

BIOLOGY 524
ADVANCED VERTEBRATE MORPHOLOGY
-OSTEOLOGY-

SKULL – II
DERMATOCRANIUM

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INTRODUCTION

RECALL:

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 in development and makes up the outer casing of the skull. It protects the brain above, and protects the entire braincase from below as the plate.

Embryology of the Dermatocranium

All components of the vertebrate dermatocranium form intramembranously from neural crest cells. In fact, it is unfortunate, as this type of formation used to be known as “dermal bone formation” (because of the proximity of the ne to the skin. However, even though we no longer use the term dermal formation, we still use the term dermatocranium.

Notably, whereas the entire dermatocranium is derived from neural crest forms intramembranously, it is not the only part of the skeleton derived from neural crest (also the splanchnocranium, which forms endochondrally), and it is not the only part of the skeleton that forms intramembranously (also significant parts of the pectoral girdle, which is derived from mesoderm).

In general, more primitive vertebrates have a greater number of individual dermatocranial bones. Through vertebrate evolution, any number of them fuse together to make bones that are a composite of multiple more primitive bones. Regardless, all dermatocranial elements remain derived from neural crest. Additionally, by the time amniotes have developed, a number of dermal elements fuse to chondrocranial or splanchnocranial elements.

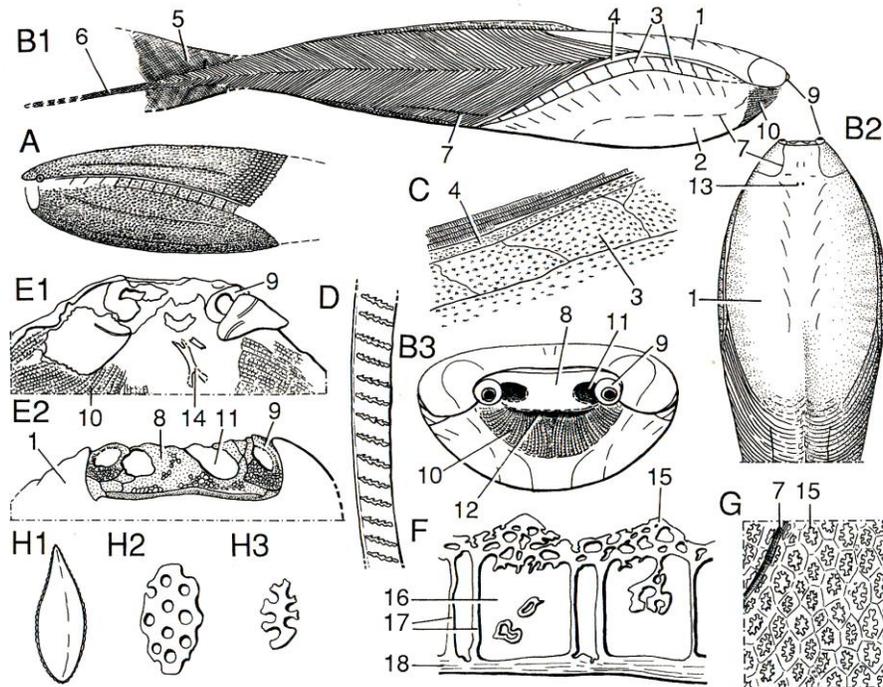
Primitive Dermatocranium

Although the splanchnocranium is generally considered the most primitive part of the skull skeleton, the dermatocranium is also very old. Many of the earliest jawless vertebrates had extensive dermal armor covering the head, and often head plus body. In most cases, this extensive dermal armor is difficult to homologize with the dermal elements of later fishes and tetrapods, but it is important to recognize the means of depositing dermal bone is likely a very ancient one.

BRIEF (PARTIAL) SURVEY OF DERMAL COVERINGS OF ANCIENT JAWLESS VERTEBRATES

ARANDASPIDAE

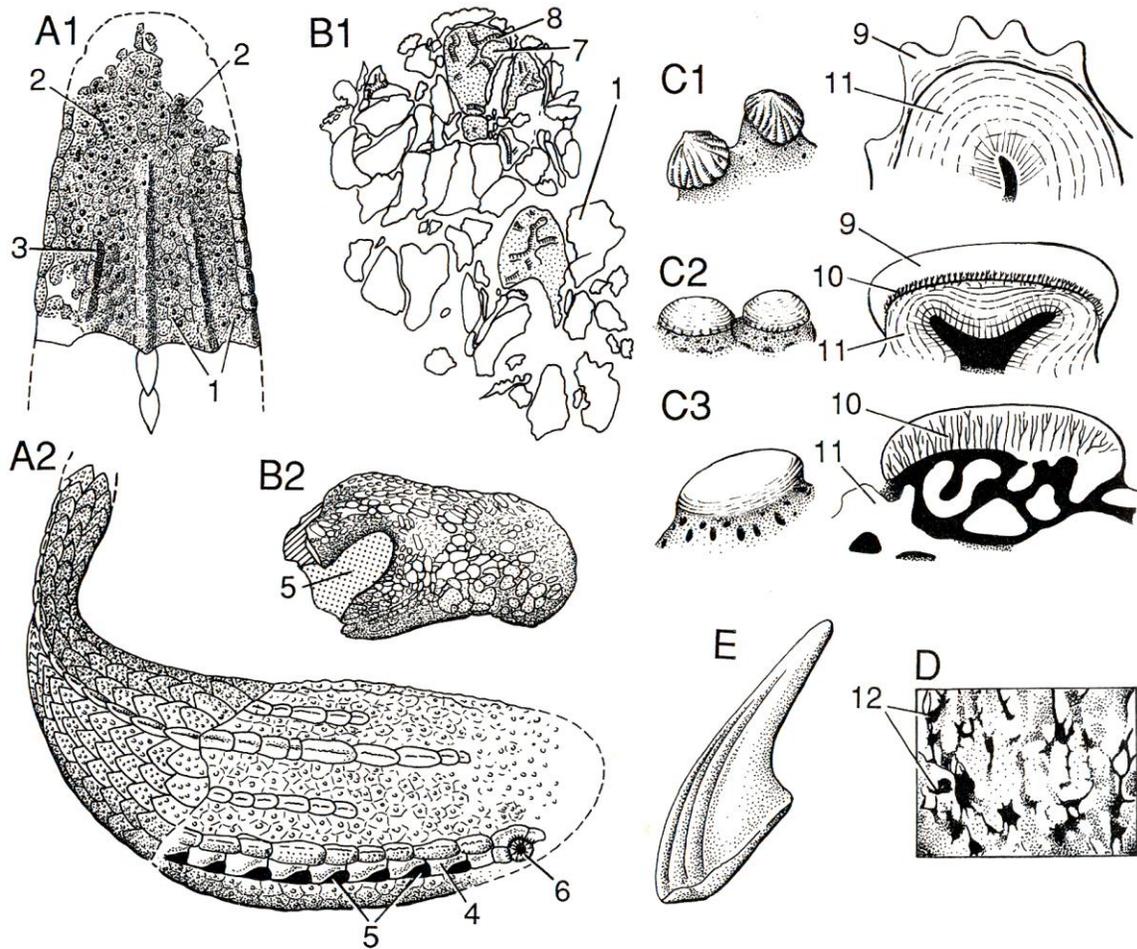
Arandaspids had an extensive dermal covering on both the dorsal and ventral sides of the head.



Arandaspida. A, *Arandaspis*, Early Ordovician of Australia, reconstruction of the head in lateral view ($\times 0.5$); B–G, *Sacabambaspis*, Ordovician of Bolivia; B, reconstruction in lateral (B1, $\times 0.5$), dorsal (B2), and anterior (B3) view; C, detail of the branchial platelets of the right side; D, detail of a portion of flange scale; E, sketch of the anterior part of the head in two of the best-preserved specimens known so far, in ventral (E1) and dorsal (E2) view respectively; F, vertical section through the exoskeleton of the dorsal shield ($\times 30$); G, aspect of the external surface of the dorsal shield, showing the grooves that mark the limits between the exoskeletal units; H, tubercles of the dermal ornamentation of *Arandaspis* (H1), *Porophoraspis* (H2), and *Sacabambaspis* (H3), brought to the same scale ($\times 20$). 1, dorsal shield; 2, ventral shield; 3, branchial platelets; 4, epibranchial plate; 5, caudal fin; 6, chordal lobe; 7, lateral-line grooves; 8, T-shaped plate; 9, presumed sclerotic ring; 10, oral plates or scales; 11, presumed nostrils; 12, mouth; 13, pineal and parapineal openings; 14, dumbbell-shaped bone or calcified cartilage; 15, tubercle; 16, cancellae; 17, double walls of the cancellae; 18, laminar basal layer. (A, H1, H2, from Ritchie and Gilbert-Tomlinson (1977); B–H3, based on Gagnier (1993a) and original material.)

ASTRASPIDAE

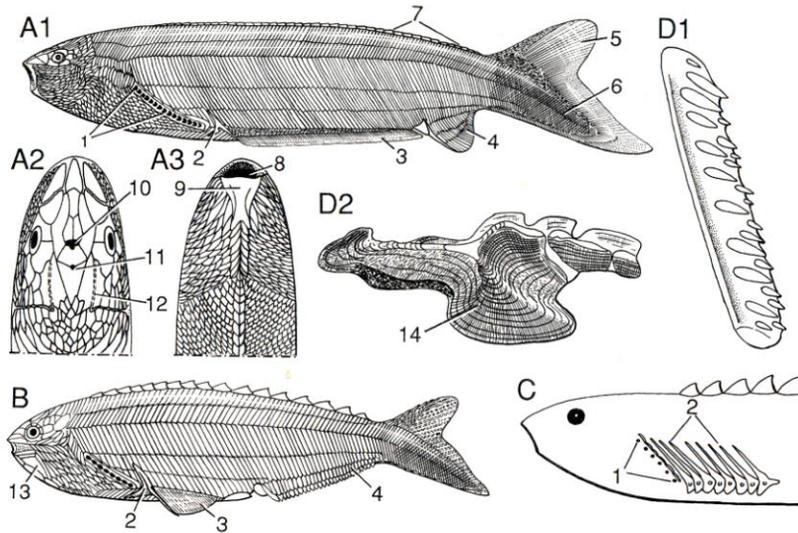
Astraspids had a mosaic of dermal bone and scales covering the head region as a dorsal head shield.



