

CARTILAGE

Cartilage and **bone** are specialized connective tissues that provide support to other tissues and organs. Cartilage occurs where flexibility is required, while bone resists deformation.

Cartilage is composed of cells, fibers, and a highly-hydrated ground substance. The fibers provide tensile strength, while proteoglycans in the ground substance make cartilage resilient by trapping water.

Three types of cartilage are recognized based on differences in fiber composition:

- **Hyaline cartilage** - type II collagen
- **Elastic cartilage** - elastic fibers and type II collagen
- **Fibrocartilage** - type I and II collagens

Cartilage is avascular and its cells rely on diffusion for nutrients. Because of this, damaged cartilage heals poorly after injury.

- is a specialised type of connective tissue.
- consists, like other connective tissues, of cells and extracellular components.
- does, unlike other connective tissues, not contain vessels or nerves.
- is surrounded by a layer of dense connective tissue, the perichondrium.

Cartilage is rather rare in the adult humans, but it is very important during development because of its firmness and its ability to grow rapidly. In developing humans, most of the bones of the skeleton are preceded by a temporary cartilage "model". Cartilage is also formed very early during the repair of bone fractures.

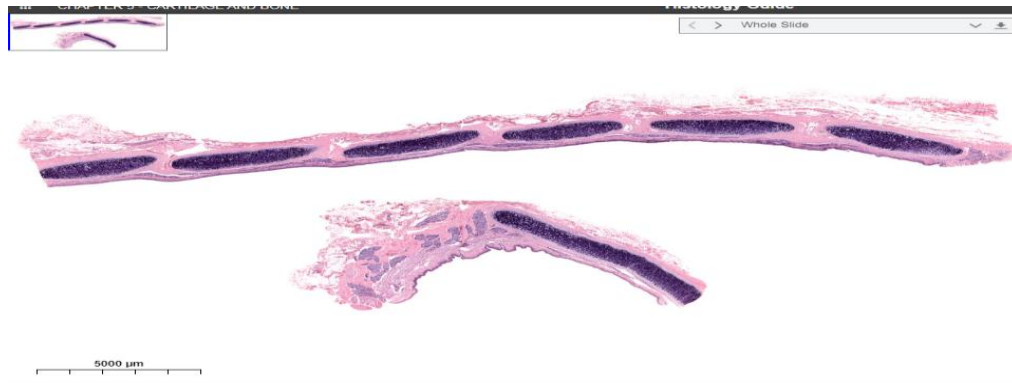
Types of Cartilage

Hyaline Cartilage

Hyaline cartilage develops, like other types of connective tissue, from mesenchymal cells. From about the fifth fetal week precursor cells become rounded and form densely packed cellular masses, [centres of chondrification](#). The cartilage-forming cells, chondroblasts, begin to secrete the components of the extracellular matrix of cartilage. The extracellular matrix consists of, ground substance (hyaluronan, chondroitin sulfates and keratan sulfate*) and tropocollagen, which polymerises extracellularly into fine collagen fibres.

* Keratan sulfate (KS) proteoglycan (PG) is one of the major components of the cornea, and suggested to have important roles for **corneal development and maintenance of transparency of the tissue**. KS-PG is consists of two different components, core proteins and attached carbohydrates called glycosaminoglycans (GAGs).

Hyaline cartilage contains type II collagen fibers and a highly-hydrated ground substance. It is the most common cartilage and is found on articular surfaces of bone, walls of the respiratory system (trachea and bronchi), and epiphyseal plates.



Hyaline Cartilage

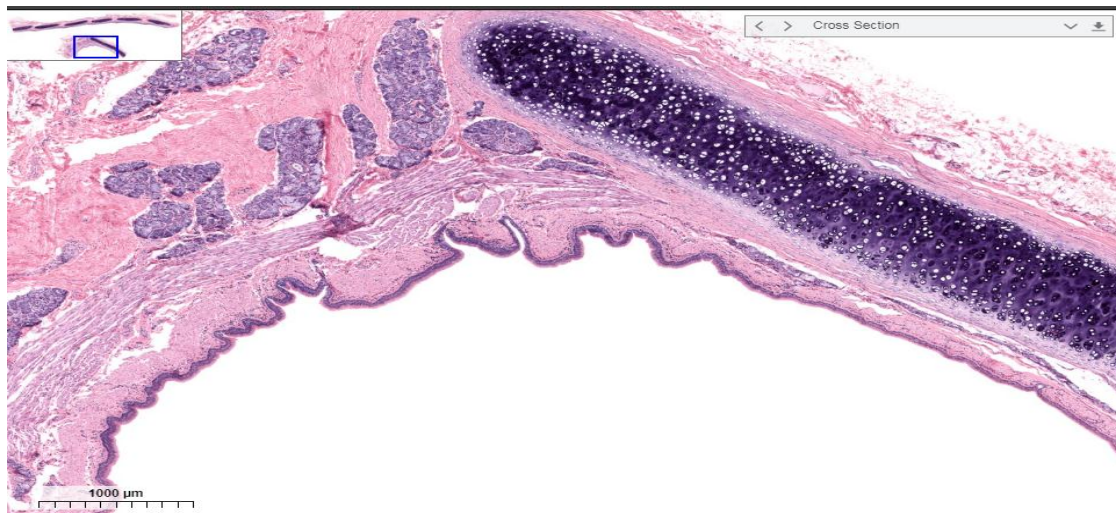
This slide contains a cross section and a longitudinal section of the trachea.

Hyaline cartilage provides structural support in the respiratory system (larynx, trachea and bronchi).

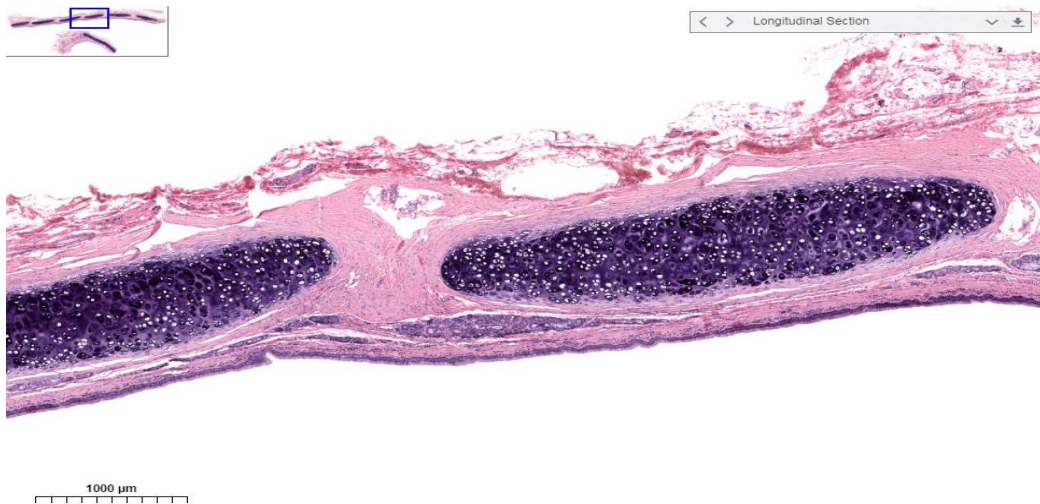
The airway of the trachea is held open by cartilaginous rings of hyaline cartilage:

- Perichondrium - a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:
- Outer Fibrous Layer - contains fibroblasts that produce the type I collagen on the outer surface of the perichondrium.
- Inner Chondrogenic Layer - contains fibroblast-like cells that can differentiate into chondroblasts, initiate matrix production (type II collagen) and become immature chondrocytes.
- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.
- Matrix - composed mostly of type II collagen and a ground substance of proteoglycans.
- Territorial Matrix - basophilic area immediately around chondrocytes.
- Interterritorial Matrix - less intensely stained area between isogenous groups of chondrocytes.

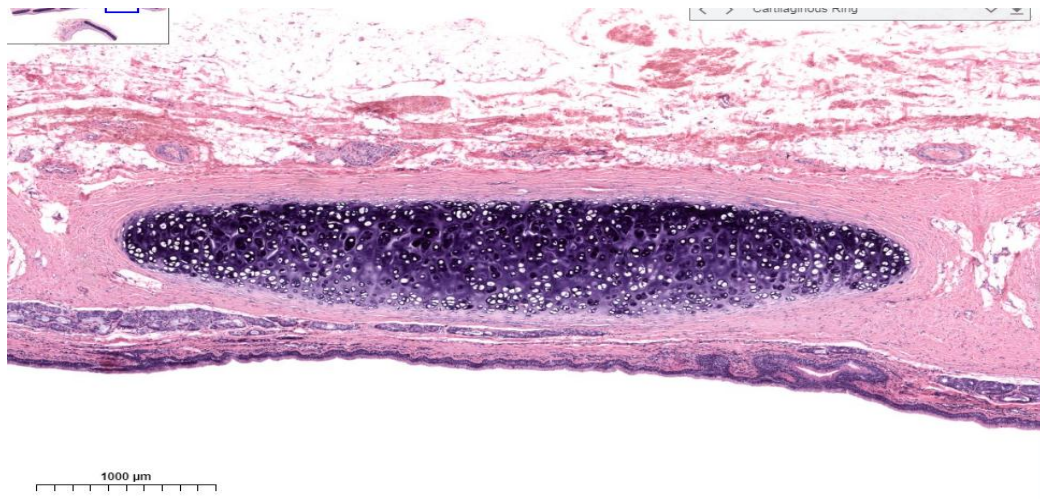
Hyaline cartilage contains no blood vessels or nerves.



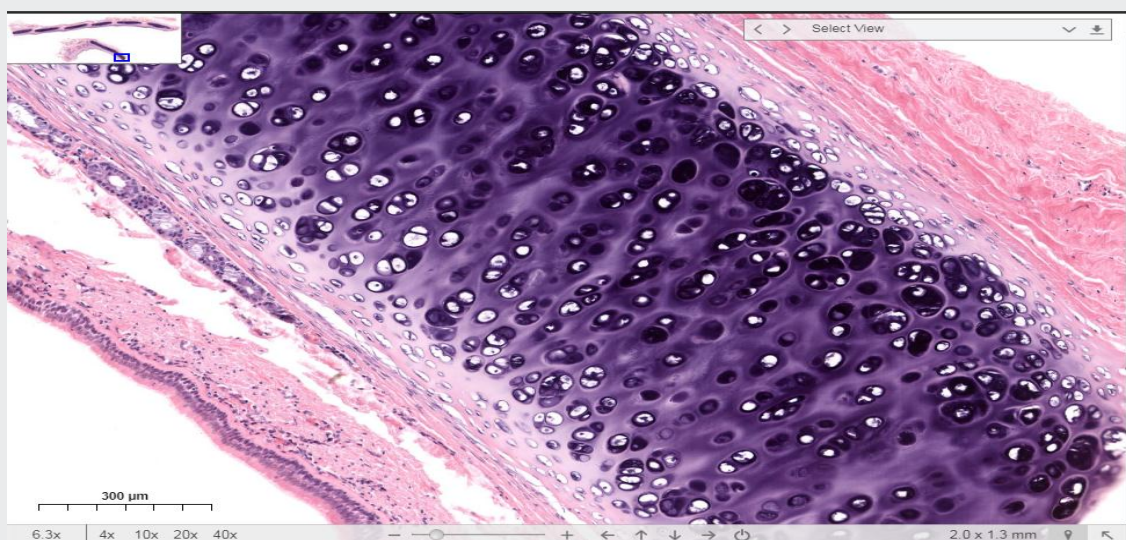
This slide contains a cross section and a longitudinal section of the trachea.

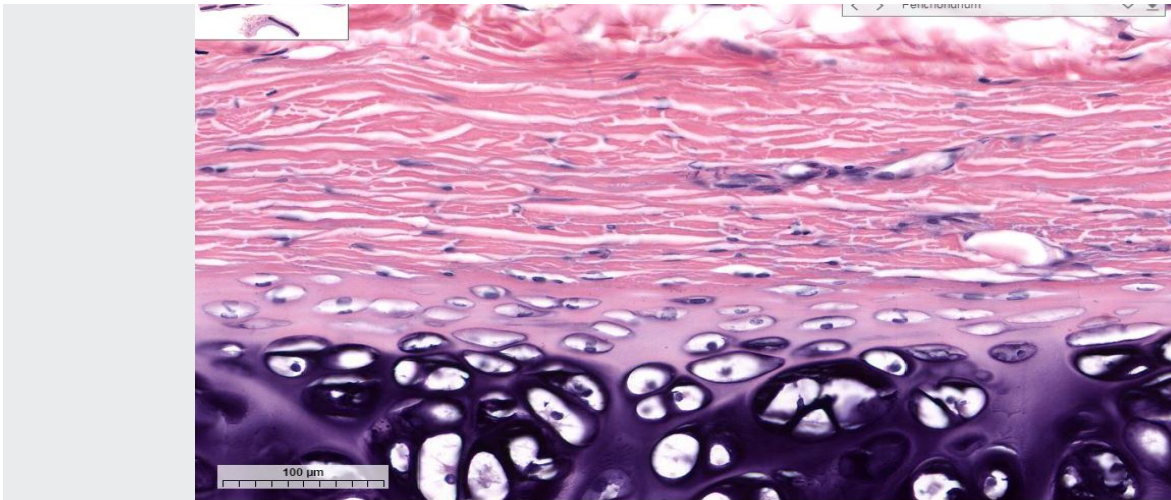


longitudinal section of the trachea.

