BIOLOGY 524
ADVANCED VERTEBRTE MORPHOLOGY
-OSTEOLOGY-

SKULL – I
BRAINCASE/CHONDROCRANIUM

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PREFACE
Terms You Should [already] understand

- Ectoderm
- Endoderm
- Mesoderm
- Neural Crest
- Endochondral
- Intramembranous
- Dorsal hollow Nerve cord
- Notochord
- Cartilage
- Bone

INTRODUCTION

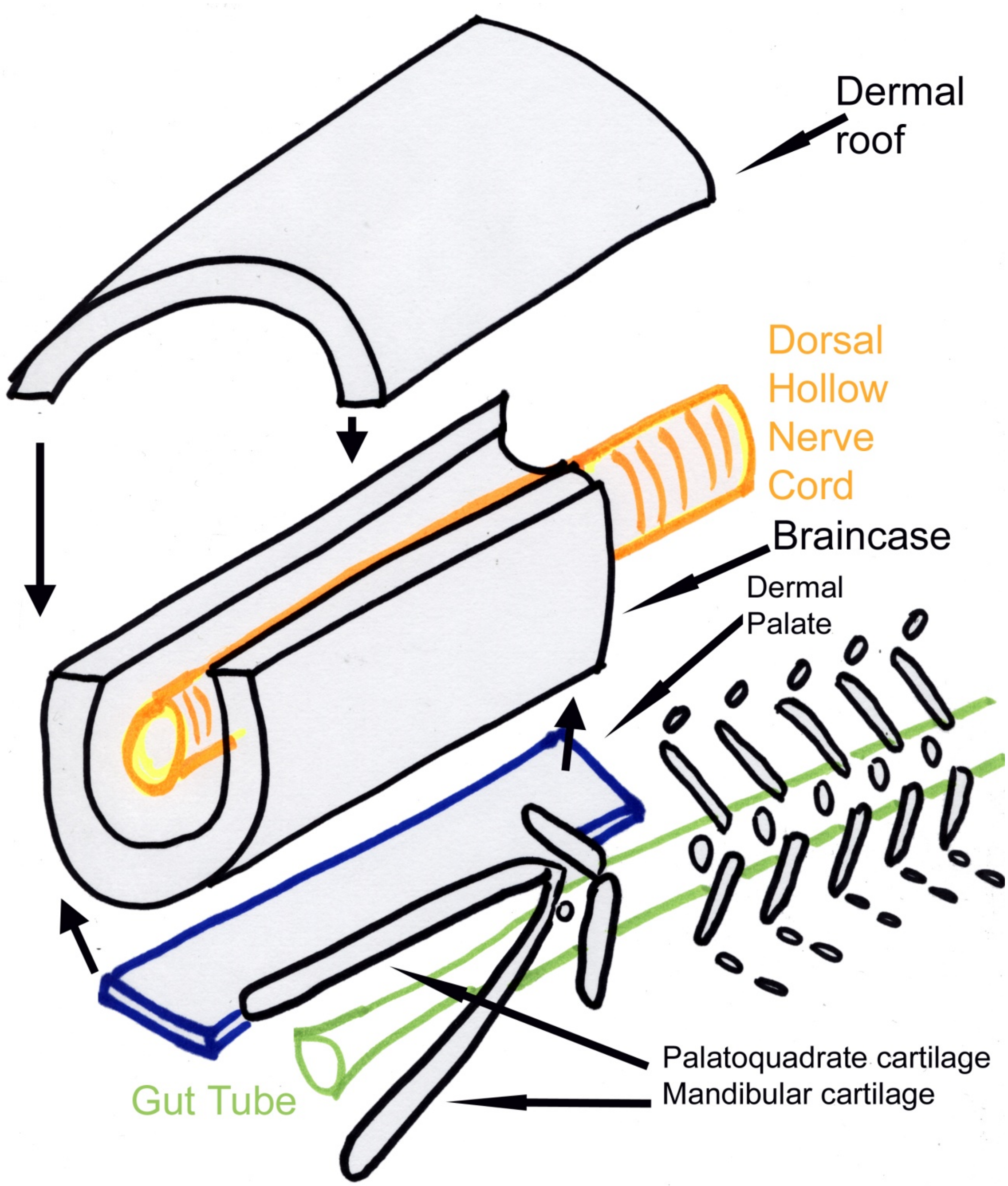
The vertebrate skull is a complex, composite structure formed from three distinct parts. Each of the parts has a distinct phylogenetic origin, and each part has (predominantly) characteristic combination of mode of formation (intramembranous or endochondral) and embryological derivation (mesoderm + neural crest, or just neural crest)

SPLANCHNOCRANIUM – 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.

CHONDROCRANIUM – The chondrocranium is a cradle that supports the underside of the brain itself. Its components form endochondrally, and can be derived from either mesoderm or neural crest. The chondrocranium is derived from multiple individual structures that fuse to become this cradle. Not all components ossify, with some remaining as cartilage.

DERMATOCRANIUM – The dermatocranium is slightly later development that makes up the out casing of the skull. It protects the brain above, from below, and protects the entire braincase from below as the plate.

A diagrammatic representation of the major parts of the skull of a gnathostome (jawed vertebrate) are shown following with their topographic relationships relative to each other and the two major tubes of the head: the nerve tube and the gut tube. (Please note, the colors of the braincase components here have no particular significance.)



CHONDROCRANIUM

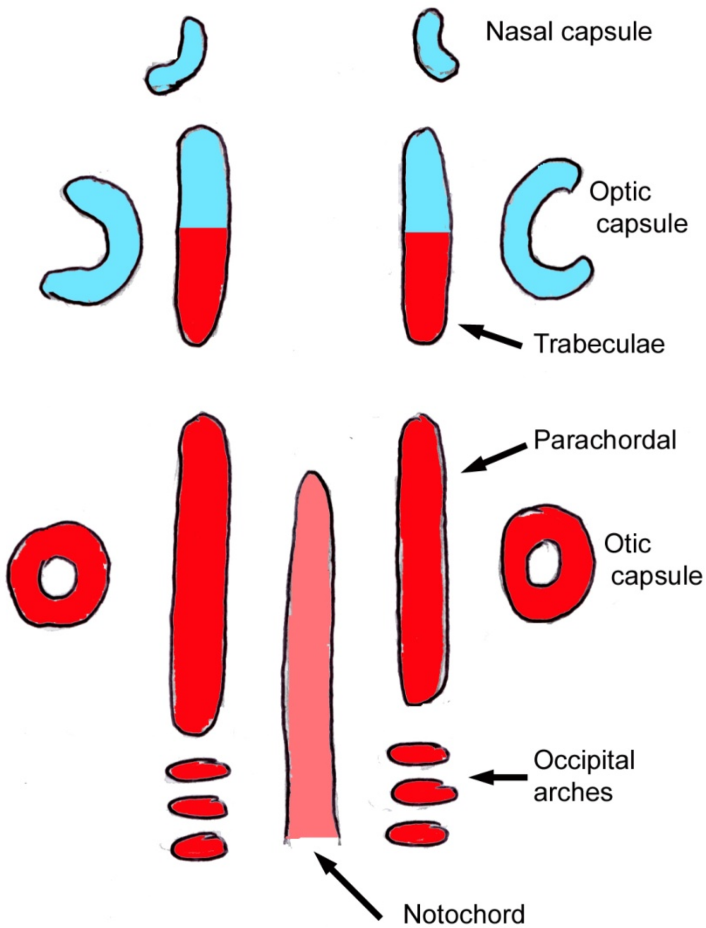
Embryology of the Chondrocranium

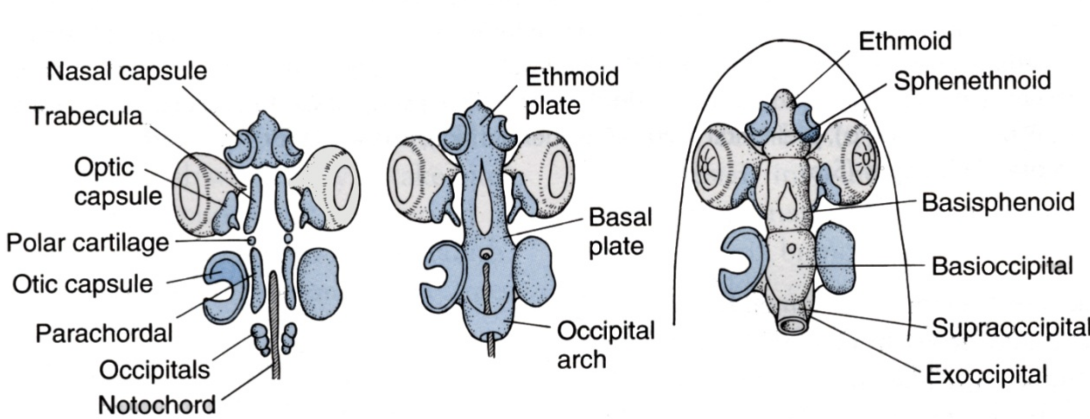
The developing chondrocranium is composed of a series of cartilages that lie cranial to the vertebral column, ventral to the dorsal hollow nerve cord, and just lateral to the midline axis defined by the notochord.

From rostral (nose-ward) to caudal these are the trabeculae, parachordal cartilages (named for their position next to the notochord), and a series of occipital arches derived from the sklerotome of the anteriormost somites. In addition to these are the paired, right and left cartilages that support major sensory organs – the nasal capsules, optic capsules, and otic capsules.

A summary of these structures follows:

Embryonic Braincase Structure	Embryonic derivation	Adult structure
Nasal capsule	Neural crest	Ethmoid (in part)
Trabeculae		
Anterior trabeculae	Neural crest	Ethmoid in part; anterior part of sphenethmoid
Posterior trabeculae	Mesoderm	Basisphenoid
Optic capsule	Neural crest	
Parachordal cartilage	Mesoderm	Basioccipital
Otic capsule	Mesoderm	Otic capsule and part of basioccipital
Occipital arches	Mesoderm	Basioccipital in part; paired exooccipitals; supraoccipital


Nasal capsule
Optic
capsule
Trabeculae
Parachordal
Otic
capsule
Occipital
arches
Notochord


Nasal capsule
Trabecula
Optic
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Polar cartilage
Otic capsule
Parachordal
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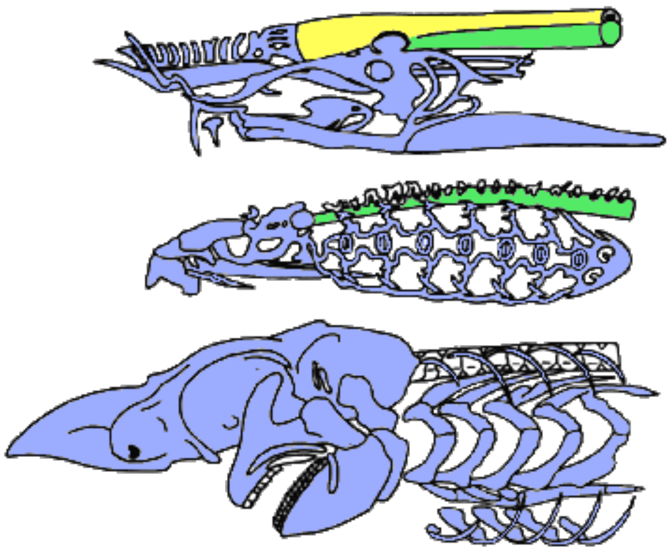
Notochord
Ethmoid
plate
Basal
plate
Occipital
arch
Ethmoid
Sphenethnoid
Basisphenoid
Basioccipital
Supraoccipital
Exoccipital

