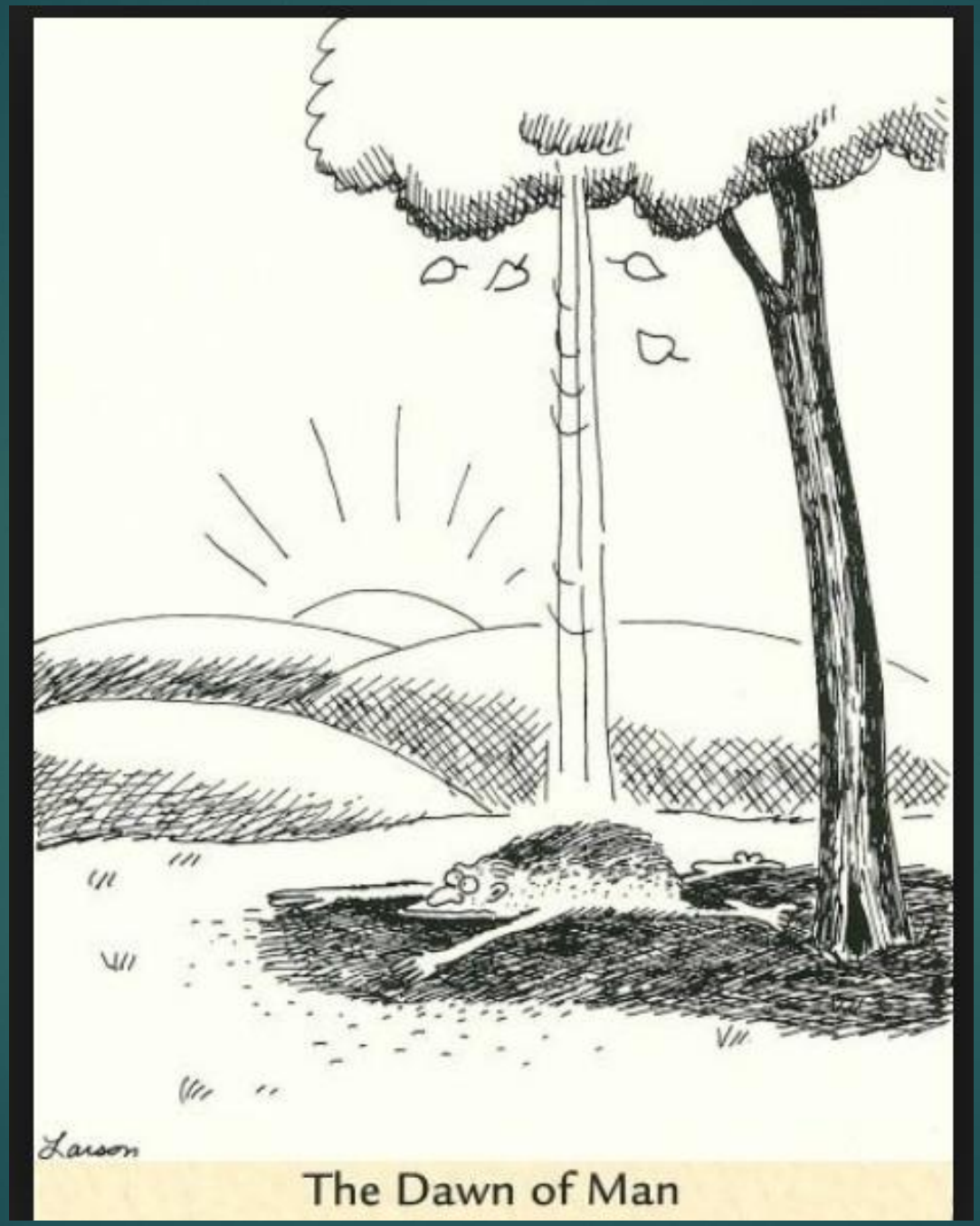
Earliest Hominins

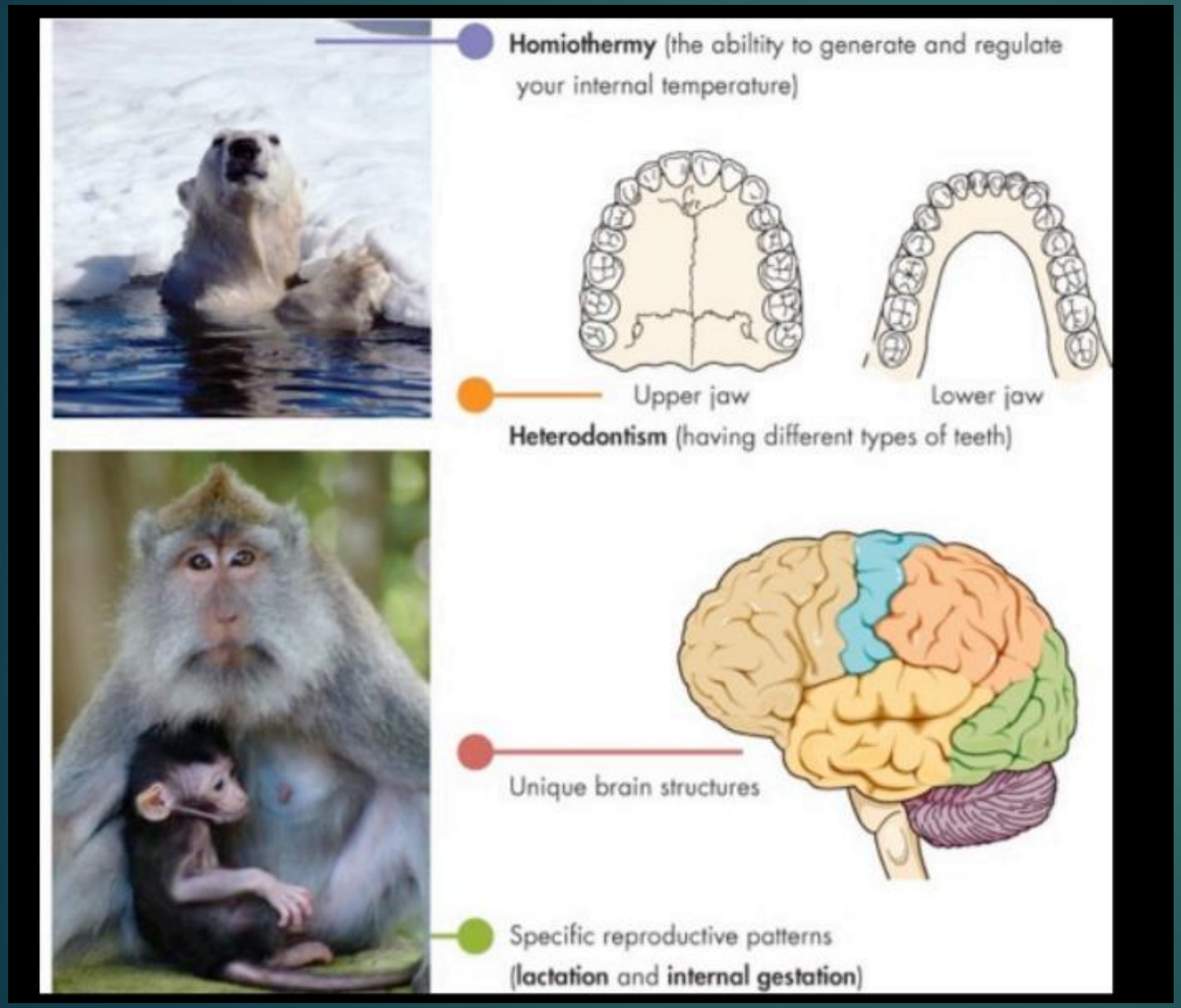
CHARLES J VELLA, PHD

JULY 25 2018



This is latest theory of how Lucy died!

We are Mammals



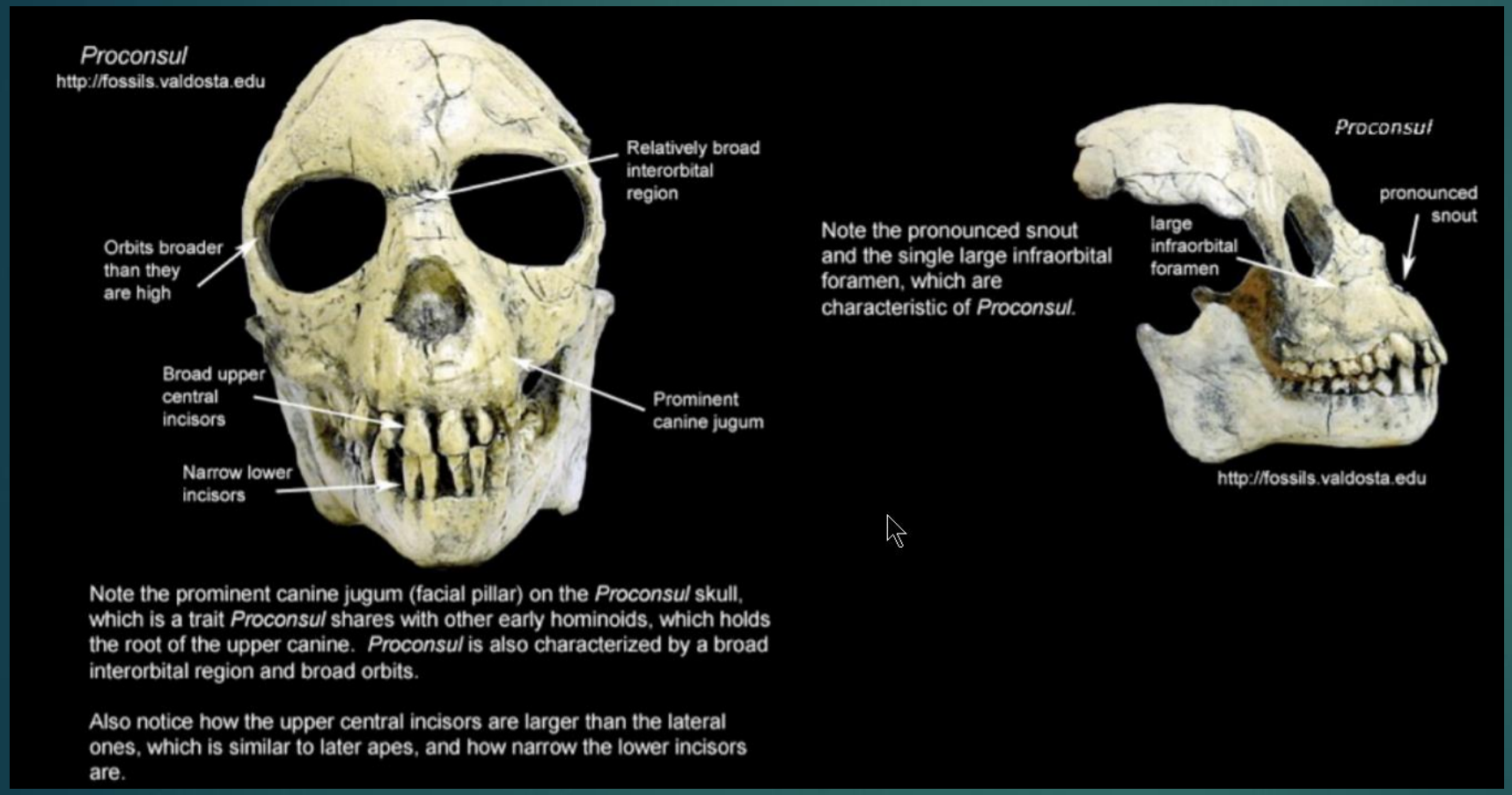
3 defining mammalian traits: hair, mammary glands, homeothermy

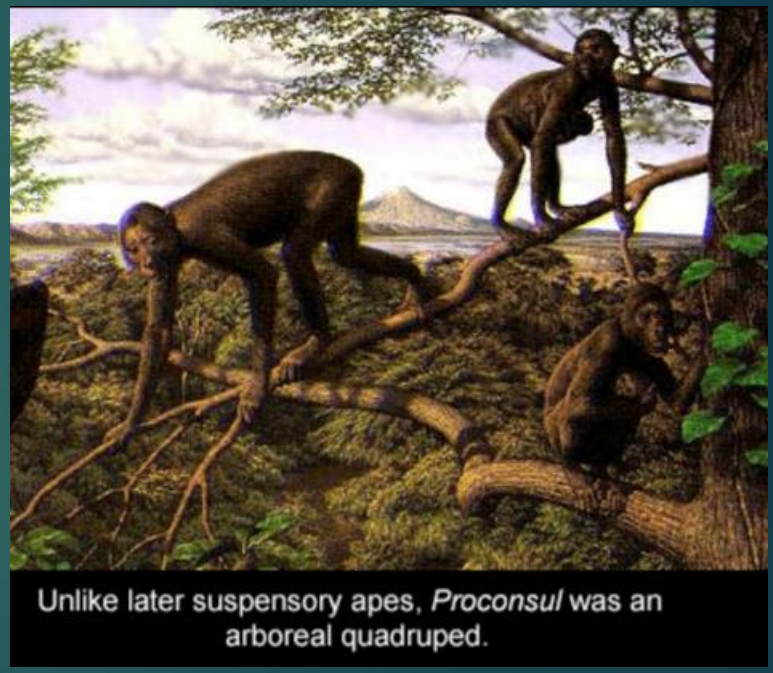
Mammalian traits show an adaptation for adaptability

Miocene era: 23 to 5 Ma, Warmer global period

- Ape grade: Planet of the apes
- Over 30 genera and 100 species of ape – compared with 6 today
- Location: Africa and Eurasia

Proconsul: 25 to 23 Ma, during Miocene; arboreal quadruped




Unlike later suspensory apes, *Proconsul* was an arboreal quadruped.

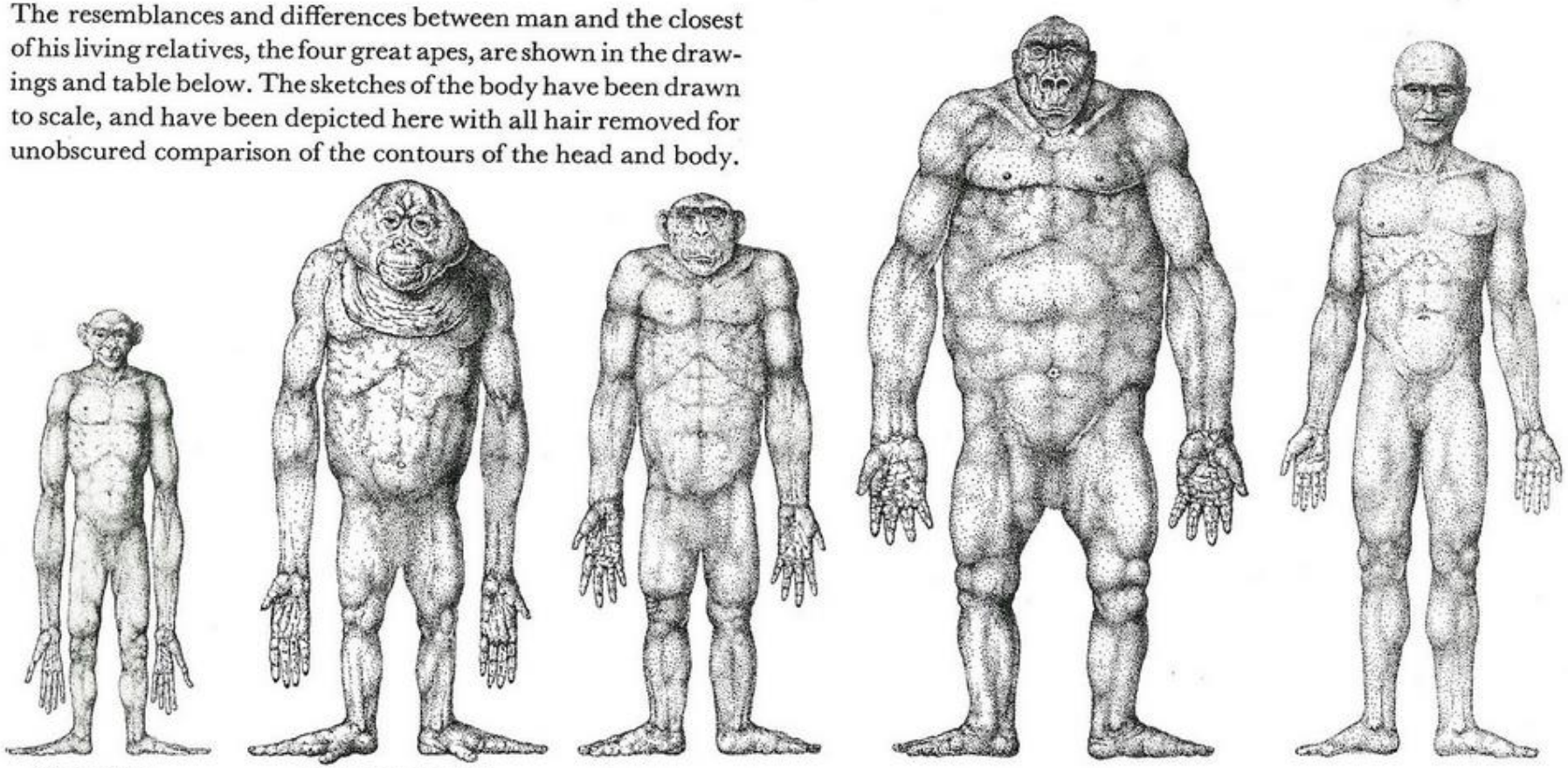
Primates

- Larger body size
- Larger brain
- Complete stereoscopic vision
- Longer gestation, infancy, life span
- More k-selected (tend towards single offspring)
- Greater dependency on learned behavior
- More social

Great Apes

A Comparison of Apes and Man

The resemblances and differences between man and the closest of his living relatives, the four great apes, are shown in the drawings and table below. The sketches of the body have been drawn to scale, and have been depicted here with all hair removed for unobscured comparison of the contours of the head and body.



GIBBONS
Hylobatidae

ORANG-UTAN
Pongo pygmaeus

CHIMPANZEE
Pan troglodytes

GORILLA
Gorilla gorilla

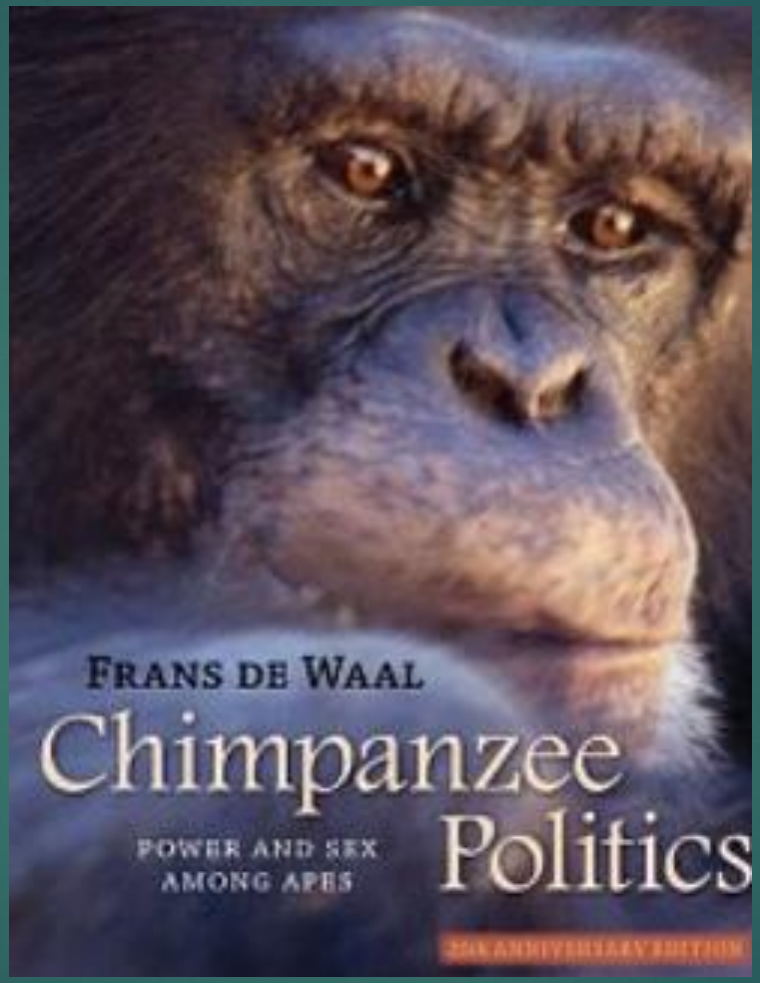
MAN
Homo sapiens

Bonobos and Chimps split ~1 Ma

Superfamily: Hominoidea

- Gibbons, Gorillas, Orangutan, Chimpanzee, Human
  - Greater encephalization (brain to body ratio) = smarter
  - larger body,
  - brachiation,
  - social complexity,
  - lack of tail

Why did Newt Gingrich recommend this book to all new politicians?



Detailed and thoroughly engrossing account of ape rivalries and coalitions.
Machiavellianism**:** political behavior is rooted at a level of development that is below the cognitive and is as much instinctive as it is learned.

de Waal 1982

De Waal: Machiavellian IQ

- Machiavelli's *The Prince*: Frans de Waal introduced the term 'Machiavellian Intelligence' to describe the social and political behavior of chimpanzees

- Social behaviors: reconciliation, alliance, and sabotage

- Tactical deception in primates:
  - Vervet monkeys use false predator alarm calls to get extra food
  - Chimpanzees use deception to mate with females belonging to alpha male

Chimpanzee cultures

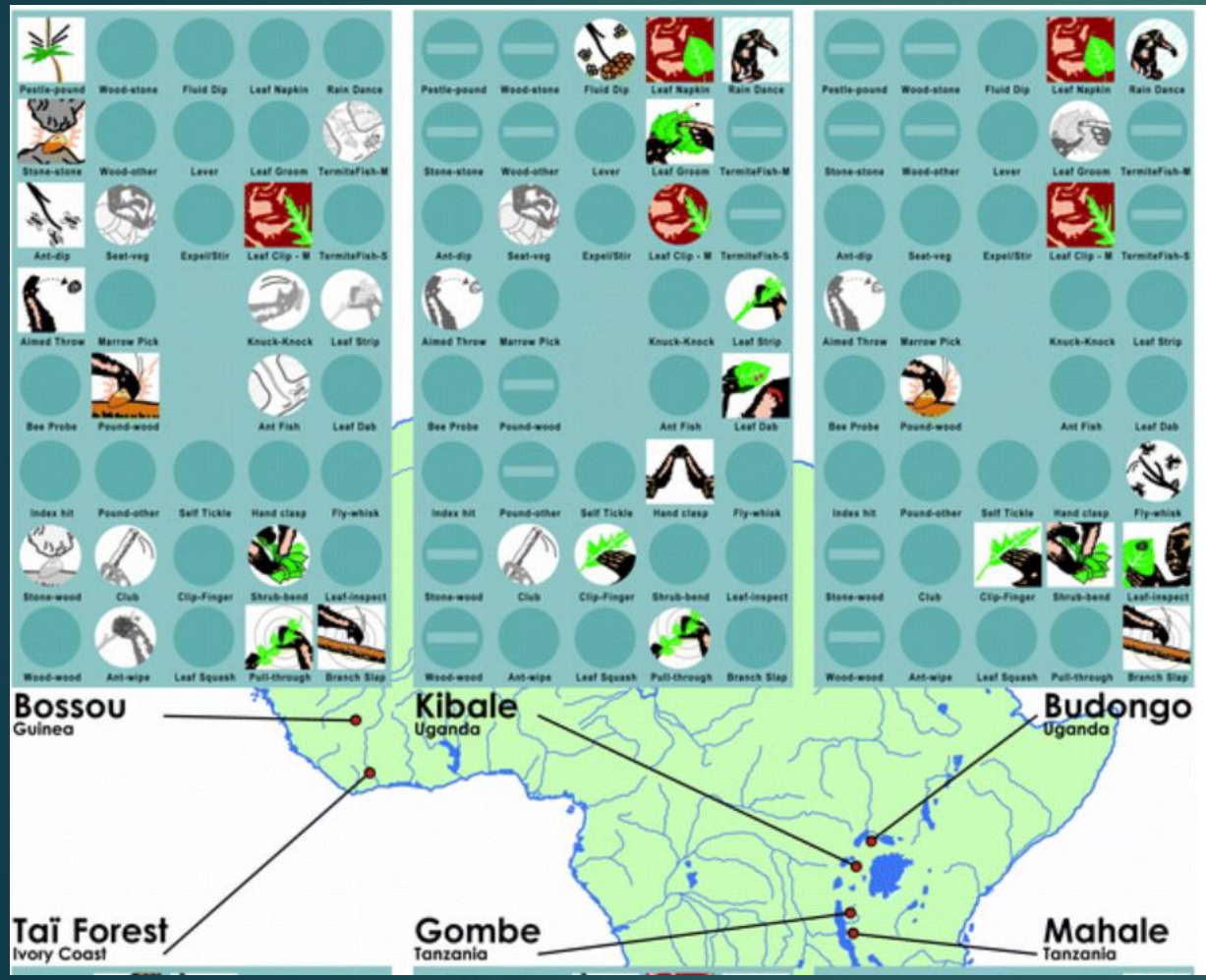
- Chimp Cultures: shared behaviors in different communities:
  - pounding actions
  - fishing;
  - probing;
  - forcing
  - comfort behavior
  - miscellaneous exploitation of vegetation properties
  - exploitation of leaf properties;
  - grooming;
  - attention-getting.

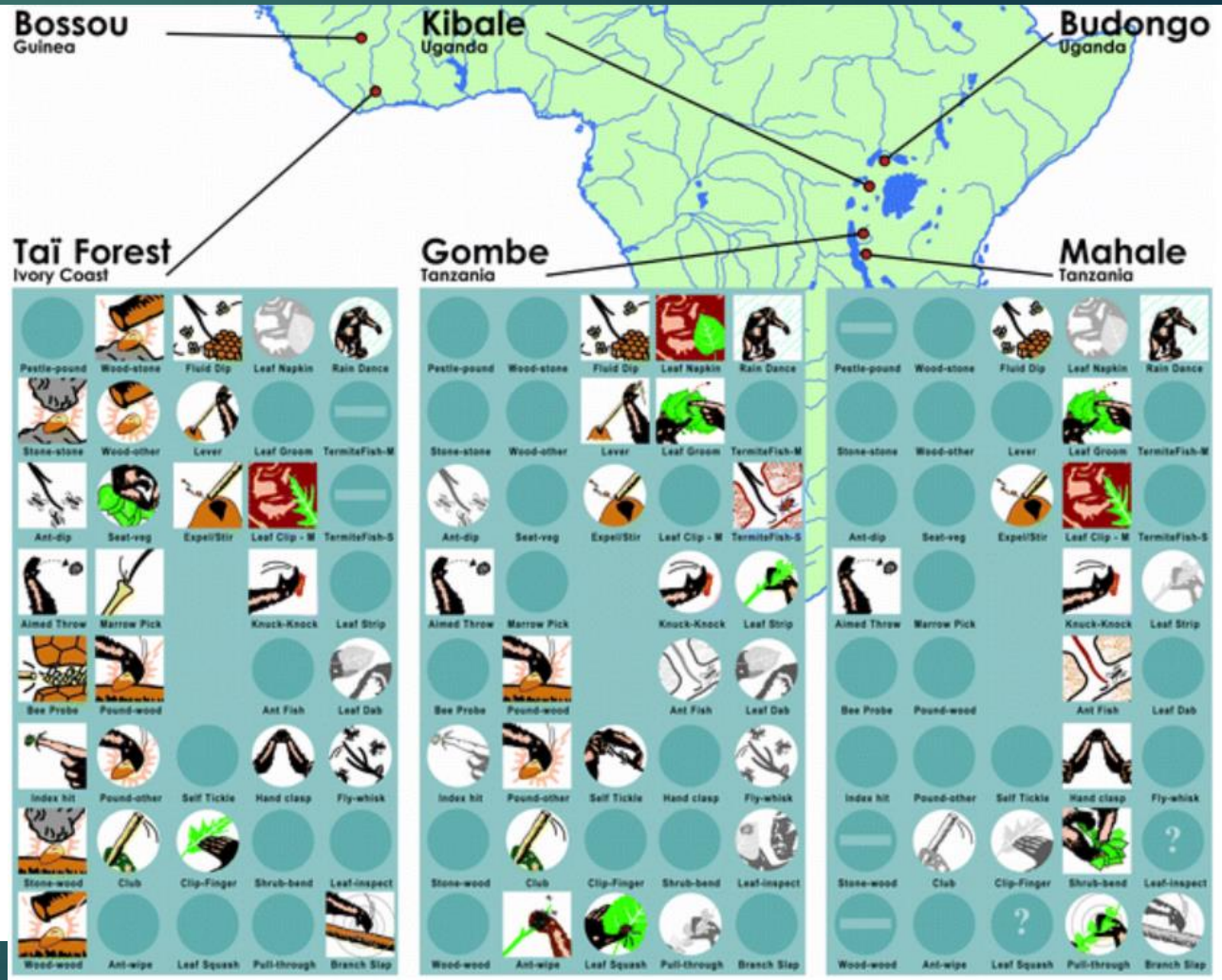
Andrew Whiten et al., Nature, 1999

Chimpanzee cultures

Andrew Whiten et al., Nature, 1999

Different communities of chimpanzee display their own particular patterns of behavior, giving rise to the idea that each has its unique cultural tradition. Color icons, customary; circular icons, habitual; monochrome icons, present; clear, absent; horizontal bar, absent with ecological explanation; question mark, answer uncertain.





Molecular clock: How do we find Last Common Ancestor (LCA)

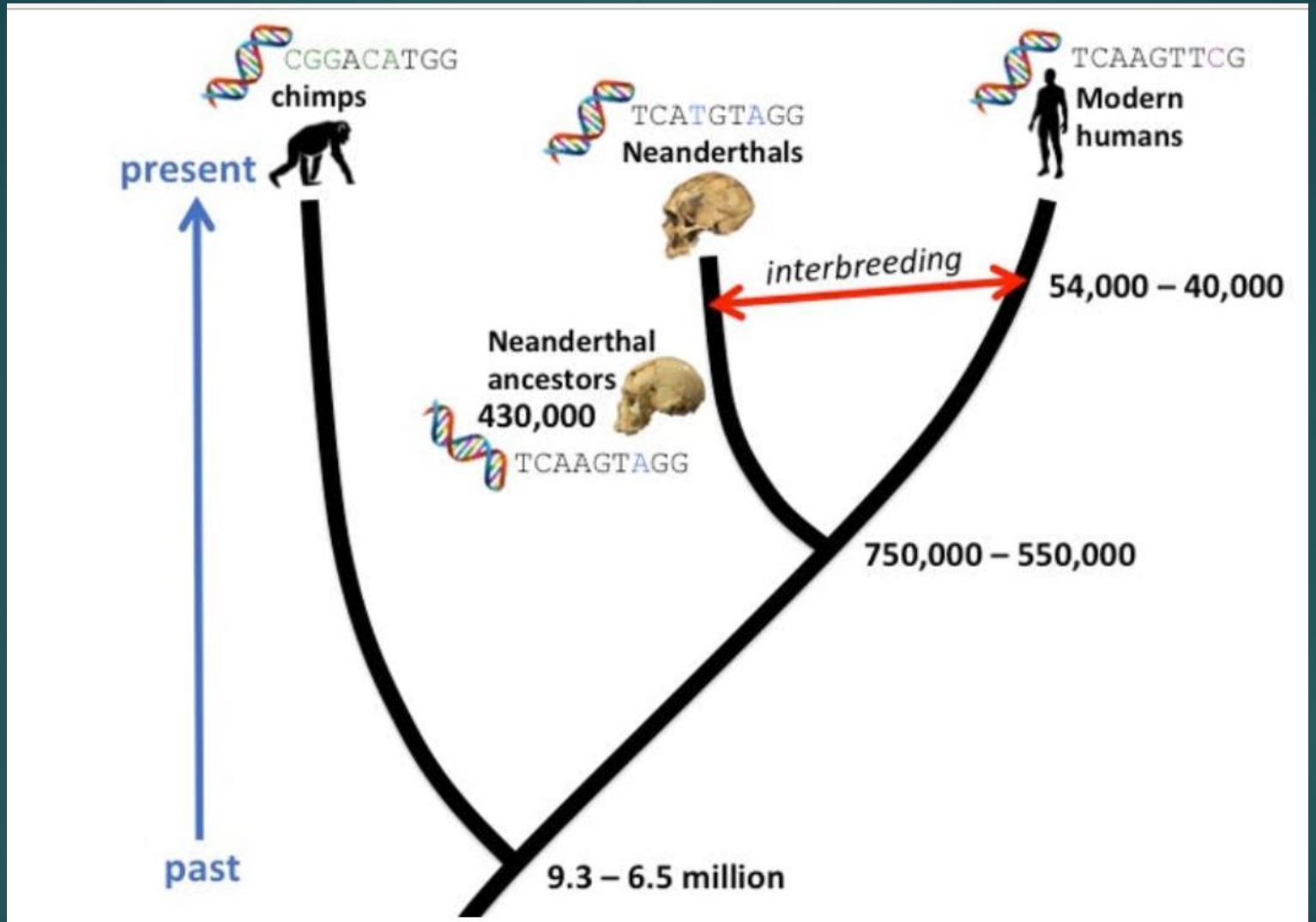
- Molecular clock method: use the amount of genetic divergence between 2 organisms to extrapolate backwards to estimate date for LCA.

- This method compares the amount of genetic difference between living organisms and computes an age based on well-tested rates of genetic mutation over time.

- Since genetic material (like DNA) decays rapidly, the molecular clock method can't date very old fossils. It's mainly useful for figuring out how long ago, living species shared a common ancestor, based on their DNA.

Molecular clock 2

- This means that most mutations do not produce phenotypic results and are not subject to natural selection
- Amount of genetic differences, given steady rate of mutations, gives us way to estimate how far back in past a LCA is.
  - rate of mutation is not constant,
  - varies across lineages;
  - slower in humans & great apes;
  - 5-7 Ma to LCA
- The molecular clock alone can only say that one time period is twice as long as another: it cannot assign concrete dates. Needs collaboration.



