Lesson 16

- Lesson Outline:
  - Phylogeny of Skulls, and Feeding Mechanisms in Fish
    - Agnatha
    - Chondrichthyes
    - Osteichthyes (Teleosts)
  - Phylogeny of Skulls and Feeding Mechanisms in Tetrapods
    - Temporal Fenestrations
    - Cranial Kinesis
    - Evolution of Ear Bones
    - Palatal Evolution
    - Cranial Akinesis in Mammals
    - Hyoid Apparatus and Larynx

- Objectives:
  At the end of this lesson, you should be able to:
  - Describe the structure and function of the skulls of fish
  - Describe the feeding mechanisms in jawless fish (agnathans)
  - Describe cranial kinesis in fish and relate the various degrees of kinesis to styles of feeding
  - Describe the manner in which adaptations for chewing and mastication versus seizing have altered the structure of the skull
  - Discuss the significance of the differences in the anapsid, diapsid and synapsid skull
  - Discuss the significance of cranial kinesis and akinesis discussing where these occur and why this is important
  - Describe how adaptations for feeding gave rise to the bones of the ear and why this in significant in tetrapods
  - Discuss how adaptations for mastication gave rise to the evolution of the palate, hyoid apparatus and larynx

- References:
  - Chapter 9: 162-198

- Reading for Next Lesson:
  - Chapter 9: 162-198

Phylogeny of Skulls and Feeding Mechanisms

Neurocranial-Dermatocranial- Splanchnocranial Complex - Phylogeny of Skulls and Feeding Mechanisms

Skulls first appear in the craniates.

Protchordates:

Microphagous feeding employing cilliary currents and mucus entanglement.
Well adapted to aquatic forms leading a sedentary lifestyle.
Still found in amocoetes larvae.

Agnatha:

Jawless and feed in a number of specializes ways.

Without jaws, feeding mechanisms are limited to bottom feeding, sucking, mud swallowing, scavenging and parasitism.

Lampreys: Parasitic, sucking, feed on blood and tissue.

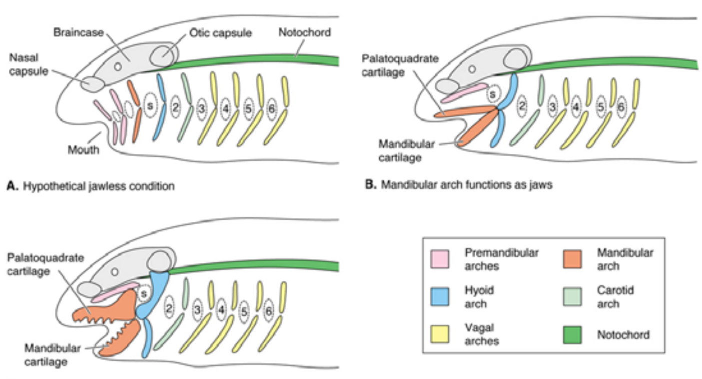
Attach by the round oral disk or mouth and create suction by forcing water out through the gills. Have a "velar valve" separating the oral cavity from the buccal cavity. They have a rasping tongue that abrades the flesh of their prey. The velar valve separates the oral cavity during feeding while the pharyngeal or buccal cavity is used for breathing. They continue to breathe both in and out through the pharyngeal slits.

Hagfish: Scavengers. Cannot attach to prey. Have no jaw but have paired, toothed oral plates that open and close like the leaves of a book. Are feeble for grasping and holding.

Use cutaneous respiration for gas exchange while buried into prey and back out and breathe every 3-4 minutes. Can suffocate prey by secreting mucous and then scavenge on the corpse.

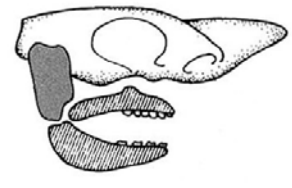
First step towards gill-arch jaws was the enlargement of the mouth, an adaptation for taking in larger pieces of food - not for predation.

