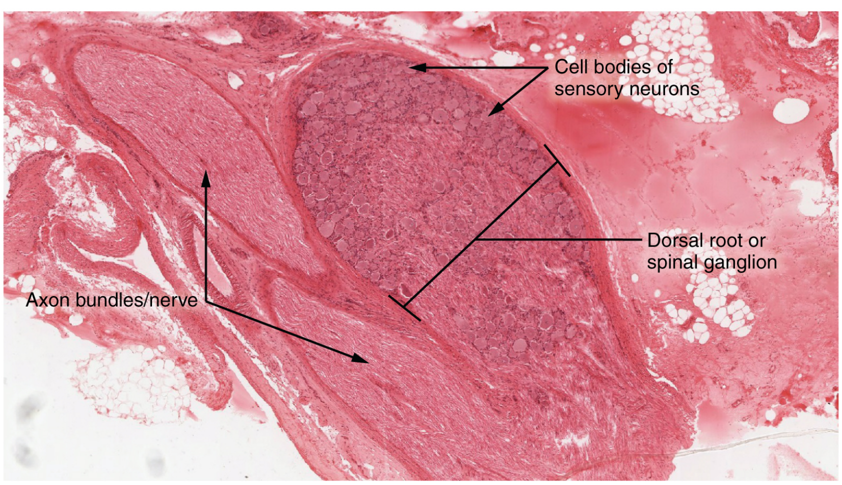
Central and Peripheral Nervous Systems

The CNS includes the brain and spinal cord. The PNS is not as contained as the CNS because it is defined as everything that is not the CNS. Some

peripheral structures are incorporated into the other organs of the body. In describing the anatomy of the PNS, it is necessary to describe the common structures, the nerves and the ganglia, as they are found in various parts of the body. Many of the neural structures that are incorporated into other organs are features of the digestive system; these structures are known as the enteric nervous system and are a special subset of the PNS.

Ganglia

A ganglion is a group of neuron cell bodies in the periphery. Ganglia can be categorized, for the most part, as either sensory ganglia or autonomic ganglia, referring to their primary functions. The most common type of sensory ganglion is a dorsal (posterior) root ganglion. These ganglia are the cell bodies of neurons with axons that are sensory endings in the periphery, such as in the skin, and that extend into the CNS through the dorsal nerve root. The ganglion is an enlargement of the nerve root. Under microscopic inspection, it can be seen to include the cell bodies of the neurons, as well as bundles of fibers that are the posterior nerve root. The cells of the dorsal root ganglion are unipolar cells, classifying them by shape. Also, the small round nuclei of satellite cells can be seen surrounding—as if they were orbiting—the neuron cell bodies.

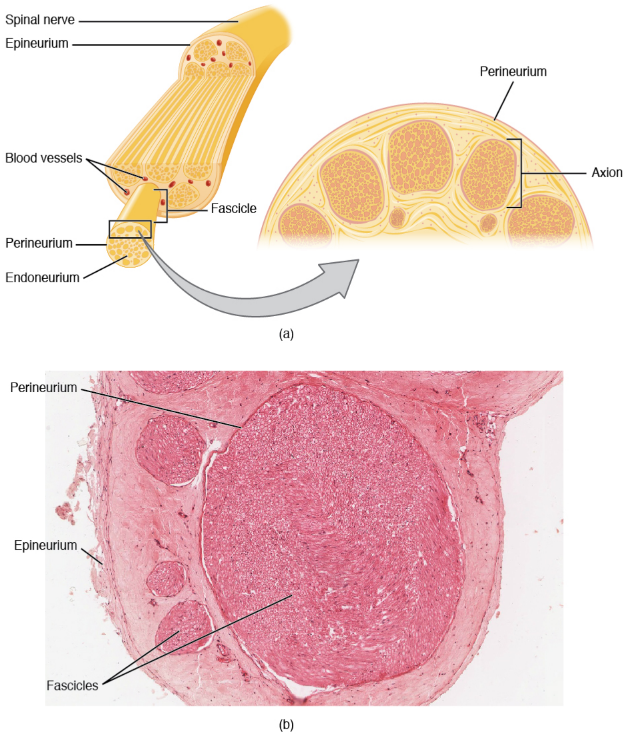


Unipolar sensory neurons in a dorsal root ganglion of a dog. Light microscopy, magnified 40x. (Image provided by the Regents of

University of Michigan Medical School © 2012).
More details.

Nerves

Bundles of axons in the PNS are referred to as nerves. These structures in the periphery are different than the central counterpart, called a tract. Nerves are composed of more than just nervous tissue. They have connective tissues invested in their structure, as well as blood vessels supplying the tissues with nourishment. The outer surface of a nerve is a surrounding layer of fibrous connective tissue called the epineurium. Within the nerve, axons are further bundled into fascicles, which are each surrounded by their own layer of fibrous connective tissue called perineurium. Finally, individual axons are surrounded by loose connective tissue called the endoneurium. These three layers are similar to the connective tissue sheaths for muscles. Nerves are associated with the region of the CNS to which they are connected, either as cranial nerves connected to the brain or spinal nerves connected to the spinal cord.



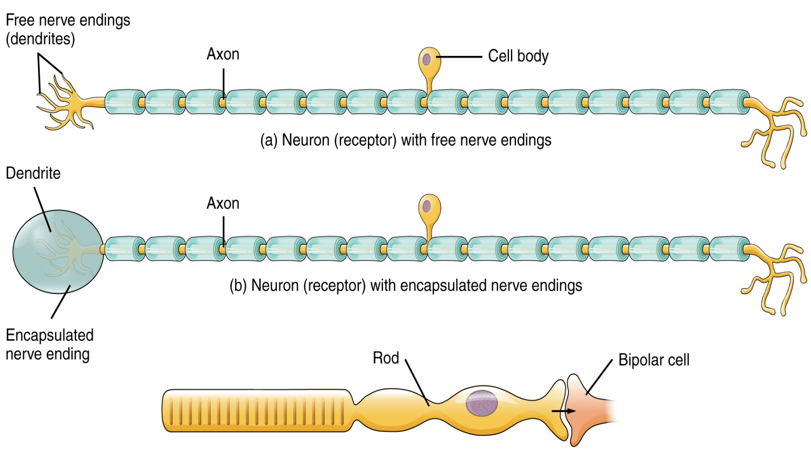
The structure of a nerve. Light microscopy, magnified 40x. (Micrograph provided by the Regents of University of Michigan Medical School © 2012). More details.

Sensory Receptors

Stimuli in the environment activate specialized receptor cells in the peripheral nervous system. Different types of stimuli are sensed by different types of receptor cells. Receptor cells can be classified into types on the basis of three different criteria: cell type, position, and function. Receptors can be classified structurally on the basis of cell type and their position in relation to stimuli they sense. They can also be classified functionally on the basis of the transduction of stimuli, or how the mechanical stimulus, light, or chemical changed the cell membrane potential.

Structural Receptor Types

The cells that interpret information about the environment can be either (1) a neuron that has a free nerve ending, with dendrites embedded in tissue that would receive a sensation; (2) a neuron that has an encapsulated ending in which the sensory nerve endings are encapsulated in connective tissue that enhances their sensitivity; or (3) a specialized receptor cell, which has distinct structural components that interpret a specific type of stimulus. The pain and temperature receptors in the dermis of the skin are examples of neurons that have free nerve endings. Also located in the dermis of the skin are lamellated corpuscles, neurons with encapsulated nerve endings that respond to pressure and touch. The cells in the retina that respond to light stimuli are an example of a specialized receptor, a photoreceptor.



Receptor cell types can be classified on the basis of their structure. Sensory neurons can have either (a) free nerve endings or (b) encapsulated endings. Photoreceptors in the eyes, such as rod cells, are examples of (c) specialized receptor cells. These cells release neurotransmitters onto a bipolar cell, which then synapses with the optic nerve neurons. More details.

Another way that receptors can be classified is based on their location relative to the stimuli. An exteroceptor is a receptor that is located near a stimulus in the external environment, such as the somatosensory receptors that are located in the skin. An interoceptor is one that interprets stimuli from internal organs and tissues, such as the receptors that sense the increase in blood pressure in the aorta or carotid sinus. Finally, a proprioceptor is a receptor located near a moving part of the body, such as a muscle, that interprets the positions of the tissues as they move.

Functional Receptor Types

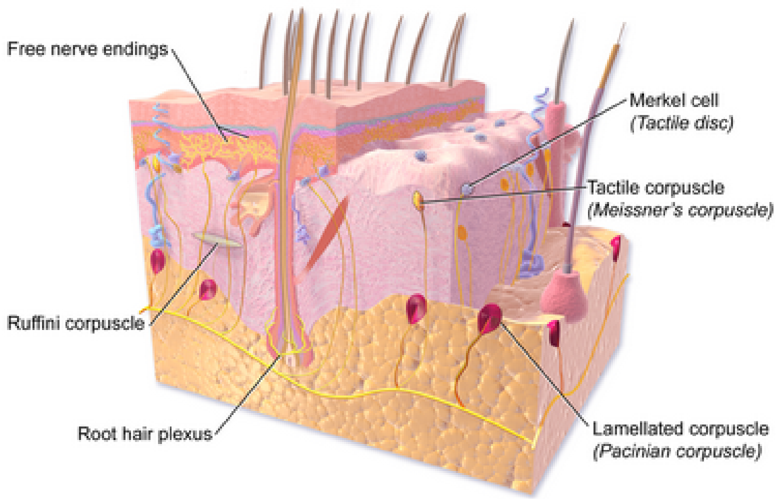
A third classification of receptors is by how the receptor transduces stimuli into membrane potential changes. Stimuli are of three general types. Some stimuli are ions and macromolecules that affect transmembrane receptor proteins when these chemicals diffuse across the cell membrane. Some stimuli are physical variations in the environment that affect receptor cell membrane potentials. Other stimuli include the electromagnetic radiation from visible light. For humans, the only electromagnetic energy that is perceived by our eyes is visible light. Some other organisms have receptors that humans lack, such as the heat sensors of snakes, the ultraviolet light sensors of bees, or magnetic receptors in migratory birds.

Receptor cells can be further categorized on the basis of the type of stimuli they transduce. Chemical stimuli can be interpreted by a chemoreceptor that interprets chemical stimuli, such as an object’s taste or smell. Osmoreceptors respond to solute concentrations of body fluids. Additionally, pain is primarily a chemical sense that interprets the presence of chemicals from tissue damage, or similar intense stimuli, through a nociceptor. Physical stimuli, such as pressure and vibration, as well as the sensation of sound and body position (balance), are interpreted through a mechanoreceptor. Another physical stimulus that has its own type of receptor is temperature, which is sensed through a thermoreceptor that is either sensitive to temperatures above (heat) or below (cold) normal body temperature.

Somatosensation (Touch)

Somatosensation is considered a general sense, as opposed to the special senses discussed in this section. Somatosensation is the group of sensory modalities that are associated with touch, proprioception, and interoception. These modalities include pressure, vibration, light touch, tickle, itch, temperature, pain, proprioception, and kinesthesia. This means that its receptors are not associated with a specialized organ, but are instead spread throughout the body in a variety of organs. Many of the somatosensory receptors are located in the skin, but receptors are also found in muscles, tendons, joint capsules, ligaments, and in the walls of visceral organs.

Two types of somatosensory signals that are transduced by free nerve endings are pain and temperature. These two modalities use thermoreceptors and nociceptors to transduce temperature and pain stimuli, respectively. Temperature receptors are stimulated when local temperatures differ from body temperature. Some thermoreceptors are sensitive to just cold and others to just heat. Nociception is the sensation of potentially damaging stimuli. Mechanical, chemical, or thermal stimuli beyond a set threshold will elicit painful sensations. Stressed or damaged tissues release chemicals that activate receptor proteins in the nociceptors. For example, the sensation of heat associated with spicy foods involves capsaicin, the active molecule in hot peppers. Capsaicin molecules bind to a transmembrane ion channel in nociceptors that is sensitive to temperatures above 37°C. The dynamics of capsaicin binding with this transmembrane ion channel is unusual in that the molecule remains bound for a long time. Because of this, it will decrease the ability of other stimuli to elicit pain sensations through the activated nociceptor. For this reason, capsaicin can be used as a topical analgesic, such as in products such as Icy Hot™.



Tactile receptors of the skin. More details.

If you drag your finger across a textured surface, the skin of your finger will vibrate. Such low frequency vibrations are sensed by mechanoreceptors called Merkel cells, also known as type I cutaneous mechanoreceptors. Merkel cells are located in the stratum basale of the epidermis. Deep pressure and vibration is transduced by lamellated (Pacinian) corpuscles, which are receptors with encapsulated endings found deep in the dermis, or subcutaneous tissue. Light touch is transduced by the encapsulated endings known as tactile (Meissner) corpuscles. Follicles are also wrapped in a plexus of nerve endings known as the hair follicle plexus. These nerve endings detect the movement of hair at the surface of the skin, such as when an insect may be walking along the skin. Stretching of the skin is transduced by stretch receptors known as bulbous corpuscles. Bulbous corpuscles are also known as Ruffini corpuscles, or type II cutaneous mechanoreceptors.

Other somatosensory receptors are found in the joints and muscles. Stretch receptors monitor the stretching of tendons, muscles, and the components of joints. For example, have you ever stretched your muscles before or after exercise and noticed that you can only stretch so far before your muscles spasm back to a less stretched state? This spasm is a reflex that is initiated by stretch receptors to avoid muscle tearing. Such stretch receptors can also prevent over-contraction of a muscle. In skeletal muscle tissue, these stretch receptors are called muscle spindles. Golgi tendon organs similarly transduce

the stretch levels of tendons. Bulbous corpuscles are also present in joint capsules, where they measure stretch in the components of the skeletal system within the joint.

Mechanoreceptors of Somatosensation			
Name	Historical (eponymous) name	Location(s)	Stimuli
Free nerve endings	*	Dermis, cornea, tongue, joint capsules, visceral organs	Pain, temperature, mechanical deformation
Mechanoreceptors	Merkel's discs	Epidermal–dermal junction, mucosal membranes	Low frequency vibration (5–15 Hz)
Bulbous corpuscle	Ruffini's corpuscle	Dermis, joint capsules	Stretch
Tactile corpuscle	Meissner's corpuscle	Papillary dermis, especially in the fingertips and lips	Light touch, vibrations below 50 Hz

Mechanoreceptors of Somatosensation			
Lamellated corpuscle	Pacinian corpuscle	Deep dermis, subcutaneous tissue	Deep pressure, high-frequency vibration (around 250 Hz)
Hair follicle plexus	*	Wrapped around hair follicles in the dermis	Movement of hair
Muscle spindle	*	In line with skeletal muscle fibers	Muscle contraction and stretch
Tendon stretch organ			

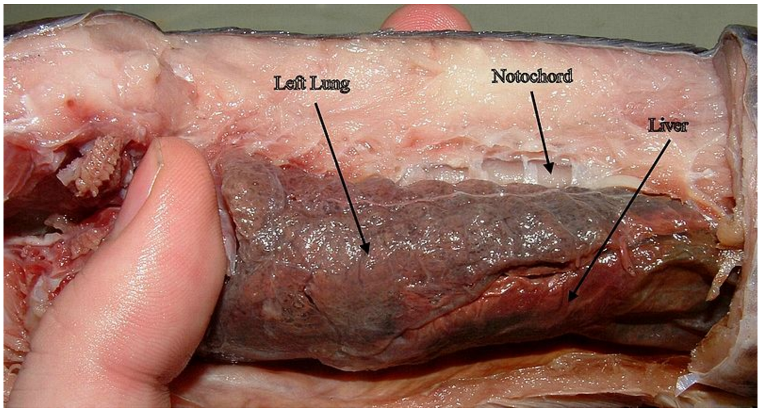
Chordates

Chordates are animals that have a notocord. This includes cephalochordates (lancelets), urochordates (sea-squirts) and all vertebrates. The body of a lancelet resembles that of a fish and it has a notocord but lacks a skeleton. Sea-squirts are mostly marine filter-feeders with a sessile adult form that lives attached to the bottom, but a free-swimming larva that presents a notocord.

A major distinctive feature of chordates in relation to other animals is the ability of producing three closely-related hard tissues: cartilage, bone and teeth. Most of the fossil record available for the group derives from these hard tissues which improved the defense, locomotion and feeding abilities of these animals.

The diagnostic feature of a chordate is having a notochord, which is a flexible rod made out of a material similar to cartilage. If a species has a notochord, it is a chordate. The notochord lies along the anteroposterior ("head to tail") axis. It is usually found closer to the dorsal than to the ventral surface of the animal, and it is composed of cells derived from the mesoderm. Many functions have been attributed to the notochord. These include serving as a site of muscle attachment, a vertebral precursor, and a midline tissue that provides signals to the surrounding tissues during development.

Notochords are thought to be advantageous (both in an evolutionary and developmental context) because they provide(d) rigid structure for muscle attachment, but were still flexible. In some chordates, it persists throughout life as the main axial support of the body, while in most tetrapods it becomes the nucleus pulposus of the intervertebral disc. The notochord plays a key role in signalling and coordinating development. Embryos of vertebrates still form transient notochord structures today during the gastrulation phase of development. The notochord is found ventral to the neural tube.



Notochord of the spotted African lungfish (*Protopterus dolloi*). More details.

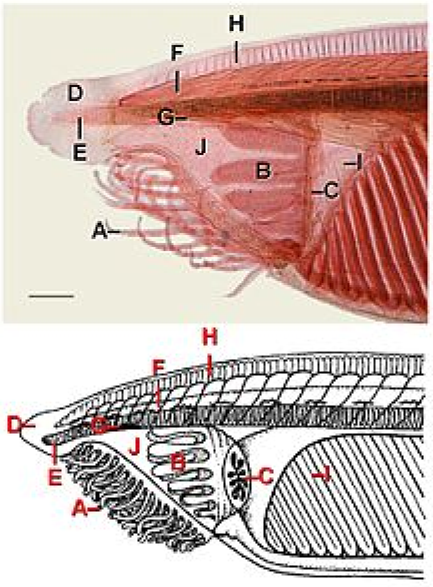
The phylum Chordata is formed by three major groups: Cephalochordata (lancelets), Tunicata (sea squirts) and Craniata (vertebrates).

Lancelets

Lancelets make the oldest of the three. They comprise about 32 species of fish-like marine chordates in the order **Amphioxiformes**, with a global distribution in shallow temperate (as far north as Scotland) and tropicalseas, usually found half-buried in sand. They are the modern representatives of the subphylum Cephalochordata. In Asia, they are harvested commercially as food for humans and domesticated animals. Although lancelets split from vertebrates more than 520 million years ago, their genomes hold clues about evolution, particularly how vertebrates have employed old genes for new functions.

Lancelet (*Branchiostoma lanceolatum*). More details.

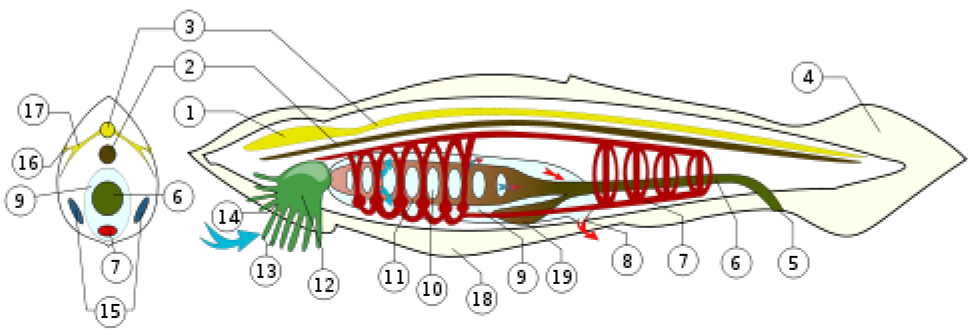
Lancelets are typically 5 cm (2.0 in) long, or 7 cm (2.8 in) at the longest. They have a translucent, somewhat fish-like body, but without any paired fins or other limbs. A relatively poorly developed tail fin is present, so they are not especially good swimmers. While they do possess some cartilage-like material stiffening the gill slits, mouth, and tail, they have no true skeleton.



Anterior anatomy of the lancelet. A: buccal cirri, B: wheel organ, C: velum, D: rostrum, E: notochord extending beyond nerve cord, F: nerve cord, G: Hatschek's pit, H: fin rays, I: gill bar, J: buccal cavity (vestibule). More details.

Lancelets also have oral *cirri*, thin tentacle-like strands that hang in front of the mouth and act as sensory devices and as a filter for the water passing into the body. Water passes from the mouth into the large pharynx, which is lined by numerous gill-slits. The ventral surface of the pharynx contains a groove, called the endostyle, which, connected to a structure known as Hatschek's pit, produces a film of mucus. Ciliary action pushes the mucus in a film over the surface of the gill slits, trapping suspended food particles as it does so. The mucus is collected in a second, dorsal, groove, and passed

back to the rest of the digestive tract. Having passed through the gill slits, the water enters an atrium surrounding the pharynx, then exits the body via the *atriopore*.



Internal morphology of the lancelet. 1. brain-like blister 2. notochord 3. dorsal nerve cell 4. post-anal tail 5. anus 6. food canal 7. blood system 8. abdominal porus 9. overpharynx lacuna 10. gill's slit 11. pharynx 12. mouth lacuna 13. mimosa 14. mouth gap 15. gonads (ovary/testicle) 16. light sensor 17. nerves 18. abdominal ply 19. hepatic caecum. More details.

Both adults and larvae exhibit a "cough" reflex to clear the mouth or throat of debris or items too large to swallow. In larvae the action is mediated by the pharyngial muscles while in the adult animal it is accomplished by atrial contraction.

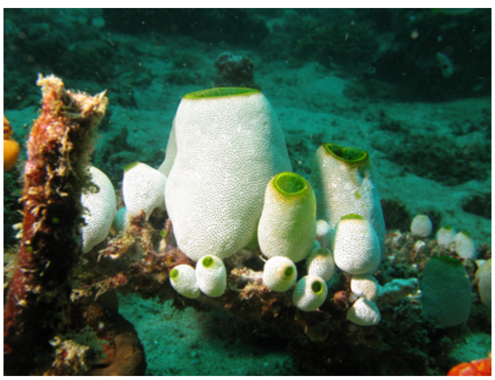
The remainder of the digestive system consists of a simple tube running from the pharynx to the anus. The hepatic caecum, a single blind-ending caecum, branches off from the underside of the gut, with a lining able to phagocytize the food particles, a feature not found in vertebrates. Although it performs many functions of a liver, it is not considered a true liver but a homolog of the vertebrate liver.

Lancelets have no respiratory system, breathing solely through their skin, which consists of a simple epithelium. Despite the name, little if any

respiration occurs in the gill slits, which are solely devoted to feeding. The circulatory system does resemble that of primitive fish in its general layout, but is much simpler, and does not include a heart. There are no blood cells, and no haemoglobin.

Sea squirts

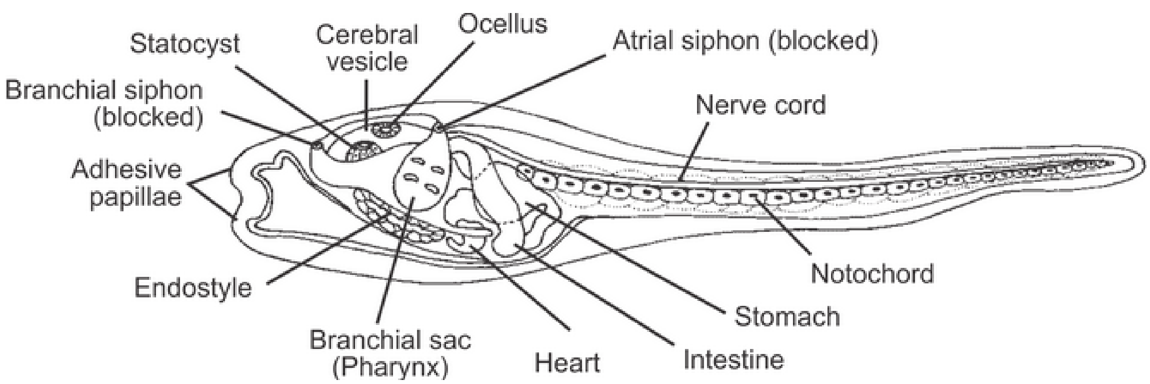
Tunicates live as solitary individuals, but others replicate by budding and become colonies. They are marine filter feeders with a water-filled, sac-like body structure and two tubular openings, known as siphons, through which they draw in and expel water. During their respiration and feeding, they take in water through the incurrent (or inhalant) siphon and expel the filtered water through the excurrent (or exhalant) siphon. Most adult tunicates are sessile, and are permanently attached to rocks or other hard surfaces on the ocean floor. Others, such as salps, doliolids and pyrosomes, swim in the pelagic zone of the sea as adults. Various species are commonly known as sea squirts, sea pork, sea livers, or sea tulips.



A colony of the sea squirt *Didemnum molle*. More details.

The earliest species of tunicate appeared in the fossil record in the early Cambrian period. Despite their simple appearance and very different adult

form, their close relationship to the vertebrates is evidenced by the fact that during their mobile larval stage, they possess a notochord or stiffening rod and resemble a tadpole. Their name derives from their unique outer covering or "tunic", which is formed from proteins and carbohydrates, and acts as an exoskeleton. In some species, it is thin, translucent, and gelatinous, while in others it is thick, tough, and stiff.



Anatomy of a larval tunicate. More details.

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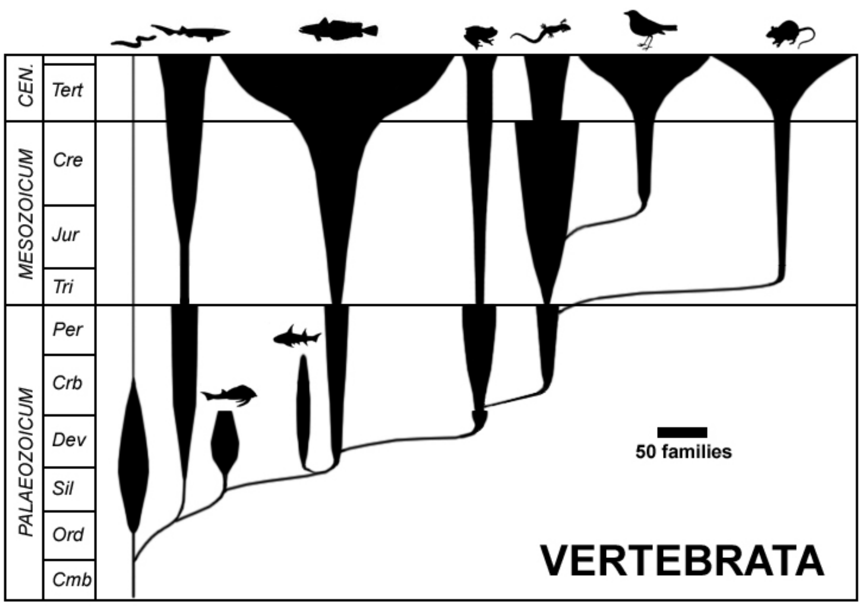
Vertebrates

While a notocord is a common feature of chordates, a cartilaginous or bony skull is a more recent feature and it is only found in vertebrates. Bony jaws make another feature that evolved later in groups of fishes that became highly diverse.

While lancelets and sea squirts had a notochord, they lacked a skull and vertebral column. These features are only found in the subphylum Vertebrata (also called Craniata) containing about 64,000 species. Vertebrates include the jawless fish and the jawed vertebrates, which include the cartilaginous fish (sharks and rays) and the bony fish. All tetrapods (amphibians, reptiles, birds and mammals) originated from bony fish.



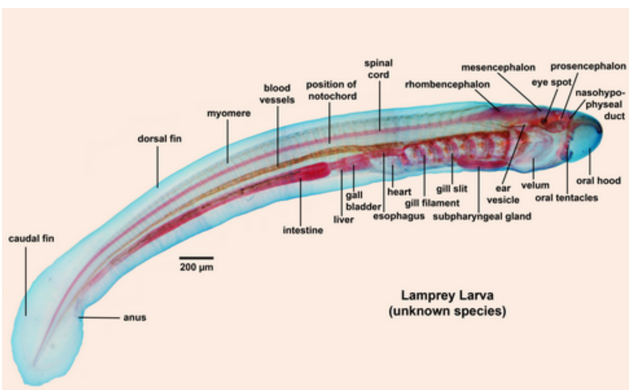
Evolution and species richness of the vertebrate classes. More details.

The oldest vertebrates are the jawless fish (Agnatha). Their cranium is normally represented by a trough-like basket of cartilaginous elements only partially enclosing the brain, and associated with the capsules for the inner ears and the single nostril. The oldest fossil agnathans appeared in the

Cambrian, and two groups still survive today: the lampreys and the hagfish, comprising about 120 species in total.

Lamprey

Adults superficially resemble eels in that they have scaleless, elongated bodies. They have a cartilaginousskeleton (including skull) and can range from 13 to 100 cm (5 to 40 inches) in length. Instead of true vertebrae, they have a series of cartilaginous structures called arcualia arranged above the notochord. Lacking paired fins, adult lampreys have large eyes, one nostril on the top of the head, and seven gill pores on each side of the head.



Morphology of a larval lamprey.
More details.

The adult lamprey may be characterized by a jawless, toothed, funnel-like sucking mouth. The teeth are actually keratinous structures. They lack dentin an enameloid (a broader term that comprehends enamel and several variants), and they are not homologous to vertebrate teeth. The pharynx is subdivided: the ventral part forms a respiratory tube that is isolated from the mouth by a valve called the velum. This is an adaptation to how the adults feed. It prevents the prey's body fluids from escaping through the gills or interfering with gas exchange, which takes place by pumping water in and out of the gill pouches instead of taking it in through the mouth. Near the

gills are the eyes, which are poorly developed and buried under skin in the larvae. Parasitic lampreys feed on prey as adults by attaching their mouths to the target animal's body, then using their teeth to cut through surface tissues until they reach blood and body fluid.

[link]

Lampetra fluviatilis from the German North sea. More details.

[link]

Hagfish

These are eel-shaped, slime-producing marine fish (occasionally called **slime eels**) about 0.5 m (19.7 in) in length. They are the only known living animals that have a skull but no vertebral column. Along with lampreys, hagfish are jawless; they are the sister group to vertebrates, and living hagfish remain similar to hagfish from around 300 million years ago. The skin of hagfish has copious slime glands, the slime constituting their defense mechanism. The slime can sometimes clog up enemy fishes' gills, causing them to die.

Pacific hagfish resting on the ocean bottom, at 280 m depth off the Oregon coast. More details.

Other jawless fishes (Ostracoderms) were prominent in the oceans of the early Paleozoic. Cyclostomes (lamprey and hagfish) apparently split from the other agnathans before the evolution of dentine and bone, which are present in many fossil Ostracoderms. They were frequently armored with heavy bony plates. These Ostracoderms reached the high point of their evolution in the Late Silurian. Most of them, such as thelodonts, osteostracans, and galeaspids, were more closely related to the gnathostomes than to the cyclostomes (lamprey and hagfish). Agnathans declined in the Devonian and never recovered.

Jawed vertebrates

The infra-phylum Gnathostomata is comprised of vertebrates with jaws. It is believed that the jaws evolved from anterior gill support arches that had acquired a new role. Instead of being used for biting, their main role was to pump water over the gills by opening and closing the mouth more effectively – the buccal pump mechanism. The mouth could then grow bigger and wider, making it possible to capture larger prey. This close and open mechanism would, with time, become stronger and tougher, being transformed into biting jaws.

Jawed fishes had two large initial radiations (Placodermi and Acanthodii) but both became extinct during the Paleozoic. Placoderms were the oldest and they had the head and thoracis highly armored. Some of them reached very large sizes, like *Dunkleosteus terrelli* measuring up to 6 m (20 ft) long and 1 ton in weight. It was an apex predator.

The placoderm*Dunkleosteus* , an early jawed vertebrate. More details.

The Acanthodii shared features with both bony fish and cartilaginous fish. In form they resembled sharks, but their epidermis was covered with tiny rhomboid platelets like the scales of holosteans (gars, bowfins). They represent several independent phylogenetic branches of fishes leading to the still-extantChondrichthyes.

The remaining main radiations of fishes are the cartilaginous fishes (Chondrichthyes) and the bony fishes (Osteichthyes).

Cartilaginous fishes

This group includes sharks, rays and a few other fishes. They are distinguished from all other jawed fishes by having a cartilaginous skeleton. This is believed to be a secondary loss because the common ancestor of

jawed fishes is thought to have been a placoderm fish with bony skeleton. A notochord, is present in young cartilaginous fishes, but it is gradually replaced by cartilage.

[link]

Great white shark, *Carcharodon carcharias*. More details.

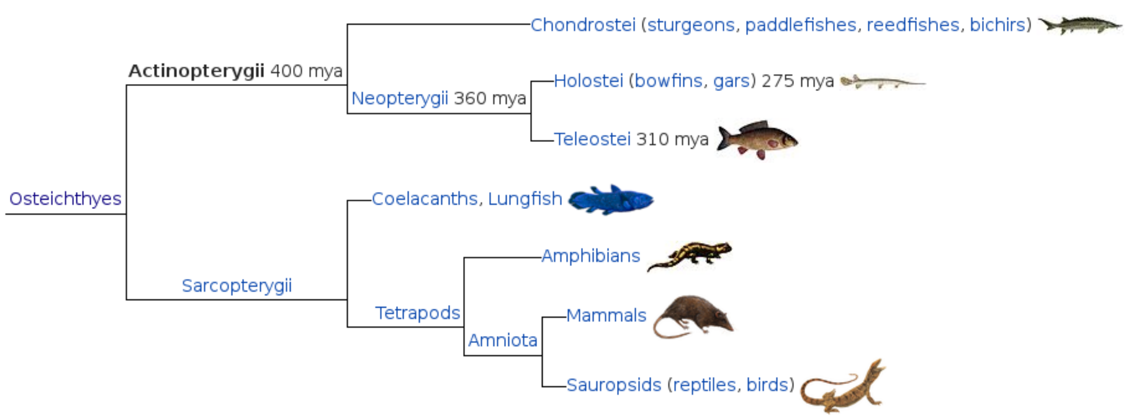
[link]

Cartilaginous fishes, such as sharks and rays have simple skull structures. The cranium is a single structure forming a case around the brain, enclosing the lower surface and the sides, but always at least partially open at the top as a large fontanelle. The most anterior part of the cranium includes a forward plate of cartilage, the rostrum, and capsules to enclose the olfactory organs. Behind these are the orbits, and then an additional pair of capsules enclosing the structure of the inner ear. Finally, the skull tapers towards the rear, where the foramen magnum lies immediately above a single condyle, articulating with the first vertebra. There are, in addition, at various points throughout the cranium, smaller foramina for the cranial nerves. The jaws consist of separate hoops of cartilage, almost always distinct from the cranium proper.

Bony fishes

Bony fishes (Osteichthyes) are characterized by a relatively stable pattern of cranial bones with medial insertion of a mandibular muscle in the lower jaw. The head and pectoral girdles are covered with large dermal bones. The eyeball is supported by a sclerotic ring of four small bones, but this characteristic has been lost or modified in many modern species. The labyrinth in the inner ear contains large otoliths. The braincase, or neurocranium, is frequently divided into anterior and posterior sections divided by a fissure. They also have an operculum, which helps them breathe without having to swim. Mucus glands coat the body and most species have smooth and overlapping scales.

The Osteichthyes are divided into two groups: ray-finned fish (Actinopterygii) and lobe-finned fish (Sarcopterygii). The former group accounts for 99% of the nearly 30,000 known species of fish. Although currently small, the later group gave origin to all tetrapods.



Phylogeny of bony fishes and tetrapods. More details.

Ray-finned fishes

There has been considerable modification from the primitive skull pattern in ray-finned fishes. The roof of the skull is generally well formed, and although the exact relationship of its bones to those of tetrapods is unclear, they are usually given similar names for convenience. Other elements of the skull, however, may be reduced; there is little cheek region behind the enlarged orbits, and little, if any bone in between them. The upper jaw is often formed largely from the premaxilla, with the maxilla itself located further back, and an additional bone, the symplectic, linking the jaw to the rest of the cranium.

Skeleton of the lingcod (*Ophiodon elongatus)*, a ray-finned fish. More details.

Lobe-finned fishes

Early lobe-finned fishes were bony fish with fleshy, lobed, paired fins, which are joined to the body by a single bone. All sarcopterygians possess teeth covered with true enamel. They present a well developed internal skeleton and the ability of breathing air. Most species of lobe-finned fishes are extinct. The largest known lobe-finned fish was *Rhizodus hibberti* from

the Carboniferous period of Scotland which may have exceeded 7 meters in length. Among the two groups of extant (living) species, the coelacanths and the lungfishes, the largest species is the West Indian Ocean coelacanth, reaching 2 m (6.5 ft) in length and weighing up 110 kg (240 lb). The largest lungfish is the African lungfish which can reach 2 m (6.6 ft) in length and weigh up to 50 kg (110 lb). These fishes share many morphological characteristics with the common ancestors of tetrapods due to common ancestry.

Queensland lungfish. More details.

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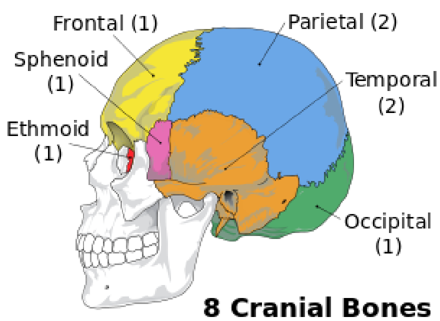
Tetrapods
As vertebrates colonized the ground, they evolved stronger and simpler skulls. These have basically two parts: the neurocranium protecting the brain, and the splanchnocranium forming the face. The neurocranium is further divided into dermatocranium and endocranium based on the developmental history of its bones. Several of the skull bones fuse during development, resulting in fewer bones in adults.

The skulls of the earliest tetrapods closely resembled those of their ancestors amongst the lobe-finned fishes. The skull roof is formed of a series of plate-like bones, including the maxilla, frontals, parietals, and lacrimals, among others. It is overlaying the endocranium, corresponding to the cartilaginous skull in sharks and rays. The various separate bones that compose the temporal bone of humans are also part of the skull roof series. A further plate composed of four pairs of bones forms the roof of the mouth; these include the vomer and palatine bones. The base of the cranium is formed from a ring of bones surrounding the foramen magnum and a median bone lying further forward; these are homologous with the occipital bone and parts of the sphenoid in mammals. Finally, the lower jaw is composed of multiple bones, only the most anterior of which (the dentary) is homologous with the mammalian mandible. In living tetrapods, a great many of the original bones have either disappeared or fused into one another in various arrangements.

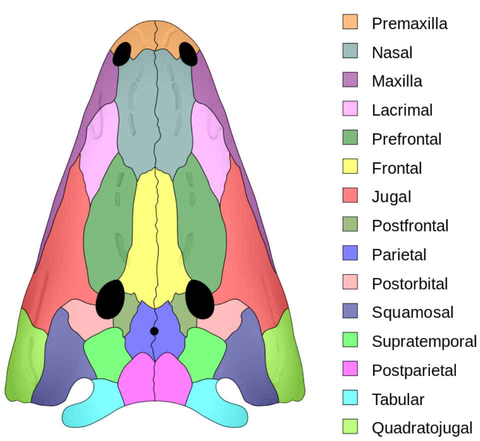
The structure of the tetrapod skull

The skull can be divided into neurocranium (braincase, calvaria) which is formed by the bones surrounding the brain, and the splanchnocranium (fascial skeleton) which is formed by the bones of the face.



The eight bones that form the human neurocranium. The splanchnocranium is shown without color. More details.

The neurocranium is further divided into dermatocranium (skull roof), which is the squamous shell formed through intramembranous ossification, and the endocranium (chondrocranium), which is formed from a cartilage template, by endochondral ossification. The dermatocranium is a set of bones covering the brain, eyes and nostrils in bony fishes and all land-living vertebrates.



The full complement of bones of the tetrapod skull roof, as seen in the labyrinthodont*Xenotosuchus*. More details.

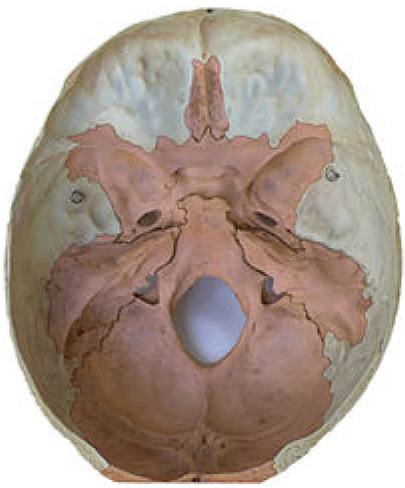
The early armoured fish did not have a skull in the common understanding of the word, but had an endocranium that was partially open above, topped by dermal bones forming armour. The dermal bones gradually evolved into a fixed unit overlaying the endocranium like a heavy "lid", protecting the animal's head and brain from above. Cartilaginous fish whose skeleton is formed from cartilage lack a continuous dermal armour and thus have no proper skull roof. A more or less full shield of fused dermal bones was common in early bony fishes of the Devonian, and particularly well developed in shallow water species.

The endocranium has a boxlike shape, open at the top. The posterior margin exhibit the *foramen magnum*, an opening for the spinal cord. The floor of the endocranium has several paired openings for the cranial nerves, and the anterior margin holds a spongy construction, allowing for the external nasal nerves to pass through. All bones of the structure derive from the cranial neural crest during fetal development and form by endochondral ossification.

In humans and other mammals, the endocranium forms during fetal development as a cartilaginous neurocranium, that ossifies from several centers. Several of these bones merge, and in the adult primates (including humans), the endocranium is composed of only five bony elements (from front to back):

- The Ethmoid bone, lying behind the nose.
- The Sphenoid bone, underlying the forward portion of the brain
- Paired petrous part of the temporal bones, containing the inner ear structures
- The Occipital bone, surrounding the *foramen magnum*

Notice that several of these bones also have a squamous region that is formed by dermal bone. Therefore only a portion of them is really part of the endocranium.



The ossified endocranium of a human skull. Endocranial elements colored in pink. More details.

Figure credits

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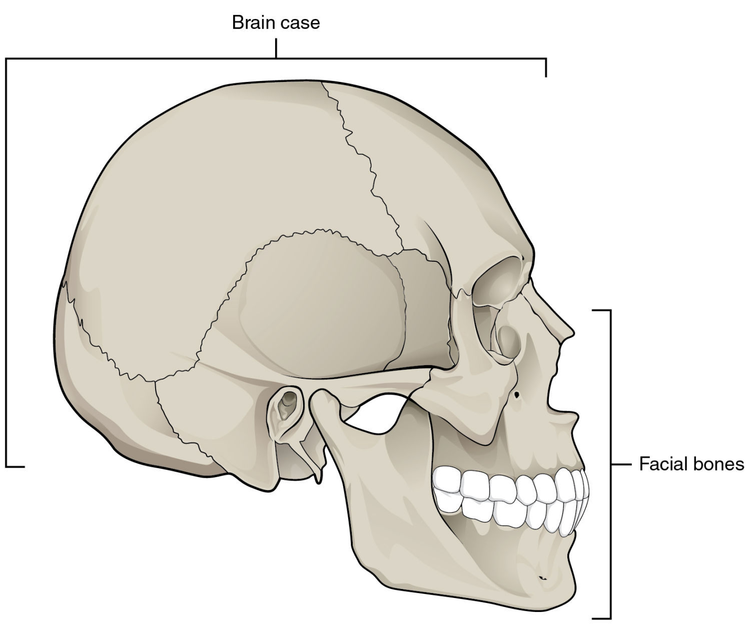
Overview of the Human Skull
The human skull is formed by 22 bones. Eight of them form the cranium, which surrounds and protects the brain. The face is formed by 14 bones: three pairs in the nasal region, three pairs in the oral region and two unpaired bones which are the mandible and the vomer. The skull also has accessory bones which include the hyoid and three pairs of auditory ossicles.

The Human Skull

The cranium (skull) is the skeletal structure of the head that supports the face and protects the brain. It is subdivided into the facial bones and the brain case, or cranial vault. The facial bones underlie the facial structures, form the nasal cavity, enclose the eyeballs, and support the teeth of the upper and lower jaws. The rounded brain case surrounds and protects the brain and houses the middle and inner ear structures.

In the adult, the skull consists of 22 individual bones, 21 of which are immobile and united into a single unit. The 22nd bone is the mandible (lower jaw), which is the only movable bone of the skull.

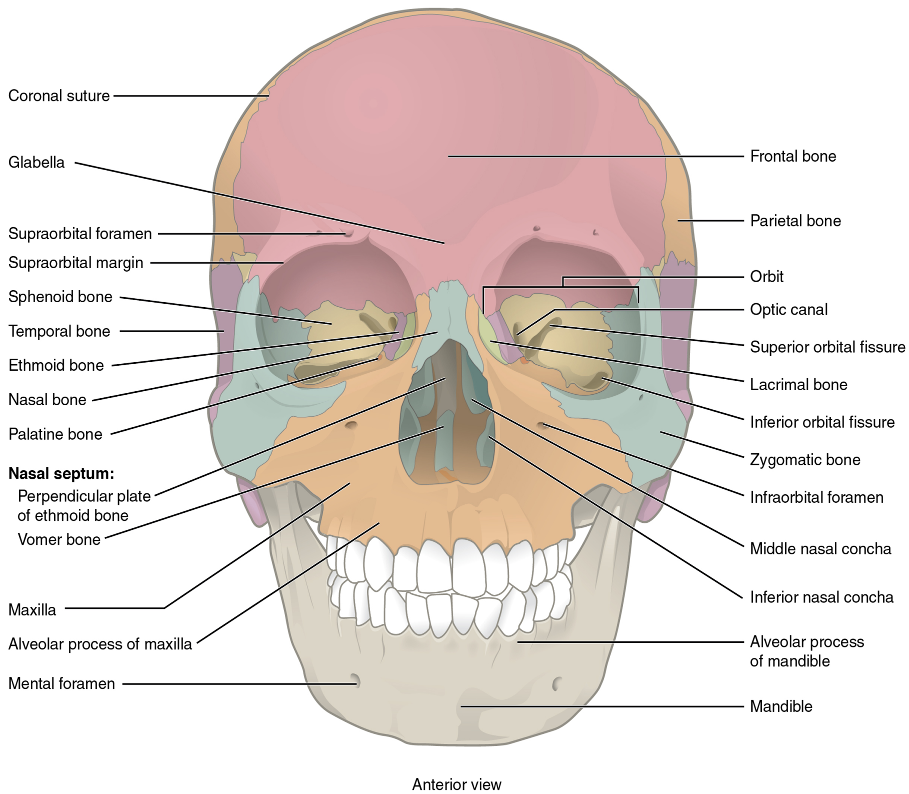


The skull consists of the rounded brain case that houses the brain and the facial bones that form the upper and lower jaws, nose, orbits, and other facial structures. More details.

Anterior View of Skull

The anterior skull consists of the facial bones and provides the bony support for the eyes and structures of the face. This view of the skull is dominated by the openings of the orbits and the nasal cavity. Also seen are the upper and lower jaws, with their respective teeth.

The orbit is the bony socket that houses the eyeball and muscles that move the eyeball or open the upper eyelid. The upper margin of the anterior orbit is the supraorbital margin. Located near the midpoint of the supraorbital margin is a small opening called the supraorbital foramen. This provides for passage of a sensory nerve to the skin of the forehead. Below the orbit is the infraorbital foramen, which is the point of emergence for a sensory nerve that supplies the anterior face below the orbit.



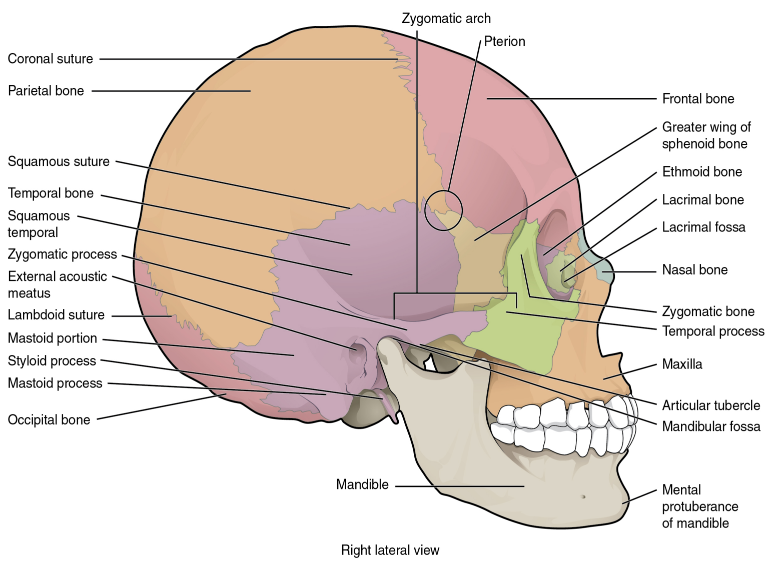
An anterior view of the skull shows the bones that form the forehead, orbits (eye sockets), nasal cavity, nasal septum, and upper and lower jaws. More details.

Inside the nasal area of the skull, the nasal cavity is divided into halves by the nasal septum. The upper portion of the nasal septum is formed by the perpendicular plate of the ethmoid bone and the lower portion is the vomer bone. Each side of the nasal cavity is triangular in shape, with a broad inferior space that narrows superiorly. When looking into the nasal cavity from the front of the skull, two bony plates are seen projecting from each lateral wall. The larger of these is the inferior nasal concha, an independent bone of the skull. Located just above the inferior concha is the middle nasal concha, which is part of the ethmoid bone. A third bony plate, also part of the ethmoid bone, is the superior nasal concha. It is much smaller and out of sight, above the middle concha. The superior nasal concha is located just lateral to the perpendicular plate, in the upper nasal cavity.

Lateral View of Skull

A view of the lateral skull is dominated by the large, rounded brain case above and the upper and lower jaws with their teeth below. Separating these areas is the bridge of bone called the zygomatic arch. The zygomatic arch is the bony arch on the side of skull that spans from the area of the cheek to just above the ear canal. It is formed by the junction of two bony processes: a short anterior component, the temporal process of the zygomatic bone (the cheekbone) and a longer posterior portion, the zygomatic process of the temporal bone, extending forward from the temporal bone. Thus the temporal process (anteriorly) and the zygomatic process (posteriorly) join together, like the two ends of a drawbridge, to form the zygomatic arch. One of the major muscles that pulls the mandible upward during biting and chewing arises from the zygomatic arch.

On the lateral side of the brain case, above the level of the zygomatic arch, is a shallow space called the temporal fossa. Below the level of the zygomatic arch and deep to the vertical portion of the mandible is another space called the infratemporal fossa. Both the temporal fossa and infratemporal fossa contain muscles that act on the mandible during chewing.



The lateral skull shows the large rounded brain case, zygomatic arch, and the upper and lower jaws. The zygomatic arch is formed jointly by the zygomatic process of the temporal bone and the temporal process of the zygomatic bone. The shallow space above the zygomatic arch is the temporal fossa. The space inferior to the zygomatic arch and deep to the posterior mandible is the infratemporal fossa. More details.

Figure credits

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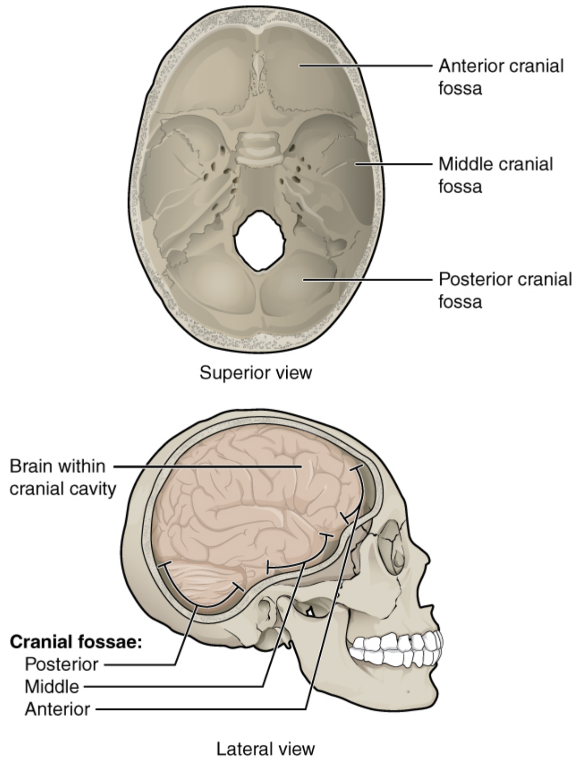
Cranial Bones
The cranium is formed by eight bones: two pairs and four single bones. The paired bones are the parietal and temporal bones. The single bones are the occipital, frontal sphenoid and ethmoid bones. All of these bones form part of the braincase which surrounds and protects the brain.

Bones of the Brain Case

The brain case contains and protects the brain. The interior space that is almost completely occupied by the brain is called the cranial cavity. This cavity is bounded superiorly by the rounded top of the skull, which is called the calvaria (skullcap), and the lateral and posterior sides of the skull. The bones that form the top and sides of the brain case are usually referred to as the “flat” bones of the skull.

The floor of the brain case is referred to as the base of the skull. This is a complex area that varies in depth and has numerous openings for the passage of cranial nerves, blood vessels, and the spinal cord. Inside the skull, the base is subdivided into three large spaces, called the anterior cranial fossa, middle cranial fossa, and posterior cranial fossa (fossa = “trench or ditch”). From anterior to posterior, the fossae increase in depth. The shape and depth of each fossa corresponds to the shape and size of the brain region that each houses. The boundaries and openings of the cranial fossae (singular = fossa) will be described in a later section.



The bones of the brain case surround and protect the brain, which occupies the cranial cavity. The base of the brain case, which forms the floor of cranial cavity, is subdivided into the shallow anterior cranial fossa, the middle cranial fossa, and the deep posterior cranial fossa. More details.

The brain case consists of eight bones. These include the paired parietal and temporal bones, plus the unpaired frontal, occipital, sphenoid, and ethmoid bones.

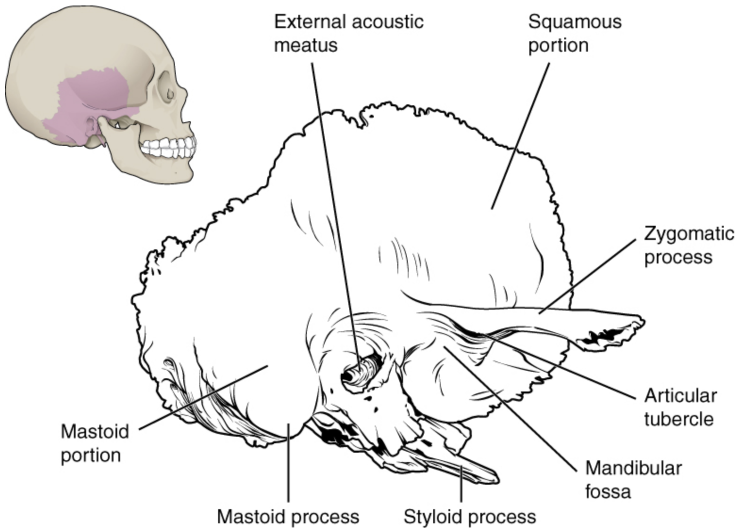
Parietal Bone

The parietal bone forms most of the upper lateral side of the skull. These are paired bones, with the right and left parietal bones joining together at the top of the skull. Each parietal bone is also bounded anteriorly by the frontal bone, inferiorly by the temporal bone, and posteriorly by the occipital bone.

Temporal Bone

The temporal bone forms the lower lateral side of the skull. Common wisdom has it that the temporal bone (temporal = "time") is so named because this area of the head (the temple) is where hair typically first turns gray, indicating the passage of time.

The temporal bone is subdivided into several regions. The flattened, upper portion is the squamous portion of the temporal bone. Below this area and projecting anteriorly is the zygomatic process of the temporal bone, which forms the posterior portion of the zygomatic arch. Posteriorly is the mastoid portion of the temporal bone. Projecting inferiorly from this region is a large prominence, the mastoid process, which serves as a muscle attachment site. The mastoid process can easily be felt on the side of the head just behind your earlobe. On the interior of the skull, the petrous portion of each temporal bone forms the prominent, diagonally oriented petrous ridge in the floor of the cranial cavity. Located inside each petrous ridge are small cavities that house the structures of the middle and inner ears.



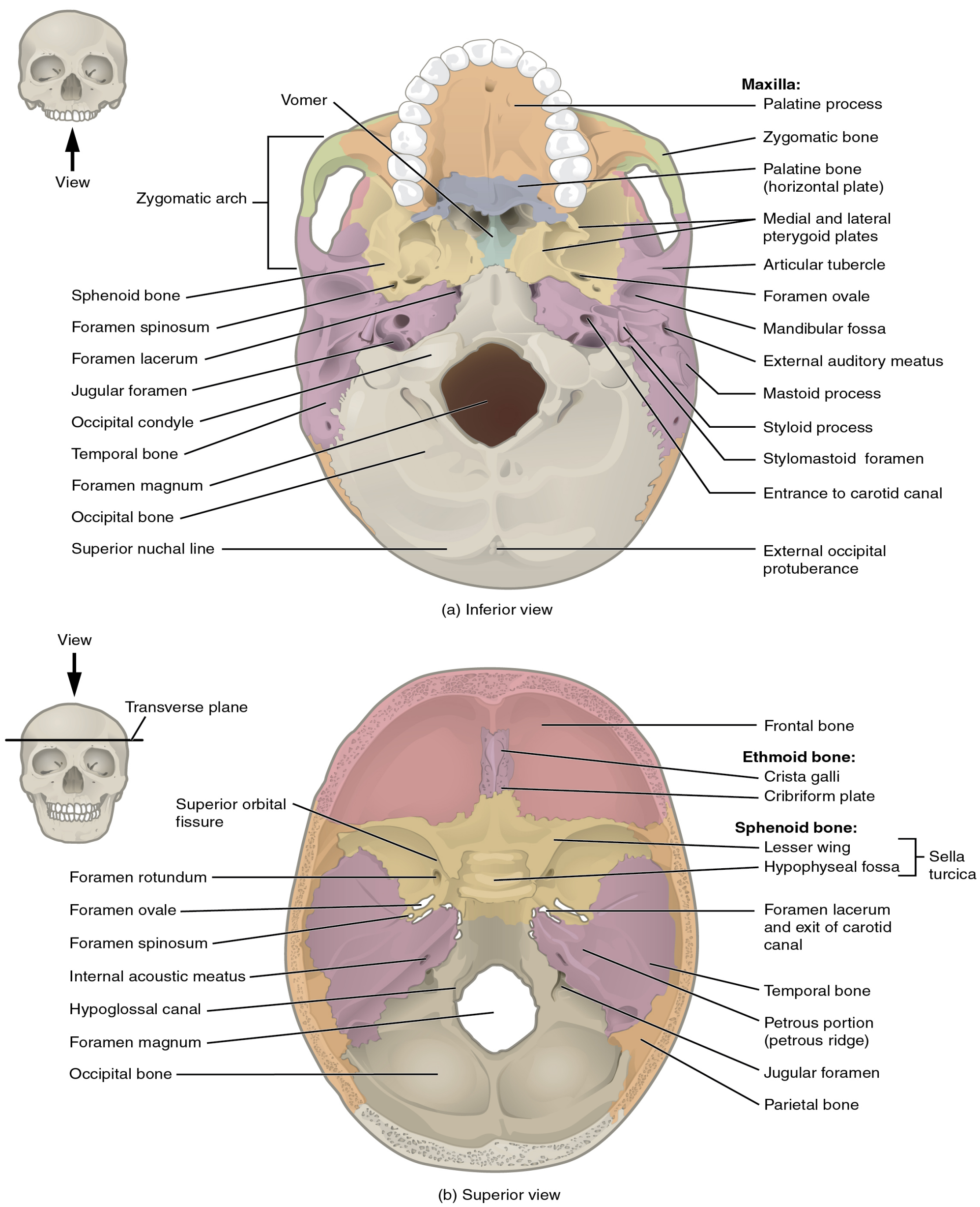
A lateral view of the isolated temporal bone shows the squamous, mastoid, and zygomatic portions of the temporal bone. More details.

Important landmarks of the temporal bone, include the following:

- External acoustic meatus (ear canal)—This is the large opening on the lateral side of the skull that is associated with the ear.
- Internal acoustic meatus—This opening is located inside the cranial cavity, on the medial side of the petrous ridge. It connects to the middle and inner ear cavities of the temporal bone.
- Mandibular fossa—This is the deep, oval-shaped depression located on the external base of the skull, just in front of the external acoustic meatus. The mandible (lower jaw) joins with the skull at this site as part of the temporomandibular joint, which allows for movements of the mandible during opening and closing of the mouth.
- Articular tubercle—The smooth ridge located immediately anterior to the mandibular fossa. Both the articular tubercle and mandibular fossa contribute to the temporomandibular joint, the joint that provides for movements between the temporal bone of the skull and the mandible.
- Styloid process—Posterior to the mandibular fossa on the external base of the skull is an elongated, downward bony projection called the

styloid process, so named because of its resemblance to a stylus (a pen or writing tool). This structure serves as an attachment site for several small muscles and for a ligament that supports the hyoid bone of the neck.

- Stylomastoid foramen—This small opening is located between the styloid process and mastoid process. This is the point of exit for the cranial nerve that supplies the facial muscles.
- Carotid canal—The carotid canal is a zig-zag shaped tunnel that provides passage through the base of the skull for one of the major arteries that supplies the brain. Its entrance is located on the outside base of the skull, anteromedial to the styloid process. The canal then runs anteromedially within the bony base of the skull, and then turns upward to its exit in the floor of the middle cranial cavity, above the foramen lacerum.



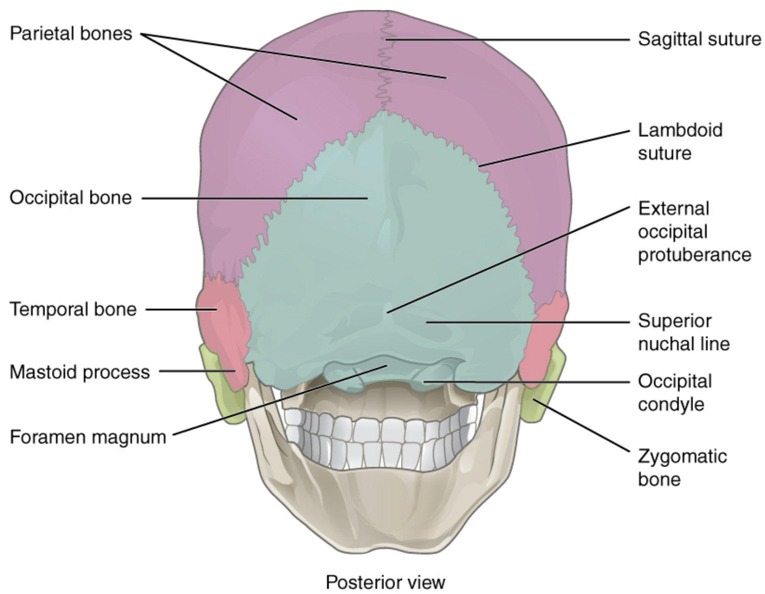
(a) The hard palate is formed anteriorly by the palatine processes of the maxilla bones and posteriorly by the horizontal plate of the palatine bones. (b) The complex floor of the cranial cavity is formed by the frontal, ethmoid, sphenoid, temporal, and occipital bones. The lesser wing of the sphenoid bone separates the anterior and middle cranial fossae. The petrous ridge (petrous portion of temporal bone) separates the middle and posterior cranial fossae. [More details](#).

Frontal Bone

The frontal bone is the single bone that forms the forehead. At its anterior midline, between the eyebrows, there is a slight depression called the glabella. The frontal bone also forms the supraorbital margin of the orbit. Near the middle of this margin, is the supraorbital foramen, the opening that provides passage for a sensory nerve to the forehead. The frontal bone is thickened just above each supraorbital margin, forming rounded brow ridges. These are located just behind your eyebrows and vary in size among individuals, although they are generally larger in males. Inside the cranial cavity, the frontal bone extends posteriorly. This flattened region forms both the roof of the orbit below and the floor of the anterior cranial cavity above.

Occipital Bone

The occipital bone is the single bone that forms the posterior skull and posterior base of the cranial cavity. On its outside surface, at the posterior midline, is a small protrusion called the external occipital protuberance, which serves as an attachment site for a ligament of the posterior neck. Lateral to either side of this bump is a superior nuchal line (nuchal = “nape” or “posterior neck”). The nuchal lines represent the most superior point at which muscles of the neck attach to the skull, with only the scalp covering the skull above these lines. On the base of the skull, the occipital bone contains the large opening of the foramen magnum, which allows for passage of the spinal cord as it exits the skull. On either side of the foramen magnum is an oval-shaped occipital condyle. These condyles form joints with the first cervical vertebra and thus support the skull on top of the vertebral column.



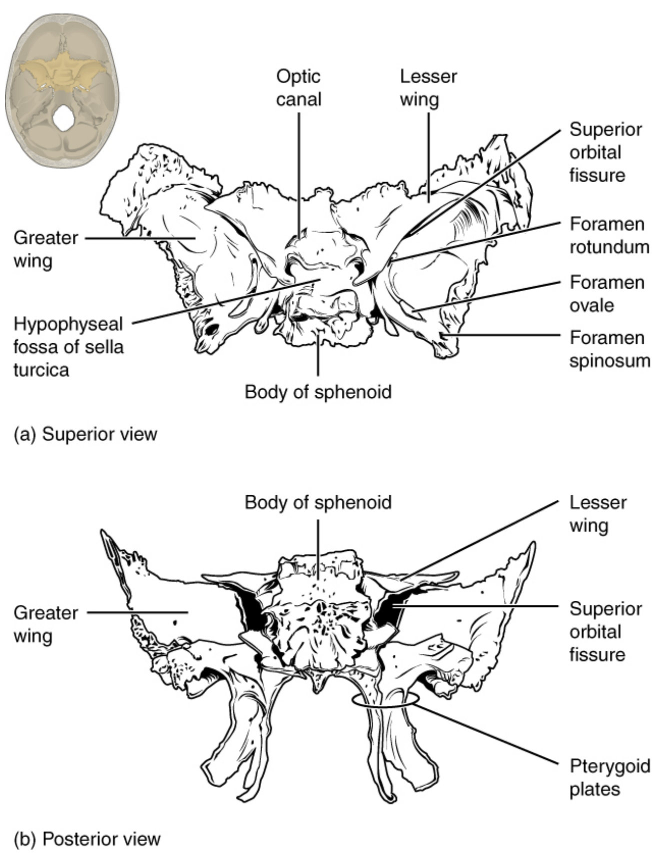
This view of the posterior skull shows attachment sites for muscles and joints that support the skull. More details.

Sphenoid Bone

The sphenoid bone is a single, complex bone of the central skull. It serves as a “keystone” bone, because it joins with almost every other bone of the skull. The sphenoid forms much of the base of the central skull and also extends laterally to contribute to the sides of the skull. Inside the cranial cavity, the right and left lesser wings of the sphenoid bone, which resemble the wings of a flying bird, form the lip of a prominent ridge that marks the boundary between the anterior and middle cranial fossae. The sella turcica (“Turkish saddle”) is located at the midline of the middle cranial fossa. This bony region of the sphenoid bone is named for its resemblance to the horse saddles used by the Ottoman Turks, with a high back and a tall front. The rounded depression in the floor of the sella turcica is the hypophyseal (pituitary) fossa, which houses the pea-sized pituitary (hypophyseal) gland. The greater wings of the sphenoid bone extend laterally to either side away from the sella turcica, where they form the anterior floor of the middle

cranial fossa. The greater wing is best seen on the outside of the lateral skull, where it forms a rectangular area immediately anterior to the squamous portion of the temporal bone.

On the inferior aspect of the skull, each half of the sphenoid bone forms two thin, vertically oriented bony plates. These are the medial pterygoid plate and lateral pterygoid plate (pterygoid = “wing-shaped”). The right and left medial pterygoid plates form the posterior, lateral walls of the nasal cavity. The somewhat larger lateral pterygoid plates serve as attachment sites for chewing muscles that fill the infratemporal space and act on the mandible.



Shown in isolation in (a) superior and (b) posterior views, the sphenoid bone is a single midline bone that forms the anterior walls and floor of the middle cranial

fossa. It has a pair of lesser wings and a pair of greater wings. The sella turcica surrounds the hypophyseal fossa. Projecting downward are the medial and lateral pterygoid plates. The sphenoid has multiple openings for the passage of nerves and blood vessels, including the optic canal, superior orbital fissure, foramen rotundum, foramen ovale, and foramen spinosum. More details.

Ethmoid Bone

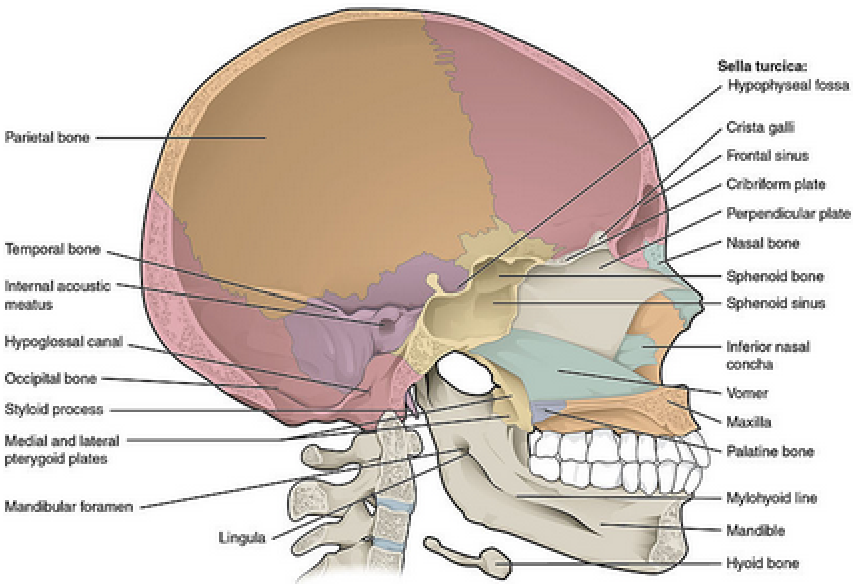
The ethmoid bone is a single, midline bone that forms the roof and lateral walls of the upper nasal cavity, the upper portion of the nasal septum, and contributes to the medial wall of the orbit. On the interior of the skull, the ethmoid also forms a portion of the floor of the anterior cranial cavity.

Within the nasal cavity, the perpendicular plate of the ethmoid bone forms the upper portion of the nasal septum. The ethmoid bone also forms the lateral walls of the upper nasal cavity. Extending from each lateral wall are the superior nasal concha and middle nasal concha, which are thin, curved projections that extend into the nasal cavity.

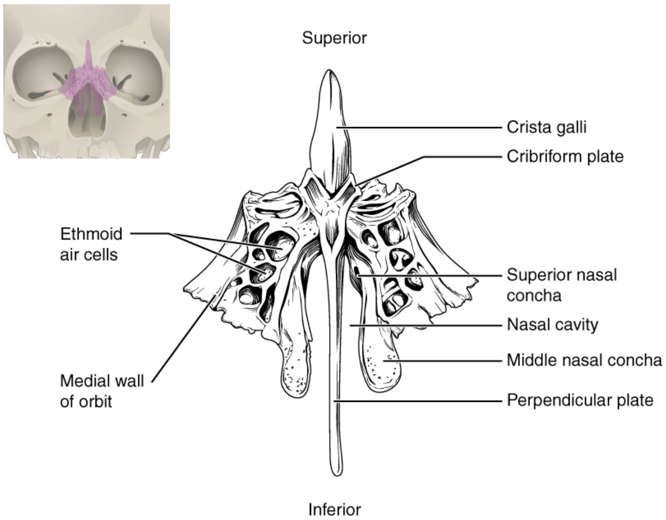
In the cranial cavity, the ethmoid bone forms a small area at the midline in the floor of the anterior cranial fossa. This region also forms the narrow roof of the underlying nasal cavity. This portion of the ethmoid bone consists of two parts, the crista galli and cribriform plates. The crista galli (“rooster’s comb or crest”) is a small upward bony projection located at the midline. It functions as an anterior attachment point for one of the covering layers of the brain. To either side of the crista galli is the cribriform plate (cribrum = “sieve”), a small, flattened area with numerous small openings

termed olfactory foramina. Small nerve branches from the olfactory areas of the nasal cavity pass through these openings to enter the brain.

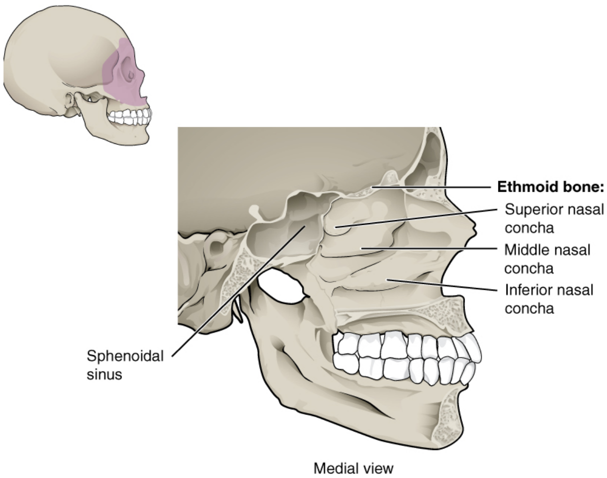
The lateral portions of the ethmoid bone are located between the orbit and upper nasal cavity, and thus form the lateral nasal cavity wall and a portion of the medial orbit wall. Located inside this portion of the ethmoid bone are several small, air-filled spaces that are part of the paranasal sinus system of the skull.



This midline view of the sagittally sectioned skull shows the nasal septum. More details.



The unpaired ethmoid bone is located at the midline within the central skull. It has an upward projection, the crista galli, and a downward projection, the perpendicular plate, which forms the upper nasal septum. The cribriform plates form both the roof of the nasal cavity and a portion of the anterior cranial fossa floor. The lateral sides of the ethmoid bone form the lateral walls of the upper nasal cavity, part of the medial orbit wall, and give rise to the superior and middle nasal conchae. The ethmoid bone also contains the ethmoid air cells. More details.



