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# Bones

A few years ago, I suggested to a paleo professor that it would be interesting to run a graduate seminar around individual bones. Much is written about bones as synapomorphies, bones as functional units, and, of course, naked lists of bones for students to memorize are infamous; but there is little continuity. It might be interesting to look at these pieces of anatomy as individual units of evolutionary change. Not only might this give us a new perspective on evolution, but also perhaps some new ideas about the meaning of homology and the evolution of function.

That project was well beyond me, and remains so. However, if I were one to wait on competence before execution, these Notes would not exist. So, as with the remainder of these notes, I will do my learning in public, like a mental web-cam. As with everything else here, we will evolve, rather than build. The coverage will begin generally with the head, but fairly randomly otherwise. It is not a project designed to be completed, or remain static. So the reader may expect the usual incomplete format changes, unexplained gaps in coverage, substantive and typographical errors.

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**Links:** For a compact treatment of the dermal cranial bones, see Justin Tweet's glossary. Some of the Tree of Life pages by Michael Laurin and colleagues are very useful, although their use of color is distracting. See, for example, Phylogeny and Classification of Amniotes. The Dinosaur Encyclopedia is a (literally) bare-bones, but serviceable, guide to dinosaur osteology. For mammals, there is an excellent set of figures and text at the University of Michigan Animal Diversity Web Contents. Another useful mammalian osteology site is Prof. LC Todd's *Bison* osteology page. ATW031129.

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# The Braincase: Overview

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# First Iteration: General Layout & Vague Concepts

The individual bones of the braincase are primarily embryological units. In the adults of most vertebrates, the braincase is largely fused into a single solid mass. The braincase may be bone, cartilage, or (most commonly) mixed. However, the various embryonic cartilages and centers of ossification are not separated by obvious sutures in the manner of the dermal bones, and there is rarely any marked kinesis between sections of the brain. Nevertheless, there are certain more or less persistent regions and landmarks that are frequently mentioned. These are illustrated schematically in Figure 1.

It should be emphasized that braincases come in a vast array of shapes and sizes. The otico-occipital boundary is sometimes almost seamless. Likewise the sphenethmoid area is frequently a single unit. It is almost always relatively easy to distinguish the otico-occipital and sphenethmoid units, although the ventral fissure is not always present. By way of example, see the braincase of *Trilophosaurus* from Parks (1969). Fig. 2.

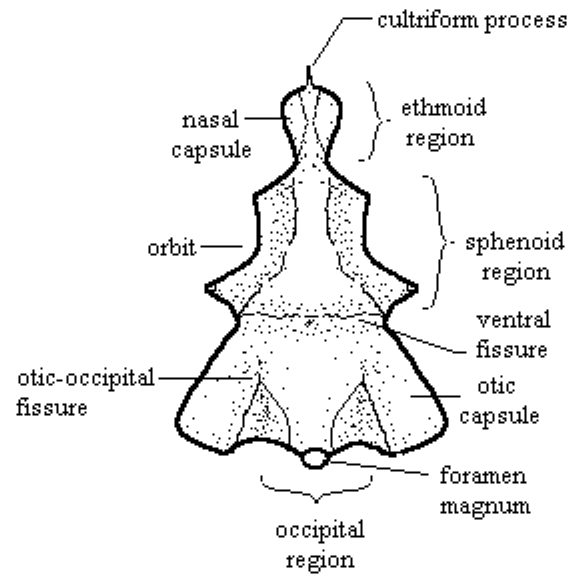

**Fig. 1. Generalized vertebrate braincase in ventral view**

It is interesting, as well as a useful aid to memory, to note that the principal braincase regions are each strongly associated with different sensory functions. The occipital region is defined by the bones of the occiput (the basi-, ex-, and supra-occipitals) which surround the foramen magnum. This is the point where the notochord and the sensory (and motor) nerves from the body enter the brain. The otic capsule partially surrounds the semi-circular canals of the labyrinth, which sense motion and orientation, as well as the organs of hearing in tetrapods. The sphenoid region is essentially defined by the orbit, and the ethmoid region is associated with chemosensation.

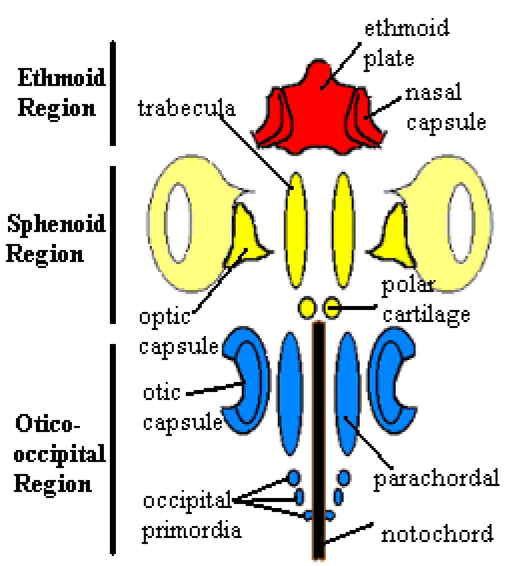

**Figure 3. Schematic view of vertebrate braincase development**

Vertebrate braincase development is relatively stereotyped, even if the final result is extremely variable. Neural crest cells migrate into the head region lateral and anterior to the notochord and condense into a pair of elongate cartilage bars, the trabeculae or prechordal bars, and a pair of small polar cartilages. A similar pair of parachordal cartilages develop posteriorly from mesoderm, flanking the notochord. Occipital cartilages form just posterior to the parachordals. Later in development, the bars widen laterally and extend up around the sides dorsally to form a trough. An ethmoid plate forms anteriorly. The embryonic composition of the ethmoid plate is not known with certainty.

In addition, a pair of sensory capsules develops adjacent to each set of axial cartilages: the nasal capsules, optic capsules and the otic capsules. Later in development, all of these growing regions of cartilage fuse. The product of this fusion is the chondrocranium.

Ancestrally, the chondrocranium was an open-topped pan that housed the brain in a trough chondrichthyans have a chondrocranium that is only slightly modified from this condition. The dorsal surface closes off medially to form a roof over the brain. In bony vertebrates, endochondral bones form from centers of ossification in the chondrocranium, although much of the braincase often remains cartilage. In teleost fish, and occasionally in other groups, separate ossifications occur in the ethmoid region. In mammals, the ethmoid ossifies to form the turbinals, convoluted bones in the nasal cavity that are covered by olfactory sense organs. Parts of the sphenoid region frequently ossify to form the basi-, orbito-, pre-, latero-, etc. sphenoid bones. These, along with the basioccipital, form the platform on which the brain rests. There are several ossification centers in the otic region, notably the prootic and opisthotic. In mammals, this region ossifies into a structure called the petrosal, which houses the inner ear. Finally, around the foramen magnum, these bones develop as the supra-, para-, and basioccipitals. See **The Occiput**.

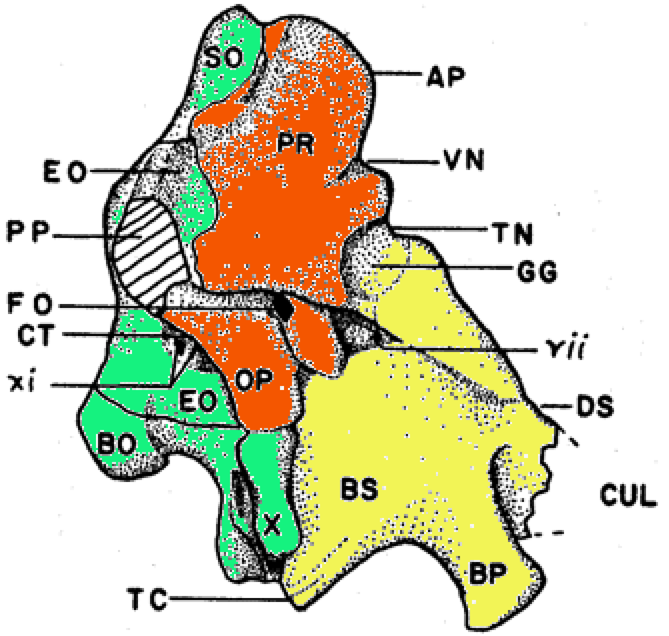

**Fig. 2. The braincase of *Trilophosaurus buettneri* in right lateral view with the sphenethmoid in yellow, otic in orange and occipital in green.**

The anatomical relations of the adult braincase are complex and somewhat variable. For simplicity, this discussion is restricted to the more conventional gnathostomes. Dorsally, the braincase and the brain are covered by the dermal bones of the vault series (frontals, parietals, and so on), or the equivalent dermal plates in placoderms. The chondrichthyans, of course, lack dermal skull bones, and here the braincase itself grows up over the brain and forms a completely enclosed capsule. Ventrally, the basioccipital (the ventral member of the occipital series) lies on or over the parasphenoid and pterygoid of the dermal palatal series. Again, sharks are the exception. The shark braincase is perhaps the major structural anchor of the skull and, in primitive forms, it supports the palatoquadrate directly. The occipital series is itself the main support of the posterior skull, and it also serves to bind the braincase to the notochord, primitively the main axial support of the entire organism.

The problem area, in terms of evolutionary engineering, appears to have been lateral support. The dorsolateral portion of the skull is dominated by the jaw adductor muscles. The location, size, orientation and mechanical advantage of these muscles has probably been more critical to vertebrate evolution than any other single body element, the brain included. As humans, our cultural progress has often been driven by speech. But, in evolutionary terms, its how you *close* your mouth that counts. This creates a serious evolutionary conflict: how can we provide lateral stability for a big, delicate brain sitting in the middle of big, active, important muscles whose size and orientation is critical to survival?

Evolution has devised any number of solutions to the problem, and it would be impossible to cover even the more significant approaches. One of the most frequent designs has involved a posterolaterally directed brace, frequently through the stapes, which extends roughly from the level of the braincase's center of mass down and back towards the heavily stabilized occiput. Another, more radical, design is the peculiar system of the always-aberrant mammals. They circumvent the entire issue by placing the jaw muscles largely outside the dermal bones. This lets the brain get very big indeed without losing stability, but it requires a reoriented, shorter jaw with very little snap. This, in turn, has only been successful because mammals have unique teeth which can process food by grinding, a process driven by the masseter muscles rather than the classical jaw adductors. Whatever the solution, it is important to keep track of how these paramount issues interact: brain size and stability vs. jaw musculature.

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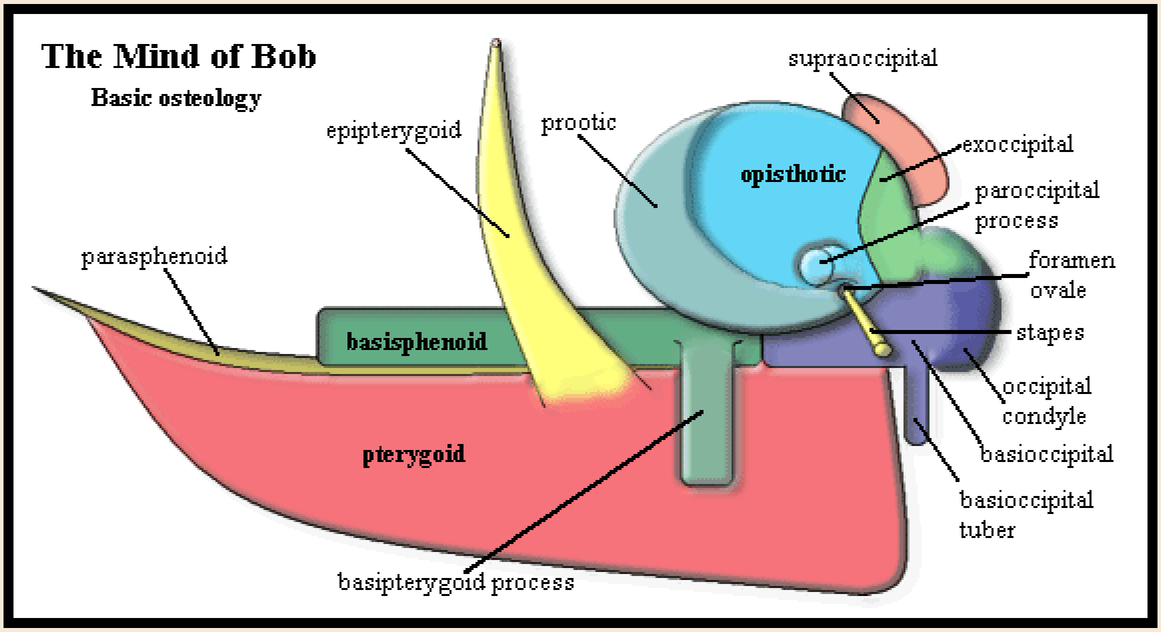
# Second Iteration: Schematic Guide to the Brain of Bob

By definition, Bob the Basal Amniote has the Standard Condition -- in this case the standard brain. While Bob is not a creature of towering intellectual prowess, we nonetheless value his companionship because of his congenial disposition and straightforward anatomy. Even so, we are perhaps not yet ready to tackle a real braincase head on, as it were. Instead, we will first describe the state of his mind as a schematic, or rather two of schematics of increasing complexity. At this stage, we will restrict ourselves to bones. This, for all practical purposes, eliminates the unossified front half of the braincase.

The thing at right which looks like a badly drawn dhow is in fact a badly drawn amniote braincase. Only the basic osteology is shown. We also provide an occipital view for reference. Beginning with the supraoccipital and moving roughly clockwise, we'll go through the essential information about each of the main structures.



The **supraoccipital** is essentially an unpaired dermal bone of the occiput. It is a bone found only in tetrapods and develops by ossification of a membrane joining the two otic capsules. The supraoccipital contacts the parietals of the skull table dorsally and the exoccipitals ventrally. It usually forms at least the dorsal edge of the *foramen magnum*.

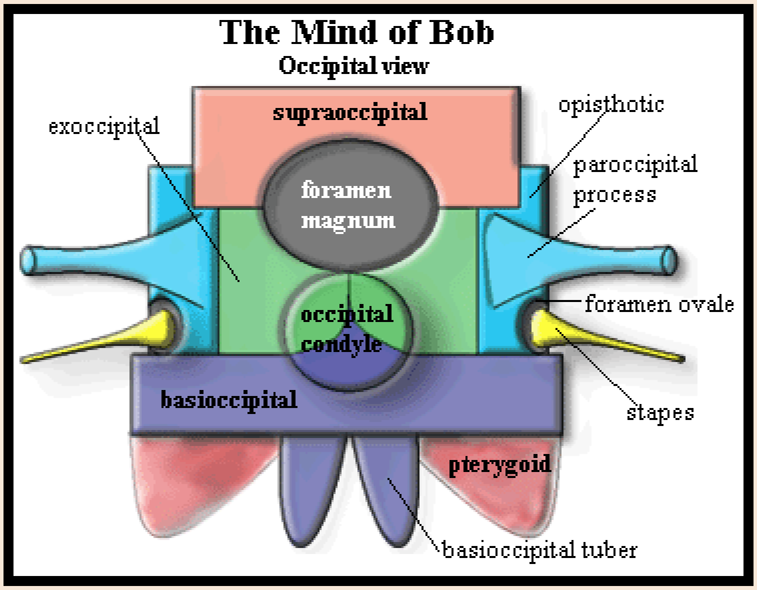
The **exoccipitals** are paired bones of the occiput. They derive from the neural arch elements of embryonic vertebrae which have been incorporated into the braincase. Dorsally, the exoccipitals contact the supraoccipital and the *foramen magnum*. Ventrally, they contact the basioccipital. The exoccipitals often form part of the *occipital condyle*.

The **opisthotic** is the posterior of the two bones making up the otic capsule and is usually fused to the prootic, the anterior otic bone. The opisthotic is an endochondral bone. It is usually the largest contributor to the paroccipital process and to the structures of the middle and inner ear. It normally contacts all of the occipital bones and the prootic, and may contact the basisphenoid. It often forms part of the edge of the *foramen ovale*, the door to the inner ear.

The **paroccipital process** may be considered a process of the opisthotic, but the process may be formed by bones in addition to, or even instead of, the opisthotic. The paroccipital process runs horizontally (and sometimes dorsally) across the back of the skull. It joins the occiput and braincase to the quadrate, squamosal and the other dermal bones of the "cheek."

The *foramen ovale* (= *fenestra ovalis*) is the only one of the various holes in Bob's head which makes our list of basic bits and pieces. It is a membrane covered manhole between the middle ear and inner ear. *See*, generally, **The Ear**. It is covered by the footplate of the stapes. The *foramen ovale* is normally located anterodorsal to the paroccipital process, between the prootic and opisthotic.

The **stapes** is an incarnation of the hyomandibular. Originally, it may have been the main upper element of a gill arch. It later appears as the hyomandibular, an accessory jaw element. In early tetrapods, it becomes a stout bone bracing the braincase against the quadrate. As the paroccipital process took over this function, the stapes was reduced, eventually becoming specialized for hearing as the *columella*, in sensible amniotes, or the stapes, in mammaliforms. The stapes bears a footplate which fits over the foramen ovale.



The **occipital condyle** is a rounded protuberance (or a pair in some taxa) forming the ball of a ball & socket joint by which the head rotates on the neck. It is usually formed by some combination of the basioccipital and the exoccipitals.

The **basioccipital** is an unpaired median bone of the occiput which derives from the centra of embryonic vertebrae which have been incorporated into the braincase. It forms the floor of the braincase under the posterior part of the otic capsule. It contacts the exoccipitals dorsally and almost always forms at least part of the occipital condyle.

The **basioccipital tubera** are a pair of ventrolaterally directed blobs descending from the basioccipital. They are sometimes simply referred to as "basal tubera." However, the basisphenoid may also bear tubera. Presumably the basioccipital tubera act as attachment sites for ligaments stabilizing the head on the neck.

The *basipterygoid processes* are (despite the name) processes of the basisphenoid. They act to join the braincase to the palate. In many basal tetrapods and their ancestors, this was a moveable articulation. In most derived tetrapods, it simply staples the braincase to the palatal bones.

The **pterygoid** is not, of course, a braincase bone. It is the dermal palatal bone which grew up over the old palatoquadrate and eventually took over many of its functions. It is a very complex and interesting bone which, fortunately, we can skip over for present purposes. We have more than enough complex and interesting stuff to go 'round just dealing with the braincase.

The **basisphenoid** forms the floor of the braincase anterior to the basioccipital. Ventrally it is covered by a dermal bone, the parasphenoid. The fusion between these two is so close that some workers refer to the complex as the "parabasisphenoid." The basisphenoid gives rise to the basipterygoid process and other structures dealt with elsewhere.

The **parasphenoid** is the dermal bone normally found fused to the basisphenoid on its ventral surface. The parasphenoid generally extends far anteriorly on the midline of the palate as a narrow *cultriform process*. The upper surface of the parasphenoid (and the vomers) may be associated with the olfactory tracts. However, the anterior braincase is normally unossified in tetrapods such as Bob.

The **epipterygoid** is another misnomer. Like the quadrates, the epipterygoids are ossified portions of the palatoquadrate (the original upper jaw which, like the hyomandibular, is homologous with an upper gill arch segment). They often appear to arise from the pterygoid, but do not. The epipterygoids are the true, old stuff of the palatoquadrate, while the pterygoid is but common dermal bone with pretensions. In fact, the epipterygoids are the original braincase articulations of the palatoquadrate. They demonstrate this ancient nobility by rising up in a graceful curve to reach the bones of the skull roof, like the last remaining columns in the abandoned temple of some forgotten god. **[1]**

The **prootic** is the anterior of the two endochondral bones making up the otic capsule. It is usually fused to the other otic capsule component, the opisthotic. The extent and geometry of the prootic are quite variable. In addition to its fusion with the opisthotic, the prootic may contact the basisphenoid and any of the elements of the occiput. ATW031205.

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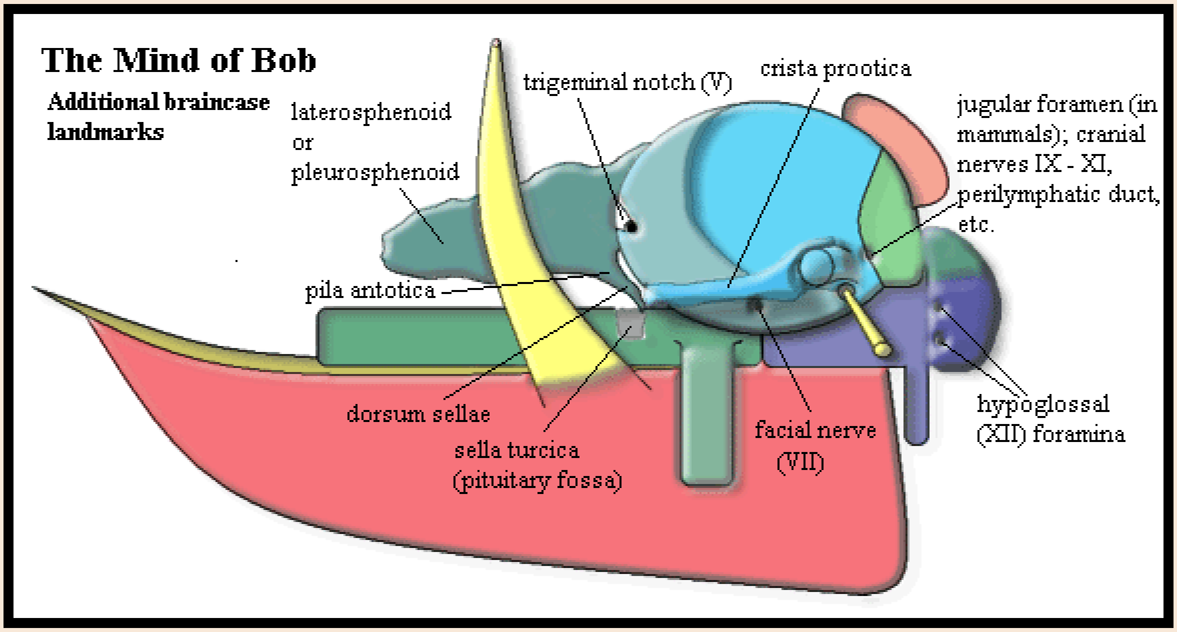
# Third Iteration: Some Landmarks



Having disposed of the osteology, we add some landmarks. Here, we are hampered by vague, shifting, and inconsistent nomenclature as well as the more usual obstacles -- among which lack of artistic ability ranks prominently. Nevertheless we have persevered in order to illustrate some critical details, as well as to familiarize the reader with some of the prestigious optional features which are available in luxury models of the tetrapod braincase. Again, we will begin in the upper right hand (posterodorsal) corner and work clockwise.

The first feature is called by a variety of names, such as **jugular foramen**, **vagus foramen**, or **perilymphatic foramen**, depending on the taxon and anatomical features of interest. Nearly every tetrapod has some sort of major foramen located on the boundary between the exoccipitals and the opisthotic, near the base of the paroccipital process.

The basioccipital may bear several small foramina for the hypoglossal (XIIth) nerve near the base of the occipital condyle.

Anterior, and usually a bit ventral, to the *fenestra ovalis* is a foramen for the facial (VIIth) nerve. The foramen is often accompanied by a groove, fossa, or what-have-you for the palatine branch of the nerve.

Just anterior to the otic capsule is perhaps the most complex and ancient area of the vertebrate brain. This is the boundary between the embryonic trabeculae and parachordals, the ancient anterior terminus of the notochord, the transition from anterior trabecular prechordal ectoderm to posterior neural crest tissue, the site where palatal (stomodeal) ectoderm invades the brain embryonically, the location of the pituitary, the origin of the optic nerve (II) and critical optic muscles, the seat of the *basipterygoid process*, the division between forebrain and mesencephalon, and so on. In short, almost everything that distinguishes the vertebrates begins right there, in a suite of features separated only by millimeters. We will mention only a few of these landmarks, but the critical importance of this region cannot possibly be overstated.

The basisphenoid bears a deep, central depression at this point called the *sella turcica* or **pituitary fossa**. The *sella* contains the pituitary (or hypophysis), a structure formed cooperatively of brain tissue and palatal ectoderm which has invaded during development via Rathke's pouch. This is taken up in detail elsewhere. A small sheet of bone rises up vertically at the posterior margin of the *sella turcica*. This is the *dorsum sellae*. The right and left corners of the *dorsum sellae* are usually prolonged anterodorsally. These are the right and left *pilae antotica*, called the **posterior clinoid processes** in mammals. The *pilae* may disappear during development, remain cartilaginous, or ossify in a number of ways. Here, we have shown the pilae ossifying dorsally, as an irregular sheet of bone running roughly between the *pila antotica* and a similar band of cartilage which comes off the top of the otic capsule, the *taenia marginalis*. In this position, the bone is referred to as a **laterosphenoid** or **pleurosphenoid**. In other taxa, a sheet of bone develops ventrally, between the *pila* and the basisphenoid. In that case, the bone is a **presphenoid**.

The prootic is quite often emarginated on its anterior border. This is the **trigeminal notch** which, not surprisingly, contains the exit of the trigeminal (Vth) nerve.

Finally, particularly in lepidosaurs, the prootic bears a lateral crest which runs anteriorly from near the base of the paroccipital process, over the facial foramen, to the anterior margin of the otic capsule. When present, this crest, the *crista prootica*, is a particularly good landmark since it is quite easy to spot. ATW031206.

# Mental Status Examination

This is as far as we can fruitfully go at the moment. We have not discussed the unossified anterior portions of the tetrapod brain, the brains of fishes of all kinds, or the innermost cavities, such as those between the otic capsule and the basicranial bones. Some of these areas are discussed in connection with particular taxa or particular bones. However, this is a reasonable place to stop for the moment, since the information above is all that one really needs to know for most purposes. ATW031206.

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**[1]** Sure, it's an idiotic conceit! But you're not likely to forget it, are you?

### "Headnotes"

**Dermosphenotic:** The dermosphenotic is a dermal bone in the otic region of many actinopterygian fishes, perhaps including groups as early as the guildayichthyiforms. It is typically found at the posterodorsal corner of the orbit and bears a portion of the postorbital sensory canal (sometimes referred to as an extension of the infraorbital canal). The neuromasts of this canal are the only ones to be innervated by the otic branch of the facialis (VIIth) nerve, or by its superficial ophthalmic branch. It typically articulates, or even fuses, with the supraorbitals and may appear to be serially homologous with them. The dermosphenotic may also articulate with the postorbital or infraorbital series and with the nasals and/or frontals. Posteriorly, the dermosphenotic articulates with the dermopterotic, to which it is developmentally related. The dermosphenotic overlies the autosphenotic, a bone of the neurocranium; and the two are frequently fused to form the sphenotic. *See* Adriaens & Verraes (1998); Lund (2000).

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# Braincase: Basisphenoid

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### Status

Like the ethmoid, the basisphenoid is a big and complex topic, intimately connected with the brain and the total design of the skull. Accordingly, after a very brief overview, we will content ourselves for the moment with a more detailed consideration of one portion of the bone: the *sella turcica.*

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## Overview

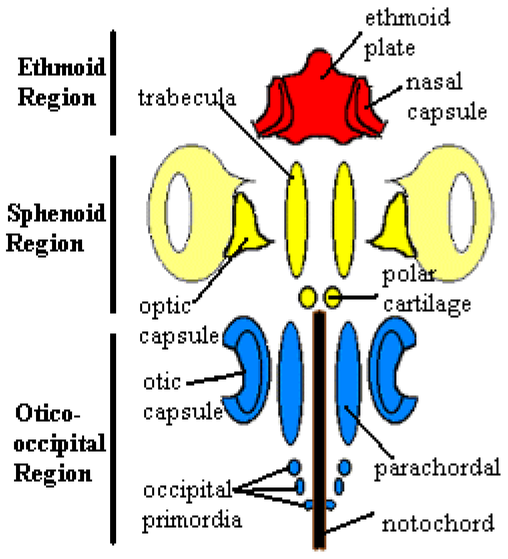

**Figure 3. Schematic view of vertebrate braincase development**

We may begin with what may now be familiar: an overview of the embryonic vertebrate braincase. The basisphenoid develops largely from the parachordals, mesodermal analogues of the trabecular cartilages, which are derived from embryonic neural crest tissue. Classically, it was supposed that the parachordals formed the basisphenoid, while the trabeculae formed the sphenethmoid and related bones. In fact, as we will see, the matter is not so simple.

The basisphenoid forms the floor of the braincase under the mid- and hind-brain in many vertebrates. It may extend forward under the forebrain as well. This is relatively common in tetrapods, since the anterior braincase of tetrapods is often unossified for reasons given elsewhere. In such organisms, the basisphenoid is the only ossified ventral element of the braincase. Under the braincase, the basisphenoid is integrated with the bones of the palate which, among many other functions, serve to support the basisphenoid on the marginal bones of the jaw, principally the maxillae. In turn, the basisphenoid acts as a strong longitiudinal beam for the palatal bones forming the roof of the mouth. See, for example the turtle skull at Skull of the Snapping

Turtle.

In many cases, these anterior supporting roles are taken over by a dermal bone, the parasphenoid. In such cases, the basisphenoid plays a more posterior role as a broad plate, well integrated into the occiput and supporting the otic capsule. Another possible arrangement involving both bones can be seen in the plesiosaur figure at Plesiosaur Skull Anatomy. Frequently, the two are also indistinguishably fused (e.g. *Thrinaxodon*).

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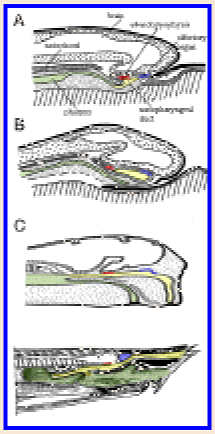
# The Sella Turcica and the Pituitary

"Sella turcica" is Latin for "Turkish saddle." If this is an accurate description, we may marvel all the more at the success and longevity of the Ottoman Empire. The term is doubtless an early product of the same scientific whimsy that brought us *Sonic Hedgehog*, colored quarks, and Maxwell's Demon. Thus the sella turcica may never have seated Spahis (Ottoman -- and, later, French -- heavy cavalry). However, it does seat the adenohypophysis, also known as the anterior lobe of the pituitary. The sella is at a key point in the skull, as judged by several criteria. It lies almost at the geometrical center of the skull. It is just anterior to the rostral limit of the embryonic notochord, about at the junction of the trabeculae and parachordals, and also at the posterior limit of the forebrain. Dorsoventrally, it sits between the most ventral portion of the brain and the palate. The pituitary it protects is a union of brain tissue and pharyngeal ectoderm. Phylogenetically, the pituitary has deep connections with the nasal placodes and chemosensation. However, genetically, it is closer to the optic placodes and shares with them a number of gene regulation pathways, including *pax6*, *six3*, and *lim3*. Kondoh *et al*. (2000); Kioussi *et al.* (1999). In fact the adenohypophysis transiently expresses species- appropriate lens crystallins during development and can be genetically transdetermined to form a more or less normal lens. Kondoh *et al*. (2000). **[2]**

Developmentally, the sella turcica is a fairly simply cavitation in the surface of the basisphenoid. Apparently, the posterior ends of the trabeculae are not actually parallel, as in the image above. Rather, they spread apart slightly so that there is a depression on the dorsal surface of the basisphenoid as it forms. I have not seen any reference to a similar separation of the parachordals, but it may turn out that this occurs. In any case, the result is that the basisphenoid has more than one embryonic origin. The anterior part is trabecular prechordal ectoderm and the posterior is neural crest parachordal tissue. Consequently, some writers refer to the bone as if it were two different ossifications: the "basipresphenoid" and "basipostsphenoid." The sella turcica itself is at the boundary between the two embryonic domains and includes contributions from both sources. Couly *et al.* (1993); Le Douarin *et al.* (1993). **[3]**.



All this antero-posterior patterning is interesting enough, but it is the dorsoventral interactions which have received all the press. This attention actually relates to the developmental molecular biology of the pituitary, rather than to osteology. In spite of having accumulated a stack of reprints and notes *this* high, your editor will be absolutely damned if he can make that subject particularly relevant to the present discussion. Furthermore, it amounts to little more than stamp-collecting at the moment because the system is far too complicated for our present, primitive grasp of bioinformatics and gene-level developmental regulation. In essence, the pituitary is the point at which *all* of the regulatory domains of the developing head overlap.

For our purposes, a brief developmental overview is sufficient. See, generally, UNSW Embryo- Endocrine System- Pituitary. After neurulation is complete and the basic body plan establishes itself, the head structures begin to differentiate. The vertebrates are deuterostomes. That is, the gut is formed butt-first. The mouth and pharynx are derived by a secondary infolding of superficial ectoderm called the *stomodeum*. See Gilbert (2000: 490-492). The stomodeum is originally a simple layer of ectoderm blocking the anterior end of the gut. However, as the fore- and mid-brain differentiate from the anterior neural tube, they grow and inflect downwards. As a result, the ectodermal cells of the stomodeum are folded in under the brain and come close to the diencephalon. See Brain Function Diencephalon. A portion of the ectoderm associated with the roof of the stomodeum then invaginates dorsally, pinches off from the stomodeum, and migrates into physical contact with the base of the diencephalon at the site of the sella turcica. **[4]** This is Rathke's Pouch, which is the primordium of the adenohypophysis in most vertebrates. Eventually, the ectoderm of Rathke's Pouch differentiates into 5 to 7 different cell types which produce the various classes of pituitary hormones.

In almost all living vertebrates, all this activity has nothing at all to do with the development of the nasal passages. Sadly, our interest is mostly in *dead* vertebrates. So, we must digress from our discursion from our detour to touch on the nose. The nasal placodes are initially formed high up on the developing head. As the brain expands, they appear to migrate down and to the front of the face. At the same time, they begin to develop their own internal passages. These are lined by a thick layer of nasal epithelium surrounded by the mesenchyme (?) of the placode. In tetrapods, the orderly separation between nasal passages and pharynx breaks down quickly. The nasal and oral passages coalesce, and the adult nasal passage is formed by the construction of a secondary palate which repartitions the combined space. See, generally, Untitled Document.

Now, finally, we have fashioned some crude conceptual tools with which to dissect the structure of earlier and more aberrant forms. The figure at right shows succesive stages in the development of the hagfish *Myxine*. These are adapted from Janvier (1986: 46-47), rescaled (and, in the case of 'C', redimensioned) for comparability. The hagfish has no forebrain inflection to speak of, and the conventional teaching is that the adenohypophysis develops from gut endoderm, so that the hagfish is unlike all other vertebrates. As the figure shows, this is may be incorrect. In fact, the nasopharyngeal duct -- an extension of the nasal cavity -- is in exactly the right place with what is probably ectodermal epithelium. Thus, we may suppose that the adenohypophysis has always been an ectodermal structure with the same basic genetic regulatory mechanisms in development. This supposition -- and the tight connection between the olfactory organs and the hypophysis -- is supported by the fact that both are derived from the anterior neural ridge, a very small area of ectoderm just in front of the anteriormost neural plate. Kouki *et al.* (2001); Takuma *et al.* (1998). Thus, what we are probably seeing in *Myxine* is not a nasopharyngeal duct, but a nasohypophyseal duct which happens to communicate with the pharynx. This sort of structure is quite common among early vertebrates.

There is no solid explanation for the function of this arrangement, but a glance at the known functions of the diencephalon (Brain Function Diencephalon) suggests many possibilities. The hagfish is guided largely by olfactory information. Hagfish have little ability to see or hear, and the hagfish brain primitive. It simply lacks the ability to integrate complex sense perceptions at a neural level. It is reasonable to suppose that much of the integration is therefore performed at a chemical level. The olfactory organ, connected with what passes for higher brain centers in the hagfish, might control immediate behavior: finding the food source or mate, fleeing the predator, etc. A downstream organ, part sensory and part endocrine, would receive direct sensory input from the environment and/or secondary messengers from the olfactory organ, and set in motion longer term preparations: to digest, to discharge gametes, to mobilize energy reserves or defensive mucous secretions. Similar arrangements, with or without connection to the pharynx, are found in the osteostracans, galeaspids, and probably heterostracans. The lamprey condition is essentially the same except for the peculiarity of the single median dorsal nostril.

In gnathostomes, the case is quite different. Here, the nasal placodes separate and move to opposite sides of the cranium. Presumably they are effectively pushed out of the way by the expanding brain. In any event, they lose contact with the hypophysis. So what happens to the old nasohypophysial duct? Why, nothing. It's still there. Recall that the very development which caused the stomodeum to fold inwards *and* separated the nasal placodes was the expansion of the forebrain. The logical consequence is that the median area of the anterior neural ridge is pushed right down into the mouth and becomes part of the infolding stomodeum. Presto! Instead of a nasohypophyseal duct invaginating from the face, we have Rathke's Pouch developing from the oral ectoderm. At the same time, and by the very same token, the enlarged forebrain permits increased *neuronal* procesing of olfactory information, so the tight chemical coupling between olfaction and endocrine release is no longer so necessary. The nasohypophyseal duct may thus be abridged and simplified. However, it is still apparently possible, albeit under rather bizarre experimental conditions, to induce chick embryos to form an ectodermal hypophyseal tube developing from the "face" even in the absence of a gut, much less a stomodeum. Withington *et. al.* (2001). The authors of that study conclude that the stomodeal ectoderm is induced by some other endoderm. It seems much more likely that the stomodeum has nothing to do with the case. Since brain inflexion is very limited in the absence of gut endoderm (see *Id.*) the old nasohypophyseal duct is simply making its way to the diencephalon from the outside, just as it did 400 million years ago.

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**[2]** This is not one of those nearly useless experiments in which some tissue extract of unknown properties is used to create weird effects in ectoderm generally. See, *e.g.* Gleiberman *et al.* (1999). Kondoh used homozygous *yot* mutant zebrafish. These mutants have an altered *gli2* gene which seems to lack specificity and shuts down several promoters in response to *shh* (Sonic Hedgehog). The most likely conclusion is that, up to the point of *gli2* protein expression, presumptive lens and presumptive adenohypophysis are very similar, suggesting that they may be homologous if one goes back far enough. This is a particularly interesting speculation if one recalls that hagfish lack both lens *and* the ectodermal component of the adenohypophysis. All other living vertebrates (probably!) have both except those that are secondarily lensless.

**[3]** These papers are both products of the famous chicken-quail chimera experiments from the laboratory of Prof. Nicole Le Douarin (Commandeur dans l'Ordre de la L�gion d'Honneur, Grand Officier dans l'Ordre National du M�rite, etc., etc. You don't see many academic resumes like this one!). Her wonderful experimental system is described in a brief and fairly non-technical manner by Gilbert (2000: 13).

**[4]** Physical contact is required for differentiation. At least some of the critical factors are *not* diffusible substances. Gleiberman *et al.* (1999). This ought to set off alarms. The warning here is that we must be very cautious -- far more cautious than many published papers -- in assuming that DNA transcription, RNA translation and protein activity are all co-localized. RNA transport, for example, is a well-known developmental phenomenon. The fact that RNA is made in one location does not mean that it expressed as protein in the same cell.

ATW 010804.

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# The Ethmoid

# Preliminary Note

The ethmoid is really a region, rather than a bone. In any case, it is somewhat too big a bite to swallow at once. Accordingly, after a brief overview, this first pass will be restricted to one of the easier elements of the ethmoid region, the cribiform plate.

# Overview

The ethmoid generally is the most anterior region of the braincase. In early development, two pairs of cartilaginous rods form parallel to the notochord in the cranium: the anterior trabeculae and the posterior parachordals. At the same time, the nasal placodes are developing within the cartilaginous nasal capsules formed by invading neural crest ectoderm. This ectodermal component also contributes at least to the anterior portion of the trabeculae. In some groups, including humans and most other mammals, the entire thing congeals into an ethmoid ossification, or ethmoid plate, incorporating the nasal capsules and the anterior portion of the trabeculae.

There is considerable variability on this general theme. For example, the mormyrid family of osteoglossomorph teleosts has members both with and without an ethmoid bone. Cichlids appear to have only the lateral ethmoids, which I take to be largely derived from the nasal capsules. By contrast, in eels, the fusion includes not only the elements listed above, but also the vomers and the premaxillae. See OceanLink Answers to Miscellaneous Fish Questions. In tetrapods other than mammals, the ethmoid region is not ossified at all. In general,

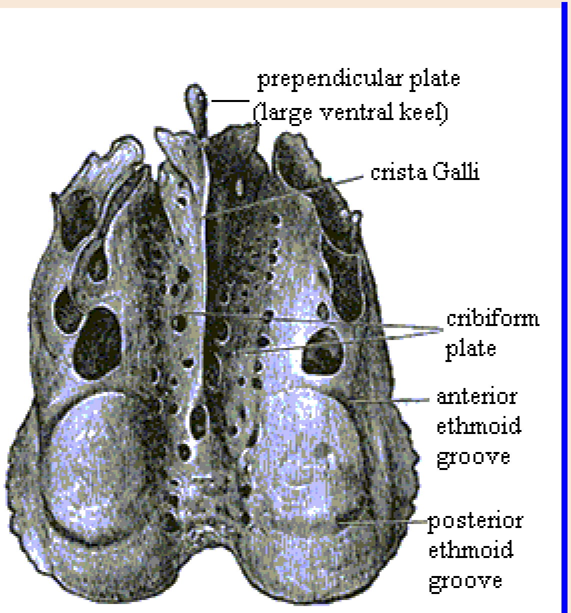


**Fig. 1. Human ethmoid in "superior" view (i.e. view from inside the brain cavity, looking forward and down.)**

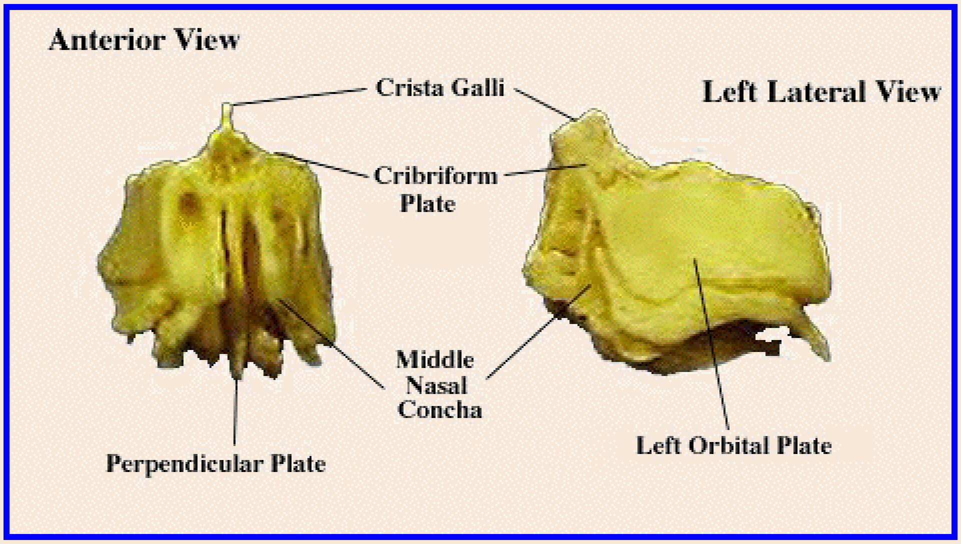
it may be best to consider the ethmoid as containing three "bones": (a) the paired lateral ethmoids (presumably derived largely from the nasal capsules) and (b) the mesethmoid (presumably derived largely from the fused anterior ends of the trabeculae). For those with a perverse desire to see the whole thing in humans, see: II. Osteology. 5a. 6. Ethmoid bone. Gray, Henry. 1918. Anatomy of the Human Body. One relevant illustration from Gray's is reproduced as Figure 1.

The ethmoid articulates with the sphenoid(s) posteriorly and frequently co-ossifies in species (fish) in which these braincase elements ossify. It typically articulates with the vomers and may co-ossify with these palatal elements as well. Other palatal articulations are possible, particularly the ascending process of the palatine.

The ethmoid has a number of persistent structures:

(1) the cribiform plate: a sieve-like barrier between the nasal cavity and the brain through which olfactory neurons communicate between the two chambers.

(2) perpendicular plate: forms nasal septum with participation of cartilage, vomers, etc. The plate can be extremely deep, as in *Homo*. It splits the ethmoid in two lengthwise and descends all the to the palate, where it often articulates with the ascending processes of the vomers and palatines.



(3) the crista galli: continues the perpendicular plate dorsally, above the roof of the nasal cavity where it may partially separate the two hemispheres of the brain in mammals. The crista galli and perpendicular plate can be envisioned together as a thin sheet of bone oriented straight up and down.

(4) conchae (turbinals) which provide a sensory surface for olfaction and prevent water loss by recovering respiratory water.

(5) orbital plates: lateral processes of the ethmoid which, if present, may define part of the medial wall of the orbits.

There is a very good discussion and figures of the human ethmoid at Dept of Anth: Ethmoid Page, from which the image at left is derived. ATW 010622.

# The Cribiform Plate

The cribiform plate of the ethmoid is apparently a linguistic redundancy, since both terms refer to the sieve-like nature of the braincase at the roof of the nasal cavity. The structure seems to have been first noted by the Roman physician Galen who, like many physicians, was an acute observer but sometimes a defective reasoner. Galen believed that nasal mucous represented the drainage of excess matter from the brain through the cribiform.**[1]**

In fact, the flow of information is the other way. The sieve-like holes in the cribiform permit the axons of olfactory receptor neurons in the nasal mucosa to synapse directly with the mitral neurons in the olfactory bulbs. The axons of the mitral cells make up the first cranial ("olfactory") nerve. However, the olfactory bulb is somewhat more than a nerve terminus and contains a rather complex neural structure of its own. Limbic System.

How the other neural inhabitants of the olfactory bulb affect the sensory function is not clear, but certainly some substantial information processing occurs even at this level. The olfactory bulb is organized into perhaps two thousand small glomeruli. According to some sources, each glomerulus is believed to be specialized around one or a few specific smells. According to another, the glomeruli are presumed to be redundant, with the response of each encoded in a sort of 24-bit binary code, corresponding to some 16 million different smells. Both explanations seem somewhat simplistic. The nasal epithelium also contains more mundane receptors sensitive to temperature and pressure. However, these do not communicate with the brain via the specialized olfactory glomeruli, but rather through the trigeminal (Vth) nerve. ATW 010622.

# Turbinals, Turbinates, Conchae, or Whatever

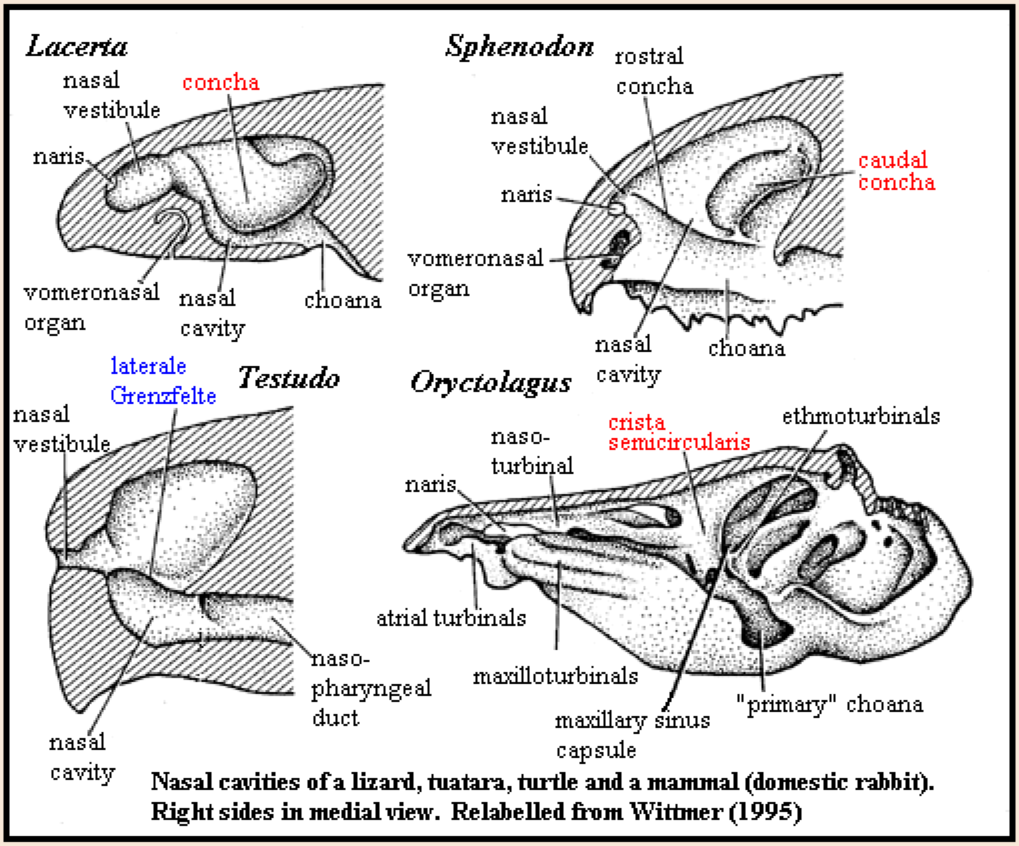
This manifestation of the ethmoid has received considerable attention since John Ruben and co-workers argued that turbinals (to pick one of the three names by which these structures are known), or their functional equivalents, are more or less indispensable for endothermic animals. See, e.g., Ruben *et al*. (1997). Since non-avian dinosaurs are seem to lack ossified turbinals, or even the enlarged nasal cavities necessary to contain them, the inference was that these dinosaurs were not endothermic. Others have argued that the lack of *ossified* turbinals is meaningless and that the volume of the nasal cavity is larger than Ruben had supposed. Much has been written on this topic by both capable students of physiology and serious scholars of the Dinosauria. We cannot count ourselves among the number of either company. Consequently, we have nothing to contribute to this debate, although we will touch on some its parameters.

The turbinals are often described as "scroll-like," although that phrase does poor justice to their complexity and variety. See image at right from Will's Skull Page (used with permission). Some very high-quality images and notes on the mammalian system may be found at nasal. They are, in any event, very thin and delicate bones of great complexity. Frequently, they are not bones at all, but unossified cartilage covered with a thin sheet of epithelium. At least in mammals, turbinals come in at least two functional varieties. The ethmoturbinals are associated with the cribiform plate. They are covered with olfactory epithelium. Primarily, they serve to increase the surface area over which olfactory receptor neurons can come in contact with respiratory air. These olfactory receptor nerves then synapse with the mitral cells of the olfactory lobes through the cribiform plate in the manner described above. Some very high-quality images and notes on the mammalian system may be found at nasal.

Meles meles (European badger) skull showing turbinals in nasal cavity.

What gets all the press are the maxilloturbinals, which are located anterior and ventral to the braincase and are covered with respiratory epithelium. These turbinals are in direct contact with the bulk respiratory air, rather than the small aliquot which is shunted aside for olfaction. In mammals, the maxilloturbinals are part of a complex countercurrent scheme which adjusts for the difference in temperature and humidity between the environment and the lungs. If colder and drier outside air were allowed to penetrate directly to the lungs, it would damage the very delicate alveolar membranes. Conversely, if warm, moist air from the lungs were allowed to escape directly, this might cause a devastating loss of heat and water. These effects are not particularly serious for a large-bodied ectotherm.. Its respiratory requirements are not ambitious, and some loss of body heat is generally only inconvenient. However, the problem is severe for an endotherm, particularly a small endotherm, which must maintain a steady internal temperature and has a considerably greater demand for respiratory oxygen. The presumed function of the maxilloturbinals is thus to create a large, vascularized surface area to recover water and heat from exhalant air, and to introduce water and heat into colder inhalant air. Note that, when an animal pants, it by-passes this nasal cavity system, deliberately increasing evaporative heat loss in order to recover from temporary overheating.

# Phylogeny of the Turbinals



Nasal cavities of a lizard, tuatara, turtle and a mammal (domestic rabbit). Right sides in medial view. Relabelled from Wittmer (1995)

In the following discussion, we generally follow Wittmer (1995). This is the most recent review of a topic which has frustrated anatomists since Gegenbaur in the 1870's. The principle difficulties are two. First, it is almost impossible to determine the form or even existence of turbinals in extinct species. Turbinals are only ossified in birds and derived synapsids. Even when ossified, they are so thin and delicate that they are very rarely preserved. Second, the position of turtles is unclear. Assuming (likely, but not certain) that turtles diverged from Eureptilia after synapsids, there remains the problem of whether turtles have turbinals.

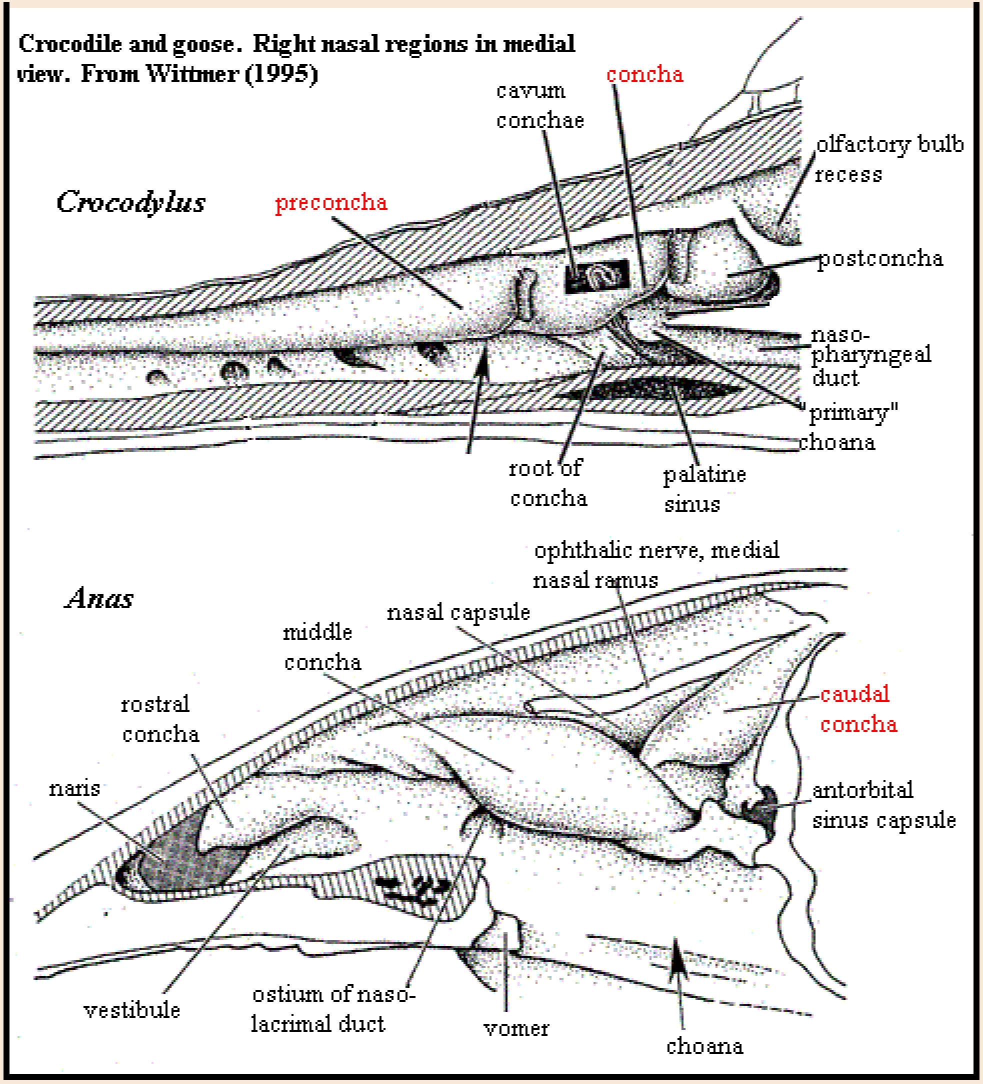
Turbinals are probably an apomorphy of the Amniota. As mentioned, the problem is turtles. There are no obvious turbinals, nor is there the kind of nasal capsule in which the concha of lizards, *Sphenodon* or some archosaurs is found. There is, however, the laterale Grenzfelte, a laminar protuberance from the wall of the nasal capsule which seems very similar to the rostral concha of *Sphenodon*. These structures *may* be related. However, Wittmer finds nothing particularly close in any other living taxon.

What Wittmer does find is a very close and convincing homology between the conchae (turbinals, cristae, etc.) marked in red in the figures adapted from his review. That is concha of lizards, the caudal concha of tuataras and birds, the crista semicircularis of mammals, and the concha plus preconcha of crocodilians are all the same structure. For convenience, we will follow Wittmer and refer to this structure as the "primary concha." In order to follow the argument, we will need to look more deeply than usual into the fundamental issue of homology.

In drawing this conclusion, Wittmer sticks very close to the strict Patterson formalism for homology. That is, in order to be homologous, structures must satisfy the tests of similarity, congruence and conjunction. These tests can be summarized as follows: **Similarity**: Each homologue must have the same 1:1 topographical relationship with other structures. In practice, we may add "or a really good developmental explanation of why it differs."

**Congruence:** The presence of the homologous character must be congruent with the cladogram. That is, the homolology must be a synapomorphy of some clade.

**Conjunction:** If two structures



Crocodile and goose. Right nasal regions in medial view. From Wittmer (1995)

are homologous, then both can never appear in the same organism.

This is, obviously, a rather strict definition, perhaps too strict in some respects. However, the primary concha generally satisfies these tests. In particular, the primary concha forms at or near the juncture of two major nasal cartilages (the paranasal and parietotectal); is the first conchal structure to form in development; is situated directly opposite the choana or its homologues (it starts and has its roots here in crocs); has a fixed relationship to the ophthalmic nerve; and contacts the lacrimal where present. In most cases, it also forms a capsular structure, the cavum conchae. Turtles present a problem for the congruence test which cannot be completely resolved. However, the general constriction of the nasal cavity in turtles probably results in secondary loss of the concha.

## Smelling Trouble

The problem with Wittmer's hypothesis -- and its only a small problem -- is really in the conjunction test. He essentially ignores this aspect of the equation and therein may have missed the forest for the trees. The fact is that there are a *bunch* of conchae in several derived forms. Even *Sphenodon* has two. Birds and crocs have three, and mammals may have six, or perhaps more. Significantly, as Wittmer notes, the primary concha in crocodilians splits into two parts during development, forming the concha and the pre-concha. Both in archosaurs and mammals, all of the conchae are structured in a similar way. Furthermore, when a particular species has conchae which are of a distinct form, it appears (from a *very* cursory review of a limited sample) that *all* of the conchae in that species have the same aberration.

So, its possible that a "concha" is not so much a particular structure as a rather general genetic program that can be duplicated and may operate at many points along the ethmoid and nasal capsule derivatives. This actually takes very little away from Wittmer's main argument. The similarities of the primary concha across many taxa are too strong to ignore. But, at the same time, we cannot fairly conclude that the other conchae are "neomorphs." The concha program may simply have been expressed more than once. In one case, the turtles, it may have been expressed *only* once, but not in the usual place. That is, it may be that the concha program has been activated in the laterale Grenzfelte, instead of the usual position. We see that both can also happen in *Sphenodon*. We might conclude that there is a fairly broad area, perhaps the entire ethmoid plus nasal capsule region, in which the concha program may be activated, with the most probable location being the primary concha.

Thus, this supposition has at least a bit more explanatory power than simple homology. However, it is virtually impossible to test without the techniques of genetic manipulation. Unfortunately, it may be some time before we have available "knock-out" turtles or crocodiles. In the mean time, strict homology is probably the best bet, so long as we don't take it too seriously. ATW021026.

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[1] A similar anatomical belief seems implicit in the writings of another noted authority, Mick Jagger.

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# The Mastoid (Human Otic Capsule)

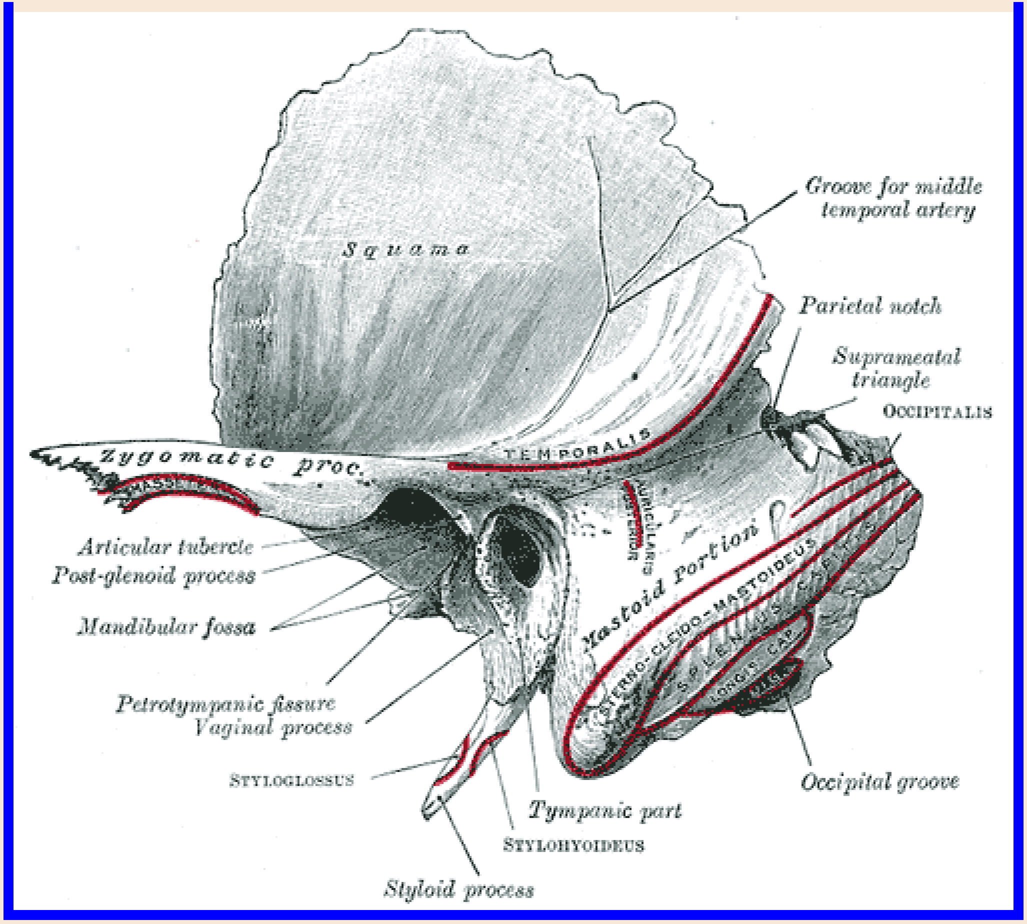
| Bones | Braincase | Otic Region |
|---|---|---|
| **Bones Overview**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**Sphenoid**<br>**References** | Demosphenotic: see Overview (Dermosphenotic)<br>Mastoid<br>Opisthotic<br>Prootic |

The mastoid is one of those repulsive little osteological features which mammals seem to have evolved solely for use as a badge of distinction, like a secret handshake or a fraternity code word. Indeed the possession of a particularly flagrant and obnoxious mastoid was once held to be the mark of man's superiority over the ape and the European's superiority over everyone else. By this reasoning, the world should rightfully be run by kangaroo rats, which have notably expanded "mastoids." But then, given the general direction of things, perhaps the world *is* being run by kangaroo rats.