An evolutionary tree displays the divergence and interbreeding dates that researchers estimated with molecular clock methods for these groups. Bridget Alex, CC BY-ND

Closer to root species, more difficult to recognize

- Species close to branching points:

- The closer a species is to its speciation event, the more difficult it is to recognize. It will look almost identical to species it originated from. They will look a lot like each other, than to descendants

- Fossils of such a species will be difficult to differentiate.

Identifying the first hominins

- In Last Common Ancestor (L.C.A.), look for anatomical features shared by humans and living great apes
- Starting from there, 1st hominins must have evolved at least one feature that we see only in modern humans
- Scientists focus on anatomy related to bipedalism
- Large brain size, hard evidence for culture, language, etc., come much later.

LCA characteristics

- LCA: fossil and comparative evidence indicates it was more similar to living apes than to living humans.
- The HumanChimp-LCA would have had:
  - Ape-sized brain and body,
  - Finger bones would be curved; adapted for climbing
  - A grasping foot that allowed it to forage in the trees.
  - Limbs adapted to walk both on all fours and on hind limbs alone
  - More prognathic/snoutlike face, not flat; elongated jaws
  - Modest-sized teeth, prominent canines, large upper incisor teeth
  - Canine teeth were probably large and sharp, as seen in several Miocene hominoids.
  - Canines were probably **sexually dimorphic**, with males having much larger canines.
  - Relatively long arms and fingers
- The idea that, like living apes it would have walked quadrupedally (on all fours) when on the ground, is now being questioned.
- Its diet would have consisted almost entirely of plant foods, primarily fruit and leaves.
- The first human-like traits to appear in the hominin fossil record are **bipedal** walking and smaller, blunt **canines**.

Ardipithecus:

Shows that today's common chimpanzees are highly specialized in their:

- Behavior ("demonic males": chimp male violence)
- Diet (fruit specialists)
- Locomotion (knucklewalkers)
- Habitat preferences (tropical forest)

The last common ancestor we shared with chimpanzees…was NOT a chimpanzee.

LCA: ? of knuckle walking

- Parsimony (simplest explanation)-based appeals to knuckle walking (KW) in contemporary African apes have been used to argue that this locomotor mode must have been the primitive condition for our last common ancestors with them.
- However, despite intensive searching of African, European, and Asian deposits, no compelling Miocene evidence of KW has so far been found; *Ar. ramidus* strongly suggests that none will be, at least in any candidates for the last common ancestor
- Many adaptations must have evolved after chimps split with the hominid clade: territoriality and intergroup aggression, complex male alliances, strong intragroup competition and aggression linked to “advertised” female estrus, and unusually robust sperm competition resulting from extreme female promiscuity.
- Hominids appear to have emerged by developing a search-intensive terrestrial feeding niche, accompanied perhaps by food transport and sharing in less densely forested but still wooded areas.

Derived Chimp characteristics per Tim White

Derived traits in chimpanzees:

- Long metacarpals
- Large incisors
- Short backs
- Flexible grasping feet
- Knucklewalking and vertical climbing
- Frugivorous diets
- Social structures

So these were not present in LCA

Paleoenvironments and early hominids

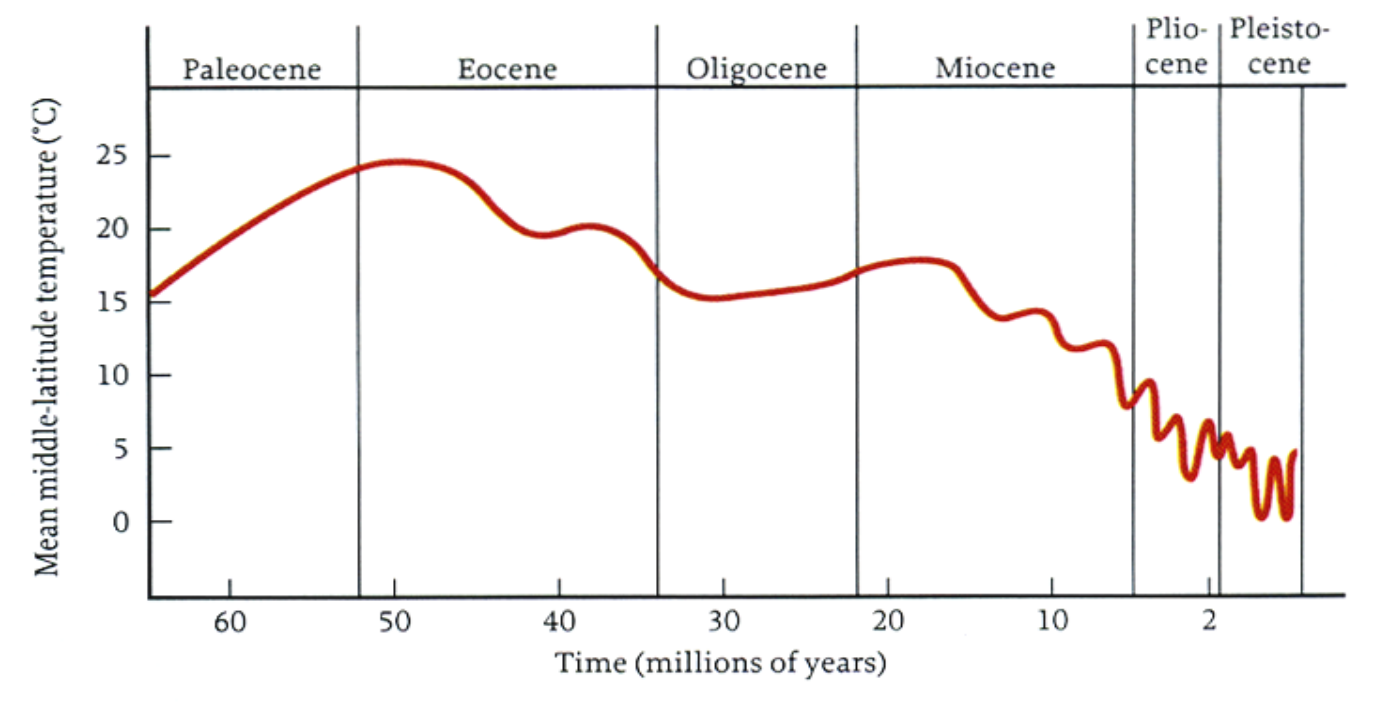
- Andrew Hill: Baringo Paleontological Project, Tugen Hills, Kenya

- 1 - Origin of Hominids: walking on 2 legs related to changing environment; origin of savanna grasslands?
  - What was environment like when hominins originated?
  - Woodlands and forest or grasslands?

- 2 – Climate change forced by astronomical variations (earth wiggles around the sun) affect local environment in Africa.
  - Did this actually affect human evolution

Climate change in late Miocene/Pliocene

Hominins evolved ~6 mill yrs ago



Falling temperatures changed climate in African tropics:

- Rain fall declined, became more seasonal
- Tropical forests shrank; woodlands, grasslands expanded

Climate change

- 8 Ma: Africa was mostly thick forests interspersed with rivers and lakes; most primates were tree dwellers
- 8 to 5 Ma: the earth experienced beginnings of long-term drying and cooling trend because earth's moisture was locked up in ice sheets, extended further from north and south poles. Temperatures fell.
- Hominin evolution began in Africa at time of these climatic changes.
- Dense forests were gradually replaced with open woodland. Grasslands began to appear between large patches of trees.
- Today's savannahs are recent event.

Environments of African Ancestors

- Originally thought that LCA probably lived in dense forest. Some descendants adapted to new landscapes.
- But recent data suggests earliest hominins lived in a mosaic of habitats: woodland, grassland, lakes, and gallery forests along rivers.
- No early hominin fossils have been found in an exclusively densely forested habitat.

African Ancestors

- Earliest hominins were adapted to both tree living and ground living.
- Trees provided fruit, nesting sites, protection from predators.
- Grassland had new food sources (tubers), while water sources offered fish and mollusks.
- Unlikely that they lived in caves (primates do not live in them), despite some fossils being found there.

Climactic Conclusions

- In Rift Valley, environments were varied, but primarily woodlands or forest at time of human origins and afterwards.
- Astronomical variations caused changes in climate and environment in Rift Valley
- Not always lakes, but significant environmental change
- Causes breakup and recombination of communities of animals and hominids
- A perfect scenario for Darwinian speciation

Climate: grasslands

- Two moments in our evolutionary history show a tantalizing connection between climate swings and the life and death of key members of our family tree.
- Starting just after 3 Ma, the species *Australopithecus afarensis* vanished, and the groups *Paranthropus* and *Homo* (our own genus) appeared.
- During this period, changes in carbon isotope ratios from land and ocean sediments show that dry grasslands rapidly expanded and wetter woodlands shrank.
- Starting after two million years ago, *Homo erectus* appeared and migrated out of Africa.

Climate

- Again, the carbon evidence shows grasslands got another boost. Yet carbon in the teeth from *H. erectus* indicates the consumption of a mixed diet and an ability to find food from a variety of sources even as grasslands enlarged.

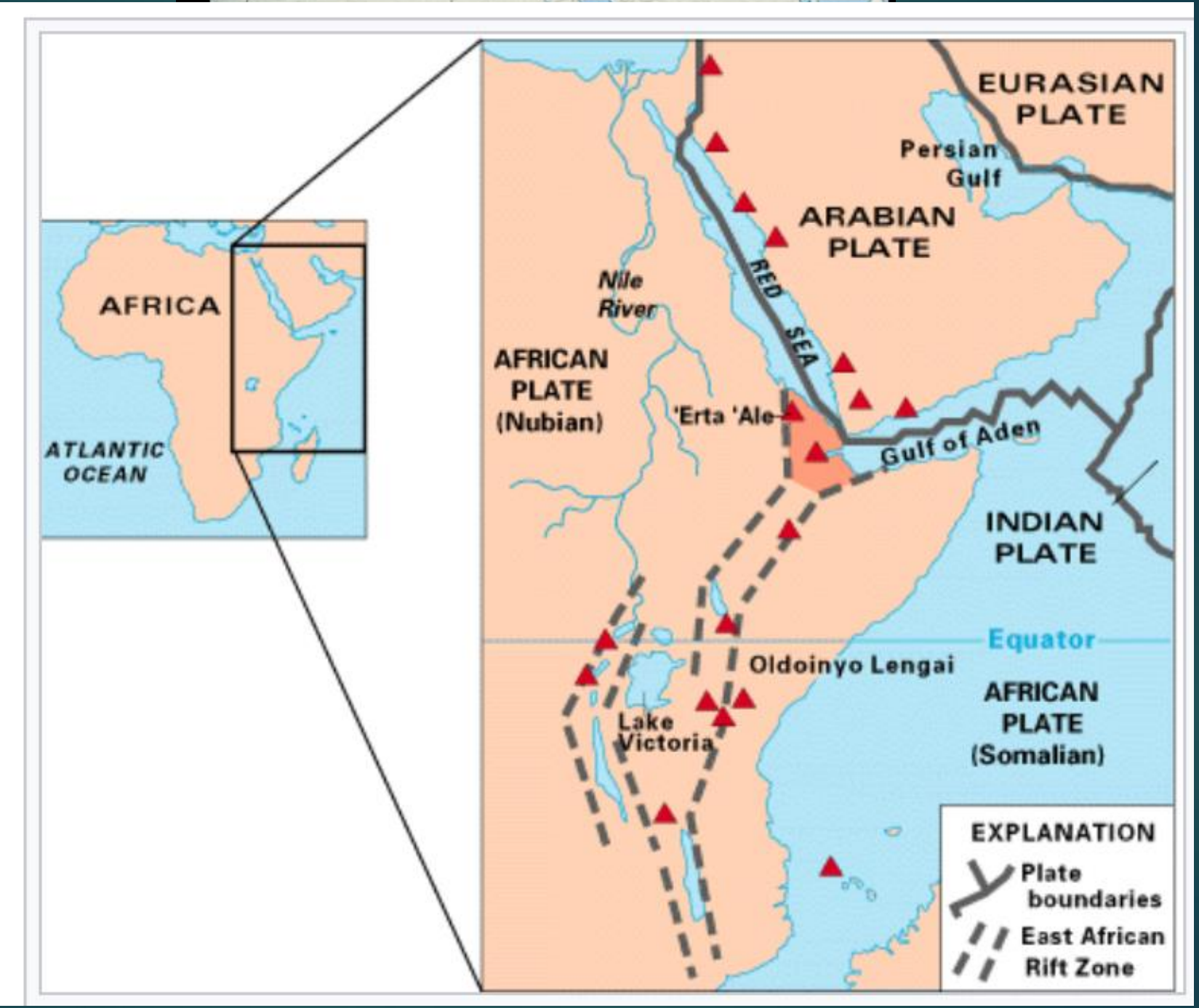
- *Paranthropus* teeth, however, showed the group (like an earlier extinct forebear, *Kenyanthropus*) was restricted to eating from grassy surroundings. They die out.

Big Picture

- 8-15+ Ma: Planet of the Apes; no hominins
- 7+ Ma: Last common ancestor of chimpanzees & humans;
- 6+ Ma: Hominin clade established (Ardipithecus, etc.)
- 4.3 Ma: Adaptation to heavily masticated diets: *Australopithecus* established
- 2.7 Ma: Homo clade established
  - Oldowan technology and large mammal butchery
- >1.8 Ma: First hominin expansion from Africa
- 600 Ka: Neanderthal/Denisovan clades established
- 200 Ka: Anatomical modern *Homo sapiens;* mini *Floresiensis* persist
- 143 Ka: *H. erectus* goes extinct
- 30 K: Neandertals go extinct

East African Rift Valley:

3 plates splitting at 6–7 mm annually

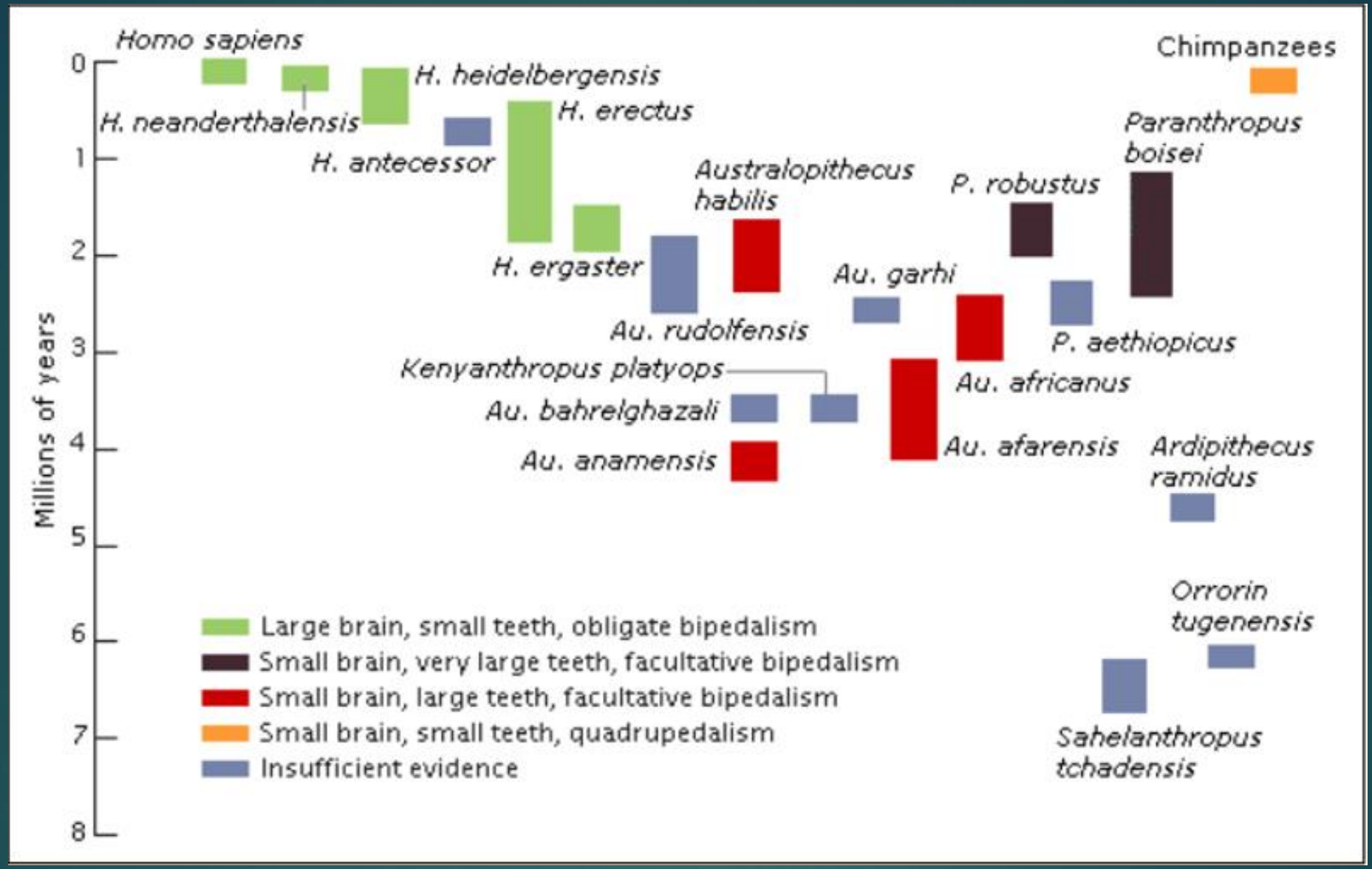


“Phases” of human evolution

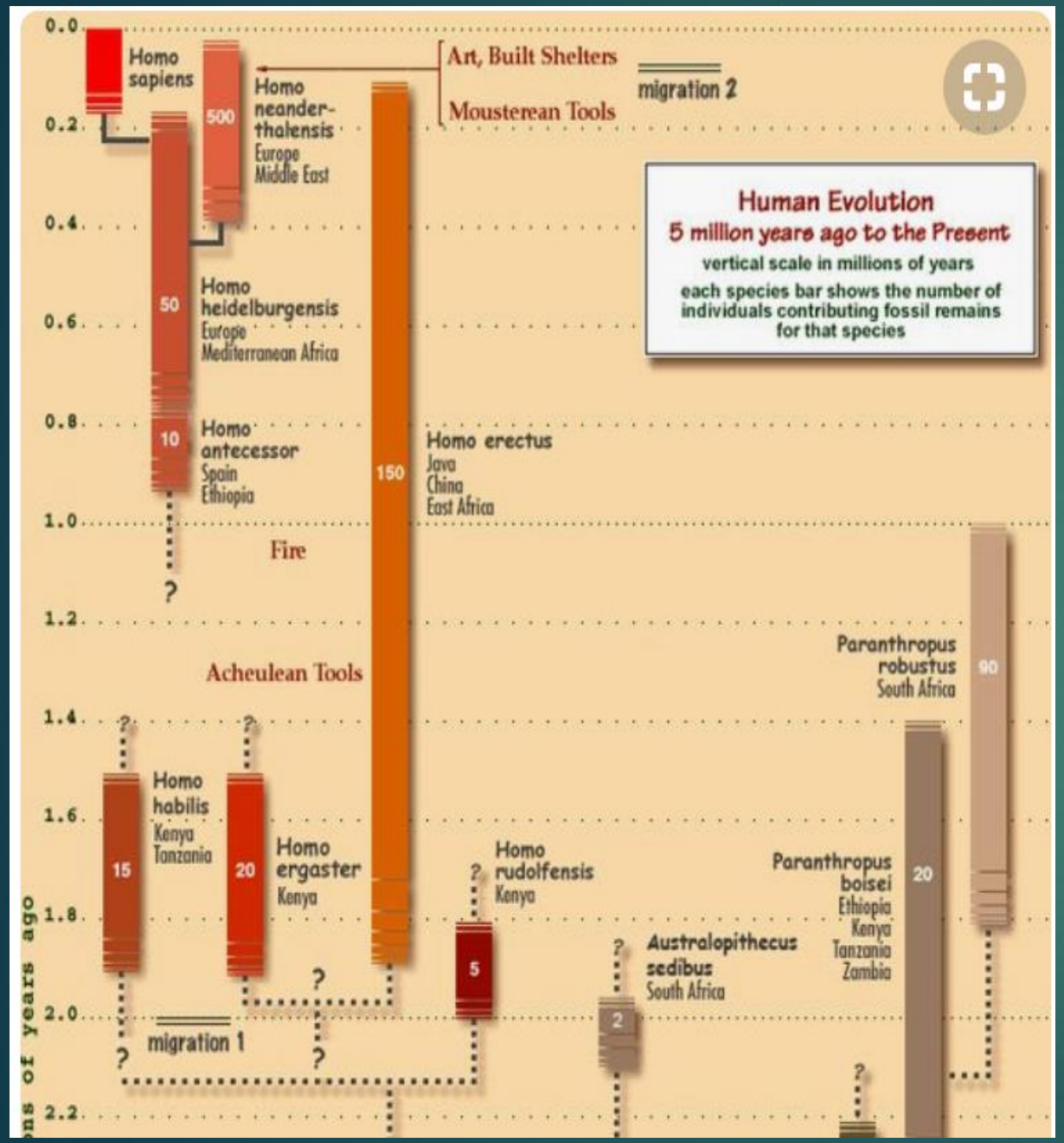
- Early phase: 7-4 Ma – Africa – Still poorly known – Earliest bipeds? Canines reduced. Largely ape-like?

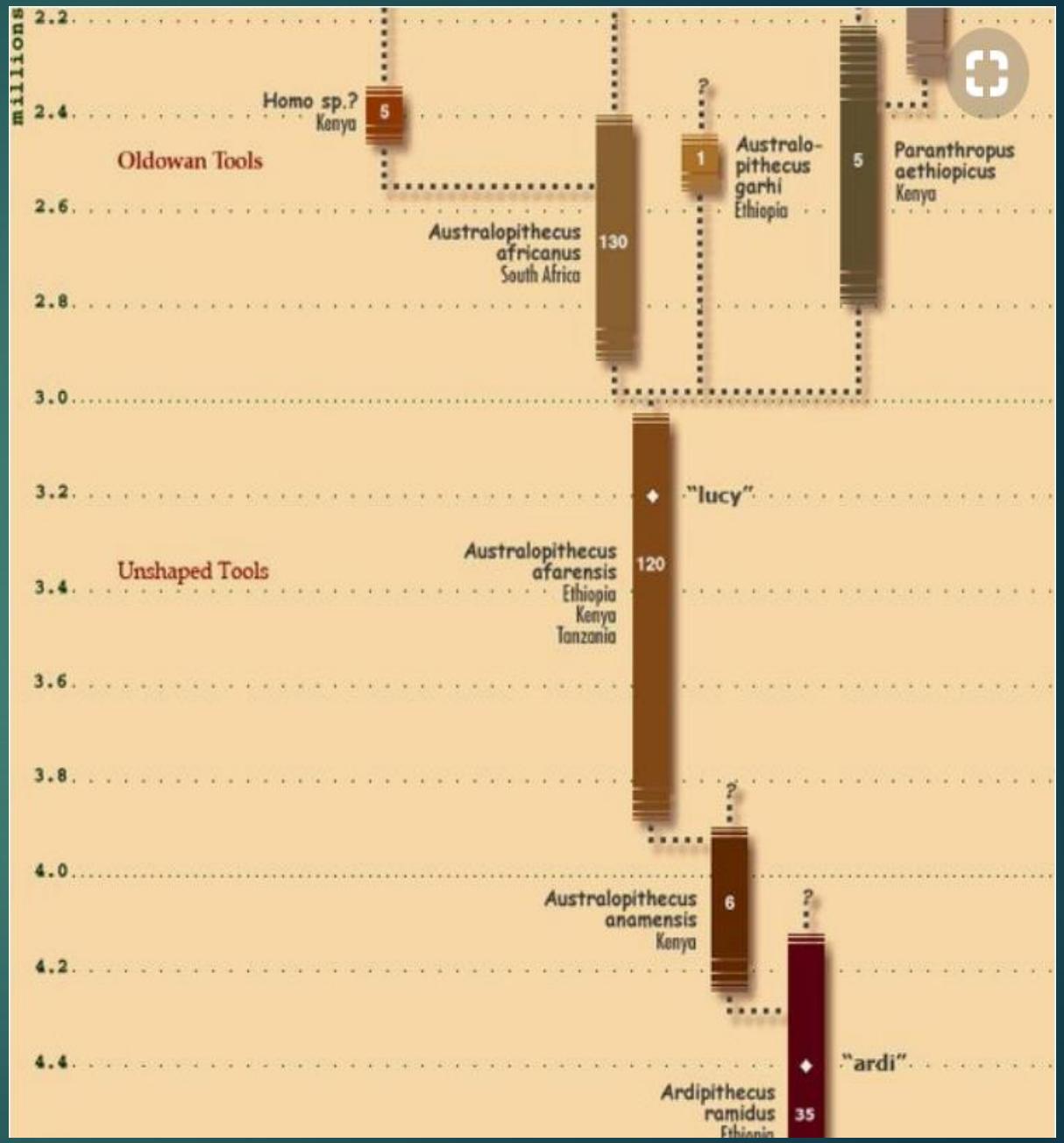
- Australopithecine phase: 4-2 Ma – Many species, widespread in Africa. Bipedal but still partly arboreal? Early tool use? Still some what ape-like?

- Human phase: 2-0 Ma – several species; global spread; “Human” anatomy; encephalized (brain larger than body size requirement); greater dietary range; behavioral complexity



Note: as many as 4-5 species living at same time;
Multiple instances of a parental species continuing to exist for time after a daughter species evolved.
Not all paleoanthropologists agree with this scheme.


Human Evolution
5 million years ago to the Present
vertical scale in millions of years
each species bar shows the number of individuals contributing fossil remains for that species
Homo sapiens
500
Homo neander-thalensis
Europe
Middle East
Art, Built Shelters
Mousterean Tools
migration 2
50
Homo heidelburgensis
Europe
Mediterranean Africa
10
Homo antecessor
Spain
Ethiopia
150
Homo erectus
Java
China
East Africa
Fire
Acheulean Tools
Paranthropus robustus
South Africa
90
15
Homo habilis
Kenya
Tanzania
20
Homo ergaster
Kenya
Homo rudolfensis
Kenya
5
2
Australopithecus sedibus
South Africa
Paranthropus boisei
Ethiopia
Kenya
Tanzania
Zambia
20
migration 1
millions of years ago
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2


millions
2.2
2.4
2.6
2.8
3.0
3.2
3.4
3.6
3.8
4.0
4.2
4.4
Homo sp.?
Kenya
5
Oldowan Tools
Australopithecus africanus
South Africa
130
1
Australo-pithecus garhi
Ethiopia
5
Paranthropus aethiopicus
Kenya
"lucy"
Unshaped Tools
Australopithecus afarensis
Ethiopia
Kenya
Tanzania
120
Australopithecus anamensis
Kenya
6
"ardi"
Ardipithecus ramidus
Ethiopia
35

A Tour Through 7 Million Years of Human Evolution

No clear fossil evidence of last common ancestor between the line that would lead to chimps and the line that would lead to modern humans has been found yet

However, many other intermediates have been found.....

May 2017: Graecopithecus freybergi (El Graeco), 7.2 Ma

Scientists recovered a jaw fossil belonging to the earliest human-chimp relative in Greece. Photo by Wolfgang Gerber/University of Tubingen

The type mandible of *Graecopithecus freybergi* from Pyrgos (7.175 Ma) and the single tooth (7.24 Ma) from Azmaka (Bulgaria) represent the first hominids of Messinian age from continental Europe. Our results suggest that major splits in the hominid family occurred outside Africa.

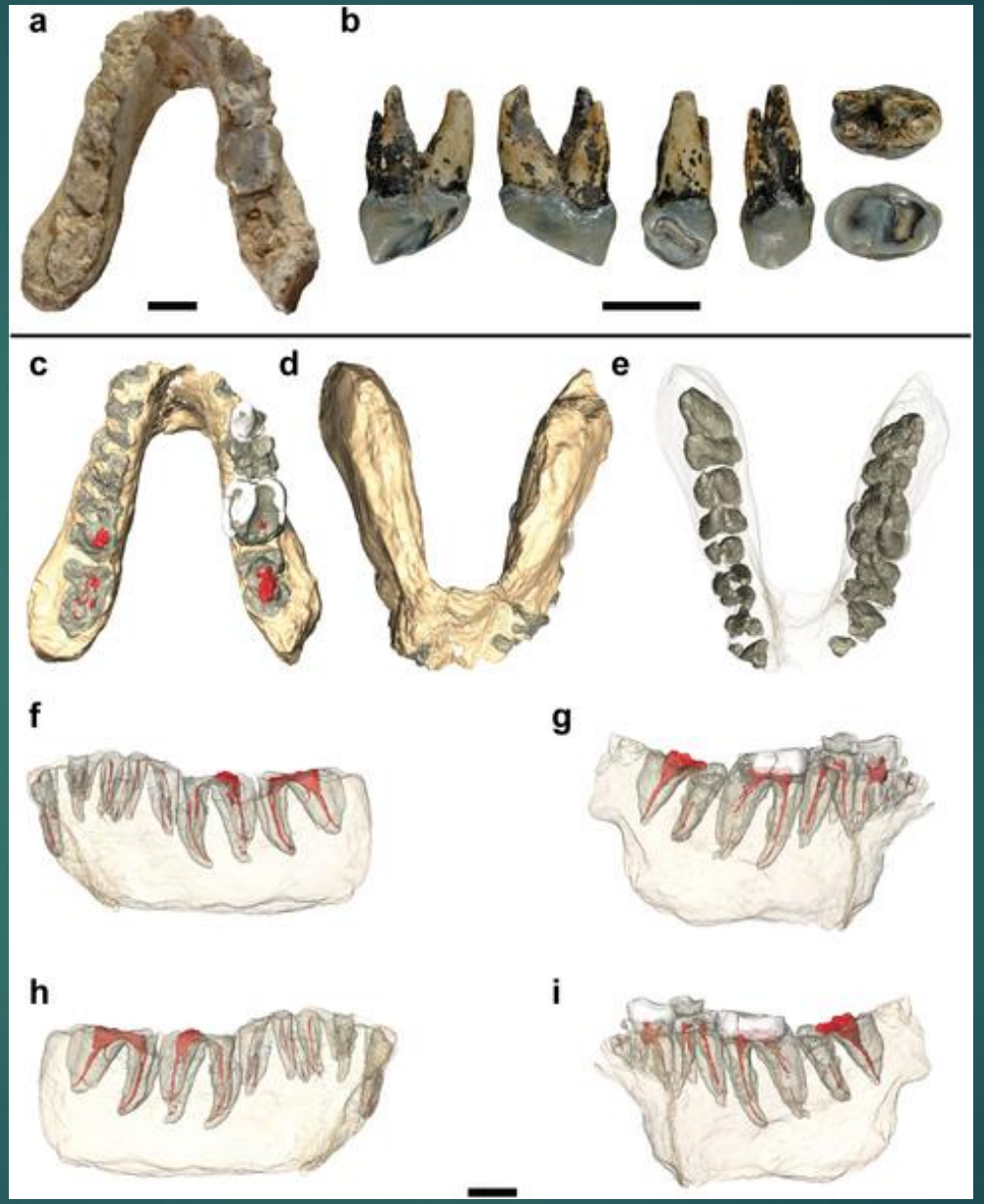
See also: *The Real Planet of the Apes* by David R. Begun

Madelaine Böhme, et al. 2017

•Jochen Fuss, et al., 2017

Studied specimens and virtual reconstructions of the holotype of Graecopithecus.

David Begun argues controversially that Graecopithecus was a hominin, not an ape; and that hominins may have originated in Europe & migrated to Africa



Tim White at the UC, Berkeley, says the new research "tries to resurrect Begun's tired argument with a long-known crappy fossil, newly scanned".

