Class Mammalia

I. Mammalian origins
  A. Mammals are members of the Synapsida
  B. Trends in Mesozoic mammalian evolution
  C. Evolution of the middle ear
II. The “true” mammals
  A. *Morganucodon* was the first mammal
  B. The three major mammalian radiations
  C. Systematics of extant groups

I. Mammalian origins

A. Mammals are the remaining members of the Synapsida, so mammalian history begins with the early synapsid radiations (see fig. 17-1, 2 pp. 480-1; handout at end of notes)

1. The first synapsid radiation was the first amniote radiation, extending from the early Carboniferous to the early Permian
    a. members included both herbivorous and carnivorous forms (this will be true in all subsequent radiations)
    b. body sizes ranged from 10 - 200 kg
    c. synapsids were, at this time, the most abundant terrestrial vertebrates
2. Second radiation involved the “non-mammalian therapsids” (or early therapsids) in the late Permian
    a. animals were generally heavy-bodied
    b. carnivorous forms were top predators in terrestrial habitats
3. Many groups went extinct during end-Permian mass extinction; throughout the Mesozoic, terrestrial environments were dominated by diapsids (including dinosaurs)
    a. during this time, one lineage of therapsids – the cynodonts – were undergoing extensive evolutionary changes
    b. these changes set the stage for the final synapsid radiation – the Cenozoic radiation of “true mammals” beginning after the end-Cretaceous mass

extinction

B. "Trends" in synapsid (pre-mammalian) evolution through the Mesozoic are associated with increasing adaptation to the "small, highly active, nocturnal insectivore" niche

1. in overview, trends result in
   a. decreasing body size:
      i. early cynodonts, already smaller than pelycosaurs, were the size of large dogs
      ii. late cynodonts were the size of rabbits
      iii. early mammals were the size of shrews (< 10 cm)
   b. increasing locomotor efficiency
      i. limbs carried directly beneath the body
      ii. dorso-ventral flexion of vertebral column helps power locomotion
   c. increasing feeding efficiency
      i. larger, more complex jaw muscles with improved mechanics
      ii. **heterodonty** = teeth differentiated for a variety of food types
   d. increased brain size
   e. increased respiratory efficiency
   f. fully mammalian energetics, including elevated metabolic rate, endothermy, etc.
2. Some key changes (see handout at end of notes; fig. 17-6 p. 489 and associated text section 17.3 pp. 488-491)
   a. increased size of temporal fenestra = opening permitting jaw muscles to originate on surface of braincase indicates a large volume of jaw musculature
   b. postorbital bar (absent in pelycosaurs) bowed out away from the braincase indicates new jaw-closing muscle (the masseter) – this becomes the zygomatic bar/arch in late cynodonts and early mammals

c. improved mechanical efficiency of lower jaw and jaw joint
   i. the dentary = the tooth-bearing bone becomes enlarged, eventually replacing all other bones of the lower jaw and forming new articulation with upper jaw
   ii. coronoid process on dentary = site of attachment of one group of jaw-closing muscles (the temporalis), allowing hard, fast bite from wide gape
d. increased specialization of dentition
   i. heterodont dentition = teeth vary in size, shape, function
   ii. mammals have complex (rotary) chewing with precise occlusion of teeth for improved food processing
      a) "pre-mammals" have simple up/down chewing (like reptiles)
      b) mammals use rotary motion of jaws with precisely occluding teeth to grind/slice food
         i) increases digestive efficiency
         ii) means more energy assimilated more quickly
   iii. mammals are **diphyodont**: only two sets of teeth (and only one set of molars)
      a) current thinking is that diphyodonty is necessary to maintain precise occlusion
      b) note that "replaced teeth" (non-molariforms) don't require as precise occlusion as molars do – and we only get one set of those
e. 2' palate of hard and soft tissue separates nasal airways from oral cavities
   i. eliminates possibility of cranial kinesis
   ii. but allows eating and breathing; suckling and breathing at same time
   iii. presumably helps support elevated metabolic rates
   iv. note that therapsids/cynodonts also had **turbinate bones** (fig. 17-11 p. 496)
      a) scroll-like bones lining nasal passages