The three nasal conchae are curved bones that project from the lateral walls of the nasal cavity. The superior nasal concha and middle nasal concha are parts of the ethmoid bone. The inferior nasal concha is an independent bone of the skull. More details.

Sutures of the Skull

A suture is an immobile joint between adjacent bones of the skull. The narrow gap between the bones is filled with dense, fibrous connective tissue that unites the bones. The long sutures located between the bones of the brain case are not straight, but instead follow irregular, tightly twisting paths. These twisting lines serve to tightly interlock the adjacent bones, thus adding strength to the skull for brain protection.

The two suture lines seen on the top of the skull are the coronal and sagittal sutures. The coronal suture runs from side to side across the skull, within the coronal plane of section. It joins the frontal bone to the right and left parietal bones. The sagittal suture extends posteriorly from the coronal

suture, running along the midline at the top of the skull in the sagittal plane of section. It unites the right and left parietal bones. On the posterior skull, the sagittal suture terminates by joining the lambdoid suture. The lambdoid suture extends downward and laterally to either side away from its junction with the sagittal suture. The lambdoid suture joins the occipital bone to the right and left parietal and temporal bones. This suture is named for its upside-down "V" shape, which resembles the capital letter version of the Greek letter lambda (Λ). The squamous suture is located on the lateral skull. It unites the squamous portion of the temporal bone with the parietal bone. At the intersection of four bones is the pterion, a small, capital-H-shaped suture line region that unites the frontal bone, parietal bone, squamous portion of the temporal bone, and greater wing of the sphenoid bone. It is the weakest part of the skull. The pterion is located approximately two finger widths above the zygomatic arch and a thumb's width posterior to the upward portion of the zygomatic bone.

Cranial Fossae

Inside the skull, the floor of the cranial cavity is subdivided into three cranial fossae (spaces), which increase in depth from anterior to posterior. Since the brain occupies these areas, the shape of each conforms to the shape of the brain regions that it contains. Each cranial fossa has anterior and posterior boundaries and is divided at the midline into right and left areas by a significant bony structure or opening.

Anterior Cranial Fossa

The anterior cranial fossa is the most anterior and the shallowest of the three cranial fossae. It overlies the orbits and contains the frontal lobes of the brain. Anteriorly, the anterior fossa is bounded by the frontal bone, which also forms the majority of the floor for this space. The lesser wings of the sphenoid bone form the prominent ledge that marks the boundary between the anterior and middle cranial fossae. Located in the floor of the anterior cranial fossa at the midline is a portion of the ethmoid bone,

consisting of the upward projecting crista galli and to either side of this, the cribriform plates.

Middle Cranial Fossa

The middle cranial fossa is deeper and situated posterior to the anterior fossa. It extends from the lesser wings of the sphenoid bone anteriorly, to the petrous ridges (petrous portion of the temporal bones) posteriorly. The large, diagonally positioned petrous ridges give the middle cranial fossa a butterfly shape, making it narrow at the midline and broad laterally. The temporal lobes of the brain occupy this fossa. The middle cranial fossa is divided at the midline by the upward bony prominence of the sella turcica, a part of the sphenoid bone. The middle cranial fossa has several openings for the passage of blood vessels and cranial nerves.

Openings in the middle cranial fossa are as follows:

- Optic canal—This opening is located at the anterior lateral corner of the sella turcica. It provides for passage of the optic nerve into the orbit.
- Superior orbital fissure—This large, irregular opening into the posterior orbit is located on the anterior wall of the middle cranial fossa, lateral to the optic canal and under the projecting margin of the lesser wing of the sphenoid bone. Nerves to the eyeball and associated muscles, and sensory nerves to the forehead pass through this opening.
- Foramen rotundum—This rounded opening (rotundum = “round”) is located in the floor of the middle cranial fossa, just inferior to the superior orbital fissure. It is the exit point for a major sensory nerve that supplies the cheek, nose, and upper teeth.
- Foramen ovale of the middle cranial fossa—This large, oval-shaped opening in the floor of the middle cranial fossa provides passage for a major sensory nerve to the lateral head, cheek, chin, and lower teeth.
- Foramen spinosum—This small opening, located posterior-lateral to the foramen ovale, is the entry point for an important artery that supplies the covering layers surrounding the brain. The branching pattern of this artery forms readily visible grooves on the internal

surface of the skull and these grooves can be traced back to their origin at the foramen spinosum.
- Carotid canal—This is the zig-zag passageway through which a major artery to the brain enters the skull. The entrance to the carotid canal is located on the inferior aspect of the skull, anteromedial to the styloid process. From here, the canal runs anteromedially within the bony base of the skull. Just above the foramen lacerum, the carotid canal opens into the middle cranial cavity, near the posterior-lateral base of the sella turcica.
- Foramen lacerum—This irregular opening is located in the base of the skull, immediately inferior to the exit of the carotid canal. This opening is an artifact of the dry skull, because in life it is completely filled with cartilage. All the openings of the skull that provide for passage of nerves or blood vessels have smooth margins; the word lacerum ("ragged" or "torn") tells us that this opening has ragged edges and thus nothing passes through it.

Posterior Cranial Fossa

The posterior cranial fossa is the most posterior and deepest portion of the cranial cavity. It contains the cerebellum of the brain. The posterior fossa is bounded anteriorly by the petrous ridges, while the occipital bone forms the floor and posterior wall. It is divided at the midline by the large foramen magnum ("great aperture"), the opening that provides for passage of the spinal cord.

Located on the medial wall of the petrous ridge in the posterior cranial fossa is the internal acoustic meatus. This opening provides for passage of the nerve from the hearing and equilibrium organs of the inner ear, and the nerve that supplies the muscles of the face. Located at the anterior-lateral margin of the foramen magnum is the hypoglossal canal. These emerge on the inferior aspect of the skull at the base of the occipital condyle and provide passage for an important nerve to the tongue.

Immediately inferior to the internal acoustic meatus is the large, irregularly shaped jugular foramen. Several cranial nerves from the brain exit the skull

via this opening. It is also the exit point through the base of the skull for all the venous return blood leaving the brain. The venous structures that carry blood inside the skull form large, curved grooves on the inner walls of the posterior cranial fossa, which terminate at each jugular foramen.

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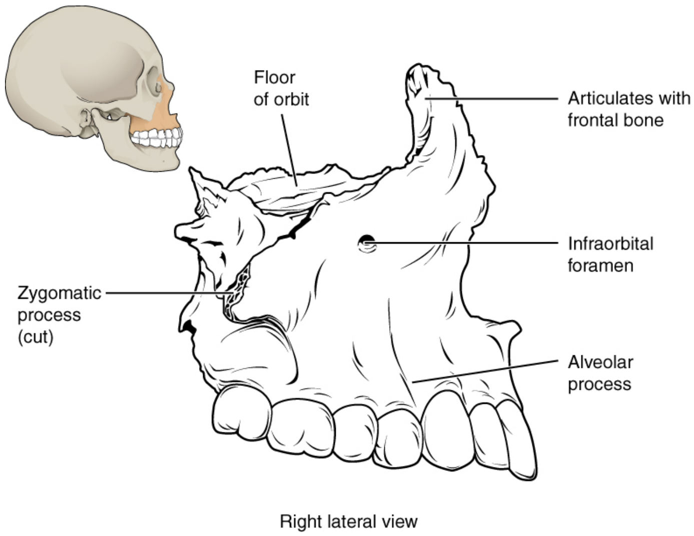
Facial Bones
The human face has 14 bones. Three pairs are found in the nasal region: the inferior conchae, lacrimal, and nasal bones. Three more pairs are found above the mouth: the maxillary, palatine and zygomatic bones. Two single bones complete the face: the mandible and vomer bones.

Bones of the Human Face

The facial bones of the skull form the upper and lower jaws, the nose, nasal cavity and nasal septum, and the orbit. The facial bones include 14 bones, with six paired bones and two unpaired bones. The paired bones are the maxilla, palatine, zygomatic, nasal, lacrimal, and inferior nasal conchae bones. The unpaired bones are the vomer and mandible bones. Although classified with the brain-case bones, the ethmoid bone also contributes to the nasal septum and the walls of the nasal cavity and orbit.

Maxillary Bone

The maxillary bone, often referred to simply as the maxilla (plural = maxillae), is one of a pair that together form the upper jaw, much of the hard palate, the medial floor of the orbit, and the lateral base of the nose. The curved, inferior margin of the maxillary bone that forms the upper jaw and contains the upper teeth is the alveolar process of the maxilla. Each tooth is anchored into a deep socket called an alveolus. On the anterior maxilla, just below the orbit, is the infraorbital foramen. This is the point of exit for a sensory nerve that supplies the nose, upper lip, and anterior cheek. On the inferior skull, the palatine process from each maxillary bone can be seen joining together at the midline to form the anterior three-quarters of the hard palate. The hard palate is the bony plate that forms the roof of the mouth and floor of the nasal cavity, separating the oral and nasal cavities.



The maxillary bone forms the upper jaw and supports the upper teeth. Each maxilla also forms the lateral floor of each orbit and the majority of the hard palate. More details.

Palatine Bone

The palatine bone is one of a pair of irregularly shaped bones that contribute small areas to the lateral walls of the nasal cavity and the medial wall of each orbit. The largest region of each of the palatine bone is the horizontal plate. The plates from the right and left palatine bones join together at the midline to form the posterior quarter of the hard palate. Thus, the palatine bones are best seen in an inferior view of the skull and hard palate.

Zygomatic Bone

The zygomatic bone is also known as the cheekbone. Each of the paired zygomatic bones forms much of the lateral wall of the orbit and the lateral-inferior margins of the anterior orbital opening. The short temporal process of the zygomatic bone projects posteriorly, where it forms the anterior portion of the zygomatic arch.

Nasal Bone

The nasal bone is one of two small bones that articulate (join) with each other to form the bony base (bridge) of the nose. They also support the cartilages that form the lateral walls of the nose. These are the bones that are damaged when the nose is broken.

Lacrimal Bone

Each lacrimal bone is a small, rectangular bone that forms the anterior, medial wall of the orbit. The anterior portion of the lacrimal bone forms a shallow depression called the lacrimal fossa, and extending inferiorly from this is the nasolacrimal canal. The lacrimal fluid (tears of the eye), which serves to maintain the moist surface of the eye, drains at the medial corner of the eye into the nasolacrimal canal. This duct then extends downward to open into the nasal cavity, behind the inferior nasal concha. In the nasal cavity, the lacrimal fluid normally drains posteriorly, but with an increased flow of tears due to crying or eye irritation, some fluid will also drain anteriorly, thus causing a runny nose.

Inferior Nasal Conchae

The right and left inferior nasal conchae form a curved bony plate that projects into the nasal cavity space from the lower lateral wall. The inferior concha is the largest of the nasal conchae and can easily be seen when looking into the anterior opening of the nasal cavity.

Vomer Bone

The unpaired vomer bone, often referred to simply as the vomer, is triangular-shaped and forms the posterior-inferior part of the nasal septum. The vomer is best seen when looking from behind into the posterior openings of the nasal cavity. In this view, the vomer is seen to form the entire height of the nasal septum. A much smaller portion of the vomer can also be seen when looking into the anterior opening of the nasal cavity.

Mandible

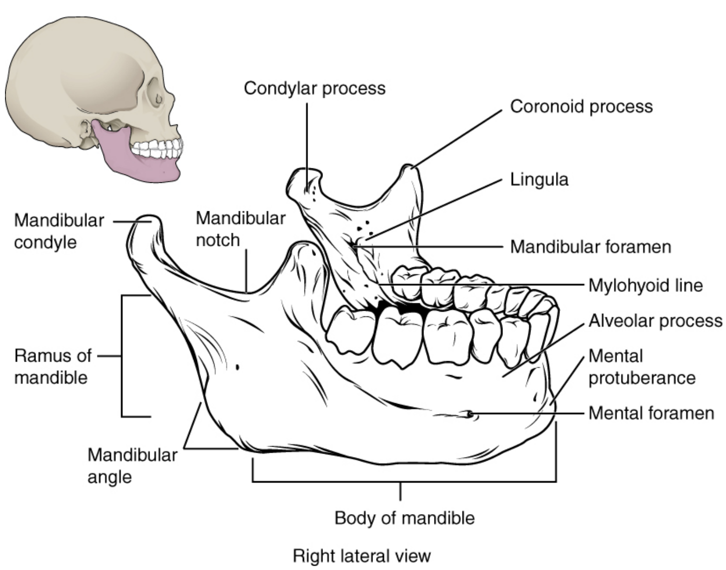
The mandible forms the lower jaw and is the only moveable bone of the skull. At the time of birth, the mandible consists of paired right and left bones, but these fuse together during the first year to form the single U-shaped mandible of the adult skull. Each side of the mandible consists of a horizontal body and posteriorly, a vertically oriented ramus of the mandible (ramus = "branch"). The outside margin of the mandible, where the body and ramus come together is called the angle of the mandible.

The ramus on each side of the mandible has two upward-going bony projections. The more anterior projection is the flattened coronoid process of the mandible, which provides attachment for one of the biting muscles. The posterior projection is the condylar process of the mandible, which is topped by the oval-shaped condyle. The condyle of the mandible articulates (joins) with the mandibular fossa and articular tubercle of the temporal bone. Together these articulations form the temporomandibular joint, which allows for opening and closing of the mouth. The broad U-shaped curve located between the coronoid and condylar processes is the mandibular notch.

Important landmarks for the mandible include the following:

- Alveolar process of the mandible—This is the upper border of the mandibular body and serves to anchor the lower teeth.
- Mental protuberance—The forward projection from the inferior margin of the anterior mandible that forms the chin (mental = "chin").

- Mental foramen—The opening located on each side of the anterior-lateral mandible, which is the exit site for a sensory nerve that supplies the chin.
- Mylohyoid line—This bony ridge extends along the inner aspect of the mandibular body. The muscle that forms the floor of the oral cavity attaches to the mylohyoid lines on both sides of the mandible.
- Mandibular foramen—This opening is located on the medial side of the ramus of the mandible. The opening leads into a tunnel that runs down the length of the mandibular body. The sensory nerve and blood vessels that supply the lower teeth enter the mandibular foramen and then follow this tunnel. Thus, to numb the lower teeth prior to dental work, the dentist must inject anesthesia into the lateral wall of the oral cavity at a point prior to where this sensory nerve enters the mandibular foramen.
- Lingula—This small flap of bone is named for its shape (lingula = “little tongue”). It is located immediately next to the mandibular foramen, on the medial side of the ramus. A ligament that anchors the mandible during opening and closing of the mouth extends down from the base of the skull and attaches to the lingula.



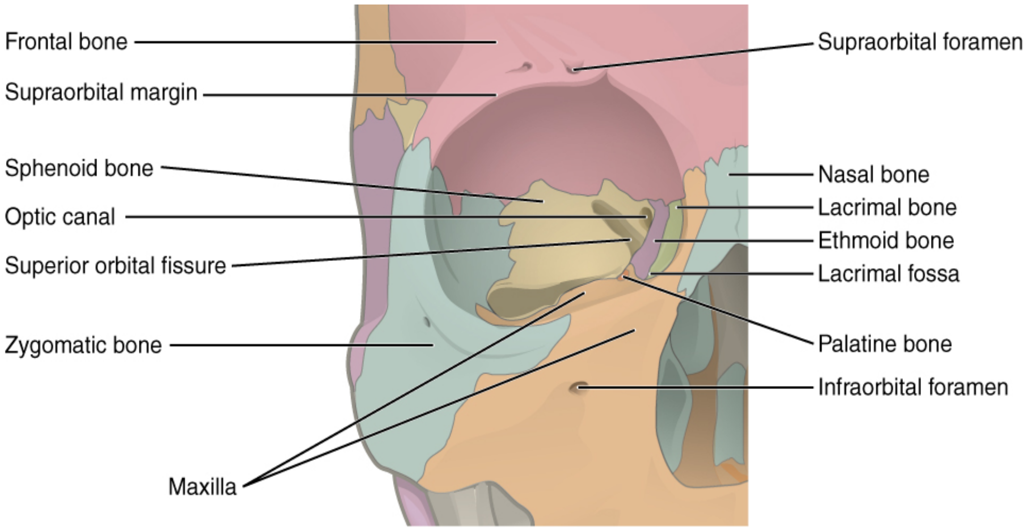
The mandible is the only movable bone of the skull. [More details](#).

The Orbit

The orbit is the bony socket that houses the eyeball and contains the muscles that move the eyeball or open the upper eyelid. Each orbit is cone-shaped, with a narrow posterior region that widens toward the large anterior opening. To help protect the eye, the bony margins of the anterior opening are thickened and somewhat constricted. The medial walls of the two orbits are parallel to each other but each lateral wall diverges away from the midline at a 45° angle. This divergence provides greater lateral peripheral vision.

The walls of each orbit include contributions from seven skull bones. The frontal bone forms the roof and the zygomatic bone forms the lateral wall and lateral floor. The medial floor is primarily formed by the maxilla, with a small contribution from the palatine bone. The ethmoid bone and lacrimal bone make up much of the medial wall and the sphenoid bone forms the posterior orbit.

At the posterior apex of the orbit is the opening of the optic canal, which allows for passage of the optic nerve from the retina to the brain. Lateral to this is the elongated and irregularly shaped superior orbital fissure, which provides passage for the artery that supplies the eyeball, sensory nerves, and the nerves that supply the muscles involved in eye movements.



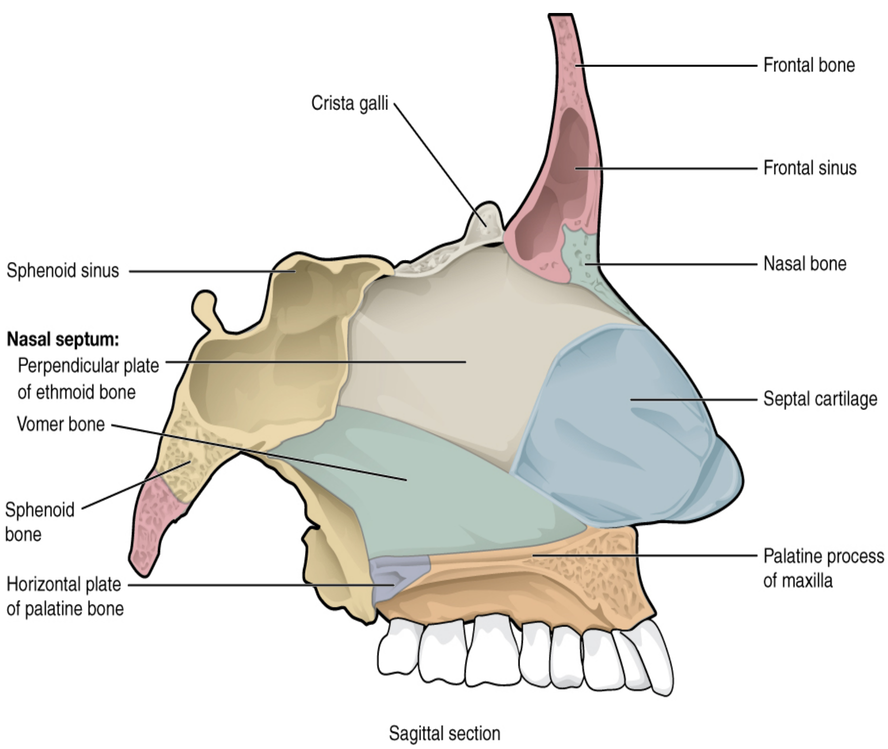
Seven skull bones contribute to the walls of the orbit. Opening into the posterior orbit from the cranial cavity are the optic canal and superior orbital fissure. More details.

The Nasal Septum and Nasal Conchae

The nasal septum consists of both bone and cartilage components. The upper portion of the septum is formed by the perpendicular plate of the ethmoid bone. The lower and posterior parts of the septum are formed by the triangular-shaped vomer bone. In an anterior view of the skull, the perpendicular plate of the ethmoid bone is easily seen inside the nasal opening as the upper nasal septum, but only a small portion of the vomer is seen as the inferior septum. A better view of the vomer bone is seen when looking into the posterior nasal cavity with an inferior view of the skull, where the vomer forms the full height of the nasal septum. The anterior nasal septum is formed by the septal cartilage, a flexible plate that fills in the gap between the perpendicular plate of the ethmoid and vomer bones. This cartilage also extends outward into the nose where it separates the right and left nostrils. The septal cartilage is not found in the dry skull.

Attached to the lateral wall on each side of the nasal cavity are the superior, middle, and inferior nasal conchae (singular = concha), which are named

for their positions. These are bony plates that curve downward as they project into the space of the nasal cavity. They serve to swirl the incoming air, which helps to warm and moisturize it before the air moves into the delicate air sacs of the lungs. This also allows mucus, secreted by the tissue lining the nasal cavity, to trap incoming dust, pollen, bacteria, and viruses. The largest of the conchae is the inferior nasal concha, which is an independent bone of the skull. The middle concha and the superior conchae, which is the smallest, are both formed by the ethmoid bone. When looking into the anterior nasal opening of the skull, only the inferior and middle conchae can be seen. The small superior nasal concha is well hidden above and behind the middle concha.

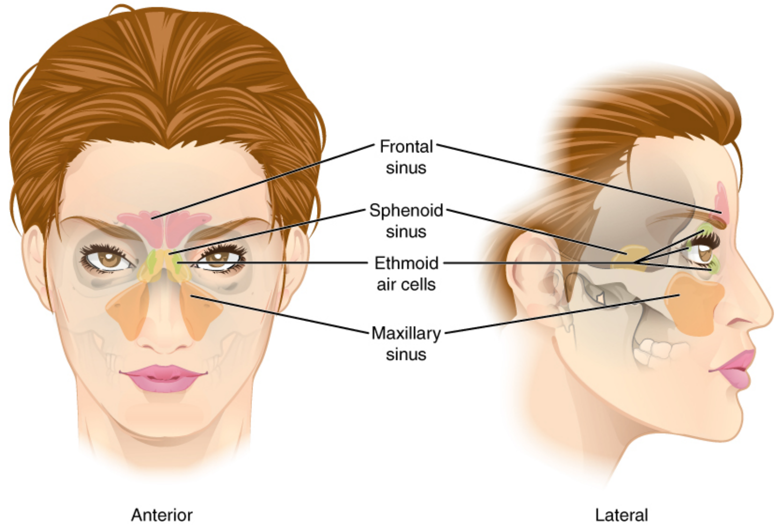


The nasal septum is formed by the perpendicular plate of the ethmoid bone and the vomer bone. The septal cartilage fills the gap between these bones and extends into the nose. More details.

Paranasal Sinuses

The paranasal sinuses are hollow, air-filled spaces located within certain bones of the skull. All of the sinuses communicate with the nasal cavity (paranasal = “next to nasal cavity”) and are lined with nasal mucosa. They serve to reduce bone mass and thus lighten the skull, and they also add resonance to the voice. This second feature is most obvious when you have a cold or sinus congestion. These produce swelling of the mucosa and excess mucus production, which can obstruct the narrow passageways between the sinuses and the nasal cavity, causing your voice to sound different to yourself and others. This blockage can also allow the sinuses to fill with fluid, with the resulting pressure producing pain and discomfort.

The paranasal sinuses are named for the skull bone that each occupies. The frontal sinus is located just above the eyebrows, within the frontal bone. This irregular space may be divided at the midline into bilateral spaces, or these may be fused into a single sinus space. The frontal sinus is the most anterior of the paranasal sinuses. The largest sinus is the maxillary sinus. These are paired and located within the right and left maxillary bones, where they occupy the area just below the orbits. The maxillary sinuses are most commonly involved during sinus infections. Because their connection to the nasal cavity is located high on their medial wall, they are difficult to drain. The sphenoid sinus is a single, midline sinus. It is located within the body of the sphenoid bone, just anterior and inferior to the sella turcica, thus making it the most posterior of the paranasal sinuses. The lateral aspects of the ethmoid bone contain multiple small spaces separated by very thin bony walls. Each of these spaces is called an ethmoid air cell. These are located on both sides of the ethmoid bone, between the upper nasal cavity and medial orbit, just behind the superior nasal conchae.



The paranasal sinuses are hollow, air-filled spaces named for the skull bone that each occupies. The most anterior is the frontal sinus, located in the frontal bone above the eyebrows. The largest are the maxillary sinuses, located in the right and left maxillary bones below the orbits. The most posterior is the sphenoid sinus, located in the body of the sphenoid bone, under the sella turcica. The ethmoid air cells are multiple small spaces located in the right and left sides of the ethmoid bone, between the medial wall of the orbit and lateral wall of the upper nasal cavity. More details.

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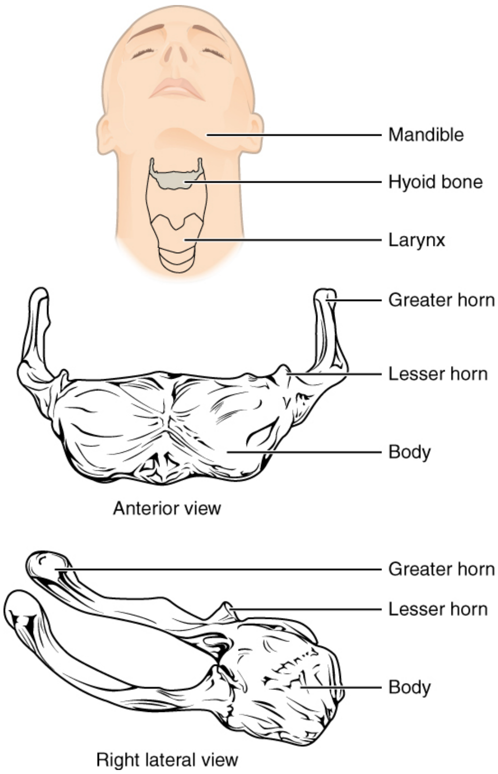
Accessory Bones of the Skull

The accessory bones of the skull comprise the hyoid and the auditory ossicles. The hyoid is suspended in position by muscles and ligaments but it does not articulate with any other bone. The auditory ossicles are not visible upon external examination of the skull because they are housed inside the temporal bone. They are the malleus, incus and stapes.

Some bones are found in the head but are not directly attached to the main bones of the skull, or are not immediately visible when the skull is examined. These accessory bones include the hyoid and the auditory ossicles.

Hyoid Bone

The hyoid bone is an independent bone that does not contact any other bone and thus is not part of the skull. It is a small U-shaped bone located in the upper neck near the level of the inferior mandible, with the tips of the "U" pointing posteriorly. The hyoid serves as the base for the tongue above, and is attached to the larynx below and the pharynx posteriorly. The hyoid is held in position by a series of small muscles that attach to it either from above or below. These muscles act to move the hyoid up/down or forward/back. Movements of the hyoid are coordinated with movements of the tongue, larynx, and pharynx during swallowing and speaking.

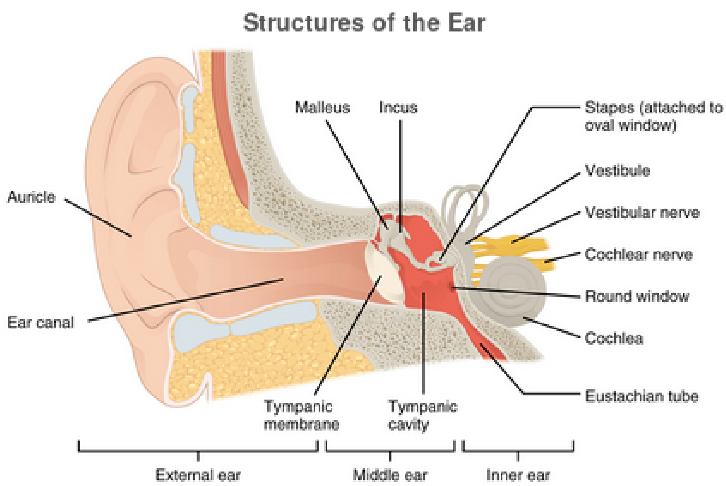


The hyoid bone is located in the upper neck and does not join with any other bone. It provides attachments for muscles that act on the tongue, larynx, and pharynx. More details.

Auditory Ossicles

The temporal bone of the skull has an auditory part that encloses the middle and the inner ear. The middle ear consists of a space spanned by three small bones called the auditory ossicles. These are the malleus, incus, and stapes, which are Latin names that roughly translate to hammer, anvil, and stirrup. The malleus is attached to the tympanic membrane (eardrum) and articulates with the incus. The incus, in turn, articulates with the stapes. The

stapes is then attached to the inner ear, where the sound waves will be transduced into a neural signal. The auditory ossicles are the smallest bones in the body, and the stapes is the smallest.



The middle ear is a hollow space inside the temporal bone. It contains the auditory ossicles and is connected to the pharynx by the auditory (Eustachian) tube. More details.

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Adaptations for Ingestion
A wide diversity of facial adaptations that facilitate food ingestion can be found in animals. Examples include trunks, beaks, tentacles, whiskers, cheek pouches, suction cups, keratin denticles, and a baleen. These structures vary with phylogenetic history but also with prey type and feeding behavior.

Ingestion

Ingestion is the consumption of a substance by an organism. In animals, it normally is accomplished by taking in the substance through the mouth into the gastrointestinal tract, such as through eating or drinking

Diversity

Animals have evolved a great variety of mouth shapes and sizes in response to the selective pressures associated with feeding. The first fishes had mouths, but bony jaws evolved later and allowed for an impressive diversification in the group. Fishes, amphibians, reptiles and mammals have bony jaws and hard teeth for powerful biting, piercing and grinding. Birds, on the other hand, evolved much lighter keratinized beaks that facilitate flight. Outstandingly long mouths and tongues can be found in nectar feeders and anteaters. Strong beaks and skulls are present in woodpeckers that hit tree trunks with the beak to find insect larvae for food. Some examples of structural adaptations for feeding are presented below.

Trunk

The trunk, or proboscis, is a fusion of the nose and upper lip, although in early fetal life, the upper lip and trunk are separated. The trunk is elongated and specialised to become the elephant's most important and versatile appendage. It contains up to 150,000 separate muscle fascicles, with no bone and little fat. These paired muscles consist of two major types: superficial (surface) and internal. The former are divided into dorsals, ventrals, and laterals while the latter are divided into transverse and

radiating muscles. The muscles of the trunk connect to a bony opening in the skull. The trunk encloses two air passages that run side by side and are separated by a nasal septum composed of tiny muscle units that stretch horizontally between the nostrils. A unique proboscis nerve, formed by the maxillary and facial nerves, runs along both sides of the trunk. It controls the muscles to produce lateral flexion, ventral flexion and extension of the trunk, the dilation of its walls for sucking in water, the compression of its walls, to expel the water into the mouth and a pinching movement at the tip of the trunk, which allows the animal to manipulate small objects precisely.

Elephant trunks have multiple functions in addition to bringing food to the mouth. These include breathing, olfaction, touching, grasping, and sound production. The trunk's ability to make powerful twisting and coiling movements allows it to collect food, wrestle with other elephants, and lift up to 350 kg. The trunk can be used for delicate tasks, such as wiping an eye and checking an orifice, and it is capable of cracking a peanut shell without breaking the seed. An elephant can reach items at heights of up to 7 m with its trunk and dig for water under mud or sand. Elephants can suck up water both to drink and to spray on their bodies. An adult Asian elephant is capable of holding 8.5 liters of water in its trunk. When swimming, the elephant uses its trunk as a snorkel. Trunks are most developed in elephants, but they are also found in several other mammals, such as the tapir and elephant seal.

Asian elephant using its trunk to eat a

watermelon. More details.

Beak

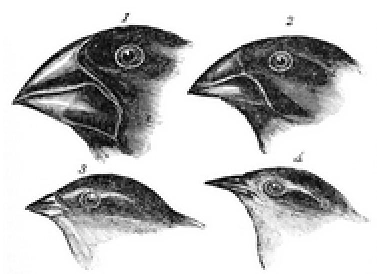
The beak, bill, or rostrum is an external anatomical structure of birds that is used for eating and for grooming, manipulating objects, killing prey, fighting, probing for food, courtship and feeding young. The terms *beak* and *rostrum* are also used to refer to a similar mouth part in some dicynodonts, Ornithischians, cephalopods, cetaceans, billfishes, pufferfishes, turtles, Anurantadpoles and sirens.

Although beaks vary significantly in size, shape, color and texture, they share a similar underlying structure. Two bony projections—the upper and lower mandibles—are covered with a thin keratinized layer of epidermis known as the rhamphotheca. In most species, two holes known as nares lead to the respiratory system. In contrast with mammal jaws, the beaks of some birds (like seagulls) can articulate at multiple points instead of two. This allows them to widen the beak as they open it, and swallow a wider food item than would fit the width of the closed beak. This is specially useful for birds as they that lack teeth and most of them have to swallow food items whole.

The bony core of the beak is a lightweight

framework, like that seen on this barn owl's skull. More details.

As the jaws and teeth of mammals, bird beaks have been shown to evolve in close association with the physical properties of the most common food items in the diet. A classical example is the radiation of Darwin's finches in the Galapagos Islands (Fig. 8). A single species arrived to the islands from the continent and colonized them. It then gradually diversified into several species that specialized in the consumption of different seeds. The morphology of the beak evolved quickly to better exploit the food resource of each specialized new species.



Darwin's finches. Large ground finch, medium ground finch small tree finch, green warbler-finch. More details.

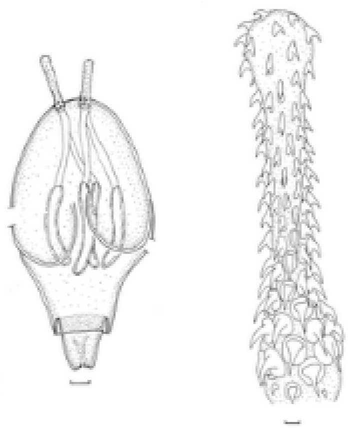
Tentacles

A tentacle is a flexible, mobile, elongated organ present in some species of animals, most of them invertebrates. In animal anatomy, tentacles usually occur in one or more pairs. The tentacles of animals work mainly like muscular hydrostats. Most forms of tentacles are used for grasping and feeding. Many are sensory organs, variously receptive to touch, vision, or to the smell or taste of particular foods or threats. Examples of such tentacles are the "eye stalks" of various kinds of snails. Some kinds of tentacles have both sensory and manipulatory functions.

Blue tentacles of the sea anemonie *Macrodactyla doreensis* from Thailand. More details.

A variety of shapes and sizes of tentacles is found around the mouths of Cnidarians, Molluscs and Bryozoans. Trypanorhynchcestodes are parasitic tapeworms found in fishes. Their scolex shows four tentacles covered by spines (Fig. 2). These tentacles help the adult cestode to attach to the intestine of the shark or ray host. The same tentacles are also present in the larvae. Among vertebrates, two short tentacles are found in the legless amphibians called caecilians. They are located on each side of the head, between their eyes and nostrils. Their function, however is most likely olfactory or tactile, but it is not used to direct food into the mouth. Similarly, the star-nosed mole, *Condylura cristata*, of North America, has

22 short but conspicuous tentacles around its nose. They are mobile and extremely sensitive, helping the animal to find its way about the burrow and detect prey. They are about 1–4 mm long and hold about 25,000 touch receptors, giving this mole a very delicate sense of touch. These tentacles have not been seen to direct food toward the mouth either.



The fish parasite tapeworm *Nybelinia basimegacantha* (left) with an enlarged view of a tentacle (right) that it uses to attach to its host. Scale bars: 0.1 mm (cestode) and 0.01 mm (tentacle). More details.

Barbels and Whiskers

Many fishes have barbels around the mouth. Birds and especially mammals commonly have long whiskers (vibrissae) on each side of the mouth. These structures have sensory roles, providing their bearers with exquisite tactile sensitivity. They seem not to have, however, a role in ingestion.

The channel catfish has four pairs of barbels. More details.

A chinchilla with large vibrissae. More details.

A possible exception might be rictal bristles which are hair-like feathers that arise around the base of the beak and project anteriorly. These are mostly found in insectivorous species like nightjars, swallows, and flycatchers (Fig. 4). Nightjars are medium-sized birds in the family Caprimulgidae, characterized by long wings, short legs and very short bills. They are mostly active in the late evening and early morning or at night, and feed predominantly on moths and other flying insects. They beak is surrounded by stiff vibrissae arranged in parallel and pointing anteriorly, forming a “basket” around the beak. It was been suggested that the birds may used them as a net, to direct into the mouth flying prey that would have otherwise escaped predation. This hypothesis has not been experimentally tested and a valid alternative role for the vibrissae would be that of a tactile receptor.

The front-pointing vibrissae of the Puerto Rican nightjar (*Caprimulgus noctitherus*). More details.

Cheek and floor of the mouth

Cheek pouches are pockets on both sides of the head of some mammals between the jaw and the cheek. They can be found on mammals including

the platypus, some rodents, and most monkeys,as well as the marsupialkoala. The cheek pouches of chipmunks can reach the size of their body when full. Cheek pouches allow the rapid collection of food, serving for temporary storage and facilitating transport. In monkeys of the subfamily of Cercopithecinae, they collect predigested food and allow the animals to carry their food to safer locations.

Chipmunk storing a peanut in its cheek pouch. More details.

Pelicans are well-known for having a large pouch that can contain several liters of water. The animal opens the beak and scoops a volume of water containing small fish into the pouch. Specialized muscles then contract, expelling the water from the pouch and forcing the fish down the throat.

Australian Pelican (*Pelecanus conspicillatus*) showing its throat pouch. More details.

Jaws and Teeth

An amazing variety of jaws and teeth arrangements has evolved in vertebrates, as a result of their radiation and occupation of a broad range of ecological niches. The position, size and strength of jaws and teeth evolves to match diet and foraging mode. As an example, both in fishes and tadpoles, species that feed on the surface, midwater and bottom tend to have their mouths oriented upward, forward and downward, respectively.

Some fishes use their mouths as an anchorage device to attach to a host. This can be used for dispersal, non-invasive feeding or invasive feeding. The candiru (vampire fish) is a species of parasiticfreshwatercatfish in the family*Trichomycteridae*. It is native to the Amazon Basin where it is found in Bolivia, Brazil, Colombia, Ecuador and Peru. It attacks larger fishes by swimming under the operculum and into the gills, where it latches onto aortic arteries and feeds on blood for 1-4 min. After feeding, the candiru leaves the host and remains buried at the bottom of the river while digesting the meal.

Half of the known species of lamprey are also parasitic fish. They are jawless and have the mouth organized as a suction cup, with series of

rasping teeth arranged in circles. Parasitic lampreys feed on prey as adults by attaching their mouths to the target animal's body, then using their teeth to cut through surface tissues until they reach blood and body fluid. Secretions in the lamprey's mouth prevent the victim's blood from clotting. Victims typically die from excessive blood loss or infection. After one year of hematophagous (blood) feeding in salt water, lampreys ascend a river to spawn and die.

Lampreys attached to a lake trout. More details.

Concentric circles of sharp teeth can be found around the suction cup shaped mouth of the jawless lampreys. These parasitic fishes use their teeth to harvest lymph and blood from their host until it is killed or badly debilitated. The keratinized teeth of lampreys are thought to have evolved independently from the enamel covered teeth of most other vertebrates.

Mouth of the sea lamprey*Petromyzon marinus*. More details.

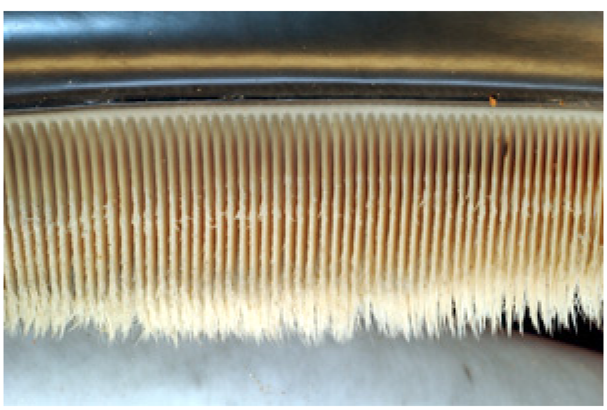
In contrast with the candiru and lamprey, remoras (family Echeneidae) do not use their mouths to attach to their hosts. Instead, their first dorsal fins are modified into suction organs. While remoras move around attached to the body of the host, they are not parasites. Remoras feed on food particles of feces of the host in a commensal relationship that may even be somewhat mutualistic as the remoras may remove some ectoparasites and loose flakes from the host's skin.

A modified dorsal fin forms the attachment structure of the remora *Echeneis*

naucrates. More details.

Baleen

Baleen whales have evolved baleens which are series of parallel plates of calcified keratin attached to the upper jaw and used for filter feeding. The whale opens its mouth widely and scoops in dense shoals of prey (such as krill, copepods, small fish and sometimes birds that happen to be near the shoals), together with large volumes of water. It then partly shuts its mouth and presses its tongue against its upper jaw, forcing the water to pass out sideways through the baleen, thus sieving out the prey which it then swallows. This is a form of suction feeding and it allows the whale to capture multiple prey items at once. Whales are mammals and as such they were terrestrial animals before they moved into the sea. The availability of food as many small prey items is thought to have driven the loss of teeth and the evolution of suction feeding and baleen. The baleen is a keratinous structure that bears no resemblance with the structure of teeth. It has most likely evolved from the epithelium of the gums, in a similar way as to how the epithelium of the mammal skin produces nails, horns and hair, which are all made of keratin.



Parallel baleen plates attach to the upper jaw of a baleen whale. More details.

Tongue

Many animals use the tongue as the primary way of taking food from the environment. Chameleons project a sticky tongue that adheres to the prey, whereas woodpeckers impale pray items with their barbed tongues. Giraffes have long and versatile tongues with which they harvest leaves from trees as they feed. The general structure of the tongue, specializations, and its role in gustation are discussed in the chapter Tongue and Gustation.

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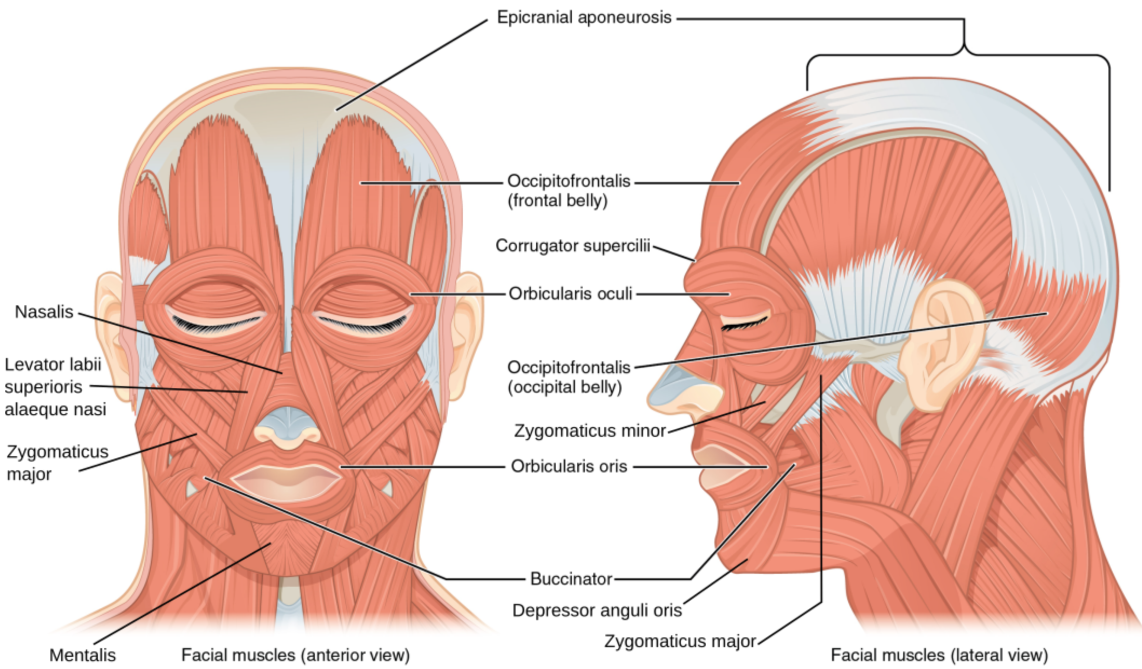
Muscles that Move the Lips, Nose and Ears

The muscles that move the lips, nose and ears have attachments to the skin and are part of the muscles of facial expression. They are the most superficial skeletal muscles of the head.

The skeletal muscles are divided into axial (muscles of the trunk and head) and appendicular (muscles of the arms and legs) categories. This system reflects the bones of the skeleton system, which are also arranged in this manner. The axial muscles are grouped based on location, function, or both. The axial muscles include the muscles of the head and neck presented below.

The origins of the muscles of facial expression are on the surface of the skull. The insertions of these muscles have fibers intertwined with connective tissue and the dermis of the skin. Because the muscles insert in the skin rather than on bone, when they contract, the skin moves to create facial expression.



Human muscles of facial expression. [More details](#).

The orbicularis oris is a circular muscle that moves the lips, and the orbicularis oculi is a circular muscle that closes the eye. The occipitofrontalis muscle moves up the scalp and eyebrows. The muscle has a frontal belly and an occipital (near the occipital bone on the posterior part of the skull) belly. In other words, there is a muscle on the forehead (frontalis) and one on the back of the head (occipitalis), but there is no muscle across the top of the head. Instead, the two bellies are connected by a broad tendon called the epicranial aponeurosis, or galea aponeurosis (galea = “apple”). The physicians originally studying human anatomy thought the skull looked like an apple.

A large portion of the face is composed of the buccinator muscle, which compresses the cheek. This muscle allows you to whistle, blow, and suck; and it contributes to the action of chewing. There are several small facial muscles, one of which is the corrugator supercilii, which is the prime mover of the eyebrows. Place your finger on your eyebrows at the point of the bridge of the nose. Raise your eyebrows as if you were surprised and lower your eyebrows as if you were frowning. With these movements, you can feel the action of the corrugator supercilli. Additional muscles of facial expression are presented in Table 1.

Table 1. Human muscles of facial expression.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Brow					
Furrowing brow	Skin of scalp	Anterior	Occipito-frontalis, frontal belly	Epicraneal aponeurosis	Underneath skin of forehead
Unfurrowing brow	Skin of scalp	Posterior	Occipito-frontalis, occipital belly	Occipital bone; mastoid process (temporal bone)	Epicraneal aponeurosis
Lowering eyebrows (e.g., scowling, frowning)	Skin underneath eyebrows	Inferior	Corrugator supercilii	Frontal bone	Skin underneath eyebrow
Nose					
Flaring nostrils	Nasal cartilage (pushes nostrils open when cartilage is compressed)	Inferior compression; posterior compression	Nasalis	Maxilla	Nasal bone
Mouth					
Raising upper lip	Upper lip	Elevation	Levator labii superioris	Maxilla	Underneath skin at corners of the mouth; orbicularis oris
Lowering lower lip	Lower lip	Depression	Depressor labii inferioris	Mandible	Underneath skin of lower lip
Opening mouth and sliding lower jaw left and right	Lower jaw	Depression, lateral	Depressor angulus oris	Mandible	Underneath skin at corners of mouth
Smiling	Corners of mouth	Lateral elevation	Zygomaticus major	Zygomatic bone	Underneath skin at corners of mouth (dimple area); orbicularis oris
Shaping of lips (as during speech)	Lips	Multiple	Orbicularis oris	Tissue surrounding lips	Underneath skin at corners of the mouth
Lateral movement of cheeks (e.g., sucking on a straw; also used to compress air in mouth while blowing)	Cheeks	Lateral	Buccinator	Maxilla, mandible; sphenoid bone (via pterygomandibular raphae)	Orbicularis oris
Pursing of lips by straightening them laterally	Corners of mouth	Lateral	Risorius	Fascia of parotid salivary gland	Underneath skin at corners of the mouth
Protrusion of lower lip (e.g., pouting expression)	Lower lip and skin of chin	Protraction	Mentalis	Mandible	Underneath skin of chin

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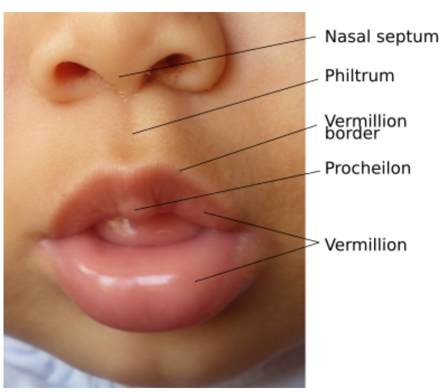
Lips
The lips control the entrance into the mouth, probe the physical characteristics of food items and manipulate them before ingestion. They are sexually dimorphic in humans and their appearance can influence attractiveness.

The lips control the entrance into the mouth. They are positioned by an elaborate musculature and in many animals the lips can manipulate food items extensively before ingestion. The lips have one of the highest concentrations of touch and temperature receptors in the body and they can probe the physical characteristics of potential food items. The development of the lips is modified by sex hormones and they are a target of sexual selection. During kissing behavior, the lips are a central structure of interaction between individuals.

Structure

The upper and lower lips form the border between the mouth and the exterior environment. The juncture where the lips meet the surrounding facial skin is the vermilion border, and the typically reddish area within the borders is called the vermilion zone. The fleshy protuberance located in the center of the upper lip is a tubercle known as procheilon, tuberculum labii superioris, or labial tubercle. The vertical groove extending from the procheilon to the nasal septum is called the philtrum.



Anatomy of the

human lips shown in a baby. More details.

Anatomy of the human lips shown in a baby. More details.

The skin of the lip looks pink or red because the its blood vessels are more apparent then in other parts of the skin. This is because:

- The skin of the lips has three to five cellular layers, making it very thin compared to typical facial skin, which has up to 16 layers.
- It contains fewer melanocytes and less melanin (dark pigment).
- Its keratinocytes contain mostly eleidin instead of keratin, and eleidin is more transparent.

The lip skin is not hairy and does not have sweat glands. Therefore, it does not have the usual protection layer of sweat and body oils which keep the skin smooth, inhibit pathogens, and regulate temperature. The lips therefore dry out faster and become chapped more easily than the surrounding skin.

Internally, both lips have membranous medial attachments to the gums. The *frenulum labii inferioris* is the frenulum of the lower lip. The f*renulum labii superioris* is the frenulum of the upper lip.

Innervation

The lips contain one of the highest densities of sensory receptors in our skin, including thermoreceptors, free nerve endings and various types of touch receptors. Neural signals originating at these receptors are transmitted to the brain by branches of the trigeminal nerve (one of the cranial nerves):

- The infraorbital nerve is a branch of the maxillary branch. It supplies not only the upper lip, but much of the skin of the face between the upper lip and the lower eyelid, except for the bridge of the nose.

- The mental nerve is a branch of the mandibular branch (via the inferior alveolar nerve). It supplies the skin and mucous membrane of the lower lip and labial gingiva (gum) anteriorly.

Blood supply

The facial artery is one of the six non-terminal branches of the external carotid artery. It supplies the lips by its superior and inferior labial branches, each of which bifurcate and anastomose with their companion artery from the other side.

Musculature

The muscles that move the lips were covered in chapter 7: Ingestion .

Functions

Food intake

Lips are used for holding food or to get it into the mouth. In addition, lips serve to close the mouth airtight shut, to hold food and drink inside, and to keep out unwanted objects. Through making a narrow funnel with the lips, the suction of the mouth is increased. This suction is essential for babies to breast feed. Lips can also be used to suck in other contexts, such as sucking on a straw to drink liquids.

In most vertebrates, the lips are relatively small folds of tissue lying just outside the jaws. However, in mammals, they become much more prominent, being separated from the jaws by a deep cleft. They are also more mobile in mammals than in other groups, and have muscles embedded in them. In some teleost fishes, the lips may be modified to carry sensitive barbels. In birds and turtles, the lips are hard and keratinous, forming a solid beak.

Keratinous lips of the turtle *Trachemys scripta*. More details.

Communication

Lips are used in vocal sounds, to produce speech and to play musical instruments. People also unconsciously or consciously lip read to understand speech in noisy conditions.

The lips contribute substantially to facial expressions. The lips visibly express emotions such as a smile or frown, iconically by the curve of the lips forming an up-open or down-open parabola, respectively. Lips can also be made pouty when whining, or perky to be provocative.

Sensory

The lip has many nerve endings and is very sensitive to touch and temperature. It provides an important opportunity for problem detection before an item is brought into the mouth. With their high sensory sensitivity, the lips are also an erogenous zone. The lips play a crucial role in kissing and other acts of intimacy.

Mate attraction

Several facial features diverge between men and women after puberty. The sex hormone estrogen causes, among other effects, females to develop thick (full) lips. This is a feature that enhances facial attractiveness as perceived by men. A woman's lipstick (or lip enhancement) attempts to make her more attractive by creating the illusion that she has more estrogen than she actually has and thus indicating higher fertility.

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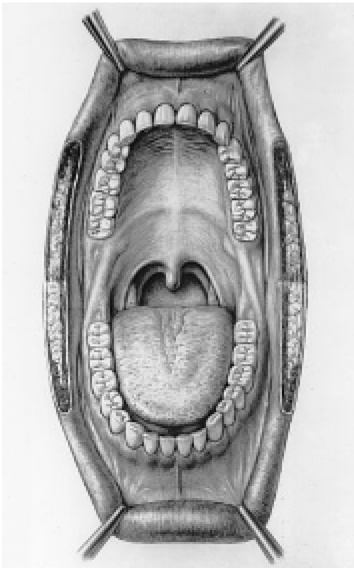
The Oral Cavity
The oral cavity is formed by the vestibule and the oral cavity proper. The vestibule is delimited by the teeth, lips and cheeks. The oral cavity proper is delimited by the teeth, fauces, roof and floor of the mouth. The oral cavity is lined with oral mucosa, which can be keratinized or nonkeratinized and contains mucous and salivary glands.

Internal structure of the human mouth. More details.

The cheeks, tongue, and palate frame the mouth, which is also called the oral cavity or buccal cavity. At the entrance to the mouth are the lips, or labia (singular = labium). Their outer covering is skin, which transitions to a mucous membrane in the mouth proper. The lips cover the orbicularis oris muscle, which regulates what comes in and goes out of the mouth. The labial frenulum is a midline fold of mucous membrane that attaches the inner surface of each lip to the gum.

Vestibule

The anterior and lateral portions of the mouth form a U-shaped cavity between the teeth, lips and cheeks. This area is called the vestibule.



Vestibule and oral cavity proper in a human. More details.

Cheeks are muscular in humans and cover the teeth, forming the lateral aspect of the face. The inside of the cheek is lined with a mucous membrane (buccal mucosa) which is part of the oral mucosa. During mastication (chewing), the cheeks and tongue between them keep the food between the teeth.

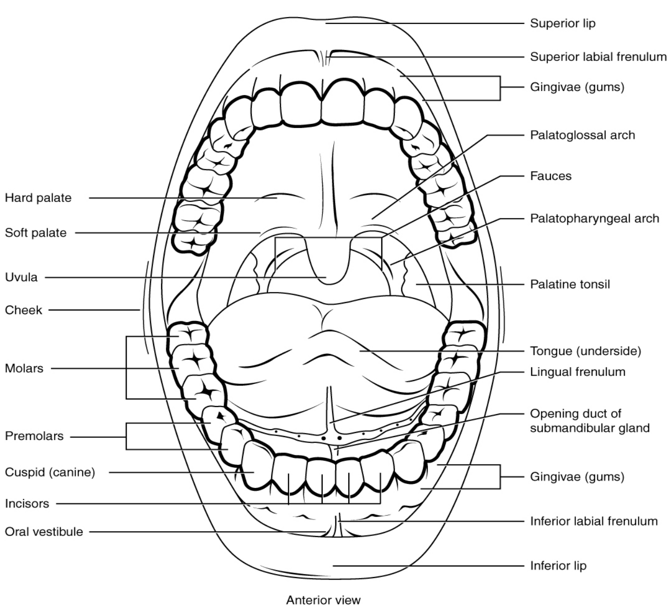
The cheeks are covered externally by hairy skin, and internally by the mucous membrane. This membrane is comprised by a sheet of stratified squamous epithelium and a sheet of areolar connective tissue. The epithelium is mostly smooth, but may have caudally directed papillae (for example, in ruminants). The mucosa is supplied with mucous or salivary secretions from the buccal glands located between the mucous membrane and the buccinator muscle. In carnivores, a superior buccal gland is large and conspicous. It is called the zygomatic gland, because it is found above the zygomatic arch. Between the skin and mucous membranes are connective tissue and buccinator muscles. During chewing, food that gets

crushed by premolars and molars tends to fall on the tongue or into the vestibule. Contraction of the buccinator muscle pushes the cheeks against the teeth. This helps to direct food that would fall into the vestibule back in between the teeth for further reduction of particle size. The buccinator muscle may also help in suckling by babies.

Some mammals such as squirrels and hamsters have highly distendable cheeks. Their vestibules form buccal (cheek) pouches that are used for temporary storage of food or during foraging. These pouches are most common in rodents and monkeys but they are also present in the platypus and the marsupialkoala. The cheek pouches of chipmunks can reach the size of their body when full. The females of some species of hamster are known to hide their young in their cheek pouches to carry them away when they fear danger. Other species of hamsters are known to fill their pouches with air to increase bouyancy while they swim.

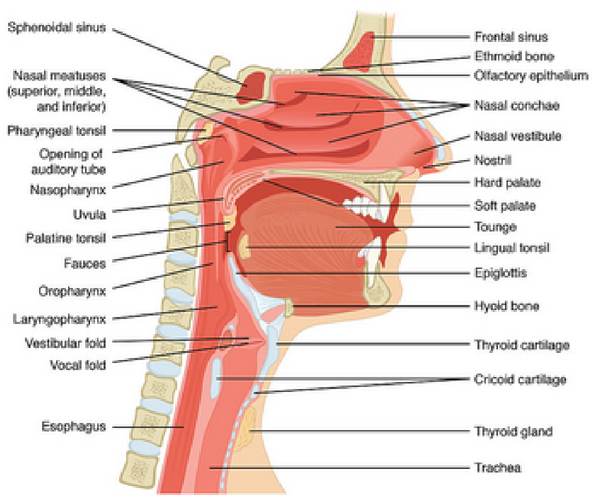
Oral Cavity Proper

The part of the oral cavity (mouth) that is not the vestibule is called the oral cavity proper. It is delimited by the teeth, the pharynx, the roof of the mouth and the tongue, or floor of the mouth.



Structure of the oral cavity. More details.

Simultaneous chewing and breathing is made possible by the roof of the mouth, which is called palate. The anterior region of the palate serves as a wall (or septum) between the oral and nasal cavities as well as a rigid shelf against which the tongue can push food. It is created by the maxillary and palatine bones of the skull and, given its bony structure, is known as the hard palate. If you run your tongue along the roof of your mouth, you'll notice that the hard palate ends in the posterior oral cavity, and the tissue becomes fleshier. This part of the palate, known as the soft palate, is composed mainly of skeletal muscle. We move the soft palate subconciously to yawn, swallow, or sing. During swallowing, contraction of two muscles that attached to the soft palate move it upward to close the passage into the nasal cavity and direct the food into the oropharynx.



The hard palate separates the oral from the nasal cavities. The fauces separates the oral cavity from the pharynx. The teeth separate the vestibule

from the oral cavity proper.
More details.

A fleshy tissue called uvula extends down from the center of the posterior edge of the soft palate. It has been suggested that the uvula is a vestigial organ, but it may have a role in preventing unintended early swallowing of items in the mouth during chewing. The space between the uvula and the base of the tongue is the fauces and it marks the limit between the oral cavity and the pharynx. Two muscular folds extend downward from the soft palate, on either side of the uvula. Anteriorly, the palatoglossal arch lies next to the base of the tongue. Posterior to it, the palatopharyngeal arch forms the superior and lateral margins of the fauces. Between these two arches are the palatine tonsils. These are clusters of lymphoid tissue that protect the pharynx from pathogens. The lingual tonsils are located at the base of the tongue.

Oral mucosa

The oral mucosa is the mucous membrane lining the inside of the mouth and consists of stratified squamous epithelium termed oral epithelium and an underlying connective tissue termed lamina propria. Some alterations in the oral mucosa lining the mouth can reveal systemic conditions, such as diabetes, vitamin deficiency, or chronic tobacco or alcohol use.

Classification

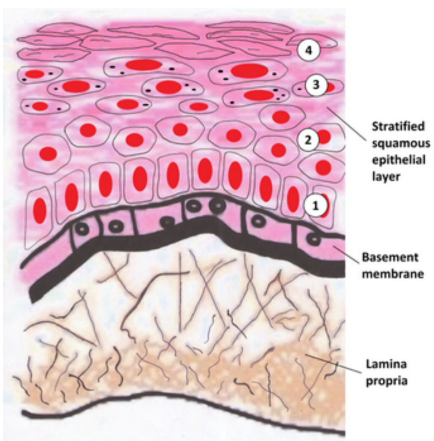
It can be divided into three main categories based on function and histology:

- **Masticatory mucosa**, keratinizedstratified squamous epithelium, found on the dorsum of the tongue, hard palate and attached gingiva.
- **Lining mucosa**, nonkeratinized stratified squamous epithelium, found almost everywhere else in the oral cavity, including the:

- Buccal mucosa lining of the cheeks.
- Labial mucosa lining of the lips internally.
- Alveolar mucosa refers to the mucosa between the gums and the buccal/labial mucosa.

- **Specialized mucosa**, specifically in the regions of the taste buds on lingual papillae on the dorsal surface of the tongue that contains nerve endings for general sensory reception and taste perception.

Structure



The keratinized oral mucosa is formed by stratified squamous epithelium containing: 1. stratum basale; 2. stratum spinosum; 3. stratum granulosum; 4. stratum corneum. More details.

The epithelium of the oral mucosa may be keratinized or nonkeratinized. Keratinization is the differentiation of keratinocytes in the stratum granulosum into nonvital surface cells or squames to form a stratum corneum very rich in keratin.

Keratinized squamous epithelium is present in the attached gingiva and hard palate as well as areas of the dorsal surface of the tongue. Nonkeratinized squamous epithelium covers the soft palate, inner lips, inner cheeks, and the floor of the mouth, and ventral surface of the tongue.

In keratinized oral mucosa, the epithelium consists of four layers:

- Stratum basale (basal layer)
- Stratum spinosum (prickle layer)
- Stratum granulosum (granular layer)
- Stratum corneum (keratinized layer)

In nonkeratinized epithelium, the two deep layers (basale and spinosum) remain the same but the outer layers are termed the *intermediate* and *superficial* layers.

Deep to the epithelium, the connective tissue layer (lamina propria) has two layers: papillary and dense. The papillary layer is superficial and consists of loose connective along with blood vessels and nerve tissue. The tissue has similar amounts of fibers, cells, and ground substance. The deeper dense layer contains a larger amount of fibers. Between the papillary layer and the deeper layers of the lamina propria is a capillary plexus, which provides nutrition for the all layers of the mucosa and sends capillaries into the connective tissue papillae.

A submucosa may or may not be present deep to the dense layer of the lamina propria, depending on the region of the oral cavity. If present, the submucosa usually contains loose connective tissue and may also contain adipose tissue or salivary glands, as well as overlying bone or muscle within the oral cavity.

A variable number of Fordyce spots or granules are scattered throughout the non keratinized tissue. These are visible as small yellowish bumps on the

surface of the mucosa. They correspond to deposits of sebum from sebaceous glands in the submucosa.

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Health Conditions of the Mouth
Several health conditions manifest themselves in tissues of the mouth. Oral herpes is a viral infection that commonly causes cold sores and ulcers. Oral thrush is caused by the yeast Candida and commonly affects infants and people with weakened immune systems forming white patches on the oral mucosa. Oral cancer can originate in salivary glands, tonsils and skin cells, having alcohol and tobacco as the main risk factors. Periodontal disease and caries are discussed in chapter 15.

Dental and periodontal infections are very common and represent major public health issues in a global scale. They are covered in chapter 15 Dental Disease and Treatment. A number of other relevant health conditions can manifest themselves in the oral cavity and the main ones are discussed below.

Herpetic Gingivostomatitis

Infections by herpes simplex virus type 1 (HSV-1) frequently manifest as oral herpes, also called acute herpes labialis and characterized by cold sores on the lips, mouth, or gums. HSV-1 can also cause acute herpetic gingivostomatitis, a condition that results in ulcers of the mucous membranes inside the mouth. Herpetic gingivostomatitis is normally self-limiting except in immunocompromised patients. Like oral herpes, the infection is generally diagnosed through clinical examination, but cultures or biopsies may be obtained if other signs or symptoms suggest the possibility of a different causative agent. If treatment is needed, mouthwashes or antiviral medications such as acyclovir, famciclovir, or valacyclovir may be used.

(a) This cold sore is caused by infection with herpes simplex virus type 1 (HSV-1). (b) HSV-1 can also cause acute herpetic gingivostomatitis. (credit b: modification of work by Klaus D. Peter).

Oral Thrush

The yeast *Candida* is part of the normal human microbiota, but overgrowths, especially of *Candida albicans*, can lead to infections in several parts of the body. When *Candida* infection develops in the oral cavity, it is called oral thrush. Oral thrush is most common in infants because they do not yet have well developed immune systems and have not acquired the robust normal microbiota that keeps *Candida* in check in adults. Oral thrush is also common in immunodeficient patients and is a common infection in patients with AIDS.

Oral thrush is characterized by the appearance of white patches and pseudomembranes in the mouth and can be associated with bleeding. The infection may be treated topically with nystatin or clotrimazole oral suspensions, although systemic treatment is sometimes needed. In serious cases, systemic azoles such as fluconazole or itraconazole (for strains resistant to fluconazole), may be used. Amphotericin B can also be used if the infection is severe or if the *Candida* species is azole-resistant.

Oral thrush is an infection by the years *Candida*, which forms white patches on the oral mucosa. (credit: modification of work by Centers for Disease Control and Prevention).

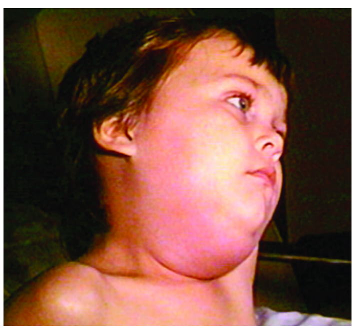
Mumps

The viral disease mumps is an infection of the parotid glands, the largest of the three pairs of salivary glands. The causative agent is mumps virus (MuV), a paramyxovirus with an envelope that has hemagglutinin and neuraminidase spikes. A fusion protein located on the surface of the envelope helps to fuse the viral envelope to the host cell plasma membrane.

Mumps virus is transmitted through respiratory droplets or through contact with contaminated saliva, making it quite contagious so that it can lead easily to epidemics. It causes fever, muscle pain, headache, pain with chewing, loss of appetite, fatigue, and weakness. There is swelling of the salivary glands and associated pain. The virus can enter the bloodstream (viremia), allowing it to spread to the organs and the central nervous system. The infection ranges from subclinical cases to cases with serious complications, such as encephalitis, meningitis, and deafness. Inflammation of the pancreas, testes, ovaries, and breasts may also occur and cause

permanent damage to those organs; despite these complications, a mumps infection rarely cause sterility.

Mumps can be recognized based on clinical signs and symptoms, and a diagnosis can be confirmed with laboratory testing. The virus can be identified using culture or molecular techniques such as RT-PCR. Serologic tests are also available, especially enzyme immunoassays that detect antibodies. There is no specific treatment for mumps, so supportive therapies are used. The most effective way to avoid infection is through vaccination. Although mumps used to be a common childhood disease, it is now rare in the United States due to vaccination with the measles, mumps, and rubella (MMR) vaccine.



Child showing the characteristic parotid swelling associated with mumps. (credit: modification of work by Centers for Disease Control and Prevention).

Oral cancer

Also known as mouth cancer, oral cancer is a type of head and neck cancer and is any cancerous tissue growth located in the oral cavity. It may arise as a primary lesion originating in any of the tissues in the mouth, by metastasis from a distant site of origin, or by extension from a neighboring anatomic structure, such as the nasal cavity. It may involve multiple tissues (teratoma), salivary glands (adenocarcinoma), tonsils (lymphoma), melanocytes (melanoma), keratinocytes (squamous cell carcinomas), or skin stem cells (basal cell carcinoma). The most common form is squamous cell carcinoma involving the tongue, the floor of the mouth, cheek lining, gingiva (gums), lips, or palate (roof of the mouth). In 2013 oral cancer resulted in 135,000 deaths up from 84,000 deaths in 1990. In the United States, fewer than 63% of the patients survive more than 5 years after diagnosis.

Oral cancer on the side of the tongue, a common site along with the floor of the mouth. More details.

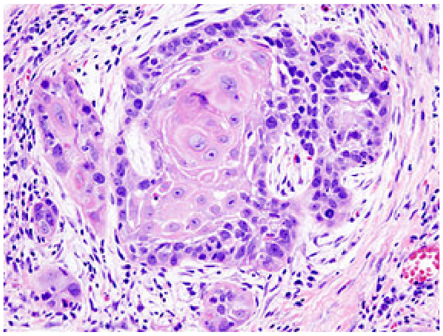
Symptoms

In its early stages, it can go unnoticed. It can be painless with slight physical changes. Early symptoms can include persistent red or white patches, a non-healing ulcer, progressive swelling or enlargement, unusual surface changes, sudden tooth mobility without apparent cause, unusual oral bleeding or epitaxis and prolonged hoarseness.

Late stage symptoms can include thickened skin, tingling or dysesthesia of the tongue or lips, airway obstruction, chronic middle ear infections, pain in the ears, locked jaws, eating disorders, cervical lymphadenopathy, persistent pain or referred pain and altered vision.

Causes

Around 75 percent of oral cancers are linked to modifiable behaviors such as tobacco use and excessive alcohol consumption. Infection with human papillomavirus (HPV), particularly type 16 (there are over 180 types), is a another risk factor for oral cancer. Other factors include poor oral hygiene, irritation caused by ill-fitting dentures and other rough surfaces on the teeth, poor nutrition, and some chronic infections. If oral cancer is diagnosed in its earliest stages, treatment is generally effective.



Histopathologic appearance of a well differentiated squamous cell carcinoma specimen.

Hematoxylin-eosin stain. More details.

Oral cancer often presents as a non-healing ulcer (shows no sign of healing after 2 weeks). In the US, oral cancer accounts for about 8 percent of all malignant growths. Men are affected twice as often as women, particularly men older than 40.

Management

Surgical removal of the tumor is usually recommended if the tumor is small enough, and if surgery is likely to result in a functionally satisfactory result. Radiation therapy with or without chemotherapy is often used in conjunction with surgery, or as the definitive radical treatment, especially if the tumor is inoperable.

Following treatment, rehabilitation may be necessary to improve movement, chewing, swallowing, and speech. Speech and language pathologists may be involved at this stage.

Figure credits

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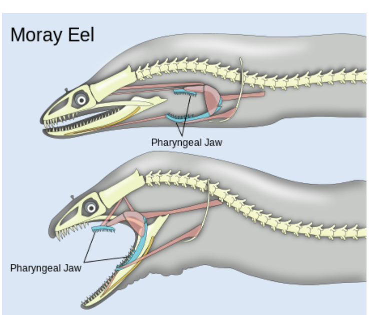
Jaw Diversity
Vertebrates have evolved a wide diversity of mandibular structures. Some, like the moray eel, have evolved a second jaw that independently of the oral jaw and helps to ingest the food.

Biting in vertebrates is based on muscular action on a bony framework typically formed by a maxillary bone and mandible. More than a simple hinge, the joint between the jaws supports complex movements in chewing, allowing for extended angular opening and dealing with high stresses during biting. This chapter examines the diversity of the joint, its structure and movement, and common clinical issues in humans.

Diversity

Vertebrates have evolved a great diversity of jaw structures and joint adjustments in order to cope with ecological selection pressures. Most of these pressures relate to the characteristics of the most common food items, such as size, texture and ingestion method. As an extreme example, some types of fishes have evolved a second set of jaws, called pharyngeal jaws.

Pharyngeal jaws are contained within an animal's throat, or pharynx, distinct from the primary or oral jaws. They are believed to have originated as modified gill arches, in much the same way as oral jaws.



Movement of mandibular and pharyngeal jaws

in the more eel during prey capture. More details.

Most fish species with pharyngeal teeth do not have extensible pharyngeal jaws. Among the ones that do, a notable example is the highly mobile pharyngeal jaw of the moray eel. Moray eels live in tight burrows and they may be restricted in their suction behavior as lateral clearance is necessary for the wide opening of the opercular cover of the gills that creates negative pressures in the mouth. Pharyngeal jaws might be an evolutionary response to such limitation. When the moray attacks, instead of using suction to bring the prey into the mouth, it first bites normally with its oral jaws, capturing the prey. Immediately after, the pharyngeal jaws are brought forward and bite onto the prey to grip it. They then retract, pulling the food item down the moray eel's gullet, allowing it to be swallowed.

Figure credits

Figure 1 by Zina Deretsky, National Science Foundation (after Rita Mehta, UC Davis); Ryan Wilson (pbroks13) - Pharyngeal jaws of moray eels.jpg, which is in turn from http://www.nsf.gov/news/news_images.jsp?cntn_id=109985&org=NSF, CC BY 3.0, https://commons.wikimedia.org/w/index.php?curid=5982756

Joint Types of the Head
Joints are classified by the amount of movement that they permit between the bones and by their structure. A synarthrosis allows for no movement, an amphiarthrosis allows for reduced movement and a diarthrosis allows for extensive movement. Structurally, joints can be based on fibers, cartilage or bone. At the head, the most relevant articulations are the fibrous sutures (synarthrosis) between the bones of the cranium, the fibrous gomphosis (synarthrosis) between the teeth and the jaw bones, and the synovial join (diarthrosis) between the mandible and the temporal bone.

A joint, also called an articulation, is any place where adjacent bones or bone and cartilage come together (articulate with each other) to form a connection. Joints are classified both structurally and functionally. Structural classifications of joints take into account whether the adjacent bones are strongly anchored to each other by fibrous connective tissue or cartilage, or whether the adjacent bones articulate with each other within a fluid-filled space called a joint cavity. Functional classifications describe the degree of movement available between the bones, ranging from immobile, to slightly mobile, to freely moveable joints. The amount of movement available at a particular joint of the body is related to the functional requirements for that joint. Thus immobile or slightly moveable joints serve to protect internal organs, give stability to the body, and allow for limited body movement. In contrast, freely moveable joints allow for much more extensive movements of the body and limbs.

