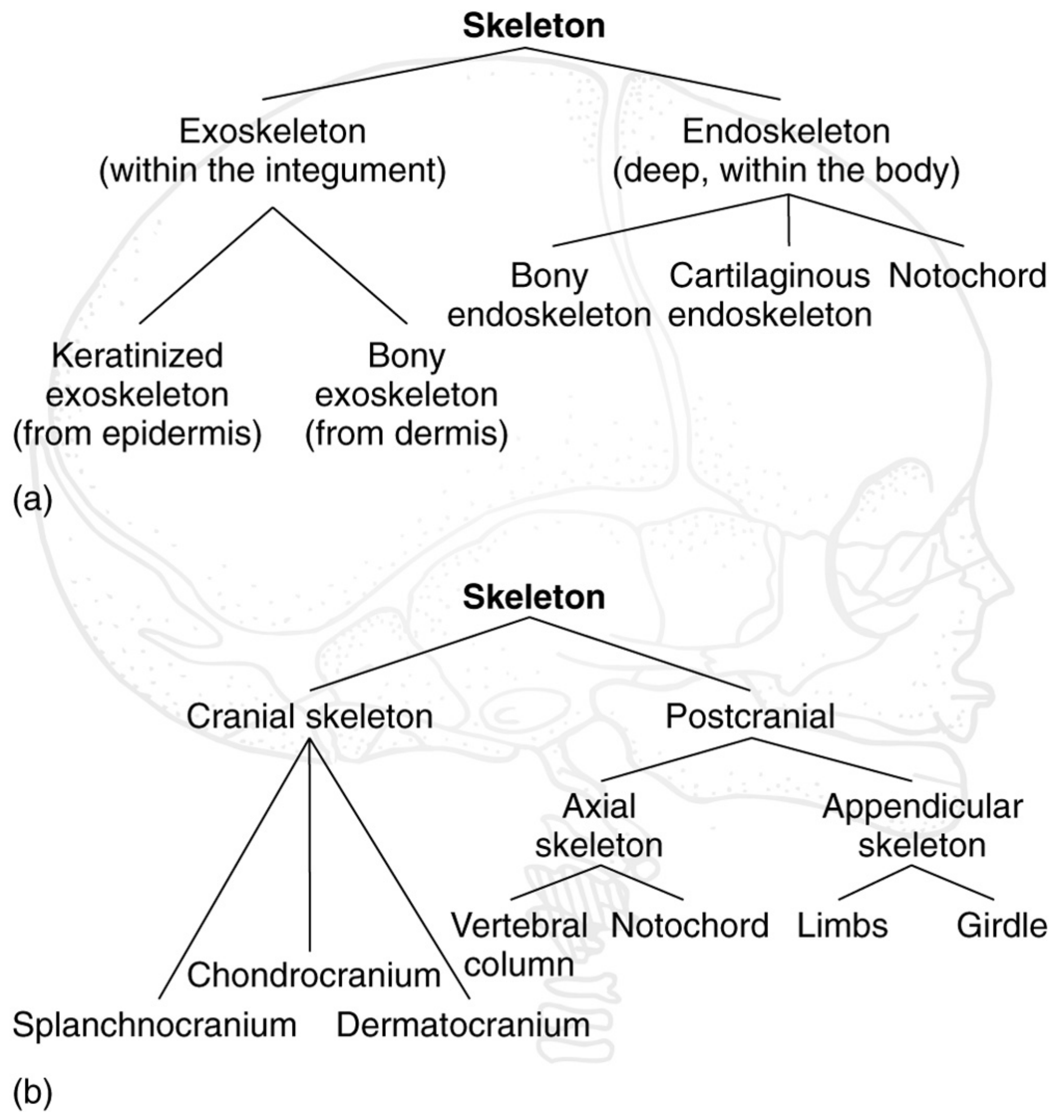
Skeletal System: The Skull

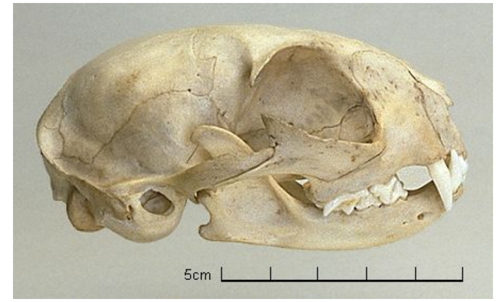

Skeleton
Exoskeleton
(within the integument)
Endoskeleton
(deep, within the body)
Bony
endoskeleton
Cartilaginous
endoskeleton
Notochord
Keratinized
exoskeleton
(from epidermis)
Bony
exoskeleton
(from dermis)
(a)
Skeleton
Cranial skeleton
Postcranial
Axial
skeleton
Appendicular
skeleton
Vertebral
column
Notochord
Limbs
Girdle
Chondrocranium
Splanchnocranium
Dermatocranium
(b)

1 - neurocranium (also called endocranium or chondrocranium)

2 - dermatocranium (membrane bones)

3 - splanchnocranium (or visceral skeleton)

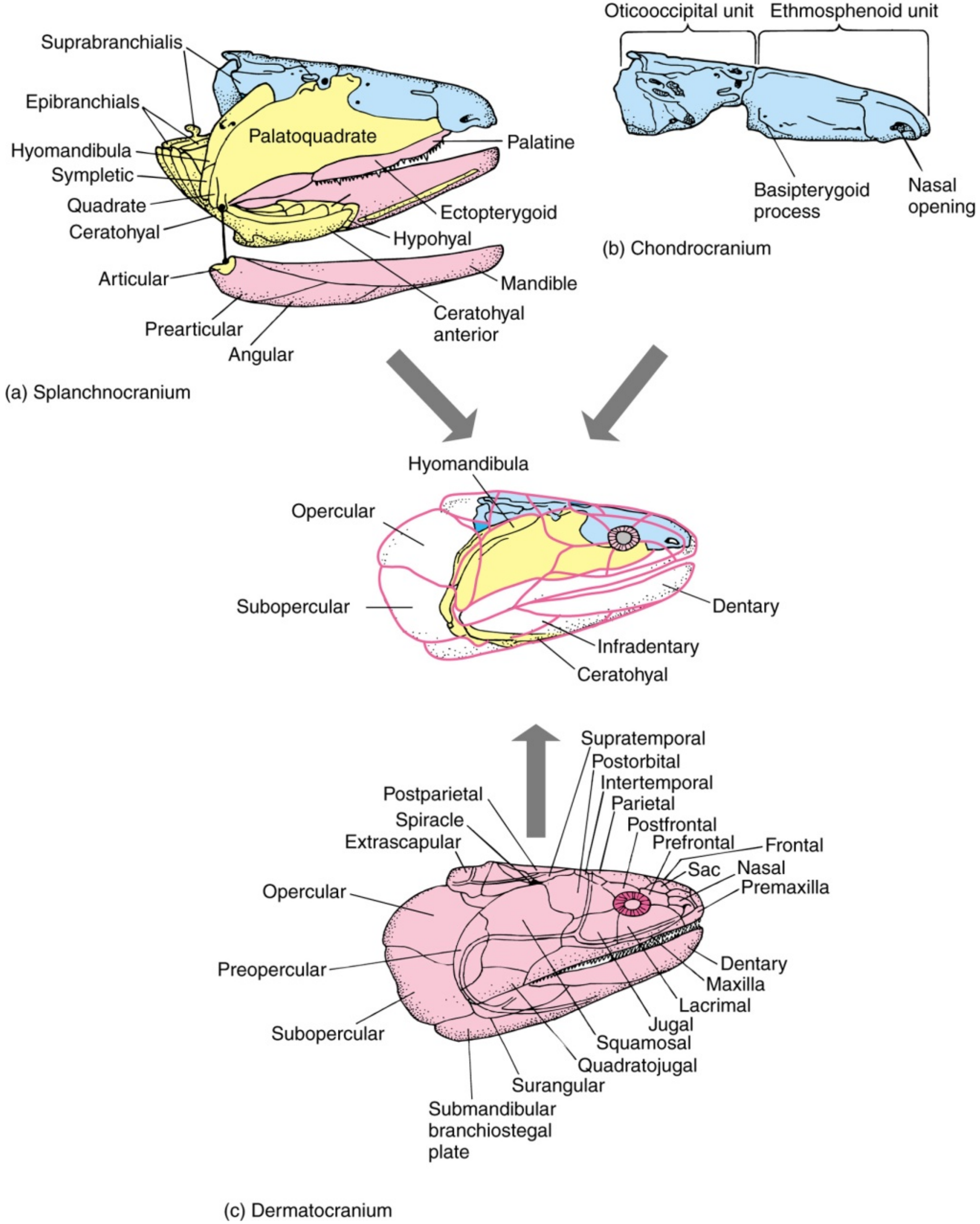
The Vertebrate Skull consists of:



1.The **neurocranium/chondrocranium** includes the box that encloses the brain and the capsules surrounding the sense organs. It protects the brain.

2.The **splanchnocranium** is the visceral portion of the skull that supports the gills and contributes to the jaws.

3.The **dermatocranium** is the dermal bone that is believed to be derived from the external armor of primitive fish.
This bone contributes to the brain case and the jaws.


Suprabranchialis
Epibranchials
Hyomandibula
Sympletic
Quadrate
Ceratohyal
Articular
Prearticular
Angular
Palatoquadrate
Palatine
Ectopterygoid
Hypohyal
Mandible
Ceratohyal anterior
(a) Splanchnocranium
Oticooccipital unit
Ethmosphenoid unit
Basipterygoid process
Nasal opening
(b) Chondrocranium
Hyomandibula
Opercular
Subopercular
Dentary
Infradentary
Ceratohyal
Supratemporal
Postorbital
Intertemporal
Parietal
Postfrontal
Prefrontal
Frontal
Postparietal
Spiracle
Extrascapular
Sac
Nasal
Premaxilla
Opercular
Preopercular
Subopercular
Submandibular branchiostegal plate
Surangular
Quadratojugal
Squamosal
Jugal
Lacrimal
Maxilla
Dentary
(c) Dermatocranium

General Embryological Development of the Skull

1. Shortly after the initial formation of the embryological CNS, mesenchymal cells surrounding the CNS begin to differentiate. The outermost layer begins to aggregate into units or centers that form cartilage. In some vertebrates this cartilage will ossify to form replacement bone .

The developing **neurocranium/ chondrocranium** forms cartilage at 6 pairs of isolated regions.

a. parachordal (posterior pair)

b. polar (middle pair, only in some vertebrates)

c. trabeculae (anterior pair)

c. The occipital

d. The otic, optic and nasal capsules

Neurocranium begins as cartilage that is partly or entirely replaced by bone (except in cartilaginous fishes)

Cartilaginous stage:

-neurocranium begins as pair of parachordal & prechordal cartilages below the brain

