Mammalogy Lecture 3 – Mammaliaformes, Early Mammals & Monotremes

I. Early lineages – There are several early groups known as **Mesozoic mammals**. There have been lots of groups discovered rather recently, and we'll only address a few that are significant for one reason or another. (Note Mammaliaformes vs. Mammalia).

A. Morganucodontids – Remember that this node represents the stable, clade-based definition of Mammalia (Ruta et al. 2013; others consider these to be mammaliaforms).

These are some of the earliest known mammals, from the latest Triassic and early Jurassic, and they're best known from the genus *Morganucodon* (which I mentioned earlier).

We actually have pretty good, complete fossils for this group, so we can make quite a few inferences.

They were small; the skull length was around **3 cm** and total length around **10 cm**.

The skull had large nasal cavity. We can infer that there were great olfactory capabilities and that there were respiratory turbinates; so, they were probably endothermic.

They had a well-developed inner ear region, with a large petrosal. They probably had very good hearing.

In addition, they had very large eye sockets.

Based on this, as well as the olfactory and auditory capabilities, we can infer that they were probably nocturnal.

The pectoral girdle was like early cynodonts, even early synapsids; the scapula, anterior & posterior coracoids, clavicle and intercalvicle were all present and the pelvic girdle was unfused.

The dentary was greatly expanded and articulated with the squamosal. The articular was small and still present (but did not form the jaw joint) and was beginning to pull away from the dentary medially.

They had no auditory bullae. The tympanic bone was not fused to cranium; rather the angular was on mandible (labelled ectotympanic).

The cheek teeth had three cusps: large middle cusp, with the anterior and posterior cusps offset.

They had alternate side chewing

The upper & lower molars slid past each other and we see wear facets that resulted in shearing.

They probably were insectivorous.

They almost certainly had vibrissae (whiskers), based on pits and openings in the snout; so, they had hair.

B. Docodonts

The next group (of mammliaformes, under the crown-group definition; or of mammals under the most stable clade-based definition) is the early-diverging docodonts. Oldest fossils are known from the Middle Jurassic, and the first known, *Docodon*, was discovered in the mid 1800's in North America.

As is the case for many of these early groups, a lot has been discovered relatively recently. For example, there were forms with aquatic adaptations, such as *Castoricauda*.

A quite new discovery (2019) is the genus *Microdocodon*, that has the hyoid apparatus preserved. This is the skeletal support structure for the tongue, and it suggests that *Microdocodon* lapped milk and that these therefore lactated.

C. Haramiyidans

The haramiyidans were an old and persistent group; they first appeared ~220 MYA and persisted for ~80 MY.

Again, our knowledge of them has increased greatly in the last several years, and they had dentition that was adapted for herbivory. There were chisel-like incisors, a diastema (gap between incisors and cheek teeth).

They retained the ancestral single ear ossicle; there was an articular in the mandible and quadrate in the cranium.

There's increasing evidence that many were arboreal.

There are controversies regarding their phylogenetics, but the Luo et al. (2015) phylogeny seems the best supported (and corroborated by Huttenlocker et al. 2018).

D. Australosphenids (Mammals using either definition)

Some really cool Australian fossils called *Bishops* & *Ausktribosphenos* were discovered in the late '90s that exhibit a particular tooth type called tribosphenic molars (Rich et al. 1997.

Science, 278:1438 – pdf on course website). It was originally thought that these were eutherians, based on these molars. This would have been the (by far) earliest evidence of eutherians in Australia, so garnered lot of attention.

However, the phylogenies I referenced (Lou et al. 2015 – see the copy on course website) indicate that these fossils (e.g., *Bishops, Ausktribosphenos*) are related to Monotremes, in the clade called Australosphenida.

This is still quite interesting, though, because it implies that this molar type evolved at least twice.

E. Triconodonts – For several decades, triconodonts were known only from teeth and a few other skeletal fragments.

These teeth are similar to Morganucodontids', except the cusps are linear.

A complete Triconodont skeleton was discovered in China in 1999, the genus *Jeholodens*.

A really spectacular aspect of *Jeholedens* is that they have a very mammalian pectoral girdle - only a scapula and clavicle were present, because the interclavicle and both pairs of coracoids are lost.

However, the pelvic girdle is still ancestral; the ilium, ischium and pubis are unfused, epipubic bones are present.

Retained had a very sprawling posture; the limbs were not rotated under the body.

It's therefore a good demonstration of mosaic evolution. The pectoral girdle is derived, but the pelvic girdle is primitive.

About 18 years ago (2005), an incredibly cool triconodont was discovered, *Repenomamus giganticus*.

These also had the derived mammalian pectoral girdle but retained the ancestral pelvic girdle; it's these characters that support their place in the phylogeny inside crown mammals.

This is the largest mammal known from the Mesozoic, about a meter long, and probably was carnivorous. In fact, in one specimen of the genus, a collection of bones from a small dinosaur were found where the stomach would have been, suggesting predation on dinosaurs (Hu et al. 2005, Science, 433:139. – pdf on website).

F. Multituberculates - a.k.a "Rodents of the Mesozoic"

This was a very diverse and persistent group. It is first known from the upper Jurassic and ranged from mouse-sized to marmot-sized.

They extend through the Cretaceous into the Tertiary and existed with modern mammals.