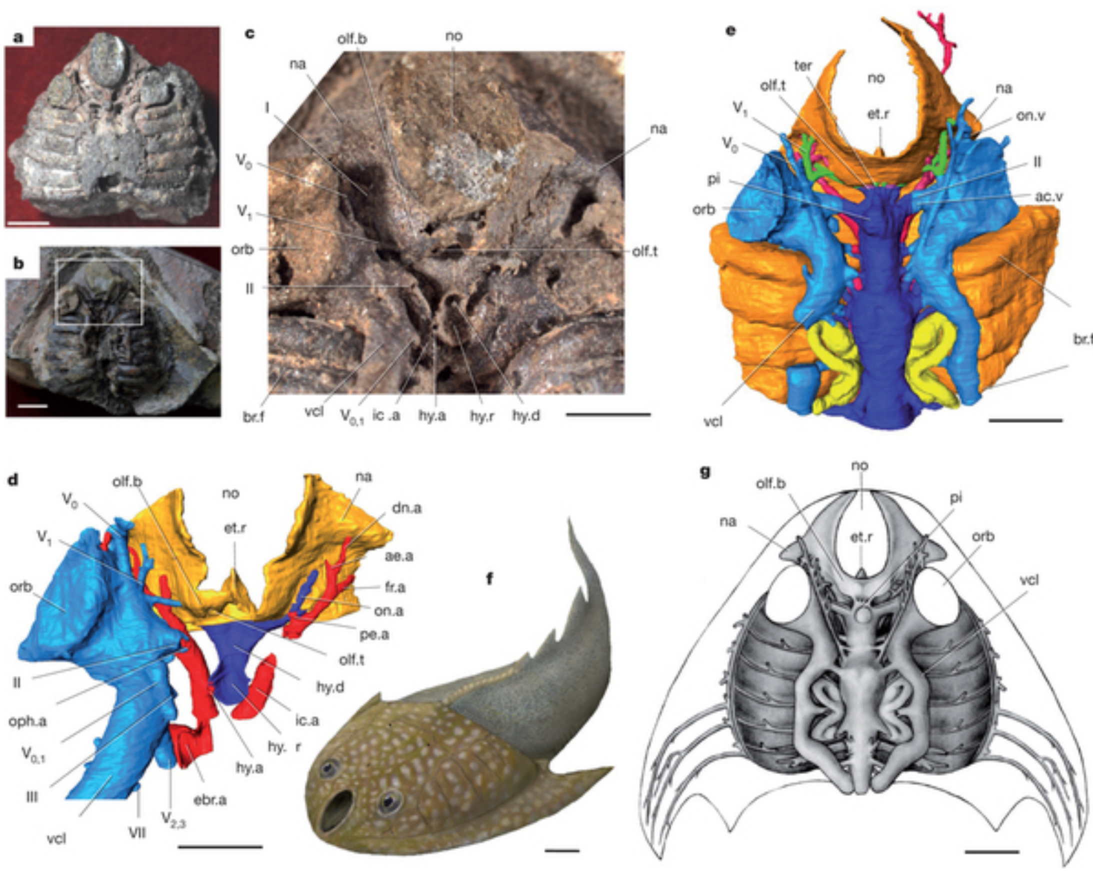
DIVERSITY OF BRAINCASE STRUCTURE



AGNATHANS:

The skulls of jawless fishes are – to be blunt – fairly minimal. Above, the skull of a hagfishes consists of cartilaginous bars (blue), but the brain is mostly surrounded by a fibrous sheath (yellow) underlain by the notochord (green). The skull of a lamprey (middle) has a more elaborate braincase. Behind it is a large "branchial basket" surrounding the gills. In the gnathostomes (bottom example, a shark), the braincase is generally closed.

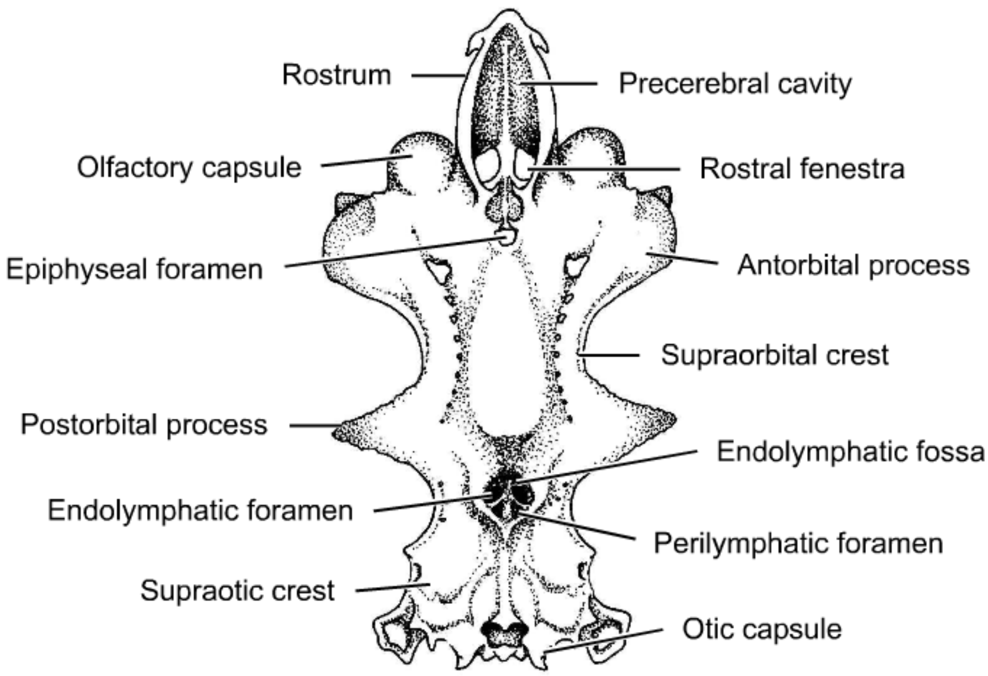
Notably, the jawless fishes illustrated above are the relics of a once much more diverse group of organisms. The extinct bony jawless fishes, often known as “agnathans” often had all their cranial structures covered by an elaborate coating of dermal bone. This has allowed vertebrate paleontologists, most notably Erik Jarvik to examine them in great detail. By thin sectioning them, and reconstructing the slices, extraordinarily detailed views of jawless fish braincases have been produced.



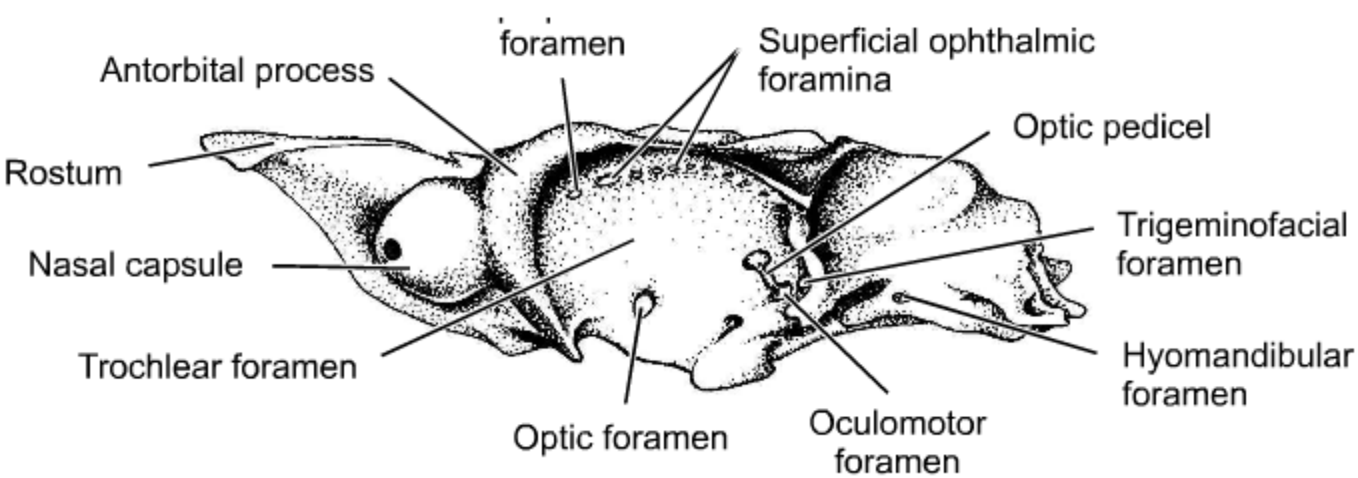
GNATHOSTOMES

The shark is often used as a classic example of a gnathostome, but their braincases are a pain in the ass. All of the embryonic components fuse into a single cartilaginous structures with not sutural distinctions. Therefore, one can only name regions and foramina.

Dorsal view:

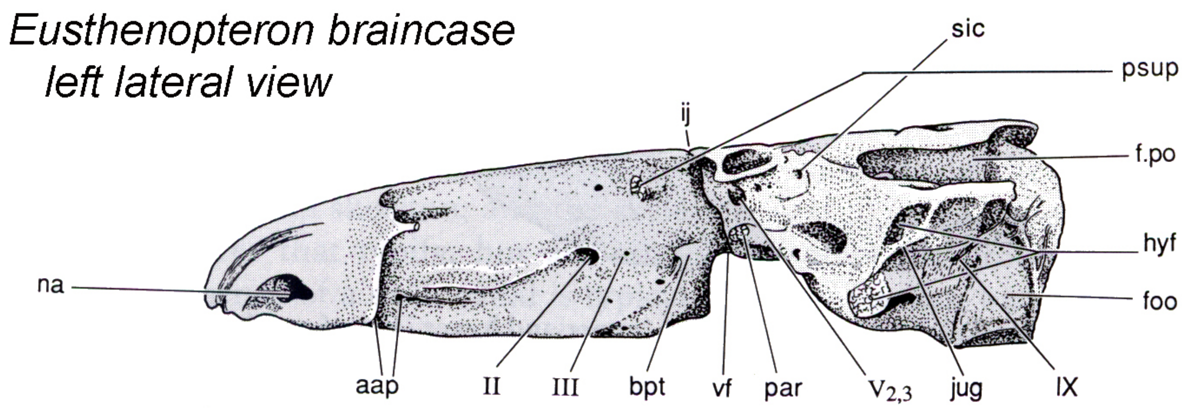


Lateral View:



BONY FISHES

Following is an illustration of the chondrocranium of a crossopterygian fish, then one of a basal tetrapod (often called "labyrinthodont amphibians" because the infolded ridges of their teeth were called "labyrinthine). These are amongst the most useful of the images we have because we can work forward and backward from these.



Note that in the crossopterygian there is an intracranial joint(!) (Here labeled "ij". The sphenethmoid region could actually move on the otico-occipital region. Note particularly the structure labeled "bpt". This is the basipterygoid process. It is at this point that the braincase contacts/articulates with the palatal structures. Note also that it is virtually immediately ventral to the intracranial joint. Crossopterygian fishes had very mobile heads!

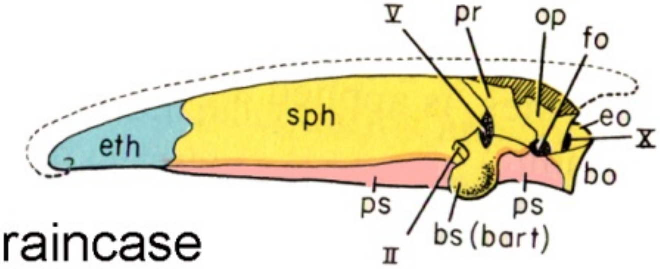
Among other bony fishes, the ethmoid region frequently remains unossified as cartilage.

