Limb Development in Mammals

- Interspecies Limb Diversity
  - Bone size, shape, # of bones, type, etc.
  - Muscles, skins, feathers, etc.
- Reflection of animals habitat
- Important for movement, feeding, and social behavior.
Limb Function

- **Movement/Locomotion**
  - Walking, running, climbing, etc.

- **Feeding**
  - Ability to grasp food

- **Social behavior**
  - Mating rituals
Skeletal Diversity in Living Mammals

Mammalia*

- Monotremata
- Theria
  - Eutheria
  - Metatheria

*Refers to the earliest common ancestor to have an exclusively dentary squamosal jaw joint.
Mammalia

- **Mammalia**
  - **Therians** - Several tooth morphologies (Heterodonts)
    - Eutheria – Placental mammals
      - **Archonta** - primates, bats, and flying lemurs
      - **Ungalata** - Perissodactyls (horses, rhinos, and tapirs) and Artiodactyls (pigs, camels, and cattle).
  - **Metatheria** – Marsupials
    - **Diprotodontia** - kangaroos, wombats, possums, and koalas.
  - **Monotremata** - Egg laying mammals
    - **Platypoda** – Duckbilled platypus; echidna.
Mammalian Limb

- Fewer number of bony elements but more muscles compared to most other vertebrates.
  - Scapula - reduction of pectoral girdle to a single bone (except in monotremes).
  - Carpals reduced to 9 or fewer.
  - Tarsals reduced to 7 or fewer.
- Highly developed processes
  - Ulna - Olecranon process
  - Femur - Greater Trochanter
  - Calcaneum - Tubercle
Limb Development & Posture

- **Rotation of Limbs**
  - Upright posture - Femur & humerus vertical to ground.
  - Astragalus (Talus) positioned on top of calcaneum.

- **Reorganization of pectoral & pelvic girdle in Therians**
  - Associated with changes in posture and greater efficiency in locomotion compared to ancestors.
**Limb Postures**

- **Plantigrade** - Entire foot rests on the ground.
  - Bears, wombat, humans, etc.

- **Digitigrade** - Digits rest on ground while posterior part (ankle or wrist) is elevated above the ground.
  - Dogs, cats, etc.

- **Unguligrade** - Tips of digits rest on ground; associated with cursorial (running) locomotion.
  - Horses, antelopes, goats, etc.
Limb Postures

- **Plantigrade**—Feet allows greater forward propulsion than digitigrade and unguligrade mammals (Brown and Yalden, 1973)

- **Digitigrade**—Extra limb segment; longer distal limbs allowing longer strides which increases speed; forward thrust more dependent on proximal limb.

- **Unguligrade**—More limb segments and increased length of distal limbs (metacarpals) results in quicker/more efficient movement.
Pectoral Girdle

- In Therians, the pectoral girdle is composed of scapula, coracoid, and often clavicle (which connects scapula and sternum).
- In Monotremes, anterior clavicle and interclavicle is retained (unlike Therians)
- Provides support, propulsive power, and helps absorb impact of forelimbs during locomotion.
- Point of origin for muscles of the arm.
Scapula

- Spine-Divides supraspinous and infraspinous fossae.
- Glenoid fossa- Receives humeral head.
- Dorsal portion of scapula composed of cartilage in adult perissodactyls & artiodactyls.
Scapula

- Shape, size, and muscle attachments reflect the animal’s type of movement, posture, etc.
- Primary functional components:
  - Blade width from teres process to cranial border → determines movement arms of flexors & extensors in shoulders.
  - Orientation of scapular axis → determines extent of scapula’s contribution to limb flexion and extension.
  - Size and shape of acromion & coracoid processes → determines size and moment arms of shoulder muscles.
Scapula