As the mouth enlarges, it crowds backwards onto the gill arches. The first gill arch becomes the jaw, and forms the palatoquadrate and Meckel's cartilage. It becomes the base for the teeth that evolve from dermal denticles.



Chondrichthyes

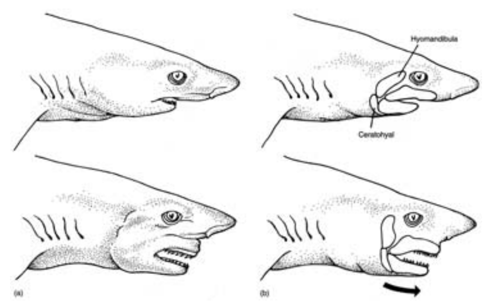
The mandibular arch is not attached directly to the chondocranium in sharks but is attached to the hyoid arch – which is attached to the skull. This is referred to as an amphystylic suspension.



Amphistyly
(Primitive fish)

The palatoquadrate is attached at its anterior end by a loose ligamentous articulation with the braincase near the nasal capsule. At the posterior end, it articulates with the lower jaw (Meckel's cartilage) as well as with the hyoid arch (ceratohyal). The hyomandibula, in turn, is attached firmly but movably to the otic region of the chondocranium. This is the attachment of the jaw to the cranium. As a result, the upper jaw can drop down at its posterior end, and swing forward with a pendulum like motion, to increase the size of the mouth opening.

This is protrusion. This achieves several things. It allows both upper and lower jaws to strike the prey at the same time and it allows the mouth to open wider.



This does disrupt the streamlined body silhouette, which would reduce swimming efficiency. This style of jaw allows the animal to protract the jaw for feeding and retract the jaw for swimming.

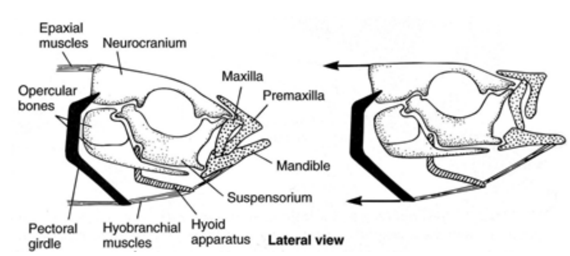
The function of the jaws and teeth of most species of shark are restricted to grasping prey and to cutting off pieces small enough to swallow. They do not use the jaws and teeth for killing prey directly. The jaws are not strong, their support is weak and the muscle arrangement is too weak to allow a strong bite (poor hinge, poor mechanical advantage). Sharks use the force of swimming to sink their teeth into their prey, not the force of the bite. They then use one set of teeth to hold and move the cutting teeth using lateral movements, against the holding teeth to cut off bites. They may assist this by rotating their entire bodies. They have processes on the upper jaw to strengthen it against lateral strain. This is effective. Large tiger sharks have been known to be able to cut marine turtles into bite sized pieces, shell and all.

Osteichthyes:

Actinopterygians (Chondrosteans - Teleosts)

Show a progressive improvement in a fundamentally predaceous feeding mechanism. The trend is for the liberation of bony elements to serve diversified functions in food procurement.

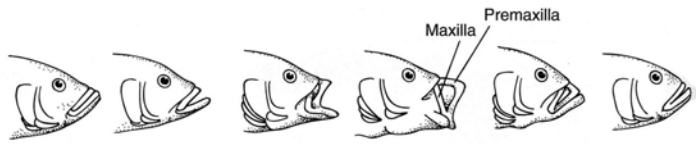
Early actinopterygians were predators, biters and swallowers. They employed rapid suction feeding. Rapid expansion of the buccal cavity sucked food into the mouth, and once captured, teeth hold the prey. Relative to suspension feeders, this required a more muscular buccal region and strong jaws. They had sharp pointed teeth, an oblique jaw opening, a rigid upper jaw and palate.



1) The first improvement was the freeing of the maxilla (hyostyly).

2) This allows the upper jaw to drop when the mouth is opened increasing the gape.