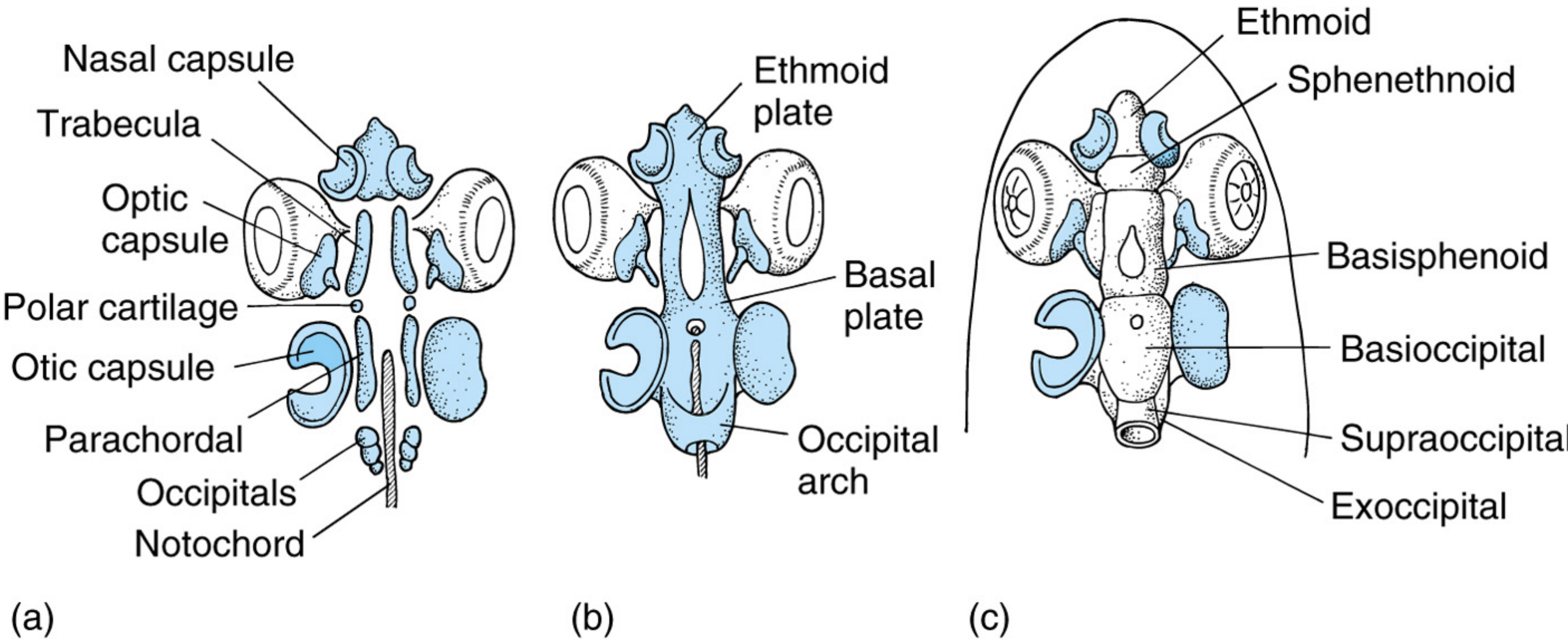
-parachordal cartilages expand & join; along with the notochord from the **basal plate**

-prechordal cartilages expand & join to form an **ethmoid plate**

-Cartilage also appears in the

olfactory capsule (partially surrounding the olfactory epithelium)

otic capsule (surrounds inner ear & also develops into sclera of the eyeball)



Embryonic development of the chondrocranium. Cartilage (blue) appears first but in most vertebrates is replaced by bone (white) later in development.The chondrocranium includes these cartilaginous elements that form the base and back of the skull together with the supportive capsules around sensory organs. Early condensation of mesenchymal cells differentiates into cartilage (a) that grows and fuses together to produce the basic ethmoid, basal, and occipital regions (b) that later ossify (c), forming basic bones and sensory capsules.

Cartilaginous fishes - retain a cartilaginous neurocranium (or chondrocranium) throughout life

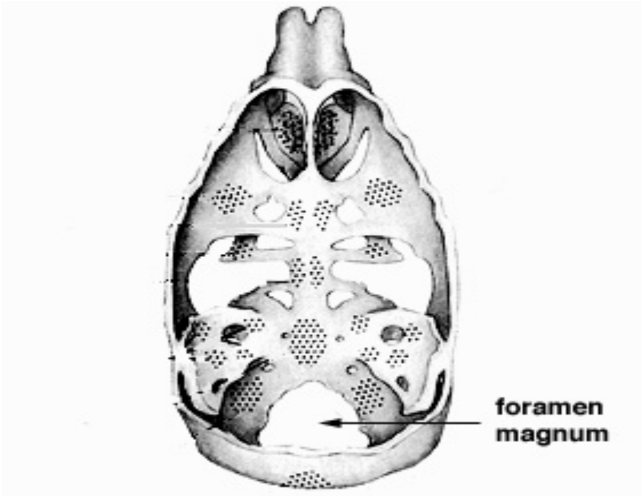
Bony fishes, lungfishes, & most ganoids - retain highly cartilaginous neurocranium that is covered by membrane bone

Other bony vertebrates - embryonic cartilaginous neurocranium is largely replaced by replacement bone (the process of endochondral ossification occurs almost simultaneously at several ossification centers)

Neurocranial ossification centers:

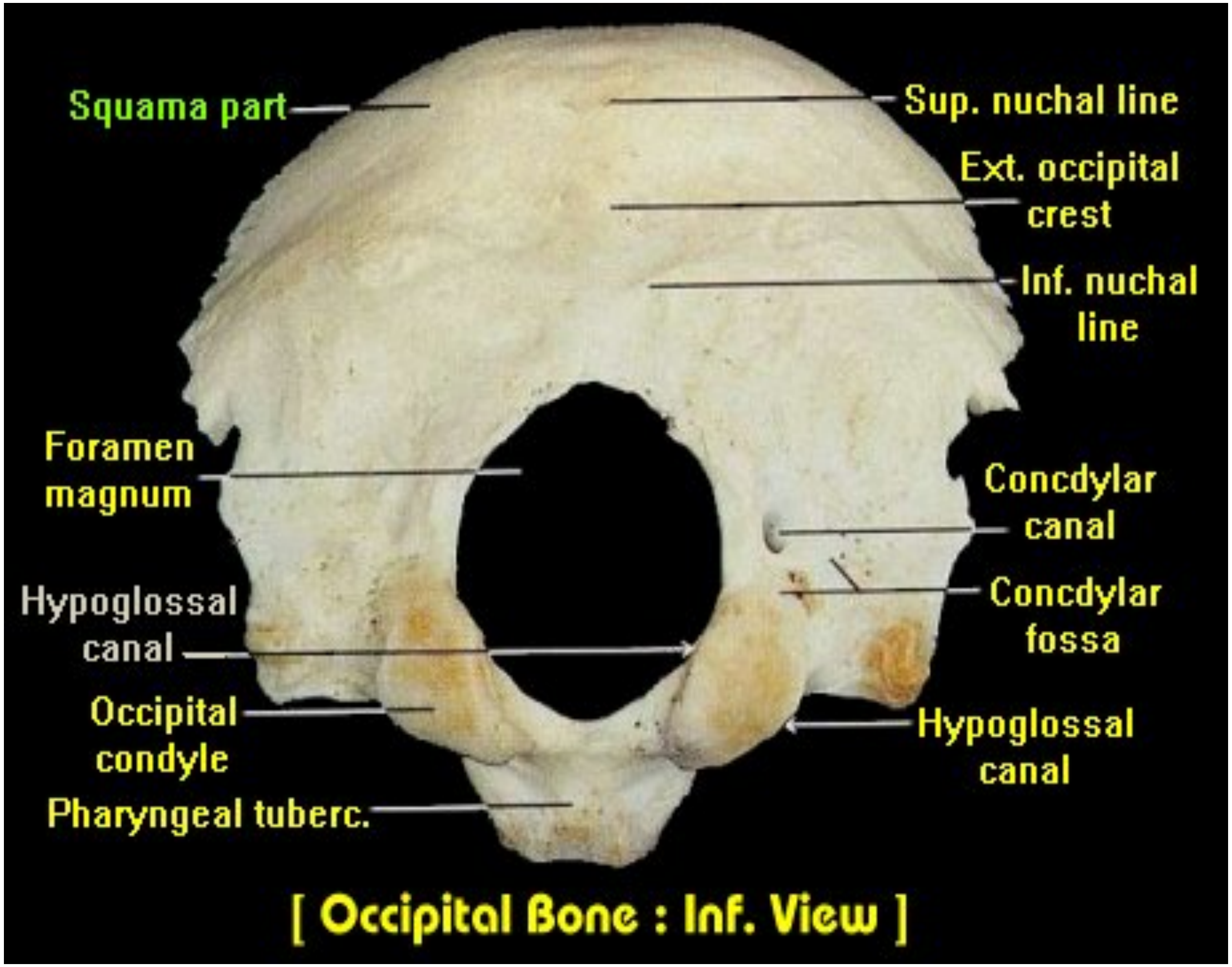
1 - **Occipital centers**
cartilage surrounding the foramen magnum may be replaced by as many as four bones:

- Basioccipital
- Exoccipital (2)
- Supraoccipital



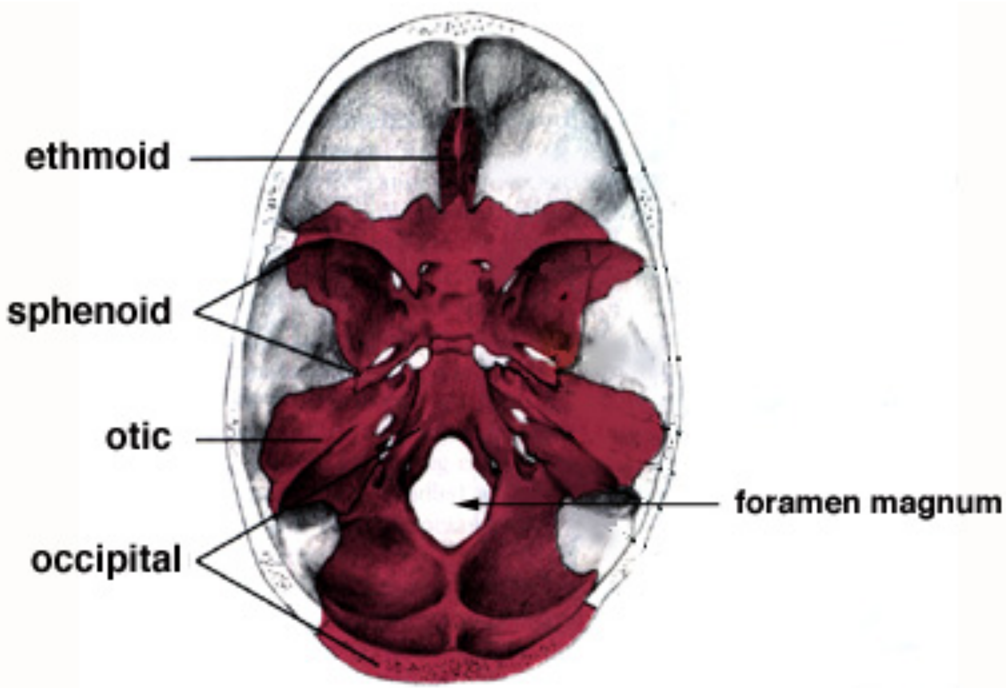
Mammals - all 4 occipital elements typically fuse to form a single occipital bone

Tetrapods - neurocranium articulates with the 1st vertebra via 1 (reptiles and birds) or 2 (amphibians and mammals) occipital condyles (see human skull below)



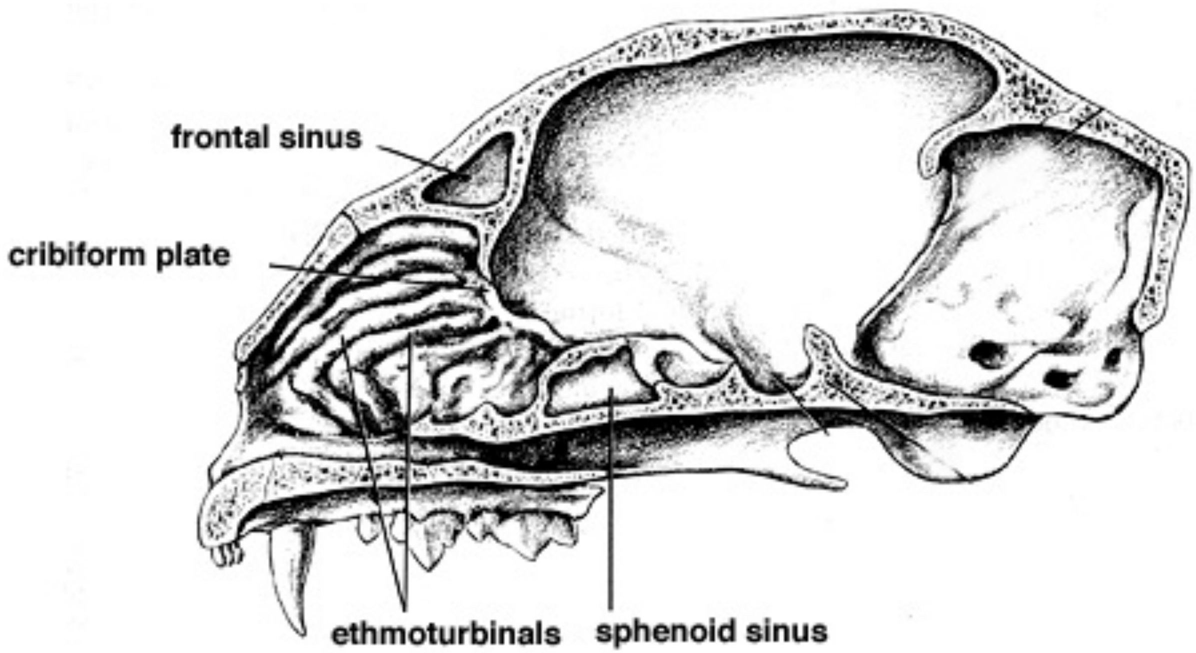
Squama part
Sup. nuchal line
Ext. occipital crest
Inf. nuchal line
Foramen magnum
Concdylar canal
Concdylar fossa
Hypoglossal canal
Occipital condyle
Hypoglossal canal
Pharyngeal tuberc.
[Occipital Bone : Inf. View]

