

Mammalogy Lecture 2 - Origin of Mammals

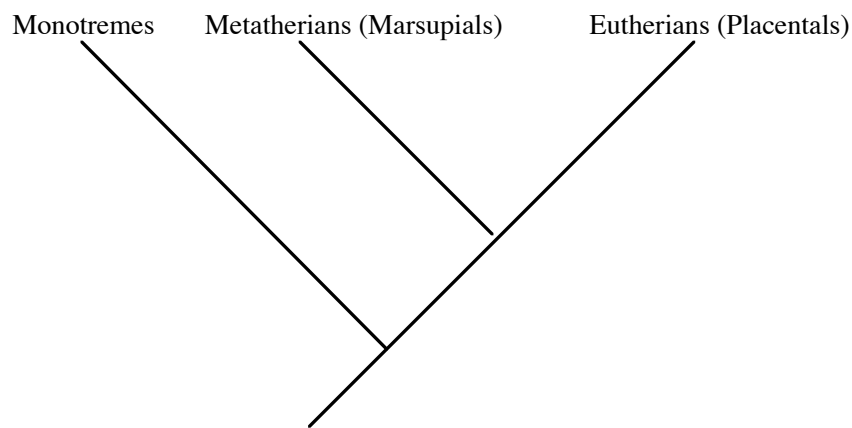
Introduction to the **Geologic Time Scale**.

We'll go back to the Carboniferous (Mississippian), ~ 360 MYA.

I. First, however, we'll note that there are three major living (extant) groups of mammals

- A. Monotremes – egg-laying mammals (echidna)
- B. Metatherians – marsupial mammals (kangaroo)
- C. Eutherians – Placental mammals (pangolin)

These are related by the following evolutionary tree or phylogeny

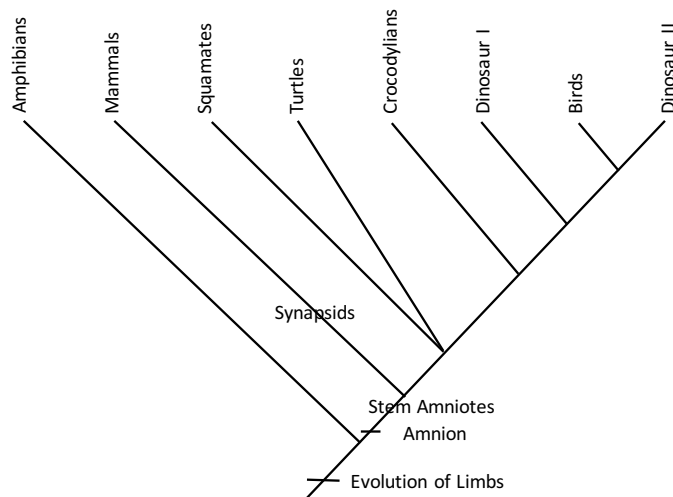


Node - Divergence Event

Branch - Common Ancestor

Marsupials and placentals share an ancestor not shared by monotremes.

II. A. In order to understand the origin of mammals, we have to look farther back, as I said, ~360 MYA to the relationships among tetrapod vertebrates.



We can mark evolutionary changes along this phylogeny; the evolution of limbs, the evolution of the amnion, etc.

It's this lineage labeled Synapsida that we'll examine in order to understand the origin of mammals. In addition to serving as the name of the group, the term **Synapsid** ("together/arch") describes a skull condition that is unique to this lineage.

We need to understand the situation just prior to this in the "stem amniotes" (a.k.a. stem reptiles), the ancestors to mammals, birds, turtles, and other reptiles.

Stem Amniotes.

B. In the Carboniferous, ca. 350 MYBP, the stem amniotes were present, and the synapsid lineage diverged from these 30 MY later 320 MYA, and it's this lineage that will eventually lead the modern mammals.

Stem amniotes were anapsid; they had no temporal fenestra.