3) Ligaments develop between the maxilla and the lower jaw. Now when the lower jaw is depressed, the maxilla is pulled forward increasing the number of teeth available for grasping prey.

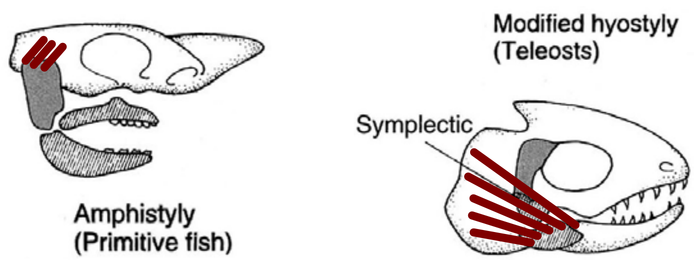


4) Following on from the origin of the moveable suspension of the maxilla is the free articulation of the premaxilla.

5) The neurocranium is also free to move at its spinal attachment and can be lifted.

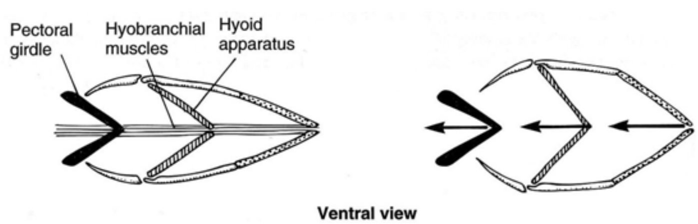
This leads to a highly kinetic, protrusible upper jaw that allows the fish to project its upper jaw towards food with greater rapidity than was possible by maxillary movement alone.

6) This permits expansion of the adductor muscles, can now increase mass and complexity. Their origin extends to the brain case, to the ventral surface of the skull roof, back of the palate and hyomandibular apparatus. This increases the force of the bite.



7) The coronoid process develops as an upward extension of the dentary bone and this increases the surface area for muscle attachment and the torque that can develop around the jaw articulation.

8) The hyoid apparatus (cerato and basi hyal plus other elements) forms struts within the floor of the buccal cavity which, when pulled backward during mouth opening, push out the lateral walls of the buccal cavity and help expand the cavity creating suction.



We get a stronger bite with more freedom of movement but still a basic predaceous biting pattern.

This now allows the mouth to also be used for other things than seizing and ripping. This gives rise to an enormous variety of feeding mechanisms in teleost fishes - and promoted the successful exploitation of food sources not available previously (nibbling on coral reefs or in the rocky intertidal) (imagine bobbing for apples if we had a protrusible premaxilla).

For predators, the predaceous mouth requires a solid footing for the upper jaw. The premaxilla must resist the impact of hitting prey with force and provide a solid foundation for the lower jaw to snap closed against. In highly predaceous teleosts (barracuda, pike), the premaxilla has secondarily lost its mobility and modifications arise that increase the strength and rigidity of the jaw.

Tetrapods

The earliest amphibians had conical teeth for grasping, a rigid jaw articulation, and an oblique gape. They were just like early fish. This only allows simple vertical movements.

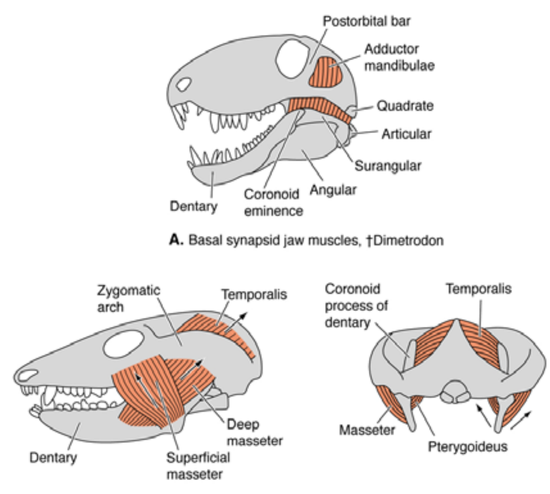
Within the tetrapods we see the development of two basic patterns of jaw action. These occur separately in many cases but also occur together in others (They are not mutually exclusive).

