Human Evolution
Scientific Update

October 2023

by

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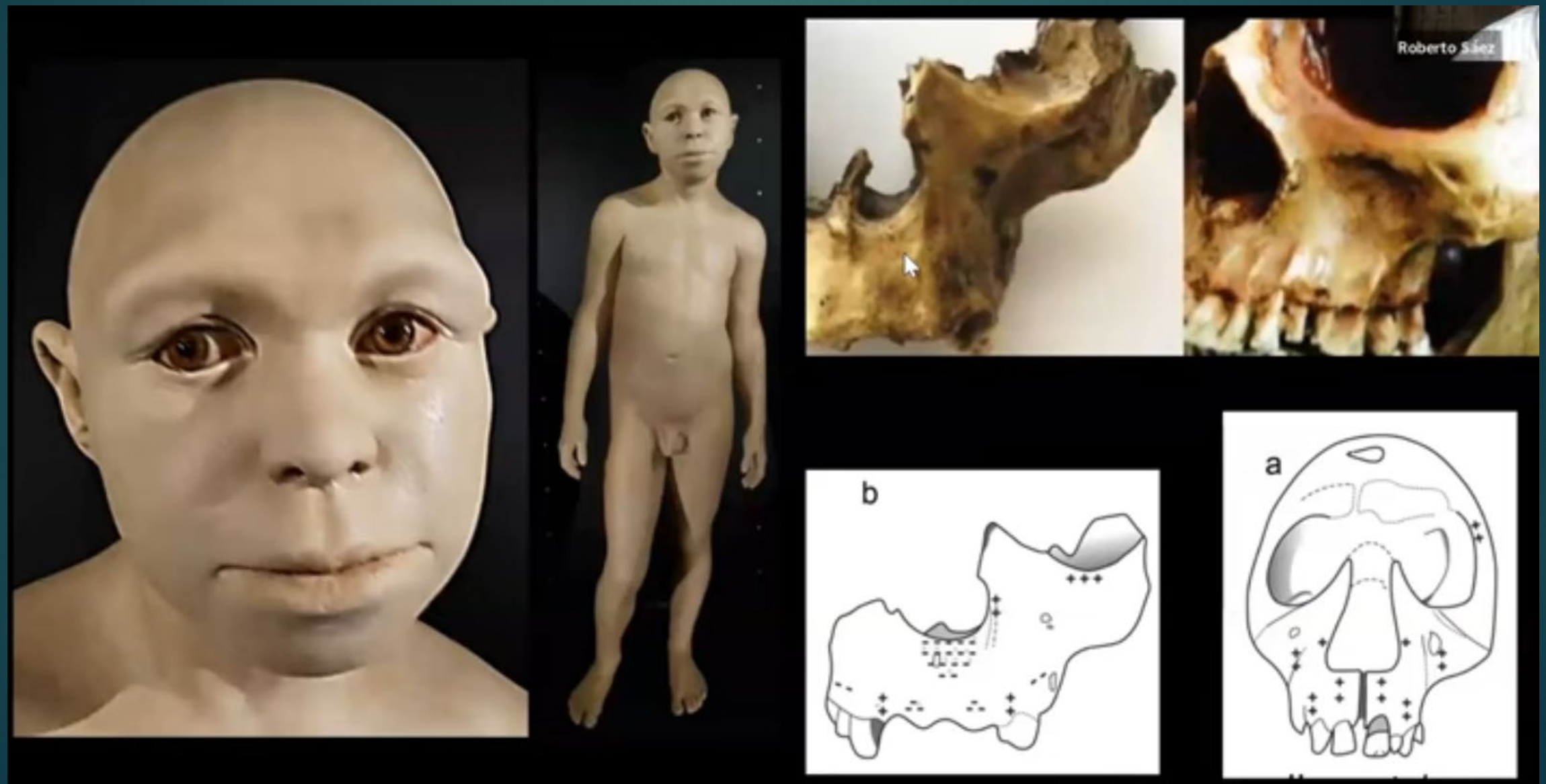
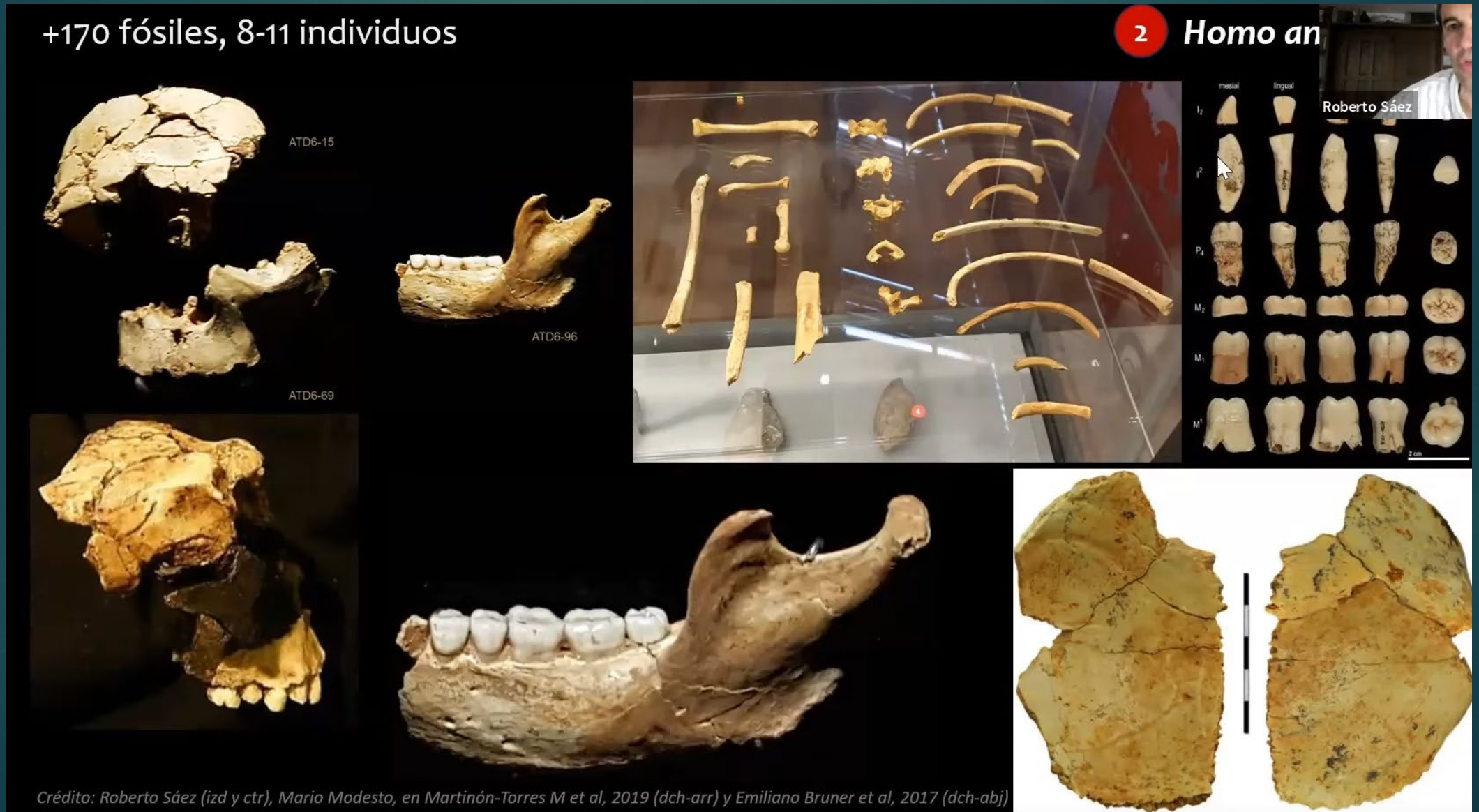
Five Hominin Species at Atapuerca

