Mammalogy Lecture 2 - Origin of Mammals

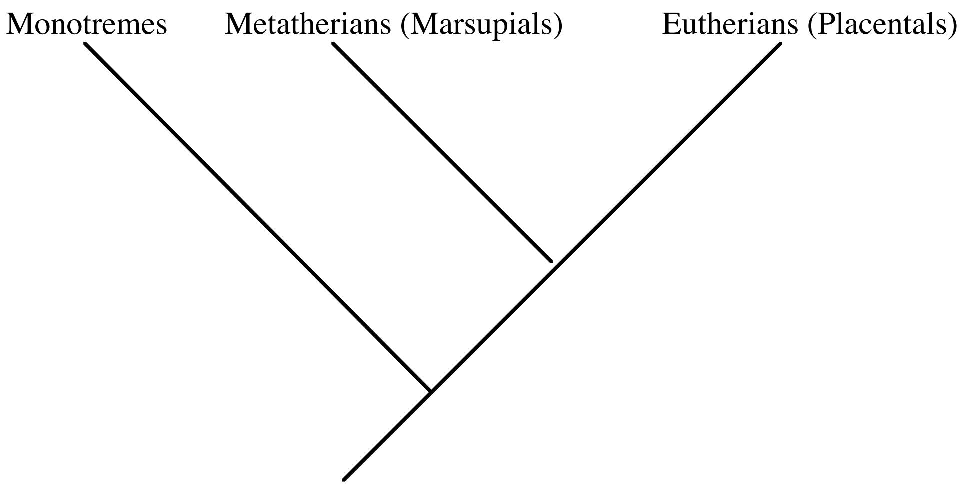
I. There are three major living (extant) groups of mammals

A. Monotremes - egg laying mammals

B. Metatherians - marsupial mammals

C. Eutherians - Placental mammals

These are related by the following evolutionary tree or phylogeny

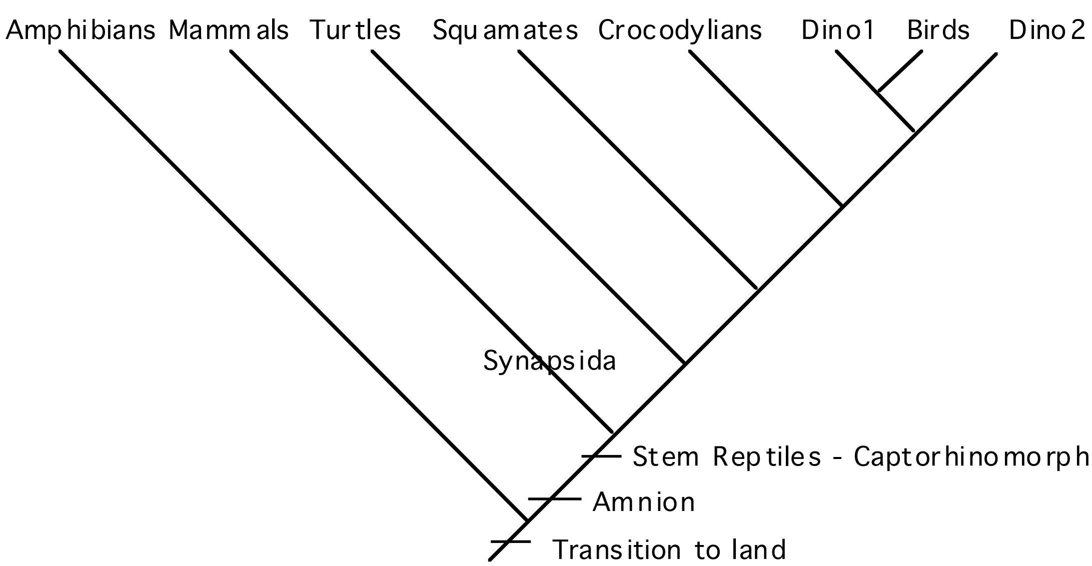


Node - Divergence Event

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, into the Paleozoic (350 MYA), and look at relationships among the tetrapod vertebrates. So we'll start by going deeper in time, and work our way back up to this level in the phylogeny.



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.

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

Captorhinomorphs.

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

Synapsid - "together arch" describes a skull condition that is unique to this lineage.

The word "synapsid" is also used to refer to the group of organisms that exhibit this condition.

