Overview: Bipedalism is a defining characteristic of modern humans that evolved over millions of years. Therefore, identifying evidence for bipedalism in the fossil record can help determine what selective pressures may have affected human evolution. This lesson examines the significance of bipedalism, anatomical adaptations exhibited by hominins, and discusses possible climatic influences on bipedal evolution. Students should have a basic understanding of osteology (i.e. skeletal anatomy).

Objectives:
- To understand the significance of identifying bipedal evidence within the fossil record.
- To learn the morphological adaptations associated with bipedalism.
- To become familiar with the environmental and behavioral pressures that may have affected bipedal locomotion.

Outline: A. Introduction to Bipedalism
B. Anatomical Evidence for Bipedalism
C. Fossil and Geologic Evidence
D. Conclusions
E. Activity: Bipedalism Features Chart
F. Activity: Brain vs. Bipedalism
G. Review Questions
H. References
I. Answer Key

Strategy:
- You will identify the fossil evidence for the evolution of bipedalism
- You will hypothesize about the evolutionary pressures affecting bipedal behavior
- You will familiarize yourself with the adaptations necessary for habitual, or obligate bipedalism.

Required Materials: Pen, pencil, digital calipers (or ruler), life-size cast of human cranium (if available), copies of attached sections A-H of this lesson.
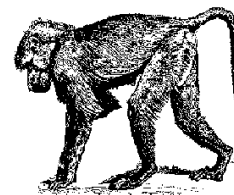
Expected classroom hours: 2 hrs (Assigning reading as homework will decrease classroom hours).

Suggested Supplemental Lessons or Resources:
- On the Track of Prehistoric Humans
- Human Evolution: Genera *Australopithecus* and *Parathropus*
- *Who is Lucy?* eFossils Lesson
- eSkeletons.org
- eFossils.org or eLucy.org Glossary

What is Bipedalism?

Bipedalism refers to locomoting (e.g., walking, jogging, running, etc.) on 2 legs. It is not uncommon to see animals standing or walking on 2 legs, but only a few animals practice bipedalism as their usual means of locomotion. Animals, including chimpanzees and gorillas, that assume bipedalism on a temporary basis in order to perform a particular function practice a form of locomotion called **facultative bipedalism**. For example, octopodes sometime walk bipedally in order to camouflage themselves from predators[1]. The octopus piles 6 of its 8 limbs on top of its head, assuming the shape of a drifting plant, and then uses the 2 remaining limbs to quite literally walk away. As for quadrupeds

Sketch of a baboon practicing quadrupedalism.

(animals that move on four limbs), it is not uncommon to see antelope standing on their 2 hind limbs while supporting themselves on their forelimbs when reaching for food in high branches. Chimpanzees have been documented walking on 2 legs in order to carry things with their hands.

**Habitual bipedalism**, or obligate bipedalism, is rare. This is the form of bipedalism that is assumed as a regular (i.e., habitual) means of locomotion. Today, very few mammals (e.g., humans and kangaroos) demonstrate habitual bipedalism. However, many early hominins (i.e., a classification term that includes modern humans and all their bipedal fossil relatives) show a combination of primitive and novel adaptations that suggest these species utilized bipedalism but still engaged in arboreal behaviors.

Gerenuck in bipedal feeding pose. Image by Steve Garvie (via Flickr).

Bipedalism Geological Age and Climate

Around 7 or 8 million years ago (Ma), the earth's climate underwent a dramatic cooling event which lowered land and ocean temperatures. Growth in the Antarctic ice cap during this time resulted in a dramatic drop in sea levels, including the Mediterranean Sea[2]. As a result of these sea level changes in the Mediterranean, water sources availability within nearby continents like Africa were severely limited. Thus, the extensive, moisture-dependent forests of these continents were reduced as their water sources dried up. This shift toward less dense forests and the subsequent growth in woodland environments may have been a driving force for bipedal evolution in hominins[4-9].
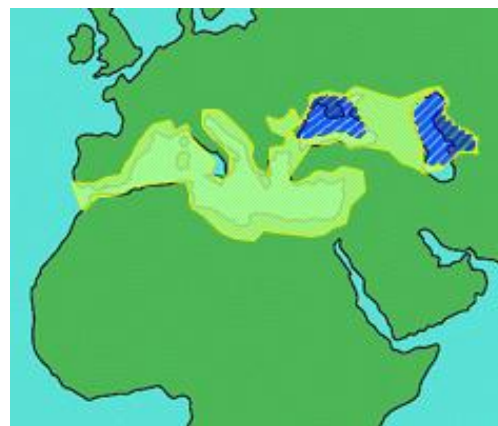
As a result of climatic cooling and tectonic activity, the Mediterranean Sea almost complete evaporated between 5 – 6 Ma. This event is known as the Messinian Salinity Crisis[3].

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Recent studies have determined that the early ancestors of humans probably lived in some sort of wooded habitat, perhaps a woodland savanna[4-9]. Climbing trees in search of food or to escape predators would have been a common behavior for organisms living a wooded or forest environment, and it is possible that early bipedal ancestors retained features (i.e., long arms, and curved fingers and toes) that were adapted to arboreal locomotion. In fact, some of the early hominin fossils do exhibit morphological adaptations conducive to tree climbing[8-12].

If bipedalism is one of the defining characteristics for hominins, then bipedal characteristics may be used to pinpoint the first appearance of hominins. To put it another way, although the DNA evidence suggests that apes and humans shared a common ancestor sometime between 7 and 8 Ma, characteristics of this shared ancestor remain somewhat debated. The identification of early bipedal adaptations within the fossil record may help to identify this shared ancestor, or perhaps help to determine what characters would be expected in this ancestor. Therefore, understanding the evolution of bipedalism remains an important study in the story of human origins.

Why bipedalism?

Habitual bipedalism is not necessarily the fastest and most effective form of running or walking, but bipedalism has a number of advantages over certain specialized forms of quadrupedalism. It is not clear why early hominins adapted a bipedal behavior. However, many hypotheses propose that environmentally-based selection pressures operated to drive the evolution of bipedalism[8-10,12-14]. As forests receded due to climatic conditions, hominins began to venture out into the expanding savannas where standing up to see over the tall grass aided in survival.

Older hypotheses about bipedal origins include the ability to carry food or other portable items over longer distances; the freeing of forelimbs for foraging, tool use, or protection; moving more energy-efficiently than other forms of primate quadrupedalism; and the development of long distance running. Another possible explanation for bipedalism is as an adaptation to efficiently cool the body in hot temperatures, known as thermoregulation. In a hot savanna environment a tall, lean upright posture exposes less surface area to the sun's heat overhead, while also promoting heat loss by exposing the greatest amount of surface area (i.e. the sides of the body) to cooling winds and air.

Despite a lack of consensus about the origins of bipedalism, many if not most of these proposed hypotheses are not mutually exclusive. Some combination of different selection pressures may have been responsible for driving bipedal evolution.
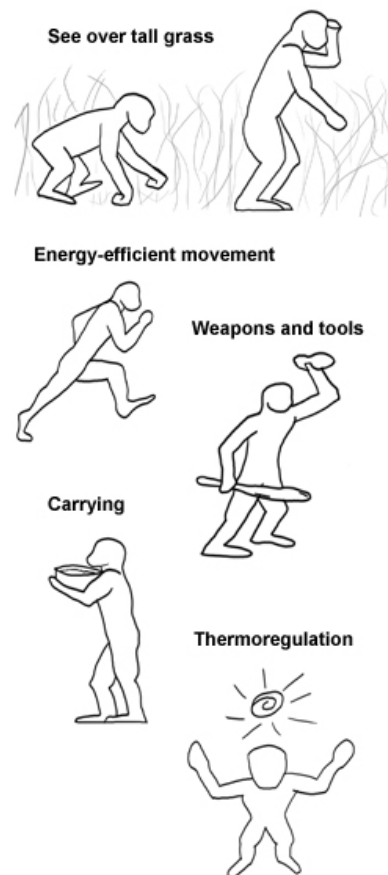

Proposed selective pressures for bipedal evolution. Modified from Setp and Betti as seen in Figure 17.11 in Fleagle 1999[13].