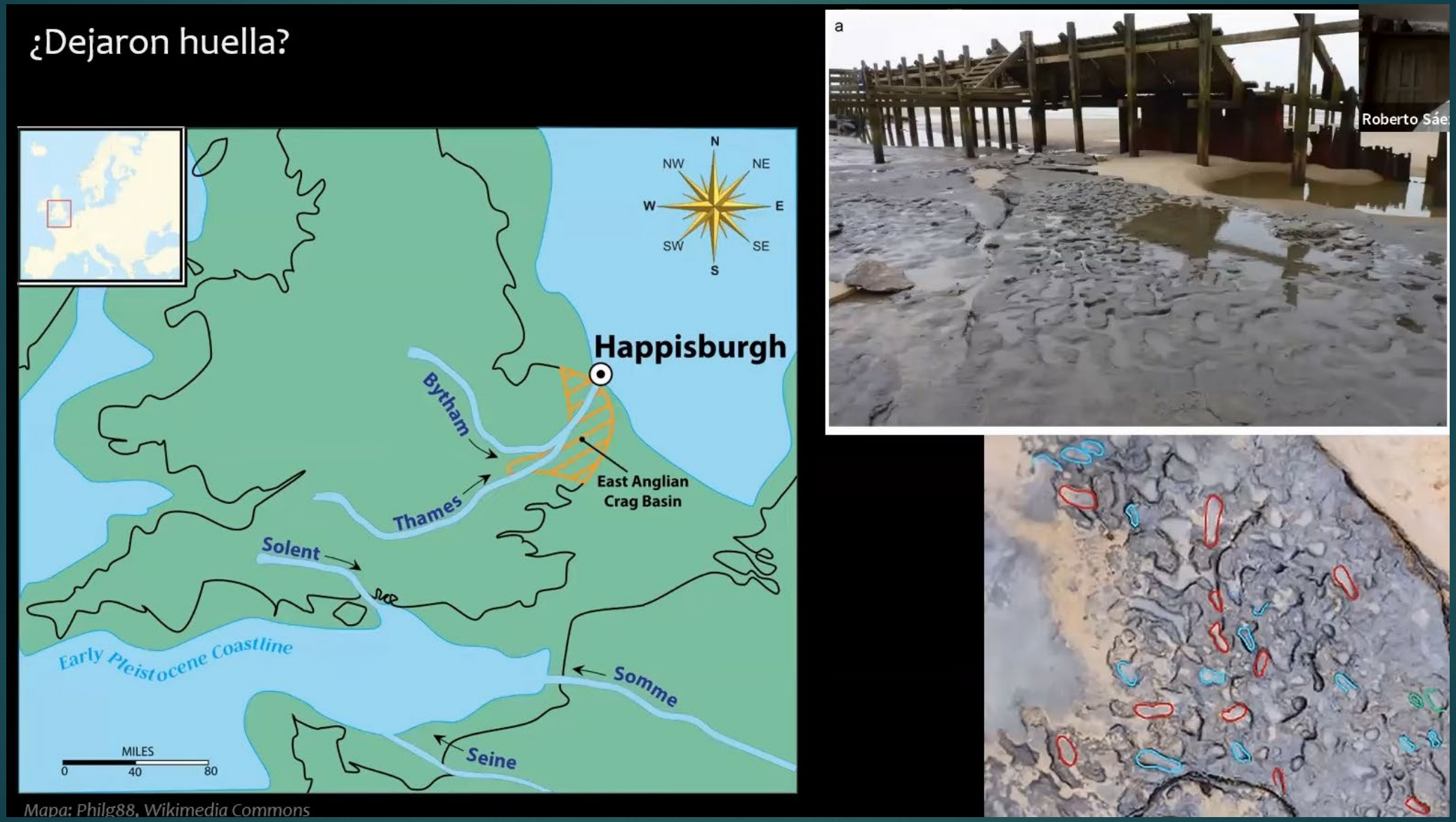
Homo antecessor, 900 Ka



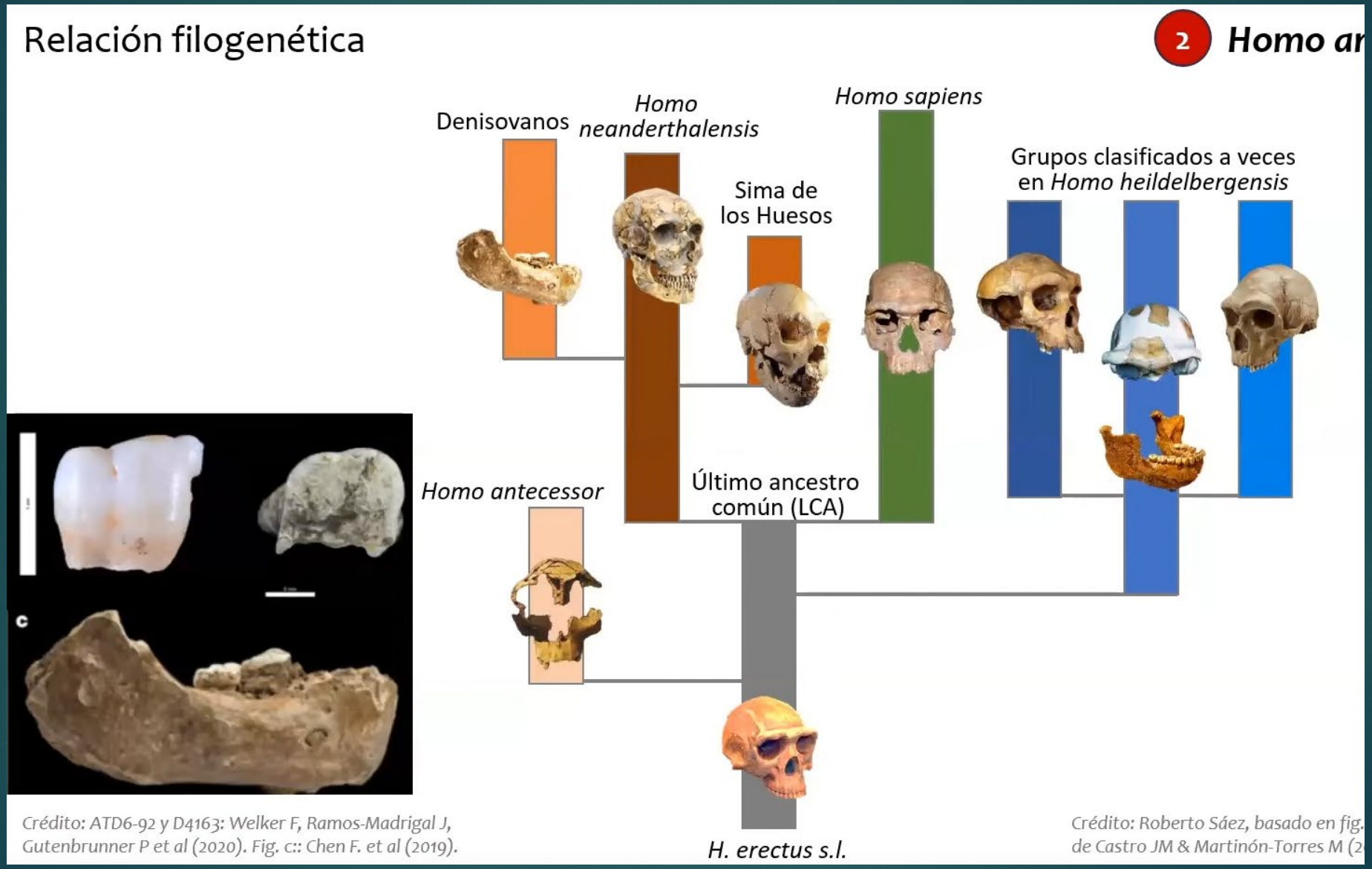
H. antecessor



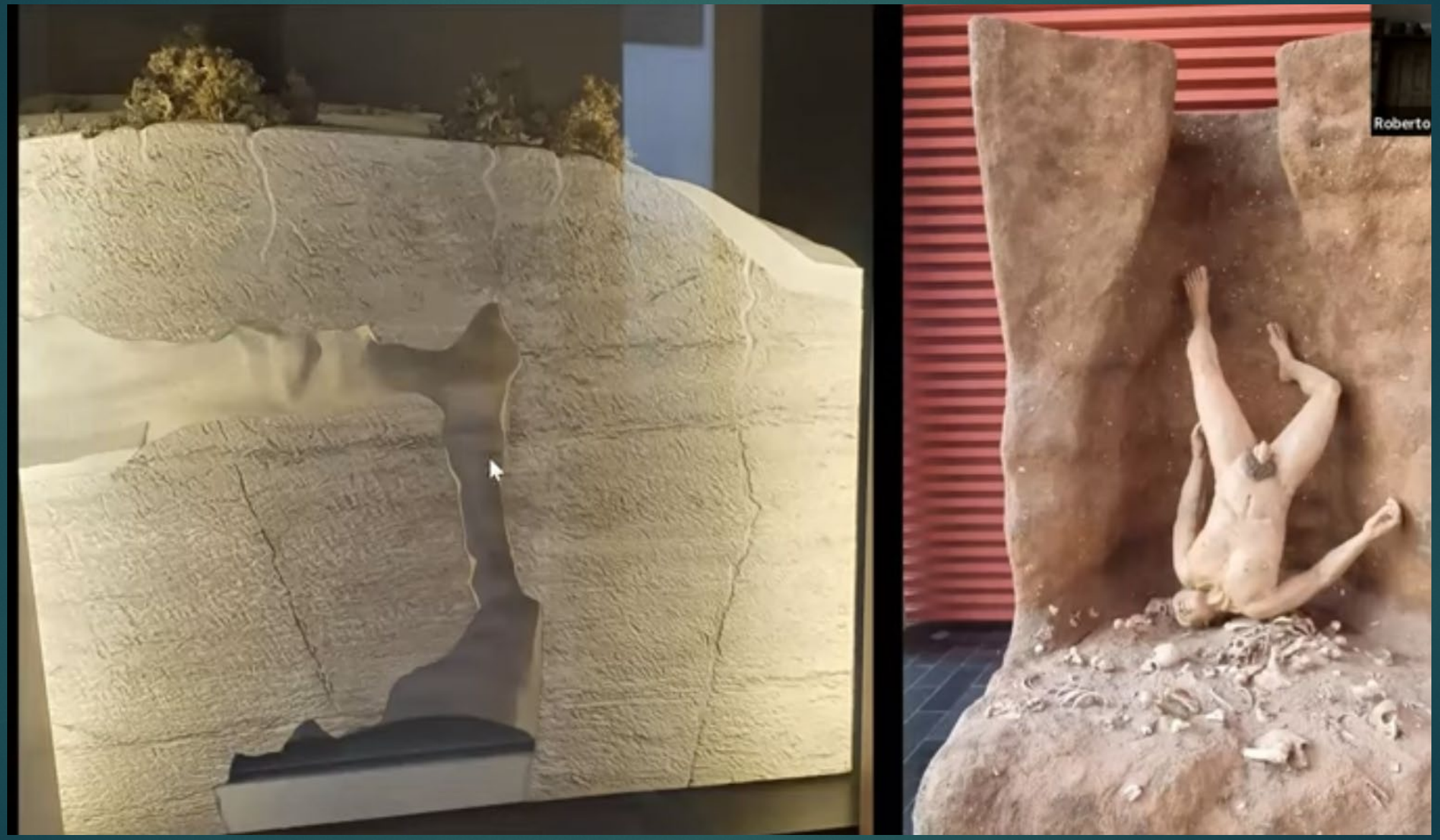
Antecessor? “They left their mark?”



Phylogenetic relationships



Sima de los Huesos (Pit of the Bones): early Neandertals



Sima de los Huesos: 28 skulls; Skull 5 = DNA, 420 Ka

Sima de los Huesos: no longer *H. heidelbergensis*

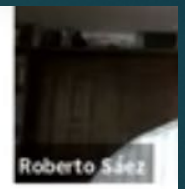
1997: *Homo heidelbergensis*

Arsuaga JL, Martínez I, Gracia A, Lorenzo C (**1997**). The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative Study. Journal of Human Evolution 33, 219-281.

Only terminal species or species without any descendants (such as Neandertals in our opinion) are diagnosable in terms of uniquely derived traits. But in the European Middle Pleistocene sample each single fossil (even within the Sima de los Huesos sample) exhibits a unique combination of plesiomorphies and Neandertal apomorphies, because these traits were polymorphic and more or less independent in the Middle Pleistocene. The fossils included in the European Middle Pleistocene species could show any combination of some derived traits shared with Neandertals, together with many primitive traits not present in Neandertals. Incipient Neandertal-like traits (i.e., not the plesiomorphy nor the apomorphy, but intermediate character states that may be called "mesiomorphies"), could also be used.

One possible name for this exclusively European Middle Pleistocene species is *H. heidelbergensis* Schoetensack, 1908, but the problem is that it is difficult to say if the Mauer mandible (the holotype) belongs to a human population that shared derived features with Neandertals. We consider this possibility very likely, because Mauer is closer to other European Middle Pleistocene fossils, as the Sima de los Huesos sample, than to the Lower Pleistocene fossils from the Gran Dolina site, also in the Sierra de Atapuerca (Carbonell *et al.*, 1995). So, the redefined *H. heidelbergensis* species would include all the known European Middle Pleistocene fossils (including the Sima de los Huesos sample), with the exception (provisional) of Ceprano and that of the very Neandertal-like fossils of the end of this period, as Biache-Saint-Vaast or La Chaise Suard.

2014: ~~*Homo heidelbergensis*~~



Arsuaga et al. (**2014**). Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344, 1358.

Concerning the taxonomy of the SH fossils, we have long maintained that the SH hominins are members of the Neandertal lineage (*16*, *40*). Based on the cranial evidence, we have proposed that the SH fossils, as well as the rest of the European early and middle Middle Pleistocene specimens, should be assigned to the species *Homo heidelbergensis* defined in a broad sense to include fossils with a generally more primitive morphology than the late Middle Pleistocene and Late Pleistocene Neandertals, even if they exhibit some derived Neandertal traits (*19*). However, the difficulty with identifying derived Neandertal features in the Mauer mandible, the type specimen of *H. heidelbergensis*, contrasts strongly with the presence of numerous Neandertal apomorphies in the SH mandibles (*41*). On this basis, we suggest that the SH sample be removed from the *H. heidelbergensis* hypodigm. An alternative view of *H. heidelbergensis* is as a Middle Pleistocene taxon that includes only fossils that lack any Neandertal apomorphies, and, in this restricted sense, the species is seen as the stem group for Neandertals and modern humans (*7*).

In addition, the new evidence presented here based on cranial morphology confirms that the SH population differs from some other European MPHs, such as Ceprano and Arago, that do not exhibit the suite of derived Neandertal features seen in SH. Thus, more than one evolutionary lineage appears to have coexisted during the European Middle Pleistocene (*42*), with that represented by the SH sample being phylogenetically closer (i.e., a sister group) to the Neandertals.

Underrepresentation of African genomes

- People of African ancestry are among the most genetically diverse in the world, yet they make up less than 0.5% of participants in genetic studies and are still underrepresented in major genetic databases.

- In the UK Biobank, one of the largest in the world, about 1.6% of the 500 K participants identify as Black or Black British.

- And although the U.S. National Institutes of Health's (NIH's) All of Us study aims to build a diverse biobank, only about 17% of the roughly 500,000 fully enrolled participants recruited so far identify as Black, African American, or African.

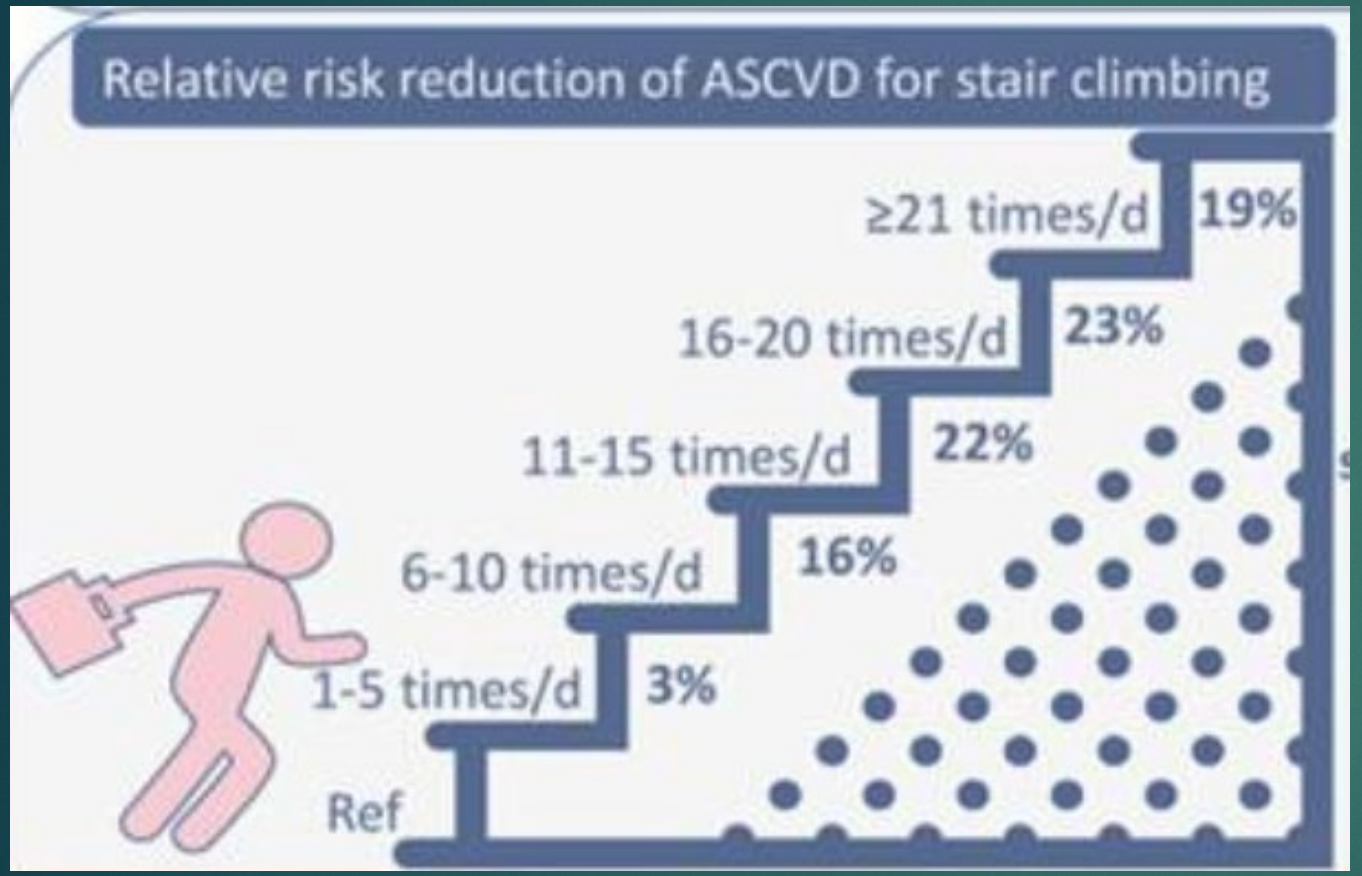
New African Genomic Initiative

- The lack of representation means disease-causing mutations unique to Africans are missed. And tools for predicting disease risks or treating patients that were developed with data from those of European descent—may not work as well in patients with African ancestry. These “are aspects of human genomes that can only be studied in African populations,