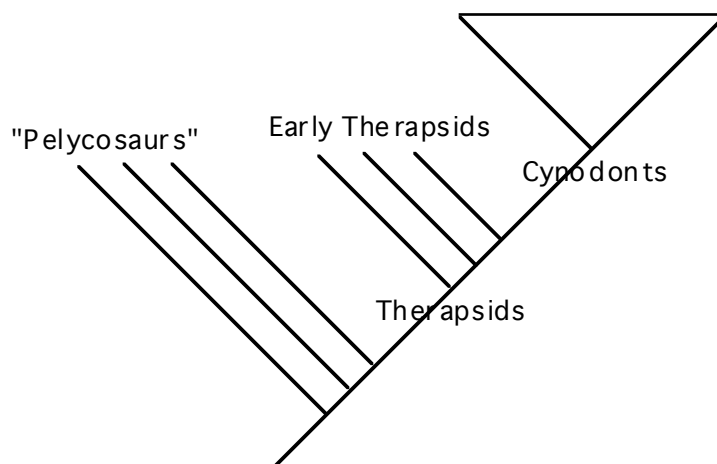
The temporal region (temple) is a solid shield of bone. Lower jaw musculature (jaw adductors) is anchored to inside the shield of bone. This condition is still present in some turtles. Modern tetrapod groups have different modifications of this ancestral anapsid condition (we saw these in lab).

Early synapsids evolved an opening in this temporal shield, the temporal fenestra. This provides a much more solid anchor for the lower jaw musculature.

In early synapsids, the fenestra opens below the suture between the squamosal and postorbital bones.

In later synapsids, including modern mammals, both the temporal fenestra and the braincase expand greatly, and the original dermal shield becomes very reduced.

C. Phylogeny of Synapsid Lineage



1. Pelycosaur lineages (a.k.a. non-therapsid synapsids, or stem mammals)

These arose in the Late Carboniferous (Pennsylvanian)/Early Permian, **prior to the diversification of dinosaurs** (ca. 323 MYA).

In the mid 1980's, we thought these were entirely carnivorous; only a single lineage had been discovered. This is what I learned and is based primarily on the frequently represented genus *Dimetrodon*.

Since then, early additional synapsid fossils have been discovered; it's clear that they were much more diverse than we previously thought and there were multiple lineages. For example, there was much more variation in both diet & activity than we once thought and there were also both herbivorous & insectivorous lineages.

Some (*Dimetrodon*) had a large dorsal sail that probably was thermoregulatory (some postulate it was used in mate choice).

Most were **rather large**, about 3M long,

All demonstrate many of the ancestral skeletal characters we've discussed.

1. They were only weakly heterodont,
2. They had only a small temporal fenestra, through which only little of the jaw adductors passed.
3. The dentary was not greatly enlarged, with several post-dentary bones in the mandible (including the angular and articular bones).
4. The jaw joint was formed by the quadrate bone (upper) and the articular bone (lower).
5. They had no secondary palate and the two nares opened into front of oral cavity.
6. They had a single occipital condyle.

And **many other** ancestral characters (e.g., limb girdles, palatal teeth, cervical and lumbar ribs).

2. Therapsids: By the Middle Permian (ca. 270 MYA), one lineage became dominant. These are known as **therapsids** (sometimes called “advanced synapsids”).

Early therapsids were actually quite large → 3-5 meters.

The therapsids were very diverse in the mid Permian.

They were large (3 -5 M).

There were lots of groups, including herbivores, carnivores, etc.

All were rather active.

This was still prior to the origin of dinosaurs, & therapsids were the dominant terrestrial vertebrates.

Most went extinct during the Permo-Triassic extinction.

Therapsid fossils exhibit a mixture of ancestral and derived character states.

They exhibited an enlarged temporal fenestra.

They gradually evolved deeply thecodont dentition.

There was a partial secondary palate; we see gradual evolution of the palate.

It's in one particular therapsid lineage that we see the sweeping sets of changes in skull and jaw morphology, which we'll go through in more detail later.

At the end of the Permian, ca. 250 MYA, there was a mass extinction. 90% of all species, including most of the therapsids, went extinct. This was the massive Permo-Triassic extinction, and a paper published a few years ago ([Broadly et al., 2018.](#)) describes evidence that vulcanism released halogens, and that these destroyed the ozone.

One lineage, the cynodonts, survived the Permo-Triassic extinction.

3. Cynodonts: The “advanced therapsids” arose, as I said, in the very late Permian and survived the Permo-Triassic mass extinction.