Bipeds have adapted a number of interdependent morphological characteristics that solve challenges posed by habitual bipedalism. These anatomical adaptations evolved over millions of years and differences exist between earlier and later hominin species (i.e., *Australopithecus*, *Paranthropus*, and *Homo*). Australopith and paranthropine evolution represents a notable step in the evolution of humans because these species are among the earliest hominins known to have evolved the adaptation of bipedalism.

Major morphological features diagnostic (i.e., informative) of bipedalism include: the presence of a bicondylar angle, or valgus knee; a more inferiorly placed foramen magnum; the presence of a reduced or nonopposable big toe; a higher arch on the foot; a more posterior orientation of the anterior portion of the iliac blade; a relatively larger femoral head diameter; an increased femoral neck length; and a slightly larger and anteroposteriorly elongated condyles of the femur. Each of these features is a specific adaptation to address problems associated with bipedalism.

All of the anatomical adaptations necessary for habitual bipedalism can be found in the fossil record. By reconciling the fossils evidence with the geologic time scale, it is possible to hypothesize about the evolutionary origins of bipedalism. The following is a detailed discussion of each morphological adaptation for habitual bipedalism.

Comparison of foramen magnum placement in a modern human and an extant chimpanzee.
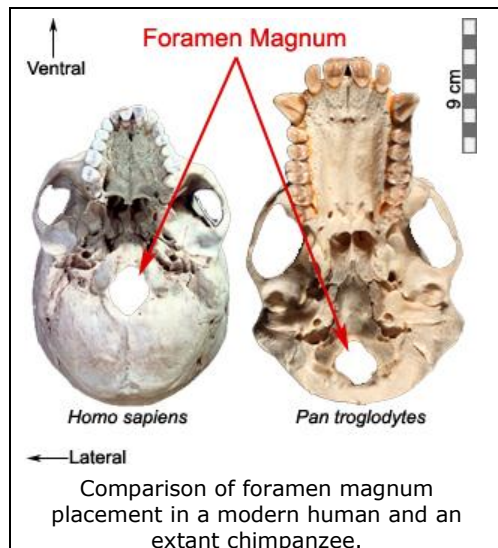
Cranium:

The placement of the foramen magnum, the large hole on the cranium through which the spinal column passes, is directly related to the orientation of the cranium. Consider that a primate holds their mandible (or chin) parallel to the ground. In a quadruped, the spinal column also runs parallel to the ground so the foramen magnum is more dorsally placed (i.e., toward the back of the cranium). In a bidped, the spinal column runs perpendicular to the mandible and the ground. The foramen magnum is located more inferiorly (more on the bottom of the cranium). Australopiths have a more inferiorly placed foramen magnum[8-10].

Lumbar vertebra:

Maintaining balance is critical when walking on two legs. In part of the walking cycle, a biped must balance on one leg while lifting the other foot off the ground and swinging it forward. In most quadrupedal hominins, the center of gravity is located near center on the torso. In modern humans, the center of gravity is closer to the center of the pelvis. As the legs alternate swinging forward during the walking cycle, the center of gravity shifts from one side of the pelvis to the other, making a pattern similar to the figure 8. The lumbar curvature on the spine helps to bring the center of gravity closer to the body's midline and above the feet.

Estimated center of gravity in modern humans and extant chimpanzees.
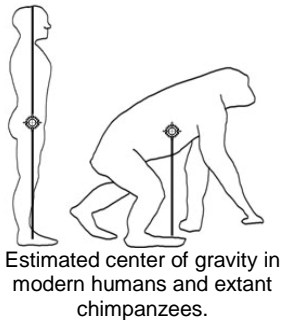
The number and size of the lumbar vertebrae in humans is different than in apes. Humans usually have 5 comparatively larger lumbar vertebrae. Most large apes typically have 4 lumbar vertebrae that are relatively smaller than human lumbar vertebrae. The greater number and size of the vertebrae forms a more flexible lower back that permits the hips and trunk to swivel forward when walking. Because the ape lower back is less flexible, the hips must shift a greater distance forward with each step when an ape walks bipedally.
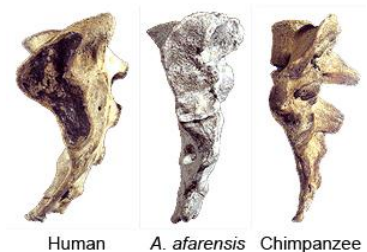
Australopithecus lumbar vertebral bodies were broad for effective weight transmission from the upper body to the pelvis. Australopiths had 5 or 6 lumbar vertebrae that articulated to form a distinctive lumbar curvature, similar to the morphology of modern humans[8,9,15].

The lumbar curvature (shown in the box above) allows the hips and trunk to swivel forward while walking.

The *Australopithecus* sacrum is broad, similar to modern human.
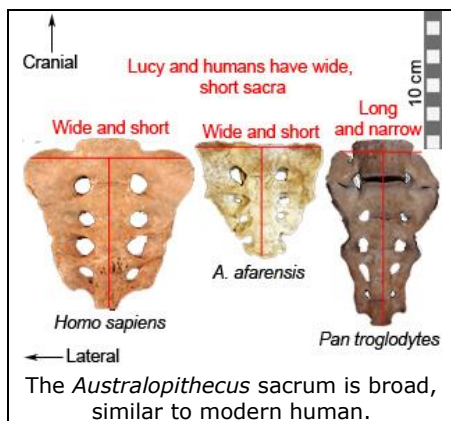
Sacrum:

The sacrum articulates with last lumbar vertebra, and also with the pelvis at the sacroiliac joint. The shape of the sacroiliac joint is a reflection of the lumbar curve. The sacrum is relatively broad in modern humans with large sacroiliac joint surfaces. Modern chimpanzees have a relatively smaller sacroiliac joint surface. These size differences are related to the different patterns of weight transmission through the pelvis during quadrupedal and bipedal locomotion. The australopith sacrum has relatively large, but less curved sacroiliac joint than that seen in modern humans[9].
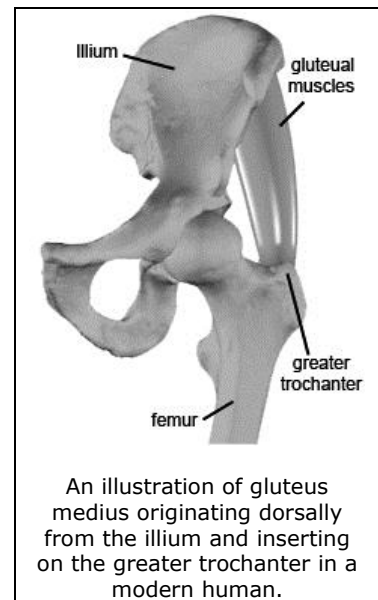

The australopith sacrum is more curved and has a larger sacroiliac joint than an extant chimpanzee, but it is not as curved as a modern human. (Not to scale.)

