Homo heidelbergensis: “Archaic” Homo Sapiens

The Muddle in the Middle

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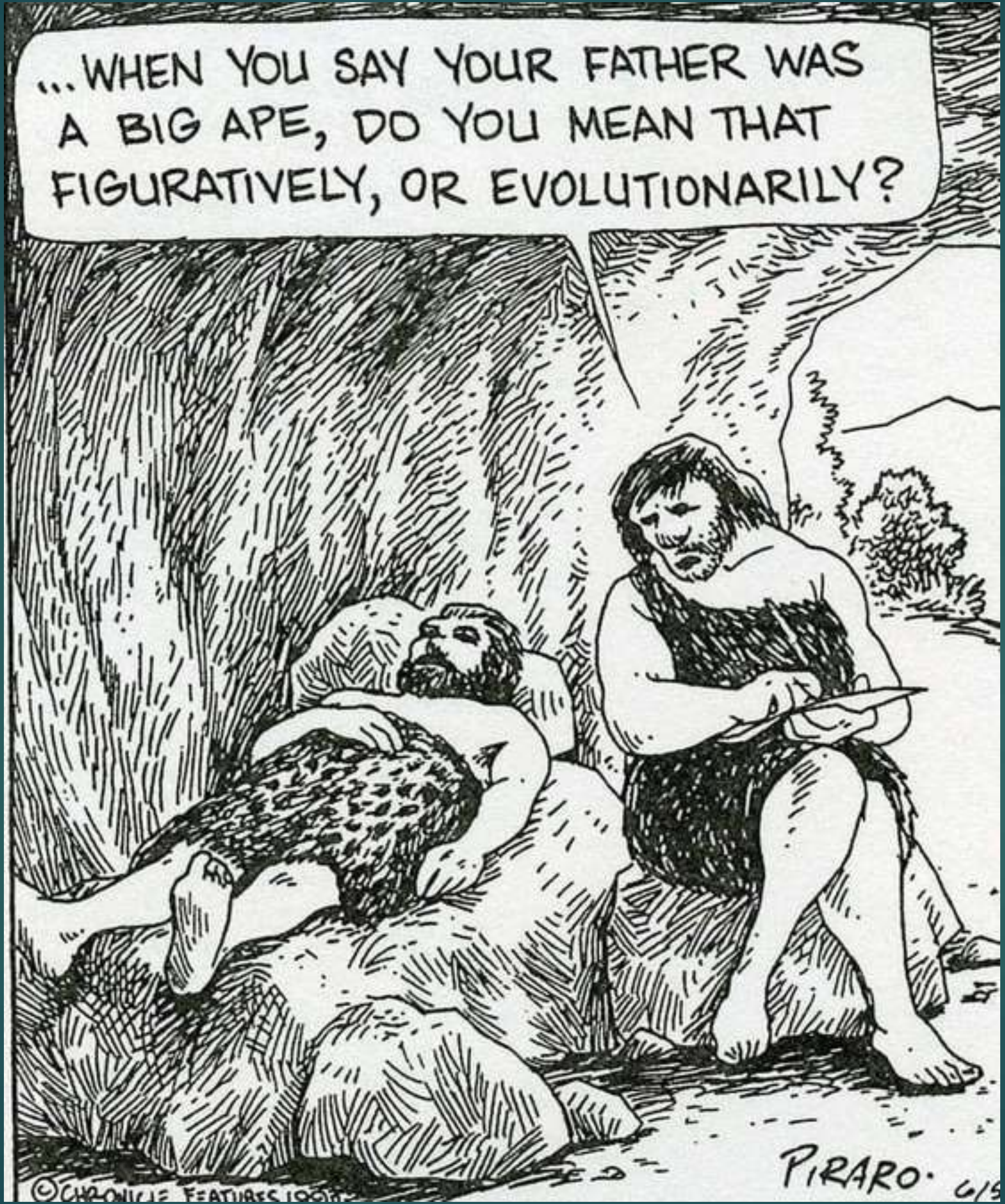
2020

Stephen Gould

“Life is a copiously branching bush,
continually pruned by the grim reaper of extinction,
not a ladder of predictable progress.”


...WHEN YOU SAY YOUR FATHER WAS A BIG APE, DO YOU MEAN THAT FIGURATIVELY, OR EVOLUTIONARILY?
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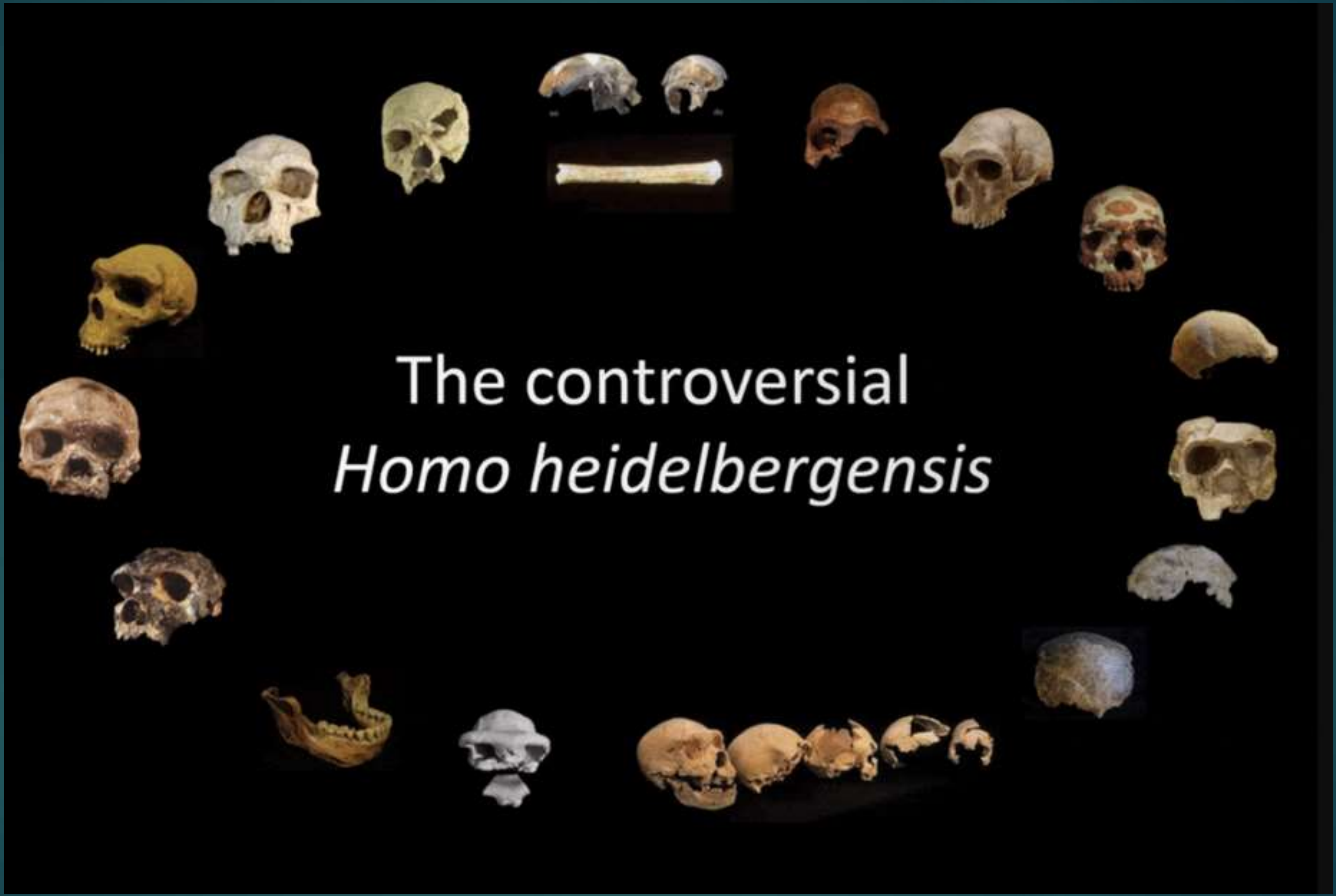
The Pleistocene

- The Pleistocene, often called the Ice Age, was marked by advances and retreats of massive continental glaciations.
  - In Europe at least 15 major and 50 minor glacial advances.
  - Hominins were impacted as the climate, flora, and animal life shifted.

- *** Middle Pleistocene
  - 780 Ka – 125 Ka:
  - period of *H. heidelbergensis*

- Upper Pleistocene (125 Ka to 10,000 y.a.)



The controversial *Homo heidelbergensis*

600 to 250 Ka in Eurasia: Defeating the cold

- After end of 1st major Eurasian glaciation, circa 600 Ka, new kind of hominin appears in Europe and Africa bearing Acheulean axes and wooden spears
- Hunters and gatherers
- More extensive occupation of Europe (or better researched locale)
- Maintained presence through multiple glaciations
- This was *Homo heidelbergensis;* for whom evidence is far richer in Europe than in Africa
- Represents a migration out of Africa or Asia before 1 Ma
- Ancestor of Eurasian *Homo neanderthalensis* and African *Homo sapiens*

Muddle in the Middle: 780-126 K

- What's the problem? The Middle Pleistocene (780-126 K) is often referred to as the 'muddle in the middle' (G. Isaac, 1976) — an apt description given the great debate over which hominin species should be recognized and the attribution of fossils to those species.
- Until recently no securely dated archeological evidence was known from western Europe to suggest permanent occupation there before 500 Ka; then Gran Dolina & Sima del Elefante in Spain were discovered.
- The status of *Homo heidelbergensis* as a distinct type of hominin is controversial.
- Very little well-dated evidence from the period between 500 and 300 Ka

Current Biology 24: L. Buck & C. Stringer

Homo heidelbergensis

Prior to 600 Ka: the African branch of *Homo* is thought to have started evolving towards anatomically modern humans in Africa and the Eurasian branch towards Neanderthals.

Reconstruction based on Kabwe by John Gurche

"Archaic" Homo sapiens *of the Middle Pleistocene: Homo heidelbergensis*

- By 800 Ka, African *H. erectus* were supplanted by or evolved into, a highly variable group of hominins that spread into all of Africa and Europe's ecological niches
- *H. heidelbergensis* is the Hominin during the Middle Pleistocene (780 - 126 Ka)
- Most researchers used the term "archaic *H. sapiens*" until Chris Stringer resurrected the nomen "*H. heidelbergensis*" (type specimen name for the Mauer jaw)
- No DNA yet, except for Sima de los Huesos
- *Homo heidelbergensis: considered as* direct ancestor of:
  - *Homo neanderthalensis,*
  - *Homo denisova*
  - *Homo sapiens*

Three Major Evolutionary Transitions: Middle Pleistocene

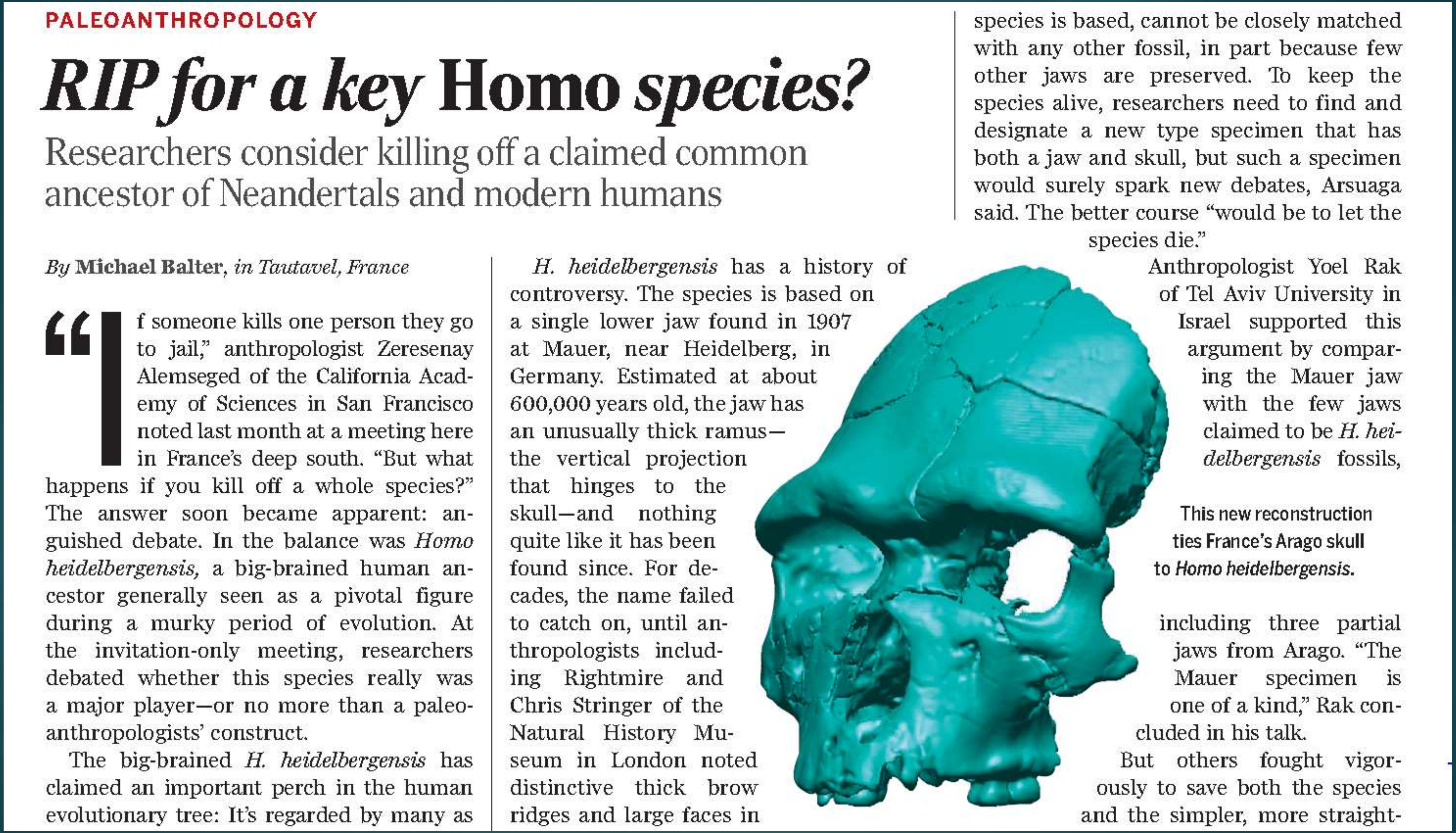
1. Early *Homo* to *H. erectus* - only in Africa.

2. Leading to more transitional archaic hominins (*H. heidelbergensis*), Not geographically limited, but occurred slowly and unevenly.

3. Evolution from *H. heidelbergensis* to classic Neandertals of Europe and anatomically modern *H. sapiens* in Africa.

“Archaic” *Homo sapiens*/*Homo heidelbergensis* definition

- *H. heidelbergensis* are ancestral members of the species *Homo sapiens* (including Neandertals)
- Who preceded “anatomically modern *Homo sapiens*” (i.e. Omo, Qafzeh and Cro-Magnon) but
- are different from, yet retained some characteristics of, *Homo erectus*
- and lack the full set of characteristics diagnostic of modern *Homo sapiens* . . .



PALEOANTHROPOLOGY

RIP for a key Homo *species?*

Researchers consider killing off a claimed common ancestor of Neandertals and modern humans

By **Michael Balter**, *in Tautavel, France*

"If someone kills one person they go to jail," anthropologist Zeresenay Alemseged of the California Academy of Sciences in San Francisco noted last month at a meeting here in France's deep south. "But what happens if you kill off a whole species?" The answer soon became apparent: anguished debate. In the balance was *Homo heidelbergensis,* a big-brained human ancestor generally seen as a pivotal figure during a murky period of evolution. At the invitation-only meeting, researchers debated whether this species really was a major player—or no more than a paleoanthropologists' construct.

The big-brained *H. heidelbergensis* has claimed an important perch in the human evolutionary tree: It's regarded by many as

H. heidelbergensis has a history of controversy. The species is based on a single lower jaw found in 1907 at Mauer, near Heidelberg, in Germany. Estimated at about 600,000 years old, the jaw has an unusually thick ramus—the vertical projection that hinges to the skull—and nothing quite like it has been found since. For decades, the name failed to catch on, until anthropologists including Rightmire and Chris Stringer of the Natural History Museum in London noted distinctive thick brow ridges and large faces in

species is based, cannot be closely matched with any other fossil, in part because few other jaws are preserved. To keep the species alive, researchers need to find and designate a new type specimen that has both a jaw and skull, but such a specimen would surely spark new debates, Arsuaga said. The better course "would be to let the species die."

Anthropologist Yoel Rak of Tel Aviv University in Israel supported this argument by comparing the Mauer jaw with the few jaws claimed to be *H. heidelbergensis* fossils, including three partial jaws from Arago. "The Mauer specimen is one of a kind," Rak concluded in his talk.

But others fought vigorously to save both the species and the simpler, more straight-

This new reconstruction ties France's Arago skull to *Homo heidelbergensis.*

M. Balter, *Science*, 2014

R.I.P. for a homo species?

- *Homo heidelbergensis* is regarded by many as the common ancestor of modern humans and the Neandertals. Dating to roughly 600 Ka, it is thought to link those species and the earlier *H. erectus.*
- *H. heidelbergensis* has a history of controversy. The species is based on a single lower jaw found in 1907 at Mauer, near Heidelberg, Germany, dated to 600 Ka; the jaw has an unusually thick ramus and nothing quite like it has been found since.
- P. Rightmire argues that this species fits up to 20 specimens from Europe, Africa, and Asia dated to between 800 and 200 Ka, just before *H. sapiens* appears in Africa.
- Often designated as “archaic” *Homo sapiens*

Michael Balter, *Science*, 2014

R.I.P.?

- Most of these skulls had a larger brains than *H. erectus*, ~1250 cc
- In the 1970s, Stringer and others postulated a single species spanning Europe, Africa, and Asia, and resurrected the "*H. heidelbergensis*" name to describe it.
- One classic position used to be the consideration of *Homo heidelbergensis* as the **common ancestor** of *Homo sapiens* and *Homo neanderthalensis*.
- Alternative hypotheses place *Homo heidelbergensis* as a Western European niche, while the African fossils are assigned to *Homo rhodesiensis*.
- *H. heidelbergensis* got a big boost in the 1990s when researchers working at the site of Sima de los Huesos in Spain attached the name to the remains of 28 hominins found there.

European Middle Pleistocene specimens

Mauer (Germany)
600 Ka.

Steinheim an der Murr
(Germany)
250-300 Ka.

Arago
Tautavel (France)
450 Ka.

Petralona (Greece)
350 Ka.

African Middle Pleistocene specimens

Bodo (Ethiopía)
600 Ka.

Kabwe (Zambia)
300 Ka.
Broken Hill

Saldanha (Sudáfrica)
500 Ka.

Ndutu (Tanzania)
350 Ka.

European Middle Pleistocene specimens

Vértesszőllős (Hungary)
500 Ka.

Boxgrove (UK)
500 Ka.

Swanscombe (UK)
400 Ka.

Bilzingsleben (Germany)
370 Ka.

Asian Middle Pleistocene specimens

Zuttiyeh Cave (Israel)
300 Ka.

Yunxian (China)
581 Ka.

Maba (China)
132 Ka.

Jinniushan (China)
280 Ka.

Dali (China)
200 Ka.

No longer *Homo heidelbergensis*

Altamura
Grotta di Lamalunga (Italy)

DNA analysis in 2014 confirmed its assignment to H. neanderthalensis 170 Ka.

Sima de los Huesos Atapuerca (Spain)
430 Ka.

DNA analysis in 2015 confirmed their relationship to H. neanderthalensis

The key *H. heidelbergensis* fossils with locations & dates

- Mauer (Germany): 1907
- Broken Hill (Zambia): 1921
- Steinheim (Germany): 1933
- Saldanha/Elandsfontein (South Africa): 1953
- Petralona (Greece): 1960
- Arago (France): 1964
- Bodo (Ethiopia): 1976
- Atapuerca (Spain): 1994
- Boxgrove (England): 1994

Rise of post-*erectus* hominins: G. Philip Rightmire

- These key fossils above differ from *Homo erectus* in brain size and other aspects of their morphology.
- Evidence for sophisticated stone tools, hunting large herbivores, and probably controlling fire to prepare food.
- However, the skulls retain numerous primitive features that set them apart from modern humans:
  - Faces are massively built with strong supraorbital tori
  - Frontal bones are flattened
  - Skull vaults remain low
  - Less parietal expansion than is evident in *Homo sapiens*.

Rise of post *erectus* hominins

- Evidence from Africa and Europe suggests a speciation event in which *Homo erectus* gave rise to a daughter lineage.
- At or before the beginning of the Middle Pleistocene, these new populations spread across Africa and into western Eurasia.
- It is possible that additional splitting occurred subsequently, as the hominins in Europe became increasingly isolated from other groups.
- It is very likely that a *H. heidelbergensis* lineage established in Africa produced the first populations resembling *Homo sapiens*.
- How the fossils from Africa and Europe should be grouped into species continues to be debated.

H. erectus to H. heidelbergensis speciation event: brain size

- *Homo erectus*: well-represented by fossil crania. The mean capacity for 30 crania is 973 cc. Within this group there is substantial variation, but brain size increases in specimens from later time periods (up to 1250 cc).
- Middle Pleistocene (781–126 ka) crania differ from those of *Homo erectus*.
- Characters of the facial skeleton, vault, and cranial base suggest that fossils from sites such as Arago Cave in France, Bodo in Ethiopia, Broken Hill in Zambia, and perhaps Dali in China belong to the taxon *Homo heidelbergensis*.
- Ten of these hominins have brains averaging 1,206 cc in volume.

G. P. Rightmire, Am J Phys Anthropol, 2003.

Rise of post-*erectus* hominins

- The (significant) increase in brain volume documented for the Middle Pleistocene individuals is not simply a consequence of larger body mass. They have higher encephalization quotients (3.7 to 4.2 vs. MH's 5.4).

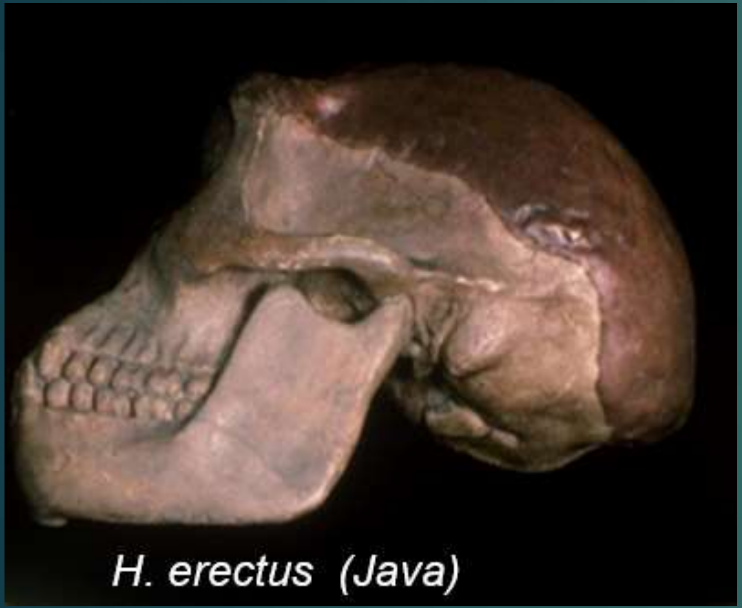
- These changes in absolute and relative brain size can be taken as further corroborative evidence for a speciation event, in which *Homo erectus* produced a daughter lineage.

- It is probable that *Homo heidelbergensis* originated in Africa or western Eurasia and then ranged widely across the Old World.

Erectus vs. Sapiens

- The primary morphological characters of *H. erectus:* a long and low cranium, a pronounced supraorbital torus, a pronounced postorbital constriction, thick cranial bones, an angled occipital torus, a cranium that is widest at the base, the absence of a chin, and a cranial capacity of ~1,000 cc. *H. erectus* **postcrania** fall within the range of modern *H. sapiens*, but generally are more robust
- The primary morphological traits of *H. sapiens* that distinguish it from *H. erectus:* more rounded and high cranium, a reduced supraorbital torus, the lack of a postorbital constriction, a less angled occipital torus, a cranium that is widest at the top of the parietals rather than at the base, a chin, and a cranial capacity of ~1,350 cc.
- The primary distinctions between the two species appear to be morphological variation found in the crania.

Bae, C. J. (2013) . Nature Education Knowledge 4(8):4



H. erectus (Java)

H. heidelbergensis

H. neanderthalensis

H. sapiens

Erectus, archaic *Sapiens*, *Sapiens* 2

- Fossils that do not fit the above two sets of traits were allocated to archaic *H. sapiens/H. heidelbergensis*.
  - The African fossils include Bodo, Broken Hill, Ndutu, and Elandsfontein,
  - while the western Eurasian fossils include Mauer, Arago, Petralona, and possibly Zuttiyeh from Israel.
  - The primary Chinese fossils are from Dali, Jinniushan, and Maba, while the late Solo fossils from Indonesia can also be included.

- The ages of these hominin fossils range from ~600 Ka (Bodo) to as recently as about 120 Ka (Maba)

Petralona

Kabwe

Figure 2

Frontal (top) and lateral (bottom) views of typical *Homo heidelbergensis* crania from Europe and Africa (left: Petralona; right: Kabwe).

Maba

Dali

Figure 3

Frontal (top) and lateral (bottom) views of typical archaic *Homo sapiens* crania from China (left: Maba; right: Dali).

“Archaic” *Homo sapiens*

- Almost modern-sized brains, but set off as ‘archaic' because of their primitive looking cranial morphology"
- The primary morphological characteristics of archaic *H. sapiens* (Rightmire 2004, 2008) are:
  - 1) average cranial capacity (~1,200 cc) and a proportional increase in **encephalization** that places them between modern *H. sapiens* (~1,350 cc) and *H. erectus* (~1,000 cc);
  - 2) a reduced postorbital constriction, to account for the increase in cranial capacity;
  - 3) the degree of overall cranial robustness somewhere between *H. erectus* and *H. sapiens*;
  - 4) and compared to *H. erectus*, a more rounded and less angled occipital region.
- Few post-cranials have been found; bones suggest cold adaptation in Europe

Now *H. heidelbergensis*

- Over the past several decades, there has been a push by a number of paleoanthropologists to refer to the Middle Pleistocene archaic *Homo sapiens* as *H. heidelbergensis*, following the original designation of the Mauer mandible which is the **holotype** of the taxon (Schoetensack 1908).
- There is a great deal of morphological variation within and between the European and African *H. heidelbergensis* fossils
- Besides Early Pleistocene occupations in higher latitudes by *Homo erectus* in Georgia, for the most part Middle Pleistocene archaic *Homo sapiens* were the most widely and northerly ranging hominin group prior to the arrival of modern *H. sapiens*
- However, occupation of higher latitudes was probably restricted to interglacial stages.

Relationships: Europe vs Africa

- In Europe, *H. heidelbergensis* is taken to have given rise to *H. neanderthalensis* circa 240 Ka (a conventional date dictated by a fossil gap)

- Late *H. heidelbergensis* in Europe prior to 240 Ka is also called "pre-Neanderthal" or "ante-Neanderthal").

- *Homo sapiens* most likely derived from *H. rhodesiensis* (African *H. heidelbergensis*) after ~300 Ka.

Dating

- The date of the fossil range of:
  - *H. heidelbergensis* spans about 600 to 400 Ka
  - cladistically, *H. heidelbergensis* is estimated to have developed from *H. erectus* (or *H. antecessor*) around 800 to 700 Ka
  - and given rise to *H. neanderthalensis* (and *H. sapiens* via *H. rhodesiensis*) around 400 to 300 Ka
- Neither the derivation of *H. heidelbergensis* from *H. erectus*, nor the derivation of anatomically modern humans and Neanderthals from *H. heidelbergensis*, are clear-cut and are the object of debate.

Relationships

- It is uncertain whether *H. heidelbergensis* is ancestral to *Homo sapiens*, as a fossil gap in Africa between 400 to 260 Ka obscures the presumed derivation of *H. sapiens* from *H. rhodesiensis*.
- Genetic analysis of the Sima de los Huesos fossils (Meyer et al. 2016) seems to suggest that
  - *H. heidelbergensis* in its entirety should be included in the Neanderthal lineage, as "pre-Neanderthal" or "archaic Neanderthal" or "early Neanderthal",
  - while the divergence time between the Neanderthal and modern lineages has been pushed back to before the emergence of *H. heidelbergensis*, to about 600 to 800 Ka, the approximate time of disappearance of *Homo antecessor*

Relationships: *H. antecessor*

- Recent theory that *H. heidelbergensis* is derived from *Homo antecessor* around 800,000 to 700,000 years ago.

- The oldest-known fossil classified as *H. heidelbergensis* dates to around 600 Ka (Bodo in Africa), but the flint tools found in 2005 at Pakefield in Suffolk, England, with teeth from the water vole *Mimomys savini*, a key dating species, suggest human presence in England at 700 Ka, assumed to correspond to a transitional form between *H. antecessor* and *H. heidelbergensis*.

- Fifty prehistoric hominin footprints dated to 1 Ma were discovered in Happisburgh, England. They are likely members of *Homo antecessor* that lived from 1.2 Ma to 800 Ka

Relationships

- Hublin (2013): Middle Pleistocene humans in Eurasia underwent a succession of population bottlenecks due to glaciations.
- Chris Stringer (2012): *Homo heidelbergensis* as an independent chronospecies. A 2013 genetic study on the Sima de los Huesos fossils classified them as *H. heidelbergensis* or "early Neanderthal“
- White et al. (2003): Rhodesian Man (Kabwe) as ancestral to *Homo sapiens idaltu* (Herto Man)

Is *Homo heidelbergensis* a distinct species?

- The discovery of new fossils in Africa, Asia, and Europe, and the recognition of a greater diversity in the middle Pleistocene fossil record, has led to a reconsideration of the species *Homo heidelbergensis*.
- This nomen, formulated by Schoetensack in 1908 to describe the Mauer jaw (Germany), was almost forgotten during most of the past century.
- Numerous fossils have been attributed to it but no consensus has arisen concerning their classification.
- The holotype anatomical traits are still poorly understood, and numerous fossils with no mandibular remains have been placed in the taxon.

Aurélien Mounier François Marchal, Silvana Condemi, 2008

Homo heidelbergensis

Location: East and South Africa, Europe and Western Asia: Africa (Broken Hill/Kabwe, Bodo, Omo), Europe (Arago, Atapuerca– Sima de los Huesos, Petralona, Schoeningen, Steinheim, Swanscombe), Asia (Dali)

As yet, no *H. heidelbergensis* DNA has been sequenced

Date range: 780 Ka – 130 Ka

Brain size: ~ 950-1390 cc (average 1250 cc) = core feature of species

Tool use: Acheulean, Mousterian/Levallois (later in Europe); Oldowan (in Asia)

- First definite controlled use of fire; Definite evidence for hunting

- First species build permanent shelters. Evidence for semi-permanent shelters

Homo heidelbergensis firsts

- Several attributes of the human species appear first in *H. heidelbergensis*.
- *H. heidelbergensis* was the first *Homo* with a body shape that enabled it to withstand colder temperatures, paving the way for its successors to adapt for even colder landscapes: *H. heidelbergensis* could conserve more body heat to endure harsher climates because its body was comparatively wide in relation to its height.
- The apparently earliest documented case of odontogenic orbital cellulitis, a severe eye infection that develops from an abscess in the mouth, occurred in *H. heidelbergensis*; also of a meningioma in brain

Post *erectus hominins*

- Use of ocher pigmentation
- Prepared core technology: Levallois circa 400-300 Ka in Africa; then at 200 Ka outside of Africa
- Regular fire use; Fire was used, although further evidence is needed to establish whether this was a controlled use of fire.
- Spear hafting
- Use of projectiles

Post *erectus hominins*

- Cold adaptation in Europe

- *Homo heidelbergensis* hunted large animals for food. The fossilized bones of these animals have shown that large animals including rhinos, hippopotamus, bears, horses and deer were targeted.

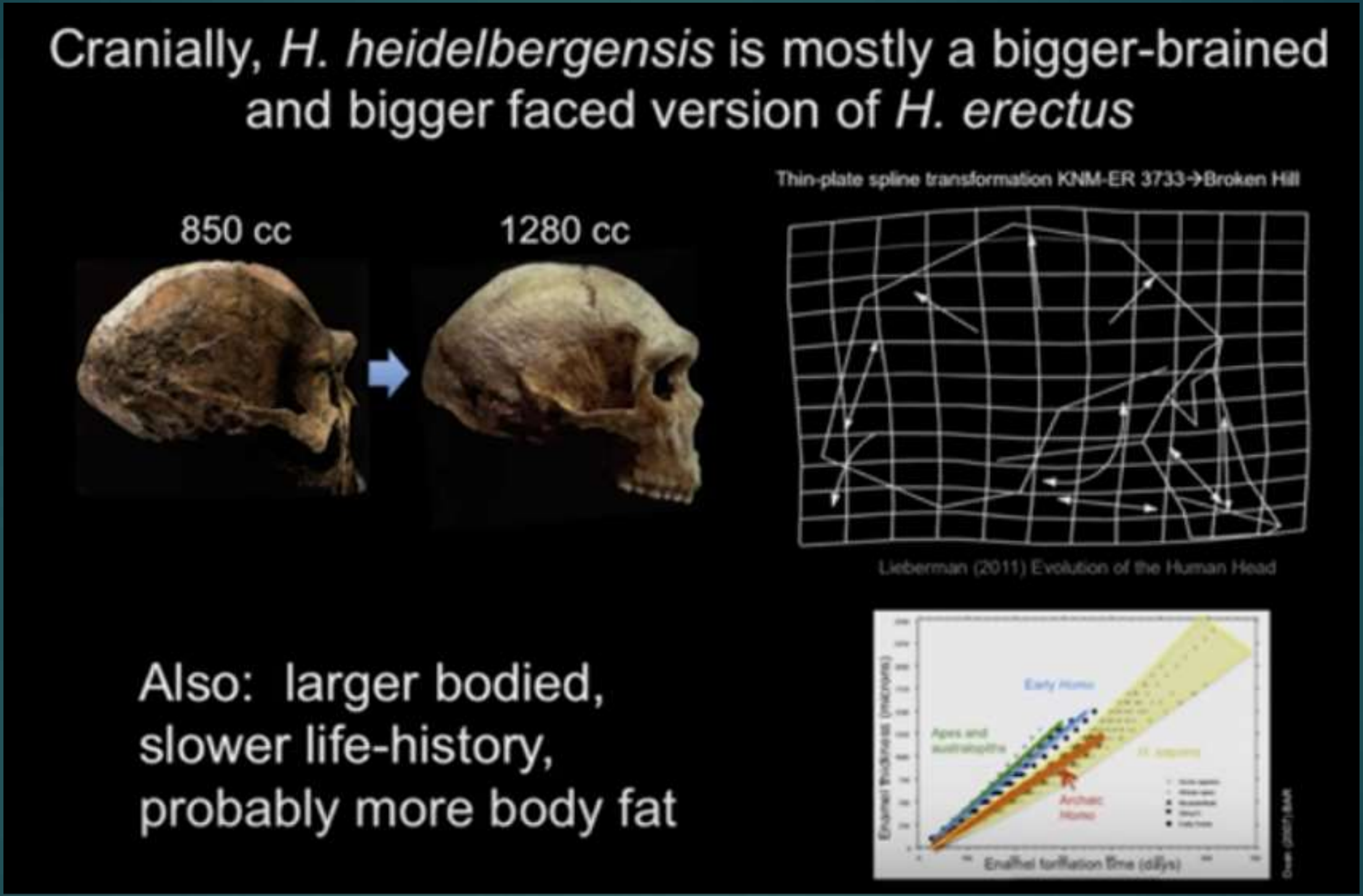
- Animal hide clothing may have been worn, especially by populations living in the cooler European areas. No direct evidence of clothing currently exists.

H. heidelbergensis: Skeletal Morphology

- In Africa, circa 600 Ka,
  - Skull is more rounded than in *H. erectus*: its face is large, and its nose is broad
  - Braincase is higher and more filled out, especially at the sides, which is indicative of a larger average brain size—closer to modern humans than to *H. erectus*.
  - Lack the characteristically horizontal and thick brow ridges seen in *H. erectus; flatter face*
  - Cranial capacity = 1250 cc (vs 1000 cc for *H. ergaster & erectus*)
  - Further reduction of size of jaws and molars
  - Thicker & stronger limb bones; joint surfaces are larger than MHs

H. heidelbergensis: ancestral to Ns

- Ancestral to Ns
- Appearance of classical Neandertal morphology after 130 Ka in Middle East and Europe:
  - long, low skull;
  - wide, large nose;
  - large front teeth with common heavy wear;
  - forward-projecting face;
  - no chin;
  - wide body trunk: short limbs



Cranially, *H. heidelbergensis* is mostly a bigger-brained and bigger faced version of *H. erectus*

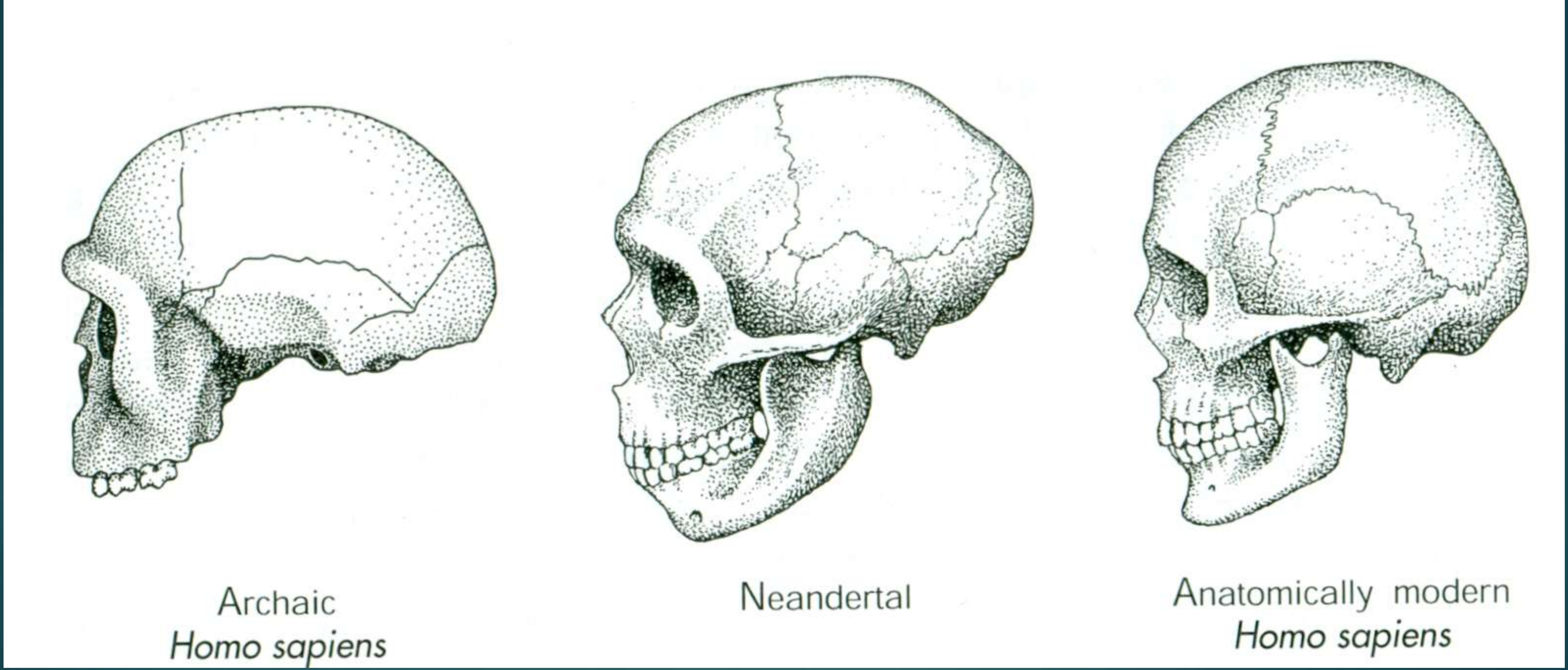
Lieberman (2011) Evolution of the Human Head

Also: larger bodied, slower life-history, probably more body fat

Homo heidelbergensis is blown up version of *H. erectus;*
With a newer slower development in life history

Cranial capacity =

1250 cc 1450 cc 1350 cc



Homo heidelbergensis

2016: Composite Digital of common ancestor of MHs & Ns (based on comparison of 797 elements)

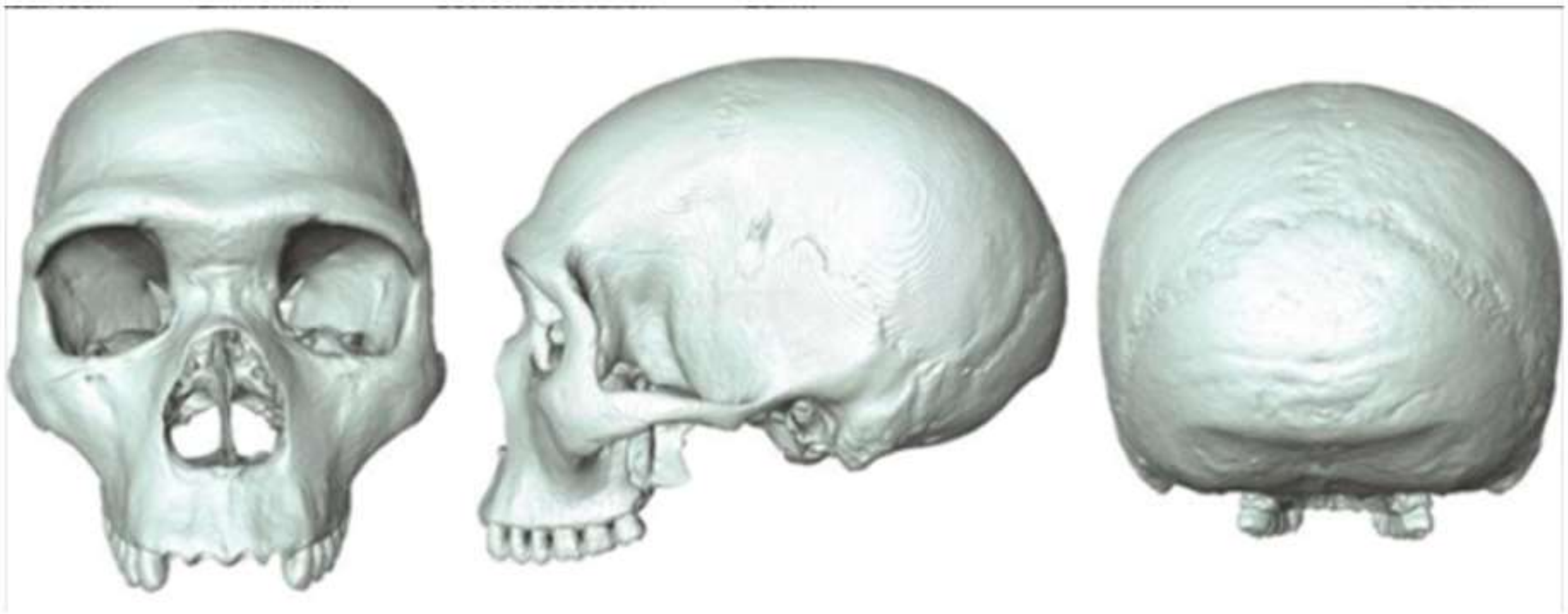
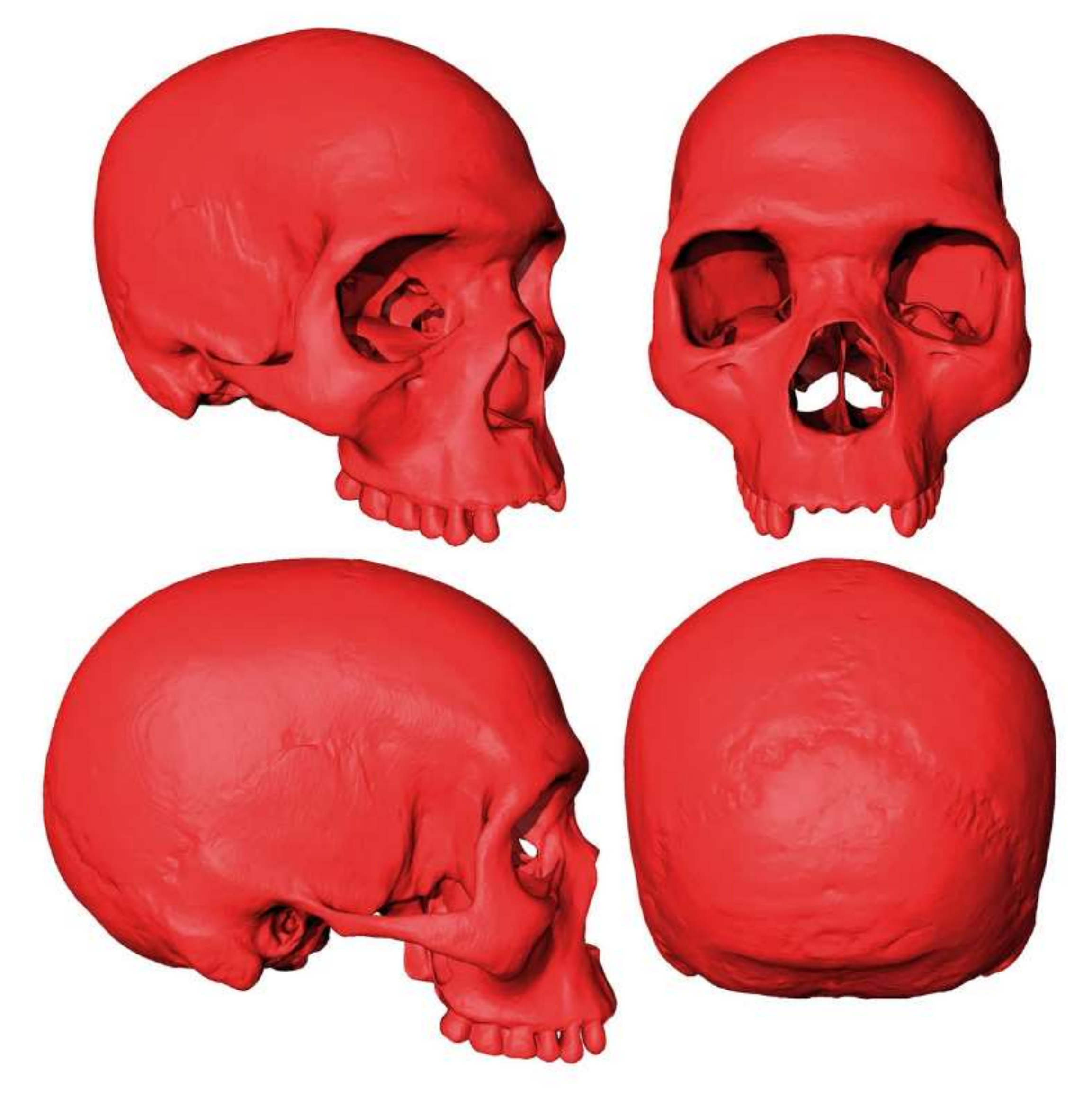


Photo credit: Aurélien Mounier, University of Cambridge

The composite common ancestor skull looks a great deal like the recovered skulls of *Homo heidelbergensis*.

Aurélien Mounier & Marta Mirazón Lahr, 2016

2019:



A computer reconstruction of a skull that may have belonged to the earliest common ancestor of living humans.

- A virtual skull belonging to the Last Common Ancestor of all modern humans, who lived in Africa about 300 Ka.
- Based on 260 MH skulls & fossil skulls
- Rendering of this ancestral skull shows the same vaulted braincase that we have today. But it also has heavier brow ridges and a protruding lower face.

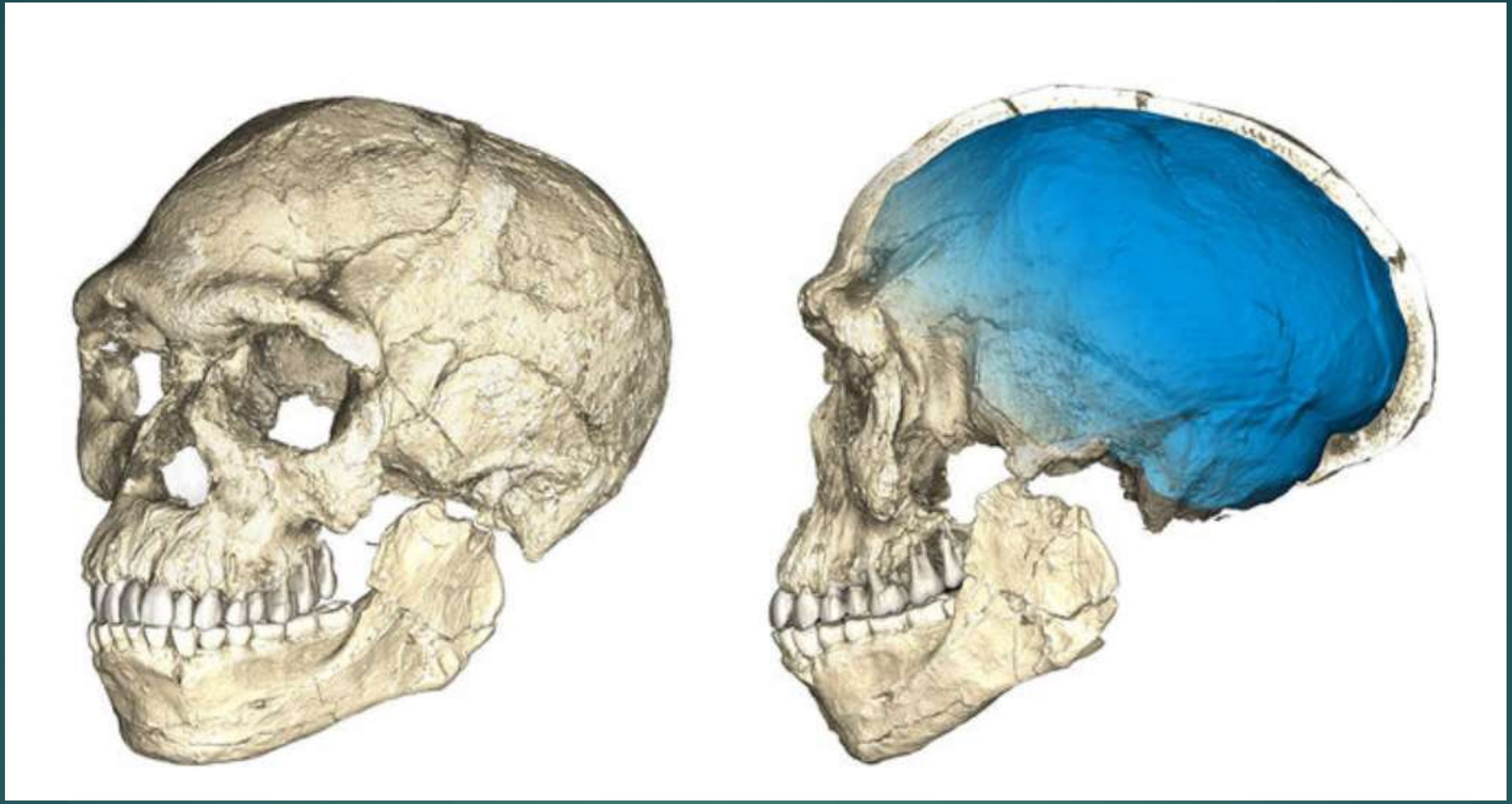
Aurélien Mounier & Marta Mirazón Lahr, 2019

1967: 2 oldest *Homo Sapiens,* Omo 196 Ka & Herto, 160 Ka:
Curved parietal, high forehead, chin

Homo sapiens (Omo I)
At 196 Ka, the 2nd oldest known fully anatomically modern human fossil

Homo sapiens idaltu, 160K Herto, Ethiopia; Bou-VP-16-1: 160 Ka

2017: Oldest *Homo sapiens*, Jebel Irhoud, Morocco, 300 Ka



A composite computer reconstruction of fossils from Jebel Irhoud shows a modern, flattened face paired with an archaic, elongated braincase; 100 K older than Omo II skull. Evolutionary processes behind the emergence of H. sapiens involved the whole African continent. The fossils suggest that faces evolved modern features before the skull and brain took on the globular shape seen in the Herto fossils and in living people.

Anne Gibbons, Science, 2017

Homo heidelbergensis *cranial* traits

- Often a *mosaic of* ***H. erectus*** *and* ***H. sapiens*** *features*
- Things to note:
  - Size of brain: > 1250 cc
  - *H. erectus* features
  - Size of supraorbital tori
  - Increased parietal lobes
  - Rounder occipital lobe; without the characteristic angular occipital shape of *H. erectus*
  - Widest part of skull high in parietal area; but some in lower temporal
  - Reduced total facial prognathism

H. heidelbergensis cranial traits

- Thick cranial bones*
- Front View:
  - Relatively flat face
  - Large middle part of the face
  - Less robust but still large brow ridges; separate brow ridges over each eye; more arched
  - nasal opening was relatively wide
- Side View:
  - Bony keel along the top of skull
  - Large braincase; 1250 cc
  - No vertical forehead; broader frontal bones
  - Somewhat prognathic lower face
  - Sides of skull more vertical
  - Flexed base of skull
  - Reduced postorbital constriction

H. Heidelbergensis Traits: African postcranials

- *Homo heidelbergensis* fossils tend to have features that are intermediate between those of *Homo ergaster* and either *Homo neanderthalensis* or *Homo sapiens*.
- Body size and shape
  - leg bones tended to be thick and strongly built.
  - lower leg bones were relatively long.
  - Limb proportions such as these represent an adaptation to tropical conditions as they provide a larger skin surface to help cool the body. These limb proportions are similar to those found later in *Homo sapiens* and contrast with the short lower legs that developed in the Neanderthals.
  - large lower limb joints
- Klein: Postcranial bones fail to differentiate *H. ergaster, H. erectus, H. heidelbergensis, and H. neanderthalensis*, they all imply similar terrestrial lifestyle.

H. Heidelbergensis Traits: Jaws and teeth

- teeth were smaller than earlier species but were larger than in modern humans
- teeth arranged in a parabolic shape (curved at the front then splayed out toward the back)
- some had a gap, called the retromolar space, behind the third molars (or wisdom teeth) at the back of the jaw.
- jaws were shorter than those of earlier species resulting in a face with only a slight projection
- lower jaw was strongly built for the attachment of strong chewing muscles
- lower jaw did not have a chin; some had incipient chin

B. Wood:

- *Characteristics and inferred behavior*:
- Unique morphology of the cranium and the robustness of the postcranial skeleton.
- Brain cases were always more robustly built with a thickened occipital region
- The crania of *H. heidelbergensis* lack the specialized features of *H. neanderthalensis* such as the anteriorly projecting midface and the occipital bun.
- But some European fossils have an incipient suprainiac fossa (dent in the back of the head), common in Ns

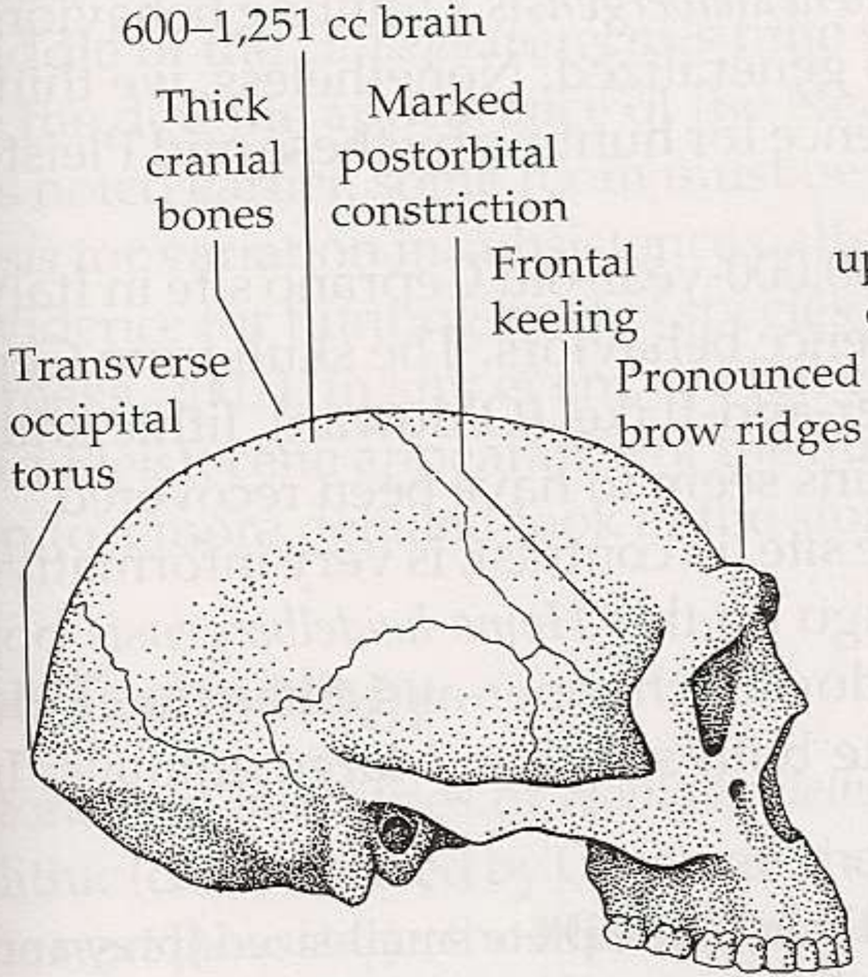
Body Types

- European *H. heidelbergensis:*
  - large and muscular, like boxers or football players; cold adapted
  - Specialized ambush hunters, using wooden spears in close combat against sizeable prey in river valleys

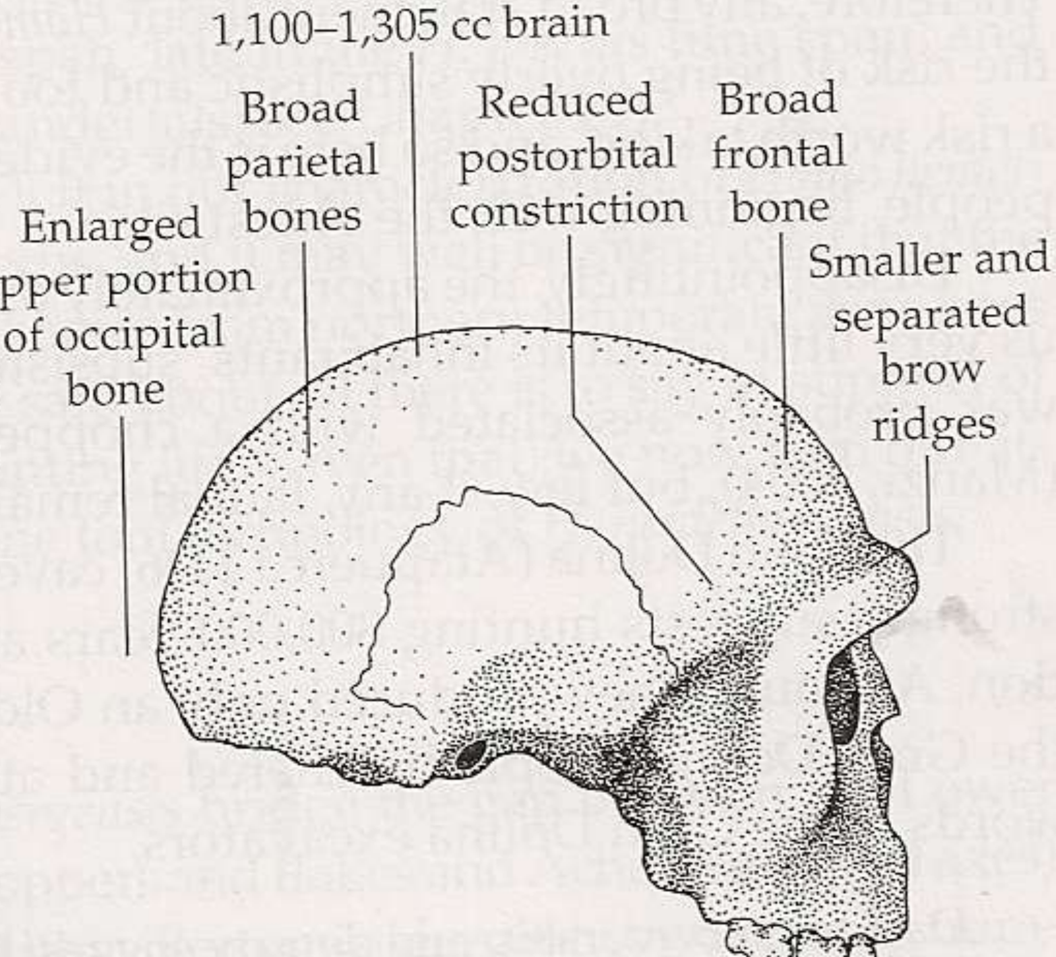
- African *H. heidelbergensis*:
  - tall and slenderer; heat adapted
  - Assumptions: Threw spears; run down overheated prey over long distances; endurance pursuit running in hot landscape

Characteristics of Homo heidelbergensis

Trait	*Homo heidelbergensis*
Height	Male 1.75 m (5 ft 9 in; 5’7” at SH) Female 1.57 m (5 ft 2 in)
Weight	Male 62 kg (136 lb) – Female 51 kg (112 lb)
Brain size	1,212 cc mean (1,100-1,305 cc range)
Cranium	Compared to *Homo erectus:* smaller and separated brows; higher cranial vault; less prognathic face



Homo erectus



Homo heidelbergensis

Cranial capacity: Africa (600-130 Ka)

Taxa (age)	Cranial Capacity (cc)	Source
Early African *H. sapiens/H. heidelbergensis*		
	1,201 ± 281 (N=8)	
Jebel Irhoud 1	1,305	Holloway et al. 2004
Jebel Irhoud 2	1,400	Holloway et al. 2004
Salé	880	Holloway et al. 2004
Singa	1,340	Stringer et al. 1985
Bodo	1,250	Conroy et al. 2000b
Lake Ndutu	1,100	Rightmire 1983
Kabwe	1,325	Holloway et al. 2004
Elandsfontein	1,225	Drennan 1953

R. Klein, Human Career

Cranial capacity: Europe (530-130 Ka)

Taxa (age)	Cranial Capacity (cc)	Source
“Early” European *H. neanderthalensis/H. heidelbergensis*		
	1,248 ± 148 (*N*= 9)	
Swanscombe	1,325	Holloway et al. 2004
Arago 21/47	1,166	Holloway et al. 2004
Biache-Saint-Vaast	1,200	Stringer et al. 1984
Atapuerca SH 4	1,390	Arsuaga et al. 1997b
Atapuerca SH 5	1,125	Arsuaga et al. 1997b
Atapuerca SH 6	1,220	Lorenzo et al. 1998
Reilingen	1,430	Holloway et al. 2004
Steinheim	1,150	Howell 1960
Petralona	1,230	Stringer et al. 1979
China		
Dali	1,120	Wu & Poirier 1995
Jinniushan	1,390	Wu & Poirier 1995

R. Klein, Human Career

Cranial capacity: N & MH: 140 Ka & later

▶ European and West Asian classic Neanderthals (130-40 ka)	1,435 ± 184 cc (N= 15) Holloway et al. 2004
▶ West Asian (Skhul-Qafzeh) "near modern" humans (120-90 Ka)	1,535 ± 27 (N=5) Trinkaus 1983
▶ Early Upper Paleolithic (fully modern humans) (35-24 Ka)	1,577 ± 135 (N=11) Trinkaus 1983
▶ Current modern humans:	1350 cc

Europe

- *Heidelbergensis sites are found in Africa, Europe, and Asia*.
- Hominins first appear in Europe circa 1 Ma (Homo erectus, or Homo Antecessor, or Homo heidelbergensis – from Africa or Asia?)
- First glaciation circa 650 Ka in Europe, with more arid Africa
- Incipient Neandertal traits by 500 Ka -- local evolution or new arrival?
- Neandertals take on distinctive N form by 250 Ka, as well as develop Mousterian tools (which appears simultaneously in Europe, Western Asia, & Southern Africa)
- Warming period circa 130 Ka, allowed both N and MH to move into Western Asia; shortly after 130 Ka, both reach Near East

A Partial Record of *Homo heidelbergensis* sites

Geographic Area	Site	Age
Africa	Ngaloba (LH18)	150,000-90,000
	Singa (Sudan)	170,000-150,000
	Jebel Irhoud	190,000-90,000
	Omo Kibish 2	195,000
	Florisbad	-260,000
	Kabwe	-400,000
	Elandsfontein	-400,000
	Ndutu	-400,000
	Bodo	600,000
Asia	Xujiayao	125,000 -100,000
	Maba	140,000 -119,000
	Dali	230,000 - 180,000
	Jinniushan	280,000 - 200,000
	Yunxian	-580,000
	Narmada, India	600,000 – 400,000

A Partial Record of *Homo heidelbergensis* Sites

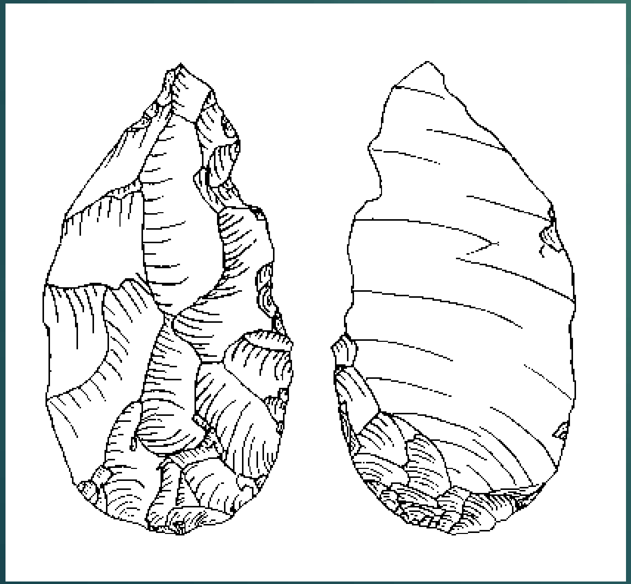
Geographic Area	Site	Age
Europe	Bilzingsleben	~300,000
	Petralona	400,000-250,000
	Swanscombe	400,000-250,000
	Steinheim	400,000-300,000
	Vértesszôllôs	~400,000
	Arago	~ 450,000
	Boxgrove	500,000
	Mauer	500,000
	Atapuerca (Gran Dolina, TD6)	~ 800,000
	Ceprano	~ 850,000

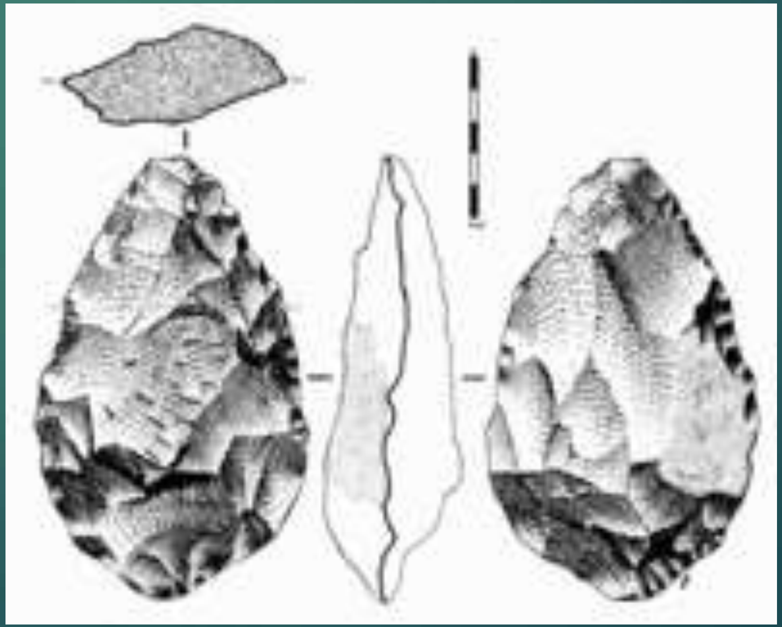
Homo heidelbergensis Lithic Cultures

Geographic Area	Site/Fossil	Age (Years bp)	Tool Kit
Africa	Jebel Irhoud	190,000-90,000	Mousterian, Levallois-flaked tools
	Kabwe	-400.000	Sangoan tools
	Elandsfontein	-400.000	Acheulean tools (probable)
	Ndutu	-400.000	Acheulean tools
	Bodo	600,000	Acheulean tools
Asia	Xujiayao (China)	125,000-100,000	Flake tools (no hand axes)
	Dali (China)	230,000-180,00	Flake tools (no hand axes)
	Narmada (India)	600,000-400,000	Acheulean tools
Europe	Vértesszôllôs	-400.000	Flake tools, choppers (no hand axes)
	Swanscombe	400,000-250,000	Flakes, choppers and Acheulean tools
	Bilzingsleben	-300,000	Flake tools (no hand axes)
	Arago	450,000	Late Acheulean, including small flake tools
	Boxgrove	500.000	Early Acheulean hand axes
	Gran Dolina	~800,000	Flake tools, choppers (no hand axes)

H. heidelbergensis began making new kinds of tools

- Continued to make **Mode 2** until 300 Ka
  - Acheulean
  - cores flaked along sides to extend cutting edge





Homo heidelbergensis: Tools

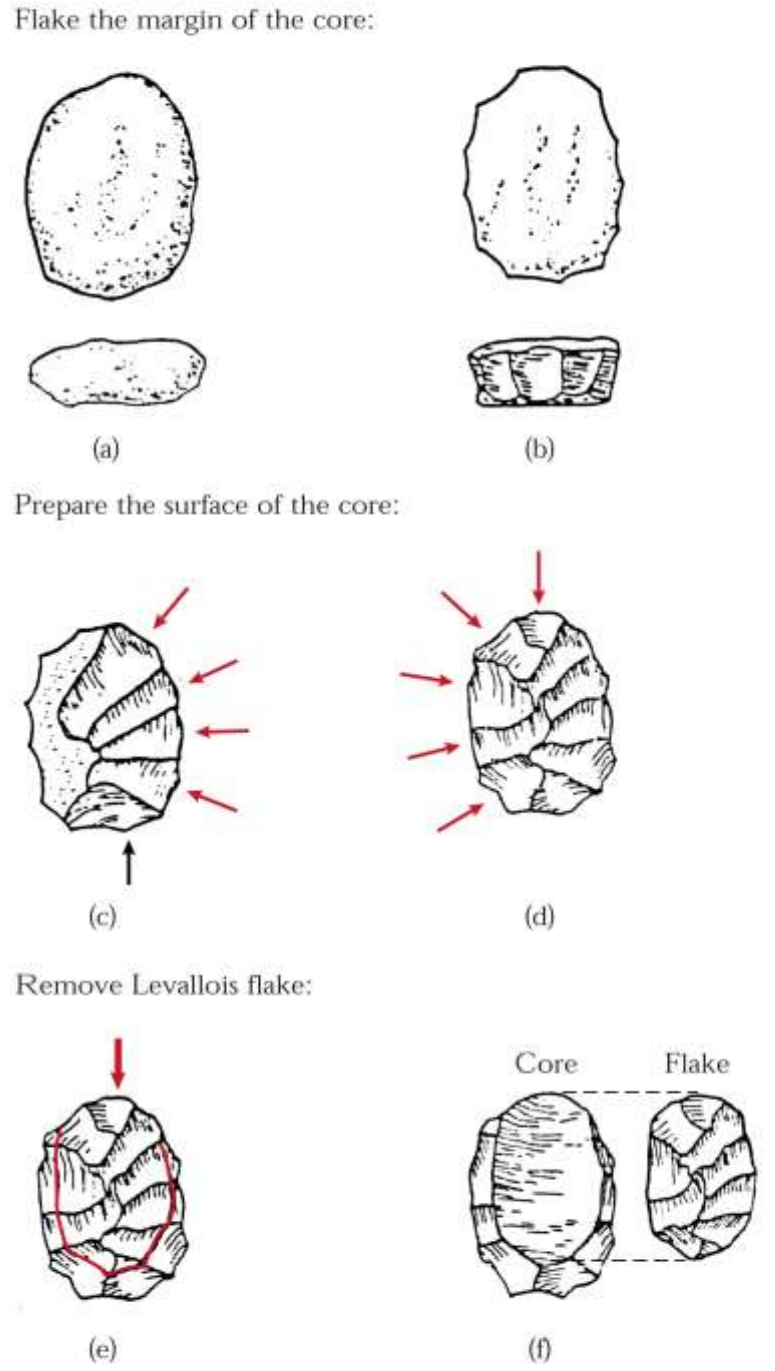
- ~300 Ka, *H. heidelbergensis* started making flake tools Mode 3, Mousterian

- About 200 Ka, a new stone-working technology appeared that was associated with *H. heidelbergensis*, the Levallois technique.

- Some later populations are known to have also made tools from deer antler, bone and wood. These materials were modified into scrapers, hammers and sophisticated wooden throwing spears.

