Early *Homo:*

Homo habilis,
the 1470 and 1813 groups,
the Ledi-Geraru *Homo*

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Abbreviations of Locales

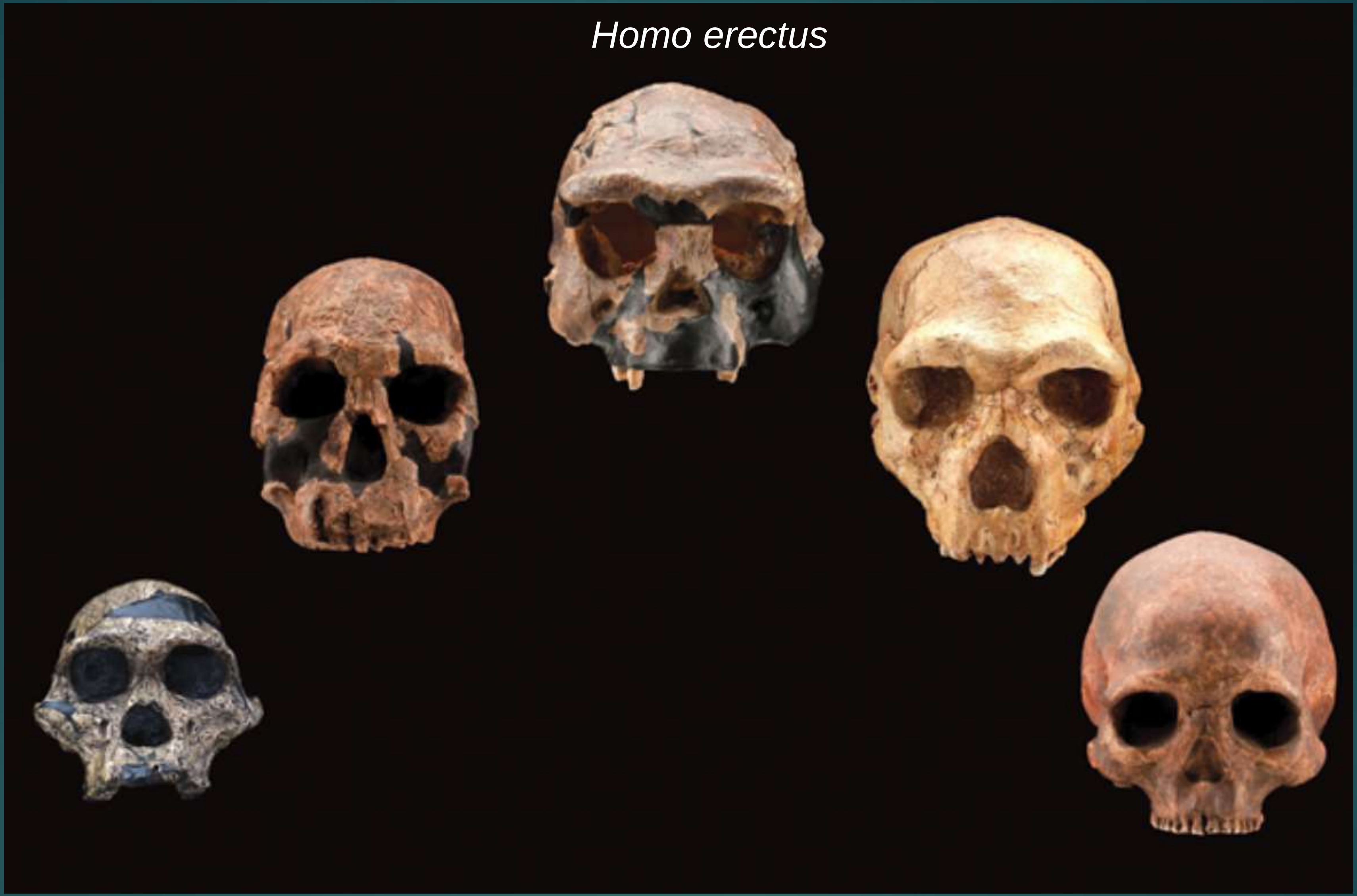
AMNH	American Museum of Natural History
DK	Douglas Korongo (a locality at Olduvai Gorge)
FLK	Frida Leakey Korongo (a locality at Olduvai Gorge)
FLKNN	FLK North—North (a locality at Olduvai Gorge)
KBS	Kay Behrensmeyer Site (at East Turkana)
KNM-ER	Kenya National Museums—East Rudolf
KNM-WT	Kenya National Museums—West Turkana
LH	Laetoli Hominid
MLD	Makapansgat Limeworks Deposit
MNK	Mary Nicol Korongo (a locality at Olduvai Gorge)
NMT	National Museum of Tanzania
NMT-WN	National Museum of Tanzania—West Natron
NMT	National Museum of Ethiopia
NMT-WN	National Museum of Ethiopia—West Natron
OH	Olduvai Hominid
SK	Swartkrans
Sts	Sterkfontein site (TM designation)

Stw	Sterkfontein site (UW designation)
TM	Transvaal Museum
UW	University of the Witwatersrand

Charles Darwin, “*Descent of Man*” (1871, p. 230):

“….it would be impossible to fix on any point when the term “man” ought to be used…”

- Paleontologically, whether a fossil is *Homo* turns out to be very complicated.



Three-dimensional skull casts of early hominins (left to right): *Australopithecus africanus*, 2.5 Ma from Sterkfontein in South Africa; *Homo rudolfensis*, 1.9 Ma from Koobi Fora, Kenya; *Homo erectus*, 1 Ma from Java, Indonesia; *Homo heidelbergensis*, 350 Ka from Thessalonika, Greece; and *Homo sapiens*, 4,800 years old from Fish Hoek, South Africa. Credit: Smithsonian Institution.

10 Current Species of Genus *Homo*

1. *Homo habilis (& Homo rudolfensis)*
2. *Homo erectus (Asian) [& Homo ergaster (African)]*
3. *Homo antecessor ("archaic" Homo sapiens) ?*
4. *Homo heidelbergensis ("archaic" Homo sapiens)*
5. *Homo neanderthalensis*
6. *Homo sapiens subsp. Denisova (D0, D1, D2)*
7. *Homo floresiensis*
8. *Homo luzonensis*
9. *Homo naledi*
10. *Homo sapiens*

1964: *Homo habilis*

- Increase in cranial capacity from earlier hominins
  - Cranial capacity: 600 cc

- Found with Oldowan toolkit, used for both meat and plant food.

Number of evolutionary species

- Known fossil record is an underestimate of diversity of actual species
- Primate species on average have a longevity of 1 M years
- Robert Martin calculations: 6000 primate species have existed throughout entire history of primate evolution
- 200 living primate species = 3% of this total
- 84 species of hominoids are estimated to have existed in past 35 M years; less than half are known from fossil record

Number of evolutionary species

- Less than half of the predicted number of hominin species have been identified

- Current fossil record is clearly an underestimate

- Phylogenetic charts are probably missing +25% of their branches

Lumpers and splitters

- Problem of the interpretation of anatomical variability in new fossil finds
- Lumping: some see fewer species; anatomical variation seen as intraspecific; within same species
- Splitting: see more species; anatomical variation seen as interspecific; each variant seen as separate species

History of lumping and splitting

- In early years, field dominated by splitters (i.e. Louis Leakey); every new find = new species

- Sentiment in the 1960s switched to lumping, which underestimates species richness; Less than half of the predicted number of hominin species have been identified; Current fossil record is clearly an underestimate

- Led to "single-species" hypothesis of Loring Brace & Milford Wolpoff in 1960-1970s; explained all anatomical differences as within-species variation; Only 1 hominin species existed - a progression of a species through time, to *homo sapiens*

Lumpers and splitters

- While this single-species theory is invalid, there continued to be the tendency to interpret anatomical differences as within-species variation rather than as more species variation

- due to fact that there is no relationship between speciation and morphological change

- Recently move away from lumping; true hominin tree is almost certainly more bushy, with more species that have not yet been found

Early Homo*:*

- *Homo habilis* was the first non-*erectus* species of early *Homo* to be recognized,
- A single species that is:
  - larger brained and smaller toothed than *Australopithecus,*
  - yet smaller brained and slightly larger toothed than early African *Homo erectus*.
- For a time, all other early, relatively small-brained African hominins were lumped into this species.

Major Adaptive radiations of early hominins

- Concept of *adaptive radiation* in evolution: when a group of descendent species diversifies from a single ancestral stock or lineage to occupy different ecological niches; occurs when new way of exploiting an environment arises; produces bushy phylogenies (i.e.1500 rodent species; 51 rat species)
- Early hominin evolution suggests several phases of radiation

- 1 – African ape lineage: 6-7 Ma; diverged from LCA; immigration from Asia, across Africa; earliest hominins are sister clades of other apes, exploiting equatorial tropic environments; include ancestors of living great apes, *Sahelanthropus, Orrorin, Ardipithecus;* result of dispersals of new fauna spreading into all available habitat

Major Adaptive radiations of early hominins

- 2 – Early *australopithecines*: 4-3.5 Ma; originating in E. Africa, diversifying into E and S Africa;
  - includes *A. anamensis, A. afarensis, A. africanus, A. garhi, K. platyops;*
  - bipedalism as fundamental reason for their success

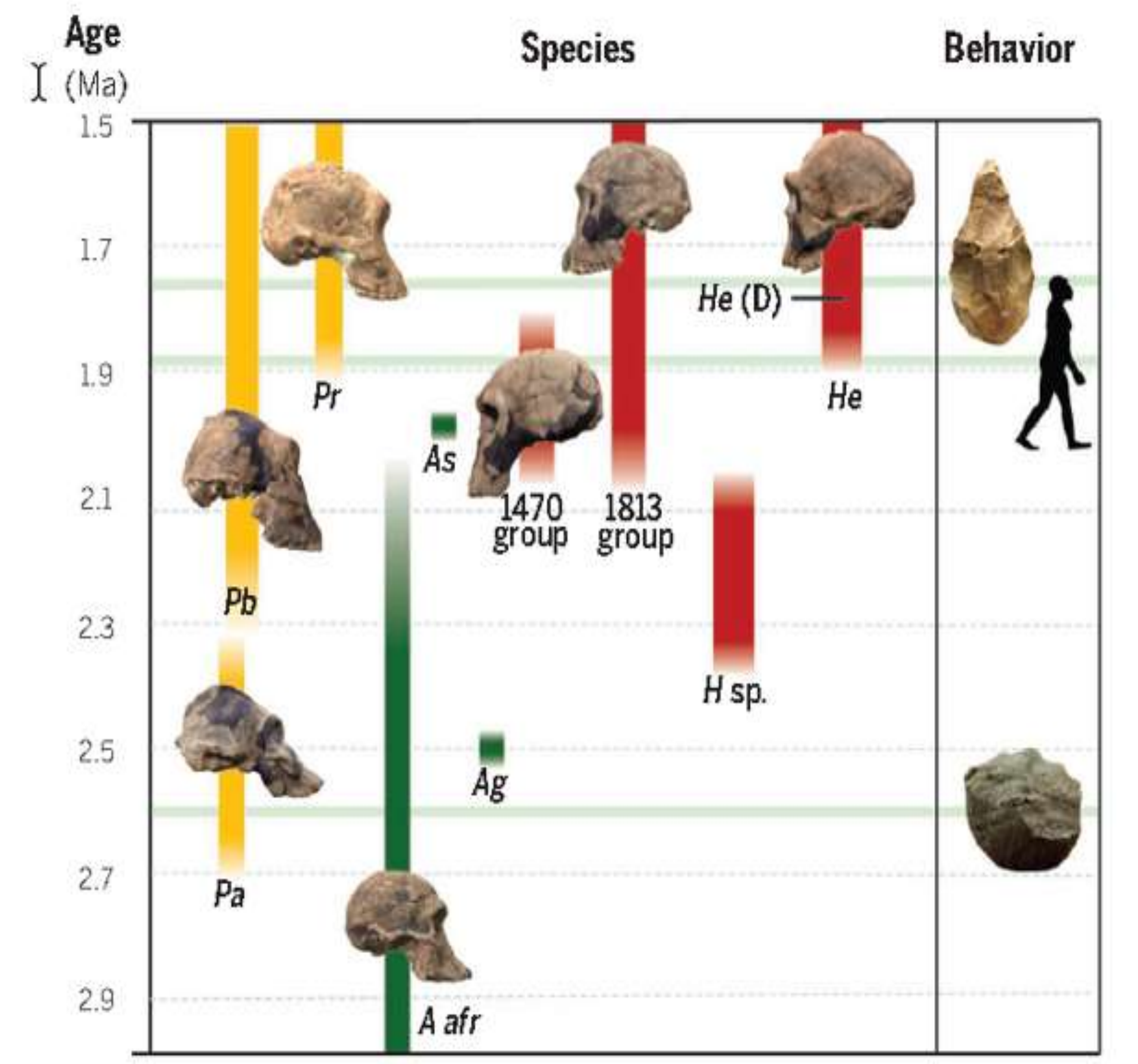
- 3 – Robust *australopithecines*: 2-1 Ma;
  - characterized by their megadontic dental specializations
  - includes *P. aethiopicus, P. boisei, & P. robustus;*
  - decreased global temperatures; increased aridity in E. Africa; more open, seasonal environments

Adaptive radiations of early hominins

- 3 – Robust *australopithecines*:
  - large teeth as adaptations to processing large quantities of coarse, fibrous, gritty plant materials (vegetation of more seasonal, drier environments)
  - evidenced by teeth microwear; by time a *P. boisei's* third molar erupted, first & second molars were worn down to dentine
  - successful strategy given its widespread distribution, being most common Pliocene hominin fossil, lasting 1 M years.

- *4* – Large brained hominins: *H. habilis, H. rudolfensis, H. ergaster/erectus*

- These radiations may not be entirely discrete events; clearly continuity between earlier and later australopiths; dental size differences is one of degree, not kind



Susan C. Antón, Richard Potts, Leslie C. Aiello, 2014

- **Hominin evolution from 3.0 to 1.5 Ma.** (Species)
- Currently known species temporal ranges for *Pa*, *Paranthropus aethiopicus*; *Pb*, *P. boisei*; *Pr*, *P. robustus*; *A afr*, *Australopithecus africanus*; *Ag*, *A. garhi*; *As*, *A. sediba*; *H* sp., early *Homo* >2.1 million years ago (Ma); 1470 group and 1813 group representing a new interpretation of the traditionally recognized *H. habilis* and *H. rudolfensis*; and *He*, *H. erectus*. *He* (D) indicates *H. erectus* from Dmanisi.

- (Behavior) Icons indicate from the bottom the
  - first appearance of stone tools (the Oldowan technology) at ~2.6 Ma,
  - the dispersal of *Homo* to Eurasia at ~1.85 Ma,
  - and the appearance of the Acheulean technology at ~1.76 Ma.
  - The number of contemporaneous hominin taxa during this period reflects different strategies of adaptation to habitat variability.

Different adaptive strategies

1 - Australopithecus, Paranthropus, Homo habilis and rudolfensis

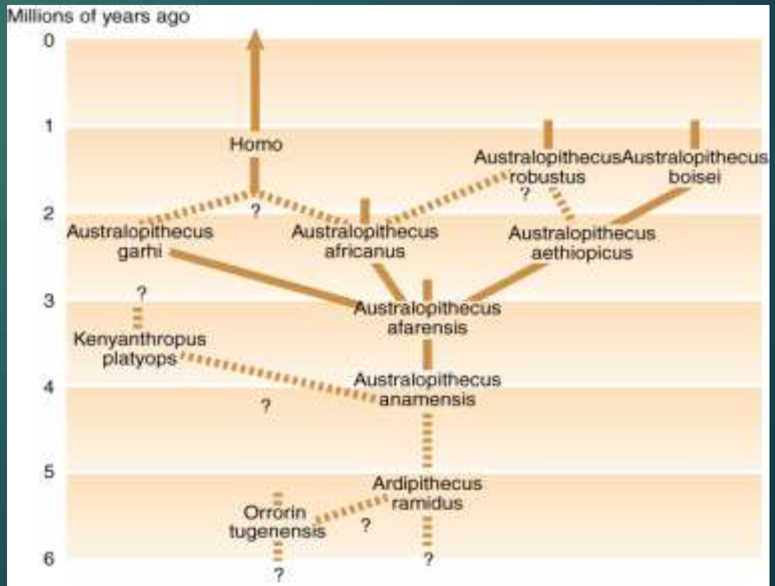
- Ape-sized brains
- Body mass (low) and shape more suited to closed environments, e.g. forest
- Ape-like plant-based diet; vegetarians
- Ape-like faster development pattern (earlier molars & sexual maturity, less longevity)
- Combined locomotion of bipedalism and arboreality (substantial amount of time in trees)
- Small male canines; heavy masticatory stress reflected in jaws & teeth
- Gracile lines become extinct circa 2 Ma
- Robust lines see an intensification of adaptation to hard object feeding; extinct by 1.2 Ma

Wood & Collard, 2001: Meaning of Homo

Who was ancestral to *Homo*?

- Not robustus: General agreement that the robust australopithecines became extinct after ~1.2 Ma and did not give rise to modern humans

- Who did?
  - Major candidates
    - *Australopithecus africanus*
    - *Australopithecus garhi*
    - *Kenyanthropus platyops*



Collard and Wood would define *Homo* by its adaptive zone

- 2 - *Homo erectus/ergaster, Homo heidelbergensis, Homo neanderthalensis*
  - larger brain & body size
  - brain reorganized (lateralization & language regions)
  - flatter faces
  - more modern postcranial skeleton: Body mass and shape more like ours; long legged build, suited to hotter, more open habitats
  - Ecological flexibility
  - Tool manufacture
  - terrestrial bipedalism and limited arboreality

Collard and Wood would define *Homo* by its adaptive zone

- 2 - *Homo erectus/ergaster, Homo heidelbergensis, Homo neanderthalensis*
  - relatively smaller chewing teeth
  - Increased dietary quality, similar to modern *H. sapiens*; Added meat to diet (scavenging/hunting?)
  - extended developmental hx and longevity
  - use of fire
  - larger home range
  - increased social cooperation

Evolution of early *Homo: not a single package*

- Many of the above features associated with *Homo sapiens* were once thought to have evolved near the origin of the genus in response to heightened aridity and open habitats in Africa.

- These features are mostly true for *Homo erectus*; but have now been challenged in *Homo habilis*

- Recent analyses of fossil, archaeological, and environmental data indicate that *Homo sapiens* traits did not arise as a single package.

- Instead, some arose substantially earlier and some later than previously thought. Mosaic development of these traits is the rule.

Evolution of early *Homo: not a single package*

- From ~2.5 to 1.5 Ma,
  - 3 lineages of early *Homo (H. habilis, rudolfensis, erectus)* evolved in a context of
  - habitat instability and fragmentation
  - on seasonal, intergenerational, and evolutionary time scales.

- These contexts gave a selective advantage to traits, such as dietary flexibility and larger body size, that facilitated survival in shifting environments.
  - Environmental/ecological niche differentiation
  - resulting from obligate bipedalism and dietary breadth

Early Homo Who, When, and Where Susan C. Antón, *Cur Anthro*, 2012

Homo

- Main evolutionary hominin trend between 5 MA to 1.5 Ma is megadontia

- *Homo* represents reversal of this trend:
    - dentition is reduced;
    - face & cranium lack muscular specializations (i.e. sagittal crest)

- *Homo* clade originates between 3 - 2.5 Ma;
    - associated with *H. habilis or H. rudolfensis/1470*, or another species.
    - Basis is larger cranial capacity and smaller dentition

What was first trigger for evolution of *Homo*?

- Adam Van Arsdale:
- Best supported model by the fossil record is that
    - the evolution of stone tools, their first appearance, and
    - the associated ecological changes,
- are the key driver in the *Homo* lineage.

Identifying Homo: Association with tools

- In the modern era, beginning with *Homo habilis*, behavior was the first criterion applied to identify and assess *Homo*
- The key criteria, was that at Olduvai Gorge, *Homo habilis*, was found with stone tools; whether they were made and used there is uncertain

- *H. habilis* was historically the first hominin to be found with stone tools

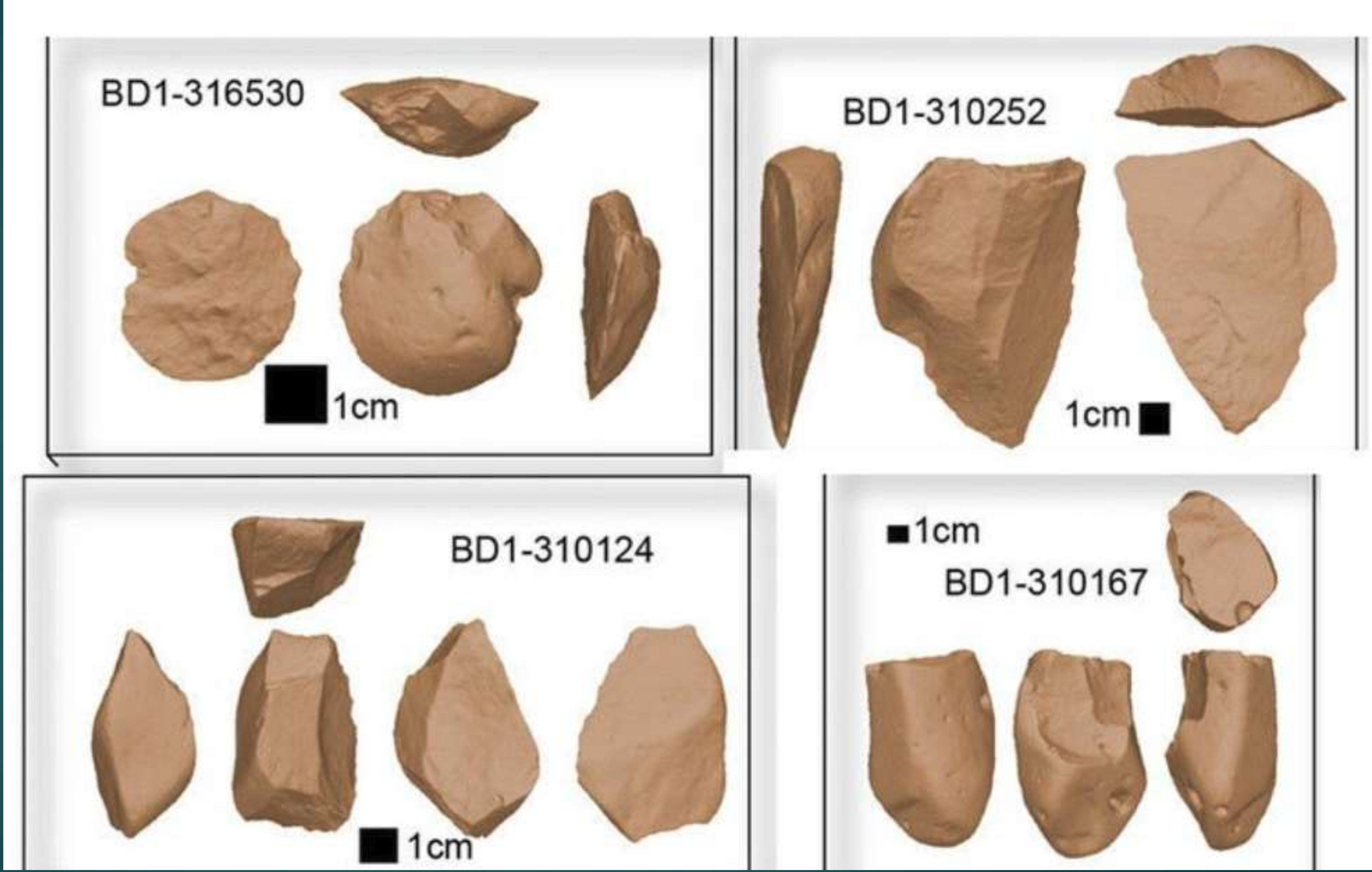
- At that time, the Australopiths of S Africa had not been associated with stone tools.
- Now know of stone tools at 3.3 Ma at Lomekwi & cutmarks at Dikika

2019: Bokol Dora, Ethiopia: Earliest known Oldowan artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia

- Recent discoveries from Ledi-Geraru, Ethiopia, place the first occurrence of *Homo* ~250 thousand years earlier than the Oldowan at Gona.
- A new Oldowan locality (Bokol Dora 1) that dates prior to 2.6 Ma. A substantial assemblage (327 stone tools) of systematically flaked stone tools excavated in situ from a stratigraphically constrained context, at LG bracketed between 2.61 and 2.58 Ma. Found 3 miles from Ledi-Geraru jaw (dated to 2.78 Ma).
- This discovery at the Bokol Dora 1 site in Ethiopia’s Afar Basin, push the origins of early human tool-making back by some 10,000 years earlier than previously believed. Additionally, the research suggests that multiple groups of prehistoric humans invented stone tools on separate occasions, adapting increasingly complex techniques in order to best extract resources from their environment.

David R. Braun, et al., 2019

Bokol Dora, Ethiopia



Shift in stone tools & smaller teeth

- Something changed by 2.6 million years ago, and our ancestors became more accurate and skilled at striking the edge of stones to make tools. The BD 1 artifacts captures this shift.
- It appears that this shift in tool making occurred around the same time that our ancestor's teeth began to change. This can be seen in the *Homo* jaw from Ledi-Geraru. As our ancestors began to process food prior to eating using stone tools, we start to see a reduction in the size of their teeth. Our technology and biology were intimately intertwined even as early as 2.6 million years ago.
- The lack of clear connections with earlier stone tool technology suggests that tool use was invented multiple times in the past.

Lomekwian stone tools, 3.3 Ma

- 3.3 million-year-old stone tools known as "Lomekwian" tools predate the new 2.6 Ma Oldowan trove, these were likely made by members of early hominin groups such as Australopithecus afarensis rather than members of the *Homo* genus.
- Until now, the oldest known *Homo* tools—dubbed "Oldowan" in honor of the Olduvai Gorge in Tanzania where the first examples of such artifacts were found—dated to between 2.55 and 2.58 million years ago. Excavated in Gona, Ethiopia, the sharpened stones are technologically distinct from the more rudimentary Lomekwian tools, in West Turkana, Kenya, in 2015.
- Compared with the Gona tools and other Oldowan artifacts, the latest finds are actually rather crude. The instruments have "significantly lower numbers of actual pieces chipped off a cobble than we see in any other assemblage later on,"

- Compared to the Oldowan tools found in Gona and now Bokol Dora, the earlier Lomekwian tools are decidedly less advanced.

Homo habilis: stone tools and meat

- The Oldowan toolkit is associated with *Homo habilis*; hence the nickname, handy man.
  - These are simple water-smoothed rocks roughly 3–4 inches across, modified by knocking some flakes or chips off one or two faces to make a sharp edge.
  - According to paleoanthropologist Richard Leakey, these simple stone tools allowed these hominins to more quickly cut meat and bones off a carcass, making the addition of meat to the diet, through scavenging.

Earliest *Homo* species

- Contentiousness regarding who belongs to early *Homo*

- At least 3 (perhaps more) *Homo* species
  - *Homo habilis/1318 group* = 2 - 1.6 Ma
  - *Homo rudolfensis/1470 group* = 2 - 1.8 Ma
  - *Homo erectus* (aka *H. ergaster*) = 1.8 - .03 Ma.

Homo habilis, 1.9-1.6 Ma

- *Homo habilis* was named in 1964 by Louis Leakey and colleagues based on fossils from Olduvai Gorge (Tanzania) now dated to 1.9–1.6 Ma
- *H. habilis* was regarded as intermediate between australopithecines and *Homo sapiens*, due to its larger brain and smaller posterior dentition.
- This ‘handy man’ purportedly had manual adaptations that facilitated toolmaking,
- Tool use is argued to coincide with changes in cognition and diet, including increased meat eating, another supposed distinction between *Homo* species and australopithecines

Leakey et al., 1964, Antón, 2004; Harmand et al., 2015; Wood, 2012; Lockwood, 2013.

Relaxation of who was in genus *Homo*

- 1758: Linnaeus - *Homo sapiens*; Type specimen: None designated
- 1864: King - *Homo neanderthalensis;* Type specimen: Neanderthal 1
- 1908: Schoetensack- *Homo heidelbergensis;* Type specimen: Mauer mandible
- 1921: Woodward - *Homo rhodesiensis*; Type specimen: Kabwe 1
- 1932: Oppenoorth - *Homo (Javanthropus) soloensis*; Type specimen: Ngandong 1 (by implication)
- 1944: Mayr - *Homo erectus;* Type specimen: Trinil 1
- **1964: Leakey, Tobias and Napier - *Homo habilis;* Type specimen: OH 7**

Wood & Collard: 6 historical steps in relaxing the criteria for belonging to genus *Homo*

- 1. Naming the original N skeleton from Feldhofer by William King as a new species of *Homo*, *H. neanderthalensis*.

- 2. Naming the Mauer mandible from Germany as a new species of *Homo*, *Homo heidelbergensis*.

- 3. Weidenreich recommending that *Pithecanthropus erectus* should be transferred to the genus *Homo* as *Homo erectus.*

- 4. Designating the new gracile species from Olduvai as a new species of *Homo*, *Homo habilis.*

Wood & Collard: 6 historical steps in relaxing the criteria for belonging to genus *Homo*

- 5. Allocating KNM-ER 1470 from Koobi Fora to a new species of *Homo*, *Homo rudolfensis*.

- 6. Changing inclusive interpretations of *Homo habilis* over time. Additions of specimens from Sterkfontein, Swartkrans, Hadar, Dmanisi

- *Homo* now runs the gamut of Australopith-like postcranial forms & brain size seen in *H. habilis* to those features of modern humans.

- Early hominin brain size range from 500 cc to 850 cc

Genus *Homo*

- Our own genus, *Homo*, first appeared in the fossil record of Africa 2.8-2.0 Ma.

- Has traditionally been divided into 3 time-successive species, or chronospecies, *H. habilis*, *H. erectus*, and *H. sapiens.*

- This model reflects the view that we represent a single anagenetic lineage (one characterized by a gradual accumulation of changes from an ancestor to descendants thru time)

- Question: how many species of *Homo* during this period?

Inferences about *Homo*, 2.8-1.5 Ma

- Increased bipedalism (evidence: postcranials)
- Increased dexterity related to tool making (hand bones, tools)
- Stones & animal bones carried repeatedly to specific sites
- Use of tools to procure & process food
- Dietary increase in protein & fat from large animals (cut marks, animal bones)
- Scavenging & possible hunting of large animals (animal limb bones)
- Increased cognitive capacities associated with tool making, foraging, social interactions (brain size increase from 1/3 to ½ of MH)
- Increased mobility and predator defense (*H. erectus* large skeleton)

Questions pertaining to *Homo*

- Some of the ongoing controversies facing paleoanthropologists as they study the genus *Homo:*

- How can early *Homo* be distinguished from gracile australopiths?
- Is the range of variation in form subsumed under the name *H. habilis* too great for a single species?
- If so, what other taxa are represented?
- Does the definition of *Homo* need to be modified, and if so, how?
- Is *Homo habilis* ancestral to *H. erectus*?

Early *Homo*: *critique*

- B. Wood and M. Collard (1999):
  - if body size and rigorous cladistic analysis considered, early *Homo* falls adaptively with australopiths;
  - grade change only with *H. ergaster/erectus*; (grade = group of organisms which share common adaptation)

- Roger Lewin & Robert A. Foley:
  - early hominins = closer to apes than to humans;
  - highly sexually dimorphic,
  - largely apelike guts and brains;
  - pattern of growth & life history closer to apes;
  - restriction to Africa;
  - these are bipedal apes, not protohominins

Redefining *Homo*: Does our family tree need more branches?

- Do all current *Homo* species, with their wide diversity of physical and cultural traits, actually belong in the same genus?
- Traditionally, early hominin fossils have been classified into either the genus *Homo* or *Australopithecus*, with *Homo* dating back to about 2.8 million years and the oldest Australopiths dating back to about 4 million years ago.
- The original fossil described by Leakey had a brain slightly bigger than the average Australopith, but the brains of subsequent *H. habilis* specimens were smaller, between 340 and 500 cubic centimeters.
- Some believe the genus *Homo* has become a wastebasket of names with very little meaning

Mary Caperton Morton, 2016

Debate over taxonomy of *H. habilis*

- B. Wood: “If you include *Homo habilis* in *Homo*, you end up including a species that had limb proportions that are closer to *Australopithecus*, as well as dentition and a jaw whose scaling in relation to body mass is closer to *Australopithecus* and a brain size closer to *Australopithecus*,”.
- However, just because *Homo habilis* does not belong in *Homo* doesn’t mean it’s an Australopith.
- But some anthropologists think we need more options. Ian Tattersall: “Right now, we are stuck in a false dichotomy, where if it isn’t an Australopith, it must be *Homo* and if it isn’t *Homo*, it must be an Australopith,” “My sense is that *Homo habilis* should belong to its own genus, neither Australopith nor human.”

Redefining *Homo*

- As an example, by the mid-20th century there were more than a dozen different named genera, most of which were actually the same species: *Homo neanderthalensis*.

- The first paleontologists were experts in anatomy, not taxonomy. They were splitters.

- In 1963, taxonomist and ornithologist Ernst Mayr tried to set everybody straight by dragging the field in the opposite lumping direction. He was the original lumper.

Redefining *Homo:* Ernest Mayr

- Despite never having seen a hominin fossil, Mayr declared there was:
  - only one genus in the hominin family — *Homo*
  - and that there were only three species, each giving way to the next in an orderly fashion:
    - *Homo transvaalensis* (the Australopiths)
    - gave rise to *Homo erectus*,
    - which paved the way for *Homo sapiens* to populate the planet.

- Mayr grouped members simply on the basis of bipedalism: everything bipedal was automatically Homo. He never looked at fossils and never looked at the literature

Tattersall on Mayr

- Tattersall: It’s mind-boggling that the field of paleoanthropology is still being influenced to this day by a nonpaleoanthropologist. We’ve effectively been mired in Mayr’s misunderstanding since 1963.

- When Linnaeus was laying out his case for a binomial naming system, he bestowed Latin genus and species names on a number of plants and animals, including humans. For humans, he simply wrote, “Nosce te ipsum,” or “Know thyself.” No type specimen.

- *Homo sapiens* has not been properly defined, despite being the type fossil for *Homo*.

Redefining *Homo*: A list of features

- In 1795, anatomist Johann Friedrich Blumenbach compiled a list including a
  - chin,
  - small jaws,
  - small canines next to small incisors,
  - a large braincase balanced atop a vertical vertebral column,
  - erect posture,
  - bipedalism,
  - a bowl-shaped pelvic girdle,
  - buttocks
  - and a long thumb.

Criteria for *Homo*

- 4 historical criteria for inclusion in *Homo* (Wood & Collard) :
  - 1 – absolute brain size: History of cerebral “Rubicon” for membership in *Homo*:
    - Keith (1948): 750 cc for *Homo*
    - Leakey (1964): 600 cc for *Homo habilis*
    - Burger: 500 cc, *Homo naledi*
    - *Brown: 400 cc, Homo floresiensis*

  - 2 – possession of language

  - 3 – manufacture of stone tools – Leakey thought this was major criteria

  - 4 – possession of modern precision grip based on opposable thumb

Criteria for *Homo 2*

- But none of these criteria is satisfactory for inclusion in *Homo.*

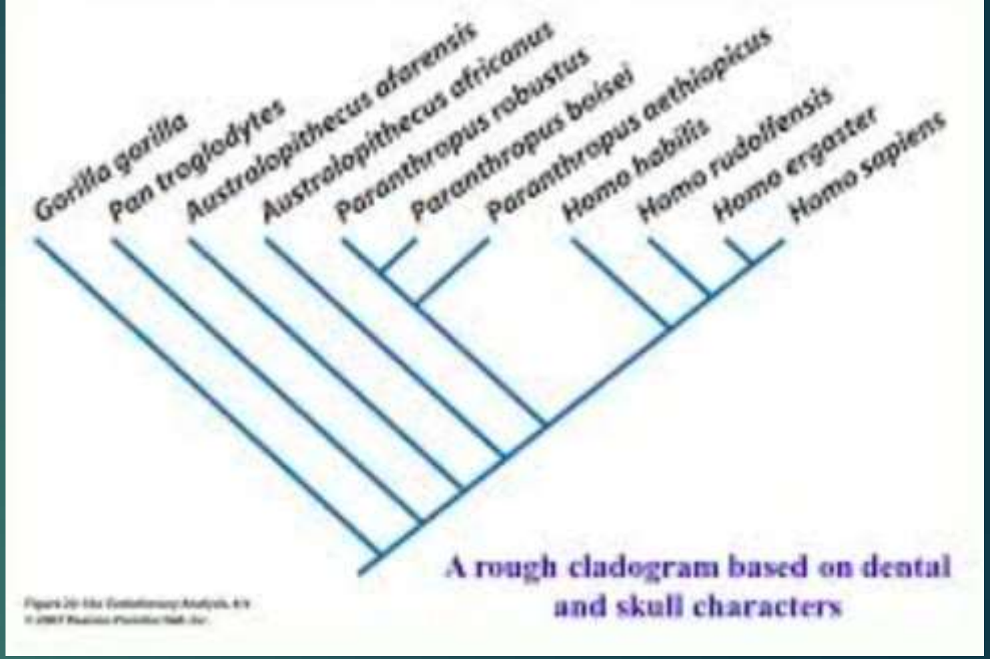
- These criteria are either of questionable biological significance or are often incapable of being determined from evidence in fossil record;

  - brain size (without body size) and language are difficult to verify in fossil endocasts

  - stone tools now predate appearance of *Homo*

  - grip not restricted to *Homo* and is hard to identify

Criteria for *Homo* 3



A rough cladogram based on dental and skull characters

- B. Wood & M. Collard:
- 2 criteria for *Homo* –
  - 1 – cladistic analysis should indicate species more closely related to type species of *H. sapiens*
  - 2 - body mass and shape, locomotion, pattern of tissue development, relative dentition size are more closely related to type species

Origins of *Homo*

- Several morphological differences distinguish fossil members of the genus *Homo* from those of *Australopithecus* and *Paranthropus*, including:
  - reduction in tooth and jaw size,
  - re-organization of craniofacial morphology,
  - perhaps changes in body shape and size.
    - suggest underlying adaptive shifts at the origin of the genus *Homo*
    - the adaptive zone of *Homo* related to cranial expansion and masticatory reduction and/or to increased locomotor efficiency and ranging relative to *Australopithecus*.

Origins of *Homo*

- S. Antón: Genus *Homo* is recognized on the basis of the following mostly derived craniodental characters relative to *Australopithecus:*
- 1. *Cranial expansion*. Size-adjusted cranial capacity relative to orbit size is above 2.7.
- 2. *Shape of the face and palate*. The palate is deep and broad. The anterior maxillary profile, as seen from above, is round to square (not triangular). The subnasal prognathism is mild, the nasoalveolar clivus is sharply angled to the nasal floor, and the nasal margin is everted
- 3. *Size and shape of the dentition*. The canine crown is symmetrical. Premolars lack substantial molarization in crown and root form (buccolingually narrow) but are not sectorial. The molars, especially the first, are somewhat mesiodistally elongated but may retain a large crown-base area. M2 is “rhomboidal” in shape (dominated by mesial cusps)

Origins of *Homo:* almost no postcranial *Homo* remains

- Postcranial differences are not used here to distinguish *Homo* and *Australopithecus* because few postcranial remains are certainly associated with species-diagnostic cranial remains of early *Homo*.

- Additionally, those that are, do not support a major locomotor difference between *H. habilis* sensu lato on the one hand and *H. erectus* on the other.

- Using this standard, *H. habilis* and *H. rudolfensis* are recognized as *Homo* because both differ in distinct craniodental ways from *Australopithecus*.

Origins of *Homo:* South Africa vs. East Africa

- In South Africa, fewer fossils from the period 2.6 to 2.0 Ma or older have been suggested to represent either early *Homo* or a species of *Australopithecus* derived in the direction of *Homo*.

- These include the cranial base, Sts 19, and juvenile cranial fragments, Stw 151, from Sterkfontein. However, both are commonly attributed to *Australopithecus africanus*. It is unclear which species is directly ancestral to *Homo*.

- However, the origin of the lineage is likely to be at 2.5 Ma or earlier given that by 2.3 Ma there is incipient evidence of two dental morphs.

Origins of *Homo*

- Based on the current record, the earliest accepted *Homo* appear to be in the northern part of eastern Africa; however, this does not preclude an ancestor from another part of the continent.
- Early *Homo* (2.0–1.44 Ma) members of "non-*erectus*" *Homo* are better represented after 2 Ma and range in age from about 2.0 to 1.44 Ma. They are best known from Kenya and Tanzania, although at least one South African morph also appears to be present.
- It is generally agreed that there is some fossil evidence for at least one member of early *Homo* in South Africa; however, there is no consensus concerning which species are present or whether these also occur in East Africa.

Origins of *Homo: South Africa*

- The remains in question date (roughly) between 2.0 and 1.5 Ma and come from Sterkfontein, Swartkrans, and Drimolen. The Swartkrans remains are most frequently linked with *H. erectus.*

- The Sterkfontein remains include isolated teeth, two partial mandibles, and the cranium Stw 53,

- The isolated teeth from Sterkfontein and Drimolen lend strong support to the identification of an as yet unnamed early non-*erectus Homo* in South Africa. Because they do not affiliate strongly with the East African teeth, they are considered as early non-*erectus Homo*.

Origins of *Homo*

- The first recognizable members of the genus *Homo* appear at approximately 2.3 Ma, suggesting that
  - The genus evolved earlier,
  - but substantial fossil evidence does not appear until about 2.0 Ma.

- A strong case can be made for at least three different morphs between 2.0 and 1.5 Ma:
  - an 1813-group (*Homo habilis; OH 7 type*),
  - a 1470-group (*Homo rudolfensis*),
  - *Homo erectus/ergaster*

Origins of *Homo*

- S. Antón avoids the use of taxonomic names for the 1813-group and 1470-group because of uncertainty over group affiliation of type specimens for early *Homo* species (e.g., *Homo habilis* and *Homo rudolfensis*).

- This lecture provides an introduction to what is now known about the distinct features that separate the three different morphs from each other and from *Australopithecus*

Origins of *Homo 6*

- On average,
    - early *Homo* is larger of body and brain than *Australopithecus*,
    - *H. erectus* is larger than other early *Homo.*
    - But size overlap is usually underestimated.

- That said, the surprising facts are the degree of diversity within the morphs and that, in some ways, the morphs are more similar to each other than has been previously imagined.

- For example, all early *Homo*, including *H. erectus*, may exhibit substantial amounts of sexual dimorphism, and *H. erectus* is less fully modern in body proportions than has been previously claimed.

Importance of Dating

- Discovery of radioactivity resulted in radiometric dating;
  - Arthur Holmes pioneered the use of radiometric dating of minerals
  - Age of the earth was dated to 1.6 to 3 Billion years in 1911.

- Age of the earth:
  - In 1926, National Academy of Science: 4.5 Billion years old based on galena specimen, but question as to whether a terrestrial rock has retained its original composition;
  - In 1956, meteorite dating (primitive material from which the accreting solar disk was formed): 4.55 ± 0.07 billion years

- Prior to 1960s, no exact chronology of mankind's history was available

Evolution of the genus *Homo*

- Classic conceptual division of genus *Homo* into 3 successive species:
  - *Homo habilis* (2.5 to 1.7 Ma),
  - *Homo erectus* (1.8 Ma to 100 Ka),
  - *Homo sapiens* (> 300 Ka);
  - each distinguished by larger brain size

- *R. Klein, 2009*:
  - *H. habilis*,
  - then *H. ergaster* in Africa,
  - which gave rise to *H. erectus* in Eurasia;
  - *H. ergaster* in Africa gave rise to *H. heidelbergensis* in Africa, which spread to Eurasia (700-600 Ka),
  - which gave rise to *H. neanderthalensis* in Eurasia, and *H. sapiens* in Africa.
  - But it was clearly even more complicated.

Evolution of early *Homo: not a single package*

- From ~2.5 to 1.5 Ma,
  - 3 lineages of early *Homo (H. habilis, rudolfensis, erectus)* evolved in a context of
  - habitat instability and fragmentation
  - on seasonal, intergenerational, and evolutionary time scales.

- These contexts gave a selective advantage to traits, such as dietary flexibility and larger body size, that facilitated survival in shifting environments.
  - Environmental/ecological niche differentiation
  - resulting from obligate bipedalism and dietary breadth

Early Homo Who, When, and Where Susan C. Antón, *Cur Anthro*, 2012

Homo

- Main evolutionary hominin trend in the Australopiths between 5 MA to 1.5 Ma is megadontia

- *Homo* represents reversal of this trend:
    - dentition is reduced;
    - face & cranium lack muscular specializations (i.e. sagittal crest)

- *Homo* clade originates between 3 - 2.5 Ma;
    - associated with *H. habilis/1813 or H. rudolfensis/1470*, or another species.
    - Basis is larger cranial capacity and smaller dentition

Relation of neural growth & behavioral change

- Temporal coincidence
  - between brain expansion in *Homo* & appearance of first archeological sites between 2.6 & 2.0 MA
  - suggests functional link between neural and behavioral change (stone technology)

- Additional brain enlargement that occurred 1.8-1.7 Ma in emergence of *H. ergaster* may have been equally tied to nearly simultaneous appearance of Acheulean biface artifacts.

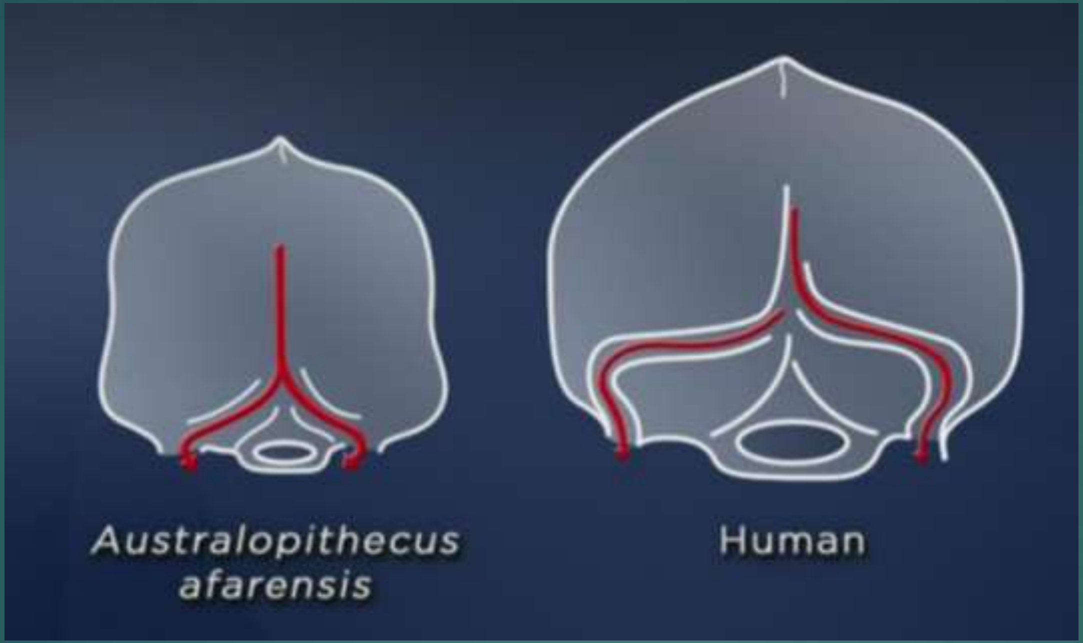
- At both 2.5 and 1.7 Ma, neural change may not only have allowed new behaviors, but new behaviors in turn may have selected for more neural change

Inferences about *Homo*, 2.8-1.5 Ma

- Increased bipedalism (evidence: postcranials)
- Increased dexterity related to tool making (hand bones, tools)
- Stones & animal bones carried repeatedly to specific sites
- Use of tools to procure & process food
- Dietary increase in protein & fat from large animals (cut marks, animal bones)
- Scavenging & possible hunting of large animals (animal limb bones)
- Increased cognitive capacities associated with tool making, foraging, social interactions (brain size increase from 1/3 to ½ of MH)
- Increased mobility and predator defense (*H. erectus* large skeleton)

Heat constraints of the brain: Dean Falk noted venous drainage differences in hominins (veins act as heat regulators for brain)

Radiator theory: *A. Afarensis* and *Homo sapiens* venous drainage – allowed better drainage & larger brains



Thermoregulation adaptation: Occipital marginal drainage vs more efficient transverse drainage; allows blood to drain from the back of the head; these occipital veins in humans have been shown to cool the brain under conditions of hyperthermia. Thus, the network of veins in the lineage leading to *Homo* acted as a radiator that released a thermal constraint on brain size; Bigger brains need better drainage for less heat

What was first trigger for evolution of *Homo*?

- Adam Van Arsdale, 2014:

- First trigger for evolution of Homo?

- Best supported model by the fossil record is that
    - the evolution of stone tools and their first appearance, and
    - the associated ecological changes,
- are the key driver in the *Homo* lineage.

Redefining *Homo:* the toolmaker

- In the 1960s, the idea of defining *Homo* solely based on tool use was very much in vogue.

- “‘Man the toolmaker’ was an interesting notion at the time, but like a lot of interesting notions, it’s a hypothesis that has been modified

- Tool use criterion: not unique to *Homo* because there is now evidence that *Australopithecus* also used tools.

Tool use and hunting in chimpanzees

- Chimps use tools:
  - use tree roots as anvils for cracking hard nuts of kola and Panda trees with stone or wood hammers;
  - some hammers from 100 meters away;
  - females engage in such tool use more frequently than males;
  - these stone tools are not usually used for hunting
  - if females hunt, share more than males
- Male chimps hunt red colobus monkeys; chaotic male bands, not really cooperative; although meat is shared; and no meat exchange for sex
- 2019: Bonobos hunt Weyn's duikers in female-led groups; female control of carcasses is frequent but not exclusive, and meat sharing in bonobos is primarily passive but not without aggression.

Chimps and Savanna

- Patterns of tool use and hunting by chimpanzees argue vs view that savanna living provided the critical impetus for hominin tool manufacture or meat eating
- Forest living chimps have been found to use more tools, make them in more different ways, hunt more frequently and more often in groups & show more frequent cooperation than do savanna-living chimps.
- Exploitation of the savanna habitat, in and of itself, is not sufficient to explain the evolution of such human-like behavior, as increased tool use, cooperative hunting, or food sharing.
- It increasingly seems likely that the cognitive basis for tool use was probably present in the last common ancestor of chimps and modern humans.

Boesch-Achermann & Boesch, 1994; Mitani et al., 2002

Where did *Homo* originate?

No scientific answer currently accepted by everyone

Adrienne Zihlman, 1978: Pygmy chimpanzee hypothesis

- A. Zihlman's 'pygmy chimpanzee hypothesis' (Zihlman *et al*. 1978): proposed that the Bonobo *Pan paniscus* is "the best prototype for the common ancestor of humans and [other] African apes": best representative in anatomy and behavior of a *Pan-parent* population that gave rise to 3 ape lineages
  - Least sexual dimorphism compared to other 2 ape groups (gorilla, chimp)
  - Most propensity for bipedality
  - Occupy most diverse habitats
  - Undeterred by water
- Zihlman proposes that LCA was a knucklewalker and that hominins then lost knucklewalking trait via increasing upright bipedality. But note T. White disagrees.

Zihlman et al. 1978; Zihlman 1984, p. 39.

A. Zihlman

- Congo basin as the crucible for ancestral origins of 3 ape lineages
- Last Common Ancestor (LCA): Widely distributed parent population of apes that resembled *P. paniscus* in:
    - Moderate body size
    - Locomotor versatility, with effective ground travel and a tendency for bipedal behavior
    - Omnivorous and diverse diet
    - Facility with objects and manipulative skills
    - Social and ecological flexibility

Adrienne Zihlman

- 2019: LCA of modern apes expanded from Congo basin:
  - Gorillas went West to forests, circa 6.5 Ma;
  - Australopithecines went East to mosaic savannah with new ecological niches, circa 4.5 Ma, developing from knuckle-walking to bipedality, which allowed greater foraging distances; going east & south
  - Chimpanzees went West; Pan troglodytes, due to competition with gorillas, underwent alternation to their physiology (larger, more aggressive, larger canines);
  - Then went East and South;
  - Bonobos & Pan troglodytes separate at 1 Ma

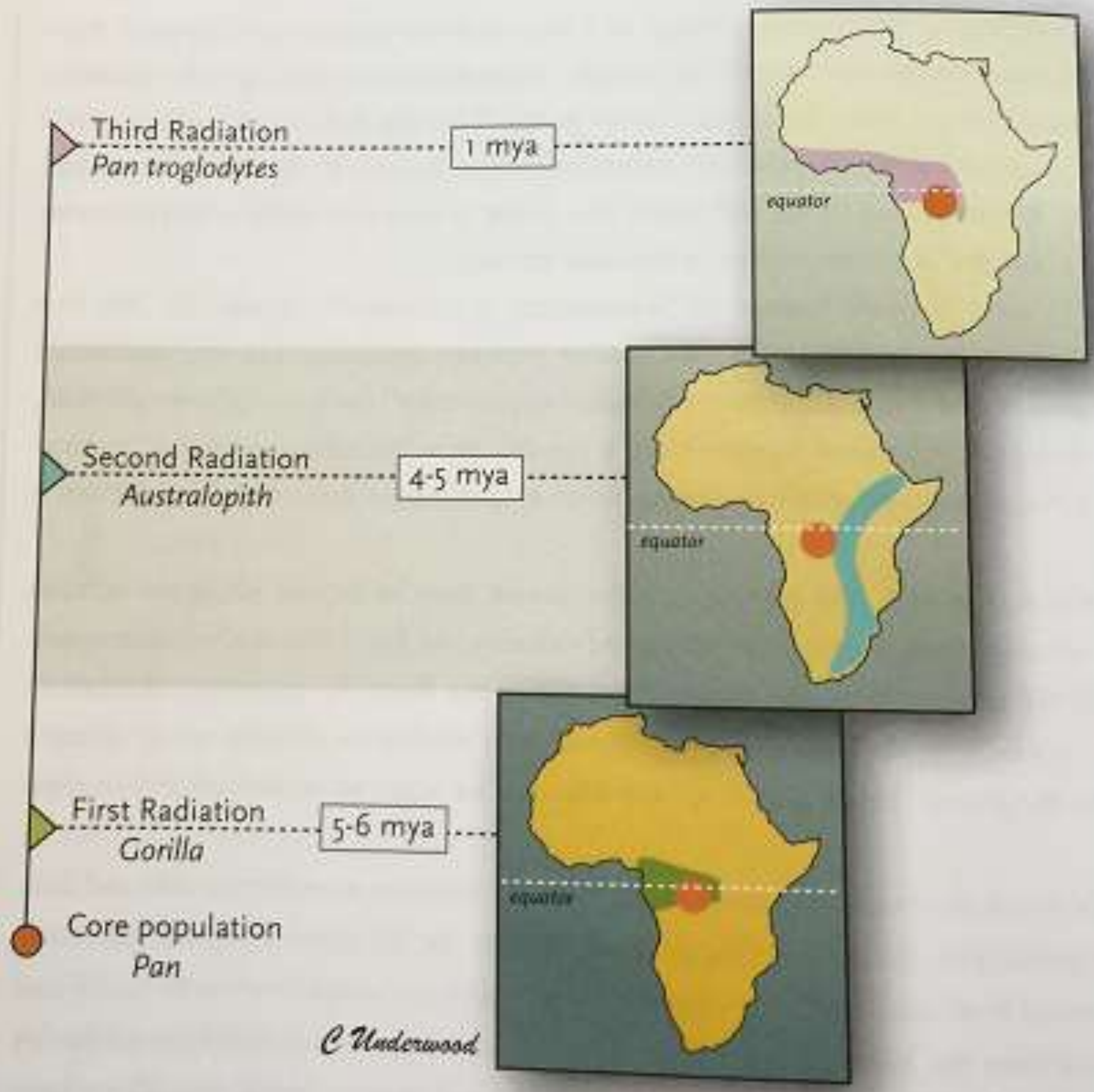
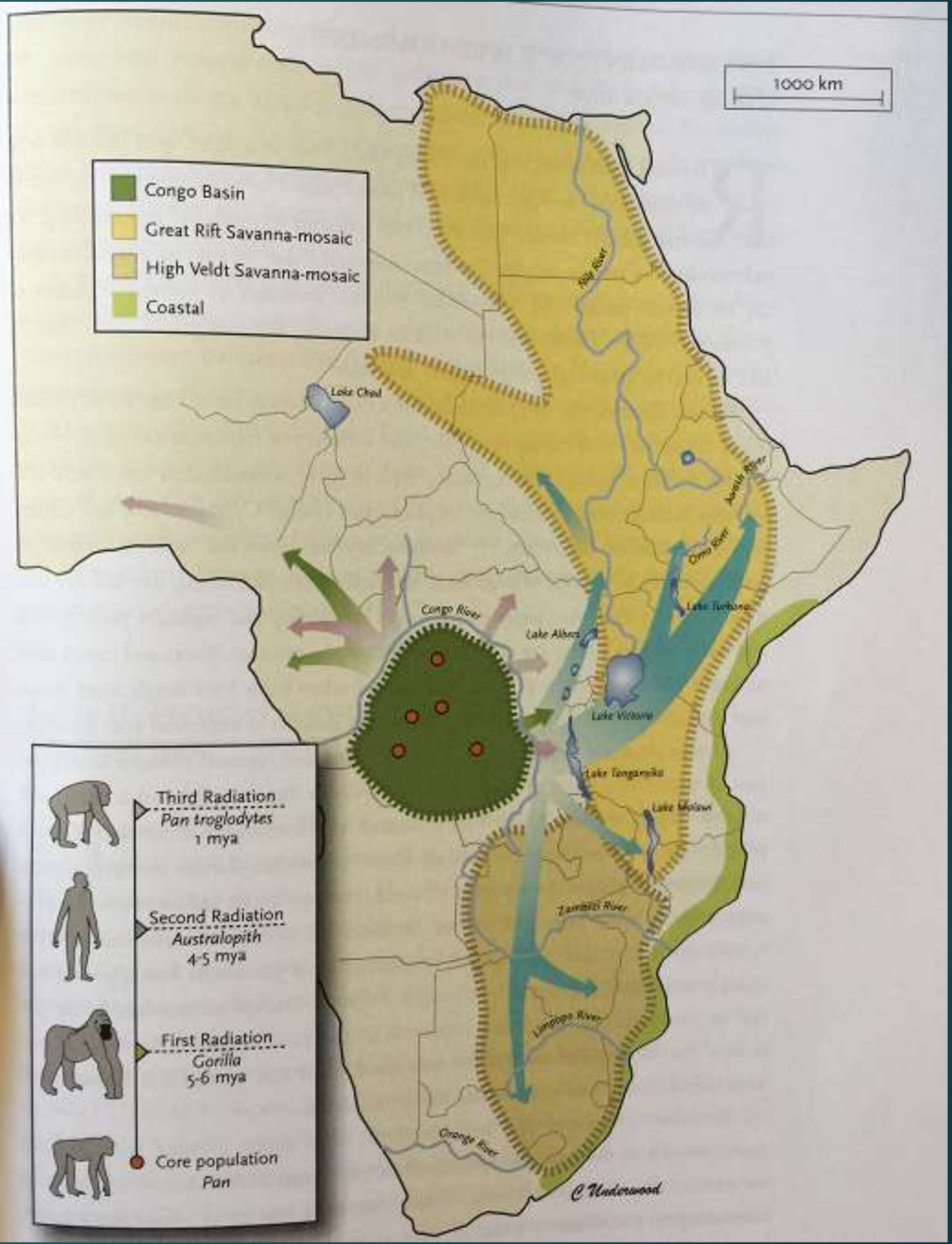
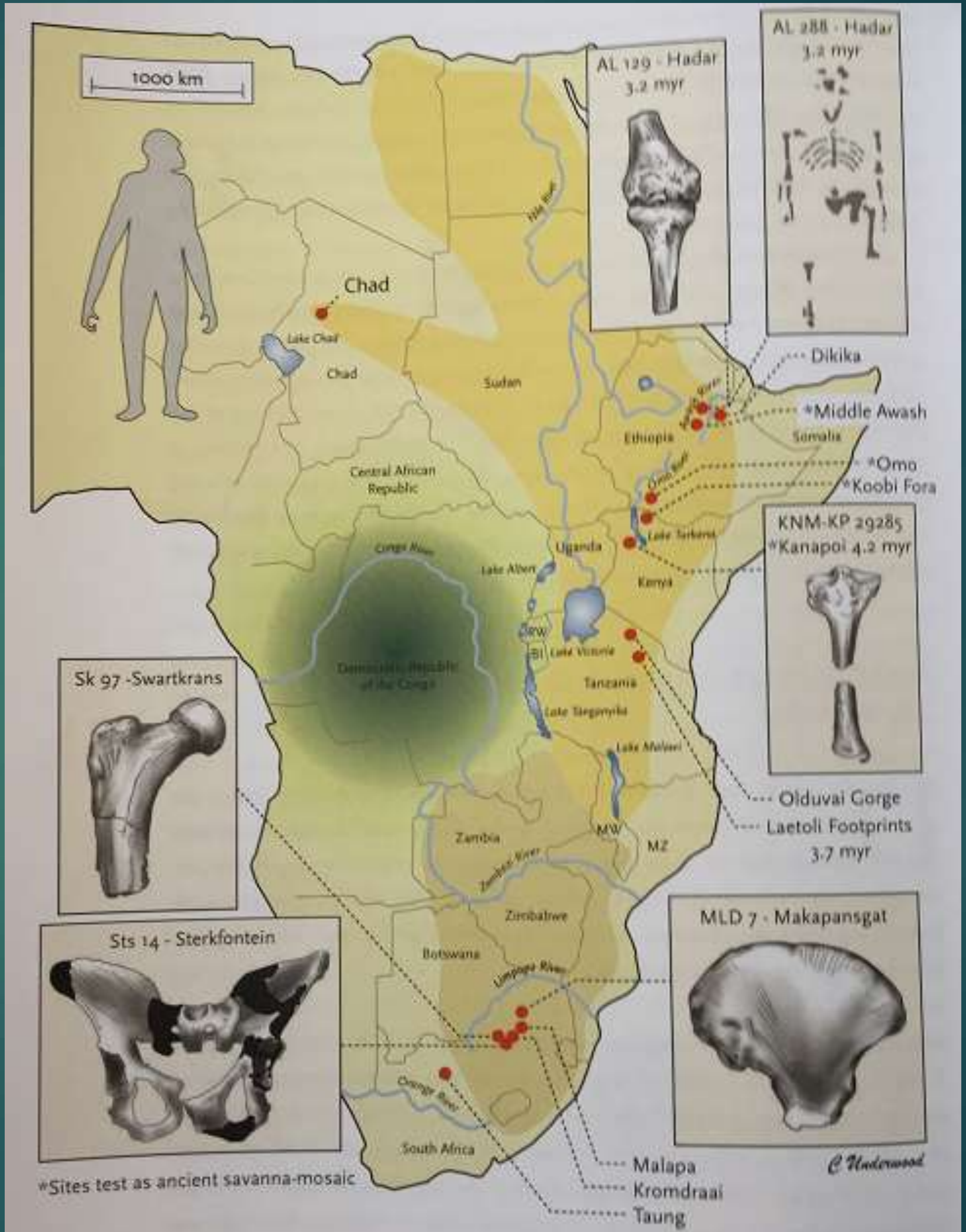


FIGURE 15.2. Timing of three lineages from the Congo Basin.



Australopith sites with fossil evidence for bipedal locomotion.



A. Zihlman

- Key to human origins: we were part of African ape evolution; Apes arose from arboreal setting; all came down from trees & started moving on the ground
- Where did hominins come from: Congo basin were all other apes originated
- LCA was knucklewalker; hominins adapted to bipedality
- Related to rise of bipedal locomotion and food source location
- 65% of body mass of apes is in locomotor system
- Size of bones do not necessarily correlate with muscle mass (Orangs: foot bone = 38% of hindlimb, but thigh = 54% of muscle); fossils may fool you

Chimps differ from other apes & are similar to hominins

- More locomotor versatility: more time on ground locomotion, travel farther
- Food items: expanded diversity of food (meat, insects, honey)
- Manipulative skills (know wood/branch properties; build comfortable nest every night)
- Problem solving (tool use, material manipulation)
- Foot: heel down, toe off
- Tools: make pestle to gain pulp from palm trees; spear to stab small animals in tree hollows, to pry open bee nest for honey; stone hammers to smash open hard-shelled nuts; don’t have to be a biped to do these
- Termite Toolsets: 2 different tools (plant wand & stick); find, select, modify; transport to site; probe & dig; insert wand & extract; females are star tool users; child learns from watching M

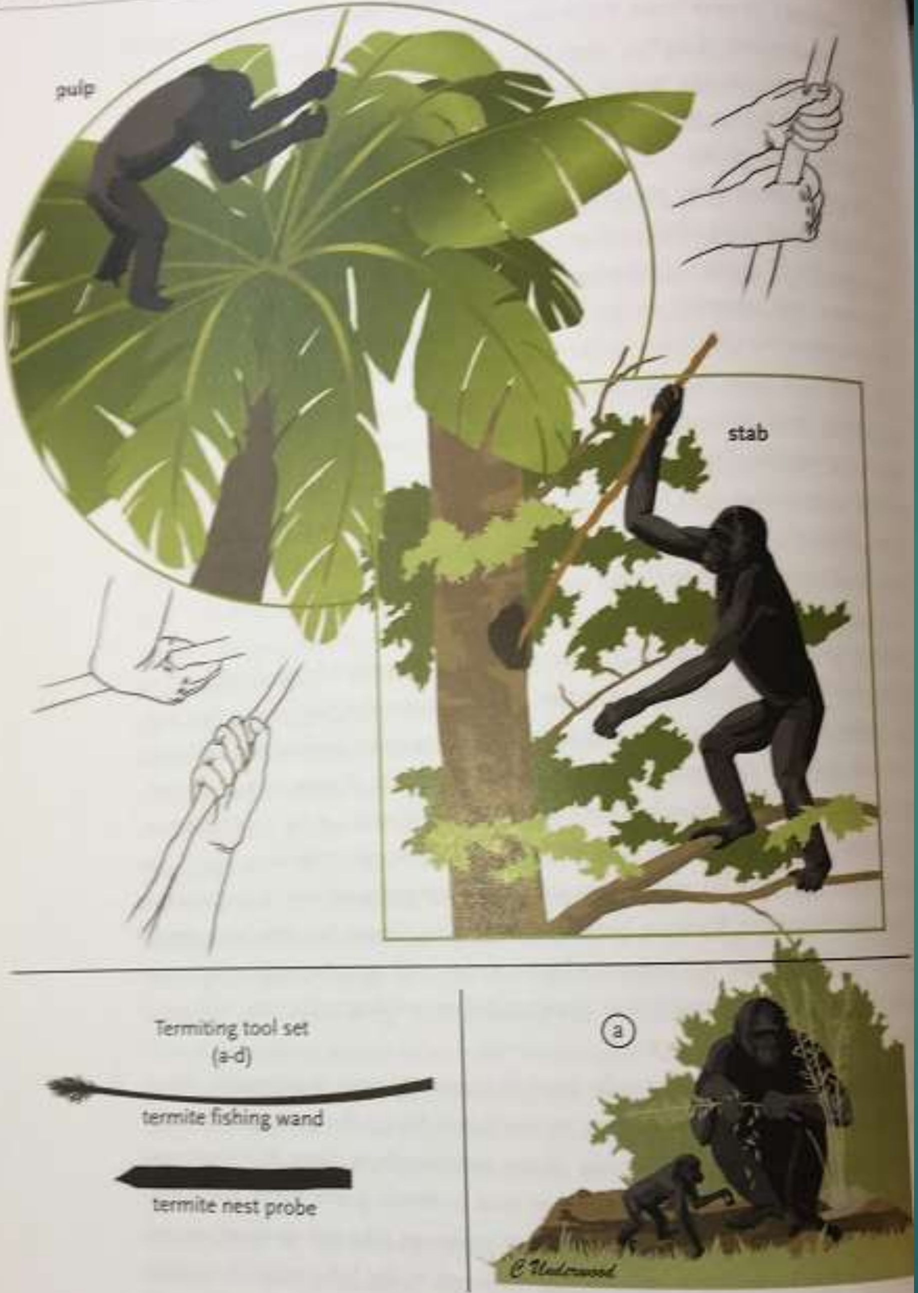


FIGURE 8.15. Whole body, hand and foot positions during tool use.

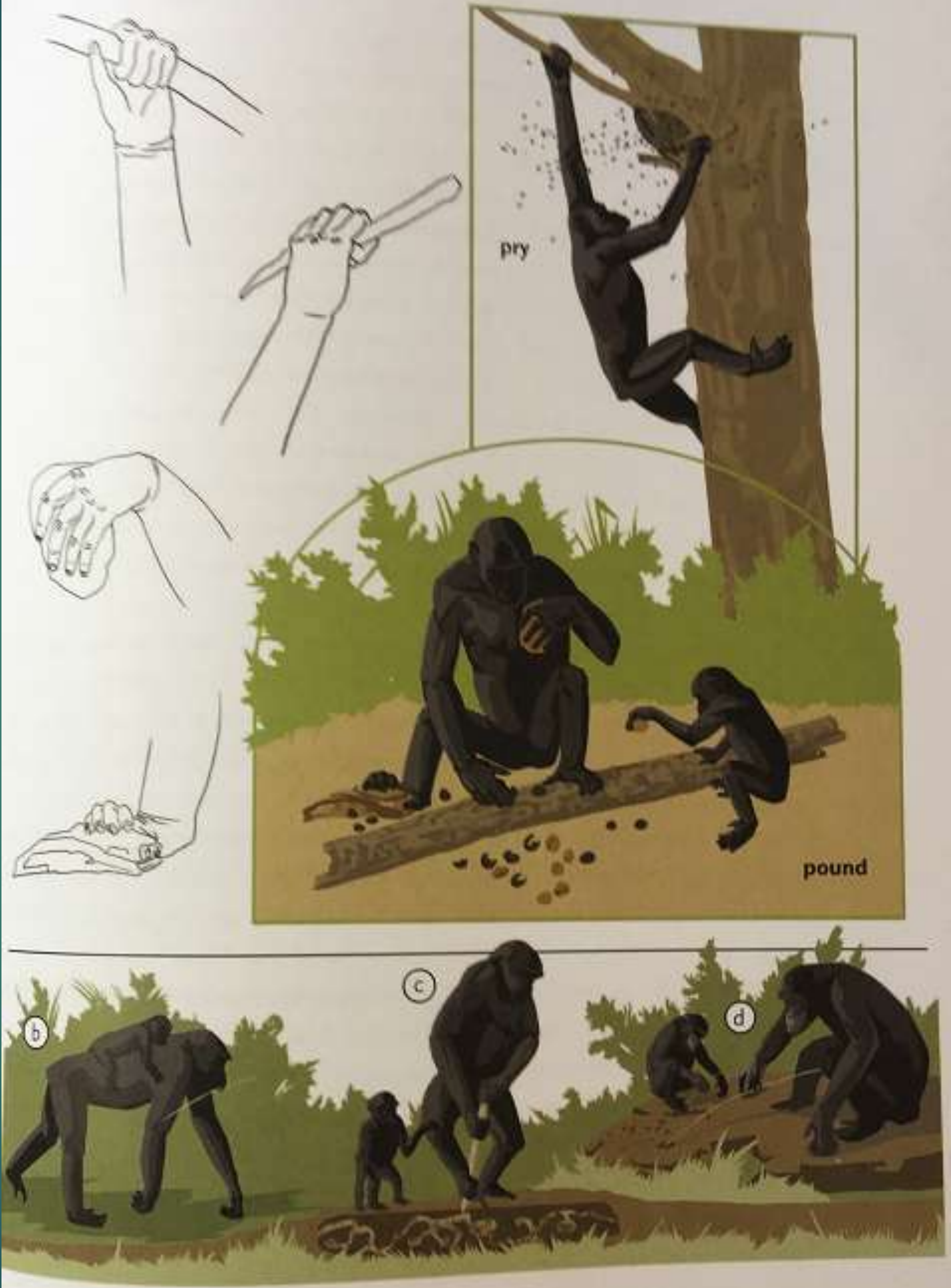


FIGURE 8.16 Whole body, hand and foot positions during tool use.