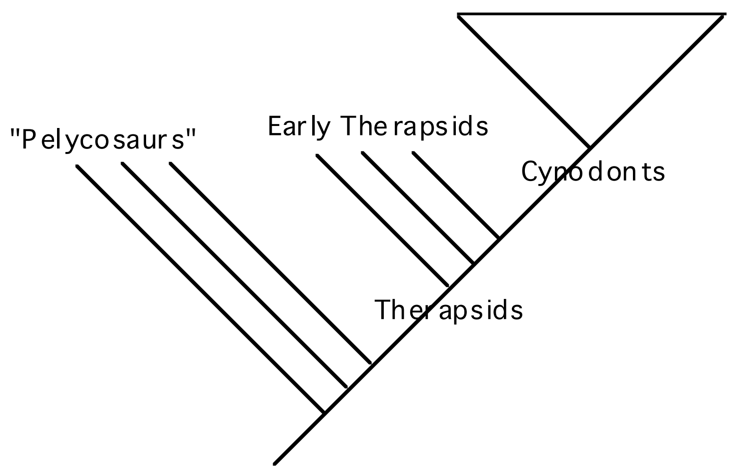
Anapsids: Lower jaw musculature (jaw adductors) anchored to inside of this shield of bone. Still present in some turtles. Modern tetrapod groups have different modifications of this ancestral anapsid condition. Captorhinomorphs were anapsid – has no temporal fenestra.

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

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

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

C. Synapsid Phylogeny



1. Pelycosaurs (a.k.a. non-therapsid synapsids)

Arose in the Early Permian - **prior to the diversification of dinosaurs** (ca. 320 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 synapsid fossils have been discovered that were clearly herbivorous, and others that were insectivorous; 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 pelycosaurs.

Still though, they were **all rather large**, about 3M long,

- They had a large dorsal sail that probably was thermoregulatory (some postulate it was used in sexual selection).
- They had many ancestral characters:
- They were only weakly heterodont,

- They had only a small temporal fenestra, through which only little of the jaw adductors passed.
- The dentary was not greatly enlarged, with several post-dentary bones in the mandible.
- The jaw joint was formed by the quadrate bone (upper) and the articular bone (lower).
- They had no secondary palate – nares opened into fort of oral cavity.
- They had a single occipital condyle.

2. Therapsids: By the Middle Permian (ca. 265 MYA), a separate 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.

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

All were rather active.

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

They exhibited an enlarged temporal fenestra.

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, there was a mass extinction. 90% of all species, including most of the therapsids, went extinct. Permo-Triassic extinction.

3. Cynodonts – "advanced therapsids" arose in the very late Permian, and survived the 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.
- 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 & braincase.
- Strongly heterodont dentition arises.

It’s almost certain 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.

Classic thinking has been that cynodonts represent the ancestral stock from which modern mammals evolved, and the extinction of the dinosaurs at the end of the Cretaceous permitted the radiation of modern mammals.

D. So there are several issues that we’ll be interested in examining the origin of mammals.

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

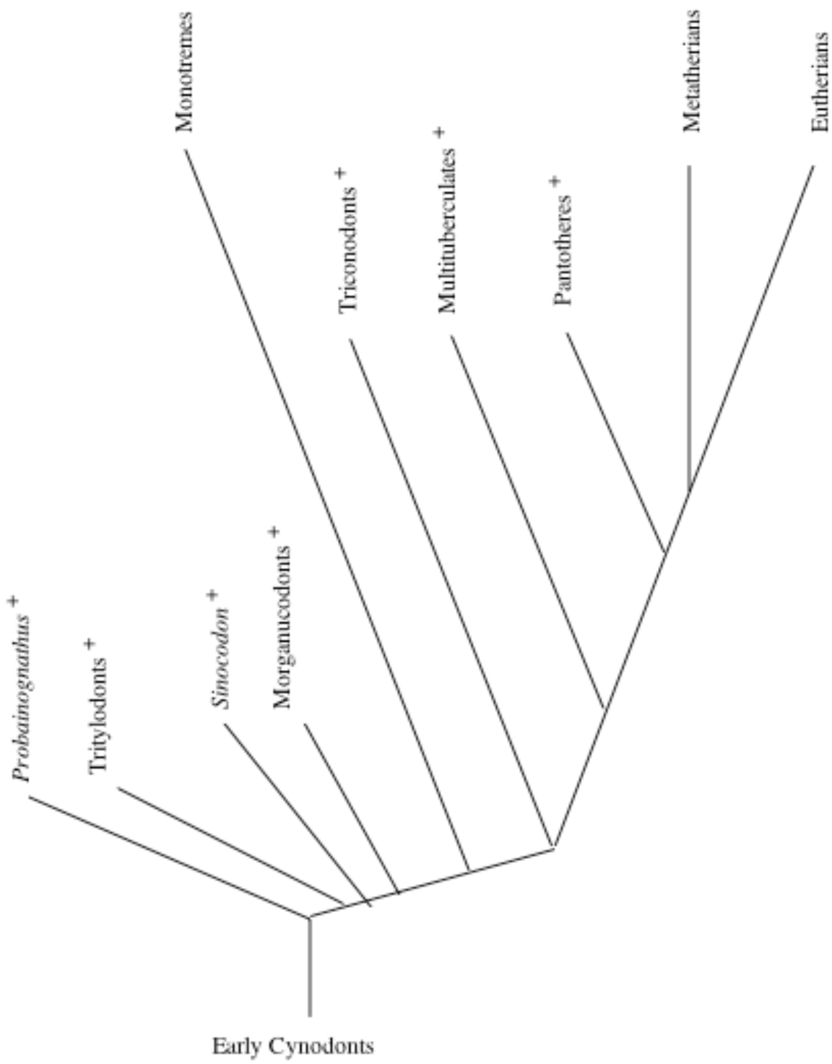
2) Which groups were Mammals.

