

BIOLOGY 524 ADVANCED VERTEBRATE MORPHOLOGY -OSTEOLOGY-

SKULL – III SPLANCHNOCRANIUM

S. S. SUMIDA

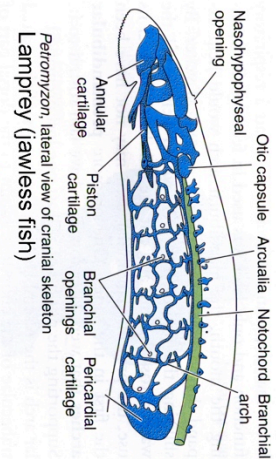
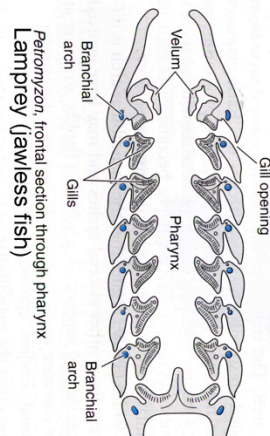
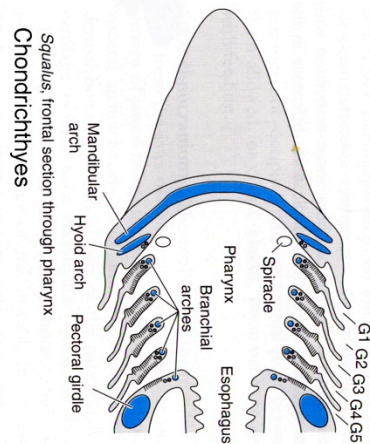
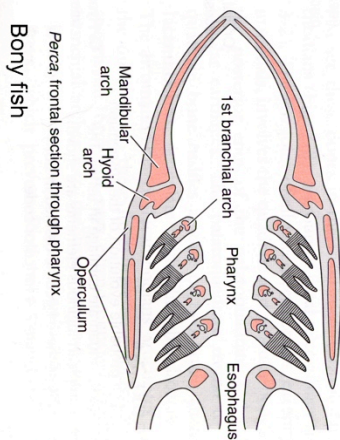
INTRODUCTION

RECALL:

The splanchnocranium (sometimes called the viscerocranium) is the phylogenetically most ancient part of the skull. It arose even before vertebrates themselves to support the pharyngeal gill slits of protochordates. Within the vertebrates, it supports gill structures or their evolutionary derivatives. The cartilagenous or bony components are derived from neural crest, and form endochondrally. Components of the upper and lower jaw are derived from this.

Gills

Gills of fishes are openings from the pharynx, through the body wall, to the outside of the body, allowing water to pass over the gills but leave the gut tube before heading to the remainder of the gut tube.



Embryology of the Splanchnocranium

All components of the vertebrate splanchnocranium form endochondrally from neural crest cells.

Notably, whereas the entire splanchnocranium is derived from neural crest and forms endochondrally, it is not the only part of the skeleton derived from neural crest (also the dermatocranium, which forms intramembranously), and it is not the only part of the skeleton that forms endochondrally (also almost all of the postcranial skeleton, and parts of the parts of the chondrocranium, which are derived from mesoderm).

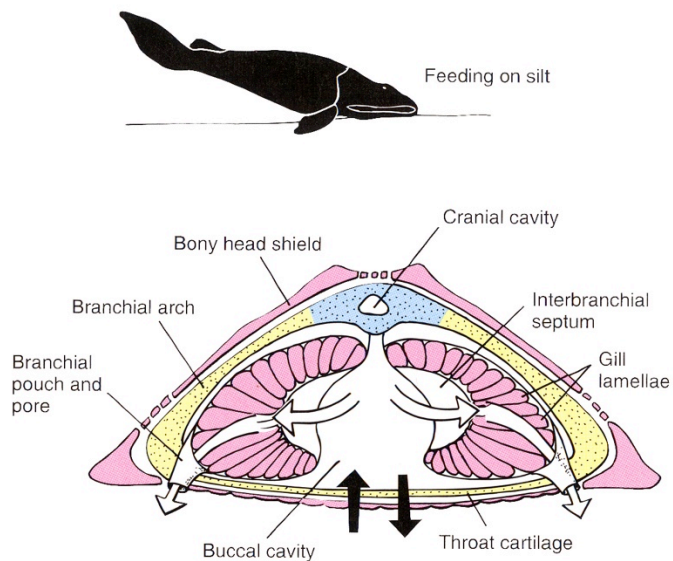
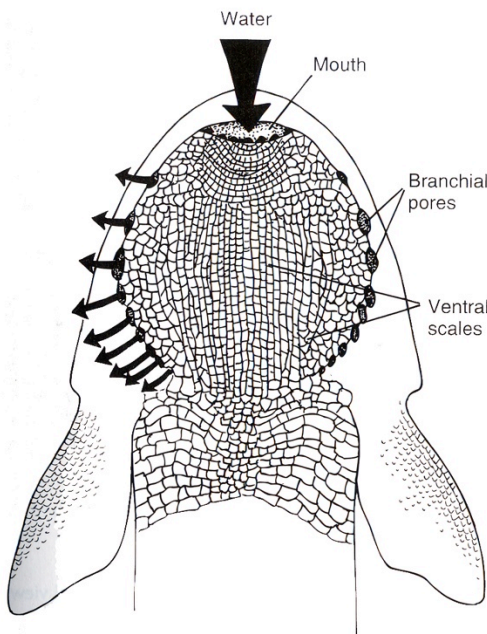
Primitive Splanchnocranium

The splanchnocranium is generally considered the most primitive part of the skull skeleton. The splanchnocranium is the skeleton of the gill structures, and gills, or gill-like structures are more broadly distributed amongst chordates, so the skeleton accompanying it presumably was in place at or near the origin of vertebrates.

BRIEF (PARTIAL) SURVEY OF SPLANCHNOCRANIUM OF JAWLESS VERTEBRATES

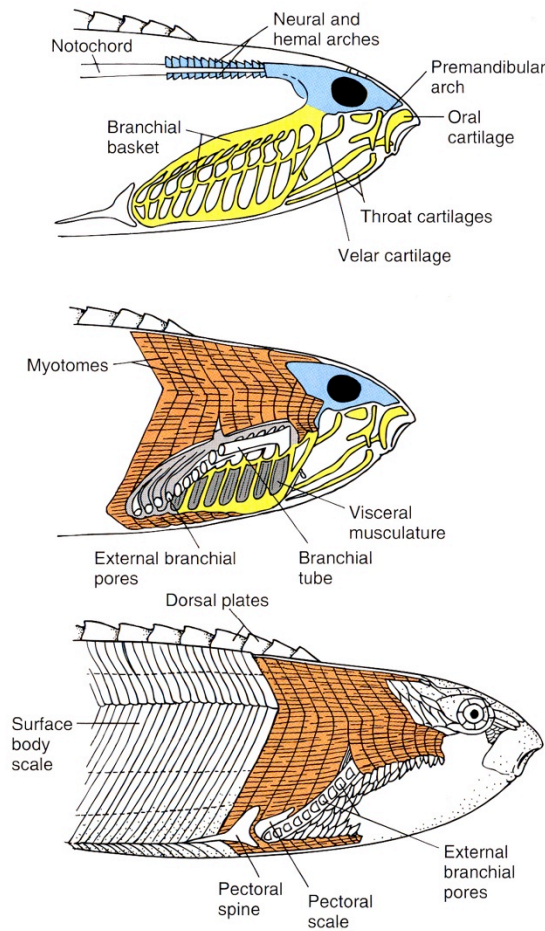
In the most primitive jawless vertebrates, the head region is dominated by the gill apparatus.

