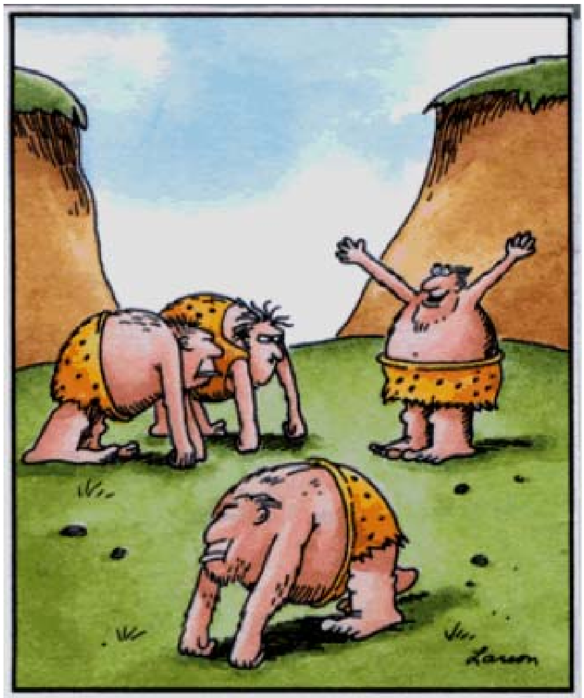
Name ____________________________ Lab section _________________________

Lab 5: Investigating bipedalism

This laboratory will examine anatomical features related to bipedalism in fossil and living hominins.



"Hey! Look! ... No hands!"

Introduction

We are members of the species known as *Homo sapiens*. The most important adaptation of our lineage is that we walk upright on our hind legs at all times, which is an extremely unusual way of getting around for a mammal. We are the only habitual and obligate bipeds among living primates.

Origins of bipedalism

Habitually walking around on the hind limbs is an unusual mode of locomotion. Once our ancestors had adopted an upright stance, many things associated with being human became possible, such as fine manipulation with the hands, and the carrying of food back to a base camp. It is important to remember, however, that we cannot argue that more than 4 million years or so ago early hominins evolved upright walking in order to use their hands in refined ways or to develop a food-sharing economy, because evolution does not work in a goal-oriented manner (as part of an inevitable trend towards modern humans). Behaviors such as tool use and food sharing did not arise until several million years **after** bipedalism. Although many hypotheses have been proposed, no single adaptive explanation exists for the origin of this unusual mode of locomotion.

Australopithecus afarensis

Australopithecus afarensis is a fossil hominin species that lived 3.9 to 3.0 million years ago (Ma). *A. afarensis* is significant in part because this is the first hominin for which we have abundant and unequivocal evidence for bipedalism, although the evidence from older fossils suggests that bipedalism may have evolved by 6 Ma. Today you will look at some fossils of *A. afarensis* and other *Australopithecus* and pre-australopith species in order to examine some of the morphological features that led researchers to assign these species to the hominin lineage; in other words, you will look for evidence of bipedal locomotion in their skeletons.

Anatomical adaptations to bipedality

The vertebral column

In previous labs we have noted that the position of the foramen magnum (the large hole through which the spinal cord enters the cranium) is centered underneath the skull in humans. This condition contrasts sharply with that of the quadrupedal great apes, in which the foramen magnum is located more posteriorly, near the rear of the skull (Fig. 1). A centralized foramen magnum positions the skull over the long axis of the body and helps maintain the center of gravity in bipeds.