Fuss J, Spassov N, Begun DR, Böhme M (2017) Potential hominin affinities of Graecopithecus from the Late Miocene of Europe. PLOS ONE 12(5): e0177127. https://doi.org/10.1371/journal.pone.0177127
http://journals.plos.org/plosone/article?id=10.1371/journal.pone.0177127

Early hominin footprints at Trachilos near Crete at 5.7 Ma

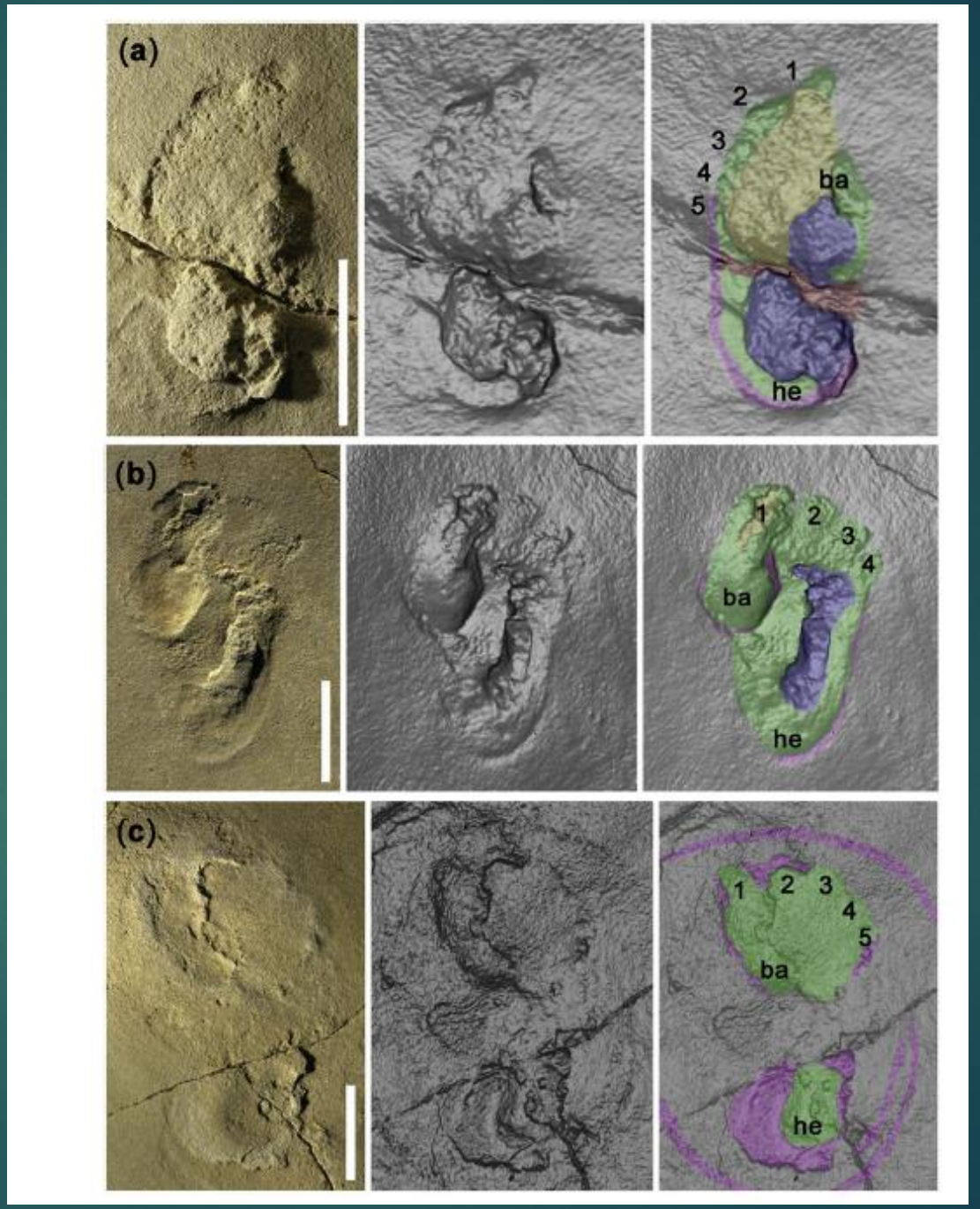
- Researchers have found 5.7 million-year-old, human-like footprints in Crete, complicating the story of human evolution. Oldest prior footprints at Laetoli, Tanzania, Africa, dated 3.7 Ma.
- Most researchers believe the first pre-humans evolved in southern and eastern Africa, remaining on the continent for several million years before migrating to Europe and Asia. The discovery of human-like feet in Crete complicates the narrative.
- The newly discovered "Trachilos" tracks are unmistakably human-like, indicating bipedality, walking on soles of its feet, not its toes. The prints showcase a human-like big toe and the ball shape found on the sole of human feet.
- Until recently, no hominin fossils older than 1.8 million years had been discovered outside of Africa.

Gierlinski, et al., 2017

Trachilos footprints, 5.7 Ma

1 theory: Hominin who walked bipedally;

Alternative theory: an ape that walked bipedally some of the time



From Ape to hominin: the early hominins

- **Proto-hominins (Opportunistic bipeds)**
  - *Sahelanthropus tchadensis*
  - *Orrorin tugenensis*

- **Transitional Opportunistic-into-Habitual Bipeds**
  - *Ardipithecus ramidus* / kadabba
  - *Australopithecus anamensis*

- **First True Habitual Bipeds**
  - *Australopithecus afarensis* / *A. africanus* / *A. garhi*
  - *Australopithecus robustus* / *A. boisei*

Early hominin species

- *Sahelanthropus tchadensis, Orrorin tugenensis, Ardipithecus ramidus*

- General characteristics: These taxa are generally considered to be very close to the point of divergence from LCA with *Pan.*
  - Poorly known, but probably the size range of a large chimpanzee (35-45 kg),
  - They may or may not be bipedal. Discoverers believe they are bipedal.
  - Overall they are probably frugivorous/omnivorous apes.
  - Brain size and sexual dimorphism are unknown, but probably similar to *Pan.*
  - These taxa perhaps indicate the geographical origin of *Homininae* in northeastern Africa.

- Variation:
  - earliest hominins are highly variable (three genera)
  - some showing indications of bipedalism
  - some also possessing primitive traits.

Contenders for Title of Earliest Hominin: 4-7 Ma

- *Ardipithecus ramidus*
  - 1992
  - Middle Awash in Ethiopia
  - Previously thought to be older than 5 Ma, now dated to 4.4 Ma
- *Orrorin tugenensis*
  - 2001
  - Tugen Hills in Kenya
- *Sahelanthropus tchadensis*
  - 2002
  - Toros-Menalla in Chad
- *Ardipithecus kadabba*
  - 2004
  - Middle Awash in Ethiopia

Significance of late Miocene hominins

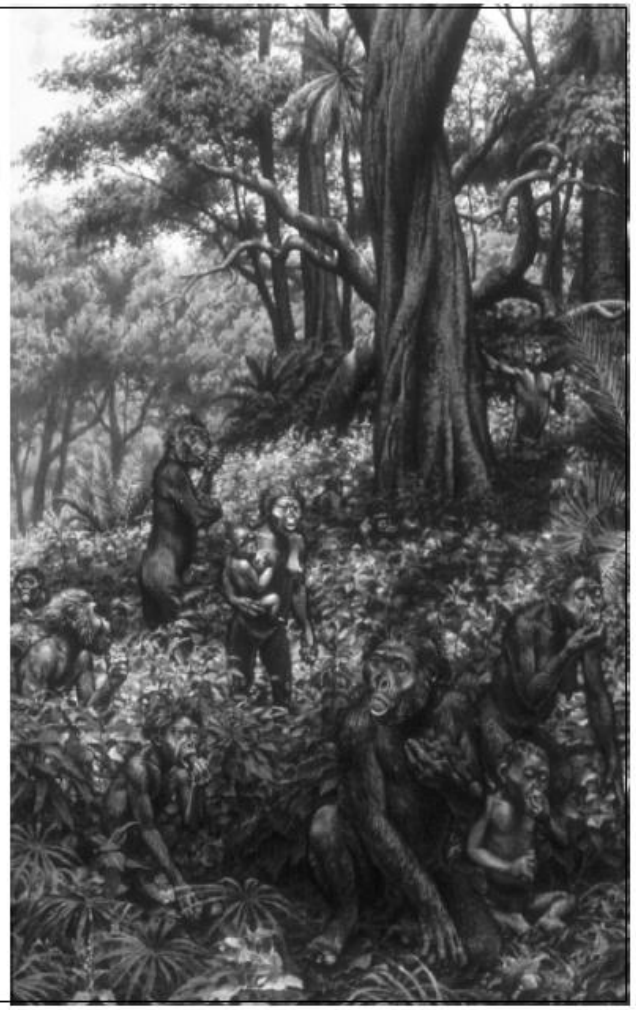
- Pushes back fossil record of hominins by 2-3 million years
  - Until early 1990s, earliest hominins were less than 4 Ma
  - Now appears that multiple, diverse hominins may date to late Miocene (8 to 5 Ma)

- Forces rethinking of bipedalism
  - Early hominins appear to have inhabited forested environments, not open savannas
  - Challenges some scenarios for adaptive value of bipedalism
    - Having hand free to use tools doesn't seem important since bipedalism predates tool use by 3 My

Savanna Hypothesis

Problem with savanna hypothesis?

Earliest bipeds all found at sites with forests



Evolution of hominins & African apes

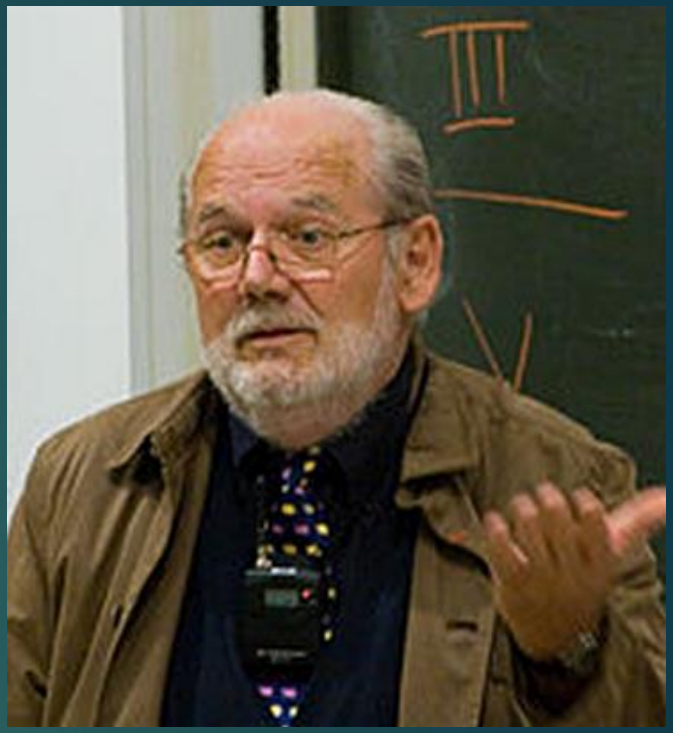
- LCA of chimp/human per Tim White: palmigrade arborealist, dimorphic canines; forest frugivore/omnivore
- Ardi (~6 to 4 Ma): partially arboreal; facultative (capable, but not usual) biped; feminized (smaller) canines; woodland omnivore
- Australopithecus (~4 to 1 Ma): striding terrestrial biped; postcanine megadontia; Pan-African; Wide niche
- *Homo* (< -2.5 Ma): enlarged brain; dentognathic reduction; technology-reliant; Old World range

White, 2009

Sahelanthropus tchadensis

Michel Brunet (1940-):

Sahelanthropus tchadensis

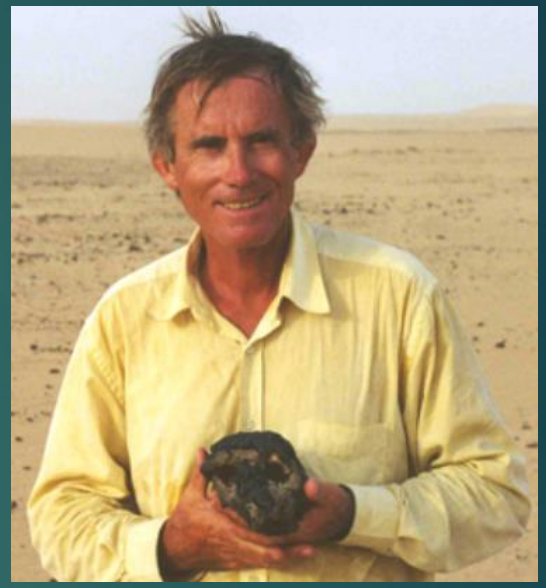


- French paleontologist & professor at the University of Poiters.
- Formed the French-Chadian Paleoanthropological Mission (*Mission Paléoanthropologique Franco-Tchadienne* or MPFT)
- 1995: with MPFT, in Koro Toro, Chad, discovered *Australopithecus bahrelghazali;* (KT-12, Abel, type specimen in 1996), 3.5M
- 2001: with MPFT, Toros-Menalla, Chad, discovered *Sahelanthropus tchadensis* (Toumai)

Alain Beauvilain:

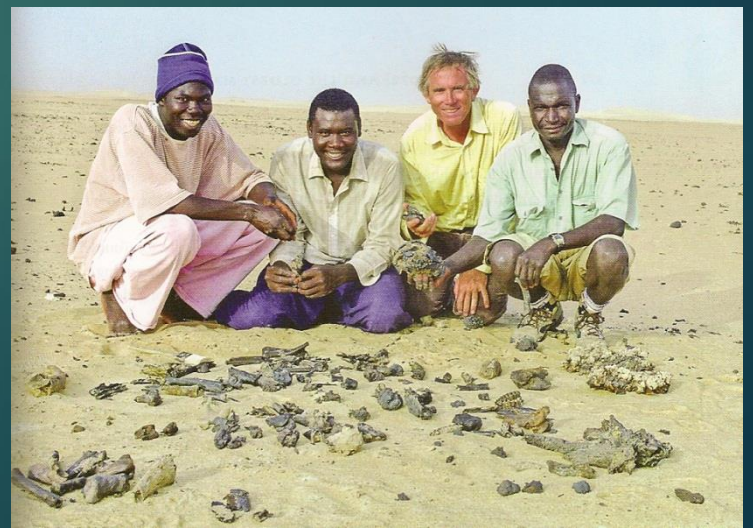
Sahelanthropus tchadensis

- French geographer



- 1995: with MPFT, discovery of *Australopithecus bahrelghazali;*

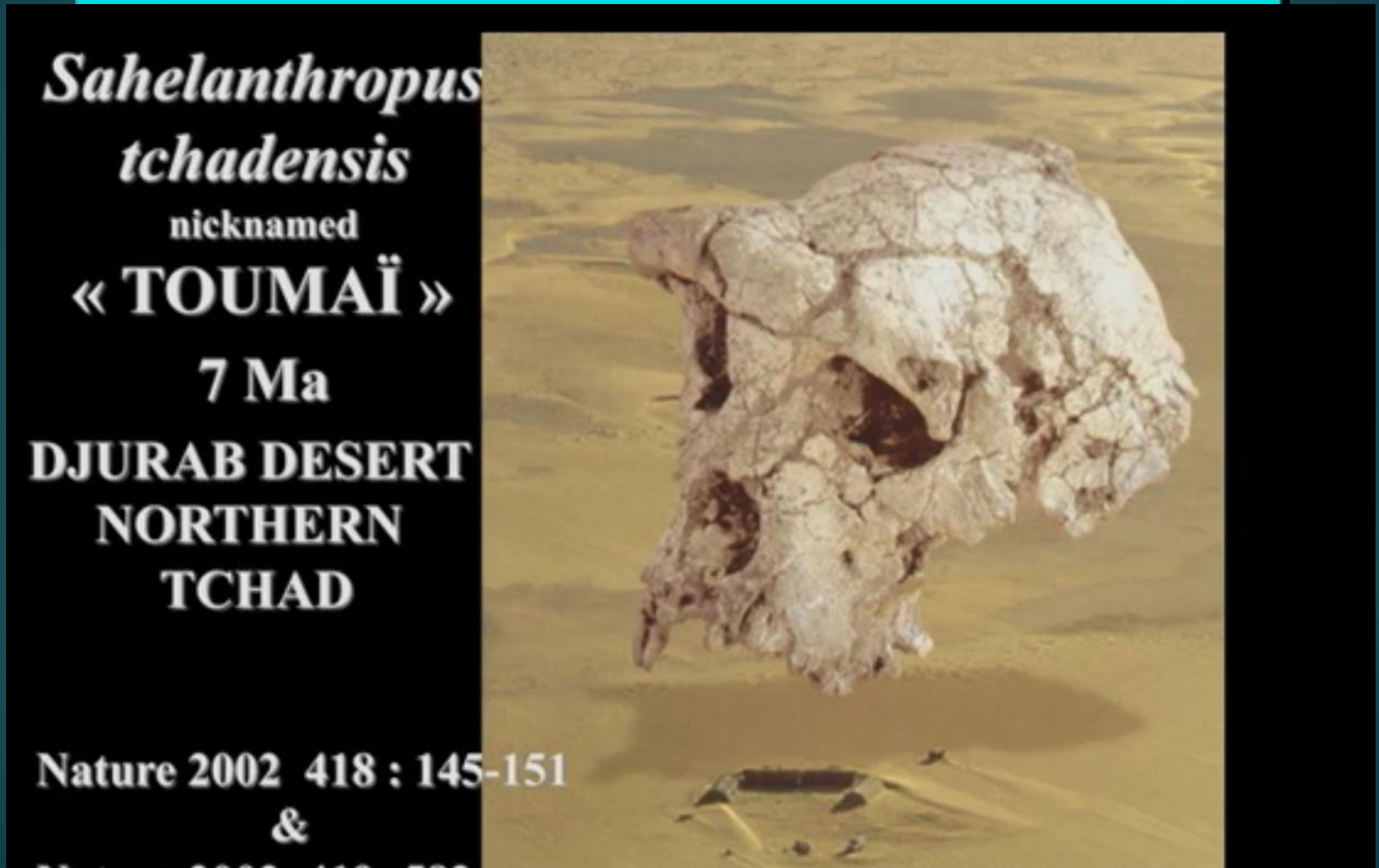
- 2001: with MPFT, Toros-Menalla, Chad, discovery of *Sahelanthropus tchadensis;* (Toumai)



Michel Brune

Changing environment: Toumai lived in forest area

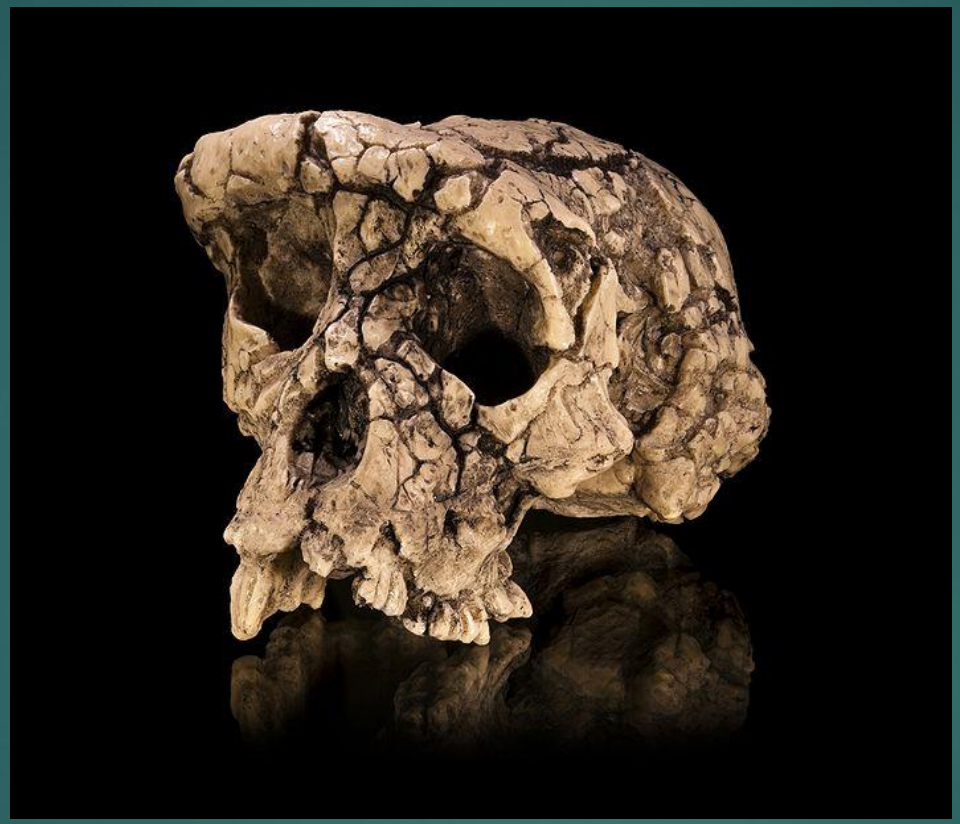
Chad: 3 to 8 Ma; Abel at 3.5 Ma;



On 26th expedition into desert of N. Chad

Dated to 6.83 to 7.12 Ma

Sahelanthropus tchadensis:
About 7 million years old, status as human ancestor unclear



This skull, nearly complete, though flattened by distortion, is also known by its nickname, ‘Toumai,’ which means ‘hope of life’ in the local Dazaga language of Chad.

Brunet, M., et al., 2002. A new hominid from the Upper Miocene of Chad, central Africa. Nature 418(6894), 145-151

Sahelanthropus tchadensis

- ***Sahelanthropus tchadensis*** (“Toumai”) was discovered in Chad, in the southern Sahara desert.
- It is dated at 6 to 7 Ma. Oldest known species in the human family tree.
- Toumai is a nearly complete cranium with a very small brain between 320 and 380 cc, comparable in size to that of a chimpanzee.
- A cranium, jaw fragment, and several teeth were found. It has widely-spaced eye orbits and small canines.
- It is not certainly known whether *S. tchadensis* was bipedal because no lower limb bones have been discovered. It has both apelike and hominin features.
- This species may be close to the hominin chimpanzee ancestor split.

Sahelanthropus tchadensis

- **Diet:** Unfortunately, most of *Sahelanthropus*' teeth are heavily worn; no studies of its tooth wear or tooth isotopes to indicate diet; infer based on its environment, that it ate a mainly plant-based diet. This probably included leaves, fruit, seeds, roots, nuts, and insects.

- **Habitat and Distribution:** Western Africa (Chad)

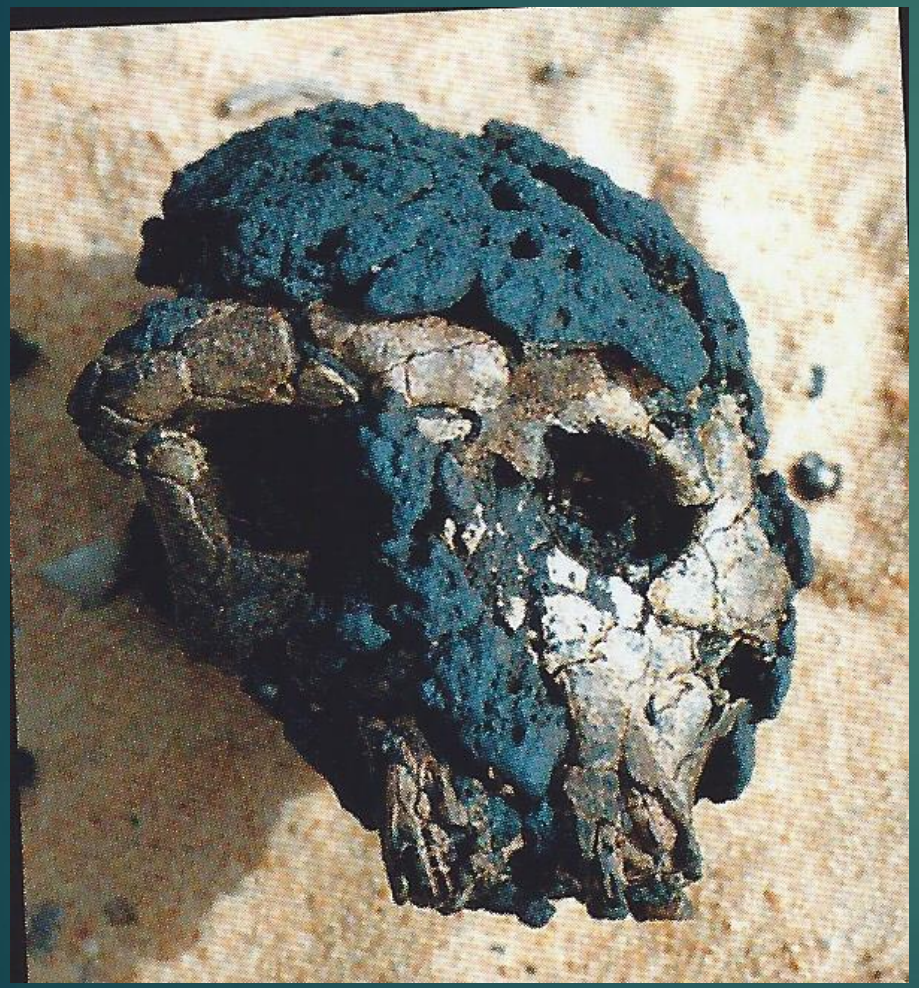
- Whether it was before or after chimp-human split cannot be determined until additional fossils are found from the same time period.

Sahelanthropus tchadensis

Discovered by the Mission Paléoanthropologique Franco-Tchadienne,
May be the oldest hominin recovered thus far

Brunet, et al., 2002

2001: *Sahelanthropus tchadensis*, Chad, 7M*:*
Extension of range of early hominins



Sahelanthropus tchadensis

(*Type:* TM 266-01-060-1)

Discoverer: Ahounta Djimdoumalbaye

Locality: Toros-Manalla, Chad,

Date: 2001

Age: 6-7M

Sahelanthropus

Reconstruction based on CT data

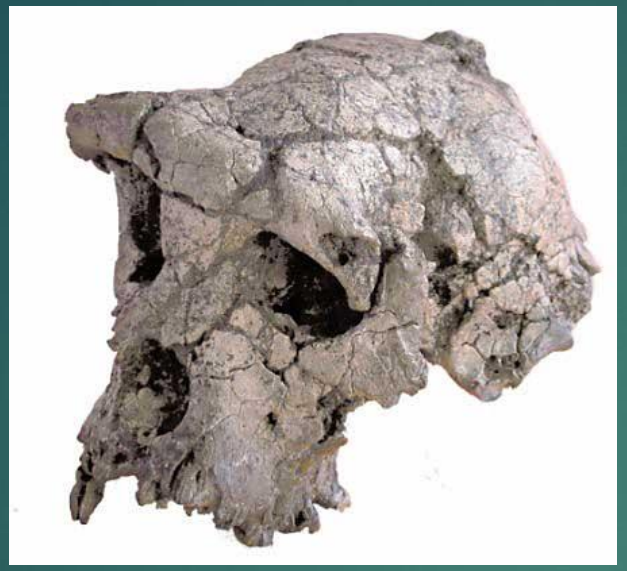
- Major features:
  - Prominent supraorbital torus
  - Fairly large canines (smaller than Chimp)
  - Flat, human like face

Brunet, M. and e. al. "A new hominid from the upper Miocene of Chad, Central Africa." Nature 418 (2002): 145 - 152.
Vignaud, Patrick, et al. "Geology and paleontology of the Upper Miocene Toros - Menalla hominid locality, Chad." Nature 418 .6894 (2002): 152 - 155.

Sahelanthropus tchadensis: Location

- First Hominin in central Africa
- Location: West Central Africa
- Major site: Toros-Menalla, Chad (just below Sahara)
- Implication: if hominin, they occupied much wider area in Africa

2001: *Sahelanthropus tchadensis*, Chad, 7-6 M



Remarkably complete but distorted cranium & 2 mandibles; no postcranials

Has been virtually remodeled

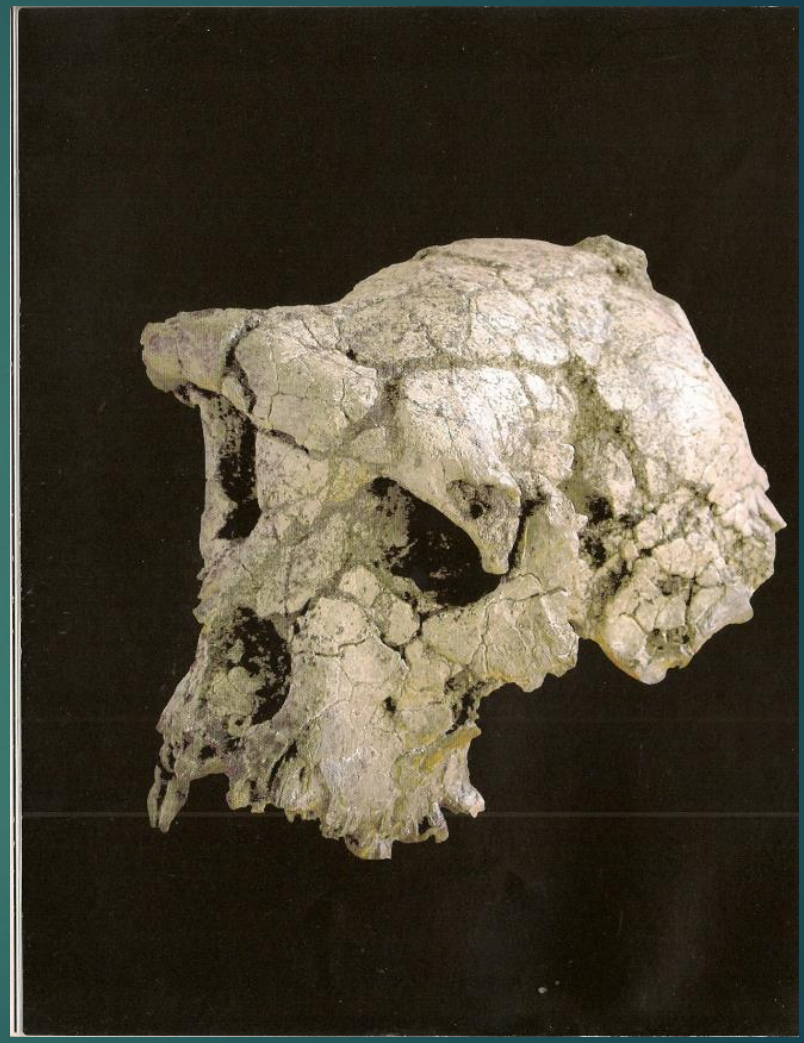
Largest hominoid browridge ever discovered

Smaller size than Ardi

Foramen magnum shape and forward positioning indicate bipedalism (like Ardi; both upright posture)

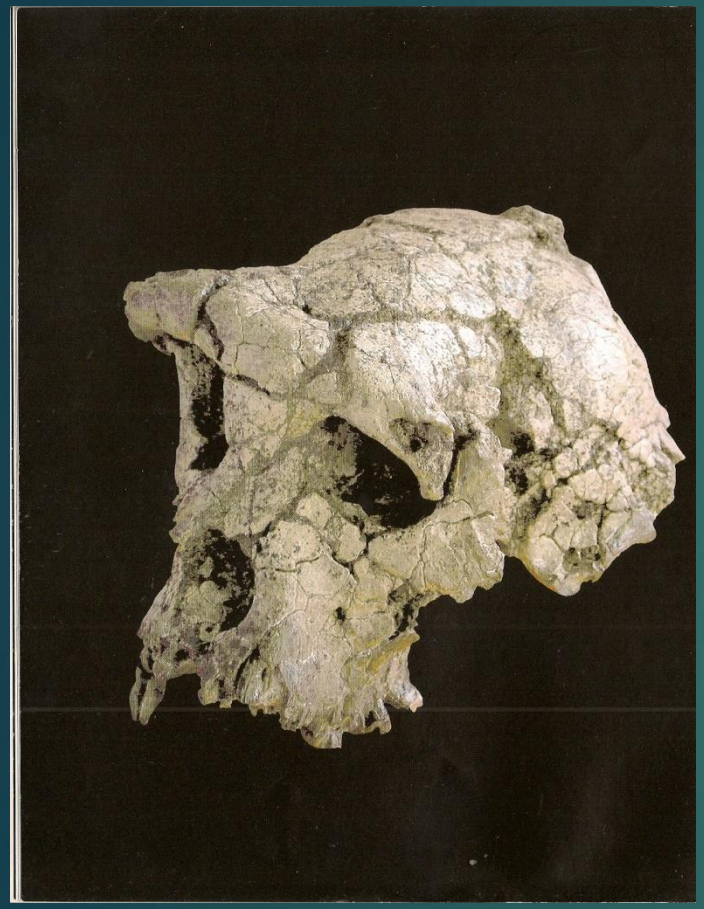
Canines smaller and shorter than those of the male chimp; thick enamel

Sahelanthropus tchadensis

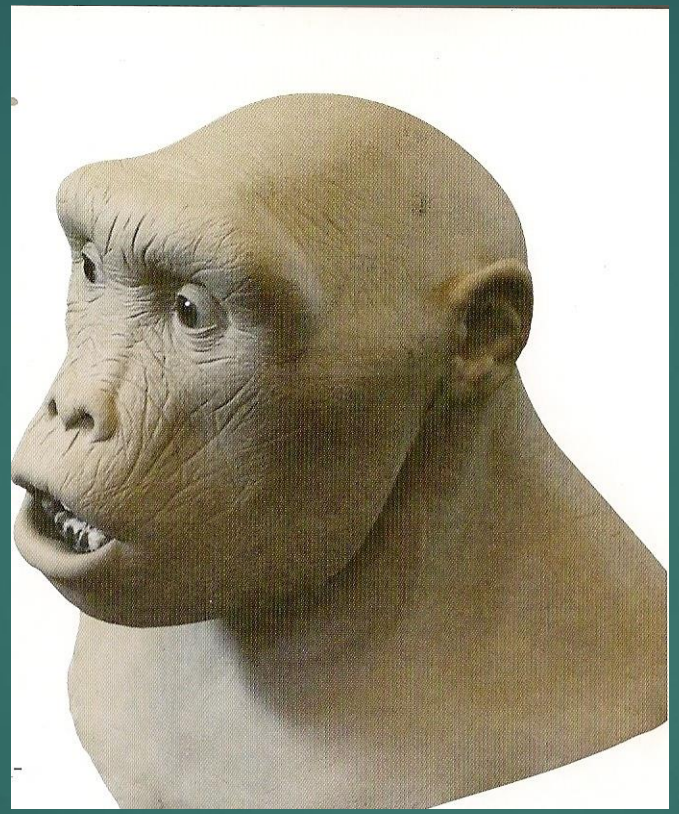


Single Skull (9 cranial elements); no skeleton

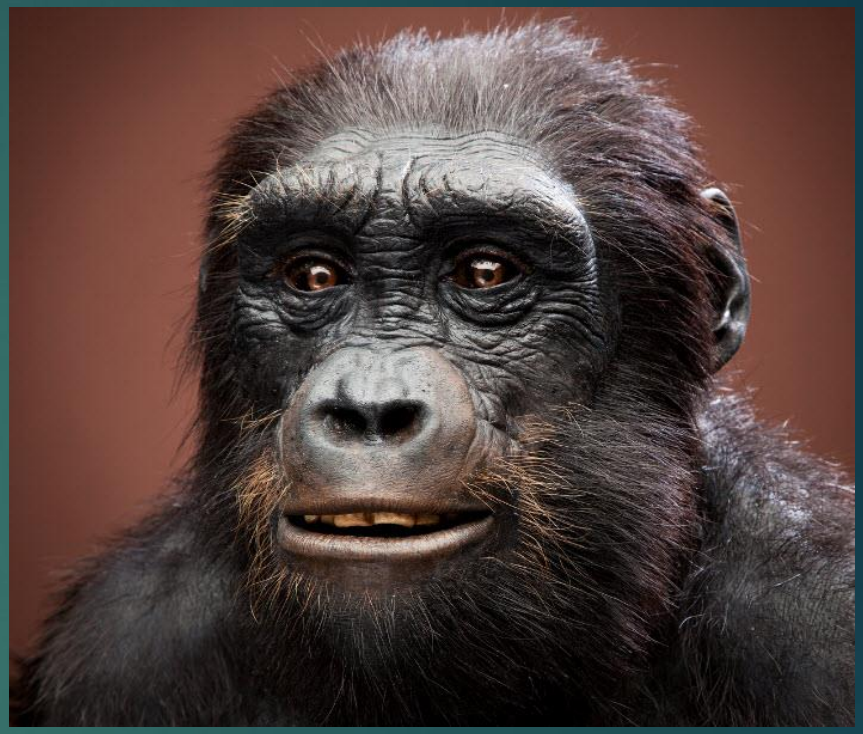
Sahelanthropus tchadensis:



2001 Sahara Desert



6 to 7 Million years old



Reconstruction

Late Miocene ape or hominin ancestor?