2 - **Sphenoid centers** form:
-basisphenoid bone (anterior to basioccipital)
-presphenoid bone
-side walls above basisphenoid & presphenoid form:
  - -orbitosphenoid
  - -pleurosphenoid
  - -alisphenoid



3 - **Ethmoid centers** tend to remain cartilaginous & form

-anterior to sphenoid
-cribiform plate of ethmoid & several conchae (or ethmoturbinal bones)



The ethmoid region is clearly visible within the bisected skull above. In most mammals, the nasal chamber is large & filled with ridges from the ethmoid bones called the turbinals or ethmoturbinals. These bones are covered with olfactory epithelium in life and serve to increase the surface area for olfaction (i.e., a more acute sense of smell).
Another ethmoid bone, the cribiform plate, separates the nasal chamber from the brain cavity within the skull.

4 - Otic centers - the cartilaginous otic capsule is replaced in lower vertebrates by several bones:
prootic
opisthotic
epiotic

One or more of these may unite with adjacent replacement or membrane bones:

Frogs & most reptiles - opisthotics fuse with exoccipitals
Birds & mammals - prootic, opisthotic, & epiotic unite to form a single petrosal bone; the petrosal, in turn, sometimes fuses with the squamosal to form the temporal bone

The developing **splanchnocranium** is also characterized by paired cartilaginous aggregates that form pharyngeal arches. It's derived from neural crest cells. The neural crest cells migrate into the walls of the pharynx to form pharyngeal arches between the gills. The anterior branchial arches that support the mouth are the jaws

The mandibular arch becomes divided into dorsal and ventral components.

The **dorsal** component is called the quadrate cartilage or **palatopterygoquadrate bar**.

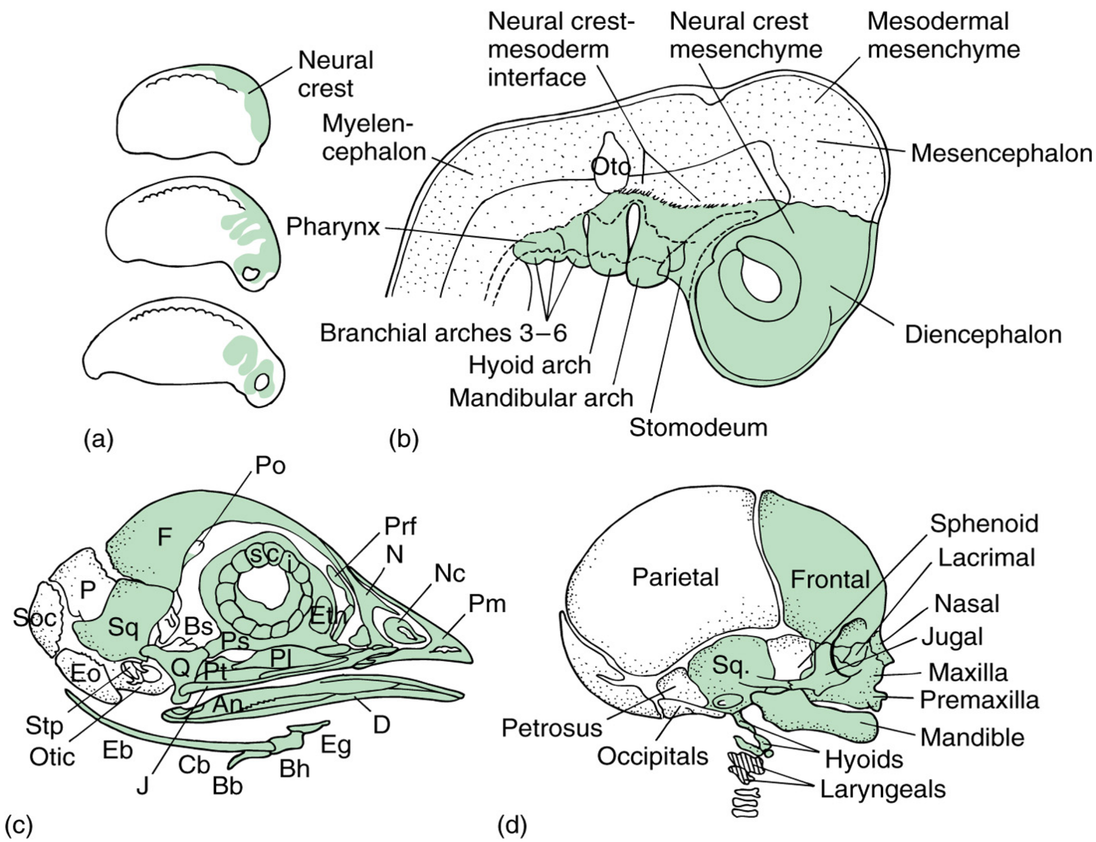
The **ventral** component is called Meckel's cartilage.

b. The **hyoid arch**:

c. The **branchial** arches **or visceral arches**:

Subsequent Development in Humans:

In man, the major changes that take place in the neurocranium include the spread and eventual fusion of the paired cartilages.



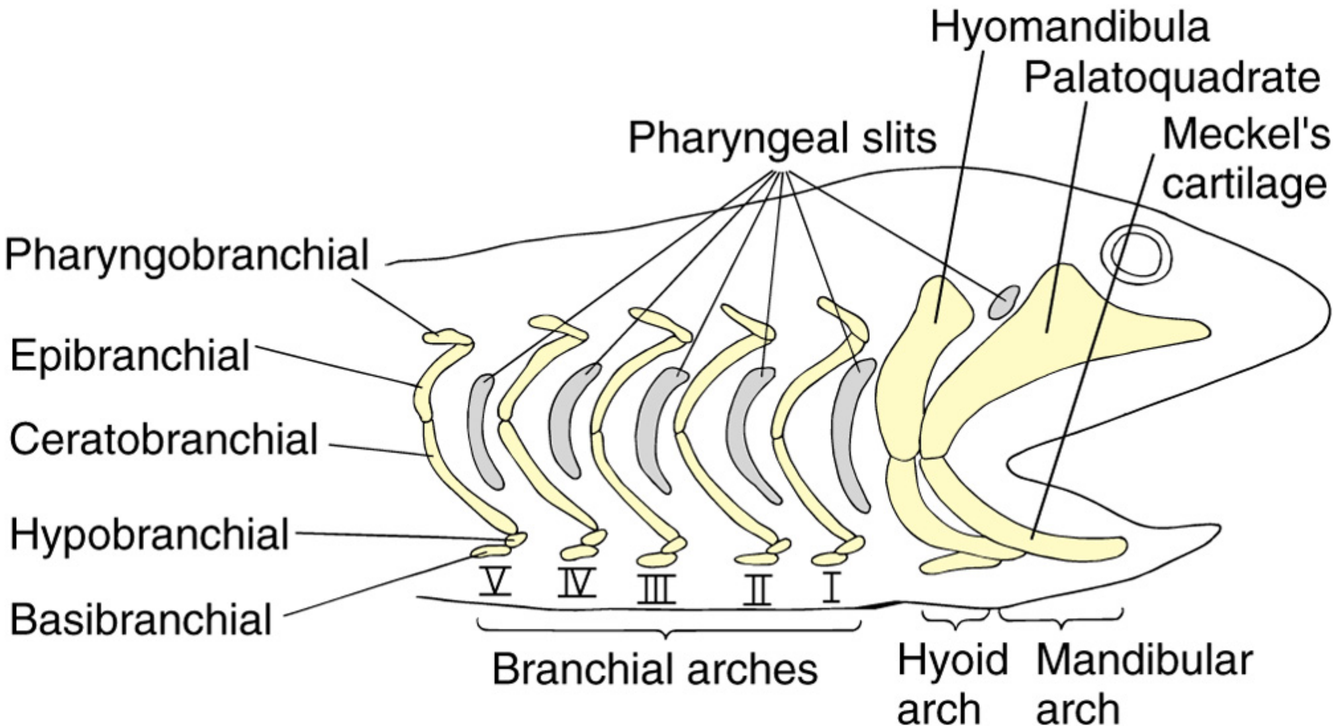
Neural crest contributions to the skull. (a) Salamander embryo illustrating the sequential spread of neural crest cells. During early embryonic development, neural crest cells contribute to the head mesenchyme, which is called the ectomesoderm because of its neural crest origin. (b) Also contributing to the head mesenchyme are cells of mesodermal origin, the mesodermal mesenchyme.The position of the mesodermal (stippled) and the neural crest (shaded) mesenchyme, and the approximate interface between them, are indicated in the chick embryo. Skull of a chick (c) and a human fetus (d) show bones or portions of bones derived from neural crest cells (shaded).

The **first arch** is called the **Mandibular Arch** and it's divided into dorsal and ventral

Elements:
A- dorsal element-called the **paeloquadrate**. It contributes to the upper jaw
B- ventral element-called **Meckel's cartilage**. It contributes to the lower jaw

The **second arch** is called the **hyoid arch**, most prominent component is the **hyomandibula**. In mammals, the ventral portion is involved in support the tongue, muscles used for swallowing and jaw movements.

Branchial arches I-V are associated with the gill apparatus. In mammals they eventually contribute to the larynx



Primitive splanchnocranium. Seven arches are shown. Up to five elements compose an arch on each side, beginning with the pharyngobranchial dorsally and in sequence to the basibranchials most ventrally.The first two complete arches are named: mandibular arch for the first and hyoid arch for the second that supports it.The characteristic five arch elements are reduced to just two in the mandibular arch: the palatoquadrate and Meckel’s cartilage.The large hyomandibula, derived from an epibranchial element, is the most prominent component of the next arch, the hyoid arch. Behind the hyoid arch are variable numbers of branchial arches I, II, and so on.

Subsequent development in Humans

In **Neurocranium** two major changes (Chondrocranium)
-Spread/fusion of paired cartilages

1- parachoradal cartilages fuse to form the basal plate

2- prechordals fuse with the nasal capsules to form the ethnoid region

3- parachordal/occipital region fuse with the auditory and orbital cartilages resulting in a single unit chondrocranium

In **Splanchnocranium**:

1-Meckel’s cartilage attaches to the auditory region

2- Hyoid arch and branchial arches form the hyobranchial appparatus

Following these changes, replacement bone forms and dermal bone is added

-the dermal bone covers the anterior region of the chondrocranium , eventually fuse to encase the brain. Growth of these bones continue after birth.

-At birth, temporary gaps called fontanelles are found between plates of dermal bones

- -molding during birth
- -accomodation for rapid growth of the brain

-After birth

- -fontanelles close typically between 18-24 months
- -suture lines form to hold the skull together.

The **dermatocranium** lies superficial to neurocranium, has a large number of bones.