- Cursorial (running) mammals usually equipped with longer, more narrow scapulae which is positioned more vertically compared to ambulatory (unspecialized) mammals.
  - Stride length increased.
- Fossorial (digging) and natatorial (swimming) mammals equipped with triangular scapulae and larger teres process.
  - Provides greater leverage from teres major muscle resulting in more powerful adduction of forelimb.
Clavicle

- Only bone to be retained in the therian pectoral girdle.
- Clavicle connects scapula to sternum.
  - Present in only some mammals.
  - Cleidocranial dysplasia-reduced/absent clavicle.
    - Mutation in cbfa I gene(s) in humans (Mundlos, 1999).
- Has different function in monotremes.
Clavicle

- Bone function depends on configuration of muscles that attach to it. Functions include:
  - Shoulder movement.
    - Climbing, flying, manipulating objects, etc. (Howell, 1937b).
  - Maintains distance between shoulder joint and sternum.
  - Lifting the shoulder by acting as a lever and manubrium (upper sternum) as the fulcrum (Williams and Warwick, 1980).
  - Evolutionary loss of the clavicle allows shoulders to move parallel to the thorax; this is seen in cursorial mammals.
Humerus

- Insertion point for muscles in brachium; forelimb and muscles of the manus originate here.
- Support anterior body weight (quadrupeds).
- Head articulates with glenoid fossa (scapula); condyle articulates with radius and ulna.
- Entepicondylar foramen found in ancestral mammals; reduction of foramen restricts ability to abduct humerus and supinate the forearm.
Humerus

- Range of movements of limb (and thus function) is dependant on size, shape, orientation of tubercles and heads, etc.
  - In antelopes (*Antilocarpa americana*): deltoid tuberosity positioned approx. ¼ distance down shaft; shortened moment arm for deltoid & teres major muscles allows rapid but weak flexion/extension of forearm.
  - In otters (*Lutra canadensis*): deltoid tuberosity positioned further down shaft allowing greater flexion/extension of forearm.
  - Variation in size of epicondylar region: broader epicondyles in otter provides longer moment arms for pronator/supinator muscles thus allowing more powerful pronating/supinating abilities for swimming and manipulating food.
Humerus

- Other features such as the animal’s body size is also associated with these features in the humerus.
  - Cursorial mammals that lack the ability to supinate their forearms, have a restricted body mass.
  - Ambulatory (unspecialized/generalized) mammals that retain supination can reach larger body sizes (Andersson and Werdelin, 2003).
Radius and Ulna

- Support anterior body weight (quadrupeds).
- Ulna: point of insertion for elbow extensors; stabilizes elbow joint.
- Radius and ulna fused in some mammals, particularly cursorial mammals.
- Proximal end (olecranon process & radial head) articulates with humerus.
- Distal end (styloid processes) articulates with scaphoid and lunate bones of carpus.
  - Styloid processes homologous to radiale & ulnare of ancestral tetrapods (Cihak, 1972).
Radius and Ulna

- **Limb function dependant on:**
  1) *Degree of fusion between radius and ulna.*
  2) *Shape of radial head and the ulnar surface it articulates.*
  3) *Proportional length of the olecranon process.*
  4) *Proportional position of the radial and ulnar tuberosities.*
Degree of fusion & Radial head shape

- Determines range of pronation-supination of manus.
  - Cursorial mammals - restricted pronation-supination.
  - Scansorial (climbing) mammals - manus completely supinates.
- Round radial heads roll easier (compared to flat heads) making supination possible (allowing distal end of radius to cross over ulna).
Radius and Ulna

- **Length of olecranon process**
  - Affects moment arm of effort for forelimb extension.
    - Longer olecranon in fossorial & natatorial mammals; shorter in cursorial mammals.