The Pelvis:

The gluteus medius and gluteus minimus muscles originate on the dorsal side of the ilium and insert on the greater trochanter of the femur. Their actions are critical to propulsion and stability while walking. Since bipedalism requires special adaptations, the orientation (and thus the function) of the gluteal muscles, is different in bipedal humans and quadrupedal apes. In apes, the flat portion of the iliac ala is roughly parallel with the plane of the back, while in humans the iliac ala is shifted laterally and flares more on the sides. This relatively lateral orientation of the alae in humans abducts *(*i.e., move away from the body) the hip joint. In turn, the gluteal muscles act to stabilize the area by preventing the hip on the supported side (the standing leg) from collapsing toward the unsupported side (the swinging leg). In apes, these muscles are attached relatively dorsal (i.e., more toward the back and less on the sides) and act as hip extensors, which move the leg backward when the primate takes a step[9].

An illustration of gluteus medius originating dorsally from the illium and inserting on the greater trochanter in a modern human.

The australopith pelvis exhibits widely flaring iliac ala. This flare is a critical component of the lever system of the hip and acts to increase the mechanical advantage of the lesser gluteals by increasing their lever arm. However, the lateral flare of the australopith ala is more pronounced than typically seen in modern humans. Shape similarities between the australopith and modern human pelves indicate that *Australopithecus* was fully bipedal. However, the unique morphology seen in australopiths suggests the species did not utilize the modern gait seen in later *Homo*[9].
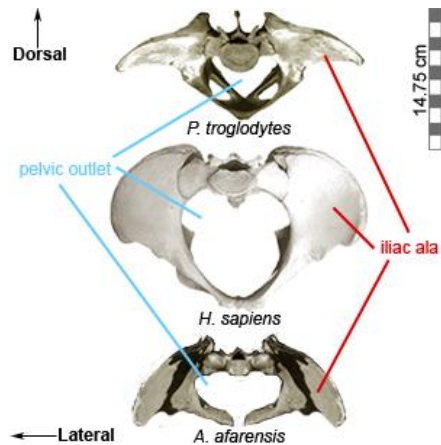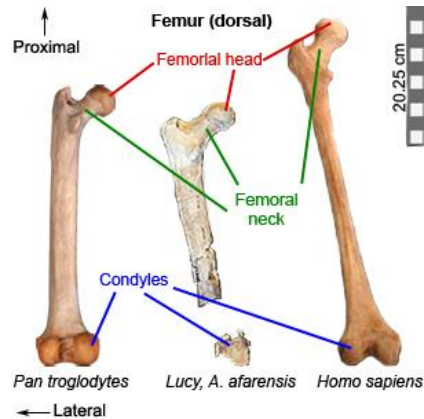

Both humans and *Australopithecus* have flaring iliac ala, curving toward the front of the body. The pelvis outlet is also increased in size in the human and *Australopithecus.*

The modern human pelvis has relatively larger hip joints and larger pelvic outlet relative to australopiths or modern apes. These differences appear to be a compromise between two functional needs: 1) efficient bipedalism; and 2) allowing enough space for wide shouldered, large brained infants to pass through the birth canal.

In bipeds, the hips support and balance the weight of the torso during locomotion. However, as the size of the pelvic outlet increased, the hip joints were repositioned relatively further from the center line of the body. As a result, more force is exerted on the hip joint as the joint (acetabulum and femoral head) moves further away from the body's center of gravity, and thus affects stability as the weight of the torso presses downward toward the middle of the body. This issue is resolved through several adaptations in the pelvis and femur. In the pelvis, an enlarged hip joint allows more stress to be absorbed and accommodates a larger femoral head[9,16].

Femur:

The entire weight of the torso is transferred through the legs and into the feet during bipedal standing and walking. Therefore, the femur in bipeds is one of the most critical links between the pelvis, vertebral column, and lower legs. The femur is also the distal

Comparison of a Chimpanzee, *A. afarensis* and *H. sapiens* femora, size, shape and bicondylar angles.

attachment point for the gluteal muscles that provide the propulsive force for locomotion.

The rounded femoral head articulates with the pelvis at the acetabulum (hip joint). The femoral shaft is generally straight, ending in two bulbous condyles. These condyles are larger and more elliptical in bipeds when compared to the relatively smaller and rounder condyles seen in quadrupeds. The distal end of the femur articulates with the tibia (lower leg) and patella (knee cap) at the knee joint.

The amount of force exerted on the hip joint and the femoral head increases as the acetabulum moves further away from the body's center of gravity. The size of the femoral head reflects the amount of force absorbed at the hip joint. A femoral head with a larger diameter is able to absorb more stress. Another adaptation to counteract the increased stress on the hip joint is a longer femoral neck, which increases the mechanical advantage of the lesser gluteal muscles by lengthening their lever arm.

Australopithecus has a relatively smaller femoral head and longer femoral neck compared to later *Homo* who have a relatively and absolutely larger femoral head[9,17].

Knee (Distal Femur and Proximal Tibia):

A critical adaptation for efficient bipedalsim relates to the need to keep the body's center of gravity balanced over the stance leg during the stride cycle. Birds solved this issue by having the entire leg (from the hips all the way to the feet) as close as possible to the body's center line. In humans, whose hips are wide apart, the shaft of the femur is

angled so that the knee is closer to the body's midline than the hips. This angle is called the **bicondylar angle**, and the resulting knee joint is referred to as a **valgus knee**[9]. The effect is to bring the knees closer together, placing the feet directly below the center of gravity.
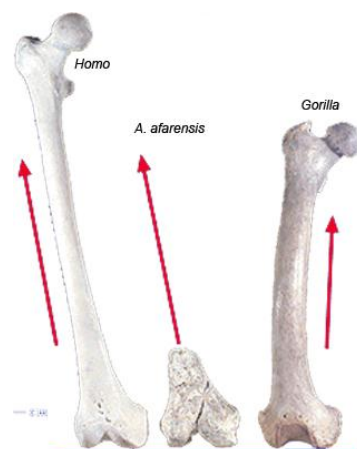
Compared to modern humans, an ape femur is almost vertical within a horizontal plane. In quadrupeds the positioning of the center of gravity during locomotion is less critical since the quadruped is usually supported by 2 or more legs during the stride cycle rather than just 1 as with humans. Australopiths have a human-like bicondylar angle[9,18].
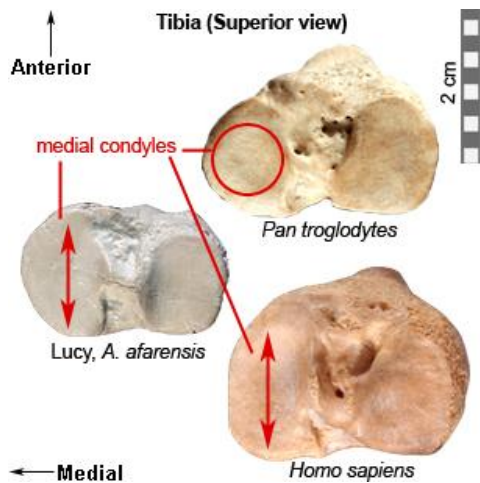
The superior view of the right tibia illustrates the antero-posterior elongation of the medial condyle in bipeds. The condyles in chimpanzees are more circular.
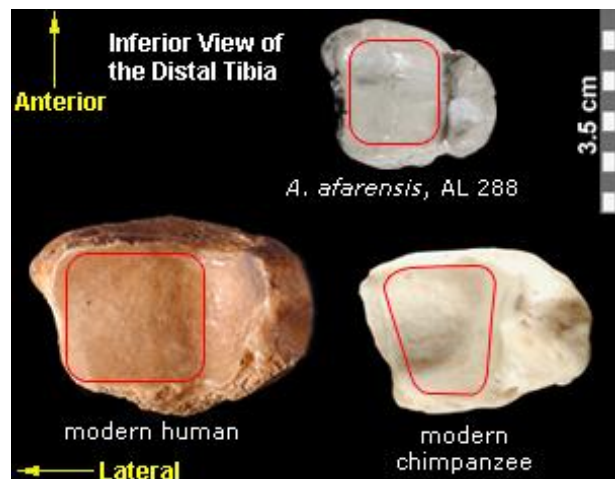
A result of the femur's bicondylar angle pulling the knees inward is that the tibia stands almost parallel with the body's center of gravity. Unlike the femur, the tibial shaft lies at a right angle to its proximal surface. Also of note, the human medial and lateral proximal articular condyles (i.e., the flattened surfaces on the top of the tibia that articulate with the femur) are relatively larger and elongated anteroposteriorly (i.e., longer front to back) compared to quadrupeds. The comparatively larger lateral proximal condyle (also seen on the femur and helps to create the bicondylar angle) is an adaptation to increased weight transfer through the femur and into the foot. In addition, modern human condyles are more concave and elliptical in shape to accommodate the elliptical femoral distal condyles. Quadrupeds tibial condyles appear relatively spherical and are more convex. The elliptical shape in humans helps to lock the knee in place and create straight-forward forward leg movement[9].