In this lineage, we see the very gradual evolution of many mammalian characters we’ve already discussed, with tons of transitional fossils.

- It’s here that we first see a complete secondary palate.

 - It evolved gradually; first just the premaxillae met at the midline.

- Two occipital condyles are present.

- There is a gradual enlargement of the dentary and shrinking of post-dentary bones.

- There is a vast expansion of the temporal fenestra.

- Strongly heterodont dentition arises.

Again, these arose in the late in the Permian and survived the P-T extinction.

There’s increasing evidence that cynodonts interacted with dinosaurs directly. It may well have been that cynodonts were preyed upon rather heavily by dinosaurs, which diversified and became dominant in the early Triassic.

For whatever reason, competition, predation, or something else, by the late Triassic the cynodonts were nearly all small and inconspicuous.

It’s very well supported that cynodonts represent the ancestral stock from which modern mammals evolved. The extinction of the dinosaurs at the end of the Cretaceous is thought to have permitted the radiation of modern mammals, although timing of placental mammal diversification remains pretty controversial.

D. So there are several issues that we’ll examine regarding the origin of mammals.

- 1) What are the key groups of cynodonts and how are they related?

- 2) Which groups were Mammals.

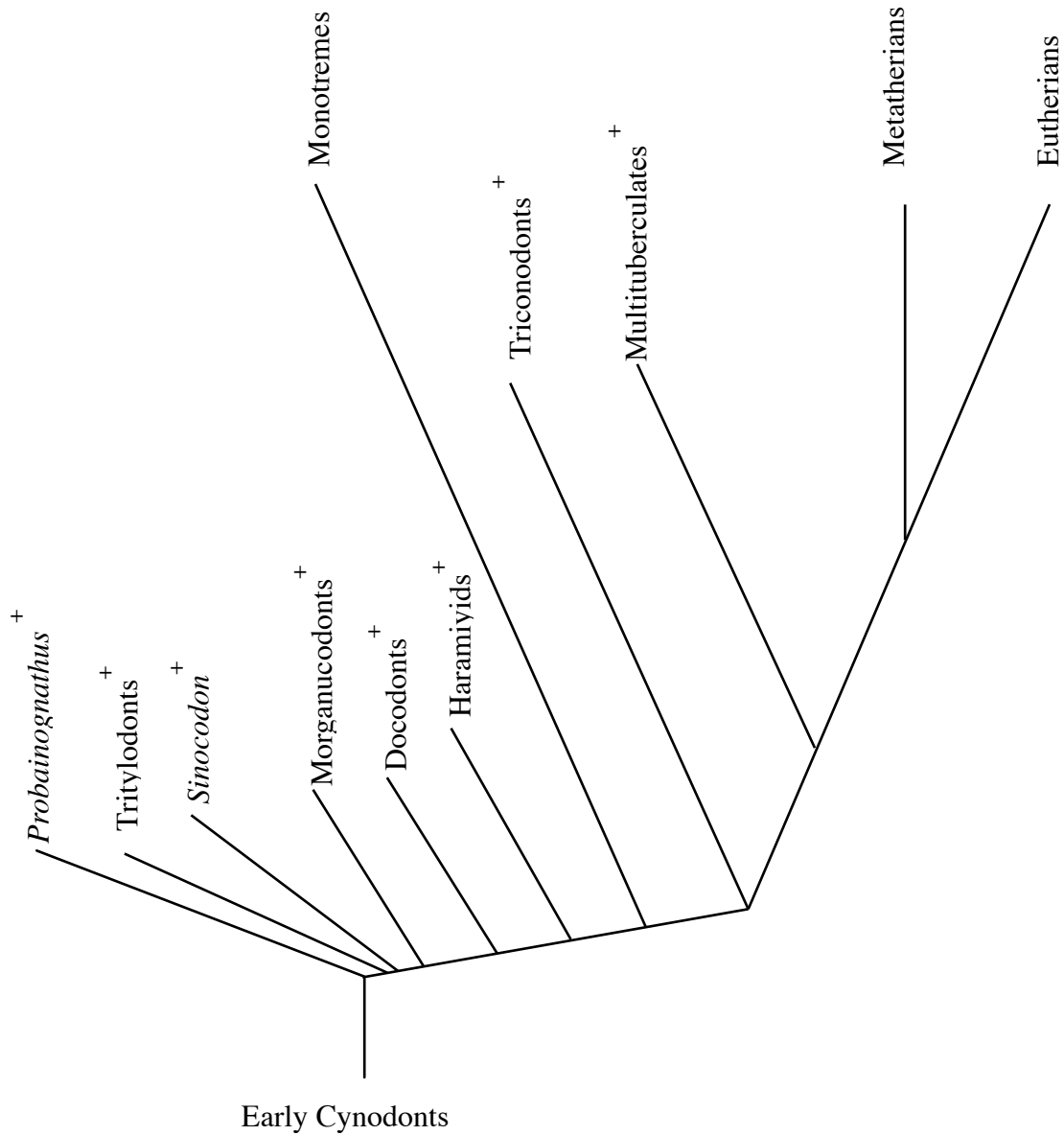
- 3) Why and how did so many characters evolve.