Astraspida and other Ordovician vertebrates. A, *Astraspis*, Late Ordovician of North America, dorsal shield in dorsal view (A1, $\times 0.7$) and reconstruction in dorsolateral view (A2); B, *Eriptychius*, Late Ordovician of North America, partially articulated snout in dorsal view (B1, $\times 1$), showing masses of globular calcified cartilage with canals (stippled), and isolated branchial plate (B2, $\times 2$); C, comparison of the aspect and structure (vertical sections) of the tubercles of the dermal ornamentation in *Astraspis* (C1), *Pycnaspis* (C2), and *Eriptychius* (C3) from the Ordovician of North America; D, cell spaces (lacunae) in the basal bone of an undetermined tubercle from the Ordovician of North America (about $\times 150$); E, *Stereocoonus*, Ordovician of Siberia, a possible vertebrate dermal denticle ($\times 50$). 1, tesserae; 2, supraorbital sensory line; 3, longitudinal ridges; 4, branchial plates; 5, branchial openings; 6, eye; 7, calcified endoskeleton (globular calcified cartilage); 8, grooves for subaponevrotic vessels; 9, enameloid; 10, dentinous tissue (meso- or metadentine); 11, aspidine; 12, cell space. (A1, from Halstead (1973b); A2, from Elliott (1987); B1, from Denison (1967); B2, C, based on Ørvig (1958, 1989); D, from M. M. Smith (1991); E, from Moskalenko (1973).)

ANASPIDAE

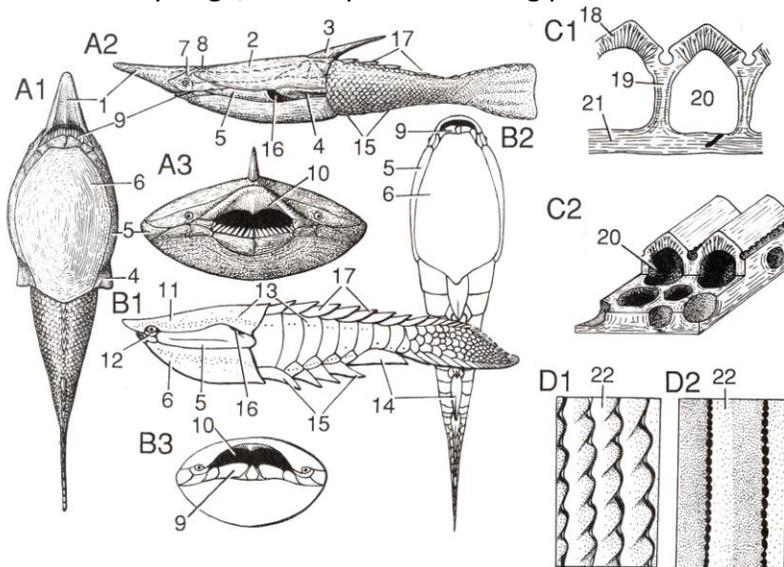
Anaspids also had a mosaic of dermal bones covering the skull region. Although some of the elements appear superficially to resemble some of the dermal skull roofing elements of gnathostomes, it is not likely they are homologous.



Anaspida. External morphology and histology. A, *Pharyngolepis*, Early Silurian of Norway, reconstruction in lateral view (A1, $\times 1$), and head in dorsal (A2) and ventral (A3) view; B, *Rhyncholepis*, Early Silurian of Europe, reconstruction in lateral view ($\times 1$); C, *Lasanius*, Early Silurian of Scotland, head in lateral view ($\times 2$); D, flange scale in external view (D1) and transverse section (D2, $\times 70$). 1, external branchial openings; 2, tri-radiate postbranchial spine; 3, paired fins; 4, anal fin; 5, epichordal lobe of caudal fin; 6, chordal lobe of caudal fin; 7, median dorsal scutes; 8, mouth; 9, oral plate; 10, presumed nasohypophysial foramen; 11, pineal foramen; 12, sensory-line groove; 13, ventral 'gular' plate; 14, laminar aspidine. (A, combined from I. C. Smith (1957), Ritchie (1964), and Stensjö (1964); B, from Ritchie (1980); C, from Parrington (1958); D, from Gross (1958).)

HETEROSTRACI

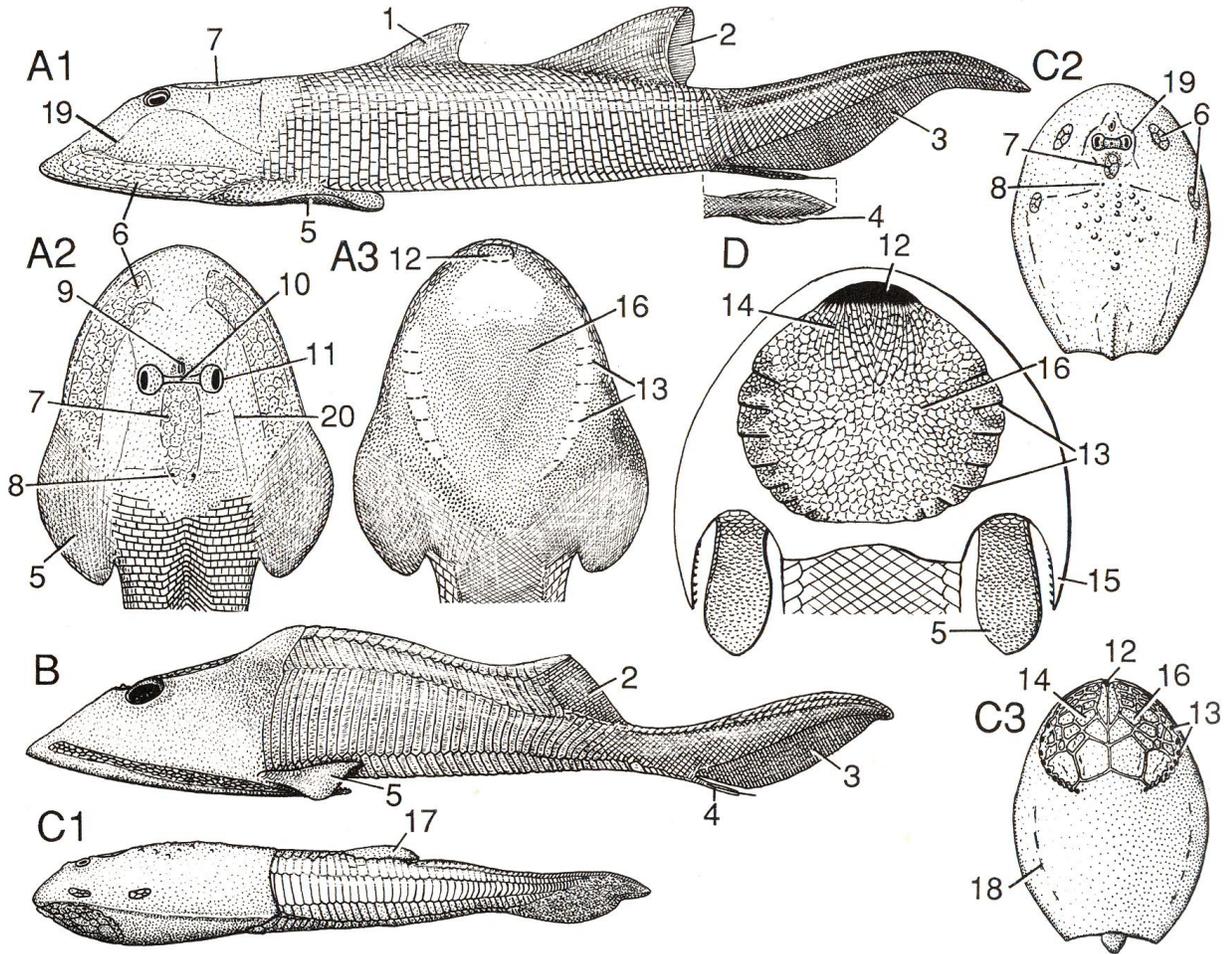
Many heterostracans have very large, robust plates covering parts of the skull.



Heterostraci. External morphology and histology. A, the pteraspidiiform *Errivaspis*, Early Devonian of Europe, in ventral (A1, $\times 0.5$), lateral (A2), and anterior (A3) view; B, the cyathaspidiform *Anglaspis*, Early Devonian of Europe, in lateral (B1, $\times 1$), ventral (B2), and anterior (B3) view; C, generalized structure of the heterostracan exoskeleton in vertical section (C1, $\times 25$) and in block diagram, showing the cancellar middle layer (C2); D, external aspect of the dermal bone ornamentation in pteraspidiiform heterostracans (D1, $\times 50$) and cyathaspidiform heterostracans (D2, $\times 50$). 1, rostral plate; 2, dorsal disc; 3, dorsal spinal plate; 4, cornual plate; 5, branchial plate; 6, ventral disc; 7, orbital plate; 8, pineal plate; 9, oral plates; 10, prenasal groove; 11, dorsal shield (fused rostral, pineal, orbital epitega + dorsal disc); 12, suborbital plate; 13, sensory-line pores; 14, postanal plate; 15, preanal ridge; 16, common external branchial opening; 17, median dorsal ridge; 18, dentine; 19, aspidine; 20, cancella; 21, basal layer; 22, dentine ridge. (A, from E. I. White (1935) and Bleick (1984); B, from Kiaer (1932) and Bleick and Heintz (1983); C1 from Novitskaya (1971); D, from Bleick (1982a).)

OSTEOSTRACI

Osteostracans had extensive dermal armor coving virtually their entire bodies. Dorsal head shields are very solid, but areas presumed to be “sensory fields” were covered with a much thinner mosaic layer. Nerves leading away from the sensory field regions indicate that these were probably the surfaces of electro-sensing organs.