Structural Classification of Joints

The structural classification of joints is based on whether the articulating surfaces of the adjacent bones are directly connected by fibrous connective tissue or cartilage, or whether the articulating surfaces contact each other within a fluid-filled joint cavity. These differences serve to divide the joints of the body into three structural classifications. A fibrous joint is where the adjacent bones are united by fibrous connective tissue. At a cartilaginous joint, the bones are joined by hyaline cartilage or fibrocartilage. At a synovial joint, the articulating surfaces of the bones are not directly connected, but instead come into contact with each other within a joint

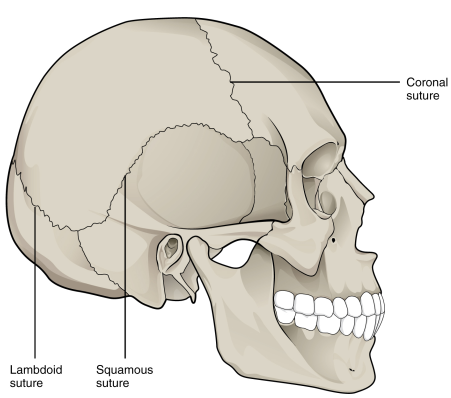
cavity that is filled with a lubricating fluid. Synovial joints allow for free movement between the bones and are the most common joints of the body.

Functional Classification of Joints

The functional classification of joints is determined by the amount of mobility found between the adjacent bones. Joints are thus functionally classified as a synarthrosis or immobile joint, an amphiarthrosis or slightly moveable joint, or as a diarthrosis, which is a freely moveable joint (arthroun = "to fasten by a joint"). Depending on their location, fibrous joints may be functionally classified as a synarthrosis (immobile joint) or an amphiarthrosis (slightly mobile joint). Cartilaginous joints are also functionally classified as either a synarthrosis or an amphiarthrosis joint. All synovial joints are functionally classified as a diarthrosis joint.

Synarthrosis

An immobile or nearly immobile joint is called a synarthrosis. The immobile nature of these joints provide for a strong union between the articulating bones. This is important at locations where the bones provide protection for internal organs. Examples include sutures, the fibrous joints between the bones of the skull that surround and protect the brain, and the manubriosternal joint, the cartilaginous joint that unites the manubrium and body of the sternum for protection of the heart.



The suture joints of the skull are an example of a synarthrosis, an essentially immobile joint. More details.

Amphiarthrosis

An amphiarthrosis is a joint that has limited mobility. Examples of this type of joint include the pubic symphysis and the cartilaginous joint that unites the bodies of adjacent vertebrae through an invertervertebral disc.

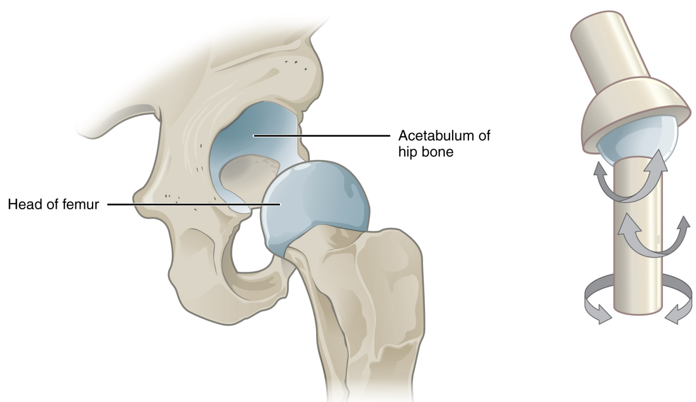
Diarthrosis

A freely mobile joint is classified as a diarthrosis. These types of joints include all synovial joints of the body, which provide the majority of body movements. Most diarthrotic joints are found in the appendicular skeleton and thus give the limbs a wide range of motion. In the head, the joint between the mandible and the temporal bone is a diarthrosis and it allows for extensive movement of the lower jaw.

Diarthroses are divided into three categories, based on the number of axes of motion provided by each. An axis in anatomy is described as the movements in reference to the three anatomical planes: transverse, frontal, and sagittal. Thus, diarthroses are classified as uniaxial (for movement in one plane), biaxial (for movement in two planes), or multiaxial joints (for movement in all three anatomical planes).

A uniaxial joint only allows for a motion in a single plane (around a single axis). The elbow joint, which only allows for bending or straightening, is an example of a uniaxial joint. A biaxial joint allows for motions within two

planes. An example of a biaxial joint is a metacarpophalangeal joint (knuckle joint) of the hand. The joint allows for movement along one axis to produce bending or straightening of the finger, and movement along a second axis, which allows for spreading of the fingers away from each other and bringing them together. A joint that allows for the several directions of movement is called a multiaxial joint (polyaxial or triaxial joint). This type of diarthrotic joint allows for movement along three axes. The shoulder and hip joints are multiaxial joints. They allow the upper or lower limb to move in an anterior-posterior direction and a medial-lateral direction. In addition, the limb can also be rotated around its long axis. This third movement results in rotation of the limb so that its anterior surface is moved either toward or away from the midline of the body.

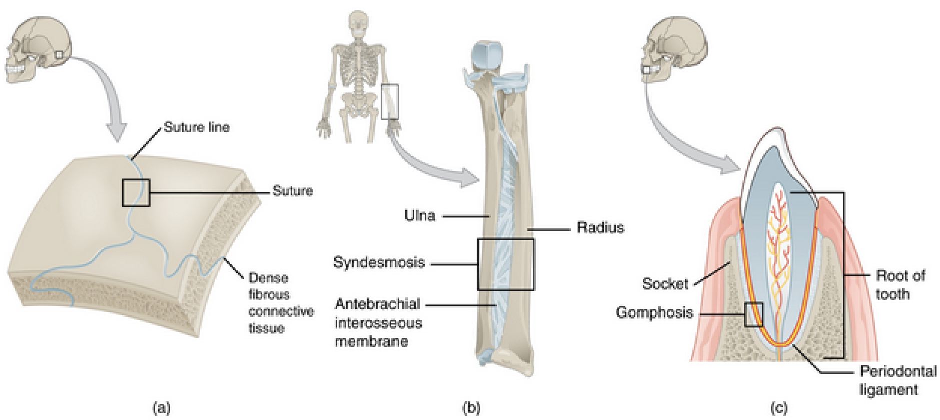


A multiaxial joint, such as the hip joint, allows for three types of movement: anterior-posterior, medial-lateral, and rotational. More details.

At a fibrous joint, the adjacent bones are directly connected to each other by fibrous connective tissue, and thus the bones do not have a joint cavity between them. The gap between the bones may be narrow or wide. There are three types of fibrous joints. A suture is the narrow fibrous joint found between most bones of the skull. At a syndesmosis joint, the bones are more

widely separated but are held together by a narrow band of fibrous connective tissue called a ligament or a wide sheet of connective tissue called an interosseous membrane. This type of fibrous joint is found between the shaft regions of the long bones in the forearm and in the leg. Lastly, a gomphosis is the narrow fibrous joint between the roots of a tooth and the bony socket in the jaw into which the tooth fits.

Main joint types found in the head



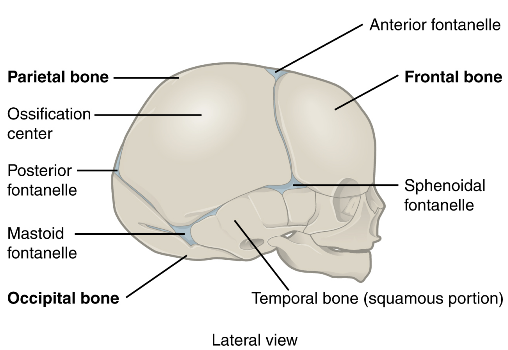
Fibrous joints form strong connections between bones. (a) Sutures join most bones of the skull. (b) An interosseous membrane forms a syndesmosis between the radius and ulna bones of the forearm. (c) A gomphosis is a specialized fibrous joint that anchors a tooth to its socket in the jaw. More details.

Suture

All the bones of the skull, except for the mandible, are joined to each other by a fibrous joint called a suture. The fibrous connective tissue found at a suture (“to bind or sew”) strongly unites the adjacent skull bones and thus

helps to protect the brain and form the face. In adults, the skull bones are closely opposed and fibrous connective tissue fills the narrow gap between the bones. The suture is frequently convoluted, forming a tight union that prevents most movement between the bones. Thus, skull sutures are functionally classified as a synarthrosis, although some sutures may allow for slight movements between the cranial bones.

In newborns and infants, the areas of connective tissue between the bones are much wider, especially in those areas on the top and sides of the skull that will become the sagittal, coronal, squamous, and lambdoid sutures. These broad areas of connective tissue are called fontanelles. During birth, the fontanelles provide flexibility to the skull, allowing the bones to push closer together or to overlap slightly, thus aiding movement of the infant's head through the birth canal. After birth, these expanded regions of connective tissue allow for rapid growth of the skull and enlargement of the brain. The fontanelles greatly decrease in width during the first year after birth as the skull bones enlarge. When the connective tissue between the adjacent bones is reduced to a narrow layer, these fibrous joints are now called sutures. At some sutures, the connective tissue will ossify and be converted into bone, causing the adjacent bones to fuse to each other. This fusion between bones is called a synostosis ("joined by bone"). Examples of synostosis fusions between cranial bones are found both early and late in life. At the time of birth, the frontal and maxillary bones consist of right and left halves joined together by sutures, which disappear by the eighth year as the halves fuse together to form a single bone. Late in life, the sagittal, coronal, and lambdoid sutures of the skull will begin to ossify and fuse, causing the suture line to gradually disappear.



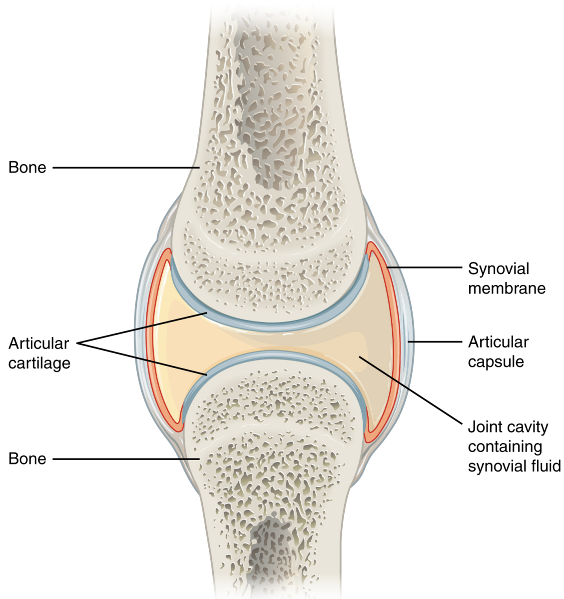
The fontanelles of a newborn’s skull are broad areas of fibrous connective tissue that form fibrous joints between the bones of the skull. More details.

Gomphosis

A gomphosis (“fastened with bolts”) is the specialized fibrous joint that anchors the root of a tooth into its bony socket within the maxillary bone (upper jaw) or mandible bone (lower jaw) of the skull. A gomphosis is also known as a peg-and-socket joint. Spanning between the bony walls of the socket and the root of the tooth are numerous short bands of dense connective tissue, each of which is called a periodontal ligament. Due to the immobility of a gomphosis, this type of joint is functionally classified as a synarthrosis.

Synovial joint

Synovial joints are the only type of diarthrosis and they form the most common type of joint in the body. A key structural characteristic for a synovial joint that is not seen at fibrous or cartilaginous joints is the presence of a joint cavity. This fluid-filled space is the site at which the articulating surfaces of the bones contact each other. Also unlike fibrous or cartilaginous joints, the articulating bone surfaces at a synovial joint are not directly connected to each other with fibrous connective tissue or cartilage. This gives the bones of a synovial joint the ability to move smoothly against each other, allowing for increased joint mobility.



Synovial joints allow for smooth movements between the adjacent bones. The joint is surrounded by an articular capsule that defines a joint cavity filled with synovial fluid. The articulating surfaces of the bones are covered by a thin layer of articular cartilage. Ligaments support the joint by holding the bones together and resisting excess or abnormal joint motions. More details.

Structural Features of Synovial Joints

Synovial joints are characterized by the presence of a joint cavity. The walls of this space are formed by the articular capsule, a fibrous connective tissue structure that is attached to each bone just outside the area of the bone’s

articulating surface. The bones of the joint articulate with each other within the joint cavity.

Friction between the bones at a synovial joint is prevented by the presence of the articular cartilage, a thin layer of hyaline cartilage that covers the entire articulating surface of each bone. However, unlike at a cartilaginous joint, the articular cartilages of each bone are not continuous with each other. Instead, the articular cartilage acts like a Teflon® coating over the bone surface, allowing the articulating bones to move smoothly against each other without damaging the underlying bone tissue. Lining the inner surface of the articular capsule is a thin synovial membrane. The cells of this membrane secrete synovial fluid (synovia = “a thick fluid”), a thick, slimy fluid that provides lubrication to further reduce friction between the bones of the joint. This fluid also provides nourishment to the articular cartilage, which does not contain blood vessels. The ability of the bones to move smoothly against each other within the joint cavity, and the freedom of joint movement this provides, means that each synovial joint is functionally classified as a diarthrosis.

Outside of their articulating surfaces, the bones are connected together by ligaments, which are strong bands of fibrous connective tissue. These strengthen and support the joint by anchoring the bones together and preventing their separation. Ligaments allow for normal movements at a joint, but limit the range of these motions, thus preventing excessive or abnormal joint movements. Ligaments are classified based on their relationship to the fibrous articular capsule. An extrinsic ligament is located outside of the articular capsule, an intrinsic ligament is fused to or incorporated into the wall of the articular capsule, and an intracapsular ligament is located inside of the articular capsule.

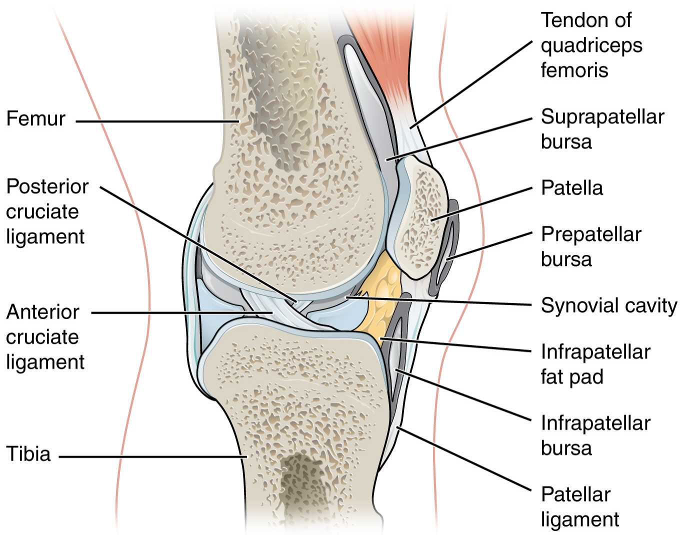
At many synovial joints, additional support is provided by the muscles and their tendons that act across the joint. A tendon is the dense connective tissue structure that attaches a muscle to bone. As forces acting on a joint increase, the body will automatically increase the overall strength of contraction of the muscles crossing that joint, thus allowing the muscle and its tendon to serve as a “dynamic ligament” to resist forces and support the

joint. This type of indirect support by muscles is very important at the shoulder joint, for example, where the ligaments are relatively weak.

Additional Structures Associated with Synovial Joints

A few synovial joints of the body have a fibrocartilage structure located between the articulating bones. This is called an articular disc, which is generally small and oval-shaped, or a meniscus, which is larger and C-shaped. These structures can serve several functions, depending on the specific joint. In some places, an articular disc may act to strongly unite the bones of the joint to each other. Examples of this include the articular discs found at the sternoclavicular joint or between the distal ends of the radius and ulna bones. At other synovial joints, the disc can provide shock absorption and cushioning between the bones, which is the function of each meniscus within the knee joint. Finally, an articular disc can serve to smooth the movements between the articulating bones, as seen at the temporomandibular joint. Some synovial joints also have a fat pad, which can serve as a cushion between the bones.

Additional structures located outside of a synovial joint serve to prevent friction between the bones of the joint and the overlying muscle tendons or skin. A bursa (plural = bursae) is a thin connective tissue sac filled with lubricating liquid. They are located in regions where skin, ligaments, muscles, or muscle tendons can rub against each other, usually near a body joint. Bursae reduce friction by separating the adjacent structures, preventing them from rubbing directly against each other.



Bursae are fluid-filled sacs that serve to prevent friction between skin, muscle, or tendon and an underlying bone. Three major bursae and a fat pad are part of the complex joint that unites the femur and tibia of the leg. More details.

A tendon sheath is similar in structure to a bursa, but smaller. It is a connective tissue sac that surrounds a muscle tendon at places where the tendon crosses a joint. It contains a lubricating fluid that allows for smooth motions of the tendon during muscle contraction and joint movements.

Figure credits

Figure 1 by OpenStax College – Anatomy and Physiology. Chapter 9.1, Fig. 1. http://cnx.org/content/col11496/1.6/

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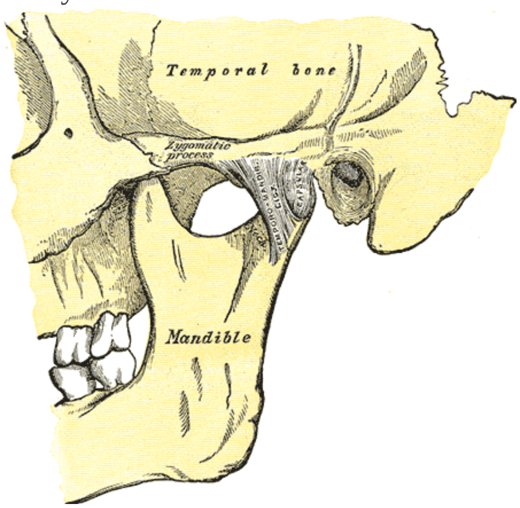
Figure 5 by OpenStax College – Anatomy and Physiology. Chapter 9.4 Fig. 1. http://cnx.org/content/col11496/1.6/

Figure 6 by OpenStax College – Anatomy and Physiology. Chapter 9.4 Fig. 2. http://cnx.org/content/col11496/1.6/

The Temporomandibular Joint
The temporomandibular joint (TMJ) is the synovial articulation between the mandibule and the temporal bone. The mandibular condyle articulates with the mandibular fossa but the two bones are separated by an articular disc. The TMJ is a highly versatile joint, allowing for protraction, retraction, elevation, depression and excursion of the mandible. These movements are executed by the masseter, temporalis and pterygoid muscles, innervated by the anterior mandibular division of the trigeminal nerve and irrigated by the maxillary artery.

The temporomandibular joint (TMJ) allows for opening (mandibular depression) and closing (mandibular elevation) of the mouth, as well as side-to-side (mandibular excursion) and protraction/retraction motions of the lower jaw. This joint involves the articulation between the mandibular fossa and articular tubercle of the temporal bone, with the condyle (head) of the mandible. The main components are the joint capsule, articular disc, mandibular condyles, articular surface of the temporal bone, temporomandibular ligament, stylomandibular ligament, sphenomandibular ligament, and lateral pterygoid muscle.

The capsule is a dense fibrous membrane that surrounds the joint and incorporates the articular eminence. It attaches to the articular eminence, the articular disc and the neck of the mandibular condyle.

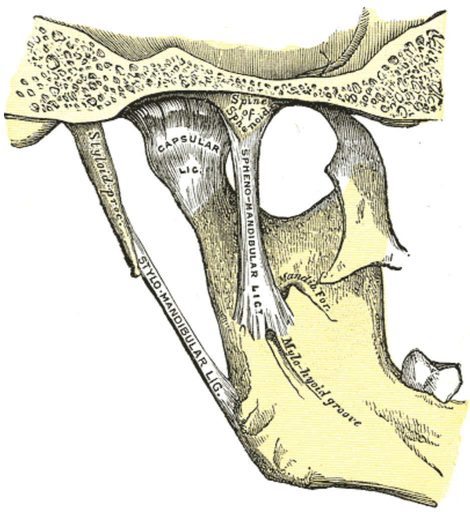


Ligaments reinforcing the lateral aspect of the temporomandibular joint. More details.

Ligaments

There are three ligaments associated with the temporomandibular joints: one major and two minor ligaments. These ligaments are important in that they define the border movements, or in other words, the farthest extents of movements, of the mandible. Movements of the mandible made past the extents functionally allowed by the muscular attachments will result in painful

stimuli, and thus, movements past these more limited borders are rarely achieved in normal function.



Ligaments reinforcing the medial aspect of the temporomandibular joint. More details.

The major ligament, the temporomandibular ligament, is actually the thickened lateral portion of the capsule, and it has two parts: an outer oblique portion (OOP) and an inner horizontal portion (IHP). The base of this triangular ligament is attached to the zygomatic process of the temporal bone and the articular tubercle; its apex is fixed to the lateral side of the neck of the mandible. This ligament prevents the excessive retraction or moving backward of the mandible, a situation that might lead to problems with the joint. More details.

The two minor ligaments, the stylomandibular and sphenomandibular ligaments are accessory and are not directly attached to any part of the joint.

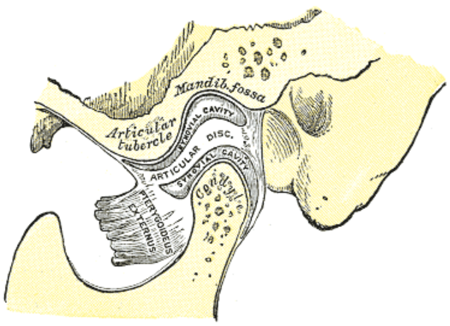
The stylomandibular ligament separates the infratemporal region (anterior) from the parotid region (posterior), and runs from the styloid process to the angle of the mandible; it separates the parotid and submandibular salivary glands. It also becomes taut when the mandible is protruded.

The sphenomandibular ligament runs from the spine of the sphenoid bone to the lingula of mandible. The inferior alveolar nerve descends between the sphenomandibular ligament and the ramus of the mandible to gain access to the mandibular foramen. The sphenomandibular ligament, because of its attachment to the lingula, overlaps the opening of the foramen. It is a vestige of the embryonic lower jaw, Meckel cartilage. The ligament becomes accentuated and taut when the mandible is protruded.

Synovial cavity

The unique feature of the temporomandibular joint is the articular disc. The disc is composed of dense fibrous connective tissue that is positioned between the two bones that form the joint. The temporomandibular joints are one of the few synovial joints in the human body with an articular disc, another being the sternoclavicular joint. The disc divides each joint into two. These two compartments are the upper and lower synovial cavities. The synovial membrane lining the joint capsule produces the synovial fluid that fills these cavities.

The posterior region (retrodiscal tissue) has blood vessels and nerves. The anterior portion, in contrast, is avascular and lacks innervation. Few cells are present, but fibroblasts and white blood cells are among them. This area is thinner but denser than the peripheral region.

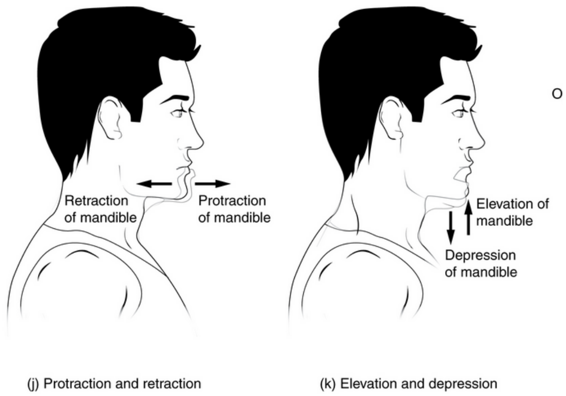


Internal structure of the temporomandibular joint, seen in parasagittal section. More details.

Movements of the mandible

Protraction and Retraction

Protraction and retraction are anterior-posterior movements of the scapula or mandible. Protraction of the scapula occurs when the shoulder is moved forward, as when pushing against something or throwing a ball. Retraction is the opposite motion, with the scapula being pulled posteriorly and medially, toward the vertebral column. For the mandible, protraction occurs when the lower jaw is pushed forward, to stick out the chin, while retraction pulls the lower jaw backward.



Movements of the mandible. More details.

Depression and Elevation

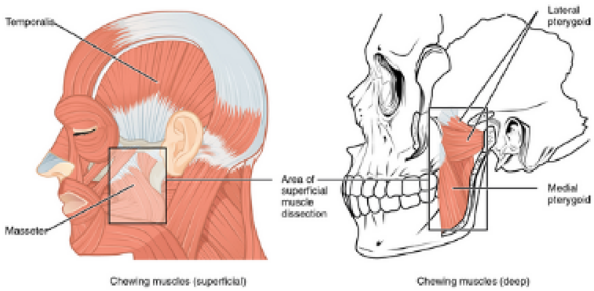
Depression and elevation are downward and upward movements of the scapula or mandible. The upward movement of the scapula and shoulder is elevation, while a downward movement is depression. These movements are used to shrug your shoulders. Similarly, elevation of the mandible is the upward movement of the lower jaw used to close the mouth or bite on something, and depression is the downward movement that produces opening of the mouth.

Excursion

Excursion is the side to side movement of the mandible. Lateral excursion moves the mandible away from the midline, toward either the right or left side. Medial excursion returns the mandible to its resting position at the midline.

Muscles That Move the Lower Jaw

In anatomical terminology, chewing is called mastication. Muscles involved in chewing must be able to exert enough pressure to bite through and then chew food before it is swallowed. The masseter muscle is the main muscle used for chewing because it elevates the mandible (lower jaw) to close the mouth, and it is assisted by the temporalis muscle, which retracts the mandible. You can feel the temporalis move by putting your fingers to your temple as you chew. Although the masseter and temporalis are responsible for elevating and closing the jaw to break food into digestible pieces, the medial pterygoid and lateral pterygoid muscles provide assistance in chewing and moving food within the mouth. The muscles of mastication are derived from the first pharyngeal arch during development.



Muscles that move the lower jaw. They are typically located within the cheek and originate from processes in the skull. This provides the jaw muscles with the large amount of leverage needed for chewing. More details.

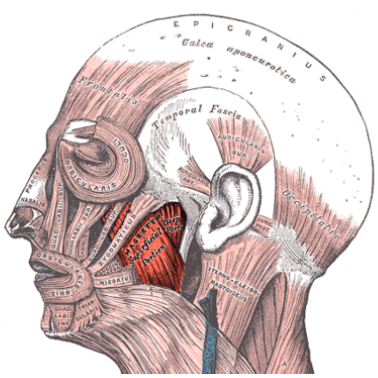
Muscles of the Lower Jaw

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Closes mouth; aids chewing	Mandible	Superior (elevates)	Masseter	Maxilla arch; zygomatic arch (for masseter)	Mandible
Closes mouth; pulls lower jaw in under upper jaw	Mandible	Superior (elevates); posterior (retracts)	Temporalis	Temporal bone	Mandible

Muscles of the Lower Jaw					
Opens mouth; pushes lower jaw out under upper jaw; moves lower jaw side-to-side	Mandible	Inferior (depresses); posterior (protracts); lateral (abducts); medial (adducts)	Lateral pterygoid	Pterygoid process of sphenoid bone	Mandible
Closes mouth; pushes lower jaw out under upper jaw; moves lower jaw side-to-side	Mandible	Superior (elevates); posterior (protracts); lateral (abducts); medial (adducts)	Medial pterygoid	Sphenoid bone; maxilla	Mandible; temporo-mandibular joint

Masseter

The masseter is a thick, somewhat quadrilateral muscle, consisting of two heads, superficial and deep. The fibers of the two heads are continuous at their insertion.



The left masseter muscle (red highlight). More details.

Superficial head

The superficial head, the larger, arises by a thick, tendinous aponeurosis from the maxillary process of the zygomatic bone, and from the anterior two-thirds of the inferior border of the zygomatic arch. Its fibers pass inferior and posterior, to be inserted into the angle of the mandible and inferior half of the lateral surface of the ramus of the mandible.

Deep head

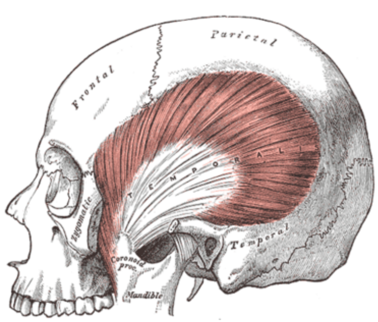
The deep head is much smaller,and more muscular in texture. It arises from the posterior third of the lower border and from the whole of the medial surface of the zygomatic arch. Its fibers pass downward and forward, to be inserted into the upper half of the ramus as high as the coronoid process of the mandible. The deep head of the muscle is partly concealed, anteriorly, by the superficial portion. Posteriorly, it is covered by the parotid gland.

Temporalis

In humans, it arises from the temporal fossa and the deep part of temporal fascia. It passes medial to the zygomatic arch and forms a tendon which inserts onto the coronoid process of the mandible, with its insertion extending into the retromolar fossa posterior to the most distal mandibular molar. In other mammals, the muscle usually spans the dorsal part of the skull all the way up to the medial line. There, it may be attached to a sagittal crest, as can be seen in early hominins like *Paranthropus aethiopicus*.

The temporalis muscle is covered by the temporal fascia, also known as the temporal aponeurosis. This fascia is commonly used in tympanoplasty, or surgical reconstruction of the eardrum.

The muscle is accessible on the temples, and can be seen and felt contracting while the jaw is clenching and unclenching.



The temporalis muscle. The zygomatic arch and masseter have been removed. More details.

Function

The temporalis muscle is the most powerful muscle of the temporomandibular joint. It can be divided into two functional parts: anterior and posterior. The anterior portion runs vertically and its contraction results in elevation of the mandible (closing the mouth). The posterior portion has fibers which run horizontally and contraction of this portion results in retrusion of the mandible.

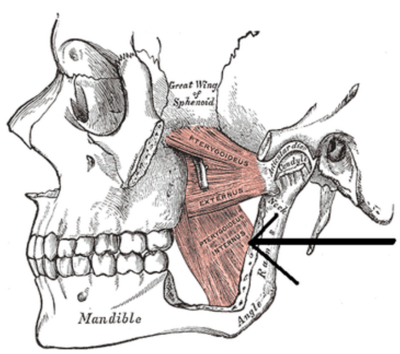
When lower dentures are fitted, they should not extend into the retromolar fossa to prevent trauma of the mucosa due to the contraction of the temporalis muscle.

Medial pterygoid

It has of two heads: superficial and deep.

- The bulk of the muscle arises as a deep head from just above the medial surface of the lateral pterygoid plate.
- The smaller, superficial head originates from the maxillary tuberosity and the pyramidal process of the palatine bone.

Its fibers pass downward, lateral, and posterior, and are inserted, by a strong tendinous lamina, into the lower and back part of the medial surface of the ramus and angle of the mandible, as high as the mandibular foramen. The insertion joins the masseter muscle to form a common tendinous sling which allows the medial pterygoid and masseter to be powerful elevators of the jaw.



The pterygoidei muscles. The zygomatic arch and a portion of the ramus of the mandible have been removed. More details.

Function

Given that the origin is on the medial side of the lateral pterygoid plate and the insertion is from the internal surface of the ramus of the mandible down to the angle of the mandible, its functions include:

- Elevation of the mandible (closes the jaw)
- Minor contribution to protrusion of the mandible
- Assistance in mastication
- Excursion of the mandible; contralateral excursion occurs with unilateral contraction.

Lateral pterygoid

The upper/superior head originates on the infratemporal surface and infratemporal crest of the greater wing of the sphenoid bone, and the lower/inferior head on the lateral surface of the lateral pterygoid plate.

Inferior head inserts onto the neck of condyloid process of the mandible; upper/superior head inserts onto the articular disc and fibrous capsule of the temporomandibular joint.

Function

The primary function of the lateral pterygoid muscle is to pull the head of the condyle out of the mandibular fossa along the articular eminence to protrude the mandible. A concerted effort of the lateral pterygoid muscles helps in lowering the mandible and open the jaw whereas unilateral action of a lateral pterygoid produces contralateral excursion (a form of mastication), usually performed in concert with the medial pterygoids.

Unlike the other three muscles of mastication, the lateral pterygoid is the only muscle of mastication that assists in depressing the mandible (opening the jaw). At the beginning of this action it is assisted by the digastric, mylohyoid and geniohyoid muscles.

Mouth opening

Movement at the TMJ during opening and closing of the mouth involves both hinge motion (mandibular rotation) and gliding (mandibular translation) of the mandible. With the mouth closed, the mandibular condyle and articular disc are located within the mandibular fossa of the temporal bone. During the first 20 mm of mouth opening, the mandibular condyle rotates within the lower synovial cavity and the mandible moves like a hinge (mandibular rotation).

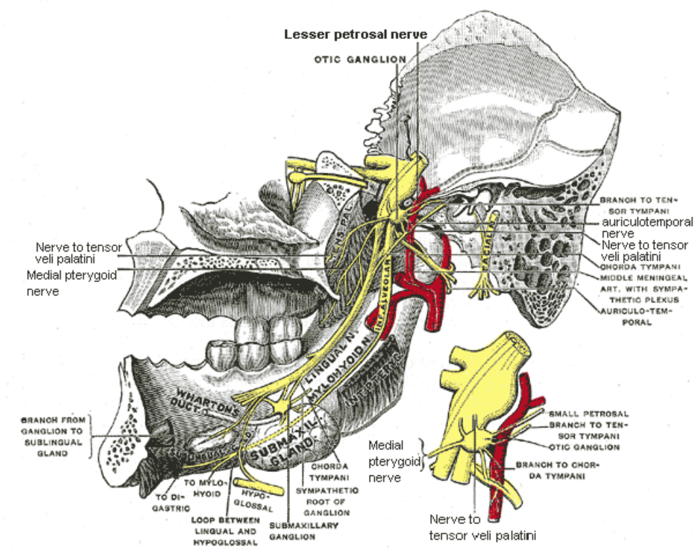
Further opening the mouth is helped by the lateral pterygoid muscle. This muscles originates in the palatine and sphenoid bones, and its two heads insert into the anterior surfaces of the neck of the mandibular condyle (inferior head) and articular disc (superior head). Contraction of the lateral pterygoid muscle protracts the mandible, pulling anteriorly on the mandibular condyle and articular disc. This produces mandibular translation, which is the gliding of the articular disc out of the mandibular fossa and over the eminence of the articular tubercle. The net result is a forward and downward motion of the condyle and mandibular depression.

Mandibular rotation and translation allow us to open the mouth and produce strong biting over a wide range of angles. At any angle, the articular disc is positioned between the mandibular condyle and the temporal bone. It cushions the stresses of biting and we do not feel pain because the disc lacks neural terminals.

Watch the MRI video at https://upload.wikimedia.org/wikipedia/commons/c/c1/Real-time_MRI_-_Temporomandibular_Joint.ogv. By Byomedizinische NMR Forschungs GmbH am Max-Planck-By Institut für biophysikalische Chemie Am Fassberg 11 37077 Göttingen, http://www.biomednmr.mpg.de.

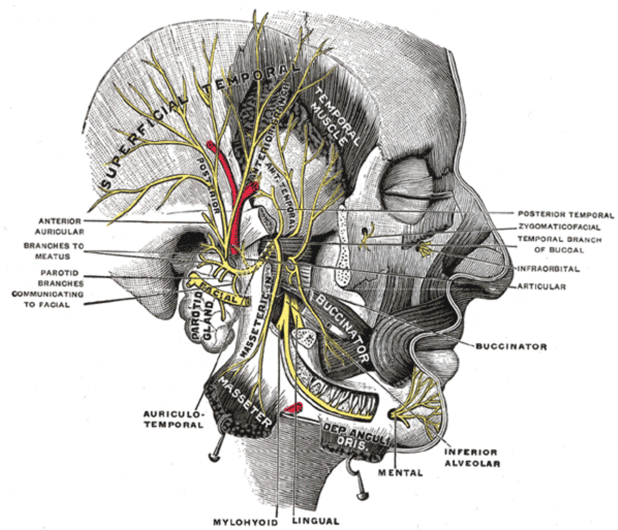
Innervation

The four muscles of mastication (masseter, temporalis, medial pterygoid, and lateral pterygoid), are innervated by the mandibular division of the trigeminal nerve. The mandibular nerve has sensory and motor function and it passes through the foramen ovale of the sphenoid bone. The medial pterygoid muscle is innervated by nerve to medial pterygoid, which is the second branch off of the mandibular nerve.



Branches of the maxillary and mandibular nerves. After forming the medial pterygoid nerve, the mandibular nerve divides into a thin anterior branch and a large posterior branch. The anterior branch is lateral to the bones and is not shown. The posterior branch originates the lingual and inferior alveolar nerves. More details.

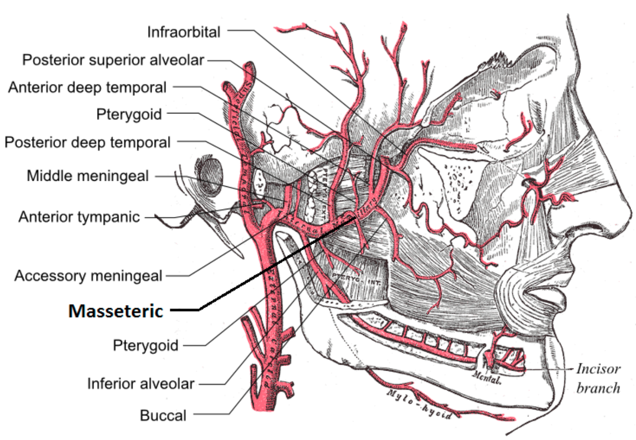
Further down, the mandibular nerve divides into small anterior and a large posterior branch. The masseter, temporalis and lateral pterygoid muscles are innervated by branches of the anterior division of the mandibular nerve. The masseter is innervated by the masseteric nerve. The temporalis muscle is innervated by the anterior and posterior deep temporal nerves. And the lateral pterygoid muscle is innervated by the lateral pterygoid nerve.



Branches of the mandibular nerve, showing the innervation of the muscles of mastication. More details.

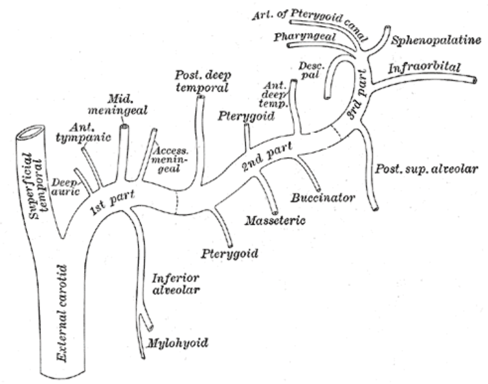
Blood supply

The common carotid artery is the main artery that supplies the head with blood. It branches into internal and external carotid arteries. The internal carotid mostly serves structures in the brain, whereas the external carotid serves structures in the neck and face. T external carotid forms many branches, including the maxillary artery, which supplies the muscles of mastication.



Branches of the maxillary artery that irrigate the muscles of mastication. More details.

The masseteric artery passes over the mandibular notch and supplies the masseter muscle. The pterygoid arteries, variable in position and number, irrigate the lateral and medial pterygoid muscles. The anterior and posterior deep temporal arteries which anastomose with the middle temporal artery, supply the temporalis muscle.



Branching pattern of the maxillary artery. More details.

Temporomandibular joint disorders

Disc displacement is the most common disorder of the TMJ. This occurs when the articular disc is dislocated anteriorly with the mouth closed. The retrodiscal tissue is found in between the mandibular condyle and the mandibular fossa. Biting in this condition can be very painful as compression of the retrodiscal tissue will damage it and stimulate its pain receptors.

If the mouth opens fully, the condyle slides anteriorly, over the articular disc. The posterior end of the articular disc might form a salience, however, representing an obstacle to the movement. This will cause clicking sounds when the mouth is opened or closed and the mandibular condyle passes over the salience back and forth between retrodiscal tissue and articular disc. This condition is called disc displacement with reduction.

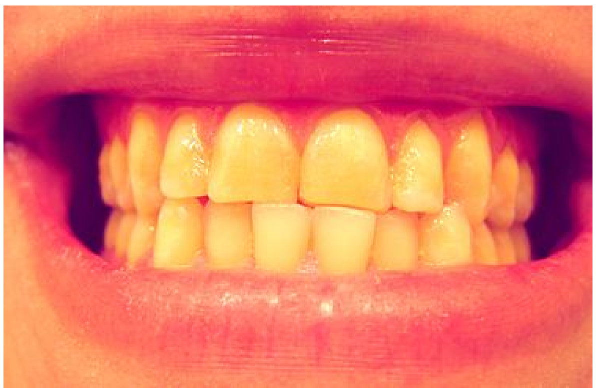
If the salience formed by the posterior end of the articular disc becomes too prominent, it may prevent the mandibular condyle from sliding over the articular disc. There is no click, but mandible is locked, unable to produce translation. Mouth opening is limited to the 20 mm allowed by mandibular rotation. This condition is called disc displacement without reduction.

Dislocation of the TMJ may occur when opening the mouth too wide (such as when taking a large bite) or following a blow to the jaw, resulting in the mandibular condyle moving beyond (anterior to) the articular tubercle. In this case, the individual would not be able to close his or her mouth. Temporomandibular joint disorders may also arise due to arthritis, wearing of the articular cartilage, muscle fatigue from overuse or grinding of the teeth, damage to the articular

disc within the joint, or jaw injury. Temporomandibular joint disorders can cause headache and impaired chewing. Pharmacologic agents for pain or other therapies, including bite guards, are used as treatments.

Bruxism

Bruxism is excessive teeth grinding or jaw clenching. It occurs at times other than eating or talking. It is a common problem affecting 8–31% of the general population. Bruxism causes hypersensitive teeth, aching jaw muscles, headaches, tooth wear, damage to dental restorations (e.g. crowns and fillings) and damage to teeth.



Teeth worn by grinding (bruxism). More details.

The tooth grinding can occur during sleep or during wakefulness. Dental damage may be similar in both cases. The symptoms of sleep bruxism tend to be worse on waking and improve during the course of the day, whereas the symptoms of awake bruxism may not be present at all on waking, and then worsen over the day.

The causes of bruxism are not well understood and various factors seem to influence it, but social stress seems to be commonly involved. Several treatments are in use, including medications, psychological intervention, stress relief therapies, dental guards (to reduce further damage) and dental treatment.

Dental guard for wear reduction in cases of tooth grinding. More details.

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Diversity of Jaw Movements
Vertebrates with jaws can bite, and their feeding effectiveness is greatly increased by suction. Lateral expansion of the operculum and lowering of the mouth floor provide such suction, whereas projection of the jaws accelererates the containment of prey. Both mechanisms promoted the increase in number of articulations between cranial and facial bones. Across vertebrates, the need for ingestion of large pray items whole has promoted cranial kinesis, whereas the need for strong biting has promoted bone fusion. Mammals seem to have lost their skull kinesis in favor of improved suckling through the evolution of a hard palate.

The evolution of jaws was a big event among fishes. It permitted biting and it provided structural support for the buccal pump. Jawed fishes could maintain a high rate of water flow through their gills using the buccal pump. This would keep the blood well oxigenated even if the fish was not actively swimming. The buccal pump made possible another important advancement, however: suction feeding!

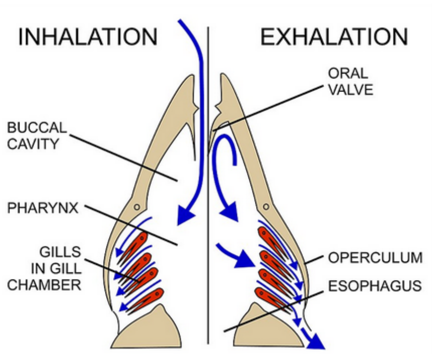
Suction feeding

This is a method of ingestion in which the food item enters the mouth of the organism carried by a volume of medium that is sucked in. It is typically accomplished by the predator expanding the volume of its oral cavity and/or throat, resulting in a pressure difference between the inside of the mouth and the outside environment. When the mouth is opened, the pressure difference causes water to flow into the predator's mouth, carrying the prey in with the flow.

Illustration of large

mouth bass with mouth open for prey ingestion. More details.

Suction is produced by extensive expansion of the oral cavity, involving lateral displacement of the operculum (the cover of the gills) and lowering of the floor of the mouth. This feeding mechanism is enhanced by simultaneous fast upper jaw protrusion, which directs the suction and accelerates the containment of the prey. Watch this video on suction feeding by the WainwrightLab at the University of California, Davis.



Suction by lateral expansion of the oral cavity in fishes. More details.

Ram feeding is an alternative method of ingestion employed by many fishes. Instead of sucking in the water with food, in ram feeding the fish swims forward with the mouth and the gill slits open. Water flows through the mouth and exits through the gills, while food items are retained in the mouth and directed to the esophagus. Many fishes are not restricted to suction or ram feeding but alternate between these methods or employ a

combination of them, adding some suction to the forward motion of the body when an item of interest is detected.

Ram feeding by a basking shark (*Cetorhinus maximus*). This is one of the three species of plankton-eating sharks. It grows up to 8 meters in length and feeds by swimming slowly near the surface with the mouth open. More details.

Cranial kinesis

Cranial kinesis is the amount of movement between skull bones. It is not restricted to the bones of the brain case but also applies to the upper jaws.

Most vertebrates have some form of kinetic skull. The amount of cranial kinesis is usually influenced by diet and feeding habit. Animals which must exert powerful bite forces, such as crocodiles, often have rigid skulls with

little or no kinesis, for maximization of strength. Kinetic skulls, frequently with numerous mobile joints are usually found in animals that:

- Swallow large prey whole (snakes).
- Grip awkwardly shaped food items (parrots eating nuts).
- Feed in the water via suction feeding.

In cartilaginous fishes (sharks and rays) there is no attachment between the hyomandibular and the quadrate bones, and instead the hyoid arch suspends the two sets of jaws like pendulums. Sharks can swing their jaws outwards and forwards over the prey.

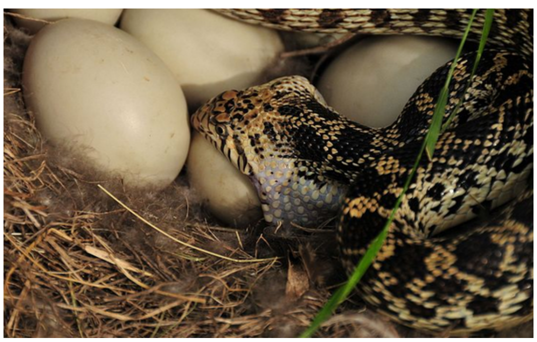
White shark biting on bait. More details.

Ray-finned fishes possess a wide range of kinetic mechanisms, mostly linked expansion of the oral cavity and to protrusion of the mandible during suction feeding. As the group diversified using suction feeding a general trend arose of liberating more and more bony elements to allow greater skull motility. A common arrangement in ray-finned fishes is a four component kinetic system. The hyoid is linked to the mandible by ligaments and moves together with it. The hyoid articulates with the ceratohyal bone which articulates with the suspensorial bone. In a four-part movement that also involves the cranium and shoulder girdle, the lower jaw can be extensively protracted. The width of the mouth can also be greatly expanded, producing the water inflow that is necessary for suction feeding.

Like mammals, lobe-finned fishes mostly use the masseter (homologous with that of mammals) to elevate the lower jaw, and a sternohyoid muscle (also homologous) to retract the hyoid, in order to open the mouth. The protractor hyoideus in fishes and the

geniohyoid and digastric in mammals are analogous however, in serving the role of depressing the lower jaw, but having distinct evolutionary origins.

Reptiles exhibit a wide variety of kinetic mechanisms. The most spectacular examples are snakes which use highly kinetic joints to allow them to swallow large items whole. Some snakes can eat bird eggs with a much greater diameter than that of their own bodies. The mandibular bone is typically connected to the neurocranium via the quadrate and squamosal bones.



Bullsnake (*Pituophis catenifer sayi*)preying on an egg in a mallard (*Anas platyrhynchos*) nest. More details.

Birds show a vast range of cranial kinetic hinges in their skulls. Opposite to the common perception that bird’s beaks are completely rigid, cranial kinesis in birds has been categorized in three different classes. These articulations allow shore birds to probe the mud with their beaks and curve

the tips, to use them like forceps. Other birds can curve the beak to increase the height or the width of the passage, increasing the range of food item sizes that they can swallow.

Mammals have akinetic skulls. This is most likely due to the evolution of the secondary palate, the bony separation between the oral and nasal cavities. This in turn is a consequence of the need to create suction during suckling.

Credits

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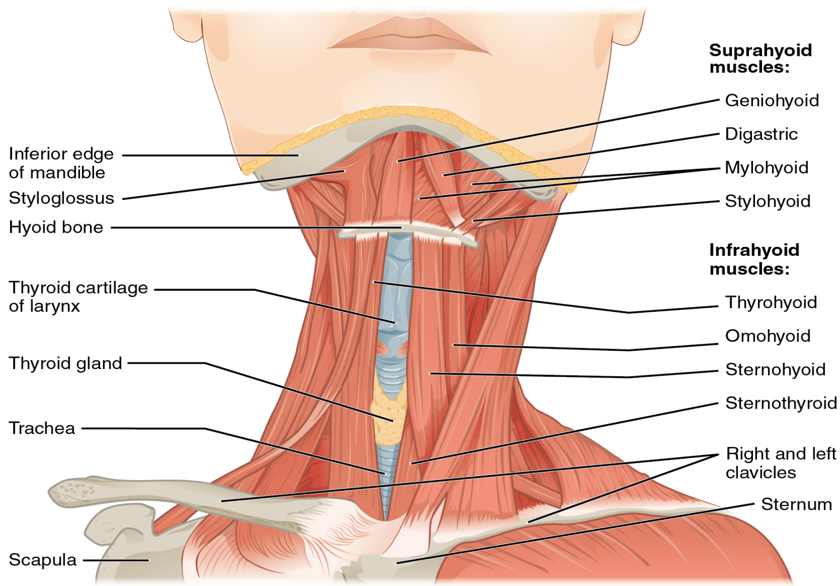
The Anterior Muscles of the Human Neck
The anterior muscles of the neck control the depression of the larynx and the positions of the hyoid bone and larynx. In addition to depression of the mouth for eating and drinking, this control is necessary for swallowing and voice.

While the lateral pterygoid protrudes the mandible for translation (see chapter 9 Biting), gravity and various muscles of the anterior portion of the neck assist in depressing the mandible. These muscles attach to the hyoid bone, which is posterior and inferior to the mandible. Contraction of these muscles tends to produce protrusion and elevation of the hyoid, but this can be prevented by other muscles that attach to the hyoid and to the temporal bone, larynx, sternum, clavicle and scapula. At other times, movement of the hyoid and larynx can be demanded for other activities including deglutition (swallowing) and speech. The anterior muscles of the neck control the positions of the larynx and the hyoid bone. They are categorized according to their position relative to the hyoid bone. Suprahyoid muscles are superior to it, and the infrahyoid muscles are located inferiorly.



Anterior muscles of the human neck. More details.

The suprahyoid muscles depress the mandible or raise the hyoid bone, the floor of the mouth, and the larynx during deglutition. These include the digastric muscle, which has anterior and posterior bellies. The stylohyoid muscle moves the hyoid bone posteriorly, elevating the larynx, and the mylohyoid muscle lifts it and helps press the tongue to the top of the mouth. The geniohyoid depresses the mandible in addition to raising and pulling the hyoid bone anteriorly.

The strap-like infrahyoid muscles generally depress the hyoid bone and control the position of the larynx. The omohyoid muscle, which has superior and inferior bellies, depresses the hyoid bone in conjunction with the sternohyoid and thyrohyoid muscles. The thyrohyoid muscle also elevates the thyroid cartilage, whereas the sternothyroid depresses it to create different tones of voice.

Table 1. Anterior muscles of the human neck.

Movement	Target	Target motion direction	Prime mover	Origin	Insertion
Moves tongue up; retracts tongue back into mouth	Tongue	Superior (elevates); posterior (retracts)	Styloglossus	Temporal bone (styloid process)	Tongue undersurface and sides
Flattens tongue	Tongue	Inferior (depresses)	Hyoglossus	Hyoid bone	Sides of tongue
Bulges tongue	Tongue	Superior (elevation)	Palatoglossus	Soft palate	Side of tongue
Swallowing and speaking					
Raises the hyoid bone in a way that also raises the larynx, allowing the epiglottis to cover the glottis during deglutition; also assists in opening the mouth by depressing the mandible	Hyoid bone; larynx	Superior (elevates)	Digastric	Mandible; temporal bone	Hyoid bone
Raises and retracts the hyoid bone in a way that elongates the oral cavity during deglutition	Hyoid bone	Superior (elevates); posterior (retracts)	Stylohyoid	Temporal bone (styloid process)	Hyoid bone
Raises hyoid bone in a way that presses tongue against the roof of the mouth, pushing food back into the pharynx during deglutition	Hyoid bone	Superior (elevates)	Mylohyoid	Mandible	Hyoid bone; median raphe
Raises and moves hyoid bone forward, widening pharynx during deglutition	Hyoid bone	Superior (elevates); anterior (protracts)	Geniohyoid	Mandible	Hyoid bone
Retracts hyoid bone and moves it down during later phases of deglutition	Hyoid bone	Inferior (depresses); posterior (retracts)	Omohyoid	Scapula	Hyoid bone
Depresses the hyoid bone during swallowing and speaking	Hyoid bone	Inferior (depresses)	Sternohyoid	Clavicle	Hyoid bone
Shrinks distance between thyroid cartilage and hyoid bone, allowing production of high-pitch vocalizations	Hyoid bone; thyroid cartilage	Hyoid bone: inferior (depresses); thyroid cartilage: superior (elevates)	Thyrohyoid	Thyroid cartilage	Hyoid bone
Depresses larynx, thyroid cartilage, and hyoid bone to create different vocal tones	Larynx; thyroid cartilage; hyoid bone	Inferior (depresses)	Sternothyroid	Sternum	Thyroid cartilage
Rotates and tilts head to he side; tilts head forward	Skull; cervical vertebrae	Individually: medial rotation; lateral flexion; bilaterally: anterior (flexes)	Sternocleid-omastoid; semispinalis capitis	Sternum; clavicle	Temporal bone (mastoid process); occipital bone
Rotates and tilts head to the side; tilts head backwards	Skull; cervical vertebrae	Individually: lateral rotation; lateral flexion; bilaterally: anterior (flexes)	Splenius capitis; longissimus capitis		

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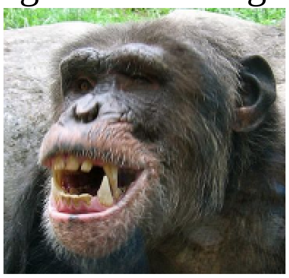
The Origin of Dental Tissue

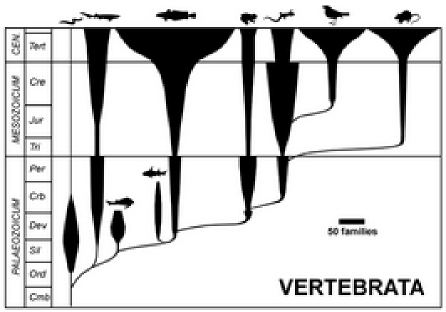
Teeth with pulp, dentin and enameloid have evolved in jawed fishes. Other fishes and many invertebrates have tooth-like structures formed by keratin. Teeth may have evolved from dermal denticles or may have originated in the mouth and the earliest evidence of complete teeth in the mouth was found within the latest group of placoderms, which is thought to have originated cartilaginous fishes, bony fishes and tetrapods.



A chimpanzee displaying its teeth which are key to feeding and communication. More details.

The evolution of new types of hard tissues like cartilage, bone, dentin and enameloid was key to the diversification and success of chordates. This chapter reviews the origin of teeth, their diversification in the major groups of vertebrates and their organization in mammals. Human teeth are studied in detail in the next chapter.

Origins of hard tissues and teeth



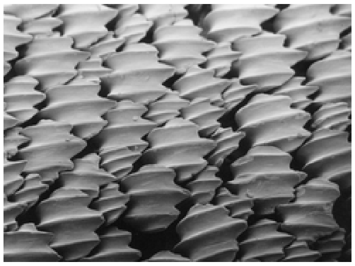
Evolution and species richness of the vertebrate classes. More details.

As studied in the chapter on skull, the evolution of progressively harder tissues in chordates promoted the origin of vertebrae, skulls, jaws and teeth. Lampreys and hagfishes lack bones or a mandible but they have a cartilaginous skeleton. Lampreys use sharp “teeth” to attach to their prey, but these teeth are hardened by keratin and they lack any dentin or enameloid. They are analogous (similar function) but not homologous (originated by common descent) to our teeth.

Teeth with dentin and enamel evolved in fishes, and modern paleontological evidence is gradually revealing when and how. Several hypotheses have been proposed as to how teeth evolved, and they can be grouped into Outside-In and Inside-Out propositions.

The outside-in propositions are based on the finding that most cartilaginous fishes like sharks and rays have a tough skin covered with tiny tooth-like scales (placoid scales or dermal denticles). In most species, all dermal denticles are oriented in one direction, making the skin feel very smooth if rubbed in one direction and very rough if rubbed in the other. Each placoid scale has a pulp, covered by a softer and a harder mineralized layer of tissue that resemble dentin and enamel, respectively. These scales are proposed to have originated the teeth of tetrapods. The scales would have covered the entire body as a protective structure. At the edge of the mouth, however, these structures could become useful at improving the grip of a bite. They

would then be selected to become more internalized, larger and assume specialized shapes for capturing prey and processing food.



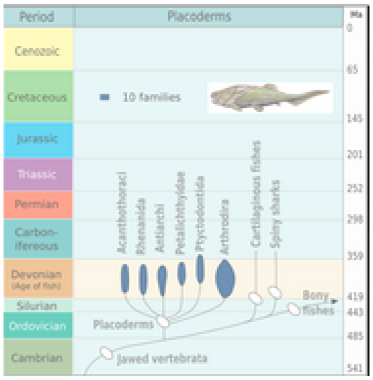
Placoid scales as viewed through an electron microscope. Also called dermal denticles, these are structurally homologous to tetrapod teeth. More details.

The inside-out hypotheses suggest that teeth could have evolved in the mouth first, and then covered the body as dermal denticles. Several types of fishes have pharyngeal teeth, which are saliences on the walls of the pharyngeal arches (which also hold the gills) that help to grip and retain food items. Dentin and enamel could have evolved in the pharyngeal teeth of fishes, then spread through the mouth and the outer skin. The teleost bony fish *Denticeps clupeoides* has most of its head covered by dermal teeth, which were not present in the common ancestors of bony fish. This shows that dermal teeth could originate from oral teeth.

As an alternative to both directions of spread of teeth, dermal and oral teeth could have evolved independently. The evidence for oral teeth, however, seems to indicate a single origin.

Pharyngeal teeth on the pharyngeal arch of a goldfish. More details.

Dermal and oral teeth are common and well developed in cartilaginous fishes. When uncovering older evidence, researchers have to carefully establish the evolutionary history of a fossil and the homology of the structures being compared across species. The current fossil record has many gaps and some evidence is tentative, but it seems most likely that dermal scales evolved much before teeth with dentin. Dermal scales have been found in various groups of jawless ostracoderm and placoderm fishes, whereas enameloid teeth are not found at all in most placoderms. Teeth with dentin and a pulp cavity are first seen in arthrodirans which form the most recent subgroup of placoderms. Pharyngeal teeth have been described from older jawless fishes (ostracoderms), but studies failed to find evidence of common structure between them and modern teeth and developmental studies did not reveal any major separation between the origin of oral teeth and dermal denticles. The most recent evidence is therefore favoring the outside-in hypothesis, in which dermal scales would have covered the body and started to specialize as teeth in arthrodiran placoderm fishes, which originated the cartilaginous and bony fishes, and all tetrapods.



Evolution and extinction of placoderm fishes. The diagram shows the traditional view of the group having common ancestry. The most recent evidence however indicates a series of separate origins, with Arthrodira being the most recent group and the ancestor of cartilaginous and bony fishes. More details.

Credits

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Homodont animals
Homodont animals have all teeth of a same type. A great diversity of tooth structures is found among species, however. Diet and feeding habit are the main driving forces shaping the evolution of teeth. Specializations are found for cutting meet, seizing prey, crushing seeds, dealing with abrasion by grass, and injecting venom.

Tooth types

Most toothed vertebrates exhibit repetitions of a single type of tooth (homodont) that varies in size across the dentition. Diet and feeding habit can cause natural selection to gradually mold tooth shape producing remarkably specialized teeth. Carnivory in fishes favors the evolution of flat teeth with a sharp edges for cutting meat. They tend to be triangular with a pointy tip to facilitate penetration. Piranhas are South American freshwater fish with carnivorous habit. They are famous for having very sharp teeth and quickly aggregating and dismantling large animals at the first sign of blood in the water.

Dry-preserved piranha showing relatively large and flat triangular teeth used for biting into the flesh of prey. More details.

Other morphological adaptations observed in carnivore fish include serrated teeth, commonly found in sharks. A serrated cutting edge has many small points of contact with the material being cut. By having less contact area than a smooth blade or other edge, the applied pressure at each point of contact is greater and the points of contact are at a sharper angle to the material being cut. The tooth produces many small splits in the surface of the material being cut and merges them as it moves.

The serrated edges of tiger shark teeth. More details.

Some herbivore fish, on the other hand, specialize in eating seeds and have broad and flat teeth designed for crushing hard items. The pacu (order Characiformes) is a relative of the piranha with very different teeth that grossly resemble human molars. Pacus can reach large body sizes (> 80 cm) and they mostly feed on nuts that fall from the trees into the rivers that they inhabit.

Pacus are neotropical freshwater fish that can deliver powerful bites and have teeth with flat crowns designed for crushing nuts. More details.

Living amphibians typically have small teeth, or none at all, since they commonly feed only on soft foods. These pedicellate teeth are flexible due to connective tissue and uncalcified dentine that separates the crown from the base of the tooth. In addition to the tiny denticles found along the jaws, some frogs have vomerine teeth, found on the roof of the mouth. These tend to be sharp and inclined posteriorly to help prevent the loss of food items in the mouth.

An alligator has conical teeth

designed to retain prey. More details.

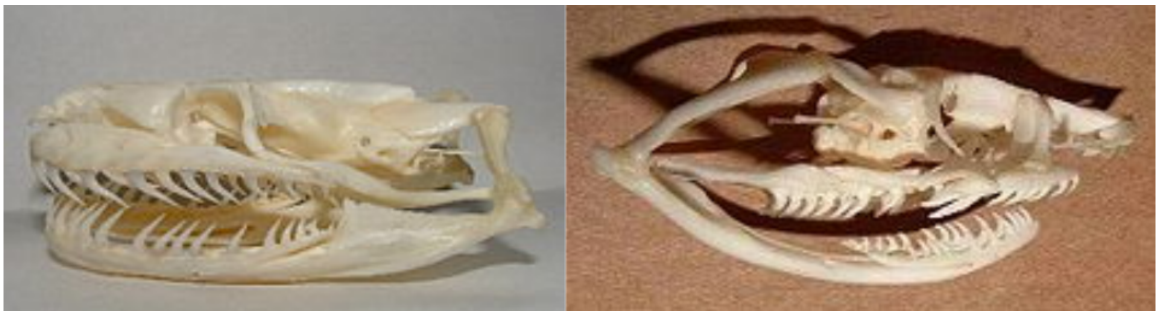
Reptile teeth are generally simple and conical in shape. Most lizards and crocodilians have large numbers of conical teeth designed to perforate and retain live food items. They mostly ingest their prey whole as opposed to biting pieces off such as carnivore fishes with blade-like teeth do. An interesting variation can be seen in snakes, in which some of the teeth are specialized into venom-injecting fangs.

The anterior teeth of the Gaboon viper (*Bitis gabonica*) are specialized for the injection of venom. More details.

The position and size of the fangs and the associated venom glands is highly variable in snakes. Their teeth also vary in the presence and position of groves on the teeth, which serve the role of transporting venom from the base to the tip of the tooth. Most snakes can be placed into one of four

groups, based on their teeth, and this grouping correlates strongly with lineage and venom type.

Aglyphous (lacking groves) snakes have no specialized teeth. All teeth are similar in shape and often size. Most aglyphous snakes, including boas and pythons are non-venomous. Some are considered mildly venomous, but they are generally not harmful to humans.



Snakes classified by fang type. Left: Dentition of an aglyphous snake. A Burmese python skull (*Python bivittatus*). More details. Right: Dentition of an opisthoglyphous snake. A hognose snake skull (*Heterodon nasicus*). More details.

Opisthoglyphous (*rearward grooves*) snakes use a pair of enlarged teeth at the back of the maxillae to inject venom. These bones normally angle backward and are grooved to channel venom into the puncture. Since these fangs are not located at the front of the mouth the snake must move the prey into the rear of the mouth and then penetrate it with its fangs. Opisthoglyphous snakes such as garter snakes are found in family Colubridae.

Snakes classified by fang type. Left: Proteroglyphous king cobra skull (*Ophiophagus hannah*). More details. Right: Solenoglyphous rattlesnake skull (*Crotalus sp.*). More details.

Proteroglyphous (*forward grooved*) snakes have shortened maxillae bearing few teeth except for a substantially enlarged fang pointing downwards and completely folded around the venom channel, forming a hollow needle. Because the fangs are only a fraction of an inch long in even the largest species these snakes must hang on, at least momentarily, as they inject their venom. Some spitting cobras have modified fang tips that allow them to spray venom at an attacker's eyes. Proteroglyphous dentition is unique to elapids such as coral snakes and cobras.

Solenoglyphous (*pipe grooved*) snakes have the most derived venom delivery method of any snake. Each maxilla is reduced to a nub supporting a single hollow fang and it can rotate over its articulation with the skull. The fangs, which can be as long as half the length of the head, are folded against the roof of the mouth, pointing posteriorly. The fangs rotate erecting anteriorly when the jaws open. Solenoglyphous snakes open their mouths almost 180 degrees allowing their fangs to penetrate deep into the prey. Solenoglyphus dentition is unique to vipers.

Most dinosaurs had conical teeth like those of lizards and crocodilians. As notable exceptions, several carnivore species had flattened triangular teeth, some of them with serrated edges. Large herbivore species faced accelerated wearing of the teeth through abrasion produced by the silicon

crystals contained in the grass that they consumed. Hadrosaurs exhibited 'tooth batteries' with rows of teeth densely packed side by side on the jaw and also over each other forming vertical layers.

Dental batteries from an adult and juvenile hadrosaur. Both Batteries are part of the lower jaw. More details.

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Heterodont animals
Mammals evolved a heterodont dentition with four classes of teeth: incisors, canines, premolars and molars. Each tooth is formed by 1-5 cusps. Maxillary cusps are called cones whereas mandibular ones are called conids. Hypsodont teeth erupt high beyond the gum line while brachydont teeth do not protrude much. The shape and arrangement of tissues in the molar teeth is grouped into several classes that reflect the diet and phylogeny of the animals.

Mammalian teeth

The tiger (*Panthera tigris*) presents an example of heterodont dentition with four types of teeth. More details.

Mammals have evolved heterodont dentitions. They are unique in having four tooth classes: incisors, canines, premolars and molars. These classes are found in the majority of species, and always in the same order (but in variable numbers) from the midline to the sides. Each type is formed by 1-5 cusps, which are round projections of the crown pointing toward the opposing tooth.

Incisors are the most medial and anterior teeth. They vary in number from none in armadillos, to 18 in opossums. They are broad and flat, and their single cusp forms a broad cutting line called the incisal edge. The general function of incisors is seizing food and biting off pieces of food items. Mammals that gnaw, like rabbits and mice, have relatively large incisors lacking on the posterior surface. As enamel wears more slowly than dentin, the tooth maintains a chisel shape with a sharp incisal edge. Elephants have highly specialized incisors that evolved into a round shape and extended out of the mouth to form tusks.

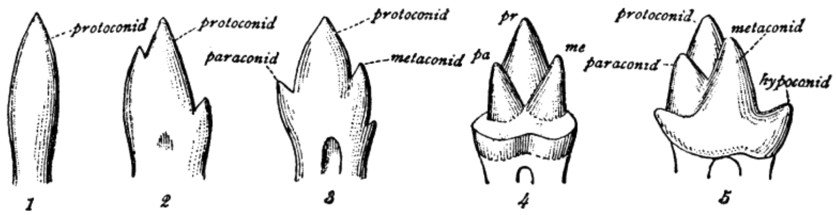
Canines are round and pointy, frequently being the longest teeth of mammals. They present a single cusp and are also called cuspids. Mammals have 0-4 canines, which are used to puncture the food item during biting, producing a firm hold helping to kill prey. Hervibores commonly lack canines, or have them modified into tusks, like walruses and pigs, to serve as weapons or have other uses.

Early mammals had premolars with a single cusp and molars with three cusps, but they later evolved premolars with up to three cusps and molars with four or five cusps. These teeth process the food in the mouth by cutting, slicing or grinding.

Cusps

Upper molar cusps are called cones, whereas lower molar cusps are called conids. A prefix is added to the name to specify their position on the tooth. These prefixes are proto-, para-, meta-, hypo-, and ento-. A paracone is therefore the anterior external cusp of a maxillary molar.

Tribosphenic molars with three cusps were found in early mammals and are still found in insectivores. Many modern mammals such as primates (humans), racoons and hedgehogs have quadrate molars however, containing four or five cusps.



Evolution of the arrangements of cusps in molar teeth of reptiles and early mammals. 1, Reptile; 2, *Dromatherium*; 3, *Microconodon*; 4, *Spalacotherium*; me, metaconid; pa, paraconid; pr, protoconid; 5, *Amphitherium*. (After Osborn.). More details.

Crown height

Hypsodont teeth are characterized by high crown with enamel that extends far past the gum line into the bone. These teeth are commonly found in grazing herbivores because they provide extra material for wear and tear. The tooth keeps erupting slowly as it is worn off. Some examples of animals with hypsodont teeth are cows and horses. These animals usually die in nature of other causes before their molars wear off completely. But domesticated animals like old horses are frequently reported to loose to functionality of their molars because of extensive wearing. Rabbits and some rodents, on the other hand, incisors that continue growing after they erupt, adding new tissue at the roots as wearing progresses at the incisal edge.

The opposite condition to hypsodont is brachydont. It is a type of dentition characterized by low-crowned teeth (brachys = short). Human teeth are brachydont. The tooth has a crown above the gingival line and a neck just below it, and at least one root. A cap of enamel covers the crown and extends down to the neck. Cementum is only found below the gingival line, covering the root.

Shape and arrangement of enamel and dentin

Bunodont

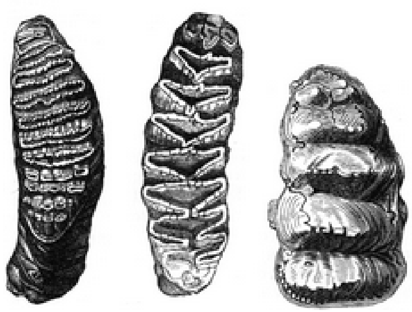
The cusps are rounded instead of sharp or pointy. These molars are most common among omnivores such as pigs, bears and humans. Bunodont molars are effective crushing devices and often quadrate in shape.

Pig molars are bunodont teeth. More details.

Lophodont

These teeth are identified by the patterns of ridges or lophs of enamel interconnecting the cusps on the crowns. Present in most herbivores, these

patterns of lophs can be a simple ring-like edge, as in mole rats, or a complex arrangement of series of ridges and cross-ridges, as those in odd-toed ungulates (Perissodactyla), such as horses, tapirs and rhinoceroses.



Molars of the Asian elephant (*Elephas;* left), African elephant (*Loxodonta;* center) and Mastodon (right). Elephants are mostly grazers with lophodont molars, whereas mastodons are believed to have been browsers of trees, shrubs and swamp vegetation and their molars were not lophodont. More details.

Lophodont molars have hard and elongated enamel ridges called lophs oriented either along or perpendicular to the dental row. Lophodont molars

are common in herbivores that grind their food thoroughly. Examples include tapirs, manatees, and many rodents.

When two lophs form transverse, often ring-shaped, ridges on a tooth, the arrangement is called bilophodont. This pattern is common in primates, but can also be found in lagomorphs (hare, rabbits, and pikas) and some rodents.

Extreme forms of lophodonty in elephants and some rodents (such as *Otomys*) is known as loxodonty. The African elephant belongs to a genus called *Loxodonta* because of this feature.

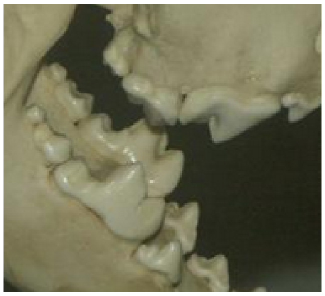
Selenodont

The major cusp in this type of molar is elongated into a crescent-shaped ridge. This is found in most even-toed ungulates (Artiodactyla), such as cows and deer.

Selenodont teeth of a mountain goat. More details.

Secodont

Many carnivorous mammals have enlarged and blade-like teeth especially adapted for slicing and chopping called carnassials. A general term for such blade-like teeth is secodont or plagiaulacoid.



Carnassials of a Eurasian wolf. More details.

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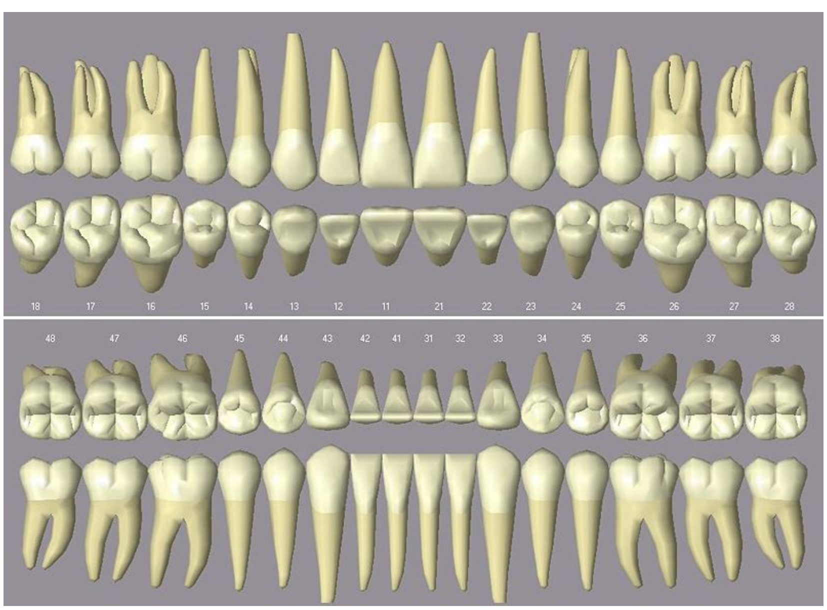
Dental Position and Structure
Humans have a succedaneous dentition in which a set of primary teeth is replaced once by a set of permanent teeth. All teeth are classified as incisor, canine, premolar or molar. For dental notation, quadrants are numbered clockwise starting with the upper right. Teeth are numbered sequentially or medio-distally depending on the notation system in use. Positional terms and surface landmarks are used to refer to specific locations on each tooth. Human teeth have a live dental pulp surrounded by dentin and covered by enamel at the crown and by cementum at the root. It is irrigated by the maxillary artery and innervated by the trigeminal nerve, with sensory receptors for pain, vibration and temperature.