We are used to gnathostomes usually having five gill openings, rarely six or seven in some sharks. However some awless vertebrates had as many as a dozen or even more. Note below the numerous gill openings of the agnathan *Hemiclaspis* and how they dominate the mass of the head.



Below the heterostracan agnathan *Pterolepis* shows numerous gill openings.

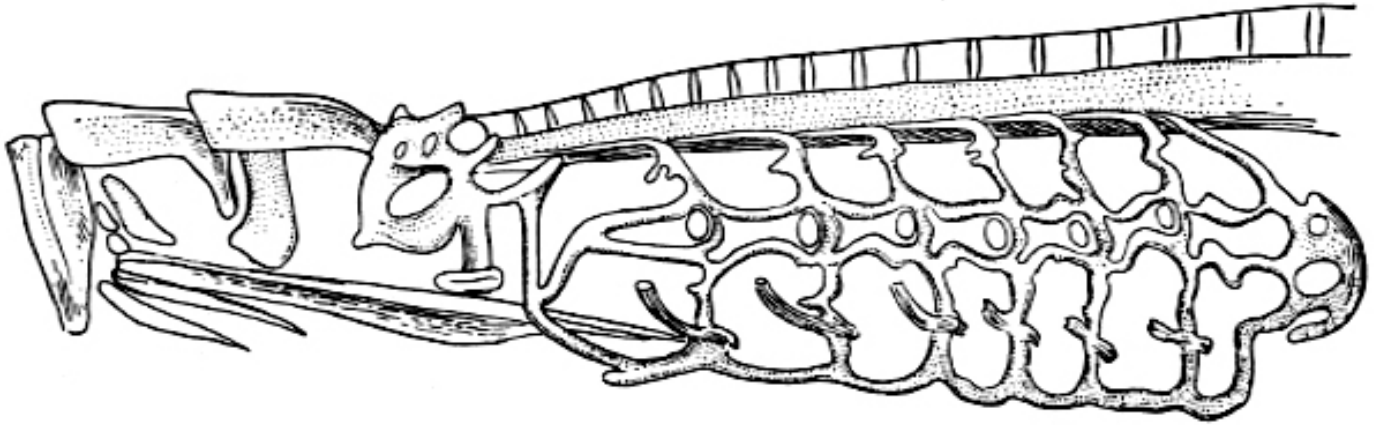
Also, note the well developed supporting skeletal structure. Individual components of the structure supporting the gill structures cannot be differentiated, so it is referred to as a **BANCHIAL BASKET**.



LIVING AGNATHANS

Only two groups of living agnathans remain, the hagfishes and lampreys. They bear little resemblance to extinct agnathans, but they do retain the simple branchial basket as seen above.

On the next page can be seen the branchial basket in the lamprey *Petromyzon*. It is a flexible cartilaginous structure that can compress and expand under the influence of branchial musculature to help the animal ventilate its gills.



In this course, we will be concerned primarily with the splanchnocranium of gnathostomes. It is generally accepted that the jaws are derived from primitively unmodified gill skeletal structures, or visceral arches.

The homologies of the visceral arches of gnathostomes is matter of some debate. There is little argument that they are homologous to one or more primitively unaltered visceral arches. The question is which one (or one)? Some authors suggest:

Jaw Origin Hypothesis 1:

There was an arch rostral to the one that became the jaws. It was subsequently lost, and is referred to as the premandibular arch. This is supported by the fact that part of the trigeminal nerve, the never of the jaw arch, or MANDIBULAR ARCH, has three major branches.. Most have two branches (one strictly sensory, the other sensory+motor). The trigeminal has an additional sensory branch reaching forward of the other two, and it is generally thought that this is the sensory branch of the old premandibular arch that was “captured” by the trigeminal.

Jaw Origin Hypothesis 2:

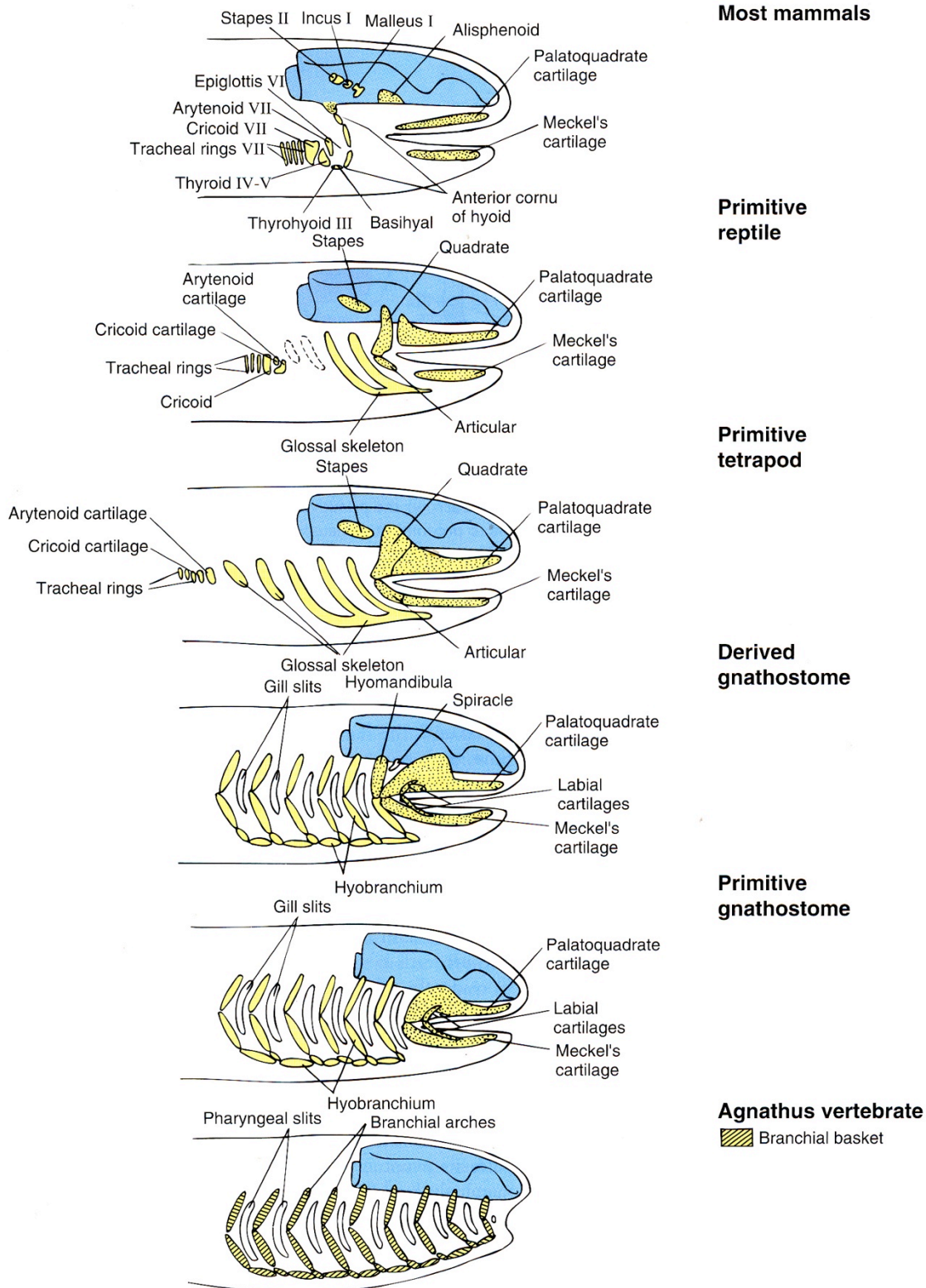
Some researchers suggest there were two premandibular arches. But, as the arches are long gone, it is impossible to test.