Lavallois technique (Mode 3)

- Involves striking flakes from a prepared core
- A striking platform is formed at one end
- Core's edges are trimmed by flaking off pieces around the outline of the intended flake
- Large, symmetrical flakes are struck off of the core
- This method provides much greater control over the size and shape of the final flake
- More efficient use of available stone
- Greater level of planning & abstract thinking



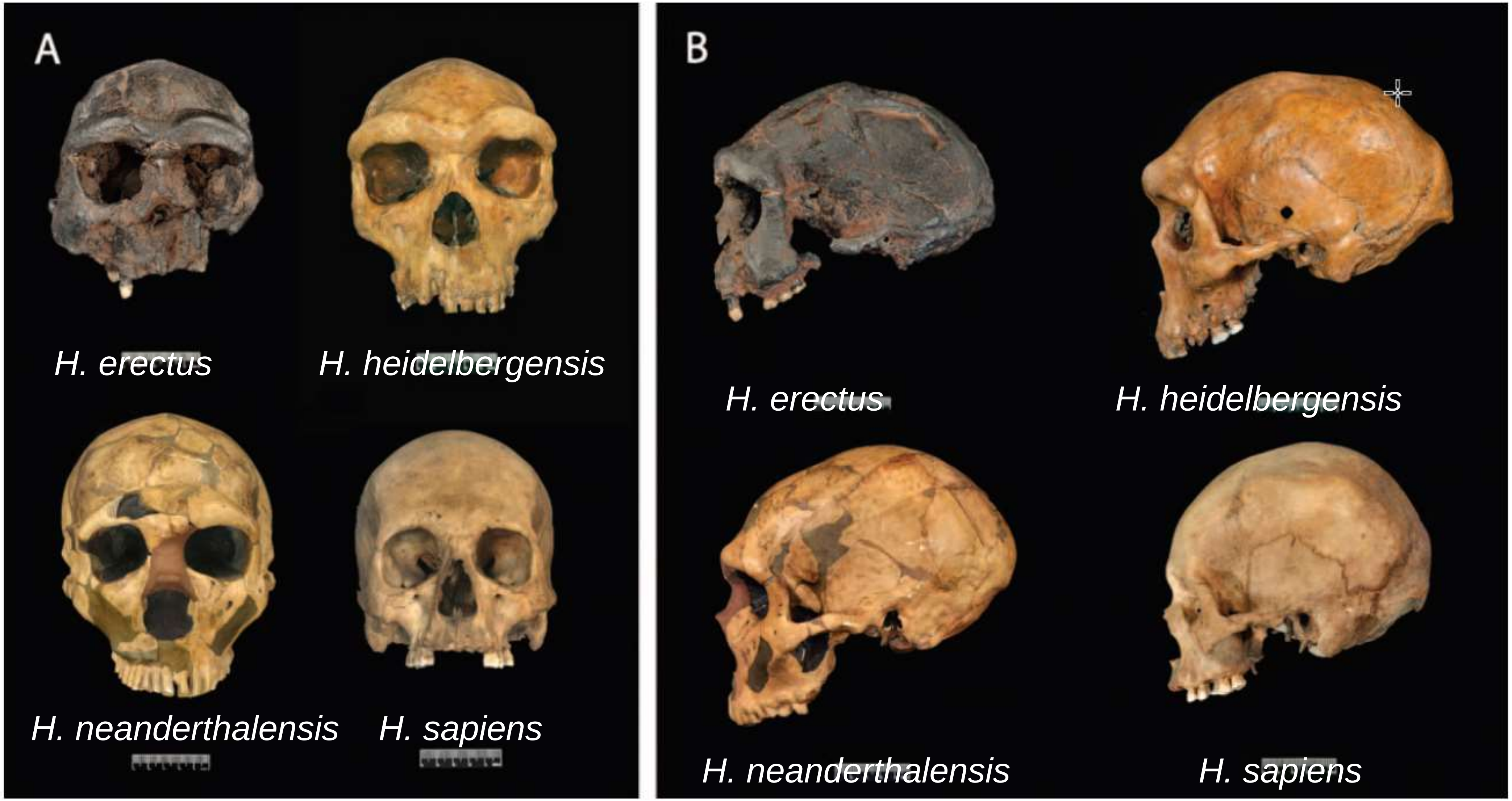


Figure 2. Facial (A) and lateral (B) views of crania. Clockwise from top left: *Homo erectus* (replica, Sangiran, Java), *heidelbergensis* (Broken Hill, Zambia), *sapiens* (recent, Indonesia), and *neanderthalensis* (replica, La Ferrassie, France). All pictures © The Natural Histroy Museum London. (Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.)

First hunting of big game

- Hunting:
  - *H. heidelbergensis* was also the first hunter of large game animals;
  - remains of animals such as wild deer, horses, elephants, hippos, and rhinos with butchery marks on their bones have been found together at sites with *H. heidelbergensis* fossils.

Locations of important *homo heidelbergensis* localities across the Old World.

Various *Homo Heidelbergensis*

Bilzingsleben, Germany: 300-414 Ka

Petralona, Greece, 400K

Arago 21, France, 320-400 K

Steinheim skull, 250-350 Ka

Jinniushan, China, 200K

Bodo, 600K

Dali, China, 250K

1907: Mauer, Germany: *Homo heidelbergensis,*

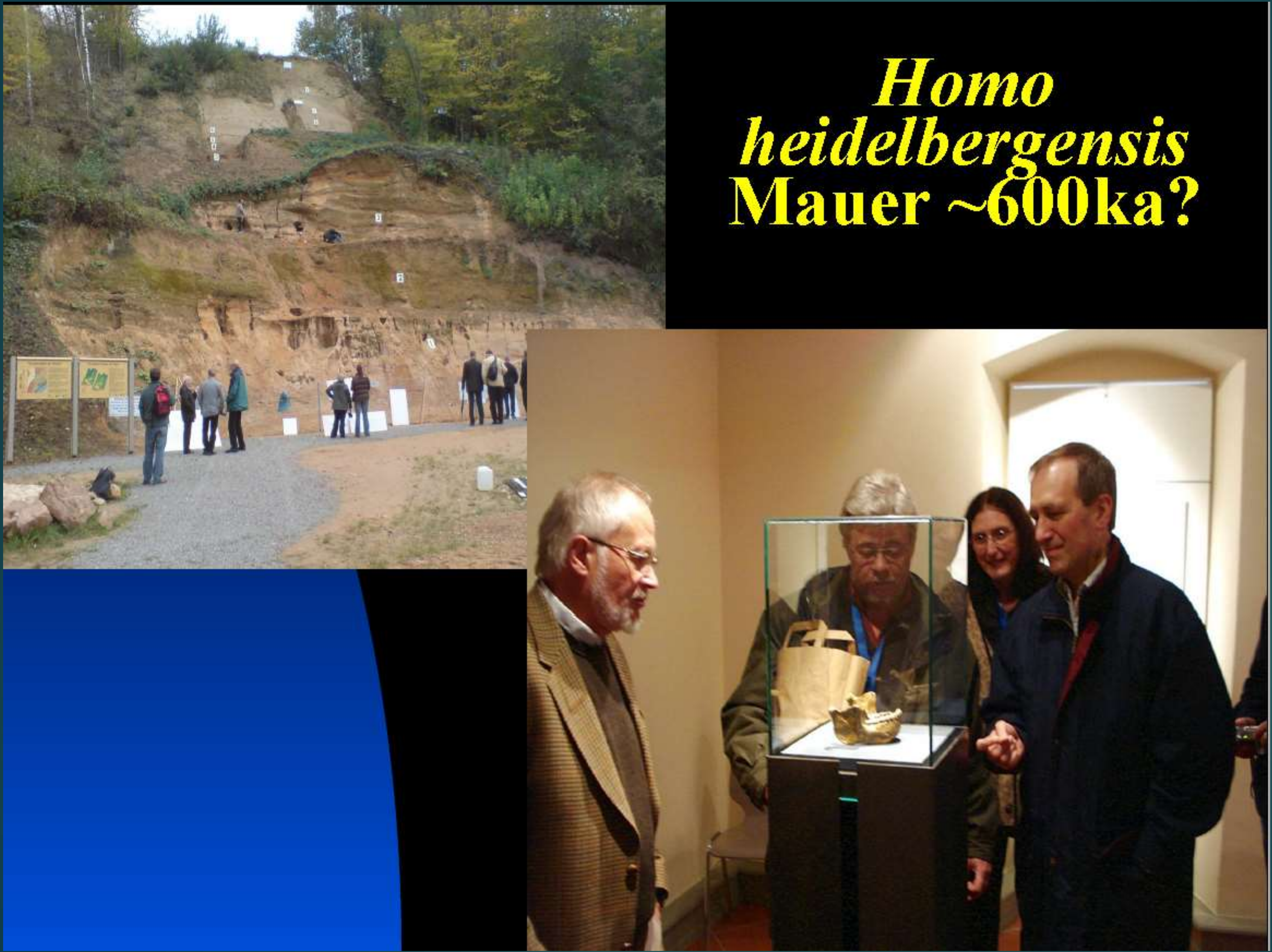
Mauer mandible, 610 Ka; type specimen; one of oldest European fossils

Despite 5000 faunal bones found by 1962, jaw is only hominin find

Mosaic of features intermediate between *H. erectus & H. sapiens:* Combination of primitive features (high corpus thickness, very wide ramus, receding chin, and receding symphysis) and more recent human features, (small dentition, small molars, esp. the canines and anterior teeth)

Homo heidelbergensis
(Mauer 1, type)
Discoverer: Daniel Hartman, workman for Joseph Rosch
Date: 1907
Locality: Mauer sand pits, Germany
Age 610 K

Ma

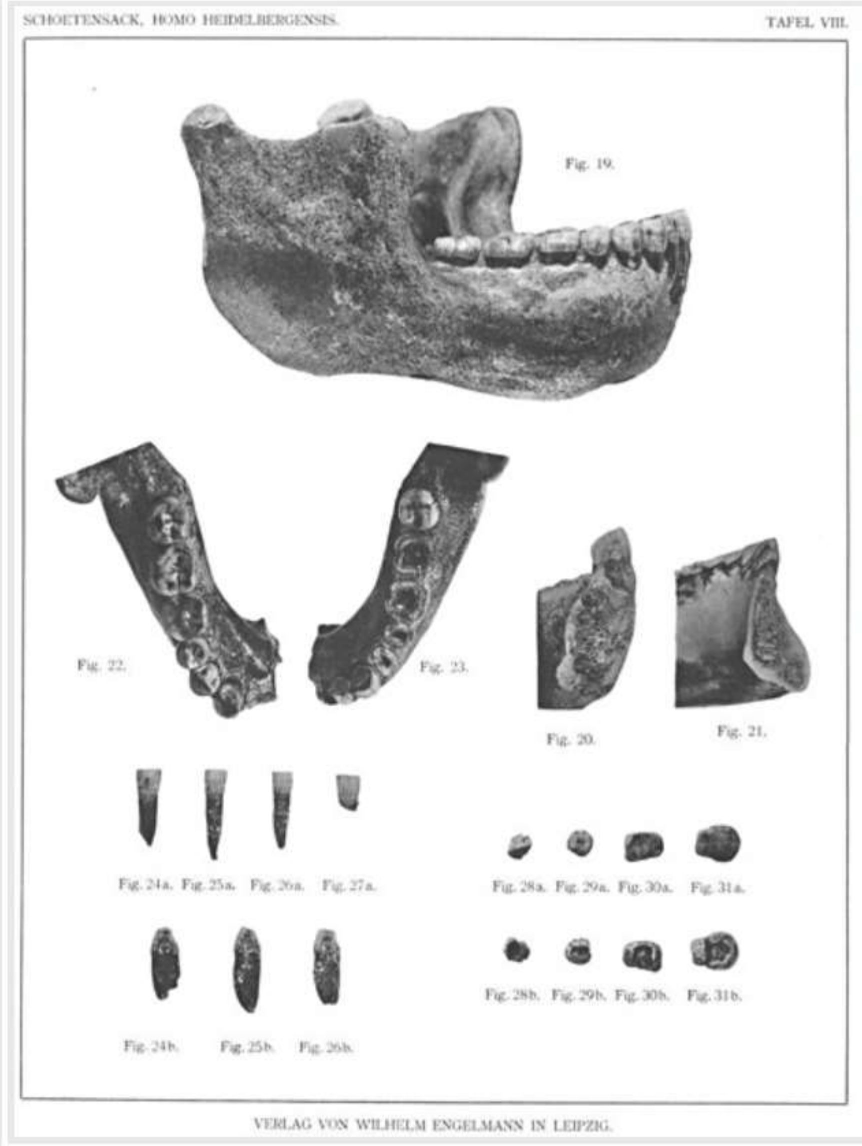


Homo heidelbergensis

Mauer ~600ka?

Heidelberg
University
Geological Museum

Mauer Jaw, 610 Ka, young female



SCHOETENSACK, HOMO HEIDELBERGENSIS.

TAFEL VIII.

Fig. 19.

Fig. 22. Fig. 23.

Fig. 20. Fig. 21.

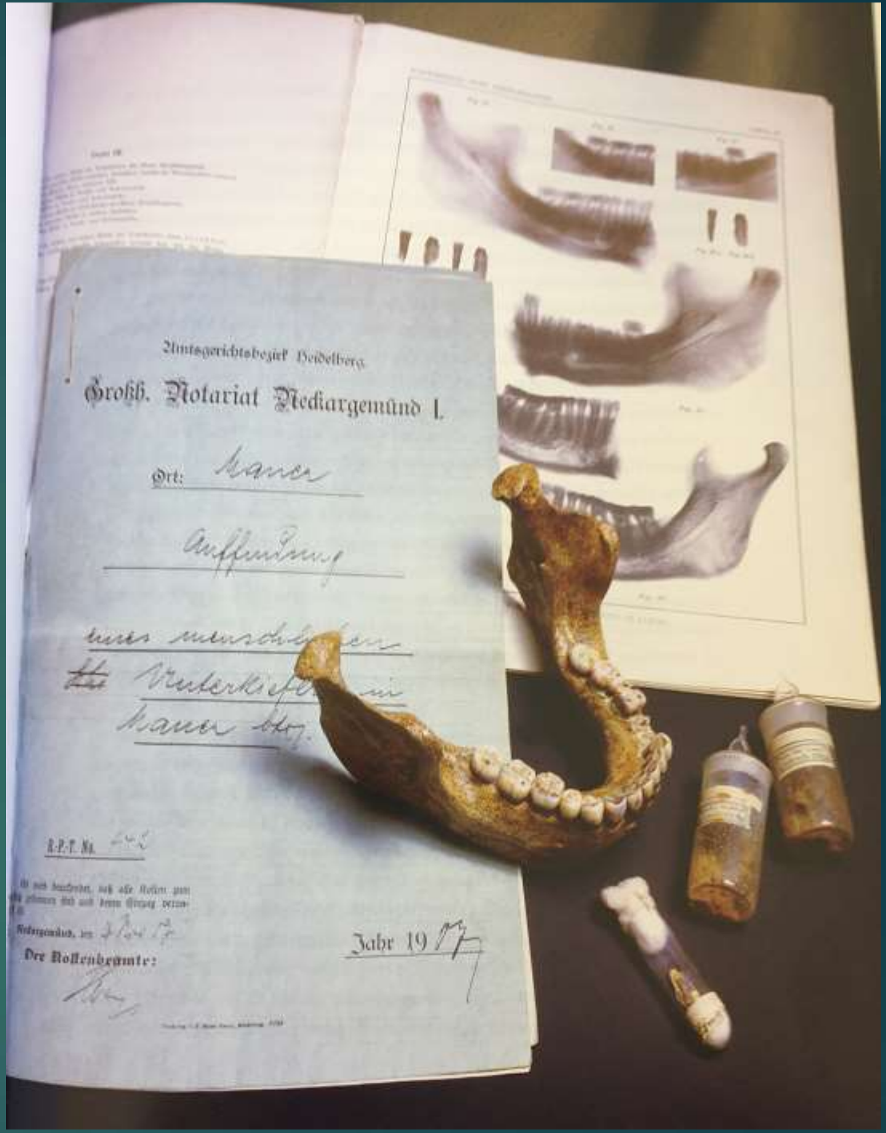
Fig. 24a. Fig. 25a. Fig. 26a. Fig. 27a.

Fig. 28a. Fig. 29a. Fig. 30a. Fig. 31a.

Fig. 24b. Fig. 25b. Fig. 26b.

Fig. 28b. Fig. 29b. Fig. 30b. Fig. 31b.

VERLAG VON WILHELM ENGELMANN IN LEIPZIG.



Amtsgerichtsbezirk Heidelberg.

Großh. Notariat Neckargemünd I.

Ort: Mauer

Auffindung

eines menschl[illegible]en
Unterkiefe[illegible] in
Mauer [illegible]

R.-P.-T. Nr. 442

Neckargemünd, den [illegible]

Der Rollenbeamte:

Jahr 1907

Innovative: He had it notarized & x-rayed in 1908

Mauer mandible: problematic

- The mandible itself is large, and robustly built like that seen in *Homo erectus*, with broad ascending ramus. The corpus of the mandible is deep and thicker than a modem human's. The lack of a projecting chin is another morphological difference from modem humans.
- Schoetensack proposed the species name *Homo heidelbergensis* for the Mauer specimen. Robust morphology of the jaw shows affinities to *Homo erectus,* yet the tooth morphology is decidedly more "modem" in appearance. Most researchers agree that the Mauer mandible is not *Homo erectus*.
- First considered as "Archaic" *Homo sapiens.* Recently, a separate species name: *Homo heidelbergensis.*

Mauer?

- Unfortunately, there is no way to absolutely date the Mauer specimen. However, faunal correlation (comparing the animal fossils found at this site with other sites for which dates have been determined) has placed the find within the Middle Pleistocene, ~610 Ka.
- Some argue that the Mauer mandible should not be used to name this larger Mid-Pleistocene group.
- As the quote (attributed to William Straus) goes: “While the skull is the creation of God, the jaw is the work of the devil.”
- There are very few other MP mandibles; but this mandible does not have a large number of taxonomically diagnostic features.

First Europeans

- The earliest hominin occupation of Europe is one of the most debated topics in paleoanthropology.

- However, the purportedly oldest of the Early Pleistocene sites in Eurasia lack precise age control and contain stone tools rather than human fossil remains.

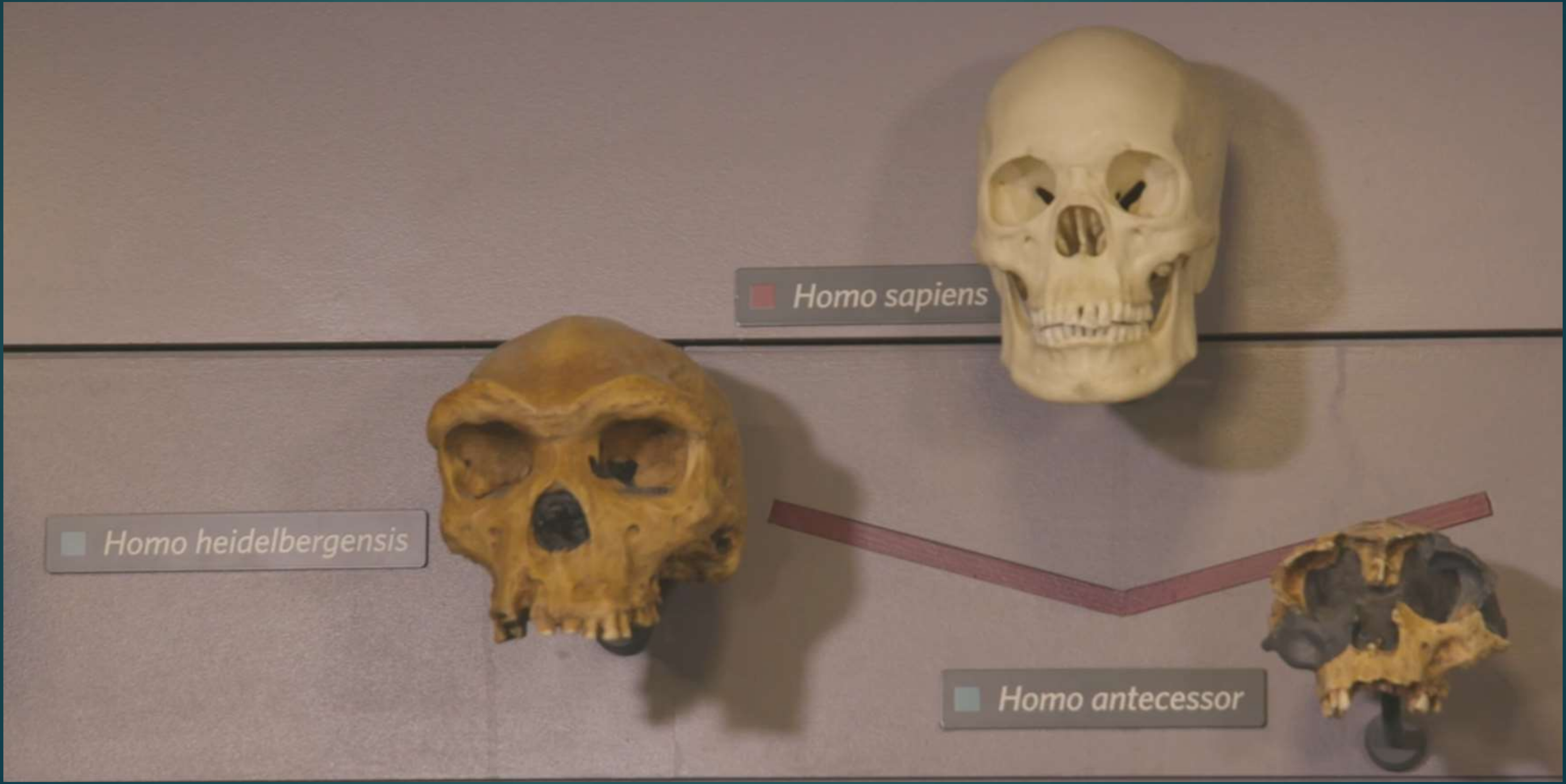
- Until Atapuerca discovery, earliest finds were after 500 Ka.

Papagianni & Morse, 2015

First Europeans

- First Europeans (pre 600 Ka) in Spain & Britain:
  - Seem to represent an isolated migration from Africa or possibly Asia
  - Either reached a dead end or retreated out of Europe when climate deteriorated
  - Were probably not ancestral to Neandertals
- Circa 650 Ka, Europe underwent 40 ky of sustained glaciation; probably ended the above earliest migration

Who was ancestral to *H. sapiens*?



Who were the first Europeans? 4 Hypotheses

- **1)** Descendants of *H. ergaster* gave rise at 1 Ma to *H. antecessor* in Africa. This was the first human species arriving to Europe and evolved to the forms we call pre-Neandertals, which we find at 500 Ka developing typical Neandertal features like the N face and the dentition. Later in time, *H. antecessor* evolved in Africa from *H. rhodesiensis/heidelbergensis*, which in turn ended up evolving into *H. sapiens*.
- **2)** A set of populations descendant from the Asian *H. erectus* could also trace the fertile valleys in Central Europe. Some of them would successfully settle some parts of Southern Europe for some time, and even would contribute to the genetic mosaic.

First Europeans

- **3)** Descendants of *H. ergaster* gave rise ~600 Ka in Africa to new form called *H. heidelbergensis*. This species left Africa toward Europe. But in Europe there were some pre-existing human forms… or not, because they could have become extinct before. Later in time, *H. heidelbergensis* evolved in Africa independently towards the lineage of *H. sapiens*. In Europe they started to become the lineage of *H. neanderthalensis*.
- **4)** *H. antecessor* was a local form developed in Europe by isolation. Alternatively, some morphological similarities with certain Asian specimens could suggest a potential migration of *H. antecessor* from Asia. This species could be close to the 'mother population' that evolved to the lineage *H. heidelbergensis-neanderthalensis.*
- Some of these hypotheses from the previous scenarios are not exclusive.

Sima del Elefante, Atapuerca, Spain

- The Sima del Elefante Site is located in the Sierra de Atapuerca, northern Spain, in the proximity of the well-known sites of Gran Dolina, Galerıa and Sima de los Huesos.

- In 1978, a mining company train track excavation revealed karst, limestone caves. Valley has two rivers running through it.

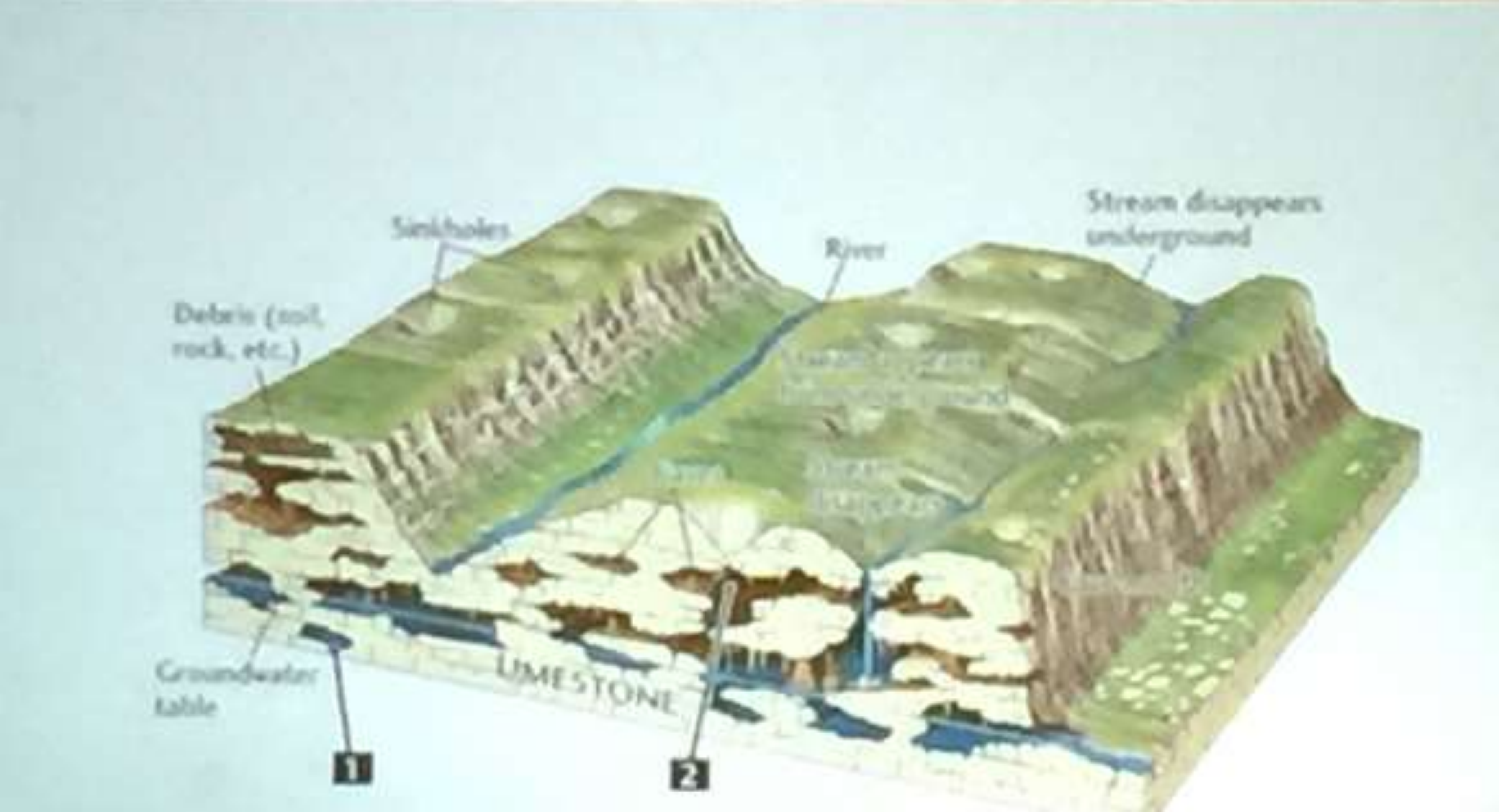
- All of them have yielded hominin fossils attributed to:
  - *Homo antecessor* (approximately 860 Ka) in Gran Dolina
  - *Early Homo neanderthalensis* in Galerıa and Sima de los Huesos (430 Ka)

Earliest Europeans: before 1.2 Ma

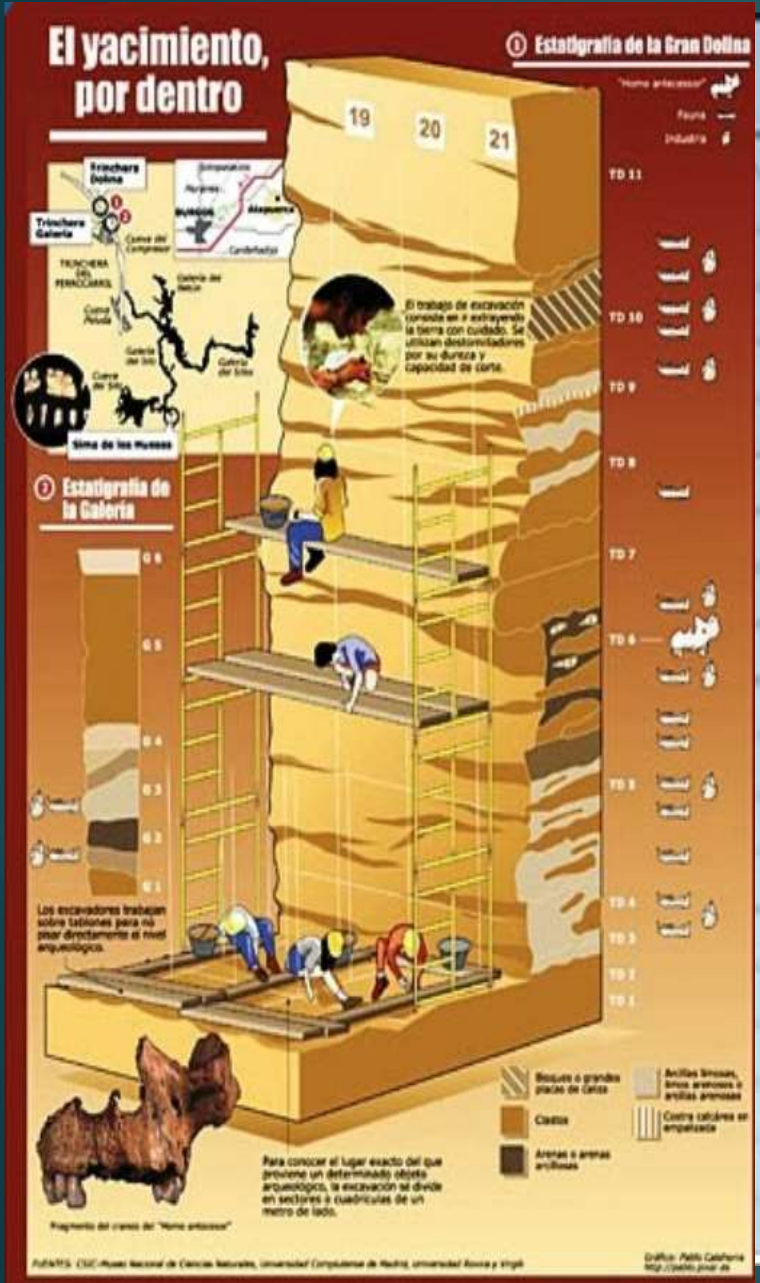
- Assuming that *Homo antecessor* arrived in Western Europe c. 1 Ma (at Gran Dolina at Atapuerca & Happisburgh at Norfolk Coast):
- There is growing evidence of hominin presence in southern Europe well before 1 Ma:
  - 1.2-1.3 Ka in **Northern Spain** (Sima del Elefante at Atapuerca)
  - 1.3-1.5 Ka in **Southern Spain** (Barranco León and Fuente Nueva 3 at Orce, Andalusia);

- Barranco León hominin (1 tooth; 1.4 Ma) is the oldest from Western Europe
- Orce: In **2015**, the excavation work has recovered 160 Oldowan stone tools in levels of 1.4-1.5 Ma and 2,700 faunal remains of 1.3 Ma.
- Fuente Nueva: More than 2,000 Oldowan stone tools have been found there, together with fossil evidences of cutting legs, marrow extraction and head dismantling.

Atapuerca, Northern Spain



Gran Dolina: layer TD1 = bottom layer; TD10 = 300-400 Ka; TD35 = 1 Ma



El yacimiento, por dentro

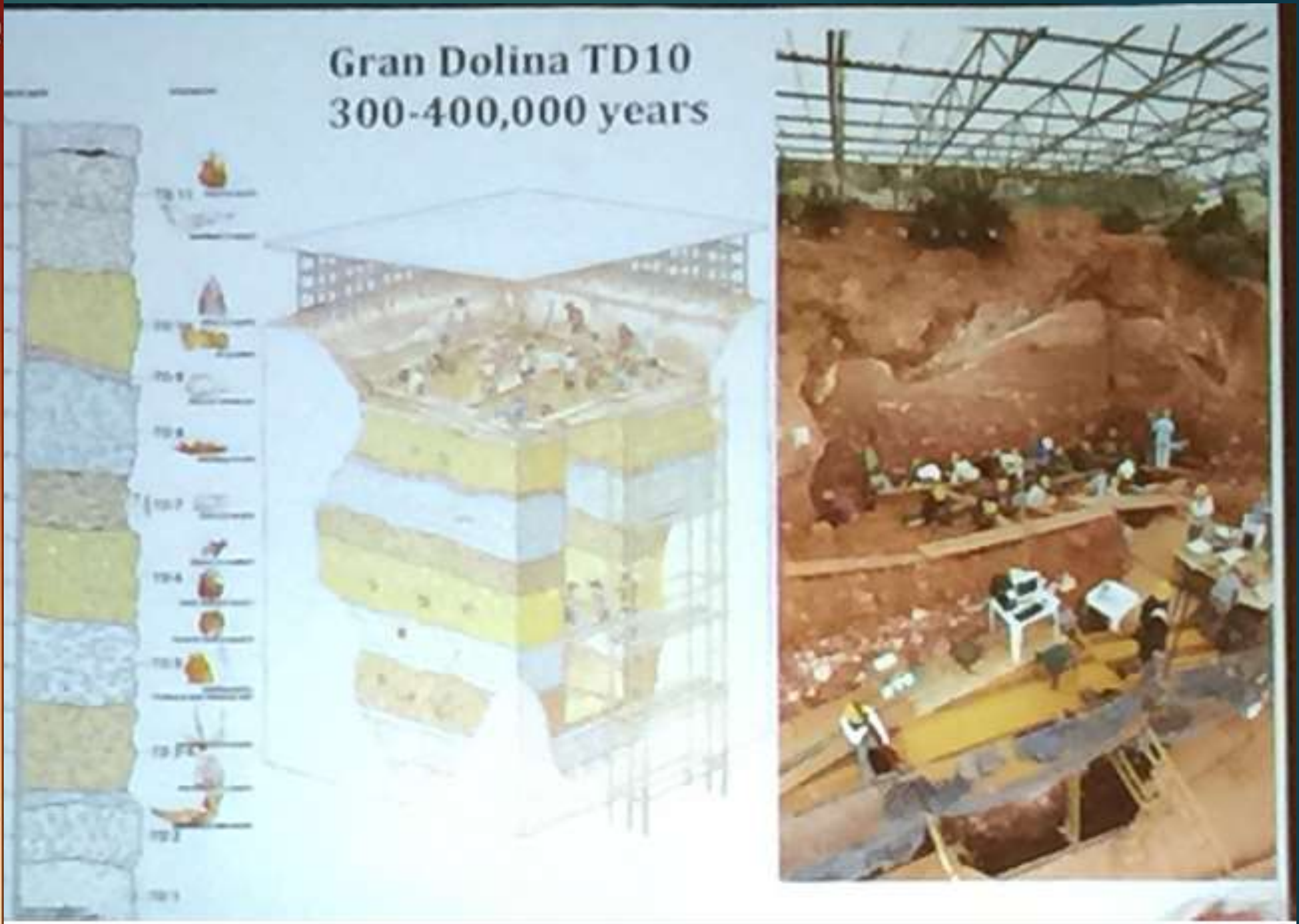
El trabajo de excavación consiste en ir extrayendo la tierra con cuidado. Se utilizan destornilladores por su dureza y capacidad de corte.

Los excavadores trabajan sobre tablones para no pisar directamente el nivel arqueológico.

Para conocer el lugar exacto del que proviene un determinado objeto arqueológico, la excavación se divide en sectores o cuadrículas de un metro de lado.

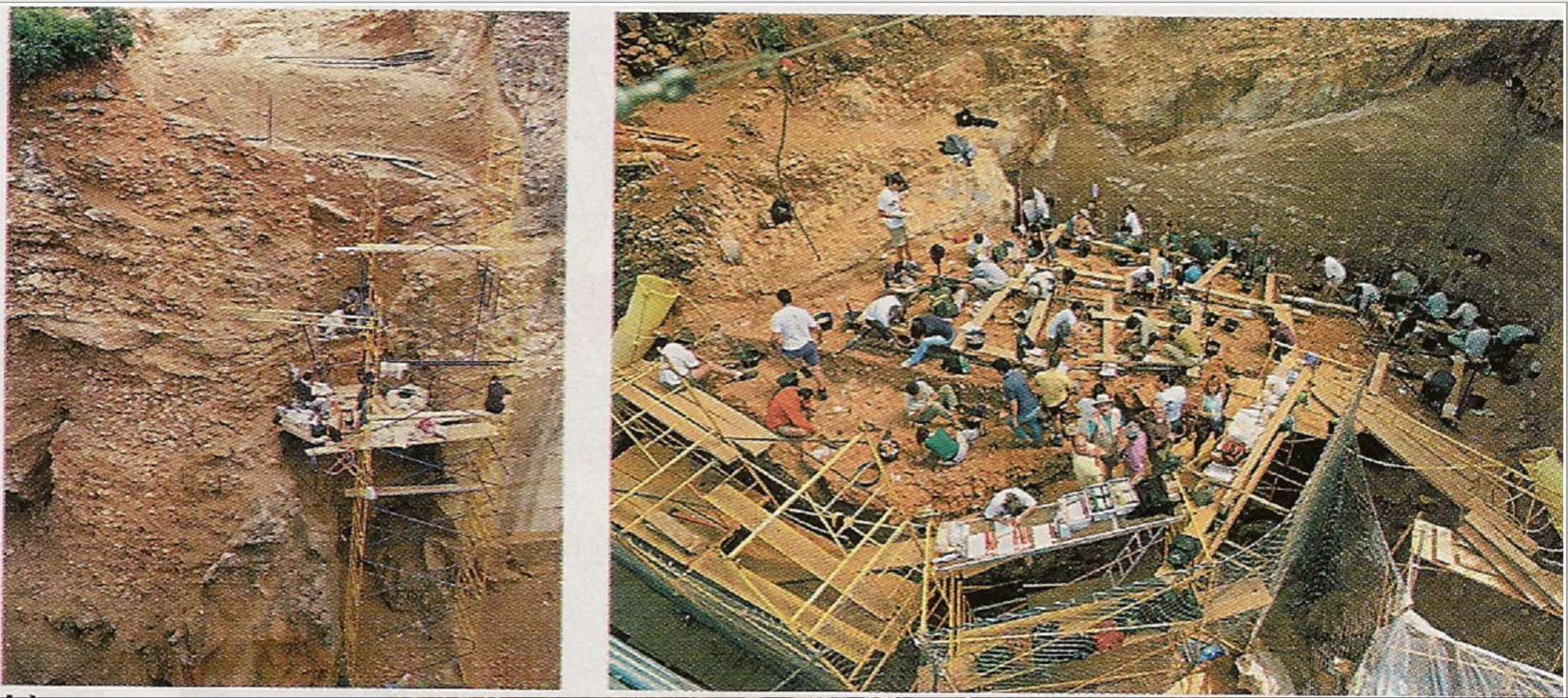
Fragmento del cráneo del "Homo antecessor"

FUENTES: CSIC-Museo Nacional de Ciencias Naturales, Universidad Complutense de Madrid, Universidad Rovira y Virgili



Gran Dolina TD10
300-400,000 years


El mapa de los yacimientos
REGISTRO CRONOLÓGICO
PRINCIPALES HALLAZGOS
VISTA AÉREA
GRAN DOLINA
ENTRE 1.000.000 Y 200.000 AÑOS



Atapuerca, Spain: First Europeans

- Gran Dolina cave: earliest evidence of European population: *Homo antecessor* (1.2 Ma); evolutionary link between *H. ergaster* and *H. heidelbergensis*?
- 1997: Jose-Maria Bermudez de Castro made ATD 6-5 mandible the type specimen of *Homo antecessor*
- Sima de Elefante: first fossil from Western Europe (molar dated to 1.2–1.1 million years

The Invasion of Europe: Spain

- Sima del Elefante, Atapuerca, Spain:

  Oldest securely dated site in Europe

  - 1.2-1.1 Ka; tooth, jawbone fragment, & part of finger; assigned in 1997 to *Homo antecessor*
  - Oldowan tools; Animal bones with cut marks
  - Similar to Asian *H. erectus*; may not have survived Europe's 2nd glaciation c 850 Ka
  - Dental plaque: uncooked food
  - *Homo antecessor, Homo erectus*, or *Homo heidelbergensis?*

Carbonell, et al., 2008

Sima del Elefante

- These early European populations, sometimes referred to as *Homo antecessor*, are considered by some to have been:
    - ancestral to the later, European, *Homo heidelbergensis* and to Neanderthals?
    - but may also represent unsuccessful early episodes of colonization that ended in local extinctions.

Carbonell et al. 2008; Bermudez de Castro et al. 1997

2008: Sima del Elefante, Atapuerca: 1.2 Ma, mandible

- Eudald Carbonell made discovery of a human mandible associated with an assemblage of Mode 1 lithic tools and faunal remains bearing traces of hominin processing, in stratigraphic level TE9 at the site of the Sima del Elefante, Atapuerca, Spain.

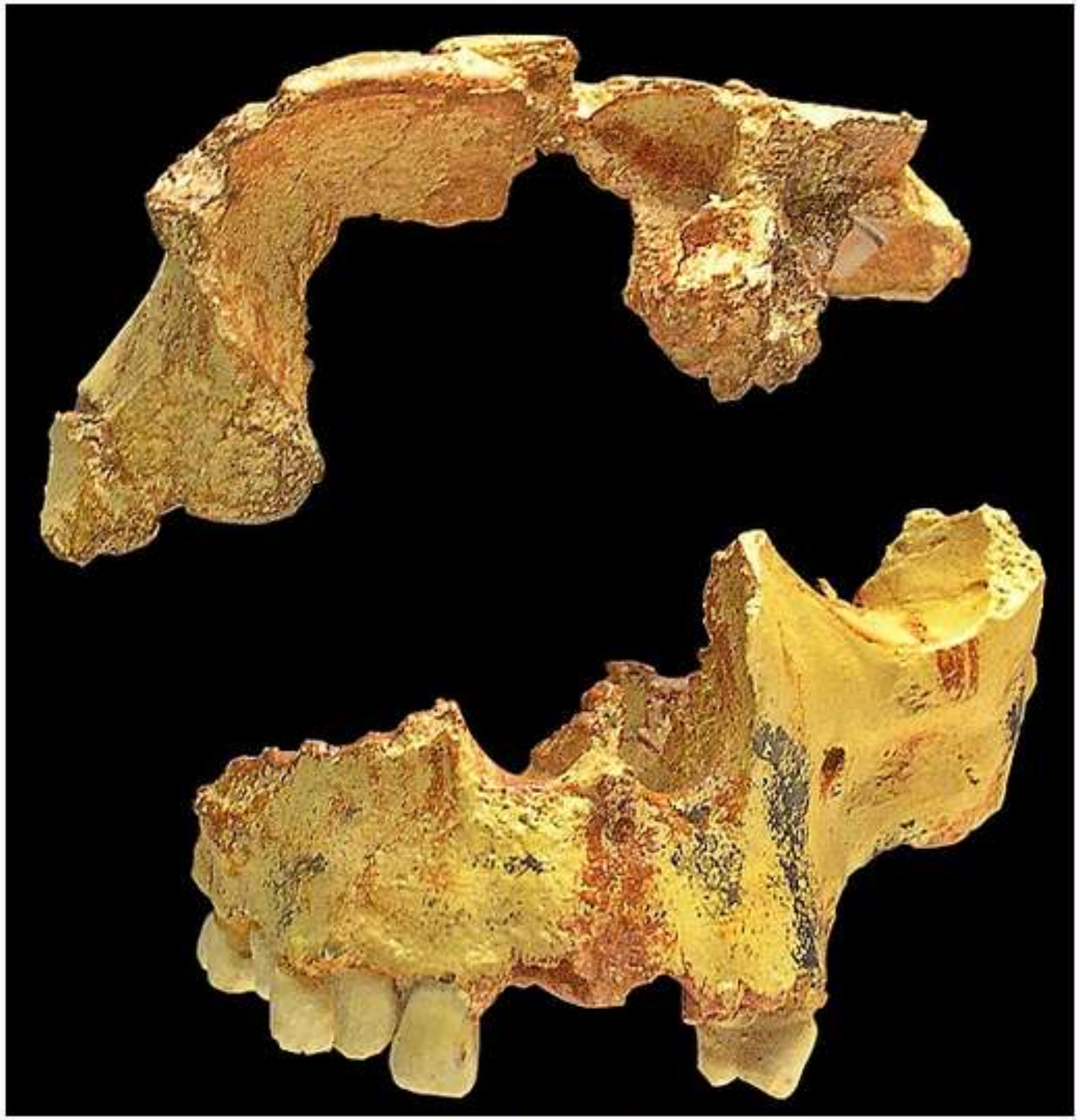
- Level TE9 has been dated to the Early Pleistocene, 1.2–1.1 Ma.

- The Sima del Elefante site thus emerges as the oldest, most accurately dated record of human occupation in Europe.

Eudald Carbonell, et al., 2008

Gran Dolina,
TD6, 860 Ka
H. antecessor

ATD6-15 (front)
ATD6-69 (maxilla)



Skull known as the child of the Gran Dolina.

Gran Dolina, TD6, *H. antecessor*, 860 Ka

- TD6 level: 860 Ka, via 6 different dating techniques; 15 individuals/160 fragments, 200 Oldowan stone tools and 300 animal bones

- These remains resemble *Homo heidelbergensis*, or *Homo ergaster* due to the characteristics of its forehead and teeth, but it also has more modern characteristics, such as the flat face, typical of *Homo sapiens*; so it was decided to make the attribution to a new species, *H. antecessor*.

- All juveniles; ATD6 = 9 yo; 160 bone fragments from 15 individuals

Homo antecessor: 860 Ka, 1000 cc, Oldowan tools

- Atapuerca, Gran Dolina, Spain:
  - 2nd oldest site in Europe
- ~800-960 Ka: - 160 fossils of 15 individuals, ages 3 to 20, share many physical similarities with *Homo erectus*
- Homo antecessor male would have stood approximately 5”2”- 5’9” (1.6-1.8 meters) tall, weighing around 90 kg.
- Cranial capacity: 1,000-1,150 cc
- 200 Oldowan stone tools
- 160 hominin fossil remains, all attributed to a single species, *H. antecessor*.

Homo antecessor

- The species *Homo antecessor* is another very controversial species designation. The species was designated by J.L. Arsuaga et al. to the remains of several individuals found at the Gran Dolina site, Spain.

- The discovery was significant because the remains have been securely dated at 860 Ka. This makes the material one of the earliest known European specimens.

- The find breathed new life into the argument for the validity of *H. heidelbergensis,* as well as creating a whole new species: *Homo antecessor.*

Figure 2 | Mandible ATE9-1. **a**, Frontal view. Arrowheads point to the position of the anterior marginal tubercle, and the arch of the marked incisura submentalis. **b**, Superior view. Arrowheads point to the mental protuberance, the subvertical alveolar planum and the slight alveolar prominence. Note also the parabolic arc formed by the alveolar part of the corpus. **c**, Median sagittal cross-section of the symphysis based on a three-dimensional computed tomography reconstruction. Fossils are housed at the Centro Nacional de Investigación sobre la Evolución Humana. **d**, Distal view of the LP4 of ATE9-1. **e**, Occlusal view of the LP4; mesiodistal dimension: 8.9 mm; buccolingual dimension: 11.4 mm (estimated).

Homo antecessor: 860 Ka

- Discoverers suggest *H. antecessor* may have evolved from a population of *H. erectus* living in Africa more than 1.5 million years ago and then migrated to Europe, further arguing that *H. antecessor* gave rise to *H. heidelbergensis*, which then gave rise to Neanderthals

Maxilar ATD6-69 of hominin 3 of TD6

Less prognathic than *H. erectus*

B. Wood: Antecessor traits

- *Nature of the evidence*: The partial cranium of a juvenile, parts of mandibles and maxillae and isolated teeth.

- Researchers who found the remains claim the combination of
  - a modern human-like facial morphology
  - with the large and relatively primitive crowns and roots of the teeth
  - is not seen in *H. heidelbergensis*.

- The Gran Dolina remains also show no sign of any derived *H. neanderthalensis* traits.

- Its discoverers suggest *H. antecessor* is the last common ancestor of Neanderthals and *H. sapiens*.

H. antecessor

- TD6: 13 layers, not a single event, but a practice
- 15 individuals, many children (ages 3, 4, 6, 9); 160 specimens of *H. antecessor.* The most complete specimen is hominin 3, which is also the type specimen for *H. antecessor.*
- This is unusual because hominin 3 is a 10-year old, and therefore has not fully developed its skeletal characteristics.


JAVIER TRUEBA/MADRID SCIENTIFIC FILMS

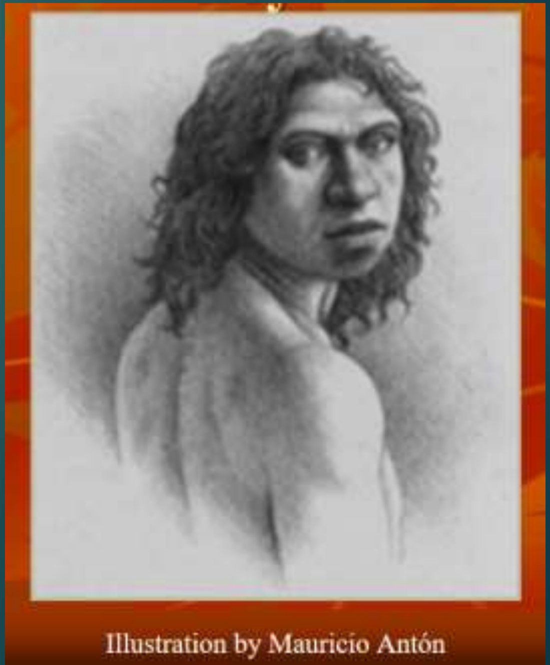


Illustration by Mauricio Antón

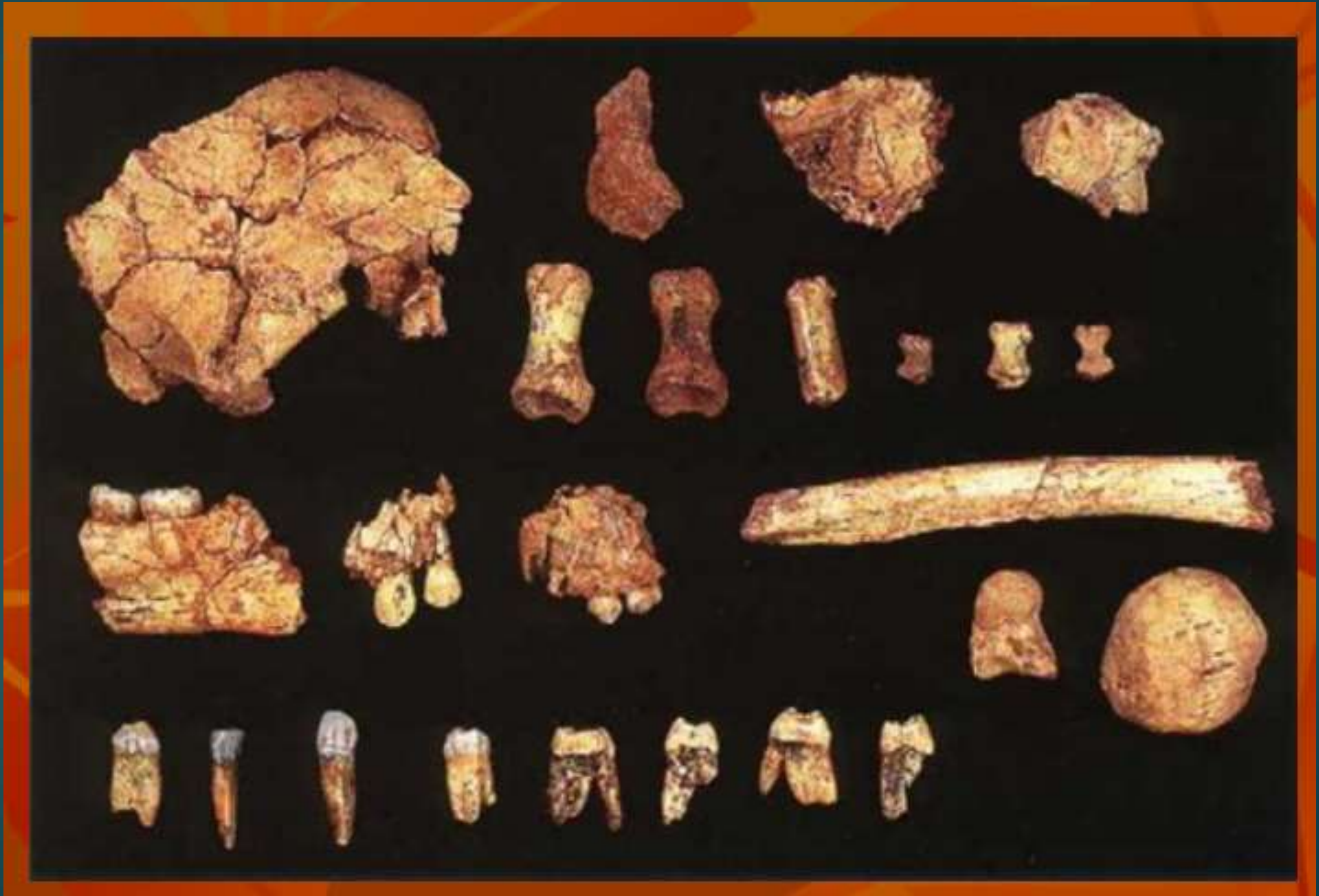
First Direct Dating of *Homo antecessor*: 772-949 Ka

- Direct dating of a fossil tooth of *Homo antecessor* from the unit TD6 of the archaeological site of Gran Dolina in the Sierra de Atapuerca (Burgos, Spain). In the work, a time range of between 772 and 949 Ka was found for this species of the Lower Pleistocene, so confirming earlier indirect datings.
- Used Uranium-Thorium analysis and Electron Spin Resonance, as well as precise paleomagnetic study of the deposits of the stratigraphic unit TD6
- Makes it the oldest known fossil human species in Western Europe

Mathieu Duval, et al., 2018

Homo antecessor

Gran Dolina Site



Fossils of Homo antecessor found at level TD6 of Gran Dolina /J.M. Bermúdez de Castro,

Homo antecessor remains from Atapuerca (Credit: Javier Trueba/MSF/Science Photo Library)

Homo antecessor traits

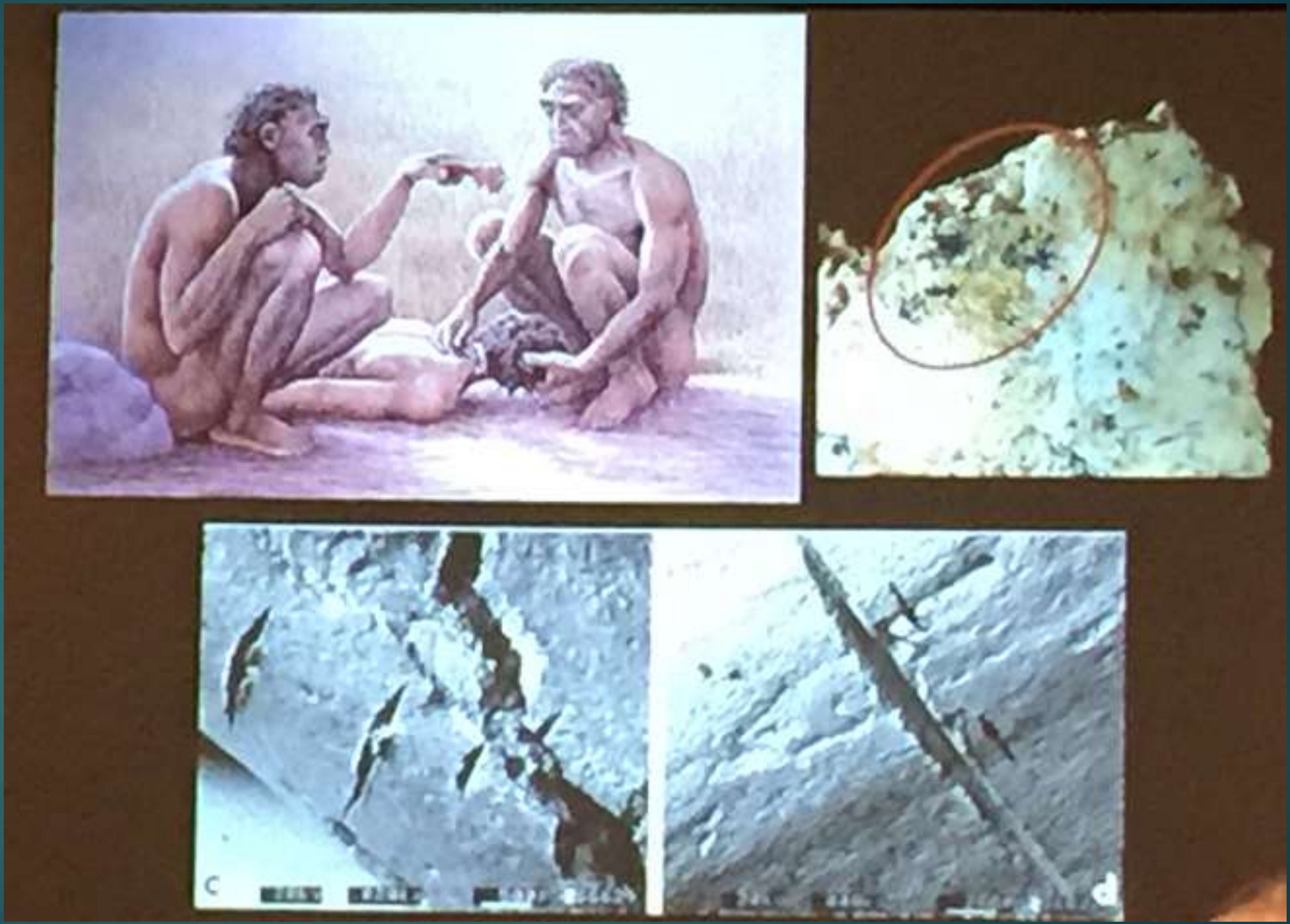
- Has a marked double-arched browridge (like later Neanderthals and Chinese erectus).
- An approximate brain size of 1,000-1,150 cc.
- Reduced mandibular thickness when compared to *ergaster* or early *erectus*.
- Has small postcanines that resemble those of the habilines (*habilis* and *rudolfensis*), but they are still within the *ergaster*/*erectus* range.
- Shovel-shaped maxillary incisors (ancestral condition).

Gran Dolina flake tools

Tools found with the Gran Dolina fossils include simple cutting flakes.

Cut marks left by tools on human bones indicate the bodies were defleshed after death, possible evidence of cannibalism (Javier Trueba/Madrid Scientific Films).

Cannibalism



Cut marks on metacarpals

Cannibalism at Gran Dolina

- Oldest evidence of human cannibalism: Nutritional cannibalism, -since the marks found on the bones of animals and humans have suggested a process of dismemberment, meat extraction and surface scraping.
- All hominin remains exhibit evidence of butchering (cutmarks, dismembering, skinning, defleshing); hominin fossils mixed in with food debris; same type of cuts as on all the animals
  - At El Sidrón, Spain: 12 Ns also show signs of cannibalism;
  - Also at Vindija Cave, Croatia
- Cannibalism: Reason?; Despite it being a period when it was warm and had multiple available animals. Many theories: nutritional, ritual, kill offspring of enemies

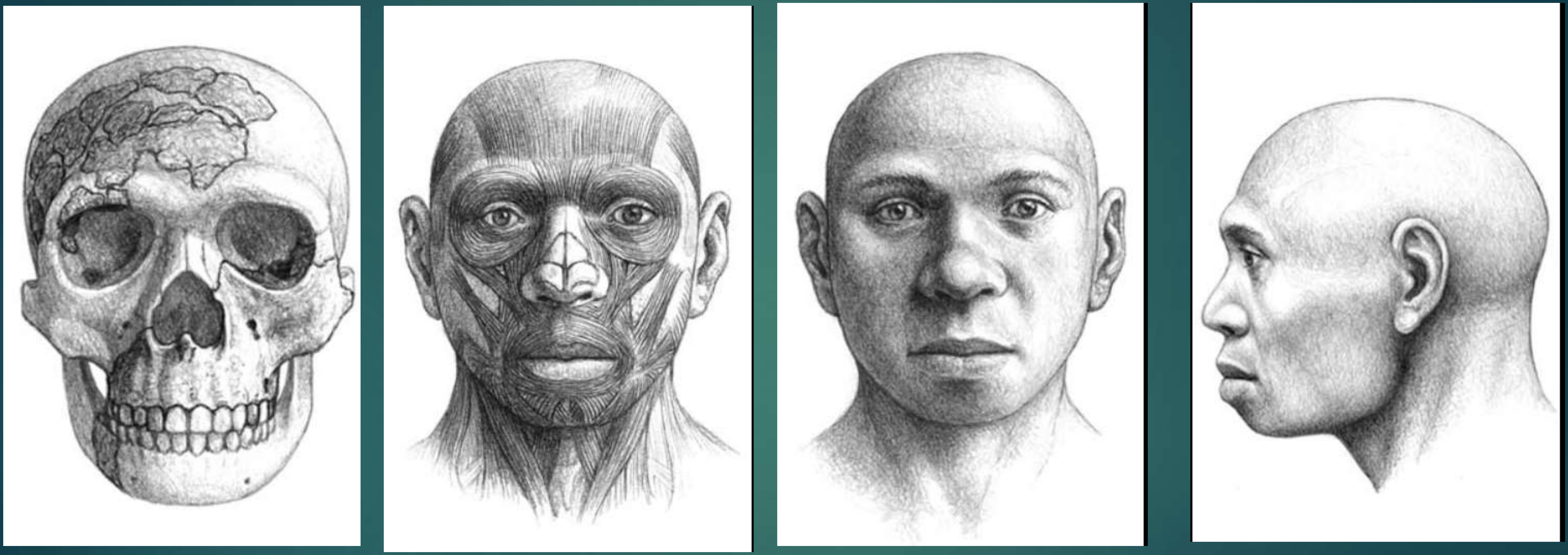
Homo antecessor: Many doubts

- The mid-facial area of *antecessor* seems very modern, but other parts of the skull such as the teeth, forehead and brow ridges are much more primitive.

- Many scientists are doubtful about the validity of *H. antecessor*, partly because its definition is based on a juvenile specimen. The sample for this species is small, fragmentary, and mostly subadult specimens.

- At present, the evidence suggesting the Gran Dolina specimens represent a distinct species is scant and many researchers attributed these fossils to *H. heidelbergensis*.

Reconstruction: modern like face



Cueva Negra: Oldest handaxe and fire, 840 Ka

- Cueva Negra del Estrecho del Río Quípar **(**Caravaca de la Cruz, Murcia, SE Spain**)**: the oldest stone hand axe, along with the creation of the oldest fire known in Europe, dated to 810 to 865 Ka.

- Biochronological analysis on the teeth of a mammal that were found near the special Acheulean hand axe, and the location of the fire hidden in the rock shelter, it was determined that the site would have been in use between 810 to 865 Ka; there were hominin teeth as well

- Could either be *Homo erectus, Homo heidelbergensis, or Homo antecessor.*

Antonio López Jiménez, et al., 2018

TN2, mode 2

TG10, mode 2

TG7, mode 2

TG10, mode 2

Cueva Negra stone axes

Raw Diet at 1.2 Ma at Sima del Elefante

- A large assemblage of animal bones suggests meat consumption, while stone tools provide evidence for meat processing and marrow extraction

- Dental calculus evidence: earliest direct evidence for foods consumed in the genus *Homo*.

- Starchy carbohydrates from two plants, including a species of grass from the Triticeae or Bromideae tribe, meat and plant fibers.

- All food was eaten raw; no evidence for processing of the starch granules; evidence of toothpick use (groves)

Cluster of starch granules

Karen Hardy, et al., 2016

Sima de los Huesos- “Pit of Bones”

- In a cave not far from Gran Dolina, lies one of the most remarkable sites in all of paleoanthropology: Sima de los Huesos, or the Pit of the Bones.

- The bottom of the pit is crammed with bones from such animals as cave bears, lions, foxes and wolves, as well as archaic modern hominins

- World’s largest assemblage of Middle Pleistocene hominin fossils

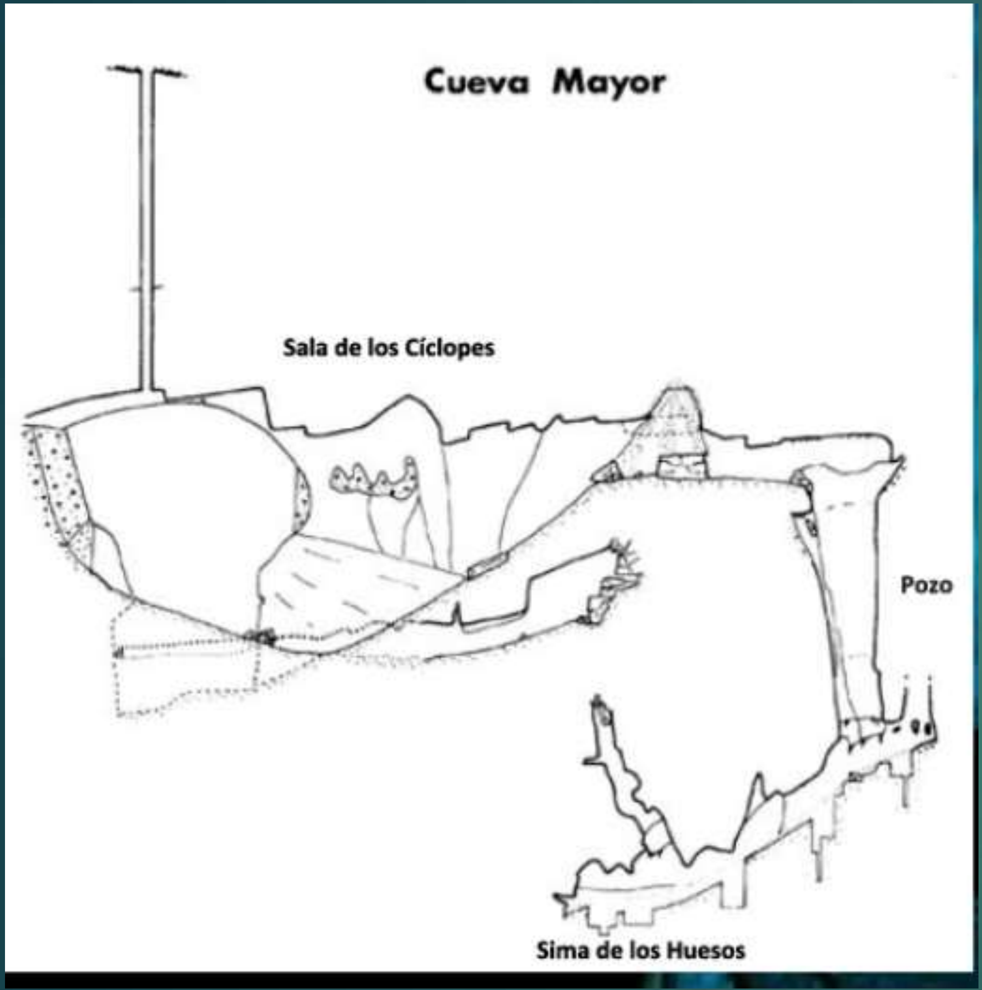
- Now dated to around 430 Ka.