They are named for their unique dentition, and the thinking is that this is what allowed them to persist as long as they did and become diverse.

There are chisel-like incisors or front teeth, with a large diastema (gap between front and cheek teeth). This arrangement is associated with herbivory.

They had very complex, grinding molars; this is the character for which they're named. Many of these are characteristic of modern herbivorous mammals.

They probably retained the ancestral sprawling limb posture (Keilan-Jarowoska & Hurum 2006).

There's good evidence that at least some of the multituberculates were arboreal.

Their success is thought to be related to their dentition, in that their diversification coincides with the early Cretaceous diversification of flowering plants (angiosperms). The hypothesis is that, because of their specialized dentition, they were able to diversify into the many new herbivore niches that were available with the diversification of flowering plants.

A really intriguing aspect of this group is that, as judged by their pelvis, they may have been viviparous, although that's a difficult inference to test.

E. Some other groups – In addition to the groups we've just discussed, other new fossil material has become available in the last couple decades or so. I'll just mention a few examples.

1. The genus *Hadrocodium* is very old mammaliaform fossil. It was discovered in 2001 (Luo et al. 2001. Science 292:1535) and appears to be ca. 195 MY old. As you can see, it's a very tiny specimen, and there's controversy over whether it's an adult or not. **It is among the earliest known fossils to have three ear ossicles. As we'll see, they evolved this state independently!**
2. The genus *Juramaia sinensis* was discovered a dozen years ago (Luo et al., 2011. Nature 476: 442. doi:10.1038/nature10291 – pdf on website). This is the oldest known eutherian, ca. 160 MY old, and has a number of adaptations that suggest it was scansorial (adapted for climbing).

Over the next several years, it'll be very interesting to see how the increasing knowledge of non-mammalian cynodonts and early mammals impacts hypotheses such as the size refugium hypothesis.

The classical view was that all Mesozoic mammals were shrew-like, but a new understanding of their diversity has been emerging for around 15 years (Luo et al. 2007): semiaquatic, carnivorous, fossorial, arboreal, and gliding forms have been discovered.

II. Living Mammals - Monotremes vs. Therian Mammals.

Metatherians and Eutherians form a clade called Theria. The older literature uses a term called Prototheria to include monotremes, miltutuberculates, morganucodontids and triconodonts. You'll still see the term used, but it's not a monophyletic group, so we won't use it.

A. O: Monotremata. "one hole" - refers to cloaca which is the Latin word for sewer.

The cloaca is a single opening receives the large intestine, ureters, and reproductive tract. This is a very primitive trait among vertebrates.

Earliest fossils are from the early Cretaceous, ~120MYA.

Fossil record is still poor, but it is increasing. In the early 90's, 63 MY old platypus fossil teeth were discovered in Argentina. These teeth are similar to the teeth living platypus has when young.

B. We often hear monotremes called **primitive mammals**. This really is inaccurate because monotremes are **mosaics of both primitive and derived traits.**

Primitive Characters

- Cloaca, which is still present in other tetrapod groups.
- Skull characters
  - still possess pre- and post-frontal bones.
  - no auditory bulla
  - lacrimal bones absent
- Pectoral girdle
  - interclavicle
  - anterior coracoids
  - posterior coracoids
  - intercalvicle
- Epipubic bones present; they were present in early synapsids.
- Cervical ribs are present and free, that is, not fused to vertebrae.
- Reproductive characters
  - oviparous
  - eggs have huge amount of yolk relative to therian ova
  - eggs are shelled - have a shell gland
  - mammary glands have separate openings, no nipple, and young lap milk from tufts of fur rather than suckling.
  - male lacks a scrotum, and testes remain in the abdominal cavity.
  - males lack seminal vesicles

Derived Characters

- Leathery bill or beak.
- Venom - male platypuses have a venomous spur. This is very unusual in mammals.
- As adults, instead of teeth they have horny raspy pads.
- Electroreceptors in bill in platypuses
- One group has spines

It's a mischaracterization to call a group primitive.

C. Two living groups - both restricted to Australia and New Guinea

1. F: Tachyglossidae - Echidnas - occur in both Aust. & N.G.

Both forms have large spines - not barbed like those of porcupines, when threatened, echidnas will roll up into a ball.

Pinnae (external ears) are moderately large.

Limbs are powerful and adapted for digging.

Typically lay single egg that is incubated in a temporary pouch for 7-10 days.

Echidnas hibernate, that is, when ambient temperature drops to 5^{o}C, T_{body} drops to 5.5^{o}.

Males have spurs, but these are non-venomous.

Tachyglossus - short beaked echidna, specializes on ants and termites, has copious sticky saliva.

Zaglossus - long beaked echidna, specializes on earthworms.

2. F: Ornithorhynchidae - Platypus found only in Australia

Ornithorhynchus - Aquatic, swims with forefeet, which are webbed (as are hindfeet) - digits retain claws.

Bird/Snout - feed primarily on aquatic crustaceans - submerge for around a minute.
- dense pelage, and under fur is wooly
- males have venomous spurs that enlarge during reproductive season → male-to-male combat.

- young platypus have teeth that actually never erupt.
- burrow into stream bank make a den
- usually lay two eggs, which are incubated for 10 days in the plugged burrow.