We see changes in the shape of the jaw and the angle of insertion of the jaw muscles. These changes determine the basic functions of the jaw.

The structure of the jaw in early tetrapods allowed the development of rapid motion starting at the open position, but the jaws at rest in the occlusal position could exert little force. When open, the muscles were pulling at right angles to the lower jaw (good strength) but as the jaw closes, the muscles are now working obliquely. The action was a simple vertical movement. Once motion is initiated, it was the velocity and mass of the jaws that did the work. This allowed rapid mouth closure and drove piercing teeth into prey. It was not a good design for holding or grasping with the mouth closed or for nibbling, etc.

With the enlargement of the lower jaw and evolution of the coronoid process, and the development of the temporal fossa, the angle of insertion of many muscles changes. These changes allow much more force to be developed with the jaw in the occlusal position. Further changes in both the articulation of the jaw and the angle of insertion of muscles may also allow lateral as well as anterior-posterior movement.

The driving force for these changes was chewing or mastication rather than seizing.



A. Basal synapsid jaw muscles, †Dimetrodon

B. †Probainognathus

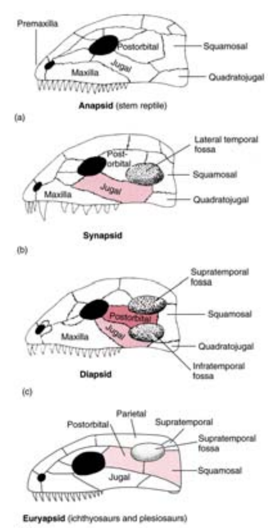
C. †Probainognathus

Throughout the amniotes we see a number of trends:

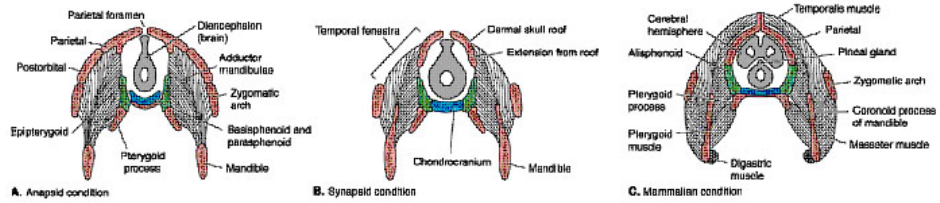
1) Temporal Fenestrations

In an earlier lecture we discussed the different types of temporal fenestrae and their use for studying the evolution and classification of amniotes. Thus skulls could be:

anapsid
diapsid
synapsid
euryapsid



In the lab you have now seen many examples. Although useful to taxonomists, what is their functional significance? Fenestrae or fossa are absent in amphibians and primitive reptiles (turtles). They are normally associated with strong jaw adductor muscles leading to two hypotheses:



They evolved to provide space in the skull for the muscles to expand during contraction. Good idea but hard to find a preadaptation that would explain how this came about.

It has been suggested that the rims of the fenestrae offer a more secure attachment site for muscle than flat bone. Muscle tendons fuse with the bone periosteum and distribute the forces over greater area. This too, however, does not offer any idea of pre-adaptation.

Whatever the origin of the openings, they certainly now provide sites for muscle attachment, muscle swelling during contraction and lead to the evolution of stronger jaws.

2) Cranial Kinesis

Within the reptiles and birds, skull elements show varying degrees of freedom and movement, just as they do in teleost fishes. The most extensive motions are found in lizards and snakes

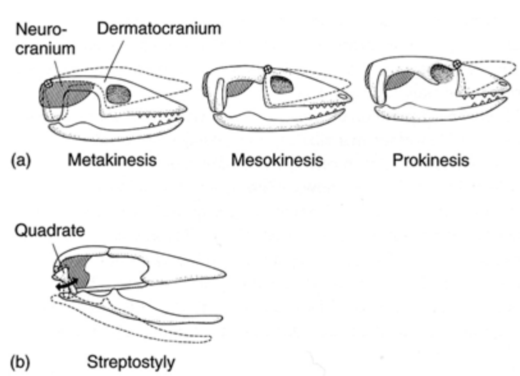
There are often transcranial joints across the full width of the top of the skull. This allows the tip of the snout to be raised independently.