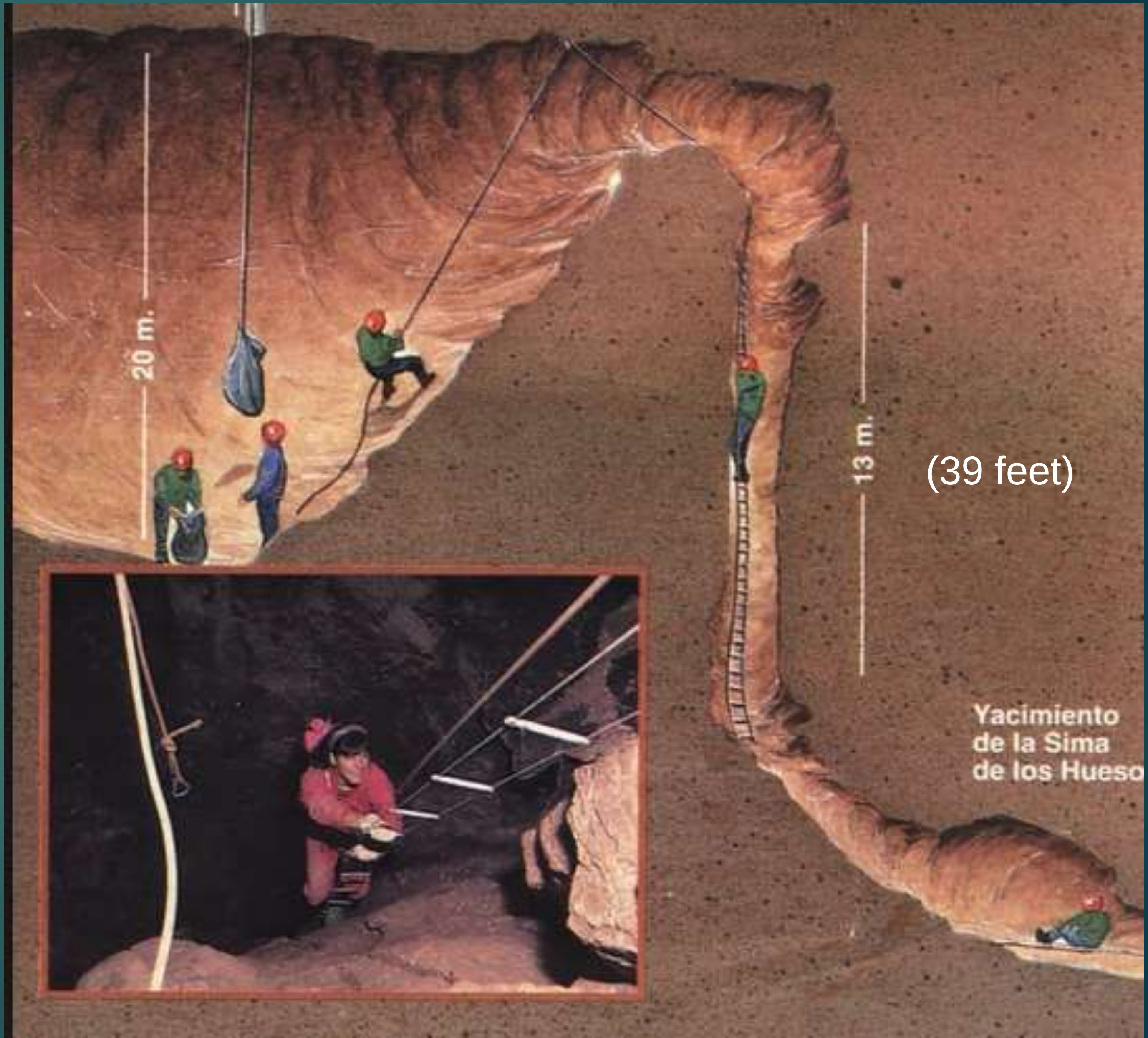
“Pit of Bones”

AMNH

Ursus spelaeus
“Cave Bear”

1992: Sima de los Huesos (Pit of the bones), Atapuerca, Spain

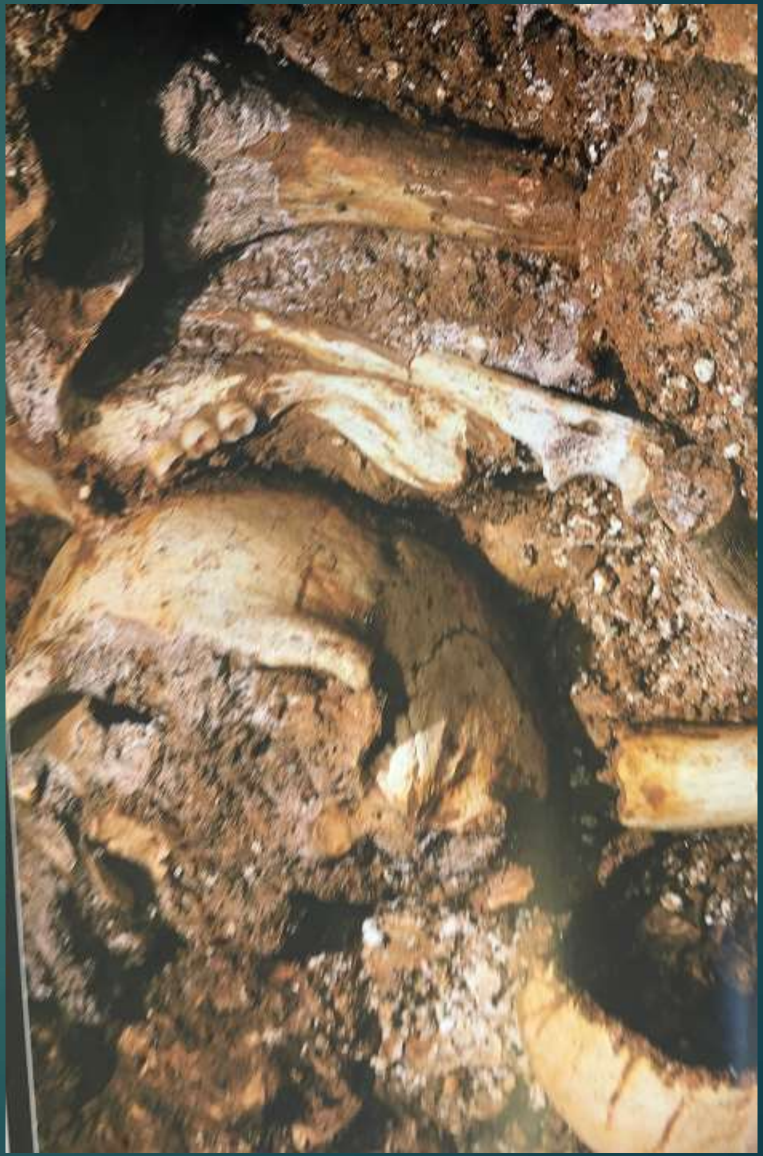




(39 feet)

Originally cave entrance was close to surface

Sima de los Huesos: small space, 8 m x 6 m, 1 excavator only

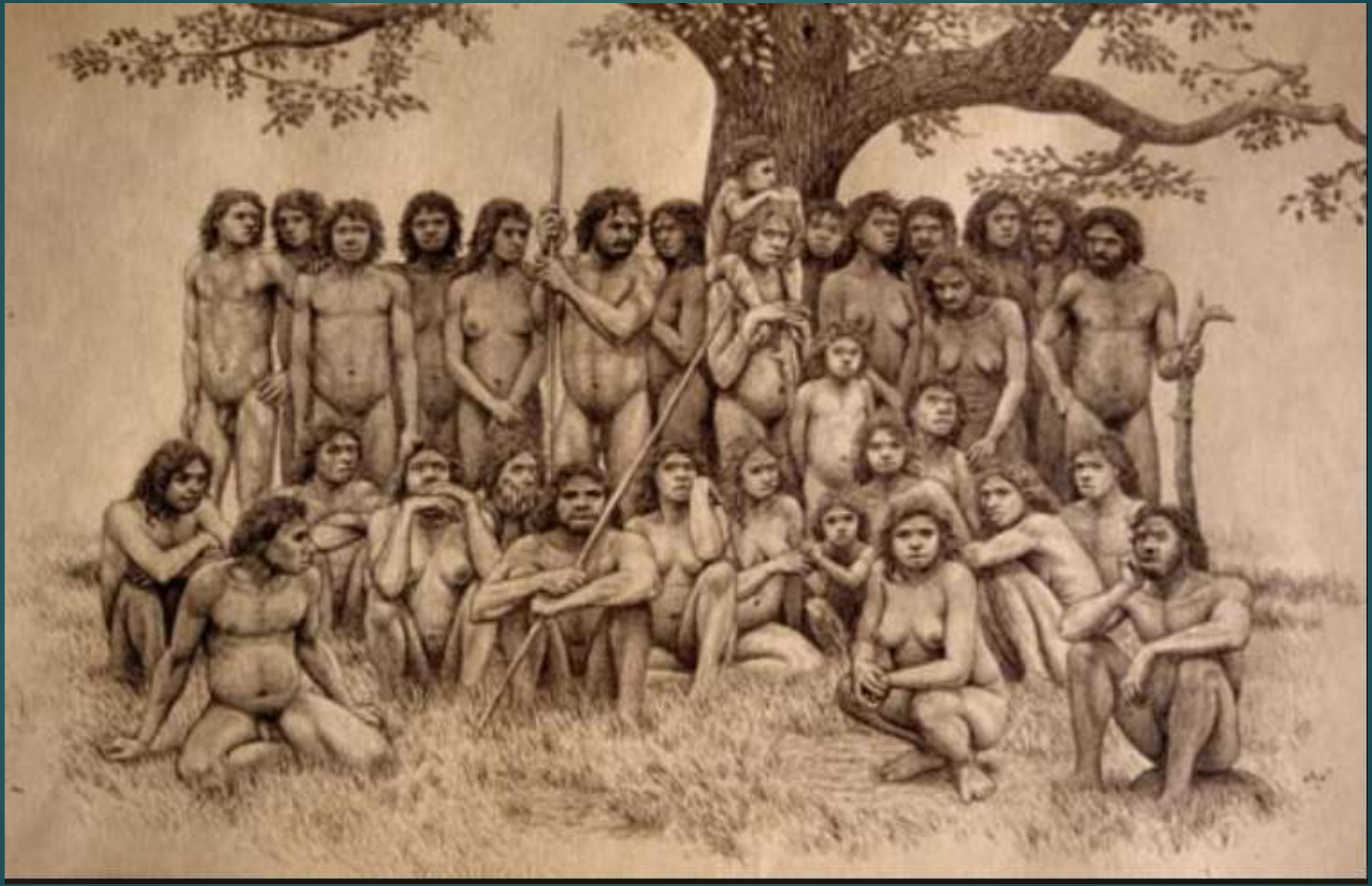


Sima de los Huesos:

Sima de los Huesos, Atapuerca, Spain

7000+
fossil
bones

Wonderful, but misleading depiction of the Sima de los Huesos findings



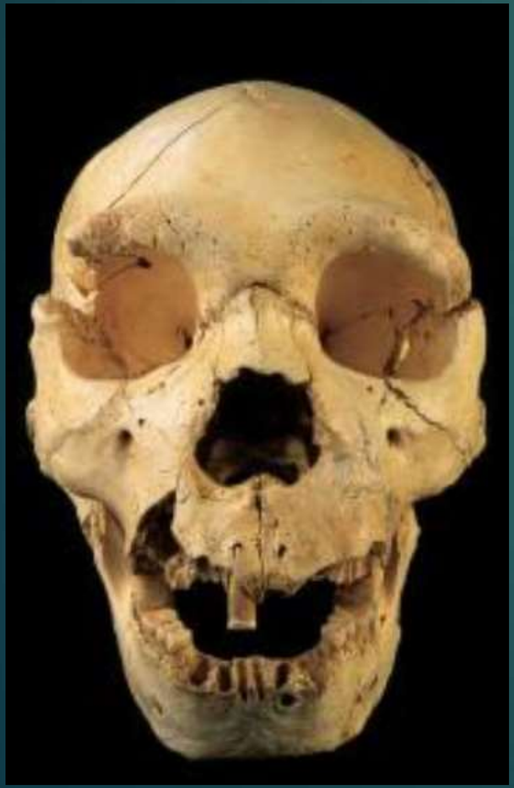
By Mauricio Antón

Sima de los Huesos

1 specimen is 93 kilos (205 lbs); not tall, but stocky; apex of weight in *Homo* line; lower wgt since

Sima de los Huesos: 17 crania; 430 Ka, 1125-1400 cc; ave 1232 cc

- 17 skulls from Sima de los Huesos
- Atapuerca, Spain; pre-Neandertal



1992: Sima de los Huesos (Pit of the Bones): Historical debate about species designation

- Example of the difficulties of paleoanthropology: Long debate over species designation.
- 1992, Juan Arsuaga: remains of 28 bodies (6500 bones); the world's greatest single haul of ancient *Homo* fossils; originally dated at 600 Ka; now dated to 430 Ka
- Arsuaga: originally designated as *Homo heidelbergensis*
- Chris Springer: Neanderthal remains that are no more than 400 Ka

Arsuaga, et al., 1991-1997

Are the Sima de los Huesos Fossils part of *H. heidelbergensis*?

- Mosaic combination of *heidelbergensis*-like and Neanderthal-like features

- Originally dated to >530 Ka (600+/-66 Ka); reinforced the Atapuerca team's preference for assigning the material to *H. heidelbergensis*

- C. Stringer preferred to regard the SH material as an archaic form of *neanderthalensis*, based on the presence of Neanderthal-like features such as an incipient suprainiac fossa and midfacial projection in the crania, dental and mandibular traits, and numerous postcranial characters.
- Mandibles of the Sima sample are virtually identical to the Neandertal mandible

- SH sample reinforces idea that some of *H. heidelbergensis* hominins document an early stage of N evolution

The complexity of fossil interpretation at Sima de los Huesos:

- *Heidelbergensis* or *Neanderthalensis*? The more than 7500 fossils from that site show distinctive Neanderthal features, but have often been included in the *H. Heidelbergensis* taxon because of their supposed great original dating (up to 600 ka).

- 2014 mtDNA: closely related to the lineage leading to mitochondrial genomes of Denisovans; 400 Ka
  - via common ancestor of Neanderthals and Denisovans, and some of their descendants later headed east and became the Denisovans?
  - Or Neanderthal ancestors, and came after the species split from Denisovans & Ns lost mtDNA later

Matthias Meyer *et al*. 2016

The complexity of fossil interpretation at Sima de los Huesos 2

- In 2015, new nuclear DNA results show that the SH hominins carry mtDNAs more closely related to those of Denisovans in Asia than Neanderthals, even though their nuclear genomes show that they are more closely related to Neanderthals.

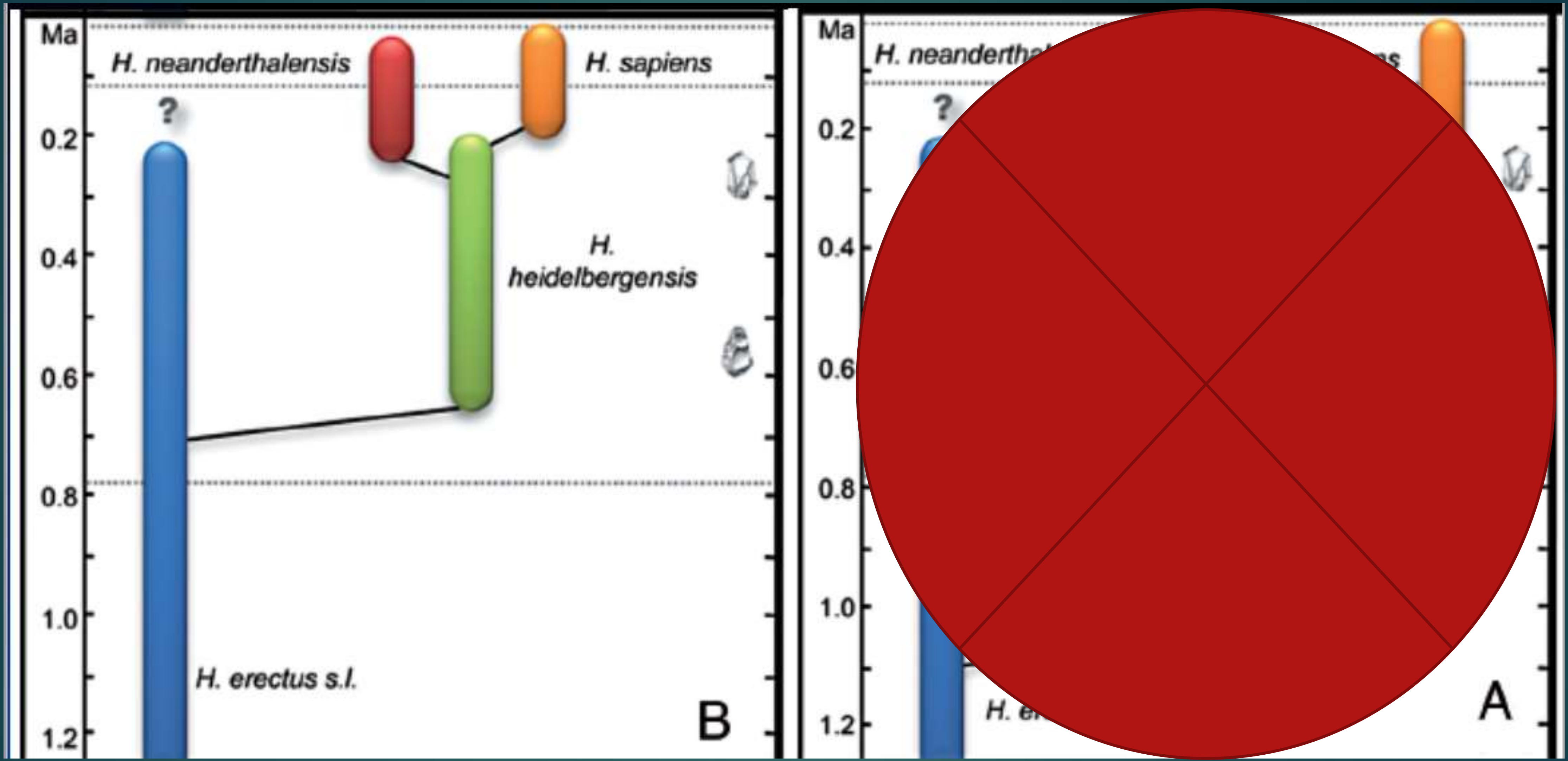
- 2015 Nuclear DNA: Sima de los Huesos hominins were related to Neanderthals rather than to Denisovans.

- This is the oldest dated DNA currently achieved in a hominin, at 430 Ka

- Anatomical and molecular studies have demonstrated that these hominins are phylogenetically related to Neanderthals, thus making them the earliest unquestionable representatives of the Neanderthal lineage.

- It also indicates that the population divergence between Neanderthals and Denisovans predates 430 Ka (estimated at 550 to 750 Ka)

2 scenarios before genetic data arrived in 2015



New model post revelation of Sima de Los Huesos fossils being 430 Ka Neandertals

Sima de los Huesos: Genus switch

- Starting in the 1990s, 7,000+ hominin fossils dated to 430 Ka have been found at **Sima de los Huesos** in Atapuerca.

- They constitute more than 80% of the total hominin fossil record of the Middle Pleistocene; 90% of all *H. neanderthalensis* fossils

- Therefore, in 2014 the Atapuerca team argued that those hominins do not belong to *H. heidelbergensis*.

Sima de los Huesos

- Largest hominin collection in the world; 7000+ fragments; repetition of all body parts
- 17 crania (adult), 1 fragmentary cranium (immature), 450 teeth, 5 mandible fragments, postcranial remains, 2 human-like hyoid bones
- Catastrophic distribution?: 50% teenager; prime age people; no very young or old. The most represented group is between 13 and 17-year-old specimens. Only 3 individuals were over 30.
- Some children (Cr. 3, 6, 9, 11, 14 yrs). , but none under 3. The sex of 18 individuals: half men, half women.
- Males were 1.75 m tall and females 1.70 m tall.
- The SH paleodeme can be characterized as relatively tall, wide, and muscular individuals

La Sima de los Huesos (The Pit of Bones)

- Teeth show heavily worn teeth, probably caused by the consumption of uncooked fruit or vegetables, but not a single cavity has been found.
- Incipient N features; nuDNA indicates they were early Ns, dated to 430 Ka
- Grooving on posterior teeth imply use of toothpicks and/or use of teeth for sinew processing
- Fossil animal bones of 100s of cave bears & other predators (lions, wolves, foxes); lack of herbivore bones

Sima was not a living space

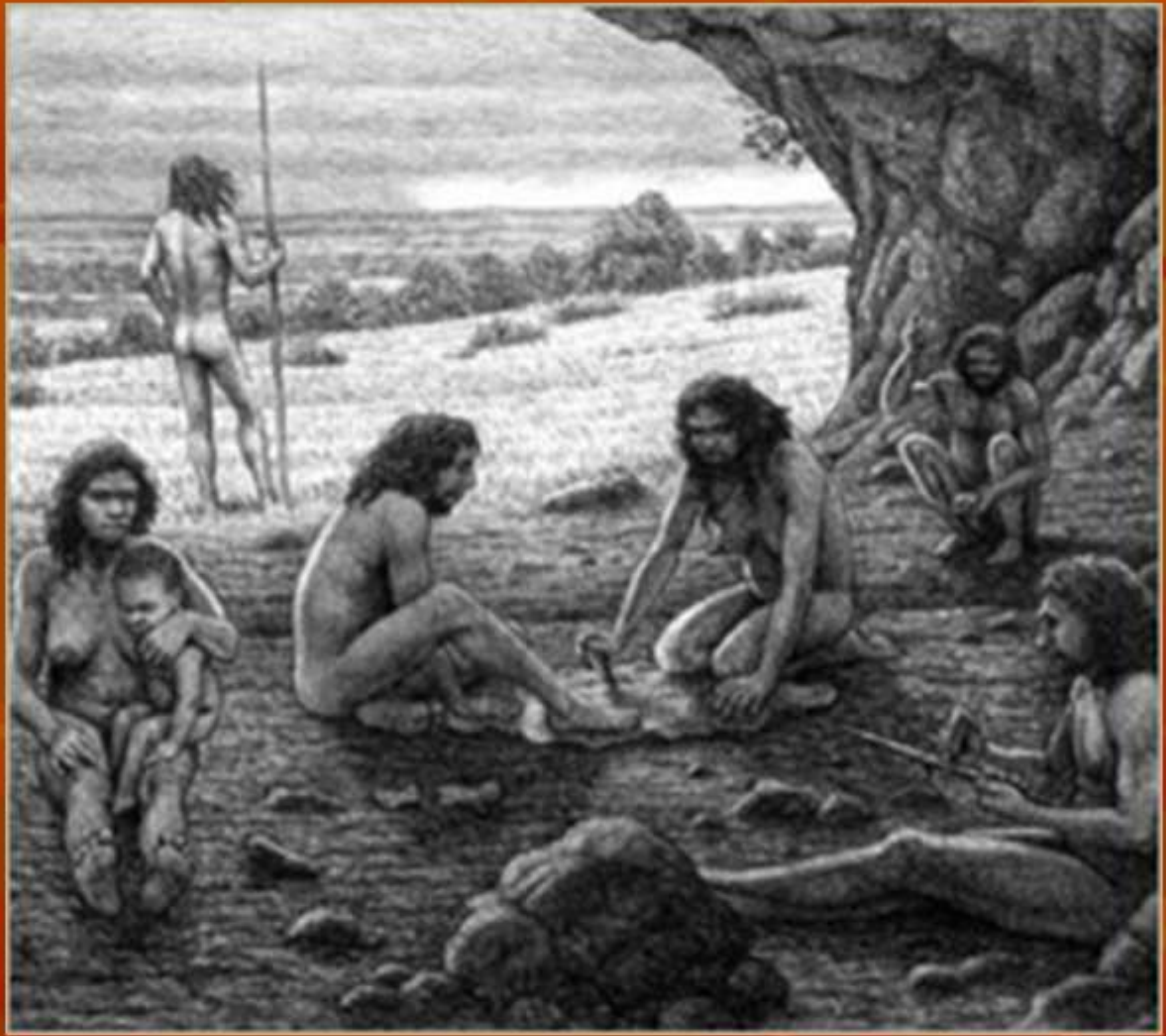


Illustration by Mauricio Antón

How did the bones of the Sima hominins end up in the cave?

- There are no indications that the hominins ever lived in the cave—for example, there is no evidence of fire or tools there.
- 30 individuals, many of them teenagers and young adults. have been found
- If the Sima hominins had fallen in accidentally, we would expect to see a wider range of ages represented.
- Original researchers have speculated that the hominins disposed of these bodies by carrying them over to the cave and then throwing them in.
- There is evidence of bodies being carried in by predators

Sima de los Huesos: “Elvis” the pelvis

- Most complete pelvis in fossil record

- Invalid?: As well as being hunched, he had a slipped vertebra which must have constantly and painfully rubbed against its neighbor. He’d also developed a bony growth on another vertebra.

Sima de los Huesos: Disabled not left behind

- The ear canals in ‘Agamenón’ are blocked, suggesting long-term deafness.

- Cranium 17 shows evidence of two fractures produced by the same object in a face-to-face interpersonal conflict.

- 9-year-old with occipital suture early closing: Craniosynostosis

Sima de los Huesos

- Petalias are a type of cerebral asymmetry, with greater protrusion of the surface of one hemisphere beyond that of the opposite hemisphere. The most typical configuration in modern humans is for the combination of a right frontal lobe petalia and a left occipital lobe petalia. Brain endocast asymmetries.
- Right handed (stronger right arm bones; right frontal lobe petalia and a left occipital lobe petalias); wear on the preserved teeth suggest that food was usually brought to the mouth with the right hand (right oblique orientation of labial striations on the anterior dentition)
- Bodybuilder physiques: Pronounced muscle markings; thick leg bones; Thick layers of hard bone around central marrow cavities; 95 kg (209 lbs) – largest hominin in history to that time; modern sexual dimorphism
- Cranial capacity ranged from 1204 cc (Cranium 5) to 1246 cc (Cranium 4)

Cranium 5

Sima de los Huesos: more primitive endocranial N traits

- The Sima de los Huesos (SH) endocranial sample includes 17 complete or partial endocasts

- The description of endocranial variation in this population is fundamental to shedding light on the evolution of the Neanderthal brain.

- Results indicate that the SH hominins show a transitional state between a primitive hominin endocranial configuration (which is found in *Homo erectus* and non-SH Middle Pleistocene *Homo*) and the derived configurations found in Neanderthals and modern humans, without a clear anticipation of classic Neanderthal endocranial traits.

SH Ns endocasts

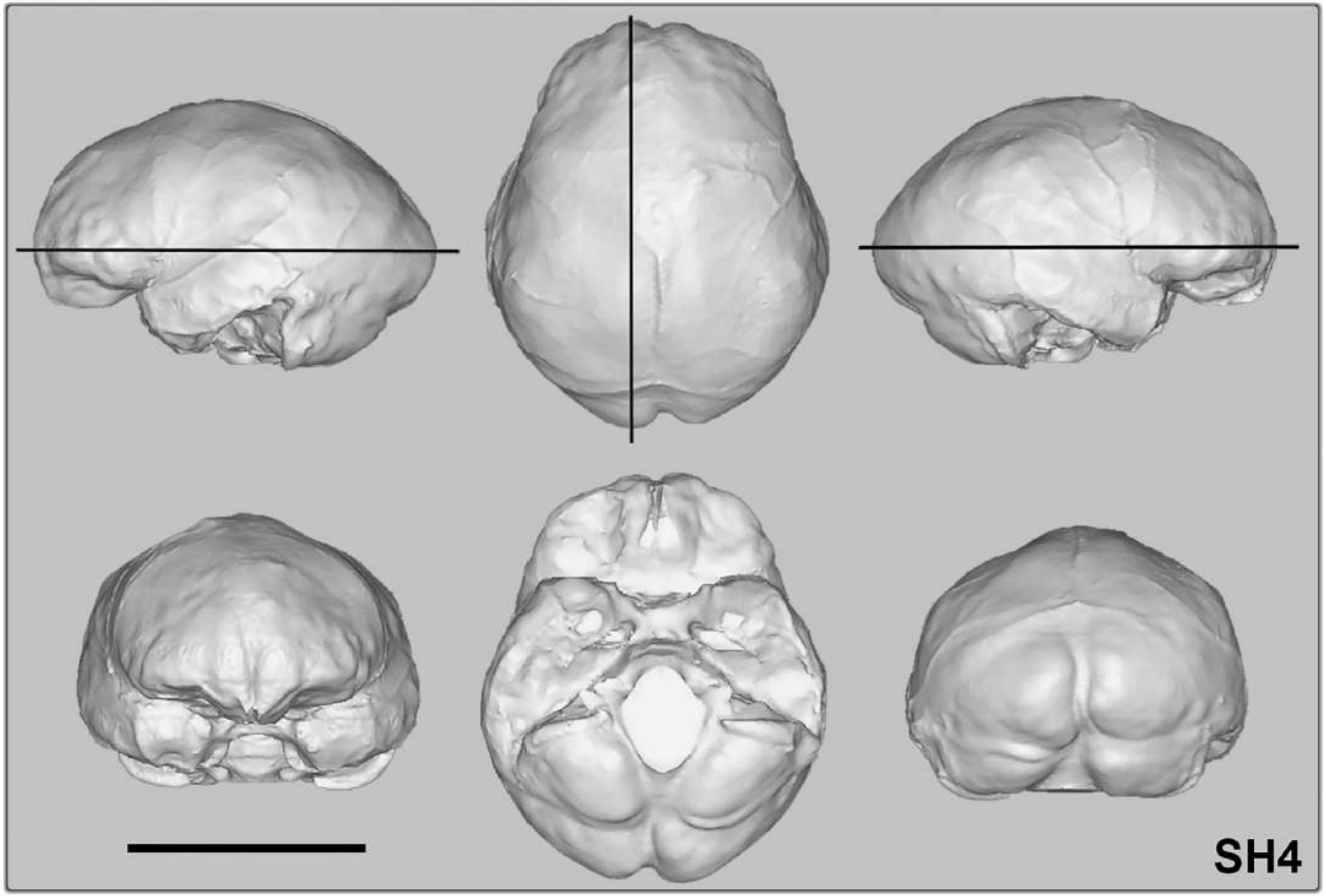
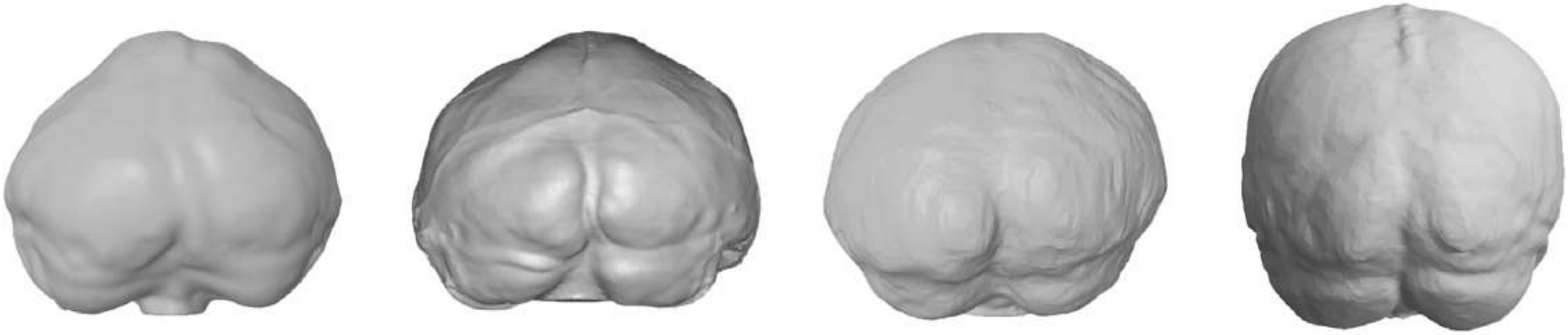


Figure 6. Endocast SH4. Six different views are provided (top row: left lateral, superior, right lateral; bottom row: anterior, inferior and posterior). Scale bar is 10 cm.



H. erectus SH H. neanderthalensis H. sapiens

Figure 20. Posterior view of four hominin endocasts showing the configurations observed in *H. erectus* (tent-like or “en tente”, Zhoukoudian 12), SH-hominins (roof-like, SH4), *H. neanderthalensis* (rounded or “en bombe”, Saccopastore 1) and *H. sapiens* (house-like or “en maison”, recent modern human). Endocasts are not to scale.

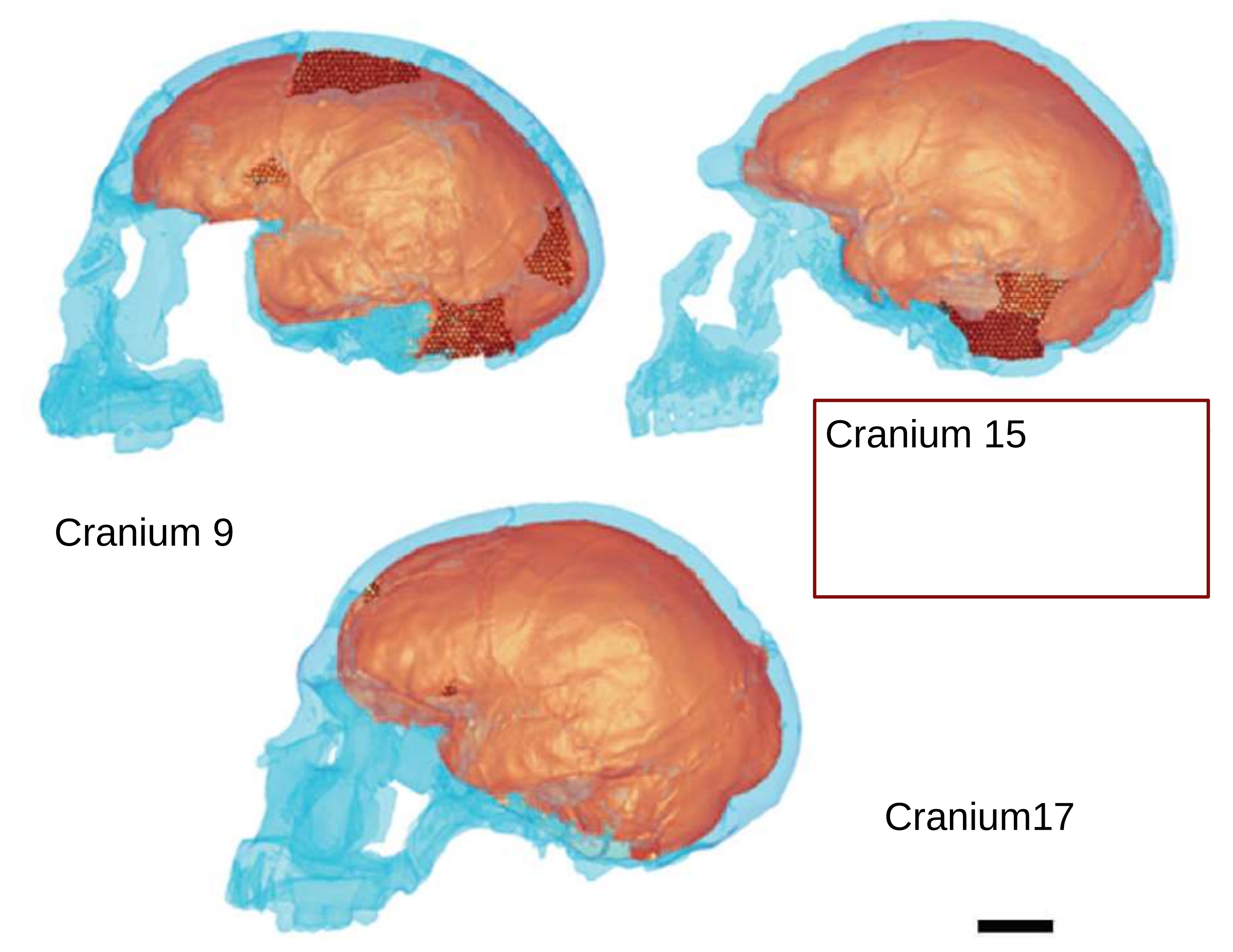
Sima de los Huesos: more primitive endocranial N traits

- In comparison with other cranial and postcranial traits that show a fully Neanderthal or clear pre-Neanderthal condition in the SH collection, endocranial variation in these hominins is surprisingly primitive and shows no Neanderthal affinity.

- These results and the comparison with other cranial traits confirm that Neanderthals evolved in a mosaic fashion.

- Traits related to mastication (dental, facial and mandibular anatomy) led the Neanderthalization process, whereas neurocranial anatomy must have acquired a fully Neanderthal condition considerably later.

Endocranial volume: mean = 1230 cc



Sima hominins are pre-Neandertals

- Some of the Neandertal traits showed by the Sima individuals: pronounced browridge, not sunk over the nose; cheeks projected towards the nose, giving a triangular look to the face
- The braincases are not Neandertal-type. Their average brain size is less than modern humans and less than Neandertals.
- SH5: cranial capacity is only 1230 cc
- Neandertals developed larger brain separately, and later.

Cranium SH 5

Miguelón

Age: 30-40

Javier
Trueba

Atapuerca, Cranium 5

SH5: Some primitive features, but mainly derived Neandertal features of face

Cranium 5 is one of the most important discoveries in the Sima de los Huesos, Atapuerca (Spain).
The mandible of this cranium appeared, nearly intact, some years after its find, close to the same location.

Cranial Capacity
1100 cc – 1400 cc

Average: 1200 cc

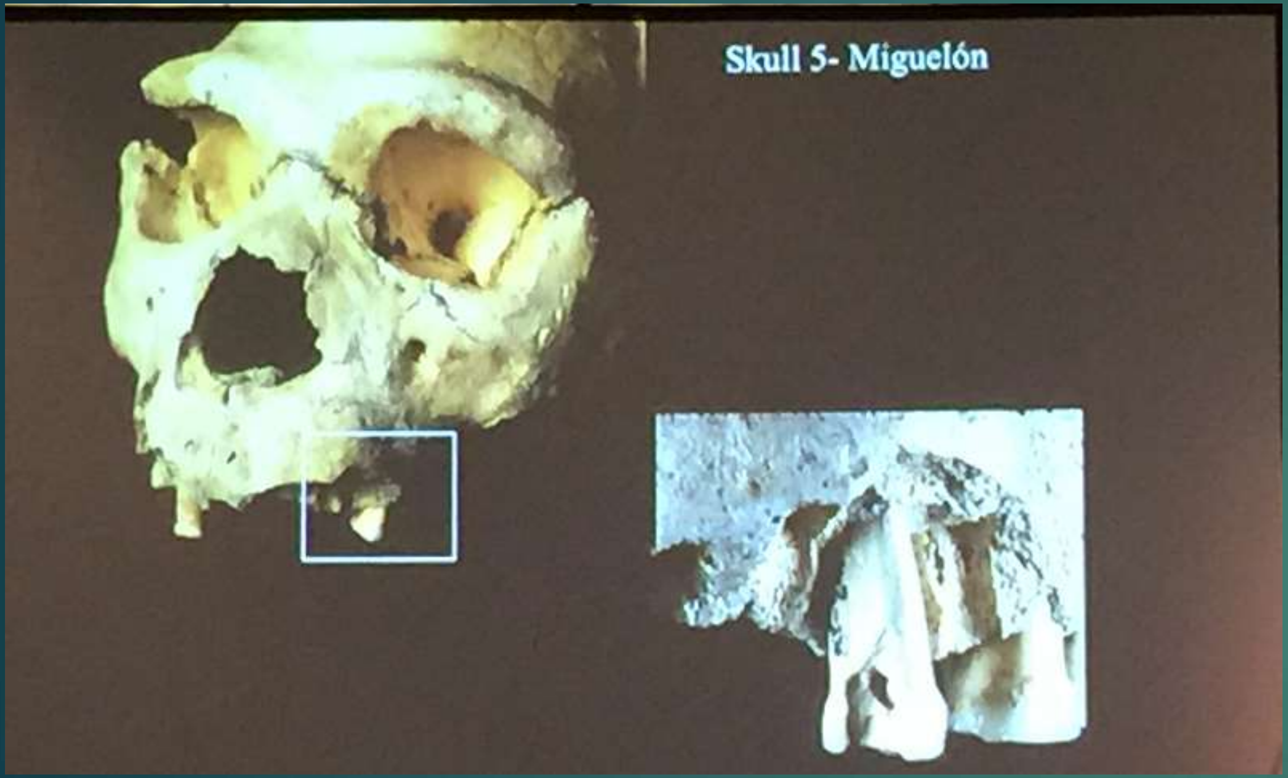
Pronounced brow ridge

Wide eye sockets

Wide nose bridge

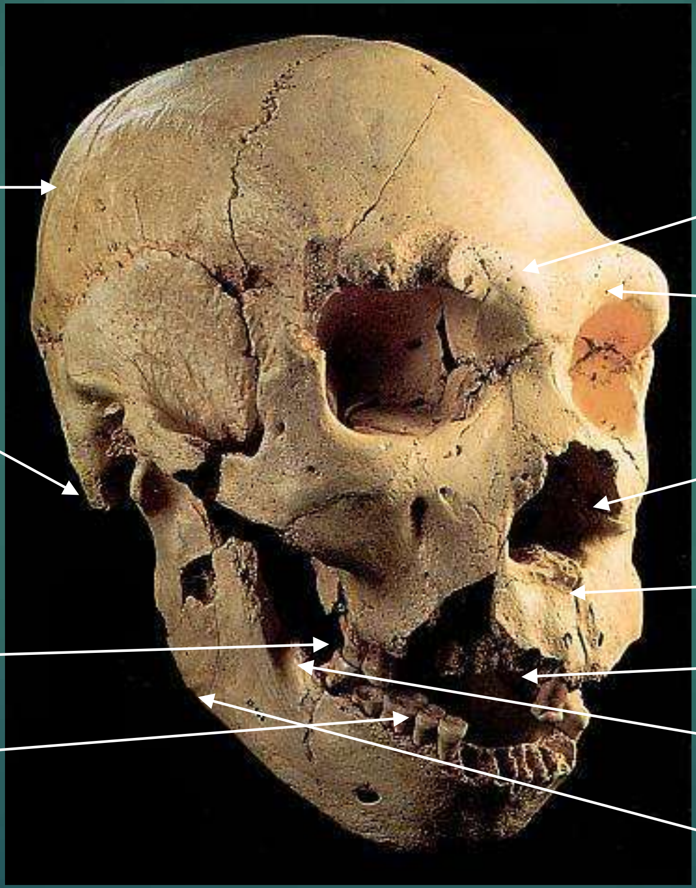
No chin

Skull 5: broken premolar, open cavity, affected left mandible and side of nose and face



Suffered traumatic rupture of the first upper left premolar, which caused a wound in the oral cavity and its subsequent infection. This pathology could cause a generalized fatal septicemia.

SH5: These hominins are pre-N: Some primitive features, but mainly derived Neandertal features of face; SH5 has all N facial features



Not "en bombe"

Large mastoid

Molars don't slope much

Molars not taurodont

N-like features

Deep glabella

Evenly circular supraorbital tori

Nasal protrusion

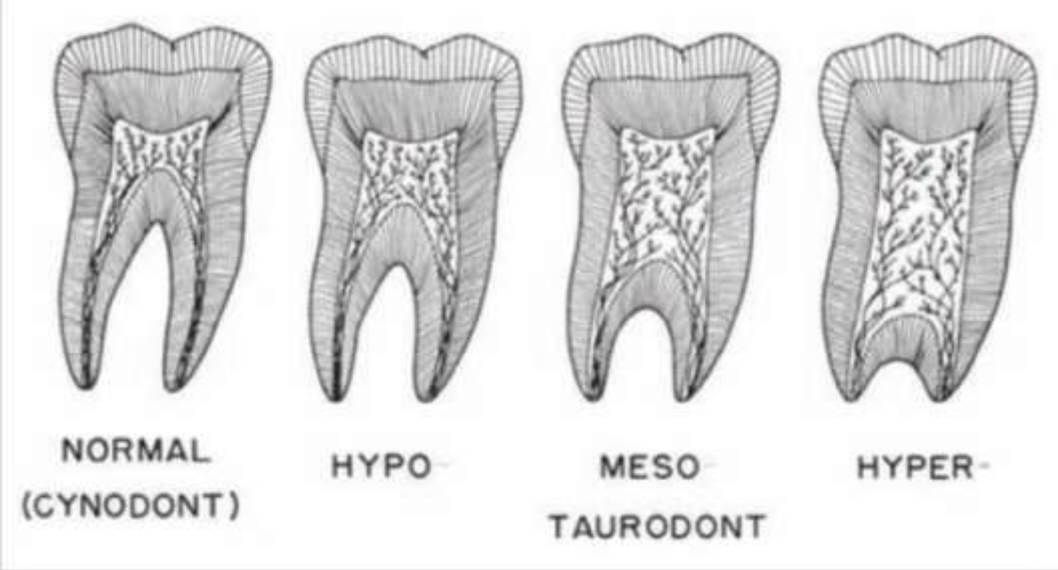
Some midfacial protrusion

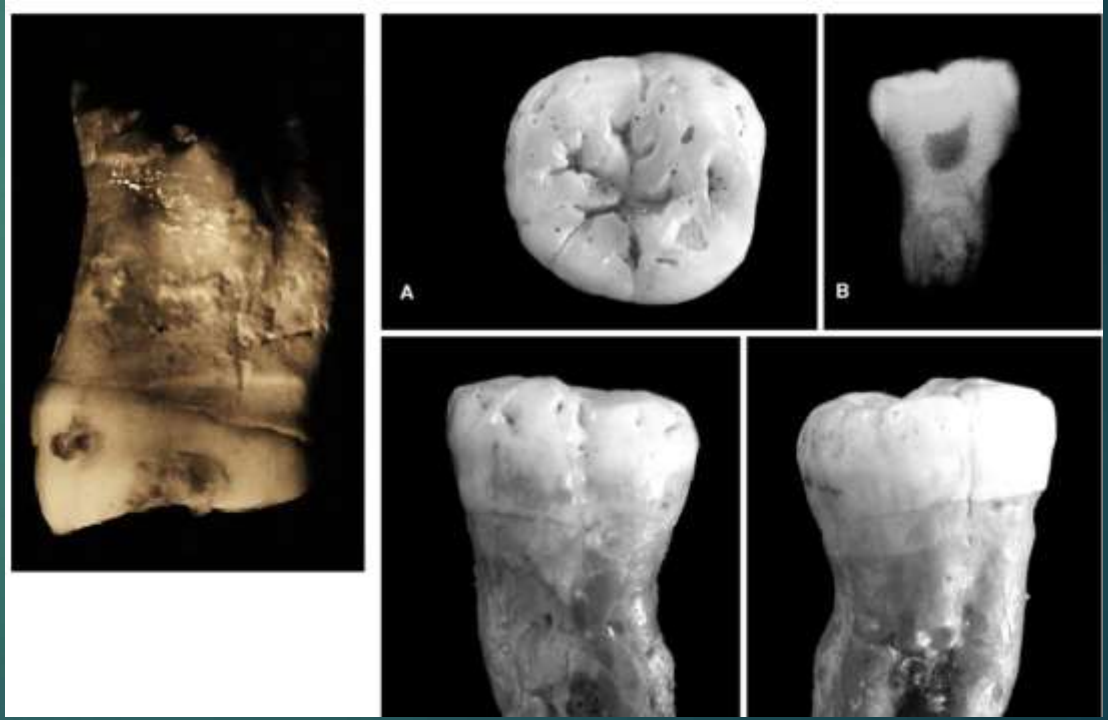
Maxillary sinus seems large

Retromolar space

Truncated jaw angle

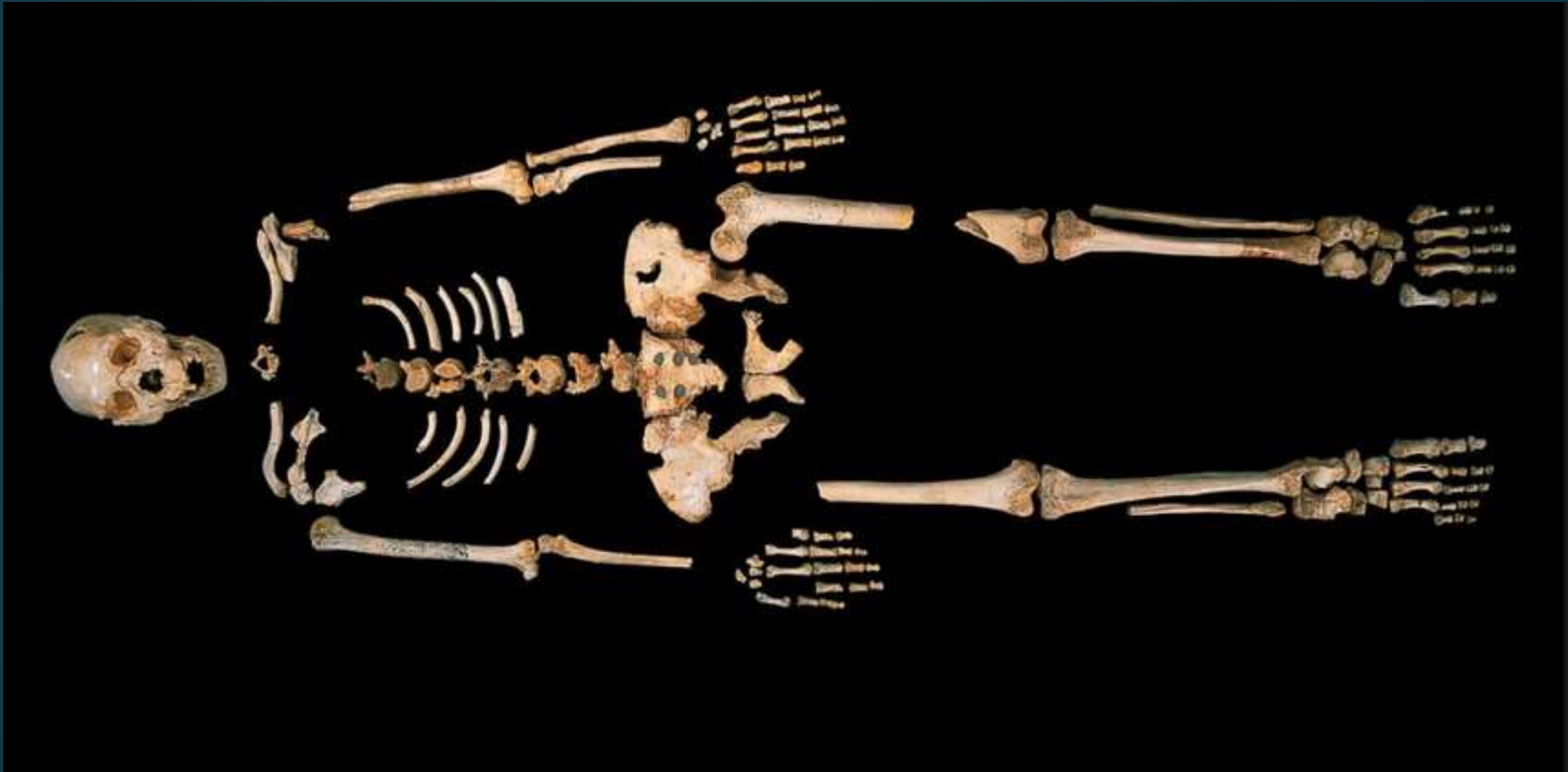
Taurodontism: not 2 tooth roots, but square shape; classic N trait





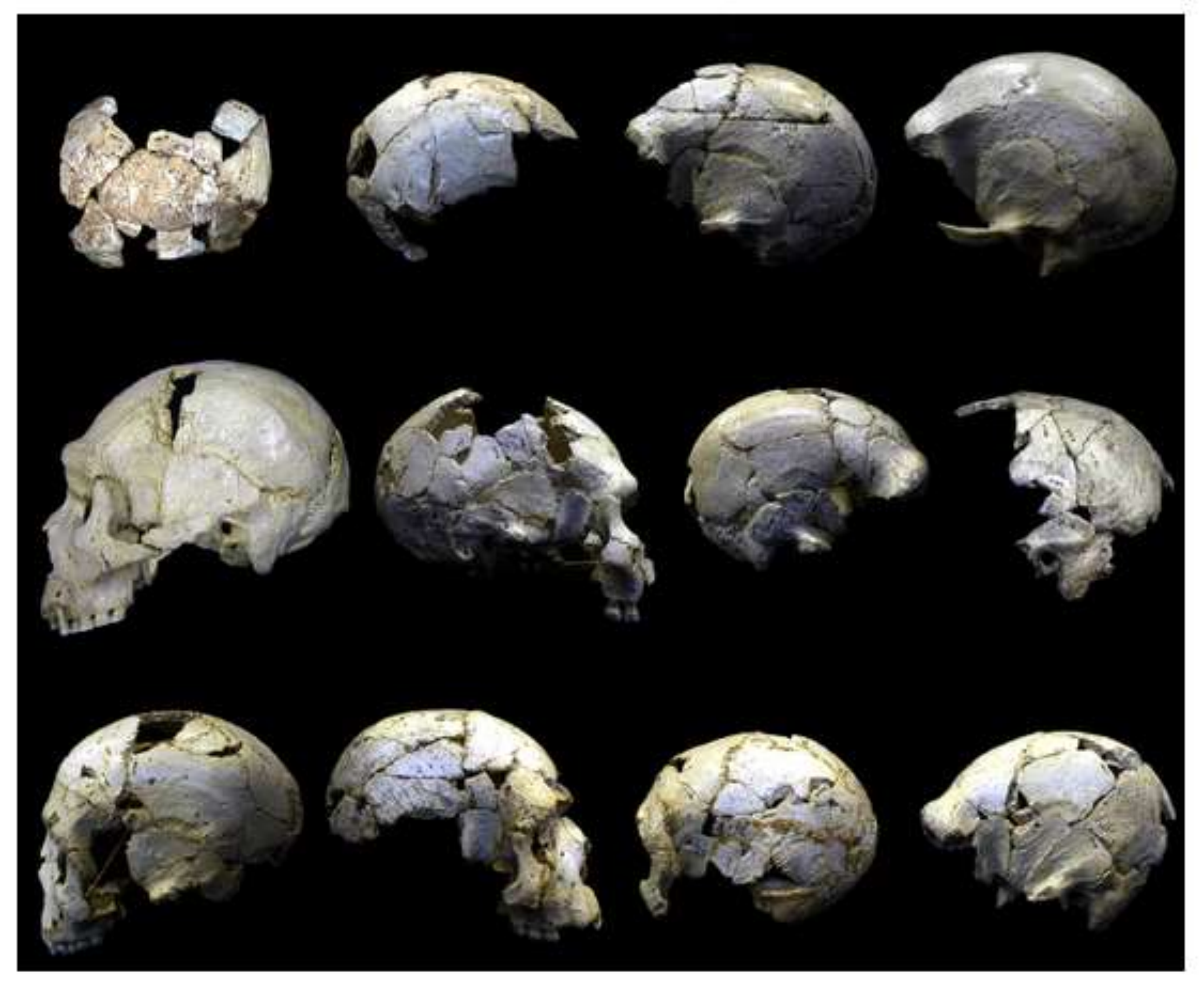
Shovel shaped incisors from Sima de los Huesos

Robust



17 skulls at Sima: the largest collection of hominin crania in the fossil record

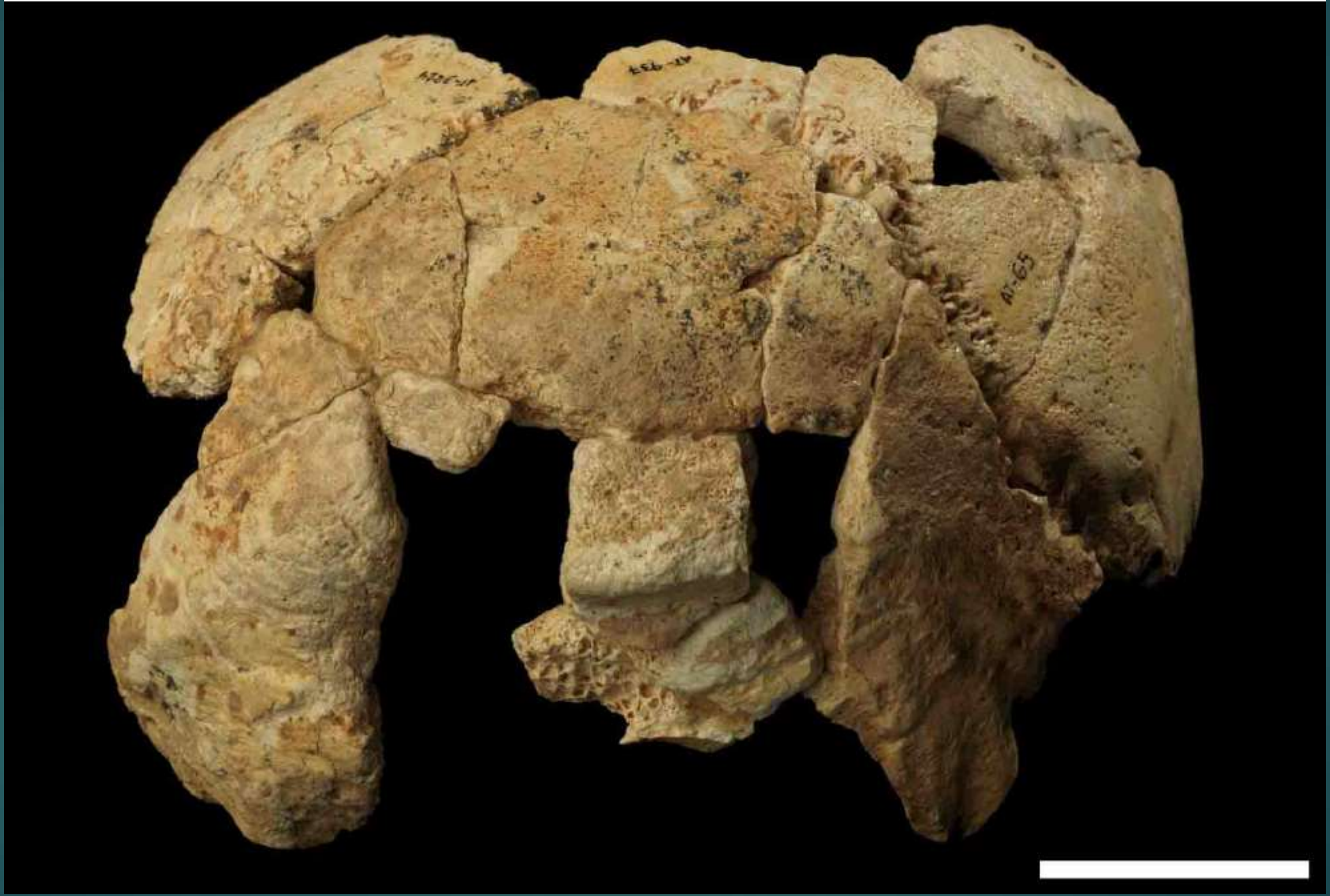
Meeting a violent end at Sima de los Huesos



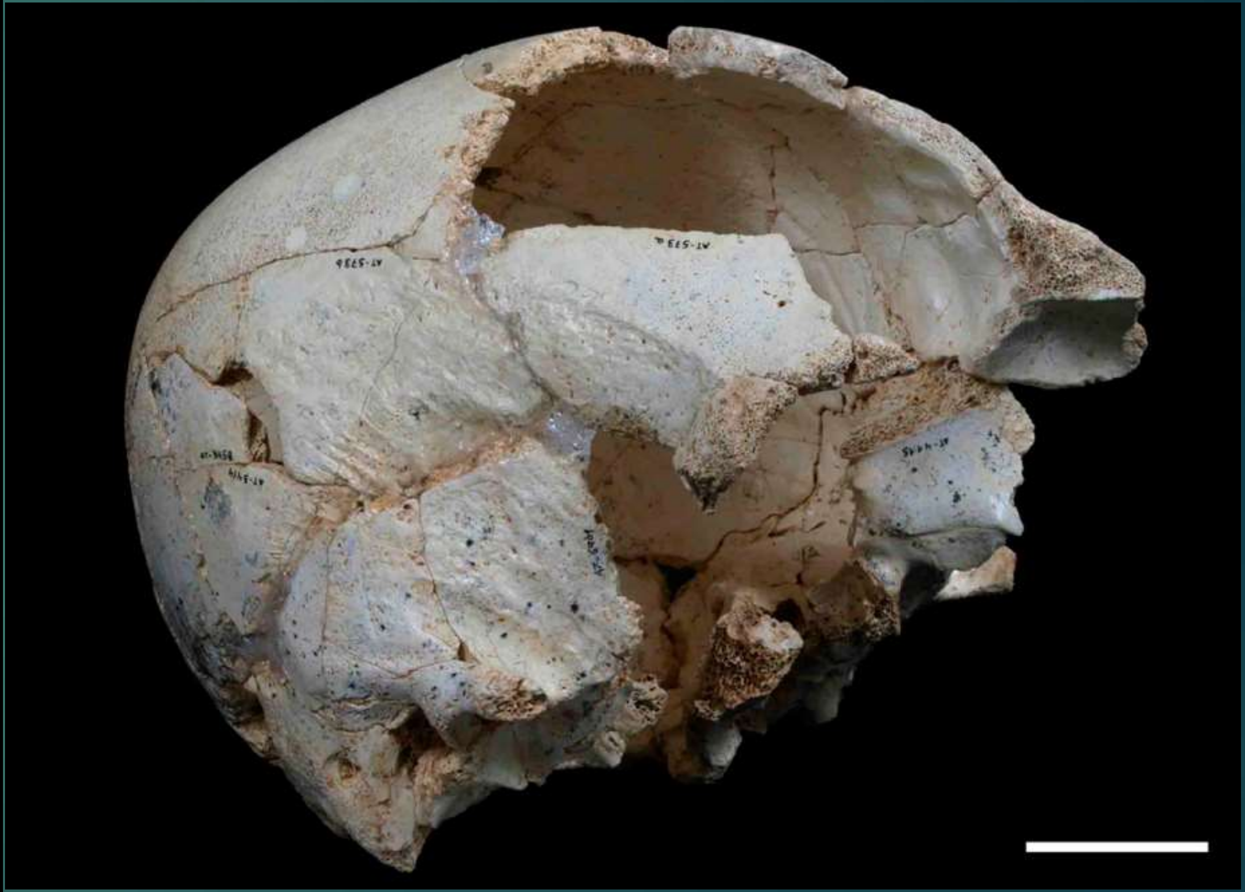
- One theory of interpersonal violence:
- The fractures found in all seventeen crania from SH display a postmortem fracturation pattern, which occurred in the dry bone stage and is compatible with collective burial assemblages.
- Eight crania also display some typical perimortem (at time of death) traumas.
- Interpersonal violence as a cause for the perimortem fractures can be confirmed for one of the skulls, Cranium 17 and is probable for Cranium 5 and Cranium 11.
- For the rest of the crania, although other causes cannot be absolutely ruled out, the violence-related traumas are the most plausible scenario for the perimortem fractures. If this hypothesis is confirmed, the team may be able to interpret that interpersonal violence was a recurrent behavior in this population from the Middle Pleistocene.

Putting SH craniums together

Cranium 1 (adult)



Cranium 2 & 3



Cranium 4

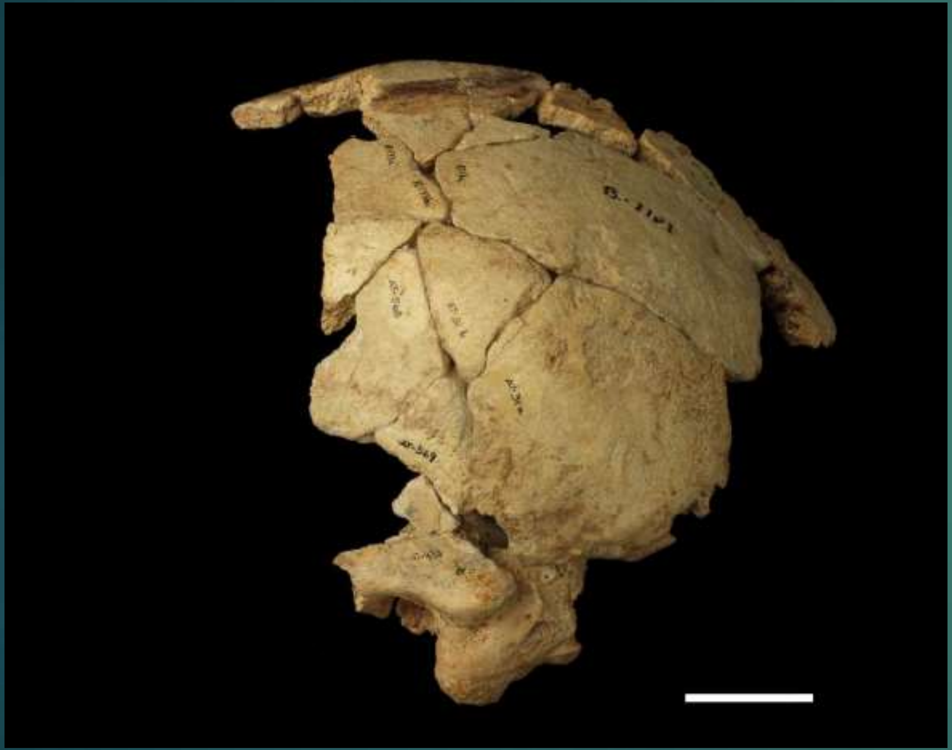
Cranium 4 (adult)

Cranium 5 (adult)

Cranium 6

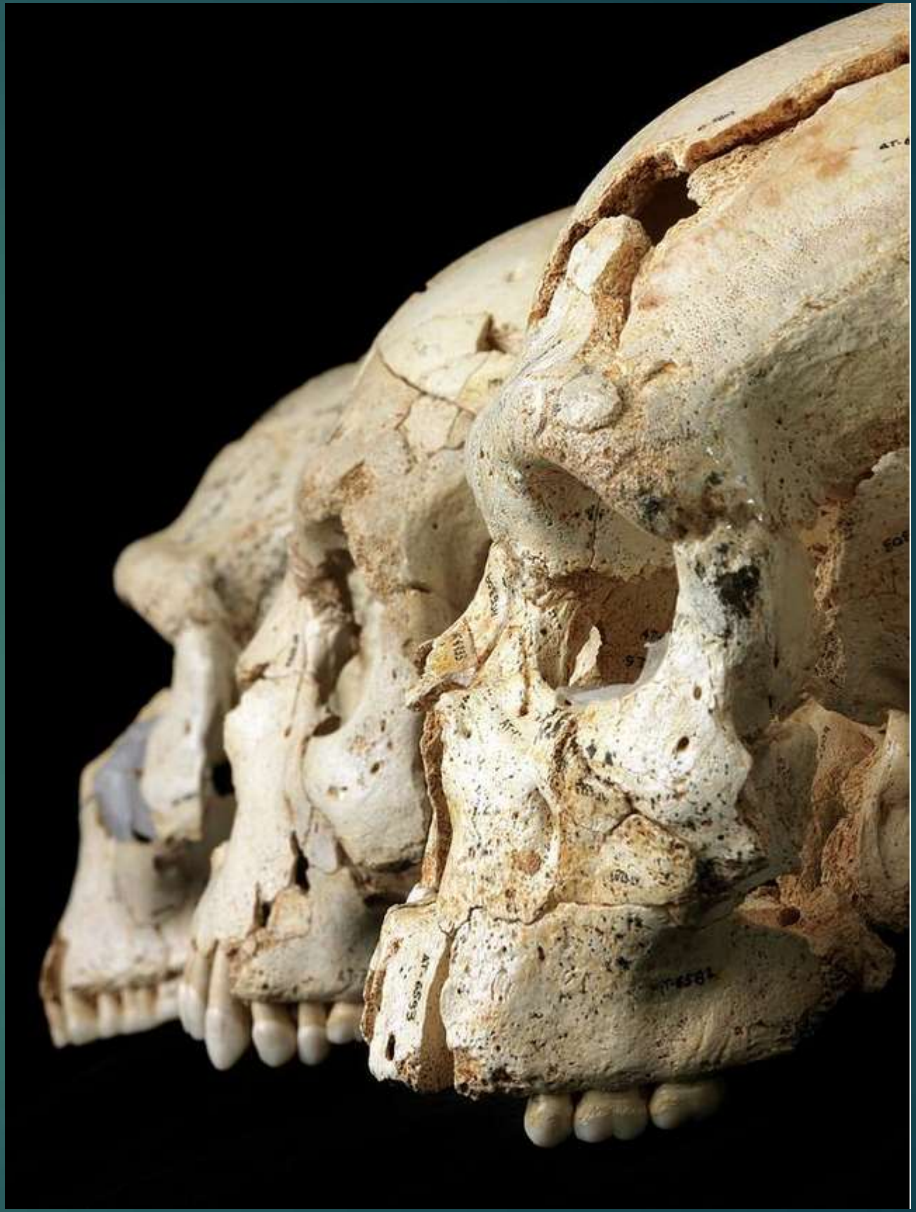
- Cranium 7

Cranium 8



Cranium 9

Cranium 9 (child)

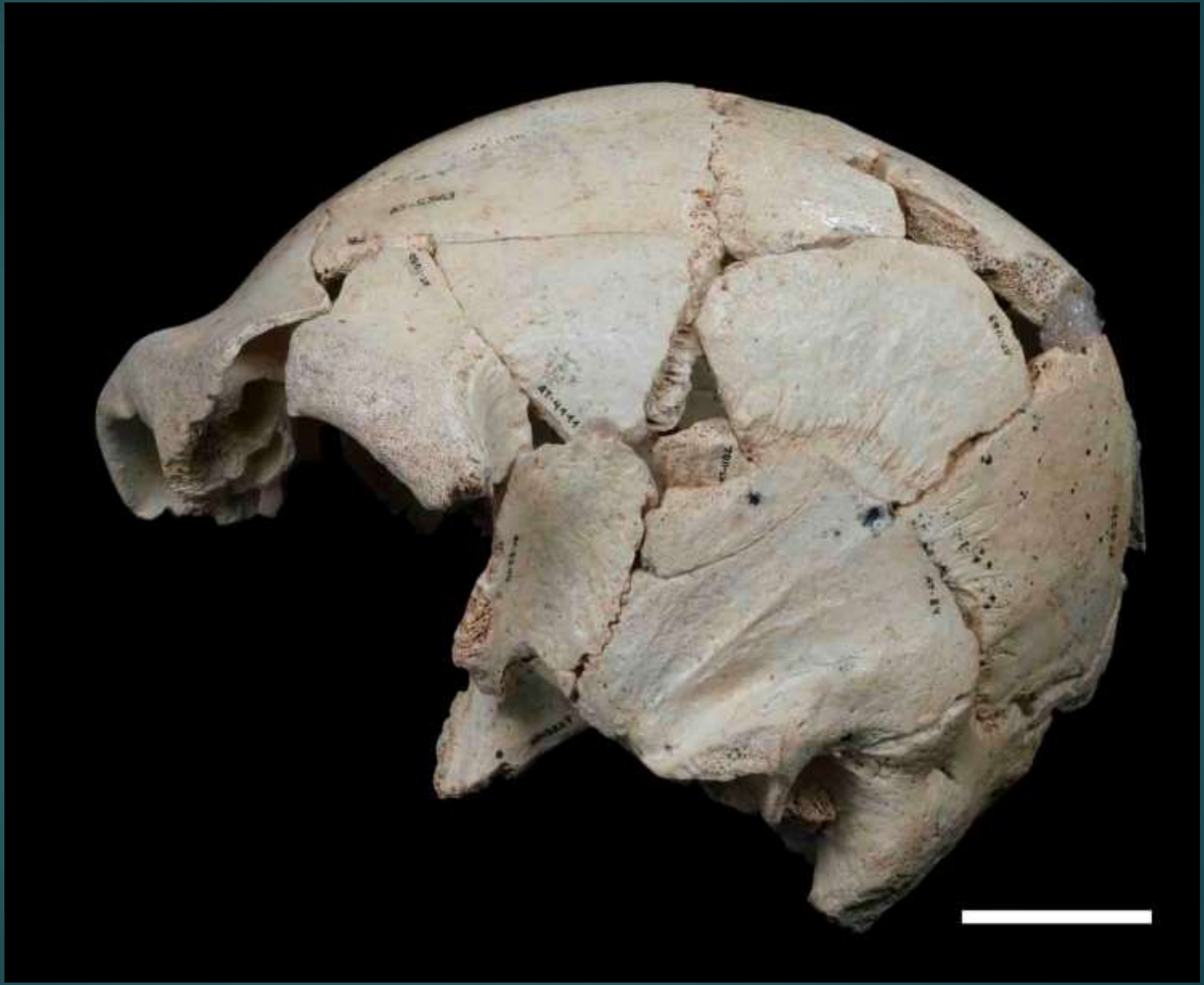


Cranium 15 (adult, left), cranium 9 (immature, center) and cranium 17 (adult, right)

Cranium 10

Cranium 11

Cranium 12



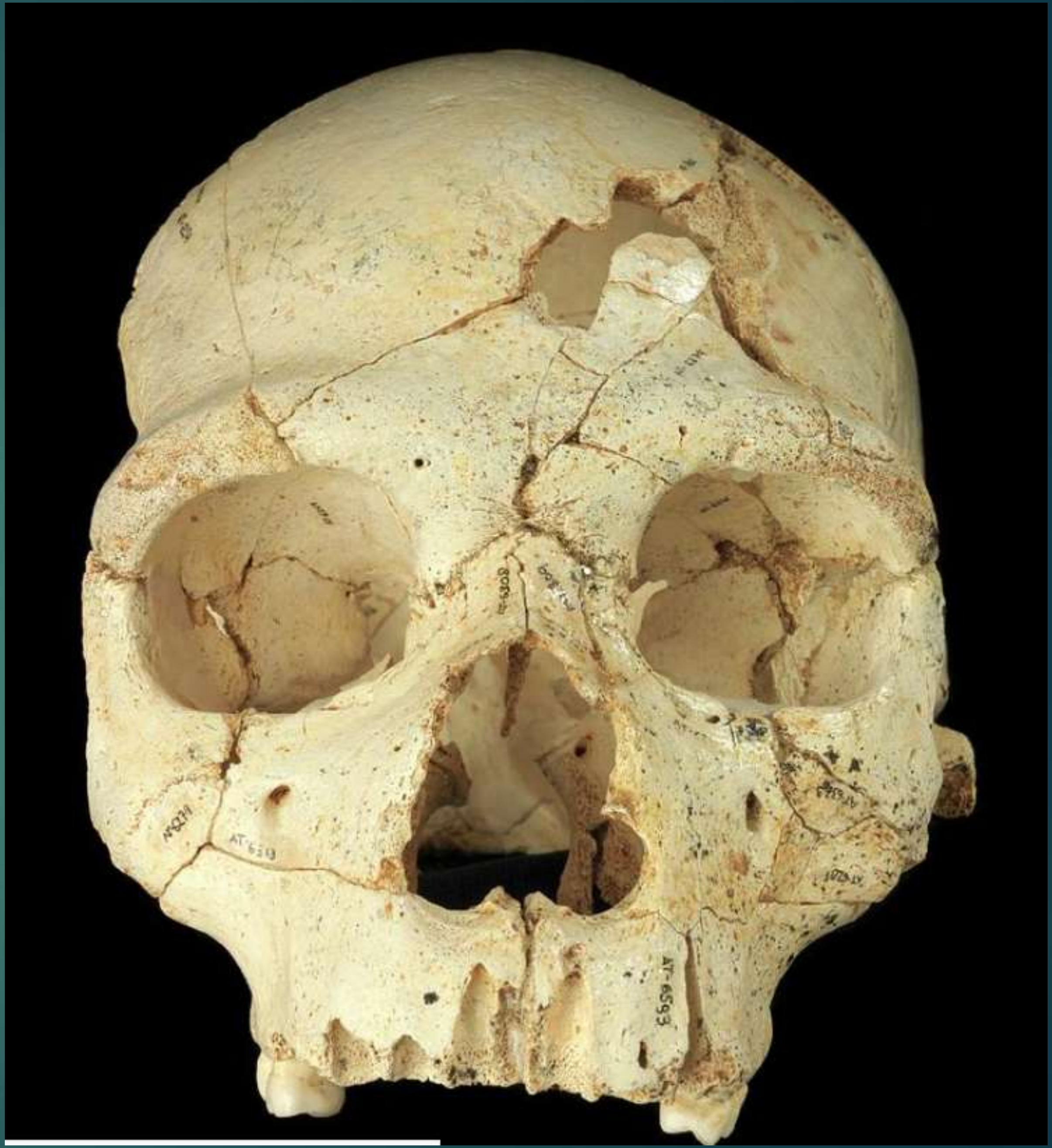
Cranium 13

Cranium 14

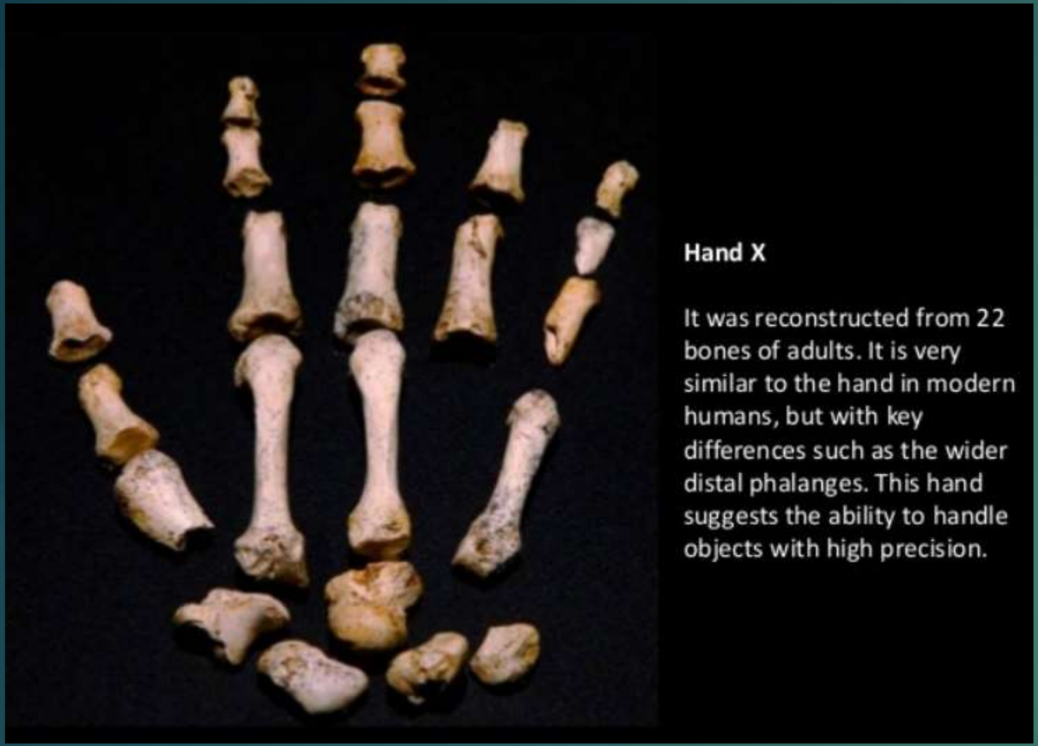
Cranium 15

Cranium 16

Cranium 17



SH hand and foot



Hand X

It was reconstructed from 22 bones of adults. It is very similar to the hand in modern humans, but with key differences such as the wider distal phalanges. This hand suggests the ability to handle objects with high precision.