Whether or not we are the pawns of xerophillic, megalomaniacal rodents bent on world domination, we must expose the truth, which is that the mastoid is not really anything new or different. It is simply another name for the periotic, which is identical to the petrosal, which is more or less the same thing as the otic capsule: *i.e.*, the opisthotic plus the prootic. The "mastoid" is simply the homologous human variant of this structure. Accordingly, we will use this page as a place to summarize the status of the otic complex in human beings. In humans, the otic capsule has fused with the squamosal and various other odds and ends to form the temporal bone. The mastoid is then that portion of the temporal bone which encloses the middle ear and forms the outer wall of the inner ear in humans. It differs from the same structure in basal mammals and mammaliforms primarilly in its outer aspect. That is, it comes equipped with an outer ventral process, the mastoid process, to which a group of muscles attach. In humans, and a number of other mammalian taxa, the structure is also expanded and heavily pneumatized. This is said to have something to do with auditory acuity, but no one seems to know exactly what.

## Anatomy & Attachments of the Otic Capsule in Humans

The figure on the right, lifted from the estimable Dr. Gray, shows the human left temporal bone in the sort of antero-latero- and- a- bit- dorsal view physicians use to talk down to patients without risking



unseemly eye contact. The dorsolateral surface of the mastoid portion forms a shelf, sometimes referred to as the occipital ridge (since it lacks a ridge and is nowhere near the occiput). The shelf provides an attachment point for two vital muscles, the *mm auricularis* and *occipitalis*. These serve, respectively, to wiggle the ears and raise the eyebrows.

After this promising start, the mastoid shelf abruptly gives up, as if discouraged by such pointless activity, and drops down, flat and wrinkled, to a roughly rounded point ventrally. This is the mastoid process, named for its supposed resemblance to a breast. From this nomenclature we may charitably conclude that the medical anatomists responsible for the simile were perhaps unfamiliar with the secondary female characters of their own species. Attached to the mastoid process are the *mm. sternocleidomastoideus, splenius capitis,* and *longissimus capitis*. If one were, for example, to hang one's head sadly and slowly shake it back and forth as if ruefully contemplating some new and distressing demonstration of the perversity of fate, one would then be exercising all of these mastoid faculties.

The narrow space on the medial face of the mastoid process provides a shelter for the occipital artery, and also anchors the posterior body of the *m. digastricus*. This muscle inserts on the hyoid. Lifting the hyoid through the *digastricus* aids in swallowing and in opening the jaw. Note how easily the simple act of opening the mouth, while repeating the mastoid exercise described above, converts a sophisticated gesture of world-weary resignation into an expression of feckless and bovine stupidity. Surely there is some sort of lesson to be learned here.

Internally, the mastoid is hollowed out to form the *epitympanic recess* to accomodate the ossicles of the middle ear. At the blind end of this chamber, the bone forms the *tegmen tympani*. Actually, the *tegmen* is not a blind end, since it communicates with a complex of small air-filled chambers in the mastoid. As noted above, the function of these pneumatized pockets is unknown. ATW030519

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# The Occiput

| Bones | Braincase | Occiput |
|---|---|---|
| **Bones Overview**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**Sphenoid**<br>**References** | **Occiput** |

## Anatomy

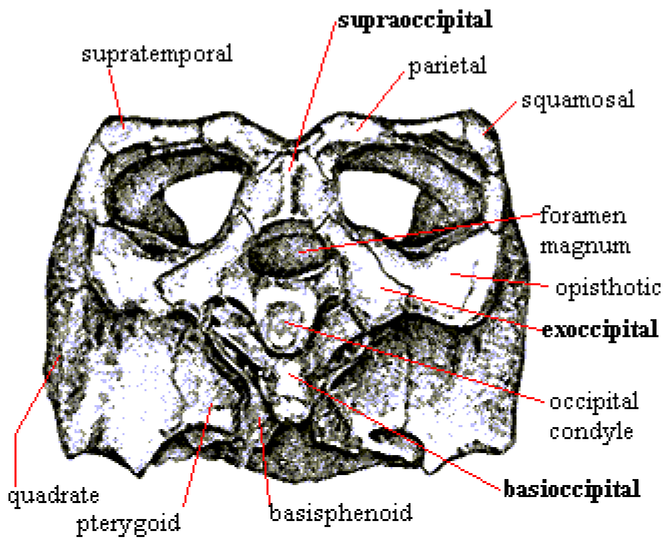

**Fig. 1. Stylized early amniote in occipital view, emphasizing elements of the occipital series**

The occiput is most typically a series of four endochondral bones: the supraoccipital, the basioccipital and the paired exoccipitals. Together, or in various combinations, they usually form the occipital condyle(s), the cranial side of the articulation of the skull with the vertebral column, and define the boundaries of the *foramen magnum* (Latin for "big hole") where the spinal nerves exit the brain. Together with the quadrates, the opisthotics and various dermal bones, such as the parietals and the squamosals, the bones of the occiput form the back of the skull. A typical arrangement, that of our old friend, Bob the Basal Amniote, is shown in **Figure 1**. **[1]**

The triangular configuration of the three dorsal elements is fairly typical and also rather easy to understand. The supraoccipital ties the occiput to the dermal skull table, while the exoccipitals are braced, directly or through the opisthotics, to the quadrate, squamosal, and whatever other elements form the posterolateral columns of the skull. Together, the supraoccipital and the exoccipitals define the top and sides of the foramen magnum.

Bob's occipital condyle is formed entirely by the basioccipital. The exoccipitals also frequently participate with the basioccipital in the occipital condyle, particularly when there is more than one craniospinal articulation. Bob's condyle is also a rather simple socket for a basic ball-in-socket articulation. However, the rest of the basioccipital is a very complicated affair. The "pockets" flanking the condyle are probably shaped to accept elements of the first cervical vertebra which limit lateral and/or dorsoventral rotation of the skull with respect to the spinal column and resist hyperextension of the neck. These brakes on rotation are critical to prevent bending stresses on the spinal cord. In addition, the basioccipital must be braced strongly against compression by articulating with basicranial elements such as the basisphenoid and pterygoid. The design problem is acute, because the basioccipital is performing its structural duties dorsally, and there is no direct ventral support.

# Functions

Most of the functions of the occiput have been discussed above:

1) *formation of the foramen magnum*. In lower vertebrates, the occiput (or its functional equivalent) is organized around the penetration of the anterior notochord into the cranium, and separate foramina for the major vessels and the spinal nerve cord. However, the same principles apply.

2) *formation of the craniospinal articulation*, including the occipital condyle(s) and accessory articulations primarily designed to keep rotation, flexion, and compression of the skull with respect to the spine within a physiologically safe range.

3) *structural support for the rear wall of the skull*. The occiput usually has considerable help here from other elements.

4) *structural support for the otic capsules, palate and basicranium* (as well as vice-versa).

# Phylogeny

## Chondrichthyes

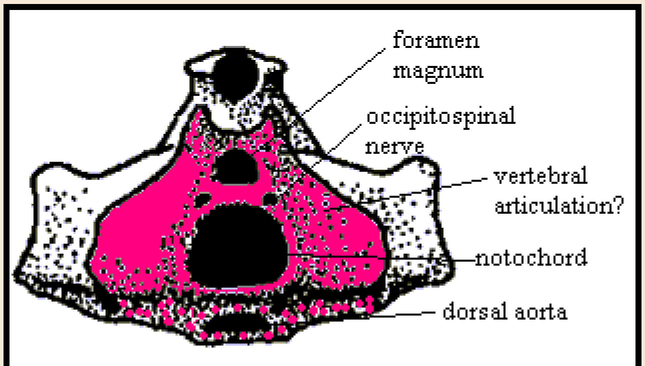

**Fig. 2. Occiput of Stethacanthus, modified from Coates & Sequeira (1998). The unlabelled foramen at the top is the endolymphatic duct, actually about 15mm anterior to the occiput.**

Although the standard occipital bones are a more recent phenomena, all craniates must, by definition, have an articulation between the braincase and the notochord (or vertebral column). Actually, it appears that the articulation in more basal vertebrates was far more complex than in Recent tetrapods. We are accustomed to think of the occipital articulation as involving two elements: (a) a mechanical coupling with the vertebrae and (b) a neural coupling with the spinal cord. In more basal forms, there were actually *five* different couplings which are (roughly from ventral to dorsal): (a) the dorsal aorta, (b) a cotylus or pit for the anterior notochord, (c) connections for the XIth cranial nerve (the spinal accessory or occipitospinal nerve), (d) mechanical coupling for the vertebrae, and (e) the foramen magnum for the spinal cord. The occiput of the Lower Carboniferous shark *Akmonistion*, shown in **Figure 2**, illustrates one such arrangement. See Coates & Sequeira (1998). The very complexity of this arrangement may have created the need for an otico-occipital fissure to prevent excessive strain on the various components. Modern sharks are notably different. As shown in **Figure 3**, the notochord and dorsal aorta have been re-engineered so as not to participate directly in the occiput, and the occipital condyle has become a more prominent, paired structure dorsolateral to the foramen magnum.

## Osteichthyes

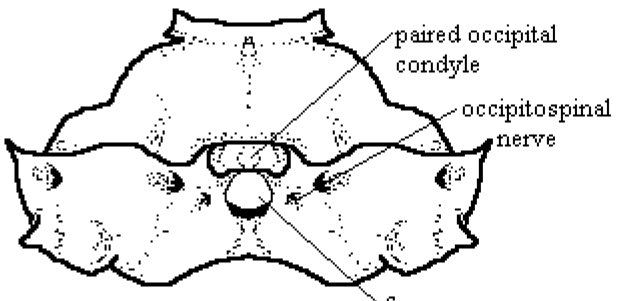

**Fig. 3. Occiput of generalized neoselachian shark (after Kardong & Zalisko (1998)).**

We have spent some extra time with the sharks in order to focus on the structure of the occiput as a whole, without the distraction of individual bones. The osteichthyans actually show a rather similar pattern of development, with mammals eventually arriving at an occipital structure that is somewhat similar to the neoselachian condition. Unfortunately (slipping, momentarily, out of the editorial "we") I have been unable to come up with enough information on the basic actinopterygian or sarcopterygian plans to comment much except to make the following tentative points. (1) The supraoccipital does not seem to have been part of the original complement of occipital ossifications. In teleosts, the supraoccipital is not clearly part of the occiput at all, but tends to form an anteroposterior crest on the top of the skull -- anchored in, but not part of, the occiput. The space between the foramen magnum and the roof of the skull (specifically, the post-parietals) is occupied by the opisthotic. (2) As in sharks, the dorsal aorta is lost from the occiput first, presumably because it is functionally replaced by the carotid arteries.

# Tetrapoda

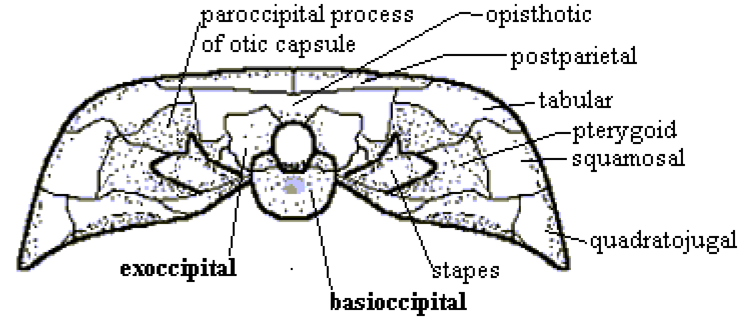

**Figure 4. Generalized occiput of early tetrapod. Note absence of supraoccipital and participation of exoccipitals in occipital condyle.**

A generalized early tetrapod occiput is shown in **Figure 4**. Like the opercular bones, the notochordal cotyle of the occiput vanishes with or perhaps even before, the transition to land. In fact, it disappears almost as soon as there are any tetrapods to be found. Note that the exoccipitals participate in the occipital condyle -- a feature which is present, for example, in the eogyrinid *Palaeoherpeton* and becomes quite common in amniotes.

At least in the colosteid *Greererpeton*, the exoccipitals articulate directly with the postparietals, which may participate directly in the foramen magnum. In slightly more derived forms, the opisthotic appears on the surface of the occiput and separates the foramen magnum from the postparietals. In amniotes, the supraoccipital is added as well. This is consistent with the common observation that the height of the braincase tends to increase in more derived tetrapods*. Note that, although the global trend in tetrapods is to reduce the number of cranial bones, bones are actually being added in the occiput.

# Lepidosauria

The general pattern of the lepidosaur occiput is essentially the same as in early tetrapods, except that (a) the supraoccipital replaces the opisthotic and the opisthotic becomes a paired element lateral to the exoccipitals. In other words, the pattern is the same as for Bob the Basal Amniote.

**Figure 5** shows the same basic pattern in *Anomochilus*, a fairly basal snake (modified from Cundall & Rossman (1993)). As those authors note, "the posterior braincase of *Anomochilus* appears remarkable in shape but unremarkable in organization." *Id.* at 246. In more derived snakes, most of the occipital elements are fused, forming essentially the only akinetic structure in the skull. However, the organization of the occiput remains the same.

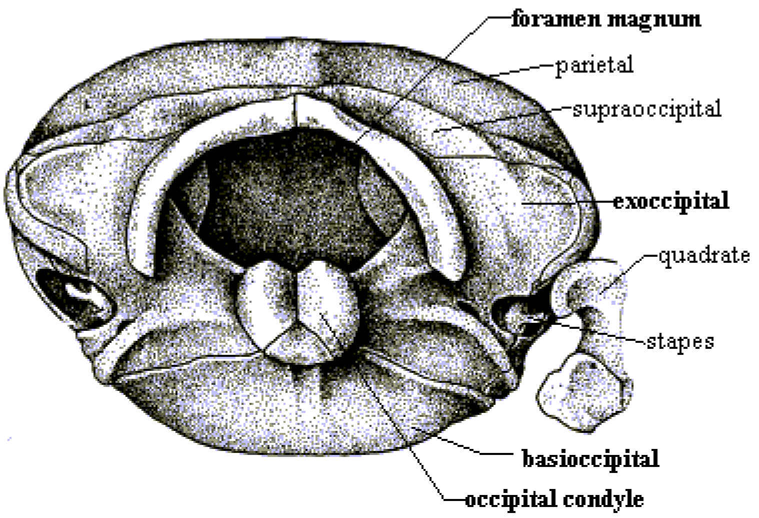

**Figure 5. Occiput of Anomochilus weberi. Modified from Cundall & Rossman (1993).**

# Archosauria

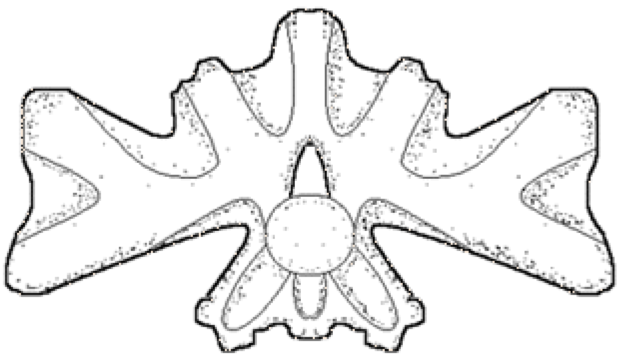

**Figure 6. Chasmosaur occiput, after Dodson (1996).**

The archosaur occiput also differs very little from the basic tetrapod pattern. Frequently, the occipital elements are fused, so that the occiput appears to be a single block. In particular, the exoccipitals are usually completely fused with the opisthotics, always so in theropods. Currie & Zhao (1993). Consistent with that trend, there is a tendency for some foramina disappear so that, for example, the XIth nerve no longer exits the brain in the occiput itself. In addition, the occipital condyle tends to be in a more dorsal position relative to the skull as a whole. This does not appear to be due to restructuring of the occiput so much as to the elongation of the quadrate ventrally. That is, the skull becomes deeper while the occiput remains more or less unaffected. Finally, the fused exoccipital-opisthotic element forms a broad bar joining the occiput to the quadrates on either side. Because of the increasing fenestration of the back of the skull, the entire occipital complex may appear to form a sort of Maltese cross, as in the rough sketch of the occiput of *Chasmosaurus* in **Figure 6** (after Dodson (1996)). Here, much of the edge of the occiput is not in contact with any other bone. The lateral edges articulate with the quadrates, the very top is attached to the parietals, and the base rests more broadly on the basisphenoid.

# Aves

In birds (**Figure 7**), all the evolutionary labor of the archosaurs is undone. Broadly speaking, The bird skull is formed from the dinosaur skull by pushing all of the dorsal bones posteriorly. Conceptually, one might create bird from dinosaur by taking the heel of one's hand and kneading a theropod skull from front to back. The parietal is pushed onto the posterior face of the skull and may actually overhang portions of the occiput as an occipital crest. The foramen magnum and occipital condyle are pushed almost to the bottom -- even onto the ventral surface -- of the skull.

As in derived lepidosaurs, all of the elements in Figure 7 are fused in the adult skull. Accordingly, the divisions between individual ossifications are somewhat arbitrary. Note that the

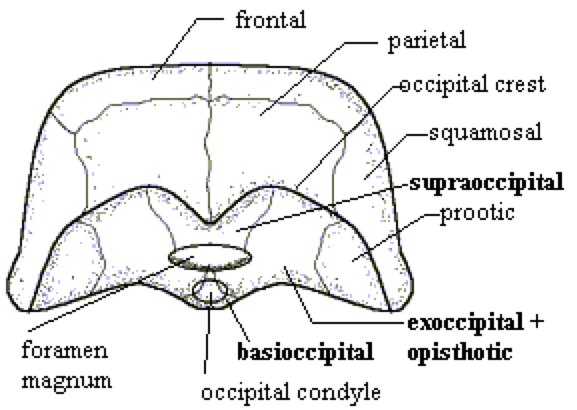

**Figure 7. Generalized neornithine occiput**

exoccipitals still participate in the occipital condyle. Since the bird condyle is rather small, and since one would expect an evolutionary premium on a smooth, even condylar head, it is hard to understand why evolution has preserved this 3-bone design.

# Synapsida

As mentioned above, the synapsids develop a doubled occipital condyle, like neoselachians **[2]**. This development occurs at the level of the therapsids. *Thrinaxodon*, for example, clearly has two occipital condyles, although they remain -- perhaps somewhat awkwardly -- below the level of the foramen magnum. In eucynodonts, the condyles "migrate" dorsally so that they come to flank the foramen magnum. This arrangement completely prohibits lateral rotation of the head and thus requires a fully developed mammal-like atlas-axis complex (which permits a wide range of rotation between the first and second cervical vertebrae). The offsetting advantage is that shearing strains on the spinal nerves are minimized since the axis of flexion now passes through the spinal cord, rather than below it.

# Additional Note

Two days after this essay was originally completed, I came across David Berman's *Origin and early evolution of the amniote occiput* (see Berman (2000)) -- which may be a greater comment on the shallowness of my original research than on the perversity of chance. In any case, this is a very fine paper combining a lot of careful, old-fashioned anatomy with a careful cladistic treatment of the results to yield an interesting and (despite the author's disclaimer) novel result. Crucial to this work is Berman's observation that the supraoccipital in tetrapods evolved independently at least twice, apparently from different embryonic structures.

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**[1]** Actually, in most typical early amniotes, the temporal opening would be less visible from this perspective, and the quadrate might be a smaller element. For the curious, this is a heavily edited, retouched, distorted and relabeled version of *Proganochelys*, an early turtle. The original is in Gaffney, ES & LJ Meeker (1983), *Skull morphology of the oldest turtles: a preliminary description of* ***Proganochelys quenstedi***. **J. Vert. Paleontol.** 3: 25-28, *vide* Carroll (1988).

**[2]** Also like placoderms. However, the placoderm occiput is so unique that it is not really homologous to any of the structures addressed here. In placoderms, my (possibly deranged) understanding is that the craniospinal articulation has no condyle. The hinge between head and body is posterior to the braincase and consists of a usually doubled condyle joining the posterior cephalic and anterior thoracic plates.

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# The Opisthotic

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- **Bones Overview**
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- **Ear**
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**Braincase**

- **Overview**
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**Otic Region**

- Demosphenotic: see Overview (Dermosphenotic)
- Mastoid
- Opisthotic
- Prootic

## 1. General

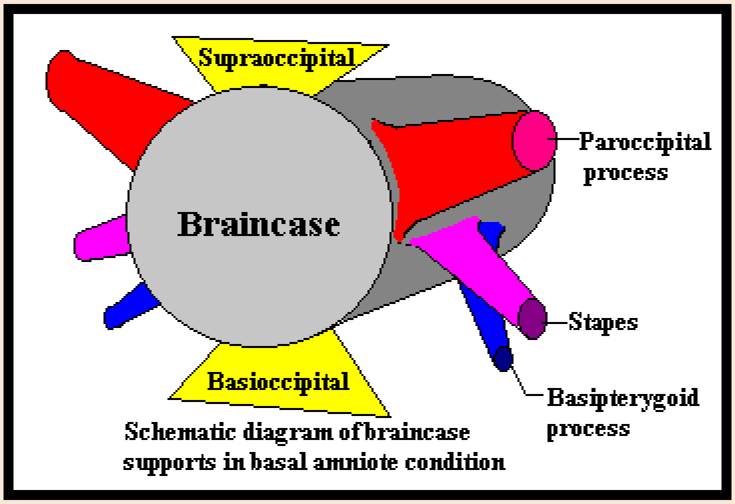
The opisthotic is, as the name might suggest, behind the prootic. Conceptually, it is the posterior half of the otic capsule. In this capacity, it is a rather boring bone. Usually, it is hopelessly fused to other things, forming yet another set of inscrutable speed bumps and pot holes on the braincase and providing the basis for yet another set of hopelessly inappropriate anatomical terms in an extinct language. In this case the terms usually begin with *crista, tecta, sella*, or (who knows?) *taiga, tundra*, and the like. Braincase terminology is somewhat fractal. Each level of obscure anatomical referents turns out to be made up of parts and variants with even more eldritch anatomical names. Just as the essentially Greek braincase regions are made up of little Latin structures, there is probably an entire vocabulary of component substructures which is represented in Babylonian pictograms, the true meaning of which is revealed only to a secret hereditary caste of anatomical hierophants.

Fortunately, the opisthotic has another and more democratic nature. Like the premaxilla, it has been recruited to perform a variety of external functions whose nature is open and accessible to all. Almost every student who has looked a figure including the occiput -- the bones at the back of the head – has seen the "paroccipital process" and has asked, plaintively, "the paroccipital process of *what*?" Here, all will be revealed. The paroccipital process is actually a process of the opisthotic. However, the process is a truly public structure and other elements tend to get involved, including the exoccipitals, supraoccipital, and even the prootic. In fact, there are "paroccipital processes" that do not even involve the opisthotic. Thus the structure tends to be referred to as if it were a separate bone.

Accordingly, the opisthotic has a two-fold personality. On the one hand, it is an obscure and secretive braincase element. On the other, a flamboyant and out-going external structural element of the occiput. We will concentrate primarily on the latter aspect. It is not only more accessible, but has recently been the subject of an odd and interesting study by Dr. David Berman of the Carnegie Museum, better known as the co-discoverer of the Bounding Bolosaur -- *Eudabimus*. Berman *et al.* (2000). But Berman (2000) is a very different kind of paper. Here, Berman carefully develops his theory of the evolution of the amniote occiput. Although it has all the appropriate cladistic tools and terminology, it is essentially a pre-cladistic work in the best tradition of Huxley's *On the Theory of the Vertebrate Skull*. That is, it begins with a few key developmental and anatomical insights and works them through numerous taxa to arrive at a unified picture of evolution at work. This kind of essentially intuitive work is still critical, and always will be. The cladistic analysis of numerical characters is the almost magical rocket engine driving contemporary paleontology. Still, someone has to point the thing in the right general direction and send us the postcards telling us where it has been. Berman (2000) is that kind of paper. Unfortunately, Berman's paper involves some aggressive reinterpretation of a number of well known taxa. So, it is a hard paper to evaluate. Nevertheless, it contains a good deal of information and raises a good many useful issues.

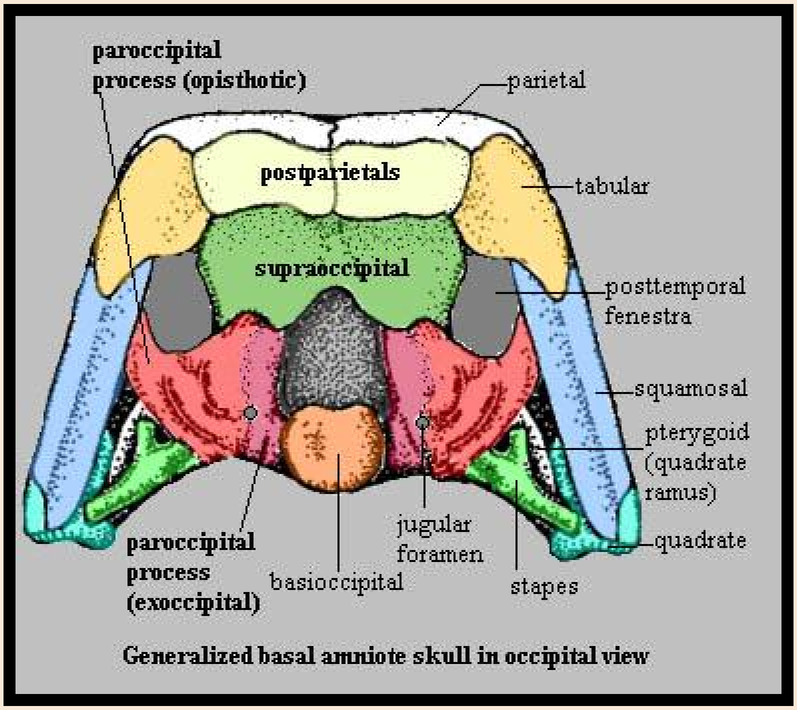
## 2. The Standard Condition

As usual, Bob, the Basal Amniote, is the standard bearer of the Standard Condition. However, even before we begin our customary visit to Bob, it is useful to look at a schematic. This is a sort of roadmap. If we model the braincase (very inaccurately) as a cylinder, we see that it is braced primarily towards the posterior end. Ventrally, it is supported by the basioccipital, which usually articulates with the pterygoids. Dorsally, the supraoccipital braces the braincase against the skull table, usually through some combination of the parietals, postparietals and tabulars. From the opisthotic at the rear of the otic capsule, the paroccipital process extends laterally, usually in combination with the exoccipitals but often including other elements. The paroccipital process typically terminates at the squamosal. Finally, the stapes creates a ventrolateral brace, joining the braincase with the quadrate at the ventrolateral corner of the occiput.



Schematic diagram of braincase supports in basal amniote condition

These are very broad generalizations, with numerous exceptions. However, they give us some basic landmarks. Landmarks are frequently necessary because, unlike more orderly bones, the opisthotic doesn't seem to grow so much as it *runs*. That is, it behaves like melted plastic and thoughtlessly fails to leave visible sutures. For that reason, three other historic landmarks merit a very brief side trip:



Generalized basal amniote skull in occipital view

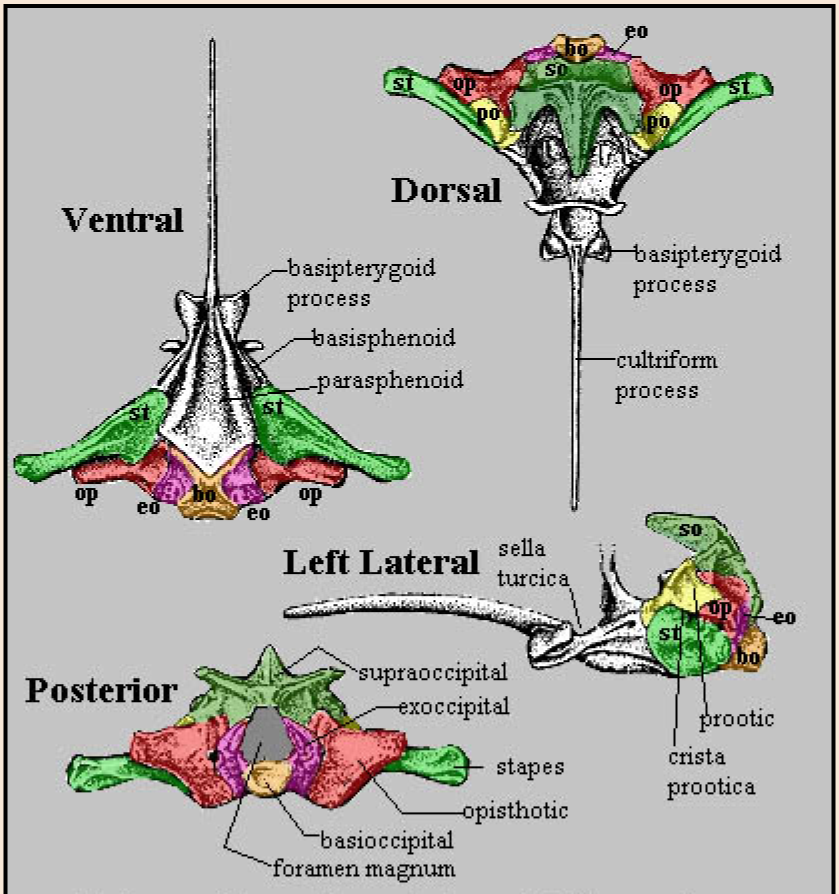
(a) The **posttemporal fenestra**: This structure is of greatest significance in non-amniotes. It is an opening in the back of the skull between the paroccipital process and the bones of the skull table. In amniotes, it tends to get covered over or obliterated.

(b) The **jugular foramen**: Another landmark of occasional interest is the jugular foramen – a small hole where the jugular vein exits the braincase. It generally marks the exit of the Xth and XIth nerves, as well. This jugular foramen is normally located along the articulation between the opisthotic and the exoccipitals.

(c) The **fenestra ovalis** (a/k/a fenestra vestibulae): This is the sensory "port" for the inner ear, as described in more detail at **The Ear**. It is frequently found along the prootic-opisthotic boundary.

With this roadmap, we can start to get into Bob's head. **[1]** In the case of Bob, the paroccipital process incorporates the exoccipitals. As mentioned above, the paroccipital process frequently includes other elements such as the supraoccipital or prootic. Bob has a very large posttemporal fenestra. Frequently much of the fenestra is obscured because the margin of the tabular which forms the dorsal border of Bob's fenestra develops into an opisthotic process which contacts the dorsal margin of the paroccipital process. A final variation is found in a number of basal amniotes, including the original model for Bob, *Paleothyris*. In these forms, the paroccipital process never reaches the squamosal. Instead, the process is present as a large, plate-like slab of bone lying between the supraoccipital and skull table, on one side, and the ventral margin of the occiput, on the other.

Before leaving the standard condition, it is worthwhile to take a careful look at the appearance of the braincase In another early amniote, *Eocaptorhinus*. Unfortunately, in real fossils, there are no convenient color codes or even detectable sutures in most of the braincase. Some of the boundaries shown in figure are only approximate. Still, they give us a pretty good idea of how the opisthotic is laid out with respect to the other bones of the brain case and occiput.



**Braincase of Eocaptorhinus, showing occipital bones and various other points of interest. From Carroll (1988: 195)**

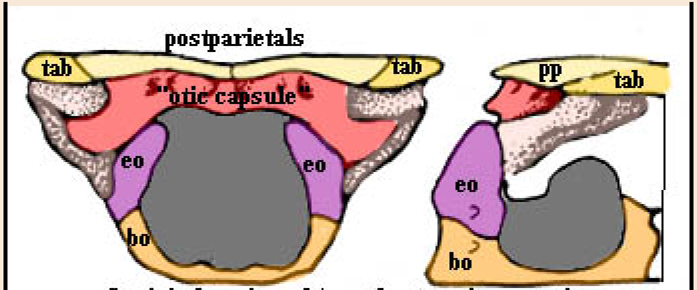
Note that at this level of vertebrate evolution, the stapes is a really massive element. While it is certainly possible that the stapes was connected in some way to hearing, it could not have performed the task in the same way as the columella of later diapsids. Another interesting feature is the size and complex topology of the supraoccipital. The dorsal and dorsolateral processes of the supraoccipital grab tightly onto the bones of the skull table like a three- fingered claw. The exoccipitals, opisthotics and prootics form a tight band around the braincase which is further stapled into position by the broad footplate of the stapes.

In fact, the basic structure seems so strongly constructed that one wonders why it was necessary to evolve a strong paroccipital process in addition. One might speculate that the evolutionary impetus was, as it often is, the drive to develop always stronger faster, and more flexible jaw muscles. That is, the development of large temporal fenestrae for jaw musculature would interfere with a structure which depended on strong attachment to the skull table. Furthermore, the growing jaw muscles would themselves be constrained by the massive stapes. Thus, it may have been advantageous for an organism to have a strong cross brace at the back of the skull which would leave more room for the development of jaw muscles anteriorly.

But we are getting a head of ourselves, so to speak. First we must try to determine how this distinctively amniote occipital structure evolved from its fishy forbearers. For this portion of the story, we must turn to a careful analysis of occiput evolution from *Acanthostega* to the Age of Bob. As with most early tetrapod problems, the inquiry gets bogged down in the swamps of the Carboniferous. But we will tread lightly and try not to get sucked in.

# 3. The Rise of the Opisthotic: from *Acanthostega* to Bob

Not to belabor the obvious, but our ancestors were fish. For that reason the earliest terrestrial vertebrates did not come equipped with an occiput, as we understand the term. Fishes live in a relatively supportive medium. The are quite happy with an

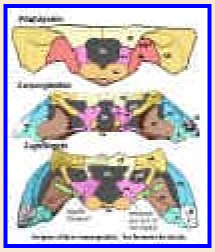


Occipital region of Acanthostega in posterior and right lateral views. From Berman (2000).

unrestricted notochord. Consequently, they have no need for an elaborate joint between the spine and the cranium. To be sure, teleost fishes have a bone which is called the opisthotic. However, it is not homologous to the tetrapod opisthotic and the teleost otic capsule is all of a piece.

The occiput of *Acanthostega*, such as it is, is therefore a relatively simple affair. Apparently the exoccipitals lie directly under the otic capsule which itself forms the dorsal margin of the foramen magnum. At least this is the way it is illustrated by Berman (2000). Jarvik's interpretation of *Ichthyostega* is quite different. However, the present fashion is to regard *Acanthostega* as closest to the tetrapod stem, while *Ichthyostega* is relegated to the role of an atypical offshoot.

This being the case, the interpretation given to the colosteid, *Greererpeton*, may be a little surprising. However, here there is no controversy. All seem to be agreed that the exoccipitals rest almost on top of the otic capsule. This is important, because *Greererpeton* is probably the most primitive well-known occiput from something that is clearly not a fish. "Fish" is, of course, not a term with much precision. *Greererpeton* was probably an aquatic organism. It may well have had gills, at least in some larval form. However, it did not have opercular bones; and its pectoral girdle was largely free of the skull. Given that *Greererpeton* was as close as we can find to *Acanthostega* in the direction of the amniotes, it may be legitimate to ask whether its exoccipitals are really homologous with those of *Acanthostega*. But that is a question for another day and another bone. For our purposes it is sufficient to note that *Greererpeton* certainly did have a paroccipital process of sorts. However, given its orientation and position -- a short anterodorsal bar terminating on the tabular -- it looks more like a process of the prootic than an occipital contribution from the opisthotic. Because the otic capsule is not divided into separate ossifications, we can't tell whether this structure is really a paroccipital process of the type found in other terrestrial vertebrates. In any case, this is clearly a very primitive occiput.



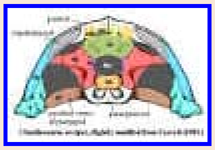
Since *Greererpeton* is generally felt to be closest to the temnospondyls, the next logical step is to compare it with the temnospondyls. **[2]**. But here we run into something rather unexpected. Berman bases his model of the temnospondyl occiput on *Platyhystrix*. He illustrates this organism as having a broad, plate like opisthotic lateral to the exoccipitals, with a squarish corner homologous to the paroccipital process. Perhaps a more typical example of the temnospondyl condition is found in *Luzocephalus*. *Luzocephalus* and many other temnospondyls have something a great deal more like a paroccipital process which is created by a laterodorsal process of the exoccipital sutured to a corresponding ventromedial extension of the tabular. Other temnospondyls form a similar structure with the exoccipital and the postparietals. At least one temnospondyl, *Lapillopsis*, apparently has both structures.

Note that in *Lapillopsis*, the stapes articulates with a process of the "exoccipital." Furthermore, the jugular foramen -- usually at the exoccipital-opisthotic boundary -- is well inside the exoccipital. What this suggests is that the exoccipital and opisthotic are fused or, perhaps more likely, that they are the same bone. Therefore, the "paroccipital process" of *Greerpeton* and *Platyhystrix* is quite possibly an unrelated process of the prootic or the old, unitary otic capsule. Conceivably, the exoccipital of *Acanthostega* may also be unrelated to the temnospondyl bone of the same name or, perhaps the opisthotic is itself derived from an extension of the exoccipital onto the otic capsule instead of a subdivision of the original otic capsule. **[3]** This supposition may be supported by the very primitive temnospondyls *Eryops* and *Edops*, in which the exoccipitals unite above the foramen magnum and roof the cranial cavity above the otic capsule. Berman (2000: 945).

This looks orderly, but rather strange. What happens if we take a step in another direction from *Greerpeton*, toward the amniotes? Possibly the closest we can come to this is *Megalocephalus*, a baphetid. The baphetids are weird, possibly alligator-like forms with enormous keyhole orbits. Their position is much debated, but the general feeling is that they diverged from the line leading to amniotes later than the temnospondyls. This is an area of phylospace we have not explored much, so it is hard to comment (undoubtedly this is for the best). At this level, something which is clearly related to the amniote opisthotic appears on the surface and forms a process joining with the tabular. In baphetids and anthracosaurs, the opisthotics join medially over the top of the foramen magnum. In amniotes, this central region is replaced by a (usually) unpaired supraoccipital formed from the ossification of cartilaginous bands which normally join the two otic capsules. Berman asserts that the supraoccipital is already present at this level and is continuous with the opisthotic.

While we have skipped over a great deal of detail, including the entire point of Berman's paper and all of the strange variations worked on these basic themes among the lepospondyls and living amphibians, this brings us more or less up to the level of Bob. It is clear only that the origin and evolution of the opisthotic is closely tied to the exoccipitals and the supraoccipital. However, the precise relationships are still vague. Note that Bob's opisthotic is more or less continuous with the exoccipitals -- an apparently primitive configuration -- and that this seems to be the normal pattern for reptiles. In some closely related basal or earliest amniotes like *Diadectes* and in early synapsids, the arrangement looks more like *Megalocephalus*, where the opisthotic and supraoccipital are more intimate. Turtles, fittingly enough, seem to begin somewhere in between, although parieasaurs have the Bob-like reptilian pattern.

# 4. Beyond Bob



We have spent an unusually long time trying to understand the Standard Condition, and without much success at that. This page threatens to become so encumbered that it resembles one of Prof. Paul Olsen's bandwidth-busting Mesozoic life pages, sadly without the quality that marked his work. We must now race through the amniotes like Benni McCarthy running past a couple of winded fullbacks.

Among the reptiles, as we've seen, the opisthotic tends to consort with the exoccipitals. It has little choice in the matter, since the supraoccipital tends to retreat into austere seclusion as a vertical element dedicated to loftier, or at least more dorsal, goals such as keeping the skull table together with the occiput. This is particularly necessary because the tabular, supratemporal and postparietal bones retreat over the course of the Permian. Those vertical anchors are weakened and finally lost. Both of these developments have a liberating effect on the opisthotic, which now combines with the exoccipitals to stretch across the back of the skull to form the lateral arms of the typical "Maltese Cross" occiput of archosaurs, illustrated elsewhere. As we can see from *Claudiosaurus* [Carroll (1981)], this pattern was well-established in basal diapsids, before archosaurs and lepidosaurs diverged.

Each of these groups has a minor variation on the general theme. In pythonomorphs and varanoids, the crista prootica is particularly well developed and actually extends posteriorly to participate in the paroccipital process. Rieppel & Zaher (2000). In archosaurs, there is a strong tendency for the entire occiput to fuse into one inseparable mass, invariably so in theropods. Currie & Zhao (1993). However, developmentally, the pattern is the same as in all other reptiles.

In synapsids, this simplification does not take place. the tabulars and postparietals are retained. The opisthotic-supraoccipital complex is likewise retained as a massive, plate-like paroccipital element. However, as the temporal fenestra expands to ludicrous proportions in the cynodonts, the skull table is reduced to a saggital crest formed by the parietal. The postparietals, tabulars *and* the paroccipital plate are all squeezed into a vertical triangular occipital area at the back of the skull, framed by the squamosals. Since there is no particular advantage to having separate ossifications in such a structure, this development set the stage for the more or less unitary skull of the mammals **[4]**.

# 5. Parting Shots

The opisthotic is unlike any other bone we have reviewed thus far. Its origins, relationships and evolution remain uncertain. It is nominally a chondrocranial bone of the braincase, but its most obvious function and associations are with bones of the occiput. It is closely associated, and often fused with either the exoccipitals, the supraoccipital, or even both. It may, in fact, share a common origin with one or both. Since it has no real homologues outside the "Amphibia," it ought to be , as Berman argues, a good phylogenetic marker for the tetrapod stem group; but somehow, its pattern seems to elude accurate classification.

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**[1]** Bob is loosely based on *Paleothyris* from Carroll (1988: 194). However, numerous changes have been made to better illustrate the general amniote condition, and any resemblance to actual occiputs, living or dead, is purely coincidental.

**[2]** *Platyhystrix* is taken from Berman (2000), labeled in accordance with the original. *Luzocephalus* is from Warren (1998). The original is unlabelled. I had some difficulty with this figure, and some areas (not those of major interest) may be mislabeled or shown with misplaced borders. *Lapillopsis* is from Yates (1999). This is labeled per the original, except for the jugular foramen which is unlabelled in the original.

**[3]** Readers should not have to be reminded to take these speculations with a massive grain of salt. As always, the analysis is for amusement and exercise, and should not be confused with real science.

**[4]** It seems to be one of those unwritten rules of paleontology that no one illustrates a mammaliform in occipital view. To be sure, there isn't a lot to show. Nevertheless, this is somewhat frustrating for those of us who wish to illustrate the full range of vertebrate cranial morphology.

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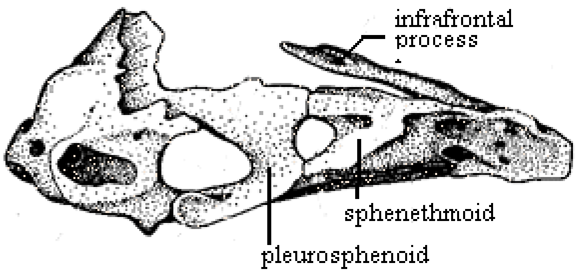
# Braincase: Pleurosphenoid

| Bones | Braincase | Sphenoid Region |
|---|---|---|
| **Bones Overview**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**Sphenoid**<br>**References** | Overview<br>Basisphenoid<br>Pleurosphenoid<br>Sphenethmoid<br>Sphenoid (see Overview) |

# Status



**Braincase of Grandisomia, an extant caecilian, in right lateral view. Modified from Carroll (1988)**

About three years ago (1999) we posted a small paragraph on the pleurosphenoid at the bottom of the Braincase Overview page. Here, we essentially accused the profession of having made the whole thing up. We received several emails from pleurosphenoid *afficionados* objecting that one or the other reptile actually had this no-doubt essential piece of vertebrate headgear. Eventually (2001), we grudgingly admitted that at least some Gymnophiona had a pleurosphenoid. See the *Grandisonia* braincase at right. More recently, we dealt with the evolution of the jaw in Holocephali, as illuminated by Grogan *et al*. (1999). This important article leads us back to the middle of the braincase and a re-evaluation of a number of structures, including the pleurosphenoid. While we are not yet willing to yield the pleurosphenoid a seat at the High Table of serious cranial structures, we can at least relieve it of the singular indignity of being a footnote among head bones.

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# Overview

Unlike many cranial bones, the function of the pleurosphenoid is easier to determine than its structure or lineage. In gnathostomes generally the anterior braincase is the province of a sphenethmoid ossification which develops, more or less, from the trabeculae. However, something rather dramatic occurred in the tetrapod lineage during the later part of the

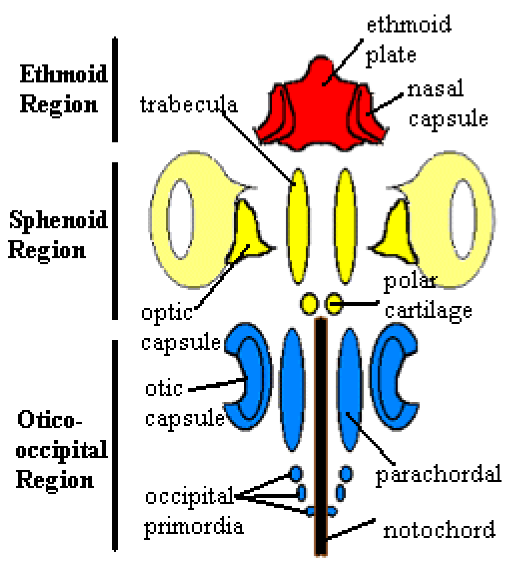
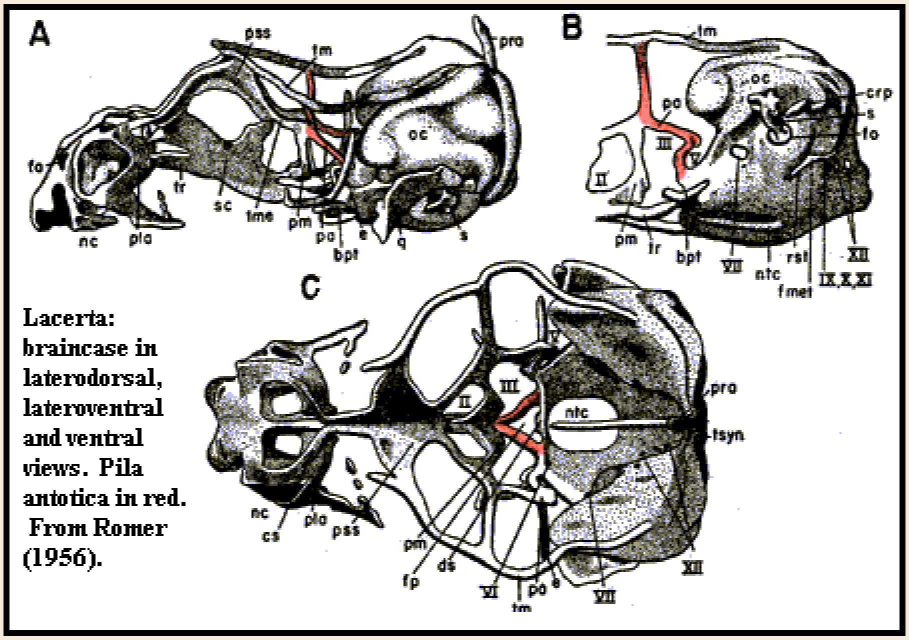


**Figure 3. Schematic view of vertebrate braincase development**

Early Carboniferous. At this point, temnospondyls, lepospondyls and reptilomorphs diverged. None of these taxa has a "normal" gnathostome sphenethmoid, although the lepospondyls come close. In most cases, the anterior braincase is unossified, or the degree of ossification is reduced, presumably as a result of adapting to a terrestrial or partially terrestrial existence.

This leaves things like crocodiles, theropods, and even birds and mammals, with a real problem. The braincase can be made cartilagenous without a great deal lost. However, it is still necessary to shore up the sides of the skull if one is to develop a really formidable rostrum. Furthermore, it is important to keep things like eyeballs, maxillary veins, and nasal epithelia from sloshing around and generally getting in each others' business. Thus, many tetrapod taxa re-invented the sidewall for the anterior braincase, or at least bits and pieces of it.

The pleurosphenoid is oneof those bits and pieces. It is distinguished (if at all) by its position relative to certain embryological markers, notably the *pila antotica*. On the off-chance that some particularly obtuse or forgetful reader may be unfamiliar with this ever-popular landmark of lizard embryology, we will explain.



**Lacerta: braincase in laterodorsal, lateroventral and ventral views. Pila antotica in red. From Romer (1956).**

The sphenethmoid does not simply disappear over the course of tetrapod evolution. Rather, like a decrepit dwelling, it gradually sheds superstructure until only a few main beams remain. In development, the embryo still dutifully constructs these beams as a latticework of cartilage, although the frame will never be built out or ossified. One of these beams is the *pila antotica.* These *pilae* **[1]** (since there are actually a pair) arise from either side of the *dorsum sellae*, the sturdy process which guards the pituitary fossa just in front of the hind-brain. With reference to our standard diagram, the *dorsum sellae* is located just about at the point where the polar cartilages are shown. Dorsoventrally, it is more or less at the bottom of the brain. The *pilae* rise anteriorly and medially from the *dorsum sellae* until the two processes meet in the middle. It then rises to the *taenia marginalis* which runs sagitally along the midline of the skull table, just under the dermal bones.

In some forms, as in Multituberculata, the *pila antotica* itself may ossify. In such cases, it is referred to as the *taenia clino-orbitalis* **[2]**. More frequently, as in birds, crocs, and ocasional others, the *pilae* allegedly come to support small and variable ossification above, more or less as minor anterior extensions of the otic capsule. These, we are told, are the pleurosphenoids.

And so, although we are still inclined to suspect that we have been taken in by some bizarre anatomical jest, we have done full justice to the subject and will say no more. ATW020917.

**[1]** *Pila* is normally translated as *pillar*, but is more acurately a generic Latin word for any long, vaguely cylindrical object. It also has a few other meanings, including *ball, ball game,* and *bookstore*. Thus: *pilam pilarum inter pilas pilae ludabamus* (we were playing a game with balls among the pillars of the bookstore).

**[2]** No, I am *not* kidding.

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# The Prootic

| **Bones** | **Braincase** | **Otic Region** |
|---|---|---|
| **Bones Overview**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**Sphenoid**<br>**References** | Demosphenotic: see Overview (Dermosphenotic)<br>Mastoid<br>Opisthotic<br>Prootic |

## Anatomy

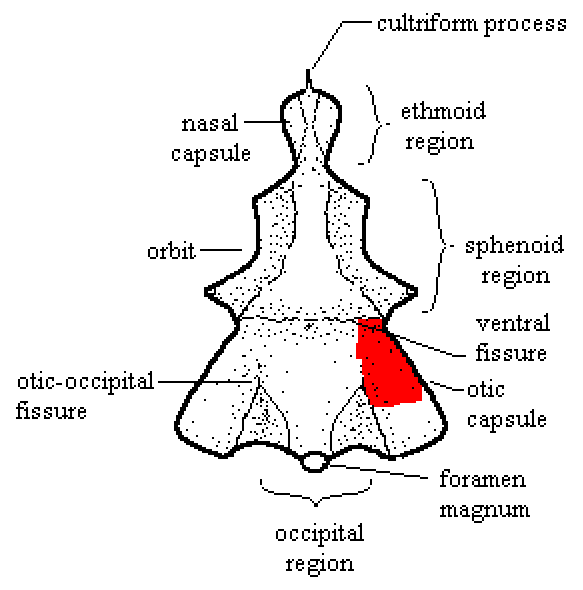

**Fig. 1. Generalized vertebrate braincase in ventral view. Prootic region in red.**

The prootic (in older or European texts, the "pro�tic") is an endochondral bone of the braincase. It typically forms the anterior and dorsal surface of the otic capsule. The otic capsule contains, in addition to the otic region of the brain itself, the labyrinth and inner ear. The labyrinth is the sensory organ which informs the brain about its orientation and acceleration in a gravity field. As with most endochondral bones (bones pre-formed in cartilage) the prootic does not form neat sutures, but tends to merge seamlessly with the other centers of ossification. It co-ossifies with the opisthotic, the other major bone of the otic capsule in many vertebrates, which is usually integrated into the external occipital wall (i.e. the back surface of the skull). The prootic itself may also articulate internally with the occiput, e.g., through the exoccipitals or the supraoccipital. It may also articulate with various dermal bones of the roof or sides of the skull for support, normally the squamosal and parietal. In dinosaurs, for example, the otic capsule can be fixed indirectly by the depression it leaves on the internal surface of the lateral wall of the skull. Most significantly, however, the prootic articulates with the quadrate. In more basal vertebrates, the quadrate simply braces the braincase. In more derived tetrapods*, this articulation forms the fenestra ovalis (fig. 2). In this case, the stapes forms a tight seal with an open area defined by the prootic and opisthotic and transduces airborne sound vibrations to vibrations in the liquid-filled inner ear. The prootic may also bear ventrolateral processes which staple it to the occiput or to one of the sphenoids underlying the braincase, or posterior processes which may reach the external surface of the occipital region.

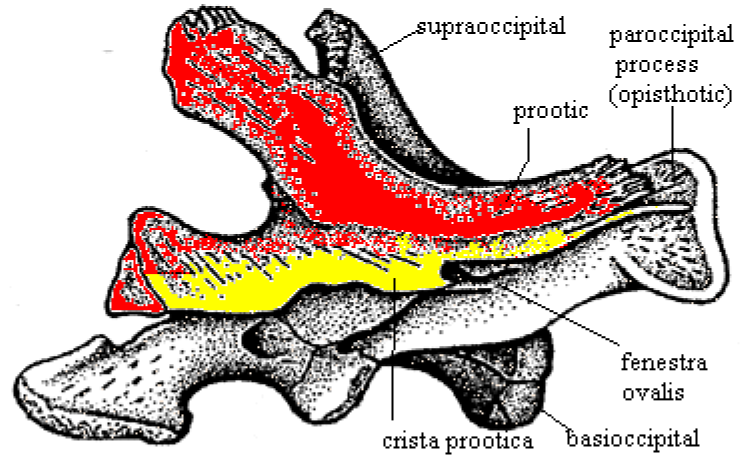

**Fig. 4. Braincase of Varanus in left lateral view showing crista prootica (in yellow). Modified from Rieppel & Zaher (2000).**

One of the more reliable landmarks on the prootic is the *crista prootica*. The crista prootica is a ridge or ledge of the prootic which runs antero-posteriorly along the side of the braincase above the otic capsule. **Figure 4**, modified from Rieppel & Zaher (2000). As shown in the figure, the crista prootica can be elaborated into a major braincase component. In *Varanus* (the monitor lizard), as in *Trilophosaurus* and other reptiles, the crista may join with the opisthotics or exoccipitals to form the paroccipital process. This process acts as a sort of horizontal cross-bar across the back of the skull. Anteriorly, the crista may be elaborated into a kind of awning which shelters the foramina from which other cranial nerves communicate with the brain.

## Functions

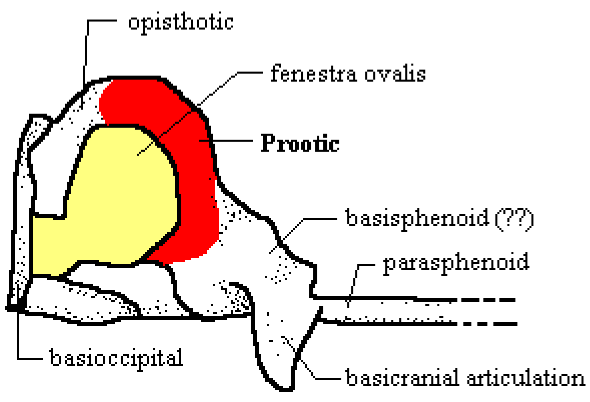

**Fig. 2. Temnospondyl otico-occipital braincase in right lateral view.**

The prootic is associated with the following functions:

(a) *Protection of the labyrinth and inner ear*: This is perhaps the most ancient and invariable function of the otic capsule generally. The labyrinth consists of the semicircular canals which, in turn have hair cells with small otoliths (roughly, pebbles attached to the hair cells). The canals each have a specific orientation and are so arranged that the movement of the otoliths can be integrated by the brain to determine orientation in a gravity field or acceleration. Since an organ which can detect motion in liquid can detect (on a finer scale to be sure) *vibration* in liquid, it isn't hard to see how this apparatus might evolve an auditory function. In derived tetrapods, the inner ear contains both the auditory and "balance" sensors. In addition to forming all or part of the otic capsule, the prootic may bear a crista prootica which provides a second layer of protection for the otic capsule and other neural structures.

(b) *Lateral support of the braincase*: As discussed above, the prootic is a rather protean bone which can attach itself to a variety of supports. See the braincase overview for the importance of lateral support. Again, the crista prootica elaborates on this function by participating in the paroccipital process of the occiput.

(c) *Support of/by the stapes*: Primitively, the stapes was a rather large bone which provided ventrolateral bracing to braincase through the otic capsule. However, in this position, it naturally carried some external vibrations to the otic capsule. In many early tetrapod lineages, the primary function of the otic capsule became hearing, and the prootic-stapes junction became the fenestra ovalis. In advanced tetrapods*, the stapes loses its support function altogether and becomes a minute element specialized for sound transduction. Thus, the respective roles of the two bones are reversed, with the prootic serving to support the stapes as a sound transducer, rather than being supported by the stapes.

## Phylogeny

Osteostracans have a distinct vestibular chamber, but no otic capsule or prootic as such. The placoderms and chondrichthyans both show at least some capsular protuberance of the braincase, but the braincase is a single, undivided mass, whether or not ossified. Interestingly, even at this stage, the braincase frequently bears a shelf or ridge over the otic capsule, so that homologues of the crista prootica may predate the

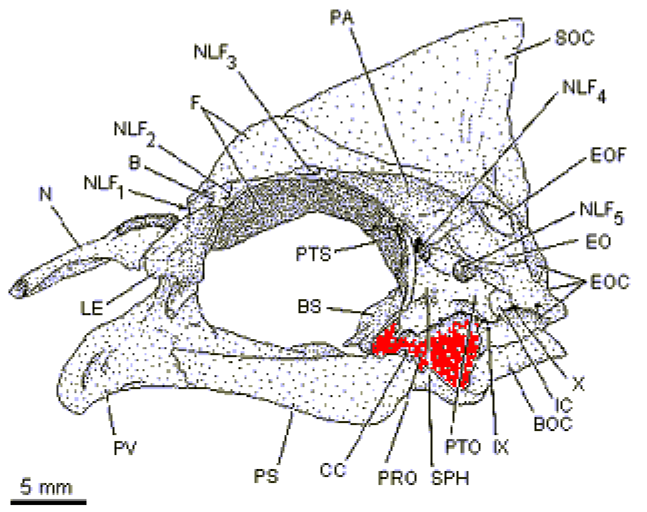

**Fig. 3. Skull of a teleost, the basal chichlid Heterochromis multidens. B: blind cavity (not lateral line). BOC: basioccipital. BS: basisphenoid. CC: carotid canal. EO: epioccipital. EOC: exoccipital. EOF: facet of EO for posttemporal. F: frontal. IC: intercalar. IX: glossopharyngeal nerve. LE: lateral ethmoid. N: nasal. NLF: lateral line foramina. PA: parietal. PRO: prootic. PS: parasphenoid. PTO: pterotic. PTS: pterosphenoid. PV: vomer. SOC: supraoccipital. SPH: sphenotic. X: vagus nerve.**

prootic itself. See, e.g., Coates & Sequeira (1998).

Acanthodians and most sarcopterygians are believed to have had a single and undivided otico-occipital ossification. Teleosts have a prootic ossification, but (like a number of teleost bones), it is not clear that this is homologous with the tetrapod bone of the same name. Fig. 3. The teleost prootic may be integrated with the lateral dermal bone through the dermopteric and pterotic, bones which have no straightforward analogs in land animals. The basal tetrapods possessed a recognizable prootic ossification, more or less similar to that shown in Figure 2. One, somewhat aberrant and interesting example (the frog), may be seen at Prootic Bone. Note how the whole otic complex has been oriented laterally and suspended between the squamosals and the pterygoids.

In amniotes, the enlarged supraoccipital links the occiput with the otic capsule, perhaps freeing the stapes to evolve further in the direction of a purely sensory transducer. In cryptodire turtles, the prootic also assumes a special role in supporting and redirecting the force of the major jaw adductor muscles. Among cynodont synapsids, the jaw joint moved anteriorly, and the jaw muscles became associated with the *external* surface of the dermal bones and in the "new" masseter muscles inside the zygomatic arch. This removed a good many constraints on the size of the brain and the position of the otic capsule. In this lineage, the prootic becomes a much smaller, peripheral element closely associated with the squamosal, eventually merging with the opisthotic to form the petrosal in early mammals.

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Figure 3 from Mike Oliver's **Malawi Cichlids** site, and originally from Oliver, MK (1984), **Systematics of African cichlid fishes: Determination of the most primitive taxon, and studies on the haplochromines of Lake Malawi (Teleostei: Cichlidae)**. Unpublished Ph.D. dissertation, Yale Univ. 326+ pp. � 1984 by Dr. Oliver and reproduced here by permission.

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# The Sphenethmoid

| Bones | Braincase | Sphenoid Region |
|---|---|---|
| **Bones Overview**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**References** | Overview<br>Basisphenoid<br>Pleurosphenoid<br>Sphenethmoid<br>Sphenoid (see Overview) |

**Anatomy**: The sphenethmoid, sometimes called the ethmosphenoid, is something between a region and a bone. In primitive gnathostomes, the embryonic trabeculae (see Overview) fuse to form a single ossification which includes the entire braincase from the ethmoid plate, anteriorly, to the otic region posteriorly. This region is marked by the orbits, laterally, and often the articulation between the braincase and the palatoquadrate. Its posterior extent was coincident with the original anterior limit of the notochord and the ventral fissure. Ventrally, the ethmosphenoid normally contains foramina for the internal carotid artery and the Vth cranial (trigeminal) nerve, or at least the profundus branch of that nerve. The sphenethmoid also usually bore the basicranial articulation, the old major articulation between the palate and the braincase.

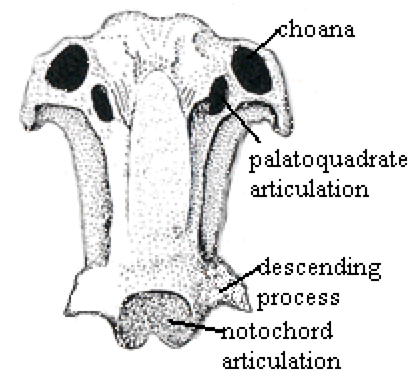

**Figure 1a. Sphenethmoid of generalized dipnomorph in palatal view**

However, in early tetrapods, this portion of the braincase began to take on a rather different character. With the development of skulls constructed of strong dermal bones, the importance of the sphenoid was reduced. The basicranial articulation was no longer the anchor for the palate, and the palatoquadrate was functionally replaced by its dermal *anlagen*, the maxillae. By the level of the amniotes, the sphenethmoid had disappeared altogether. Instead, the midbrain was roofed by dermal bones, and the principle sphenoid ossifications became a series of bar-like bones which supported the brain ventrally and sometimes laterally. These are the various sphenoid bones which will be dealt with separately. The remainder of the anterior sphenoid region was unossified.