A chimpanzee's tibia retains smaller lateral proximal condyles, and may exhibit an obtuse angle between the tibial proximal surface and the shaft. The australopith tibia has a nearly right angle between the shaft and proximal surface.

Tibia and Talus (Ankle):

The distal end of the tibia articulates with the talus at the ankle. In humans, the tibia's articular surface for the talus is situated relatively more inferior when compared to the anteroinferior orientation in quadrupeds. In addition, the shape of the distal tibia in apes is relatively trapezoid when compared to the square shape of modern humans. This is because the anterior aspect is relatively wider mediolaterally in African apes[34].

The talar superior articular surface which articulates with the distal tibia sits almost directly superior, or nearly parallel with the talar body in humans. Plantar articulation surfaces on the talus (i.e., the calcaneal articular surface and the navicular articular surface) are also less angled than typically seen quadrupeds.

Inferior view of the 3 distal tibiae: Lucy, an extant chimpanzee, and a modern human. Articular surfaces outline in red. Note the elongated anterior aspect seen in chimpanzees.

Instead, these surfaces trend downward, forming a plantarly oriented foot when standing. Both the ankle and the subtalar joint are situated directly at the end of the tibia's long axis, which helps to transmit stress loads from the legs through the foot[33,34].
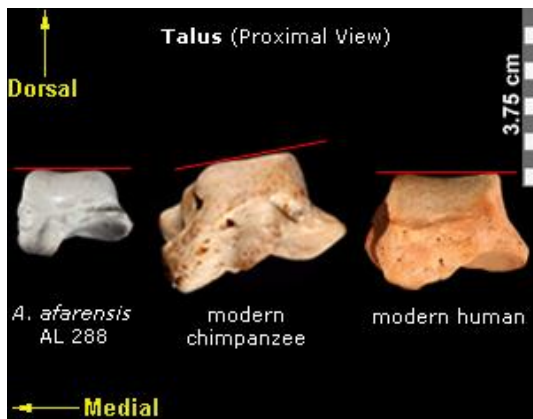
Proximal View of 3 right tali: Lucy, an extant chimpanzee, and a modern human. Note the medially oriented superior articular surface as outlined by the red line.

Additionally, the relatively inflexible midfoot and horizontal orientation of the ankle joint encourage a straighter foot path during walking. The talus is also relatively robust in humans, which helps absorb stress during foot strike.

In comparison with humans, corresponding articular surfaces in chimpanzees appear more angled. For example, the superior articular surface on the chimpanzee talus is relatively more medially angled than in humans[33]. This medial orientation of the talar superior articular surface may be associated with the inverted position of the foot used during vertical climbing[33]. Likewise, the calcaneal articular surface is more rounded suggesting relatively agile mid-foot flexibililty typical of arboreal primates.

The *A. afarensis* distal tibia articular surface is oriented relatively inferior, as seen in modern humans. The talus is relatively derived in that it is positioned at the end of the tibia's long axis, and the articular surfaces sit relatively parallel with the talar body[34]. The fossil material suggests that *A. afarensis* had an inflexible midfoot, although perhaps not as restrictive as seen in modern humans[34].

Fingers:

Among hominins, the degree of curvature observed in the phalangeal shaft correlates with the frequency of arboreal behavior. Species that spend a lot of time grasping or suspending from curved branches have dramatically curved fingers and toes which allows for a more powerful grip. Non-arboreal primates, such as humans, have relatively flat manual and pedal phalanges, an adaptation reflecting a lack of regular arboreal activity. This, in turn, has facilitated the evolution of precise hand movements necessary for making and using tools. Highly curved phalanges reduce the capacity for precision grips.

Australopith phalanges are intermediately curved between those of modern humans and great apes, suggesting that climbing and arboreal behavior continued to play some role in the lifestyle of these early hominins[6,9,12].
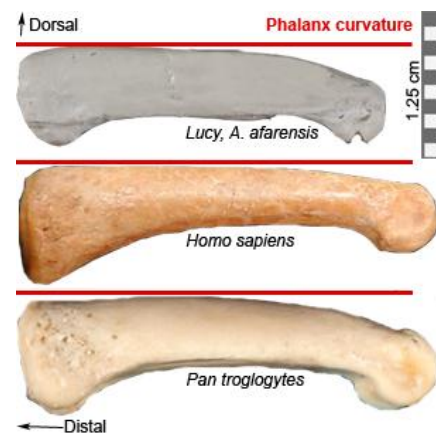
Compared to extant chimpanzees and modern humans, australopiths have intermediately curved phalanges.
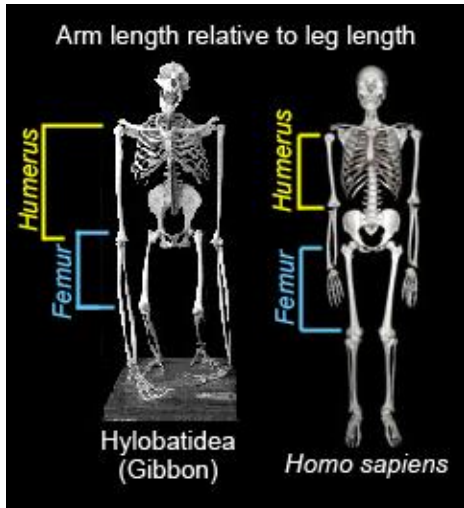
Arboreal gibbons have much longer arms than legs, while bipeds typically have arms and legs of similar size. Not to scale.

Arms and Legs:

Most quadrupedal and arboreal primates have either longer arms relative to their legs, or arms and legs of equal length. Most bipeds have relatively longer legs than arms. Based on this information, it is possible to estimate the positional behavior of a species by calculating the humerofemoral index. This index is the length of the humerus divided by the length of the femur, multiplied by 100:

$$\frac{\text{humerus length}}{\text{femur length}} \times 100$$

Results of the humerofemoral index calculate the overall body proportion of an organism which can then be compared to others. The higher the index value, the longer the arms and the more likely a primate is to be arboreal. Most arboreal primates have ratios close to 100. For example, the mean ration for the common chimpanzee is 97.8. Humans average a lower ratio at approximately 71.8. The ratio of the famous *A. afarensis* "Lucy" is intermediate between modern humans and chimpanzees at 84.6[9,10].