TETRAPODS

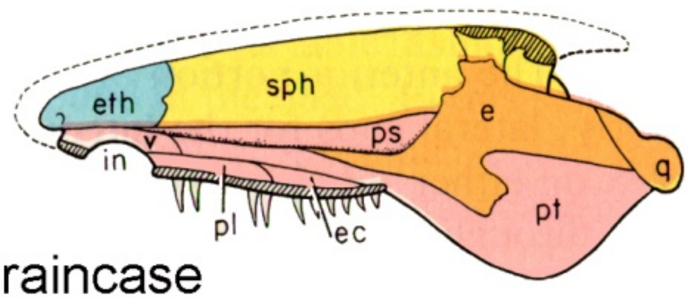
Following is an illustration of a basal tetrapod (often called "labyrinthodont amphibians" because the infolded ridges of their teeth were called "labyrinthine).

Note that the components of the skull are extraordinarily similar to those of the crossopterygian.

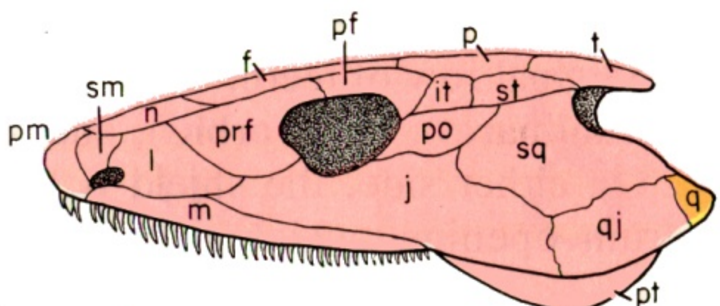
- The ethmoid region may or may not be ossified but if not it remains as cartilage.
- The basipterygoid process (for articulation/connection with the palate) is more robust, but remains a mobile joint).
- The basioccipital, exoccipitals, and suprocciopital remain distinct structures.
- Note particularly that the jugular foramen for exit of the jugular vein and cranial nerve X is ***between*** otic and occipital region.
- The extension rostrally of the presphenoid is called the "cultriform process".



Braincase



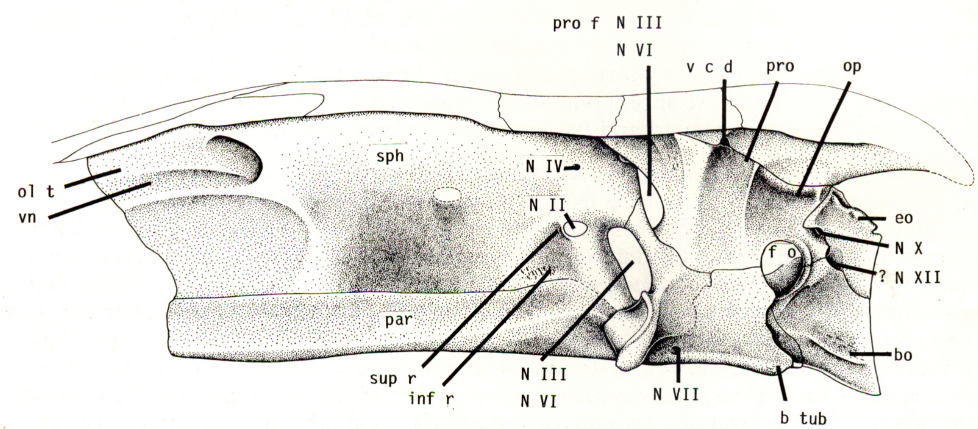
Braincase
Dermal palate added



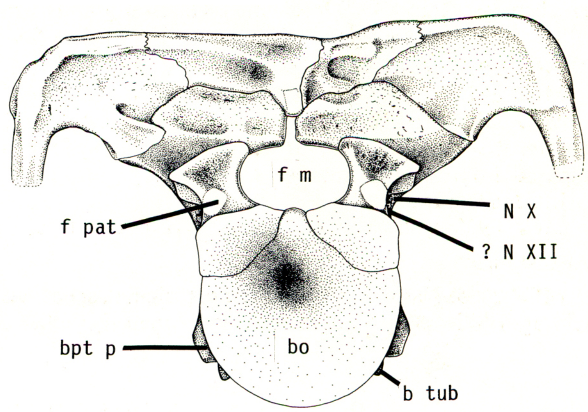
Dermal
skull roof overlaid

The image above is an idealized average structure of a labyrinthodont amphibian. Following is one such labyrinthodont, from the subset of labyrinthodonts called temnospondyls. Following on the next page is the braincase in left lateral view of the embolomorous amphibian *Archeria* (named for Archer County, Texas). Embolomeres are on the lineage leading toward amniotes. They are defined primarily by their vertebral construction, which we will discuss in the lecture for week five. (Be sure to come back to this section once the the embolomere condition is clearer.

The Embolomere Amphibian *Archeria*
Note the overall similarity to the condition retained from crossopterygian fishes.



So far all of the views have been lateral (aide) views of the skull or its internal component parts. The image below is an occipital view Clearly visible in the rear of the skull where the foramen magnum permit passage of the dorsal hollow nerve cord.



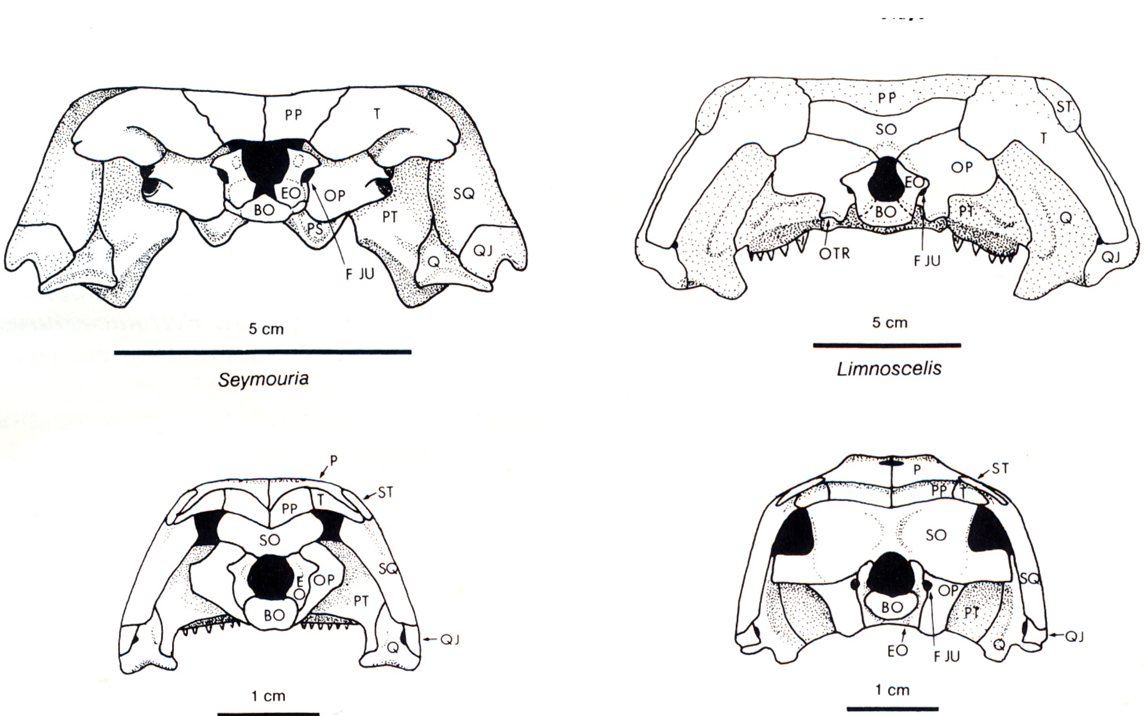
THE TRANSITION TO REPTILES

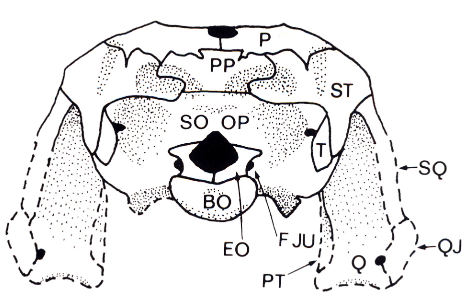
The transition from advanced amphibians to basal reptiles is a gradual and blurry one. Reptiles are part of Amniota, and whereas many fossil groups appear to be highly terrestriall adapted like amniotes, we can never be certain lacking fossil evidence of an amniotic egg. In the next few figures we will start to see th chane in the braincase across this transition as well.

- In the figure following, you can see the condition at the upper left of an advanced amphibian, *Seymouria*. Note the basioccipital ventral to the foramen magnum.
- Significantly, it is the basioccipital that will be the location of the occipital condyle.
- The exoccipitals can be seen on either side of the foramen magnum.

- (*Seymouria* is unusual in that its supraoccipital does not ossify.)
- Just lateral to the exoccipitals the opisthotic – the back part of the otic capsule – is well developed. Remember, this is the otic capsule, and thus capsule for the inner ear. Significantly, it is here that the stapes will articulate. In the case of these animals, it stapes acts as a brace between the braincase and the cheek portion dermal skull roof.

In the upper right portion of the figure as well as in the lower tier of the figure are amniotes or amniote-like organisms. At the upper right is *Limnoscelis*, a member of Diadectomorpha – the likely sister group to Amniota. It is very amniote like. Note that though large and rubust, it shares many features in common with the basal reptile *Protorothyris* and the primitive diapsid reptile *Petrolacosaurus*:
- Basioccipital well developed, still carries the occipital condyle.
- Right and left exoccipitals well developed.
- Supraoccipital very well developed, well ossified, providing a robust dorsal margin for the foramen magnum.
- Note the consistent placement of the jugular foramen between otic and occipital regions.





The image to the left is an occipital view of another diadectomorph, *Diadectes*. As with *Limnoscelis*, it is very amniote-like. In this case it has taken consolidation of the skull to an extreme by fusing the opisthotic and supraoccipital. But note the jugular foramen remains exactly where you would expect it.