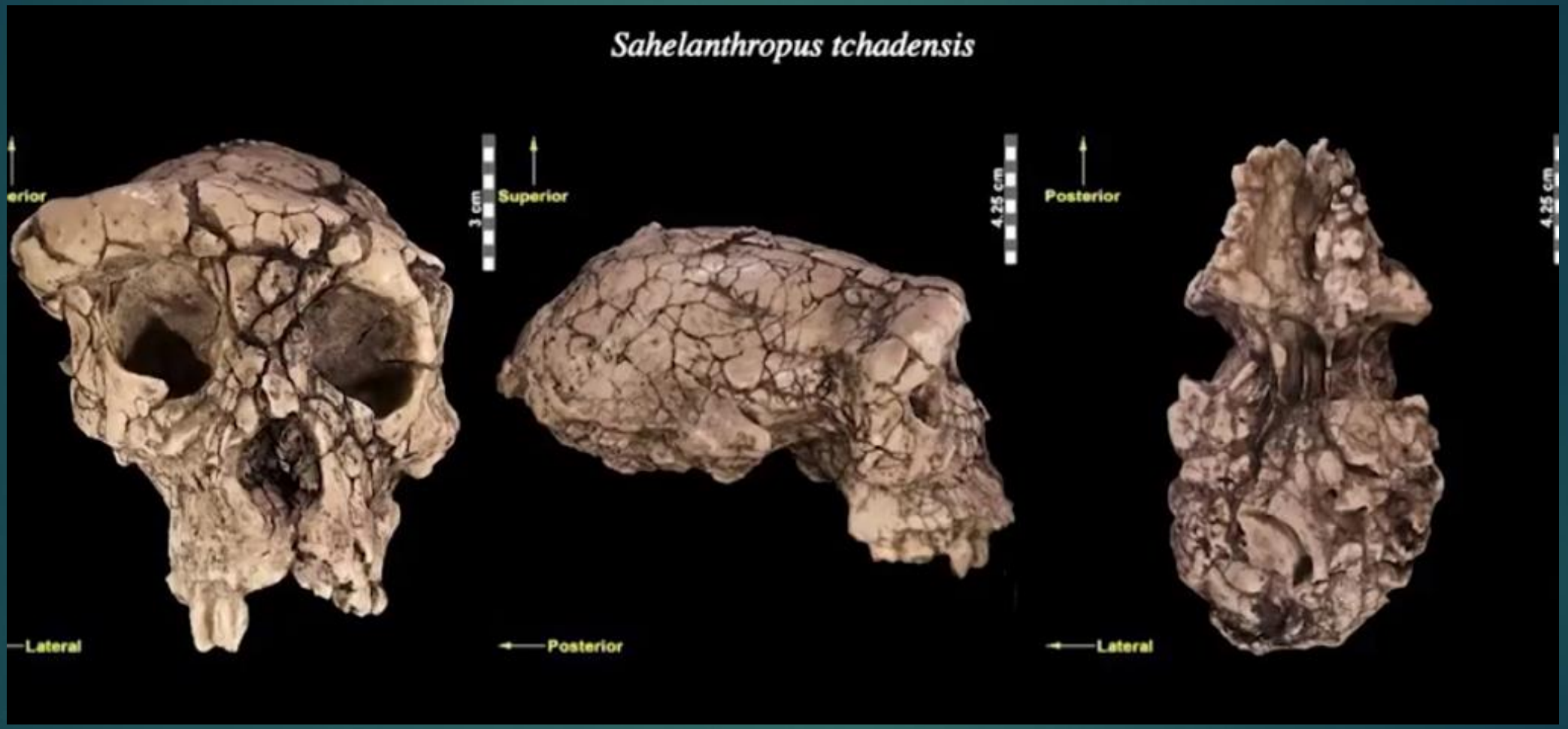
Sahelanthropus tchadensis

- Discovered in 2001; new dental and mandibular specimens reported in 2005
- Estimated 6-7 Ma (relative biochronological methods)
  - Fits with humans if older human-chimp divergence is use
  - Habitat was lakes, grassy woodland, rivers bordered by forests (lakeshore sediments; freshwater fish vertebrates
- Unique mix of humanlike and apelike features
  - Apelike features were an elongated skull, very small brain, massive brow ridges, and no forehead. Back of skull very apelike
  - Humanlike features were a short middle part of the face, smaller canine teeth, and the foramen magnum locale beneath the skull.
- No postcranial fossils known
- Could be hominoid, probably not hominin

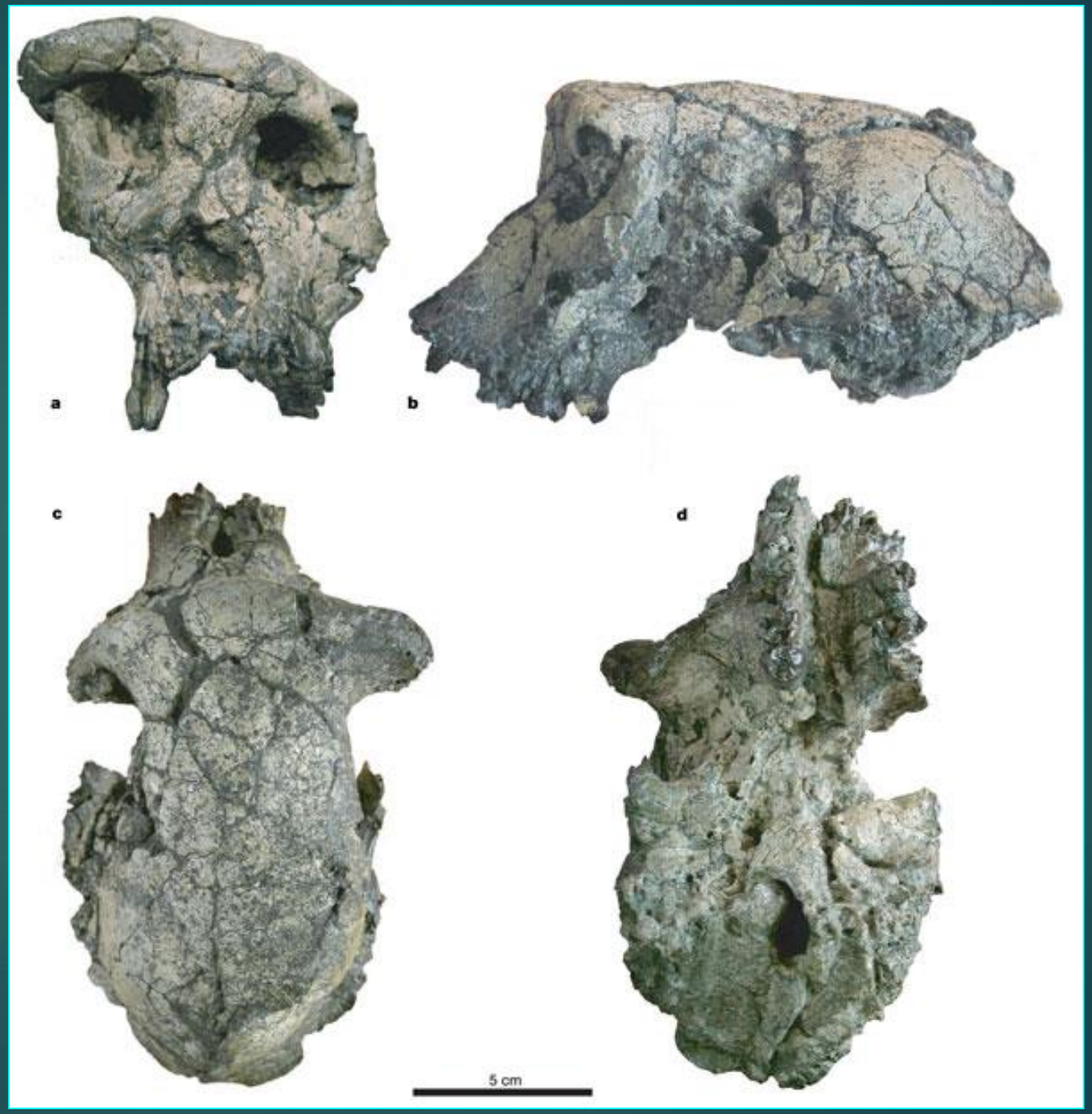
Toumaï

Cranium

Actual skull: not well preserved: distorted, fragments, cracks, warped bones



The seven-million-year-old Sahelanthropus tchadensis skull, known as Toumai, viewed from different sides. Image: Didier Descouens/Wikicommons


a
b
c
d
5 cm

Sahelanthropus tchadensis

- 1 - Shape of skull suggests it was chimp size
- 2 - Average cranial capacity: Unpublished (~ 320–380 cc)
- 3 - Larger supraorbital torus than any other hominin or living ape; continuous & much thicker than any modern ape; prob. a male
- 4 - Face is short and relatively flat (similar to later bipedals)

Sahelanthropus tchadensis

- 5 – Teeth: Canines smaller and shorter than those of a male chimp; worn down only at tip, not on sides like in chimps; cheek teeth larger & shorter than chimp; enamel slightly thicker than chimp (diet with less fruit?); small canine teeth in this male skull distinguished it from other apes. There may have been less competition among *Sahelanthropus tchadensis* males.
- 6 – Foramen magnum: oval, not rounded as in chimp; shape & forward position imply upright walking; Don't know if habitual biped
- 7 – Mandible: thicker than jaw of living chimps
- 8 -The species probably lived in a wooded environment near a lake, perhaps even in a swampy locale

Sahelanthropus tchadensis

- It has a mosaic of features, both of ape and early hominins.
- The face has reduced prognathism and a continuous brow ridge.
- The forward position of the foramen magnum, while not enough evidence to reliably infer habitual bipedalism, still makes such an inference reasonable.
- The primary investigators claim that this form represents the oldest and most primitive hominin, possibly close to the divergence of hominins and chimpanzee ancestors.
- Walking upright may have helped this species survive in diverse habitats, including forests and grasslands.
- Some of the oldest evidence of a humanlike species moving about in an upright position comes from *Sahelanthropus*.

(Zollikofer *et al*. 2005)

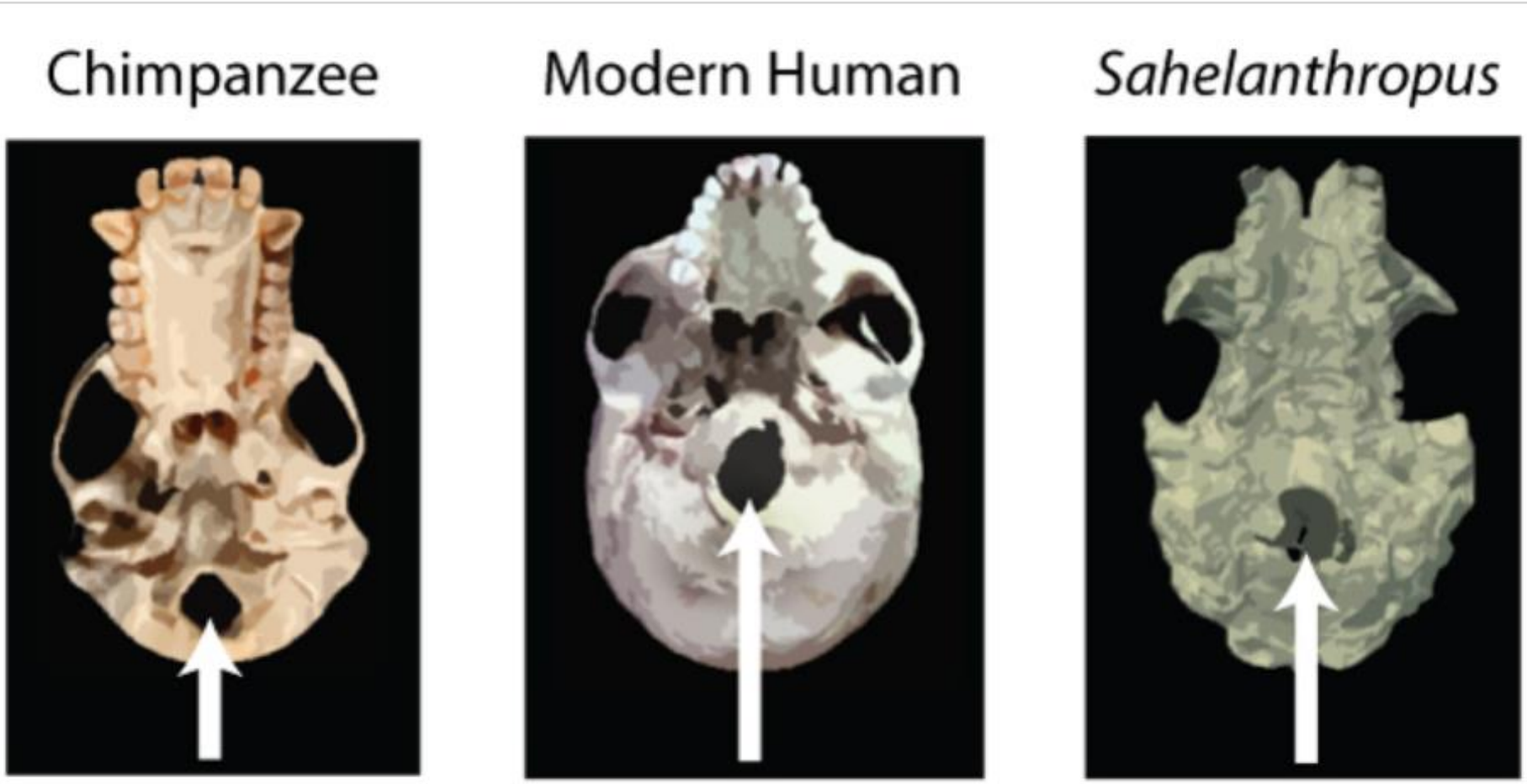
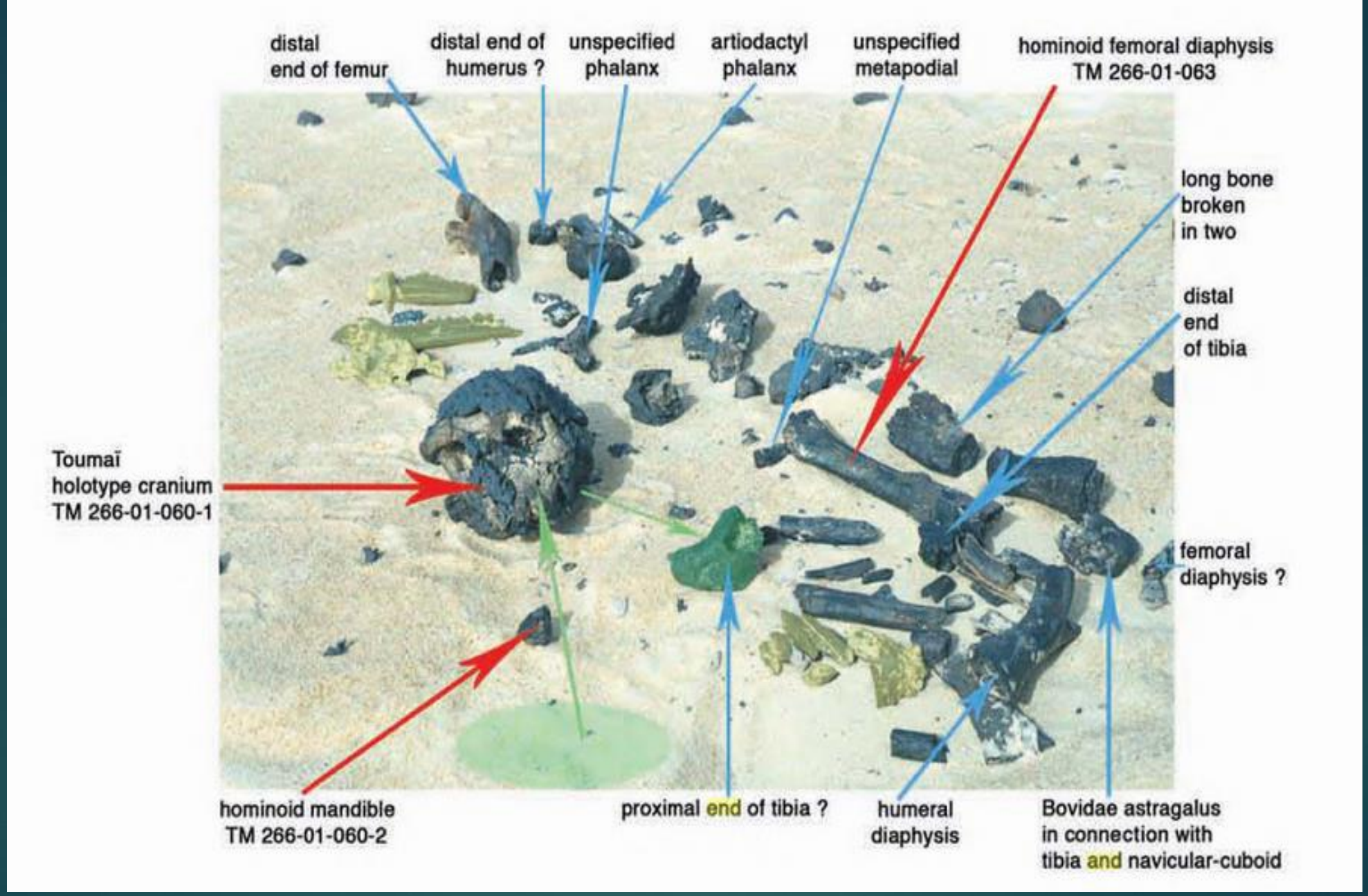


Figure 2: A comparison of the position of the foramen magnum (marked by white arrows) in chimpanzee, modern human and *Sahelanthropus*.

This is a view of the underside of the skull. Note that the foramen magnum of the chimpanzee is positioned posteriorly (to the back of the skull), while that of the modern human is positioned anteriorly (to the front of the skull). The foramen magnum of Sahelanthropus is positioned more anteriorly than that of the chimpanzee and is closer to the human condition, suggesting to Brunet *et al.* (2002, 2005) that it held its head in a similar fashion to humans and was thus bipedal.

Publications

Toumaï: Nature 2005 a&b, 2002 a&b, 1995; Science 2006 a&b; PNAS 2008, 2006, 2005 a&b



Did camel herders rebury Toumai facing Mecca?

Controversies

- Milford Wolpoff and John Hawks: aspects of the skull would have prevented the species from keeping its head upright—and therefore it couldn't have been a bipedal walker; Thus, they suggested, *Sahelanthropus* was not a hominid, just some kind of ape. Some of the dental similarities *Sahelanthropus* shared with hominids could be cases of parallel evolution.
- Beauvilain and Watté paper: picture of bones in 2 straight lines (rearranged toward Mecca?), a burial
- Data still not fully published, 15 years later
- Beauvilain (2008) claimed that Toumaï had not been discovered *in situ*
- Toumaï's skull was found alongside a femur**:** describers of *Sahelanthropus* have never once mentioned femur in print.

A femur

- The primate femur found at the TM 266 locality, originally numbered TM 266-01-63. Photo credit: Aude Bergeret
- Hawks: it will be more difficult to make a case that this femur is a biped than it was for *Orrorin*.

Biochronologic Dating

- The age of *Sahelanthropus* was first determined **biochronologically** (Vignaud *et al*. 2002).

- Unlike eastern African sites, Toros-Menalla lacks volcanic tuffs, which precludes the use of **radiometric dating**.

- Although an age range of 7–6 Ma is suggested for *Sahelanthropus*, cosmogenic nuclide dating using ^{10}Be indicates that the sediments from which the fossils derive are at the older end of that range at 7.2–6.8 Ma (Lebatard *et al*. 2008).

Controversy

- If it is a male (based on torus), then canines are relatively small
- Has distal wear on back of tooth and apical wear (tip, crown wearing); humans mastication produces wear on tip of tooth, not posteriorly as in apes
- Because of distortion, foramen magnum position is hypothesized as being anteriorly located
- Another argument: relative position of the orbits compared to the base of the skull, as measured by the foramen magnum: humans have an angle between the foramen magnum and the orbits that approaches 90 degrees; apes have a more acute angle, again associated with the posterior foramen magnum position that they have. Humans have an angle between the foramen magnum and the orbits that approaches 90 degrees, apes have a more acute angle, again associated with the posterior foramen magnum position that they have. Sahelanthropus has the human like 90 degrees

Controversy

- Various researchers have suggested that the link between browridge size and sex is tenuous — a more parsimonious conclusion is that the cranium belongs to a female individual (Wolpoff *et al*. 2002, Andrews & Harrison 2005), specifically that of a female ape (and not a hominin at all) in whom canines are more likely to be worn at the tip (Wolpoff *et al*. 2002, 2006).
- They further argue that without diagnostic postcranial elements with clear adaptations for obligate bipedalism, such as the pelvis and femur, any inference made about the positional and locomotor behavior of *Sahelanthropus* is premature, because the taxonomic value and functional significance of shortened cranial base and foramen magnum position are unclear (Wolpoff *et al*. 2002, 2006, Andrews & Harrison 2005, Wood & Harrison 2011).

Controversy

- Several derived features with later hominins that confirm its status as a member of the hominin clade.
  - small canines worn at the tip, implicative of a reduced or absent C/P3 honing complex,
  - short cranial base with a foramen magnum that is positioned anteriorly and orthogonal to the orbital plane, suggestive of an upright posture and habitual bipedality
- There is, however, much contention that *Sahelanthropus* is a hominin based on these traits.
- The determination of the small relative size of the canine is dependent on the supposition that the cranium is male as inferred from its large browridges.

Sahelanthropus reconstruction

Most recent reconstruction

Orrorin *tugenesis*

Orrorin tugenesis

Tugen hills of Kenya

Martin Pickford (1943-): *Orrorin tugenensis*

- English paleoanthropologist
- Chair in Paleoanthropology and Prehistory at the Collège de France and researcher at the Département Histoire de la Terre in the Muséum national d'Histoire.
- 1974: lower molar tooth crown discovered
- 2000: with Brigette Senut, in Tugen Hills, Kenya, discovered *Orrorin tugenensis;* 6-5 M

Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K., & Coppens, Y. (January 20, 2001). First hominid from the Miocene (Lukeino Formation, Kenya). Comptes Rendus Academie Des Sciences Paris Serie 2 Sciences De La Terre Et Des Planetes Fascicule A, 332, 137-144.

Brigette Senut (1954-):
Orrorin tugenensis

- French paleontologist
- Professor of Paleontology in the Department of Earth History National Museum of Natural History

- 2000: with Martin Pickford, in Tugen Hills, Kenya, discovered *Orrorin tugenensis*

- 2001: B. Senut make BAR 1000’00 the type specimen

- 12 other specimens discovered since 2000

2000: *Orrorin tugenensis*

6 Ma - bipedality

Orrorin tugenensis

BAR 1000'00 - type

Discoverer:
Kiptalam Cheboi

Locality: Tugen Hills, Kenya

Date: 2000

Age: 6.2-5.5 M (potassium/argon dating of sandwich layers); 6.1-5.8 M (magnetic dating)

Orrorin’ s features

- • Humerus and femur suggest bipedalism
- • Thick enamel
- • Small teeth
- • Large upper canines
- Dentition is morphologically more similar to that of apes, particularly the canine, which is large, triangular and pointed at the apex

Orrorin tugenensis: First bipedal hominin?

- *Orrorin tugenensis* was named in July 2001 on the basis of fossils discovered in the Lukeino Formation, near Lake Baringo in western Kenya (Senut et al. 2001).
- The 13 fragmentary remains include portions of an arm and thigh bones, lower jaws, and teeth of 5 different individuals.
- They date to between 6.1 and 5.8 Ma and are therefore of Miocene age.
- They were discovered by a expedition led by Brigitte Senut and Martin Pickford of the Muséum national d'Histoire naturelle in 2000. Believe it was an ancestral hominin
- The limb bones, about 50 percent longer than those of Lucy, suggest that *Orrorin tugenensis* was about the size of a chimpanzee

Orrorin tugenesis

Evidence is very fragmentary:

- Only postcranial bones found
- Femur more humanlike than Australopithecines
- Humerus (large muscle attachments) and curved finger bone retains evidence of arboreal adaptations

Evidence of leopard-like fang marks on bone (cause of death)

Orrorin tugenensis, 6 Ma

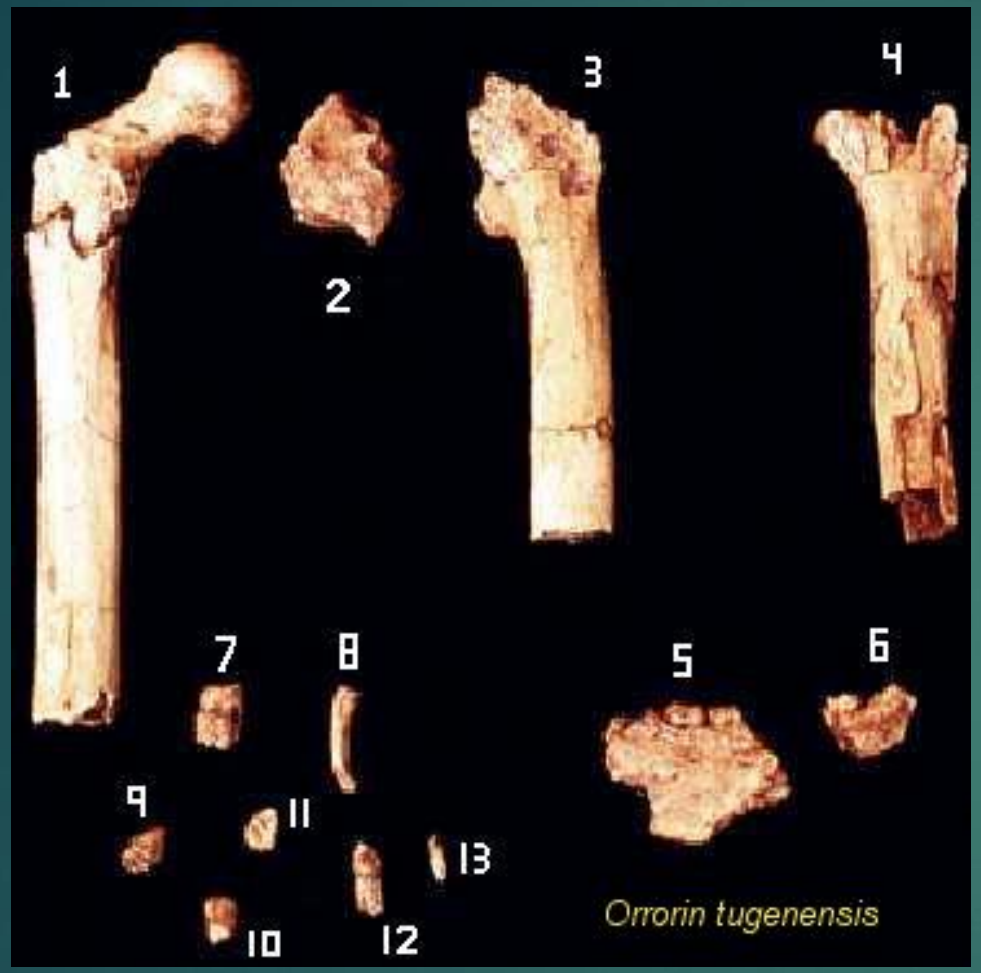
- No cranial fossils recovered
  - Keeps controversy alive (could be *Ardipithecus* per T. White)

- Mixture of apelike-humanlike
- Incisors, canines, premolars, arm and fingers like chimpanzees;
- Humerus and finger bone retains evidence of arboreal adaptations
- Large central incisor and upper canine – more apelike
  - Thick enamel

- Bipedalism inferred from femur anatomy

• There's a little bit of a groove (obturator externus groove). This is a groove that's associated with the contact between a particular muscular tendon and the neck of the femur that come in contact, actually, during bipedal locomotion. Not present at birth, develops through bipedality

Orrorin tugenensis



- Canines / premolars extremely ape-like BUT with thick tooth enamel (like hominins)
- Inferior side of femoral neck (#1 on picture) is thick (like hominins)
- Maybe bipedal (no knee, which is easiest way to tell bipedality)

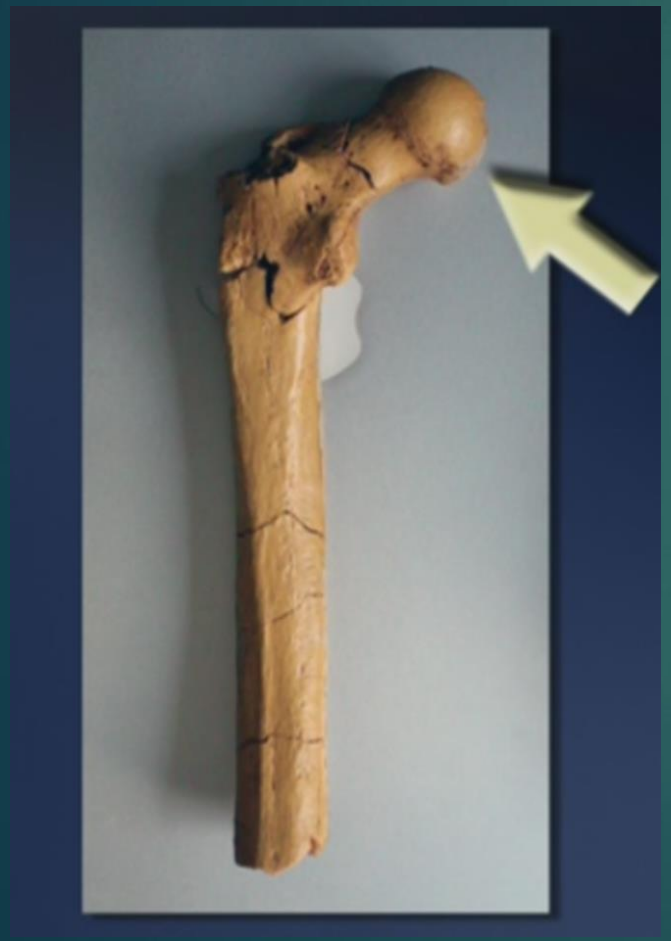
Criticisms

- Criticism about claims that *Orrorin* is hominin:
  - 1 - Morphology of *Orrorin* femur is not much different from that of primates that move in trees
  - 2 – Not demonstrated within higher primates that thick tooth enamel is confined to hominins
  - 3 – Much of morphology of teeth of *Orrorin* is “apelike”

- But researchers have shown that external shape of femur is like that of later archaic hominins

- Best to regard *Orrorin* as creature close to LCA of panins & hominins, but not enough evidence to be sure it is hominin

Orrorin: proximal end of femur: groves on it for muscles that keep it upright; vertical posture in legs (Ardi does not have this)



Evidence for being hominin:

Part of femur just below hip joint:
In climbing primates, outer bone is equally thick all round the neck of femur,
But in habitual bipeds the thickening is greatest at top and bottom of the neck
(back & forward motion of walking)

Senut & Pickford claim outer bone of neck of *Orrorin* femora is also thickened on top & bottom of neck; CT images are indistinct

Orrorin tugenensis

Evidence for being hominin:

- Thick enamel on molar & premolar teeth (not found in panins & only in later hominins)
- Back teeth look human, front teeth look like chimp
- Pulverizing teeth (nuts, seeds, etc.)