Chimp anatomy & bipedal function

- Chimps have most muscular lower limbs of all apes
- Foot structure adapted for ground surfaces
- Long lower limbs relative to upper limb and trunk length

- All these would transition to hominin anatomy
- LCA had anatomy something like chimpanzees
- It would be a small step to become full fledged biped based on chimp anatomy
- 1966 polio outbreak in Gombe; Jane Goodall’s chimp Faben, age 18, got polio, right limb paralyzed & became bipedal overnight; for 9 years

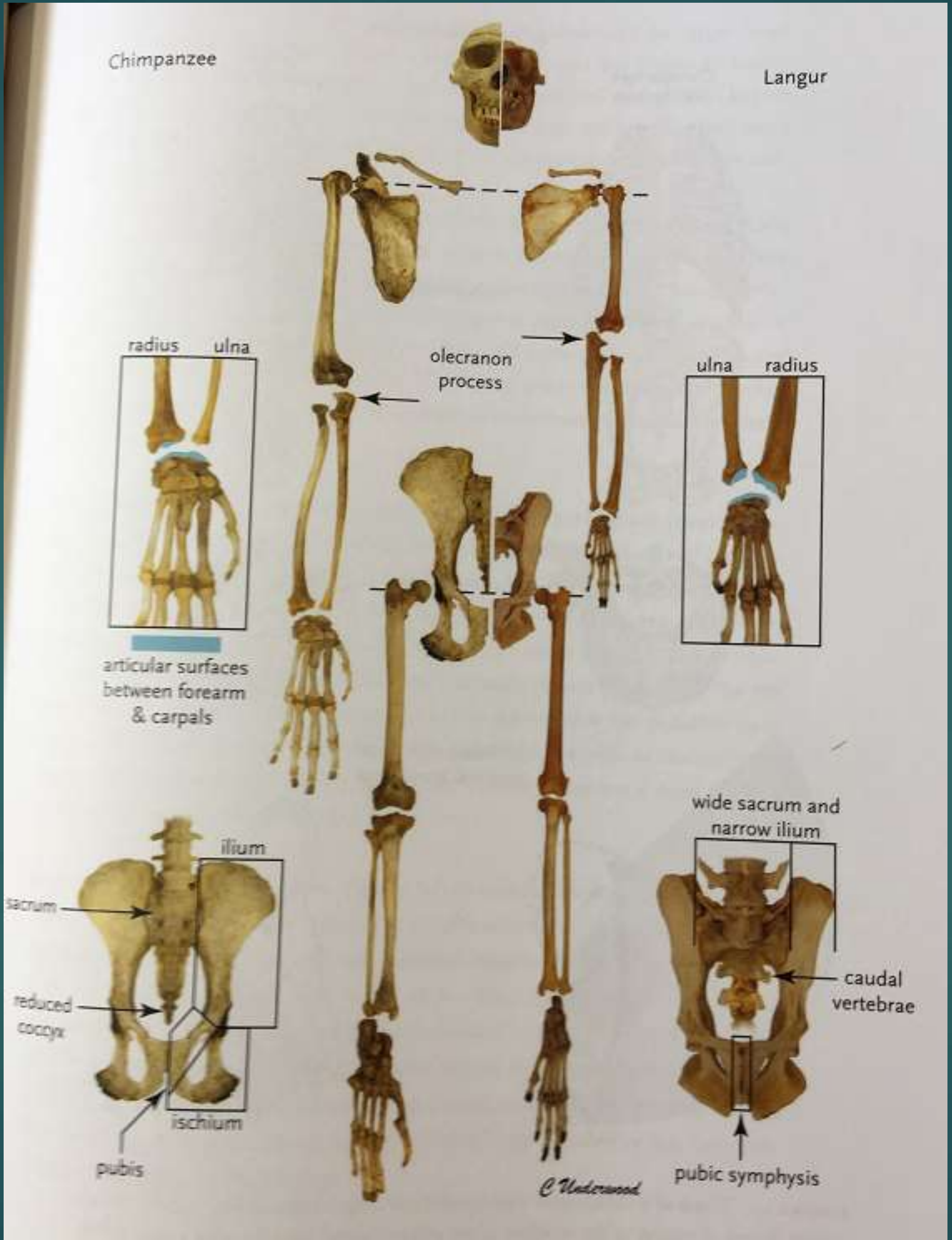
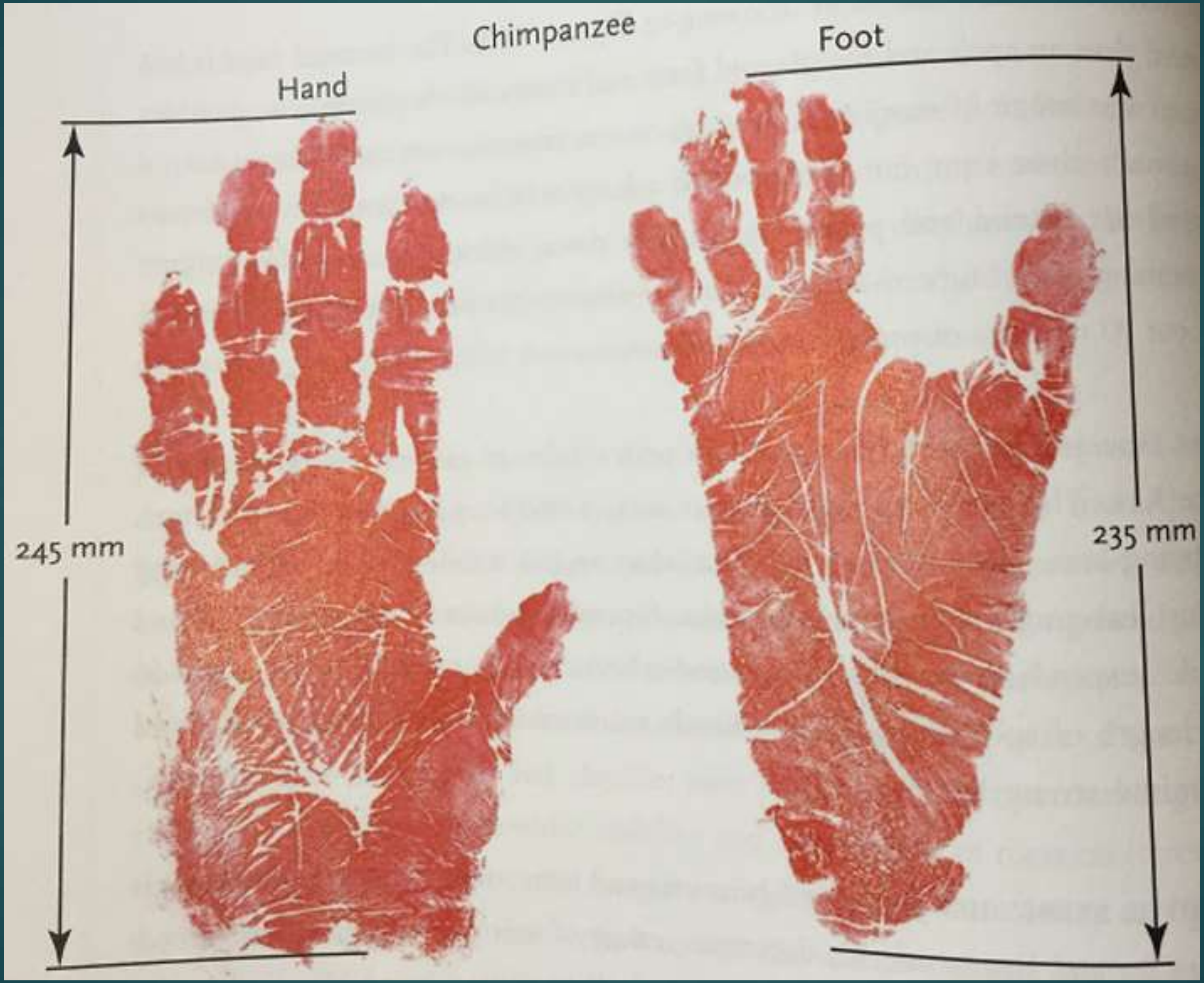


FIGURE 3.5. Split image: chimpanzee female (37.2 kg); langur male (23.5 kg).


Chimpanzee
Hand
Foot
245 mm
235 mm

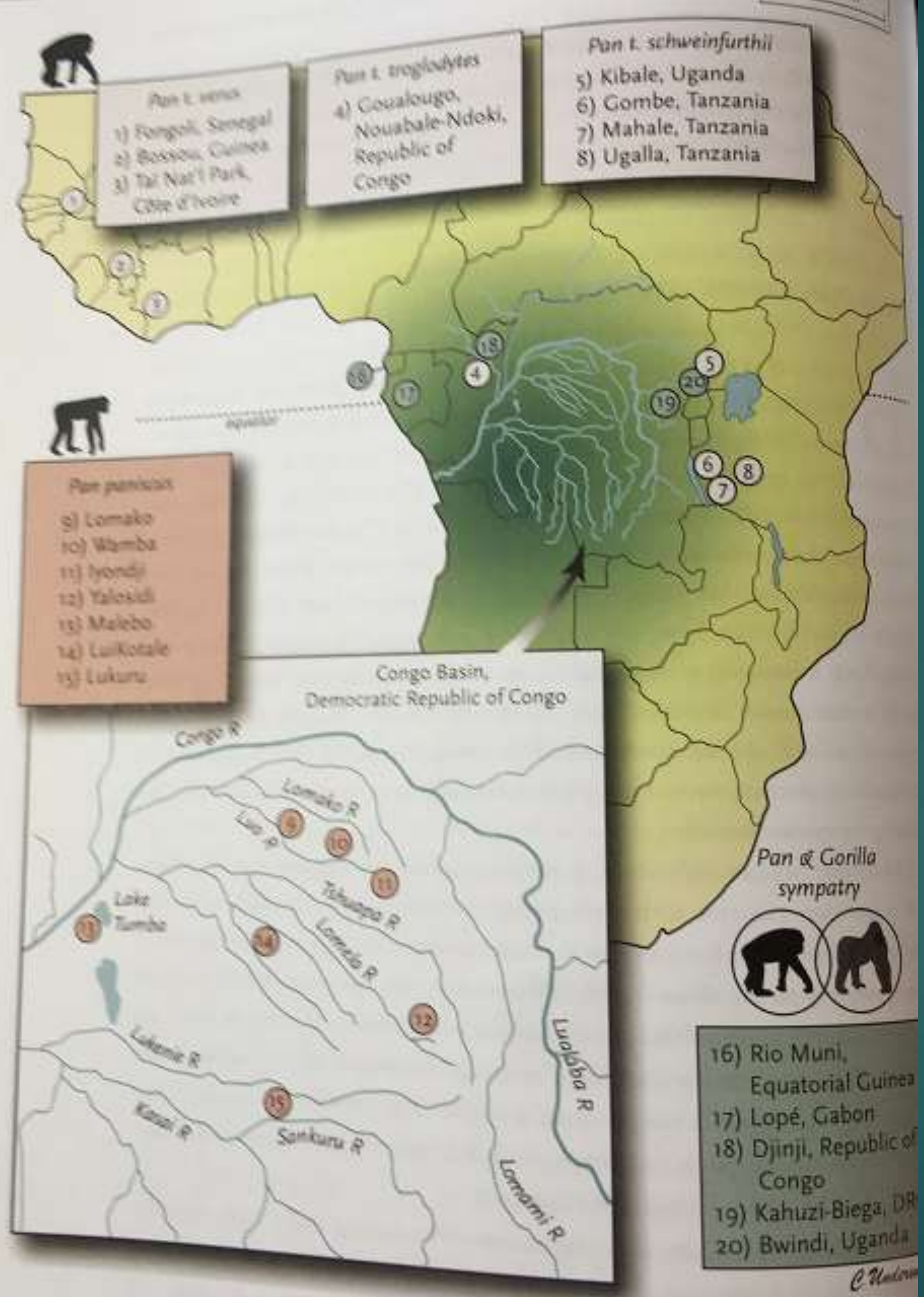
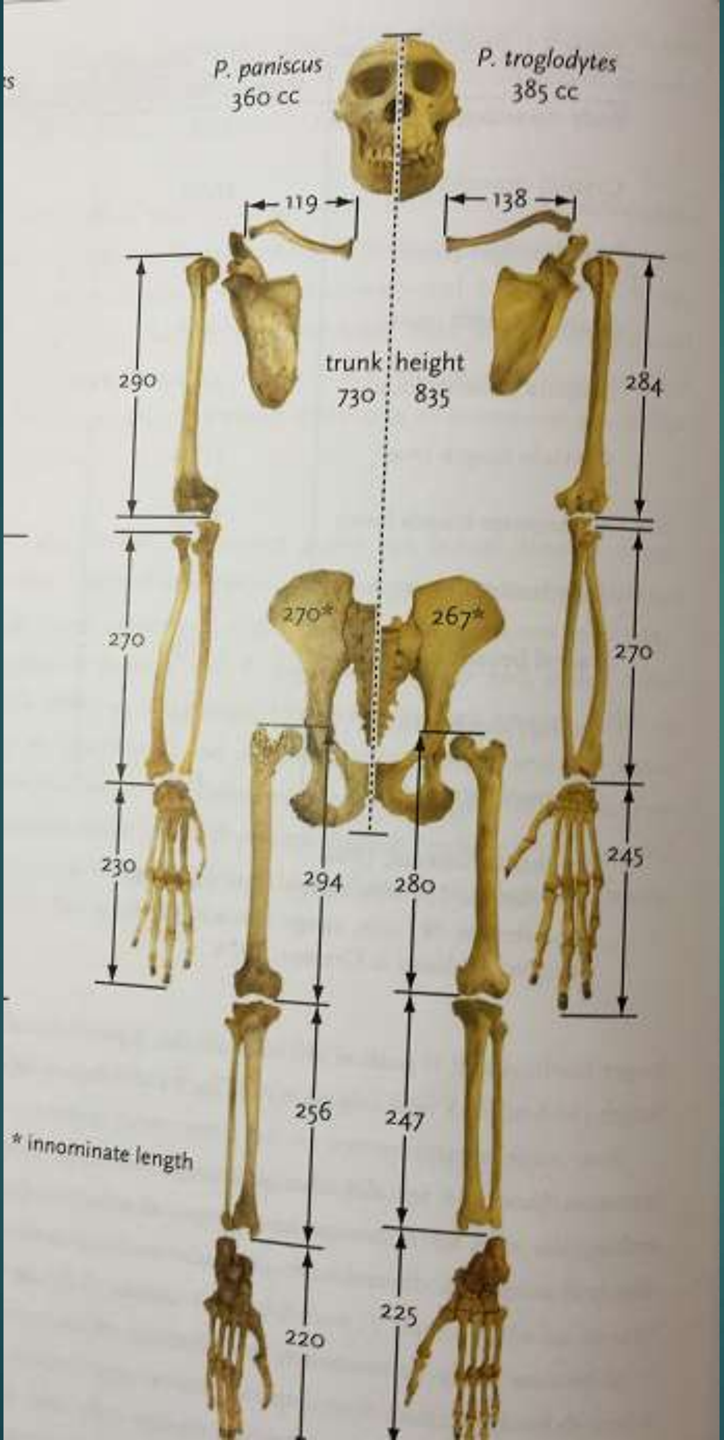
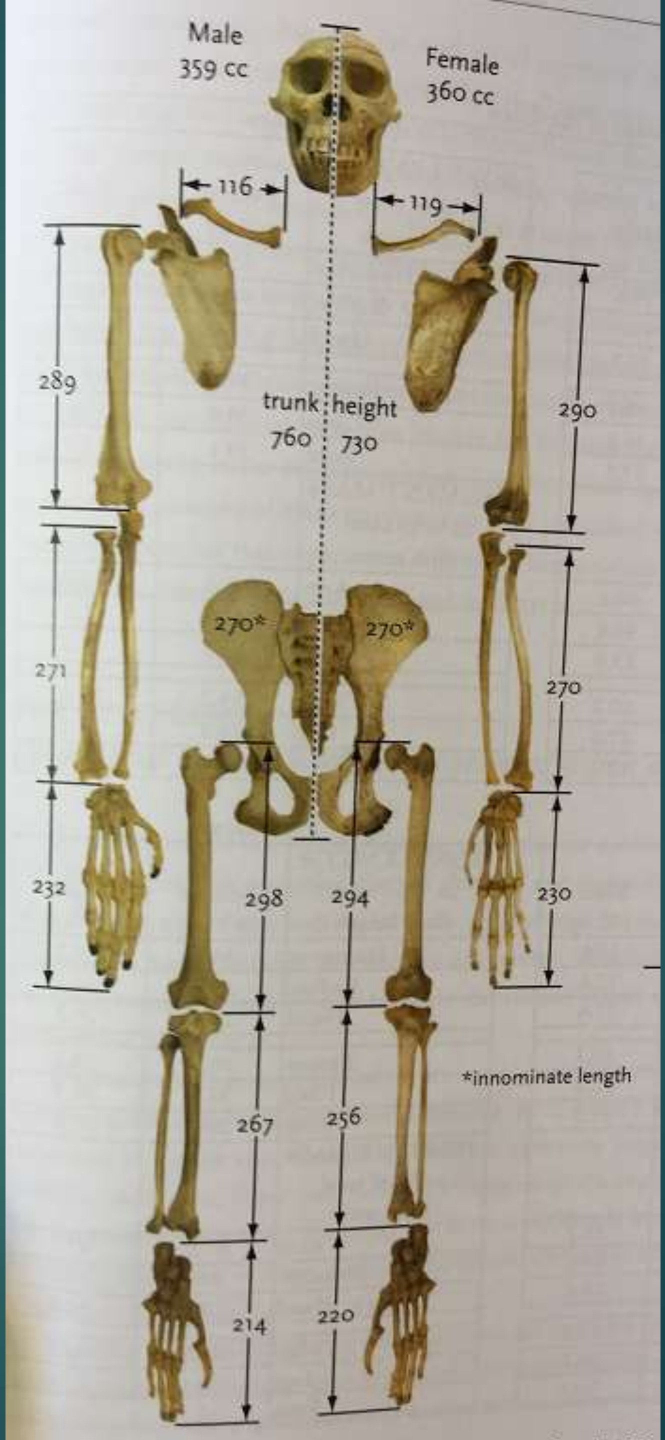


FIGURE 8.1. Map: Study sites of *Pan.*

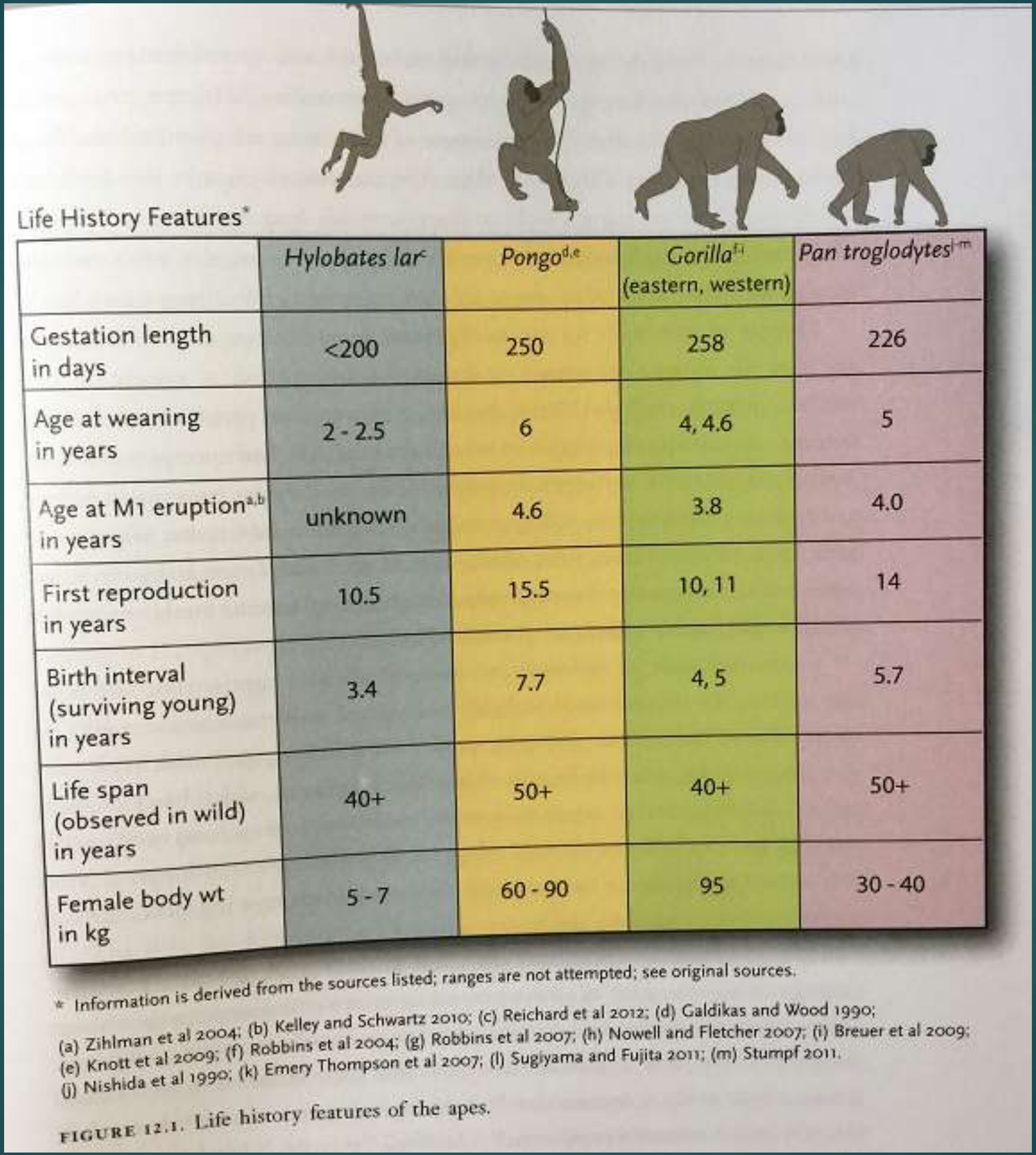


* innominate length



*innominate length

Life History features of the apes



Life History Features*

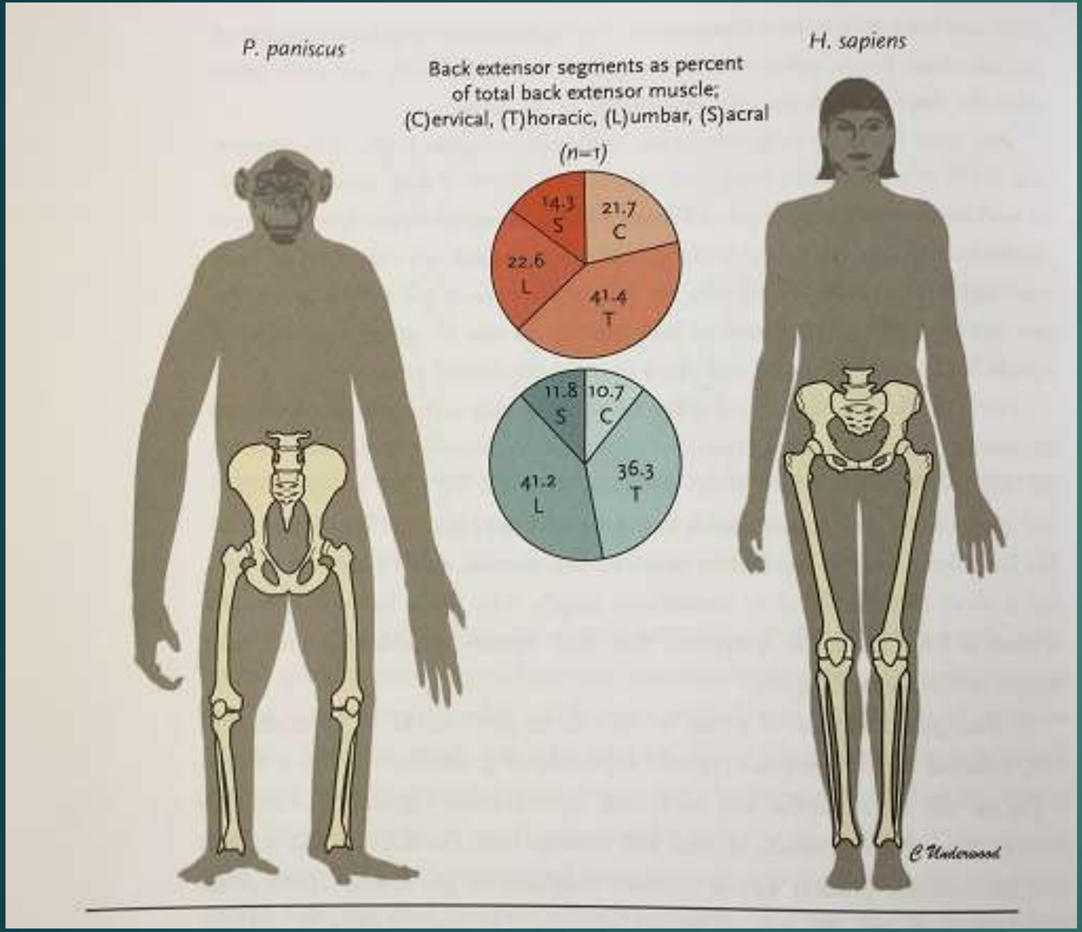
	Hylobates lar[c]	*Pongo*[d,e]	*Gorilla*[f-i] (eastern, western)	*Pan troglodytes*[j-m]
Gestation length in days	<200	250	258	226
Age at weaning in years	2 - 2.5	6	4, 4.6	5
Age at M1 eruption[a,b] in years	unknown	4.6	3.8	4.0
First reproduction in years	10.5	15.5	10, 11	14
Birth interval (surviving young) in years	3.4	7.7	4, 5	5.7
Life span (observed in wild) in years	40+	50+	40+	50+
Female body wt in kg	5 - 7	60 - 90	95	30 - 40

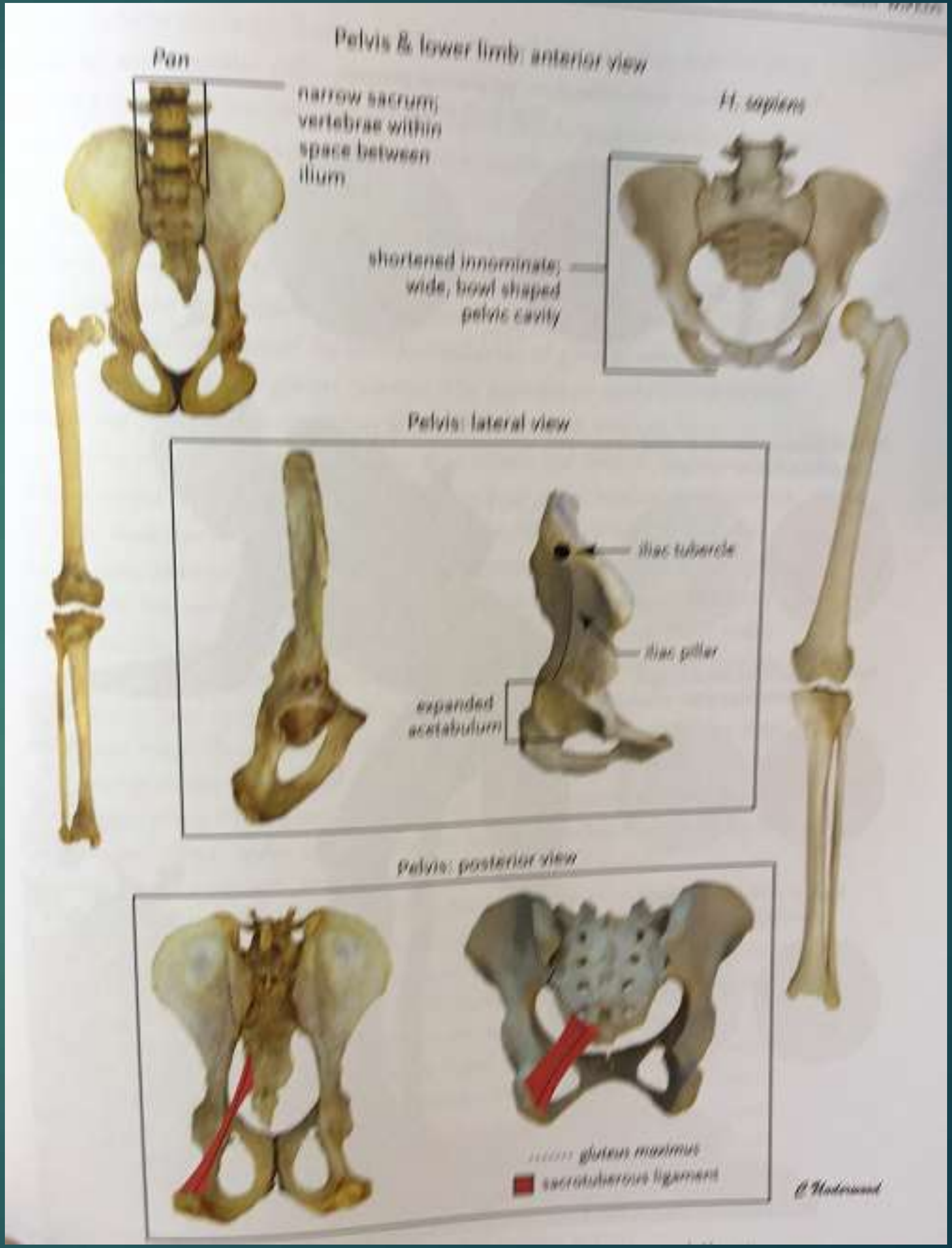
* Information is derived from the sources listed; ranges are not attempted; see original sources.

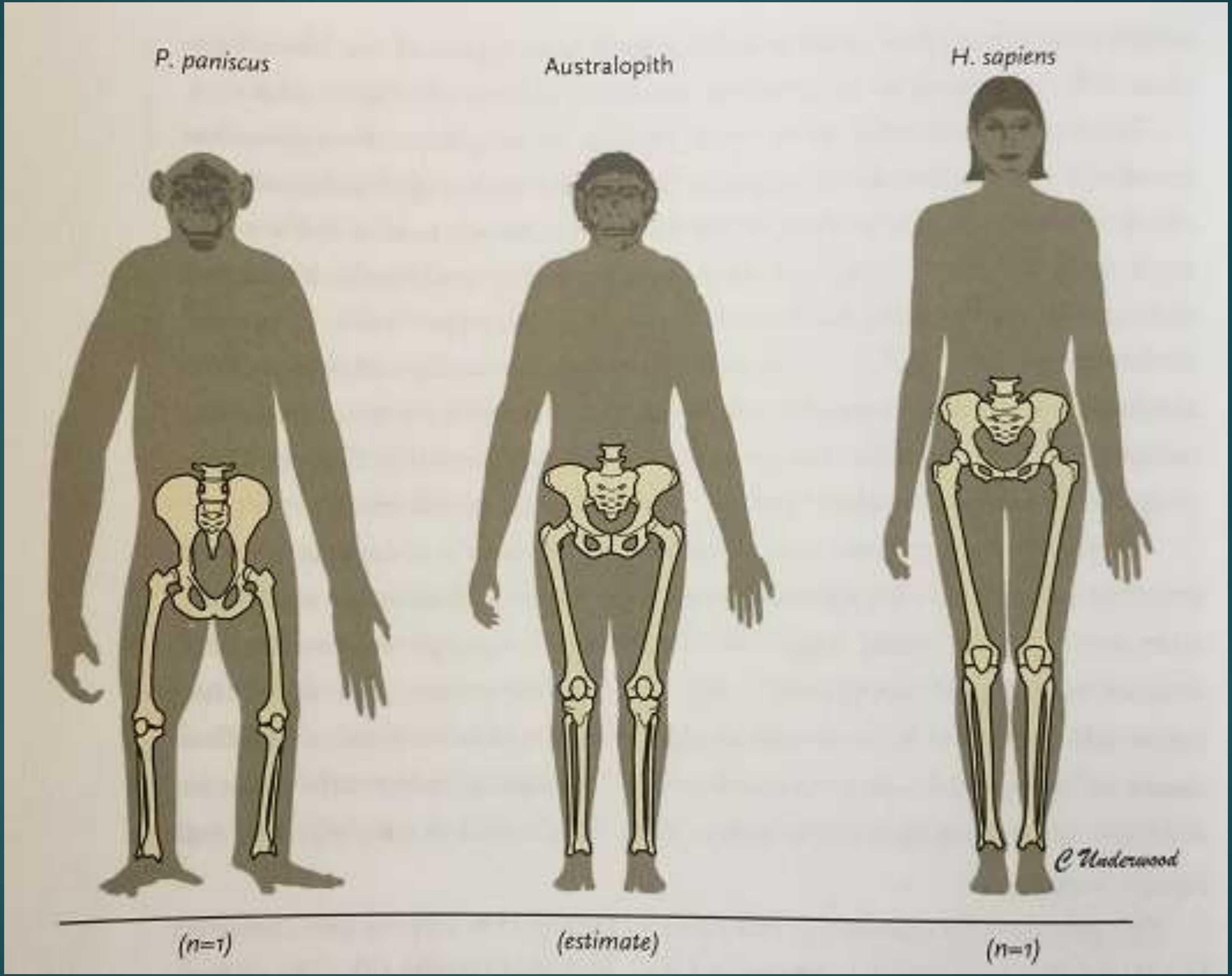
(a) Zihlman et al 2004; (b) Kelley and Schwartz 2010; (c) Reichard et al 2012; (d) Galdikas and Wood 1990; (e) Knott et al 2009; (f) Robbins et al 2004; (g) Robbins et al 2007; (h) Nowell and Fletcher 2007; (i) Breuer et al 2009; (j) Nishida et al 1990; (k) Emery Thompson et al 2007; (l) Sugiyama and Fujita 2011; (m) Stumpf 2011.

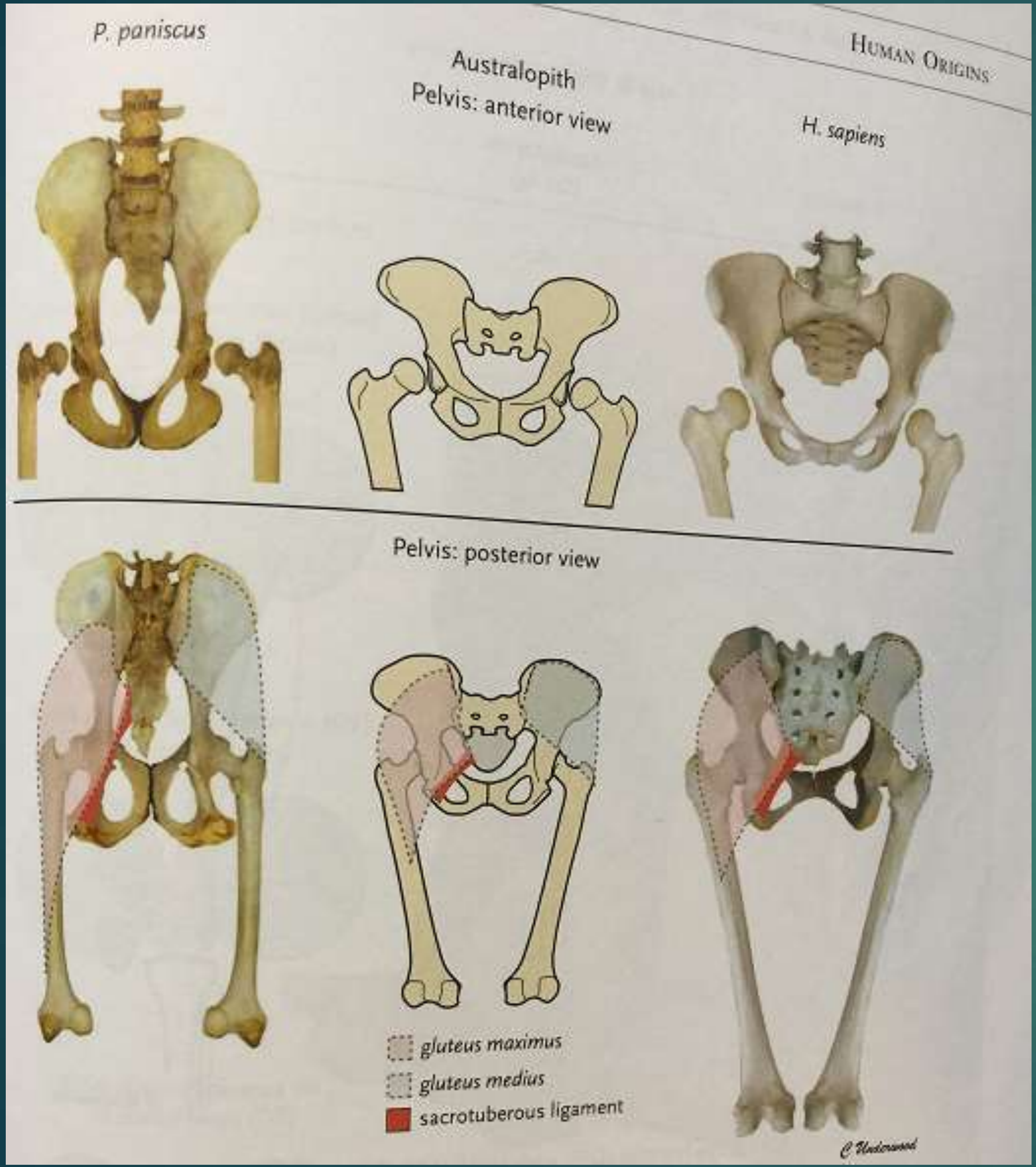
FIGURE 12.1. Life history features of the apes.

FIGURE 11.1. Sex diff


P. paniscus
H. sapiens
Back extensor segments as percent of total back extensor muscle; (C)ervical, (T)horacic, (L)umbar, (S)acral
(n=1)
14.3 S
21.7 C
22.6 L
41.4 T
11.8 S
10.7 C
41.2 L
36.3 T
C Underwood


Pelvis & lower limb: anterior view
Pan
narrow sacrum; vertebrae within space between ilium
H. sapiens
shortened innominate; wide, bowl shaped pelvic cavity
Pelvis: lateral view
iliac tubercle
iliac pillar
expanded acetabulum
Pelvis: posterior view
gluteus maximus
sacrotuberous ligament
C Underwood


P. paniscus
Australopith
H. sapiens
C Underwood
(n=1)
(estimate)
(n=1)



HUMAN ORIGINS

P. paniscus

Australopith

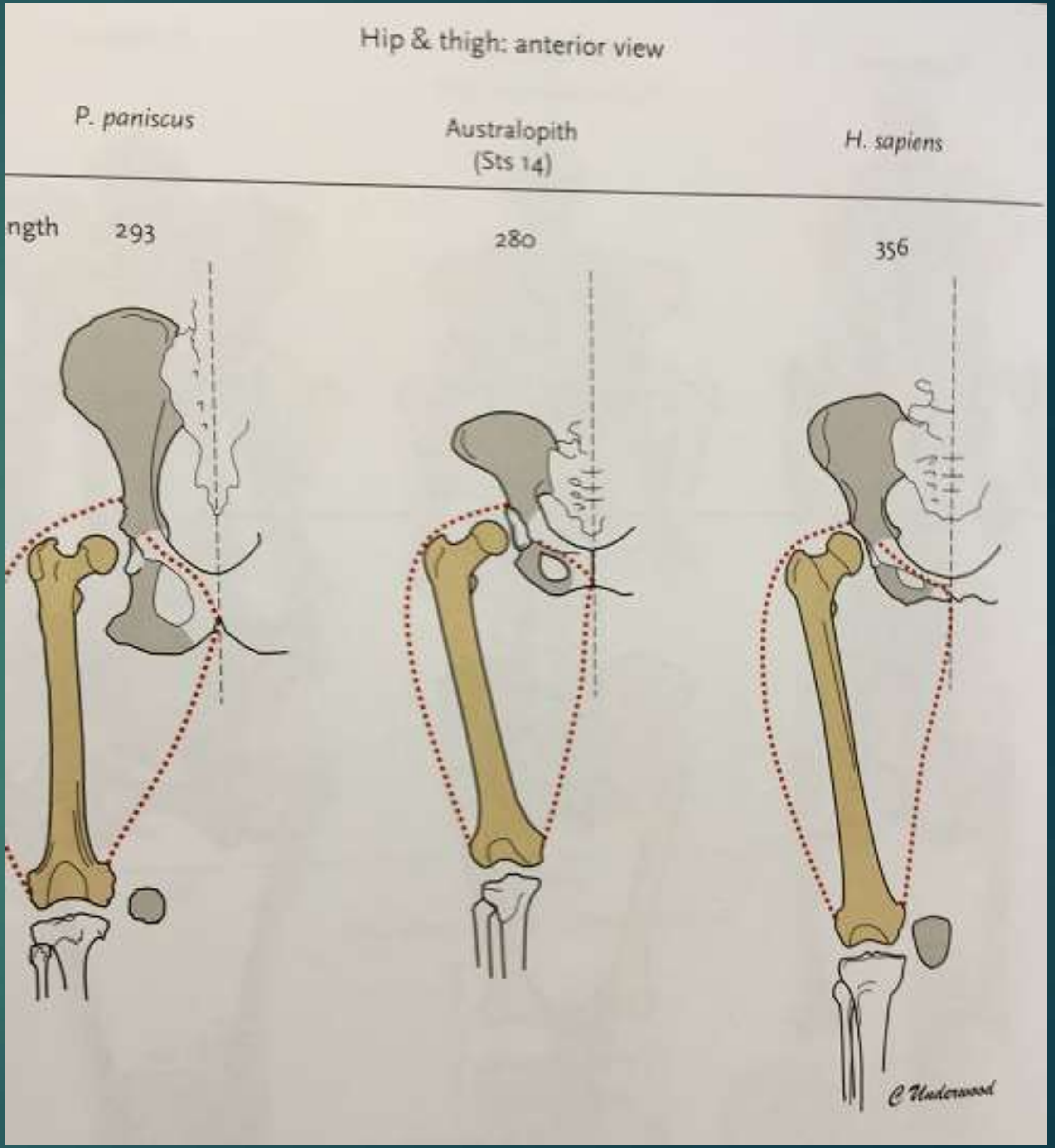
Pelvis: anterior view

H. sapiens

Pelvis: posterior view

- ▨ *gluteus maximus*
- ▨ *gluteus medius*
- 🟥 sacrotuberous ligament

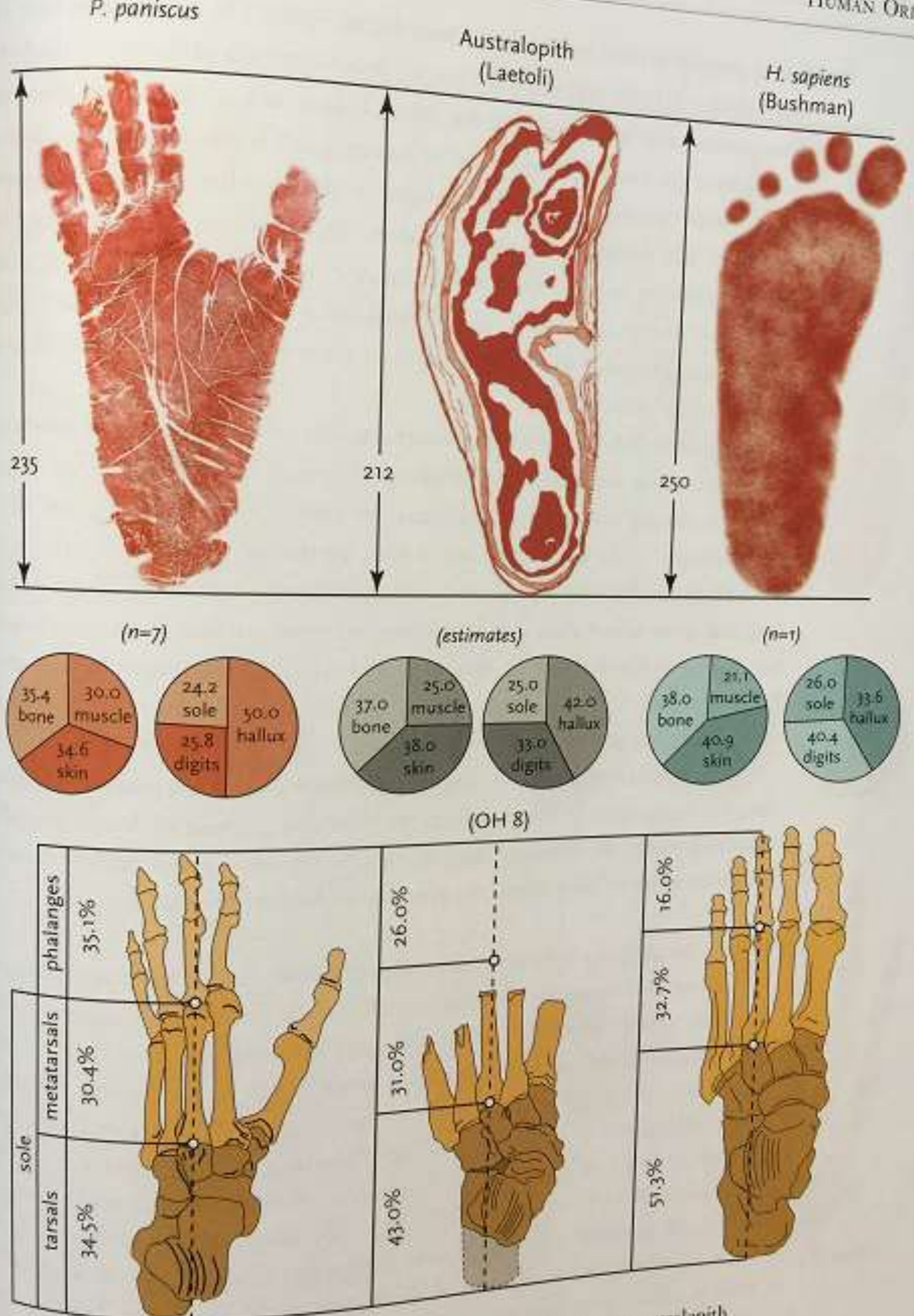
C Underwood



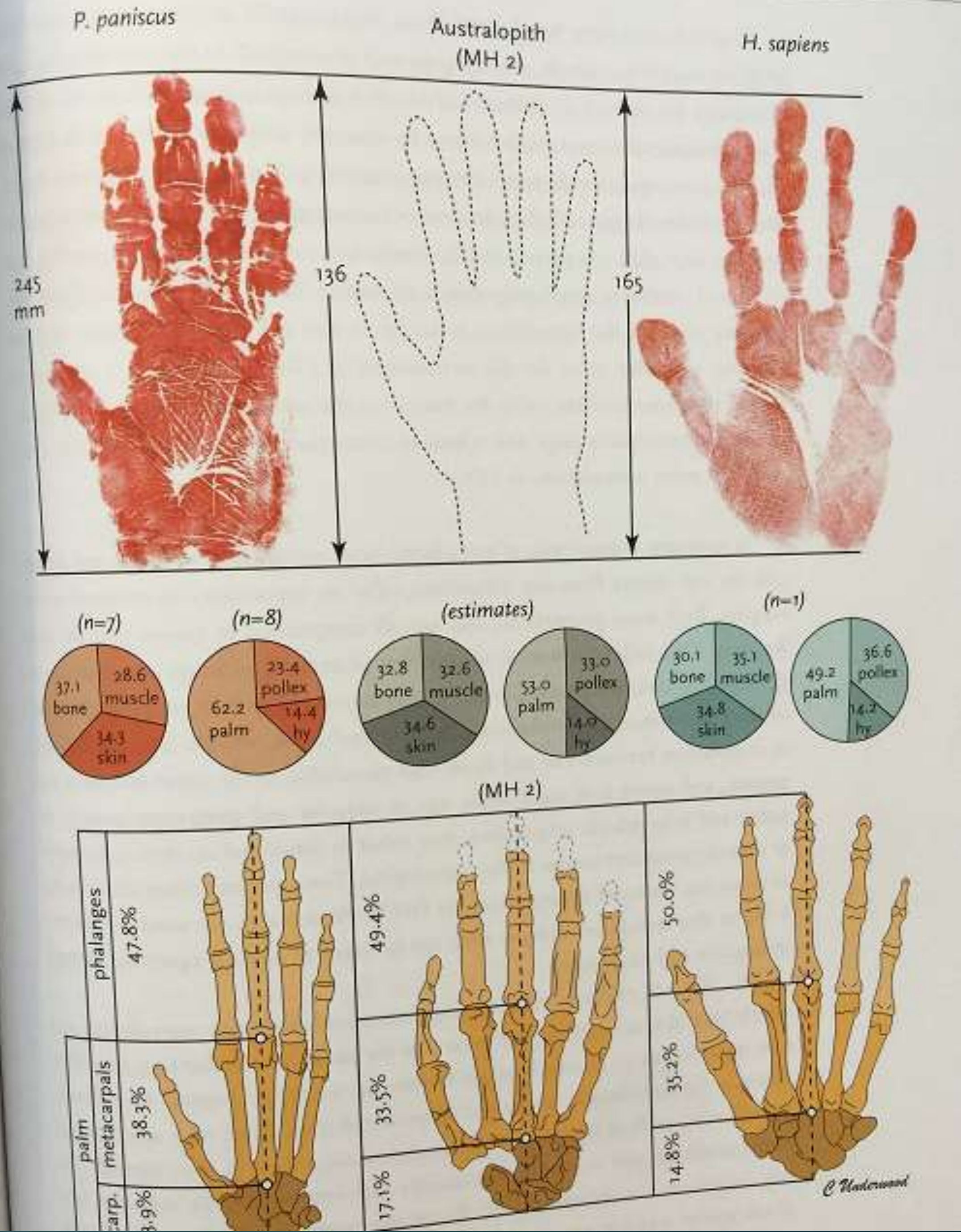
Hip & thigh: anterior view

	P. paniscus	Australopith (Sts 14)	H. sapiens
ngth	293	280	356

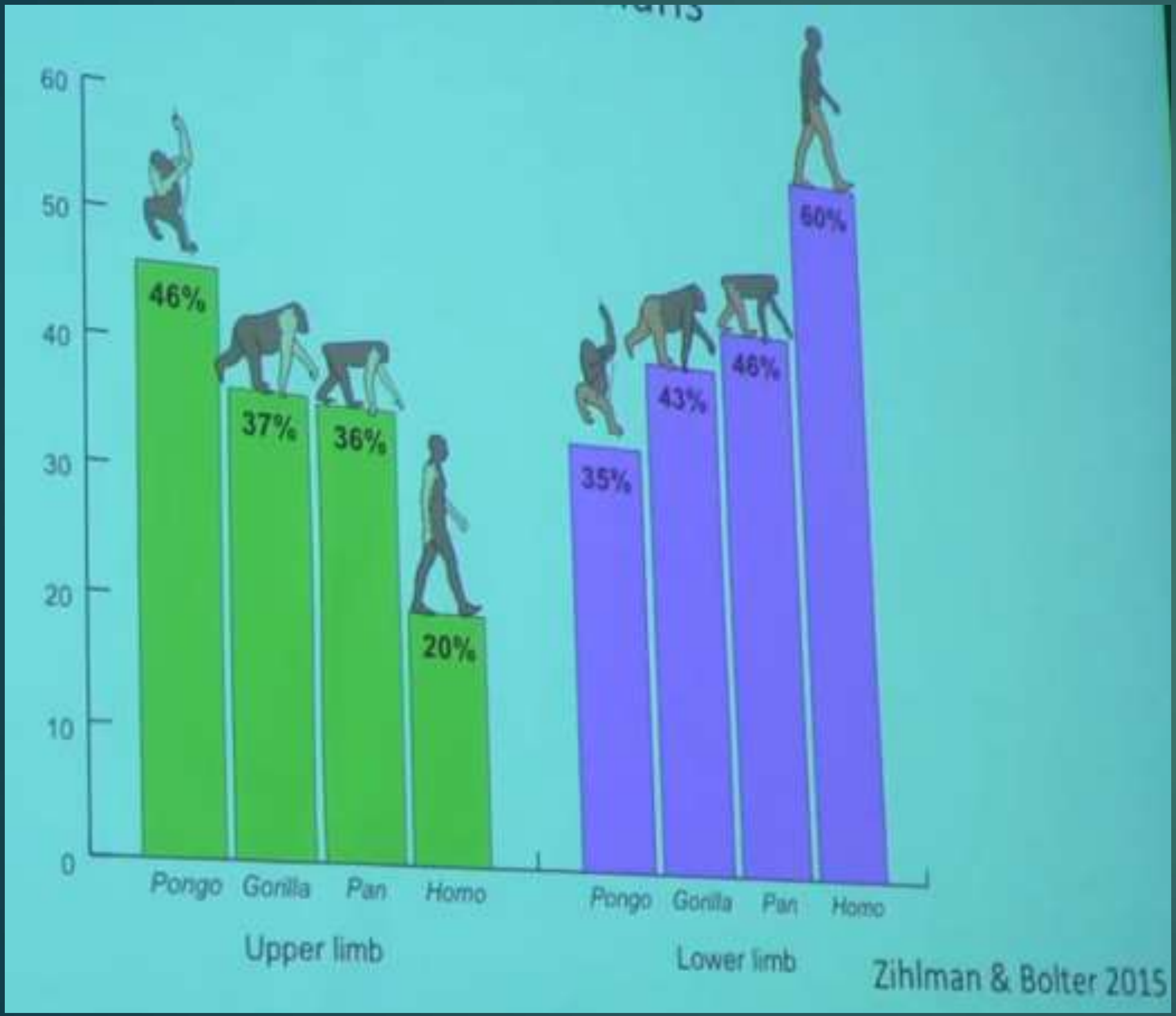
C Underwood



lerons. *P. paniscus*, australopith



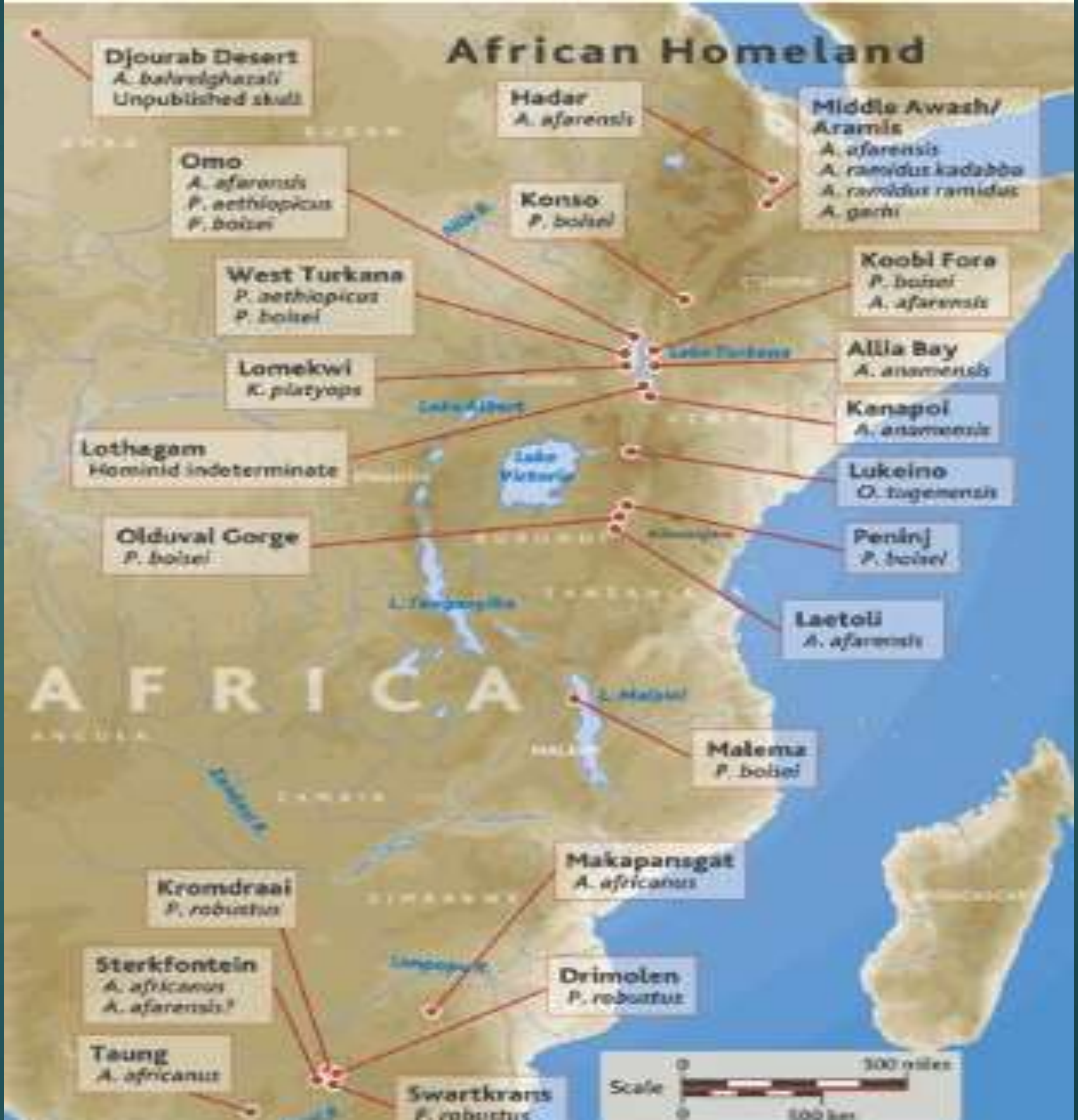
Distribution of body muscle in apes and humans



Zihlman & Bolter 2015

- Forelimbs become shorter & lighter, hindlimb longer & heavier
- Loss of mass/muscle in upper body and gain mass/muscle in lower body (hip and thigh)

Major African Hominin Fossil Sites



First discovery at Olduvai Gorge, Tanzania, 1913, OH 1:

Burial of a modern Masai into older geological layers; 900 yo

History of discovery: Betting on Africa

- In 1931, Louis Leakey began intensive prospecting and excavation at Olduvai Gorge, 33 years before he announced the first human species.
  - Only finds by 1955 =
    - Hans Reck's 1913 human skeleton (Olduvai Hominid 1),
    - In 1930s, the Leakeys found stone tools in Olduvai.
    - 2 thick *H. erectus* cranial vault fragments (OH 2) by Mary Leakey
- First trace of the potential toolmaker were two hominin teeth (giant molar & a canine (OH 3)) in 1955. But these were milk teeth, which are not as easy to link to taxa as permanent teeth.

- When primitive stone-chopping tools were uncovered at Olduvai Gorge in Tanzania, Louis Leakey became convinced that this is where he would find the earliest stone-tool makers, who he assumed would belong to our genus.

Human evolution: Fifty years after *Homo habilis*, Bernard Wood, 02 April 2014

OH 4

Teeth

OH 6

Cranial
Fragments

1959 – *Annus Mirabilis* at Olduvai

- Jul 1959: Heselon Mukiri found first remnant of *H. habilis,* a molar tooth in Bed I, OH 4
- 17 Jul 1959: Mary Leakey finds cranium of *A. (Zinjanthropus) boisei,* the type specimen of *P. boisei,* OH 5
  - Louis reacts – "nothing but a goddam robust *australopithecus";*
  - P. Tobias nicknames the latter "Nutcracker Man" at a conference
- Leakey initially claimed Zinj is ancestral to MHs, because he was found with some stone tools; therefore Leakey claimed Zinj was a toolmaker
  - *P. boisei* has in fact been found with stone tools in S. Africa; so ironically Leakey may have been right!
- Until 1960, *H. erectus* had been found only in Asia; theory that Asia was original home of mankind

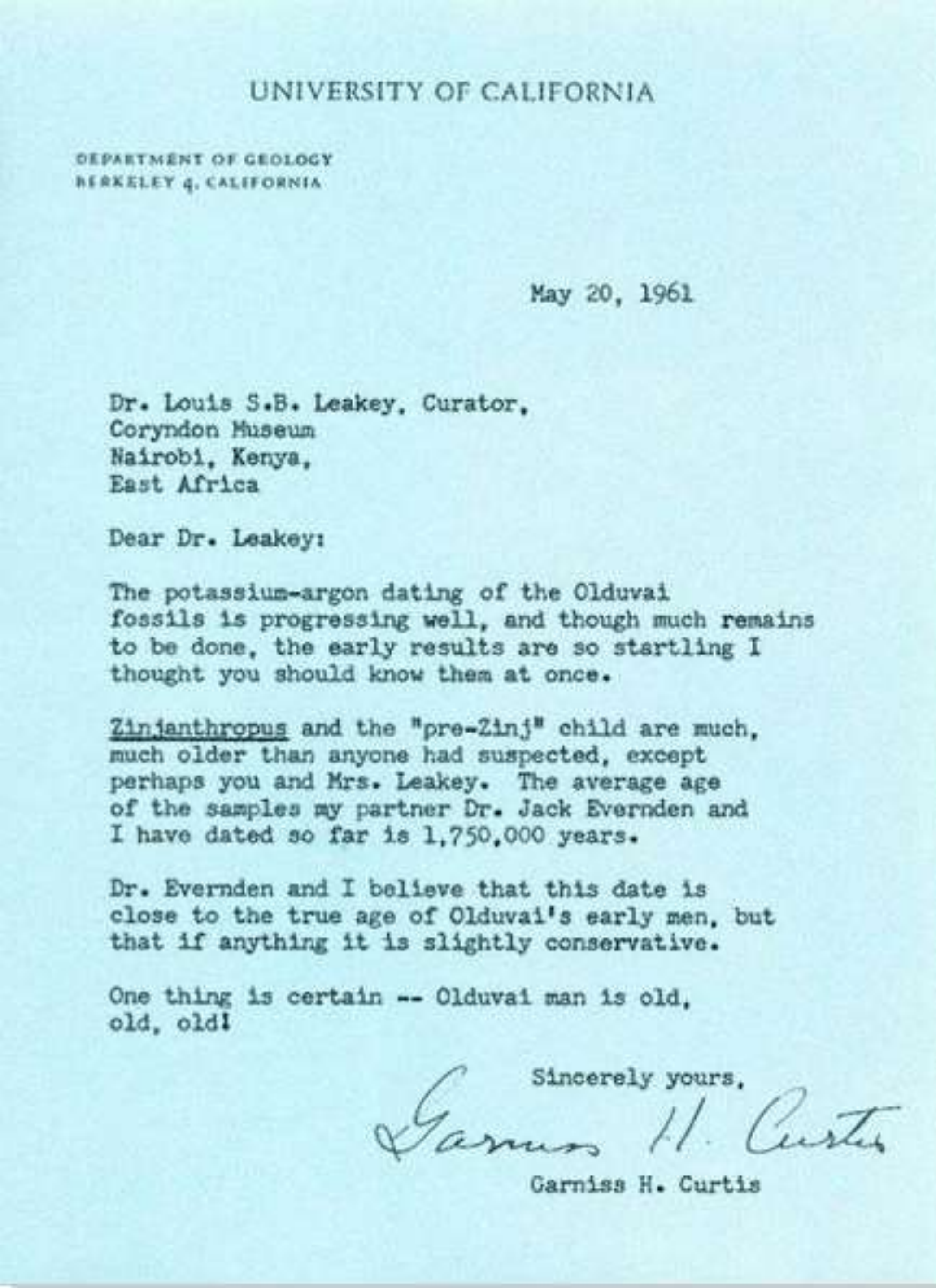
Accepted Dating beliefs until 1961

- Evolution of mammals = several million years
- Evolution of humans = few 100 thousand years old
- It was hard to determine exact chronological sequence of fossils
- Other fossil mammals were used to help correlate dates, i.e. pig teeth
- Dating was an insoluble problem until new technology came along

Zinj = startlingly old; 1.7 MA

Dating of Zinj rocked the anthropological world when age established at 1.75 Ma

Zinjanthropus, pushing back the then-accepted age of the Pleistocene by 1 million years.



UNIVERSITY OF CALIFORNIA

DEPARTMENT OF GEOLOGY
BERKELEY 4, CALIFORNIA

May 20, 1961

Dr. Louis S.B. Leakey, Curator,
Coryndon Museum
Nairobi, Kenya,
East Africa

Dear Dr. Leakey:

The potassium-argon dating of the Olduvai fossils is progressing well, and though much remains to be done, the early results are so startling I thought you should know them at once.

Zinjanthropus and the "pre-Zinj" child are much, much older than anyone had suspected, except perhaps you and Mrs. Leakey. The average age of the samples my partner Dr. Jack Evernden and I have dated so far is 1,750,000 years.

Dr. Evernden and I believe that this date is close to the true age of Olduvai's early men, but that if anything it is slightly conservative.

One thing is certain -- Olduvai man is old, old, old!

Sincerely yours,

Garniss H. Curtis

Garniss H. Curtis

Geologist Garniss H. Curtis, a professor emeritus of earth and planetary science at the University of California, Berkeley, whose pioneering use of radioactive isotopes to date relatively young rocks provided the first solid timeline for human evolution; Used potassium/argon method in volcanic rock

"His major contribution was putting numbers on the timescale of human evolution."

1959: *Paranthropus boisei:*
Most famous Olduvai Gorge fossil; "Zinj": 1.75 M

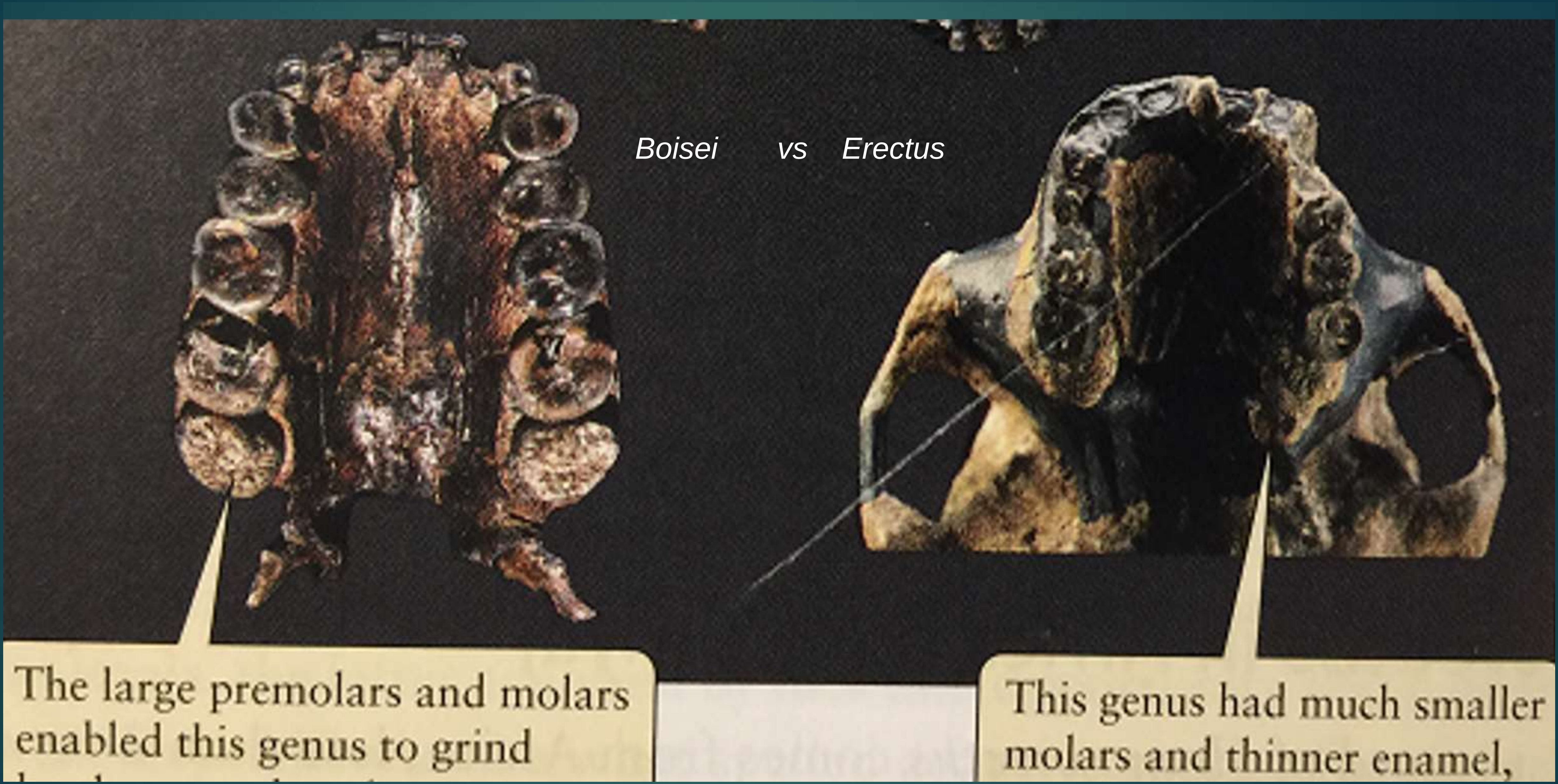
Disappointed Louis Leakey: "Why it's nothing but a god-damned robust australopithecine!"

1959: Zinj, OH 5, 1st dated fossil

Paranthropus boisei
(OH 5, type)
Discoverer: Mary Leakey

The greatest significance of *Paranthropus boisei* is that its 1959 discovery convinced the scientific world that the place to look for the earliest humans is Africa

Boisei vs *Erectus*



The large premolars and molars enabled this genus to grind

This genus had much smaller molars and thinner enamel,

Boisei is no longer “Nutcracker Man”; ate grasses and sedges

Early *Homo*

- *Homo habilis* is best known from deposits dated to 1.9-1.8 Ma at Olduvai Gorge & Koobi Fora (East Turkana)
- But other isolated specimens imply that it emerged much earlier, perhaps about 2.5 Ma
- The findings of KNM-ER 1470/*rudolfensis* and KNM-ER 1813/*habilis* at Koobi Fora with their varying morphologies implies at least two contemporaneous species.

Hominin species according to a 'splitter's' taxonomy (i.e., speciose taxonomy)

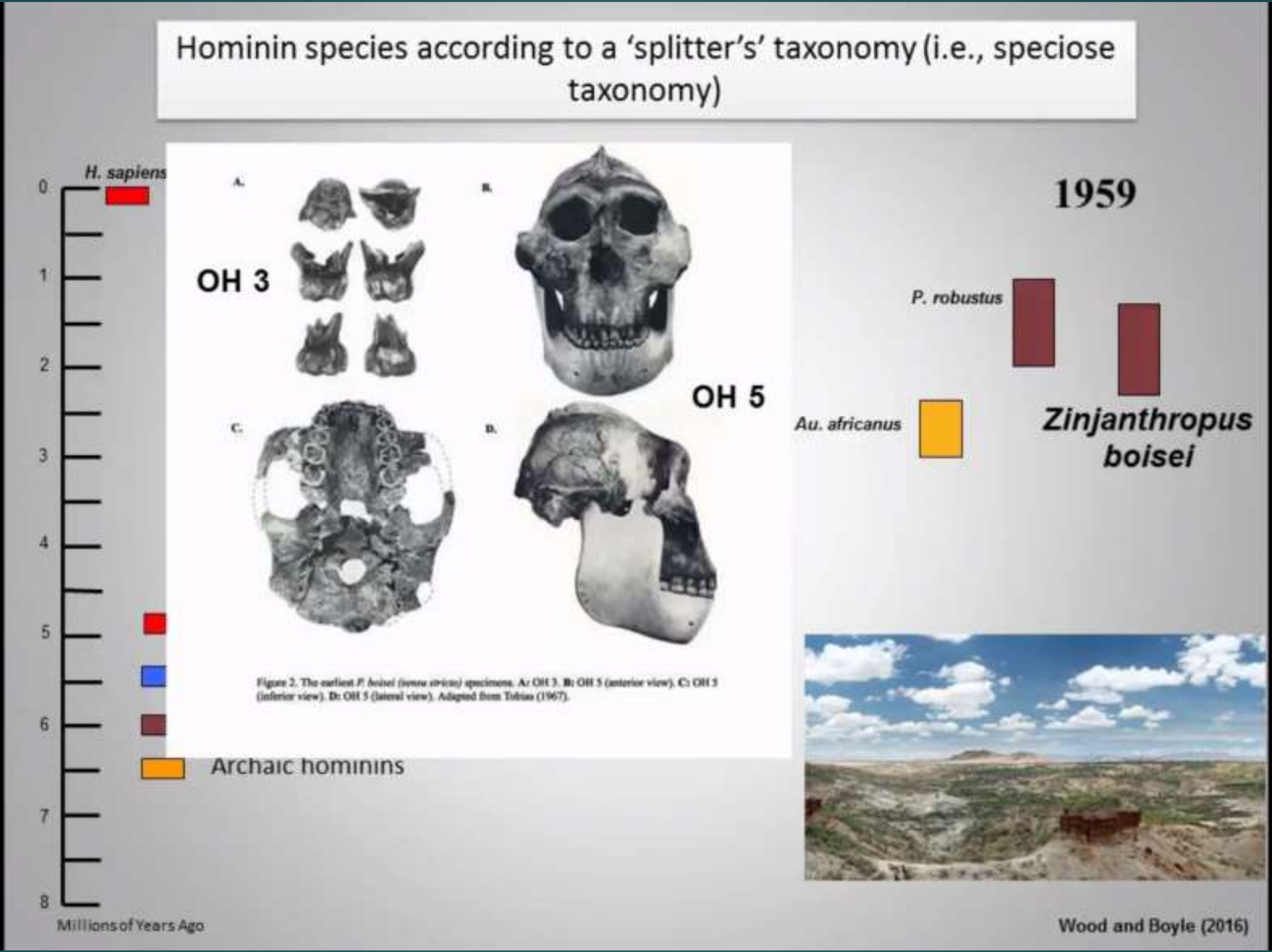


Figure 2. The earliest *P. boisei* (*sensu stricto*) specimens. A: OH 3. B: OH 5 (anterior view). C: OH 5 (inferior view). D: OH 5 (lateral view). Adapted from Tobias (1967).

Wood and Boyle (2016)

Louis, Mary, Jonathan Leakey: discovery of OH 7 mandible

History of discovery

- On 4 Nov 1960, Jonathan Leakey, Louis & Mary’s eldest son, found a juvenile lower jaw with teeth (OH 7, the type specimen of *H. habilis*), the 2 parietals, & 21 hand bones of a juvenile (12-13 y) hominin.
- Dubbed Jonny's Child; definitely did not belong to the same species as 'Zinj', and the Leakeys began to suspect that it was the real toolmaker.
- The parietals were larger than any known australopithecine parietal bones; Phillip Tobias measures cranial capacity at 680 cc, 50% larger than *A. africanus* (ave. of 441 cc); a difference of 10 standard deviations.