We’ll start examining these issues by looking at cynodont phylogeny. We won’t worry about all the groups, just those that contribute to our understanding of mammals.

Huttenlocker et al. (2018 – pdf on website) have produced a well-supported hypothesis of cynodont and early mammal relationships.

The phylogeny in the paper is very comprehensive and excellent for research, but we'll use a simplified version that only includes a few relevant groups.

Simplified Cynodont Phylogeny
(Following Huttenlocker et al. 2018)



At this point, then, we get to the second issue; how do we **classify** these fossils? That is, which ones were mammals? Note that “mammal-like reptiles” is an old term used for early synsids, therapsids, and non-mammalian cynodonts.

The traditional paleontological approach has been to look for “**key characters**” – if the animal has this character, we can call it mammal.

This approach worked well for a while, as long as the fossil record was spotty; the **dentary/squamosal** jaw articulation was the key character and for decades we knew of no transitional forms.

If a fossil had a dentary/squamosal articulation it was considered a mammal.

If it had a quadrate/articular jaw joint, it was considered a non-mammalian cynodont.

When this was the approach, Morganucodontids were the first mammals (*Sinoconodon* has a D/S jaw joint, but wasn't discovered until 1975)

Problem arose when intermediate forms were found; evolution of the derived jaw joint has been caught in action by fossil intermediates.

Probainognathus -- both jaw joints present. Q/A still present but D/S has evolved.

Medial Q/A jaw joint

Lateral D/S jaw joint

Diarthognathus -- both jaw joints present. Q/A still present but D/S has evolved.

Paleontologists responded that we can't use a single key character, we should use a **suite of characters**. This is the approach taken by Feldhamer et al.

- 1) D-S jaw joint
- 2) Strongly heterodont dentition
- 3) Molar surfaces complex, with wear facets, indicating precise occlusion.
- 4) Alternate side chewing, implying complex jaw musculature
- 5) Well-developed inner ear region, and presence of petrosal (inner ear bone)
- 6) Small
- 7) Axial skeletal characters - dorso-ventral flexion, placement of ribs, etc.

So, by this approach, if a fossil has most or all these characters, it was called a mammal.

It's no surprise that this approach led to application of the name Mammalia at the Morganucodontid node; the set of characters were chosen by those who already considered Morganucodontids the first mammals

Both these two approaches, based on **key character** and based on a **suite of characters**, represent what are called **grade-based definitions**. That is, we have some concept of what constitutes a mammal and if some organism achieves a certain grade of organization, we can call it a mammal.

Problems with a grade-based approach

- Because quite gradual evolution is represented in these fossils, and there are lots of transitional fossils, it's rather difficult and very arbitrary to assign a cut-off point based on achievement of some perceived critical "mammalian grade."
- Many of these characters evolve independently at different places on the phylogeny & we could have mammals evolving at various places (e.g., Heterodont dentition. Size. Parasagittal posture).

Thus, using either grade-based approach to classification is potentially problematic. In order to address these problems, we need to think about **what we require of our classifications**.

1) Classification must reflect evolutionary history. What this means is that we only want to recognize monophyletic groups. Monophyletic group represents an ancestor plus all of its descendants.

2) Classifications should be stable. That is, they shouldn't be changing all the time.