Humans are born without teeth. A primary dentition is formed by age 6, then the milk teeth are gradually replaced by permanent teeth in a process that completes itself around age 12. Additional teeth erupt up to age 20 when the full permanent dentition is completed. In this chapter we will examine the morphology and development of human teeth.

Identification

Nomenclature



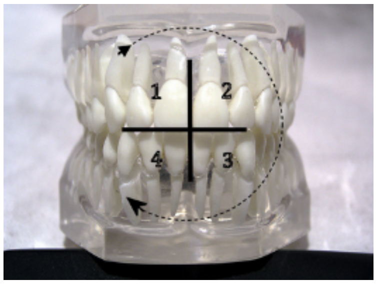
The permanent dentition of humans. Top panel: maxillary teeth in buccal (top) or occlusal (bottom) view. Bottom panel: mandibular teeth in buccal (top) or occlusal (bottom) view. More details.

Teeth are named by their sets and also arch, class, type, and side. Teeth can belong to one of two sets of teeth: primary (also called deciduous or baby) teeth or permanent (adult) teeth. Teeth of the permanent dentition that replace primary teeth are called succedaneous. Teeth are further named based on the arch on which they are found. Maxillary teeth are found in the upper jaw and mandibular teeth are found in the lower jaw. There are four classes of teeth: incisors, canines, premolars, and molars. Premolars are found only among the permanent teeth; there are no deciduous premolars. Incisors are divided into types: central and lateral incisors. There are first and second premolars, and first, second, and third molars. The side of the mouth in which a tooth is found may also be included in the name. For example, a specific name for a tooth may be "permanent maxillary left lateral incisor."

Dental notation

When working with teeth, it is often necessary to have a faster way of referring to a tooth than, for example, saying “permanent mandibular right second molar”. Several systems for dental notation have been proposed and adopted at various times and locations. Among them, the Universal Numbering System, is most widely used in the United States, whereas the the ISO System is most common in the rest of the world. The American Dental Association (ADA) accepts both systems, while the World Dental Federation (FDI) and the World Health Organization (WHO) use the ISO System.

ISO System



The first digit of the code in the ISO system identifies the quadrant where the tooth is located. Quadrants are numbered starting from the right maxillary arch and moving left, down and right. More details.

This system, more specifically ISO 3950, is based on the dental notation system previously adopted by the FDI, which was called the FDI System or the International System. It uses two-digits to identify teeth. The first digit represents a tooth's quadrant and the second digit represents the number of the tooth from the midline of the face. For permanent teeth, the upper right teeth begin with the number 1. The upper left teeth begin with the number 2. The lower left teeth begin with the number 3. The lower right teeth begin with the number 4. For primary teeth, the sequence of first digits is 5, 6, 7, and 8, respectively. When speaking about a certain tooth such as the

permanent maxillary central incisor, the notation is pronounced “one-one” instead of “eleven”.

Dental notation for the maxillary (left) and mandibular (right) permanent teeth in the ISO System. More details (left, right).

Table 1. The ISO System dental notation for permanent and primary teeth.

Permanent Dentition																
Upper right								Upper left								I - incisor C - canine P - premolar M - molar
18	17	16	15	14	13	12	11	21	22	23	24	25	26	27	28	
48	47	46	45	44	43	42	41	31	32	33	34	35	36	37	38	
Lower right								Lower left								
Primary Dentition																
Upper right								Upper left								I - incisor C - canine M - molar
			55	54	53	52	51	61	62	63	64	65				
			85	84	83	82	81	71	72	73	74	75				
Lower right								Lower left								

Universal numbering system

Although it is termed "universal numbering system", it is most commonly used in the United States. It is also called the "American system". The uppercase letters *A* through *T* are used for primary teeth and the numbers 1 - 32 are used for permanent teeth. The tooth designated "1" is the maxillary right third molar ("wisdom tooth") and the count continues along the upper teeth to the left side. Then the count begins at the mandibular left third molar, designated number 17, and continues along the bottom teeth to the right side. Each tooth has a unique **number** or **letter**, allowing for easier use on keyboards.

Table 2. The Universal System dental notation for permanent and primary teeth.

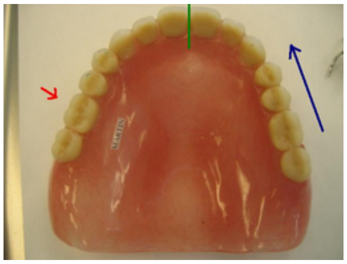
Permanent Dentition																
Upper right								Upper left								I-incisor C-canine P-premolar M-molar
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	
32	31	30	29	28	27	26	25	24	23	22	21	20	19	18	17	
Lower right								Lower left								
Primary Dentition																
Upper right								Upper left								I-incisor C-canine M-molar
			A	B	C	D	E	F	G	H	I	J				
			T	S	R	Q	P	O	N	M	L	K				
Lower right								Lower left								

Primary Dentition – Alternative System																
Upper right								Upper left								I-incisor C-canine M-molar
			1d	2d	3d	4d	5d	6d	7d	8d	9d	10d				
			20d	19d	18d	17d	16d	15d	14d	13d	12d	11d				
Lower right								Lower left								

Directional terms and surfaces

Several specific directional terms are used to locate structures in the mouth and they are commonly used to specify a certain surface on a tooth.

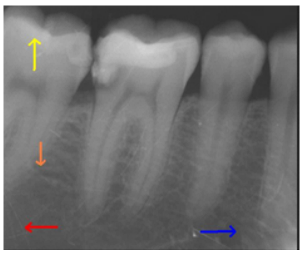
Anterior teeth include the incisives and canines, whereas posterior teeth include the premolars and molars. Structures that are nearest the cheeks or lips are referred to as vestibular or facial, They can also be referred to more specifically as buccal, when found near the cheeks (posterior teeth), or labial, when found near the lips (anterior teeth). On the opposite sides of the teeth, structures are called oral. Their position can also be further refined as lingual for mandibular structures, or palatal for maxillary structures. The term lingual is sometimes used referring to all oral structures but this is confusing because the tongue is generally associated with the mandibular portion of the mouth.



Occlusal view of a maxillary denture. The dental midline (green) separates left from right. The buccal surface (red arrow) of each tooth is opposite to the palatal or lingual surface. Structures and surfaces are mesial toward the midline (blue arrow)

and distal toward the third molar. More details.

The dental midline passes between the central incisors and along the plane of symmetry (sagittal plane) of the face, separating left from right. Mesial refers to a structure that is close to or faces the dental midline. The direction away from the midline toward the furthest teeth is called distal.



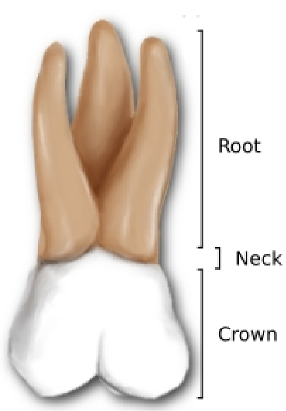
X-ray image of teeth in the lower right quadrant. The arrows point in the following directions: distal (red), mesial (blue), coronal (yellow) and apical (orange). More details.

Along the length of the tooth, structures are called apical when near the apex of the root. Tissues surrounding the apex are called periapical. On the other end, structures found near the crown are called coronal. Alternatively, the terms occlusal, for molars and premolars, or incisal, for incisors and canines, are also used and refer more specifically to the very biting surface. Structures found near the junction of the crown and root are referred to as cervical.

Directional terms are frequently used in pairs, combined into a single word, such as distopalatal or buccocervical. This is commonly used to specify the position of a surface on a tooth, or a direction from which the tooth is seen or approached. Two letter abbreviations can be used in conjunction with these terms, as long as the word is spelled out and followed by the abbreviation on the first time that it appears in the text, for example, distolingual (DL).

External anatomy

Crown, neck and root



Model of the crown,

neck and root of a human maxillary molar. More details.

The crown is the part between the neck of the tooth and the opposing tooth. The crown is completely covered in enamel. The neck is the constricted region that contains the junction between enamel and cementum. The root is the region between the neck of the tooth and the apex of the tooth. The root is covered in cementum.

The crown can be further specified as “anatomical crown” meaning the part covered in enamel or “clinical crown” meaning the part that is visible in the mouth. While they usually correspond to the same, they may differ, for example, when a receded gingiva exposes part of the root of the tooth.

Cusp

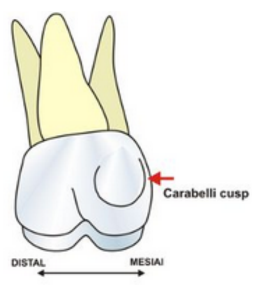
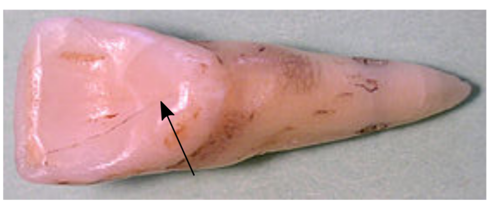


Diagram of maxillary molar with cusp of Carabelli.

More details.

A cusp is an elevation on an occlusal surface of posterior teeth and canines. It contributes to a significant portion of the tooth's surface. Canines have one cusp. Maxillary premolars and the mandibular first premolars usually have two cusps. Mandibular second premolars frequently have three cusps: one buccal and two lingual. Maxillary molars have two buccal cusps and two lingual cusps. A fifth cusp that may form on the maxillary first molar is known as the cusp of Carabelli. Mandibular molars may have five or four cusps.

Cingulum



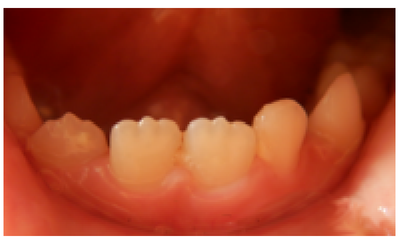
Lingual view of an upper central incisor showing the cingulum (arrow). More details.

A cingulum is a convexity on the cervical third of the lingual surface of anterior teeth. It is frequently identifiable as an inverted V-shaped ridge, and its appearance is comparable to a girdle. All anterior teeth are formed from four developmental lobes. Three are located on the facial side of the tooth, and one on the lingual side. The cingulum forms from this lingual developmental lobe. On lower incisors, the cingulum usually is poorly

developed or absent. Maxillary canines have a large, well-developed cingulum, whereas the cingulum of mandibular canines is smoother and rounded.

Mamelon

Mamelons are usually seen as three small bumps on the incisal edges of newly erupted anterior teeth. They are the remnants of the three labial developmental lobes that form the tooth (the fourth lobe forms the cingulum). Mamelons are mostly visible soon after the eruption of the tooth. Their tips are soon eroded giving place to a straight incisal edge. The presence of mamelons in adults is an indication of misalignment problems that prevent the tooth from being used and worn normally.



Mamelons on the newly-erupted lower central and right lateral incisors of a seven year old boy. The incisal edge of the left lateral incisor is smooth because it is a deciduous tooth that had erupted years before. More details.

Ridge

Ridges are any linear, flat elevations on teeth, and they are named according to their location. The buccal ridge runs cervico-occlusally in approximately the center of the buccal surface of premolars. The labial ridge is one that runs cervico-incisally in approximately the center of the labial surface of canines. The lingual ridge extends from the cingulum to the cusp tip on the lingual surface of most canines. The cervical ridge runs mesiodistally on the cervical third of the buccal surface of the crown. These are found on all primary teeth but only on the permanent molars.

Cusp ridges are ridges that radiate from cusp tips. There are two marginal ridges, mesial and distal, present on all teeth. On anterior teeth, they are located on the mesial and distal borders of the lingual surface; on posterior teeth, they are located on the mesial and distal borders of the occlusal surface. Triangular ridges are those that project from the cusp tips of premolar and molars to the central groove. Transverse ridges are formed by the union of two triangular ridges on posterior teeth. The joining of buccal and lingual triangular ridges is usually named as an example. The oblique ridge is found on the occlusal surfaces of maxillary molars. It is formed by the union of the distal cusp ridge of the mesiolingual cusp and the triangular ridge of the distobuccal cusp. The oblique ridges usually forms the distal boundary of the central fossa.

Groove

Groves are elongated depressions on the surface of the tooth. They are most numerous on posterior teeth and less marked in anterior teeth . Groves that mark the separation between the developmental lobes that formed the tooth are called developmental grooves.

Embrasure

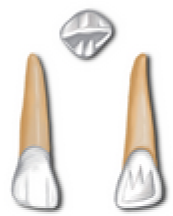
Due to the rounded shapes of teeth, V-shaped spaces form around their points of contact. These spaces are occlusal, cervical, vestibular or lingual to the contact between teeth . They provide a spill way for food to escape during chewing. This prevents food from being forced between teeth, which could result in periodontal pain. The cervical embrasures are normally occupied by the gums, but they can become exposed as large open spaces when the gums receed.

Tooth classes

Incisor

Maxillary central incisor in occlusal (top), labial (left) and oral (right) views. More details.

Each quadrant of the mouth presents a central and a lateral incisor, both in the primary and in the permanent dentition. Their function is shearing or cutting food during biting. Both have a single root and a sharp, straight incisal edge as opposed to round cusps.



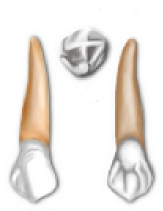
Maxillary lateral incisor in occlusal (top), labial (left) and oral (right) views. More details.

The maxillary central incisors are usually the most visible teeth, because they are centered and anterior to the mandibular incisors. The crown of the permanent maxillary central incisor is the widest (mesiodistally) of the anterior teeth and it is wider than it is tall. It is also less convex than the lateral incisor on its labial surface.

Maxillary central incisors are larger than their mandibular counterparts. This is the most contrasting size difference between teeth in equivalent

positions of the two arches. It provides a strong indication as to which arch a dental cast represents.

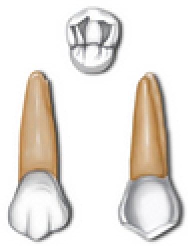
Canine (cuspid)



Maxillary canine in occlusal (top), labial (left) and oral (right) views. More details.

There is a single canine in each quadrant of the primary and of the permanent dentitions. Both maxillary and mandibular canines are the third tooth of the quadrant and separate the premolars from the incisors. Their location and function is intermediate between those of the incisors and premolars. The most common action of human canines is tearing food. There is a single root and cusp on canines. The maxillary canine is the longest tooth in the mouth from root to incisal edge.

Premolar (bicuspid)

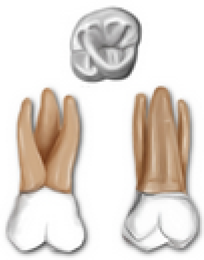


Maxillary first premolar in occlusal (top), labial (left) and oral (right) views. More details.

Each quadrant of the permanent set has 2 premolars that are found distal to the canines and mesial to molars. The first premolar is mesial to the second premolar. There are no deciduous premolars. Instead, the teeth that precede the permanent premolars are the two deciduous molars. The maxillary premolars have two cusps and two roots. Mandibular first premolars have two cusps and one root, which sometimes may be bifurcated. The buccal cusp is well developed but the lingual cusp is small and not active in chewing, making the tooth resemble a small canine. The second mandibular premolar has three cusps. It has a large buccal cusp and two well-developed lingual cusps, which make this tooth resemble a first molar. A less common

two-cusp morphology can also be found, with similar crown dimensions but lack of separation into two lingual cusps.

Molar



Maxillary first molar in occlusal (top), labial (left) and oral (right) views. More details.

Molars are the most posterior teeth in the mouth and the last ones to complete their eruption. Each quadrant has two molars in the primary set and three molars in the permanent set. One or several third molars (wisdom teeth) are commonly missing in modern humans.

Their function of molars is to crush and grind food. The number of cusps varies among the different molars and between people. There are great differences between deciduous and permanent molars, even though their functions are the same. Permanent molars are not preceded by deciduous teeth, because the primary molars are followed by permanent premolars.

Deciduous molar

Smaller than permanent molars in all aspects, deciduous molars are the largest of the primary teeth. They have three to five cusps. They may also have a Cusp of Carabelli, which is most common on the second maxillary molar. Maxillary molars have three roots whereas mandibular ones have two roots.

Permanent maxillary molar

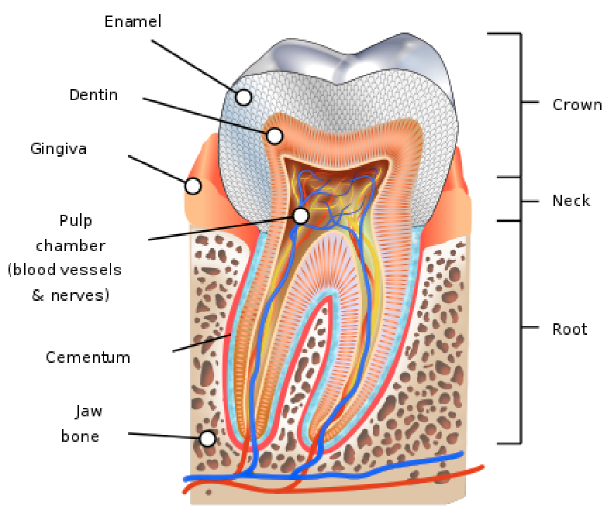
The maxillary first molar has the largest occlusal surface, followed by the second and the third molars. The first molar usually has four cusps: two buccal and two palatal. In many cases there is also a fifth cusp, called the Cusp of Carabelli, located on the mesiolingual aspect of the tooth. The second and third molar usually have four cusps: two buccal and two palatal. Maxillary molars have three roots: two buccal and one lingual.

Mandibular first molar

The mandibular first molar is the reference for occlusion (see chapter 17 Dental Alignment). There are usually five well-developed cusps: two buccal, two lingual and one distal. Second molars most commonly have four cusps: two buccal and two lingual. Mandibular molars most frequently have two roots: mesial and distal.

Internal anatomy

Under the cover of enamel, the bulk of the crown is composed of dentin, which surrounds and protects the pulp chamber of the tooth. The root lacks enamel and is instead covered by a thin layer of a hard tissue called cementum. Dentin composes most of the root forming root canals that contain pulp tissue. A tooth can have a single or multiple roots. The tooth is supported at the root by an attachment apparatus called periodontium. This attachment apparatus connects the tooth to the alveolus of the jaw bone. The entire tooth is enclosed within the jaw bone before the tooth erupts, but after eruption the crown is entirely visible in an anatomically normal and healthy tooth.



Internal anatomy of the tooth. More details.

Enamel

This is the hardest and most highly mineralized substance of the body. It is one of the four major tissues which make up the tooth, along with dentin, cementum, and dental pulp. It is normally visible and it is supported by

underlying dentin. The composition of enamel is mostly mineral (96%), with water and organic material comprising the rest. The normal color of enamel varies from light yellow to grayish white. Enamel is semitranslucent, therefore the color of dentin and any restorative dental material deep to the enamel strongly affects the appearance of a tooth. Enamel varies in thickness over the surface of the tooth and is often thickest at the cusp, up to 2.5mm, and thinnest at its border at the neck of the tooth.

Enamel's primary mineral is hydroxyapatite, which is a form of calcium phosphate. The large amount of minerals in enamel accounts not only for its strength but also for its brittleness. Dentin is less mineralized and less brittle than enamel. Unlike dentin and bone, enamel does not contain collagen fibers. The mains proteins involved in the development of enamel are ameloblastins, amelogenins, enamelins and tuftelins, which help to form a supporting framework. Ameloblasts secrete the enamel layer during tooth development but the mature tissue is acellular (no cells).

Dentin

Dentin is the substance between enamel or cementum and the pulp chamber. It is secreted by the odontoblasts of the dental pulp. This porous, yellow-hued material is made up of 70% inorganic materials, 20% organic materials, and 10% water by weight. Because it is softer than enamel, it decays more rapidly if exposed, but it is normally completely covered in enamel or cementum.

Dentin is a mineralized connective tissue with an organic matrix of collagenous proteins. Dentin has microscopic channels, called dentinal tubules, which radiate outward through the dentin from the pulp cavity to the exterior cementum or enamel border. The diameter of these tubules ranges from 2.5 μm near the pulp, to 1.2 μm in the midportion, and 900 nm near the dentino-enamel junction. Although they may have tiny side-branches, the tubules do not intersect with each other. Their length is dictated by the radius of the tooth. Although the dentin is acellular, the dentinal tubules allow odontoblasts in the pulp cavity to maintain the mineral composition of the dentin through long cytoplasmatic extensions.

Cementum

Cementum is a specialized bone-like substance covering the root of a tooth. It is approximately 45% inorganic material (mainly hydroxyapatite), 33% organic material (mainly collagen) and 22% water. Cementum is excreted by cementoblasts within the root of the tooth and is thickest at the root apex. Its coloration is yellowish and it is softer than dentin and enamel. The main role of cementum is to serve as a medium by which the periodontal ligaments can attach to the tooth for stability. The cementum is acellular (lacks cells) at the cementoenamel junction and cervical portions of the root. The more permeable form of cementum, cellular cementum, covers about one third of the root near the apex.

Dental Pulp

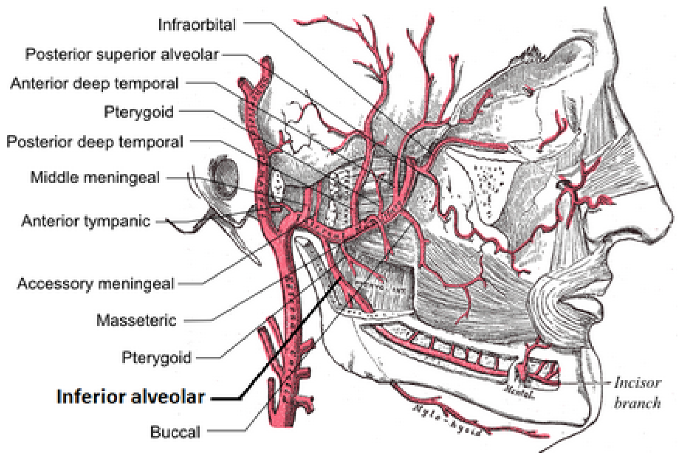
The dental pulp is the central part of the tooth filled with soft connective tissue. This tissue contains blood vessels and nerves that enter the tooth from a hole at the apex of the root (apical foramen). Along the border between the dentin and the pulp are odontoblasts, which form and maintain the dentin. Other cells in the pulp include fibroblasts, preodontoblasts, macrophages and T lymphocytes.

From the central pulp chamber, a pulp horn extends into each root and forms a radicular canal that ends at the apical foramen. Through this foramen, the pulp receives a dental artery and emits a vein. It also receives a dental nerve with sensory but no motor fibers. Arteries and neural plexuses in the jaw bones originate the tiny vessels and nerves that supply each tooth.

Vascularization

Maxillary

The branches of the external carotid artery include the maxillary artery. This artery forms many branches that irrigate muscles of the head. Most anteriorly, the maxillary artery forms the infraorbital artery. The anterior superior alveolar artery branches off from the infraorbital artery and irrigates the upper incisors and canines. The posterior superior alveolar artery (posterior dental artery) originates directly from the maxillary artery and divides into numerous branches to supply the molar and premolar teeth.



Irrigation of the maxillary teeth by the infraorbital and posterior superior alveolar arteries, and of the mandibular teeth by the inferior alveolar artery and its incisor branch. More details.

Mandibular

Mandibular teeth are irrigated by another branch of the maxillary artery, the inferior alveolar artery (inferior dental artery). It descends with the inferior alveolar nerve into the mandibular foramen on the medial surface of the ramus of the mandible. It runs along the mandibular canal inside the bone,

accompanied by the nerve. At the first premolar tooth it divides into two branches, incisor and mental. The incisor branch is continued forward beneath the incisor teeth as far as the middle line, where it anastomoses (fuses) with the artery coming from the opposite side.

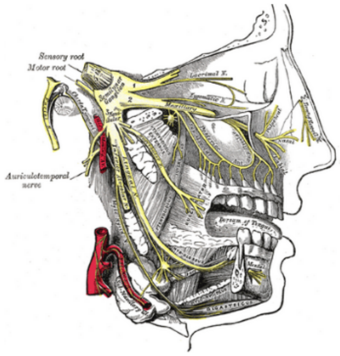
The inferior alveolar artery and its incisor branch during their course through the substance of the bone originate a series of branches which correspond in number to the roots of the teeth: these enter the minute apertures at the extremities of the roots and supply the pulp of the teeth.

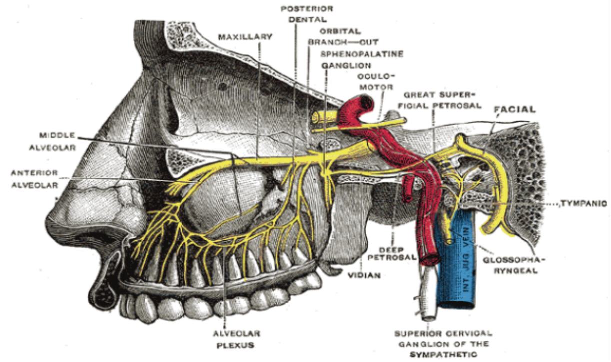
Innervation

Our teeth receive sensory innervation from cranial nerve V, the trigeminal nerve. It has three major branches: ophthalmic, maxillary and mandibular that innervate the face. The maxillary nerve leaves the cranium through the foramen rotundum whereas the mandibular nerve extends through the foramen ovale.

Maxillary

The maxillary branch of the trigeminal nerve receives the sensory input from our teeth. Branches of the maxillary nerve called posterior superior alveolar nerve, middle superior alveolar nerve, and anterior superior alveolar nerve form the superior dental plexus which supplies the upper jaw. These branches are somewhat variable in structure: the middle superior alveolar nerve is sometimes missing, whereas the posterior superior alveolar nerve is most frequently split into a pair of nerves.

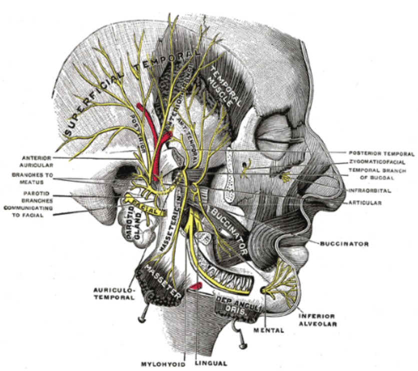




Innervation of the maxillary teeth by the superior dental plexus. More details (left, right).

Mandibular

The mandibular teeth are innervated by the mandibular branch of the trigeminal nerve. The mandibular nerve produces several branches, including the inferior alveolar nerve, which enters the mandibular foramen.



Innervation of the mandibular teeth by the inferior alveolar branch of the

mandibular nerve.
More details.

While in the mandibular canal within the mandible, it supplies the lower teeth (molars and second premolar) with sensory branches that form the inferior dental plexus. Anteriorly, the inferior alveolar nerve originates the mental nerve which exits the mandible via the mental foramen and supplies sensory branches to the chin and lower lip. The inferior alveolar nerve continues anteriorly as the mandibular incisive nerve to innervate the mandibular canines and incisors.

Sensory reception

Pain

The most abundant sensory receptors in a tooth are nociceptors, a class of receptors specialized in conveying pain stimuli. The dental nociceptors are classified as A-fibers or C-fibers. A sharp pain is typically originated at A-fibers reacting to cold or mechanical stimuli, such as cold drinks or toothbrushing. C-fibers are usually involved in long-lasting dull pain produced by inflammation of the pulp. A-fibers tend to be thick and myelinated, which are neuronal traits associated with fast stimulus conduction. C-fibers are usually thin and non-myelinated.

Dental nociceptors are distributed in the entire pulp. They are found near the odontoblasts and they can extend into the dentinal tubules. These nociceptors are found at highest density and they extend furthest into the dentine at the occlusal portion of the dentin-pulp border.

Mechanical stimuli

Mechanoreception inside the teeth seems to be based on responses of odontoblasts in the pulp. When the enamel cover of the tooth is removed or damaged, the peripheral end of the dentinal tubules may be opened, and stimuli in the surrounding medium may produce fluid displacement in the tubules. Stretch-activated potassium channels on the cellular membrane of the odontoblasts are activated, leading the cell to release chemicals that activate adjacent nociceptors.

Outside the tooth, mechanoreceptors are present on the periodontal ligaments. These are collaginous fibers that anchor the root of the tooth to the surrounding alveolar bone. A type of stretch receptor called Ruffini receptor is found on the periodontal ligaments. It has finger-like projections which extend into the surrounding tissue to detect the deformation of collagen fibers. Its role is to respond to accidental movement of the tooth in its socket, such as when you bite into a hard object in your food, and activate a nociceptive reflex that causes immediate relaxation of the muscles of mastication.

Temperature

In addition to acting as mechanoreceptors, the odontoblasts of the pulp can also respond to changes in temperature. Like the thermoreceptors in our skin, odontoblasts have transient receptor potential (TRP) ion channels on their membranes. Many types of TRPs have been described, and each one opens at a certain temperature range. This allows odontoblasts to respond to cold or hot stimulation of the tooth (especially if the enamel cover is removed) and convey the stimulus to the surrounding sensory neurons (nociceptors).

Reflexes

The stimuli transduced by the sensory receptors of the teeth, together with stimuli originating in stretch receptors within the muscles of mastication, are transmitted to the CNS by the trigeminal nerve. They are processed in the spinal trigeminal nucleus at the medulla oblongata. The reticular

formation then transmits them to the thalamus, from where they are conveyed to the primary sensory cortex, allowing us to become aware of the sensation in the tooth.

Our neural system also uses these stimuli to direct immediate reflex responses that do not require our awareness. One class of reflexes involves the use of feedback from the muscle spindles (stretch detectors) in the muscles of mastication to detect the position of the mandible and adjust the contraction of each muscle for stable and effective chewing. This myotatic response goes beyond simply stimulating the muscle when it is stretched. The response is dependent on chewing task, phase of movement, and site of stimulation.

Another type of reflex is triggered by Ruffini receptors in the periodontal ligaments, which signal traumatic displacement of a tooth. When activated, this reflex causes immediate relaxation of the main muscles of mastication. This is thought to be a protective response designed to prevent tooth damage by further biting into a hard object.

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Figure 4 = Table 1.

Figure 5 = Table 2.

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Tooth Formation

Teeth start to develop very early during embryonic life. Each tooth develops in its own bud formed by the dental lamina. Ectoderm forms and enamel organ in which ameloblasts for enamel. The ectomesenchyme originates a dental papilla that forms dentin and pulp, and dental follicle which originates the periodontium. Odontoblasts in the pulp secrete the dentin and maintain it through cellular processes that extend into dentinal tubules. The pulp is irrigated by branches of the maxillary and inferior alveolar arteries. It is innervated by sensory fibers of the maxillary and mandibular branches of the trigeminal nerve. The tooth contains pain receptors and the odontoblasts respond to mechanical and thermal disturbance of the fluid in the dentinal tubules. Roots can complete their development years after the crown. Healthy dental formation requires Ca, P and vitamins A, C and D.

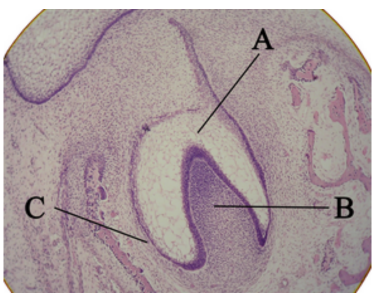
Odontogenesis is the process by which tooth form, grow, and erupt in the mouth. For human teeth to have a healthy oral environment, all parts of the tooth must develop during appropriate stages of fetal development. Primary (baby) teeth start to form between the sixth and eighth week of development, and permanent teeth begin to form in the twentieth week. If teeth do not start to develop at or near these times, they will not develop at all, resulting in hypodontia (missing teeth) or anodontia (no teeth).

Radiograph of lower right molars in different stages of development. More details.

Overview

Watch the animations at https://www.youtube.com/watch?v=t3hR2YGdqWk or https://www.youtube.com/watch?v=wkriancp4kM for a visual introduction to the subject.

The development of a tooth seems to be initiated by a factor within the tissues of the first pharyngeal arch. The tooth germ is an aggregation of cells that eventually forms the tooth. These cells are derived from the ectoderm of the first pharyngeal arch and the ectomesenchyme of the neural crest. The tooth germ is organized into three parts: the enamel organ, the dental papilla and the dental sac or follicle.



Developing tooth bud: A. Enamel organ, B. Dental papilla, C. Dental follicle. More details.

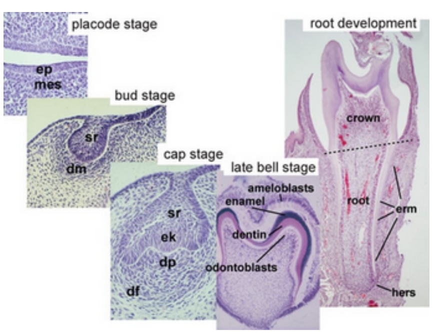
The enamel organ is composed of the outer enamel epithelium, inner enamel epithelium, stellate reticulum and stratum intermedium. These cells give rise to ameloblasts, which produce enamel and become a part of the reduced enamel epithelium (REE) after maturation of the enamel. The location where the outer enamel epithelium and inner enamel epithelium join is called the cervical loop. The growth of cervical loop cells into the

deeper tissues forms Hertwig Epithelial Root Sheath, which determines the root shape of the tooth. During tooth development there are strong similarities between keratinization and amelogenesis. Keratin is also present in epithelial cells of the tooth germ and a thin film of keratin is present covering the enamel on a recently erupted tooth (Nasmyth's membrane or enamel cuticle).

The dental papilla contains cells that develop into odontoblasts, which are dentin-forming cells. Additionally, the junction between the dental papilla and inner enamel epithelium determines the crown shape of a tooth. Mesenchymal cells within the dental papilla are responsible for formation of tooth pulp.

The dental sac or follicle gives rise to three important cells: cementoblasts, osteoblasts, and fibroblasts. Cementoblasts form the cementum of a tooth. Osteoblasts give rise to the alveolar bone around the roots of teeth. Fibroblasts are involved in developing the periodontal ligament which connects teeth to the alveolar bone.

Stages



Stages of tooth development, from dental placode (top left) to maturation (right). Ep, epithelium; mes,

mesenchyme; sr, stellate reticulum; dm; dental mesenchyme; dp, dental papilla; df, dental follicle; ek, enamel knot; erm, epithelial cell rests of malassez; hers, hertwig's epithelial root sheath. More details.

Tooth development is commonly divided into the following stages: initiation stage, bud stage, cap stage, bell stage, and maturation. The staging of tooth development is an attempt to categorize changes that take place along a continuum. It has great didatic value but it is not perfect. It can be difficult to assign a stage to a particular developing tooth when it is passing from one stage to the next.

Initiation Stage

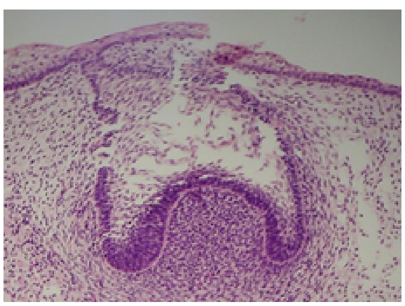
At the beginning of tooth development, two stripes of thickened epithelium called vestibular lamina and the dental lamina can be differentiated at the sites were the teeth will form. The epithelium of the dental lamina is connected to the epithelium lining the mouth and it forms several placodes. Each placode contains the thickened dental lamina and some underlining mesenchyme. It acts as a center of chemical signaling that triggers the development of several teeth. Only one tooth buds out directly from a placode, however. The other teeth that it triggers develop from the primed dental lamina.

Bud stage

The bud stage is characterized by the appearance of a tooth bud without a clear arrangement of cells at the location where the tooth will form. This occurs when epithelial cells of the dental lamina proliferate into the underlying ectomesenchyme of the jaw. Typically, this occurs when the fetus is around 8 weeks old. The tooth bud itself is the group of cells at the periphery of the dental lamina.

Ten tooth buds develop on each arch. These correspond to the 10 primary maxillary and mandibular teeth. Each bud is separated from the ectomesenchyme by a basement membrane. Some ectomesenchymal cells congregate deep to the bud and form a cluster of cells.

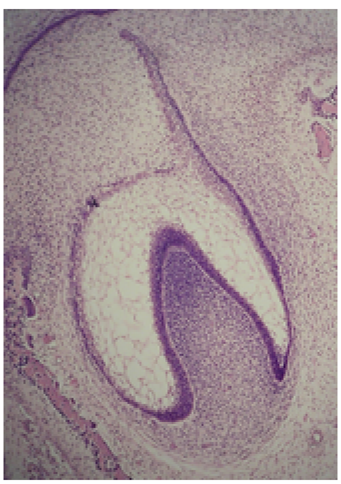
Cap stage



Developing tooth in cap stage. Notice the differentiation of the cells of the dental papilla and follicle in relation to the remaining ectomesenchyme in the picture. More details.

The cap stage is marked by the differentiation of cells. Some ectomesenchymal cells stop producing matrix and form an aggregation of cells called dental papilla. The epithelial portion of the tooth bud grows around the dental papilla, taking on the appearance of a cap, and becomes the enamel organ covering the dental papilla. The closest surrounding ectomesenchymal cells differentiate forming the dental sac (dental follicle). The enamel organ will eventually produce enamel, the dental papilla will produce dentin and pulp, and the dental sac will produce all the supporting structures of a tooth, the periodontium.

Bell stage

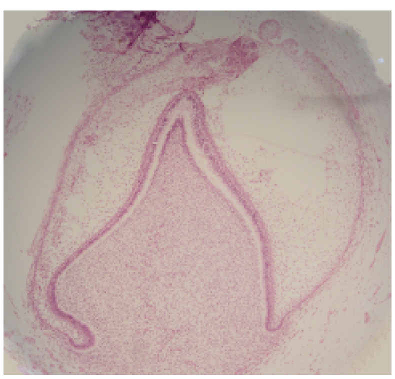


Developing tooth in early bell stage. This stage is marked by the differentiation of the epithelial tissues in the enamel organ

into four layers. More details.

The enamel organ extends further and becomes bell-shaped during this stage. The majority of its cells are called stellate reticulum because of their star-shaped appearance. Cells on the periphery of the enamel organ differentiate into four layers: 1) A layer of cuboidal cells form the periphery of the enamel organ and it is known as the outer enamel epithelium (OEE); 2) Most of the internal volume of the enamel organ is occupied by the stellate epithelium; 3) A layer of columnar cells is found adjacent to the enamel papilla and it is known as the inner enamel epithelium (IEE); 4) Some cells remain between the IEE and the stellate reticulum and are called stratum intermedium.

Other events occur during the bell stage. The dental lamina disintegrates, breaking the epithelial connection between the developing tooth and the epithelium of the oral cavity. The developing tooth is at this point completely surrounded by ectomesenchyme. The two epithelia will not join again until the final eruption of the tooth into the mouth.



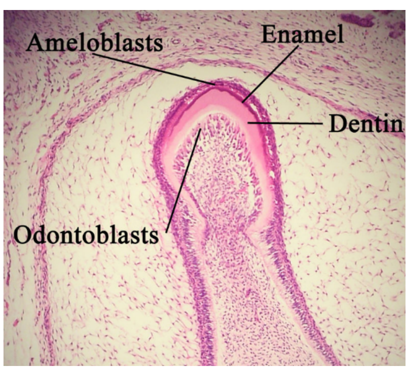
Developing tooth in late bell stage. The connection with the oral

epithelium through the dental lamina has been lost. More details.

The crown of the tooth is shaped during this stage. The chemical signaling that drives the shaping of different tooth types in different tooth buds (ex.: incisors vs. canines) is an area of active research but the mechanism has not yet been fully explained.

Maturation stage

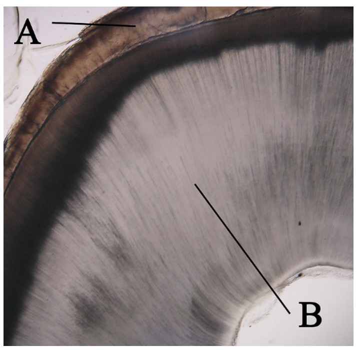
Hard tissues, including enamel and dentin, develop during the crown or maturation stage. In prior stages, all of the IEE cells were dividing to increase the overall size of the tooth bud. At the maturation stage, however, the rate of mitosis is drastically reduced where the cusps of the teeth form. The first mineralized hard tissues form at this location.



Developing tooth in maturation stage. Ameloblasts form enamel while odontoblasts form

dentin. More details.

The IEE cells change in shape from cuboidal to columnar and become preameloblasts. These cells become polarized as their nuclei move closer to the stratum intermedium and away from the dental papilla.



Hard tissues in a cross-section of the crown of a tooth. Notice the tubular appearance of dentin. A: enamel. B: dentin. More details.

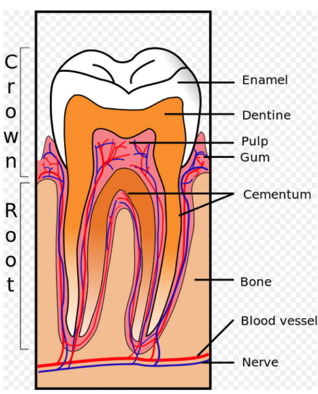
At the dental papilla, the layer of cells adjacent to the IEE increases in size and differentiates into odontoblasts, which are the cells that form dentin. The odontoblasts secrete an organic matrix named predentin towards the enamel organ. As they do so, they congregate at the center of the dental papilla which becomes surrounded by the secreted matrix. Thus, the layer

of dentin grows inward. Cytoplasmic extensions are left behind as the odontoblasts move inward. These form the dentinal tubules, which can be observed in mature teeth.

After dentin formation begins, the cells of the IEE differentiate into ameloblasts and secrete an organic matrix against the dentin. This matrix mineralizes and becomes the initial layer of the tooth's enamel. The continued deposition of enamel pushes the ameloblasts outward. Enamel is therefore deposited in the opposite direction of dentin.

Hard tissue formation

Enamel



Internal anatomy of an erupted mature molar tooth. More details.

Enamel formation is called amelogenesis. It occurs during the maturation stage of tooth development. Amelogenesis itself is divided into three stages:

initiation, secretory and maturation stages. Proteins and an organic matrix form a partially mineralized enamel in the secretory stage; the maturation stage completes enamel mineralization.

During the initiation stage, the formation of predentin induces differentiation in the IEE. Its cells elongate and their nuclei migrate away from the ectomesenchyme forming ameloblasts.

In the secretory stage, ameloblasts release a soft matrix containing enamel proteins for structure. The matrix is then mineralized by the enzyme alkaline phosphatase. This phase occurs around the 3rd or 4th month of pregnancy and it marks the first appearance of enamel in the body. Ameloblasts make enamel where the cusps of the teeth will be located.

In the maturation stage, the ameloblasts transport some of the substances used in enamel formation out of the enamel. Their function changes from enamel production, as occurs in the secretory stage, to transportation of substances. Most of the materials transported in this stage are proteins used to complete mineralization, including amelogenins, ameloblastins, enamelins, and tuftelins. By the end of this stage, the enamel has completed its mineralization.

Newly erupted teeth of both dentitions may be covered by Nasmyth's membrane. This membrane consists of the outer layers of the enamel epithelium, the oral epithelium, and the dental cuticle. The later is a layer of keratin placed by the ameloblasts on the outer surface of the newly formed enamel. Nasmyth's membrane easily picks up stain from food debris. It is shortly worn away by mastication and cleaning.

Dentin

Dentin formation, known as dentinogenesis, is the first identifiable feature in the maturation stage of tooth development and it precedes the formation of enamel. As opposed to enamel, dentin can be produced throughout the live of a tooth. Four types of dentin have been identified: mantle dentin, primary dentin, secondary dentin, and tertiary dentin.

Odontoblasts differentiate from cells of the dental papilla. They begin secreting an organic matrix against the enamel organ. The organic matrix contains collagen fibers with large diameters (0.1–0.2 μm in diameter). The secretion of matrix drives the odontoblasts toward the center of the tooth. They leave behind a cellular extension called odontoblast process. This process promotes the secretion of hydroxyapatite crystals and mineralization of the matrix, which is called mantle dentin grows to about 150 μm thickness.

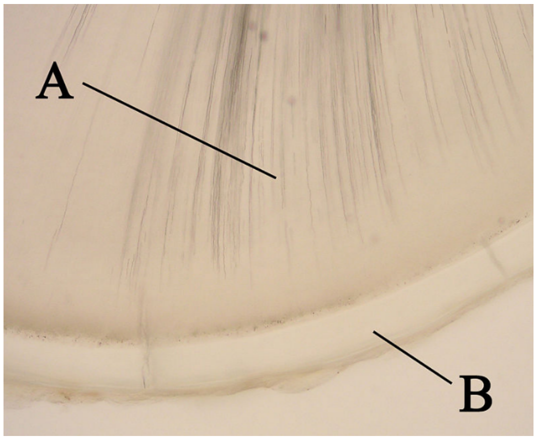
Primary dentin forms through a different process. As odontoblasts mature, they enlarge and become more tightly packed. This reduces the contribution of other materials in the dental papilla to the new matrix. The amount of collagen in the matrix is reduced and the resulting dentin is denser and more mineralized than mantle dentin.

Secondary dentin is formed after root formation is finished and the tooth has erupted. It occurs at a very slow rate, however. The dentin forms faster inside the crown of a tooth. This development continues throughout life and makes the pulp chamber smaller and enclosed in a wider-walled crown in older individuals than in younger ones.

Tertiary dentin is also known as reparative dentin. It involves new, localized and accelerated secretion of dentin. The process is triggered by an external stimulus such as attrition or dental caries.

Cementum

Cementum formation is called cementogenesis and occurs late in the development of teeth. Cementoblasts are the main cells active in cementogenesis. There are two types of cementum: cellular (with cells) and acellular (without cells).



Cross-section of the root of a tooth. Notice the clear, acellular appearance of cementum. A: dentin. B: cementum. More details.

Acellular cementum forms first. The cementoblasts differentiate from follicular cells. They need to contact the cervical edges of the dentin in the enamel organ, but they can only reach there when the tooth is in the maturation stage, after the epithelial cover (Hertwig's Epithelial Root Sheath) of the enamel organ has begun to deteriorate. The cementoblasts secrete fine collagen fibrils along the root surface at right angles before migrating away from the tooth. As the cementoblasts move, more collagen is deposited to lengthen and thicken the bundles of fibers. Other proteins, such as bone sialoprotein and osteocalcin, are also secreted. This forms a cementum matrix rich in proteins and fibers. The fibers deposited along the surface eventually join the forming periodontal ligaments.

Cellular cementum develops after most of the tooth formation is complete and after the tooth starts occluding against a tooth in the opposite arch. This type of cementum forms around the fiber bundles of the periodontal ligaments. The cementoblasts forming cellular cementum become trapped in the cementum they produce. Cellular cementum is usually absent in teeth with one root. In premolars and molars, cellular cementum is found only in the apical 1/3 of the roots.

Human tooth development timeline

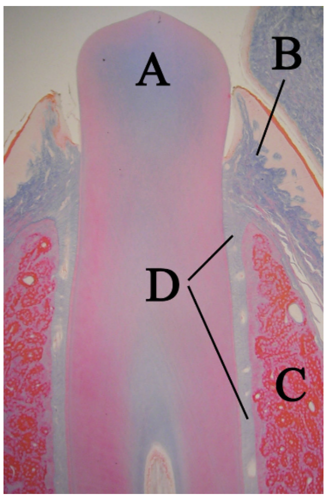
All dental follicles are formed before birth. Their development into erupted teeth, however, follows very different time courses depending on dental set (primary or permanent), class (incisor, canine, etc) or arch.

Table 1. Developmental timeline of human teeth. Times for the initial calcification of primary teeth are for weeks *in utero, while other times are relative to birth*. Wk = weeks; mo = months; yr = years.

	Incisors		Canine	Premolar		Molar		
	Central	Lateral		First	Second	First	Second	Third
Deciduous teeth								
Maxillary								**(* weeks in utero)**
Initial calcification	14 wk*	16 wk*	17 wk*			15 wk*	19 wk*	
Crown completed	1.5 mo	2.5 mo	9 mo			6 mo	11 mo	
Root completed	1.5 yr	2 yr	3.25 yr			2.5 yr	3 yr	
Mandibular								
Initial calcification	14 wk*	16 wk*	17 wk*			15.5 wk *	18 wk*	
Crown completed	2.5 mo	3 mo	9 mo			5.5 mo	10 mo	
Root completed	1.5 yr	1.5 yr	3.25 yr			2.5 yr	3 yr	
Permanent teeth								
Maxillary								
Initial calcification	3–4 mo	10–12 wk	4–5 mo	1.5–1.75 yr	2–2.25 yr	birth	2.5–3 yr	7–9 yr
Crown completed	4–5 yr	4–5 yr	6–7 yr	5–6 yr	6–7 yr	2.5–3 yr	7–8 yr	12–16 yr
Root completed	10 yr	11 yr	13–15 yr	12–13 yr	12–14 yr	9–10 yr	14–16 yr	18–25 yr
Mandibular								
Initial calcification	3–4 mo	3–4 mo	4–5 mo	1.5–2 yr	2.25–2.5 yr	birth	2.5–3 yr	8–10 yr
Crown completed	4–5 yr	4–5 yr	6–7 yr	5–6 yr	6–7 yr	2.5–3 yr	7–8 yr	12–16 yr
Root completed	9 yr	10 yr	12–14 yr	12–13 yr	13–14 yr	9–10 yr	14–15 yr	18–25 yr

Formation of the periodontium

The supporting structure of a tooth is called periodontium. It consists of the cementum, periodontal ligament, gingiva, and alveolar bone. Only the cementum is part of a tooth. Alveolar bone surrounds the roots of teeth to provide support and creates what is commonly called a "socket". Periodontal ligaments connect the alveolar bone to the cementum, and the gingiva is the surrounding soft tissue visible in the mouth.



Main elements of the periodontium in a tooth erupting into the mouth. A. Tooth; B. Gingiva; C. Bone; D. Periodontal ligaments. More details.

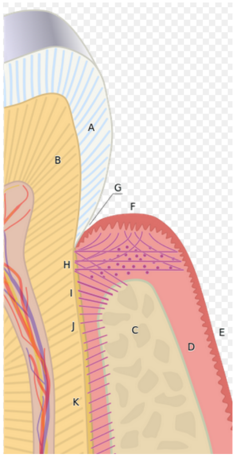
Periodontal ligament

Cells from the dental follicle give rise to the periodontal ligament (PDL). Some details of the process vary between deciduous and permanent teeth and among species of animals. Fibroblasts from the dental follicle secrete collagen and bind it to fibers on the surfaces of adjacent bone and cementum. These attachments develop as the tooth erupts into the mouth. The periodontal ligament is the part of the periodontium that attaches the tooth, at the cementum, to the alveolar bone. It contains fibroblasts, epithelial cells, undifferentiated mesenchymal cells, bone cells and cementum cells. It also contains bundles of collagen fibers arranged in various orientations and attachments.

Five types of fibers attach the cementum at one end to the alveolus at the other end:

- Alveolar crest fibers run from the cervical part of the root to the alveolar bone crest;
- Horizontal fibers run perpendicular to the long axis of the tooth, attaching the cementum to the alveolus;
- Oblique fibers are the most numerous fibers in the periodontal ligament, running obliquely from the cementum into a more coronal point on the bone.
- Apical fibers are found radiating from cementum around the apex of the root to the bone, forming base of the socket or alveolus.
- Interradicular fibers are found between the roots of multirooted teeth.

A sixth type of fiber called transseptal extends over the alveolar bone crest and is embedded in the cementum of adjacent teeth. It forms an interdental ligament. These fibers help to keep all the teeth aligned. Transseptal fibers may be considered part of the gingiva because they do not attach to the alveolus.



Arrangement of the fibers of the periodontium. A. Enamel; B. Dentin; C. Alveolar bone; D,E,F. Gingiva; H. Transseptal fibers; I. Crest fibers; J. Horizontal fibers; K. Oblique fibers. More details.

The occlusion of teeth continually affects the structure of the periodontal ligament. This perpetual maintenance of the periodontal ligament involves the formation of groups of fibers in different orientations, such as horizontal and oblique fibers.

Alveolar bone

As root and cementum formation begin, bone tissue is eroded where space is needed and produced where empty spaces are created. Alveolar osteoblast cells form from the dental follicle. Similar to the formation of primary cementum, collagen fibers are created on the surface nearest the tooth, and they remain there until attaching to periodontal ligaments.

Like any other bone in the human body, alveolar bone is remodeled throughout life. Osteoblasts create bone matrix and osteoclasts erode it, especially if force is placed on a tooth. An area of bone under compressiveforce tends to locally increase the activity of osteoclasts, resulting in bone resorption. This removal of bone tends to reduce the pressure, mitigating the problem. This is common when movement of teeth is attempted through orthodontic treatment using bands, wires, or appliances. An area of bone receiving tension, on the other hand, tends to locally increase the number of osteoblasts, resulting in bone formation. The addition of bone tissue tends to reduce the tension, again mitigating the problem. Teeth therefore can slowly move along the jaw in order to minimize mechanical stresses and balance them across the dentition.

Gingiva

The connection between the gingiva and the tooth is called the dentogingival junction. Hemidesmosomes form the primary epithelial attachment by anchoring the epithelium to small protein filaments on the enamel, remnants of ameloblast activity.

For details on gingival development, please refer to the chapter dedicated to the gums.

Innervation and vascularization

Nerves and blood vessels that run parallel to each other in the body are frequently formed simultaneously in the same location. This is not the case for nerves and blood vessels of teeth, however.

Nerve fibers start to near the tooth during the cap stage of tooth development and grow toward the dental follicle. Once there, the nerves develop around the tooth bud and enter the dental papilla when dentin formation has begun. Nerves never proliferate into the enamel organ.

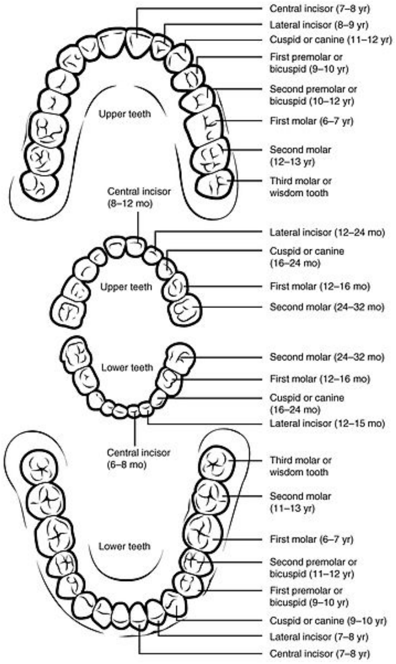
Blood vessels grow in the dental follicle and enter the dental papilla in the cap stage. The vascularization increases until the pulp of the tooth is formed. Throughout life, the amount of pulpal tissue in a tooth decreases, and the blood supply to the tooth decreases with age. The enamel organ is devoid of blood vessels because of its epithelial origin, and the acellular tissues of enamel and dentin do not need nutrients from blood.

Tooth eruption

Tooth eruption is when a tooth ruptures the oral epithelium and becomes visible in the mouth. Osteoclasts erode the bone to create a passage for the tooth follicle, while osteoblasts add alveolar bone to the spaces behind the tooth. Tooth loss is called exfoliation, and it is naturally initiated when a primary tooth is due to be replaced by a permanent one.

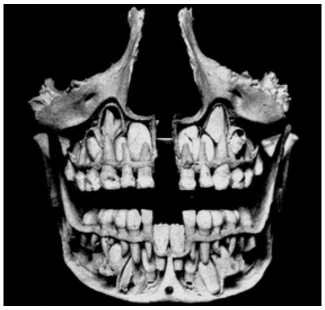
The mechanism that controls the movement of the tooth during eruption is not yet fully understood. Some ideas that have been disproven over time include that the tooth is pushed upward by: (1) growth of the root; (2) growth of the bone around the tooth; (3) vascular pressure; and (4) a cushioned hammock. The cushioned hammock concept postulated that a ligament below a tooth was responsible for eruption. Later, the proposed "ligament" was determined to be merely an artifact of histological technique. Tooth eruption is currently believed to be based on gradual changes to the attachments of the periodontal ligament.

Although tooth eruption occurs at different times for different people, a general eruption timeline exists. Typically, humans have 20 primary (baby) teeth and 32 permanent teeth. Tooth eruption has three stages. The first, known as deciduous dentition stage, occurs when only primary teeth are visible. Once the first permanent tooth erupts into the mouth, the teeth are in the mixed (or transitional) dentition. After the last primary tooth falls out, the teeth are in the permanent dentition.



Eruption times of primary and permanent teeth in humans. More details.

The period of primary dentition starts with the eruption of the mandibular central incisors, usually at eight months of age. It lasts until the first permanent molars appear in the mouth, usually when the child is six years old. The primary teeth typically erupt in the following order: (1) central incisor, (2) lateral incisor, (3) first molar, (4) canine, and (5) second molar. In general, four teeth erupt every six months, mandibular teeth erupt before their maxillary equivalents, and teeth erupt sooner in females than males. While the child has a primary dentition, the tooth buds of permanent teeth develop below the primary teeth, close to the palate or tongue.



Infant's mandibule and maxillary bones with their vestibular walls removed to expose the developing permanent teeth below the roots of primary teeth. More details.

A mixed dentition is formed by both primary and permanent teeth. This period starts when the first permanent molar appears in the mouth, usually at six years of age, and lasts until the last primary tooth is lost, usually at eleven or twelve years. Permanent teeth in the maxilla erupt in a different order from permanent teeth on the mandible.

Order	Maxillary	Mandibular
1	first molar	first molar
2	central incisor	central incisor
3	lateral incisor	lateral incisor
4	first premolar	canine
5	second premolar	first premolar
6	canine	second premolar
7	second molar	second molar
8	third molar	third molar

Table 2: Order of eruption of permanent teeth in each arch.

Since there are no premolars in the primary dentition, the primary molars are replaced by permanent premolars. If any primary teeth are lost before permanent teeth are ready to replace them, some posterior teeth may drift forward and cause space to be lost in the mouth. This may cause crowding when the permanent teeth erupt.

Mandibular teeth of a

seven-year-old, showing primary left lateral incisor and canine, the site of a recently exfoliated primary central incisor, and a fully erupted permanent right central incisor with mamelons. More details.

The permanent dentition stage begins when the last primary tooth is lost, usually at age 11 or 12, and lasts for the rest of a person's life or until all of the teeth are lost (edentulism). During this stage, third molars (also called "wisdom teeth") are frequently extracted because of decay, pain or impactions. The main reasons for tooth loss are decay and periodontal disease.

Nutrition and tooth development

As in other aspects of human growth and development, nutrition has an effect on the developing tooth. Essential nutrients for a healthy tooth include calcium, phosphorus, and vitaminsA, C, and D. Calcium and phosphorus are needed to properly form the hydroxyapatite crystals, and their levels in the blood are maintained by Vitamin D. Vitamin A is necessary for skin growth (formation of keratin), and vitamin C for production of collagen.

Fluoride, although not a nutrient, is incorporated into the hydroxyapatite crystal of a developing tooth and bones. Low levels of fluoride incorporation and fluoride in saliva reduce enamel demineralization and decay. Fluoride ingestion can delay eruption of teeth for as much as a year. This delay has been suggested as the reason for the apparent reduction in decay among the youngest children. Excessive fluoride ingestion during tooth development can lead to a permanent condition known as fluorosis with varying levels of severity.

Mild fluorosis. In its usual mildest form, it appears as opaque white patches on the enamel. More details.

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Variation in Dental Development
Developmental variation in tooth number is not uncommon. One or a few missing teeth is common, with the third molars being the most commonly missing teeth. Extranumerary teeth are less common and normally involve a single tooth between the central incisors or around the maxillary molars. An entire set of teeth can be missing in rare conditions that impair ectodermal differentiation. Teeth that fail to erupt may be harmless, may contract caries or may compromise erupted teeth. In the later cases, management most likely includes their extraction.

Tooth Number

Most vertebrates have dozens of teeth and some variation is usually found around the most common number of teeth within each species. Most humans, for example, have 20 teeth in the primary dentition and 32 in the permanent dentition. One or more third molars are absent in 20–23% of the population, followed in prevalence by missing second premolars and lateral incisors. Without considering the third molars, about 3.5–8.0% of humans lack some other tooth.

The condition of naturally having fewer teeth than the most common number in a species is called hypodontia. The condition mostly results from developmental abnormalities with genetic origin. Selective Tooth Agenesis ("STHAG") has been associated with the genes MSX1, PAX9, LTBP3 and several others associated with the differentiation of the ectoderm. When identical twins lack a tooth, it tends not to be the same one. This indicates that environmental factors, in addition to genetic ones, are involved in the patterning of hypodontia. Common environmental factors include infection, trauma and some drugs.

If many (more than five) teeth are missing the condition is called partial anodontia or oligodontia. Anodontia is the complete absence of primary or permanent teeth. It generally has a genetic basis and involves congenital obstruction of the development of the dental lamina. Partial or complete anodontia frequently accompany major genetic syndromes (ectodermal dysplasia, Down syndrome, Riegar syndrome), particularly those that affect ectodermal development.

Primary dentition of patient with ectodermal displasia, showing missing teeth and conical shaped teeth. The maxillary incisors have been restored with composite material to conceal their conical shape. More details.

Hyperdontia is the development of extra (supernumerary) teeth. They can appear in any area of the dental arch and they are most common in the permanent maxillary arch. It occurs in 1–3% of Caucasians but it is more frequent in Asians. It is more frequent in men than in women. A single extra tooth is most common (86% of cases) and it is most commonly found among the maxillary incisors. Many supernumerary teeth never erupt and not cause any complication. They may, however, delay eruption of nearby teeth or cause other problems which might require their extraction. Dental X-rays are often used to diagnose hyperdontia.

Supernumerary teeth can be classified by shape and by position. The shapes include the following:

- Supplemental (where the tooth has a normal shape for the teeth in that class);
- Tuberculate (also called *barrel shaped*);
- Conical (also called *peg shaped*);
- Compound odontoma (multiple small tooth-like forms);

- Complex odontoma (a disorganized mass of dental tissue)

When classified by position, a supernumerary tooth cay be a:

- Mesiodens. The most common form. A conical tooth that occurs between the maxillary central incisors.
- Paramolar. Extra tooth found buccal or lingual to the molars. Most commonly small, rudimentary and located in the maxillary arch.
- Distomolar. Fourth and fifth molars that form distal to the third molars.
- Accessory tooth. Located anywhere else in the mouth.

Plaster model showing mesiodens and accessory tooth immediately palatal to the right central incisor. Paramolar tooth buccal to the maxillary third molar. More details (left, right).

Like hypodontia, hyperdontia tends to be hereditary with a strong genetic basis modified by environmental factors. It can be found in association with a variety of genetic syndromes that affect ectodermal differentiation.

Timing, Shape and Composition

Most babies are born without teeth. Natal and neonatal teeth involve teeth erupting before birth or sooner than usual. It occurs in about one in 2,500

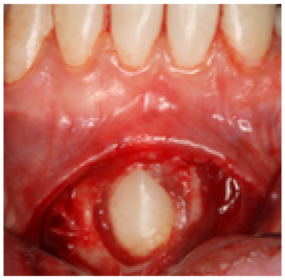
births. Natal teeth are more frequent, approximately three times more common than neonatal teeth. The most common location is the mandibular region of the central incisors. Natal teeth and neonatal teeth can be caused by genetic syndromes.

Tooth development can be delayed by deficient nutrition or endocrine disorders, anemia, renal failure, heavy metal intoxication or tobacco smoke. Enamel hypoplasia is specific to the development of the enamel’s organic matrix and it is clinically visible as enamel defects. It may be caused by nutritional factors, trauma or diseases (celiac disease, chicken pox, congenital syphilis).

Dilaceration is an abnormal bend found on a tooth, and is nearly always associated with trauma that moves the developing tooth bud. As a tooth is forming, a force can move the tooth from its original position, leaving the rest of the tooth to form at an abnormal angle. Cysts or tumors adjacent to a tooth bud are forces known to cause dilaceration, as are primary (baby) teeth pushed by trauma into the gingiva where it moves the tooth bud of the permanent tooth.

Impacted teeth

An impacted tooth fails to erupt into the dental arch within the expected developmental window. It may be retained throughout the individual's lifetime unless extracted or exposed surgically. Teeth may become impacted because of adjacent teeth, dense overlying bone, excessive soft tissue or a genetic abnormality. Most often, the cause of impaction is lack of space in the dental arch. The wisdom teeth (third molars) are most frequently impacted and among them, mandibular molars are more frequently impacted than maxillary ones.



Mandibular canine impacted in the chin. More details.

Erupted teeth that are adjacent to impacted teeth are predisposed to periodontal disease. Since the distal surface of the last teeth are difficult to reach, an impacted third molar frequently results in gingival inflammation around the second molar that can result in periodontitis and compromise the tooth. Impacted third molars frequently contract dental caries when a minor communication is established with the oral cavity.

Pericoronitis is an infection of the soft tissue that covers the crown of an impacted tooth and is usually caused by the normal oralmicrobiota. For most people there exists a balance between the host defenses and the oral micriobiota but if the host defenses are compromised like during minor illness such as a flu or a cold, pericoronitis may result. Pericoronitis can present as a mild infection or severe infection.

Impacted teeth are classified with base on position, orientation and degree of eruption for dicussion of a treatment plan. The most common treatment is extraction.

Figure credits

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The Anatomy of the Gum

The gingiva is the part of the masticatory mucosa that surrounds the teeth and extends to the alveolar mucosa. It is firmly attached to the jaw bone and it has keratinized stratified squamous epithelium. The free gingiva is separated from the tooth by the gingival groove and it it very narrow. Most of the gum is the attached gingiva. The interdental gingiva occupies the cervical embrasures in healthy gums but periodontal disease may cause it to receede. Gingival fibers attach the gums to the neck of the tooth. They also provide structure to the gingiva and connect the free to the attached gingivae.

Maxillary gingiva of a dog. More details.

This chapter is about the gums, which are also called gingivae (singular gingiva). The text will describe the structure of the gingiva and explain its role in periodontal diseases, from gingivitis to abscesses in humans and other mammals.

Structure

The gingiva is part of the masticatory mucosa of the mouth. This mucosa is formed by keratinized stratified squamous epithelium and it covers the dorsum of the tongue and hard palate in addition to forming the gingivae.

The gingiva surrounds the teeth and contacts the alveolar mucosa. More details.

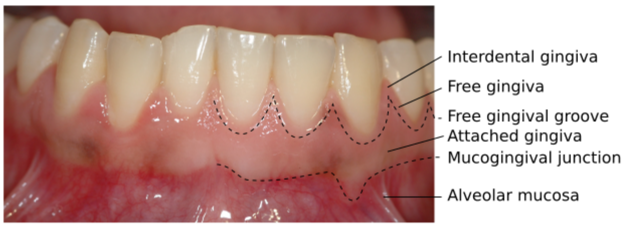
The gingivae surround the teeth and provide a seal around each of them. They are tightly bound to the underlying bone. This helps them resist friction against food during mastication. A healthy gingiva is an effective barrier against external threats to deeper tissue. The gingiva interfaces with the alveolar mucosa which is non-keratinized, darker and much looser as a lining of the oral cavity than the masticatory mucosa (Fig. 2). The line of contact between the gingiva and the alveolar mucosa is called mucogingival junction.

Healthy gums range from light pink to tan depending on the person’s skin color. Accumulation of bacterial plaque, however, can cause inflammation with increased redness together with swelling and a tendency to bleed. A chronic inflammation of the gingiva can affect the deeper tissue of the periodontium and potentially compromise the tooth.

The gingiva is divided anatomically into three areas called free (marginal), attached and interdental gingivae (Fig. 3).

Free gingiva

The free (also called marginal) gingiva is the edge of the gingiva, the portion where it is not attached to the tooth ("free" in this case refers to not attached). It is delimited by the free gingival groove, a shallow depression on the surface of the gum that is visible in about half of the population. This groove is most prominent in mandibular incisors, canines and premolars.



The anatomical structure of the gingiva. More details.

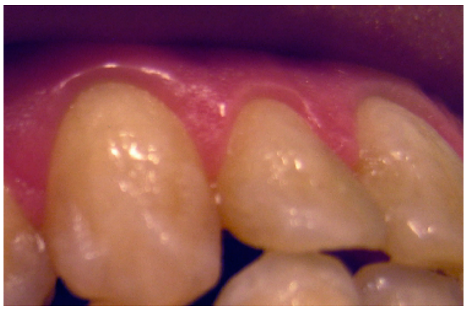
The free gingiva varies in width from 0.5 to 2 mm from the free gingival crest to the attached gingiva. The marginal gingiva has a similar appearance to that of the attached gingiva being slightly more translucent. The free gingiva lacks stippling (textured surface), however, and it is more movable for not being attached the underlying tooth. The free gingiva is stabilized by gingival fibers that have no bony support. The gingival margin, or free gingival crest is the most coronal part of the free gingiva. The gingival sulcus is the space between the free gingiva and the tooth.

Attached gingiva

The attached gingiva is continuous with the free gingiva. It is firm, resilient, and tightly bound to the underlying periosteum of alveolar bone. The facial aspect of the attached gum extends to the relatively loose and movable alveolar mucosa with the limit marked by the mucogingival junction. The attached gingiva frequently presents surface stippling, a roughened texture

that derives from the organization of epithelial ridges and dermal papillae. The degree of stippling is highly variable among individuals.

The attached gingiva is widest in the incisor region (3.5 to 4.5 mm in the maxilla and 3.3 to 3.9 mm in the mandible) and narrowest in the first premolar region (1.9 mm in the maxilla and 1.8 mm in the mandible).



Stippling may be visible as a texture on the surface of the attached gingiva but not of the free gingiva, which is always smooth. More details.

Interdental gingiva

The interdental gingiva (also called interdental papilla) lies between the teeth occupying the gingival embrasure, which is the close proximity space apical to the area of tooth contact. This gingiva tends to have a pyramidal shape in the vestibular and in the lingual aspects with a less extended ridge between them, forming a concave structure.

Gingival fibers

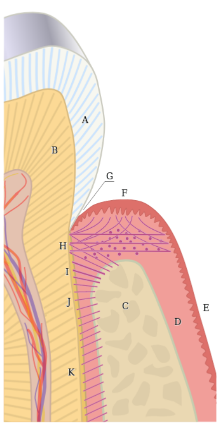
The gingiva is held firmly against the tooth by gingival fibers composed of connective tissue. These fibers differ from those of the periodontal ligament in attaching the tooth to the gingival tissue rather than to the alveolar bone.

Gingival fibers have several roles:

- They connect the base of the free gingiva to the tooth.
- They provide internal structure to the free gingiva to help it withstand the forces of mastication.
- They reinforce the connection between the free and the attached gingivae.

Damage to the gingival fibers promotes periodontitis. With reduced fiber anchorage, the gingival sulcus (labeled G in the Fig. 5) broadens and increases in depth apically. This facilitates the entrance of debris and bacteria between the root of the tooth and the alveolar bone.

Types of gingival fibers



The fibers of the periodontiu

m attach the tooth to the alveolar bone (periodontal ligament) and to the gingiva (gingival fibers). A. Enamel. B. Dentin. C. Alveolar bone. D, Subepithelial connective tissue. E, Oral epithelium. F. Free gingival margin. G. Gingival sulcus. H. Principal gingival fibers. I. Alveolar crest fibers of the periodontal ligament (PDL). J. Horizontal fibers of the PDL. K. Oblique

fibers of the PDL. More details.

Gingival fibers are arranged in three groups:

- **Dentogingival group** - there are three types of fibers within this group:
    - Fibers that extend towards the free margin of the gingiva;
    - Fibers that extend laterally to the outer surface of the gingiva; and
    - Fibers that extend laterally past the alveolar crest, and then apically along the cortex of the alveolar bone.
- **Circular group** - fibers found entirely within the gingiva with no connection to the tooth.
- **Transseptal group** - fibers that make mesiodistal connections between teeth. They are mostly found in the gingiva between teeth but also extend through the gingiva around teeth.

Figure credits

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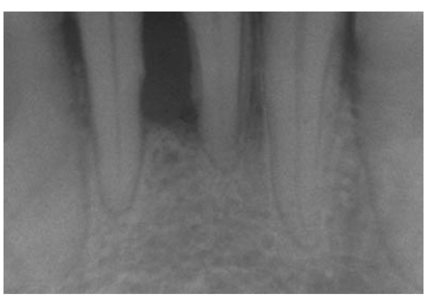
Periodontal Disease

Peritoneal disease starts with gingivitis when microbes in the dental plaque irritate the gums. Without proper oral hygiene, the microbes can infect the gingival tissue and attack the fibers that attach it to the tooth causing gingival recession. They also attack the periodontal ligament, loosening the tooth. Exposure of the roots increase the risk of cavities on the tooth. If the pulp of the tooth is infected and the infection extends down to the roots, it can pass through the apical foramina and infect the gum tissue. The body responds with immune defenses and pus is produced in the area around the apex of the root, forming a dental abscess.

Clinical significance of the gingiva

Improper eating or insufficient oral hygiene can lead to many gum disorders, including gingivitis and periodontitis, which is a major cause of tooth failure. Gingival recession involves an apical retraction of the gingival margin away from the biting (occlusal) surface. It may result from periodontitis or from forceful displacement of the marginal gingiva away from the tooth (harsh brushing or flossing). Gingival retraction exposes the dental neck causing root sensitivity, increasing the risk of caries in the dental root and reducing the area of attachment of the tooth.



Radiograph showing significant bone loss between the two roots of a tooth (black region). The alveolar bone has

receded at the site of infection, weakening the support of the tooth. More details.

Periodontal disease

This is actually not one but a set of inflammatory diseases affecting the tissues that surround the tooth. It involves progressive loss of the alveolar bone around the teeth. If left untreated, it can lead to loosening and subsequent loss of teeth.