Foot, nicknamed 'Vicente del Bosque'

It belonged to an adult male who was 1.73 m tall and had a weight of 90 kg. It is the right foot, reconstructed from all the bones found of the ankle, heel and instep of the same individual.

Ear bones

Ear bones: vibration between 3000 to 5000 Hz (similar as human speech)

Neandertal Roots: Sima de los Huesos

- The hominin-bearing layer dates to 430 Ka. SH: 7000 human fossils from at least 28 individuals are represented in a single stratigraphic level

- The sample shows a consistent morphological pattern with derived Neandertal features present in the face and anterior vault, many of which are related to the masticatory apparatus.

- This suggests that facial modification was the first step in the evolution of the Neandertal lineage, pointing to a mosaic pattern of evolution, with different anatomical and functional modules evolving at different rates.

J. L. Arsuaga, et al., 2018

Accretion model

- Theory known as the "accretion model" rests on two hypotheses:
  - Timing of the origin of the Neandertal lineage: Under this model, the Neandertals originated in the Middle Pleistocene, branching off as early as 400 Ka, or even earlier.
  - Pattern of morphological change: full suite of derived Neandertal features did not emerge as a single package, but that different features appeared separately and at different times.
- In particular, Neandertal facial morphology evolved first, followed later by changes in the brain.

Rightmire: Accretion hypothesis of N development

- Gradual accumulation of the derived Neandertal traits in the middle Pleistocene European populations.
- In this framework, *H. heidelbergensis and H. neanderthalensis* are considered to be chronospecies of an exclusively European lineage
- “Accretion” hypothesis: distinctive Neanderthal characters appear first in the facial skeleton.
- Such traces can be identified in the Mauer and Arago remains.
- Ancestors of Neanderthals became increasingly isolated through time as a consequence of colder climate conditions.
- Isolation in this relatively harsh environment led to the full expression of the morphology that distinguishes Neanderthal skulls and postcranial bones from those of other populations.

N Roots: SH dated to 434 Ka

- U-series dating of a cave raft speleothem deposited directly on a hominin cranium (Cranium 4) from LU-6 yielded a minimum mean age of 434 +36/–24 Ka. With this new age, the SH hominins are now the oldest reliably dated hominins & oldest to show clear Neandertal apomorphies (unique derived traits).

- Cranial capacities and encephalization quotient (EQ): The mean of the SH cranial capacities (1232 cc; n = 15) is clearly above the Asian Homo erectus mean. It is also well below the Neandertal and Pleistocene *H. sapiens* means

- Occipital plane exhibits a certain degree of curvature, it is considerably less curved than in Neandertals, and there is no occipital bun.

N Roots: SH

- SH is a mosaic of ancestral and derived features relative to Ns.

- In SH group, the maximum cranial breadth consistently lies in a low position, but the lateral cranial walls are either parallel or slightly convergent superiorly.

- Most of the SH crania show a supraorbital torus that is double-arched and rounded. Similar to Ns.

- Thus, there is an advanced degree of midfacial prognathism in the SH midface, but it is not as inflated, smooth, and retreating as in Neandertals.

- N clade begins with masticatory specialization (facial, dental, and

SH postcranial morphology

- The SH hominins show the following:
  - (i) wide bodies, a plesiomorphic character in the genus Homo
  - (ii) statures that can be found in modern hominin middle-latitude populations that first appeared 1.6–1.5 Ma
  - (iii) large femoral heads in some individuals
-
- Size variation in SH shows that the level of dimorphism was similar to modern humans (MH), but the SH hominins were less encephalized than Neandertals.

- The evolution of the postcranium occurred in a mosaic mode

Disposing of the dead?

Illustration by Mauricio Antón

- Researchers who discovered the Sima fossils speculated that the hominins disposed of these bodies by carrying them over to the cave and then throwing them in.

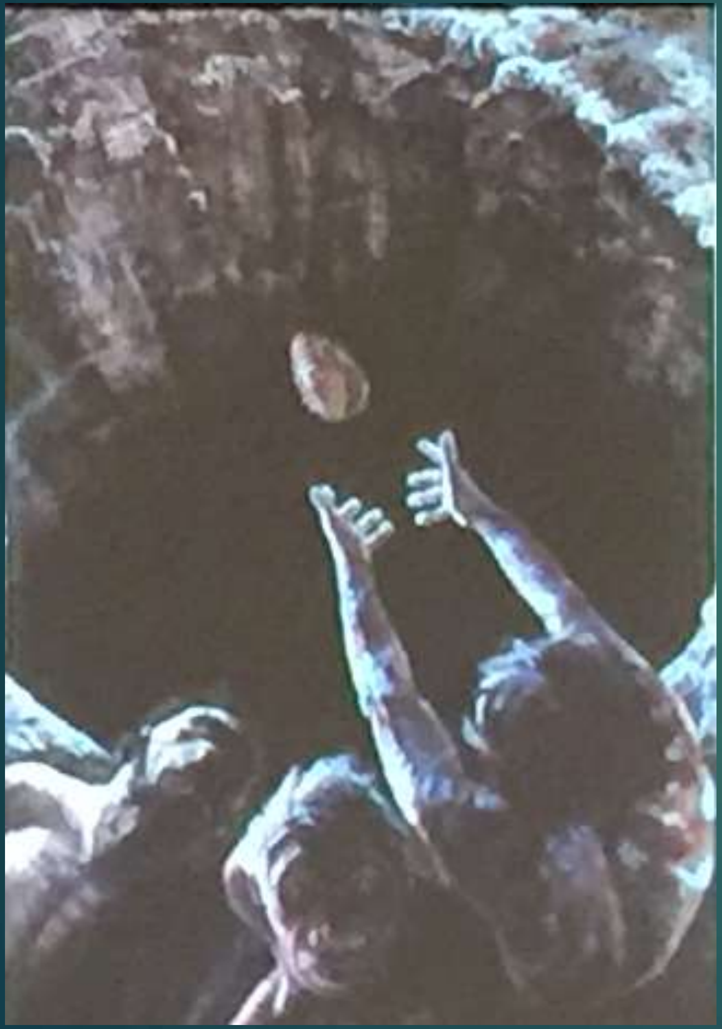
- There is no evidence, however, that this practice was part of a tradition of planned burial.

- The Neanderthals were the first hominins known to engage in such behavior, beginning under 100 Ka.

Sima de los Huesos: a symbolic ritual act?

- Presence of only 1 unused tool
- Postmortem mortuary practice? / body disposal / washed in?
- 1 handaxe: “One handaxe does not a ritual make.” – C. R. Smith

Only 1 stone tool at Sima de los Huesos:



- “Excalibur”
- Only stone tool in cave; considered never used, but…
- Red and green quartzite – uncommon in area

Bones, bones, bones….

Why the Sima de los Huesos Site was not a burial: A Taphonomical Review

- David Rabadà i Vives, 2015: SH has the largest accumulation of human remains from the Middle Paleolithic known to date. It has more than 6500 human remains found in only 4 cubic meters of sediments, representing 28 individuals, representing 80% of the global MP fossil record..

- SH was originated by different taphonomical mechanisms.
  - Competition between *Homo* and other predators for the cavity, accidental death by falling into the pit and a feeding trough for felines and canines while the cave had other entrances, blocked nowadays, explain this fossil association.

David Rabadà i Vives, 2013 & 2015

Taphonomical processes

- Processes:
  - *Homo* was victim of large predators that carried the corpses inside or around the pit.
  - Foxes and other scavengers came later for feeding.
  - The bears fell by accident or died while hibernating there.
  - The water flows in the cave during heavy rainfalls produced dispersion, mixing and abrasion in all these skeletal remains.
  - During all these processes a low sedimentation rate and a continuous supply of corpses produced the observed fossil concentration.

Facts revision

- Traceology studies reveal that the hand axe does not show use-wear traces because there is microscopic erosion on the edges of the hand axe. According to experimental data, this abrasion was produced by sandy sediments. Therefore, this hand axe was a reworked element as the rest of human remains.
- CONCLUSIONS
- According to geological and taphonomical data review this outcrop was originated by different mechanisms than by human burial.
- Competition between *Homo* and other predators for the cavity, accidental death by falling into the pit and a feeding trough for predators while the cave had other entrances blocked nowadays explain this fossil association.
- Furthermore, there had been time differences between bears, humans and others bone remains accumulations events.

Homo heidelbergensis: Middle Pleistocene 780 Ka – 125 Ka

"Archaic" Homo sapiens of the Middle Pleistocene: Homo heidelbergensis

- By 800 Ka, African *H. erectus* were supplanted by or evolved into, a highly variable group of hominins that spread into all of Africa and Europe's ecological niches
- *H. heidelbergensis* is the Hominin during the Middle Pleistocene (780 - 126 Ka)
- Most researchers used the term "archaic *H. sapiens*" until Chris Stringer resurrected the nomen "*H. heidelbergensis*" (type specimen name for the Mauer jaw)
- No DNA yet, except for Sima de los Huesos
- *Homo heidelbergensis: considered as* direct ancestor of:
  - *Homo neanderthalensis,*
  - *Homo denisova*
  - *Homo sapiens*

“Archaic” *Homo sapiens*

- Almost modern-sized brains, but set off as ‘archaic' because of their primitive looking cranial morphology"
- The primary morphological characteristics of archaic *H. sapiens* (Rightmire 2004, 2008) are:
  - 1) average cranial capacity (~1,200 cc) and a proportional increase in **encephalization** that places them between modern *H. sapiens* (~1,350 cc) and *H. erectus* (~1,000 cc);
  - 2) a reduced postorbital constriction, to account for the increase in cranial capacity;
  - 3) the degree of overall cranial robustness somewhere between *H. erectus* and *H. sapiens*;
  - 4) and compared to *H. erectus*, a more rounded and less angled occipital region.
- Few post-cranials have been found; bones suggest cold adaptation in Europe

Homo heidelbergensis

Location: East and South Africa, Europe and Western Asia: Africa (Broken Hill/Kabwe, Bodo, Omo), Europe (Arago, Atapuerca– Sima de los Huesos, Petralona, Schoeningen, Steinheim, Swanscombe), Asia (Dali)

As yet, no *H. heidelbergensis* DNA has been sequenced

Date range: 780 Ka – 130 Ka

Brain size: ~ 950-1390 cc (average 1250 cc) = core feature of species

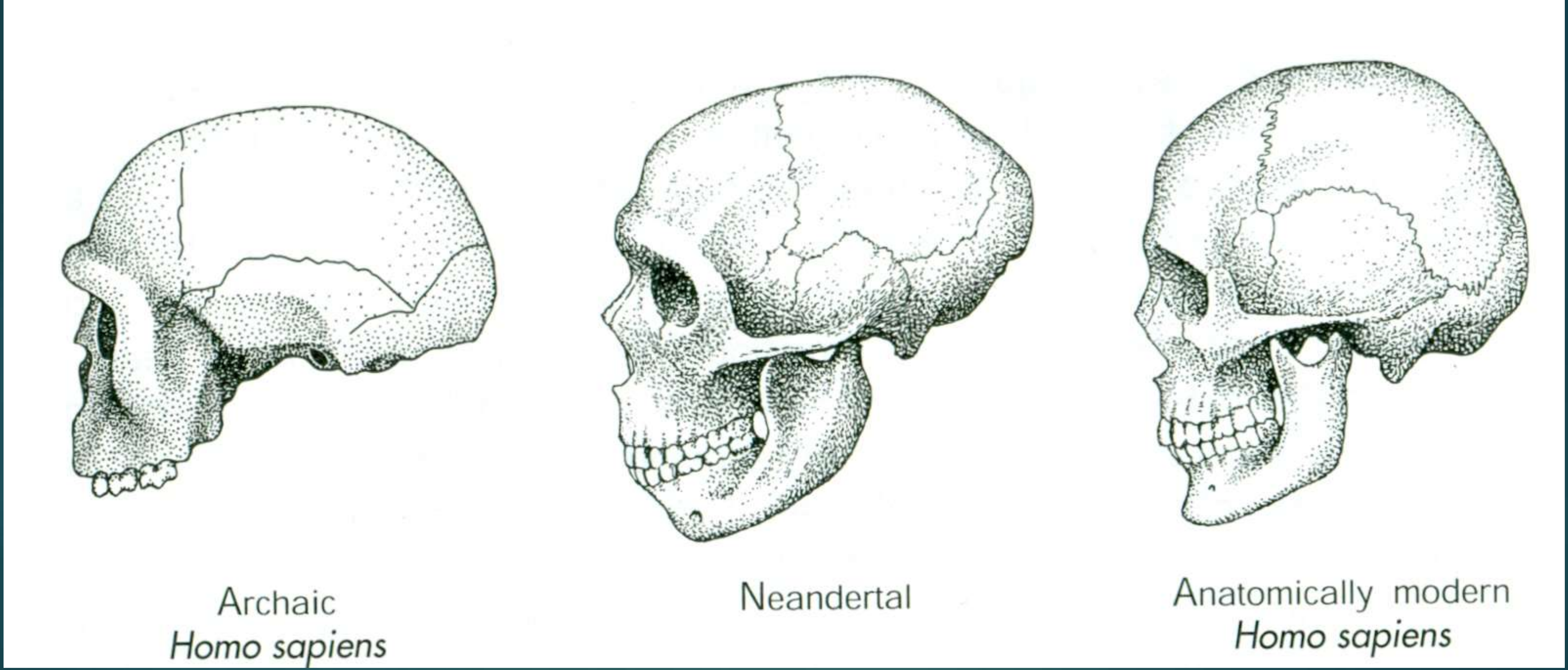
Tool use: Acheulean, Mousterian/Levallois (later in Europe); Oldowan (in Asia)

- First definite controlled use of fire; Definite evidence for hunting

- First species build permanent shelters. Evidence for semi-permanent shelters

Cranial capacity =

1250 cc 1450 cc 1350 cc



Homo heidelbergensis

First Britons: *Homo heidelbergensis* in England, 500 Ka

- At 500 Ka: Evidence of human occupation in at least 13 European locations

- 1985: Boxgrove, England: 500 Ka; best preserved butchery site of this period; elephants & rhinos

Boxgrove: Evidence of a thrown spear in a horse scapula

- Horse scapula with hole, 500 Ka = oldest evidence of hunting
- The semicircular wound on this fragment of a horse shoulder blade was made by a thrown spear, indicating it was killed by early humans.
- Other horse bones from the same site have butchery marks from stone tools. 500,000 years old (England)

Boxgrove, England: Single long, very robust tibia, 362-423 Ka

- 1994: Single long, very robust tibia (lower leg bone): 5’10” to 6’3” & wgt of 200 lbs
- The elevated robusticity of the specimen indicates exceptional shaft strength and/or cold adapted body proportions paralleling those of the Neanderthals. A specific assignment for the Boxgrove tibia is problematic. The tibia can only definitely be assigned to non-modern *Homo* sp., with possible further reference to *Homo heidelbergensis*

Pakefield, Suffolk, England, Stone tools, ~ 650 Ka

The flint tools discovered in Pakefield were evidently crafted from riverside stones and may have been used to cut meat
(Image: Harry Taylor/Natural History Museum)

In 2005, 32 stone tools, made of black flint, and teeth from the same strata as fossils of the water vole *Mimomys savini*, a key dating species, were found in the cliffs at Pakefield near Lowestoft in Suffolk, England.

Pakefield: a lesson in dating – 700 Ka

- 32 flint tools: dated using several methods.
- Younger than 780 K: The magnetic polarity of iron-containing minerals in the sedimentary rocks where the tools were found is aligned north-south, just as it is today. The Earth’s magnetic field underwent a polarity reversal 780 Ka, so the site must be younger than that.
- Older than 450 K: The tools were found beneath glacial deposits laid down during a period 450 Ka when the region was blanketed in ice, so they must be older than this.
- Older than 500 K: Also present were fossils of a water vole *Mimomys*, which was replaced by another vole species called *Arvicola* ~ 650 Ka.

Pakefield: a lesson in dating – 700 Ka

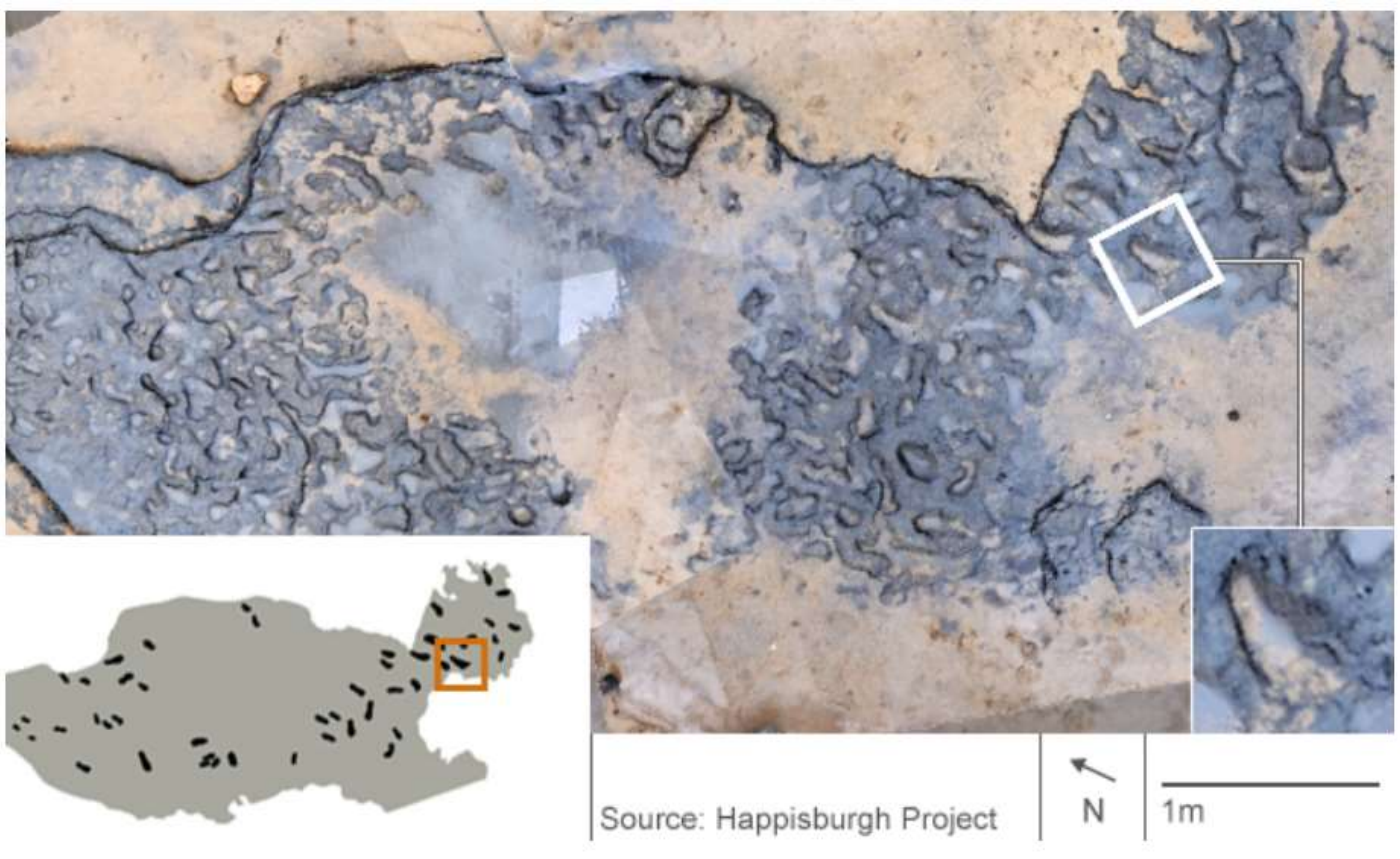
- A new amino-acid dating technique supports this estimate.
- The authors concluded that the tools are dated to ~700 Ka.
- This suggests that hominins existed in England at 700 Ka, when Britain was connected to Europe during warm period;
- Chris Stringer: Either *Homo antecessor* or *Homo heidelbergensis*.

Other early sites: Happisburgh, England, 950 Ka

- Happisburgh, Norfolk, England
  - In 2010, 80 stone tool finds were reported in Happisburgh, Norfolk, England, thought to have been used by *H. antecessor*, suggesting that the early hominin species also lived in England at 950 Ka—the earliest known population of the genus *Homo* in Northern Europe.

  - In 2013, sets of fossilized footprints were discovered in an estuary at Happisburgh. They are thought to date from 800 Ka and are theorized to have been left by a small group of people, including several children and one adult male. The tracks are considered the oldest human footprints outside Africa and the first direct evidence of humans in this time period in the UK or northern Europe, previously known only by their stone tools.

Happisburgh Footprints: now washed away

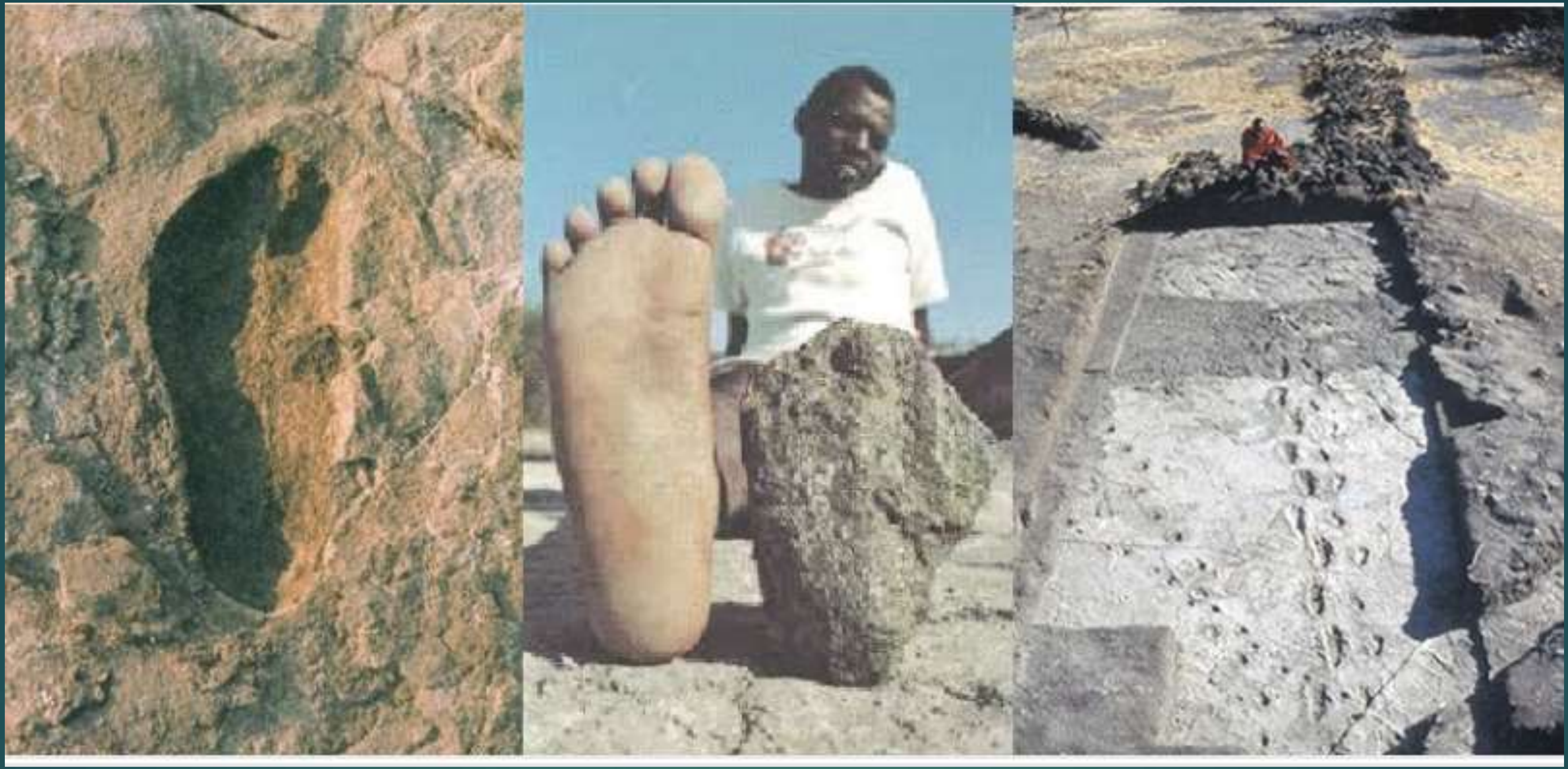


Source: Happisburgh Project

Happisburgh Footprints: 800 Ka, earliest footprints outside Africa

- Shores of Happisburgh, Norfolk, England
- Homo antecessor?
- Now washed away

Footprints: Laetoli, Tanzania. 3.66 Ma, *A. afarensis*



Site G, found in 1978: 70 footprints made by three *Australopithecus afarensis*.

Site S (150 m away from Site G), found in 2015: 14 footprints made by two *Australopithecus afarensis* walking in the same time frame, in the same direction and at a similar moderate speed as the other three. One of them (hominin S1) had an average stature between 161-168 cm.

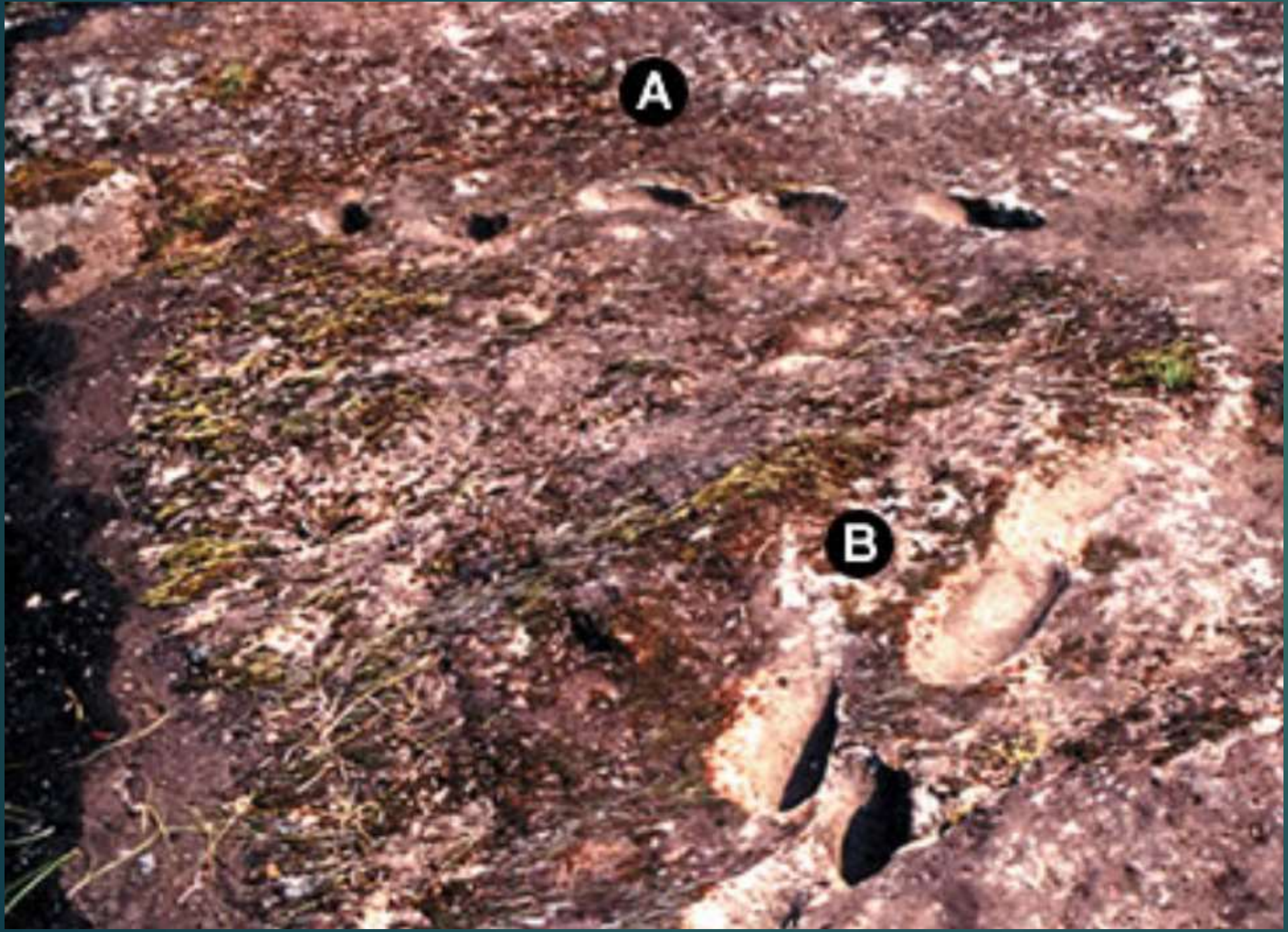
Ileret, Kenya: 1.5 Ma. *H. erectus*

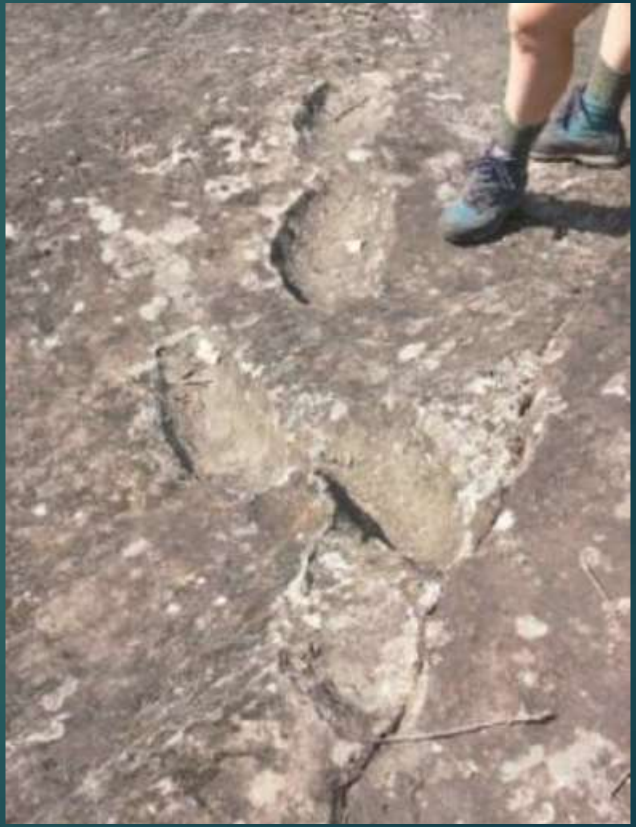
They are 97 footprints left by at least 20 *Homo erectus* individuals, who had a modern foot and stride: a mid-foot arch, straight big toe and heel-to-toe weight transfer. The footprints are indistinguishable from our own.

Margalla Hills, Pakistan. 2 footprints, *Homo erectus*, *1 Ma*

History of footprints: Terra Amata, France footprint, circa 380 Ka

Footprints on 3 tracks, 325-385 Ka, Roccamonfina volcano in southern Italy, 20 cm long and 10 cm wide; *H. heidelbergensis*

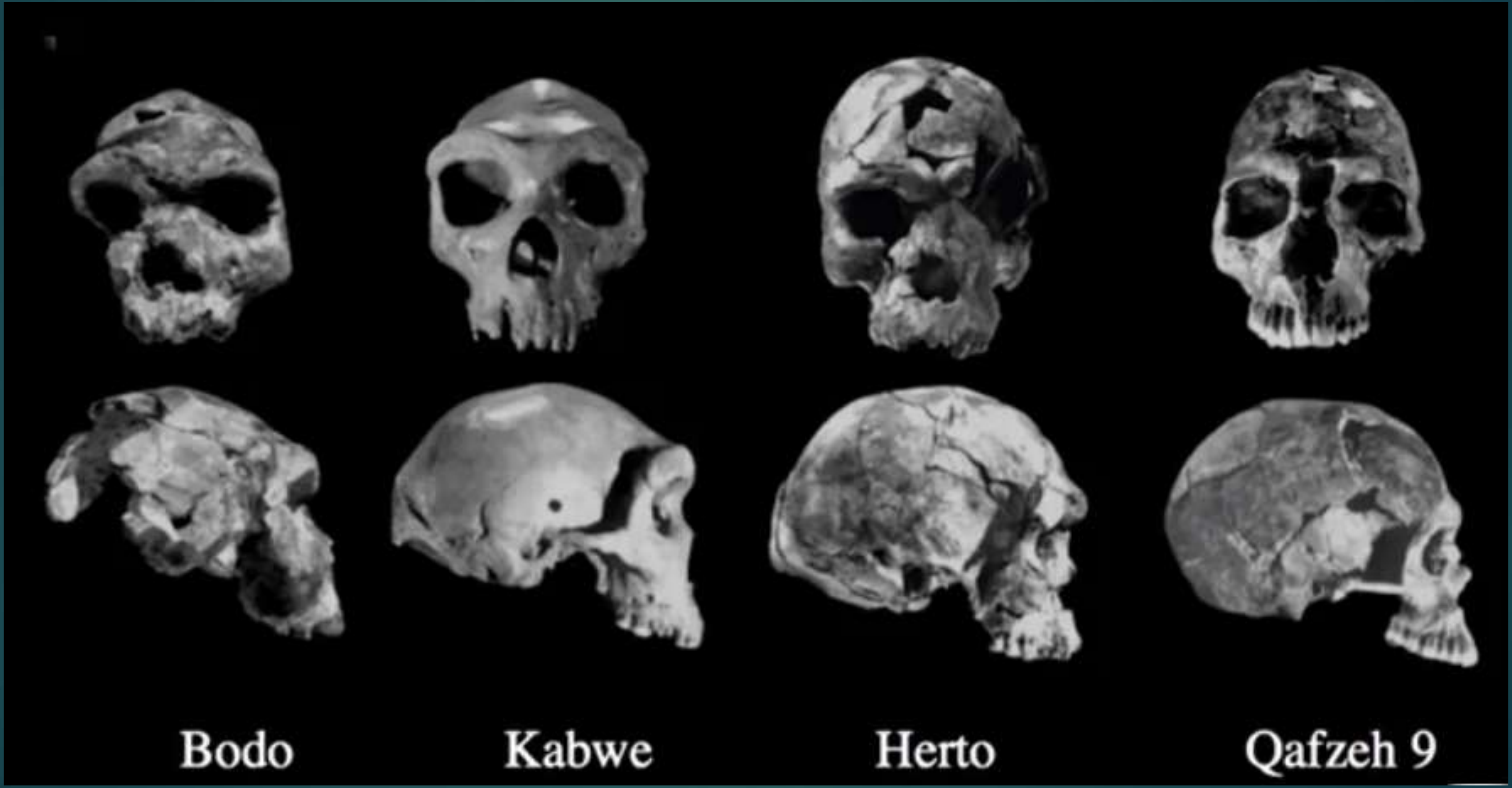




Langebaan Lagoon, South Africa. 117 Ka. *H. sapiens*

Called ‘Eve’s footprint’, because they are the oldest known footprints of an anatomically-modern human. This is very relevant considering that less than 40 hominin fossils from the period 100 to 200 Ka have been found.

Africa: a record of continuity towards a modern appearance within Africa.



Herto & Qafzeh are MHs, more globular cranium

Archaic Hominins: Africa

- African *H. heidelbergensis* group:
    - Kabwe (Broken Hill)
    - Saldanha (Hopefield)
    - Bodo
    - Ndutu
    - Eyasi
    - Turkana region

Middle & Upper Pleistocene sites in Africa

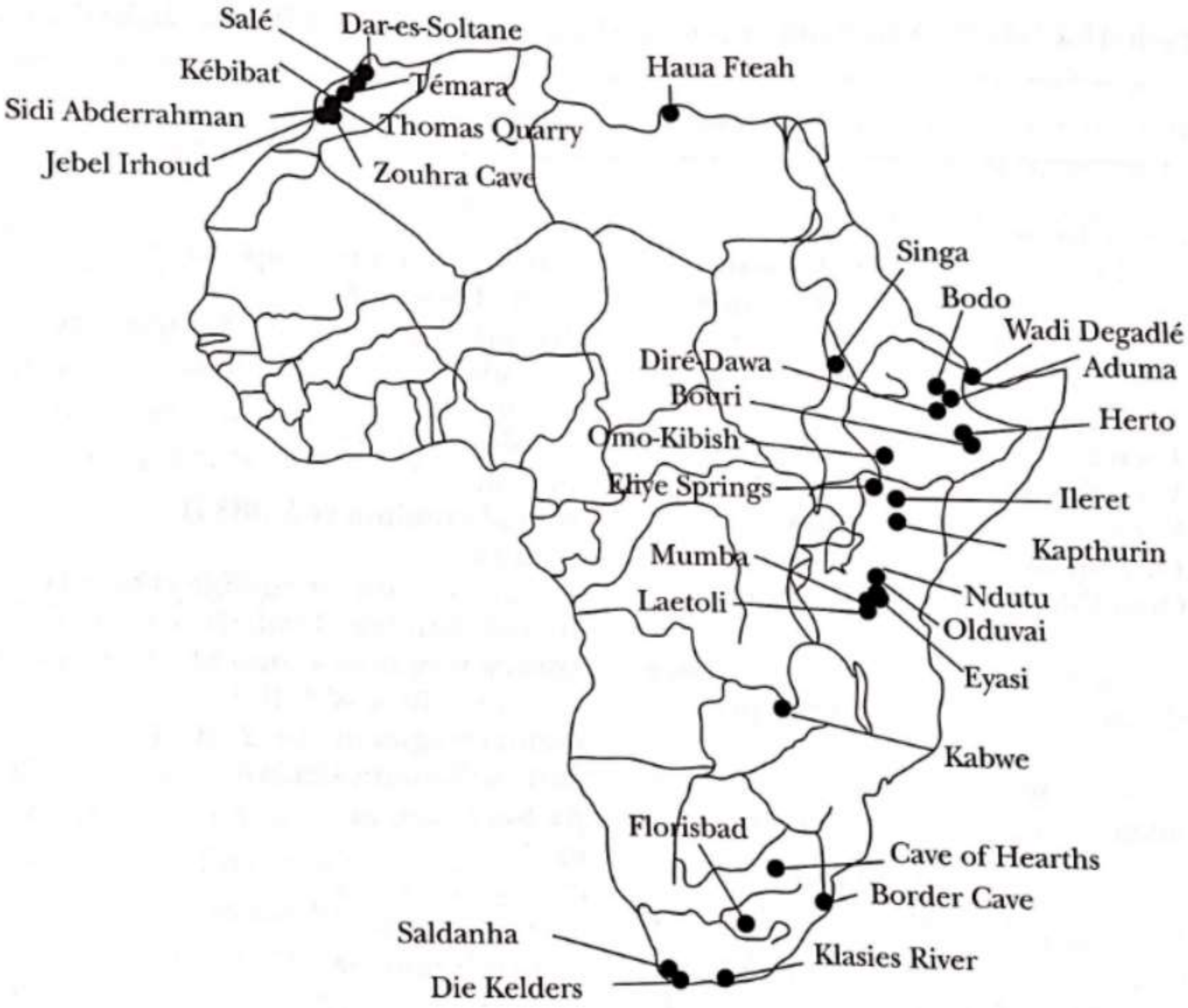


Fig. 11.10. Middle and early late Pleistocene hominin sites in Africa. (From Brauer, 2008.)

G. Conroy & H. Pontzer, 2012

Invention of hafted weapons in Africa

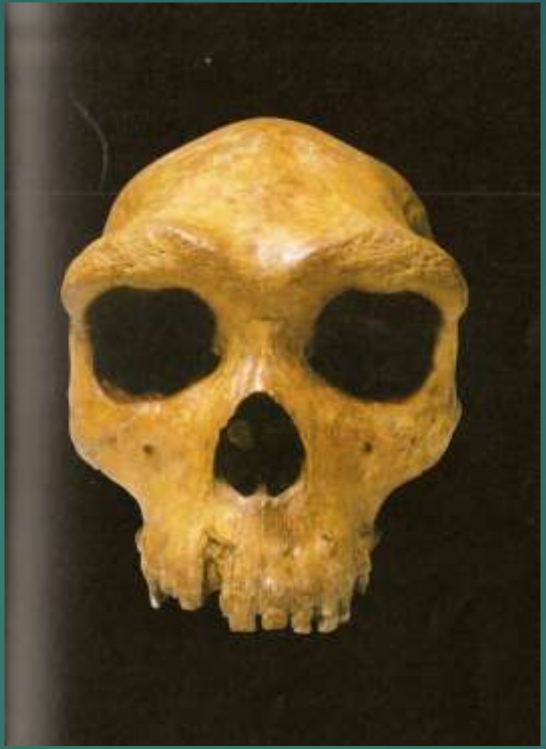
- By 200 Ka, crucial change took place in archaeological record of Africa that related to a major technological breakthrough: the invention of tools with handles by which they could be attached or hafted to pieces of wood for use as spears or knives.

- Disappearance of large Acheulean bifaces and their replacement by assemblages of smaller bifaces and Middle Paleolithic flake technology

1921: BH1 (Rhodesian Man); *Homo heidelbergensis*, (Broken Hill,) Kabwe, Zambia

- The first archaic hominin fossil discovered in Africa

10 cavities, left ear wound



Homo heidelbergensis
(Broken Hill 1)
Discoverer: Tom Zwigelaar
Locality: Kabwe, Zambia
Date 1921
Age: 300 Ka

Tom Zwiglaar
(photo by Aleš Hrdlička)

Kabwe skull

- Once thought to be less than 40,000 years old, the Kabwe skull (also known as the Broken Hill skull) was used at one time to validate the supposed "primitiveness" of African peoples, demonstrating that while Europeans had evolved to the "level" of Cro-Magnon, African populations still looked essentially like *Homo erectus.*
- This assumption was shown to be flawed on many accounts, most crucially in that the date for this site based on the associated animal fossils found is *at least* 300 Ka.
- Some researchers have proposed that Kabwe may be a member of the African population from which all modem humans descended, although this cannot be definitively proven.

‘Kabwe’ or ‘Broken Hill 1’ Homo heidelbergensis skull. Discovered: 1921 in Kabwe (formerly Broken Hill), Zambia. It combines primitive features such as a wide face, thick arching browridges. and a sloping forehead with a large brain capacity of 1280 cc.

Broken Hill cranium: comparatively largest browridges of any known hominin

Figure 3. Facial and lateral views of the Broken Hill cranium. Broken Hill is one of the most complete Middle Pleistocene specimens, here attributed to *Homo heidelbergensis*. Along with increased brain volume, the cranium exhibits features of the nasal region, palate, occiput and base that distinguish it from *Homo erectus*.

Includes ancient features such as prominent browridges and modern features such as a globular-shaped brain case—could represent a transitional step in human evolution circa 300 Ka; Failed DNA attempt in 2016

Fossil Colonialism: Repatriation?

- Soon after its discovery, mining officials sent the Kabwe fossils to the British Museum for study.

- In subsequent years, the skull and other remains stayed in the U.K., and today they reside in London's Natural History Museum. They have never been returned to Zambia.

- There is a replica in the Museum in Livingstone, Zambia.

- Zambia has been trying to get them back for decades, to no avail.

Broken Hill 1: pathology

- The cranium shows evidence of disease and wounds that occurred in the lifetime of this individual.
- Ten of the upper teeth have cavities, and dental abscesses of the upper jaw are clearly visible in the upper photograph (above the right incisor/canine) and the middle photograph (above the first molar).
- Additionally, a partially healed wound on the skull is visible above and anterior of the hole for the ear.
- This wound measured roughly a quarter-inch-across, and was made by either a piercing instrument or the tooth of a carnivore. Exactly which is unclear

- BH1 was originally dated to approximately 700–300 ka, mainly using faunal correlations with other middle Pleistocene sites in southern and eastern Africa (Klein 2009; Millard 2008). New ESR and U-series dating, however, is currently underway; preliminary results suggest that the cranium is younger, dating to approximately 250–300 ka; direct date of 110 Ka for this specimen measured by aspartic acid racemization
- The specimen's *H. erectus, H. sapiens*, or supposed Neandertal1 affinities alternately were highlighted over the next few decades. Recently, BH1 often has been included *in H. heidelbergensis*, where it has formed an important part of the Euro-African hypodigm for this taxon for many researchers

Broken Hill: 1280 cc

Heavy browridges, slightly keeled & constricted frontal bone, short parietals that show little bossing,
acutely flexed occiput with prominent occipital torus, lateral expansion of the mastoid & supramastoid regions,
and extensive paranasal sinus development; severe dental decay; several pathological lesions in left temporal bone

Computerized endocast (1280 cc)

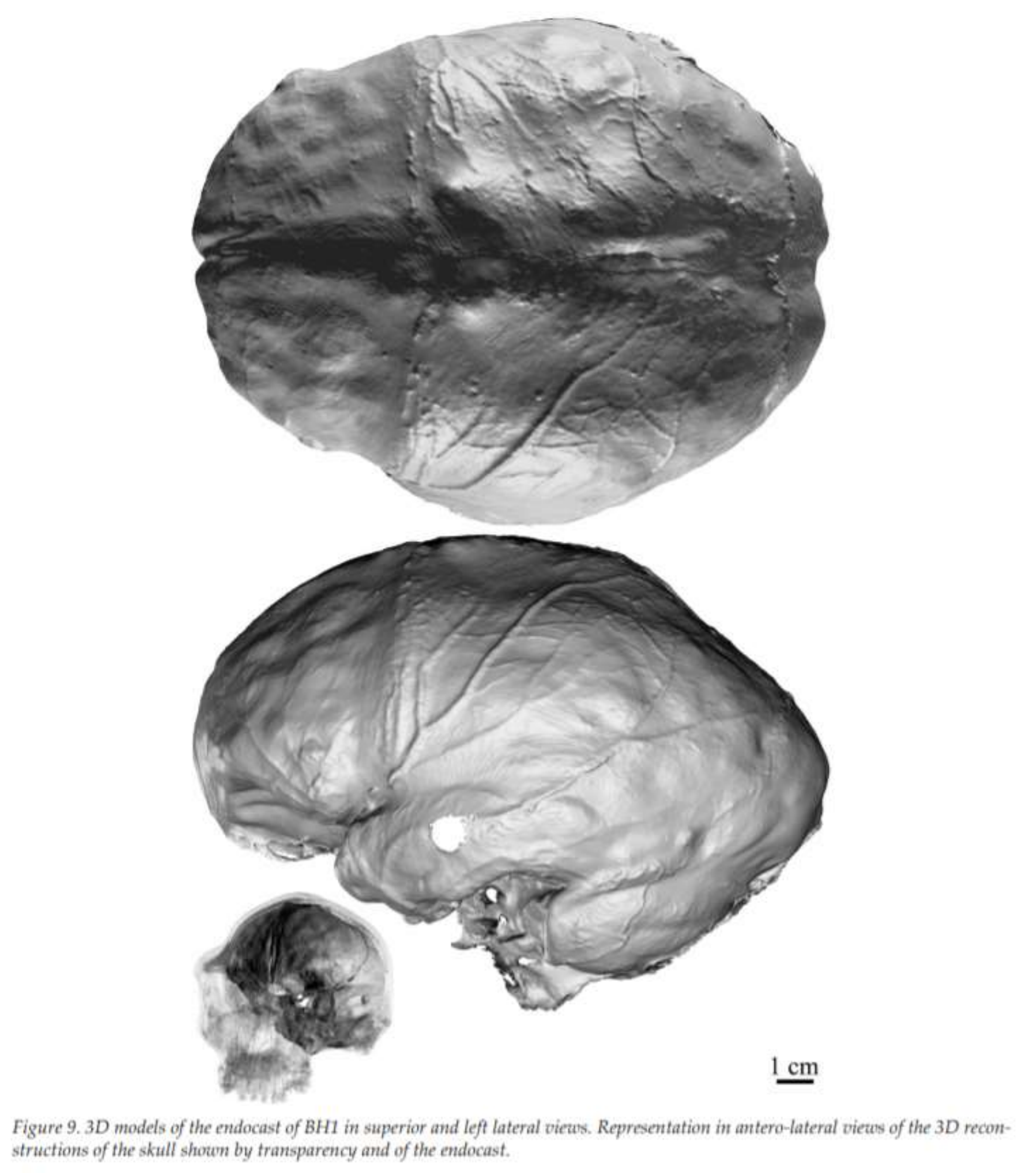


Figure 9. 3D models of the endocast of BH1 in superior and left lateral views. Representation in antero-lateral views of the 3D reconstructions of the skull shown by transparency and of the endocast.

The study of BH1 shows that this relatively large endocast is long and low.

Globally, the morphometric analyses further illustrate that its shape does not display the specific features of either Neandertals or H. sapiens.

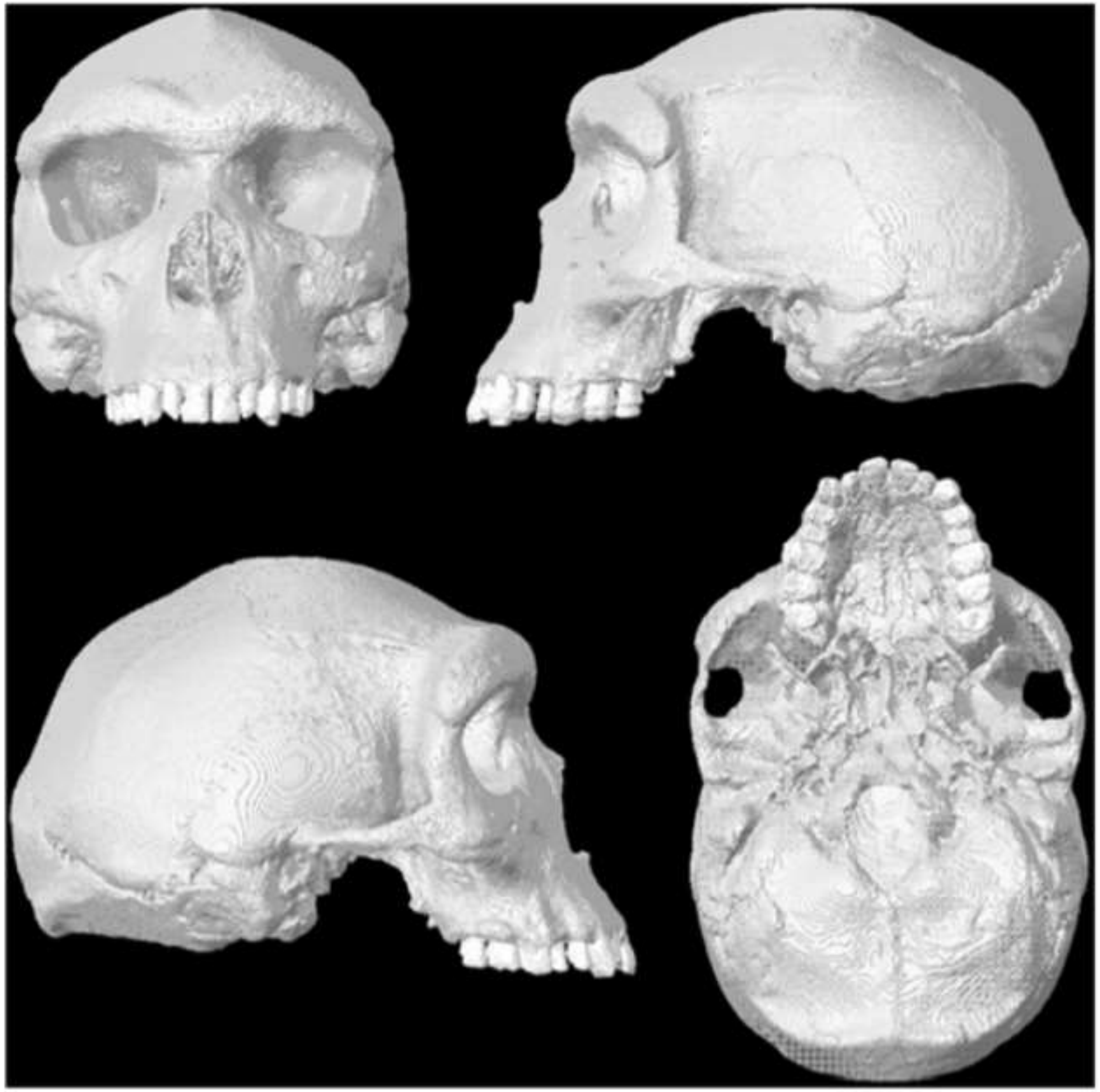


Figure 1. Reconstruction of the Kabwe 1 cranium.

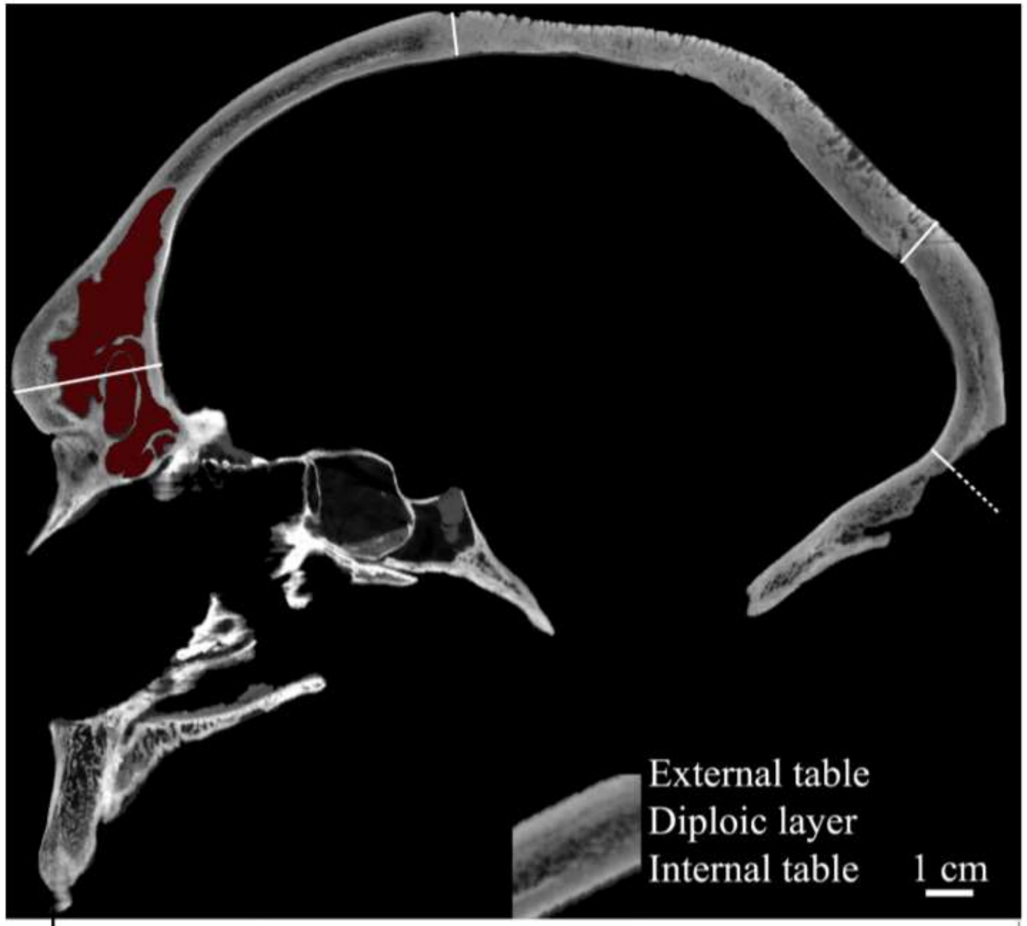


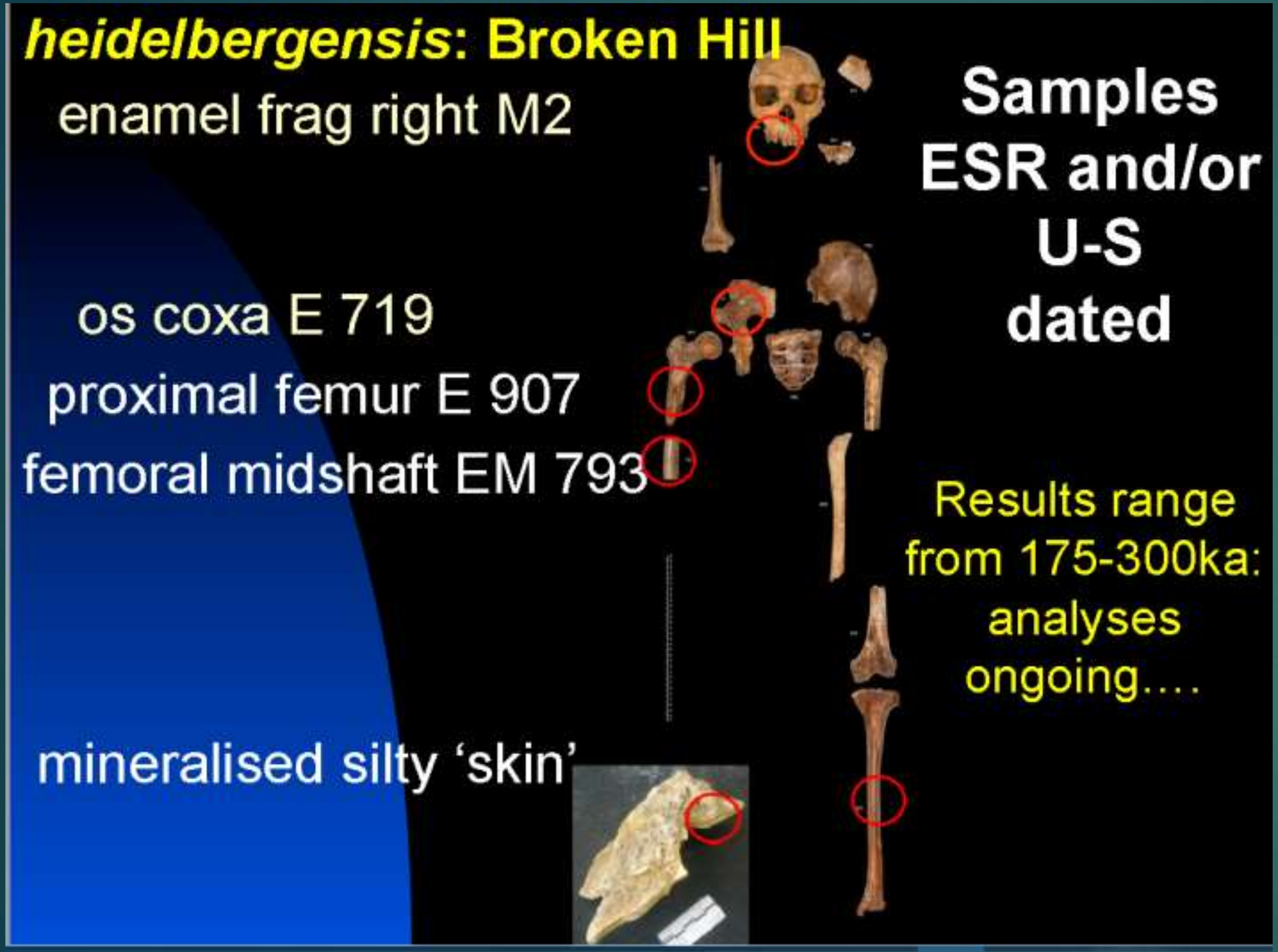
Figure 1. Anterior (A), posterior (P), medial (M), and lateral (L) views of the Broken Hill E691 left tibia.

- In 1921, one of the most complete pre-Late Pleistocene human tibiae was discovered at Broken Hill, Kabwe, Zambia, apparently directly associated with the Broken Hill 1 cranium.

- Currently dated to the middle or earlier Middle Pleistocene, the Broken Hill *E691 tibia* derives from a large Pleistocene individual. There were also 9 other skeletal remains.

- It is the only essentially complete human tibia from the Middle Pleistocene and one of the few known prior to the later Late Pleistocene.

Postcranials at Broken Hill



***heidelbergensis*: Broken Hill**

enamel frag right M2

os coxa E 719

proximal femur E 907

femoral midshaft EM 793

mineralised silty 'skin'

Samples ESR and/or U-S dated

Results range from 175-300ka: analyses ongoing….

- In addition to the cranium, an upper jaw from another individual, a sacrum, a tibia, and two femur fragments were also found

- Femoral fragments lack erectus elongated femoral neck, but have thickened cortical bone on lateral side; tibia has modern rounded anterior crest and posteromedial/lateral angles; otherwise modern postcranially

Bodo, Ethiopia, 1976, *Homo heidelbergensis, 600 Ka, 1250 cc*

Photograph by Donald Johanson.

Photograph by Donald Johanson.

- Discoverers: Alemayhew Asfaw, Paul Whitehead, and Craig Wood

Bodo: *H. heidelbergensis*

Broadest nasal aperture in the human fossil record.

Earliest Evidence of *Homo Heidelbergensis* in Africa: 600 Ka


© Robert Franciscus, University of Iowa

- Very thick cranium; supraorbital ridges are thick, arched, separated by prominent glabellar region
- Unique depth, width, & robustness of zygomatic bone (more than some Ns)
- Less postorbital constriction
- More modern: Cranial capacity = 1250 cc; broadest at parietal area; vertical nose area
- 1981: discovery of *H. erectus*-like parietal bone from 2nd individual at Bodo

Bodo was defleshed

- Associated with Acheulean tools, much later than in other areas (1.7 Ma)
- Cut marks indicate oldest postmortem defleshing of bone
- The skull has 17 cut marks made on fresh bone, suggesting that immediately after the death of this individual stone tools were used to remove the flesh from the bone.

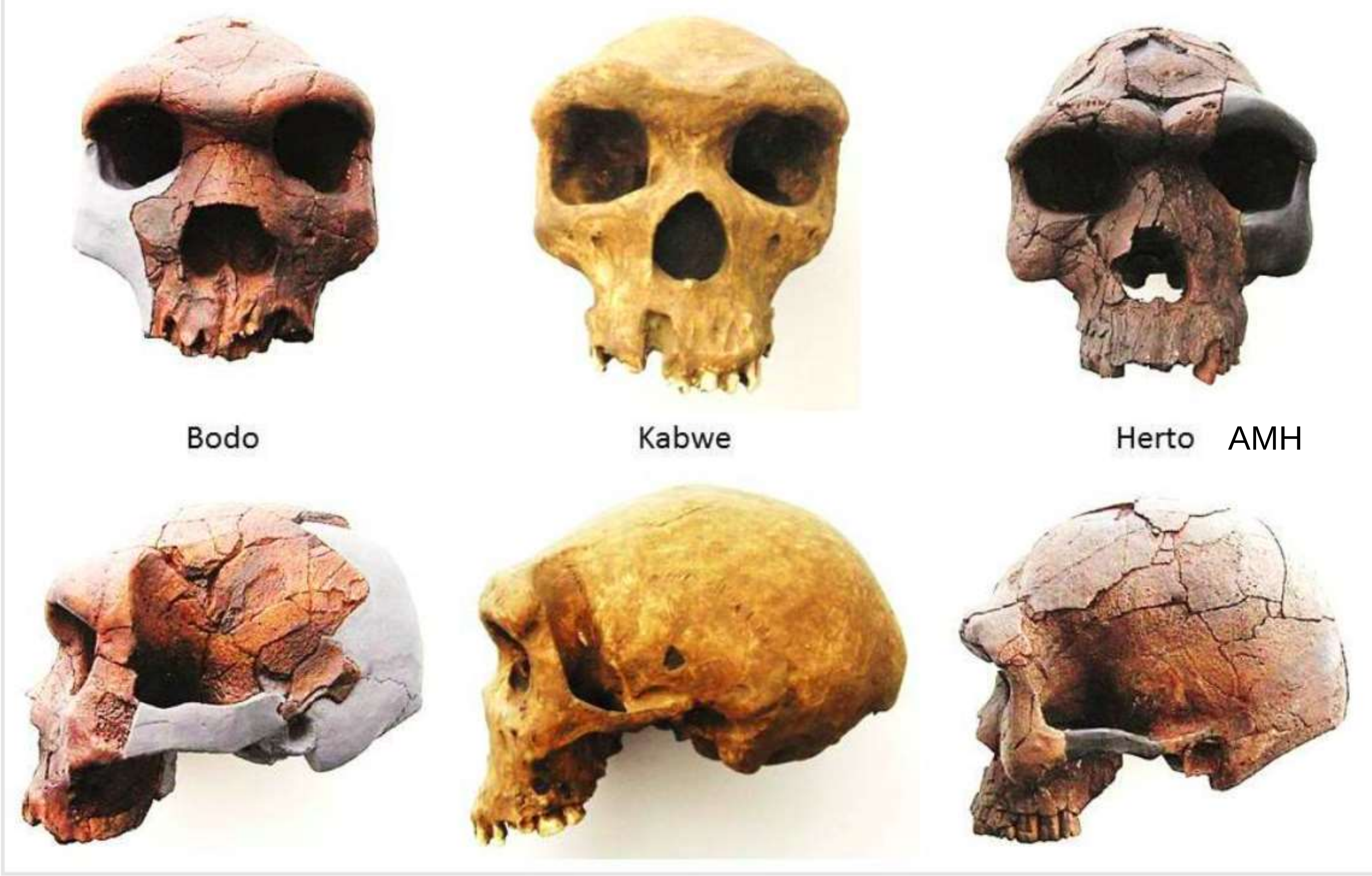


Photo: Roberto Sáez

Bodo

- Bodo is one of the first archaic specimens we can consider closer to *Homo sapiens*, likely an ancestor of the modern human populations that appear in East Africa at 200 Ka.
- Very thick, double-arched supraorbital torus, but interrupted at the glabella.
- Broadest nasal aperture in the human fossil record.
- Projecting and broad middle face below the nasal bones.
- Bodo remains were associated with several hippo skeletons and Acheulean tools.

2017: Gruta da Aroeira, Portugal, Cranium 3, 425-390 Ka

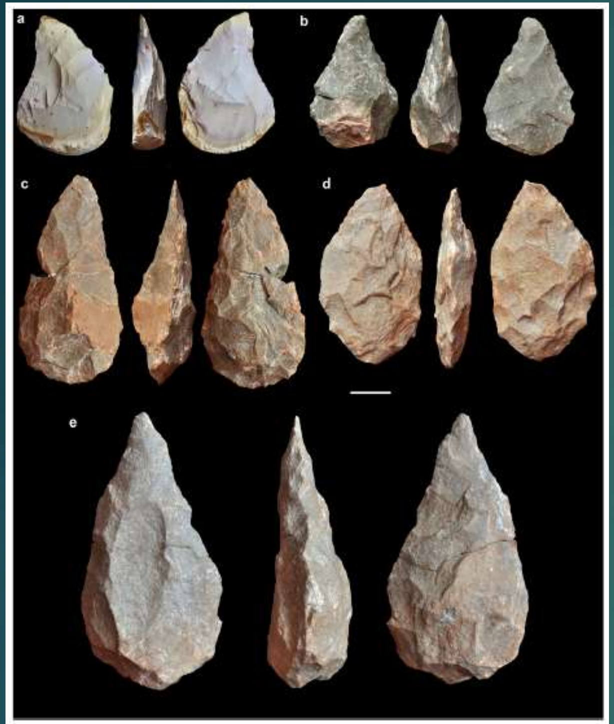


Fig. 52. Acheulean handaxes (bifaces) from level Xb/c. (A) Flint. (B–E) Quartzite.

Cranium 3 was in direct association with abundant faunal remains and stone tools, & with burnt bones suggests a controlled use of fire.

It is the westernmost Middle Pleistocene cranium of Europe; one of the earliest fossils from this region associated with Acheulean tools; reminiscent of the Steinheim specimen

Joan Daura, et al., 2017

Gruta da Aroeira

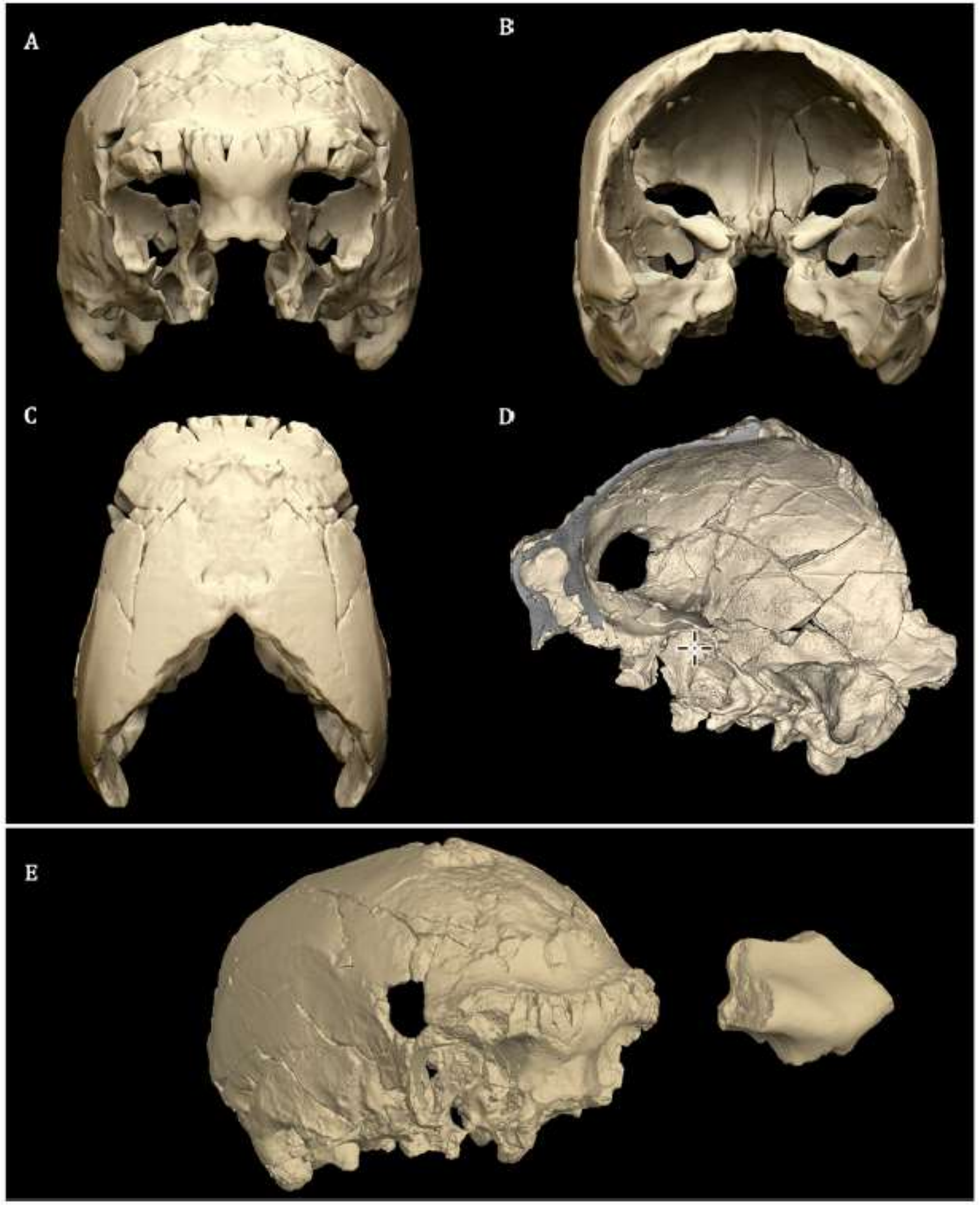
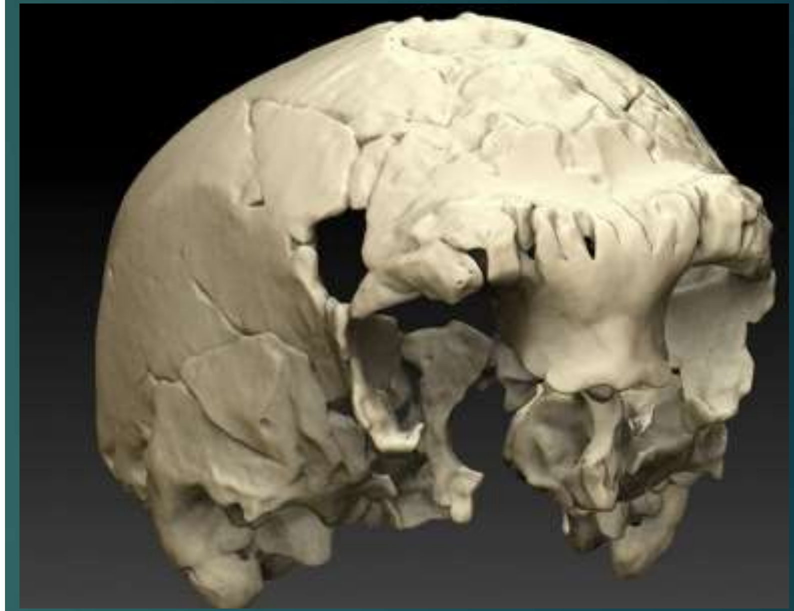


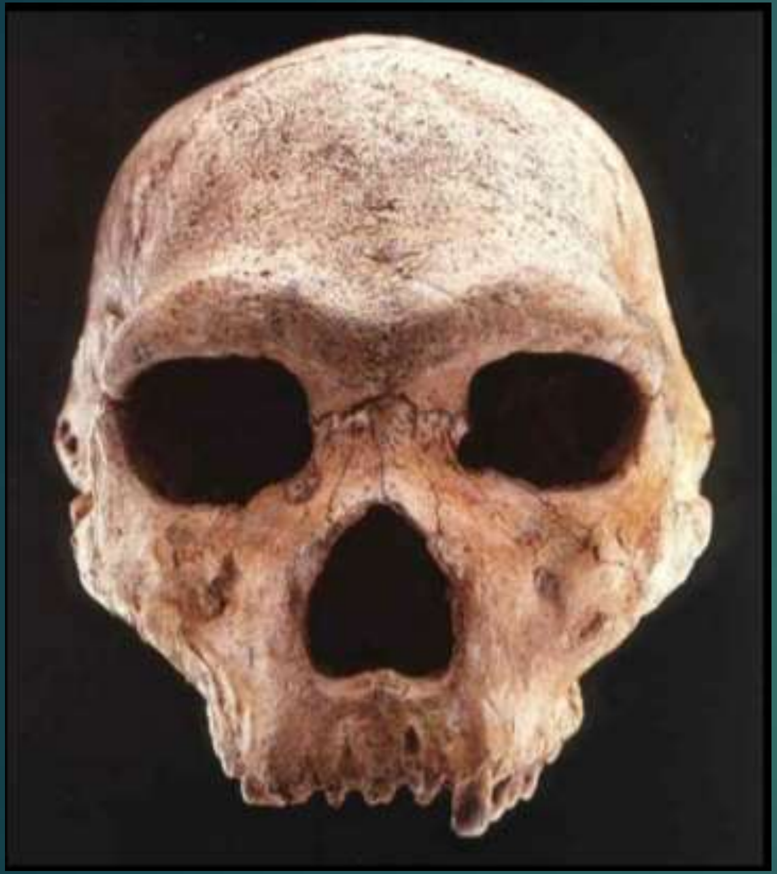
Fig. S5. Virtual reconstruction of the Aroeira 3 cranium in frontal (*A*), posterior (*B*), superior (*C*), and endocranial (*D*) views. The frontal sinus in *D* is exposed in a parasagittal section located 4 mm to the right of the sagittal plane. (*E*) Virtual reconstruction of the Aroeira 3 cranium in a three-quarters view compared with Bilzingsleben B1 (cast).