The bottom line of all this is that the Standard Condition for the sphenethmoid cannot be defined with reference to our usual informant, Bob the Basal Amniote. Bob simply doesn't have a sphenethmoid. Instead, it is convenient to define the Standard Condition by reference to some, vaguely dipnomorphic, sarcopterygian whom we will call "Judy," after another primitive, schizocephalic blockhead not otherwise discussed in these Notes. Judy's isolated sphenethmoid is shown in palatal view in **Figure 1a.** (Figures 1a, 1b and 1c are modified from illustrations of

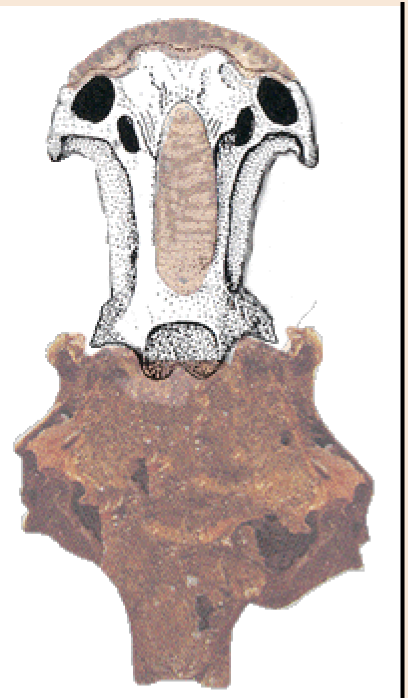

Figure 1b. Same as 1a, with premaxilla, parasphenoid and otico-occipital braincase

*Gogonasus andrewsae* in Long, 1995). As in many sarcopterygians, Judy's sphenethmoid is confluent with the ethmoid and nasal capsules. This the choanae lead dorsally right into the nasal capsules. The orbit and jaw adductors fit into the 'C'-shaped cavities on either side of the long sphenoid stem region.

In **Figure 1b**, we add ghost-like images of Judy's premaxilla, parasphenoid and the otico-occipital region of the braincase. The premaxillae fit tightly onto the anterior end of the ethmoid region and add a tooth row. As discussed at The Premaxilla, the premaxilla continues its contact with the nasal capsules and becomes involved with the external nares as well. The parasphenoid is a tooth- or denticle-covered plate which is attached to the sphenoid stem. The otico-occipital braincase attaches to the posterior. Note how the descending processes of the sphenethmoid hook onto anterolateral facets of Judy's prootic to form a kind of hinge joint on which the intercranial joint can flex. The otico-occipital portion is not only more massive than the sphenethmoid, but it is stabilized by the notochord which enters through the posterior "stem" region, runs all the way through the otico-occipital braincase and terminates at a socket joint at the end of the sphenethmoid, providing yet another mobile contact which allows the sphenethmoid to flex downward. The muscular workings of the *intracranial joint* are discussed in more detail (with yet another complicated diagram in *lateral* view) in connection with the main entry on porolepiforms.

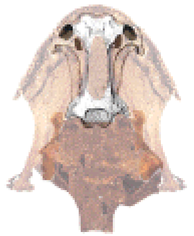

Figure 1c. As 1b, with addition of maxilla, palatines and pterygoids

Finally, we are ready to add some additional palatal roofing bones. These are shown in **Figure 1c.** The maxilla extends the skull outward from the sphenethmoid to make room for Judy's big mouth and, perhaps more importantly, a larger, more posterior adductor chamber for the all-important jaw-closing muscles. Her palatines supply an additional row of teeth and the pterygoids almost complete the roof of the palate. This is as far as we will take the assembly, but the palate is still incomplete. For example, the blank area between the choanae would be covered by the vomers. The second tooth row might be extended by toothed ectopterygoids. A second layer of denticle-bearing dermal bones, such as entopterygoids and parasphenotic plates, might cover all or part of the pterygoids.

Dorsally, the sphenethmoid is in contact with the dermal bones of the facial, orbital and vault series. However, in dipnomorphs, these bones tend to be rather non-standard (see figure at Dipnoi), so that the articulations are not what one might normally expect.

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**Functions:** In the Standard Condition, the sphenethmoid is associated with the following, fairly obvious, functions:

1) *Formation of the anterior braincase*. The sphenethmoid is intimately connected with the olfactory nerves, the entire optic apparatus and the fore- and mid-brain.

2) *Anterior articulation of the palatoquadrate*. Technically, this is part of the ethmoid, but the two are confluent in the Standard Condition.

3) *Medial support of the palate*. In sarcopterygians, including basal tetrapods, the mouth is very large. It is stable only because the sphenethmoid (and its later successors) provide a roof beam which supports the center of the palate.

4) *Intracranial articulation*. The sphenethmoid is the moving part of the intracranial joint. In many sarcopterygians, the joint gradually became immovable, or only slightly flexible as in the living actinistian,

*Latimeria*. However, it seems to have played an important role in the evolution of the structure of the sarcopterygian head which the tetrapods inherited.

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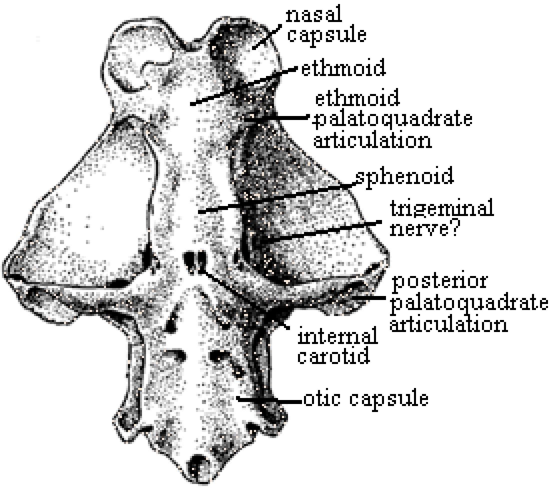
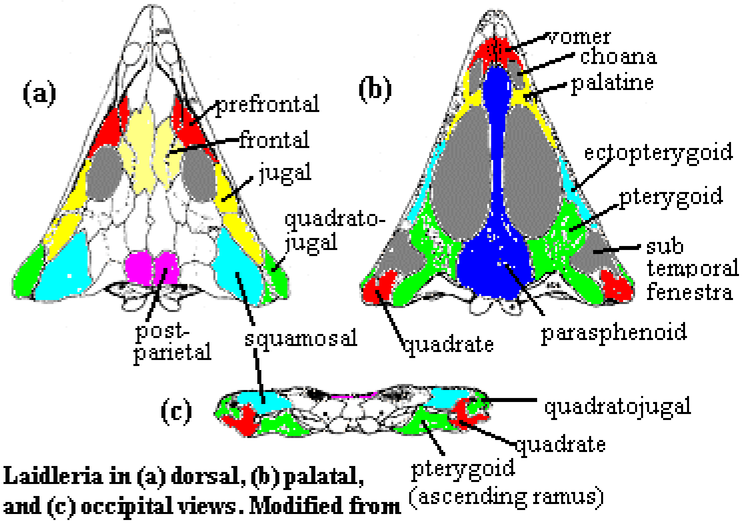


**Figure 2. Braincase of Stethacanthus in ventral (palatal) view. Modified from Coates & Sequeira (1998)**

**Phylogeny:**

1) *Basal gnathostomes*: There will always be a sphenoid, if for no other reason than that there must be something between the nose and the otic capsules. **Figure 2** shows as primitive a gnathostome braincase as we are likely to know for some time. This is the early symoriid chondrychthian, *Stethacanthus.* In spite of the vast phylogenetic gap between *Stethacanthus* and dipnomorphs, many of the sphenethmoid landmarks are recognizable. These include the palatoquadrate articulation at the posterior boundary of the ethmoid, the long, thin sphenoid region, and the trigeminal and internal carotid foramina. In fact, not a great deal separates the sphenethmoid areas of *Stethacanthus* and the Standard Condition except for the absence of both endochondral bone and the intracranial fissure in the former. Not surprisingly, the sphenethmoid of the basal sarcopterygian *Psarolepis* is more or less intermediate between the two. Yu (1998).

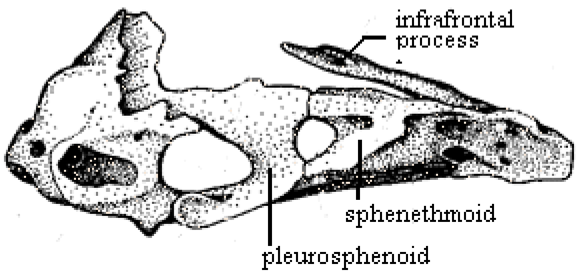
2) *Basal tetrapods*: The advanced sarcopterygian *Eusthenepteron* also has the Standard Condition, except that the trigeminal nerve foramina are all posterior to the intracranial division. Since the Vth nerve elements would then have to cross the intracranial divide, this suggests (as do some subtle changes in geometry) that the intracranial joint was less flexible. The sphenethmoid region as a whole already shows a trend toward closer integration with the dermal bones dorsally, with a more open structure on the dorsal surface of the braincase. By contrast, the ventral surface of the sphenethmoid is much broader in proportion to the total width of the head, looking more like a beam than a hammer.



**Laidleria in (a) dorsal, (b) palatal, and (c) occipital views. Modified from Warren (1998)**

With the move onto land, tetrapods* lost the constant support of an aqueous medium. As a result, there was considerable adaptive advantage to reducing the mass (and so the moment arm) of anterior element of the head. The labyrinthodonts still had fairly elaborate dermal shoulder girdles which could allow the arms to support the back of the head directly. However, the anterior elements were unsupported and enormous energy would be required to hold them off the ground -- similar to the difference between holding a bowling ball at arms' length, rather than close to the body. As a result, it is not surprising that temnospondyls and other stem tetrapods rearranged their skulls significantly. Thus the basicranial articulation was moved to the otico-occipital region, and the ethmosphenoid became a largely unossified element located half-way out on a long, thin beam created by the cultriform process of the parasphenoid which passed through the middle of two large, empty (of bone) "interpterygoid vacuities" The general scheme can be seen in the figure of *Laidleria*, a moderately derived temnospondyl, at right. Warren (1998). Here, the otico-occipital unit would be supported by the posterior body of the parasphenoid, while the remaining sphenethmoid would be a small element attached to the long anterior cultriform process of the parasphenoid.

3) *Lepospondyls and Lissamphibia*: Microsaurs adopted more or less the same design as temnospondyls, but the evolutionary constraints they faced were not as severe because of their relatively small size and aquatic habit. In the microsaur *Rhynkconkos*, for example, the sphenethmoid loses the basicranial articulation and the trigeminal nerve, as in temnospondyls. Likewise it is restricted to a narrow section dorsal to the cultriform process. However, it is still a long, fairly substantial element which is in direct contact with the basisphenoid and the otico-occipital section of the braincase.



**Braincase of Grandisomia, an extant caecilian, in right lateral view. Modified from Carroll (1988)**

Caecilians, generally speaking, took the microsaur body plan and consolidated it for their difficult, fossorial mode of life. As shown in the figure, the sphenethmoid makes a modest comeback as a major cranial bone, but its former territory is split with a pleurosphenoid ossification. The caecilians have also developed a unique paired infrafrontal process of the sphenethmoid which may help support the dermal skull bones against the considerable forces generated by digging.

A rather similar arrangement occurs in frogs. However, the anuran ethmoid plate widens out considerably at the anterior of the skull, so that the whole external aspect of the skull is changed. The premaxilla and maxilla look like a large arch supported at the apex by a pillar made up of the cultriform process of the parasphenoid with its attached sphenethmoid (and a more posterior ossification which is likely a pleurosphenoid).

4) *Amniotes*: There are occasional references to ossified sphenethmoids in the amniote literature. See, e.g., Currie (1997) (dinosaurs). However I have not yet found anything specific. At least generally speaking, the sphenethmoid is not ossified in amniotes.

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# Braincase: Sphenoid

| Bones | Braincase | Sphenoid Region |
|---|---|---|
| **Bones Overview**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**References** | Overview<br>Basisphenoid<br>Pleurosphenoid<br>Sphenethmoid<br>Sphenoid (see Overview) |

## Status

In the absence of an Overview essay for the sphenoid region, this survey of the sphenoid ossification must do for now as an introduction to this region. The following is drawn largely from medical sources, and may or may not apply in non-humans.

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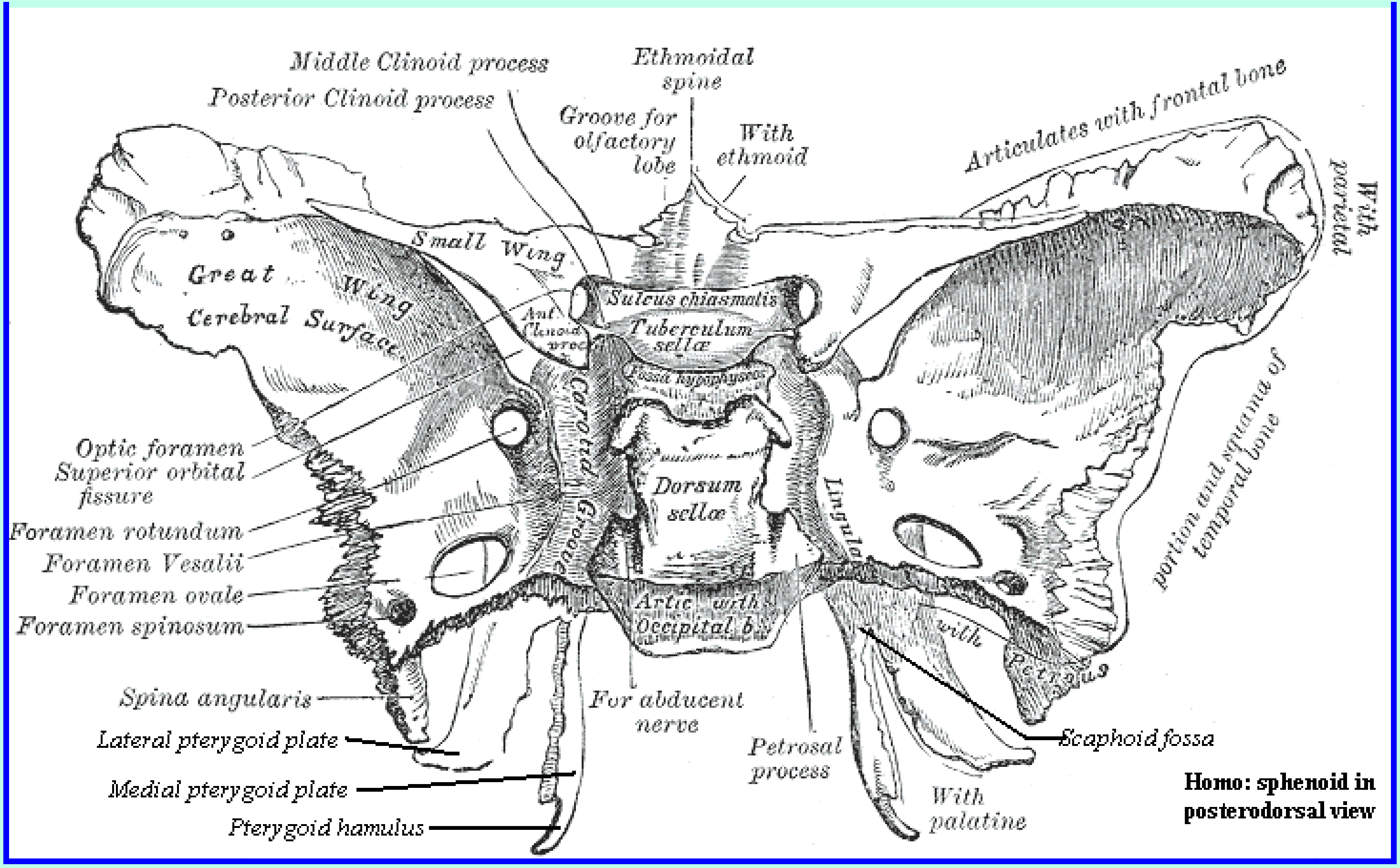


**Homo: sphenoid in posterodorsal view**

# Overview

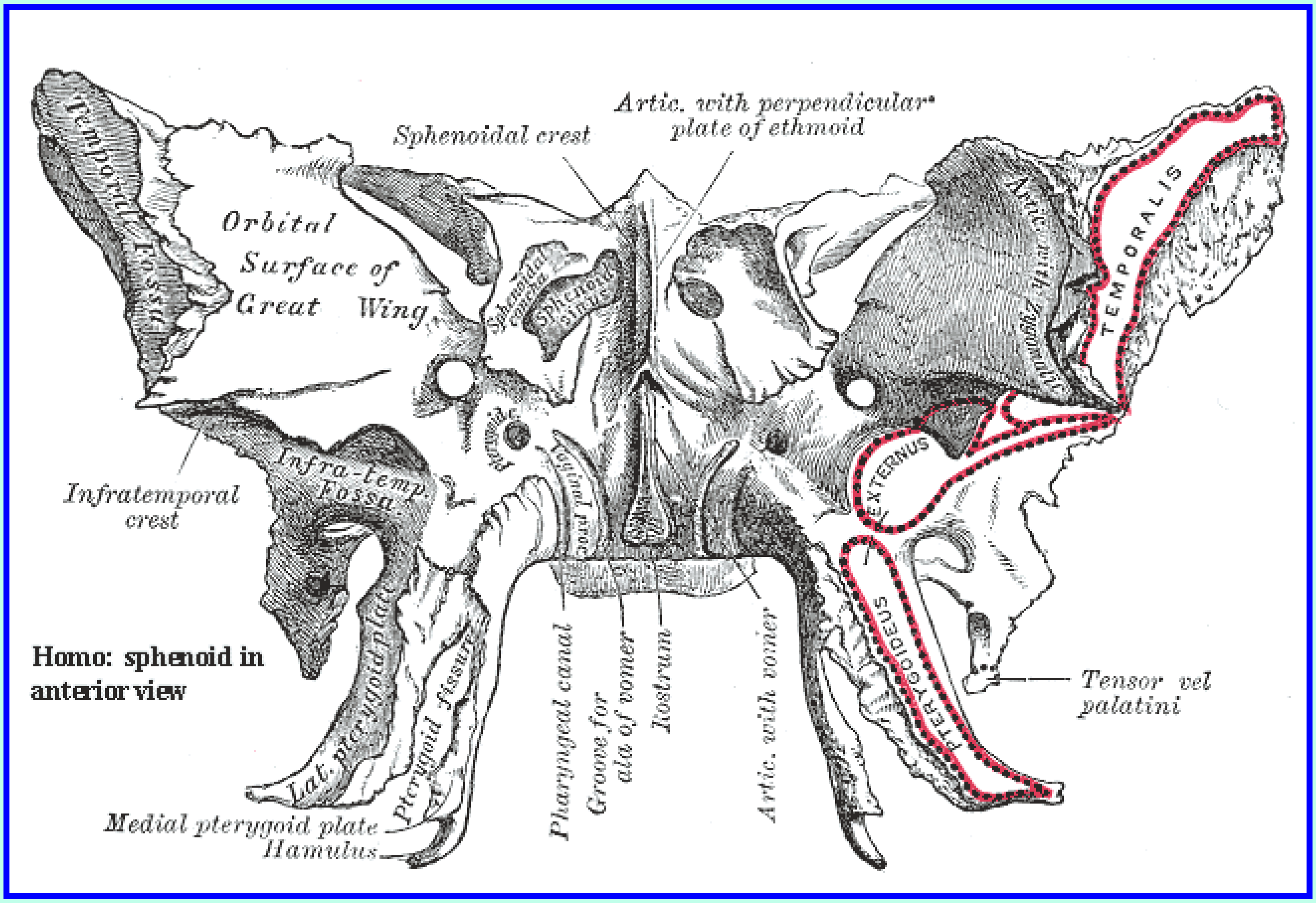
The sphenoid is the object looking like a giant ossified butterfly in the images on this page. Like the ethmoid it is both a region and a bone.

Considered as a region, the sphenoid is the second of the four main sectors of the braincase. Structurally, it underlies and supports the bulk of the brain. In addition, it tends to get involved in lateral support of the brain as well, and includes the alisphenoids, orbitosphenoids and similar vague, accessory ossifications, the primary purpose of which is to keep things from sloshing around. Like the ethmoid and otic regions, it is strongly associated with a suite of important sensory structures. The sphenoid region is most obviously associated with the orbit and the neural hardware supporting the sense of vision. However, it also includes the *sella turcica*, which is not only the home of the adenohypophysis but also has strange and poorly understood relations to the eyes. See **The Basisphenoid**. Finally, and even more mysteriously, the sphenoid region supports the portion of the brain containing the median light-sensitive organs of the *pineal* and associated structures. Vision, like hearing and smell/taste, is not entirely a unitary sense, particularly when considered in evolutionary perspective.

Considered as a bone, the sphenoid is a basisphenoid with ambition. If the *sella turcica* is the "Turk's saddle," then the sphenoid bone is a sort of Ottoman Empire: heterogeneous, loosely assembled and built generally on the grounds of its imperial predecessor, the sphenethmoid. In some derived mammals, such as *Homo*, the sphenoid combines the basisphenoid, alisphenoid, orbitosphenoid, and presphenoid (an ethmoid ossification, or perhaps an anterior extension of the basisphenoid), as well as incorporating portions of the pterygoid. As a reminder, the pterygoid is a dermal bone; and the alisphenoid is retreaded epipterygoid which traces its ultimate origin to the palatoquadrate and the gill arch series. The sphenoid thus incorporates derivatives of all three embryonic skull tissues: the endochondral bone of the neurocranium, the dermal bones of the palate, and gill arches.

The sphenoid, at least in its most expansive form, is apparently found only in some mammals. In fact, I have not seen any mention of anything like the human sphenoid outside the primates. Then again, what I have or have not seen is a poor proxy for the actual state of the universe. It may be that the components of the sphenoid vary considerably from one mammalian taxon to another. In any event, we lack sufficient reliable information for a phylogenetic survey and must be content with tunnel visions of our medical brethren.

The description below follows closely the classical (1918) description in Grey's Anatomy, which Bartleby's has thoughtfully placed on-line, along with a number of other priceless references. "Follows closely" is, of course, a euphemism for blatant plagiarism. However, the discussion here is reorganized and edited for relevance to areas of potential interest in our usual inquiries. A good deal of the nomenclature has also been changed. Thus suitably translated, the treatment in Gray's remains remarkable useful. The illustrations from Grey's, also reproduced here, tend to have a somewhat cubist quality. That is, strict perspective is occasionally sacrificed for the sake of showing as many features as possible in a single illustration. On the internet today, just as in Grey's time, too many images make a reference unreasonably bulky and expensive to produce. Thus, these stylistically simple, but highly detailed line drawings are once again perfect for a low-budget guide, so long as the reader is cautious.



**Homo: sphenoid in anterior view**

## Basisphenoid + Presphenoid

The dorsal surface of the sphenoid body consists of the basisphenoid and presphenoid ossifications. The body is marked anteriorly by a prominent spine, the ethmoidal spine, which articulates with the cribriform plate of the ethmoid. The ethmoidal crest is continuous with a sphenoidal crest on the anterior face which articulates with the perpendicular plate of the ethmoid and forms part of the nasal septum.

Behind the ethmoid spine is a smooth surface slightly raised in the midline, and grooved on either side for the olfactory lobes of the brain. This surface is bounded behind by a ridge, which forms the anterior border of a narrow, transverse groove, the chiasmatic groove (*optic groove*), posterodorsal to which lies the optic chiasma. The groove ends on either side in the optic foramen, which allow the optic nerve and ophthalmic artery into the orbital cavity. Behind the chiasmatic groove is an elevation, the tuberculum sellae; and still more posteriorly, a deep depression, the sella turcica, the deepest part of which holds the adenohypophysis. The anterior boundary of the sella turcica is completed by two small eminences, one on either side, called the middle clinoid processes, while the posterior boundary is formed by a square-shaped plate of bone, the *dorsum sellae*, ending at its dorsolateral corners in two tubercles, the posterior clinoid processes. The posterior clinoid processes deepen the sella turcica, and support the *pila antotica*, in organisms in which the *pila* is present. See also discussion at the pleurosphenoid. On either side of the dorsum sellae is a notch for the passage of the abducens nerve (cranial nerve VI). The abducens enervates the lateral rectus muscle of the eye which rotates the eyeball laterally. Below the abducens notch is a sharp process, the petrosal process, which articulates with the anterior apex of the petrosal (or the petrous portion of the temporal bone), and forms the medial boundary of the (anterior?) lacerate foramen. Behind the dorsum sellae is a shallow depression, the clivus, which slopes obliquely backward, and is continuous with the groove on the basioccipital (basilar portion of the occipital bone). The lateral surfaces of the basisphenoid section are fused with the great wings and the medial pterygoid plates. Above the attachment of each great wing is a broad groove, curved something like the italic letter *f*. This groove holds the internal carotid artery, and is thus unsurprisingly named the carotid groove. The rectangular posterior surface is joined to the basioccipital by a plate of cartilage. In humans, the connection ossifies during early adulthood.

The anterior surface of the sphenoid body is dominated by the sphenoidal crest, discussed above. On either side of the crest are air sinuses, the sphenoid sinuses, which are partially roofed over by the sphenoid conchae. The sphenoid sinuses are also subdivided by irregular ridges of bone. The sinus systems are quite variable even among the mammals, and are briefly taken up in the discussion of the turbinals.

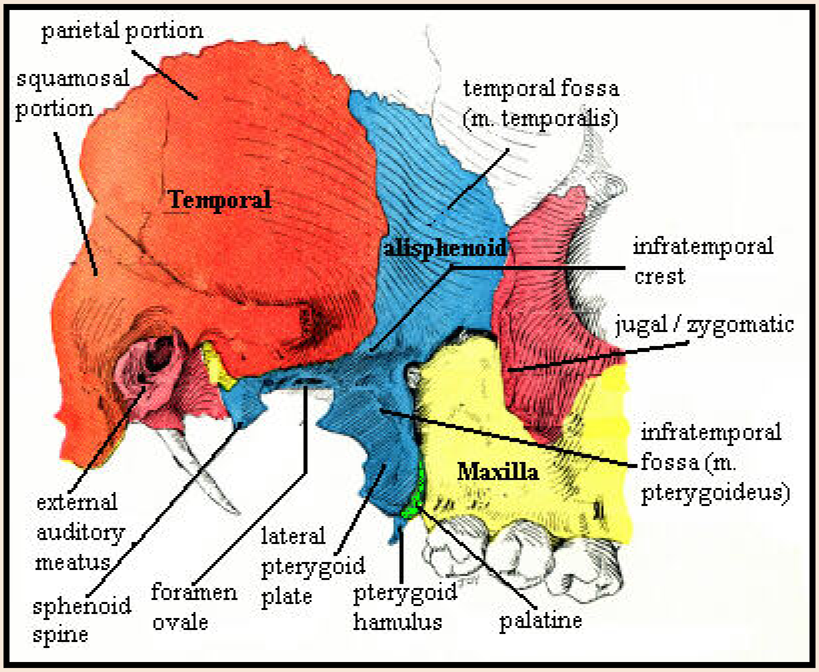
The ventral surface of the sphenoid body bears a triangular spine along the midline, the sphenoidal rostrum, which is continuous with the sphenoidal crest on the anterior surface, and articulates with a deep fissure between the wings of the vomer. On either side of the rostrum is a projecting lamina, the vaginal process. This process is directed medially from the base of the medial pterygoid plate, with which it is described below.

# The Alisphenoids

The great wings are the alisphenoid contribution to the sphenoid. "Alisphenoid" = *ala* (L. for "wing") + sphenoid. So now you know. The alisphenoids grow out laterally from the basisphenoid + presphenoid, and are curved dorsolaterally and posteriorly. The posterior part of each alisphenoid forms a triangular process which fits into the angle between the squamosal and the petrosal. The posterior end of the alisphenoid also bears a ventral process, the spina angularis (*sphenoidal spine*). Presumably, this is an evolutionary remnant of the quadrate ramus of the epipterygoid (= alisphenoid).

The dorsal surface of each alisphenoid is deeply concave, and is ornamented with depressions for the convolutions of the temporal lobe of the brain. Anteromedially, the alisphenoid is pierced by the foramen rotundum, through which the *maxillary nerve*, (= CN V2, or the maxillary branch of the trigeminal nerve) exits the braincase. Posterolateral to the foramen rotundum is the foramen ovale, for the exit of (most significantly) the mandibular nerve (=CN V3, or the mandibular branch of the trigeminal nerve).

The lateral surface of the alisphenoid is difficult to describe in isolation, and is most readily conceived in osteological context, as shown in the third figure (the colored image on the right). This surface is divided into dorsal and ventral halves by a transverse ridge, the infratemporal crest. The dorsal or temporal portion, forms a part of the temporal fossa. The *m. temporalis* originates broadly on this surface and inserts on the coronoid process of dentary. Its primary function is to close the jaw. The concave ventral or infratemporal surface forms part of the infratemporal fossa. Together with the infratemporal crest, this surface is the origin of the upper head (at least) of the *m. pterygoideus externus*, a/k/a *pterygoideus lateralis*. The lateral pterygoideus inserts on the back of the jaw and on the capsule of the temporomandibular joint itself. It acts to open the jaw, as well protracting (protruding) the lower jaw.



Posteriorly, the alisphenoid is pierced by the foramen ovale. The posterior end bears the sphenoid spine (*spina angularis*), which is frequently grooved on its medial surface for the chorda tympani nerve. The primary purpose of the sphenoid spine appears to be the attachment of the dorsal end of the sphenomandibular ligament. This ligament is derived from the middle section of Meckel's cartilage. The more posterior sections are adapted as the maleus and incus of the middle ear. Since the sphenomandibular ligament represents the more distal portion of Meckel's cartilage, we find, as we might expect, that the ventral attachment of the ligament is located on the lower jaw, on a ridge of bone adjacent to the mandibular foramen.

The orbital surface of the alisphenoid is smooth, generally quadrilateral in shape, and is directed anteromedially. It forms part of the lateral orbital wall. Its articulates dorsally with the frontal. Its lateral margin and articulates with the jugal (zygomatic).

# The Orbitosphenoids

The lesser wings of the sphenoid are formed by the orbitosphenoids. The orbitosphenoids are thin triangular plates, which arise from the anterodorsal part of the body, *i.e.* the presphenoid. They project laterally, ending in sharp points. The dorsal surface of the orbitosphenoid is flat, and supports part of the frontal lobe of the brain. The dorsal surface forms the inner part of the roof of the orbit. The anterior border of the orbitosphenoid articulates with the frontal. The posterior border, smooth and rounded, inserts into the lateral fissure of the brain. The medial end of this border forms the anterior clinoid process. The orbitosphenoid is connected to the presphenoid by two roots, the upper thin and flat, the lower thick and triangular; between the two roots is the optic foramen, for the transmission of the optic nerve and ophthalmic artery.

# The Pterygoid Processes

The pterygoid processes, one on either side, descend perpendicularly from the regions where the sphenoid body and alisphenoids unite. Each process consists of a medial and a lateral plate, the upper parts of which are fused anteriorly. A vertical *sulcus*, the pterygopalatine groove, descends on the front of the line of fusion. The plates are separated below by an angular cleft, the pterygoid fissure, the margins of which are rough and articulate with the pyramidal process of the palatine. The two plates diverge behind and enclose between them a V-shaped fossa, the pterygoid fossa, which contains the medial pterygoid muscle (= *m. pterygoideus internus*). Above this fossa is a small, oval, shallow depression, the scaphoid fossa. The anterior surface of the pterygoid process is broad and triangular near its root, where it forms the posterior wall of the pterygopalatine fossa and presents the anterior orifice of the pterygoid canal.

The lateral pterygoid plate is broad, thin, and everted; its lateral surface forms part of the medial wall of the infratemporal fossa, from which the lateral pterygoideus muscle originates, as mentioned above. The medial pterygoid plate is narrower and longer than the lateral. It curves laterally at its distal end into a hook-like process, the pterygoid hamulus, around which the tendon of the Tensor veli palatini glides. The lateral surface of this plate forms part of the pterygoid fossa. The medial surface constitutes the lateral boundary of the choana. Superiorly the medial plate is prolonged on to the under surface of the body as a thin lamina, named the vaginal process, which articulates in front with the sphenoidal process of the palatine and behind this with the ala of the vomer. On the under surface of the vaginal process is a furrow, which is converted into a canal by the sphenoidal process of the palatine bone, for the transmission of the pharyngeal branch of the internal maxillary artery and the pharyngeal nerve from the sphenopalatine ganglion. The anterior margin of the plate articulates with the posterior border of the vertical part of the palatine bone. ATW021117.

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# Braincase References

| **Bones** | **Braincase** | **References** |
|---|---|---|
| **Bones Overview**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Ethmoid Region<br>**Occiput**<br>Otic Region<br>**Sphenoid**<br>**References** | |

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# The Facial Series

| Bones | Dermal Bones | Facial Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | Overview<br>Internasal<br>Premaxilla<br>Septomaxilla |

The facial series of the dermatocranium consists of the maxillae, premaxillae, and nasals. Where present, the series also includes the septomaxillae, small bones normally located under the premaxilla which define the internal shape of the external nares. For lack of any better place to put them, the facial series also includes a variety of small rostral bones which occur in various taxa under various different names. From a functional point of view, the facial series defines the rostral region of the skull, some or all of the distal and internal outline of the nares, and the primary tooth-bearing units of the upper jaw. However, this generalization is subject to many exceptions, and should not be taken too literally.

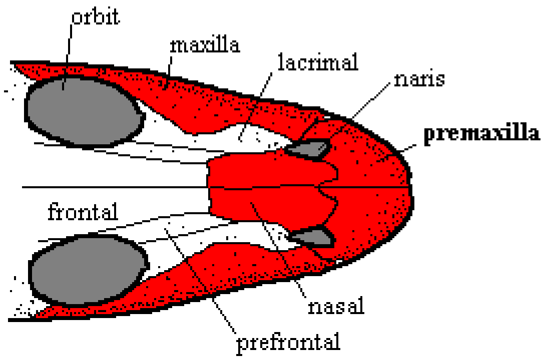

**Fig. 1. Anterior portion of generalized primitive amniote skull in dorsal view**

In fact, the facial series does not appear to behave as a strong unit of phylogenetic anatomy. We cannot make generalizations about the evolution of the facial series in the same way as we might speak of evolutionary trends for organ systems or individual bones. The series is simply a convenient way to break up the long list of dermal bones as an aid to memory.

This, in itself may be an important datum. These bones clearly articulate with each other and must be coordinated, at least developmentally, in order to do so. Yet the way in which they fit together does not appear to be under stringent control, or at least under no different control than may be explained by the selective forces acting on the individual bones.

Before running too far with this speculation, it is important to point out some exceptions. The teleost jaw, described elsewhere represents a case in which the development of the premaxilla as the principle tooth-bearing element is part of the more complex structural evolution of the protrusible jaw. Similarly, the concerted retooling of the rostrum towards consolidation in various different fossorial forms, or towards radical kinesis in advanced snakes, appear to represent selection acting on the entire facial series as a unit. However, these exceptions can be explained as cases in which the "normal" (whatever this means) degree of movement between the functional units of the skull has been eliminated in order to deal with the extraordinary stresses imposed by underground, fossorial life. In the case of snakes, and probably mammaliforms, the lineage has rediscovered terrestrial life after a period of mainly fossorial evolution. In these cases, the changes wrought by fossorial specialization have had irreversible effects, with the result that the skull responds in a more unified fashion to selective pressures. Thus, the specialized teleost jaw is the only true exception.

This pattern is consistent with a genetic tale which goes something like this. Once upon a time there were fishes that developed dermal bones as plate armor. Initially, the main selective pressure was to find a pattern of ossification centers which made it convenient, from a developmental perspective, to cover whatever needed to be covered -- normally the braincase, jaws, and sensitive areas around the sensory organs of the head -- with minimum fuss and bother during embryogenesis. In these far-off days before *Cheirolepis*, this meant that the number and location of dermal ossifications would change almost as frequently as the shape of the head or the type of food preferred. The centers simply grew until they encountered other osteocytes and then quit.

However, anything worth doing consistently is worth doing genetically. By the Late Silurian, a number of different kinds of fish happened on the practice of using dermal bone for secondary functions which required more consistency: bearing teeth being probably the first and best example. This required a greater degree of gene-level control. Dermal bones could no longer develop simply in response to the shape of the underlying epidermis, but began to respond directly to specific genetic signals from neural crest and mesenchymal messengers. Now the best way to ensure consistent and coordinated obedience to such signals is to give the signals early to a single population of stem cells and let them execute the program, with only occasional developmental nudging. Thus, the centers of dermal ossification came to be identified with discrete structural roles. Once even one dermal bone becomes "dependable" in this developmental sense, the bones around it become "dependable" to some degree, since they will stop growing at the defined boundaries of the fixed bone. This means that the surrounding bones are more fixed and consistent, thus more consistently able to take up secondary roles which, in turn, will tend to bring them under genetic control.

If correct, this explains why various different gnathostome lineages developed distinct, but rather different, patterns of dermal bone or abandoned dermal bone altogether by the mid-Devonian. The tooth-bearing function acted as a catalyst for genetic control of the entire dermatocranium. Granted, the sample size is not large: a half dozen different placoderm lineages, the similar, but not identical, actinopterygian and sarcopterygian patterns. But only one non-gnathostome group shows this trait, the possible exception being an advanced group of pteraspidiforms which seem to have developed a fairly consistent, if rather simple, pattern of dermal bones. Even here, the exception may prove the rule. Basal heterostracans have an upper and lower head shield, plus a rather variable set of small plates between them. The excurrent duct for the gills forms generally at the posterior limit of these small plates. While nowhere near as precise a function as tooth-bearing, the formation of this duct might have acted as a nucleus for spreading genetic control of the dermatocranium in a similar, if less stringent way. In fact, the multi-part dermal skeleton remains more or less restricted to a sort of medial belt defined by the gill slit and associated lateral "fins", the upper margin of the mouth, and the rostrum.

Thus the concept of the bone as a unit of evolutionary change has a possible basis in real biology in a way which is less applicable to bigger or smaller anatomical units. As we have seen with the premaxilla, further stabilization may occur when the same bone is subject to multiple genetic controls. However, selection works on larger units only in extreme circumstances which force simultaneous changes in multiple areas of the skull.

# Specific Bones:

1. Internasal
2. Premaxilla

# Minor Bones:

# 1. Internasals

A variety of different bones are referred to as "internasals." It is almost certain that these elements are not homologous. As discussed elsewhere, the premaxilla originally functioned largely as a second tooth-bearing bone in the upper jaw. In very primitive gnathostomes, the space between the margin of the jaw and the nares was filled with a number of small rostral bones. In this group, the internasals are generally paired small bones of this type just distal to the nasals. Unfortunately, the term is also used to describe a teleost bone of dermal origin which forms part of the braincase, with a position which seems to be analogous to the mesethmoid in advanced mammals.

In tetrapods, a number of groups occasionally produce small, *unpaired* bones between the paired nasals which may also articulate with the premaxilla. See, for example, Phylogeny of stegocephalians. *Ichthyostega* has a central bone of this type. Possibly, these are homologous with the teleost bone of the same name. Such bones are occasionally observed even in humans. Virtual Hospital: Nasal Bone. Thus, the phylogenetically random appearance of internasals in tetrapods may simply be the sampling of random individual variation, or random genetic drift of a minor mutation which has no immediate selective consequences. In fact, the most interesting point may be that there do *not* appear to be any significant consequences. This is entirely consistent with the general observation that there is at least a bit of slack in the fit of bones before selection becomes significant. ATW 010115

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# The Facial Series: Premaxilla

| Bones | Dermal Bones | Facial Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | Overview<br>Internasal<br>Premaxilla<br>Septomaxilla |

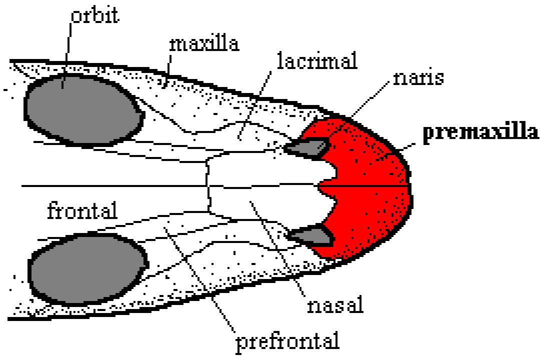

**Fig. 1. Anterior portion of generalized primitive amniote skull in dorsal view**

**Anatomy**: The premaxillae are paired dermal bones of the facial series, a series which also includes the maxillae and nasals. The morphology of the premaxilla is highly variable. It frequently takes the form of a '**C**' in lateral view, with the top covering the tip of the rostrum, and the bottom forming the most anterior section of the upper jaw. It may be a major dermal component which plays a significant role in the margin of the nares (Fig. 1). Occasionally, as in hadrosaurs, the premaxilla is extensively elaborated in almost fanciful ways. See, for example, Hadrosauridae. In addition, the premaxillae may become invested externally with keratinous structures forming a beak or bill (rhamphotheca), as in the anomodont synapsids, birds, trilophosaurs and turtles (Fig. 2). In these cases, the dorsal surface of the bone will often be roughened and show pits and channels. Where a rhamphotheca is absent, the premaxilla is usually a tooth-bearing bone. Most commonly, the premaxillae articulate with the maxillae and nasals, although borders with the frontals, prefrontals and other dermal bones are also possible.

Ventrally, the premaxilla's tooth-bearing surface normally articulates with the vomers, dermal bones of the anterior palate, as well as the maxilla. It may also contact the palatines or their derivatives (dermal bones of the palate which are also closely associated with the maxilla) and even the parasphenoid. The premaxilla generally participates in the margin of the internal nares (choana). As with the dorsal surface, the ventral premaxilla may also become a major element, as it is in birds. See, e.g., paleognathous bird palate. More typically, its ventral exposure is fairly limited (Fig. 3.). In a number of different groups, there is a gap in the tooth row, referred to as a diastema, corresponding to the articulation between the maxilla and premaxilla. This may be associated with a flexible premaxilla which is not completely sutured to the maxilla. See, for example, *Ornithosuchus*. Such an arrangement allows at least some independent movement of the tip of the rostrum.

**Links:** Vertebrate Paleontology Photo Gallery (equid);

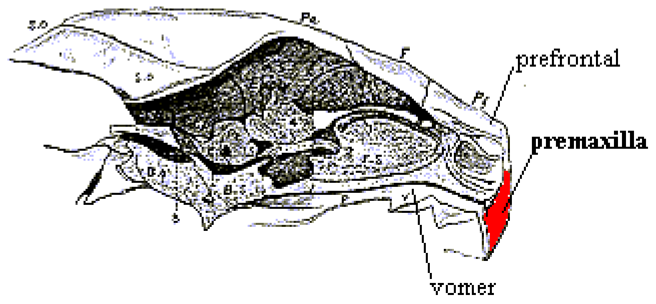

**Fig. 2. Sagittal section of turtle head. Modified from Huxley (1859).**

Phylogeny and Classification of Amniotes (early amniotes); Synapsid classification and autapomorphies (early synapsids); Pre-maxilla (theropod); http://biol1.bio.nagoya-u.ac.jp:8000/Taxonomy.html (teleost); Skulls (crocodile).

**Functions:** As largely discussed above, the premaxillae seem to be associated with the following functions:

1) *Bearing the anterior-most teeth*: for many carnivores, one might suppose that the front teeth would be of particular importance in capturing prey. While this may be true, the premaxillary teeth are not often specialized except in the therapsid line.

2) *Supporting a beak.* A wide variety of tetrapods have developed keratinous beaks for piercing or cutting food. Most are herbivores, but carnivorous birds and probably various closely related theropod dinosaurs also developed beaks.

3) *Defining and supporting the chemosensory apparatus*: The premaxilla normally defines a large portion of the naris and covers much of the nasal cavity.

3) *Protection of the rostrum*. For the simple reason that the premaxilla is usually the animal's most anterior bone, it is frequently the part that gets into trouble first. Quite likely this provided a powerful selective force favoring the formation of a fairly small, thick bone in this position, separate from the main body of the maxilla. In this way, an unexpected blow from the front is less likely to destroy the entire upper jaw or the structure of the face.

4) *Specialized structures.* In fish, the premaxilla is an important element in a number of different arrangements which allow protrusion of the mouth to suck in and envelop prey (see, *infra*). As noted above, the premaxilla may also become involved in the structure of facial ornament such as crests and the elaboration of the nasal passage in hadrosaurs.

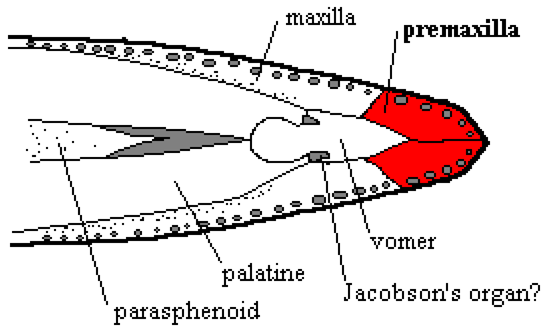

**Fig. 3. Anterior portion of the skull of Plesiosaurus in palatal view; after Storrs (1997)**

**Phylogeny:** Every elongate organism has to have a front end. So, in a sense, analogs of the premaxilla go as far back as chordates with bone. However, the premaxilla, even considered as a functional unit of the skull and without regard for phylogeny, is a much more complicated object. As fully developed in advanced tetrapods, it has a three-fold structure. (1) Ventrally it is involved with prey capture and dentition. (2) Dorsally, it protects the rostrum, a portion of the body far more likely than most to suffer damage. (3) Internally, it is involved with respiration and chemosensation. In a very broad sense, the premaxilla seems to have acquired these functions in the order listed.

In *Cheirolepis*, one of the most basal animals with more or less "standard" bones, the premaxillae appear to have been primarily tooth-bearing bones. Externally, they also formed the broad base of a fairly tall rostrum dominated by the rostral bones and a series of small dermal bones with no clear correspondence to those of living species. In more derived actinopterygians, the orbit is much further back on the skull so that the rostrum is no longer vertical, but slopes gradually upward from the terminal mouth. As a result, the external exposures of the premaxillae are naturally stretched out and

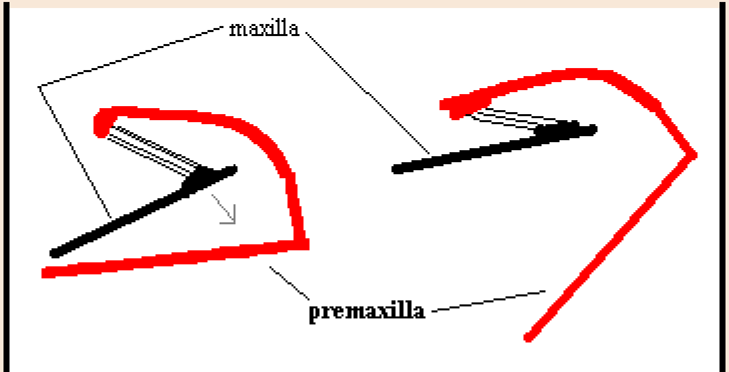

Fig. 4. Schematic illustration of teleost jaw mechanics

angled back from the mouth. During the same evolutionary sequence, the premaxillae generally became the principle tooth-bearing element of the upper jaw, while the maxilla developed into a lever, structured so as to protrude the premaxilla and drop the floor of the mouth for suction feeding. As this arrangement requires a mobile premaxilla, things get quite complicated. One might anticipate that the premaxillae would then lose their dorsal, external exposures. Instead, the "ascending processes" are retained, although modified, and become part of a lever used to swing the ventral, internal, portion of the premaxilla down and out. The mechanics of this type of arrangement are illustrated (rather inadequately, to be sure) in Figure 4.

The sarcopterygian premaxilla appears to be homologous to the actinopterygian bone, although the case is not as clear as it might be. Some dipnomorphs, for example, develop a fused parietoethmoidal shield, which unites the parietals with the rostral bones in a single plate. Others break up the dermal skull in ways which bear no relation to the standard pattern. However, the most common arrangement of the premaxillae is quite similar to *Cheirolepis*. The significant difference is that the sarcopterygian orbit is so far forward that the nares are brought into close proximity with the premaxilla. In addition, the sarcopterygian brain is sharply divided anteroposteriorly, with the anterior ethmoid practically pushed against the internal surface of the premaxilla. In tetrapods, the premaxillae frequently participate in the margin of the internal nares, the choana. However, this appears to be a late development. The choanae originally opened at the intersection of the vomer, palatine and maxilla -- similar, and perhaps homologous to the vomeronasal or Jacobson's organ of the later snakes and plesiosaurs.

From that point forward, the premaxilla has been extraordinarily stable. In some groups with highly consolidated skulls, such as turtles, the premaxilla is small or disappears. In others, as noted above, it becomes prominent. Generally speaking, it seems to have taken over a larger role as a rostral bone, and lost ground in the palate. This trend is especially clear in archosaurs, but is reversed in birds. On the whole, however, there is remarkably little change in form or function, except perhaps in highly derived snakes. Even in mammals, the relative position and articulations of the premaxillae are quite similar to those in sarcopterygians, allowing for the sloppy tendency of mammals to fuse everything together.

This series of essays is far too new at this date (November, 2000) to be drawing conclusions, but the extraordinary stability of this bone calls for some explanation. Perhaps (and solely as a tentative hypothesis going forward) diversity of function generates phylogenetic stability. The premaxilla is not only integrated with a dermal skull "program." It is deeply involved in the prey capture and mastication programs, as well as the chemosensation system. Thus different developmental genetic pathways are so deeply entangled at this junction that it becomes very difficult for mere selection or genetic drift to cause really significant change in the morphology of this bone. ATW001103.

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# The Facial Series: Septomaxilla-1

| Bones | Dermal Bones | Facial Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | **Overview**<br>Internasal<br>Premaxilla<br>Septomaxilla |

## The Standard Condition

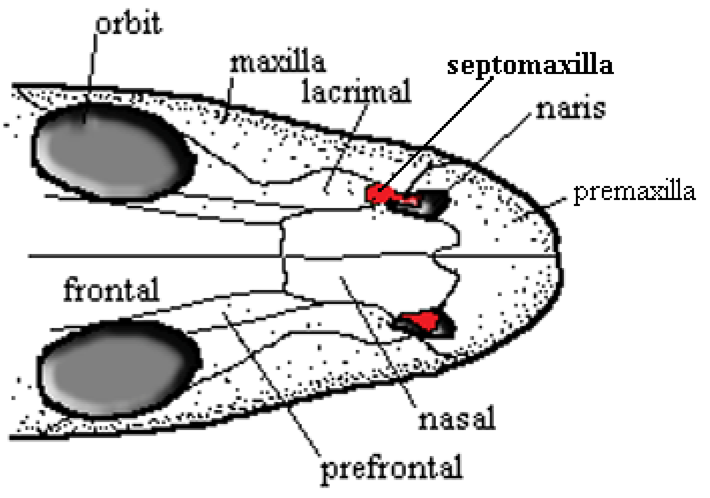
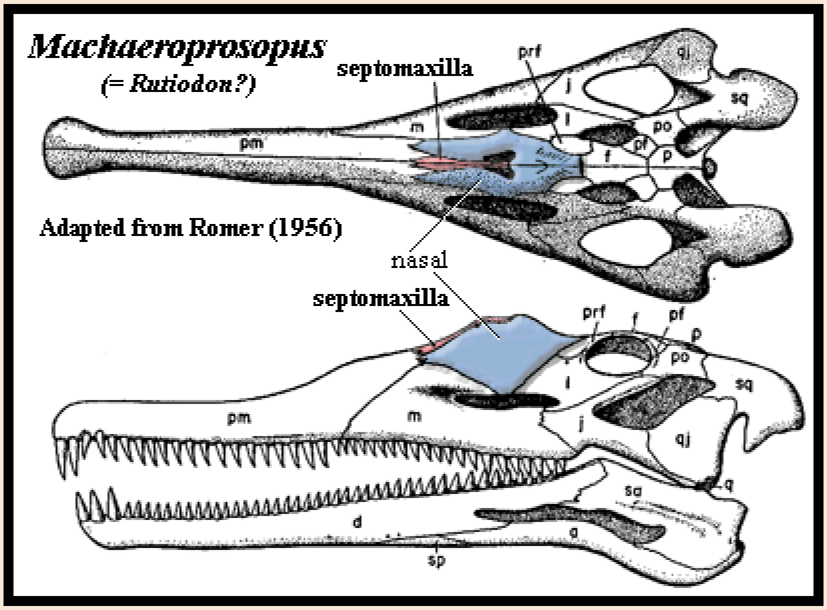


**Fig. 1. Anterior portion of generalized primitive amniote skull in dorsal view**

The septomaxilla is a small, usually delicate bone which is closely associated with the nares. In most cases some or all of the bone lies below the level of the dermal surface bones and inside the narial opening. On the right is the familiar dorsal shot of the snout of *Bob*, the Basal Amniote. In order to illustrate the obscure workings of the septomaxilla, we have been forced to magnify Bob a bit, which must surely gratify his basal amniotic ego. However, we have offset this minor flattery by making him asymmetrical. In fact, we have attempted -- albeit with limited success -- to illustrate *three* basic types of septomaxilla on one individual. With some exceptions, these three types are fairly distinct, and we will refer to them by letter designation.

**Type A**: (left side of Bob) the septomaxilla is often sutured to the lacrimal and appears to be an extension of that bone. Alternatively, it has a long external, posterior process towards the orbit. In either case, it is probably associated with the nasolacrimal duct. In this morph, it may or may not have additional structure inside the naris.

**Type B**: the septomaxilla is entirely inside the naris. It lies on the lateral or ventral inner surface, in contact with the underlying vomer. In this position it often bears a distinct dorsally or medially - directed process which, from the outside, appears to divide the naris into anterior and posterior compartments.

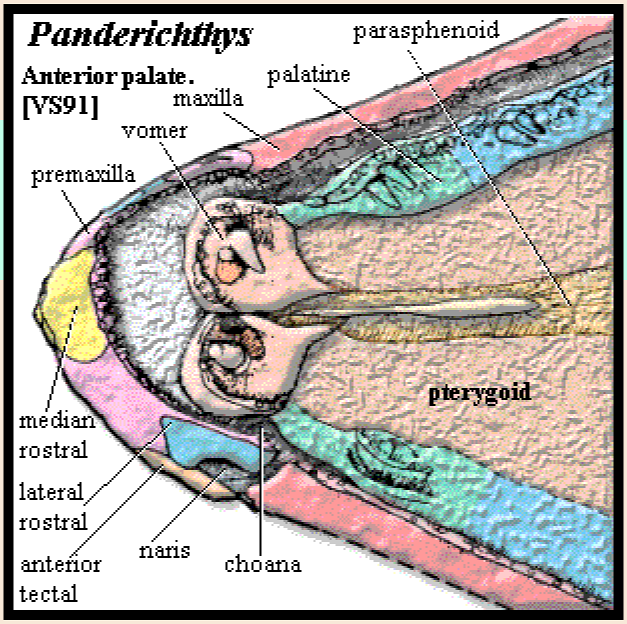


**Type C**: (right side of Bob) the septomaxilla lies almost entirely external to the naris. It is sutured to the nasal and extends ventrally or laterally to partially obscure the naris.

Perhaps the differences between these types may be explained by the different inductive influences these septomaxillae experience during development. The Type A bone is seems to function as an extension of the lacrimal and/or the nasolacrimal duct. Type B works with the vomer to form the floor of the naris and the shunt out of the nasal passage to the *vomeronasal organ*, or possibly the *choana*. Type C is a conventional dermal roofing bone which extends the nasal out over the naris. Thus, Types A, B, and C could be thought of as, respectively, nasolacrimal, vomeral and nasal septomaxillae. Our type designations have some phylogenetic utility, but they are not infallible. In some cases, as we will see, the type flips back and forth in a way which would be unbecoming of a reliable synapomorphy.

There are a number of bones which, by convention, are called "septomaxillae" but may well be neomorphs. For example, phytosaurs have a pair of small median bones, sutured on the midline. These are actually located anterior to the nares, which are dorsal and closely spaced. They are referred to as septomaxillae. In fact, they might actually *be* septomaxillae of a modified Type C, since they are flanked by the nasals. However, the phytosaur nares are unique, and it is difficult to be certain.

Finally, since septomaxillae are usually small, fragile bones, they are simply not recovered in many cases. In many forms, they may also fail to ossify. As a result, the phylogenetic distribution of the bone is uncertain.

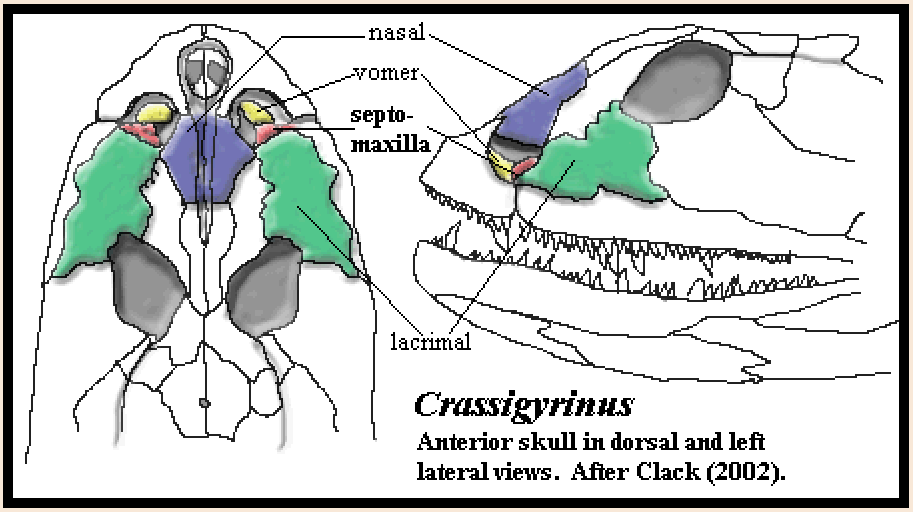


# Functional Considerations

The three different structural morphs of the septomaxilla reflect its differing roles in various branches of the tetrapod tree. The Type A septomaxilla primarily involved in maintaining the nasolacrimal duct, either alone or in combination with the lacrimal. The Type B bone is similarly employed together with the vomer in reaching the vomeronasal organ and/or the choana. Both the B and C types -- perhaps all three types -- may also anchor muscles which close off or flare the nostrils. Clack (2002).

# Origin of the Septomaxilla

In the high and far-off days of the Middle Devonian the immediate ancestors of the Rhipidistia experienced some unknown selective force which caused the conventional pattern of rostral bones to fragment into a kaleidoscope of random-looking shards of bone. In the Dipnomorpha, the process eventually disassembled virtually all of the conventional dermal bones of the skull. Among our own ancestors, the Tetrapodomorpha, the process stopped early on, and eventually reversed course. In the transition back to a tidier skull, the tetrapodomorphs developed regular, if unconventional, sets of bones between the tip of the rostrum and the orbit -- series which were gradually simplified over the course of time and phylogeny.



*Crassigyrinus*
Anterior skull in dorsal and left lateral views. After Clack (2002).

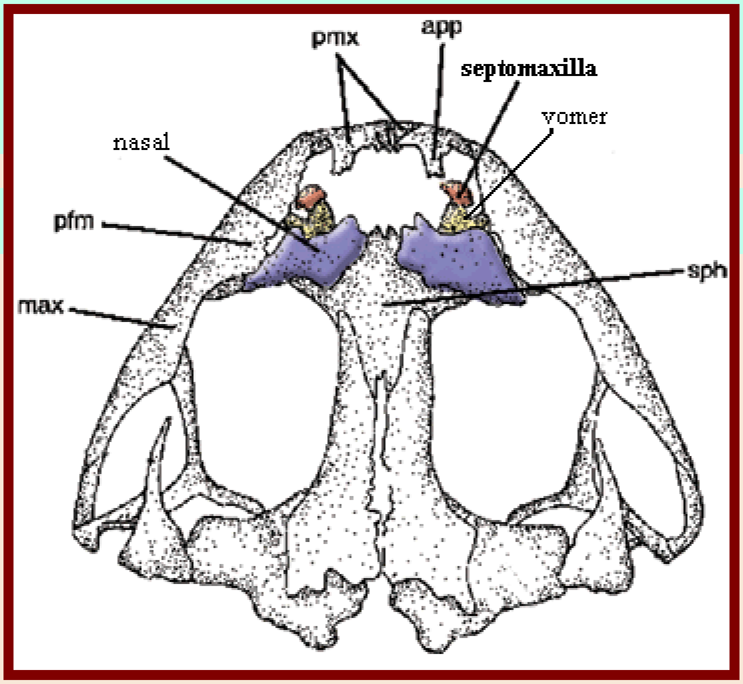
The two series which concern us are the rostral series, on and around the edge of the rostrum, and the tectal series, which occupied the more dorsal regions which would later be occupied by the nasal and lacrimal.

By the time we reach *Panderichthys*, on the borderlands of the Tetrapoda, four bones are in contact -- or near contact -- with the nares: the premaxilla, the maxilla, the lateral rostral, and the anterior tectal. One of the latter two bones is the immediate precursor of the septomaxilla. Clack (2002) (anterior tectal); Schultze & Arsenault (1985) (lateral rostral). The anterior tectal makes a more convincing precursor for a Type A or C septomaxilla, but the lateral rostral looks more like a Type B septomaxilla.

As shown in the image from Vorobyeva & Schultze (1991), the premaxilla had a tendency to slip in under the lateral rostral and meet the maxilla directly. All that would be required for a Type B septomaxilla is for the premaxilla to, instead, overlie the lateral rostral. Conversely, the anterior tectal is already behaving exactly like a Type C septomaxilla. So, since we lack any living osteolepiform fishes with which to experiment, it is impossible to say which is the more plausible candidate **[1]**.

# Phylogeny of the Septomaxilla

## Tetrapoda

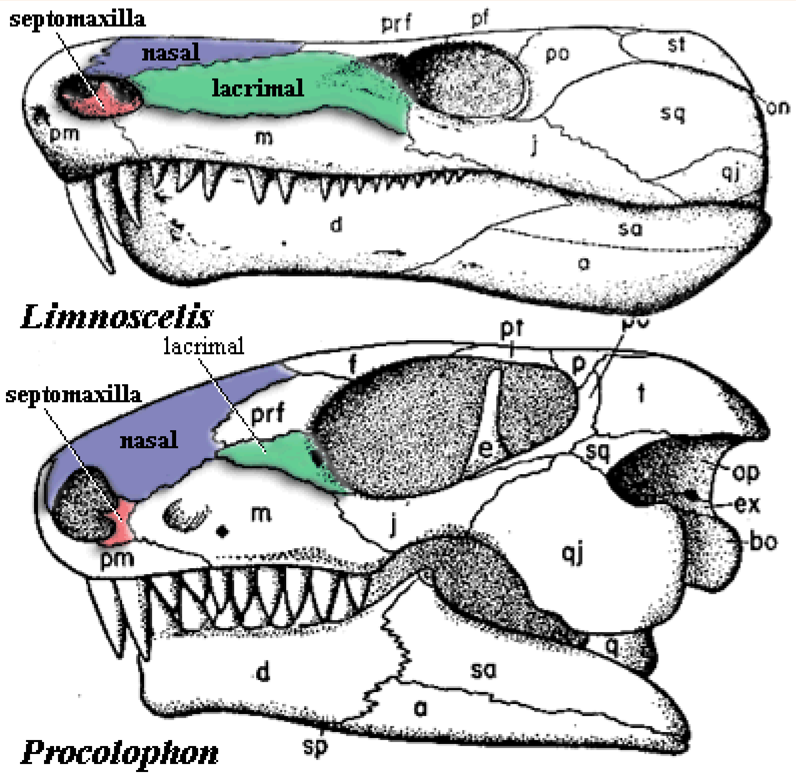


The first tetrapod septomaxillae which we meet are plainly of Type C, which favors a tectal origin. Both *Acanthostega* and *Ichthyostega* have this morphology. Clack (2002) **[2]**. However, *Crassigyrinus*, which may also be quite basal (or not!), has a very different septomaxilla, essentially of Type B. The septomaxilla lies entirely within the naris and below the surface of the dermal bones (*id.*), it bears a small dorsomedially directed process, and it is closely associated with the vomer. The two help form an unusual *external* (but probably subdermal) duct leading into the oral cavity. However, the septomaxilla is also in an essentially posterior position and flush with the lacrimal, as in Type A. Thus *Crassigyrinus* is somewhat anomalous, as it is in many other ways.