Periodontal disease is caused by microorganisms that adhere to the tooth's surfaces along with an over-aggressive immune response against these microorganisms. A diagnosis is reached through inspection the gingivae and radiographs to determine the amount of bone loss around the teeth.

Classification

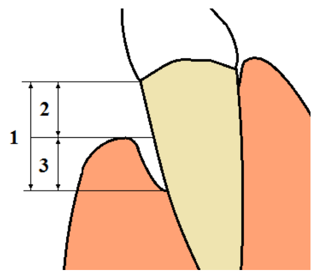
The 1999 classification system for periodontal diseases listed seven categories:

1. Gingivitis. Irritation and inflamation of the gingiva.
2. Chronic periodontitis. Inflammation with slow detachment from tooth and bone loss.
3. Aggressive periodontitis. Inflammation with rapid detachment from tooth and bone loss.
4. Periodontitis as a manifestation of systemic disease. Gingival inflammation caused by conditions of the heart, respiratory system or diabetes.
5. Necrotizing ulcerative gingivitis/periodontitis. Death of gingival tissues, periodontal ligament and alveolar bone, usually linked to

systemic diseases.
6. Abscesses of the periodontium
7. Combined periodontic-endodontic lesions

The severity of disease is assessed with base on the amount of gingival retraction and depth of the gingival sulcus. These determine the area of tooth surface over which periodontal ligament fibers have been lost. The disease can be:

- Mild: 1–2 mm of attachment loss
- Moderate: 3–4 mm of attachment loss
- Severe: ≥ 5 mm of attachment loss



Determination of the clinical attachment loss of a tooth. The total loss of attachment (1) includes the amount of gingival recession (2) and the depth of the gingival

sulcus (3).
More details.

Signs and symptoms

Symptoms may include:

- Redness or bleeding of gums while brushing teeth, using dental floss or biting into hard food (e.g., apples)
- Gum swelling that recurs
- Halitosis (bad breath) or a persistent metallic taste in the mouth
- Gingival recession
- Deep pockets between the teeth and the gums
- Loose teeth

Gingival inflammation and bone loss are largely painless, so people may underestimate the importance of the symptoms of periodontitis and allow the condition to develop to an advanced stage before seeking treatment.

Causes

The primary cause of periodontal disease is poor or ineffective oral hygiene, which leads to the accumulation of a mycotic and bacterial matrix at the gum line, called dental plaque. Other contributors are poor nutrition and underlying medical issues such as diabetes. Smoking also increases the occurrence of periodontitis and may hinder its treatment. Genetic predisposition also influences the risk of a person developing the disease.

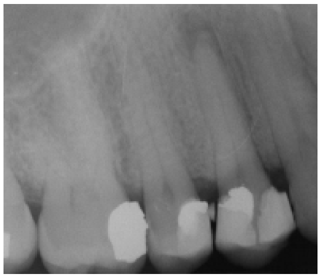
Progression

As dental plaque accumulates on the tooth near and below the gums, its microbial composition changes from a dominance by *Streptococcus* to a

dominance by *Actinomyces*. The gingiva becomes irritated and inflamed, a condition called gingivitis. A person can have gingivitis for years and the condition may not progress. When the microorganisms in plaque start attacking the periodontal ligament, the condition changes to periodontitis. The gingiva tends to bleed and a predominantly gram-negative bacterial flora is established.

Top: typical presentation of gingivitis. Bottom: healthy gingiva. More details.

If left undisturbed, microbial plaque calcifies to form calculus (tartar). Calculus must be removed to prevent damage to the gingival fibers, which is when gingivitis develops into periodontitis. The gingiva progressively separates from the tooth. This widens the gingival sulcus which becomes a deep periodontal pocket. Microorganisms colonize the periodontal pockets and cause further inflammation in the gum tissues with progressive bone loss.



Filling materials that exceed the natural contours of restored teeth are called "overhangs". They trap microbial plaque and can lead to localized periodontitis. More details.

Prevention

Oral hygiene measures to prevent periodontal disease include:

- Brushing and flossing properly to physically remove bacteria and fungi
- Using an antiseptic Chlorhexidine gluconate-based mouthwash.
- Regular dental check-ups and professional teeth cleaning.

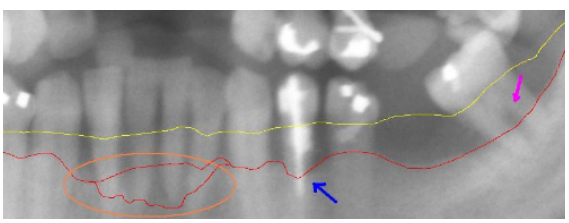
Dental hygienists and dentists use special instruments to remove plaque beyond the reach of toothbrushes and floss. After professional cleaning,

microbial plaque growth tends regress. The patient's daily oral hygiene routine is complementary, however, to professional cleaning.

Treatment

Periodontal treatment starts with establishing a routine of brushing twice a day and flossing once. Removal of microbial plaque and calculus may involve mechanical cleaning below the gumline in a procedure called scaling and root planing. This may require multiple visits and local anesthesia.

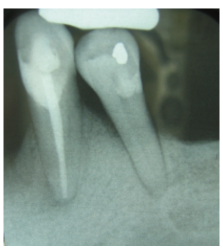
Nonsurgical scaling and root planing are usually successful if the periodontal pockets are shallower than 4-5 mm (0.16–0.20 in). The need for further treatment is determined through monitoring of gingival inflammation. Pocket depths greater than 5-6 mm (0.20–0.24 in) with bleeding upon probing indicate an active disease with further bone loss over time.



Jaw bone resoption due to periodontal disease. Yellow line: Original gum line. Red line: Current gum line. Pink arrow: exposed bifurcation of the molar roots. Blue arrow: loose tooth with > 80% attachment loss. Orange circle: Extensive bone loss and demineralization of

existing bone at incisors.
More details.

Surgery may be needed to stop progressive bone loss and regenerate lost bone. The goal is complete calculus removal and correction of bony irregularities which have resulted from the disease process to reduce pockets as much as possible. In flap surgery, the gum is detached from the tooth for complete removal of tartar. Sutures are used to position the gum back into place until the tissue reattaches to the tooth. In more advanced cases, bone and tissue grafts may be required. These involve the placement of synthetic or natural tissues in the area of tissue loss. The transferred material is taken from another part of the patients body.



Radiography of the lower left first premolar and canine, exhibiting severe bone loss. The neighboring teeth were lost. More details.

Other animals

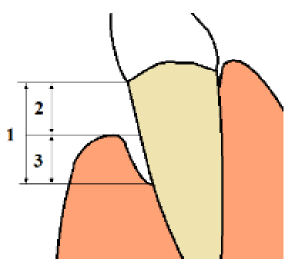
Periodontal disease is the most common disease found in dogs. It affects more than 80% of dogs aged three years or older. Its prevalence increases with age, but it is less common in large than in small animals. Systemic disease may develop because the gums are very vascular (have a good blood supply). The blood stream transports these anaerobic micro-organisms to the kidneys and liver, the organs that are most commonly damaged. They may also attack the heart valves and lungs.

Gingival recession

It is the exposure in the roots of the teeth caused by a loss of gum tissue and/or retraction of the gingival margin from the crown of the teeth.

The main causes are:

- Periodontal disease.
- Overaggressive brushing or flossing.
- Genetic predisposition through fragile or insufficient gingival tissue.
- Dipping tobacco, which weakens the mucous membrane lining in the mouth.



Characterization of gingival recession. 1. Total loss of attachment is

the sum of 2. Gingival recession and 3. Probing depth. More details.

Gum recession is a common problem in adults over the age of 40, but it may also occur in adolescents or children. It occurs with or without a decrease in crown-to-root ratio, which indicates recession of the alveolar bone. In most cases, the condition progresses gradually over the years and patients tend not to notice the recession. It may remain undetected until severe symptoms start to occur.

Gingival recession, most noticeable in the right mandibular central incisor. More details.

Elimination of the cause of gingival recession is frequently enough to resolve it. In advanced cases, however, soft-tissue graft surgery may be used to create more gingiva. Depending on the extent and shape of the gum recession, it can be regenerated with new gum tissue using a variety of grafting procedures. These procedures are typically conducted under local anesthesia. The graft may be a:

- Pedicle graft. Repositioning of adjacent gum tissue to cover the recession.
- Free gingival graft. A thin layer of skin from the palatal gingiva.
- Subepithelial connective tissue graft. Tissue removed deeper in the palate.
- Acellular dermal matrix. Processed skin from a human donor.

Receded gingiva near maxillary lateral incisor, canine and first premolar before grafting, immediately after and at the end of the treatment. More details (left, center, right).

Healing from such procedures requires 2–4 weeks. The new tissue may need some adjustment for improved results. Nearly complete coverage of the recession area is achievable, especially in cases that do not involve alveolar bone loss.

Acute Necrotizing Ulcerative Gingivitis

Colloquially known as trench mouth, this is a common, non-contagious infection of the gums with sudden onset. The main features are painful bleeding gums and ulceration of inter-dental papillae. This disease normally develops from the non-acute form which has milder symptoms. The name "trench mouth" arose during World War I as many soldiers developed the disease, probably because of poor conditions and extreme psychological stress.

Mild acute necrotizing ulcerative gingivitis at the typical site on the gums of the lower front teeth. More details.

The cause is mostly anaerobic bacteria, including fusobacteria and spirochete species. Predisposing factors include poor oral hygiene, smoking, malnutrition, psychological stress and immunosuppression. When the attachments of the teeth to the bone are involved, the disease is called necrotizing ulcerative peritonitis. Treatment is by debridement (removal of dead and infected tissue) and antibiotics in the acute phase, and improving oral hygiene to prevent recurrence. Although the condition has a rapid onset and is debilitating, it can usually be resolved quickly without further complications.

Dental abscess

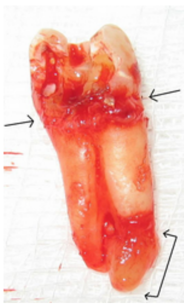
A dental abscess (dentoalveolar abscess, tooth abscess or root abscess), is a localized collection of pus associated with a tooth. The most common type of dental abscess is a periapical abscess and the second most common is a periodontal abscess.

Periapical abscess

It is usually caused by a bacterial infection in the soft, often dead, pulp of the tooth. The infection may derive from tooth decay, a broken tooth or extensive periodontal disease. A failed root canal treatment may also create an abscess.

A periapical abscess in a decayed tooth with a dead pulp. It is draining pus into the mouth via an intraoral sinus (gumboil) visible on the vestibular aspect of the gingiva. More details.

A dental abscess usually produces increased pressure inside the pulp chamber, which leads to a continuous pain that may be described as extreme, sharp, or throbbing. The area may be swollen and sensitive to touch. Adding pressure or warmth on the tooth may induce extreme pain. Swelling may be present at either the base of the tooth, the gum, and/or the cheek. In some cases, a tooth abscess may perforate bone and start draining into the surrounding tissues creating local facial swelling. The closest lymph nodes in the neck may become swollen in response to the infection.



Maxillary right second premolar after extraction. The top arrows point to the cementoenamel junction separating the crown (in this case, heavily decayed) from the roots. The bottom (double) arrow shows the extent of the abscess that surrounds the

apex of the palatal root. More details.

Treatment

Successful treatment of a dental abscess centers on the reduction and elimination of the offending organisms. If the tooth can be restored, root canal therapy is performed. Non-restorable teeth must be extracted and the infected tissues removed by curettage of all apical soft tissue. The infection is also treated with drainage and antibiotics.

If left untreated, a severe tooth abscess may become large enough to perforate the jaw bone and spread either internally or externally. External drainage may begin as a boil which bursts allowing pus to drain from the abscess intraorally (usually through the gum) or extraorally. Chronic drainage will allow an epithelial lining to form in this communication establishing a pus draining canal called fistula. Sometimes this type of drainage will relieve some of the painful symptoms associated with the pressure buit up in the pulp chamber.

Internal drainage is more dangerous as the growing infection affects the tissues surrounding it. The infection can cause severe complications requiring immediate hospitalization if it spreads into the mediastinum where it can affect vital organs such as the heart. Another complication is a risk of infection of the blood (septicemia), which is a life-threatening condition.

Periodontal abscess

A periodontal abscess (lateral abscess or parietal abscess) is a type of dental abscess that is localized within the tissues of the periodontium. It occurs alongside a living tooth, therefore the infection does not originate in a dead

tooth, like in a periapical abscess. Periodontal abscesses are acutebacterial infections classified primarily by location.

A periodontal abscess between the lower left canine and first premolar. More details.

A periodontal abscess most commonly occurs as a complication of advanced periodontal disease. An inflammatory response occurs if bacteria invade and multiply within the soft tissue of the gingival sulcus and periodontal pocket. A pus-filled abscess forms when the immune system responds and attempts to isolate the infection from spreading. Communication with the oral environment is usually maintained via the opening of the periodontal pocket.

The main symptom is pain, which can be deep and throbbing. The closest tooth may feel raised and prominent in the bite and it may become mobile due to destruction of the periodontal ligament and alveolar bone by the infection. When pus forms, the pressure increases, with increasing pain, until it spontaneously drains and relieves the pain. When pus drains into the mouth, a bad taste and smell are perceived. Usually drainage occurs via the periodontal pocket, or else the infection may spread into the surrounding tissues.

Periodontal abscesses may be difficult to distinguish from periapical abscesses. This distinction is important because while root canal therapy is

the main component in the treatment of periapical abscess, it may be unnecessary in a periodontal abscess.

The treatment of a periodontal abscess involves pain relief and control of the infection through drainage and antibiotics. The pulp of the closest tooth is usually alive and the tooth can be maintained throughout the treatment. Sometimes the periodontal support is significantly compromised, however, and extraction or root canal therapy may be considered.

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Dental Plaque
Saliva contains glycoproteins that form a protective pellicle on the crown of each tooth. Microorganisms in saliva bind the the pellicle and form a biofilm called plaque. Most of them ferment carbohydrates in the mouth and form lactic acid. Which can demineralize the enamel. They also secrete proteolytic enzymes that cause periodontal disease. The pellicle with plaque is mechanically removed during brushing and flossing. If proper cleaning is not done, multiple layers of plaque accumulate and make it more difficult to remove. It later mineralizes forming calculus which has to be removed with scalers at the clinic.

The oral environment

Our teeth are moistened with saliva produced by various salivary glands in the mouth. Healthy saliva has a neutral pH and and electrolyte composition that resembles that of plasma with an increased abundance of phosphate and a few other ions. It also contains larger molecules that form mucus, enzymes, antimicrobials and other substances. Among those, some glycoproteins can bind to the exposed surface of enamel. They form a protective film, called dental pellicle, attached to the crown of each tooth. The pellicle is removed with tooth brushing but it forms again moments after the clean tooth makes contact with saliva.

Human saliva is also populated by microorganisms, including dozens of species of bacteria, fungi and archea. Most of them ferment dietary sugars and produce lactic acid. They can bind to the glycoproteins of the pellicle and remain attached to the tooth.

Plaque formation

When microorganisms grow attached to a surface, they may also secrete a sticky extracellular matrix that further stabilizes them in place. This forms a biofilm, a thin layer of microorganisms + extracellular matrix. Dental plaque is biofilm that forms on the surfaces of the crown , along the gumline, or within the gingival sulci.

The bulk of the microorganisms that form the biofilm are *Strepcoccus mutans*, *Fusobacterium* and *Actinomyces*. *Streptococcus* and other anaerobes are the initial colonisers of the pellicle and play a major role in the establishment of the early biofilm community. As more microbes attach and secrete matrix, the plaque becomes thicker. The substances secreted by them gradually alter the chemical environment within the plaque and this favors the establishment of new types of microorganisms, called the later colonizers.

The bacterial equilibrium position varies at different stages of formation. Below is a summary of the bacteria that may be present during the phases of plaque maturation:

- Early biofilm: primarily Gram-positive cocci
- Older biofilm (3–4 days): increased numbers of filaments and fusiforms
- 4–9 days undisturbed: more complex flora with rods, filamentous forms
- 7–14 days: *Vibrio* species, spirochetes, more Gram-negative organisms[9]

Early colonizers

Most genera listed below include multiple species that form plaque.

- *Streptococcus (60-90% of bacteria in plaque)*
- *Eikenella*
- *Haemophilus*
- *Prevotella*
- *Priopionibacterium*
- *Capnocytophaga*

Late colonizers

- *Actinomyces*

- *Prevotella*
- *Eubacterium*
- *Treponema*
- *Porphyromonas*

Fusobacterium is another very common group of colonizers that appears between the early and late colonisers, linking them together.

Environment

The warm and moist environment of the mouth and the presence of teeth, makes a good environment for growth and development of dental plaque. Teeth make great settlement surfaces for the biofilm. Unlike other parts of the body, tooth surfaces are firm and non shedding. The main ecological factors that contribute to plaque formation are pH, saliva, temperature and availability of oxygen. The normal pH of saliva is neutral and plaque flourishes at pH 6.7 to 8.3. Variation in pH within the mouth favors the development of specific types of microorganisms in plaque. Saliva acts as a buffer maintaining the pH in the mouth between 6 and 7. The normal temperature of the mouth ranges between 35 °C and 36 °C, and a two-degree change has been shown to drastically shift the dominant species in the plaque. Oxidizing reactions are carried out by aerobic bacteria. Their metabolism influences the oxygen levels in plaque and affects the composition of its microbial community.

The microorganisms in plaque are normally unable to harm the teeth. They attach to the pellicle and grow at a moderate speed forming a thin plaque. The lactic acid that they secrete diffuses easily into the saliva where it is buffered and it does not affect the enamel which is protected by the pellicle. Most of the cover of pellicle and plaque is removed daily at each event of tooth brushing and flossing. Plaque is therefore present most of the time, but is it prevented from growing thick.

Enamel demineralization and remineralization

The hydroxyapatite crystals $Ca5(PO4)3(OH)$ in enamel are influenced by the pH at the pellicle and the concentrations of of Ca^{++} and $PO4^{---}$ in saliva. Low pH stimulates dissolution of the hydroxyapatite crystals which leads to demineralization of the enamel. At high pH, calcium, phosphate and hydroxyl groups from saliva crystalize into hydroxyapatite, remineralizing the enamel.

The teeth can be protected further by exposure to fluoride in saliva. Fluoride forms fluorapatite which is incorporated into the dental enamel. Fluoride reduces the rate of tooth enamel demineralization and increases the rate of remineralization of teeth.

This dynamic balance between demineralization and remineralization of enamel allow teeth to recover from minor acidic attacks by plaque microorganisms. Failure to remove plaque by regular tooth-brushing, however, allows plaque to proliferate unchecked. With the build up in a thick layer, plaque can become difficult to remove and it can harm the tooth and the gingiva, causing various dental diseases.

Top: Typical case of extensive plaque growth along the dentogingival margin accompanied by gingivitis. Bottom: Healthy gingiva 9

days after cleaning.
More details.

Plaque build-up and consequences

The first kind of plaque to form after the teeth are brush is supragingival biofilm, which is a dental plaque that forms above the gingiva. It is most common between the teeth, in the pits and grooves of the teeth and along the gums. It is rich in aerobic bacteria but if allowed to grow thick, anaerobic bacteria may dominate its composition.

Heavy plaque growth on teeth with inadequate hygiene.
More details.

Plaque located under the gums is called a subgingival biofilm. It follows the formation of the supragingival biofilm which grows along the dentogingival attachment line until it manages to bypass it. The subgingival biofilm is mostly made of anaerobic bacteria. As this plaque attaches in a pocket under the gums, it is less exposed to oxygen.

Gingivitis is the most common result of plaque build-up around the gingival tissues (see chapter 14 Gingiva). The bacteria found in the biofilm secrete

acids and proteolytic enzymes that cause a localized inflammation of the tissue. This is characterized by a red, puffy appearance of the gums and bleeding during brushing or flossing. Gingivitis due to plaque can be resolved by removal of the plaque. If left for an extended period of time, however, the inflammation may begin to affect the periodontal ligament, in a progression referred to as periodontitis.

In periodontitis, bacteria in plaque release enzymes that attack not only the collagen but also the bone. At the same time, osteoclasts in the bone erode it to prevent further infection. This can be treated with brushing and cleaning in between the teeth as well as with surgical debridement (removal of decayed tissue).

Caries is an infectious disease caused primarily by *Streptococcus mutans*, characterized by acid demineralization of the enamel and deeper dental tissue. When the plaque becomes very thick, saliva is unable to penetrate and cannot neutralize the acid produced by the bacteria. These acids then lead to demineralization of the tooth surface.

Detection of plaque build-up

There are two main methods of detecting dental plaque in the oral cavity: visually or through the application of a disclosing gel or tablet.

Dental plaque may present as a yellow, tan or brown stain on the tooth. It can be detected thorough contact as a rough surface and it collects in the instrument if the tooth is scraped. The most common areas where plaque is found is between the teeth and along the cervical margins.

Disclosing agents are applied to the teeth and stain the tooth with one or multiple colors to indicate the amount, location and age of plaque build-up. Clean surfaces of the teeth do not retain the disclosant after the mouth is rinsed, but surfaces covered in plaque do. Plaque disclosing agents are available for use at home or in the dental clinic. These gels provide a visual aid in the management of dental plaque.

Disclosing tablets used to indicate surfaces of increased growth of plaque. These are most commonly areas of ineffective brushing. Their disclosure allows the patient to adjust the oral hygiene routine in order to avoid complications. More details.

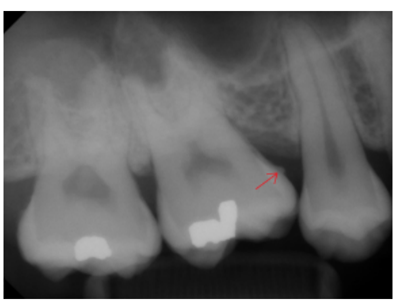
Calculus (tartar)

Calculus is a form of hardened dental plaque. It is caused by precipitation of minerals from saliva in plaque on the teeth. This process of precipitation kills most bacteria within dental plaque, but the rough and hardened surface that is formed provides an ideal surface for further plaque formation. Calculus buildup compromises the health of the gingiva (gums) and teeth.

Heavy staining and calculus deposits exhibited on the lingual surface of the mandibularanterior teeth, along the gumline.

Calculus deposits on inferior incisors. More details.

Like plaque, calculus can be supragingival or subgingival. It should be removed mechanically but brushing and flossing are not effective because it is more firmly attached to the tooth than plaque. Calculus buildup has to be removed at the clinic with dental hand instruments or with an ultrasonic scaler.



Localized calculus deposit on x-ray image. More details.

Calculus is composed of about 50% inorganic (minerals) and 50% organic (cellular and extracellular matrix) components. The mineral part consists of various forms of calcium phosphate crystals. The organic component is approximately 85% microorganisms and 15% extracellular matrix. The cells are primarily bacterial, but also include at least one species of archaea (*Methanobrevibacter oralis*) and several species of yeast (e.g., *Candida albicans*). The organic extracellular matrix in calculus consists primarily of proteins and lipids (fatty acids, triglycerides, glycolipids, and phospholipids).

Plaque and calculus in animals

Calculus formation in animals is less well studied than in humans, but it is known to form in a wide range of species. Domestic pets, such as dogs and cats, frequently accumulate large calculus deposits. Grazing animals rarely form thick deposits and instead tend to form thin calculus deposits that often have a metallic or opalescent sheen. In some animals, calculus can be confused with crown cementum. The entire tooth is covered by cementum which is gradually worn away through abrasion, but remnants of it may be visible in the cervical region of the tooth.

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Caries
The acid produced by bacteria in plaque through lactic fermentation causes gradual demineralization of the enamel. As it progresses deeper, the infection forms a cavity and the structural damage cannot be reversed anymore. Pain starts when the infection reaches the dentin. The pulp reacts making the dentin sclerotic at the site of the infection and this may stop the pain temporarily. The pulp also responds producing tertiary dentin. Infection of the pulp causes pulpitis and can produce intense pain. The infection can extend through the roots and form an abscess in the jaw bone.

Caries (dental cavity, tooth decay) is a breakdown of teeth caused by bacteria. Symptoms include pain and difficulty with eating. Complications may include inflammation of the tissue around the tooth, tooth loss, and infection or abscess formation.

Destruction of a tooth by dental caries. More details.

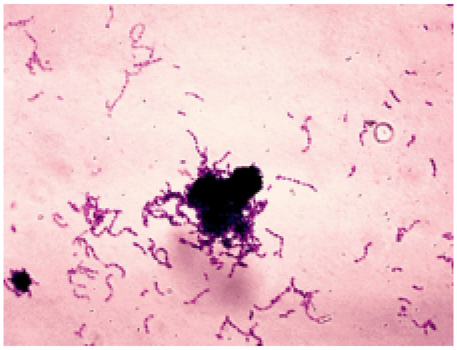
Cause

The cause of caries is acid from bacteria in dental plaque dissolving the hard tissues of the teeth (enamel, dentin and cementum). The acid is produced by the bacteria when they ferment food debris or sugar on the tooth surface. The mouth contains a wide variety of microorganisms but only a few bacteria are believed to cause dental caries infecting the enamel. *Streptococcus mutans* and *Lactobacillus* species among them.

[link]

“Stephan curve", showing sudden decrease in plaque pH following glucose rinse, which returns to normal after 30–60 min. They yellow aread indicates demineralization of dental hard tissues below pH 5.5. More details .

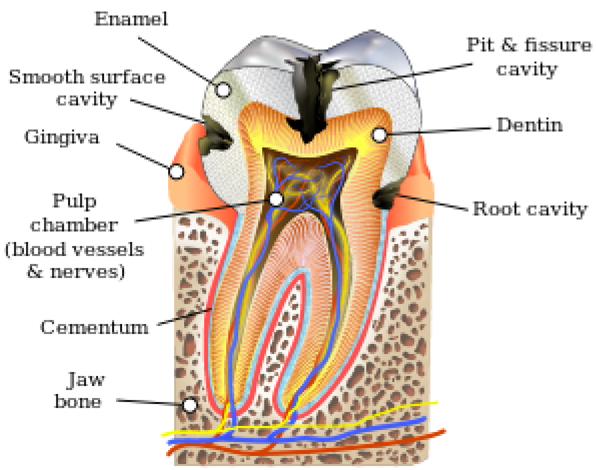
Streptococcus mutans are gram-positive plaque builders and early colonizers of the dental pellicle. These organisms can produce high levels of lactic acid through fermentation of dietary sugars and are resistant to the adverse effects of low pH, properties essential for cariogenic bacteria. As the cementum of root surfaces is more easily demineralized than enamel on crown surfaces, a wider variety of bacteria can cause root caries, including *Lactobacillus acidophilus*, *Actinomyces*, *Nocardia*, and *Streptococcus mutans*.



A gram stain image of *Streptococcus mutans* the main bacterium causing of tooth demineralization. More details.

Progression

A grows of plaque results in caries when it produced irreversible demineralization of the tooth. This can be very localized and some sites are more vulnerable than others. S ites with a low rate of salivary flow such as the grooves on the occlusal surfaces of molar and premolar teeth protect plaque from saliva and potentially from the tooth brush. Interproximal surfaces between teeth are another site where the plaque has a reduced likelihood of being removed .



Types of tooth decay by dental surface feature. More details.

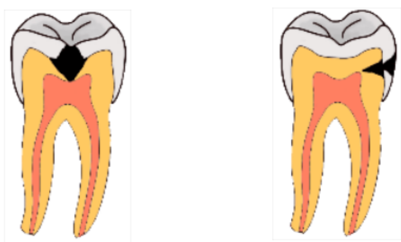
Enamel

A person experiencing caries may initially not be aware of the disease. No pain is experienced and no reaction by the tooth is produced while only the enamel is being affected. The earliest sign of a new carious lesion is the appearance of an opaque white spot on the surface of the tooth, indicating an area of demineralization of enamel. This is referred to as a white spot lesion, an incipient carious lesion or a "microcavity".

As the lesion continues to demineralize, it can turn brown but will eventually turn into a cavitation ("cavity"). Before the cavity forms, the process is reversible, but once a cavity forms, the lost tooth structure cannot be regenerated. A lesion that appears dark brown and shiny suggests dental caries were once present but the demineralization process stopped, leaving a stain. Active decay is initially light in color and opaque in appearance.

Enamel is a highly mineralized acellular tissue and caries act upon it through slowly through chemical demineralization. The hydroxyapatite crystals in enamel are organized in enamel rods which mostly run

perpendicularly from the dentin to the surface of the tooth. Some curvature is added to this orientation, however, around surface features such as groves, ridges and pits. Demineralization of enamel by caries tends to follow the direction of the enamel rods. Knowledge of the patterns of orientation of enamel rods in the tooth, therefore, allows the dentist to predict the shape of the caries and facilitates its treatment.



The effect of the orientation of enamel rods and dentinal tubules on the shape of caries. Pit and fissure caries (left) approximates the shape of a diamond whereas smooth surface caries (right) develops as two triangles. More details (left, right).

Cementum

The protection that cementum offers to the tooth against caries is reduced in comparison to that offered by enamel. The roots are therefore more

susceptible to caries than the crown. The incidence of cemental caries increases in older adults as gingival recession occurs from either trauma or periodontal disease.

Dentin

Once the infection reaches the dentin , it produces transient or constant pain which worsens upon exposure to heat, cold, or sweet foods and drinks. This is because the dentinal tubules, which extend into the pulp, transmit chemical and physical stimuli to the odontoblasts and pain receptors in the pulp.

Unlike enamel, the dentin reacts to the progression of dental caries. After tooth formation, the ameloblasts, which produce enamel, are destroyed once enamel formation is complete and thus cannot later regenerate enamel after its destruction. On the other hand, dentin is produced continuously throughout life by odontoblasts, which reside at the border between the pulp and dentin. After the tooth erupts, the odontoblasts greatly decelerate the speed of dentin production, switching from manufacturing primary to secondary dentin. Caries stimulate the odontoblasts to intensify the production of dentin. These defense mechanisms include the formation of sclerotic and tertiary dentin.

In dentin from the deepest layer to the enamel, the distinct areas affected by caries are the advancing front, the zone of bacterial penetration, and the zone of destruction. The advancing front represents a zone of demineralised dentin due to acid and has no bacteria present. The zones of bacterial penetration and destruction are the locations of invading bacteria and ultimately the decomposition of dentin. The zone of destruction has a more mixed bacterial population where proteolytic enzymes have destroyed the organic matrix. The innermost dentin caries has been reversibly attacked because the collagen matrix is not severely damaged, giving it potential for repair. The outer more superficial zone is highly infected with proteolytic degradation of the collagen matrix and as a result the dentin is irreversibly demineralized.

Sclerotic dentin

Dentinal tubules radiate outward from the pulp chamber to the cementum or enamel border. The diameter of the dentinal tubules is largest near the pulp (about 2.5 µm) and smallest (about 900 nm) at the junction of dentin and enamel. The carious process expands through the dentinal tubules. This gives rise to the triangular patterns shape of caries within dentin.

In response to the caries, the fluid inside the tubules brings immunoglobulins (antibodies) from the immune system to fight the bacterial infection. At the same time, there is an increase of mineralization of the tubules. This results in a constriction of the tubules, which slows down the bacterial progression. In addition, as the acid from the bacteria demineralizes the hydroxyapatite crystals, calcium and phosphorus are released, allowing for the precipitation of more crystals which fall deeper into the dentinal tubule. These crystals form a barrier and slow the advancement of caries. After these protective responses, the dentin is considered sclerotic.

Since sclerotic dentin blocks the connection between the carious infection and the pulp pain that would otherwise serve as a warning of the invading bacteria may not develop. Consequently, dental caries may progress for a long period of time without any sensitivity of the tooth. Without pain, the caries may remain untreated for longer and result in greater loss of tooth structure.

Tertiary dentin

As another response to dental caries, odontoblasts may intensify the production of new dentin (tertiary dentin) toward the pulp. This additional dentin is produced to protect the pulp for as long as possible from the advancing bacteria. As more tertiary dentin is produced, the size of the pulp decreases. This type of dentin has been subdivided according to the presence or absence of the original odontoblasts. If it is produced by the original odontoblasts that formed the tooth the dentin produced is called reactionary dentin. If new odontoblasts differentiate in the pulp to produced it the dentin is called reparative dentin.

Pulp

When the caries reaches the pulp it causes inflammation of the pulpar tissue (pulpitis). Since the pulp is surrounded by hard tissue, the swelling caused by the inflammatory response causes a pressure build up in the pulpar chamber. This exerts pressure on the nerves of the tooth and can lead to intense pain and throbbing.

Pulpitis can also result from dental trauma or from exposure to heat. In such cases it can be reversible, but when caused by caries it almost always results in the death of tooth. The pressure build up and accompanying pain are relieved when the crown is opened (by the dentist or by the caries). If left untreated, the infection extends along the radicular pulp and passes through the apical foramina of the roots to enter the jaw bone. This forms an abscess (see chapter 15 Periodontal Disease). The abscess may form a fistula, a passage that extends from the abscess and opens at the surface of the gums or skin to relief the pressure and to drain the pus that is formed by the inflammation.

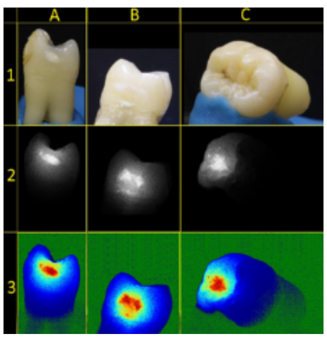
The infection can also expand from the abscess into other body tissues and become life-threatening. The tooth should be treated with root canal therapy, which involves removing all pulpar tissues, cleaning the pulp chamber and roots, filling them with a synthetic material and fitting a prosthetic crown to the tooth.

Diagnosis

The tip of a dental explorer used in the diagnosis of

caries. More details.

The presentation of caries is highly variable. However, the risk factors and stages of development are similar. Initially, it may appear as a small chalky area (smooth surface caries), which may eventually develop into a large cavitation. As the enamel and dentin are destroyed, the cavity becomes more noticeable. The affected areas of the tooth change color and become soft to the touch.



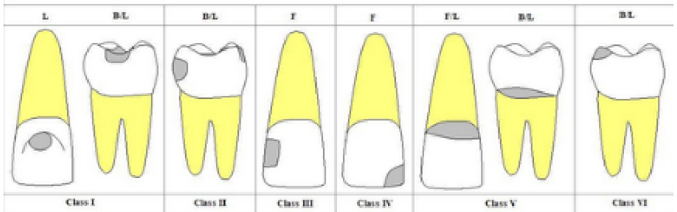
Tooth samples imaged with a a continuous light source (row 1), Laser Speckle Imaging (LSI, row 2) and computer-generated colored reconstruction based on LSI data (row 3). More details.

Primary diagnosis involves inspection of all visible tooth surfaces using a good light source, dental mirror and explorer. Visual and tactile inspection along with radiographs are employed frequently among dentists, in particular to diagnose pit and fissure caries. Early uncavitated caries is often diagnosed by blowing air across the suspect surface. This removes moisture and facilitates the detection of shine and texture differences between the unmineralized enamel and the surrounding healthy tissue. Dental radiographs (X-rays) may show dental caries before it is otherwise visible or when it is concealed as when it develops between the teeth. Laser imaging can also be used to reveal the shape and size of caries before initiating the treatment.

Classification

Caries are be classified by location, severity, and affected hard tissues. The G.V. Black classification is frequently used to indicate the type of tooth and position of the cavity:

- Class I. Occlusal surfaces of posterior teeth, buccal or lingual pits on molars, lingual pit near cingulum of maxillary incisors.
- Class II. Proximal surfaces of posterior teeth.
- Class III. Interproximal surfaces of anterior teeth without incisal edge involvement.
- Class IV. Interproximal surfaces of anterior teeth with incisal edge involvement.
- Class V. Cervical third of facial or lingual surface of tooth.
- Class VI. Incisal or occlusal edge is worn away due to attrition.



G.V. Black’s classification of
cavities by position and tooth class.
More details.

The severity of caries is described with four categories:

- Incipient. Caries advanced through less then half of the enamel cover.
- Moderate. Caries passed half of the enamel but did not reach the dentin.
- Advanced. Caries advanced through less then half of the dentin cover.
- Severe. Caries advanced through more then half of the dentin cover.

Prevention

Oral hygiene

The risk of caries can be reduced with proper brushing and flossing daily. The goal is to remove all plaque from the surfaces of the teeth. Plaque growths faster and produces more acid when carbohydrates in the food are left on teeth after every meal or snack. The toothbrush is highly effective at removing plaque on accessible surfaces, but it is not as useful between teeth. When used correctly, dental floss removes plaque between teeth. Additional aids include interdental brushes, water picks, and mouthwashes.

Toothbrushsing is a traditional and effective way of removing most plaque . More details.

Daily brushing prevents periodontal disease more than tooth decay. This is because food forced inside pits and fissures of posterior teeth cannot be removed by the brush or the floss and it is not exposed enough to the protective action of saliva. The majority of caries in children occur on the oclusal surfaces of posterior teeth. The teeth at highest risk for carious lesions are the permanent first molars in part because they are the first permanent teeth to erupt and they frequently do so before children become effective and performing their oral hygiene.

Professional dental hygiene involves regular examination and cleaning. Examination includes both visual and x-ray screening whereas cleaning targets the removal of plaque and calculus.

Diet

The risk of cavities increases with the frequency of sugar consumption. Minimizing snacking is recommended, especially with chewy and sticky sweets (candy, cookies, potato chips, and crackers) that tend to adhere to teeth for long. Parents should limit the frequency of consumption of drinks with sugar by children.

Other measures

Dental sealants are frequently used to prevent cavities in the occlusal surfaces of posterior teeth. A sealant is a thin plastic-like coating applied to the chewing surfaces of the molars to prevent food from being trapped inside pits and fissures. Sealants are usually applied on the teeth of children, as soon as the teeth erupt. They are effective but they can wear out and fail, so regular inspection is important.

Sodium fluoride tablets used for cavity prevention at home. More details.

Fluoride binds to the hydroxyapatite crystals in enamel and hinders demineralization while also inhibiting the attachment of bacteria to the tooth. Topical fluoride can be found in some treated tap water (varies with city), toothpaste, mouthwash and fluoride tablets. It can also be applied as a varnish by dental professionals.

Trays commonly used in dental clinics for local application of fluoride. More details.

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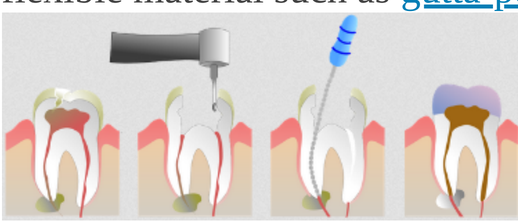
Root Canal Therapy
Root canal treatment is conducted when the pulp is infected or otherwise compromised. The crown is opened with a drill and the pulp is removed. Removal of the pulp from the roots and widening of the canal is done manually with flexible files because the roots are long, thin and curved. This is done in conjunction with antiseptic irrigation that washes out the debris and sterilizes the canal. All roots of the tooth are treated and filled with gutta-percha. Permanent restoration of posterior teeth requires a prosthetic crown to reduce the risk of tooth fracture. The alternative treatment to root canal therapy is dental extraction.

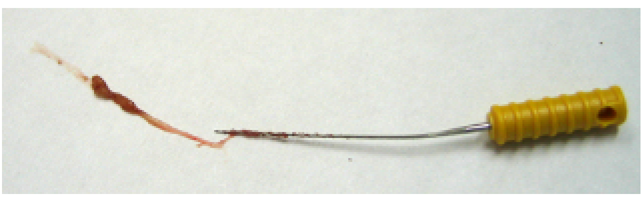
Endodontic therapy, also known as endodontic treatment or root canal therapy, is a treatment sequence for the infectedpulp of a tooth which results in the elimination of infection and the protection of the decontaminated tooth from future microbial invasion. Endodontic therapy involves the removal of the dental pulp, the subsequent shaping, cleaning, and decontamination of the hollows with small files and irrigating solutions, and the filling of the decontaminated canals. Filling is typically done with a flexible material such as gutta-percha and an eugenol-based cement.



Root canal therapy. The unhealthy tooth, opening of the crown with a dental handpiece and removal of the pulp, cleaning of the root canals with an endodontic file, and restoration with gutta-perchafilling and a crown. More details.

Diagnostic and preparation

When a tooth is threatened by an infection of the pulp, a pulpectomy (removal of the pulp tissue) is conducted. If the inflammation is extensive, the tooth can be unroofed to allow drainage and help relieve pressure, the abscess may be drained, antibiotics prescribed, and the treatment continued after the inflammation has been mitigated. The dentist then drills into the pulp chamber and removes the infected pulp. Next, the tissues in the root canal(s) are extracted with long needle-shaped hand instruments known as files (H files and K files). All debris and bacteria have to be completely removed from the empty root canals and from the abscess, if present, in preparation for the tooth to be restored.



Pulp tissue removed during endodontic therapy with a file. More details.

This preparation is challenging because the root canals are long and narrow, surrounded by hard tissue (dentin) and they are curved. The root canals are cleaned and widened through manual use of files which are long, thin and flexible, to adjust to the curvature of the root. This cleaning and widening is done as an iterative process in which the filing is alternated with irrigation using antiseptic solutions that wash out debris and kill microorganisms. The procedure usually requires multiple visits over a period of weeks.

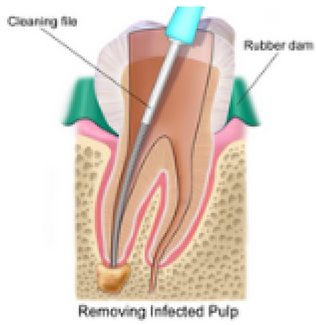
Upper left second premolar after removal of the decay. The roof of the pulp chamber has been removed exposing the pulp chamber (red oval). More details.

Several compositions of irrigant solutions may be used in root canal therapy:

- 5% sodium hypochlorite (NaClO)
- 2% chlorhexidine gluconate
- 17% ethylenediaminetetraacetic acid (EDTA)
- Framycetin sulfate
- Mixture of citric acid, doxycycline, and polysorbate 80 (detergent) (MTAD)

Sodium hypochlorite and chlorhexidine are the most commonly used irrigants and their antimicrobial activity has been verified in vitro. Irrigation

is a key component of root canal therapy, not only to clean and sterilize the root canal but also the abscess and fistula, when present.



Manual use of the file for removal of infected pulp during root canal therapy. More details.

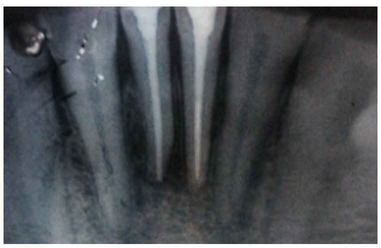
The root canal(s) can be temporarily filled with calcium hydroxide paste. This strong base is left in for a week or more to disinfect and reduce inflammation in the surrounding tissues.

It may take several visits until the inflation is mitigated and all the infection and debris are removed from the tissues. A temporary filling material is applied to the crown between the visits. Maintaining a coronal seal throughout root canal therapy is important for the success of the treatment.

Filling the root canal

After all the debris and infected tissue have been removed, the dentist fills each of the root canals and the pulp chamber with an inert material and seals the opening. The standard filling material is gutta-percha, a natural

polymer prepared from latex from the percha (*Palaquium gutta*) tree. Its main characteristics of interest are that this is a fairly rigid yet flexible material and it is highly inert (does not cause reactions) in relation to the body tissues. A cone gutta-percha is inserted into each clean root canal along with a sealing cement. Gutta-percha is radiopaque, allowing for x-ray verification that the root canal passages have been filled without leaving any voids.



Radiography of central mandibular incisors with treated root canals. The white structures are the root canals filled with radiopaque material. More details.

Final restoration

Molars and premolars that have had root canal therapy should be protected with a crown that covers the cusps of the tooth. This is because the access made into the root canal system removes a significant amount of tooth structure. Molars and premolars are the primary teeth used in chewing and fracture more frequently after root canal treatment without cuspal coverage.

Anterior teeth typically do not require full coverage restorations after a root canal, unless there is extensive tooth loss from decay. Placement of a crown is also recommended because it will best seal the root treated tooth.

Success of the treatment

After endodontic therapy a tooth is considered dead for not having life cells in it anymore. It should not be considered inert, however. The tooth is still prone to decay and without proper hygiene in can develop caries in its remaining enamel and dentin. This can occur without the patient's knowledge because with the removal of the pulp, the development of new caries does not produce in pain. Caries is the main reason for extraction of teeth after root canal therapy.

Endodontic treatment may fail because of inadequate cleaning of the root canal or incomplete sealing of the crown. In both cases, contamination of the gutta-percha by oral bacteria can reinitiate tooth decay. The contaminated gutta percha would have to be replaced in a retreatment procedure to minimise the risk of failure.

Another potential source of complication is that the dentist may fail to find, clean and fill all of the root canals within a tooth. The number of roots is variable among individuals, such that about half of the maxillary molars have four canals instead of three. An infected canal that is missed during the treatment may later inflame and require treatment.

Alternatives

If extensive loss of tooth structure occurs, extraction may be the only treatment option. It is also conducted when the treatment needs to be completed in a single session or when the endodontic equipment or expertise are not available. Following tooth extraction, options for prosthetic replacement may include dental implants, a fixed partial denture (bridge), or a removable denture.

Figure credits

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Dental Restoration
Dental restoration involves tooth preparation and filling. The preparation is mostly influenced by the extent of decay and the structural state of the tooth. All decayed tissues and healthy tissues without structural support are removed. Many options are available for filling materials and procedures. Direct restorations are produced in the tooth, whereas indirect restorations are produced in the lab and cemented onto the tooth. Considerations in the choice of materials and techniques include durability, cost, appearance, position, size of the cavity and type of tooth (deciduous or permanent). Composite resin and amalgam are most common in direct fillings whereas gold and ceramic are most common in crowns.

A dental restoration or dental filling is a treatment to restore the function, integrity, and morphology of missing tooth structure resulting from caries or external trauma. A restoration can be direct and indirect and it is classified by location and size. A root canal filling, for example, is a restorative technique used to fill the space where the dental pulp normally resides.

Tooth preparation

Upper right first molar being prepared for filling. The white outer enamel appears

intact, while the yellow, underlying dentin appears recessed. This is because a large amount of decayed dentin was removed. This portion of the enamel is now unsupported, and should be removed to prevent future fracture. More details.

Restoring a tooth to good form and function requires two steps: (1) preparing the tooth for placement of restorative material or materials, and (2) placement of these materials. The process of preparation usually involves removing the decayed material from the tooth with a rotary dental handpiece and dental burrs. If permanent restoration cannot be carried out immediately after tooth preparation, temporary restoration may be performed.

A number of considerations will determine the type and extent of the preparation. The most important factor to consider is decay. The extent of the decay greatly influences the extent of the preparation, and in turn, the subsequent method and appropriate materials for restoration. Another consideration is unsupported tooth structure. When preparing the tooth to receive a restoration, unsupported enamel is removed to allow for a more predictable restoration. While enamel is the hardest substance in the human body, it is particularly brittle, and unsupported enamel fractures easily.

Direct restorations

This technique involves placing a soft or malleable filling into the prepared tooth and building up the tooth. The materials used are most commonly gold, amalgam, dental composites, glass ionomer cement, or porcelain. The material is then set hard and the tooth is restored. The advantage of direct restorations is that they usually set quickly and can be placed in a single procedure. The decision of which material to use is usually made based on the location and severity of the cavity.

Indirect restorations

In this technique the restoration is fabricated outside of the mouth using dental impressions of the prepared tooth. Common indirect restorations include inlays and onlays, crowns, bridges, and veneers. Usually a dental technician fabricates the indirect restoration from records the dentist has provided. The most commonly used materials are gold and ceramics. The finished restoration is bonded permanently with a dental cement. The treatment is often done in at least two separate visits to the dentist because time is needed for the fabrication of the restoration after the impression is obtained. While the indirect restoration is being prepared, a temporary restoration is used to cover the prepared tooth and allow the patient to bite. This usually consists of a softer dental cement that can easily be removed with the dental drill.

Removable dental prostheses (mainly dentures) are a form of indirect dental restoration, as they are made to replace missing teeth. There are numerous types of precision attachments (also known as combined restorations) to aid removable prosthetic attachment to teeth, including magnets, clips, hooks, and implants which may themselves be seen as a form of dental restoration.

Materials used

Casting alloys are mostly used for making crowns, bridges and dentures. Titanium, usually commercially pure but sometimes a 90% alloy, is used as

the anchor for dental implants as it is biocompatible and can integrate into bone.

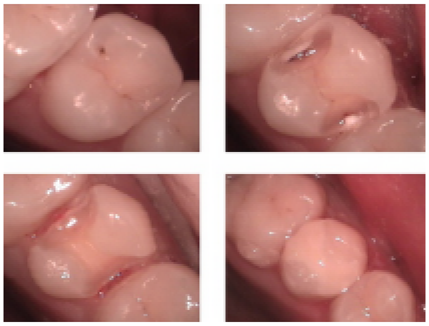
Metals and alloys

- gold (high purity: 99.7%) and gold alloys (with high gold content)
- gold-platinum alloy
- silver alloy
- cobalt-chrome alloy
- nickel-chrome alloy
- Amalgam: 65% Silver, 29% Tin, 6% Copper, 2% Zinc, 3% Mercury

Dental Amalgam is widely used because it is easily made into rigid direct fillings, completed in single appointment, with acceptable strength, hardness, corrosion, and toxicity properties. Its preparation is more forgiving than that of composite resins. Amalgam is now mainly used for posterior teeth (less visible) because of its gray color. Although the mercury in cured amalgam is not available as free mercury, concern about its toxicity has existed since its invention as a dental material. It is banned or restricted in Norway, Sweden and Finland.

Composite resin

Dental composites, also called "white fillings", are a group of restorative materials used in dentistry. In addition to fillings done at the clinic, composite resins are also used to manufacture crowns and in-lays in the laboratory. The greatest advantage of these materials is that they can be made tooth-colored. Their strength and durability is not as high as porcelain or metal restorations and they are more prone to wear and discoloration. Compositions vary widely, with proprietary mixes of resins forming the matrix, as well as engineered filler glasses and glass ceramics.



Composite resin is most commonly used in direct fillings because its color can be made to closely match that of the tooth. More details.

An initiator substance begins the polymerization reaction of the resin when light is applied at a specific wavelength (460-480 nm blue light) to yield necessary free radicals and start the process. This process is quick and safe, but it require the composites to be applied in thin layers as determined by their opacity. Immediately after light induced curing, the final surface can be be shaped and polished.

Glass ionomer cement

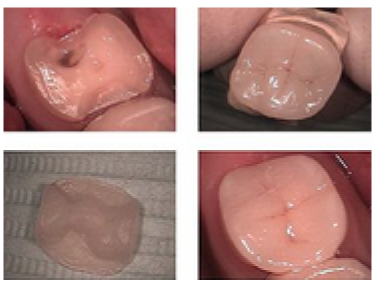
A glass ionomer cement (GIC) is one of a class of materials commonly used in dentistry as filling materials and luting cements. These materials are based on the reaction of silicate glass powder and polyalkenoic acid. These materials can also have the color of the tooth and they were used to restore anterior teeth before composite resins were developed.

As they bond chemically to dental hard tissues and release fluoride for a relatively long period, modern-day applications of GICs have expanded. The desirable properties of glass ionomer cements make them useful in

restorations at low-stress areas on primary teeth. They do not need to be applied layer by layer, like in composite fillings.

Porcelain (ceramics)

Various types of dental porcelain (ceramic fired at high temperatures) are used in indirect fillings and crowns. They are also used as in-lays, on-lays, and aesthetic veneers. A veneer is a very thin shell of porcelain that can replace or cover part of the enamel of the tooth. Full-porcelain restorations are particularly desirable because their color and translucency mimic natural tooth enamel. Porcelain can be combined with metal to provide strength to a crown or bridge. These restorations are more durable than porcelain used alone.



All-ceramic dental onlay for a molar tooth. More details.

Comparison of filling materials

- Composites and amalgam are used mainly for direct restoration. Amalgam is more durable but composites can be made to match the

color of the tooth and the surface of the restoration can be polished after the procedure has been completed.
- Amalgam fillings expand with age, possibly cracking the tooth and requiring filling replacement.
- Composite fillings shrink with age and become prone to infiltration. If not noticed early, this results in new decay.
- Fillings are recommended for small to medium size restorations.
- Inlays and onlays are more expensive indirect restoration alternatives to direct fillings. They should be more durable than composite direct fillings, however.
- Porcelain, cobalt-chrome, and gold are used for indirect restorations like crowns and partial coverage crowns (onlays). Traditional porcelains are brittle and are not always recommended for molar restorations.

Complications

Irritation of the pulp

When a deep cavity is filled, the vibration, heat and chemical stimulation that the tooth receives may irritate the pulp and generate pulpitis (inflammation of the pulp). This can result in pain when biting on the treated tooth or sensitivity to cold and hot substances. It may settle down spontaneously with time. If not, root canal treatment is usually conducted to resolve the pain and save the tooth.

Weakening of tooth structure

In situations where a relatively larger amount of tooth structure has been lost or replaced with a filling material, the overall strength of the tooth may be affected. This significantly increases the risk of the tooth fracturing in the future when excess force is placed on the tooth, such as trauma or grinding teeth at night. The standard treatment of large cavities and root canal therapy in premolars and molar includes sealing with a crown because this reduces the risk of fracture.

Figure credits

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Coming Soon!
Just a place holder to allow previewing the navigation bar. The system will not allow a collection to be published without having modules inside each of its subcollections.

Coming soon!

Tooth Occlusion
Human teeth occlude forming a curved surface that is convex inferiorly, both in the anterior-posterior axis and the left-right axis of the mouth. Malocclusion can affect many teeth when the size of position of the jaw bones is involved. Based on the relative positions of the mandibular and maxillary first molars, Angle’s classification recognizes three major classes of malocclusion involving the length of the jaws bones. Cephalometric analysis is used to identify misposition or misproportion of structural elements that support the teeth. Anterior teeth can also exhibit abnormal position, inclination, rotation or eruption. Tooth position is dynamically adjusted through life due to alveolar remodeling and rearrangement of the periodontal ligament. This makes orthodontic treatment possible.

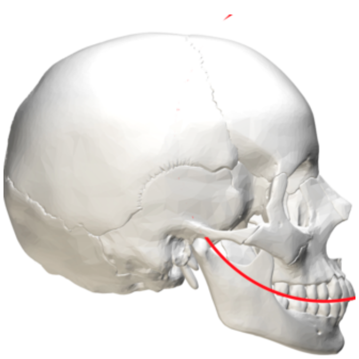
The performance of an organism in biting and chewing is strongly influenced by the alignment of the teeth. It takes a precisely tuned developmental program not only to form each tooth and bring it into position, but also to account for the replacement of deciduous teeth without significant loss in functionality. The fine positioning of the teeth is based on remodeling of the alveolus in the supporting bone, and adjustment to the periodontal ligaments, the collagen fibers that attach the tooth to the bone. This mechanism remains active throughout life, constantly adjusting the position of the teeth in response to any changes in the forces experienced during mastication. Orthodontics is the study of tooth movement and alignment. It includes normal and abnormal tooth movement, bone growth, tooth eruption and shedding of baby teeth. Orthodontists study these mechanisms to make adjustments to the alignment of the teeth. This chapter explains the processes above, introduces the most common problems and treatment in humans and reviews dental alignment in other mammals.

Dental occlusion

Occlusion, in dentistry, means the contact between teeth. With the teeth ideally positioned, all mandibular teeth should touch maxillary teeth at the same time during mouth closure. The real condition tends to be very close to this ideal due to feedback-driven adjustment of tooth position. Tooth eruption progresses until it is inhibited by pressure received from the opposing tooth at the occlusal surface. Similarly, the position of the tooth

along the mesio-distal axis is also adjusted such that the alveolar bone tends to grow in areas of high pressure between teeth and be resorbed in areas of low pressure between teeth. These processes tend to position teeth to spontaneously maintain tight occlusion along the entire dentition and to approximate even spacing among teeth along the arcades.

The occlusal plane is the imaginary surface formed by the occlusal surfaces of the teeth with the mouth closed. This surface is actually curved in humans. The Curve of Spee is the curvature of the mandibular occlusal plane beginning at the tip of the lower incisors and following the buccal cusps of the posterior teeth, continuing to the posterior molar. According to another definition the curve of Spee is an anatomic curvature of the occlusal alignment of the teeth, beginning at the tip of the lower incisor, following the buccal cusps of the natural premolars and molars and continuing to the anterior border of the ramus. It is named for the German embryologist Ferdinand Graf von Spee (1855–1937), who was first to describe the anatomic relations of human teeth in the sagittal plane.



Curve of Spee in the human dentition. More details.

The pull of the main muscle of mastication, the masseter, is at a perpendicular angle with the curve of Spee. This directs force to the teeth in alignment with their longitudinal axis, which is structurally favorable. The longitudinal axis of each lower tooth is also nearly parallel with its arch of closure. The curve of Spee is, essentially, a series of sloped contact points between upper and lower teeth. It is of importance to orthodontists as a flat or mild curve of Spee is essential to an ideal occlusion.

The curve of Spee is at a right angle with the curve of Wilson, which is the upward (U-shaped) curvature of the maxillary and mandibular occlusal planes in the coronal plane. The occlusal surfaces of the mandibular molars are slightly higher on the vestibular side than on the lingual side because the teeth are tilted inwards. Both curves (Spee and Wilson) are believed to be relevant for stability of the temporomandibular joint and for the appropriate distribution of the forces of mastication on the teeth and supporting bones.

Curve of Wilson formed by the inward tilting of the mandibular molars. More details.

Malocclusion

A malocclusion is a misalignment or incorrect relation between the teeth of the two dental arches when they approach each other during mouth closure. Malocclusions are common, although usually not serious enough to require treatment. Severe malocclusions may involve craniofacial anomalies and require orthodontic or sometimes surgical treatment (orthognathic surgery) to correct the problem. Correction of malocclusion may reduce the risk of tooth decay and prevent damage to the temporomandibular joint. Orthodontic treatment is also used to correct minor misalignments for aesthetic reasons.

Malocclusions can involve teeth that are mispositioned, tilted, rotated, deformed extranumerary or missing, and with dozens of teeth in the mouth, diagnosis can be a complicate process. Angle (1899) produced one of the oldest and simplest way of classifying malocclusions. It focuses on the position of the teeth. Several other classification systems have been proposed later to account for the limitations of Angle's system. This includes classifications by Martin Dewey (1915), Benno Lischer (1912, 1933), Simon (1930, the first 3D system), Jacob A. Salzmann (1950, based on skeletal structures) and James L. Ackerman and William R. Proffit (1969).

Angle's classification of malocclusions

Edward Angle used the position of the first molars to classify malocclusion. Molars tend to be more stable than front teeth and the first molars erupt early. The choice of the first molars for reference resulted in a system that is still widely used today. According to Angle, the mesiobuccal cusp of the upper first molar should align with the buccal groove of the mandibular first molar. The teeth should all fit on a line of occlusion which, in the upper arch, is a smooth curve through the central fossae of the posterior teeth and cingulum of the canines and incisors, and in the lower arch, is a smooth curve through the buccal cusps of the posterior teeth and incisal edges of the anterior teeth.

He classified malocclusions in three major types:

Class I: Neutrocclusion

The molars are correctly positioned as described above, but there are misalignment problems involving the front teeth.

Neutrocclusion with severe crowding and labially erupted canines. More details.

Class II: Distocclusion

The lower first molar is distal to the neutral position. Usually the mesiobuccal cusp of the upper first molar rests in between the first mandibular molar and second premolar. There are two subtypes:

- Class II Division 1: The anterior teeth are protruded (tilted anteriorly).
- Class II Division 2: The central anterior teeth are tilted inwards.

Distocclusion showing the mandibular first molar displaced distally. More details.

This condition commonly results from the development of a short mandible.

Class III: Mesiocclusion

The lower first molar is mesial to the neutral position. The mesiobuccal groove of the mandibular first molar lies anterior to the mesiobuccal cusp of the maxillary first molar. The lower front teeth are frequently more prominent than the upper front teeth. This condition commonly results from the development of a large mandible.

Angle’s classification offers a useful framework and terminology for diagnosis of the general alignment of the dentition. A complete diagnosis of malocclusion involves further characterization of each tooth in position, tilt, rotation and level of eruption.

- Dislocation: Describes the position of the tooth. It can be mesial or distal, buccal or lingual.
- Inclination: Describes the tilt angle of the tooth. It can be mesial or distal, buccal or lingual, depending on which direction the crown of

the tooth is leaning.
- Rotation: Describes the turning of the tooth around its longest axis. It is mesiolingual the mesial aspect of the tooth is turned toward the tongue or it is distolingual if the distal aspect of the tooth is turned toward the tongue.
- Eruption: Describes the vertical position of the occlusal surface of the tooth in relation to the occlusal plane formed by the rest of the teeth. In an infraocclusion, the tooth has not erupted enough to reach the occlusal plane, whereas in a supraocclusion the tooth has overerupted.

While the maxillary first molars (used in Angle's classification) provide a reasonably stable position reference for the other teeth, they can also be mispositioned. It is therefore important to consider the dimensions of the mandible and maxilla, and the position of the entire dentition in relation to the skull. A cephalometric analysis is conducted to accomplish this step.

Cephalometric analysis

Cephalometry is the the study of the dimensions of the head. In a dental cephalometric analysis, molds of the dentition are combined with x-ray or tomographic images of the head to analyze the position and size of all the facial structures involved in mastication.

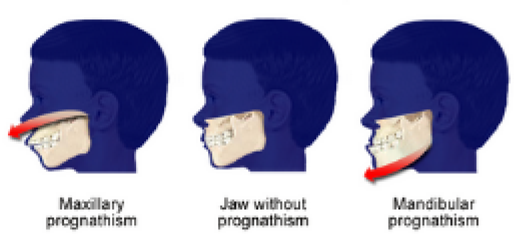
Lateral cephalometric radiograph used for skull

analysis. More details.

This allows for the diagnosis of developmental issues involving the maxilla, mandible and other support tissues in addition to the teeth. Most commonly, the analysis involves the identification of a series of standard landmarks on the images, measurement of distances and angles between them and comparison to the normal distribution of such measurements in the population. Various methods of analysis have been devised, and they differ in which landmarks are used. With today's computing power, several methods involve digitization of the landmark positions and generation of 3D models of the patient's skull and teeth to facilitate a comprehensive diagnosis of malocclusion.

Prognathism and retrognathism

Cephalometric analysis allows for comparison of the positions of the mandible and maxilla in relation to the skull. Prognathism is when either of the jaws protrudes beyond an imaginary plane (usually that of the forehead) that is parallel to the coronal plane of the skull. The word *prognathism* derives from Greek (*pro* = forward and *gnáthos* = jaw). Prognathism may result in malocclusion.



Classification of jaw position in relation to the skull. More details.

Prognathism can involve a projecting maxilla, mandible or both and it is usually the result of extensive growth of these bones. Not all alveolar prognathism is anomalous, and significant differences can be observed among ethnic groups. Prognathism, if not extremely severe, can be treated in growing patients with orthodontic functional or orthopaedic appliances. In adult patients this condition can be corrected by means of a combined surgical/orthodontic treatment.

Alveolar prognathism is a special case in which the maxilla and the mandible have normal size and position but the incisors are tilted labially. This condition can be exaggerated or caused by thumb sucking or tongue thrusting. Functional appliances can be used by growing children to help modify behavioral habits and avoid this condition. Otherwise, alveolar prognathism can be corrected with fixed orthodontic therapy.

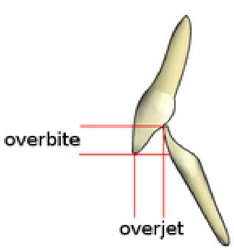
Alveolar prognathism caused by thumb sucking and tongue thrusting in a 7-year-old girl. More details.

Retrognathism is a condition in which the maxilla or mandible, particularly the mandible, has an abnormally posterior position relative to the rest of the skull.

A child with Treacher Collins syndrome showing retrognathism and microtia (small ear). More details.

Alignment of anterior teeth

In a normal dentition, the incisive edge of the inferior incisor occludes against the cingulum of the superior incisor. The incisive edges of the two teeth do not touch but move past each other, creating some overlap between the teeth. The horizontal overlap is called overjet, whereas the vertical overlap is called overbite.



Central

incisors in mesial view showing the horizontal and vertical overlap at occlusion. More details.

Conditions of malocclusion can exaggerate the overlap, reduce it or even invert the positions of the teeth. The inferior incisors have most commonly 30-50% of their height overlapped by the superior incisors. Both increased and reduced overlaps may be considered malocclusions. An excessive overlap is also called deep bite whereas a lacking overlap is called open bite (Fig. 7).

Maxillary or alveolar prognathism and mandibular retrognathism tend to increase the overjet. Mandibular prognathism, on the other hand, reduces the overjet and can result in negative overjet, with the mandibular incisors occluding anteriorly to the maxillary ones. The condition of negative overjet is also called underbite or anterior crossbite. Notice that overbite is a quantitative property of the alignment of incisors, whereas underbite refers to a condition of malocclusion characterized by negative overjet.

Crossbite

This is a malocclusion in which at least one tooth is closer to the tongue or to the cheek (or lips) than the normal position, making it occlude in an abnormal position. It can involve anterior or posterior teeth and it can involve one or both sides of the arcade. A crossbite can be caused by dental

issues such as crowding or delayed loss of primary teeth. It can also result from skeletal issues affecting the development of the maxilla or mandible.

Unilateral posterior crossbite. More details.

Teeth are dynamically positioned

Each of our teeth articulate at an alveolus of the maxillary bone or mandible. The shape and position of the alveolus is adjusted by our body through the process of bone remodeling. This process is most intense during development allowing, the growth of jaw bones and the replacement of the primary dentition.

Alveolar remodeling occurs constantly throughout our lives, however. Adjustments are made in response to external forces, particularly occlusal forces. Bone is removed from areas where it is no longer needed and added to areas where it is needed. Osteoblasts are found in large numbers in the areas of the alveolus where tension is high, whereas osteoclasts are found in large numbers where the tissues are being compressed. These forces also influence the density and alignment of trabeculae inside the bone. The bony trabeculae are aligned in the path of tensile and compressive stresses to provide maximum resistance to occlusal forces with a minimum of bone substance. When forces are increased the bony trabeculae also increase in number and thickness.

The fibers of the periodontal ligament hold the tooth in the alveolus, allowing for a minimal amount of movement of the tooth. They also rely on mechanical stimulation to preserve their structure. Within physiologic limits, the fibers become thicker in response to increased stresses. If occlusal forces are reduced, the fibers become thin. This phenomenon is called *disuse atrophy*.

Tooth mobility

Healthy teeth are not completely immobile inside the alveolus. It is normal for them to move about 0.25 mm in response to pressure in the bucco-lingual direction. This is because the tooth is not fused to the bones of the jaws but is connected to the alveolus by the periodontal ligament. This slight mobility accommodates forces exerted on the teeth during chewing without damaging them. Milk (deciduous) teeth also become looser naturally just before their exfoliation. This is occurs through gradual resorption of their roots and periodontal ligaments when stimulated by the developing permanent tooth underneath.

Tooth mobility is evaluated by applying pressure with the ends of 2 metal instruments and trying to rock a tooth gently in a bucco-lingual direction. Multiple classifications of tooth mobility have been proposed:

Grace & Smales Mobility Index

- Grade 0: No apparent mobility
- Grade 1: Perceptible mobility < 1 mm in bucco-lingual direction
- Grade 2: < 2 mm
- Grade 3: > 2 mm < or can be depressed in the alveolus

Miller Classification

- Class 1: < 1 mm (horizontal)
- Class 2: >1 mm (horizontal)
- Class 3: > 1 mm (horizontal+vertical)

Teeth become loose when they loose their attachments or when they are exposed to abnormal mechanical forces. Loss of attachment includes

periodontal disease, and dental abscesses. Abnormal mechanical forces include those produced in bruxism (tooth grinding or clenching), dental trauma (blow), or when a new filling or crown is too prominent and concentrates the pressure of the bite on a single occlusal surface.

Figure credits

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Orthodontic Treatment
Orthodontic treatment starts with a planning phase that considers many medical, asthetical, developmental, behavioral, cultural and financial aspects. The final goal and method of treatment are defined in agreement with the patient. Malocclusions that involve jaw structure are considered first and can be treated with functional appliances in growing children or orthognatic surgery in adults. Tooth extraction for spacing of teeth is common but has not been proved necessary. Fixed appliances (braces) are the most common tools used for tooth alignment. A bracket is cemented onto each tooth and a tensed archwire transfers forces to the bracket that gradually produce movement of the tooth. Clear aligners are a less visually-disruptive alternative to braces, which can produce comparable results when smaller adjustments to tooth position are needed. Malocclusion also affects animals such as rodents, cats, dogs and horses, and orthodontic treatment can be equally necessary and effective in them.

Treatment planning

Teeth can be successfully repositioned through the introduction of moderate and sustained mechanical forces in the mouth, sometimes in combination with surgery. An orthodontic treatment aims to improve the function and/or aesthetics of the mouth by realigning the teeth.

The planning of orthodontic treatment involves a precise characterization of the structure of the oral structure, consideration of the potential for change which can be strongly influenced by age and health condition, and the determination of the precise goal of the treatment. The planning phase can be challenging in its technical aspects. It requires a profound understanding of the mechanical forces involved in mastication and of the responses of the teeth, ligaments and bones to the added mechanical forces. Determining the origin of a malocclusion may not be easy, but it may be crucial for successful realignment and retention of the teeth in the new position.

The ethical aspects of the planning phase can also be challenging. The borderline between normal variation and malocclusion is not clearly delimited from either functional or aesthetical points of view. The plan should consider the patient’s age, diet, feeding habits, health condition, and

need or desire for aesthetic modification. Similarly, the final alignment pursued with the treatment and how closely it needs to be matched are not absolutely defined and need to be decided in agreement with the patient.

Diagnosis

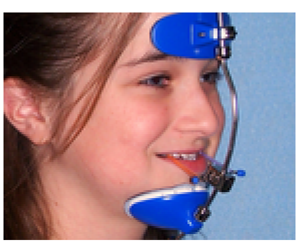
The diagnosis most commonly involves a detailed cephalometric analysis (see Tooth Alignment in this chapter) combined with careful analysis of a cast of the dentition, usually obtained through alginate impressions. The cast can be digitized and allow for tridimensional analysis in the computer.

The structure of the skull is analyzed with focus on the size and position of the jaw bones. The position and tilt of each tooth, erupted or developing is taken into account and each aspect of malocclusion is identified.

Treatment

Functional appliances

Malocclusions involving the structure of the jaws in children are usually treated with facial growth modification through the use of orthopedic devices. A variety of devices called functional appliances is available to address malocclusions. These appliances can be fixed (ex: Herbst appliance) or removable (chin cup, face mask, head gear) and they apply forces the the jaws that modify the growth of the bones, altering their final length and position.



A face mask used to

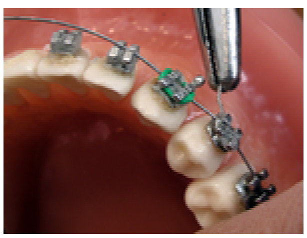
protract the upper jaw in the treatment of a class III malocclusion through growth modification. The is a removable appliance attached to the braces by easily removable elastic bands. More details.

In adults, orthognatic surgery may be required in combination with orthodontic treatment. For instance, a segment of bone may be surgically removed from the mandible of an adult with mandibular prognathism. The bone is exposed through an incision in the gums to leave no externally visible scars. The mandible is then shifted and the cut ends are held against each other by a small plate and screws as the mandible heals.

Space for the teeth on the arch can be managed with or without the extraction of permanent teeth. The discussion of the advantages and disadvantages of each approach has been controversial, and research has failed to provide evidence of a clear advantage to either approach in the function, aesthetics or stability of the final result of the treatment.

Braces

The teeth can be aligned through the use of fixed appliances (braces) or removable devices (clear aligners). Braces became popular during the 20th century, especially after 1970, when it became feasible to hold small brackets against the teeth using removable adhesives. The treatment involves the attachment of one bracket to the surface of each tooth and the installation of an archwire that goes through all brackets in the arch, connecting them. A different shape of bracket is designed for each tooth in the dentition. Arch wires vary in diameter and shape (round or square in cross-section). The choice of the precise placement for the bracket and the selection of wire diameter and shape make it possible to control the dislocation of each tooth and adjust its inclination and rotation. Elastics (rubber bands) may also be attached to the brackets to help position the teeth.



Practice of bracket and archwire installation on a plastic model. More details.

The appliance is adjusted with repositioning of brackets and archwires as the teeth move and new applied forces are necessary to conduct the teeth to the desired position. Several aspects of malocclusion may be dealt with at overlapping time frames. In general, the teeth are leveled and aligned to form a smooth curve of Spee, then class II and III malocclusions are

corrected, the upper and lower arches are coordinated to achieve proper overbite and overjet, space is created and used to align the teeth and the final position, inclination and rotation of each tooth is fine-tuned. The treatment may also involve the use of other appliances, such as a headgear to promote anteroposterior jaw or tooth adjustments or a transpalatal bar or lingual arch to adjust the width of the arch and/or produce space anteriorly. Variations of braces include ceramic braces in which the tooth-colored brackets are less visually disruptive, lingual braces in which the brackets and arch wire are attached to the lingual surfaces of the teeth to conceal the entire appliance, and gold-plated or titanium braces for patients allergic to the nickel in the stainless steel.

A fixed palatal bar between the first molars produced a 4.5% increase in the width of the arch. The bar was welded against a metal band that wraps around each first molar and anchors the archwire. More details.

Clear aligners

Clear aligners have been conceived in the middle of the 20th century and became popular at the turn of the millennium. They are a less aesthetically disruptive alternative to braces. Treatment with clear aligners was initially only applicable when the necessary changes were small and restricted to the

front teeth, but the development of the technique has greatly expanded its applicability to posterior teeth and to complex and profound corrections of tooth positioning. Its effect on skeletal elements is reduced, however, especially when lateral adjustments are needed. Hyrax or Herbst appliances are commonly included in the treatment to promote such adjustments.

Clear aligner (left; Invisalign) individually designed for the maxillary arch of the patient. A clear aligner is barely noticeable in the smile of the patient (right). More details (left, right).