b) support epithelium that helps resorb water from exhaled air
c) strong correlate of elevated respiratory rates – therefore strong correlate of elevated metabolic rates

f. parietal foramen present in pelycosaurs, lost in cynodonts
   i. provides opening to pineal gland, used in behavioral thermoregulation
   ii. loss suggests switch from behavioral (ectothermal) thermoregulation to endothermy
g. Increased locomotor efficiency with limb posture moving from sprawling to upright –
   i. this indicates more efficient, rapid locomotion and, therefore, higher activity levels
   ii. involves numerous changes to postcranial skeleton, including
      a) remodelling pelvic girdle in association with switch to use of gluteal muscles for propulsion
      b) remodelling pectoral girdle to lighten the girdle and allow it to participate in stride
      c) reduction in tail length
      d) improved mechanics of hands and feet as they become actively involved in rapid locomotion
h. changes to the vertebral column associated with changes in locomotion and respiration
   i. loss of lumbar vertebrae in cynodonts indicates “switch” to system allowing breathing, rapid locomotion to take place simultaneously
      a) recall that lateral undulation + costal ventilation precludes this
      b) with limbs beneath the body, dorso-ventral flexion of vertebral column adds to stride length (improving speed)
      c) costal ventilation replaced by muscular diaphragm
      d) mechanics of new system “automatically” coordinates

expansion/contraction of diaphragm with stride

ii. also get loss of ribs on cervical vertebrae; reduction in number of c.v. to 7

i. shortened tail in conjunction with switch in locomotor modes

C. Coolest "story" in mammalian evolution: evolution of the middle ear (see pp. 491-494 & box 17-1 p. 493)

1. remember that, in mammals, the dentary and squamosal replace the quadrate and articular as the bones of the jaw joint
2. Embryological studies over a hundred years ago demonstrated homologies between mammalian inner ear bones and "old" jaw bones:
   a. **stapes** homologous to **hyomandibular** (note this homology also holds for the columella of amphibians and reptiles with tympanic ears)
   b. **malleus** homologous to **articular**
   c. **incus** homologous to quadrate
3. We also have a good fossil record of the "transition" between the two articulations, including fossils with both sets of bones participating (these are the diarthrognathines = "double-jointed jaw")
4. Question is, what selection pressures were responsible for driving this shift in structure/function?
   a. "old hypothesis" = changes in jaw mechanics "freed" quadrate/articular to participate in middle ear: this hypothesis holds that
      i. selection for increased feeding efficiency drove changes in the structure of the jaws, including:
         a) enlarged dentary for increased strength, longer toothrow
         b) reduced post-dentary bones, including articular
         c) new and more powerful jaw muscles to allow use of wide range of food types
      ii. as jaw mechanics changed and jaw got stronger, increased stress was placed on quadrate/articular (remember that these are relatively small

bones)

iii. portions of the dentary (adjacent to articular) and squamosal (adjacent to the quadrate) shift position to add support to the quadrate/articular

iv. because they're bigger, stronger bones, the presence of the dentary/squamosal articulation "released" quadrate and articular from previous function, allowing them to become increasingly modified for participation in sound transduction

b. alternative hypothesis = middle ear bones evolved out of conflict between twin functions of hearing and feeding: this hypothesis holds that

i. starting at least with derived pelycosaurs, the quadrate and articular had dual functions:

a) articulate the jaw

b) help transmit sound vibrations from typanum to stapes

ii. selection was favoring changes in the jaw mechanics for more powerful biting, chewing (as above)

iii. this created "conflict" in functions for quadrate/articular:

a) to be good sound conductors, bones should be light, "loose" = free to vibrate

b) to support a strong jaw, bones should be robust and tightly articulated to surrounding bones

iv. initial solution was to "move" bulk of jaw musculature onto enlarged dentary, somewhat isolating quadrate and articular from the feeding apparatus

v. selection could then act "independently" on the two systems:

a) increasing the strength of the dentary and associated jaw muscles, which would eventually bring the dentary into contact with the squamosal on the upper jaw

b) decreasing the size of the quadrate/articular for improved sound transmission

vi. once dentary and squamosal came into contact, quadrate/articular were completely freed from involvement in feeding, and selection would favor the changes that we know led to modern middle ear structure/function