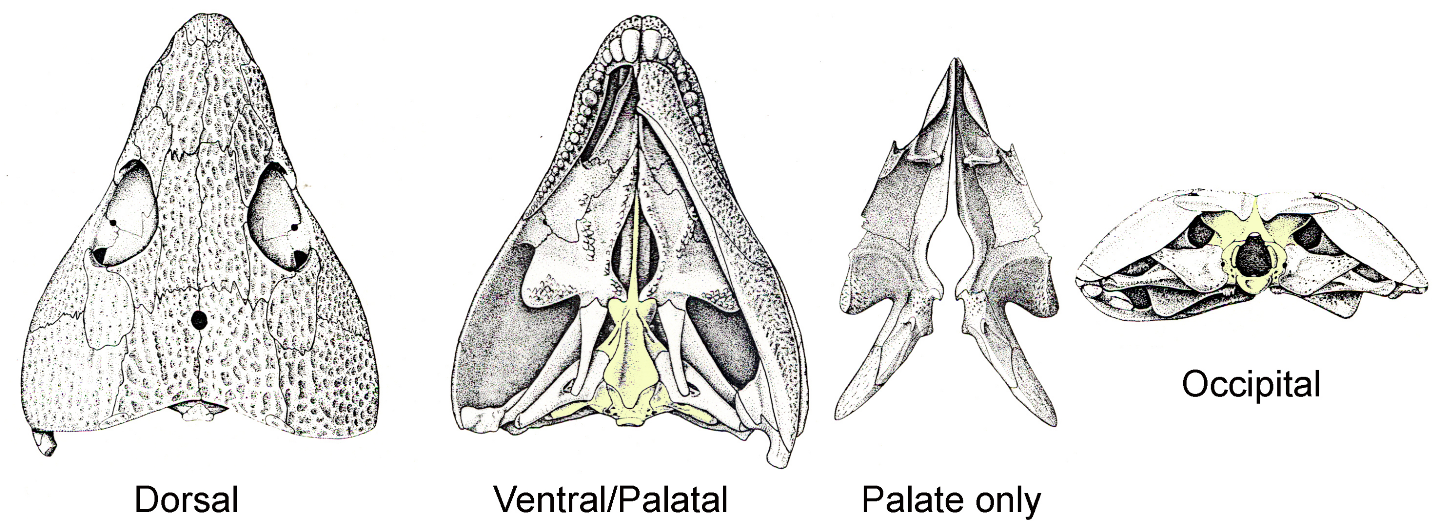
REPTILIA

Although some of the proportions change, reptiles and other basal amniotes continue the standard pattern that originated with crossopterygian fishes.

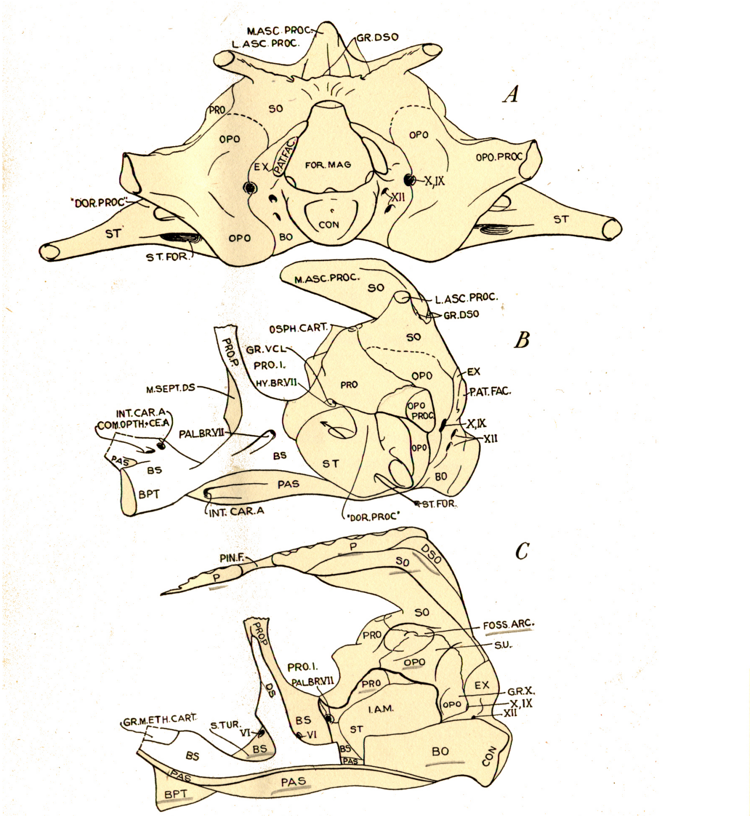
The next image is (a right lateral view) of the basal reptile Captorhinus – which belongs to a very primitive reptilian family called the Captorhinidae.

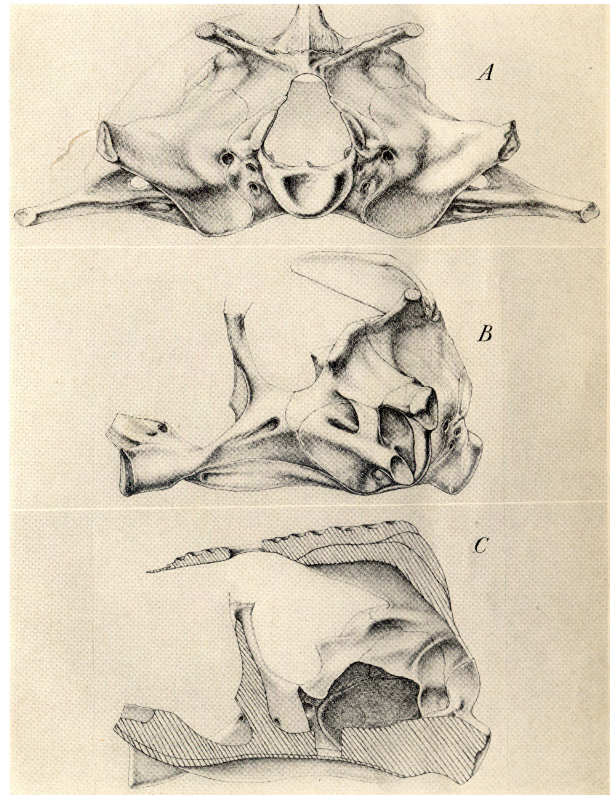
- Generally the ethmoid region is only present in cartilage.
- The remaining sphenethmoid (derived from the trabeculae) is present, sometimes as a vertical plate.
- The basipterygoid process is well developed, and indicates a mobile basipterygoid articulation persists.
- Both the basisphenoid and orbitosphenoid components ossify.
- Both the opisthotic and prootic remain distinct structures.
- The same set of occipital components are present: basi-, ex-, and supraoccipital.

Following is a ventral view of the skull to see the position of the braincase relative to the palatal structures.

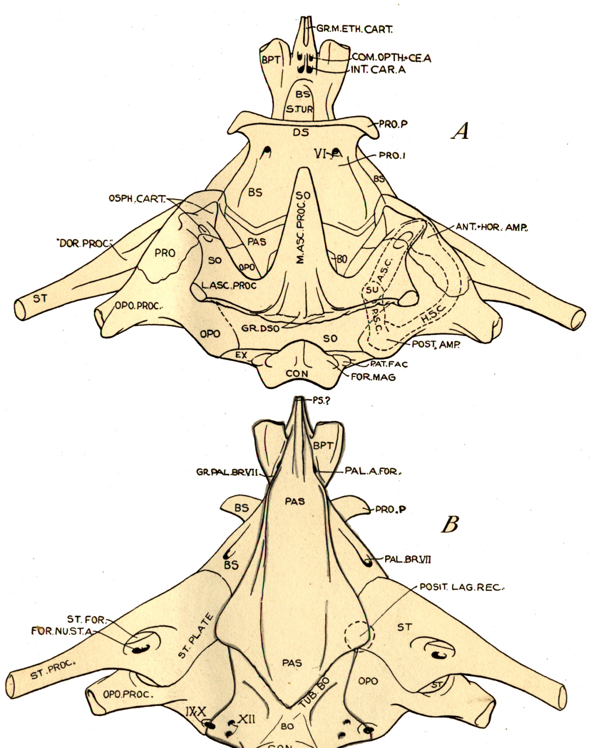


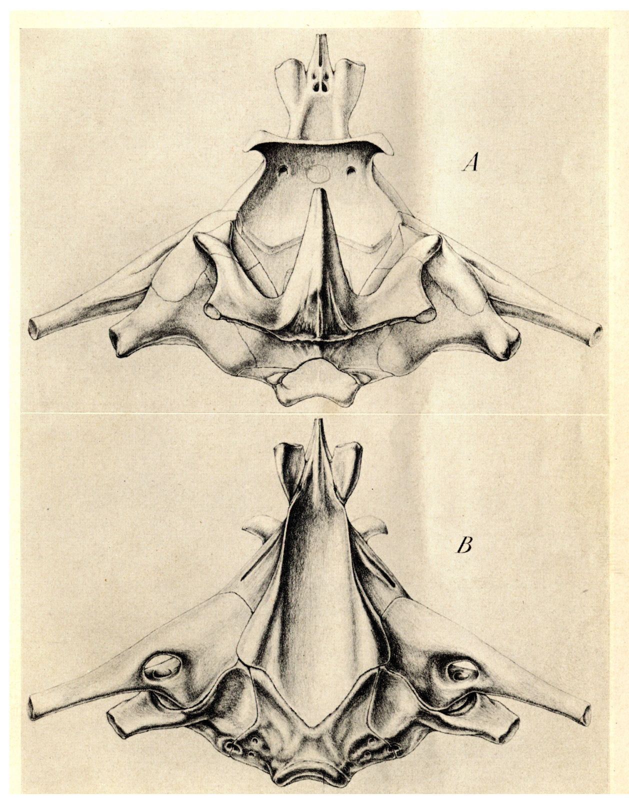
Below: *Captorhinus*. (A) occipital view; (B) left lateral view; (C) sagittal view.



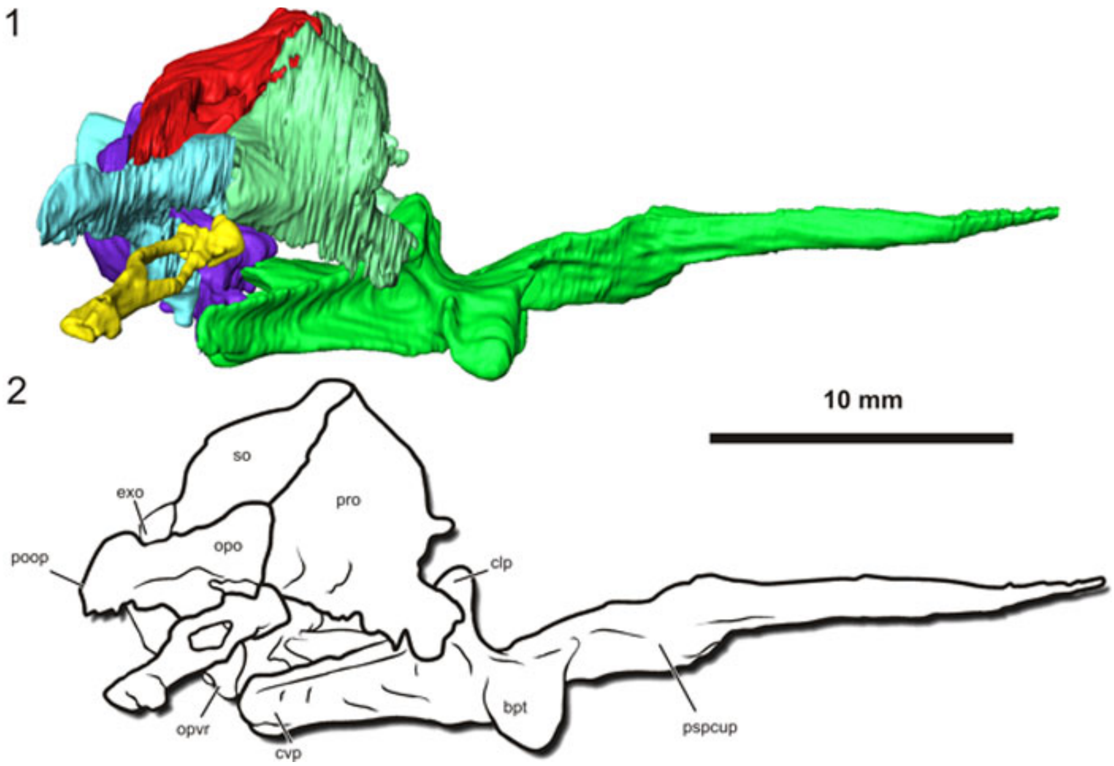


Below: *Captorhinus*. (A) dorsal view; (B) ventral view.