- **Position of tuberosities**
  - Affects moment arm of effort for forelimb flexion.
Manus

- Consist of carpus (wrist), metacarpus, and digits.
  - Carpals - Articulates with radius and ulna; number and shape of bones vary among mammals.
    - Three proximal carpels in ancestral therians: the scaphoid & lunate (articulates radius; may be fused) and triquetral (articulates the ulna).
    - Distal carpels (medial to lateral): trapezium, trapezoid, capitate, and hamate.
**Manus**

- **Metacarpals**
  - Number of bones varies among the different groups.
  - 1-5 bones which usually corresponds to number to digits present.
  - Equids (i.e. horses) have reduced number (only one metacarpal bone present) while other retain ancestral number of five metacarpals.

- **Digits**
  - Distal to metacarpals
    - One digit per metacarpal bone
  - Each digit composed of three phalanges (proximal, middle, and distal).
Manus

- Manus is highly variable (especially in eutherians) among the different mammalian groups.
  - Cursorial mammals usually have digits reduced.
  - Bats have elongated digits which support wing membranes.
- Most metatherians (marsupials) retain all five digits.
  - Less diversity in limb development.
  - May be due to fact that they have to climb to the nipple after birth, so well developed forelimb required.
Pelvic Girdle

- Composed of ilium, ischium, pubis, Supports and protects internal organs in posterior body cavity.
- Acetabulum—Receives femoral head.
Pelvis

- Shape of pelvis associated with animal’s locomotory habits and body mass.
  - Orientation of iliac crest associated with posture (i.e. bipedal or quadrupedal).
    - Orthograde/Bipedal mammals- Iliac crest is “upright” – reflection of dorsally directed position as crawling quadruped.
    - Pronograde/Quadrupedal mammals- Iliac crest is horizontal and parallels their horizontal vertebral column (Schultz, 1936).
Pelvis

- Pelvic orientation in quadrupeds
  - Upright- often seen in larger, more heavy mammals.
    - Vertical orientation allows greater support without dislocating sacroiliac joint.
    - Horizontal vertebrae also supports greater weight without placing more torsion on vertebral column.
Pelvis

- Shape of acetabulum associated with animal’s locomotory style (Jenkins and Camazine 1977).
  - Unspecialized (ambulatory) mammals have a shallow and open acetabulum which allows a broad range of movements.
  - Cursorial (running) mammals have a deeper and more narrow acetabulum.
    - Length and angles of muscle insertion sites (such as the ischiatic tuberosity) also associated with animal’s locomotory style
      - Determine the moment arms for hip extension which is associated with the degree of forward momentum.
Femur

- Position of trochanters determine lever advantage for flexor and extensor muscles of the hip.
- Patellar groove located between medial and lateral condyles.
  - Length and depth of groove associated with locomotory type.
Femur

Primary functional components of femur

- Length and orientation of the greater trochanter.
  - Functions as primary lever for hip extension; mammals adapted for running have a long and robust greater trochanter.

- Size of the third trochanter
  - Also function as lever for hip extension; well developed in cursorial mammals.

- Shape of femoral head and position of fovea (pit/depression).
  - Broader head provides greater abduction during locomotion.

- Depth of patellar groove.
  - Longer and deeper in cursorial and saltatory (leaping) mammals.
Crus

- Composed of fibula, tibia, and some sesamoid bones.
- Tibia usually larger and supports majority of body weight.
  - Point of fibular articulation varies greatly among different groups.
    - Eutherians-articulation distal to margin of lateral condyle.
    - Metatherians & Montremes-articulation usually on margin of lateral condyle and head extending to distal femur (Szalay, 1994).
Crus

- Most notable difference seen in distal articular surface of tibia.
  - Deeply grooved in cursorial mammals
  - Spiraled which allows greater limb abduction and hindfoot reversal (ambulatory and scansorial mammals respectively).
  - Flattened in scansorial and some ambulatory mammals.