Osteostraci. External morphology. A, *Ateleaspis*, Early Silurian of Scotland, reconstruction in lateral view (A1, $\times 0.8$), and head in dorsal (A2) and ventral (A3) view. B, zenaspidid osteostracan, Early Devonian of Scotland, reconstruction in lateral view ($\times 0.5$); C, *Tremataspis*, Late Silurian of Estonia, reconstruction in lateral view (C1, $\times 1$), and head in dorsal (C2) and ventral (C3) view; D, generalized cornuate osteostracan, head and paired fins in ventral view. 1, anterior dorsal fin; 2, posterior dorsal fin; 3, caudal fin; 4, horizontal caudal lobe; 5, pectoral fin; 6, lateral fields; 7, median field; 8, endolymphatic duct; 9, nasohypophysial opening; 10, pineal foramen; 11, sclerotic ring; 12, mouth; 13, external branchial openings; 14, oral plates; 15, cornual process; 16, scales or dermal plates covering of oralbranchial chamber; 17, median dorsal scute; 18, ventral trunk sensory line; 19, infraorbital sensory line; 20, main lateral sensory line. (A, from Ritchie (1967); C, from Janvier (1985b); D, partly based on specimens of ‘*Cephalaspis*’ *cradleyensis* in White and Toombs (1983).)

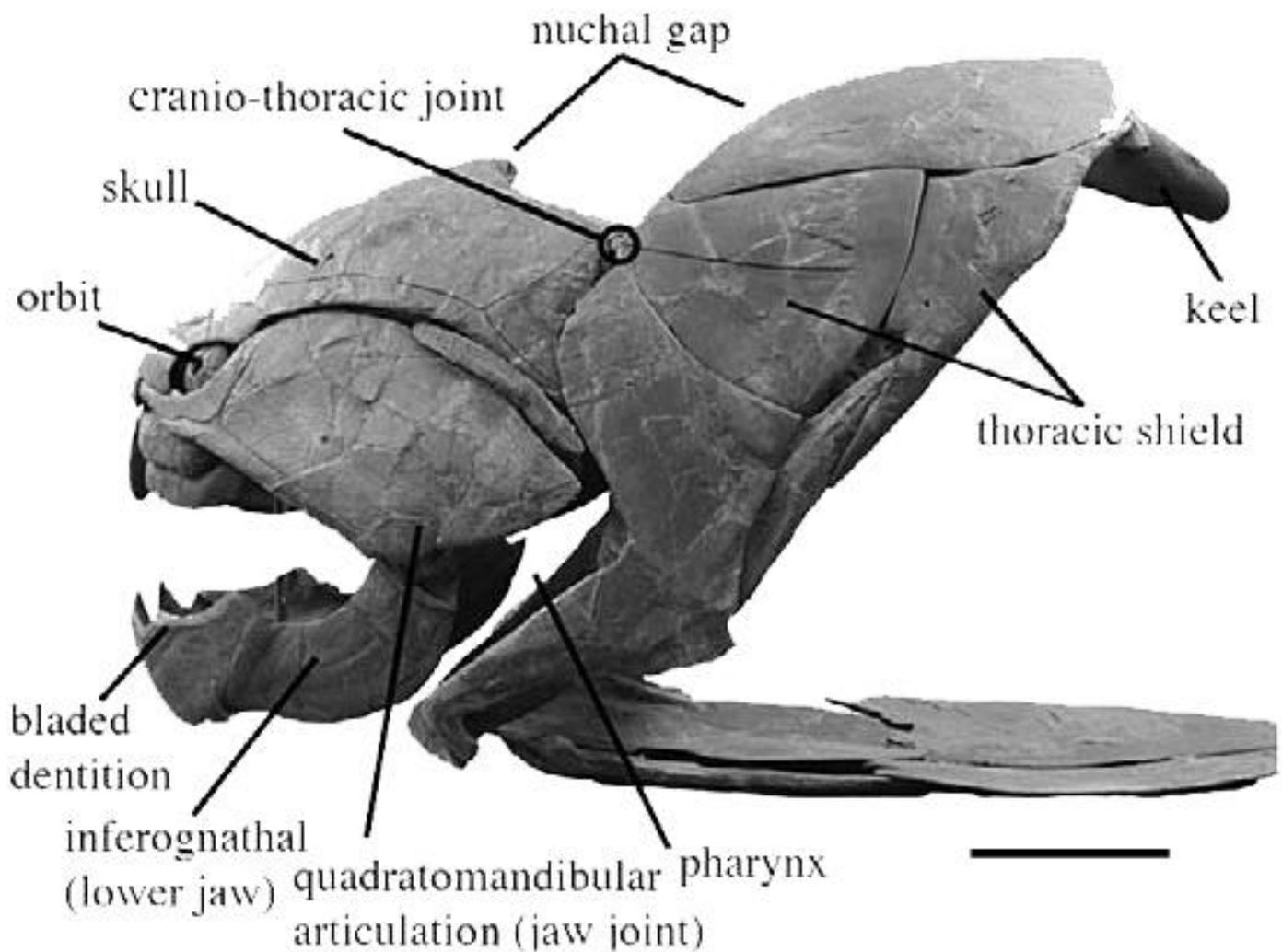
BRIEF (PARTIAL) SURVEY OF DERMAL COVERINGS OF BASAL GNATHOSTOMES

PLACODERMI

Placoderms were a moderately diverse group of basal gnathostomes. They have well developed jaws, which were equipped with robust cutting plates, but no teeth. Thus it is likely that the acquisition of jaws and teeth were independent events.

One of the most notable features of placoderms was that the head shield region articulated with the shoulder region with a peg-and-socket joint.

Amongst the most dramatic of the placoderms was *Dunkleosteus*, a form named for the paleoichthyologist Dave Dunkle, which could get as large as a school bus.



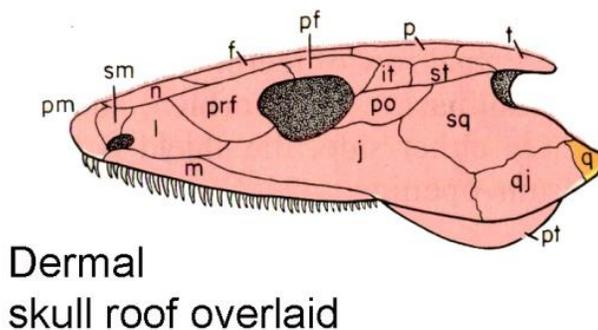
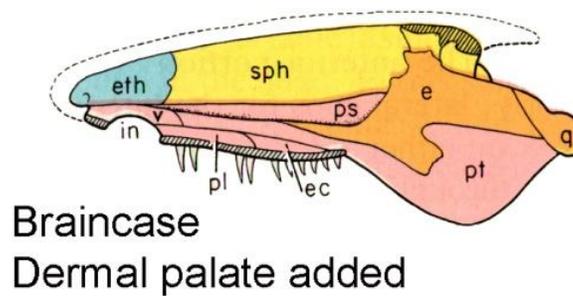
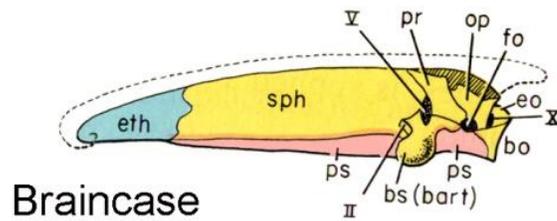
OTHER GNATHOSTOMES

Sharks are amongst the most notable of ancient lineages of gnathostomes, but as strictly cartilaginous fishes (other than their teeth) they possess no dermal bones of any kind.

Acanthodians, often referred to as “Spiny Sharks” do possess dermal bone in their skulls. Significantly, they demonstrate the standard fish condition with the pectoral girdle attached to the caudal end of the skull.

OVERVIEW OF THE EVOLUTION OF THE DERMAL SKULL ROOF IN OTHER VERTEBRATES

Recall that the dermal skull roof in a curved roof for the skull that protects the brain from above and creates a “cheek” region laterally. Below the braincase the dermal palate provides the roof of the pharynx. Although part of the splanchnocranium, it is important to remember that the upper jaw element of the mandibular arch, the palatoquadrate cartilage, fuses to each lateral edge of the palate (orange below).



REGIONS AND COMPONENTS OF THE DERMAL BONES

The dermal bones of the skull roof include:

MIDLINE OR MEDIAN SERIES: from rostral to caudal: nasal, frontal parietal, postparietal*.

MARGINAL TOOTH-LAERAL TOOTH-BEARING BONES: premaxilla, maxilla, septomaxilla* (though some include this in the circumorbital series)

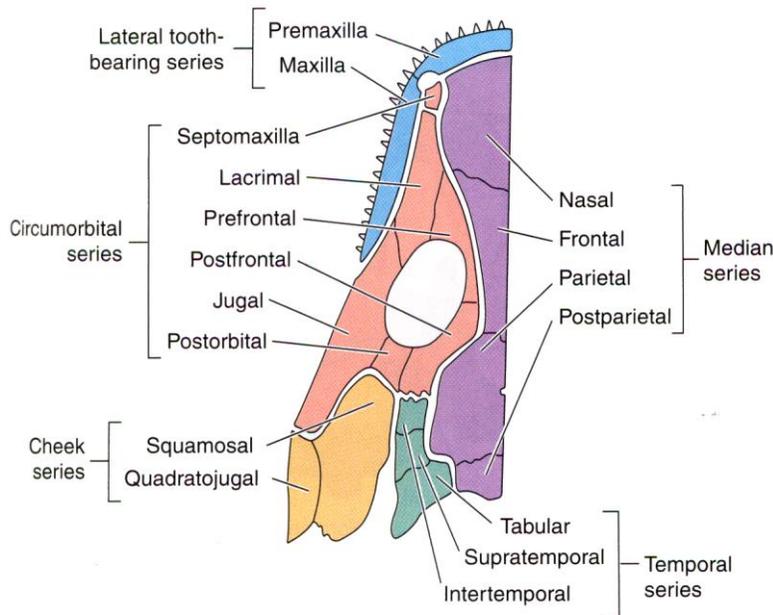
CIRCUMORBITAL SERIES (BONES CURROUNDING THE ORBIT): septomaxilla* (though some include this in the marginal toothed series, lacrimal, prefrontal*, postfrontal*, postorbital*, jugal.