Feet and Toes:

Humans have the most distinctive feet of all the apes. Since only the hindlimbs (or lower limbs) are used for propulsion, the body's entire torso weight (all of the forces generated by running, walking, and jumping) pass through only 1foot at a time as the biped moves between the swing and stance phases of locomotion. As a consequence, the foot anatomy must be robust enough to accommodate these forces, while also providing efficient toe-initiated push-off for propulsion. As an example, the hallux (i.e., big toe) in humans is much larger and more robust than the other four toes.
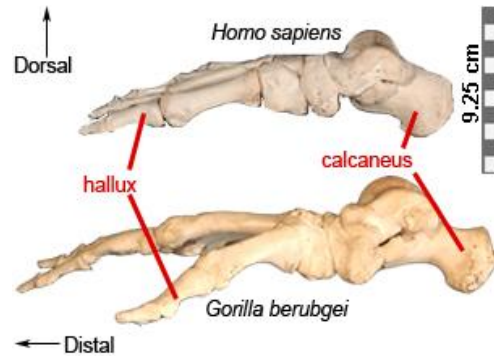
The calcaneus is comparatively more robust in bipeds than quadrupeds. Note that the hallux sits parallel to the rest of the toes in humans, but is more divergent in extant apes.

The calcaneus, or heel bone, is also relatively large and robust in humans compared to chimpanzees, especially the posterior portion known as the calcaneal tuberosity. As the first foot bone to contact the ground during the stride cycle, the robust size of the calcaneus provides stability and helps to absorb the high forces encountered during heel strike. In addition, the shape of the calcaneus provides attachment points for strong ligaments that run from the arch of the foot to the tibia. These ligaments add support, creating a double arch system that helps to absorb stress as the foot hits the ground.

The metatarsals are long thin bones in the middle of the foot between the tarsals (on the distal side) and the phalanges, or toe bones (on the proximal side). Bipedalism can be inferred by examining the shape of the articular surfaces on tarsals that articulate with metatarsal I (i.e., the hallux). For example, the rounded articular surface on the ape medial cuneiform permits a wide range of abduction. The human medial cuneiform, however, has a flattened articular surface which restricts the hallux to an adducted position. This means that the human hallux lies parallel to the other toes and lateral movement is severely limited.

The fully adducted hallux in humans is commonly referred to as a **non-opposable big toe**. In general, human toes are shorter in relative length than in other primates; and comparatively, humans have almost no grasping ability in their toes and feet. However, walking bipedally with longer toes and a divergent hallux would be energetically costly and impede efficient bipedalism, so relatively toe length is likely an adaptation for obligate bipedalism[9,19].

Evidence from the Laetoli Tracks in Tanzania, where footprints from several australopiths were preserved in volcanic ash, indicates that *Australopithecus* had relatively short toes, and an intermediately adducted hallux.
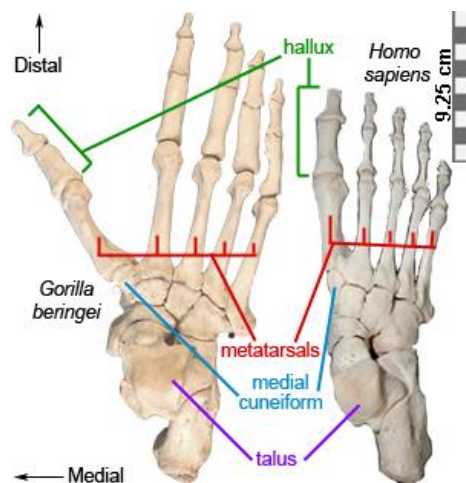
The rounded articular surface of the medial cuneiform in quadrupeds permits a wide range of movement in the hallux. In humans, the hallux sits parallel to the rest of the toes allowing for greater push-off during walking.

Fossil Evidence of Bipedalism:

The fossil record offers clues as to the origins of bipedalism, which in turn helps us to identify those species ancestral to modern humans. One of the most abundant sources for early bipedalism is found in *Australopithecus afarensis*, a species that lived between approximately 4 and 2.8 Ma. *Au. afarensis postcrania* fossils clearly shows hip, knee, and foot morphology distinctive to bipedalism.

An illustration of the Laetoli tracks, left by three *A. afarensis* individuals. These tracks date to 3.7 million years ago. Drawn from PBS:Evolution 2001[30].

In addition to the postcranial material, *Au. afarensis* also left behind a 27 meter long set of footprints known as the Laetoli Tracks in Tanzania. Approximately 3.7 Ma, 3 *Au. afarensis* individuals walked through a muddy layer of volcanic ash that preserved their foot prints after the ash hardened[20]. From the Laetoli tracks it is clear that *Au. afarensis* walked with an upright posture, with a strong heel strike and follow-through to the ball of the foot, with the hallux making last contact with the ground before push-off. Interestingly, the prints provide evidence of a slight gap between the hallux and the other toes. This gap suggests that even though the hallux was not fully divergent, it was also not yet fully adducted as seen in modern humans[8-10,21-23].

Though australopith material offers a strong case for habitual bipedalism, earlier hominins dating as far back as 7 Ma also provide exciting evidence for early bipedalism. The oldest known hominin to show definitivebipedal adaptations is the extinct species *Orrorin tugenensis* that dates to 6 Ma. A femur and tibia recovered in Kenya and assigned to *O. tugenensis* exhibits feature typical of bipeds, including a bicondylar angle[24-26]. However, a 7 Ma fossil discovered in Chad in 2001, known as *Sahelanthropus tchadensis,* exhibits a more inferiorly positioned foramen magnum consistent with bipedalism, rather than the relatively dorsal position seen in quadrupeds[27,28]. No postcranial material has been associated with *Sahelanthropus,* but if proven to be bipedal, *Sahelanthropus* may substantiate the hypothesis that bipedal evolution was influenced by climate trends beginning in the late Miocene (i.e., a geologic epoch that dates between 23 and 5.3 Ma). Faunal analyses from these early hominin sites suggests *S. tchadensis* and *O. tugenensis* lived on lake margins, near the edge of woodlands and grasslands.

Cranium of *S. tchadensis* specimen TM 266-02-060-1

About 2 million years younger than *O. tugenensis* is a hominin known as *Ardipithecus ramidus* that dates to approximately 4.4 Ma. Known as Ardi, *Ar ramidus* material exhibits a mosaic of primitive and derived features, including a fully abductable hallux (primitive), relatively inflexible midfoot (derived), arms and legs of similar proportions (primitive), relatively broad iliac ala (derived), and an inferiorly placed foramen magnum[8-10,31,32].

The oldest evidence for australopith bipedalism is found in the species *Australopithecus anamensis* (4.2 to 3.9 Ma). Found in Kenya, *Au. anamensis* most likely lived in a wooded savanna. Fossil evidence for this species includes a preserved tibia that exhibits bipedal characteristics such as a right angle between the shaft and the proximal surface, and

proximal articular condyles of nearly equal size. An abundance of the younger species *Au. afarensis* (4 to 2.8 Ma) and *Australopithecus africanus* (3 to 2 Ma) fossils also show clear signs of bipedalism, including a bicondylar angle, an anteriorly placed foramen magnum, laterally flaring iliac blades, longer femoral necks and heads, and the presence of a lumbar curve. Though *Au. afarensis* seems to have originated in Ethiopia and *Au. africanus* is found only in South Africa, both of these species lived in open habitats, possibly wooded savanna areas near a lake[8-10].
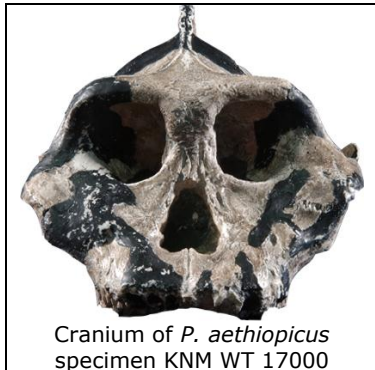
Cranium of *P. aethiopicus* specimen KNM WT 17000

Paranthropines are larger and more robust than australopiths, but have similar postcranial morphology, including bipedal adaptations similar to *Australopithecus*. The oldest paranthropine was found in Ethiopia and is known as *Paranthropus aethiopicus* (2.6 – 2.5 Ma). Although postcranial material is scarce, a possible *P. aethiopicus* calcaneus may exhibit bipedal adaptations. The younger paranthropine species, *Paranthropus robustus* (1.75 to 1.5 Ma) and *Paranthropus boisei* (2.5 to 1 Ma), exhibit the same bipedal adaptations as *Au. africanus*, which include an inferiorly oriented foramen magnum, modern human-like talus, relatively long femoral neck, and a bicondylar angle. In addition, the hand anatomy of *P. robustus* implies a grip capable of tool use, while the radius of both *P. robustus* and *P. boisei* implies *Paranthropus* retained the ability to effectively climb trees. Paleoecological studies suggest these species were living in open woodland or savanna habitats.