Jaw Origin Hypothesis 3:

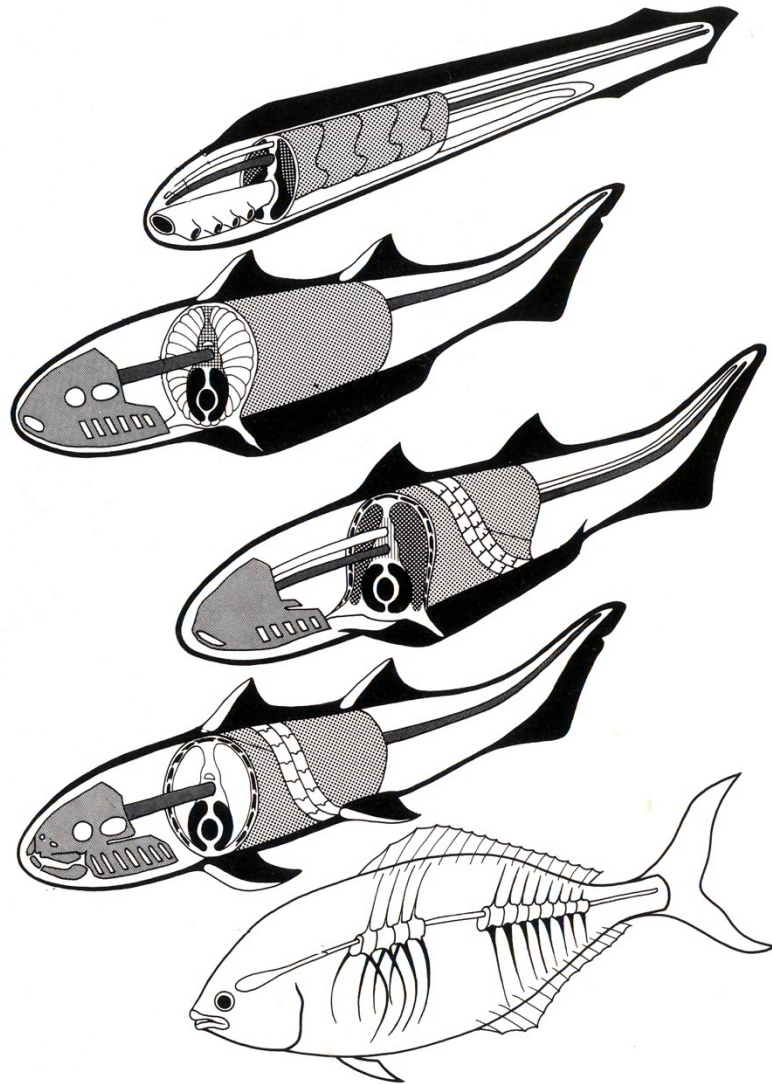
Some researchers suggest that not only was there a premandibular arch, but that there could have been another. This theory known as the COMPOSITE THEORY suggests that the resulting Mandibular arch as components of numerous adjacent arches incorporated.

In all of the above hypotheses, at least one premandibular arch is suggested. The additional branch of the trigeminal nerve is cited as support for this hypothesis. Additional, many would suggest that the paired trabeculae of the rostral underside of the braincase are homologous to premandibular visceral arch elements.

Immediately caudal to the mandibular arch, the next arch, known as the hyoid arch is also highly modified, in part to facilitate suspension of the jaws on the underside of the braincase.



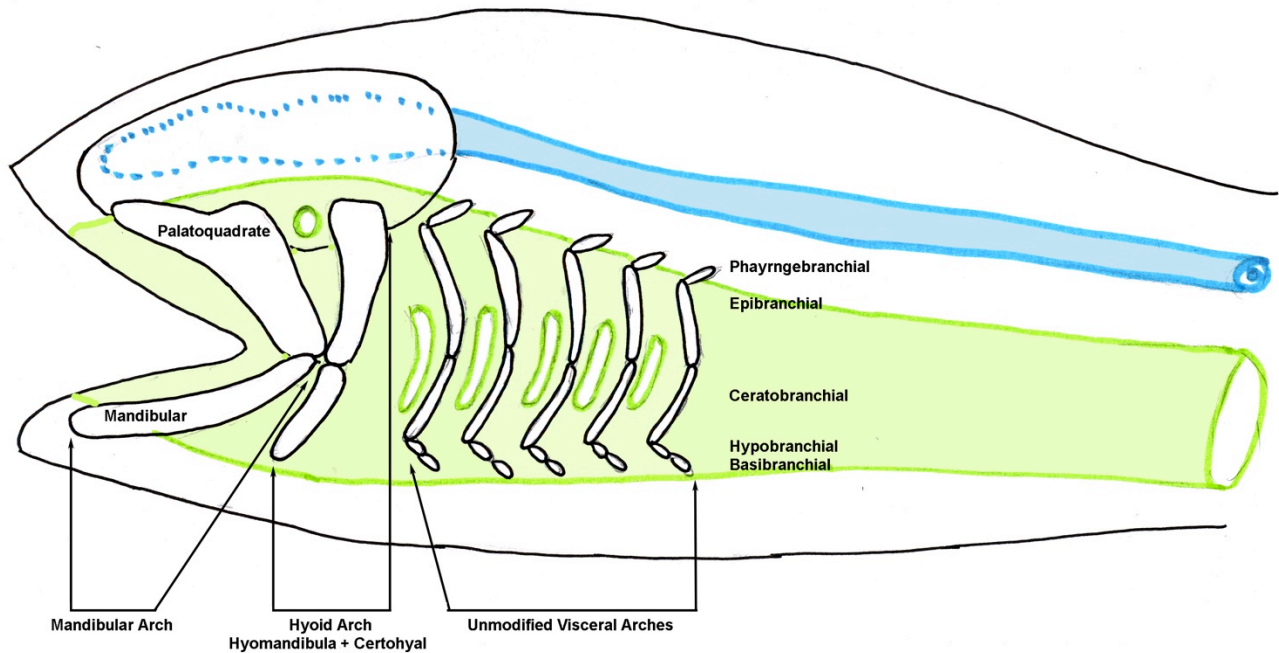
In the image below, a comparison of the Bauplans (“Body-plan” or “Body-organization”) from nonvertebrate chordates to jawless fishes, and ultimately to gnathostomes.