CHEEK: squamosal*, quadratojugal*.

TEMPORAL SERIES: intertemporal*, supratemporal*, tabular*.

(IN FISHES) : OPERCULAR SERIES: preopercular, opercular, (in some accessory opercular), subopercular, branchiostegals (large midventral elements are often called gulars).

All of the opercular series is lost between fishes and tetrapods. Elements indicated with a "*" may be lost or fused to other elements in various amniote lineages.



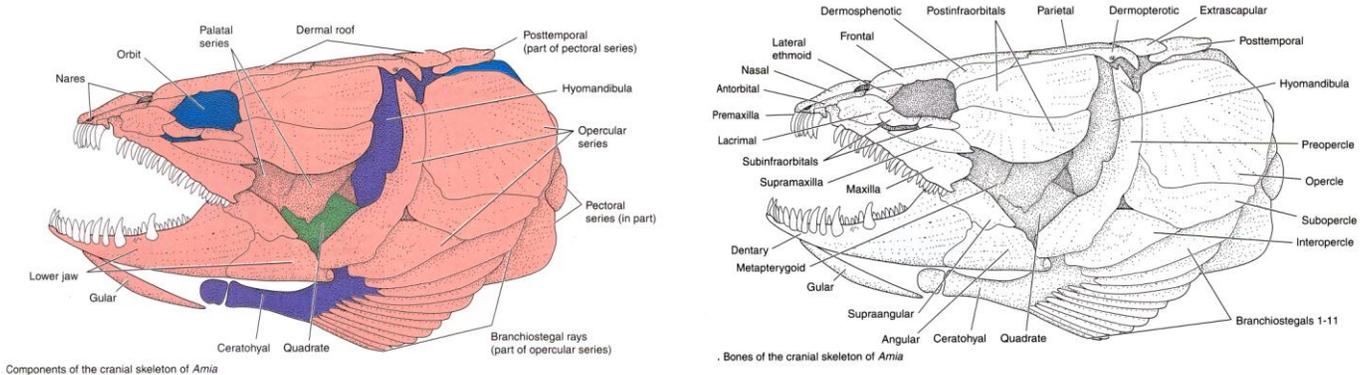
The dermal bones of the palate include:

MIDLINE SERIES: Vomer, pterygoid*

LATERAL SERIES: palatine, ectopterygoid*

DERMAL ELEMENTS OF FISHES

Amongst bony fishes, the entire complement of dermal bones are present – and then some. Many actinopterygian fishes have an additional set of median ones interpolated between the nasal bones (if present), usually referred to as the ROSTRALS. Additionally, dermal element that facilitate connection of the pectoral girdle to the skull are present caudal to the postparietals and tabulars, the EXTRASCAPULARS.



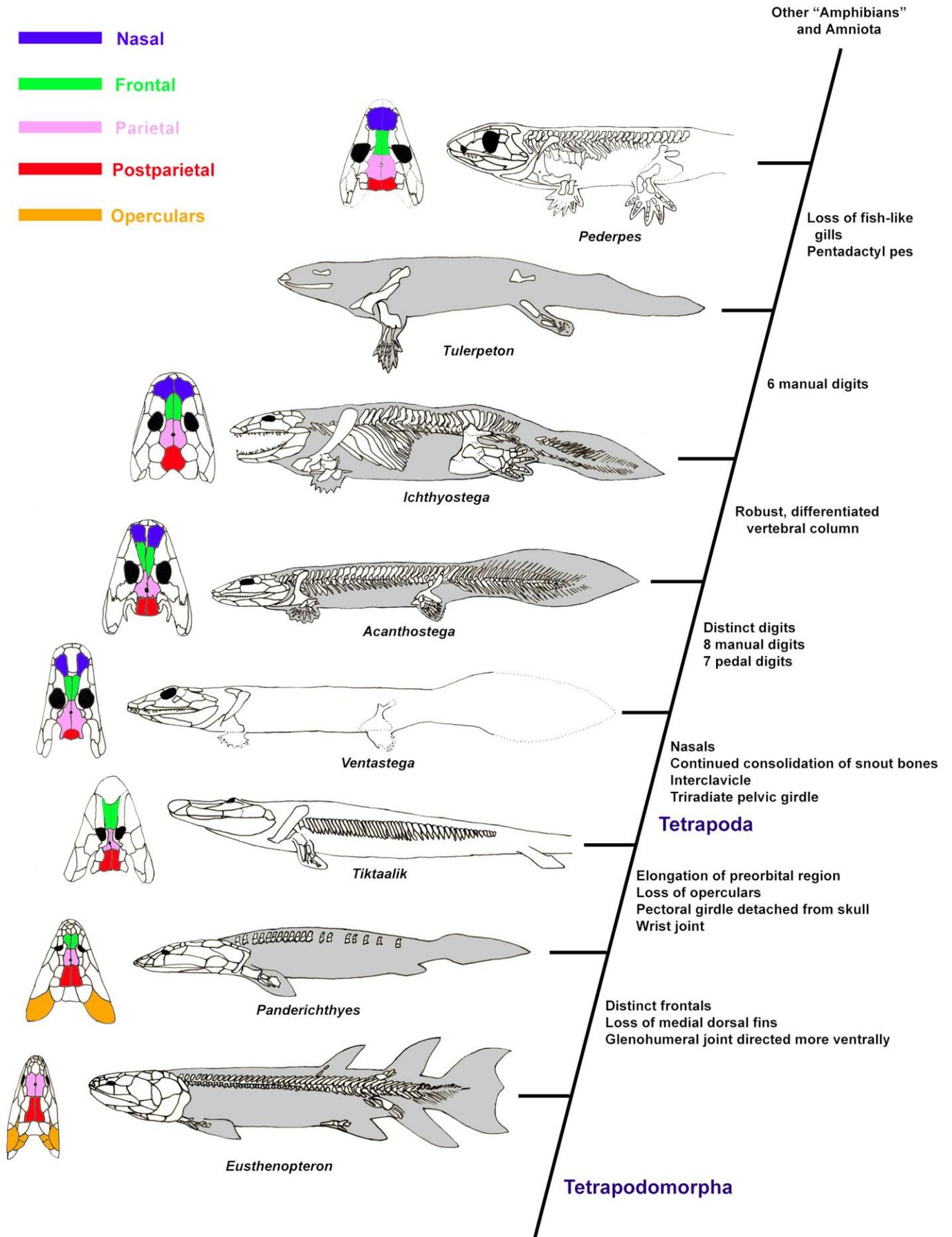
Crossopterygian fishes tend not to have well developed nasals, with the snout region essentially a mosaic of numerous bones, many of which are not even named. (Lungfishes are so odd their dermal bones can't even be homologized with those of crossopterygians or tetrapods, and they are just designated by numbers and letters.)

In the progression from crossopterygian fishes to early tetrapods, we see the following trends:

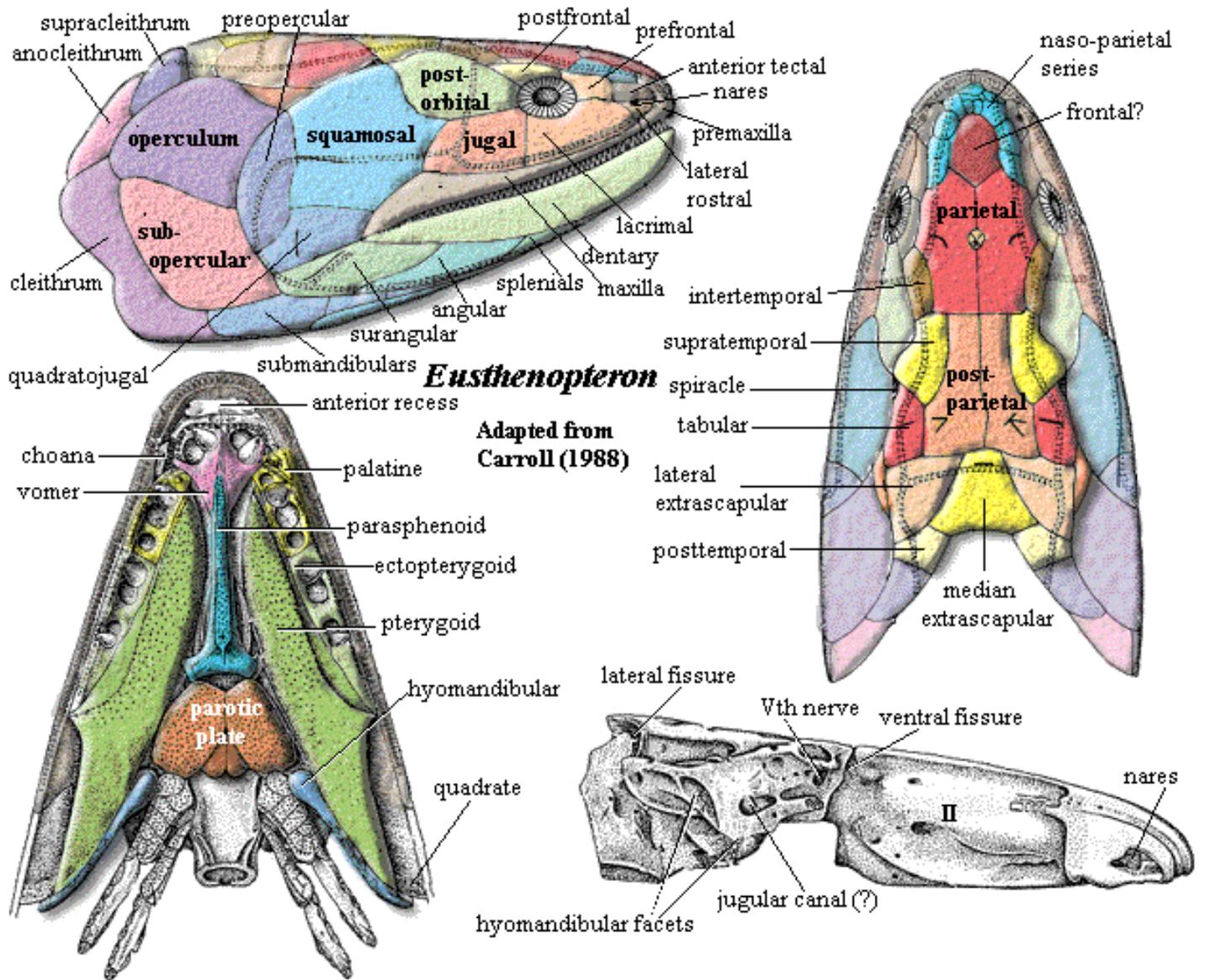
- Consolidation of the bones of the snout region
- Recognition of a clear nasal bone.
- Elongation of the preorbital region – i.e the snout.
- Correlated shortening of the postorbital region – i.e. the back of the head.
- Loss of opercular bones.
- Loss of extrascapular bones.
- Loss of connection between the skull and the pectoral girdle.