Jackson Njau: Olduvai Gorge,
a wetland bordered by a river, with crocodiles

Left: This right p
crocodile bite ma

ssible

Homo habilis leg bone (tibia) bearing tooth punctures on the distal

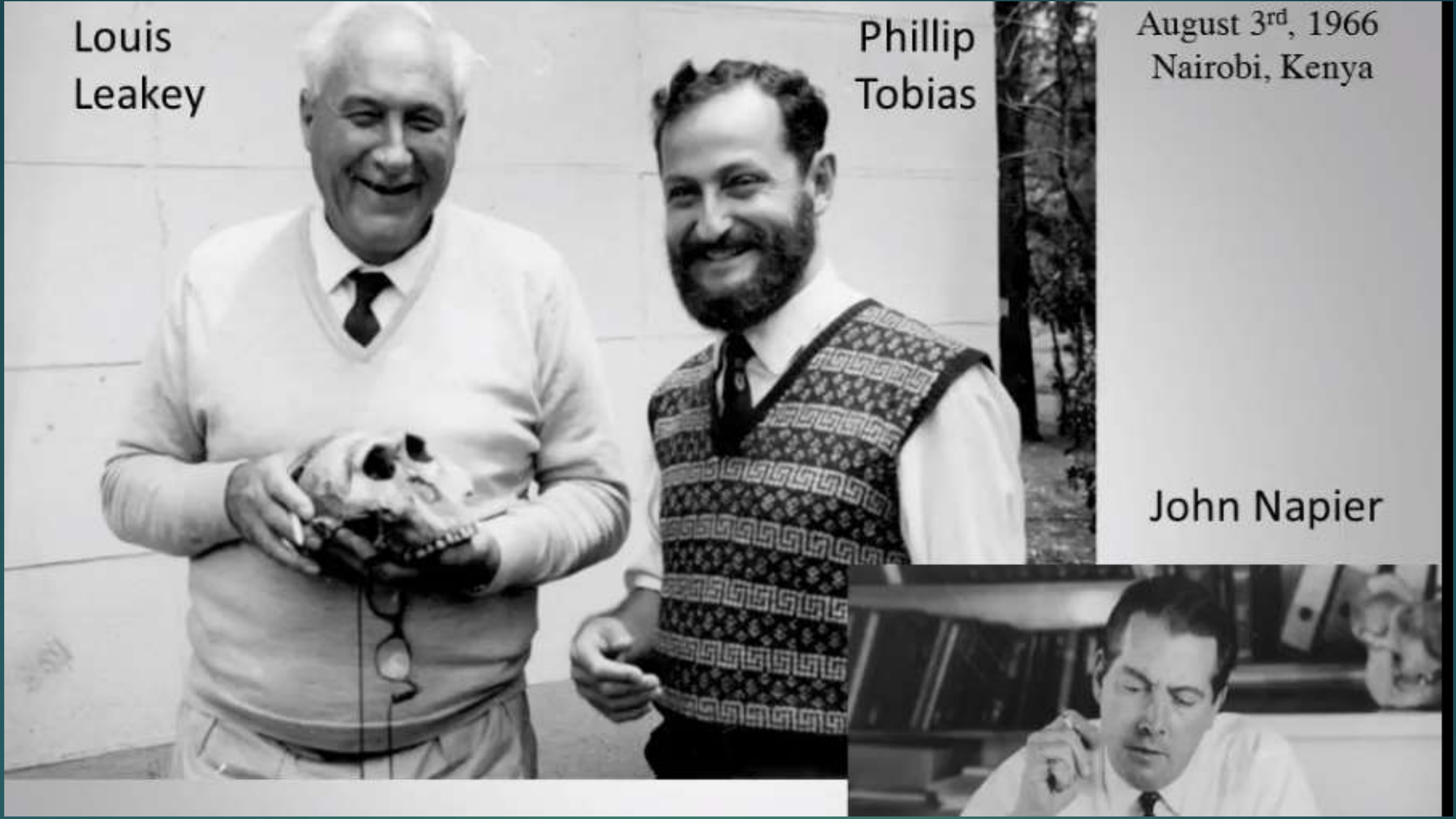
On second thought, this is stone tool maker
because has bigger brain

OH 7: Parietals found at FLKNN I in 1960 and mandible in 1961

1960

OH 8: Found at FLKNN I in 1960

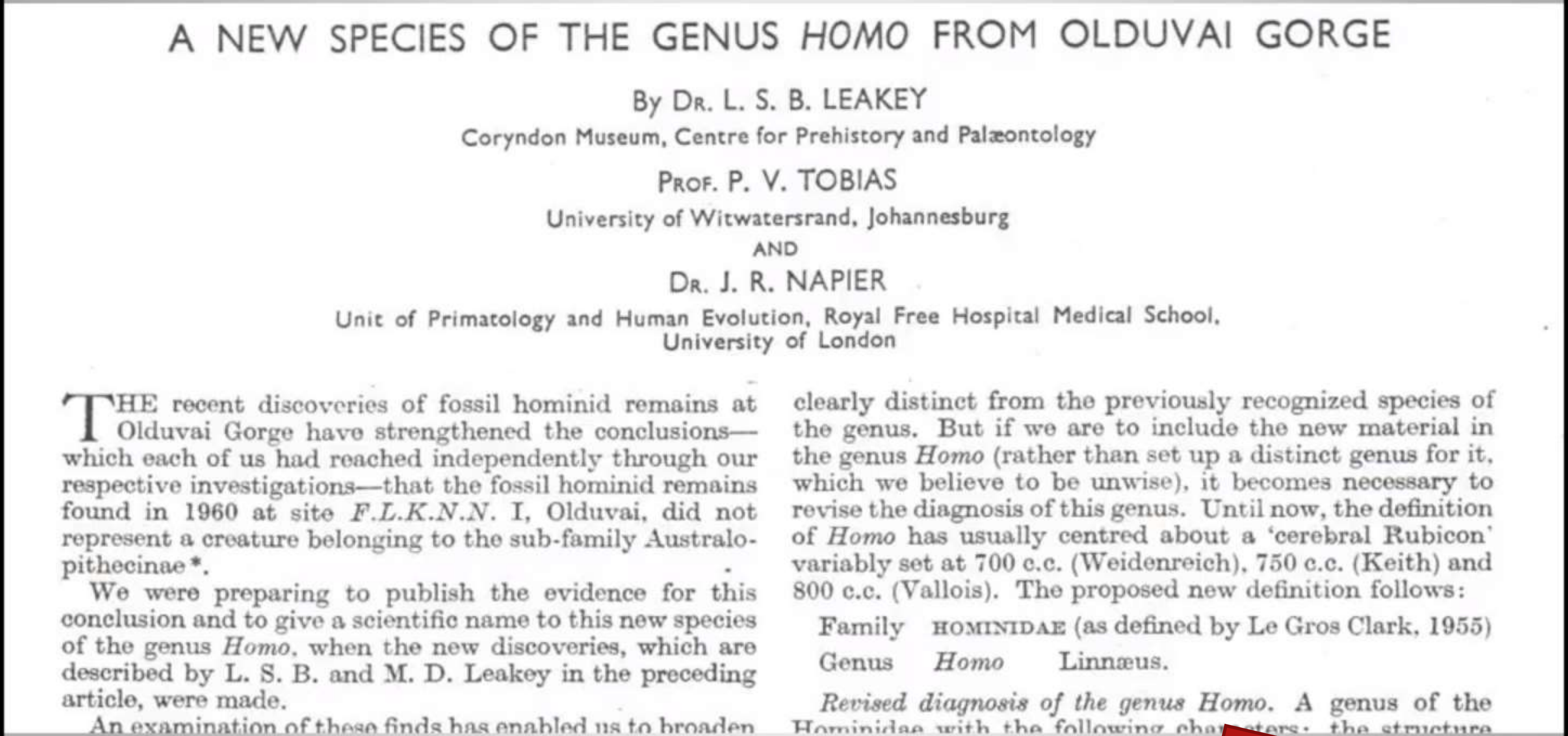
John Napier: Strident biped



Phillip Tobias was recruited to analyze Zinj, so the Leakeys turned to him to analyze the juvenile cranium. He initially thought it was *A. africanus.* Only when OH 13 (“Cindy”, ~600 cc) was discovered, was he convinced that *H. habilis* was a genus.

John Napier, a specialist in hand anatomy (as well as sleight-of-hand magic tricks) was recruited to examine wrist and hand bones found with the skull.

NATURE APRIL 4TH 1964



A NEW SPECIES OF THE GENUS *HOMO* FROM OLDUVAI GORGE

By DR. L. S. B. LEAKEY
Coryndon Museum, Centre for Prehistory and Palæontology

PROF. P. V. TOBIAS
University of Witwatersrand, Johannesburg

AND

DR. J. R. NAPIER
Unit of Primatology and Human Evolution, Royal Free Hospital Medical School,
University of London

THE recent discoveries of fossil hominid remains at Olduvai Gorge have strengthened the conclusions—which each of us had reached independently through our respective investigations—that the fossil hominid remains found in 1960 at site *F.L.K.N.N.* I, Olduvai, did not represent a creature belonging to the sub-family Australopithecinae*.

We were preparing to publish the evidence for this conclusion and to give a scientific name to this new species of the genus *Homo*, when the new discoveries, which are described by L. S. B. and M. D. Leakey in the preceding article, were made.

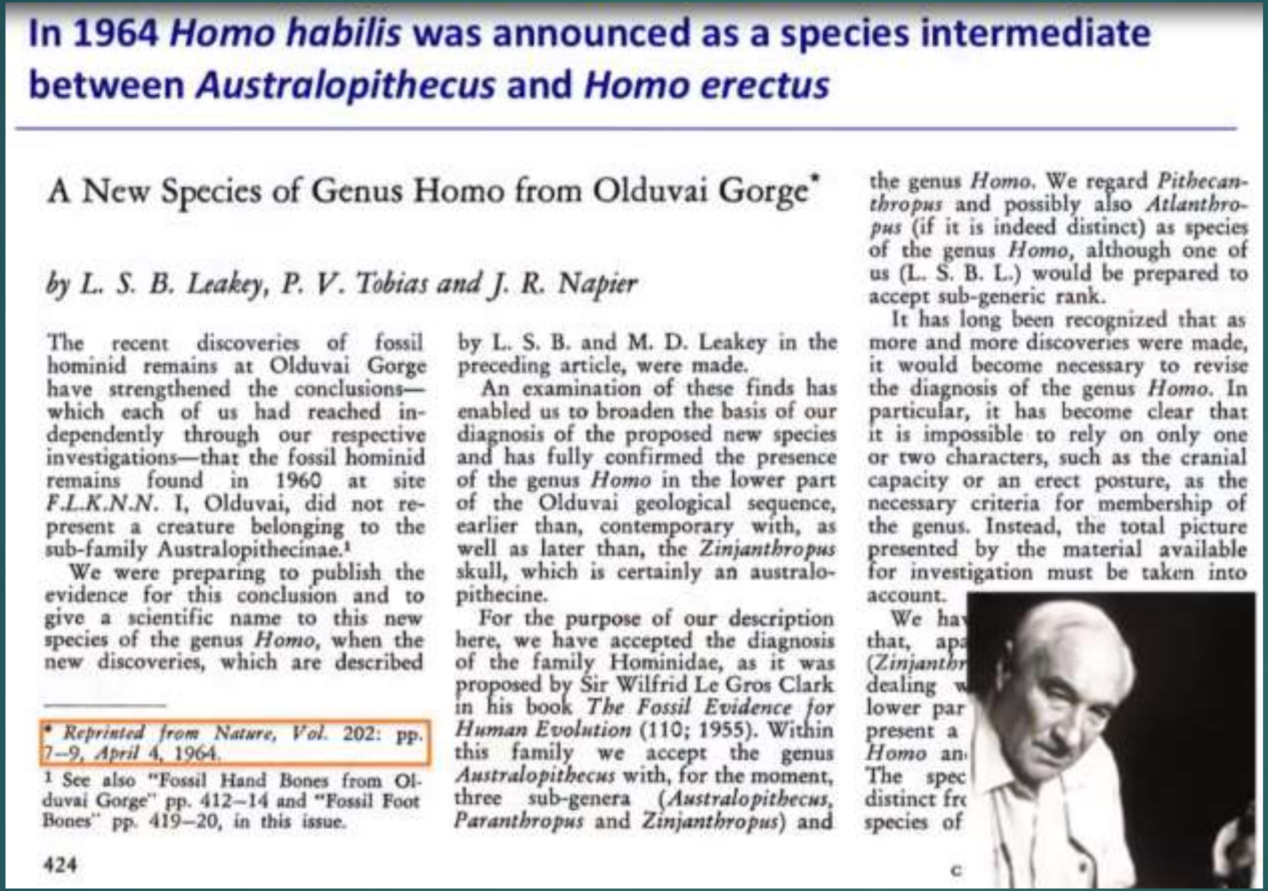
An examination of these finds has enabled us to broaden

clearly distinct from the previously recognized species of the genus. But if we are to include the new material in the genus *Homo* (rather than set up a distinct genus for it, which we believe to be unwise), it becomes necessary to revise the diagnosis of this genus. Until now, the definition of *Homo* has usually centred about a 'cerebral Rubicon' variably set at 700 c.c. (Weidenreich), 750 c.c. (Keith) and 800 c.c. (Vallois). The proposed new definition follows:

Family HOMINIDAE (as defined by Le Gros Clark, 1955)
Genus *Homo* Linnæus.

Revised diagnosis of the genus Homo. A genus of the Hominidae with the following characters: the structure

Leakey, Tobias, and Napier, 1964,
A new species of the genus *Homo* from Olduvai Gorge



In 1964 *Homo habilis* was announced as a species intermediate between *Australopithecus* and *Homo erectus*

A New Species of Genus Homo from Olduvai Gorge*

by L. S. B. Leakey, P. V. Tobias and J. R. Napier

The recent discoveries of fossil hominid remains at Olduvai Gorge have strengthened the conclusions—which each of us had reached independently through our respective investigations—that the fossil hominid remains found in 1960 at site F.L.K.N.N. I, Olduvai, did not represent a creature belonging to the sub-family Australopithecinae.[1]

We were preparing to publish the evidence for this conclusion and to give a scientific name to this new species of the genus *Homo*, when the new discoveries, which are described by L. S. B. and M. D. Leakey in the preceding article, were made.

An examination of these finds has enabled us to broaden the basis of our diagnosis of the proposed new species and has fully confirmed the presence of the genus *Homo* in the lower part of the Olduvai geological sequence, earlier than, contemporary with, as well as later than, the *Zinjanthropus* skull, which is certainly an australopithecine.

For the purpose of our description here, we have accepted the diagnosis of the family Hominidae, as it was proposed by Sir Wilfrid Le Gros Clark in his book *The Fossil Evidence for Human Evolution* (110; 1955). Within this family we accept the genus *Australopithecus* with, for the moment, three sub-genera (*Australopithecus, Paranthropus* and *Zinjanthropus*) and the genus *Homo*. We regard *Pithecanthropus* and possibly also *Atlanthropus* (if it is indeed distinct) as species of the genus *Homo*, although one of us (L. S. B. L.) would be prepared to accept sub-generic rank.

It has long been recognized that as more and more discoveries were made, it would become necessary to revise the diagnosis of the genus *Homo*. In particular, it has become clear that it is impossible to rely on only one or two characters, such as the cranial capacity or an erect posture, as the necessary criteria for membership of the genus. Instead, the total picture presented by the material available for investigation must be taken into account.

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* *Reprinted from Nature, Vol.* 202: pp. 7–9, *April* 4, 1964.

[1] See also "Fossil Hand Bones from Olduvai Gorge" pp. 412–14 and "Fossil Foot Bones" pp. 419–20, in this issue.

New species: between
A. australopithecus and
H. erectus

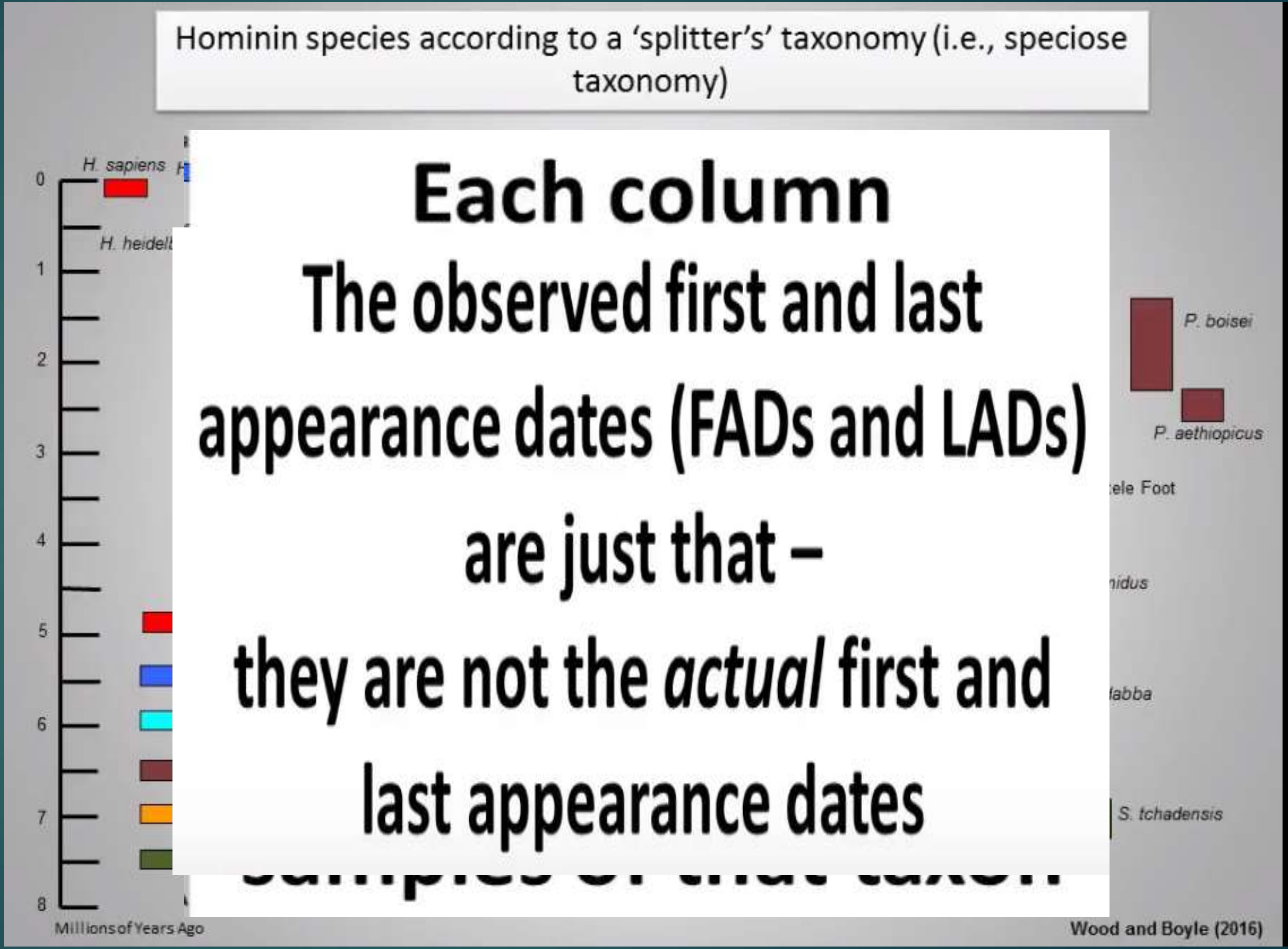
More like *erectus*

"We have come to the conclusion that, apart from *Australopithecus (Zinjanthropus),* the specimens we are dealing with from Bed I and the lower part of Bed II at Olduvai represent a single species of the genus *Homo* and not an australopithecine. The species is clearly distinct from previously recognized species of the genus."

Origin of *Homo*

B. Wood:
Homo begins
with African
H. erectus

FADs & LADS
= fossil record data



Hominin species according to a 'splitter's' taxonomy (i.e., speciose taxonomy)

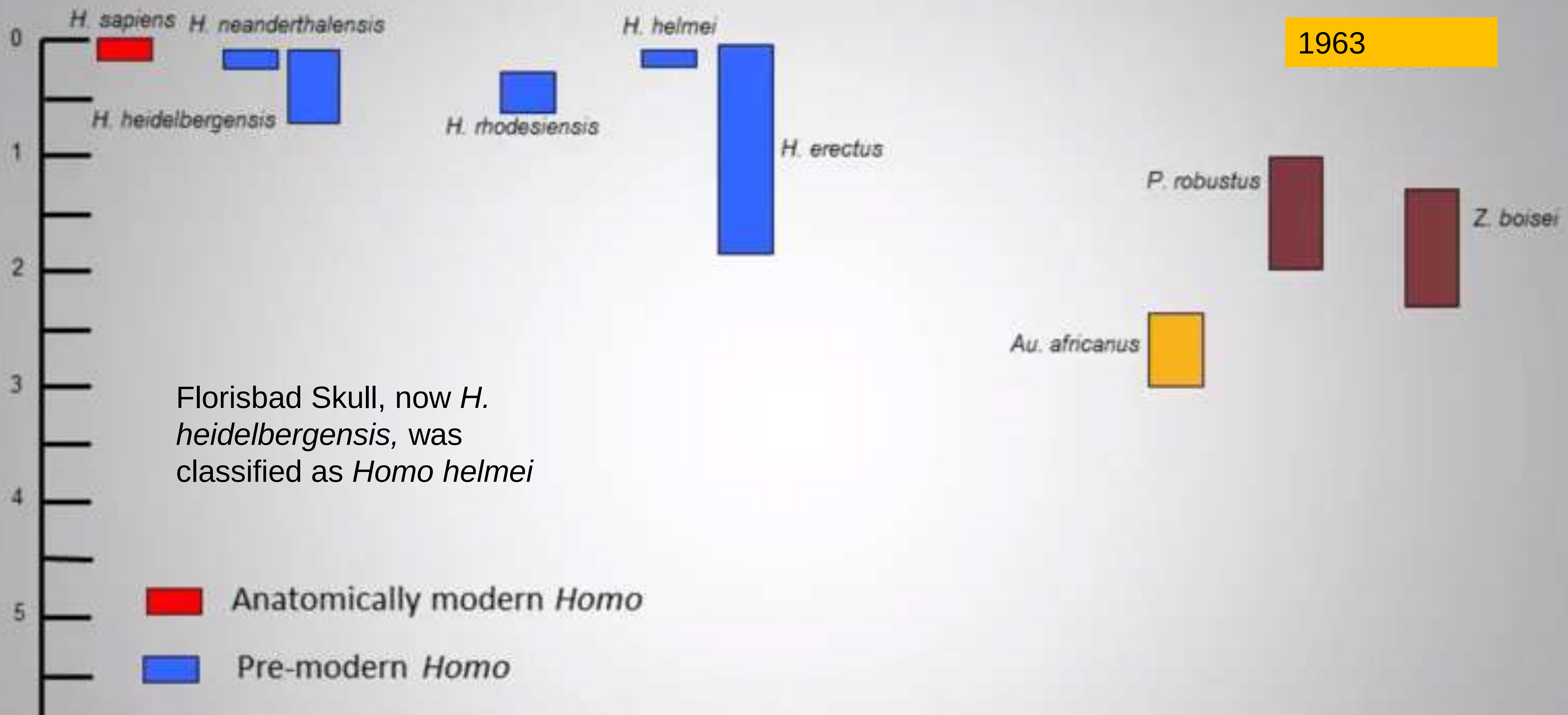
Each column

The observed first and last appearance dates (FADs and LADs) are just that –

they are not the *actual* first and last appearance dates

Wood and Boyle (2016)

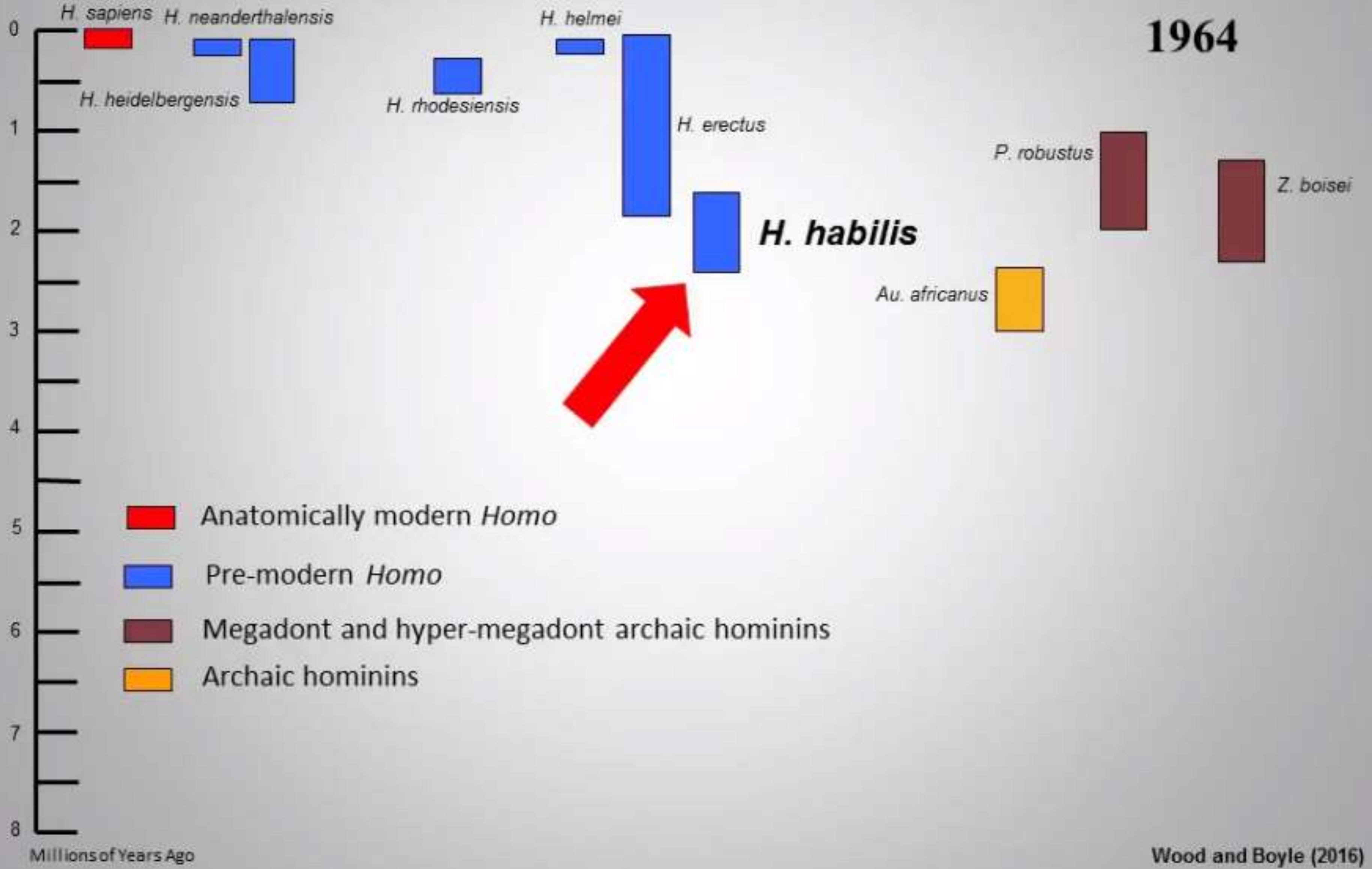
Hominin species according to a 'splitter's' taxonomy (i.e., speciose taxonomy)



1963

Florisbad Skull, now *H. heidelbergensis,* was classified as *Homo helmei*

Hominin species according to a 'splitter's' taxonomy (i.e., speciose taxonomy)



1964

Wood and Boyle (2016)

What is a genus?

Which taxa should be included in our own genus, *Homo,* and **why?**

When and **where** did *Homo* originate?

1960: Olduvai Gorge: OH 7, *Homo habilis*

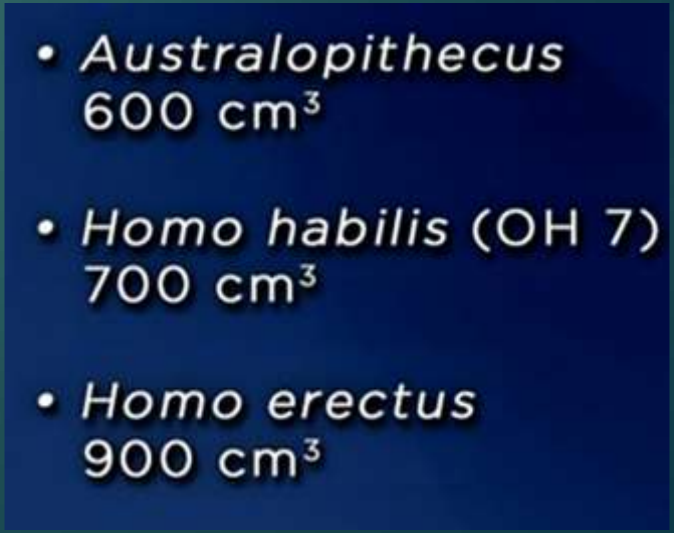

OH 7
(Olduvai Hominid 7)

Fragmentary and distorted type specimen

It's molar size is between Australopithecines and MHs

The only mandible at Olduvai

Original cranial size estimate: 642-723 cc



- *Australopithecus*
  600 cm³
- *Homo habilis* (OH 7)
  700 cm³
- *Homo erectus*
  900 cm³

1960: *Homo habilis,* 1.7 M, OH 7: First Stone Tool Use?

Note central crack

Homo habilis

OH 7 mandible is made the type in 1964

Discoverer: Jonathan Leakey
Locality: Olduvai Gorge, Tanzania
Age: 1.75 M
Discovery Date 1960

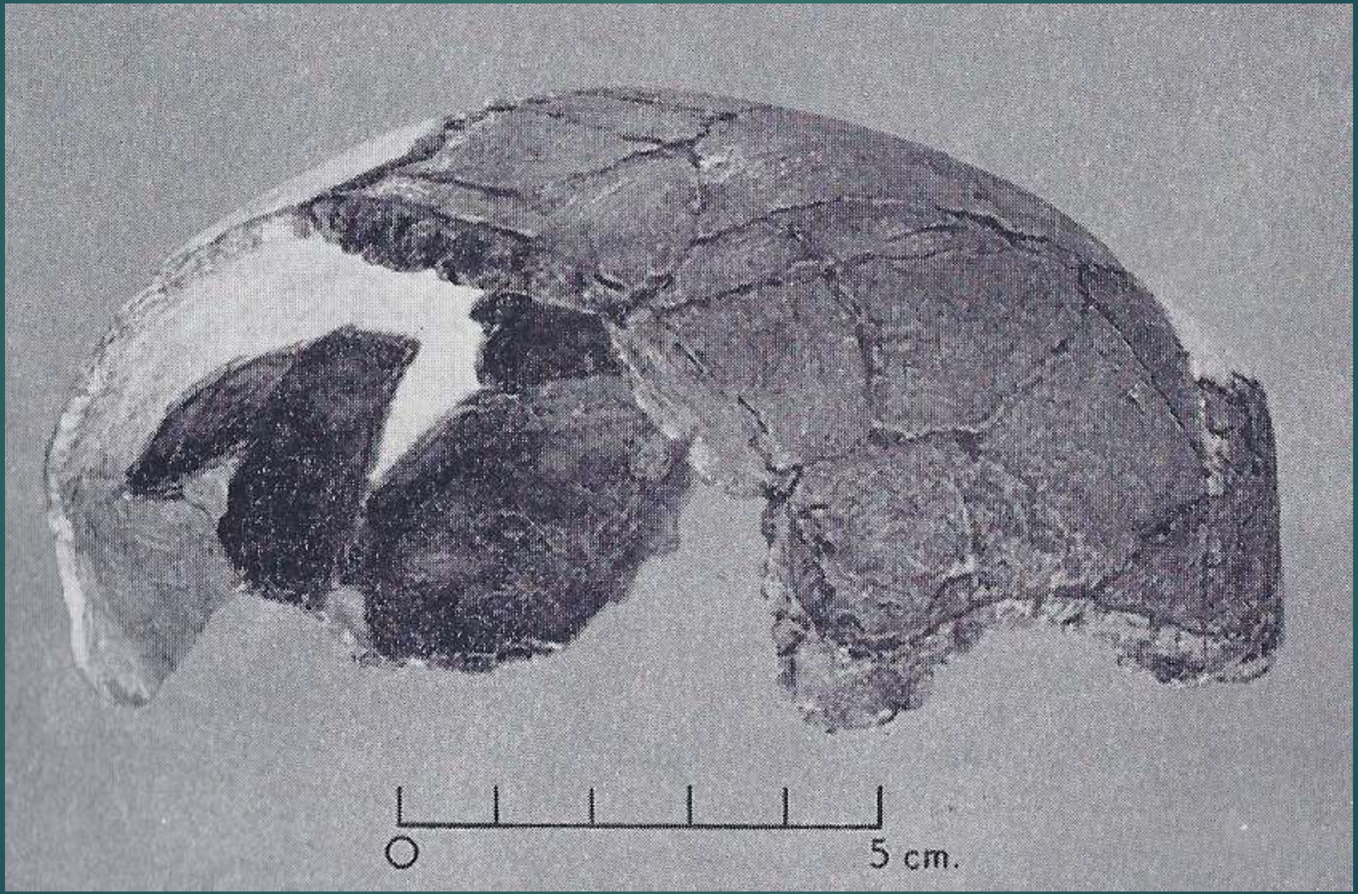
The only mandible at Olduvai
Original cranial size estimate: 642-723 cc

Controversy: Sits between *australopithecines* and *Homo erectus*.
Is it *Homo* or *Australopithecine?*

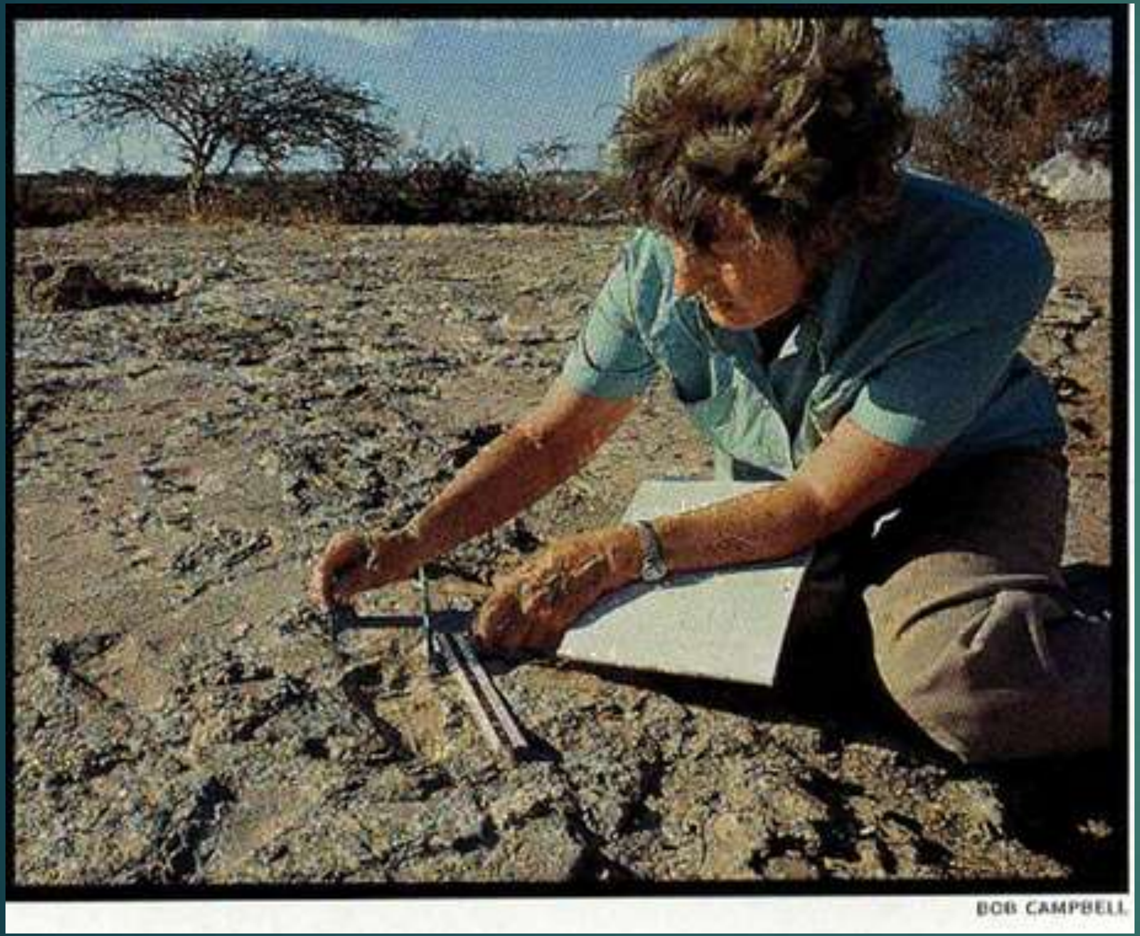
OH 7
Mandible

Australopithecus afarensis type specimen the LH 4 jaw bone from Laetoli

OH 7 Parietal bones



1960: Louis & Mary Leakey: discovered the skull and hand of *Homo habilis*, 1.75 million years old. She is not mentioned in 1964 paper.



- Mary Douglas Nichol Leakey:
- Discoverer of
  - Zinj,
  - Laetoli footprints,
  - World expert on Oldowan typology

Leakey, Mary. D. 1971 Olduvai Gorge: volume 3, excavations in Beds I and II, 1960–1963. Cambridge, UK: Cambridge University Press

Transitional Hominins

- Even today scientists continue to debate whether these fossils belong to genus *Homo,* or to a larger-brained *Australopithecus*.

- In 1961, John Robinson distinguished between tool-use, which he accepted for *Australopithecines*, and tool-making, exclusive to the genus *Homo*.

- Leakeys then found incomplete skull of an adolescent, more cranial fragments, a lower jaw, and teeth.

- Cranial remains showed no sign of sagittal crests (like Zinj, *P. boisei*), and the premolars and molars were much smaller than those of *P. boisei.*

Olduvai Gorge, Tanzania

Highest level *Homo erectus*

Homo habilis (female, Cinderella)

Homo habilis (male, George)

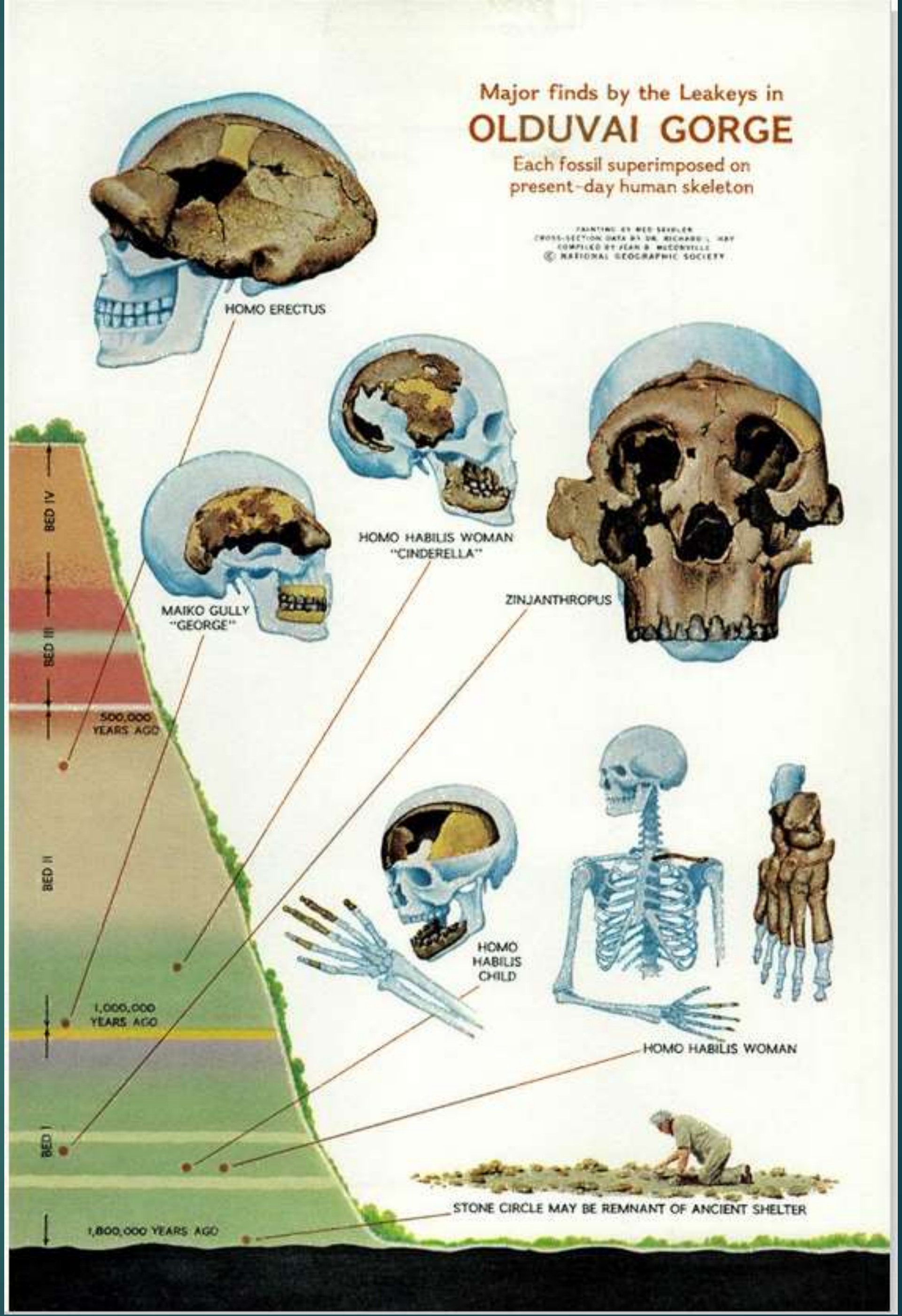
Zinjanthropus (1st found)
(*Paranthropus boisei*)

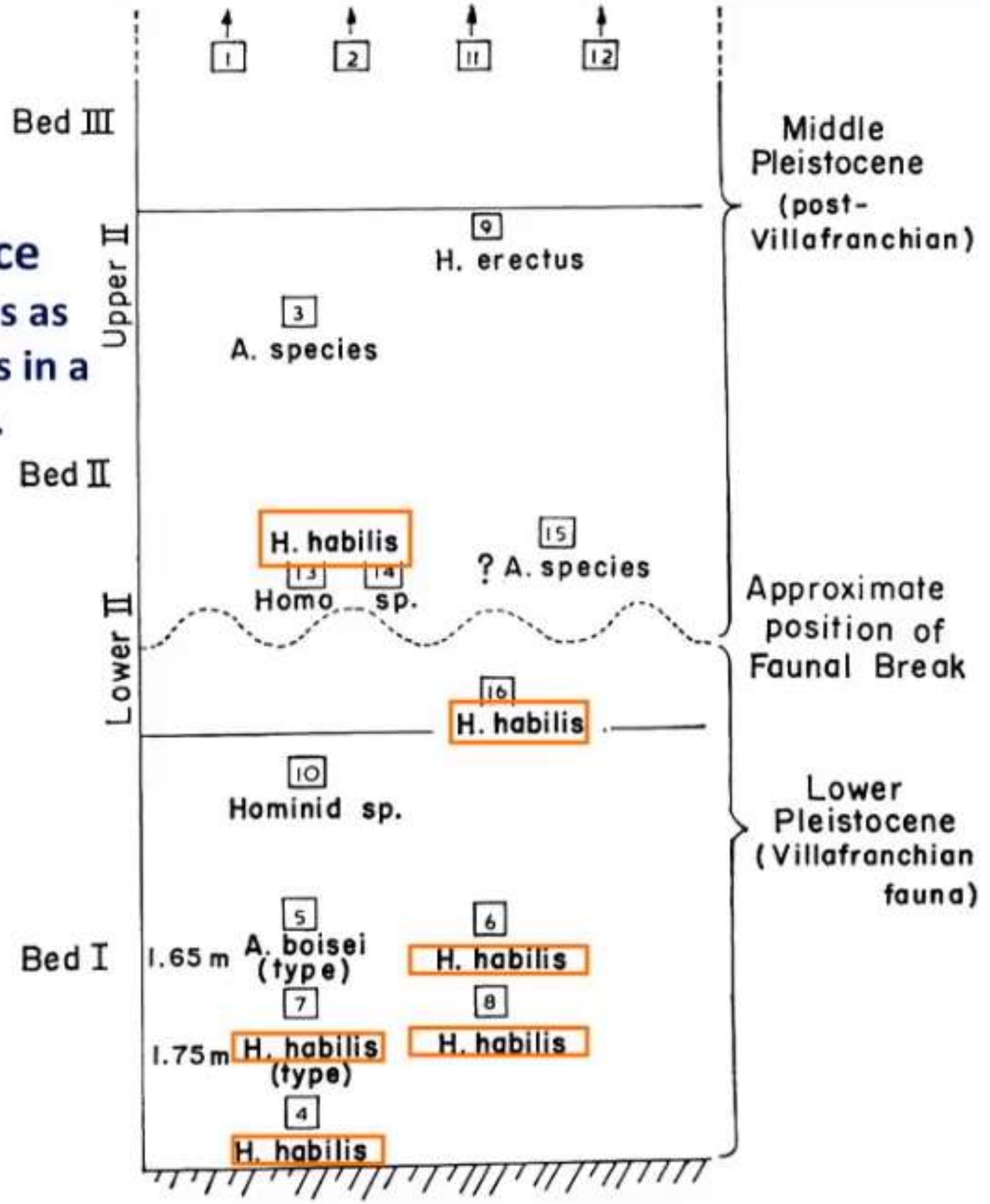
Homo habilis (type) (child, Jonny)

Lowest level

Homo habilis (female)

Homo erectus remains were found in the upper portions of Bed II, making them contemporaries of *P. boisei*, but not of *Homo habilis;* at least at Olduvai





Olduvai Sequence

***H. habilis* specimens as illustrated by Tobias in a 1965 *Science* paper.**

Olduvai Sequence:
described by Tobias

Australopithecus was earlier;
Erectus was later;
Habilis was in between.

Upper bed *habilis* was much more like *erectus* than lower bed *habilis*

Genus *Homo*: Evolution of our species

- In 1964, announcement by Mary and Louis Leakey at Olduvai Gorge;
- OH 7 jaw is type specimen:
  - smaller molar size
  - smaller premolars
  - in conjunction with Oldowan tools and finger bones indicating precision grip
  - and cranial size increase (45% larger than *A. africanus*).
  - Later found: caps over cortical motor speech areas of Broca & Wernicke's: speech

History of Discovery

- **“Handy” hypotheses: In** the *Nature* paper of April 1964, Leakey, Tobias and Napier made the case for adding the 'handy man' to the genus *Homo* as *H. habilis*.
  - Olduvai fossils met three key criteria set out in Le Gros Clark’s 1955 definition of *Homo*:
    - upright posture,
    - a bipedal gait
    - dexterity to fashion primitive stone tools
  - Relaxed the brain-size criterion (A. Keith’s Cerebral Rubicon = 750 cc) to accommodate the smaller brain (~ 600 cc)
  - Name suggested by Raymond Dart, and means “handy man,” in reference to tool making; not “brainy” man

History of discovery: controversy

- The proposal was met with considerable skepticism. Some thought that the fossils were too similar to *Australopithecus africanus* to justify a new species.
- Assault on *H. habilis*: LeGros Clark, K. Oakley, David Pilbeam, Clark Howell, Loring Brace, John Robinson, Milford Wolpoff – not *Homo*. Opposition for 20 years.
- John Robinson, a leading authority on australopiths, suggested that *H. habilis* was a mix of earlier *A. africanus* and later *H. erectus* bones.
- Very few accepted that it was the earliest human.

Homo habilis. Olduvai Gorge (642 cc): ~1.7 Ma

4 Olduvai cranial specimens: Jonny’s Child, Twiggy, Cindy, George

“**Jonny’s Child**”, *H. habilis*, OH 7, 1.7 M, 642-723 cc, type specimen

Homo habilis: Diagnostic Features

- It is particularity hard to list the features of *Homo habilis*, because the specimens attributed to *habilis* (and the reasons the material was placed there) vary widely.

- OH 7 is the type specimen of *habilis*.
- The specimen consists of
  - nearly complete left parietal,
  - a fragmented right parietal,
  - most of the mandibular body (including thirteen teeth),
  - an upper molar,
  - and twenty-one finger, hand, and wrist bones.
  - 12-13 year old male.
  - Cranial capacity = 590–710 cc.

Homo habilis (ER 1813): Expansion of brain

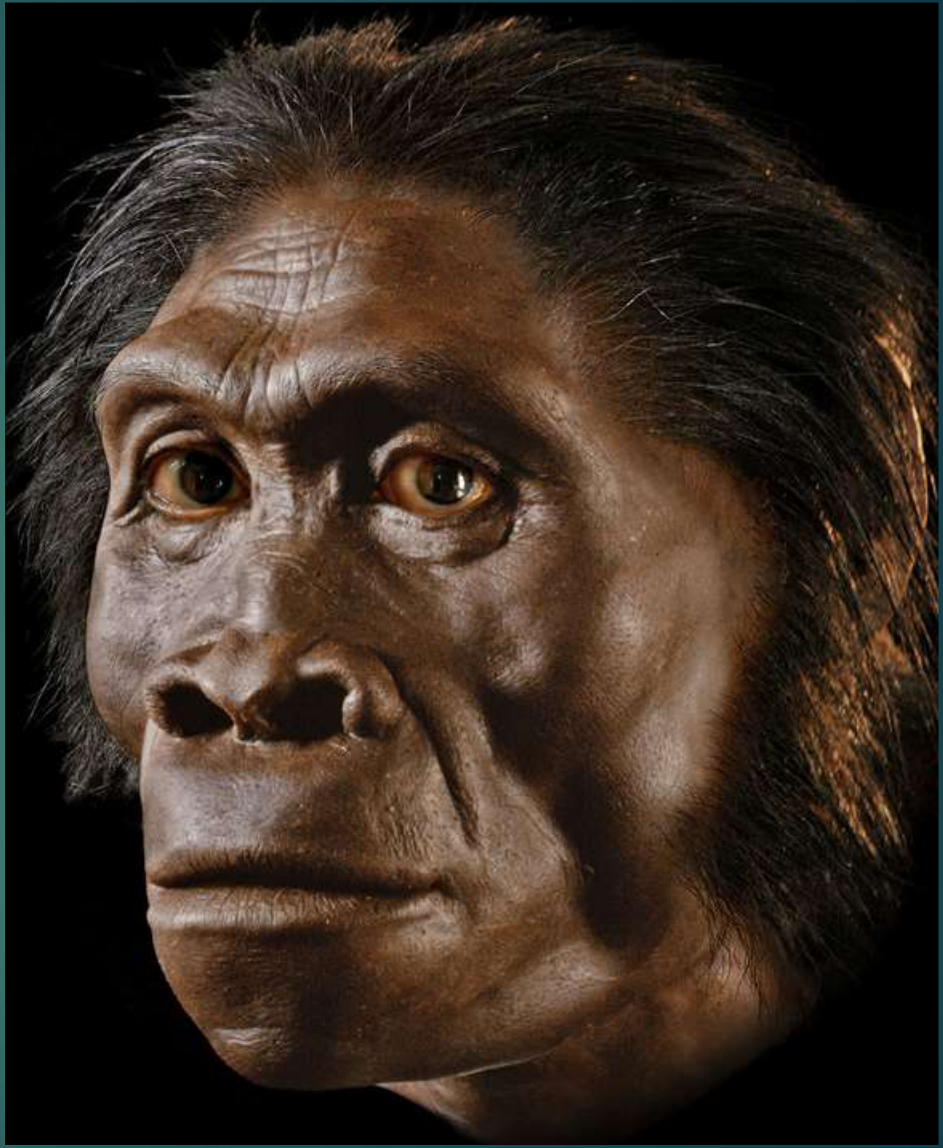
- Sloping, elevated forehead
- Expansion of frontal lobe area
- Cranial capacity: 600-800 cc

21 bones of a hand

Distal tuffs (tip of finger end bones are enlarged) – capable of precision gripping; unlike *A. afarensis*

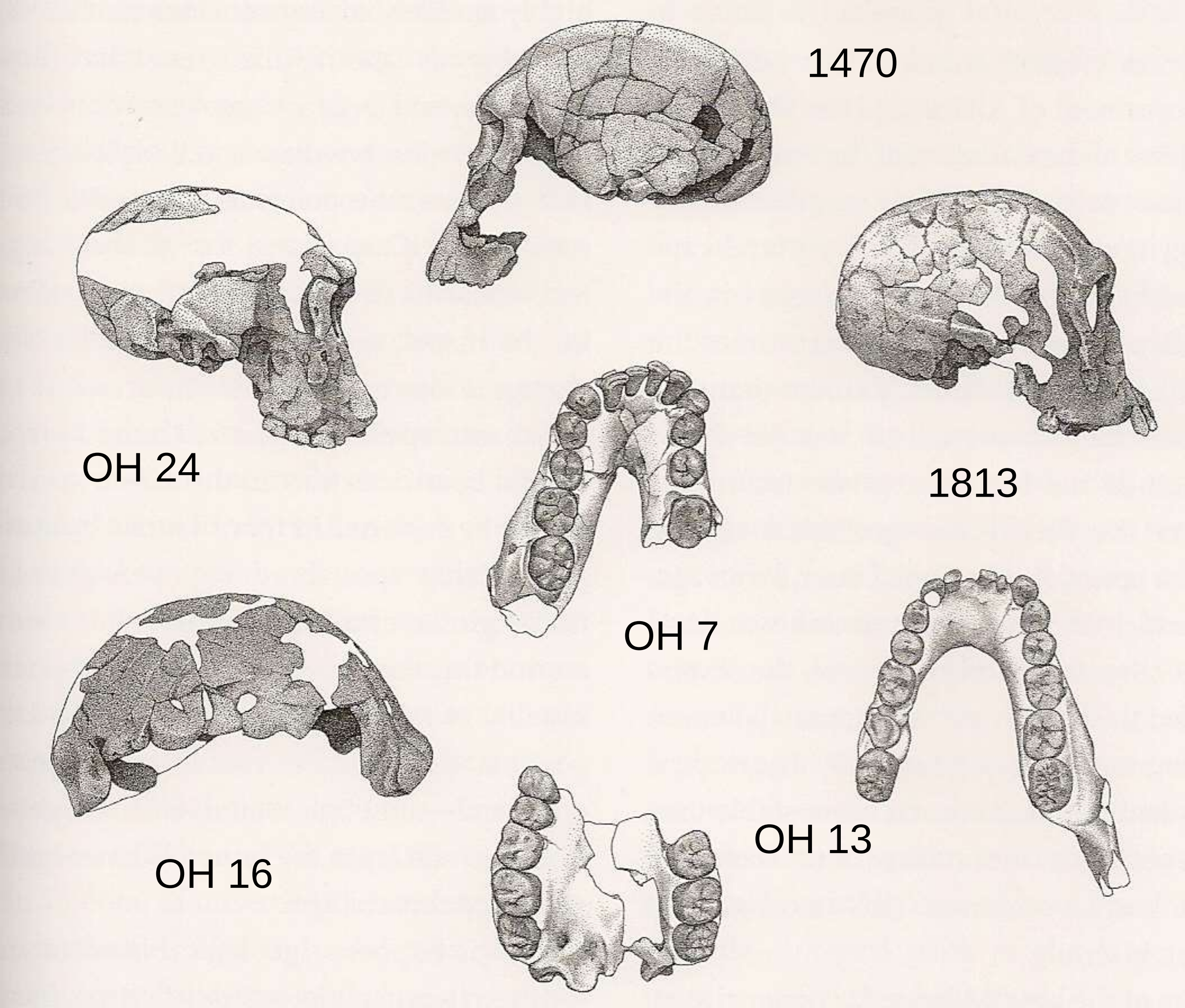
Reconstructions of *H. habilis*

Deek brothers



John Gurche

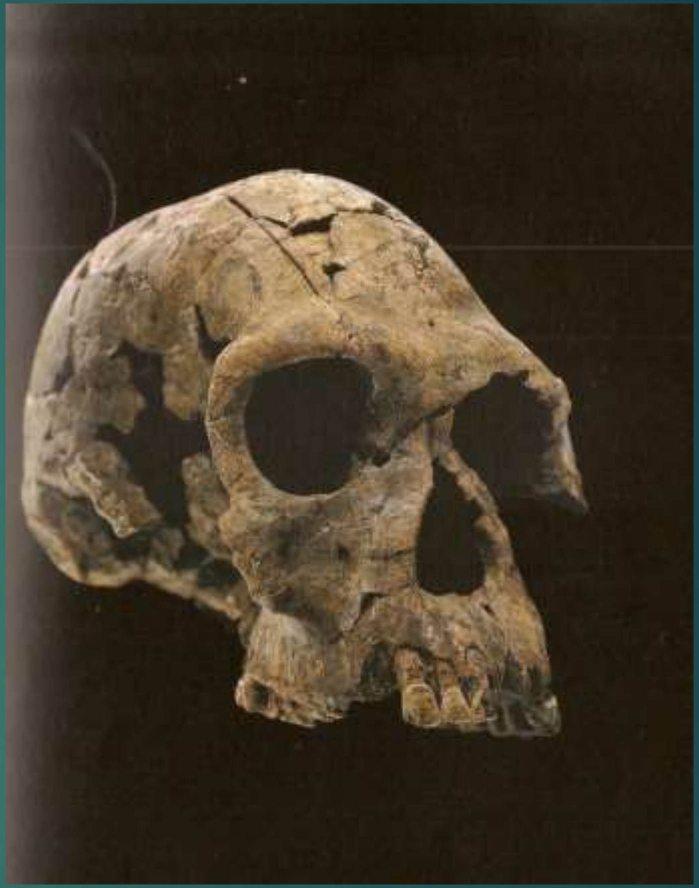
Reconstructions of *H. habilis*



by Don McGranaghan

- Specimens originally all placed in *Homo habilis:*
  - Type OH7, center,
  - Olduvai; clockwise from top
  - KNM-ER 1470 & 1813
  - Kenya; OH13 mandible & maxilla
  - OH16 (George)
  - OH 24 (Twiggy)

Homo habilis: Handy Man



2.4-1.6 Ma: long arms, short legs, but more advanced upper jaw

Average cranial capacity of *H. habilis:* original estimate*:* 631 cc

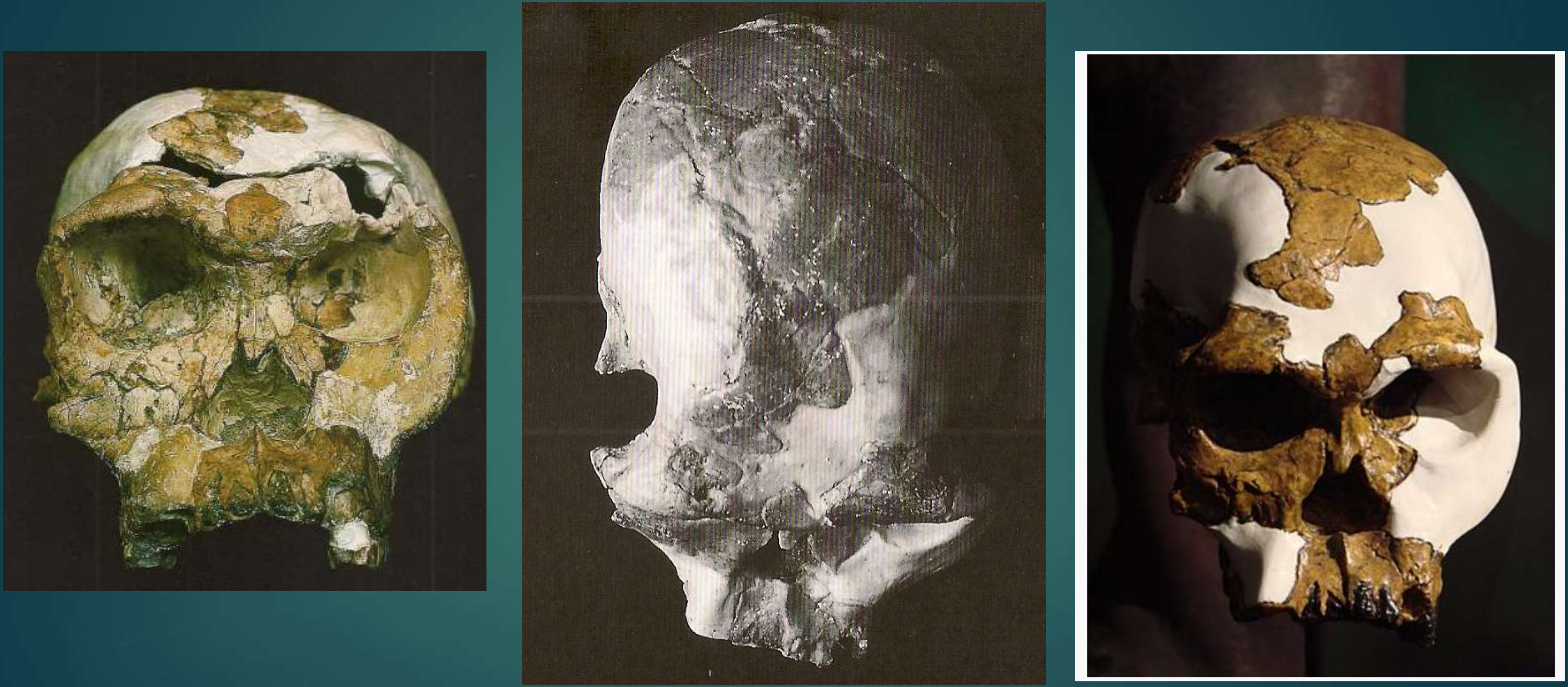
“Twiggy”, *Homo habilis*, OH 24, 1.8 M, pancaked flat

OH 24: Restored (L) and unrestored (R) from Bed I

A crushed cranium from the lowest strata at Olduvai:

Nixed Robinson's argument that *H. habilis* was a mix of an australopith and *H. erectus*.

OH 24

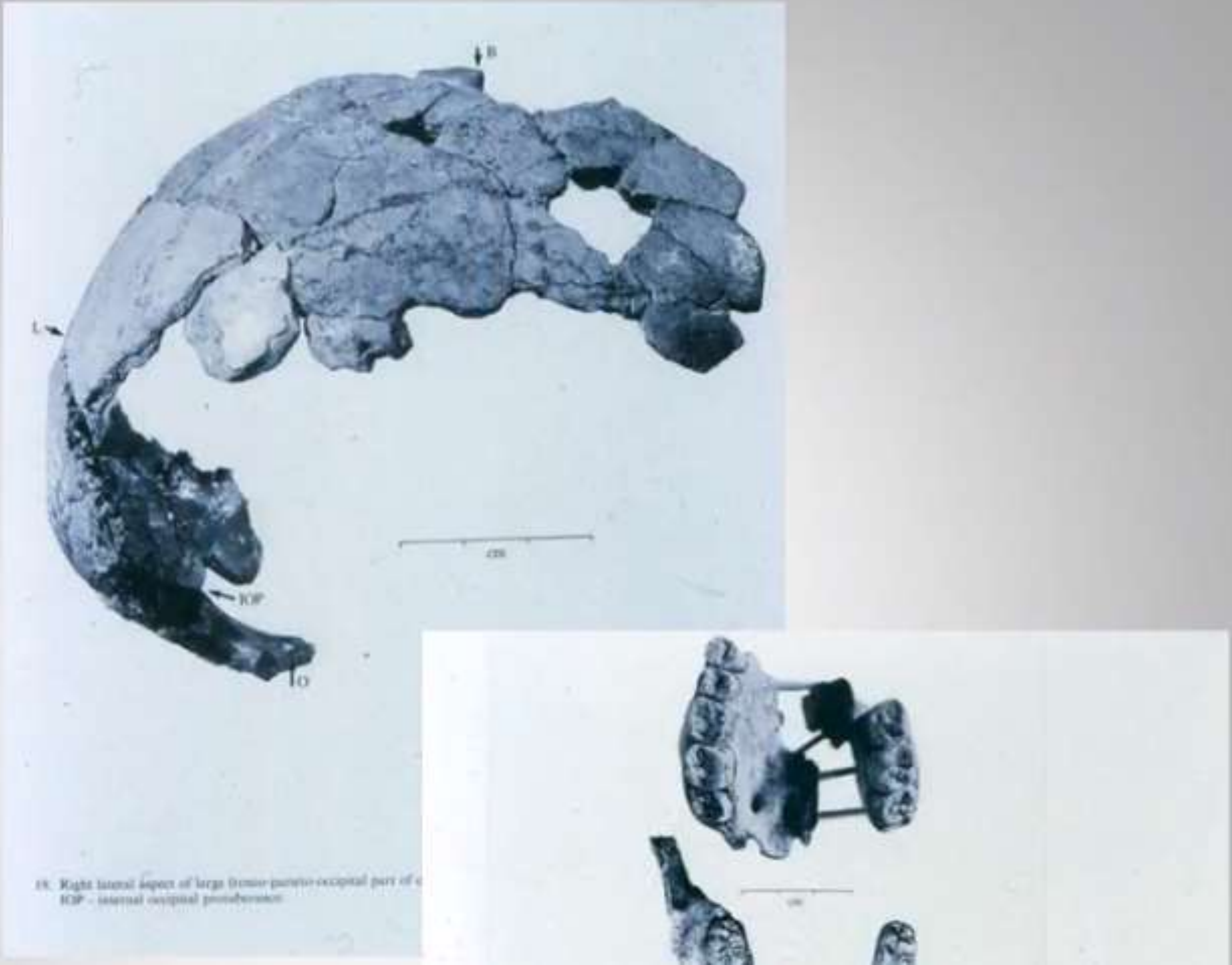


OH 24

OH 24, Twiggy

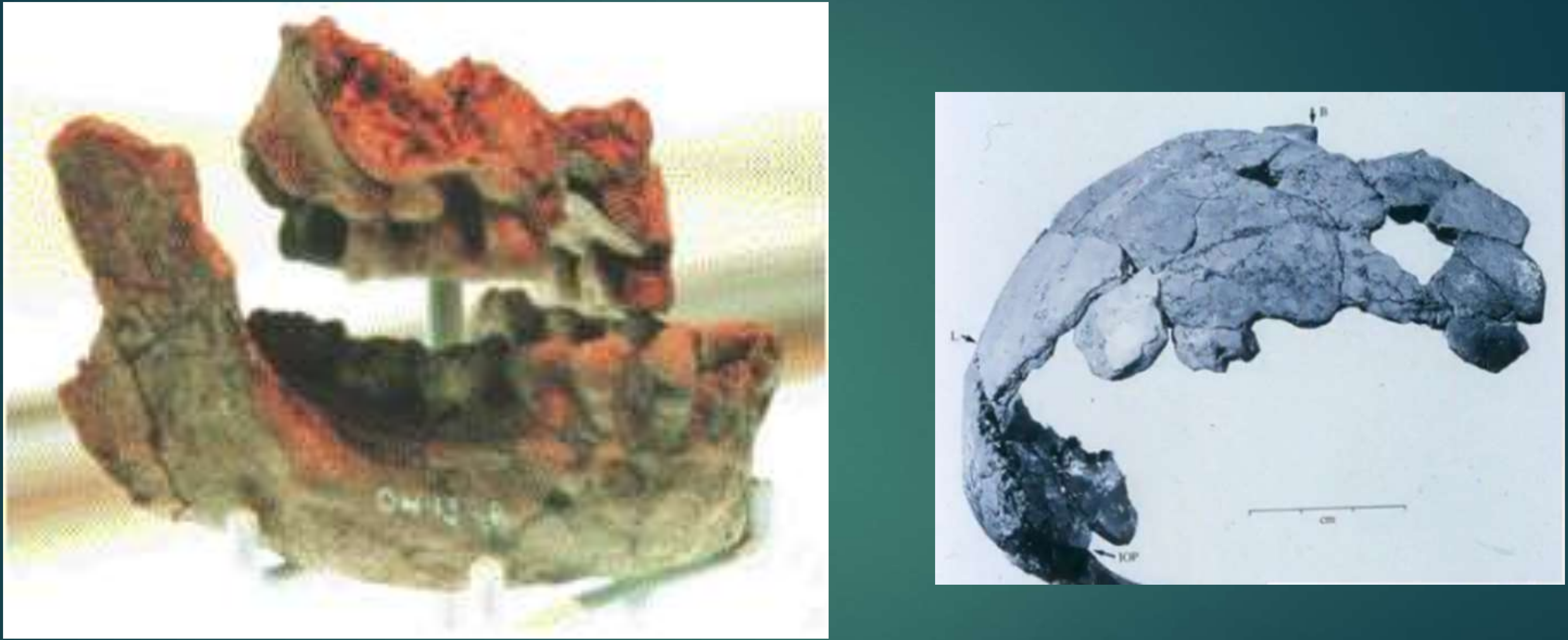
- OH 24 ("Twiggy") is the most australopithecine-like of specimens attributed to *H. habilis;* may be more highly correlated with *A. africanus*.
- The skull was found crushed almost flat and was therefore named after the famously skinny model of the time, Twiggy.
- Found completely fractured, cemented together in a coating of limestone.
- Ron Clarke: reconstruction, which left out 100 small fragments
- Hence, the specimen is extremely distorted, making an accurate estimate of its brain size very difficult; Holloway - estimate of 590 cc (many researchers believe that number is too high).

OH 13: “Cindy” Cranial vault and dentition from Bed II



18. Right lateral aspect of large fronto-parieto-occipital part of c
IOP - internal occipital protuberance

“**Cindy**”, *H. habilis*, OH 13 , 1.6 M, ~ 650 cc



Mandible & teeth, bits of maxilla, cranial fragment.

Homo habilis: OH 13, Cindy

- OH 13 – “Cinderella”: This is a poorly preserved and fragmentary specimen of a 15–16 year-old female *habilis*
- Dated to 1.7 Ma; the most recent habilis specimens known.
- The material consists of the mandible and the maxilla, several teeth, pieces of the cranial vault, and some postcranial elements, including a small piece of proximal ulna.
- This specimen (along with OH 16, “George”) were the object of much inaccurate brain size estimations, which originally lead to the two being classified as *H. erectus*.
- More recent estimates put the brain size at around 500 cc, and along with an estimated body size near that of AL 288–1, gives this specimen a relative brain/body weight ratio similar to OH 7.

Mary Leakey found OH16 (George): Unfortunately trampled by Masai cattle; much of the skull was lost.

“**George**”, *Homo habilis*, OH 16, 1.7 M, Approx. 500-640 cc.

Teeth & skull fragments.

OH 16

Homo habilis: OH 16

- OH 16, "George": found in 1963, consisted of teeth and some very fragmentary parts of the skull. Estimated age is 1.7 Ma, and the brain size was about 640 cc.

- Very large teeth (close to *australopithecus* in size).

- The individual was age 15–16 when he died.

- The individual had very bad caries on one side of its jaws (very unusual in ancient specimens), which lead to differential chewing on the other side, causing it to develop a huge temporalis muscle on that side.

First Skeletal bones: OH 62

Johanson and White in 1986; 3-4 feet tall

OH 62:

- Screening of dirt revealed 18,000 bone fragments; 308 attributed to OH 62

First postcranials of *H. habilis*

OH 62: only partial skeleton attributed to *Homo habilis*

Controversial

OH 62, *Homo habilis*

- First skeleton of *Homo habilis* with both cranial & postcranial fragments found together;
- It is the only fossil in which limb bones have been securely assigned to *H. habilis*.
- A tiny, old, long armed female
- 1.8 Ma

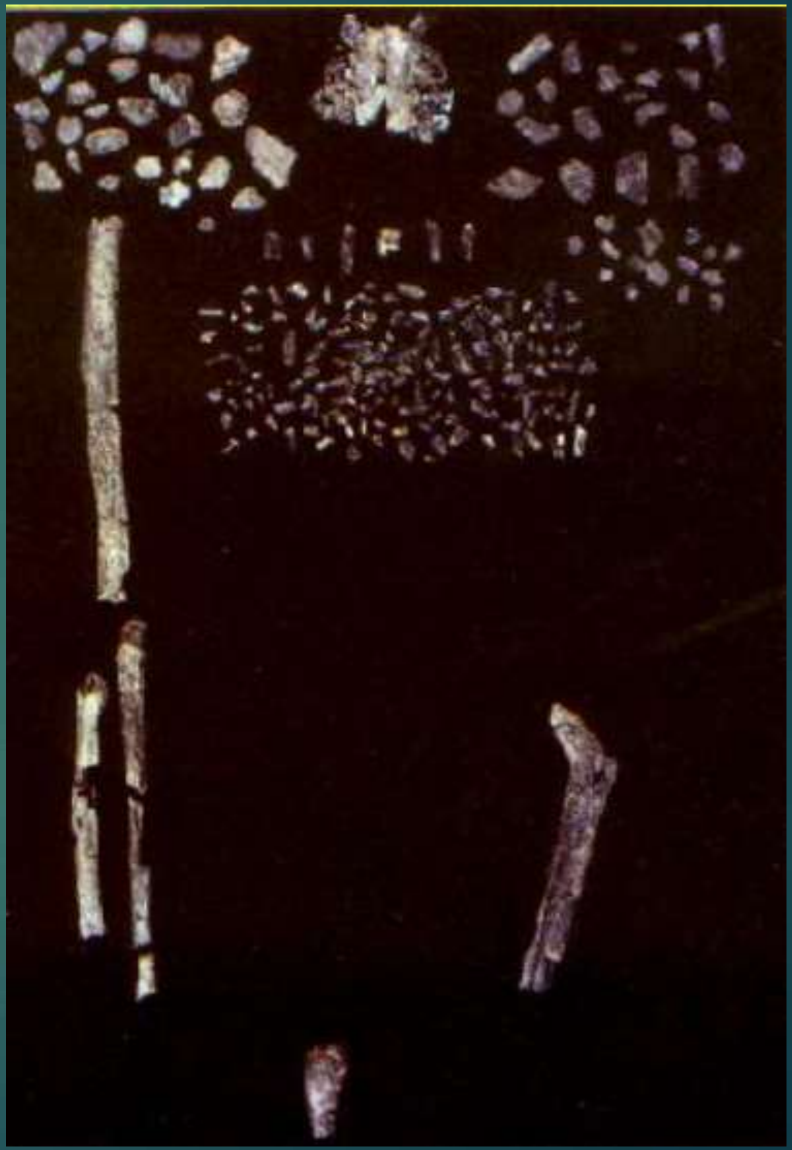
OH 62 maxilla:
Worn teeth; not like OH 7

Homo habilis: OH 62

- OH 62. Publicized widely as "Lucy's Child" by Johanson, it is a very scrappy collection of 308 bone fragments. The maxilla permitted identification as *H. habilis*.
- The entire specimen is problematic; raises many questions as to sexual variation and behavior.
- The most controversial aspect of the specimen was the Johanson et al. calculation of a humero-femoral index of 95% (higher = more arboreal) (humans, 70%, Lucy 85%). It is unclear why Johanson et al. calculated the index in the manner they did. It is generally not accepted.
- Arms long (longer than Lucy's), legs short (shorter than Lucy's); more apelike than *A. afarensis*, its presumed ancestor

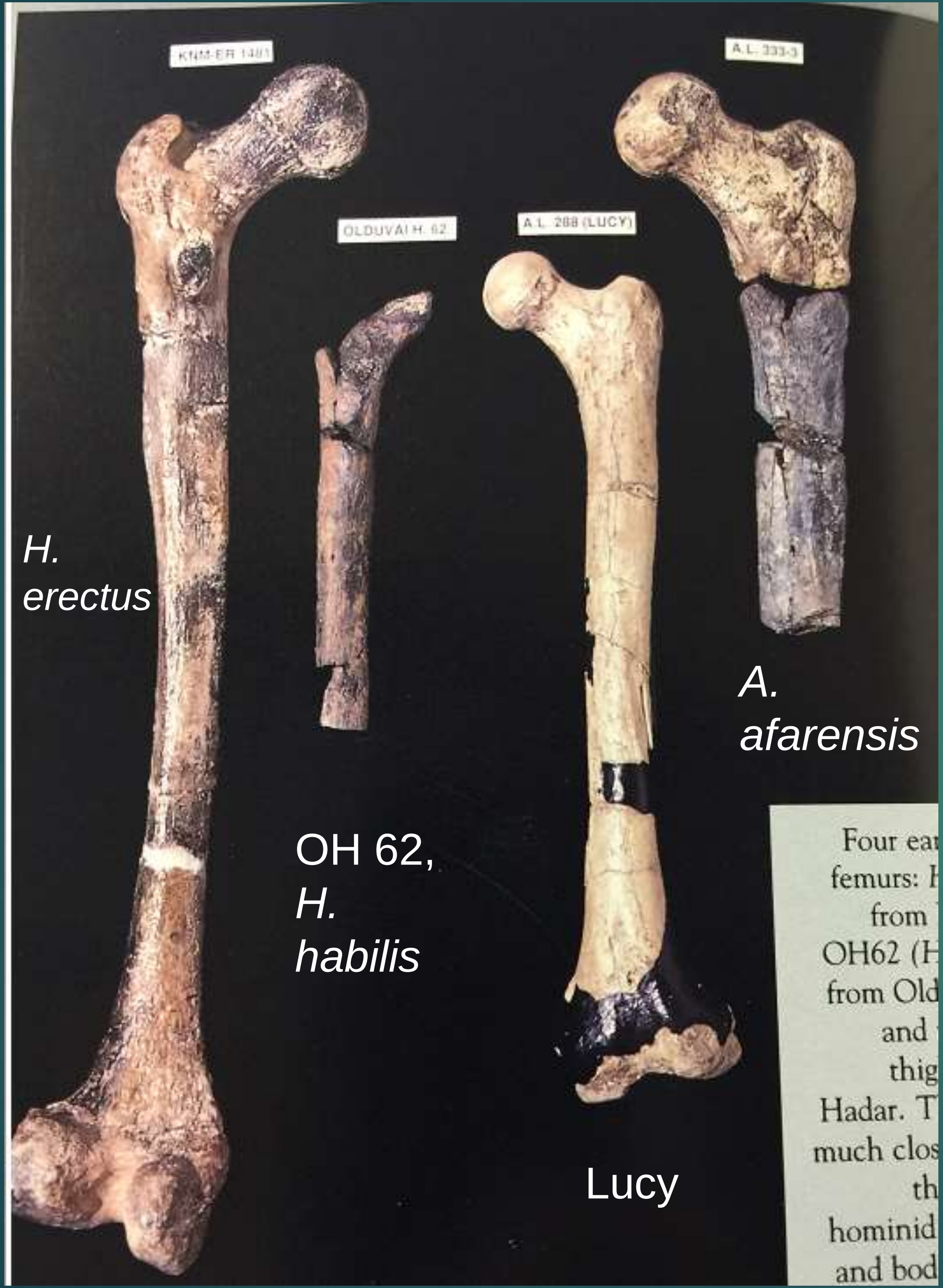
1986: Body size of *Homo habilis*, OH 62, is like Lucy; ape-like arms longer than Lucy

- Limb sizes and proportions nearly identical to australopithecines; arms as long as *A. africanus*
- Called dik-dik hominin because found in the droppings of a dik-dik.
- Height estimated at 3 feet 5 inches tall; very small for the species.