These are described below as bone series rather than individual elements

1. **Facial series**: Premaxilla, Maxilla, Nasals

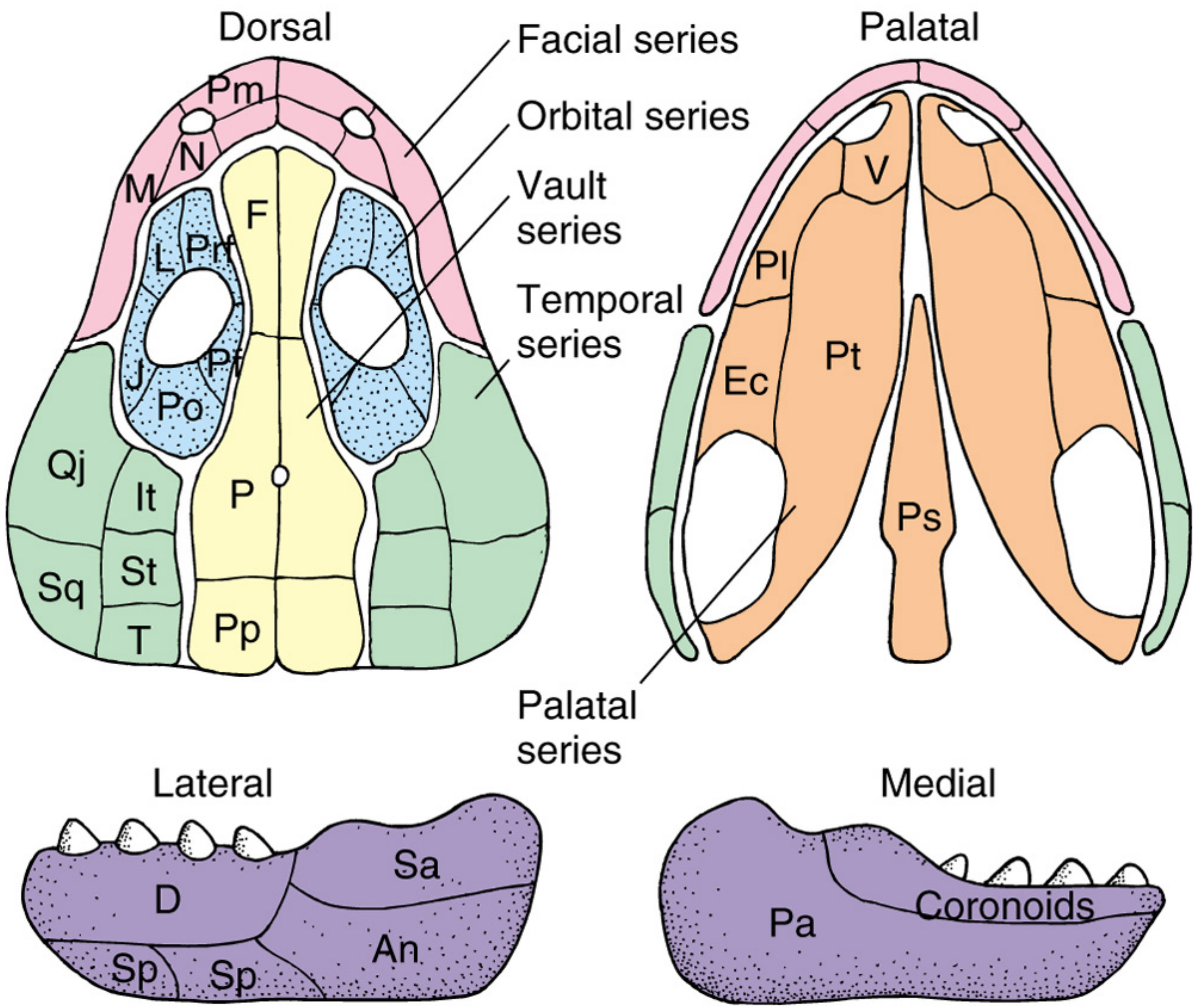
2. **Orbital series**: Lacrimal, Prefrontal, Postfrontal, Postorbital, Jugal

3. **Temporal series**: Intertemporal, Supratemporal, Tabular, Squamosal, Quadratojugal

4. **Vault series**: Frontal, Parietal, Postparietal

5. **Palatal series**: Vomer, Palatine, Ectopterygoid, Pterygoid, Parasphenoid

6. **Mandibular series**: Lateral bones: dentary, splenials, angular, surangular. Medial bones: prearticular, coronoids


Dorsal
Facial series
Palatal
Orbital series
Vault series
Temporal series
Pm
N
M
F
L
Prf
Pf
J
Po
Qj
It
P
Sq
St
T
Pp
V
Pl
Ec
Pt
Ps
Palatal series
Lateral
Medial
Sa
D
An
Sp
Sp
Pa
Coronoids

Phylogeny of the Skull

The skull is a composite structure derived from the splanchnocranium, dermatocranium, and chondrocranium. Each component comes from a separate phylogenetic source. The skull evolution is complex reflecting complex feeding styles.

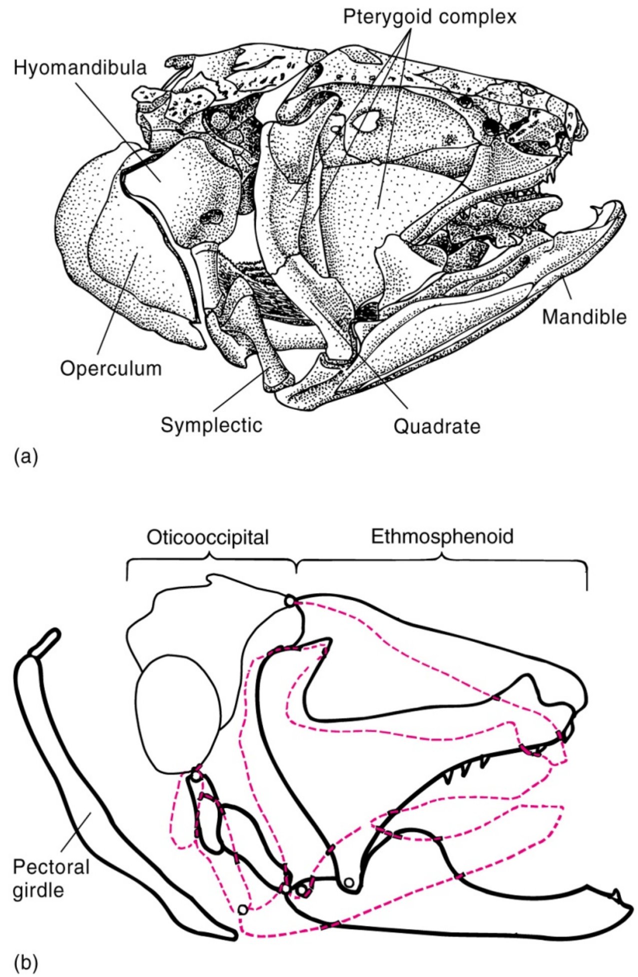
Fishes (Crossopterygians or Sarcopterygians)

1. In early fish the neurocranium was well ossified.

2. One notable feature of the crossopterygian skull is the presence of a movable hinge.

3. The dermal regions of the skull consisted of medium sized bones arranged in a pattern similar to the generalized vertebrate skull.

4. The jaw hinge involves two replacement bones.



Cranial kinesis of a coelacanth, *Latimeria*. (a) Lateral view of the skull.
(b) Biomechanical model of major functional elements showing displacement pattern during jaw opening (solid lines) compared with closed position(dashed lines). Pterygoid complex includes entopterygoid, ectopterygoid, and epipterygoid.

Labyrinthodont Amphibians

The skull structure of the labyrinthodonts is similar to that of crossopterygians with a few notable changes:

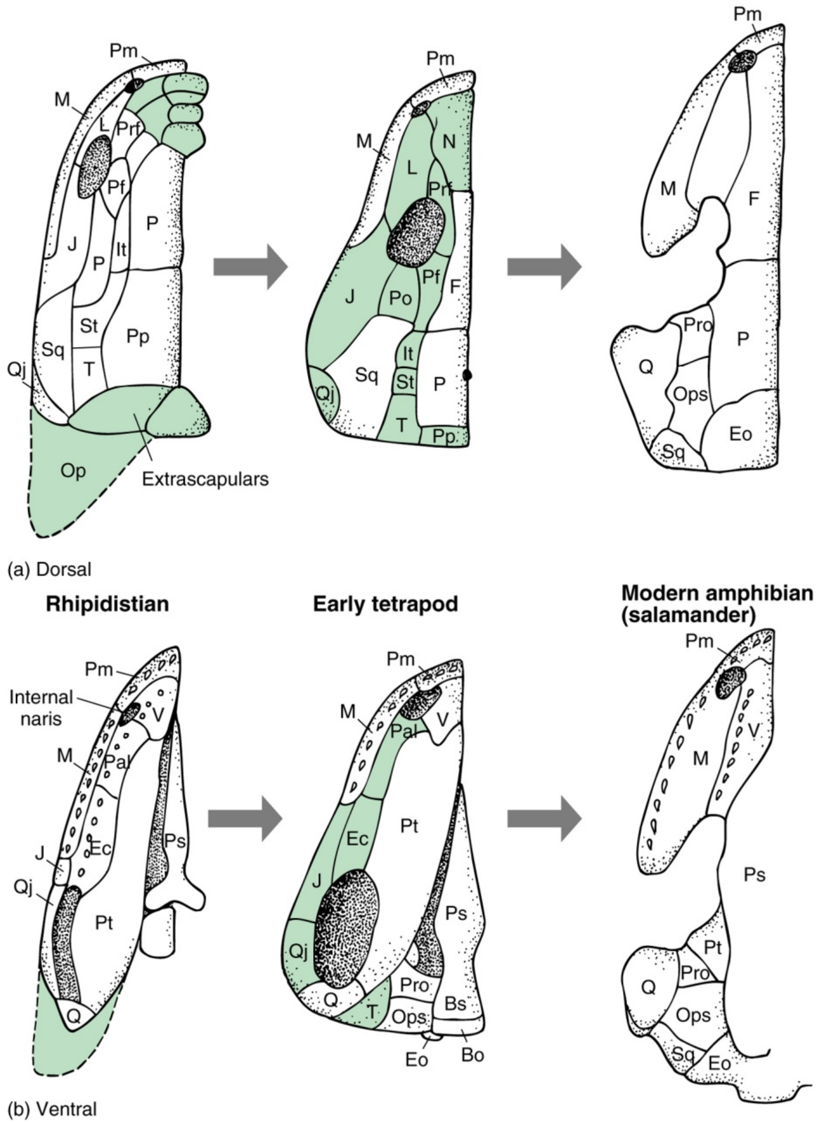
a. The proportions of the skull changed in that in the labyrinthodonts the regions anterior to the orbitals were elongated and the posterior regions were shortened.

b. There is a reduction in the number of dermal bones.