All species included in the genus *Homo* are obligatory bipeds and show evidence of tool use, beginning with the species *Homo habilis* (i.e. "Handy Man") that dates between approximately 2.6 to 1.6 Ma, and continuing to the modern species *Homo sapiens* that dates between approximately 190,000 years ago (Ka) to present[8-10].

H. ergaster specimen KNM WT 15000, is a nearly complete skeleton and exhibits many hallmarks of bipedalism, such as the bicondylar angle and longer legs relativeto the arms.

Bipedalism vs. Brain size?

Early researchers hypothesized that brain enlargement was the first hallmark of the hominin lineage. Beginning in the mid 1800's until the early 1900's, almost all known fossil hominins had relatively large brains. The large brain hypothesis was falsified after the discovery of early hominin fossils exhibiting ape-sized brains and bipedally-adapted morphology.

Lateral view of the *A. africaus* specimen known as Taung Chilld (3-2 Ma). Note the preserved endocast. Raymong Dart proposed that bipedalism evolved before larger brains as a result of examining this fossil.

In 1924, Raymond Dart identified the first australopith fossil, known as the Taung Child, from South Africa. This specimen belonged to the species *Au. africanus* and had a relatively small brain similar to the size of a modern chimpanzees. The inferior placement of the foramen magnum, Dart argued, suggested that the Taung Child was bipedal. Dart's hypothesis that bipedalism evolved before larger brains ran counter to the scientific consensus at the time. Because of his small sample size and fragmentary remains, debate about the timing of bipedalism and brain size continued for the next 50 years.

Illustration of "Lucy", a 3.2 Ma *A. afarensis* specimen that exhibits bipedal morphology. Drawn after Johanson and Edgar 2006.

Everything changed in 1974 when Donald Johanson found the nearly complete fossilized skeleton of Lucy, a member of the species *Au. afarensis* dating to 3.2 Ma. Lucy was unique at that time because she was one of the first fossils to exhibit both small relative brain size *and* the highly derived features characteristic of bipedalism. As other contemporaneous and older fossils (perhaps as old at 7 Ma) are found, scientists continue to revise the bipedalism timeline. Today, the evidence undoubtedly demonstrates that bipedalism was one of the first hallmarks of the hominin lineage and may have led to many more advances. For example, one advantage of bipedalism is that the hands are freed, which allowed for the production of more technologically advanced stone tools. In turn, the production of more complex tools may have led to a higher protein diet that affected brain size[8-10,27-29].

The functional demands of bipedalism have exerted a strong influence on the postcranial skeletal adaptations of modern humans as well as extinct hominins. For example, australopiths share with modern humans many of the essential features of bipedalism such as reorganized pelvic and lower back anatomy, a valgus knee, and a relatively robust calcaneus. However, australopiths have many unique features that differ from modern humans in significant ways. Humans do not share the long ala of the ilia, the relatively smaller femoral heads, or the curved fingers and toes seen in *Australopithecus*. This combination of primitive and derived features leads many researchers to support the idea that australopiths engaged in a form of locomotion that was not identical to that of modern humans, including a greater amount of time engaged in climbing and suspensory behaviors. *Australopithecus* may, then, represent a mosaic of evolutionary adaptations for life on the ground and in the trees.
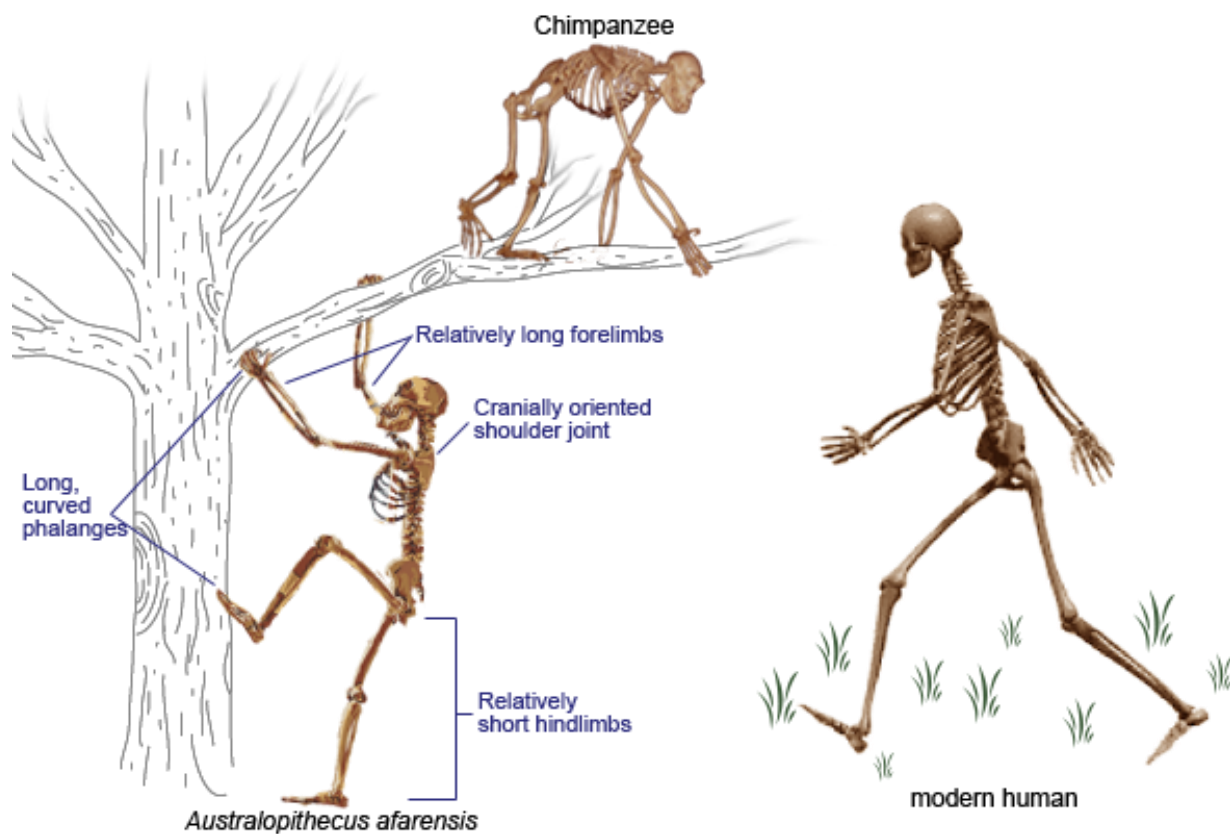
Illustration of *A. afarensis*, modern chimpanzee, and modern human forms of locomotion.
Note that *A. afaresnsis* exhibits traits that suggest the species walked bipedally while on the ground, but remained agile when climbing trees. Modified from Fleagle 1999[13].