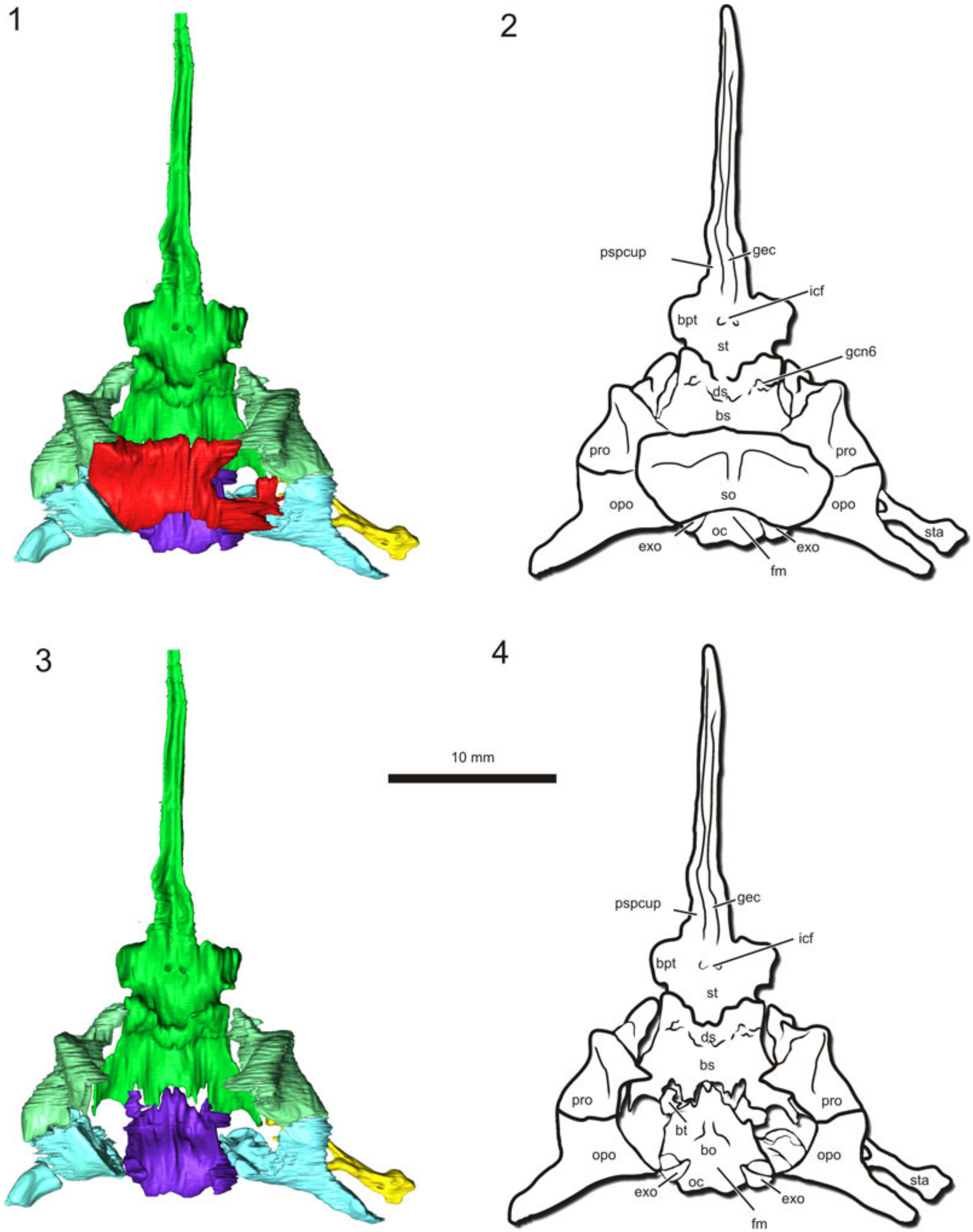


We see a similar condition in the primitive diapsid reptile known as *Youngina.* This example was digitally reconstructed from CT scans.



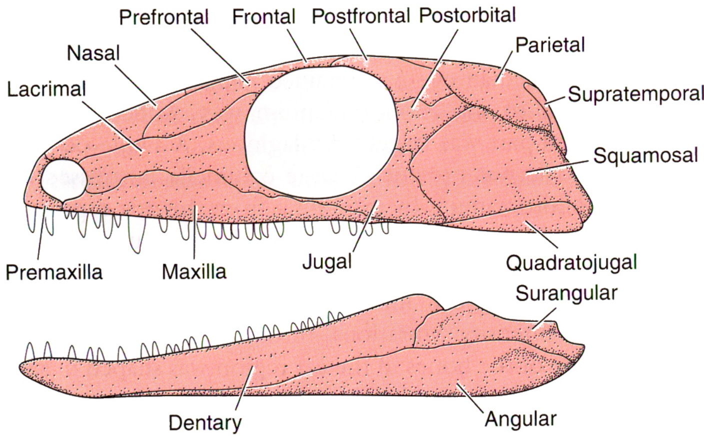
Following are views of a *Youngina* braincase, in dorsal view (1-2), then ventral view (3-4). So, in 1-2, the brain would lie between the braincase and the viewer, as you are looking at the internal surface of the cradle for the brain.

Why does the braincase appear to be getting smaller? In part because a component of the palatoquadrate (upper jaw) is joining to the sidewall of the braincase – an element called the epipterygoid. (We will discuss this in much greater detail in the next lecture.)

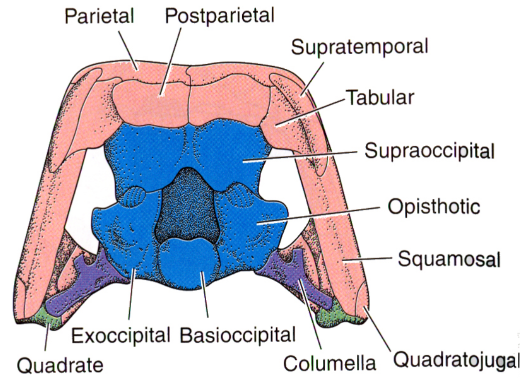


Note in each of the above images, the yellow element is not a part of the braincase, but rather the stapes, which articulates with the braincase.

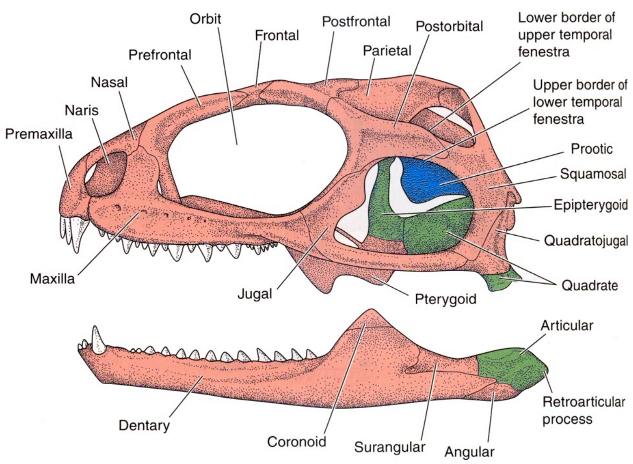
In the images that follow, note the braincase is color-coded blue.



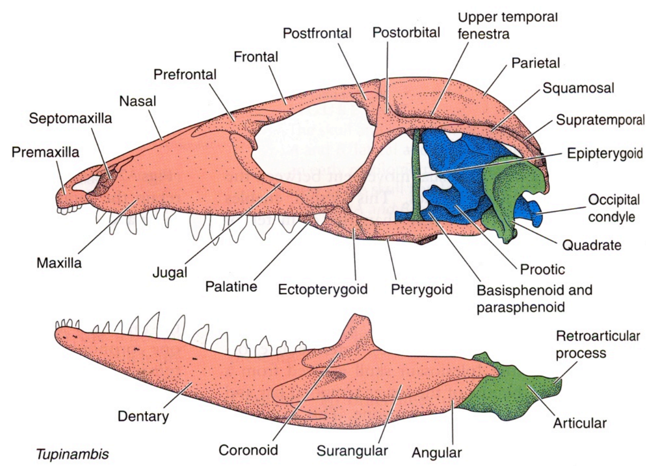
Lateral view of †*Paleothyris*



Posterior view of †*Paleothyris*



Sphenodon (basal diapsid reptile)

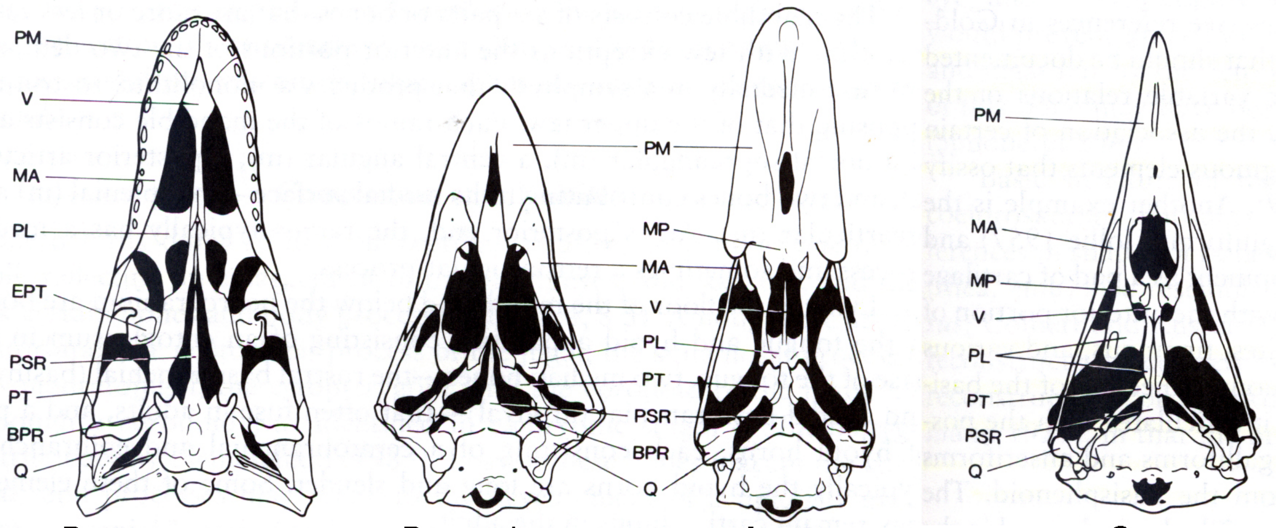


Tupinambis (extand varanid lizrd)