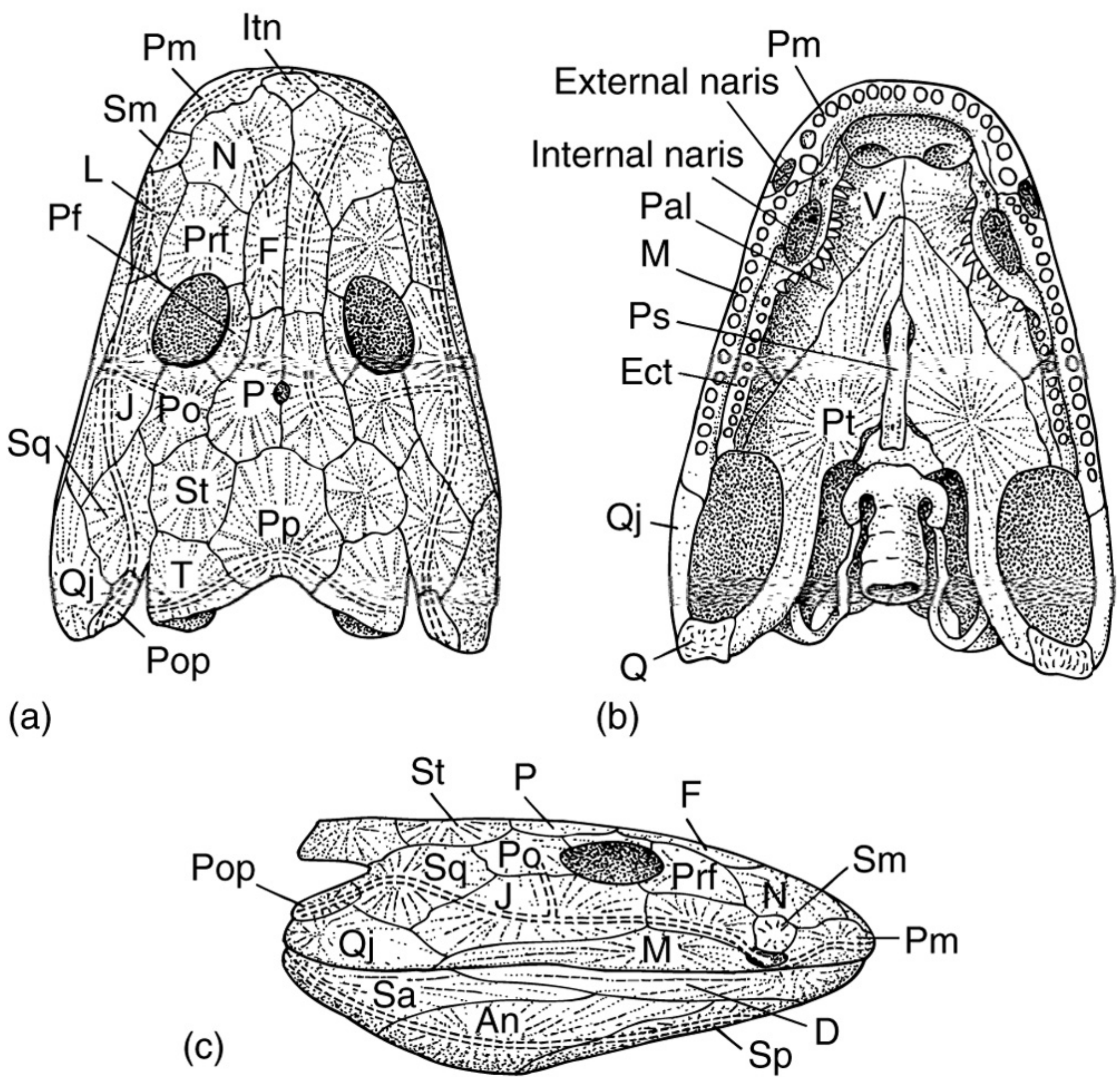
c. The gills and operculum were eliminated.

d. The jaw attachment was modified.

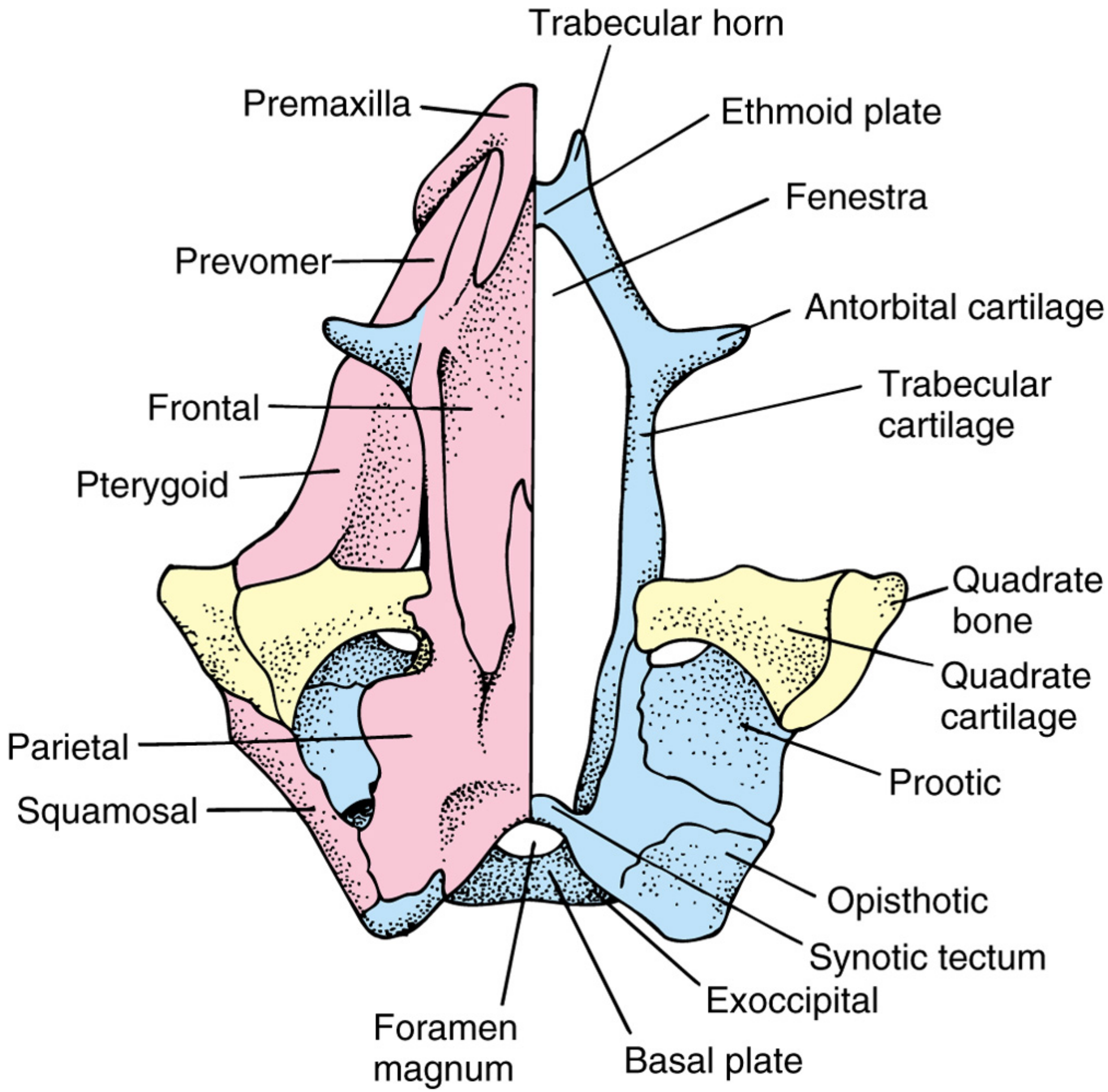
e. The movable hinge connecting the anterior and posterior endocranium in crossopterygians is lost in the labyrinthodonts.



Diagrammatic views of skull modifications from rhipidistian to early tetrapod to modern amphibian (salamander).
(a) Dorsal views. (b) Ventral (palatal) views.
Skull bones lost in the derived group are shaded in the skull of the preceding group.



Skull of Ichthyostega, a primitive tetrapod of the late Devonian.



Skull of Necturus, a modern amphibian. Superficial skull bones are indicated on the left. These bones have been removed to reveal the chondrocranium and derivatives of the splanchnocranium on the right.

Reptiles

1. The primary difference between early reptiles and amphibians involves the proportions of the skull. The skull in reptiles is higher and narrower. Later reptiles exhibited a number of modifications.

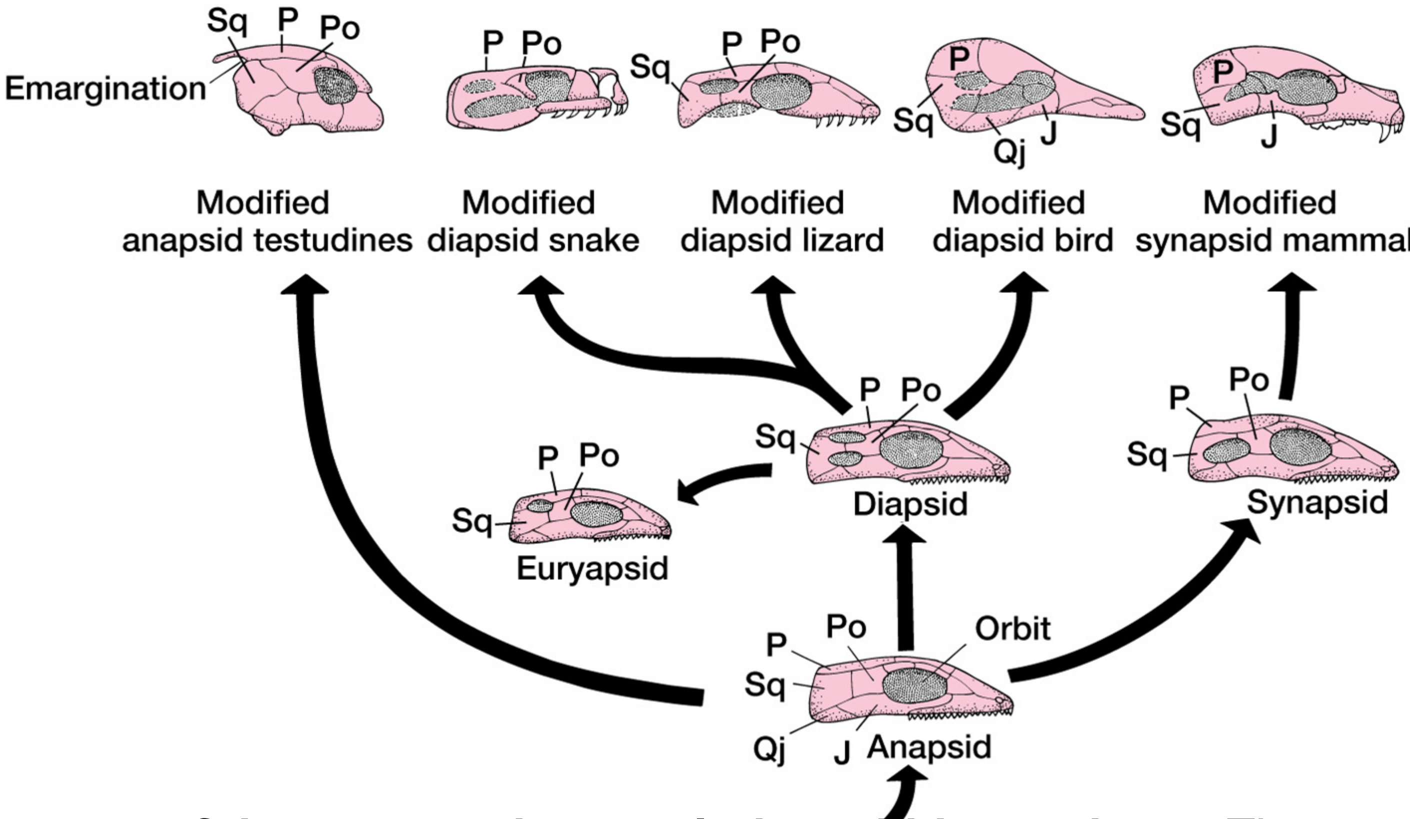
a. Again, there is a reduction in size or the outright elimination of some of the dermal bones.

b. There is the appearance of openings in the posterior side of the skull. Reptiles having two openings on each side (Diapsida) provide the stem for birds and modern reptiles with the exception of the turtles ((anapsides) .