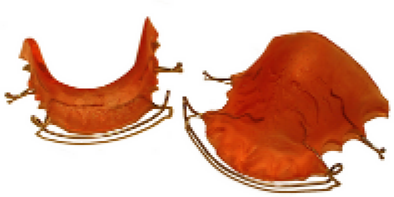
A precise digital 3D model of the mouth of the patient is built and software is used to calculate the movements needed in each tooth for the dentition to reach the targeted alignment. The model is usually built after digitization of a cast of the patient's dentition. Intraoral scanners (wands with light and camera) are becoming available, however, for direct digitization at the clinic, eliminating the need for a cast.

Software is used to estimate the forces needed to be applied to each tooth. It then balances the forces and designs a series of aligners that will gradually reposition all teeth. Each clear aligner covers multiple teeth and has a fixed shape although it is slightly flexible. Small patches of composite material called “attachments” may be added at specific positions on some teeth to improve the anchorage of the aligner and facilitate specific tooth movements. The patient wears each aligner for a certain amount of time and

switches to the next one, reaching aligned teeth at the end of the series. The treatment may be interrupted near the middle for a reevaluation with new aligners being produced based on a new scan of the mouth. This accounts for eruption or loss of teeth, modification of their shape due to restorative treatment (cavities), noncompliance of the patient or changes in plans. A second interruption (called refinement) with scanning and production of new aligners may take place near the end of the treatment. The goal is to correct for teeth that did not respond exactly as predicted to the applied forces. This final adjustment usually results in a fine-tuned alignment that closely matches the targeted one.

Retainers

Relapse is a tendency of teeth to return to their original position after being dislocated through orthodontic treatment. It is a concern both when braces or clear aligner are used in the orthodontic treatment. Tooth relapse may occur due to recoil of periodontal fibers, pressure from surrounding soft tissues, occlusal forces, and the patient's continued growth and development. Orthodontic retainers are custom-made devices, usually made of wires or clear plastic, that hold teeth in position after they reach their targeted positions. By using retainers to hold the teeth in their new position for some time, the surrounding tissues are allowed to stabilize in the new condition and reduce the risk of relapse. The advisable duration of retainer usage depends on many factors involving the extent and type of orthodontic procedure, and the physiology and behavior of the patient. Some patients are advised to wear retainers for life.



Upper and lower

jaw Hawley retainers. Commonly used to maintain the position of the teeth after the conclusion of the orthodontic treatment. More details.

The most common retainers (Hawley type) are movable. They should be worn at night and the need to wear them during the day has not been established. They consist of wires that surround the anterior teeth and insert into an acrylic base. They are custom-molded for each patient. Other types of retainers include vacuum-formed removable retainers, which are made or plastic and can be transparent like clear aligners, and fixed retainers.

Orthodontic treatment in animals

Malocclusions are common in pets. These animals do not encounter in captivity the variety of food items that they would find in the wild. Their diet may be inappropriate or too limited, leading to gastrointestinal diseases, cavities and abscesses that develop into malocclusions. Animals with constantly growing teeth (ex: rodents, lagomorphs) are frequently fed insufficiently abrasive diets. They experience excessive growth of incisors and molars which inevitably lead to acquired malocclusion. Treatment frequently includes trimming with a diamond-impregnated cutting disc and dietary advising of the pet owner.

Animals such as dogs and cats naturally have canines that greatly exceed the length of the other teeth. In a normal bite, the mandibular canine remains anterior to the maxillary canine. Both teeth have a buccal inclination that prevents them from piercing the opposing arch. Developmental misalignment of the canines can lead to severe and painful damage to the palate, the gums or to neighboring teeth. Such conditions can

be treated with extractions, bone surgery or with fixed appliances resembling “customized braces”. Fixed appliances can be highly effective but their use is complicated by the great variation in facial size and morphology present in the group and by the patient's attempts to remove the appliance.

Normal occlusion in a dog, showing the anterior position of the mandibular canine in relation to the maxillary one. More details.

Horses can present any of the basic three classes of malocclusions recognized in humans. Class II malocclusions are common and can result in overjets of 2-3 cm between mandibular and maxillary incisors. They are usually treated with a bite plane or with wiring techniques (braces). A bite plane is a rigid pad (usually acrylic) that is attached to the maxillary incisors, providing and anteriorly-inclined plane for the mandibular incisors to occlude against. Biting then produces anterior traction on the mandible which helps it to grow longer, in juveniles, reducing the malocclusion. Class III malocclusions are commonly seen in miniaturized breeds. Chewing in horses involves substantial lateral excursion of the mandible but also some antero-posterior movement. This later movement is impaired by abnormally long teeth during chewing. The treatment of a malocclusion

can also include shortening of an overlong tooth to unlock the movements of the mandible for normal chewing.

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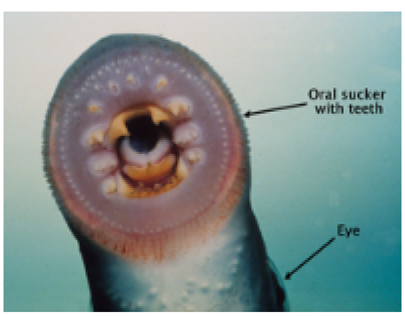
The Biology of the Tongue

The tetrapod tongue with mucosa and muscles originated in amphibians. It diversified greatly with key roles in food ingestion, gustation, swallowing and communication. The human tongue has four intrinsic and four extrinsic muscles, all innervated by the hyoglossal nerve. Its mucosa receives sensory innervation from four cranial muscles because it is formed with tissue contributions from four pharyngeal arches. Specializations of tongue structure and function are found in all classes of tetrapods, particularly among predator species.

Evolutionary origin

Most vertebrates have tongues. Cartilaginous and bony fishes have a "tongue" attached to the floor of the mouth but their structure does not contain muscle. Jawless fish like lampreys do have a muscular tongue. After they attach to the body of a host using their mouth as a suction cup with keratinous "teeth", they use their tongue muscles to rasp their abrasive tongue against the scales and skin of the host to cause the oozing of the body fluids on which they feed. The tongue structure and associated muscles in the lampreys are not homologous (did not have the same origin) to those of the tongues of tetrapods. There is no evidence, therefore, that the tetrapod tongue would have appeared among fishes.



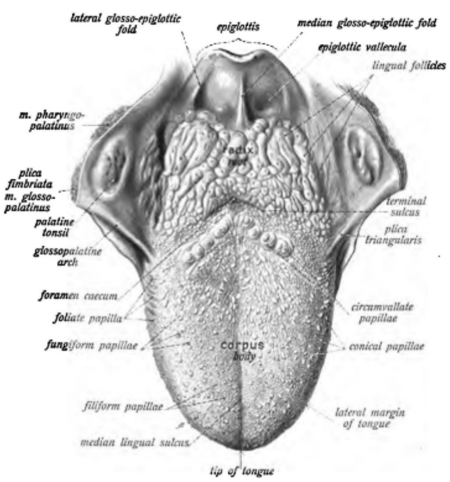
Jawless mouth of a river lamprey showing the abrasive tongue in

the center. More details.

The tongues of tetrapods seem to have originated among amphibians. Frogs and salamanders have muscular tongues that they use to ingest food and the structure is generally homologous to those of other classes of vertebrates.

The human tongue

The tongue has many roles including ingestion , deglutition (swallowing), chemical digestion (lingual lipase), sensation (taste, texture, temperature), swallowing, and speech. It is positioned over the floor of the oral cavity, attached to the mandible, the styloid processes of the temporal bones, and the hyoid bone.



The structure of the human tongue and attached structures (larynx, tonsils). More details.

The tongue is divided into two parts, an anterior oral part (body) and a posterior pharyngeal part (root). The separation is made by a V-shaped groove called terminal sulcus. The apex of the terminal sulcus points posteriorly and it is marked by a blind foramen, the foramen cecum, which is the remnant of a duct to an embryonic sac (thyroid diverticulum) that connected the tongue to the thyroid gland during early embryonic development.

The left and right sides of the tongue are separated along most of its length by a vertical section of fibrous tissue (lingual septum or median septum) that forms a groove (median sulcus) on the tongue's surface. An adult human tongue has a length of about 10 cm and a mass of about 65 g, mostly formed by skeletal muscle. The surface of the tongue is divided into dorsal (the upper, visible surface) and ventral (the inferior surface that faces the floor of the mouth) and it is formed by mucosa, a sheet of connective tissue + squamous epithelium that secretes mucus.

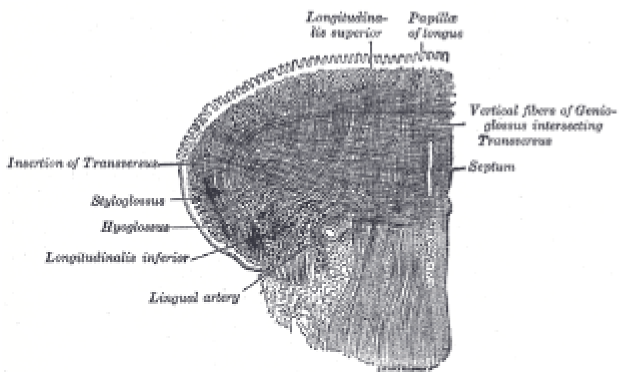
Muscles

Deep to the mucous membrane covering, the tongue is composed of four intrinsic muscles and four pairs of extrinsic muscles. The intrinsic tongue muscles insert into the tongue from origins within it, whereas the e xtrinsic tongue muscles insert from outside origins. The extrinsic muscles move the entire tongue in various directions, whereas the intrinsic muscles change the shape of the tongue (ex: curling or flattening it).

The intrinsic muscles are are the superior longitudinal muscle, the inferior longitudinal muscle, the vertical muscle, and the transverse muscle. The superior longitudinal muscle runs along the upper surface of the tongue under the mucous membrane, and elevates, assists in retraction of, or deviates the tip of the tongue. It originates near the epiglottis, at the hyoid bone, from the median fibrous septum.

The inferior longitudinal muscle lines the sides of the tongue, and is joined to the styloglossus muscle. The vertical muscle is located in the middle of the tongue and joins the superior and inferior longitudinal muscles. The

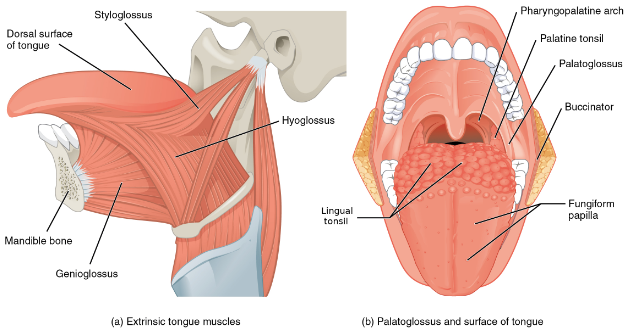
transverse muscle divides the tongue at the middle and is attached to the mucous membranes that run along the sides.



Coronal section of tongue showing its intrinsic muscles. More details.

The extrinsic muscles all include the word root glossus (glossus = “tongue”) and the muscle names are derived from where the muscle originates. The genioglossus (genio = “chin”) originates on the mandible and allows the tongue to move downward and forward. The styloglossus originates on the styloid bone, and allows upward and backward motion. The palatoglossus originates on the soft palate to elevate the back of the tongue, and the hyoglossus originates on the hyoid bone to move the tongue downward and flatten it.

Working in concert, these muscles perform three important digestive functions in the mouth: (1) position food for optimal chewing, (2) gather food into a bolus (rounded mass), and (3) position food so it can be swallowed.



The human tongue. Extrinsic muscles move the organ (left). Gustatory papilla contain the sensory receptors for taste and are located on the dorsum of the tongue (right). More details.

Mucosa

The dorsal surface of the tongue is formed by the masticatory oral mucosa. It contains areolar connective tissue with a variety of lingual glands and a keratinized stratified squamous epithelium . Lingual glands in the connective tissue secrete saliva, mucus and a watery serous fluid that contains the enzyme lingual lipase, which plays a minor role in breaking down fat but does not begin working until it is activated in the stomach.

The dorsal mucosa contains a high density of four types of lingual papillae. Filiform papillae cover most of the dorsal surface of the anterior 2/3 of the tongue, with fungiform interspaced. Filiform papillae are small, long, thin and lack taste buds. They have touch receptors are keratinized to create an abrasive surface on the tongue. Fungiform papillae are mushroom shaped with taste buds on their upper surface. Foliate papillae are four or five short vertical folds and are present on each side at the back of the tongue. They lack keratin and bear many taste buds. Circumvallate papillae are dome-shaped. Humans have 8 to 12 aligned in a V-shape immediately anterior to

the foramen cecum and sulcus terminalis. Each papilla consists of a projection of mucous membrane surrounded by a circular depression. The wall of the projection is called (vallum), and the circular sulcus is called fossa. Numerous taste buds are found in the vallum. Ducts of lingual salivary glands, known as Von Ebner's glands, empty a serous secretion into the fossa.

Human tongue with a conspicuous median sulcus and many fungiform papillae (red dots) distributed over the dorsal surface. More details.

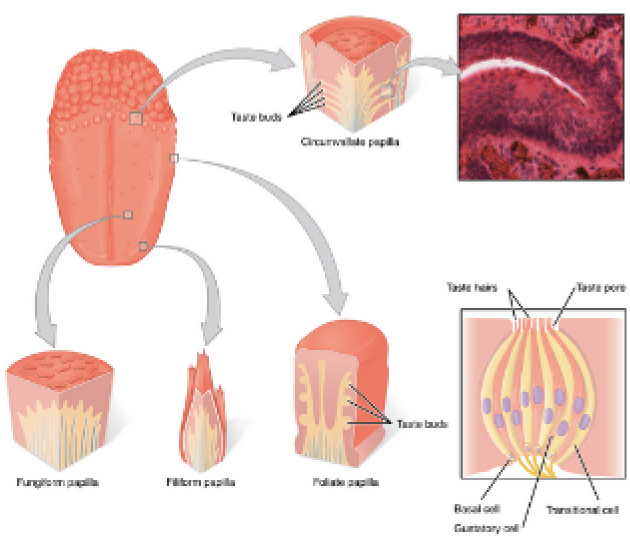
The mucosa of the ventral side of the tongue is mostly non-keratinized. A medial fold on it, the lingual frenulum, tethers the tongue to the floor of the

mouth. People with the congenital anomaly ankyloglossia, also known by “tongue tie,” have a lingual frenulum that is too short or otherwise malformed. Severe ankyloglossia can impair speech but it can be resolved with a simple surgery.

Gustation

Gustation is the special sense associated with the tongue. Within the structure of the papillae are taste buds that contain specialized gustatory receptor cells for the transduction of taste stimuli. The taste buds of the lingual papillae are round epithelial structures containing basal (stem) cells, gustatory receptor cells and supporting cells.

The gustatory receptor cells are sensitive to the chemicals contained within foods that are ingested, and they release neurotransmitters based on the amount of the chemical in the food. Neurotransmitters from the gustatory cells can activate sensory neurons in the facial, glossopharyngeal, and vagus cranial nerves.



The tongue and its four types of lingual papillae, three of which containing taste buds, which in turn house the gustatory receptor

cells. Chemicals in food bind to membrane receptors in the gustatory receptors cells, which then send neural stimuli to the brain. More details.

Salty taste is simply the perception of sodium ions (Na+) in the saliva. When you eat something salty, the salt crystals dissociate into the component ions Na+ and Cl–, which dissolve into the saliva in your mouth. The Na+ concentration becomes high outside the gustatory cells, creating a strong concentration gradient that drives the diffusion of the ion into the cells. The entry of Na+ into these cells results in the depolarization of the cell membrane and the generation of a receptor potential.

Sour taste is the perception of H+ concentration. Just as with sodium ions in salty flavors, these hydrogen ions enter the cell and trigger depolarization. Sour flavors are, essentially, the perception of acids in our food. Increasing hydrogen ion concentrations in the saliva (lowering saliva pH) triggers progressively stronger graded potentials in the gustatory cells. For example, orange juice—which contains citric acid—will taste sour because it has a pH value of approximately 3. Of course, it is often sweetened so that the sour taste is masked.

The first two tastes (salty and sour) are triggered by the cations Na+ and H+. The other tastes result from food molecules binding to a G protein–coupled receptor. A G protein signal transduction system ultimately leads to depolarization of the gustatory cell. The sweet taste is the sensitivity of gustatory cells to the presence of glucose dissolved in the saliva. Other monosaccharides such as fructose, or artificial sweeteners such as aspartame (NutraSweet™), saccharine, or sucralose (Splenda™) also activate the sweet receptors. The affinity for each of these molecules varies, and some will taste sweeter than glucose because they bind to the G protein–coupled receptor differently.

Bitter taste is similar to sweet in that food molecules bind to G protein–coupled receptors. However, there are a number of different ways in which this can happen because there are a large diversity of bitter-tasting molecules. Some bitter molecules depolarize gustatory cells, whereas others hyperpolarize gustatory cells. Likewise, some bitter molecules increase G protein activation within the gustatory cells, whereas other bitter molecules decrease G protein activation. The specific response depends on which molecule is binding to the receptor.

One major group of bitter-tasting molecules are alkaloids. Alkaloids are nitrogen containing molecules that are commonly found in bitter-tasting plant products, such as coffee, hops (in beer), tannins (in wine), tea, and aspirin. By containing toxic alkaloids, the plant is less susceptible to microbe infection and less attractive to herbivores.

Therefore, the function of bitter taste may primarily be related to stimulating the gag reflex to avoid ingesting poisons. Because of this, many bitter foods that are normally ingested are often combined with a sweet component to make them more palatable (cream and sugar in coffee, for example). The highest concentration of bitter receptors appear to be in the posterior tongue, where a gag reflex could still spit out poisonous food.

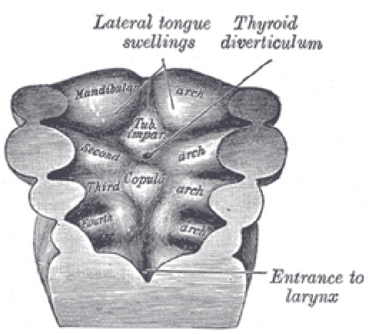
The taste known as umami is often referred to as the savory taste. Like sweet and bitter, it is based on the activation of G protein–coupled receptors by a specific molecule. The molecule that activates this receptor is the amino acid L-glutamate. Therefore, the umami flavor is often perceived while eating protein-rich foods. Not surprisingly, dishes that contain meat are often described as savory.

Once the gustatory cells are activated by the taste molecules, they release neurotransmitters onto the dendrites of sensory neurons. These neurons are part of the facial and glossopharyngeal cranial nerves, as well as a component within the vagus nerve dedicated to the gag reflex. The facial nerve connects to taste buds in the anterior third of the tongue. The glossopharyngeal nerve connects to taste buds in the posterior two thirds of the tongue. The vagus nerve connects to taste buds in the extreme posterior of the tongue, verging on the pharynx, which are more sensitive to noxious stimuli such as bitterness.

Development

The tongue begins to develop in the fourth week of embryogenesis. Its mucosa is formed with contributions from the first four pharyngeal arches. The first step is the development of a median swelling called tuberculum impar on the first pharyngeal arch.

In the fifth week a pair of lateral swellings, the lateral lingual swellings*(distal tongue buds)* one on the right side and one on the left, form on the first pharyngeal arch. These lingual swellings quickly expand, cover the tuberculum impar and continue to develop through prenatal development. They form the anterior part of the tongue that makes up two thirds of the length of the tongue. The line of their fusion is marked by the median sulcus.



Floor of the pharynx in a human embryo about twenty-six days old. The major components that will form the tongue develop from the first four pharyngeal

arches. More details.

In the fourth week a swelling appears from the second pharyngeal arch, in the midline, called the copula. During the fifth and sixth weeks the copula is overgrown by a swelling from the third and fourth arches (mainly from the third arch) called the hypopharyngeal eminence, and this develops into the posterior part of the tongue (the other third). The hypopharyngeal eminence develops mainly by the growth of endoderm from the third pharyngeal arch. The boundary between the two parts of the tongue, the anterior from the first arch and the posterior from the third arch is marked by the terminal sulcus. The terminal sulcus is shaped like a *V* with the tip of the V situated posteriorly. At the tip of the terminal sulcus is the foramen caecum, which is the point where the embryological thyroid begins to descend.

In contrast with the origin of the mucosa described above, the intrinsic and extrinsic muscles of the tongue do not originate from the pharyngeal arches. The are formed by a group of cells from the somites of the embryo. These cells migrate ventrally and anteriorly to enter the mouth and form the lingual musculature. They are innervated by the hypoglossal nerve which provides the motor control to the tongue.

Innervation

The tongue is innervated by motor fibers, special sensory fibers for taste, and general sensory fibers for sensation.

- Motor supply for all intrinsic and extrinsic muscles of the tongue is supplied by the hypoglossal nerve (CN XII)

Innervation of taste and sensation is different for the anterior and posterior part of the tongue because they are derived from different embryological structures.

Anterior two thirds of tongue (anterior to the terminal sulcus):

- Touch: lingual branch of the trigeminal nerve (CN V from 1st arch)

- Taste: chorda tympani branch of the facial nerve (CN VII from 2nd arch)

Posterior one third of tongue:

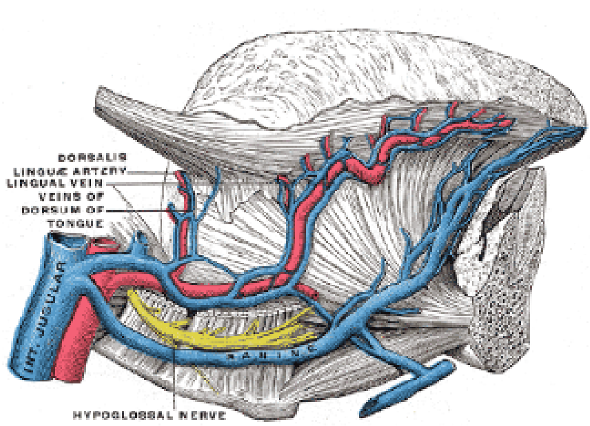
- Touch and taste: glossopharyngeal nerve (CN IX from 3rd arch)

Base of tongue

- Touch and taste: internal branch of the superior laryngeal nerve (itself a branch of the vagus nerve, CN X from 4th arch)

Blood supply

The tongue receives its blood supply primarily from the lingual artery, a branch of the external carotid artery. The lingual veins drain into the internal jugular vein. The floor of the mouth also receives blood from the lingual artery. The tongue has secondary blood supplies from the tonsillar branch of the facial artery and the ascending pharyngeal artery.



Blood supply of the human tongue. More details.

Diversity

The tongue has assumed an extensive variety of sizes and shapes in tetrapods, commonly reflecting the diet and foraging modes of animals. Its association with the hyoid allows it to have a cartilaginous or even bony structure in many species.

Many mammals have a tongue that is much longer, relative to body size, and versatile than that of humans. This is particularly true in quadruped herbivores. Having their forelimbs on the ground, many of these animals use their tongues to collect and manipulate food before ingesting it.

A giraffe uses its long and versatile tongue to harvest leaves and other food items. Specimen at the National Museum of Natural History. More details.

Some predators have tongues that are specially adapted for catching prey. Examples such as woodpeckers, anteaters, frogs and cameleons are present in all classes of tetrapods. The tips of the tongues can be pointy, sticky and have barbs to stick to or impale their prey. The tongue is usually long for increased range of action and it can be projectible.

Anteaters

The giant anteater has no teeth and is capable of only very limited jaw movement. It relies on limited rotation of the lower jaw to open and close its mouth. This is accomplished by its relatively underdeveloped masticatory muscles. Jaw depression creates an oral opening large enough for the slender tongue to flick out.

The giant anteater, *Myrmecophaga tridactyla*, with its tongue extended. More details.

The tongue is typically 60 cm long with a small rounded tip. Along its length it is covered in backward-curving papillae and coated in thick, sticky saliva secreted from large salivary glands. This allows the giant anteater to collect insects by extending the tongue into ant or termite mounds. During feeding, the tongue moves in and out around 160 times per minute and the anteater swallows at a higher rate than most other mammals.

Woodpeckers

Woodpeckers feed mainly on insects and their grubs taken from living and dead trees, and other arthropods, along with fruit, nuts and sap from live trees. The family is noted for its ability to acquire wood-boring grubs using the bill for hammering. The insect prey most commonly taken are those found inside tree trunks and in crevices in the bark. These include beetles and their grubs, ants, termites, spiders, and caterpillars. They may be obtained either by gleaning or, more famously, by excavating wood. Having hammered a hole into the wood, the prey is impaled by a long tongue that is pointy and barbed near the tip. The long tongue is then retracted into the mouth. The muscle slides over the hyoid cartilage which has posterior horns that can extend around the brain to attach to the superior base of the beak. This allows room to fit the entire retracted tongue into the mouth.

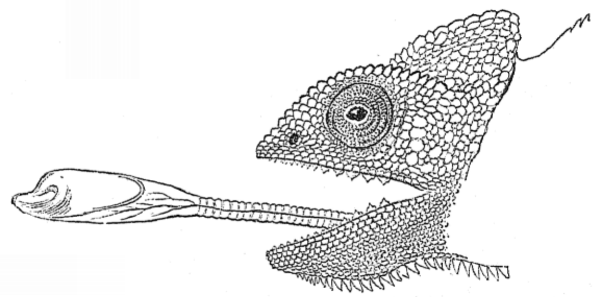
The tongue of the great spotted woodpacker *(Dendrocopos major*) is barbed at the tip to effectively retrieve insect larvae after impaling them. More details.

Chameleons

The chameleon has a catapult system that allows it to launch the tongue up to 1.5 body lengths away to catch prey. Tongue projection occurs extremely quickly, reaching the prey in as little as 0.07 seconds with an accelerations that exceed 40 gravities. The power with which the tongue is launched (~3000 W kg−1) exceeds the physiological limit of muscles, indicating the presence of an amplification system. The muscle therefore loads an elastic system that launches the tongue when triggered.

This system is formed by a highly modified hyoid bone, tongue muscles, and a collagenous sheath. The hyoid bone has an elongated projection, called the entoglossal process. A cylindric sheath of collagen covers the entoglossal process and connects it to the surrounding accelerator muscle. This muscle is also cylindric and its fibers are arranged radially. When the accelerator muscle contracts around the entoglossal process, it becomes thinner and has to expand longitudinally along the length of the bone because muscle tissue is not compressible. This longitudinal expansion stretches the collagenous sheath longitudinaly, storing a large amount of energy that will produce the work when the tongue is launched. Continued contraction of the accelerator muscle triggers the system. The entoglossal process end abruptly at its anterior end. When the accelerator muscle expands longitudinally it slides over the entoglossal process until some of it slides off the tip. This produces and anterior anchorage that allows the collagen sheath to release the stored energy like a stretched rubber band, launching itselft and the accelerator muscle anteriorly.

If the target is hit, the prey is usually captured in the sticky pad that covers the anterior end of the tongue. A retractor muscle, the hyoglossus, connects the accelerator muscle to the hyoid and is responsible for drawing the tongue back into the mouth.



Tongue projection by the chameleon *Chamaeleon calcaratus*. More details.

Other groups of animals also exhibit specializations of elongated structures that facilitate ingestion. These organs may be analogous to tongues, such as the proboscis of a butterfly or the radula on a mollusc. These structures are not homologous with the tongues found in vertebrates, however, and important differences in structure and function can be observed. For example, the proboscis of a butterfly is formed by two jaws held together to form a tube and it is used to suck instead of licking.

Figure credits

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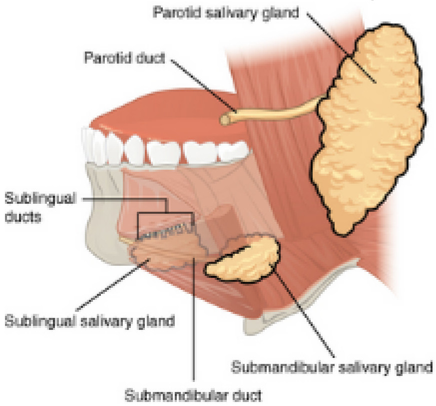
The Salivary Glands

Saliva has many important roles such as lubricating the mouth, hydrating, lubricating and digesting the food before swallowing, washing away and digesting food particles from the teeth and supporting some remineralization of the enamel. Saliva is produced by major and minor salivary glands. The major glands are the parotid, submandibular and sublingual salivary glands. Minor salivary glands are very small but very numerous and distributed over the entire oral mucosa. Salivary glands vary in the composition of their product, ranging from highly serous to highly mucous. Saliva has some special uses in animals, forming the venom of vipers, being used as glue for nest building by swifts or as a defense by camels.

Saliva is a watery substance formed in the mouths of animals, secreted by the salivary glands. Human saliva is motly water with electrolytes, mucus, white blood cells, epithelial cells, glycoproteins, enzymes (such as amylase and lipase), antimicrobial agents such as secretory IgA and lysozyme. Saliva keeps the oral mucosa wet, protecting the tissues and facilitating gustation. It also hydrates and lubricates the food with mucus, to facilitate swallowing. The enzymes found in saliva begin the digestion of starches and fats in the mouth. This helps breaking down food particles entrapped within dental crevices and protects the teeth from bacterial decay.

Estimates of daily production range from 0.75 to 1.5 liters but salivation nearly stops during sleep. In humans, the submandibular gland secretes 70–75% of the saliva while the parotid gland secretes about 20–25% and small amounts are secreted by the other salivary glands.



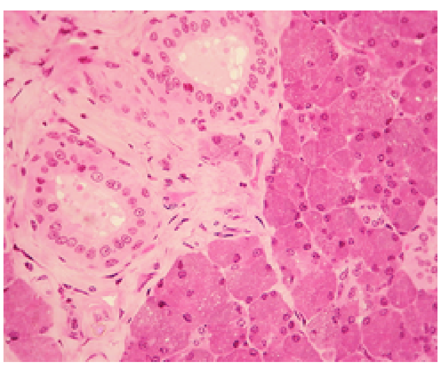
The major salivary

glands are located outside the oral mucosa and deliver saliva into the mouth through ducts. More details.

Various animals have special uses for saliva. Some swifts use a gummy saliva to build nests on the walls of caves. Many snakes hunt with venomous saliva injected by fangs. Some caterpillars secrete silk from their salivary glands.

Anatomy of mammalian salivary glands

Salivary glands are divided into lobules containing acini and ducts. Secretory cells are found in a group, or acinus (plural acini). Each acinus is located at the terminal part of the gland connected to the ductal system, with many acini within each lobule of the gland. Each acinus consists of a single layer of cuboidal epithelial cells surrounding a lumen, a central opening where the saliva is deposited after being produced by the secretory cells. The three forms of acini are classified in terms of the type of epithelial cell present and the secretory product being produced: serous, mucoserous and mucous.

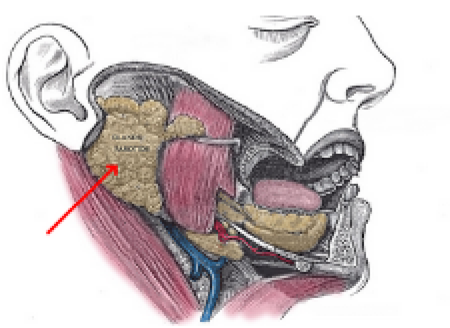


Histological section of the parotid gland, showing acini and ducts. More details.

Secretions from the acini are drained by intercalated ducts which join to form striated ducts. These drain into ducts situated between the lobes of the gland (called interlobar ducts or secretory ducts). All of the human salivary glands terminate in the mouth.

Parotid gland

A pair of mainly serous salivary glands located below and in front of each ear canal, draining their secretions into the vestibule of the mouth through the parotid duct. Each gland lies posterior to the mandibular ramus and anterior to the mastoid process of the temporal bone. It has four surfaces: superficial or lateral, superior, anteromedial, and posteromedial. It also has three borders: anterior, medial, and posterior. The gland can be easily palpated as it rests immediately deep to the skin.



Lateral view of the major salivary glands. More details.

The parotid duct, a long excretory duct, emerges from the anterior surface of each gland, superficial to the masseter muscle. The duct pierces the buccinator muscle and opens into the mouth on the inner surface of the cheek, usually opposite the maxillary second molar. The parotid papilla is a small elevation of tissue that marks the opening of the parotid duct on the inner surface of the cheek.

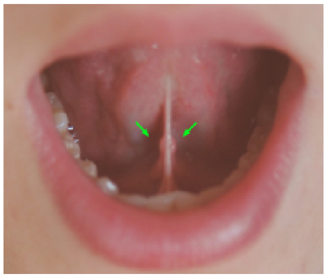
The papilla of the parotid duct drains saliva from the parotid gland into the mouth. More details.

The superficial temporal and the maxillary artery are the branches of the external carotid artery that supply the parotid gland. Venous return is to the retromandibular veins.

Submandibular gland

The paired submandibular gland is located next to the lower jaw, superior to the digastric muscle. It is divided into superficial (most of the gland) and deep lobes, which are separated by the mylohyoid muscle. Its products are

drained by the submandibular duct or duct of Wharton. This is a 5 cm long duct drains saliva into the mouth through the sublingual caruncles on each side of the lingual frenulum on the ventral surface of the tongue.



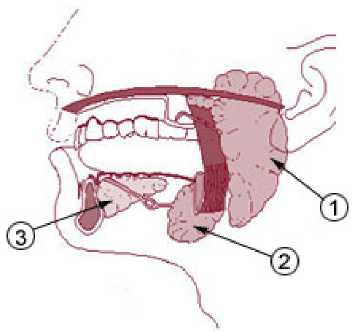
Location of the sublingual caruncle where the submandibular duct empties the saliva produced by the submandibular gland. More details.

The secretion produced is a mixture of both serous fluid (rich in salivary amylase) and mucus. Approximately 65-70% of saliva in the oral cavity is produced by the submandibular glands, even though they are much smaller than the parotid glands. This gland can be palpated at a position inferior and medial to the angle of the mandible .

Within each lobule, the acini (also called alveoli) of the submandibular glands are grouped in adenomeres. The acini within an adenomere are all composed of serous or mucous cells. The gland is classified as tubuloacinar. It has long striated ducts and short intercalated ducts.

The submandibular gland receives its blood supply from the facial and lingual arteries. The gland is supplied by sublingual and submental arteries and drained by common facial and lingual veins.

Sublingual gland



Location of the major salivary glands. 1. Parotid gland, 2. Submandibular gland. 3. Sublingual gland. More details.

The sublingual glands are a pair of major salivary glands located inferior to the tongue, anterior to the submandibular glands. They are the smallest, most diffuse, and the only unencapsulated major salivary glands. The secretion produced is mainly mucous in nature, however, it is categorized as a mucoserous (mixed) gland. Saliva is secreted through 8-20 excretory ducts known as the Rivinus ducts. The largest of all, the sublingual duct (of Bartholin) joins the submandibular duct to drain through the sublingual caruncle. Approximately 5% of saliva entering the oral cavity comes from

these glands. The gland receives its blood supply from the sublingual and submental arteries.

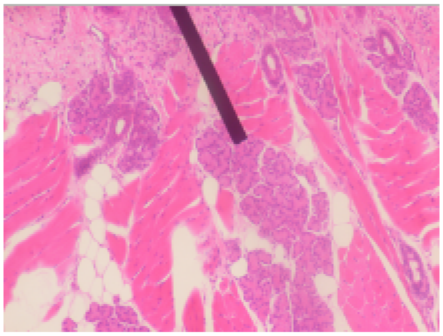
Minor salivary glands

There are 800 to 1,000 minor salivary glands located throughout the oral cavity within the submucosa of the oral mucosa in the tissue of the buccal, labial, and lingual mucosa, the soft palate, the lateral parts of the hard palate, and the floor of the mouth. They are 1 to 2 mm in diameter and unlike the major glands, they are not encapsulated by connective tissue, only surrounded by it. The gland has usually a number of acini connected in a tiny lobule. A minor salivary gland may have a common excretory duct with another gland, or may have its own excretory duct. Its secretion is mainly mucous and the innervation is provided by the facial cranial nerve (CN VII).

Von Ebner's glands

Von Ebner's glands are seroussalivary glands which reside adjacent to the fossae of the circumvallate and foliate papillae just anterior to the terminal sulcus. These glands secrete many enzymes including lingual lipase and begin lipidhydrolysis in the mouth. They empty their serous secretion into the fossae of the foliate and circumvallate papillae. This secretion presumably flushes material from the moat to enable the taste buds to respond rapidly to changing stimuli.

Von Ebner's glands are innervated by cranial nerve IX, the glossopharyngeal nerve.



Human Von Ebner's gland. More details.

Innervation

Salivary glands are innervated by the parasympathetic and sympathetic divisions of the autonomic nervous system. Parasympathetic stimulation evokes a copious flow of saliva. In contrast, sympathetic stimulation produces either a small flow rich in protein or no flow at all.

- Parasympathetic innervation to the salivary glands is carried via cranial nerves. The parotid gland receives its parasympathetic input from the glossopharyngeal nerve (CN IX) via the otic ganglion, while the submandibular and sublingual glands receive their parasympathetic input from the facial nerve (CN VII) via the submandibular ganglion.
- Sympathetic innervation of the salivary glands takes place via spinal nerves in the thoracic segments T1-T3. The pre-ganglionic neurons synapse in the superior cervical ganglion. The postganglionic neurons release norepinephrine which binds β-adrenergic receptors on the acinar and ductal cells of the salivary glands and leads to increased salivation.

In the absence of food, parasympathetic stimulation keeps saliva flowing at appropriate levels for speech, swallowing, rest and sleep. Salivation increases when you smell, see, taste or think about food, even if you do not eat it. Drooling is an extreme instance of overproduction of saliva. During times of stress, such as before speaking in public, sympathetic stimulation

takes over inhibiting parasympathetic stimulation thus reducing salivation. This results in the symptom of dry mouth that we associate with anxiety. If you dehydrate, salivation is reduced causing the mouth to feel dry and prompting you to drink water.

While you are eating, food chemicals stimulate taste receptors on the tongue. These send neural signals to the superior and inferior salivatory nuclei in the brain stem. These two nuclei then send back parasympathetic stimuli through the glossopharyngeal and facial nerves to stimulate salivation. Even after you swallow food, salivation is increased to cleanse the mouth and to water down and neutralize any irritating chemical remnants, such as that hot sauce in your burrito. Most saliva is swallowed along with food and is reabsorbed, so that fluid is not lost.

Development

The salivary glands arise as epithelial buds in the oral cavity between week 6 to 7 and extend into the underlying mesenchyme. The first sign is a thickening of the epithelium on the side of the tongue, outside the dental lamina in the labiogingival sulcus.

The parotid salivary glands are the first major salivary glands formed. The epithelial buds of these glands are located on the inner part of the cheek. These buds grow posteriorly toward the developing ears and branch to form solid cords with rounded terminal ends near the developing facial nerve. Later, at around 10 weeks of prenatal development, these cords are canalized and form ducts, with the largest becoming the parotid duct for the parotid gland. The rounded terminal ends of the cords form the acini of the glands. Secretion by the parotid glands via the parotid duct begins at about 18 weeks of gestation.

The submandibular salivary glands appear late in the sixth week of prenatal development. They develop from epithelial buds in the sulcus surrounding the sublingual folds on the floor of the primitive mouth. Solid cords branch from the buds and grow posteriorly, lateral to the developing tongue. The cords of the submandibular gland later branch further and then become canalized to form the ductal part. The submandibular gland acini develop

from the cords' rounded terminal ends at 12 weeks, and secretory activity via the submandibular duct begins at 16 weeks. Growth of the submandibular gland continues after birth with the formation of more acini. Lateral to both sides of the tongue, a linear groove develops and closes over to form the submandibular duct.

The sublingual salivary glands are the last major salivary glands to develop. They appear in the eighth week of prenatal development. They originate from epithelial buds in the sulcus surrounding the sublingual folds on the floor of the mouth, lateral to the developing submandibular gland. These buds branch and form into cords that canalize to form the sublingual ducts associated with the gland. The rounded terminal ends of the cords form acini.

Composition of saliva

Saliva is essentially (98 to 99.5 percent) water. The remaining 4.5 percent is a complex mixture of ions, glycoproteins, enzymes, growth factors, and waste products. The most important ingredient in saliva is likely the enzyme salivary amylase for initiating the breakdown of carbohydrates. Food does not spend enough time in the mouth to allow all the carbohydrates to break down, but pancreatic amylase can continue the job in the intestines. Bicarbonate and phosphate ions function as chemical buffers, maintaining saliva at pH 6.35 to 6.85. Salivary mucus helps lubricate food, facilitating movement in the mouth, bolus formation, and swallowing. Saliva contains immunoglobulin A, which prevents microbes from penetrating the epithelium, and lysozyme, which makes saliva antimicrobial. Saliva also contains epidermal growth factor (EGF), which maintains and renovates the epithelium of the digestive tube.

Each of the major salivary glands secretes a unique formulation of saliva according to its cellular makeup. For example, the parotid glands secrete a watery solution that contains salivary amylase. The submandibular glands have cells similar to those of the parotid glands, as well as mucus-secreting cells. Their saliva also contains amylase but in a liquid thickened with mucus. The sublingual glands contain mostly mucous cells, and they secrete the thickest saliva with the least amount of salivary amylase.

Saliva sampled in the mouth contains water, electrolytes, mucus, antibacterial compounds and various enzymes.

- Water: 99.5%
- Electrolytes:
    - 2–21 mmol/L sodium (lower than blood plasma)
    - 10–36 mmol/L potassium (higher than plasma)
    - 1.2–2.8 mmol/L calcium (similar to plasma)
    - 0.08–0.5 mmol/L magnesium
    - 5–40 mmol/L chloride (lower than plasma)
    - 25 mmol/L bicarbonate (higher than plasma)
    - 1.4–39 mmol/L phosphate (higher than plasma)
    - Iodine (concentration is usually higher than plasma but varies with diet)
- Mucus (mucopolysaccharides and glycoproteins)
- Antibacterial compounds (thiocyanate, hydrogen peroxide, and secretory immunoglobulin A)
- Epidermal growth factor (EGF): regenerates spithelium.
- Various enzymes
    - α-amylase, or ptyalin, secreted by the acinar cells of the parotid and submandibular glands. Starts the digestion of starch in the mouth at neutral pH.
    - Lingual lipase, which is secreted by the acinar cells of the sublingual gland. It has a pH optimum around 4.0 so it is not activated until entering the acidic environment of the stomach.
    - Kallikrein, an enzyme that catalyzes the production of bradykinin, a vasodilator. It is secreted by the acinar cells of all three major salivary glands
    - Antimicrobial enzymes
        - Lysozyme
        - Salivary lactoperoxidase
        - Lactoferrin
        - Immunoglobulin A

- Proline-rich proteins (function in enamel formation, Ca2+-binding, microbe killing and lubrication)[5]
- Minor enzymes include salivary acid phosphatases A+B, N-acetylmuramoyl-L-alanine amidase, NAD(P)H dehydrogenase (quinone), superoxide dismutase, glutathione transferase, class 3 aldehyde dehydrogenase, and glucose-6-phosphate isomerase.

- Cells: some white blood cells and many bacterial cells
- Opiorphin, a pain-killing substance found in human saliva.
- Haptocorrin, a protein which binds to Vitamin B12 to protect it against degradation in the stomach.

Clinical issues

Sialolithiasis is the development of a salivary calculus or stone which may block the duct causing pain and swelling of the gland. Symptoms occur in 0.5% of the population, most commonly in the submandibular duct of men. The stones can grow to several millimeters in diameter and their removal may involve hydration, massage, shock waves or surgery.

A white salivary stone (arrow) seen in the right submandibular (Wharton’s) duct. More details.

Dysfunctions of the s alivary gland usually present as hypofunction (reduced production of saliva) which causes xerostomia (dry mouth). Salivary gland dysfunction is a predictable side-effect of radiotherapy in the head and neck region. Chemotherapy may also impair salivary flow. Both treatments tend to injury the epithelial cells of the salivary glands due to their high metabolism.

Lack of saliva increases the risk of dental caries. Saliva has antimicrobial agents as well as ions that promote the remineralization of tooth enamel. Conditions that cause salivary gland hypofunction as well as conditions that lead the patient to sleep with the mouth open tend to be correlated with increased occurrence of cavities.

Mumps is a viral infection of the nasal passages and pharynx by the paramyxovirus and it most commonly attacks the parotid glands. Enlargement and inflammation of the parotid glands is typical, causing a characteristic swelling between the ears and the jaw. Symptoms include fever and throat pain, which can be severe when swallowing acidic substances such as orange juice. Mumps vaccines have greatly reduced the incidence of mumps, however. According to the U.S. Centers for Disease Control and Prevention (CDC), only 11 cases were reported in the US in 2011.

Diversity

The salivary glands of many species produce amylase, but in some species they are modified to produce other proteins. The venom glands of venomous snakes, Gila monsters, and some shrews are modified salivary glands. In insects, salivary glands can be used to produce silk or glues. In the salivary glands of flies, the high demand for gene transcription is met by polytene chromosomes that have thousands of DNA strands (copies) in them.

Glue to construct bird nests

Birds in the swift family, Apodidae, generally build nests on very exposed surfaces of rocks to avoid predators. They produce a viscous saliva during the nesting season to glue together materials to construct a nest. As an extreme, two species of swifts in the genus Aerodramus build nests on the walls of caves using only their saliva.

Spitting

Camels and llamas may spit at a threat as a defensive behavior . They can use it against wolves or people. In addition to a considerable volume of saliva, some stomach contents may also be added to the spit.

Wound licking

It is an instinctive response of many vertebrates to lick an injury. Dogs, cats, small rodents, horses, and primates are commonly observed licking their wounds. Saliva contains tissue factor which promotes blood clotting, and lysozymes that attack bacteria. Wound liking may increase the risk of bringing an infection into the mouth and digestive tract and it is not recommended to humans with access to clean water and medication for treating wounds. The behavior is understandable in animals living in the wild where the the benefits of sanitizing a wound with saliva may overcome the risks of infecting the mouth.

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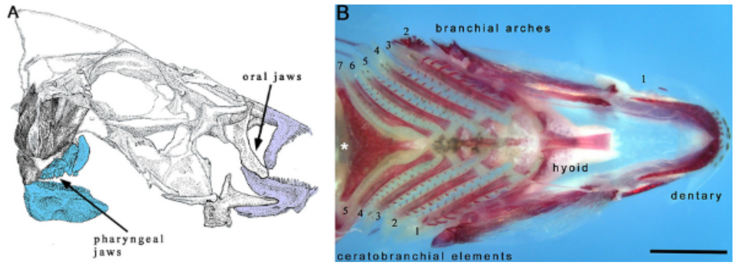
Mechanisms of Deglutition
Swallowing is the transport of food from the mouth into the stomach. The general mechanism is peristalsis of the digestive tube, but fishes can help it using mucociliary transport or pharyngeals jaws. Frogs add a muscular tongue and retraction of the eyes and some birds use gravity. Mammals have a palate and a muscular soft palate that protects the nasal cavity from the entrance of food. The epiglottis prevents food from entering the larynx. Its effectiveness is reduced in adult humans, however, because our larynx is permanently descended and the epiglottis does not contact the soft palate. Imperfect swallowing results in chocking or pulmonary aspiration. The human larynx has most likely descended in response to selection for loud and low pitched voice. In newborns, the larynx is not yet descended however and they suckle by producing negative pressures in the mouth to extract milk from the nipple.

Swallowing or deglutition is the transport of a substance from the mouth to the stomach. It is an important part of eating and drinking. The portion of food or drink that is transported in one swallow is called bolus. Deficient swallowing is called dysphagia and it may allow some of the bolus to enter the airways causing choking or pulmonary aspiration.

Diversity of mechanisms

Vertebrates have incorporated a variety of mechanisms to facilitate the transport of food from the mouth into the esophagus. Several groups make use of multiple mechanisms simultaneously.

Fishes use the water flow produced by ram ventilation or the buccal pump to bring food into the mouth. The flowing water exits through the gill openings and does not enter the esophagus. Food items in the mouth are moved into the esophagus by contractions of the pharyngeal musculature and movement of the pharyngeal jaws, when present.



Mouth structure of a cichlid fish. A. Schematic drawing of the bony elements including pharyngeal jaws with teeth. B. Dorsal view of the lower pharyngeal and oral elements of a cleared and stained skeleton in a juvenile *Dimidiochromis compressicepsa.* Notice the spaces between the gill arches through which most water exits the mouth. More details.

The mouths of many fishes and amphibians are lined by a ciliated epithelium that employs mucociliary transport to move any particles in the mouth toward the esophagus. Touch receptors in the oral mucosa stimulate the beating of the cilia when a particle contacts the epithelium. The entire lining of the mouth therefore works as a conveying belt transporting food into the esophagus. Frogs can transport and entire cricket from the mouth into the esophagus through mucociliary transport alone.

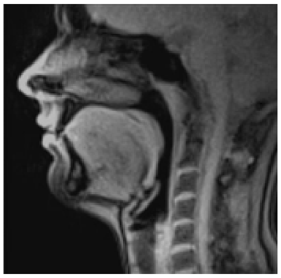
Many frogs have relatively large eyes that protrude on the surface of the head and can be retracted for protection. When the eyeballs are retracted into the think skull, however, they intrude into the roof of the mouth, forming a convexity that reduces the free internal volume of the mouth. The animals actively use this to facilitate food transport into the esophagus. When a frog swallows, it both retracts its eyeballs and contracts the floor of the mouth to push the food contained in the mouth posteriorly.

Pelican swallowing a fish. More details.

Many birds use gravity to facilitate swallowing. In events such as a seagull swallowing a fish or a stork swallowing a frog, swallowing consists largely of the bird lifting its head with its beak pointing up and guiding the prey with the tongue and jaws so that the prey slides down the pharynx and esophagus.

Swallowing in humans

The entire process takes about 4 to 8 seconds for solid food and about 1 second for very soft food and liquids. Although this sounds quick and effortless, deglutition is, in fact, a complex process that involves both the skeletal muscle of the tongue and the muscles of the pharynx and esophagus. It is aided by the presence of mucus and saliva. Swallowing consists of three phases: an oral, pharyngeal and esophageal phase. It involves many smooth muscles of the pharynx and esophagus. The oral phase is voluntary and controlled by the cerebral cortex whereas the autonomic nervous system (ANS) coordinates the pharyngeal and esophageal phases.



Swallowing movements during juice drinking filmed in MRI. Click to watch.

Phases

Oral phase

Posterior displacement of the bolus

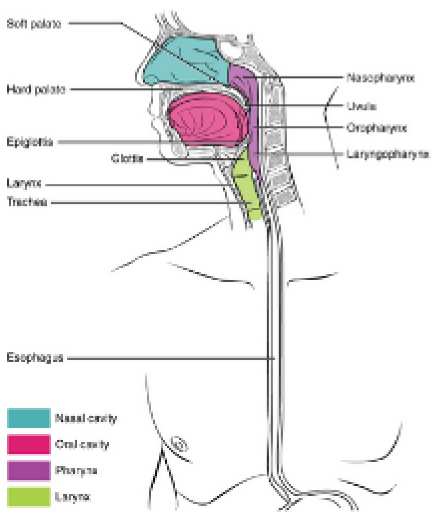
During the oral phase of swallowing, food has already been mechanically broken down and mixed with saliva at the mouth, forming a bolus. The tongue propels the bolus posteriorly into the pharynx. The superior longitudinal muscle elevates the apex of the tongue to make contact with the hard palate and the bolus is propelled to the posterior portion of the oral cavity. Once the bolus contacts the palatoglossal arch of the oropharynx, it triggers the pharyngeal phase, which is involuntary. Touch receptors initiating this reflex are scattered over the base of the tongue, the palatoglossal and palatopharyngeal arches, the tonsillar fossa, uvula and posterior pharyngeal wall.

Pharyngeal phase

For the pharyngeal phase to work properly all other exit routes from the pharynx must be occluded, including the nasopharynx and the larynx. When the pharyngeal phase begins, other activities such as chewing, breathing, coughing and vomiting are inhibited.

Closure of the nasopharynx

The soft palate is tensed by the tensor palatini muscle and elevated by the levator palatini muscle. The closure of the passage is helped by simultaneous approximation of the walls of the pharynx to the posterior free border of the soft palate. This movement is carried out by the palatopharyngeus muscle and the upper part of the superior pharyngeal constrictor muscle.



The pharynx extends from the nasal cavity to the esophagus passing posterior to the oral cavity and the larynx. More details.

The pharynx, larynx and hyoid are elevated to receive the bolus

The pharynx and larynx are pulled upward and forward by the stylopharyngeus, salpingopharyngeus and palatopharyngeus muscles. The hyoid is also elevated by the digastric and stylohyoid muscles, further lifting the pharynx and larynx with it. The entrance into the airways is closed by: 1) Retroversion of the epiglottis, which covers the entrance; 2) Adduction of the aryepiglottic folds. The aryepiglotticus muscle contracts, causing the arytenoids to appose each other and bring the aryepiglottic folds together; 3) Adduction of the false vocal folds; 4) Adduction of the true vocal folds by contraction of the lateral cricoarytenoids and the oblique and transverse arytenoid muscles.

This phase of the swallowing reflex is controlled through cranial nerves V, X, XI and XII. The respiratory center of the medulla is directly inhibited by the swallowing center for the brief time that it takes to swallow, causing deglutition apnea.

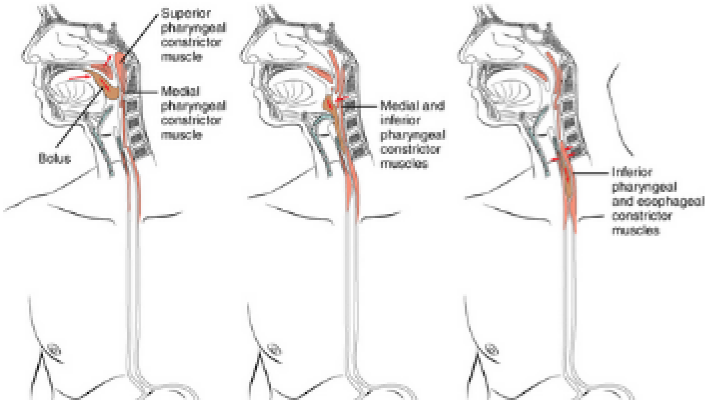
Opening of the auditory tube

The auditory (Eustachian) tube is and air-filled passage that connects the nasopharynx to the middle ears but it remains collapsed most of the time. The actions of the levator palatini, tensor palatini and salpingopharyngeus muscles in the closure of the nasopharynx and elevation of the pharynx open the auditory tube. This equalizes the pressure between the nasopharynx and the middle ear. It does not contribute to swallowing, but happens as a consequence of it. This is why swallowing helps alleviate pressure in the ears when a plane is taking off or landing.

Closure of the oropharynx

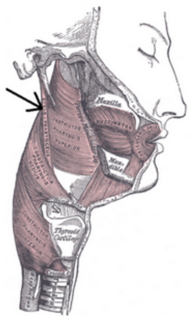
The oropharynx is kept closed by the tongue, preventing the bolus from returning into the mouth. The tongue is held in position by the palatoglossus muscle, the styloglossus muscle and the intrinsic muscles of tongue.

Bolus is moved through the pharynx



Deglutition includes the voluntary phase and two involuntary phases: the pharyngeal phase and the esophageal phase. More details.

The bolus moves down towards the esophagus by pharyngeal peristalsis which takes place by sequential contraction of the superior, middle and inferior pharyngeal constrictor muscles. The lower part of the inferior constrictor is normally closed and only opens for the advancing bolus. Gravity plays only a small part in swallowing and it is possible to swallow solid food with the body upside down.



Sequential contraction of the three pharyngeal constrictor muscles moves the bolus from the pharynx into the esophagus. More details.

Esophageal phase

Esophageal peristalsis

Like the pharyngeal phase of swallowing, the esophageal phase of swallowing is under involuntary neuromuscular control. The upper esophageal sphincter relaxes to let food pass. The bolus is then pushed down by the striated constrictor muscles of the pharynx, then by peristalsis of the esophageal walls. Finally, relaxation of the lower esophageal sphincter allows the bolus to enter the stomach.

Relaxation phase

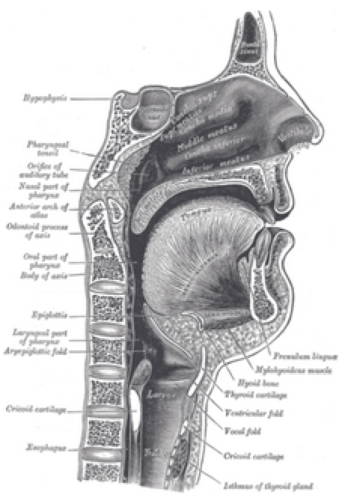
The larynx, pharynx and hyoid move down together at first, mostly by elastic recoil. Then the larynx and pharynx move down in relation to the

hyoid also by elastic recoil.

The descent of the larynx

Swallowing in humans is a rather complicate process and it frequently fails, causing chocking or aspiration of fluids into the lungs. It makes one wonder why do the digestive and respiratory systems have to share the oropharynx? And why do we not see dogs, cats or horses choking when they drink water?

It turns out that while the mechanism of swallowing described above is common to vertebrates, the anatomy of the pharynx is modified in humans. Our unique feature is having a descended larynx in which the epiglottis does not contact the soft palate. The entire oropharynx fits into the gap between the epiglottis and the soft palate in humans.



Sagittal view of the human head with its long oropharynx. [More details](#).

Other mammals have the entire larynx positioned closer to the nasopharynx and the epiglottis rests in contact with the soft palate. The epiglottis is hinged ventrally and forms a dorsal opening into the larynx. In this position:

- Air can flow directly between the nasopharynx and the larynx.
- Large food particles in the mouth hit the epiglottis and are blocked until the epiglottis is retroverted, covering the entrance of the larynx.
- Fluids and small food particles can follow the vallecula and go around the larynx as it is thinner than the pharynx. This morphology raised the interesting possibility that mammals other than humans could possibly drink fluids without interrupting their breathing. Recent assessments through live imaging techniques have failed to confirm simultaneous drinking and breathing though. The animals execute instead a rhythmic alternation between airflow and swallowing.

Dog head in sagittal section. Notice the contact between the larynx and the soft palate. More details.

Humans have a permanently descended larynx. Our newborns start with the general mammal condition but the larynx descends rapidly as the baby grows. In men, the increase in male sex hormones that takes place during

puberty causes the larynx to become larger and descend further than in women.

The descended larynx has other effects in addition to making swallowing more challenging. The low position of the larynx renders the trachea shorter and the pharynx longer. The shorter trachea tends to facilitate vocalization by reducing the attenuation and delay that the duct imposes to air pressure changes that are generated at the lungs and are converted into voice at the larynx. A larger pharynx allows for more cavity resonance, emphasis in lower frequencies of voice and potentially a wider range of resonance patterns. This translates into louder and lower pitched voice with a potentially greater variety of producible vowels.

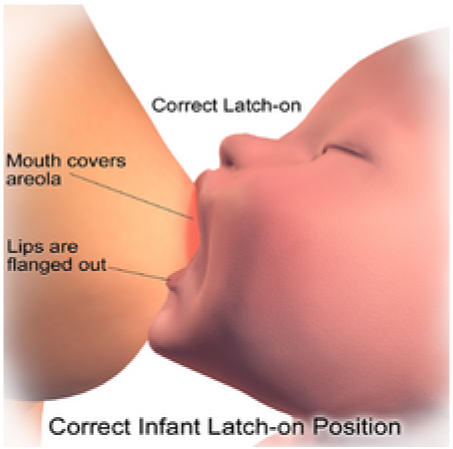
Vocal communication is extremely elaborate in humans. The advantages that the descended larynx confer for vocal communication may have generated the selective forces that drove the descent of the larynx. Other vocal primates also benefit from a lowered larynx but they only lower it during vocalization, whereas we have the larynx permanently lowered and have to elevate it to swallow. The physical association between loud and deep voice with large body size and the common involvement of men in territorial disputes may explain the enlargement and increased descent in the male human larynx at sexual maturation.

The lack of laryngeal descent in human newborns could be a reflection of special mechanical needs for nursing or of different selective pressure on vocal communication at that age. The fact that milk can flow around the open epiglottis and into the esophagus without entering the larynx raised the question of simultaneous drinking and breathing during nursing in newborns. Again, modern assessments have found evidence of rhythmic patterns of alternation between respiration and swallowing in newborns of humans and other mammals.

Suckling

Nursing in newborns was a major innovation in vertebrates and promoted the diversification of mammals into an entire class of organisms. Nursing allows females to give birth to small offspring and then continue to transfer

nutrients to them until they can forage on their own. A key aspect to suckling is the mechanical coupling and transfer of milk from the mammary gland into the stomach of the offspring.



Nursing position of human newborn. More details.

The nipple of the mammary gland, also called teat, is held between the tongue and the palate. The need for effective nursing is likely to have been the selective force that drove the evolution of the palate in mammals. The mandible, the anterior and posterior portions of the tongue, the lips, the buccinator and other muscles of the mouth move in complex rhythmic coordination during suckling.

There has been a long debate about the basic mechanism of suckling, as completely opposite processes seemed plausible. In one hand, milk could be squeezed out of the teat by compression between the tongue and the palate. On the other hand, milk could be extracted out of the teeth by suction produced mainly through lowering of the tongue. Detailed analyzes of live ultrasound imaging during nursing revealed that the tip of the teat retracts when the mandible and tongue are elevated and it protracts when the mandible and tongue are depressed. This conforms with the expectations for

milk extraction by suction when the volume of the mouth is increased but not with the expectation for compression when the mandible and tongue are elevated.

Figure credits

Figure 1 by Fraser G. J., Hulsey C. D., Bloomquist R. F., Uyesugi K., Manley N. R. and Streelman J. T. - "An ancient gene network is co-opted for teeth on old and new jaws". (2009) PLoS biology, 7 (2): e1000031. doi:10.1371/journal.pbio.1000031, CC BY-SA 3.0, https://commons.wikimedia.org/w/index.php?curid=37208634

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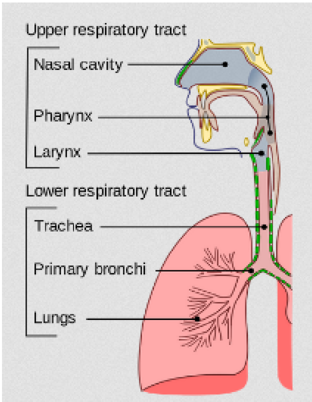
Choking and Dysphagia

Swallowing is the transport of food from the mouth into the stomach. The general mechanism is peristalsis of the digestive tube, but fishes can help it using mucociliary transport or pharyngeals jaws. Frogs add a muscular tongue and retraction of the eyes and some birds use gravity. Mammals have a palate and a muscular soft palate that protects the nasal cavity from the entrance of food. The epiglottis prevents food from entering the larynx. Its effectiveness is reduced in adult humans, however, because our larynx is permanently descended and the epiglottis does not contact the soft palate. Imperfect swallowing results in chocking or pulmonary aspiration. The human larynx has most likely descended in response to selection for loud and low pitched voice. In newborns, the larynx is not yet descended however and they suckle by producing negative pressures in the mouth to extract milk from the nipple.

The most common complications with swallowing are choking and dysphagia.

Choking

Choking is a life-threatening medical emergency the passage of air passage into the lungs is blocked by food or another object. This obstruction can be partial or complete. The disruption of normal breathing by choking hinders oxygen delivery to the body, resulting in asphyxia. Although oxygen stored in the blood and lungs can keep a person alive for several minutes after breathing stops, chocking is potentially fatal. It is a major cause of unintentional injury-related death.



Regions of the human respiratory tract. More details.

Deaths from choking most often occur in the very young (< 1 year old) and in the elderly (> 75 years). The obstruction of the airway most commonly occurs at the pharynx or the trachea. Foods that can adapt their shape to that of the pharynx such as bananas, marshmallows, or gelatinous candies are particularly dangerous.

Choking is frequently caused by tumors, swelling of the airway tissues due to infections, and physical compression in strangulation. Complications

- Brain damage typically occurs if the body is deprived of air for three minutes.
- Death will usually occur if breathing is not restored in six to eight minutes.

Causes

Children younger than age three are especially at risk of choking because they explore the environment by putting objects in their mouth. Their

airway is smaller in diameter than an adult's airway and their coughing may not be as effective as that of an adult in clearing an airway obstruction. In adults, choking is most often caused by food. Risk factors include:

- Medical conditions that affect the coordination of swallowing such as:
    - Strokes
    - Parkinson disease
    - Alzheimer disease
- Using alcohol or sedatives.
- Undergoing a procedure involving the oral cavity or pharynx.
- Wearing oral appliances.

Prevention

The risk of chocking in children can be reduced by:

- Waiting until 6 months of age before introducing solid foods to infants.
- Supervision of children while eating or playing.
- Removal of hazardous objects from the reach of your children.
- Governmental safety regulation and inspection of children's toy products.

In adults with difficulty swallowing, selection of food items with appropriate particle size, texture and humidity can reduce the risk of chocking.

Treatment

Choking can be treated with various basic techniques or advanced techniques.

Basic Treatment

For the conscious choking victim, most protocols recommend encouraging the victim to cough. If not effective, hard back slaps are attempted and if none of these procedures work, abdominal thrusts (Heimlich maneuver) or chest thrusts are applied. If the choking victim becomes un conscious, CPR is recommended.

Back Blows (or Slaps)

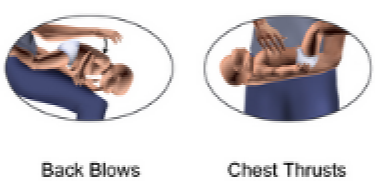
These are performed by leaning the choking victim forward, then delivering blows with the heel of the hand onto the victim's back, in between their shoulder blades. Back slaps must be performed with the head lower than the chest (patient bent over), otherwise the blow may drive the object deeper into the person's throat.

Abdominal Thrusts (Heimlich Maneuver)

Abdominal thrusts are usually recommended for their simplicity and effectiveness. They can be followed by chest thrusts, if abdominal thrusts are not effective. Abdominal thrusts are performed with the rescuer standing behind the person choking and exerting inward and upward pressure with their hands on the choking person's abdomen. The purpose of abdominal thrusts is to create pressure that will expel any object lodged in the airway upwards to relive the obstruction. The procedure is similar in chest thrusts, except that the pressure is applied around the chest. Chest trusts might be more effective on obese people.

Demonstration of abdominal thrusts on a person showing signs of choking. More details.

For children less than 1 year old, the American Heart Association recommends performing cycles of 5 back blows (or slaps) followed by 5 chest compressions. Abdominal thrusts are not recommended because they can cause liver damage.



Back blows (or slaps) and chest compressions for treating an infant

less than 1 year of age. More details.

Advanced Treatment

There are many advanced medical treatments to relieve choking or airway obstruction. These include inspection of the airway with a laryngoscope or bronchoscope and removal of the object. Emergency cases in which the appropriate conditions to remove the object are not available may require cricothyrotomy (tracheostomy). It involves making an incision between the cricoid and the thyroid in the anterior aspect of the neck and inserting a tube into the trachea in order to bypass the upper airways. This procedure is only performed when the basic methods have failed and other options are not available.

Dysphagia

Dysphagia is difficulty in swallowing. It can have various causes and involve different parts of the swallowing mechanism or anatomy. It frequently produces coughing, chocking or pulmonary aspiration (food or liquid going into the lungs) and subsequent aspiration pneumonia. Dysphagia can also lead to dehydration and weight loss.

Oropharyngeal dysphagia includes difficulty controlling the position of food in the mouth, difficulty initiating a swallow, nasal regurgitation and gurgly voice after swallowing. Patients identify the mouth or neck as the site of the problem. These problems are common among older individuals, patients who have had strokes, head and neck cancer and progressive neurologic diseases like Parkinson's disease, dementia or multiple sclerosis.

In esophageal dysphagia patients indicate an inability to swallow solid food, saying that it is held up before it reaches the stomach or is regurgitated. Various diseases in or adjacent to the esophagus can result in dysphagia and the treatment will depend on the cause. Achalasia is an exception to usual

pattern of dysphagia in that patients report more difficulty swallowing fluids than solids. It is caused by a degeneration of neural tissue in the esophagus which results in peristaltic failure.

The diagnosis of dysphagia commonly requires specialized techniques due to the concealed nature of the swallowing mechanism. Endoscopic techniques involve the lowering of a camera into the mouth, pharynx and esophagus and allow for imaging of the structure in action. Videofluoroscopy can also be useful, providing live x-ray images of the neck structures while the patient swallows a radio-opaque fluid.

Many treatments are used in dysphagia because it is not a disease, but a symptom or condition associated with a wide variety of diseases. Treatments can include swallowing therapy, dietary changes, feeding tubes, certain medications, and surgery.

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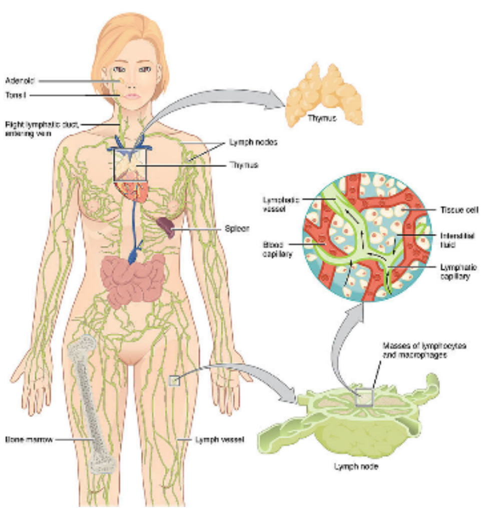
The Biology of the Tonsils

Tonsils are lymphatic nodules that form the first immunological defense of the digestive tube, at the pharynx. There are pharyngeal, tubal, lingual and palatine tonsils. They have tonsillar crypts that facilitate the entrance of antigens and pathogens deep into the tonsil, where they are processed and destroyed. During respiratory infections, tonsils can become swollen or inflamed. When the palatine tonsils become severely swollen they can hinder swallowing or even breathing. The situation can usually be controlled with medication but when infections are frequent, the palatine tonsils may be surgically removed.

The immunological defense of the body is a function of the lymphatic system, which also drains the excess fluids between cells. This system is composed of:

- Lymphoid organs
- Lymph nodes
- Lymphoid nodules
- Lymphatic vessels

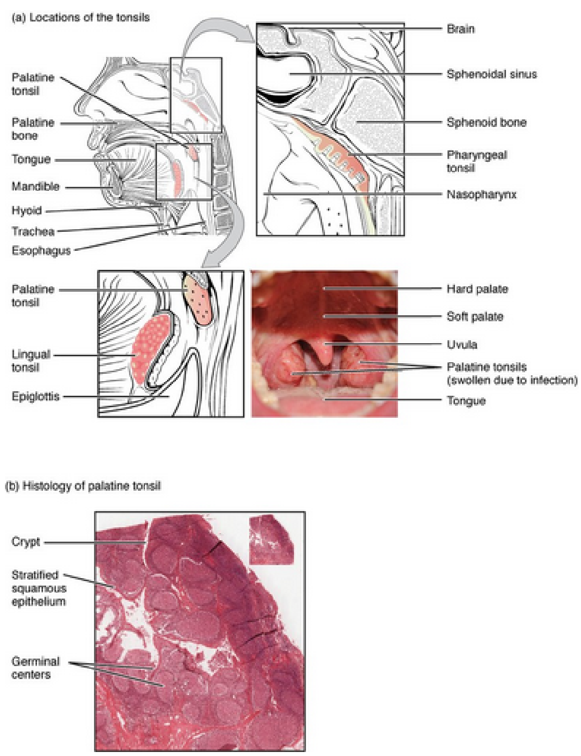


The immunological defense system of the human body. [More details](#).

Lymphoid nodules have a simpler architecture than the lymphoid organs or lymph nodes. They consist of a dense cluster of lymphocytes without a surrounding fibrous capsule. These nodules are located in the respiratory and digestive tracts, areas routinely exposed to environmental pathogens.

Tonsils are the lymphoid nodules located along the inner surface of the pharynx. They form Waldeyer's tonsillar ring (pharyngeal lymphoid ring) which is the first line of immunological defense of the digestive tract. It surrounds the naso- and oropharynx, with some tonsils located above and some below the soft palate. The ring consists of (from top to bottom):

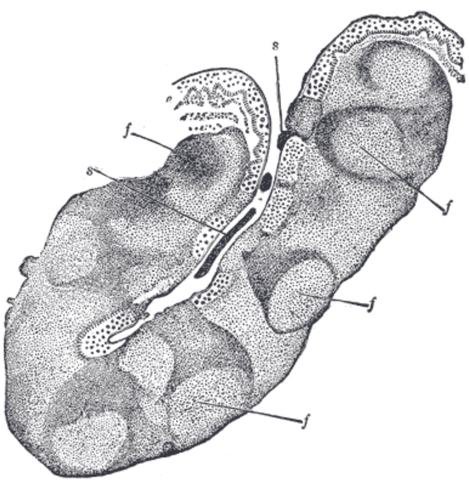
- 1 pharyngeal tonsil (adenoid) on the roof of the nasopharynx.
- 2 tubal tonsils posterior to the opening each auditory tube on each side.
- 2 palatine tonsils (tonsils) on the lateral walls of the oropharynx.
- 1 lingual tonsil on the posterior 1/3 of the tongue.



Location and histological structure of the tonsils in the human pharynx. More details.

Some books list two pharyngeal tonsils for considering the left and right halves of the pharyngeal tonsil as separate structures. Similarly the lingual tonsil is frequently considered as a group because it consists of a number of little prominences (rounded masses). This can be confusing, but it reflects differences in wording, rather than differences in biological structure.

Like other lymphoid nodules, tonsils are not enclosed in a complete fibrous capsule. The epithelium of the pharynx invaginates deeply into the tonsil to form tonsillar crypts. These structures, which accumulate all sorts of materials taken into the body through eating and breathing, actually "encourage" pathogens to penetrate deep into the tonsillar tissues where they are acted upon by numerous white blood cells and eliminated.



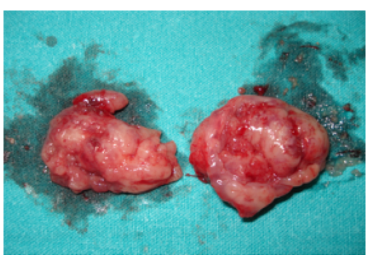
Section through one of the tonsillar crypts (running diagonally) as it opens onto the surface of the throat (at the top). Stratified epithelium covers the throat's surface and continues as a lining of the crypt. Beneath the surface are numerous nodules (f) of

lymphoid tissue. More details.