Among the baphetids, the septomaxilla is known in *Megalocephalus*. Here, it is essentially in the conventional Type B position. It sutures only (and narrowly) with the maxilla and premaxilla. Beaumont (1977). The bone appears depressed below the general surface of the skull in reconstruction. However, it is ornamented and thus presumably had some surface exposure. Thus, given the evidence from *Crassigyrinus* and *Megalocephalus*, one could question whether this is really the same bone as the septomaxilla of *Ichthyostega*. It might perhaps be a different ossification, derived from the lateral rostral.

## Temnospondyli

However, a brief review of the



Septomaxillae of two reptilomorphs from Romer (1956)

temnospondyls shows no pattern at all. Many temnospondyls either lack a septomaxilla, or the bone has never been recovered. It appears to be absent both in the basal *Dendrerpeton* and the derived Parotosuchids. Steyer (2002). When present, it is quite variable in size. *Id*. It may be entirely internal (Trematopidae) or have broad surface exposure (*Thoosuchus*). Clack (2002), Shishkin *et al*. (2000). One rather revealing exercise is to compare *Thoosuchus yakovlevi*, as described by Ryabinin in 1925, with precisely the same specimen, as described by Shishkin *et al*. in 2000. The position and dermal exposure of the septomaxilla is entirely different in the two. The septomaxilla is, once again, a small and delicate bone and it is often only weakly sutured to other components of the skull. Thus, it is not always possible to assume that a particular reconstruction is accurate at the level we are examining this bone.

## Lissamphibia

Living amphibians are. as usual, too derived to be of much help in working out early phylogeny. The frog septomaxilla appears to be of Type B, but the skull is so highly modified that this is not a particularly meaningful statement.

## Reptiliomorpha

According to Romer (1956), the plesiomorphic condition for the amniote stem lineage is Type A. This is a bit peculiar, since this is the one type we have not seen much of in the basal tetrapods (*Crassigyrinus* being perhaps the only exception). However it makes good sense in a mechanistic kind of way. The Type A septomaxilla is involved in the nasolacrimal duct. The nasolacrimal duct is important only for truly terrestrial animals, and there aren't any truly terrestrial tetrapods until we get into the immediate neighborhood of the amniotes. According to Romer, in this group -- seymouriamorphs, diadectomorphs, and so on -- the septomaxilla is usually found attached to the lacrimal in the posterior corner of the naris.

However reasonable this may be, it is not entirely clear that Romer is correct. So, for example, *Limnoscelis* bears a Type B septomaxilla of classic morphology. It is entirely internal, clearly ventral, has minimal (if any) contact with the lacrimal, and bears a robust dorsal process which would have done justice to Cyrano de Beregerac -- had he been, for example, a temnospondyl.

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# The Facial Series: Septomaxilla - 2

| Bones | Dermal Bones | Facial Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | Internasal<br>Premaxilla<br>Septomaxilla |

## Things that Go BMP in the Night: A Developmental Digression

It is at this point in phylospace that the septomaxilla begins to behave in a much more consistent and phylogenetically meaningful way. But, before describing this behavior, let us pause a moment to reflect on the implications of that last sentence. The ugly truth is that some morphological characters can be very useful phylogenetic indicators over certain ranges and completely misleading over others. Why should this be?

Development proceeds by a series of genetic cascade mechanisms. Suppose for example, that some high-level organizer is turned on, a *Hox* gene for example. In some cases, the *Hox* gene product is exported and binds directly to receptor sites in another cell which cause that cell to differentiate into some particular definitive type. More often, the *Hox* gene product promotes the production and release of secondary signals. Which secondary signals are promoted depends on the developmental state of the receptor cell. These secondary signals then go out into the world and, again, either have direct effects or induce the production of tertiary signals -- and so on. Undifferentiated target cells probably receive a variety of conflicting signals. However, at some point, a threshold is reached and the cell becomes irreversibly committed to some particular histological fate.

These ultimate signals, carried by "bone morphogenic proteins" ("BMPs") and the like, launch sometimes complex developmental programs. However, the signal itself is simple, and the programs are rather stereotyped. One "fast twitch"

muscle fiber is pretty much like another, everywhere in the body. While turning an undistinguished group of mesenchymal cells into muscle is a complex transformation, that transformation can be turned on or off with a set of very simple commands. What's more, these commands are part of the developmental vocabulary of mesenchyme cells generally, and are understood in more or less the same way throughout the embryo.

In the later Ottoman Empire, the first official act of the a new Sultan was normally to order the execution of any male siblings and, just to be on the safe side, selected first cousins as well. Embryos have a clear understanding of this salutary principle. There can only be one Sultan, one left jugal, one right coracoid, and so on. Literally the first thing a developing structure must do is to suppress the development of any other primordia which might show any ambition to become a jugal, coracoid, or, for that matter, a Sultan. Thus, there are a variety of negative signals as well, including signals instructing cells to die.

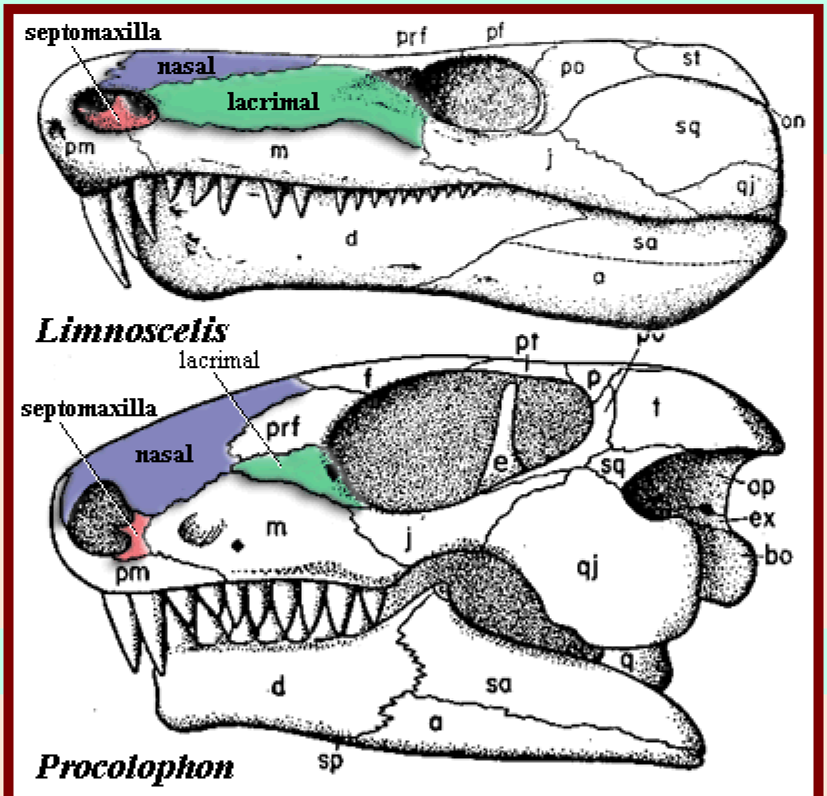
All embryonic cells, particularly in an area as complex as the vertebrate head, are subject to a variety of these signals. Which signal(s) ultimately activate differentiation depends on timing, geometry, and what the cell's neighbors are doing as well as the concentration of the inducers and repressors. However, clear differentiation is still the rule. A cell which is half muscle and half bone is useless for either function. Relatively sharp boundaries can be maintained because (a) the final developmental programs are mutually exclusive and (b) the Sultan Effect discussed above. Thus, we shouldn't be too surprised if a developing ossification center, such as the septomaxilla, has a discontinuous distribution of forms. Depending on small details of development, it may get sucked into the developmental pattern of low-level inducers generated by the cells shaping the nasolacrimal duct, the nasals, or the vomeronasal organ. However, its likely to be one form or the other -- not something in between.

For a small bone located at the intersection of several different developmental domains, the result is phylogenetic variability. The septomaxilla may be a good character for mapping temnospondyl families, for example, but its useless, and possibly misleading for broader scale studies. It can't tell us much about the relative position of temnospondyls and frogs, because it changes too fast and too often. The problem is a form of "long branch attraction" and exactly comparable to the problem of saturation in molecular studies. *See* discussion elsewhere.

But, what happens if the cells of the septomaxilla later become receptive to higher level inducers? Now, instead of responding to the simple messages, it responds first to high-level inducers like *pax* and *hox*. The state of the bone stops changing with every new family. We may observe a whole new set of smaller morphological changes as synapomorphies at the family level. Among the temnospondyls such slight changes would be ignored as phylogenetic noise -- at most apomorphies at the species level. These are now significant for higher order clades, while the bigger changes, such as the Types described above -- lose utility because they are essentially invariant.

Unfortunately, we can't expect that this sort of modal change will occur only at the borders of the phylospace of interest. So, together with all the other homology problems that plague cladistic analysis, we have to be concerned with whether we have this sort of problem as well. The typical parsimony analysis treats all changes as equal and all states with the same character score as homologous. How good are those assumptions in real life?

# Amniotes: Back to the Script



Septomaxillae of two reptilomorphs from Romer (1956)

With these vague and imponderable concerns behind us, we may return to the main line of our story refreshed and unburdened of all such feckless speculation. The only actual relevance of the foregoing osteological idyll is that the character of the septomaxilla does indeed change among the amniotes. No longer a volatile child of sudden, simple passions, it becomes a steady, but sophisticated, bone with a variety of intriguing specialized functions -- or disappears entirely.

## Anapsida

Notwithstanding our concerns about *Limnoscelis*, the anapsid septomaxilla does appear to begin as a Type A morph as exemplified by *Procolophon* on the previous page. The bone is located on the posterior margin of the naris and includes a posterior process with significant external exposure. However, this is one of the few cases in which the typology is not completely clear, since the *Procolophon* septomaxilla also has an *anterior* process extending into the naris. This process looks suspiciously like the dorsal process of a Type B septomaxilla which has been rotated 90 degrees counterclockwise. Furthermore, the lacrimal has retreated from the naris in *Procolophon*, and the septomaxilla comes nowhere near it. It is, once again, hard to know how seriously to take detailed reconstructions of small, fragile elements such as the septomaxilla. However, something quite similar seems to be going on in some millerettids, in *Bolosaurus*, whose lacrimal does reach the naris, as well as in *Acleistorhinus*, where it doesn't.

In short, there seems to be the beginnings of a synapomorphic anapsid condition of the septomaxilla. Unfortunately, the whole thing peters out pretty quickly. In lanthanosuchids and pareiasaurs, the septomaxilla is strongly reduced or absent; and no turtle is known to possess one. There is nothing mysterious about this. The anapsids start out with elongate jaws and rostra, but the entire muzzle becomes progressively shorter across their phylospace. Perhaps this is a consequence of the reorganization of the jaw muscles towards the peculiar condition in turtles, in which the force of the adductor contraction is redirected over a "pulley" on the braincase or the pterygoid. Thus the force on the lower jaw is almost vertical. This gives great strength and efficiency to the jaw, eliminating the advantage (particularly in herbivores) and utility of a long tooth row.

## Diapsida

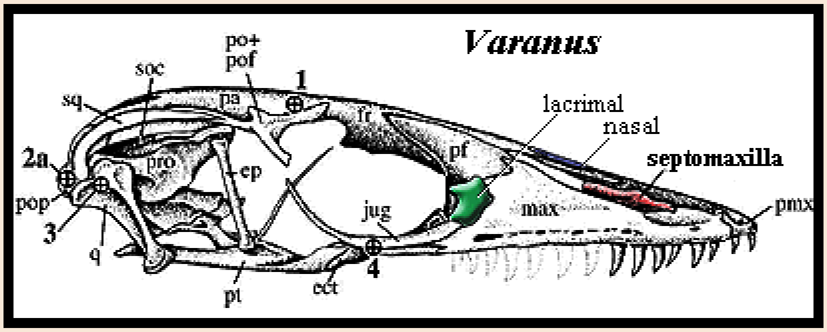
The septomaxilla does not seem to have been much of a success among early Diapsida. The best known basal diapsids were aquatic, and the region around the nares was frequently unossified. *Youngina*, for example, seems to have had a septomaxilla, but its shape and position are unclear in Carroll's (1981) discussion. As we have mentioned, there is some correlation between the development of the septomaxilla and terrestriality. It would seem that this applies in reverse, as well. We have seen no report of a septomaxilla in any ichthyosaur or sauropterygian.

## Lepidosauria

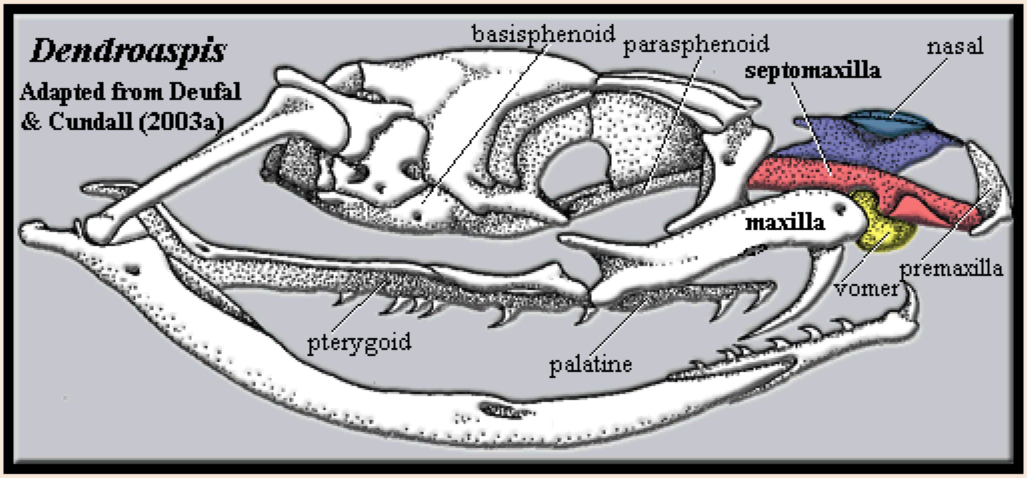
Wherever the diapsids were hiding the genetic potential for developing a septomaxilla, it must have remained, since both rhynchocephalians and squamates have them. The bone is entirely internal to the naris and apparently tends to become involved in forming the nasal septum. However, we do not feel safe in referring to it as Type B. Not only is it relatively large and plate-like, but it immediately begins to behave in a rather peculiar fashion among the squamates.


*Uma notata*
A phrynosomatid lizard from the Sonoran Desert (Arizona, USA).

For example, in the Phrynosomatidae, a family of desert lizards, the septomaxilla is posteriorly elongate and forms a "sink trap" for particulates entering the nares during subsurface burrowing. This is a **U**-shaped passage in which fine particles settle, allowing air to continue on freed of most contamination. When the lizard resurfaces, it expels the particulates with a violent sneeze. In *Xenosaurus*, the posterior septomaxilla penetrates deeply to participate in the choana. Wu & Huang (1986).



In snakes, this posterior process of the septomaxilla becomes ever more elaborate. As we have learned to expect, the septomaxilla is not known in the aquatic mosasaurs. However, even the very basal scolecophidian snakes have large septomaxillae. These are in extensive contact with the premaxilla anteriorly and the nasals medially. Ascending, medial processes of the premaxillae also lock this element between the nasals, so that the whole complex is tightly bound and interlocked, consistent with an important role in burrowing. The septomaxilla also bears a broad posterior process which clasps the vomers. Together with the vomers, the septomaxilla forms the floor of the nasal cavity and encloses the vomeronasal organ. Although a lacrimal is absent, the prefrontal bears the nasolacrimal duct which continues onto the septomaxilla. Romer (1956). The functional significance of this unique system is that it frees other palatal elements, particularly the pterygoids and maxillae, to move independently. In effect, the septomaxilla replaces both the lacrimal and the usual palatal bones as links between the mouth and the braincase. **[3]**



Adapted from Deufal & Cundall (2003a)

As the jaws become progressively loosened in more derived snakes, the septomaxilla-vomer complex undergoes a peculiar transformation from an incidental component of the nasal cavity to a major structural support. Thus, in aniloid snakes the septomaxilla - prevomer complex is still tightly bound to the palate by stiff ligaments. This stabilizes the upper jaw, but requires translational movement of each side of the entire complex (vomer + septomaxilla + palate) to "walk" the mouth over large prey items. Kley (2001). In colubroids, such as *Dendroaspis* pictured at right, the transformation is essentially complete. The main strut of the anterior skull is the septomaxilla, and its posterior process binds directly to the parasphenoid to brace the snout on the braincase. The pterygoid and palatine are unconstrained and able to move independently, while the maxilla rotates on the round vomer which serves as a sort of ball joint. Deufel & Cundall (2003); Deufel & Cundall (2003a).

# Archosauromorpha

A septomaxilla "is an element that has never been reliably identified in any crowngroup archosaur." Hill *et al.* (2003). In fact, we are not aware of a septomaxilla in any archosauromorph. However, septomaxillae continue to be identified -- unreliably, one presumes -- in all kinds of archosaurs: phytosaurs, ankylosaurs, and confuciusornithid birds. For the most part, this proves only that a small snout bone is easy to misidentify.

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# The Facial Series: Septomaxilla - 3

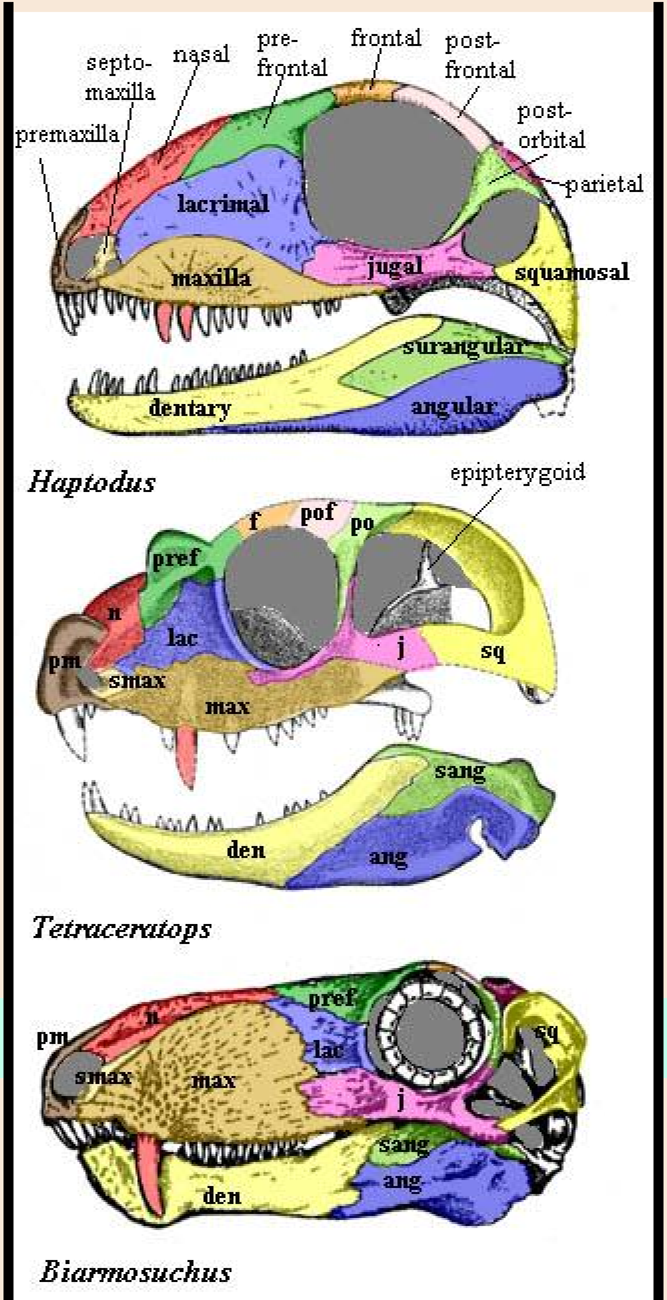
| Bones | Dermal Bones | Facial Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | Internasal<br>Premaxilla<br>Septomaxilla |

## Synapsida

It has been reported that the nasolacrimal duct opens into the vomeronasal organ in both synapsids and lepidosaurs. Hillenius (2000). This may well explain the relative success of the septomaxilla in these two lineages. In any event, the septomaxilla is a relatively large, Type A structure in pelycosaurs. It may also have had a role in giving some minor flexibility to the snout, as it tends to insert ventrally between the maxilla and premaxilla, and dorsally between the nasal and premaxilla. This last character is best developed in sphenacodonts, and particularly in *Haptodus*. In the basal therapsids, this character is very marked, and the elongate posterior extension of the septomaxilla on the external skull is considered a strong synapomorphy of Therapsida.

The septomaxilla is lost in several synapsid branches, including the anomodonts and most therian mammals, presumably coincident with the uncoupling of the nasolacrimal duct from the vomeronasal organ. However, the bone is rather persistent otherwise, and has been identified, for example, in tritylodontids, *Morganucodon*, *Gobiconodon*, and monotremes, although it is absent in multituberculates.

What is difficult to explain is the presence of a septomaxilla in the Xenarthra. This may be an argument for a pacing them outside the Eutheria. However, it more likely another case of a non-homologous neomorph.



Skulls of Haptodus, Tetraceratops and Biarmosuchus in left lateral view from Carroll (1988), Lauren & Reisz (1996), and Ivakhnenko (1999), respectively.

## An Odd Bone

The septomaxilla is, obviously, a bone characterized by ambiguities. It probably originates from the anterior tectal of osteolepiforms, where it depended from the nasal and flexibly covered part of the external naris -- a Type C conformation. On the other hand, a lateral rostral origin cannot be ruled out. The lateral rostral looks much more like a Type B septomaxilla and a clear Type C is known only from *Acanthostega* and *Ichthyostega*.

The septomaxilla is highly mutable in anamniote groups. Both its form and presence seem labile on a family level. However, among the amniotes, we find great stability in some lineages and permanent loss in others. This stability appears to be linked to a tight association with the nasolacrimal duct. However, the connection with the vomer and the vomeronasal organ can't be eliminated, either. In fact, its greatest success is among the squamates, where it plays an increasingly important palatal role in more derived species.

This is all a puzzle that anatomists are unlikely to be able solve alone. Eventually, we have argued, we will need a much deeper understanding of the fine points from molecular developmental biology. ATW040312.

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**[1]** However, we do have remarkably complete developmental series for one osteolepiform, *Eusthenopteron*. *See* Cote *et al*. (2002). Possibly something could be learned from an examination of these fossils.

**[2]** In fact, Clack refers to the bone in both cases as an "anterior tectal".

**[3]** Although we have left the typology of the early tetrapods behind, not how the enlarged septomaxilla of snakes incorporates the characteristics of all three basal septomaxilla types. It is associated with the nasolacrimal duct as in Type A, bears a dorsal process within the nasal cavity as in Type B, and is strongly bound to the nasal, as in Type C.

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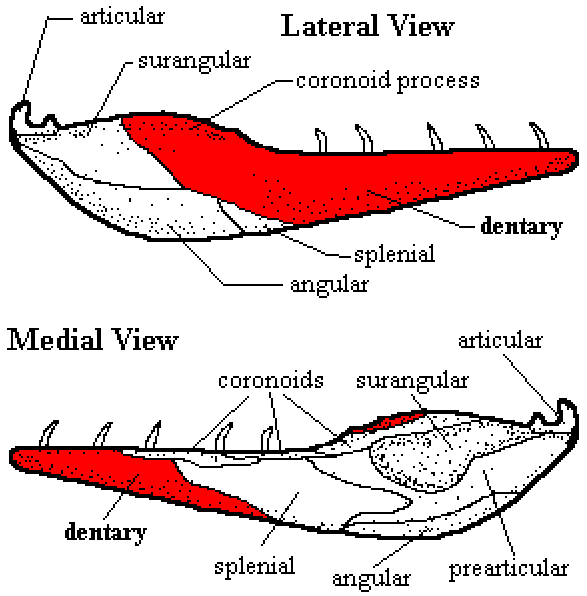
# The Mandibular Series: Dentary

| Bones | Dermal Bones | Mandibular Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series | **Dentary**<br>**Gulars**<br>Infradentaries<br>**Surangular** |

## The Standard Condition



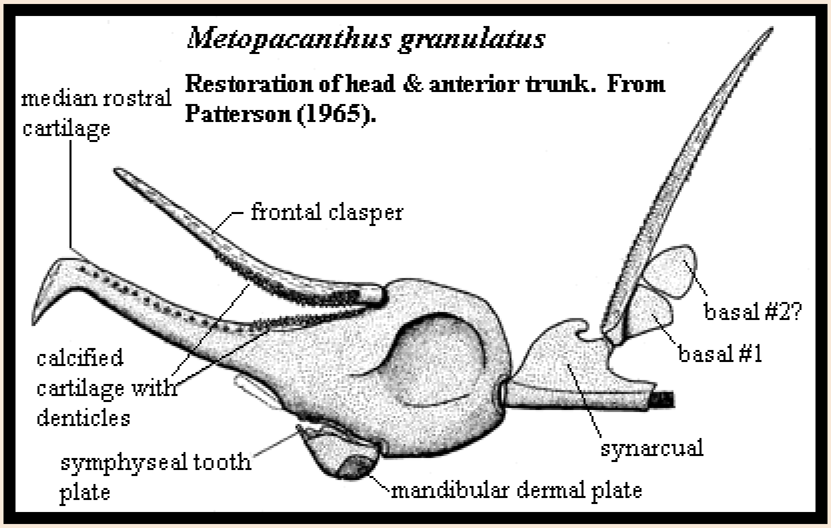
Standard Condition: Bob's lower jaw in lateral & medial views

To our right is the jaw of Bob, the standard critter with the Standard Condition. This particular avatar of Bob is so unlike anything that ever lived that we must exercise extra caution. Know ye that Bob is a member of the taxon Didactomorpha, meaning that this jaw is designed to support points of view, rather than points of teeth. However, with that said, know also that in this case, the Standard Condition is *extremely* standard and applies generally to more or less everything from *Cheirolepis* on except for a few durophagous, or otherwise pathological forms, and the usual lot of osteological outcastes and untouchables -- the mammals.

The dentary has had minor ups and downs in vertebrate phylospace. The dentary almost always covers the outside of the mandible and holds the outer marginal dentition. Much of its life among tetrapods consists of a slow war of attrition against the coronoids, splenials and prearticular internally and the angular and surangular externally. Generally speaking, the dentary has made gradual and irregular progress in displacing these bones, although it has acheived decisive victory only among the mammals. At the level of Bob, roughly the very basal Amniota, the dentary was carrying all before it on the outside of the jaw. The entire anterior part of the outer jaw was already covered by the dentary. Posteriorly, it was encroaching on the coronoid process and taking large bites from the former territory of the splenial(s) and surangular.

However, these victories were somewhat hollow, or at least the jaw was. The inner surface was still controlled by the archaic splenial, sometimes multiple splenials, as well as the coronoids. The latter still competed with the dentary as the main tooth-bearing elements of the mandible.

# The Origin of the Dentary



The developmental source of the dentary is quite clear. Like most dermal bones, it began by contour ossification of structural cartilage. Patterson's (1965) restoration of *Metopacanthus*, a Jurassic myriacanthoid chimaera, provides us with one possible model of how the dentary may have begun. Here, the working parts of the jaw are all cartilagenous, but a small plate of dermal bone has developed at the bottom of the jaw, either for muscle attachment or to guard against mechanical stress and abrasion.

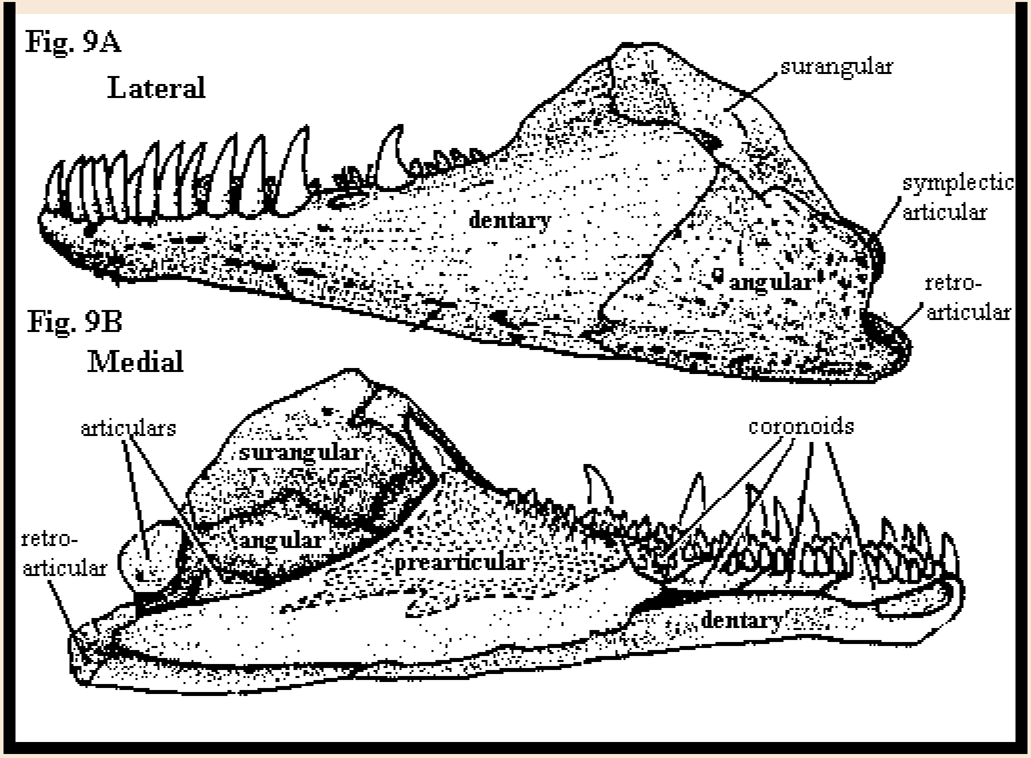
All members of the mandibular series may have began in this fashion (except the articular, which is not a dermal bone). However, the dentary was a bit different because it early assumed the role of supporting the most marginal tooth row. As it turned out, this was an excellent career move, because most major terrestrial vertebrate groups increasingly came to rely on this dentition alone.

However, it may not have happened in this fashion. In the Middle Paleozoic, a range of competing designs existed which might have given rise to the dentary. All are found in the Acanthodii -- another indication of the possible paraphyly of this group. Many acanthodians bore teeth directly on the Meckelian cartilage, which was ossified in most cases (like placoderms), but may have remained cartilagenous in others (like sharks). The "typical" condition, if such a thing exists for acanthodians, seems to have involved a mixture, with the Meckelian ossified both proximally and distally, but remaining cartilaginous in the middle. However, regardless of the ossification state of the Meckelian, most acanthodians also developed dermal bones on the mandible, which might have developed denticles. Any of these might be homologous or at least analogous to the early dentary. However, it is striking that none of these dermal bones are presently known to have supported teeth. Long (1995).

Among the Climatiiformes, the Meckelian is ossified and bears denticles, but the main tooth-bearing function is taken over by an (unnamed?) "dentigerous jaw bone" which lies along the apex of both the upper and lower jaws. Janvier (1996). This is not an ornamented external dermal, but appears to be a special purpose novelty. This, also, is a possible origin for the dentary. However, this model suffers from the opposite problem: none of these bones are known to have developed any significant degree of external exposure. Accordingly, we are forced to retire in confusion, without a clear idea whether the dentary was a normal ordinary dermal bone exapted to hold teeth or a dentigerous bone which aspired to a front office job.

# Phylogeny

However it began life, the dentary "appears full blown," albeit from the head of *Cheirolepis* rather than Zeus. Both branches of the Vertebrata at the actinopterygian - sarcopterygian split inherited the Standard Condition. Among the ray-finned fishes, this was maintained at least through the living neopterygian



*Amia*, which is shown at right. The sarcopterygian fishes developed a tendency to minimize the dentary, but trend was reversed with the evolution of land-dwelling tetrapods.

Despite the structural advantages of a one-piece jaw, most vertebrates have kept the Standard Condition because it constitutes a workable compromise for any organism with an essentially kinetic jaw mechanism. To explain, Bob, and most other vertebrates apply most of the force of the jaw-closing muscles when the jaws are wide open, relying on momentum to follow it through. This is sound strategy, because it makes efficient use of the adductors, and adductor musculature has probably been *the* most important limiting factor for tetrapods. Unless one wishes to go to the absurd extravagence of evolving molars, the main thing for a predator is to place nutritionally appropriate organisms (or portions thereof) in the oral cavity and swallow them as quickly as possible. Anything else is essentially waste motion. Thus, the range of action of the adductors should be from mouth open to mouth closed. As muscles work best in the middle of their range of motion, it follows that an efficient adductor system will apply most force to the jaw when the mouth is still fairly wide open.

This is efficient, but not entirely safe. As anyone knows who has ever bitten down hard on something that wasn't there, a kinetic system has certain disadvantages when the cushioning medium of water is absent. Thus, it made sense for land animals to retain a flexible, multi-element jaw with its hollow or cartilagenous core. This design permits a long but lightweight jaw, lots of surface area for teeth, and the flexibility to avoid the worst consequences of miscalculation. Even lineages which have departed from this model have sometimes found it expedient to return to the original inspiration. Review, for example, the *jaw of Tyrannosaurus*, which differs from Bob's jaw only in its adaptations for great mass. Note particularly how the immediate ancestors of *Tyrannosaurus* reinvented the multiple coronoids in the guise of a "supradentary".

We might speculate on why the result was different for mammals. Mammals differ because they expect their teeth to do the work of a gizzard or large, muscular gut. Unlike some mammalian adaptations, molars are probably not simply a matter of caprice or willful indifference to the legitimate interests of anatomists. A warm-blooded creature has to eat a lot. Since internal processing takes a long time, one either has to develop a gut of truly Brobdignagian proportions or find a way to process food outside of the stomach. Since McDonald's was unavailable in the Mesozoic, it was necessary for the early mammals to pre-process their own food. Molars were thus helpful co-conditions for the development of a fully warm-blooded lifestyle. Oral food processing, in turn, meant that muscles evolved which worked while the mouth was nearly closed. With less need for a kinetic jaw, this constraint on the growth of the dentary was removed. ATW021223.

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# The Mandibular Series: Gulars

## Bones

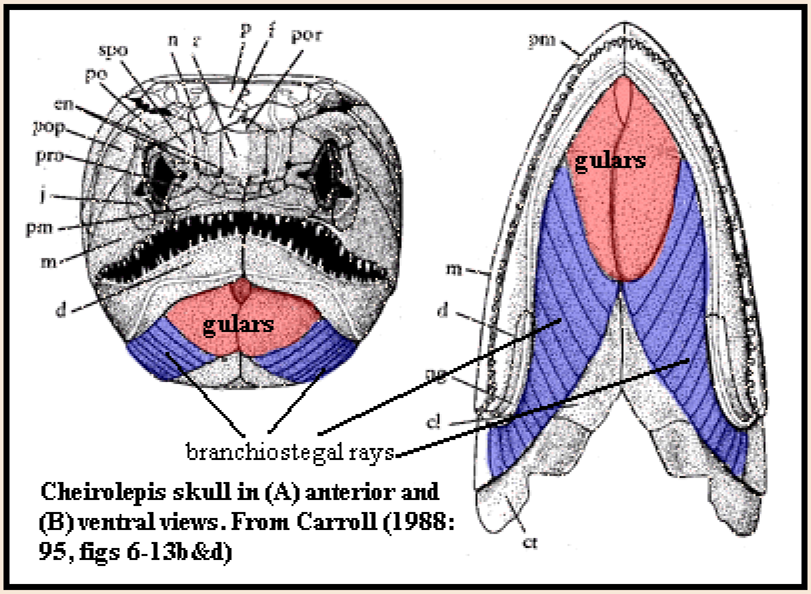
**Bones**
**Braincase**
Dermal Bones
**Ear**
**Gill Arches**
**Teeth**

## Dermal Bones

**Facial Series**
Mandibular Series
**Opercular Series**
Orbital Series
Palatal Series

## Mandibular Series

**Dentary**
**Gulars**
Infradentaries
**Surangular**

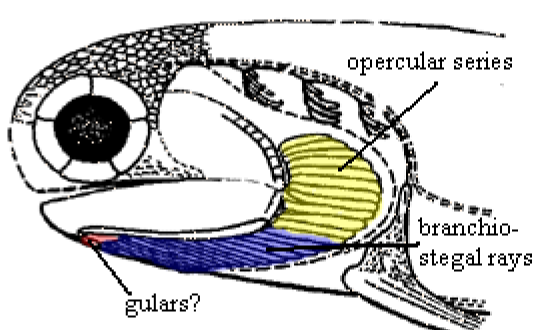


**Cheirolepis skull in (A) anterior and (B) ventral views. From Carroll (1988: 95, figs 6-13b&d)**

The gulars are restricted to various fish groups and are not terribly interesting bones in themselves. They would not normally be worth much attention. However, they do provide an occasion to add a rarely noticed footnote to the jaw story which, as frequently remarked elsewhere, is the central plot in our tale of the vertebrate skull.

The gular is defined in Fishbase as a "median, dermal bone between the dentary bones of some primitive fishes (e.g. *Latimeria* and *Elops*)." As has been our general rule with bones with this kind of phylogenetic distribution, we will define the Standard Condition with reference to *Cheirolepis*. For once, there seems not to be any reason to suspect that the actinopterygian and sarcopterygian versions of this bone are independently derived.

From the figure, it is almost painfully obvious that the gulars are serially homologous with the branchiostegal rays -- the series of dermal bones that provide the flexible bone floor to the mouth in many different fish lineages. What is less often remarked is that the same relationship holds for the opercular series. The acanthodian *Mesacanthus* (see figure) shows this relationship well. This complete continuity between the opercular and branchiostegal series is also present in *Mimia*; and even the highly derived dipnoan, *Griphognathus*, suggests the same relationship. We can even follow the trail of supposition a little further out and remark on the similarity to



**Mesacanthus: head in left lateral view.**
**From Janvier (1996: 176, fig. 4.60B)**

the infradentary series, just lateral to the branchiostegal series, which was discussed in connection with the derivation of the surangular, and perhaps even the splenials on the inside of the jaw.

What this all suggests is that there may be a common derivation for structures as diverse as the opercular, the surangular and the gular. All of these seem to have evolved from serial repetition of a simple laminar pattern of small dermal plates running along the outside of the "mandibular arch."

ATW011207.

**Note added in proof:** more than eight years after this page was first written it now seems to be generally accepted that the gulars are simply the most anterior extension of an "opercular-gular" system. The extension of this system under the jaw turns out to have been present in *Onychodus* after all, as well as in *Psarolepis* and *Guiyu*. Zhu *et al*. (2009). We have accordingly deleted an earlier note expressing doubt about our original position. ATW090328.

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**checked ATW090328**
**modified ATW090328**

# The Mandibular Series: Surangular

| Bones | Dermal Bones | Mandibular Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series | **Dentary**<br>**Gulars**<br>Infradentaries<br>**Surangular** |

**Anatomy**: The surangular is a dermal bone of the lower jaw (fig. 1). It typically covers much of the dorsal and lateral surface of the posterior jaw and variably extends onto the medial (inside) surface. The surangular articulates with and supports the articular, which forms the jaw joint with the quadrate in most vertebrates, and is in turn supported by the angular. More distally, the surangular bridges the mandibular fenestra, if one is present. It may also bear a raised dorsal coronoid process, an important attachment site for the mandibular adductors. At its distal (or rostral) end, the surangular meets the dentary, the main tooth-bearing bone of the lower jaw in most vertebrates. In certain fishes, an "infradentary" separates the two. On the medial face of the jaw, the surangular broadly articulates with the prearticular which covers much of the posterior medial face of the lower jaw. Across the jaw line, the surangular faces the quadratojugal and/or the jugal bones of the cheek region. The surangular is highly variable in shape, but most typically is slightly arched, either upward (as in fig. 1) or downward (as in fig.2).

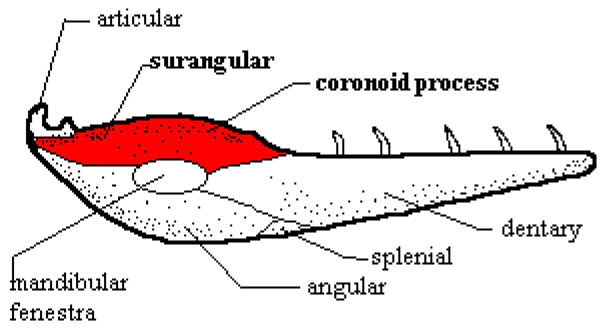

**Fig. 1. Generalized archosaur right lower jaw in lateral view**

**Functions:** Functionally, then, the surangular is associated with the following processes.

1) *Support and orientation of the articular*. In many cases, for example dinosaurs, the articular is reduced to a small, specialized articular surface, and the entire structural role is taken over by the surangular.

2) *Attachment of jaw adductors.* The surangular normally lies over the center of mass of the lower jaw, and thus occupies the most mechanically advantageous site for the attachment of the muscles closing the jaw. This is presumably why the mandibular fenestra is located there. The fenestra and the coronoid process provide additional surface area for muscle attachment at this critical site. In lepidosaurs and some other forms, the coronoid may be a separate element, and the mandibular fenestra is unique to the archosaurs.

3) *Lengthening the jaw.* Many vertebrates rely heavily on the speed of jaw closure for prey capture.

Strength is less important than speed in capturing small prey. This gives a selective (and mechanical!) advantage to jaw which is long, particularly distal to the adductors. One important "function" of the surangular is simply to make a longer lever arm between the hinge and the business end with teeth.

4) *Jaw kinesis.* This function takes no standard vertebrate form. However, the surangular may work with other jaw elements to provide a mid-jaw "hinge" allowing the jaw to bend outward (laterally) or up-and-down (dorso-ventrally).

**Phylogeny:** A surangular, sometimes labeled "supraangular," appears as soon as the dermal bones of the cranium begin to stabilize with the earliest osteichthyans. Here, the surangular is an irregularly-shaped element which caps the lower jaw. In neopterygians, it may develop a coronoid process, as in tetrapods. Nevertheless, it is not completely clear that this surangular is homologous with the surangular in tetrapods. Sarcopterygians tend to have a series of vaguely rib-like bones posterior to the dentary. They are oriented more-or-less diagonally and are often referred to as "infradentaries." In early tetrapods, the opercular (gill cover) series is lost, and these "infradentary" bones come to lie horizontally and extend further posteriorly on the skull. In that case, the most dorsal of the series is referred to as the surangular; and it is this bone that is clearly homologous with the surangular of all later tetrapods.

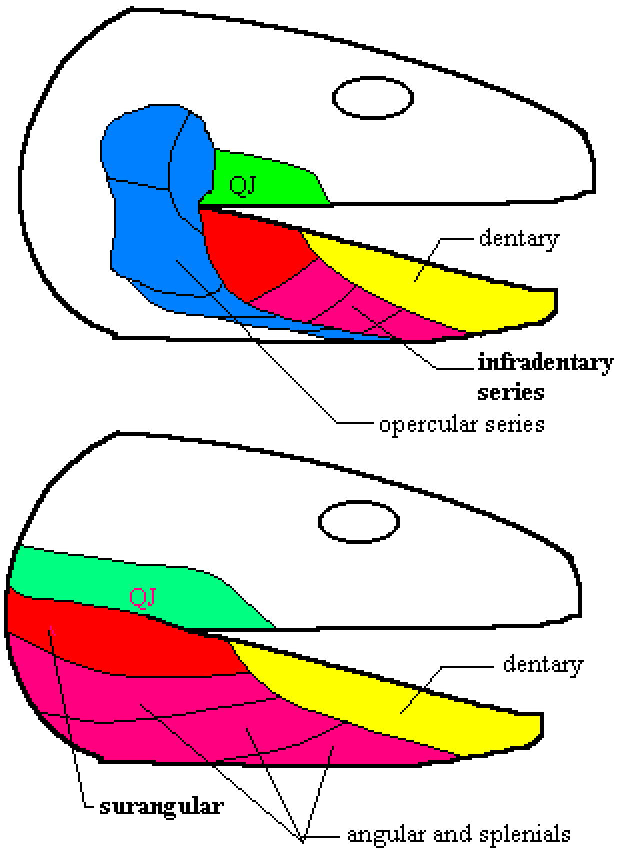

Fig. 2. Hypothetical (a) sarcopterygian and (b) early tetrapod skulls in right lateral view, showing homology of infradentary and angular series.

The later fate of this bone varies in different lineages. In some lepospondyls, and in frogs and salamanders, the surangular is absent. However, it becomes increasingly significant in the anthracosaur lineage. In turtles, it is one of the two principle bones of the lower jaw. In lepidosaurs, it is less important because of the development of a separate coronoid bone. In advanced lizards and pythonomorphs, it may fuse with the articular and perhaps other bones and loses its separate identity. Its function in archosaurs has been discussed above. See also Anatomical Dictionary.

In syanapsids, a secondary jaw joint develops between the surangular and the squamosal, which becomes the unique mammalian jaw articulation. However, the surangular fuses with the dentary and becomes the unitary mammalian "mandible" without a separate identity.

ATW 000930.

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**Some arguably relevant links:** Anatomical Dictionary (dinosaurs); cranial (more dinosaurs); Skull of Einiosaurusprocurvicornis in lateral view (yep, another one).

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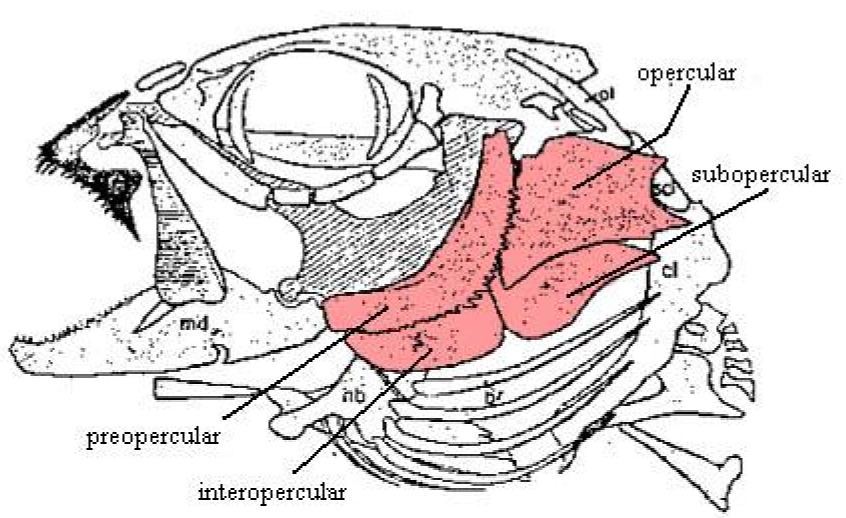
# The Opercular Series: Overview

| Bones | Dermal Bones | Opercular Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | **Overview**<br>**Opercular** |

The opercular is a plate-like bone which covers the operculum, the structure which protects and operates the internal gills. There is simply no getting around the fact that, in order to have an opercular series of dermal bones, it is necessary to have an operculum. Consequently, the opercular series is present only in aquatic Osteichthyes. At this point, of course, some sniveling pedant will insist on bringing up the so-called operculum of the Holocephali. However, the likelihood that these soft tissue structures have any relationship whatsoever to the structures of interest to us, is beyond remote. Chondrichthyan gills operate in a quite different fashion. Accordingly, we will treat this disgraceful interruption with the scorn and derision it deserves. In fact, it is not even clear that the opercula of the Actinopterygii and Sarcopterygii are precisely the same structure, although we will assume that they are closely homologous.

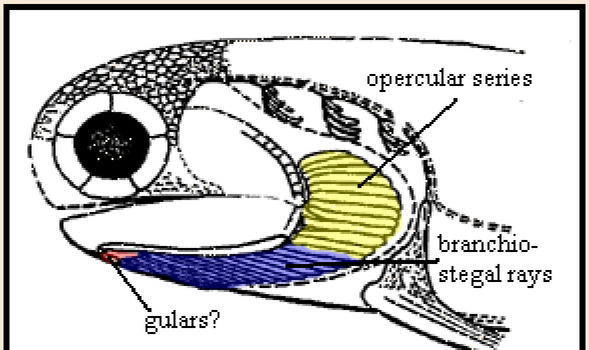
# The Standard Condition



Generalized teleost showing Standard Condition of the opercular series

The Standard Condition (for a teleost) is shown at right. The *opercular series* comprises each gill cover (operculum) and generally consists of four bones. The *preoperculars* are flattened, J-shaped bones that usually bear heavy serrations on their posterior margins. It is not clear that they have the same origin as the operculum and the remainder of the series. Lying below each preopercular is a thin *interopercular*. Each interopercular normally possesses a small, dorsally-oriented projection on its anterior end. Posterior to each preopercular is the largest bone in the series, the *opercular*. Each somewhat triangular operculum has a large fossa on its upper anterior margin that articulates with the hyomandibular. Below each operculum is an oblong bone, the *subopercular*. The opercular series is connected to the lower jaw by a series of ligaments so that the jaws and opercula act in synchrony.

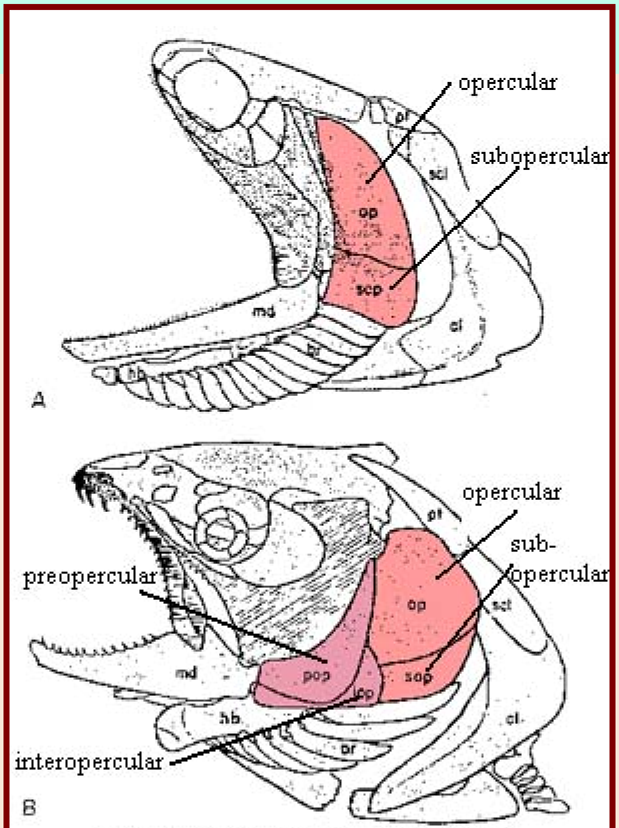
# The Origin of the Opercular Series



**Mesacanthus: head in left lateral view.**
**From Janvier (1996: 176, fig. 4.60B)**

As we discussed in connection with the **gulars,** the opercular series seems to have developed from serial repetition of a simple overlapping laminar series of scales, as exemplified in some Acanthodii. The development from this stage is easily determined from the series at right and below, ultimately leading to the Standard Condition in teleosts. As noted above, it is not obvious that the interoperculars and -- in particular -- the preoperculars are derived in exactly the same fashion. In that connection, the very basal guildayichthyiform actinopterygian *Guildayichthys* demonstrates an interesting condition. Lund (2000). A moderately detailed image can be seen *here*. *Guildayichthys* has an extensive series of interoperculars parallel to the branchiostegal rays. They appear to have arisen by duplication of the entire branchiostegal series in a more dorsal position. This fish also has two long, thin preoperculars which, unlike the other members of the series, may well have been derived by the same sclerotic - orbital route which produced the **jugal**. However, that is a matter which can be taken up together with a more detailed consideration of those particular bones. The plot line is clear, even if we have not completely accounted for all of the characters.

# Some Functional History



**Opercular series in (A) a generalized basal actinopterygian and (B) Amia**

Primitively, the operculum functioned as a sort of pump-and-valve-system for respiration. It seems likely that there has always been some connection between respiration and feeding in fishes. However, the operculum was essentially a respiratory structure, operating as part of a dual pump. The dual pump consists of a buccal and opercular pump, which act in synchrony. The first phase is he suction phase, in which the buccal and opercular cavities expand and water is drawn in. The opercular valve is closed at this point and lower pressure in the opercular cavity draws water across he gills. In the second, force phase, the mouth is closed and he opercular valve open. Muscle compression forces water posteriorly and out. The result is unidirectional flow. respiration.pdf.

At the level of the Halecostomi and above, things get more involved as the nature of the jaw changes. In essence, the posterior end of the lower jaw is depressed -- dropping the floor of the mouth -- by using the interopercular as an extension of the lower jaw. The trick is done by contraction of the *m. levator operculi* (derived from the primitive opercular adductor muscle). The levator causes a dorsal rotation of the entire opercular series (operculum, subopercular and interopercular) which is applied as a posteroventrally directed force on the posterior end of the jaw via the *interoperculomandibular ligament*. Lecture 2.

*Wakarimashta*?

Let's try it again: review the image of *Amia* at right. if one could grip the opercular series like a dial and twist it counter-clockwise, that would force the far end of the interopercular down and to the right. The left end of the interopercular and the right end of the lower jaw are connected by a ligament, so that end of the jaw moves the same way. That drops the whole floor of the mouth.

Now, if we're an advanced teleost, the whole thing looks like this:

1. First the fish must prepare. During the preparatory phase the volume of the buccal cavity is reduced. Basically the floor and the sides (i.e. the hyoid region and the suspensorium region) of the fish�s mouth squeeze together.

2. Next the fish expands the volume of the buccal cavity, opens its jaws, and in some species also protrudes its upper jaw. During this phase water and prey are sucked into the fish�s mouth. There are three musculoskeletal couplings that are involved in this expansion phase.

a. epaxial muscles lift the cranium and the roof of the mouth, expanding the buccal cavity.

b. The lower jaw is depressed. This occurs when the operculum is rotated via the *levator operculi* and interopercular-mandibular ligament as explained above.

c. Additionally, the hypaxial muscles depress the lower jaw. Hypaxial and the sternohyoid muscles act on the bones of the floor of the mouth (the hyoids) and also depress the lower jaw.

3. During the compression phase, the jaws are closed by the adductor mandibulae (see Fig. B below) Also the sides of the fishes mouth are squeezed in (the suspensorium is adducted), and the cranium returns to its original position. If the buccal cavity is being squeezed in, where does the water in the mouth go? During the compression phase, the operculum valve opens and the water in the buccal cavity flows over the gills, past the operculum and out of the fish. The protruded jaw returns to its original position also.

4. During the recovery phase, the muscles and bones return to their original positions. The length of this phase is longer when large prey are consumed. Perch supplement2.pdf.

These complex steps are coordinated with movements of the gills and the strange dance of maxilla and premaxilla which seems almost backward to those of us more accustomed to the simple-minded hinge of the tetrapod jaw. See, e.g., **Premaxilla**.

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**Links:** Lecture 2 (important stuff on helecostomes); Perch supplement2.pdf; Untitled Document (important figure & figures of mechanism above); MsoDockBottom; gibbpage/pvfeed.pdf (the case of flatfish); respiration.pdf; Biology 356; The materials provided with the previous exam; Fall'96Syllabus. ATW020817.

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# The Opercular Series: The Opercular

| Bones | Dermal Bones | Opercular Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | **Overview**<br>**Opercular** |

The opercular, sometimes called the "opercle" is, obviously, the first and principle component of the opercular series. As we have mentioned, it is likely that the opercular is serially homologous with the branchiostegal rays and that both began as a series of dermal opercular scales as is observed in some acanthodians. However, the embryology of the operculum in the zebrafish suggests that the operculum may also have some deep connection with the splanchnocranial (gill-arch derived) bones. It is probably too early to say much. This is another of those interesting regions in which two very different developmental domains converge. See the discussion in Meckel's Cartilage and the basisphenoid for other, much more complex, examples.

The desirability of having some kind of hinged cover for the gills is plain. Even the chondrichthyans, who have multiple gill slits and no dermal bone to speak of, have independently evolved the operculum twice, and probably three times (Holocephali, Iniopterygii & Hypnosqualea). However, the importance of this particular bone and its homologues varies considerably, even between taxa which are fairly closely related. Thus, for example, Porolepiformes had rather small opercula, while Actinistia have unusually large opercula. Among actinopterygians, the Amiidae have a large operculum, Pycnodontiformes had small opercula, and the Chondrostei may have none at all. In general, these differences seem to correlate with lifestyle factors, such as how hard the gills have to work to get oxygen and whether dirt and parasites are likely to gain entrance to the sensitive gill membranes.

This correlation lends itself to some interesting lines of speculation, if we may extrapolate the same observations back to earlier forms. First, were the early jawless fishes ecologically restricted because of the absence of opercula? If so, the operculum may have been a key ingredient in the radiation of fishes onto the broad, shallow continental seas of the Late Silurian and Devonian. Second, all but the most feeble gill covering must be mechanically coordinated with respiration or it will interfere with gill function. But once a muscular gill cover is coordinated with respiration, it gains the potential to assist in *actively* pumping water over the gills and so (a) increasing ecological range to more poorly aerated waters and (b) speeding oxidative metabolism in well-oxygenated waters. In fact, under the right circumstances, one might even imagine an early analogue of the opercular apparatus driving the development of jaws, rather than vice-versa.

The (at least tacit) assumption seems to be that the primitive operculum was only marginally coordinated with the jaw. However, as far back as we can study jaw mechanics with any confidence, there seems to have been some level of coordination. Thus, in *Mimia* and *Cheirolepis* the opercular is braced against the hyomandibular, which is braced against the palatoquadrate. Accordingly, when the jaw is opened, the opercular must move, although the specifics of its movement are not so easily determined. At least some acanthodians (Climatiiformes, in particular) seem to have had a similar arrangement, although reconstructing the details of cranial anatomy in this group still involves a fair amount of guesswork, and the mechanics are complicated by auxiliary gill covers which were not mechanically coupled to the hyomandibular in any obvious way. Interestingly, a preopercular is already present in many of these early fishes. The function of this latter bone is normally to couple the opercular series with the dermal bones of the jaw, *i.e.* the maxilla. So, its early appearance argues for an early mechanical relationship between operculum and jaw movements. This is also consistent with embryological evidence which shows that the operculum and preoperculum substantially precede the other elements of the opercular series in development.

Whenever muscular control of the operculum was established (presumably very early), it was probably based on the cleithrum. The cleithrum is the origin of the hypaxial musculature which generally serves to open the mouth and expand the gill chamber. In any case, the braincase and cleithrum are virtually the only stable platforms from which cranial muscles can act in these early fishes. The first evidence of a completely independent set of muscular controls comes from the Halecostomi. The halecostomes, of which *Amia* is an example, have an opercular dilator muscle originating on the mandible which opens the operculum. It is unclear just how novel this muscle really is at this level. Although it is apparently unknown in chondrosteans, it is believed to be homologous to lamprey velar muscles. Schilling & Kimmel (1997). Since chondrosteans have minimized the opercular as a whole, they are not a particularly good basis on which to draw any conclusions. These dilators are opposed by opercular adductors originating on the hyoid arch. *Id.*

What is truly new at the halecostome level is the *m. levator operculi* which runs the other way, so to speak, raising the opercular as a method for depressing the jaw. The levator muscle is what creates the "new jaw" of the neopterygians. As this has been discussed in the overview section, and in connection with Neopterygii, we will refrain from repeating it all again. ATW030207.

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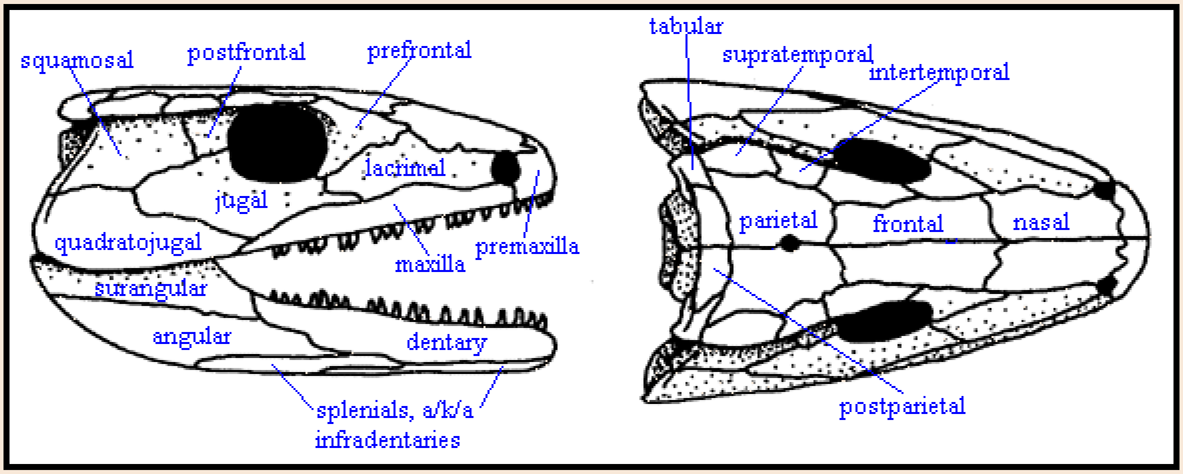
# The Orbital Series: Jugal (1)

| Bones | Dermal Bones | Orbital Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series | Jugal<br>Jugal (2) |

Unlike many of the odder bones with which we have been required to deal, the jugal is almost an open book. It is generally easy to locate and identify. Its structural role is straightforward; and its position and properties have been quite stable over time. Each of these rules is subject to some exceptions; but, by and large, we can coast on this one.

# The Standard Condition

The Standard Condition of the jugal is shown at right. In this case, our model is not Bob, our basal amniote. Instead, we have selected a slightly more primitive relative, *Eoherpeton*. The image is relabeled from Smithson (1985), *vide* Clack (2002).