- New initiative aims to sequence half a million genomes of people with African ancestry for health studies

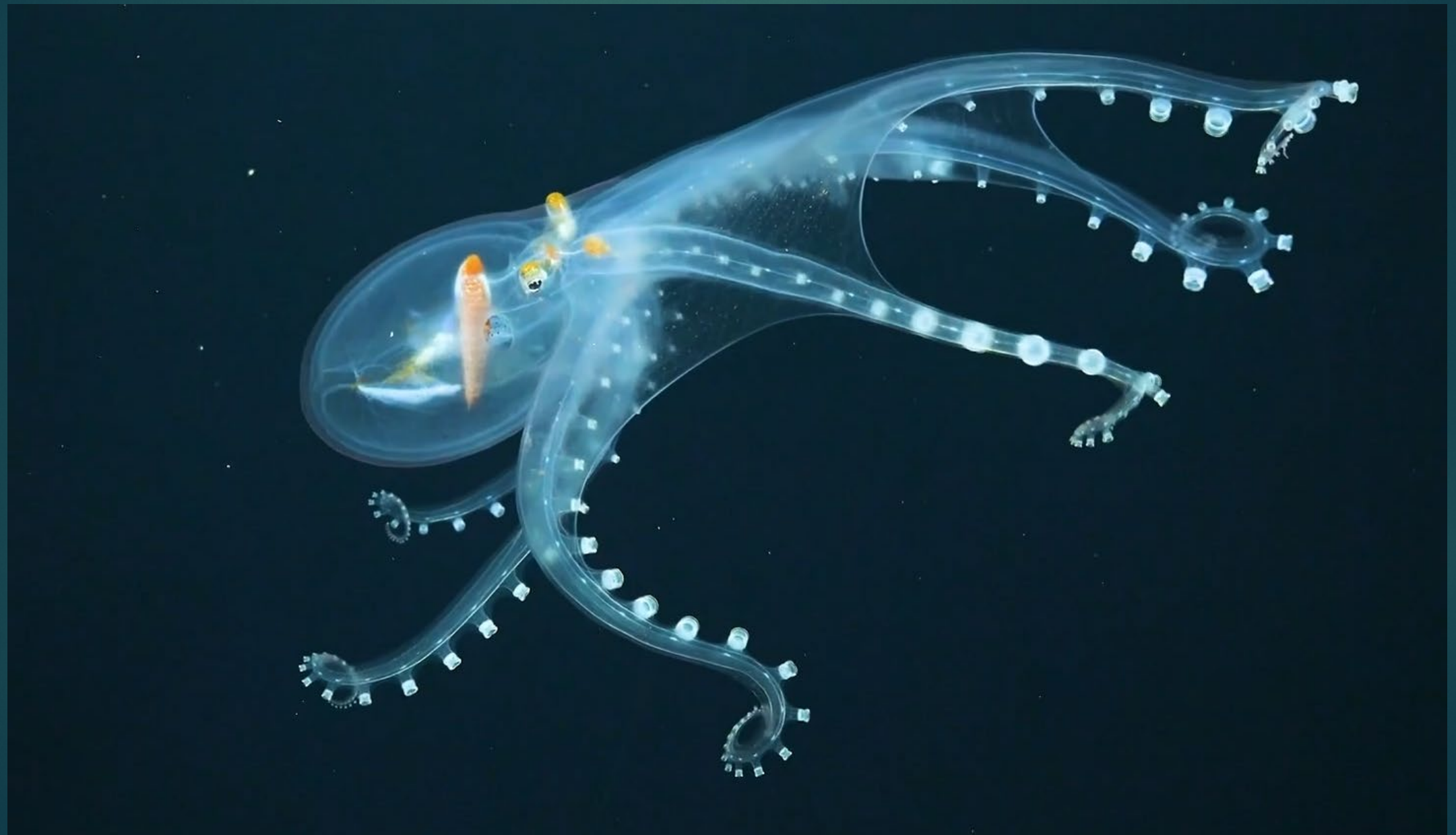
- All the partner organizations will have exclusive access to the sequencing data.

Forget walking 10,000 steps a day. Taking at least 50 steps climbing stairs each day could significantly slash your risk of heart disease.

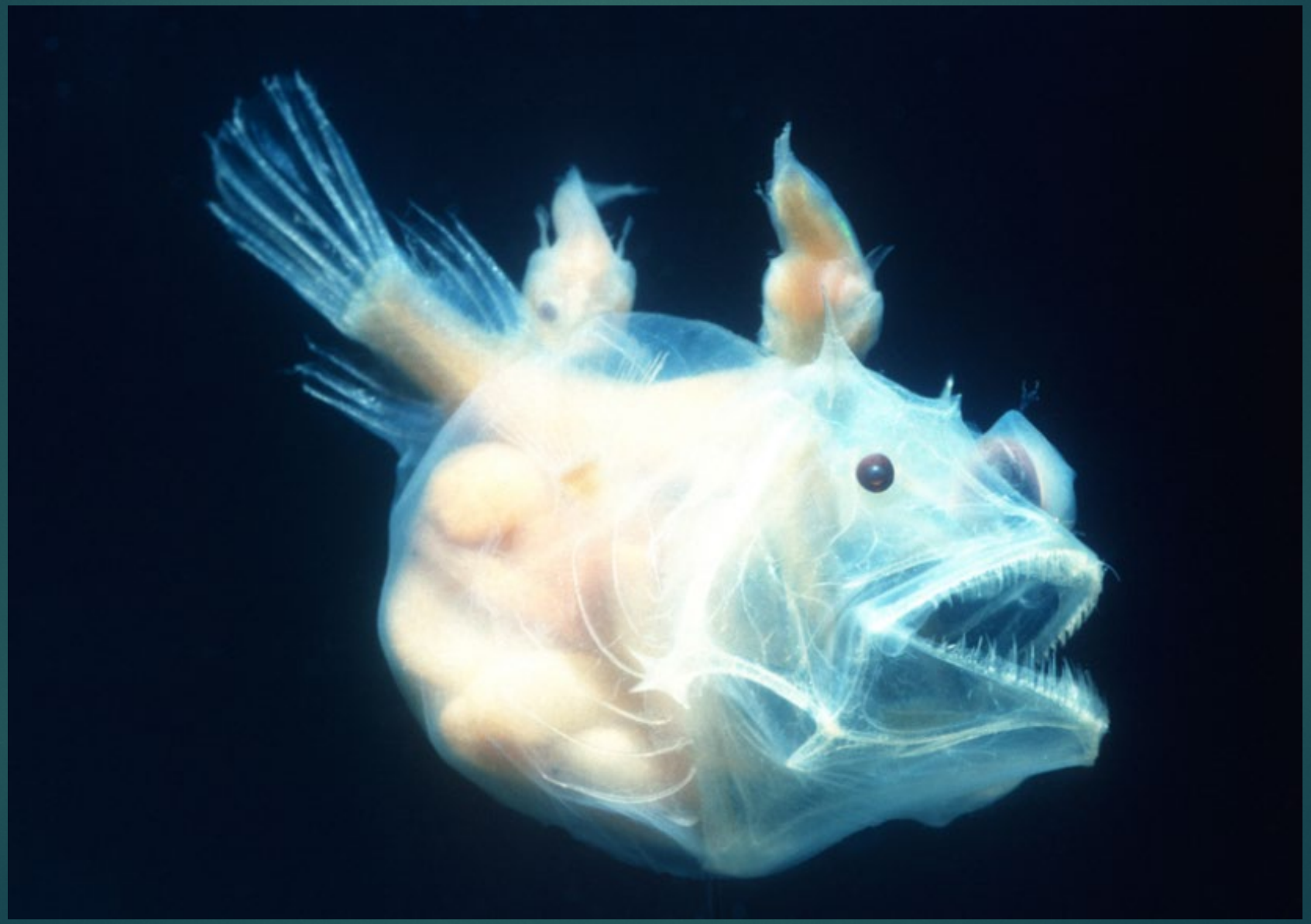


Climbing more than five flights of stairs (approx. 50 steps) daily was associated with a lower risk of ASCVD types independent of disease susceptibility. Participants who stopped stair climbing between the baseline and resurvey had a higher risk of ASCVD compared with those who never climbed stairs.

Glass octopus



A kiss that lasts: a parasitic male provider of sperm on-tap



Russian orca beached after swallowing 7 whole sea otters

Acheulean Handaxes in Medieval France: An Earlier 'Modern' Social History for Palaeolithic Bifaces

- Study investigate the shape, color and potential flake scarring on a handaxe-like stone object seen in the Melun Diptych, painted by the French fifteenth-century artist Jean Fouquet, and compare its features with artefacts from diverse (including French) Acheulean handaxe assemblages.
- Our results strongly support the interpretation that the painted stone object represents a flint Acheulean handaxe, likely sourced from northern France, where Fouquet lived.
- In the mid 1600s, widespread gravel aggregate extraction, the rise of antiquarianism and the European Enlightenment resulted in increased discovery rates of, and subsequent interest in, these unusually flaked stone objects. It is known that from 1656 onwards handaxes started to be formally investigated and went on to become a major focus in the emerging field of archaeology, and later, prehistoric archaeology.

Alastair Key, et al., 20023

Acheulean handaxes

- Prior to the Enlightenment handaxes were often considered to be of natural origin and were thought to have been ‘shot from the clouds’ when lightning struck the ground.
- Sixteenth-century natural historians across Europe noted the presence of ‘ceraunia’ or ‘thunderstones’, which were ‘curiously shaped stone objects … treated as a naturally occurring geological phenomenon’ formed through lightning strikes
- The object under discussion appears in *Étienne Chevalier with Saint Stephen*, an oil-painting on wood that is currently housed in the Gemäldegalerie, Staatliche Museen zu Berlin (Germany). Painted *c.* 1455, it is one of the two panels of the so-called Melun Diptych.

St. Stephen in blue. He was stoned to death

Cannibalism was a common funerary rite in northwest Europe near end of last ice age

- New study: evidence of Magdalenian cannibalism in human remains unearthed at Gough's Cave in western England dating to about 15,000 years ago.
- Research suggests cannibalism was a funerary rite for the Magdalenian people in northwest Europe, but others preferred to bury their dead.
- Cannibalism was common in northwest Europe between 14,000 and 19,000 years ago; the Magdalenians used it in their rituals to dispose of the dead.
- But cannibalism seems to have ended when the Magdalenians were supplanted by another group of prehistoric people known as the Epigravettians, who instead buried their dead.

Tom Metcalfe, 2023

Gough’s Cave, Cheddar, England: evidence of cannibalism

The human remains from Gough's Cave in the west of England are dated to about 15,000 years ago. Many of the remains show clear signs of cannibalism. (Image credit: Trustees of the Natural History Museum)

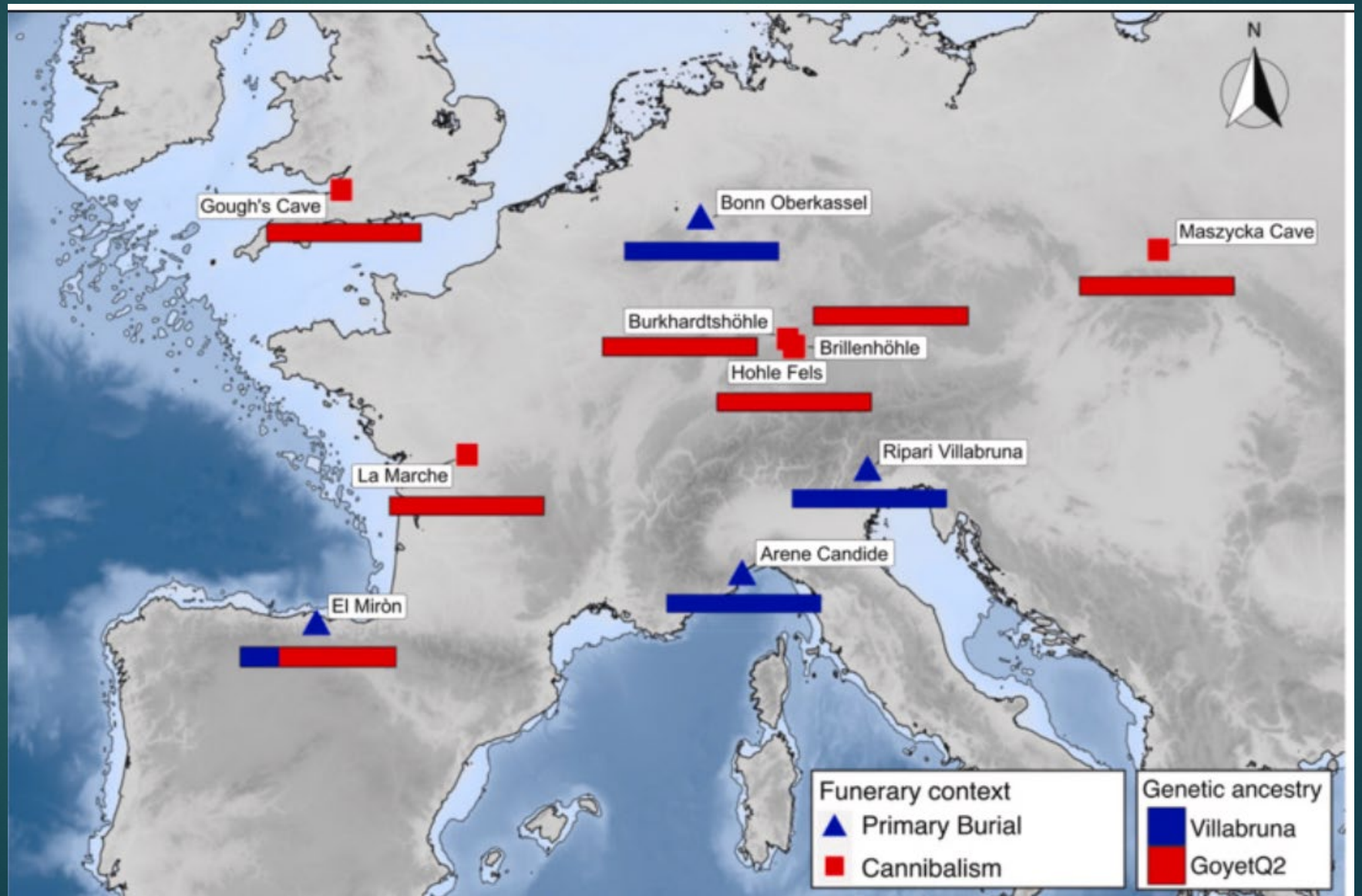
Gough's Cave

- The remains show clear cut marks and indentations made by human teeth. Some of the largest bones have been broken, presumably to scoop out their marrow, and several skull fragments found there have been shaped into cups or bowls, which were probably used for drinking.
- Study found widespread evidence of cannibalism throughout northwest Europe at this UP time. But they also found a curious cultural link: Genetic research suggests cannibalism was widespread among Magdalenian groups in northern and western Europe but not among Epigravettian groups, who occupied eastern and southern Europe.
- The conclusions hinge on a small genetic sample — the ancestry of just eight individuals could be reliably determined from their remains.