- Degree of fusion between tibia and fibula associated with animal’s body mass.
  - Fused at distal ends in smaller (sometimes saltatory & cursorial) mammals.
  - Lesser degree of fusion in fibula allows greater abduction/adduction of the ankle.
    - Important for scansorial (climbing) mammals.
Pes

- Consists of tarsals, metatarsals, and digits
- Ancestral therians had 7 tarsal bones following loss or fusion of bony elements.
- Tarsal bones
  - Calcaneum and Astragalus (talus).
    - Talus: articulates with the crus.
  - 3 Cuneiforms
    - Lateral, intermediate, and medial
  - Navicular and Cuboid.
    - Along with the 3 cuneiforms, these bones articulate with the metatarsals.
Pes

- **Major joints and axis of rotation**
  - Unlike manus where pronation/supination occurs by movement in the forelimb, inversion and eversion of the pes are done at the tarsal joints.
  - Upper ankle joint (between talus and tibia)—primary joint for dorsiflexion and plantarflexion.
    - In metatherians, the joint is smooth allowing some abduction/adduction of the foot as well as dorsiflexion/plantarflexion.
    - In eutherians, the joint may have two ridges on edges of the astragalar trochlea which restricts plantarflexion thus stabilizing the ankle.
      - Seen in cursorial and saltatorial mammals.
Ecomorphologic Diversity

- **Categorization of Mammalian Limbs**
  - Locomotory types based on gaits, musculoskeletal features, limb ratios, and/or the combination of these features.
  - Ecomorphological types
Ambulatory Mammals

- Specialization for generalized mammals (raccoons, humans, etc.)
  - Mobile joints
  - Ability to protinate/supinate manus
  - Five digits
  - Plantigrade to semi-digitigrade posture
  - Triangular scapula- provides more powerful moment arm for greater flexion of forearm.
  - Unfused radius and ulna- allow supination of manus.
  - Open acetabulum- allows broad range of hip movements.
  - Unrestricted tarsal joints- allows variety of foot movement.
Cursorial Mammals

- Specialization for running mammals (horses, etc.)
  - Long limbs; distal limb segments generally longer.
  - Digitigrade or Ungiligrade posture.
  - Restricted limb joints providing parasagittal motion.
    - Contributes to joint stabilization
  - Carpals and Tarsals oriented closely
  - Cylindrical acetabulum helps maximize parasagittal motion.
Saltatory Mammals

- Specialization for jumping mammals (kangaroos, jerboas, etc.)
  - Exaggerations of cursorial features (i.e. long distal limbs, high gear ratios, reduced digits, etc.)
- Forelimbs similar to ambulatory mammals
- Tail acts as counterbalance for bipedal movement.
- Tridactyl foot provides weight support and stabilization for propulsion.
Scansorial Mammals

- Specialization for climbing and arboreal mammals (lemurs, monkeys, etc.)
  - Mobile limbs
  - Ability to grasp with hands (sometimes feet).
  - Plantigrade posture
  - Elongated manus and pes (of monkeys); curved claws (of sloth).
  - Capable of pronation/supination.
  - Clavicle which stabilizes the shoulder.
  - Triangular scapula.
Fossorial Mammals

- Specialization for digging mammals (moles, badgers, etc.)
  - Emphasis on strength of forelimbs rather than speed.
    - Long teres (scapula) and olecranon (ulna) processes provides longer moment arms.
    - Shortened and inflexible manus elements
    - In moles, the humerus has large tubercles for flexion, extension, abduction, and adduction muscles.
Natatorial Mammals

- Specialization for swimming and aquatic mammals (seals, beavers, etc.)
  - Similar specializations as fossorial mammals in regards to the forelimb, but specialization is also seen in hindlimb.
    - Elongated manus (unlike fossorial mammals) particularly in the digits.
    - Shortened femur and long crus
    - Paddle-like pes (flippers) or toes may be webbed
Graviportal Mammals

- Specialization for mammals with extremely large body masses (elephants, bison, etc.)
  - Limb bones have large diameters to support higher body mass (Schmidt-Nielsen, 1984).
  - Vertical orientation of the ilium.
Variation in limb morphology due to genetic factors.