(Johanson and Shreeve 1989; Johanson et al. 1987)

Femurs (upper leg bone)



Four early hominin femurs:

1 *Homo erectus* from Koobi Fora

2 OH62 (*Homo habilis*) from Olduvai Gorge

2 other *afarensis* thighbones from Hadar.

Though living much closer in time to the Koobi Fora *H. erectus*, OH 62's size & body proportions resemble those of Lucy, 2nd from right.

OH 62 possibilities

- Postcranially primitive; long arms; it would be smaller than any known hominin, if accurate; more similar to apes than Lucy (1 My older)

- Possibilities:
  - 1 – OH 62 is not *H. habilis*; did not lead to *H. erectus*
  - 2 – OH 62 is not *H. habilis*; dead end
  - 3 – OH 62's limb proportions have been reconstructed incorrectly (probable, given fragmentary nature)
  - 4 - If OH 62 is accurate, suggests that body plan combining long humanlike legs with long australopith-like arms persisted for at least 600 Ka after *Homo* emerged.

Homo habilis: basics

- **Fossil Record:**
  - 2.4 to 1.5 Ma
  - Some specimens attributed to *H. habilis* may have too wide a range of morphological variation to be considered one species.
  - Some of the larger specimens have been placed in the species known as *Homo rudolfensis*/group 1470.
- **Habitat and Distribution**: Tanzania, Kenya, Ethiopia, and southern Africa.
- Major Location: Mainly East Africa
- Major site(s): Olduvai Gorge, Koobi Fora/East Lake Turkana, Sterkfontein

Homo habilis: features

- *Homo habilis is* very similar to australopithecines in many ways.
  - The face is still primitive but projects less than in *A. africanus*.
  - The back teeth are smaller but still considerably larger than in modern humans.
  - Brain size varies between 509 and 800 cc, overlapping the australopithecines at the low end and *H. erectus* at the high end.

Homo habilis

- The original reasons for including the *H. habilis* fossils in the genus *Homo* are twofold.
  - First, *Homo habilis* shows a notable increase in brain size, from the average of about 480 cc for *Australopithecus* and *Paranthropus* to an average of 509 cc to 800 cc for *Homo*
  - Second, the presence of stone tools indicates that those larger brains may have been capable of more complexity of thought, not seen in the other two hominin genera.
  - 15 Olduvai sites from the early *Homo* period contain stone flakes, tools, and animal bones.

Diagnostic features

- P. Tobias and L. Leakey used three traits that set *habilis* apart, as a transitional species between *A. africanus* and *H. erectus:*
  - Expanded cranial capacity (relative to *A. africanus*).
  - Reduced postcanine tooth size.
  - The presence of a precision grip (determined from the hand bones present in OH 7), which provides the anatomical basis for tool-making.

Homo habilis: cranial capacity, teeth, hand

- General features of the specimen seems to support these three traits (whether or not it is transitional from *africanus* to *erectus*):
- Larger cranial capacity (though very problematic). Tobias gives an estimate of 647 cc, Holloway gives an estimate of 710 cc, and Wolpoff has estimated it at 590 cc; most recently, Spoor gives 729-824 cc
- Molar megadontia is gone, with molars longer than they are wide. Still larger than MH.
- Hand: less interlocked bones, which allowed more movement.
- The distal phalanges have apical tuffs (finger tip pads), more capable of precision grip.

H. habilis basics

- **Height** F: 3.3 ft (100 cm) M:?
- **Weight** F: 71 lb (32 kg); M: 82 lb (37 kg) (F about 86% of M)
- **Brain size** 612 cc mean (509-674 cc range)
- **Cranium:**
  - Somewhat prognathic face
  - incipient brow ridge
  - foreshortened palate
  - no sagittal crest
  - rounded mandibular base

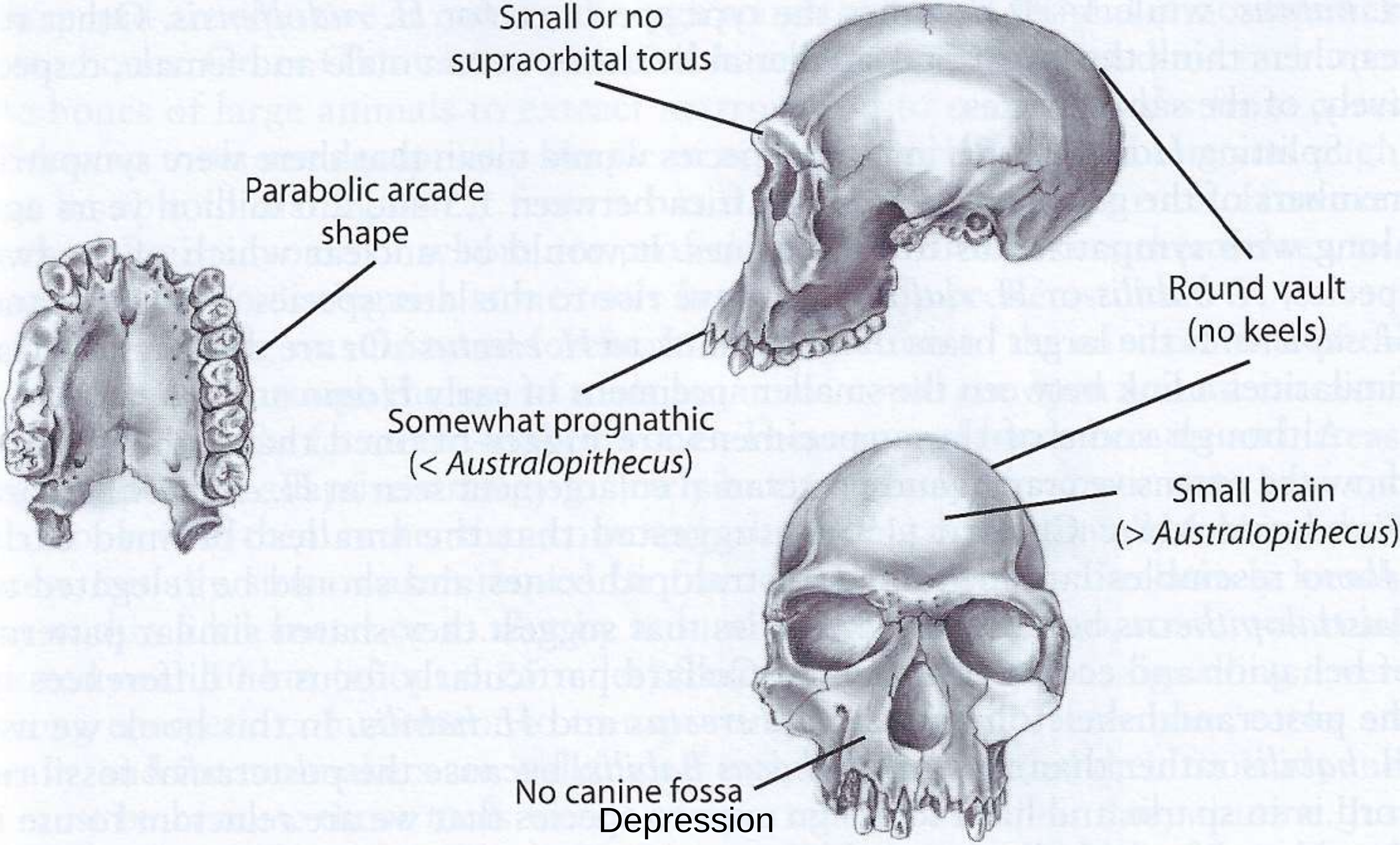


FIGURE 12.1 Key anatomical features of *Homo habilis* include reduced facial size, a parabolic palate, and some brain enlargement.

H. habilis basics

- Dentition
  - Narrower lower grinding teeth than in *Homo rudolfensis*
  - mostly single-rooted lower premolars
  - much larger teeth than we do, relative to our body size.
- Limbs
  - Possibly, longer arms and shorter legs than modern humans
  - feet retaining adaptations for climbing
- Locomotion
  - Bipedalism (probably relatively modern)
- Dates: 2.5 -1.6 Ma

Redefining *Homo*

- Issue of who would be “in” and who would be “out” of *Homo*?
- B. Wood: “I would allow *Homo erectus* in, but I would draw the line at *Homo habilis.*”
- The origin of genus *Homo* is arguably one of the most exciting topic in paleoanthropology today.
- *Homo habilis* is the original problem child of the paleoanthropological community.

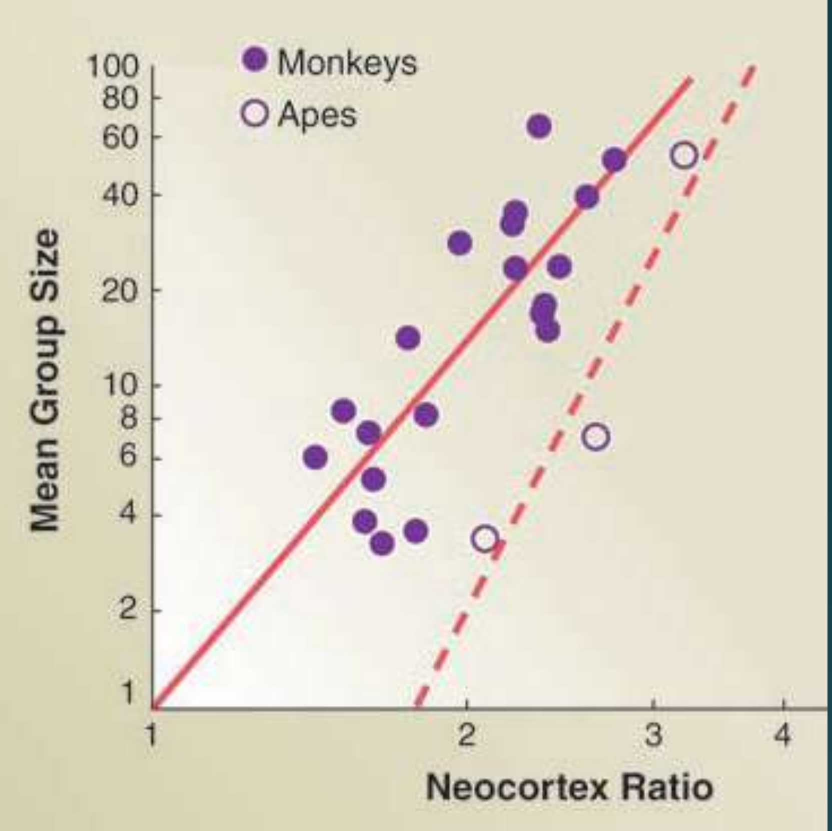
Genus *Homo*: Evolution of our species

- Modern history of the study of genus *Homo* begins in 1964 with discovery & recognition of *Homo habilis* by Louis & Mary Leakey

- The announcement of *Homo habilis* in 1964:
  - Was a turning point in paleoanthropology.
  - Shifted the search for the first humans from Asia to Africa
  - Began a controversy that endures to this day;
  - But a convincing hypothesis for the origin of *Homo* remains elusive.

Dunbar’s Social brain hypothesis

- Robin Dunbar (1992): brain size in primates, expressed in terms of neocortex ratio, shows an outstanding correlation with the size of the social group.
- Dunbar: Average social group size correlates with the ratio of neocortex to the rest of the brain.
- Dunbar’s number: 150



R. I. M. Dunbar, *et al.* 2007. Evolution in the Social Brain. *Science* 317, 1344-1347.

Social Complexity and Brain size

- Dunbar found a close correlation between the ratio of neocortex to the rest of the brain on the one hand, and social group size and complexity of social relationships on the other.

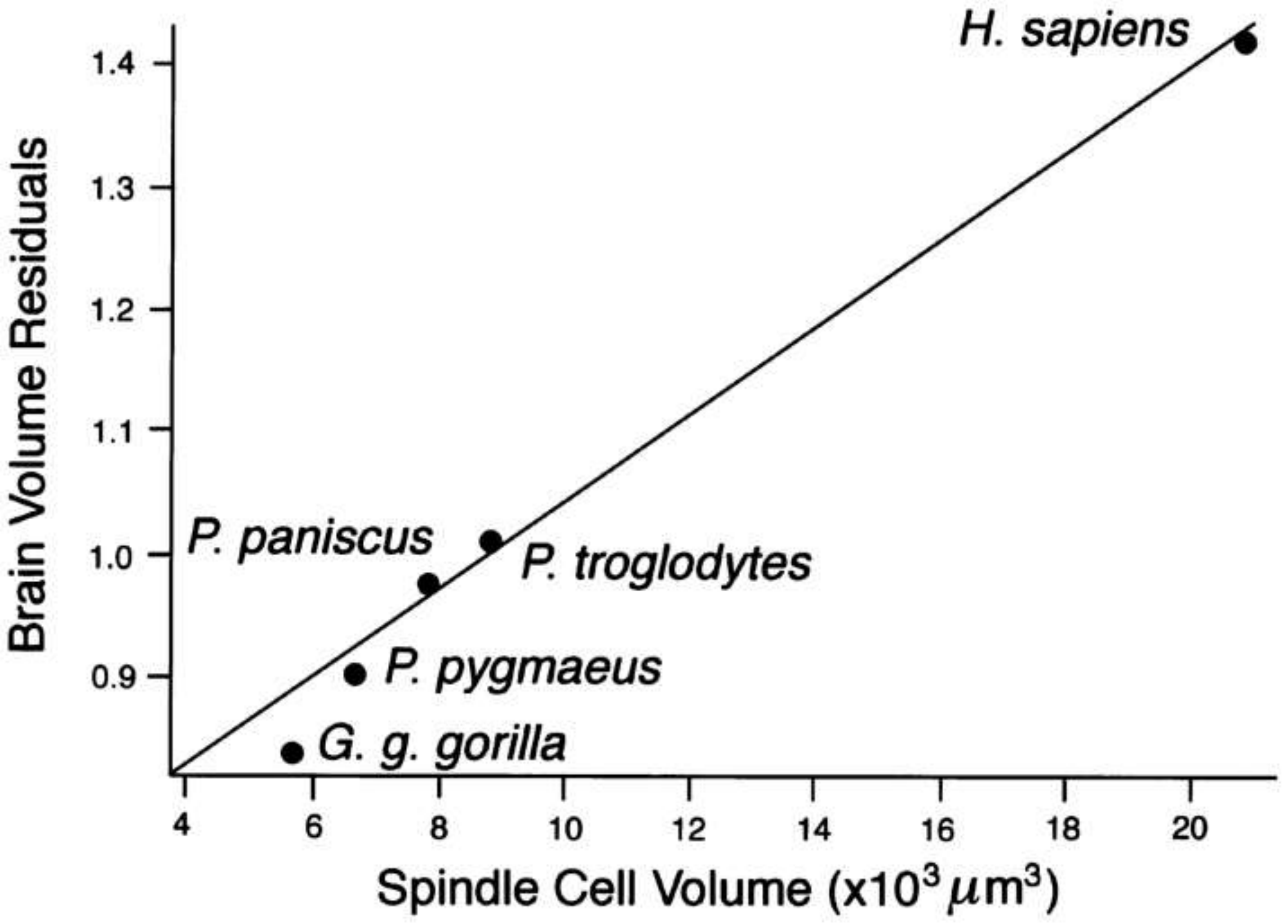
- For example, Baboons show a remarkably high degree of sociability and have the largest neocortex of Old World monkeys.

- Byrne and Whiten: highly significant correlation between neocortical size and the prevalence of tactical deception (sex while alpha chimp isn’t watching).

Von Economo Cells

- VENs: Damage to uniquely human VENS result in significant social impairment
- Fastest and largest neurons located primarily in the anterior cingulate and insula (layer Vb)
- Only 3 groups with significant VENs: primates/humans, certain cetacians, elephants; those with largest brains and most social species
- Evolved to speed information around a big brain for social analysis

Comparison of number of VENs and relative brain volume



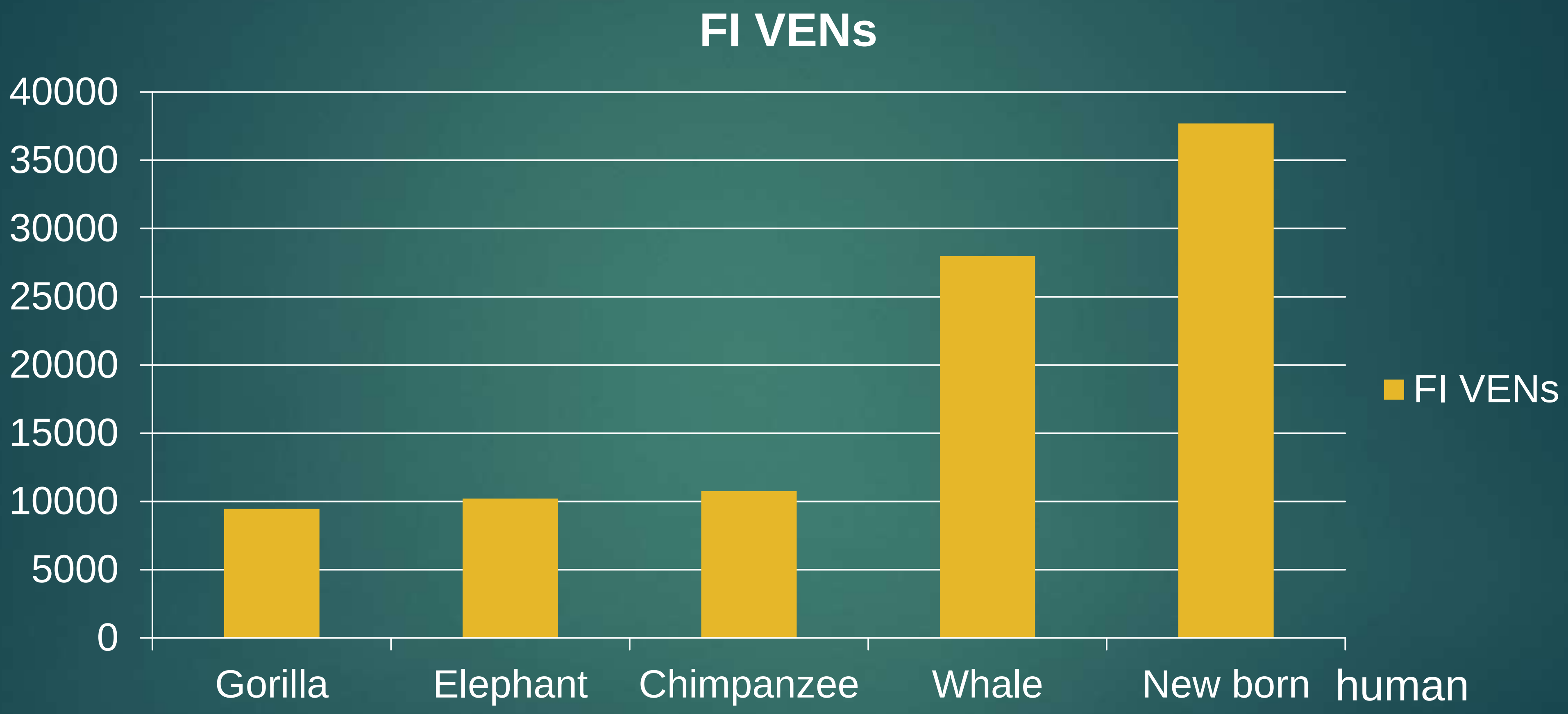
Nimchinsky E A et al. PNAS 1999;96:5268-5273

VENS: Von Economo Neurons

- Found in Frontal Insula & anterior cingulate; few in hippocampus & dlPFC
- 30% more abundant in the right hemisphere
- Pruned to adult status ~ 8 y
- Absent in monkeys and lesser apes
- Humans>>>chimps>gorillas>Orangs
- Correlated with increased encephalization (IQ)

Nimchinsky et al., 1995, Allman et al., 2010, W. Seeley lecture, 2011

VENs in right anterior insula



(Allman et al., 2010, 2011; Butti et al., 2009; Hakeem et al., 2009; Hof and Van der Gucht, 2007; Nimchinsky et al., 1999).

VENs: Involvement in neuropsychiatric disorders

- If you alter VENS, you produce instant deficits in social ability
- Frontal Temporal Dementia: destruction of Salience Network
  - 70% reduction VENs in ACC & FI; none in Alzheimer's
  - Correlates with social behavioral severity of bvFTD

Seeley, Allman, and others 2007; Seeley and others 2006; Kim, et al. 2011

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FTD Social-Emotional Deficits

- Emotional empathy (empathic concern)
- Cognitive empathy (perspective taking)
- Interpersonal warmth
- Emotion recognition of faces (negative emotion↓)
- Emotion recognition of music
- Emotional moral judgment
- Prosocial sentiments (guilt, pity, embarrassment ↓)
- Other critical sentiments (anger, disgust ↓)
- Mutual gaze during dyadic interactions

Rankin et al., 2006, Eslinger et al, 2011; Omar et al., 2011,
Sturm et al, 2006, 2008, 2011

Major fossil locales of *H. habilis/rudolfensis:*

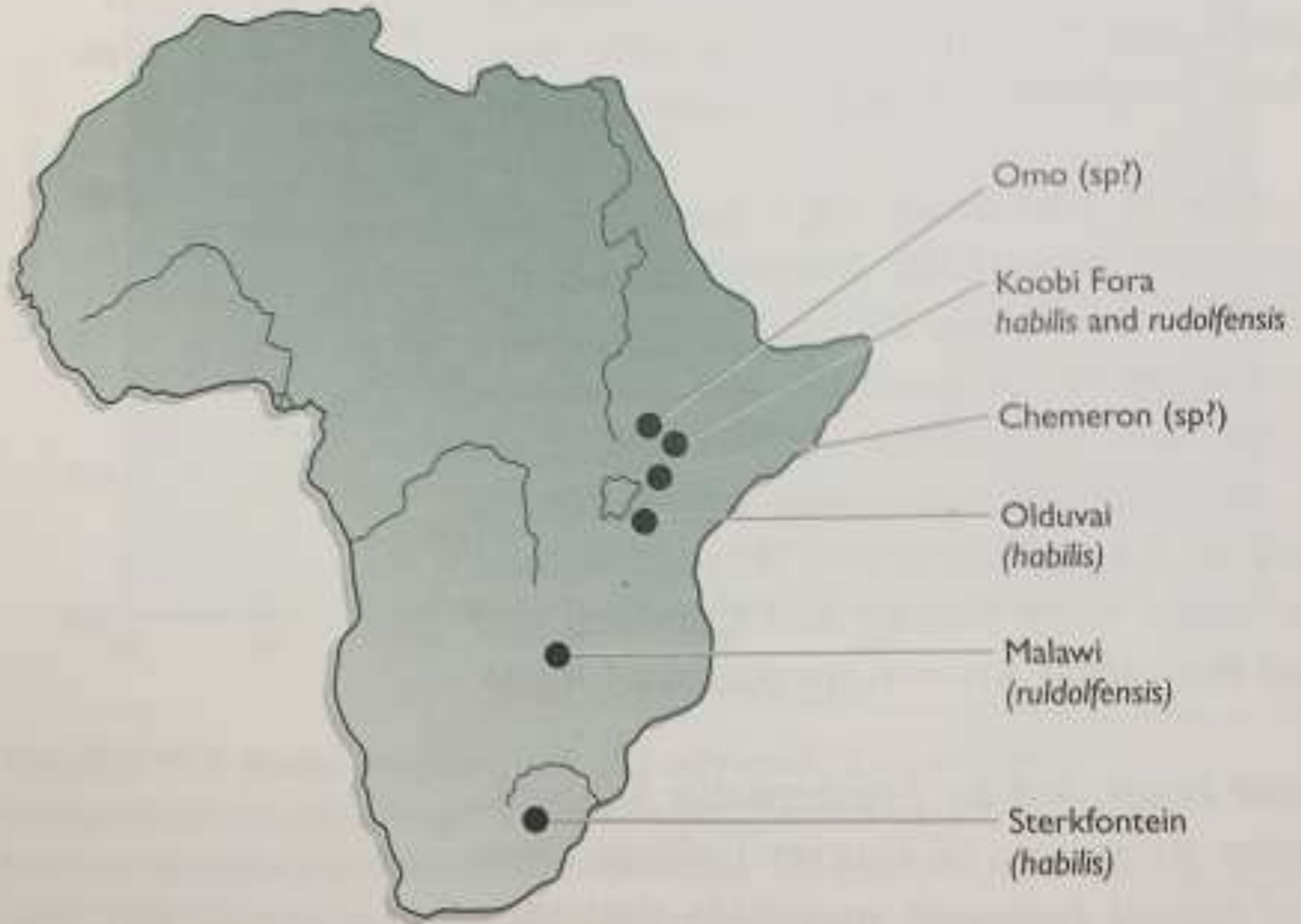


FIGURE 11.6 Sites of early *Homo* fossil finds: This shows sites in Africa with specimens that have been attributed to genera other than *Australopithecus* and which are Pliocene or very early Pleistocene.

African Oldowan Stone Tool Sites, 2.4 – 1.5 Ma

Site	Locality	Age (Ma)	Bones
Gona, Ethiopia	West Gona 1	2.4	Yes
Hadar, Ethiopia	AL 666 & AL 894	2.4-2.3	Yes
West Turkana, Kenya	Lokalelei 1	2.35	Yes
Omo, Ethiopia	Omo 57, Omo 123	2.4-2.3	Yes
Fejej, Ethiopia	FJ1	1.88	Yes
Melka Kunturé, Ethiopia	Gomboré IB and Karre I	1.7	Yes
Koobi Fora, Kenya,	FxJj 1,3, and 10	1.9	Yes
Kanjera South, Kenya	KSl, 2, and 3	2.2	Yes
Olduvai Gorge, Tanzania	FLK NN 1 (“Zinj”)	1.76	Yes
Nyabusosi, (Toro- Uganda), Uganda	NY 18	1.86 >1.5	Yes

R. Klein, 2009

Oldowan Sites 2

Site	Locality	Age (Ma)	Bones
Upper Semliki Valley, Congo	Senga 5a,	?2.3	Yes
Chiwondo Beds, Malawi	Mwimbi	?2.4-1.6	Yes
Sterkfontein Cave, S. Africa	Member 5	2-1.7	Yes
Swartkrans Cave, S. Africa	Members 1- 3	1.8-1.5	Yes
Chemoigut, Kenya	Gnji 1/5,1/6E,10/4,10/5	>1.42	Yes

Homo habilis

- Very few post-cranial fossils

- Assessing sexual dimorphism is extremely difficult for early *Homo:*
  - from the small number of fossils in each group
  - the disagreement about taxonomic assignments

- Sexual dimorphism (male-female body size difference) is uncertain because most post-cranial remains have
  - not been attributed to a particular species
  - or to being male or female

- The smaller Dmanisi, Georgia specimens were so similar to *H. habilis* that they were initially put into *H. habilis;* eventually designated as *H. erectus.* Dmanisi revolutionized concept of *erectus.*

Origins of *Homo:* Sexual dimorphism

- Ideally, we should identify males and females independent of overall body size, such as through canine size and robusticity.
- The ER 1813 group is the only one in which it is possible to try to assess sexual dimorphism in this way (canines), but such characters are few.
- Complicating issues of sexual assignment:
  - possibility of misidentifying of large females and small males
  - Inadequate, non-representative, sampling of the fossil record.

Origins of *Homo:* Sexual dimorphism

- For the postcranial skeleton, if the small OH 62 skeleton is female and the larger KNM-ER 3735 is male, then if they are typical of their sexes, sexual dimorphism in body mass could be as much as 1.5 (male/female weight dimorphism as compared with chimpanzees at about 1.3 and *H. sapiens* about 1.1).
- These values are lower than those for early African and Georgian *H. erectus*, particularly for cranial capacity.
- If we take instead all the early non-*erectus Homo*, regardless of group affiliation, the cranial CVs are still lower than those for *H. erectus*, but their body mass CVs are significantly greater.

Homo habilis: similar to Australopiths

- There is little to distinguish *H. habilis* from the australopiths.
  - When relating size of jaw and teeth to estimates of body size, *H. habilis* is more similar to the australopiths than to later *Homo*.
  - Postcranial skeleton of *H. habilis* differs very little from *Australopithecus* and *Paranthropus*. Limb proportions indistinguishable from *A. afarensis*
  - Hand bones found at Olduvai suggest *H. habilis* was capable of manual dexterity involved in manufacture and use of stone tools, but this is also true of hand bones of *A. afarensis* and *P. robustus*.

Homo habilis was right-handed based on right oblique teeth marks

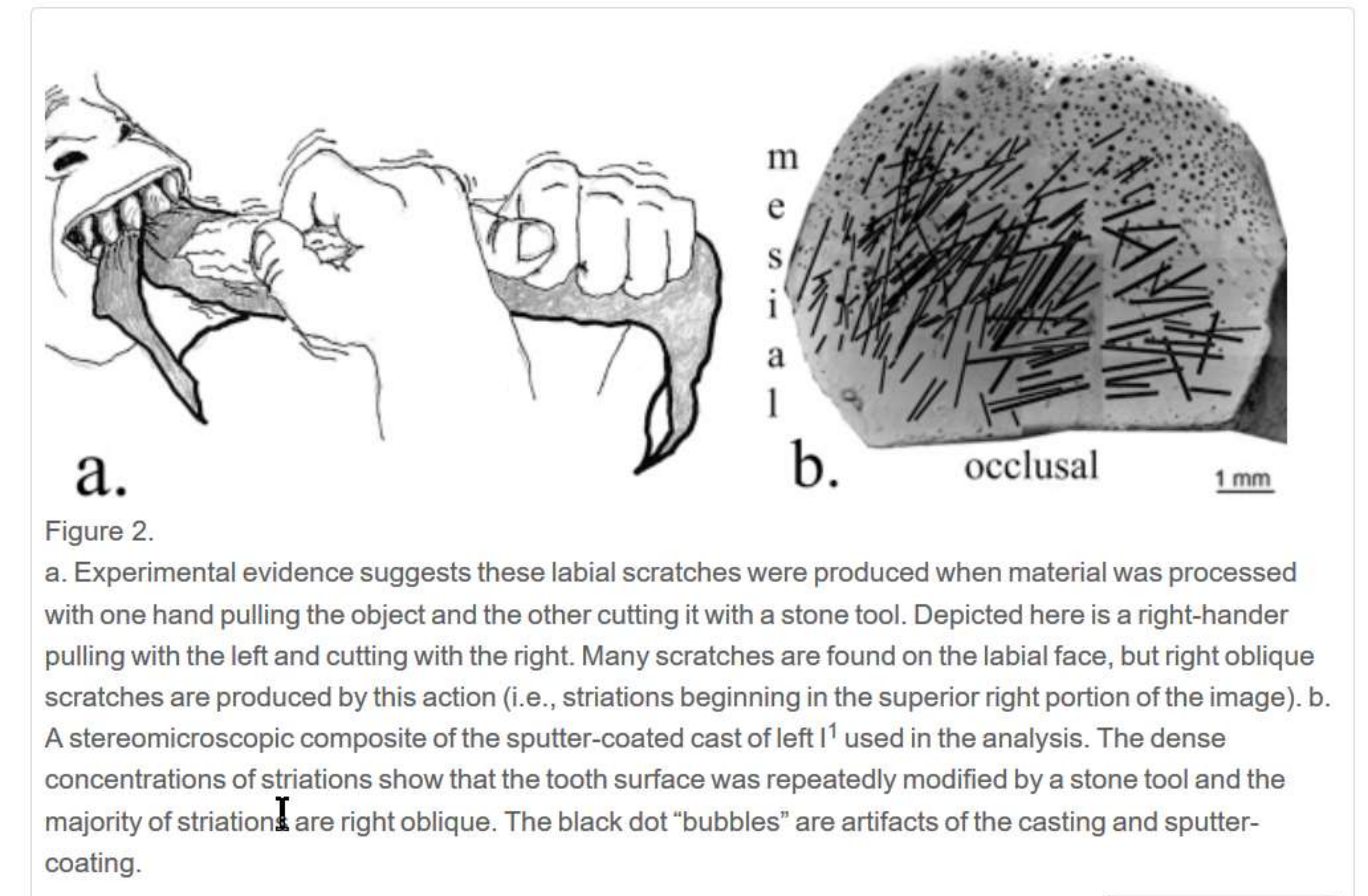


Figure 2.

a. Experimental evidence suggests these labial scratches were produced when material was processed with one hand pulling the object and the other cutting it with a stone tool. Depicted here is a right-hander pulling with the left and cutting with the right. Many scratches are found on the labial face, but right oblique scratches are produced by this action (i.e., striations beginning in the superior right portion of the image). b. A stereomicroscopic composite of the sputter-coated cast of left I^1 used in the analysis. The dense concentrations of striations show that the tooth surface was repeatedly modified by a stone tool and the majority of striations are right oblique. The black dot “bubbles” are artifacts of the casting and sputter-coating.

O

1.8 M; found 1995

D. Frayer, et al., 2016

Early Homo was right-handed based also on stone tool evidence

- Knappers usually holds hammerstone in dominant hand and core in nondominant hand. Right hand to strike flakes from pebble held in left hand.
- First flakes bear cortex (weathering outer rind) whose position tends to reflect which hand held the hammerstone. Right sided flakes (strike scare on left & cortex on right) produced by right handers.
- Right-handed knappers produce 56 flakes with cortex on right side for every 44 with cortex on left; left hander, the opposite ratio.
- Oldowan stones from Koobi For a have ratio of 57 right to 43 left, implying right handers made them
- Right handedness correlates with brain lateralization; developed by 2-1.5 Ma

H. habilis skull features, relative to *A. africanus*

- Larger endocranial volume (range 510-750 cc, with a mean of 630 cc); with little increase in mean body size;
- Brain case had become fuller and more rounded due to expansion of the brain, with less body size increase; more human cortical sulcal pattern (Broca's area); question of brain reorganization
- Beginnings of a slight forehead were appearing; Expanded frontal and esp. parietal region
- More rounded occipital contour
- Face had a small, arched brow ridge, which was smaller and shorter than those of earlier ancestors
- More anterior (located in the center of the skull base) foramen magnum, indicating bipedality

Features of *H. habilis*

- Less facial projection (reduced prognathism - less forward projecting jaws)
- Less postorbital constriction (gutter between supraorbital torus & frontal bone)
- A broad and short cranial base. Cranial bone is thick.
- Less convex and bulging zygomatics, and more vertically oriented.

Homo: reduction in postcanine dental size

- Jaw and dentition are less massive: Absence of postcanine megadontia. Postcanine dental reduction is characteristic of *Homo*
- Large front teeth relative to the postcanines. Some incisors are getting broader. Teeth tucked under face
- Thinner enamel; elongated premolars; although the incisors were still relatively large; = dietary change
- More parabolic (rounded) dental arcade
- Premolars especially are smaller
- Dental reduction reflects an ecological change in terms of the diet of early Homo-- smaller teeth because presumably, they don't need the large kind of chewing teeth

Diagnostic traits of *Homo habilis* (Wood, 1992)

- 1 - Traits distinguishing this species (and all other hominins') from *Ardipithecus, Australopithecus,* and *Paranthropus:*
- increased cranial vault thickness
- reduced postorbital constriction (same degree seen in *A. garhi)*
- increased contribution of the occipital bone to cranial sagittal arc length
- increased cranial vault height
- more anteriorly situated foramen magnum
- reduced lower face prognathism
- narrow tooth crowns, particular in the lower premolars
- reduced molar toothrow length

Diagnostic traits of *Homo habilis* (Wood, 1992)

2) Traits distinguishing this species from *Homo rudolfensis:*

- smaller mean brain size
- greater occipital contribution to the sagittal arc
- complex suture pattern of skull
- incipient supraorbital torus
- upper face exceeds midface in breadth
- nasal margins sharp and everted
- zygomatic surface vertical or nearly so

Diagnostic traits of *Homo habilis* (Wood, 1992)

- palate foreshortened
- relatively deep mandibular fossa
- rounded base on body of mandible
- lower premolars and molars show more buccolingual narrowing
- reduced talonid on P_4
- lower premolars mostly single-rooted

- 3) Traits distinguishing this species from *Homo erectus* and all later hominins:
- elongated anterior basicranium
- mesiodistally elongated and M_2
- narrow mandibular fossa

Distinguishing morphological features of *Homo habilis*

- *Cranial and mandibular*
  - Maxilla and mandible smaller than in *Australopithecus* but equivalent in size to *H. erectus* and *H. sapiens*
  - Brain size greater than *Australopithecus* but smaller than *H. erectus* Slight to strong muscular markings
  - Parietal bone curvature in the sagittal plane varying from slight (i.e., homine) to moderate (i.e., australopithecine)
  - Relatively open-angled external sagittal curvature to occipital
  - Retreating chin, with a slight or absent mental trigone

Distinguishing morphological features of *Homo habilis*

- *Dental*
  - Incisors large with respect to those of *Australopithecus* and *H erectus*
  - Molar size overlaps the ranges for *Australopithecus* and *H. erectus* Canines large relative to premolars
  - Premolars narrower than in *Australopithecus* and within the range of *H. erectus*
  - *All* teeth relatively narrow buccolingually and elongated mesiodistally, especially the mandibular molars and premolars

Distinguishing morphological features of *Homo habilis*

- Postcranial: mosaic
  - Clavicle resembles that of *H. sapiens*
  - Hand bones have broad terminal phalanges and capitate and metacarpophalangeal articulations resembling those of *H. sapiens,* but differ with respect to the scaphoid and trapezium, attachments of the superficial flexor tendons, and the robusticity and curvature of the phalanges
  - Foot bones resemble those of H. sapiens in the stout and adducted big toe and well-marked foot arches, but differ in the shape of the trochlear surface of the talus and the relatively robust third metatarsal
  - Bipedal & capable of powerful grasping

- From Leakey et al. (1964).

H. habilis features

- Limbs
- features of the leg and foot bones indicate that this species walked on two legs.
- legs were relatively short, providing this species with arm and leg proportions that were relatively ape-like and similar to those of the australopithecines.
- finger bones are slightly curved and intermediate in shape between the curved finger bones of quadrupedal apes and the straight finger bones of modern humans
- finger bone proportions suggest the human-like ability to form a precision grip

Homo habilis: Foot

- OH 8 – a fairly complete foot – was found near OH 7; was initially determined to be from another individual. This was due to the fact that OH 7 was known to be from an adolescent around age 12, and the foot seemed to be of a more advanced age, due to the presence of arthritis in the specimen.
- However, the partially gnawed remains have arthritis due to a sustained injury, and the actual age runs close to OH 7, making it likely they are from the same individual (many researchers consider this part of OH 7 now, rather than OH 8).
- The remains show clear signs that this was an obligate biped, including:
  - Presence of digital shortening.
  - Enlargement of the hallux, as well as being fully abducted.
  - Alignment of digits 2–5.
  - Thickened metatarsal shaft with a humanlike cross-sectional shape.
  - A fully developed double arch to the lower surface.
  - Mechanically set up for efficient weight transmission at the ankle.

Homo habilis

- While it shows definite obligate bipedalism, the specimen also has a marked tubercule for the tibialis posterior muscle, an invertor of the foot that could be useful for climbing.
- So it is possible that while this individual was an obligate biped, it still spent some time in the trees

- From the talus, H. McHenry calculated an estimated weight of 31.7 kg. Using the various estimated brain size, one gets brain/body weight ratios of:

Brain size

- **Wolpoff: 590 cc brain = 1.86%**
- **Tobias: 647 cc brain = 2.04%**
- **Holloway: 710 cc brain = 2.24%**

- Even using the smaller brain estimate, this is one of the largest relative brain size for any male hominin up to the time period this individual lived (1.75 Ma).

- When compared to primate allometry, the OH 7 brain size is at the top of the allometric expectations within non-human primates. This is a large brained specimen relative to its body size.

Cranial capacity

- *H. habilis* brain size has been shown to range from 550 to 687 cc, rather than from 363 cubic centimeters (22.2 cu in) to 600 cubic centimeters (37 cu in) as previously thought.
- A virtual reconstruction published in 2015 estimated the endocranial volume at between 729 milliliters (25.7 imp fl oz; 24.7 US fl oz) and 824 milliliters (29.0 imp fl oz; 27.9 US fl oz), larger than any previously published value. *H. habilis'* brain capacity of around 640 cm^3 (39 cub. in.) was on average 50% larger than australopithecines,
- These hominins were smaller than modern humans, on average standing no more than 1.3 meters (4 ft 3 in).
- The body proportions for *H. habilis* are in accordance with craniodental evidence, suggesting closer association with *H. erectus*.

Postcranial features of *H. habilis*

- Postcranial skeleton of *H. habilis* is poorly known.
- A few foot bones: Foot bones resemble those of MHs in the stout and adducted big toe and well-marked foot arches
- Long arms, short legs (OH 62): if accurate, suggest body plan combining long humanlike legs with long australopith-like arms persisted for at least 600 K after *Homo* emerged.
- OH 7 hand bones include robust, curved proximal and middle phalanges that imply apelike ability to hang below branches; apelike climbing ability persisted until *H. ergaster* emerged.

Body Size

- Body size cannot be compared between the groups because only the 1813 group has associated postcranial remains (i.e., OH 62 on maxillary form).
- Collectively, these remains suggest that the largest end of the early *Homo* body size range is just under 5 ft. tall (150 cm), and the average weight is 97 lbs (44 kg (range 31–65))

Origins of *Homo: OH62 was a climber*

- The OH 62 humerus is relatively stronger compared with its femur than is true of recent humans and is like those of *Pan.*

- Thus, OH 62 participated in substantial arboreal locomotion as well as terrestrial (bipedal) locomotion. Arm strength proportions appear to link OH 62 with *Australopithecus*

- Long legs and efficient bipedal locomotion were in place well before the origin of the genus *Homo*; hind-limb length proportions do not actually differ between *Australopithecus* and early *Homo*.

Evolution of early *Homo:* Locomotion

- Locomotor efficiency:
  - large-bodied finds of *Australopithecus*
  - and small-bodied *Homo*
  - show no difference in hind limb proportions or inferred bipedal efficiency;
  - this is because locomotor efficiency in walking and running is a function of leg length, which is allometrically related to body size

Early *Homo:* Locomotion

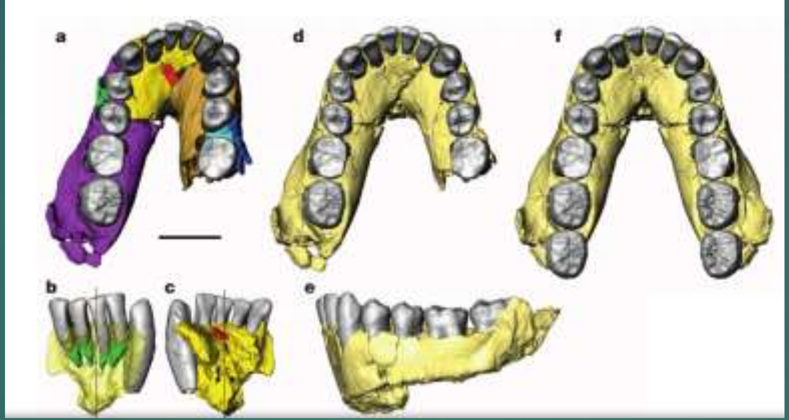
- Similarly, the *A. afarensis* foot possessed close packed arches, another sign of bipedal adequacy. Although there may have been multiple modes of bipedality among the early hominins, long legs and efficient bipedal locomotion were in place well before the origin of the genus *Homo* and cannot necessarily be used to distinguish among genera or species.
- Regardless of the taxonomy of early *Homo* or morphological differences between species, recent fossil finds and new analytical techniques suggest that all early *Homo* differ from Australopithecus in having larger average body and brain sizes.
- Given these observations, what is the evidence for distinct morphological groups in the fossil record of *Homo* before and contemporaneous with *H. erectus*? speculative.

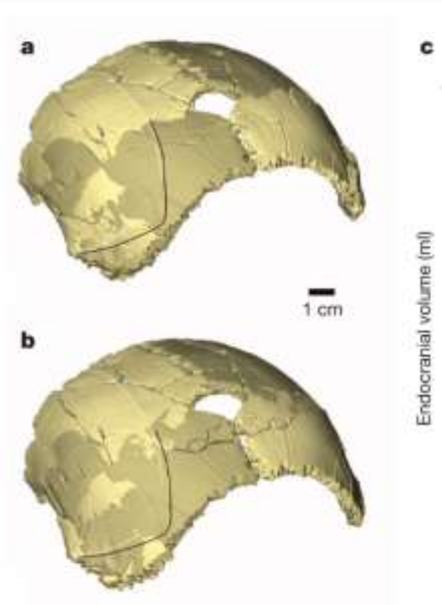
Homo: Brain size increases

- Increased brain size is the most critical trait in identifying members of the early members of the genus *Homo*.
- Ave. brain size of Australopithicines: <500 cc
- Ave. brain size of *Homo (habilis & rudolfensis*) by 2 Ma: 770 cc
- At lower end, overlaps with higher brain sized australopiths
- Partially due to increase in body size
- Movement toward larger relative brain size in *Homo*
- Also increase in brain reorganization (see endocasts)

2015 Digital reconstruction of *Homo habilis*, OH 7, 1.8 Ma

Cranial size of 729-824 cc





Mandible is remarkably primitive; more similar to *A. afarensis* than to parabolic jaw of *Homo erectus*

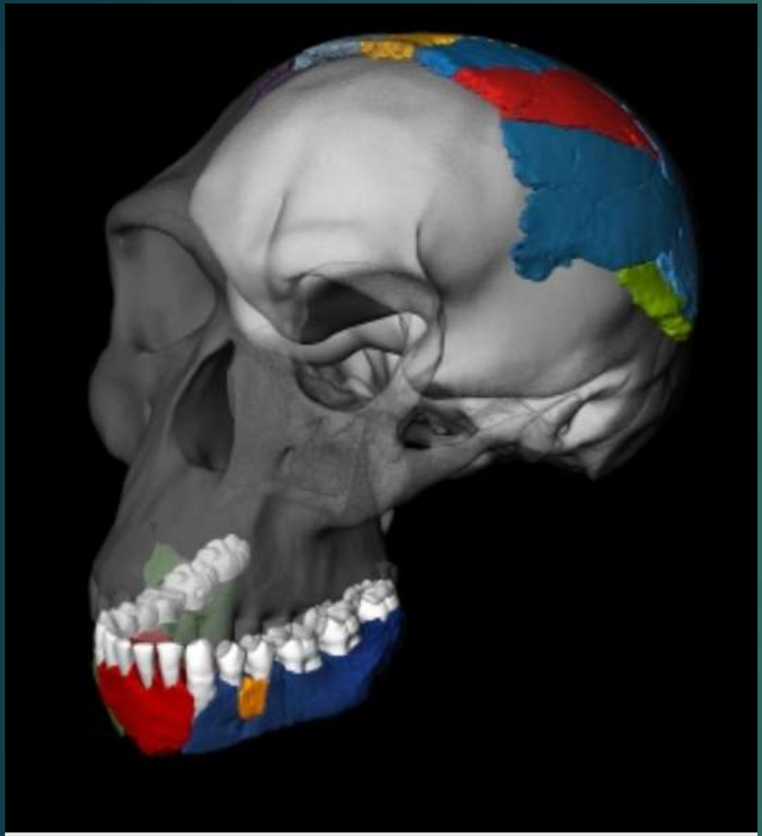
Jaw is not consistent with any single species of early *Homo, including Homo rudolfensis;* implies origin of *Homo* species before 2.3 Ma;

Parietal lobe reconstruction implies endocranial volume of 729-824 cc;

Homo habilis, Homo rudolfensis, and early Homo erectus cannot be distinguished by their brain size, in contrast to their major differences in facial morphology

F. Spoor, et al., 2015

2015: Jaws, Not Brains, Define Early Human Species



Philipp Gunz, Simon Neubauer and Fred Spoor

The reconstructed Homo habilis skull based on bones from Olduvai Gorge, Tanzania.

Fred Spoor: Reconstructing the original H. habilis pieces revealed that the jaw was more primitive-looking . It was long and thin, and the rows of teeth on opposite sides were nearly parallel — more like an *Australopithecus*'s jaw than a human's rounder one.

A reconstruction of the skull bones revealed that the brain was larger than expected, similar in size to that of *H. erectus*.

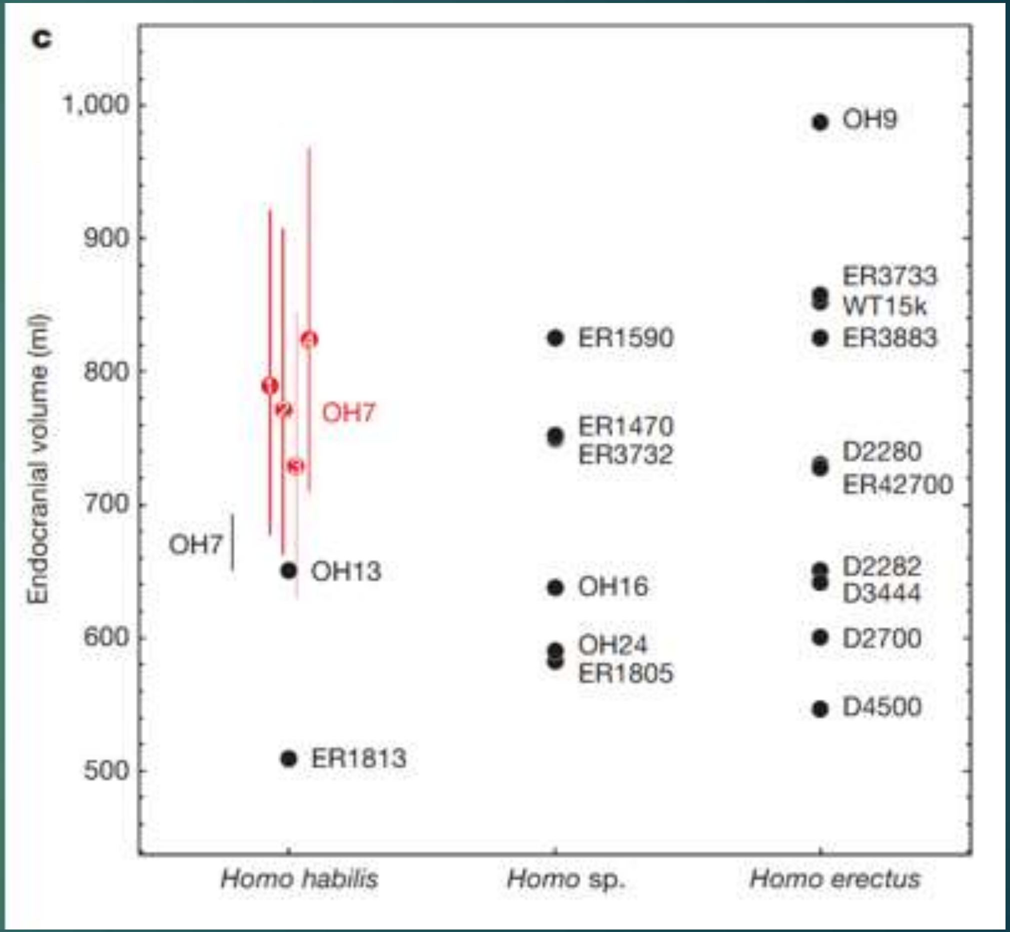
Previously discovered upper-jaw fossils classed as *H. habilis*, and dating back as far as 2.3 million years ago, look too different from the newly reconstructed jaw to belong to the same species

This suggests that the species that predated *H. erectus* were a diverse bunch.

Lieberman: 'Early *Homo*' species showed lots of variation, yet none stands out as an obvious ancestor of *H. erectus*.

One theory: It was face protrusion, not brain capacity, that differentiated very early *Homo*

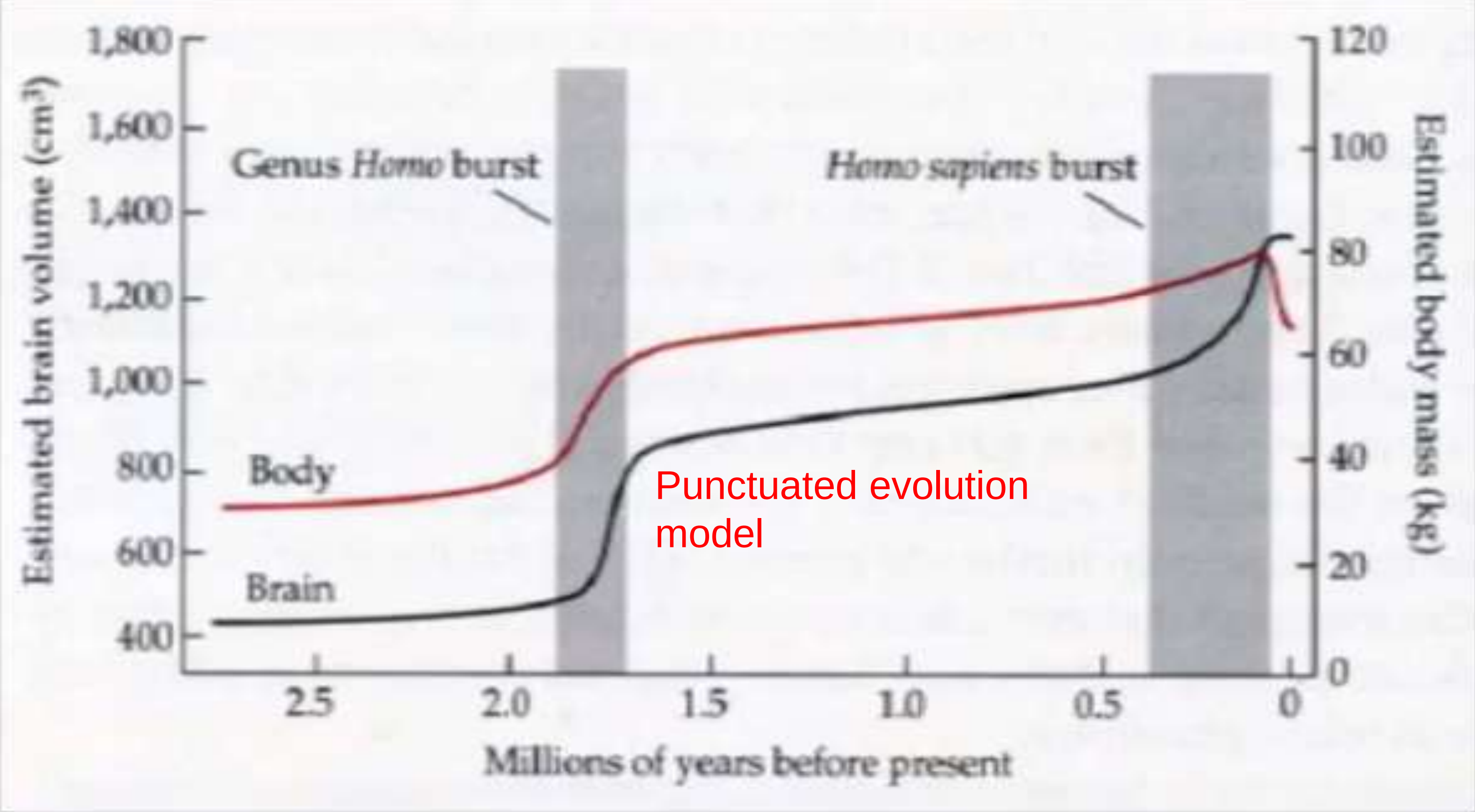
- Implication that cranial capacity of *Homo habilis, Homo rudolfensis, and Homo erectus*, who were alive between 2.1 and 1.5 Ma, were all within the range of 500-900 cc.
- Early *Homo* characterized more by facial morphology (gnathic diversity) than by cranial size difference.



Function-related studies since 1999

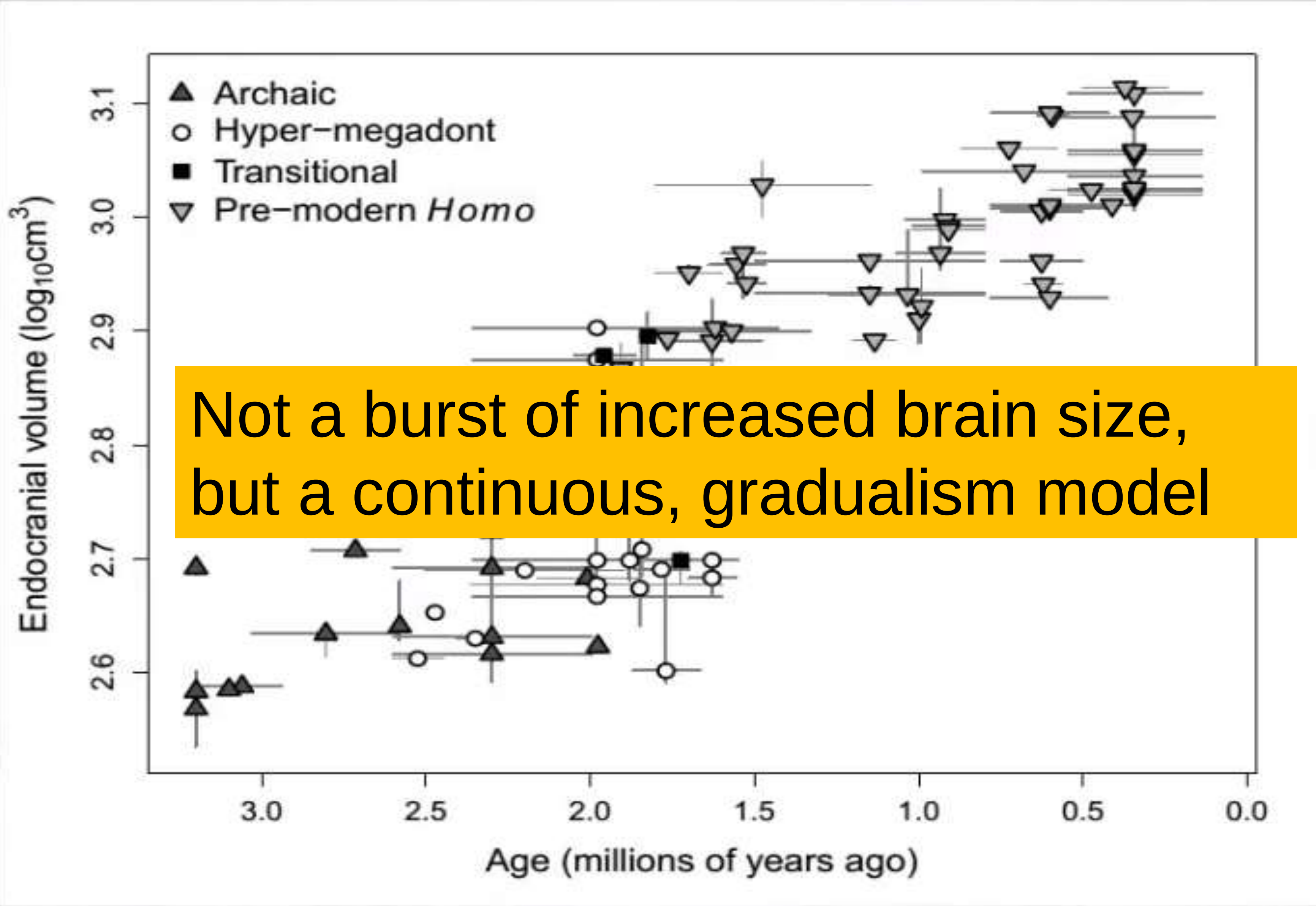
- Body size and shape - Richmond *et al.* 2002 (but see Haeusler and McHenry 2004, 2007)
- Locomotion – Locomotion both arboreally & on land Gebo and Schwartz, 2006; Larson 2007; Ruff 2009
- Cognition - Du *et al.* 2018
- Dexterity - Tocheri *et al.* 2007
- Diet - McHenry & Coffing 2000; Ungar *et al.* 2006, 2011; Ungar and Sponheimer 2012; Cerling *et al.* 2013; Sponheimer *etal.* 2013; Patterson *et al.* in preparation
- Life history - Dean 2001

Nature of Brain size increase, starting at 1.8 Ma



Punctuated evolution model

Striedter (2005)



Not a burst of increased brain size, but a continuous, gradualism model

Du *et al*. 2018

Behavior

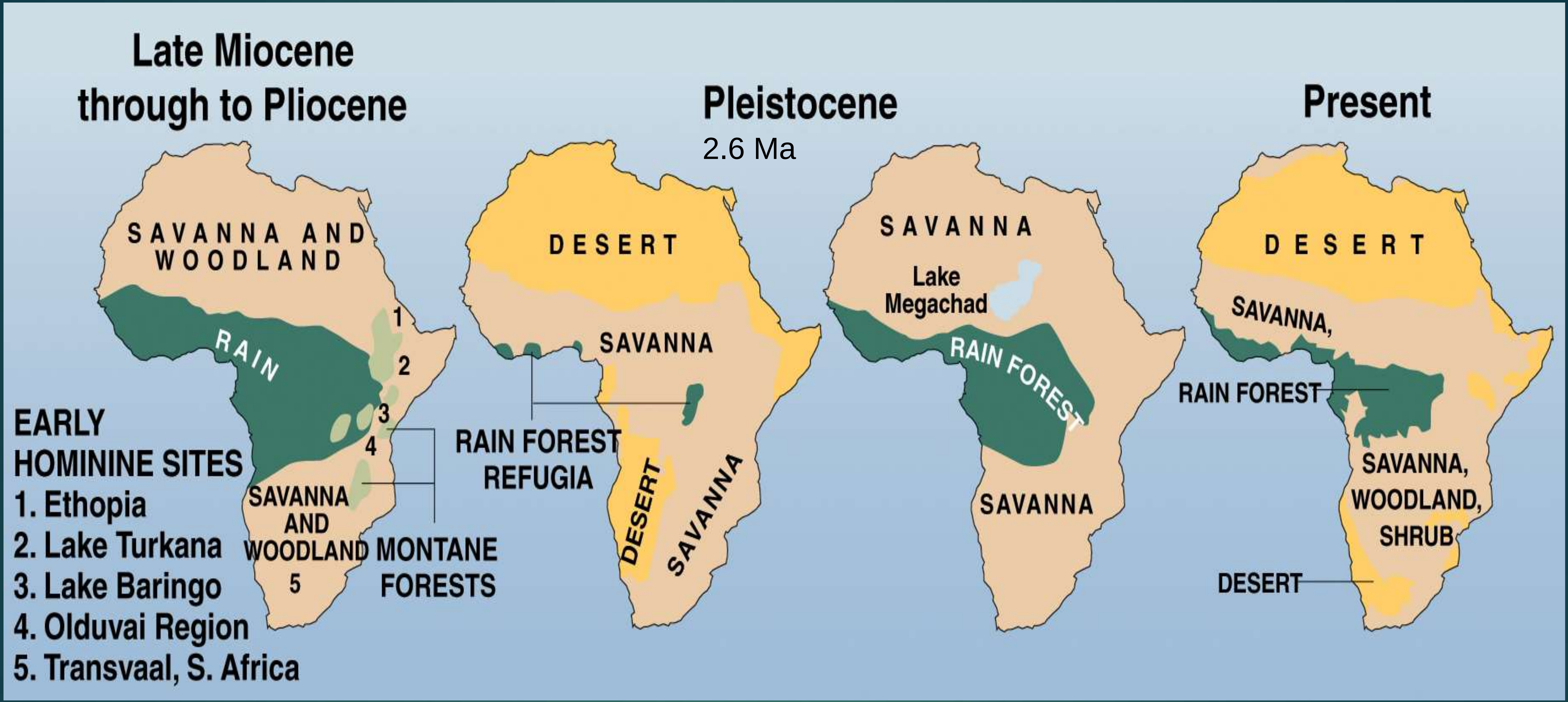
- Tool use: *Homo habilis* is thought to have mastered the Lower Paleolithic Oldowan tool set, which used stone flakes. *H. habilis* used these stones to butcher and skin animals. These stone flakes were more advanced than any tools previously used, and gave *H. habilis* the edge it needed to prosper in hostile environments previously too formidable for primates. Whether *H. habilis* was the first hominin to master stone tool technology remains controversial, as *Australopithecus garhi*, dated to 2.6 million years ago, has been found along with stone tool implements.
- Co-existence: *Homo habilis* coexisted with other *Homo*-like bipedal primates, such as *Paranthropus boisei*, some of which prospered for many millennia. However, *H. habilis*, possibly because of its early tool innovation and a less specialized diet, became the precursor of an entire line of new species, whereas *Paranthropus boisei* and its robust relatives disappeared from the fossil record. *H. habilis* may also have coexisted with *H. erectus* in Africa for a period of 500,000 years.

Homo habilis

- *Homo habilis* is the oldest hominin assigned to the genus *Homo*, and perhaps the least similar to extant humans (*Homo sapiens*).
- *Homo habilis* may be:
    - a direct human ancestor (only some accept this hypothesis),
    - a dead-end side-branch that led nowhere
    - or even an invalid species whose designated examples belong in other species.
- But its facial structure and small teeth, large cranial capacity, and the precision of its grip, have convinced most paleoanthropologists that *habilis* should be placed in *Homo*

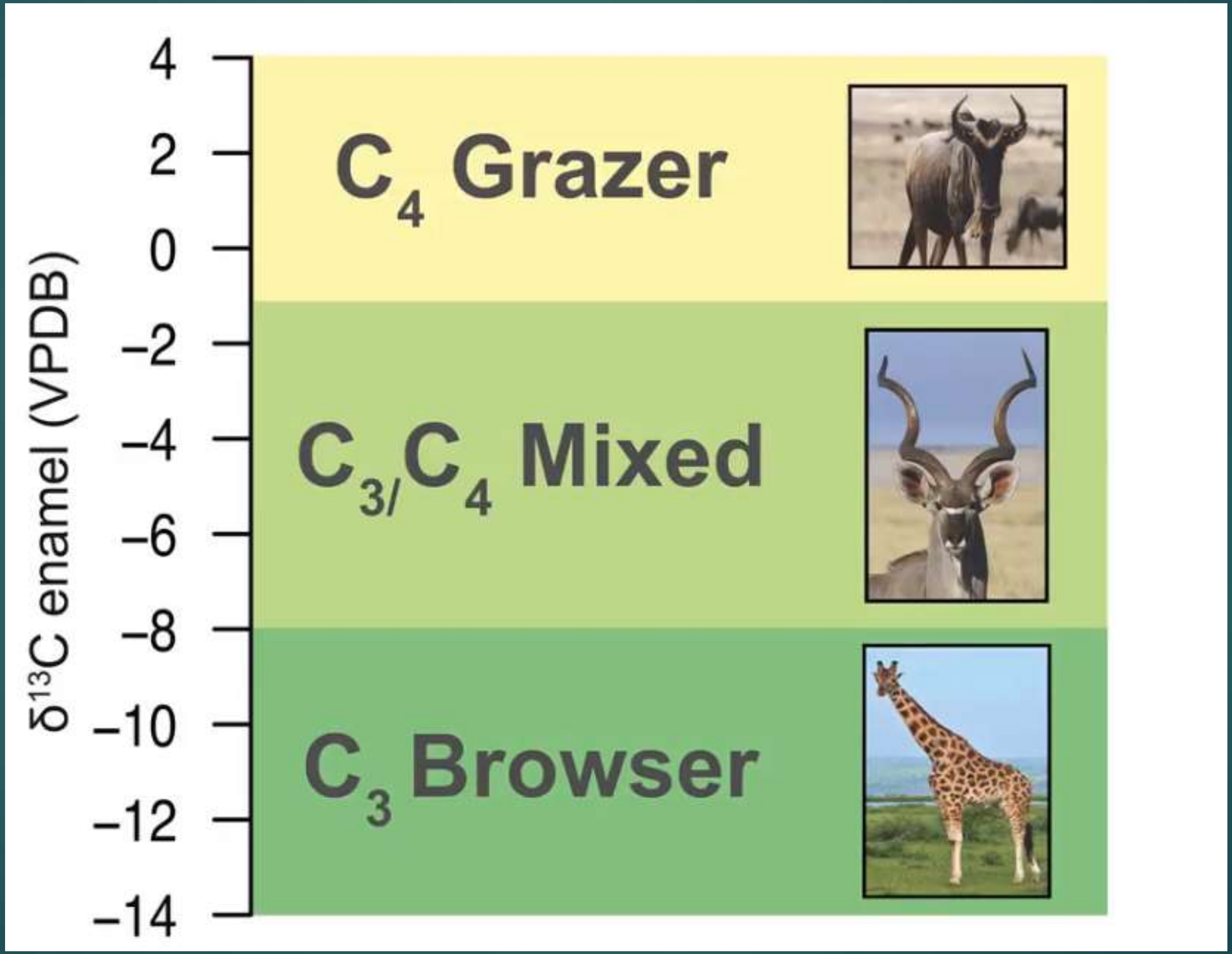
Behavioral changes: Diet

- Now, we realize that some of the key behavioral changes that can be associated with the beginnings of *Homo* were dietary.
- Ecological changes in E. Africa: In many parts of Africa change from closed to open habitats occurred gradually from about 4 Ma on, when there was a major increase in arid and grazing adapted mammals.
- By 2.5 Ma the environment had become increasingly arid, seasonal, and in many places C4-dominated as the rain belt contracted toward the equator in response to increasing ice volume at high latitudes.