This did not happen all at once. It was a progression from animals we know to be completely fish-like, through transitional forms. From fishes with some tetrapod features such as *Elpistostega* and *Tiktaalik*, to tetrapods with some fish-like features such as *Ventastega* and the ichthyostegalians.

In the diagram on the following page, note these progressive changes as indicated by the color-coded median elements. (Also, note, this diagram will be of use to you again when we study the vertebral column and the limbs.)



An examination of the palate of a crossopterygian fish (in this case *Eusthenopteron*), note that the vomers and pterygoids are paired, as are the palatines and ectopterygoids lateral to them. The more lateral palatines and ectopterygoids carry large tusks, and the vomers and pterygoids are covered by a shagreen of smaller teeth.

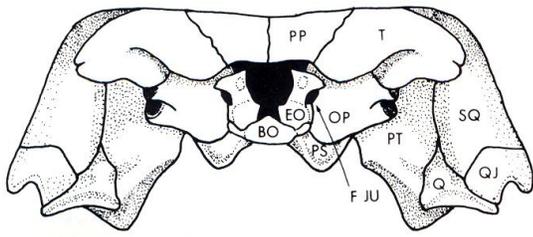


DERMAL ELEMENTS IN BASAL TETRAPODS

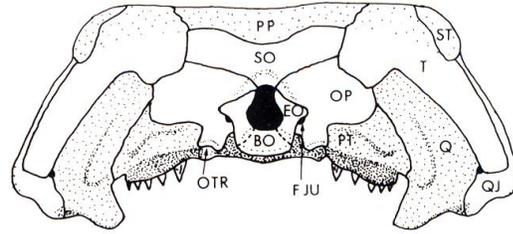
The standard set of dermal elements in more derived labyrinthodont amphibians may be seen in the illustrations at the beginning of this overview.

The braincase was examined in occipital view in the previous lecture. At that point, we noted the positions of the occipital series, with the supraoccipital positioned most dorsally. Immediately dorsal to that could be seen the postparietals. Note that as the elements caudal to them have been lost in tetrapods, the postparietals

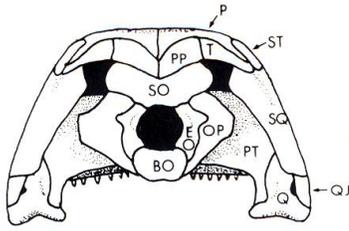
have some exposure on the occipital surface of the skull. Note them in the illustration following that includes both advanced amphibians, as well as basal amniotes.



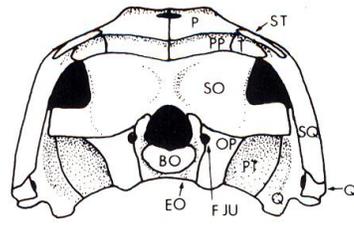
5 cm
Seymouria



5 cm
Limnoscelis



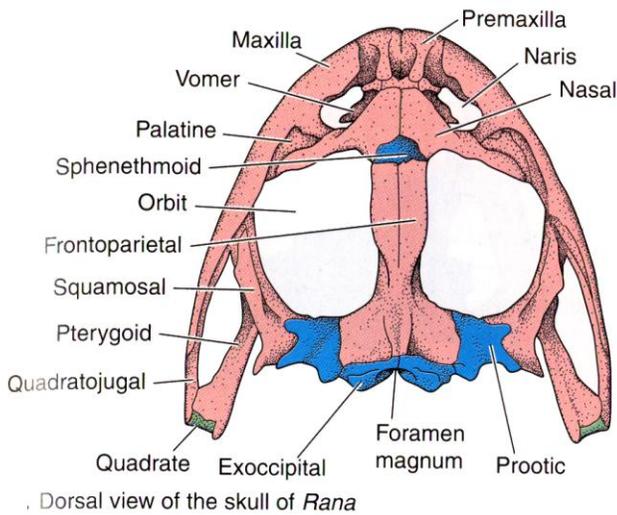
1 cm



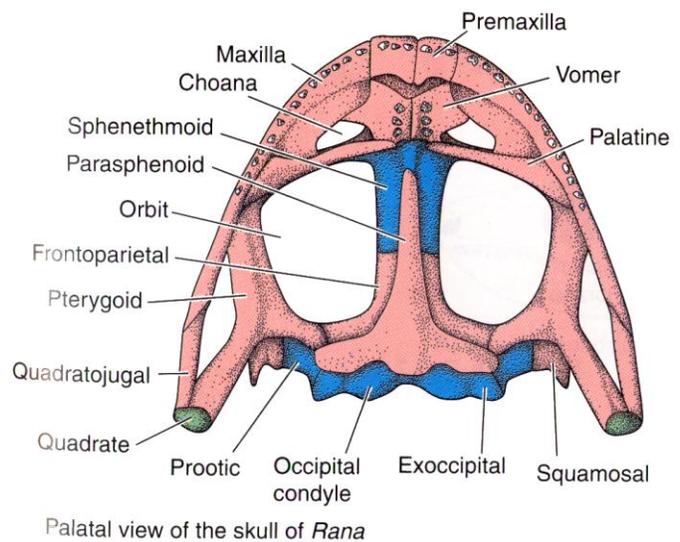
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DERMAL ELEMENTS IN EXTANT AMPHIBIANS

For the most part, extant amphibians show a marked reduction in elements, with many elements fusing, and many of the circumorbital series lost or fused to other elements. Below is an example of the frog *Rana*.

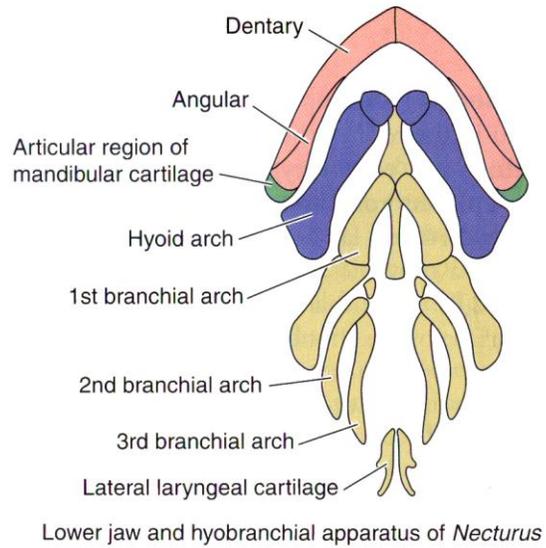
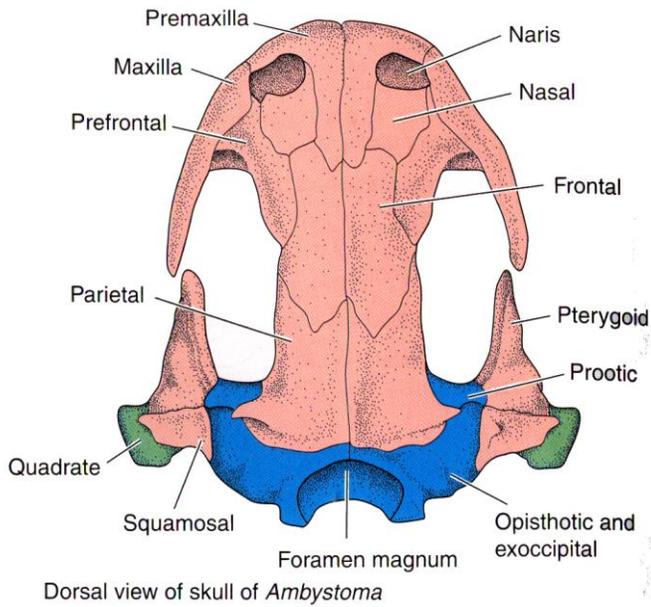


Dorsal view of the skull of *Rana*



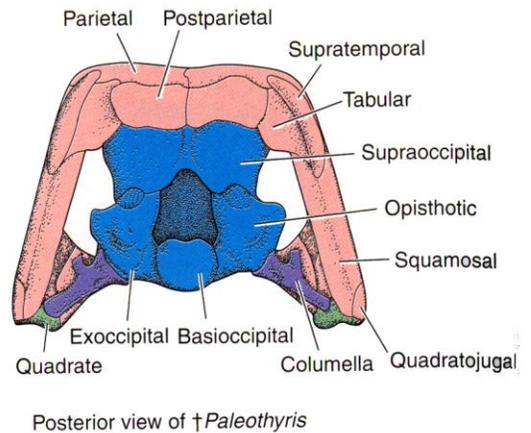
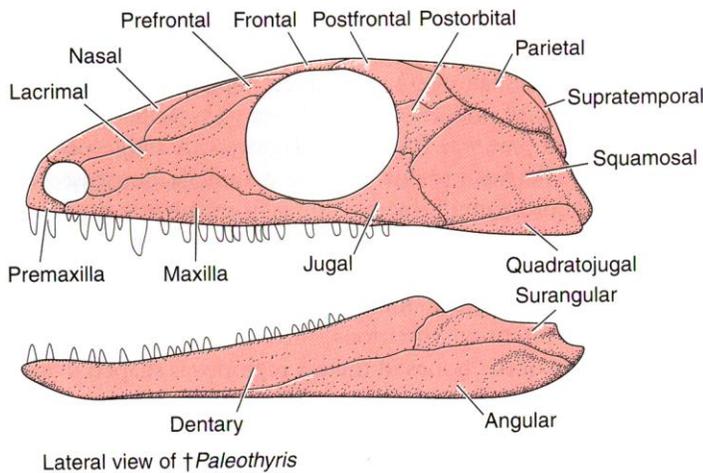
Palatal view of the skull of *Rana*

Below is the salamander *Ambystoma*.