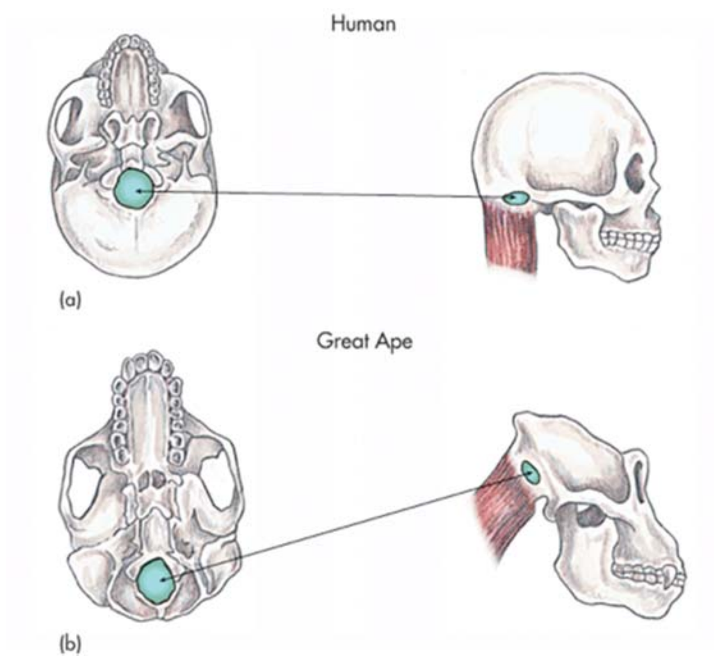


Fig. 1. Position of foramen magnum in (a) human and (b) great ape.

The shape of the vertebral column is also restructured in bipeds relative to quadrupeds. Quadrupeds have a C-shaped spine with one main convex curvature in the thoracic region. Bipeds have two secondary concave curvatures in the cervical and lumbar regions in addition to this main thoracic curve, which gives the spine an S-shape (Fig. 2). This unique shape helps stabilize the bipedal body – if bipeds had retained a C-shaped spine, the center of gravity would actually fall in front of the feet. The additional curvatures function to bring the center of gravity directly over the feet.

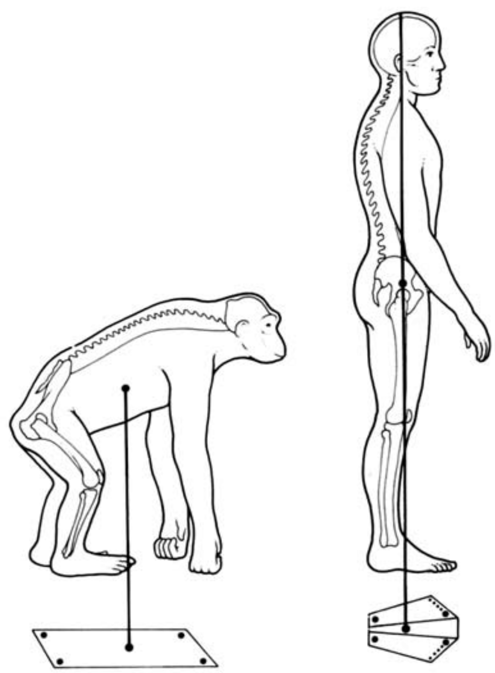


Fig. 2. Spinal curvature and center of gravity in chimpanzee and human.

The pelvis

Some of the most striking differences between quadrupeds and bipeds can be observed in the pelvis. In quadrupeds the ilium is long, narrow, and flat, and the acetabulum (femoral socket) is small and shallow. In bipeds the pelvis has a broad, bowl-like shape with a wide and short ilium, which brings the sacrum closer to the large, deep acetabulum. These anatomical changes increase the support of the entire upper body in an upright position and transmit the weight of the trunk directly to the legs.