II. "True mammals"

A. Currently, we recognize *Morganucodon* as the earliest mammal – from the late Jurassic ~ 210 mybp – but why?

1. among extant vertebrates, mammals are distinguished by the presence of fur, mammary glands – but those don't fossilize
2. historically, we recognized fossil mammals as those having a dentary-squamosal jaw articulation – but the presence of "double-jointed" specimens makes that untenable
3. currently, the "hallmark" of "true" mammals is a combination of
   a. small body size -- first fossil mammals are much smaller than derived cynodonts
   b. skull characters suggesting an enlarged brain and expanded sensory organs
   c. complex teeth with precise occlusion – which also suggests lactation (read p 499):
      i. because mammals have only two sets of teeth (and one set of molars), precise occlusion can only occur when teeth are ~ "adult" size
      ii. if precise occlusion is important for feeding, then need some mechanism for nourishing young while jaw develops to ~ adult size, so "adult-size" teeth can erupt
      iii. according to this model, lactation is a pre-condition for the evolution of precise occlusion
      iv. so, if we can identify specimens with precise occlusion, we can infer that they had lactation
4. On your own, read Blackburn's hypothesis for the evolution of lactation and the

discussion of the selective benefits of lactation (p. 500)

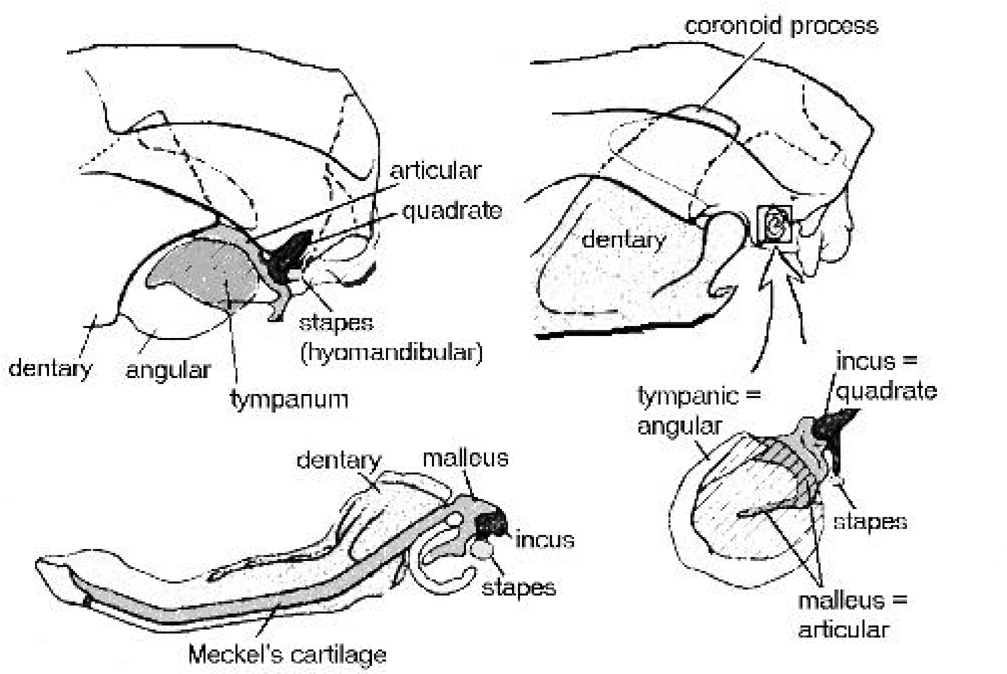
B. "True mammals" had three major periods of radiation:
   1. two Mesozoic radiations produced multiple lineages, but limited morphological/ecological variation:
      a. from the Jurassic to Early Cretaceous
         i. monotremes probably arose at this time
         ii. most members of this radiation went extinct by the end of the Mesozoic
      b. Early Cretaceous – at about the same time as the radiation of angiosperms
         i. marsupials and placentals had diverged from monotremes and from each other by this time
      c. most mammals at this time were relatively small insectivores and/or omnivores
   2. Major radiation began in the Cenozoic, after the final extinction of dinosaurs
      a. major diversification in form and function continued through the Miocene
      b. major extinction of large mammals at the end of the Pleistocene