Studies in mice indicated that different limb elements had a different degree of heritability.

- Higher inheritance in length of limb elements in offspring compared to skull and body traits (Leamy, 1974).
- Forelimb elements displayed higher heritability than hindlimb elements.

Despite the high heritability of limb traits, molar and skull traits seem to evolve more quickly on a microevolutionary time scale.
Quantitative Variability

- Genetic factors in limb development.
  - The different limb morphologies are the results of many genes (Lande, 1978).
    - Hox genes - involved in patterning the segments of limbs.

- Other factors contributing to limb variation.
  - Muscular and vascular systems
  - Nervous system
  - Interactions between the limb elements themselves.
  - Behavior
Polymorphic Variability

- Polymorphic variability of limb elements may occur within the same population.
  - Most common polymorphisms involve missing bones.
    - May be caused by arterial malformations rather than the skeletal system itself during the embryonic stage (Packard et al., 1993).
      - Development of arterial and skeletal systems are closely related (Karsenty, 2003).
  - “Luxate”- Polydactylus condition where tibia is reduced or absent.
    - Result of a genetic mutation in the Fgf-8 gene (Yada et al., 2002).
Diversification of Mammalian Limb

- Ancestral therian mammals
  - Suggestions that they were arboreal mammals (Matthew, 1904).
    - Ancestral eutherians may have had opposable digits on manus and pes.
    - Metatherians may have had arboreal ancestors (Huxley 1880; Dollo 1899).
  - Opposing views suggest that the earliest known eutherians were terrestrial (Haines, 1958).
    - In addition, additional studies suggest that the scansorial adaptations seen in these eutherians were not homologous to those seen in metatherians (Szalay, 1994).
Chapter 16
Skeletal Adaptations for Flight

Stephen M. Gatesy and Kevin M. Middleton
Ancestral Amniote

- Musculoskeletal elements of forelimb provide support and help deform wings during flight.
- Adaptations for flight in bats and birds arose independently from Amniota who had a less specialized forelimb.
Ancestral Amniote

- **Amniote shoulder girdle:**
  - Paired scapulae, coracoids, clavicles, and cleithra.
  - Unpaired median interclavicle (Sumida, 1997).

- **Distal elements**
  - Tetrahedral humerus (Romer, 1956).
  - Limited pronation/supination (Sumida, 1997).
  - Manus was pentadactyl (with digit IV being the longest) and specimen was from an obligate quadruped (Sumida, 1997).
Pterosaurs

- First amniotes to have flight adaptations.
- Fossil record dates them back to the Late Triassic (~210 million years ago).
- Bones (such as the humerus and phalanges) are highly distinctive.
  - Digit IV of metacarpal bones
  - Pteroid bone
- Some believe that the pterosaurs to capable of flapping flight despite the fact that some pterodactlyloids may have used the winds for soaring (Bramwell and Whitfield, 1974).
Pterosaurs

- **Pectoral girdle**
  - Dermal elements are absent
  - Fused sternal plates
    - Allows attachment of enlarged muscles adapted for flight.
  - Paired scapulae and coracoids (Romer, 1956).
Pterosaurs

- **Distal elements**
  - Saddle shaped humerus
  - Four carpal bones (except in primitive pterosaurs).
    - Pteroid bone – supports anterior wing membrane.
  - Offset condyles on metacarpal IV
    - Allows wing finger (IV) to supinate during upstroke (Padian, 1983) and tuck along body when not in flight (Bramwell and Whitfield 1974).
  - Elongated phalanges in digit IV
    - Supports posterior wing membrane.
Birds

- Theropod ancestry (Cracraft 1986; Gauthier 1986).
- Fossil record dates them back to the Late Jurassic (~145 million years ago).
- Over 9000 extant species of birds globally.
  - Flying and flightless species.
Birds

- **Expanded edge (keel) of sternum**
  - Supports enlarge flight musculature (supracoracoideus and pectoralis muscles).
  - Keel is absent in some flightless species.