Bilzingsleben, Germany: 300-414 Ka

- In 1927, naturalist Adolf Spengler found a molar at Bilzingsleben, Germany; quarry reopened in 1969 and fossils found in 1974 & 1977
- 25 cranial fragments, 7 molars, 100 K artifacts (ivory points, wooden staffs, incised objects); remains of at least three individuals
- 2 occipital fragments, 2 frontal bones, 1 parietal
- Stone, bone, antler tools
- Use of fire: burned flint tools, charcoal traces
- *Most H. erectus-like*

1960: *Homo heidelbergensis*: Greece
Petralona skull, 400 Ka



Homo heidelbergensis
(Petralona 1)
Discoverers: J. Malkotsis, J. Stathis, B. Avaramis, C. Sarijanides, & C. St. Hantzarides
Date: 1960
Locality: Katsika Hill, Petralona, Greece
Age 400 K

Notice this older male's worn teeth and huge brow ridges.

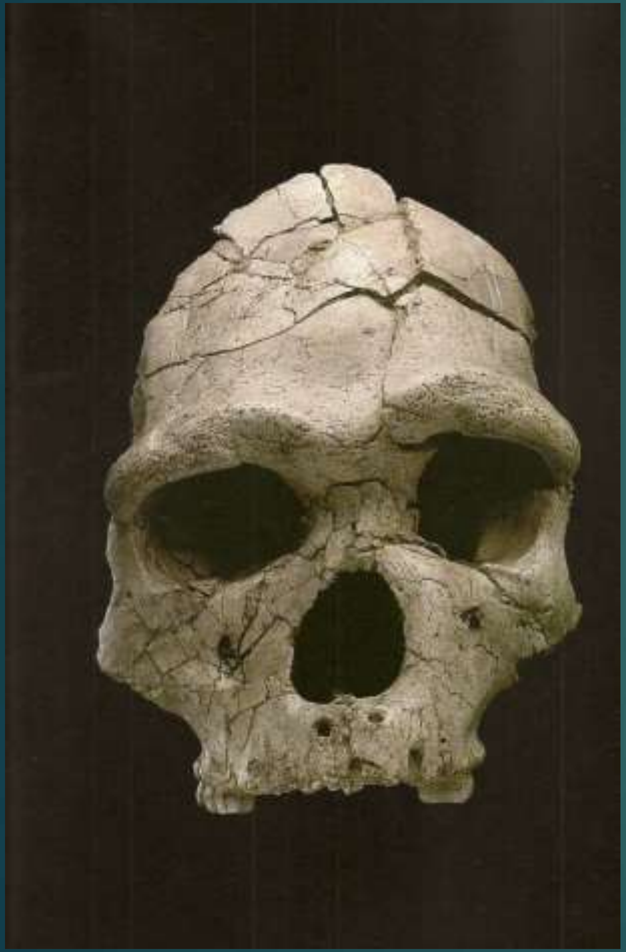
Petralona

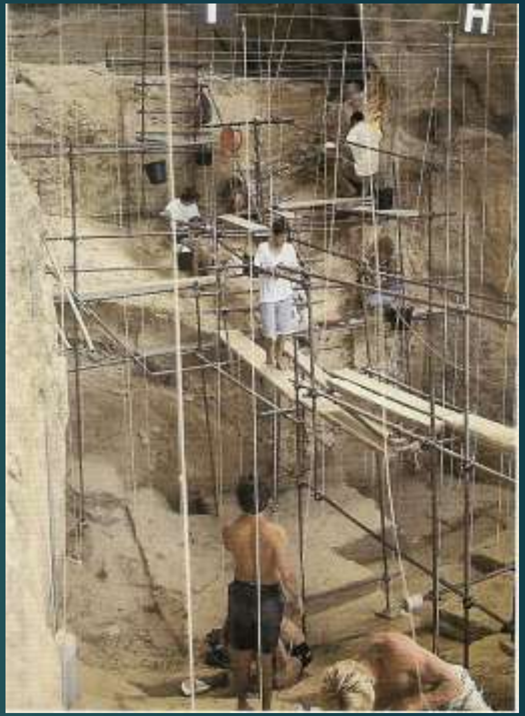
Petralona

- Well preserved cranium; originally encased in pink stalagmite

- Mosaic of *H. erectus & sapiens* features:
  - Primitive: low cranial vault with receding forehead; occipital features and cranial thickness;
  - Derived: cranial capacity of 1220 cc; supraorbitals are massive, but contours are like early *H. sapiens & Neandertals*
  - Skull larger than any *H. erectus*

1964: *Homo heidelbergensis*, Arago 21, France, 320-400 Ka





Arago cave, near
Tautavel, France

Homo heidelbergensis
(Arago 21)
Discoverer: Henry de Lumley
Date: 1964
Locality: Caune de l'Arago
Tautavel, France
Age: 320-400 K
Cranial capacity: 1100 cc

The features of this cranium are most similar to much larger specimens of *Homo heidelbergensis*.

- Cast of Arago 21, a skull and lower jaw discovered in Arago Caves, Tautavel, France.

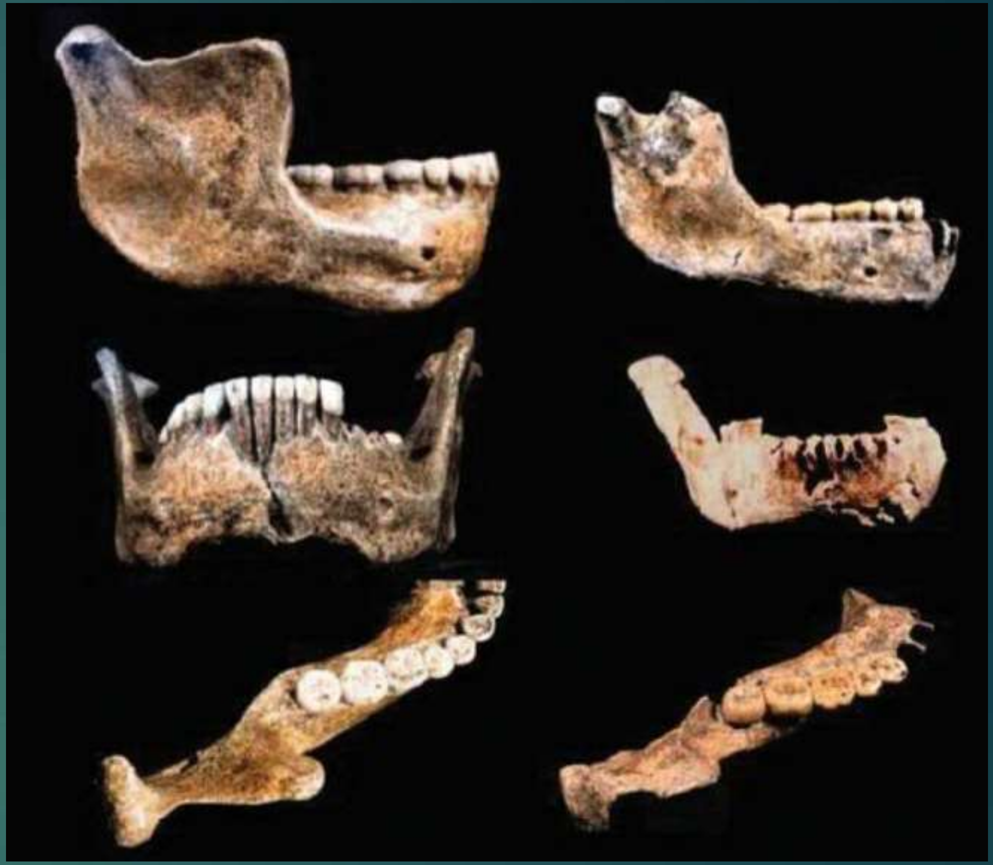
- Thousands of stone tools and the bones of many types of animals have also been uncovered at this site.

- The Arago 21 skull is relatively complete but it was distorted either before or during fossilization. Its features are typical of this species but its size and robust facial features suggest that it is the skull of a female or young male.

Arago, France

- Cranial & postcranial remains of 4 adults & 3 children: 2 mandibles, distorted face (Arago 21); associated cranial bones; and part of left pelvis
- Arago 21 cranium: thick supraorbital tori separated from long, flat frontal bone by deep supratoral sulcus; low rectangular orbits; broad, blat midfacial region; prognathism; occipital has true angular torus
- Cranial capacity of 1100 cc
- Tools: stone, bone, antler, wooden

Argo II & XXIII



Mauer Mandible vs. Arago 13 Mandible

A female older than forty (Arago II), This skull shows a mixture of features of H. heidelbergensis and *Homo erectus*, to which it is sometimes assigned. It consists of a fairly complete face, with five molars and part of the brain case.

Ceprano, Italy: 487 Ka, 1185 cc

Site: Ceprano, Italy
Year of Discovery: 1994
Discovered by: Italo Biddittu
Age: Original dating - 487 Ka
Species: *Homo heidelbergensis*

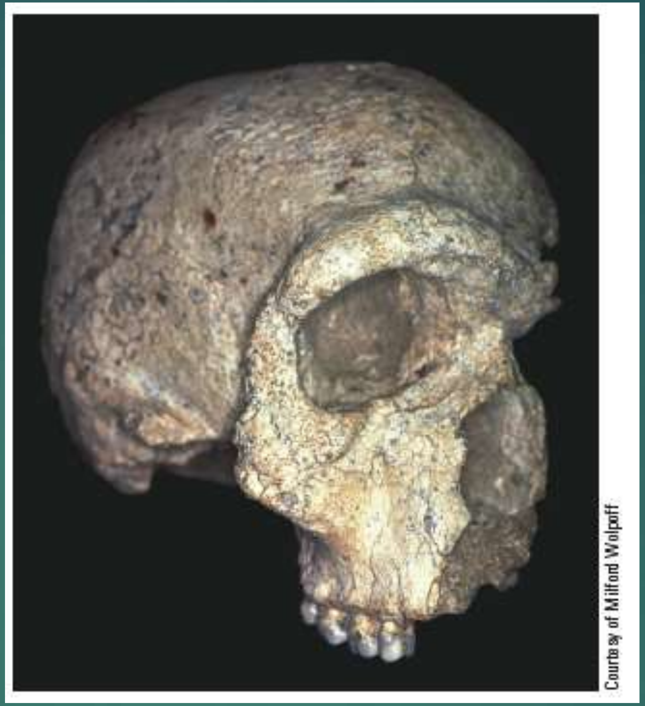
Homo erectus or heidelbergensis?

- Low cranial vault, flattened receding forehead; massive shelf-like supraorbital ridges; angle between occipital & nuchal planes; cranium has large breadth relative to length
- Difference from *H. erectus*: shorter cranial vault, thicker cranial bones, more massive & double arched supraorbital torus, larger cranial capacity; widest near temporal squama; no frontal keeling
- Cranial capacity: 1185 cc
- Oldowan tools

Ceprano

- The peculiar morphology of the Ceprano calvarium has no equivalent in Europe or elsewhere and its taxonomic status has been so far controversial, being alternatively viewed as
  - a "late" *H. erectus*,
  - a possible adult individual of *H. antecessor*,
  - or the holotype of a new species named *H. cepranensis*.
- Ceprano is a possible representative of an ancestral stock of *H. heidelbergensis*

1933: Steinheim skull, 250-350 Ka



Courtesy of Milford Wolpoff

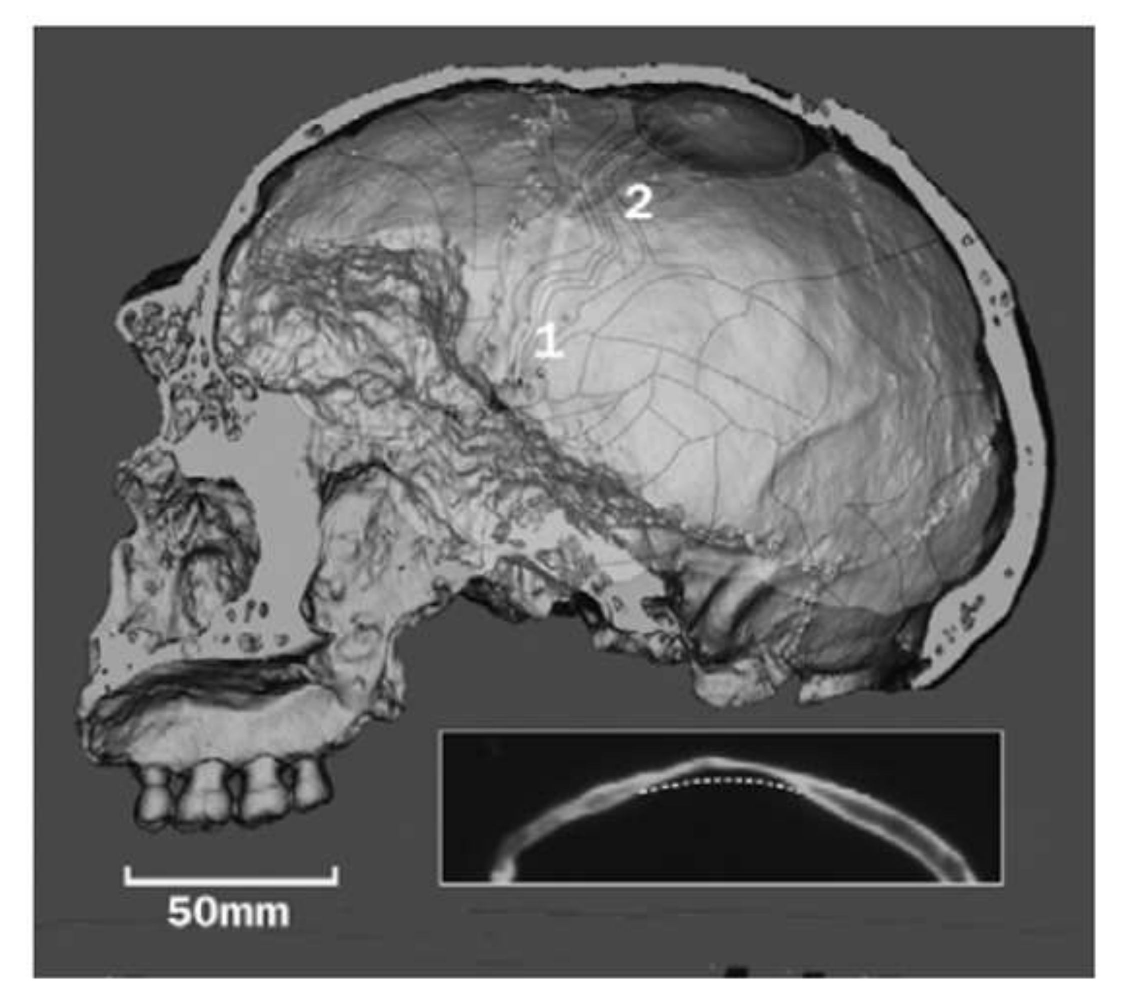
Homo heidelbergensis
(Steinheim)
Discoverer: Karl Sigrist, Jr.
Date: 1933
Locality: Sigrist gravel pit, Steinheim Germany
Age: 250-350 K
Cranial capacity: 1100 cc

Steinheim, 1140 cc

Cast of a skull discovered in 1933 in Steinheim, Germany. It dates to ~ 250 Ka.

The cranium, however, is Neanderthal-like as it is very rounded at the rear and has a slight depression in the occipital bone at the back of the skull. Suprainiac fossa present; C. Stringer = N

Homo heidelbergensis: Steinheim:
First evidence of a brain meningioma



- Age: 250-350 Ka
- Cranial capacity: 1100 cc

- The owner of the skull suffered from a brain meningioma (evidenced by a depressed area of the parietal bone; a classic sign for a meningioma).

- It is the earliest evidence of a meningioma tumor on record. The tumor did not produce loss of skull on right side.

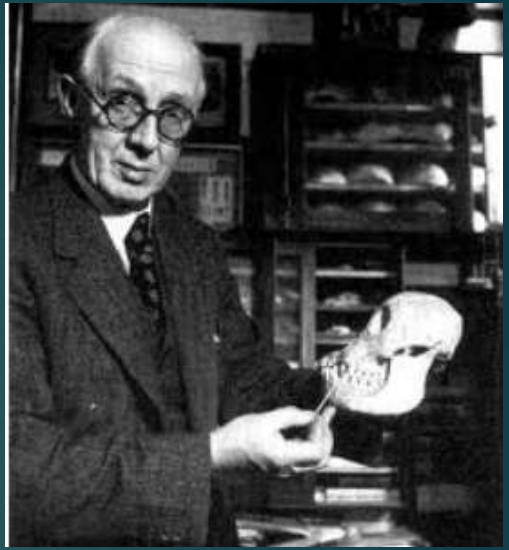
1935: *Homo heidelbergensis*, Swanscombe, England, 400 Ka

- Occipital is rounded; lack the marked angulation between occipital & nuchal planes seen in *H. erectus* crania
- Parietals are thick
- Horizontal oval-shape depression on occipital bone (suprainiac fossa); a distinctive N like feature; oldest skull to show such a feature; Stringer thinks = N
- Cranial capacity = ~1325 cc

Oldest human remains in Europe directly associated with Acheulean tools (400 Ka)

Alvin T. Marston (1889-1971):

Homo heidelbergensis at Swanscombe



- English dentist
- 1935: Found the Swanscombe occipital (1935) and left (1936) and 26 Acheulean tools in the Barnfield Pit, Kent
- 1955: right parietal of the skull found
- Got Oakley to use fluorine dating on it: 400K; and to test Piltdown specimens

“This may hurt, but I am afraid I’ll have to remove the whole jaw!” (Punch)

Swanscombe in England, 1935, 1936 & 1955

1935: Original fossil was complete occipital bone;

1936: left parietal bone

Occipital is more Neandertal; no browridge found

1955: right parietal discovered

Reilingen, Germany, 200 Ka, 1429 cc

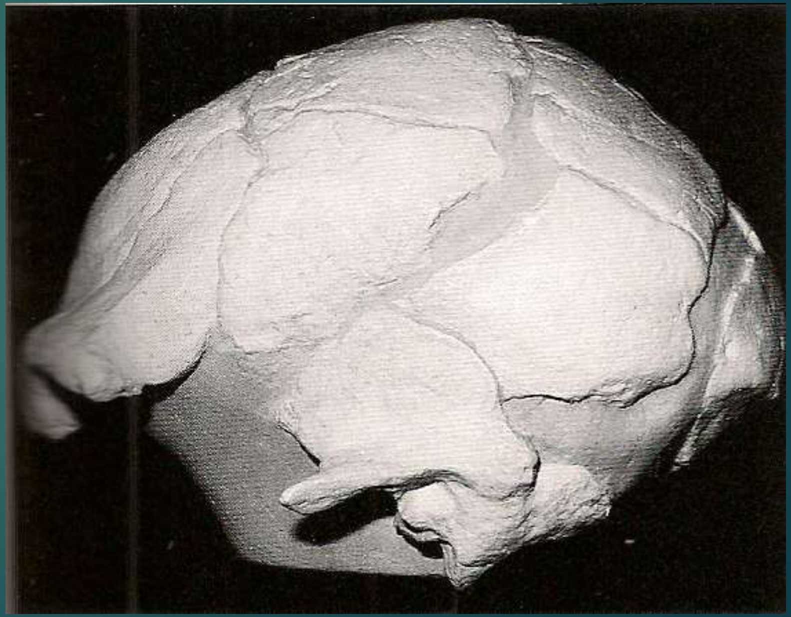
- Discovered in 1978; dated at >200 Ka
- Both parietals, most of R temporal, and much of occipital
- Archaic hominin features: Max cranial breadth at supramastoid crests; presence of angular torus; shortened squamous temporal, strong mastoid
- N-like features: presence of suprainiac fossa, protuberant occipital torus; lambdoid flattening
- Cranial estimate: 1429 cc
- Tattersall: *H. heidelbergensis* with N features; Arsuaga 1 of first true N; Papagianni: N via cranial capacity

David Dean, J. Hublin, et al., 1998

I. Tattersall, 2011

- Two European groups in Middle Pleistocene:
  - Neanderthal predecessors: Sima de los Huesos, Steinheim, Reilingen: became Neandertals in UP
  - *Homo heidelbergensis* group: died out in Europe

Ehringsdorf, Germany



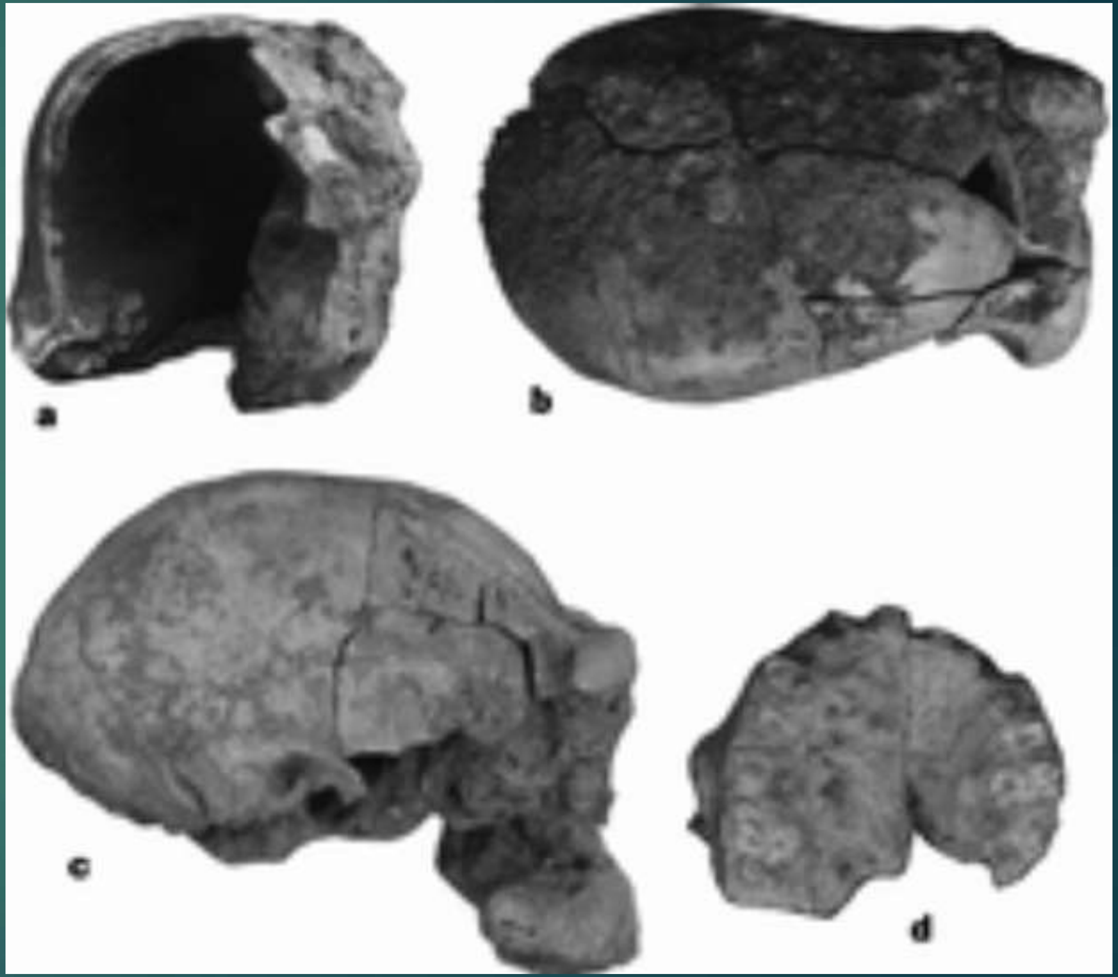
Weidenreich, 1929

- 9 hominins
- Discovered 1908 and 1925
- 186-245 Ka
- N like size of the brow ridges, the long and low brain case, and the strong lower jaw lacking a chin
- Rounded occipital, high skull & forehead, large brain
- Weidenreich considered it Neandertal;

  now *H. heidelbergensis*

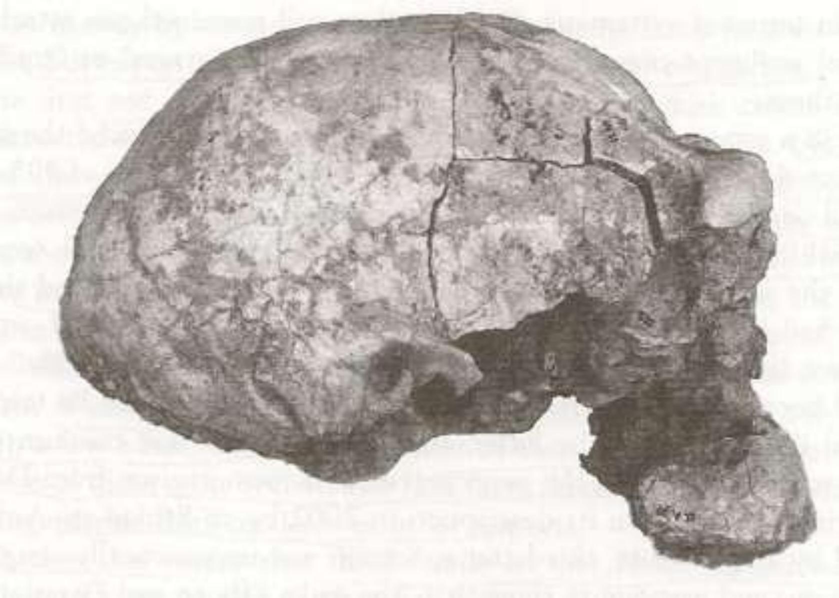
Buia, Eritrea: UA 31: 1 Ma, 750-800 cc, large Parietals

- Northern Danakil (Afar) Depression, Eritrea, Africa
- The skull is long and oval, pointed at the back, and has massive browridges, all features characteristic of *Homo erectus*, as is the small brain capacity.
- Where the skull differs from *erectus* is in the parietal bones, which form the curved sides and top of the skull. They are much wider at the top than those of *H. erectus* and are typical of *Homo sapiens*.
- Conroy (1980) believes it is *H. heidelbergensis*); but also notes that some sapiens like features had begun to evolve in Africa by about 1.0 Ma



Buia, Eritrea: UA 31

Buia, Eritrea



Ndutu, Tanzania, 350 Ka

- **Ndutu**
- **Site:** Lake Ndutu, Tanzania
- **Year of Discovery:** 1973
- **Discovered by:** A team led by A. A. Mturi
- **Age:** ~ 350 Ka
- **Species:** *Homo heidelbergensis*

- Found with stone tools
- *H. erectus*-like in contour and form of occipital with thickened nuchal torus, size of mastoid region, inferred size of supraorbital torus, great thickness of cranial bones

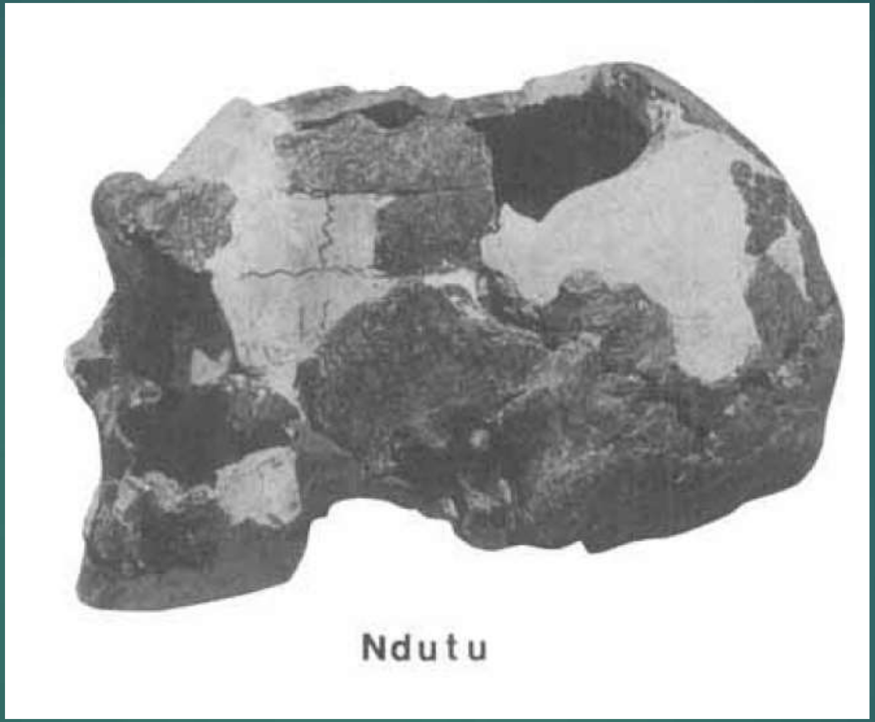
- Like MHs in greatest width high up on parietal region, pronounced parietal bosses, more vertical sides of cranial vault, presence of ossified styloid process, absence of sagittal keel, presence of raised articular tubercle

- Cranial capacity = 1100 cc

Ndutu, Tanzania: 500-300 Ka, 1,100 cc

Lake Ndutu in northern Tanzania

1973, A. A. Mturi
Clark Reconstructed
Rightmire: archaic *Homo sapiens* found in Africa



Eyasi Lake, Tanzania, 132 Ka, 1250 cc

. The hominid frontal bone (EH06) from superior (a), basilar (endocranial) (b), anterior (c), partial lateral (d), and lateral (e) views.

- Lake Eyasi, Tanzania, near Olduvai Gorge
- Discovery: 1934-1940, German Ludwig Kohl-Larsen Expedition; originally thought to be *H. erectus*
- 250 small pieces; few fit together
- Now classified as *H. heidelbergensis*
- Lacks *erectus*-like continuous occipital torus, supraorbital torus, postorbital constriction
- Has widest breadth high on parietals, less thick cranial bones
- Cranial capacity = 1250 cc
- Date = 88 to 132 Ka

M. Domınguez-Rodrigo, et al., 2008

Florisbad, South Africa: 259 Ka, 1,400 cc

Site: Florisbad, Republic of South Africa
Year of Discovery: 1932
Discovered by: Prof. T.F. Dreyer
Age: About 259 Ka
Species: *Homo heidelbergensis*

Frontal & Parietal pieces, incomplete right side of face; Low, broad prognathous face; rectangular orbits; flattened nasal bridge; rounded projecting browridges; rounded forehead

A very important Middle Stone age sample presents a mix of modern and ancient features. Whether Florisbad should be classified as *Homo heidelbergensis* or *Homo helmei* has been a subject of prolonged debate.

But with the anatomical features observed in 315 Ka Jebel Irhoud specimen, Florisbad skull can be more securely described as an early *Homo sapiens* form.

Florisbad debate

- The difficulty of placing the fossil in either *H. heidelbergensis* or *H. sapiens* have prompted McBrearty and Brooks (2000) to revive the designation *H. helmei*.
- In 2016 Chris Stringer argued that the Florisbad Skull, along with the Jebel Irhoud and Eliye Springs specimens, belong to an archaic or "early" form of *Homo sapiens*.
- The Florisbad Skull was also classified as *Homo sapiens* by Hublin et al. (in 2017), in part on the basis of the similar Jebel Irhoud finds from Morocco.
- Scerri et al. (2018) adduce the fossil as evidence for "African multiregionalism", the view of a complex speciation of *H. sapiens* widely dispersed across Africa, with substantial hybridization between H. sapiens and more divergent hominins in different regions.
- Lahr and Mounier (2019) also classify the Florisbad Skull as an example of early *H. sapiens*, which they suggest arose between 350,000 and 260,000 years ago from the merging of populations in East and South Africa.

Saldanha (Elandsfontein)
South Africa, 500 Ka

Found with Acheulean tools;
low receding forehead; large supraorbital tori;
Supratoral groove; thickened cranial bone; prominent
Occipital crest; mandible (460m away) has broad ramus;

- **Site:** Elandsfontein, Republic of South Africa
- **Year of Discovery:** 1953; 30 pieces
- **Discovered by:** Keith Jolly
- **Age:** Between 500 to 200 Ka
- **Species:** *Homo heidelbergensis*

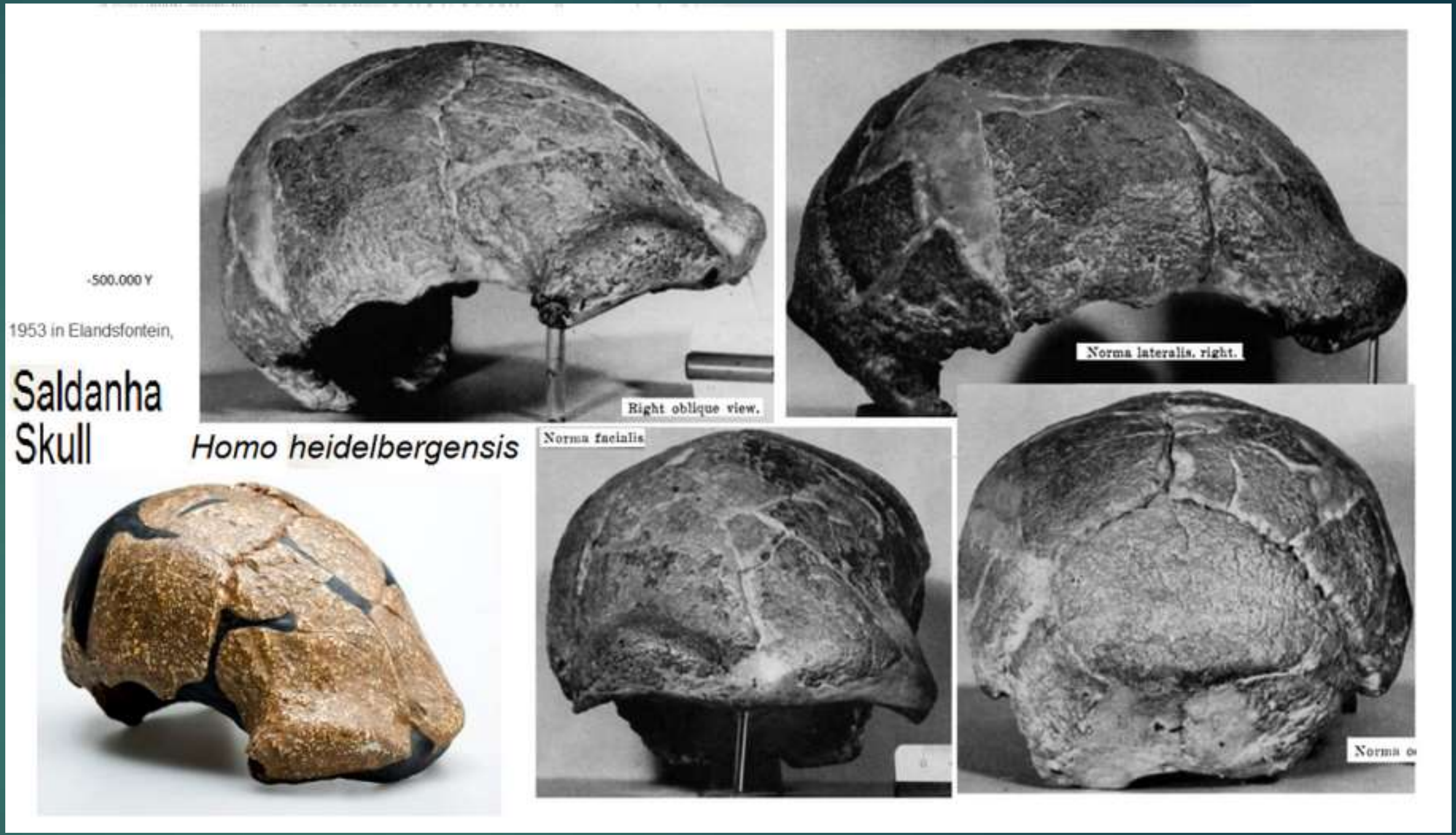
Saldanha: 500 Ka, 1225 cc

- Found in in 1953 Elandsfontein, Saldanha Bay, S. Africa

- *Homo heidelbergensis*

- This skullcap closely resembles the Broken Hill 1 skull in having large brow ridges, a broad, sloping forehead and a rear skull wall that is vertical rather than rounded or sloping.

Saldanha



Saldanha cranium, found in 1953 in South Africa was subject to at least three taxonomic revisions from 1955 to 1996.

Narmada, India

- December 5, 1982. On the banks of the Narmada at Madhya Pradesh's Hathnora village, geologist Arun Sonakia
- 500-600 Ka
- Associated with Acheulean tools
- estimates for the Narmada cranial vault fell between 1,155 and 1,421 cc
- Sheela Athreya, 2015: Narmada hominin falls between *H. heidelbergensis* and *H. erectus* in morphology. Narmada appears to have a mosaic of African and Asian *H. erectus* traits but these results suggest that it is more similar to *H. erectus*; based on brain size, would be *H. heidelbergensis*

Narmada cranium

Asian *H. heidelbergensis*?

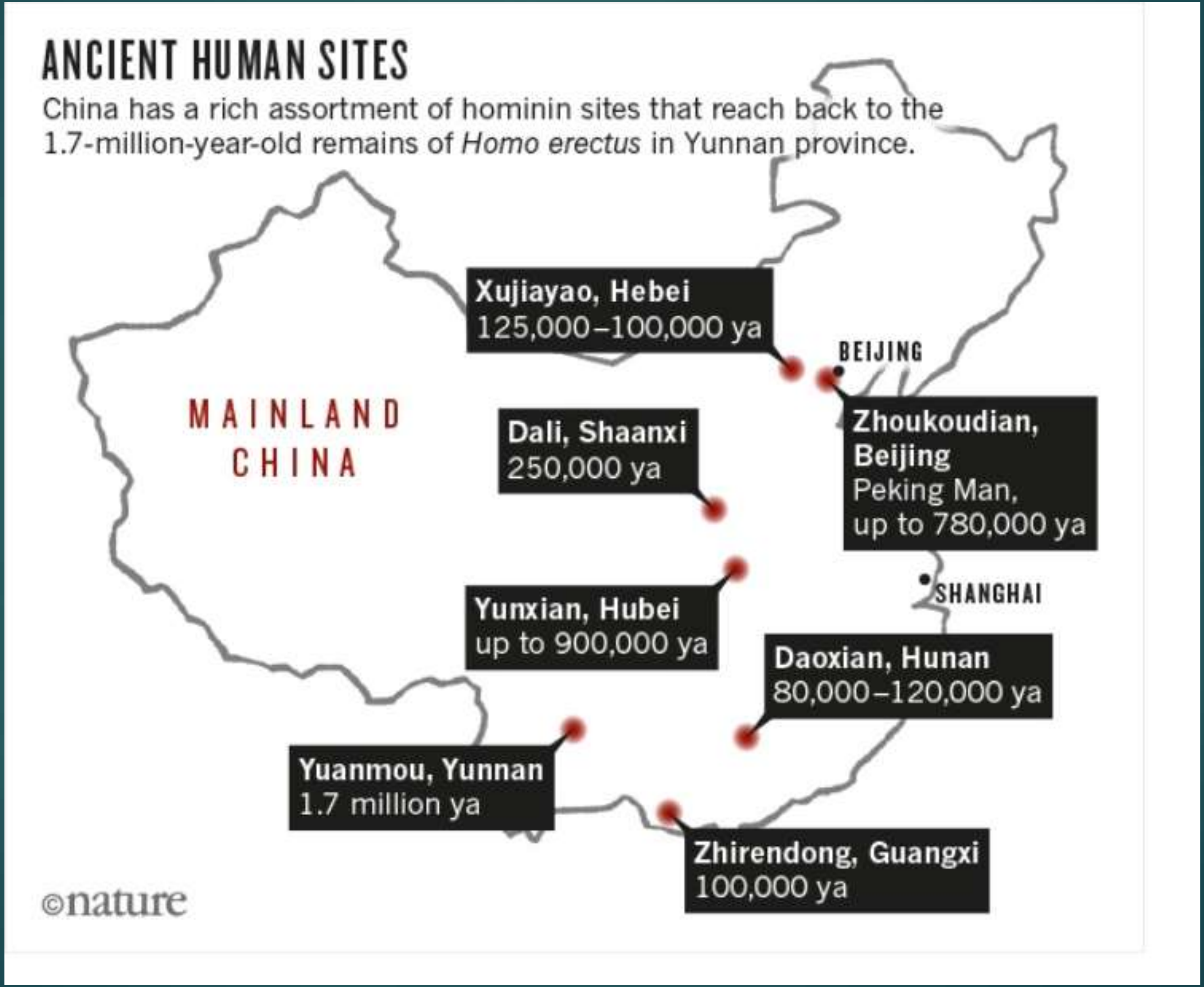
Yunxian

Dali

Narmada

Jinniushan

China hominins: 1.7 to 125 Ka



ANCIENT HUMAN SITES

China has a rich assortment of hominin sites that reach back to the 1.7-million-year-old remains of *Homo erectus* in Yunnan province.

Xujiayao, Hebei
125,000–100,000 ya

Dali, Shaanxi
250,000 ya

Zhoukoudian, Beijing
Peking Man,
up to 780,000 ya

Yunxian, Hubei
up to 900,000 ya

Daoxian, Hunan
80,000–120,000 ya

Yuanmou, Yunnan
1.7 million ya

Zhirendong, Guangxi
100,000 ya

©nature

Chinese hominins: 900 to 125 Ka

- Chinese hominins in these dates clearly represent more advanced species than *H. erectus*, but nobody knows what they are because they don't seem to fit into any categories we know.

- The fossils' transitional characteristics have prompted researchers such as C. Stringer to lump them with *H. heidelbergensis*.

- Because the oldest of these forms, two skulls uncovered in Yunxian in Hubei province, date back 900 Ka
- Stringer even suggests that *H. heidelbergensis* might have originated in Asia and then spread to other continents.

Chinese hominins

- Studies of modern Chinese populations show that 97.4% of their genetic make-up is from ancestral modern humans from Africa, with the rest coming from extinct forms such as Neanderthals and Denisovans.
- This genetic data does not support multiregional model. If there had been significant contributions from Chinese *H. erectus*, they would show up in the genetic data

R. Klein: Chinese *H. heidelbergensis*

- Klein: Chinese fossils (Jinniushan, Xujiayao, Dali, Maba) are like Narmada skull in combination of primitive and derived features. They can be *H. heidelbergensis*, but they are much younger than 400 Ka.

- Their inclusion would imply that west to east gene flow intensified after 400 Ka or that the features that define *H. heidelbergensis* (esp. the cranial brain size increase) evolved later in the east than in the west.

- If the Chinese fossils are included in *H. heidelbergensis* and they acquired their features independently, then *H. heidelbergensis* would become a grade concept (united by gross morphological traits), with no phylogenetic utility.

Yunxian

CT based reconstruction: cranial capacity of Yunxian Man was 1,065 cubic centimeters,

Chinese believe it is H. erectus

Li Tianyuan of the institute in Wuhan discovered the two fossilized human skulls at a site in Yunxian County in 1989 and 1990.

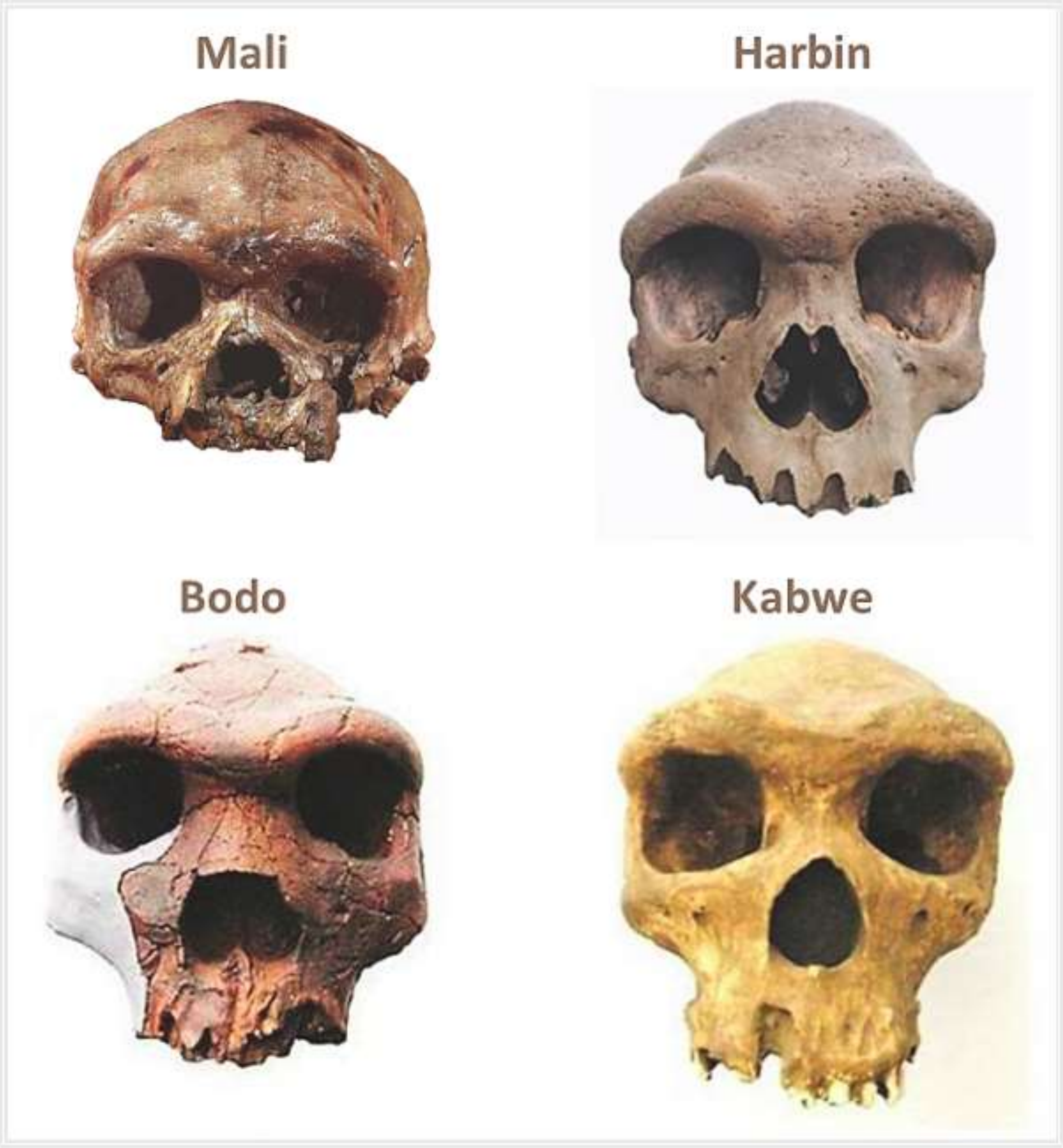
No. 2 skull, although badly damaged and without a jawbone, was the most complete human skull of its age ever found in China. It was determined to be 350,000 to 500,000 years old.

Harbin, Heilongjiang province, China: 2018, Hidden for 85 years

- *Homo heidelbergensis*
- estimated age of between 200-400 Ka.

Chinese Denisovans??: Harbin

- The **Harbin** skull, which remains unpublished to date, except a few photographs in the Chinese press. Incredibly, it remained hidden in private hands from its discovery in 1933 until September 2018. It seems very similar to Dali on the face, supraorbital tori, frontal and orbits.
- It was handed over to professor Ji Qiang at Hebei GEO University by an acquaintance, a farmer, who wanted to ensure the fossil would be safe. The farmer said that the skull had been dug up by a co-worker of his grandfather back in 1933 in the sediment of Songhua River in Harbin, Heilongjiang province.
- Realizing the skull was unusual, the grandfather hid it from the Japanese army in a well. As he was dying, he told his son and grandson about it.



Middle Pleistocene skulls: Mali, Harbin, Bodo, Kabwe. Sources: Mali (peterbrown-palaeoanthropology.net/dali.html), Harbin (China Institute of Geological Environmental Monitoring), Bodo and Kabwe (Roberto Sáez)

Dali, China, 250K

- *H. heidelbergensis*
- Discovered in 1978

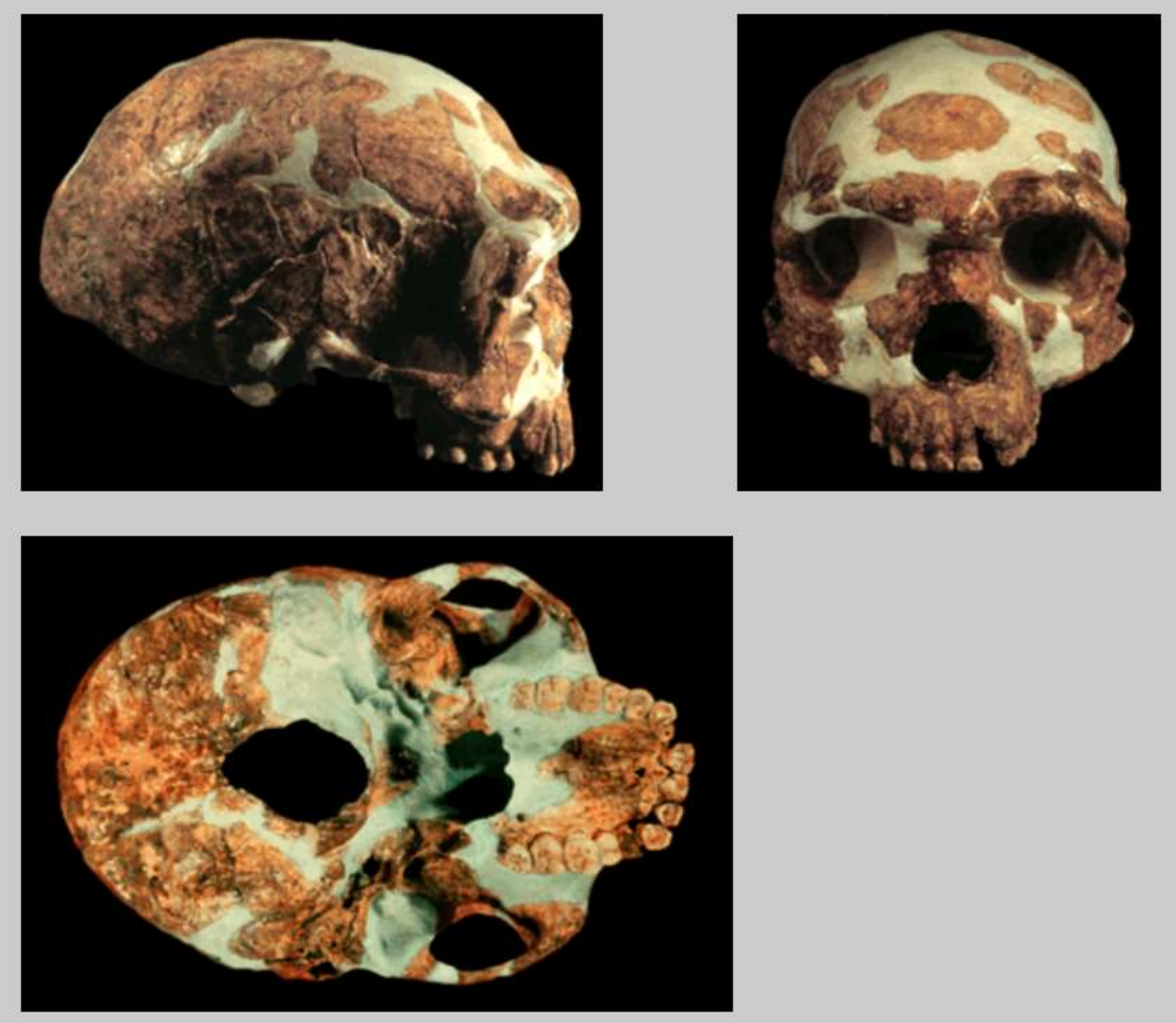
- near Jiefang Village, Dali County,
- Shaanxi Province

- Cranial capacity = 1200 cc

  - Face is broad & short (possibly crushed); broad bell-shaped nasal aperture, massive supraorbital tori; unlike Eurasian N

- 200 Oldowan stone tools
  - Chinese paleontologists: Has a bigger braincase, a shorter face and a lower cheekbone than most *H. heidelbergensis* specimens, suggesting that the species was more advanced.

Jinniushan, China, 200 Ka, 1300 cc, EQ 4.1



- Discovered in 1984 in cave near Sitian Village, southwest of Yinkou in Liaoning Provence, China

- Second largest cranial capacity (1300 cc) & thinnest cranial bones of any Chinese archaic fossil

- Broad nasal bridge, shovel-shaped incisors, prominent cheekbones differentiate early Chinese *H. sapiens* from Eurasian archaics (used to support Multiregional theory)

- Hominins in China used the same type of simple stone instruments from about 1.7 million years ago to 10,000 years ago.

- Question of hearths
- Cranium & pelvis may be female

Dali vs Jinniushan

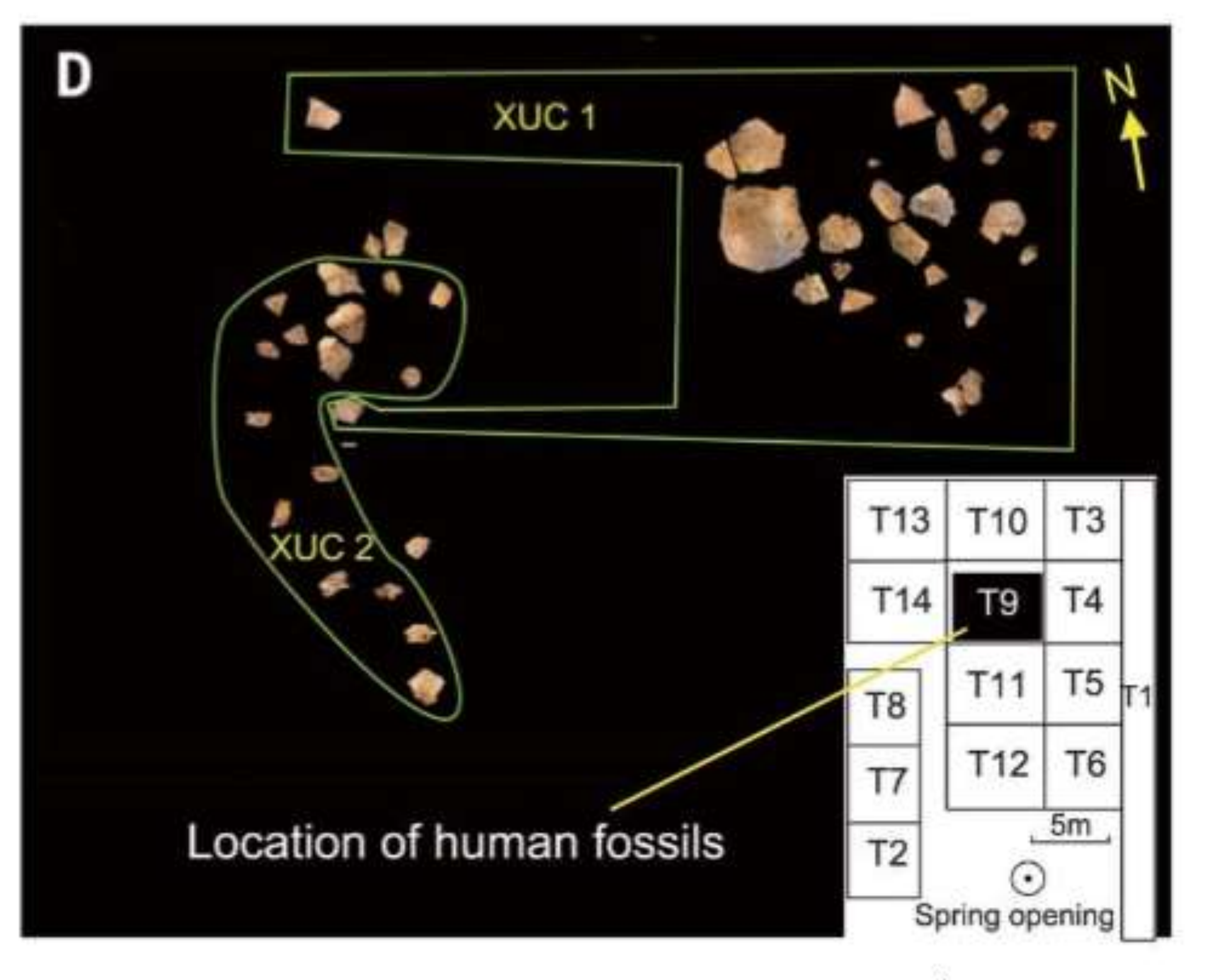
Maba, China, 229 Ka, most pronounced forehead

Similarities to Eurasian N: shape of supraorbital tori, thickest in medial third; rounded orbits lacking supraorbital notches

Maba
Site: Guangdong Province, China
Year of Discovery: 1958
Discovered by:
Age: 169-229 Ka
Species: *Homo heidelbergensis*

Maba, China: 1120 cc

2017: Xuchang 1 cranium: example of how fragmented fossil findings can be



Location of human fossils

2017: Xuchang crania, 105-125 Ka, 1800 cc

- Excavated in situ between 2007 and 2014, the Xuchang 1 and 2 crania (plus additional elements) from the Lingjing site in Xuchang County, Henan Province, China are considered to be archaic human, dated between about 105 and 125 Ka
- The endocranial volume of Xuchang 1, ~1800 cc, is at the high end of Neandertal and early modern human variation. It indicates marked encephalization. It is associated with lateral expansion of the parietal bones. The vault height is low, similar to those of the Neandertals. Widest point is low, on the temporal bones, as in most earlier crania, rather than on the parietal bones, as among Neandertals and most modern humans
- Xuchang 1 and 4 exhibit prominent supraorbital tori, their tori are modest in thickness, similar in that respect to those of Neandertals and some early modern humans. Their cranial gracility is evident in their modest parietal thicknesses. The maximum cranial breadth is the largest known in the later Pleistocene.

Zhan-Yang Li, et al., 2017

2017: Digital Xuchang 1 cranium

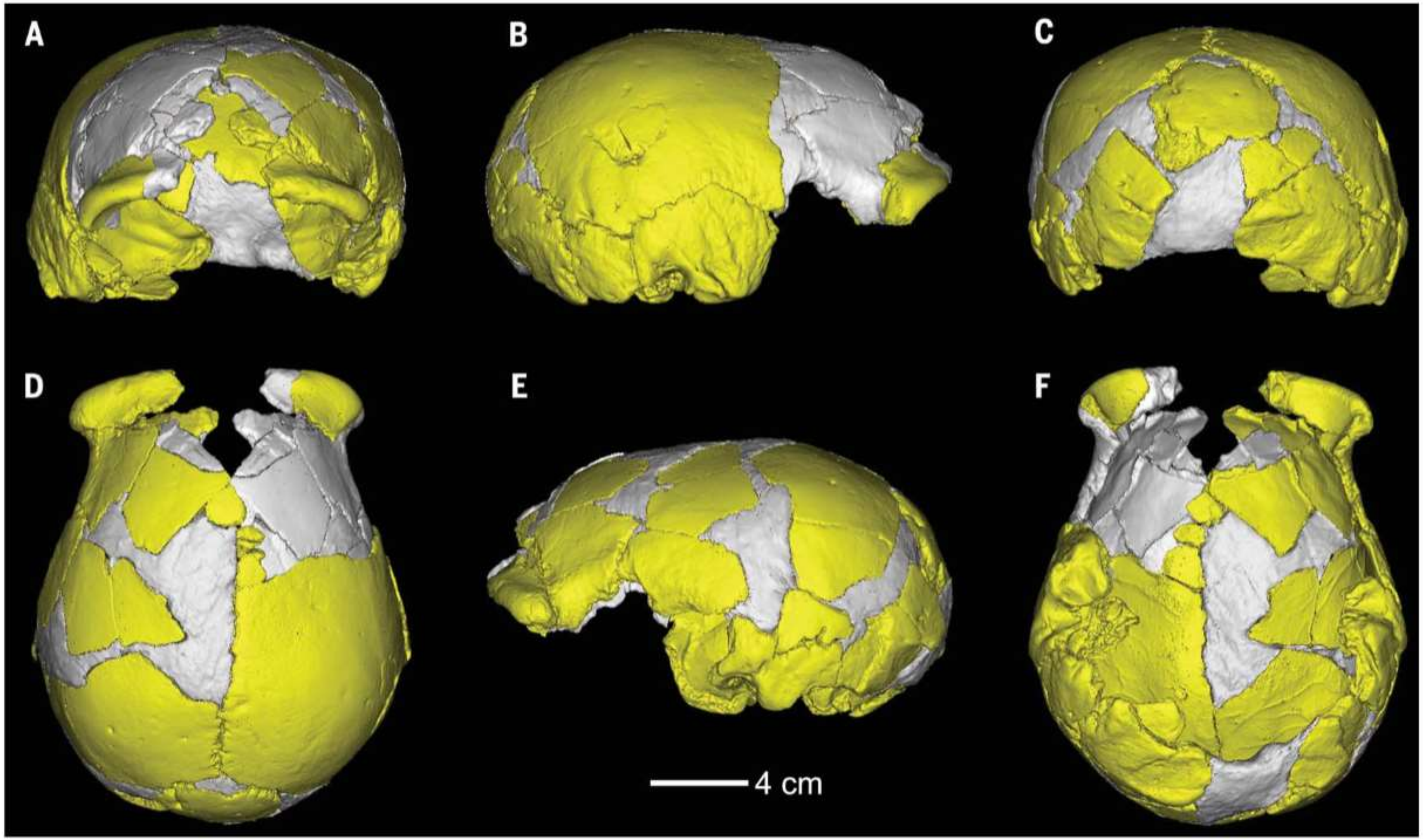


Fig. 2. Virtual reassembly of the Xuchang 1 cranium. (**A**) Anterior, (**B**) right lateral, (**C**) posterior, (**D**) superior, (**E**) left lateral, and (**F**) inferior views. Gray, filled-in absent portions and mirror-imaged right frontal squamous portion.

2017: Xuchang 2

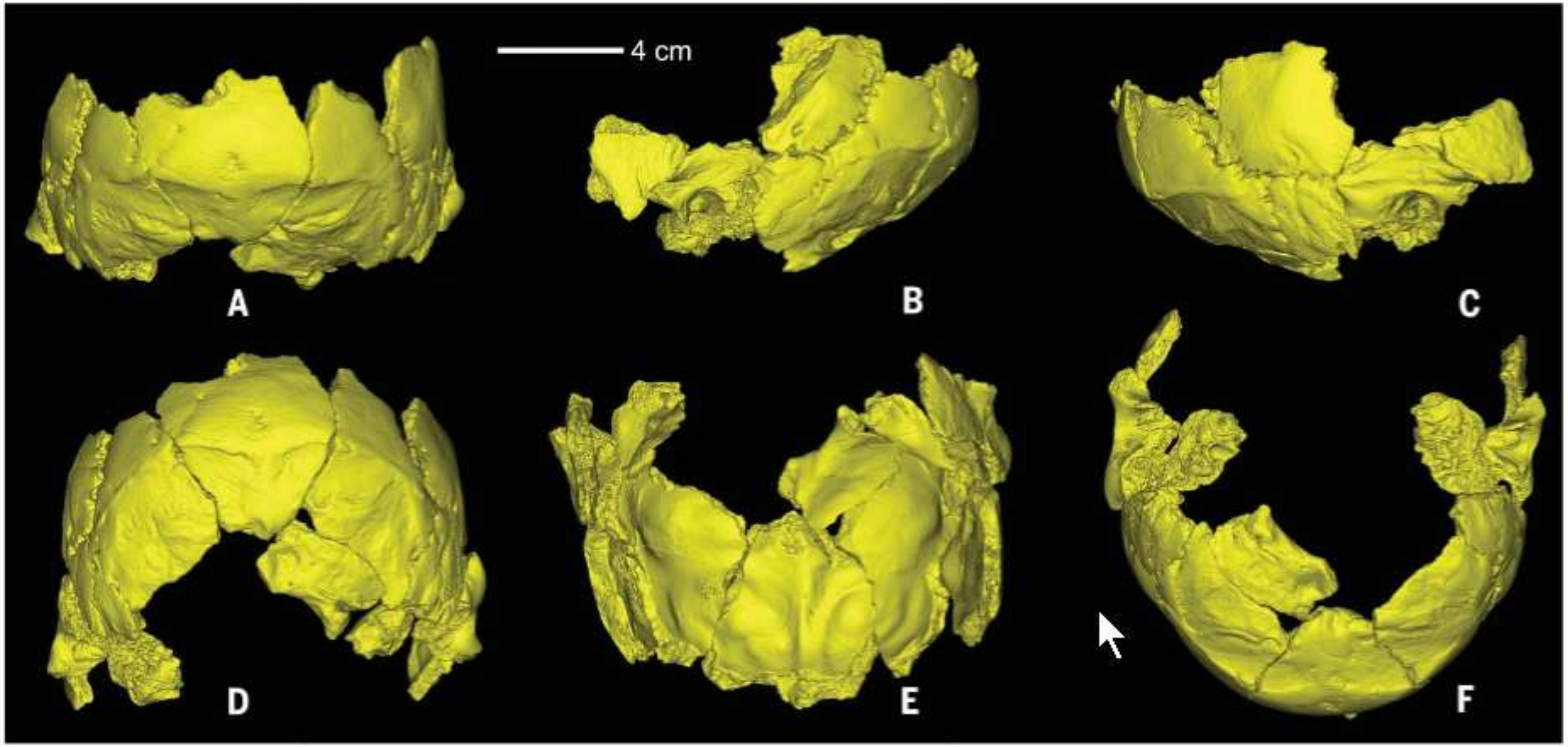


Fig. 3. Virtual reassembly of the Xuchang 2 cranium. (**A**) Posterior, (**B**) left lateral, (**C**) right lateral, (**D**) posteroinferior, (**E**) superior, and (**F**) inferior views.

2017: Xuchang 1 cranium: N features (suprainiac fossa & temporal labyrinths)

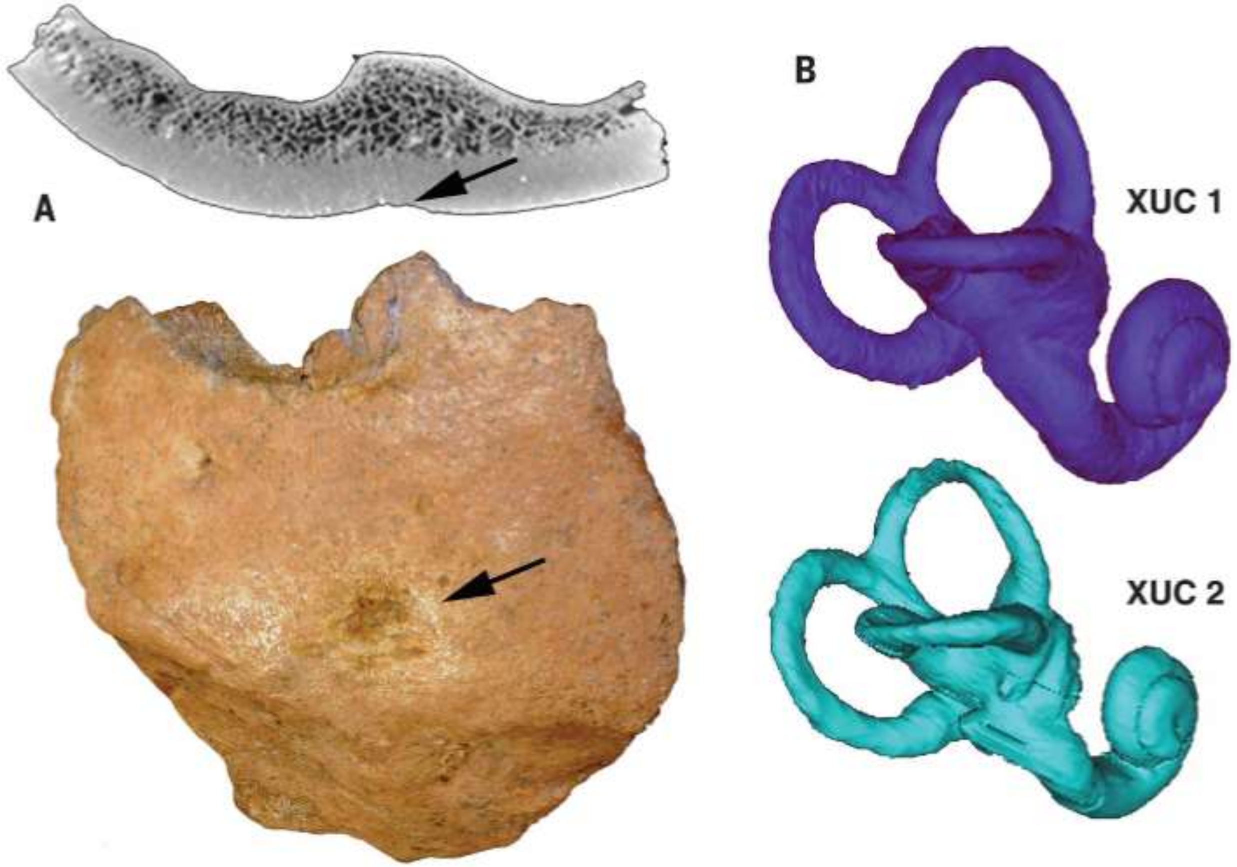


Fig. 4. Neandertal features of the Xuchang cranial remains. (**A**) External view of the Xuchang 2 suprainiac fossa with the superior nuchal line (bottom) and micro–computed tomography (μCT) section through the Xuchang 2 suprainiac fossa (top), showing the continuous external table thickness. (**B**) μCT-extracted temporal labyrinths of the Xuchang 1 and 2 right petrous bones, in lateral view, showing the relatively small anterior canals and the more superior lateral versus posterior canals. [Not to scale]

Hualongdong, China: ~300 Ka, 1,150 cc

- 2019: The Hualongdong (Hualong Cave) site (30° 06′ 34.1" N, 116° 56′ 54.2" E, elev. 40 m asl) is located in Pangwang village, Yaodu town, Dongzhi County, Anhui Province, China

- New Middle Pleistocene (~300 Ka) human remains from Hualongdong (HLD), China, provide further evidence for regional variation and the continuity of human biology through East Asian archaic humans. The HLD 6 skull is notable for its low and wide neurocranial vault and pronounced brow ridge, but less projecting face and modest chin.