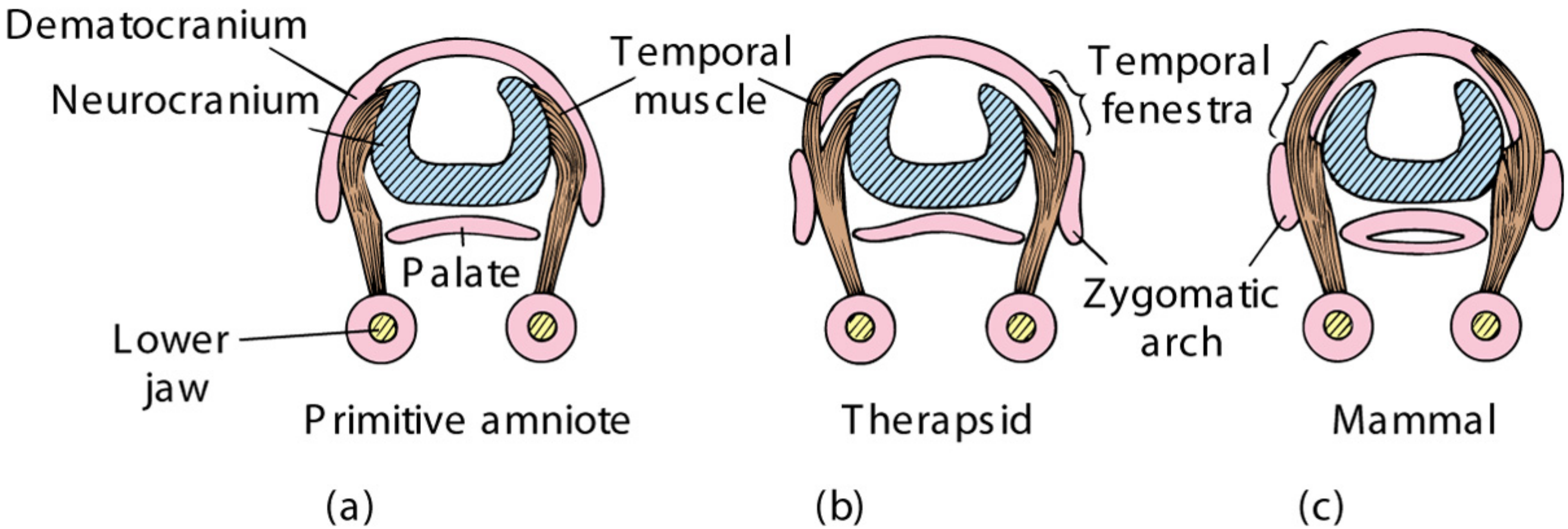
c. The neurocranium is ossified and most forms have a single occipital condyle.

d. Jaw articulation

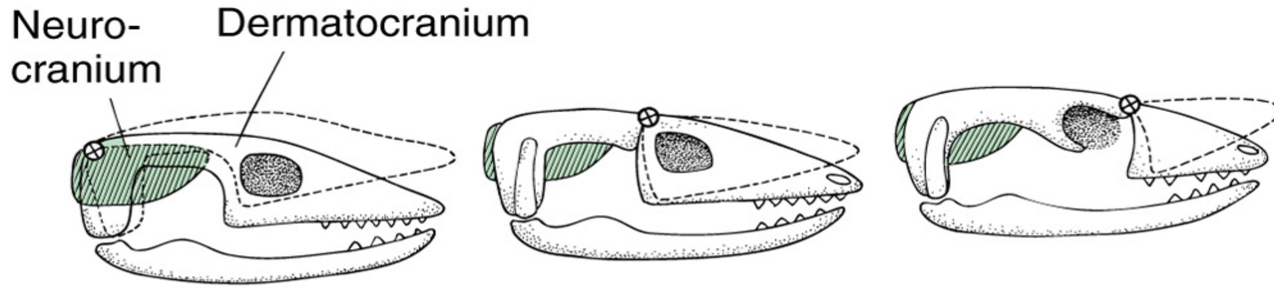
The hyomandibula is represented by the stapes. The hypobranchial apparatus is represented by the lower portion of the hyoid arch and the branchial arches.



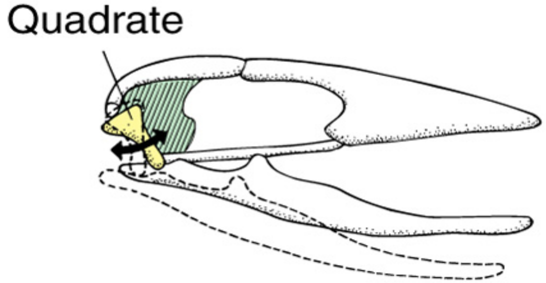
Major lineages of dermatocranium evolution within amniotes. The anapsid skull occurs in cotylosaurs and their modern descendants, turtles and tortoises.Two major groups, the diapsids and synapsids, independently evolved from the anapsids. Sphenodon and crocodilians retain the primitive diapsid skull, but it has been modified in diapsid derivatives such as snakes, lizards, and birds. Shading indicates positions of temporal fenestrae and orbit.Abbreviations: jugal (J), parietal(P), postorbital (Po), quadratojugal (Qj), squamosal (Sq)



Temporal fenestrae. The shift in jaw muscle attachment to the skull is shown. (a) Anapsid skull. In early amniotes, temporal muscles run from the neurocranium to the lower jaw. Such a skull is retained in modern turtles. (b) Perforation in the dermatocranium opens fenestrae, and attachment of jaw muscles expands to the edges of these openings. (c) Extensive attachment of jaw muscles to the surface of the dermatocranium. Such development of fenestrae characterizes the diapsid and synapsid radiations.



(a) Metakinesis Mesokinesis Prokinesis



(b) Streptostyly

Cranial kinesis in squamates.(a) There are three types of cranial kinesis based largely on the position at which the hinge (X) lies across the top of the skull. The hinge may run across the back of the skull roof (metakinesis), behind the orbit (mesokinesis), or in front of the orbit where the snout articulates (prokinesis). (b) The ability of the quadrate to rotate about its dorsal end is called streptostyly.

Therapsids

Therapsids- mammal like reptiles believed to be the precursors of mammals.
Several notable changes in skull structure were present in this group.

1- Therapsids were synapsid: one single opening located on the temporal region of the skull. The postorbital bone separating the two openings reduced in size in some forms.

2- Therapsids had a pair of occipital condyles, bones which articulate with the atlas of the spinal cord. Early amphibians, most reptiles, and birds only have one (modern amphibians have two)

3- Therapsids exhibited increased size of the dentate bone in lower jaw (dermal bone of the mandibular series). The articulate and quadrate bone (derived from 1st arch) are smaller and tend to be shifted posteriorly.

In some therapsids, the articulate and quadrate lost their position as jaw hinges and jaw articulation between the squamosal bone (temporal) and dentate become evident.

4- Therapsids had a further reduction of bone numbers either through loss or fusion. E.g. jaw: dentate bone of the mandibular series enlarges and 5 other bones in the series are lost or reduced.

5. The therapsids also exhibit some changes related to feeding. Amphibians and reptiles bolt their food. Air entry from the external nares to the anterior mouth region is not important. In the therapsids, two factors made this undesirable:

a. the transition to endothermy was accompanied by an increase in the rate of respiration.

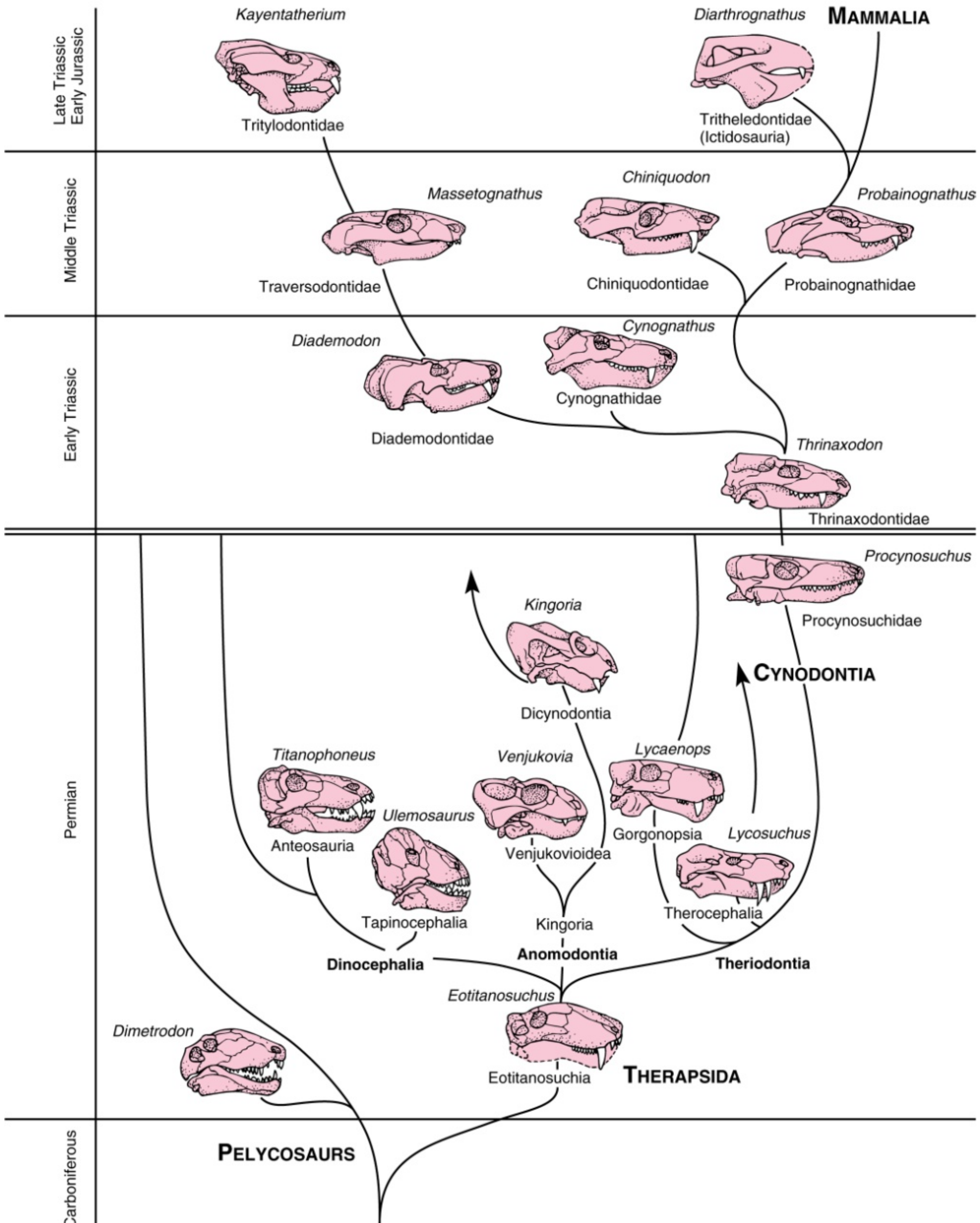
b. the therapsids had a tendency to chew and tear their food rather than bolt it down.

Both the increase in respiratory rate and the prolonged presence of food in the mouth disrupts air flow in the anterior portion of the mouth. Several changes in bone structure allowed a bypass of the anterior mouth region:

a. Two of the bone pairs in the palatal series, the parasphenoid and pterygoids, are reduced.

b. The vomer fused and the palatine bones and maxilla grew to the midline to form a secondary palate. In addition, the internal nares moved posteriorly and merged.

The result is that air moves from the external nares to the internal nares to deliver the air to the pharynx while bypassing the chewing region.


Late Triassic
Early Jurassic
Middle Triassic
Early Triassic
Permian
Carboniferous
Kayentatherium
Tritylodontidae
Diarthrognathus
MAMMALIA
Tritheledontidae
(Ictidosauria)
Massetognathus
Traversodontidae
Chiniquodon
Chiniquodontidae
Probainognathus
Probainognathidae
Diademodon
Diademodontidae
Cynognathus
Cynognathidae
Thrinaxodon
Thrinaxodontidae
Procynosuchus
Procynosuchidae
Kingoria
Dicynodontia
CYNODONTIA
Titanophoneus
Anteosauria
Ulemosaurus
Tapinocephalia
Venjukovia
Venjukovioidea
Lycaenops
Gorgonopsia
Lycosuchus
Therocephalia
Kingoria
Anomodontia
Dinocephalia
Theriodontia
Eotitanosuchus
Eotitanosuchia
THERAPSIDA
Dimetrodon
PELYCOSAURS

Mammals

In mammals most of the trends noted in the therapsids are continued, including fusion and bone rearrangement to accommodate larger brain size.