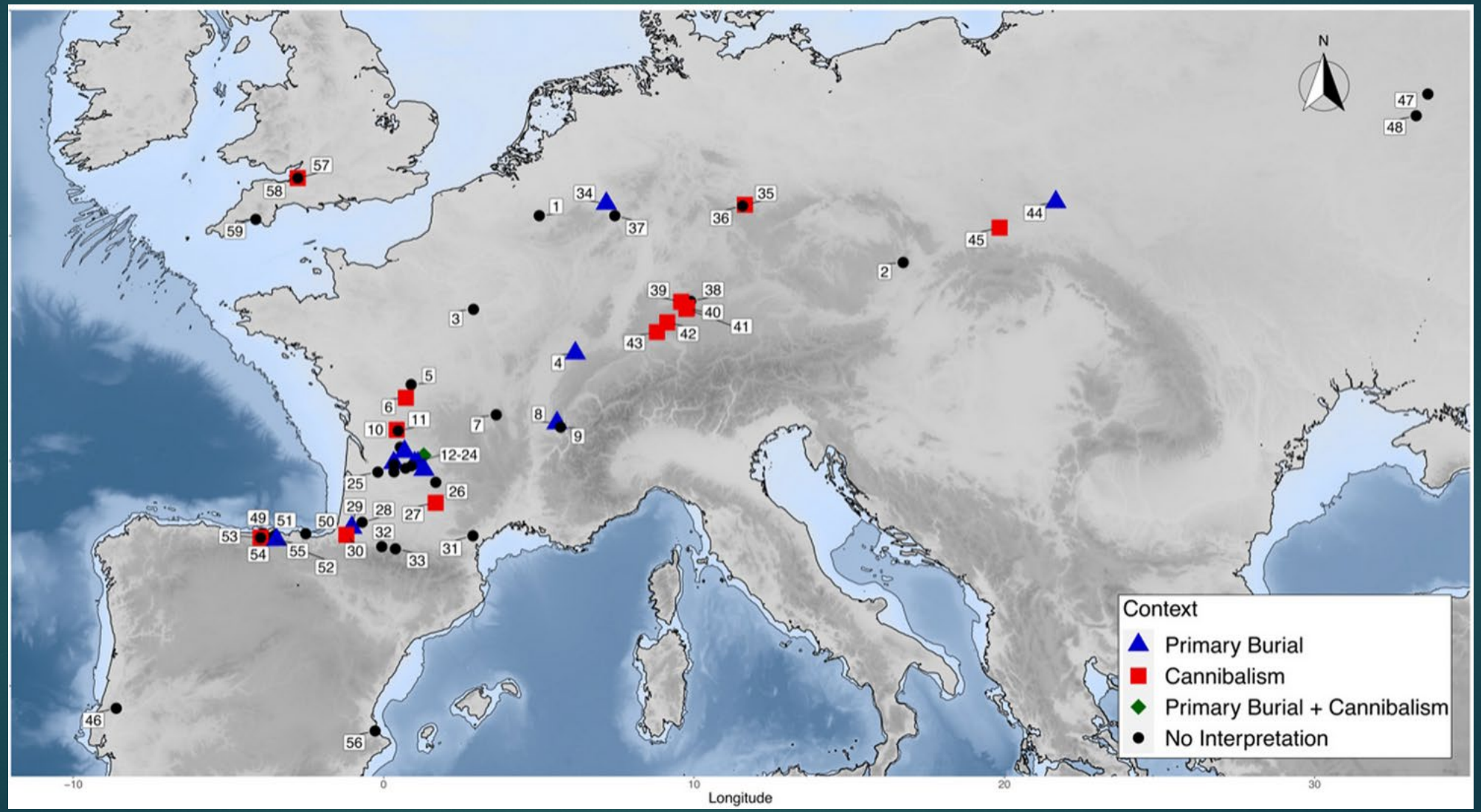
Cultural cannibalism: skull cups at Gough's Cave

Among the remains at Gough's Cave are several human craniums that have been deliberately made into "skull cups," possibly for drinking from. (Image credit: Trustees of the Natural History Museum)

Map of Magdalenian and Epigravettian sites from where both funerary context and genetic data are available



Researchers found evidence of cannibalism only at archaeological sites they attributed to Magdalenian hunter-gatherers, and not at sites they attributed to the Epigravettian people



Artistic reconstruction of a group of hominins in direct competition for carrion with a hyena

Hominin scavenging vs giant hyenas ~1.2-.8 Ma

- Passive scavenging could be a very successful strategy for late-early Pleistocene hominins in Europe, even in competition with giant hyenas.
- Hominins may have been capable of competing with giant hyenas for carcasses abandoned by saber-toothed cats and jaguars during the late-early Pleistocene era (approximately 1.2 to 0.8 million years ago) in southern Europe. The findings of this modeling study are published in *Scientific Reports* and suggest that moderately sized groups of hominins may have been the most successful at scavenging.
- Previous research has theorized that the number of carcasses abandoned by saber-toothed cats may have been able to sustain early hominin populations in southern Europe

J. Rodriquez, et al., 2023

Food chain = saber-toothed cats – hyenas - hominins

- Carcasses of large ungulates abandoned by the two saber-toothed species.

- If cats killed one prey every week, based on a conservative estimate, only one-third of the edible energy in the carcass would be consumed before killing a new prey. This estimate supports the claims linking the extinction of the giant hyena in Europe to the extinction of saber-tooth cats.

- Moreover, scavenging large carcasses in competition with other carrion eaters may have led hominins to coordinate their movements, group cohesion, defense, cooperation, and communication. A relationship between scavenging and language emergence was proposed.

Importance of group size and cohesion

- Evidence from Fuente Nueva and Dmanisi suggests that cobbles and limestone blocks could be used as throwing stones to drive away predators and competitors, reducing the risk of the confrontation

- Group size had to be moderate in order to maximize the energetic efficiency of the activity. Scavenging does not require advanced technology only group cohesion and cooperation and was likely an important source of meat and fat for Homo sp. in Europe, especially in winter when plant resources were scarce.

Early *Homo erectus* lived at high altitudes and produced both Oldowan and Acheulean tools

- The fossil and archaeological sites of Melka Kunture, Ethiopia. The new research re-evaluates the geological age of some of the earliest archaeological levels in this area, in the excavations at the locality designated Garba IV.

- With new paleomagnetic dating results, Mussi et al. show that levels D, E, and F are between 2.02 million and 1.95 million years old.

- Most interesting is that level D includes what is now the earliest Acheulean assemblage in the world, and level E has produced the partial jaw of a very young *Homo erectus* individual.

- The Garba IVE jaw is now one of two earliest *H. erectus* individuals known anywhere, in a virtual tie with the DNH 134 cranial vault from Drimolen, South Africa.

Margherita Musi, et al., 2023

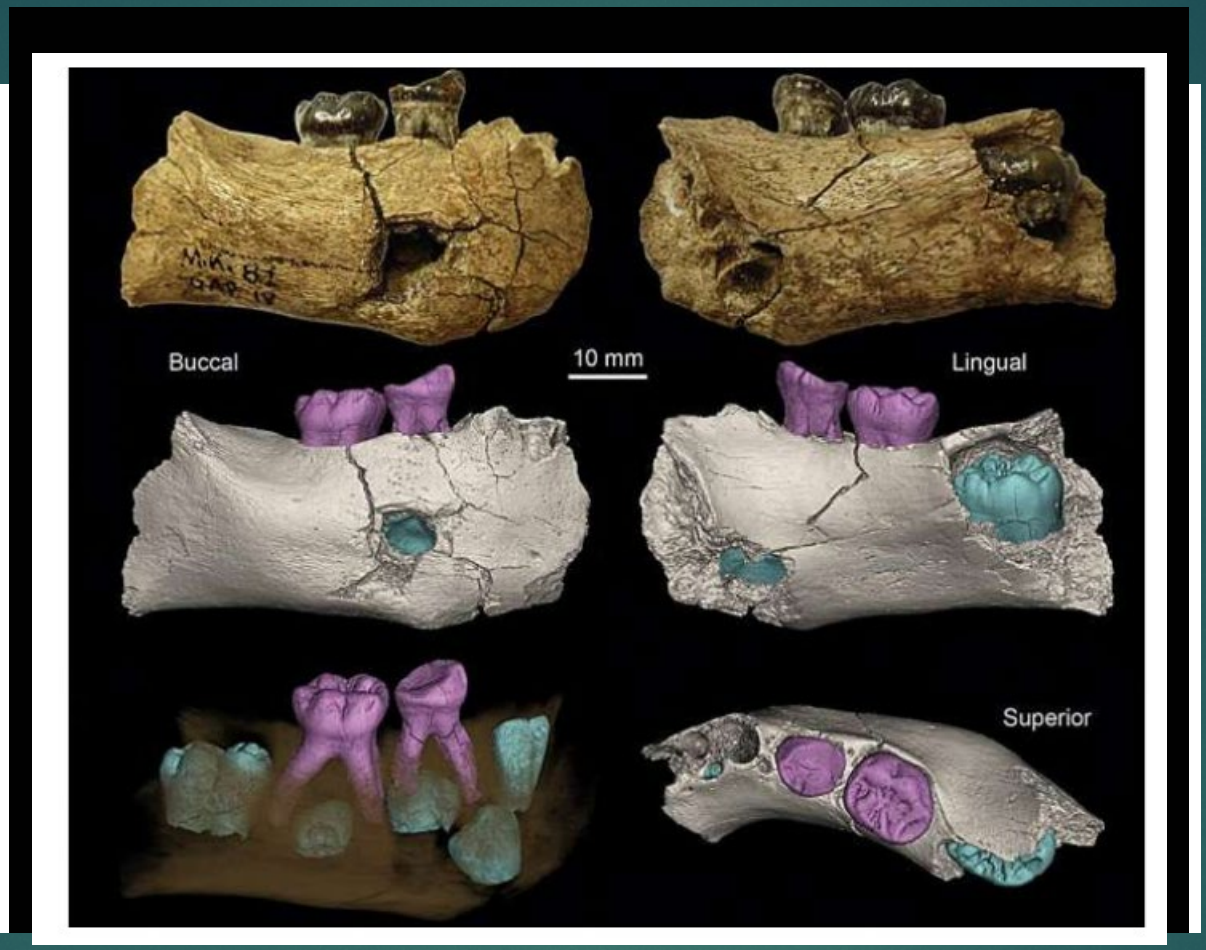
Oldest H. erectus and Acheulean tools

- The infant mandible discovered in level E at Garba IV (Melka Kunture) on the highlands of Ethiopia: direct association with an Oldowan lithic industry.