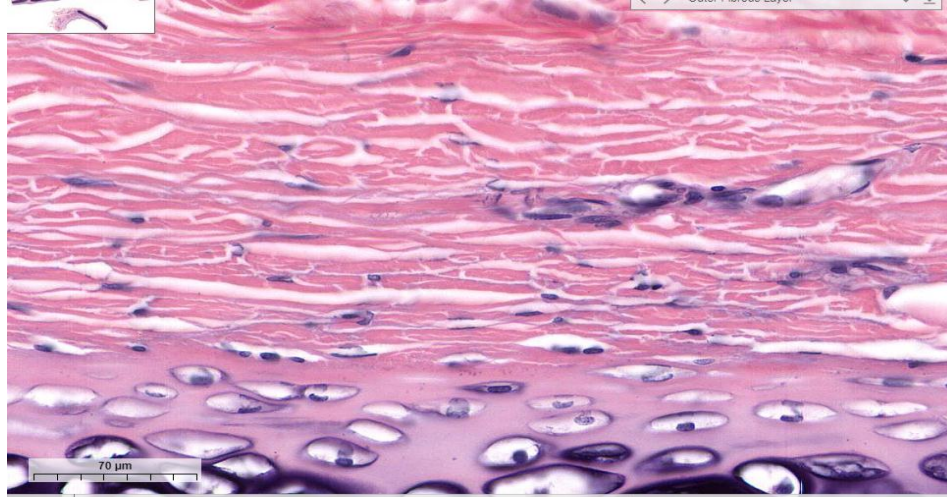


The airway of the trachea is held open by **cartilaginous rings** of hyaline cartilage:

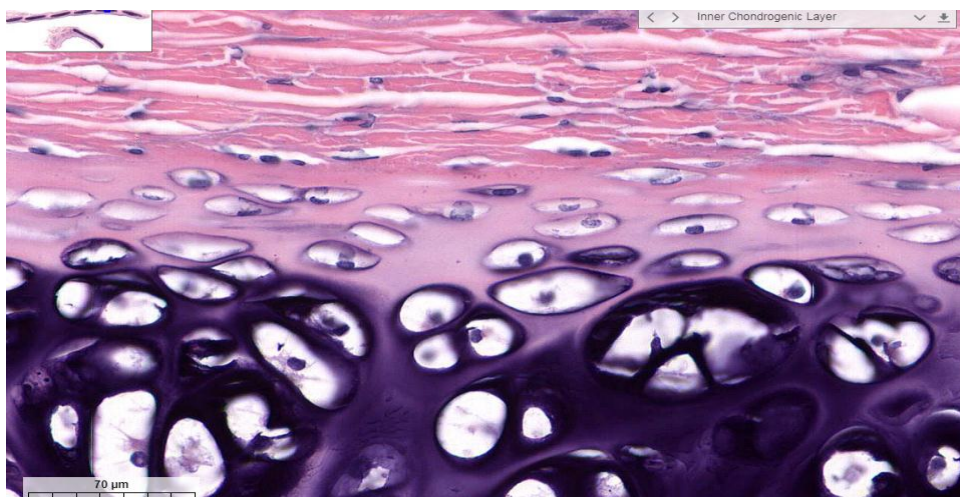




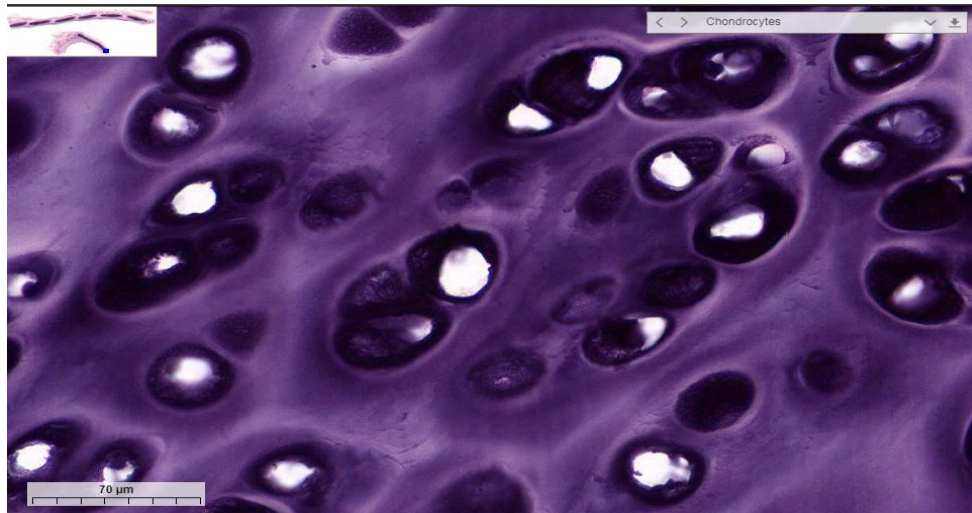
Perichondrium - a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:



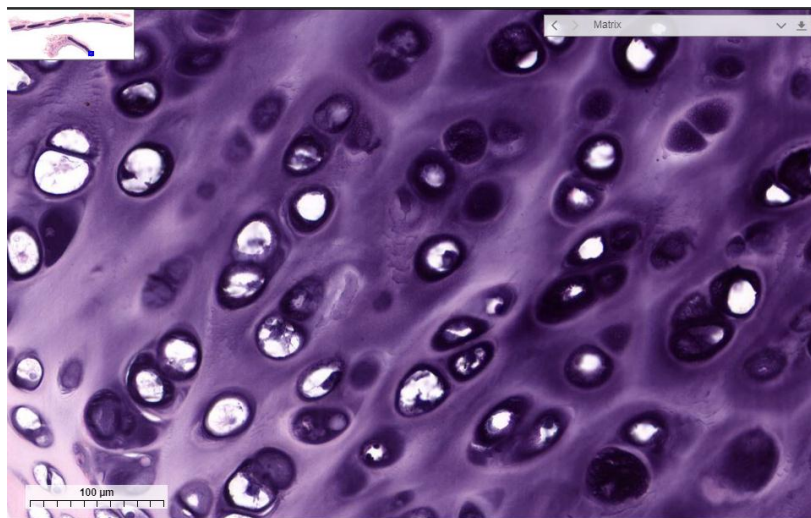
- **Outer Fibrous Layer** - contains fibroblasts that produce the type I collagen on the outer surface of the perichondrium.



- **Inner Chondrogenic Layer** - contains fibroblast-like cells that can differentiate into chondroblasts, initiate matrix production (type II collagen) and become immature chondrocytes.

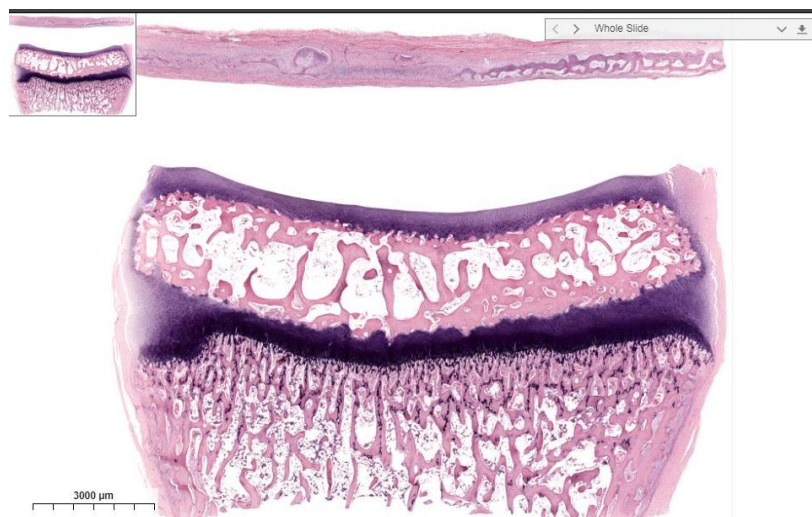


- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.



- Matrix - composed mostly of type II collagen and a ground substance of proteoglycans.
- Territorial Matrix - basophilic area immediately around chondrocytes.
- Interterritorial Matrix - less intensely stained area between isogenous groups of chondrocytes.

Hyaline cartilage contains no blood vessels or nerves



Hyaline Articular Cartilage

Hyaline cartilage also lines the articular surfaces of synovial joints, where it acts as a self-lubricating shock absorber with low friction properties.

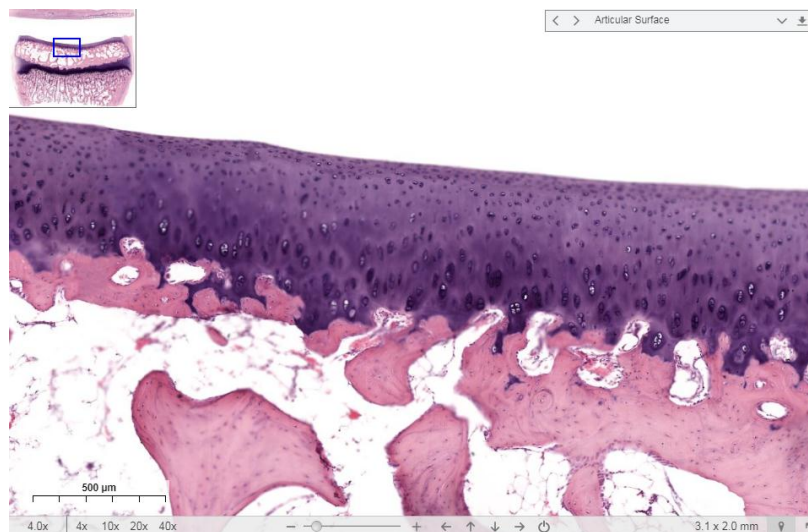
Unlike most hyaline cartilage, articular hyaline cartilage does not have a perichondrium on either surface.

- Free (articular) Surface - exposed to synovial fluid within the joint.
- Basal Surface - is in direct contact with the underlying bone.

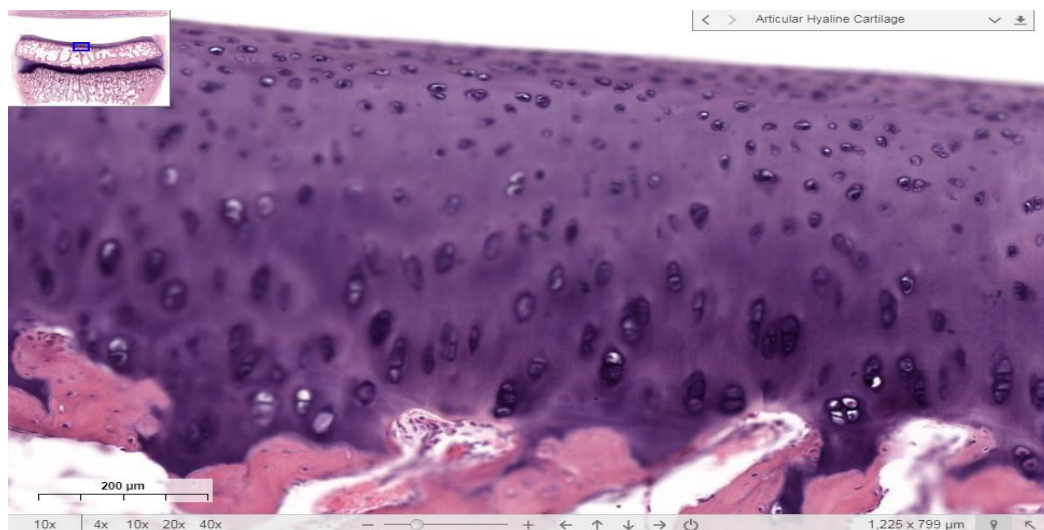
Articular cartilage is a remnant of the hyaline cartilage that formed the template for the developing bone.

New articular cartilage is limited to interstitial growth because of the absence of a perichondrium.

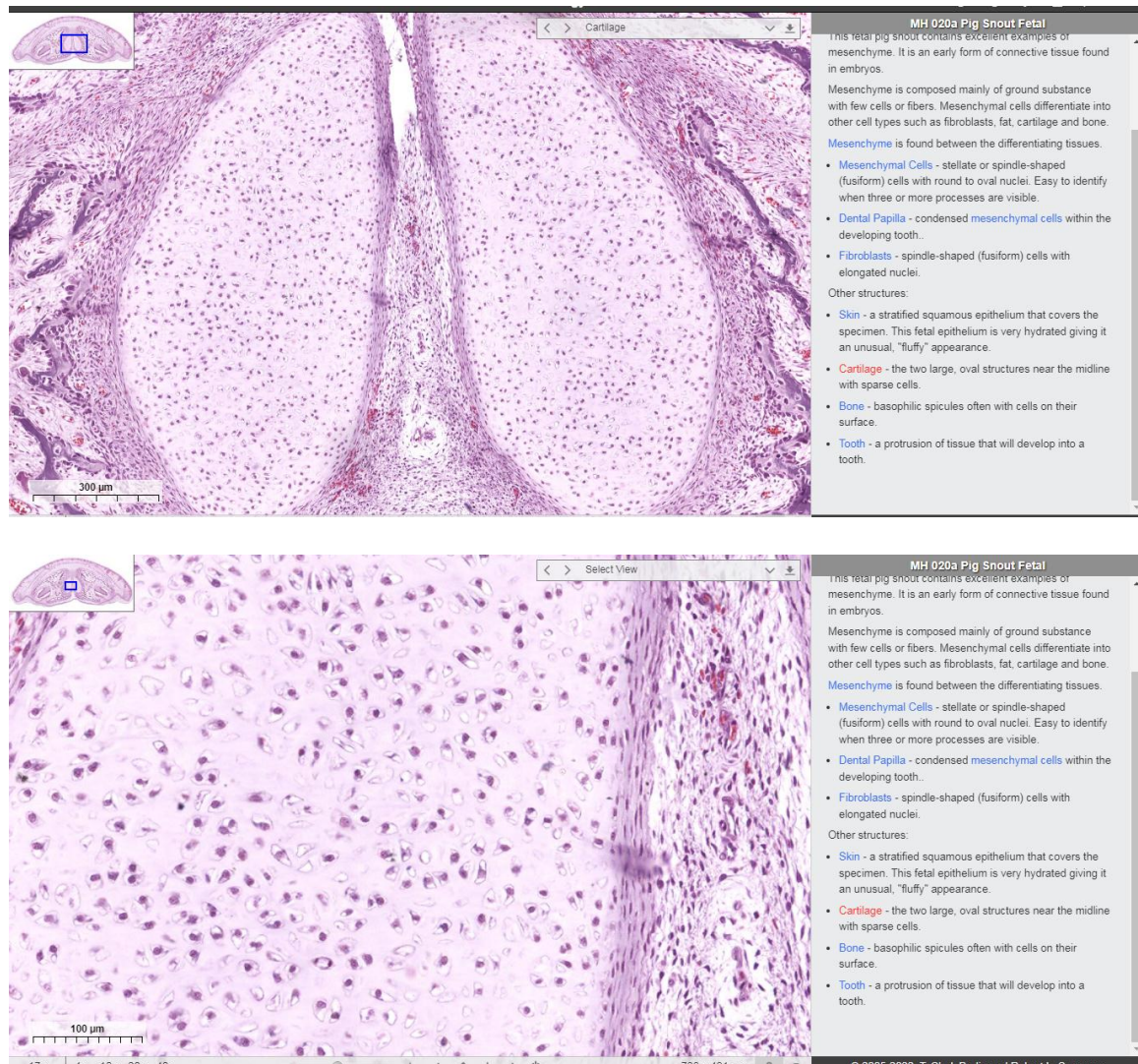
Articular cartilage contains no blood vessels or nerves.