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.

Cynodont Phylogeny & Origin of Mammals

Following Luo et al. (2002)



At this point, then we get to the second issue; how do we **classify** these fossils? That is, which ones were mammals?

The traditional paleontological approach has been to look for "**key characters**" -- if the animal has this character -> we can call it mammal.

For a while, when the fossil record was really spotty, this worked well. There were no transitional forms and the dentary/squamosal jaw articulation was the key character.

If a fossil had a dentary/squamosal articulation -> Mammal

If it had a quadrate/articular jaw joint -> reptile

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

Problem arose when intermediate forms were found -- synapsid evolution represents a continuum.

Probainognathus -- both jaw joints *Diarthognathus* -- both jaw joints

So paleonotlogists responded that we can't use a single key character, we need to 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. --Occlusion--
4) Alternate side chewing, implying complex jaw musculature
5) Well-developed inner ear region.
6) Small
7) Axial skeletal characters - dorso-ventral flexion, placement of ribs, etc.

So by this approach, if a fossil has most or all of 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 of these two approaches, based on **key character** and based on a **suite of characters**, represents what we call a **grade-based definition**. That is, we have some concept of what constitutes a mammal and if some organism achieves a certain grade of development we can call it a mammal.

Problems with a grade-based approach

- Because we have really gradual evolution represented in these fossils, and there are lots of transitional fossils, it's really difficult and very arbitrary to assign a cut off point based on achievement of some perceived critical "mammalian grade."
- Many of these characters evolve at a lot of places on the phylogeny & we could have mammals evolving at various places. D-S jaw joint. Heterodont dentition. Size.

So using either grade-based approach is potentially problematic. We're really talking about calssification here, so 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 and ancestor plus all of its descendents. **Use the Reptile example**.

2) Classifications should be stable - that is, they shouldn't be changing all the time. To some degree these to conflict. When they do - evolutionary history has priority.

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

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

About 15 years ago, a new wave of mammologists (paleontologists) decided to change the approach & restrict Mammalia to the most recent common ancestor of all living mammals.

To me, there's no doubt that a clade-based approach is a more appropriate approach. But restricting Mammalia in this way would leads to instability.

So for our purposes, we'll use apply the clade-based definition to the Morganucodontid node.

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. This is arbitrary, but objective and based on phylogenetics 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--There are several elements of this hypothesis**.**

Much of this rests on the physical law relating S/V with body size....Inverse relationship increase body size --> decrease S/V and vice versa.

1. Early therapsids were relatively large ectotherms. Initial selection for large body size. because of size, 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 100 MY that they were large.

2. In the 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 therapsids 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 is pretty common in vertebrates.

4. Once endothermy had evolved, there 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 – Increase carrying capacity for O_2 in blood.
- Separation of oxygenated blood from deoxygenated blood and evolution of 4-chambered heart.
- More efficient breathing – restriction of ribs to thoracic vertebrae and muscular diaphragm.
- Respiratory turbinates - recover 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 for insulation

ii. Development of olfactory and auditory capabilities

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

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.