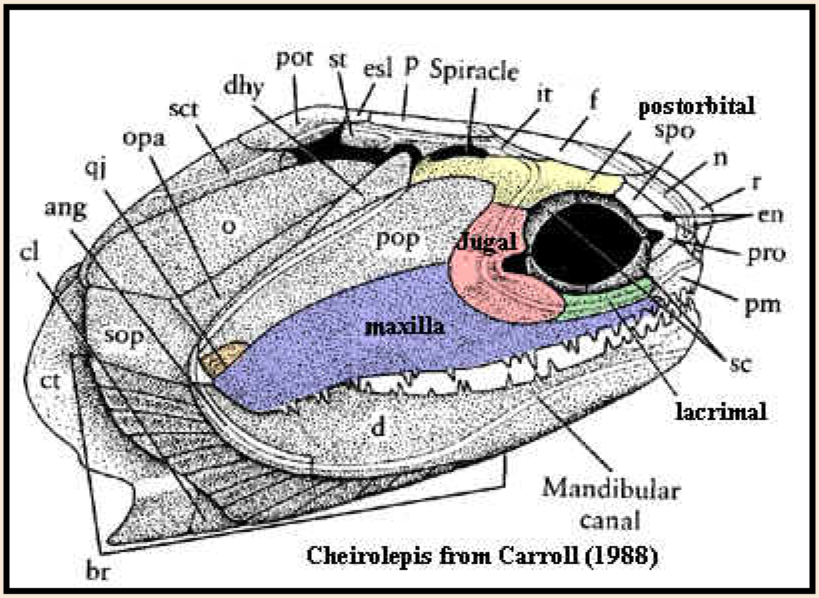


At least at this stage, the jugal almost always underlies the orbit, and contacts the lacrimal anteriorly. The relationship of jugal and maxilla is variable, although they are almost always in contact. Generally, the jugal passes dorsal to the maxilla to terminate anteriorly on the lacrimal. Romer (1956). Sometimes, as in *Eoherpeton*, the maxilla and quadratojugal exclude the jugal from the lower margin of the skull. More often, the jugal forms the ventral margin and separates the quadratojugal and maxilla. The jugal's contacts dorsally are a bit more variable due to the variety of temporal fenestration seen in the amniotes.

In general, its dorsal partners are the squamosal and either the postfrontal or postorbital.

Among amniotes, it is useful (but not always accurate) to think of the jugal as a three-pronged bone centered posteroventral to the orbit. From this perspective, the three *rami* are : (1) an anterior or suborbital process which passes under the orbit and terminates at the lacrimal and/or maxilla; (2) a posterior or subtemporal process which forms the bar (if any) under the temporal fenestra (if any) and terminates at the quadratojugal; and (3) a dorsal or postorbital ramus which forms part or all of the postorbital bar and terminates on the postfrontal, postorbital, or whatever. In this avatar as a *trimurti*, the jugal obviously plays an important role, defining and limiting the degree of the skull's lateral flexibility, as well as joining together the disparate portions of the dermal skull at this central point. This, in fact, may be the source of its name, as *iugare* is the Latin meaning to bind together, as in a marriage or a team of horses (*iugales*).

# The Origin of the Jugal



Cheirolepis from Carroll (1988)

In a sense, the jugal traces its ancestry to some of the oldest specialized dermal bones, for practically since vertebrates had eyes, they have had small, specialized, dermal bones around and behind the eye to protect it from damage or deformation. Thus, the arandaspid *Sacbambaspis* is believed to have had a *sclerotic ring*. Janvier (1996: 86), And the anaspid *Rhyncholepis* had a small circle of dermal bones surrounding the orbit. Janvier (1996: 101). Many placoderms had one or both, and it is from this circumorbital series that the jugal seems to have derived.

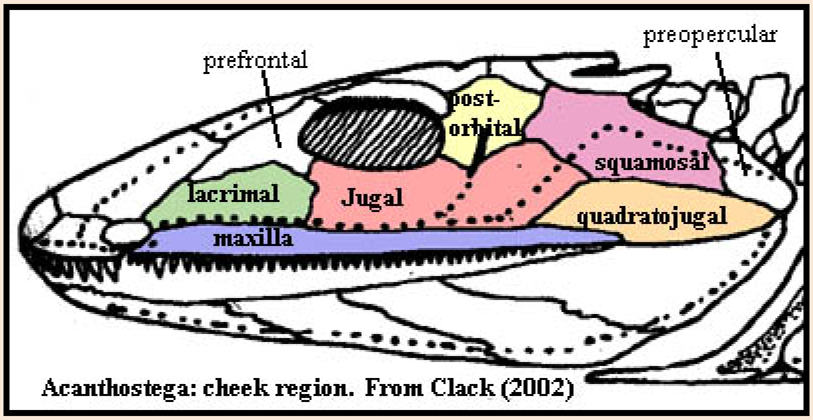
Already in the Acanthodii, one of the circumorbital bones, at the posteroventral corner of the orbit, has become notably enlarged and carries the infraorbital sensory line on its surface -- the mark of the jugal in fish. By time we reach *Cheirolepis*, our usual starting point for dermal bones, the jugal is relatively large and beginning to take on a structural role beyond the simple job of holding the eye in place. However, at this point, the jugal has no relation to the quadratojugal, nor any role in the ventral margin of the skull.

# Phylogeny

**Actinopterygii:** Subsequent to its development in *Cheirolepis*, the jugal has not had a distinguished career among the ray-finned fish. Because of the fundamental reorganization of the jaw in this group, the maxilla is short and mobile in all derived forms. Consequently, there is little need for a stout bone in this position. The jugal simply blends back in to a series of undistinguished and almost indistinguishable suborbitals that serially absorb the strains imposed by movement of the maxilla against the relatively stationary preopercular, posteriorly, and the skull table, dorsally.

**Sarcopterygii:** By contrast, the maxilla is relatively immobile in sarcopterygians. Indeed, in the Actinistia (*e.g.* the coelacanth) and Dipnoi (lungfishes), the upper jaw is completely immobile and ultimately fused to the braincase. In these forms, it is the maxilla which disappears and the jugal (or other suborbitals) which provide the dermal covering of the anterior part of the upper jaw. Along the main line of sarcopterygian evolution, the case was not so extreme. The jugal became an important arbiter between the conflicting claims of the jaw, the orbit and, most importantly, the squamosal. This last was a novel bone which was beginning to contend with the traditional opercular series for domination of the lateral skull.

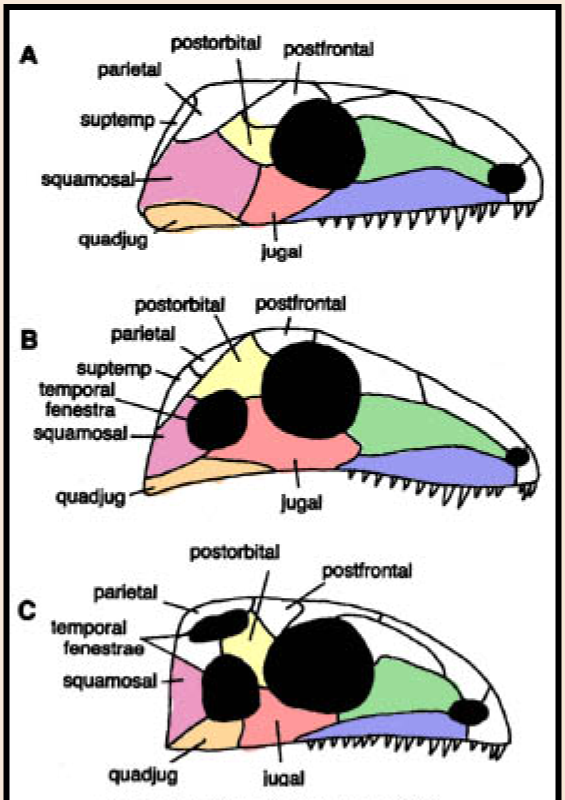
In our own ancestors, the Rhipidistia, the maxilla is slight, but the jaw, maxilla and all, is considerably elongated -- presumably to a point at which it became impractical to rely on an immobile shoulder girdle for ultimate posterior support. But that is another story. Here, the point is that the long jaw and skull made support for the postorbital skull problematic, particularly given the little sliver of maxilla and the growth of more massive jaw adductors. As a result, the jugal becomes a massive plate stretching back through the enlarged former territories of the maxilla and preopercular to reach a similarly behemoth quadratojugal.



Acanthostega: cheek region. From Clack (2002)

**Tetrapoda:** Thus, by the Late Devonian *Acanthostega*, the skull looked somewhat like the figure at right from, Clack (2002). Note that the squamosal has been interposed anterior to the rapidly shrinking preopercular. Note the shape of the jugal. If we consider its home range as a circumorbital bone, it almost appears as if the jugal had been doubled or repeated, with the two halves joined. This impression is only reinforced by comparing the respective courses of the sensory lines through the jugal in *Cheirolepis* and *Acanthostega*.

**Temnospondyls:** Perhaps there is something to the last thought, since the orbit seems to roll back and forth on the jugal within basal tetrapods and early temnospondyls. In *Dendrerpeton*, the orbit is well forward on the jugal, narrowing the jugal almost to a point, so that it makes only slight contact with the lacrimal. In *Eryops*, the orbit is more dorsal and posterior. Here, the jugal broadly contacts, not just the lacrimal, but also the prefrontal as in *Acanthostega*. The latter scheme, involving a jugal extending well anterior to the orbit, is asserted to be a synapomorphy of the Stereospondylomorpha. Yates & Warren (2000). However, some Triassic temnospondyls, such as *Laidleria*, exhibit the pattern of *Dendrerpeton*, with the jugal and prefrontal broadly sutured, and the orbits well back on the skull. Warren (1998). Perhaps it may be more accurate to suppose that the position of the orbit changes, while the form and relationships of the jugal remain rather constant. Interestingly, in few, if any, temnospondyls does the jugal contribute to the ventral margin of the skull. This appears to be a more stable phylogenetic character and is less dependant on the relative position of mutable markers like the position of the orbits.



The jugal in basal amniotes: (A) Captorhinus, (B) Archaeothyris, and (C) inPetrolacosaurus. From Clack (2002).

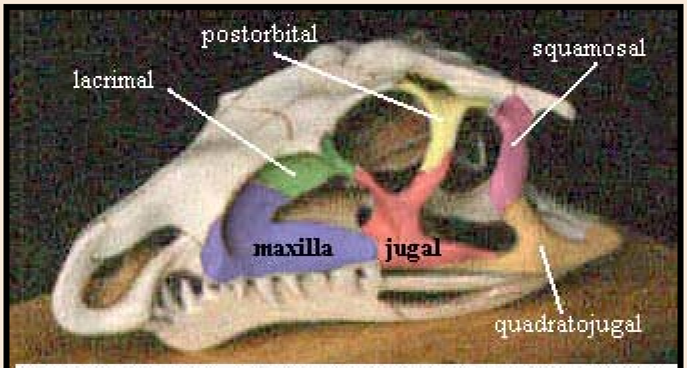
**Lepospondyli & Lissamphibia:** The pattern of the jugal in lepospondyls is generally conservative, more or less like *Acanthostega* except that the jugal finally reaches the ventral margin of the skull in some forms, such as the microsaurs *Hapsidopareion* and *Rhynchonkos* and the Nectridia. (Carroll 1988) A "normal" jugal is present also in the Early Jurassic gymnophionan *Eocecilia*. Jenkins & Walsh (1993). However in the Late Jurassic *Karaurus*, an early salamander, and in all later Lissamphibia, the jugal is usually absent altogether. While the details are obscure, to us at least, this development may relate to the development of specialized structures to project the tongue, with emargination of the ventral skull margin to accommodate the necessary musculature.

**Reptiliomorpha:** Here, again, the conservative basal stock maintains the traditional form, but the jugal increasingly tends to separate the maxilla and quadratojugal along the ventral rim of the skull. This is particularly significant because it brings the jugal into contact with the ectopterygoids, giving the jugal at least a peripheral palatal role. As we will see, this has sometimes resulted in a more frank expression of the jugal on the palate. With the introduction of fenestration in the amniote skull, the jugal begins to adopt the triradiate form in which it is commonly found in Mesozoic and Cenozoic tetrapods*.

**Anapsida:** Many of the more bizarre members of this group, such as the Lanthanosuchidae and Pareiasauria had widely flaring jugals. Turtles seem to have gone almost the other direction. Turtles lack the ectopterygoid bone and have a large *medially* directed process of the jugal bone. The patterns of skull emargination in the turtles are so varied, that it is difficult to make generalizations, but there are certainly unique arrangements in this group. For example, in the Podcnemoidae, the jugal makes contact with the parietal, the postorbital being very reduced. Gaffney & Meylan (1988). In the Cryptodira, the jugal is a relatively flat bone along the ventral margin of the skull between the maxilla and the quadratojugal.

**Eureptilia:** Among the eureptiles, the jugal adopts its conventional, triradiate form and becomes quite resistant to change. This (for once) is consistent with the hypothesis we posited in connection with the premaxilla, *i.e.* that a dermal bone which acquires specialized relationships with different parts of the skull becomes fixed in form. This is not quite correct, but the exception seems to prove the rule. Among Lepidosauriformes, particularly the Squamata, the lower temporal bar tends to be lost, the result being that the jugal is freed from its contact with the quadratojugal and the posterior process is lost. Caldwell & Lee (1997). This liberates the jugal to begin behaving strangely, which it does. So, for example, the jugal of the Anguoidea meets the squamosal *above* the lower temporal fenestra. Perhaps more typically, as in snakes, the jugal is simply lost.

**Archosauromorpha:** The archosoauromorpha are very conservative indeed, which is scarcely surprising, since the addition of an antorbital fenestra makes the jugal effective tetraradiate. Another fairly constant character of the archosauromorphs is the long *scarf joint* between the jugal and quadratojugal, as shown in the image of *Riojasuchus*. A similar joint developes between the jugal and postorbital, giving some degree of mobility to both the posterior and dorsal processes.



Riojasuchus skull. Model and photograph courtesy of Steve Harvey (Wiccart)

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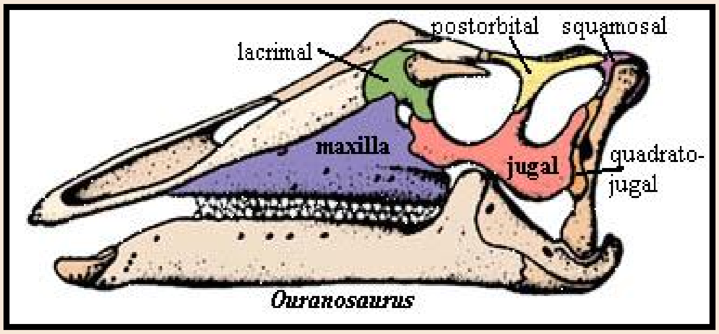
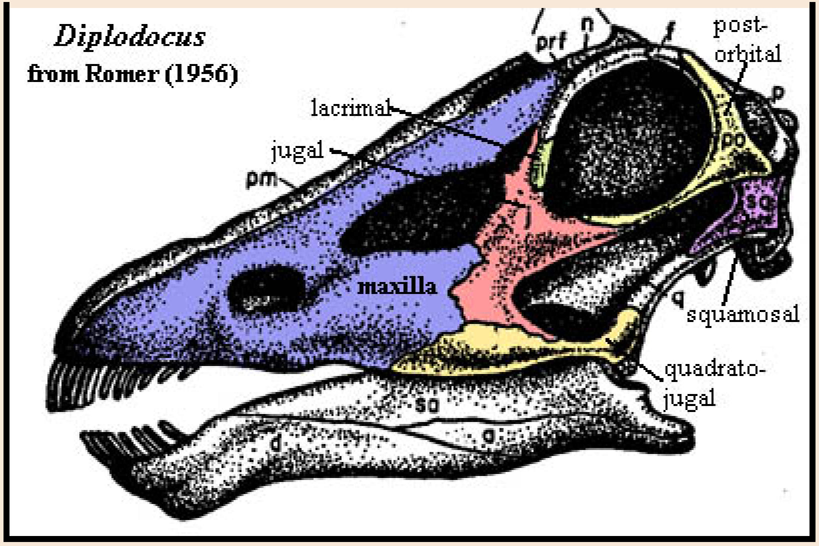
# Dermal Bones: The Orbital Series: Jugal (2)

| Bones | Dermal Bones | Orbital Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series | Jugal<br>Jugal (2) |



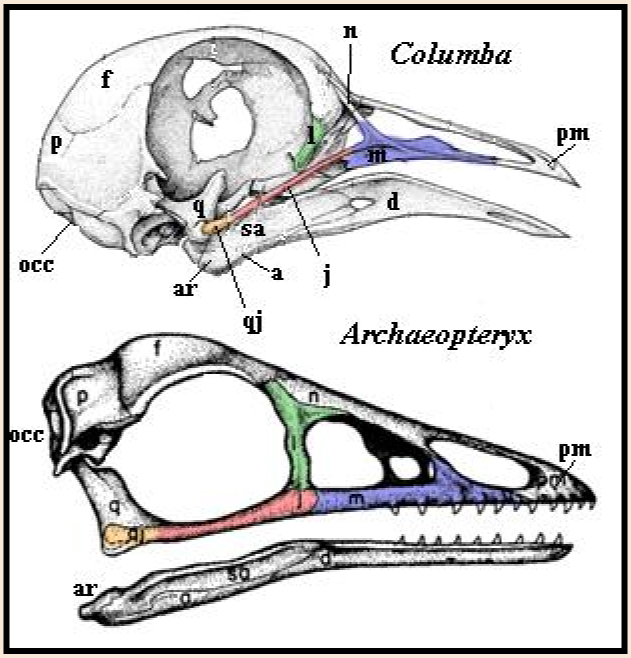
**Ornithischia**: The Ornithischia frequently have lateral elaborations of the jugal, particularly the posterior process, bearing a variety of bosses, knobs, horns and other ornaments. This sort of ornament seems to have developed a number of times: in the Ankylosauria (Coombs & Maryanska, 1990), Heterodontosauridae, and Ceratopsia. However, this is probably a common consequence of herbivory, since similar developments are seen in pareiasaurs, *Estemmenosuchus*, and (less clearly) in rhynchosaurs. The lateral expanse of the jugal is simply too good a place to hang cheeks and jowls. The development in the Hadrosauroidea has more phylogenetic and anatomical interest. Here, the jugal is rather solidly attached at both ends, *i.e.*, to the quadratojugal and the maxilla. However, the bone is thin, expanded dorsoventrally, and has only slight or sliding contact with the lacrimal and postorbital. Head (1998); Sereno (1986), *vide* Norman (1990). Presumably, this permitted the jugal to bow outward to accommodate the unique hadrosaur style of chewing. In more derived forms, the jugal reacquires its accustomed scarf joint with the quadratojugal and loses contact with the ectopterygoid, permitting even greater flexibility. Head (1998).

**Saurischia**: The Saurischia are characterized by a synapomorphy of the jugal. The posterior process is forked and grasps the quadratojugal with two or three tines. *See, e.g.*, figure and discussion at Sinraptoridae; Currie & Zhao (1993). Another peculiar jugal worth noting is that of the Neosauropoda. The retraction of the nares to the top of the skull causes a bizarre rearrangement with the

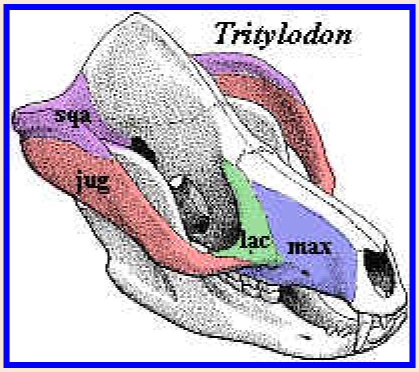


result that the "anterior" and "posterior" processes of the jugal may actually merge, as shown in the image of *Diplodocus*. For those who may not have had much practice with sauropod skulls, remember that the cavity in the anterior part of the maxilla is *not* a nostril. It is a second antorbital fenestra. The nostrils are on top of the head, above the orbits.

**Aves:** Oddly enough, one of the *first* adaptations of birds was a fairly radical reorganization of the jugal area and the reduction of the jugal to a slim *jugal bar*, actually consisting of a fused jugal and quadratojugal, connecting the maxilla and upper beak to a quadrate which is moveable on the occiput. This development was presumably preceded by a loss of the postorbital bar since, even in *Archaeopteryx*, the postorbital is present -- at most -- as a thin ridge on the anterior face of the quadrate. A slight contact with the lacrimal is maintained, but there is no palatal exposure. Note that, despite the reorganization, the jugal maintains all of its primary articulations except for the postorbital, and even this is a close call.



**Synapsida:** Recall that in the Standard Condition, the jugal contacts the squamosal. In the Diapsida, this connection is broken by the appearance of the lower temporal fenestra. In synapsids, the connection is generally maintained, with profound results. We say "generally," since the connection is believed to exist in the Eothyrididae, but is not known with complete certainty. Langston (1965). In some of the Varanopseidae, the squamosal definitely does not contact the jugal. Reisz *et al*. (1998); Romer & Price (1940). However, the subtemporal bar is slender and fragile in all of these forms, and we may maintain a healthy degree of uncertainty without intending any criticism of these authors.



**Therapsida:** Certainly, by the level of the therapsids, the jugal-squamosal connection is well-established. See the images at the Profusely Illustrated Guide. In fact, the squamosal seems to have developed by a sort of competitive exclusion of the quadratojugal, which eventually disappears entirely, with all of its functions being gradually subsumed by the squamosal. The interesting part here is that we may speculate that the jugal seems attracted (in some unspecified sense) to the squamosal generally, not to some particular part or functionality. In this connection, note that the squamosal is a large, plate-like bone in synapsids which seems to have rather vague parameters. Unlike the jugal, it doesn't just connect things. It covers area. If these generalizations are meaningful we may suspect that the establishment of the jugal's squamosal connection, together with the elimination of the constraining connection with the quadratojugal, created a genetic condition in which the jugal had a lot of freedom. That is, in any case, what we actually observe in the therapsid lineage. The weird bulbous projections of *Estemmenosuchus*, the quasi- vertical jugal of *Tapinocaninus*, and the almost incomprehensible *Lystrosaurus*. Eventually, of course, all of this sudden Permo-Triassic creativity collapses into the mundane familiarity of the mammalian zygomatic arch, as in *Tritylodon* or *Probainognathus*. At this level, the jugal again is forced to give up its irresponsible behavior and is harnessed to the exacting task of providing an attachment for the powerful new masseter musculature. Rubidge & Sidor (2001).

**Mammaliformes:** But, if that is the case, how do we derive the jugal of the Allotheria or, if one happens to be an unbeliever in this clade, the Multituberculata? Here, the jugal is reduced almost to a sliver wrapped up on the median side of a zygomatic process of the maxilla, very much like one of the postdentary bones being swallowed up by the dentary in contemporary cynodonts. Contrast this condition with the basal mammaliform *Morganucodon*, in which the zygomatic arch is dominated by the jugal. Kermack *et al.* (1981). The logical answer is that such a transformation, from the starting point of *Tritylodon*, is not very likely. In that event, the Allotheria (or Multituberculata, as the case may be) are more rationally considered a separate derivation from within the Cynodontia. Thus, the Mammaliformes, as commonly understood, may be polyphyletic.

**Mammalia:** However, we could still be well offside in jumping to this conclusion. The jugal seems to retain a good deal of plasticity in later forms. Thus, for example, the jugal is reduced or absent in the Monotremata and Insectivora, while, in the Didelphimorphia and Hyracoidea, it becomes so long that it actually contributes to the jaw articulation. It is likely that there is a strong correlation here with the development of the masseters and lateral jaw movements. So, for example, the jugals are particularly stout and well developed in the Rodentia, while strongly reduced in groups that do not chew or gnaw in the way of rodents.

# What Makes a Difference?

The jugal is an interesting exercise because our information is good enough that we can attack issues such as: what has really made a difference in the evolution of this bone? We can make a short list as follows:

1. transformation from a sclerotic ring element to a circumorbital bone in contact with other dermal bones;

2. stabilization on the skull, probably by a relationship to the maxilla (recall that the reorganization of the maxilla in actinopterygians is associated with destabilization of the jugal);

3. loss of contact with the preopercular and contact with the quadratojugal and squamosal. This (a) may have been associated with a duplication of the jugal and (b) seems to have introduced some degree of instability in the posterior connections of the jugal, as seen in the anapsids;

4. stabilization of the jugal on the ventral margin of the skull in the reptilomorphs, which, oddly enough, seems to be associated with fixing its position relative to the orbit (compare the condition in the temnospondyls);

5. fenestration of the skull, resolving the posterior connection in favor of the quadratojugal, in diapsids, or the squamosal, in synapsids;

6. a number of, often homoplastic, changes in form related to vegetarianism without much real change in the underlying osteological relationships;

7. gradual specialization and fixation of the jugal as an important element of the zygomatic arch (note that this results in loss of the palatal contact);

8. a growing functional interdependence on the masseter musculature, with reduction or loss of the jugal associated with loss or reduction of this musculature.

It is hard to derive too much guidance from these generalizations. However, it does seem, once again, that the classical anatomists were correct. As in the business world, one's contacts make all the difference. It takes a very significant functional reorganization to disturb the relative stability of the fundamental osteological relationships. And, as we first observed in the premaxilla, in increased number of separate contacts results in progressive stabilization.

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# Dermal Bones: The Palatal Series: Palatines

| Bones | Dermal Bones | Palatal Series |
|---|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Facial Series**<br>Mandibular Series<br>**Opercular Series**<br>Orbital Series<br>Palatal Series<br>**References** | Palatines |

**Anatomy**: The palatines are dermal bones in the mid-palate. They are derived from neural crest ectoderm, like many other dermal bones. As has become customary, we will begin our tour with a visit to Bob, the Basal Amniote. **Figure 1**. This time, Bob is shown in palatal view, i.e., looking at the roof of Bob's mouth with the entire lower jaw removed. Bob, as usual, has the Standard Condition. In this case, the Standard Condition means that the palatine contacts the maxilla broadly, along almost its entire posterior length. This is a very important landmark, since the palatines almost *never* lose contact with the maxilla. On the anterior section, the palatines lose contact with the maxilla and form the edge of the internal nasal openings, the choanae. Medially, the palatines contact the vomers and the pterygoid. Posteriorly, they terminate at the ectopterygoid which, despite the name, seem to have developed as one of several dermal bones on the edges of the palate. That is, the ectopterygoids may be serially homologous with the palatines.

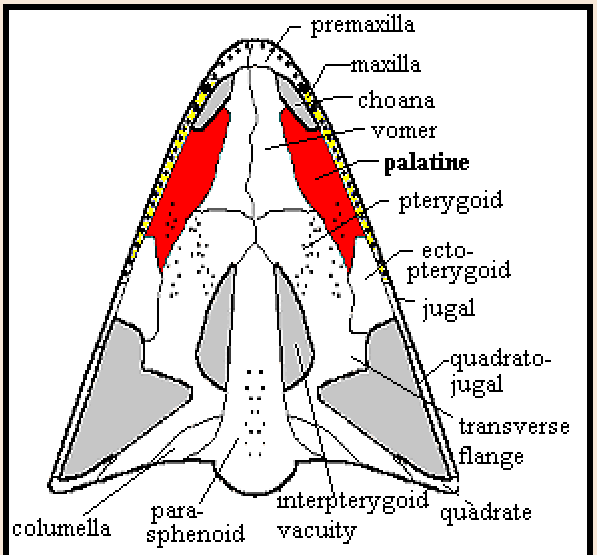

**Figure 1. Generalized basal amniote showing "standard" condition of palatines**

Many of the variations on the Standard Condition in more derived tetrapods involve moving the bone more posteriorly. In this case, the ectopterygoids tend to be reduced and the posteromedial edge of the palatine comes to rest on the transverse flange of the pterygoid. The posterior movement of the palatines may be associated with elongation of the anterior jaw. In this case, the maxilla itself develops its own medial flange anterior to the choana and the area between the posterior edge of the choanae and the transverse flange is compressed.

Another frequent variation, particularly in basal forms occurs when the palatine develops a tooth-bearing marginal ridge in apparent serial homology with the maxilla. In some sarcopterygians, for example, the palatines actually bear the larger marginal teeth and the maxilla's tooth-bearing role is "marginalized." On the other side, several different lineages have developed secondary bony palates in which the palatines overgrow the central bones and meet medially.

**Functions:** As mentioned above, the palatines have an extraordinarily stable association with the posterior maxilla. This surely has some important functional correlate, but it is not easy to see what this might be. It does seem that the palatines are associated with the following special functions.

(a) *The lateral roof of the palate*: the first and most obvious function is that the palatines for part of the roof of the palate.

(b) *Secondary palate*: as mentioned above, several very different lineages, including crocodiles and mammals have gone further and adapted the palatines as an important element of a full secondary palate, separating the business of breathing from the business of eating.

(c) *Margin of the choana*. In choanates, the palatines are strongly associated with the border of the choana. The exact relationship is variable. As we will see, the interaction in, for example, mammals can become quite complex.

(d) *Tooth bearing*: There are some clear advantages to having big teeth on an interior bone, since the tooth-bearing structure can be supported on both sides. In fact. it is harder to guess why this function was generally abandoned than why it was adopted.

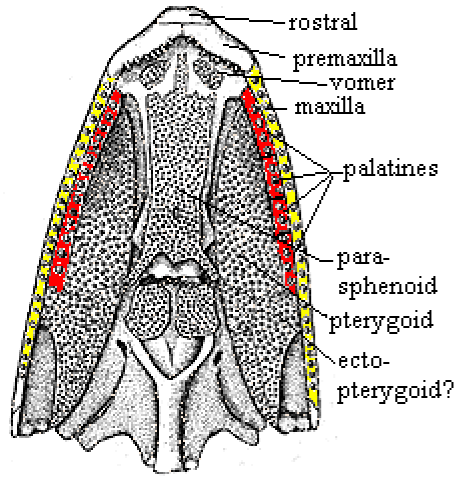

**Figure 2. Palate of Mimia. Modified from Carroll (1988)**

**Phylogeny:** Unlike many of the obscure bones in this section, there is an enormous amount of easily accessible data on the phylogenetic vagaries of the palatines. Obviously, no vertebrate has palatines until dermal bones appear on the palate. Presently, the earliest reasonably well-known fish palate is from *Mimia*, an early actinopterygian from the Late Devonian Gogo of Australia. The arrangement in *Mimia* is weird, but recognizable. *See* **Figure 2.** *Mimia* has no less than 8 palatines, 4 serial homologues on each side. They are all marginal, tooth-bearing bones with no detectable roofing function. The lateral roofing bone is, instead, the pterygoid. The center of the palate is dominate by a broad, tooth-bearing braincase element, the parasphenoid.

A plate-like dermal bone forming the rim of the adductor chamber in the posterior corners is identified as the ectopterygoid. However, in view of later developments, it may be that the ectopterygoid is actually derived from one of the posterior palatines. In modern actinopterygian fish, as in tetrapods, there is only one palatine per side, and it bears no teeth. The ectopterygoid is immediately posterior and is likewise toothless. However, in sarcopterygians such as *Eusthenopteron*, a fish close to the tetrapod line, *both* bones bear marginal teeth. Thus, the palatine of tetrapods and actinopterygians is probably the same bone. However, the tetrapod ectopterygoid is likely derived from one of the ancestral palatine serial homologues. Whether this is homologous to the ectopterygoid of modern fish is unclear.

By the level of *Eusthenopteron* and *Ichthyostega,* the palatines already approach the Standard Condition. Both the palatines and the ectopterygoids retain their raised marginal dentition. However, they both have developed substantial roofing processes into the palate. The parasphenoid has retreated, and the pterygoid has become the main roofing bone. The marginal palatine ridge curves inward at the choanae, similar to the Standard Condition except for the large tooth-bearing ridge. The same condition, with minor variations, applies to all of the basal tetrapods, including the temnospondyls. However, in temnospondyls, the interpterygoid vacuities are sometimes so large that the pterygoids are edged out, and the palatines border directly on the vacuities. See, for example the figure at Thoosuchinae.

Lissamphibia are, as usual, so strange that it is not easy to determine what has happened. Oddly, Caecilians make the most sense. As the figure at *Eocaecilia* shows, this Jurassic form has essentially the Standard Condition, apparently as with other microsaurs. In modern caecilians, the maxilla has developed its own roofing process and the palatines are pushed inward, but still retain large teeth (not merely denticles). In salamanders, the bone is simply lost -- possibly fused with the vomers as is asserted to be the case in *Karaurus*. In frogs, the palatine is retained, but only as a slight rim around the huge vacuity on each side of the braincase bones of the central palate.

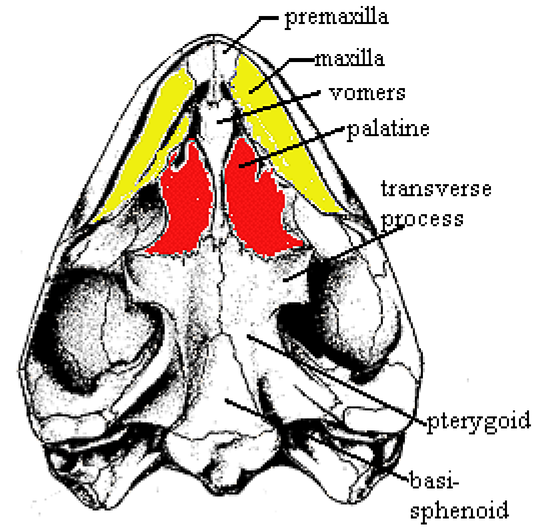

Figure 3. Plesiochelys, an Upper Jurassic turtle in palatal view. Modified from Carroll (1988).

Back on the main line of tetrapod evolution, we have reached the level of Bob. Most forms between anthracosaurs and the Sauria have the Standard Condition, except that there is a persistent tendency to reduce or fuse the ectopterygoid with the palatines. As mentioned above, this is associated with compression of the middle palate, with the palatines pressed back on the transverse process of the pterygoid. Turtles, whether considered as parareptiles or aberrant diapsids, show this condition to a marked degree. **Figure 3** shows an example. Note that the maxillae have developed their own roofing processes, typical of more advanced tetrapods, and that the palatines are approaching the midline of the palate -- typical of chewing or diving animals that need a strong seal to separate the breathing and eating functions. All basal diapsids show either the Standard Condition or one of the same variations exhibited by turtles.

Most Sauropterygia and other lepidosauromorphs are likewise unremarkable. One interesting study are the placodonts. The placodont palate bears a rather striking resemblance to the turtle palate except that both the palatines and the maxillae bear huge crushing teeth. However, given the limited range of variation seen in this entire phylogenetic neighborhood, the resemblance could easily be a matter of functional similarity leading to convergent results. The absence of the basisphenoid from the palate of *Placodus* is also a probably significant difference.

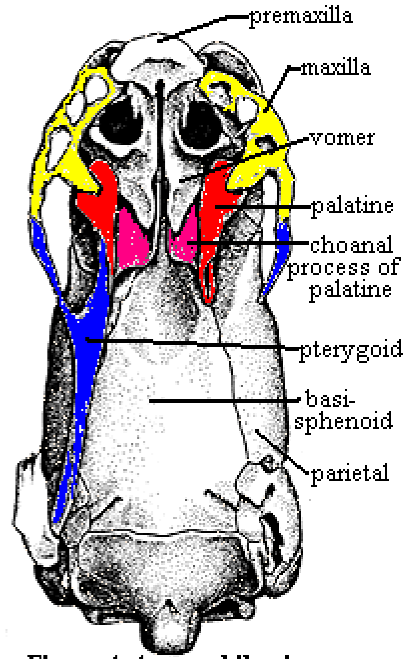

Figure 4. Anomochilus in palatal view. Modified from Cundall & Rossman (1993).

Snakes, too are a notable exception to the rule. In fact anomalepidid and some boid snakes are the only vertebrates in which the palatines lose contact with the maxilla. *Anomochilus* (**Figure 4**, modified from Cundall & Rossman (1993)) shows a transitional form. Note how, even in this highly derived design, the basic relationships of palatine, vomer, pterygoid and maxilla are preserved, as is the basic architecture of the choana, between the vomers and the choanal process of the palatines.

In archosauromorphs, the pattern is a bit different from the Standard Condition in that the palatines are almost always in contact with the transverse flange of the pterygoid. Consequently, the ectopterygoids are pushed out of the way and become fairly marginal elements. At the same time, many crocodylomorphs developed secondary palates which, as mentioned above, tends to involve expanding the palatines medially to meet at the midline. Since the palatines tended to move posteriorly and medially, the pterygoids could not reach the anterior palate. Consequently, crocs tend to elaborate the roofing processes of the premaxilla, anterior maxilla and the vomers.

With the dinosaurs, things begin to get decidedly more strange. In ornithischians, the medial migration of the tooth rows completes the separation of the palatines from the anterior palate elements. **Figure 5** (modified from Weishampel & Horner, 1990)) shows the palate of the hadrosaur, *Brachylophosaurus*. Here, the pterygoid has been pushed back so far posteriorly that a portion actually appears as an element of the occipital wall at the back of the skull.

Theropods, too have moved the pterygoid to the back of the palate and the vomer is recruited as the central bone of the anterior and middle palate. However, the transformation is not as drastic as in the plant eaters. Even the pattern in the Mesozoic bird, *Ichthyornis* is still recognizable, with effort. Modern, neornithine birds (**Figure 6**), however, are difficult to make out based on the Standard Condition. In fact, the avian palate looks quite a bit like an ornithischian palate

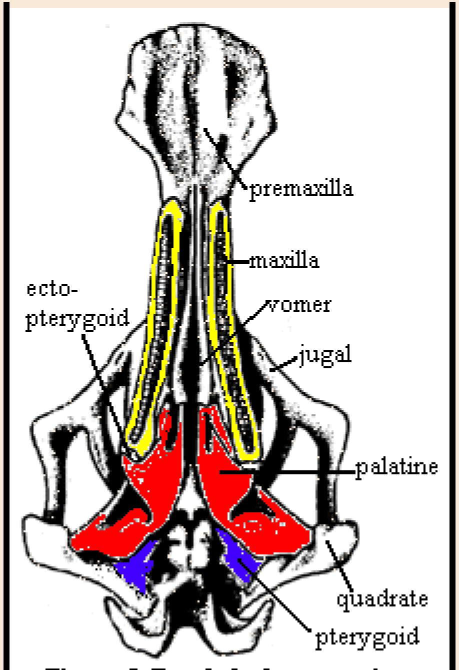

**Figure 5. Brachylophosaurus in palatal view. Modified from Weishampel & Horner (1990)**

except that (a) most of the pieces are fused together and (b) the elements are stretched out along the upper jaw to an even greater degree.

Basal synapsids are but one step removed from Bob, and thus show the Standard Condition. In fact, the anterior palate of early proto-mammals looks a bit like a turtle or a pareiasaur. However there is no maxillary roofing process and the palatines take up the slack in, for example, *Ennatosaurus*. This resemblance is increased in the therapsids which *do* develop roofing processes of the maxilla.

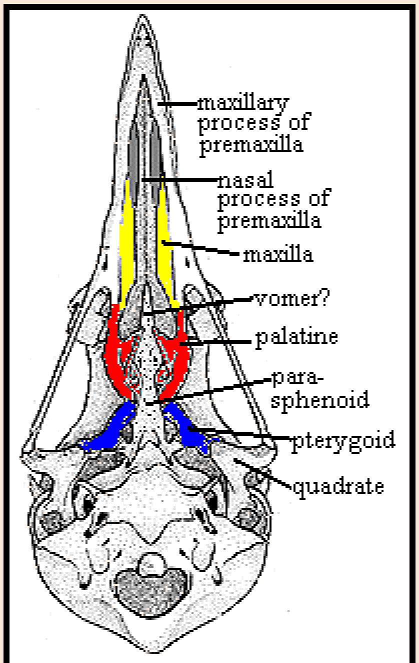

**Figure 6. Columba (dove) in palatal view. Modified from Proctor & Lynch (1993).**

The critical change occurs at the level of *Thrinaxodon*. The palate of *Thrinaxodon* can be seen "live" at Thrinaxodon CAT Scan Rendering or in a more conventional diagram at Estes, R., 1961 (figure 2). What is happening here is that the palatine has developed a process which is anterior to the choana. In basal cynodonts, this amounts to no more than a little ridge of bone running along the labial edge of the choana. By the level of *Thrinaxodon*, this ridge has developed its own roofing process which has grown back over the choana as a sort of reflected process of the palatine. In fact, it begins to grow back over the palatine itself. **Figure 7** shows the general configuration in a slightly more derived form in the eucynodont, *Probainognathus*. This species is well on its way to developing a full secondary palate. Both the maxillary and premaxillary roofing processes and the reflected process of the palatines are continuous and meet their opposite numbers at the midline. The choana is completely covered by the reflected palatine at least as far as the level of the orbit.

This is the basic mammalian pattern. The therian mammals merely extend this pattern. The roofing processes of the maxillae grow posteriorly and medially along the full length of the maxilla. The "reflected" palatines are then reduced to smaller, medial elements around the level of the mid-orbit. This simplicity is deceiving, since the palatine then develops a complex dorsal process which contributes to the definition of the nasal cavity. The original palatine is lost and the pterygoid is positioned more posteriorly. In some forms, notably primates, the remaining palatine elements fuse with the maxillae to form a continuous bony secondary palate.

**Discussion:** The palatine is an interesting contrast to the premaxilla. The premaxilla has a number of quite different and exacting functional roles which froze its general form and position quite early in tetrapod evolution. The palatine, by contrast, has far fewer constraints, particularly in those lineages in which it no longer provides a tooth-bearing ridge. Nevertheless it maintains strong contact with the maxilla in virtually all vertebrates. This consistency is hard to understand in

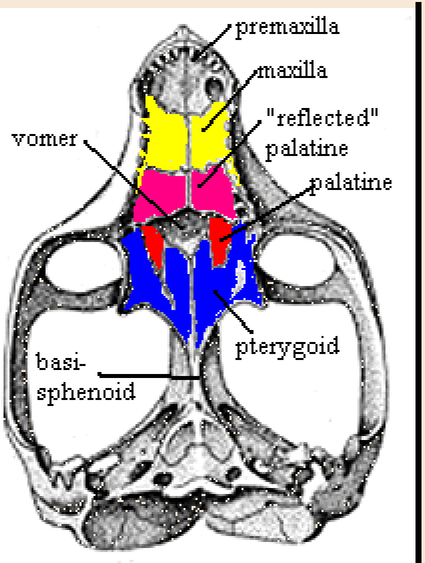

**Figure 7. Probainognathus in palatal view. Modified from Carroll (1988)**

functional terms, although it makes reasonably good sense from an embryological perspective.

Another interesting feature is the tendency of both the maxilla and premaxilla to develop their own roofing structures which "compete" with the palatines. This suggests that the maxilla has always had this capability and that the original series of palatines were derived from an earlier generation of maxillary roofing processes. To take the chain of speculation one step further, this suggests that the maxilla itself was originally a flat dermal plate of some kind, possibly homologous to the superognathal of placoderms. ATW 010417.

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**Links:** muscle actions; II. Osteology. 5b. 5. The Palatine Bone. Gray, Henry. 1918. Anatomy of the Human Body.; Dept of Anth: Palatine Page; Skull of the Sea Turtle; PPT Slide.

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# The Ear: Overview (1)

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  References

### The Ear and Hearing (Overview)

Why, you may be asking, is there a section on hearing in Bones? In part, it is here because there was no other reasonable place to put it. However, the choice is not entirely random. Many of the more confusing, difficult and significant osteological debates in paleontology and evolution have surrounded the collection of mechanoreceptors concentrated in the ear. For those who have been through Carroll (1988) or some equivalent text, consider how much debate and effort has gone into issues such as (a) the number and shape of the semicircular canals in jawless fishes, (b) the presence or absence of an otic notch in stem tetrapods, (c) the embayment of the quadrate or squamosal to support a tympanic membrane in various amniote lineages, (d) the shape, mass and orientation of the stapes as a sound conductor, or (e) the transformation of the post-dentary jaw bones into auditory ossicles in early mammals. All of these issues are significantly related to the ear and its sensory functions. Therefore, it makes some sense to digress into the anatomy and physiology of the ear as a phylogenetic and functional unit.

With our customary functional and phylogenetic approach, we will begin with a brief overview of the functions of the ear. After this we will approach the subject from the inside out, beginning with the oldest and most basic functional units of mechanoreception in the inner ear and moving on to progressively higher levels of organization and more recent evolutionary developments.

# I. The Senses of the Ear

Some text writers (as well as earlier portions of these Notes) have persisted in the naive description of the ear as the sensory home of "hearing.". In fact, the ear is unique in being the center of at least three senses, each associated with a different set of physically separate receptors: (1) hearing, (2) angular acceleration, and (3) gravitational orientation (or linear acceleration). Probably there is at least one more "sense" involving (4) detection of low frequency vibrations, but it seems to overlap with the gravitational sense in the macular receptors (explained below). Much of the detailed physiology is poorly understood, even today. Furthermore, it appears that these senses do not merely supply information, but also elicit hard-wired reflex responses without going through the brain at all.

# II. The Sensory Units

## A. The Hair Cell

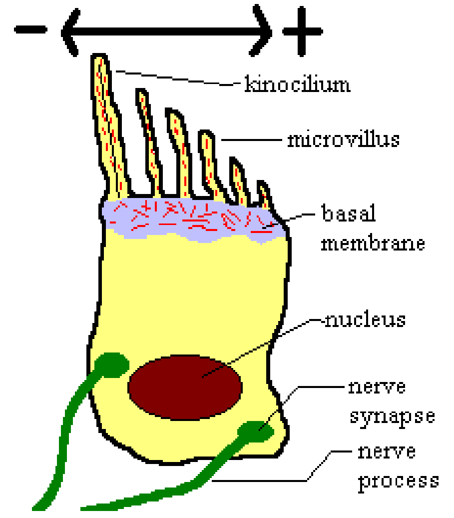


**Fig. 1. Hair cell. Red lines are actin filaments. Deformation of villi toward the left decrease rate of signals to nerves. Deformation to right increases signal rate.**

All of the senses in the ear, as well as the lateral line system of fish, are based on **mechanosensation**: the detection of physical displacement. The **hair cell** is the basic cellular unit of mechanosensation. It is characterized by the presence of oriented **microvilli** and a single **kinocilium**. The microvilli are stiffened by the presence of numerous oriented contractile **actin** fibers and are embedded in a basement membrane which includes randomly-oriented actin. When the microvilli are deformed by mechanical pressure or vibration, the cell increases or decreases the rate at which it sends an electrical signal to the nerve cells with which it is coupled. The "stiffness" of the microvilli, and hence their degree of response to a deforming force, can be regulated by the contractile state of the actin filaments.

Frequently, hair cells are highly directional. If the villi are bent on one direction, the rate of discharge increases. In the opposite direction, the rate decreases. If the villi are deformed at right angles to this axis (into or out of your screen in Figure 1), there is no change in the signal rate.

## B. The Neuromast Organ

neuromast organ

In living organisms, the hair cells are organized into **neuromast organs**. The neuromast organ consists of hair cells and support cells embedded in a gelatinous *cupula*. The hair cells within the neuromast are sometimes oriented in opposite directions, but in only in those two directions. If Figure 2 represented such a case, no hair cells would be oriented into or out of the plane of the screen.

The cupula, particularly in the macular, "gravitational" receptors, may bear **otoconia**, also known as **otoliths**. These are tiny **[1]** mineral grains, usually calcium carbonate. The otoliths supply the mass necessary to deform the entire cupula in response to linear acceleration or orientation in a gravity field. Some fishes use mineral grains from the environment for this purpose, and a few taxa manufacture calcium phosphate otoliths.

# III. The Inner Ear

The inner ear is located a cavity formed by the prootic or equivalent portion of the braincase in close association with the otic region of the brain and the VIIIth cranial nerve. It contains the **vestibular apparatus** which is shown, in extremely generalized form, in Figure 3. The vestibular apparatus us suspended by ligaments to isolate it from random vibrations in the skull. The vestibular apparatus is geometrically quite variable. However, it can be broken down into functionally constant regions, if at the risk of some over-simplification.

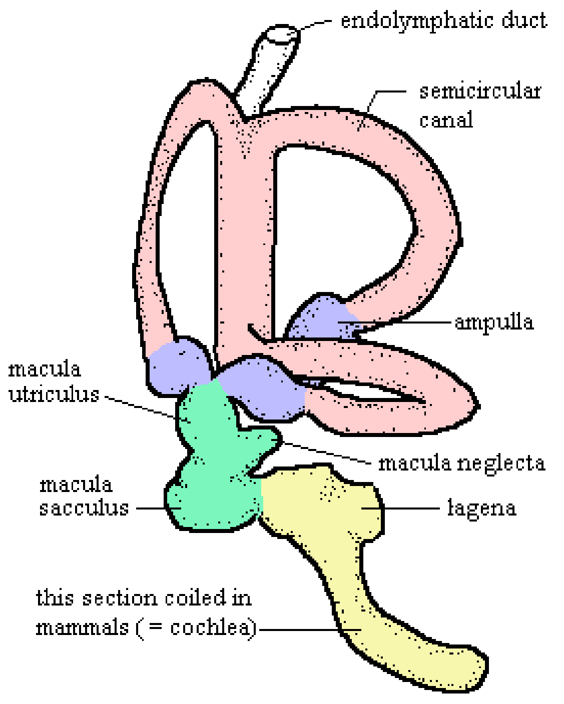


**Fig. 3. Vestibular apparatus of inner ear. Neuromast structures are found in the ampullary organs (blue), macular regions (green), and lagena (yellow).**

## A. The Endolymphatic duct (white area)

The vestibular apparatus must have some method of equalizing pressure, or it would explode during changes in pressure. I am therefore a bit skeptical when it is described as a closed system. However, this style of pressure regulation is particularly important in aquatic vertebrates, since they must respond to rapid changes in external pressure with water depth. So, for example, in elasmobranchs, the inner ear is explicitly connected to the environment via the endolymphatic duct.

## B. The Labyrinth (red and blue areas)

The **labyrinth** is composed of the **semicircular canals** (SCCs) and associated **ampullae**. In almost all vertebrates, there are three SCCs (*but see, e.g.*, *Ateleaspis*), each oriented roughly 90 degrees from the other two, such that they correspond to the three spatial planes. The SCCs themselves have no sensory role. They are simply fluid-filled structures. Their importance lies in how they slosh.

Imagine that Figure 3 is quickly rotated clockwise. For the most part, there will be no net movement of the fluid in two of the SCCs (the horizontal canal and the canal directed into the screen) relative to the walls of these canals. However, in the SCC facing to the right, the inertia of the fluid will cause it to flow counter-clockwise relative to the walls of this canal.

This current will move through the **ampulla** at the bottom of the SCC. Each ampula contains a *crista*, a very large neuromast organ, which stretches across the ampulla. When the fluid in the SCC flows, it creates a shearing force on the cupula. The hair cells communicate this movement to the brain. Thus, the ampulary receptors are sensitive to rotation or, more generally, angular acceleration. Because of the geometry of the SCCs, the deformation signals in the three ampulae can be combined to determine the rate and direction of rotation.

## C. The Maculae (green area)

The **maculae** consist of rather shapeless compartments known as the **sacculus** and **utriculus**. elasmobranchs and perhaps other groups posses a third macula, the **macula neglecta**. The macular neuromast organs bear otoliths, as described above. Thus, they are sensitive to orientation in a gravity field or, more generally, to linear acceleration. The neuromasts in the sacculus are apparently oriented oppositely from those in the utriculus. However the geometry of these spaces is sufficiently complex that there is no simple correspondence between the macula and any particular orientation, at least in humans.

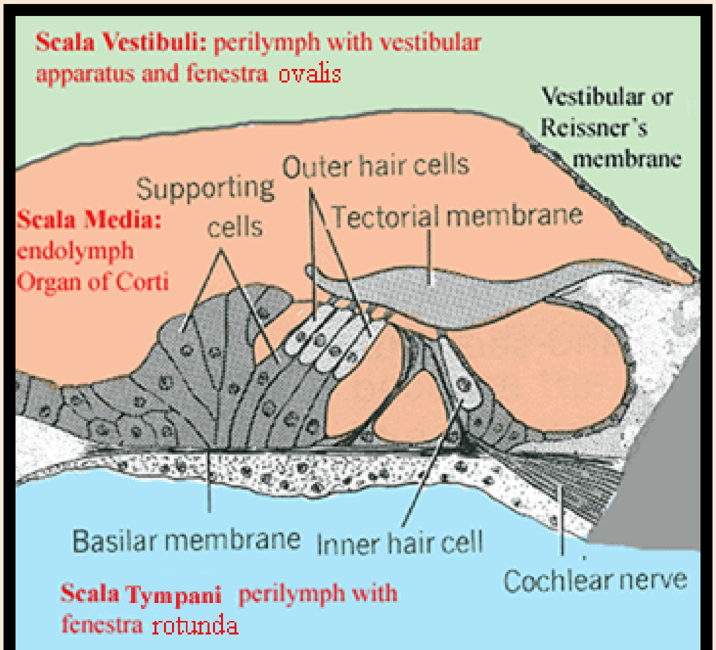
In addition, the macular receptors are involved in the perception of low frequency sound. Exactly how this works seems to be unsettled. The macular receptors are the primary organ of hearing in fishes, where the inner ear may be coupled to vibrations in the medium through a variety of mechanisms discussed below. In amphibians the inner ear is mechanically coupled to the pectoral girdle through the **operculum**. This mechanical coupling results in a "seismic" sense, which detects low-frequency vibrations in the substrate, such as those caused by platoons of loutish undergraduates dragged out on field trips to collect amphibians.

Even in humans, at least some macular hair cells are involved in the perception of loud, low-frequency sounds. These inputs may, according to one recent story, have deep psychological effects, presumably because macular inputs can completely bypass higher brain processing. Think, for example, of the effects of thunder, marching, resonant choral singing, of singing alone (which is internally very loud and resonates in the skull), or of a roaring or growling animal. Sounds which are deep enough or loud enough to literally rattle your bones are generally perceived differently from normal sounds and often have irrationally strong psychological impacts. This appears to be tied to the unusual wiring of this ancient, auxiliary sense provided by the macular receptors, which may bypass the higher processing centers of the brain.

## D. The Lagena (yellow area)

The *lagena*, as a structure, is almost as ancient as the labyrinth. However, it appears as just another macular compartment in fish and early tetrapods. An elongated distal process of the lagena is a common character of all of the amniote lineages, so we may suppose that the development of this structure predated, or was coincident with, the amniote divergence. In mammals, the lagena is coiled and is referred to as the **cochlea**. The lagena is the site of hearing, as that term is generally understood.

The physiological details of the auditory sense are somewhat beyond the scope of this essay. However, since the original version of this page was written, we have learned that some aspects of this exceedingly technical subject are germane to paleontology. This horrifying discovery was revealed to us through the work of Dr. Zhe-Xi Luo. See, *e.g.* Luo & Eastman (1995). We are thus presented with an acute moral dilemma. On the one hand, Dr. Luo's work is important. On the other hand, this stuff takes anatomical obscurity to a whole new level. Now, the astute (or simply cynical) reader may already have observed that moral considerations rarely seem to slow us down much. True. But Dr. Luo has also said some very kind things about this site, and flattery is hard to come by. Accordingly, we will -- not for the first time, to be sure -- allow the dictates of our bloated ego to overcome our better pedagogical judgment and so attempt a brief explanation.



Semi-schematic view of cochlear apparatus. Adapted from Hildebrand (1974).

The illustrations in this section show the **vestibular apparatus** (the structures in Figure 3, taken as a whole) as if they simply floated in the perilymph of the inner ear. For the bulk of the vestibular apparatus, that is approximately true, although the general orientation is maintained by loose ligamentous connections. However, around the lagena (or cochlea) things are a bit more organized. Here the soft tissue lining the inner ear narrows to form a vessel, the **perilymphatic duct**. The perilymphatic duct runs along one side of the lagena for its entire length, from proximal (near the rest of the vestibular apparatus) to distal (away from the vestibule).

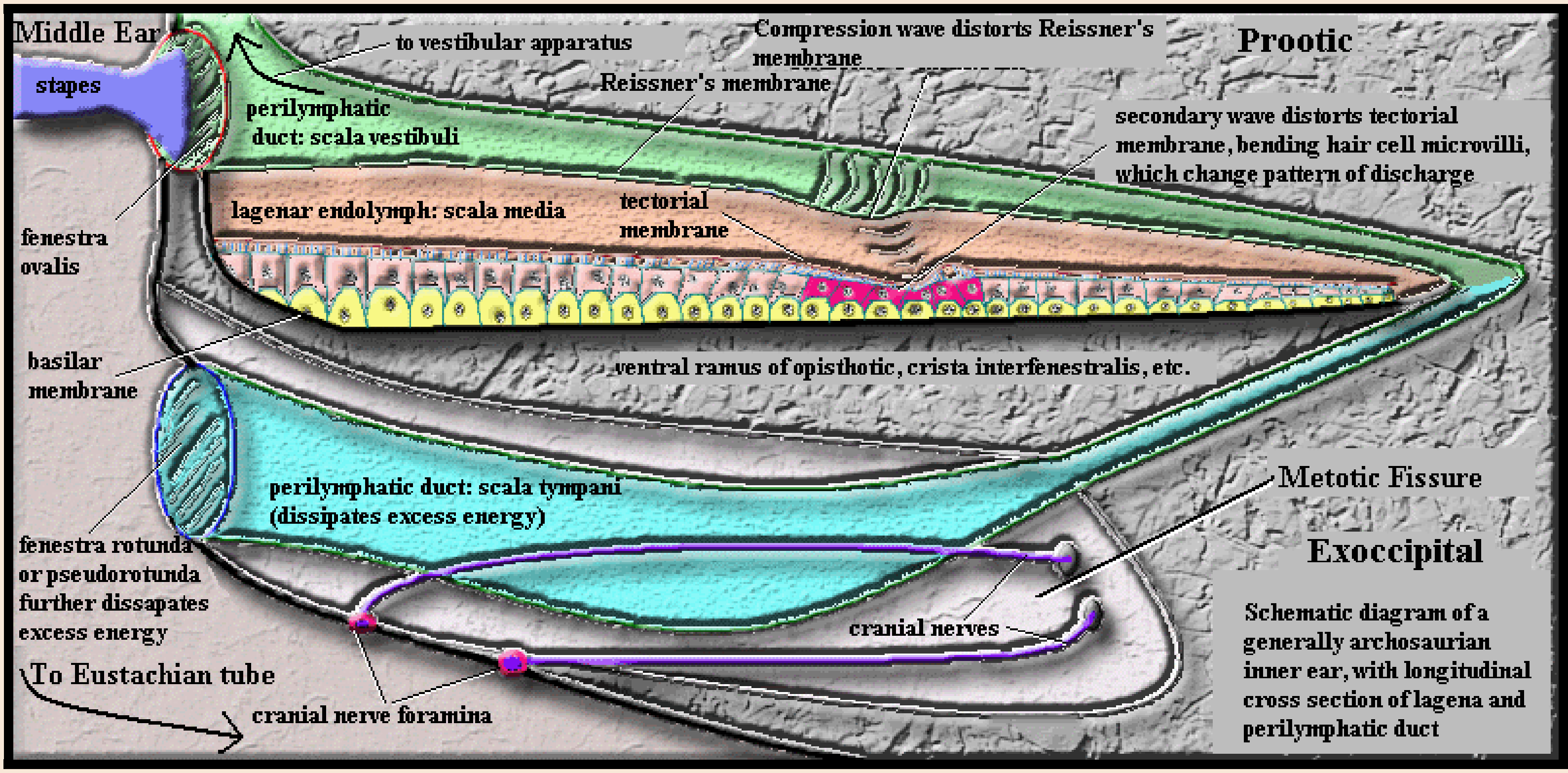
Looking only at this region, we may consider the inner ear to consist of two elongate, fluid compartments, running side by side. The image shows a cross-section of the structure. Ignore the blue area for the moment, and imagine the orange and green areas as tubes which run into and out of the screen. The green area is the perilymphatic duct. Since it is confluent with the perilymph around the rest of the vestibular apparatus, this compartment is called the *scala vestibuli*. The orange area is the endolymph-filled body of the lagena. It is referred to as the *scala media*. These two compartments are separated only by a thin, flexible membrane: the vestibular or **Reissner's membrane**.

Inside the lagena, another membrane runs the length of the *scala media*. One side of this membrane is anchored on a lateral wall of the lagena, but the other side floats more or less freely in the middle of the lagenar tube. This is the **tectorial membrane**. The free side of the tectorial membrane is in contact with the microvilli of a column of hair cells, very much the same as the hair cells in a lateral line system. These hair cells are mounted on supporting cells, and eventually anchored in a **basilar membrane** on the side of the lagena opposite the perilymphatic duct. For our purposes, we may consider the basilar membrane as a fixed, rigid, and inflexible platform. This is nearly correct, particularly in reptiles.

# E. How We Hear

So much for structure. How does it all work? Know that matters are so arranged that the base of the perilymphatic duct is the part of the inner ear sitting on top of the *fenestra ovalis*. We will discuss this structure in excruciating detail below. Briefly, the *fenestra ovalis* is the small membrane "window" between the inner and middle ears. Sound is conducted through the middle ear via the **stapes** or **columella** (both are ear ossicles derived from the hyomandibular). The stapes has a footplate which fits over the *fenestra ovalis*. Sound vibrations in the stapes thus cause the footplate to rattle the window of the *fenestra ovalis*. Because the open end of the perilymphatic duct is sitting on the *fenestra ovalis*, each jerk of the membrane in the *fenestra* causes a compression wave to go shooting down the length of the scala vestibuli, which is side-by-side with the thin Reissner's membrane of the lagena. As each pulse moves along the perilymphatic duct, it pushes on the thin fabric of Reissner's membrane. Like running a finger along the side of a water balloon, this impulse generates a complex wave in the lagena. The internal wave in the lagena causes the free end of the tectorial membrane to wobble. Since the tectorial membrane is connected to the thin microvilli of hair cells which are essentially fixed, the microvilli experience shear -- exactly as in a lateral line neuromast, and with the same result.

The linear extent of the system also allows pitch discrimination. Exactly how this works is still not completely understood and may differ somewhat among lizards, crocs, dinosaurs, and mammals, each of which independently evolved this system **[2]**. Relatively recently, it has been learned that the hair cell response is **not** the signal which is passed directly to the brain as sound in mammals. Rather, the outer hair cells control a complex and poorly-understood system of positive and negative mechanical feedback systems, the net effect of which is to sort incident vibrations by frequency. Hair cells near the base of the cochlea respond to high-frequency sounds, while cells near the end of the cochlea respond to low frequencies. Outer hair cells which respond to the appropriate frequency reduce the propagation velocity of the membrane vibration to zero and maximize its amplitude. In effect, they trade the translational kinetic energy of a traveling wave for more displacement energy (i.e. amplitude) in a standing wave. It is this coordinated, high-amplitude displacement which registers on the inner hair cells, and the inner hair cells tell the brain about sound of a particular frequency.