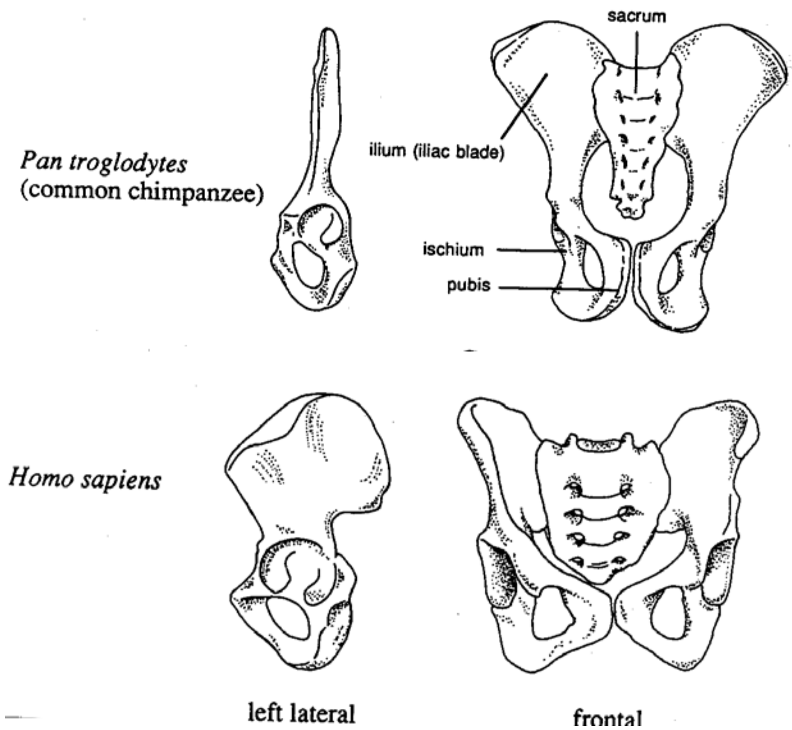


Fig. 3. The pelvis in chimpanzees and modern humans.

The knee

Differences also exist between the knee joints of bipeds and quadrupeds. In quadrupeds the femur and tibia form a straight line, which is an ideal arrangement for a form that bears its weight on all four limbs. When walking bipedally, however, this arrangement means that with each step the body's center of gravity must be swung inefficiently in a circle around the supporting leg. In contrast, the knee joints of bipeds have a carrying or **valgus** angle, so that the femora come together at the knees (Fig. 4). This angle brings the knees and lower limbs directly over the center of gravity (Fig. 2). This angle is achieved in part by having a larger inner part (medial condyle) of the distal femur than the side part (lateral condyle).

There are differences in the morphology of the tibia that parallel the differences in the femora. In bipeds, the proximal surface of the tibia is flat, and the medial side is larger than the lateral side. In quadrupeds, the proximal surface is more sloping, both sizes are more equal in size. In addition, the tibial shaft of bipeds is more robust and straight, whereas in quadrupeds it is more gracile and curved.

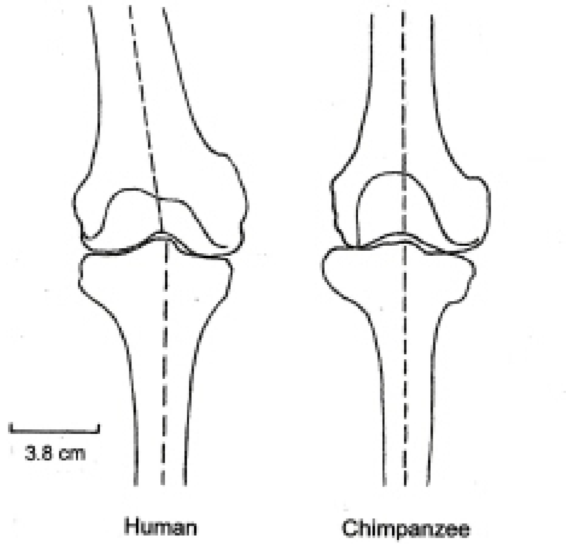


Fig. 4. Valgus angle in human compared to chimpanzee.

The foot

Bipedal locomotion places entirely new demands upon the foot. When comparing the foot anatomy of quadrupedal apes and bipedal hominins, there are many differences because of different ways in which weight is transmitted along the feet. In quadrupeds the foot is placed flat on the substrate, the weight rolls forward along the center of the foot, and the push-off is from the center of the foot because the big toe (hallux) is **abducted** (divergent, away from the midline of the foot). In a bipedal stride there is a heel strike and body weight is transmitted along the outside of the foot, then internally across the ball of the foot, and finally push-off is made by the **adducted** big toe (non-divergent, in line with the midline of the foot) in a motion known as “toe-off” (Fig. 5). Although all quadrupeds have transverse arches in their feet, bipeds have an additional longitudinal arch. These arches act as shock-absorbers.