The quadrate bone can be free to move to some extent around its connection with the braincase allowing more movement to the jaw.

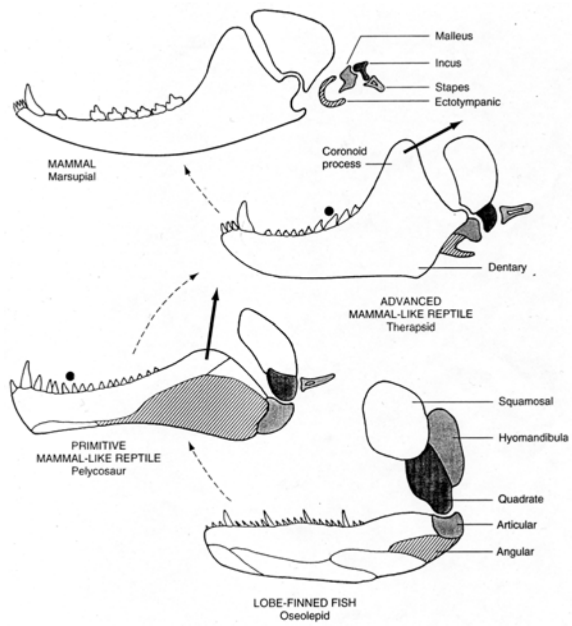
In many reptiles the lower temporal bar is lost. This gives the skull even more flexibility.

This combination of features permits the jaw to operate more efficiently. Rather than close like a pair of scissors, the angle of the jaw cannot be altered so that the upper and lower jaws close and meet the prey at the same time, delivering forces directly to the prey (they won't squirt out the front) and involving more teeth.

This is taken to a further extreme in snakes where the upper and lower temporal bars are lost, the lower jaw unfused in the midline, and there is more freedom of movement in many of the bones of the skull. The great freedom of rotation between elements of the skull, the independent movements of each and the ability to flare the jaws outward allow them to accommodate bulky prey items larger than their heads.



3) Evolution of Ear Bones

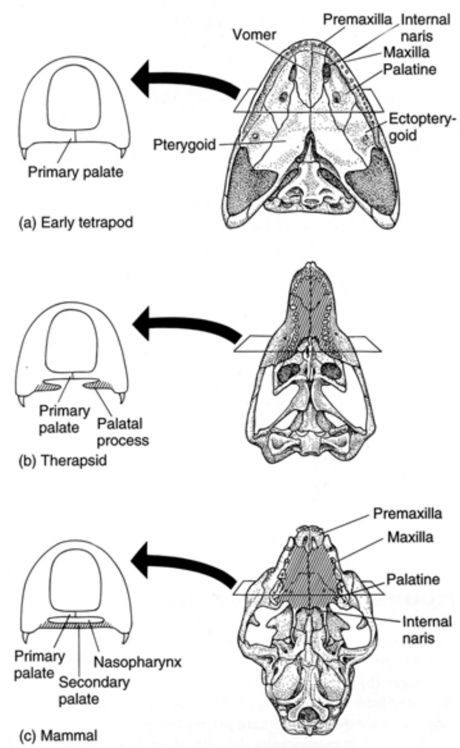


We discussed types of jaw suspensions and the fate of the quadrate and articular bones from the splanchnocranium last day.

Note here that the reason that these bones become free to take on these alternate functions is because of the changes in the shape of the jaw and the muscle attachments associated with feeding adaptations. As processes develop for muscle attachment and the distribution of the muscle forces changed, the bite became stronger but the forces on the joint decreased. At the same time, a part of the dentary bone began to articulate with the squamosal bone of the skull and slowly this articulation took over.