Xiu-Jie Wu et al., 2019

HLD 6

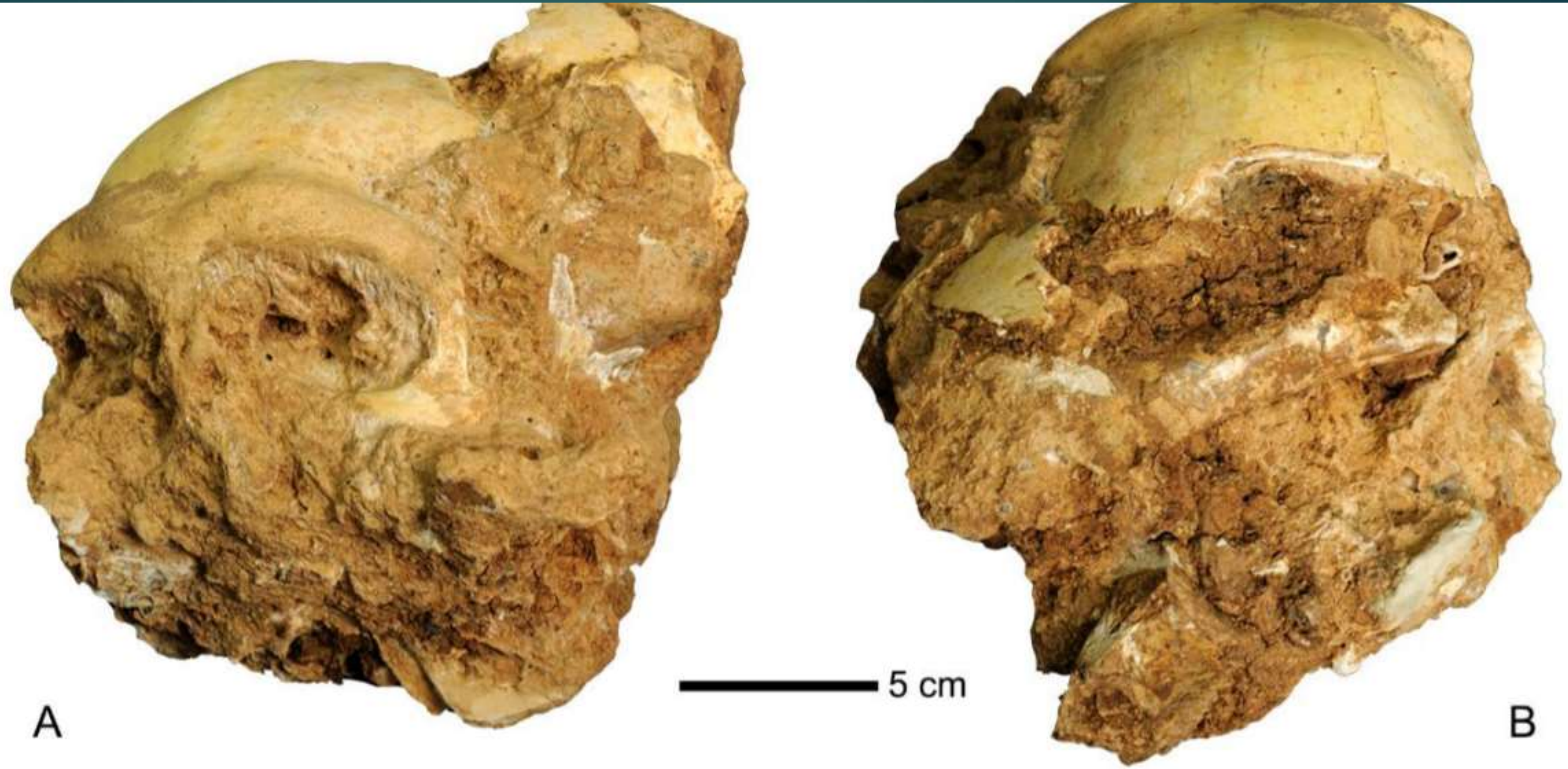
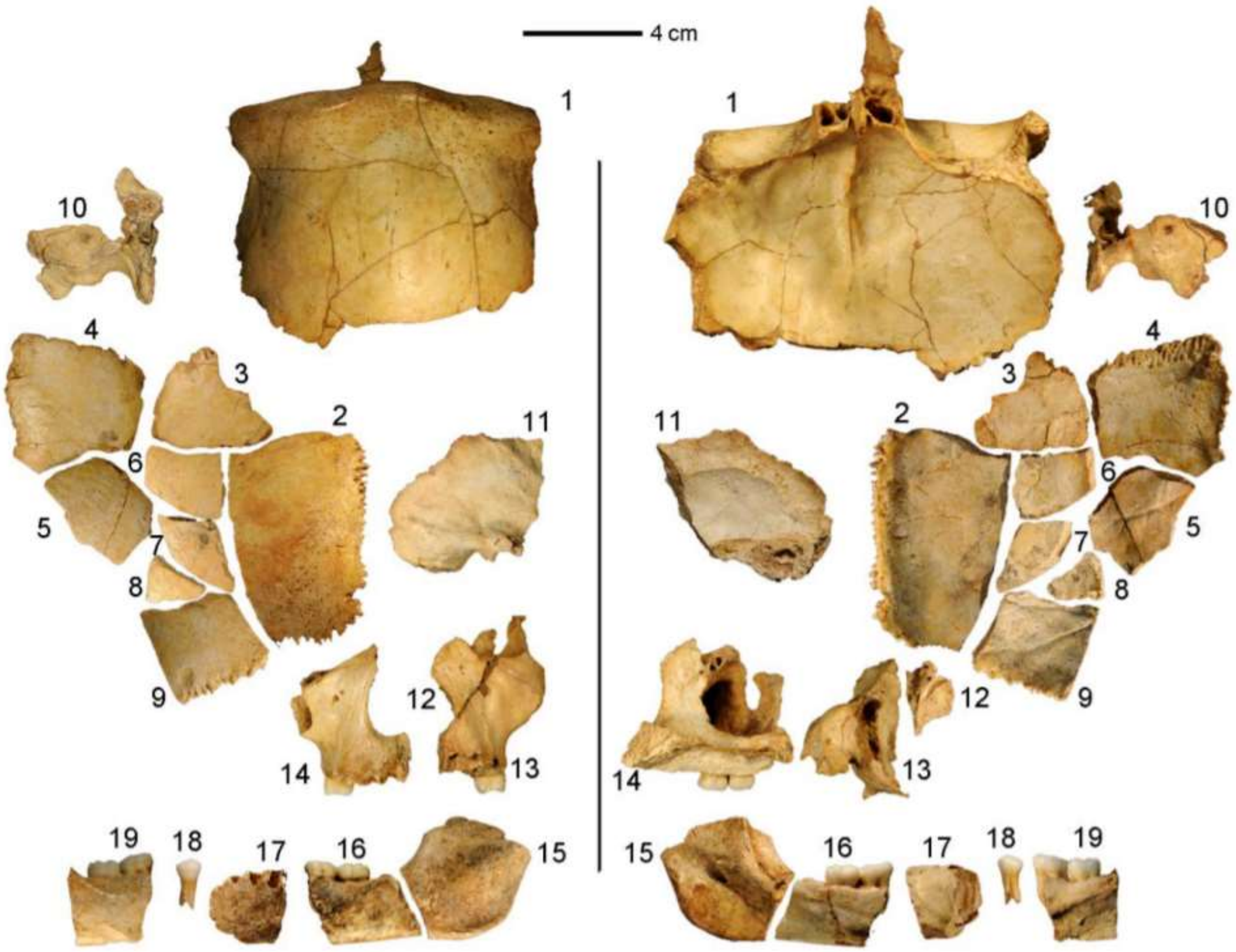


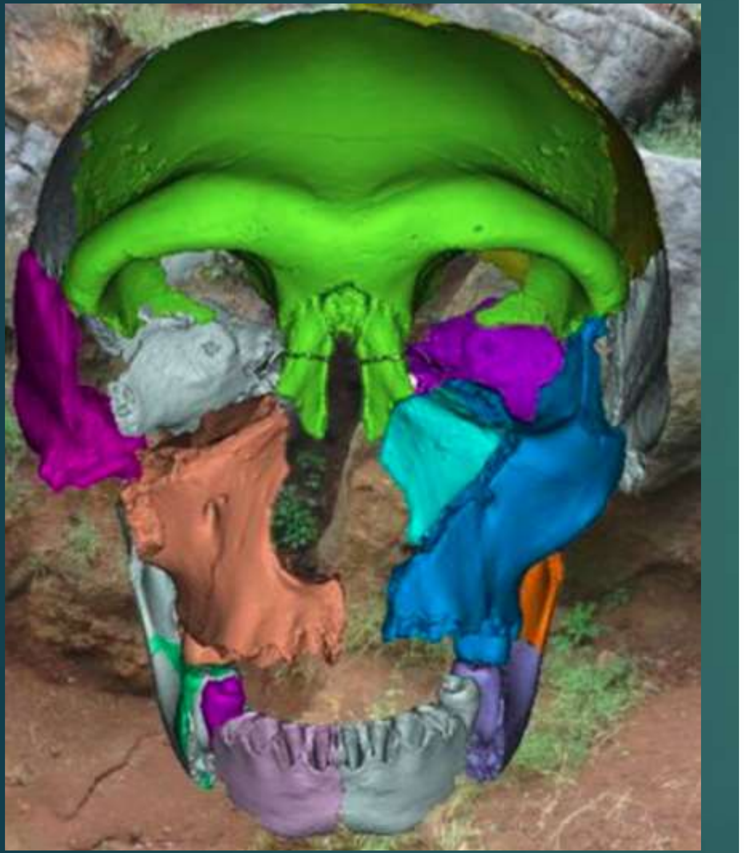
Figure S12. Anterior lateral (A) and superior (B) views of the HLD 6 partial skull as embedded in the brecciated sediment matrix.

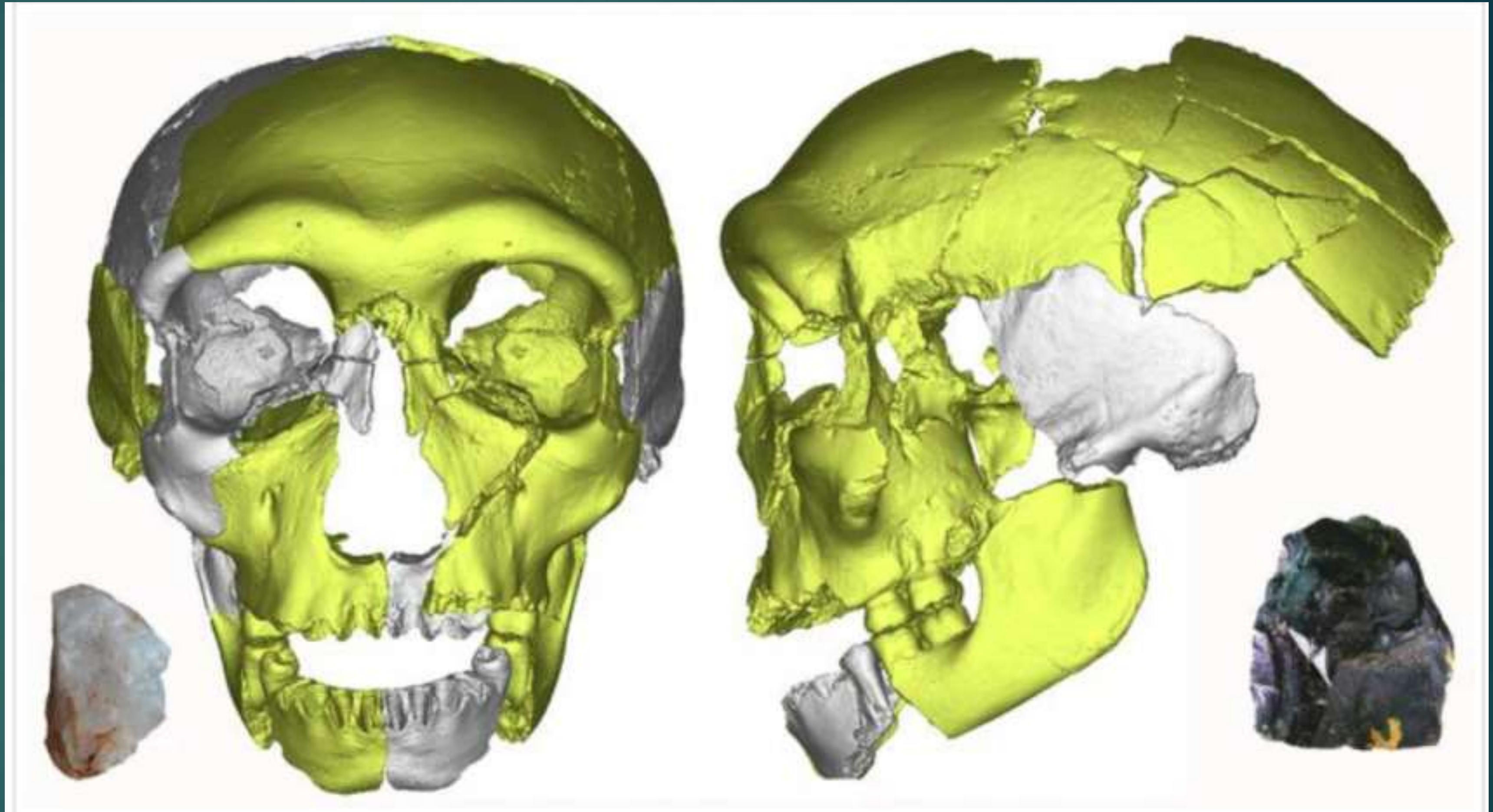
Endocranial volume ≈ 1,150 cc

Figure S13. Exterior (left) and interior (right) views of the nineteen pieces of HLD 6 cranium (number 1-14) and mandible (number 15-19).



Hualongdong, China: HLD 6





Researchers created a virtual reconstruction of the mostly complete Hualongdong skull (yellow) by mirror-imaging the missing pieces (gray). Stone tools found at the site appear in lower corners of the image. *(Credit: Wu Xiujie)*

Chinese Fossils & Denisovans?

- Recently there has been a tendency to link a group of Chinese hominin fossils, including Maba, Xujiayao, Dali, and Jinniushan, previously considered to be "archaic *Homo sapiens*", with the Denisovans. Current DNA is going on in an attempt to prove this hypothesis
- C. Stringer: In addition, the presence of relatives of the Neanderthals in the Far East forcefully reminds us how much our views are biased by the attention paid to the European and African records.
- We cannot exclude an Asian origin for *heidelbergensis*, given the similar ages (~600 ka) assigned to the earliest potential examples in Germany (Mauer), China (Yunxian), and Ethiopia (Bodo).

First evidence of Shelters circa 400 Ka

- Shelter: *H. heidelbergensis* probably took advantage of natural shelters but this species was also the first to build simple shelters.

- Evidence for this comes from hearths found at the German site of Bilzingsleben, and the French sites of Terra Amata and Lazaret. The hearth, on which fire had been maintained, was preserved; broken animal bones, charcoal, and worked stones were found in shelters.

Middle Pleistocene Culture: Dwellings

- Definitive dwellings with fire appear for the first time by 400 Ka
- Terra Amata, France

No forms of art have been uncovered for *H. heidelbergensis*, although red ochre, a mineral that can be used to mix a red pigment which is useful as a paint, has been found at Terra Amata excavations in the south of France.

Built Shelters: post hole evidence

- Terra Amata and Lazaret - evidence of possible huts in the form of post molds
- Lazaret-internal pattern of remains that also suggests an enclosure (controversial- not as coherent as some have suggested)

- Chichibu, Japan hut circa 500 Ka

- This suggests that the technology of *Homo heidelbergensis* extended beyond stone tools to include materials and knowledge in order to deal with the cold in these higher latitude areas.

Shelter: Terra Amata, France, 400 Ka, post holes

Reconstruction illustration of
400 Ka shelter from
Terra Amata, France

Date of discovery: 1966
Discovered by: Henri de Lumley

- Post holes and other evidence of multiple shelters at this site. Some shelters were as long as 14.9 m (49 ft)

Image Credit: Courtesy of Karen Carr Studio

Reconstructions of Shelter at Amata

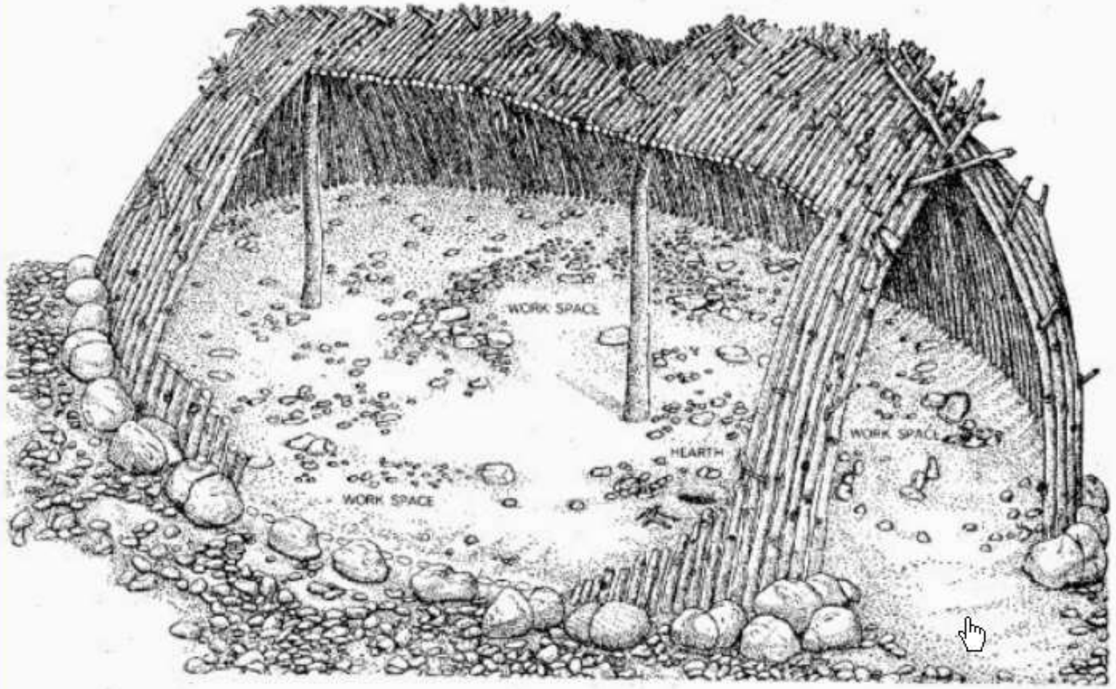


Fig. 2.2 Terra Amata (France), prehistoric hut, ca. 400,000 B.C.; reconstruction drawing.

A drawing of the structure at Terra Amata, made by Homo Heidelbergensis around 400-200 kya

An artist's impression of the structure at Terra Amata

Chichibu, Japan, 500 Ka

A drawing of one of the structures near Tokyo Japan, made by Homo Erectus around 500 kya

Schöningen, 8 throwing spears; 400 Ka, 6-7 feet long

Associated with
Homo heidelbergensis

Schöningen: wooden spears alongside masses of horse bones

Given that chimps make spears,
It is preposterous to think that early hominins
did not make spears before 400 Ka.

Wooden spears simply do not preserve well

Oldest Wooden Spears: Schöningen, Germany; 400 Ka


Wooden thrusting spear, Schöningen, Germany, about 400,000 years old.

- 8 wooden spears like this one were found at Schöningen, Germany, along with stone tools and the butchered remains of more than 10 horses.
- These spears are currently the oldest known wooden artifacts in the world.
- Along with some still embedded in horses.
- Schöningen spears had ballistic qualities indicating that they were thrown as javelins
- These spears were created by using stone tools to sharpen both ends of 2-meter long spruce shafts that had been scraped smooth.
- The humerus and shoulder morphology is associated with overarm throwing.

Wooden thrusting spear, Schöningen, Germany, ~400 Ka.
Image Credit: Chip Clark, Smithsonian Institution

Date of discovery: 1995
Discovered by: Hartmut Thieme
Site: Schöningen, Germany

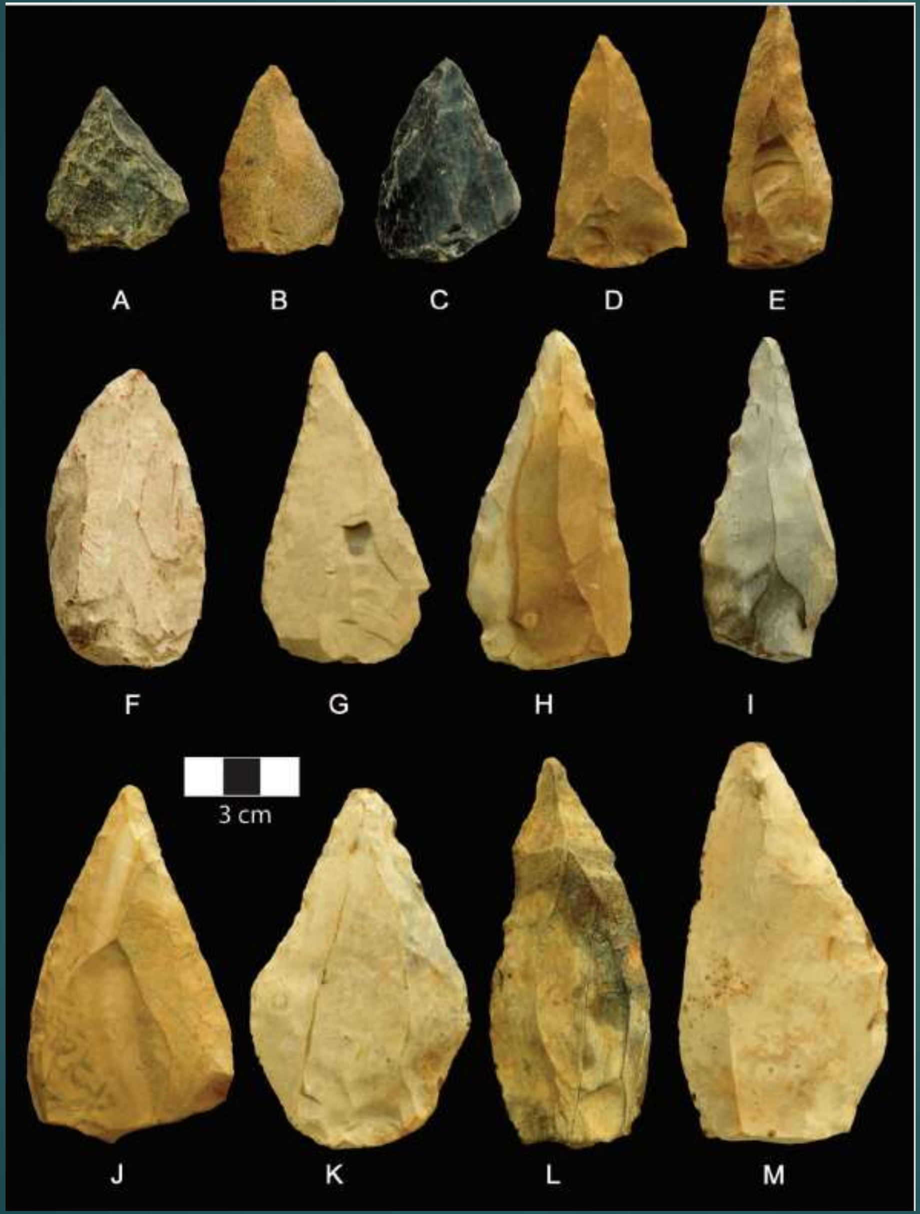
Clacton, England, spear point; 300-450 Ka

- Remains of animals such as wild deer, horses, elephants, hippos, and rhinos with butchery marks on their bones have been found together at sites with *H. heidelbergensis* fossils.

- Direct evidence of wooden implements also comes from the time of *H. heidelbergensis*: in England at the site of Clacton, a preserved wooden spear point made from yew. Oldest wooden artifact ever found in Britain. Fire hardened??. Estimates of its age range from 300-450 Ka.

15 x 1 ½ inches

Kathu Pan 1, South Africa: ~500 Ka stone points functioned as spear tips.



- Evidence for Early Hafted Hunting Technology:

- Multiple lines of evidence (damaged edges) indicate that ~500,000-year-old stone points from the site of Kathu Pan 1 (KP1), South Africa, functioned as spear tips.

- *Homo heidelbergensis*

Jayne Wilkins, et al., 2011

Hypotheses of Social life of *H. heidelbergensis*

- If their life was similar to modern hunting people, then:
  - Male-male cooperation during hunting
  - Sexual division of labor
  - Food sharing
  - Knowledge, skill, learning
  - Male aggressiveness (?)
  - Interdependence of men & women to raise children
  - Pair-bonding

Fire

- Perhaps the most striking behavioral advance associated with *Homo erectus* is the purposeful use of fire—fire used consistently in the same place over a period of time
- Fire: for warmth, cooking, social gathering
- Occurrence of charcoal is difficult to interpret
- Surest evidence of regular fire use:
  - Need fireplace with circular stones, and ash and charcoal lens inside
  - Unequivocal hearths are commonplace only in European MP (Mousterian) and African MSA sites postdating 200 Ka; S. African sites with stacked fireplaces circa 100 K

Fire

- “Burned” darkened wood and reddened sediments found at a site in northern Germany, now a coal mine called Schöningen, were really colored by water exposure and soil decomposition, not ancient flames.

- Fire origin: natural blazes, human made spark, lightening

- Whether people were using those fires “regularly,” and whether that means every week, year, or decade.

- Fire: warmth, protection, and a method for cooking food. Richard Wrangham: cooking meat and tubers lead to *H. erectus*

H. heidelbergensis: Fire use

- First early human species to live in colder climates, their short, wide bodies were a likely adaptation for conserving heat.

- Fire: There is evidence that *H. heidelbergensis* was capable of controlling fire by building hearths, or early fireplaces

- Most frequently noted evidence of controlled use of fire ~ 790 Ka in the form of fire-altered tools and burnt wood at the site of Gesher Benot Ya-aqov in Israel. Social groups probably gathered around their hearths, sharing food, staying warm, and warding off predators.

Naama Goren-Inbar, et al., 2004

Wetlands and hydrothermal cooking at Olduvai, 1.7 Ma

- 2019 study: The role of tectonics and hydrothermalism in early human evolution at Olduvai Gorge:
- Although use of fire at this time is controversial, hot springs may have provided an alternative way to thermally process dietary resources available in the 1.7 Ma Olduvai wetland.
- Hot springs may have enabled hominins to cook animal tissues and tubers with minimal effort
- Hot springs may have provided a convenient way to cook food that would have required minimal effort, which, at the same time, decreased digestibility-reducing and toxic compounds in starches. Cooking may, thus, have had a simple pre-fire stage during human evolution.

Ainara Sistiaga, et al., 2019

Controlled use of Fire

- 34 fire sites from 1.7 Ma to 730 Ka: natural brush fires, hearths, charcoal, burned bone/lithics, lightening caused cave fires; campfire temperatures are hotter.
- Burned materials:
  - 1.5 Ma, burned stones at Koobi Fora (2019 study; good evidence)
  - 1 to 1.5 Ma, burned bones with cutmarks at the Swartkrans
  - 1.0 Ma at Wonderwerk Cave, S. Africa: earliest solid evidence that *Homo erectus* were using fire. The plant and bone ash was found thirty meters inside the Wonderwerk Cave — beyond the reach of a lightning strike.
  - 690-790 Ka, at a site in Israel called Gesher Benot Ya`aqov; burned flint, and fragments of burned fruit, grain and wood scattered about.
  - By 125 Ka: Widespread control of fire by MHs

Stone Age barbecue? Koobi Fora, Fire + humans at 1.5 Ma

- 2019 research by Sarah Hlubik
- Evidence from FxJj20 site at Koobi Fora, Kenya suggest association of fire & human behavior at 1.5 Ma at open air site
- Patches of reddened dirt surrounded by relatively dense clusters of stone tools and burned bone
- Handful of stone tool fragments have curved appearance, which occurs only when a stone is being made near a fire; they crack and curl along stress lines

Sarah Hlubik, et al., 2019

Koobi Fora, Fire + humans at 1.5 Ma

- This work demonstrates the presence of fire associated with human behavior. This is the earliest documented site in the record to display this association. Proves a demonstrated association of fired material and artifacts and bone recovered at FxJj20 AB.

- This association does not prove that hominins were controlling fire, or could make fire, but it provides evidence of the association between fire and hominin behavior in the Early Pleistocene

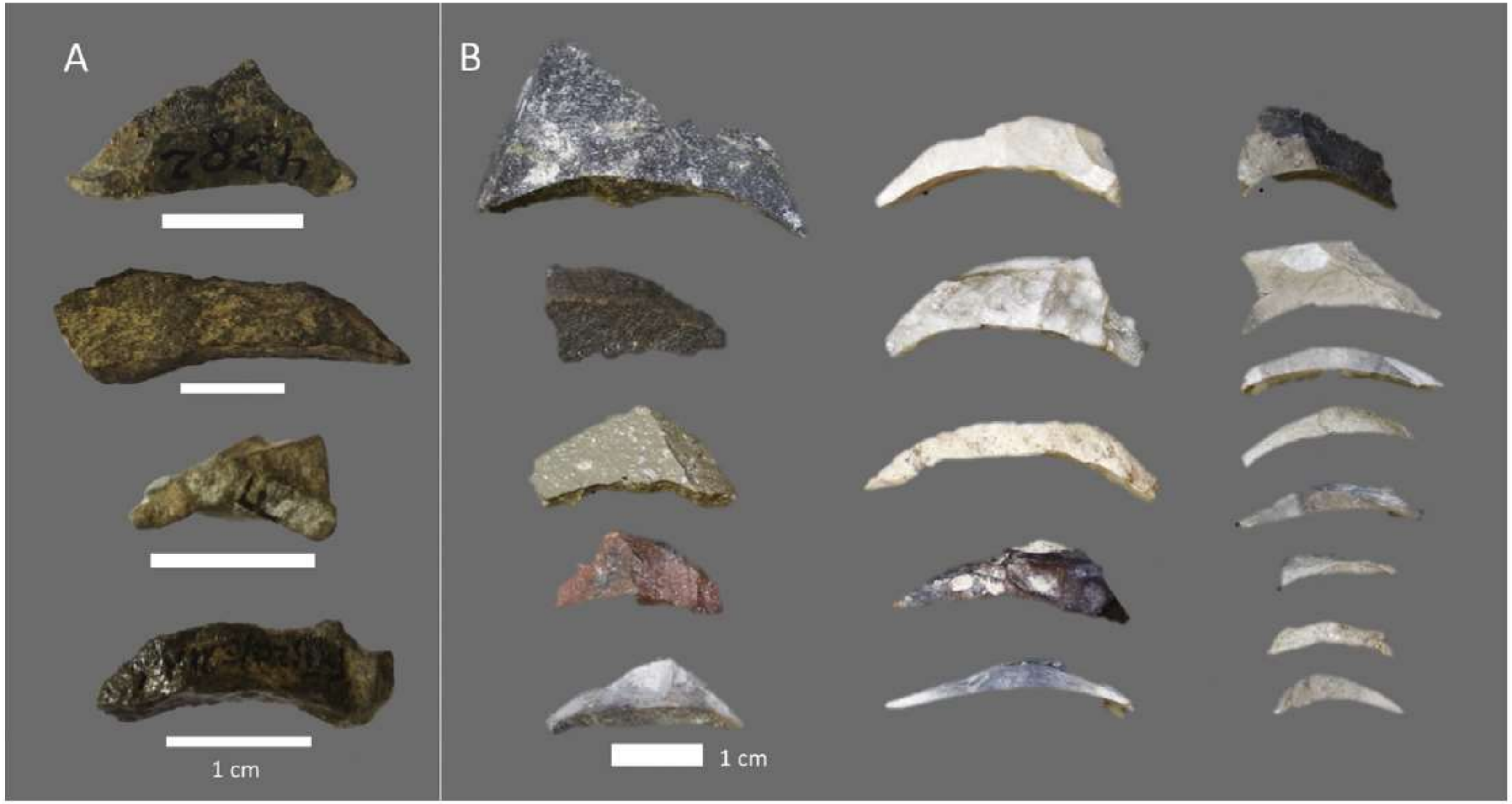


Figure 11. Thermal curved-fractures (TCFs). The potential TCF on top demonstrates statistically similar morphology and was recovered in situ at FxJj20Main during 1970s excavations and labeled "angular fragment" in collections housed at the National Museums of Kenya. On the bottom is an experimentally-derived example from a firing event exceeding 550°C. Scale = 1 cm.

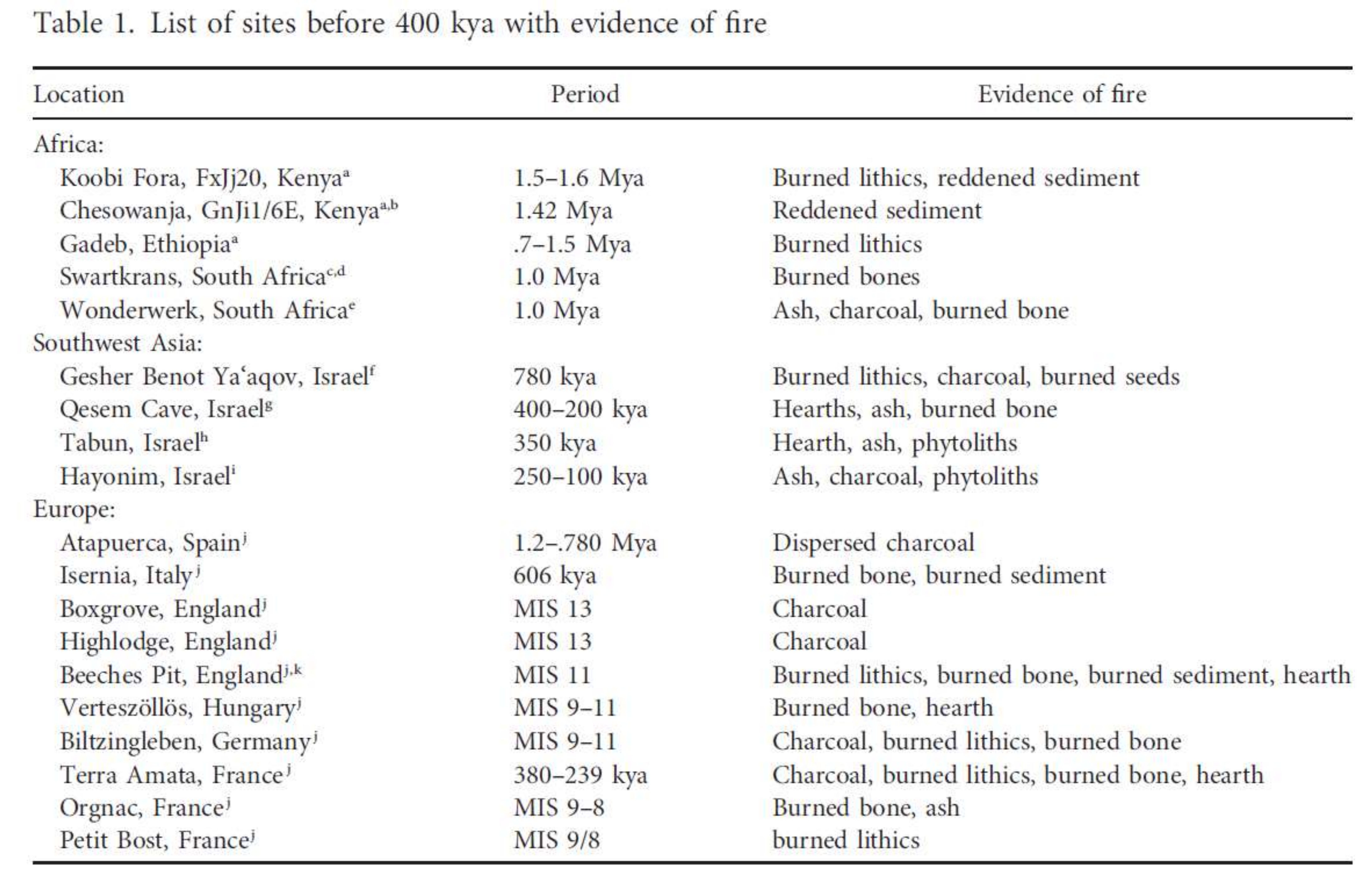


Table 1. List of sites before 400 kya with evidence of fire

Location	Period	Evidence of fire
Africa:		
Koobi Fora, FxJj20, Kenya[a]	1.5–1.6 Mya	Burned lithics, reddened sediment
Chesowanja, GnJi1/6E, Kenya[a,b]	1.42 Mya	Reddened sediment
Gadeb, Ethiopia[a]	.7–1.5 Mya	Burned lithics
Swartkrans, South Africa[c,d]	1.0 Mya	Burned bones
Wonderwerk, South Africa[e]	1.0 Mya	Ash, charcoal, burned bone
Southwest Asia:		
Gesher Benot Ya'aqov, Israel[f]	780 kya	Burned lithics, charcoal, burned seeds
Qesem Cave, Israel[g]	400–200 kya	Hearths, ash, burned bone
Tabun, Israel[h]	350 kya	Hearth, ash, phytoliths
Hayonim, Israel[i]	250–100 kya	Ash, charcoal, phytoliths
Europe:		
Atapuerca, Spain[j]	1.2–.780 Mya	Dispersed charcoal
Isernia, Italy[j]	606 kya	Burned bone, burned sediment
Boxgrove, England[j]	MIS 13	Charcoal
Highlodge, England[j]	MIS 13	Charcoal
Beeches Pit, England[j,k]	MIS 11	Burned lithics, burned bone, burned sediment, hearth
Verteszöllös, Hungary[j]	MIS 9–11	Burned bone, hearth
Biltzingleben, Germany[j]	MIS 9–11	Charcoal, burned lithics, burned bone
Terra Amata, France[j]	380–239 kya	Charcoal, burned lithics, burned bone, hearth
Orgnac, France[j]	MIS 9–8	Burned bone, ash
Petit Bost, France[j]	MIS 9/8	burned lithics

Richard Wrangham: *H. erectus*, fire, cooking

- Richard Wrangham, in Catching Fire: How Cooking Made Us Human, 2009, credits the transformation of *Homo* to the harnessing of fire to cook meat and tubers.
- Cooking food, he argues, allowed for easier chewing and digestion, making extra calories available to fuel energy-hungry brains.
- Common fireplace pushed for more sociality; More safety at night with fireplace: Firelight could ward off nighttime predators, allowing hominins to sleep on the ground, or in caves, instead of in trees.
- The altered anatomy of *H. erectus*, Wrangham wrote, indicates that these beings, like us, were "creatures of flame."

Fire

- Wrentham's thesis is that around 1.9 Ma, our ancestors learned to control fire, which until then had been a hit-and-miss event.

- Lightning-initiated fires on the African savannah were irregular phenomena, but at some point our habiline forebears figured out how to start a fire (probably with sparks produced by striking pyrite rocks with flint).

- But when one of them accidentally dropped a slab of meat into a fire — the first barbecue — that's when the transition from ape to human really got underway.

Cooking?

- There is no archaeological evidence that *Homo erectus* cooked their food. The idea has been suggested, but is not generally accepted
- It is known, from the study of microwear on handaxes, that meat formed a major part of the *H. erectus* diet.
- Flaws in the cooking hypothesis:
  - Many of the adaptations attributed to cooked food such as large brains could have arisen through an increase in raw meat consumption.
  - More researchers accept Expensive Tissue hypothesis: The mainstream explanation is that human ancestors, prior to the advent of cooking, turned to eating meat, which then caused the evolutionary shift to smaller guts and larger brains

Fire: East Africa – controlled vs natural fires

East African sites:

- At Koobi Fora, two sites show evidence of control of fire by *Homo erectus* at about 1.5 Ma, with reddening of sediment associated with heating the material to 200–400 degrees Celsius (392–752 °F).
- At Chesowanja, near Lake Baringo, Koobi Fora, fire-hardened clay fragments, dated to 1.42 Ma. The clay must have been heated to about 400 °C (752 °F).
- At a "hearth-like depression" at a site in Olorgesailie, Kenya, some microscopic charcoal was found—but that could have resulted from natural brush fires.

Controlled use of Fire

- 1.5 Ma– living sites with burnt bones - S. Africa, Swartkrans cave, Wonderwerk Cave: The cave contains the earliest solid evidence that our ancient human forebears (probably *Homo erectus*) were using fire, dating to 1 MA. The plant and animal ash was found thirty meters inside the Wonderwerk Cave — beyond the reach of a lightning strike. Collected flames from wildfires and brought them into the cave; ash layer is missing evidence of a structured fire

- Zhoukoudian, China: 670-400 Ka – burnt bones, ash; Northern latitude of Dmanisi and China findings at 1.6 M – could they survive without fire? Recent climate analysis indicates not as cold as once thought.

- Difficult to prove whether this use was controlled.

Controlled use of Fire: Gesher Benot Ya`aqov, Israel: 790 Ka

- Gesher Benot Ya’aqov, a lakeside site in Israel, was considered to have the oldest generally accepted evidence of human-controlled fire. Evidence of burned flint, and fragments of burned fruit, grain and wood scattered about.

- Gesher Benot Ya`aqov, Israel: 790 Ka, clusters of burnt chips – evidence of controlled use of fire; The distribution of the site's small burned flint fragments suggests that burning occurred in specific spots, possibly indicating hearth locations. Wood of six taxa was burned at the site, at least three of which are edible—olive, wild barley, and wild grape.

Gesher Benot Ya'aqov, Israel: 790 Ka: Fire altered stone tools


Burned flint from the 790,000 year old site of Gesher Benot Ya'aquov, Israel.

Burned flint from the 790 Ka site of Gesher Benot Ya'aquov, Israel.

Image Credit: Chip Clark, Smithsonian Institution

Gathering at the hearth
Scientists found this debris from stone toolmaking that had been scorched by fire at the site of Gesher Benot-Ya’aqov, Israel.

Close by were concentrations of burned seeds and wood, marking the location of early hearths.

Date of discovery: 2004
Discovered by: A team led by Naama Goren-Inbar
Species:
Site: Gesher Benot-Ya’aqov, Israel

Naama Goren-Inbar, et al., 2004

Gesher Benot Ya`aqov: controlled use of fire

- The site includes 12 layers of remains from different groups of early humans covering a 100,000-year span
- Site has been dated to 790 Ka
- The remains included 500,000 chips of broken flint, produced as the early humans crafted their stone axes and knives. Roughly 2% of these chips were cracked and charred by fire, and the team mapped where each burnt fragment came from.
- The analysis revealed that the charred remains were tightly clustered around certain areas, suggesting the flint chips had fallen into a campfire as early humans honed their tools by the fireside.
- Because these charred remains exist in all 12 layers of the site, every society must have had access to fire. It's unlikely that all 12 societies would have been lucky enough to find a natural source of fire, so they must have been able to create it themselves. The exact technique still remains unclear, since no obvious means of ignition were found at the site.

Fire & *H. erectus: 790 Ka,* Gesher Benot Ya`aqov, Israel; 1000s of Achuelean stone tools; burned edible plants

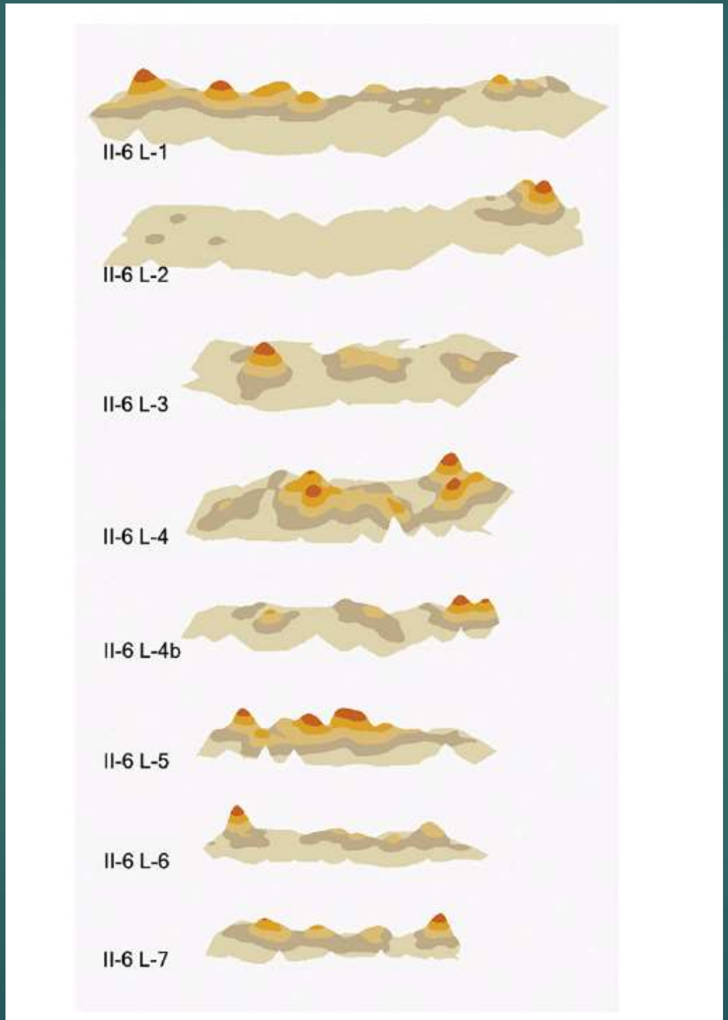


Fig. 2. The sequential occurrence of phantom hearths in Layer II-6 by level, from the topmost (youngest) level 1 to the lowermost (oldest) level 7; see Table 1 and Fig. 1 in Supplementary data for data on the excavated areas.

The sequential occurrence of phantom hearths in Uyer 11-6 by level, from the topmost (youngest) level 1 to the lowermost (oldest) level 7;

Phantom hearth = archaeological features that can be evident through observable patterns of artifacts' spatial distributions

Use of fire in Europe: 800 Ka

- Charred bone, heat-rippled stone in Spanish cave date back 800,000 years
- The oldest evidence of fire making in Europe and support proposals that members of the human genus, *Homo*, regularly ignited fires starting at least 1 million years
- Excavations conducted since 2011 at the Spanish cave, Cueva Negra del Estrecho del Río Quípar, have uncovered more than 165 stones and stone artifacts that had been heated, as well as about 2,300 animal-bone fragments displaying signs of heating and charring; had been heated to between 400° and 600° Celsius, consistent with having been burned in a fire.

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Use of Fire, Thailand

- Kao Poh Nam rock shelter, Thailand, 700 Ka; fire hearth with butchered, burned animal bones
- Fire cracked basalt cobbles were found with artifacts and bones.
- The rocks were not native to the shelter and were probably carried in by hominines.
- The bones in the hearth show evidence of butchering and burning.

Qesem Cave, Israel: 300 Ka

Qesem Cave in Israel, where these charred bits of animal bones were found, is one of the earliest known sites showing somewhat persistent fire usage by humans

- Qesem (“Kesem”) Cave in Israel, which hominins started using about 300,000 years ago. The cave is full of wood ash.
- A 300 Ka hearth was unearthed in a central part of the cave. Layers of ash was discovered in the pit, and burnt animal bones and flint tools used for carving meat were found near the hearth, suggesting it was used repeatedly.

It’s possible that fire tending happened in fits and starts before it was cemented in human habits.

Neandertals and Fire, 100-40 Ka

- D. Sandgathe and archaeologist Harold Dibble: Neanderthals who inhabited sites the pair have excavated in France, which date to between 100 to 40 Ka. They found some layers of sediment containing ash and burned tools and bone, and some layers without.

- Oddly, it’s the more recent, coldest time periods when fire seems to be absent. They hypothesize that Neanderthals couldn’t make fire and that they had better access to it during warm periods when lightning strikes were frequent.
- 75 Ka, it was really cold. The average temperature was probably about 5 to 10 degrees Celsius colder than today

Fire: Neandertals

- Others doubt that Neanderthals' fire usage really died away. "I'm pretty sure they knew how to make it," says Sarah Hlubik.
- Another explanation for Sandgathe and Dibble's findings, she speculates, is that Neanderthals might have had to rely on animal dung, instead of wood, for fuel during cold and relatively treeless periods. Perhaps they wanted to keep the stinky fumes of fires for cooking or toolmaking away from their home caves, and so they lit those fires farther afield—where the evidence more easily washed away, or hasn't yet been found.
- Pyrite & flint: solid evidence, in a hand-grooved nodule of pyrite from Belgium, that some humans set fires this way around 13,000 years ago.
- Sorensen: examined several such tools from Neanderthals who inhabited southwest France about 50,000 years ago. Neanderthals were almost certainly making fire during the last glacial period," says Sorensen, referring to a time about 100,000 to 35,000 years ago.

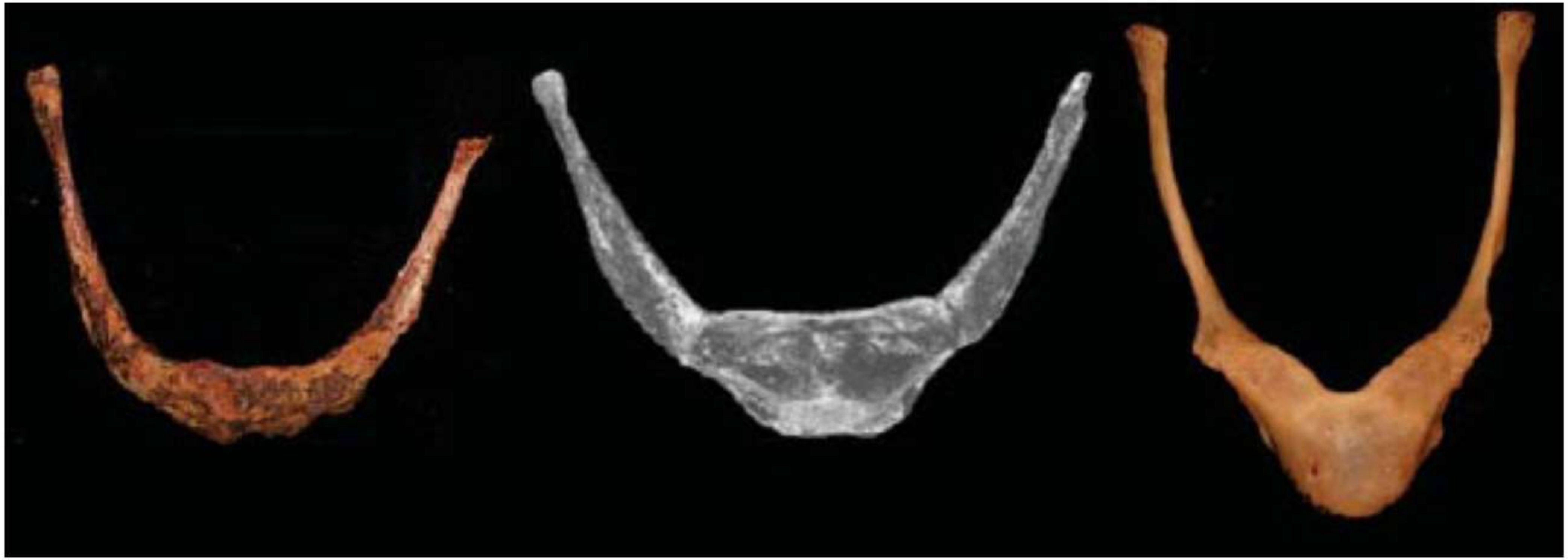
Language

- *Homo heidelbergensis* is thought to have been the first ancestor of modern humans not to have air sacs, which are laryngeal diverticula involved in vocalization.
- The loss of air sacs may have contributed to humans' ability to develop vocal language. Ancestors such as *Australopithecus afarensis* did have air sacs, as do other great apes.
- Furthermore, there is evidence that *Homo heidelbergensis* was right-handed. Handedness is associated with the development of language among hominins.
- A recent study that compared the speech frequency of humans and chimpanzees reported that *H. heidelbergensis* speech abilities more closely resemble those of modern-day humans.
- More specifically, "the Atapuerca SH hominins show[ed] a bandwidth that [wa]s slightly displaced and considerably extended to encompass the frequencies that contain relevant acoustic information in human speech."

Language?

- H. heidelbergensis had FOXP2 gene
- Endocast of the Kabwe *Homo heidelbergensis* cranium is well within the modern range in terms of size
- Demonstrates:
  - modern pattern of left occipital and right frontal petalias,
  - left ventral premotor cortex (Broca's area) is enlarged relative to the right
  - Basicranium is more angled, a feature that has been linked to lengthening of the pharynx
  - Diameter of the hypoglossal canal is in modern range (passage in cranial base (through which pass the nerves that enervate the tongue)-enlarged canal suggest greater control of tongue

Hyoid bone



The hyoid bone viewed superiorly in humans (left), Neanderthals (center), and chimpanzees (right). *(Credit: Steele et al.)*

Based on these results, most researchers agree Neanderthals were capable of emitting and hearing complex vocalizations. However, they disagree over the implications. While some consider the findings indicative of speech-based language in Neanderthals, others propose these features could have evolved for other reasons, like singing. Neanderthals may have lacked the cognitive abilities for language, but possessed the physical anatomy for musical calls to attract mates or sooth infants.

Language in *Homo heidelbergensis & H. neanderthalensis*

- The evidence points to modern speech capacities in the common ancestor of Neandertals and modern humans.
- The auditory specializations for speech on the modern bandwidth are present, the morphology of the larynx looks modern, and air sacs have been replaced by a finely controlled pulmonic airstream mechanism for vocalization. In addition, the language gene *FOXP2*, has its modern form.
- All these changes occurred in the transition from *Homo erectus* to *Homo heidelbergensis*, the common ancestor to both Neandertals and modern humans. We suggest therefore that this common ancestor was an articulate mammal.
- Complex tool making of the Mousterian kind involves hierarchical planning with recursive sub-stages which activates Broca's area just as in analogous linguistic tasks. The chain of fifty or so actions and the motor control required to master it are not dissimilar to the complex cognition and motor control involved in language

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Rightmire: a Eurafrican species

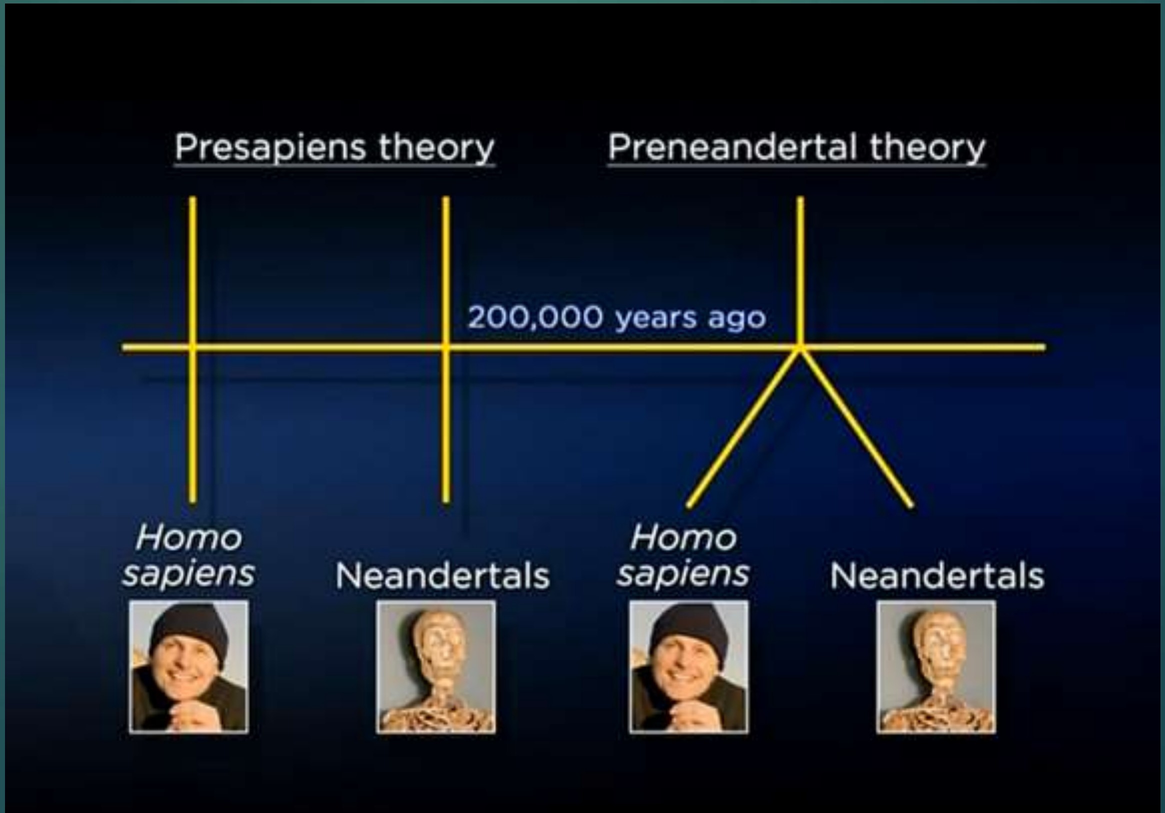
- Steinheim & Swanscombe skulls: The occipital bones of both specimens display signs of <u>a suprainiac fossa</u> (a centrally placed elliptical depression with a pitted floor unique to Ns). Swanscombe possesses a transverse torus that is weak near the midline but bilaterally projecting. <u>These traits are diagnostic for the N lineage</u>. The <u>Sima de los Huesos at Atapuerca</u> confirms that Neanderthal features are present in an assemblage at 430 Ka
- <u>In Rightmire's view, all of the earlier Middle Pleistocene hominins share both *erectus*-like features and a suite of derived traits common to later humans</u>. <u>It is hard to find any morphological basis for restricting *Homo heidelbergensis* to Europe</u>.
- This taxon may well have evolved elsewhere. However, these people did reach Europe at an early date. Sometime later, as climatic conditions changed and populations became isolated by ice barriers, speciation produced the first Neanderthals
- Rightmire (1998) has the best comparisons of Homo heidelbergensis skull morphologies.

Competing historical theories

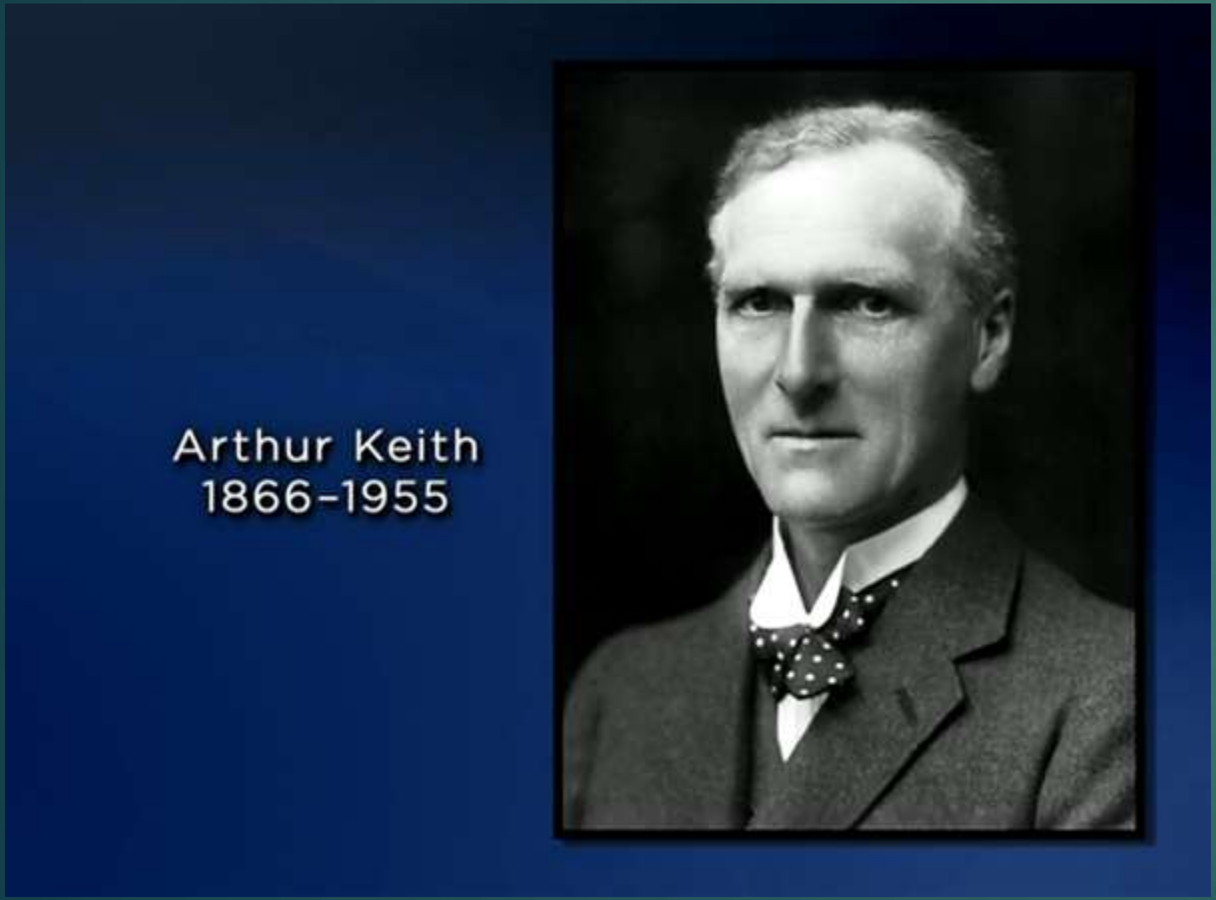
- Archeology is guided by theories
- In early 20th century, two theories were predominant
- Presapiens theory: ancient human branch existed in Europe and was ancestor of MHs; the line to modern humans was said to have branched off before the appearance of the Neanderthals.
- Preneandertal theory: No solitary MH ancestor, but a more archaic human that was ancestor of both MH and N
- Before 200K, a fossil hominin in Europe began to develop larger brain

Presapiens theory: Before 200K, fossil hominins divided into 2 branches and distinctly developed into later N and MH

Preneandertal theory: Before 200K, only 1 ancestral branch that developed after last interglacial into both N and MH

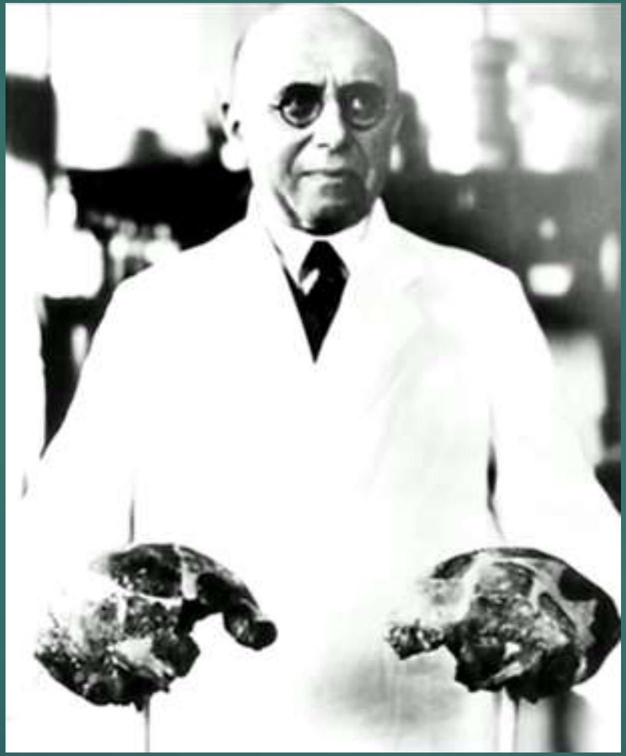


Presapiens theory: Arthur Keith and Henri Vallois

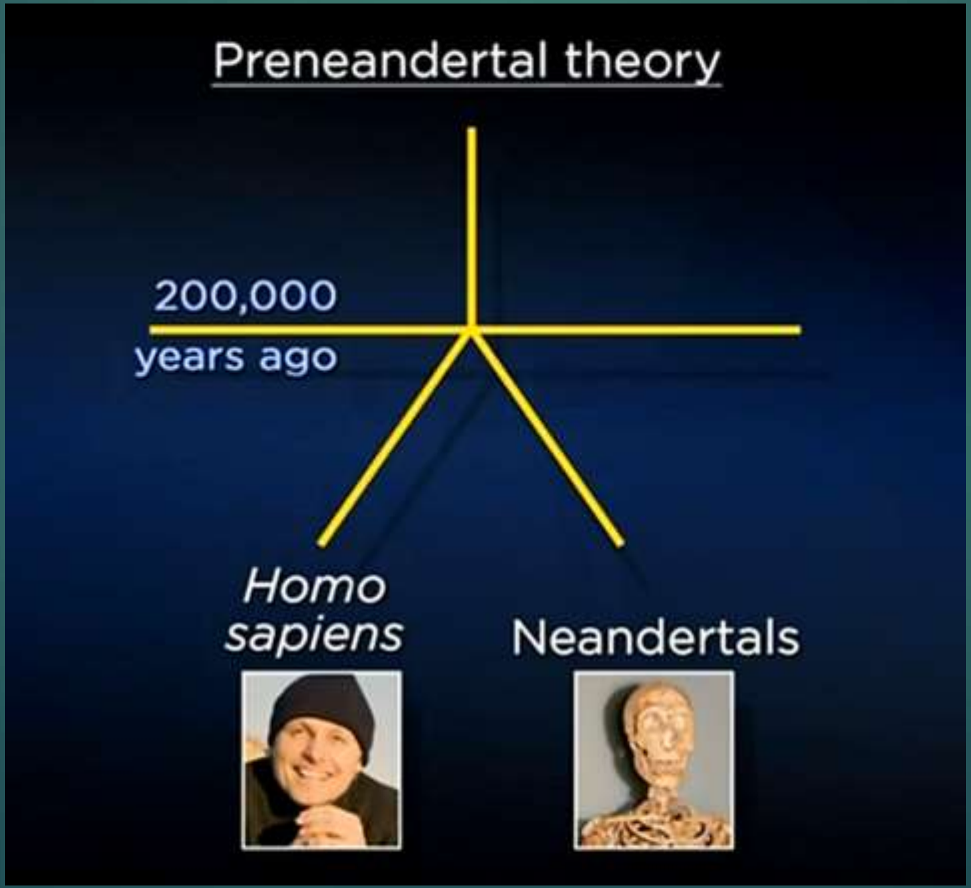


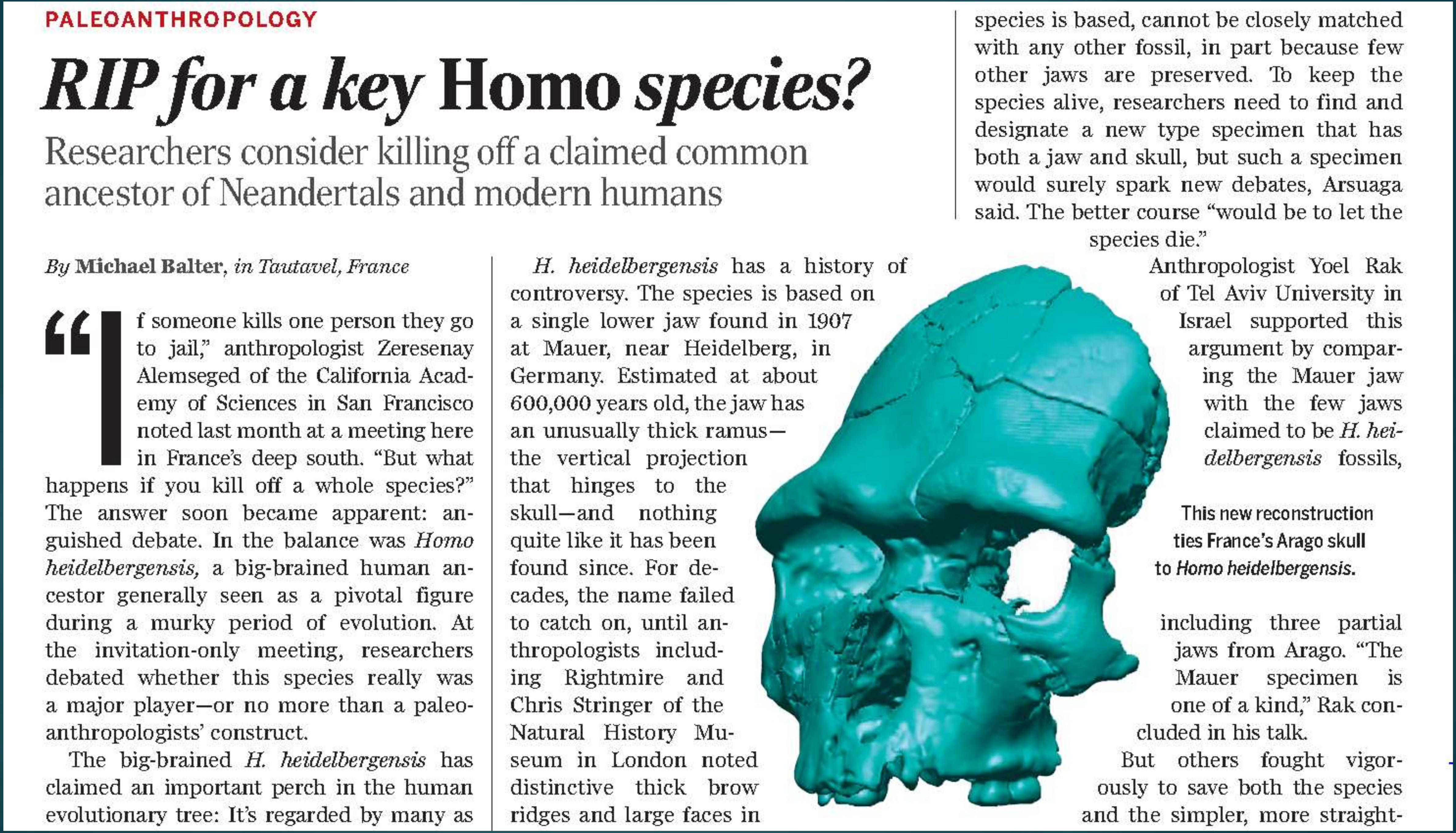
1889-1981

Preneandertal theory: Marcellin Boule in 1915, Franz Weidenreich in 1923, and Ales Hrdlicka never accepted Piltdown



All diversity of anatomy at Atapuerca is toward Neandertal; Presapiens theory was wrong, Preneandertal theory was correct; LCA much earlier than 200 Ka





PALEOANTHROPOLOGY

RIP for a key Homo *species?*

Researchers consider killing off a claimed common ancestor of Neandertals and modern humans

By **Michael Balter**, *in Tautavel, France*

"If someone kills one person they go to jail," anthropologist Zeresenay Alemseged of the California Academy of Sciences in San Francisco noted last month at a meeting here in France's deep south. "But what happens if you kill off a whole species?" The answer soon became apparent: anguished debate. In the balance was *Homo heidelbergensis,* a big-brained human ancestor generally seen as a pivotal figure during a murky period of evolution. At the invitation-only meeting, researchers debated whether this species really was a major player—or no more than a paleoanthropologists' construct.

The big-brained *H. heidelbergensis* has claimed an important perch in the human evolutionary tree: It's regarded by many as

H. heidelbergensis has a history of controversy. The species is based on a single lower jaw found in 1907 at Mauer, near Heidelberg, in Germany. Estimated at about 600,000 years old, the jaw has an unusually thick ramus—the vertical projection that hinges to the skull—and nothing quite like it has been found since. For decades, the name failed to catch on, until anthropologists including Rightmire and Chris Stringer of the Natural History Museum in London noted distinctive thick brow ridges and large faces in

species is based, cannot be closely matched with any other fossil, in part because few other jaws are preserved. To keep the species alive, researchers need to find and designate a new type specimen that has both a jaw and skull, but such a specimen would surely spark new debates, Arsuaga said. The better course "would be to let the species die."

Anthropologist Yoel Rak of Tel Aviv University in Israel supported this argument by comparing the Mauer jaw with the few jaws claimed to be *H. heidelbergensis* fossils, including three partial jaws from Arago. "The Mauer specimen is one of a kind," Rak concluded in his talk.

But others fought vigorously to save both the species and the simpler, more straight-

This new reconstruction ties France's Arago skull to *Homo heidelbergensis.*

R.I.P. for a homo species?

- *Homo heidelbergensis* is regarded by many as the common ancestor of modern humans and the Neandertals. Dating to roughly 600 Ka, it is thought to link those species and the earlier *H. erectus.*
- *H. heidelbergensis* has a history of controversy. The species is based on a single lower jaw found in 1907 at Mauer, near Heidelberg, in Germany, dated to 600 Ka, the jaw has an unusually thick ramus and nothing quite like it has been found since.
- Rightmire argues that this species fits up to 20 specimens from Europe, Africa, and Asia dated to between 800 and 200 Ka, just before *H. sapiens* appears in Africa.

Michael Balter, *Science*, 2014

R.I.P.?

- Most of these skulls had a larger brains than *H. erectus*, ~1200 cc
- In the 1970s, Stringer and others postulated a single species spanning Europe, Africa, and Asia, and resurrected the *H. heidelbergensis* name to describe it.
- Stringer noted similarity of Petralona in Europe and Broken Hill in Africa (a larger brain, a high temporal bone, a more gracile tympanic, a face that is less projecting in total)
- One classic position used to be the consideration of *Homo heidelbergensis* as the **common ancestor** of *Homo sapiens* and *Homo neanderthalensis*.

R.I.P.?

- Alternative hypotheses place *Homo heidelbergensis* as a Western European niche, while the African fossils are assigned to *Homo rhodesiensis*.