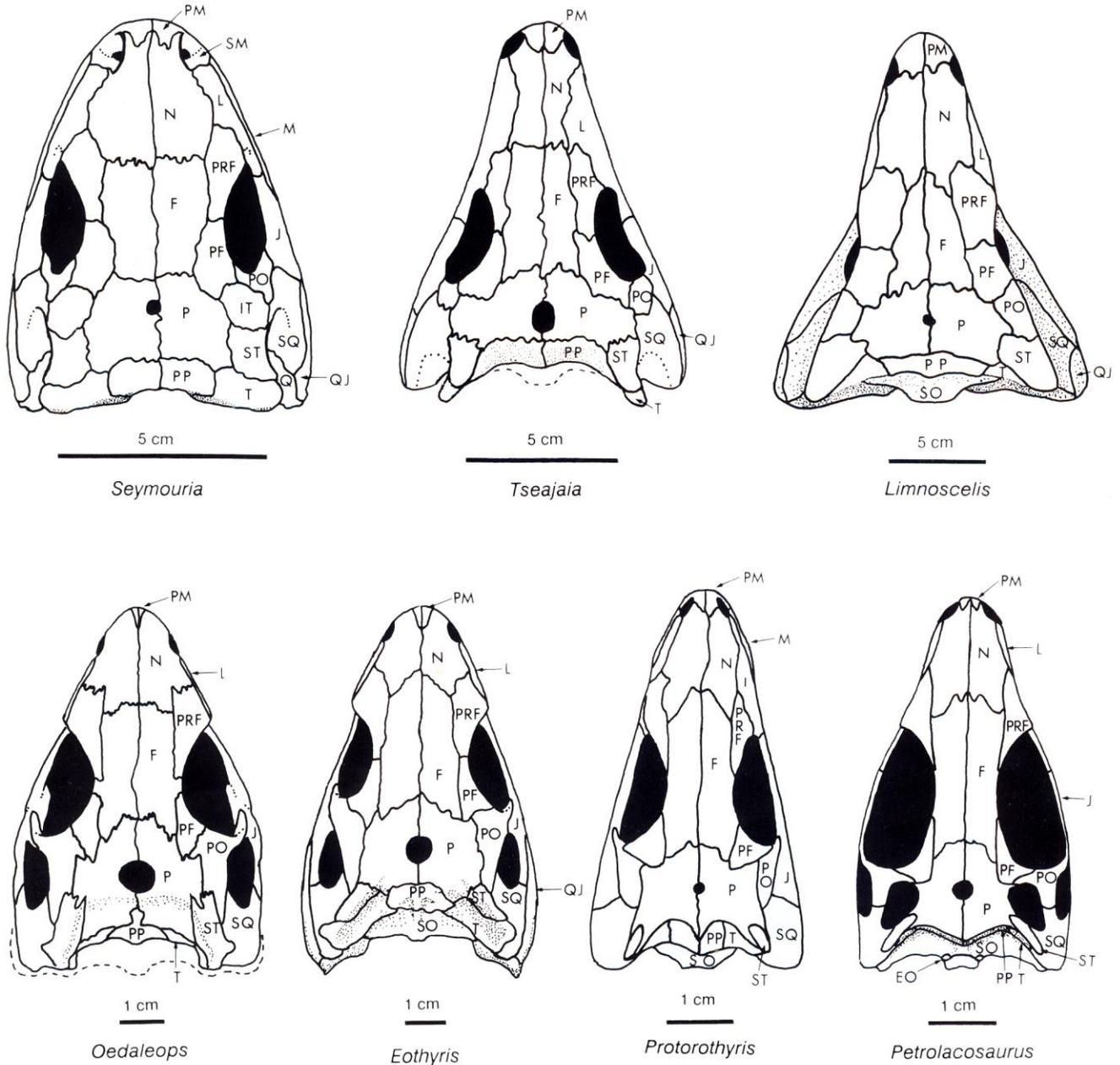


DERMAL ELEMENTS IN BASAL AMNIOTES

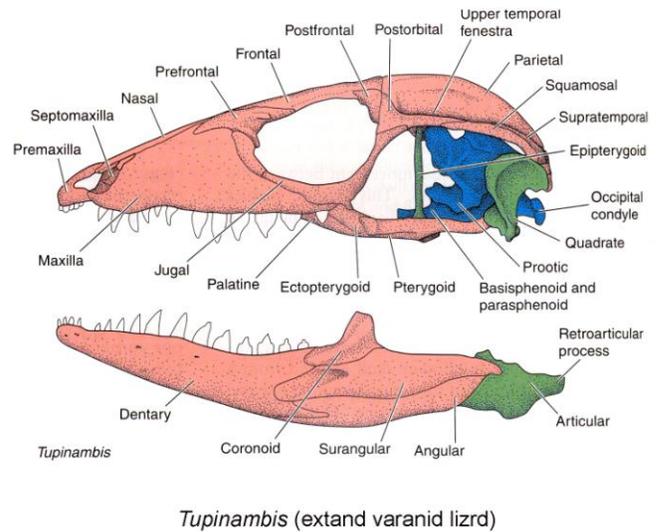
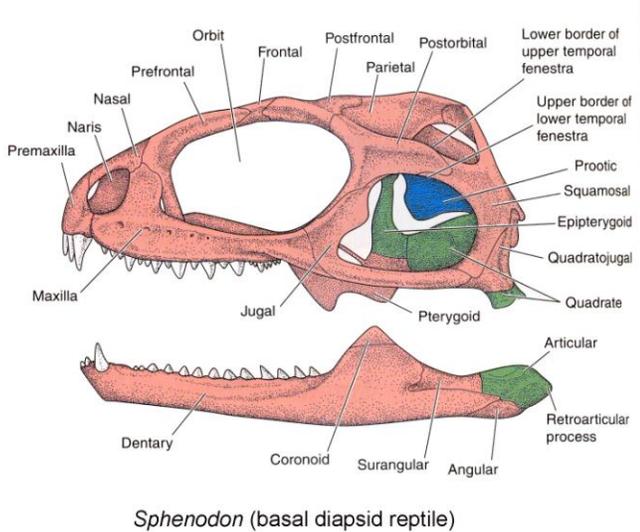
Basal amniotes retain almost all of the roofing and dermal elements seen in earlier non-amniote tetrapods. Notably, the proportions of some may change, and with that the postparietals are often pushed to having only an occipital exposure. Following is an illustration of the primitive reptile *Paleothyris*. Note how the stapes (a splanchnocranial element) acts as a strut, bracing the cheek region of the dermal roof relative to the braincase.



One of the synapomorphies of Amniota is the loss of the intertemporal bone. In fact, it more likely became fused to the parietal, and is probably the lateral extension of the parietal known as the PARIETAL LAPPET. In the following illustrations, note that *Seymouria*, an animal that is definitely classified as an amphibian, retains the intertemporal; whereas the remaining taxa have lost the intertemporal. Diadectomorphs are not generally considered amniotes *sensu stricto* because we cannot prove they had an amnion, but their skull structure suggests they were amniote like in their cranial patterning. Otherwise, they have the complete suite of dermal bones, including the septomaxilla.



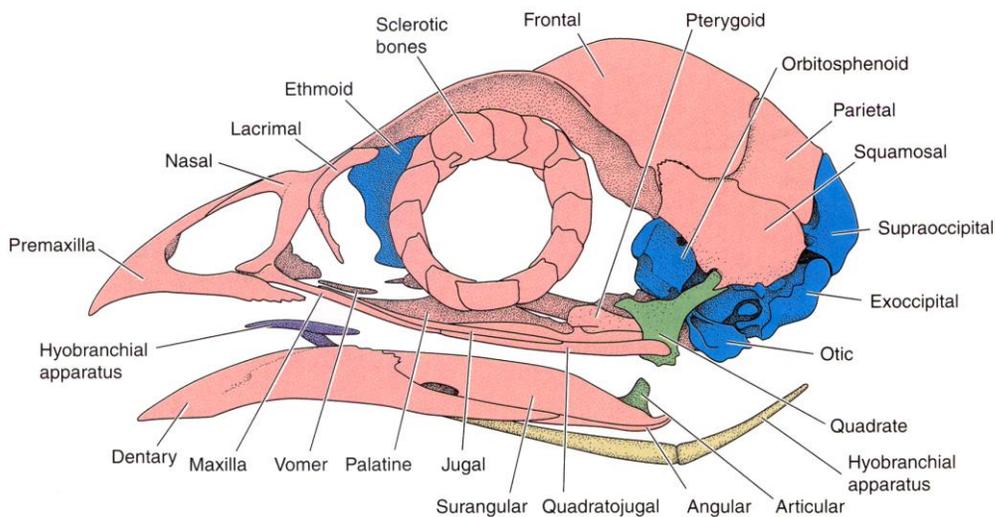
The next illustration is also a reptile, but slightly more derived. The diapsid reptiles *Sphenodon* and *Tupinambis* (a varanid lizard) show examples of the large openings in the side of the skull, known as temporal fenestrae (singular: fenestra).