Schematic diagram of a generally archosaurian inner ear, with longitudinal cross section of lagena and perilymphatic duct

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# The Ear: Overview (2)

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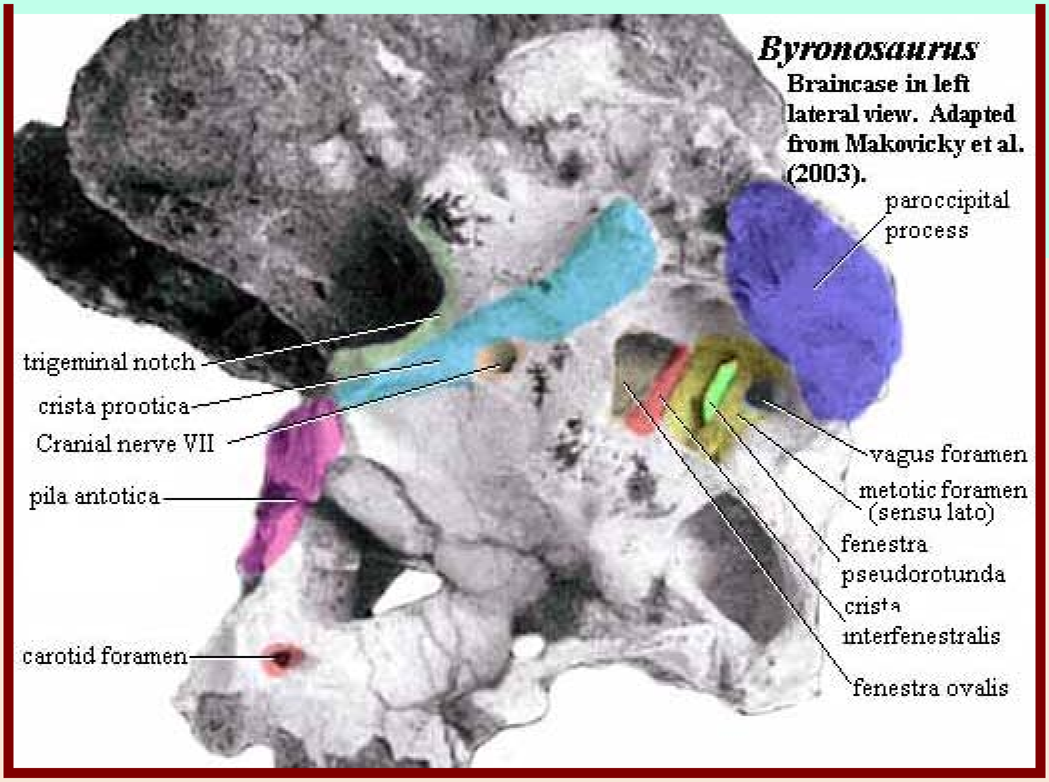
## F. Heard Enough? The *Scala tympani*.

What about the blue area, the *scala tympani*? One design problem for the perilymphatic duct is that it is very small, and entirely too efficient at capturing the energy generated at the *fenestra ovalis*. If the perilymphatic duct simply hit a dead end, any sufficiently loud sound would reflect back along the duct, causing untoward interference waves -- or the perilymphatic duct might simply explode. To prevent this, the duct has to dissipate excess sound energy which has reached the end of the lagena. Physics allows us two ways to do this, both of which are also used by university administrations to control the excess energies of noisy faculty committees. Either (a) the noisy vibrations (or faculty) are allowed to bounce around randomly in an enclosed space, until their excess energy is used up in mutual interference and frictional heat, or else (b) the vibrations are used coherently to perform some important-looking, but actually useless work, such as pushing on elastic membranes or piles of reporting forms, until they are exhausted.

The *scala tympani* uses both approaches, to different degrees in different lineages. Basal reptiles, even those without an elongate lagena, simply run the perilymph into a large sinus in the brain or in the metotic fissure between the otic capsules, where compression waves bounce around and dissipate like echoes in a cavern. Other organisms tend to combine this strategy with an extension of the perilymphatic duct which runs out through the metotic foramen and ends at an elastic membrane, the *fenestra rotunda*. Since the *fenestra rotunda* is, properly speaking, a specialized mammalian structure, the membrane is frequently referred to as the *fenestra pseudorotunda* in reptiles. This fenestra faces out into some effectively infinite pressure sink, such a Eustachian tube connected to the pharynx.

Mammals, as we have learned to expect, employ a bizarre and pointlessly complicated variation on the straightforward and logical reptilian plan. The mammalian lagena, called a cochlea, is spiral-shaped and drills into the surrounding bone like a corkscrew opening some debased Australian vintage stoppered with bone. The perilymphatic duct has, of course, no choice but to follow along. The problem is that, at the end of the spiral tunnel, the perilymphatic duct finds itself deep inside the temporal bone, with no place to go. Perhaps realizing its tactical error, the duct sheepishly turns around and stumbles back out the way it came, but on the other side of the cochlea, following the basilar membrane.

# G. Anatomical Correlates of the Inner Ear in Reptiles



***Byronosaurus***
**Braincase in left lateral view. Adapted from Makovicky et al. (2003).**

Sometimes we are lucky enough to find nice fossil impressions of these inner ear structures. Then again, if we were generally that lucky, we would be living on a yacht off some notorious Caribbean tax haven, surrounded by fawning sycophants and unimaginable luxuries, enjoying the myriad fruits of our multiple lottery winnings. Fate is rarely so generous. We have to make do with bones for the most part. Fortunately, there are some hard tissue correlates which can sometimes give us an idea of what was going on inside the inner ear.

One such outward sign is the *crista interfenestralis*, shown in the braincase of the troodont, *Byronosaurus*. Makovicky *et al*. (2003). In the image, we have included some other landmarks which may be familiar from our discussion of the generalized amniote braincase. However, the point of the image is the *crista interfenestralis* which divides the inner ear into two parts. Other structures (or the same structure with other names) may perform the same job. For example, in the crurotarsan *Batrachotomus*, shown below, the inner ear is divided by a ventral ramus of the opisthotic (dark blue). The *crista interfenestralis* and the ventral ramus of the opisthotic may, in fact, be the same thing.

However the inner ear is divided, the osteological result is the same. On the anterior side is the *fenestra ovalis*, where the columella (or stapes or hyomandibular, depending on the taxon and your tastes in nomenclature) makes contact with the inner ear. The *fenestra ovalis* frequently has a triangular shape, as in *Byronosaurus*. In organisms with an elongate lagena, we will observe a long lagenar recess, since the hearing mechanism for these animals requires a fixed basilar membrane and a carefully controlled interface with the perilymphatic duct. Sometimes, too, an additional bone (the *crista vestibuli*) walls off the lagena + perilymphatic duct from the rest of the vestibular apparatus. The functional significance of this wall is probably both structural stability and acoustic insulation. The presence of such a barrier bespeaks a lifestyle which requires both acute hearing and a high degree of pitch discrimination.

On the posterior, *scala tympani* side of things is a whole complex area of foramina which we will refer to as the *metotic foramen*, *sensu lato*. This posterior region requires some energetic sorting out, and we will now set about that task.

Embryologically, the metotic fissure is the gap between the developing otic placodes and the parachordal bars which serve as the foundation for the entire head posterior to the *sella turcica*. All of the cranial nerves exiting the posterior part of the brain exit into this space, particularly, cranial nerves IX, X, XI & XII, as well as some of the important veins which drain the braincase. This is also the space in which the perilymphatic duct

Batrachotomus ventral braincase.  Gower (2002)

terminates, in more primitive vertebrates, with a dead end cistern used to absorb excess noise.  In early development, there's lots of room here.  Only the ventral part is closed off, by the parachordal mesoderm.  So, what happens when, over the course of development (and evolution), the following happen:

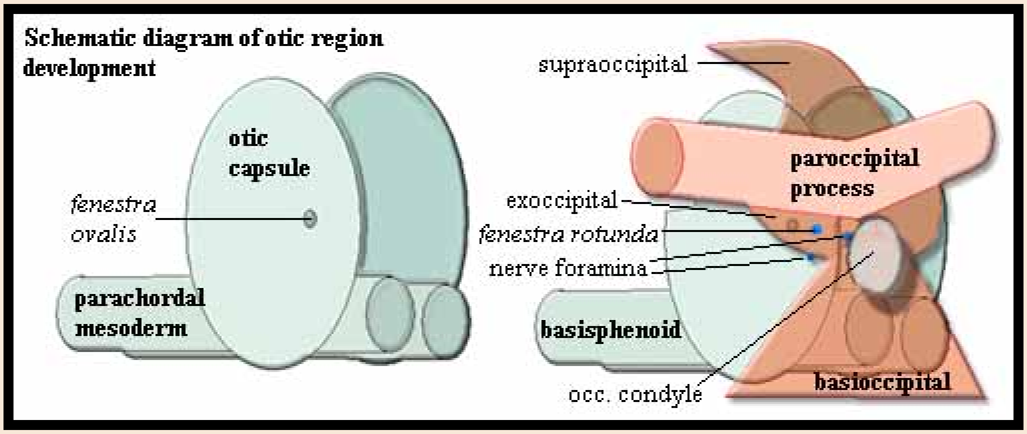
(a) the anterior end is closed by the lateral commisure, the joining of the otic capsules to the brain;

(b) the dorsal part is closed off by various outgrowths of the capsules (the supraoccipital, epiotic, and membranous precursors) as well as the dermal skull bones;

(c) the posterior part is filled up and blocked off by the recruitment of embryonic proto-vertebrae to form the occipital bones; and

(d) everything grows and expands?

What happens is that the animal simply runs out of room.  Everything gets squeezed into a little metotic foramen (the purple area in the figure of *Batrachotomus*).  There's no room for a perilymphatic cistern, so excess pressure has to be relieved some other way -- a *fenestra rotunda* or equivalent.  Initially, at least in an evolutionary sense, everything tries to escape by this same door, the metotic foramen.  Eventually, there's no room for the nerves or veins to exit either, so they find other ways out.  Typically, they develop their own foramina between or around the embryonic neural arches which form the exoccipitals.  The most prominent of these exits is the vagus foramen, homologous to the jugular foramen or "posterior lacerate foramen" of mammals.  Quite often the hypoglossal (XIIth) nerve develops its own exit, the *hypoglossal foramen*.



When most of the nerves, veins and other riff-raff have been evicted, the remnants of the old metotic foramen can begin to relax.  Since it no longer has to accommodate a group of distracting nerves and veins, this fenestra can now specialize to dissipate excess sound energy, usually by pushing a membrane into an external pressure sink, as discussed above.  At this point, we may refer to the metotic foramen as the *fenestra rotunda* -- or, more precisely, as a  fenestra pseudorotunda in reptiles.

# IV. The Middle Ear

The function of the inner ear is, then, to package an enormous amount of information from mechanoreceptors into a form usable by the brain or, in some cases, directly by motor neurons. It transduces various inputs into neural electrical signals. The function of the middle ear and of certain functionally analogous structures is also *signal transduction*. In this case, the signals are transduced from vibrations, usually airborne, to vibrations in the fluid medium of the perilymph in the inner ear. Fish, of course, don't have this problem. The sounds of concern to them are largely water-borne. However terrestrial animals must get vibrational information from the air to the mechanoreceptors in the fluid-filled inner ear.

The principle difficulty here is that water is different from air. The standard textbook explanation invokes density, the implication being that it takes relatively more energy to get a fluid vibrating, simply because the medium is denser. But, even more importantly, air and water are chemically different. The modes, characteristic frequencies, and speed of propagation of vibration differ between the two media. As anyone knows who has tried to hear while diving, most airborne sound is reflected from the surface of a fluid (or dissipated as random heat). This is the difference in acoustic *impedance* which is actually what is invoked in the phrase "*impedance-matching ear*." The design problem for a terrestrial organism is to evolve an ear that transduces vibration from air to fluid over the considerable barrier posed by the difference in impedance.

Figure 4 shows, in very schematic form, how the trick is done. The tympanic membrane receives the airborne vibration. Unlike a fluid surface, it is locally more rigid. Thus it responds as a unit to average air pressure changes over a considerable distance. Much acoustic energy is reflected away still, but the microscopic oscillation of individual air molecules has been traded for a macroscopic and highly coordinated mechanical movement of the membrane surface. Thus, despite a serious loss of total signal energy, the signal to noise ratio is very favorable and the signal energy has been captured in a form available to do mechanical work.

These macroscopic movements of the tympanum are transmitted through the *columella* and *extracolumella* in most sensible tetrapods, or through a Rube Goldberg machine of three weirdly shaped bones in mammals. In either case, the system is in part designed to achieve a high ratio between the area of the tympanum and the area of the *fenestra ovalis*. This achieves an impressive amplification of the signal. The columella is attached to the fenestra ovalis by flexible ligaments which allow the movement of the bone to transmit a corresponding vibration to the fluid surrounding the vestibular apparatus.

[**Speculation:** presumably, the system has also evolved to transmit information about high frequency overtones. A two-dimensional resonator, such as the tympanum, does not simply vibrate in and out as a whole. Overtones are carried as a complex pattern of vibration, with the surface partitioned into different areas moving in different directions. The length of the columella, as well as the projections from its contact with the tympanum, appear to allow it to transmit information about such overtones as *lateral* forces.]

Since water-based fluids are incompressible for all practical purposes, the inner ear also has a second membrane-covered window, the *fenestra rotunda* ("round window") which flexes in the opposite sense from the base plate of the columella (or the stapes in mammals). Pressure changes in the middle ear itself are accommodated through the *Eustachian tube* which communicates with the throat, as discussed in a previous section.

In fish (which have no middle ear) and amphibians, some taxa have developed additional devices for transmitting sound to the inner ear. Some fish, for example, have processes from the swim bladder to the inner ear to transmit airborne vibrations. Others have developed a series of small bones, the Weberian ossicles, which perform the same function. In amphibians, the columella shares the oval window with a second bone, the *operculum*, which communicates by way of an opercular muscle with the pectoral girdle. Apparently, this is the primary route of transmission of the "seismic sense" in basal tetrapods.

# The Outer Ear

Our tour of the vertebrate ear ends with the outer ear, which seems to be fairly uninteresting from a phylogenetic perspective. In mammals, the ear is typically ornamented with a cartilaginous *pinna* (what we colloquially refer to as the "ear"). This optimizes the external channel that sound follows to reach the tympanum, which is referred to as the *external auditory meatus*, so that sound is focused on the tympanic membrane and the directionality of the signal is optimized.

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# Some useful sites:

Hearing in Stegocephalians; Morten Buhl J�rgensen's homepage; What is acoustic impedance?; Surgical Technique of Jean-Bernard CAUSSE, M.D. (1/4); Anatomy and Physiology; Music for the sacculus: A blast from the past; Springer LINK: Pfl�gers Archiv - Abstract Volume 435 Issue 1 (1997) pp 82-90; Grand_Rounds ... Vestibular_Physiology_1992 (very nice, but unillustrated, tour of the human vestibular apparatus); Histology and Microscopic Anatomy of the Ear.

# Specific Bones:

1. Incus

# Notes:

**[1]** Not always tiny. Some coelacanths have very large otoloths for reasons which are not only obscure, but hard to understand on functional grounds.

**[2]** All in the Early Triassic, it would appear -- which is downright odd. Was there something in the nature of the End-Permian extinction which selected for terrestrial vertebrates with pitch discrimination, or at least high-frequency hearing?

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# The Incus

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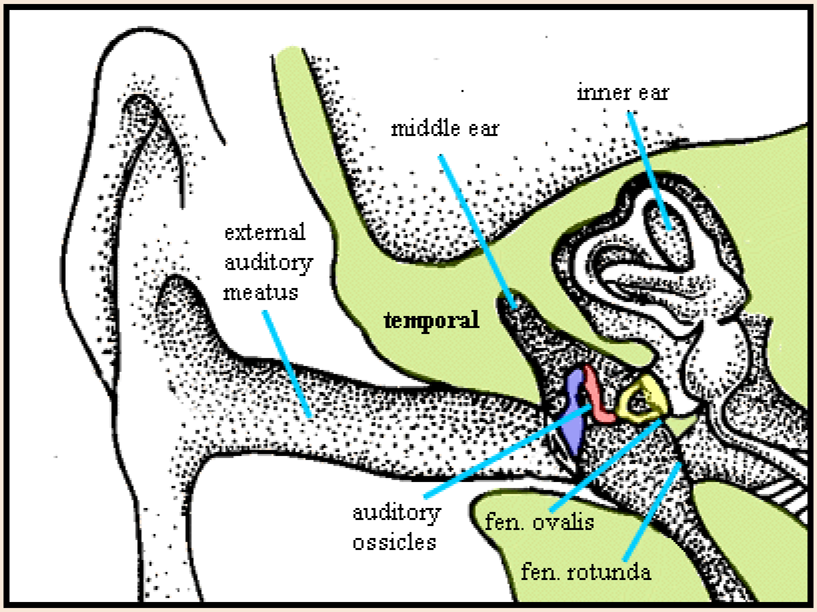
The incus is the first of the palatoquadrate derivatives we will take up. As we will discuss if, as, and when the palatoquadrate essay is ever written, the hypothetical first gill arch of chordates (or, alternatively, the velar skeleton) begat the palatoquadrate and Meckel's cartilage. The palatoquadrate begat a number of things, but most importantly the epipterygoid and the quadrate. The quadrate, in turn, begat the incus.

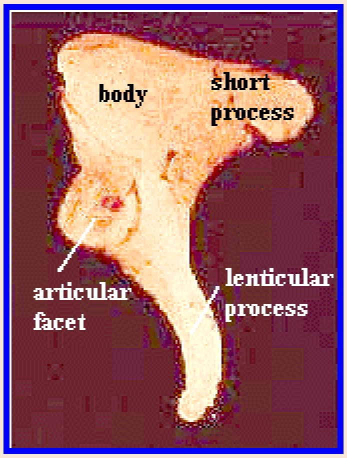
Thus, the ossification which became the incus has served, in one taxon or another, as a support element in filter feeding and possibly respiration, as a structural part of the occiput, the cheek, and the braincase, and as a critical mechanical element in the jaw and in hearing. Despite this enormous variety of functions, in thousands of vertebrate families and over five hundred million years of evolution, this bone has retained an articulation with Meckel's cartilage, or *its* progeny, the articular and the maleus. Over all or most of that same range (depending on your understanding of the origin of jaws), it has almost always retained a separate articulation with the hyomandibula or its progeny, the stapes and columella. If we are ever to develop a theory of vertebrate osteology, this is one of the most remarkable facts it will have to explain.



Fortunately, our task here is much simpler: to give a brief account of the middle bone of the three mammalian auditory ossicles. In reptiles with auditory ossicles, the entire job is done by the stapes or columella, with or without an accessory extracolumella. Only in mammals are there three ossicles: the maleus, incus, and stapes. There is undoubtedly a great and interesting body of literature on the functional anatomy of the ossicles, but we will have to be content with bare structure for the moment.

As an overview and reminder, at right is schematic vertical section of the human ear adapted from that most excellent of overviewers and reminderers, Kardong (1998: 659). Some additional background information (and probably misinformation) can be gleaned from **The Ear**. Briefly, Sound vibrations in air are funnelled down the external auditory meatus, at the end of which is the tympanic membrane. Having no place else to go, the pressure waves in the air cause the tympanic membrane to flutter. The movement of the membrane is picked up by the maleus (blue), which is in direct contact with the tympanum, and pased through the incus (red), and finally the stapes (yellow). The stapes has a large footplate which fits into the oval window of the inner ear and transduces the physical movement of the bones back into pressure waves in the perilymph of the inner ear. These pressure waves are *again* transduced into electrical impulses by cells in the inner ear complex related to the ancient lateral line system of fishes. Ultimately (i.e. microseconds later), we perceive the electrical disturbance as sound.

A more realistic view of the ossicles in articulation is shown at left. It is actually the long process of the maleus, the *manubrium*, whch makes the primary contact with the tympanum. The manubrium is, in fact, the remote ancestor of the retroarticular process of the articular. The maleus makes contact with a broad facet on the head of the incus. The incus has a *lenticular process* or *crus longum* which articulates with the stapes.



The geography of the incus is shown in a bit more detail at right. The articular facet (the *incudomalleal joint*) is close to the lenticular process. The joint faces anteromedially (except in whales) and is freely moveable on a cartilagenous surface -- not a sutural connection. The short process, or *crus breve*, is the attachment point for a ligament which binds it to the wall of the epitympanic recess, that is, the end of the middle ear opposite the Eustachian tube. Another ligament attaches to the body of the incus and binds it to the roof of the middle ear (*tegmen tympani*). Thus the movement of the incus inresponse to the maleus is probably constrained fairly tightly, although one can't tell just from the anatomy whether it is effectively constrianed to one dimension. Perhaps, like the loose quadrate-articular joint from which it evolved, there is significant play in at least two planes.

The joint between the incus and stapes is likewise a cartilagenous joint, with a tendency to ossify in older humans. Again, the implication is that the movement at this joint is constrained, but not necessarily confined to stereotyped motion in single plane. In fact, evolution seems to have avoided this solution – one it could easily have been acheived, given the quadrate as starting material. This may have important implications for the hearing. A question raised before in these Notes, and not yet answered, is whether this system is delivering one, or two-dimensional information to the inner ear. It is not necessary that the tympanum react as a one-dimensional ocillator or, even if it does, that it vibrate only to a single frequency to the exclusion of, for example, harmonics. Obviously mammals are capable of hearing more than one frequency at a time. This could be accomplished by decomposing a complex one-dimensional wave representing the superposition of all frequencies. However, it is equally possible that some of the decomposition is performed mechanically, before the impulse is transduced to the inner ear. Recall that the lateral line mechanoreceptors are exquisitely sensitive to the direction, as well as the magnitude, of shearing forces. The more elegant solution might be to evolve a system which takes advantage of this feature by supplying a vector signal to the inner ear: one with direction as well as magnitude. However, this is all speculation, and we must leave the matter to the physiologists with real data.

One peculiarity of the incus is that, at least according to some sources, not all of the bone is derived from the quadrate, or from any part of the first pharyngeal (mandibular) arch. The lenticular process is actually derived from mesenchyme attributed to the second branchial (hyoid). perhaps it may more appropriately be viewed as a part of the stapes, rather than the incus. Thus, from an evolutionary perspective, the lenticular process may be homologous to the shaft of the stapes and result from fusion of the former quadrate- stapes articulation.  This speculation is consistent with the observation that artiodactyls have a very short lenticular process (Thewissen & Hussain (1993)), with perhaps greater length to the corresponding process of the stapes.

The most obvious matter has been left for last, i.e. why bother with this complex arrangement? At least with regard to the incus, the answer seems to relate to amplification. The lenticular process is substantially longer than the arm of the manubrium which connects the tympanum to the articular facet. The result is that displacement of the malleus is amplified because it results in a *larger* displacement of the lenticular process. In essence, the incus acts as a lever with the body as the fulcrum, held steady by the ligamentous connections described above. This explains why the body, whichis not involved in sound conduction, is so much more massive and compact than the lenticular process. Its function is precisely *not* to move, but to hold the system steady. See Ear Physiology* for a rather 19th century-style diagram of the system. This is only one of several amplification and control mechanisms in the middle ear. However, the others relate to the malleus and stapes. ATW030125.

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## Additional Links

Howstuffworks \How Hearing Works\ basic mechanics, with some oversimlification of certain points.
Bio203 the ear: pictures of large plaster models.
PICTURES OF OSSICULAR CHAIN RECONSTRUCTION, INCUS REPLACEMENT, ... better, but mostly concerned with prosthetics

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# The Ear: References

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|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Ear Overview**<br>The Incus<br>References |

Carroll, RL (1988), **Vertebrate Paleontology and Evolution**, WH Freeman & Co., 698 pp. The Ear.

Gower, DJ (2002), *Braincase evolution in suchian archosaurs (Reptilia: Diapsida): evidence from the rauisuchian Batrachotomus kupferzellensis*, **Zool. J. Linn. Soc.** 136: 49-76. Ear.

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Makovicky, PJ, MA Norell, JM Clark & T Rowe (2003), *Osteology and relationships of Byronosaurus jaffei (Theropoda: Troodontidae)*. **Amer. Mus. Nov.** 3402, 21 pp. The Ear.

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# The Gill Arches: The Epibranchials

| Bones | Gill Arches |
|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Epibranchials<br>Hypohyal<br>Meckel's Cartilage<br>References |

## Summary

The epibranchials are the main upper elements of the **gill arches**. Fish with jaws usually have five functional pairs of gill arches. The last arch is sometimes simplified, so the typical fish has either 4 or 5 pairs of epibranchials. The lower ends of the epibranchials are attached to the ceratobranchials. The upper ends attach to pharyngobranchials or some related bone. The epibranchials may also support comb-like *gill rakers*, tooth plates for pharyngeal (throat) teeth, or various flanges for the attachment of muscles. The most important soft tissue attachments are the gills themselves, which project outward from the epibranchials, opposite the rakers and/or pharyngeal teeth. The epibranchials also have a variety of soft tissue attachments to the wall of the throat, gill muscles, and any interbranchial septa (tissues separating the gill chambers).

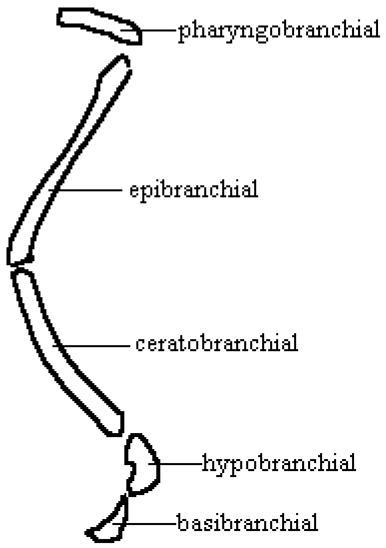
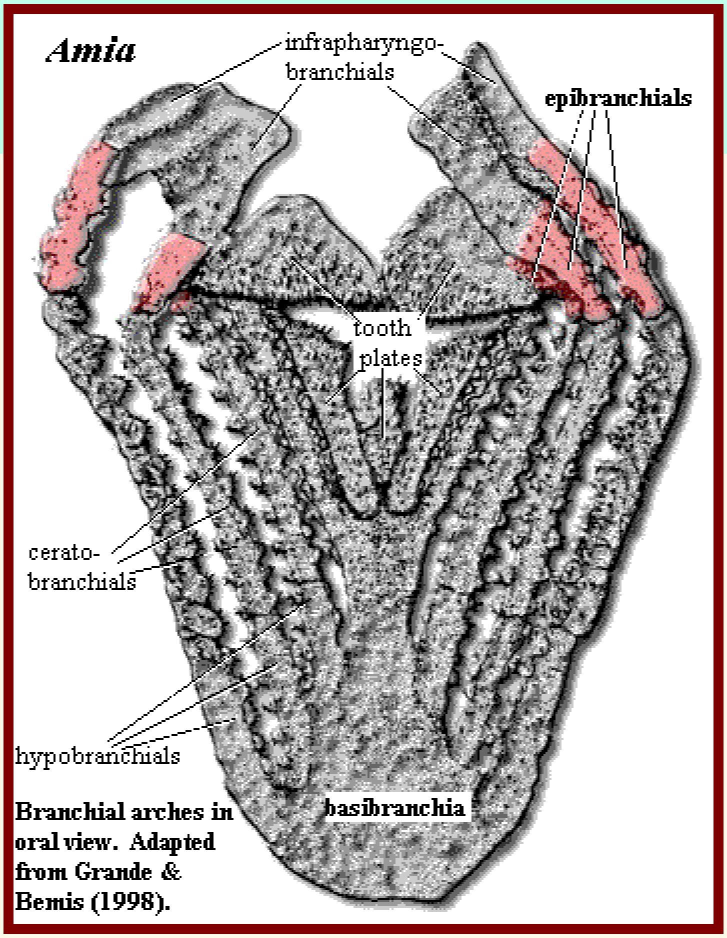


**Fig. 1. Typical gill arch elements**

The epibranchials have an interesting long-term evolutionary relationship with the ceratobranchials. Generally, the epibranchials follow "Williston's Law." That is, the number of epibranchials decreases and their degree of individual specialization increases. However, this seems to occur by shifting the core respiratory function onto the ceratobranchials, which change very little.

The epibranchials can perhaps be traced back into the jawless, osteostracan fishes. In sharks and actinopterygians we see some very similar trends, including (a) reduction in size (b) cross-linking or specialization to support terminally cross-linked pharyngobranchials, and (c) loss of 1-2 posterior epibranchials. In the teleosts, the epibranchials also develop a series of processes and flanges for the attachment of branchial muscles.

# The Standard Condition



**Branchial arches in oral view. Adapted from Grande & Bemis (1998).**

To the left is a nonstandard view of the Standard Condition, as exemplified by our usual standard in matters branchial, *Amia calva*. Here we are staring down the throat of *Amia,* a perspective normally obtained only by unfortunate prey items in their final moments before maceration on the pharyngeal tooth plates lining the throat. Petty distractions, such as dermal bones, jaws, and the hyoid arch, have been removed. *Amia*, as has been observed elsewhere, is well-endowed with teeth -- on the jaws, on the palate, and abundantly on the gill arches.

In *Amia* as in many other fishes, there are five branchial arches, but only four epibranchials. The first two epibranchials support infrapharyngobranchials which are fused dorsally on each side. Epibranchials 3 & 4 support the massive upper tooth plates. In *Amia*, as in many actinopterygian fishes, the ceratobranchials do much of the mundane work and heavy lifting. The epibranchials are short and appear more concerned with higher matters, such as the support and orientation of a variety of other dorsal elements, the infrapharyngobranchials and additional tooth plates.

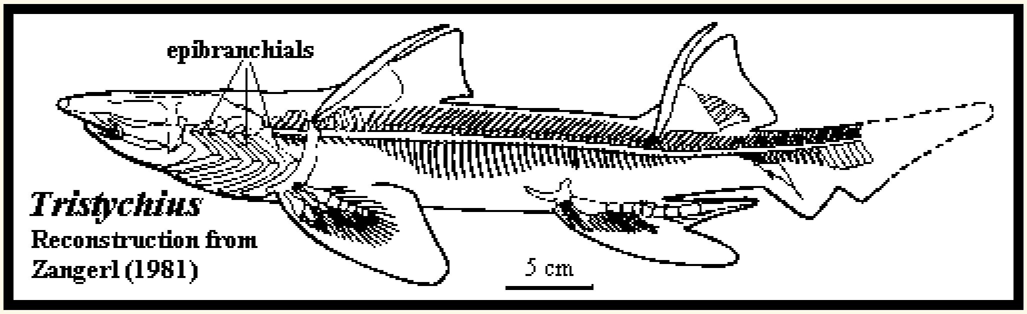
This is an interesting example *and* counter-example of Williston's Law at work. Williston's "Law" is that, in any given lineage, the number of serially homologous elements tends to decrease while the individual elements tend to become more different and specialized. Some of the best examples are the cranial bones and the teeth of mammals. Of course, there are no "laws" in paleontology equivalent to those in the harder sciences, but it is a common pattern. Here, the number of epibranchials has been reduced, and their functions have diverged somewhat from each other, in accordance with the "law." However, the epibranchials' original core function of supporting the gills is not one that can easily be abandoned. Instead, this function has been shifted progressively shifted to the ceratobranchials which have retained the ancestral number (5) and remain quite uniform in morphology.

One suspects that this is one of those chaotic processes in which a small random event has set in motion an irreversible cascade of consequences. For, as soon as any epibranchial is slightly adapted to functions other than gill support, two things happen. First, selective pressure increases on the corresponding ceratobranchial *not* to diverge, but to take up the respiratory slack. Second, the epibranchial's divergence must result from some interference in the regime of genetic regulation which originally caused it to develop as a serial structure in the first place. The breaking of this genetic assembly line for one serial element necessarily means that it is more easily possible to divert other serial elements, since all are created from the same package of genes. Thus, each change increases the tendency of epibranchials to diverge, and the tendency of ceratobranchials *not* to diverge.

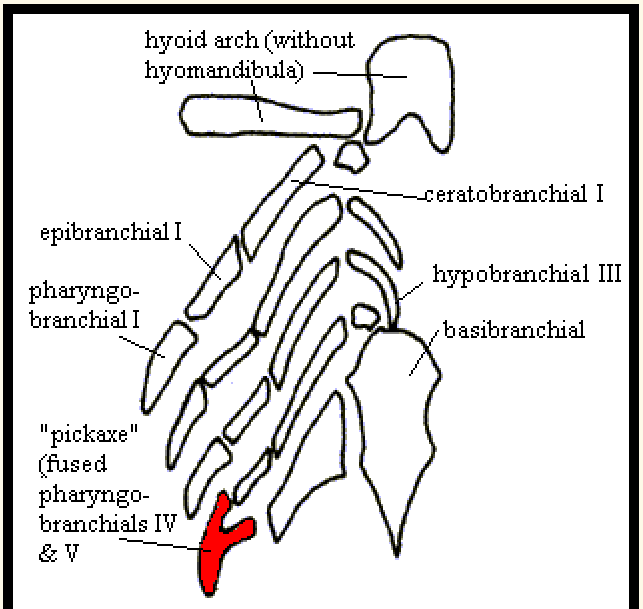
That second point is rather abstract. Let's try a molecular biology example. Suppose a very slightly aberrant regulatory element in a structural gene related to the epibranchials becomes slightly sensitive to some universal regulator -- like one of the bone morphogenetic proteins (call it *BMP-x*). Subsequently, an ancestor develops with slightly elevated levels of BMP-x during development, near epibranchial 2. The result is a slightly misshapen bone which, perhaps, has some slight advantage in allowing the pharyngobranchial elements to converge and fuse (as in *Amia*). If that animal were to live long and prosper, the structural gene in its descendants will tend to evolve a stronger and more consistent quantitative response to BMP-x. But the same gene is used in *all* of the serially homologous epibranchials. Thus, every member of the entire series becomes sensitive to relative levels of BMP-x in its particular developmental environment. This sensitivity, in turn, renders *all* the epibranchials subject to regulation by BMP-x antagonists and enhancers so that divergence becomes increasingly likely. In the process, the epibranchials will likely become less optimally adapted to gill support, which puts selective pressure on the ceratobranchials to focus all the more strongly on their core function. The result of the original tiny mutation, is a cascade of events in two directions, with the epibranchials becoming ever more individualized and the ceratobranchials becoming increasingly dour and conformist.

# Phylogeny

**Jawless Fishes:** The history of the epibranchials presumably begins wherever vertebrates first developed a jointed, internal branchial arch rather than an unjointed, external branchial basket. In thelodonts, perhaps the denticle patches with fused bases found in the pharyngeal area near the presumed gills of loganiids (Marss & Ritchie (1998); Van der Brugghen & Janvier (1993)) are the first possible indication. If so, this is particularly interesting because the reconstructions of the furcacaudiform thelodonts suggest branchial bars of the external variety. Wilson & Caldwell (1993); Wilson & Caldwell (1998). Certainly osteostracans are supposed to have had internal gill arches, either as part of, or supported by, the cranial cartilage. Janvier (1996).



**Placodermi and Chondrichthyes:** Very little is known about the branchial arches in early gnathostomes. Placoderms, in particular seem to have had branchial elements which were almost entirely cartilaginous. Janvier (1996). As for sharks, "[t]he branchial arches are so poorly known in Paleozoic forms that little need be said about their specific morphology." Zangerl (1981: 26). To the extent that these structures are known, the gill arches of early Chondrichthyes seem to have had a classically symmetrical, 'V' shape with apex of the 'V' posteriorly directed. The epibranchials were then relatively long, straight elements. The word *relatively* should be stressed, since the entire branchial apparatus tended to be quite small and still compressed under the braincase, as in living Holocephali. This morphology remains consistent into the elasmobranchs and Neoselachii, but the entire apparatus becomes much larger and is located much further back, largely behind the neurocranium. *Id.* (The image shows a somewhat intermediate form, *Tristychius*, a Carboniferous (Vis�an) elasmobranch. Here, the branchial arches are large, but are still closely related to the braincase.)



***Pseudocharcharias kamoharai*** **: left gill arch elements in dorsal view, with dorsal sections pulled outward to show "pharyngobranchial pickaxe"**

Even in *Tristychius*, the epibranchial has lost the secondary function it performed in the Osteostraci, that of fixing the gills to the cranial cartilage. That function has been taken over by specialized pharyngobranchials. By the level of the extant lamniform sharks, we see some of the same specializations found, convergently, in the Standard Condition: epibranchials of reduced size, supporting terminally fused pharyngobranchials, and loss of 1-2 posterior epibranchials. Curiously, this same condition is found in the rays and skates (Hypnosqualea), despite a very different body form. Compagno (1999a). These may be primitive traits for Neoselachii; but their persistence, and the degree of convergence with *Amia*, are initially startling.

**Acanthodii and Actinopterygii:** An image of the acanthodian gill arches can be seen in the discussion of the **Hypohyal**. The basic morphology of the epibranchial is almost identical to *Tristychius*. Note, however, the presence of tiny ossifications along the shaft. These are *gill rakers*. Gill rakers are found in both chondrichthyans and in Osteichthyes, as well as acanthodians. Although no one seems willing to swear that rakers are homologous in all three groups, it does seem likely **[1]**. Perhaps gill rakers are also the forerunners of the pharyngeal teeth in the Standard Condition, although many advanced teleosts (*e.g.*, labroids) have both, and the two populations of tooth-like bones seem to be distinct. Barlow (2000).

We are straying somewhat from the epibranchial itself, but it is all for a good cause. The primary practical importance of the epibranchial in fish work is as the bearer of gill rakers and various dorsal structures. The fine structure of fish phylogeny, particularly among the teleosts, is built on such distinctions. Even to experts, one anchovy looks very much like another. Thus, distinctions are diagnosed by the size and number of gill rakers and the presence or absence of rakers on the posterior face of the third epibranchials.

**Neopterygii and Teleostei:** The tendency to cross-link certain arches dorsally continues. Typically this occurs through fused pharyngobranchials, as in *Amia*. However, the epibranchials also become directly involved. For example, an interarcual cartilage frequently connects the first epibranchials with the second infrapharyngobranchials. In cyclosquamates, an elongated (*uncinate*) process of the second epibranchial contacts the third pharyngobranchial. Another teleost refinement is the levator process on the epibranchials, presumably for the *levator brachialis* muscles, as well as the uncinate process mentioned above. The presence, absence, size and position of these elements can be of considerable significance. *See*, generally, Esociformes, Wilson & Veilleux (1982), Johnson & Patterson (1997).

What all this might be telling us is that the gill arches are being recruited directly to assist in the active pumping of water across the surface of the gills, maceration by the pharyngeal teeth, and similar matters. Generally, the burden of adapting to these functions is falling on the dorsal elements for the reasons discussed above in connection with the Standard Condition **[2]**. The epibranchials thus (a) become shorter, increasing their mechanical advantage as levers to move the ceratobranchials, (b) cross-link, to improve resistance to muscular stresses, and (c) develop flanges and processes which facilitate muscle attachment and fine control of the more dorsal elements, such as the tooth plates. This reaches something of a logical extreme in cichlids, with their fully developed pharyngeal jaws. Barlow (2000).

**Sarcopterygii & Tetrapoda:** Even applying our customarily debased threshold of expertise, we lack sufficient knowledge of the sarcopterygian branchial apparatus to say much of anything meaningful. Since sarcopterygians developed neither pharyngeal teeth nor the advanced suction feeding methods of the teleosts, the general structure of the gills seems to have remained primitive. If one's basic feeding strategy is to get the largest possible mouth around the biggest possible food item and move it into the stomach as quickly as possible, then all anatomical subtlety is wasted. Our ancestors' lack of branchial refinement merely reflects their absence of manners or sophistication in matters of feeding.

As most sarcopterygian groups were moving (or being pushed) toward shallow, deoxygenated waters or even onto land, the utility of gills for ventilation decreased. *Acanthostega*, although fully aquatic, had only three, relatively modest, pairs of functional gills. It may have used its lungs to obtain most of its oxygen, with the gills specialized to shed excess carbon dioxide. Clack (2002). Perhaps for this reason, some basic gill structures survived for a very long time, particularly in the temnospondyl lineages. *Id.*

**Crown Tetrapoda*:** In most tetrapods*, the epibranchials lose their separate identity and are merged into structures in which their homology cannot be accurately determined. The first epibranchial is incorporated into the posterior horn of the hyoid. It sometimes emerges from this obscure retirement post to form a dramatically enlarged portion of the tongue skeleton in tetrapods* with extensible tongues (*e.g.*, birds and salamanders). The other epibranchials are lost or merged tracelessly into the thyroid or tracheal rings. ATW030830.

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**[1]** We know of no evidence for gill rakers in placoderms, but so little is known of placoderm branchial arches that it is hard to exclude the possibility. I have always considered it particularly weird that *Bothriolepis*and related antiarchs have structures on the medial face of the pectoral "limb" which look for all the world like gill rakers. This is one more indication of a deep, if recondite, relationship between the pectoral fins and the gills.

**[2]** This tendency is also related to the trend for the hypobranchials to transform from stick-like extensions of the ceratobranchials into rounded bearings on which the ceratobranchials can move relative to the basibranchium. *See*, the **Hypohyal**.

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# The Gill Arches: Overview

| Bones | Gill Arches |
|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Epibranchials<br>Hypohyal<br>Meckel's Cartilage<br>References |

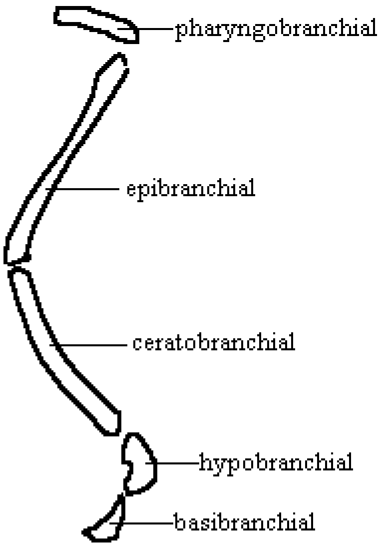

**Fig. 1. Typical gill arch elements**

We will begin and, until later revision, also end with a brief discussion of gill arches. The working hypothesis here will be that the primitive jaw, consisting of the palatoquadrate and Meckelian cartilage, is derived from a hypothetical ancestral "*mandibular arch*" and that the hyomandibular and related elements are derived from a second (and much less hypothetical) *hyoid arch*. Elements derived from the hyoid arch are most conspicuously present in jaw support. Opinions vary on the mandibular arch, and it may still be that the jaw has some completely different ancestral homologue. However, the gill arch theory is not only elegant, but has the virtue of being easy to learn and remember, which may be why it has dominated the discussion for the last century or so.

The segments of a typical gnathostome gill arch are shown in Figure 1. By convention, the corresponding parts of the hyoid arch are named by using the suffix *-hyal*, as in *ceratohyal or basihyal,* with the exception of the *epihyal*, which is more commonly called the *hyomandibular*, *columella* or *stapes*, depending on the subject matter and taxon under consideration and how badly the writer wishes to confuse you. Only the ceratal and epal elements of the mandibular arch are known. By other perverse conventions, the bone which would be the "epimandibular" is referred to as the *palatoquadrate* and the presumed "ceratomandibular" is *Meckel's cartilage*. The latter is named after Johann Friedrich Meckel (1781 - 1833), a Prussian physician and anatomist who had an abnormal fascination with abnormal human physiology*.

The phylogeny of the gill arches is of intense interest because of their possible involvement in the development of both the jaws and the paired appendages. For the past few years, the near-consensus has been that basal craniates had gills that were supported by a *branchial basket*, if they were supported at all. The branchial basket was braced against the body wall and unjointed, as in lampreys. It is derived from the hypomeres ( = lateral plate mesoderm). By contrast, the gill arches of gnathostomes are internal, jointed, and derived from the epimeres via the mesenchyme (i.e. with an admixture of neural crest ectoderm). This embryonic origin of the gill arches has been thought to be a good argument for their involvement with the jaw, but against their relationship with the limbs.

The recent discovery of the Cambrian craniate *Haikouichthys* (Chen et al. (1999)) has confused matters somewhat. Whatever else *Haikouichthys* may be, it is certainly not a gnathostome. It appears (study Chen et al.'s Figure 4 carefully) to have external gill arches (7?), as expected. However, (a) the gill arches seem to be jointed and (b) they appear to be closely related to paired fin-folds on the anaspid model. Indeed, Chen's cladogram places *Haikouichthys* basal to the anaspids and very close to the lampreys and *Jamoytius*. Thus, the possibility exists that the paired limbs of gnathostomes are derived from the ancient, *external* gill arches which have otherwise completely disappeared outside of the lampreys.

ATW 001118.

* This is, of course, is a very unfair summary of the life of an interesting scholar who studied with Cuvier and seems to have done a great deal of useful work in a variety of areas. Unlike many anatomists of the age, he made a study of vertebrate soft tissues and (according to one off-hand reference which gave no details) actually had the temerity to question Special Creation.

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# The Gill Arches: The Hypohyal

| Bones | Gill Arches |
|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Epibranchials<br>Hypohyal<br>Meckel's Cartilage<br>References |

The hypohyal is a ventral element of the hyoid arch which links the ceratohyal and the basihyal. If your reaction to this, "well, of course!" then you probably don't need to be reading this page. For those who did not imbibe splanchnocranial anatomy with their mother's milk, we will return to fundamentals.

The gill arches have two basic parts, dorsal and ventral. Each part is associated with a main gill arch segment, the (dorsal) *epal* and (ventral) *ceratal* segments, respectively. Thus, each of the *branchial arches*, the arches which actually function as respiratory arches in fishes, has an epibranchial and a *ceratobranchial*. The *hyoid arch* is a an additional arch anterior to the first branchial arch. The hyoid is often involved in respiration, but its primary functions are related to jaw support and extension. The ceratal and epal segments of this arch are called the *ceratohyal* and the *hyomandibula*, respectively.

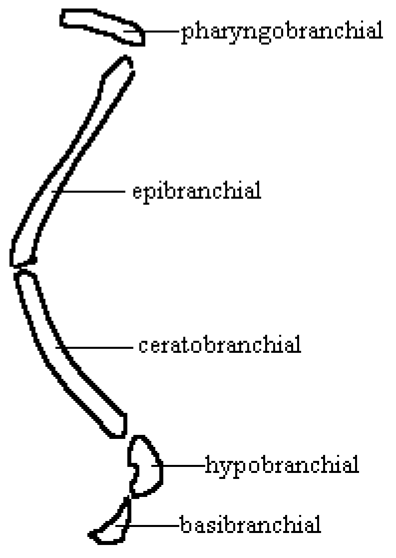
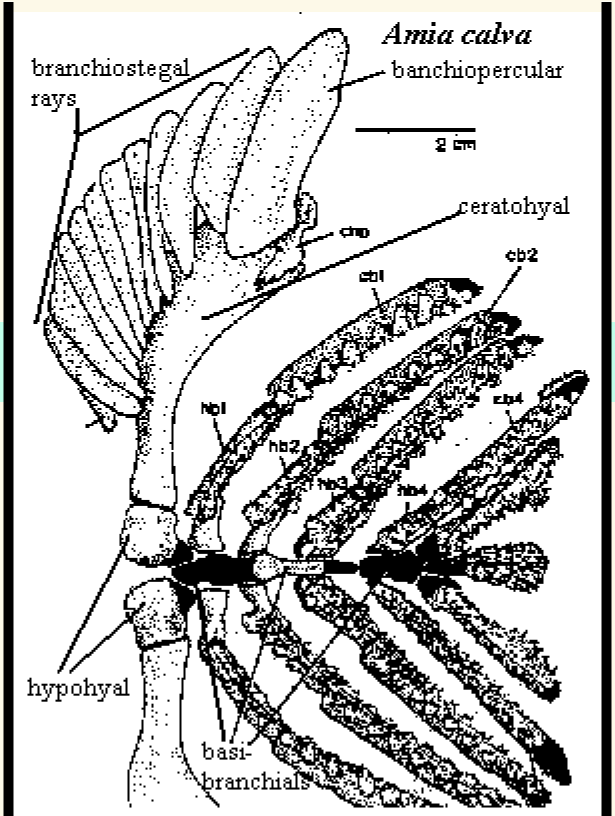


**Fig. 1. Typical gill arch elements**

Most gnathostomes have some kind of ventral extension of the gill arches, a basal component, and these usually lie flat along the ventral "throat" of the fish. The basal elements of adjacent arches are often closely interlocked, or even fused. The basal element of the hyoid arch, the *basihyal*, is no exception.

Now, the ceratal segment is typically long and relatively rigid and at least slightly vertical, while the basal elements are typically fused and/or tightly bound to the base of the gullet in a horizontal orientation. Keeping these elements in articulation as they move in different planes requires a complex joint. This is normally supplied by a small element of complex shape. This element is the *hypobranchial* or, in the case of the hyoid arch, the *hypohyal*.



**Ventral gill arch segments in dorsal (oral) view. From Grande & Bemis (1998).**

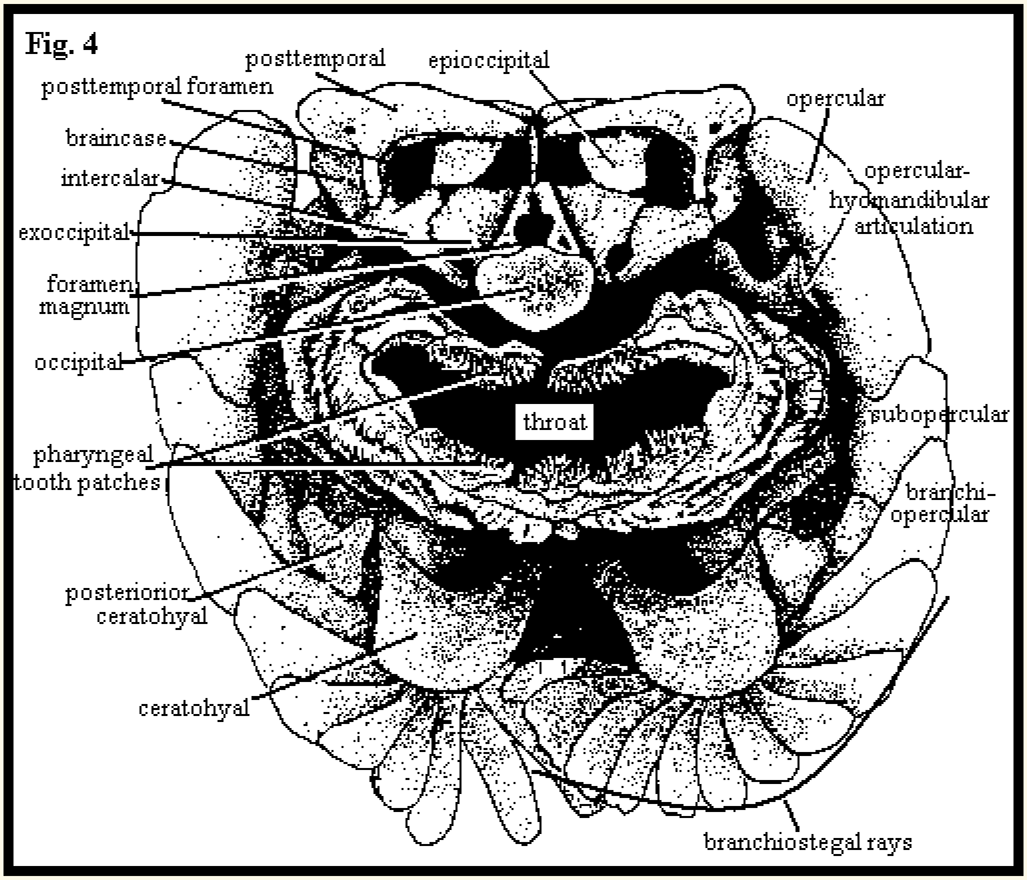
# The Standard Condition

We may define the Standard Condition by reference to the amiable *Amia calva*. I say "by reference to" since *Amia* itself has some relatively non-standard features. However, the excellent images of Grande & Bemis (1998) dictate our choice. Finding good images of the hypohyal is, as we have discovered, not a simple proposition.

Note that the hypohyal in *Amia* seems to have a rather solid and immobile articulation with the ceratohyal. In fact, the articular surface is cartilagenous. However, most of the mobility in the hypohyal is in the contact between the hypohyal and the basibranchials. *Amia* departs from the Standard Condition, as we will define it, in that there is no separate basihyal. The hypohyals directly contact the basibranchials, which are fused into a more or less continuous "basibranchial copula," although the basibranchials are only partially ossified. The hypohyals are also seldom completely ossified. Even in the rather large individual shown in the image, the hypohyal remains partially cartilagenous. This is a typical condition in actinopterygians.

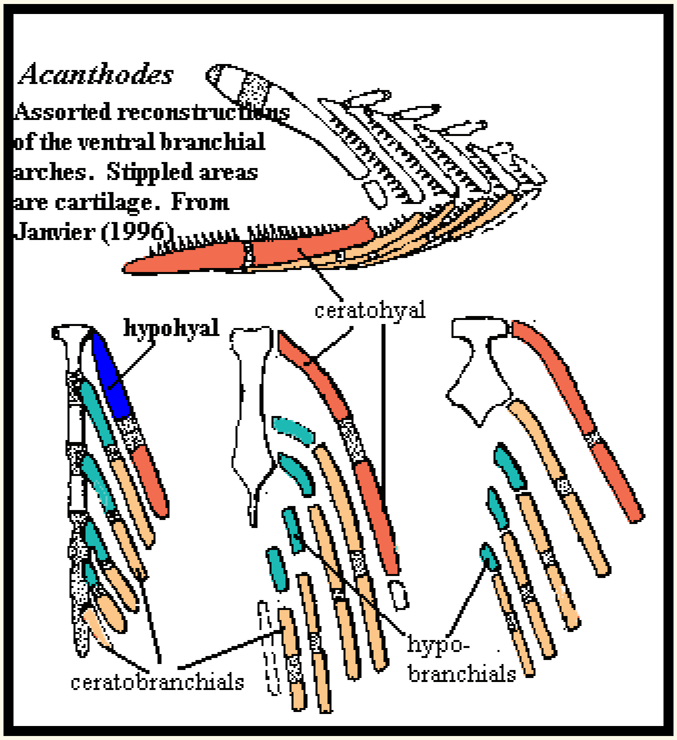
The position of the hypohyals shown in the image is not life-like. In life, the first 3-5 branchiostegal rays of each side overlap their counterparts on the opposite side. This is possible because the ceratohyals are strongly curved as shown in the occipital view in the figure at right. Accordingly, the hypohyals must be directed amost ventrally. In this orientation, the articular "head" of the hypohyal probably articulates with the hypobranchials of Branchial Arch I as well as with the basibranchial copula. It also seems likely that the two hypohyals also make rolling contact with each other in the process of raising and lowering the floor of the pharyngeal cavity via the branchiostegal rays.

Fig. 4



# Phylogenetic Summary

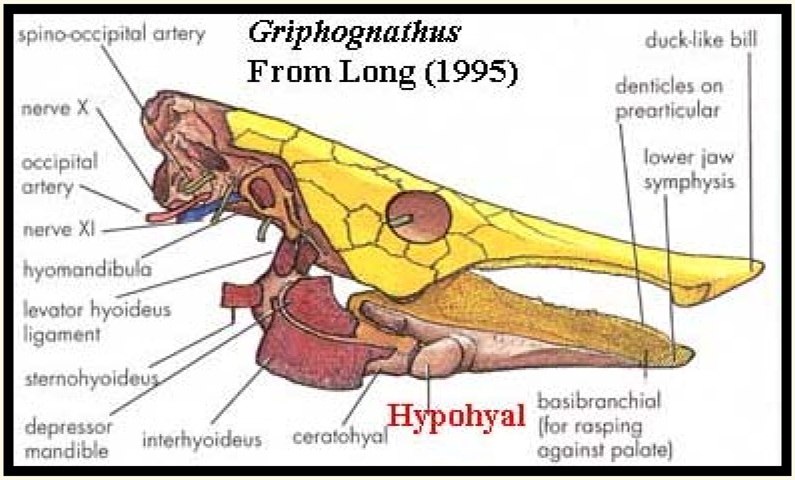
Janvier (1996) takes the hypohyal to be general for the Gnathostomata. This is unclear. The ventral branchial arch segments of placoderms are so poorly known that nothing useful can be said. Apparently, placoderm ventral arch elements were almost entirely cartilagenous. In at least many Chondrichthyes, the hypobranchials are well developed, although they point posteriorly. However, there is no hypohyal. The ceratohyal articulates directly with the basihyal or basibranchial copula. Thus, we might suppose that the hypohyal is a special feature connected with the development of the branchiostegal apparatus.


***Acanthodes***

**Assorted reconstructions of the ventral branchial arches. Stippled areas are cartilage. From Janvier (1996)**

This suspicion is confirmed from at least some reconstructions of the hyoid arch in Acanthodii. The branchial arches in the Acanthodii are not well ossified, so the issue is murky. The ceratobranchials tend to have two ossification centers. What seems to be unsettled is whether this is also true of the ceratohyal, so that the more ventral of the two ceratohyal segments becomes the hypohyal, or whether both segments are parts of the ceratohyal and the hypohyal was inserted later, as a neomorph. In the latter case, the hypohyal is possibly polyphyletic, *i.e.* convergently developed in actinopterygians and sarcopterygians.

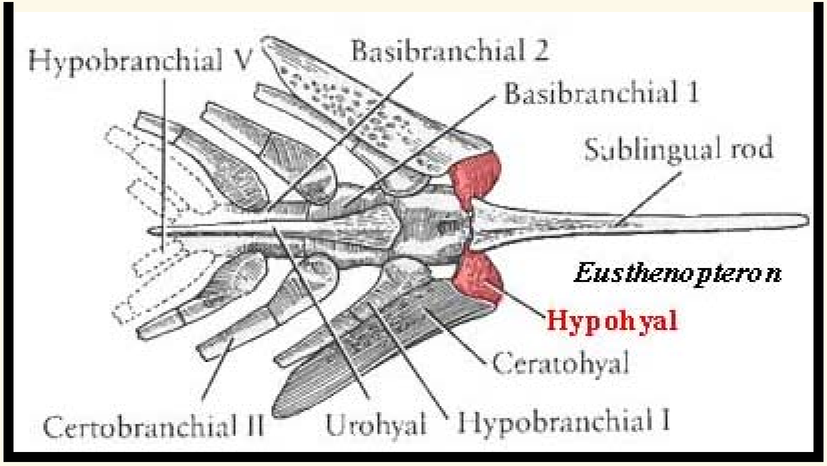
Neither one of these possibilities is particularly appealing. But, of the two, we tend to prefer the former on morphological grounds. The Late Devonian actinopterygian *Mimia*, for example, has a well-preserved hypohyal which looks quite like the ceratohyal, as in *Acanthodes*. It is only as we approach the Neopterygii and the Standard Condition that the hypohyal becomes short, rounded and joint-like. Development beyond the basal Neopterygii is a matter of adding an additional hypohyal -- presumably increasing speed, flexibility and control of the movement of the branchiostegal apparatus as teleosts developed more and more elaborate specializations related to suction feeding. *See, e.g.,* image at *Novumbra*.


***Griphognathus***

**From Long (1995)**

On the other side of the teleostome divide lie the the sarcopterygians. Here, and particularly in the durophagous forms, the ceratohyal and an anterior extension of the basibranchial copula become strongly involved in supporting the lower jaw, rather than in lowering the floor of the mouth. So, in *Glyptolepis*, for example, the ceratohyals are rather large, flat elements supporting the lower jaw and the hypohyals are correspondingly stout joints providing the necessary flexibility between the ceratohyals and the fused basibranchials. This trend reaches something of a logical extreme in Dipnoi, such as *Griphognathus*, in which the basibranchial copula *is* the lower jaw and the hypohyal effectively takes the place of the articular. Long (1995).

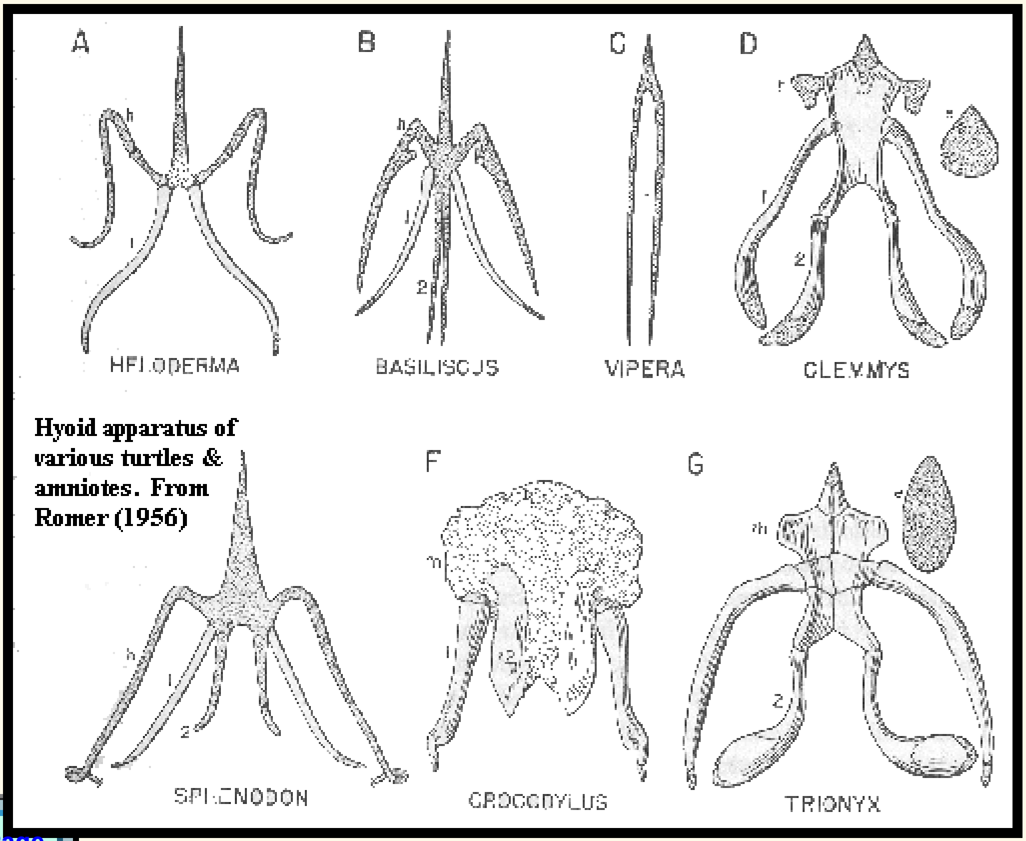
Our own inheritence from the basal sarcopterygian tradition is a bit less extreme, as can be seen in the branchial apparatus of *Eusthenopteron*, shown at left in a figure from Carroll (1988). The basibranchial copula has been drawn anteriorly with a long, but slim, sublingual rod. The hypohyal is round and stout, providing an articular bearing between both the sublingual rod and the copula proper, on the one hand, and the ceratohyal, on the other. Note that, contrary



to the Standard Condition, the hypohyal appears to have a fixed contact on the copula and a moving contact with the ceratohyal.

This conformation remains oddly constant over the loss of functional gills in the Tetrapods. Unfortunately the hyoid apparatus is almost invariably unossified and, worse, the terminology changes. The furthest we have been able to go with a hypohyal, *eo nomine*, is the salamander *Necturus*. The hyoid apparatus of *Necturus* looks quite a bit like a truncated version of *Eusthenopteron*, without the sublingual rod and with only the hyoid and first branchial arches. Since the sublingual rod is missing, the two hypohyals meet medially and cap the the basibranchial copula.