Based on the reading, identify the species (not including the genus *Homo*) that show evidence of bipedalism, the geological dates associated with each species, and the morphological features that demonstrate possible bipedalism. Where possible, identify any environmental or behavioral changes that may have affected adaptations for bipedal locomotion. Remember to write down only information for which there is evidence.

Hominin	Date Range	Morphological Features	Environmental or Behavioral Factors

Anthropologists struggled for years with the question "Which came first: larger brains or bipedalism", until the fossil record provided the evidence needed. Determine the evolution of bipedalism in relation to the increase in relative brain size by completing the exercise.

Part A: *Foot Measurements*: Determine whether *A. afarensis* had feet that more closely resembled modern humans or modern chimpanzees. (Remember that the primitive, or earliest, condition is expected to be more like that of a modern chimpanzee).

- In this section of the activity, you will take three measurements: the distance between the hallux (big toe) and the second toe, foot length (the length from the tip of the longest toe to the back of the heel), and foot width (the widest part of the foot usually around the toe area). Actual size outlines of a chimpanzee foot and from an *A. afarensis* foot print preserved at Laetoli have been provided for you.

    1. Trace your bare foot on a clean sheet of paper (you can use the back of this lesson).

    2. Using digital calipers or a ruler, measure in cm the distances according to the instructions. Write your results in the space provided on the graph.

    3. Calculate the hallux divergence index by dividing the foot width by the foot length.

    4. Answer these questions based on your results:

        Did *A. afarensis* have a divergent big toe?

        Did *A. afarensis* have a derived foot similar to modern humans, or a primitive foot more like that of an extant chimpanzee? Give a reason for your answer.

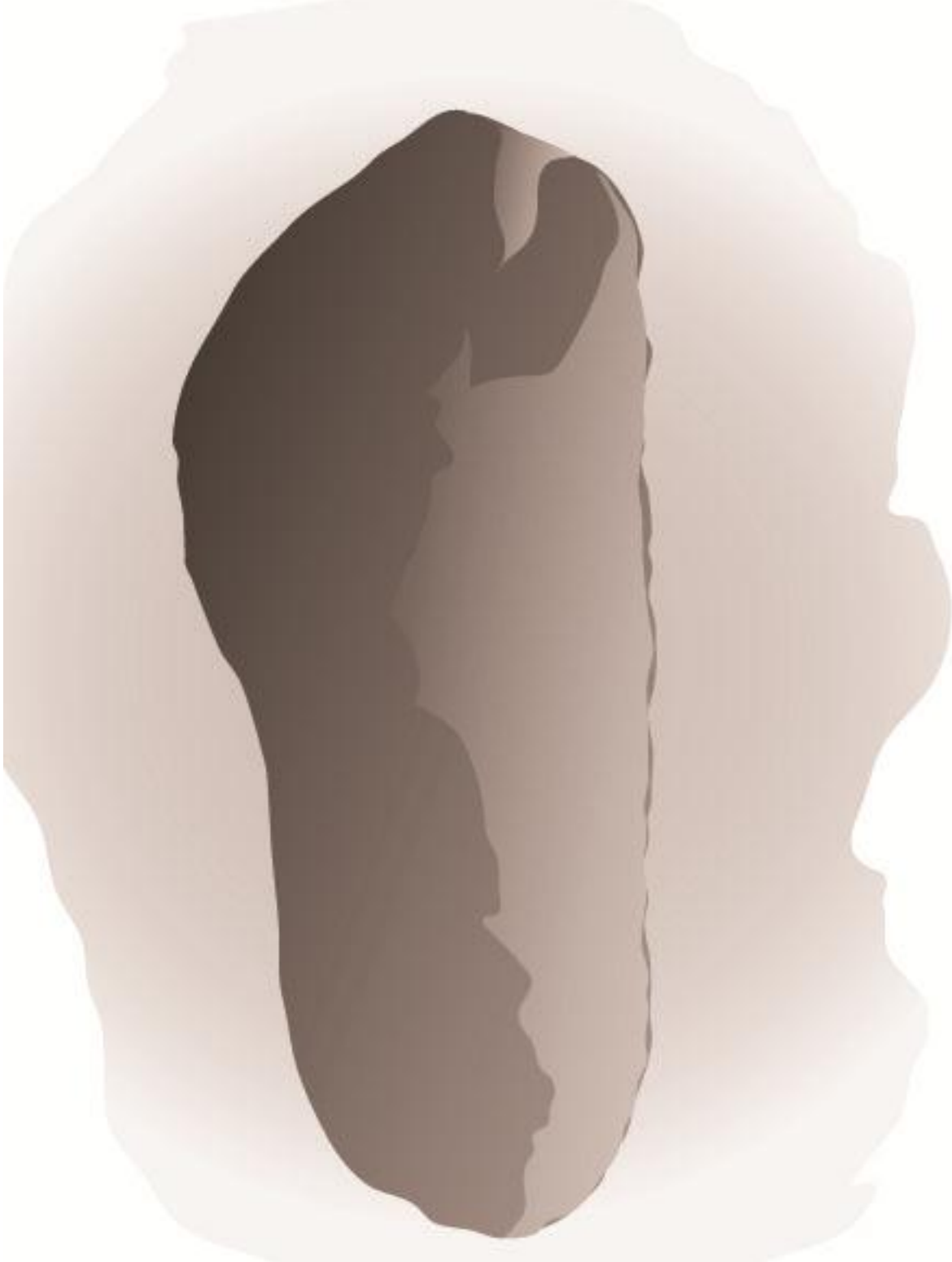| Taxon	Distance between hallux & 2nd toe	Foot length	Foot width	Foot width/ Foot length
modern human				
A. afarensis				
extant chimpanzee				

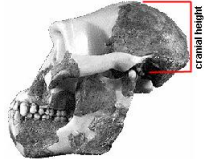**Chimpanzee Foot (unknown male or female), actual size**

Actual Size Outline of a Laetoli Footprint (Redrawn from Johanson and Edgar 2006[10])

Part B: *Cranial Measurements*: Determine whether the relative brain size of *A. afarensis* was more similar to modern humans or modern chimpanzees. (Remember that the primitive condition is expected to be more like that of a modern chimpanzee).

- In this section of the activity, you will take 3 measurements: cranial width (the widest part of the skull), cranial length (the distance from the forehead just behind the eyebrows to the back of the skull), and cranial height (the distance from the top of the cranium to just below the ear). Use the images in the chart as your guide.

  1. There are 2 options for the skull measurements. If your school has access to casts of a modern chimpanzee, a modern human, and an australopith skull, use digital calipers to measure in cm the width, length, and height of each cranium. Or you can use the images available in the online bipedalism lesson on eFossils.org and eLucy.org. Estimate the cranial width, length and height using the scale provided in the top right corner of the images.

  2. Calculate the cranial volume for the three specimens by multiplying the cranial width, cranial length, and cranial height by 1.333 x 3.14, then divide your answer by 10. Measurements for a chimpanzee and *A. afarensis* are provided for you.

  3. Answer the question based on your results.

     Was the brain size of *A. afarensis* more similar to modern humans or chimpanzees?

Taxon	Cranial Width	Cranial Length	Cranial Height	Multiply by	Cranial Volume
modern human				$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	
A. afarensis	9.83 cm	13.00 cm	8.07 cm	$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	
modern chimpanzee	9.92 cm	11.48 cm	7.11 cm	$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	

Based on your reading and the above exercise, complete the following questions.

1. What is bipedalism?

2. What is habitual or obligate bipedalism? How is it different from facultative bipedalism? For what reason(s) would a quadruped use the bipedal form of locomotion?

3. What are the earliest fossil hominins to show physical evidence of bipedalism?

4. What are some of the theories put forward by scientist for the evolution of bipedalism? Which one do you think is the most plausible and why? Do you think there is more than one?