BIRDS AS REPTILES

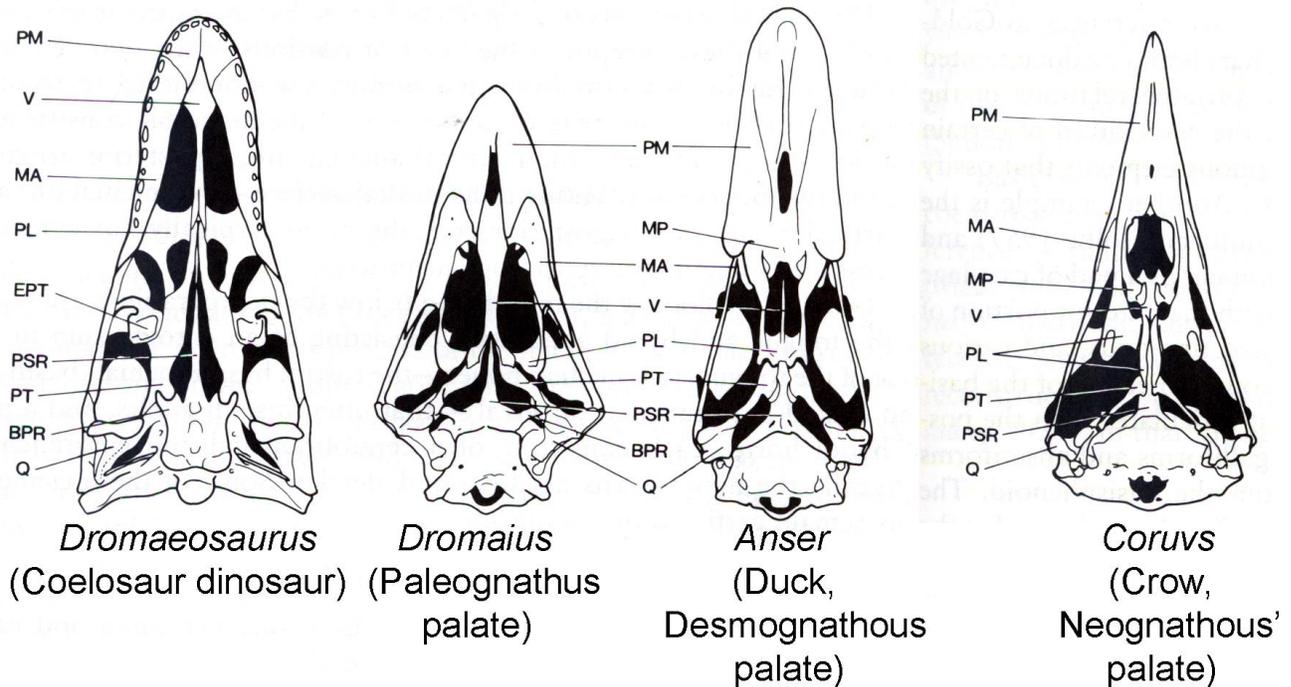
As derivatives of the dinosaurs, birds are properly a subset of reptiles. In fact, though their dermatocranium is dramatically lightened, they demonstrate most of the same elements found in reptiles. Some of the individual bones become quite thin and splint-like, for example, the quadratojugal and vomer.

Primitive birds did have teeth, though modern birds are edentulous. Despite this they still have the maxillaries, and well developed premaxillae for support of the upper part of the beak. In the illustration below can be seen the well developed SCLEROTIC RING, for support of the very large eyes. This is not unique to birds, as it is found in many reptilian groups, including the most primitive of reptiles.



Like reptiles, primitive birds have the full compliment of palatal bones.

- Ectopterygoids are lost.
- Although paired in their dinosaurian ancestors, the vomer in birds is a single fused, midline bone.
- The palatines become very thin, splint-like bones.
- Pterygoids are retained, but are very reduced in size, and in neognathous birds acts as a brace to stabilize the quadrate component of the jaw joint.



DERMAL ELEMENTS (AND THE REDUCTION IN THEIR NUMBER) IN MAMMALS.

Mammals retain the median series of dermal bones, but the remainder of the dermal series undergo modification and/or consolidation. Although it is often said that mammals “lose” many of the dermal roofing bones, it is more correct to say that they are incorporated into other elements.

Skull Roof Changes; Midline Series:

- The midline elements are intact, but the nasals become very small.
- The postparietals fuse to the supraoccipital, becoming the squamous portion of the OCCIPITAL bone.

Skull Roof Changes; Tooth Margin Series:

- Some, though not all, fuse the premaxilla and maxilla to become only right and left maxillae.
- The right and left maxillae develop secondary shelves that develop medially to create a separation between the old braincase and the oral cavity. This subdivided the pharynx into a nasal pharynx and an oral pharynx, and the maxillae (plus palatines, see below) are the SECONDARY PALATE.

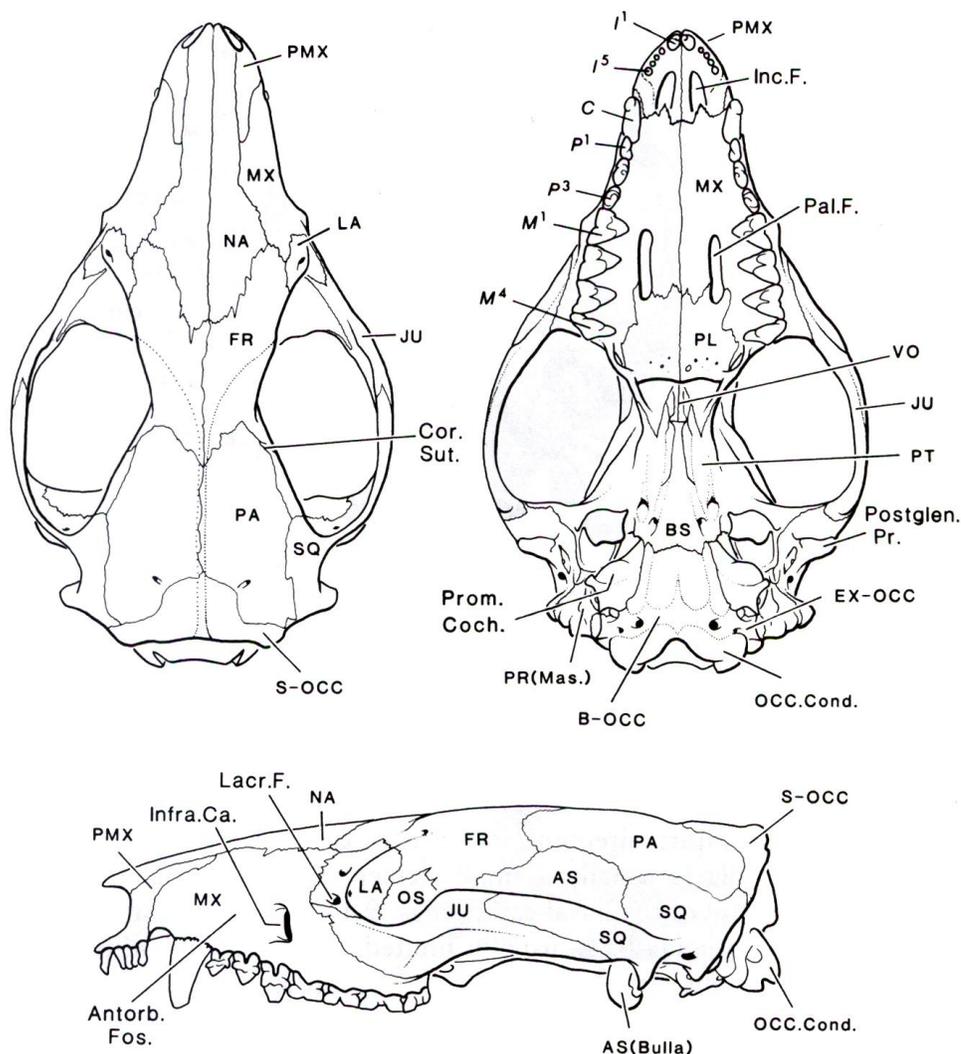
Skull Roof Changes; Circumorbital Series:

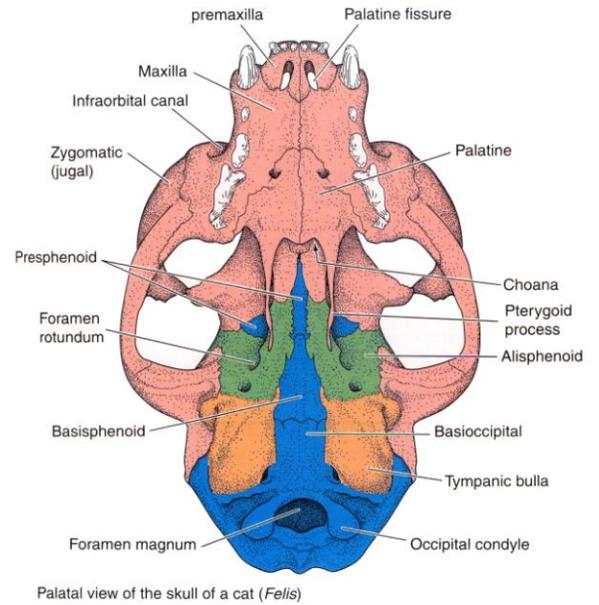
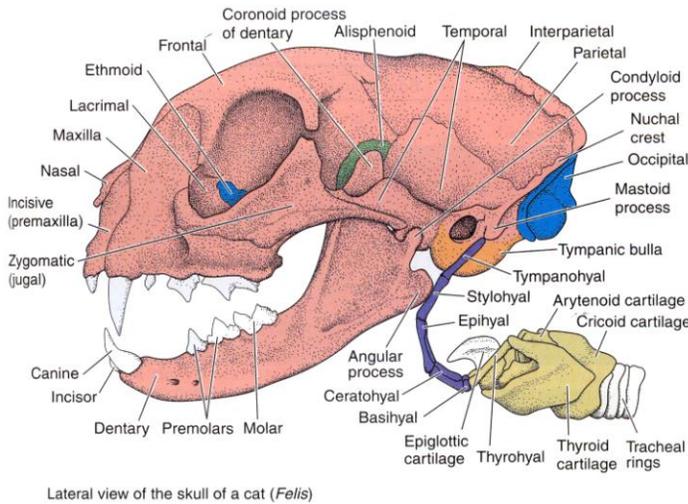
- The jugal is renamed as the ZYGOMATIC bone.
- The squamosal fuses to the otic structures and becomes the squamous portion of the compound temporal bone.
- The lacrimal remains, but becomes extremely small and thin, essentially restricted to the orbit.
- The prefrontal fuses to the frontal.
- The postfrontal fuses to the frontal, becoming the postorbital process of the frontal when present.
- The postorbital fuses to the jugal to become part of the zygomatic, generally its posorbital process.