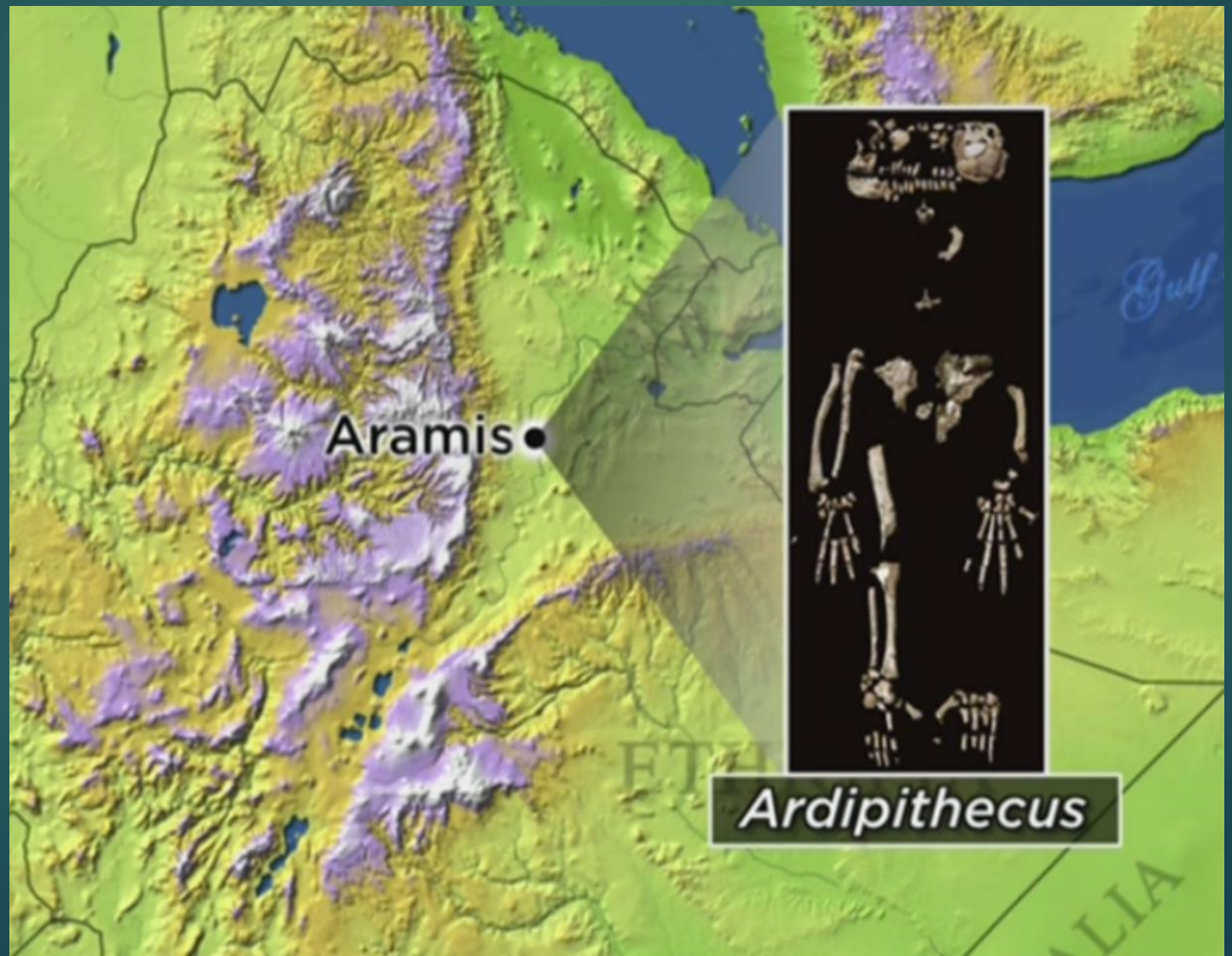
Ardipithecus ramidus

“Ardi”

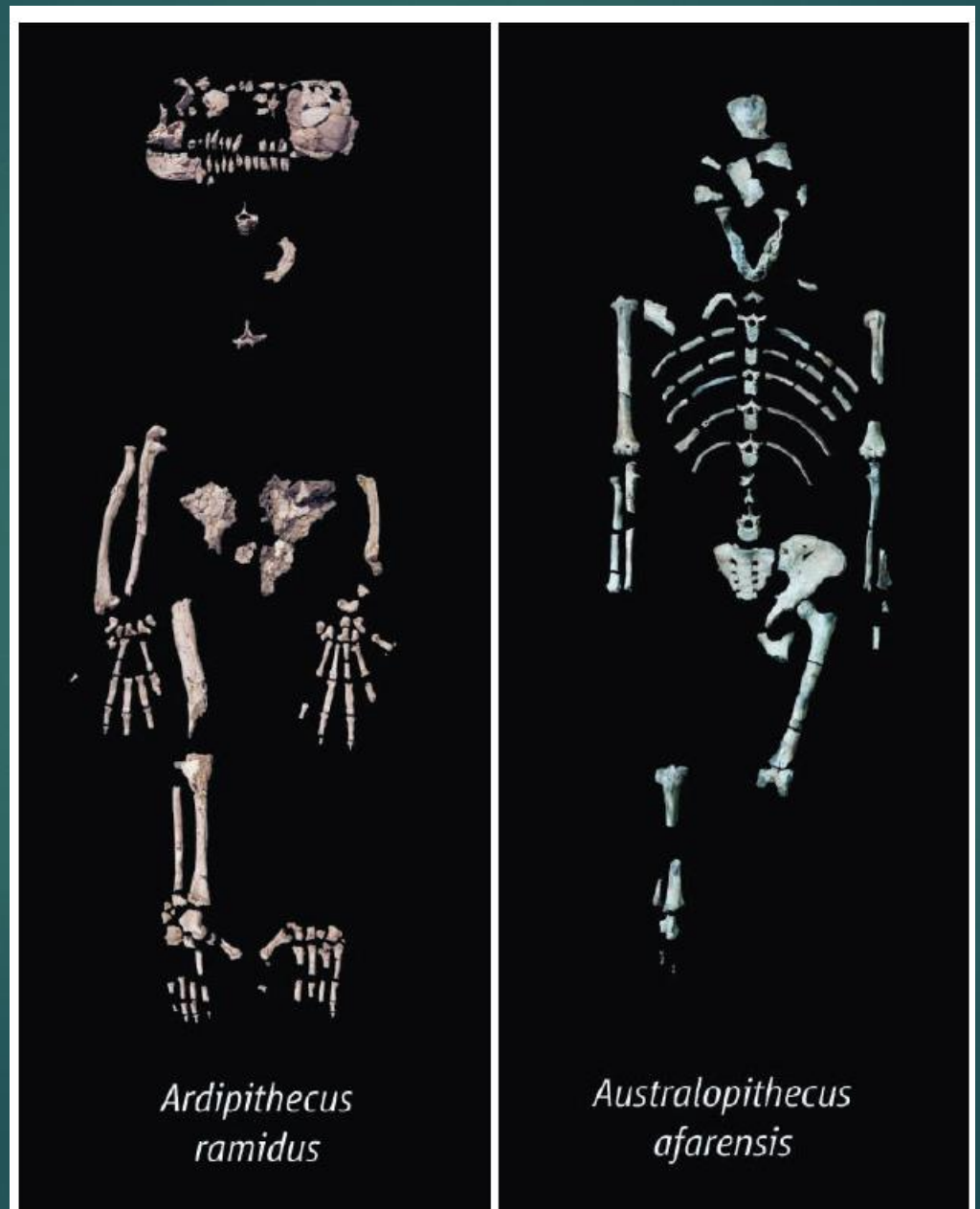
First there were the Australopiths: Then came Ardi…

- Tim White: *Australopithecus* can no longer be legitimately viewed as a short-lived transition between apes and humans. Rather, it represents an adaptive plateau occupied for ~3 Ma by up to four species of small-brained African bipeds.
- Savanna hypothesis: Because *Australopithecus* is often found in open environments, hominid origins are frequently presented as the tale of a tropical forest ape forced to adapt to open savannas that expanded via global climate change. Ardipithecus disrupts such given wisdom.
- Note the importance of complete fossil finds. Ardi preserves so many anatomical parts—in such clear ecological context—that it transforms our understanding of early hominid evolution. It allows assessment of locomotion, diet, habitat preference, and even social behavior.

Tim White's group discovers *Ardipithecus ramidus* (4.4 Ma) at Aramis, Ethiopia, 1992



Ardi vs Lucy: 4.4 Ma vs 3.6 Ma



20 years of study at Aramis, Ethiopia

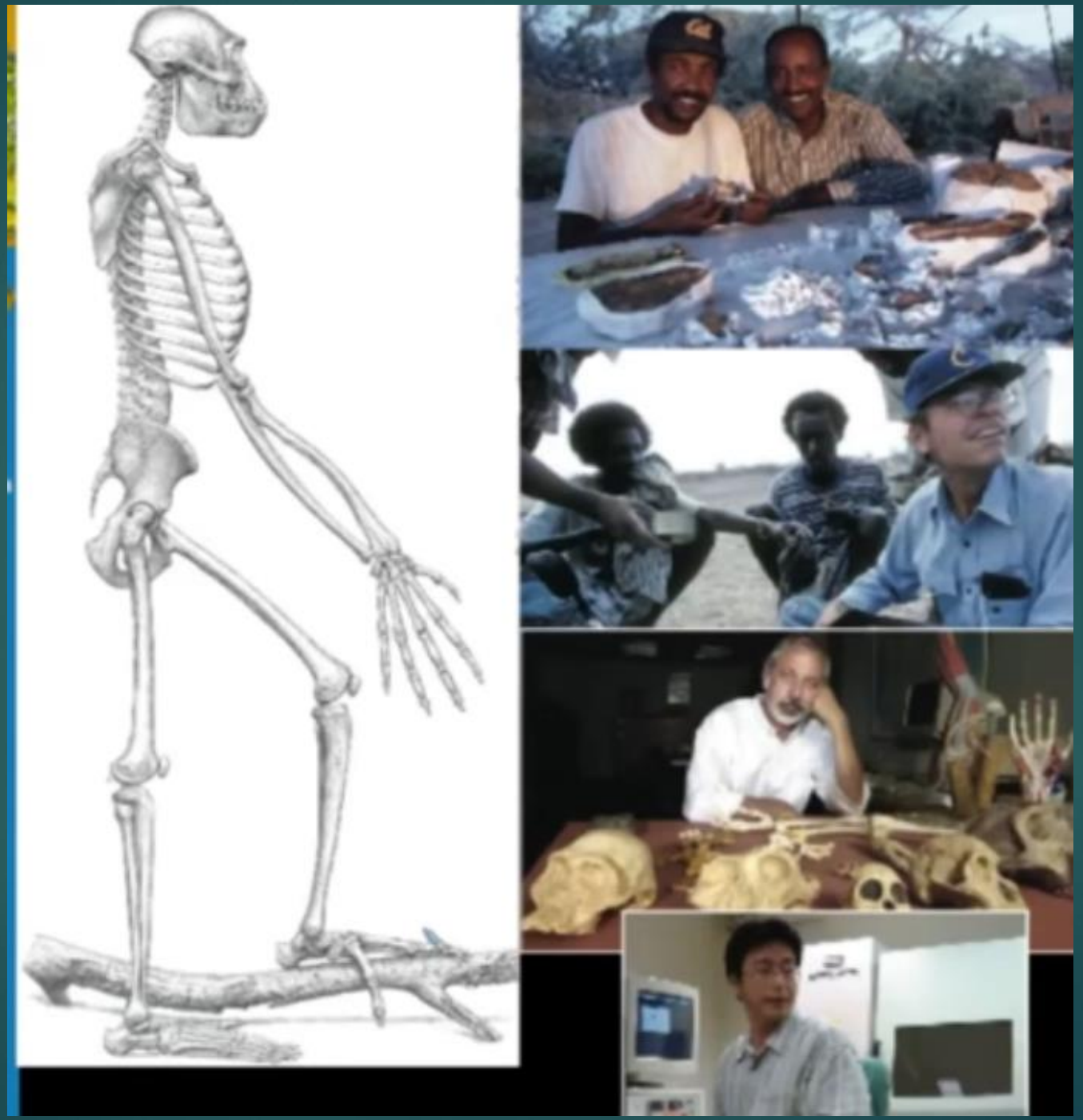
- Lower Aramis Member vertebrate assemblage:
  - totals >6000 cataloged specimens,
  - 109 hominid specimens that represent a minimum of 36 individuals.
  - 135,000 recovered fragments of bone and teeth from this stratigraphic interval
- Once exposed by erosion, destruction after deposition of the fossils by decalcification and fracture is typical.
- The identification of larger mammals was most often accomplished via teeth.
- In the field, the fossils were so soft that they would crumble when touched.
- They were rescued as follows:
  - Exposure by dental pick, bamboo, and porcupine quill probe was followed by in situ consolidation.
  - The encasing sediment was dampened to prevent desiccation and further disintegration of the fossils during excavation.
  - Each of the specimens required multiple coats of consolidant, followed by extraction in plaster and aluminum foil jackets.

Paleontology is difficult profession; but exciting

CONTEXT

- ~6,500 catalogued vertebrates
- ~150,000 vertebrate fragments
- Invertebrates
- Soil and enamel isotopes
- Phytoliths, pollen, seeds, wood

Ardi researchers



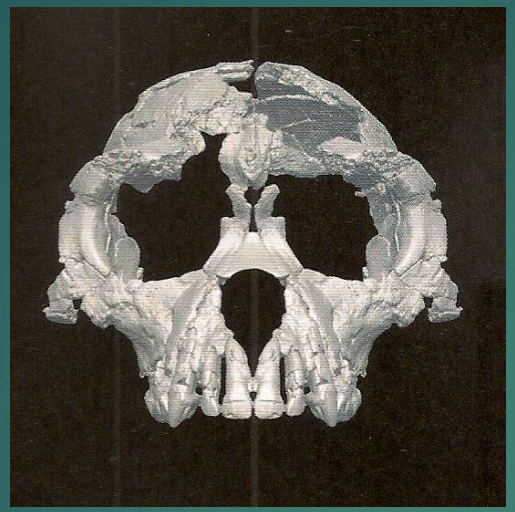
Yohannes Haile-Selassie
Berhane Asfaw

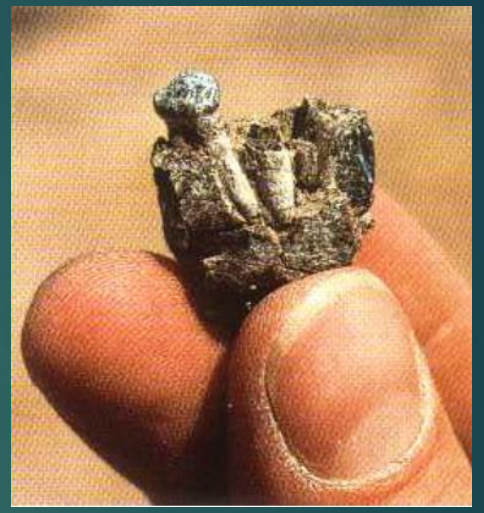
Tim White

Owen Lovejoy

Gen Suwa

1992: *Ardipithecus ramidus*, 4.4 M





Type specimen
ARA-VP-1/129

Discoverer:

Alamayehu Asfaw

Locality: Aramis, Middle Awash, Ethiopia

Age: 4.4 M

Project participant and famous hominid fossil finder Alemayehu Asfaw discovered a hominid lower jaw on February 9, 2006.
Photo by Yohannes Haile-Selassie.

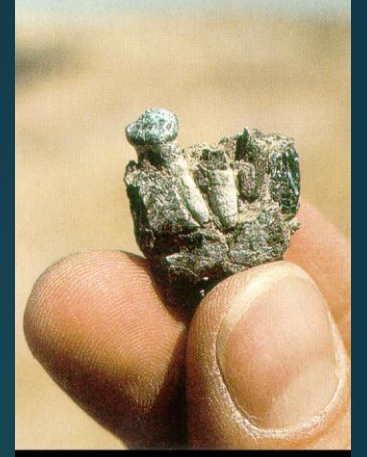
Tim White

- 1992: White with Gen Suwa, discovered ***Australopithecus ramidus*** in Aramis, Ethiopia; a milk tooth; 4.4M

- 1994: The first piece of “Ardi” was found; Yohannes Haile-Selassie found a partial hand bone. Tim White and colleagues make ARA-VP-6/1 (10 teeth) the type specimen of *Australopithecus ramidus*

- 1995: *A. ramidus* transferred to *Ardipithecus ramidus*. *Ardi* means "ground/floor" and *ramidus* **means** "root".

- White’s team have uncovered over 100 fossil individuals of *Ar. ramidus*



Ardi canine

Pan canine

Ardipithecus ramidus: Discovery announced, 1994

- First identified and named in 1994 – thought to be older than 5 Ma
- 15 years to excavate;
- Skull >100 fragments; reassembled via CT, e.g. >1000 hours on skull (Gen Suwa)

ARTICLES

Australopithecus ramidus, a new species of early hominid from Aramis, Ethiopia

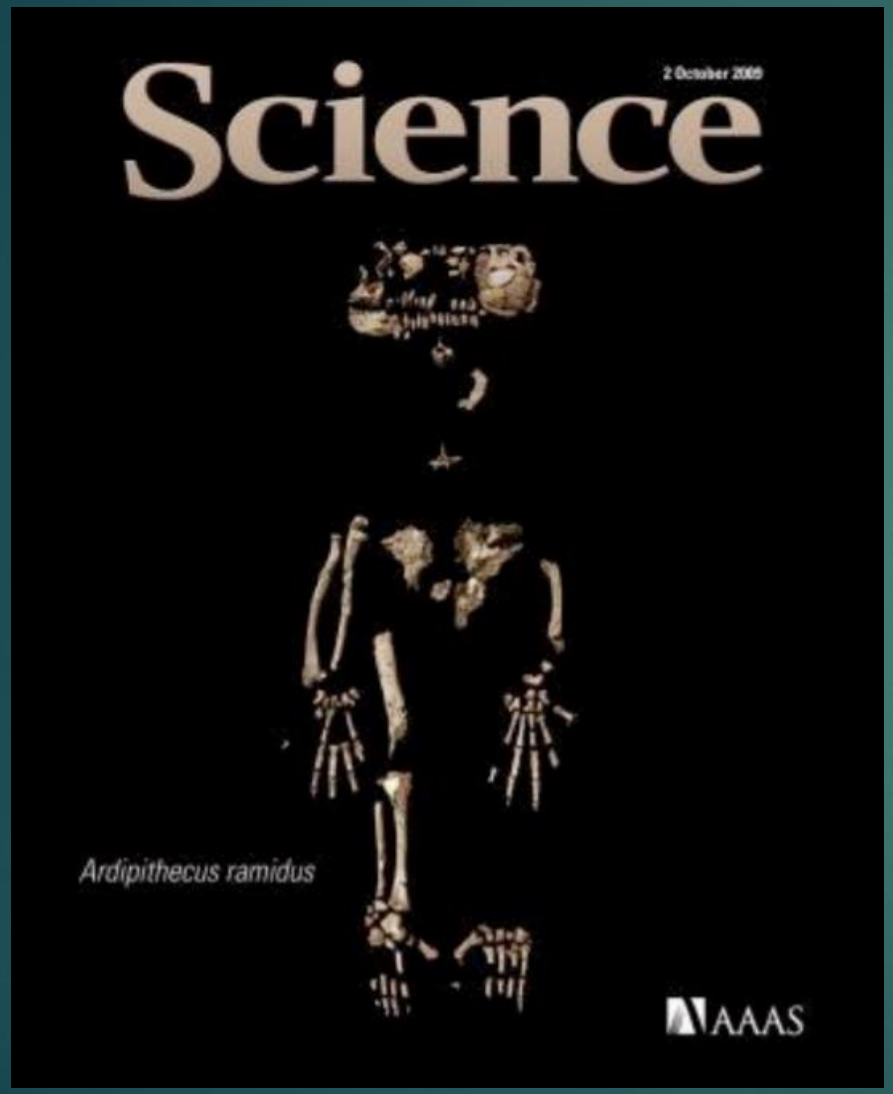
Tim D. White*, Gen Suwa† & Berhane Asfaw‡

Laboratory for Human Evolutionary Studies, University of California, Berkeley, California 94720, USA
† Department of Anthropology, University of Tokyo, Bunkyo-Ku, Hongo, Tokyo 113, Japan
‡ Ethiopian Ministry of Culture and Sports Affairs, Paleoanthropology Laboratory, PO Box 5717, Addis Ababa, Ethiopia

Seventeen hominoid fossils recovered from Pliocene strata at Aramis, Middle Awash, Ethiopia make up a series comprising dental, cranial and postcranial specimens dated to around 4.4 million years ago. When compared with *Australopithecus afarensis* and with modern and fossil apes the Aramis fossil hominids are recognized as a new species of *Australopithecus*—*A. ramidus* sp. nov. The antiquity and primitive morphology of *A. ramidus* suggests that it represents a long-sought potential root species for the Hominidae.

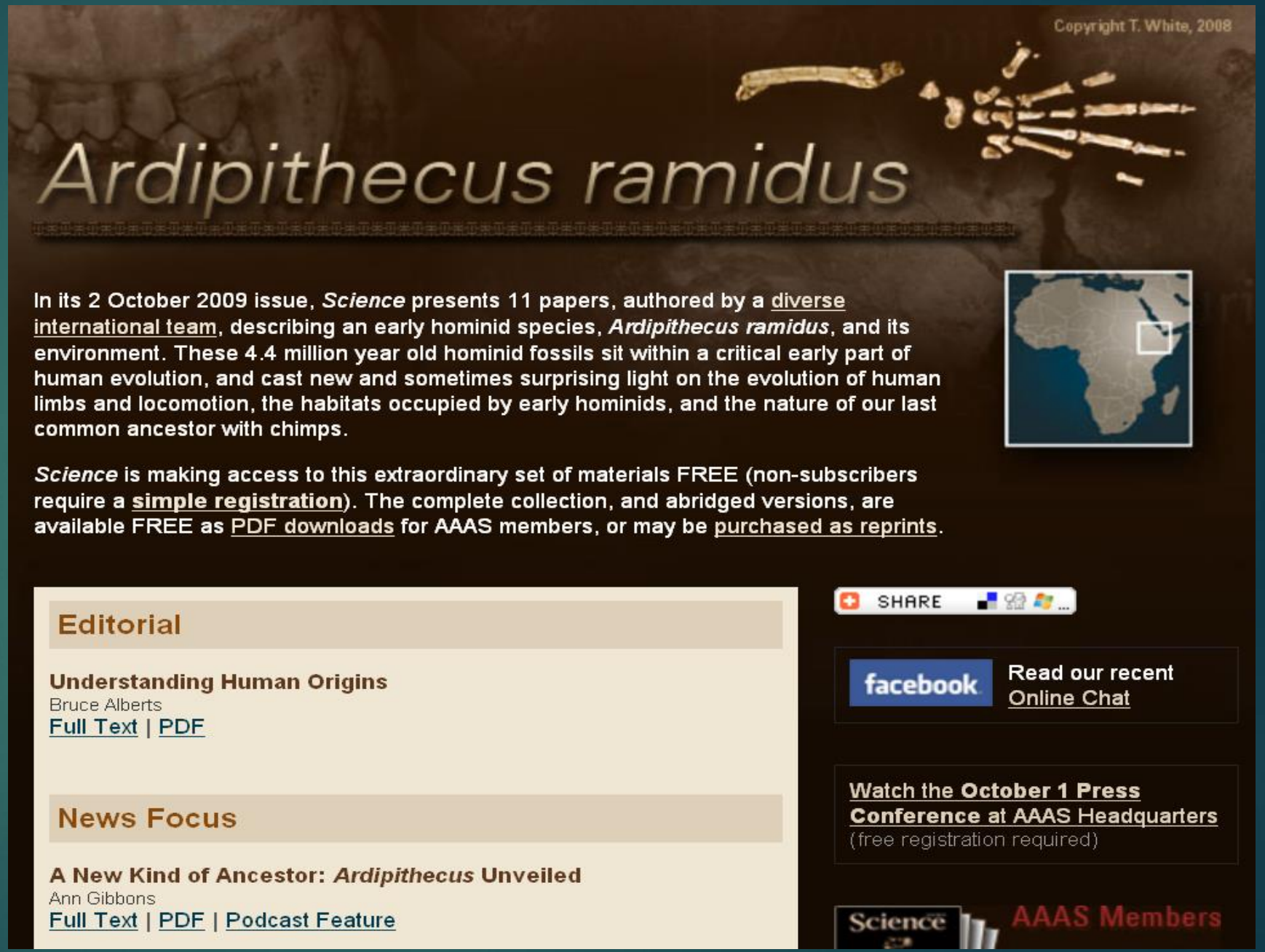
Nature 371: 306-312 (1994)

Publication: White *et al*. 2009



Publication:

- 17 years later
- 11 papers; ~250 pages of a single issue of Science in 2009
- *Ardipithecus ramidus*



T. White: Ardi, Middle Awash, 4.4 Ma, 600 pages, 17 years later

Mission to the Pliocene: 47 authors from 10 countries; 11 papers, *Science*, 10/2/ 2009

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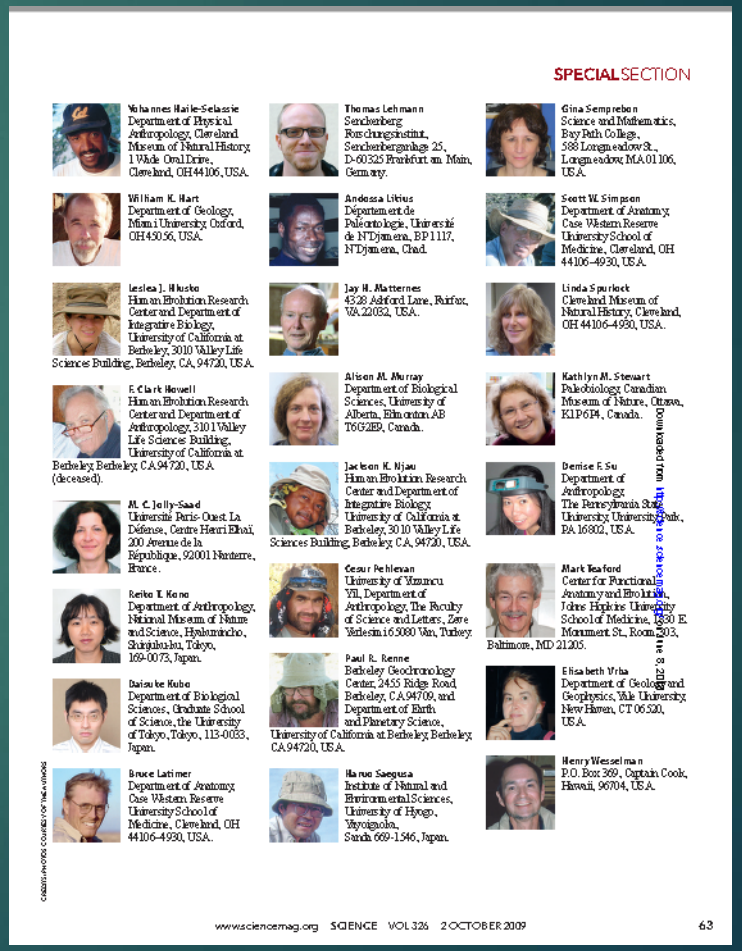

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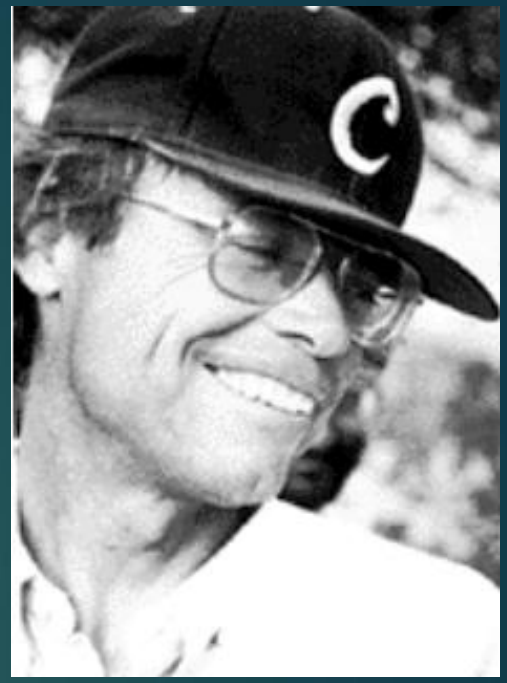
Tim Douglas White (1950-): Lucy, Ardi, *A. garhi*, *H. sapiens idaltu*

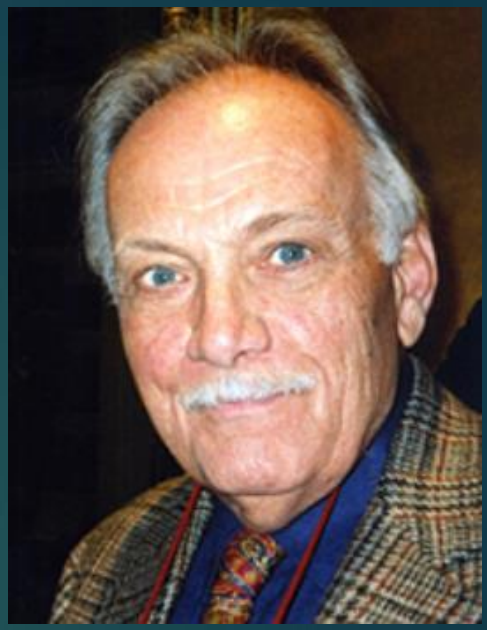


- American paleoanthropologist; student of Milford Wolpoff; Professor of Integrative Biology at the UC, Berkeley
- Head of the Laboratory for Human Evolutionary Studies at the UC, Berkeley
- 1974: White worked with Richard Leakey's team at Koobi Fora, Kenya and then with Mary Leakey at Laetoli, Tanzania.
- 1974: With Don Johanson, discovered Lucy, ***A. afarensis***
- *1992: Discovery of Ardipithecus ramidus*
- 1996: with Berhane Asfaw, discovered ***Australopithecus garhi***; 2.5M, in Bouri Formation, Ethiopia
- 1997: co-discovered ***Homo sapiens idaltu***, with Berhane Asfaw, & F. Clark Howell, at Herto Bouri near the Middle Awash, Afar, Ethiopia; ("Idaltu" is derived from a Saho-Afar word and translates to "elder" or "first born“)
- Fellow of CAS

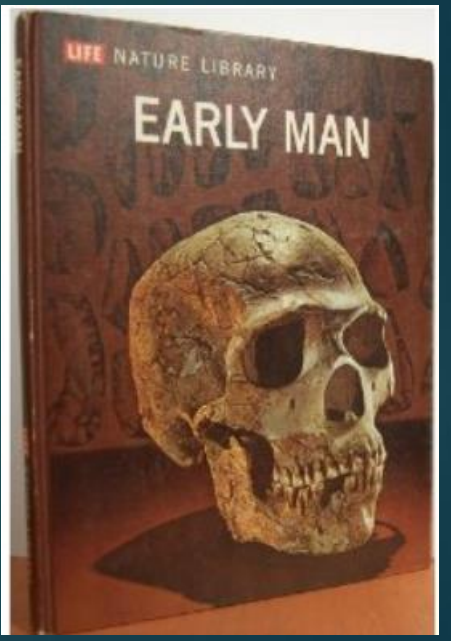
Berhane Asfaw:
Ardi, *A. garhi*, *H. sapiens idaltu*

- Ethiopian paleontologist; Africa's senior paleontologist; crania specialist
- 1981: co-director of the **Middle Awash project with Tim White**
- 1988: **First Ethiopian to receive a doctorate from an American university, UCB**
- 1992: co-discovered, with Tim White, ***Ardipithecus ramidus***
- 1997: discovered ***Australopithecus garhi***, 2.5 M;
- 1997: co-discovered, with Tim White, ***Homo sapiens idaltu*** (elder), 1M.

Francis Clark Howell (1925-2007):



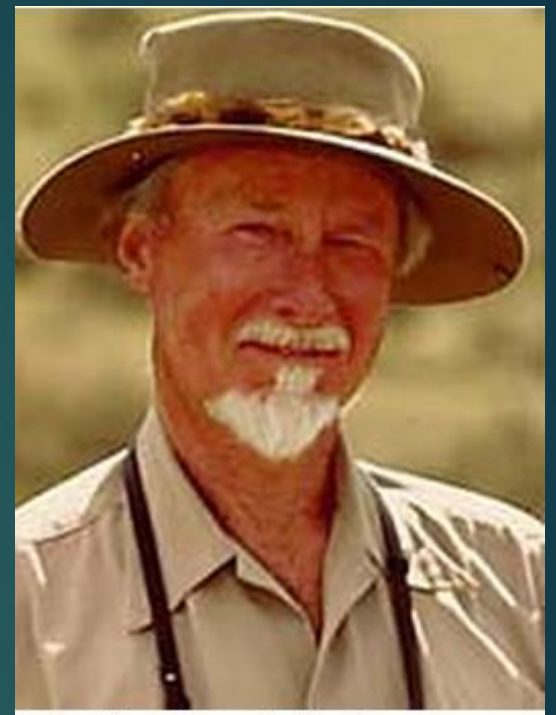
- American anthropologist;
- Father of Modern Paleoanthropology
- Leader of an **Omo Basin expedition**
- Co-director with Tim White of the Human Evolution Research Center
- With Tim White, **description of *Ardipithecus ramidus & Homo sapiens idaltu***
- Instrumental in the creation of the L.S.B. Leakey Foundation; Ex-president of CAS

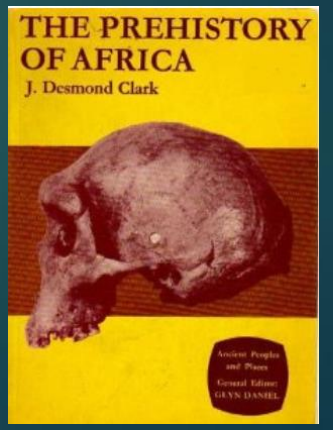


J. Desmond Clark (1916-2002): Middle Awash Project, Ethiopia

- British archaeologist
- Professor of Anthropology at the University of California, Berkeley
- Co-leader for 20 years with T. White and Ethiopian archaeologists of the **Middle Awash Project**; excavated the stone tools
- Middle Awash Project discoveries:

  Ardipithecus, Ardipithecus kadabba and *Australopithecus garhi*
- 18 books, 300 articles


John Desmond Clark



Gen Suwa (1954 -)
Ardipithecus ramidus & CT Scan

- Japanese paleoanthropologist
- University of Tokyo

- 1990: Student of Tim White: working in Ethiopia with the Middle Awash team

- 1992: Found first tooth of *Ardipithecus* in Aramis;

- Worked on the analysis and reconstruction of *Ardipithecus ramidus; 1000 hours on analysis of skull*

- Specialist with CT scan technology

- 2007: *Chororapithecus abyssinicus*, 10.5-Myr, Miocene ape with gorilla-sized dentition; basal member of the gorilla clade?

Ardipithecus ramidus

- One of the most complete early human skeletons scientists have ever found, and only one of 10 known early human partial skeletons over 1 million years old.

- Later, between 1999 and 2003, a team headed by Sileshi Semaw, of Indiana University, discovered fragmentary remains from nine separate *Ardipithecus ramidus* individuals at As Duma in the Kada Gona river valley on the western margin of the Afar.

- *Ardipithecus ramidus* is unusual among the earliest hominin species in having a large sample size (110 specimens from Aramis) — the most complete and important of these is the recently described partial skeleton (ARA-VP-6/500), nicknamed "Ardi" (White *et al*. 2009).

