Radiation and Diversity of Nonamniote Paleozoic Tetrapods

From the late _____ to the Early _____, nonamniote tetrapods radiated into a variety of terrestrial and aquatic forms

Relationships between organisms are unclear:

- There are large gaps in the fossil record
  - In particular, there are few _____ representatives of many groups
- _____ and _____ evolution were widespread

Nonamniote tetrapods – what are they?

- Often called "amphibians"
  - The term "amphibian" is now reserved for living nonamniote tetrapods, the _____ (frogs, salamanders, and caecilians)
- It is misleading to think of primitive Paleozoic tetrapods as being amphibians
  - Many were larger than any living amphibians and would have been more crocodile-like in appearance and habit
  - They would have lacked the specializations of modern amphibians (many had _____ _____, so they could not have used cutaneous respiration)
  - Many were more closely related to _____ than to modern amphibians

Devoniant Tetrapods

- Based on fossil evidence, substantial diversity had evolved among tetrapods by this time
- Ichthyostega and Acanthostega are examples
- Ranged from .5 to 1.2 meters in length
- Had differences-
- Acanthostega was more _____ than Ichthyostega
  - Its forelimb was less robust and its elbow was unable to bend in a way that it could have supported the body out of the water
  - Articulating surfaces of the vertebrae were _____, the neural arches were _____ ossified, the ribs were short and straight, and the fin rays on the tail are longer than those of Ichthyostega
  - Acanthostega appears to have retained internal gills, but Ichthyostega had both lost the postbranchial lamina on the cleithrum, suggesting that they did not have an _____ gill chamber like that of Acanthostega
- The combination of ancestral and derived features of Devonian tetrapods suggests that the origin of _____ and the origin of _____ life were two separate events

Carboniferous-Mesozoic Nonamniote Tetrapods

- Paleozoic tetrapods were **originally** divided into groups called "labyrinthodonts" and "lepospondyls"
  - _____ were small forms with a single, spool-shaped vertebral centrum and without the labyrinthine form of enamel.
  - _____ were mainly larger forms with multipartite vertebral centrum and teeth with complexly infolded enamel (labyrinthodont teeth)
- Are these "real" groups?
  - Labyrinthodont- large forms
    - The form of the vertebral centra and the enamel of the teeth are most likely related to body size
      - Bipartite _____ for twisting movements of the spinal column on land
        - Heavy head would tend to rotate around the trunk axis during locomotion
      - Labyrinthodont teeth probably reflect the reliance on _____ feeding
        - Feeding with only a simple snap of the jaws, without fine control of jaw movement
        - The teeth might need to be strong to resist the forces generated during this kind of feeding
    - This suggests that Labyrinthodont is probably not a real group
      - Actually a diverse taxonomic grouping
      - Some were stem reptiles
      - Some were closely related to modern amphibians
      - Some were more closely related to amniotes
    - Current groups of "large" nonamniote tetrapods:
      - Temnospondyls and Anthracosaurs
      - Temnospondyls
        - More aquatic
        - Characterized by _____, immobile skulls and a reduction of the hand to _____ fingers
        - Frogs may have had their origin in this group
      - Anthracosaurs
        - More terrestrial
        - Characterized by domed skulls retaining some kinetic ability
        - Have _____-fingered hand
        - Amniotes may originate within this group

- Lepospondyls
  - Different groups may not be closely related
  - Some or all of them may be closely related to amphibians
  - Some or all of them may be closely related to amniotes

- Origins of Lissamphibia are questionable
  - Current (competing) hypotheses:
    - Lissamphibia derived from one group within the temnospondyls
    - _____ and other amphibians are derived from multiple groups within the temnospondyls