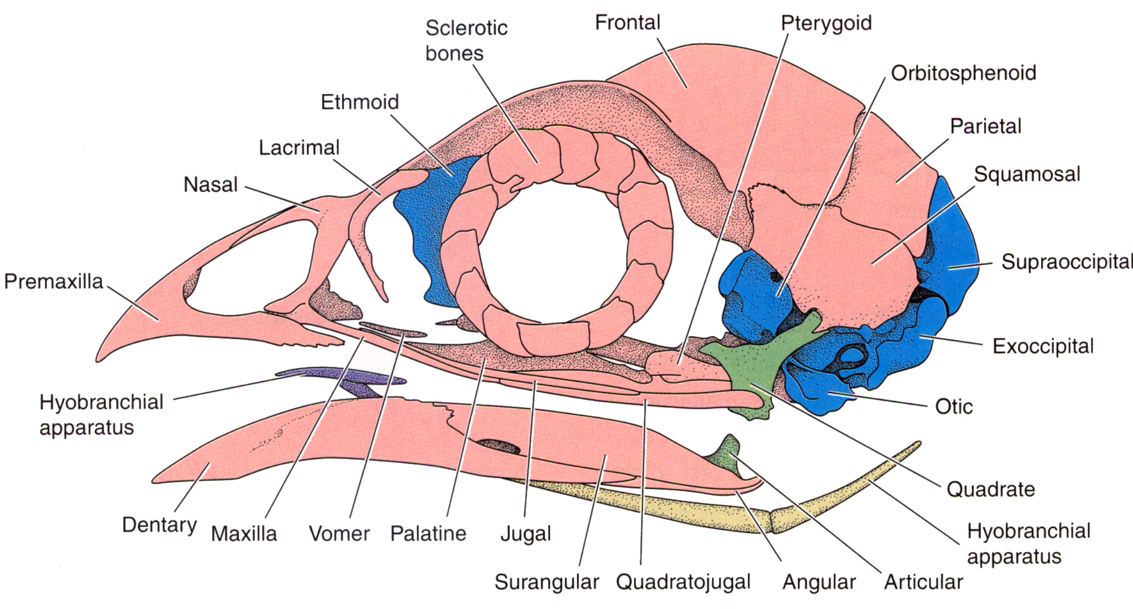
BIRDS

In birds, many skull structures tend to fuse, obliterating the sutural boundaries between elements. However, basal birds still clearly possess the standard braincase elements:

- All of the occipital structures are present, but tend to fuse into a single occipital element surrounding the foramen magnum.
- From rostral to caudal, the braincase shortens, presumably to help accommodate the function of the bill.
- The basisphenoid can often still be seen as a distinct element in palatal/ventral view
- The parasphenoid has only a blunt rostral extension, and no extended cultriform process as was seen in reptiles.

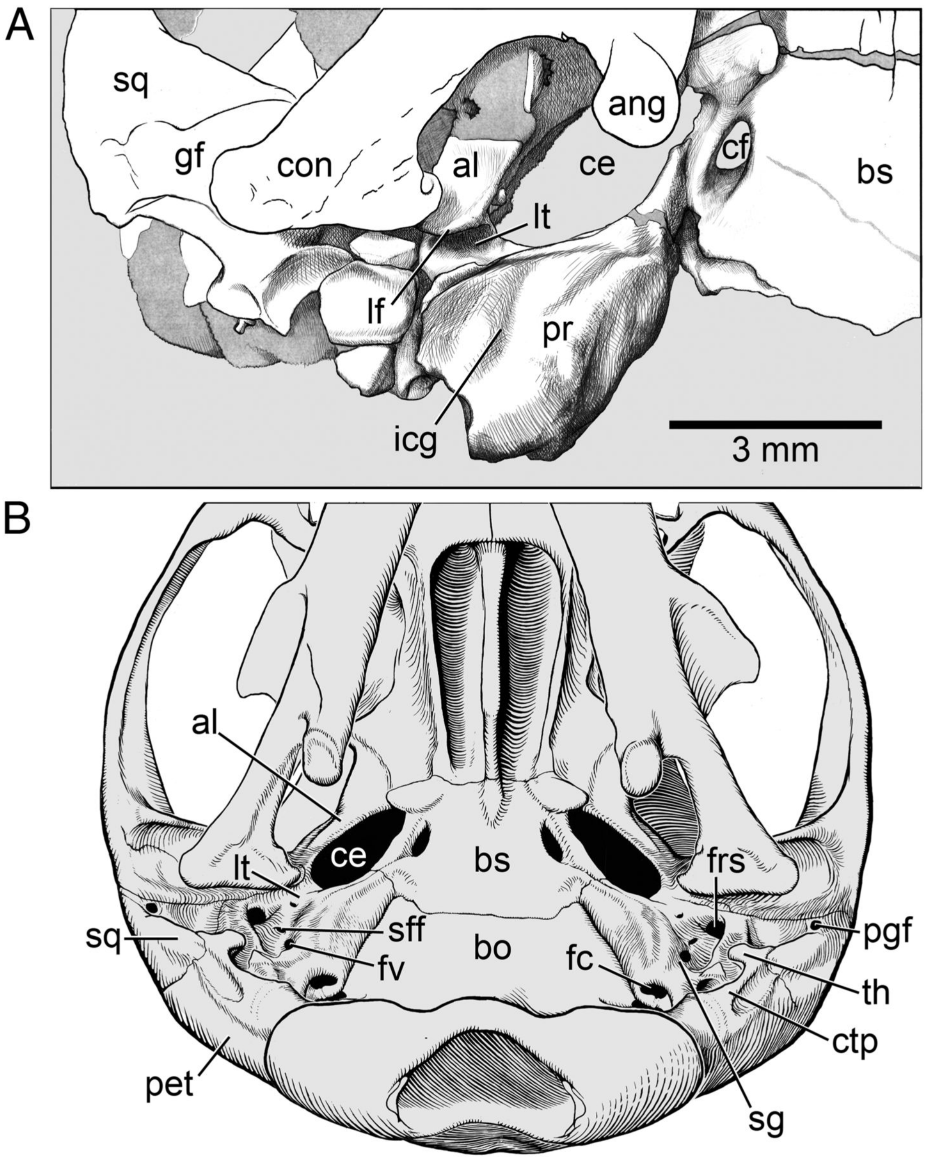


Dromaeosaurus (Coelosaur dinosaur) *Dromaius* (Paleognathus palate) *Anser* (Duck, Desmognathous palate) *Coruvs* (Crow, Neognathous' palate)



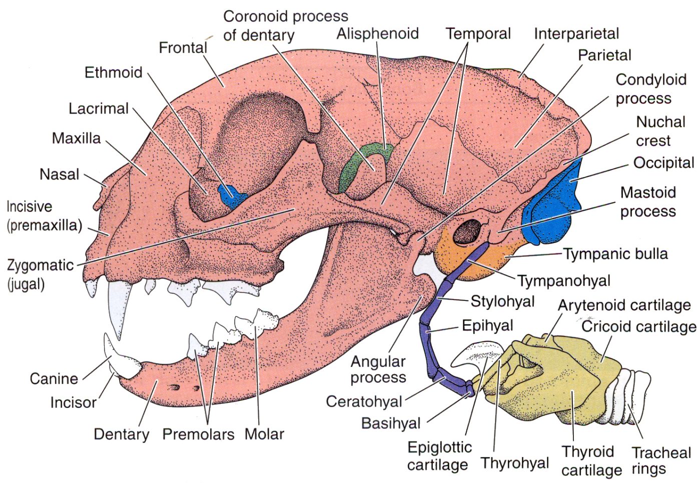
MAMMALS

- Mammals continue the process of consolidation.
- Ethmoid is fully ossified.
- In most (but not all) mammals, contributions from the nasal capsules for a midline cartilaginous structure that helps for the septum between the ethmoid and the dermal vomer – called the ***mesethmoid***.
- All of the occipital elements fuse around the foramen magnum to comprise the endochondral component of the occipital bone.
- Basisphenoid and presphenoid are generally present as distinct elements (except in humans and some other great apes).
- The prootic and opisthotic components of the otic casule ombine to form the petrosal portion of the temporal bone (itself a fusion of multiple components).

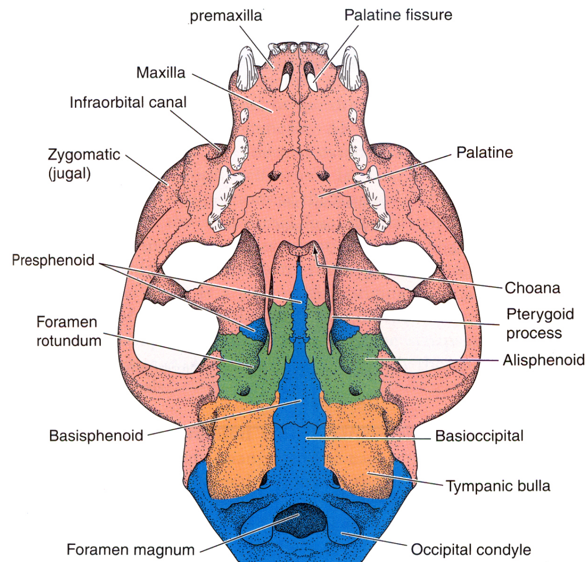


As with the earlier reptile illustration, the braincase components here are also color-coded blue.

The alisphenoid, which is frequently cited as part of the lateral part of the brincase, is actually homologous to the epiperygoid, and thus derived from the palatoquadrate cartilage.

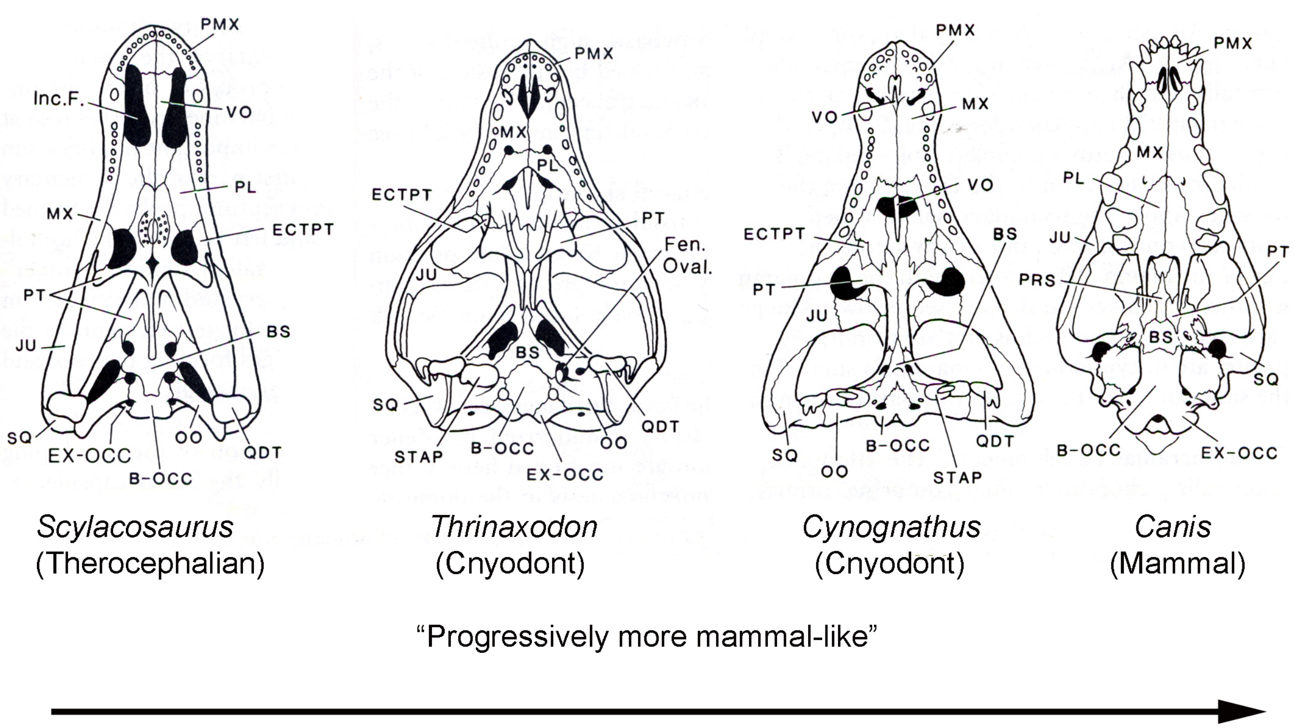


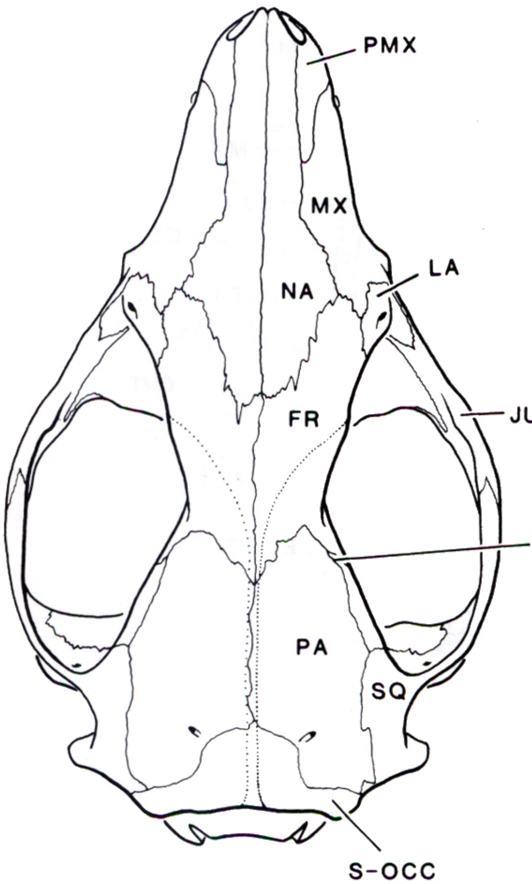
Lateral view of the skull of a cat (*Felis*)

