Mammalogy Lecture 7 - Evolution of Lower Jaw and Middle Ear

I. To begin, let's examine briefly the end point, that is, modern mammalian ears.

Inner Ear - cochlea - contains sensory cells for hearing and balance.

- lies embedded in the braincase.

Middle Ear - connects the outside world to the inner ear & contains the ossicles

- functions as a transducer; transmits ground and air vibrations to the inner ear; is surrounded by the auditory bulla in many eutherians.

Outer Ear - cartilaginous pinna.

II. We're going to examine the evolution of the ear ossicles, and this is intimately tied to the evolution of the lower jaw in mammals.

This evolution is integral to mammalian biology – feeding diversity/dietary specialization

To me, this is one of the most remarkable examples of some common features of evolution.

1. Gradualism → Evolution is often very gradual. Change from one morphology to another very different morphology occurs through a series of intermediates. This documents transitional forms.

2. Modification of existing structures → For the most part, evolution modifies what's already there, and when new structures arise they split off existing structures (masseter).

3. Constraints → Organisms are integrated wholes, and changes to a particular system don't occur in a vacuum; characters are non-independent and **functions change over time.**

III. In addition, we'll begin to explore functional morphology.

Analyze biological structures using principles of physics. We'll restrict our attention to very simple principles.

1) In equilibrium, any force that is being exerted is resisted by an equal and opposite force.

2) We'll learn a little about force vectors.

VI. Ancestral Condition: Pelycosaurs, early synapsids.

1. Remember: Solid skull roof with very small temporal fenestra.

2. Lower jaw had many bones.

3. Quadrate/Articular jaw articulation.

4. There was no tympanum/typmanic bone - angular was in the lower jaw.

5. There was a very large stapes.

    This connected the inner ear to the jaw, via the quadrate.

    Vibrations at the jaw joint were transmitted to the inner ear by the stapes.

    Inference is that this is how pelycosaurs detected low frequency sounds.

    They rested their lower jaw on the ground to detect vibrations.

    So the chain of transmission would have been:

    Dentary ---> Articular ---> [Jaw Joint] ---> Quadrate ---> Stapes ---> Inner Ear.

This is the condition seen in many modern snakes.

The Quadrate & Articular functioned both as the jaw articulation and in sound transmission.

There's a interesting diagram of this at the following web site:

http://www.palaeos.com/Vertebrates/Units/Unit420/420.300.html

This diagram can be useful in understanding how the Q-A jaw functions… but can be very confusing on first glance. You won't be required to reproduce this diagram…use it at your own discretion.

The structure of the Q-A jaw sets the stage for subsequent evolution.

Jaw Musculature:

Jaw Adductors were simple. Temporalis is the only muscle we've seen evidence for.

Temporalis formed essentially a straight line from C.P. to the braincase.

Coronoid Process was rather low.

Key Point: The force of the temporalis was directly vertical, and right over the Coronoid.

Because the upward force of the temporalis and the downward force of the bite resistance are off-set, there is a lever action. This then generates forces in both directions at the jaw joint.

So in early synapsids, a powerful bite resulted in strong forces acting right at the jaw joint. As a result, the joint needs to be strongly braced, and the quadrate and articular were constrained to be very robust bones.

V. Cynodonts - Late Therapsids

A. First major change in jaw adductors. They become larger and more complex, and this is associated with cynodonts' higher activity.

This is where we see the first evidence of a **masseter**. This new muscle actually splits off from the temporalis. We see this embryonically in modern mammals.

B. Of course, as we've discussed, we also see a huge and gradual increase in the size of the temporal fenestra, as well as an expansion of the braincase.

C. In addition, we see a concurrent expansion of the coronoid process.

Temporalis - up and back
Masseter - up and forward

Now - if we analyze force vectors - The line of action of the temporalis intersects the line of action of the masseter well out over the jaw -- actually right over the bite point.

So we can resolve the vectors around the bite point.

All forces cancel out --- no stress at the jaw joint.

Because of the height of the coronoid process and the evolution of the masseter, Cynodonts could produce much bite force without imposing any stresses at all at the lower jaw.

So now, the quadrate and articular are free of the **constraint** of having to be large and robust in order to withstand the stress of feeding.

They can now respond to selection for increasing efficiency of transmission of sound vibrations. They still form the jaw joint, but now are free to become small.

This is illustrated remarkably clearly in the fossil record. As the coronoid process expands, the quadrate and articular become gradually smaller.

See ***http://www.talkorigins.org/faqs/comdesc/section1.html***

D. At the same time, we see the first evidence of an eardrum, or tympanum, supported by the lower jaw, specifically by the laminar process of the angular.

At this point, then, there is a new chain of transmission.

Cynodont chain of transmission:

Tympanum --> Angular --> Articular --> {JJ} --> Quadrate --> Stapes --> Inner ear.

Again, the bones involved in transmission of sound vibrations would have been under selection to become small because smaller objects transmit vibrations more efficiently.

The quadrate and articular are still functioning as the jaw joint, but have responded to selection to become smaller.

As these get smaller, the dentary in the lower jaw, and the squamosal bone, in the cranium, expand (to fill the space).

Eventually the dentary and squamosal come into contact.

We saw this in *Probainognathus* and *Diarthognathus*

Again, check out the site: http://www.palaeos.com/Vertebrates/Units/Unit420/420.300.html.

Once this happens, the quadrate and articular are no longer constrained to form the jaw joint. **We see a second release from constraints.**

Articular migrates off the lower jaw --> Malleus
Quadrate migrates off the upper jaw --> Incus

The angular is then lost off the lower jaw, and fuses to the braincase --> tympanic which encases the others in the middle ear cavity.

So there still is an articulation that is homologous to the ancestral jaw joint.

If we look at the developing *Didelphis* embryo, we see the malleus first ossifies on the lower jaw and the incus ossifies on the cranium and actually articulates with the malleus there. In addition, the tympanic bone ossifies on the lower jaw right where the angular is in fossil cynodonts.

At the point in development when the braincase expands, these three elements move away from the lower jaw and fuse to the cranium!

New chain of transmission:

Tympanum --> Malleus --> Incus --> Stapes --> Inner ear