To some degree these two can conflict; when they do, evolutionary history has priority.

We'll use the "Reptilia" example to demonstrate how what we name things influences how think about them.

This leads to the current **clade-based** approach; a clade is a monophyletic group.

This has the advantage of basing the classification on the phylogeny rather than some arbitrary set of characters.

About 35 years ago, a wave of mammalogists (paleontologists) decided to change the approach & restrict Mammalia to the most recent common ancestor of all living mammals (Rowe 1988 – pdf on website). This created the need for a new name, Mammaliaformes, for

things like Morganucodonts, Docodonts, & Haramiyids. Lots of folks follow this classification.

To me, there's no doubt that a clade-based approach is a more appropriate approach. But restricting Mammalia in this way leads to instability, so I prefer the older classification and apply the clade-based definition to the Morganucodontid node (Ruta et al., 2013 – pdf on website).

For classification, then, the facts that heterodont dentition evolved several times, that the D-S jaw articulation evolved at least twice, that a secondary palate evolved several times independently don't matter.

Any newly discovered fossil that shares a common ancestor with morganucodontids is a mammal (or mammaliaform). This is arbitrary, but objective and based on phylogenetic analysis.

We can address the last question - what were the forces that lead to the evolution of these characters - only by inference. That is, we can propose hypotheses, and choose that which we deem to be most plausible given the available evidence.

E. The Size-Refugium Hypothesis (see McNab 1978 - pdf on website) --There are several elements of this hypothesis.

Much of this rests on the physical law relating surface area to volume ratio (S/V) with body size. There's an inverse relationship: increase body size → decrease S/V; and vice versa.

1. The early synapsids and the early therapsids were relatively large ectotherms.

Because of size and low S/V, they had large **thermal inertia**; once warm, they took a long time to cool and experienced a fairly constant body temp. This is called **gigantothermy**.

They were homeotherms.

This is consistent with living large ectotherms like leatherback turtles.

Under this hypothesis, therapsids became physiologically adapted to a high and constant body temperature over the tens of MY time span that they were large.

Selection favored large body sizes.

2. In the mid Triassic, dinosaurs radiated and became dominant, so under this hypothesis, there would have been selection for smaller size to escape competition and/or predation. This is where the name of the hypothesis comes from.

3. But as size decreases, thermal inertia is lost and heat loss increases.

Small objects lose heat faster than do large objects.

If cynodonts were already constrained for homeothermy, selection would have favored animals with the ability to produce their own heat. There would have been selection for endothermy. Partial endothermy (Mesothermy) is pretty common among vertebrates (e.g., sharks, billfish, pythons).

4. The evolution of endothermy had are a number of far-reaching implications.

A. Energy requirements – An endotherm burns calories to maintain body temperature and requires ca. 10X energy as a similar sized ectotherm.

Selection favored:

i. Increased efficiency of food processing

- Complex & specialized dentition with precise contact between upper and lower teeth.

- Specialized jaw musculature → evolution of a new muscle the masseter.

- Formation of secondary palate

ii. Increased cardiopulmonary efficiency

- Extrusion of nuclei from Red-blood cells increases carrying capacity for O₂ in blood.

- Separation of oxygenated blood from deoxygenated blood and evolution of 4-chambered heart.

- More efficient breathing due to restriction of ribs to thoracic vertebrae and muscular diaphragm.

- Respiratory turbinates permit recovery of water lost with increased respiration.

B. Behavioral implications – Because endotherms can generate own heat, they can be active on cold nights.

Endothermy permitted nocturnality.

Selection favored:

i. Hair as insulation.

- ii. Olfactory and auditory capabilities as means of gathering information in the dark.

Under this hypothesis, the evolution of endothermy generated the selective forces that favored most of the traits we consider to be mammalian traits.

Other hypotheses have been proposed that include other aspects of biology of endotherms (e.g., parental care).

Throughout Jurassic and Cretaceous, these mammal groups remained very small and inconspicuous.

The classic thinking has been that the extinction of the dinosaurs at the end of the Cretaceous allowed for the radiation of mammals and the diversity that we see today to evolve. This is quite controversial right now: O'Leary et al. (2013) argue in favor of it, but I think they've introduced bias in their analysis (Springer et al. 2013).