Hyaline cartilage also lines the articular surfaces of synovial joints, where it acts as a self-lubricating shock absorber with low friction properties.




Unlike most hyaline cartilage, articular hyaline cartilage does not have a perichondrium on either surface.



Collagen type II is the dominant form in almost all types of cartilage.

As the amount of matrix increases the chondroblasts become separated from each other and are, from this time on, located isolated in small cavities within the matrix, the lacunae.

Concurrently the cells differentiate into mature cartilage cells, chondrocytes .



Growth occurs by two mechanisms

- **Interstitial growth** - Chondroblasts within the existing cartilage divide and form small groups of cells, isogenous groups, which produce matrix to become separated from each other by a thin partition of matrix. Interstitial growth occurs mainly in immature cartilage.
- **Appositional growth** - Mesenchymal cells surrounding the cartilage in the deep part of the perichondrium (or the chondrogenic layer) differentiate into chondroblasts. Appositional growth occurs also in mature cartilage.

Like all protein-producing cells, chondroblasts contain plenty of rough endoplasmatic reticulum while they produce matrix. The amount of rough endoplasmatic reticulum decreases as the chondroblasts mature into chondrocytes. Chondrocytes fill out the lacunae in the living cartilage.

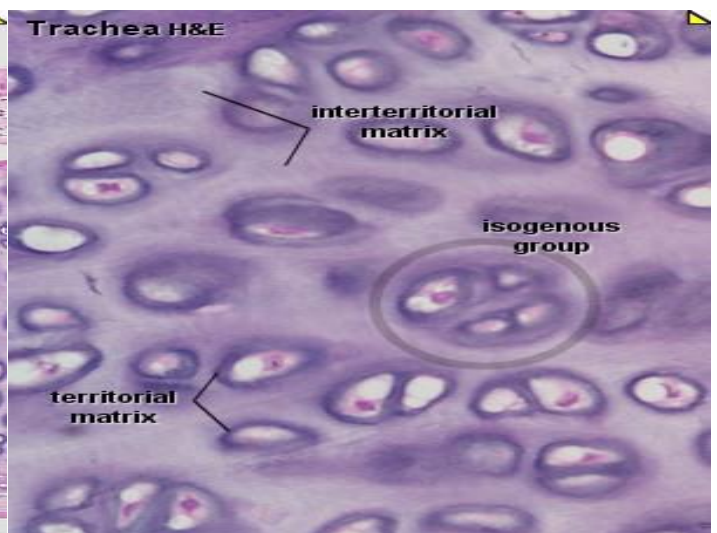
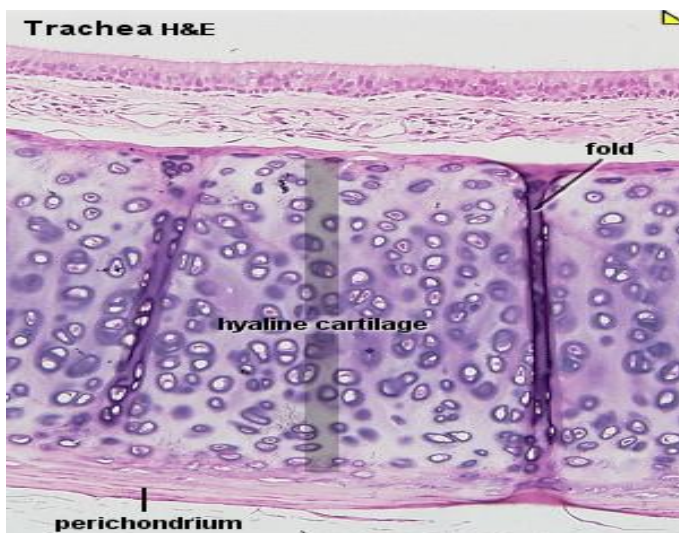
The matrix appears structureless because the collagen fibres are too fine to be resolved by light microscopy ($\sim 20\text{nm}$), and because they have about the same refractive index as the ground substance. Collagen accounts for $\sim 40\%$ of the dry weight of the matrix.

The matrix near the isogenous groups of chondrocytes contains larger amounts and different types of glycosaminoglycans than the matrix further away from the isogenous groups. This part of the matrix is also termed territorial matrix or capsule. In H&E stained sections the territorial matrix is more basophilic, i.e. it stains darker. The remainder of the matrix is called the interterritorial matrix. Fresh cartilage contains about 75% water which forms a gel with the components of the ground substance. Cartilage is nourished by diffusion of gases and nutrients through this gel.

Suitable Slides

sections of the trachea or larynx - H&E, van Gieson

Trachea, cat, H&E and Trachea, cat, van Gieson Both stains are equally well suited to look at the organisation of hyaline cartilage. The van Gieson method stains collagen red. The cartilage appears as a wide red zone underneath the epithelium and loose connective tissue, which line the lumen of the trachea. The staining may appear a little lighter close to the lacunae. This lighter stained zone defines the territorial matrix surrounding the lacunae and chondrocytes. Colour intensities appear reversed in the H&E stained section. The two compartments of the matrix are usually better defined than in van Gieson stained sections. The interterritorial matrix appears very light; the territorial matrix is somewhat darker. Groups of chondrocytes surrounded by these lighter (van Gieson) or darker (H&E) staining zones belong to the same isogenous group. A layer of dense connective tissue surrounding the cartilage and blending with it is the perichondrium. The isogenous groups may form small "squares" (e.g. four chondrocytes, separated by thin cartilage membranes, in a 2×2 arrangement) or short columns (e.g. four chondrocytes in a 1×4 arrangement). Draw a small section of the cartilage and identify in your drawing territorial matrix, interterritorial matrix, isogenous groups, and chondrocytes. Think about how the spatial arrangement of chondrocytes in the isogenous group may reflect patterns of cell divisions.



Elastic Cartilage

Elastic cartilage is similar to hyaline cartilage but also contains elastic fibers. It occurs where flexibility is required, such as the epiglottis, external ear, and auditory tubes.

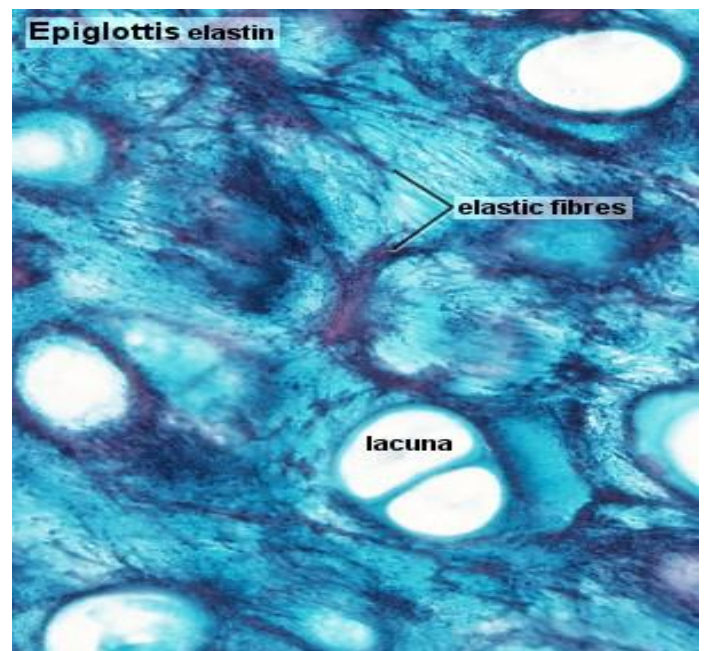
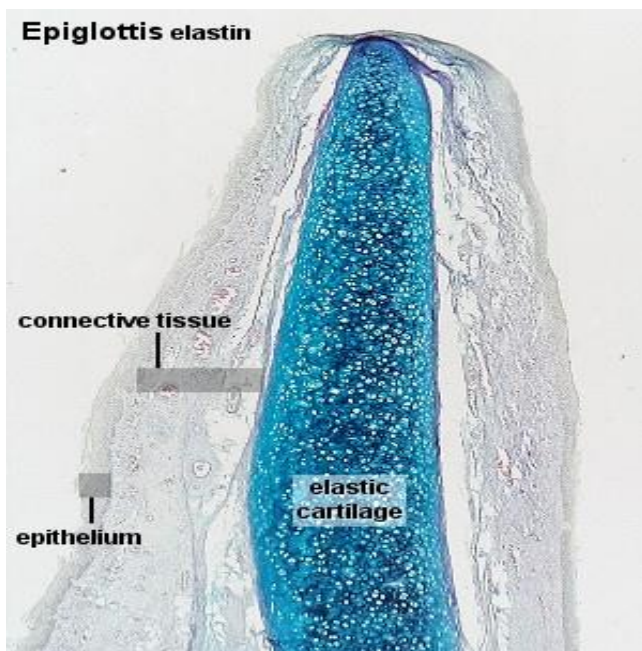
Elastic Cartilage

- occurs in the epiglottic cartilage, the corniculate and cuneiform cartilage of the larynx, the cartilage of the external ear and the auditory tube.
- corresponds histologically to hyaline cartilage, but, in addition, elastic cartilage contains a dense network of delicately branched elastic fibres.

Suitable Slides

Sections of the epiglottis - elastin

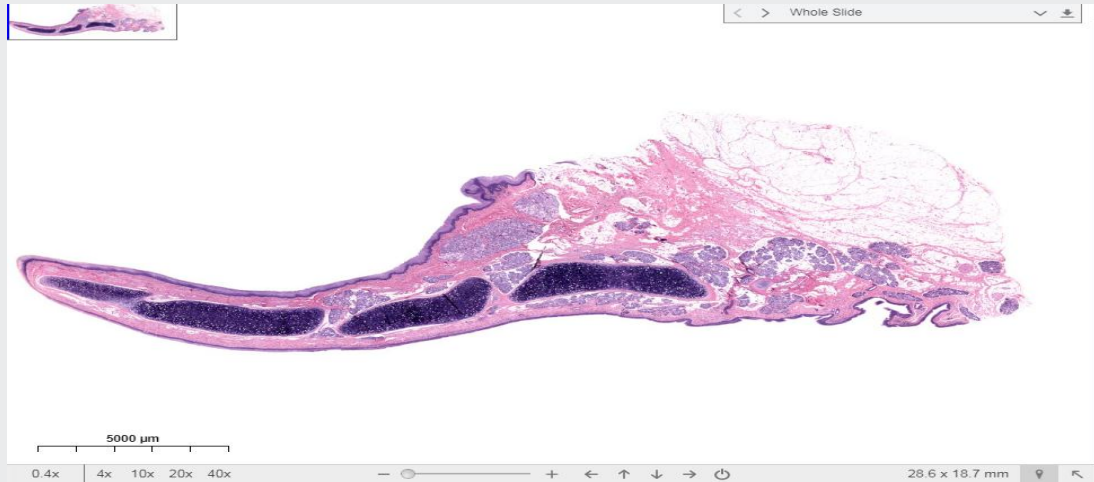
Epiglottis, human, elastin Preparations of the epiglottis are usually dominated by the cartilage surrounded by varying amounts of connective tissue and epithelia. The appearance of the cartilage (in this preparation a blue-green colour) will depend on the method used to show tissue components other than elastic fibres. Although the matrix appears blue-green, the typical organisation of cartilage is readily visible. Within the green matrix you can see the fine elastic fibres which give this cartilage its elastic properties. The elastic fibres may form dense masses in which individual fibres are difficult to distinguish. The staining of these masses of fibres may appear more reddish than dark-violet. A change of the colour of the stain in intensely stained tissue areas is called "metachromatic staining".



Draw and label a small section of elastic cartilage.

Depending on the quality of tissue preservation on your slide, it may be possible to identify the [types of epithelia](#) present in the section. It wouldn't hurt trying.

Elastic Cartilage(H&E)



The epiglottis is a cartilaginous structure at the root of the tongue that folds over the glottis to prevent food or liquid from entering the trachea during swallowing.

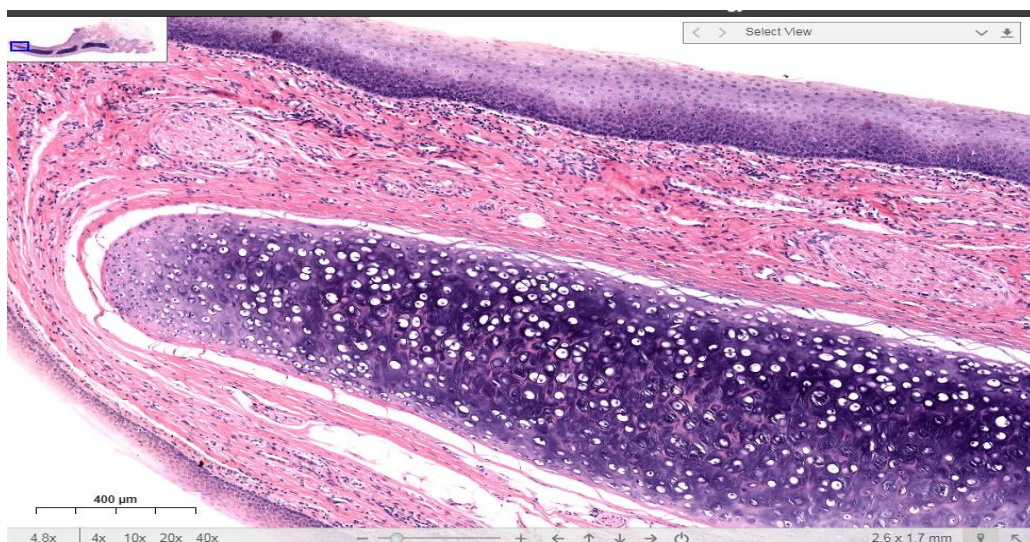
Elastic cartilage is similar to hyaline cartilage except that the matrix also contains a dense network of branching and anastomosing elastic fibers. It provides flexible support and is present in the outer ear and epiglottis.