Amniotes also have a hyoid apparatus. Some examples are shown in the figure from Romer (1956). It appears, in the case of *Heloderma* that there is a separate cartilage between the ceratohyal and the basibranchial body. This may or may not be homologus to the hypohyal. However, in almost all other taxa, the ceratohyal merges indistinguishably with the copula. In the synapsid lineage, the pieces are perhaps better differentiated, but mammallian anatomy has developed its nomenclature along a very different path, and the homologies are, in any case, far from clear. ATW030328



**Hyoid apparatus of various turtles & amniotes. From Romer (1956)**

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# The Gill Arches: Meckel's Cartilage

| Bones | Gill Arches |
|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Epibranchials<br>Hypohyal<br>Meckel's Cartilage<br>References |

Meckel's Cartilage, also known as the Meckelian Cartilage (hereinafter the "MC") is best known as the original and most primitive lower jaw. However, it is quite different from anything previously attempted in Bones, and not just because it has a funny name. Meckel's cartilage is not one of those *arriviste* dermal bones that had no family history prior to *Cheirolepis*. It is not even a bourgeois endochondral braincase element dating to the origins of Gnathostomata. The MC dates back before the gnathostomes: quite possibly into early chordate and Precambrian times. Further, it lies at the heart of one of the truly large questions of paleontology: the origin of jaws. It has been said (if only because I said it myself, just now) that the history of the vertebrates *is* the history of jaws. Efficiencies in intake drove increases in mobility and metabolism in vertebrates. Further efficiencies and specializations drove further evolutionary changes in the skull and spread vertebrates over a huge range of environments. We may not be *what* we eat; but, most certainly, we are *how* we eat.

The anatomy of the MC is not worth a great deal of attention. Its derivatives get somewhat complex. These include the malleus, the articular, and the amphibian mental bone, as well as some ligaments and soft tissues. But these will be dealt with under their own names in later sections. The MC itself is merely a cylindrical piece of gristle without much character or flavor. The phylogeny is what we will focus on. As a result, the history of the MC will be taken very slowly, with attention to a phylogenetic story that is lengthy, but still very incomplete. We will then review some of what is known about the embryology of the MC and its developmental molecular biology. Finally, we will briefly reassess the evolutionary story in light of this information.

## 1. Phylogeny

### a. Pre-craniates

As noted in the gill arch overview, the MC is supposedly the "ceratomandibular," the lower main element of a hypothetical primitive first gill arch, the "mandibular" arch. Current thinking is that the branchial apparatus was originally not designed for respiration. The early chordates were small and inactive enough to directly absorb oxygen over the epidermis generally. Indeed some sizeable turtles and lissamphibians are able to get by in this fashion even today. Organisms along the lines of the cephalochordate amphioxus use the gill apparatus for filter feeding. The branchial slits, in this context, are simply vents to release excess water which has been filtered for nutrients. Already, in this group, the branchial apparatus is supported by a series of external pharyngeal bars. As we will see, these are analogous, but not homologous, to gill arches. Anterior to the "gills," amphioxus has a velum, but it is merely a passive regulator of intake which works a bit like the iris of a camera. The flow of water is actually provided by a battery of microscopic cilia.

## b. Basal Craniates

Amphioxus is a virtually sessile filter feeder. Basal craniates run much larger than amphioxus and appear to be designed for a higher degree of energetically expensive mobility. To judge from hagfish and lampreys, the only living jawless fish, the basal craniates had also taken up moderately taxing hobbies, such as parasitism and scavenging dead or weakened fellow craniates.**[1]** In order to support these disgusting habits, some taxa developed adaptations for sucking in both food and respiratory water. The most common respiratory pump was an adaptation of the velum. Among craniates, it became an active pump rather than a regulator. The detailed anatomy and workings of the velum are not yet tackled here. Suffice to say that the velum is a sail-like curtain of tissue (hence the name) which pushes water into the pharyngeal passage and is supported and controlled by a velar skeleton. Significantly, the velum lies immediately adjacent to the otic capsule.

By the level of the Osteostraci and lampreys, i.e. at least as early as the Silurian, a typical large fish might have a velum supported by a velar skeleton towards the center of the branchial passage, and several respiratory gills, externally reinforced by an interwoven "branchial basket" of bone or cartilage braced against the body wall and connecting the gill pores, like a chicken wire fence. In addition, Mallatt (1996) has argued, based on a detailed analysis of the ammocete larvae (see image) of lampreys, that an internal pharyngeal skeleton was also present. Although lost in adult lampreys, the ammocete larva seems to have both internal and external pharyngeal supports.

Mallatt argues that such internal arches were the rule, rather than the exception, despite the lack of specific fossil evidence. Thus, for example, he argues that such elements were present in osteostraci, but failed to fossilize. This is perhaps a bit hard to swallow, so to speak, because the incredibly well-preserved remains of many osteostracans from Spitzbergen and Estonia clearly show even the most delicate neural structures. Not only are internal gill arches not found, but one might well ask why the osteostracan gill would require any terminal support at all, inside *or* out, given that all of the gills were embedded in one enormous, solid block of head shield cartilage for their entire length.**[2]** Perhaps the jointed gill arches of the fossil lamprey relative *Haikouichthys* (Chen et al. (1999)) provide better confirmation of the theory, but only if one is willing to interpret these structures as internal to the gills. In this connection, however, note that these elements are not very different from the undoubtedly *external* structures found in the Anaspida generally, particularly the triradiate bone which is the singular synapomorphy of the clade.

The alternative argument, advanced by Janvier (1996) is in fact not all that different. Janvier agrees that gills, and perhaps the external branchial skeleton, are primitive to the chordates. However, he sees the *internal* branchial skeleton as a neomorphic gnathostome character. To simplify, the matter comes down to the velum, which is agreed by all to be related in some manner to the mandibular arch. Mallatt views the velum as an accessory structure anterior to the mandibular arch which may or may not have been present in the ancestor of gnathostomes, but which disappeared in that line without a trace. However, the velum provided a major evolutionary (as well as hydrostatic!) pressure to stabilize the gills with an internal skeleton. By contrast, Janvier sees the velum as the first development and asserts that the internal branchial skeleton was developed by serial duplication and adaptation of the velar skeleton in early gnathostomes. To Mallatt, the velum is, at most, an *evolutionary* precondition of the branchial arch. To Janvier, it is a *structural* precondition.

## c. Gnathostomes

We are now ready to sink our teeth into the core problem: the origin of jaws. Mallatt's

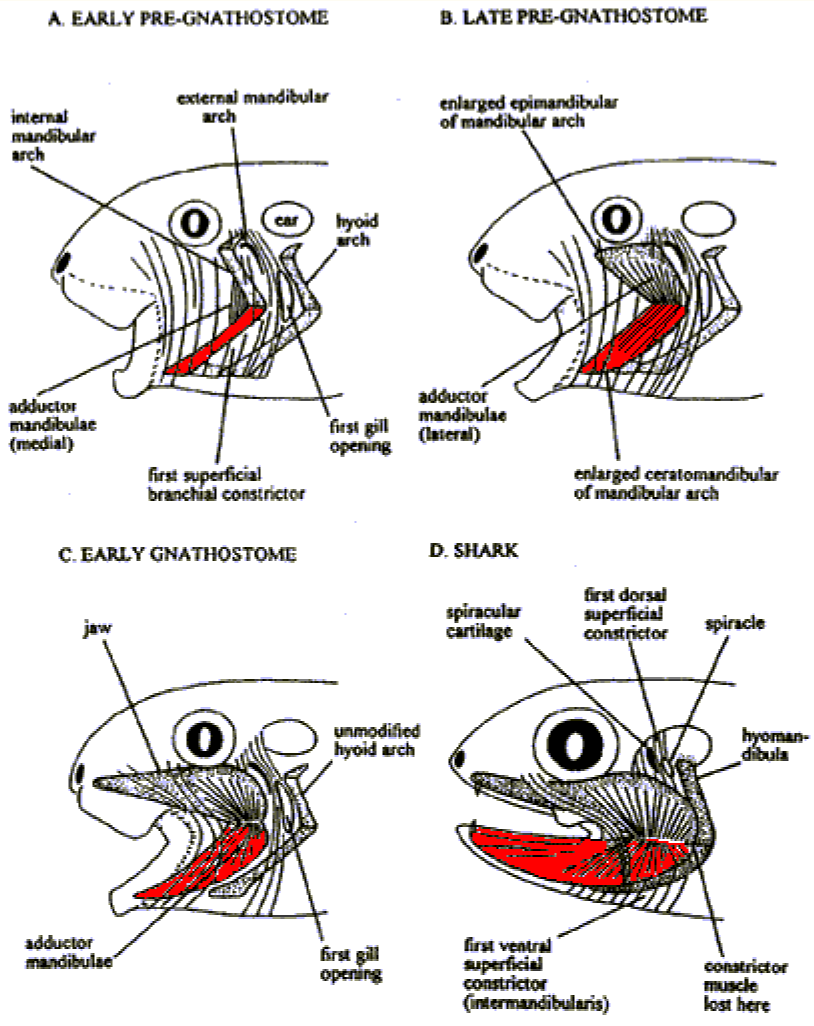

**Fig. 1. Development of gnathostome jaw from mandibular arch, modified from Mallatt (1996). Meckel's Cartilage shown in color.**

transformation series is well known. **Figure 1**. In this view, the jaw is derived from an ordinary respiratory arch, with the lower jaw, the MC, being derived from the ceratomandibular. The embryos of some fish doing a very convincing imitation of this series during development. The external mandibular skeleton disappears altogether. Mallatt sees this transformation as driven by increased need for ventilation, and only later becoming a grasping jaw. During this sequence, the external branchial basket disappears, except for some remnant cartilage which is still found externally supporting the gills of chondrichthyans. During development, the mandibular and hyal arches are coopted into the jaw and the first gill opening is reduced to a small spiracle.

Janvier points out a number of problems with this evolutionary scenario. For example, no fossil form is known in which the first gill arch has a respiratory function, with the *possible* exception of very derived pteraspidomorphs, which are well off the gnathostome line. Mallatt reconstructs the osteostraci as having a respiratory mandibular arch. However, although gill impressions are known in this group, they do not occur at this anterior position. Thus Janvier reconstructs the osteostraci as having a velum, but of course there is no evidence of a velar skeleton either. Janvier also notes that the spiracle is not an outlet, like the gill slits, but an entrance. Further, the external gill skeleton of jawless fish is never known to reach as far forward as the supposed mandibular arch.

Janvier's transformation series is shown in **Figure 2**. In this version, both the gill arches and the jaws are serial homologues of the velar skeleton. Janvier posits that both developed from the velar skeleton at the same or similar times. However, there is nothing in his hypothesis which really demands this result.

Truthfully, it is impossible to make a firm decision based on anatomical grounds alone. In fact, it is impossible even to summarize the anatomical evidence in an even-handed manner within the body of an essay of this scope. Mallatt's theory has the virtue of elegance, and he may have the edge in anatomical evidence (except possibly neuroanatomy) from living species. Janvier's hypothesis has a corresponding advantage on the fossil record. One suspects, however, that these apparent differences may be related to the fact that Mallatt has simply spent more time cutting up fish while Janvier has spent more time staring at rocks.

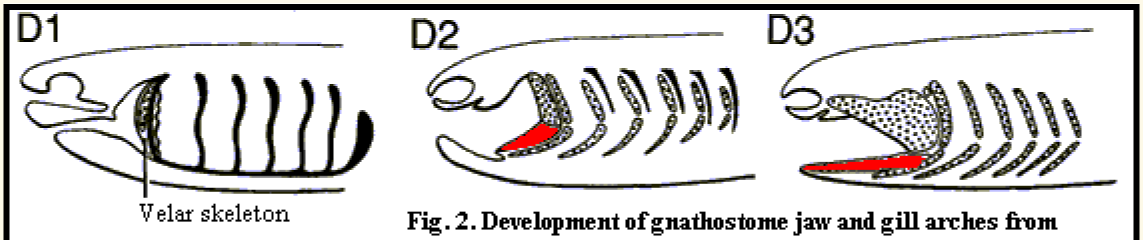

**Fig. 2. Development of gnathostome jaw and gill arches from velar skeleton. Modified from Janvier (1996).**

So, the question may now be framed: is the jaw a serial homology of the internal branchial arches, or were both jaw and branchial arches independently derived from a velar skeleton? Were we all Americans, we might now take a vote, after which a black-robed chorus of elderly lawyers, solicited at great expense, could tell us what it was we had decided. Fortunately, there may be marginally more satisfactory ways of arriving at the truth of this matter. The effort will require us to abandon the warm and familiar neighborhood of anatomy and venture out into some rather cold, serious and very new molecular biology. From that radically different perspective we will see that Janvier is probably correct. First, however, not to completely lose the thread of our story, we will briefly review the last 400 My of evolution of the MC.

## d. Later events

The gnathostomes are generally accepted as monophyletic, but the method by which the jaw is attached to everything else has been quite varied from the very beginnings. That is really part of the palatoquadrate story, and we will not review it here. In both placoderms and chondrichthyans the MC continued to serve as the primary lower jaw element directly. In this capacity, it came to bear a very wide variety of cutting surfaces, from the inferognathals of arthrodire placoderms to the bizarre spiral symphysial tooth whorls of *Helicoprion*. The very diversity of these forms of dentition is perhaps a strong argument that the MC first became a jaw element in the chondrichthyans, since other gnathostome clades have, by comparison, a rather limited repertoire of tooth forms.

In osteichthyans, the jaw adductors insert medially in the lower jaw, and the MC comes to be covered by dermal bones, including the dentary, angular, surangular and splenials. Although the MC remains a simple rod-like cartilage as a whole, the proximal end ossifies and becomes the articular bone which continues to form the lower jaw articulation (or one of the lower jaw articulations in the case of teleostomes and advanced therapsids) in virtually all groups except mammals.

The transition to land seems to have had almost no effect on the MC except that, in some lissamphibian groups, the distal end of the MC also may ossify as the mental bone. Despite numerous changes in dentition, the dermal bone covering, and various episodes of radical kinesis or equally radical skull consolidation, the MC has remained a small, but consistent element of the lower jaw. In some lepidosauromorphs, including sauropterygians and agamid lizards, the MC even makes a modest come-back as a superficial element on the inner (lingual) surface of the mandible.

This constancy in the very teeth (!) of obsolescence may relate to two factors. First, the MC may still provide some marginal advantage by providing those qualities that favor cartilage over bone: flexibility and elastic compressibility (*i.e.*, the ability to act as a shock absorber). Probably more importantly, the MC is still the embryonic lower jaw. The correct positioning and shape of the adult mandible depends on the MC regardless of whether the MC has any functional significance for the adult. This may constitute another, and rather different, example of the rule suggested in our discussion of the premaxilla: an element which becomes involved in several different functional units acquires evolutionary stability. However, the stability of the MC requires us to ask a more refined question. Is this a rule enforced by physiology or by ontogeny? To put the matter another way, are the constraints which stabilize a bone most likely to be imposed by survival and reproduction of the adult, or by the effect it has on the development of other units? Arguably, we now have an example of each. The premaxilla is a relatively late developmental and evolutionary component which has no obvious ontological significance but has important adult functions in several disparate areas. The MC is a critical component in development, but probably has little functional importance in the adult.

Again, I will attempt no answers. However, it may be significant that the functions of the adult MC can be changed more radically than the functions of the adult premaxilla. Thus, during mammalian development, the proximal region of the MC is transformed into the malleus (or the malleus and incus, depending on who you read), an ossicle in the mammalian middle ear. However, this is probably only a further transformation of the already transformed articular bone. The MC itself has remained resistant to any pressures that may exist for evolutionary change -- a notable stability considering the radical re-engineering of the mammalian jaw. This constancy is particularly interesting in view of the variety of transformations seen in the other mammalian gill arch derivatives. **See Figure 3**. This may be a hint that there is something a little special about the mandibular arch, or at least the MC. However, to get more than hints, we must turn to microscopes and molecules.

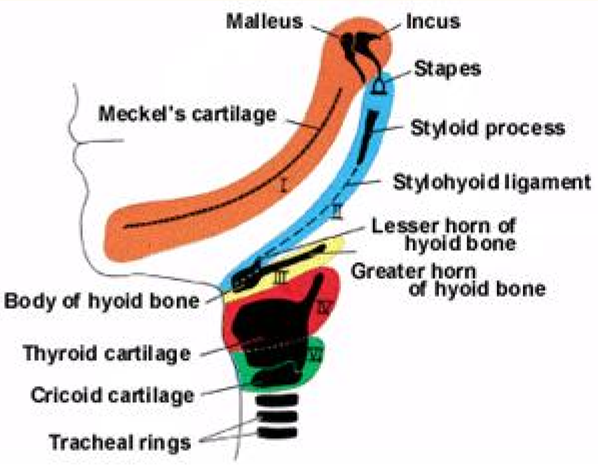

Fig. 3. Gill arch derivatives in mammals. Note the Meckelian Cartilage has not transformed significantly.

# 2. Some embryology and molecular biology

## a. Embryology

The best and most comprehensive source of WWW information on branchial arch development is at School of Anatomy - ANAT2310 Session 2 Lecture 2, including the notes at UNSW Embryo- Head and Neck Development 1. Although this is a medical site, we lack an equivalent site dedicated, for example, to shark embryology. So we must parasitize the medical profession for now. As it turns out, the human gill arches are not really all that atypical.

Humans have five gill arches, which are conveniently known as arches 1, 2, 3, 4, and 6. Arch 5 is omitted, presumably for neuroanatomical reasons. We will quickly gloss over this issue by pretending we had not noticed the numerical anomaly. Interestingly, arches 1 and 2, the mandibular and hyoid, develop well before the others. At this point, the gross anatomy appears as in Figure 4.

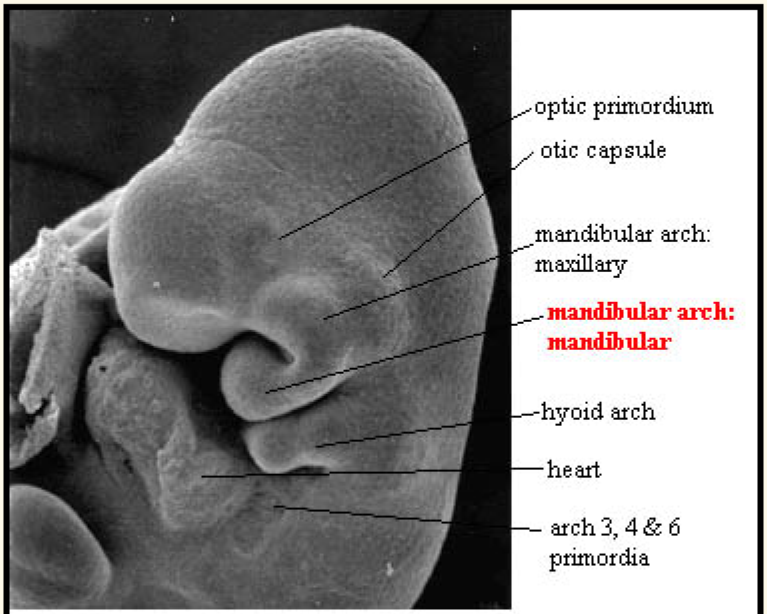

Fig. 4. Embryonic Homo with early gill arch structures.

There are several features of interest. As mentioned, the mandibular and hyoid arches develop well ahead of the others. Note also the close relationship of the mandibular arch to the otic capsule. This is a typical feature. Although we have foresworn neuroanatomy, it is worth remembering that the mandibular arch is always enervated by the Vth cranial nerve. Even in osteostracans, where the gills are somewhat distant from the brain, the first arch (velum or gill, according to your preference) appears to be enervated by this nerve. The proximity to the otic capsule and this pattern of enervation are both found in the ammocete velum.**[3]**.

The branchial arches begin as cylindrical cores of mesenchyme sandwiched between continuous sheets of epidermal ectoderm and internal endoderm. The mesenchyme is then infiltrated by neural crest ectoderm migrating from the brain and the rhombomeres of the neural tube. (Some of these terms are explained a bit more at **Early Development Notes**.) The origin and targets of these agents are quite specific. Ectoderm from the mesencephalon and rhombomere 1 specifically migrates to the mandibular arch primordium, and rhombomere 4 infiltrates the hyoid arch. The remaining arches recruit variously from rhombomeres 7 and 8. Again, we see that the mandibular and hyoid arches are developmentally different from the rest of the series.

## b. Molecular genetics

Recently, a number of molecular tools have been worked out which will allow us to look in more detail at these key events. At the moment, what is available is a series of very suggestive, but not yet decisive, experiments using the usual battery of knock-out mice, random *Danio* (zebrafish) mutants, ectopic addition of control factors and so on. Although the pathways are far from being worked out, all suggest that the mandibular arch contains the ground plan and that this plan is suppressed in the hyoid and subsequent arches, probably by homeobox genes, in favor of the gill arch plan. In particular, *hox* gene products are absent from the mandibular arch, but present in other arches. *Hox* genes specify the polarity and antero-posterior patterning of the vertebrate body and limbs, other than in some areas of the head. The pattern seems to be imposed on the various arches by the migrating neural crest ectoderm.

Thus, knockout *hoxa-2* mutant mice exhibit (a) lack of mesenchymal neural crest cell derivatives in the hyoid arch; (b) change of second arch neural crest cell identity to first arch identity; (c) homeotic transformation of second to first arch skeletal elements, including: (i) duplication of ossification centers of bones of the middle ear and (ii) duplication of Meckel's cartilage adjacent to the otic capsule. Rijli *et al*. (1993); Gendron-Maguire *et al*. (1993). These workers attribute their result to reversion of the hyoid arch to a ground pattern established by mandibular arch patterning. Interestingly, a human mutant with similar, but less drastic, symptoms, has been described. Rodriguez *et al*. (1997).

By contrast, the posterior gill arches seem to be well-integrated into the post-cranial *hox* system. Specifically, these arches respond to *hox* gene products which are introduced from the neural crest ectoderm. Some of these wandering neural crest cells are merely tourists, passing through the region on their way to the heart, which lies at the posterior end of the gill arch series. In fact, the pericardial membrane is primitively co-extensive with the gill membranes.

A screen for point mutants in *Danio* revealed a class of mutation which affected *only* the first and second arches point mutants. Piotrowski *et al*. (1997). Curiously, these mutants showed deformations largely in the ceratal components, i.e. the MC and the hyomandibula. It is not yet clear what significance these mutants will have, although the *Danio* system is obviously an important one for our purposes.

More generally, experiments with various mouse systems suggest that MC differentiation is governed by a more primitive system based on epithelial-mesenchyme interactions involving gradient regulators such as *shh, msx-1, msx-2, prx-1, prx-2,* as well as growth factors of great generality such as *EGF, BMP-2* and *BMP-4*. Barlow & Francis-West (1997); Lu et al. (1999); Shum et al. (1993); ten Berge et al. (1998). These regulatory systems are referred to as "primitive" because they appear to share at least some of the following characteristics: (a) a degree of dose-dependency, (b) partially redundancy (except for *shh*), (c) rather generalized effects in multiple areas of the embryo, (d) they, and their DNA targets, are scattered in the genome rather than being found in *hox*-boxes or similar arrangements, and (e) the regulatory pathways seem dependent on feedback loops between epithelium and mesenchyme. Time will tell whether "primitive" is a reasonable label. It is certainly a *different* system from the regulation of the posterior branchial arches. These have been thoroughly integrated into the post-cranial *hox* system.

## c. Conclusion

Given this new information, we can tentatively conclude that Janvier has the better argument. We can, at least, say with confidence that there is no simple homology between the mandibular arch and the posterior gill arches. Obviously they share some common ancestral structure. However, the basal structure seems more likely to have been the velar skeleton than an internal gill arch. The posterior arches differ because (a) they are *hox*-regulated (b) appear later in development (c) are developmentally linked more closely with the heart (as one might expect for gills) than the head **[4]**; and (d) at least the hyoid arch can be made to revert to the mandibular form by loss-of-function mutations. All things considered, this is a fairly strong set of indicators that the posterior arches are derived from a velar "arch," which has never had a respiratory function.

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**[1]** One wonders if the prevalence of this type of predation in the Silurian might not be the true reason for the nearly universal adoption of dermal armor among early gnathostomes, as well as its near universal abandonment by the Late Mesozoic.

**[2]** This may be unfair. Janvier (1996) is of the opinion (*contra* Stensi�) that the osteostracan gill apparatus, whatever it may have been, was "floating" freely in the head shield, rather than being integrated in the cartilaginous matrix. However this may be, mechanical support would not seem to have been a major evolutionary constraint inside this blockhouse skull.

**[3]** Hagfish have a homologous cranial nerve, including a "mandibular" component; but I have not been able to determine what it innervates.

**[4]** Recall that the heart is a relatively late craniate development. The hagfish has several "hearts" and the atrium and ventricle of the post-branchial pump are cleanly separated.

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# Gill Arch References

| Bones | Gill Arches |
|---|---|
| **Bones**<br>**Braincase**<br>Dermal Bones<br>**Ear**<br>**Gill Arches**<br>**Teeth** | **Overview**<br>Epibranchials<br>Hypohyal<br>Meckel's Cartilage<br>References |

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# Teeth: Overview-1

| Bones | Teeth |
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# Teeth and Scales: Structure, Development and Evolution

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## Introduction

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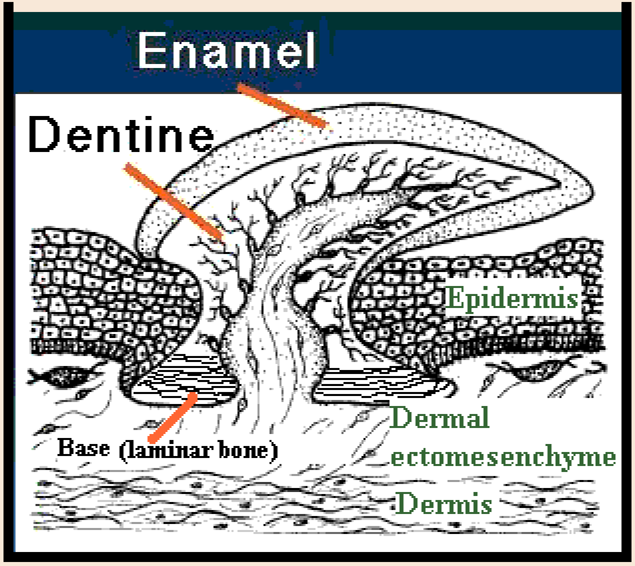
The purpose of this somewhat tedious essay is to unite and expand on a number of themes discussed in other parts of Palaeos. In particular, this discussion follows up some obscure hints dropped in our treatment of corvaspid scales. There we made various disparaging remarks about the Scandinavian School of "scale theory," and predicted that it was nearly hopeless to try and dig out of the dark scientific hole in which the Scandinavian School had left us. Since then, we have encountered the recent work of Philip Donoghue, Jean-Yves Sire, and others. Whether they will dig us out is hard to say, but they are certainly wielding their shovels with tremendous energy. All this furious activity has briefly roused us from despondent lethargy to toss a little sand about, as well.

What's at stake here is just about everything that a vertebrate uses to meet the environment except bare skin. Unlike black holes, vertebrates have hair -- and feathers and scales and teeth and so on. Over the last 500 million years or so, the vertebrates have come up with a fair selection of bits and pieces which stick out of the skin. The structure and development of all of these fashion accessories has many common features -- so many that it is virtually certain that they all derive from a common source [W+04]. Here, we will focus on the evolution of that system in



body scales (presumably the system in which the whole business first evolved) and the way it was adapted to form teeth.

Teeth and early vertebrate scales are generally treated as arising from a fundamental unit, the *odontode* or *lepidomorium*. The differences between these two (theoretical) structures will be discussed in due course. For the moment, we will speak of the odontode as it is usually discussed. The basic odontode unit is identical to the *placoid scale* of chondrichthyans [SA04] [S+98]. The odontode has three parts: (a) a *dentine*-covered cone with an internal pulp cavity (b) attached to a base of laminar bone or cartilage, and (c) capped by hypermineralized tissue [S+98], often loosely referred to as "enamel."

It turns out that we can approach the structure and development of scales and teeth (and hair and, for that matter, feathers, and even limbs) as if the three components of the odontode were three separable evolutionary modules **[4]**. These modules interact, but they are indeed separable and have often been separated in the course of evolution. This point is worth emphasizing because it is frequently forgotten in reviews of scale/tooth evolution, which tend to treat the usual three-part odontode system as if it were a fundamental unit of development. Counterexamples are not hard to find. Almost all early integumentary systems have some kind of laminar bone or cartilage as a base layer. However, this is not true of more derived structures of the same class, such as feathers [W+04], or the *elasmoid scales* of most living actinopterygians [SA04]. Galeaspid scales have a base of laminar bone, as well as an enameloid cap, but lack any trace of a dentine-covered pulp cavity [J96]. Psammosteid heterostracans have basal bone and dentine-covered odontodes, but lack enamel, or any other hypermineralized surface layer [T64].

Thus, in all probability we can treat these components separately, because they are, in fact, three different structures which have evolved in somewhat different ways and at rather different rates. Nevertheless, we will begin with a general discussion of tooth development in the most highly derived systems. As we will discuss a little later on, denticle formation on the gill arches predated the time that the mandibular arch was reconfigured as a jaw. However, we know little about those systems and will concentrate on phylogenetically uninteresting, but better-understood, systems such as the mouse. This is followed by somewhat more specific consideration of the enamel and dentine compartments. For our purposes, we will ignore the attachment module. It is quite variable and apparently shows little phylogenetic consistency [S+98]. We will then look at some aspects the evolution of this system, followed by a brief review of some "scale theory."

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# Nature, Read in Tooth and Claw: Tooth Development in Highly Derived Systems

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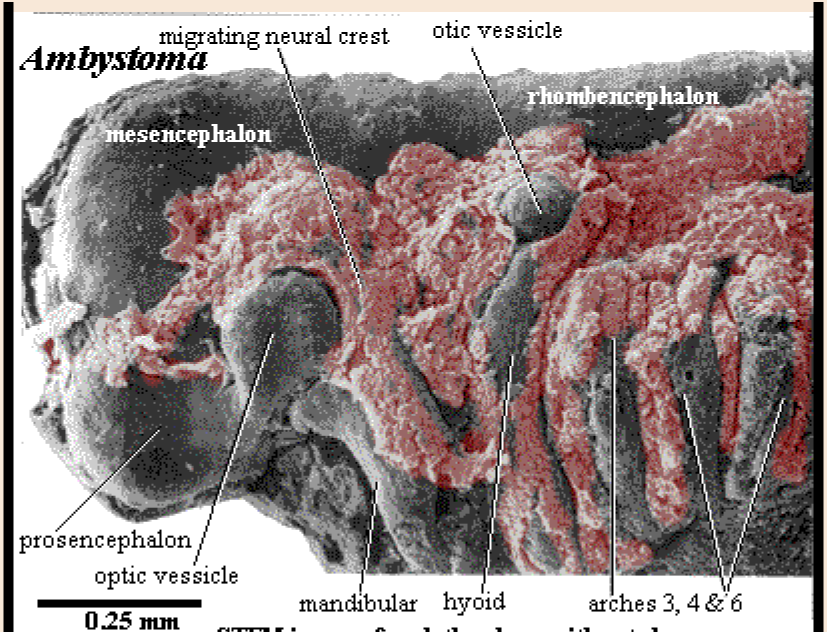
## Orientation

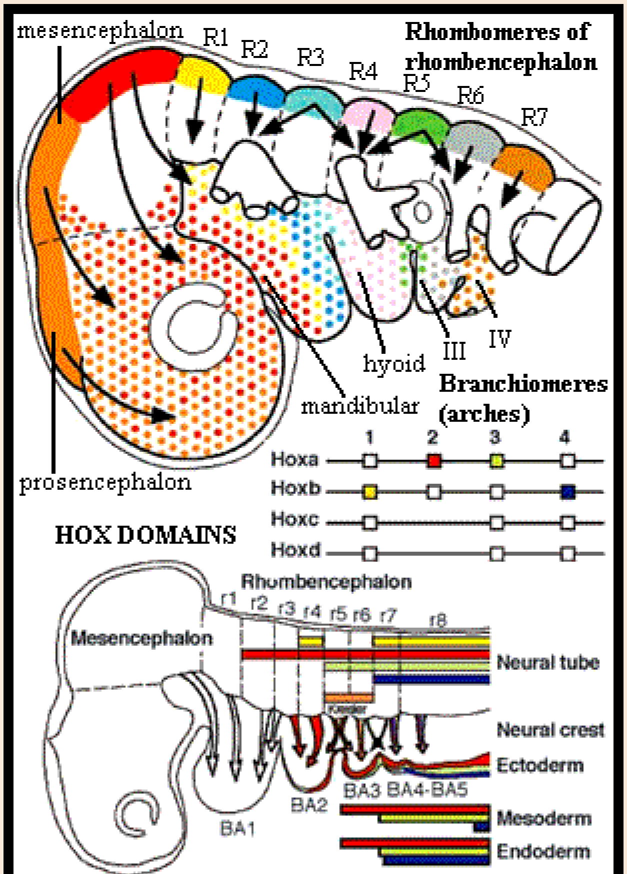
Neurulation is the process by which vertebrates form the "neural tube" which eventually differentiates into the spinal chord and related structures. The presumptive neural tube tissues



**STEM image of axolotl embryo with ectoderm removed to show migrating neural crest.**

consist of a layer of ectoderm along the dorsal midline of the embryo, between the notochord and an outer layer of epidermis. The underlying notochord produces the well-known transcription factor, Sonic hedgehog ("Shh") **[5]**. The overlying epidermis secretes another factor, BMP4. Under the influence of this Shh/BMP4 gradient, the neural ectoderm thickens, elongates, and rolls up into a tube.

The developmental hall mark of the vertebrates is neural crest ectomesenchyme. As the neural tube closes, the ectodermal cells continue to grow and divide very rapidly. Many of these cells detach from the tissue matrix and become nomadic -- that is, they form an ectoderm-derived mesenchyme, or ectomesenchyme. This neural crest mesenchyme migrates down the sides of the embryo, beneath the epidermis, to locations where it differentiates into a wide variety of structures. This wandering population of neural crest cells is quite large, particularly in the head region. The patterns of mesenchyme migration are quite specific. The cells migrate from specific portions of the neural crest to specific destinations. Many are apparently already terminally committed to the tissues they will form on arrival. In addition, they act as messengers, bearing molecular orders to the mesoderm and endoderm which they contact on arrival.



**Chick cranial neural crest patterns and hox domains. Adapted from Couly et al. (2002).**

It may be useful at this point, although perhaps not strictly necessary, to review the basic pattern of vertebrate cranial segmentation during development. The neural tube of the body tends to segment in an orderly way along the boundaries between somites. In the head, there are no somites, and the situation appears chaotic. The neural tube is broad and divides flaccidly into three parts: an anterior prosencephalon, a middle mesencephalon, and a posterior rhombencephalon. The rhombencephalon then subdivides into 7 or 8 rhombomeres. These ectodermal neural tube "segments" are superimposed on separate "segments" of mesodermal somitomeres and endodermal branchiomeres (the developing jaw, hyoid, and gill regions). This unwieldy and complex interrelationship of patterns invariably confuses humans, but the neural crest mesenchyme cells navigate this weird landscape with ease, passing from specific brain segments or rhombomeres to specific ventral destinations **[6]**.

Now, while all this dorsal to ventral activity has been going on, the endodermal gut has been continuing its stately progress through the center, from posterior to anterior, forming embryonic gill pouches and other dull, but essential structures of proper embryonic administration. However, when the endoderm reaches the future mouth region, it finds itself blocked by an unruly mass of oral epithelium, the *stomodeum*. The two opposing forces butt up against each other and form a buccopharyngeal membrane. Behind this protective wall, the endoderm holds intense, delicate discussions with the branchial neural crest to negotiate the definitive boundaries of the branchial arches, including the jaws. As it turns out, the boundaries are established largely by reference to the *Hox* messages carried by the mesenchyme from the neural crest rhombomeres. But, just as order is established, the stomodeum bursts inward like an army of clowns with cream pies, covering the mandibular arch -- in fact the whole buccopharyngeal region -- with messy and complicated layers of oral epithelium, mesenchyme from the anterior parts of the brain, and gut endoderm.

# Initiation: Don't I know You?

It is in this complex and disorderly world that the teeth are supposed to develop. The cells of the odontode are all derived from the same population of dermal *ectomesenchyme* cells derived from the *neural crest*. More specifically the future dental cells are derived from the mesenchyme of the first rhombomere and anterior brain, at least some of which were introduced from the stomodeum. Because of their anterior origin, they are Hox-less. This appears to be essential for tooth formation in normal development. [C+02]. These cells include the dentine-producing odontoblasts of the cone, as well as the cells producing the ligaments and bone of attachment [S+98].

Odontodes develop through a variety of interactions between the epithelium -- usually, but not always, of ectodermal origin -- and underlying neural crest ectomesenchyme. In the case of teeth, the initial signal is, as one might expect, given by the stomodeal epithelium. In mammals, the stomodeal invasion establishes a gradient, with *FGF8* expression over the presumptive molars and *BMP4* over the incisors. The first observable step in tooth formation, the initiation stage, is a thickening of the epithelium and condensation of the neural crest mesenchyme at sites of tooth formation [D02]. The epithelium seems to initiate this conversation with the mesenchyme, presumably using some tacky, but well-rehearsed pick-up line involving its *FGF8* and/or *BMP4*.

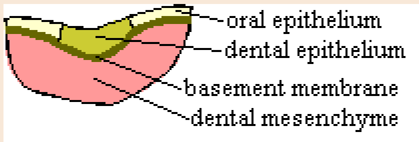
The *BMP4* gene product, in particular, is a common early epithelial signal found in many types of epithelial-mesenchyme systems. Thus, the primary result of experimentally induced over-expression of the *BMP4* gene is a variety of aberrations in hair, vibrissae, claws, teeth, and sweat glands [W+04]. In the mammalian tooth, *BMP4* is used and re-used at several different points. It is probably the initial epidermal signal to the underlying ectomesenchyme in all systems. In mouse tooth, epidermal BMP4 triggers the mesenchyme to produce Msx1 (and sometimes Msx2) [W+04], just as in the development of the vertebrate limb. It also induces its own production in mesenchyme, and the interaction of these signals appears to be a continuing feature of tooth development [C+97]. However, *Msx1* is a homologue of, and usually identical to, *Hox7*. Thus, we may wonder aloud if the dentine cone and pulp cavity are homologues of some far more ancient structure constructed on the main highway of homeobox-directed antero-posterior patterning.

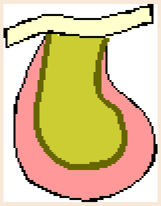
However this may be, and if the mesenchyme is not too busy adjusting its make-up, it responds to the epithelial greeting with a slight up-tick in its own *Pax9* production. In evoking this response, FGF is invariably more successful than BMP, which is one reason incisors are smaller than molars **[8]**. Thus, the initial gradient of these low level factors results in a gradient of *Pax9* responses. The increase in *Pax9* expression in turn seems to encourage the epithelial expression to become more discontinuous, as it concentrates its charms where they seem to be having the desired effect.

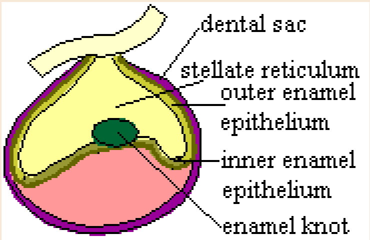
# Cap and Bell Stages: Can I Buy You a Drink?

The basic picture of tooth morphogenesis is shown below, as depicted by the authors of the **Gene Expression in Tooth** site of the University of Helsinki.

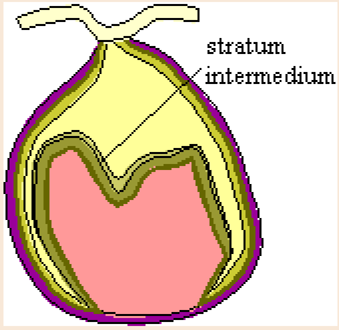
| **Initiation stage**<br>ED 10-11 | **Bud stage**<br>ED 11-13 | **Cap stage**<br>ED 13-15 | **Bell stage**<br>ED 15-17 |
|---|---|---|---|
| | | | |

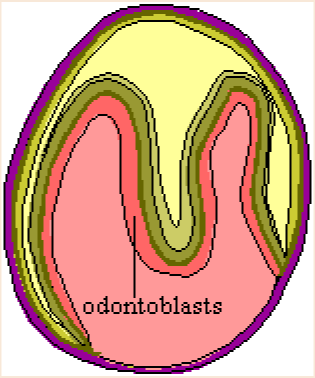
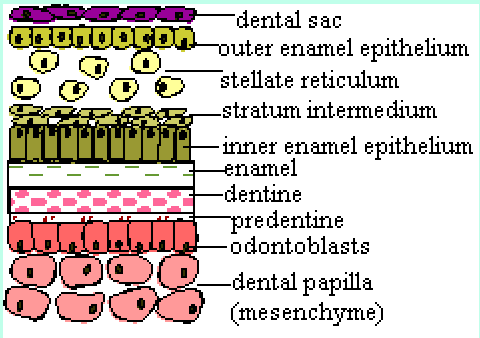
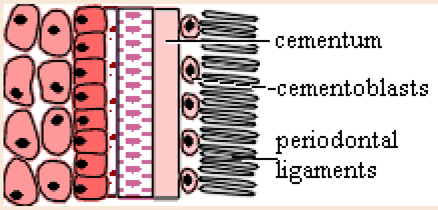






Note: basement membrane still surrounds the entire enamel epithelium



| Differentiation stage<br>ED 17-newborn | Secretory stage crown<br>newborn and onwards | Secretory stage root<br>day 3 and onwards |
|---|---|---|
|  |  |  |

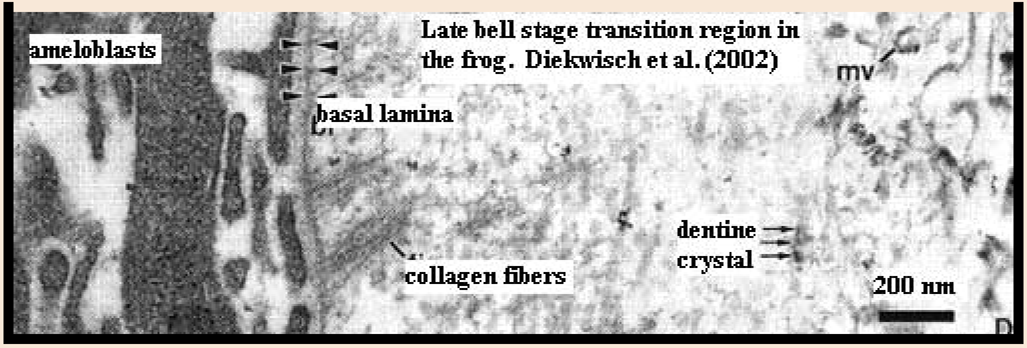
**Stages of tooth development in the mouse.** This image is adapted from The **Gene Expression in Tooth** site of the University of Helsinki. The image slices are linked to the incomparable molecular biology resources at that site.

As the result of the ensuing complex conversation among transcription factors, each tooth bud forms what is called the "enamel knot" in dental systems. This is terribly misleading nomenclature, since the knot does not produce enamel. Rather it is a small group of non-dividing cells which serves as the organizer for morphological development of the tooth [J+03]. The current thinking is that the mesenchyme is ultimately persuaded to also express *BMP4*. Things now get rather more serious, as this regulates the production of *Sonic hedgehog* (*Shh*) which has an important role in establishing and maintaining the enamel knot in teeth and equivalent organizers structures in many other epithelial-mesenchyme systems [Z+00]. Of course, meaningless noises like "important role" are tools to avoid the dizzying view down into the vast, foaming pit of ignorance around which we are carefully treading a slippery footpath of experimental evidence. Still, this is progress.

Not surprisingly, the establishment of this organizer tends to get things organized. With the epithelial enamel knot well and truly knotted up, the transfer of inducing potential passes from the epithelium to the mesenchyme. As in all other budding relationships, he eventually runs out of rehearsed lines, and it becomes her move. Classical embryology long ago demonstrated that grafting dental epithelium onto non-dental mesenchyme could produce tooth-like structures if the experiment were performed early enough in development. Somewhat later on, this no longer works, but the reciprocal experiment (grafting dental mesenchyme onto foreign epithelium) still induces teeth [D02]. The establishment of the enamel knot at the bell stage appears to be the key event in this transition, and *Shh* one of the key components of the organizer.

# Morphogenesis: "Not on a First Date!"

The organizer now kicks the morphogenetic program into gear. It is associated with the formation of a critical boundary structure, necessary for all healthy relationships. This is the "basement membrane" of light

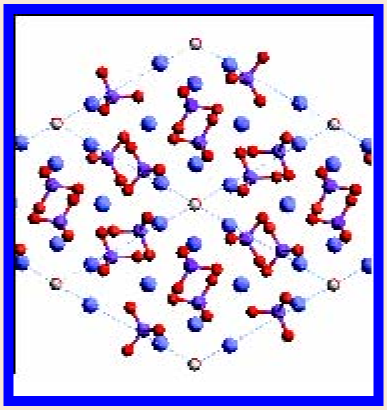


microscopists. This we take to be a pseudonym of the "basal lamina" of the electron microscopists [D+02]. This lamina separates the dentine module from the enamel module in tooth development and presumably mediates the interactions between them. Generally speaking, differentiation now proceeds in both directions away from the basal lamina, with odontoblasts creating dentine in the dental papilla (pulp cavity) and, on a somewhat slower schedule, ameloblasts creating enamel in the other direction [D+02]. When this process is well under way, the basal lamina usually begins to break down. In sharks and certain teleosts, the lamina is particularly thick and is apparently retained.

With the initiation of morphogenesis, the enamel knot also breaks down. BMP4-induced apoptosis may play a part in this step [J+03]. The pattern of *Shh* expression spreads out and/or moves to secondary organizers corresponding to individual cusps [J+00]. The pattern of cusps in the definitive tooth is primarily controlled by timing. Secondary knots which are formed earlier yield larger cusps. That is, according to current thinking, all secondary enamel knots are at least serially homologous and perhaps identical. Cusp patterns are created by differences in timing [D02], rather than under the control of *Shh* or some homeobox organizer. This has vast implications for mammalian tooth phylogenies, but too little is known at this point, and with too little certainty, to make much use of this tentative conclusion.

The details of further morphogenesis are considerably less general than the early stages described above. Morphogenesis of teeth, particularly in the very complex mammalian system, is also guided in part by a complex group of amelogenins and transcription factors of the *Fgf*, *Pax*, *Msx*, *Dlx* and *Lef* families, which seem to have considerable, but poorly understood specificity [J+03]. At any event we will now leave these teeth to develop in decent privacy and move on to other matters.

# A Digression into Dentine



Before going further into the subject, we need to look briefly into the non-cellular hard stuff that is really the whole point of the exercise. The mineral component of dentine (and enamel) may be any of several materials. Almost all are variants of apatite. At this point, textbooks usually toss out a vague comment to the effect that apatite is "essentially calcium phosphate," perhaps further obscured by rote recitation of some obviously unbalanced chemical formula for hydroxyapatite such as $Ca_5(PO_4)_3OH$. The reason for this evasive, or even disingenuous, behavior is that chemists consider apatite to be far too complex to explain to mere bio or paleo types. To our undying embarrassment, this humiliating assessment turns out to be correct -- if one insists on asking chemists to do the explaining. However, we really don't need, or even want, a mental picture of the crystal structure of apatite at 0.2 nm resolution. What we need is qualitative information on apatite structure which explains its biological properties. This we can supply this without resorting to Fourier transforms, planes of symmetry, etc. See the glossary entry at *apatite* for the relevant explanation. The most familiar apatite derivative is hydroxyapatite ("HAP"), the bulk mineral constituent of bone. Chondrichthyans may produce fluorapatite, in which a fluoride ion, rather than a hydroxyl ion, is inserted into the calcium phosphate matrix; or they may jettison apatite altogether and substitute calcium carbonate, $CaCO_3$ [D+02].

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# Teeth: Overview - 2

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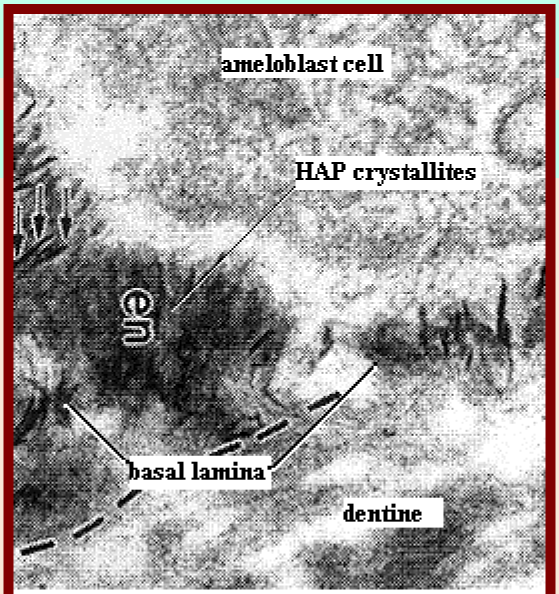
## The Hypermineralized Cap

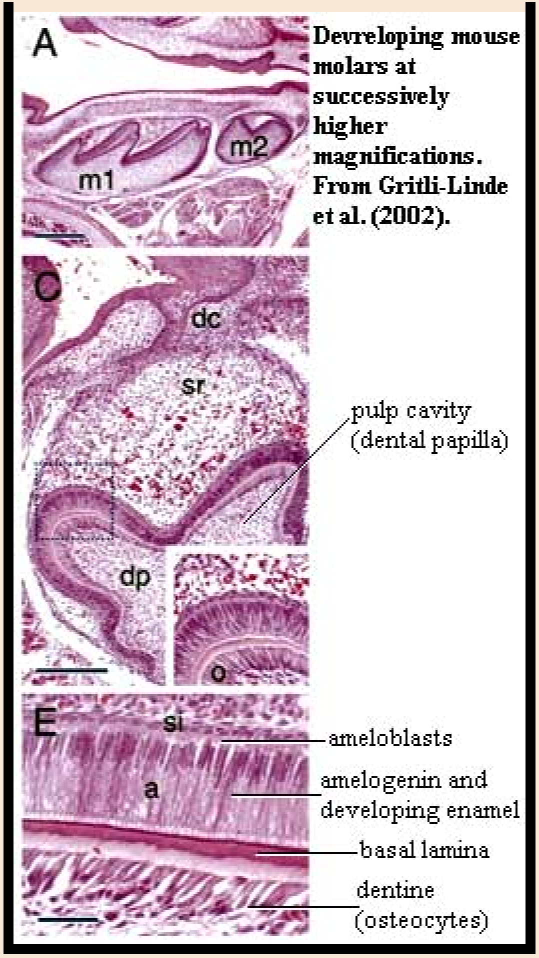
### 1. Enamel

The hypermineralized layer in mature individuals typically contains only 2% to 10% protein. When the protein content of bone drops to about 3% (*i.e.*, 97% hydroxyapatite), the material is referred to as enamel or enameloid. The difference between enamel and enameloid is discussed in the next section. For the nonce, we focus on enamel. Sarcopterygians and closely related fishes have "true" enamel. Enamel is characterized developmentally by a protein template largely composed of amelogenin, a protein secreted by cells of the epithelium. Amelogenin binds tightly to calcium and -- oddly -- also to cell surfaces [H+02]. Initially, the cap area is almost all protein, 90% of which is amelogenin [MP00]. As the tooth matures, the protein matrix is gradually degraded until the fully developed hypermineralized condition is reached, with close packing of the enamel structures [D+01].



Enamel development in frog (Rana). 1cm = ~200 nm. Diekwisch et al. (2002).

In most vertebrates, these enamel structures are formed of "semiparallel" crystallites of HAP which radiate outward from a rather distinct enamel-dentine junction [MP00]. This junction is clearly visible as a dark band or *basal lamina* in electron micrographs of developing vertebrate teeth. Most of these features can be seen in the image of the developing dental enamel in the frog, *Rana*. Mammals have evolved yet a further refinement on this system. Mammal teeth develop cylindrical or hemicylindrical *enamel prisms*. These prisms



**Devreloping mouse molars at successively higher magnifications. From Gritli-Linde et al. (2002).**

begin with "bundled" parallel crystallites, a structure found in many vertebrates, including sharks (see images at Synechodontiformes) and frogs (triple arrows in image at right). However, in mammals, these are bounded by other crystallites oriented at a sharp angle to the parallel bundles [MP00] (see image and text at glossary entry).

In all cases, the process of enamel growth and orientation is under the control of the specialized epithelial cells known as ameloblasts. Ameloblasts control the process less through the differential deposition of enamel than through the amelogenin matrix they construct. Mammals, again, add a further element of ameloblast control. Each mammal ameloblast has a terminal *Tomes process* which assists in creating and orienting the enamel prism created by that cell. The arrangement gets progressively more complicated in higher mammals, with several different amelogenins and the addition of other proteins to shape various different patterns of enamel deposition depending on the tooth type, enamel layer and location on the tooth [MP00].

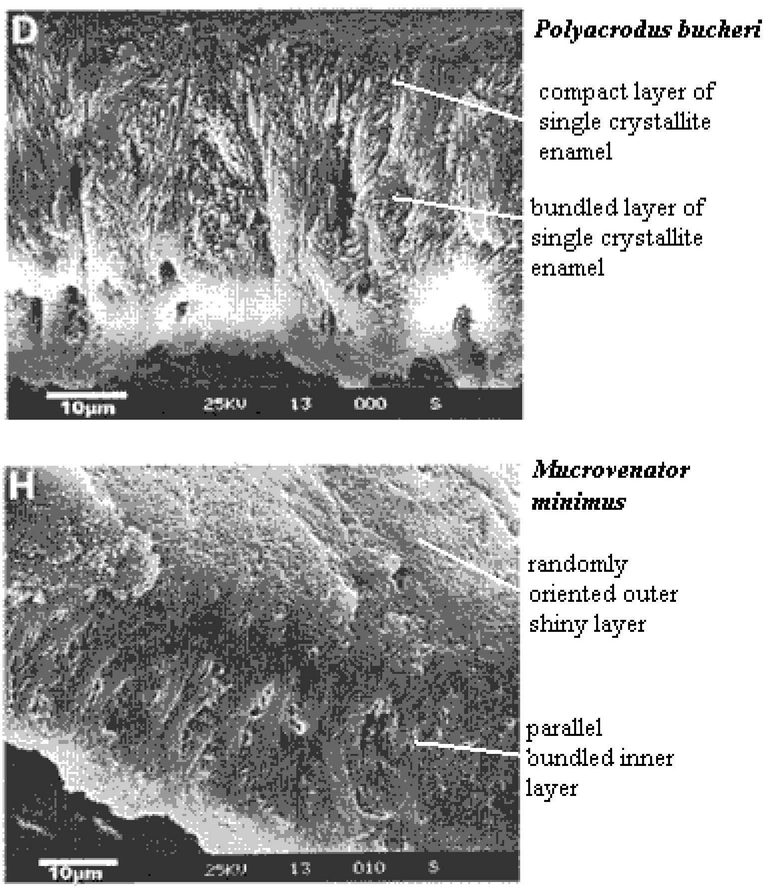
Thus, the evolution of enamel largely relates to the evolution of amelogenin. Delgado *et al* [D+01] have tried valiantly to solve this riddle, but it turns out to be a particularly hard nut to crack. There are any number of problems. First, the amelogenin gene transcript is spliced in several different ways to yield several different mRNAs in the same organism [MP00]. Thus, part of the evolutionary story is hidden -- we can probably reconstruct the gene, but we can't tell how the alternate splicing forms developed, or at what phylogenetic level. Second, amelogenin is *only* used to develop enamel and the gene is lost quickly in all lines that don't use enamel. For example, turtles and birds, which have no teeth, have no amelogenin gene. Worse, the gene has absolutely no identifiable homologues. This is almost unprecedented. Despite these problems, Delgado & Co. develop an elaborate molecular phylogeny of amelogenin. However, their model is all based on the homologues of a single, very small, exon (transcribed gene segment) which codes for a peptide (short sequence of amino acids) involved in protein transport through the endoplasmic reticulum. This purpose of this peptide is to allow amelogenin to be transported out of the cell. There is no indication that this peptide is one of the functional components of amelogenin, once exported, and there is no reason to believe that it can serve as a phylogenetic proxy for the rest of the protein.

## 2. Enameloid

We have taken enamel first, because we at least understand what enamel is, and its development is comparatively well understood in mammals and (albeit to a lesser extent) other tetrapods. Enamel*oid* development, by contrast, is poorly understood. In fact, in order to discuss the topic at all, we are forced to impose our own, possibly heterodox, notions on the unfortunate and much-abused reader. Worse, we must do so without much in the way of literature support.

Our tragic quest began in happy innocence, with a routine search for a pithy, consensus definition of "enameloid" with which to enliven this turgid discourse. Our naive curiosity soon turned to bewilderment, rapidly degenerating into a desperate and disorganized hunt for any kind of definition at all. A few hours later, out of the depths of a swirling maelstrom of paleodental chaos, it suddenly became very clear -- from no particular source -- that the absence of a positive definition enameloid is an inevitable consequence of its true nature. Enameloid is not a particular structure, but simply the name we give to a continuum of hard tissues. Enamel lies at one extreme of this continuum. A theoretical dentine-like substance lies at the other extreme.

What all enameloids seem to have in common is a significant mesenchymal component to the protein matrix in which the mineral (not always hydroxyapatite) is laid down. That is, rather than amelogenin dropping like gentle rain from epithelial ameloblasts outside the basal lamina, other proteins, rising like writhing worms from odontoblasts in the depths of the underlying mesenchyme, form some or all of the protein matrix. The protein in question is usually, or predominantly, collagen, but other proteins may play important roles.



**Enamel layers of a hybodont (Paolyacrodus) and basal synechodont (Mucrovenator) from the same location with similar preparation.**

In real life, there is no clean differentiation. Stuff that looks suspiciously like true enamel still appears adjacent to, or as a layer of, many enameloids. Basal actinopterygians sometimes have both substances. Living sharks have no true enamel (we are told), but amelogenin mRNA transcripts can be found around the developing tooth. In fact, the enameloid teeth of neoselachians, urodeles and some teleosts has three layers: (a) a rather dense layer of rather randomly-oriented small crystallites, often with considerable residual collagen, near the basal lamina, (b) a layer of long parallel crystallites, which may or may not be bundled into distinct strands, and an amorphous surface layer [C+01] [D+02]. Unfortunately, there appears to be little phylogenetic importance to this arrangement, since more primitive elasmobranchs have a completely different arrangement involving an inner parallel bundled layer and a more enamel-like outer, single-crystallite layer [C+01]. Hence the lack of any dependable definitions for enameloid. The substance varies even within teeth and between organisms, depending on the nature and degree of odontoblast (or perhaps other mesenchymal) participation.

**Update:** We have now been enlightened by Gillis & Donoghue (2007). To our surprise and dismay, it turns out that this description is essentially correct. Frankly, we were hoping the story would turn out to be more strange and interesting -- but we will settle for comprehensibility. The authors define enameloid as "a hypermineralized tissue with a matrix of mixed ameloblastic (ectodermal) and odontoblastic (ectomesenchymal) origin." SEMs of living and fossil material shows that enameloid is probably plesiomorphic for gnathostomes. ATW080227

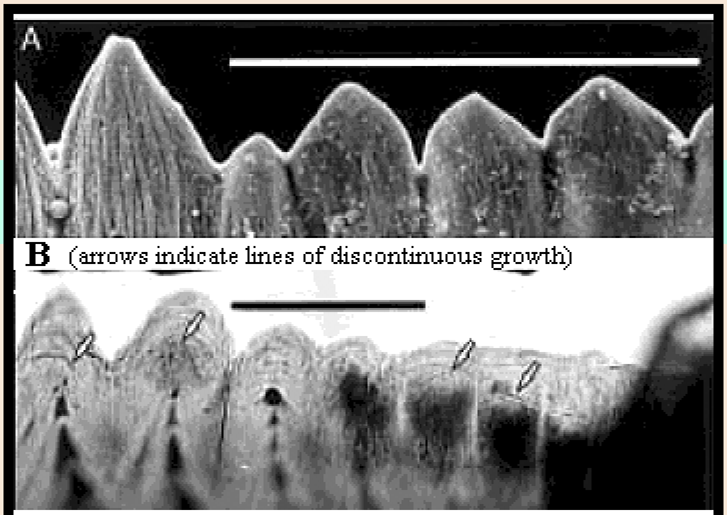
Whatever the protein matrix, mineralization proceeds more or less as in enamel teeth [D+02]. That is, mineralization begins with the deposition of tiny amorphous mineral grains. These serve as nuclei for the formation of small, randomly oriented crystal platelets 5-20 nm in diameter [D+02]. These platelets may not be apatite, but rather calcium carbonate or phosphate in the process of conversion to apatite. In any event, the small platelets probably coalesce to form the long crystals which soon dominate the enameloid layer. Presumably, in enameloid layers with parallel crystallites, the protein matrix is so arranged that an elongating crystal is increasingly forced to orient along an axis perpendicular to the basal lamina [D+02].

The further morphogenesis of the cap region is also rather variable. For example, in mouse teeth, *Shh* transcription ends fairly soon after the organizer is formed. Secondary organizers take over cusp development in mammals, but it is uncertain what, if any role *shh* plays in this process. By contrast, in elasmoid scales, *Shh* appears quite late and continues to be produced in a posteriorly migrating zone equivalent to the basal lamina of teeth and (presumably) ancient scales [SA04]. However, both of these are highly derived systems, and it would probably be a mistake to assume that either is typical of development in deep time.

# Odontode Evolution

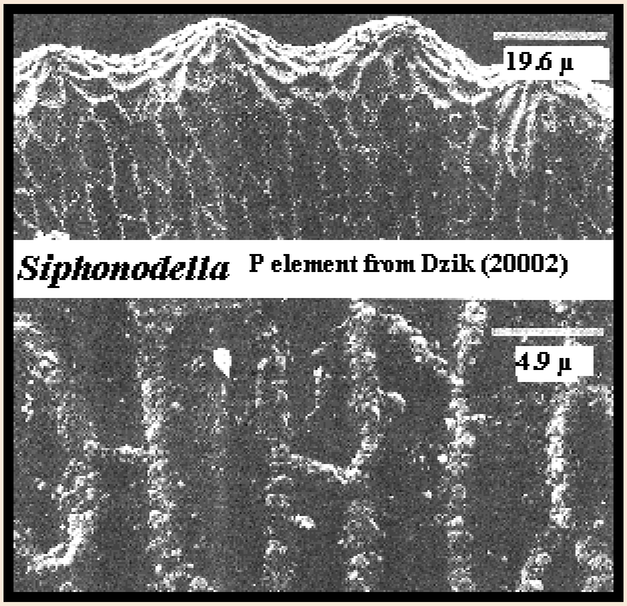
Now, if all this is true -- though we make no promises and disclaim all warranties -- we may be able to trace some of the main themes in the evolution of the system.