- Nonamniote tetrapods reached the peak of diversity in the late Carboniferous and early Permian
  - Consisted of:
    - Fully aquatic forms
    - Semi-aquatic forms
    - Terrestrial forms
  - Most lineages were extinct by the mid-Permian
  - Only groups to survive into the Mesozoic were the ancestors of the modern amphibians and the fully aquatic temnospondyls
    - Temnospondyls were extinct in most of the world by the end of the Triassic, except in Australia
      - In Australia, they died out in the Early _____
  - Ecological and Adaptive Trends
    - Many early tetrapods returned to a fully aquatic mode of life
      - Colosteids, ambolomerous, anthracosaurids, and groups within temnospondyls and lepospondyls had forms that were apparently fully aquatic as adults
      - Many living salamanders and some frogs are fully aquatic as adults
      - Some of the most bizarre aquatic forms were found among _____
        - Keraterpetonid cecteridians had broad, flattened skulls with enlarged _____ bones
          - These tabular bones were up to 5 times the width of the anterior part of the skull and were covered by a skin flap extending back to the shoulder.
          - These horns may have acted as a hydrofoil to help in underwater locomotion
          - These horns may have supported highly _____ skin to help in underwater respiration
      - The temnospondyls were the only group of amniote tetrapods to suvive the Paleozoic, and all of the Mesozoic forms were large, flattened, fully aquatic predators with apparently independent origins from less specialized forms

- Capitosaurids were large, crocodile-like forms, but with very small _____
- Plagisaurids had broad, short heads, and were extremely _____
  - They retained external gills as adults
  - They may have evolved via the process of _____ (retention of juvenile characters into adult life)
    - neoteny = retention of larval or embryonic characteristics past the time of reproductive maturity
    - paedomorphosis = condition in which a larva becomes sexually mature without attaining the adult body form. Paedomorphosis may be achieved by neoteny
- t_____ evolved the elongated snout characteristic of specialized fish-eaters and are found in marine beds
  - Raises questions about osmoregulation
  - Even if they evolved reptile-like impermeable skin, the larvae would have gills as a site of water loss.
  - They may have retained high levels of urea to raise internal osmotic pressure

- "anthracosaurs" were predominantly terrestrial as adults
- may have been mistaken for early _____
- evolution of forms with elongated bodies and limbs that are greatly reduced or lost entirely
  - Probably associated with an aquatic or _____ mode of life as in the living limbless caecilian amphibians

Amniotes

- Derived tetrapods
- Include most of the _____ alive today
- Name refers to the amniotic egg
- Amniotes appeared later in fossil record than the earliest tetropods of the Devonian
  - Earliest known examples are 20 million years younger than the earliest known tetrapods
- Initial radiation occurred in the Permian
  - Radiated into many life zones originally occupied by non-amniote tetrapods

- Key event in radition may have been the diversification of _____ in the Late Carboniferous, probably in response to increases in quantity and diversity of terrestrial vegetation
- Most terrestrial vertebrates were _____ rather than herbivorous
  - Diadectes may have been an herbivorous non-amniote
  - No adult _____ among living forms is herbivorous
- The non-amniotes of the late Paleozoic were diverse morphologically and ecologically
  - As they diversified, terrestrial nonamniotes became less varied
  - Survivors were mostly flattened, fully aquatic forms.
- From the start of the Mesozoic onward, terrestrial habitats were dominated by a series of radiations of amniote tetrapods

Derived Features of Amniotes

- Amniotes represent a more derived kind of tetrapod than both the living amphibian and the Paleozoic nonamniote tetrapods
- Skin is sometimes used as a defining character of amniotes
  - Amniotes have a _____ skin than amphibians
  - They have a _____ epidermis
  - The presence of _____ in the skin makes it relatively impermeable to water
  - Compared to amphibians, they have greater variety of skin elaborations
    - Scales, hair, and feathers are all formed from _____
- Amniotes have costal ventilation of the lungs
  - Helps with conservation of water, since the skin doesn't need to be kept _____
- Amniotic egg
  - Shell provides _____ protection while being porous enough to allow movement of _____ gases and water vapor
    - May be leathery and flexible (as in many lizards and turtles)
    - May be calcified and rigid (as in other lizards, turtles, and birds)
  - _____ (egg white)
    - Gives protection against mechanical damage
    - Provides a reservoir of water and protein
  - Yolk provides energy for the developing embryo
    - At the beginning of development, the embryo is essentially a few _____ resting on top of the yolk
    - As development proceeds, these cells multiply and endodermal and _____ tissue surrounds the yolk
      - Enclosing the yolk forms the yolk sac
      - The yolk sac is part of the developing gut

- Blood vessels differentiate rapidly in the mesodermal tissue surrounding the yolk sac and transport food and gases to the _____
- By the end of development, only a small amount of yolk remains
  - This is absorbed before or shortly after hatching

Note: to this point the amniotic egg does not differ from nonamniotic eggs of amphibians and fishes….except the shell, that's new. Confused yet?