OVERVIEW OF ORGANIZATION OF THE SPLANCHNOCRANIUM IN FISHES

The condition in gnathostome fishes provides us our point of departure for the majority of this lecture, and completes the major components influencing the organization of the skull.

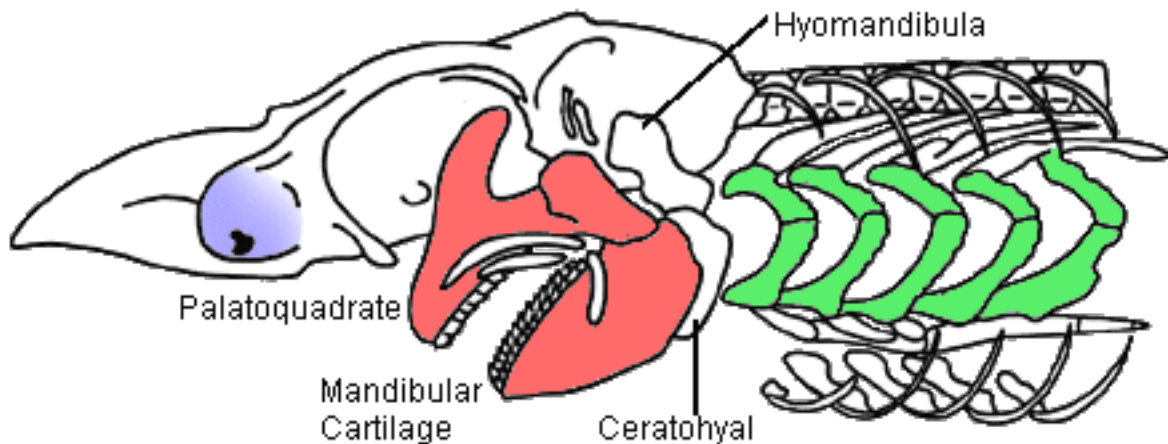
The vertebrate head is dominated by two great tubes: the dorsal hollow nerve tube, and the gut tube. The nerve tube’s influence on the skull derives from the protective function of the braincase and dermatocranial skull roof. The gut tube’s initial influence is due to the pharyngeal position of the gill sits, near to the head, and particularly the influence of the mandibular arch (jaws) and hyoid arch on skull structures.



The story of the splanchnocranium's influence on the skull is essentially that of the influence of the mandibular and hyoid arches. But before we do that, we need to look at the situation in fishes first.

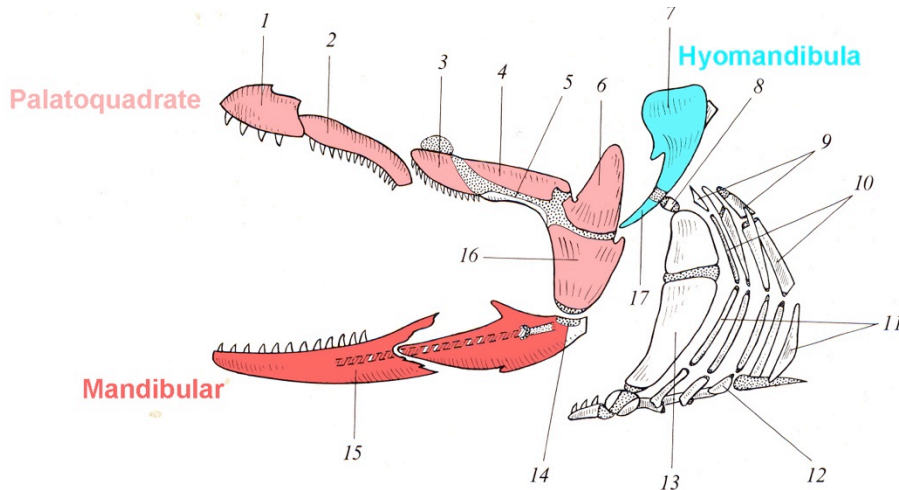
SPLANCHNOCRANIUM IN CHONDRICHTHYES

Cartilaginous fishes have no dermatocranium, and so their heads are dominated by the chondrocranium and the splanchnocranium. Elements of the splanchnocranium are essentially those of the illustration at the top of the page.



SPLANCHNOCRANIUM IN BONY FISHES

In bony fishes, the mandibular arch, hyoid arch, and unmodified visceral arches are similar to the illustration at the top of the page. Separate ossifications point out that neither the upper jaw nor the lower jaw are single elements. Note particularly the jaw joint here is between the **QUADRATE** of the upper jaw and **ARTICULAR** of the lower jaw.



Schema des isolierten Kiefer-Hyalapparates und des Kiemenkorbes eines Teleosteers.

(Nach GOODRICH, 1930)

1 Praemaxillare	5 Ectopterygoid	9 Pharyngobranchialia	14 Articulare
2 Maxillare	6 Metapterygoid	10 Epibranchialia	15 Dentale
3 Palatinum	7 Hyomandibulare	11 Keratobranchialia	16 Quadratum
4 Entopterygoid	8 Interhyale	12 Hypobranchiale	17 Symplecticum
		13 Keratohyale	

UPPER JAW ELEMENTS IN FISHES

Note the distal two most elements are the premaxilla and the maxilla. The neural crest components of these come to be covered by a sheath of intramembranous bone, and in more derived organisms they come to be incorporated into the lateral margin of the dorsal skull roof. (Those with * are later lost.)

- Premaxilla
- Maxilla
- Palatine
- Entopterygoid*
- Ectopterygoid
- Metapterygoid*
- Quadrate

LOWER JAW ELEMENTS

- Dentary
- Articular

Note particularly the jaw joint here is between the quadrate and articular elements of the upper and lower jaws respectively.