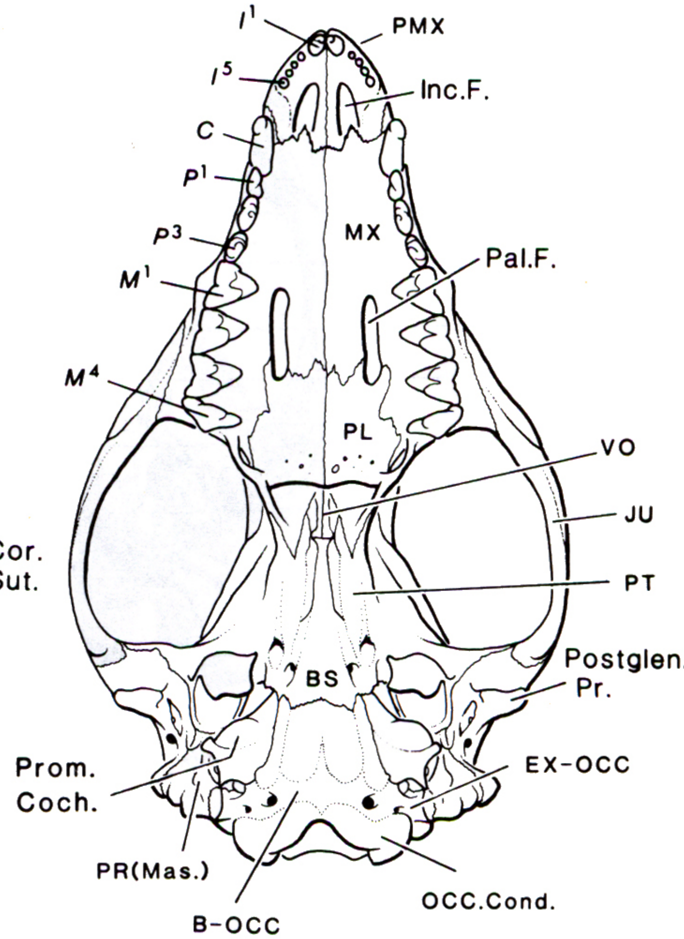


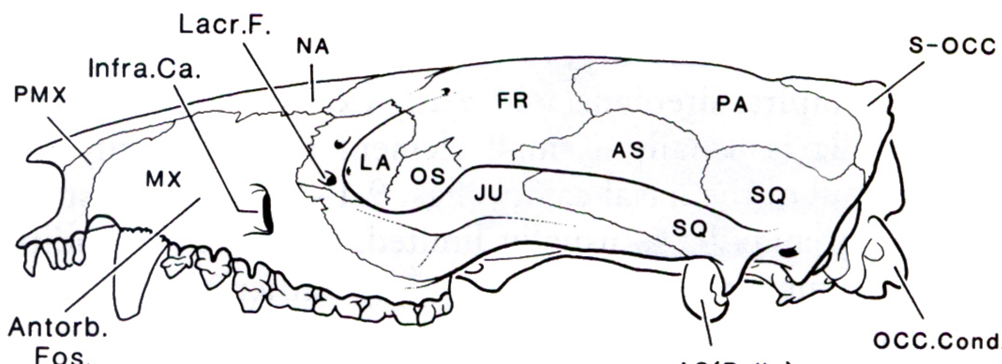
Palatal view of the skull of a cat (*Felis*)

As synapsids become progressively more mammal-like, it appears that their braincase gets smaller. Rather, it's that temporal fenestra and passing temporalis muscle are expanding.

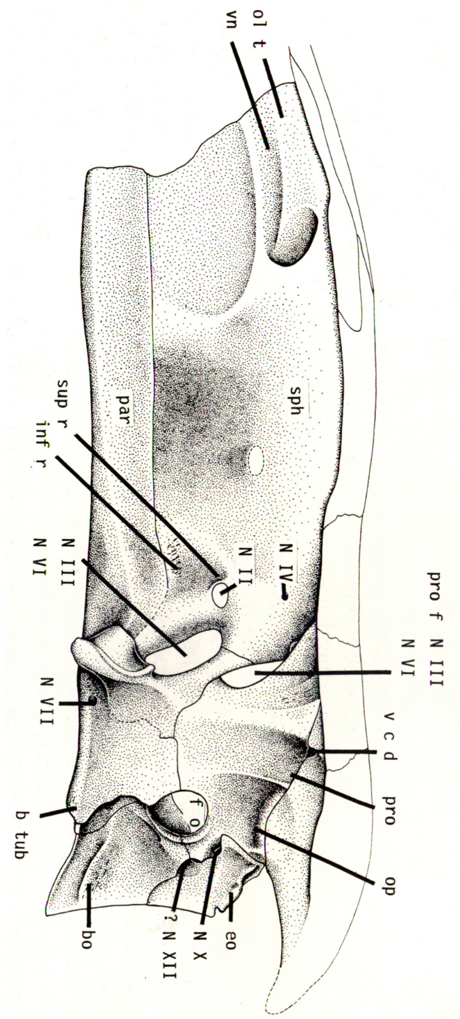








On each of the following pages are composite images for reference, study, and practice.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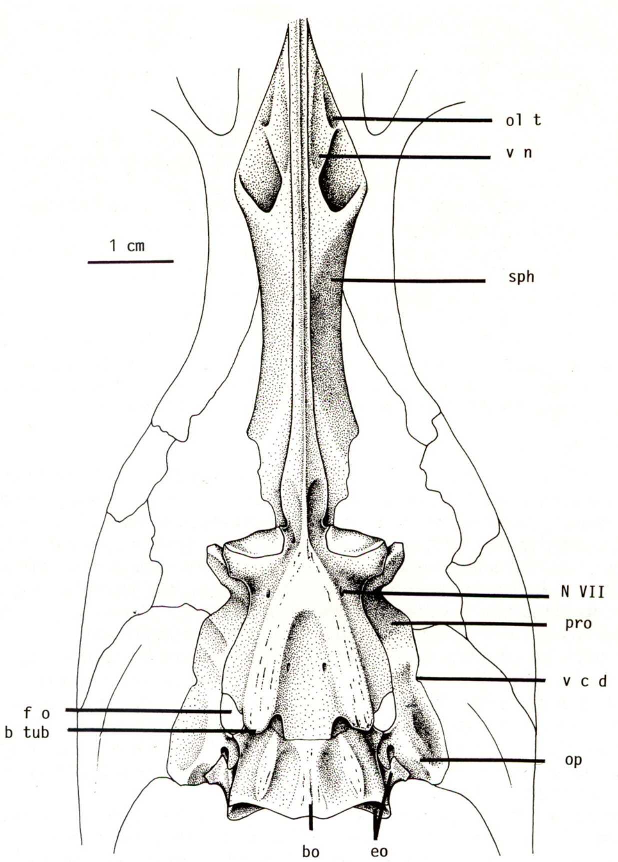
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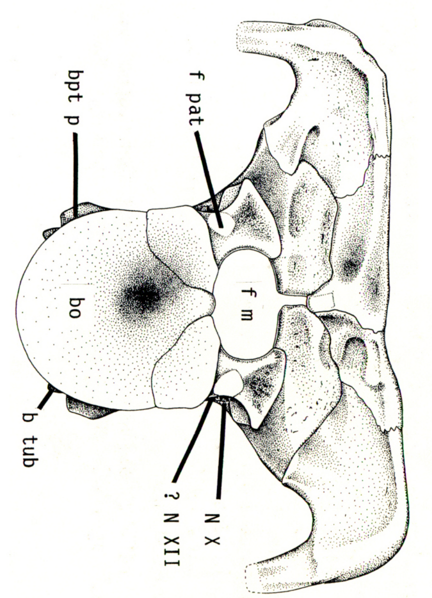
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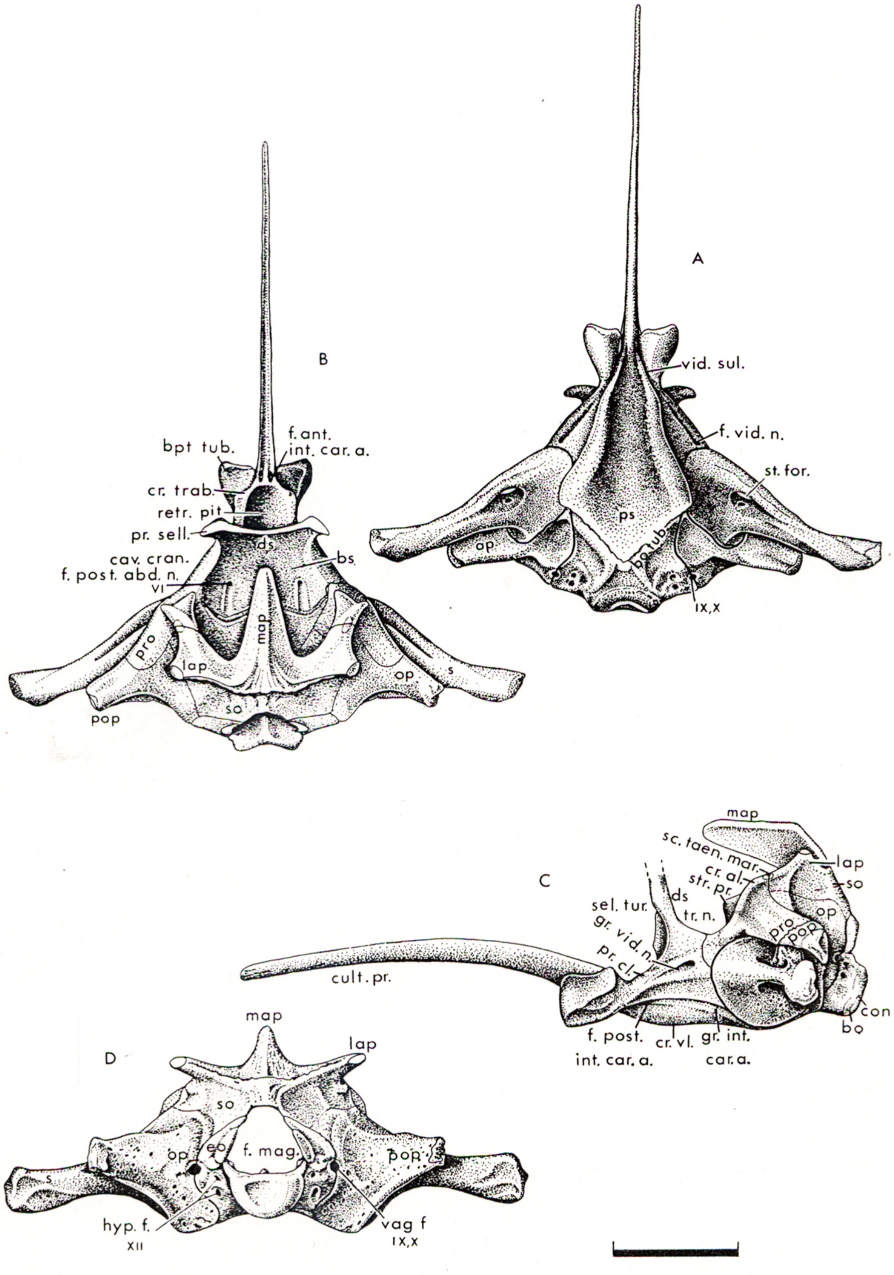
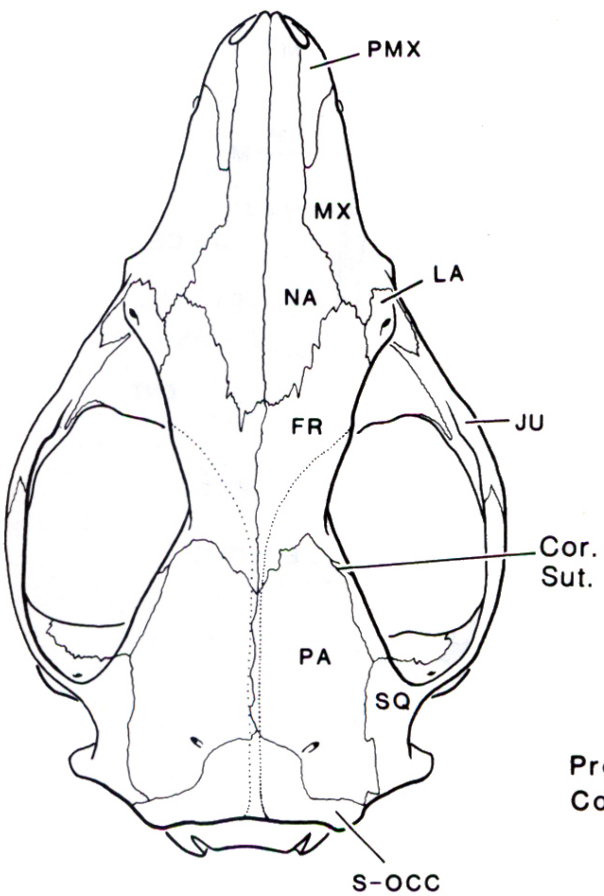