- _____ and Amnion
  - Develop as outgrowths of the body wall at the edges of the developing plate-like embryo
  - The two pouches spread outward and around the embryo until they meet
  - At their junction, the membranes merge and leave an outer membrane and an inner membrane
  - The outer membrane is the _____
    - The chorion surrounds the embryo and yolk sac
  - The inner membrane is the _____
    - The amnion surrounds the embryo itself

- Allantoic membrane develops as an outgrouwth of the hindgut posterior to the yolk sac and lies within the _____
  - Appears to have evolved as a storage place for _____ wastes produced by the metabolism of the embryo
  - The urinary bladder of the adult grows out from its base
  - Allantois also serves as a respiratory organ
    - It is _____ and can transport oxygen from the surface of the egg back to the embryo (and transmit carbon dioxide the opposite direction)
  - The allantois is left behind in the egg when the embryo emerges, and the nitrogenous wastes stored in it do not have to be reprocessed

- Why might the amniotic egg have evolved?
  - Only very _____ non-amniotic eggs may be laid on land
    - Eggs larger than 10 mm in diameter may be too large for _____ of oxygen across their surface
    - They may collapse under their own weight
    - Presence of additional embryonic membranes would enable large eggs to be supported (as would a shell) and to provide exchange of respiratory gases

- Evolution of the amniotic egg might have allowed an increase in the _____ of adults that could lay eggs on land

- How might we infer the reproductive mode of fossil animals called amniotes?
  - Capacity to lay an amniotic egg is not preserved in features of the _____
  - We can make an estimate from the tetrapod phylogeny
    - The synapsids (mammals and extinct relatives) branched off from other reptiles very early on
    - All other fossil animals that we consider to be amniotes are more closely related to living reptiles and birds
    - Because mammals have the same type of egg as other living amniotes, all animals higher than the common ancestor of mammals, reptiles, birds, etc (higher than node 13 on figure 8-13 on page 195) must have inherited this type of egg.
    - _____ did not have amniotic eggs
      - Larval forms with external gills and lateral lines are known, which means that they still had aquatic larvae
    - _____ have morphological features that suggest they were herbivorous
      - Herbivorous young must ingest symbiotic microorganisms needed to aid in digesting herbage immediately after hatching
      - These must be obtained from _____ microbial decomposers
      - It might be inferred, therefore, that diadectomorphs had a fully terrestrial form of reproduction and hence possessed the amniotic egg

Patterns of Amniote Temporal Fenestration

- Temporal fenestration refers the number of _____ in the head
- Major configurations:
  - Anapsid- seen in primtive amniotes and in turtles
    - Without an arch
  - _____- seen in mammals and their ancestors
    - With a single arch
  - _____- seen in other reptiles and in birds
    - With a double arch
  - "Arch" refers to the temporal bars lying below and between the holes
  - The phylogenetic pattern of acquisition of holes suggests that the condition arose independently in the synapsid and dispsid lineages, because more primitive sauropsids than diapsid lack holes entirely

- What is the function of these holes?
  - They provide room for muscles to bulge
    - Amniotes have larger and more differentiated jaw muscles than nonamniotes, and the notion of room for bulging was originally the preferred evolutionary explanation
  - The initial evolutionary reason for developing these holes was something different
    - Only a large hole will allow enough room for a bulging muscle
    - What could have been the evolutionary advantage of an initial small hole?
    - Why does no nonamniote ever develop a temporal fenestration?
    - Answers are related to complexity and orientation of the jaw muscles
      - In fishes and nonamniote tetrapods, the jaw muscles are a simple, little-differentiated mass, and the feeding movements consist of a simple _____
      - Domed skull of amniotes allows muscles to originate directly from the _____ of the skull and run vertically down to the jaw
      - This new orientation of part of the group of muscles allows static pressure between the teeth when the jaws are closed
      - The other portion of the original adductor complex is now the _____ muscle, originating from the pterygoid flange on the palate
      - Such a condition would not be useful for a non-amniote with a short flat skull, because it would not allow the mouth to open very widely

OK, so the muscles differentiated in amniotes. What about the holes?