Elastic and hyaline cartilage have similar appearances when stained by H&E because elastic fibers are unstained. Compare with the next specimen stained with Verhoeff.

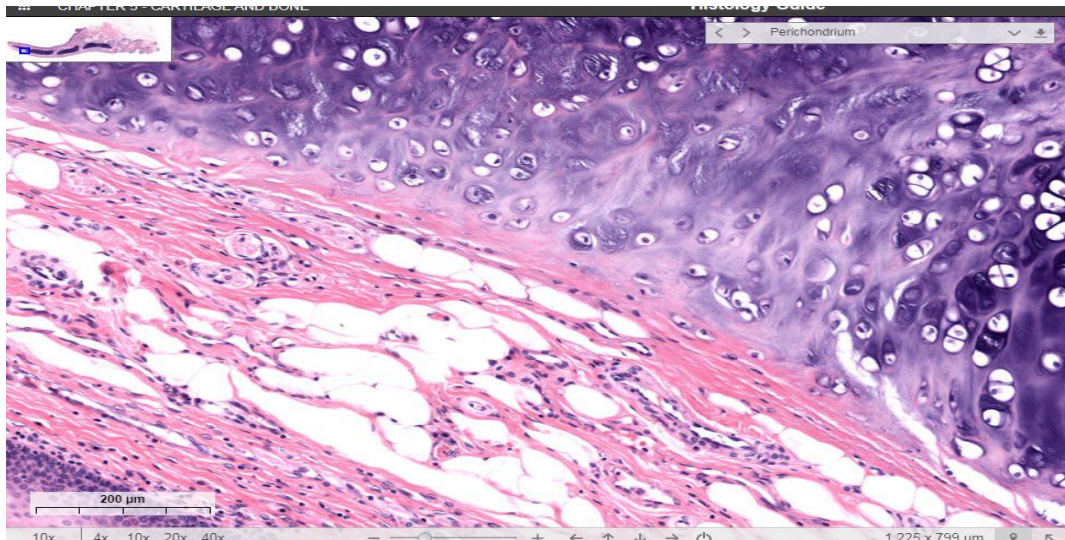
Elastic cartilage forms the core of the epiglottis:

- Perichondrium - a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:
- Outer Fibrous Layer - fibroblasts that produce the type I collagen on the outer surface of the perichondrium.
- Inner Chondrogenic Layer - contains mesenchymal cells that differentiate into chondroblasts, initiate matrix production (elastin and type II collagen) and become immature chondrocytes.
- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.
- Matrix - composed mostly of elastic fibers, type II collagen and a ground substance of proteoglycans. The streaks of pink within the matrix are due to the presence of elastic fibers.

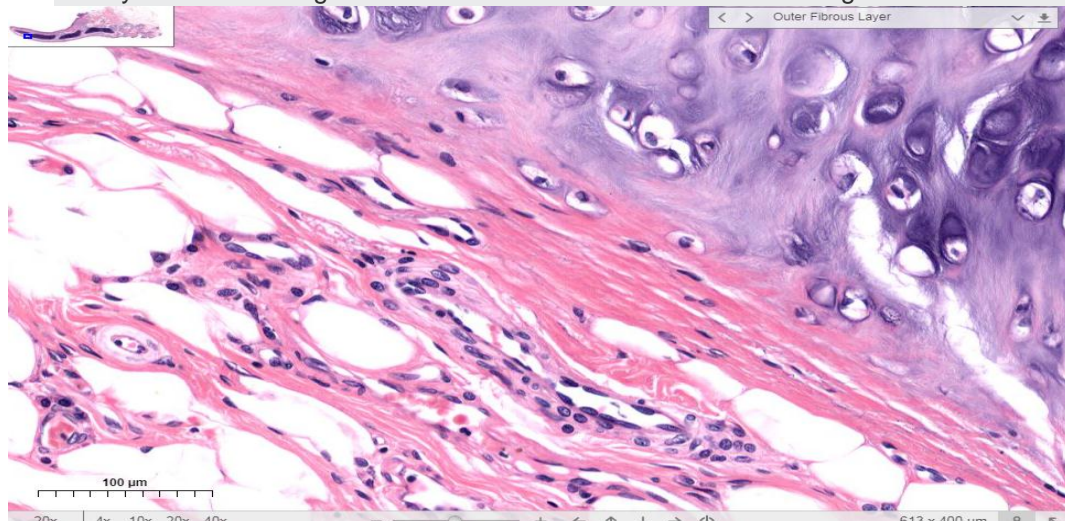
Elastic cartilage contains no blood vessels or nerves.



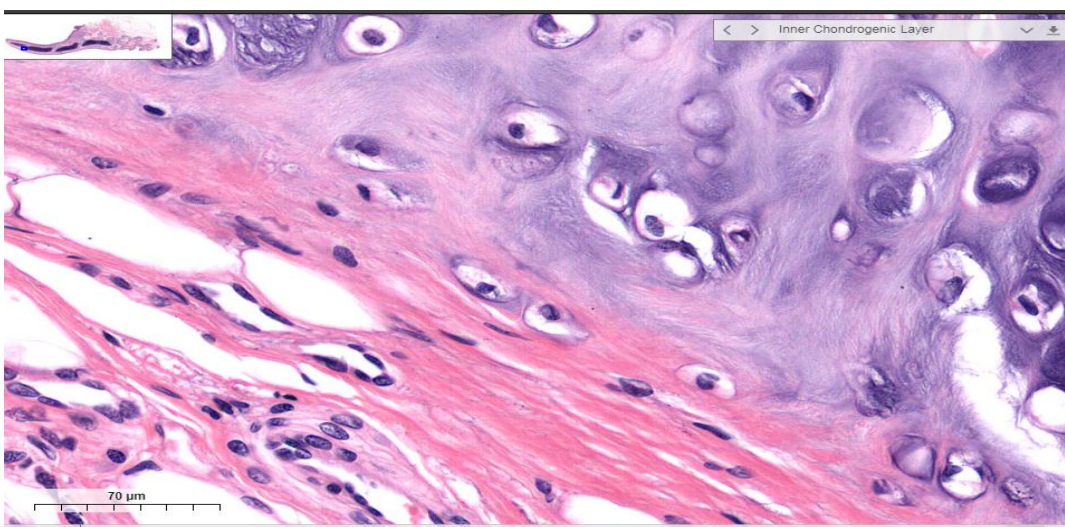
Elastic cartilage



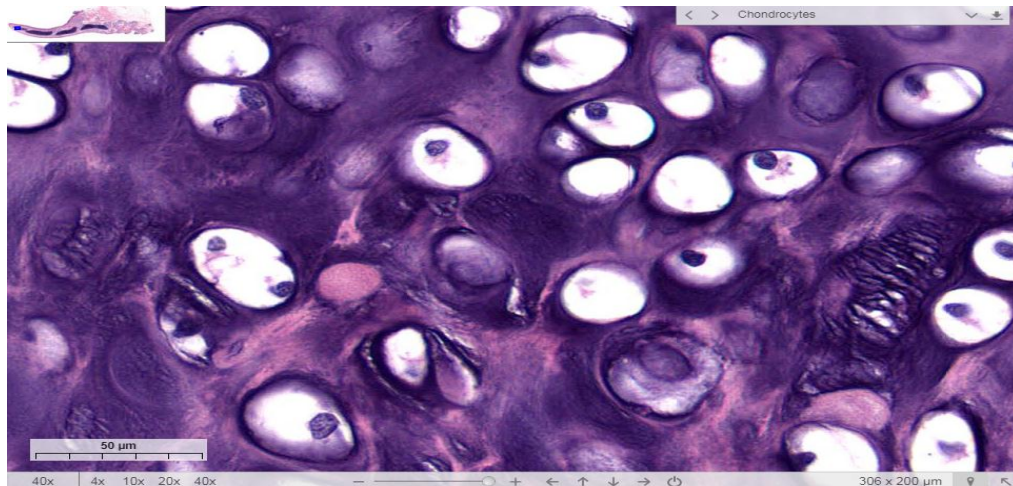
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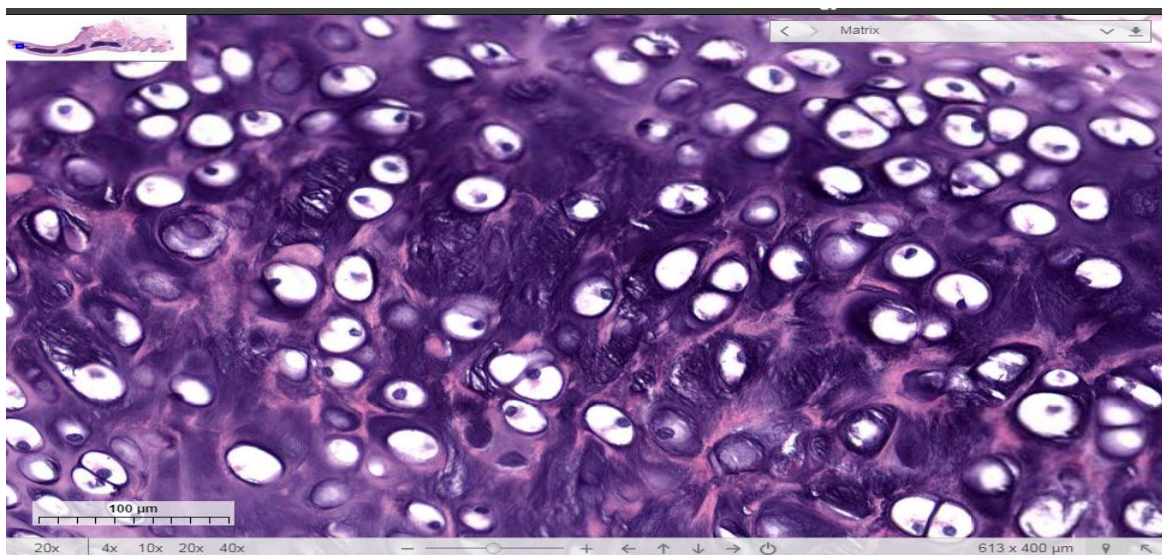
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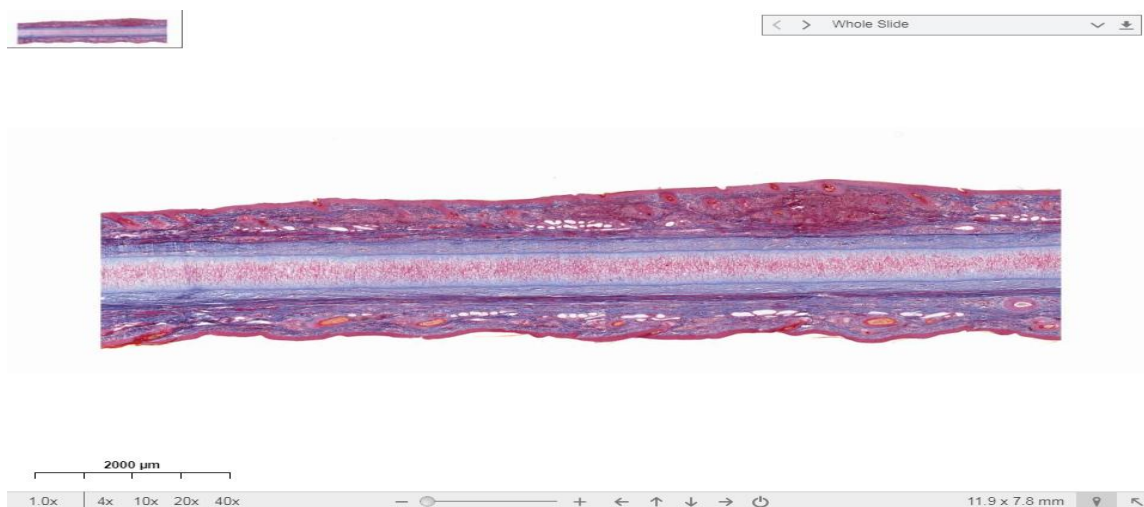


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- Matrix - composed mostly of elastic fibers, type II collagen and a ground substance of proteoglycans. The streaks of pink within the matrix are due to the presence of elastic fibers.

Elastic cartilage contains no blood vessels or nerves.



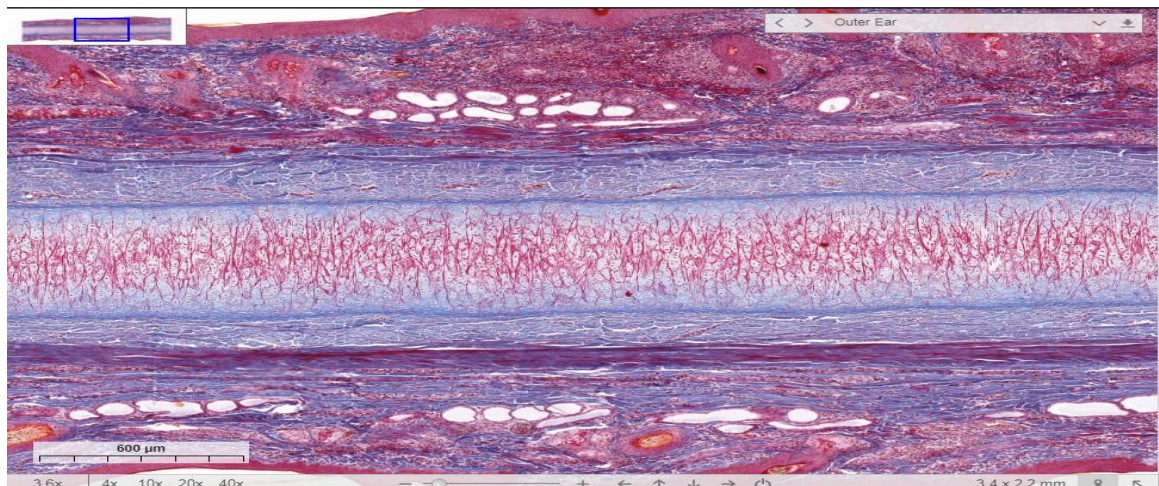
Elastic Cartilage (Masson's Trichrome / Aldehyde Fuchsin)

Elastic cartilage is similar to hyaline cartilage except that the matrix also contains a dense network of branching and anastomosing elastic fibers. It provides flexible support and is present in the outer ear and epiglottis.