Tonsils have specialized antigen capture lymphocytes called M cells that allow for the uptake of antigens produced by pathogens. These M cells then alert the underlying B and T lymphocytes in the tonsil that a pathogen is present and an immune response is stimulated. B cells are activated and proliferate in areas called germinal centers in the tonsil. These germinal centers are places where B memory cells are created and antibodies are produced.

This seems to be the major function of tonsils—to help children's bodies recognize, destroy, and develop immunity to common environmental pathogens so that they will be protected in their later lives. Tonsils tend to reach their largest size near puberty, and they gradually undergo atrophy thereafter. However, they are largest relative to the diameter of the throat in young children.

Clinical significance



A pair of palatine tonsils after surgical removal. More details.

Tonsils can become enlarged or inflamed (tonsillitis). The most common treatment is with anti-inflammatory drugs such as ibuprofen or with antibiotics if bacterial in origin. Tonsilitis involving palatine tonsils is dangerous because the swelling may interfere with breathing and/or swallowing. Tonsillectomy, the surgical removal of the palatine tonsils was common in the past. The development of modern drugs has greatly reduced the need for such removal, but it is still conducted in children who frequently develop throat infections with swelling of the tonsils.

The adenoid (pharyngeal tonsil) can enlarge nearly to the size of a ping pong ball and completely block airflow through the nasal passages. The patient switches to inhalation through an open mouth. The enlarged adenoid can also obstruct the nasal airway enough to affect the voice even without actually stopping nasal airflow altogether.

Another type of clinical occurrence involving tonsils is the development of tonsilloliths. These tonsil stones are calcified aggregates of bacterial and cellular debris that form in the tonsillar crypts, the crevices of the tonsils. While they occur most commonly found in the palatine tonsils, they may also occur in the lingual tonsils. Tonsilloliths can grow to a few millimeters in diameter before they are noticed. They may produce no symptoms, they may cause bad breath, or produce some pain during swallowing. Larger stones may be associated with an infection of the tonsil.

A tonsillolith lodged in the left palatine tonsil. More details.

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Figure 3 by Henry Vandyke Carter - Henry Gray (1918) Anatomy of the Human Body (See "Book" section below)Bartleby.com: Gray's Anatomy, Plate 1027, Public Domain, https://commons.wikimedia.org/w/index.php?curid=566973

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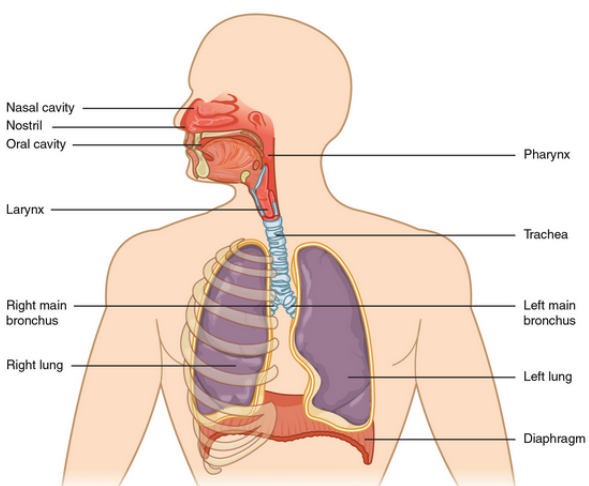
The Upper Respiratory System
The mouth is an important air passage in mammals during accelerated respiration. It is also a key component of the buccal pump in fishes and amphibians. The nose is cartilaginous and muscular and can be stirred to direct the olfaction. The vomeronasal organ analyses non-volatile odorants collected from the environment. The nose develops from the frontonasal and the medial nasal prominences of the embryo. The respiratory turbinates in the nasal cavity humidify, warm up and clean the inspired air. They also cool down and remove humidity from the expired air. The olfactory turbinates contain the olfactory epithelium. The upper respiratory system is lined with pseudostratified ciliated columnar eiphelium, except for the mouth, oropharynx and laryngopharynx with are lined with stratified squamous epithelium.

The upper respiratory system includes the nose, nasal cavity, mouth, pharynx, and larynx. This chapter deals with the structure and respiratory role of the nose, mouth, and nasal cavity. The pharynx is reviewed in the chapter on swallowing and the larynx in the chapter on voice.

The roles of the mouth



The human respiratory system.
More details.

The mouth is of primary importance to both digestion and respiration. Vertebrates other than mammals lack a palate and the air that enters the nostrils travels through the mouth before reaching the larynx. Mammals also use the mouth for respiration. While humans tend to breath through the nose at rest, most air is transported through the open mouth when running. Dogs breath through the mouth (panting) to cool the body in hot weather or after exercise.

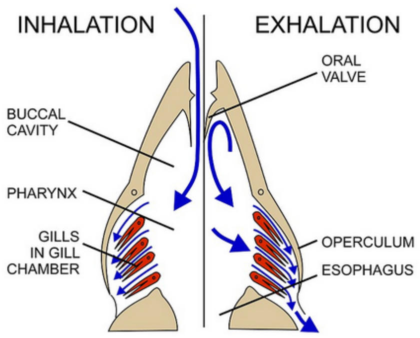
Dog panting for thermoregulation. More details.

The evolution of the palate in mammals separated the nasal cavity from the oral cavity from the face to the pharynx. This allowed the nasal cavity to become dedicated to respiration and promoted the evolution of elaborate olfaction in mammals.

The Buccal Pump

Fish exchange gases by pulling oxygen-rich water through their mouths and pumping it over their gills. The gills push the oxygen-poor water out through openings in the sides of the pharynx. Some fish, like sharks and lampreys, possess multiple gill openings. However, bony fish have a single

gill opening on each side. This opening is hidden beneath a protective bony cover called an operculum.



Ventilation movements and water flow in a fish. More details.

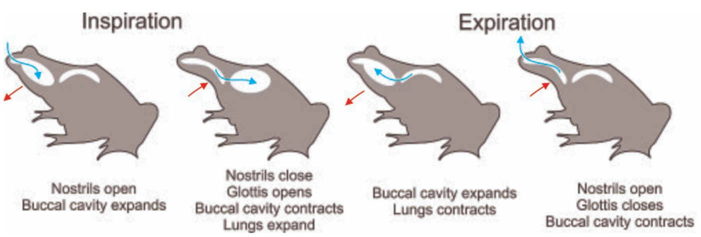
Respiration in fishes is greatly enhanced by the ability to force a flow of water by the gills (ventilation). Fishes evolved the buccal pump, a mechanism in which muscular contractions at the mouth produce ventilation. In a cyclic patter, the mouth is opened and the gill openings are closed. The oral cavity is then expanded by lowering the floor of the mouth and/or expanding the operculum laterally. This causes an inflow of water through the mouth. The mouth is then closed and the gill openings are opened. The volume of the oral cavity is reduced by elevation of the floor of the mouth and/or contraction of the opercular muscles. This forces water in the oral cavity to pass by the gills and leave through the gill openings.

Some cartilaginous fishes have diminished or abandoned buccal pumping as a method of ventilation. These animals swim constantly and they can produce flow by their gills by simply opening the mouth as they swim. This forces them, however, to never stop swimming, or to switch to buccal pumping when they stop.

Buccal pumping is also used by amphibians as their only method of ventilation. These animals lack a diaphragm and they have very short ribs that do not form a rib cage. They ventilate by moving the floor of the mouth in a rhythmic manner that is externally apparent.

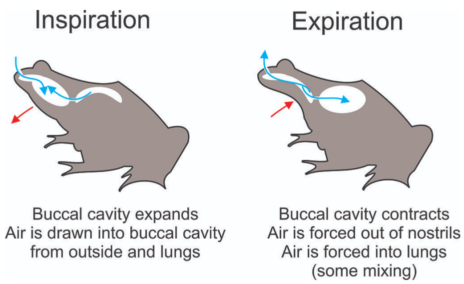
Fishes and amphibians employ two methods of buccal pumping, defined by the number of movements of the floor of the mouth needed to complete both inspiration and expiration.

Four-stroke buccal pumping is used by some basal ray-finned fishes and amphibians. First, the glottis (opening to the lungs) is closed, and the nostrils are opened. The floor of the mouth is then depressed (lowered), drawing air in. The nostrils are then closed, the glottis opened, and the floor of mouth raised, forcing the air into the lungs for gas exchange. To deflate the lungs, the process is reversed.



Four-stroke buccal pumping in a frog.
More details.

Two-stroke buccal pumping is found amphibians. It has simpler mechanics but involves some mixing of used and fresh air. The floor of the mouth is lowered, drawing air from both the outside and lungs into the buccal cavity. When the floor of the mouth is raised, the air is pushed out and into the lungs; the amount of mixing is generally small, about 20%.



Two-stroke buccal pumping in a frog. More details.

With the exception of some lizards, amniotes have abandoned buccal pumping as a ventilation mechanism and adopted aspiration breathing instead. The organization of the musculature of the floor of the mouth, which drives the buccal pump in amphibians, was maintained in amniotes.

Nose

The nose of a tapir. More details.

All vertebrates have nasal cavities and the nostrils form the entrance into the respiratory system. A protruding nose is a specialization mostly

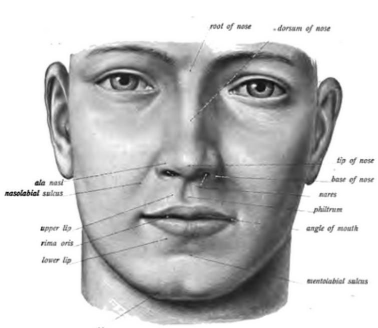
observed in mammals and it is highly variable in size and structure. In cetaceans, the nose has been reduced to the nostrils, which have migrated to the top of the head and allow the animal to breathe while mostly submerged. Other mammals have evolved muscular noses that can be stirred to direct the sense of olfaction. Aquatic species have muscular control over the closure of the nostrils, to prevent flooding of the nasal cavity during dives. An extreme development is observed in the elephant, in which the nose (trunk) is used not only for breathing and smelling, but also to manipulate objects and transport water.

Elephants have prehensile noses. More details.

The rhinarium (or nose pad) is the naked skin surface surrounding the external openings of the nostrils in most mammals. It is typically crenellated (wrinkled or embossed) but its structure and role is variable among mammals according to ecological niche. In aquatic species, development of lobes next to the nostrils allow them to be closed for diving. In mammals that dig or root with their noses, the rhinarium often develops into a resilient pad, with the nostrils off to the side or below, and capable of closing for exclusion of dust. Examples include the common wombat, marsupial mole, and members of the Chrysochloridae. In the elephants it has become a tactile organ. In the walrus, it is covered with stiff bristles to protect it during foraging for shellfish. In many other species, the role of the rhinarium remains to be elucidated. The philtrum (or medial cleft) is a

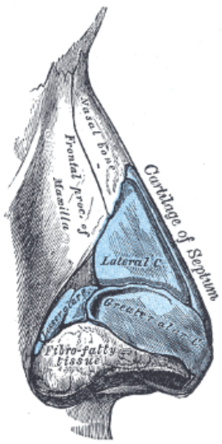
vertical groove in the middle of the upper lip, extending up to the nose. In most mammals, the philtrum is a narrow groove that may carry dissolved odorants from the rhinarium to the vomeronasal organ via ducts inside the mouth. For humans and most primates, the philtrum survives only as a vestigial medial depression between the nose and upper lip.

A dog's rhinarium with conspicuous crenellation. More details.



Nasal region in the human face. More details.

The human nose has a pair of nostrils containing nasal hairs that remove larger particles or insects from the inspired air. It is structured by the nasal bone, the maxilla and six cartilages: the cartilage of the septum, greater alar cartilage, lateral nasal cartilage, lesser alar cartilages, vomeronasal cartilage and the accessory nasal cartilages. Several skeletal muscles provide some limited movement to the nose and flaring of the nostrils.

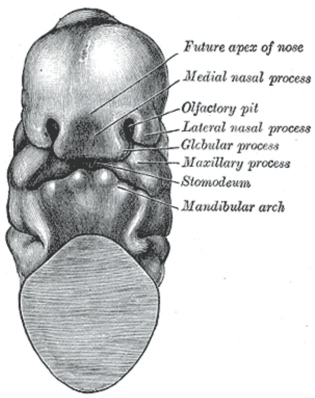


Cartilages of the human nose. More details.

Development of the nose

The facial prominences are five swellings that appear in the fourth week of development and derive from the first and second pharyngeal arches. They are basically made of mesenchyme that derives from the neural crest. The

frontonasal prominence originates the nose, the medial part of the upper lip and the primary hard palate. The maxillary prominences (one on each side) form the secondary hard palate, and the sides of the upper jaw and lip. The mandibular prominences (one on each side) form the lower jaw.



Face development in human embryo (30-31 days). More details.

The frontonasal prominence is ventral to the forebrain. It is derived from neural crest cells, which have an ectodermal origin. These neural crest cells migrate from the ectoderm as the forebrain closes, invading the space that will form the frontonasal prominence. The maxillary and mandibular prominences are derived from the first arch. The maxillary prominence is initially located superior/lateral to the stomodeum (primitive mouth) while the mandibular prominence is located inferior to it and will fuse early on.

The frontonasal prominence originates a medial nasal prominence and two lateral nasal prominenses. As the maxillary prominences grow, they fuse with the medial nasal prominences. This establishes the bridge of the nose and the intermaxillary segment, which is the region of the medial nasal

prominence located inferior to the bridge of the nose and superior to the mandibular prominence. The intermaxillary segment yields the portion of the upper lip containing the philtrum, the upper jaw with 4 incisors, and the primary palate. The medial prominence fuses with the maxillary prominence, giving rise to a smooth upper lip while fusing the primary and secondary palate. Meanwhile, the lateral nasal prominence gives rise to the alae of the nose and fuses with the maxillary prominence, forming the nasolacrimal duct. This duct is formed when the ectoderm thickens into a cord and sinks into the underlying mesenchyme.

Development of the nasal cavity

The separation of the medial from the lateral nasal prominences forms two nasal pits. The nasal pits deepen and develop the nasal sacs in the sixth week. These new structures grow dorsocaudally in front of the forming brain. In the beginning, the nasal sacs are separated from the oral cavity by the oronasal membrane. This membrane disappears in the seventh week leaving a connection between the nasal cavities and the oral cavity, called the primitive choanae. Later, when the development of the secondary palate occurs, the choanae is displaced to the junction of the nasal cavity and the pharynx. The nasal septum grows as a descending growth from the merged nasal prominences and fuses with the palatine process between the ninth and eleventh week. Finally, the lateral walls and the superior, middle and inferior conchae develop in each nasal cavity.[4][9]

Nasal cavity

The nasal cavities in mammals are exceptionally large among vertebrates, typically occupying up to half the length of the skull. In some groups, however, including primates, bats, and cetaceans, the cavity has been secondarily reduced, and these animals consequently have a relatively poor sense of smell. The nasal cavity of mammals has been enlarged, in part, by the development of a palate that separates the entire upper surface of the original oral cavity The palate therefore forms a new roof to the mouth. The

cavity also extends into neighbouring skull bones, forming additional air cavities known as paranasal sinuses.

The enlarged nasal cavity contains complex turbinates (or conchae) which are convoluted structures of thin bone or cartilage. They are lined with mucous membranes that can perform two functions: 1) They can improve the sense of smell by increasing the area available to absorb airborne chemicals; 2) They can warm and moisten inhaled air, then extract heat and moisture from exhaled air to prevent desiccation of the lungs.

Turbinates are divided in two functional types. Olfactory turbinates are found in all living tetrapods, whereas respiratory turbinates have been found in mammals, birds and possibly some reptiles. Dogs and other canids possess well-developed nasal turbinates. These turbinates allow for heat exchange between small arteries and veins on their maxilloturbinate (turbinates positioned on maxilla bone) surfaces in a counter-current heat-exchange system. Dogs are capable of prolonged chases, in contrast to the ambush predation of cats, and these complex turbinates play an important role in enabling this (cats only possess a much smaller and less-developed set of nasal turbinates). This same complex turbinate structure help conserve water in arid environments. The water conservation and thermoregulatory capabilities of these well-developed turbinates in dogs may facilitate their survival in the harsh Arctic environment.

Nasal turbinates in the skull of a

bear. More details.

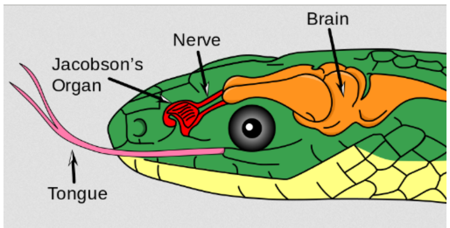
Olfactory turbinates that are involved in sensing smell rather than preventing desiccation. While the maxilloturbinates are located in the path of airflow to collect moisture, sensory turbinates are positioned farther back and above the nasal passage, away from the flow of air. These are commonly called ethmoturbinates due to their proximity to the ethmoid bone.

Vomeronasal (Jacobson's) organs

Many animals, including most mammals and reptiles, but not humans, have two distinct and segregated olfactory systems: a main olfactory system, which detects volatile stimuli, and an accessory olfactory system, which detects fluid-phase stimuli. Behavioral evidence suggests that these fluid-phase stimuli often function as pheromones, although pheromones can also be detected by the main olfactory system. In the accessory olfactory system, stimuli are detected by the vomeronasal organ, located in the vomer, between the nose and the mouth. Snakes use it to smell prey, sticking their tongue out and touching it to the organ. Some mammals make a facial expression called flehmen to direct stimuli to this organ.

The sensory receptors of the accessory olfactory system are located in the vomeronasal organ. As in the main olfactory system, the axons of these sensory neurons project from the vomeronasal organ to the accessory olfactory bulb, which in the mouse is located on the dorsal-posterior portion of the main olfactory bulb. Unlike in the main olfactory system, the axons that leave the accessory olfactory bulb do not project to the brain's cortex but rather to targets in the amygdala and bed nucleus of the stria terminalis, and from there to the hypothalamus, where they may influence aggression and mating behavior.

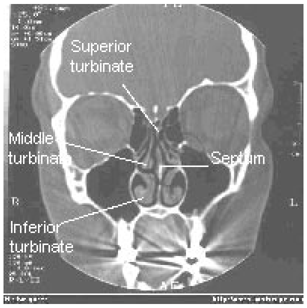
The vomeronasal organ of mammals is generally similar to that of reptiles. In most species, it is located in the floor of the nasal cavity, and opens into the mouth via two *nasopalatine ducts* running through the palate, but it opens directly into the nose in many rodents. It is, however, lost in bats, and in many primates, including humans.



Placement of Jacobson's organ in a snake. More details.

Human Nasal Cavity

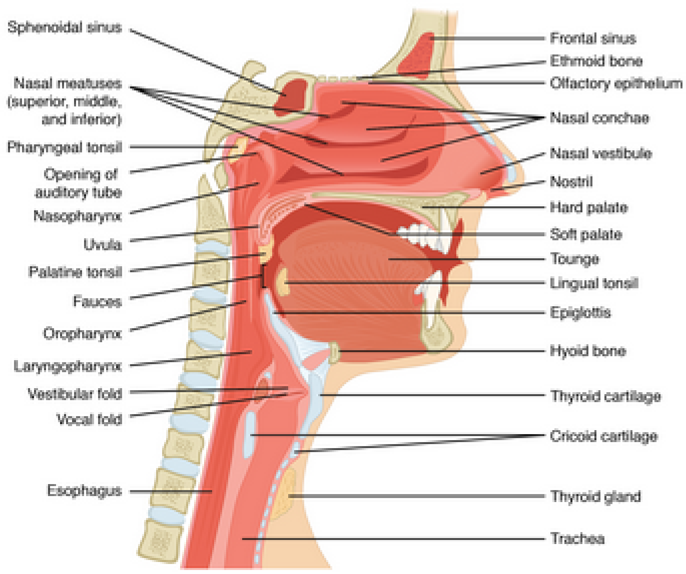
In humans, the nasal cavity is separated into left and right sections by the nasal septum. The nasal septum is formed anteriorly by a portion of the septal cartilage (the flexible portion you can touch with your fingers) and posteriorly by the perpendicular plate of the ethmoid bone (a cranial bone located just posterior to the nasal bones) and the thin vomer bones (whose name refers to its plough shape).



CT scan of human nasal cavity (frontal section) showing turbinates and sinuses. More details.

Each lateral wall of the nasal cavity has three bony projections, called the superior, middle, and inferior nasal conchae. The inferior conchae are separate bones, whereas the superior and middle conchae are portions of the ethmoid bone. Conchae serve to increase the surface area of the nasal cavity and to disrupt the flow of air as it enters the nose, causing air to bounce along the epithelium, where it is cleaned and warmed. The conchae and meatuses also conserve water and prevent dehydration of the nasal epithelium by trapping water during exhalation.

The floor of the nasal cavity is composed of the palate. The hard palate at the anterior region of the nasal cavity is composed of bone. The soft palate at the posterior portion of the nasal cavity consists of muscle tissue. Air exits the nasal cavities via the internal nares and moves into the pharynx. The internal nares are the narrowing that marks the passage from the nasal cavity to the nasopharynx.



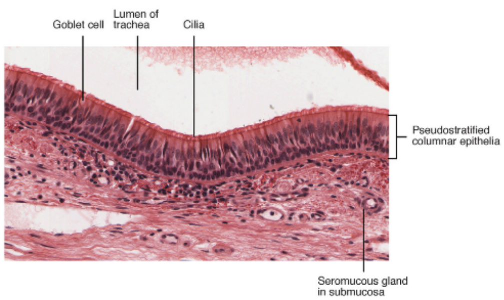
The nasal cavity of humans. More details.

Several bones that help form the walls of the nasal cavity have air-containing spaces called the paranasal sinuses, which serve to warm and humidify incoming air. Sinuses are lined with a mucosa. Each paranasal sinus is named for its associated bone: frontal sinus, maxillary sinus, sphenoidal sinus, and ethmoidal sinus. The sinuses produce mucus and lighten the weight of the skull.

The nares and anterior portion of the nasal cavities are lined with mucous membranes, containing sebaceous glands and hair follicles that serve to prevent the passage of large debris, such as dirt, through the nasal cavity. An olfactory epithelium used to detect odors is found deeper in the nasal cavity.

The conchae, meatuses, and paranasal sinuses are lined by respiratory epithelium composed of pseudostratified ciliated columnar epithelium. The epithelium contains goblet cells, one of the specialized, columnar epithelial cells that produce mucus to trap debris. The cilia of the respiratory epithelium help remove the mucus and debris from the nasal cavity with a constant beating motion, sweeping materials towards the throat to be

swallowed. Interestingly, cold air slows the movement of the cilia, resulting in accumulation of mucus that may in turn lead to a runny nose during cold weather. This moist epithelium functions to warm and humidify incoming air. Capillaries located just beneath the nasal epithelium warm the air by convection. Serous and mucus-producing cells also secrete the lysozyme enzyme and proteins called defensins, which have antibacterial properties. Immune cells that patrol the connective tissue deep to the respiratory epithelium provide additional protection.



Ciliated pseudostratified columnar epithelium with goblet cells lines the nasal cavity. More details.

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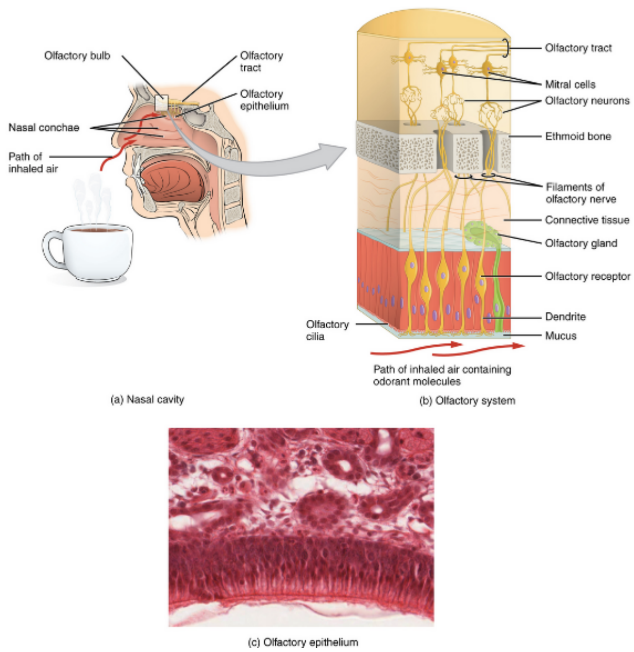
The Olfactory System
Olfactory receptor cells are found in the olfactory epithelium located on the roof of the nasal cavity. When stimulated by odorants, these cells produce action potentials which travel down the axon through the cribriform plate of the ethmoid bone and into the brain. Olfactory information is processed in various parts of the brain, but mostly in the olfactory cortex of the cerebrum. The sense of olfaction tends to be well developed in nocturnal animals and least developed in visually-oriented diurnal animals such as most birds. This sense is used for food detection and analysis, and species and individual recognition such as in territoriality, mate attraction and kin recognition.

Structure

The sense of smell, or olfaction, is responsive to chemical stimuli. The olfactory receptor neurons are located in a small region within the superior nasal cavity. This region is referred to as the olfactory epithelium and contains bipolar sensory neurons. Each olfactory sensory neuron has dendrites that extend from the apical surface of the epithelium into the mucus lining the cavity. As airborne molecules are inhaled through the nose, they pass over the olfactory epithelial region and dissolve into the mucus. These odorant molecules bind to proteins that keep them dissolved in the mucus and help transport them to the olfactory dendrites. The odorant–protein complex binds to a receptor protein within the cell membrane of an olfactory dendrite. These receptors are G protein–coupled, and will produce a graded membrane potential in the olfactory neurons.



The olfactory epithelium in humans. More details.

The axon of an olfactory neuron extends from the basal surface of the epithelium, through an olfactory foramen in the cribriform plate of the ethmoid bone, and into the brain. The group of axons called the olfactory tract connect to the olfactory bulb on the ventral surface of the frontal lobe. From there, the axons split to travel to several brain regions. Some travel to the cerebrum, specifically to the primary olfactory cortex that is located in the inferior and medial areas of the temporal lobe. Others project to structures within the limbic system and hypothalamus, where smells become associated with long-term memory and emotional responses. This is how certain smells trigger emotional memories, such as the smell of food associated with one's birthplace. Smell is the one sensory modality that does not synapse in the thalamus before connecting to the cerebral cortex. This intimate connection between the olfactory system and the cerebral cortex is one reason why smell can be a potent trigger of memories and emotion.

The nasal epithelium, including the olfactory cells, can be harmed by airborne toxic chemicals. Therefore, the olfactory neurons are regularly replaced within the nasal epithelium, after which the axons of the new neurons must find their appropriate connections in the olfactory bulb. These new axons grow along the axons that are already in place in the cranial nerve.

Sensitivity and Roles of Olfaction

The odor detection threshold is the lowest concentration of a certain odor compound that is detectable by the an organism's sense of smell. The threshold of a chemical compound is determined in part by its shape, polarity, partial charges, and molecular mass.

Most mammals have a good sense of smell, whereas most birds do not, except the tubenoses (e.g., petrels and albatrosses), certain species of vultures, and the kiwis. Among mammals, it is well developed in the carnivores and ungulates, which must always be aware of each other, and in those that smell for their food, such as moles. Having a strong sense of smell is referred to as *macrosmatic*.

Based on experiments in which animals animals are exposed to aromas in known extreme dilutions, dogs are estimated to have an olfactory sense approximately ten thousand to a hundred thousand times more acute than a human's. Bloodhounds were bred for the purpose of tracking humans and they can detect a scent trail a few days old. Bears are also highly sensitive, and this is essential for locating food underground. Using their elongated claws, bears dig deep trenches in search of burrowing animals and nests as well as roots, bulbs, and insects.

Fishes have a well-developed sense of smell. Salmon utilize their sense of smell to identify and return to their home stream waters. Catfish use their sense of smell to identify other individual catfish and to maintain a social hierarchy. Many fishes use the sense of smell to identify mating partners or to alert to the presence of food.

The sense of smell is less developed in the primates, including humans. In many species, olfaction is highly tuned to pheromones. Comparisons between species of mammals have revealed some correlation between the size of the nasal cavity, the elaboration of the ethmoturbinates, the area lined with olfactory epithelium and the olfactory sensitivity of the animal. There are many exceptions to this pattern, however, and few species have been studied in detail.

Food Detection and analysis

Animals vary greatly in diet, method of foraging (searching for food) and sensory abilities. Some foods are more easily detected through olfaction, while others might be easier to find visually. For example, ripe cherries may be located visually by a diurnal animal whereas the nectar of a flower that opens at night may be better detected through olfactory cues.

The evaluation of olfactory sensitivity for food detection should not be restricted to the ability of detecting odorants at low concentration. It can be equally important to quantify the number of odorants to which a species is sensitive and its ability to discriminate between the combinations of odors that emanate from various sources.

In addition to simply locating a source of food, it is frequently important to analyze its quality before ingesting it. Many plants keep fruits protected by high levels of indigest alkaloids until the fruits are ripe and the seeds ready for dispersal. Other resources such as ripe sweet fruits falling from a tree or a recently killed prey may decompose quickly and it may be important for an opportunistic consumer to evaluate, before consumption, if the nutrient gain will be worth the associated load of toxins.

Territoriality - Scent Marking

Scent marking, also known as territorial marking or spraying when this involves urination, is a behavior used by animals to identify their territory.

Most commonly, this is accomplished by depositing strong-smelling substances contained in the urine, faeces, or, from specialized scent glands located on various areas of the body. Often, the scent contains pheromones or carrier proteins such as the major urinary proteins to stabilize the odours and maintain them for longer. The animal sniffing the scent frequently displays a flehmen response to assist in detecting the mark.

Felids such as leopards and jaguars mark by rubbing themselves against vegetation. Prosimians and New World monkeys also use scent marking, including urine washing (self-anointing the body with urine), to communicate. Many ungulates, for example the blue wildebeest, use scent marking from two glands, the preorbital gland and a scent gland in the hoof.

Territorial scent marking may involve behaviors specific to this activity. When a wolf marks its territory, it lifts a hind leg and urinates on a scent post (usually an elevated position like a tree, rock, or bush). This raised leg urination is different from normal urination, which is done while squatting.

In the Eastern carpenter bee, *Xylocopa Virginica*, both sexes have glands that evolved for marking the nest. Males, although they have the gland, are unable to produce the marking substance. Females secrete it near the nest site entrance to establish their territory.

Mate attraction

Many vertebrates use chemical signals (pheromones) to attract mates. Pheromones are chemical substances released in the urine or feces of animals or secreted from sweat glands that are perceived by the olfactory system and that elicit both behavioral and endocrine responses in conspecifics. Sex pheromones are used to arouse, attract, and elicit specific behavioral responses from the opposite sex. In mammals, chemical signals and the scent glands that secrete them are frequently found only in adults of one sex, are often only secreted during the breeding season and are used exclusively in mating.

Mammalian pheromones can elicit both long-lasting effects that alter the hormone levels of the recipient animal, and short-term effects on its behavior. For example, detection of male pheromones by female mice has been found to encourage onset of puberty, however the detection of female pheromones have been found to delay the onset of puberty.

There is vast evidence for the use of pheromones in mating behaviors. For example, when boars become sexually aroused, they salivate profusely dispersing pheromones into the air. These pheromones attract receptive sows, causing them to adopt a specific mating posture known as standing, which allows the male boar to mount and copulate.

Major histocompatibility complex (MHC) proteins are membrane molecules that are expressed in every cell of an individual and are used by the immune system to distinguish between self cells and invasive cells. An organism usually contains many loci with MHC genes and there are many alleles of the gene. In addition to its role in immune function, studies suggest that the MHC is also involved in mate choice for many vertebrates through olfactory cues. Several studies have detected odor-based mate choice in rats and other mammals resulting in the selection of mates with different MHC background than the individual making the selection. These mating preferences could be adaptive and maintain the enormous allelic diversity of the MHC complex.

Individual or kin recognition

Social cooperation is frequently mediated by cue-based and context-based mechanisms, such as familiarity, imprinting and phenotype matching. The cues are most frequently sensory information gathered from visual, olfactory and auditory stimuli. The belding ground squirrel kin produce similar odors in comparison to non-kin. The squirrels spent longer investigating non-kin scents suggesting recognition of kin odor. They produce at least two scents arising from dorsal and oral secretions, giving two opportunities for kin recognition. Among arthropods, studies suggest that the bald-faced hornet, *Dolichovespula maculata*, can recognize nest

mates by their cuticular hydrocarbon profile, which produces a distinct smell.

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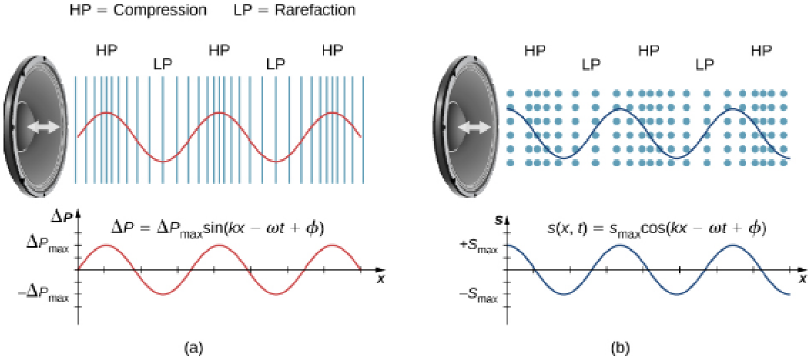
Introduction to Sound

Sound is a traveling disturbance in an elastic medium. It is a mechanical wave characterized by amplitude, frequency and phase. The simplest waves are sinusoids. When sinusoids of different frequencies occur together, they interfere forming complex waves. Natural sounds are mostly complex waves. They can be factored into a set of sinusoids, which frequently form a harmonic structure. Vocal fold usually produce a harmonic structure and the amplitudes of the harmonics are modified by resonances in the vocal tract. Oscillograms, amplitude spectra and spectrograms are the graphical representations most commonly employed to visualize sound. The range of sound intensities that vertebrate hearing systems are sensitive to is very wide. Sound intensities and sound pressures are most frequently expressed as levels, using the decibel scale. If either the source or the receiver of the sound are in movement the perceived frequency is shifted due to the Doppler effect.

The physical phenomenon of sound is a disturbance of matter that is transmitted from its source outward. Sound is a wave. On the atomic scale, sound is a mechanical disturbance of atoms.

A speaker produces a sound wave by oscillating a cone, causing vibrations of air molecules. As it oscillates back and forth, part of the speaker's energy goes into compressing and expanding the surrounding air, creating slightly higher and lower local pressures. These compressions (high-pressure regions) and rarefactions (low-pressure regions) move out as longitudinal pressure waves having the same frequency as the speaker. They are the disturbance that forms the sound wave.



Vibrations produced in air by the cone of a loudspeaker. As the speaker oscillates, a

series of compressions and rarefactions moves out as a sound wave. Left. The red graph shows the gauge pressure of the air versus the distance from the speaker. Right. The blue graph shows the displacement of the air molecules versus the position from the speaker. More details.

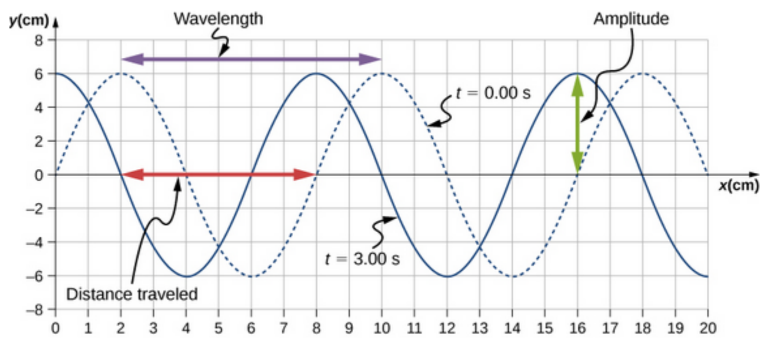
The amplitude of a sound wave decreases with distance from its source, because the energy of the wave is spread over a larger and larger area. The energy is also absorbed by objects and converted into thermal energy by the viscosity of the air. In addition, during each compression, a little heat transfers to the air while during each rarefaction even less heat transfers from the air. These heat transfers reduce the energy in the sound until it dies off.

Properties of sound

Amplitude, frequency and phase

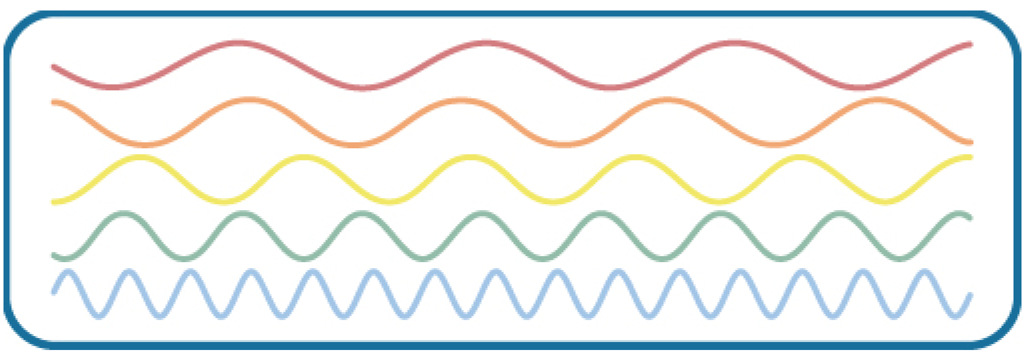
The simplest sounds are sinusoid wave which can be described by three properties: amplitude, frequency and phase. Amplitude is the air pressure or molecule position at a given moment in relation to the condition without sound. It is constantly oscillating between positive and negative values around the baseline. It is most commonly measured as sound pressure with a microphone and expressed in pascals (Pa). Frequency is the number of cycles (waves) produced by unit of time. It is expressed in hertz (Hz). Phase is the position of the wave in the cycle at a given moment and it is expressed in degrees or in radians.

The amplitude of a wave is the height of a wave as measured from the highest point on the wave (peak or crest) to the baseline. It is sometimes measured from the positive peak to the negative peak (trough) and referred to as peak-to-peak amplitude.



Some properties of a sound wave. More details.

Wavelength is the inverse of frequency (wavelength = 1/frequency) and it refers to the length of a wave (expressed in meters) from one peak to the next. Period is is also measured between peaks but in time. It quantifies the duration of a cycle and is expressed in seconds.

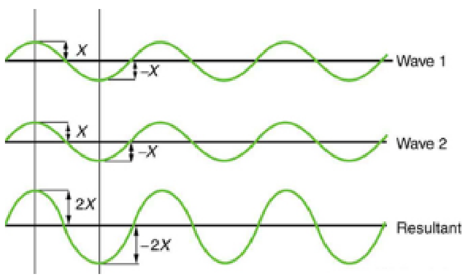


Waves with various wavelengths or frequencies. Sounds with short wavelength have high frequency and vice-versa. More details.

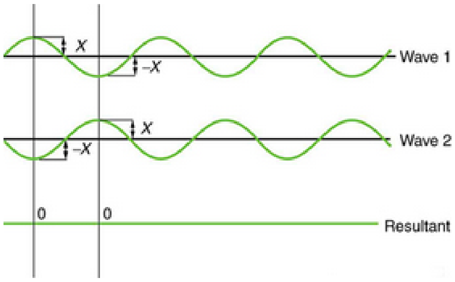
Summation and factoring of waves

The simplest waves may be created by a simple oscillation and have a sinusoidal shape with all the energy contained in a single frequency. Most natural waves do not look very simple though. They appear complex because they result from several sinusoid waves adding together. Luckily, the rules for adding waves are quite simple.

When two or more waves arrive at the same point, they superimpose themselves on one another. The resulting wave is a simple addition of the disturbances of the individual waves. If the disturbances are along the same line, the wave amplitudes will sum up to a higher value. If the disturbances go in opposite directions, they cancel each other out.

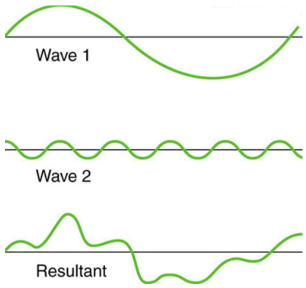


Interference between two identical waves produces a wave with doubled amplitude but the frequency is not changed. This is called constructive interference. More details.



Interference between two waves that are identical except for having opposite phases produces zero amplitude (complete cancellation). This is called destructive interference. More details.

While pure constructive and pure destructive interference do occur, they require precisely aligned identical waves. The superposition of most waves produces a combination of constructive and destructive interference and can vary from place to place and time to time. Sound from a stereo, for example, can be loud in one spot and quiet in another. Varying loudness means the sound waves add partially constructively and partially destructively at different locations. A stereo has at least two speakers creating sound waves, and waves can reflect from walls. All these waves superimpose.



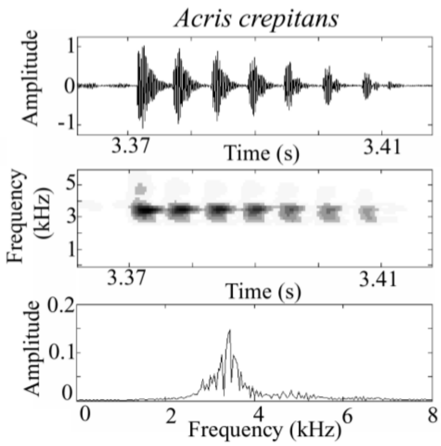
Superposition of non-identical waves exhibits both constructive and destructive interference and usually results in a complex wave. More details.

Any number of sinusoidal waves can be summed to form a single complex wave. Likewise, any complex wave can be decomposed into a set of sinusoids. The math for the decomposition is not that simple, however. It is most frequency calculated with a Fast Fourier Transform (FFT). The frequency content is not calculated over a point in time, but over a period, because the FFT quantifies periodic disturbances. This process involves a trad-off in which frequency resolution is increased with the input of longer segments of signal, whereas time resolution is improved using shorter segments of sound.

A plot of the wave form having time in the abscissa and amplitude in the ordinate is called an oscillogram. This representation of sound is ideal for examination of onset, offset, trills and modulations (changes) in sound

amplitude. Frequency can be easily determined in signals formed by a single sinusoid but it quickly become impossible to quantify the frequency content when the wave is complex.

Factoring the complex wave through an FFT allows one to plot frequency in the abscissa and amplitude in the ordinate. This is called an amplitude spectrum (or power spectrum). This representation allows for a direct quantitative visualization of the amplitude of each frequency in the sound. But it does not incorporate time.



Graphical representations of a single pulsed chirp from the advertisement call of a cricket frog from Texas. Oscillogram on top, spectrogram in the middle and amplitude spectrum at the bottom. The amplitudes are relative measurements because the recordings were not calibrated to

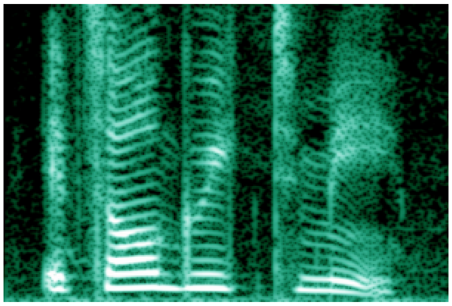
reflect absolute sound
pressure.

In order to visualize frequency modulation (change in frequency over time) a spectrogram (sometimes called sonogram for sound) is used. This is a 3D plot with time in the abscissa, frequency in the ordinate and amplitude encoded in color or darkness of the trace. It is formed by a series of FFTs calculated from successive segments of sound. They are frequency calculated with some overlap to produce a smoother graphical representation.

Harmonics

Natural vibrating structures tend not to produce perfectly symmetric movements in each direction and the shape of the resulting wave is seldom sinosoidal. Since a simple sound with all the energy in a single frequency must be sinusoidal, this means that natural sounds tend to be a combination of many frequencies. When the waves produced by natural sources are factored through FFT, the result is commonly a harmonic structure.

A set of equally-spaced energy bands is characteristic of a harmonic structure when examined in an amplitude spectrum or spectrogram. The difference in frequency between bands of energy is constant and all frequency bands are integer multiples of a fundamental frequency. For example, for a fundamental frequency = 100 Hz, H2 = 200 Hz, H3 = 300 Hz, H4 = 400 Hz, etc.



The spectrogram of the human voice reveals its rich harmonic content. More details.

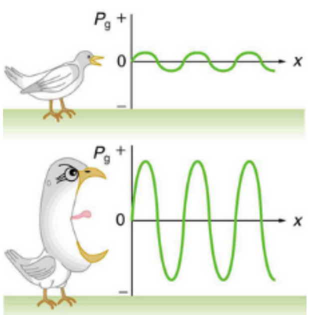
In vocal systems, vibration of the vocal folds tends to produce sounds with an extensive harmonic structure having the most energy in the fundamental frequency and gradually fading levels of energy in the upper harmonics. Resonances and filtering in the vocal tract, however (see below) can profoundly alter the amount of energy in each harmonic. The fundamental frequency could even go missing from the final output whereas higher harmonics could be emphasized. The most energetic frequency (be it the fundamental or some other harmonic) is called the dominant frequency.

Sound intensity and pressure

In a quiet forest, you can sometimes hear a single leaf fall to the ground. After settling into bed, you may hear your blood pulsing through your ears. But when a passing motorist has his stereo turned up, you cannot even hear what the person next to you in your car is saying. We are all very familiar with the loudness of sounds and aware that they are related to how energetically the source is vibrating. In cartoons depicting a screaming person (or an animal making a loud noise), the cartoonist often shows an open mouth with a vibrating uvula, the hanging tissue at the back of the mouth, to suggest a loud sound coming from the throat. High noise

exposure is hazardous to hearing, and it is common for musicians to have hearing losses that are sufficiently severe that they interfere with the musicians' abilities to perform. The relevant physical quantity is sound intensity, a concept that is valid for all sounds whether or not they are in the audible range.

Intensity is defined to be the power per unit area carried by a wave. Power is the rate at which energy is transferred by the wave. In equation form, intensity $I=PA$,where $P$is the power through an area A. The SI unit for I is W/m2 .



Graphs of the gauge pressures in two sound waves of different intensities. The more intense sound is produced by a source that has larger-amplitude oscillations and has greater

pressure maxima and minima. Because pressures are higher in the greater-intensity sound, it can exert larger forces on the objects it encounters. More details.

Sound intensities are measured in watts per meter squared. More frequently, however, sound intensities are approximated from sound pressure measurements which can be obtained using simple microphones. They are not the same, however: intensity is a property of a sound, whereas sound pressure is a property of the environment. The measured sound pressure is formed by the interaction of all sound sources present in an environment at a given moment.

Sound pressure levels are quoted in decibels (dB) much more often than in pascals (Pa). Decibels are the unit of choice in the scientific literature as well as in the popular media. The decibel scale has interesting characteristics. It is logarithmic, which makes it compress the variation in the data. This allows us to plot sounds separated by a 10,000 fold difference in amplitude within the same figure. This is also intuitive because when we perceive sound amplitude differences as equally spaced, they are actually multiples of each other. The other feature of the decibel scale is that values are expressed in levels which are ratios of the measured amplitude of a sound by that of a reference. When comparing sound pressures of two sounds, the decibel level expresses the amplitude of one sound in relation to the other. Ex: The sound pressure was reduced by 30 dB after the ear plugs

were installed. When the sound pressure of a single sound is to be characterized, it is usually compared to the threshold of human hearing at 1000 Hz (0.00002 Pa).

The sound pressure level is defined as β(dB)=20*log10(P/*Pref*), where *Pref* is a reference sound pressure. As a ratio, the decibel level is a unitless quantity telling you the level of the sound relative to a fixed standard. It is widely used not only for sound pressure but also for intensity and power. The decibel sign (dB) is used to indicate this ratio. The bel, upon which the decibel is based, is named for Alexander Graham Bell, the inventor of the telephone.

Sound pressure level (dB)	**Sound pressure (Pa)**	**Example**
0	0.00002	Threshold of hearing at 1000 Hz
10	0.000063	Rustle of leaves
20	0.0002	Whisper at 1-m distance
30	0.00063	Quiet home
40	0.002	Average home
50	0.0063	Average office, soft music
60	0.02	Normal conversation
70	0.063	Noisy office, busy traffic

Sound pressure level (dB)	Sound pressure (Pa)	Example
80	0.2	Loud radio, classroom lecture
90	0.63	Inside a heavy truck
100	2	Noisy factory, siren at 30 m
110	6.3	Damage from 30 min per day exposure
120	20	Loud rock concert; threshold of pain
140	200	Jet airplane at 30 m
160	2000	Bursting of eardrums

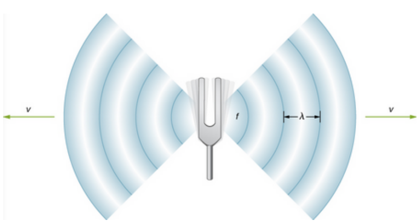
Each factor of 10 in sound pressure corresponds to 20 dB. For example, an 8 0 dB sound compared with a 60 dB sound has 2 0 dB higher level and generates 10 times more sound pressure. Another rule of thumb is that a 6 dB increase or decrease doubles or halves the sound pressure, respectively.

Speed

Sound, like all waves, travels at a certain speed and has the properties of frequency and wavelength. You can observe direct evidence of the speed of sound while watching a fireworks display. You see the flash of an explosion well before you hear its sound and possibly feel the pressure wave, implying both that sound travels at a finite speed and that it is much slower than light.

When a firework shell explodes, we perceive the light energy before the sound energy because sound travels more slowly than light does. More details.

The difference between the speed of light and the speed of sound can also be experienced during an electrical storm. The flash of lighting is often seen before the clap of thunder. You may have heard that if you count the number of seconds between the flash and the sound, you can estimate the distance to the source. Every five seconds converts to about one mile. The velocity of any wave is related to its frequency and wavelength by ($v=f\lambda$), where *v* is the velocity of the wave, *f* is its frequency, and λ is its wavelength.



A sound wave

emanates from a source, such as a tuning fork, vibrating at a frequency *f*. It propagates at speed *v* and has a wavelength *λ*. More details.

The table below shows that the speed of sound varies greatly among media. The speed of sound in a medium depends on how quickly vibrational energy can be transferred through it. To calculate this velocity, one needs to know the type of medium and its temperature. In general, the speed of sound in a medium equals the square root of the elastic property of the medium divided by its inertial property. In a fluid, v=square root(B/ρ), where B = bulk modulus and the ρ = density.

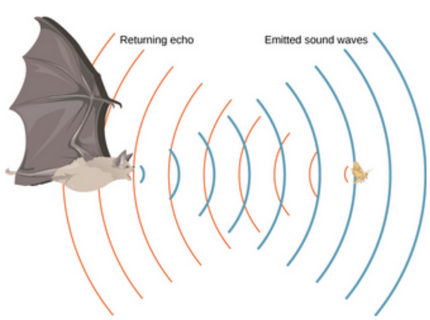
In general, the more rigid (or less compressible) the medium, the faster the speed of sound. Also, the greater the density of a medium, the slower the speed of sound. The speed of sound in air is low, because air is easily compressible. Because liquids and solids are relatively rigid and very difficult to compress, the speed of sound in such media is generally greater than in gases.

Medium	**Sound speed (m/s)**
Air at 0°C	331
Air at 20°C	343

Medium	Sound speed (m/s)
Hydrogen at 0°C	1290
Fresh water at 20°C	1480
Sea water at 20°C	1480
Human tissues	1480
Steel	5960

Because the speed of sound depends on the density of the material, and the density depends on the temperature, there is a relationship between the temperature of given medium and the speed of sound in it. For air at sea level, the speed of sound is given by *v*=331 * root square(1+(Temp/273)), where v= velocity in m/s, and Temp = temperature in °C.

Animals take advantage of the predictability of the propagation properties of sound in a medium. In echolocation, bats clue on to the time that it takes for the echoes of their voice to return in order to estimate the distance to nearby objects.



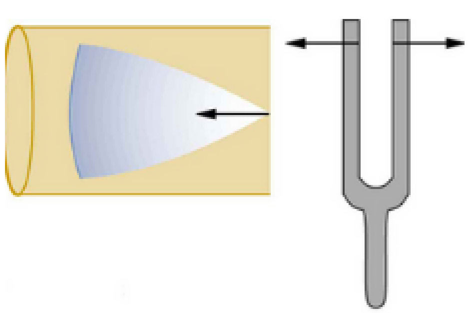
A bat uses sound echoes to find its way about and to catch prey. The time

for the echo to return is directly proportional to the distance. More details.

Resonance

All sound resonances, such as in musical instruments, are due to constructive and destructive interference. Only the resonant frequencies interfere constructively to form standing waves, while others interfere destructively and are absent. From the toot made by blowing over a bottle, to the characteristic flavor of a violin's sounding box, to the recognizability of a great singer's voice, resonance and standing waves play a vital role.

Suppose we hold a tuning fork near the end of a tube that is closed at the other end. If the tuning fork has just the right frequency, the air column in the tube resonates loudly, but at most frequencies it vibrates very little. This observation just means that the air column has only certain natural frequencies. A disturbance travels down the tube at the speed of sound and bounces off the closed end. If the tube is just the right length, the reflected sound arrives back at the tuning fork exactly half a cycle later, and it interferes constructively with the continuing sound produced by the tuning fork. The incoming and reflected sounds form a standing wave in the tube with greatly increased amplitude.



Resonance of air in a tube closed at one end, caused by a tuning fork. A disturbance moves down the tube. More details.

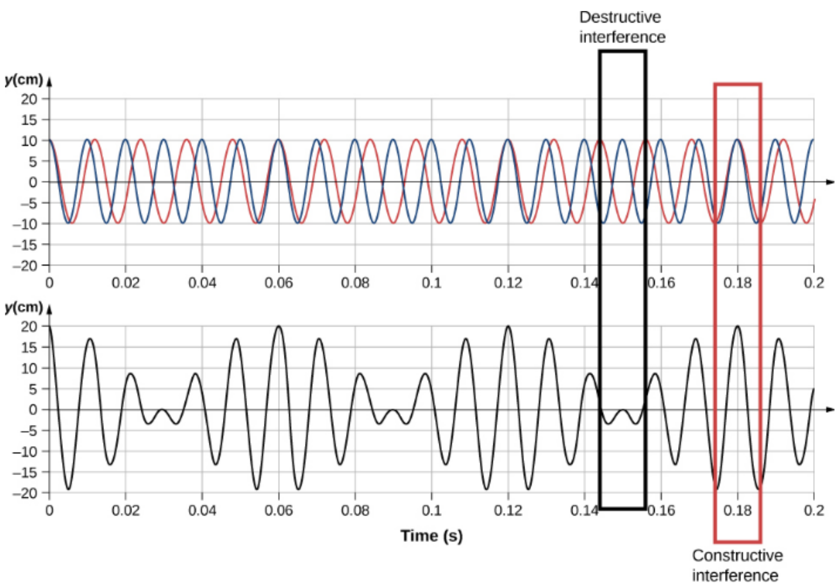
Resonance therefore depends on the distance between the walls of the cavity and on the speed of sound in the medium that fills it. Cavities with complex shapes like those in the human vocal tract can resonate at various frequencies. Behavioral modification of the shapes of the cavities by motion of the tongue, jaws, palate and pharynx can greatly modify the frequency content of the sounds produced by the larynx through resonance.

Given that maximum air displacements are possible at the open end and none at the closed end, there are other, shorter wavelengths that can resonate in the tube, such as the one shown in Figure. Here the standing wave has three-fourths of its wavelength in the tube, or $L=(3/4)\lambda'$, so that $\lambda'=4L/3$. Continuing this process reveals a whole series of shorter-wavelength and higher-frequency sounds that resonate in the tube. We use specific terms for the resonances in any system. The lowest resonant frequency is called the fundamental, while all higher resonant frequencies are called overtones. All resonant frequencies are integral multiples of the fundamental, and they are collectively called harmonics. The fundamental is the first harmonic, the first overtone is the second harmonic, and so on. Figure shows the fundamental and the first three overtones (the first four harmonics) in a tube closed at one end.

Beats

The study of music provides many examples of the superposition of waves and the constructive and destructive interference that occurs. An interesting phenomenon that occurs due to the constructive and destructive interference of two or more frequencies of sound is the phenomenon of beats. If two sounds play simultaneously with slightly different frequencies, they will

oscillate between constructive and destructive interference and the resulting wave will exhibit a pulsating amplitude pattern called beating.



Beats produced by the constructive and destructive interference of two sound waves that differ in frequency. The closer they are in frequency, the slower the beating. More details.

The frequency of beats is the difference between the frequencies of the two interfering sounds. These beats can be used by piano tuners to tune a piano. A tuning fork is struck and a note is played on the piano. As the piano tuner tunes the string, the beats have a lower frequency as the frequency of the note played approaches the frequency of the tuning fork.

The Doppler effect

The sound of a motorcycle buzzing by is an example of the Doppler effect. If you are standing on a street corner and observe an ambulance with a siren sounding passing at a constant speed, you notice two characteristic changes

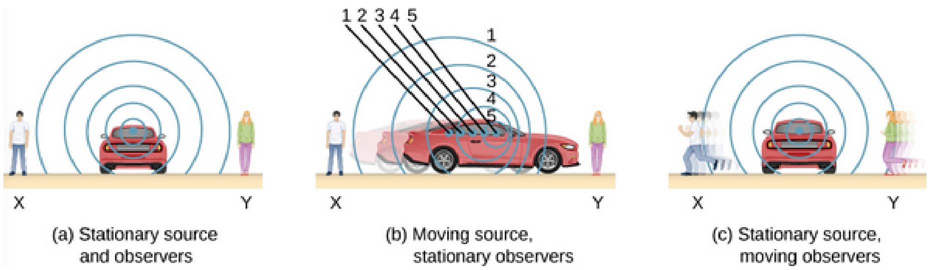
in the sound of the siren. First, the sound increases in loudness as the ambulance approaches and decreases in loudness as it moves away, as expected. But in addition, the high-pitched siren shifts dramatically to a lower-pitched sound when it passes by you. At the moment the ambulance passes, the frequency of the sound heard by a stationary observer changes from a constant high frequency to a constant lower frequency, even though the siren is producing a constant frequency. The closer the ambulance brushes by, the more abrupt the shift. Also, the faster the ambulance moves, the greater the shift. We also hear this characteristic shift in frequency for passing cars, airplanes, and trains.

The Doppler effect is an alteration in the observed frequency of a sound due to motion of either the source or the observer. Although less familiar, this effect is easily noticed for a stationary source and moving observer. For example, if you ride a train past a stationary warning horn, you will hear the horn's frequency shift from high to low as you pass by. The actual change in frequency due to relative motion of source and observer is called a Doppler shift.

The Doppler effect and Doppler shift are named for the Austrian physicist and mathematician Christian Johann Doppler (1803–1853), who did experiments with both moving sources and moving observers. Doppler had musicians play on a moving open train car and also play standing next to the train tracks as a train passed by. Their music was observed both on and off the train, and changes in frequency were measured.

What causes the Doppler shift? The figure below illustrates sound waves emitted by stationary and moving sources in a stationary air mass. Each disturbance spreads out spherically from the point at which the sound is emitted. If the source is stationary, then all of the spheres representing the air compressions in the sound wave are centered on the same point, and the stationary observers on either side hear the same wavelength and frequency as emitted by the source (case a). If the source is moving, the situation is different. Each compression of the air moves out in a sphere from the point at which it was emitted, but the point of emission moves. This moving emission point causes the air compressions to be closer together on one side and farther apart on the other. Thus, the wavelength is shorter in the

direction the source is moving (on the right in case b), and longer in the opposite direction (on the left in case b). Finally, if the observers move, as in case (c), the frequency at which they receive the compressions changes. The observer moving toward the source receives them at a higher frequency, and the person moving away from the source receives them at a lower frequency.



Sounds emitted by a source spread out in spherical waves. (a) When the source, observers, and air are stationary, the wavelength and frequency are the same in all directions and to all observers. (b) Sounds emitted by a source moving to the right spread out from the points at which they were emitted. The wavelength is reduced and the perceived frequency is increased in the direction of motion, so that the observer on the right hears a higher-pitched sound. The opposite is true for the observer on the left, where the wavelength is increased and the frequency is reduced. (c) The same effect is produced when the observers move relative to the source. More details.

We know that wavelength and frequency are related by $v=f\lambda$, where v is the fixed speed of sound. The sound moves in a medium and has the same speed v in that medium whether the source is moving or not. Thus, f multiplied by λ is a constant. Because the observer on the right in case (b) receives a shorter wavelength, the frequency she receives must be higher.

Similarly, the observer on the left receives a longer wavelength, and hence he hears a lower frequency.

The same thing happens in case (c). A higher frequency is received by the observer moving toward the source, and a lower frequency is received by an observer moving away from the source. In general, then, relative motion of source and observer toward one another increases the received frequency. Relative motion apart decreases frequency. The greater the relative speed, the greater the effect.

The Doppler effect occurs not only for sound, but for any wave when there is relative motion between the observer and the source. Doppler shifts occur in the frequency of sound, light, and water waves, for example. Doppler shifts can be used to determine velocity, such as when ultrasound is reflected from blood in a medical diagnostic. The relative velocities of stars and galaxies are determined by the shift in the frequencies of light received from them and these measurements have implied much about the origins of the universe. Modern physics has been profoundly affected by observations of Doppler shifts.

Figure credits

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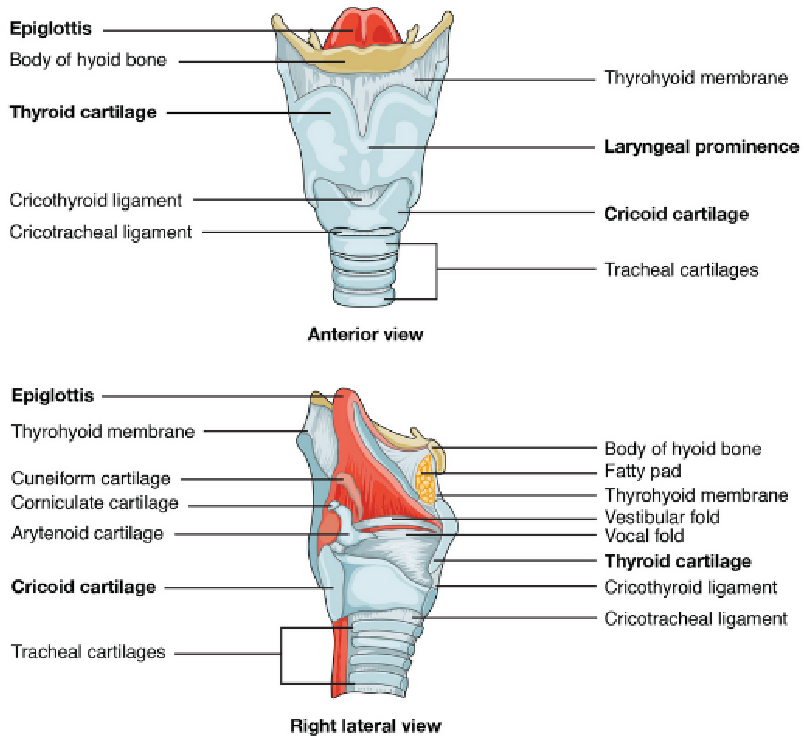
Vocal Systems

The human larynx is protects the entrance of the trachea and produces voice. It is structured by three large unpaired cartilages (thyroid, cricoid and epiglottis) and three paired cartilages (arytenoid, corniculate and cuneiform). Internally it contains a pair of true vocal folds and a second, more superior pair false vocal folds with protective role. The intrinsic laryngeal muscles control the abduction of the vocal folds for respiration and adduction for voice or for protection during swallowing. These muscles are innervated by the superior and recurrent laryngeal nerves, which are branches of the vagus nerve (CN X). The vocal folds are formed by cover of mucus, epithelium and connective tissue, a vocal ligament rich in elastin and collagen and a body formed by the thyroarytenoid muscle.

The Human Larynx

The larynx is a cartilaginous structure inferior to the laryngopharynx that connects the pharynx to the trachea and helps regulate the volume of air that enters and leaves the lungs. The structure of the larynx is formed by several pieces of cartilage. Three large cartilage pieces—the thyroid cartilage (anterior), epiglottis (superior), and cricoid cartilage (inferior)—form the major structure of the larynx. The thyroid cartilage is the largest piece of cartilage that makes up the larynx. The thyroid cartilage consists of the laryngeal prominence, or “Adam’s apple,” which tends to be more prominent in males. The thick cricoid cartilage forms a ring, with a wide posterior region and a thinner anterior region. Three smaller, paired cartilages—the arytenoids, corniculates, and cuneiforms—attach to the epiglottis and the vocal cords and muscle that help move the vocal cords to produce speech.



Cartilaginous structure of the human larynx.
More details.

The epiglottis, attached to the thyroid cartilage, is a very flexible piece of elastic cartilage that covers the opening of the trachea. When in the "closed" position, the unattached end of the epiglottis rests on the glottis. The glottis is composed of the vestibular folds, the true vocal cords, and the space between these folds. A vestibular fold, or false vocal cord, is one of a pair of folded sections of mucous membrane. A true vocal cord is one of the white, membranous folds attached by muscle to the thyroid and arytenoid cartilages of the larynx on their outer edges. The inner edges of the true vocal cords are free, allowing oscillation to produce sound. The size of the membranous folds of the true vocal cords differs between individuals, producing voices with different pitch ranges. Folds in males tend to be larger than those in females, which create a deeper voice. The act of swallowing causes the pharynx and larynx to lift upward, allowing the pharynx to expand and the epiglottis of the larynx to swing downward, closing the opening to the trachea. These movements produce a larger area

for food to pass through, while preventing food and beverages from entering the trachea.

Muscles

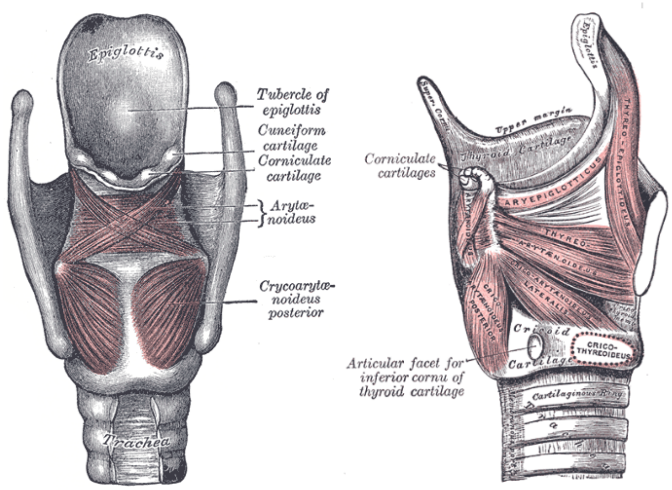
The muscles of the larynx are divided into *intrinsic* and *extrinsic* muscles.

The intrinsic muscles are divided into respiratory and the phonatory muscles (the muscles of phonation). The respiratory muscles move the vocal cords apart and serve breathing. The phonatory muscles move the vocal cords together and serve the production of voice. The extrinsic, passing between the larynx and parts around; and intrinsic, confined entirely. The main respiratory muscles are the posterior cricoarytenoid muscles. The phonatory muscles are divided into adductors (lateral cricoarytenoid muscles, arytenoid muscles) and tensors (cricothyroid muscles, thyroarytenoid muscles).

Intrinsic

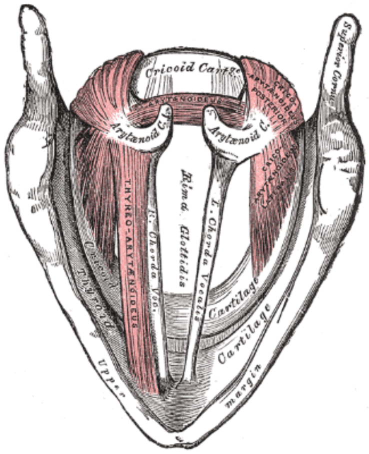
The intrinsic laryngeal muscles are responsible for controlling sound production.

- Cricothyroid muscle lengthen and tense the vocal folds.
- Posterior cricoarytenoid muscles abduct and externally rotate the arytenoid cartilages, resulting in abducted vocal folds.
- Lateral cricoarytenoid muscles adduct and internally rotate the arytenoid cartilages, increase medial compression.
- Transverse arytenoid muscle adduct the arytenoid cartilages, resulting in adducted vocal folds.
- Oblique arytenoid muscles narrow the laryngeal inlet by constricting the distance between the arytenoid cartilages.
- Thyroarytenoid muscles – sphincter of vestibule, narrowing the laryngeal inlet, shortening the vocal folds, and lowering voice pitch. The internal thyroarytenoid is the portion of the thyroarytenoid that vibrates to produce sound.



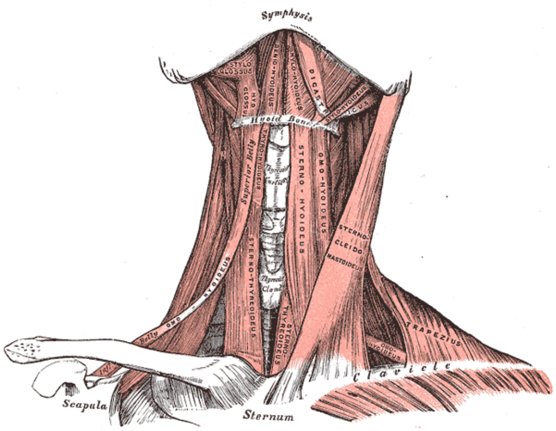
Intrinsic muscles of the larynx. Left. Posterior view of the larynx showing the posterior cricoarytenoid muscle, the transverse and the oblique arytenoid muscles (labeled arytaenoideus). Right. Medial view of sagittal cut through the larynx, showing the muscles that control the glottis and the vocal folds. More details (left, right).

Notably the only muscle capable of separating the vocal cords for normal breathing is the posterior cricoarytenoid. If this muscle is incapacitated on both sides, the inability to pull the vocal folds apart (abduct) will cause difficulty breathing. Bilateral injury to the recurrent laryngeal nerve would cause this condition. It is also worth noting that all muscles are innervated by the recurrent laryngeal branch of the vagus except the cricothyroid muscle, which is innervated by the external laryngeal branch of the superior laryngeal nerve (a branch of the vagus).



Movement of the vocal folds by pivoting of the arytenoid cartilages under the action of the intrinsic muscles of the larynx. More details.

Extrinsic



Extrinsic laryngeal muscles position the larynx in relation to the hyoid, mandible, skull and thorax. More details.

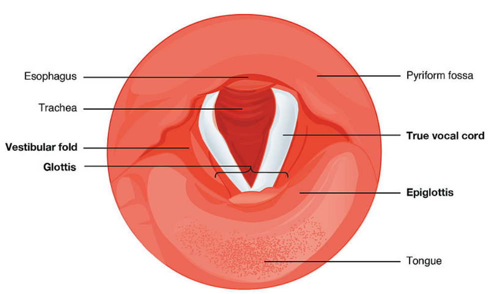
The extrinsic laryngeal muscles support and position the larynx within the trachea.

- Sternothyroid muscles depress the larynx.
- Omohyoid muscles depress the larynx.
- Sternohyoid muscles depress the larynx.
- Thyrohyoid muscles elevates the larynx.
- Digastric elevates the larynx.
- Stylohyoid elevates the larynx.
- Mylohyoid elevates the larynx.
- Geniohyoid elevates the larynx.
- Hyoglossus elevates the larynx.
- Genioglossus elevates the larynx

Vocal folds

Endoscopic view of the larynx showing the vocal folds in open position for unimpeded respiration. More details.

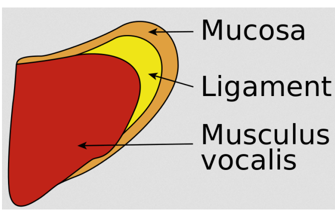
Continuous with the laryngopharynx, the superior portion of the larynx is lined with stratified squamous epithelium transitioning into pseudostratified ciliated columnar epithelium that contains goblet cells. Similar to the nasal cavity and nasopharynx, this specialized epithelium produces mucus to trap debris and pathogens as they enter the trachea. The cilia beat the mucus upward towards the laryngopharynx, where it can be swallowed down the esophagus.



The main components of the human glottis. More

details.

The vocal folds are located within the larynx at the top of the trachea. They are attached posteriorly to the arytenoid cartilages and anteriorly to the thyroid cartilage. They are part of the glottis which is the point at which the airflow is normally interrupted. Their outer edges are attached to muscle in the larynx while their inner edges, or margins, are free forming the opening called the rima glottidis.



The three layers of the human vocal fold. More details.

The tissues of the vocal folds have three major layers: cover, vocal ligament and body.

- The cover is a mucosa formed by stratified squamous epithelium bordered by ciliated pseudostratified epithelium with goblet cells. It is covered with two layers of mucus: a mucinous layer and serous layer. Both mucus layers provide viscous and watery environment for cilia beating posteriorly and superiorly. The mucociliary clearance keeps the vocal folds essentially moist, clean and lubricated. The epidermis layer is secured to the deeper connective tissue by basement

membrane. The mucosa layer vibrates at a frequency range of 100–1000 Hz and displacements of about 1mm.

- The vocal ligament is enclosed within the vocal folds and is responsible for strain during phonation. It is a band of yellow elastic tissue attached anteriorly to the angle of the thyroid cartilage and posteriorly to the vocal process of the arytenoid cartilage. Within the vocal ligament, fibrous proteins such as elastin and collagen are key in maintaining the proper elasticity while collagen is responsible for the resistance and resilience of the vocal fold to tensile strength. The normal strain level of vocal ligament ranges from 0–15% during phonation (voicing).
- The body of the vocal fold contains the thyroarytenoid (vocalis) muscle. This muscle shortens the vocal ligament letting the vocal fold relax and lower the pitch of voice. This muscle is a flat triangular band and is pearly white in color. It is actually divided into bundles with different attachments and secondary roles have been proposed for them.

False vocal folds

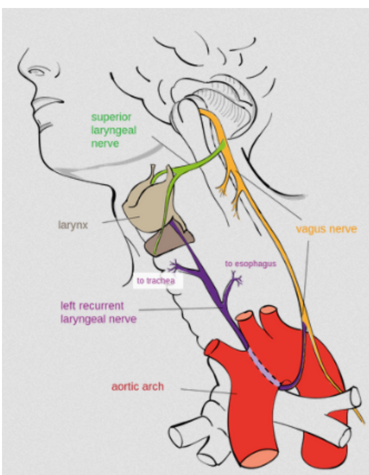
The vocal folds are sometimes called 'true vocal folds' to distinguish them from the 'false vocal folds' known as vestibular folds or ventricular folds. These are a pair of thick folds of mucous membrane that protect and sit slightly superior to the more delicate true folds. They have a minimal role in normal phonation, but are often used to produce deep sonorous tones in Tibetan chant and Tuvan throat singing, as well as in musical screaming and the death growl vocal style.