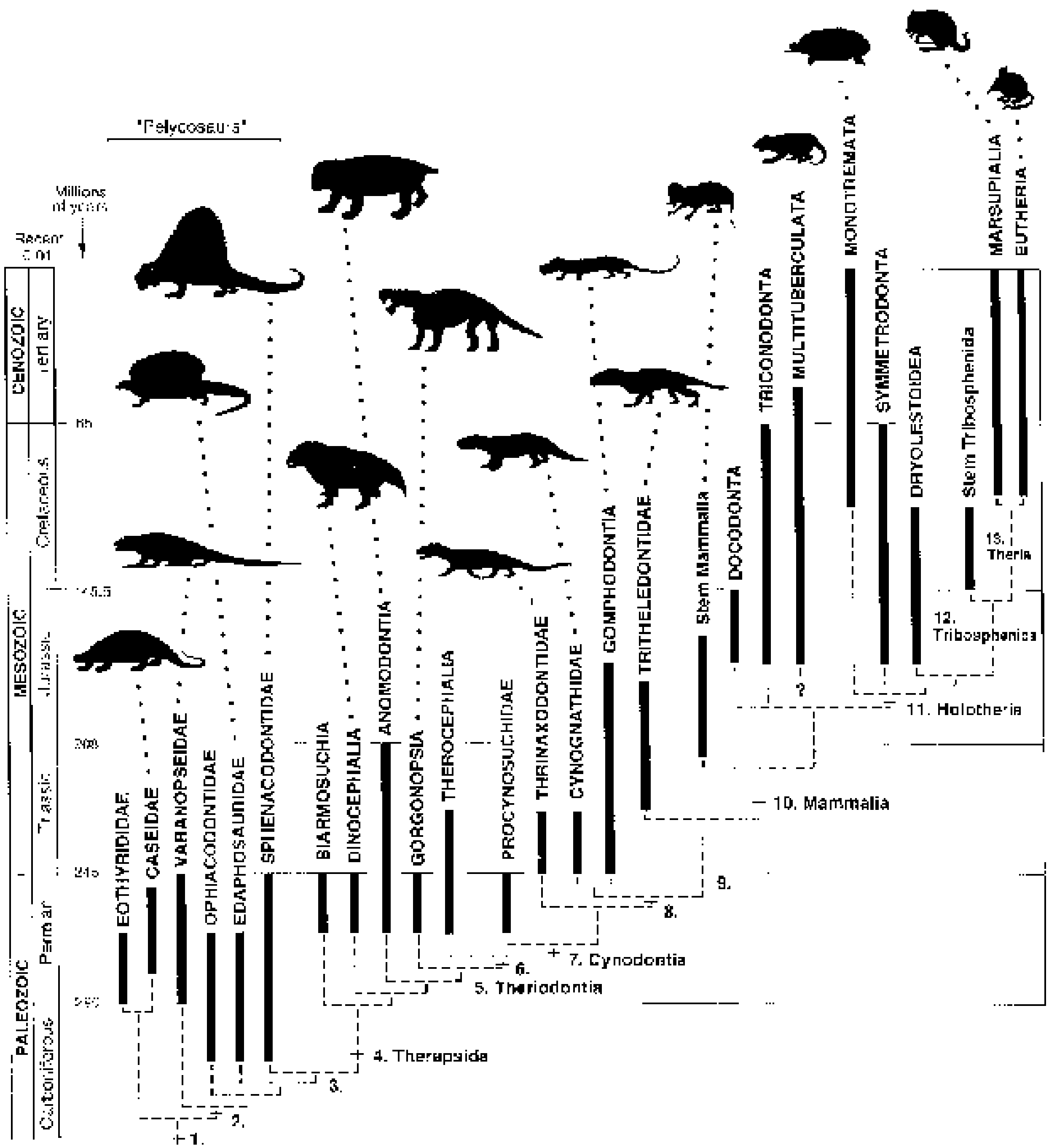
C. Systematics of modern mammals (see handout at end of notes)
   1. three major groups recognized based on reproductive mode:
      a. Monotremata = egg-laying mammals
         i. 3 species: duckbilled platypus + 2 species of spiny echidna
         ii. retain many "primitive" features of skull and limb girdles, as well as egg-laying
         iii. do have mammary glands – young lick milk from mother's fur after hatching
      b. Marsupialia = pouched mammals
         i. have placenta, but relatively non-invasive and short-lived
         ii. young are born at relatively early stage of development, but with adaptations that allow them to climb into mother's pouch, where they attach to a nipple to complete development