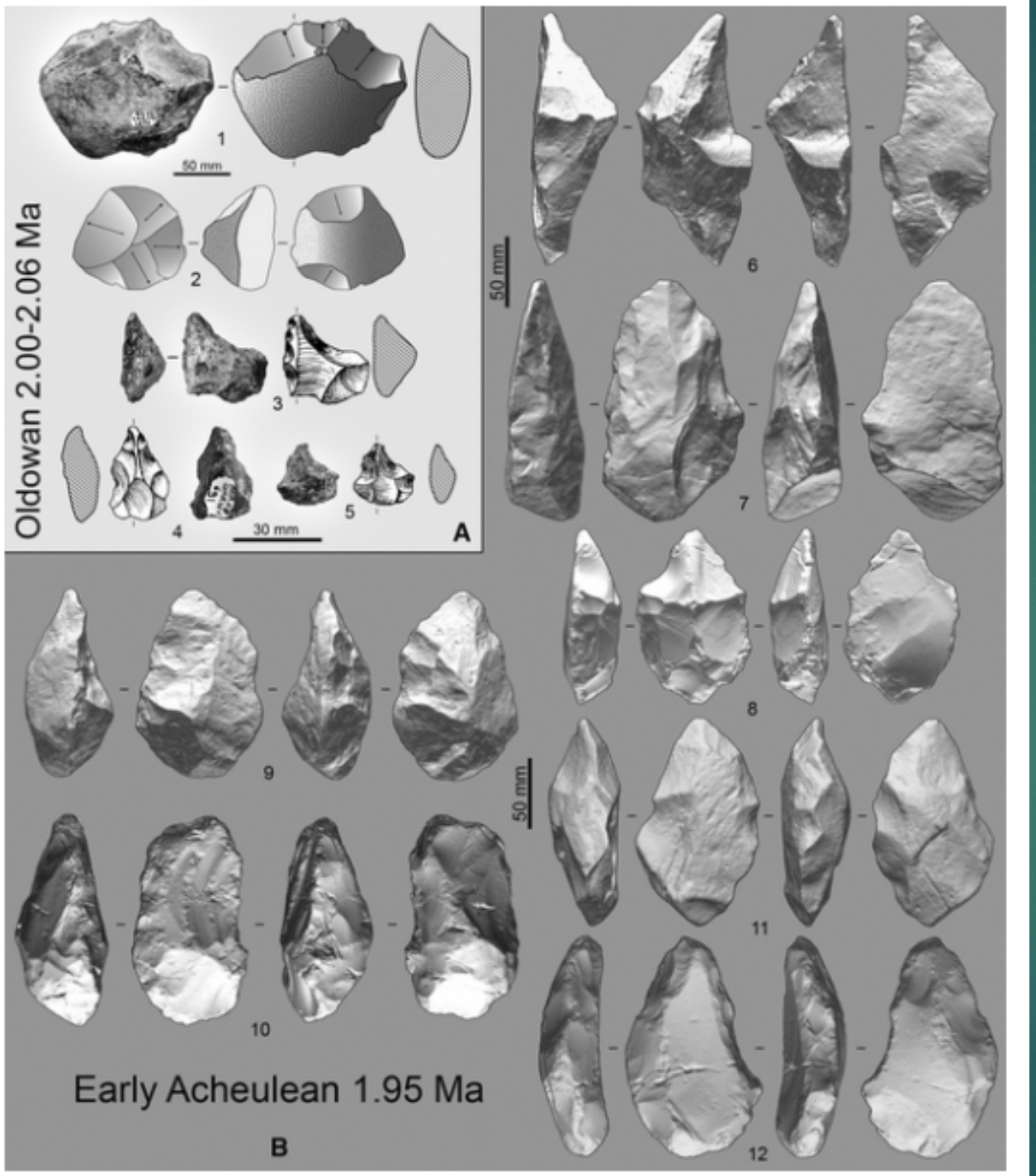
- Use synchrotron imaging to confirm its identification as *Homo erectus*.

- Additionally, we utilize new palaeomagnetic ages to show that
  - (i) the mandible in level E is ca. 2 million-years-old, and represents one of the earliest *Homo erectus* fossils, and
  - (ii) that overlying level D, ca. 1.95 million-years-old, contains the earliest known Acheulean assemblages

Two views of the Garba IV-E mandible



The Garba IVE jaw is not a new discovery: it was unearthed during excavations in 1982. From that time onward it was attributed to H. erectus and compared with other subadult mandibles from the Turkana basin such as KNM-ER 820 and KNM-ER 1477.



The features of the assemblage, including the production of large flakes and LCTs, identify it as Early Acheulean.

Thus, Garba IV documents a rapid change between Oldowan and Acheulean lithic production over a period of 50,000-100,000 years in this unique high-altitude paleoenvironment.

Conclusions

- At ca. 2 Ma, the GAR IVE mandible is one of the earliest *H. erectus* fossils so far discovered, and the only specimen whose taxonomic identification is based on teeth, which are known to have a strong taxonomic signal.
- Furthermore, it is the first to be directly associated in a sealed deposit with Oldowan stone tools in Africa. The same industry is also found in underlying level Garba IV F, pointing to a fully-ingrained behavior that we attribute to *H. erectus* activity.
- The many small, pointed tools and the systematic use of obsidian make it conspicuously different from the 2.4-1.6 Ma Oldowan found elsewhere, and notably at sites where remains of *Homo habilis* were also discovered
- Based on the current study, however, only *H. erectus* is known to have inhabited the Ethiopian highland, at or above 2000 m above sea level

Conclusions

- Around 2 Ma, there is evidence at Garba IV of *H. erectus* retaining behavioral characteristics close to those of *H. habilis*.

- It was still producing core and flake assemblages but with different features than typical Oldowan technocomplexes. Then around 1.95 Ma, the Early Acheulean emerged with archetypal bifacial tools.

- Between 2 and 1.9 Ma, the Melka Kunture site provides the earliest evidence of *H. erectus*, who quickly adjusted to a high-altitude environment first producing Oldowan technology and then developing Acheulean technology.

Everything is older than we currently assume

- On the one hand, those hominins left Africa but not 1.8 Ma ago (Dmanisi) but rather they had left much earlier, reaching China at least 2.1 Ma ago, as attested by the lithic remains in different sites (i.e. , Shangchen 2.1 Ma; Yuanmou et al., 1.7 Ma).

- We have also just discovered the surprising age of 2.9 Ma for the first Oldowan tools, with 330 artifacts in Nyayanga, next to Lake Victoria (Kenya).

- Raises questions: whose jaw was from Ledi-Geraru (2.8 Ma, Ethiopia) or who were the authors of the Lomekwi tools (3.3 Ma, Kenya). In fact, the beginnings of "the human" may still have to be sought up to a million years before Melka Kunture's erectus child.

Pierolapithecus cranium reconstruction; 12 Ma

From left, the Pierolapithecus cranium shortly after discovery, after initial preparation, and after virtual reconstruction. Credit: David Alba (left), Salvador Moyà-Solà

Pierolapithecus, ~12 Ma, European ape

- They found that Pierolapithecus shares similarities in overall face shape and size with both fossilized and living great apes, but it also has distinct facial features not found in other Middle Miocene apes.

- The results are consistent with the idea that this species represents one of the earliest members of the great apes and human family.

First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals

- We report new evidence of hunting lesions on the 48,000 old cave lion skeleton found at Siegsdorf (Germany) that attest to the earliest direct instance of a large predator kill in human history.
- A comparative analysis of a partial puncture to a rib suggests that the fatal stab was delivered with a wooden thrusting spear.
- We also present the discovery of distal lion phalanges at least 190,000 old from Einhornhöhle (Germany), representing the earliest example of the use of cave lion skin by Neanderthals in Central Europe.

Gabriele Russo, et al., 2023

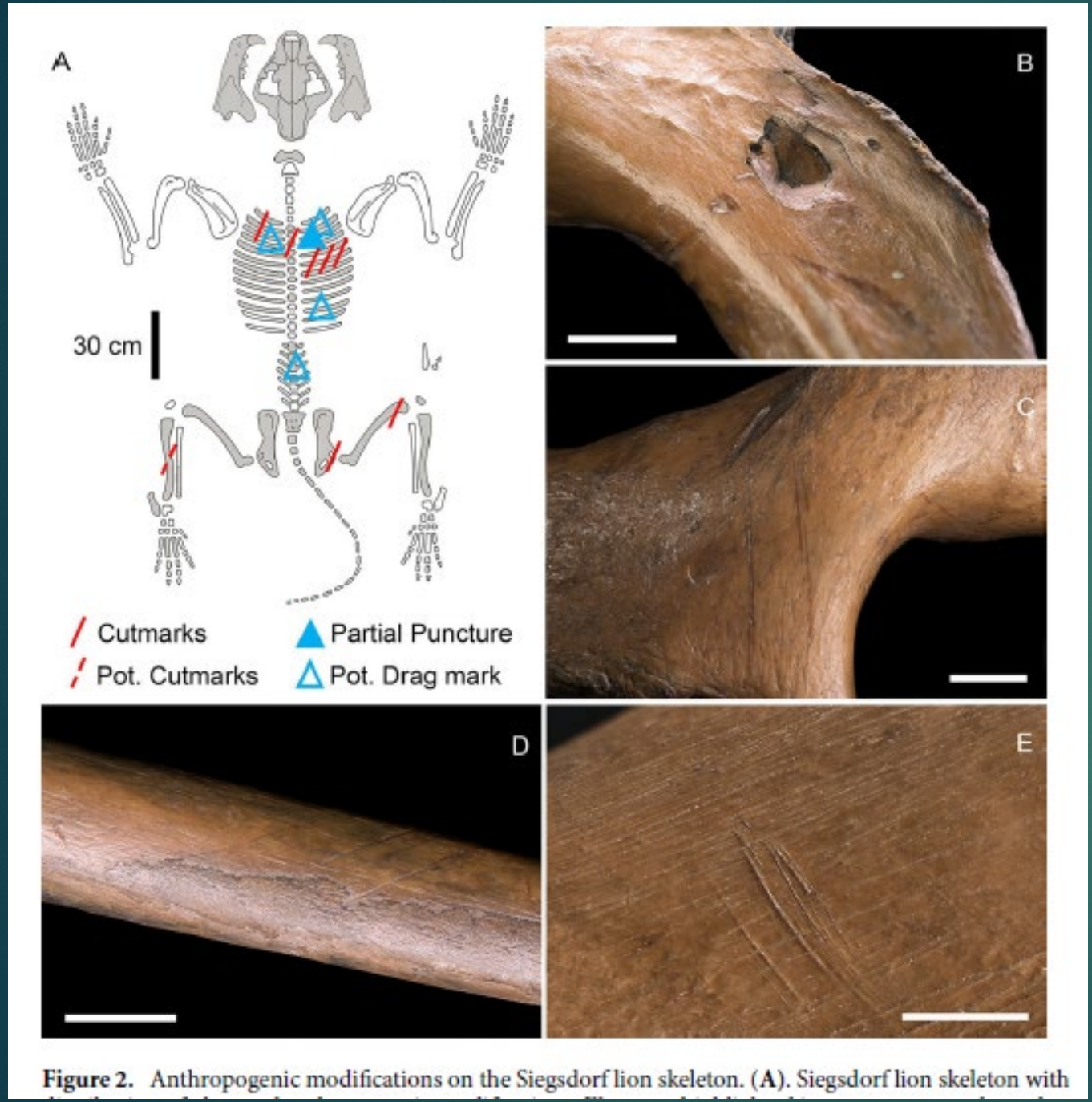


Figure 2. Anthropogenic modifications on the Siegsdorf lion skeleton. (**A**). Siegsdorf lion skeleton with

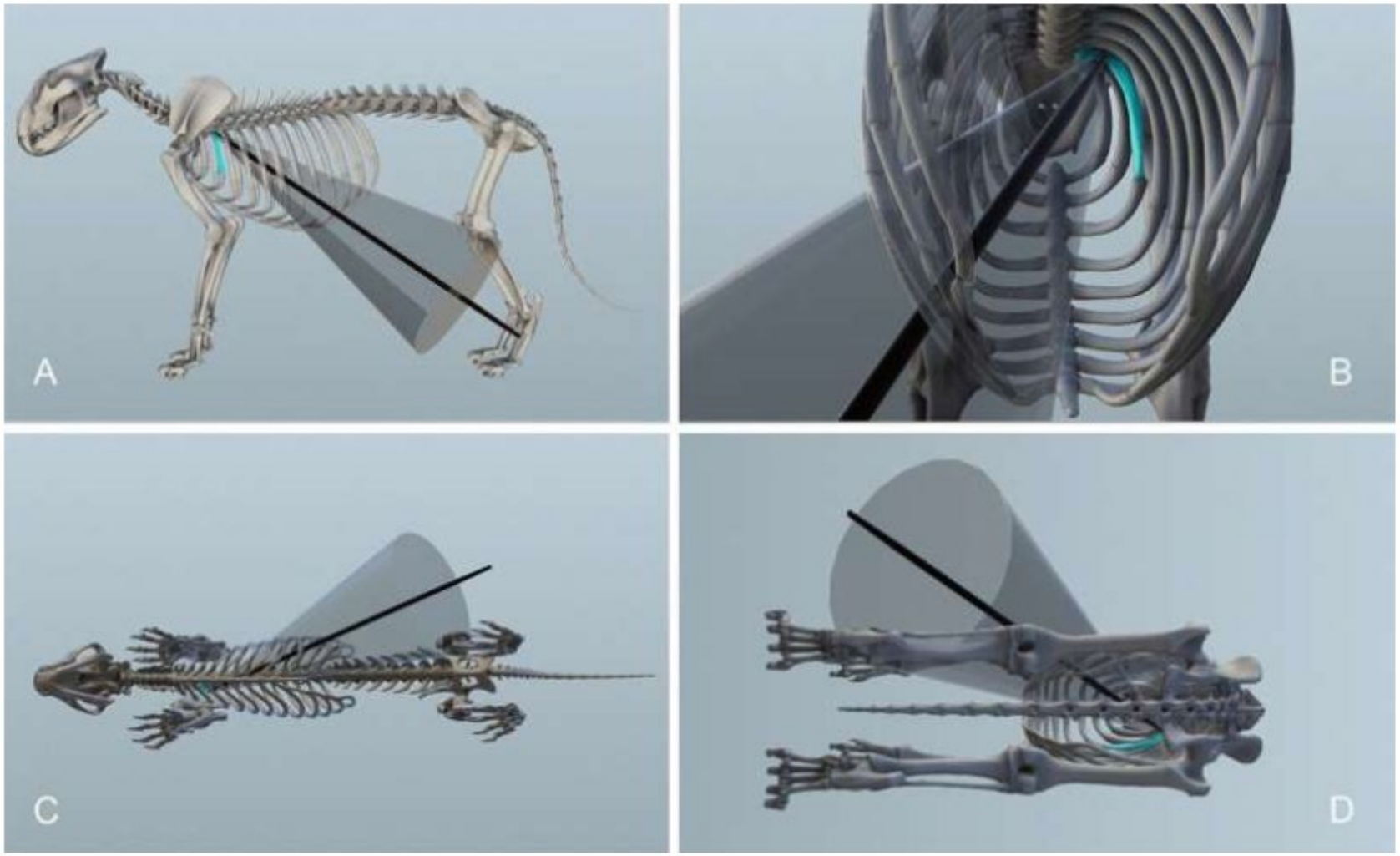
Anthropogenic modifications on the Siegsdorf lion skeleton. (**A**). Siegsdorf lion skeleton with distribution of observed anthropogenic modifications

First direct evidence of lion hunting and the early use of a lion pelt by Neanderthals

- Neanderthals hunted cave lions and used the skin of this dangerous carnivore
- Excavations at Einhornhöhle (Unicorn Cave) in the Harz Mountains (Lower Saxony, Germany) in 2019 uncovered abundant Ice Age animals, among which were a few bones of the extinct cave lion. The bones were discovered in a cave gallery approximately 30 meters from the now-collapsed entrance in a layer that dates to more than 200,000 years ago.
- Detected a toe bone with a cut mark among the remains of the cave lion. This led to the team determining that Neanderthals removed the lion's pelt with the claws attached, indicating that they used the skin for their own purposes.
- The 50,000-year-old skeleton has helped researchers to show for the first time that Neanderthals hunted cave lions. The cut marks also show that not only did they kill this apex predator, they also consumed its meat.