- Dietary adaptation to an environment changing from forests to grasslands, 3-2 mya

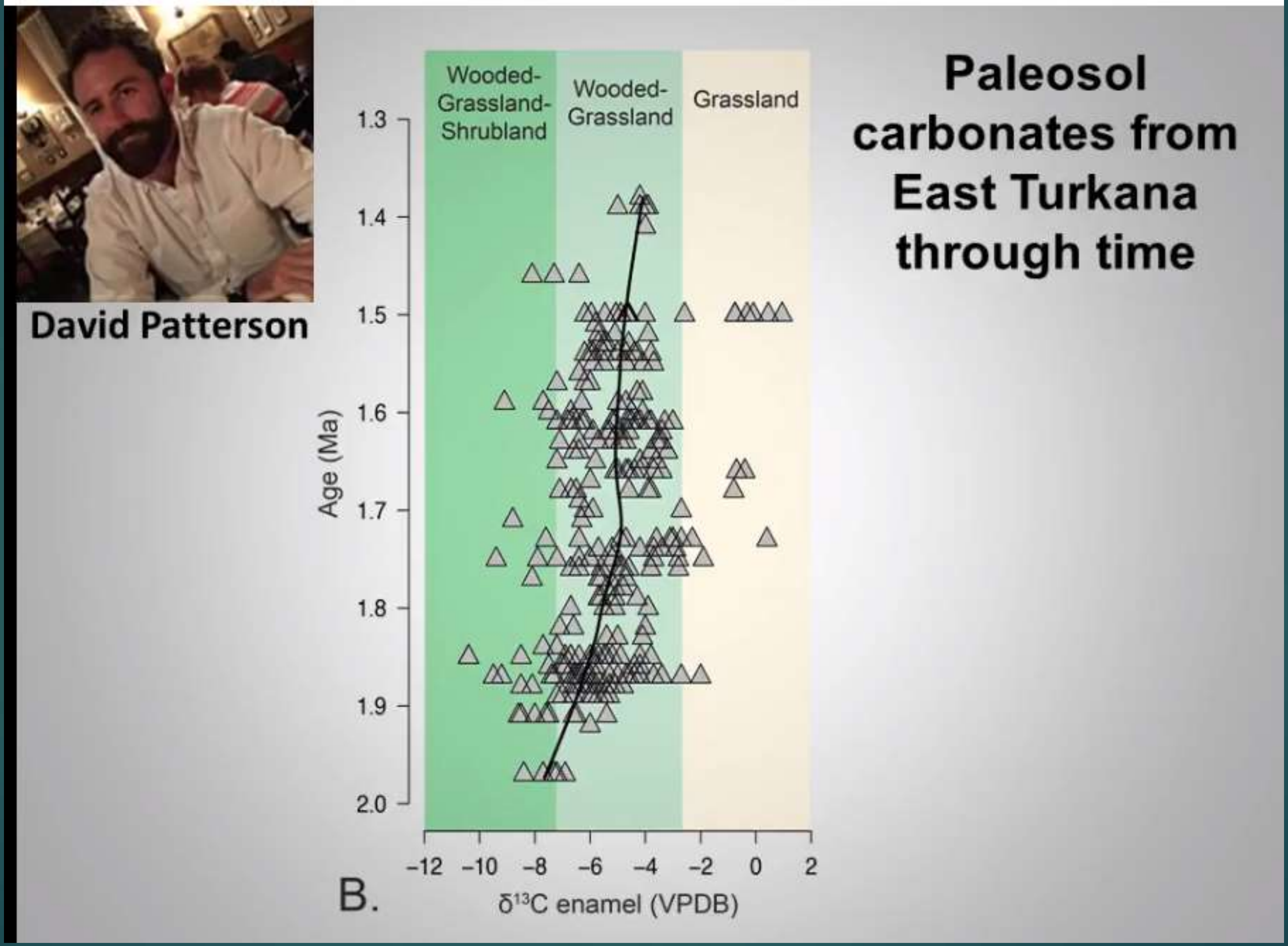
Stable Carbon Isotopes in soil



Grass

Tree, shrub leaves

C3, C4 in soil: not much change in soil, 2-1.3 Ma



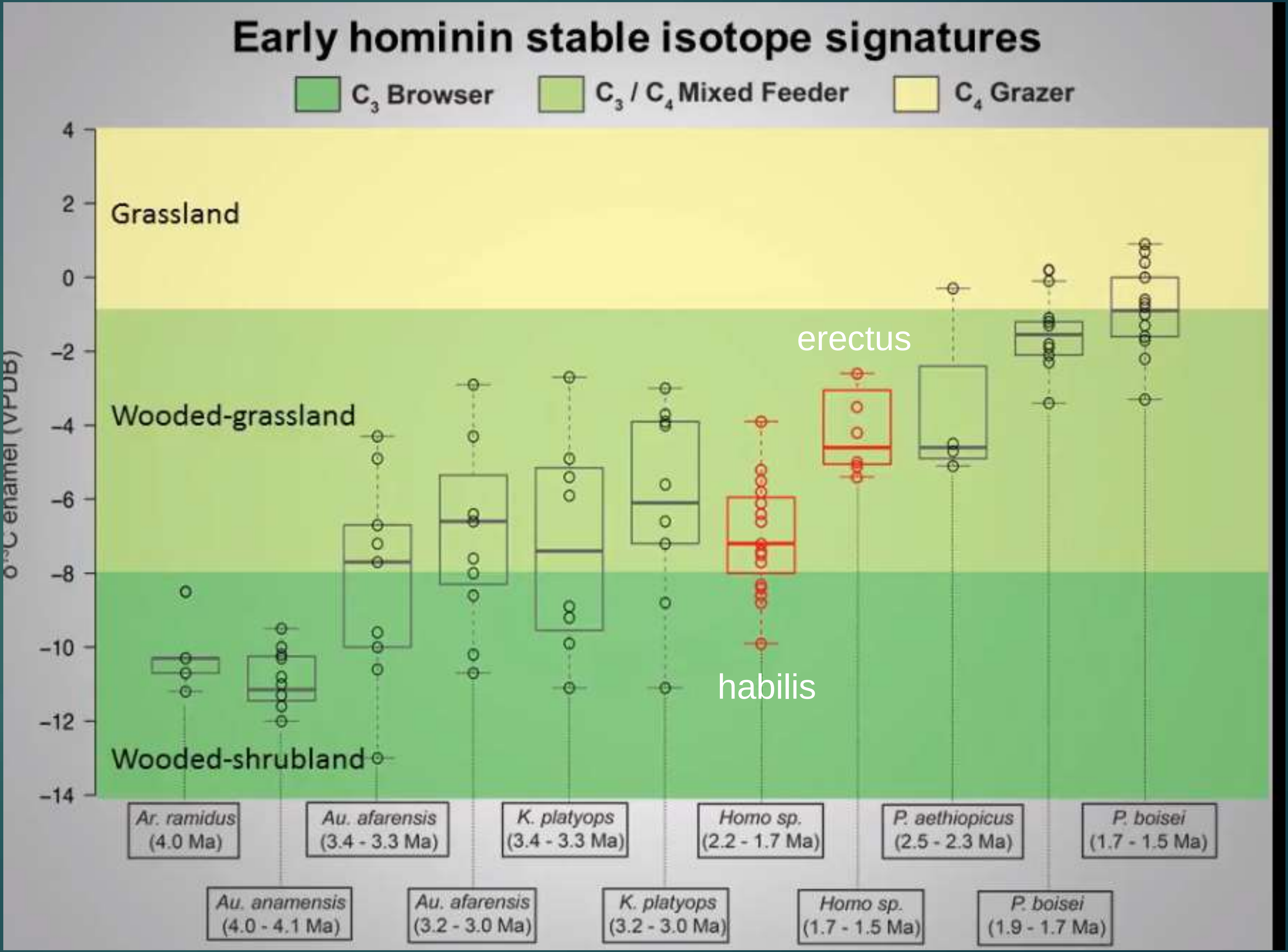
David Patterson

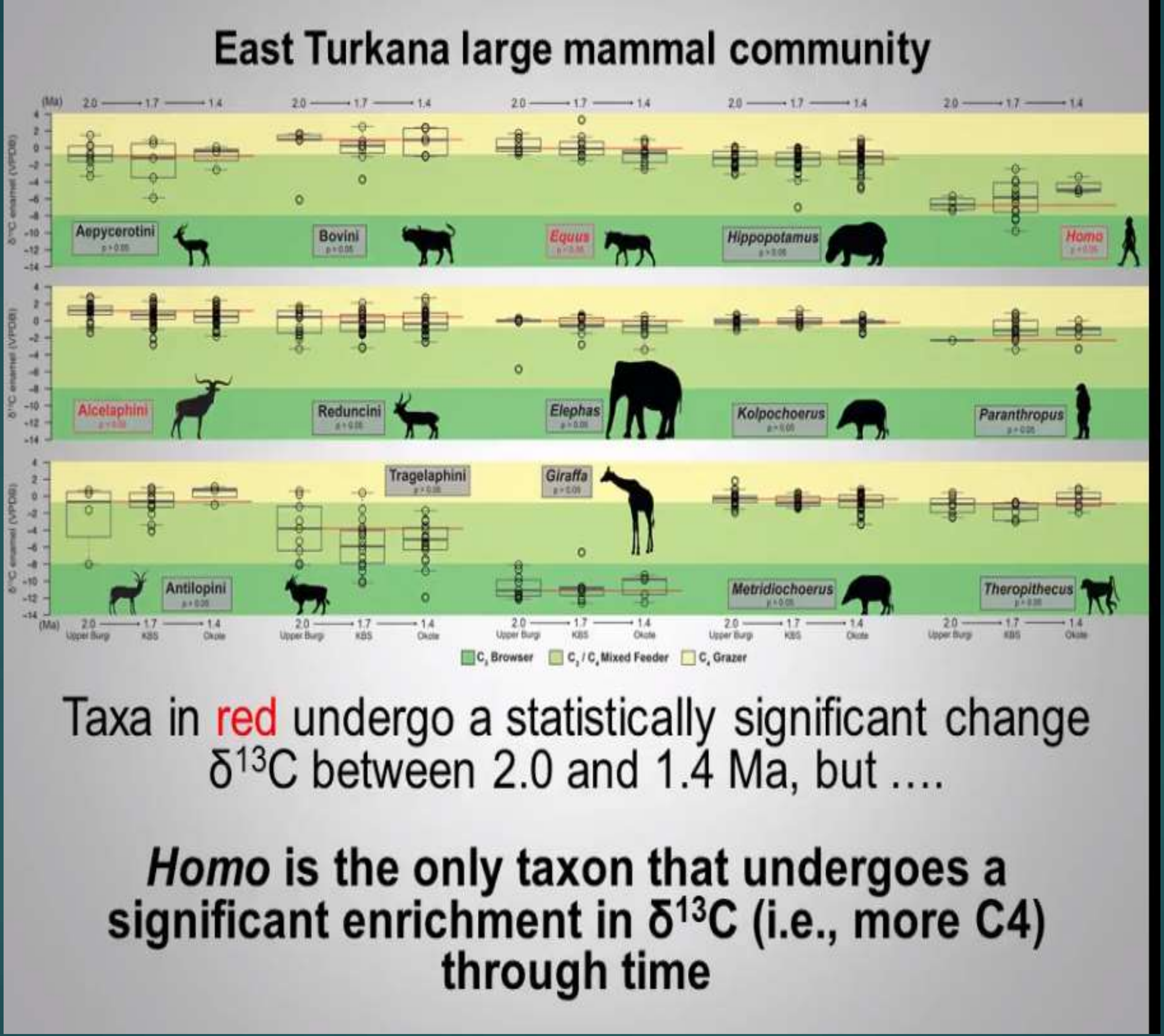
Paleosol carbonates from East Turkana through time

P. boisei =
C4 grazer

H. habilis =
Mixed, but closer to C3 Australopiths

H. erectus =
Mixed, but closer to C4 groups; eating animals that were eating grass; you are what you eat





East Turkana large mammal community

Taxa in red undergo a statistically significant change $\delta^{13}C$ between 2.0 and 1.4 Ma, but ….

***Homo* is the only taxon that undergoes a significant enrichment in $\delta^{13}C$ (i.e., more C4) through time**

C3

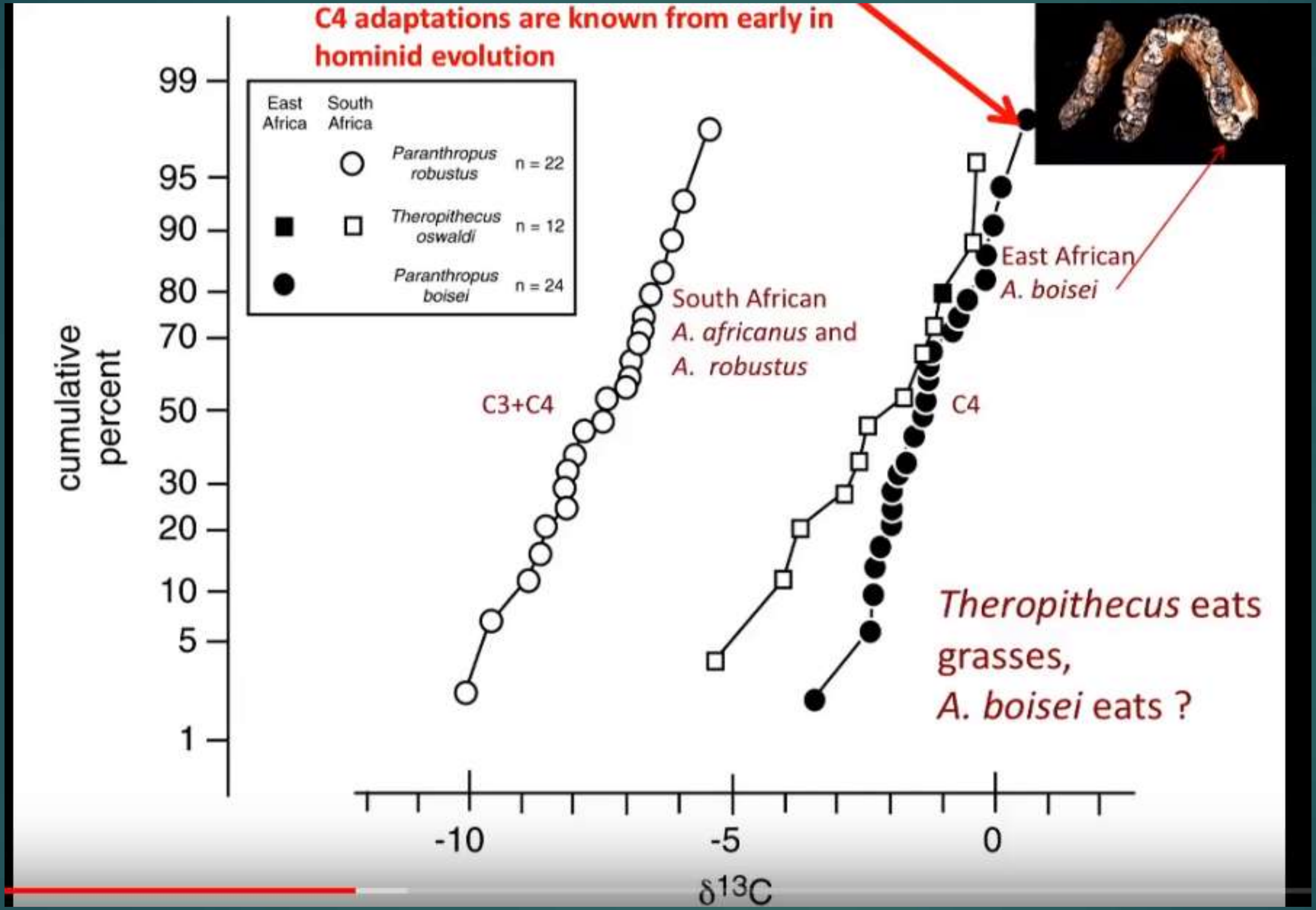
C4

All the rest stayed same or became more C3

Diet

- *Homo habilis* lived in a predominantly grassland environment.
- The climate was becoming cooler and drier and this may have been the impetus for new feeding strategies that included scavenging and tool use.
- Chemical analysis suggests that this species was mainly vegetarian but did include some meat in their diet.
- Based on dental microwear-texture analysis, *Homo habilis* (as well as other early *Homo*-class hominins) likely did not specialize on particularly tough foods.
- These measurements point to an increasingly generalized, and generally omnivorous diet in *Homo habilis*.

Dietary changes



Extinct baboon

P. boisei is a C4 eater! We are still C4 eaters (corn flakes) & meat from C4 eaters

Expensive tissue hypothesis: small teeth, big brain, small gut, better food

- Leslie Aiello’s hypothesis: if you look across mammals, the overall rate of energy production and consumption-- the basal metabolic rate-- is proportional to the overall size of the organism.
- Different body tissues use different energy amounts
- Brain is a very expensive tissue, having 2% of body mass, but using 20% of heart output
- Reduced teeth imply higher quality food

Aiello, L. C., & Wheeler, P. 1995

Expensive tissue hypothesis

- Larger brain involves a tradeoff between
  - size of brain vs.
  - size of gut

- Gut is an expensive tissue; reduced size of gut in exchange for bigger brain;
  - Gorillas have big belly because of longer guts to process low quality food;

- Higher quality food produced
  - higher metabolism
  - bigger brain
  - smaller gut
  - smaller teeth
  - = expensive tissue hypothesis

Homo habilis

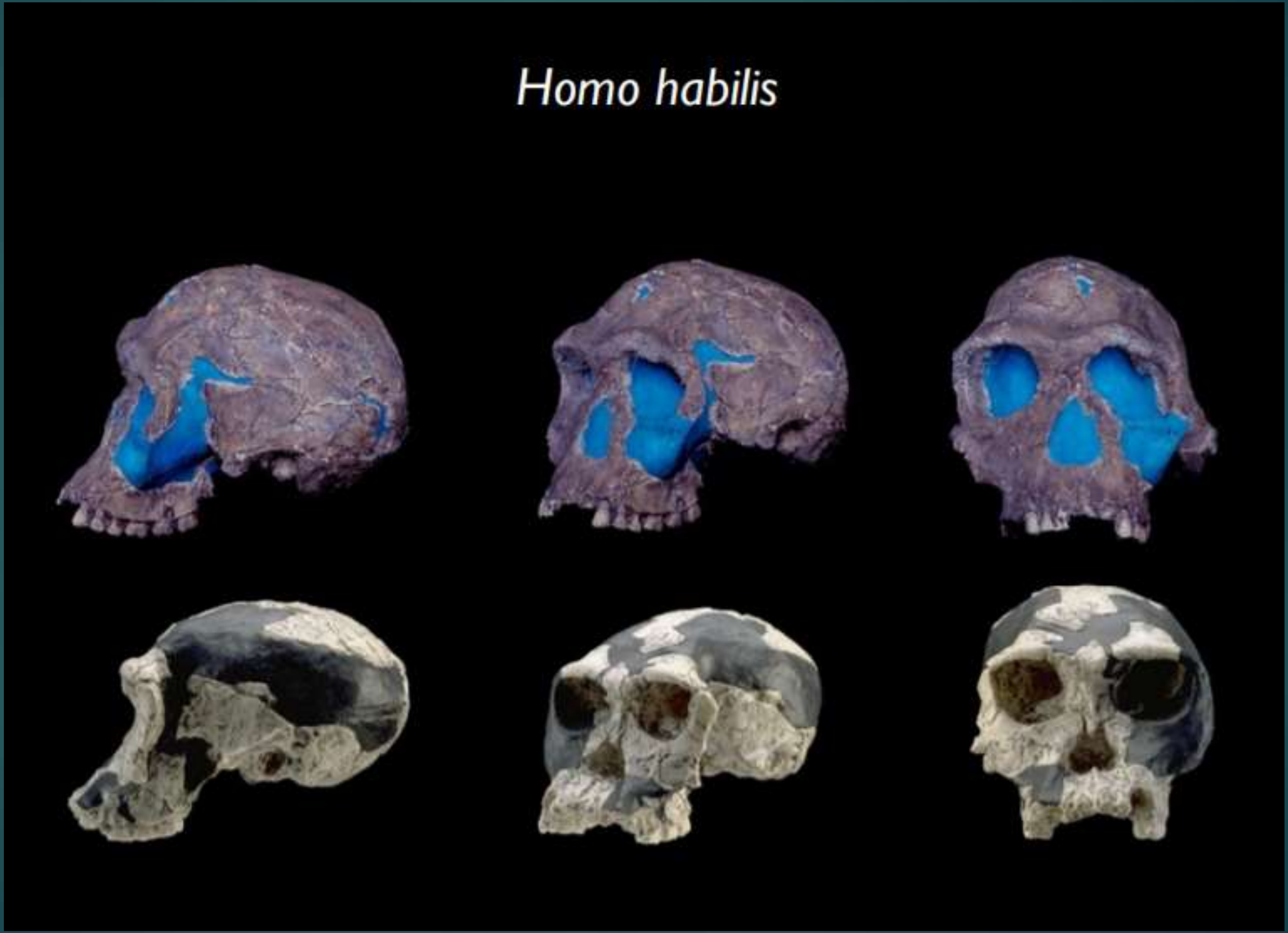
- Today, *H. habilis* is accepted as a species.
- But many of the earliest fossils assigned to *H. habilis* are
  - too fragmented and separated in time
  - To make conclusions about their relationships or species assignment
- *H. habilis* specimens with particularly large features -- brains or teeth, for instance -- are often assigned as *Homo rudolfensis*/1470 group

Is *H. habilis* ancestral to *H. erectus?*

W. Kimbel & Rightmire thinks *habilis* is at the stem of *Homo*

- If WT 15000 *H. erectus* (Turkana boy) is alive at 1.6 Ma
- And primitive OH 62 and *H. habilis*, are alive at 1.8 Ma,
- How could *H. habilis* so rapidly evolve into *erectus,* given significant skeletal differences.

Reconstructions



Early Representatives of the Genus *Homo*

Olduvai *Homo habilis*, 1.8 Ma

- 650-690 cc cranial capacity (413 cc ave for *A. afarensis*; 450 cc for *africanus* and *robustus, boisei*)
- First paleoneurological evidence for Broca's area (1 of speech areas)
- Modern-looking hands, feet
- Little difference from *Australopithecus* in body size, sexual dimorphism, and tree-climbing abilities
- Maturation rate closer to apes

Australopiths ancestral to *Homo?*

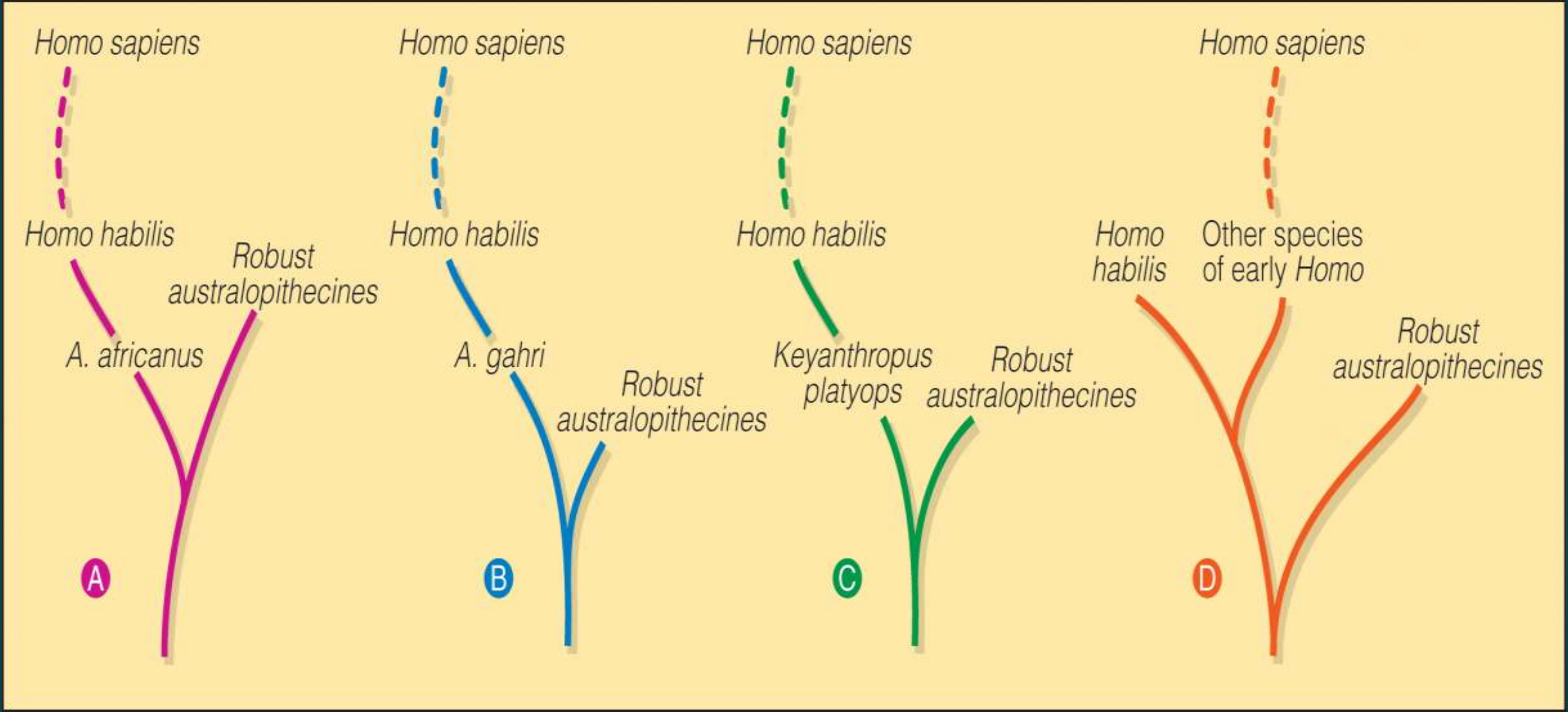
- None of the robust Australopithecines belong in the direct human lineage; they coexisted with *Homo habilis and erectus* from 2.5 to 1 Ma

- The body of *Homo habilis* had changed little from gracile Australopithecines; hence, the australopiths are likely suitable ancestors for *Homo*

- Did *Australopithecus afarensis* or *Australopithecus africanus* give rise to *Homo habilis*?

- Or was it *Kenyanthropus* to the exclusion of all Australopithecines (minority view)?

Possible trees for ancestor of *Homo*



Olduvai Gorge

- 2 million years ago Olduvai was a lake, whose shores were inhabited by robust Australopithecines, *Homo habilis* and later *Homo erectus*
- Assemblages of stone tools (2 mya) were found, associated with bones of now-extinct animals and with evidence of butchering
- On an occupation surface, 1.8 mya, there was a “stockpile” of basalt stones, forming a circle (human or pushed up by tree?)

Language origins

- Importance of cooperation, planning and foresight for *H. habilis* raises questions about communication abilities
- Humans and apes share a gesture-call system, inherited from the common ancestor
- Humans and apes share language potential (apes to the level of a 2-3 year-old)
- These shared abilities must have been possessed by the earliest hominins as well

Stone Tools, Language, & Brain Lateralization

- The cortical speech area is adjacent to that involved in precise hand control
- Manufacture of Oldowan tools require manual skills beyond those of chimpanzees using stones and anvils for nut-cracking
- *H. habilis* exhibited handedness in toolmaking which is associate with lateralization of the brain; H. habilis was right handed
- Lateralization is associated with language

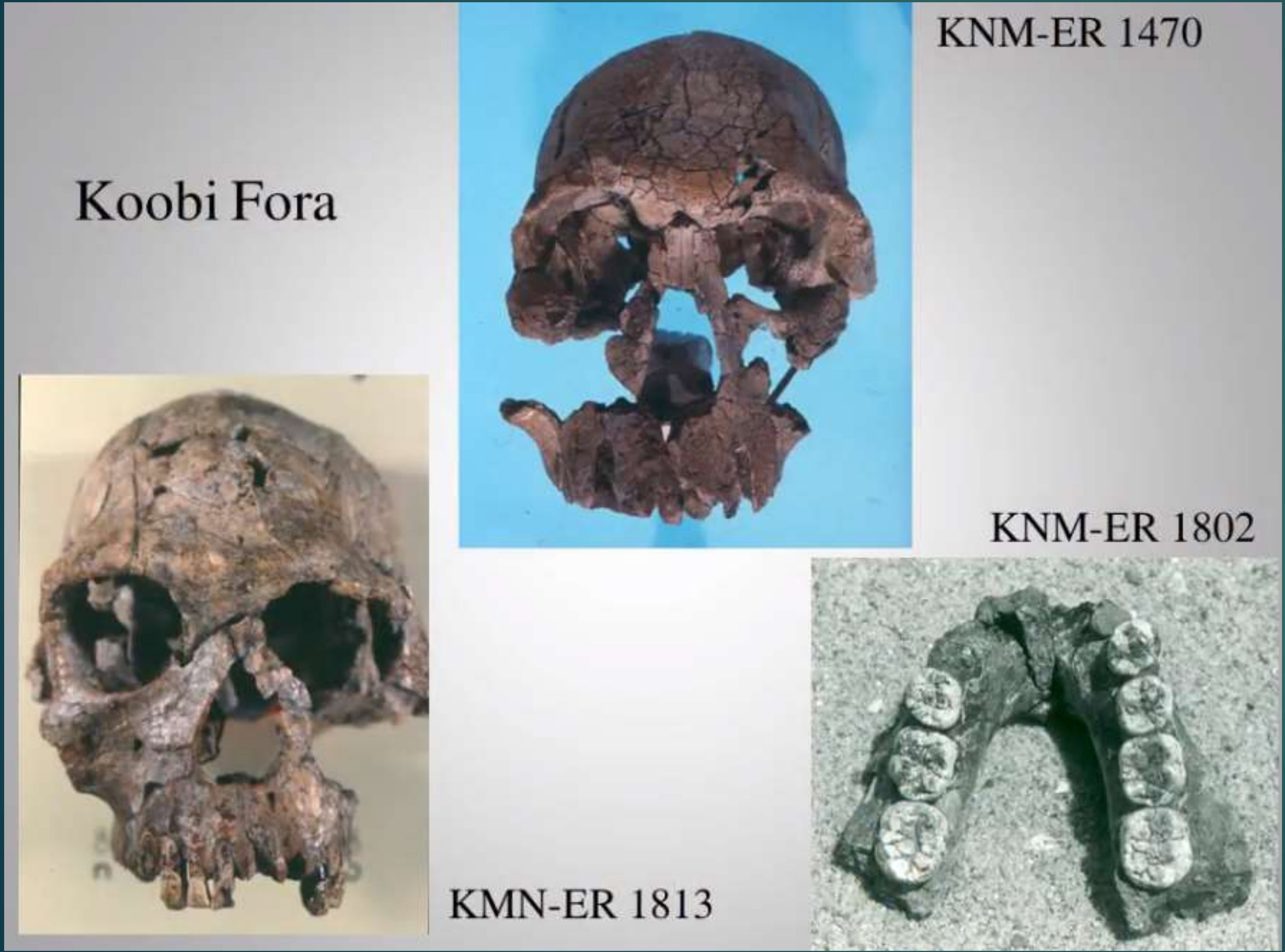
History of discovery

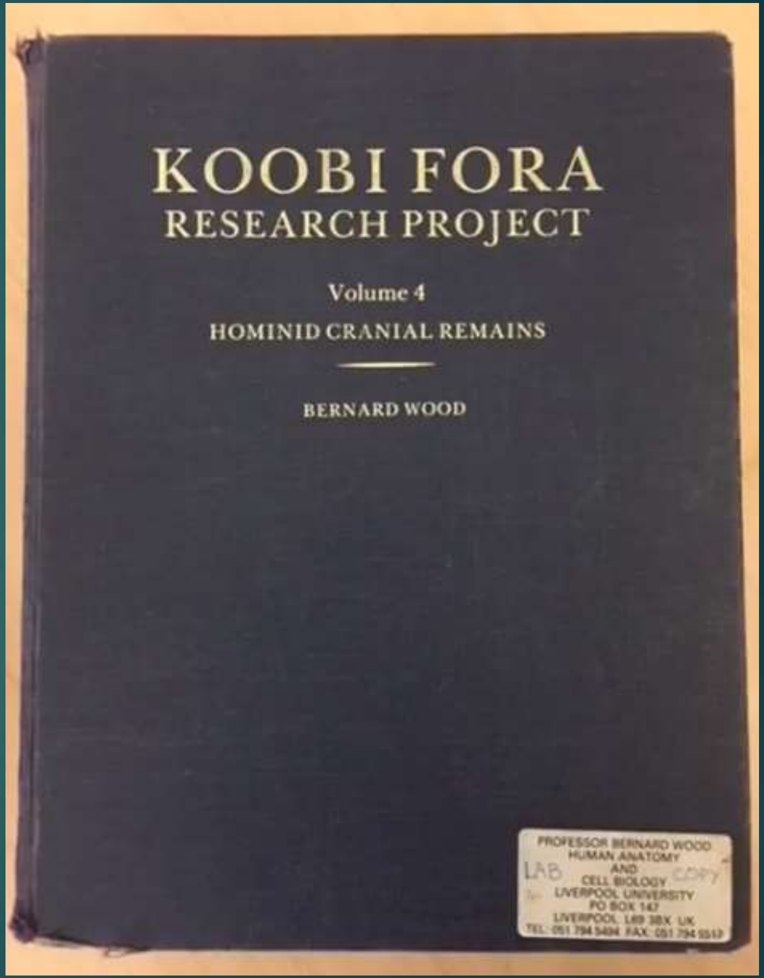
- In 1972, KNW-ER 1470 was discovered at Koobi Fora.

- By 1980, Wolpoff publishes his book, *Paleoanthropology,* acknowledging *H. habilis* as *Homo*:
  - "*Homo habilis* is a taxon whose time has come."

- But subsequent finds shaped the future debate.

Koobi Fora, Turkana, Discoveries: *H. habilis??*




KOOBI FORA
RESEARCH PROJECT

Volume 4
HOMINID CRANIAL REMAINS

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LAB COPY

1470 Group: *Homo rudolfensis? Homo habilis?*

- Flattened face
- Rounded brain case
- Compared to chimp: larger brain, vertical face, no large canines, small browridge
- Body size like the australopiths
- Smaller dentition, more human like, but still larger; difference in diet
- Broader fingertip surfaces; more powerful grip; adaptation for stone tools

History of discovery: Koobi Fora

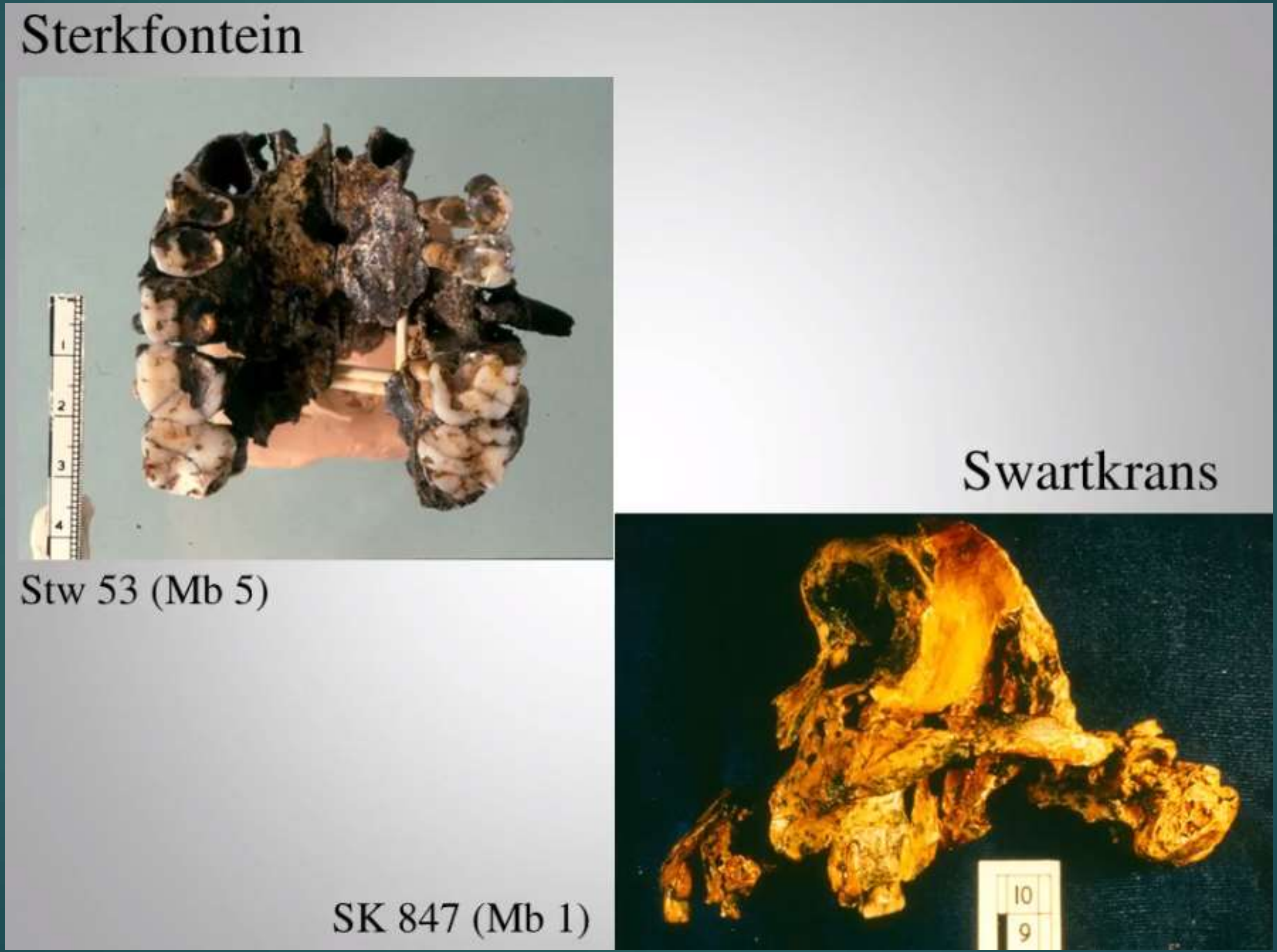
- A handful of additional specimens from Ethiopia to South Africa have since been added to *H. habilis*

- The biggest contribution to early *Homo* has come from Koobi Fora in Kenya

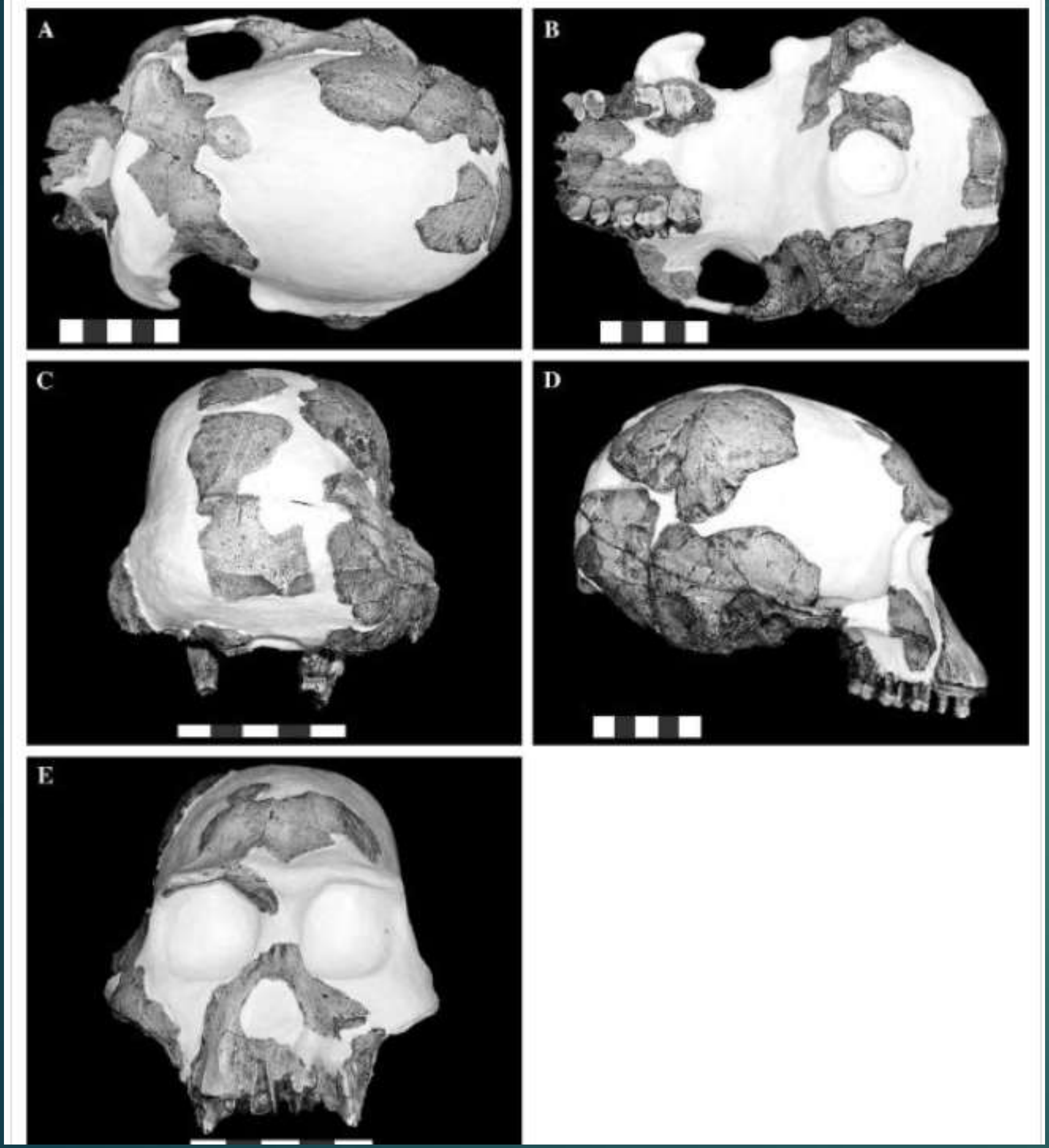
- Variation in the Koobi Fora fossils (KNW-ER 1470) was not so easily shoe-horned into a single species as those from Olduvai.

- B. Wood, 1992, “two-taxon hypothesis”:
  - two distinct types of face within early *Homo;*
  - suggested that a second early *Homo* species, *Homo rudolfensis*, should be recognized.

Then specimens from South Africa



Homo gautengensis : STW 53; *Homo habilis* or own species



Curnoe reconstruction

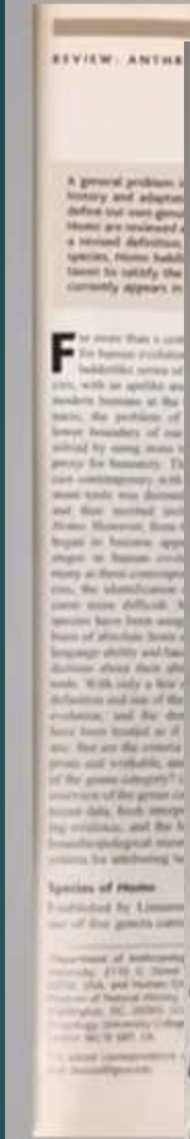
- South African, 1.5 to 2 Ma
- Stw 53 discovered in 1976 by Alan Hughes in Sterkfontein; exhibits extensive damage; stone tools present
- It’s taxonomic identification and reconstruction is heavily contested; variously affiliated with *Homo* (aff. *habilis* or sp. indet.; for the mandibles;) or *Australopithecus*.

- W. Ferguson, 1988, says *Australopithecus*
- Curnoe and Tobias 2006: *Homo habilis*

- 2010: Curnoe used it as the holotype of a new species, *Homo gautengensis:* "small-brained" and "large-toothed“; earliest *Homo*;

- evidence for burnt animal bones associated

Hughes and Tobias 1977; Darren Curnoe, 2010 us’



Wood

Scienc

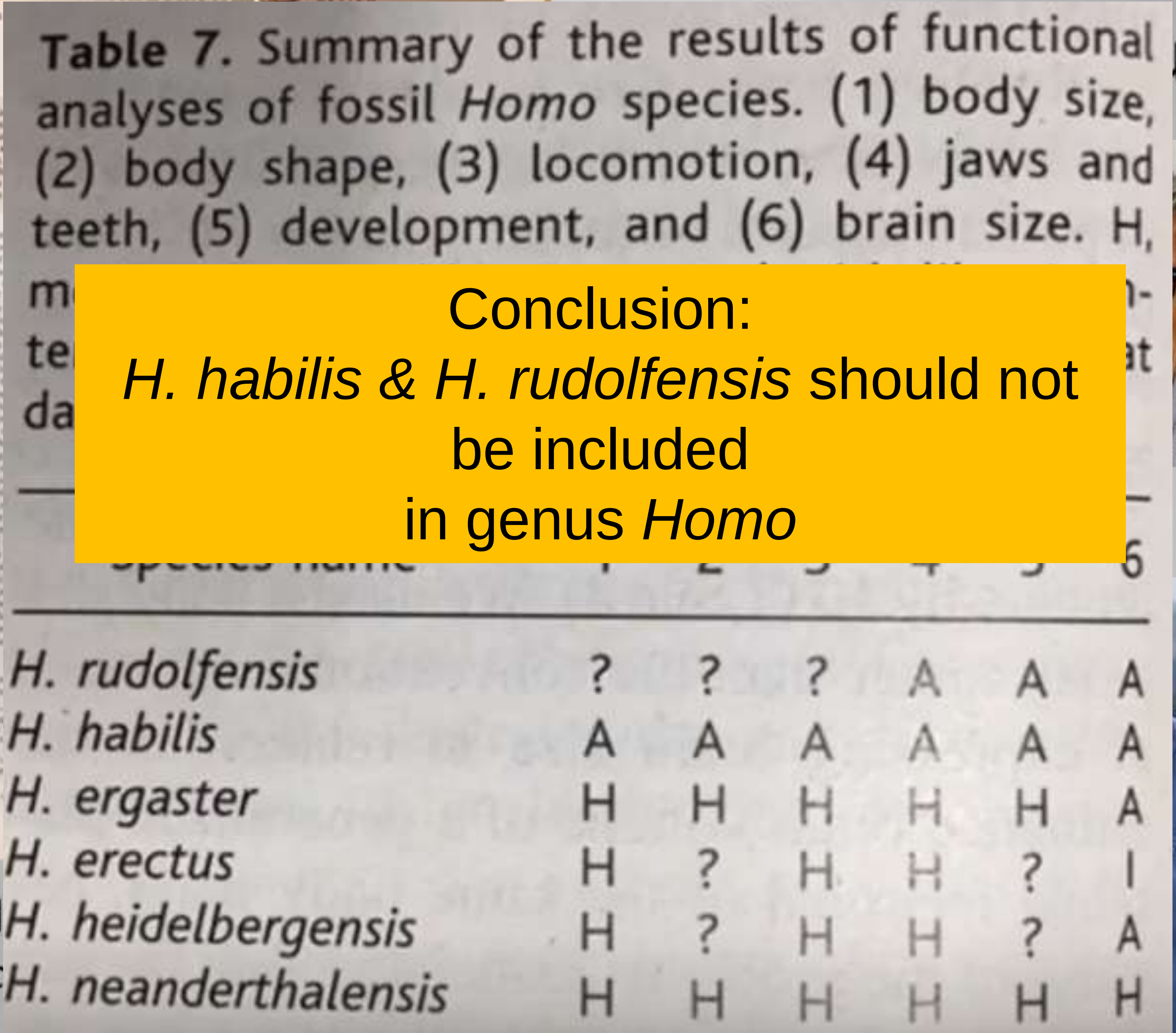


Table 7. Summary of the results of functional analyses of fossil *Homo* species. (1) body size, (2) body shape, (3) locomotion, (4) jaws and teeth, (5) development, and (6) brain size. H,

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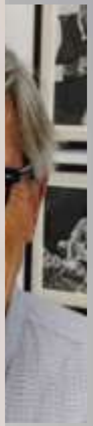
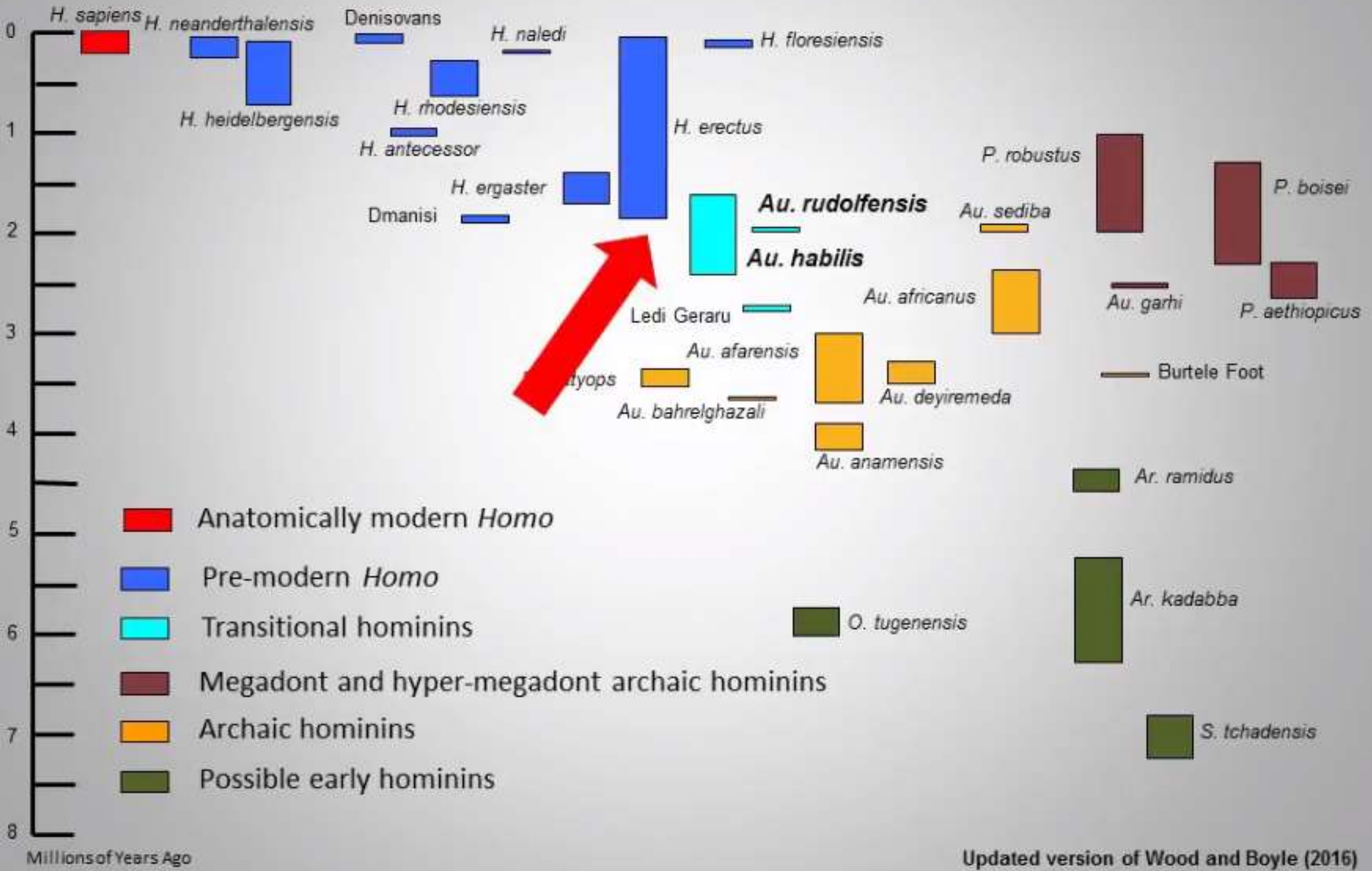
Species name	1	2	3	4	5	6
H. rudolfensis	?	?	?	A	A	A
H. habilis	A	A	A	A	A	A
H. ergaster	H	H	H	H	H	A
H. erectus	H	?	H	H	?	I
H. heidelbergensis	H	?	H	H	?	A
H. neanderthalensis	H	H	H	H	H	H

Conclusion:
H. habilis & *H. rudolfensis* should not be included
in genus *Homo*



Hominin taxa and site samples according to a 'splitter's' taxonomy (i.e., speciose taxonomy)



Updated version of Wood and Boyle (2016)

History of discovery

- 1999, Mark Collard and Bernard Wood: Defining the Genus *Homo* paper -- boundary between *Homo* and more-primitive hominins.
  - *H. habilis* is an australopithecine.

- If *H. habilis* is added to *Homo*, the genus has an incoherent mishmash of features.

- 20 years later, Meave Leakey (Richard's wife) confirmed Wood's 'two-taxon' hypothesis: a face and two lower jaws found at Koobi Fora.
  - But disproved Wood's suggestion about which jaws went with which faces.

Changing discoveries

- B. Wood & Collard, 1999: the gap between these groups suggested that earlier species such as *Homo habilis* should be excluded from *Homo*

- New discoveries and reanalysis indicated that :
  - earliest *Homo* exhibited greater diversity
  - underappreciated differences and similarities with *H. erectus*.

- New view of *Australopithecus:*
  - *Australopithecines* share many postcranial characteristics with *Homo:*
    - including a somewhat large body and relatively long legs.
    - previous overreliance on the very small “Lucy” (A.L.288-1) skeleton to characterize that species/genus (compared to a large *erectus*, Turkana boy).
    - So now we have a larger *Australopithecus afarensis* and a smaller, more variable *H. erectus* than previously known

Australopithecus, Kadanuumuu: 5’5”

anatomically arranged elements of KSD-VP-1/1;

“Big Man”

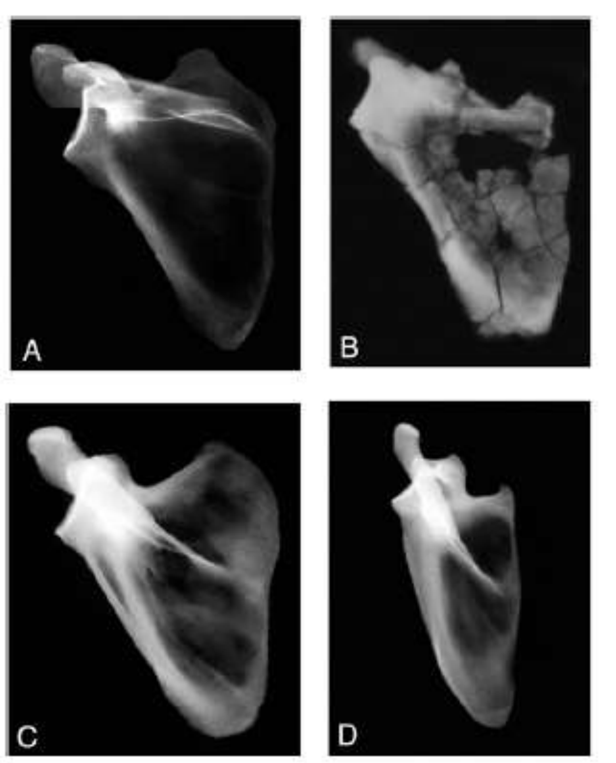
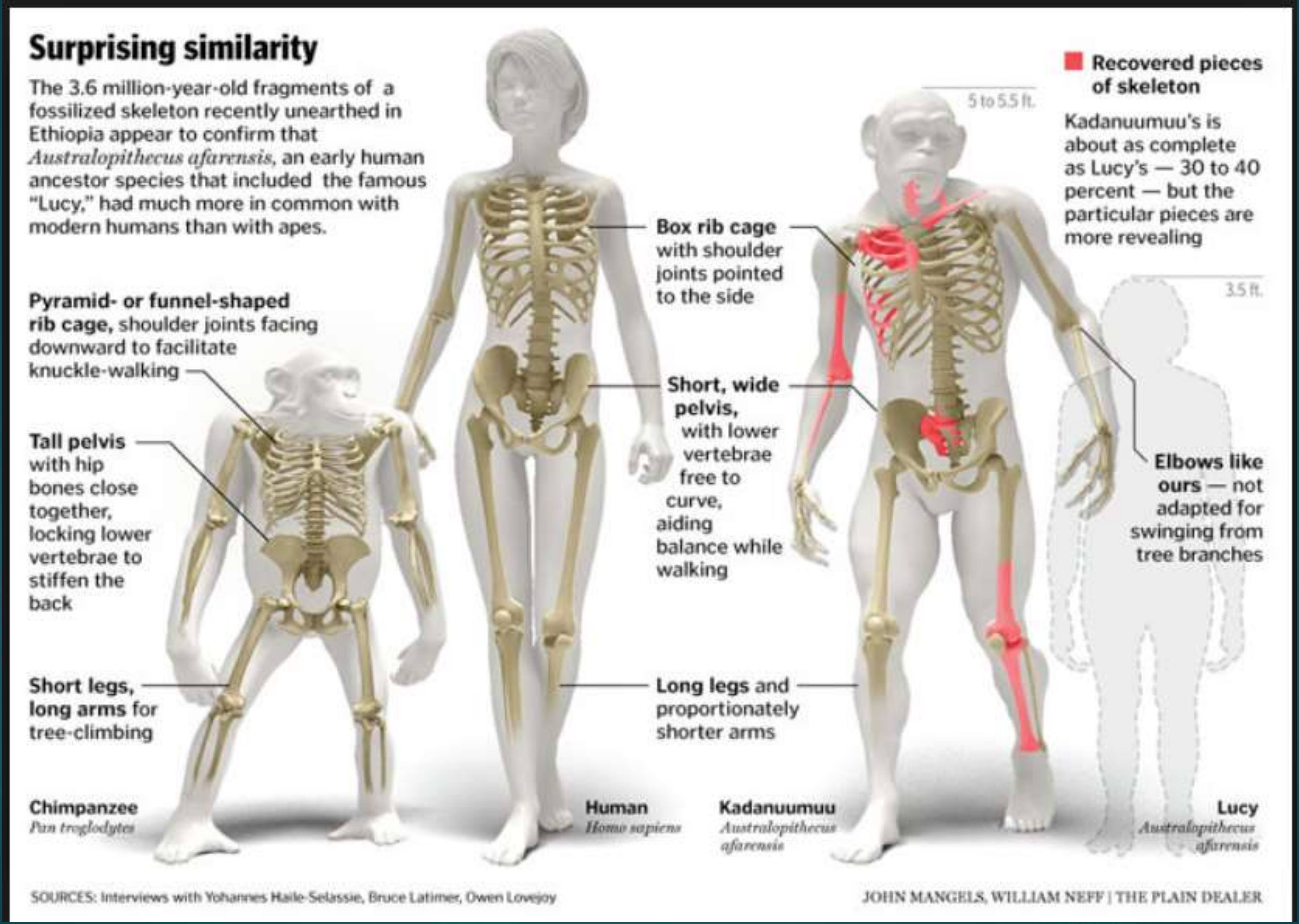


Fig. 3. X-rays of hominoid scapulas. (*A*) Modern human (CMNH-HTH-2450). (*B*) KSD-VP-1/1g. (*C*) *Gorilla* (CMNH-B-1730). (*D*) *Pan* (CMNH-B-3551). Each specimen has been scaled to the same approximate superoinferior glenoid height and aligned with its vertebral border approximately vertical. Note the uniqueness of *Pan* if a line is drawn connecting each specimen's superior and inferior angles (largely vertical in *D*). The human's glenoid angle is among the most superior in our sample (*n* = 21). All specimens, save *Pan*, have similar glenoid orientations. Both *Pan* and *Gorilla* are distinguished from the hominids by their substantially greater inferomedial spine orientation. KSD-VP-1/1g is most similar to humans. *Pan* is clearly the morphological outlier.

Spatula below (B);
similar to humans

Yohannes Haile-Selassie et al. PNAS 2010;107:12121-12126



Surprising similarity

The 3.6 million-year-old fragments of a fossilized skeleton recently unearthed in Ethiopia appear to confirm that *Australopithecus afarensis*, an early human ancestor species that included the famous "Lucy," had much more in common with modern humans than with apes.

🟥 **Recovered pieces of skeleton**

Kadanuumuu's is about as complete as Lucy's — 30 to 40 percent — but the particular pieces are more revealing

Pyramid- or funnel-shaped rib cage, shoulder joints facing downward to facilitate knuckle-walking

Tall pelvis with hip bones close together, locking lower vertebrae to stiffen the back

Short legs, long arms for tree-climbing

Box rib cage with shoulder joints pointed to the side

Short, wide pelvis, with lower vertebrae free to curve, aiding balance while walking

Long legs and proportionately shorter arms

Elbows like ours — not adapted for swinging from tree branches

SOURCES: Interviews with Yohannes Haile-Selassie, Bruce Latimer, Owen Lovejoy

JOHN MANGELS, WILLIAM NEFF | THE PLAIN DEALER

The *Homo habilis* Debate: Linear model

- It was once thought that the evolution of the genus *Homo* was an example of anagenesis, the continual and gradual change of one parent species into its daughter species in a linear fashion.
- As the fossil record began to expand and more early human fossils were found dating to the period between 2 million and 1 million years ago, some questions as to the validity of this hypothesis were raised.

History of discovery: no linear model for *Homo*

- David Lordkipanidze et al. 2013: analysis of five crania from Dmanisi, Georgia; range of shapes among these skulls equals or exceeds the variation across *H. habilis*, *H. rudolfensis* and *H. erectus*
- On that basis, Lordkipanidze proposed that all *H. habilis*-like fossils be reassigned to *H. erectus*, subsuming three species into one.
- Wood & most others disagree
- Wood, 2014: *H. habilis* should belong to its own genus, neither australopith nor *Homo*

B. Wood, Nature, 2014

History of discovery: no linear model for *Homo*

- Wood: *Homo habilis* is too unlike *H. erectus* to be its immediate ancestor; no linear model
- By 1.7-1.8 Ma in East Africa: 3 species – *H. habilis, H. rudolfensis, H. erectus*
- Ecological context in which *Homo* originated is not precisely known at present. See R. Potts
- Our ancestors probably evolved in Africa, but the birthplace of our genus could be far from the Great Rift Valley, where most of the fossil evidence has been found. See A. Zihlman
- Leakeys' iconic discoveries at Olduvai Gorge should remind us of how much we don't know, rather than how much we do.

Origins of *Homo:* few fossils

- The genus *Homo* almost certainly originated between 3.0 to 2.5 Ma.
- Yet this is a very poorly sampled period for fossils; as is the 2.5 to 2.0 Ma period
- By 2.0 to 1.5 Ma, significantly more fossils of *Homo.* But continued debate as to which bones belong to which genus of *Homo*
- Genus *Homo* characterized by longer lower extremity, forward facing shoulder joint, smaller molar teeth, diverse diet, regular use and manufacture of stone tools that functioned in butchery; association with increasingly open & wetter habitats
- But most of these chararcteristics are better defined by *H. erectus*

Fossil remains found in contemporaneous deposits at Eat Turkana during the 1970s show that four distinct species of hominins lived in the region 1.8 Ma.

Koobi Fora

- *This comparison of the skull of modern man with an early Homo skull (1) shows the fossil had a smaller braincase. The early Homo skull is more like the Homo erectus skull (2) than that of Australopithecus boisei (5).*
- *The two femurs (3 & 4) are similar to human femurs.*
- *The tibia (7) and femur (4) show the Homo erectus knee joint.*
- *The jaws are from an adult erectus (6), an erectus youth (8), and an australopithecine youth (9). The hominid jaw fragment (10) is unidentified.*
- *The teeth (11) are Australopithecus boisei.*
- *All these fossils are from Koobi Fora.*

4 species co-existed in Turkana Basin

- ~2.0-1.5 Ma: *4 hominins* co-existed in the Turkana Basin, northern Kenya:
  - *Homo habilis,*
  - *Homo rudolfensis,*
  - *Homo erectus,*
  - *Paranthropus boisei.*

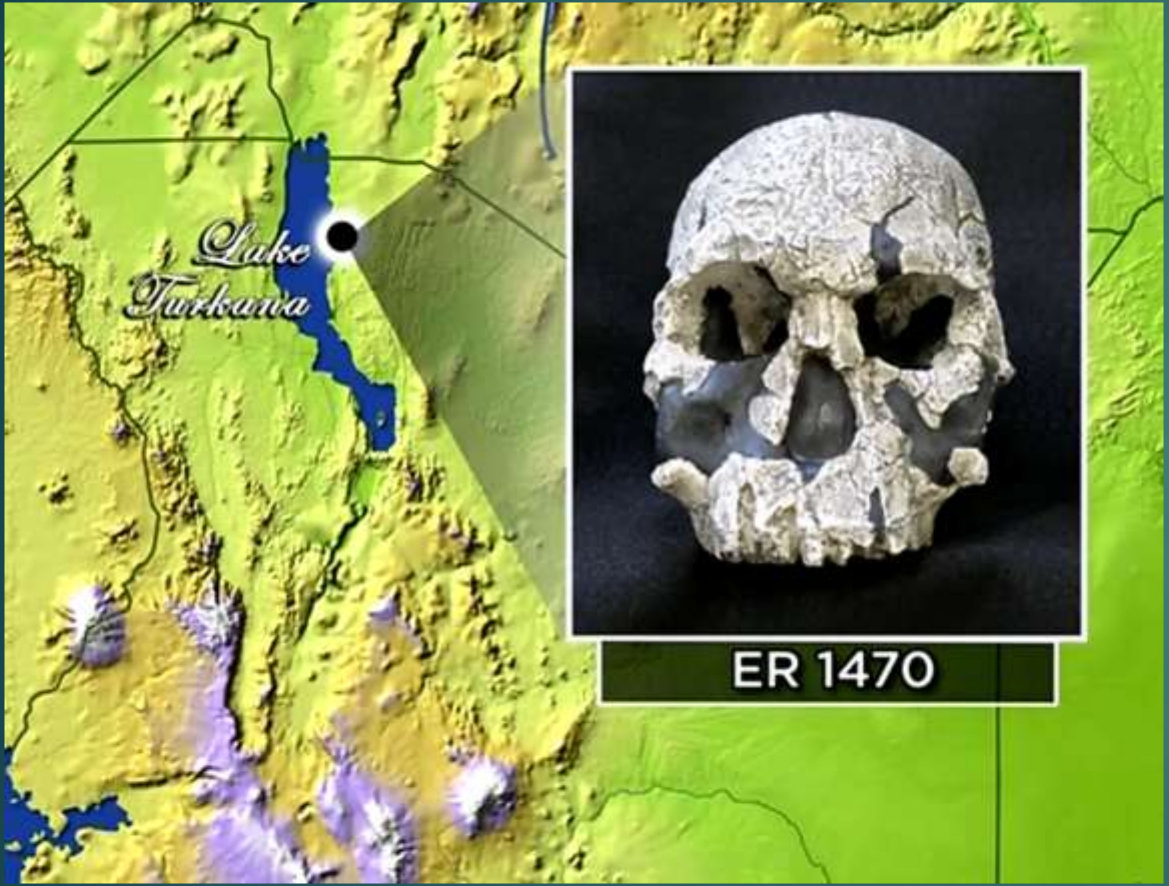
- Early *H. erectus* and early *Homo* are bigger than *Australopithecus* (~30%).

- Early *H. erectus* (including smaller Dmanisi specimens) is larger than non-*erectus Homo* (~15%–25%), but their size ranges overlap.

Bernard Ngeneo

- 1972: He discovered ***Homo Rudolfensis*** (KNM ER 1470), while working at the time with a group led by Richard and Meave Leakey, at Koobi Fora, Kenya, 1.9 MY
- 300 fragments

H. habilis rudolfensis: ER 1470, originally erroneously dated to 2.9 Ma



Koobi Fora

Brain: 750 cc

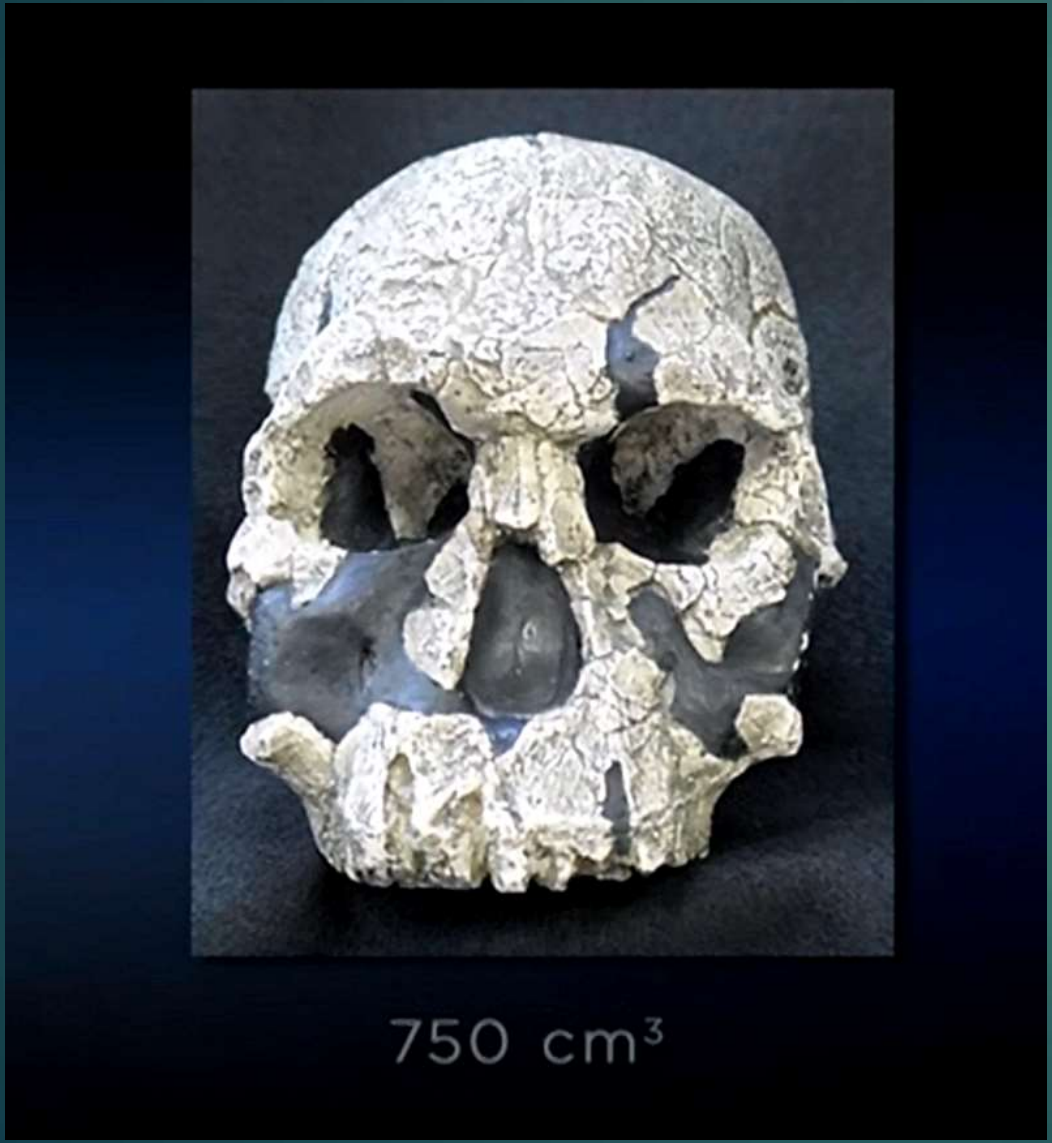
Richard Leakey & *Homo rudolfensis*

- In 1972, Richard Leakey announced the discovery of a fossil that made him world famous: KNM-ER 1470
- Larger part of a cranium pieced together from hundreds of fragments by Alan Walker and Meave Leakey
- Face was large and flat, palate blunt and wide, and teeth large; reminiscent of the australopithecines, but cranium was 750 cc
- Leakey thought it was *Homo*; Alan Walker thought it was an Australopith; published as *Homo*, but no species designation

Homo rudolfensis

- The type specimen of *Homo rudolfensis* is skull 1470 (KNM-ER 1470)
- KNM-ER = Kenya National Museum-East Rudolf
- Found by Bernard Ngeneo at Koobi Fora in 1972, on the eastern shore of Lake Rudolf, now Lake Turkana, in northwestern Kenya
- Cranial capacity: 750 cc
- Below KBS tuff (originally dated 2.9 M; later 1.8 M)

KNM-ER 1470: at first considered earliest *H. habilis*



Holloway: left, frontal Broca’s area larger:
Language? and tool making

ER-1470: Was it *H. habilis??*

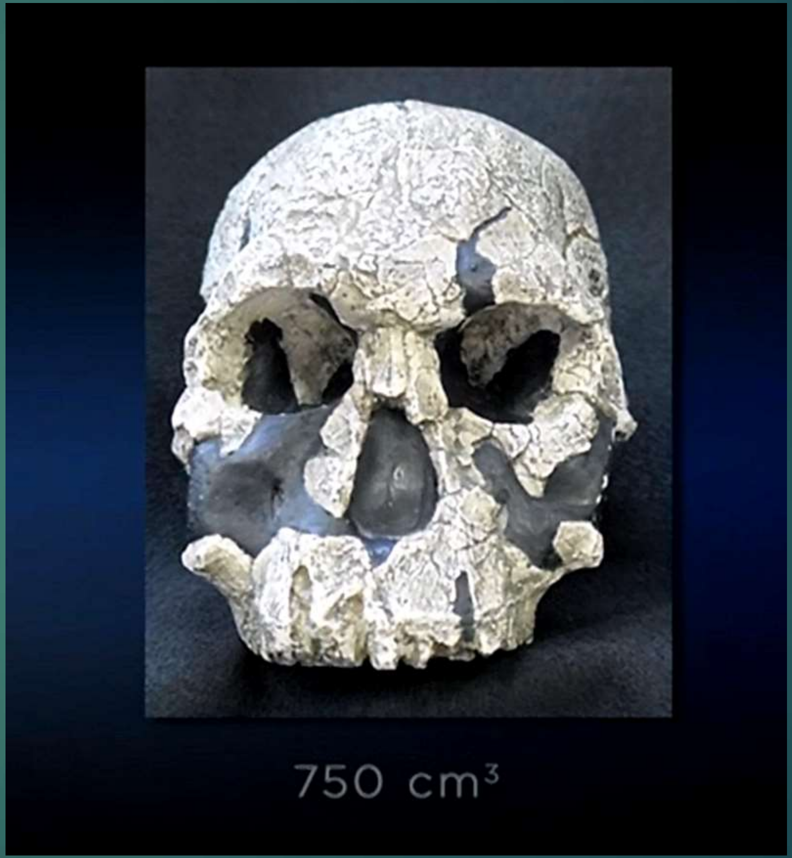
- Reluctance to call it *H. habilis:*
  - Brain was larger than 640 cc
  - 1470 was originally thought to be much older (2.9 Ma); later, using pig fauna, discovered to be 1.9 Ma, making it a contemporary of *H. habilis*
- Eventually helped convince anthropologists of validity of *H. habilis*, because demonstrated existence of another creature that was definitely different from both *A. africanus* and *H. erectus*

One year later, second cranium, KNM-ER 1813 was discovered.