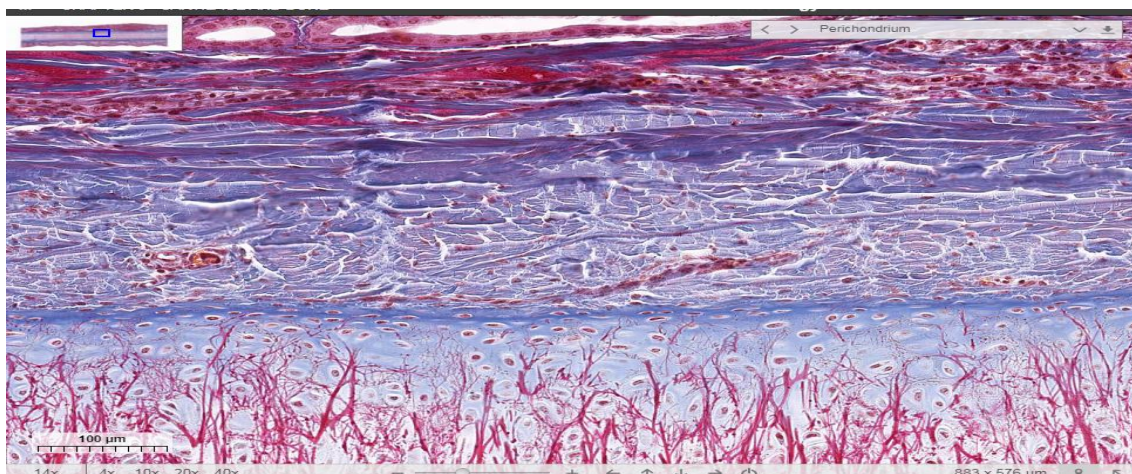
The outer ear (pinna) stained with Masson's trichrome and aldehyde fuchsin. Masson's trichrome stains connective tissue dark blue, smooth muscle and cytoplasm stain light pink, and nuclei stain dark red-purple to black. Aldehyde fuchsin stains elastic fibers pink-purple.

- Perichondrium (blue) - a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:
- Inner Chondrogenic Layer (darker blue) - contains mesenchymal cells that differentiate into chondroblasts, initiate matrix production (elastin and type II collagen) and become immature chondrocytes
- Outer Fibrous Layer (blue) - fibroblasts that produce the type I collagen on the outer surface of the perichondrium
- Matrix - composed of an extensive, dark pink-purple network of elastic fibers, type II collagen and a ground substance of proteoglycans.
- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.

Elastic cartilage contains no blood vessels or nerves.



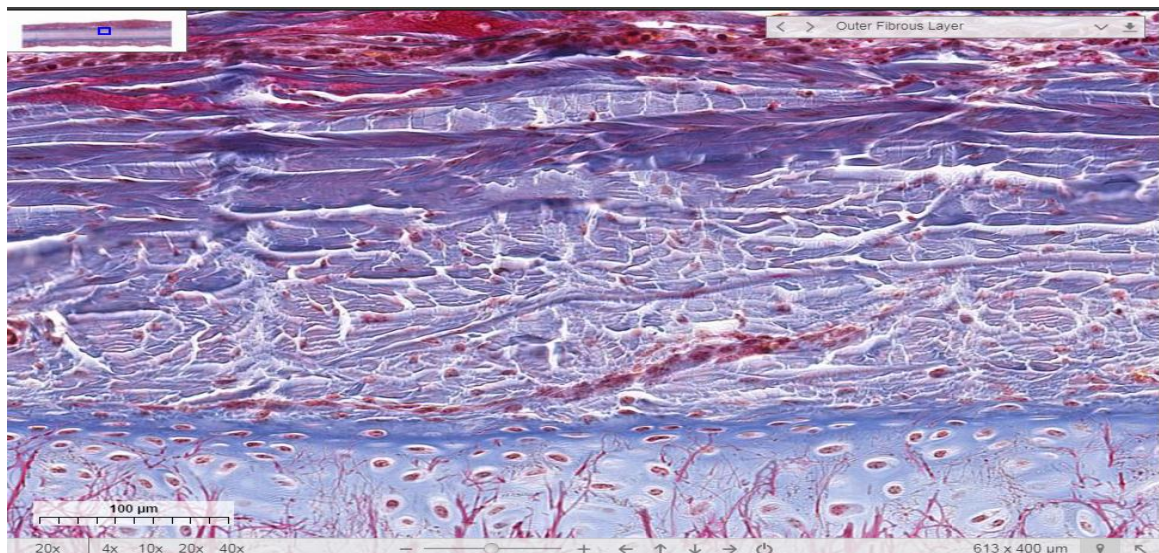
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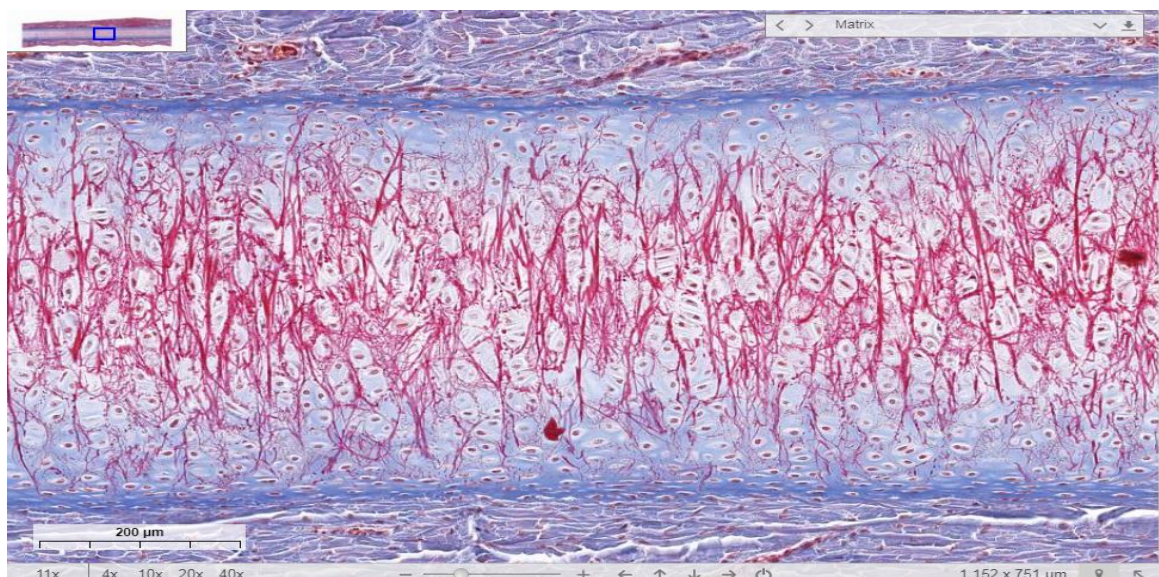
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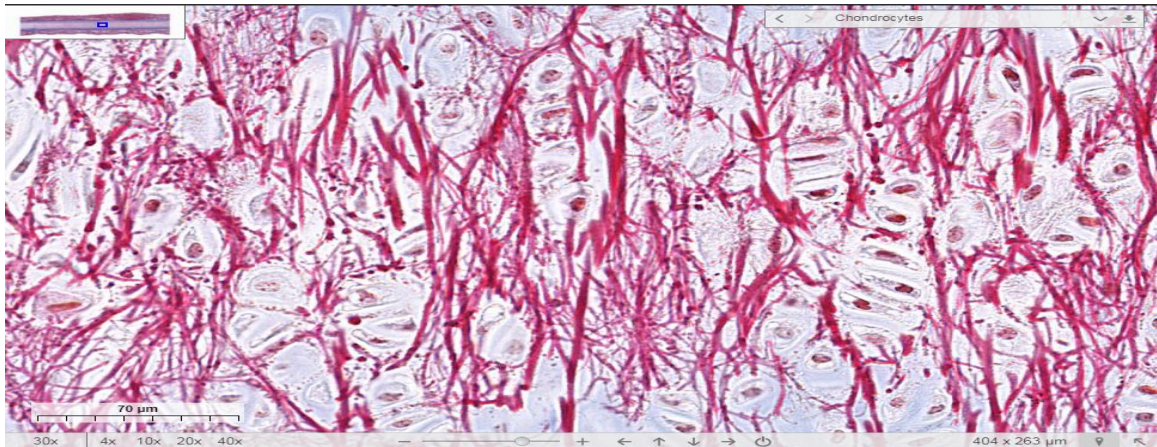
- Inner Chondrogenic Layer (darker blue) - contains mesenchymal cells that differentiate into chondroblasts, initiate matrix production (elastin and type II collagen) and become immature chondrocytes



- Outer Fibrous Layer (blue) - fibroblasts that produce the type I collagen on the outer surface of the perichondrium



- Matrix - composed of an extensive, dark pink-purple network of elastic fibers, type II collagen and a ground substance of proteoglycans.



- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups. Elastic cartilage contains no blood vessels or nerves.



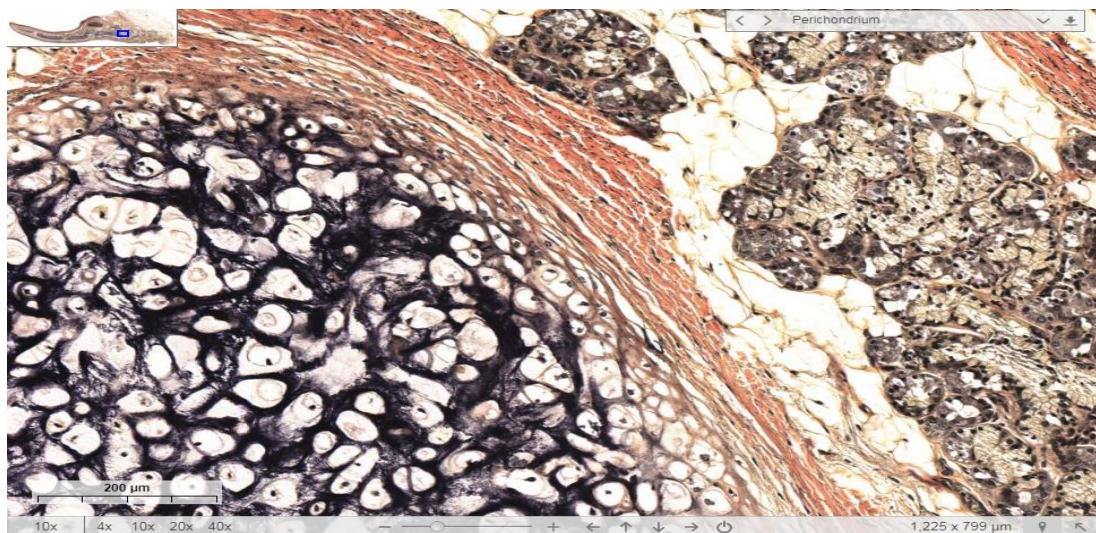
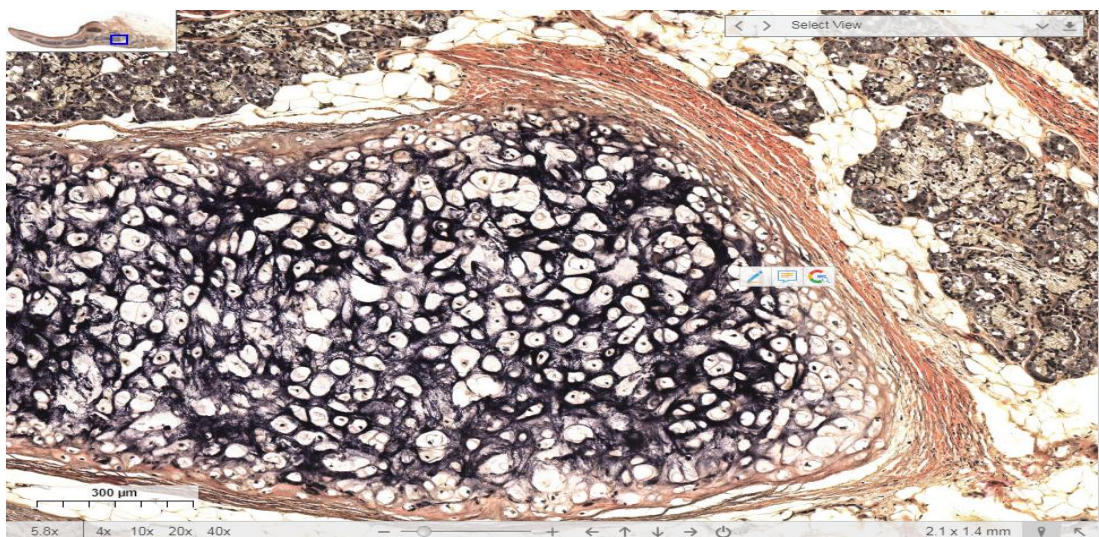
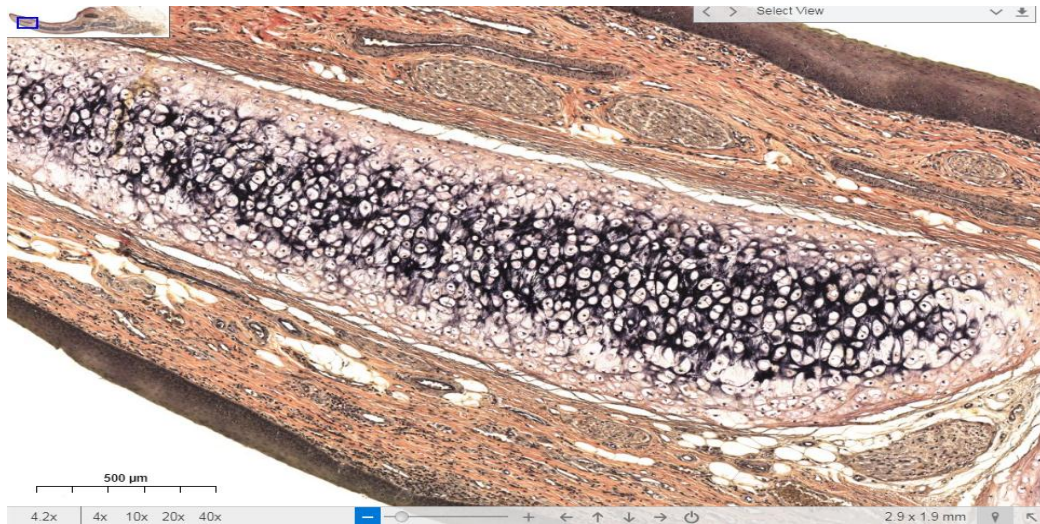
Elastic Cartilage (Verhoeff Stain)

This is the same specimen but stained with Verhoeff to show the elastic fibers, stained black, within the cartilage matrix.