- **Paired scapulae and coracoids**
  - Articulates with fused clavicles which make up the furcula (wishbone).

- **Less prominent deltopectoral crest on humerus.**

- **Radius and Ulna**
  - Articulate with carpals: radiale and ulnare.
    - Carpals articulate with the carpometacarpus: Alular major and minor; a fusion of 3 distal carpals and 3 metacarpals.
Bats

- Over 900 extant species
  - Divided into 2 groups
    - Megachiropterans (megabats) – Single family of old world fruit bats.
    - Microchiroptera (microbats) – Includes all other families of bats.
- Fossil record dates them back to the early Eocene (~53 million years ago).
Bats

- **Sternum is T-shaped**
- **Extremely large clavicles**
  - Articulates with acromion and/or coracoid process; believed to guide scapular rotation during flight.
- **Rectangular or oval scapula**
  - Large coracoid process
- **Straight/slightly sigmoid shaped humerus**
  - Olecranon fossa is rudimentary and sometimes absent.
  - Marrow-filled longbones (non-pneumatic) unlike pterosaurs.
Bats

- **Radius and ulna**
  - Radius is dominant forearm element.
  - Olecranon process of ulna is fused to the radius.
  - Distal radius interlock with carpels allowing only flexion and extension of the wrist.

- **Hands have long metacarpals and phalanges.**

- **Hand composed of 5 digits**
  - Digit I – shortened and clawed; usually for clinging.
  - Digits II-V – support wing membrane.
Wing Disparity

- **Configuration of wing skeleton**
  - During flight, skeletal elements must provide structural support against muscular, gravitational, and inertial forces.
  - Wing skeleton must also provide stability when not in flight.
    - Bats and pterosaurs were quadrupeds.
  - Wings also used in other non-flight behaviors such as feeding, brooding, defense, etc.
Wing Disparity

- Configuration of wing skeleton

- Studies of wing design primarily focus on parameters such as aspect ratio and wing loading (e.g. Pennycuick 1975; Norberg and Rayner, 1987).

- Associated with flight performance and ecology but doesn’t provide answers to many basic morphological questions; questions such as how particular skeletal elements should be organized to maximize wing function.
Wing Disparity

- How are wing skeletons proportioned?
  - A proportion morphospace can be used to study the differences in forelimb elements (Gatesy and Middleton 1997).
Forelimb Disparity

- Forelimbs with similar proportions in length restricted to one area of diagram.
- Disparate (different) spread out to larger point cloud.
Wing Disparity

- How are functional wing segments proportioned?
  - Based on where wing skeleton bends and the bones involved.
    - Bats bend wing at elbows and wrist; segments are the humerus, radius, and metacarpals + phalanges (digit 3). Plotted more medially.
    - Pterosaurs bend wing at metacarpophalangeal joint; Plotted more distally.
    - In birds, humeral, radial, and wing chord data used; Plotted more proximally.
Wing Disparity

- Specialization
  - Factors that may contribute to differences in distribution in the morphospace diagram.
    - Body size
    - Flight surface (feathers or membranous surface)
    - Forelimb’s role in terrestrial locomotion (especially in bats and pterosaurs)
Convergent Similarities

- **Skeletal adaptations for flight**
  - Enlargement (hypertrophy) of pectoral appendage and girdle.
  - Change in forelimb proportions.
    - Elongated handwing segments.
    - Digits II-V in bats; Digit IV in pterosaurs; Birds show least proportion but feathers account for most of the handwing.

- **Fusion or loss of bones**
  - Pterosaurs: digit loss (except in primitive pterosaurs) and carpal fusion.
  - Birds: fusion of 3 distal carpals and 3 metacarpals to make up Alular major and minor bones.
  - Bats: fusion of radius and ulna so that radius is dominant forearm element.