JAW SUSPENSION IN FISHES

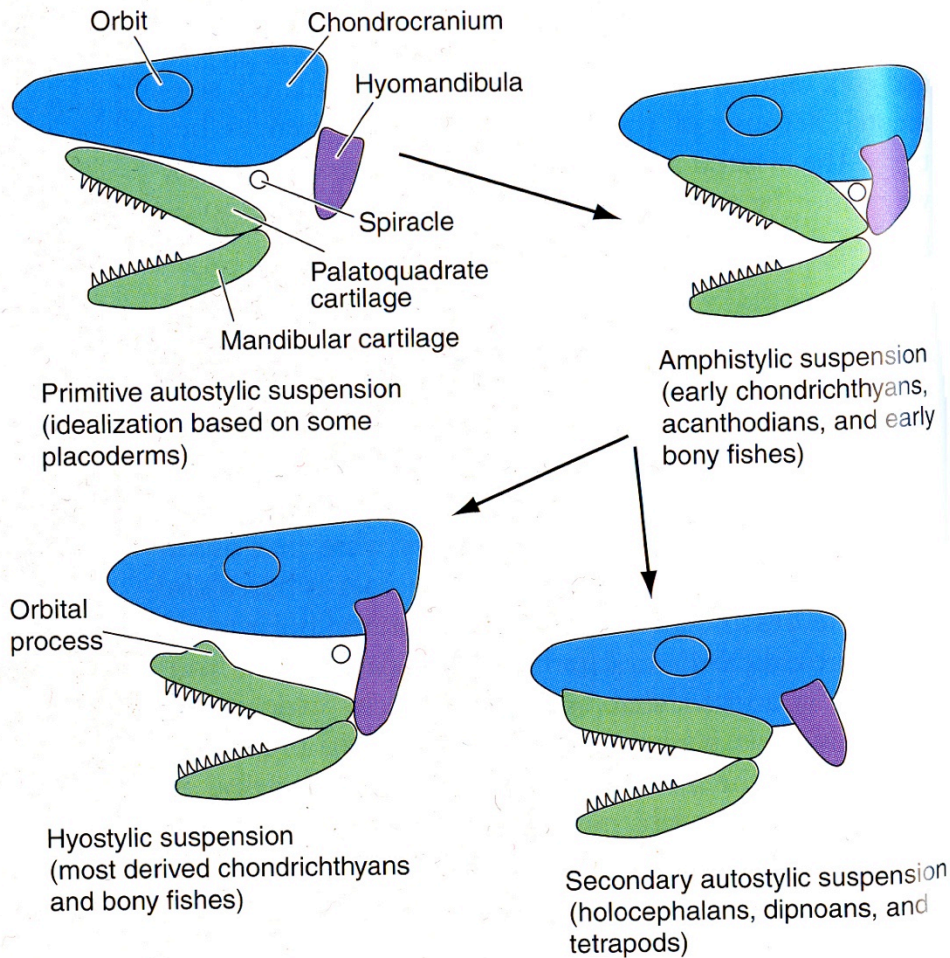
As mentioned earlier, the hyomandibula comes to play an important role in attaching the mandibular arch to the braincase. There are numerous types and styles of jaw suspension, each with a characteristic name and morphology.

AUTOSTYLIC JAW SUSPENSION: Palatoquadrate articulates with the underside of the skull. This is probably the original condition for the earliest gnathostomes.

AMPHISTYLIC JAW SUSPENSION: Upper jaw is suspended by both articulation with braincase and indirectly via hyomandibula.

HYOSTYLIC JAW SUSPENSION: Jaws suspended by the hyoid arch only.

(SECONDARY) AUTOSTYLIC JAW SUSPENSION: Palatoquadrate (again) articulates with the underside of the skull. An autostylic condition found in later groups.



THE LOWER JAW IN FISHES (AND OTHERS)

The lower jaw in gnathostomes is a multi-element structure. The largest of the elements can be seen both laterally (externally, labially) and medially (internally, lingually). Directional Terminology along the tooth row cannot be simply cranially/rostrally versus caudally, as the jaw curves medially at its symphysis. So, proper terms are mesial (toward the symphysis) and distal.

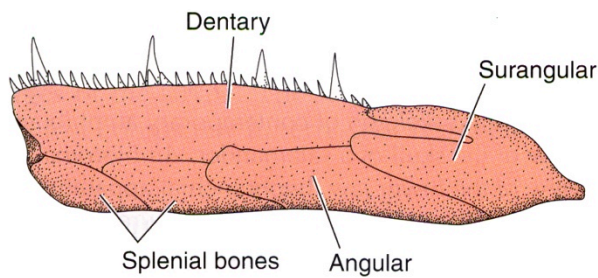
The story of the lower jaw is predominantly one of gradual loss or reduction in size of elements.

LATERALLY VISIBLE ELEMENTS OF LOWER JAW FROM MESIAL TO DISTAL:

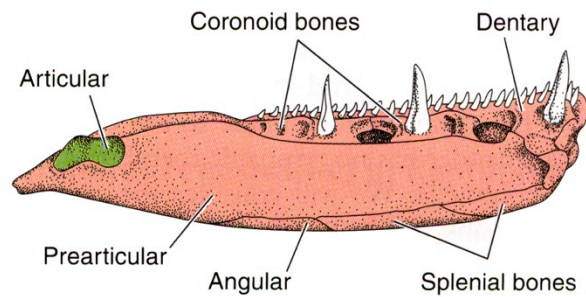
- Dentary (tooth bearing)
- Splenial(s) (When two are present, sometimes referred to as splenial and postsplenial)
- Angular
- Surangular

MEDIAALLY VISIBLE ELEMENTS OF LOWER JAW FROM MESIAL TO DISTAL:

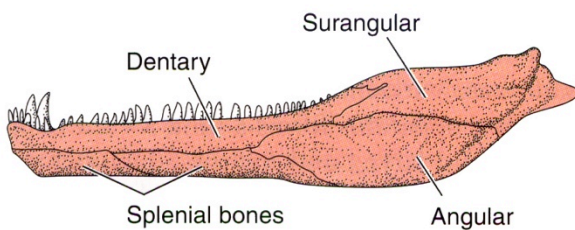
- Dentary (tooth bearing)
- Coronoid(s) (tooth/fang bearing)
- Prearticular
- Articular
- (Splenial(s) often visible at ventral margin)