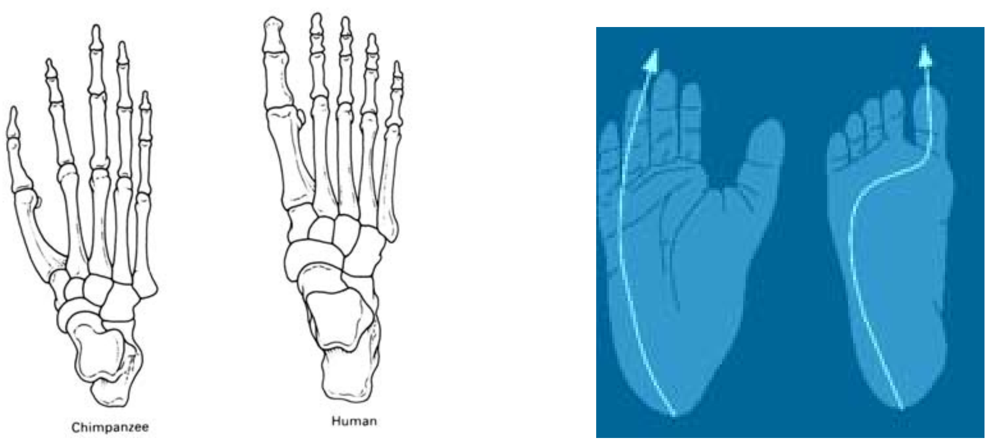


Fig. 5. Chimpanzee and human foot. Left: Articulated bones of the foot. Right: Path of weight transmission in the foot during locomotion.

Station 1. The vertebral column

For this station you will examine the vertebrae of a chimpanzee and a human using the articulated skeletons. Note again the different positions of the foramen magnum in the two articulated skeletons, and in the fossil casts of *Sahelanthropus tchadensis, Ardipithecus ramidus and Australopithecus afarensis*.

1. Looking at the articulated skeletons, what are the differences in spinal curvature between the chimpanzee and human skeletons? How does the shape of the human spine relate to bipedal locomotion?

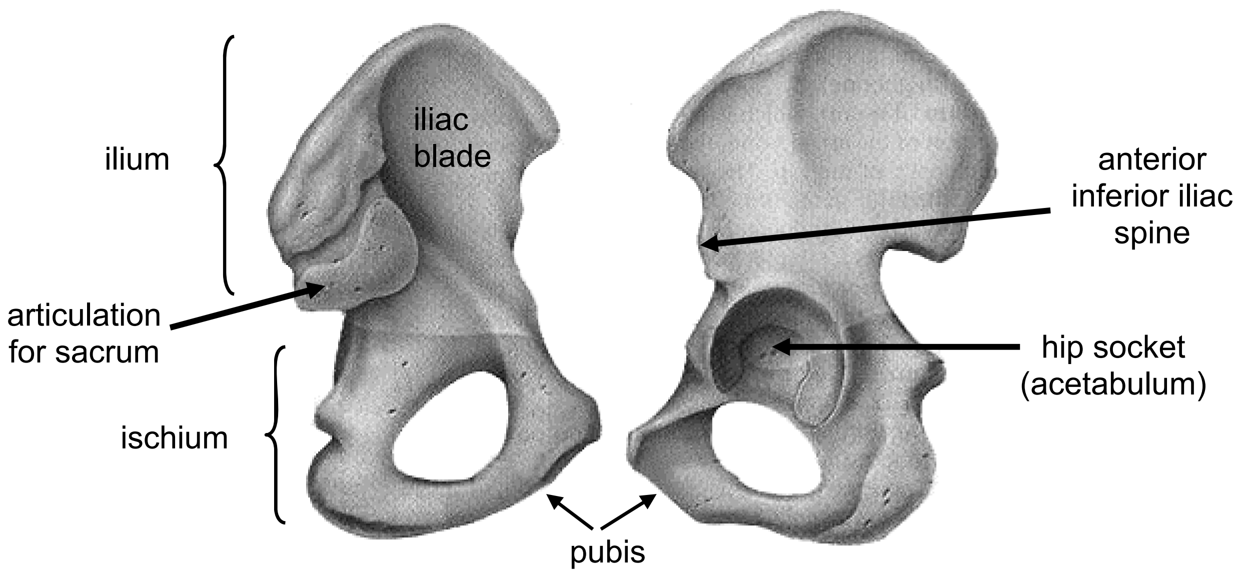
2. Take another look at the articulated skeletons. Note that even though the thorax (rib cage) is roughly the same size in the human and chimpanzee skeletons, the human vertebrae are larger than the chimpanzee vertebrae. For example, human lumbar (lower back) vertebrae are much bigger than chimpanzee lumbar vertebrae. Why do you think this is the case?