5. What are the anatomical features indicative of bipedalism? How do those features differ from a quadruped?

6. Based on the information you have recorded, did bipedalism evolve before or after an increase in brain size? In what way could brain size have been affected by bipedalism?

7. What features, if any, are unique to australopiths in comparison to modern humans and chimpanzees? What might these features indicate?

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Features Chart:

Hominin	Date Range	Morphological Features	Environmental or Behavioral Factors
Sahelanthropus	*6 - 7 Ma*	*More inferiorly-placed foramen magnum*	*possibly lake area*
A. anamensis	*4.2 - 3.9 ma*	*More human-like shape of the proximal tibia*	*wooded savanna*
A. afarensis	*3.9 - 2.8 Ma*	*Nonopposable big toe, valgus knee, inferiorly-directed foramen magnum, high foot arch, evidence of lumbar curvature, greater number and broader lumbar vertebrae, widely flaring iliac ala, wider pelvic outlet, increased femoral neck length*	*lake area surrounded by woodland savanna*
A. africanus	*2.8 - 2.2 Ma*	*Inferiorly-oriented foramen magnum*	*lake area, surrounded by savanna or open woodland*
P. aethiopicus	*2.5 - 2.3 Ma*	*No post-crania associated with this fossil*	*Unknown*
P. robustus	*1.8 - 1.0 Ma*	*Inferiorly -oriented foramen magnum, modern human-like talus, long femoral neck, valgus knee*	*lake area surrounded by open grassland*
P. boisei	*2.3 - 1.2 Ma, possibly 2.3 - 0.7 Ma*	*Inferiorly-oriented foramen magnum, long femoral neck*	*lake area surrounded by open grassland*

Brain vs. Bipedalism:

Part A: *Foot Measurements*: Determine whether *A. afarensis* had feet that more closely resembled modern humans or modern chimpanzees. (Remember that the primitive condition is expected to be more like that of a modern chimpanzee).

For Part A, check the students' math. Because of variations in the measurement procedures and between measuring instruments, measurements between students may be slightly different.

Did *A. afarensis* have a divergent big toe? *A. afarensis had a non-divergent big toe, more similar to modern humans.*

Did *A. afarensis* have a derived foot, more like that of modern humans, or a primitive foot more like that of a chimpanzee? Give a reason for your answer? *Based on the hallux divergence index, A. afarensis had a derived foot, more similar to that of modern humans.*

Part B: *Cranial Measurements*: Determine whether the brain size of *A. afarensis* was more similar to modern humans or modern chimpanzees. (Remember that the primitive condition is expected to be more like that of a modern chimpanzee).

Specimen	Cranial Width	Cranial Length	Cranial Height	Multiplication	Cranial Volume
Modern Human				$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	
A. afarensis	9.83 cm	13.00 cm	8.07 cm	$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	*431.6 cc*
Modern Chimpanzee	9.92 cm	11.48 cm	7.11 cm	$\dfrac{\text{x } 1.333 \text{ x } 3.14}{10}$	*338.9 cc*

Was the brain size of *A. afarensis* more similar to modern humans or chimpanzees? *The brain size of A. afarensis was more similar to that of chimpanzees.*

Review Questions:

1. What is bipedalism? - *Bipedalism refers to the form of locomotion (e.g. walking, jogging, running, etc.) on 2 legs.* (The Evolution of Bipedalism, page 2)

2. What is habitual or obligate bipedalism? How is it different from facultative bipedalism? For what reason(s) would a quadruped use the bipedal form of locomotion? - *Habitual bipedalism is when an animal's natural form of locomotion is on 2 legs. Facultative bipedalism is when an animal that usually locomotes on more than 2 legs assumes a bipedal position on a temporary basis in order to perform a specific action. Quadrupeds, such as African antelopes or chimpanzees may assume a bipedal position for feeding or defensive purposes.* (The Evolution of Bipedalism, page 2)

3. What is the earliest fossil hominin to show physical evidence of bipedalism? That is this geologic age? - *Possibly Sahelanthropus at 7 Ma, but more definitively Orrorin tugenensis at 6 Ma. A. anamensis at 4.2 - 3.9 Ma may also be accepted.* (The Evolution of Bipedalism, page 12)

4. What are some of the theories put forward by scientist for the evolution of bipedalism? Which one do you think is the most plausible? Do you think there is more than one? *Some of the theories about the evolution of bipedalism include an adaptation for more efficient ability to carry items over long distance, the freeing of forelimbs for foraging or tool use; a more energy-efficient manner of locomotion than quadrupedalism, and more efficient method of cooling the body.* (The Evolution of Bipedalism, page 3)

   A combination of these different selection pressures might have been responsible for driving the evolution of bipedalism.

   Instructors should score the question "Which one do you think is the most plausible" based on the critical thinking demonstrated by the student. There is no single correct answer.

5. What are the anatomical features indicative of bipedalism? What is the function of these adaptations? How do those features differ from a quadruped?

Biped	Function	Quadruped
A more inferiorly placed foramen magnum	*Reflect the orientation of the cranium*	*A more dorsally placed foramen magnum*
Broad sacroiliac joint surface indicative of a pronounced lumbar curvature	*Brings the center of gravity closer to the midline of the body and above the feet*	*Small sacroiliac joint surface indicative of little to no lumbar curvature*
Greater amount of lumbar vertebrae that are more broad	*Allows for greater flexibility of the torso*	*Relatively smaller and lower number of lumbar vertebrae*
Laterally shifted and more flared iliac ala	*Reoriented the gluteal muscles in order to stabilize the standing leg.*	*Flat iliac ala that sit in the same plane as the back.*
Relatively larger femoral head diameter	*Counteracts the forces exerted on the femur due to the widening of the pelvic outlet*	*Smaller femoral head diameter*
Increased femoral neck length	*Increases the mechanical advantage of gluteal muscles*	*Shorter femoral neck length*
A bicondylar angle or the valgus knee) due to enlarged and elongated femoral condyles	*Keeping the body's center of gravity balanced over the stance leg during the walking cycle.*	*little to no bicondylar angle and do not have a valgus knee due to smaller, rounder femoral condyles*
Ankle that sits at the bottom of the long axis of the tibia	*Helps absorb weight transmission from the leg through the foot, and forms less flexible foot*	*Ankle not under the long axis of the tibia, with flexible ankle and mid-foot.*
Robust pedal phalanges	*Larger size helps to absorb the forces during toe-off propulsion*	*Less robust pedal phalanges*
Robust calcaneus	*Larger size helps to absorb the forces during the heel strike*	*Less robust calcaneus*
Flat surface of the medial cuneiform	*Adducts the toe allowing more efficient toe-off propulsion*	*Round surface of the medial cuneiform*
Shortened toes	*Allows for more efficient bipedalism*	*Longer toes*
Less curved phalangeal shafts	*Allowed for more precise hand movements*	*More curved phalangeal shafts*
Relatively longer legs than arms	*Related to greater reliance on the legs for locomotion*	*Relatively longer arms than legs*

6. Based on the information you have recorded, did bipedalism evolve before or after an increase in brain size? In what way could brain size have been affected by bipedalism? *Bipedalism is older than larger brains. Bipedalism would have freed up the hands so that humans could produce more advanced stone tools which may have led to a better diet which in turn affected brain size.* (The Evolution of Bipedalism, page 14)

7. What features, if any, are unique to australopiths compared to modern humans and chimpanzees? What might these features indicate? *Australopiths have a long ala of the ilia, relatively small femoral heads, and curved fingers and toes. These features suggests that the gait of the australopiths was different than that of modern humans, and that australopiths may have spent more time engaged in climbing and suspensory behaviors.* (The Evolution of Bipedalism, page 15).