Gabriele Russo, et al., 2023

How to spear a cave lion

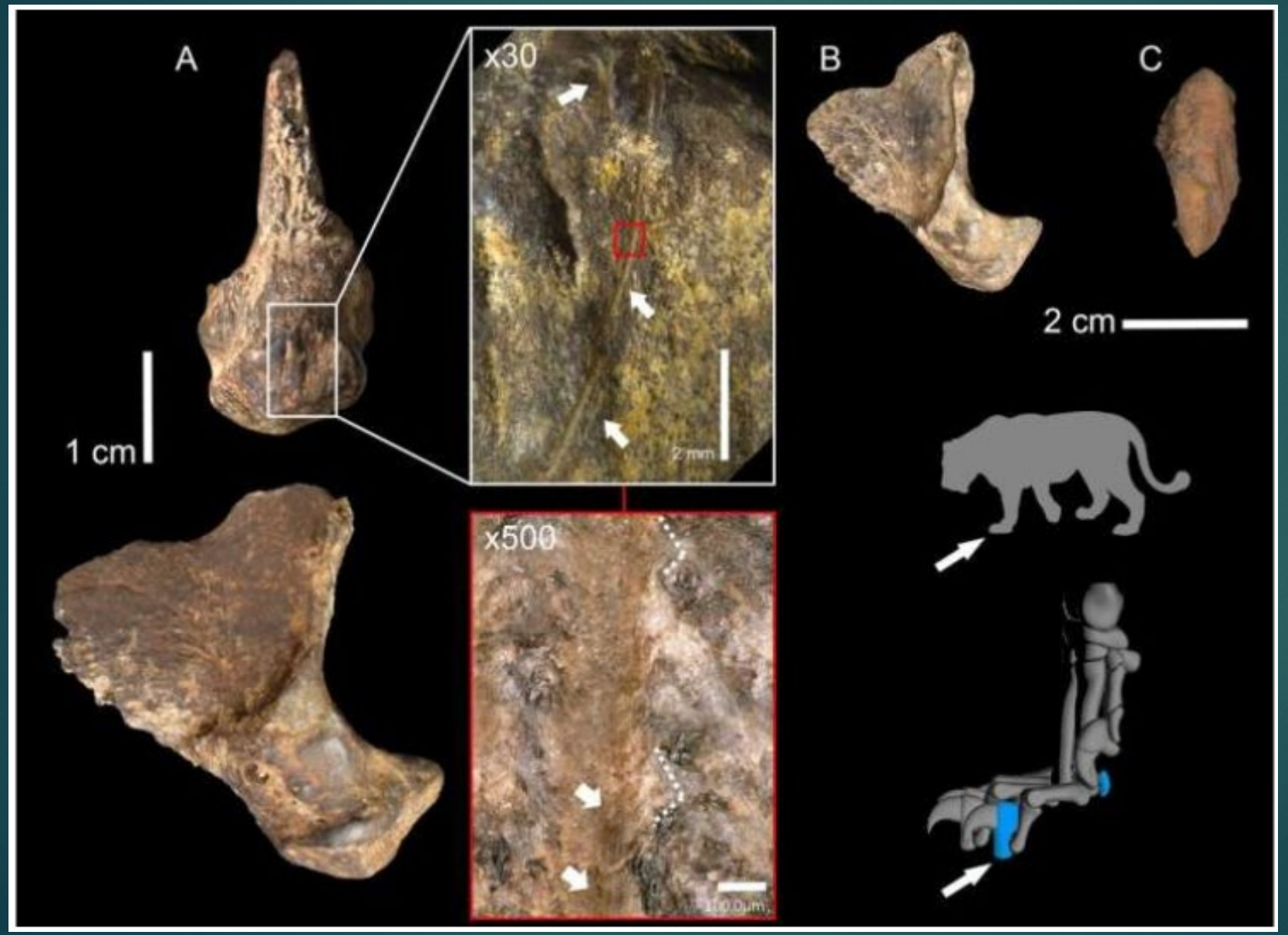


Digital ballistic reconstruction of the Siegsdorf lion spear thrust. (A). standing, l…

Approaching the animal more safely from behind and stabbing it in the lower abdomen while it was lying on its right side.

Earliest evidence of Ns using wooden spears

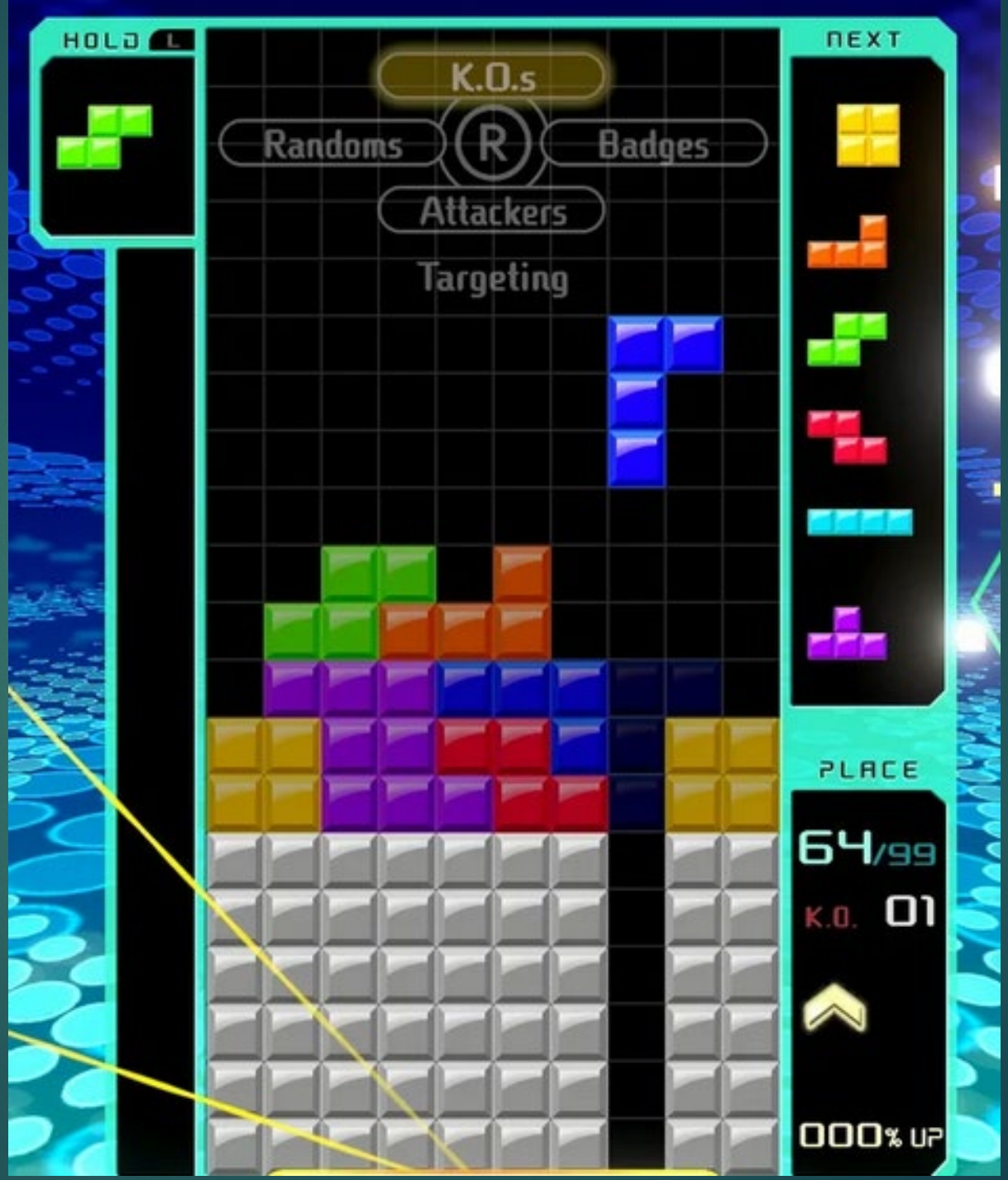
Neanderthals hunted dangerous cave lions



Cutmarks on paw of cave lion from Einhornhöhle Area 1.

For about 200,000 years the cave lion was the most dangerous animal in Eurasia, until it went extinct at the end of the Ice Age.

Tetris and PTSD



Importance of playing Tetris for reducing PTSD

- Use of the computer game Tetris on a computer or Nintendo has been shown to disrupt the visual flashbacks resulting from multiple traumatic events (childbirth, car crashes, rape, physical assault).

- Usage immediately after trauma has been shown to significantly reduce the involuntary intrusive visual flashbacks post trauma and their consequential mood alteration.

- Playing Tetris reduces the formation of visual traumatic memories in the hippocampus, which are fundamental to producing PTSD.

- Each time we recollect anything there is potential for altering that memory

Close encounters vs. missed connections? A critical review of the evidence for Late Pleistocene hominin interactions in western Eurasia

- In a new paper, Clive Finlayson and seven coauthors look critically at what we know about the connections between Late Pleistocene populations in western Eurasia.
- It is still a challenge to learn from a tooth or fragment of skull what the ancestry of an ancient individual may have been. True, there have been a handful of successes from the period of contact between Neandertal and modern populations = possibility of mixture as an explanation for a fossil's morphology, and geneticists later confirmed evidence of mixture from DNA.
- Finlayson and coworkers mention the Oase 1 mandible; J. Hawks adds the Zlatý kůň skeleton as a complementary case. Such cases may seem to increase our confidence that morphology can identify fossils accurately. But they challenge the notion that ancestors were separated as strongly as many archaeologists have assumed.

Clive Finlayson et al., 2023

Critique of prior research

- The idea of a “Neandertal trait”, or the confidence in identifying a single tooth as a Neandertal from its morphology, might be meaningful within a world where contacts between Neandertal and other populations are few and restricted in time and space.

- But those assumptions do not hold within the period from 50,000 to 35,000 years ago when populations with varied ancestry recurrently met. Mapping the eddies and currents of migration and mixture during this long period is beyond the resolution of the evidence.

Are associations of artifacts & hominins real?

- The populations of that transitional time were like today's people: Their genes came from several ancestral populations and their morphology reflects the particular combination of genes and environment. As Finlayson and coworkers end their essay: We must now not only accept the reality of the "Neanderthal inside us", but also that of "us inside the Neanderthals."

- Even today, it is common to suppose that any "advanced" elements in artifact assemblages must imply a presence of modern people. But is that true?

- Finlayson and coworkers discuss the weakness of associations of technological patterns and genetic patterns.

Even burials are potentially contaminated

- Even burials, which some archaeologists see as a “gold standard” of associating skeletal remains with artifacts, are actually poor evidence. Burials from the last Neandertals and earliest modern humans in Eurasia are extremely rare to begin with—only a handful are known.

- Finlayson and colleagues correctly emphasize that a burial is by definition intrusive into layers of sediment. In a burial, the body is covered with fill that may have been sourced from inside the hole itself. That is to say, a grave digger may have scooped dirt and old stones out of a hole, put a body into it, and then covered the body with the same dirt and old stones. Thus the potential is high that buried remains may be commingled with artifacts from a different time entirely.

Particular human taxa & particular technologies

- What this leaves is a scattered sample of rock shelters and cave sites where well-stratified layers contain a tooth or bone fragment from an ancient individual.

- In these cases, the problem of identifying mixed genetic ancestry of the individual comes to the fore.

- “In many cases, the evidence linking a human taxon with technology is supported by a small number of sites where human remains attributed to either Neanderthals or Modern Humans have been associated with a particular stone tool technology.

- This is a dangerous practice which is flawed as it assumes that particular human taxa are exclusively linked to particular technologies, which they are not

Who made what?