At the same time, we now have animals living in air where sound consists of higher frequency vibrations than in water. The stapes had evolved to form a tympanic ear and these bones became reduced in size and liberated from their previous chores, they became incorporated into the middle ear giving the ear greater capacity to respond to the higher frequency vibrations associated with sound transmission in air.

4) Palatal Evolution



Along with these changes in the lower jaw, which are associated with mastication, is the evolution of the secondary palate, also associated with mastication. The secondary palate includes a hard palate of bone and a secondary continuation of fleshy tissue, the soft palate. The hard palate forms from ingrowths from the front and the sides, form premaxilla, maxilla and palatine bones. It separates the food chamber from the respiratory passages.

It is found in some turtles and crocodilians as well as in mammals.

Most lower vertebrates deal with the problem by not breathing when eating. They have a low metabolic rate. In these animals, the jaws and mouth are an organ of prehension and food, once dead, is swallowed quickly. Food may be torn apart, but it is then swallowed unprocessed. In mammals, the feeding apparatus becomes an organ for the mechanical reduction of food. Salivary glands appear and the mouth becomes part of the digestive system.

The food of many mammals and reptiles is the same. The reason for the difference in jaw, skull and digestive morphology is the change in limb suspension in mammals. As we have already discussed, in mammals the limbs move under the body freeing them form a pure support and locomotor function so that they can be used for food handling. Prey is now usually killed before it is eaten freeing the teeth and mouth for other functions.

In mammals, along with the secondary palate, we see the evolution of the epiglottis and palato-pharyngeal folds at the back of the oral cavity that act to close off the rear of the cavity isolating the airway during mastication.

5) Cranial Akinesis

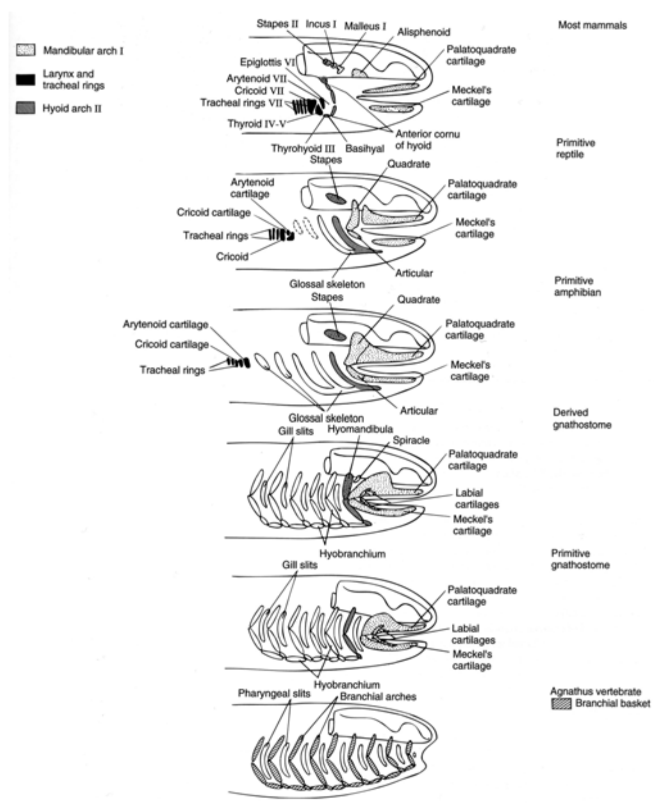
Now that the mouth is no longer used primarily to capture and hold prey, a kinetic skull is no longer an advantage.

In mammals, the trend towards fusion of bones and reduction in numbers continues. These features combined strengthen the skull, which is necessary for the new role of the jaw in mastication and chewing. The teeth change from parts for grasping to elements for cutting and chewing. The forces involved in mastication are greater than those associated with prehension. The lower jaw is now a pair of dentary bones. (This contributes to the freeing of the articular and quadrate).

Food must now be manipulated in the mouth, mixed with saliva, positioned in the tooth rows. Thus on the labial side of the tooth row we see the evolution of fleshy lips and cheeks - a development to keep the food positioned between the teeth. Because food is now processed in the mouth for significant periods of time, this is added pressure for the evolution of the secondary palate. Changes occur in the tongue.