Despite, in 1995, KNM-ER 1813 becoming the type specimen of *Homo microcranous* (Ferguson 1995), most consider it a female *H. habilis*

ER 1813,
H. habilis, Koobi Fora: more like *Australopithecus* – smaller 500 cc brain, smaller face and teeth

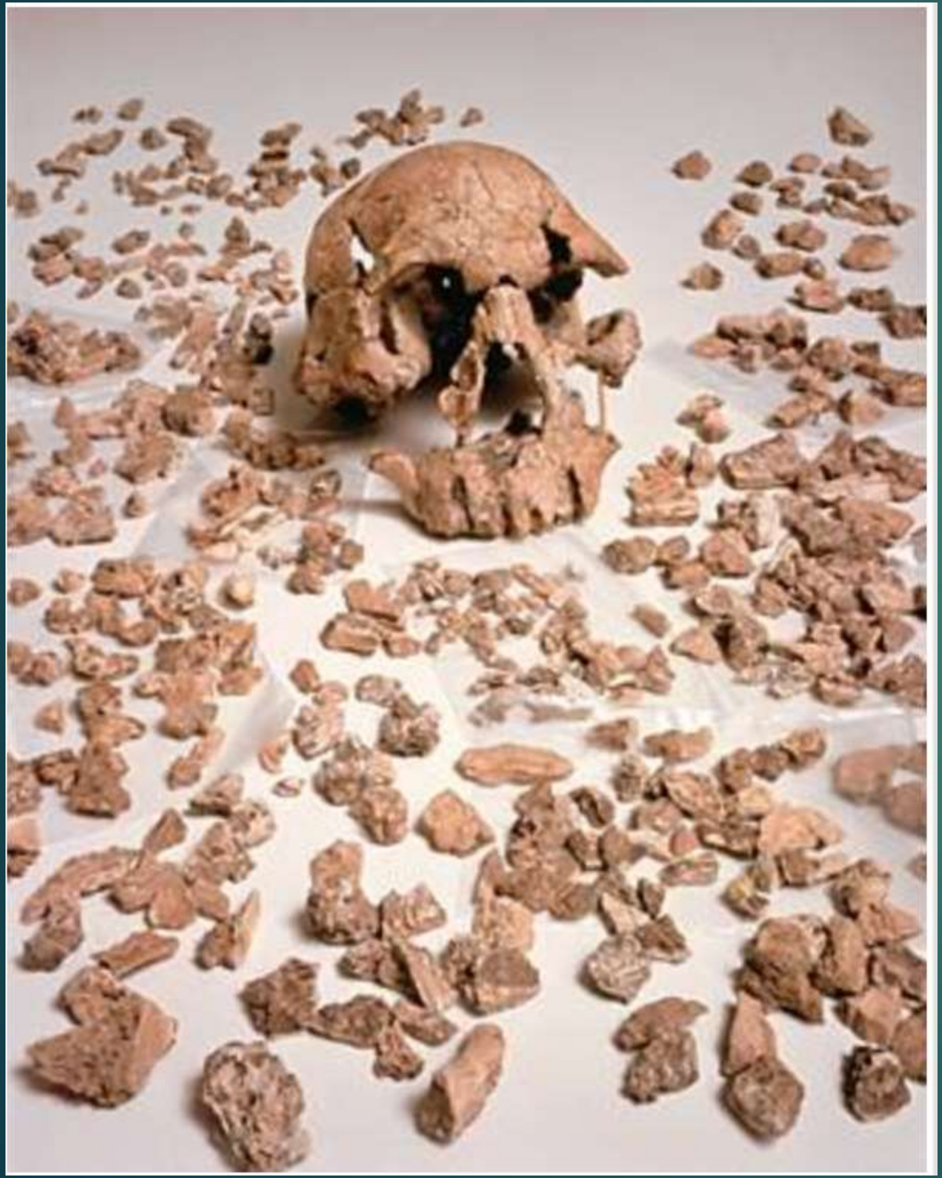
OH 7 vs. KNM-ER 1470



Homo habilis

Homo rudolfensis/1470

1470: Homo rudolfensis: 300 fragments



- Discovered by Bernard Ngeneo, a member of a team led by anthropologist Richard Leakey and zoologist Meave Leakey in 1972, at Koobi Fora in Kenya.
- Meave Leakey and Bernard Wood reconstructed KNM-ER 1470's skull from 300 fragments, revealing a large cranium with a long, wide, flat face. 150 pieces not fitted
- The brain case is much larger than any australopithecine skull and lacks the large brow ridges typical of *Homo erectus.*

2007 Tim Bromage reconstruction

- Timothy Bromage, reconstructed the skull of KNM-ER 1470.
- The new construction looked very ape-like (possibly due to an exaggerated rotation of the skull) and the cranial capacity based on the new construction was reported to be downsized from 752 cc to about 526 cc, although this seemed to be a matter of some controversy.
- Bromage said his team's reconstruction included biological knowledge not known at the time of the skull's discovery, of the precise relationship between the sizes of eyes, ears, and mouth in mammals.
- A newer publication by Bromage has since increased the cranial capacity estimate back up, from 526 cc to 700 cc.

KNM-ER 1470, Lake Turkana, 1.9 Ma

- 752 cc cranial capacity
- Cranium is more modern in appearance than in *Australopithecus*
- There are currently no stone tools found in the same layers as the *H. rudolfensis* fossils, but there are stone tools existing in the same time period that *H. rudolfensis* lived.
- Brain reorganization: Inside of the skull shows a pattern in the left cerebral hemisphere that is associated with the speech area and right-hand control of living humans
- Wear patterns on tools indicate predominance of *right-handedness*

Early Homo: Size and Proportions

- Average ranges of cranial capacity vary depending on who is included in each group.

- Regardless of whether there is one or more species of early non-*erectus Homo*, brain size across the entire group ranges from 510 to 750 cc.

Origins of *Homo: early Homo: Size and Proportions*

- Given that at least two different facial morphs seem to coexist in time and space in East Africa; what can be said about size and shape of non-*erectus Homo*?
  - 1470 group has a larger cranial capacity (750 cc) than does the
  - 1813 group (510–675 cc)
  - with the caveat that OH 7 has not been assigned to either group.
- Yet brain size among the well-preserved early *Homo* individuals (KNM-ER 1805; OH 13, 16, 24) is fairly continuously distributed between the two end members, KNM-ER 1813 and 1470.

Homo habilis: 1 or 2 species

- B. Wood (2012): Although a strong case had been made that:
  - variation among the *H. habilis* fossils from Olduvai could be subsumed within a single species,
  - The question: Do the two forms of early *Homo* found at Koobi Fora come from
    - males and females of a single species (sexual dimorphism),
    - or represented two species
- In 2012, new fossils from Koobi Fora (1.8–2 Ma), similar in shape, but not size, were published, supporting the existence of two taxa

Homo habilis: 1 or 2 species

- The Koobi Fora fossil discoveries by Richard Leakey and colleagues strengthen the case for recognizing at least:
  - That there were two evolutionary lineages at the early stages of the genus *Homo*,
  - One widely adopted “two species” scheme recognizes
    - *Homo habilis sensu stricto* (with OH 7 as its type specimen), which is known from both Olduvai Gorge and the Koobi Fora/Omo region,
    - and a second species, *Homo rudolfensis*, of which KNM-ER 1470 is the type specimen, known only from Omo region and a site in Malawi.

2 lineages

- S. Antón: Because of taphonomic damage to the type specimen of *Homo habilis*, in East Africa two species with different masticatory adaptations are better identified by their main specimen (i.e., the 1813 group and the 1470 group) rather than a species name.

- However, whether either of these two lineages was ancestral to *Homo erectus*, let alone to modern humans, remains uncertain.

- Some researchers have questioned whether either of these taxa belong in *Homo.*

H. habilis

- Initially, body proportions postcranially, in *H. habilis,* are
  - very different from later *Homo*,
  - with long arms probably demonstrating continued reliance on arborealism

- *H. habilis* has always been controversial:
  - initially because it was considered insufficiently distinct from the australopithecines and then,
  - as more material was included in the species, because some considered that it subsumed too great a morphological diversity

Lockwood, 2013; Antón et al., 2014; Wood, 2012.

Number of species in early *Homo*

- It was not easy to accommodate the variation among the Koobi Fora early *Homo* fossils within one species.

- There were two distinct facial morphologies:
  - although the larger faces could have belonged to males, and the smaller ones to females, of the same species,
  - But differences were unlike those we see between the males and females of modern humans and the living apes.

- This discrepancy led researchers to recognize B. Woods' theory of a second early *Homo* species, *Homo rudolfensis*.

Early *Homo*: Variation

- There are basically two forms –
  - a smaller and more gracile australopithecine type (*H. habilis, OH 7, 1813*) showing some brain enlargement and facial reduction; with less encephalization and a more apelike postcrania, but a more derived upper face (at Olduvai & Koobi Fora)
  - a larger, more megadontic form with larger brain (*H. rudolfensis, 1470*), with a flatter face and perhaps less apelike body proportions (only at Koobi Fora)
  - 300 K difference in age; regional variation?

- Those who argue for two species have used the name *H. rudolfensis* to distinguish the larger material. Others consider them the 1470 group.

- There is considerable doubt over their relationship; and their relationship to both H. erectus & *H. sapiens*

Wood, 2012; Leakey et al., 2012; Spoor et al., 2015

Face + jaw needed together

- Controversy: there is no single *H. rudolfensis* fossil specimen that contained both a face and a lower jaw.
- *H. habilis* (called OH 7) had a lower jaw that contained teeth, but lacked a face
- The type specimen of *H. rudolfensis* (KNM-ER 1470) had a face, but neither tooth crowns nor a lower jaw.

	***Homo habilis* (small)**	***Homo rudolfensis* (large)**	***Homo erectus***	**Archaic *Homo sapiens***	**Neandertals**	**Early Modern *H. sapiens***
Height (m)	1 meter	c 1.5 m	1.3-1.5	?	1.5-1.7	1.6-1.85
Brain size (cc)	500-650	600-800	750-1,250	1,110-1,400	1,200-1,750	1,200-1,750
Skull form	Relatively small face; nose developed	Larger, flatter face	Flat, thick skull with large occipital and brow ridge	Higher skull; face less protruding	Reduced brow ridge; thinner skull; large nose; midface projection	Small or no brow ridge; shorter, high skull
Physique	Relatively long arms	Robust but human-like skeleton	Robust but human-like skeleton	Robust but human-like skeleton	As archaic *H. sapiens*, but cold adapted	Modern skeleton; warmth adapted
Jaws/ teeth	Thinner jaw; smaller narrow molars	Robust jaw; large narrow molars	Robust jaw in larger indiv; smaller teeth than in habilis	Similar to H. erectus, but teeth may be smaller	Similar to archaic H. sapiens; teeth smaller except for incisors; chin in some	Shorter jaw than in Ns; chin; teeth may be smaller
Distribution	E & S Africa	E. Africa	Africa, Asia & Indonesia (? Europe)	Africa, Asia, Europe	Europe & W. Asia	Africa & W. Asia
Dates	2-1.6 M	2.4-1.6 M	1.8-0.3 M	400-100 K	(430) 150-30 K	130-60 K

Evolution of early *Homo:* Problems with OH 7

- Currently, only the type specimen OH 7 is affiliated with the *H. habilis* name.
- On the basis of dental anatomy, OH 7 can be excluded from *H. erectus*.
- However, taphonomic damage to the OH 7 mandible renders its arcade shape unknown.
- As a result, the crushed and distorted OH 7 mandible cannot be definitively affiliated with either 1470 or 1813 group of early *Homo*.
- 2015 digital reconstruction indicates dental arcade was primitive.

OH7, type specimen of *Homo habilis*, unaffiliated

- Although the specimen retains a mandible and dentition, extensive postmortem deformation and distortion to the mandibular symphysis and body leave the relationships among and between the anterior and posterior tooth rows unresolved.

- It is thus currently impossible to assess the fossil for the key features of arcade shape and orientation that distinguish the 1813 and 1470 groups.

- A number of specimens that can be assigned to *Homo* lack the specific arcade anatomy to be definitively assigned to one or the other non-*erectus Homo* group.

Evolution of early *Homo:* Unaffiliated early *Homo*

- These include some specimens that we consider likely to be affiliated with the 1813 group, such as KNM-ER 1802 and Uraha 501.
- These also include specimens for which we make no prediction due to missing anatomy, such as
  - OH 16 (which has relatively narrow lower incisors but does not retain palatal or mandibular structures and has a relatively large canine root) and
  - KNM-ER 1590 and 3732 – both of which have relatively large vaults (and in the case of 1590 also maxillary teeth), but which lack palatal or other facial anatomy to affiliate them definitively.
  - It should be noted that the inferior face of KNM-ER 3732 may be plastically distorted.

Evolution of early *Homo:* Unaffiliated early *Homo*

- *Postcrania*: A number of isolated postcranial limb elements cannot be affiliated with any certainty to either of the non-erectus *Homo* groups. In the past the large size of some of these has been used to argue for their inclusion with the large cranium KNM-ER 1470 – however, this seems unwarranted given the great size overlap present in the facial remains of both groups.

Evolution of early *Homo:* Paleobiology of early *Homo*

- Paleobiology: Origin and evolution of early *Homo* is related to the accommodation of these novel and/or unpredictable environments over time and space.

- Adaptive response to these ecological changes:
  - increases in average body and brain size and
  - changing dental size coupled with
  - increased toolmaking and stone transport
  - suggest dietary expansion, developmental plasticity, cognitive evolution, and social investments.

- Together these features and behaviors enabled successful accommodation of these changing environments.

Paleobiology of early *Homo*

- Diet, stone transport, and toolmaking Isotopic analysis indicates
  - a shift from reliance on C3-based foods in early Australopithecus (~4 Ma)
  - to a more diverse diet incorporating a broader range of C3- and C4-based foods
  - in both *Australopithecus* and *Homo* lineages but in different proportions.

Paleobiology

- In the same geographical area,
  - East African *Homo* has a diet that is 78% broader
  - than contemporaneous *Paranthropus*, which specialized in more C4 [and/or crassulacean acid metabolism (CAM)] foods.

- East African *Homo* has a dietary breadth that is only 63% that of *A. afarensis* and 79% that of *A. africanus*.

- This suggests that it is not dietary breadth *as reflected in isotopic breadth that was important in the evolution of Homo*, but rather the inclusion of a broader range of food stuffs within a narrower isotopic range.

OH 7, 1470, & 1813

- *Size and Postcrania*: OH 7 preserves two parietals from which a loose estimate of cranial capacity is 680 cc, which is consistent with any of the early *Homo* groups.

- The OH 7 hand elements cannot be presently compared with either group (they have no hand fossils); it retained a significant amount of arboreal behavior in its locomotor repertoire.

- Motor behavior unlike *H. erectus*, but possibly consistent with those made for the 1813 group, although they may also be consistent with the 1470 group, for which we lack positively affiliated postcranial remains.

H. habilis/1813 & H. rudolfensis/1470: 1 or 2 species?

- Our whole concept of the taxon *H. habilis* is based on the fossils from Beds I and II of Olduvai Gorge.
- Most of this material is reasonably encompassed within a single species, *H. habilis*.
- Includes OH 7 (type specimen), OH 13 (cranial parts), OH 16 (badly fragmented cranium and mandible), OH 24 (crushed cranium)

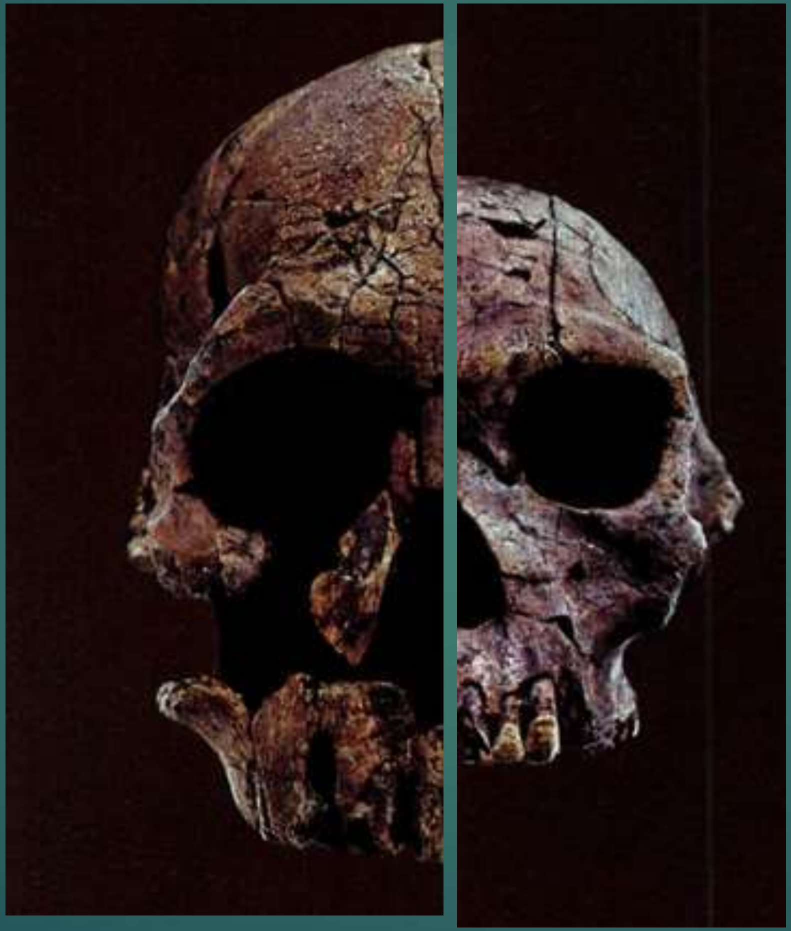
- To address the issue of 1 or 2 species, you must look at Koobi Fora, for there is where problem is.
- Koobi Fora specimens: KNM-ER 992, 1802, 1470, 1813, 1590, 1805

Are these two the same species?

Lake Turkana: Sexual dimorphism or different species?

KNM-ER 1470 :

750 CC



KNM-ER 1813:

510 CC

1813 group (*Homo habilis*) and 1470 group (*Homo rudolfensis*)

- Multiple attempts have been made to divide up these specimens, incl.
  - *H. habilis vs H. rudolfensis,*
  - *H. habilis vs H. erectus,*
  - *H. habilis* sensu stricto vs *Homo* spp, ("several species")
  - *H. habilis vs H. rudolfensis vs H. erectus*

- Some believe these are not two species, but a single species: *Homo habilis sensu lato* (in broad sense)

- But lack of agreement concerning how much variability can be subsumed within a single species is at the core of the debate surrounding the identity of the taxon *Homo habilis*

Below are two fossils, KNM ER 1813 is to the left, and KNM ER 1470 is to the right.

Originally, both were assigned to the species *Homo habilis*, with ER 1470 thought of as male and the smaller ER 1813 a female in a strongly dimorphic species.

However, the anatomies of the two skulls differ considerably.

1813 1470

1813 group (*Homo habilis*) and 1470 group (*Homo rudolfensis*)

- Paleoanthropologists disagree on the number of species that are represented by *H. habilis sensu lato* (in broad sense).
  - 1813 group: The *H. habilis* hypodigm consists of a
    - group of smaller-brained (cc = 611),
    - small-toothed individuals;
    - not an obligate biped;
    - Not reliably a clade with Homo; grade is more like Austrolopiths per Wood
  - 1470 group: *H. rudolfensis* –
    - a group of larger brained (cc = 775), individuals with
    - large teeth,
    - relatively long faced
    - less prognathism, and
    - reduced supraorbital tori;
    - no postcranial remains

KNM-ER1470 vs 1813: *H. rudolfensis vs H. habilis*

1 - *Homo rudolfensis*,
KNM-ER 1470:

large, flat face;
small browridge
small anterior teeth,
moderately sized
posterior teeth,
squared off front tooth
row, short palate;

Originally considered
to be *H. habilis;*

No stone tools found

No postcranial

2 – *Homo habilis*,
KNM-ER 1813:

Larger browridge,
Small upper jaw,
more curved tooth row,
face is flatter; third
molars were fully
erupted and showed
evidence of wear = adult

Best known *Homo*
habilis –
Turkana Basin,
Olduvai Gorge

Different species or sexual dimorphism in same species?
No mandibles for either

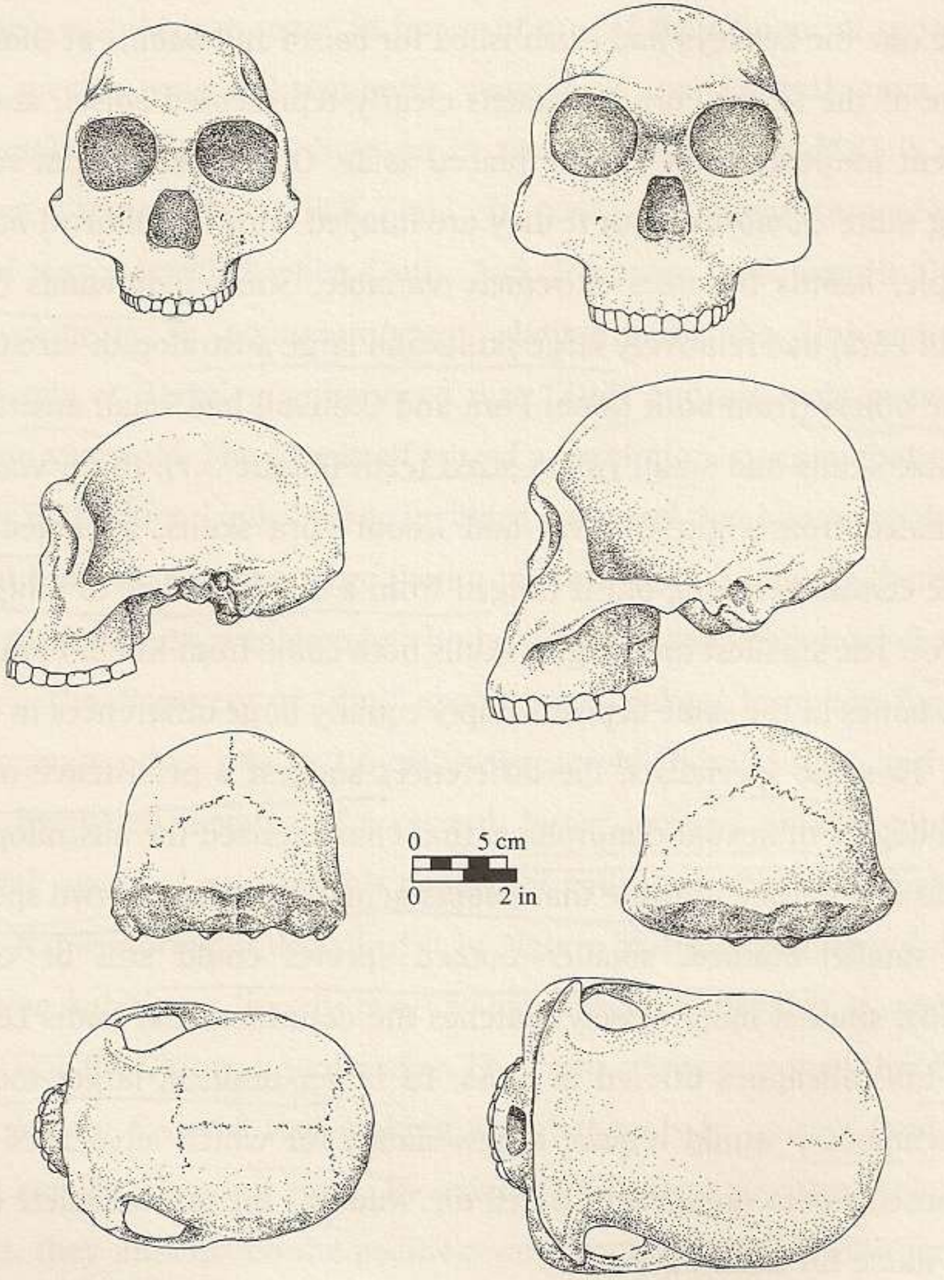
(Leakey et al., 2012)

Australopithecus africanus, *STS 5*
About 2.5 million years old
Small braincase; sloping face

Homo rudolfensis, *KNM-ER 1470*
About 1.9 million years old
Braincase larger than in earlier humans; sloping face

Homo erectus, *Sangiran 17*
About 1 million years old
Medium braincase; distinct brow ridge

- Small brain case: 510 cc
- Small face, narrower, not very flat
- Small cheek teeth
- Strong curved brow ridge
- More angulated occipital bone
- KNM-ER 1813
  (*H. habilis*)



Kenya National Museum -
East Rudolf Specimen No. 1813

Kenya National Museum -
East Rudolf Specimen No. 1470

- Fairly large brain case; 750 cc
- Broad, long, flat face
- Large cheek teeth
- Slight brow ridge
- Broader postcanine teeth
- KNM-ER-1470
  (*H. rudolfensis*)

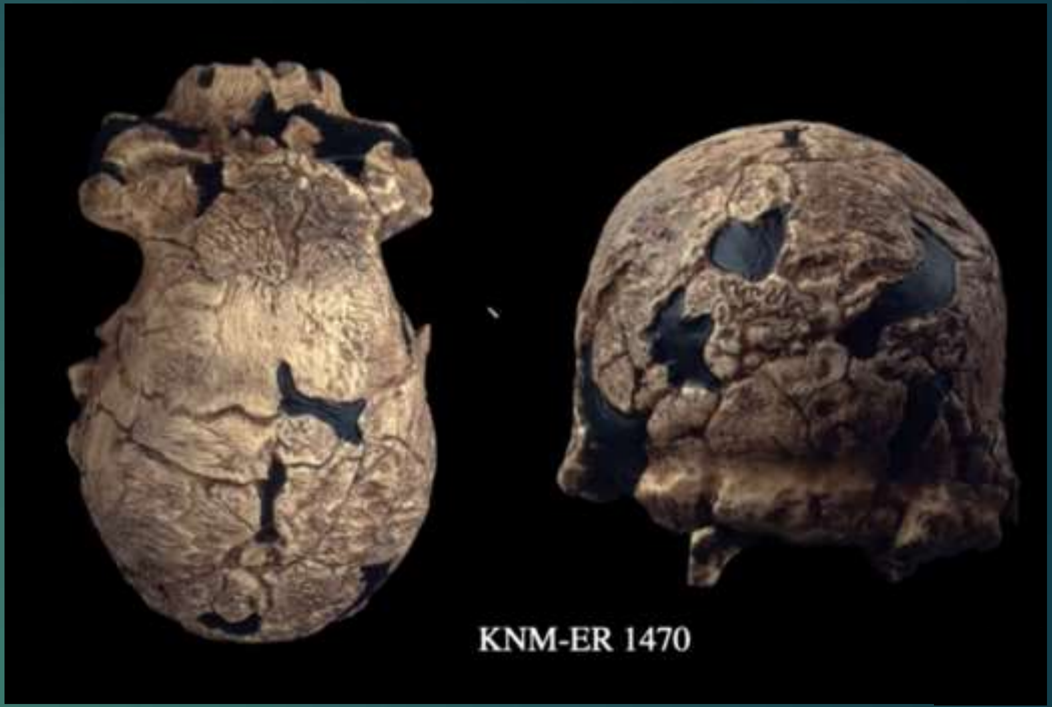
1470 and 1813

- Most researchers agree that both specimens belong to the genus *Homo*.

- Question is whether both crania could be from same species, and if so, would this be *H. habilis* as defined by Olduvai fossils?
- Based mainly on differences in
  - Cranial size and shape
  - Particularly supraorbital and cheek or molar region
  - Cranial capacity (510 cc for 1813 & 770 cc for 1470)

- Some researchers have concluded that these 2 crania show too much variation to be the same species (Walker, Leakey, Wood, Stringer, Groves)

KNM-ER1470



KNM-ER 1470

KNM-ER 1813

Left side of 1813 is compressed, distorted

Cranial Differences in 1470 and 1813

- 1813: strong supraorbital torus (horizontal bar of bone above the eye sockets)
- 1470: slight supraorbital torus, & does not have the depression behind it that is seen in 1813.
- The face of 1470 is longer than 1813's and 1470's upper jaw is square instead of rounded-off.
- There is a great discrepancy between the cranial capacities of the two individuals as well.
    - ER 1470 has a cranial capacity of 775cc,
    - ER 1813 has a cranial capacity of only 510cc (which is above the australopith average, but well below the accepted 600cc cutoff for *Homo*)

Differences

Homo habilis/1813	***Homo rudolfensis/1470***
Height: 1.0 meters	Ca. 1.5 meters
Physique: Relatively long arms	Robust
Cranial Volume: 500 – 650 cc	600 – 800 cc
Date: 2.0 – 1.6 Ma	2.4 – 1.6 Ma
Distribution: Eastern & S. Africa	Eastern Africa
Skull form: Relatively small face; nose developed	Larger, flatter face
Jaws/Teeth: Thinner jaw; smaller, narrow molars	Robust jaw; large narrow molars

Debate

- One debate in paleoanthropology today is whether or not ER 1470, and several other fossils previously identified as *H. habilis,* should be grouped into a new species, *Homo rudolfensis*.
- This classification would acknowledge that ER 1470 and the other members of *Homo rudolfensis* differ more from *Homo habilis*, sensu stricto ("in the strict sense," meaning: as originally defined), than could possibly be accounted for by variation within a population or between sexes.
- This would place two species of the genus *Homo* in Africa during the same time period in addition to two members of the genus *Paranthropus*, and, possibly, late surviving members of the species *Australopithecus africanus*.
- Far more complicated than the original neat, linear model.

1470 group: *Homo rudolfensis* (KNM-ER 1470), 1.8 M, 700-775 cc
Richard Leakey, Koobi Fora, Kenya, 1972

1986: Valery Alexeev made KNM-ER 1470 the type specimen of *Pithecanthropus rudolfensis*

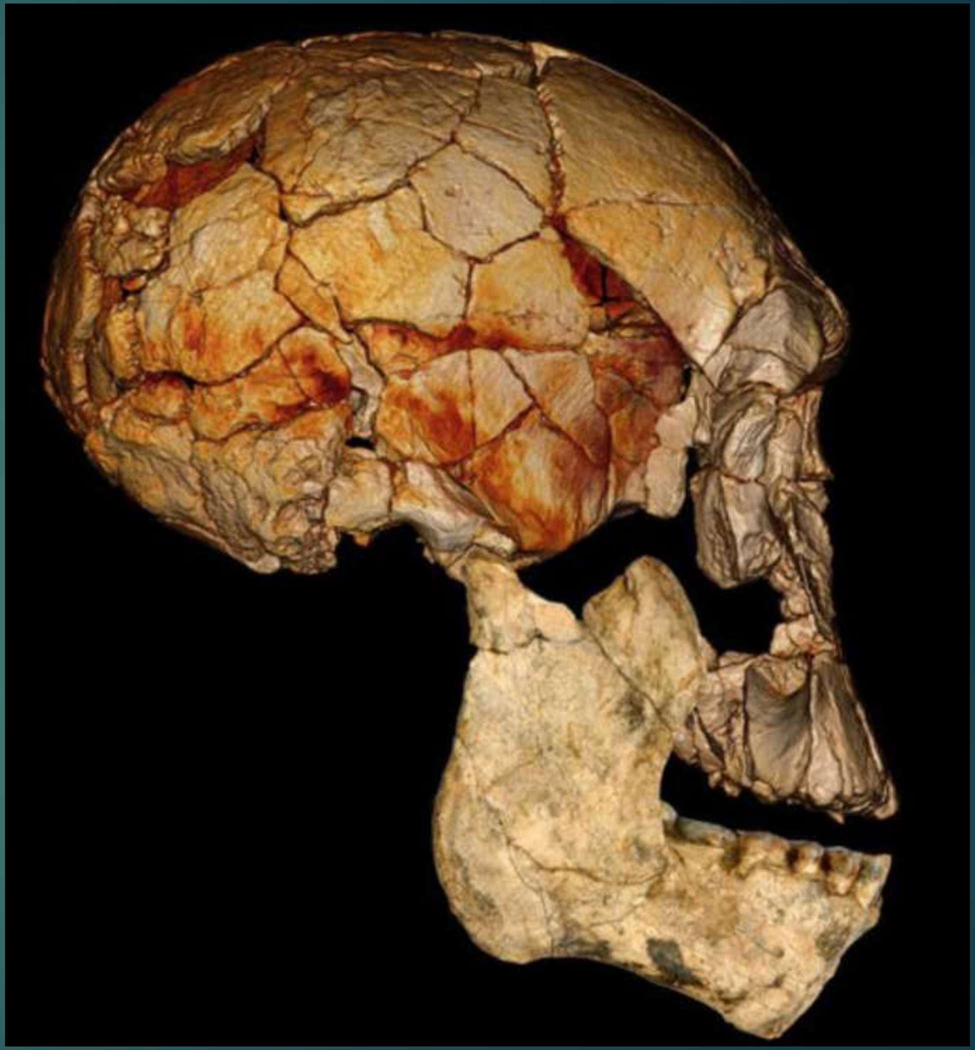
1989: Colin Groves transfers *Pithecanthropus rudolfensis* to *Homo* as *Homo rudolfensis*

Large "*H. habilis*"

Homo rudolfensis
(KNM ER 1470, type specimen)
Discoverers: Bernard Ngeneo
Date: 1972
Locality: Koobi Fora, Kenya
Age: 1.8 M

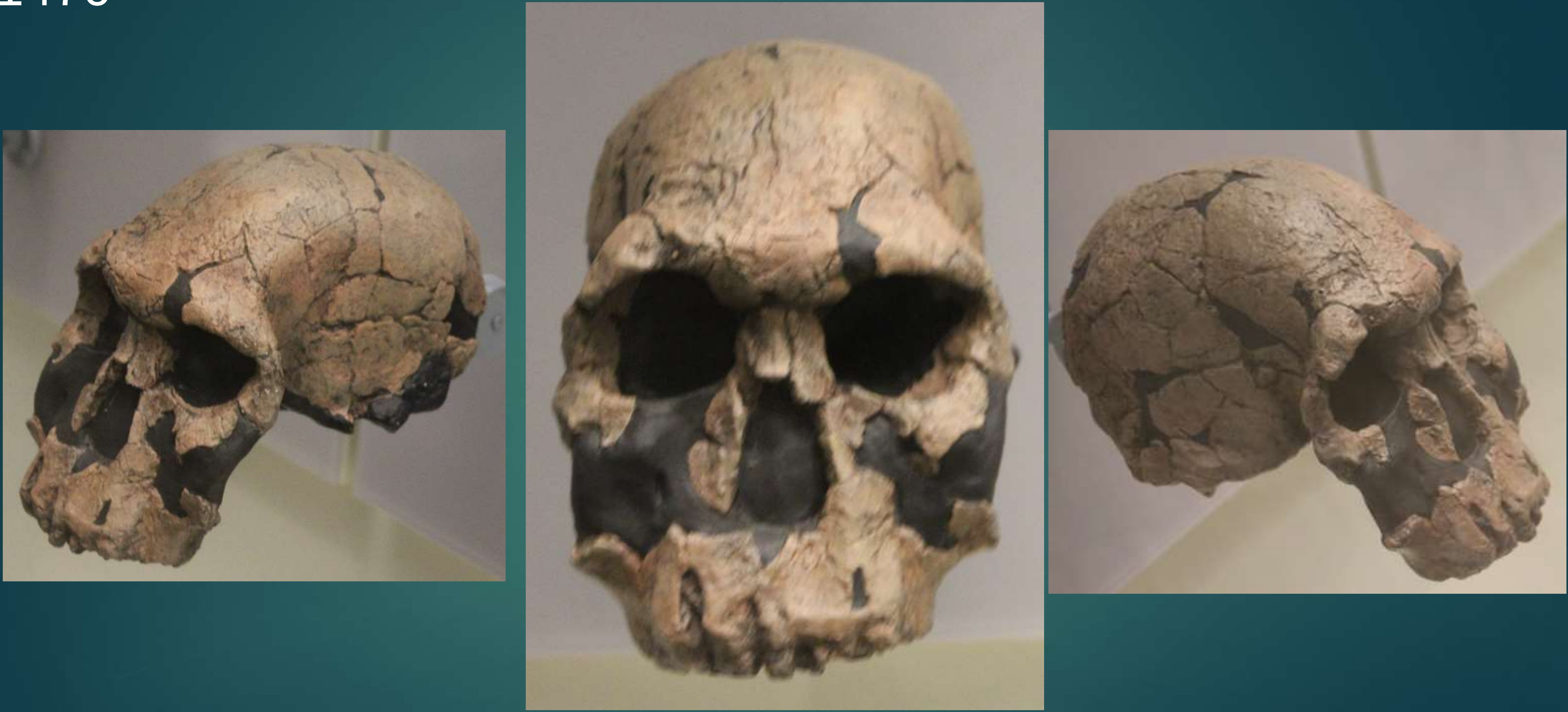
1470

1470



With ER 60000 mandible

1470



KNM-ER1470

- KNM-ER1470, Turkana, 1.8-1.9M:
  - vertically flat face,
  - large cranial capacity
- But: cast indicates 2 fxs, missing zygomatic areas (which would help distinguish it from Aust.)
- Broad palate & large root of zygomatic is primitive; postorbital constriction, no sagittal crest, bulbous cranium, nuchal torus

1470 traits

Height	4.9 ft (150 cm) (sexes combined)
Weight	F: 112 lb (51 kg) M: 132 lb (60 kg) (F about 85% of M)
Brain size	781 cc mean (752-810 cc range)
Cranium	Flat face; no brow ridge; large palate; no sagittal crest; everted mandibular base
Dentition	Broader lower grinding teeth than *Homo habilis;* multirooted lower premolars
Limbs true	Limb proportions unknown; feet possibly more like those of later humans than was *for H. habilis*
Locomotion	Bipedalism (probably relatively modern)
Known dates	2.4-1.6 Ma

Homo rudolfensis

- Is 1470 *Homo rudolfensis*? More primitive version of *Homo* and is especially characterized by larger features, especially larger features of the dentition.

- 1802 mandible: large dentition, bulbous molars, molarized premolars

- OH7, *Homo habilis,* 100-200K later: reduced premolars


KNM-ER 1802


KNM-ER 1802

Olduvai Hominin 7

1470

- As was argued in the initial proposal for two taxa, there are important differences in facial structure and perhaps dental size between the two specimens. Regardless of how it is hafted to the vault, the KNM-ER 1470 face is quite flat, with a forward-facing malar region and relatively deep and tall zygomatics that are anteriorly inclined. The anterior tooth row and the maxillary bone that holds it are somewhat retracted and narrow across the canines.
- Although the anatomy shows superficial similarities to the *Paranthropus* face, zygomatic position causes the facial flatness in *Paranthropus*, whereas the midface itself is flat in KNM-ER 1470. Wood suggested additional parallels between the two, including postcanine megadontia (albeit less marked in KNM-ER 1470). He thus described the 1470 morph as a large-brained but large-toothed early *Homo*.

1470

- KNM-ER 1470, while preserving a face and vault, lacks maxillary dental crown morphology and does not preserve a mandible.

- The large size of the vault, tooth roots, and flat anterior face suggested that large individual with a “heavy” masticatory pattern might be the best fit.
- However, there are no discrete, derived anatomical arguments beyond vault size and inferred dental size for linking KNM-ER 1470 with KNM-ER 1590, until recently the only complete maxillary dentition assigned to *H. rudolfensis*.

1470*:* controversy - Size

- Mandible (jaw) and teeth just didn’t seem to fit within acceptable limits of variation or differences for *H. habilis*.
- Even if KNM-ER 1470 was considered a large *H. habilis* male, the size difference would be too great compared to KNM-ER 1813, an established *H. habilis* female, for the two to both belong to the same species.
- Large teeth (from tooth roots), the skull lacked the massive jaw muscle features characteristic of robust australopithecines
- Today, most scientists now accept KNM-ER 1470 as belonging to *Homo rudolfensis*—a species that co-existed in the Turkana Basin, northern Kenya, with three other species sometime between 2.0 and 1.5 Ma: *Homo habilis, Homo erectus, and Paranthropus boisei.*

Anatomical features of early *Homo* groups: 1470 group

- The 1470 group is defined by the derived shape of the face, which is relatively tall and flat with the incisor/canine row squared off and the upper third premolar forming the corner of the anterior palate. Lower incisors are narrow. Premolars are mesiodistally narrow and molars are large but just slightly larger than average for all early *Homo*. There is no third molar reduction. The vault is rounded and lacks a posttoral/supratoral gutter. The posterior mandible (bigonial/bicondylar breadths) is wide relative to arcade breadth, and the corpus is relatively tall.

Anatomical features of early *Homo* groups: 1470 group

- Only the largest specimen, KNM-ER 1470, allows actual estimates of brain size (750 cc) or body size (43 to 63 kg, based on orbit size), but differences in size between KNM-ER 1470 and the more fragmentary KNM-ER 62000 suggest that the lower range of brain and body size is substantially less.
- Given that facial dimensions of KNM-ER 62000 are between 75 and 80% of those of KNM-ER 1470, S. Antón suggests ranges of 560 to 750 cc and 35 to 50 kg for this group.

1470 group

- *Cranial Vault*:
- Vault anatomy is preserved only in the largest specimen, KNM-ER 1470.
- The vault is relatively rounded in sagittal view with a steeply rising frontal lacking a supratoral gutter.
- There is moderate postorbital constriction.
- No sagittal or nuchal cresting is apparent.

1470

- Key members: cranium KNM-ER 1470; partial face 62000; mandibles KNM-ER 1482 and 60000.
- No postcranial remains are affiliated with this group. These certain and probable exclusions remove evidence for extremely large molar size in this group.
- *Facial Shape:*
- The facial skeleton is fairly derived but not specifically in the direction of later *Homo*.
- The anterior face is flat and relatively tall. Contributing to this flatness, the incisor and canine row is flat/squared-off and the zygomatic processes arise relatively far forward on the face.

- The face is relatively tall, and related to this, the broad mandibular ramus (as represented by KNM-ER 60000) sits quite high above the tooth row.
- The mandibular corpus is relatively tall compared to width and the posterior mandible is much broader (bigonial/bicondylar) than the anterior in part as a result of diverging posterior tooth rows. As a result, the extramolar sulcus is broad.

Evolution of early *Homo:* 1470 group

- *Dentition*: Lower incisor crowns are narrow with relatively short roots and the canine root is also reduced in size compared to *Australopithecus*. The posterior tooth row is relatively short due to premolar foreshortening not to molar reduction. Premolars are relatively mesiodistally compressed and are not unduly molarized, but molars are large. There is no third molar reduction.

- While the 1470 group has larger molar occlusal areas than the 1813 group, dental size is not absolutely large in the 1470 group with respect to other non-*erectus Homo*. Apparent difference in molar size is most likely an artifact of excluding a number of specimens

1470 group

- *Size*:
- Both body and brain size estimates are skewed to the larger end of the assemblage because only the largest specimen, KNM-ER 1470, preserves cranial capacity and orbit size (from which body mass may be estimated). (Orbital area is correlated with body mass at $r = 0{\cdot}987$ (John Kappelman, 1996).

- However, the fragmentary remains affiliated with one another based on palate shape display a range of size variation in which KNM-ER 1470 is the largest and KNM-ER 62000 the smallest (at only about 75-80% of KNM-ER 1470’s size).
- Estimates of the body and brain size range of 1470 group suggested by KNM-ER 62000 fragments is extensive and overlaps substantially with the 1813 group.

1470 group

- *Postcrania*: Postcranial traits and proportions are unknown given the current lack of affiliated postcranial remains.
- *Time based on East African remains*: 2.09-1.78 Ma
- Today, most scientists now accept KNM-ER 1470 as belonging to *Homo rudolfensis*

KNM-ER
1813
H. habilis

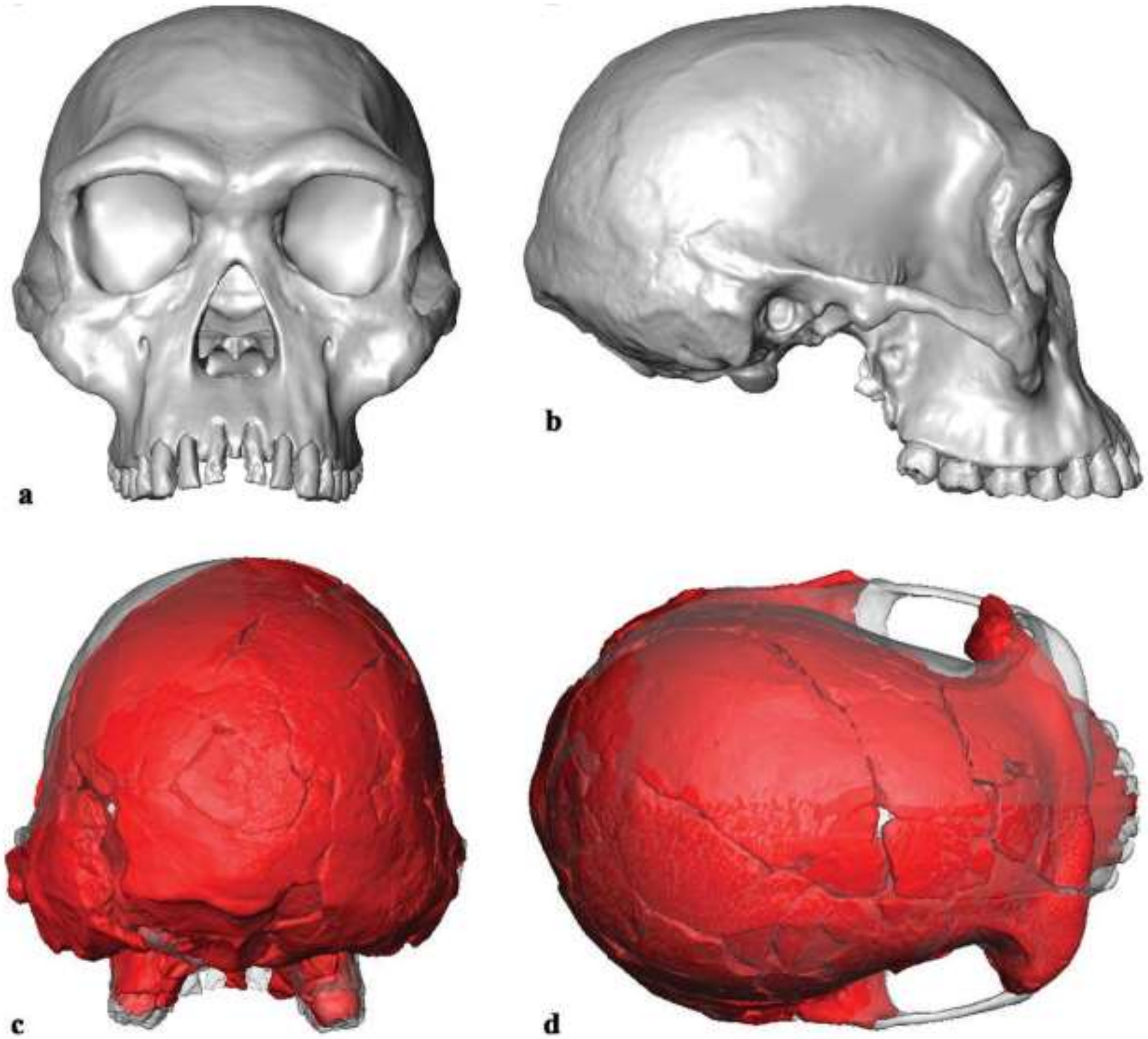


Fig. 3. The digitally reconstructed KNM-ER 1813 cranium in frontal (**a**) and lateral (**b**) view. The reconstructed cranium (transparent grey) is superimposed onto the original specimen (red) in posterior (**c**) and top (**d**) view.

KNM-ER 1813

Cast of KNM-ER 1813, a 1.9 Ma *Homo habilis* skull from Koobi Fora, Kenya; by Kamoya Kimeu in 1973; cranial capacity 500 cc; also called *Homo microcranous;* This is one of the most complete skulls of this species.

ER 1813

- Smaller build,
- smaller cranial capacity,
- gracile supraorbital torus;
- postorbital constriction,
- mild low facial prognathism,
- widest point on base of skull
- high root of zygomatic
- more primitive than 1470
- 3rd molar just erupting; late teenager

1813

1813

1805 & 1813

Other *Homo habilis:* KNM-ER 1805, & OH 13

KNM-ER 1805
Site: Koobi Fora, Kenya
Year of Discovery: 1973
Discovered by: Paul Abell
Age: About 1.7 million years old
Species: *Homo habilis*

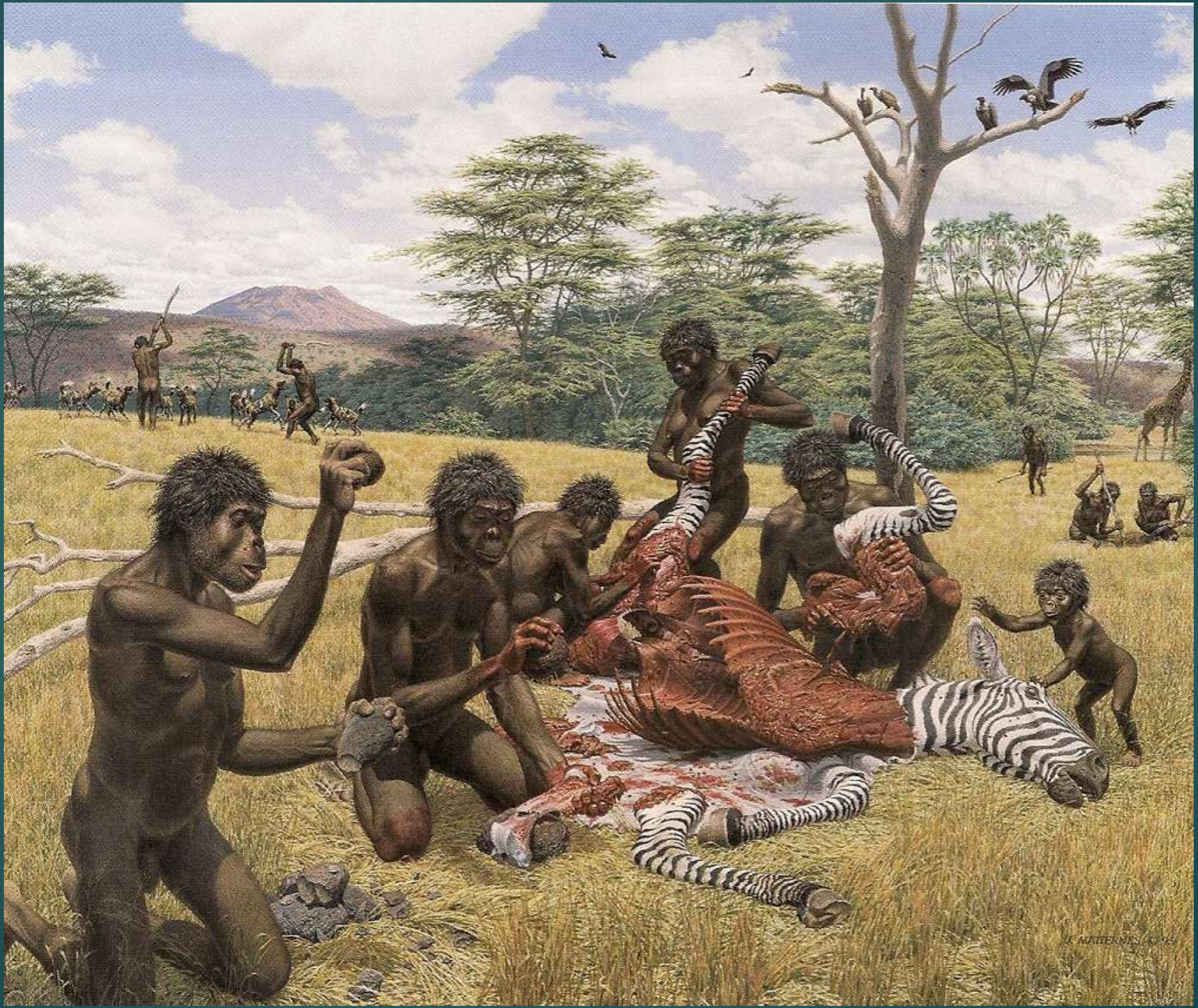
Originally placed in *Homo erectus*, but based on the degree of prognathism and the shape of the cranium (especially the prominent nuchal crest), it is now considered to belong in *H. habilis*.

OH 13 (1.66 Ma). Nicknamed "Cinderella", 16 yo female

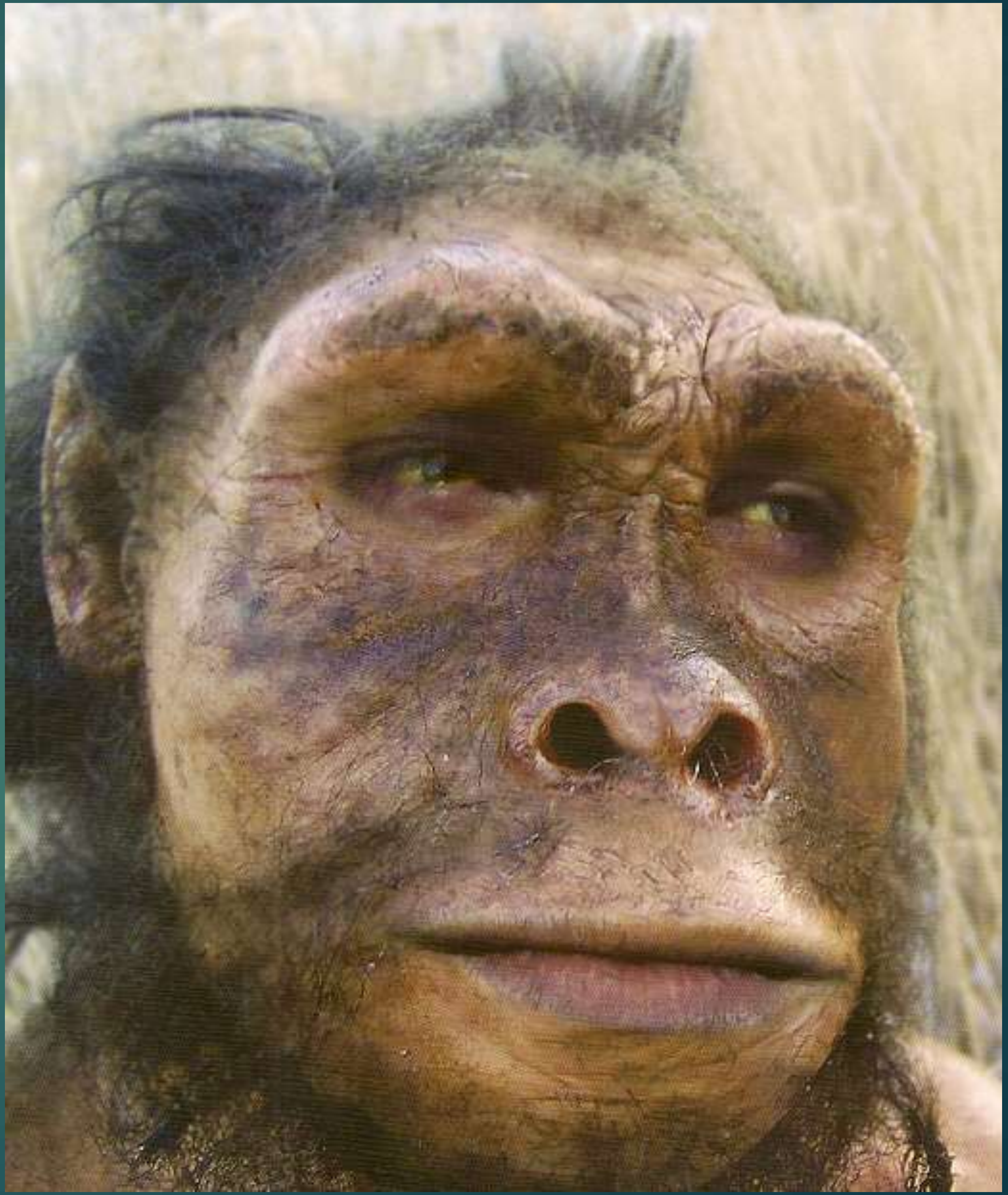
1805

1813 Reconstruction based on skull!

Homo habilis scene by Jay Matternes at AMNH



Female and male *H. habilis* by V. Deak



1813 group anatomy

- The 1813 group presents a more primitive facial architecture with a rounded anterior palate and more parallel and narrow posterior tooth rows.

- Jaw and dentition:
- Lower incisors are broader than in the 1470 group (uppers are unknown for the 1470 group).
- Molars are about the size of or slightly smaller than the 1470 group; however, if the large-molared KNM-ER 1802 is included, as we suspect it should be, these differences disappear entirely.
- There is no third molar reduction.
- Mandibular height and width are similar; rami are essentially unknown.

1813: cranial vault

- The vault is rounded with some posterior occipital cresting in some individuals (e.g., KNM-ER 1805).
- Brain size estimates from the best preserved of these yield a range of 510 to 660 cc
- S. Antón: upper range may increase to as much as 775 cc.

1813 Group: 9 specimens

- Relatively strong upper limbs compared with lower limb strength, suggesting a sustained arboreal component (perhaps related to nesting) in addition to their terrestrial locomotor repertoire.

- Body size estimates are available from only the smallest specimens and suggest ranges of 30 to 35 kg; upper range could be at least 42 kg.

- 9 Key members of 1813 Group: crania KNM-ER 1813, OH 24; partial crania and mandible KNM-ER 1805, OH 13; palate OH 65; fragmentary cranial and postcranial KNM-ER 3735, OH 62; Likely members: Mandible KNM-ER 1802 & Uraha 501; likely but not certain members of 1813 group.

1813 group

- *Facial Shape:* The facial skeleton is fairly primitive and relatively prognathic compared to the 1470 group.

- The anterior palate is rounded and more projecting (the incisors and canines do not form a flat row across the front of the palate)

- Posterior tooth rows are more parallel (less diverging) and relatively narrow.

1813: Face

- However, the face lacks features seen in the face of *Australopithecus* including facial pillars and a glabellar prominence and while more prognathic than the 1470 group is less so than *Australopithecus.*

- Additionally, the nasals are more peaked. The mandibles of the 1813 group also tend to have corpora that are more similar in their height and width than the 1470 group, which tends to have fairly tall corpus heights for width. While no complete rami are present, the partial rami would suggest that the extramolar sulcus is not as broad and probably that the bicondylar/bicoronoid breadths are not as great compared to arcade breadth as in the 1470 group, which would also partly follow from the more parallel and narrow posterior arcades.

1813 group: Dentition

- Anterior dental size is somewhat more primitive than the 1470 group with larger lower incisor crowns and canine roots.

- There is no third molar occlusal area reduction. Some specimens have smaller M1s than KNM-62000 of the 1470 group, the apparent differences in group means/ranges are likely an artifact of specimen inclusion.
- Molar and premolar size is reduced relative to the condition in *Australopithecus*.

1813: Vault & Postcrania

- The vault is rounded in sagittal view with a frontal that shows a continuous posttoral sulcus.

- There is moderate postorbital constriction.
- Cresting is apparent in some individuals.

- Greatest breadth is low in the supramastoid region, but the greatest breadth at the parietals is only marginally smaller.
- *Postcrania*: Evidence of relatively strong humeral to femoral cross-sectional properties in OH 62 have been used to argue for a substantial arboreal component to the locomotor repertoire of this group.

1813 group

- *Size*: Both body and brain size estimates are skewed to the smaller end of the assemblage because only the smallest specimens, KNM-ER 1813 and 1805, preserve cranial capacity and orbit size, and because the associated postcranial remains, OH 62, are also from a small individual.
- However, the fragmentary remains affiliated with one another based on extrapolation from KNM-ER 1813's anatomy display a range of size variation.
- OH 65 is the largest and about 15% larger than the next largest, OH 13. The body and brain size range of this group as suggested by these fragments should have a larger maximum size than exhibited by the more complete specimens and overlap substantially with the 1470 group.
- *Time based on East African remains*: 2.09-1.44 Ma

1813

- Alternatively, the KNM-ER 1813 face is more conservative in its structure, with a moderately prognathic midface, a rounder anterior maxilla, and somewhat more posteriorly positioned but more vertical zygomatic arches.

- The KNM-ER 1813 face also houses relatively smaller teeth.

- If we accept that the structural differences in the face indicate two different species, then who belongs to each group depends on direct anatomical associations between the other fossils and either 1470 or 1813.

1470 vs 1813: Different sexes?

- The differences between KNM-ER 1470 and KNM-ER 1813 can be interpreted in various ways.

- As Different Sexes –
  - Other things being equal, large bodied individuals have a bigger head and brain than small individuals.
  - KNM-ER 1813 may be a female and KNM-ER 1470 may be a male of *Homo habilis*.
  - However, they do not differ from each other in the sort of ways that males and females of modern apes (including humans) differ from one another.

1470 vs 1813: different species?

- Or as Different Species –
  - scientists claim that 1813 and 1470 represent two species, or even two genera.
  - Suggestions include *Australopithecus africanus*, *Homo habilis* and *Homo rudolfensis*.
  - The discovery of a skull of *Kenyanthropus platyops* in 1999, and its similarity to KNM-ER 1470, has led some to consider reclassifying KNM-ER 1470 into the *Kenyanthropus* genus.

Reinterpretation: 1813 vs 1470

- New fossils support the
  - presence of multiple groups of early *Homo* that overlap in body, brain, and tooth size
  - challenge the traditional interpretation of *H. habilis* and *H. rudolfensis* as representing small and large morphs, respectively
- Because of a fragmentary and distorted type specimen for *H. habilis* (OH 7):
  - two informal morphs have been proposed, the 1813 group and the 1470 group, that are distinguished on the basis of facial anatomy but do not contain the same fossils as the more formally designated species of early *Homo*.

Classic division

- *H. habilis*/1813 group, 11 specimens: smaller brained, smaller-toothed
  - 5 specimens from Olduvai Gorge: (Olduvai Hominid = OH) OH 7, 13, 16, 24, 62
  - 5 specimens from East Turkana (KNM-ER 1813, 1805, 1501, 1502, 42703)
  - Oldest: AL 666-1 maxilla from Hadar, 2.33 MA; youngest, Koobi Fora maxilla (KNM-ER 47203, 1.44 Ma)
- *H. rudolfensis*/1470 group, 6 specimens: larger brained, larger-toothed
  - well documented only by 5 specimens from East Turkana/Koobi Fora (KNM-ER 1470, 1590, 1801, 1802, 3732)
  - Olduvai: Only OH 65, a maxilla that resembles maxilla of skull 1470

Homo habilis/1813 vs. *Homo rudolfensis/1813*

- All of the crania, jaws, and teeth of specimens of *H. habilis* are more variable than one would expect for a single species.
- Many now divide it into 2 species:
  - *H. habilis/1813 group* (technically called sensu stricto ("strict sense")
  - *H. rudolfensis/1470 group*.

- *1470* has a bigger brain (700-800cc); bigger, wider face; & larger chewing teeth (latter more like robust australopiths);

- We know nothing about 1470's limbs. Case for both being *Homo* would be greatly strengthened if limb bones of *H. rudolfensis/1470* were like those of *H. ergaster.*

1470 & 1813 group controversy

- KNM-ER 1470 and KNM-ER 1813
- Are they from the same species, *Homo habilis?*
- These two fossils are still taxonomically undetermined:
  - different species or
  - their differences could be related to sexual dimorphism within a single species.
- It is argued that unless *Homo habilis* was significantly more sexually dimorphic than *Gorilla gorilla*, it is improbable that the two fossils can both be classified as *Homo habilis*. The creation of at least one new species is required.

Daniel E. Lieberman, David R. Pilbeam, Bernard A. Wood, 1988

H. habilis (1813) vs. H. rudolfensis (1470)

- Wood includes:
  - all non-australopith specimens at Olduvai in *Homo habilis*,
  - whereas Lake Turkana fossils are divided between *H. habilis/1813 and H. rudolfensis/1470*
- Wood: KNM-ER 1470 is *H. rudolfensis*; KNM-ER 1813 and KNM-ER 3735 are *H. habilis*
- *H. rudolfensis (1470)*
  - Larger brained
  - Flatter, broader face
  - Broader postcanine teeth
  - More complex crowns and roots & thicker enamel
- *H. habilis (1813):* smaller brained; archaic postcranium

1470 & 1813 Groups: facial shape differences

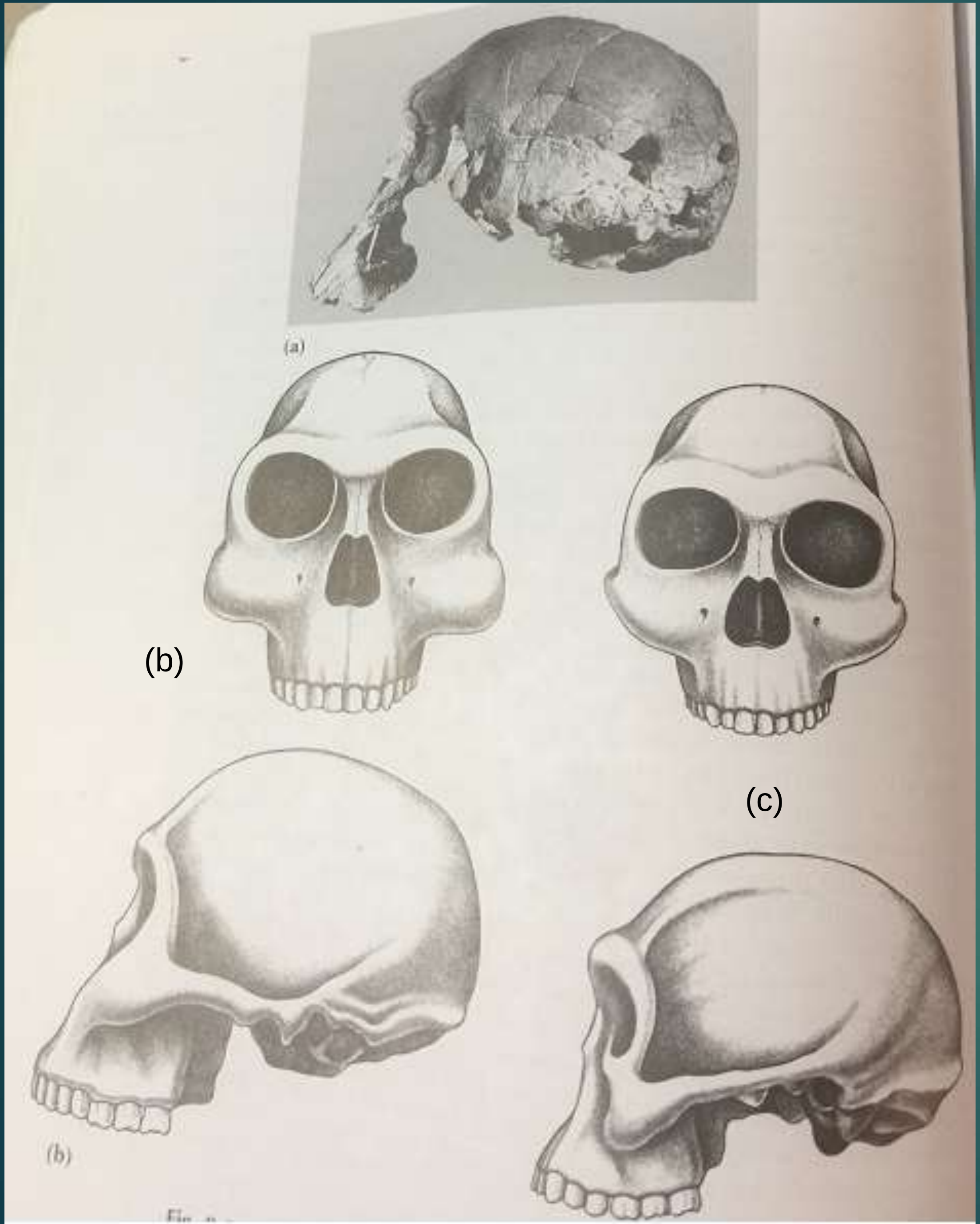
- S. Antón's model: suggests we call the groups of early non-*erectus* *Homo* after their most iconic specimens.
  - The 1470 group (2.1 to 1.8 Ma) is named for KNM-ER 1470 and is distinguished particularly by its:
    - short and flat anterior dental arcade (with a short premolar row and flat anterior tooth row)
    - and relatively tall, flat face.

S. Antón’s 2012 model

The 1813 group (2.1 to 1.4 Ma) is named for KNM-ER 1813.

  - more primitive face
  - with a round and more projecting anterior palate

- *** These groups do not comprise the same fossils as previously attributed to *H. rudolfensis* and *H. habilis*.
- R. Klein, 2009: Provisionally, attributes variability of early *Homo* in skull & dental size to extreme sexual dimorphism within a single species, designated as *H. habilis*

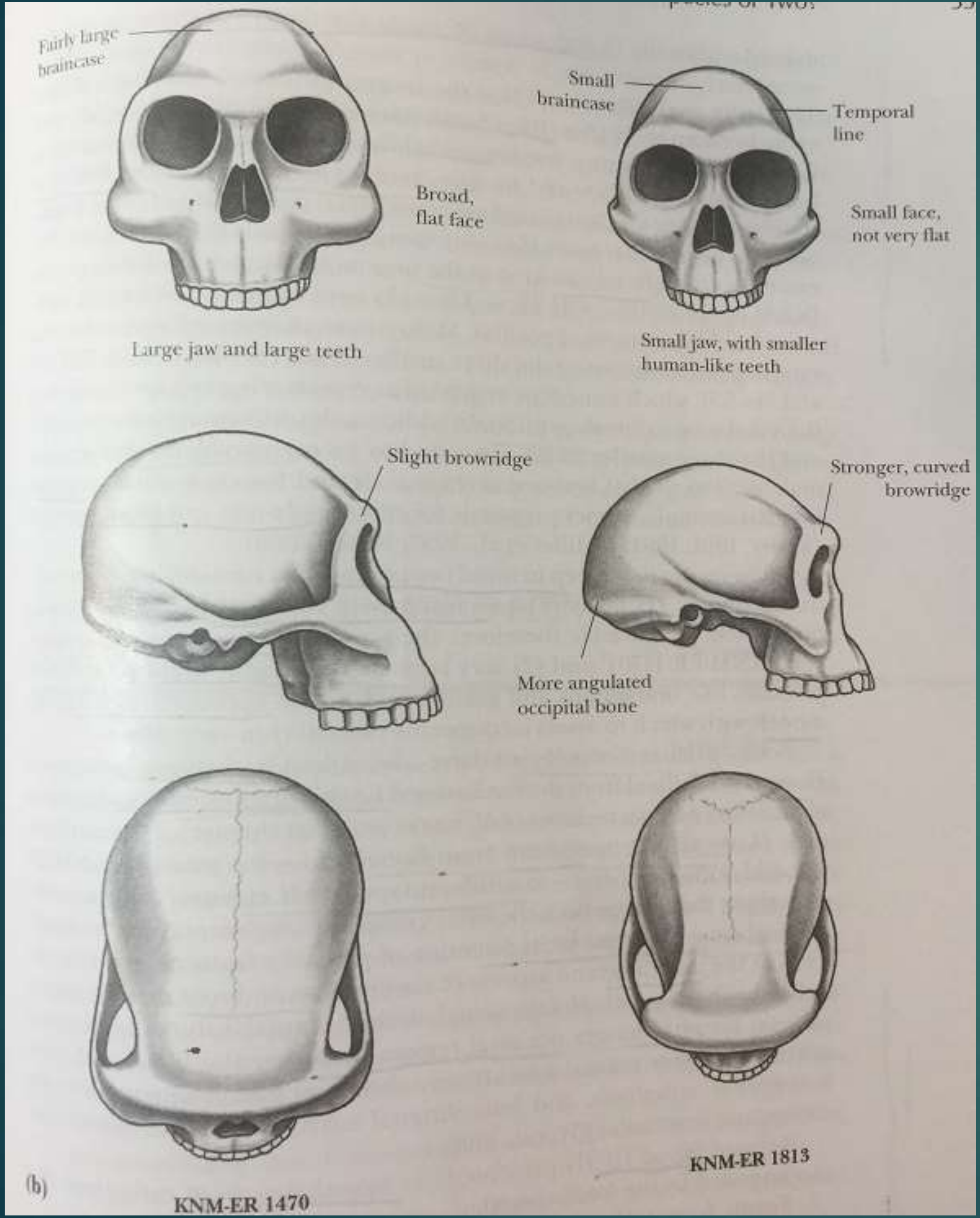


- Crania of H. habilis from Koobi Fora
- A: ER 1470, type of H. rudolfensis

- b: reconstruction of ER 1470, presumably male

- c: reconstruction of ER 1813, presumably female

Morphological differences between crania KNM-ER 1470 & 1813



More Fossils: Koobi Fora, KNM-ER 60000 & 62000

nature

THE INTERNATIONAL WEEKLY JOURNAL OF SCIENCE

A FACE IN THE CROWD

Lake Turkana fossils reveal diversity among early *Homo* species PAGES 162 & 201

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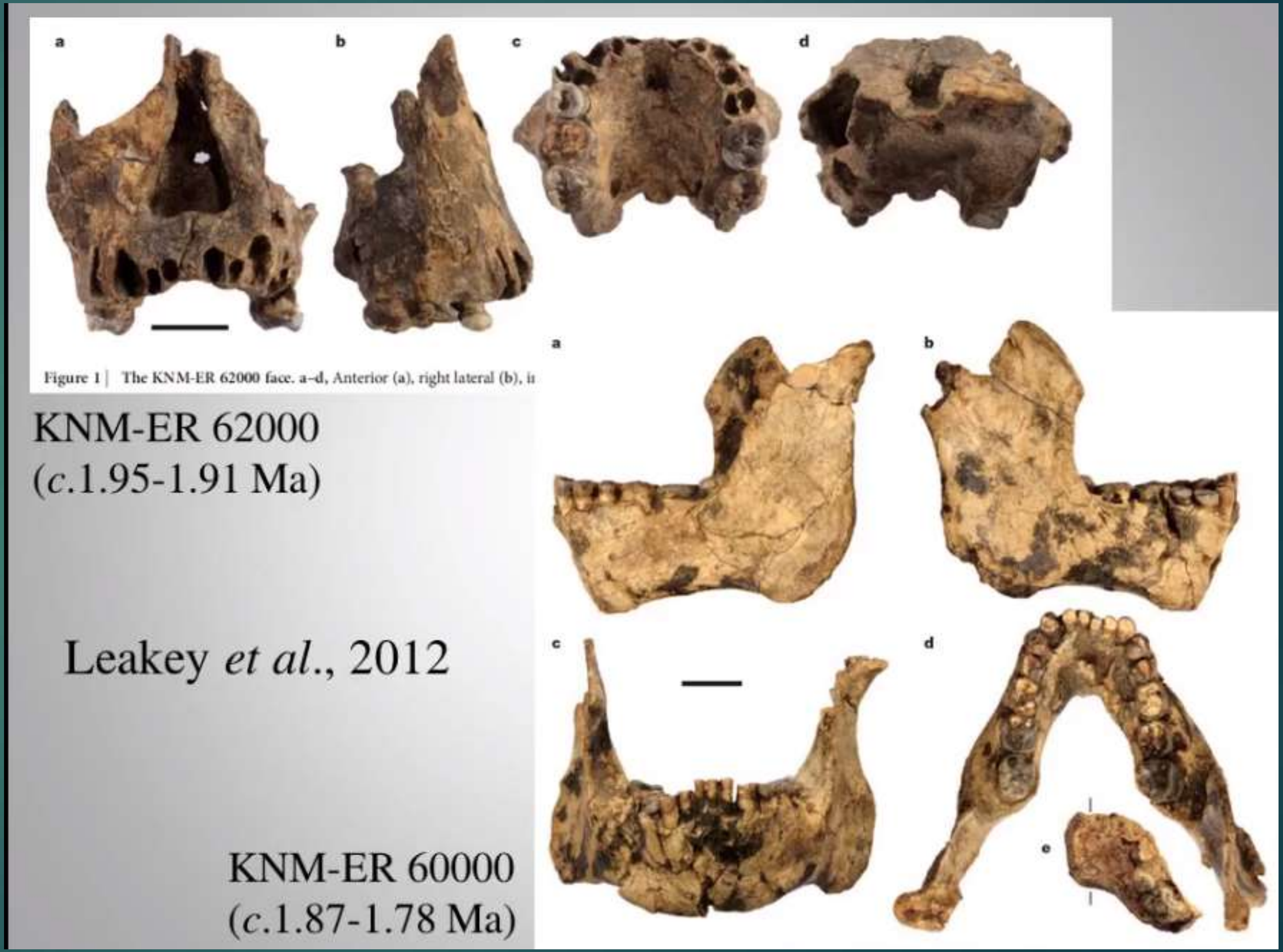


Figure 1 | The KNM-ER 62000 face. a–d, Anterior (a), right lateral (b), i

KNM-ER 62000
(*c*.1.95-1.91 Ma)

Leakey *et al*., 2012

KNM-ER 60000
(*c*.1.87-1.78 Ma)

KNM-ER 60000 & 62000

- Found within a radius of just over 10 km from 1470's location, the three new fossils are dated between 1.78 and 1.95 Ma.

