Mammalogy Lecture 8 - Evolution of Ear Ossicles

A very old hypothesis of Homology (1937) is supported by decades of new data, including comparative genomics.

I. To begin, let's briefly revisit the end point, that is, the Definitive Mammalian Middle Ear (DMME).

Inner Ear – The cochlea contains sensory cells for hearing and semicircular canals contain the sensory cells for balance.

- It lies embedded in the braincase (in the petrosal).

Middle Ear – Bounded by the tympanum and is surrounded by the auditory bulla in many eutherians.

- It connects the outside world to the inner ear & contains the ossicles, the malleus, incus and stapes.

- These function as transducers & transmit air vibrations to the inner ear.

Outer Ear – canal & cartilaginous pinna.

Chain of Transmission: Tympanum → Malleus → Incus → Stapes → Inner Ear

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, and hearing ability.

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 often occurs through a series of intermediates. This provides fantastic examples of transitional fossils.

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 splits from temporalis).

3. Constraints & Exaptation → 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. An exaptation is a feature whose current function is different than its original function.**

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

We'll analyze biological structures using (very simple) principles of physics.

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 they had a solid skull roof with very small temporal fenestra.

2. Lower jaw had many bones (e.g., dentary, angular, articular, etc.) and a low coronoid.

3. Quadrate/Articular jaw articulation.

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

5. There was a single ear ossicle, the very large stapes, and it traversed the middle ear.

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.

The inference is that early synapsids detected low frequency sounds by resting their lower jaw on the ground to detect ground-borne vibrations.

So, the chain of transmission would have been:

Dentary → Angular → 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. This dual function generated constraints.

Jaw Musculature:

Jaw Adductors were simple. The temporalis is the only muscle for which there is evidence.

Coronoid Process was rather low.

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

Key Point: The force of the temporalis was directly vertical, and right over the coronoid. We can represent that with a force vector that indicates both direction and strength.

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

So, in early synapsids, a powerful bite resulted in much stress right at the jaw joint. As a result, the joint needed to be strongly braced, and the quadrate and articular were constrained to be very robust bones (constraint #1).

This constrained them from responding to selection to increase efficiency of sound transmission and hearing was probably restricted to low frequency sounds.

V. Cynodonts - Late Therapsids

A. First major change in jaw adductors. They become larger and more complex, and this is (as we discussed) associated with cynodonts' higher activity and evolving endothermy.

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.

C. In addition, we see a concurrent expansion of the coronoid process, which extends up into the temporal fenestra.

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. There was a powerful bite, with 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 **released from the constraint** of having to be large and robust in order to withstand the stress of feeding (constraint #1).

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.

D. Concurrent with this transition, we also 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 (Mandibular Middle Ear of Cynodonts: MMEC):

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 (constraint #2) 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*

Once this happens, the quadrate and articular are no longer constrained to form the jaw joint. We see a second release from constraints (constraint #2).

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.

We can see this transition in the fossil record as well. *Morganucodon* exhibited a state called the Mandibular Middle Ear of Cynodonts (MMEC), and triconodonts and other Mesozoic mammal fossils show a transitional state called the Primitive Mammalian Middle Ear (PMME). The articular(=malleus) and angular(=tympanic) are extended away from the new jaw joint by an ossified Meckel's Cartilage. This PMME is seen in developing mammals, for example in *Ornithorhynchus*; Meckel's Cartilage is ossified early, and deteriorates during development, resulting in the DMME.

If we look at the developing *Didelphis* embryo, we see the malleus first ossifies on the lower jaw in Meckel's cartilage. The incus ossifies on the cranium in the palatoquadrate cartilage 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, leading to the DMME.

New chain of transmission (Definitive Mammalian Middle Ear: DMME):

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

The discovery in the last ~15 years of lots of diversity in Mesozoic mammals that we discussed earlier has led to a remarkable conclusion.

The origin of the DMME from the MMEC/PMME likely occurred at least 3 times independently.

Once in *Hadrocodium* (which we indicated is the earliest fossil with three ossicles).
Once in living monotremes (*Bishops* and *Asuktribosphenos* had the PMME).
And a third time in the common ancestor shared by Metatherians and Eutherians.

There are pdf files of papers on the course website (Anthwal 2017) if you want to look further into this, including the identification of the genes responsible for the development of the DMME from the PMME.