- *H. heidelbergensis* got a big boost when researchers working at the site of Sima de los Huesos in Spain attached the name to the remains of 28 hominins found there.

Sima de los Huesos

- There was a debate among scholars whether the remains at Sima de los Huesos are those of *H. heidelbergensis* or early *H. neanderthalensis*.
- In 2015, the study of mitochondrial DNA samples from three caves Sima de los Huesos revealed that they are "distantly related to the mitochondrial DNA of Denisovans rather than to that of Neanderthals."
- In 2016 nuclear DNA analysis determined the Sima hominins are Neanderthals and not Denisova hominins, and the divergence between Neanderthals, Denisovans and anatomically modern humans predates 430 Ka

R.I.P. ?

- Arsuaga went a big step further and proposed eliminating the name *H. heidelbergensis* altogether.

- He argued that the Mauer jaw, the type specimen on which the species is based, cannot be closely matched with any other fossil, in part because few other jaws are preserved

- Rightmire analyzed 34 *H. erectus* and 11 potential *H. heidelbergensis* skulls, and found that their similarities—including massive brow ridges, large faces, and flattened frontal bones—stemmed from true relatedness, rather than convergent evolution. "Calling them *H. heidelbergensis* is the correct position," he said.
- Ian Tattersall of the AMNH in NY argued that the Mauer jaw isn't so singular after all: He found close affinities between it and the Arago jaws, especially in the teeth.
- Many researches actually recognize a number of features in the Mauer mandible as neandertal-like.

Issue of divergence dates

- According to the most recent paleogenetics studies, the split between the neandertal and the modern human lineages occurred between 550-765 Ka.

- The Mauer mandible dated to 600 Ka is the oldest *Homo heidelbergensis*, and other specimens traditionally assigned to *H. heidelbergensis* are more recent than that.

- Due to their dating, these imply that *H. heidelbergensis* cannot be the common ancestor of Neandertals and modern humans.

Problems with *H. heidelbergensis*

- For some, it was the last common ancestor for the subsequent species *Homo sapiens* and *Homo neanderthalensis*;
- *Others regard it as only a European form, giving rise to the Neanderthals*.
- Following the impact of recent genomic studies indicating hybridization between modern humans and both Neanderthals and "Denisovans", the status of these as separate taxa is now under discussion.
- German Mauer jaw is type specimen: but mostly only upper craniums have been found, not mandibles; idiosyncratic morphology of the type specimen is problematic

H. heidelbergensis

- Around 700 Ka, and perhaps earlier, *H. erectus* in Africa gave rise to *H. heidelbergensis*
- *H. heidelbergensis*, often referred to as an "archaic" *Homo sapiens,* was an active big-game hunter, produced sophisticated Levallois style tools, and by at least 400 Ka had learned to control fire
- Neanderthals (*H. neanderthalensis*), cold-adapted hominins with stout physiques, complex behaviors, and brains similar in size to ours, are thought to have evolved from *H. heidelbergensis* populations in Europe by at least 430 Ka
- *Homo heidelbergensis* may reach back to 1.3 million years ago, and include early humans from Spain (‘*Homo antecessor, 1 Ma*), England (1 Ma), and Italy (Ceprano, ~ 1 Ma)

Rightmire, 2009; Roebroeks and Villa, 2011; Rightmire, 2008; Hublin, 2009.

Last common ancestor of MHs & Ns

- It is generally believed that the lineages of modern humans (*Homo sapiens*) and Neanderthals (*Homo neanderthalensis*) originated during this time, but the nature of their last common ancestor, when and where this ancestor lived, and what the ancestor should be called are continuing sources of controversy. One popular designation for the last common ancestor is *Homo heidelbergensis.*

Chris Stringer: vote for archaic H. sapiens

- For me, the pattern of anatomically modern humans is really the pattern in the skeleton we have today, particularly a high and rounded skull, a small face under the braincase, the chin on the lower jaw, a lighter-built skeleton with a narrow pelvis… which typify MHs today.
- 150 Ka to 200 Ka at least for most of that pattern in Africa, with the material from Herto 1 and 2 and Omo 1. So 200K and later.
- Ancestor of *sapiens*, Ds, Ns: Their LCA must go back beyond the date of the Sima materials, at 430 Ka. If we have a common ancestor at 600-700 Ka in Europe , there must be quite a long record of archaic *Homo sapiens* in Africa before 200 to 400 Ka.
- We need a term for *Homo sapiens* in Africa before you have the majority of modern human features. So that is where I use the term archaic *Homo sapiens*. To use that term outside of Africa is meaningless. So I am against the use of archaic *Homo sapiens* anywhere except in Africa

Chris Stringer 2: *H. antecessor* as LCA

- There was a wide-spread species in the Middle Pleistocene that fits that morphology,
- Whether that is the common ancestor of us and Neanderthals, is now a much more open question, because when you look at the deep divergence dates between us and Neanderthals, that divergence could be beyond that any of the known *heidelbergensis* fossils.
- The idea that the *sapiens* face - rather than a late development in the last 250 K years- may be primitive and it goes back deep into the Middle Pleistocene. There is better evidence that the modern-looking facial morphology that we have - this retracting face with delicate cheekbones - is there in the *H. antecessor* fossils

Stringer

- In which case, the big skulls of *H. heidelbergensis,* which does not show that modern human morphology in the face - may be not on the modern human lineage but may be part of a clade which includes the Neanderthals – having this distinctive face that is more inflated, that lacks the canine fossa… Is the common ancestor more like *H. antecessor* in the face, and less like the classic *H. heidelbergensis*?
- There were earlier African dispersals, but the majority of the DNA we find today in people even from Australia or New Guinea is coming from the ~60 K years dispersal. So that would mean that these earlier dispersals ultimately failed in the sense of continuing their DNA into the future.

Stringer: *Antecessor*

- Because the Sima fossils are now dated at 430 Ka, and as belonging to Neanderthal line, their ancestor probably lived further back in time than *Homo heidelbergensis*.
- Studies of facial evolution published earlier this year also cast doubt on *heidelbergensis* as our ancient ancestor. My view had been that *Homo heidelbergensis*'s big face could have evolved into both the Neanderthal face, with its huge nose and puffy cheekbones, and the flatter face of sapiens, with its more delicate cheekbones.
- However, a child's skull about 850 Ka assigned to the species *Homo antecessor* ("Pioneer human"), found at another site in the Atapuerca hills in 1997, looks more modern facially than *Homo heidelbergensis*, the Sima people or mainstream Neanderthals; so too do Chinese fossils such as the Dali skull, dating from around 300 Ka.
- The upshot is that it seems possible that the common ancestor of Neanderthals, Denisovans and us possessed a more modern-looking face, which we kept, the Denisovans perhaps also kept (if Chinese fossils such as the Dali skull turn out to be Denisovans, once we have their DNA), and the Neanderthals and Homo heidelbergensis lost during their evolution.
- Who exactly that common ancestor was remains to be determined, but it probably had a face like that of Homo antecessor, and it could have lived in Europe, Asia or Africa.

Two hypothesis of taxonomy of *H. heidelbergensis*

H. antecessor as LCA; Divergence at 800 Ka

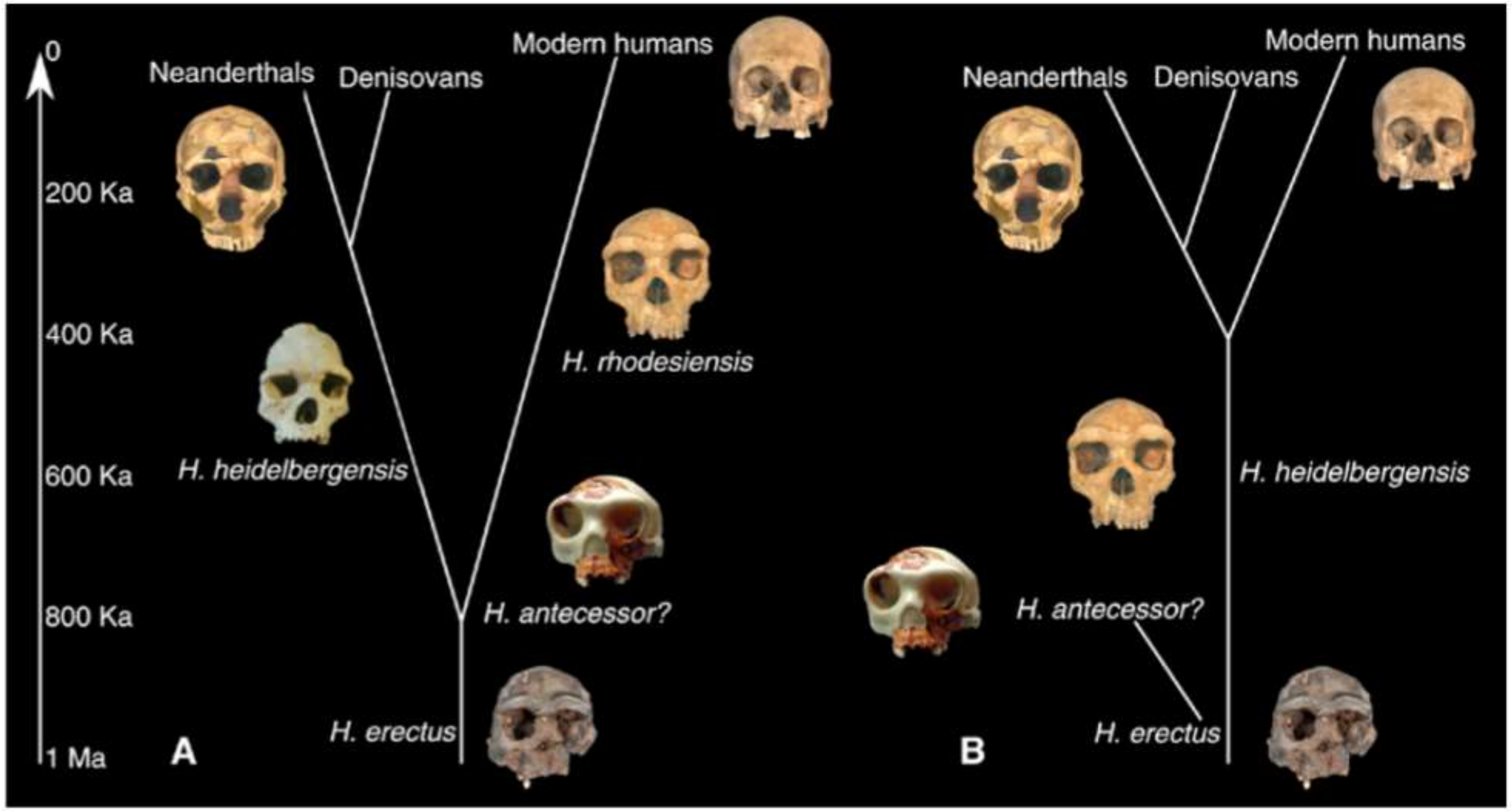
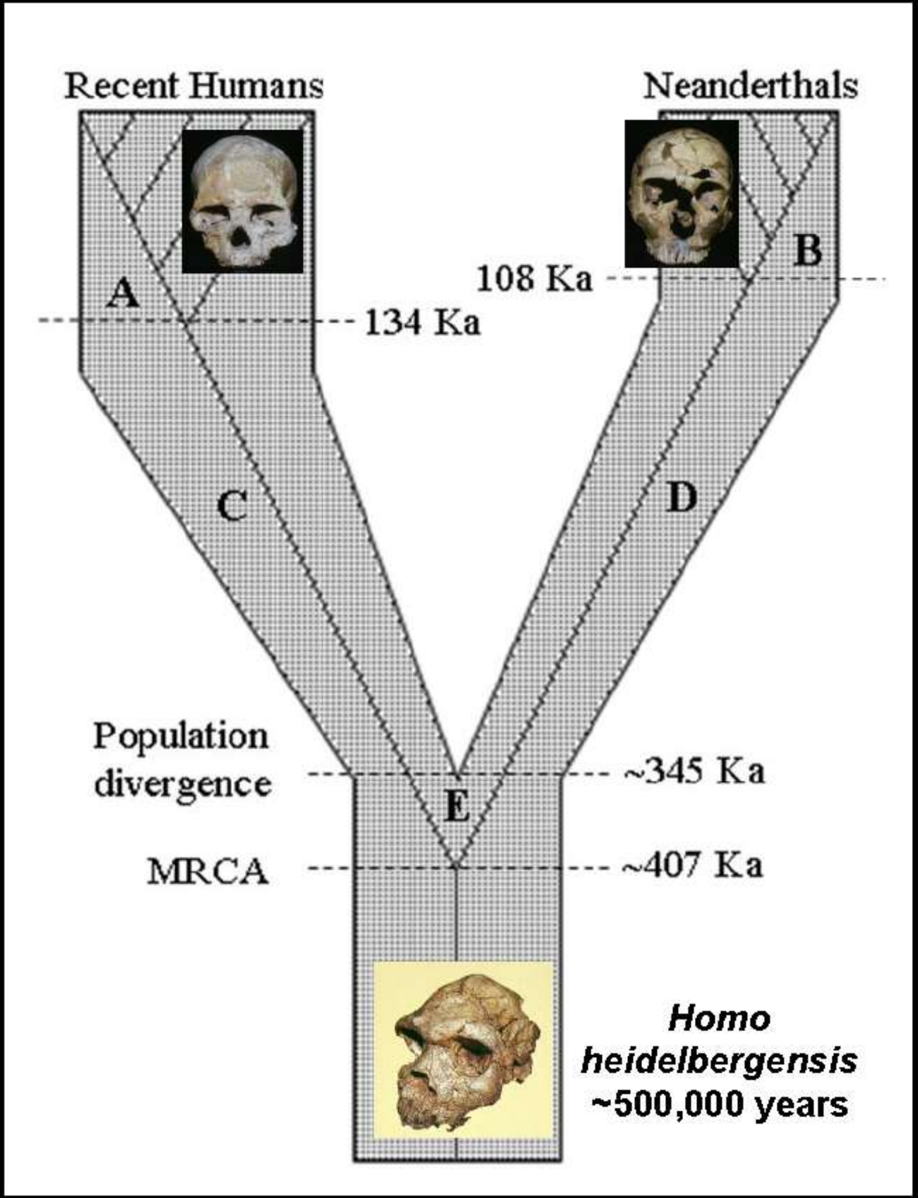


Figure 1. The two main hypotheses for the taxonomic placement of *H. heidelbergensis*. (A) European *H. heidelbergensis* as the exclusive ancestor of Neanderthals and the related Denisovans. (B) European *H. heidelbergensis* as the last common ancestor of modern humans, Neanderthals and the related Denisovans. Pictures: *H. antecessor* Wikimedia Commons; *H. heidelbergensis* (Arago) in Figure 1A: Chris Stringer; all other images with kind permission of the Natural History Museum, London.

H. heidelbergensis as LCA; Divergence at 450 Ka

The evolution of Modern Humans and Neanderthals

(based on fossil and genetic data)

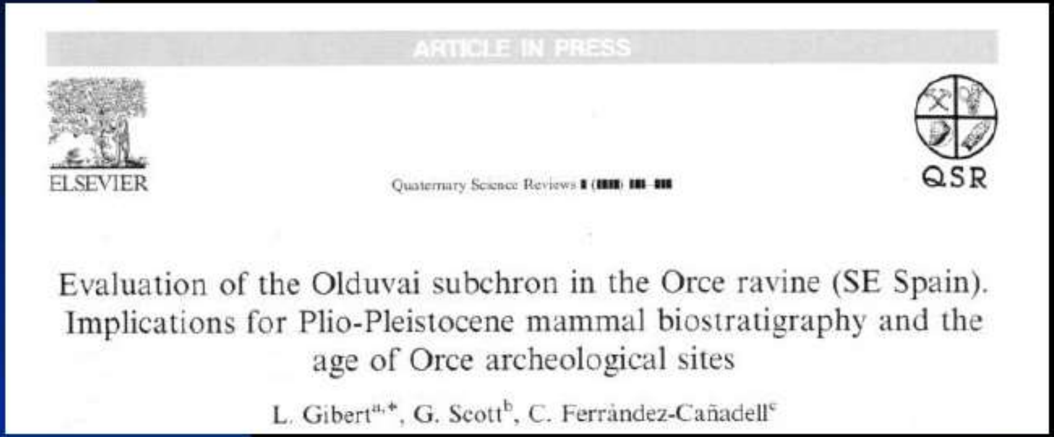


Naturwissenschaften. 2007 Feb: 94(2):107-112.

Evidence of earliest human occurrence in Europe: the site of Pirro Nord (Southern Italy).

Arzarello M, Marcolini F, Pavia G, Pavia M, Petronio C, Petrucci M, Rook L, Sardella R.

1.5 Ma?



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ELSEVIER

Quaternary Science Reviews ■ (■■■■) ■■■-■■■

QSR

Evaluation of the Olduvai subchron in the Orce ravine (SE Spain). Implications for Plio-Pleistocene mammal biostratigraphy and the age of Orce archeological sites

L. Gibert[a,*], G. Scott[b], C. Ferràndez-Cañadell[c]

1.4 Ma?

1.2 Million year old jawbone found in Sima del Elefante Atapuerca, Spain

1.2 Ma?

Homo heidelbergensis

- Zeray’s opinion, not definitive:
- Widely spread, and locally specialized version of *H. erectus*
- Or a distinct species
- In both cases, *H. heidelbergensis* is ancestor of both Ns and MHs

Revising the hypodigm of *Homo heidelbergensis*: A view from the Eastern Mediterranean (23 slides)

- The hominin mandible BH-1 from the Middle Pleistocene cave of Mala Balanica suggested the possibility that human populations in this part of the continent were not subject to the process of Neanderthalization observed in the west.
- Review of Central Balkans: fossil record of the early MP in this region suggests that Europe was inhabited by two different populations:
  - a population in the west of the continent with derived Neanderthal morphology;
  - more variable population in the east characterized by a combination of plesiomorphous and synapomorphous traits.
- We suggest that — in order to continue using the nomenclature of *Homo heidelbergensis* — the current hypodigm needs to be revised to include only the specimens from the latter group.

Roksandic, M., et al., Revising the hypodigm of *Homo heidelbergensis:* A view from the Eastern Mediterranean, Quaternary International (2017), https://doi.Org/10.1016/j.quaint.2017.10.013

MP

- The Middle Pleistocene (MP) fossil record plays a crucial role in understanding later human evolution: this was the period characterized by greater encephalization, accompanied by dental reduction and associated changes in morphology, as well as changes in behavioral repertoire.
- Since Stringer (1983) re-introduced *Homo heidelbergensis* (Schoetensack, 1908) as a species, the MP human fossil record of Europe has been associated with this nomenclature.
- What is currently considered as European *H. heidelbergensis* (H. *heidelbergensis sensu stricto*) is a mixture of specimens clearly ancestral to Neanderthals and those without demonstrable Neanderthal traits

Revising the hypodigm of *Homo heidelbergensis*

- Notably, it includes the Sima de los Huesos material, with a large number of distinctly Neanderthal traits. According to Bermudez de Castro et al. (2011, 2015), even the Early Pleistocene material from Europe (Gran Dolina-TD6) shows derived Neanderthal traits.
- Considering that morphological differences between African and European specimens are not clear cut, *Homo heidelbergensis* could be equated with a purported MP Afro-European population which was ancestral to both Neanderthal (European) and modern human (African) lineages.

Revising the hypodigm of *Homo heidelbergensis*

- Stringer (2012) suggested that *Homo heidelbergensis* as a species makes sense only if Sima de los Huesos is removed from the hypodigm which, on the other hand, could potentially include specimens as geographically distant as Mauer in Germany, Bodo in Ethiopia, and Yunxian in China (although the east Asian specimens were tentatively associated with the Denisovans).
- Thus H. *heidelbergensis* would be distinct enough from smaller-brained Erectines and represent the MRCA of Neanderthals, Denisovans, and modern humans.

Revising the hypodigm of *Homo heidelbergensis*

- The réintroduction of *Homo heidelbergensis* did not result in a greater understanding of the relationship between MP African hominins at the origin of our lineage and the MP European fossils at the origin of the Neanderthal lineage.
- Important questions remain open:
  - 1) what was the relationship of European *H. heidelbergensis* to the earlier European specimens from Gran Dolina and Sima del Elefante in Spain
  - 2) what was their relationship to the contemporaneous African specimens assigned to *H. heidelbergensis sensu lato,* or to *H. rhodesiensis*
  - 3) when did the split between the African and Eurasian lineages occur
  - 4) what was the relationship of African and European MP hominins with contemporaneous Asian specimens?

Revising the hypodigm of *Homo heidelbergensis*

- On the basis of genetic data, the split between the ancestors of Neanderthals and those of modern humans was postulated to have happened around 300-400 ka
- The oldest hominin aDNA retrieved from Sima de los Huesos shows a mitochondrial genome more closely related to “Denisovans”
- However, nuclear DNA of an additional two individuals from the same site shows a closer relatedness to Neanderthals
- Together with aDNA results and the presence of Neanderthal autapomorphies in Sima de los Huesos, the re-dating of the material to 430 ka supports the estimate of 420-770 ka for the initial separation of Neanderthal, Denisovans and contemporary African populations.

Revising the hypodigm of *Homo heidelbergensis*

- Furthermore, interbreeding between Neanderthals and modern humans, long held to be improbable based on the mtDNA evidence was confirmed by the examination of whole genome sequences of several Neanderthals, while the putative date for introgression was pushed back to 270 ka
- A recent review by Pääbo (2015) states that the genomes of Neanderthals and Denisovans suggest that "our ancestors were part of a web of now-extinct populations linked by limited, but intermittent or sometimes perhaps even persistent, gene flow" complicating the famous "muddle in the middle".
- Hawks' (2013) assertion that all three groups were part of the biological species of *Homo sapiens* — which could have been far more variable in the Middle Pleistocene than it is today — seems more plausible than ever.

Revising the hypodigm of *Homo heidelbergensis*

- Based on the current fossil record, Neanderthals are a distinctly western European-derived population whose morphology is likely linked to isolation induced by glacial cycles. This isolation should not be construed as absolute and/or resulting from insurmountable geographic barriers, but rather as a product of the peripheral position of the westernmost peninsula and its geographic distance from other contemporaneous hominin populations.
- With Sima de los Huesos at the far west of the continent presenting undeniable evidence of derived Neanderthal morphology from at least 430 ka, the lack (or attenuation) of Neanderthal traits in contemporaneous specimens from other parts of Europe needs new explanations.

Revising the hypodigm of *Homo heidelbergensis*

- Central European Middle Pleistocene specimens (Mauer, Bilzingsleben, and Vértesszôllôs) are mostly characterized by evidence of primitive Erectine traits.

- The Mauer mandible is particularly important. Dated to ca 609 ± 40 ka by a combined ESR/U-series method, it could represent the population from which both Neanderthals and modern humans were derived. However, if a specimen this old can be demonstrated to show Neanderthal traits, it should be excluded from the modern human lineage.

Revising the hypodigm of *Homo heidelbergensis:* Mauer

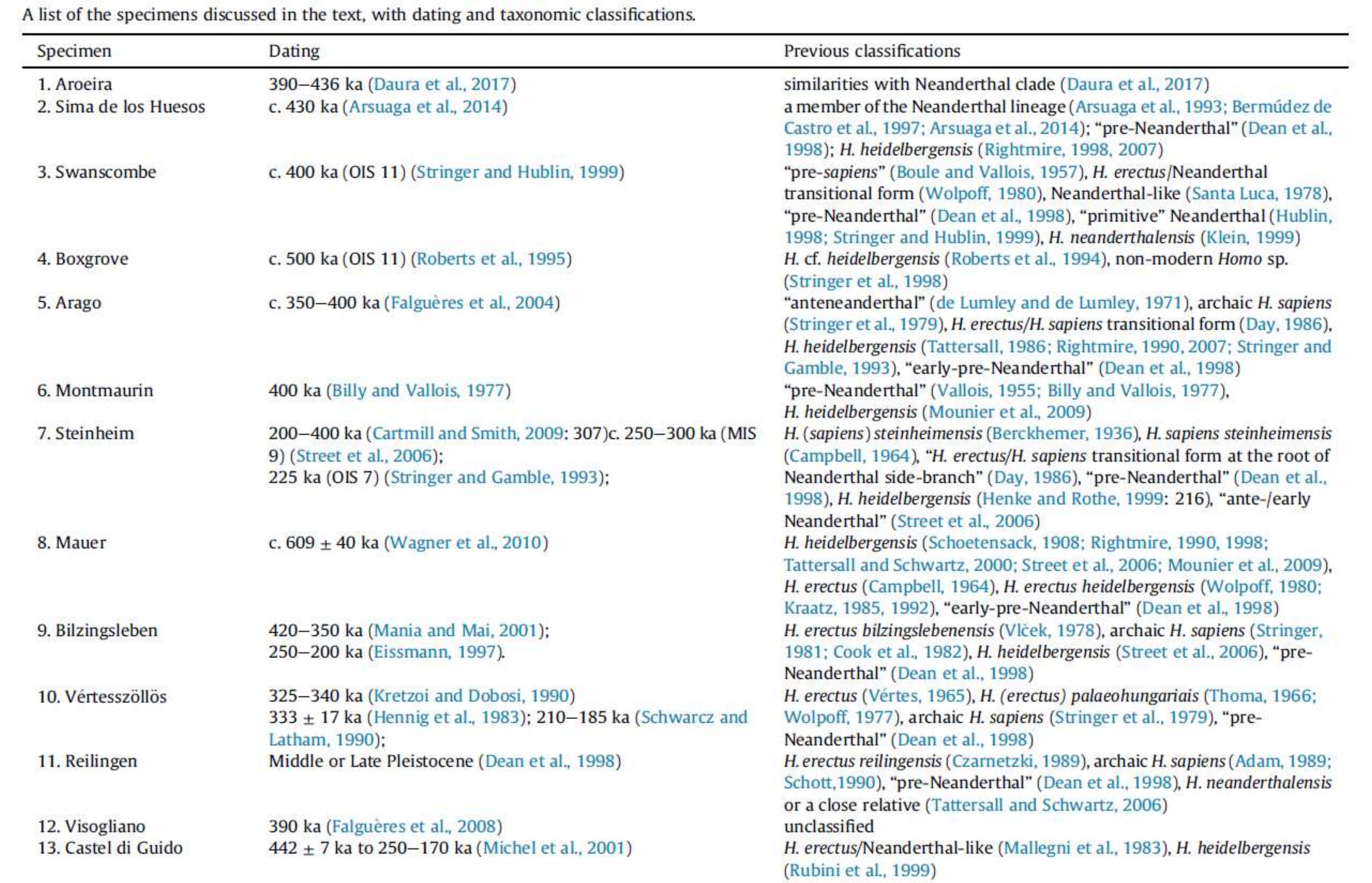
- Rosas and Bermudez de Castro (1998) argued that it shows definite Neanderthal autapomorphies in the position of the mental foramen and the existence of a retromolar space, and therefore cannot be regarded as a stem species of Neanderthals and modern humans.
- However, the position of the mental foramen falls within the range of overlap between modern humans and Neanderthals, and their definition of retromolar space does not conform to that used by other workers (Cartmill and Smith, 2009: 308).
- Mauer exhibits a posteriorly located deepest point of the mandibular notch - a trait commonly observed in Neanderthals - although, according to Wolpoff and Frayer (2005) mandibular ramus features are not diagnostic.

Mauer

- Dental traits that appear most frequently in Neanderthals (mid-trigonid crest with a deep, pit-like anterior fovea; distal trigonid crest in the third molars; and a continuous transverse crest in the lower second premolars) are not recorded in Mauer's dentition, neither in the occlusal morphology nor the morphology of the cemento-enamel junction (Martinon-Torres and Bermudez de Castro, 2015).
- In terms of enamel-dentine junction (EDJ) morphology, the single molar examined by Skinner et al. (2016) is similar to BH-1 in possessing a primitive EDJ morphology that tends to fall outside of the variation present in the *H. neanderthalensis*, Pleistocene *H. sapiens*, and recent *H. sapiens* samples. In PCA plots it is often positioned together with BH-1, between *H. erectus* on the one hand, and Pleistocene *H. sapiens* and *H. neanderthalensis* on the other hand.

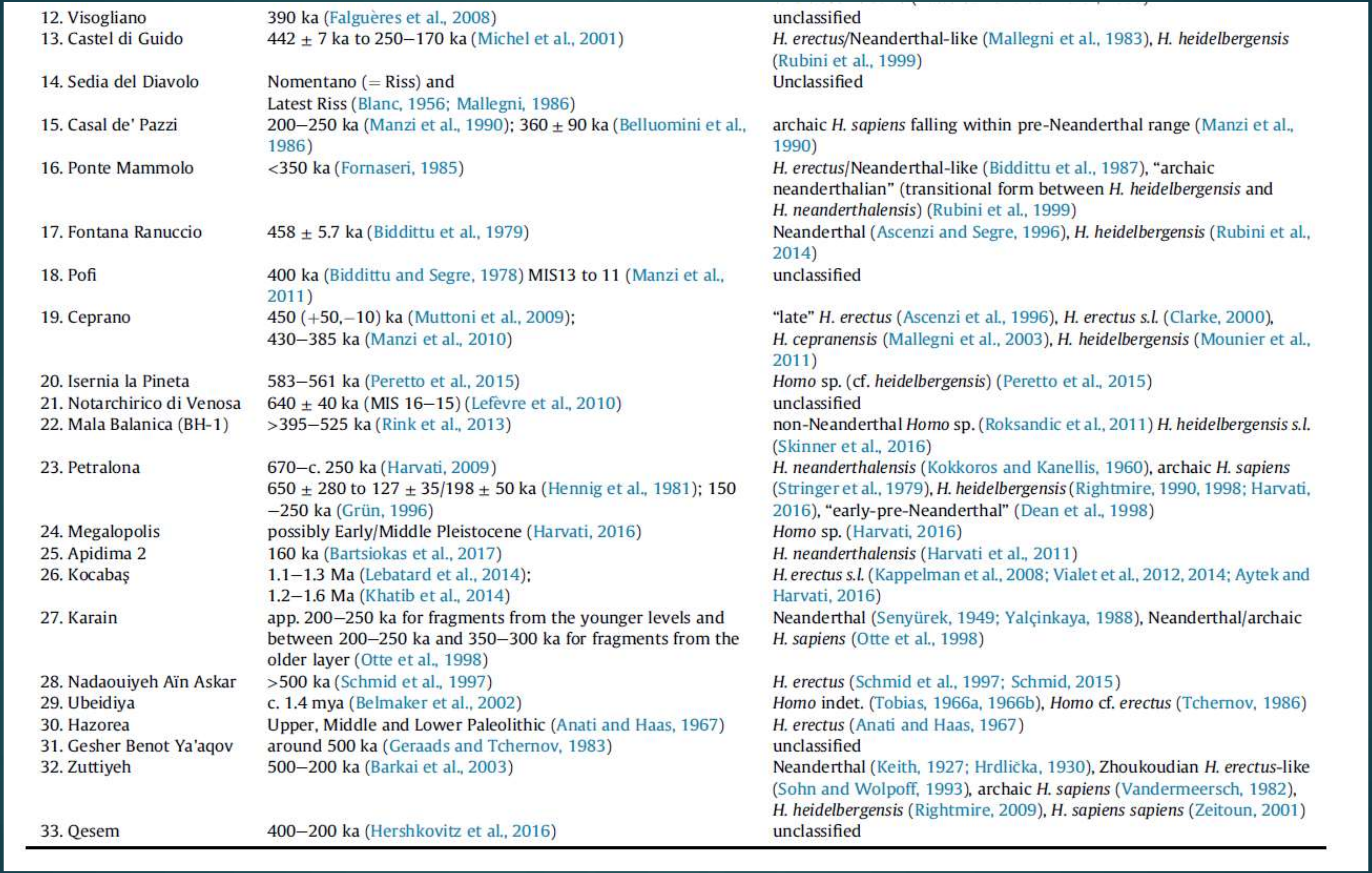
Revising the hypodigm of *Homo heidelbergensis:* Bilzingsleben

- Given that dental traits are taxonomically more informative than the more variable mandibular traits, Mauer should not be included in the Neanderthal ancestral lineage; accordingly, we agree with Arsuaga et al. (2014) that *Homo heidelbergensis* should exclude all specimens with demonstrable Neanderthal traits.
- The Bilzingsleben material consists of **28** skull fragments, one mandible and eight very fragmented teeth with worn edges, dated to 350—400 ka or 250—200 ka.
- The ensemble is characterized by a preponderance of primitive (Erectine) traits, especially in the shape of the occipital and the supraorbital torus. The robust individuals I and II are represented by a series of skull fragments, and individual III is represented by a gracile mandible.
- Individuals I and II from Bilzingsleben are most similar to OH-9 from Olduvai Gorge, although similarities were also seen with Asian *H. erectus* specimens Zhoukoudian III and Sangiran III. The mandible is most similar to Zhoukoudian mandibles HI and BI, but also has likeness to Arago II and XIII. However, a flat articular eminence on the temporal bone should be noted as a Neanderthal trait.



A list of the specimens discussed in the text, with dating and taxonomic classifications.

Specimen	Dating	Previous classifications
1. Aroeira	390–436 ka (Daura et al., 2017)	similarities with Neanderthal clade (Daura et al., 2017)
2. Sima de los Huesos	c. 430 ka (Arsuaga et al., 2014)	a member of the Neanderthal lineage (Arsuaga et al., 1993; Bermúdez de Castro et al., 1997; Arsuaga et al., 2014); "pre-Neanderthal" (Dean et al., 1998); *H. heidelbergensis* (Rightmire, 1998, 2007)
3. Swanscombe	c. 400 ka (OIS 11) (Stringer and Hublin, 1999)	"pre-*sapiens*" (Boule and Vallois, 1957), *H. erectus*/Neanderthal transitional form (Wolpoff, 1980), Neanderthal-like (Santa Luca, 1978), "pre-Neanderthal" (Dean et al., 1998), "primitive" Neanderthal (Hublin, 1998; Stringer and Hublin, 1999), *H. neanderthalensis* (Klein, 1999)
4. Boxgrove	c. 500 ka (OIS 11) (Roberts et al., 1995)	*H.* cf. *heidelbergensis* (Roberts et al., 1994), non-modern *Homo* sp. (Stringer et al., 1998)
5. Arago	c. 350–400 ka (Falguères et al., 2004)	"anteneanderthal" (de Lumley and de Lumley, 1971), archaic *H. sapiens* (Stringer et al., 1979), *H. erectus/H. sapiens* transitional form (Day, 1986), *H. heidelbergensis* (Tattersall, 1986; Rightmire, 1990, 2007; Stringer and Gamble, 1993), "early-pre-Neanderthal" (Dean et al., 1998)
6. Montmaurin	400 ka (Billy and Vallois, 1977)	"pre-Neanderthal" (Vallois, 1955; Billy and Vallois, 1977), *H. heidelbergensis* (Mounier et al., 2009)
7. Steinheim	200–400 ka (Cartmill and Smith, 2009: 307)c. 250–300 ka (MIS 9) (Street et al., 2006); 225 ka (OIS 7) (Stringer and Gamble, 1993);	*H.* (*sapiens*) *steinheimensis* (Berckhemer, 1936), *H. sapiens steinheimensis* (Campbell, 1964), "*H. erectus/H. sapiens* transitional form at the root of Neanderthal side-branch" (Day, 1986), "pre-Neanderthal" (Dean et al., 1998), *H. heidelbergensis* (Henke and Rothe, 1999: 216), "ante-/early Neanderthal" (Street et al., 2006)
8. Mauer	c. 609 ± 40 ka (Wagner et al., 2010)	*H. heidelbergensis* (Schoetensack, 1908; Rightmire, 1990, 1998; Tattersall and Schwartz, 2000; Street et al., 2006; Mounier et al., 2009), *H. erectus* (Campbell, 1964), *H. erectus heidelbergensis* (Wolpoff, 1980; Kraatz, 1985, 1992), "early-pre-Neanderthal" (Dean et al., 1998)
9. Bilzingsleben	420–350 ka (Mania and Mai, 2001); 250–200 ka (Eissmann, 1997).	*H. erectus bilzingslebenensis* (Vlček, 1978), archaic *H. sapiens* (Stringer, 1981; Cook et al., 1982), *H. heidelbergensis* (Street et al., 2006), "pre-Neanderthal" (Dean et al., 1998)
10. Vértesszöllös	325–340 ka (Kretzoi and Dobosi, 1990) 333 ± 17 ka (Hennig et al., 1983); 210–185 ka (Schwarcz and Latham, 1990);	*H. erectus* (Vértes, 1965), *H. (erectus) palaeohungariais* (Thoma, 1966; Wolpoff, 1977), archaic *H. sapiens* (Stringer et al., 1979), "pre-Neanderthal" (Dean et al., 1998)
11. Reilingen	Middle or Late Pleistocene (Dean et al., 1998)	*H. erectus reilingensis* (Czarnetzki, 1989), archaic *H. sapiens* (Adam, 1989; Schott,1990), "pre-Neanderthal" (Dean et al., 1998), *H. neanderthalensis* or a close relative (Tattersall and Schwartz, 2006)
12. Visogliano	390 ka (Falguères et al., 2008)	unclassified
13. Castel di Guido	442 ± 7 ka to 250–170 ka (Michel et al., 2001)	*H. erectus*/Neanderthal-like (Mallegni et al., 1983), *H. heidelbergensis* (Rubini et al., 1999)



12. Visogliano	390 ka (Falguères et al., 2008)	unclassified
13. Castel di Guido	442 ± 7 ka to 250–170 ka (Michel et al., 2001)	*H. erectus*/Neanderthal-like (Mallegni et al., 1983), *H. heidelbergensis* (Rubini et al., 1999)
14. Sedia del Diavolo	Nomentano (= Riss) and Latest Riss (Blanc, 1956; Mallegni, 1986)	Unclassified
15. Casal de' Pazzi	200–250 ka (Manzi et al., 1990); 360 ± 90 ka (Belluomini et al., 1986)	archaic *H. sapiens* falling within pre-Neanderthal range (Manzi et al., 1990)
16. Ponte Mammolo	<350 ka (Fornaseri, 1985)	*H. erectus*/Neanderthal-like (Biddittu et al., 1987), "archaic neanderthalian" (transitional form between *H. heidelbergensis* and *H. neanderthalensis*) (Rubini et al., 1999)
17. Fontana Ranuccio	458 ± 5.7 ka (Biddittu et al., 1979)	Neanderthal (Ascenzi and Segre, 1996), *H. heidelbergensis* (Rubini et al., 2014)
18. Pofi	400 ka (Biddittu and Segre, 1978) MIS13 to 11 (Manzi et al., 2011)	unclassified
19. Ceprano	450 (+50,−10) ka (Muttoni et al., 2009); 430–385 ka (Manzi et al., 2010)	"late" *H. erectus* (Ascenzi et al., 1996), *H. erectus s.l.* (Clarke, 2000), *H. cepranensis* (Mallegni et al., 2003), *H. heidelbergensis* (Mounier et al., 2011)
20. Isernia la Pineta	583–561 ka (Peretto et al., 2015)	*Homo* sp. (cf. *heidelbergensis*) (Peretto et al., 2015)
21. Notarchirico di Venosa	640 ± 40 ka (MIS 16–15) (Lefèvre et al., 2010)	unclassified
22. Mala Balanica (BH-1)	>395–525 ka (Rink et al., 2013)	non-Neanderthal *Homo* sp. (Roksandic et al., 2011) *H. heidelbergensis s.l.* (Skinner et al., 2016)
23. Petralona	670–c. 250 ka (Harvati, 2009) 650 ± 280 to 127 ± 35/198 ± 50 ka (Hennig et al., 1981); 150 −250 ka (Grün, 1996)	*H. neanderthalensis* (Kokkoros and Kanellis, 1960), archaic *H. sapiens* (Stringer et al., 1979), *H. heidelbergensis* (Rightmire, 1990, 1998; Harvati, 2016), "early-pre-Neanderthal" (Dean et al., 1998)
24. Megalopolis	possibly Early/Middle Pleistocene (Harvati, 2016)	*Homo* sp. (Harvati, 2016)
25. Apidima 2	160 ka (Bartsiokas et al., 2017)	*H. neanderthalensis* (Harvati et al., 2011)
26. Kocabaş	1.1–1.3 Ma (Lebatard et al., 2014); 1.2–1.6 Ma (Khatib et al., 2014)	*H. erectus s.l.* (Kappelman et al., 2008; Vialet et al., 2012, 2014; Aytek and Harvati, 2016)
27. Karain	app. 200–250 ka for fragments from the younger levels and between 200–250 ka and 350–300 ka for fragments from the older layer (Otte et al., 1998)	Neanderthal (Senyürek, 1949; Yalçinkaya, 1988), Neanderthal/archaic *H. sapiens* (Otte et al., 1998)
28. Nadaouiyeh Aïn Askar	>500 ka (Schmid et al., 1997)	*H. erectus* (Schmid et al., 1997; Schmid, 2015)
29. Ubeidiya	c. 1.4 mya (Belmaker et al., 2002)	*Homo* indet. (Tobias, 1966a, 1966b), *Homo* cf. *erectus* (Tchernov, 1986)
30. Hazorea	Upper, Middle and Lower Paleolithic (Anati and Haas, 1967)	*H. erectus* (Anati and Haas, 1967)
31. Gesher Benot Ya'aqov	around 500 ka (Geraads and Tchernov, 1983)	unclassified
32. Zuttiyeh	500–200 ka (Barkai et al., 2003)	Neanderthal (Keith, 1927; Hrdlička, 1930), Zhoukoudian *H. erectus*-like (Sohn and Wolpoff, 1993), archaic *H. sapiens* (Vandermeersch, 1982), *H. heidelbergensis* (Rightmire, 2009), *H. sapiens sapiens* (Zeitoun, 2001)
33. Qesem	400–200 ka (Hershkovitz et al., 2016)	unclassified

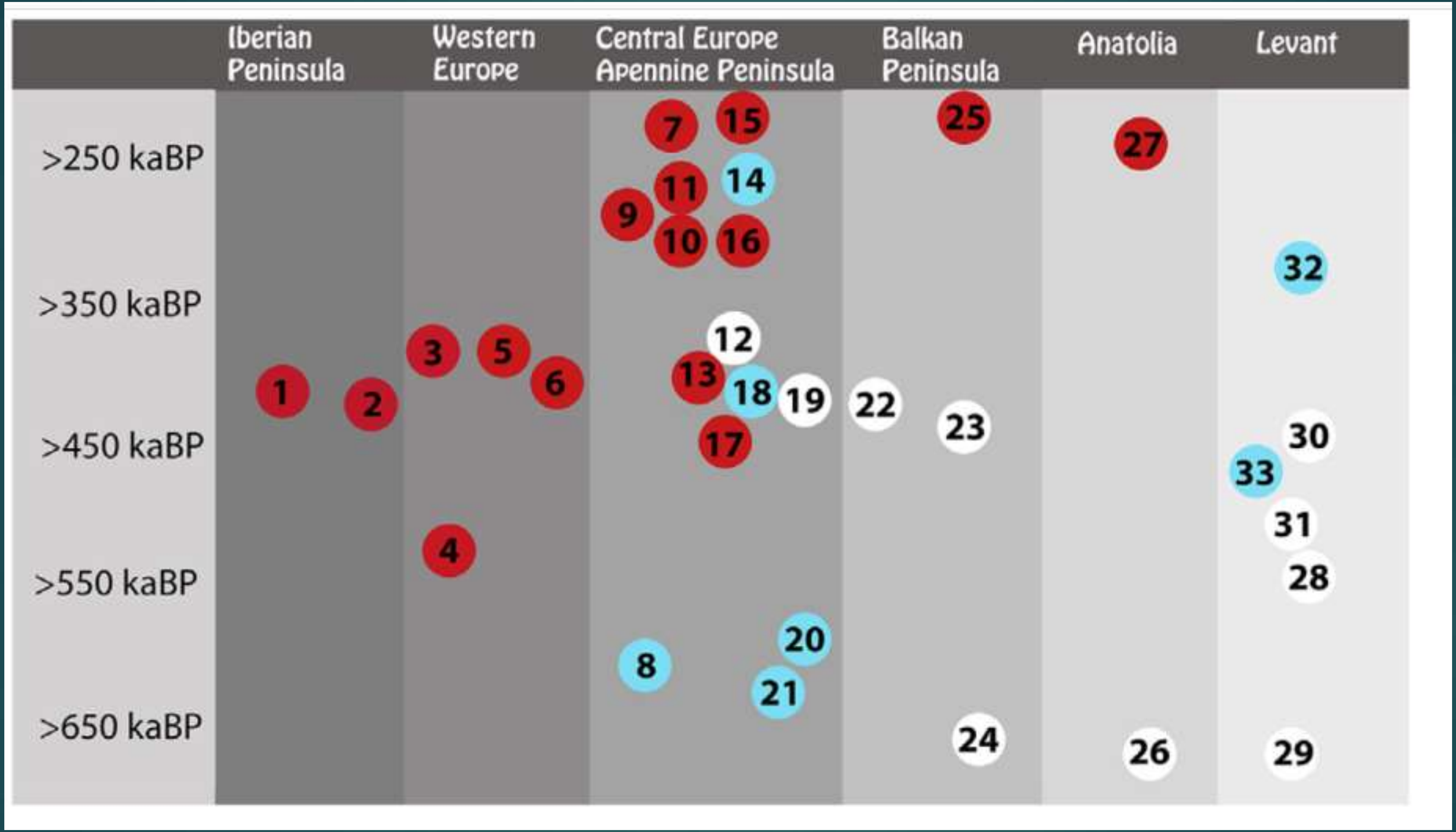
Revising the hypodigm: Vértesszôllôs

- Vértesszôllôs is represented by an almost complete occipital bone with primitive morphology, but it is tall and has a relatively large estimated cranial capacity. The hominin-bearing layer at the site was dated to 325-340 ka, although a younger date of 210-185 ka was also proposed. The occipital bone is thick, with a sharp angle between nuchal and occipital planes. A more or less continuous, deep sulcus along the superior nuchal line creates, from below, a pronounced, but only moderately wide occipital torus with no suprainiac depression above it, or an incipient one.The inion is set high and it coincides with opisthocranion (this primitive trait is also found in Bilzingsleben). The primitive morphology with a large estimated cranial capacity resulted in different taxonomic determinations and the specimen was identified as *Homo erectus, Homo (erectus* seu *sapiens) palaeohungaricus* and archaic *Homo sapiens*.

Reilingen

- A posterior part of neurocranium (occipital, parietals, right temporal) from Reilingen is dated to the Middle or Late Pleistocene (Dean et al., 1998). According to Dean et al. (1998) and Martinez et al. (2006), the specimen is characterized by a combination of primitive (low cranial vault; maximum cranial breadth at the supramastoid level; pentagonal shape in the occipital view; short parietal coronal arc with short sagittal chord; angular torus and posterior slope of the tympanic plate; separation of the vaginal crest from the mastoid process in the temporal bone) combined with a number of derived Neanderthal traits (wide and convex occipital plane; lambdoid flattening; occipital torus with bilateral projection; incipient *en bombe* shape in the occipital view; extensive suprainiac fossa; occipital bun with an inferior shelf; lambdoid flattening and strong juxtamastoid eminence; flat articular eminence; configuration of the styloid process, digastric groove, and stylomastoid foramen on the temporal portion). The relevance of Reilingen for this discussion is limited by the potentially late date of the specimen.

Revising the hypodigm of *Homo heidelbergensis*



Red = N traits

Blue = ambiguous

White = no traits

Revising the hypodigm of *Homo heidelbergensis*

- **Last slide, Fig. 1.** Schematic distribution of the hominin material over geographic and temporal span discussed in the paper. Red circles indicate unambiguous presence of Neanderthal traits; white circles represent lack of Neanderthal traits; blue circles indicate ambiguous or insufficient morphology. Please note that the dates are represented as midpoints of accepted dates and the chronological placement is not absolute.
- 1. Aroeira, 2. Sima de los Huesos, 3. Swanscombe, 4. Boxgrove, 5. Arago, 6. Montmaurin, 7. Stein- heim, 8. Mauer, 9. Bilzingsleben, 10. Vértesszôllôs, 11. Reilingen, 12. Visogliano, 13. Castel di Guido, 14. Sedia del Diavolo, 15. Casai de' Pazzi, 16. Ponte Mammolo, 17. Fontana Ranuccio, 18. Pofi, 19. Ceprano, 20. Isernia la Pineta, 21. Notarchirico di Venosa, 22. Mala Balanica, 23. Petralona, 24. Megalopolis, 25. Apidima 2, 26. I<ocaba§, 27. Karain, 28. Nadaouiyeh Ain Askar, 29. Ubeidiya, 30. Hazorea, 31. Gesher Benot Ya'aqov, 32. Zuttiyeh, 33. Qesem.

Revising the hypodigm: Sima de los Huesos

- To fully understand the "muddle in the middle" we need to move away from what Pilbeam (2002) called a "Neanderthal bias" and examine MP hominin variation as a worldwide phenomenon.
- Extensive publication of Sima de los Huesos material, with an accepted date of 427 ± 12 ka shows that definite Neanderthal autapomorphies in all skeletal elements were present early on, and more consistently expressed than would be expected under the accretion model (Hublin, 2009).
- Referring to the Sima de los Huesos material as H. *heidelbergensis* is inaccurate (Stringer, 2012; Arsuaga et al., 2014).
- Given the lack of clear Neanderthal autapomorphies in the Mauer mandible, we agree with Arsuaga et al. (2014) that H. *heidelbergensis* should be defined as a Middle Pleistocene taxon which excludes specimens with Neanderthal autapomorphies. As such, this group could represent the stem group for Neanderthals and modern humans as suggested by Stringer (2012).

Revising the hypodigm of *Homo heidelbergensis*

- As a group distributed over a wide area, which did not experience isolation, *Homo heidelbergensis* would be expected to show a combination of plesiomorphous and synapomorphous traits, and a greater degree of variation than its more isolated counterparts further to the west.
- The new *H. heidelbergensis* hypodigm therefore should include at minimum Mauer (and possibly Vértesszôllôs) from Central Europe, and Ceprano, Visogliano, Balanica, Hazorea and Nadaouiyeh Ain Askar in the Eastern Mediterranean Area. This group would not necessarily show any morphological distinction from the most recent common ancestor (MRCA) even after the Neanderthal lineage diverged.
- Glacial cycles would have played a major role in inducing and limiting the movement of hominin populations during the Pleistocene. Together with the Iberian and Italian Peninsulas, the Balkans acted as a southern refugium for plant and animal species during Pleistocene glaciations, when ice cover made most of Northern Europe inhospitable.

Revising the hypodigm of *Homo heidelbergensis*

- The combination of geographic distance and glacial barriers would have resulted in a relatively greater degree of isolation of the westernmost refugium - the Iberian Peninsula.
- The Balkans differs from the other two peninsulas as it could be reached by three overland routes throughout the Pleistocene. The contact between the Balkans, Transcaucasia and Southwestern Asia (Anatolia and Levant) was never completely severed by glaciations and impenetrable mountain ranges, notwithstanding the difficulty of migrations over the Anatolian plateau.
- Therefore, geographic isolation — an important factor in the development of Neanderthal derived morphology and the evolution of Western European populations in the Middle Pleistocene - would not have played a prominent role in the Eastern Mediterranean Area. The lack of isolation would have resulted in a more varied and morphologically more plesiomorphous population.

Revising the hypodigm of *Homo heidelbergensis*

- The notion of successive movements of hominin populations in the Early and Middle Pleistocene was recently explored by Dennell et al. (2011) in building a demographic “sinks and sources” model.
- According to the authors, hominin populations in Western Europe would be substantially reduced during glaciations, limited to groups that survived in the southern réfugia.
- The reduction in the size of population (the demographic sink) would necessitate repopulation of the west of the continent from an area acting as a demographic source. This demographic source population was postulated for South West Asia (SWA).

Revising the hypodigm of *Homo heidelbergensis*

- Through a series of successive migrations, Europe would have been re-populated by the groups from SWA, which intermixed with the residential populations from the réfugia.
- Given the lack of geographic barrier, we suggest that the area from which the source population was derived could be extended into what we define here as the Eastern Mediterranean Area.
- Neanderthals should be regarded as a Western European group which developed its recognizable morphology in relative glacial isolation. Intermixing with more eastern populations would have been possible during interglacial times, when migrations, contact and genetic exchange could have taken place in different degrees and modalities.

Revising the hypodigm of *Homo heidelbergensis*

- The exchange of genes and tool kits need not always have taken the same direction and degree. If the date of the Fontana Ranuccio teeth is correct, it would suggest that Neanderthal ancestors were on the Italian Peninsula as early as 458 ± 5.7 Ka, and in the Balkans at least as early as Apidima currently dated to 160 ka.
- The Karain mandible in Turkey indicates that Neanderthals spread into Asia by 200—250 Ka, moving later to the Levant and Central Asia.
- The Eastern Mediterranean represents a key area for research into the peopling and re-peopling of Europe,

Why the Sima de los Huesos Site was not a burial: A Taphonomical Review by David Rabada (15 slides)

- SH has the largest accumulation of human remains from the Middle Paleolithic known to date. It has more than 6500 human remains found in only 4 cubic meters of sediments, representing 28 individuals, representing 80% of the global MP fossil record.. According to Chris Stringer, they represent an early form of Ns, as does nuclear DNA.
- This study highlights the variation in taphonomic processes that can occur within a single cave system, and the complex pre- and postdepositional geological and hydrological processes that can influence the history of karstic fossil assemblages.
- SH was originated by different taphonomical mechanisms. Competition between Homo and other predators for the cavity, accidental death by falling into the pit and a feeding trough for felines and canines while the cave had other entrances blocked nowadays, explain this fossil association. Large felines feed on the human remains inside or around the pit. Foxes and other scavengers came later for feeding. The bears fell by accident or died while hibernating there. The water flows in the cave during heavy rainfalls produced dispersion, mixing and abrasion in all these skeletal remains. During all these processes a low sedimentation rate and a continuous supply of corpses produced the observed fossil concentration.

David Rabadà i Vives, 2013 & 2015

Sima facts

- Modern access to SH is via the Cueva Major entrance and 5 meters from it, Cyclops Gallery is reached and the 13 meter vertical shaft that gives access to SH. There were other access openings originally. The human fossils are in the red clay LU-6 layer.
- Only predators have been identified, no herbivores: hominins associated with bone remains of other carnivores (50% bears, humans 11%; foxes 8% (felines, wolves and weasels were a minority)); but no evidence of habitation.
- No cutmarks on animals; hominins mixed with others mammals bones and without anatomical connections; no complete bodies; 27 long bones (1.64 cm hgt)
- Some 60 % of the bodies' bones are missing, particularly vertebra, cranial elements and phalanges; high amount of jaws and limb bones
- 52 % were adolescents and young adults; 60 % were less than 19 yo, and 90 % less than 27; 1 under 10 yo

Sima facts

- Many human cranial remains with abrasions and fractures caused by impacts; more than 24% of the bones are eroded showing abrasions over surfaces of fractures; 50% of the human remains are affected by bite marks, especially femora at 96 percent and, in general, on limb bones.
- Original Ritual burial theory: evidence includes the absence of herbivores, the highest concentration of *Homo heidelbergensis* around the world, presence of one Acheulean handaxe, and the human mortality distribution.
- The absence of herbivores: carnivores didn't use the site as a den. It is more likely that human and bear bodies were already there and that carnivores came into the cave to eat the carrion. The large number of foxes and presence of other carnivores, does not favor the hypothesis that carnivores visited the site only to scavenge and eventually died there by natural causes; better theory would be that it was a natural trap to explain the carnivore accumulation. Moreover, the age-at-death profile of the bear sample fits better with a catastrophic profile than with an attritional pattern.

Sima Facts

- Bone concentration: These fossil remains are mostly concentrated inside a quite discrete sedimentary level, which cannot be explained by any kind of catastrophic event; found in only four cubic meters of sediments; the highest concentration of *Homo heidelbergensis* fossils and the most complete collection of Middle Pleistocene *Homo*; Arsuaga & Carbonell argue that it indicates human burials by this primitive *Homo* who threw their dead relatives to the cave site as a symbolical act
- Excalibur: not an occupation space or carnivore den; presence of multiple carnivore fossils may be explained as several events of natural falling, hibernation and catastrophic death, particularly clear for the bears' case. This may be supported by the fact that all these specimens are present along the whole sedimentary sequence. On the contrary, human remains are mostly concentrated inside a quite discrete sedimentary level.

Sima facts: Handaxe

- The finding of an Acheulean handaxe at the Sima de los Huesos cave site casts light on the evolution of human behavior during the Middle Pleistocene. It is a finely flaked quartzite handaxe, which is associated with the hominin assemblage. The particular nature of the deposit involving its taphonomy, paleontology, and technology points to a symbolic meaning both of the tool and the human accumulation. This would support the hypothesis of human mortuary practices at the Sima around 400 kyr ago.
- It would seem quite clear that it was not made to be used in the Sima, since the latter was clearly not employed as an occupation site and it was thrown to the chasm as a symbolic act during a ritual burial (Carbonell, 2006)
- A use-wear analysis could not demonstrate conclusively as to whether this object was actually used, due to erosion of piece's edges; according to experimental data, this abrasion was produced by sandy sediments.

Facts

- Age distribution: The lack of infants and children with an abnormally high percentage of adolescents and prime-age adults. Also, the number of adults over the age of 20 years is lower than expected in normal models. This mortality distribution could be the result of a catastrophe as a sudden death for all the Sima de los Huesos human individuals before the ritual burial
- Considering the biases of the human bone collection, the presence of one hand axe, the human remains concentration and the absence of herbivores, the recognized interpretation is that in the Sima de los Huesos there was an accumulation of human bodies where carnivores were not responsible for the accumulation of the human remains which would indicate the accumulation of human remains could be either catastrophic or the result of a mortuary practice and this explanation should be considered the null hypothesis for future tests (Arsuaga et al., 1993).
- How the human remains reached the SH is highly debated, as intentional or the result of a catastrophe.

Facts revision: taphonomical and geological data of the Sima.

- Method: Analysis of published literature from 1997 to 2013
- Location: Human remains found only in lower red clay level, LU-6. 176 bears found in both LU-6 and higher LU-7. Collection is primarily hominin, bears, and foxes, with no herbivores.
- Missing: SH contains 32 individuals from 1300 skeletal parts (Arsuaga et al., 1997); or 6500 remains from 28 individuals (Castro, 2004). The total number of skeletal parts of 32 hominins is much higher than these 1300 skeletal parts. In fact, they would have to be more than 3.000 which indicates two things. So more than 60% of the original remains are missing, especially skulls, phalanges and vertebrae. Secondly, this association fossil shows a dispersion of large bones, with no whole skeletons with anatomical connections. If human remains were carried as a sepulchral rite within in a pit we have to suppose that these were whole bodies and not parts of them. More arms and legs than any other parts.
- Abrasions on bones: There are not many cranial remains with abrasions or fractures from falls. Some authors have said that these injuries were caused by impacts of stones when they were fighting or playing with each other (Arsuaga, 1999), but it seems more logical that these scars were produced when water currents reworked the human remains in the cave because there are no signs of cranial healing. People would think that these abrasions were caused by impacts when human bodies fell into the chasm. When some animals fall in a pit inaccessible to predators they tend to generate fossil associations without bite marks, but the human remains in the Sima are full of bite marks.

Facts revision

- Experiment of throwing bodies into a pit from 13m on to concrete floor: most of the bones did not break or were damaged in any way. Altogether the proportion of complete bones was 82%, very different from the 3% in the fossil assemblage of the Sima. This fact does not support the hypothesis that other humans threw dead bodies into the pit
- There are only 3% complete human bones. Fossils from the undisturbed deposits show evidence of rounding: 24 % of transverse breaks were rounded and 20 % of spiral breaks; It has been demonstrated that abrasion by silty clay matrix may produce rounding of fossilized bones more rapidly than fresh bone, which again suggests modification some time after deposition. In summary, the fossil association of the Sima were mixed and eroded by the cave’s water currents.
- At Cueva del Angel, hominins took prey into cave for consumption, leaving many cutmarks on bones, and collections of stone tools. None of that applies at SH.

Facts revision

- Bite marks on bones: The SH human remains show many bite marks on the majority of bones.
- Arsuaga rejected the idea of carnivore predation as cause of SH bone collection due to absence of toothmarks (usually 50%; Salas found 8% had bitemarks; but did only 2400 of 6500 bones). But there are bone collections caused by carnivores with low bitemark evidence consistent with SH pattern. Carnivores gnaw less bones when hunting is abundant. A large portion of SH body parts are missing; the remains are very dispersed, suggesting a partial and selective transport of bones at SH.

- The abundance of bears found with humans originally suggested that those predators perpetrated these bite marks, but bears chew bones producing a characteristic pattern with rounded epiphyses which is not found; Namely, there are bite marks from bears on bears bones but not on human bones. On the contrary, there are bite marks from felines or foxes on human remains but not over bear bones. All these reasons indicate that bear and human remains were separated at the first time and was mixed later by water currents which involved the observed abrasion on bones.
- It has been conclusively demonstrated that the bears entered the Sima separately from the humans; and therefore bears didn't produce the human bone accumulation in the Sima de los Huesos site.

Facts revision

- Percentage of bones: We have seen that there is a clear predominance of human arms and legs remains in the Sima de los Huesos site. Limb bones (femurs, humeri and tibiae) are more frequent than ribs, vertebrae and metacarpals, which are very scarce. All these percentages involve a partial transport of bones at Sima de los Huesos site. The fact that some 60 % of the bodies' bones are missing, particularly vertebra, cranial elements and phalanges, seems to support a selective transport. In addition, limbs contain a large quantity of meat for feeding while ribs, vertebrae and metacarpals don't because they contain relatively little nutritional value. Lions, leopards, hyenas or others produced this kind of bone accumulation with predominance of arms and legs. In fact, carnivores rarely fragment metacarpals.
- 50% of the human remains at Sima de los Huesos are affected by bite marks, especially femora at 96 % and, in general, on pelvis & limb bones.
- Femora, tibiae, humeri and radii were more chewed by small scavengers. On the other hand, pelvis, and lumbar vertebrae were chewed by big predators. In fact chewing-marks by small carnivores are absent on the last elements. Therefore, these marks follow, from high to low abundance, the consumption sequence for flesh ingestion, with highest percentages on pelvis and lowest on ulna and radius. Therefore, a big carnivore is considered to have had priority access to the human bodies of SH, because hindquarter (axial parts) are affected by their teeth in higher proportions than is present in other elements.

Facts revision

- It is unclear which carnivores made bite marks on human remains at SH, but some authors think that Panthera leo fossilis and Vulpes were carnivores which produce the main bite marks. Incisions over human bones were caused by wolves, foxes and some big feline. The last of them had access to the remains before canines.
- The total of some 32 individuals at Sima de los Huesos site as preys would not be out of character with a comparatively low rate of predation on ancient humans by medium or large carnivores at the site. Therefore large carnivores hunted human individuals during Pleistocene and many carnivore species was involved. According to low fracture level in the Sima de los Huesos fossil association hyena was not the main bone-cracking producer. At the moment, big felines ate human flesh first near the Sima de los Huesos site and later scavengers chewed the rest. Femora, humeri, tibiae were chewed more by small scavengers. Pelvis and lumbar vertebrae were chewed by large predators
- Water transport, as Sima de los Huesos site, is ruled out as the primary process responsible for removing skeletal elements based on abrasion data. Instead, the feeding activity of carnivores and the ecological context appear to have been an important factor in the formation of the assemblage. Atapuerca range represented an area of ecological competition between all these carnivores, Homo included. The last suffered a high risk of contingencies as depredation by big carnivores which explains the age distribution of the bones, with a predominance of younger age and scarcity of infants and old individuals.

Facts revision

- Age distribution: Fossils can reflect the mortality rate of the original population. Infant mortality rate in current hunter-gatherer is very high followed by old people. If the Sima de los Huesos site was generated as intentional burial by Neanderthal populations, it should contain a high number of children and elders, but 52 percent of human remains were adolescents and young adults. Two hyoid bones and nearly 30 middle ear bones were found.
- The fossil preservation in Sima de los Huesos site is excellent and the distribution of human ages has to reflect the original corpses number. Humans between 0 to 11 years old and over 27 were underrepresented at SH. This predominance of middle age and scarcity of infants and old individuals doesn't indicate a mortality rate, but something very different, an accident risk rate. Teens and young adult are more risk tolerant. Higher mortality rates in this age group is consistent with greater risk taking and catastrophes happening.
- This fact involves high risk of accidents or contingencies for young humans but this accident was not falling inside the hole because the low skeletal fractures rate observed invalidates this hypothesis; the mortality distribution was the result of some kind of catastrophe for all the Sima de los Huesos human individuals; although pattern of speleothems indicate it was not a single catastrophe.

SH: carnivores

- The evidence of carnivore activity in the human sample at SH is concentrated primarily on the ends of long bones and limbs. (One study has found that femurs have highest bite mark rate (at 20%), and then the humerus). No evidence of cutmarks or defleshing which would indicate cannibalism.
- Small carnivores activity, therefore, is consistent with scavenging rather than predation. All these carnivores produced the first human bone association with high percentage of limbs. Later cave water currents transported and eroded the bones.

Facts revision

- There were once more accesses in the Sima de los Huesos. Felines and canines came in and went out of or around the actual cavity through all these old buried caves by slumps. In fact, there are different blocked passages in the Sima. At the bottom of the vertical shaft which gives access to the Sima at present, there is an opening at the end of the Sima furthest from the bone pit and topographically one or two meters above it. This passage is completely blocked by large boulders at present, but clearly at some time in the past it was not blocked. This and other entries were described in the Sima de los Huesos site but they were discarded
- The discussion about this site has to be focused on concentration mechanisms of bones. There are many causes which accumulate skeletal remains in caves and caverns
- The absence of cut marks in Sima de los Huesos bones indicates that there was not a substantial hominin colony inside or near the pit.

Facts revision

- Low sedimentation rate allowed a high bone transport in the karst, which lead to the observed bone fragmentation and abrasion by reworking by water.
- More than 24 % of the bones are eroded by water currents which transported this first fossil assemblage inside the chasm.
- The second reason is the mixed fauna found in the Sima de los Huesos site which happens very often in fossil condensation levels. And the third aspect was the different sedimentation ages found in the outcrop.
- This dispersion was due to a low sedimentation rate in the Sima de los Huesos pit. Given the actual time scale by paleomagnetism and uranium thorium, much of this fossil human accumulation covered a substantial time span in excess of 100,000 years. In summary, a continuous supply of corpses for a long period of time and a low sedimentation production produced the observed fossil concentration at the Sima de los Huesos.

Facts revision

- Traceology studies reveal that the hand axe does not show use-wear traces because there is microscopic erosion on the edges of the hand axe. According to experimental data, this abrasion was produced by sandy sediments. Therefore, this hand axe was a reworked element as the rest of human remains.
- CONCLUSIONS
- A monolithic interpretation does not explain natural processes because these are consequences of a network of causes. The Sima de los Huesos fossil association was considered only as a human burial site by other authors, but according to geological and taphonomical data review this outcrop was originated by different mechanisms.
- Competition between Homo and other predators for the cavity, accidental death by falling into the pit and a feeding trough for predators while the cave had other entrances blocked nowadays explain this fossil association. Furthermore, there had been time differences between bears, humans and others bone remains accumulations events.
- The bears fell by accident or died while hibernating there.
- Homo was victim of large predators that carried the corpses inside or around the pit.
- Foxes and other scavengers came later for feeding.
- The water flows in the karst during heavy rainfalls produced dispersion, mixing and abrasion in all these skeletal remains. During all these processes a low sedimentation rate or a continuous supply of corpses produced the observed fossil concentration.

1994: The earliest occupation of Europe:
a short chronology - Wi Roebroeks & Thijs Van Kolfschoten

- 1994 view of the earliest occupation of Europe makes for a short chronology. Starts at 500 Ka.

- An age of about one million years is considered a good estimate for the first occupation of Europe by most workers (Le Vallonet in France and Kärlich A in Germany)

- In contrast to these 'long chronologies' we suggest in this paper that Europe's earliest human traces are in fact considerably younger, dating from well into the Middle Pleistocene.

- *Before* 500,000, virtually all finds come from a disturbed, coarse matrix, afterwards we have primary context sites in fine-grained deposits. The assemblages dating from *before* 500,000 are virtually all the result of selection of isolated pieces from natural deposits, younger ones are often excavated from knapping floors

The earliest occupation of Europe

- In view of the attributes of the 'artefacts' and contexts of the pre-500,000 sites, we instead interpret these differences as *no indisputable proof for human occupation of Europe prior to about 500,000 years ago.* The first primary context sites with good archaeological evidence date from a later period within the Middle Pleistocene, possibly from about Stage 13 onwards.

- From the 'Mauer' time period onwards we have Middle Pleistocene human remains all over Europe: Arago, Atapuerca, Biache-Saint- Vaast, Bilzingsleben, Cava Pompi. Gastel di Guido, La Chaise, Ehringsdorf, Fontana Ranuccio, Fontéchevade, Grotte du Prince, Lazaret, Mauer, Montmaurin, Ofgnac III, Petralona, Pontnewydd, Steinheim. Swanscombe, Venose, Vergranne, Vértesszöllös and Visogliano, to mention them in alphabetical order

- See next slide for correction.

Wil Roebroeks: Human Colonization of Europe

- Prior to the approximately 1.7 Ma finds from Dmanisi and the at most 1.8 Ma old Indonesian fossils, all hominin fossils are from Africa.
- Most workers assume that the Asian hominins derived from representatives of the Homo ergaster/erectus s.l. group who left Africa soon after its emergence. These ‘colonizers’ consisted of (compared to the australopithecines) large-brained (700–1050 cc) hominins with a large body size and modern limb proportions, and equipped with a good locomotor system (cf. Aiello and Wells, 2002) that made them capable of sustained endurance running (Bramble and Lieberman, 2004).
- The emergence of this group has often been related to the global climate change around 2.0 Ma, which resulted in a shift to more arid conditions in Africa (de Menocal, 2004). These changes are thought to have produced new niches in grasslands and wooded grasslands for terrestrial herbivores, and slightly larger-brained and -bodied Homo individuals were to profit more from these new resources than smaller individuals (Anton et al., 2002)

Wil Roebroeks, 2006

Human Colonization of Europe 2

- The growth of the relatively large and energetically expensive brain of the Homo group was very probably financed by a shift towards a higher-quality diet in which animal products had become important (Aiello and Wheeler, 1995.) This increasing carnivory is reflected in the archaeological record by the cooccurrence of stone tools and broken and cut-marked bones of a wide variety of large mammals.

- Tool-using hominins were already exploiting animal carcasses more than 2 million years ago, as attested by the recently reported cut-marked bones from Pliocene archaeological sites at Gona, Afar, Ethiopia, from the time interval 2.58–2.1Ma.

- The exact role of carnivory in these early stages of the hominin lineage is still largely debated. There are various scenarios differently emphasizing the role of active hunting versus scavenging-related means of meat procurement, but here it is sufficient to stress that, given the biological relationships between body size, brain size, diet quality and home range size, range expansion of early Homo can be expected

Human Colonization of Europe

- Anton and colleagues (2002) estimate that the larger body size of *H. ergaster*, combined with a moderate increase in meat consumption, would have necessitated an eight- to ten-fold increase in home range size compared with that of the *australopithecines*—enough to account for the abrupt expansion of the species out of Africa in the Early Pleistocene.
- As popular as these models are, they suffer from a major drawback: they implicitly start from the assumption that East Africa was the region where all hominins (including the genus Homo) evolved.

Human Colonization of Europe 3

- Asia:
- The oldest artefacts thus far reported from Asia are from Riwat, Pakistan, where they have been assigned a minimum age of 1.9 Ma
- The first skeletal traces of a hominin presence in Eurasia are from the earlier parts of the Early Pleistocene, i.e. earlier than thought about a decade ago, when ‘Ubeidiya in Israel was considered the oldest site outside Africa. With its inferred age of 1.0–1.4Ma (Tchernov, 1987), ‘Ubeidiya is younger than the Georgian site of Dmanisi (Rightmire et al., 2006), with an age of approximately 1.7 Ma.
- According to Dennell (2003), the record of Eurasia before 1 million years ago is indicative of repeated, short-lived and modest dispersal events up to 408 N, rather than of something like a continuous residence. In Dennell’s view, we are dealing with *Visitors* for most parts of Early Pleistocene Eurasia. For major parts of Eurasia, including Europe, repeated dispersal events, not leading to a substantial hominin presence in lower latitude Eurasia, are a very prominent feature.

Human Colonization of Europe

- Europe:
  - finds from Atapuerca TD6, which point to a somewhat earlier presence of hominins in Spain
- European archaeological record changes significantly around 500 to 600 Ka, with an increasing number of sites in the Mediterranean as well as elsewhere in Europe indicating a more substantial occupation than in the period before.
- Until the recent finds from East Anglia, most workers also agreed that north of the mountain chains of the Pyrenees and Alps the first unambiguous traces of human occupation were from 500 to 600 Ka. The new finds from Pakefield, East Anglia (Parfitt et al., 2005) demonstrate that England saw a somewhat earlier presence of hominins, possibly for only a short period
- Apart from the newly reported finds from East Anglia, all unambiguous traces of human occupation north of the European mountain chains date from about 500 Ka, from the Mauer-Miesenheim-Boxgrove time horizon, probably equivalent to MIS 13.