- The face KNM-ER 62000, late juvenile, discovered by field crew member Elgite Lokorimudang in 2008, is very similar to that of 1470, showing that the latter is not a single "odd one out" individual.

- Moreover, the face's well-preserved upper jaw has almost all of its cheek teeth still in place, incl. long postcanine teeth, which for the first time makes it possible to infer the type of lower jaw that would have fitted 1470.

Meave G. Leakey, et al., 2012

Maeve Leakey & Fred Spoor: 2012, KNM-ER 60000 jawbone (with KNM-ER 1470 cranium)

Kenya’s Lake Turkana between 2007 and 2009

A composite image pairs a newfound jawbone (see above) with a 1470 cranium found in 1972. Illustration courtesy Fred Spoor.

1.78-2.0M: 6 miles from 1972 ***Homo rudolfensis/1470*** skull,

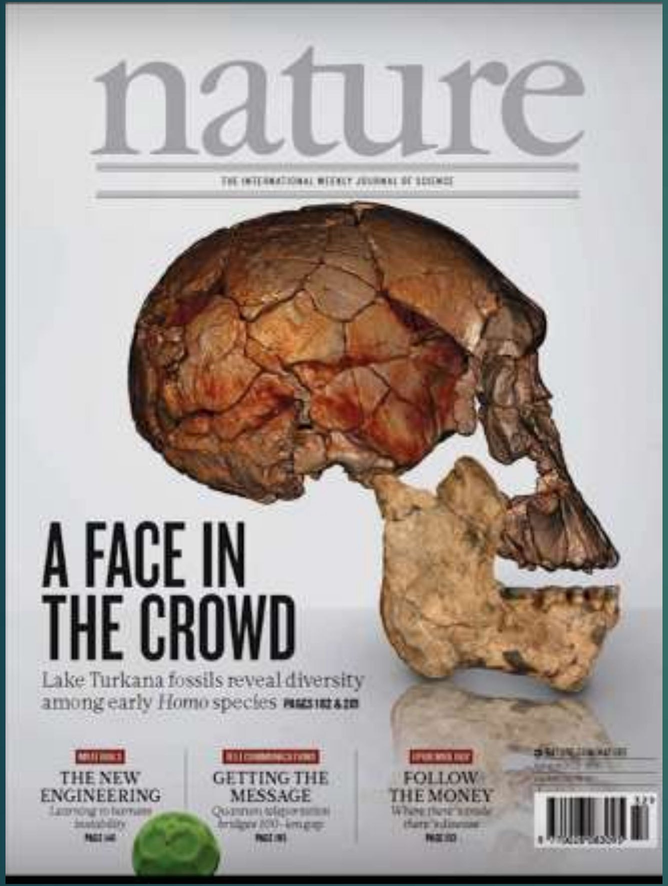
KNM-ER 60000 mandible

KNM-ER 60000 stands out as the most complete lower jaw of an early member of the genus *Homo* yet discovered.

A match for 1470?

a–d, Left lateral (**a**), right lateral (**b**), anterior (**c**) and occlusal (**d**) views of KNM-ER 60000. **e**, Occlusal view of KNM-ER 62003, with lines marking the mid-sagittal plane aligned to that of KNM-ER 60000. Scale bar, 3 cm.

Since 1999, more fossils found or reanalyzed:



nature

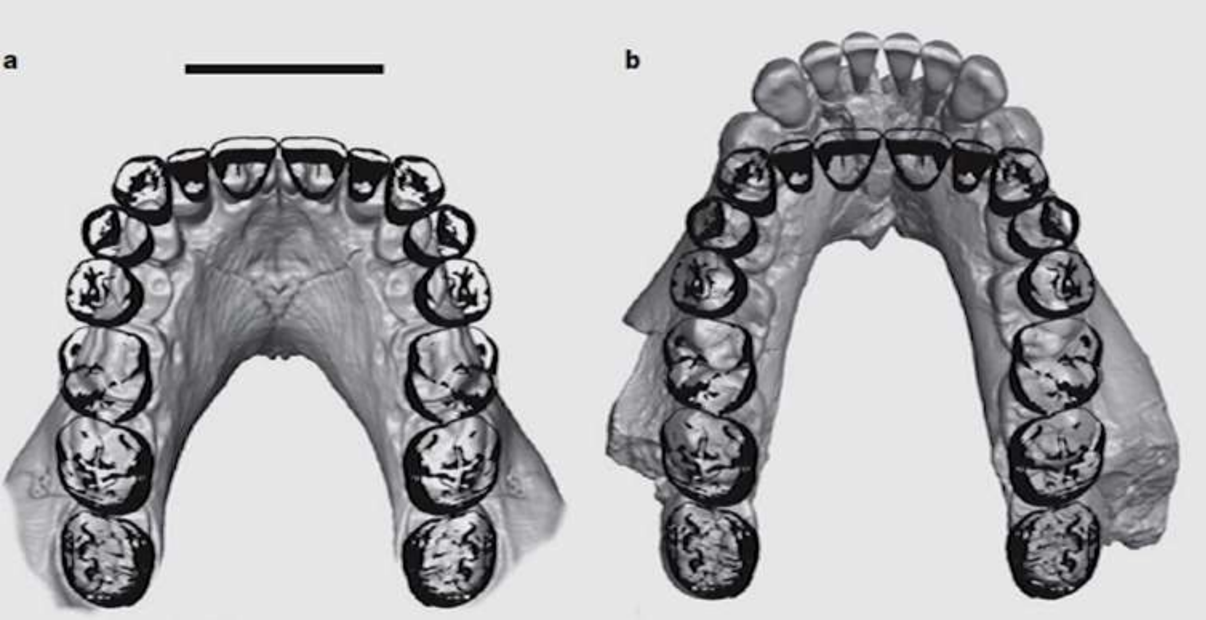
A FACE IN THE CROWD

Lake Turkana fossils reveal diversity among early *Homo* species

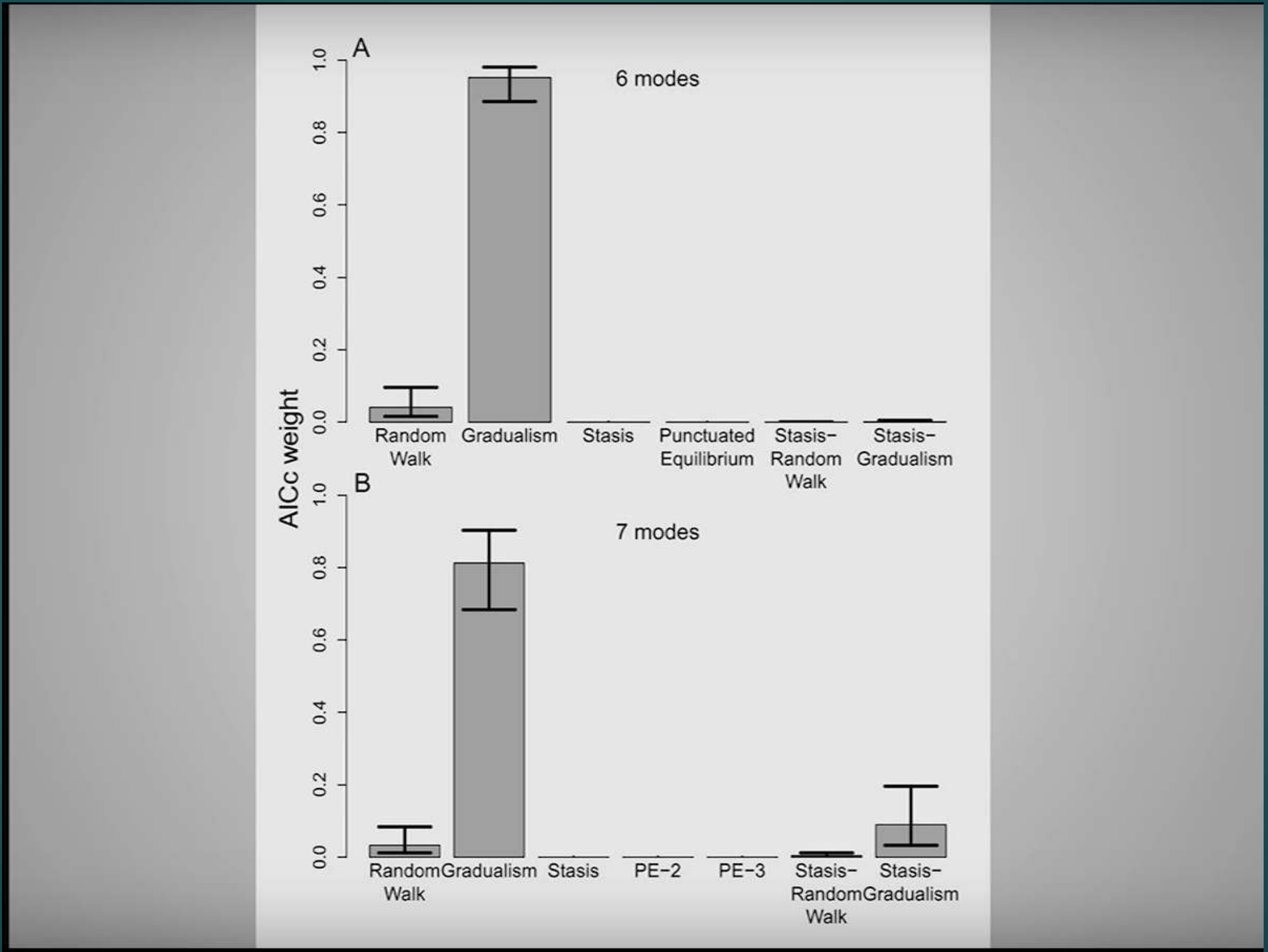
THE NEW ENGINEERING

GETTING THE MESSAGE

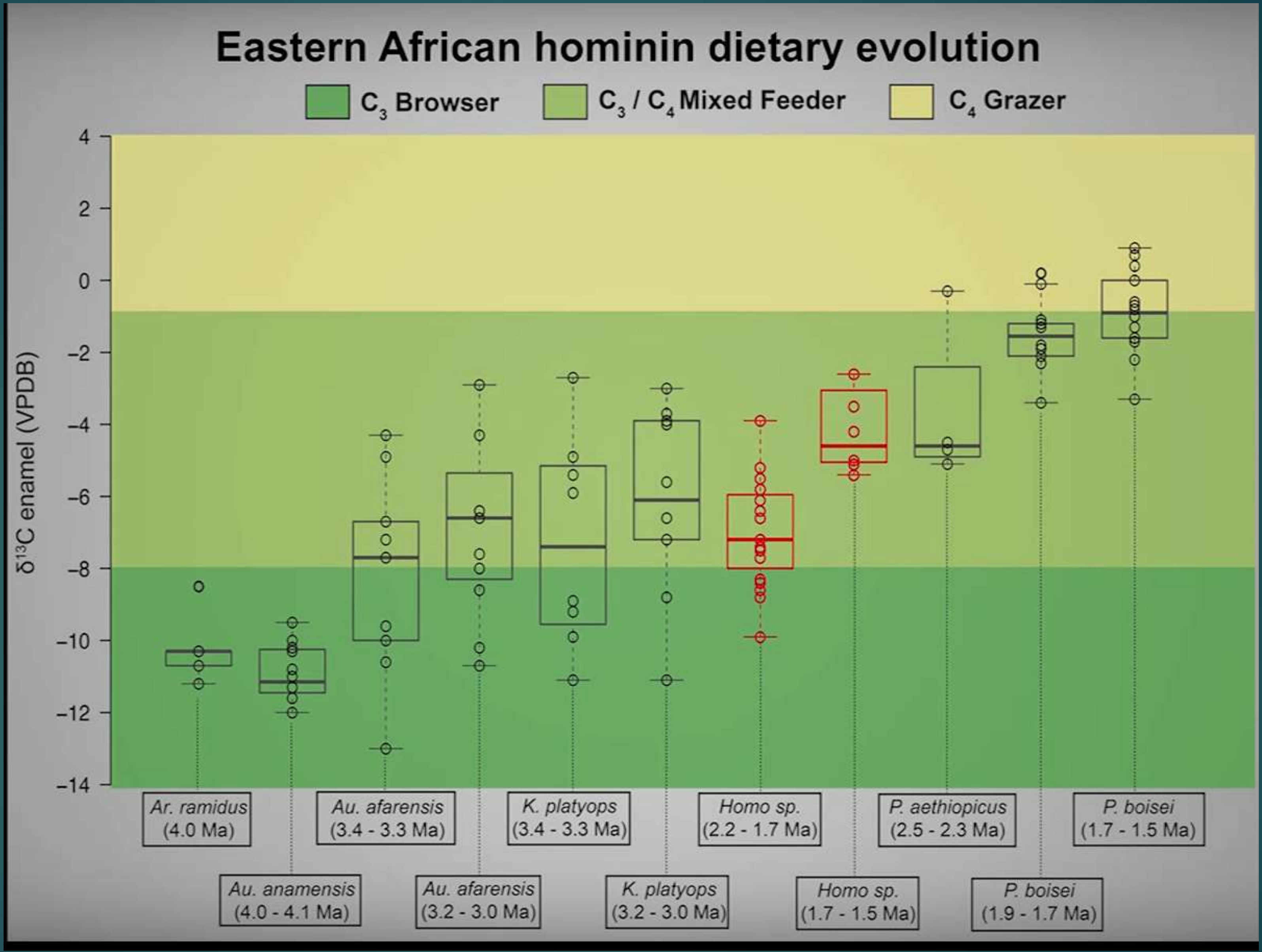
FOLLOW THE MONEY



New analysis of Aiello data (error in endocranial volume and ages) by Du: gradual increase in brain, not punctuated



Diet



H. Habilis & erectus

Australopiths

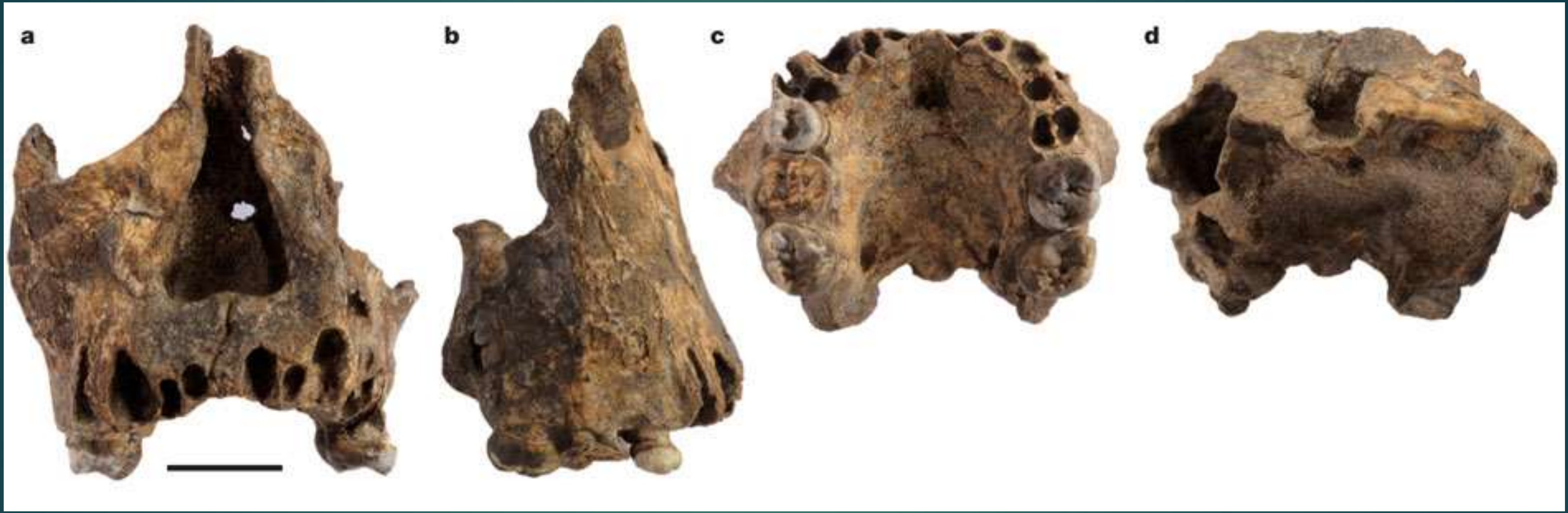
David Patterson

Homo rudolfensis: KNM-ER 62000 partial face

- A recent update: 2012 , Maeve Leakey et al., report on a group of fossils they unearthed between 2007 and 2009, along the shore of Lake Turkana in Kenya.

- The face (fossil KNM-ER 62000) was of a juvenile,
  - but had features in common with KNM-ER 1470,
  - suggesting that the 1470 skull's uniqueness is due to being a separate species,
  - rather than being a large male *H. habilis*.

KNM-ER 62000 face



a–d, Anterior (**a**), right lateral (**b**), inferior (**c**) and superior views (**d**) of the KNM-ER 62000 face. Scale bar, 3 cm.

Homo rudolfensis: KNM-ER 62000

- Fred Spoor described the face as "incredibly flat", with a straight line from the eye socket to the incisor tooth.
- The jawbones, which appeared to match KNM-ER 1470 and KNM-ER 62000, were also shorter and more rectangular than known *H. habilis* specimens.
- There were definitely two *Homo* species inhabited East Africa nearly 2 Ma.

KNM-ER 60000

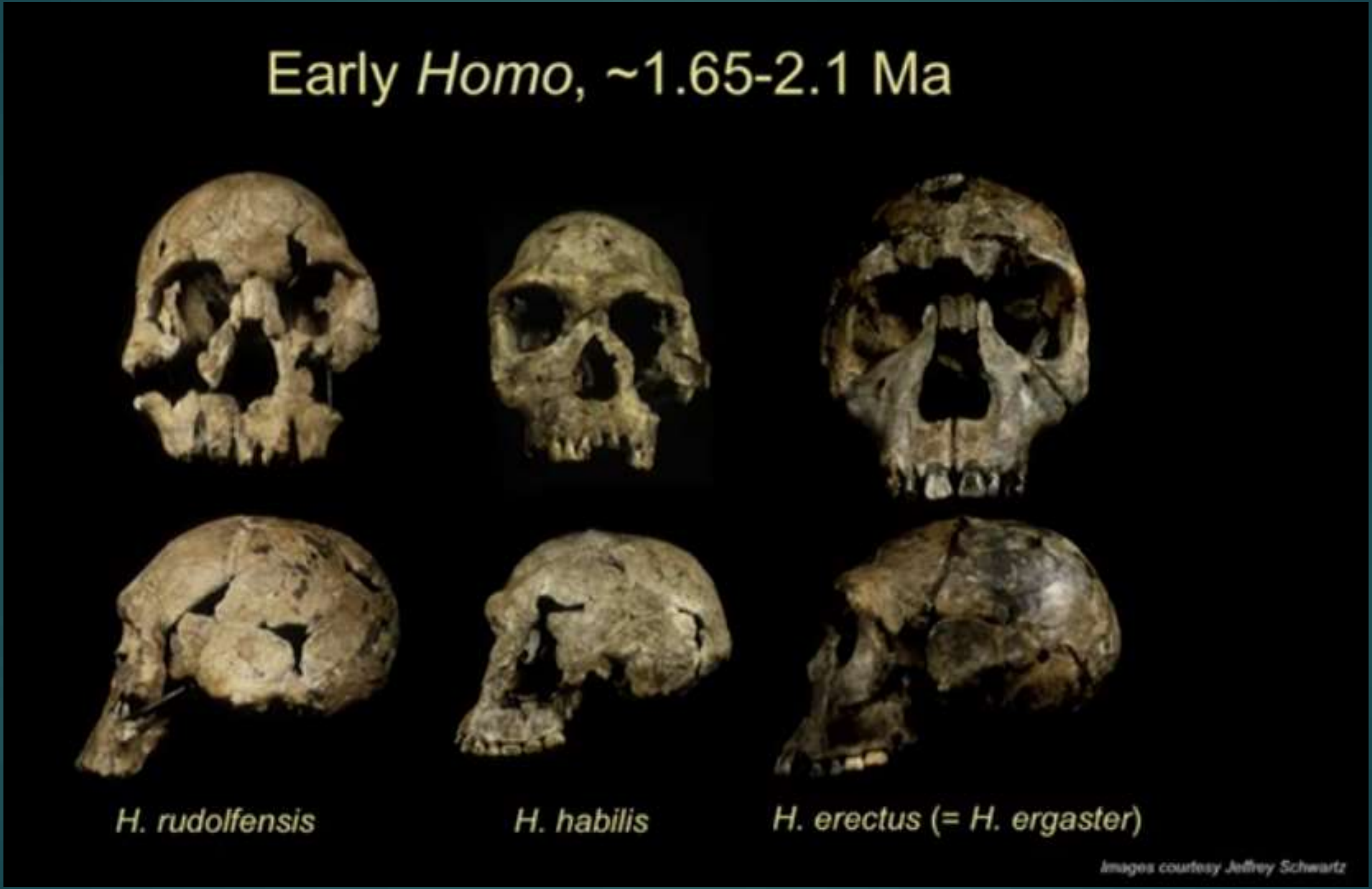
- A particularly good match can be found in the other two new fossils, the lower jaw KNM-ER 60000, found by Cyprian Nyete in 2009, and part of another lower jaw, KNM-ER 62003, found by Robert Moru in 2007.

- A dental arcade that is short anteroposteriorly and flat across the front, with small incisors;

- These features are consistent with the arcade morphology of KNM-ER 1470 and KNM-ER 62000.

- KNM-ER 60000 stands out as the most complete lower jaw of an early member of the genus *Homo* yet discovered.

3 broadly contemporaneous species, 2.1 to 1.7 Ma



Multiple adaptive packages in the genus

Evolution of early *Homo:* new ways to differentiate early *Homo*

- East African non-*erectus Homo* from this period has been assigned previously to either:
  - *H. habilis* - small brained species
  - *H. rudolfensis* - large-brained (and -bodied) species.

- New fossils from Lake Turkana, Kenya (KNM-ER 60000 and 62000), suggest multiple species of non-*erectus Homo* just after 2.1 Ma but show that the two species cannot be distinguished on the basis of cranial size.

Evolution of early *Homo*: Size does not differentiate

- The new Kenyan fossils suggest that palate and mandibular shape, especially the relative position of the anterior dentition, differentiate among the two better known groups of early *Homo*

- But taphonomic damage to the OH 7 mandible, the type specimen for H. habilis, and the fact that size may no longer be a distinguishing feature of different species of early *Homo* preclude an easy answer to the attribution of the OH 7 type

- It is unclear to which group, if either, the nomen *H. habilis* applies.

Homo habilis/1813 & Homo rudolfensis/1470

- What are other anthropologists saying?
- In reviewing *Homo habilis/1813* and *Homo rudolfensis/1470*, can we say that these are definitely human ancestors?
- Right now, most scientists seem to say that there are not enough fossils to make that determination.
- Some experts believe that the 2.5 million-year-old *Australopithecus garhi* could be a human ancestor, but again, scientists can’t say for sure at this time.
- Thus, despite their disparate human-like features in teeth, face, or brain size, the human status of these early *Homo* groups of fossils remains a matter of dispute.

No small-skulled early Turkana habilines.

- Hawks, 2019: New geological analysis at Koobi Fora; Frank Brown's group, which in a series of papers has defined and dated stratigraphic units between the major tuffs of the Koobi Fora formation, between the KBS Tuff at 1.87 Ma and the Chari tuff at around 1.38 Ma.
- Now the situation has changed. The small Turkana habiline, KNM-ER 1813, is now contemporary with the Olduvai sample.
- There are no longer any small-skulled early Turkana habilines.
- That leaves KNM-ER 1470, KNM-ER 1590, KNM-ER 3732, and KNM-ER 3735 as plausible habilines before 1.85 Ma.
- This seems like a nice sample as a possible ancestor for both later large-bodied *Homo* and later habilines

H. habilis vs. H. rudolfensis

- Chris Stringer & Richard Leakey: 2 species at Olduvai – OH 7 is *habilis*; OH 13 & OH 62 are smaller, more archaic species

- Major Consensus: 2 species at 2 Ma

- Which of the two (if either) gave rise to modern humans is still in contention:
  - *H. rudolfensis* appears to have good claim based on large brain
  - But *H. habilis* has facial and dental anatomy that fits closer to MHs
  - Some think *Kenyanthropus platyops* is a contender; others think *A. garhi*

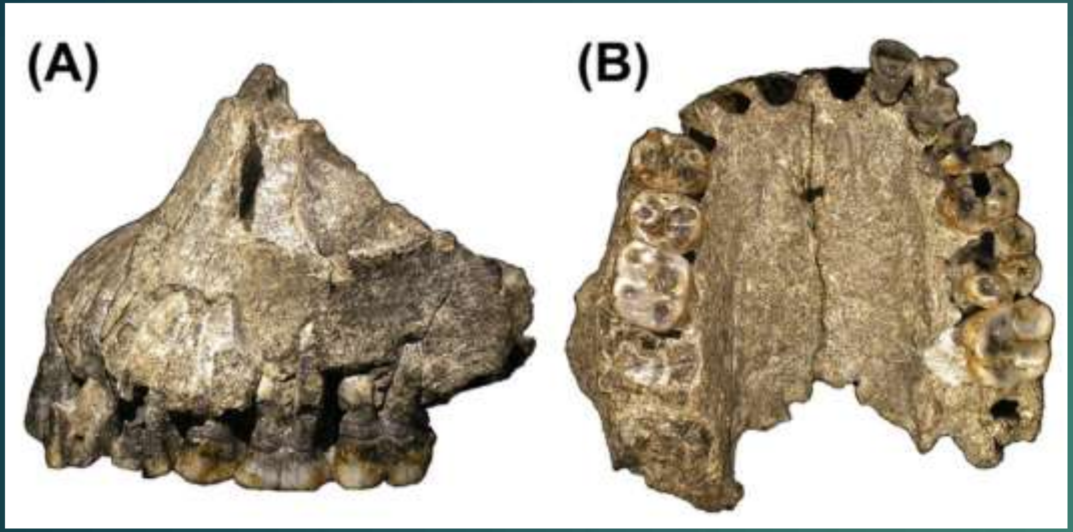
Origins of *Homo*: *Homo* before 2 Ma

- There are a small number of fossil remains of older than 2 Ma in East Africa; however, none of these can be confidently attributed to species.

- The oldest fossil *Homo* is likely to be the A.L. 666 maxilla from Hadar, Ethiopia, which is minimally 2.33 Ma. This specimen differs from *Australopithecus* in the anatomical suites of characters mentioned in items 2 and 3 above.

- A similarly aged isolated molar from West Turkana, Kenya, is also likely early *Homo*. Both have some affinities with later early *Homo* from Kenya, such as KNM-ER 1813.

Homo before 2 Ma: a maxilla & a mandible



A.L. 666-1 maxilla attributed to *Homo* cf. *habilis*, Hadar, Ethiopia, 2.33 mya.

Uraha-501 (UR-501) mandible from Malawi

1470 & 1813 Groups

- Both the 1813 and 1470 groups exhibit considerable and overlapping size variation.

- In particular,
  - molar size,
  - facial size (but not shape),
  - and very likely endocranial and body size

  - But these features cannot be used to distinguish the 1813 and 1470 groups as they once were used to distinguish H. habilis and H. rudolfensis.

H. habilis/1813 vs H. rudolfensis/1470

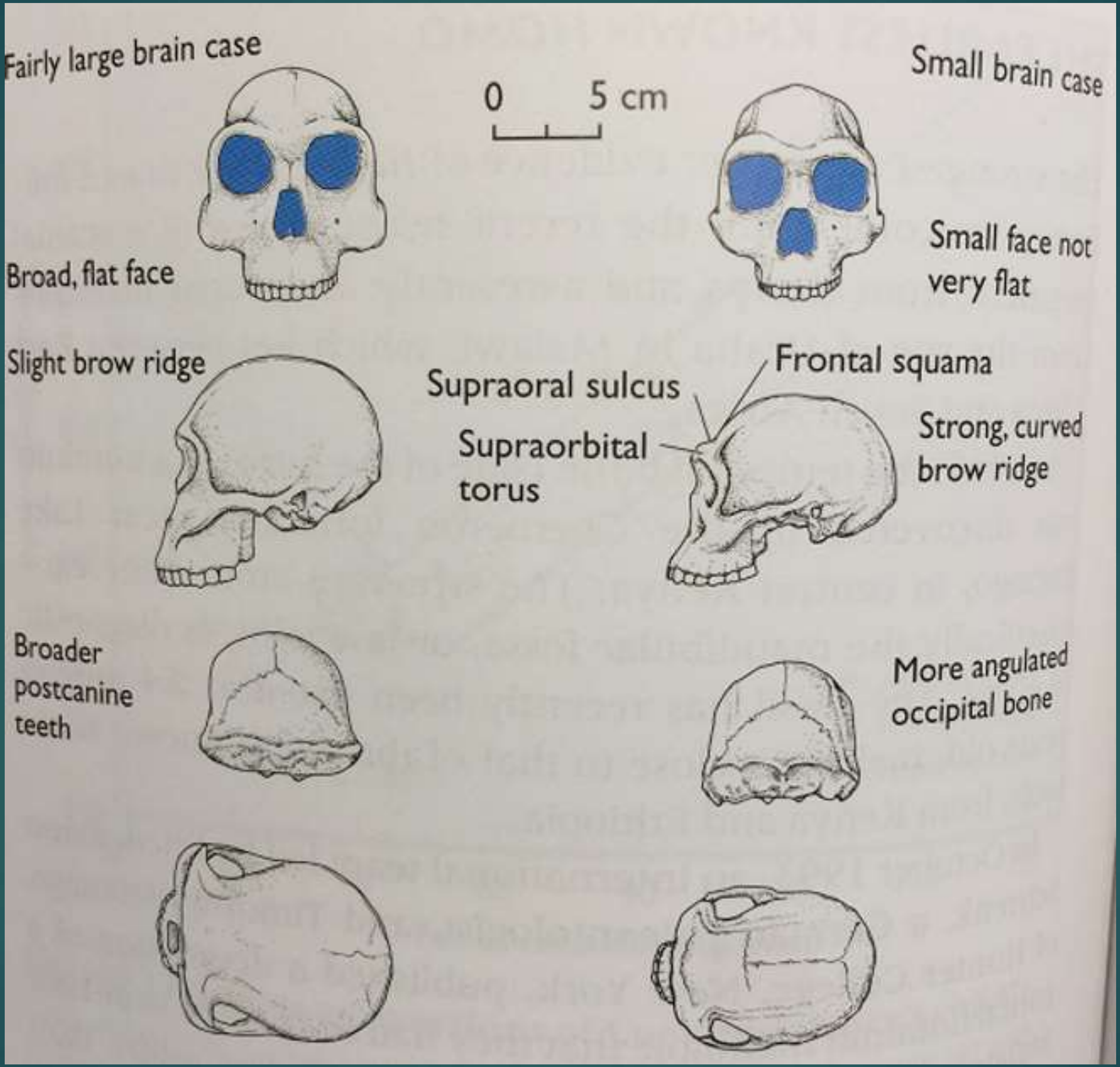
- *H. habilis & H. rudolfensis* unquestionably co-existed with *Paranthropus boisei/robustus* about 2-1.8 Ma

- If *H. habilis & H. rudolfensis* are separate species, only one could be ancestral to *H. ergaster*, which appeared in E Africa about 1.8-1.7 Ma

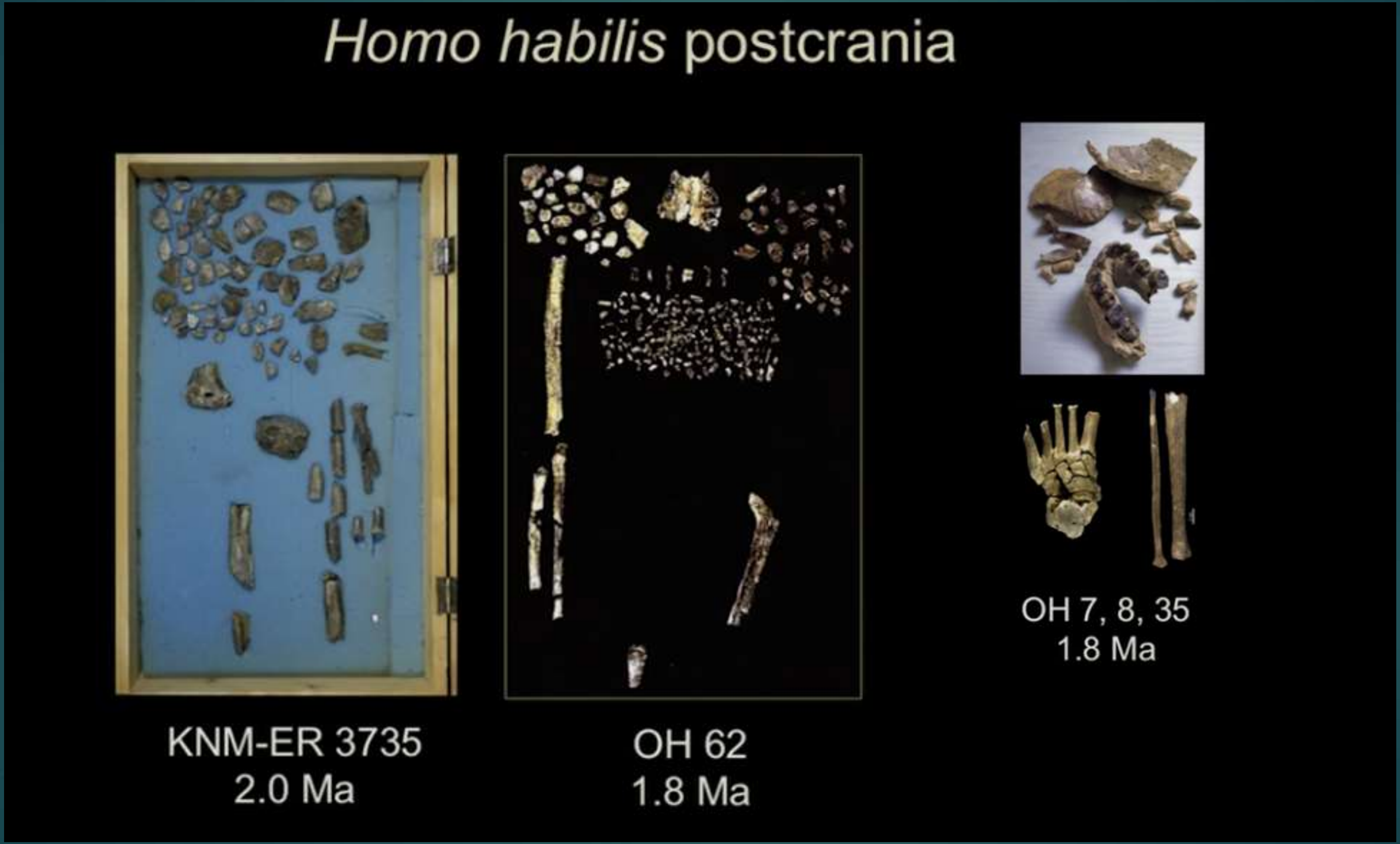
- *H. habilis* is weaker candidate: it persisted in E. Africa for 100-300 Ka after *H. ergaster* emerged

H. habilis vs H. rudolfensis

- Cranial evidence:
  - dental and facial reduction favor a line from *H. habilis* to *H. ergaster*,
  - while brain expansion supports a line from *H. rudolfensis*
- Multiple cladistic analyses:
  - craniodental characters: *H. habilis* and *H. ergaster* are more closely related;
  - other analyses link *habilis* and *rudolfensis* more closely to each other than to *Homo*;
  - some analyses suggest both species should be removed from *Homo* to *Australopithecines*


Fairly large brain case
0 5 cm
Small brain case
Broad, flat face
Small face not very flat
Slight brow ridge
Supraoral sulcus
Frontal squama
Supraorbital torus
Strong, curved brow ridge
Broader postcanine teeth
More angulated occipital bone

Homo habilis postcrania



Homo habilis postcrania

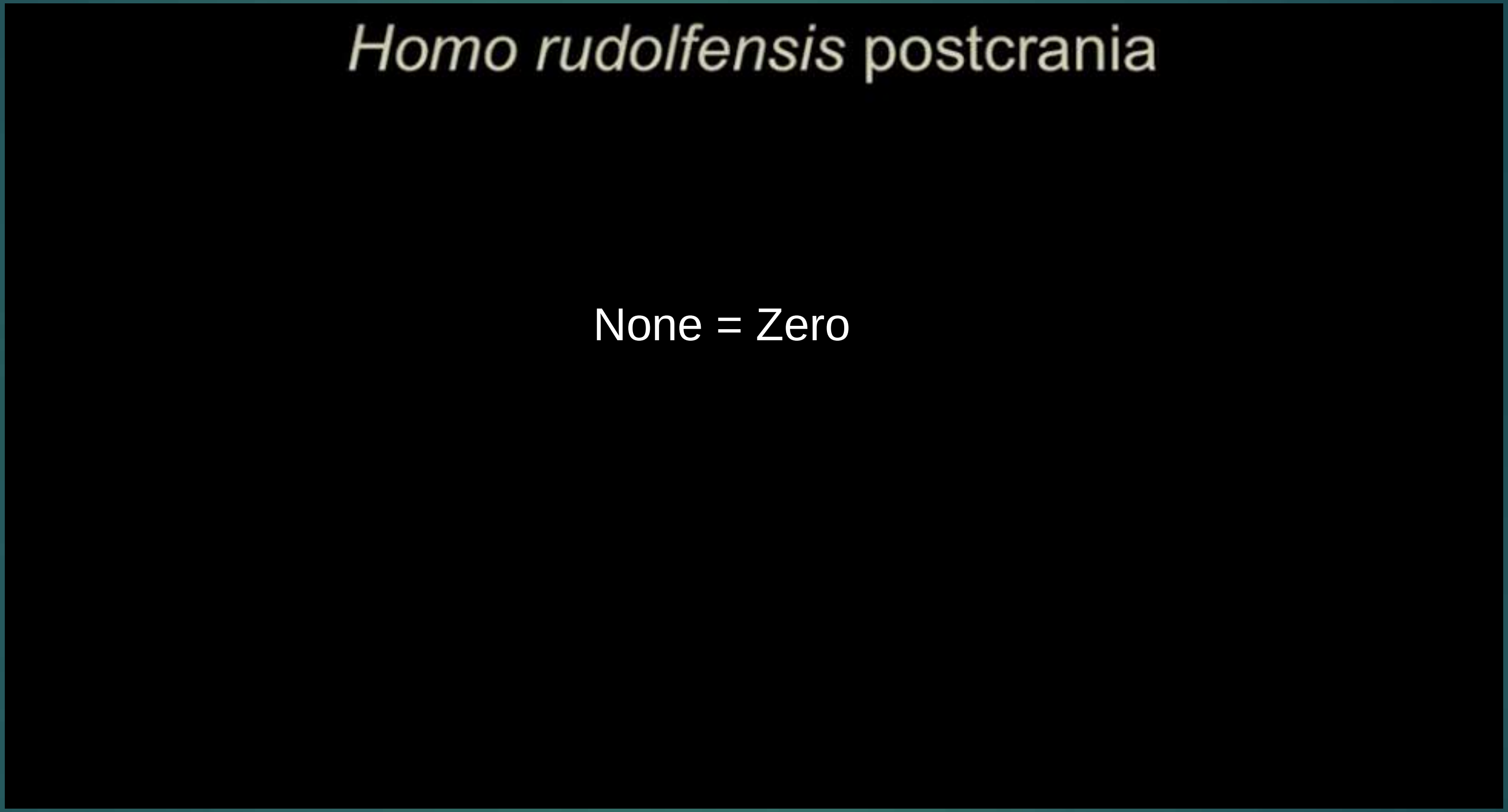
KNM-ER 3735
2.0 Ma

OH 62
1.8 Ma

OH 7, 8, 35
1.8 Ma

From type site of *H. habilis*,
But questioned.

Homo rudolfensis postcrania



Homo rudolfensis postcrania

None = Zero

Origins of *Homo: Homo* before 2 Ma

- The Uraha-501 (UR-501) mandible from Malawi has been argued to be oldest *Homo specimen*; its age, based on faunal correlations, may be as young as 1.9 Ma or as old as 2.5 Ma.
- The inclusion of UR-501 in *Homo* is based on both molar and premolar morphology & mandibular anatomy.

Oldest Early *Homo* at Ledi-Geraru, 2.8 Ma

PALEOANTHROPOLOGY

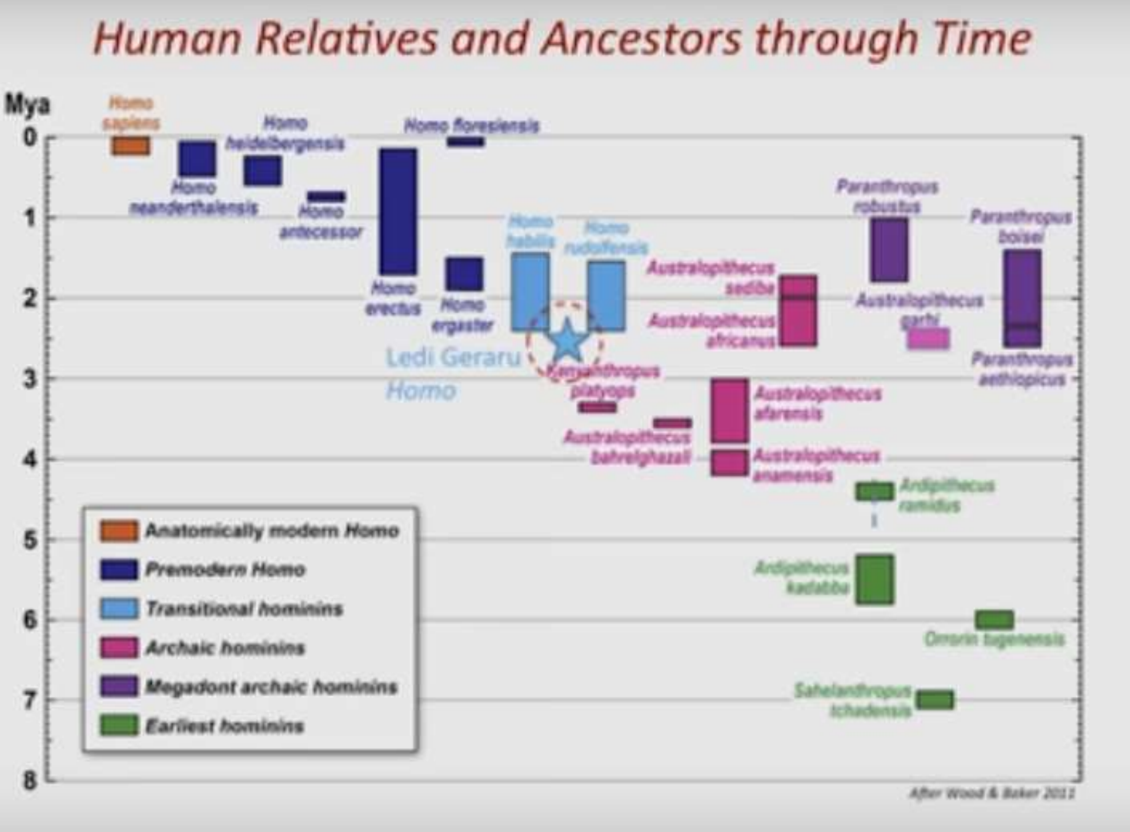
Science, 3 March 2015

Late Pliocene fossiliferous sedimentary record and the environmental context of early *Homo* from Afar, Ethiopia

Erin N. DiMaggio,[1*] Christopher J. Campisano,[2] John Rowan,[2] Guillaume Dupont-Nivet,[3†] Alan L. Deino,[4] Faysal Bibi,[5] Margaret E. Lewis,[6] Antoine Souron,[7] Dominique Garello,[8] Lars Werdelin,[9] Kaye E. Reed,[2] J Ramón Arrowsmith[8]

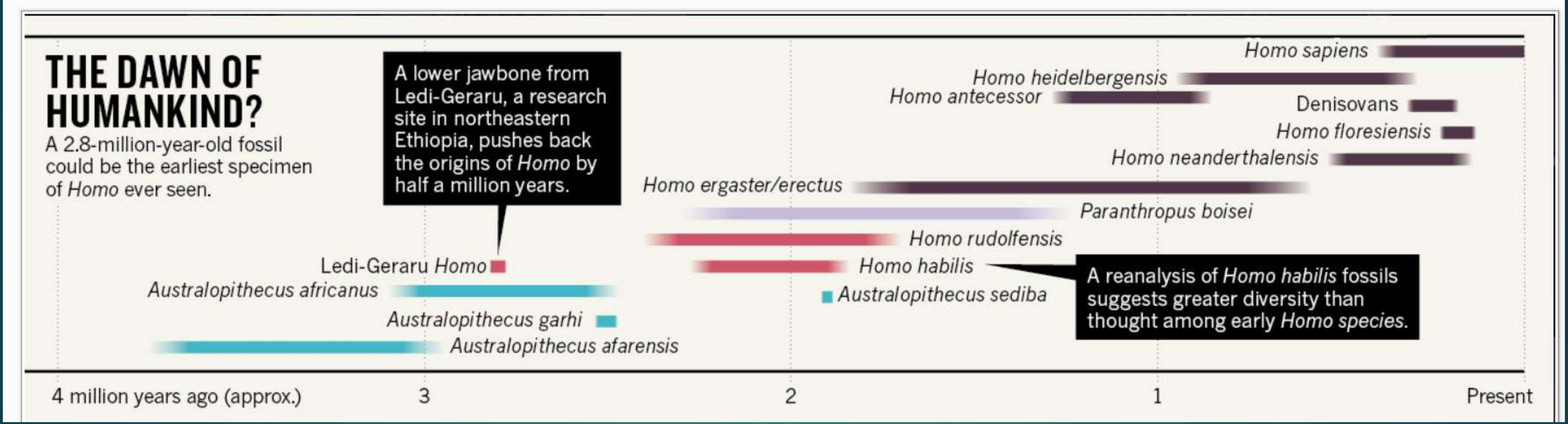
Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia

Brian Villmoare,[1,4,6*] William H. Kimbel,[2*] Chalachew Seyoum,[2,7] Christopher J. Campisano,[2] Erin N. DiMaggio,[3] John Rowan,[2] David R. Braun,[4] J Ramón Arrowsmith,[5] Kaye E. Reed[2]



After Wood & Baker 2011

Dawn of Humanity at Ledi-Geraru?



THE DAWN OF HUMANKIND?

A 2.8-million-year-old fossil could be the earliest specimen of *Homo* ever seen.

A lower jawbone from Ledi-Geraru, a research site in northeastern Ethiopia, pushes back the origins of *Homo* by half a million years.

A reanalysis of *Homo habilis* fossils suggests greater diversity than thought among early *Homo* species.

Has not yet been assigned to a particular species.

It’s worth noting, not everyone agrees the Ethiopian fossil should be classified as *Homo*.

Afar, Ethiopia

Brian Villmoare,[1,4,6]* William H. Kimbel,[2]* Chalachew Seyoum,[2,7] Christopher J. Campisano,[2] Erin DiMaggio,[3] John Rowan,[2] David R. Braun,[4] J. Ramon Arrowsmith,[5] Kaye E. Reed[2]

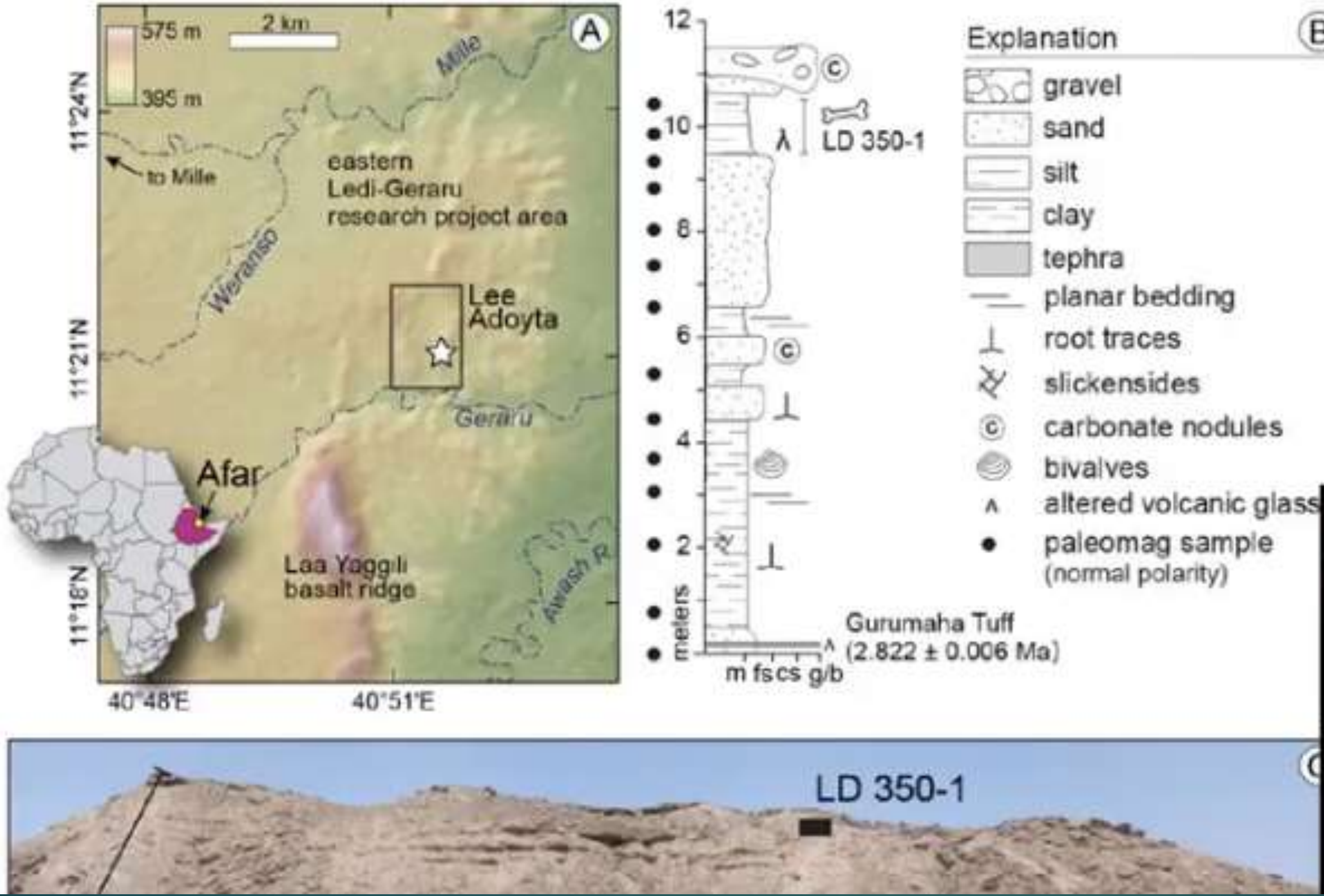
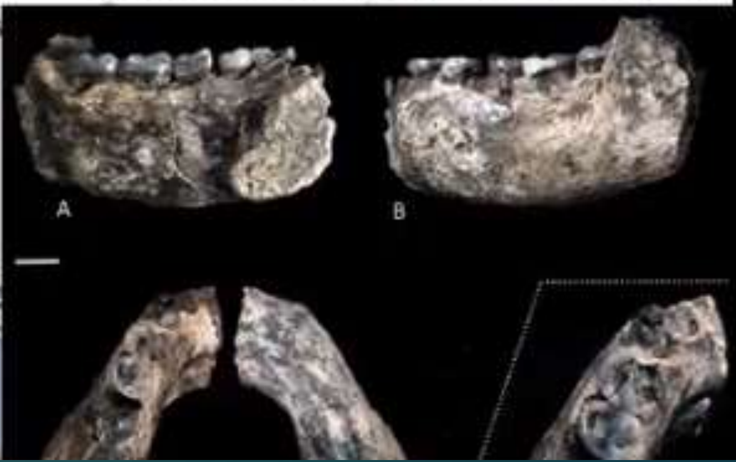


Fig. 1. (A) Map of the Lee Adoyta region in the Ledi-Geraru research area. (B) Stratigraphic section of the Lee Adoyta sequence indicating the provenience of the hominin mandible LD 350-1. (C) The LD 350 locality with the position on the surface of the LD 350-1 mandible in relation to the Gurumaha Tuff. Section in (B) is indicated by black line at left in



Ethiopian Jaw Bone, Ledi-Geraru, LD 350-1
2.8 M – oldest genus *Homo*

- Jaw bone fossil discovered in Ethiopia is oldest known human lineage remains

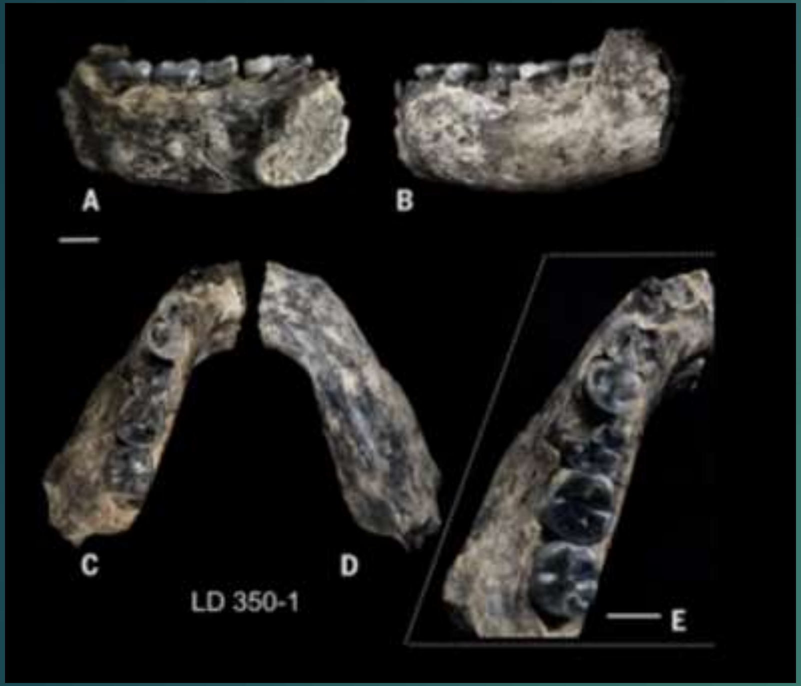
- Around 400 K years older than previous discovery of *Homo* lineage, 2.8 m-year-old jaw and five teeth was found on rocky slope in Afar region, at a site called Ledi-Geraru,

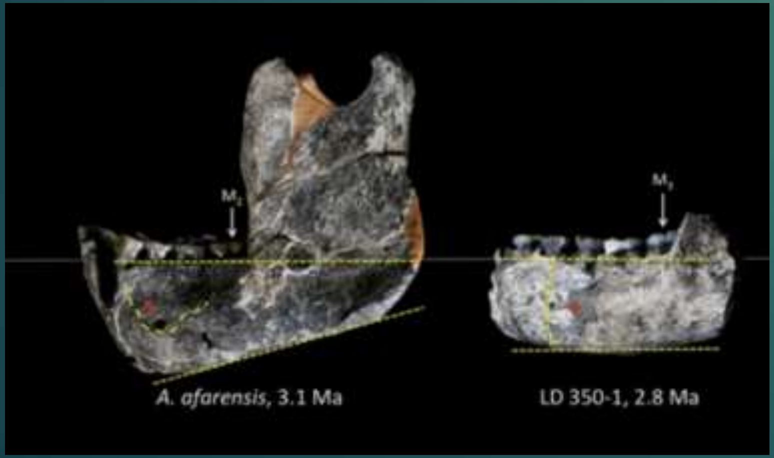
- 40 miles from where Lucy was found.

LD 350-1 mandible

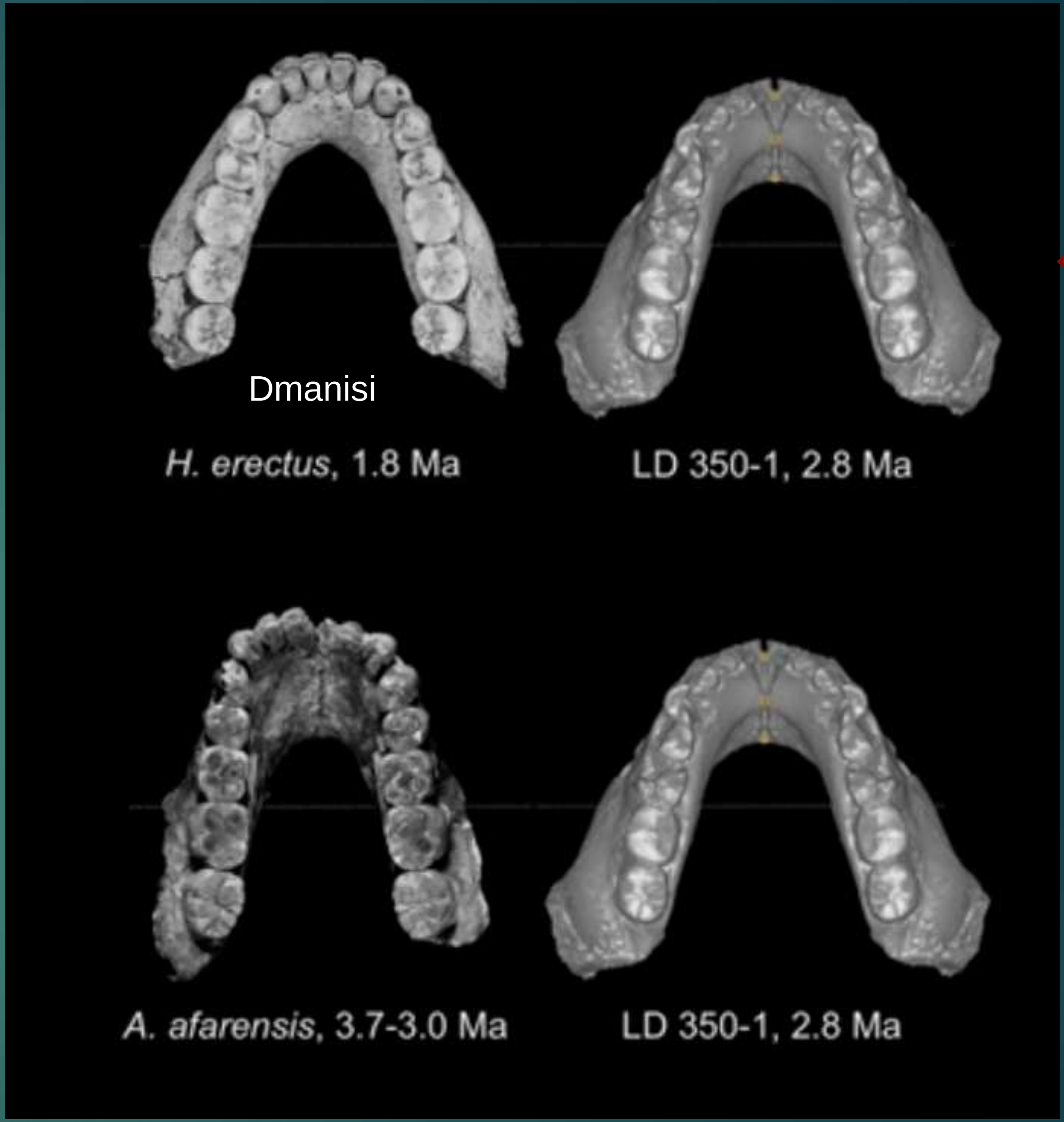
Villmoare, et al., 2015

Ledi-Geraru: LD 350, 2.8 Ma





Mandible forecasts later *Homo*



Long, narrow, fat molars
Primitive premolars

reconstructions

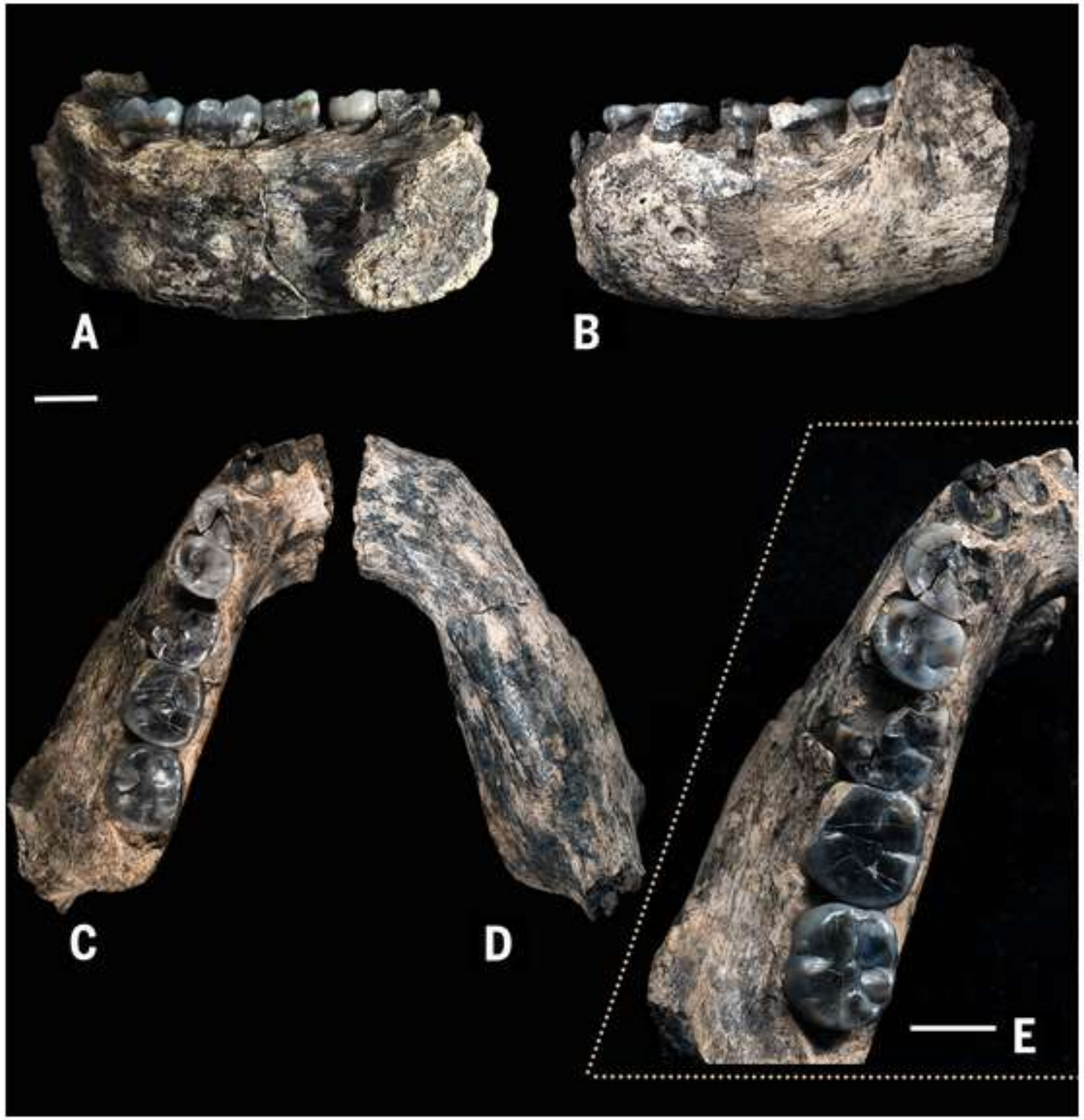
Ledi-Geraru LD 350-1 mandible: 2.8 Ma

Teeth becoming more slender than in A. afarensis.

Leading edge of the origin of the genus *Homo* was our teeth, not brain.

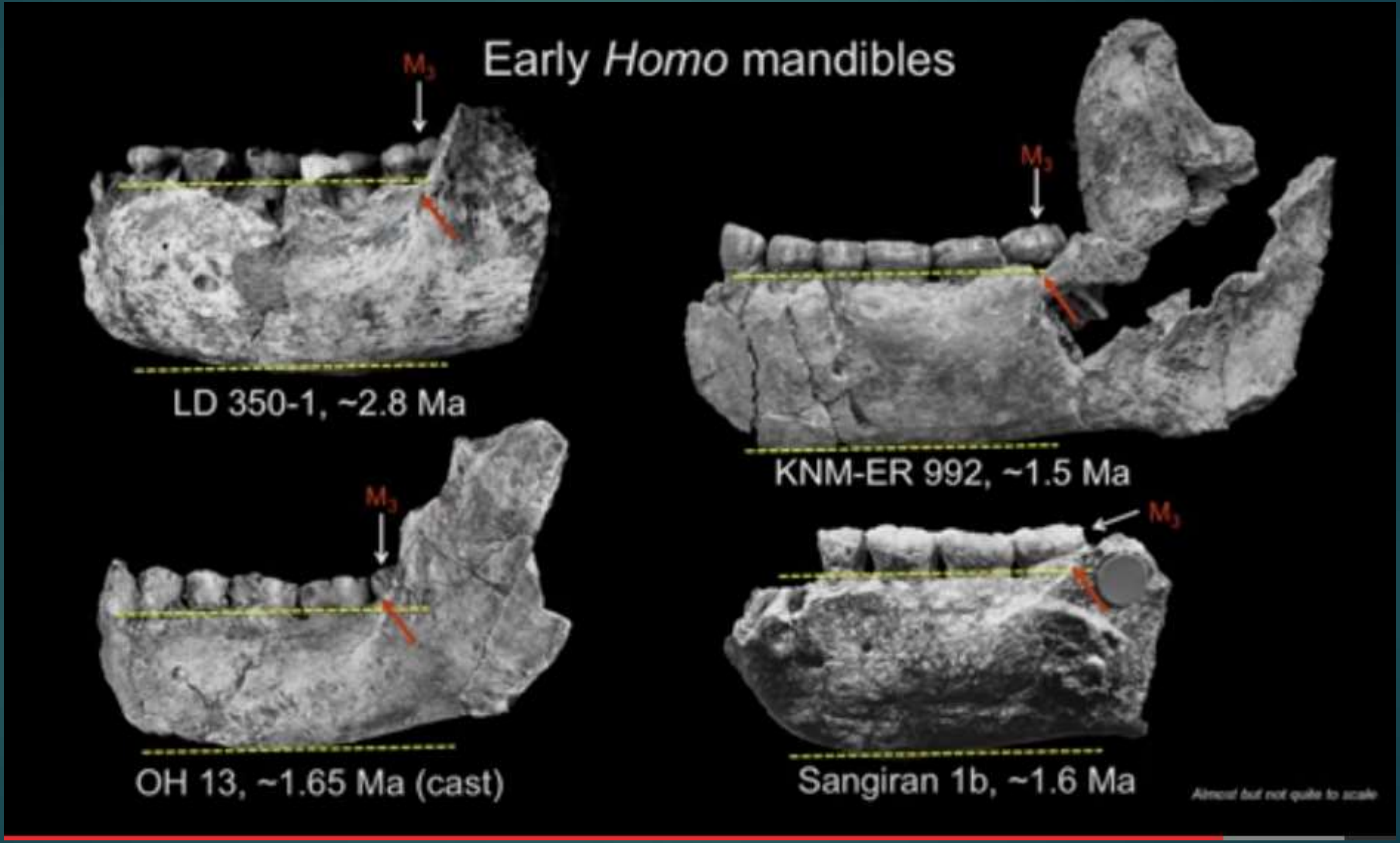
Theory: You don't need big jaws and teeth if you have stone tools to process food

Villmoare, et al., 2015



Five views of the fossilized jawbone highlight teeth that are becoming more slender, scientists say, relative to the blocky, more apelike teeth of *Australopithecus*.

Mandibles



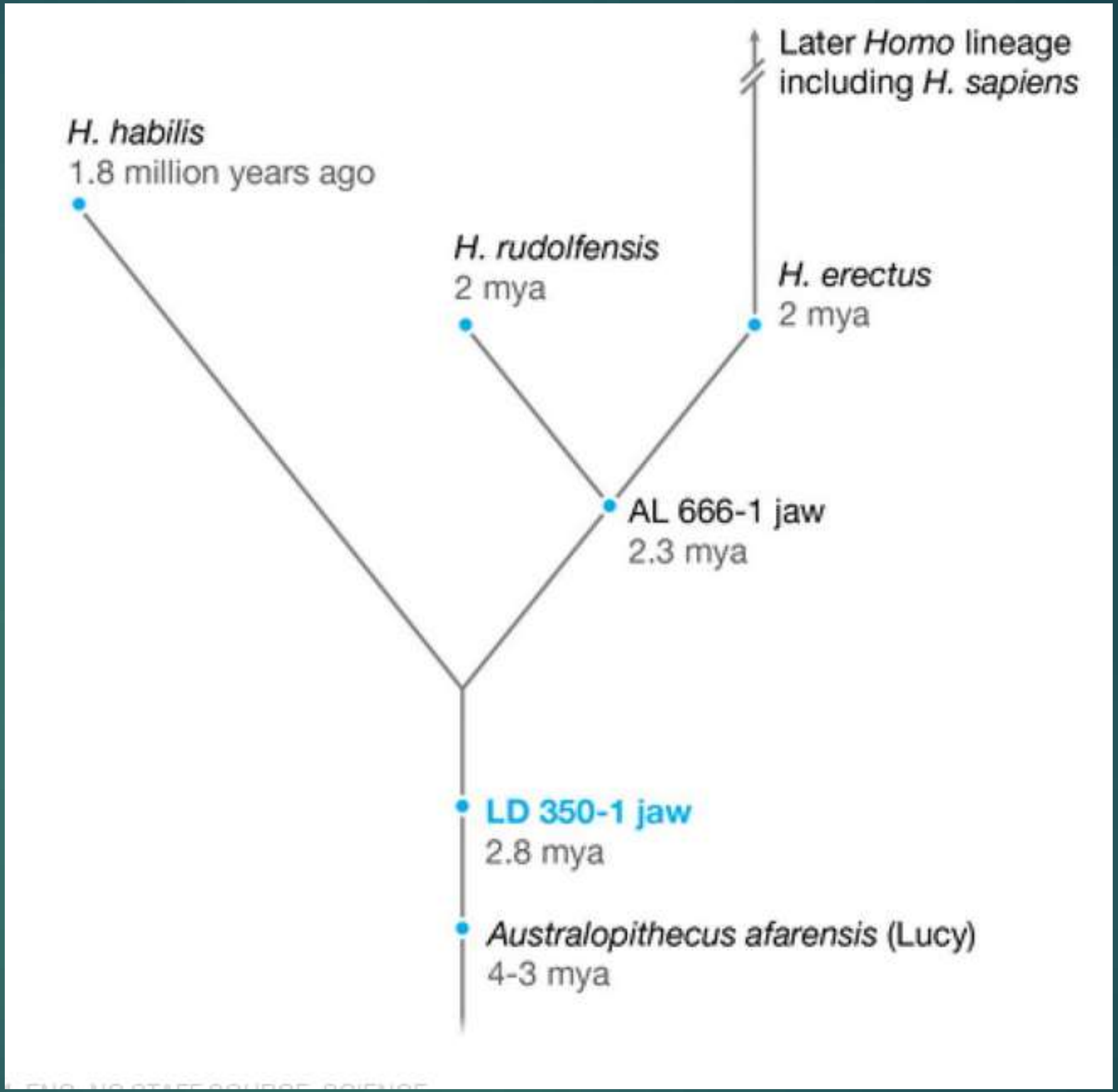
Ledi-Geraru

H. ergaster

H. habilis

H. erectus

Possible lineage



"The Ledi-Geraru jaw has turned up as if 'on request,' suggesting a plausible evolutionary link between *Australopithecus afarensis* and *Homo habilis*," says Spoor.

OH 86: Oldest modern human-like hand bone from a new >1.84-million-year-old site at Olduvai in Tanzania

OLD BUT MODERN A newly discovered hominid finger bone dating to at least 1.84 million years ago is shown from two sides (right) and overlaid on a modern human hand (left). A team of scientists regards the fossil as the oldest known humanlike hand bone.

Figure 2 | OH 86 views. The OH 86 hominin manual proximal phalanx in (from left to right) dorsal, lateral, palmar (distal is top for each) and proximal views. Scale bar, 1 cm.

From little finger of left hand; found at Tanzania's Olduvai Gorge, pinkie bone is 1.84 million years old; looks more like corresponding bones of modern humans than like finger fossils of previously discovered Olduvai hominins; new finger fossil is more humanlike than comparably ancient Olduvai hand fossils from *Homo habilis* and *Paranthropus boisei*; entire hand probably looked humanlike; tool making capability; could come from a number of species that were around at the time, including *Homo erectus* (Acheulean tools show up soon after at 1.7M).