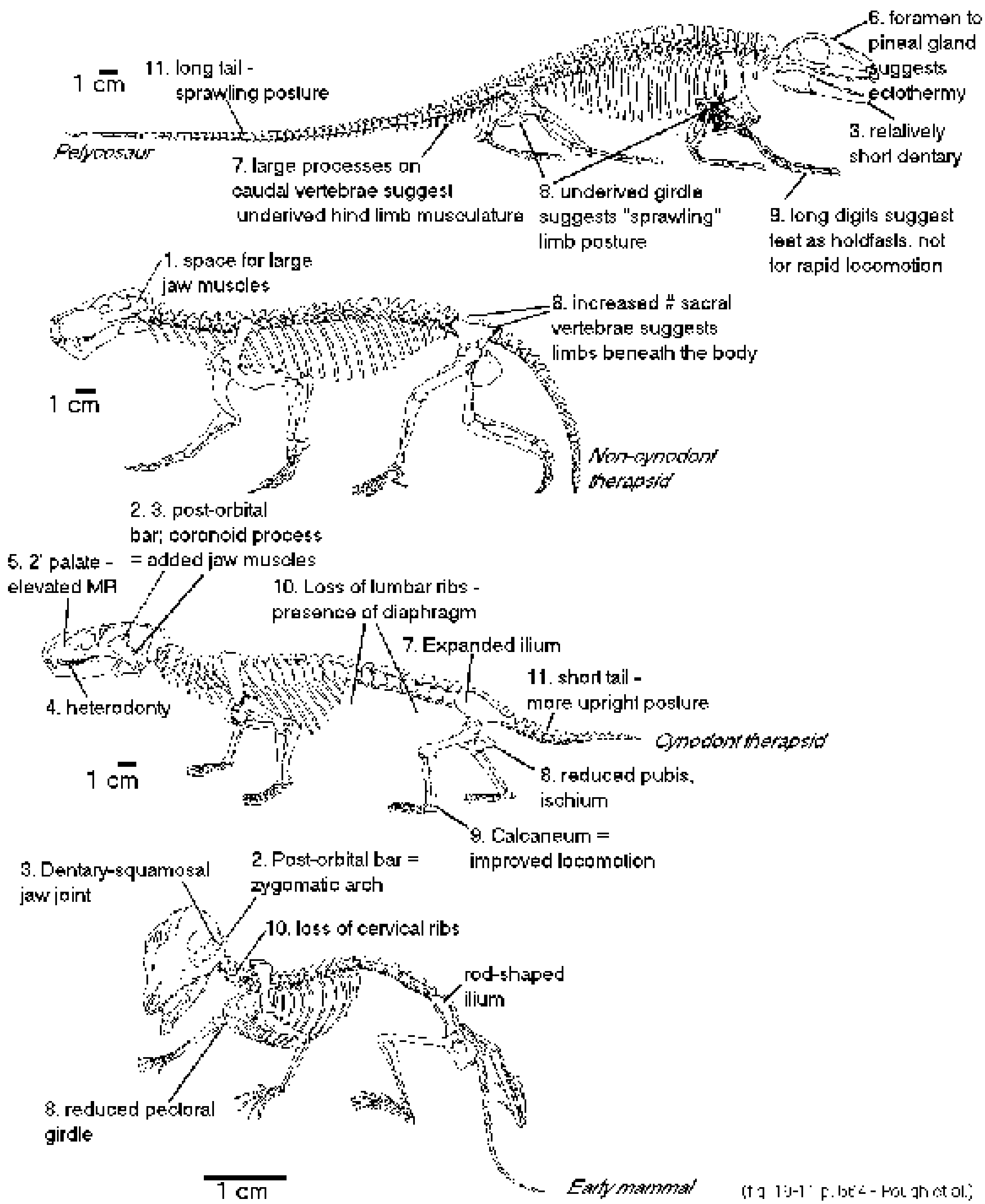
iii. evolutionary relationships between this mode and “true placental” mode still unclear