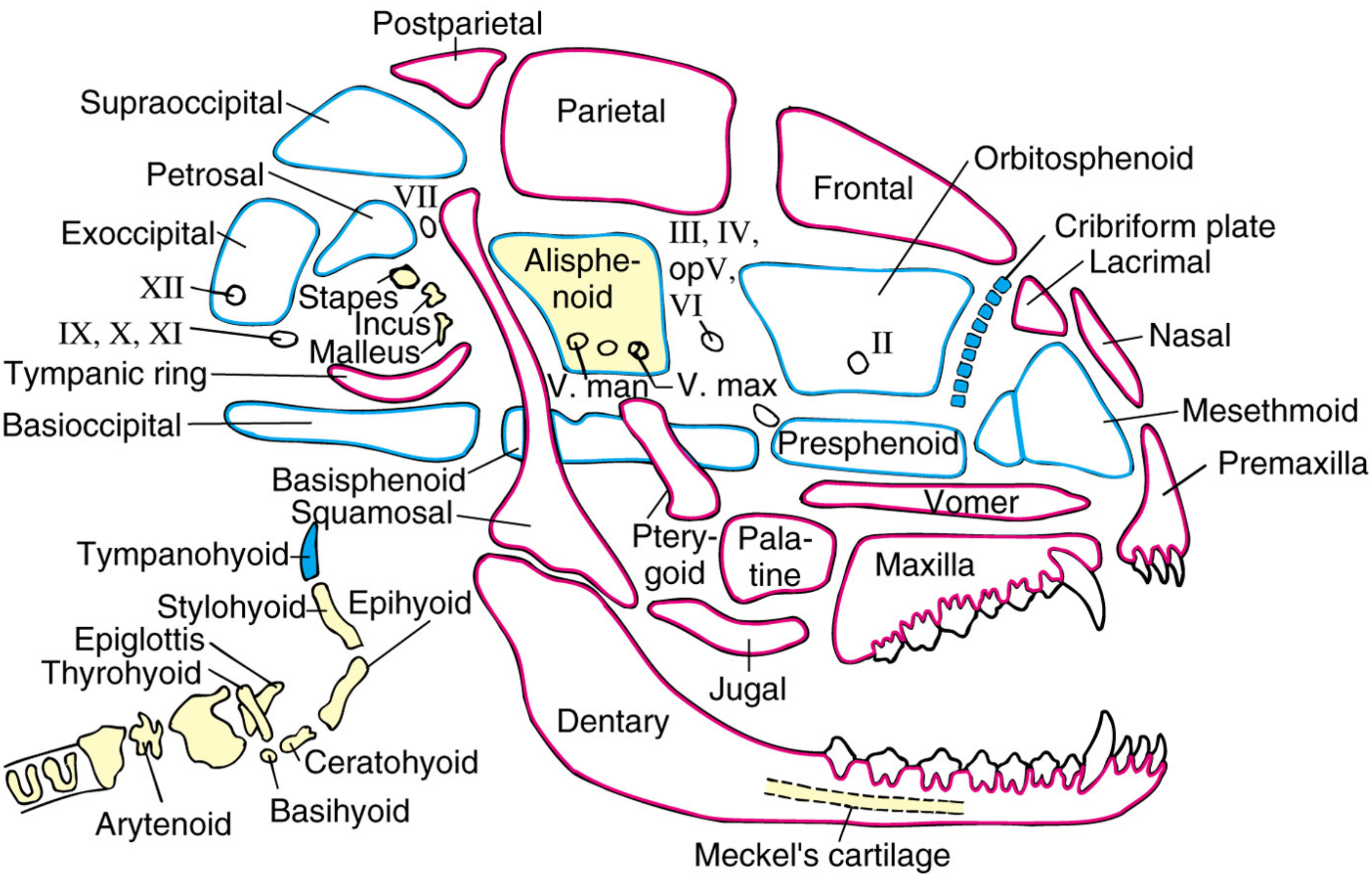
1. The tendency to reduce the postorbital bone is continued in the mammals and in marsupials. The orbital opening and the temporal opening merge to produce a modified synapsid skull. In more advanced mammals extensions of the jugal bone and the frontal bone reestablish a separation of the orbital and temporal space.

In mammals the pretorbital bone is lost and there is a loss of 4 of the 5 elements making up the orbitosphenoid group of bones. Only the lacrimal bone remains.

2. Pair of occipital condyles persist in mammals.

3. In therapsids, the dentate enlarged, other mandibular bones are lost or reduced, and the quadrate and articulate moved laterally.

In mammals, most of the original dermal elements that make up the early mandibular series of bones are lost, only dentary bone remains to make up the mandible. The jaw in mammals articulate to the neurocranium via two dermal bones: the dentary or mandible bone and the squamosal or temporal bone. The replacement bones that ancestrally served to articulate the jaw more posteriorly move to the middle ear. The quadrate forms the incus, the articulate forms the malleus. The incus is in contact with the stapes-which was first present in amphibians and reptiles as a modification of the hyoid arch.


Postparietal
Supraoccipital
Parietal
Petrosal
VII
Exoccipital
Frontal
Orbitosphenoid
Cribriform plate
Lacrimal
III, IV,
opV,
VI
Alisphe-
noid
XII
Stapes
Incus
IX, X, XI
Malleus
Tympanic ring
II
Nasal
V. man
V. max
Mesethmoid
Basioccipital
Presphenoid
Premaxilla
Basisphenoid
Vomer
Squamosal
Ptery-
goid
Pala-
tine
Maxilla
Tympanohyoid
Stylohyoid
Epihyoid
Epiglottis
Thyrohyoid
Jugal
Dentary
Ceratohyoid
Arytenoid
Basihyoid
Meckel's cartilage

4. the reduction/fusion of bones noted in the therapsids continues further. Most notably, the frontal and parietal bones enlarge to accommodate a larger brain. E.g. primates.

5. The changes in skull structure related to feeding noted in the therapsids evolve further:

a. The parasphenoid bone is lost.
b. The pterygoid bones are further reduced.
c. The phalanges or extensions of the premaxilla, maxilla and palatine extend to form the secondary palate. The internal nares remain fused and form a nasal cavity that is filled with scrolls of bone called the turbinates. The turbinates are derived from portions of the maxilla, ethmoids and nasal bones.

6.The hypobranchial skeleton is made up by portions of the lower hyoid arch (#2) and the branchial arches. Included are the:

a. hyoid apparatus- tongue movement support

b. larynx- vocal cords/prevention of foreign material to entering the lungs

c. thyroid cartilage- ventral sides of the larynx

d. cricoid cartilage- rings of cartilage surrounding the trachea

Summary:

Replacement of bones

Occipital bones present in all vertebrates: in mammals, occipital bone fuses to form one bone

Auditory region- three elements tend to be present- but in mammals they fused as one bone: periotic or petrosal bone

Sphenoid bones fused in mammals

Dermal bones

Marked changes from the prototype-loss and alteration in size

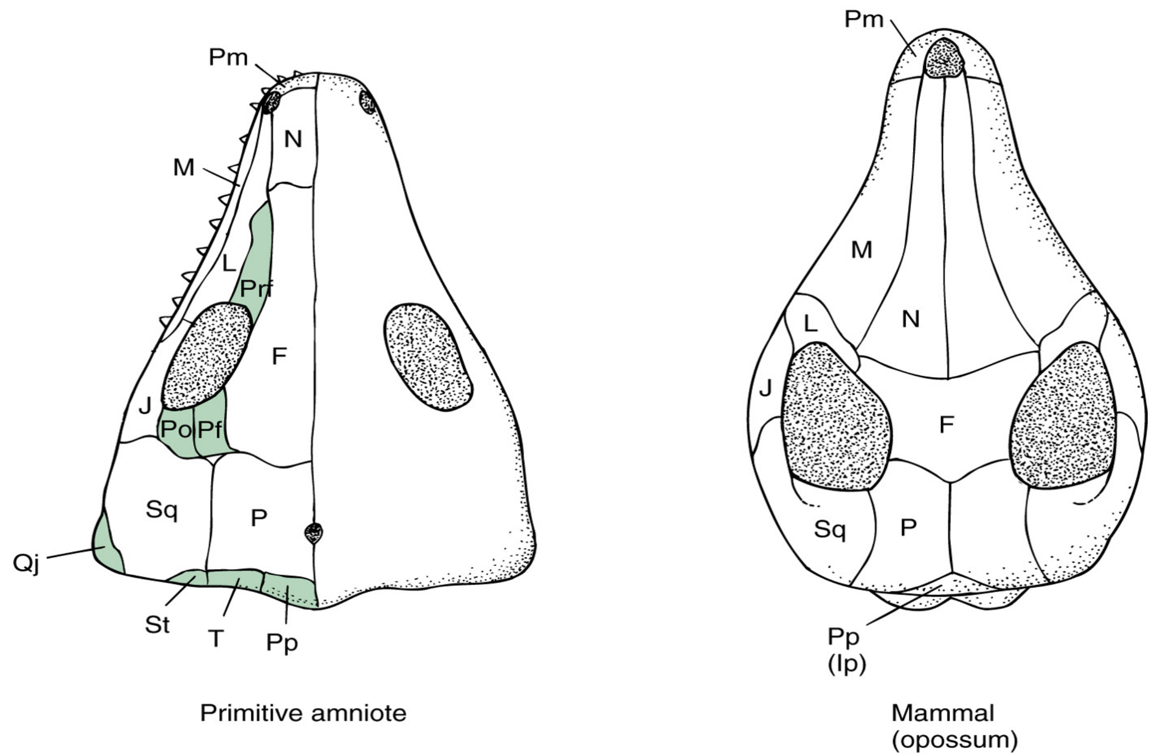
- Frontal and parietal bones form the external mammalian brain
- Orbital elements reduced to a single lacrimal bone

Dermal bones of upper jaw retained except for loss of quadratojugal in mammals, the lower jaw is reduced to the dentate in mammals.

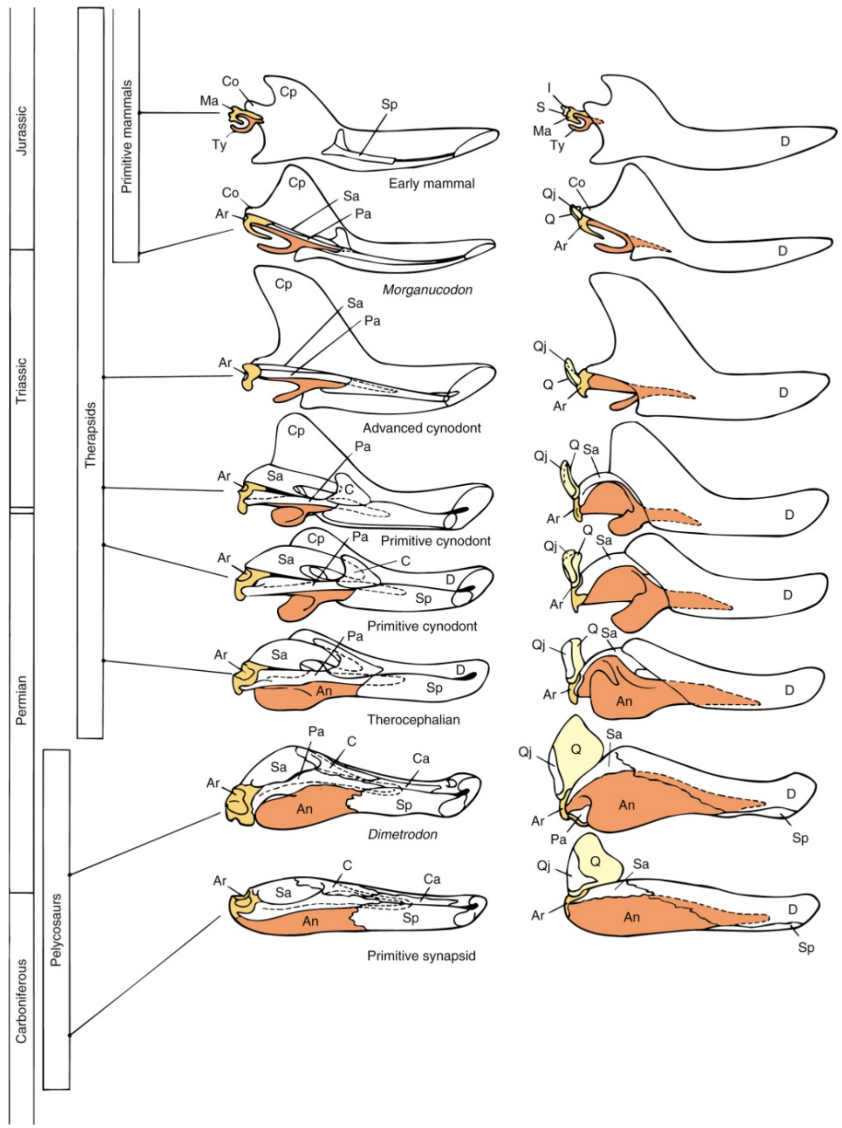
Replacement of bones of visceral arches

Articulate and quadrate from mandibular arch start as part of the jaw apparatus, tied in with the second arch derivative, hyomandibula in the crossopterygian fish.
The hyomandibula moves to form the stapes in amphibians and reptiles, while the quadrate get incorporated into the auditory wall. They have articulate-quadrate articulation
In mammals, the quadrate and articulate move to the middle ear to form the incus and malleus. Jaw suspension is by tow dermal bones: dentary and squamosal.