## Conodonts



**Idiognathodus: SEM images of Pa element denticle tips. (A) Slightly worn whole tips (B) Thin section of more heavily worn tips. Scale bars = 0.1 mm. Donoghue & Purnell (1999).**

Perhaps the most basal system in which denticulate structures are reasonably well known is the feeding apparatus of conodonts. The general form and structure of these odd "teeth" is discussed in more detail elsewhere. For our purposes here, we focus on the structure of the denticles, as shown in the image from Donoghue & Purnell [DP99]. In the image, note the fibrous structure of the denticle tips which extends almost to the end of the denticle. In cross-section, the structure of the tips is dense, but with a rather woven texture. This suggests an enameloid based on a collagen matrix, as Sansom *et al*. [S+92] have concluded. As Donoghue & Purnell point out, growth was clearly discontinuous. To judge from the literature, each growth cycle adding a layer of 1-5μ mineralized tissue. From the cross section, we can see that the pulp cavity was retreating, becoming larger, but also more distant from the tip, with each growth cycle. Thus, it seems unlikely that collagen was produced from pulp odontoblasts as in teeth. It must have been applied, probably parallel to the surface, by an epithelial layer which periodically covered the denticles, as Donoghue & Purnell suggest **[7]**.



***Siphonodella*** **P element from Dzik (20002)**

However, it is harder to accept the conclusion of some conodont workers that this is a gnathostome-style dentine-plus-enamel system [DS02]. Dzik [D00], for example, refers to the secretory cells as "ameloblasts" although his work shows quite clearly that these cells behaved as an epithelial monolayer which primarily deposited mineralized tissue as amorphous clumps in the spaces between adjacent cells.

In short, the gross morphology of conodont denticles generally resembles an odontode, but the fine structure is clearly laminar, rather fibrous, and without elongate crystals. Our interpretation of the histology is that we are seeing something close to enameloid, but applied as a series of very thin layers and without extensive crystallite development.

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# Teeth: Overview - 3

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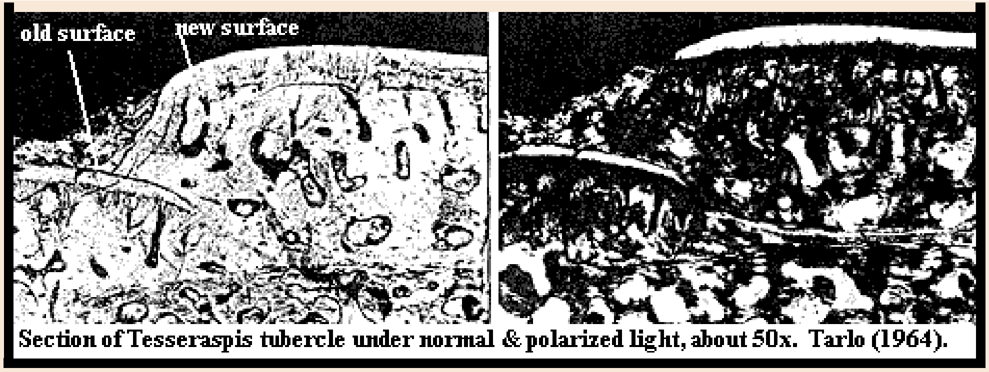
## Pteraspidomorphs

Thus , the conodont apparatus does not seem to be made of odontodes as they are understood today. Nevertheless, at least the dentine cone part of the odontode seems to have appeared *very* early in vertebrate evolution, possibly even before the vertebrates themselves. Isolated scales of this type are known from the Furongian (Late Cambrian), and the typical dentine scale cone is commonplace among both the Pteraspidomorphi and Thelodonti. The evolution of hard tissues in pteraspidomorphs was quite diverse, and the development of the mineralized integument here is still obscure. Halstead [T64] makes a compelling case that the external dentine-capped tubercles were replaced and/or repaired throughout adult life. In order to explain this phenomenon, he invokes a metabolic connection through the supposedly acellular *aspidine* matrix. This work is discussed elsewhere. The point (also made by Halstead) is that, as in conodonts, this required periodic covering of the surface with some epidermal tissue. However, in this system, mesenchymal tissue was presumably proliferating below the epidermis, creating something like familiar dentine odontode structure with its array of dentine canals.

Assuming the conodont process to be basal, it is natural to suppose that the epithelium could be engaged to apply a thin layer of acellular hypermineralized tissue to the surface. The literature is full of confusion and contradiction about whether an "enamel" layer was sometimes present on the outer surface of heterostracan plates and scales. Halstead [T64] denies this was present in psammosteids, and we have no reason to doubt him. However he also supplies some interesting comparative images of other heterostracans plates, one of which (*Tesseraspis*) is reproduced here. Note that the right and left halves show the same image, but the image on the right is taken with "crossed nichols." In this technique, light is passed through a polarization filter before reaching the specimen. Another filter, oriented at 90° to the first, is placed between the specimen and the camera. Light can only reach the camera if the light waves are rotated by the specimen. Bright regions then probably indicate crystals capable of rotating the light waves through some consistent angle.

In Halstead's image, there are two types of apparently crystalline materials:



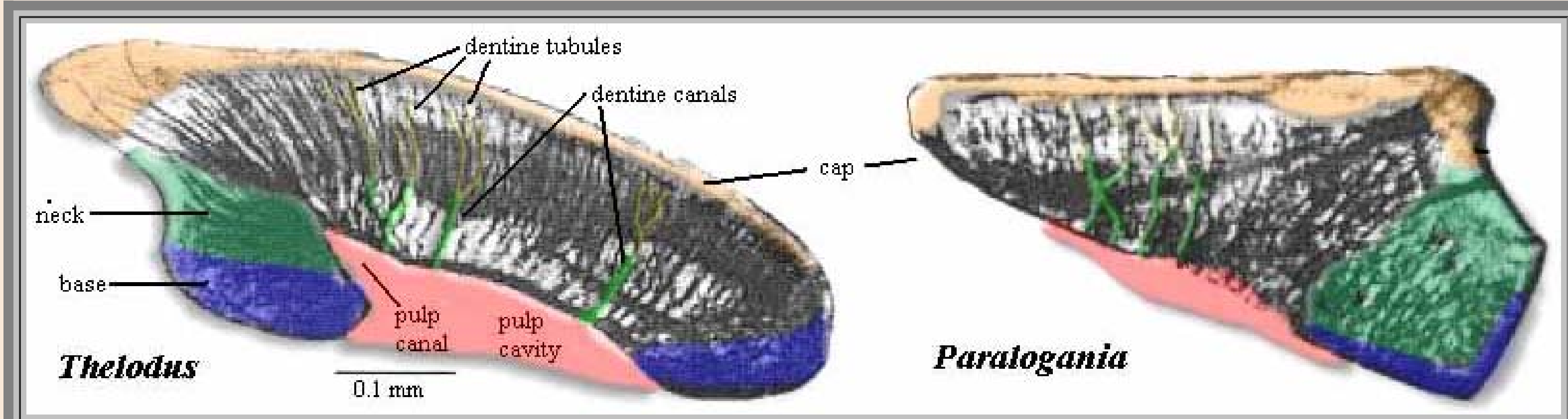
Section of Tesseraspis tubercle under normal & polarized light, about 50x. Tarlo (1964).

"lines" and shapeless blobs. The blobs correspond to vacuities in the dentine and are probably due to calcite or some other post-mortem infilling. The lines, however, are clearly dense material on the surface of both new and partially overgrown tubercles. Note especially the tubercle labeled "old surface." Here, we can observe dentine tubules around which the apatite has been partially resorbed. The tubules appear to hang down like hairs from the surface material, but they do not enter it. The tubule region is dark and probably amorphous and non-crystalline. By contrast, the surface material shines brightly, and tubules are absent. In short, we have ordered, dense, crystalline material on top of dentine tubules -- a very good indicator of an enamel-like material, without evidence of inclusions from osteoblasts. The enamel appears to be perhaps 20-30 µ thick -- thin, but much more substantial than the surface coating in conodonts. Thus, our best guess is that these are ordered apatite crystallites. The presence of some long-distance ordering should give us pause. It strongly suggests that the crystals did not form randomly, but were lined up on a regular matrix.

Does this mean that true enamel is a synapomorphy of the vertebrates? No. However, it does seem certain that the heterostracans had achieved the basic tissue configuration needed to use one of the most powerful utensils in the vertebrate developmental toolbox, the epithelial - mesenchyme interaction discussed earlier. In fact, those interactions would be hard to avoid. If Halstead is right, then during periods of plate repair, mesenchyme would proliferate from scattered dormant refugia in the aspidine and grow in the gaps between tubercles and wherever else there was room to grow. At the same time a thin epithelium would grow over the plates or scales to protect the mesenchyme. *The two tissues would meet precisely at those places where the dentine tubercles had been damaged or abraded away*. Thus, it would be natural, even unavoidable, that this contact would become the metabolic signal for the mesenchyme to produce dentine tubercles. It would be equally natural, although perhaps not unavoidable, that the epithelium would evolve a method to produce a hypermineralized "finish" to seal off the external surface of the tubercles. The physical evidence suggests that this layer was thick enough, and ordered enough, at least in some cases, to infer the presence of some protein matrix. However heterostracan "enamel" is not thick enough to be true enamel, nor does it have the multi-layered appearance of a mixed collagen-amelogenin enameloid system. What we are probably seeing is a single-layered collagen based matrix -- similar to the conodont system, but ordered by specialized epithelial cells, rather than simply painted on top in some random orientation.

# Thelodonts

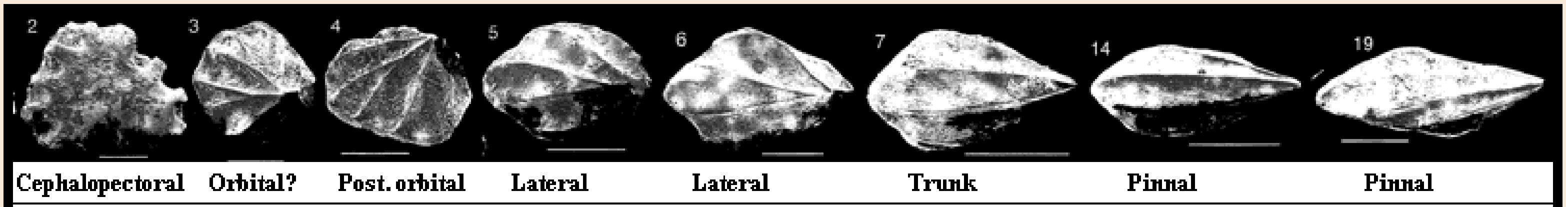
In the thelodonts, we see several critical advances. Thelodont scales presumably developed subcutaneously. This seems a small matter, but it meant that the fish no longer had to undergo periodic repair cycles and could remain active at all times. Furthermore, scales would be produced at a permanent epithelial - mesenchyme boundary, which allowed the formation of regular scales of a distinctive shape and pattern. That shape could then evolve to become more hydrodynamic, improving mobility.



**Comparison of thelodontid and loganiid scales** The **thelodontid** scale is relatively small and has a rounded crown. It has a more distinct pulp cavity with a uniformly sharp border. The dentine tubules and canals are generally straight and there are relatively few spaces (trapped cell bodies) in the crown. This histology is characteristic of orthodentine. The base is slightly inflated and (although difficult to see in this view) tends to form a toroidal opening to the pulp cavity. The **loganiid** scale is larger and has a rather flat crown. The pulp cavity is barely discernable, and its margin is rough or indistinct in the central region. The dentine tubules form a messy-looking network with numerous spaces. This histology is characteristic of mesodentine. The two examples are both from Karatajute-Talimaa & Marss (2002).

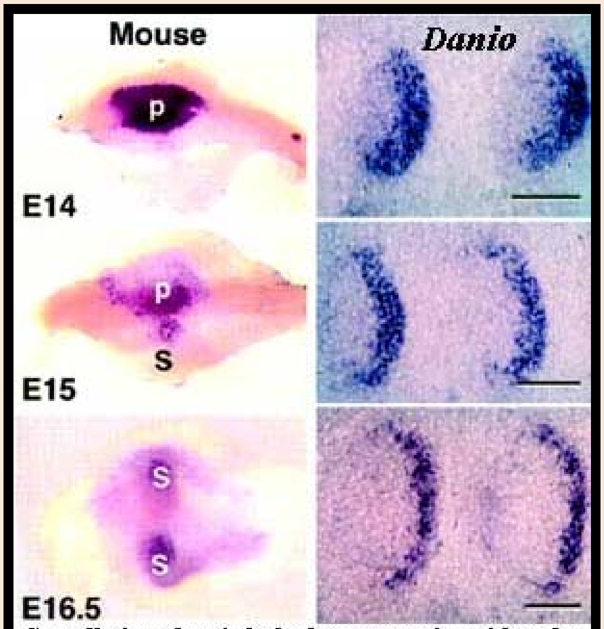
The hypermineralized cap remained very thin, although the outer surface often became very elaborately ornamented. This suggests that the epithelial interaction with the base odontode was becoming increasingly sophisticated. Thelodonts also produced several different types of dentine, as shown in the image above. This variety tends to confirm the widespread suspicion dentine histology has rather limited phylogenetic value.

Far more revealing are the long-range antero-posterior changes in the scale morphology, as shown below.



Loganellia scales arranged as an anterior to posterior transformation series. All images from Blom (1999).

This transformation series has been somewhat artificially assembled. However, it is sufficient to illustrate two differences from the heterostracan condition, each of which has specific developmental implications.



Correllation of sonic hedgehog expression with molar cusp development in mouse and scale elongation in zebrafish. From Jernvall et al. (2000) and Sire & Akimenko (2004), respectively.

**Specific center of symmetry**: Rather than some sort of vaguely pustule shaped dome, thelodont scales have one or more specific centers of symmetry. This probably correlates with an organizing center or "enamel knot." This, in turn, suggests the presence of an *Shh* pathway using the same *BMP4*-dependent signaling system discussed above.

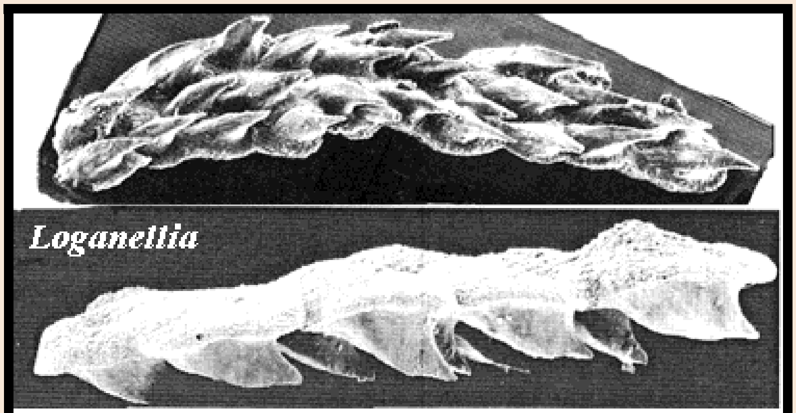
**Movement of the Axis:** Further, the center of symmetry moves posteriorly in a rather regular sequence. In both the teeth of mammals and the *elasmoid scales* of most living actinopterygians, directional "stretching" of the tooth or scale is associated with a specific pattern of *Shh* expression, late in development, in which *Shh* expression spreads out from the primary "enamel knot" into subsidiary cusps (tooth) or along a broad growth front (scales) [SA04]. This *phylogenetic bracket* (assuming we've got the phylogeny right) allows us to postulate that thelodont scale development had begun to be governed by the same mechanism.

But two things are also missing:

**No dorsoventral patterning**: Thelodont scales show very little dorsoventral patterning. It is generally not possible to tell whether a body fossil is in dorsal or ventral orientation. *See*, for example the famous debate over the holotype of *Turinia* [DS01].

**No prepatterning:** in osteichthyans, scale development proceeds from an initiation scale in regular rows, and the epidermis appears to be prepatterned in some manner to produce scales only in certain positions [SA04]. In thelodonts, the scales show no signs of a regular arrangement. There are two known exceptions, both in highly derived thelodonts. *Lanarkia* has two kinds of scales. The large, "trumpet" scales are arranged at regular intervals in lines running down the body parallel to a mid-dorsal line of ridged scales. This is interesting, but not particularly informative, as the mid-dorsal ridge line is easily explained by the unique relationship to the notochord. While we cannot know the molecular biology of thelodonts, the notochord is a notorious producer of *Shh*, thus providing a ready explanation for strange effects in this area which do not require pre-patterning. The more interesting exception occurs in *Loganellia*.

# *Loganellia*



**Pharyngeal denticle arrays in dorsal (top) and ventrolateral (bottom) views. Adapted from Smith & Coates (2001).**

The more important example for present purposes are the branchial denticle arrays found in some thelodonts [vJ93] [SC01]. Or, to be more precise, they are found in *Loganellia* -- one of the thelodonts which is most gnathostome-like in other respects. *Loganellia* did not have jaws, but it did have gill arches, and these are where the denticle arrays are believed to have come from. Jaws are quite probably related to the gill arches, and pharyngeal teeth associated with the gill arches are very common in living actinopterygians. See, for example, the elaborate gill arch dentition of *Amia* or the Ostariophysi. Similar pharyngeal denticle arrays are found in the pharynx of the early chondrichthyan, *Stethacanthus* (a/k/a *Akmonistion*), and in some acanthodians [SC01]. Most recently, similar structures have been reported from the branchial chambers of *all* major placoderm groups [JS03] **[1]**.

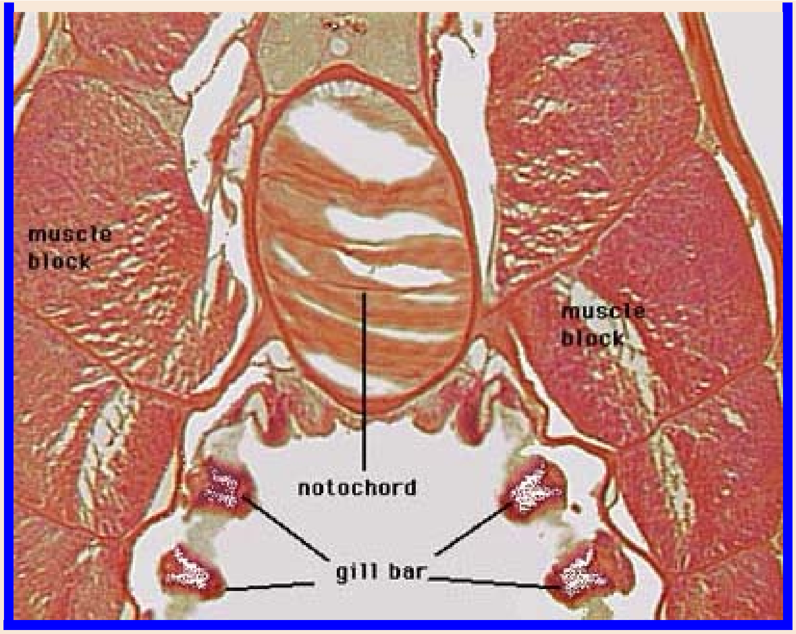
Note that these denticles are fused at the base and form roughly linear arrays. The appearance of ordering on the gill arches, but not in the integument, suggests that this patterning is related to the influence of pharyngeal endoderm. The influence of endoderm is often said to be essential to the formation of teeth [DS02]. This is, at least, subject to exceptions. *See* the discussion of *Denticeps*, below. However, sensitivity to endoderm strongly suggests the integration of the odontode development system with endodermal transcription factors, such as Pax9.

The implication here is that this linear aggregation of denticles is a key synapomorphy joining gnathostomes and *Loganellia*. This may be the case. Both *Loganellia* and *Sheilia*, another Loganiid, have been reported to possess multiple gill slits and pectoral fins. *Sheilia* may even have pelvic fins, specialized scales on the fin leading edges and some degree of dorsoventral scale specialization [M+02].

# Gnathostomata

We are now at last ready to discuss the gnathostomes and the subject of teeth. Unfortunately, at this key transition point we are also about out of things to say to which we can attach much confidence. The evo-devo of the jaw is perhaps as poorly understood as the gross morphological change it underlies. This particular question has inspired a number of inspired guesses. A few years ago a group of molecular scientists, reinforced by Philippe Janvier, nominated *Otx1* as a key inducer based on its presence in a number of characteristic gnathostome or near- gnathostome features [M+00]. In particular, *Otx1* is expressed in the horizontal *semi-circular canal* of the *middle ear*, which evolved at about the same phylogenetic level as the jaw. However, *Otx1* seems to be more or less confined to neural and brain-related tissues [Z+02] and no information to date relates it to tooth, jaw or scales. Other possible candidates might include some member of the *Wnt* series, a novel *BMP* signal, or perhaps a mutant *Shh*.

Our personal endorsement might go to something more along the lines of *Pax9*. The *Pax* family of genes code for proteins with a highly conserved, 128-amino acid, *N-terminal paired* DNA binding domain [H+00], an octapeptide of unknown function, and a *homeobox* domain. The *C-terminal* portions of the protein are rather variable. Like many vertebrate transcription factor genes, the *Pax* genes come in pairs **[2]**. *Pax1* and *Pax9* are quite similar, and both lack the homeobox domain region. The extant cephalochordate *Branchiostoma* has only one gene, which appears to be homologous to both *Pax1* and *Pax9* [H+00]. This gene, *AmphiPax1*, is expressed in the gill bars [H+00], homologous to the inner, endodermal gill pouches and (later) gill arches of vertebrates [L+01]. *Pax9* is similarly expressed in the gill arches of vertebrates



(and, it seems, in the inner ear). It is also expressed, largely in the *endoderm*, in a variety of other phylogenetically interesting places, such as the developing vertebrae [P+99], limb buds, and -- of course -- the jaw. Interestingly, it is *not* expressed in the axial "skeleton" of non-vertebrate chordates [DS02]. Given the developmental information we have, and the phylogenetic information we have inferred, one crucial test of *Pax9* is whether its expression is related to *Shh* expression. As it happens, both *Pax1* and *Pax9* are initially induced by *Shh*, from the notochord (for vertebrae) [P+99], presumably from the apical ectodermal ridge (limbs), the neural crest ectomesenchyme (for pharyngeal arches), and the enamel knot (for teeth). We understand (*i.e.* from abstracts only) that *Pax9* also induces *BMP4* production, which modulates *Shh* expression in teeth as discussed earlier. Thus it seems likely that some relatively complex feedback control mechanism is involved.

Unfortunately, more recent (*i.e.*, 2001 and later) work has uncovered whole new groups of transcription factors which appear to be involved in molding the characteristic structures of gnathostomes: *Dlx*, and *Lef* genes as well as novel *FGF*s and *Msx*s [J+03]. Thus we must retire in disorder from this otherwise entertaining subject. However, if we were forced at gunpoint to speculate, we might choke out the words "*sonic hedgehog*."

# Sonic Hedgehog?

*Shh* itself has not changed, of course. It is more or less the same gene in all metazoans. What seems to have happened is that *Shh* somehow became capable of directing traffic along induction pathways on which it was previously a mere pedestrian. It has always had the ability, as we saw in scale development, to alter polarity and shape. Why does it suddenly become a key inducer in creating a variety of new shapes and structures? A likely mechanism is not at all hard to identify: the profligate use by vertebrates of ectomesenchyme from the neural crest, combined with the equally profligate creation, discussed above, of new transcription factor paralogues during early vertebrate evolution.

Neural crest ectoderm (or ectomesenchyme) is the hallmark of the chordates. As the chordate head and brain develop, this material drips down from the dorsal neural crest over the rest of the body like water overflowing a bathtub. It comes in contact with all kinds of tissues and enters into the formation of all of the characteristic vertebrate -- and gnathostome -- structures. In particular, it forms the entire splanchnocranium (gill arches, jaws and related structures) [DS02]. *Shh* is involved at every step, usually through its ability to interact with bone morphogenic proteins (*BMP*s), as mentioned above. *Shh* is secreted by the *neural plate* and notochord during formation of the neural crest tissue, and also helps mediate cell adhesion during neural crest migration [T+01]. It is deeply involved in differentiation and, especially, morphogenesis of all of the structures of interest, again frequently through its ability to play nicely with *BMP*s.

Now, one developmental "problem" of early vertebrates would be to evolve a mechanism for managing the enormously complex morphology of these novel structures. Fortunately, the early vertebrates had handy two to four paralogues of many transcription factors thanks to the gene duplication events previously discussed. In order to control the *shapes* of the structures controlled by the pathways influenced by these factors, it would be a simple, and practically inevitable, matter to develop a mechanism by which one paralogue reacted differently than the other to either *Shh* or to *BMPs* controlled by *Shh*. By natural variation in the degree of *Shh/BMP* sensitivity, the amount of the transcription factors present, and the preexisting *Shh/BMP* interactions, practically any desirable form could be evolved in relatively short order.

Thus, quite without meaning to, we have blundered into a testable theory of gnathostome evo-devo. It should be possible to show that the paired *Pax, Otx, Lef, Msx*, and (particularly!) *Dlx* paralogues show a diverging pattern of pattern of responses to *Shh/BMP* regulation over the course of vertebrate evolution. This is really only a molecular variation on *Williston's Law*. Furthermore, we should look even more closely at molecular development in those rare vertebrates, such as the Chondrostei, which have clearly undergone additional rounds of polyploidy (genome replication) during more recent geological time. Of course, the fact that that a hypothesis is testable does not mean it is *right*; but we can, at least, look forward to day when we may be proven *wrong*.

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# Teeth: Overview - 4

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# Scale Theory: Modulation and Dissonance

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Having completed this sojourn through the arcana of molecular embryology and petrified fish scales, we may return to the subject with which we began, namely the peculiar theoretical constructs which make up "scale theory." We will begin with the dominant scale theory of the mid-Twentieth Century. Despite its numerous failings, it is still mindlessly repeated in many texts. Thus, the well-prepared student still needs to know this enemy and arm himself to extirpate any remaining germs of its false doctrine. We will then modulate to a more harmonic scale, the odontode theory of Reif, as practiced by various paleontologists today. Finally, we will bang away at various points, in a manic fashion, to demonstrate certain dissonances which may be inherent in the whole idea of a scale theory.

## Lepidomorial Theory

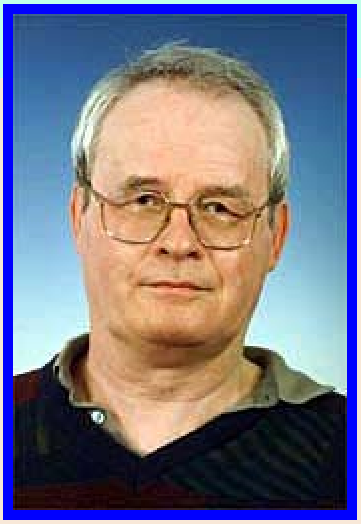
As discussed briefly elsewhere, scale theory in the middle reaches of the last century meant the Scandinavian School, of which Erik Stensiö was the best-known and most vocal proponent. This was a typological theory which attempted to explain all scales and teeth as simply differing combinations of theoretical scale units called *lepidomoria*. A lepidomorium is essentially the three-part unit we have been discussing from the beginning, consisting of bone base, a dentine-covered pulp cavity, and a hypermineralized cap. However, the Scandinavian School also supposed that the structure was fundamentally circumscribed by a single vascular loop as shown in the image. Thus, in this view, essentially all real scales and

Lepidomorium

teeth represent coalescences of these theoretical units [D02]. As Donoghue [D02] points out, the lepidomorial theory is a "concrescence" based model. Scales and teeth only recombine lepidomoria in different ways. The basic lepidomorial unit never evolves or differentiates. Despite this peculiar, almost anti-evolutionary way of looking at things, the theory was enormously influential.

However, no one has ever found a true lepidomorium. The theory could be used to *describe* any scale or dental structure, but it was unclear that it actually *explained* anything. Thus, by the 1990's, the Scandinavian School had few partisans -- but also few serious challengers. One of those few was the extraordinary **[3]** Prof. Wolf-Ernst Reif of the University of Tübingen. In about 1976, Reif began an empirical study of the squamation and dentition of sharks which lasted almost twenty years. What Reif found was difficult to reconcile with the approach taken by Stensiö and others of the Scandinavian School. Lepidomorial theory predicted that scales and teeth were simply slightly different arrangements of the same basic unit. In sharks such as *Scyliorhynchus*, in which both structures are very simple, one might expect that teeth and scales would be developmentally integrated. They're not. *See, e.g.*, [R80]. The sequence and timing of development are quite different, even in sharks with oral denticles other than teeth. Scales and teeth do not grade into each other. Teeth develop as families, while scales develop individually. The bone of attachment is derived quite differently.

# Odontode Differentiation Theory



What Reif proposed was a very different approach. First and foremost, he substituted the odontode -- a real structure found in real organisms -- for the theoretical lepidomorium. Although he still regarded the odontode as a sort of fundamental unit, Reif argued that odontodes are capable of differentiating into various types and evolving in more or less the same way as any other biological structure. As Donoghue [D02] points out, this is the very opposite of the lepidomorial theory, with its supposed integration of invariant fundamental units. Odontodes may physically merge, but they evolve by differentiation of different types of the fundamental unit. Reif, as summarized by [J96] and [D02], posits that odontodes are organized with respect to each other by a "zone of inhibition" of greater or lesser size and persistence, which inhibits the formation of other odontodes in the immediate vicinity of an existing structure (this is another example of the Sultan effect, discussed elsewhere). Donoghue [D02] argues that this kind of spatial organization is accomplished by co-expression of *Shh*, one or more *BMP*s and *FGF4*, as in the enamel knot of the developing mammalian tooth. The BMPs are Shh antagonists, but are also low molecular-weight substances which diffuse outward rapidly. Thus, the region around the source is rich in the FGF4, a promoter of *Shh*, while surrounding areas have a preponderance of BMPs, suppressing the formation of competing centers of *Shh* activity.

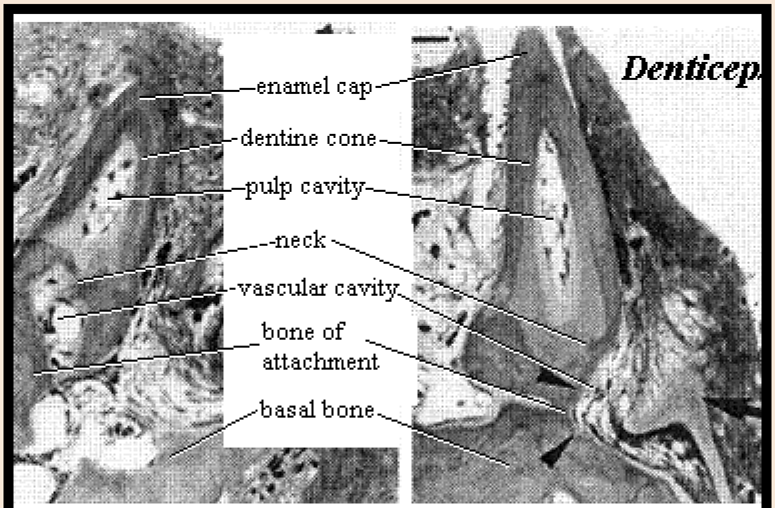
Dr. Moya Smith and others have argued cogently that tooth and scale, although presumably derived from the same source, diverged long ago. *See, e.g.*, [SC01]. Pressing this phylogenetic analogy, they assert that teeth and scales separated at a very early point in vertebrate phylogeny and have specialized in quite different ways [SC01][D02]. In a long series of papers, Smith and co-workers have developed a great deal of new information on the evolution of endoderm-influenced denticles.

# Denticles & Dissonance: the Ill-Tempered Clupeomorph

Now that we have walked our way through the basic chords of scale theory, we may explore some of its underlying problems. Actually, in our view, it has only one failing, although it is a glaring flaw. That flaw is an inheritance from the lepidomorial theory: the assumption that the odontode is an irreducible and fundamental unit of development, evolution and homology. That's a nice, rolling sentence, but what does it mean?

Look at it this way. One difficulty with the odontode specialization model is that it rests on an inexact analogy. The development of structures in organisms is *like* the evolution of the whole organisms. But the process is not the same. To the extent that oral and dermal odontodes are developed in the same fashion, they depend on the same set of developmental signals and, more generally, the same gene products. A change in any of these genes will affect *both* processes, at the same time, and very often in the same way. So, for example, the initial development of odontodes seems to depend on a very complex and stylized set of two-way epithelial - *ectomesenchyme* interactions mediated by *BMP4* and *FGF8*, among others [G00]. Any change in any of these genes, or the receptivity of common tissues to these signals, will alter both types of odontodes. Thus teeth and scales have not "diverged," "differentiated," or "specialized" in quite the same way as we might use those words to describe the evolution of two species. Two species are, by definition, no longer in genetic contact. Teeth and scales still use many of the same genetic programs in the same genome.

Consider a concrete example. As Donoghue & Sansom [DS02] point out, one problem case comes in the unlikely form of a particularly ugly Nigerian clupeomorph fish which was not discovered until the 1950's. This fish, *Denticeps clupeoides*, and a few of its close relatives, have apparently reversed the process of turning scales into teeth. That is, the teeth of *Denticeps* have escaped the jaws and pharyngeal arches and appear as isolated denticles on the surface of the dermal bones [S+98]. The result is a structure quite similar to that found in the armored catfishes and a few other teleosts, in the coelacanth [S+98], and perhaps in the more basal sarcopterygian, *Grossius* [S73]. The oral and dermal denticles have almost the same morphology and ultrastructure. In short, the teeth of *Denticeps* work perfectly well as scales, and it would not be surprising to find that different sorts of odontodes have crossed these functional borders at numerous times. Indeed, many workers believe that the scales of extant teleosts are derived from teeth, rather than from the scales of their distant ancestors [SA04].



**Denticles from dentary (left) and dermal bone (right). Adapted from Sire et al. (1998).**

Here's the issue: scale theory assumes that the odontode is the relevant unit for this analysis. It isn't. An odontode is a type: a shorthand for a series of developmental and genetic processes which often occur together and are manifested in a typical morphology. The odontode has shown a lot of stability over the last 500 My -- much more stability than most organs -- but that should not mislead us into seeing it as any more than a type. It is no more fundamental or indivisible than the fin/arm/flipper/wing or the gill arch/jaw/auditory ossicle. All of the parts of a typological odontode may be present, or they may not. We have discussed many scales which lack the enamel cap, or where the hypermineralized portion is produced in quite disparate ways. On the other hand, scales, teeth and other integument derivatives may all be affected in a coordinate fashion by genetic changes in the developmental programs which they still have in common. It is often useful and convenient to speak in terms of the odontode unit, but it is a typological fiction we should be willing to abandon the moment it ceases to be the real issue. With our rapidly increasing knowledge of the molecular underpinnings of integumentary structures, our willingness needs to all the greater.

# Footnotes

**[1]** But what about the (randomly placed) oral denticles and (linear, ordered) external mouth scales of some cyathaspidiforms, the apparently linear arrays of *external* scales in the Corvaspididae, or the serial spines of the conodont apparatus? Unlike the thelodont branchial denticles, these examples probably all have reasonable explanations which do not require us to invoke any evolutionary novelties. However, they also suggest caution.

**[2]** The tendency of many vertebrate regulatory genes is to come in groups of at least two paralogues. This is said to be the result of very broad gene duplication events which seem to have affected many regulatory genes, and perhaps the entire genome. There were probably at least two distinct duplications which occurred in the passage from early chordates to the early vertebrates [H+00].

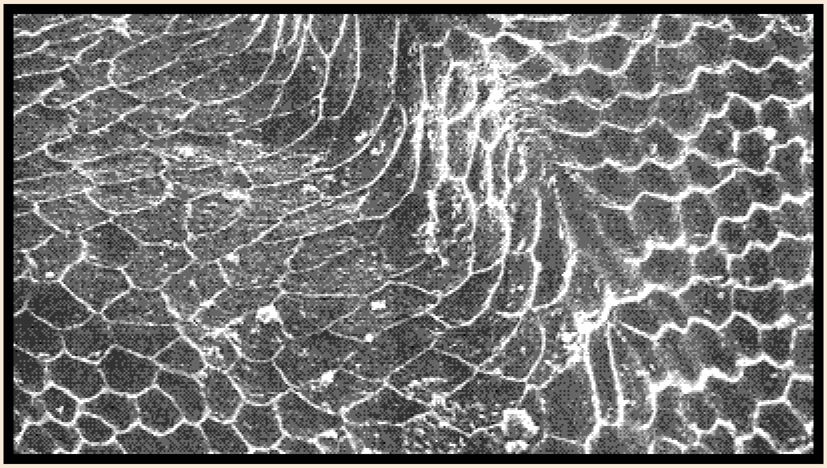
**[3]** We do not use the word lightly. Prof. Reif's name will never be a household word, but his contributions to theoretical biology (and other fields) have been, and continue to be, as remarkable as they are varied.

**[4]** The reader is warned that this approach is heterodox.

**[5]** We adhere to the convention of denoting genes in italics, with the corresponding gene products in normal typeface. Thus, the "*Shh* (gene) was active" but the "Shh (transcription factor) was present." In many cases, we are not certain whether the species exported, or even the active species, is an RNA or a protein coded for by an mRNA. For our purposes, it rarely makes a difference. Accordingly, all gene products are in normal typeface.

**[6]** This specificity is true of all known gnathostome systems. The migration of neural crest in lampreys appears to be less tightly constrained [MB03].

**[7]** Dzik [D00] argues that the conodont elements were *continuously* covered with both secretory epithelium and a keratinous ("horn") layer. However the images of both Dzik and of Donoghue & Purnell [DP99] strongly support discontinuous growth, and it is difficult to see how a thin layer of secretory cells could be maintained -- mechanically or metabolically -- under a keratin sheath. Dzik offers arguments based on the morphology of the cell outlines. The outlines are clearly elongated, with thinner lines of crystals, in locations in which the slope changes rapidly, suggesting that this reflects a slower growth rate. The argument is ingenious, but may confuse cause with effect. The shape of the surface would naturally create such a pattern if it were brought into contact with a taught, flat, elastic epithelium, approaching at a slight angle.



**[8]** Or alternatively, as stated by [D02], BMP2 and/or BMP4 inhibit the ability of FGF8 to induce *Pax9* expression.

# References

| | | | |
|---|---|---|---|
| [C+96] | Chen *et al*. (1996) | [MB03] | McCauley & Bronner-Fraser (2003) |
| [C+01] | Cuny *et al*. (2001) | [MP00] | Mathur & Polly (2000) |
| [C+02] | Couly *et al*. (2002) | [M+00] | Mazan *et al*. (2000) |

| | | | |
|---|---|---|---|
| [D00] | Dzik (2000) | [M+02] | Marss *et al*. (2002) |
| [D02] | Donoghue (2002) | [PN00] | Piotrowski & Nüsslein-Volhard (2000) |
| [DP99] | Donoghue & Purnell (1999) | [P+99] | Peters *et al*. (1999) |
| [DS01] | Donoghue & Smith (2001) | [R80] | Reif (1980) |
| [DS02] | Donoghue & Sansom (2002) | [S73] | Schultze (1973) |
| [D+01] | Delgado *et al*. (2001) | [SA04] | Sire & Akimenko (2004) |
| [G00] | Gilbert (2000) | [SC01] | Smith & Coates (2001) |
| [G+02] | Gritli-Linde *et al*. (2002) | [S+92] | Sansom *et al*. (1992) |
| [H+00] | Hetzer-Egger *et al*. (2000) | [S+98] | Sire *et al*. (1998) |
| [H+02] | Hoang *et al*. (2002) | [T64] | Tarlo (1964) |
| [J96] | Janvier (1996) | [T+01] | Testaz *et al*. (2001) |
| [JS03] | Johanson & Smith (2003) | [vJ93] | van der Brugghen & Janvier (1993) |
| [J+00] | Jernvall *et al*. (2000) | [W+04] | Wu *et al*. (2004) |
| [J+03] | Jung *et al*. (2003) | [Z+00] | Zhang *et al*. (2000) |
| [L+01] | Liem *et al*. (2001) | [Z+02] | Zhao *et al*. (2002) |

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# Tooth Implantation

Bones
- Bones
- Braincase
- Dermal Bones
- Ear
- Gill Arches
- Teeth

Teeth
- Canines
- Molars
- Tooth Implantation
- References

Mammal teeth get all the press, but even the relatively strightforward teeth of reptiles require a little study, since the mode of replacement and implantation is often of phylogenetic interest. Like mammal teeth, reptile teeth seem to have an almost magnetic quality that attracts obscure and inconsistent nomenclature. Interestingly this is also a property shared by pre-dental tooth analogues, *i.e.* scales, aspidine and so on. Is there something special about hypermineralized tissues that stuns the speech centers of the neocortex, rendering normal communication impossible?

Whatever the magical properties of apatite may be, it is necessary for us to imbibe another tun of terminology. Here we follow the widely-admired system of Motani (1997) for tooth implantation in non-mammals. Truthfully, Motani's brief summary is so succinct and so complete that most of the following is simply cribbed from his article.

Different types of tooth implantation are recognized by a combination of three features: (a) whether or not the tooth is fused (ankylosed) to the jaw (b) whether or not the teeth are set in separate sockets or in a groove; and (c) whether or not they are assymmetrically exposed as in the pleurodont example in the figure. Generally there are two "extremes." Teeth which are ankylosed to the jaw are referred to as *acrodont*, or *pleurodont* if fusion is to the side of the jaw bones. At the other extreme, teeth are said to be *thecodont* if they are set in sockets, without ankylosis. Between these two endpoints, there are a number of other possibilities, which are set out in alphabetical order below.

**Acrodont:** teeth ankylosed to the jaw bone. There are no dental sockets or grooves. Examples:somelizards, *Sphenodon*.

**Ankylosed thecodont:** teeth set in sockets, which may extend to the crown of the teeth. bones of the socket are ankylosed to the jaw. A dental groove is absent. Example: *Mixosaurus*.

**Aulacodont:** teeth set in a groove, without ankylosis to the jaw. Example: (probably) *Ichthyosaurus*.

**Labial pleurodont:** probably same as pleurodont, but involves a dental groove with a low labial wall, rather than none at all. Thus the teeth are ankylosed to the jaw on the outside (labially) and rest on a bone shelf on the inside (lingually). Example: some lizards?

**Pleuroacrodont:** same as labial pleurodont.

**Pleurodont:** teeth ankylosed to jaw. No sockets, and teeth rest in a dental groove with a high labial (outside) wall and a low or no lingual (inside) wall. Ankylosis is normally on the labial side of the tooth only, or on the labial side and at the bottom of the groove. Example: varanid and iguanid lizards.

**Pleurothecodont:** same as subthecodont.

**Prothecodont:** same as subthecodont.

**Subacrodont:** same as pleurodont.

**Subpleurodont:** a variation of pleurodonty in which (as noted above), there is well-developed bone of attachment at the bottom of the tooth in the dental groove.

**Subthecodont:** both a groove and shallow sockets, within the groove, are present. The groove has a high lbial wall and low lingual wall, as in pleurodonty. Apparantly, there is also ankylosis. Example: *Paleothyris*, *Petrolacosaurus*, some non-amniote reptilomorphs.

**Thecodont:** teeth in deep sockets, deeper than than height of tooth crowns. There is no ankylosis and roots are cylindrical. Examples: most archosaurs, including living crocodilians, mammals.

We may summarize Motani's system in the following table:

| | **Ankylosis** | **Dental sockets** | **Dental Groove** |
|---|---|---|---|
| **Acrodont** | yes | no | no |
| **Ankylosed Thecodont** | socket bones only | yes, shallow | no |
| **Pleurodont** | yes | no | yes |
| **Subpleurodont** | yes, strongly attached in groove | no | yes |
| **Subthecodont** | yes? | yes | yes |
| **Aulacodont** | no | no | yes |
| **Thecodont** | no | yes, deep | no |

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# Canines

Truthfully there is not much to be said about canine teeth. The adaptations required to develop a couple of long, sharp, recurved teeth towards the front of the jaw are simple enough. They have occurred countless times from fish to felines. The utility of such a device is fairly obvious. The teeth get plunged into the selected recipient, and any additional force serves to gouge out a pound of flesh like a heated ice cream scoop. Canines almost always occur as a single pair -- or a pair on each jaw -- since having more than that, unless they were perfectly aligned, would require the teeth to cut laterally through the prey to some degree. This is messy, inefficient and unnecessary. ATW001113.

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# Teeth: Molars

Bones
Bones
Braincase
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While it will be necessary to go into this subject in more detail at another time, this section will serve for now as a sort of temporary filling: a place to put some molar nomenclature for the tribosphenic molar until a fuller discussion is possible. For purposes of the following discussion, almost all other puns have been omitted and are left as an exercise for the reader.

## 1. Reversed triangles

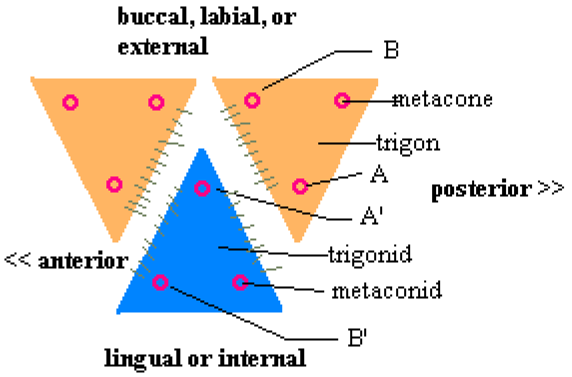


**Fig. 1. Primitive "reversed triangles" holotherian molars. Upper molars in orange, lower molar in blue. The cusps labelled A and A' are believed to be homologous to the paracone and paraconid of therian mammals**

Some conventions: for purposes of these notes, the orange/tan color is used for upper molars and the blue, for lower molars. Anything dealing with the lowers has the suffix **-id**. This gets carried to extremes in some literature, and I will try to avoid it. **Cusps** are the elevated points of teeth, and are shown as pink circles. The addition of **-ule** to a cusp name means a subsidiary cusp. Thus, the posteriormost cusp of the trigonid is the **metacone**, and a subsidiary cusp of the metaconid would be the **metaconulid**. **Cristae** are the ridges joining the cusps, and are shown (when present) as pink lines. Shearing surfaces are shown with a pattern of short grey lines, while broad crushing surfaces are stippled in grey. All figures are shown in a sort of **occlusal view**, meaning we are looking down on the business end of the tooth, similar to the last thing a prey animal ever sees. Actually, this is a kind of Cubist perspective, (see **Figure 2**, reproduced by permission), since we are attempting to view the occlusal surfaces of both upper and lower teeth at once.

The basic reversed triangles pattern for molars is shown schematically in **Figure 1**. This is the sort of dentition seen in *Kuehneotherium*, as well as symmetrodonts and other basic Mammalian types. Unfortunately, molar nomenclature was

Fig. 2. "Afficionado" by Pablo Picasso. Copyright ©1997-2000 Barewalls Interactive Art, Inc. All rights reserved.

developed for therian mammals, and some of the terminology turns out not to work very well at this fundamental level. The basic triangular units with three cusps are the **trigon** and **trigonid**. The **metacone** is the posterior cusp. The A and B cones were originally thought to be homologous with the protocone and paracone, respectively, of therians (see below). This turns out not to be the case: hence the use of letter designations.

As the trigon and trigonid meet, the slide past one another, shearing the food item on the edges of the molars as shown. Depending on the shape and length of the cusps and the sharpness and position of the cristae, the molars may also pierce, at the tips of the cusps, or even slice like the teeth of ornithischian dinosaurs. However, the principle effect is shear, since neither the cusps nor the cristae actually occlude with anything. Instead, they are designed to slide past their opposite numbers.

## 2. The Tribosphenic Molar

The "reversed triangles" molar, for all its elegance, was a somewhat limited system. Some foods resist shearing: seeds, bones, and nuts, not to mention chewing gum. Evolution, fortunately, developed a method for overcoming a potential culinary limitation to tofu, *blanc mange*, and strained peas by elaborating the upper molars lingually and creating a low posterior extension of the lower molar, the **talonid**. The margin of the talonid is surrounded by a series of cusps ("cuspids," actually, since this is a lower jaw molar) which enclose a **talonid basin**. The **protocone** and, if present, the **hypocone** of the upper molar occlude directly with this surface. Even when not reducing peanuts to peanut butter, this mechanism serves to guide the rest of the jaw into a more precise occlusion. The enlarged surface and finer occlusion also permitted the development of complex series of subsidiary cusps and other accoutrements. These include not only subsidiary cusps on the tooth surface, but ancillary **stylar cusps** on the **cingula**, the mineralized ridges at the base of the lingual face of the molar.

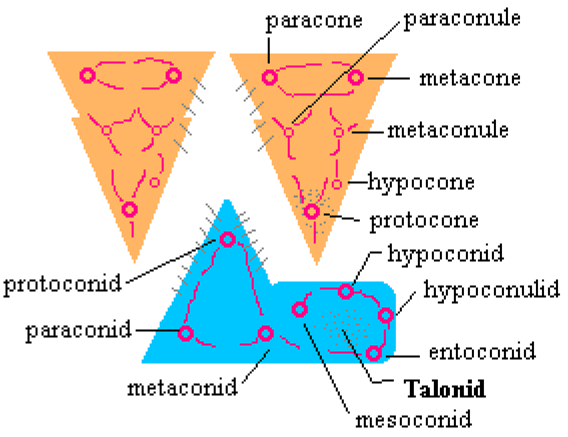
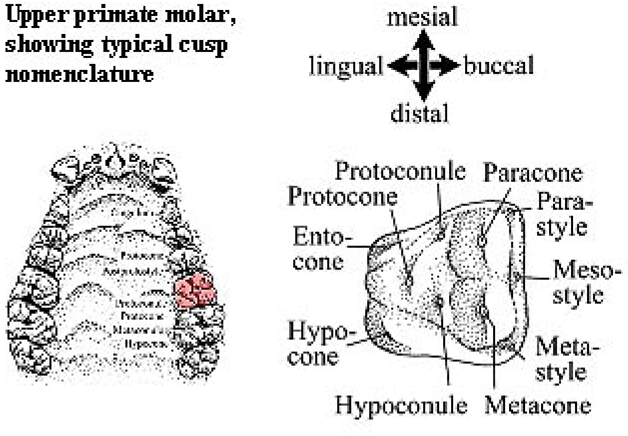


Fig. 3. Tribosphenic molar with talonid and development of accessory crushing surface in talonid basin



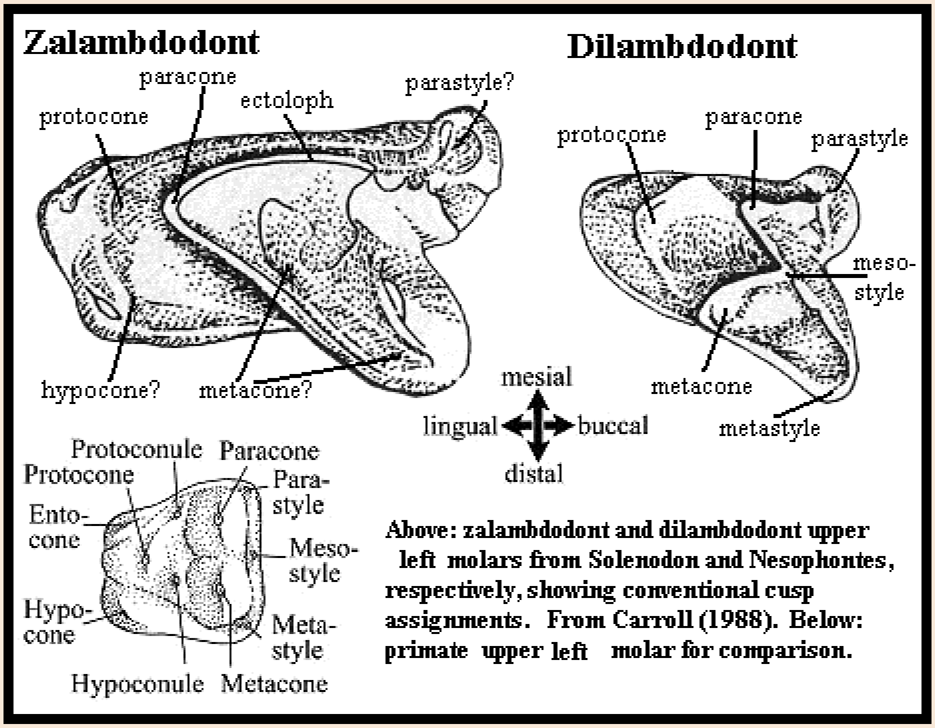
Upper primate molar, showing typical cusp nomenclature

## 3. Variations

Evolution never comes without a price; and, in this case, the price included an explosion of dental nomenclature which can be deeply unsettling -- even to hardened paleontologists who can normally chew up a Greek root faster than you can say fluorophenylphthaline. Thus, we will dodge the fine points (and, to be sure, the fine pointids, pointules, etc.). The pages at Introduction to Teeth are strongly recommended for more, and certainly better illustrated, information and some very good real-life examples. However, there are a few important variations on the basic plan which require explanation.

The **bunodont** dentition of, for example, pigs (see Ungulate teeth, More on Artiodactyla) follows the basic pattern and consists of low, rounded cusps. It is characteristic of fairly unspecialized omnivores.

Ruminants need *only* grinding and cutting teeth. Thus they tend to revert to the trigonid form, but without cusps, so that the work is done by curved ridges: **lophodont** dentition. A **loph** is a ridge of enamel. The intervening dentine wears faster than the enamel resulting in distinct, fairly sharp contact surfaces. In **selenodont** molars, the enamel ridges form characteristic crescent shapes. See More on Morphology of the Artiodactyla (figure at bottom of page); selenodont.jpg. In extreme cases the molar dentition consists of close packed lophodont teeth with a single long lingual-buccal ridge: **loxodont** teeth. See recently2 (mammoth teeth).



**Above: zalambdodont and dilambdodont upper left molars from Solenodon and Nesophontes, respectively, showing conventional cusp assignments. From Carroll (1988). Below: primate upper left molar for comparison.**

**Zalambdodont** molars have an upper molar characterized by a V-shaped crest along the margin (**ectoloph**). At the apex of the V (on the lingual side of the tooth) is usually the paracone (sometimes fused with the metacone). This looks odd, since the paracone is typically at the buccomesial corner of the molar. However, animals with zalambdodont molars have offset jaws, so that the ectoloph is occluding with the hypoflexid on the lower molar, just as the paracone typically does. Asher *et al*. (2002). The crests of the ectoloph run to stylar cusps on the labial side of the tooth. The protocone is typically absent. *See* The Diversity of Cheek Teeth. A **dilambdodont** upper molar is similar except that the ectoloph is W-shaped. The metacone and paracone are at the (lingual) base of the 'W.' Crests run from these cones to buccal stylar cusps and form the arms of the 'W.' In addition, the molar has a low shelf, lingual to the rest of the tooth, with a small protocone. See, The Diversity of Cheek Teeth.

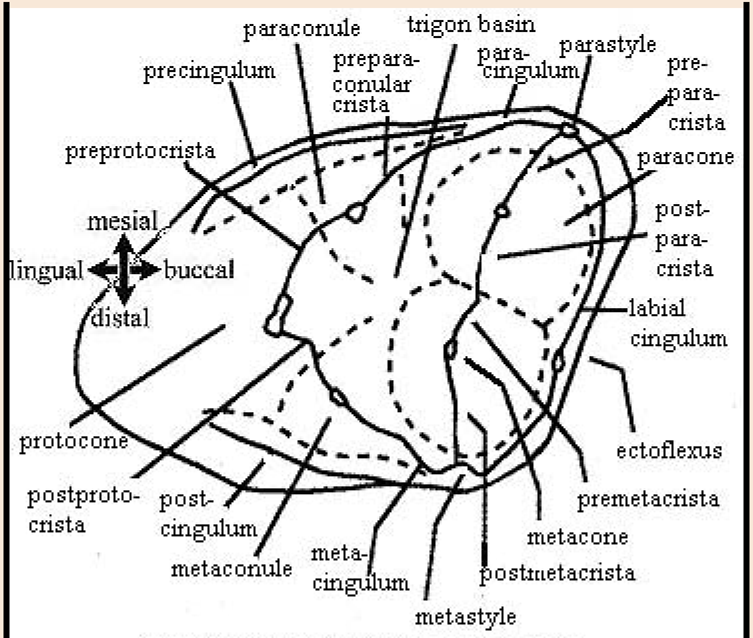
In some carnivores, one or two of the cheek teeth may be **carnassials**, specialized blade-like cutting teeth. La Brea Tar Pits.

# 4. Another Walk-through

Since the time the earlier part of this Note was written, our tastes in dentition have become a bit more refined, requiring a little more coverage and something a bit more substantial to chew on. To the right is an upper left molar adapted from de Muizon & Cifelli (2000) which will do for the purpose. I have deliberately *not* made the diagram more colorful or easier to follow than the original precisely so that we can learn to follow the usually obscure and unhelpful tooth diagrams in the literature.

First, recognize that this *is* a left molar. We are looking at in occlusal view, which in this case means the same as a palatal perspective. This reverses the usual directions. That is, the tooth would be on the *right* of the diagram if the entire mouth were shown. Accordingly, lingual (towards the tongue) is on our left and buccal on the right.

**Cones & conules:** The easiest place to start is usually with the two major buccal cusps, the paracone



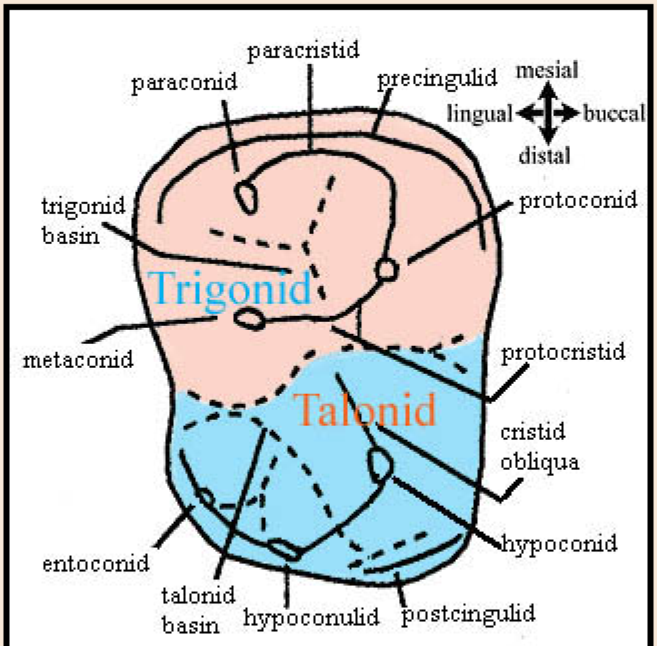
**Upper left molar, labelled according to the nomenclature of de Muizon & Cifelli (2000)**

(mesial or anterior) and metacone (distal or posterior). Each of these often has a substantial conule lingual to it, the paraconule and metaconule, respectively. Lingual to all these other cones is the protocone. The trigonid basin lies in the center of all of these cones and conules. (This particular molar lacks a hypocone. If one were present, it would lie on the ridge created by the postcingulum.)

**Cristae:** The major buccal cusps also define a line which is usually marked by a crista. The regions of this crista are named for the cusp nearest them. Thus, the postparacrista is the region behind (distal) to the paracone. Distal to this segment is the premetacrista, and so on. The same convention is used for the cristae connected to the protocone. The system breaks down somewhat for the cristae associated with the conules, but in theory it remains the same.

**Stylar cusps and cingula:** A labial (i.e. buccal) cingulum runs around the buccal side of the upper molar, and stylar cusps are often associated with the points at which the preparacrista and postmetacrista intersect the cingulum. Not surprisingly, these are the parastyle and metastyle, respectively. Frequently, an additional stylar cusp (not shown) occurs between them. This is the mesostyle. Branches of the cingulum curve around outside the trigon on its mesial and distal sides. This are called, with impeccable logic, the precingulum and postcingulum.

That is essentially all we normally have to deal with on the upper molar. A right lower molar is shown in the next figure. We are now looking down on the tooth (i.e. not a palatal view) but the subject is a right tooth, rather than left. These two effects cancel, so the chirality is the same as in the last image.



**Right lower molar labelled according to the nomenclature of de Muizon & Cifelli (2000)**

**Conids and conulids:** Unfortunately, the nomencalture is not quite as logical for lower teeth, which are a bit more complex. By analogy to the upper molar, we can orient ourselves with the paraconid and metaconid. Since this is a lower molar, these cuspids are located on the lingual, rather than the buccal side. That's why the tribosphenic molar is referred to as "*reversed* triangles." Since there's a large talonid (*particularly* large in the example), the metaconid and paraconid tend to be found in the linguomesial quadrant. Somewhere buccal to these conules will lie the protoconid, and the three will define the trigonid, with the trigonid basin in the center. Truthfully, even the trigonid cusps can be very hard to identify. For example, look at Figure 12.2m on one of the best mammal tooth sites. This molar has *no* paraconid and has a very large entoconid. Consequntly, the entoconid and metaconid are likely to be misidentified as the metaconid and paraconid, respectively. The take-home lesson is that one should double check for the constricted "waist" between the trigonid and talonid. (Not infrequently, the lower third molar (m3) will appear to have two waists and *three* compartments. This is actually very helpful because, in that case, the cusp in the most distal section can safely be identified as the hypoconulid.)

Assuming we can correctly identify the trigonid, the next step is to identify the hypoconid in the buccodistal quadrant. As previously noted, there is a chance of confusion in nomenclature since the names of the hypoconid and entoconid are sometimes reversed. Nevertheless, the large cusp in the buccodistal quadrant is usually easy to find. The hypoconulid can then be distinguished from the entoconid (if both are present) because the hypoconulid is near the distal margin, or even set off distally from the main body of the talonid, while the entoconid is near the lingual margin.

**Cristids:** On the right lower molar, the cristids of the trigonid are named as if they were a clock face. That is, the cristid clockwise from the paraconid is the paracristid. The cristid clockwise from the protoconid is the protocristid. This is, of course, reversed on the *left* lower molars. Perhaps more frequently, the entire cristid around the trigonid is referred to as the precristid. On the talonid, the crista obliqua is often of considerable interest. Its position is easily determined from its origin at the hypoconid. Again, the entire cristid associated with the talonid is often referred to as the postcristid.

**Cingulid and stylids:** Unfortunately, these are so variable that I have been unable to get a good handle on them at this point. Accordingly, discussion is deferred for the moment.

## 5. Lophodont Dentition

Ruminants and certain similar forms present special problems of nomenclature. Here, the cristae joining the cusps frequently become the primary dental surfaces. The cusps themselves may no longer be evident as separate structures. In many cases, the overall form of the cutting surface becomes so strongly simplified that no special nomenclature is necessary. However, intermediate states exist in which the form and placement of the lophs assume phylogenetic importance. The nomenclature used for lophodont forms is not always consistent. Purely by way of example, the image at left shows the nomenclature used for notoungulates, an extinct group of ungulates endemic to the early Cenozoic of South America. ATW021228.

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### Useful Web Sites

DENTITION DES VERTEBRES
Teeth, diastema lengths (**Best on the Web**)
Introduction to Teeth

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