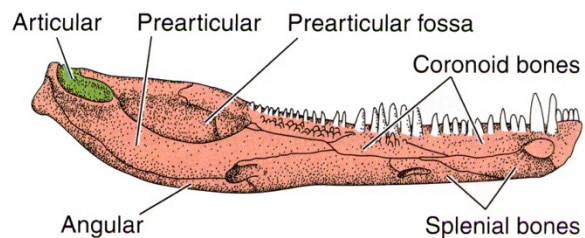
Choanate fish, lateral view



Choanate fish, medial view



Basal tetrapod, lateral view



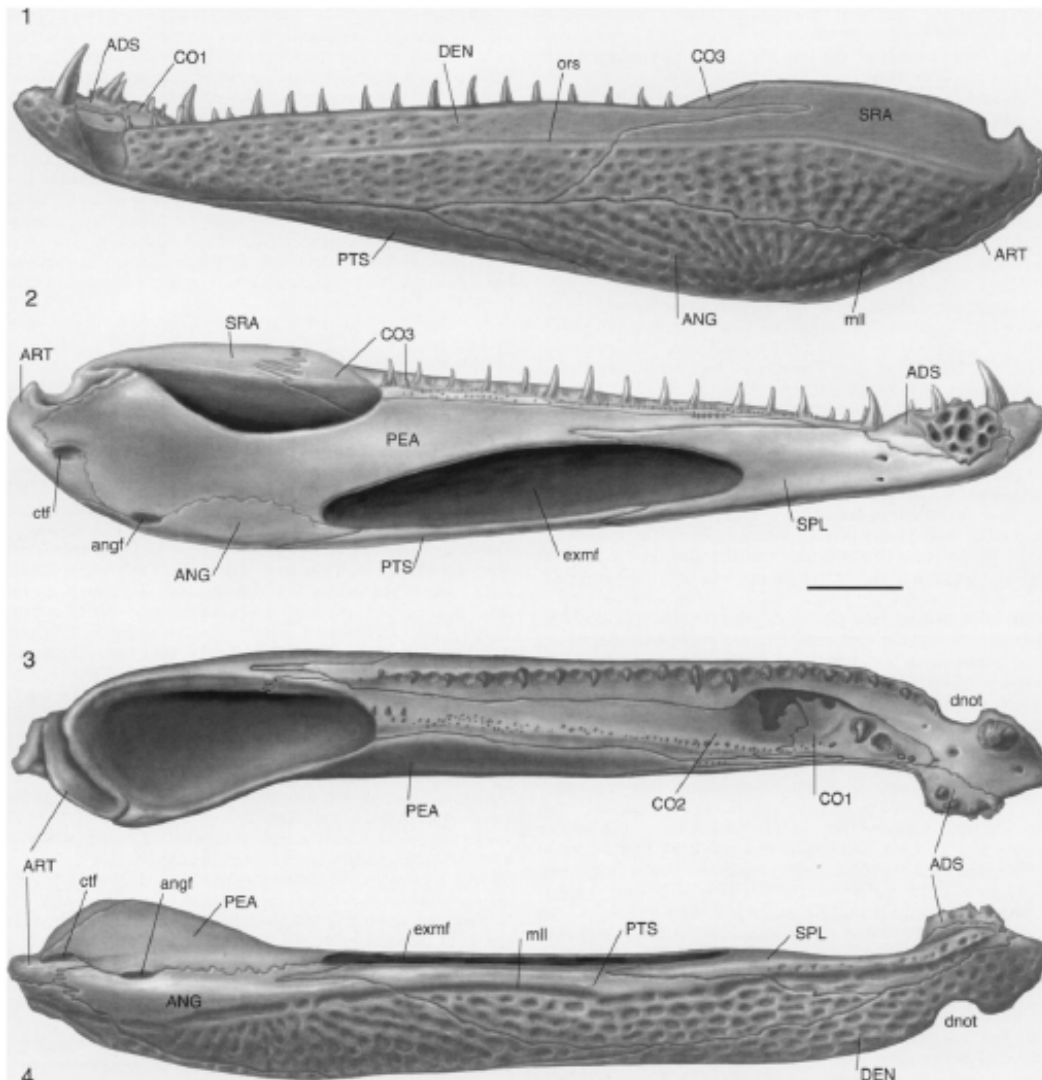
Basal tetrapod, medial view

SPLANCHNOCRANIUM IN BASAL TETRAPODS

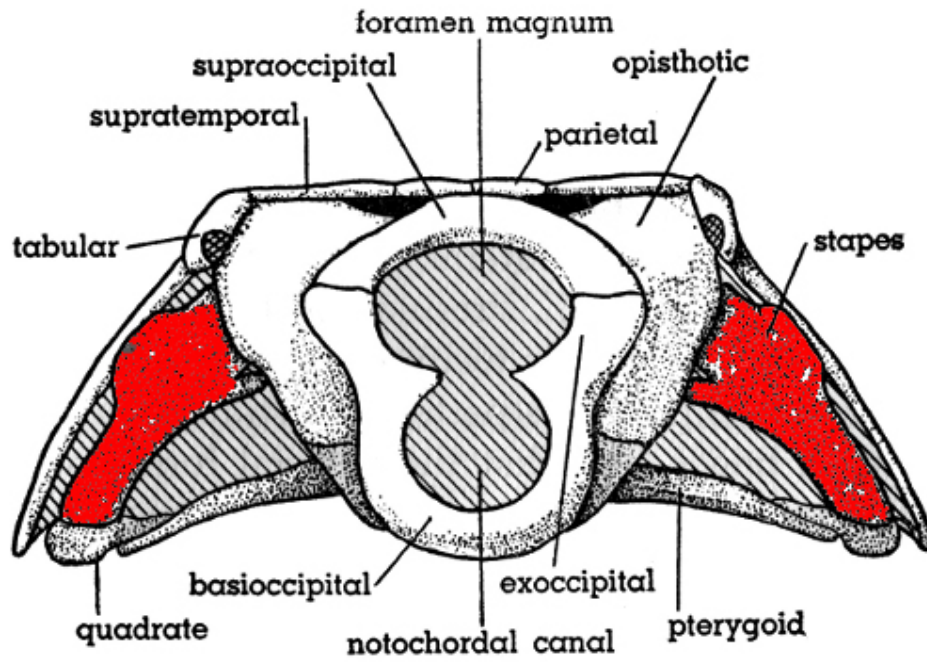
MANDIBULAR ARCH IN BASAL TETRAPODS: Ossifications of the upper jaw contribute to the skull. The epipterygoid is pieced out of the middle of the palatoquadrate cartilage. Mesially, the quadrate bone that has been incorporated into the posterolateral corner of the skull table provides the articulation with the lower jaw. This is the **QUADRATE-ARTICULAR JAW JOINT**. This jaw joint is retained through to modern extant amphibians.

The embryonic cartilage of the lower jaw is also known as **MECKEL'S CARTILAGE**. Remember, the distal-most part of the lower jaw ossifies as the articular bone - the lower jaw contribution to the quadrate-articular jaw joint. The lower jaw carries the full compliment of elements. The dentary is the primary, though not sole tooth-bearing bone. Notably there are numerous elements in addition to the dentary, including the full compliment of splenials, coronoids, angular, surangular, prearticular, articular.

On the medial surface, one or more large Meckalian foramina are sometimes present. Below is an illustration of the basal tetrapod *Greererpeton*.



HYOID ARCH IN BASAL TETRAPODS: In basal tetrapods, the hyomandibula remains relatively large. Now known as the **STAPES**, it acts as a brace between the otic capsule of the braincase, and the inner surface of the dermal skull roof, inserting into a pit in the quadrate bone. Below note the stapes in red. Other components of the branchial skeleton remain. Presumably it was well developed to support gills in larvae, and it often remains as a robust anchor for the tongue skeleton.



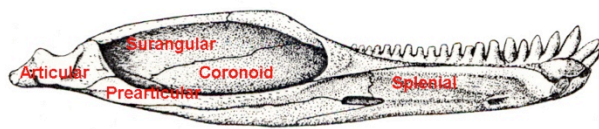
SPLANCHNOCRANIUM IN BASAL AMNIOTA

MANDIBULAR ARCH IN BASAL AMNIOTES: The condition of the jaw elements in basal amniotes is not significantly different from that of basal tetrapods. Chief differences include:

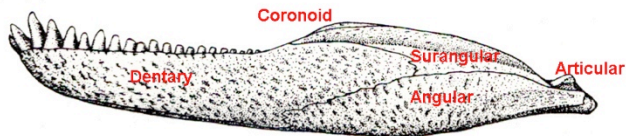
- Reduction to single splenial.
- Reduction to single coronoid.
- Development of a **RETROARTICULAR PROCESS**, a caudally directed process of the elements of the distal end of the jaw to provide greater attachment for jaw opening muscles.

HYOID ARCH IN BASAL AMNIOTES: The stapes remains as a brace between the otic capsule and the cheek region of the dermatocranium. Note the stapes is usually easy to identify due to the presence of the stapedial foramen.

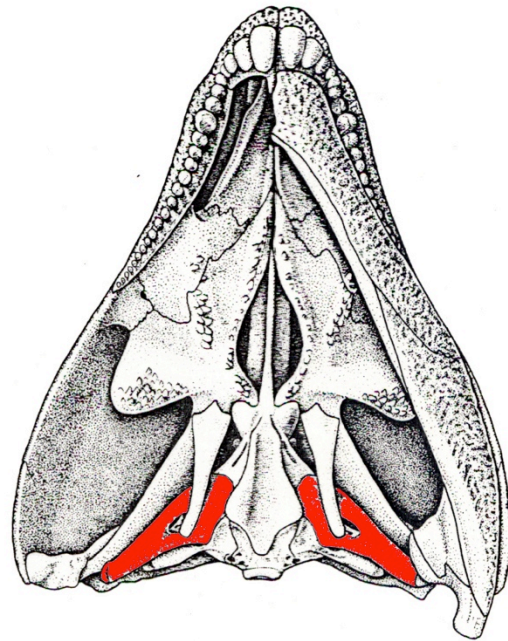
Lower Jaw and Stapes (in red) of the Lower Permian basal reptile *Captorhinus*.