- We don't really know which populations made which artifacts.
- Worse, we don't really know which populations there *were*.
- Without this kind of evidence, we are only starting to understand the technical flexibility of these populations and cultural interchange between them

Close encounters vs. missed connections? A critical review of the evidence for Late Pleistocene hominin interactions in western Eurasia – C. Finlayson, et al., 2023

- Recent advances in the study of ancient DNA recovered from fossils and cave sediments have profoundly changed our views on the biological and cultural interactions between populations and lineages of fossil *Homo* in the Later Pleistocene of Eurasia.

- A complex picture emerges, with multiple population admixture and replacement events.

- Traditional narratives about human migrations and the biological and/or cultural advantages of our own species over the Neanderthals are now giving way to the study of the biological and cultural dynamics of past human populations and the nature of their interactions in time and space.

MH-N contact

- Review current evidence regarding the interactions that appear to have taken place between hominins derived from different lineages (typically ascribed to Ns & MHs), esp in western Eurasia

- The prevalent view holds that Modern Human-Neanderthal contact resulted in complete population replacement. Specifically, in Europe – the best-documented region, the extinction of Neanderthals and the successful colonization of the continent by Modern Humans is thought to be due to biological or ecological advantages of our own lineage

- Such advantages were frequently attributed with differences in cognitive capacities

Range expansions

- We likely have underestimated the spatiotemporal complexities of human range expansions and contractions, with local and regional extinctions, subsequent range expansions and even back into areas settled in previous expansions and also back into source areas.
- In areas of contact between expanding and established populations, the outcome would have been determined by: time previously isolated, and hence the degree of genetic, phenetic and behavioral isolation, the densities of the two populations relative to environmental carrying capacity and the degree of ecological isolation

Site occupation and reoccupation

- It is now clear that, within the same site, different populations representing different lineages of hominins occupied and re-occupied and alternated with each other.
- In the case of Mandrin Cave in the Rhone Valley, France, Neanderthals and Modern Humans even alternated occupation and Neanderthals were in the cave before and after Modern Humans (Slimak et al., 2022): conclusions were derived largely from lithic evidence.
- At Denisova Cave in the Altai Mountains, Neanderthal-Denisovan population turnover was inferred from analysis of ancient DNA (aDNA) in sediment, with a final layer of Modern Human occupation.
- At Galeria de las Estatuas in Atapuerca, Spain, sediment aDNA indicated a major Neanderthal population replacement event at ~ 120 ka.

Causation of N demise

- In spite of the large number of publications on the subject of the outcome of Neanderthal-Modern Human contact, we are nowhere nearer to having a clear picture of the causes of the presumed disappearance of the Neanderthals.
- Models provide a range of possible scenarios. Scenarios range from a direct Modern Human intervention to climatic and random factors, or a mix of these.
- The only conclusion that we can draw from this motley group of disparate schemes is that it is possible to explain the disappearance of the Neanderthals – with a multitude of factors and processes, both with and without the need of Modern Human interaction.

Species concept vs lineages

- The use of species concepts in paleoanthropology is notoriously difficult. and has plagued the Neanderthal-human debate since its beginnings .
- Recommend replacing the notion of species by that of lineage.
- Since the advent of paleogenomics, the focus of N-MH discussions has shifted from species competition to lineage histories and population dynamics.
- Ancient DNA (aDNA) extraction and analysis reveal an intricate pattern of admixture events between human and Neanderthal lineages, and more generally with lineages of archaic Homo such as the “Denisovans” and hypothetical “ghost species”
- aDNA evidence: admixture events have been frequent among human populations in the Pleistocene,

Lineages and hybrids in the fossil and archaeological records

- Next problem – how do we detect hybrids in the palaeontological and archaeological records?

- While the population-level outcomes of individual encounters between groups belonging to different *Homo* lineages remain unknown, the existence of first-generation hybrids within the genus *Homo* is now indisputable (Slon et al., 2018).

- Identifying hybrids on morphological grounds from human remains from Pleistocene sites is a different matter altogether

Hybrids: difficult to ID

- While Paleogenetics can study thousands of independent discrete traits (such as SNPs) with ancestor-descendant polarity, Paleo-phylogeny (similarity of morphological trait indicates relatedness) has to content itself with comparatively few preserved skeletal traits.

- Moreover, most of these traits are continuous rather than discrete, they vary within paleopopulations, and do not exhibit clear morphological distinctiveness (phyletic polarity).

- Many hybrids are thus likely to remain undetected on morphological grounds. What may be potentially detectable are cases where phenotypic differences between the parent lineages are clearly visible (e.g. as between Neanderthals and Modern Humans), and the hybridization event is only few generations back in time, thus preserving a sufficiently strong phenotypic signal

Hybrids

- The mandible from Peștera cu Oase is a good example of postulated admixture based on morphology (Trinkaus et al., 2003) subsequently supported by genomic data.

- Some of these cases have been disputed, in itself a reflection of our ignorance of what a hybrid in the genus Homo should or could have looked like.

- Our inability to clearly define Pleistocene Modern Human fossils on the basis of morphology, or to agree on what hybrids might look like when found = problem when it comes to attempting to interpret the palaeontological data.

Misidentifications

- Are taxonomic attributions of specimens, based on small (often single) samples which give us practically no information of population variation robust enough to enable us to map, for example, a picture of the spread of Modern Humans and the range contraction of Neanderthals? Clearly, they are not.

- How certain can we be that some or all of these taxonomic allocations, currently done on the premise that they must be either Neanderthal or Modern Human, might not be mistaken and that individuals that are hybrids are being overlooked?

- In some cases, the specimens are classified even though they may show mixed and conflicting evidence, as in the case of the Kent's Cavern maxilla which was claimed to have Modern Human and Neanderthal traits and other traits which were ambiguous, but was nevertheless reported as the earliest evidence of anatomically Modern Humans in northwestern Europe (Higham et al., 2011).

Be wary of taxonomic attributions

- We should be particularly wary of taxonomic attributions based on continuous (metrical) rather than discrete traits. For example, teeth are often characterized by morphometric traits, which reveal statistically significant differences between taxon-specific mean values but overlap between taxon-specific distributions, such that single fossil specimens cannot be assigned with any certainty to one or the other taxon.

- Until such time as we are able to allocate specimens with certainty, and we clearly cannot do so today (although we may even be able to do so in isolated cases using evidence additional to morphology such as aDNA and palaeoproteomics) we should not use them to map past human distribution patterns and dispersals.

Lithics, culture and hominin lineage attribution

- When archaeologists attempt to map human distribution in the Palaeolithic, they organize their observations about the lithic evidence in terms of stone tool industries (Shea and Bar-Yosef, 2005).

- This is largely because of the paucity of fossil material available compared to the much richer lithic record.

- Lithics are used as proxies for hominin taxa. The most commonly-cited stone tool industries group together stone (and sometimes bone) artefacts excavated assemblages from multiple sites.

- In practice, a newly-identified industry's recognition, acceptance, and use depends on appeals to authority and various national research traditions

Stone tool industries

- Named stone tool industries first appear in 19th century archaeological writing as universal stages of human cultural evolution, but their number increased dramatically as 20th century archaeologists increasingly sought entities with which to describe histories of prehistoric culture change, or "prehistory" (Shea and Bar-Yosef, 2005).

- When industries appear in prehistory, they do so as proxies, or "stand ins" for groups of people, the functional equivalent of ethnographic cultures.

- This is how students use industries in current debates about replacement versus continuity among Late Pleistocene hominins.

Stone technologies

- Archaeologists customarily identify Late Pleistocene industries from Europe, western Asia and North Africa as either Upper Palaeolithic (UP), Middle Palaeolithic (MP) or MP/UP Transitional age-stages.

- Most of the differences between MP, UP, and MP/UP industries reflect greater or lesser proportions of fracture products detached from “Levallois” cores (bifacial hierarchical cores) or from “prismatic blade cores” (elongated unifacial hierarchical cores).
  - Levallois products are more common in MP assemblages,
  - prismatic blades more common in UP assemblages.
  - MP/UP Transitional industries vary widely in this respect.
  - Archaeologists consider retouched artefacts more culturally diagnostic than unretouched ones.

Tools by LP, MP, UP assignment

- Carved bone, antler, and ivory artefacts including perforated beads occur in many UP assemblages, but such artefacts rarely appear in MP ones.

- Whereas archaeologists often assign assemblages from vast areas to either MP or UP industries, those they assign to MP/UP Transitional assemblages have more restricted regional distributions.

- In spite of these major problems of taxonomic attribution, the reality is that the presumed pattern of replacement of Neanderthals by Modern Humans in Europe, in the absence of sites with human remains, has been largely inferred from archaeological sites

Stone Tech not necessarily associated with particular hominin

- In many cases, the evidence linking human taxon with technology is supported by a small number of sites where human remains attributed to either Neanderthals or Modern Humans have been associated with a particular stone tool technology.
- This is a dangerous practice which is flawed as it assumes that particular human taxa are exclusively linked to particular technologies, which they are not (Shea, 2016).
- There is no de facto reason why different human taxa should not be able to produce the same technology, especially if cultural exchanges occurred at times of genetic exchange and technologies were the product of ecological circumstances. The problem is compounded by our absence of knowledge of which technologies were associated with hybrids

Replacement theory

- Middle to Upper Palaeolithic transition in Europe and the Middle East, which is generally equated to the replacement of Neanderthals (associated with MP industries) by Modern Humans (associated with UP industries).

- The narrative: maps, based on stone tool industries as proxies for human taxa, are generally inaccurate as they assume that each industry equates to a specific sort of hominin.

- The degree of certainty of attribution is, at best, based on few sites in which the hominin-industry link has been established or is claimed to have been established

Wrong assumptions?

- How do these industries help us understand Neanderthal and Modern Human interactions? Not very well.
- No prior theory suggests that they correspond to self-conscious social groups such as ethnographic “cultures.”
- That some of them persist, minimally variable for thousands of years and across thousands of kilometers suggests named stone tool industries are virtually the opposite of actual ethnographic cultures.
- Actual cultures change rapidly and vary widely over time and space. Dividing hominins into conjectural social groups based on their lithic litter makes no more sense than dividing and grouping living humans based on the kinds of pens and pencils that appear in their trash cans.

Archeological sites and conclusions made

- Archaeologists refer industries to one or another hominin based on fossils found in the same sediments with the stone artefacts assigned to them.

- Some of these fossils appear to be deliberate burials, but many more are isolated teeth, maxillary and mandibular fragments, and finger or toe bones.

- Whether or not one can credibly assign such isolated fragments to one hominin or another depends on the bone in question and the criteria used.

Don’t assume fossils have not moved

- However, even if one can make such identifications, one cannot necessarily take the stratigraphic associations between these fossils and stone tools at face value.

- Teeth, mandibles, and phalanges are among the densest bones in the human body. Stone tools are nearly indestructible. All of these things can and do move around in sedimentary deposits, such as the surfaces of caves. Excavating consolidated cave sediments can create the illusion that, once deposited, fossils and stone tools remain in place.

- Sinking up to one’s ankles in the unconsolidated surface sediments of a modern-day cave offers a valuable corrective to this assumption.

Distribution of stone tool industries, their association with hominin taxa, chronology and geographic distribution for Europe and the Middle East in the period 50–30 ka. Stone Tool Industry and Age-stage follow Shea (2016).

Stone Tool Industry	Age-stage	Hominin	Date (ka)	Geography	Remarks
Neronian	IUPal	Modern	52–57	France (Mandrin Cave).	Slimak, et al. (2022) Neronian layers between otherwise Mousterian ones.
Late Levantine Mousterian	MPal	Uncertain. Assumed Neanderthal	43–42	Levant (Ksar Akil)	Dates have been presented at one standard error (Douka et al., 2013).
Late European Mousterian	MPal	Probably Certain. Assumed all Neanderthal	41-39 (37)	Western Europe	Higham et al. (2014). Extended to 37 ka for Iberia (Zilhao et al., 2017). Late dates of 32 ka at Gibraltar (Finlayson et al., 2006) are currently under re-examination.
Bohuncian	IUPal	Uncertain. Assumed "Modern"	50–46	Czech Republic	Retains MPal features but not considered transitional (Kuhn, 2003). (Richter et al., 2009).
Bachokiran	IUPal	Modern	47–44	Bulgaria	Fewlass et al. (2020); Hublin et al., 2017
Initial Upper Palaeolithic, Turkey	IUPal	Uncertain. Assumed "Modern"	45–39	Turkey	Hominin attributions few and unclear (Ewing, 1963; Gleń and Kaczanowski, 1982; Metni, 1999; Yazbeck, 2004; Kuhn et al., 2009). Dates have stratigraphic issues (Kuhn et al., 2009) or have been presented at one standard error (Douka et al., 2013). 50 k estimate, from TL dates of 48.2 ± 1.9 ka for Bohunice (Richter et al., 2009).
Emiran	IUPal	Uncertain. Assumed "Modern"	(50)45-36	Levant	Dates (Marks, 1983) require revision (Hublin, 2015). Dates 45–36 ka from Stutz et al. (2015).
Szeletian	"Transitional" MPal/UPal	Uncertain.	48–44	Czech Republic, Hungary	Gábori-Csánk (1983); Kaminská et al. (2004). Nigst (2012).
Uluzzian	"Transitional" MPal/UPal	Uncertain. Now Assumed "Modern"	45–40	Italy, Greece	Palma di Cesnola and Messeri (1967); Churchill and Smith (2000); Benazzi et al. (2011), 2014; Banks et al. (2013); Ronchitelli et al., 2014 Douka et al. (2014)

Châtelperronian	"Transitional" MPal/UPal	Uncertain. Assumed Neanderthal	44–40	Spanish Basque Pyrenees, southwest and central France	Leroi-Gourhan (1958); Hublin et al. (1996), 2006; Bailey and Hublin, 2006 a & b; Bailey et al. (2009); Bar-Yosef and Bordes (2010). Higham et al. (2010); Hublin et al. (2012).
Lincombian-Ranisian-Jerzmanowician (LRJ)	"Transitional" MPal/UPal	Uncertain	43–40	Southern United Kingdom, Belgium, Germany, Poland	Hublin (2015). Kozlowski (2002); Cooper et al. (2012); Flas (2011)
Ahmarian	UPal	Uncertain. Assumed "Modern"	48–40	Levant, Turkey	Juvenile ("Egbert") lost but claimed to be "Modern" (Bergman and Stringer, 1989). Rebollo et al. (2011); Douka et al. (2013) (dates have been presented at one standard error)
Kozarnikian	UPal	Uncertain	43–41	Bulgaria	Guadelli et al. (2005).
ProtoAurignacian	UPal	Possibly Certain. Assumed all "Modern"	42–38	N. Italy, S. France, N. Spain	Benazzi et al. (2015). Szmidt et al. (2010); Douka et al. (2012).
Early Aurignacian	UPal	"Modern" and Uncertain	44–35	Austria, Germany, Italy, France, Slovakia, Russia, Portugal	Hublin (2015). Haesaerts et al. (1996); Higham et al. (2012) (dates have been presented at one standard error); Nigst and Haesaerts (2012); Nigst et al. (2014).
Levantine Aurignacian	UPal	Uncertain	38–34	Middle East	Alex et al. (2017)
Later Aurignacian	UPal	"Modern" and Uncertain[21]	35–31	Czech Republic, Germany, Romania, Poland, Hungary, France, Spain	Hublin (2015).