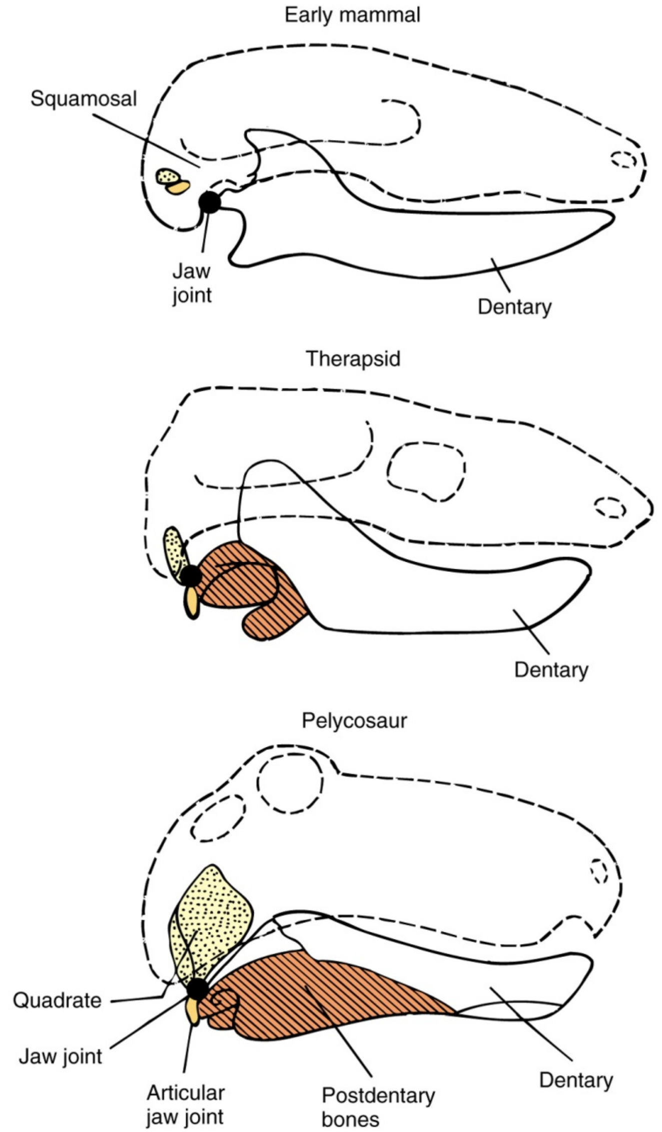
Tongue movement: hyoid arch and laryngeal cartilage formed by hyoid and branchial arches in mammals

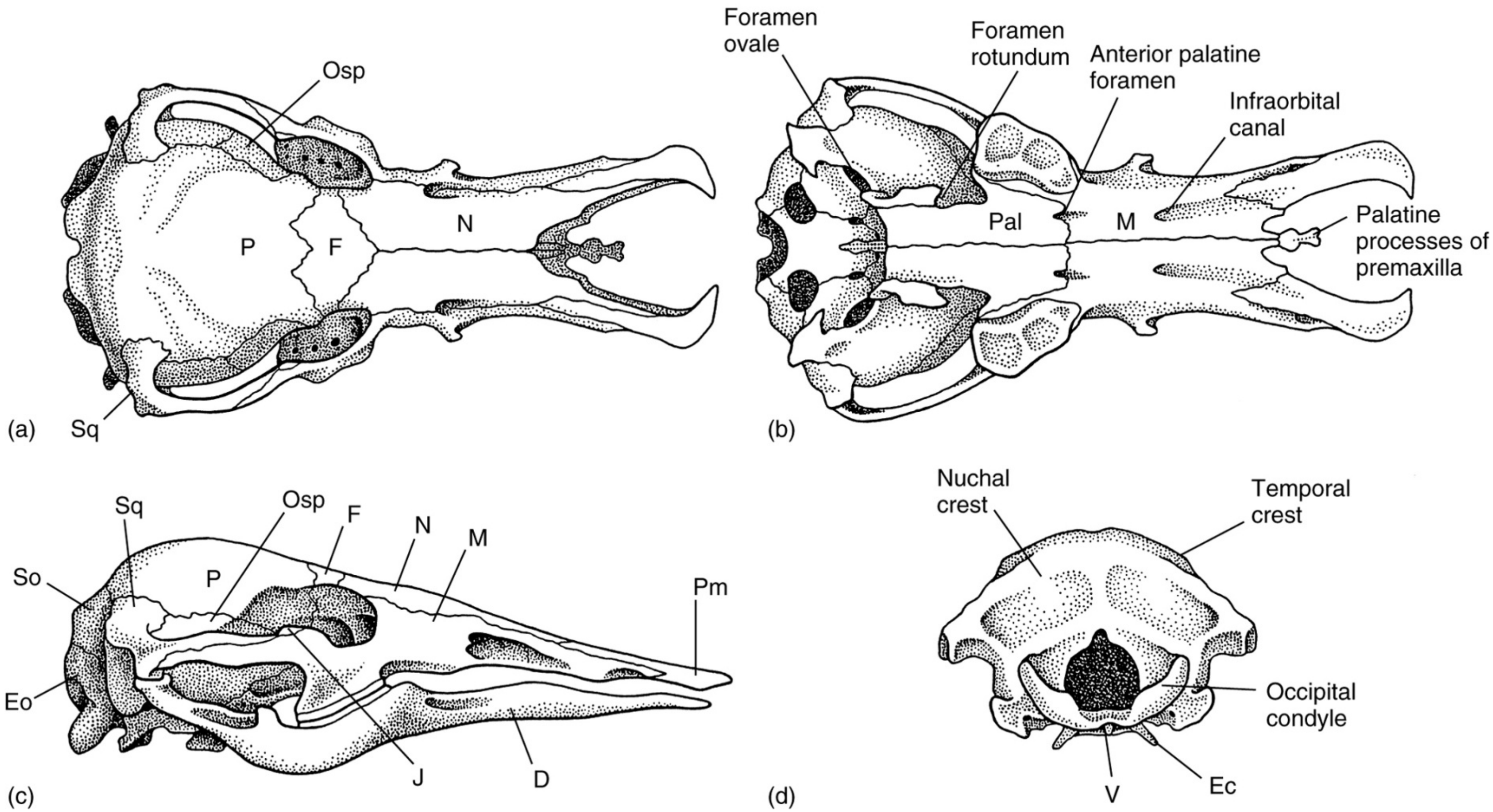


Diagrammatic comparison of a derived mammal skull with a primitive amniote skull. Bones lost in the derived mammal are shaded in the primitive amniote. In mammals, orbital and temporal openings merge.Abbreviations: frontal (F), jugal (J), interparietal (Ip), lacrimal (L), maxilla (M), nasal (N), parietal (P), postfrontal (Pf), premaxilla (Pm), postorbital (Po), postparietal (Pp), prefrontal (Prf), quadratojugal (Qj), squamosal (Sq),supratemporal (St), tabular (T).

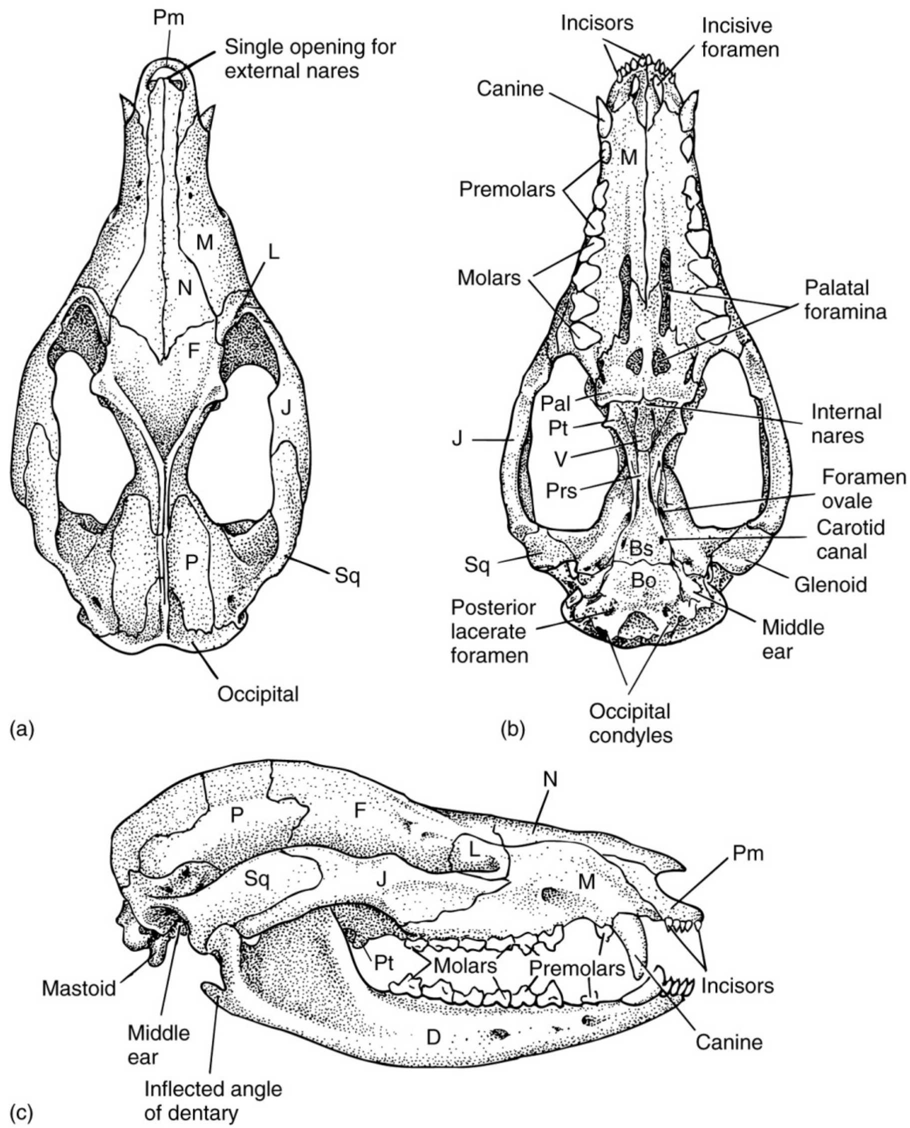


Evolution of mammalian middle ear bones


Early mammal
Squamosal
Jaw
joint
Dentary
Therapsid
Dentary
Pelycosaur
Quadrate
Jaw joint
Articular
jaw joint
Postdentary
bones
Dentary



Monotreme, skull of the duckbill platypus Ornithorhynchus. Dorsal (a), ventral (b), lateral (c), and posterior (d) views.Abbreviations: dentary (D), ectopterygoid (Ec), exoccipital (Eo), frontal (F), jugal (J), maxilla (M), nasal (N), orbitosphenoid (Osp), parietal (P), palatine (Pal), premaxilla (Pm), supraoccipital (So), squamosal (Sq), vomer (V).



Marsupial, skull of the opossum Didelphis. Dorsal (a), palatal (b), and lateral (c) views. Abbreviations: basioccipital (Bo), basisphenoid (Bs), dentary (D), frontal (F), jugal (J), lacrimal (L), maxilla (M), nasal (N), parietal (P), palatine (Pal), premaxilla (Pm), parasphenoid (Ps), pterygoid (Pt), squamosal (Sq).