Ardipithecus ramidus

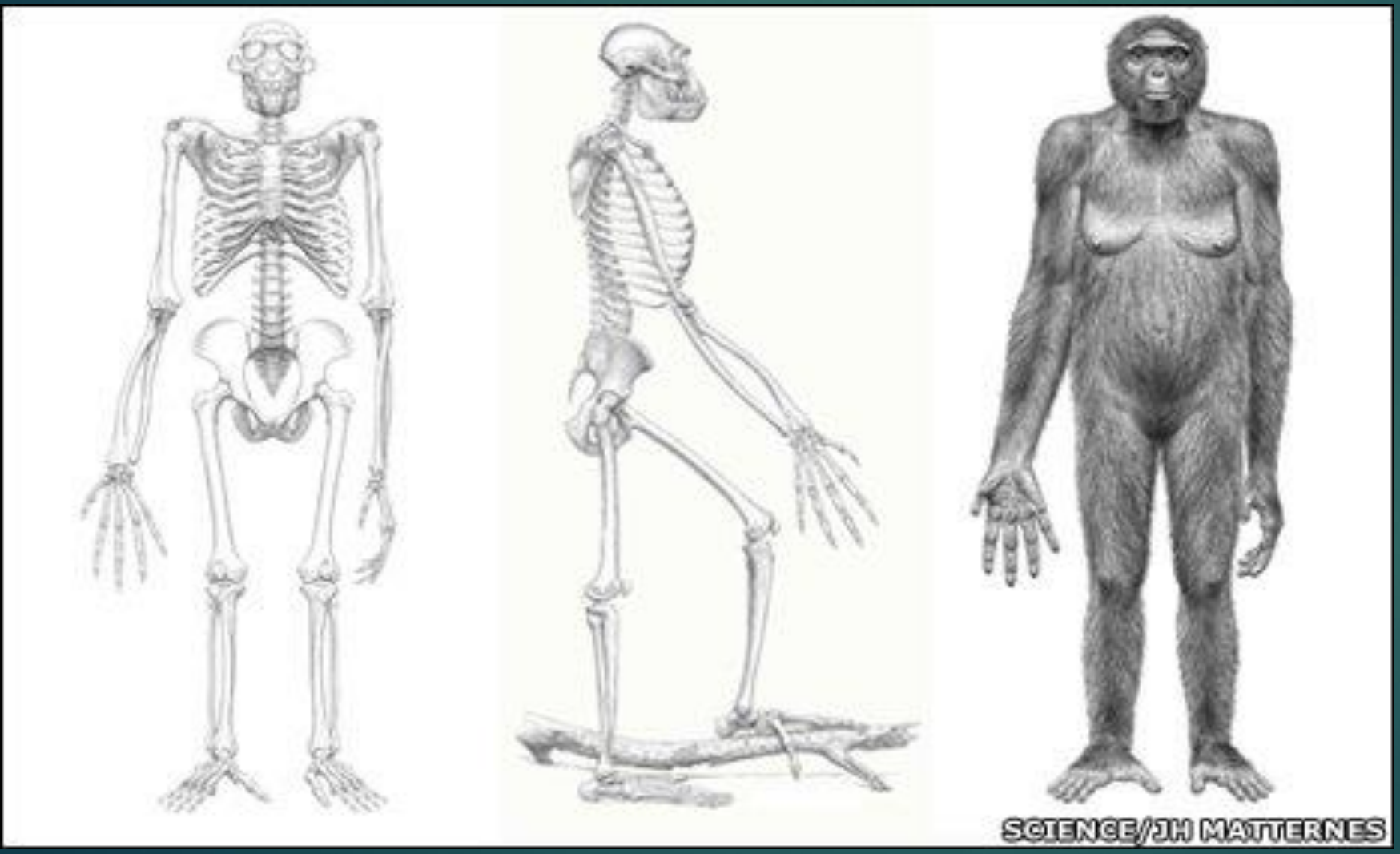
- **Between Apes and Australopithecines.** All specimens presently assigned to *Ardipithecus ramidus* date to around 4.4 Ma and show a mixture of ape-like and australopithecine-like features.

- Because *Ardipithecus ramidus* shares certain characteristics with apes, some experts think it's an ancestor of chimpanzees instead of humans.

- But the consensus considers it close to a common ancestor of both apes and humans since its teeth are intermediate between those of earlier apes and *Australopithecus afarensis*.

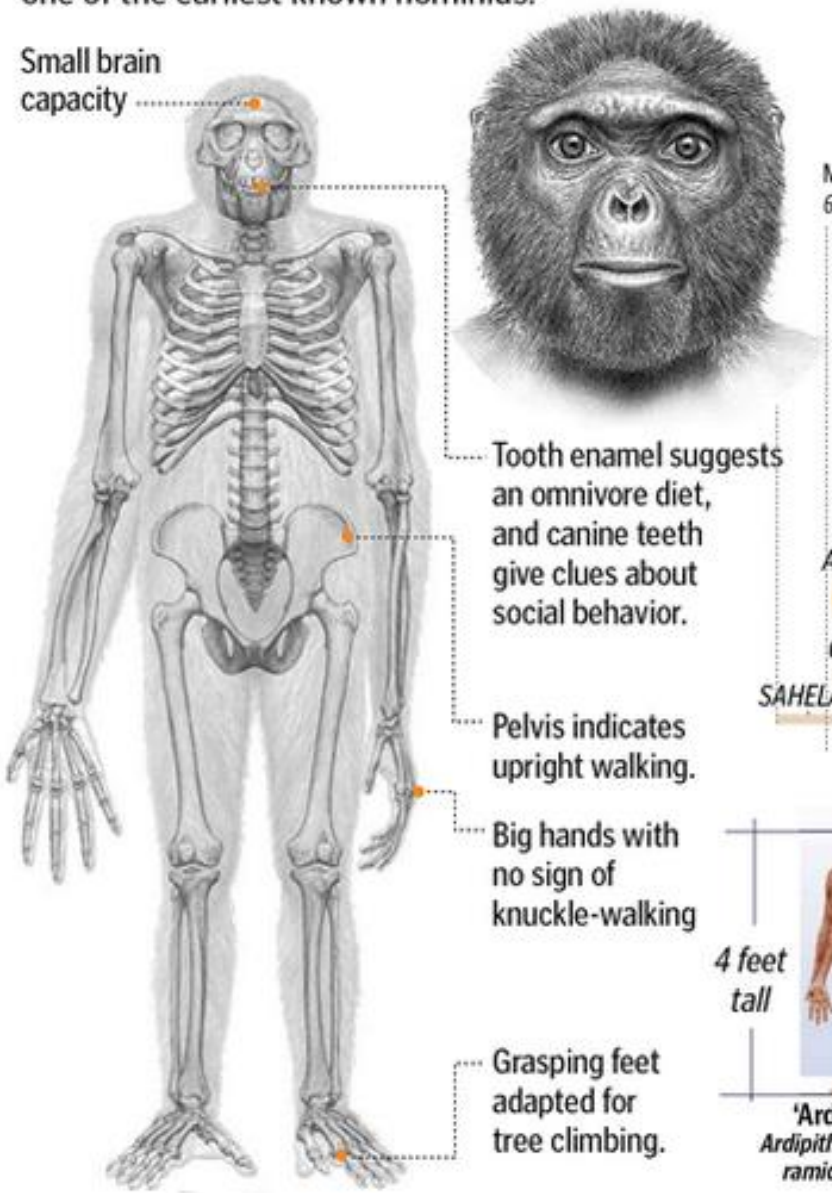
- *Ardipithecus ramidus* was bipedal when on the ground

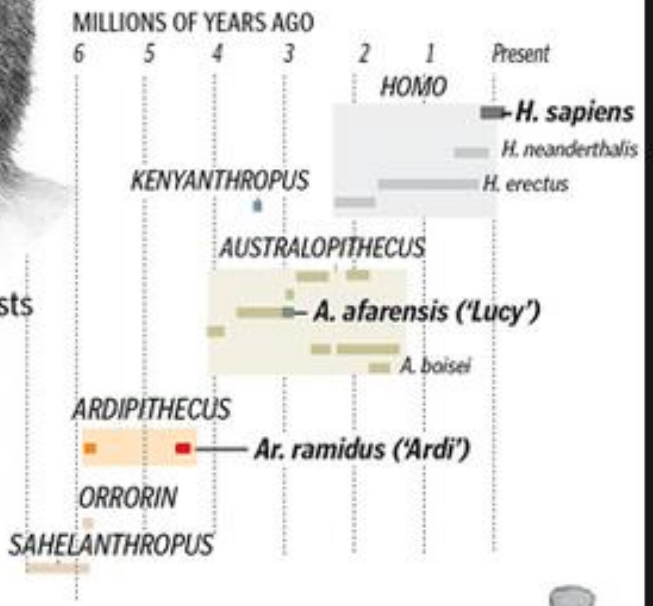
Ardipithecus: 4.4 million years ago, 300-350cc, omnivore

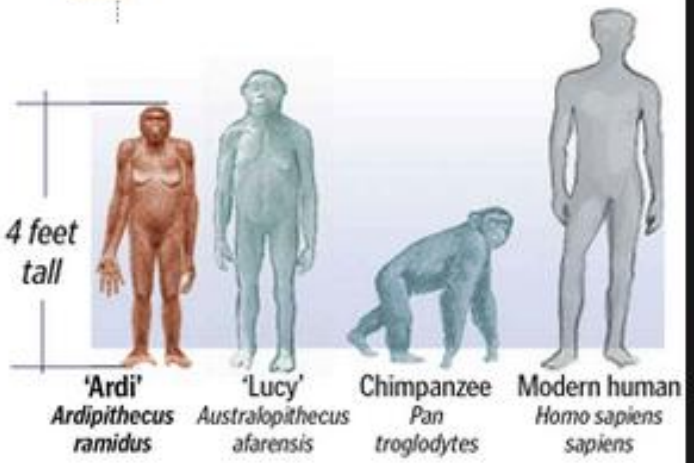


- **Height:** Females: average 3 ft 11 inches (120 centimeters)
- **Weight:** Females: average 110 lbs. (50 kg)
- Relatively low sexual dimorphism

Research on a 4.4 million-year-old skeleton — a female Ardipithecus ramidus — reveals surprising traits of one of the earliest known hominids.



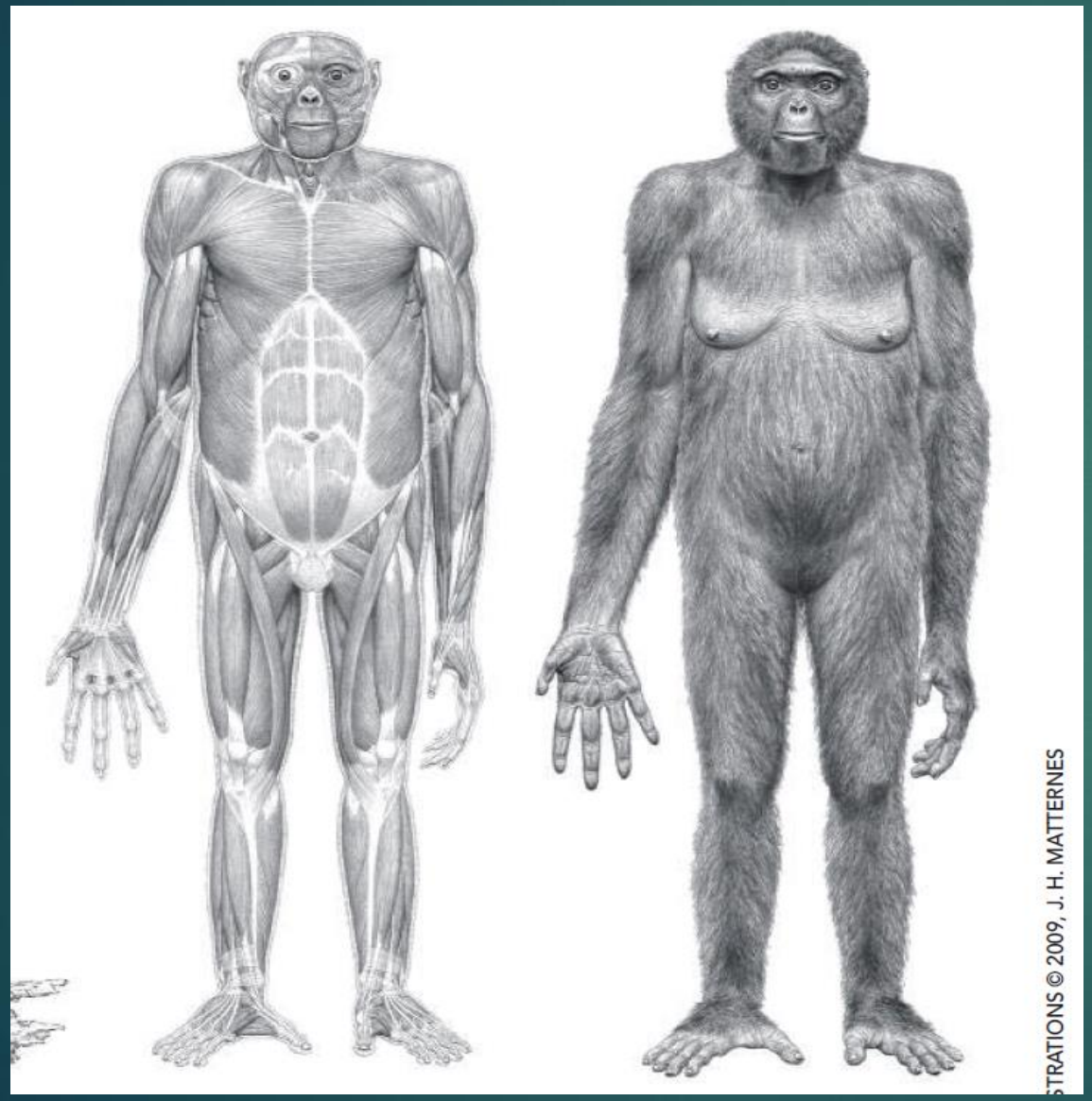




SOURCE: Science/AAAS; reconstruction by J.H. Matternes

JAVIER ZARRACINA/GLOBE STAFF

Ardipithecus ramidus – “ARDI”



- Most complete skeleton older than Lucy
- 45% of the full skeleton: sets of teeth, part of underside of cranium, parts of several jaws, and some limb bones
- Canines less apelike than *Ar. kadabba*
- Not *Australopithecus*
- Similarities to *Sahelanthropus*
  - Very early stage of human evolution

Ardipithecus ramidus

- 'Ardi' ARA-VP-6/500: A partial skeleton found in 1994, consisting of about 125 pieces, was described and published in 2009.
- It is the oldest known ***skeleton*** of a possible human ancestor.
- The individual is believed to be a female and is nicknamed ‘Ardi’.
- The skeleton was in extremely poor condition and it took the team 17 years to excavate, scan, make virtual reconstructions, assemble and then analyze.
- Finger bones were long and curving, both features useful for grasping branches.
- Upper and lower legs bones (femur and tibia) have features consistent with bipedalism.
- Feet were relatively flat and lacked arches, indicating this species could probably not walk or run long distances.
- They had a grasping abducted toe, characteristic of gorillas and chimps, combined with a rigid foot. Did not walk like us.

Ardipithecus ramidus

- *Ardipithecus ramidus* is currently represented by 110 fossil specimens, including a partial female skeleton rescued from erosional degradation.
- Little difference in body size between males and females.
- Her lower face had a muzzle that juts out less than a chimpanzee's
- The cranial base is short from front to back, indicating that her head balanced atop the spine as in later upright walkers.
- Her face is in a more vertical position than that of a chimpanzee.
- Small bodied (64-100 lbs); stood about 120 cm tall.

Ardi characteristics

White et al., 2009

- Reduced canine/premolar complex, indicative of minimal social aggression.

- Skeleton reveals that it moved capably in the trees, supported on its feet and palms (palmigrade clambering), but lacked any characteristics typical of the suspension, vertical climbing, or knuckle-walking of modern gorillas and chimps.

- More omnivorous than chimpanzees (who are ripe fruit specialists) and likely fed both in trees and on the ground.

- Consumed only small amounts of open-environment resources, arguing against the idea that a rise of grasslands was the driving force in the origin of upright walking.

Arboreal and bipedal

- Although badly fragmented, the pelvis recovered reveals a morphology quite different from that of living apes, with a shorter, more bowl-like shape that strongly suggests *Ardipithecus* walked bipedally

- However, its long forelimbs and fingers and its divergent, grasping first toe (hallux) suggest *Ardipithecus* spent much of its time in the trees.

- The overall impression is of a largely arboreal species that walked bipedally whenever it ventured to the ground.

Derived characters of Ardi

Key derived characters of Ardi shared with other hominis:

- Teeth: reduced/feminized, non-projecting, blunt canines; lack of a functional C/P3 honing complex; reduced canines similar to those of *Orrorin* and *Sahelanthropus*.
- Skull: Basicranium foreshortened; small face; anteriorly positioned foramen magnum
- Pelvis: short, broad upper pelvis, specialized for bipolarity
- Foot: lateral forefoot specialized for bipedality
- Characters inferred to be indicative of bipedality: such as the presence of a greater sciatic notch, anterior inferior iliac spine, inferred lumbar lordosis, and dorsal canting of the pedal phalanx

Ardi’s Ancestral & Derived features

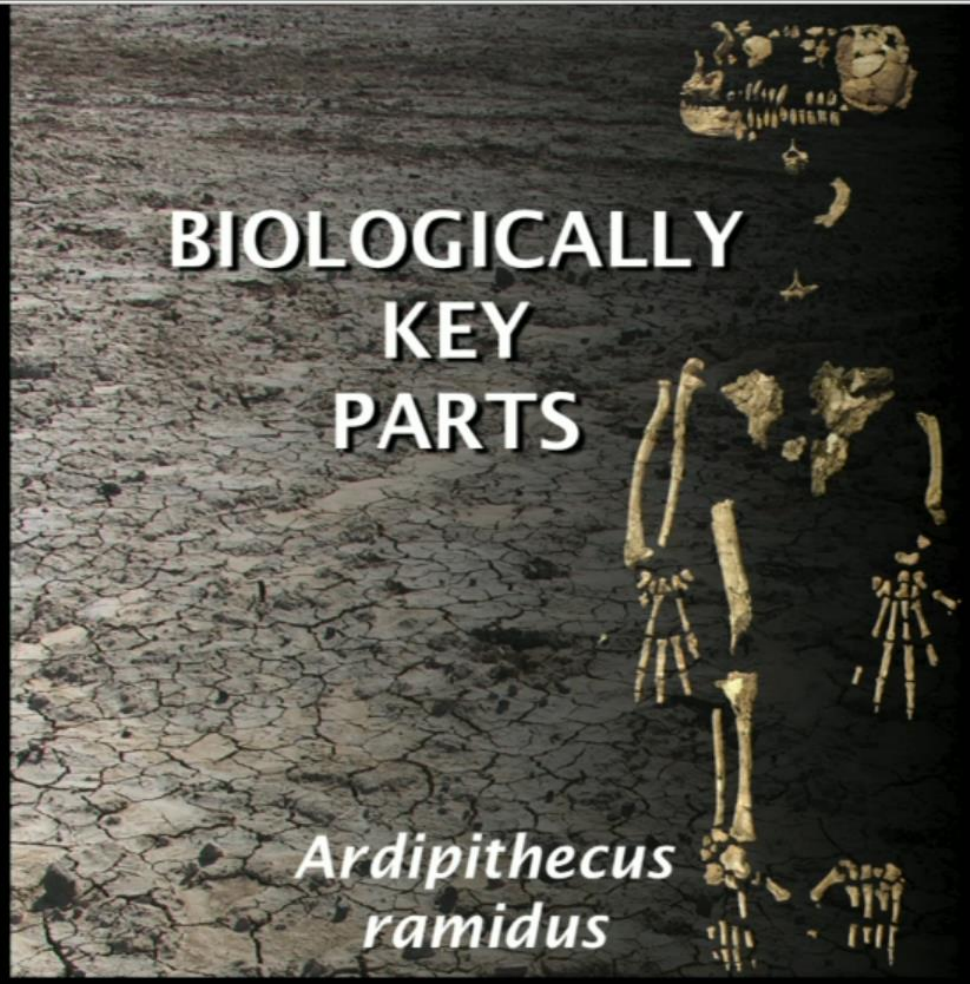
- "Ardi" also shows a number of ancestral characters, particularly in the postcranium:
  - fully opposable big toe,
  - absence of longitudinal arch in the foot,
  - relatively equal fore- to hind-limb lengths,
  - ape-like lower pelvis
  - Small brain size (300-350 cc)

- Ardi" shows an unexpected mosaic of derived and primitive features that suggest it was a facultative biped, able to climb in the trees effectively by palmigrade quadrupedalism.
- This refutes the previous assumptions that the last common ancestor was chimpanzee-like, and instead suggests that living chimpanzees are highly specialized.

Ardi

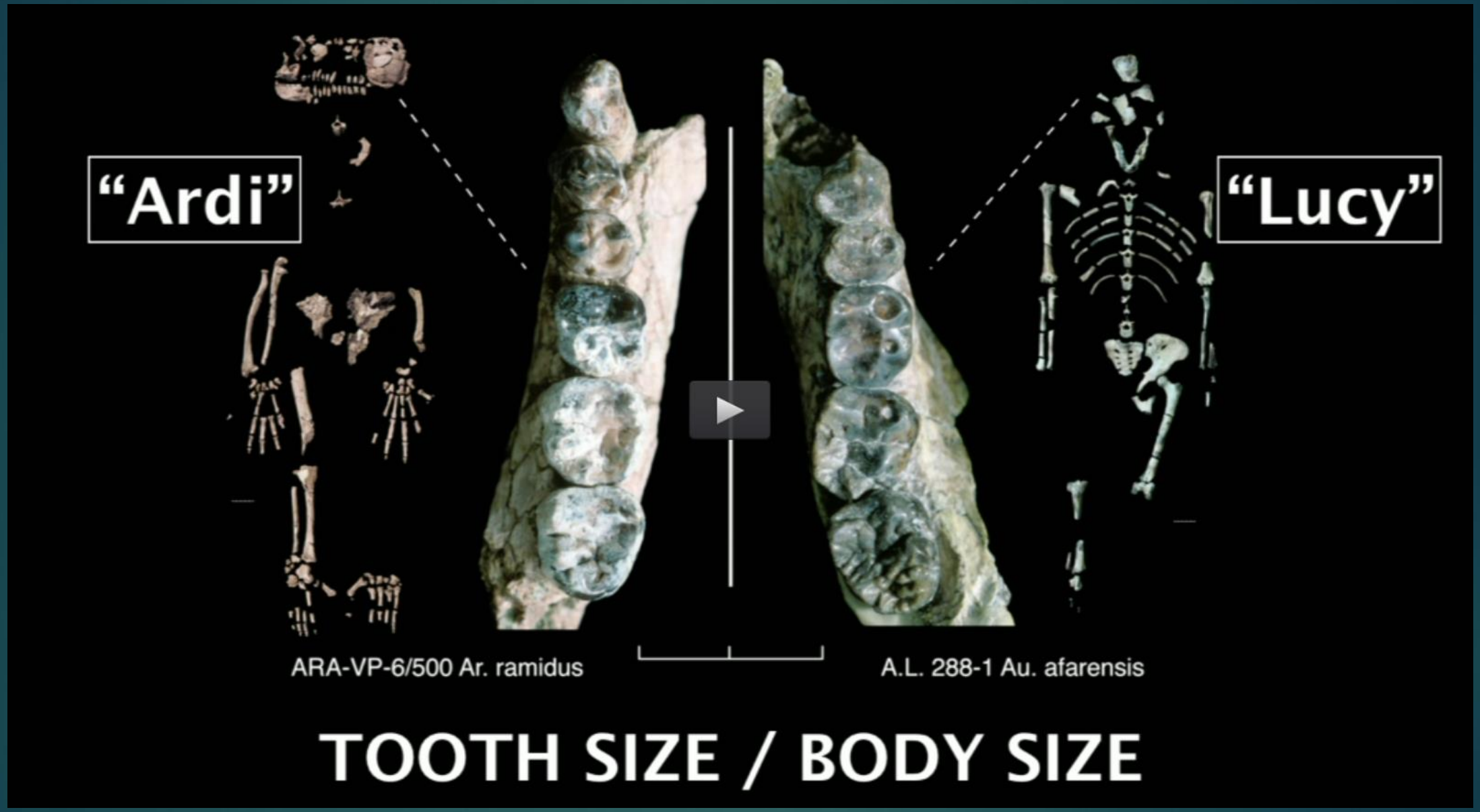
- The skull of *Ar. ramidus* is rather ape-like and broadly similar to that of *Sahelanthropus*
- Ardi's anatomy is not at all chimp-like. She was neither a knuckle-walker or a brachiating ape.
- Ardi lived in a forest setting and spent time in trees as well as on the ground.
- But her anatomy suggests she was adapted to move around in those trees almost like a large monkey might, moving cautiously on feet that – unlike gorilla and chimp feet – seem to have been unsuitable for wrapping around branches for grip.
- Put simply, Ardi looked "primitive" – and that suggested that the LCA looked primitive too.

1 individual, ~125 pieces @ 4.4 Myr



- Skull
- Teeth
- Pelvis
- Hands
- Feet

+ parts of 36 **additional** hominid males, females, children

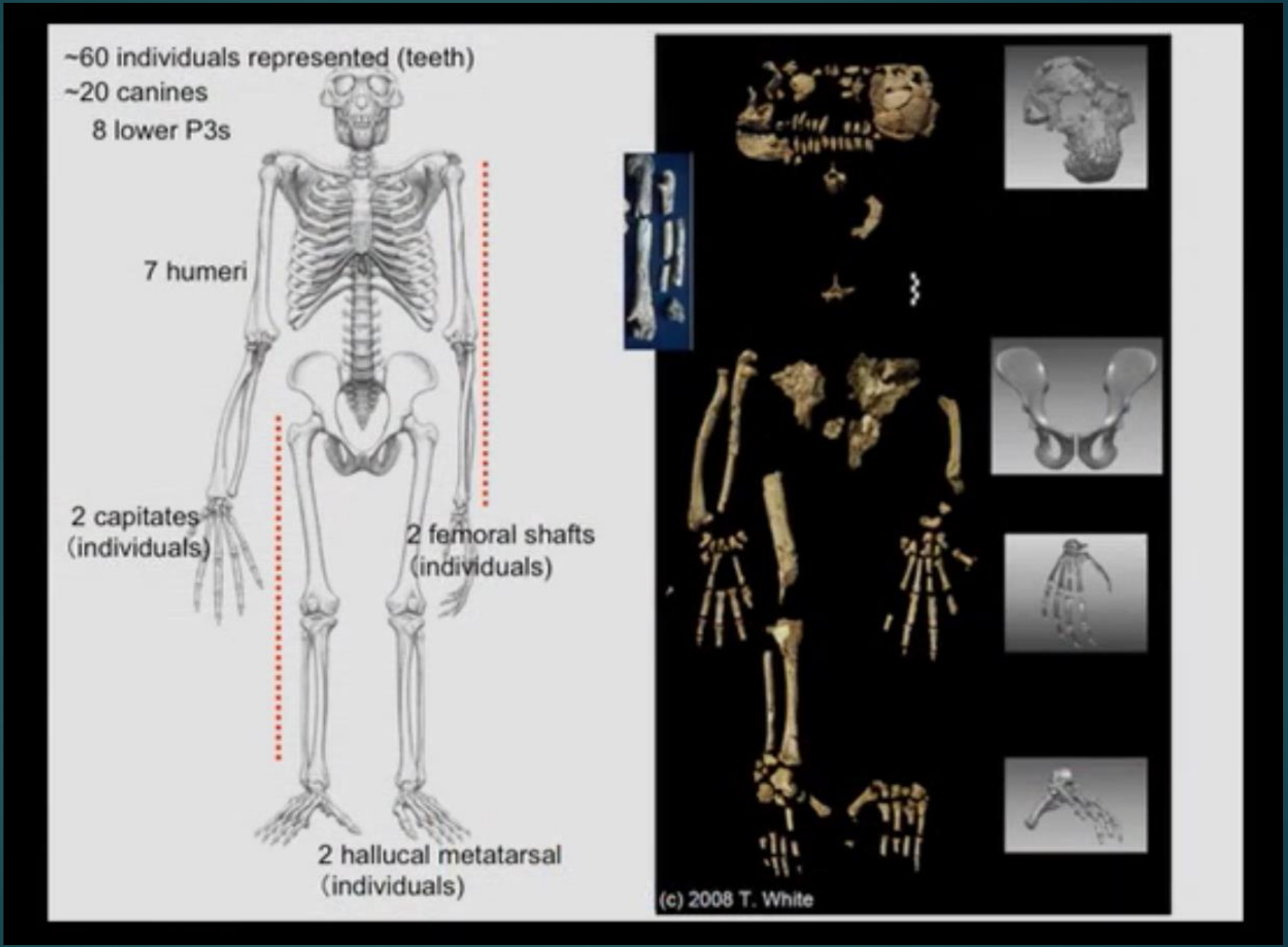


Lucy = small body, big back teeth

Ardipithecus: The ARA-VP-6/500 skeleton: a female

Widely scattered

Arm shorter than lower limb; Opposite of chimpanzee



Crushed pelvis and cranium

Almost complete hand and foot

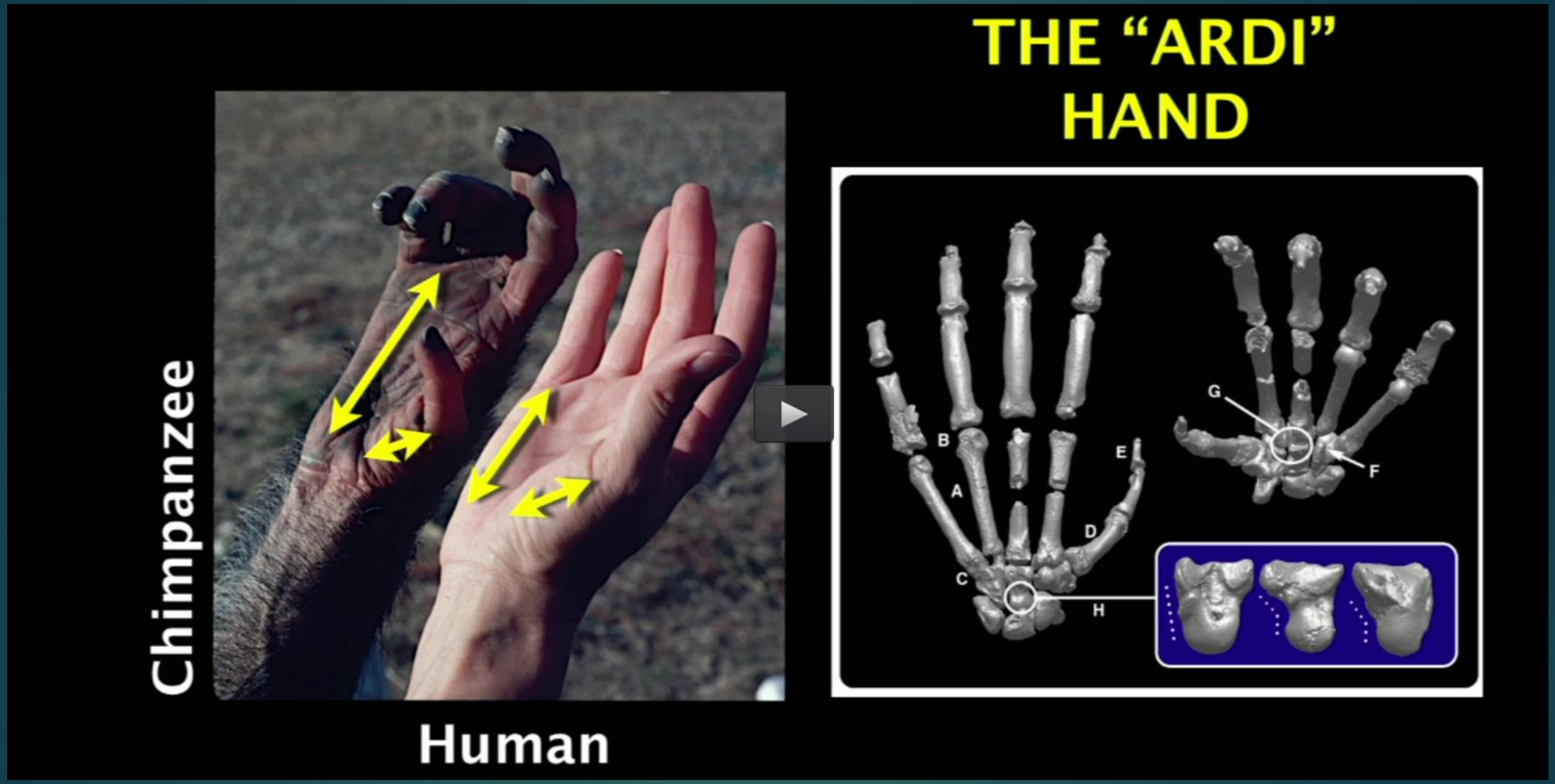
Ardipithecus ramidus

- Research has shown *Ardipithecus ramidus* was a denizen of woodland with small patches of forest.
- Scientists also learned that Ardi was probably more omnivorous than chimpanzees and was likely to feed both in trees and on the ground.
- She was a biped still living in two worlds: upright on the ground but also able to move on all fours on top of branches in the trees, with an opposable big toe to grasp limbs.
- Supported itself on its feet and palms as it moved through the trees but lacked any characteristics typical of the suspension, vertical climbing, or knucklewalking of modern gorillas and chimps.
- On land, it engaged in a form of bipedality more primitive than that of *Australopithecus* sp.
- Scientists believe that Ardi consumed only small amounts of open-environment resources, arguing against the idea that inhabiting grasslands was one of the driving forces in upright walking.

Ardi, the savannah hypothesis, and knucklewalking

- Savannah Hypothesis: The idea that our four-legged ancestors abandoned the forests, perhaps because of a change in climate conditions, and then adapted to walk on two legs is one of the oldest in human evolution textbooks.
- First proposed by Jean-Baptiste Lamarck in 1809. Ardi challenges this hypothesis.
- Ardi didn't have a chimp's adaptations for swinging below branches or knuckle-walking, suggesting chimps gained these features relatively recently. In other words, the ape that gave rise to chimps and humans may not have been chimp-like after all.
- And contrary to Lamarck's hypothesis, her feet, legs and spine clearly belonged to a creature that was reasonably comfortable walking upright.
- Yet Ardipithecus preferred wooded habitats that were neither a closed tropical forest nor open grassland savanna.
- This suggests that hominins began walking on two legs before they left the forests, not after – directly contradicting the savannah hypothesis.
- The hypothesis that opening grasslands led to hominid emergence and bipedality now stands effectively falsified.