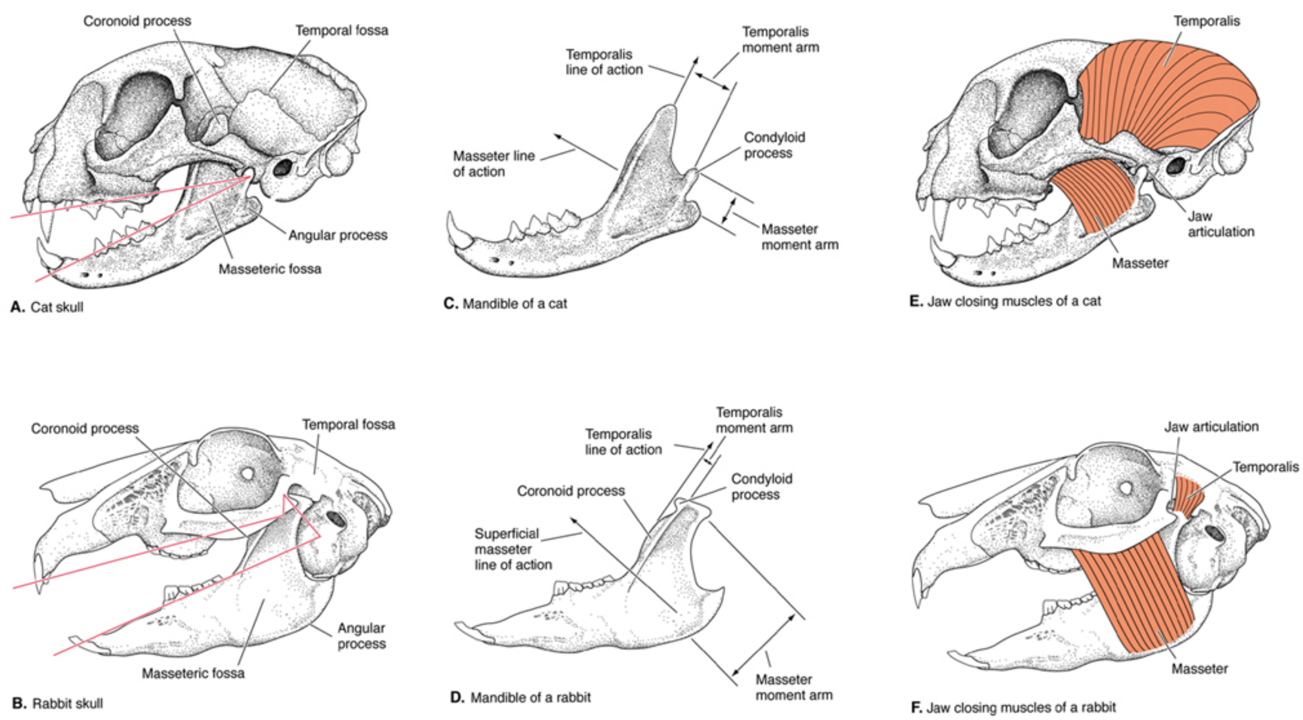
Hyoid Apparatus and Larynx

With the evolution of the secondary palate and the epiglottis and palato-pharyngeal folds we also see the evolution of the larynx. This is constructed to prevent problems during swallowing. The epiglottis arises to deflect food to either side of the glottal opening. Most of the cartilages of the larynx are derived from splanchnocranium, from parts of the other visceral arches. Thus, it would appear that the whole cranial evolution that accompanied the origin of mammals and which left its mark on almost every structure in the head, can be attributed to the mechanical requirements for mastication - a process that arose as a result of the ability to kill and/or manipulate food items prior to ingestion - a result of changes in limb structure and function. This has allowed adaptive radiation and the use of food resources unavailable to other vertebrates.



Homework Assignment

Jaw Mechanics of Carnivores versus Herbivores



How many of the differences in form that you see in this slide
Can you ascribe to differences in function?