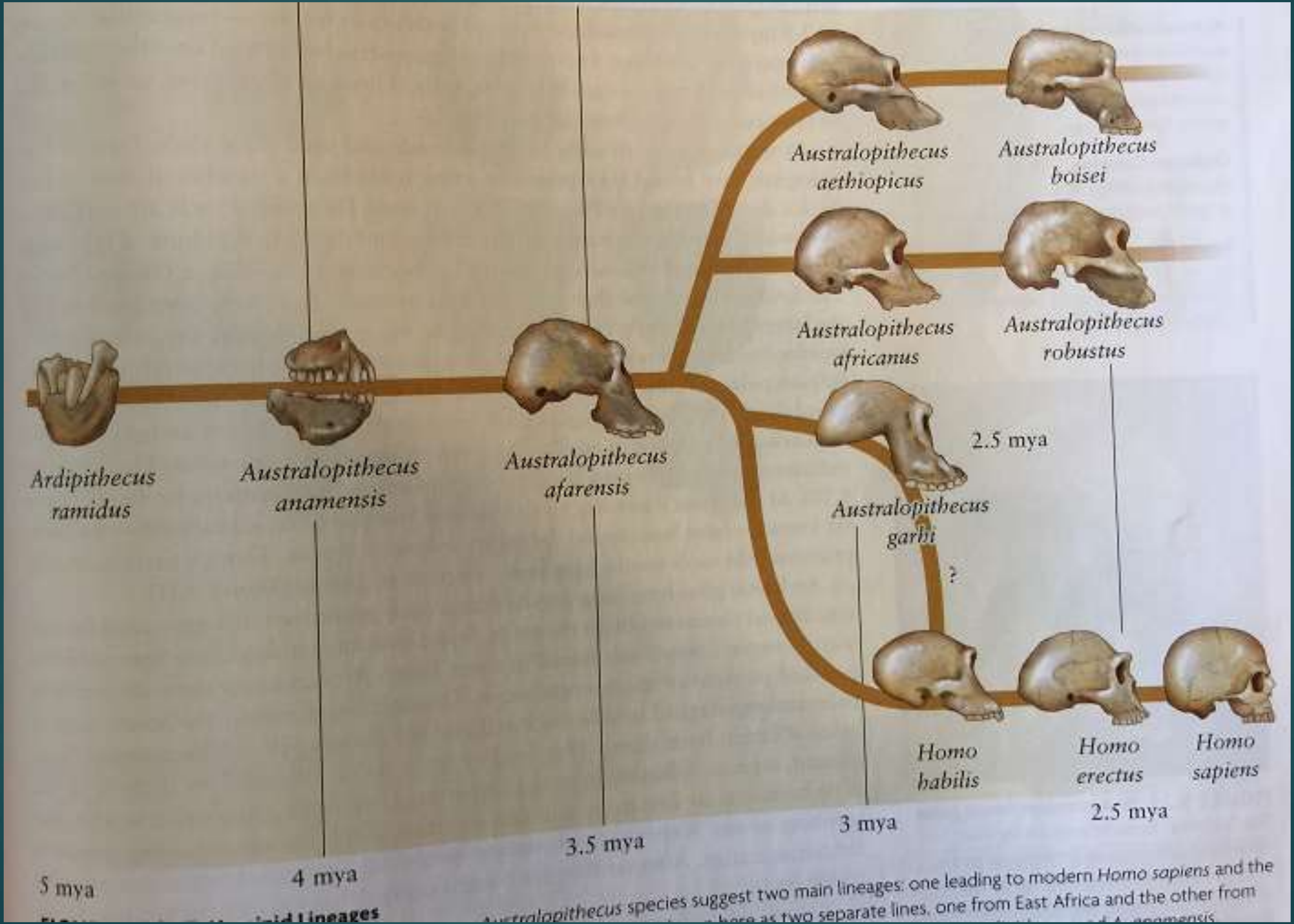
Manuel Domínguez-Rodrigo, et al., 2015

Earliest modern human-like finger bone ever found - - Phalangeal curvature comparison

Figure 4 | Phalangeal curvature in extant and fossil hominoids. (**a**) Included angle values (in degrees) in a modern and fossil sample of fifth proximal phalanges. OH 86 is (exclusively) within the modern human variation (distinct from australopiths). Boxes represent 25th and 75th percentiles, centreline is the median, whiskers represent non-outlier range and the dot is an outlier. Samples for each boxplot are *Homo sapiens* ($n = 36$), *Pan paniscus* ($n = 8$), *Pan troglodytes* ($n = 16$), *Gorilla* ($n = 22$), *Pongo* ($n = 16$) and Hylobatidae ($n = 22$). (**b**) The fossil hominin specimens analysed in this study are compared in lateral view. All pictures were taken from the originals with the exception of AL333-62 (cast) and ATE9-2 (modified from the literature[56]; Supplementary Table 4). Scale bar, 1 cm.

OH 86 represents a hominin species different from the taxon represented by OH 7, and whose closest form affinities are to modern H. sapiens. However, the geological age of OH 86 obviously precludes its assignment to H. sapiens, and ambiguity surrounding the existing potential sample African *H. erectus* (sensu lato) hand bones also prohibits its confident assignment to that species at this time. Conclusion: Just <2 Ma at least one East African hominin taxon/lineage showed marked reduction in manual phalangeal arboreal adaptations (as reflected by the proximal phalanx curvature and flexor sheath ridges development in the shaft), along with the concomitant expression of an overall MHL phalangeal morphology (as far as it is possible to infer from a single phalanx)

Hypothetical ancestry



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African Pleistocene Ecology
2.6 Ma to 12 Ka

Climate Instability, Stone Technology, Diet, Scavenging, Bones & Stones

Evolution of early *Homo* : *habitat unpredictability*

- New environmental data:
  - *Homo* evolved against a background of long periods of habitat unpredictability that were superimposed on the underlying aridity trend.
- New fossils support:
  - presence of multiple groups of early *Homo* that overlap in body, brain, and tooth size
  - challenge the traditional interpretation of *H. habilis* and *H. rudolfensis* as representing small and large morphs, respectively.

Evolution of early *Homo: Environmental Instability*

- Environmental instability as an evolutionary paradigm:
  - The diversity observed in early hominins cannot be understood apart from its environmental context.
  - A long-standing view is that human evolution was linked to the onset of global cooling, progressive African aridity and C4 grass–dominated open vegetation habitats.

- Accordingly, the spread of African savanna grasslands set the selection pressures that favored stone toolmaking, increased carnivory, and other adaptive characteristics of early *Homo* as a member of the African arid-adapted fauna.

Savanna hypothesis vs Variability Selection

- Savanna hypothesis:
  - certain adaptations, such as upright walking or tool-making, were associated with drier habitat and the spread of grasslands. According to this long-held view, many important human adaptations arose in the African savanna or were influenced by the environmental pressure of an expanding dry grassland.

- The Variability Selection Hypothesis (developed by Dr. Rick Potts):
  - key events in human evolution were shaped not by any single type of habitat (e.g., grassland) or environmental trend (e.g., drying) but rather by environmental instability.
  - Changeability of conditions drove the evolution of our big brains

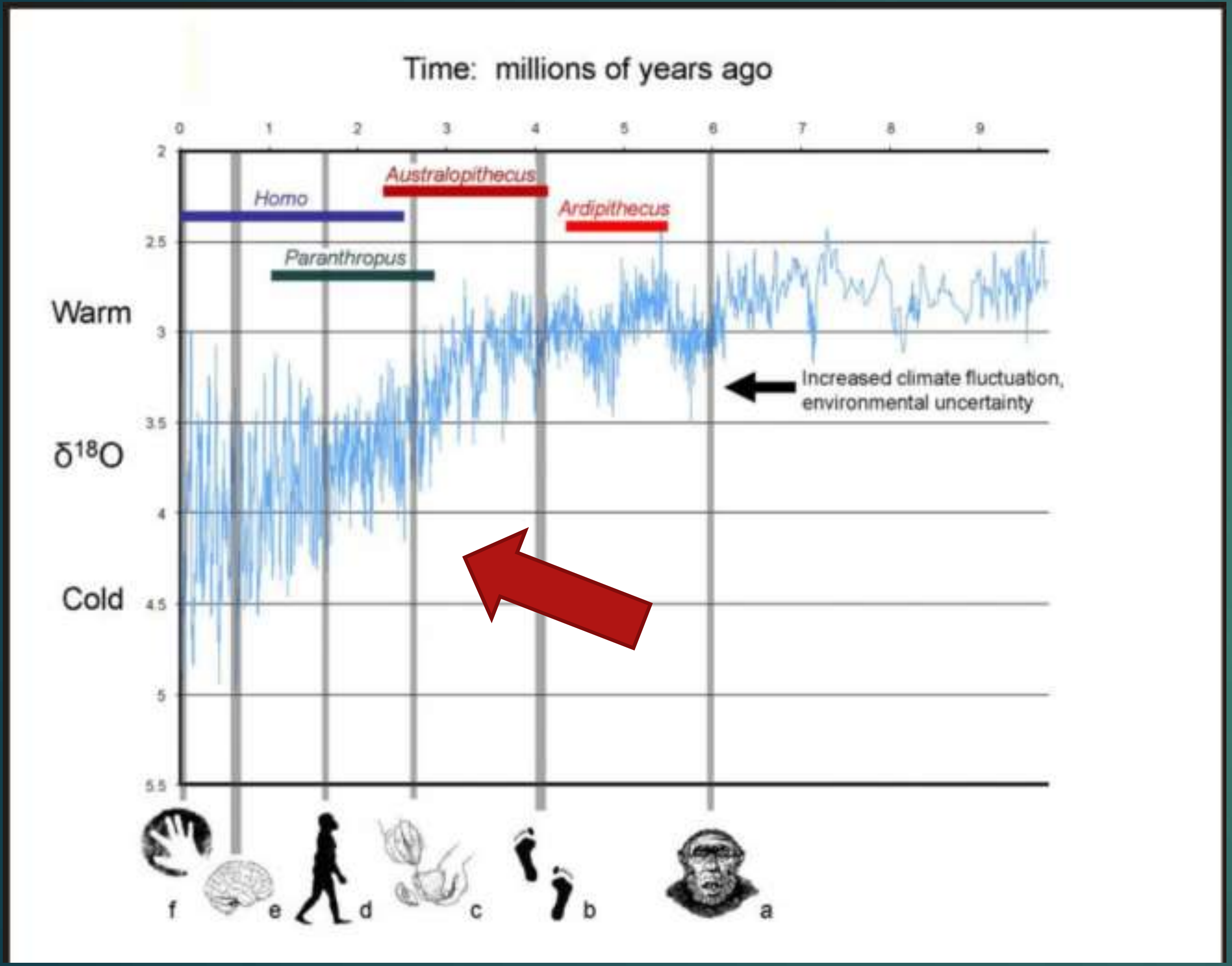
Variability Selection

- This hypothesis calls attention to the variability observed in all environmental records and to the fact that the genus *Homo* was not limited to a single type of environment.

- Over the course of human evolution, human ancestors increased their ability to cope with changing habitats rather than specializing on a single type of environment.

- Evolution of the genus *Homo* and of the adaptations that typify *H. sapiens* were associated with the largest oscillations in global climate.

Climate effect: Oxygen isotope curve (δ18O) for the past 10 million years (data from Zachos et al., 2001)



Icons: (a) hominin origins, (b) habitual bipedality, (c) first stone toolmaking and eating meat/marrow from large animals, (d) onset of long-endurance mobility, (e) onset of rapid brain enlargement, (f) expansion of symbolic expression, innovation, and cultural diversity.

- 10 M year *record of oxygen stable isotopes, measured in foraminifera recovered from deep-sea sediment cores, illustrates that global ocean temperature and glacial ice varied widely over the past 6 million years, the period of human evolution..*
- *During the course of human evolution, the overall $\delta^{18}O$ trend has been toward a cooler, glaciated world. However, the amplitude of oscillation also increased beginning around 6 Ma, and became even larger over the past 2. Ma.*
- *Evolution of the genus Homo and of the adaptations that typify H. sapiens were associated with the largest oscillations in global climate.*

Smithson.com

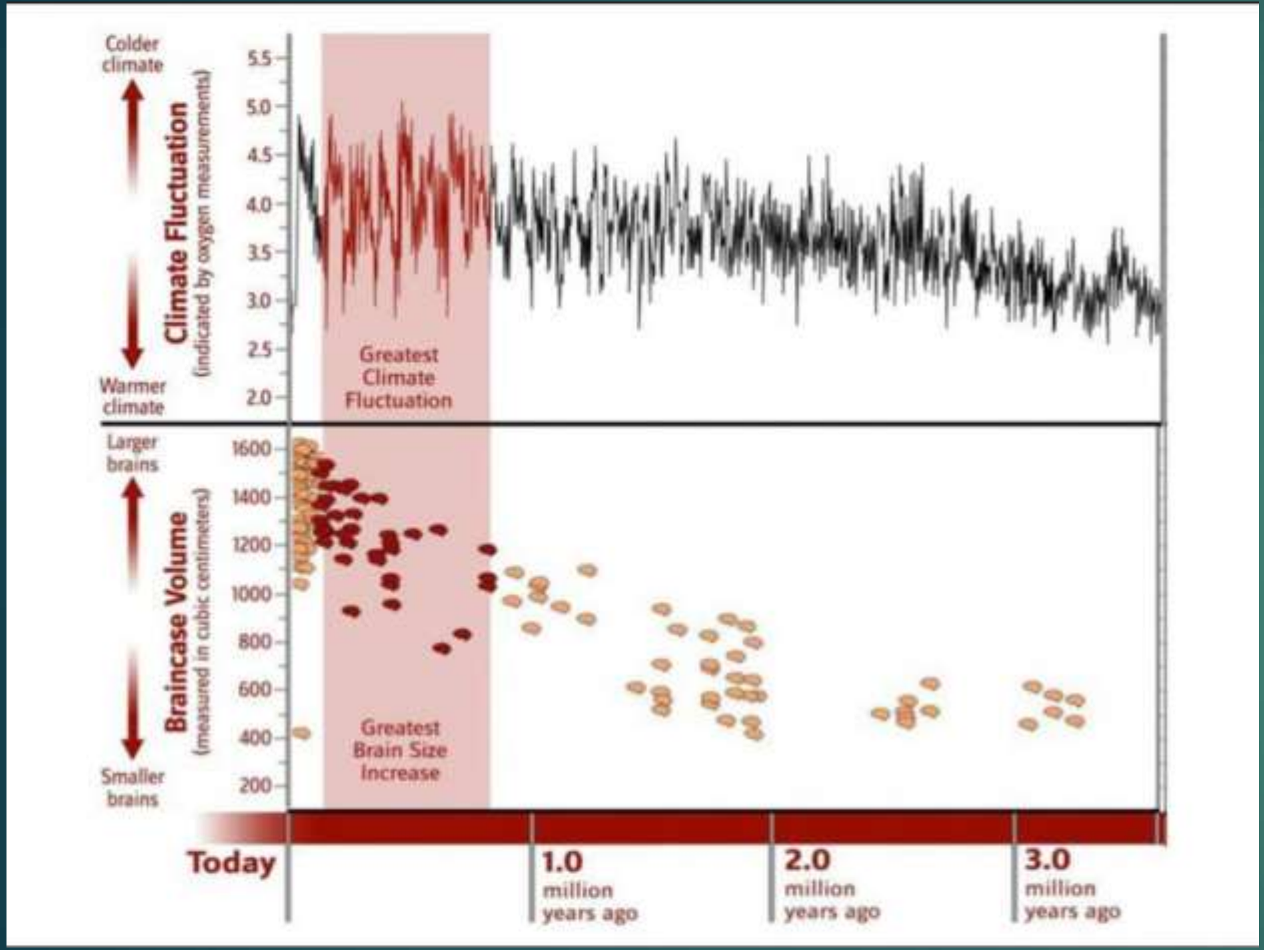
Variability

- Overall, hominins evolved during an environmentally variable time.
- Higher variability occurred as changes in seasonality-produced large-scale environmental fluctuations over periods that lasted tens of thousands of years.
- The variability selection hypothesis implies that human traits evolved over time because they enabled human ancestors to adjust to environmental uncertainty and change.

Environmental variability

- Variability Evidence:
  - capacity to use both climbing and bipedality.
  - Using stone tools also conferred versatility. Tool use would have made it easier for hominins to obtain food from a variety of different sources. Tool use would have widened the diet of hominins.
  - As predicted by the variability selection hypothesis, hominins were not found solely in one kind of habitat, but rather in a variety.
  - A major signal of the ability to tolerate different environments was the dispersal of the genus early *Homo* beyond Africa into Asian environments

Encephalization and Adaptability



- *Brain enlargement during human evolution. During the first four million years of human evolution, brain size increased very slowly.*
- *Encephalization was especially pronounced over the past 800,000 years, coinciding with the period of strongest climate fluctuation worldwide.*
- *A large brain able to produce versatile solutions to new and diverse survival challenges was, according to the variability selection hypothesis, favored with an increase in the range of environments hominins confronted over time and space.*

Climate

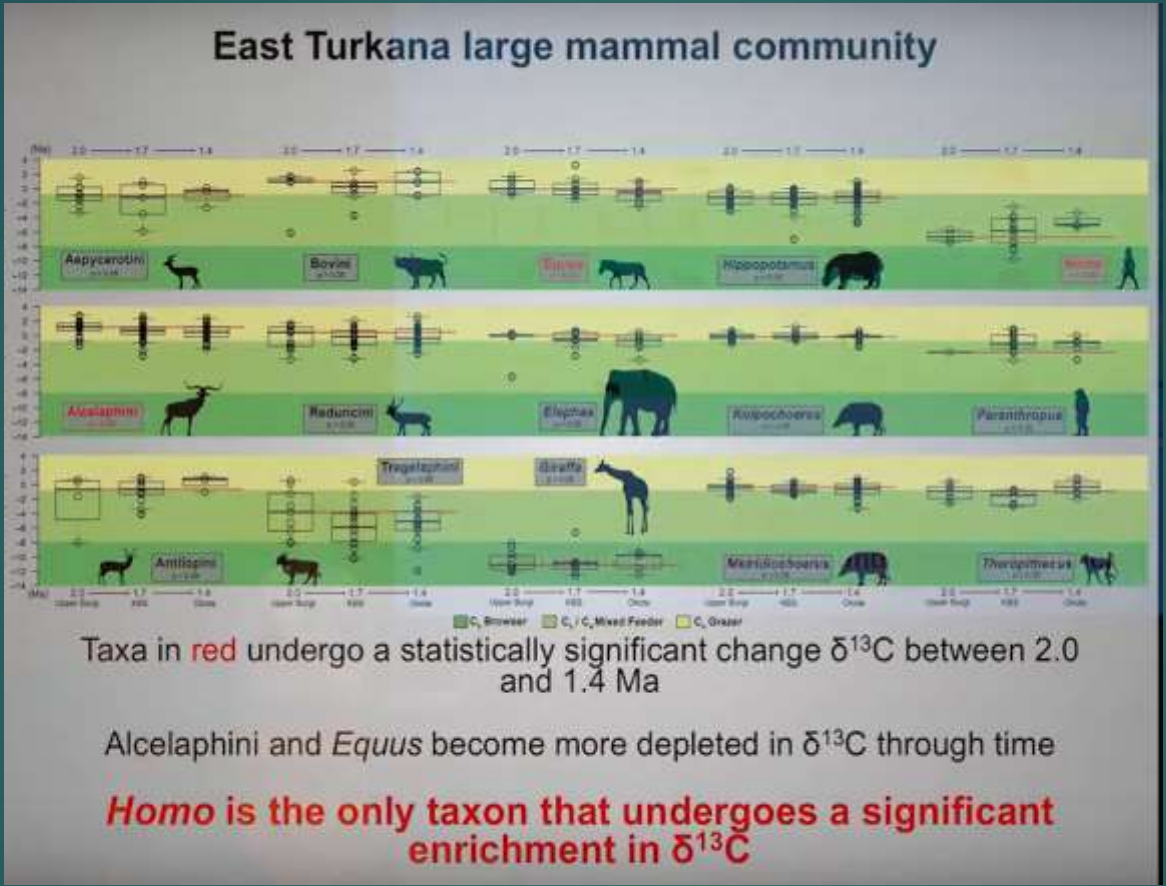
- Although populations of early *Homo* likely lived in a variety of specific environments, Potts reviewed how multiple independent paleoclimatic records show an increase in the amplitude of the climate shifts and an increasing unpredictability in their timing during the origin and early evolution of *Homo*.
- He suggests that this inherent variation in climate placed a premium on developmental plasticity—the capacity for developing individuals to respond phenotypically to environmental change—and likely behavioral plasticity as well.

- The increasing variability of climate over time suggests that both developmental and behavioral flexibility may have been selectively important

R. Potts (2012)

More C3 signal for *Homo erectus* than for *P. boisei*; dietary shift from *H. habilis to H. erectus*

Dark Green = Browsing: a herbivore feeds on leaves, soft shoots, or fruits of high-growing, generally woody, plants such as trees & shrubs; non-grasses; C4 plants; incorporate more 13C into their tissues



Taxa in red undergo a statistically significant change $\delta^{13}C$ between 2.0 and 1.4 Ma

Alcelaphini and *Equus* become more depleted in $\delta^{13}C$ through time

Homo **is the only taxon that undergoes a significant enrichment in $\delta^{13}C$**

Yellow = grazing: feeding on C3 plants grass & sedges or other low vegetation; more **$\delta^{13}C$**

$\delta^{13}C$ (delta C 13) = measure of the ratio of stable isotopes ^{13}C (1%): ^{12}C (99%); an increase in $\delta^{13}C$ in marine fossils is indicative of an increase in the abundance of vegetation.

C3 to C4 shift

- Before 4 Ma, hominins had diets that were dominated by C3 resources; like chimps
- By about 3.5 Ma, many hominins began incorporating C4 foods in their diets
- By 2.5 Ma, *Paranthropus* in eastern Africa diverged toward C4/CAM specialization
- At the same time, *Australopithecus africanus* & *P. robustus* continued to have mixed and varied C3/C4 diets, but more C3.
- Overall, there is a trend toward greater consumption of C4 foods in early hominins over time; eating C4 browsers

Material Culture: Tools and diet

- The archaeological record provides evidence of several key behaviors—including changes in dietary niche, ranging, and cognition—that are often associated with the rise of genus *Homo*.

- The manufacture and use of stone tools has long been thought to signal a foraging shift and to be associated with the origin of *Homo*.

- The first unambiguous tools appear at 2.6 Ma, with cut-marked animal bone ubiquitous in sites after this time

Potts 2012

Material Culture: Tools and diet

- However, one occurrence of cut-marked bone has been argued to occur before the emergence of *Homo*.

- Although the Oldowan is linked to carcass processing, other uses related to plant food processing are important.

- This emerging picture is consistent with dental evidence and supports a modest dietary shift to more carnivory in *Homo* and increased dietary breadth compared with *Australopithecus*.

Early *Homo* Behavior: Stone Tools

- The Oldowan Stone tool industry was named for 1.8 Ma artefacts found near the bottom of Olduvai Gorge, Tanzania.

- Attributed 1st to *P. boisei*, then to 2ndly to *H. habilis*

- Subsequent archaeological research in the Omo (Ethiopia) and Turkana (Kenya) also yielded stone tools dated to 2.3 Ma

- 1992 discovery at Gona, Ethiopia, dated to 2.6-2.5 Ma

Stone Tools

- Recent research on early technologies, by 2.5 Ma, tends to emphasize the complexity of the first lithic assemblages, contradicting previous views on the alleged simplicity of the early Oldowan; mastery of complex reduction techniques

- 2011: 150 stone tools at Lomekwi, Kenya, close to Lake **Turkana**, (*Kenyanthropus platyops* found 1 km away) dated to 3.3 Ma

- Dikika cutmarks on bone at 3.4 Ma

Stone tools made by chimpanzees

Lomekwi 3 (3.3 myr)

Lomekwi 3 tools do not differ much from the stone tools collected from chimpanzee activities. With a LCA that may be no more than 1 myr earlier, the most reasonable conclusion is that stone tool making in *Australopithecus* and *Pan* is homologous.

Very similar: perhaps stone tool making was present in LCA

Homo habilis: Tools

- At Olduvai, tools used to break long bones for marrow, found with cutmarks on faunal bones of turtles, crocodiles, big antelopes, hippos
- Evidence that meat had become part of their diet

Stone tools, dentition, brain size and diet

- Origin of *Homo* based largely on an ecological transition to higher-quality food (aided or concurrent with stone tools), correlated with a decrease in dentition and an increase in body size and brain size.

- Which came first?
  - Larger brains →→stone tools
  - or reverse
  - or concurrent

- Need high quality diet to support larger brain size

- Correlation between larger brain and smaller dentition

Stone Tools precedes large brain

- Brain replaces larger teeth with stone tools

- Stone tools appear to precede any form of increased encephalization, predating development of larger brains

- Use of stone tools → higher quality food → increased brain size and teeth size reduction

Evolution of early *Homo:* Stone tools

- Core-flake-hammerstone technology (Oldowan) is temporally persistent beginning ~2.0 Ma
  - along with the acquisition of large animal tissues at least partly by hunting and butchery,
  - exploitation of diverse terrestrial and aquatic resources,
  - tool-edge wear consistent with processing underground tubers and roots.
- Stone tools were transported from as far away as 12 km from source,

Stone tools

- Oldowan tools provided the technological basis for expansion into southern and northern Africa and western Asia by 1.85 Ma

- Appearance of the Acheulean by 1.76 Ma may have enhanced adaptive potential.

- Increasing flexibility in accommodating to habitat and resource diversity and unpredictability in eastern Africa and beyond.

Tool transport distance

- A second noteworthy change occurs at approximately 1.95 Ma with an increase in stone transport distances that suggests the movement of rock over ~12 km intervals.

- Further, by 1.76 Ma, Acheulean tools appear in the record .
  - These changes are often attributed to *H. erectus* and are used to suggest increased range, although it is worth noting that this temporal association may be coincidental and that increased transit distances may be characteristic of all post-2.0 Ma *Homo*.

- Certainly after 1.6 Ma, *H. erectus*, but not other *Homo*, is distributed across the Old World, suggesting even greater ranging.

East Africa’s unstable ecosystems may have driven human evolution

- Thanks to ice cores and other natural records, we already knew that, for the past 2.5 million years, Earth has been in an ice age
- New study: global climate changes over the past 800,000 years. They did it by using models of the past 120,000 years to develop an algorithm, which they then used to reconstruct an outline of the past 800,000 years.
- Simulated variation in vegetation. They found that many habitats were unstable 90 per cent of the time. Of the stable habitats, many were inhospitable, including the deserts of northern Africa, Arabia and southern Asia.
- This variability may have helped to drive our evolution in Africa’s habitable regions. Many suspect that it was the changeability of conditions in these areas that drove the evolution of our big brains, as our ancestors grappled to adapt to their varying environment.

Climate

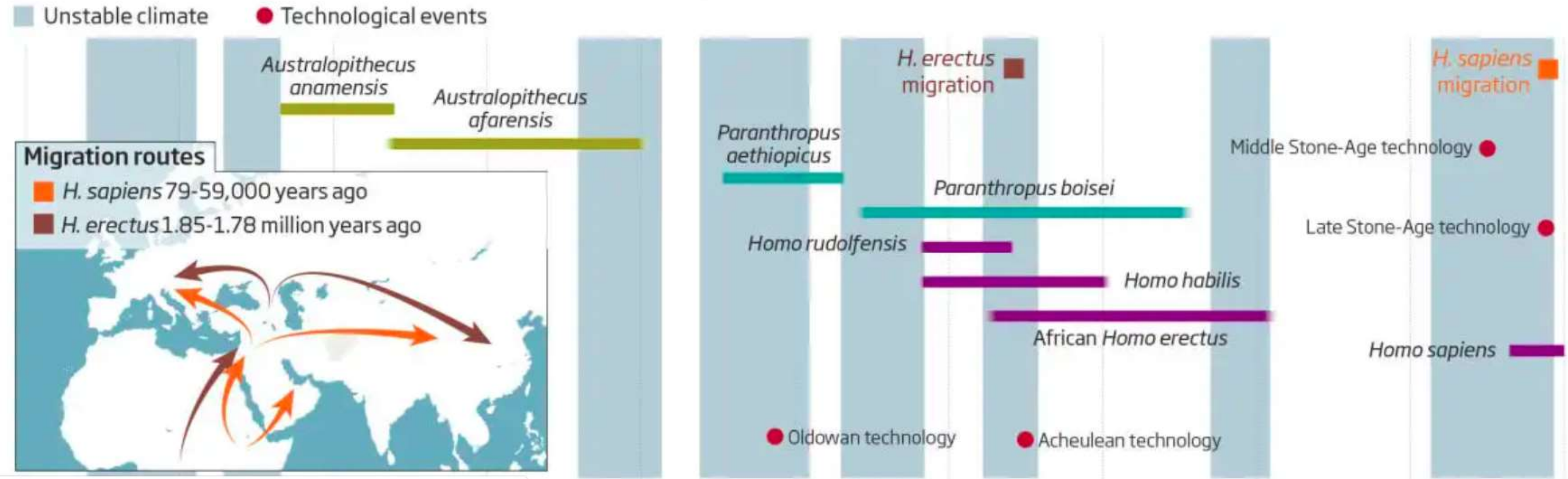
- The forests of west Africa seem to have changed little over this time.
- We don’t know what role these stable habitats may have played in our evolution. We only have fossils for about 10 per cent of Africa
- It seems very reasonable that the deserts of the Sahara, Arabia, Mongolia and Gobi probably played an important role in keeping different populations apart for long periods of time.
- The team examined sediments from Lake Tana in Ethiopia and drew a detailed timeline of rainfall variability. Using the rainfall record to work out when there was a lull in climate upheaval, their theory predicts a dispersal from the area between 97,000 and 112,000 years ago. The fossil record has wide error margins for this dispersal, but they center around 102,000 years ago.
- It suggests that human adaptability and plasticity has allowed us to ride the tide of climate change

Climate

- Darren Curnoe says it’s just as likely that what Potts and others are pointing to as natural selection might actually be other types of evolution like random genetic drift or niche construction, which would mean climate didn’t have any important role at all. “So just jumping to a selection-based scenario is putting the cart before the horse.”
- Potts disagrees. He says they tested for the idea that the associations were a result of chance or biases in fossil preservation. “We tried our best… and found that those factors can currently be discounted,”
- And indeed there is evidence that some birds evolve to be more flexible in response to variable climates – and that this helps them colonies new areas

Human evolution driver?

Some key events in the evolution of humans in East Africa, such as speciation and extinction, as well as migrations and technological innovations, have overlapped with periods of unstable climate more than expected by chance



Evolution of early *Homo*: Savannah theory

- Until recently, the evolution of the genus *Homo* has been interpreted in the context of the onset of African aridity and the expansion of open grasslands
- *Homo erectus* was considered a definite member of the genus *Homo.*
- *Older* agreement that the open-country suite of features inferred for *Homo erectus* had evolved together and provided the adaptations for dispersal beyond Africa.
- *But pre-erectus Homo (*earlier, more fragmentary fossils traditionally attributed to *Homo habilis* and *Homo rudolfensis)* was highly debated.

Susan C. Antón, et al., 2014

Early Models: Baboons & Chimps – predict early *Homo*

- Savanna Baboon model: adaptation to life on savanna
  - Savanna living baboons are the most successful ground-living primates
  - Troop size & structure, predator defense, home range size, diet, roles of hunting & scavenging
- Chimpanzee model: foraging ecology & cognitive abilities
  - Close evolutionary relationship (98.4% identical DNA)
  - Similar brain and body size to early hominins
  - Regular tool use (hammer stones, termite sticks, leaves for hygiene) – early S. African Australopiths used termite bone tools

Scavenging

- Most experts assume the intelligence and social organization of *H. habilis* were more sophisticated than typical australopithecines or chimpanzees.

- Idea that *H. habilis* used tools primarily for scavenging, such as cleaving meat off carrion, rather than defense or hunting.

- Hominins as Prey: Yet, despite tool usage, *H. habilis* was not the master hunter its sister predator species (or descendants) proved to be, as ample fossil evidence indicates *H. habilis* was a staple in the diet of large predatory animals, such as *Dinofelis*, a large scimitar-toothed predatory cat the size of a jaguar.

Scavenging

- *H. habilis* and large carnivores were active at the same locations, based on combinations of toolmarks and gnaw marks
- *Homo* may have regularly encountered abandoned kills, esp. of medium sized adult herbivores; not much left except for marrow bones and head contents; esp. from saber tooth cats (who could not crush bones); latter died off as grassland expanded circa 1.8 Ma
- Whole carcasses of animal skeletons are not represented
- Tools were made of materials that were procured at a distance
- There was repeated use of sites over periods of 5-15 years

Man the hunter; and women…

- In the 1960s and 1970s the “man the hunter” model for provisioning of the social group was supported, followed later by documenting the role of “woman the gatherer”

- Cooperation in food procurement and division of labor by sex are seen as prime factors in the success of early *Homo* in this model

- Since these factors relate to male-female differences in the distant past, they are generally attributed to biologically determined sex differences rather than gender
- Behavioral reconstructions from fragments of bone and stone rely on observations of living primates, human (e.g. modern food foragers) and nonhuman
- It is likely that the culture of *Homo habilis* played a role in food-sharing behaviors, rather than strict biological male-female differences

Higher quality food: Eating meat and marrow

- Currently, there is fossil evidence for at least three species of hominins occurring at around 2.6-2.5 Ma:
    - *Australopithecus africanus*
    - *Australopithecus garhi*
    - *Paranthropus aethiopicus*

- *H. habilis* was established by around 2.4-2.3 Ma. There are no butchered bones (or stone tools) found at stratigraphic levels associated with *A. africanus* or *P. aethiopicus*; but there are 3.3 Ma stone tools

- While butchered bones have been found near *A. garhi* fossils, it's only in the *Homo* lineage, especially in *Homo erectus*, that we see biological features often linked to meat-eating, such as a decrease in tooth and gut size and an increase in body and brain

Evidence for Meat-Eating by Early Humans

- The first major evolutionary change in the human diet was the incorporation of meat and marrow from large animals, which occurred by at least 2.6 Ma.
- Strongest evidence = butchery marks found on bones.
- The earliest well-accepted evidence for this novel dietary behavior comes from about 2.6 Ma at the site of Gona, Ethiopia

Domínguez-Rodrigo *et al.* 2005, 2010; McPherron *et al.* 2010

Evidence for Meat-Eating by Early Humans

- Circa 2.6 Ma we start to see the first evidence of archaeologically visible accumulations of stone tools (Semaw *et al.* 2003).

- There is evidence of hominin-butchered bones at 3.4 Ma at Dikika, Ethiopia, where *Australopithecus afarensis* remains have been found,

New resources: Meat

- Ability of taking advantage of meat resources and animal resources through the butchery of animal carcasses.
- Concurrent with the earliest evidence of stone tools, evidence of cut marks, of butchery of those fossil animals.
- The butchery of animal carcasses using these stone tools, both as percussion instruments and cutting elements, allowed hominins access to a lot of new resources - access fat in marrow & brain (fat)
- Access to things like tendons or cartilage or hide that could've been secondarily utilized to carry objects or store water.

Eating meat

- The carnivory of hominins is unique among primates in three ways:
  - (1) use of flaked stone tools to access animal resources
  - (2) use of meat of animals much larger than the hominins themselves
  - (3) getting meat by scavenging.

- Many zooarchaeologists who study Early Stone Age faunal assemblages think it's likely that at least some animal carcasses that were butchered by hominins, especially the larger ones, were obtained by scavenging.

Oldest evidence of meat eating

- Remains of *Australopithecus garhi*, at 2.5 Ma at Bouri, Ethiopia:
  - Antelope bones with marks that appear to be from stone tools.
  - No stone tools found
  - Oldest evidence that hominins were deliberately defleshing animal carcasses.

- The earliest well documented evidence of persistent hominin **carnivory** from ***in situ*** excavated fossil fauna occurring in association with large concentrations of stone tools is at about 2.0 Ma at Kanjera, Kenya.

- It is first clear evidence of grassland living: Kanjera is a grassland site dominated by grass-eating animals

(Ferraro *et al.* 2013).

Fat in diet: Importance of percussion of bones pre 2 Ma

- The habitual consumption of large-animal resources (e.g., similar sized or larger than the consumer) separates human and nonhuman primate behavior.
- Flaked stone tool use is often portrayed as being functionally related to this by the necessity of a sharp edge for cutting animal tissue. However, most research on both issues emphasizes sites that postdate ca. 2.0 million years ago.
- Jessica Thompson: concepts of meat-eating and tool use are too loosely defined:
  - outside-bone nutrients (e.g., meat) vs.
  - inside-bone nutrients (e.g., marrow and brains)
  - have different macronutrient characteristics (protein vs. fat),
  - mechanical requirements for access (cutting vs. percussion),
  - demanded distinct technological and behavioral solutions.
- Thompson proposes that the regular exploitation of large-animal resources—the “human predatory pattern”—began with an emphasis on percussion-based scavenging of inside-bone nutrients, independent of the emergence of flaked stone tool use.

Jessica Thompson, et al., 2019

Olduvai Gorge: Scavenging or hunting

- Bone fragments of birds, fish, amphibians, and large mammals were found at the FLK-Zinj site, many of which were scarred with marks.
- These likely were made by hominins breaking open the bones for marrow, using tools to strip the meat, or by carnivores having gnawed the bones.
- Since several kinds of marks are present together, some archaeologists including Lewis Binford think that hominins scavenged the meat or marrow left over from carnivore kills.
- Others like Henry Bunn believe the hominins hunted and killed these animals, and carnivores later chewed the bones.

AMNH: Early *Homo* Scavenging Behavior

Homo habilis, 2.3 M, scavenging food
by Jay Matternes

Stones and bones

- A study of *Homo habilis* sites was done by archaeologist Lewis Binford, starting a debate over the relationship of stones & bones.
  - He analyzed bones from several sites and found that many remains are the lower legs of antelopes. These bones carry little meat, and along with the skull, are about the only part of the animal left after a larger carnivore had finished eating. However, such bones are rich in marrow, so *H. habilis* may have eaten what little meat was left on the bones and then broken them open for the bones' rich marrow.
  - Tool marks sometimes overlapped carnivore tooth marks, indicating that the carnivore had been there first
  - *H. habilis* was a scavenger, not a hunter.

Stones & bones debate

- Stratigraphic association between stones and bones does not demonstrate a functional link.
- Associations occur almost entirely near ancient lakeside or streamside sites where stones and bones could have been brought together by various events or chance; preponderance of antelopes and other medium-sized species that tends to characterize African Stone Age sites
- Possibilities:
  - Hunting by people, followed by carnivore scavenging; or the opposite
  - Natural deaths from carnivore predation, accidents, disease, followed by human scavenging
  - Human accumulation of bones at living site/home base, followed by carnivore scavenging
  - Animal accumulation of bones at a den, followed by human scavenging
  - Coincidental association at watering holes, used at different times
  - Stream flows concentrating both

Hunting hypotheses

- 1960s: Hunting hypothesis -- cooperative hunting as primary human adaptation; driving force for human evolution
- 1970s: food sharing hypothesis – Glenn Isaac & “human” home base concept; hunting and gathering; cooperation in meat and plant food sharing; meat not as important; new human behaviors by 2.5 Ma
- 1980s: scavenging hypothesis: took “humanity” out of the picture – attribution of marginal scavenging behavior to hominins; animal foraging
- Current: Advanced scavenging hypothesis: scavenging was route to meat acquisition, but not exclusively; nutritional importance of proteins and hunting significance for all primates

Testing bones and stones hypotheses: Binford vs Isaac

- Lewis Binford: what processes brought stone artifacts and animal bones together at a site; what behaviors are implied?
- Isaac looked at Olduvai Gorge & Koobi Fora; Binford reviewed literature
- Bones & stones could be causally unrelated (washed in by stream, a hydraulic jumble; carnivores used site for feeding & hominins independently used it for stone knapping)
- Olduvai: 40 K bones, 2647 stones; not hydraulic process – Binford: no evidence of carrying food to a home – principally due to carnivore activity, with hominins as marginal scavengers; not social living floors

Living floors

- Living floors as home bases were meat was shared theory: traditionally living floors interpreted as temporarily occupied camps to which hominins returned (Glynn Isaac: use of home bases, sexual division of labor, food sharing as selective pressures that lead to language & cultural rules; i.e.. Modern hunter-gatherers)
- Criteria for scavenged assemblages: broad range of prey-animal sizes, low proportion of juveniles, skew in distribution of prey sizes toward large end
- Conflicting theories: home base, not home base (predators would be attracted to such animal processing areas; they were stone caches)

Testing bones and stones hypotheses

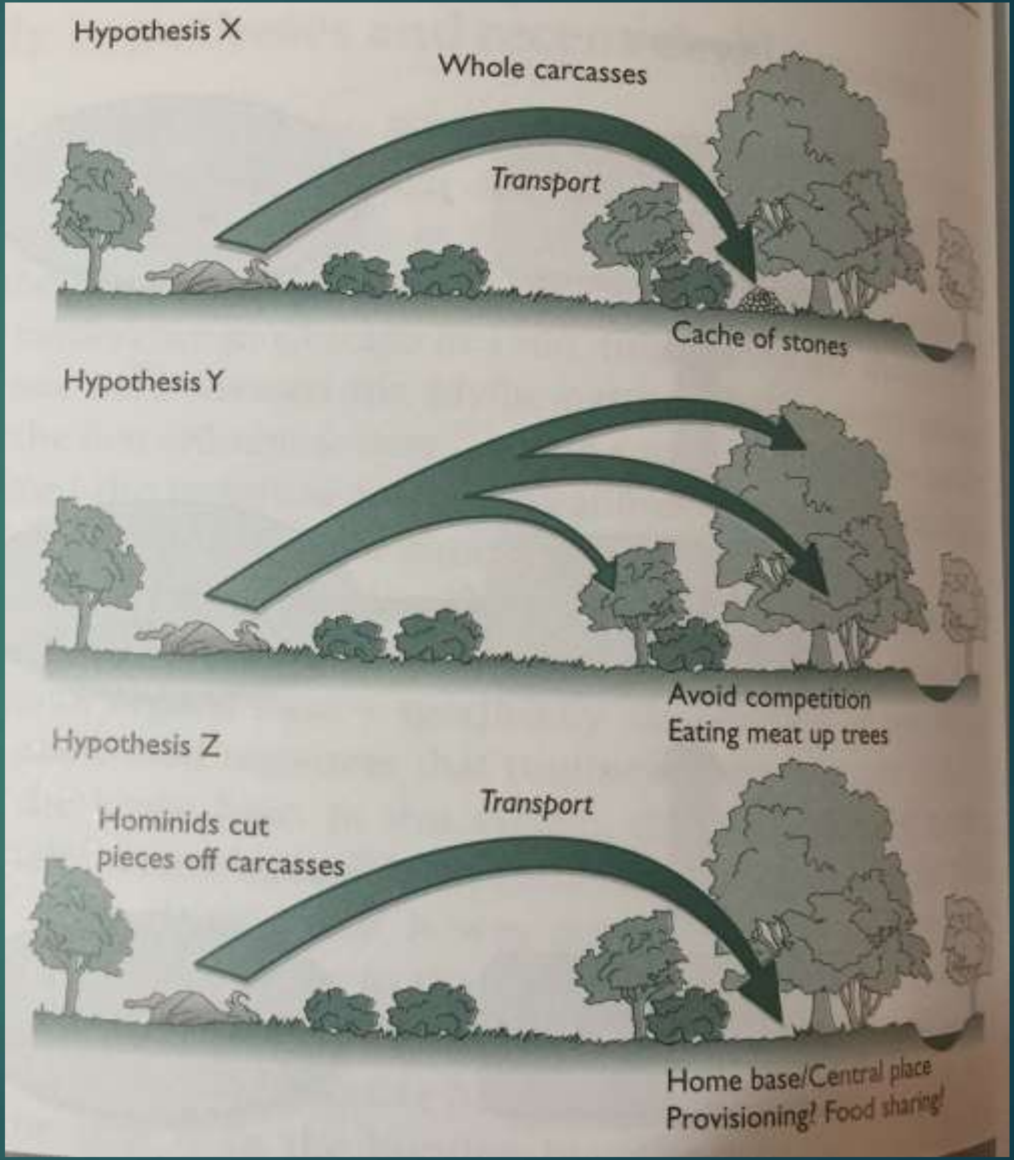
- Isaac’s associates, Rick Potts, Pat Shipman, Henry Bunn: not living floors, but different interpretations
- None agree with Binford that accumulations are primarily result of carnivore activity. All see collections as work of hominins, with carnivores visiting occasionally.
- But question of how much was hunting vs scavenging
- Potts: pattern of bone accumulation is more diverse than would be expected if just carnivore site; thinks it represents a mixture of scavenging and hunting, which can’t be distinguished
- 1979: all three discover first cutmarks on fossil bones at Olduvai; inflicted by stone tools to deflesh or disarticulate the bones; cutmarks are the most direct evidence that hominins used the bones at the site

Testing bones and stones hypotheses

- Shipman: no disarticulating bones; so bones from scavenging from carnivore kills
- Potts & Bunn: evidence of disarticulation, indicating hunting or early scavenging
- Bunn: strongly favors hunting behavior
- Potts: most carnivores are both hunters and scavengers
- Olduvai unlikely to be home base since modern hunter-gathers use home bases for social activity & safety sites for a few weeks; but Olduvai accumulated over 5 to 10 years & visited by carnivores (with both toothmarks overlapping cutmarks & vice versa)
- Potts thinks Olduvai formed around stone caches, where hominins accumulated raw material for making artifacts & brought carcasses to them

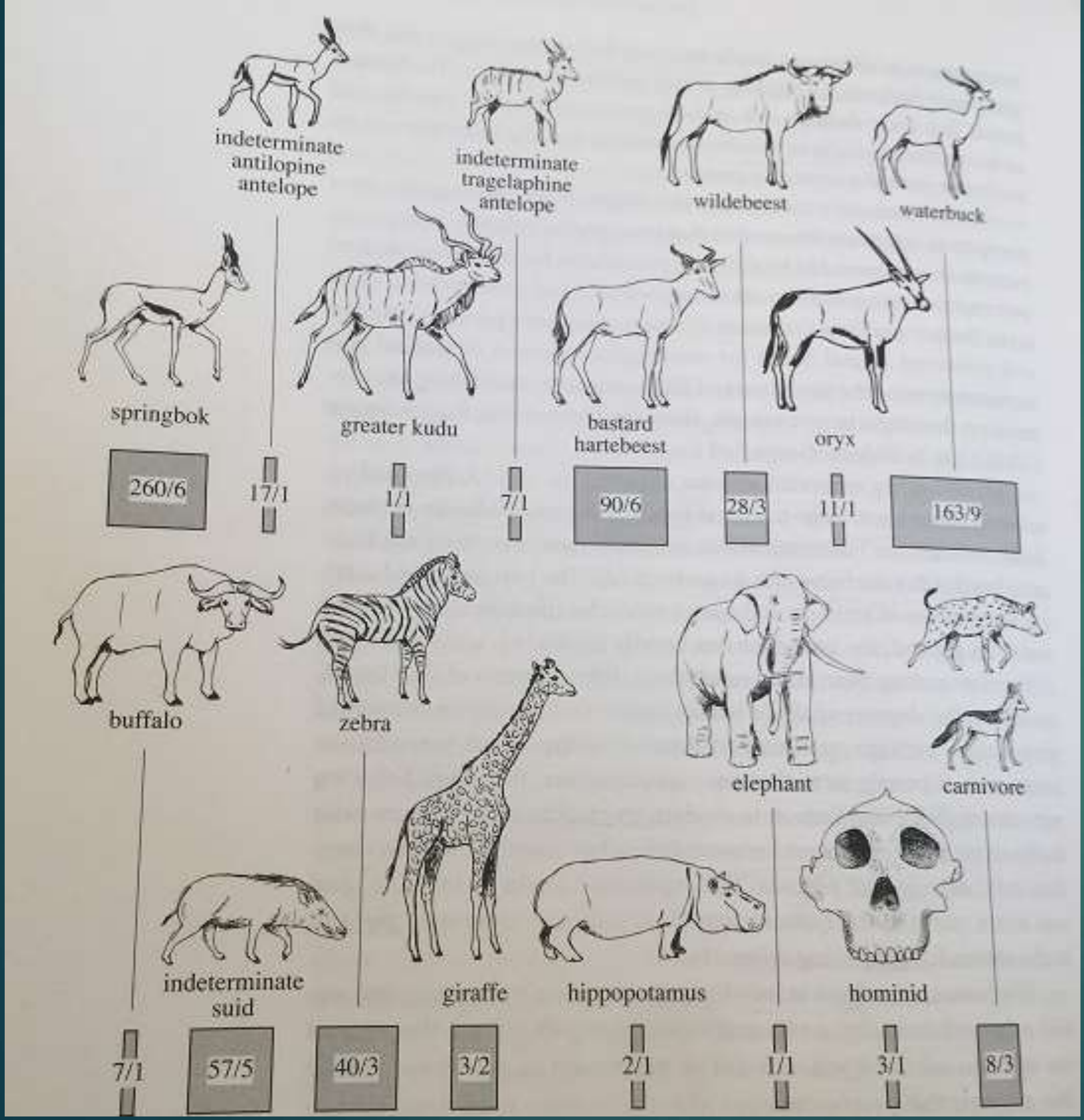
Bones and stones at a site

- Hypothesis X: hominins made caches of stones, to which they brought the more easily transported carcass fragments
- Hypothesis Y: accumulation occurs at 1 location because hominins used trees there to escape competition from other carnivores and ate meat in tree
- Both hypotheses produce same result: bones and stones at same site
- Hypothesis Z = home base theory



What was Olduvai?

- Conway: Olduvai appears to have been formed by hominins transporting stones to particular localities
- Probably also brought meat bearing bones too; the result of scavenging, but maybe hunting
- Instead of home bases, these sites appear to have been meat-processing and consumption places
- But Site 50 at Koobi Fora was not used for stone caches, because raw material is sourced at this site; and stones there used for wood whittling and plant processing; conjoinable bone fragments argue vs water accumulation
- Isaac eventually changed his theory to central-place foraging hypothesis, involving food transporting, but not purposive food sharing



The abundance of various large mammals at the FLK Zinj. site in Olduvai Gorge Bed I (data from Bunn and Kroll *[1986]*).

The bars are proportional to the minimum number of individuals by which each species is represented. The numbers superimposed on the bars are the number of bones assigned to each species over the minimum number of individuals.

The sample is small, but it still illustrates the preponderance of antelopes and other medium-sized species that tends to characterize African Stone Age sites, regardless of age.

Specialists disagree on how the animal bones accumulated at FLK, whether it was mainly through human activity and, if so, whether the people were hunting or scavenging.

Modern hypothesis about meat eating

- Current recognition of importance of meat eating:
  - Hunting exists among chimps & has a social role
  - Most of debate has been about how meat acquired, not on quantity; need only 10-20% of diet to be significant behaviorally & nutritionally
  - Evidence of cutmarks on bones associated with *A. garhi* at 2.5 Ma and cutmarks at 3.3 Ma at Dikika back the first signs of meat eating in hominin evolution
  - Expensive tissue theory (guts vs brain): rib-cage reconstructions of A. afarensis implies large gut (associated with plant eating); change in larger *H. erectus*, correlated with increasing carnivory
  - Size of larger brains requires consistent high-quality protein; meat as source

Modern hypothesis about meat eating

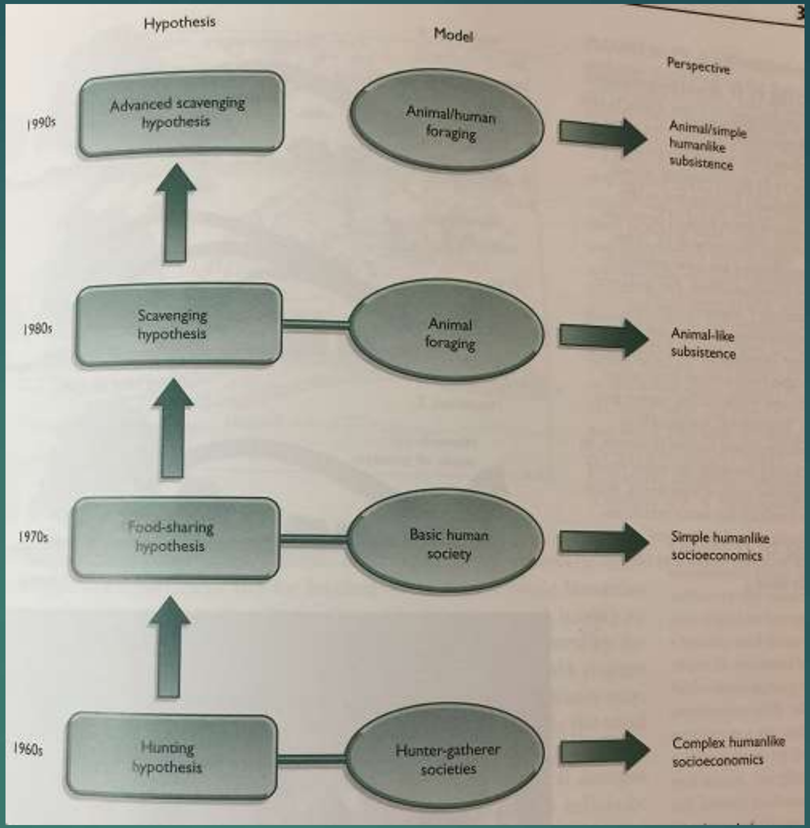
- Once *H. ergaster* is present, new scale to archeological record: much larger quantity of stone tools, clearer structure to sites, strong association with mammalian bones; suggests change in foraging behavior

- Wooden spears at 400K implies systematic hunting before this date

- Analysis of faunal remains during Lower & Middle Pleistocene: association of early hominins and very large mammals

- Meat eating clearly played a role in human evolution

Scavenging vs Hunting



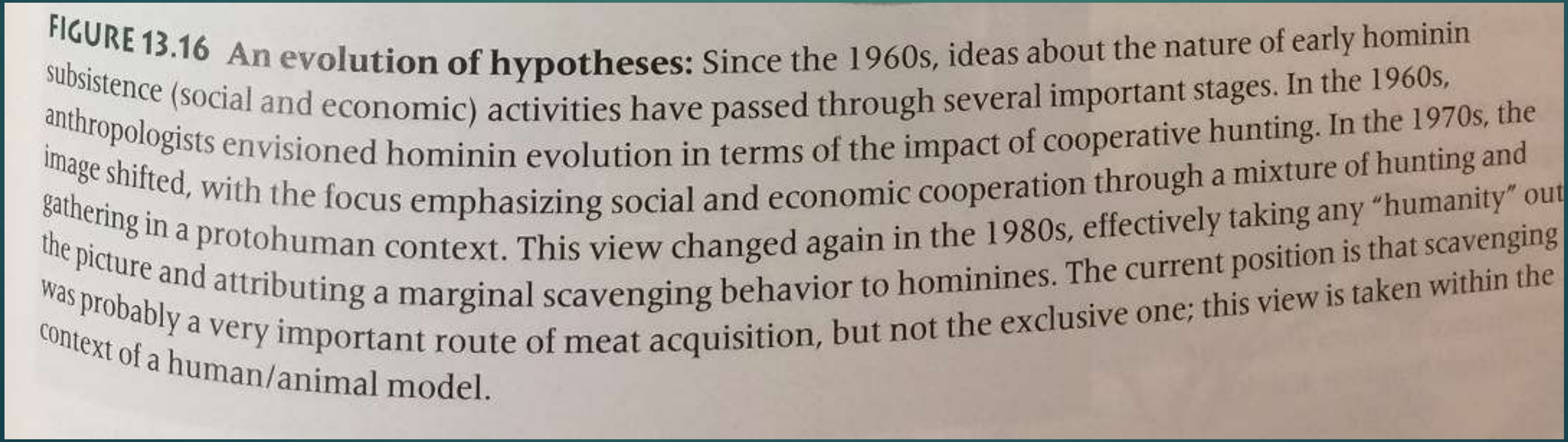


FIGURE 13.16 **An evolution of hypotheses:** Since the 1960s, ideas about the nature of early hominin subsistence (social and economic) activities have passed through several important stages. In the 1960s, anthropologists envisioned hominin evolution in terms of the impact of cooperative hunting. In the 1970s, the image shifted, with the focus emphasizing social and economic cooperation through a mixture of hunting and gathering in a protohuman context. This view changed again in the 1980s, effectively taking any "humanity" out the picture and attributing a marginal scavenging behavior to hominines. The current position is that scavenging was probably a very important route of meat acquisition, but not the exclusive one; this view is taken within the context of a human/animal model.

Homo habilis

- **Diet**:
  - Most of the animal bones found at early *Homo* sites consisted of antelope lower leg bones and skulls, about the only part of an animal left after a large carnivore has finished eating; but note Henry Bunn theory of scavenging vs. ambush hunting.
  - Early *Homo* had smaller teeth than Australopithecus, but their tooth enamel was still thick and their jaws were still strong, indicating their teeth were still adapted for chewing some hard foods (possibly only seasonally when their preferred foods became less available).
  - Dental microwear: diet of *H. habilis* was flexible and versatile

Scavenging

- Sequence of found scavenging, confrontational scavenging, and hunting
- May have contributed to rapid increase in body size from *H. habilis to H. erectus*
- At Olduvai, circ 1.85-1.7 Ma, indicates that hominins and carnivores exploited similar animal species, attracted to same body parts, overlapped spatially, and interacted directly on occasion.
- There, long bones were processed in 3-stage carnivore-hominin-carnivore sequence (longs defleshed by Carnivores, Hominins then processed intact long bones for marrow, and then Cs processed the epiphyses (rounded end of a long bone) for grease)
- Tapeworms colonized early hominins from contact with bovids, hyaenids, canids.

Henry Bunn: *Homo habilis* as hunter

- We examine the ungulate utilization by ancient hominins (e.g. *Homo habilis* and early *Homo erectus*).
- The different lines of evidence suggest that the subsistence activities of early *Homo* probably included active, confrontational scavenging to obtain mostly intact carcasses of large animals and some opportunistic hunting of small animals, both of which yielded significant quantities of meat and fat that were an important source of food.

Henry T. Bunn & Joseph A. Ezzo, 1993

Henry Bunn: *Homo habilis* as hunter

- Henry Bunn: compared the type of prey killed by lions and leopards today with the type of prey selected by hominins in those days.

- In his study, Bunn and his colleagues looked at a huge butchery site in the Olduvai Gorge in Tanzania.

- The carcasses of wildebeest, antelopes and gazelles were brought there by ancient humans, most probably members of the species *Homo habilis*, more than 1.8 Ma. The meat was then stripped from the animals' bones and eaten.

Olduvai Gorge: Scavenging or hunting

- This issue is still debated today, but archaeologist Pat Shipman provided evidence that scavenging was probably the more common practice; she published that the majority of carnivore teeth marks came before the cut marks.

- Another finding by Shipman at FLK-Zinj is that many of the wildebeest bones found there are over-represented by adult and male bones; and this may indicate that hominins were systematically hunting these animals as well as scavenging them.

- The issue of hunting versus gathering at Olduvai Gorge is still a controversial one.

Henry Bunn’s theory

- Newer analysis of Olduvai (FLK22) by H. Bunn:
  - not living floor;
  - primarily a carnivore kill site & to butcher prey;
  - a fresh water spring area that attracted prey and predator;
  - age profiles of hominin prey assemblages (ungulates with cutmarks) do not match those of felid prey assemblages;
  - these hominins were not preying on young and weak;
  - processed more for meat than marrow;
  - actively hunting prime age prey, perhaps using ambush hunting

(Bunn & Pickering, 2010)

Henry Bunn’s theory

- Ages of the animals: The results for several species of large antelope Bunn analyzed showed that humans preferred only adult animals in their prime.

- Lions and leopards killed old, young and adults indiscriminately.

- For small antelope species, humans preferred only older animals, while lions and leopards had a fancy only for adults in their prime.

- "For all the animals we looked at, we found a completely different pattern of meat preference between ancient humans and other carnivores, indicating that we were not just scavenging from lions and leopards and taking their leftovers. We were picking what we wanted and were killing it ourselves."

Henry Bunn, 2012

Henry Bunn: Hunting

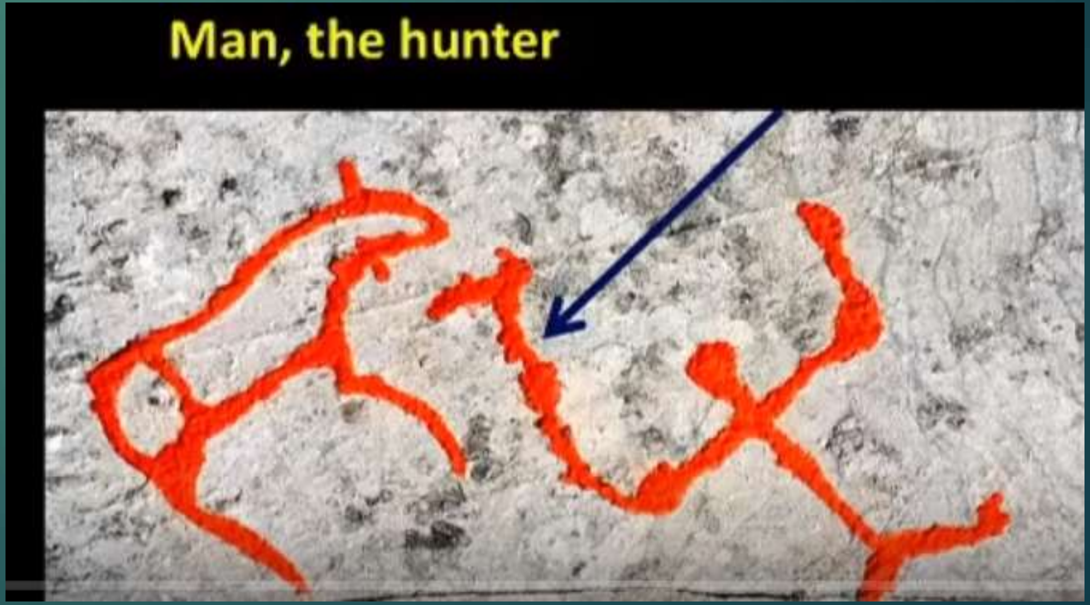
- Did hominid meat eating involve hunting or scavenging? Henry Bunn (UW) examined early hominid sites with cut-mark evidence:
- "For all the animals we looked at, we found a completely different pattern of meat preference between ancient humans and other carnivores, indicating that early hominids were not just scavenging from lions and leopards and taking their leftovers. Early hominids were picking what they wanted and were killing it themselves."

Man the toolmaker

- This brings us to tool making and tool use. From the time of "man, the tool maker", using and making stone tools was considered the key attribute of becoming human, if not its cause. This was firmly believed by Kenneth Oakley, Louis Leakey, and many other early paleoanthropologists who happened to be men.

- But it didn't last! As Mao said,

"women hold up half the world".



Ways the changing Earth shaped human evolution

- All animals evolve in response to their natural environment, and our own species, *Homo sapiens*, is no different.
- It is our environment that has shaped us. The physical features of the planet we live on enabled our species to arise, nurtured our remarkable brains, facilitated our spread across the planet
- About 55.5 Ma, Earth's thermostat spiked, for 100,000 years, up by between 5°C and 8°C, hovered for a bit, and then came back down. This brief planetary fever was hugely disruptive to life on Earth, driving the rapid evolution and divergence of whole new orders of animals, including our own. This temperature rise was due to methane.
- Gas from organic matter at bottom of ocean was became trapped within crystals of ice. The fateful spark is thought to have been a cluster of volcanic eruptions that peppered the atmosphere with enough carbon dioxide to cause an initial temperature rise. This, in turn, melted ice on the sea floor, causing methane to bubble up through the water and into the atmosphere, leading to a further temperature rise that melted yet more methane.

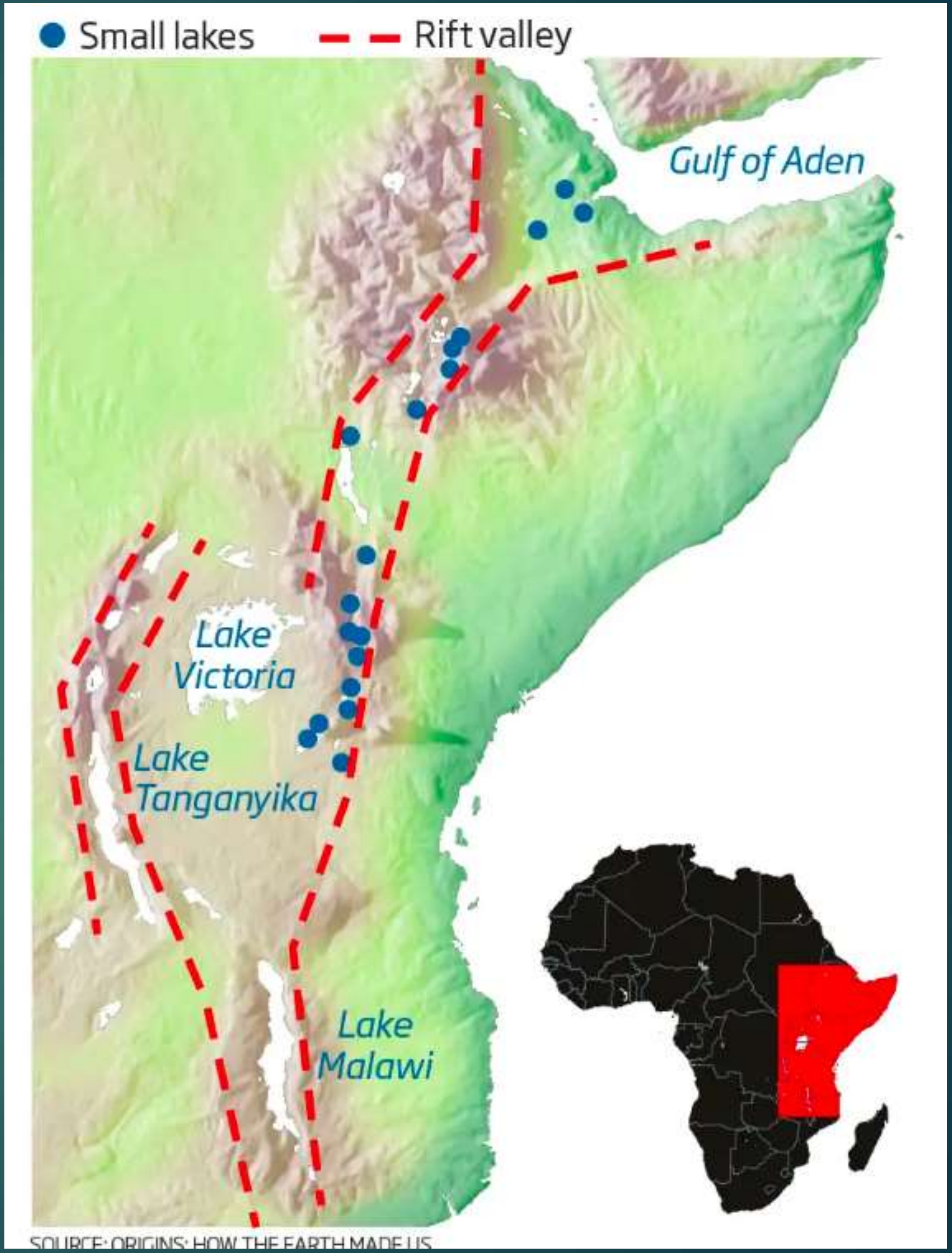
Lewis Dartnell, 2019

Ways the changing Earth shaped human evolution

- The sweltering climate resulted in a burst of evolutionary diversification. The fossil record shows that ungulates, which include modern species like the cow, goat, pig, sheep, llama, camel and horse, first emerged during this period. These large herbivores are utterly critical to human societies, providing not just a reliable source of meat, milk, hide, wool and leather, but also means of transport.
- The most significant group of mammals that sprang up during this heatwave were the primates. These early ancestors of ours, physically similar to lemurs, emerged and then rapidly dispersed across Asia, Europe and North America. But it was in the unique geology of East Africa that they took their first unsteady steps towards humanity.

Ways the changing Earth shaped human evolution

The unusual topography of the East African Rift Valley, and the sensitivity of its lakes to climate change, created a challenging environment that forced our ancestors to get smart or perish.



SOURCE: ORIGINS: HOW THE EARTH MADE US

Ways the changing Earth shaped human evolution

- The major factor that led our evolutionary family, the hominins, to split from our tree-swinging, primate ancestors was the general drying out of East Africa and the transformation of the densely forested habitat into grassy savannah. This drying trend was driven largely by forces beneath the ground. As the African continental plate bulged upwards and ripped apart to form the East African Rift Valley, wall-like mountainous ridges rose to line the valley. These peaks blocked the movement of moisture-laden clouds and kept East Africa arid.
- While the mountainous walls of the rift collect rainfall on their flanks, the valley bottom is hot and dry. That means the many lakes strung along the rift floor are highly sensitive to the delicate balance between precipitation and evaporation, and their water levels fluctuate significantly with the Milankovitch cycles. During particularly unstable climatic periods, these bodies of water rapidly flicker in and out of existence.
- This changing availability of water, and therefore vegetation, animal life and food, is thought to be what favored the evolution of humanity’s versatile behavior.

Ways the changing Earth shaped human evolution

- The three most recent periods of extreme climate variability in this region occurred around 2.6, 1.8 and 1 million years ago, and are each associated with the emergence of new hominin species in East Africa and increases in brain size.
- And once the unstable, fluctuating environment had started encouraging the growth of intelligence, it rapidly led to other big gains, including increasingly complex social interaction, language and tool use. It was in these specialized surroundings that our own species eventually emerged from other hominins around 300,000 years ago.
- During the great human dispersal starting at 2 Ma, Earth was in the depths of its most recent freeze, one of at least 40 such glaciations that have taken place over the past 2.6 million years. Not only were global temperatures much lower during these periods, but the climate was also much drier. Even beyond the reach of the advancing ice sheets, much of the land was desolate tundra. Such conditions would have been undeniably brutal for palaeolithic humans living across Eurasia, but the glaciation offered one crucial advantage to our early ancestors. The great ice sheets locked up vast amounts of water, lowering global sea levels by up to 120 meters.

Ways the changing Earth shaped human evolution

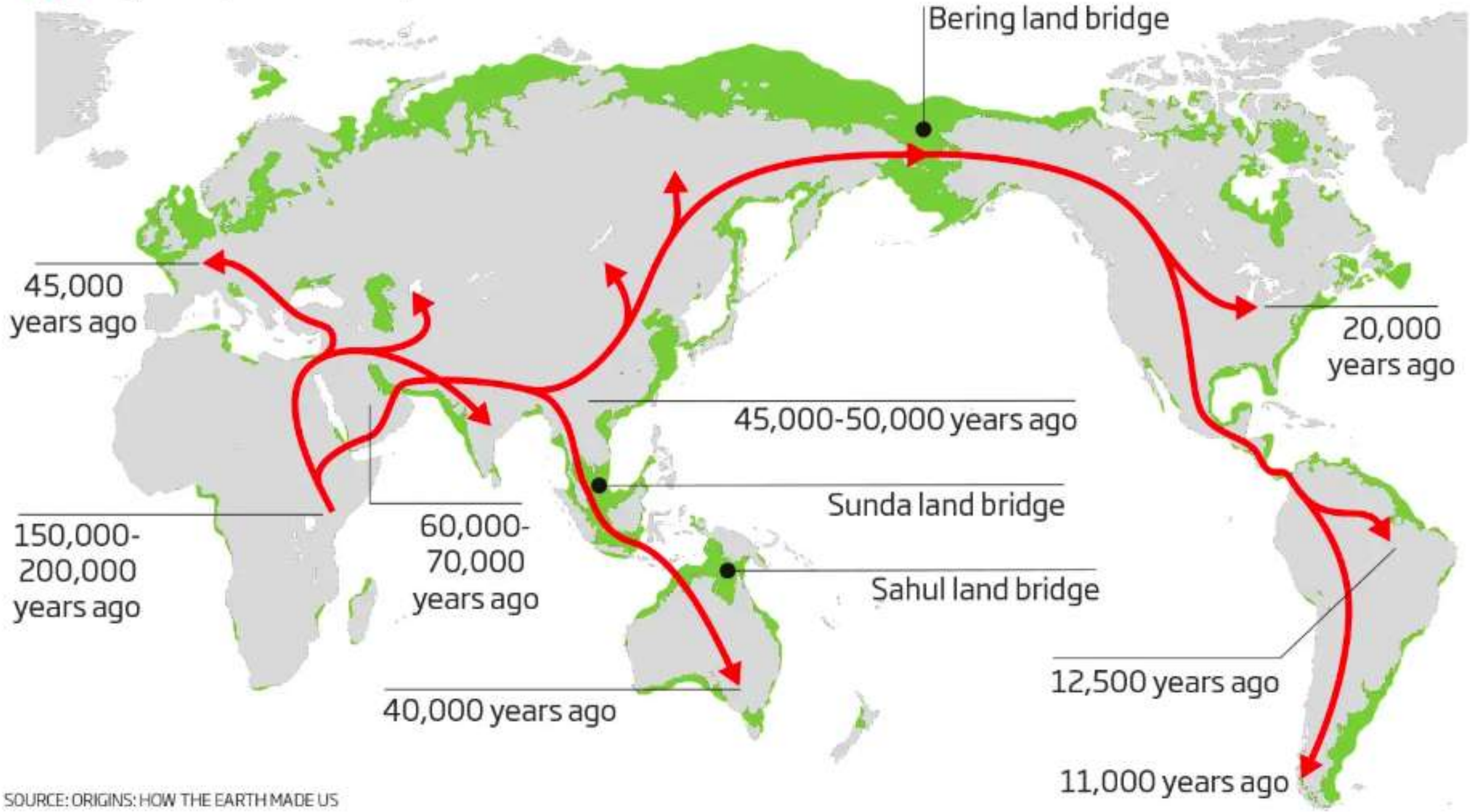
- Large tracts of the shallow continental shelves became dry land, and this offered flat plains for hunting and highways for migration. Early humans in Asia were able to simply walk across the Sunda land bridge to populate current-day Malaysia, as well as Sumatra, Java and other parts of Indonesia, while the Sahul land bridge offered easy access between what is now New Guinea and Australia.
- But perhaps most significantly for the human story, a wide corridor of land linking eastern Siberia and Alaska – the Bering land bridge – also emerged. This gave our ancestors a route of entry from Eurasia into the otherwise unreachable continent of North America, where they soon worked their way down to cross the isthmus of Panama and reach South America as well.

Ways the changing Earth shaped human evolution

Frosty reception

The lowered sea levels of Earth's frozen spells exposed more coastal land (green) that served as land bridges for *Homo sapiens* to migrate around the world. Dates are oldest evidence of *H. sapiens*

→ Migration paths of *H. sapiens*



SOURCE: ORIGINS: HOW THE EARTH MADE US