Human Colonization of Europe

- The Eurasian evidence can be summarized in three points:
  - 1. A thinly spread Early Pleistocene 'non-permanent' presence in Asia south of 408 N, from about 1.7–1.8Ma onward.
  - 2. A thinly spread presence in southern and occasionally Atlantic western Europe between 1 and 0.6 Ma (with a striking time lag between Dmanisi and the earliest circum-Mediterranean).
  - 3. A more 'permanent' presence in Europe, including its higher latitudes, from about 500–600 ka onward.

Human Colonization of Europe

- Dennell and Roebroeks (1996) have argued that the long-lasting Early and early Middle Pleistocene 408 N range limit may have been the result of limited daylight foraging hours.
- Mussi and Palombo (2001) see the human entry in Europe as part of a general faunal turnover with an increasing availability of prey: humans enter the scene for good at the beginning of the Middle Pleistocene, when middle-sized herbivores increase, but also when two new carnivore species appear, Panthera leo fossils and Panthera pardus. The common driving force may have been an increasing availability of suitable prey.
- Gamble has repeatedly stressed the importance of the scale of hominin social systems and its matching with the spatial structure of resources in the environment as an important factor in permitting colonization

Human Colonization of Europe

- Middle Pleistocene Europe:
- The European record shows that Middle Pleistocene hominins (the first ones generally referred to *Homo heidelbergensis*) were present in a wide range of environments, including full interglacial and colder steppic ones, over large (but not all) parts of Europe from about half a million years ago
- From about 500 Ka, Europe saw a continuous occupation by— occasionally very small and rather isolated—groups of hominins.
- As shown by the evidence from Schöningen and Boxgrove, these hominins were capable hunters of large mammals and had become serious members of the carnivore guild.
- By Neanderthal times they had become top carnivores (Richards et al., 2000), possibly specializing in prime-age adult ungulates, a specialization unknown in other carnivores and a good sign of niche separation (Stiner, 2002). In the Levant, late Neanderthal hunting activities may even have led to a decline of red deer and aurochs populations (Speth, 2004).

Human Colonization of Europe: meat and hunting

- A reliable supply of meat may have been a conditio sine qua non for a successful peopling of the northern latitudes, and it might be more than a coincidence that the first unambiguous traces of a substantial hominin presence in Europe tally with the first good evidence for hominin hunting.
- Given Expensive Tissue hypothesis, Neanderthal large brains and heavy bodies (cf. Sorensen and Leonard, 2001) would have involved high daily energy costs during pregnancy and lactation, implying that a regular supply of high-quality food for nursing females and cooperation between the sexes may have been in place by the time of Boxgrove and Schöningen. The ethnographic record shows that large game package size and cooperation are strongly correlated (Kelly, 1995), and the large size of many of the prey animals (e.g. the Boxgrove and Schöningen horses) is at least suggestive of fully-fledged cooperative forms of hunting

Human Colonization of Europe

- During the first half of the Middle Pleistocene hominins were mainly limited to the western and central parts of Europe.
- The time discrepancy between substantial colonization of western-central and eastern Europe is in the order of about 200 000 to 300 000 years.
- Although these first Europeans were successful hunters who colonized a wide range of environmental settings, the long-term stability of their archaeological distribution over major areas of Europe is striking.
- Stability of range boundaries may point to low population densities. The long-term stability of their geographical ranges as documented in Europe—a long-term stability in other domains, for instance in stone tool technology and use of space (cf. Gamble, 1999).
- This long-term stability in various domains, and especially in the geographical distribution of Early and Middle Pleistocene hominins is strikingly different from the archaeological record of Upper Paleolithic humans.

Human Colonization of Europe

- This stability is part of a wider, puzzling paradox: on the one hand we have indications for ‘complex’ forms of behavior of Middle Pleistocene hominins (such as fire manipulation, transmission of knowledge on how to fabricate stone and wooden artefacts, surviving in a wide range of environments by fully-fledged forms of hunting of large and sometimes dangerous mammals). On the other hand we see long-term stability and we do not see the cultural behavior as exemplified by the ratchet effect (Tomasello, 1999) that shows up when Upper Paleolithic humans appear on the European scene.
- The differences in material culture between the Upper Paleolithic and the Lower/Middle Paleolithic record are usually ascribed to between-species cognitive differences. But does this have to be the case? The paradox mentioned here calls for an alternative and less simple explanation.

Human Colonization of Europe

- The archaeological data and Henrich’s model suggest that surprisingly large populations are necessary to sustain a toolkit consisting of rather complex items
- These hominins, and especially the later Neanderthals, had relatively large bodies that needed more energy than, the slender physique of modern humans (Sorensen and Leonard, 2001), and probably subsisted at a higher trophic level (and hence at a lower population density) than modern humans, as well illustrated for the Neanderthals by stable isotope studies of their bones (Richards et al., 2000).

Human Colonization of Europe

- The virtual absence of dwelling structures (or the low investments in a built environment) (cf. Gamble, 1999) in the Lower and Middle Paleolithic record suggests that they were also more mobile than Upper Paleolithic humans.
- This again indicates that in comparable environments they would have lived at lower population densities than Upper Paleolithic humans, with the possible implications for cumulative cultural evolution suggested by Henrich.
- Paleolithic populations may have developed quite different degrees of technological complexity depending on how the availability of local resources (or, in this case, biological energetic requirements) affected the frequency and intensity of social interaction
- As suggested by Henrich (2004), the differences between Middle Pleistocene hominins and Neanderthals on the one hand and Upper Paleolithic humans on the other may result from differences in group size and sociality (the number of social learners) rather than reside in genes related to cognitive abilities that lead to improved tools and the visibility of the ratchet effect.

Mounier, 2019: Late MP skulls in Africa

- In Morocco/Northern Africa, the site of Jebel Irhoud has yielded multiple fossils since the 1960s, including a complete skull (Irhoud 1), originally dated to 130–190 Ka, and a new date estimate of 315 ka.
- Well preserved LMP hominins are more numerous in Eastern Africa. The Singa calvarium from Sudan is dated to 133 Ka. In Ethiopia, the Omo Kibish specimens, Omo I and Omo II, are dated to 200 Ka, and the three specimens from Herto, with an estimated date of 160 Ka.
- In Kenya, the Guomde calvarium (KNM-ER 3884), which lacks most of the facial and frontal bones, has been dated to 270–300 Ka with ɣray spectrometry, while an age of 200–300 Ka has been suggested for the nearly complete Eliye Springs skull (KNM-ES 1169327) on the basis of its morphology.
- Further South, a 200–300 Ka cranium (LH1829,30) was discovered in the Ngaloba Beds at Laetoli (Tanzania), and in South Africa, the site of Florisbad yielded a partially preserved cranium dated to 259 ka.
- Lastly, the recently discovered remains of H. naledi, dated to 236–335 Ka, add major complexity to the LMP hominin record of southern Africa.

Late MP skulls in Africa

- African LMP fossils exhibit extremely variable morphologies. The Omo I and Herto specimens have a modern-like anatomy that includes the presence of the two cranio-mandibular apomorphies of the species—cranial proportions that result in a tall vault (basi-bregmatic height) and a chin; and are generally considered the earliest undisputed remains of *H. sapiens*.
- All other LMP African fossils show a mosaic of derived and archaic characters. For instance, the Jebel Irhoud remains were originally described as showing strong similarities with Neandertals, while the study of the new Irhoud remains emphasizes their affinities with *H. sapiens*, despite the absence of key modern humans apomorphies (i.e., tall and globular vault, and inverted T chin).
- The Guomde, Ngaloba, Eliye Springs and Florisbad specimens along with Omo II and possibly the pathological Singa calvarium, have been mostly referred to as ‘archaic *H. sapiens*’.
- This situation challenges any attempt at identifying the evolutionary mechanisms that may explain the morphological pattern in the African LMP fossil record, as well as identifying the ancestral population, or populations, of modern humans.

Late MP skulls in Africa

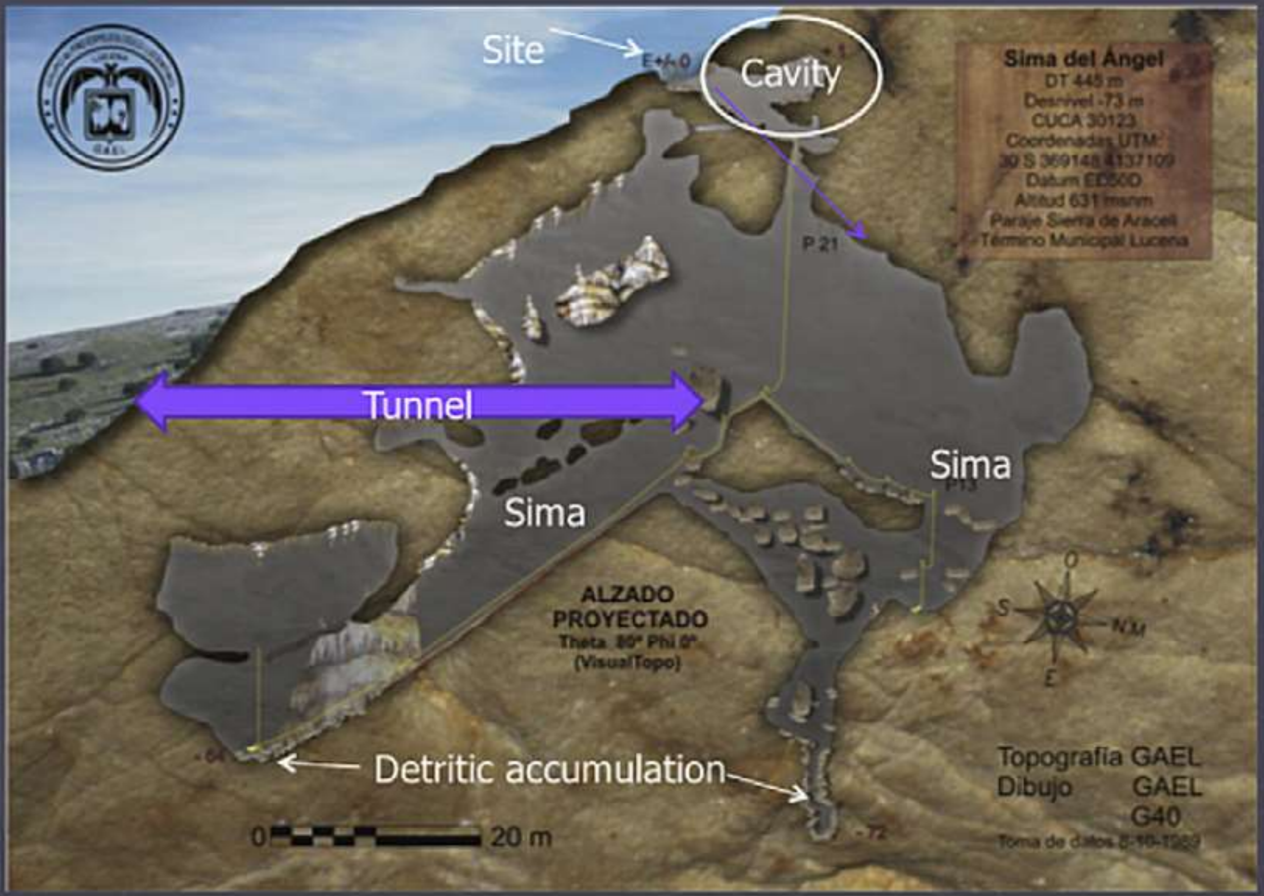
- Derived cranial features of *H. sapiens* are fully displayed in the digital vLCAs—a domed neurocranium, a reduced face and a marked basicranial flexion, and only partly balanced by more archaic features (i.e., projecting brow-ridges, marked alveolar prognathism, weakly developed mastoid processes, elongated occipital bone, weakly marked incurvatio inframalaris frontalis, and wide interorbital distance.
- The African LMP fossil mosaic morphologies combine archaic and modern characters, and the first occurrence of a full modern morphotype is not documented before Omo I (195 ka) and BOUVP16/1 specimen from Herto (160 ka).
- Given the complexity of the morphological variation within the genus Homo during the African LMP, it is likely that some LMP African fossils were not associated with any population ancestral to H. sapiens.
- We should thus expect to find LMP fossils in Africa that were members of chronologically and geographically overlapping side branches of the Pleistocene human evolution tree, as the H. naledi remains seem to be

Late MP skulls in Africa

- The speciation process for *H. sapiens* appears to have been complex, going through different phases that may not have contributed to the genetic and phenotypic structure of current modern human populations.
- A first stage of phenotypic diversification, from 350 to 200 Ka, may have happened locally with different contemporary populations forming local morphs of *pre-H. sapiens* groups as they are represented in the LMP fossil record.
- This phase may have been followed by a period of fragmentation and differential expansion of populations leading to hybridization and coalescence of groups, which could have resulted in the emergence of morphologically derived populations of anatomically modern humans between 200 to 100 ka, as exemplified by the fossils from Herto, Skhūl and Qafzeh.
- Nevertheless, our results suggest that it is unlikely that all LMP local populations would have contributed equally, or at all, to the lineage that gave rise to the population ancestral to H. sapiens; local extinctions and founder effects would have shaped considerably the emergence of anatomically modern humans.
- The morphology of the vLCAs computed in the present study appears to be closer to this last phase (i.e., 200–100 Ka) than to the former one.
- This may indicate that chronologically older fossils of anatomically modern *H. sapiens*, representing populations which outlived most of the LMP hominin groups, are yet to be found

- Both the Southern African fossil Florisbad, and the Eastern African specimens KNM-ES 11693 and Omo II show similarities with the vLCAs and early H. sapiens.
- A northern African origin is less likely, as Irhoud 1 displays a different affinity pattern, making it morphologically closer to the Neandertals.

The Cueva del Angel Karst



Cueva del Angel, near Cordoba, in Andalusia, Spain

- The Cueva del Angel (Lucena, Spain): An Acheulean hunters habitat in the South of the Iberian Peninsula, discovered in 1995.
- The Cueva del Angel archaeological site is an open-air sedimentary sequence, remnant of a collapsed cave and part of a karst complex. The faunal assemblage dominated by Equus ferus, large bovids and cervids has been subjected to intense anthropic actions reflecting selective predation.
- The Cueva del Angel lithic assemblage (dominated by non-modified flakes and abundant retouched tools with the presence of 46 handaxes) appears to fit well within the regional diversity of a well developed non-Levallois final Acheulean industry. A preliminary 230Th/234U age estimate, the review of the lithic assemblage and faunal evidence would favor a chronological positioning of the site in a period stretching from the end of the Middle Pleistocene to the beginning of the Upper Pleistocene ~121 Ka (MIS 11-MIS 5, 400-100 Ka).
- The Acheulean lithic assemblage found at the Cueva del Angel fits very well with the hypothesis of a continuation of Acheulean cultural traditions in the site, distinct from the contemporaneous uniquely Mousterian complexes witnessed in other parts of the Iberian Peninsula, and Western Europe.

Cecilio Barroso Ruíz, et. al., 2011

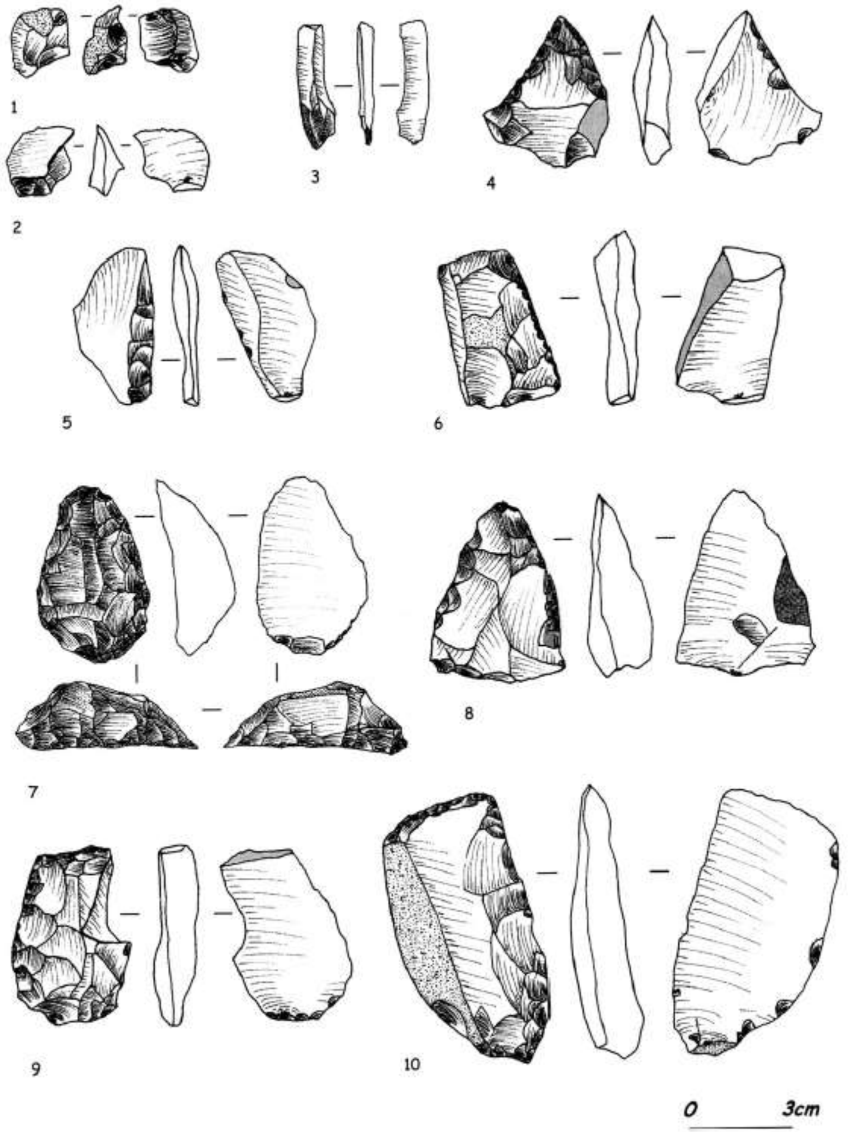


Fig. 10. Retouched tools from Cueva del Angel: (1) unidirectional flint micro core on a small flint cobble; (2) Kombewa flint flake; (3) flint bladelet; (4) flint Quinson point; (5) flint retouched edge flake; (6) flint retouched edge flake and side scraper; (7) flint protolimace; (8) flint point; (9) flint side scraper with Kostienki thinning; (10) flint side scraper. (Drawings by Vincenzo Celiberti).

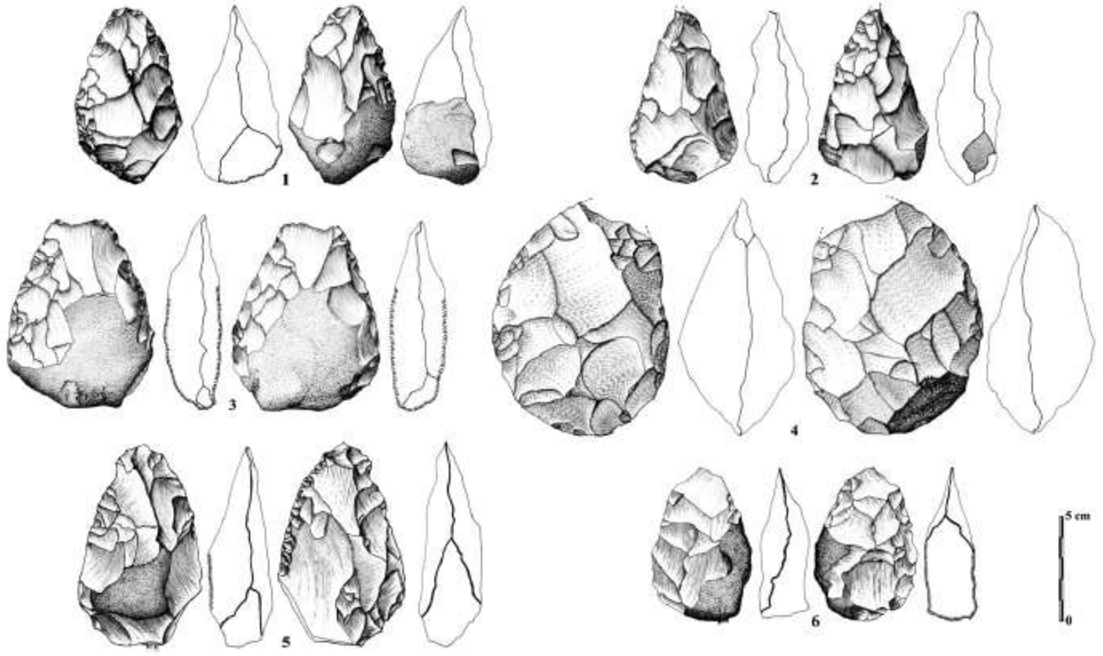


Fig. 11. Handaxes from Cueva del Angel: (1) lanceolated; (2) subtriangular; (3) cordate-cordiform; (4) oval; (5) lanceolated; (6) oval. (Drawings by D. Cauche and R. Guilard).

The Cueva del Angel lithic assemblage appears to fit well within the regional diversity of a well developed final Acheulean industry, observed generally at the end of the Middle Pleistocene in Western Europe. Raw material procurement is mainly local, which is a typical behavioral characteristic found in many Western European final Acheulean and Mousterian sites. Shows regional variation.

Source and sink model by M. Martinón-Torresa

- This study aims to present a preliminary approach to the suitability of the "source and sink" model to explain the human settlement of East Asia. We present a general overview of the hominin dental evidence with a special emphasis in some key localities with human remains that have been recently described. Our analysis suggests that the morpho-dimensional variation of the Pleistocene populations from East Asia cannot be accommodated within one single lineage. This evidence seems supportive of an intense but also more discontinuous pattern of occupation. The severe climatic oscillations, the extent of the desert areas and the possibility of intermittent exchanges between continental and insular East Asia, depending on sea level changes, are key factors to identify possible sink and sources in the region.

María Martinón-Torresa, et al., 2015

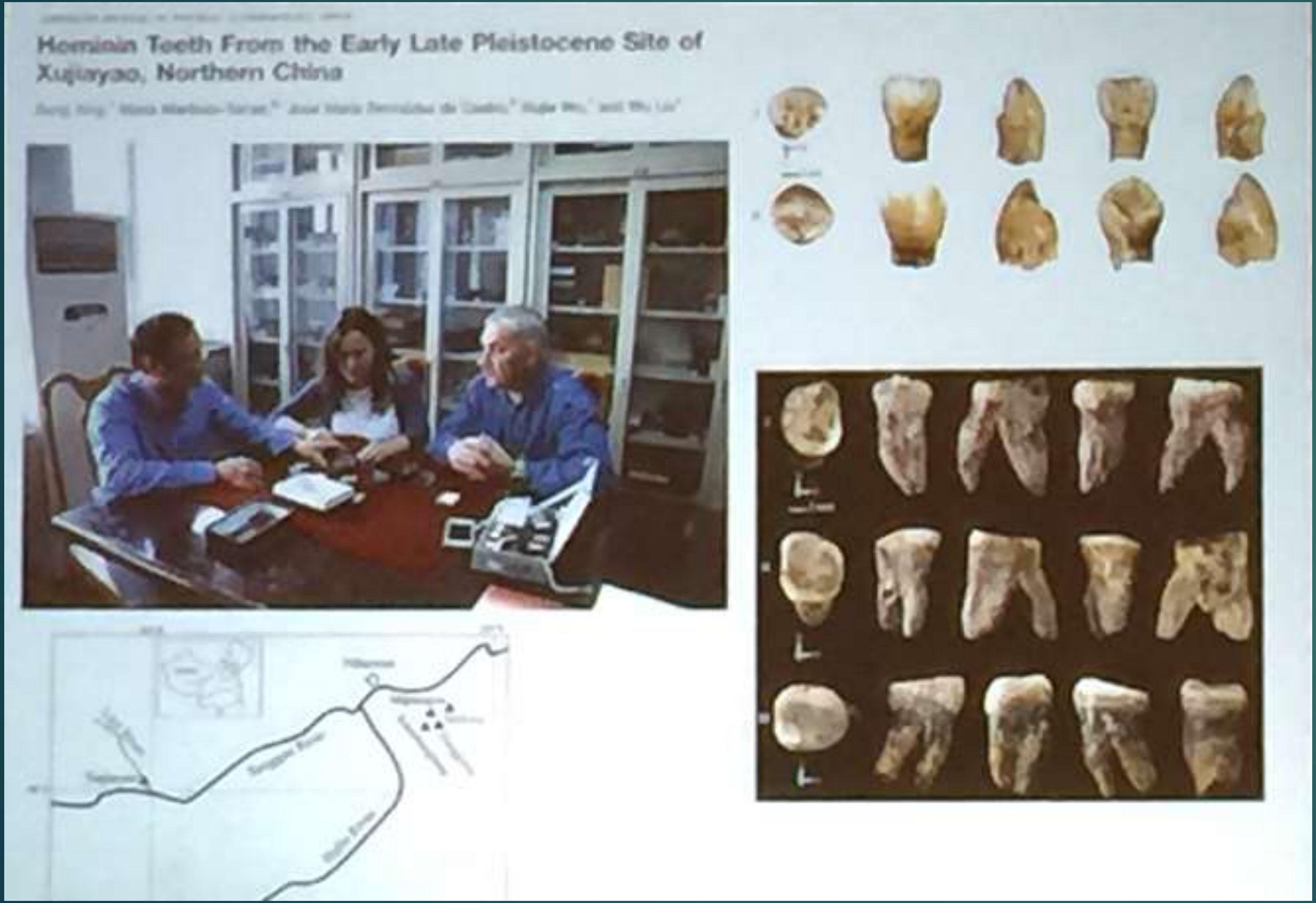
Source and sink model

- If correct, this points to a strong but discontinuous occupation of east Asia. Although Martinón-Torres doesn't believe that our species arose independently in Asia, she does think it likely that we have roots in Asia – though probably not in the Far East.
- Peking Man was a true pioneer, but most of his relatives didn't travel nearly as far, settling instead in the Middle East where the climate was more favorable. This, she suggests, was the source population of Neanderthals, Denisovans and another branch of our family tree, which migrated back to Africa before evolving there into *H. sapiens*. "Maybe Africa was not the only human cradle," she says.
- If these various species interbred, they should have left behind hybrids scattered across Asia. Indeed, the surprisingly rich variety among east Asian fossils suggests hybridization was widespread.

Source and sink model

- Hominins in Africa and Eurasia did evolve relatively independently for a long time. Study of 5000 fossil teeth spanning 2.5 million years, they found that each continent had its own distinct type of teeth – strong evidence that Eurasia was a center of speciation in its own right.
- Rather than multiregionalism, she and her collaborators suggest a "source and sink" model to explain the human settlement of east Asia.
- They believe the huge variety of fossils points to repeated colonization, interbreeding and extinctions, with populations thriving and disappearing depending on fluctuations in the climate over hundreds of thousands of years. During cold periods, much of central Asia and the northern steppe would have become uninhabitable. These are the "sinks".
- But hominins would have been able to survive in more southerly regions, on some islands and in regions where the climate remained relatively stable, such as the Middle East – the "sources".

Early Late Pleistocene site of Xujiayao, Northern China: Ns in China?



Hominin Teeth From the Early Late Pleistocene Site of Xujiayao, Northern China

Shovel and primitive teeth

Dental evidence: Asian impact on colonization of Europe

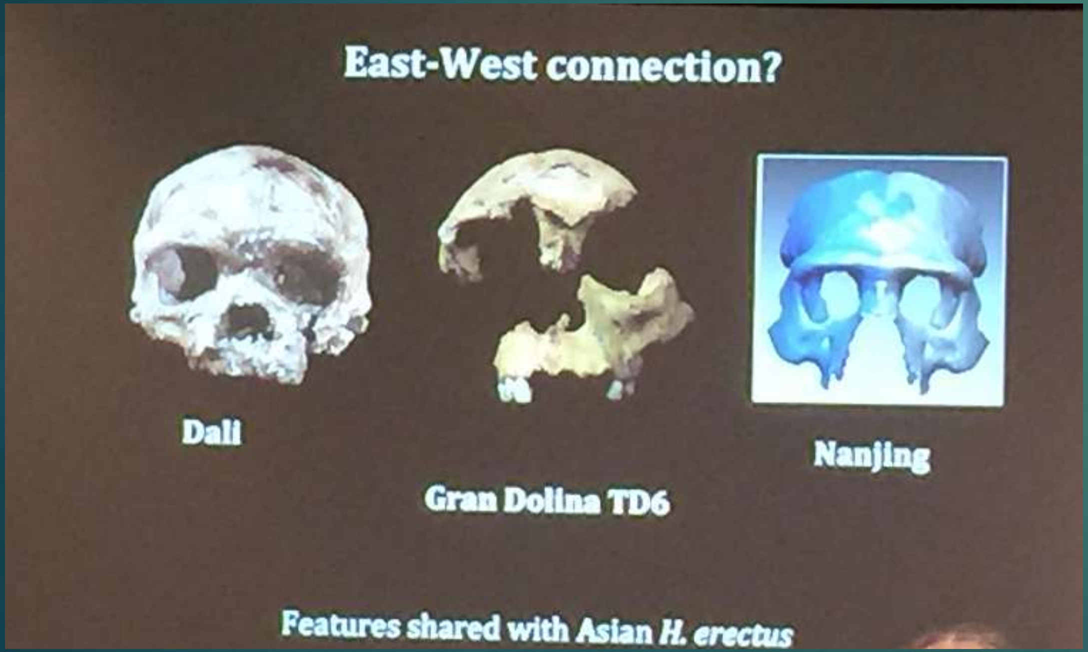
- A common assumption in the evolutionary scenario of the first Eurasian hominin populations is that they all had an African origin.
- This assumption also seems to apply for the Early and Middle Pleistocene populations, whose presence in Europe has been largely explained by a discontinuous flow of African emigrant waves.
- Only recently, some voices have speculated about the possibility of Asia being a center of speciation. However, no hard evidence has been presented to support this hypothesis.
- We present evidence from the most complete and up-to-date analysis of the hominin permanent dentition from Africa and Eurasia. The results show important morphological differences between the hominins found in both continents during the Pleistocene, suggesting that their evolutionary courses were relatively independent.
- We propose that the genetic impact of Asia in the colonization of Europe during the Early and Middle Pleistocene was stronger than that of Africa.

Martinón-Torres M, **et al., 2007**

- **O**rigin and fate of Early and Middle Pleistocene hominins found in Eurasia. Overall, the fossil evidence has been interpreted as supportive of an “out of Africa” origin, and early Asian hominins have been often interpreted as evolutionary “dead ends”.
- In this context, it has been commonly suggested that the origin of Middle Pleistocene populations of Europe lay in the arrival of African emigrants who evolved in Europe toward the Neanderthal lineage. If this hypothesis is correct, and Africa is the main cradle of the Eurasian populations, then we should expect to find an African influence or a discontinuity in the morphological pattern of the European Pleistocene populations.
- Study analyzed the crown morphology of 5,000 permanent teeth assigned to a number of hominin species from the genus *Australopithecus* and *Homo*, which covers the majority of the hominin fossil record available from the late Pliocene and Pleistocene

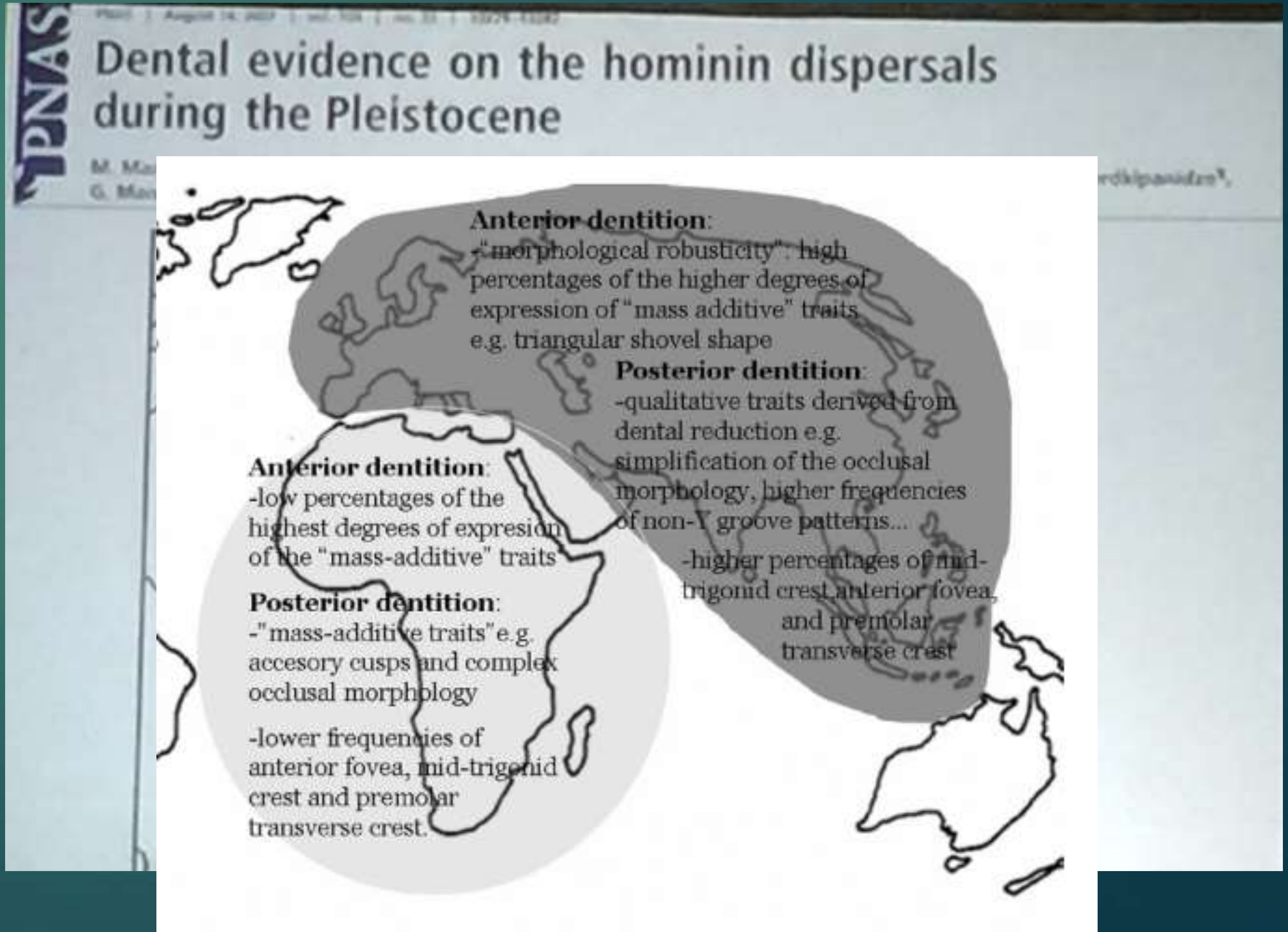
Dental East-West Connections

- 2007: Maria Martinón-Torres, et. al.:
  - 5000 dental teeth study
  - European samples closer to Asian than to African dental samples: genetic impact of Asia in the colonization of Europe during the Early and Middle Pleistocene was stronger than that of Africa



East-West connection?

Features shared with Asian *H. erectus*



PNAS

Dental evidence on the hominin dispersals during the Pleistocene

Anterior dentition:
-"morphological robusticity": high percentages of the higher degrees of expression of "mass additive" traits e.g. triangular shovel shape

Posterior dentition:
-qualitative traits derived from dental reduction e.g. simplification of the occlusal morphology, higher frequencies of non-Y groove patterns...

-higher percentages of mid-trigonid crest, anterior fovea, and premolar transverse crest

Anterior dentition:
-low percentages of the highest degrees of expresion of the "mass-additive" traits

Posterior dentition:
-"mass-additive traits" e.g. accesory cusps and complex occlusal morphology

-lower frequencies of anterior fovea, mid-trigonid crest and premolar transverse crest.

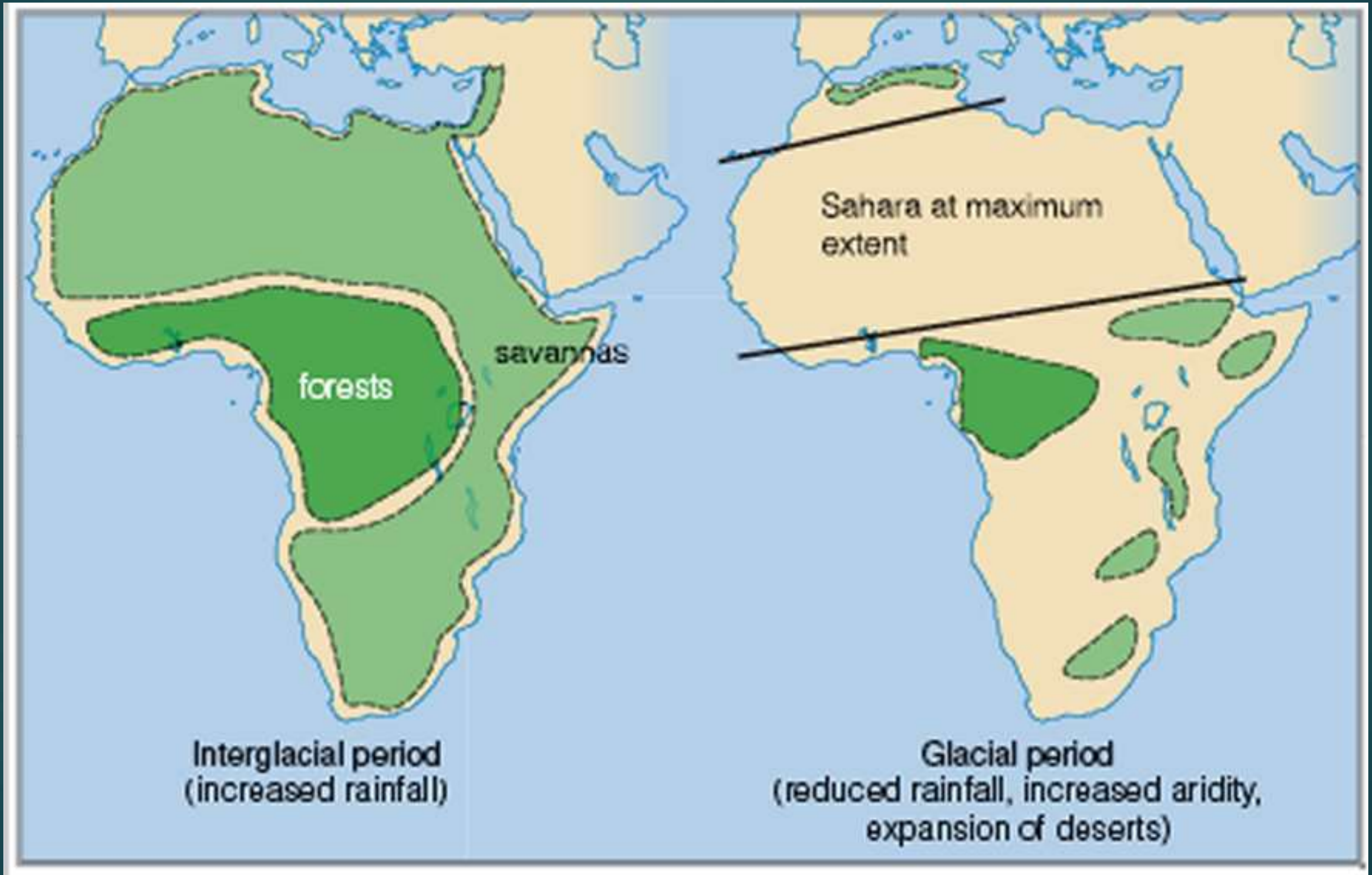
Climate

- Between 600 and 200 Ka, the climates of Africa and Europe experienced a series of warm and cool phases and the move from Africa to Europe subjected these people to generally colder climates.
- About 300 Ka, a severe cold, dry period began, and the Sahara became a barrier to movement between Africa and Eurasia, although movement may have been possible between Europe and northern Asia.
- At this time, populations in Africa and in Europe were isolated from one another and regional differences began to appear.

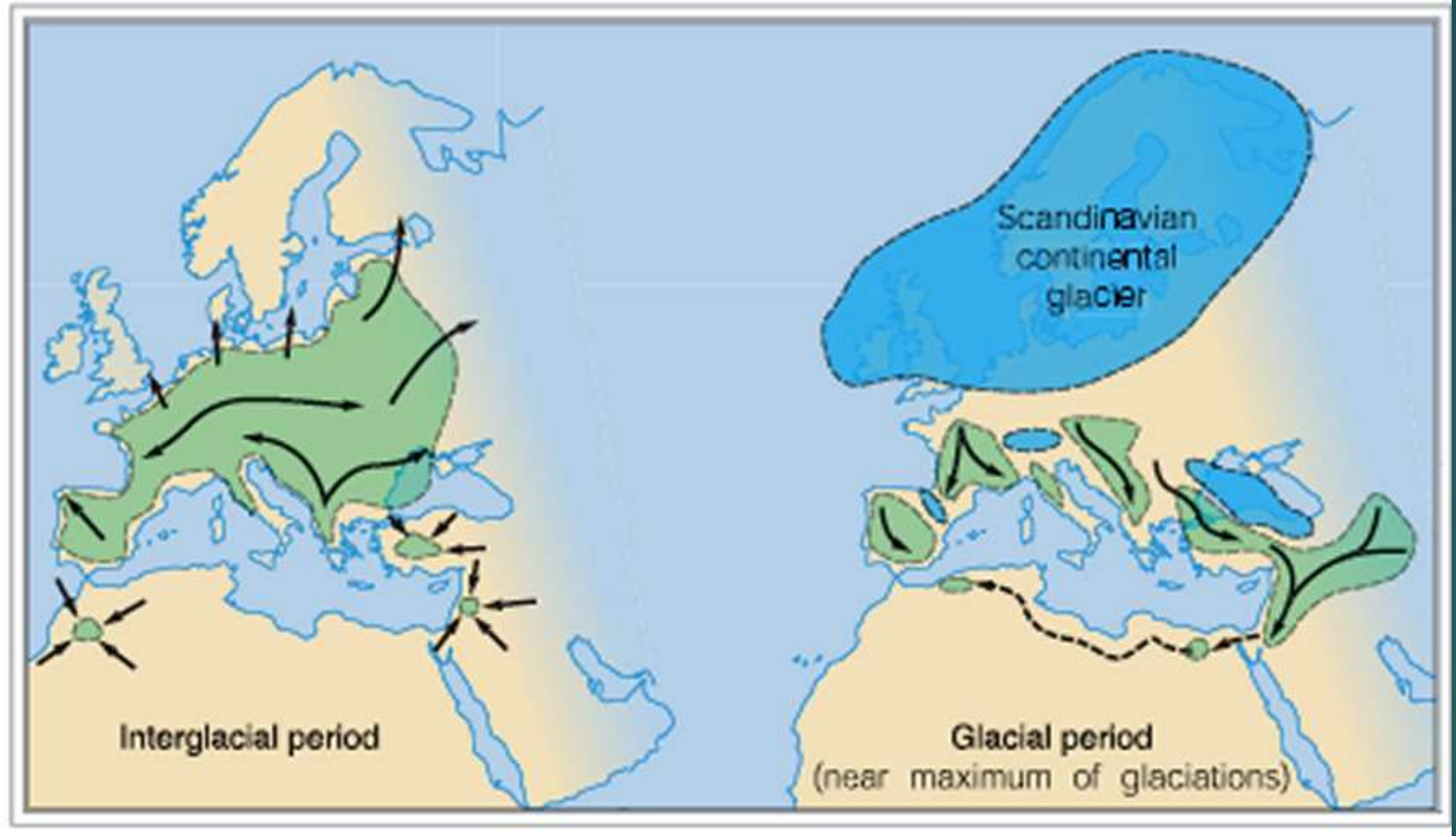
Pleistocene Climate Change

- The **Pleistocene** is the epoch from 2.6 Ma to 12 Ka covering the world's recent period of repeated glaciations.
- Glaciation in the Pleistocene was a series of glacials and interglacials, stadials and interstadials, mirroring periodic changes in climate. The main factor at work in climate cycling is now believed to be Milankovitch cycles. These are periodic variations in regional solar radiation caused by the sum of many repeating changes in the Earth's motion.
- Homo erectus came to be successful within this rapidly changing context. We think that their ability to adapt is due to their cognitive adaptations.

Changing Pleistocene Environments in Africa



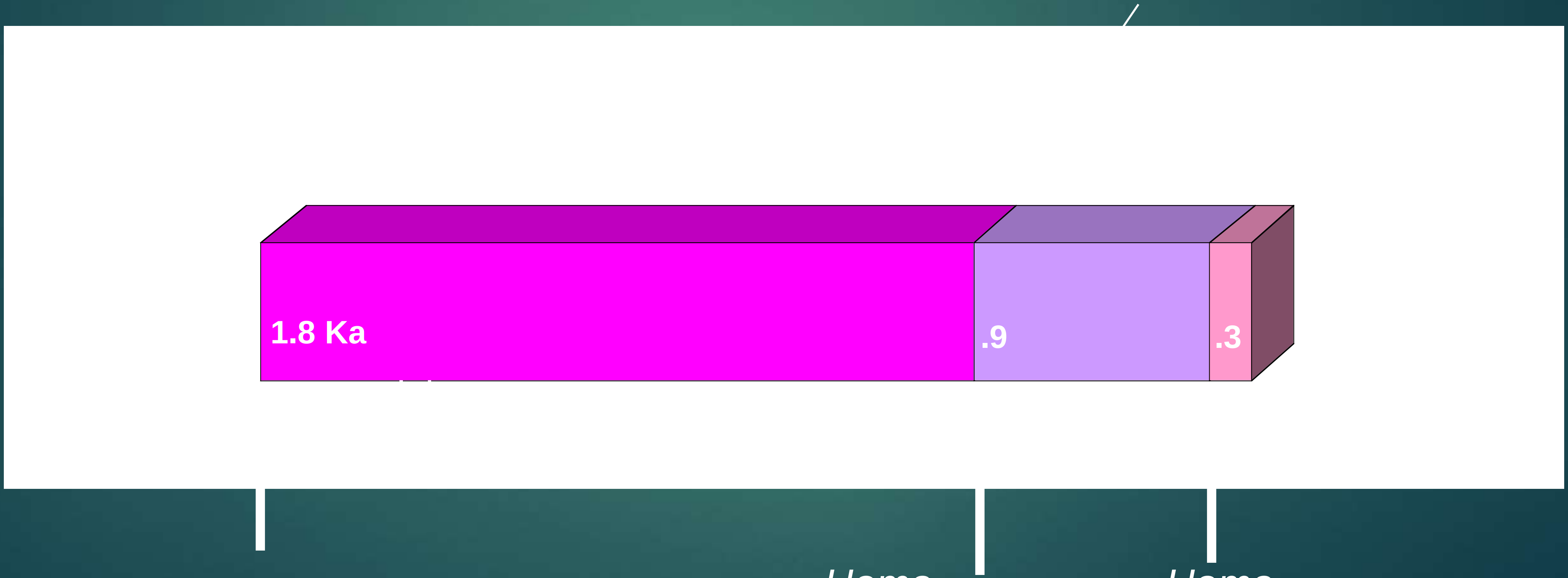
Changing Pleistocene Environments in Eurasia



- Green areas show regions of likely hominin occupation. Blue areas are major glaciers. Arrows indicate likely migration routes.

Major climatic changes occurred during Pleistocene

Glaciers cover much of Europe



Homo erectus

Homo heidelbergensis

Homo neanderthalensis

Middle Pleistocene
(900 – 300 Ka)

- Long, cold glacial periods
- Short, warmer interglacial periods

- Great variability in climate
- Next stage in hominin evolution occurred during this stage
  - More like modern humans than *Homo erectus*

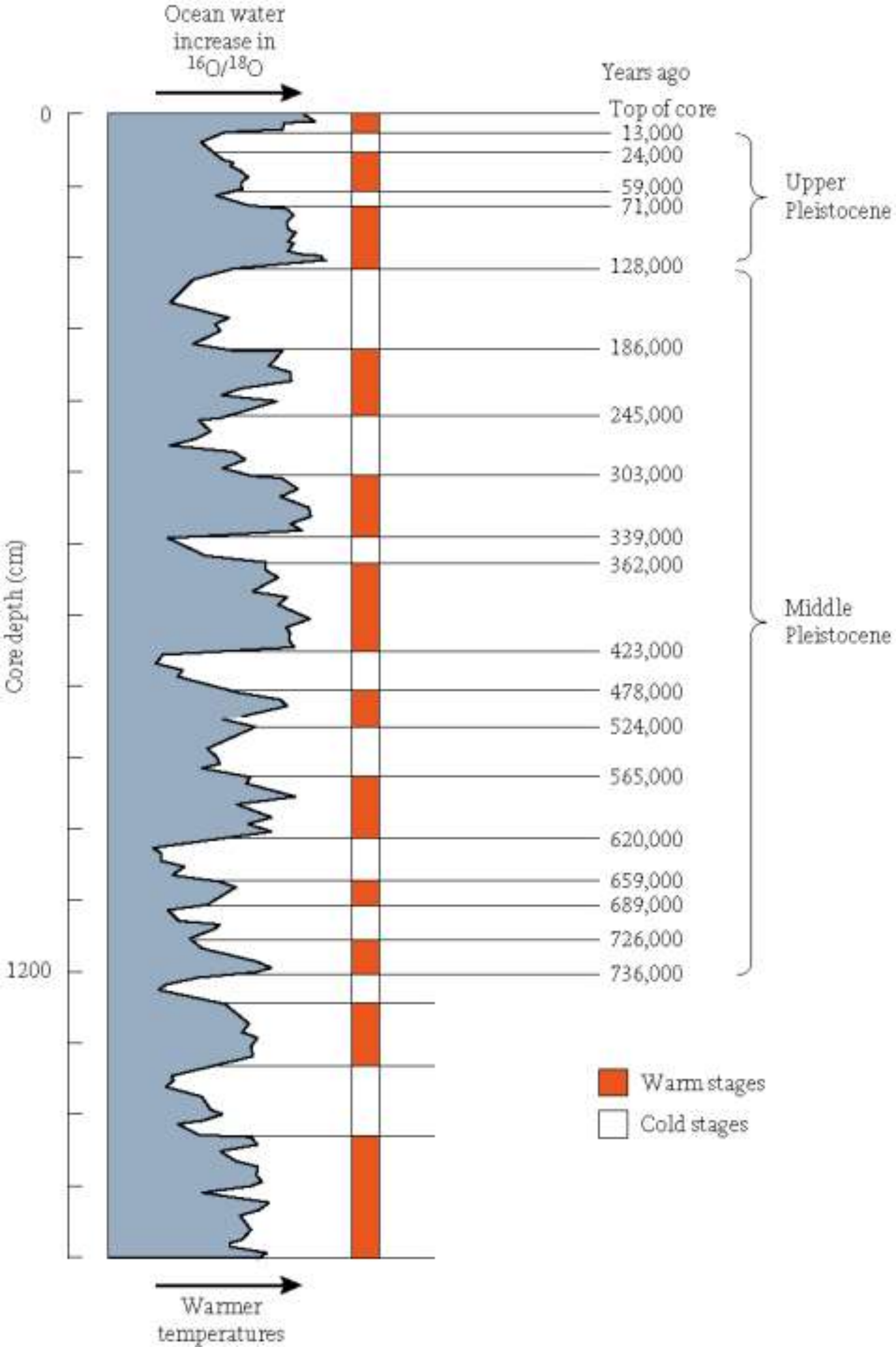
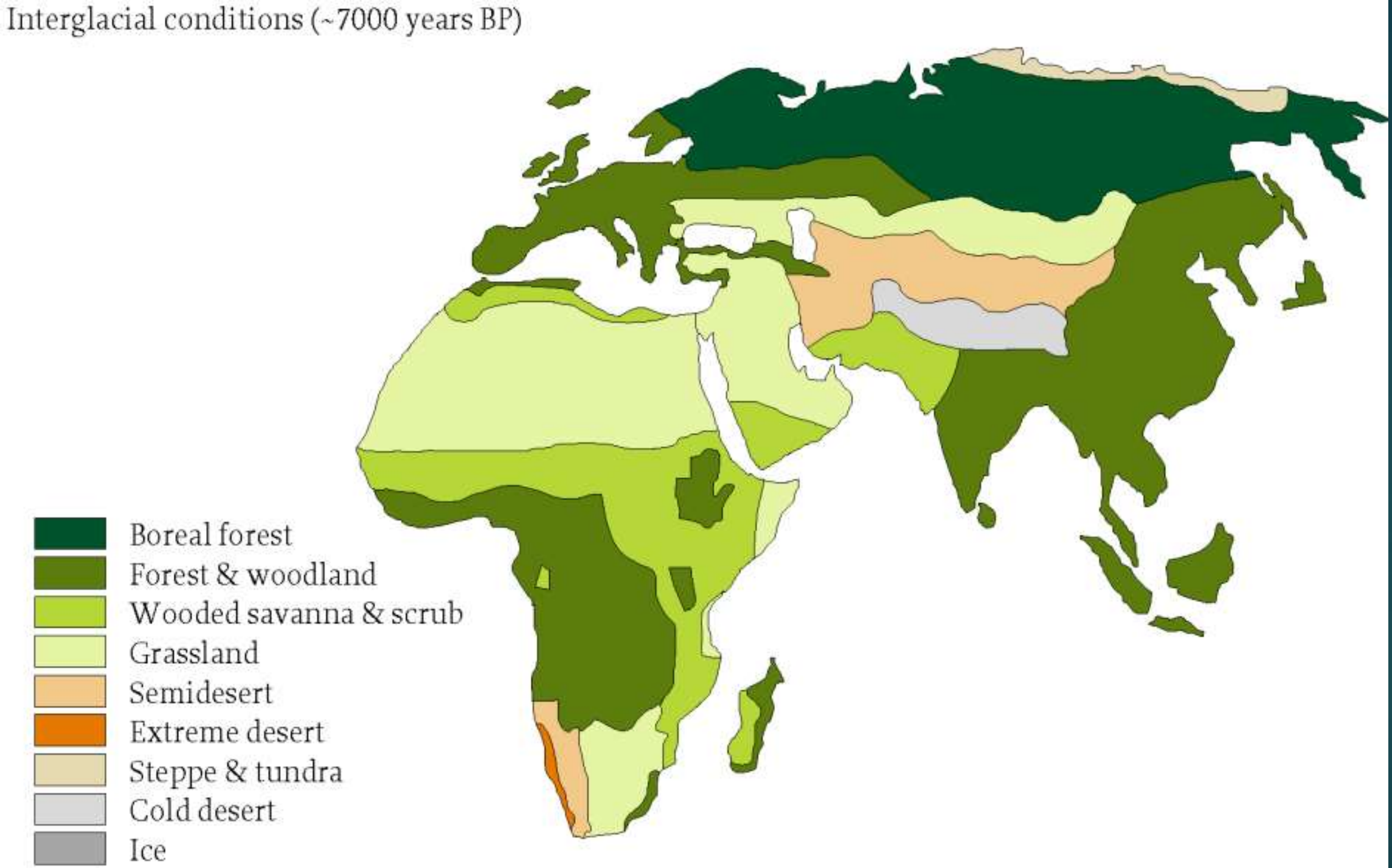
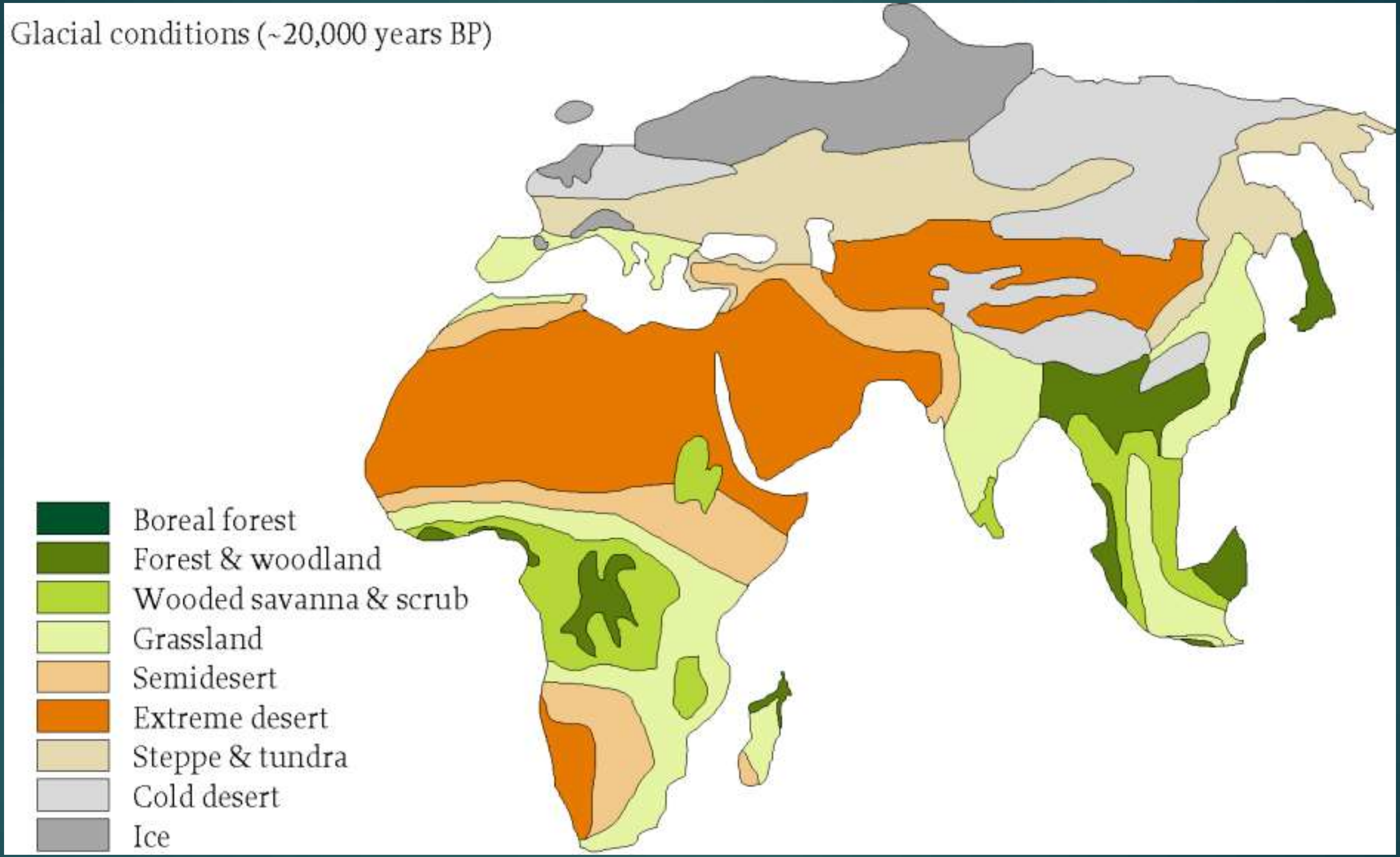


Figure 13.12a



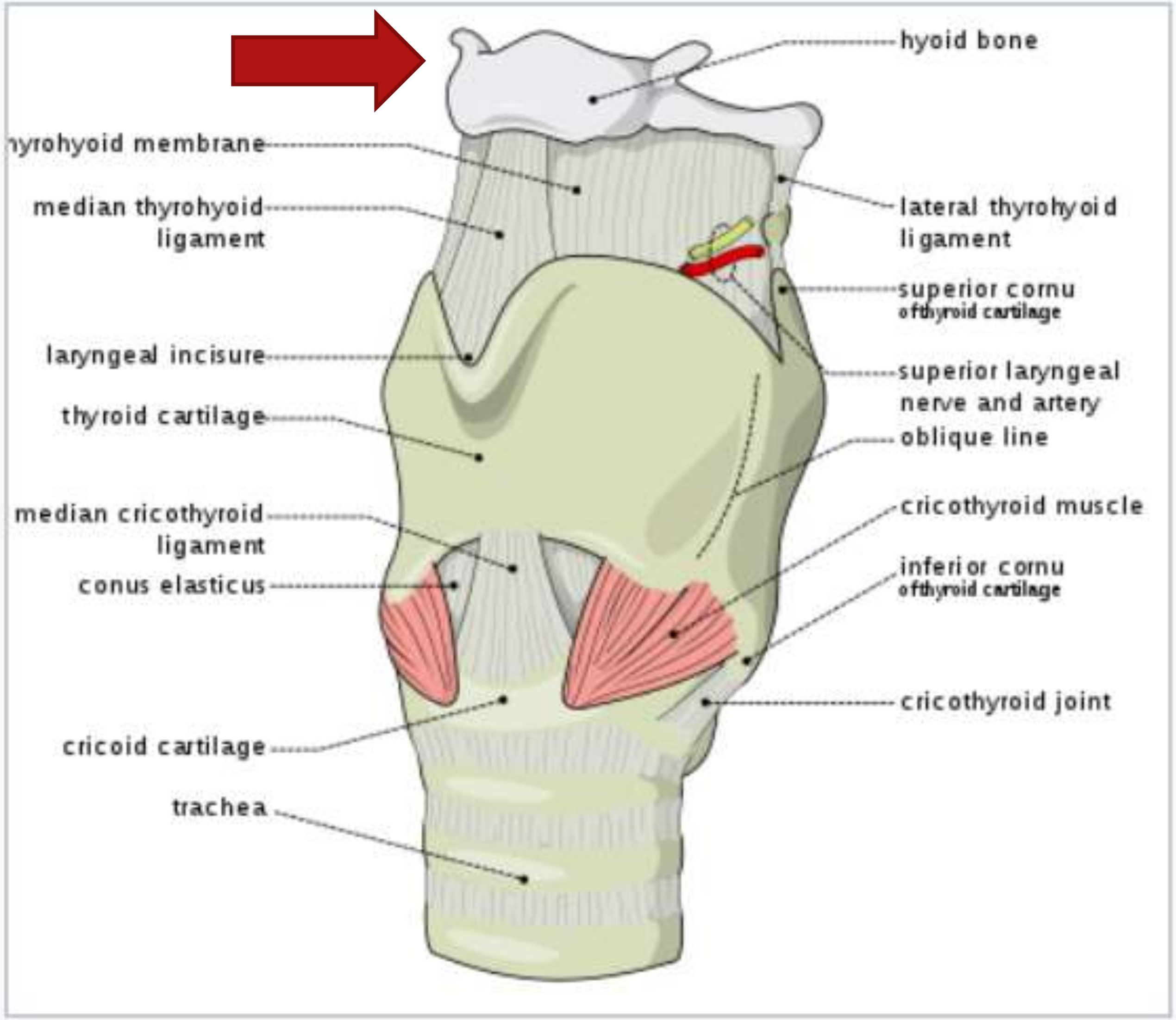
Interglacial conditions (~7000 years BP)

Figure 13.12b



Human hyoid bone:

Aids in tongue movement, breathing, swallowing and speech.
The hyoid bone provides attachment to the muscles of the floor of the mouth and the tongue above, the larynx below, and the epiglottis and pharynx behind. It lies at the level of the base of the mandible. Only bone in body not connected to another bone.



The hyoid bone sits above the thyroid cartilage

Fossil Hyoid bones

- *Australopithecus afarensis* specimen from Dikika, Ethiopia; and a “chimpanzee-like” hyoid assigned to *Australopithecus afarensis* from Dikika (Ethiopia, ~3.3 Ma) (Alemseged et al., 2006)
- *Homo erectus* specimen from Castel di Guido, Italy, 400 Ka; Capasso et al., 2008
- Sima de los Huesos, Spain—from Homo heidelbergensis; Martínez et al., 2008; Two Middle Pleistocene hyoids (AT-1500 and AT-2000) assigned to *Homo heidelbergensis* (as of 2008) from Sierra de Atapuerca (Spain) dated at ~530 ka
- Complete N hyoid, Kebara, Israel; Arensburg et al., 1989, 1990
- El Sidrón, Spain; a partial Neanderthal hyoid (SDR-034) from El Sidròn Cave (Asturias, Spain) dated to ~43 ka (Rodríguez et al., 2003)

Homo erectus hyoid bone

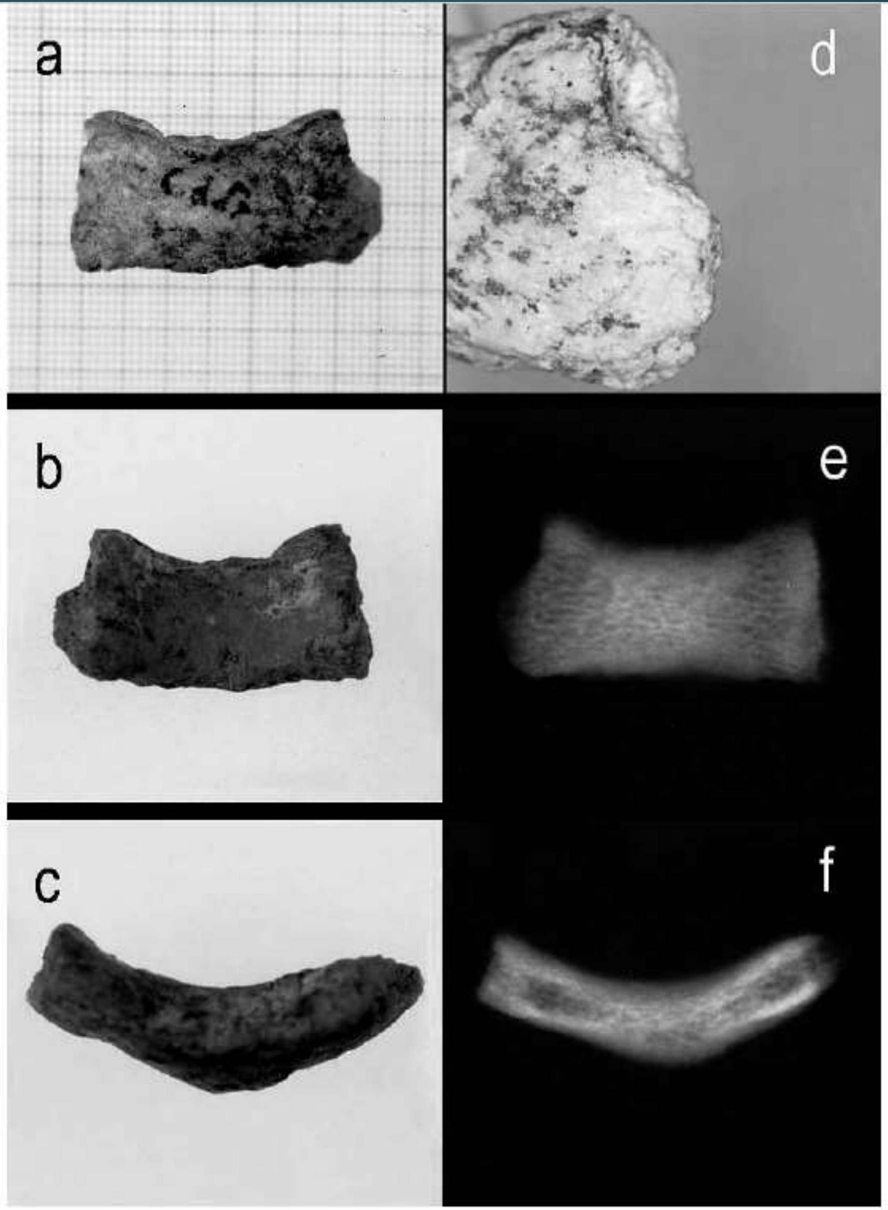


Fig. 1. Hyoid bone of Homo erectus from Castel di Guido 1: ventral (a), dorsal (b) and superior views (c); superior-lateral left margin of the body showing non-fusion of the left greater horn (d); radiographs: frontal (e) and superior (f) views.

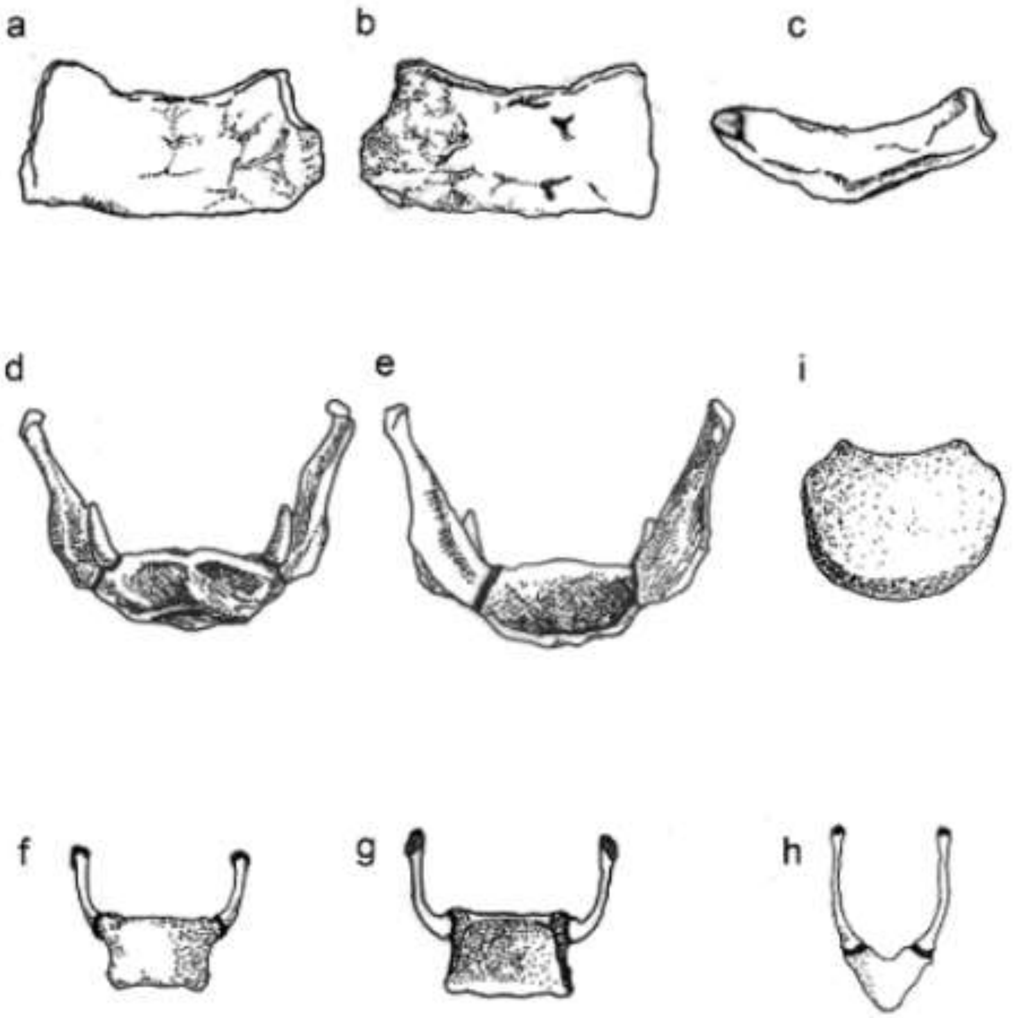


Fig. 3. This drawing compares the general morphology of the Homo erectus from Castel di Guido(CdG-1) hyoid bone (a, b, c), with the bones from the Neandertal man from Kebara (Kebara-2) hyoid bone (d, e), the extant Pan troglodytes hyoid bone (f, ventral view; g, dorsal view; and h superior view), and the Australopithecus afarensis from Dikika (DIK-1-1) hyoid bone body (i, infero-posterior view).

a,b,c: *Homo erectus*

d, e: Kebara
Neandertal

i: Dikika *A. afarensis*

f, g, h: *Pan*

A Homo erectus hyoid bone

- A hyoid bone body, without horns, attributed to Homo erectus from Castel di Guido (Rome, Italy), dated to 400 Ka. The hyoid bone body shows the bar-shaped morphology characteristic of Homo, in contrast to the bulla-shaped body morphology of African apes and Australopithecus. Its measurements differ from those of Kebara Neandertal and Australopithecus afarensis, and from the mean values observed in modern humans.
- The almost total absence of muscular impressions on the body's ventral surface suggests a reduced capability for elevating this hyoid bone and modulating the length of the vocal tract in Homo erectus. The shield-shaped body, the probable small size of the greater horns and the radiographic image appear to be archaic characteristics; they reveal some similarities to non-humans and pre-human genera, suggesting that the morphological basis for human speech didn't arise in Homo erectus.

Capasso et al., 2008

Kebara Cave Israel,
60 Ka, N hyoid bone

Gross anatomy of the Kebara 2 hyoid differs little from that of modern humans.

Two Sima de los Huesos hyoid bones

Two hyoid bones from the middle Pleistocene site of the Sima de los Huesos in the Sierra de Atapuerca (Spain). The Atapuerca SH hyoids are humanlike in both their morphology and dimensions, and they clearly differ from the hyoid bones of chimpanzees and Australopithecus afarensis. Their morphology is modern-human-like and very different from that described for the African apes and A. afarensis. The degree of metric and anatomical variation in the fossil sample was similar in magnitude and kind to living humans. Modern hyoid morphology was present by at least 530 kya and appears to represent a shared derived feature of the modern human and Neandertal evolutionary lineages inherited from their last common ancestor.

- The hyoid bones recovered from the Sima de los Huesos represent the oldest fossil evidence for the anatomy of this bone in the genus Homo.

Martinez et al., 2008

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