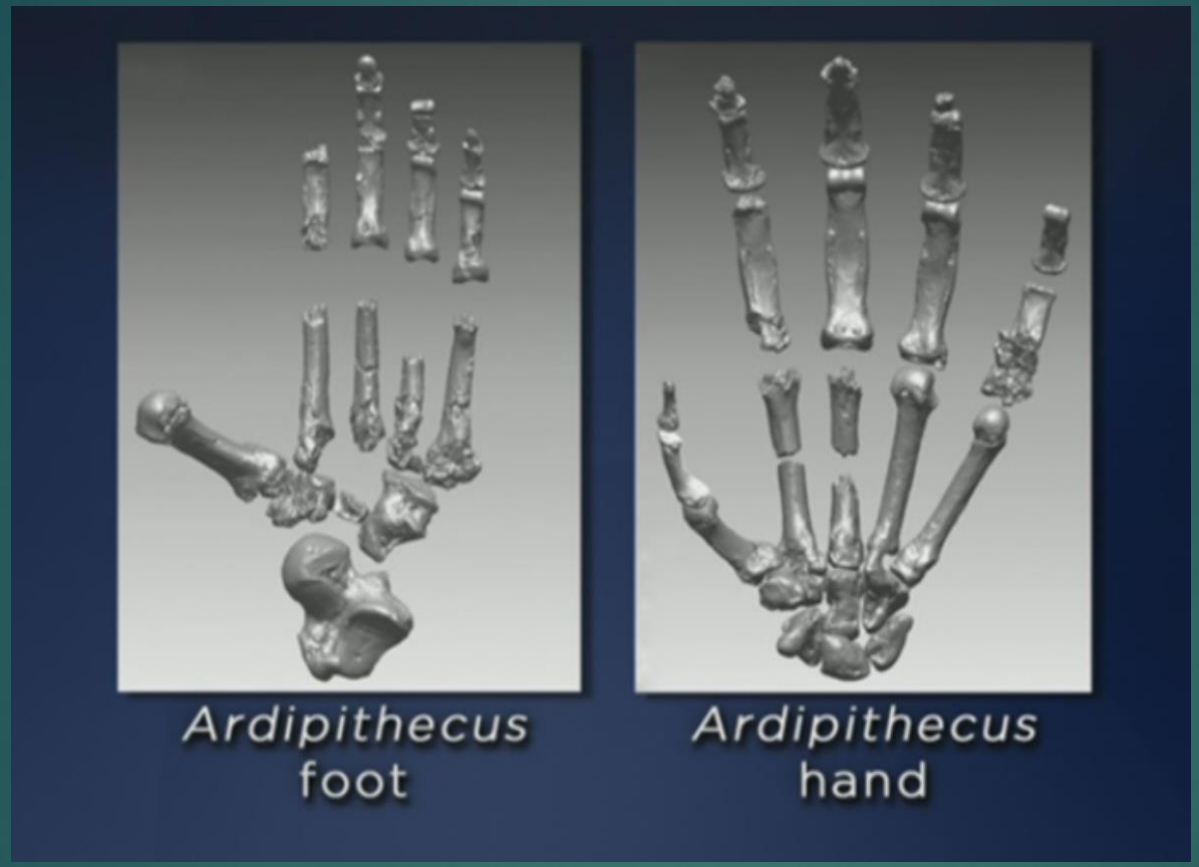
T. D. White, et al., 2014



Chimpanzee hand: suspensory; not so much for Ardi

Very long fingers

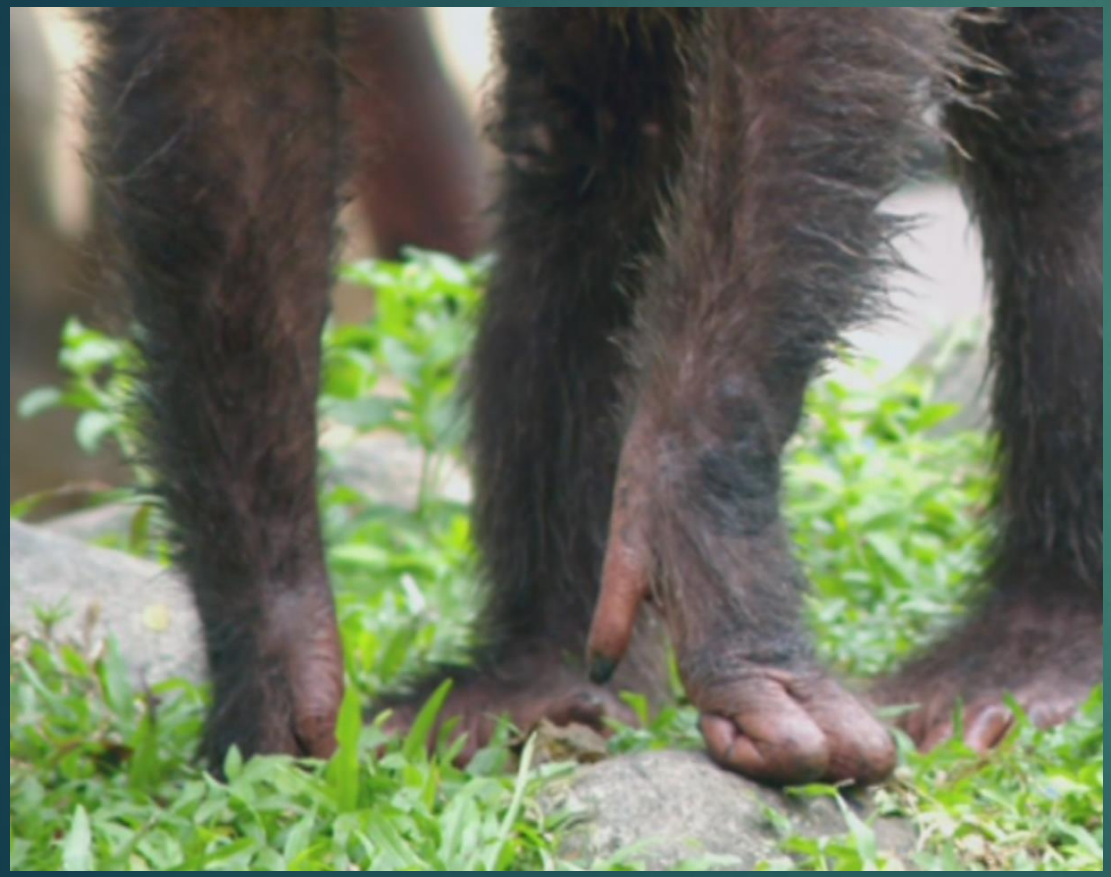
Ardi: a climber, partial walker; long fingers and toes



- Flexible wrist
- No characters for suspension or vertical climbing
- No sign of knuckle walking

She probably spent much of her time in the trees, though she probably wasn’t swinging from branches. Ardi’s hand can bend backwards at the wrist, which is unlike chimpanzees or gorillas who have stiff wrists designed for knuckle-walking. Ardi’s flexible hands allowed her to walk with four limbs carefully on top of branches (called palmigrady).

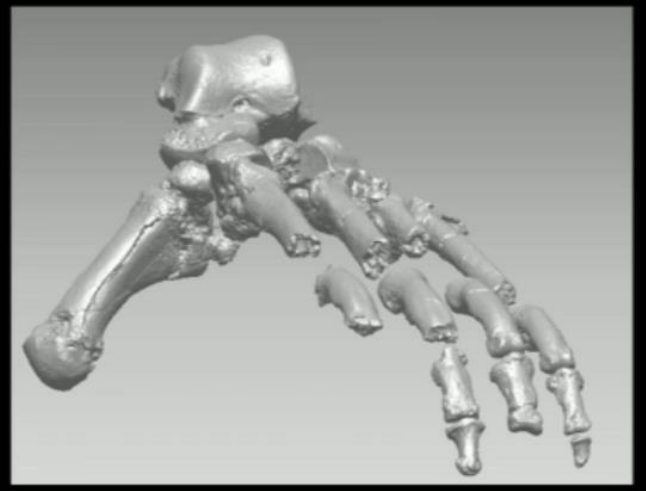
Chimps have special adaptations for weight support for knuckle walking; Ardi does not



- *Ar. ramidus* engaged in upright walking, but not knuckle-walking.
- This lead scientists to conclude that chimpanzees evolved knuckle-walking after they split from humans 6 million years ago, and humans evolved upright walking without knuckle-walking.

THE "ARDI" FOOT

Chimpanzee



Lateral foot functions as rigid lever, not a hand

Grasping feet = All primates, except humans, have divergent toe;
Ardi has divergent toe, but rest of foot is rigid lever, not a hand; more derived

Ardipithecus foot: divergent, opposable toe (first time seen in a hominin); long toes (arboreal)

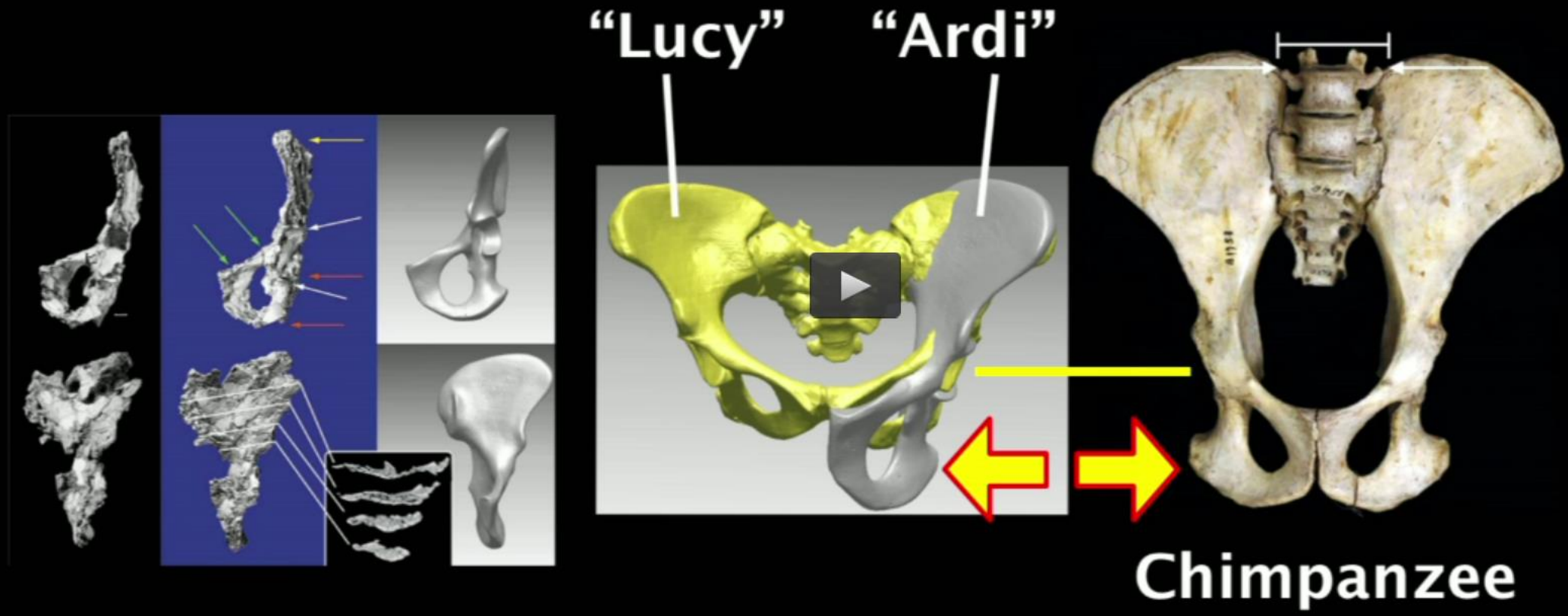
Foot

Foot skeleton of *Ar. ramidus* (bottom; reconstruction based on computed tomography rendering shown) lacked many features that have evolved for advanced vertical climbing and suspension in extant chimpanzees (*Pan*, top left). Chimpanzees have a highly flexible midfoot and other adaptations that improve their ability to grasp substrates. These are absent in *Ar. ramidus*.

- Ape-like foot
- Curved phalanges
- Grasping big toe
- No arch
- Habitual, not obligatory, biped
- Could climb

THE “ARDI” PELVIS

Pelvis: crushed, but reconstructed



Pelvis like Lucy, but lower extension like chimp = mosaic;
But not curved like bowel like later hominins for movement muscle attachments

Ardi and LCA

- Ardipithecus reveals the first hominid adaptive plateau after the chimp/human LCA.

- It combined facultative terrestrial bipedality in a woodland habitat with retained arboreal capabilities inherited from the LCA.

- The markedly primitive Ar. ramidus indicates that no modern ape is a realistic proxy for characterizing early hominid evolution.

Ardi and Last Common Ancestor

- Tim White: Ar. ramidus reveals that the last common ancestor that we share with chimpanzees (LCA) was probably a:
  - palmigrade (whole foot down),
  - arboreal, climber/clamberer that lacked specializations for suspension, vertical climbing, or knuckle-walking.
  - postcanine dentition associated with an omnivorous frugivorous diet
  - moderate canine dimorphism with minimal skull and body size dimorphism,
  - relatively weak male-male antagonism in a male philopatric social system.

T. D. White et al., 2009

C3 vs C4 plants

- Different form of carbon in different plants:
  - the ratio of carbon-13 and carbon-12 isotopes in plant tissues is different depending on the type of plant photosynthesis
  - this can be used to determine which types of plants were consumed by animals, whether in woodland or grassland
  - plants using the C_4 photosynthetic pathway (grasses); tropical, semi-tropical
  - plants using the C_3 photosynthetic pathway (most plants; trees & shrubs; fruits); temperate

Dentition

- Ardi's dentition is consistent with a partially terrestrial, partially arboreal pattern of feeding in a predominantly wooded habitat.
- Carbon isotopic evidence from the teeth of five Ar. ramidus individuals suggests that Ardipithecus and Australopithecus were distinct in dietary intake.
  - "Robust" and "nonrobust" *Australopithecus* have enamel isotope values indicating a diet of more than 30% C4 plants (grasses), with variation ranging up to ~80% C4.
  - In contrast, the known *Ar. ramidus* individuals vary only between ~10 to 25% C4; eating predominately more C3 plants; an omnivore
  - Differ from Pan troglodytes, which prefers ripe fruit and is considered closer to a pure C3 (fruit) feeder.
  - Thus, *Ardipithecus* appears to have exploited a wider range of woodland resources than do chimpanzees, but without relying on the open biotope foods consumed by later *Australopithecus*.

Ardi

- Terrestrially, it engaged in a:
  - form of bipedality more primitive than that of *Australopithecus*,
  - lacked adaptation to “heavy” chewing related to open environments (seen in later *Australopithecus*). A habitual biped, still capable of arboreality

- Its ecological habitat appears to have been largely woodland-focused.

- *Ar. ramidus* lacks any characters typical of suspension, vertical climbing, or knuckle-walking.

- *Ar. ramidus* thus indicates that the last common ancestors of humans and African apes were not chimpanzee-like and that both hominids and extant African apes are each highly specialized but through very different evolutionary pathways.

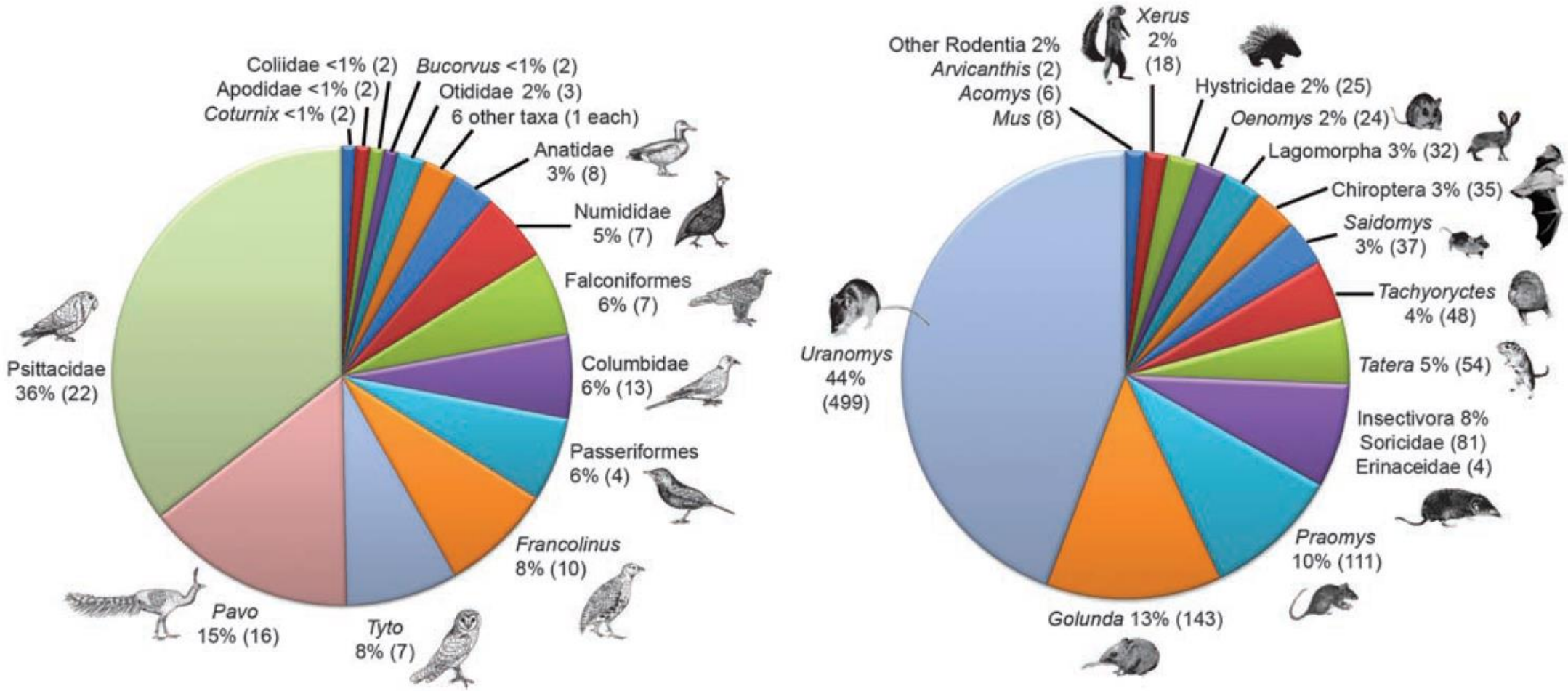
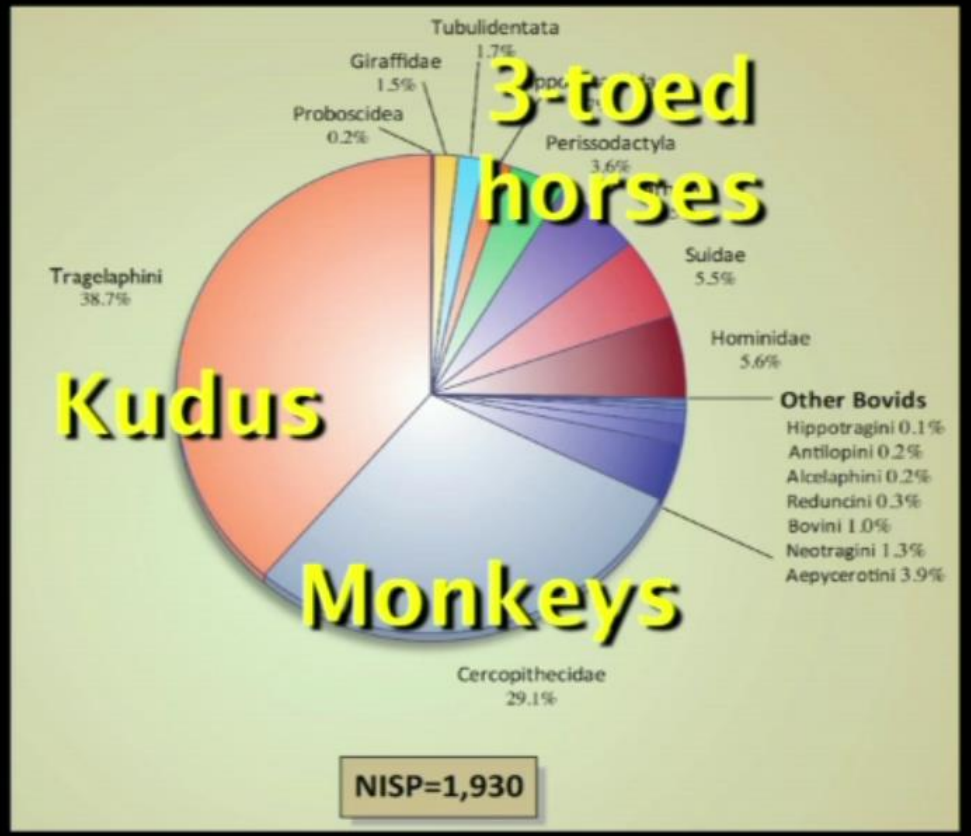


Fig. 2. Relative abundance of avian and small-mammal taxa. For each bird taxon, the pie slice and first number apply to the number of identified specimens (n = 263); the second (in parentheses) is the minimum number of individuals represented in the overall sample. For small mammals, the numbers apply to the number of identified specimens only (n = 1127), but closely reflect the minimum number of individuals because only craniodental specimens are included.

Ardi surrounded by parrots and peacocks (= woodlands), and mice; few ducks = not near water

Abundance



Lots of kudus (antelope) = leaves from tickets; and monkeys - eat leaves = trees; few horses - eat grass; Conclusion: Ardi was in woodland

Ardipithecus teeth

- Wood and Harrison point to the small canines in *Ardipithecus* and *Sahelanthropus* as possibly the most convincing evidence to support their status as early human ancestors.

- However note that canine reduction was not unique to the human lineage for it occurred independently in several lineages of fossil apes (e.g., Oreopithecus, Ouranopithecus and Gigantopithecus) presumably as a result of similar shifts in dietary behavior.

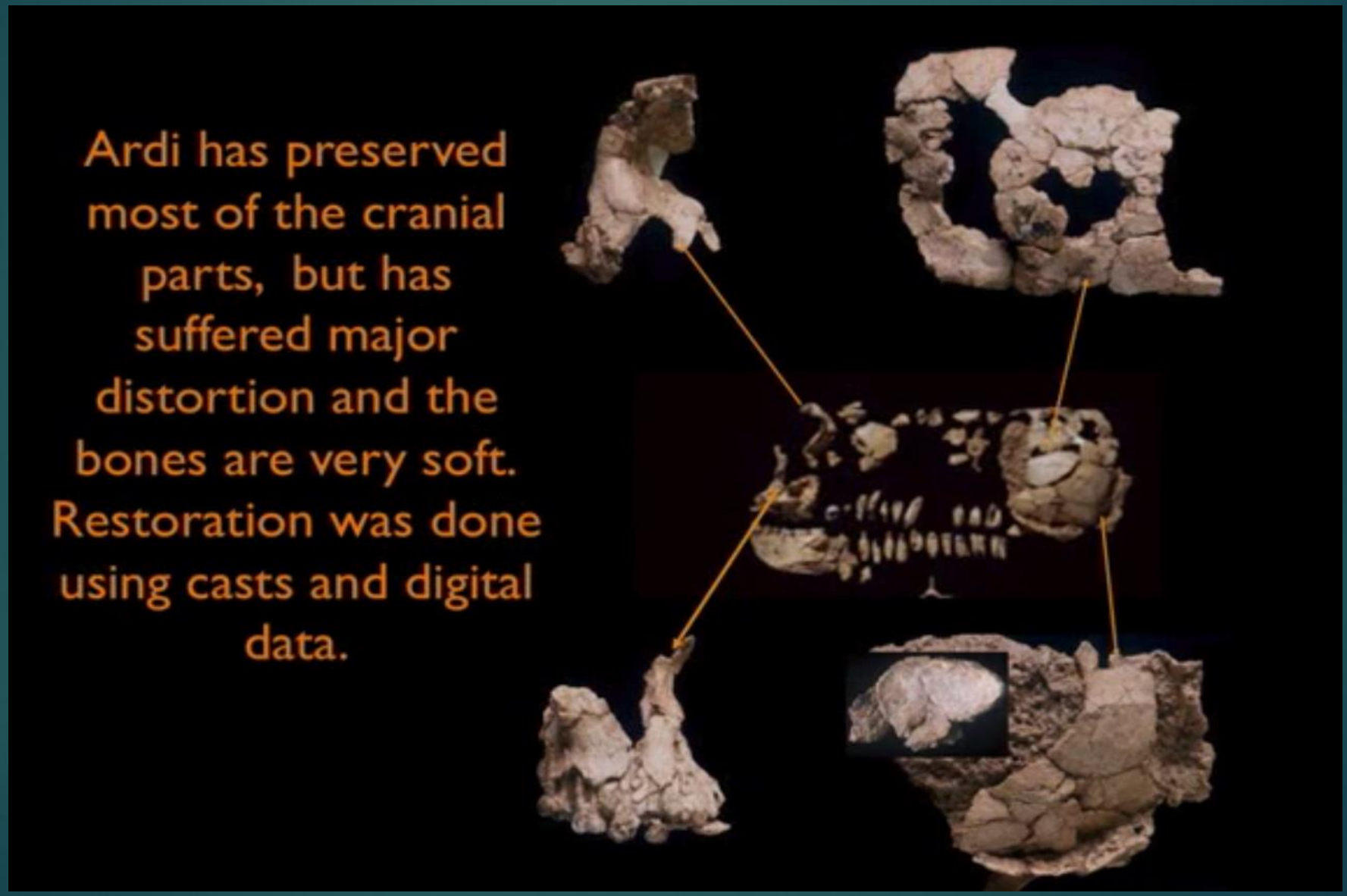
Ardi teeth: slightly bigger than Chimp molars but not as big as later hominins; canines relatively small

- Hominid family due to lack of C/P3k honing complex
- No sexual dimorphism in canines

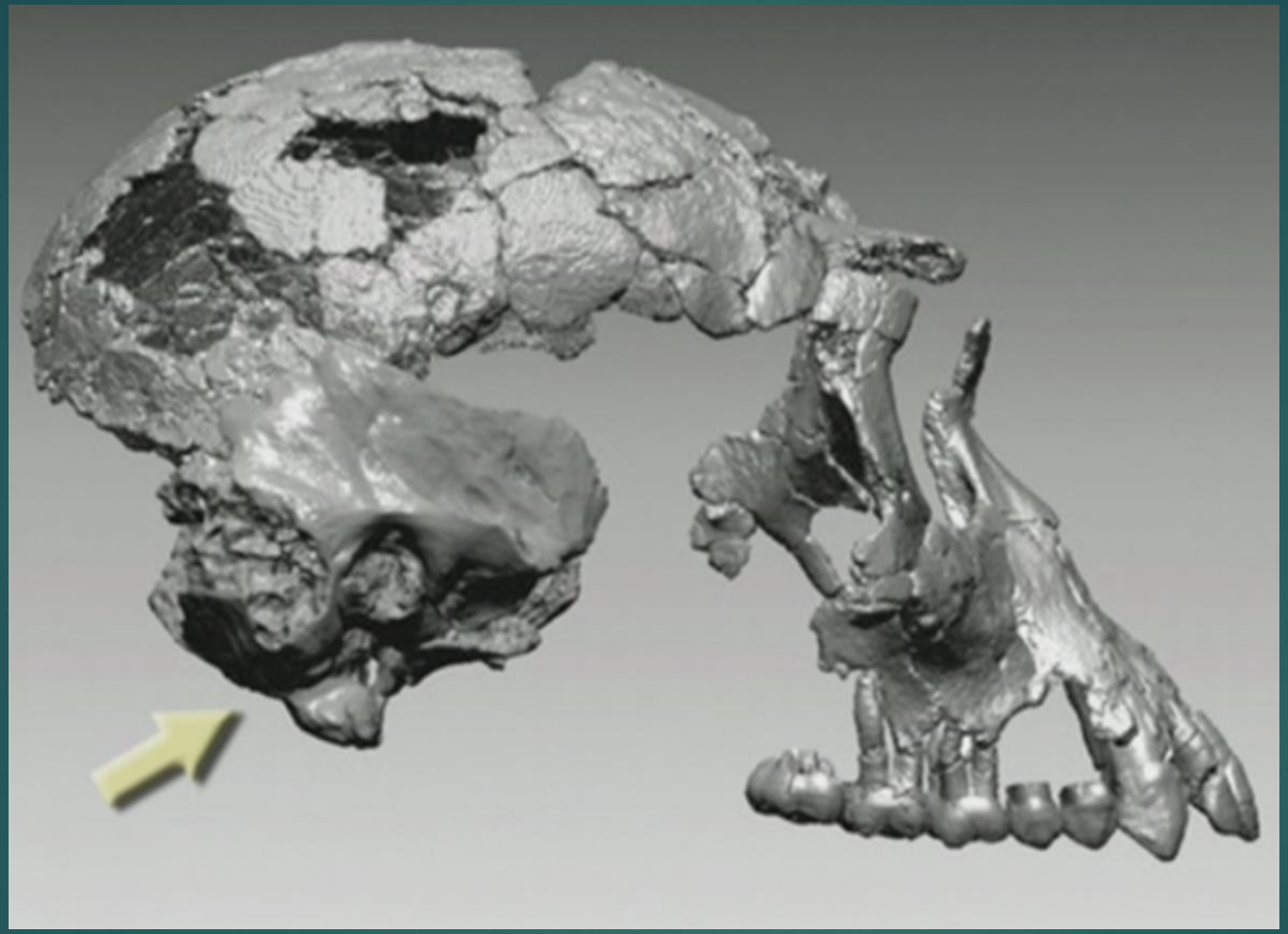
Ardi’s canine teeth: smaller, like us

A. *ramidus* has an enamel thickness between a chimpanzee’s and later *Australopithecus* or *Homo* species, suggesting a mixed diet.
B. However, the wear pattern and incisor sizes indicate *Ar. ramidus* was not a specialized frugivore (fruit-eater).