Internal (lingual) view



External (labial) view



JAW DIFFERENCES IN SELECTED REPTILIAN GROUPS:

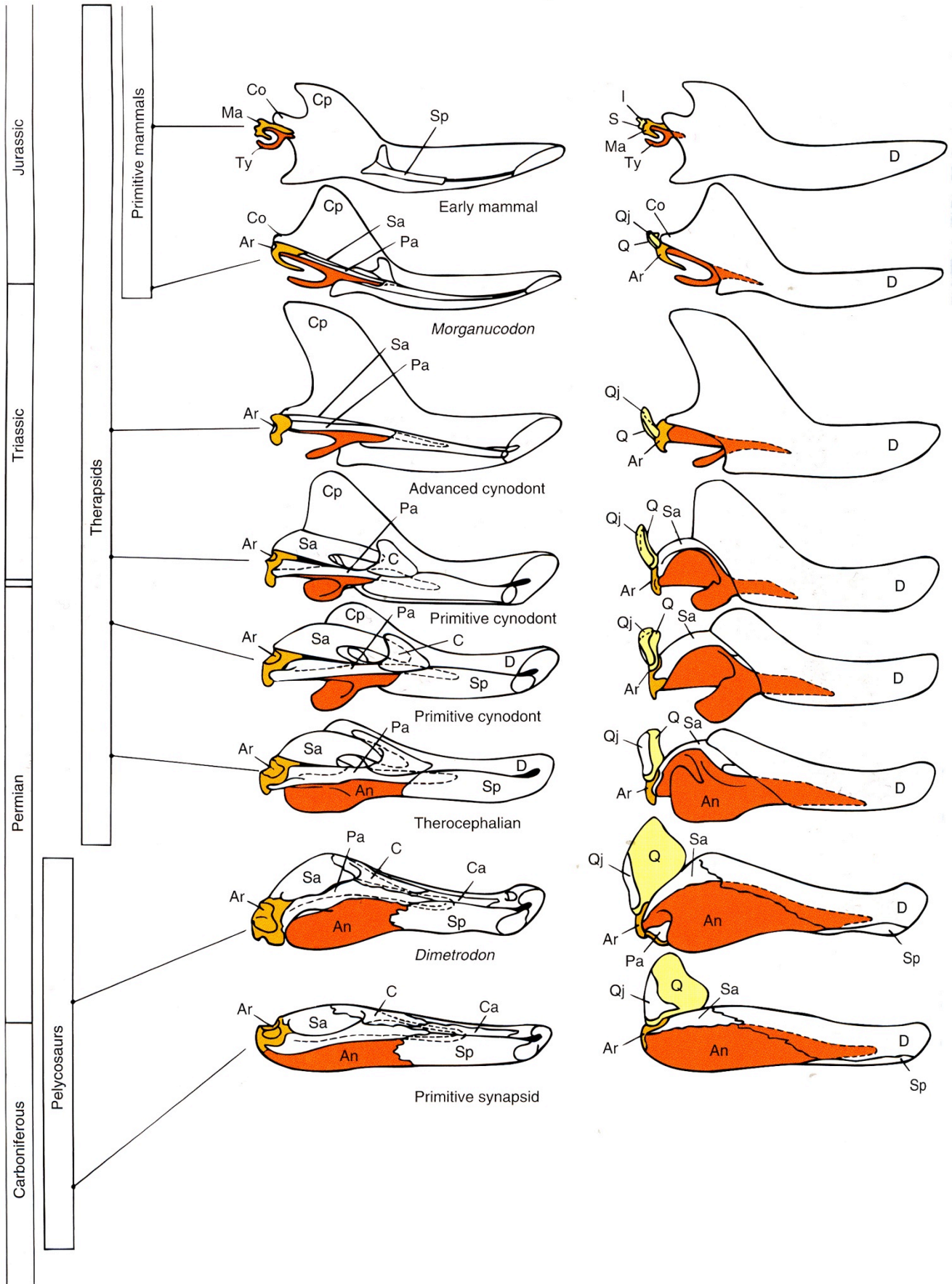
- In some herbivorous dinosaurs, the Cerapoda (which includes Ceratopsians such as *Triceratops* and iguanodonts), there is an additional bone forward of the dentary, the **PREDENTARY**. It is edentulous.
- There is extreme reduction of jaw elements in snakes, and the lower jaws do not fuse at their symphysis to allow passage of prey.
- Many reptiles have kinetic skulls to allow greater opening of the jaw, including a **NASOFRONTAL HINGE** in birds.

SPLANCHNOCRANIAL EVOLUTION IN SYNAPSIDA

The story of the transformation of the elements of the mandibular and hyoid components in the lineage leading toward mammals is perhaps one of the best known and most famous of evolutionary transformations taught in vertebrate biology. It is, briefly, the story of:

- Consolidation of palatoquadrate elements into the side-wall of the braincase.
- Reduction of post-dentary elements of the lower jaw.
- Change from the quadrate-articular jaw joint to the **DENTARY-SQUAMOSAL JAW JOINT**.
- Transformation of mandibular and hyoid arch elements into middle ear elements.

In the illustration following the progression from basal synapsid to a true mammal is shown.



In the previous illustration note:

[Left – internal/lingual view; Right – external/labial view]

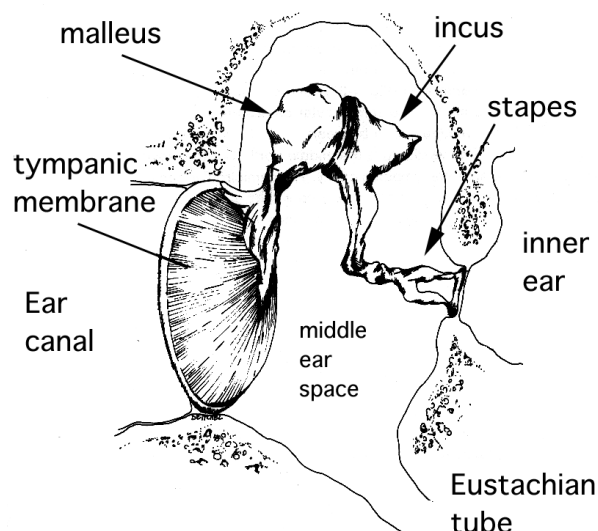
The dentary gradually becomes the dominant, then only bone of the lower jaw.

- As it does so, it becomes (by default) the only tooth bearing bone.
- The dentary develops a large, dorsally directed **CORONOID PROCESS**, which will take insertion of the **TEMPORALIS** muscle.
- As this occurs, there is a progressive and proportional reduction in the size of the postdentary bones.
- The splenial is eventually lost.
- The coronoid is eventually lost
- The surangular is eventually lost.
- The prearticular is eventually lost.
- The quadrate of the upper jaw, comes to be closely associated with the articular of the lower jaw – this is straight-forward, as they had already articulated as the quadrate-articular jaw joint of more primitive taxa.