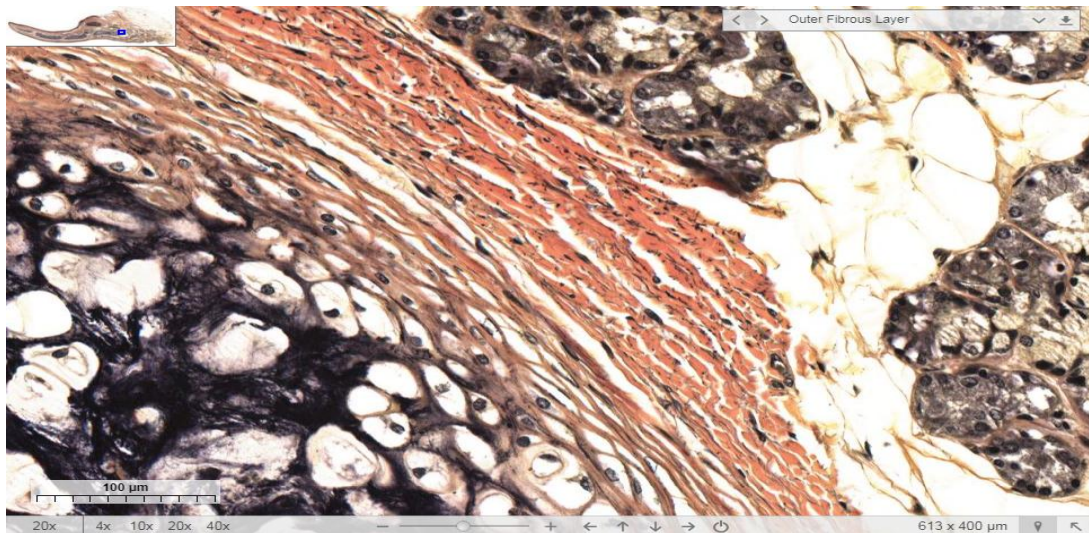
Elastic cartilage forms the core of the epiglottis:

- Perichondrium - a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:
- Outer Fibrous Layer - the type I collagen on the outer surface of the perichondrium is stained light pink/red.
- Inner Chondrogenic Layer - contains unstained fibroblast-like cells, chondroblasts, and immature chondrocytes.
- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.
- Matrix - composed mostly of elastic fibers, type II collagen and a ground substance of proteoglycans. The elastic fibers are intensely stained black.

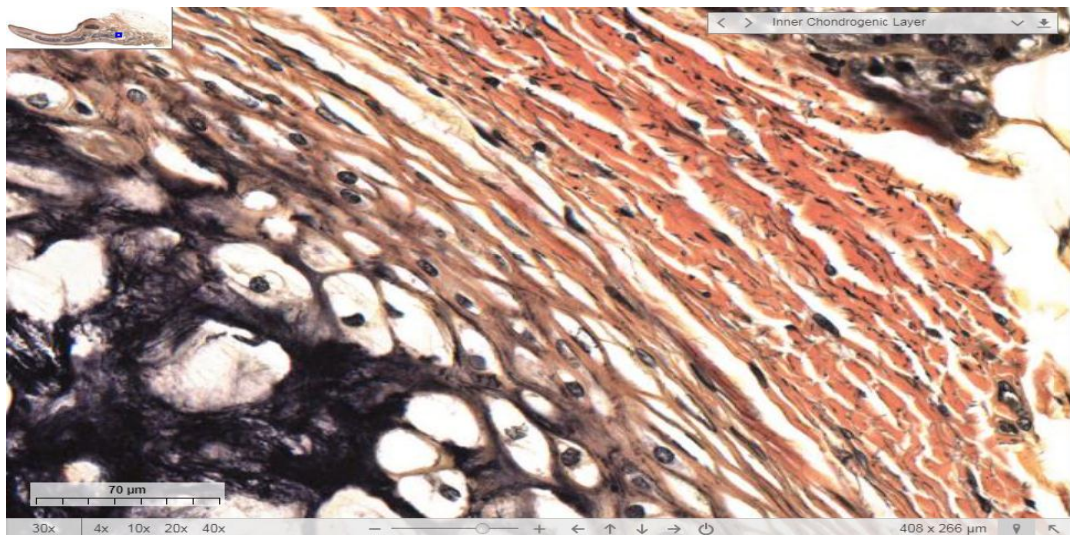
Elastic cartilage contains no blood vessels or nerves



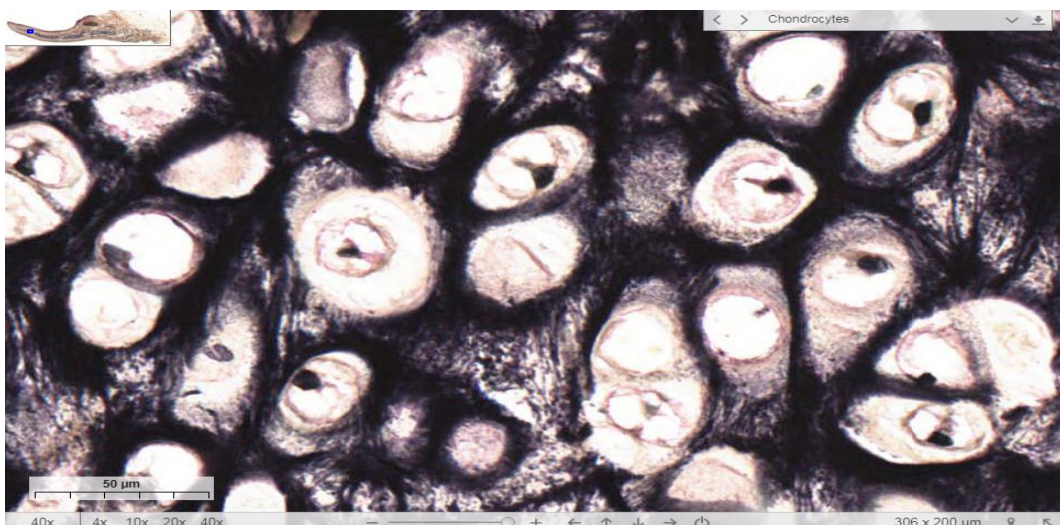
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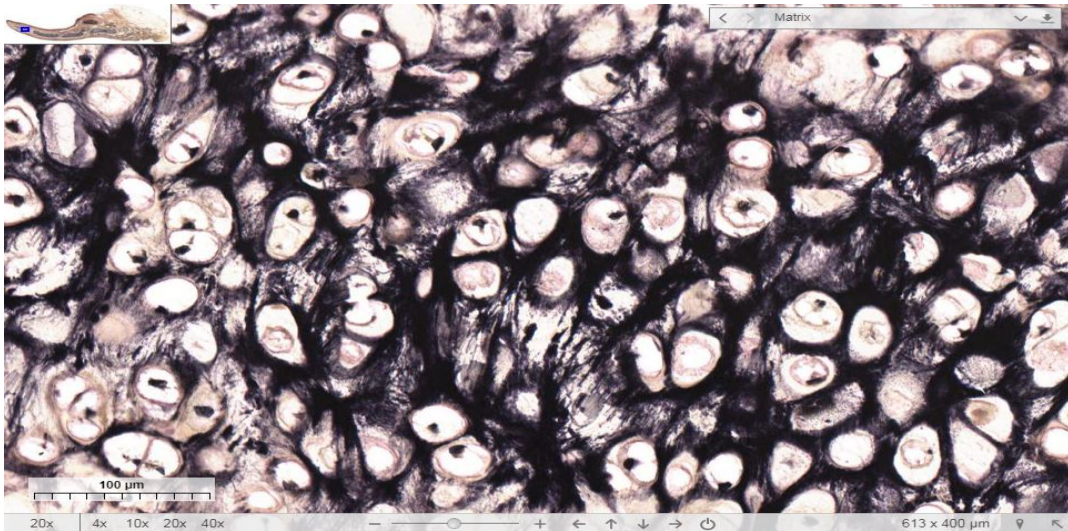
- Outer Fibrous Layer - the type I collagen on the outer surface of the perichondrium is stained light pink/red.



- Inner Chondrogenic Layer - contains unstained fibroblast-like cells, chondroblasts, and immature chondrocytes.



- Chondrocytes - cells within lacunae inside the cartilage that occur singularly or in clusters called isogenous groups.



- Matrix - composed mostly of elastic fibers, type II collagen and a ground substance of proteoglycans. The elastic fibers are intensely stained black.

Elastic cartilage contains no blood vessels or nerves.

Fibrocartilage

Fibrocartilage contains a mixture of hyaline cartilage and dense regular connective tissue. It combines the tensile strength of collagen fibers with the resistance to compression of cartilage. It is found where tendons attach to bones, menisci and intervertebral discs

Fibrous Cartilage

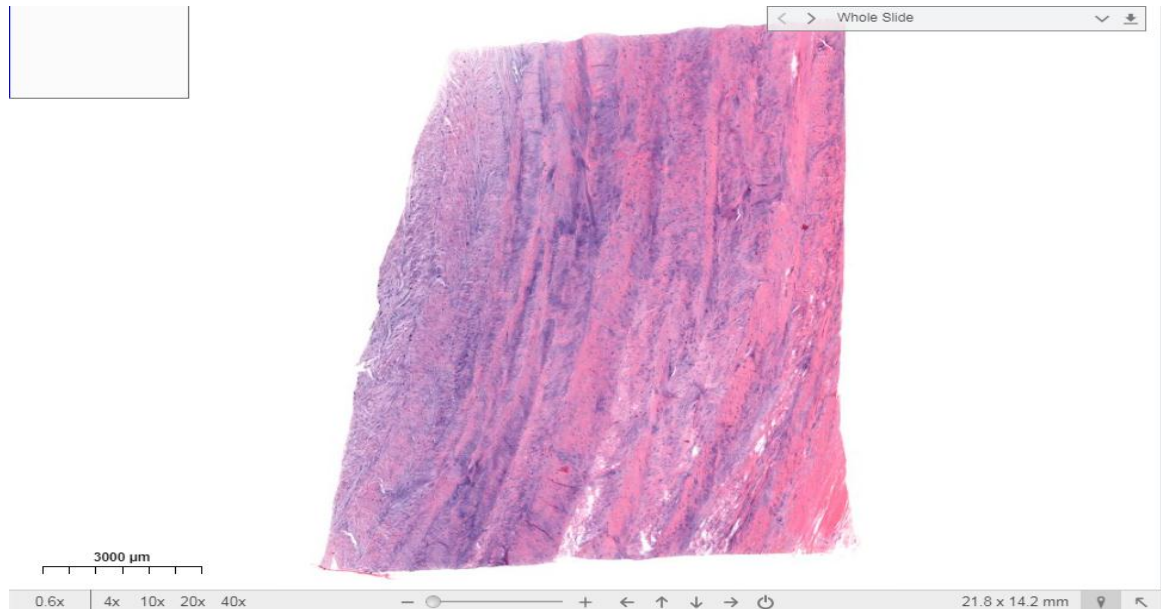
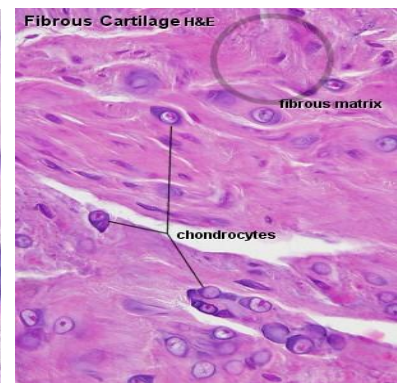
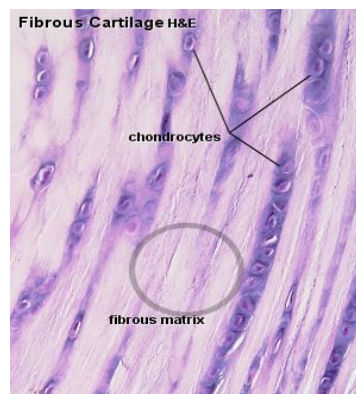
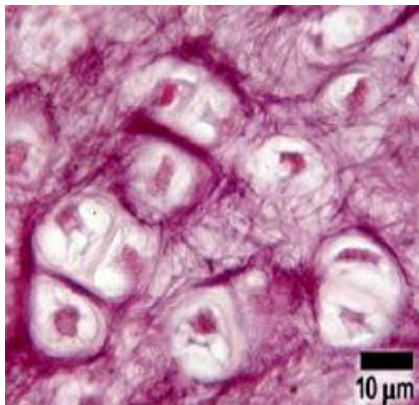
- is a form of connective tissue transitional between dense connective tissue and hyaline cartilage. Chondrocytes may lie singly or in pairs, but most often they form short rows between dense bundles of collagen fibres. In contrast to other cartilage types, collagen type I is dominant in fibrous cartilage.
- is typically found in relation to joints (forming intra-articular lips, disks and menisci) and is the main component of the intervertebral disks.
- merges imperceptibly into the neighbouring tissues, typically tendons or articular hyaline cartilage. It is difficult to define the perichondrium because of the fibrous appearance of the cartilage and the gradual transition to surrounding tissue types.