Ardi skull was crushed, pancaked

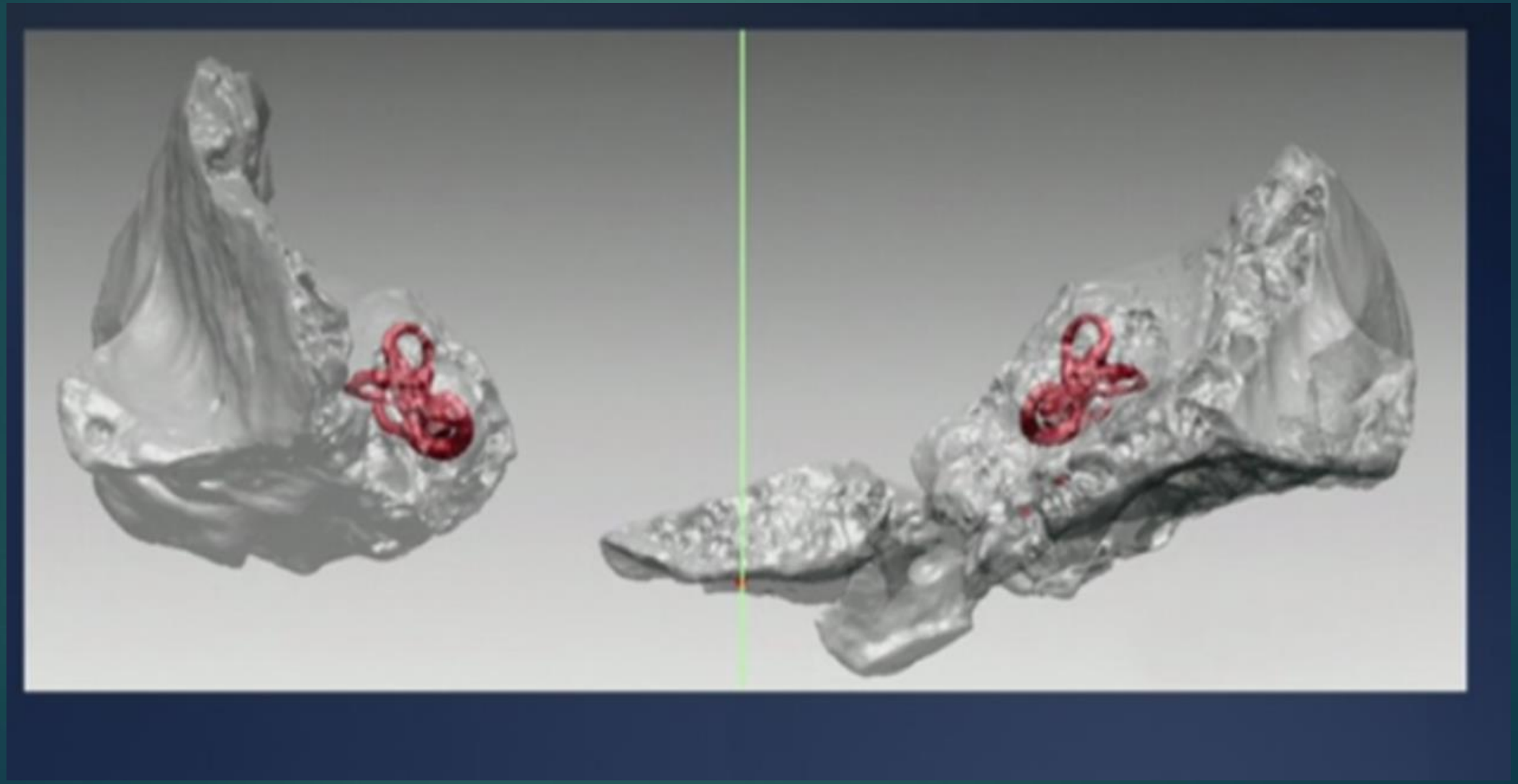


Ardi: base of skull reconstructed first



Link to hominins: foramen magnum position & relatively small canines

Temporal bone with inner ear on CT scan: helped them orient temporal bones at base of skull correctly



Digital recreation of pancaked cranium; 60 pieces

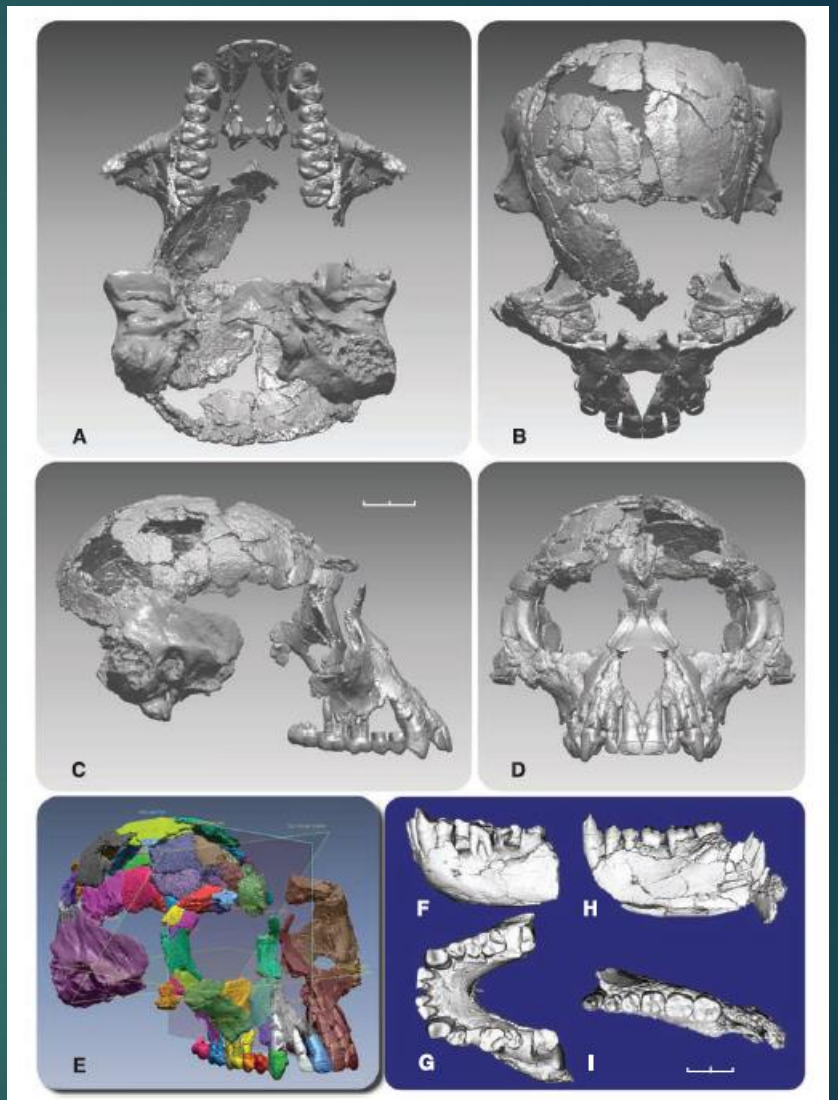
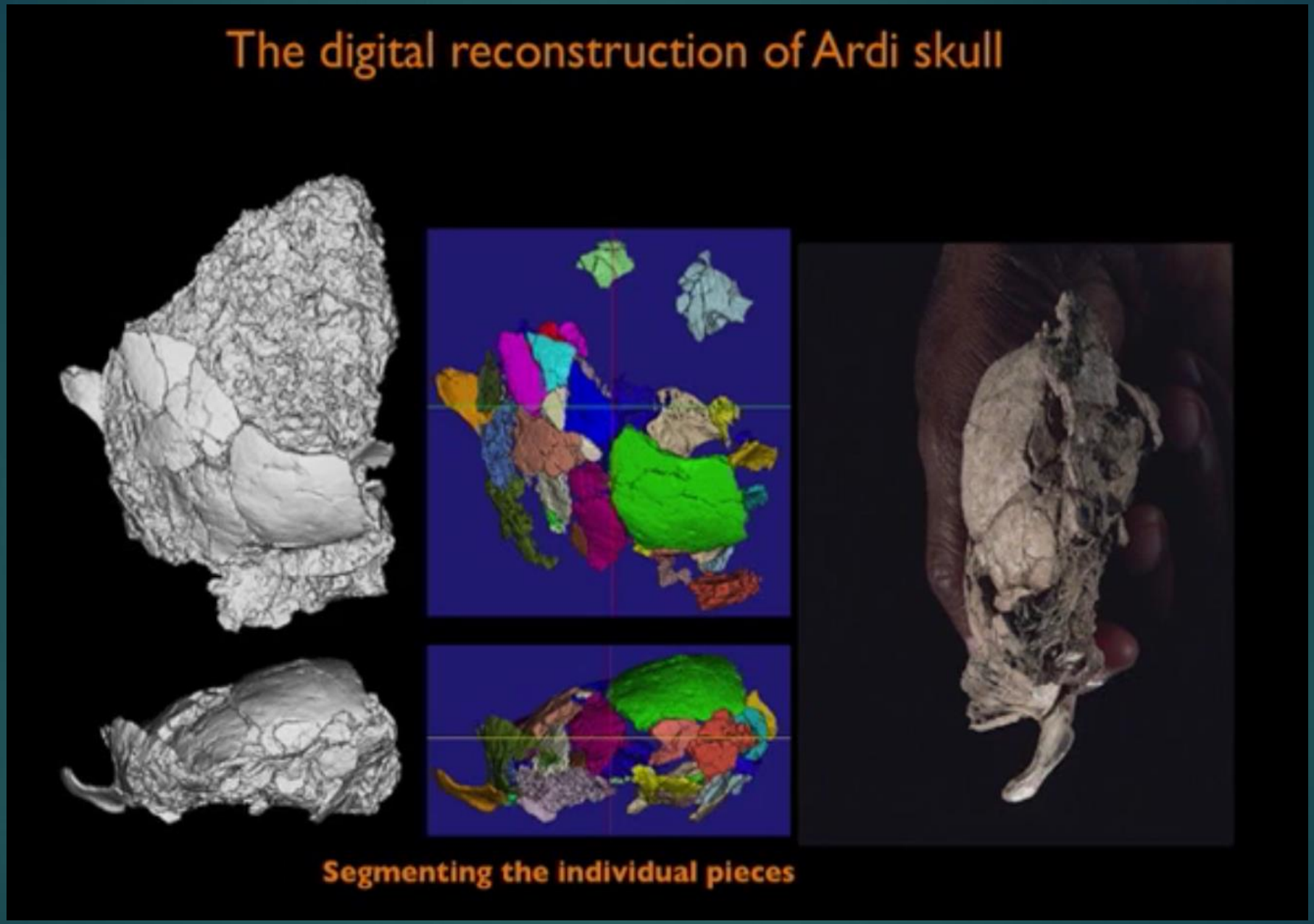
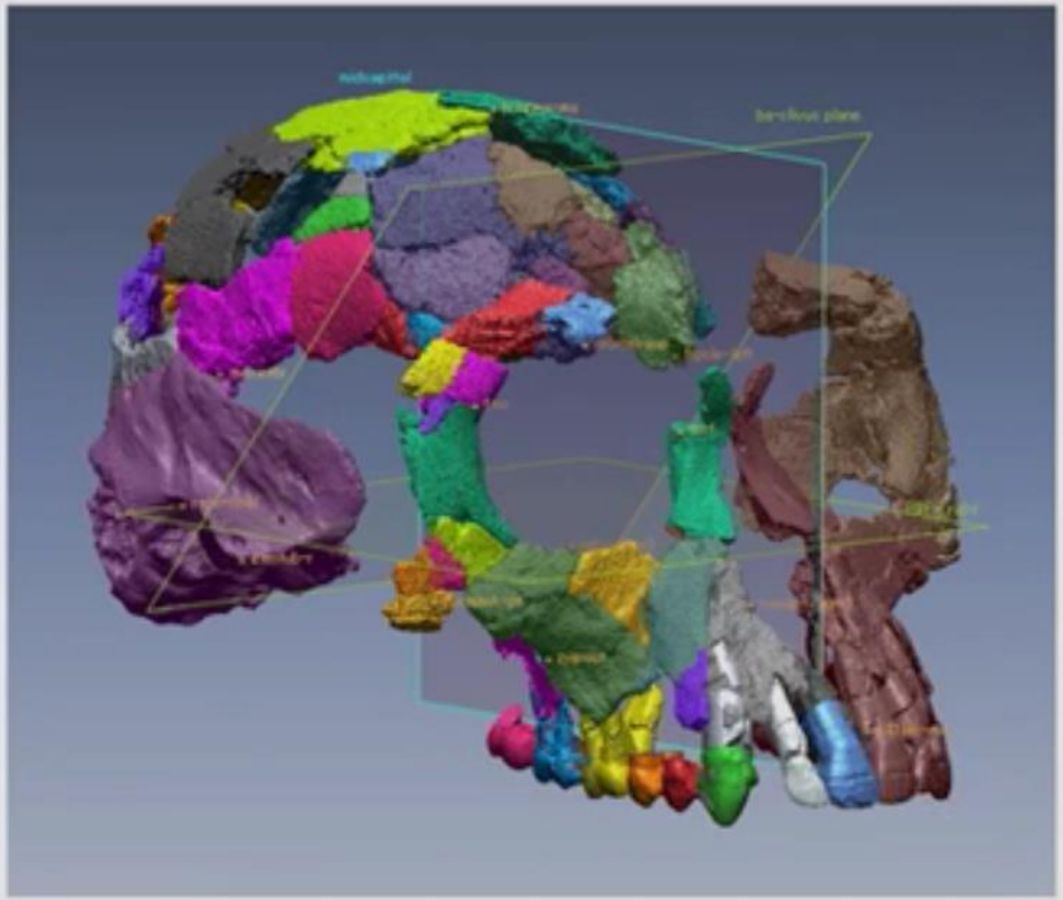


Fig. 2. Digital representations of the *Ar. ramidus* cranium and mandible. (**A** to **D**) The *ARA-VP-6/500* and downscaled *ARA-VP-1/500* composite reconstruction in inferior, superior, lateral, and anterior views (in Frankfurt horizontal orientation). (**E**) Individual pieces of the digital reconstruction in different colors. Note the steep clivus plane intersecting the cranial vault on the frontal squama (as in *Sts 5* and not apes). (**F** and **G**) Lateral and superior views of the *ARA-VP-1/401* mandible (cast). (**H** and **I**) Lateral and superior views of the *ARA-VP-6/500* left mandibular corpus with dentition.

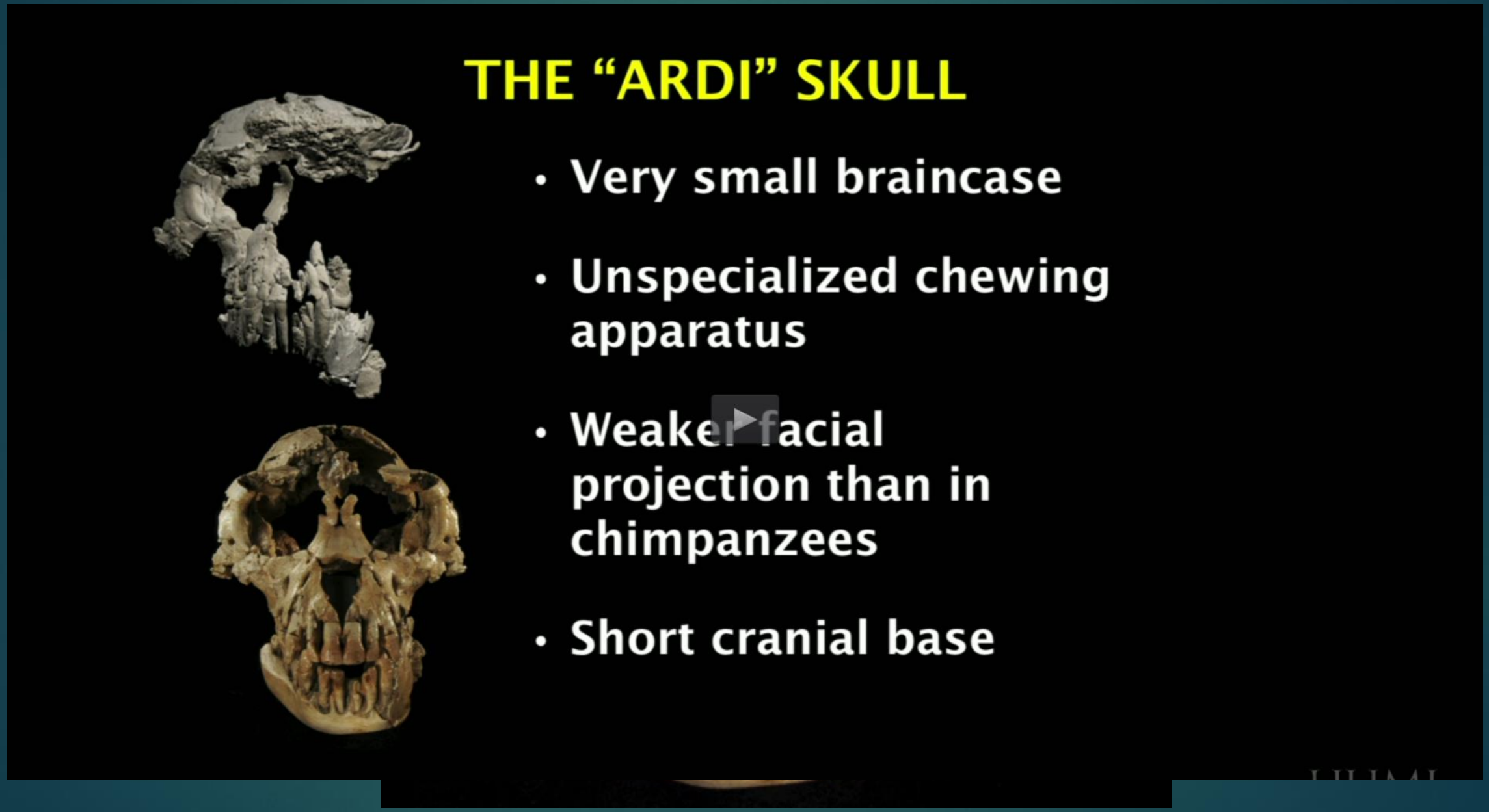


Tim White at UCB manually reconstructed casts;
Exported to Univ. of Tokyo for digital reconstruction by Gen Suwa

Showing all the 60+ digitally separated parts in the final reconstruction



Ardi, 4.4 Ma


THE “ARDI” SKULL
• Very small braincase
• Unspecialized chewing apparatus
• Weaker facial projection than in chimpanzees
• Short cranial base

Social/Reproductive Behavior

- Homo sapiens is:
  - the only living primate committed to terrestrial bipedality.
  - the only living higher primate in which the canine plays no social role,
  - only primate that engages in prolonged monogamous relationships within the context of a larger social group.
- *Ar. ramidus* shares the first two of these characters with humans, which may elucidate the third.
- All of the earliest known hominids (Orrorin, Sahelanthropus, and Ardipithecus) had apparently already abandoned the primitive C/P3 "honing" complex in which a triangular, projecting upper canine is continuously sharpened by occlusion against the anterior lower premolar, especially in males.
- However, even the male canines of *Ar. ramidus* are feminized: they are short and morphologically blunt, with tips wearing down to the level of the surrounding teeth.
- *Ar. ramidus* shows dramatic male canine height reduction; signals a fundamental change in social behavior.
- Moreover, bipedality and male canine feminization appear to have been evolutionarily coupled.

Continuity with Australopithecus

- How is *Ardipithecus* related to later hominids?
- The temporally nearest *Australopithecus* is the little-known taxon *A. anamensis*.
- Recent data suggest that this species was related to *Ardipithecus* either as a close collateral relative, or in an ancestral-descendant relationship.
- The two taxa are superimposed in the Awash area's single stratigraphic sequence.
- Despite dramatic morphological distinctions between *Ar. ramidus* and *Australopithecus* that signal niche differentiation, *Ar. ramidus* shares many details of structure and morphology with early Australopithecus.

Hypotheses tested by Ardi:

- Bipedality evolved in savanna environment

1 - Falsified. Lived in woodland

- We evolved from a knuckle-walker

2 - Falsified. No KW features

- Chimpanzees are good models for the last common ancestor we shared with them.

3 - Falsified. Chimps have their own evolution

Ardi represents a major paradigm shift in terms of how and where we should look for a model for the last common ancestor

Ardipithecus Kadabba

Ardipithecus ramidus is descendant of *Ardipithecus kadabba*

- *A. ramidus* 4.4 Ma
- *A. kadabba* 5.2-5.8 Ma

- *A. ramidus* has smaller canine than *A. kadabba*
- Anterior foramen magnum
- Non-weight bearing arm
- Grasping feet

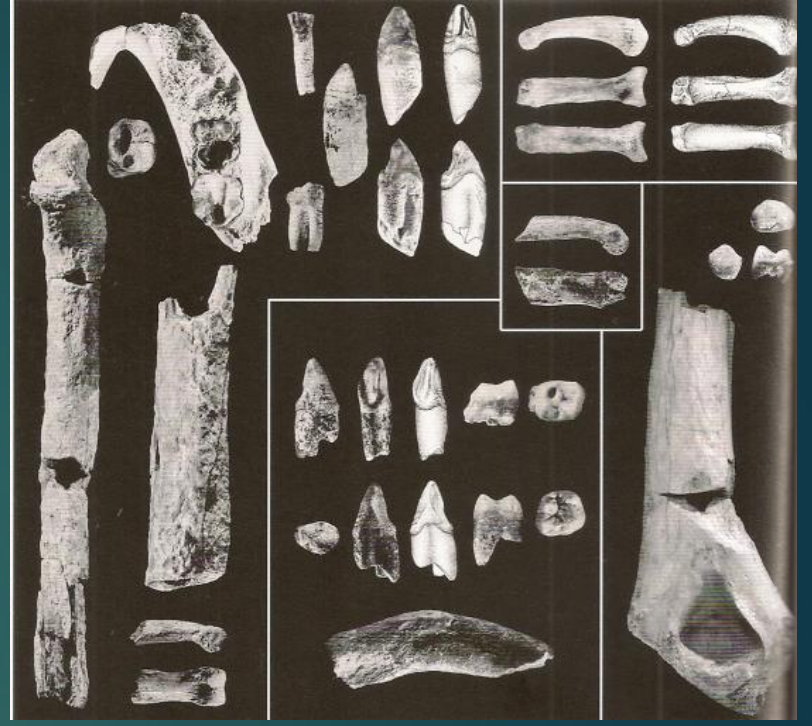
Yohannes Haile Selassie (1961-):

Ardi ramidus & kadabba, A. garhi, Kadanuumuu

- Ethiopian paleontologist
- Curator and head of the physical anthropology department at the Cleveland Museum of Natural History
- 1994: first to discover the hand-bone of the *Ardipithecus ramidus* skeleton.
- 1996: at W. Margin, Mid. Awash, Ethiopia, discovered *Ardipithecus kadabba,* c. 5.6M
- 1997: discoverer *Australopithecus garhi;* , (BOU-VP-12/130), 2.5M; named it in 2001
- *2005*: discovered Kadanuumuu ("Big Man" in the Afar language), 3.58M, partial *Australopithecus afarensis*, in the Afar Region of Ethiopia; human like gait
- 2012: Critical of Zeray's interpretation of Selam shoulder bone

Ardipithecus kadabba, 5 Ma

- Even older - 5.8 – 5.2 Ma
- Ethiopia (Middle Awash)
- Similar to *Sahelanthropus* in mix of features
- Mandibles, teeth, some postcranial bones
- Tall, pointed, upper canines; slightly smaller lower canines; resemble chimp
- 17 specimens from at least 5 individuals
- Wooded habitat
- Case for being hominin is not strong



2004 ALA-VP-2/10,
type specimen

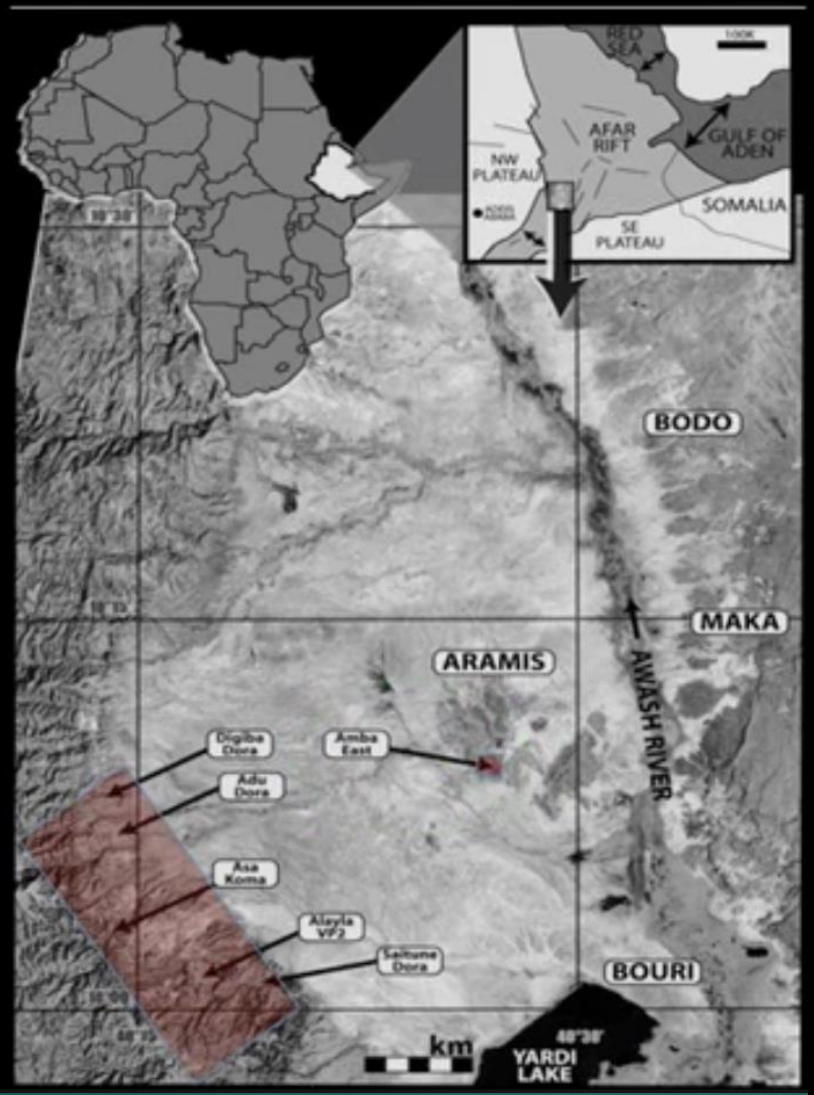
Haile-Selassie, Y., Suwa, G., White, T.D., 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. Science 303, 1503-1505.

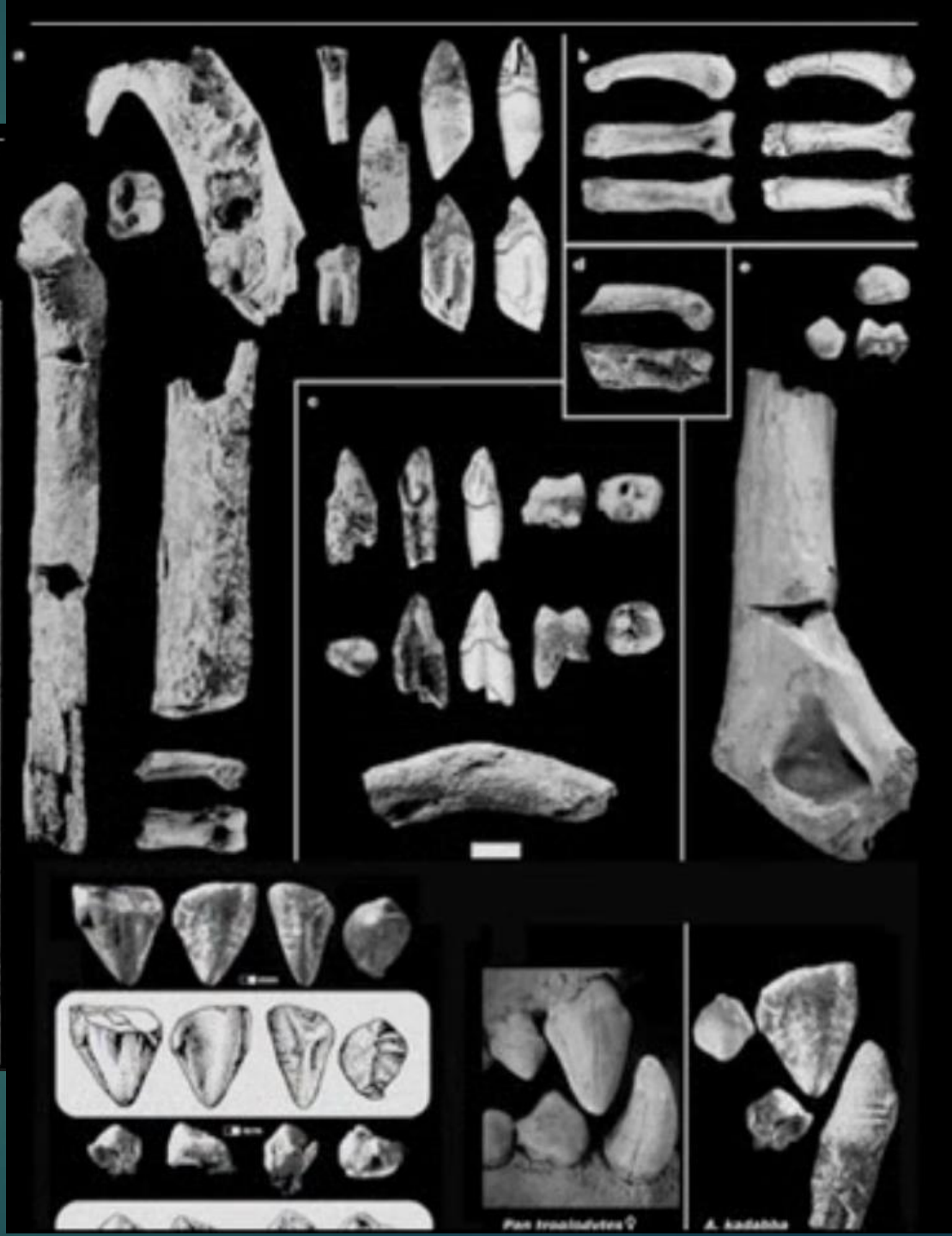
Ardipithecus kadabba, 5.5 M

- Additional fossils, discovered between 1997 and 2001, and dating to between 5.2 and 5.8 Ma, first attributed to *Ardipithecus ramidus* (Haile-Selassie 2001), were subsequently assigned to a *Ardipithecus kadabba*
- 11 specimens from at least 5 individuals; few post-cranial bones (hand and foot bones, partial arm bones, and a clavicle (collarbone)) and sets of teeth. One bone from the large toe has a broad, robust appearance, suggesting its use in bipedal push-off.
- In 2002, six more teeth were discovered in the Middle Awash at the site Asa Koma. The dental wear patterns confirmed the early human fossils were unique and not a subspecies of *Ar. ramidus*. Based on these teeth, paleoanthropologists Yohannes Haile-Selassie, Gen Suwa, and Tim White allocated the fossils in 2004 to a new species they named *Ardipithecus kadabba* ('kadabba' means 'oldest ancestor' in the Afar language).

Ardipithecus kadabba

- Mostly known from the Western Margin of the Middle Awash study area
- One specimen from the Central Awash Complex

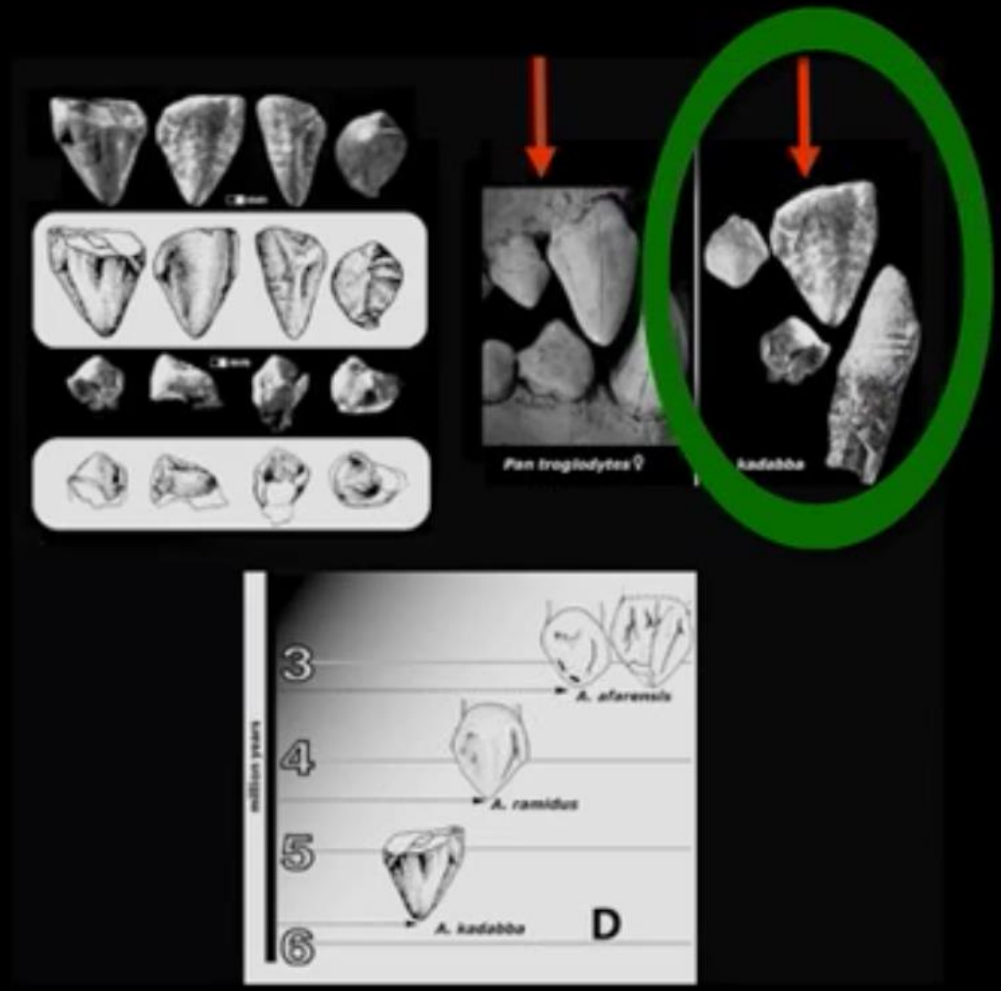




Ar. Kadabba: primitive teeth

Major character states of *Ar. kadabba*

- Canines and lower third premolar more primitive than any other known hominid younger than 5 Ma
- C/P3 complex intermediate between apes and later hominids



C/P3 overlap;
Unclear if honing

Ardipithecus kadabba

- Known from the late **Miocene** localities of the western margin of Middle Awash, Ethiopia.
- Specimens consist of mandibular fragments, isolated teeth and few postcranial elements recovered from the Asa Komi (5.54–5.77 Ma) and Kuseralee (ca. 5.2 Ma) Members of the Middle Awash study area.

- They were originally referred to as a subspecies of *Ardipithecus ramidus* (Haile-Selassie 2001), but were later elevated to a species based primarily on the primitive morphology of the C/P3 complex that implied the potential for some functional honing.
- Among the postcranial elements recovered is a pedal proximal phalanx. This feature is associated with toeing-off and is unique to bipeds — thus, linking *Ar. kadabba* to later hominins. But the pedal phalanx was recovered from the younger formation & the dentition was from the older formation have prompted some doubts regarding its association to *Ar. kadabba* (Begun 2004).

Ard. Ramidus phalanges, toe bones, 4.5 Ma., Gona

- One of these fossils is a toe bone (third) belonging to a bipedal creature, but it is a few hundred thousand years younger than the rest of the fossils.
- Habitual bipedality is still to be determined by further discoveries

Sileshi Semaw

Ar. kadabba

- Faunal (fossil animal) evidence from the site indicated that the early humans there lived in a mixture of woodlands and grasslands, and had plenty of access to water via lakes and springs.

- The back teeth of *Ardipithecus kadabba* are larger than a chimpanzee's, but its front teeth are narrower.

- This evidence suggests this species did most of its chewing in the back of its mouth. This type of chewing would focus on hard-to-eat foods like fibrous nuts.

Paleoenvironment of the Earliest Hominins

- *Australopithecus africanus* with the recovery of associated fauna indicated open habitats: posited that the origin of bipedality in our lineage had its roots in the expanding savannas of the Pliocene (Dart 1957).

- However, the ecological contexts of the earliest hominins suggest that the link between the advent of bipedalism and the expansion of savanna and grassland habitats may be tenuous.

- *Sahelanthropus* is found in a mosaic of environments, ranging from gallery forest at the edge of a lake, to savanna woodland, to open grassland, with a dominance of shrub/bushland and grassy woodland habitats within the Chadian lake basin

Paleoenvironment of the Earliest Hominins

- *Orrorin* is associated with open woodland habitats with dense woodland or forest in the vicinity, possibly along lake margins (Pickford & Senut 2001).
- *Ardipithecus ramidus* is found in closed woodland habitats with possible patches of forest at Aramis and associated with bushland and grassland habitats at Gona.
- *Ardipithecus kadabba* is associated with woodland on banks of rivers and floodplain grassland along water margins (Su *et al*. 2009).

- Combined, these paleoenvironmental interpretations of the African latest Miocene and earliest Pliocene suggest that the beginnings of our lineage did not occur in open, semi-arid to arid habitat conditions, but rather in more closed and/or wet habitats.

Paleoenvironment of the Earliest Hominins

- However, a definitive conclusion is difficult to draw at this time given the lack of detailed paleoecological reconstruction for *Orrorin*, the possibility that *Sahelanthropus* was found in more open habitats, the discordance in interpretation of the Aramis dataset, and the general paucity of late Miocene hominin-bearing sites in Africa.

- While the hominin status of *Sahelanthropus*, *Orrorin*, and *Ardipithecus* species may be debated, their significance for understanding human origins and evolution is clear.

- They open a window into the very beginnings of our lineage; we will learn more not only about their paleobiology, taxonomy, and phylogenetic relationships, but also about their environment, and how that may have influenced the evolution of our lineage.