c. Eutheria = placental mammals
    i. this includes the bulk of mammalian diversity
    ii. elaborate, highly invasive placenta for developing young in utero
    iii. is this a “better” way to be a mammal?
        a) relative advantages and disadvantages are unclear
        b) where placentals invade habitats dominated by marsupials, tend to outcompete them – but why is not understood
            i) “great American faunal interchange” of Pliocene when NA, SA connected at the isthmus of Panama: many marsupial forms went extinct in SA, but few placentals went extinct in NA
            ii) invasion of modern placentals in Australia, New Zealand is wiping out native marsupials

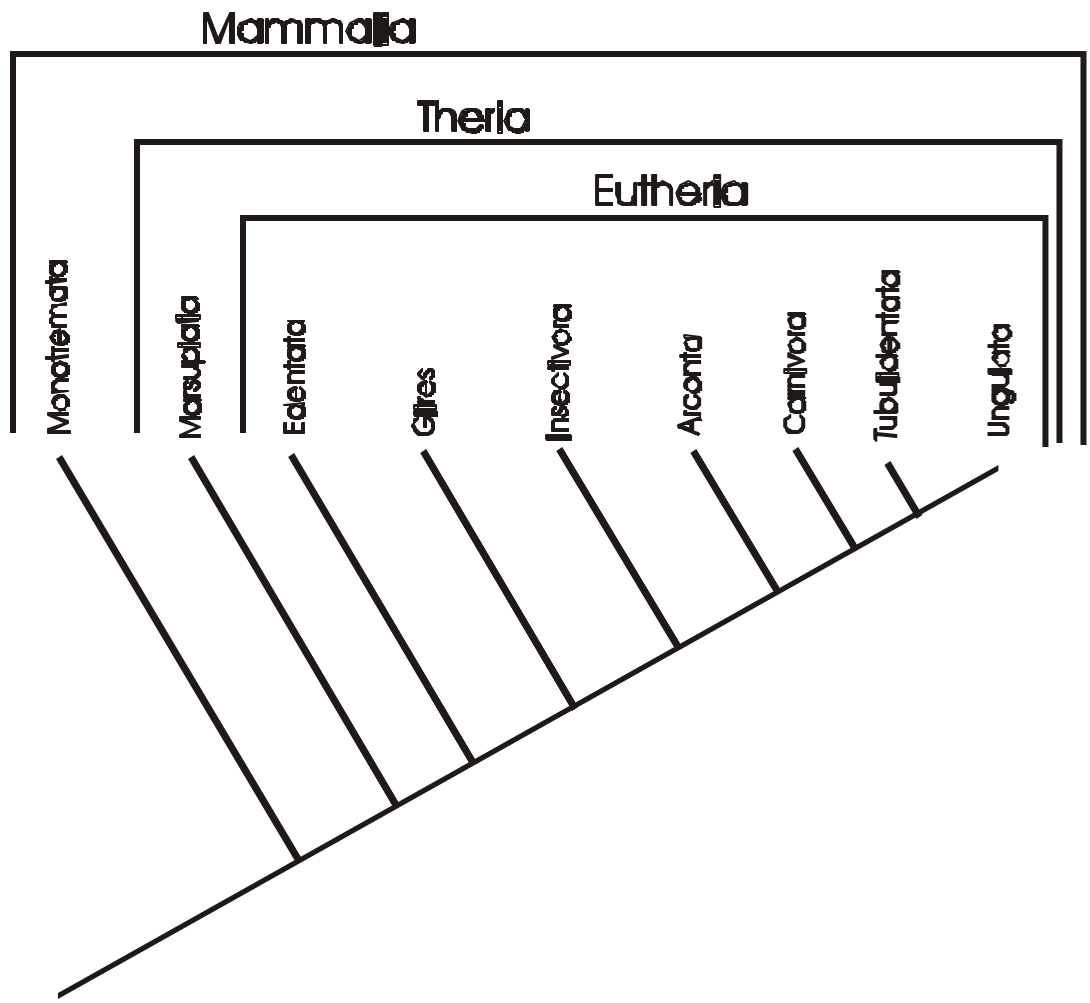
Evolution and development of middle ear ossicles (from Box 19-1)