Suitable Slides

sections of intervertebral discs or articular discs - H&E, van Gieson

Fibrous Cartilage, Intervertebral Disc, sheep, H&E and Articular Disc, rabbit, H&E
The fibrous cartilage forming the intervertebral discs varies in appearance from the center of the disc (the nucleus pulposus) to the periphery of the disc (the annulus fibrosus). Centrally, the fibrous matrix is very loose. The jelly-like consistency of the central part allows the intervertebral discs to function as a shock absorber. Towards the periphery, the fibrous matrix is organised into layers. It is often visible that the fibres of different layers are oriented at angles to each other - similar to the orientation of the thread in radial tires. Chondrocytes are very flattened in the periphery and may be difficult to find. Midway between periphery and

center of the intervertebral disc, chondrocytes are scattered singly or in small isogenous groups in the dense fibrous matrix of the cartilage. If you take a close look at the cells you will see that their appearance actually resembles that of chondrocytes in other types of cartilage - their characteristic appearance distinguishes fibrous cartilage preparations from connective tissues. The very regular arrangement of the fibres in the articular disc may initially let you guess at dense regular connective tissue. Isogenous groups of chondrocytes again identify the tissue as fibrous cartilage. **Draw a small section of the fibrous cartilage, including (if possible) a group of chondrocytes.**



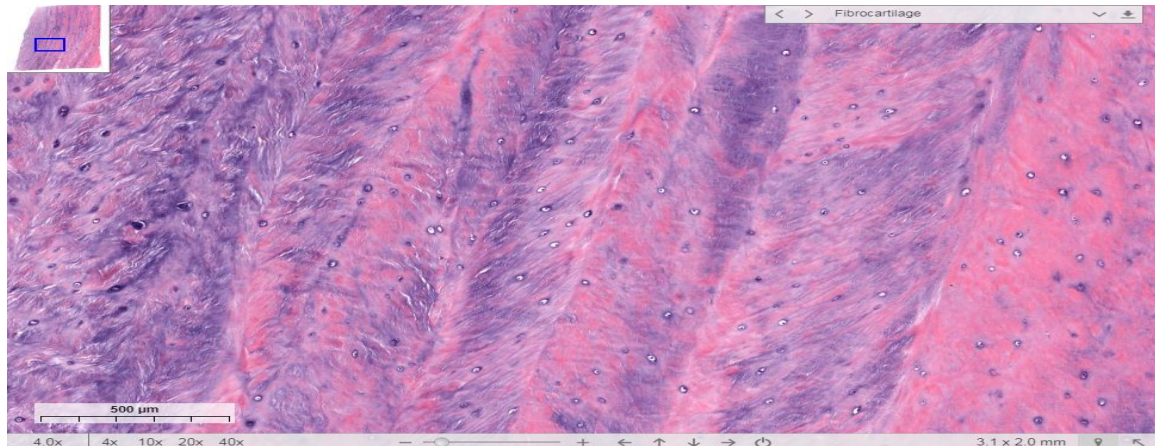
Fibrocartilage is a mixture of dense regular connective tissue and hyaline cartilage. It is found in intervertebral discs, pubic symphysis, articular discs and menisci of joints.

Intervertebral discs that are found between adjacent vertebrae of the spine contain fibrocartilage. They have a fibrous appearance of mostly collagen fibers with interspersed areas of cartilage.

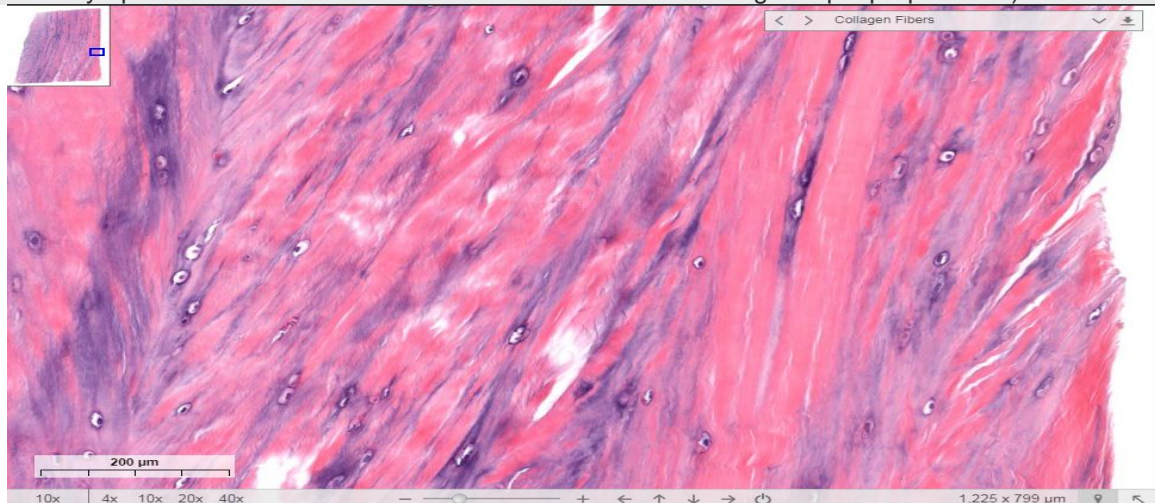
(Note that the cytoplasm has been extracted from most of the cells during sample preparation.)

- Collagen Fibers - the majority of the fibrocartilage is a mixture of type I and type II collagen. They type I collagen is stained pink/red.
- Fibroblasts - scattered cells within fibrous regions with elongated or flattened nuclei. Few are seen in this specimen.

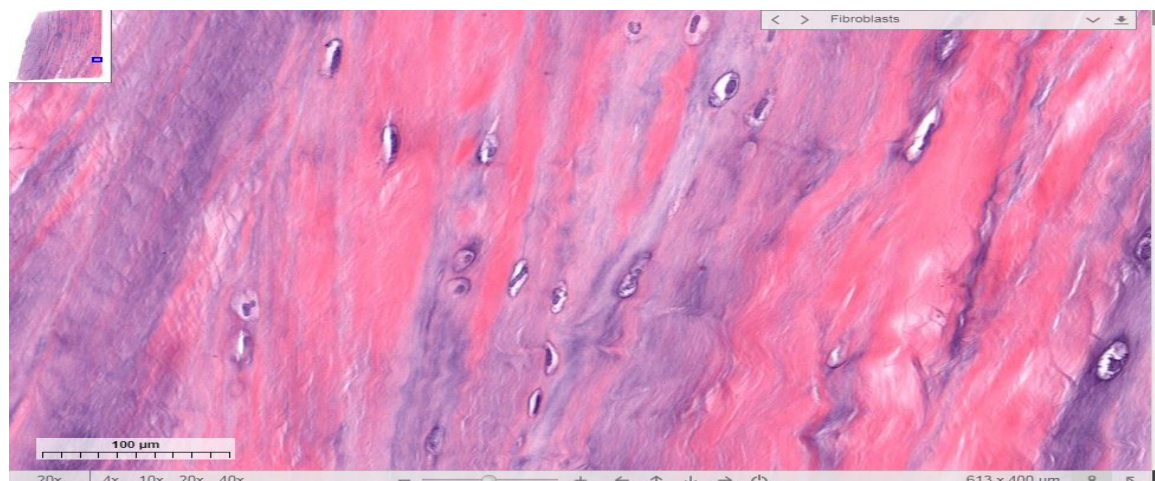
- Chondrocytes - are dispersed between collagen fibers singularly, in columns, or in isogenous groups and are surrounded by a basophilic matrix.
- Matrix - much less material surrounds each chondrocyte than in hyaline cartilage. It is composed of type II collagen and a ground substance of proteoglycans. The basophilia is due to a high content of sulfated glycosaminoglycans (GAGs).
- There is no perichondrium.



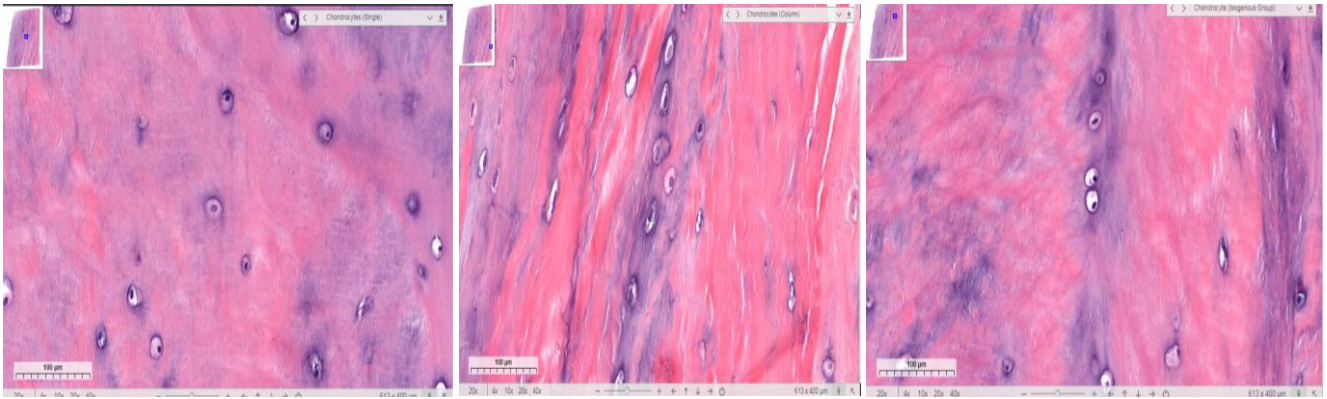
Intervertebral discs that are found between adjacent vertebrae of the spine contain fibrocartilage. They have a fibrous appearance of mostly collagen fibers with interspersed areas of cartilage.
(Note that the cytoplasm has been extracted from most of the cells during sample preparation.)



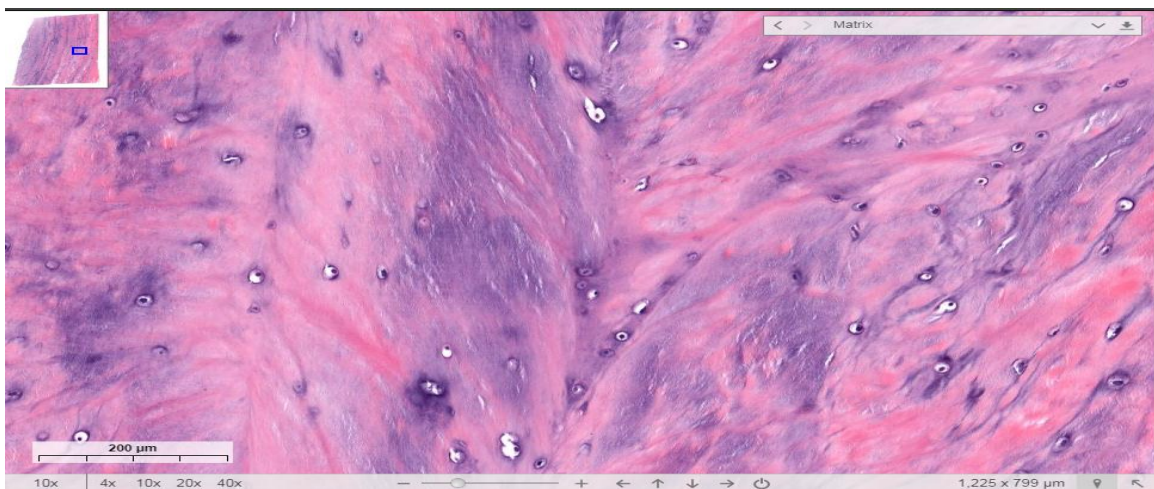
- Collagen Fibers - the majority of the fibrocartilage is a mixture of type I and type II collagen. The type I collagen is stained pink/red.



- Fibroblasts - scattered cells within fibrous regions with elongated or flattened nuclei. Few are seen in this specimen.



- Chondrocytes - are dispersed between collagen fibers singularly, in columns, or in isogenous groups and are surrounded by a basophilic matrix.



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- There is no perichondrium.

Articular Cartilage

- is a specialised form of hyaline cartilage.
- transforms the articulating ends of the bones into lubricated, wear-proof, slightly compressible surfaces, which exhibit very little friction.
- is not surrounded by a perichondrium and is partly vascularised.
- is, depending on the arrangement of chondrocytes and collagenous fibres, divided into several zones:

Tangential layer

Chondrocytes are rather small and flattened parallel to the surface. The most superficial part (lamina splendens) is devoid of cells. Collagen fibres in the matrix of the tangential layer are very fine. They run parallel to the surface of the cartilage.

Similar to the collagen fibres of the skin, the general orientation of collagen fibres in articular cartilage is determined by tensile and compressive forces at the articulating surfaces.

Transitional zone

The chondrocytes are slightly larger, are round and occur both singly and in isogenous groups. Collagen fibres take an oblique course through the matrix of the transitional zone.

Radial zone

Fairly large chondrocytes form radial columns, i.e. the stacks of cells are oriented perpendicular to the articulating surface. The course of the collagen fibres follows the orientation of the chondrocyte columns.

Calcified cartilage layer

It rests on the underlying cortex of the bone. The matrix of the calcified cartilage layer stains slightly darker (H&E) than the matrix of the other layers.

The main source of nourishment for articular cartilage is the synovial fluid, which fills the joint cavity. Additional small amounts of nutrients are derived from blood vessels that course through the calcified cartilage close to the bone. Living chondrocytes have been found in small pieces of cartilage floating in the joint cavity after damage to the articular cartilage.

Osteoarthritis, the slow progressive degeneration of articular cartilage, is the most common joint disease. It may be caused by persistent and abnormally high loads on the joint surfaces, which initially result in the loss of proteoglycans and chondrocytes from the articulating surface of the cartilage. Subsequently, the cartilage may crack (fibrillate), erode and expose the underlying bone.