Innervation

The larynx is innervated by two branches of the vagus nerve (CN X): the superior and recurrent laryngeal nerves.

The superior laryngeal nerve consists of two branches: the internal laryngeal nerve (sensory), which supplies sensory fibers to the laryngeal mucosa, and the external laryngeal nerve (motor), which innervates the cricothyroid muscle.

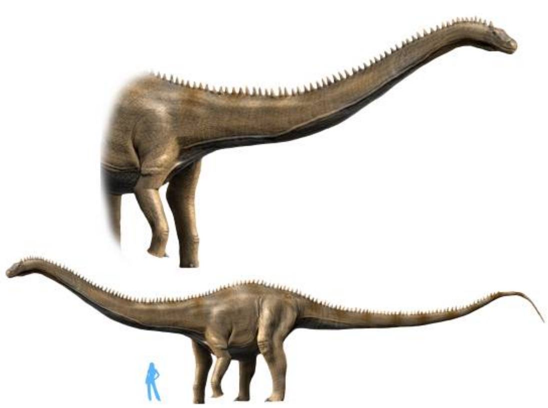
The recurrent laryngeal nerves (RLN) branch from the vagus nerve. As the name indicates, they run down into the thorax and back up to the larynx. The vagus nerves exit the skull at the jugular foramen and travel alongside the carotid arteries through the neck. The left RLN branches off the vagus at the aortic arch and the right at the right subclavian artery. The left RLN passes in front of the arch and then wraps underneath and behind it. The right RLN does the same around the right subclavian artery. Both nerves then typically ascend in a groove at the junction of the trachea and esophagus. They extend behind the posterior lobes of the thyroid gland and enter the larynx deep to the inferior constrictor muscle, just posterior to the cricothyroid joint. The terminal branch is called the inferior laryngeal nerve.



The vagus nerve extends down from the brain to the thorax, the left recurrent laryngeal nerve

branches off of the vagus nerve next to the heart and then it extends back up the neck to innervate the laryngeal muscles. More details.

The recurrent laryngeal nerves control all intrinsic muscles of the larynx except for the cricothyroid muscle. These muscles act to open, close, and adjust the tension of the vocal cords, and include the posterior cricoarytenoid muscles, the only muscle to open the vocal cords. These nerves also carry sensory information from the mucous membranes of the larynx below the lower surface of the vocal fold, as well as sensory, secretory and motor fibers to the cervical segments of the esophagus and the trachea.



The dinosaur *Supersaurus vivianae* had one of the longest necks in history. Based on the anatomy of live

reptiles, its vagus and recurrent nerves would run 28 m to deliver motor commands from the brain to the laryngeal nerves. Human profile in light blue for scale. More details.

The extreme detour of the recurrent laryngeal nerves, about 4.6 m in the case of giraffes, became famous as evidence of evolution, as opposed to Intelligent Design. The nerve's route would have been direct in the fish-like ancestors of modern tetrapods, traveling from the brain, past the heart, to the gills, as it does in modern fishes. Over the course of evolution, as the neck extended and the heart became lower in the body, the laryngeal nerve was caught on the wrong side of the heart’s main vessels. Natural selection gradually lengthened the nerve by tiny increments to accommodate, resulting in the circuitous route now observed. Sauropod dinosaurs were the vertebrates with the longest necks in record. The total length of the vagus nerve and recurrent laryngeal nerve (brain to larynx) would have been up to 28 m in *Supersaurus*.

Development

In all other mammals and in newborn infants, the larynx is initially at the level of the C2–C3 vertebrae, and is further forward and higher relative to its position in the adult body. The epiglotis rests against the soft palate, forcing food to press the epiglottis closed during swallowing and therefore preventing choking. The larynx descends later as the child grows, especially in males with the rise of testosterone levels during puberty.

Figure credits

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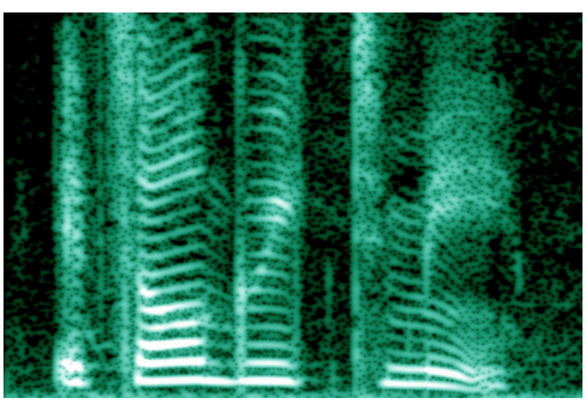
Vowels and Consonants
Articulatory phonetics is the branch of linguistics that studies how the vocal apparatus is moved to produce speech sounds. The International Phonetic Alphabet is used to represent all the sounds produced in all languages. Vocal sounds are produced as vowels, with unrestricted air flow, or consonants, with blocked or constricted airflow. Vowels are characterized not by fundamental frequency of vocal fold vibration, but by distribution of energy in their harmonics. This is a function of the resonance patterns in the vocal cavities, which can be modified by moving the anatomy of the vocal tract. Vowels are not categorically different in production mode or sound. The categorization is learned and the boundaries are variable among languages, dialects and accents. The articulation of vowels mostly involves raising, protracting or retracting the tongue. Consonants involve blocking or restricting the airflow through various manners of articulation and doing so at various places of articulation. The various possible combinations between manners and places of articulation originate the great variety of consonant sound observed in the multitude of languages spoken around the world.

Human speech

Most of the sounds that humans use in speech are produced by the vocal folds. Non-vocal sounds include clicks produced with the lips or tongue. Vibration of the vocal folds produces complex sound waves with elaborate harmonic structure. The vocal folds can be stretched or relaxed, producing voice over a wide range of fundamental frequencies.



The spectrogram of the human voice reveals its rich harmonic content. More details.

At any given fundamental frequency, the voice can be changed in a myriad of ways that influence its meaning during speech or singing. After being produced at the vocal folds, sound is modified through cavity resonances in the pharynx, mouth and nasal cavity and through constriction or interruption of the flow at the soft palate, tongue, teeth or lips. A large number of muscles can move body parts in ways that alter the quality of voice and in this way become part of the vocal system. The vocal system could be the most complex and versatile motor system in our body.

Phonetics is the branch of linguistics that studies the sounds of human speech and equivalent aspects of sign languages. It is divided into articulatory, acoustic and auditory phonetics. Articulatory phonetics is the subfield that studies how the anatomy of the vocal apparatus is used to articulate speech. It addresses the biomechanics of positioning structures, the physics of airflow and the acoustics of the articulation.

International phonetic alphabet (IPA)

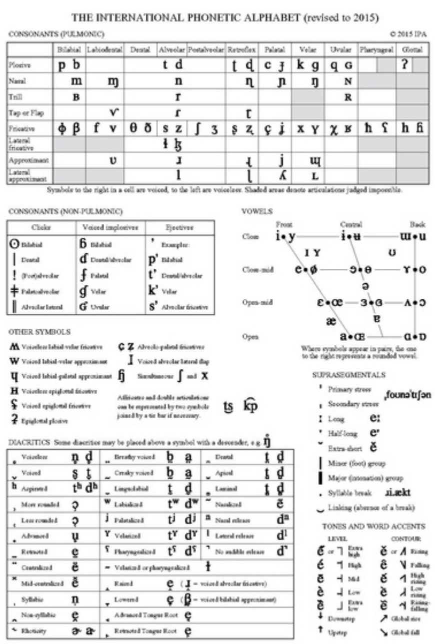
The variety of vocal sounds produced for communication needed to be cataloged using a common notation system that could be applied to any language and dialect. The International Phonetic Association created the International Phonetic Alphabet (IPA) in the late 19th century as a standardized representation of the sounds of spoken language.

IPA symbols are composed of one or more elements of two basic types: letters and diacritics. The sound of the English letter ⟨t⟩, for example, may be transcribed in IPA with a single letter, [t], or with a letter plus diacritics, [t̪ʰ], depending on how precise one wishes to be. As of 2005 the system contains 107 letters and 52 modifyiers. The letters chosen for the IPA come

mostly from Latin and Greek, but many other letters and symbols were also included.

The IPA provides one letter for each distinctive sound (speech segment). This means that:

- It does not normally use combinations of letters to represent single sounds, the way English does with ⟨sh⟩, ⟨th⟩ and ⟨ng⟩, or single letters to represent multiple sounds the way ⟨x⟩ represents /ks/ or /ɡz/ in English.
- There are no letters that have context-dependent sound values, as do "hard" and "soft" ⟨c⟩ or ⟨g⟩ in several European languages.
- It does not have separate letters for two sounds if no known language makes a distinction between them.



The official chart of the IPA as of 2015. An official chart is released after each revision of the IPA, summarizing

its structure. More details.

The IPA offers over 160 symbols for transcribing speech but only a subset of these is used to transcribe any one language. It is possible to transcribe speech with various levels of precision. A precise phonetic transcription in which sounds are described in a great deal of detail is known as a narrow transcription. A coarser transcription is called a broad transcription. The English word little, for example, may be transcribed broadly using the IPA as [ˈlɪtəl], and this broad (imprecise) transcription is a more or less accurate description of many pronunciations. A narrower transcription may focus on individual or dialectical details: [ˈɫɪɾɫ] in General American, [ˈlɪʔo] in Cockney, or [ˈɫɪːɫ] in Southern US English.

Classifications of vocal sounds

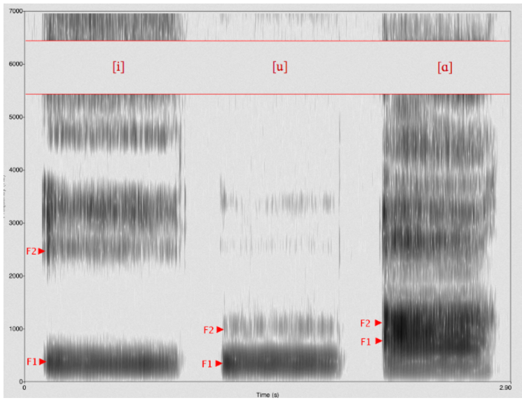
The sounds produced for vocal communication form two major groups: vowels and consonants.

- Vowels are produced by the passage of air through the larynx and the vocal tract mostly having the vocal tract open and allowing the air to escape without generating turbulent noise.
- Consonants are produced with restriction or interruption of the airflow from the lungs.

Vowels

Vowels are mostly made distinguishable by differences in the distribution of energy among their harmonics. As vowels are produced with the vocal tract open, these differences are mostly generated through appropriate positioning of the elements in the vocal tract. This alters the resonance in the vocal cavities which in turn modifies the distribution of energy among the harmonics. The acoustics of vowels can be visualized using

spectrograms, which display the acoustic energy at each frequency, and how this changes with time.



Spectrogram of vowels [i, u, ɑ]. [ɑ] is a low vowel, so its F1 value is higher than that of [i] and [u], which are high vowels. [i] is a front vowel, so its F2 is substantially higher than that of [u] and [ɑ], which are back vowels. More details.

A vowel is therefore determined by the configuration of the vocal tract and not by the tension in the vocal folds. A singer can vocalize an “ah” and change the fundamental frequency of the voice drastically while still holding a sound that can clearly be recognized as the vowel “ah”. Conversely, the singer can maintain the tension at the vocal folds constant while cycling through all the vowels.

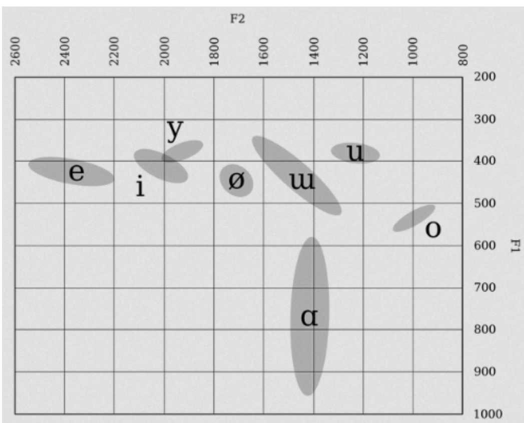
Watch the MRI video at https://upload.wikimedia.org/wikipedia/commons/9/9f/Real-time_MRI_-_Speaking_%28English%29.ogv. More details.

The frequencies that are emphasized at a given configuration of the vocal tract are called formants. When the tension in the vocal folds is changed without moving the vocal tract, the formants stay the same, but the fundamental frequency changes. This results in a different set of harmonics being matched by the formants and emphasized by resonance in the vocal tract.

One important aspect of vowel production is that the muscle contractions that produce the various vowels all occur along continual ranges without categorical steps. A person's concept of a given vowel is a learned convention that is employed when producing the vowel and when recognizing it in another person's speech. These conventions do not hold across languages and they also vary among regions that speak a same language.

Formant charts are frequently used to analyze the continuum of the vowel space and study accents, dialects, pathologies and the boundaries between vowels. The first formant, abbreviated "F1", corresponds to vowel openness (vowel height). Open vowels have high F1 frequencies, while close vowels have low F1 frequencies, as can be seen in the accompanying spectrogram. The [i] and [u] have similar low first formants, whereas [ɑ] has a higher formant.

The second formant, F2, corresponds to vowel frontness. Back vowels have low F2 frequencies, while front vowels have high F2 frequencies. This is very clear in the spectrogram, where the front vowel [i] has a much higher F2 frequency than the other two vowels. However, in open vowels, the high F1 frequency forces a rise in the F2 frequency as well, so an alternative measure of frontness is the difference between the first and second formants. For this reason, some people prefer to plot as F1 vs. F2 – F1.



A formant chart showing the stem vowel space of the Kyrgyz language. Vowels are produced in different parts of the acoustic space formed when the frequency of the first formant (F1) is plotted against that of the second formant (F2). More details.

Vowels are more traditionally defined phonetically or phonologically.

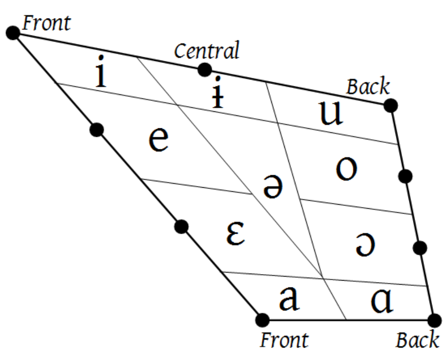
- In the phonetic definition, a vowel is a sound, such as the English "ah" or "oh", produced with an open vocal tract. It is median, oral,

frictionless and continuant, meaning that most air escapes through the middle of the tongue, through the mouth, without restriction and continuously . There is no significant build-up of air pressure at any point above the glottis. This contrasts with consonants, such as the English "sh" [ʃ], which have a constriction or closure at some point along the vocal tract.

- In the phonological definition, a vowel is defined as the nucleus of a syllable. In oral languages, phonetic vowels normally form the nucleus of many or all syllables, whereas consonants form the onset and (in languages that have them) coda.

Vowel articulation

The traditional view of vowel production is one of articulatory features that determine a vowel's quality as distinguishing it from other vowels. Daniel Jones developed the cardinal vowel system to describe vowels in terms of the features of tongue height (vertical dimension), tongue backness (horizontal dimension) and roundedness (lip articulation). These three parameters are indicated in the schematic quadrilateral IPA vowel diagram. The vowel quadrilateral is not a perfect mapping of tongue position but it is an intuitive morphological approximation to the tongue influences the acoustics of the vowels.



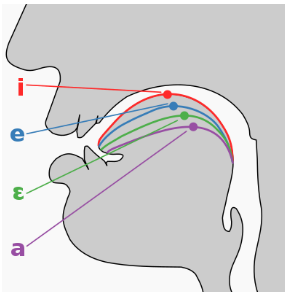
The original vowel quadrilateral, from Jones' articulation.

The vowel trapezoid of the modern IPA, and at the top of this article, is a simplified rendition of this diagram. More details. Try the current IPA chart with audio.

Articulation features of vowels

Height

Vowel height is named for the vertical position of the tongue relative to either the roof of the mouth or the aperture of the jaw. It correlates closely with the first formant (lowest resonance of the voice), abbreviated F1. In close vowels, also known as high vowels, such as [i] and [u], the first formant is consistent with the tongue being positioned close to the palate, high in the mouth, whereas in open vowels, also known as low vowels, such as [a], F1 is consistent with the jaw being open and the tongue being positioned low in the mouth. Height is defined by the inverse of the F1 value: The higher the frequency of the first formant, the lower (more open) the vowel.



Idealistic tongue positions of cardinal front vowels with highest point indicated. More details.

The International Phonetic Alphabet defines seven degrees of vowel height, but no language is known to distinguish all of them:

- close (high)
- near-close (near-high)
- close-mid (high-mid)
- mid (true-mid)
- open-mid (low-mid)
- near-open (near-low)
- open (low)

The parameter of vowel height appears to be the primary cross-linguistic feature of vowels in that all spoken languages use height as a contrastive feature. No other parameter, even backness or rounding (see below), is used in all languages. Some languages have vertical vowel systems in which at least at a phonemic level, only height is used to distinguish vowels.

Backness

Vowel backness is named for the position of the tongue during the articulation of a vowel relative to the back of the mouth. As with vowel height, however, it is defined by a formant of the voice, in this case the second, F2. In front vowels, such as [i], the frequency of F2 is relatively high, which generally corresponds to a position of the tongue forward in the mouth, whereas in back vowels, such as [u], F2 is low, consistent with the tongue being positioned towards the back of the mouth.

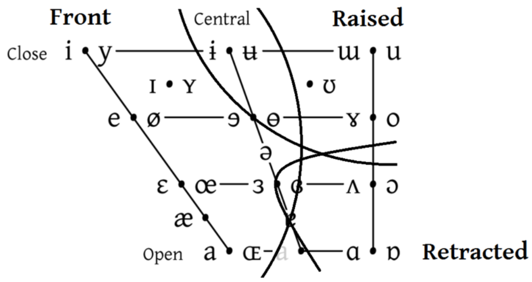
The International Phonetic Alphabet defines five degrees of vowel backness:

- front
- near-front
- central
- near-back
- back

Although English has vowels at five degrees of backness, there is no known language that distinguishes five degrees of backness without additional differences in height or rounding.

Front, raised and retracted vs. height and backness

The conception of the tongue moving independently in two directions, high–low and front–back, is not supported by articulatory evidence. The natural movements of the tongue are better characterized by the three directions of movement that it can take from its neutral position: front, raised, and retracted. In this alternative classification, front vowels can be secondarily qualified as close or open, as in the traditional conception.



Front, raised and retracted are the three articulatory dimensions of vowel space. More details.

Roundedness

Roundedness is named after the rounding of the lips in some vowels. Because lip rounding is easily visible, vowels may be commonly identified as rounded based on the articulation of the lips. Acoustically, rounded vowels are identified chiefly by a decrease in F2, although F1 is also slightly decreased.

Lip position in the two forms of vowel rounding: protrusion (left) and compression (right). More details (left, right).

In most languages, roundedness is a reinforcing feature of mid to high back vowels rather than a distinctive feature. Usually, the higher a back vowel, the more intense is the rounding.

Nasalization

Nasalization refers to whether some of the air escapes through the nose. In nasal vowels, the velum (soft palate) is depressed and some air travels through the nasal cavity. An oral vowel is a vowel in which all air escapes through the mouth. French, Polish and Portuguese contrast nasal and oral vowels.

Phonation

Voicing describes whether the vocal cords are vibrating during the articulation of a vowel. Most languages have only voiced vowels, but several Native American languages, such as Cheyenne and Totonac, contrast voiced and devoiced vowels. Vowels are devoiced in whispered speech. In Japanese and in Quebec French, vowels that are between voiceless consonants are often devoiced.

Other features

Some languages contrast between vowels made with the root of the tongue advanced or retracted, using or not secondary narrowings in the vocal tract or making tense or lax vowels.

Consonants

Consonants are classified with base on:

- Manner of articulation is how air escapes from the vocal tract when the consonant sound is made. Manners include stops, fricatives, africates, laterals and nasals.

- Place of articulation is where in the vocal tract the obstruction of the consonant occurs, and which speech organs are involved. Places include bilabial (both lips), alveolar (tongue against the gum ridge), and velar (tongue against soft palate).

While manner and place of articulation form the main features used to categorize consonants, several other features are also considered in finer analyses:

- Phonation of a consonant is how the vocal cords vibrate during the articulation. When the vocal cords vibrate fully, the consonant is called voiced. When they do not vibrate at all, it is voiceless.
- Voice onset time (VOT) indicates the timing of the interruption in relation to the onset of vocal fold vibration.
- Airstream mechanism is how the air moving through the vocal tract is powered. Most languages have exclusively pulmonic egressive consonants, which use the lungs and diaphragm, but ejectives, clicks, and implosives use different mechanisms.
- Length is how long the obstruction of a consonant lasts. This feature is borderline distinctive in English, as in "wholly" [hoʊlli] vs. "holy" [hoʊli], but it can be more distinctive in other languages.

Manners of articulation

The main manners of articulation include:

- **Stop.** Involves momentary blocking of airflow the oral vocal tract, and no nasal air flow. Examples include English p t and b. All languages have stops.

- **Nasal.** Air passes through the nose. The shape and position of the tongue determine the resonant cavity that gives different nasals their

characteristic sounds. Examples include English m, n. Nearly all languages have nasals.

- **Fricative.** There is continuous frication (turbulent and noisy airflow) at the place of articulation. Examples include English f, s, v and z. Most languages have fricatives. Indigenous Australian languages are almost completely devoid of fricatives of any kind.

- **Sibilant.** A type of fricative where the airflow is guided by a groove in the tongue toward the teeth, creating a high-pitched and very distinctive sound. These are by far the most common fricatives and include English s and z.

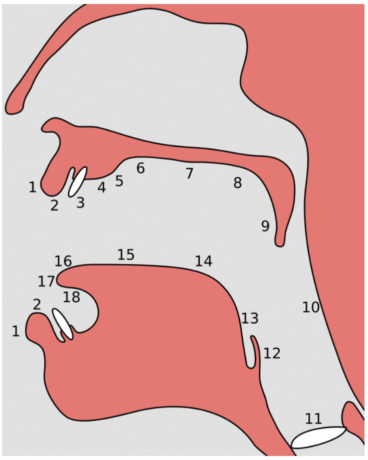
- Lateral fricative. A rare type of fricative, where the frication occurs on one or both sides of the edge of the tongue. The "ll" of Welsh is a lateral fricative.

- **Affricate**. Begins with a stop and continues as a fricative. The English letters ch and j are affricates. Affricates are common but less common than fricatives.
- **Flap.** Often called a tap, it is a momentary closure of the oral cavity. The "tt" of "utter" is a flap in North American English.
- **Trill.** The articulator (usually the tip of the tongue) is vibrated by the airstream. The double "r" of Spanish "perro" is a trill.
- **Approximant**. There is very little constriction of the airflow. Examples include English w and r.

- **Lateral.** Also calledlateral approximant, this is pronounced with the sides of the tongue. English l is a lateral.

Places of articulation

The passive place of articulation is the place on the more stationary part of the vocal tract where the articulation occurs and can be anywhere from the lips, upper teeth, gums, or roof of the mouth to the back of the throat. The articulatory gesture of the active place of articulation involves the more mobile part of the vocal tract, typically some part of the tongue or lips.



Places of articulation (passive and active). 1. Exo-labial, 2. Endo-labial, 3. Dental, 4. Alveolar, 5. Post-alveolar, 6. Pre-palatal, 7. Palatal, 8. Velar, 9. Uvular, 10. Pharyngeal, 11. Glottal, 12. Epiglottal, 13. Radical, 14. Postero-dorsal, 15. Antero-dorsal, 16. Laminal, 17. Apical, 18. Sub-apical. More details.

With respect to the place of articulation, consonants are classified within the following major groups:

- Bilabial. Produced with both lips. Ex: b, m, and p.
- Labiodental. f and v are articulated by placing the upper teeth against the lower lip.
- Interdental. "th" as in think or as in the are pronounced by inserting the tip of the tongue between the teeth.
- Alveolar. t, d, n, s, z, l, and r are produced with the tongue is raised towards the alveolar ridge. The tip of the tongue may touch the ridge (t, d, n), or the tip may be lowered so that air escapes over it (s, z). For l, the middle of the tongue is raised while air escapes around its sides. For r, the tip of tongue is curled back behind the alveolar ridge, or bunched up behind the ridge and the air escapes through the central part of the mouth.
- Palatal. j is produced by raising the front part of the tongue to the palate.
- Velar. k and g are produced by raising the back of the tongue to the soft palate or the soft palate.
- Uvular. Some sounds are produced by raising the back of the tongue to the uvula. The 'r' in French and German may be an uvular trill. These do not normally occur in English.
- Glottal. h results from the flow of air coming from an open glottis, past the tongue and lips as they prepare to pronounce the vowel that follows h.

Figure credits

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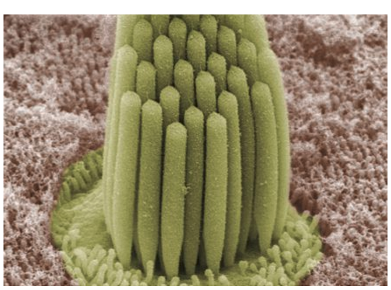
The Ears

Ion channels open when the hair bundle of hair cell is deflected by a mechanical stimulus and this leads the cell to secrete neurotransmitters and stimulate the associated sensory neuron. The mechanical stimulus is therefore transduced into a neural stimulus. This forms the base of the senses of balance and hearing. Mechanoreceptors like hair cells are found in most animals from cnidarians to vertebrates. In mammals, they are found only in the inner ears which are composed of vestibule and cochlea. The vestibule contains three semicircular canals, the saccule and the utricle. These organs detect rotational and linear accelerations of the head. The cochlea contains the organ of Corti which is specialized in detecting sound. Acoustic waves enter the ear by reflecting on the auricle, crossing the ear canal and vibrating the eardrum. The vibration is then transferred from the eardrum to oval window by the malleus, incus and stapes, the smallest bones of the body. The oval window vibrates the fluid inside the inner ear, bringing the signal to the hair cells in the organ of Corti.

The ears provide the senses of hearing and balance. Their middle portion is an air-filled cavity that connects to the mouth or nasopharynx. This connection allows for adjustment to changes in atmospheric pressure, it influences hearing and voice and it can allow for infections to spread between the two cavities. The inner portions of the ears are fluid-filled chambers that contain hair cells. These sensory detectors do not regenerate in mammals and exposure to loud noise can produce permanent hearing loss.

Hair cells



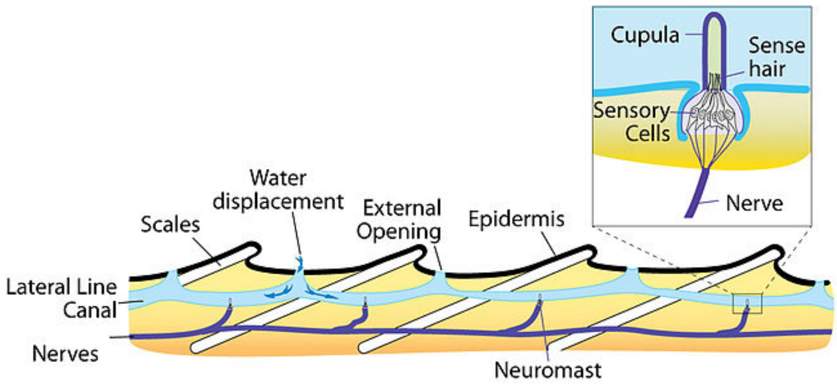
Stereocilia forming the hair bundle on the apex of a hair cell in the inner ear of a frog. More details.

Some epithelial cells have apical specializations called stereocilia. When the stereocilia are deflected, ion channels open and the cell is stimulated. This arrangement forms an ancient type of mechanoreceptor called hair cell. Various types of stimuli are detected by animals through hair cells. The stereocilia can be deflected by fluid flow or by contact with a sensory structure. The former case is found in the lateral lines of fishes and in the semicircular canals of all vertebrates, whereas the later case is found in the statocysts of invertebrates, the cochlea of mammals and the otolithic organs of all vertebrates.

The lateral lines of fishes and the statocysts of invertebrates can be found in contact with the medium.

Lateral line

The lateral line system allows the detection of movement, vibration, and pressure gradients in the water surrounding a fish, providing spatial awareness and the ability to navigate in the environment. This plays an essential role in orientation, predatory behavior, defense, and social schooling.



Structure of the lateral line in bony fishes. More details.

The functional unit of the lateral line is the neuromast. This is a mechanoreceptive organ that detects mechanical changes in water. Superficial neuromasts are located externally on the surface of the body, while canal neuromasts are located along the lateral lines in subdermal, fluid filled canals. Each neuromast consists of a group of hair cells whose hair bundles are covered by a flexible gelatinous cupula.

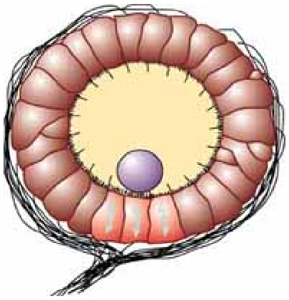
Lateral line of a goldfish. Notice the red structures on some of the golden

scales, following the longitudinal line from head to tail. More details.

Hair cells utilize a system of transduction that uses rate coding in order to transmit the directionality of a stimulus. Hair cells of the lateral line system produce a constant, tonic rate of firing. As mechanical motion is transmitted through water to the neuromast, the cupula is deflected, causing deflection of the embedded hair bundles. This results in opening of ion channels in the hair cells. Deflection towards the longest stereocilium results in depolarization of the hair cell, increased neurotransmitter release by the hair cell. Deflection towards the shorter stereocilium has the opposite effect. These electrical impulses are then transmitted by sensory neurons to the brain.

Statocysts

The **statocyst** is a balance sensory receptor organ present in aquatic invertebrates, including bivalves, cnidarians, ctenophorans, echinoderms, cephalopods, and crustaceans. The statocyst consists of a sac-like structure containing a mineralized mass (**statolith**) and numerous innervated sensory cells with apical projections (setae). The statolith's inertia causes it to push against the setae when the animal accelerates. Deflection of setae by the statolith in response to gravity activates neurons, providing feedback to the animal on change in orientation and allowing balance to be maintained.



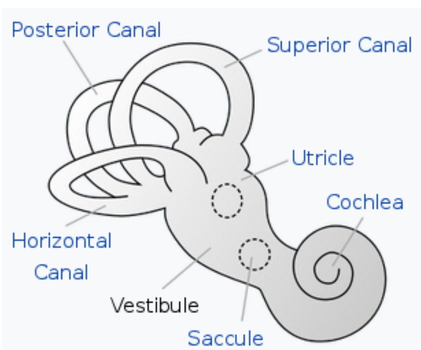
Statocyst containing a dense statolith that deflects the stereocilia of the surrounding hair cells in response to gravity or other linear acceleration. More details.

The statolith shifts as the animal moves. Any movement large enough to throw the organism off balance causes the statolith to brush against tiny bristles which in turn send a message to the brain to correct its balance. A key feature of this organ is having labeled lines. This means that the signal from each receptor cell is not merged into a single or a few axons for the entire organ. Such merging would preserve the signal but it would discard the location information. The signal from each region of the organ is transmitted to the brain through separate axons. The brain determines the direction of the movement (or gravity) by identifying the axons that are bringing in the signal. It can also use the rate of action potentials to determine the strength of the signal (acceleration on the statocyst).

Inner ear

In contrast with the lateral line and statocysts which tend to be found near the surface of the body, the cochlea, otolith organs and semicircular canals are contained in a bony enclosure immediately lateral to the braincase, inside the petrous part of the temporal bone. The soft tissues are called the membranous labyrinth, and it is surrounded by dense bone (the bony labyrinth). Together, the membranous and bony labyrinths form the inner ear.

In humans, the inner ear has six sensory regions containing hair cells: three semicircular canals, two otolith organs (saccule and utricle) and the cochlea. Because these are spots where the epithelium is differentiated from the surrounding epithelium, they are called maculae (latin for spot).

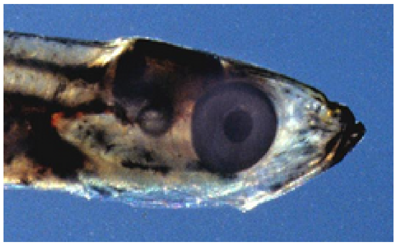


The inner ear, formed by vestibule and cochlea. Sound is primarily detected at the cochlea, whereas rotation of the head is detected by the three semicircular canals in the vestibule and linear acceleration is detected by the

saccule and utricle also in the vestibule. More details.

Otolith organs

Vertebrates have sensory structures in the inner ears that are analogous (similar function) to the statocysts of invertebrates. They are the otolithic organs: saccule, utricle and lagena (missing in mammals). These otolithic organs share the property of containing mineralized bodies called otoliths (oto = ear, lithos = stone). When the head tissues move, the otholiths lag, producing deflection of the hair bundles of neighboring hair cells. This allows vertebrates to sense head position (gravity), linear movement, or vibration. The neural signals are transmitted through the vestibulocochlear nerve to the brain stem and cerebellum.

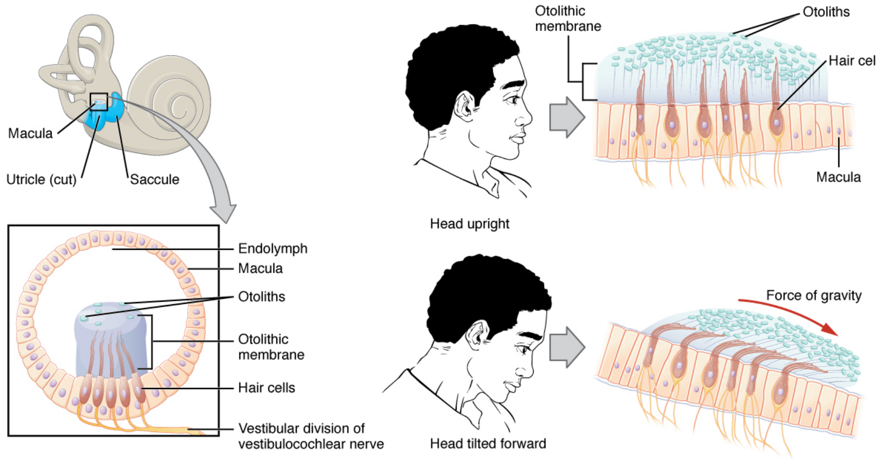


Three months old juvenile herring (body length = 30 mm). The otolith is visible by transparency, posterior to the eye, as a circle slightly smaller than the pupilla. More details.

In fishes, otoliths receive specific names for each macula. The concretion is called sagitta in the saccule, lapillus in the utricle and asteriscus in the lagena (absent in most mammals). They can reach large sizes (31.4 mm, 11% of the body length), although they remain smaller in most species. The otoliths grow throughout the life of the fish by peripheral deposition of calcium carbonate (mostly aragonite). The growth rate tends to accompany that of the body and vary along the year, resulting in the appearance of rings that resemble tree rings. By counting the rings, it is possible to determine the age of the fishes from habitats with well-defined growth seasons. After the death and decomposition of a fish, otoliths may be preserved within the body of an organism or be dispersed before burial and fossilization. Dispersed otoliths are one of the many microfossils which can be found through a micropalaeontological analysis of a fine sediment.

In addition to detection of linear acceleration, otolith organs are the primary hearing organs in fishes. In amphibians, sound detection is mostly performed by two other vestibular maculae, the amphibian papilla and the basilar papilla. In birds and mammals, the cochlea is the main hearing organ. In all vertebrates however, some auditory sensitivity can be detected at the otolith organs, especially in response to low-frequency sound.

In mammals, the utricle and saccule do not contain a single large otolith, but a large number of tiny otoliths (1-50 um diameter; otoconia) embedded in a gelatinous mass that forms the otolithic membrane. The stereocilia of the hair cells extend into the otolithic membrane. The otoliths essentially increase the inertia of the otolithic membrane, which moves separately from the macula in response to head movements. Tilting the head causes the otolithic membrane to slide over the macula in the direction of gravity. The movement of the otolithic membrane, in turn, deflects the sterocilia, causing some hair cells to depolarize as others hyperpolarize. The exact position of the head is interpreted by the brain based on the pattern of hair-cell depolarization.

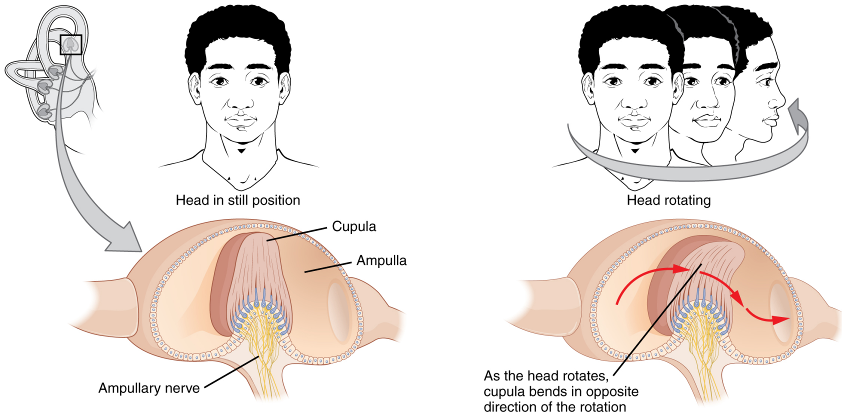


Hair cells in the saccule and utricle are covered by an otolithic membrane containing calcium crystals. Linear acceleration of the head makes the otolithic membrane lag behind the macula deflecting the stereocilia of the hair cells. More details.

The otolithic maculae of mammals are specialized for sensing linear acceleration, such as when gravity acts on the tilting head, or if the head starts moving in a straight line. The difference in inertia between the hair cell stereocilia and the otolithic membrane in which they are embedded leads to a shearing force that causes the stereocilia to bend in the direction of that linear acceleration.

Semicircular canals

A semicircular canal is a ring-like extension of the inner ear. Its enlarged base is called the ampulla. A group of hair cells is found inside the ampulla. They respond to rotational movement, such as turning the head while saying “no.” The stereocilia of these hair cells extend into the cupula, a gelatinous structure that partially obliterates the ampulla. As the head rotates in a plane parallel to the semicircular canal, the fluid lags, deflecting the cupula in the direction opposite to the head movement. The role of the semicircular canal is therefore detecting rotational movement of the head.



Rotational movement of the head is encoded by the hair cells in the base of the semicircular canals. As the head turns, fluid in the canal moves in the opposite direction, bending the cupula and stereocilia. More details.

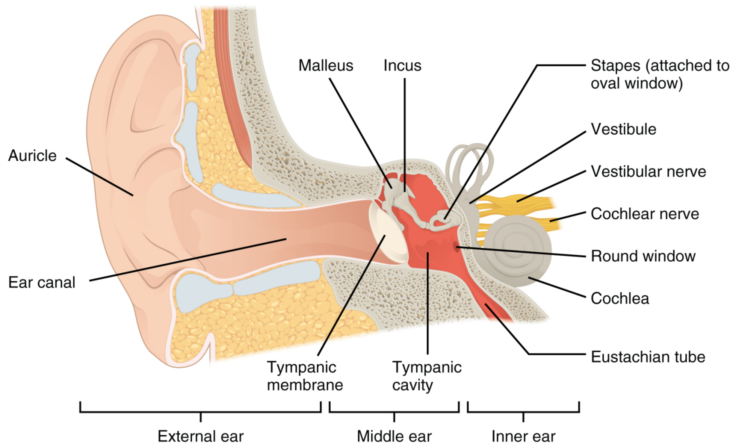
Since the hair cells are stimulated by the flow of fluid within the semicircular canal, they are not stimulated by rotational movement within in a plane that is perpendicular with the plane of the canal. This limitation was circumvented by the evolution of three semicircular canals positioned in perpendicular planes in each ear of vertebrates. Hagfishes (jawless fish) have a single semicircular canal, lampreys have two or three, and all jawed vertebrates have three semicircular canals. By comparing the relative amounts of movement detected by each ampulla, the ear can detect the direction of most head rotations within the three-dimensional (3-D) space.

Vertigo is the sensation of spinning or having one's surroundings spin about them when in reality everything is static. This may be associated with nausea, vomiting, sweating, or difficulties walking. It is typically worsened when the head is moved. Vertigo is the most common (25%) type of dizziness. The most common diseases that result in vertigo are benign paroxysmal positional vertigo (BPPV), Ménière's disease, and labyrinthitis. Less common causes include stroke, brain tumors, brain injury, multiple sclerosis, and migraines. In BPPV, some otoconia are dislodged from their usual position within the utricle, and migrate into one of the semicircular

canals (the posterior canal is most commonly affected due to its anatomical position). When the head is reoriented relative to gravity, the gravity-dependent movement of the heavier otoconial debris within the affected semicircular canal causes abnormal fluid displacement and a resultant sensation of vertigo. BPPV is often treated with a number of simple movements such as the Epley maneuver or Brandt-Daroff exercises. These maneuvers aim to move the particles from locations in the inner ear where they cause vertigo, to where they do not cause these problems. Additionally, medications may be used to alleviate the nausea.

Hearing in humans

Hearing, or audition, is the transduction of sound waves into a neural signal that is made possible by the structures of the ear. The large, fleshy structure on the lateral aspect of the head is known as the auricle. Some sources will also refer to this structure as the pinna, though that term is more appropriate for a structure that can be moved, such as the external ear of a cat. The C-shaped curves of the auricle direct sound waves toward the auditory canal. The canal enters the skull through the external auditory meatus of the temporal bone. At the end of the auditory canal is the tympanic membrane, or ear drum, which vibrates after it is struck by sound waves. The auricle, ear canal, and tympanic membrane are often referred to as the external ear. The middle ear consists of a space spanned by three small bones called the ossicles. The three ossicles are the malleus, incus, and stapes, which are Latin names that roughly translate to hammer, anvil, and stirrup. The malleus is attached to the tympanic membrane and articulates with the incus. The incus, in turn, articulates with the stapes. The stapes is then attached to the inner ear, where the sound waves will be transduced into a neural signal. The middle ear is connected to the pharynx through the Eustachian tube, which helps equilibrate air pressure across the tympanic membrane. The tube is normally closed but will pop open when the muscles of the pharynx contract during swallowing or yawning.



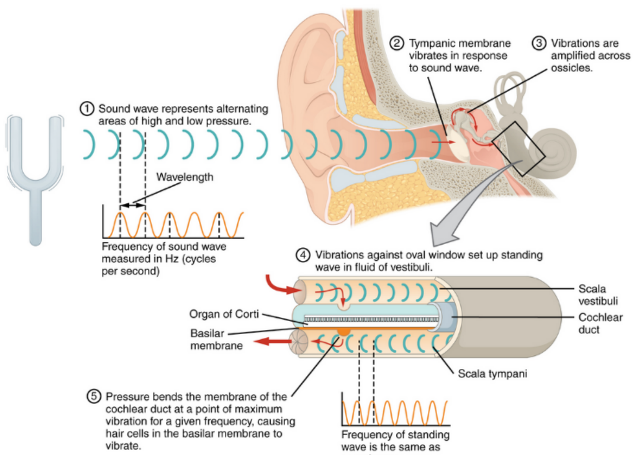
The main structures of the human ear.
More details.

The external ear contains the auricle and ear canal. The middle ear contains the tympanic membrane and the ossicles, and is connected to the pharynx by the Eustachian tube. The inner ear contains the cochlea and vestibule, which are responsible for audition and equilibrium, respectively.

The inner ear is often described as a bony labyrinth, as it is composed of a series of canals embedded within the temporal bone. It has two separate regions, the cochlea and the vestibule, which are responsible for hearing and balance, respectively. The neural signals from these two regions are relayed to the brain stem through separate fiber bundles. However, these two distinct bundles travel together from the inner ear to the brain stem as the vestibulocochlear nerve. Sound is transduced into neural signals within the cochlear region of the inner ear, which contains the sensory neurons of the spiral ganglia. These ganglia are located within the spiral-shaped cochlea of the inner ear. The cochlea is attached to the stapes through the oval window.

The oval window is located at the beginning of a fluid-filled tube within the cochlea called the scala vestibuli. The scala vestibuli extends from the oval window, travelling above the cochlear duct, which is the central cavity of the cochlea that contains the sound-transducing neurons. At the uppermost

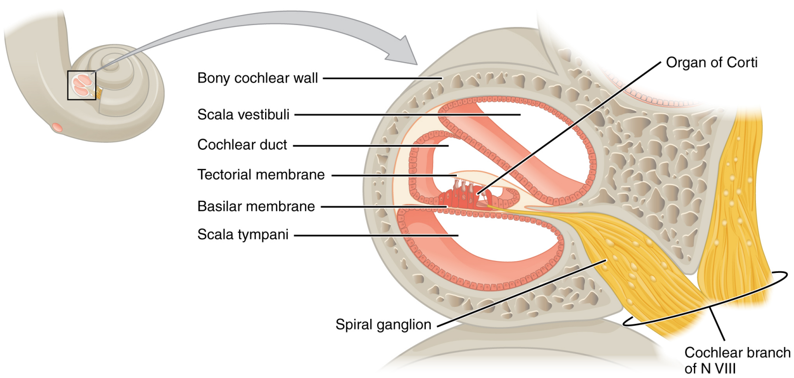
tip of the cochlea, the scala vestibuli curves over the top of the cochlear duct. The fluid-filled tube, now called the scala tympani, returns to the base of the cochlea, this time traveling under the cochlear duct. The scala tympani ends at the round window, which is covered by a membrane that contains the fluid within the scala. As vibrations of the ossicles travel through the oval window, the fluid of the scala vestibuli and scala tympani moves in a wave-like motion. The frequency of the fluid waves match the frequencies of the sound waves. The membrane covering the round window will bulge out or pucker in with the movement of the fluid within the scala tympani.



Transmission of sound waves to cochlea. More details.

A sound wave causes the tympanic membrane to vibrate. This vibration is amplified as it moves across the malleus, incus, and stapes. The amplified vibration is picked up by the oval window causing pressure waves in the fluid of the scala vestibuli and scala tympani. The complexity of the pressure waves is determined by the changes in amplitude and frequency of the sound waves entering the ear.

A cross-sectional view of the cochlea shows that the scala vestibuli and scala tympani run along both sides of the cochlear duct. The cochlear duct contains several organs of Corti, which tranduce the wave motion of the two scala into neural signals. The organs of Corti lie on top of the basilar membrane, which is the side of the cochlear duct located between the organs of Corti and the scala tympani. As the fluid waves move through the scala vestibuli and scala tympani, the basilar membrane moves at a specific spot, depending on the frequency of the waves. Higher frequency waves move the region of the basilar membrane that is close to the base of the cochlea. Lower frequency waves move the region of the basilar membrane that is near the tip of the cochlea.

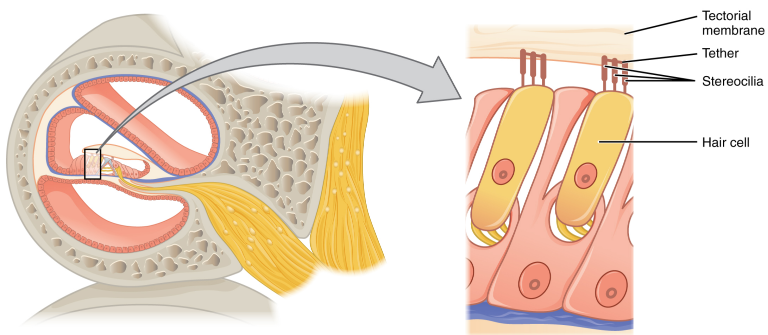


Cross section of the cochlea, showing the organ of Corti. More details.

The three major spaces within the cochlea are highlighted. The scala tympani and scala vestibuli lie on either side of the cochlear duct. The organ of Corti, containing the mechanoreceptor hair cells, is adjacent to the scala tympani, where it sits atop the basilar membrane.

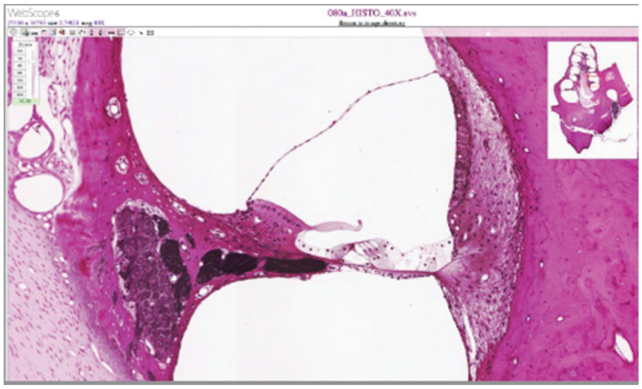
The organs of Corti contain hair cells, which are named for the hair-like stereocilia extending from the cell's apical surfaces. The stereocilia are an array of microvilli-like structures arranged from tallest to shortest. Protein fibers tether adjacent hairs together within each array, such that the array

will bend in response to movements of the basilar membrane. The stereocilia extend up from the hair cells to the overlying tectorial membrane, which is attached medially to the organ of Corti. When the pressure waves from the scala move the basilar membrane, the tectorial membrane slides across the stereocilia. This bends the stereocilia either toward or away from the tallest member of each array. When the stereocilia bend toward the tallest member of their array, tension in the protein tethers opens ion channels in the hair cell membrane. This will depolarize the hair cell membrane, triggering nerve impulses that travel down the afferent nerve fibers attached to the hair cells. When the stereocilia bend toward the shortest member of their array, the tension on the tethers slackens and the ion channels close. When no sound is present, and the stereocilia are standing straight, a small amount of tension still exists on the tethers, keeping the membrane potential of the hair cell slightly depolarized.



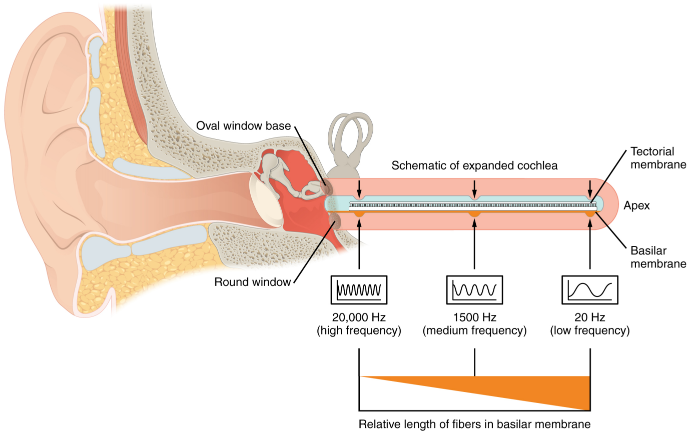
Position of the hair cells between the basilar membrane and the tectorial membrane in the organ of Corti. More details.

The hair cell is a mechanoreceptor with an array of stereocilia emerging from its apical surface. The stereocilia are tethered together by proteins that open ion channels when the array is bent toward the tallest member of their array, and closed when the array is bent toward the shortest member of their array.



Human cochlea and organ of Corti under light microscope with a magnification of 412 x . More details.

As stated above, a given region of the basilar membrane will only move if the incoming sound is at a specific frequency. Because the tectorial membrane only moves where the basilar membrane moves, the hair cells in this region will also only respond to sounds of this specific frequency. Therefore, as the frequency of a sound changes, different hair cells are activated all along the basilar membrane. The cochlea encodes auditory stimuli for frequencies between 20 and 20,000 Hz, which is the range of sound that human ears can detect. The unit of Hertz measures the frequency of sound waves in terms of cycles produced per second. Frequencies as low as 20 Hz are detected by hair cells at the apex, or tip, of the cochlea. Frequencies in the higher ranges of 20 KHz are encoded by hair cells at the base of the cochlea, close to the round and oval windows. Most auditory stimuli contain a mixture of sounds at a variety of frequencies and intensities (represented by the amplitude of the sound wave). The hair cells along the length of the cochlear duct, which are each sensitive to a particular frequency, allow the cochlea to separate auditory stimuli by frequency, just as a prism separates visible light into its component colors.



Frequency coding in the cochlea.
More details.

The standing sound wave generated in the cochlea by the movement of the oval window deflects the basilar membrane on the basis of the frequency of sound. Therefore, hair cells at the base of the cochlea are activated only by high frequencies, whereas those at the apex of the cochlea are activated only by low frequencies.

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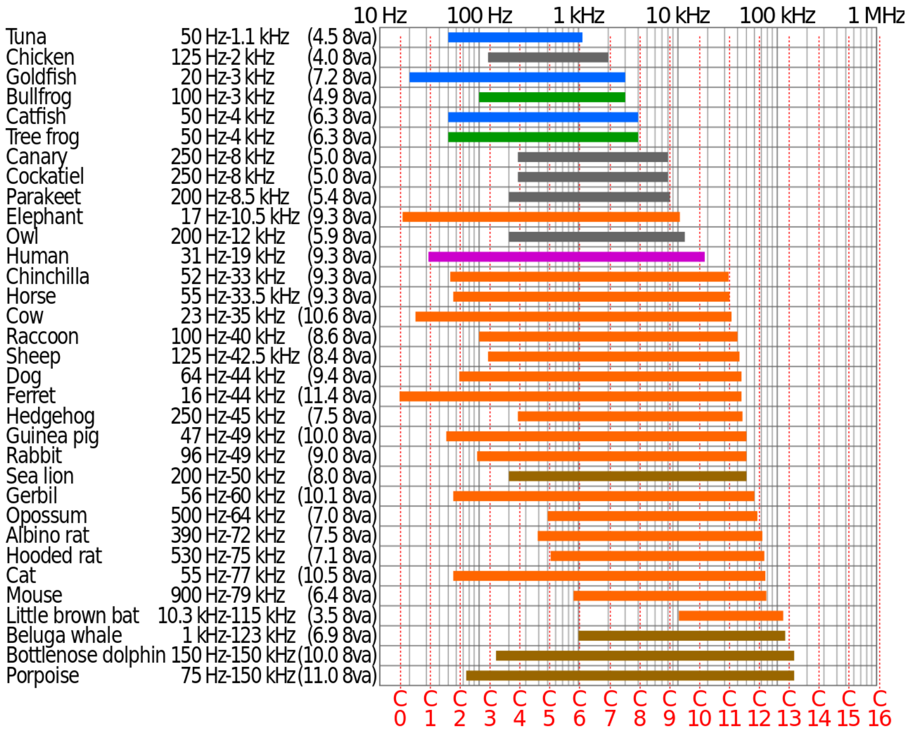
Auditory Sensitivity

The frequency range of hearing in vertebrates extends from 14 to beyond 180 kHz although no species captures the entire range. Broad ranges and high frequency hearing are most common in mammals but some frogs and fishes can also hear ultrasound. An audiogram describes how the threshold of hearing varies with frequency. Water, air and soil differ greatly in sound transmission and extensive adaptations of the hearing systems occur in evolutionary transitions between aquatic, terrestrial and subterranean environments. Low frequency and seismic sensitivity are favored underground. High frequency signaling and echolocation are favored when vision is impaired, such as in nocturnal or deep water predators. The acoustic reflex dampens the ear and protects it from excessively intense sounds. The source of the sound can be localized using cues from a single ear and differences in time of arrival and intensity between the two ears.

Frequency range

Hearing range describes the range of frequencies that can be heard by humans or other animals, though it can also refer to the range of amplitude levels. The human range is roughly 20 to 20,000 Hz, though there is considerable variation among individuals and a substantial loss of sensitivity is expected with age.

Several animals are able to hear frequencies well beyond the human hearing range. A sound with a frequency above the limit of human hearing is called an ultrasound whereas a sound with a frequency below the lower limit of human hearing is an infrasound. Some dolphins and bats, for example, can hear ultrasound at frequencies up to 100,000 Hz. Elephants can hear infrasound at 14–16 Hz, while some whales can hear frequencies as low as 7 Hz (in water).



The hearing ranges of some vertebrates. Notable omissions include fishes that can hear above 180 kHz and frogs that can hear > 30 kHz. Blue = fishes, green = frogs, gray = birds, orange = terrestrial mammals, brown = marine mammal, pink = human. More details.

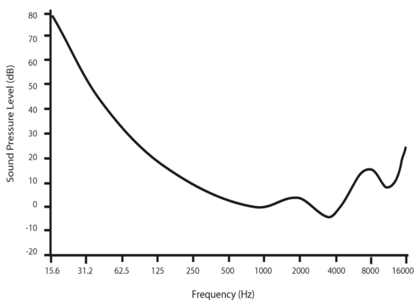
Human hearing is not outstanding when its frequency range is compared to those of other vertebrates. The broadest auditory ranges and high sensitivity are most commonly found among nocturnal predators and prey. The extremes of the frequency range are found among animals that inhabit underground or noisy environments and among some marine mammals.

As a group, mammals have the broadest hearing range among vertebrates. They are also the only vertebrates with three ossicles in the middle ear. All other groups transmit vibrations from the eardrum to the inner ear using a single ossicle (the stapes, also called columella). The wider frequency range in mammals has been traditionally attributed to a more elaborate middle ear

structure. This view has been challenged by the discovery of species of frogs in China and Borneo that can hear frequencies > 30 kHz using single-ossicle middle ears. Fishes like shad and some other clupeids are sensitive to frequencies > 180 kHz but they do not employ a middle ear with ossicles. These fishes are the main prey of dolphins which emit echolocation calls withing 80-120 kHz while foraging. The high-frequency sensitivity of clupeid fishes may have evolved in response to predation pressure by echolocating marine mammals. Most other fishes tend to have their hearing sensitivity restricted to frequencies < 4 kHz. Their thresholds are highly variable among groups, and the most sensitive species are usually in the superorder Ostariophysi (~8,000 species) which use the swim bladder and Weberian ossicles to enhance their hearing.

The audiogram

The hearing sensitivity of an organism can be characterized by an audiogram, a graph that shows the minimum detectable sound level at various frequencies throughout an organism's hearing range.



Audiogram of normal hearing in humans. More details.

Behavioural hearing tests or physiological tests can be used to find hearing thresholds. The test involves tones being presented at various frequencies (pitch) and intensities (loudness). When a human subject hears the sound, he or she indicates it by raising a hand or pressing a button. The lowest intensity that the subject can hear is recorded. This test is also done in animals, by previously training them to respond with a specific behavior (pressing a button) when they hear a sound. In human newborns or in animals that cannot be trained to press a button, the audiogram can be determined through physiological methods, such as the monitoring of brainwave activity or of very faint distortion sounds (otoacoustic emissions) that the ears produce in response to certain combinations of sound.

Environments

A great deal of variation in frequency range of hearing can be found within each group of vertebrates. Animals are selected to respond to those sounds that they encounter in their environment and that have biological relevance to them. Analogous adaptations can be found within the various vertebrates groups to cope with specials conditions encountered in specific habitats. The environment may affect the transmission or reflection of sound in ways that affect the availability of that type of sound to the animals.

Underwater

Water conducts sound much faster and farther than air . This makes it easier to detect sound from a distant source underwater, but it makes it more difficult to localize the direction of the source. The distance between the ears is covered faster, so the brain has to be sensitive to smaller differences in both amplitude and time of arrival between the ears to use the binaural cues to locate the source. Another consequence of the sounds being transmitted farther is that antropogenic (human made) noise sources have a larger footprint. Few studies had been done until recently on the effects of underwater noise on aquatic wildlife. Considering the magnitude of the diversity of aquatic live, environments and human-introduced sources of

noise, an extensive dataset is necessary to guide the proper management of subaquatic noise.

Water is a high impedance medium (molecules are more difficult to move than those in air). Since about 70% of the bodies of vertebrates are composed of water, underwater sound can cross the tissues and reach the inner ear if not blocked or absorbed by specialized tissues. A thin membrane like an eardrum is unnecessary under water and having an air-filled cavity behind it (middle ear) is problematic for divers, because the external water can produce immense pressures during a deep dive. Several types of adaptations of the auditory systems are observed in vertebrates that recolonized the underwater environment after having been terrestrial.

The ear canals in seals, sea lions, and walruses are similar to those of land mammals and seem to function the same way. In whales and dolphins, studies suggest that sound is channeled to the ear by tissues in the area of the lower jaw. In odontocetes (toothed whales) the ears are placed relatively far from each other in the head. Both the channeling of sound and the separation of the ears should assist in increasing the separation of the signals in the two ears and facilitate the localization of the sources of sounds. Odontocetes use echolocation in foraging, therefore sound source localization is key to their survival.

Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) are odontocetes with elaborate adaptations

for underwater hearing.
More details.

Underground

Many vertebrates inhabit tunnel systems under the ground. High frequencies are severely attenuated when transferring between the air in the tunnels and in the soil (seismic vibrations), and also when transferred across the variety of materials encountered in most soils. The environment is therefore dominated by low-frequency sounds.

Several groups of mammals that live underground have independently evolved enlarged middle ear ossicles (malleus or incus) as an adaptation to detect seismic vibrations. The inertia of these massive ossicles sitting in an air-filled middle ear make them lag behind the skull when the head is shaken by seismic vibrations. This movement of the ossicles relative to the skull stimulates the inner ear, which decodes the seismic vibrations as sound.

Giant golden moles (*Chrysospalax trevelyani; taxidermy*) are blind subterranean mammals that live in South Africa and use enlarged middle ear ossicles to detect

seismic vibrations. More details.

Golden moles are extremes of seismic sensitivity. They are blind and live on African deserts, burrowed in the sand. They navigate the sand mounds eating arthropods that they find mostly near vegetation. When foraging at night, they also walk on the surface of the sand but occasionally stop and dip the head into the sand. Golden moles are attracted to the seismic vibration patterns produced by sand mounds containing vegetation and insects. Their mallei are so large that the lateral surface of the skull has a bulge to fit the middle ear ossicle.

Frogs also tend to be very sensitive to seismic vibrations. They make use of their forelegs to transmit the signals through the shoulders to the middle ear through the opercular system (see previous chapter). Large mammals like elephants and whales also use low frequency signals to communicate over large distances on the ground or in the sea.

Noisy terrestrial environments

Sloped regions tend to be dominated by fast flowing streams that form noisy environments. The sound of water running over rocks characteristically has most energy at a few dozen Hz and gradually slopes down at higher frequencies. Several groups of frogs have species adapted to life in such streams. Some of them have changed to being diurnal and use visual signals for communication. These mostly include foot flagging, a behavior in which the animal suddenly raises and extends a limb to exhibit a vividly colored palm or sole.

Other species continue using sound. They communicate at high frequencies, from a few thousand Hz to ultrasound only, therefore escaping the masking that the stream noise produces at low frequencies. These species tend to have thin eardrums and light middle ear ossicles because reduced inertia is necessary for the high rate vibrations produced at high frequencies. As

extremes of high frequency communication in frogs, the concave eared torrent frog (*Odorrana tormota*) and the hole-in-the-head frog (*Huia cavitympanum*) produce and respond to calls with fundamental frequencies at 5-30 kHz. Their eardrums are transparent and recessed, allowing the stapes to be shorter and lighter.

Behavioral adjustment of auditory sensitivity

Acoustic reflex

The **acoustic reflex** (also known as the stapedius reflex, middle-ear-muscles (MEM) reflex, attenuation reflex, or auditory reflex) is an involuntary muscle contraction that occurs in the middle ear in response to high-intensity sound or during vocalization.

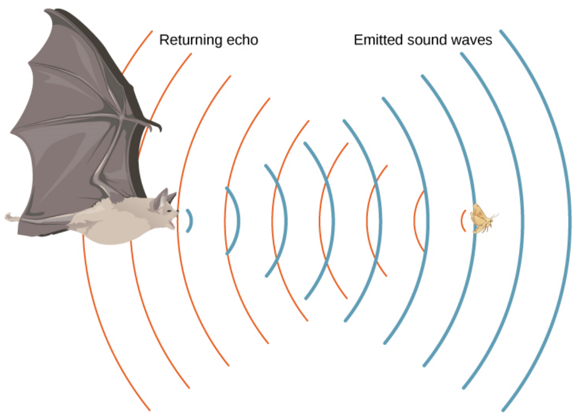
When presented with a high-intensity sound stimulus, the stapedius and tensor tympani muscles of the middle ear contract. The stapedius stiffens the ossicular chain by pulling the stapes out, away from the oval window of the cochlea. The tensor tympani muscle stiffens the ossicular chain by loading the tympanic membrane when it pulls the malleus in, toward the inner ear. The reflex decreases the transmission of vibrational energy to the cochlea, protecting the hair cells in the organ of Corti from excessive displacements.

In humans, the acoustic reflex reduces the intensity of the triggering sound by 15-20 dB at the inner ear. This provides significant but not complete protection. It takes 100-150 ms for the muscles to contract fully, and the strength of the contraction is reduced to about 50% after a few seconds. This makes the reflex less effective against sounds with a sharp onset, like hammering, and sounds with continuous long duration, like and extended beep or a jet plane taking off.

In animals that produce loud vocalizations such as advertisement or echolocation calls, the acoustic reflex can be triggered by the vocalization command immediately before the onset of sound. This offers improved protection to the ears and prevents overstimulation, which would reduce the hearing sensitivity after phonation.

Echolocation

The high frequency limit in the hearing of bats varies from 1 kHz to 200 kHz. This wide variation is mostly due to the evolution of echolocation, which drove certain species to vocalize and hear at ultrasonic frequencies.



Echolocating bats emit calls at frequencies > 20 kHz. They can locate flying insects by detecting the echo of their ultrasonic calls. More details.

An echolocating bat produces a very loud, short sound and listens to the echos that bounce back. These bats hunt flying insects which return a faint echo of the bat's call. The type of insect and how big it is can be determined by the quality of the echo and time it takes for the echo to rebound. Low frequency sound has large wavelengh and it does not reflect well in small objects like the insects that bats target. Echolocating bats therefore produce ultrasonic calls to detect small objects around them. Some bats produce calls with a constant frequency, whereas others produce frequency sweeps.

But high frequency calls are energetically expensive to produce and they die off in air very quickly. Bats tend to fly emitting echolocation calls at a

certain rate and then progressively increase the rate of calling as the approach an object of interest.

The same way a bright flash of light can blind you for a few seconds, an exposure to intense sound tends to reduce your sensitivity in the next seconds. This is a problem for bats, because they need to produce a very intense echolocation call and be able to detect a very fain echo immediately after the call. This problem can be circumvented in several ways:

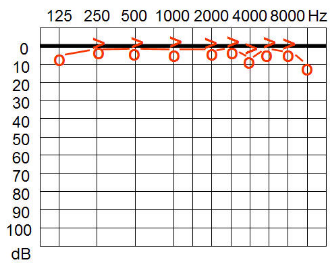
- The acoustic reflex turns on immediately before the call and it turns off immediately after the call. The middle ears are therefore highly damped during the call but are set completely unimpeded to transmit the echo.
- The fact that the bat is flying generates a Doppler shift. Due to the Doppler effect, the call returns as an echo with a slightly higher frequency than that at which it was emitted. In bats that produce calls with constant frequency, the call and the echo are detected at slightly different positions of the Cochlea (tonotopy) and therefore the hair cells that detect the echo are less likely to be overstimulated by the call.
- The audiogram of constant-frequency bats tends to show a sharp change from low to high sensitivity near the frequency of the call. The bat adjusts the frequency of its call to the speed at which it is flying, to maintain the frequency of the echo within the high sensitivity peak of the ears and that of the call in the low sensitivity range.

Echolocation is not unique to bats or to air as a medium. Several species of cave-nesting swiftlets and the unrelated oilbirds also employ less elaborate forms of echolocation than those of bats. Dolphins and toothed whales also exhibit very elaborate echolocation systems for foraging in waters where vision is hindered by high turbidity or lack of light due to depth.

Human hearing

While the range of human tends to be conveniently approximated to 20 Hz - 20 kHz, precise measurements have not produced these round numbers. U nder ideal laboratory conditions, humans can hear sound as low as 12 Hz

and as high as 28 kHz, though the threshold increases sharply at 15 kHz in adults. Humans are most sensitive to frequencies between 2,000 and 5,000 Hz. Individual hearing range varies according to the general condition of a human's ears and nervous system. The range shrinks during life, with the upper frequency limit being reduced. Typically, humans can discriminate between two sounds if their frequencies differ by 0.3% or more. For example, 500.0 and 501.5 Hz are noticeably different. At a given frequency, it is possible to discern differences of about 1 dB in sound amplitude, and a change of 3 dB is easily noticed.

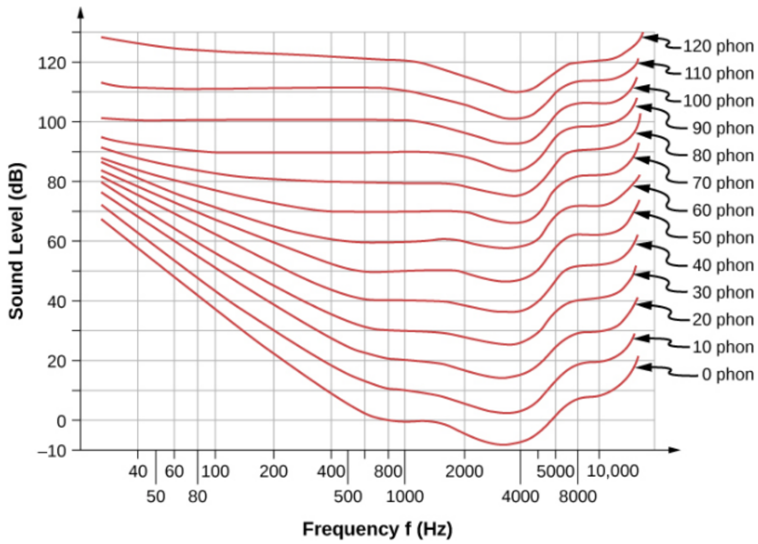


Audiogram showing a typical result for an adult with slight hearing loss . In clinical usage, audiograms usually have the frequency axis on the top of the chart and the threshold sound level is shown in relation to normal hearing (zero dB is set

to the threshold of normal hearing). This makes the results in dB express of the patient's hearing loss directly. More details.

The human ear is not equally sensitive to all frequencies. In addition, our perception of both amplitude and frequency is not linear. For example, the difference between the amplitudes of sounds at 0.1 and 0.2 Pa appears greater than the difference between sounds at 0.3 and 0.4 Pa . Scales were therefore develop to quantify our perception of the physical qualities of sound: pitch quantifies to our perception of sound frequency, whereas loudness quantifies our perception of sound amplitude.

Loudness varies with frequency, due to the sensitivity pattern described in the audiogram. A unit called phon is used to express loudness numerically. Phons differ from decibels because the phon is a unit of loudness perception, whereas the decibel is a unit of physical intensity. The loudness scale was determined by having large numbers of people compare the loudness of sounds at different frequencies and sound intensity levels. At 1000 Hz, phons were set to be numerically equal to decibels. The relationship of loudness to intensity level and frequency has the shape of the audiogram at 0 phon. Curves of equal-loudness can be separated by more or fewer decibels of sound intensity, depending on the frequency and intensity of the sound.



Relationship between loudness (phons) and intensity level (dB) in humans with normal hearing. The curved lines are equal-loudness curves. All sounds on a given curve are perceived as equally loud. More details.

Localization

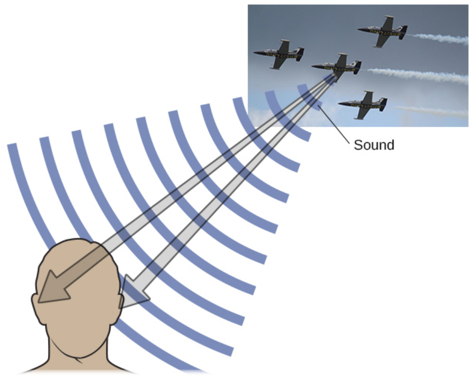
The ability to locate sound in our environments is an important part of hearing. The auditory system localizes sound by using cues that can be monaural (formed within one ear) or binaural (formed by comparison between the two ears).

Monaural cues are formed by the ways in which the complex shapes of the pinna reflect the incoming sound waves. The frequencies contained in the sound are modified in different amounts by the pinna forming a pattern. This pattern depends on the direction from which the sound arrives to the pinna. Our brain learns the patterns produced by our pinnae and uses them to help identify the direction of the source. Monaural cues can be obtained with a single ear and they help to locate sound sources both along the horizontal plane (azimuth) and the vertical plane (elevation). In any case,

the generation of a recognizable pattern depends on amplitude comparisons across frequencies. Noise and clicks have energy in many frequencies and therefore provide more reliable monaural cues than tones and whistles that have one or a few frequencies.

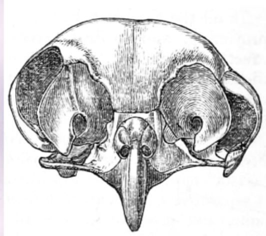
Binaural cues emerge from differences in patterns of vibration of the eardrum between the two ears. If a sound arrives from the right side of your body it is more intense at your right ear than at your left ear because your head casts an acoustic shadow over your left ear. In addition, this sound arrives first at the right ear than at the left ear. Certain brain circuits monitor these differences to infer where along a horizontal axis a sound originates.

The reliability of binaural cues exceeds by far that of monaural cues for the localization of sound sources. In addition, they function well both with noisy and tonal sounds. Binaural cues only provide information for localization along the horizontal plane (azimuth), though, because changes in elevation do not alter the time of arrival or amplitude differences between the ears. Monaural cues are therefore the primary source of information used to determine the elevation of sound sources (vertical direction).



Localization of the sound source can involve the use of both monaural and binaural cues. More details.

Binaural cues can be made useful for the determination of elevation, however, by tilting the head laterally. This is commonly observed in dogs expressing curious behavior, although its association with more precise elevation assessment is unclear. The problem of localizing the elevation of the source is magnified in foraging owls, which search for prey at night while flying. In this position, the head faces the ground and prey that would try to escape running aligned with the longitudinal axis of the body of the owl would produce sounds that would arrive identically to the two ears of the owl.



The skull of Tengmalm's owl (*Aegolius_funereus*) is asymmetric, with the right ear opening high in the head and the left one low. More details (left, right).

This problem is circumvented by the morphology of the owl's ears. While the feathers of the head make it looks symmetric, the skull underneath is asymmetric, having the opening of one ear high in the head and the other low. With this configuration, sounds with different elevations do generate binaural cues. This improves the localization ability of the birds and allow them catch mice even in complete darkness.

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