"Pelycosaurs"
Millions of years
Recent 0.01
CENOZOIC
Tertiary
65
Cretaceous
145.5
MESOZOIC
Jurassic
200
Triassic
245
PALEOZOIC
Permian
290
Carboniferous
EOTHYRIDIDAE
CASEIDAE
VARANOPSEIDAE
OPHIACODONTIDAE
EDAPHOSAURIDAE
SPHENACODONTIDAE
BIARMOSUCHIA
DINOCEPHALIA
ANOMODONTIA
GORGONOPSIA
THEROCEPHALIA
PROCYNOSUCHIDAE
THRINAXODONTIDAE
CYNOGNATHIDAE
GOMPHODONTIA
TRITHELEDONTIDAE
Stem Mammalia
DOCODONTA
TRICONODONTA
MULTITUBERCULATA
MONOTREMATA
SYMMETRODONTA
DRYOLESTOIDEA
Stem Tribosphenida
MARSUPIALIA
EUTHERIA
1.
2.
3.
4. Therapsida
5. Theriodontia
6.
7. Cynodontia
8.
9.
10. Mammalia
11. Holotheria
12. Tribosphenida
13. Theria



(fig 19-11 p. 664 - Pough et al.)



Monotremata = platypus, spiny echidnas (3 spp; SA, Aust)
Marsupialia = pouched mammals (~ 280 spp.; SA, Aust)
Edentata = sloths, anteaters, armadillo, pangolin (~ 37 spp)
Glires = Rabbits/hares, rodents, elephant shrews (~ 1900 spp; 1800 spp of rodents)
Insectivora = shrews, hedgehogs, moles, tenrecs (~ 390 spp)
Archonta = tree shrews, bats, "gliding lemurs", primates (1240 spp; ~ 990 spp bats, ~ 235 spp. primates)
Carnivora = dogs, cats, bears, mustelids (otters, skunks, weasels, badgers), sea lions, seals, walruses (~ 274 spp)
Ungulata = hoofed mammals, elephants, hyraxes, dugongs and manatees, whales and dolphins (~ 324 spp.; ~ 213 are 'even-toed = swine, deer, antelopes, hippos, etc.)