3. Is the foramen magnum in fossil hominin specimens more centrally or more posteriorly placed? Why is this feature a good indicator of the type of locomotion used by fossil taxa? *Hint: Hold the skulls up with the face positioned as in life, then note the position of the foramen magnum and think about the angle at which the spinal cord would have exited (e.g., straight down or angled backwards).*

4. Although not directly related to bipedalism, the loss of a functional canine/premolar (C/P_3) honing complex is also one of the features present in hominins. Compare the canines and premolars in the chimpanzee, human and casts of *S. tchadensis, Ar. ramidus, Au. anamensis and Au. afarensis*. Is there a diastema (gap) between the upper incisors and canines in fossil hominins? What is the morphology of the lower premolar in those taxa? Based on this evidence, did they possess a functioning C/P_3 honing complex?

Station 2. The pelvis

The pelvis in bipeds is structured differently from that of knuckle-walkers. Compare the pelves of a great ape, human and australopith, using the following images as a guide for relevant features. Be sure to note the differences between quadrupedal and bipedal pelves, as well as the differences between an *Au. afarensis and Au. africanus* and a modern human pelvis. Answer the following questions based on your observations.



Consider the following features in the three specimens:
- iliac blade: straight or curved? Tall or short?
- acetabulum: big or small?
- anterior inferior iliac spine: present or absent?
- sacrum (if available): wide or narrow? Long or short?
- distance from the acetabulum to the sacrum (if available): close or far?

5. What are the differences between the bipedal human and quadrupedal ape pelvis?

6. What features identify *Australopithecus* as habitual bipeds?

7. What differences can you identify between the pelves of *Au. afarensis* and *Au. africanus* and that of the modern human?

Station 3. The knee: femur and tibia

The structure of the knee joint is different in bipeds and quadrupeds. Examine the modern human, great ape, and casts of *Au. anamensis* and *Au. afarensis*. Place each femur on a flat surface with the articular (knee joint) surface down. Note the marked angle the shaft makes with the articular surface. This angle is called a "valgus" or a bicondylar angle. Compare this feature in the specimens.

8. Describe the differences in the angle of the femur in the chimpanzee and the human. What is the importance of the valgus angle?

9. Look at the distal femur of the chimpanzee and human from below and from the side. Are the condyles (the two protuberances that articulate with the tibia) relatively long and elliptical, or short and rounded? Which species would benefit from having a larger surface area for the articulation of the bones of the knee?

10. Examine the degree of curvature in the shafts of the chimpanzee and human tibiae.This is easiest to do by holding the bone with the articulation for the femur pointing straight up and then looking at the bone from the side. Is the bone curved (bowed) or straight for these specimens? Also remember that the proximal tibia is the complement for the distal femur – are there differences in relative surface area and/or angle between chimpanzee and human tibiae?

11. Examine the tibia of *Au. anamensis*, Lucy's femoral fragments and the knee joint of a second *Au. afarensis* individual. What traits indicative of bipedalism do you observe in those specimens?

Station 4. Feet

At this station, you will compare the foot bones of an ape and human. You can also look at the articulated feet of chimpanzee and human skeletons at Station 1.

12. What features can you observe in the foot bones of apes and humans that provide clues about locomotor behavior? Why are these features informative?

Station 5. Intermembral index

Differences in locomotor behavior can be best demonstrated by the **intermembral (IM) index**, a measurement that compares forelimb and hindlimb length. In general, species that emphasize the hindlimb in their locomotion (e.g., leapers, bipeds) have a low intermembral index (longer hindlimbs relative to forelimbs), species that emphasize the forelimb in their locomotion (e.g., suspensory, brachiators) have a high intermembral index (longer forelimbs relative to hind limbs), whereas quadrupedal species tend to have intermediate indices (forelimbs and hindlimbs similar in size).

It is calculated as shown:

$$\textbf{Intermembral index (IMI)} = \frac{\textbf{(humerus + radius)}}{\textbf{(femur + tibia)}} \times 100$$

Data collection: Using the osteometric board, record the maximum length (in centimeters) for each bone and then calculate IMI.

	Human	**Chimpanzee**
Humerus		
Radius		
Femur		
Tibia		
IMI		

13. How do the chimpanzee and human intermembral indices reflect their locomotor repertoires?