Bipedal hominid and quadrupedal apes: muscle and skeletons

Differences between the hip skeleton and musculature of bipedal hominid and quadrupedal apes.

        1. Ilium

Humans:

Reduced height, relative wideness (it is important in bipedal posture, because the weight of the body does not concentrate onto the spinal cord only).

Orientation of blade (the curvature and the mediolateral orientation of the iliac blades help the Glutei medius and minimi to act as abductors and they can also assist in support of the trunk. This curved shape also helps in balancing the upper body during locomotion, because the external and internal oblique muscles attach to the iliac crest).

Acetabular margin and the well-developed anterior inferior iliac spine (AIIS) reflects the bipedal locomotion. Rectus femoris takes its origin here, that extends the leg at the knee. Rectus femoris is very important in some of the leaping and clinging prosimians, as the galagos and lemurs, because Rectus femoris is a leaping muscle in them. Nevertheless, in apes, there is no large AIIS. AIIS is also a place for the iliofemoral ligament in humans that prevents the hip joint from overextending.

Apes:

There is no S-shaped curve visible at the iliac crest and the crest projects laterally. Therefore, the iliac fossa orients anteriorly and the gluteal surface projects posteriorly. This orientation keeps the trunk in an upright position during sitting or squatting. In case if they want to walk bipedally, the Glutei

medius and minumi muscles medially rotate the flexed thigh at the hip – while in humans they abduct the extended thigh.

The long iliac crest is an adaptation to climbing. Latissimus dorsi origins from here and inserts into the humerus. Because this is one of the most important climbing-muscles, the longer the iliac crest is, the better aid is in climbing.

The auricular surface and the iliac tuberosity are smaller in apes. It is mainly because of the fact that their weight does not focus on their pelvic region and lower limbs (hind limbs).

    1. Ischium

Humans:
Ischial tuberosity is an attachment for the hamstring muscles (Biceps femoris, Semitendinosus, Semimembranosus and Adductor magnus hamstring part). At a superior pressure during the bipedal posture, the posterior part of the sacrum elevates, and pulls upwards the ischial tuberosity. The ischial tuberosity – which is located just below the great sciatic notch – reflects the bipedalism.

Apes:

Long ischium.

The ischial tuberosity is wider in apes than it is in humans and it does not look so " pulled-up" in apes. The ischial tuberosity lacks the facets for the hamstring and adductor muscles.

    1. Pubis

Humans:

Pubic crest and pubic tubercle are important in bipedal locomotion as well, because the pubic crest serves as an attachment for Rectus abdominis that supports the guts and pubic tubercle is associated with the inguinal ligament, which helps in supporting the trunk.

The iliopubic eminence is the divider of the Anterior Superior Iliac Spine (ASIS) and the AIIS. Here takes place the iliopsoas muscle that helps in flexing the hip and supporting the upper body on the hip joint.

Apes:

Apes lack all these human characteristics at the pubis: they do not have a pubic crest nor tubercle, and because their pelvis orient differently, their ilipsoas groove and iliopubic eminence are missing.

The pubic symphysis in apes are usually fuses together, while it only rarely happens in humans.

1. Acetabulum

Humans:

The orientation of the acetabulum is inferior-lateral-anterior. The superior margin of acetabulum must cope with the biggest weight/pressure, it developed a very thick cartilage, so did the head of the femur. This is called laubrum. Very strong, Z-shaped, ligaments are present here. The depth of the acetabulum can tell us a lot about the mobility of the hip joint. If the acetabulum is shallow, it reflects more flexibility. The acetabulum in humans

is shallow compared to many of the African apes (but chimpanzees), but it is deep compared to the orang-utans.

Apes:

The ligaments are weaker than in humans.

> 1. Sacrum, coccyx

Humans:

The human sacrum contains five fused vertebrae averagely. However, it can be varied between four and six. The coccyx stands from four fused vertebrae, usually.

The sacrum in humans is wider than in apes and it is not so long as an ape sacrum. This unique shape is very distinctive regarding to bipedalism. The wider sacrum means more distance between the sacroiliac joint, which helps in transferring the weight and the pressure from pubic symphysis. A wider distance at this joint also means a larger birth-canal.

Apes:

In apes and monkeys the number of the fused vertebrae of the sacrum and coccyx may vary from species to species.

The shape of the sacrum is not so wide and more elongated. It reveals that they do not support so huge weight on their pelvic region as do the humans.

> 1. Femur

Humans:

The human femur is longer than that of an ape.

The lateral condyle in humans is more prominent.

The bicondylar surface is larger in humans than in apes. It is because of the centre of gravity of the body.

Apes:

Medial condyle is larger in apes.

More flexibility at the hip joint.

B, Actions of muscles at the knee and ankle joints during bipedal locomotion. Observed features in ancestral hominid fossils.