- Increased differentiation of the adductor muscles allows for more complex jaw movement
- It could also introduce new _____ to the periosteal covering of the bone
  - The pterygoideus muscle connects upper and lower jaw on the inside of the skull.
  - Other muscles originated from other positions on the inside of the skull. Because they are on the inside and attach at essentially a 90 degree angle, stress on the bone will be quite high in a localized area
  - This creates an area of weakness of the skull

    - To compensate for this, portions of the skull could remain _____, and muscle could originate from connective tissue covering this hole
    - Later developments would then include _____ of the hole, with muscles running through the hole to attach to the outside of the skull roof

- The previous explanation does not explaoin why the pattern is different in synapsid and diapsids and some early amniotes lack fenestration
    - _____ have skulls that are technically anapsid, but they have a posterior emargination of the skull that allows expansion of the jaw muscles
        - It is analogous to a fenestra
    - Early synapsids and diapsids were rather different kinds of animals
    - Synapsids were more _____
        - Needed them to seize and crush large, slow prey
    - Diapsids were more _____
        - Needed inertial snapping to capture small, quick prey
    - Differences in muscle actions relating to different feeding styles may have encouraged temporal fenestration to take different form in the two groups

Differences among Major Amniote Groups

- Major splits in diversification of amniotic lineages happened very early, soon after the origin of amniotes themselves
- Initial split was into synapsids (mammals and extinct relatives) and saurapsids (reptiles and birds)
    - Saurapsids split into parareptiles (probably including turtles) and eureptiles (other reptiles and birds)
        - There is some debate about the monophyletic nature of parareptiles
        - This grouping emphasizes that main lineages have little or no relationship to the living groups of reptiles (except for turtles)
- Differences between groups
    - Mammals
        - Branched off very early
        - Lack some of the derived features that we attribute to reptiles
            - Sauropsids (reptiles plus birds) have good color _____ and the anatomy of their eyes suggests diurnal ancestry

- Sauropsids have a new type of harder _____ (called beta keratin) forming the scales or feathers

- Eureptiles and parareptiles differ
  - All living eureptiles have hindlimbs longer than the forelimbs, allowing them to run _____ and bipedally
  - Middle ear and eardrum evolved separately in different groups
- Lepidosaur and archosaur (both eureptiles) differ
  - Lizards and snakes have forked _____
  - Lizards and snakes shed their _____
  - Lizards and snakes have bifurcated _____
  - Archasaurs have a muscular _____
  - Archosaurs have a more upright stance
  - Archosaurs have more complexly subdivided _____

Posture and Locomotion in Derived Amniotes

- Tetrapods such as lizards still move via _____ movements, and still experience a conflict between the use of axial muscles for locomotion and for ventilation
- Primitive tetrapods are unable to run and _____ at the same time
  - This is acceptable for ectothermal amniotes which relay primarily on _____ metabolism for short bursts of activity
  - For a more active animal, especially an endotherm, this muscle arrangement limits the capacity for _____ aerobic activity
- New posture
  - Conflict of dual use of trunk muscles is solved in part by adopting an _____ posture
    - Limbs are held more directly _____ the body
    - The trunk is held more rigidly in locomotion
    - The _____ provide the predominant propulsive force
  - In mammals, this posture is associated with a _____ stance
  - In archosarus, the upright posture was combined with a tendency towards _____
    - Running on two legs rather than four isolates the trunk from the effects of locomotor bending
    - Crocodiles are archosaurs, but their _____ stance was derived from an upright stance, and is associated with their aquatic mode of life