Eocaptorhinus laticeps. Braincase. *A*, ventral view; *B*, dorsal view; *C*, left-lateral view; *D*, occipital view. Abbreviations: *bo. tub.*, basioccipital tubercle; *bpt. tub.*, basipterygoid tubercle; *cav. cran.*, cavum cranii; *con.*, occipital condyle; *cr. al.*, crista alaris; *cr. trab.*, crista trabecularis; *cr. vl.*, crista ventrolateralis; *cult. pr.*, cultriform process; *ds.*, dorsum sella; *f. ant. int. car. a.*, foramen anterior of internal carotid artery canal; *f. mag.*, foramen magnum; *f. post. abd. n. VI*, foramen posterior of abducens (VI) nerve canal; *f. post. int. car. a.*, foramen posterior of internal carotid artery canal; *f. vid. n.*, foramen for vidian (VII) nerve; *gr. int. car. a.*, groove for internal carotid artery; *gr. vid. n.*, groove for vidian (VII) nerve; *hyp. f. XII*, hypoglossal (XII) nerve foramina; *lap*, lateral ascending process of supraoccipital; *map*, median ascending process; *pr. cl.*, processus clinoideus; *pr. sell.*, processus sellaris; *retr. pit*, retractor pit; *sc. taen. mar.*, scar for attachment of taenia marginalis; *sel. tur.*, sella turcica; *st. for.*, stapedial foramen; *str. pr.*, supratrigeminal process; *tr. n.*, trigeminal notch; *vag. f. IX, X*, vagus foramen (IX, X); *vid. sul.*, vidian sulcus. Reconstruction based on OUSM 15020B (3-0-S5), 15022 (3-1-S7), 15024 (3-1-S6), 15101 (3-0-S4), and Richards Spur captorhinid specimens. Scale equals 1 cm.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LA
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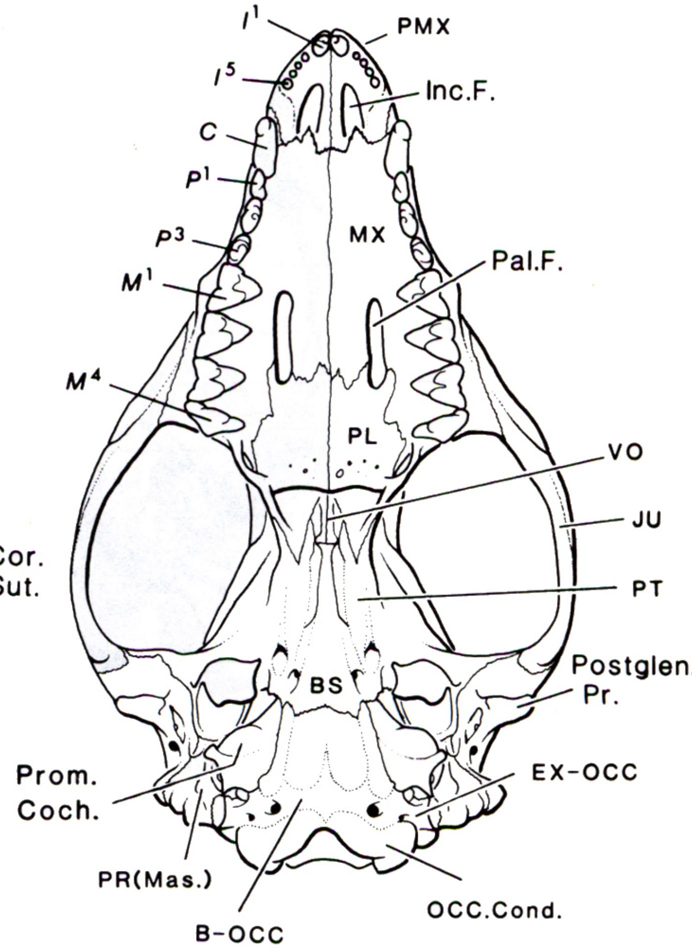
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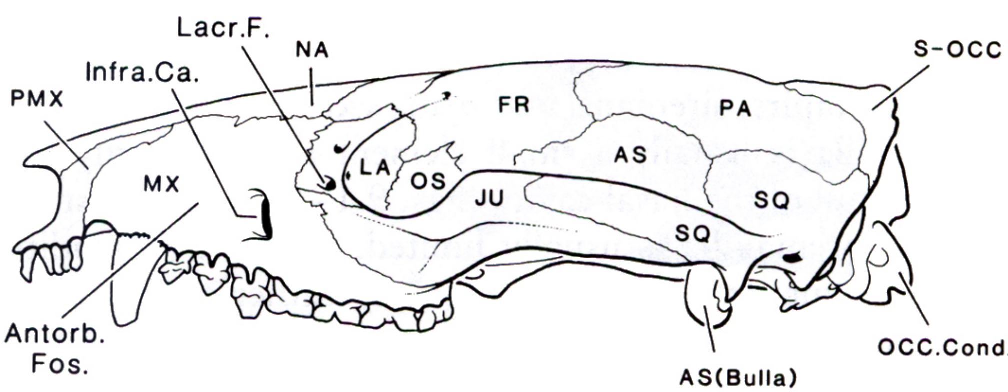
Pr.
BS
Prom.
Coch.
EX-OCC
PR(Mas.)
OCC.Cond.
B-OCC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Infra.Ca.
PMX
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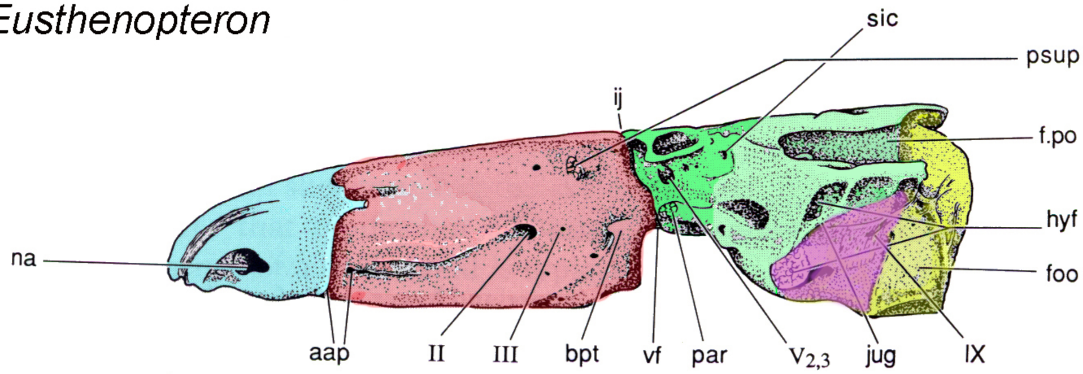
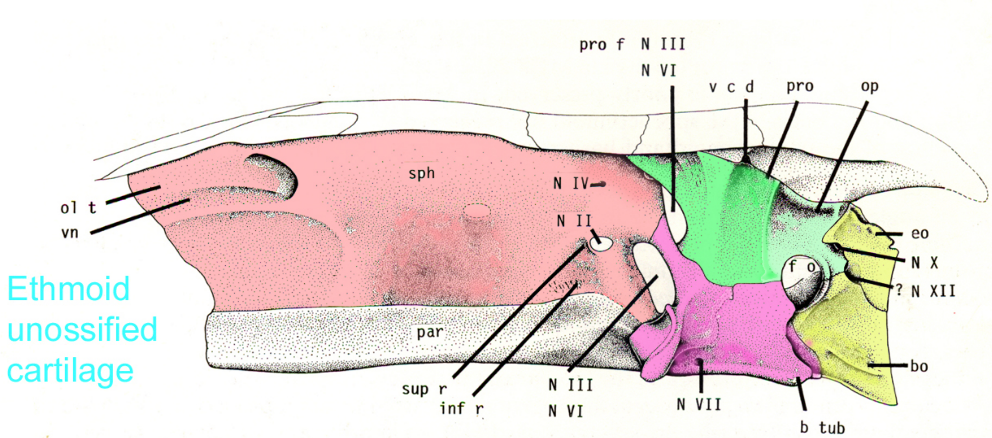
SQ
Antorb.
Fos.
AS(Bulla)
OCC.Cond.

Eusthenopteron



Archeria (temnospondyl amphibian)



Captorhinus (basal reptile)