Extensors of the leg at the knee joint:

- Tensor fasciae latae
- Quadriceps femoris muscles (Rectus femoris, Vasti lateralis, medialis, intermedius)

Flexors of the leg at the knee joint:

- Sartorius
- Gracilis (also can assist in medial rotation)
- Hamstring muscles (Biceps femoris {it is also the lateral rotator of the knee joint}, Semimembranosus, Semitendenosus {they also medially rotate the knee joint when the leg is flexed}

- Gastrocnemius

- Popliteus (weak flexor, but it is a medial rotator of the leg)

- Plantaris

Muscles that act at the ankle (talotibial) joint:

- Tibialis anterior (dorsiflexion)

- Extensor hallucis longus (dorsiflexion)

- Extensor digitorum longus (dorsiflexion)

- Peroneus tertius (dorsiflexion)

- Peroneus longus and brevis (plantar flexion)

- Gastrocnemius (plantar flexion)

- Soleus (plantar flexion)

- Plantaris (plantar flexion)

- Flexor digitorum longus (plantar flexor)

- Tibialis posterior (plantar flexor)

Fossil records:

Australopithecus afarensis:

The tibia and the fibula are quite interesting. We can observe adaptations to both arboreal and bipedal signs. This is called mosaic morphology.

The examined specimens: AL 129-1b, AL 288-1aq and AL 333x-26). Ape-like elements: short border to the lateral condyle, in the first two specimens, there are features that general in the apes (under the epicedial there was the " hollowed-out appearance") which means that the Tibialis posterior attached to the lateral side of the tibia instead of the posterior side. Other

attachments – such as semimembranosus and gracilis are also rather ape-like.

Nevertheless, other A. afarensis specimens show bipedal characteristics:

Distal articulation surface of the tibia (the angle of the ankle joint and the tibia and fibula). But, yet again, there are ape-like features also on the distal part of fibula: the direction of the articular facet, (orients distally rather than medially as in the modern humans), they have an anteriorly oriented peroneal groove on their fibulae while it faces laterally in modern humans. The A. afarensis Lucy (AL 288-1) also owns these mosaic morphological features: the posteriorly oriented distal tibial angle shows similarities with the apes, while in other afarensis specimens the angle is lateral, which is a human feature. The carrying angle at the knee joint also shows more similarities to the modern human specimens. This can reveal an individual arboreal habit of Lucy, and a more developed bipedalism in the other specimens.

Homo habilis:

The H. habilis specimens do not cause so many arguments than the australopithecines. They have more human like features in their lower legs and less ape-like features. Although, they do not lack these features (rounded anterior border of the tibia, in humans the insertion area of the Flexor digitorum longus is bigger than that of the tibialis posterior – it is quite the opposite in the habilis. The attachments of other muscles – soleus, popliteus – show sort of a transition between apes and humans, etc.).

The Neanderthals:

The fibula and the tibia are very robust, but bear the human characteristics.

Q2, Evolution of the early hominid foot

The main characteristics of the human foot include the presence of the arches, the calcaneocuboid joint, the proportions of the major parts of the foot, the shape of the ankle-joint and the fact that the hallux cannot be opposed.

The arches in foot are quite unique, the apes do not have arches (they have only one arch, the transverse arch). In humans, apart from the plantar aponeurosis, there are other ligaments that aid in having these arches: the spring ligament, the short plantar ligament and the long plantar ligament. The length of the distal digits of the toes are much shorter in humans than in apes, however, the size of the big toe is about the same.

The foot of Australopithecus afarensis, such as in the leg, shows mosaic morphology. It means that certain features are similar to the modern humans, while others share similarities with the apes.

The human-like morphology: the talus – which also has both human and ape characteristics – together with the tibia and fibula, shows a more human like joint at the talotibia. Although, the shape of the talus is rather ape-like. Other signs that reveal a more human appearance in the afarensis foot are the talar trochlear shape, the direction of the ankle joint's axis and of the Flexor hallucis longus's groove which suggest that the movements of the afarensis were very similar to those of the modern humans.

The shape of the fifth metatarsals reveal a very similar ability of dorsiflexion as it is present in modern humans. Their navicular bones in appearance are more ape-like, but the presence of the groove of the spring ligament proves that they might have similar arches than the modern humans have. The possibility of the bipedal locomotion can be traced down also by the human-like lateral cuneiform, although, its hook makes it look more ape like.

Nevertheless, the ape-like curves of the phalanges suggest that they might be arboreal. The calcareous also have both human and ape like features, the medial cuneiform is rather ape like, so is the first metatarsal's rounded head.

The foot of Paranthropus robostus has several human-like characteristics. These features are the following: the hallux probably was adducted unlike in the apes where the big toe is rather abducted, the plantar ligaments suggest similarities to the human foot, the first metatarsal suggests that it bore more weight than the apes because of its robust appearance, but other features on the first metatarsal bone reveal ape-like features, too. According to the article of Susman and Brain (1988, mentioned in Aiello and Dean), it is very likely that the Paranthropus robostus was bipedal but in a different way than the modern humans.

The foot of the Homo habilis:

The biggest argument is caused by the tarsal bones of a young Homo habilis (OH 8 from Olduvai Gorge), because some researchers do not think that the human characteristics of this specimen's foot bones are good enough to be classified as humans. The elements of the foot show the signs of the bipedalism – even those agree with this who do not think that this specimen

deserves to be included into the Homo genus – but, perhaps, in a completely different way as it is seen in the modern humans. Another talus bone, the KNM-ER 813 from Koobi Fora, has less problems with its classifications, as it shows more similarities to the talus of the modern humans. The first metatarsal is the most robust, and the fifth metatarsal bone of the OH 8 is the second, while in apes the fifth metatarsal bone is the weakest. The size of the foot length of the OH 8 is also more similar to the structure of the human foot.

The fossil record suggests that the opposability of the big toe of OH 8 is not present, but the adduction of it can be observed. The ability of grasping is also very likely, though.

The foot of the Neanderthals:

Interestingly, the evidences reveal that the opposability of the big toe might be somewhere between the modern humans and the living apes. Others deny it, because of the more human characteristics in the tarsometatarsal joint, which can be varied on a great scale even in modern humans. Typical Neanderthal features are the short proximal phalanx of the big toe and the short neck of the talus.

The possible signs of the bipedalism in the fossil evidences:

Apart from the bones of the foot other skeletal remains can reveal the erected body posture and the possible bipedal walking habits. A relative longer arm may be a sign of the arboreal life-style, or partly arboreal living circumstances. Nevertheless, Lucy has relatively short fingers, not ape-like,

long ones (JOHANSON-EDEY 1990) The shape of scapula and the orientation of the glenoid fossa also can help to answer this question. A small fragment of an Australopithecus afarensis scapula suggests that its owner had a more ape-like in this question, than human like. In apes the glenoid fossa faces towards the cranium and this feature can be observed also in case of this fragment. A more complete scapula – which derives from an A. africanus (Sts 7) – can tell us more details about the possible functions of the pectoral girdle. This scapula looks very similar to the scapula fragment of the afarensis specimen (AL 288-1l), and they both bear more similarities to the pectoral girdle of the apes, especially to the orang-utans. The ribcage has more ape-like characteristics in its appearance. The shape of the vertebral column, however, widens distally (the lumbar vertebrae are the widest) as it appears in humans, which is another possible sign of the bipedal locomotion. The pelvic girdle shows more evidences for the mosaic morphology yet again. The iliac crest is rather human-like, although it is more elongated laterally and the acetabulum orients more anteriorly. Perhaps this is the reason why A. afarensis has a relatively very long femoral neck. The iliac blades direct interiorly, as well. The shape of the sacrum is very wide – another human-like sign, however its posterior segment is not as curved anteriorly as it is in the modern humans.

According to Johanson (JOHANSON-EDEY 1990), Lucy's pelvis is adapted to the bipedal locomotion as well as to the possibility to give life to large-headed babies, as her pelvis is so wide.

All these features make likely that the A. afarensis could walk bipedally, but in a more complicated way. The anteriorly faced acetabulum could result a

very heavy bipedalism. On the femoral head, we can observe a stronger fovea than it is on the femoral head of the modern human.

In quadrupeds the tibial tuberosity is more rounded and less sharp. The " sharpness" of the tibial tuberosity is a more human (or bipedal) characteristic. This sharpness can be observed in Lucy, although her tibia looks more robust compared to the very tall juvenile, the Turkana boy (H. erectus).

In proximal femur of the Australopithecines, there are about the same number of similarities to humans (the varied presence of the intertrochanteric line and the Obturator externus groove) than to chimpanzees (the small femoral head and the non-flaring greater trochanter) and the unique features (long femoral neck, compressed femoral neck-cross section), the more similarities to humans in the question of the distal femur (the high/very high bicondylar angle, the elliptical shaped lateral epicedial profile), and its own unique phenomena in the epiphysis shape and symmetry, but the femoral shaft's more similarity to the chimpanzees gives us a very eclectic impression about the possible locomotion of the Australopithecines.

As I wrote in the 1B question, the foot of the Australopithecines show very varied picture as well. It reveals both human and ape like features – such as almost everything else in the Australopithecus skeleton. The more human like elements of the foot include the human-like ankle joint, the ability of a better dorsiflexion, the expanded base of the fifth metatarsal, the wide calcaneus and the presence of the longitudinal arch.

On the other hand, there are several ape-like characteristics, like the shape of the phalanges, the tuberosity of the calcaneous has an oval orientation, also has a huge peroneal tubercle, the already mentioned ape-like shape of the " hook" of the lateral cuneiform bone, and the rounded head of the first metatarsal.

Summarising, the mosaic morphology in the Australopithecines are very strongly present, they share similarities to the humans, as well as to the apes, but they also developed own features. It is very likely that they were adapted to the bipedal locomotion, but not in a modern human way.

The essay has been written by using the following books as a guide-line:

Aiello and Dean, 2006: An Introduction To Human Evolutionary Anatomy, reprinted in 2006, Elsevier Academic Press, London

The materials during the Demo-sessions

And

JOHANSON-EDEY, 1990: Lucy – The Beginnings of Humankind, Penguin Books, London, 1990.