And, the following key changes take place:

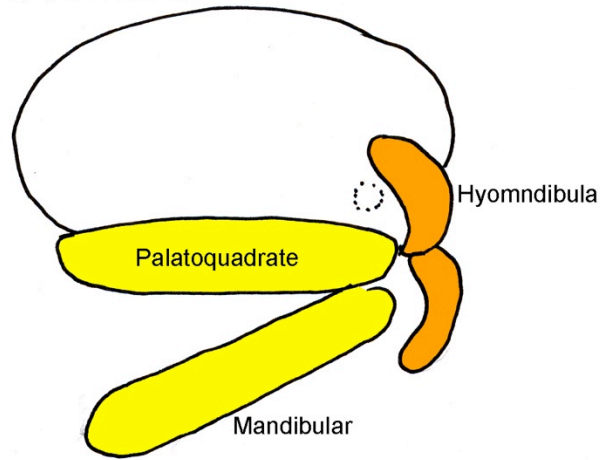
1. The angular bone does not disappear, but rather is reduced in size, detaches from the back of the jaw, attaches to the otic capsule of the skull, and becomes the circular rim of the **EXTERNAL AUDITORY MEATUS** of the temporal bone.
2. The articular – is also reduced in size. It remains lodged in the membrane that stretches across the articular rim of the external auditory meatus (**TYMPANIC MEMBRANE**), becoming the **MALLEUS** bone of the middle ear.
3. The quadrate is also reduced in size. It remains in articulation with the old quadrate (now the malleus), as the **INCUS BONE**.
4. Now that the braincase has stabilized and strengthened due to the fusion of the alisphenoid and parietal, the stapes need no longer function as a brace – so it too is reduced in size. The stapes is already in contact with the otic capsule. It comes to articulate with the incus.

Thus, the angular contributes to the temporal bone, and the articular-quadrate-hyomandibular/stapes series become the **MALLEUS-INCUS-STAPES** linkage, or **MIDDLE EAR OSSICLES**.

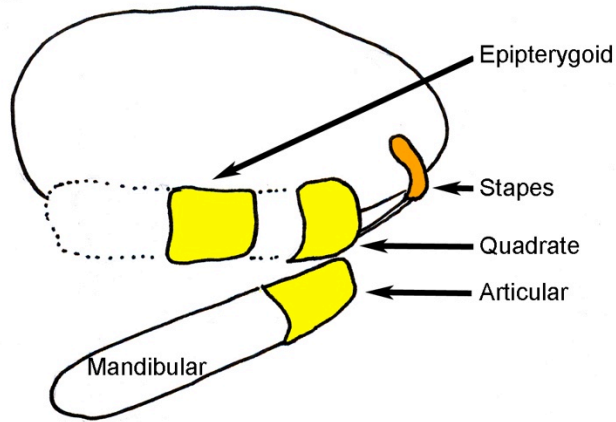


In the following simply drawn representations of vertebrate skulls, track the fate of selected elements of the mandibular and hyoid arches.

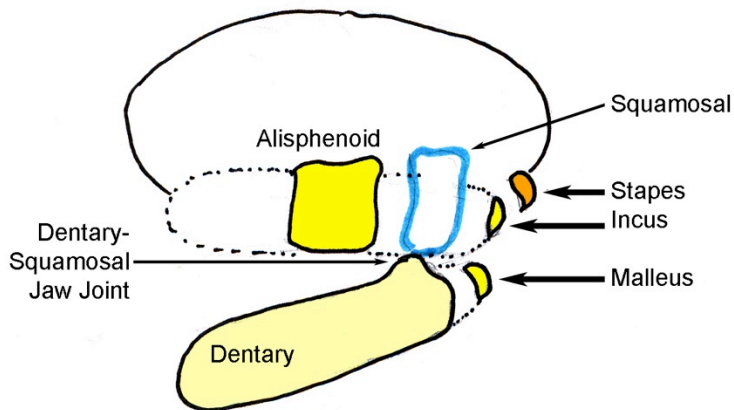
Primitive condition



Tetrapod



Mammal



COROLLARY: COMPOSITE BONES OF THE MAMMALIAN SKULL

The bone most clearly explained by this discussion is the **TEMPORAL BONE**, which has the following components:

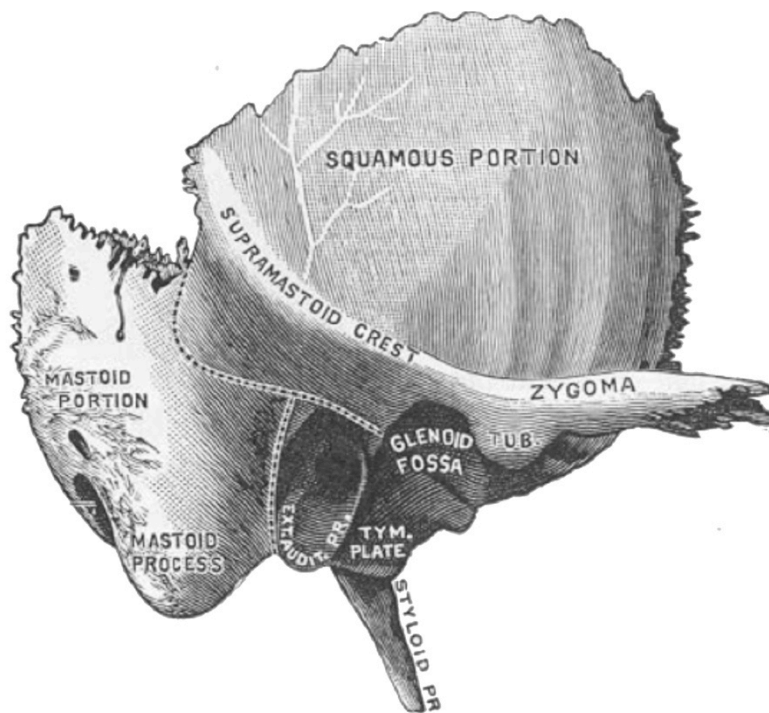
PETROUS portion – otic capsule of the chondrocranium

SQUAMOUS portion – squamosal of dermatocranium

ZYGOMATIC PROCESS – squamosal of dermatocranium

ANGULAR RIM of external auditory meatus – angular of mandibular arch of splanchnocranium

STYLOID PROCESS – hyoid arch



Other composite bones include the

OCCIPITAL BONE:

OCCIPITAL portion – supraoccipital, exoccipitals, basioccipital of chondrocranium.

SQUAMOUS portion – postparietals of dermatocranium

Note the alisphenoid is in most mammals a separate ossification.

SPHENOID BONE:

GREATER WING (WHEN FUSED) – alisphenoid (= epipterygoid) of splanchnocranium

BASISPHENOID (including sella turcica and dorsum sellae) – basisphenoid of chondrocranium

PTERYGOID WINGS – pterygoids of palatal dermatocranium

LESSER WINGS – optic capsule of the chondrocranium

Finally, following is a summary of mandibular and hyoid arch contributions to the human skull:

