BIOLOGICAL EVOLUTION
Human skeletal changes due to bipedalism

Limbs

- An increase in leg length during the evolution of bipedalism changed how leg muscles functioned in upright gait.
- In human's the "push" for walking comes from the leg muscles acting at the ankle.
- A longer leg allows the use of the natural swing of the limb so that, when walking, humans do not need to use muscles to swing the other leg forward for the next step.
- human forelimbs are not needed for locomotion, they are instead optimized for carrying, holding, and manipulating objects with great precision.
- Having long hind limbs and short forelimbs allows humans to walk upright.
- humans have femurs that are slightly angled medially from the hip to the knee. This adaptation allows our knees to be closer together and under the body's center of gravity. This permits human to lock their knees and stand up straight for long periods of time without much effort from the muscles.
- More slender limbs

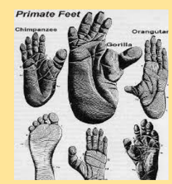
Knee

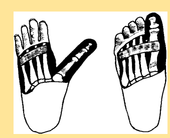
- *Human knee joints are enlarged for the same reason as the hip – to better support an increased amount of body weight.*
- *The changing pattern of the knee joint angle of humans shows a small extension peak, called the "double knee action.*
- *Double knee action decreases energy lost by vertical movement of the center of gravity.*
- *Humans walk with their knees kept straight and the thighs bent inward so that the knees are almost directly under the body, rather than out to the side, as is the case in ancestral hominins.*
- *This type of gait also aids balance.*

The Foot

- The human foot evolved to act as a platform to support the entire weight of the body, rather than acting as a grasping structure, as it did in early hominins.
- Humans therefore have smaller toes than their bipedal ancestors.
- humans have a foot arch rather than flat feet
- When non-human primates walk upright, weight is transmitted from the heel, along the outside of the foot, and then through the middle toes while a human foot transmits weight from the heel, along the outside of the foot, across the ball of the foot and finally through the big toe. This transference of weight contributes to energy conservation during locomotion.
- an arch, an energy-absorbing feature of feet that helps protect bones.
- Humans, uniquely among primates, have two arches in their feet, longitudinal and transverse, which are composed of the midfoot bones and supported by muscles in the sole of the foot. During bipedal locomotion, these arches perform two critical functions: leverage when the foot pushes off the ground and shock absorption when the sole of the foot meets the ground at the completion of the stride. Ape feet lack permanent arches, are more flexible than human feet and have a highly mobile large toe, important attributes for climbing and grasping in the trees. None of these apelike features are present in the foot of *A. afarensis*.

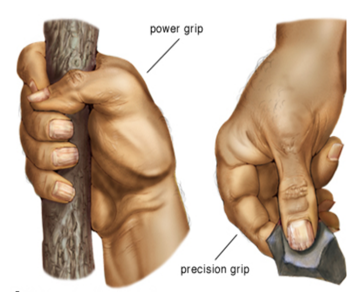
1. *Carrying Angle*
   - *Human feet are placed under the spine so that walking is carried out without swaying*
   - *Apes- Feet are below the outer side of the pelvis so there is a sideways swaying motion when walking.*
2. *Shape.*
   - *Humans- the weight is placed on the outer edge with the inner side elevated into an arch. The convex arch under the foot acts like a spring under tension and allows for a transfer of weight down the foot to the big toe, providing a shock absorber effect and a spring that facilitates long distance travelling.*
   - *Apes – have no arch*
3. *Big Toe*
   - *Humans - The foot has changed to become a platform, with short toes alongside the big toe, which is forward thrusting (non-opposable) to provide the final thrust against the ground to propel the body forward. The foot has lost all grasping ability.*
   - *Apes – is divergent (slightly opposed to allow for grasping action and anchorage in toes.*





Hands

- A fully opposable thumb gives the human hand its unique power grip (left) and precision grip
- Neandertals – exceptionally powerful grip, suggested by large apical tuft of the terminal phalanges.
- Differed from modern man in the terminal phalanx of the thumb was almost as long as the proximal one, whereas in modern humans it is significantly shorter
- Digits flexible and finger bones are straight.

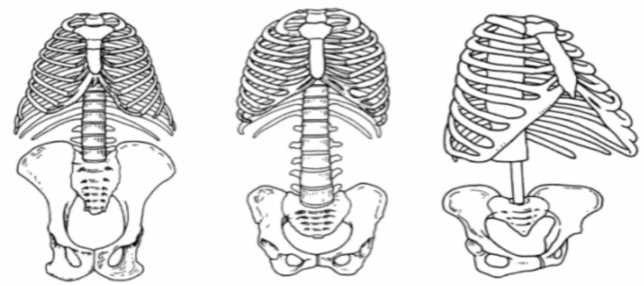


Pelvis – Shape

Humans – broader,shorter (bowl-shaped) pelvis supports an upright torso by giving greater stability. The stress of the weight of the trunk is reduced by having it transmitted directly to the legs. This improves balance, enables support of the upper body and enlarges the vulgus angle. The strong bowl shaped pelvis bones also increases the surface for the attachment of large buttock muscles (gluteus maximus). The pelvis also supports internal organs. The wide pelvis allows the birth of babies with large skulls.

Apes – Longer and narrow pelvis. The greater length provides greater attachment area for gluteus medias muscle facilitating the pelvic tilting in quadrupedal motion and gives greater support for abdominal organs.

Ribs

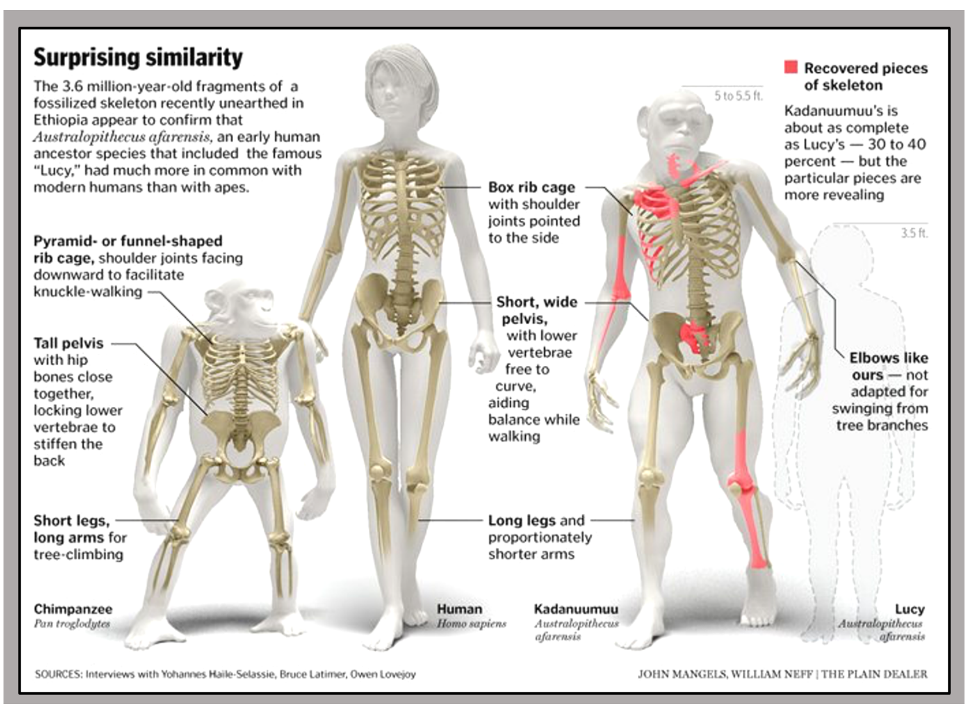


Humans - Rib cage has been flattened from front to back, so that chest centre of gravity is closer to the spine, minimising tendency to fall forward and improving balance.
Apes – chest is flattened from the sides – this creates a deeper chest.

- Vertebral bodies moved inwards into the thorax, which became slightly shorter and went from a bell-shaped appearance to that of a flatter barrel shaped one. This resulted in respiratory muscle mechanics that were more efficient for upright posture
- Modification to the chest muscles, as bipedalism developed, allowed for more breath control, which lead eventually to speech.

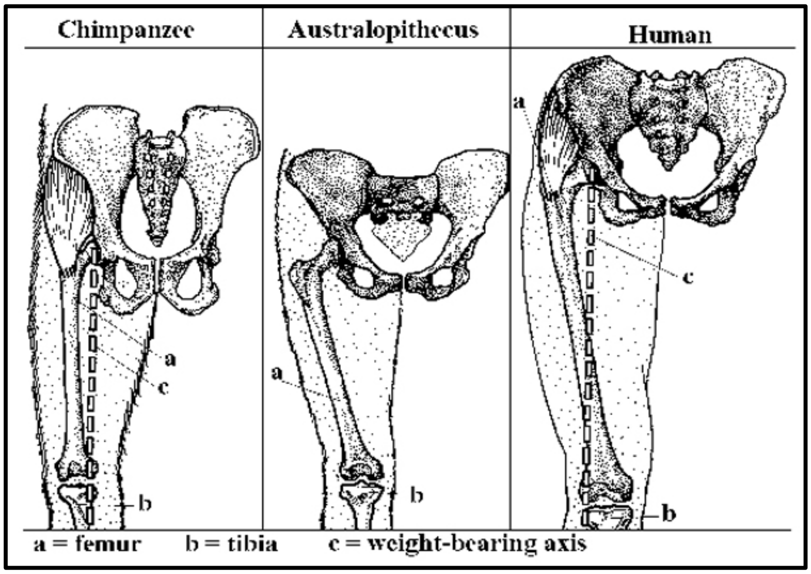
Hip

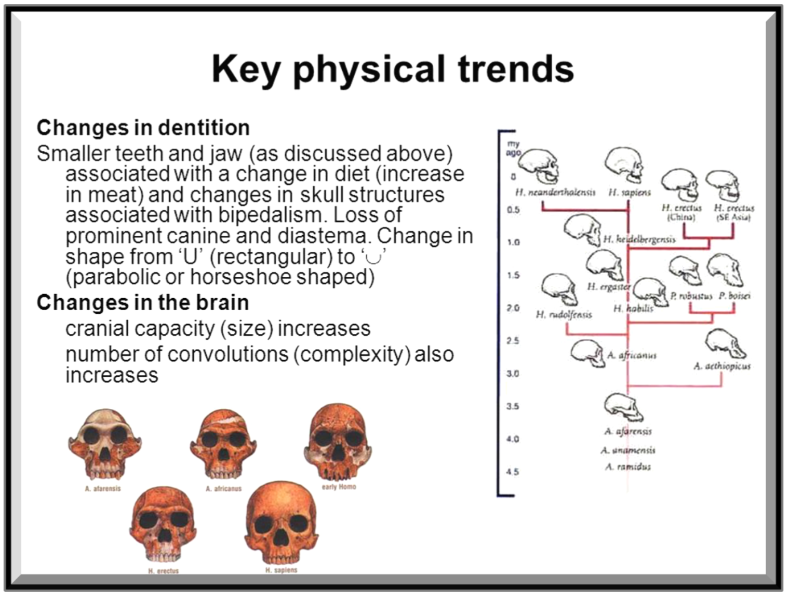
- Modern human hip joints large and provide better support the greater amount of body weight passing through them, as well as having a shorter, broader shape.
- This alteration in shape brought the vertebral column closer to the hip joint, providing a stable base for support of the trunk while walking upright.
- bipedal walking requires humans to balance on a relatively unstable ball and socket joint, the placement of the vertebral column closer to the hip joint allows humans to invest less muscular effort in balancing.
- Change in the shape of the hip may have led to the decrease in the degree of hip extension, an energy efficient adaptation.



Valgus angle

- *Humans –The human femur is longer and slants inwards from the hip. This brings the knee joints closer together and assists the upper body to be positioned above the centre of gravity for walking. This is called the valgus angle. Humans have an increased valgus angle, so better balanced when walking. Humans can fully extend their legs.*
- *Apes – The femur descends vertically from the pelvis with no slant i.e. the valgus angle=0. This enable good swinging motion (brachiating) when moving through trees. Apes are unable to fully extend their legs.*



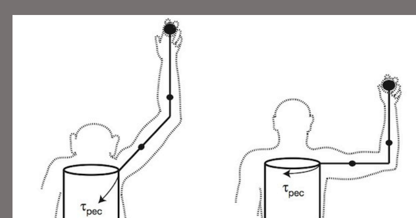


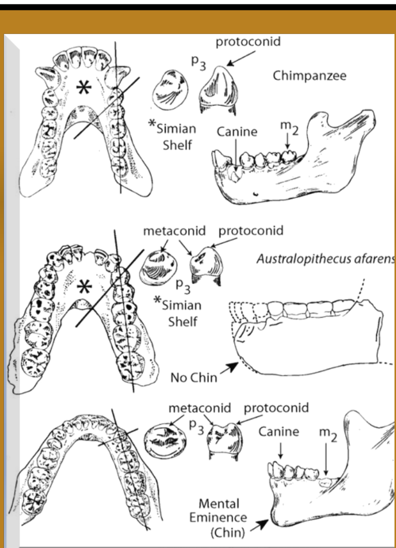
SCAPULA

Our lower, outward-facing shoulders (right), as compared to chimps (left), allow us to use our pecs to rotate our arms farther back relative to our torsos, generating more torque (represented by τ) and serving as one of the anatomical features that give us the ability to store elastic energy in our tendons and ligaments. Image via Nature/Roach et. al.

The evolution of the anatomical traits that set our throwing skills apart from chimps can be traced to roughly two million years ago, the researchers say, when our ancestors still belonged to a different species (*Homo erectus*). While it's impossible to know exactly which selective pressures led to their evolution, the researchers have an idea. "We think that throwing was probably most important early on in terms of hunting behavior, enabling our ancestors to effectively and safely kill big game," Roach said. "Eating more calorie-rich meat and fat would have allowed our ancestors to grow larger brains and bodies and expand into new regions of the world—all of which helped make us who we are today."

Eventually, the development of technologies that made hunting easier—starting with bows and arrows, then nets, blades, and eventually firearms—made our skill at hurling objects largely unnecessary. But if the authors are correct, our capacity for such invention stems from the evolutionary advantage given by high-speed throwing





Brain

- Apes have a smaller brain than humans 450cm^3 c.f. 1400cm^3
- The human brain has a well-developed cerebral cortex, which is involved with higher level thinking skills, memory, language and speech
- Humans have a better developed cerebellum than apes (this organ is involved in balance and the coordination of muscles. This is important because humans are bipedal which involves continual balancing, and they also need fine muscular coordination for their highly developed and accurate hand and finger movements.

Skull

- The human skull is balanced on the vertebral column.
- The foramen magnum is located inferiorly under the skull, which puts much of the weight of the head behind the spine.
- the flat human face helps to maintain balance on the occipital condyles - Bones supporting skull on vertebral column.
- the erect position of the head is possible without the prominent supraorbital ridges (brow ridges – hence a decrease in size) and the strong muscular attachments found in apes.
- Decrease in size of zygomatic arch, sagittal crest and nuchal crest.
- A small nuchal crest is required in humans because of there is a reduction of the muscles behind the vertebral column as the centre of gravity lies behind the spine. In apes, the centre of gravity is in front of the vertebral column so nuchal muscles must be very large and powerful to support the quadrupedal head and preventing it from sagging forward.
- Along with the evolution of the brain, the skull changed – rounded brain case (enlarged brain) with reduced sites for muscle attachment, especially those used for chewing and aggressive facial displays which were no longer called for.
- Apes have flatter brain cases.
- The changes in the skull were presumably due to an upright posture and diet changes. The larynx didn't drop for over another 1.5 million years.

Teeth

- Less dimorphism evident in teeth – eg decrease in size of canines (lead to males being more co-operative and used less as display of aggression.)
- Thinner enamel on teeth
- Lower canines show no evidence of honing – the sharpening of tooth edges against each other
- Non-honing is one of the first hominin features.
- In humans, the teeth are smaller in size and more uniform, suiting their omnivorous diet and softer cooked food. They have no distema.
- Teeth are arranged in a V like arch cf U shape of apes.

Larynx

- change in position of larynx,
- Newborn children's larynges are similar in structure to those of chimps and other primates. At 3 or 4 months, the larynx begins descending –cf. just before onset of babbling
- The larynx is high, as is the hyoid bone which helps to support the tongue and serves as an attachment point for several muscles that help to elevate the larynx during swallowing and speech.
- The hyoid bone is suspended above the larynx where it is anchored by ligaments to the skull.
- **Marks where ligaments were attached are seen in fossils**
- 3 or 4 months- begins descending –cf. just before onset of babbling
- L shaped, two-tubed vocal tract permits the articulation of the 3 point vowels, [i a u].
- Evolutionary disadvantage choking – therefore language must have been big advantage.

Jaw

- Small jaw, as teeth are smaller in humans.

Brain

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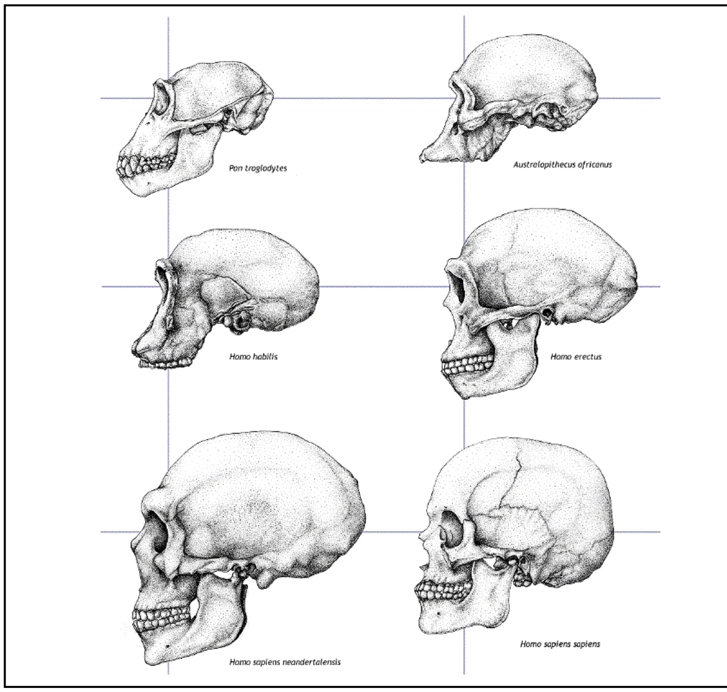
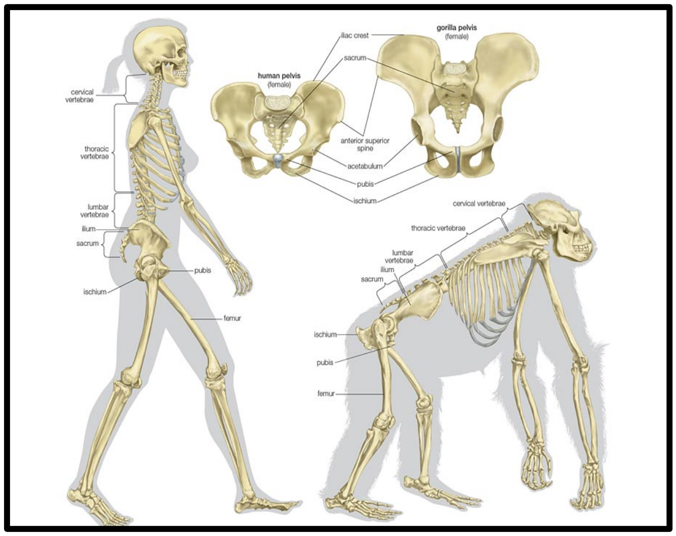
- As early humans faced new environmental challenges and evolved bigger bodies, they evolved larger and more complex brains.
- Large, complex brains can process and store a lot of information. That was a big advantage to early humans in their social interactions and encounters with unfamiliar habitats.
- Over the course of human evolution, brain size tripled. The modern human brain is the largest and most complex of any primate.
- A large brain capable of processing new information was a big advantage during times of dramatic climate change.
- Endocasts are replicas of the insides of early and modern human braincases. They represent the size and shape of the brains that once occupied the braincase.
- Humans have far more white matter in the temporal cortex, reflecting more connections between nerve cells and a greater ability to process information
- **Encephalization** is defined as the amount of brain mass exceeding that related to an animal's total body mass
- Quantifying an animal's encephalization has been argued to be directly related to that animal's level of intelligence.
- Anthropological studies indicate that bipedalism preceded encephalization in the human evolutionary lineage
- Intelligence is not just a function of brain size: relative brain size appears to be more important (brain size compared to body size). Modern humans have a brain volume three times larger than that predicted for an average monkey or ape with our body size. Another important factor is the organization of the brain, evident in the development of the areas concerned with spoken language. Two areas of the brain have become highly developed in modern humans:
    - Broca's area concerned with speech production
    - Wernicke's area concerned with comprehension of language –spoken and written.

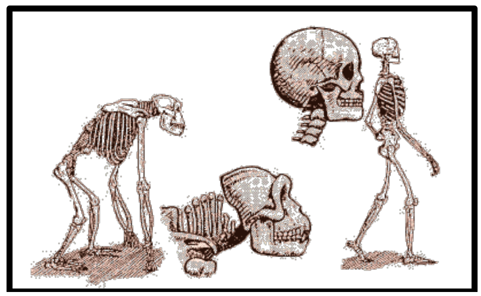


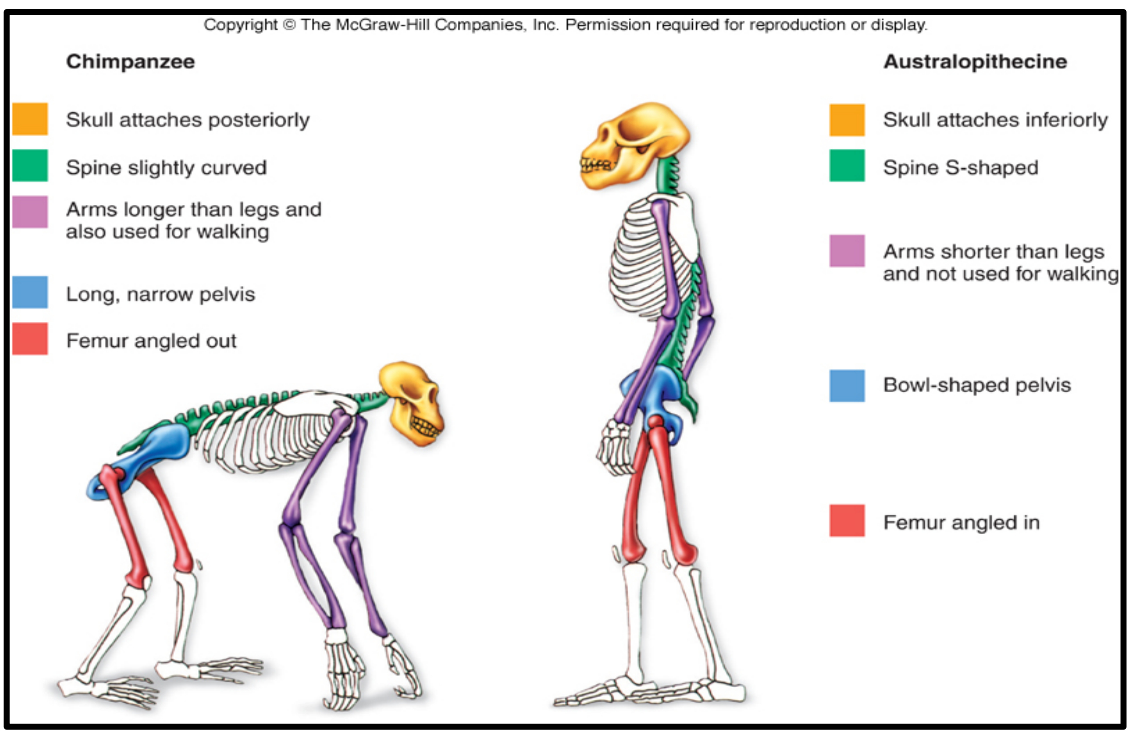
Vertebral column

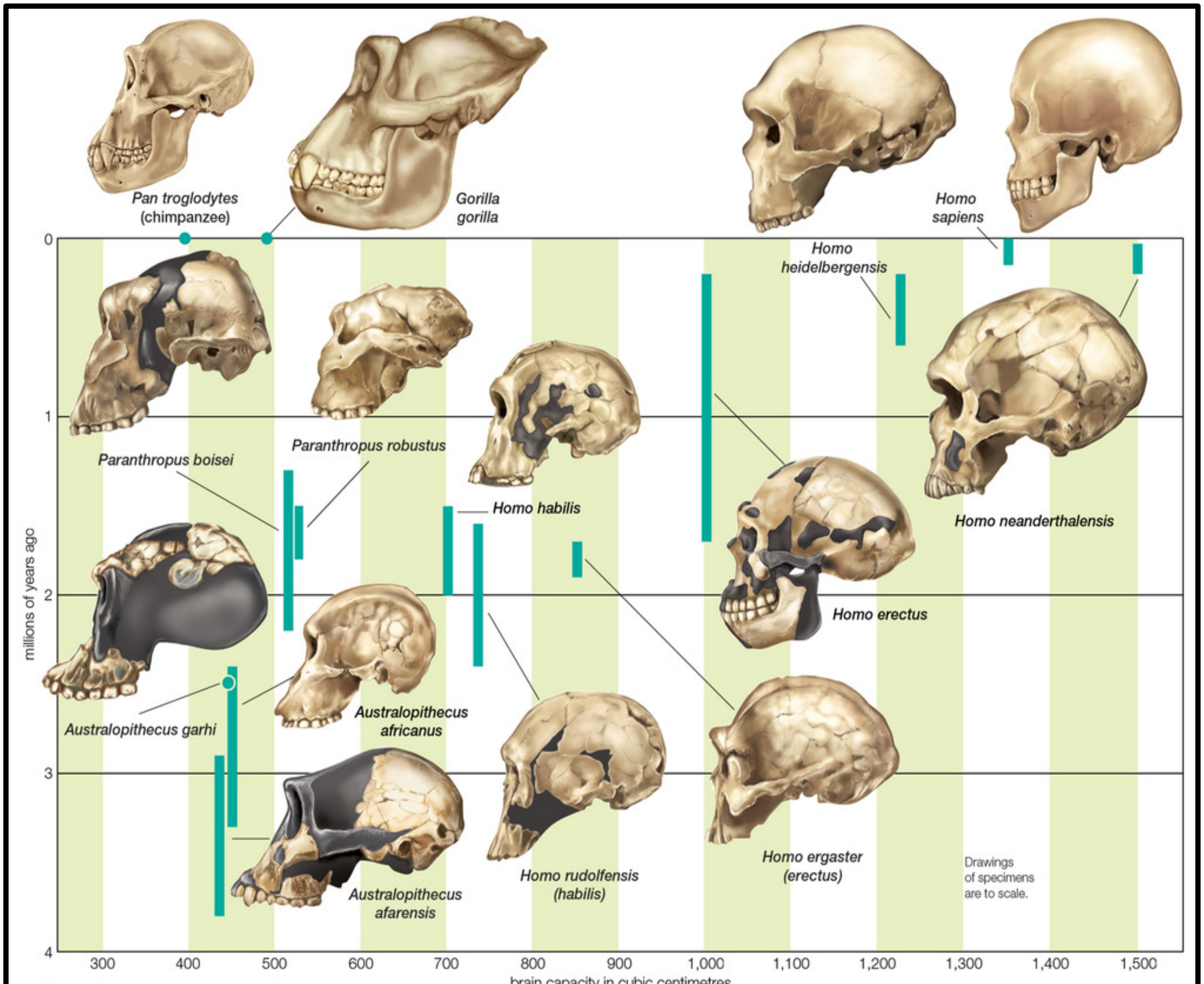
Shape –

- Humans – has a S-shaped curve to provide support and balance for the upright biped as the weight of the chest sits almost directly above the joint between the spine and pelvis.
- The vertebral column of humans takes a forward bend in the lumbar (lower) region and a backward bend in the thoracic (upper) region.
- Without the lumbar curve, the vertebral column would always lean forward, a position that requires much more muscular effort for bipedal animals.
- With a forward bend, humans use less muscular effort to stand and walk upright.
- Together the lumbar and thoracic curves bring the body's center of gravity directly over the feet.
- Changes affecting the relationship between the skull and the spinal column, together with an improved laryngeal structure (allowing vocalization), resulted in a soft and elongated oropharynx, with part of the tongue integrated into its anterior wall, and thus in an increased tendency towards upper airway collapse during sleep.
- Vertebral bodies moved inwards into the thorax, which became slightly shorter and went from a bell-shaped appearance to that of a flatter barrelshaped
  one. This resulted in respiratory muscle mechanics that were more efficient for upright posture.








Pan troglodytes (chimpanzee)
Gorilla gorilla
Homo sapiens
Homo heidelbergensis
Paranthropus boisei
Paranthropus robustus
Homo habilis
Homo neanderthalensis
Homo erectus
Australopithecus garhi
Australopithecus africanus
Australopithecus afarensis
Homo rudolfensis (habilis)
Homo ergaster (erectus)
Drawings of specimens are to scale.
millions of years ago
0
1
2
3
4
300
400
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700
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900
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1,100
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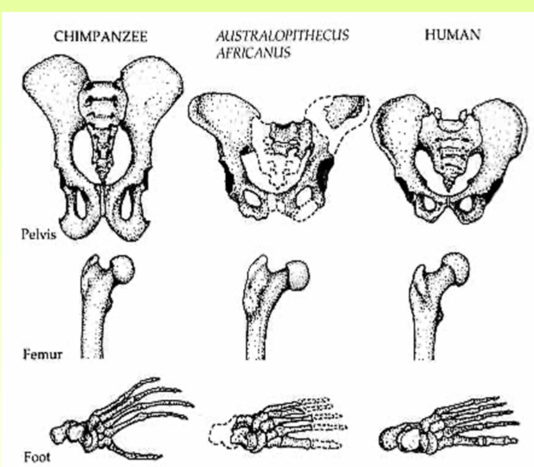
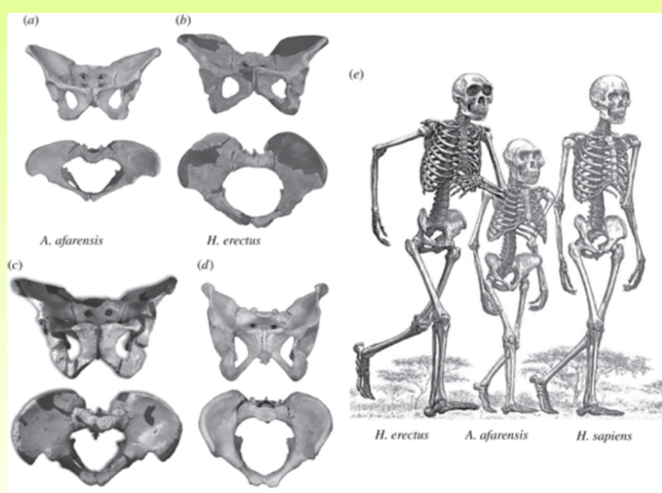
brain capacity in cubic centimetres


CHIMPANZEE
AUSTRALOPITHECUS AFRICANUS
HUMAN
Pelvis
Femur
Foot


(a)
(b)
A. afarensis
H. erectus
(c)
(d)
H. heidelbergensis
H. sapiens
(e)
H. erectus
A. afarensis
H. sapiens

SELECTION PRESSURES AND ADVANTAGES. What were the selection pressures that drove hominin evolution?

1. **Environmental pressures**
   - Environmental changes normally precipitate evolutionary changes. The major changes that were happening worldwide between 5.5 and 0.1 MYA were:
     i. Tectonic changes causing the uplift of the Tibetan Plateau.
     ii. Changes in ocean circulation
     iii. A cooler and drier earth
   - In Africa, the rainforests may have receded, being replaced by more savannah-like grasslands, and then advanced again, with the cycle being repeated. There may have also developed a more variable mosaic environment made up of forest, shrubland and grassland. These relative rapid environmental changes may have put selection pressures on our tree-dwelling ancestors, perhaps because there was less food available or less shelter.
   - Studies of fossils show that changes to different body systems occurred at different times. The change to towards bipedalism came first, then dental changes, then much later development of a large brain.

2. **Bipedalism Advantages**
   - Bipedalism gives many selective advantages:
     a) Bipedalism is more energy-efficient at walking speed than knuckle-walking, although it is less efficient than running. Bipedalism would have been better for travelling long distances to the next food force as food becomes harder to obtain.
     b) Bipedalism frees up the hands while walking. Hands could be used for carrying offspring which may have been born with feet less able to hang on to the mother. The mother may also have had less fur. It is not possible to know when humans became naked apes. Hands could also be used for carrying or using tools and for carrying food back for the others. The freeing of hands would have allowed the development of a more precise grip. All these advances, would help to accumulate the pace of evolution towards bipedalism.
     c) Bipedalism helps keep the body cool. Less surface area is directly hit by the sun during the middle of the day when walking upright and there is an increased flow of air around the body for cooling.
     d) Bipedalism gives greater height. With the head higher, predators and food are more easily seen. The higher stance may also be more frightening to predators.

3. **Height Advantage**
   - The first bipedal hominins were about the size of apes but gradually the size of hominins increased. This may have been because a greater height gave individuals and advantage because they could see food and predators more easily and they were stronger.

4. **Dentition Pressure**
   - The canines of hominins were reduced in size and the molars became larger which were perhaps adaptations to the harder vegetable food such as nuts and grains that the hominins were now having to eat.

5. **Brain Size and Development Advantages.**
   - The start of changes in brain size and organization were correlated with the first stone tool. Developments about 2.5 MYA and further innovations from about 1MYA onwards.
   - The selective advantage involved might be that once the hands were free then any individual who had a more innovative brain to devise and use technology such as tools, had a survival and therefore reproductive advantage.
   - Those hominins with larger brains and better thinking and communication skills would be able to engage in planning complex co-operative tasks which would also increase their chances of leaving offspring.

The Evolution of the Human Pelvis

- The fossil record of our evolutionary history, during which mechanical requirements for locomotion, childbirth and thermo- regulation often conflicted.
- In our earliest upright ancestors, fundamental alterations of the pelvis compared with non-human primates facilitated bipedal walking.
- Further changes early in hominin evolution produced a platypelloid birth canal in a pelvis that was wide overall, with flaring ilia.
- This pelvic form was maintained over 3–4 Myr with only moderate changes in response to greater habitat diversity, changes in locomotor behaviour and increases in brain size.
- It was not until Homo sapiens evolved in Africa and the Middle East 200 000 years ago that the narrow anatomically modern pelvis with a more circular birth canal emerged.
- This major change appears to reflect selective pressures for further increases in neonatal brain size and for a narrow body shape associated with heat dissipation in warm environ- ments.
- The advent of the modern birth canal, the shape and alignment of which require fetal rotation during birth, allowed the earliest members of our species to deal obstetrically with increases in encephalization while maintaining a narrow body to meet thermoregulatory demands and enhance locomotor performance
- the human pelvis reveals the selective priorities acting on hominin anatomy at different points in evolution.

Humans are bipeds. . The pelvis in humans has undergone radical changes in orientation and shape compared to other anthropoid primates. Many of these changes serve to adapt our muscle orientations to the requirements of upright stance and bipedal locomotion.

The most significant changes to the pelvis in humans compared to other apes are:

Ilium-The ilium (top portion of the innominate bone) in humans is shorter and broader. It curves around the trunk, whereas in apes it is flat against the back of the trunk.

Greater sciatic notch-This is very wide in apes, a function of their long, tall ilium. In humans, the notch is actually a notch.

Anterior inferior iliac spine-This feature is prominent in the hominin pelvis, absent or small in apes.

Sacrum-In humans, the sacrum is broad and short, in apes it is narrow and long, usually incorporating 6 or more sacral vertebral bodies.