Skull Roof Changes; Temporal Series:

- Both the tabular and supratemporal are no longer discreet elements. It is likely they have been incorporated into either the lateral part of the postparietals, which were incorporated into the squamous occipital. Or, the back end of the parietal. (Note, the shape of the parietals in the primitive mammal *Monodelphis*, below, would suggest this.)

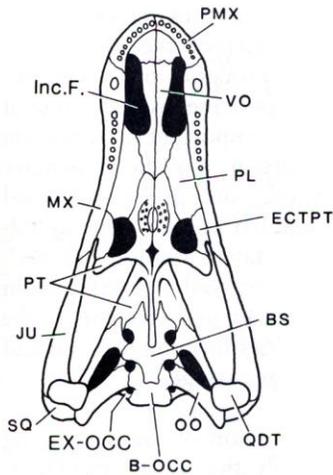
Compare the primitive mammal *Monodelphis* below (using mostly basal tetrapod bone names) with the illustration of the cat, *Felis*, following.



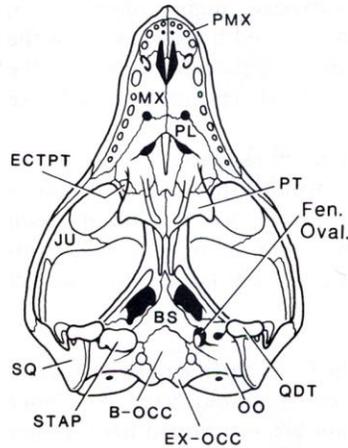


Palatal Changes:

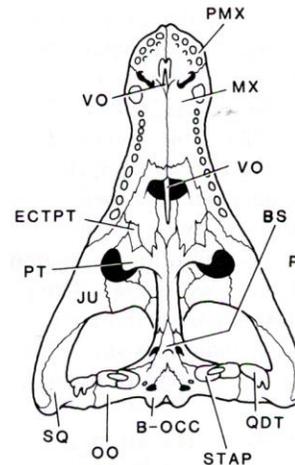
- Ectopterygoids are lost.
- The vomers fuse to become a vertically oriented midline structure.
- The pterygoids fuse to the underside of the basisphenoid, and become the pterygoid wings.
- The palatines remain, but get pushed to a position caudal to the maxillae. They can be distinguished from the maxillae because they do not carry teeth. They contribute to the secondary palate (see above).



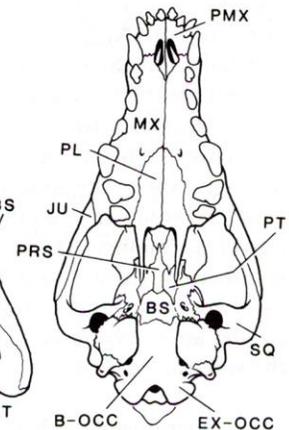
Scylacosaurus
(Therocephalian)



Thrinaxodon
(Cnyodont)



Cynognathus
(Cnyodont)



Canis
(Mammal)

“Progressively more mammal-like”



EVOLUTION OF THE TEMPORAL FENESTRAE

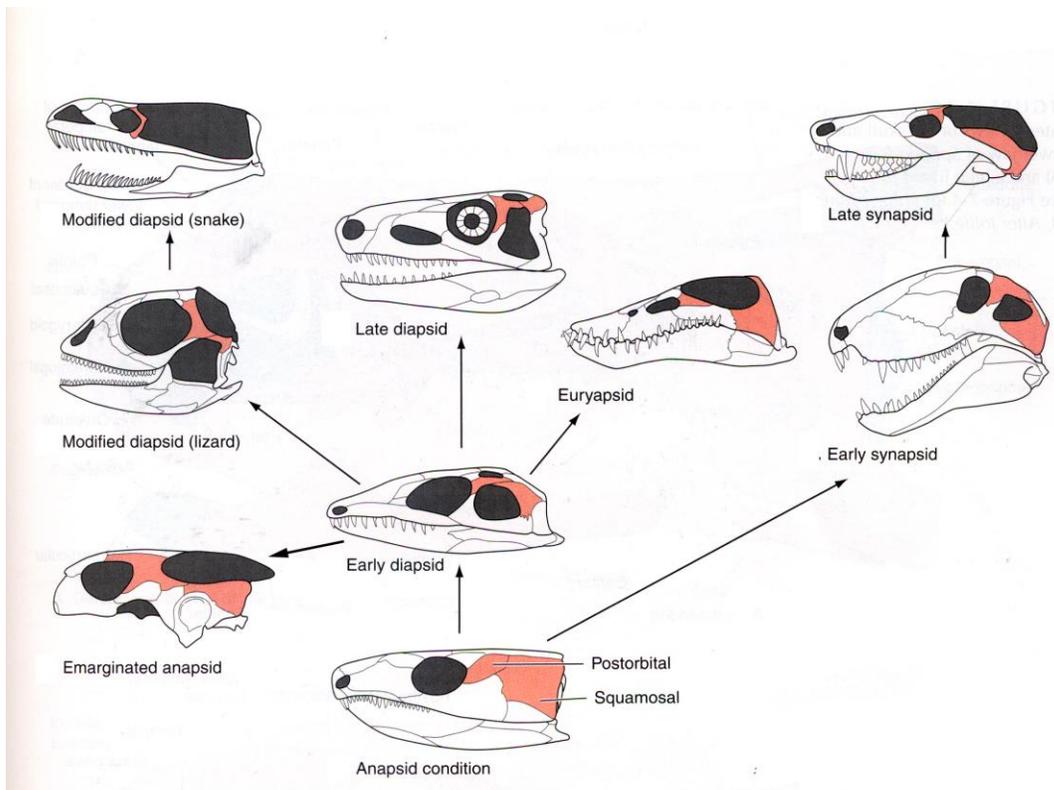
Now that we have made our way all the way to mammals, we are in a position to understand the unusual derivation of the cheek-bone, or ZYGOMATIC ARCH.

Numerous amniote lineages developed openings in the side of the dermatocranial cheek and temporal regions to facilitate the attachment of jaw adductor muscles. The primitive condition found in basal reptiles was retained from their fish and amphibian ancestors. There are three major lineages of amniotes with openings in the side of the temporal/cheek region.

SYNAPSIDA – A single opening bounded by the postorbital anteriorly, the squamosal posteriorly, and the quadrate + jugal bone. The lineage leading to mammals.

DIAPSIDA – Two openings, bounded by the parietal above the upper, the quadrate + jugal below the lower one, and the squamosal in-between them. The lineage leading to most modern reptiles, including lizards and snakes, probably turtles, dinosaurs (and thus birds).

EURYAPSIDA – A single opening, but placed higher than that of the synapsids. Bounded by the parietal above, and the squamosal + postorbital below. It had long been thought this was derived from a diapsid in which the lower opening closed secondarily, but this appears not to be the case. More likely, the euryapsid temporal opening was an independent evolutionary lineage branching from the primitive anapsid condition.



The question, is, how did this occur? We will use the progression known from synapsids as our example, as it is the best known example.

Temporal Fenestration Stage 1 – Anapsid Condition

- In this condition, the jaw adductor muscles originate on the inner surface of the dermal skull roof. This works, but it is difficult for muscle anchors (Sharpey's fibers) to attach strongly to the flat surface of the inner dermal skull roof.
- Note that medial to the adductor mandibular muscle, only a ligamentous fascial sheet separates the brain from the muscle. It reaches down from the parietal to a component of the palatoquadrate cartilage that has incorporated itself into the sidewall of the braincase – the epipterygoid. Remember, the palatoquadrate is stuck to the side of the palate.
- The braincase at this level is the basiptyergoid, and the pterygoids can be seen as the palatal structures on the underside of the braincase.
- The adductor mandibulae muscles reach down of the lower jaw. The pterygoid muscles reach from the underside of the palate to the medial (inner) aspect of the lower jaw.

Temporal Fenestration Stage 2 – Basal Synapsid (Pelycosaur) Condition

- NOW, an opening has developed in the side/temporal region of the dermal roof. This opening is the **TEMPORAL FENESTRA**.
- This provides an edge for adductor mandibular musculature to originate. Sharpey's fibers may now insert at a much higher angle.
- Note that medial to the adductor mandibular muscle, [there is still] only a ligamentous fascial sheet separates the brain from the muscle. It [still] reaches down from the parietal to a component of the palatoquadrate cartilage that has incorporated itself into the sidewall of the braincase – the epipterygoid. Remember, the palatoquadrate is stuck to the side of the palate.
- However, note: the ligamentous fascial sheet is now originating from a more ventrally directed flange of the parietal.
- The braincase at this level is [still] the basiptyergoid, and the pterygoids can [still] be seen as the palatal structures on the underside of the braincase.
- The adductor mandibulae muscles [still] reach down of the lower jaw. The pterygoid muscles [still] reach from the underside of the palate to the medial (inner) aspect of the lower jaw.

Temporal Fenestration Stage 3 – Advanced Therapsid to Mammal Condition

- The parietal has developed a sagittal crest for greater surface area of adductor origin. Much of the musculature, now called the **TEMPORALIS MUSCLE**, is attaching to the old outside of the bone.

- Meanwhile, the old epipterygoid, now called the **ALLISPHENOID** has grown dorsally to contact the parietal, encasing the brain completely.
- As mentioned earlier, the pterygoids fuse on to the basisphenoid to become the pterygoid wings. They still give rise to the pterygoid muscles.
- Part of the adductor mandibulae splits off from the temporalis, and the part originating from (all that is left of) the lower part of the dermal roof – the zygomatic arch – is distinguished as the **MASSETER MUSCLE**.