Suitable Slides

Sections of large joints - H&E Layers are difficult to identify in the articular cartilage of small joints.

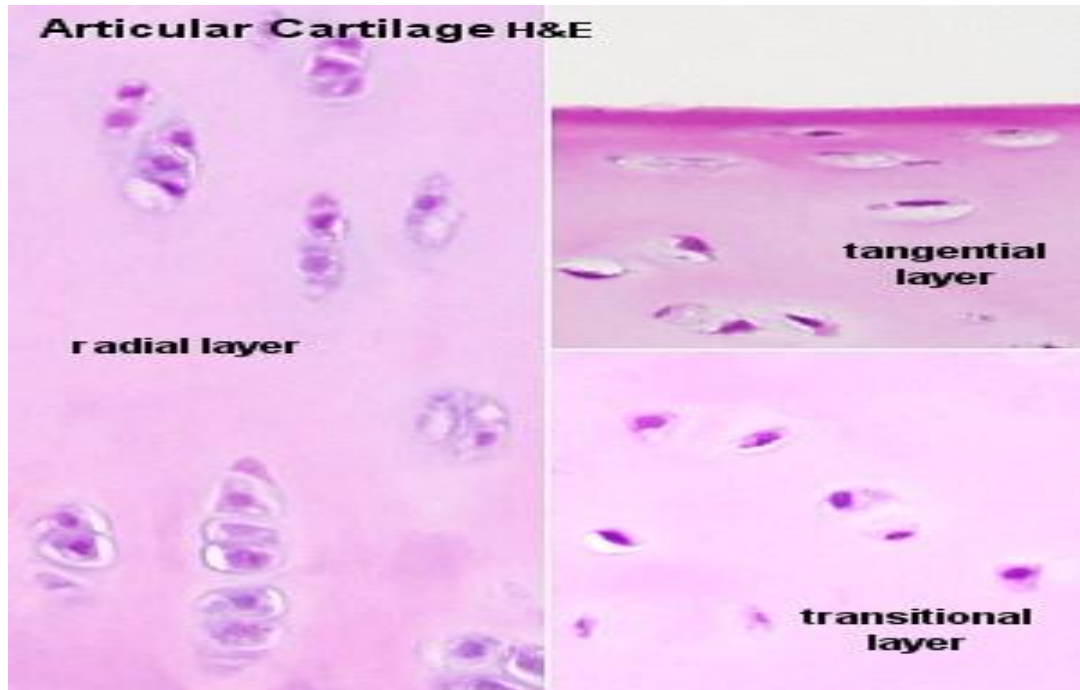
Articular Cartilage, bovine, H&E The layers of articular cartilage are easiest to identify in the cartilages covering the articulating surfaces of large joints. Note the changing orientations of the lacunae and isogenous groups at different depth in the cartilage. The changing orientations of chondrocytes and isogenous groups reflect the orientations of the collagen fibres in the matrix. The fibres are not visible in the slide. The darker hue of the cartilage close to the bone is caused by the calcification of the cartilage.

Draw the articular cartilage at low magnification. Indicate in your drawing the preferred orientations of lacunae and isogenous groups and the expected orientation of collagen fibres.

Degeneration and Regeneration of Cartilage

Due to the fairly poor access of nutrients to the chondrocytes they may atrophy in deep parts of thick cartilage. Water content decreases and small cavities arise in the matrix, which often leads to the calcification of the cartilage. This further compromises nutrition. The chondrocytes may eventually die, and the cartilage is gradually transformed to bone.

Chondrogenic activity of the perichondrium is limited to the period of active growth before adulthood. Although chondrocytes are able to produce matrix components throughout life, their production can not keep pace with the repair requirements after acute damage to hyaline or articular cartilage. If these cartilages are injured after the period of active growth, the defects are usually filled by connective tissue or fibrous cartilage. The extracellular matrix of these "repair tissues" is only poorly integrated with the matrix of the damaged cartilage.



Fortunately, cartilage is rather well suited for transplantation - the metabolism of the chondrocytes is rather slow, the antigenic power of cartilage is rather low, and it is difficult, if not impossible, for antibodies or cells of the immune system to diffuse through the matrix into the cartilage. **CARTILAGE DEVELOPMENT**

Chondrogenesis is the process by which cartilage is formed from condensed mesenchyme, differentiation into chondroblasts, and deposition of the extracellular



Chondrogenesis

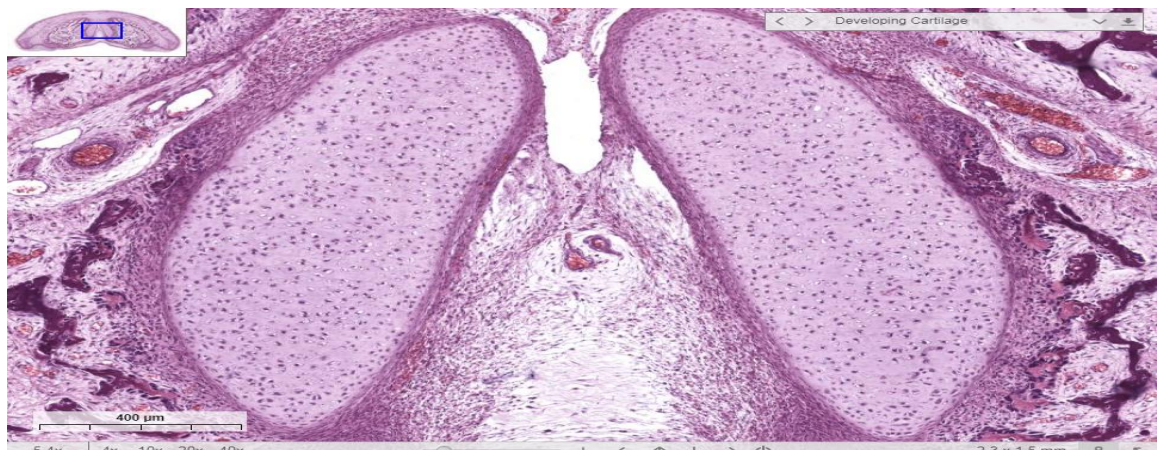
Developing cartilage occurs as two large, oval structures near the midline of this specimen. Cartilage development begins with the aggregation of mesenchymal cells that differentiate into chondroblasts. With the initiation of matrix production, the cells become surrounded by matrix and are called chondrocytes.

Cartilage growth continues by two processes:

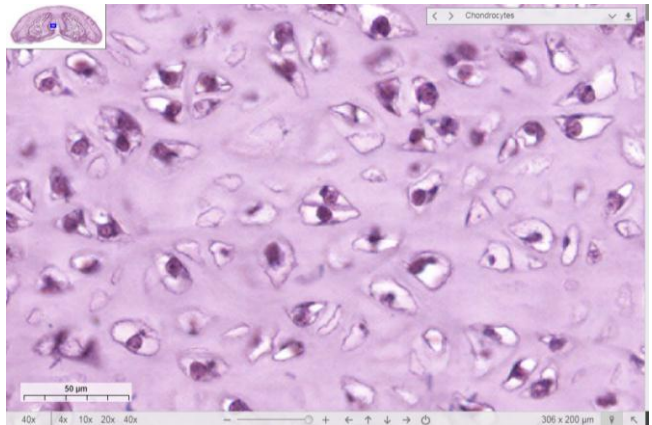
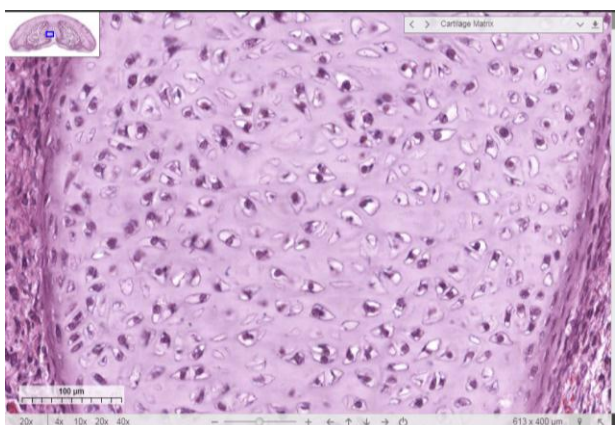
- **Appositional Growth** - forms new cartilage on the surface of existing cartilage. The perichondrium is a layer of dense irregular connective tissue that surrounds cartilage. It is divided into two layers:

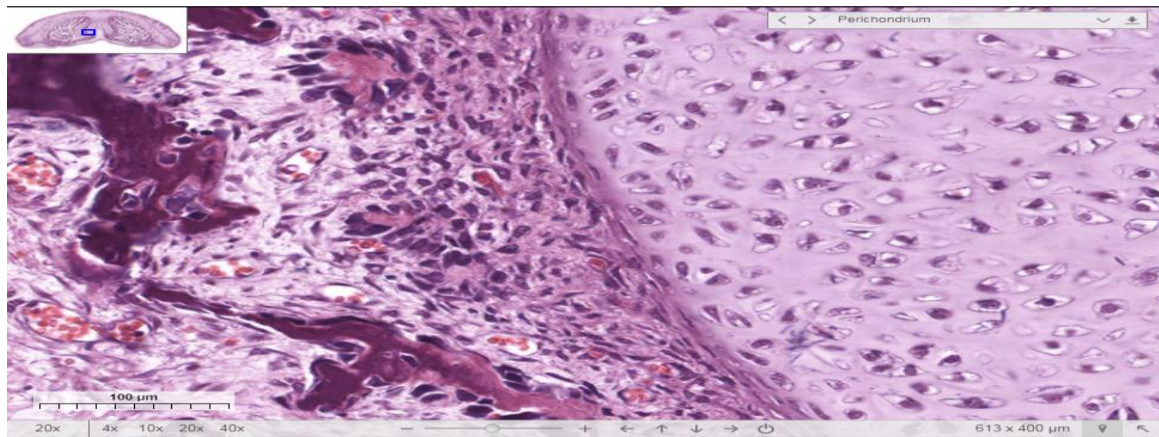
- Outer Fibrous Layer - contains fibroblasts that produce the type I collagen on the outer surface of the perichondrium.
- Inner Chondrogenic Layer - contains fibroblast-like cells that differentiate into chondroblasts, initiate matrix production (type II collagen), and become immature chondrocytes. The new matrix increases cartilage mass.
- Interstitial Growth - forms new cartilage within the existing cartilage. Chondrocytes divide and the daughter cells move apart from each other. This is only possible when the surrounding matrix is distensible.

Unlike the basophilia of mature cartilage, developing cartilage is pale staining because sulfated glycosaminoglycans (GAGs) have not been added to the matrix.

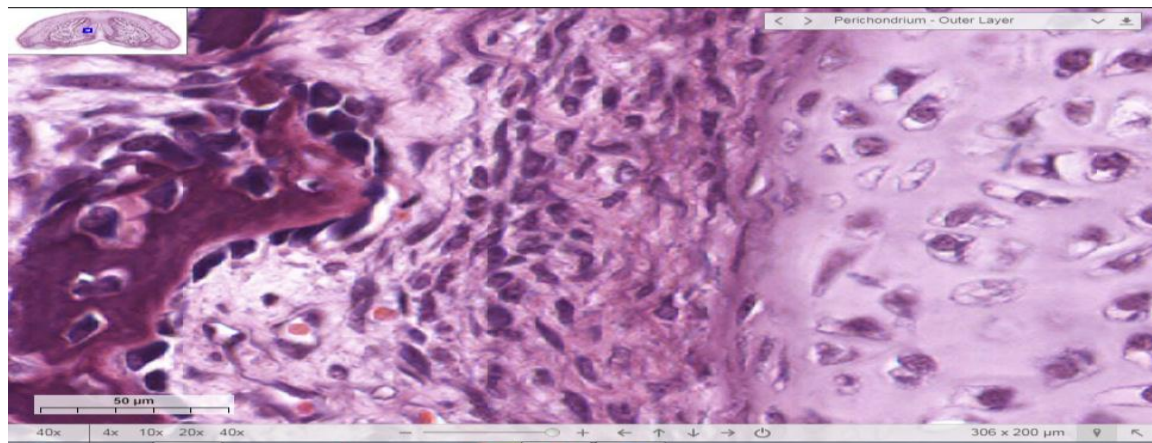


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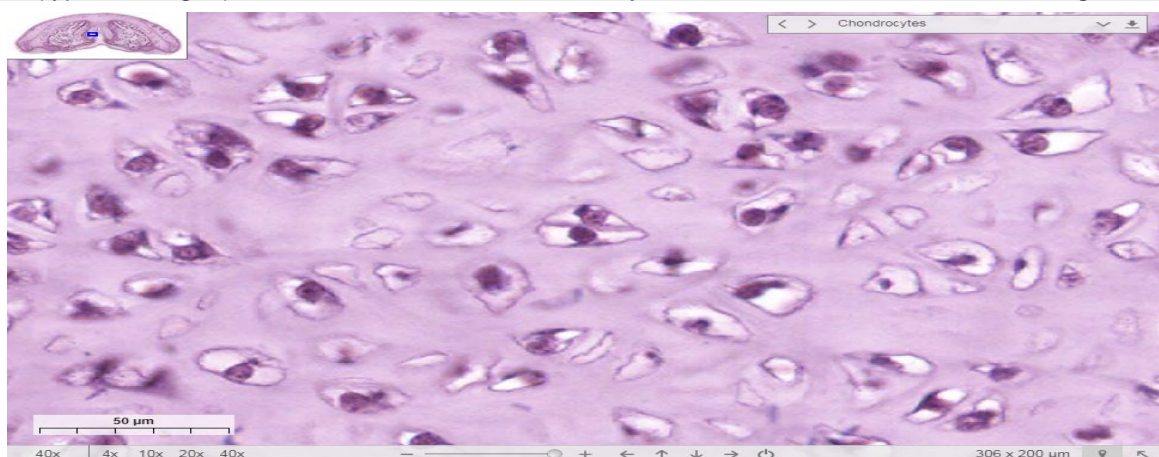




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