Burials?

- Industry-hominin attributions based on burials seem unassailable, but they are actually quite the opposite. Burials are intrusive features. The only thing one can say about them with confidence is that the buried individuals are younger than the sediments surrounding them.

- Even if one can tell how much younger, no consensus exists among archaeologists about how much of a temporal offset is sufficient to sever the hypothetical link between the fossils and the stone tools.

- Much can change in a century or two. In evaluating burial-based attributions, one also has to guard against prematurely rejecting alternative explanations for them. Some may be burials like those recent humans create in funeral rituals. Some may be natural deaths rapidly buried, or burials for hygienic reasons. Some might even be concealed homicides.

MP/Mousterian = N? Not in N Africa = MH

- The assumption that “Middle Palaeolithic/Mousterian equals Neanderthals” is so well-entrenched in European prehistory that one can easily forget that this hypothesis is demonstrably false in North Africa and the East Mediterranean Levant, the two regions most often proposed as sources for Europe’s Modern Human populations.
- Middle Palaeolithic “Mousterian” tools appear in North African sites dating between 45 and 300 Ka and together with Modern Human fossils only.
- Neanderthal remains appear at a handful of sites in the Levant together with Mousterian artefacts, but so, too, do Modern Human fossils.
- Most Levantine MP, MP/UP, and UP sites lack any hominin fossil remains
- Who made them is anybody’s guess. This being the case, perhaps we ought to ask why we bother guessing?

Who vs How questions

- Archaeologists' answers to "who questions" about extinct hominins hinge on accepting arguments about stone tool "authorship." Proving these arguments right or wrong, would require one to observe extinct hominins.

- Without a time travel device, perhaps students of human evolution should set "who questions" aside and focus instead on answering "how questions," questions about prehistoric human activities

- Early Modern Humans, and at least some Neanderthals and Denisovans, became our ancestors by overcoming obstacles to their survival. Not because of who they were, but because of what they did.

Species-specific behaviors

- If researchers still want to continue to play "Pin the Tail on the Donkey" (match hominins to stone tool industries), then they should focus on identifying species-specific behaviors, chart those behaviors' distributions in time and space, and then propose hypotheses about how different kinds of interactions among various hominins ought to affect change and variability in those behaviors.

- It is very likely that Europe and the Middle East were occupied by populations of hominins which were, in all probability, hybrids. We have virtually no knowledge of the phenotypes of these hybrids and even less their extended phenotypes. It is clear that uncertainty in the attribution of stone tool industries to hominin taxa is pervasive.
- We cannot, therefore, place any credence on maps and narratives of the spread of Modern Humans across Europe (or indeed anywhere else) in the critical period between 50 and 30 thousand years ago (ka)

Chatelperronian

- In cases where Neanderthals have been linked to technologies akin to the Upper Palaeolithic of Modern Humans, e.g. the Châtelperronian at Grotte du Renne, Arcy-Sur-Cure, France, supporters of Modern Human cognitive superiority over Neanderthals, wrongly imputing unverifiable behavioral qualities of “primitiveness” or “modernity”, have been quick to interpret these as the product of the acculturation of Neanderthals by newly arrived Modern Humans.

- Others have argued for an independent origin of these stone tool industries (d’Errico et al., 1998), giving the Neanderthals comparable cognitive abilities to Modern Humans.

Grotte du Renne: Acculturation?

- The acculturation interpretation has two major problems. On the one hand the archaeology is unable to demonstrate who acculturated whom but, more importantly, the acceptance of such acculturation in interstratified archaeological levels implies a long period of coexistence and therefore runs contrary to population replacement by competitive exclusion or the notion of Modern Human advantages, other than originality of thought.

- It is also relevant that, although the stratigraphic position of the Neanderthal remains at the Grotte du Renne have been questioned statistically validated evidence for Modern Human remains from this site is still weak, given the probabilistic nature of metric traits mentioned above.

Just working hypotheses

- The entire acculturation discussion has been based on Neanderthal remains, whose stratigraphy is questioned, versus Aurignacian stone tools and related artefacts which are attributed to Modern Humans. Given our comments above on the dangers of attributing stone tool industries to hominin taxa, the entire acculturation question must be viewed with skepticism

- Archaeologists' efforts to develop and test hypotheses about Late Pleistocene "cultural geography" in the northern and eastern Mediterranean Basin rely on a complex patchwork of equations between specific stone tool industries and specific hominins…

- In the meantime, we must retain multiple working hypotheses about any and all such equations' validity

Timing neanderthal disappearance and Modern Human arrival

- A very short period of interaction between Modern Humans and archaic humans (including the Neanderthals) when they met, the Modern Human advantage leading to a rapid replacement, is predicted by proponents of replacement.

- The argument for the involvement of Modern Humans in the Neanderthal extinction has been almost universal: "But it *is* evident that the days of the Neanderthal era in Europe were numbered when the Cro-Magnons first arrived" (Stringer and Gamble, 1993).

- The alternative, that the late entry of Modern Humans into Europe compared to other regions was due to the Neanderthal presence has received less attention.

- In actual fact, it is impossible to identify Modern Humans as the main cause of the Neanderthal extinction or Neanderthals as the main cause of the Modern Human delay, simply from an archaeological stratigraphy. From an archaeological perspective the two are indistinguishable.

MH-N overlap

- A range of scenarios have been discussed for the disappearance of the Neanderthals: from “Blitzkrieg” models, through stochastic processes, to competition.

- The case for competitive exclusion suffers fundamentally by its inability to demonstrate causality. The opposite, in fact, is what seems to have occurred: rather than a rapid replacement, Neanderthals and Modern Humans are thought to have overlapped for thousands of years.

- Based on radiocarbon data the duration of this overlap has been estimated to between 2600 and 5400 years (Higham et al., 2014), but combined paleogenetic and archaeological data suggests a more extended time period and the presence of Early Modern Humans north of the Alps 43,500 years ago has also been used to argue in favor of an extended period of contact in Europe.

Last recorded dates and overlap

- These claims must, nevertheless, be treated with caution as they rely to a large extent on stone tool industries as proxies for human taxa.
- Additionally, last recorded dates of human material at a site should not be taken to mean the last presence of that human taxon at the site but rather when the population was substantial to have been picked up in fossil material.
- Actual disappearance is expected to follow a protracted process after the last date of observation. Similarly, earliest dates at a site need not represent first arrival dates either.
- So, questions of temporal overlap need to be treated with great caution.
- The genetic evidence, on the other hand, confirms that there must have been significant, widespread and prolonged overlap.

Life in the fluctuating world of Europe and the Middle East between 50 and 30 ka

- The main conclusion that we derive from our analysis of presently available data is that there is a great deal of uncertainty regarding the patterns and processes of dispersion of populations of *Homo* in Europe and the Middle East during the long, twenty thousand-year, period between 50 and 30 ka.
- Did Modern Humans enter Europe some time between 45 and 40 ka? If we assume that Europe, prior to 50 ka, was occupied solely by Neanderthals, then it would be logical to accept that the later presence of other, non-Neanderthal, Homo populations must have come from outside.
- If so, the most parsimonious explanation would advocate a geographical expansion from the Middle East, either directly into Europe or circuitously via Central Asia.

Earlier MHs in Europe

- But could populations of Homo, attributed to Modern Humans, have been present in Europe earlier?

- The presence of populations with morphology claimed to be associated with Modern Humans in Jebel Irhoud, Morocco, at >300 ka (Hublin et al., 2017), in the Middle East at 194–177 ka (Hershkovitz et al., 2018) and in Greece at >210 ka (Harvati et al., 2019) suggests that this might well have been the case.

- The best evidence so far is of recent introgression of Modern Human Y chromosomes into Neanderthals at ~370–~100 ka (Petr et al., 2020) which indicates that contacts between these hominin taxa were taking place well before 50 ka. This makes it very likely that populations of Homo present in Europe prior to 50 ka were not exclusively Neanderthal and also included hybrids and, very probably, Modern Humans.

Interpretation of IUP

- Evidence of a ~45 ka entry of Modern Humans from the Middle East would then rest on a clear chronological demonstration of this dispersion spatially from east to west.

- The Initial Upper Palaeolithic Industries (IUP) are lumped together but there is no evidence, other than techno-typological similarities, suggesting that they were all made by the same hominin.

- In fact, a comparison of date ranges for the different IUP Industries could be equally interpreted to mean a dispersal from south-eastern Europe into the Middle East.

The IUP

- A further alternative could be that the IUP represents ways in which hominins were coping to changing environmentally-driven conditions in south-eastern Europe, Turkey and the Levant at 48–38 ka. It would be seen as a geographical alternative to similar responses at the same time across Europe (north-west Europe, East-Central Europe, Italy, the Balkans, south-west France and northern Spain) and represented by the transitional industries.
- The Protoaurignacian "family" of industries would represent alternative responses within the same time frame, but concentrated in the southern parts of the geographical area (Ahmarian in the Levant and Turkey; Kozarnikian following the Bachokiran in Bulgaria; and the Protoaurignacian in northern Italy, southern France and northern Spain).
- The Mousterian and Aurignacian would appear as partially, temporally and geographically, overlapping industries. This scenario cannot, by any stretch of the imagination, be seen as a clear signal of an east-west geographic Modern Human expansion at the expense of the Neanderthals.

Regional adaptations

- A regional adaptation by European and Middle Eastern hominins (Neanderthals, Modern Humans and hybrids) to changing environmental conditions, is a more parsimonious and biologically meaningful interpretation.
- Broadly, it would appear to correspond to an increase in the use of lightweight, long-distance, projectile technology as a response to the need to adapt to the exploitation of open tundra-steppe-desert habitats and habitat mosaics which were overrunning much of Europe and the Middle East during Marine Isotope Stage (MIS) 3.
- Rapidly and stochastically fluctuating environments would also be expected to facilitate coexistence and promote hybridization and hybrid zones with consequent adaptive advantages to colonizers of new environments or to those locally keeping up with rapid ecological change.
- It is therefore very probable that what we are observing in the tumultuously fluctuating conditions of Europe and the Middle East between 50 and 30 ka, is extensive biological and cultural interchange leading to experimentation.

Expansions & extinctions

- It would include successes (in the form of demographic and geographical expansion) and failures (demographic and geographical contraction and extinction).
- The apparent Neanderthal-Modern Human-Neanderthal turnover in Mandrin Cave, France (Slimak et al., 2023), as indeed the dynamics in the Middle East would seem to bear this out. In this scenario, hybridization and cultural exchanges can be seen as contributors to a common fitness currency, providing quick fixes as alternatives to the slower processes of natural selection of novel mutations or of independent invention.
- The flip side to the story is provided by the Iberian Peninsula. The absence of all IUP, transitional and Protoaurignacian family industries from the Iberian Peninsula), stands out in contrast to the rest of Europe and the Middle East. Here, coastal areas of the Mediterranean and Atlantic seaboards, least affected anywhere in Europe by the vicissitudes of the MIS 3 climate, were occupied by remaining makers of the Mousterian.

Late Ns in Spain?

- Current discussion on the late survival of Neanderthals in southern Iberia (Finlayson et al., 2006) remains an open question.

- The dating of late Neanderthals in southern Iberia by Higham et al. (2014) is limited to a single site in a mountainous area which was only occupied sporadically by Neanderthals, and therefore insufficient to have any level of certainty as to the wider regional picture.

- The presumed early presence of Aurignacian at another Iberian site, this time in the extreme south of the peninsula at Bajondillo, Malaga, has been taken as evidence of a correspondingly early Neanderthal extinction. This evidence has been discredited as a result of a mixed stratigraphy and non-diagnostic technology.

MH and N presences

- The additional error is in presuming that the presence of the Aurignacian (equated to Modern Humans) at one location must signify the disappearance of the Mousterian (equated to Neanderthals) over an entire region.

- There is enough evidence to show that this persistent angle of region-wide population replacement is untenable.

- Instead, the currently available evidence indicates that cultural, as well as genetic, contacts and exchanges between Middle Pleistocene Homo and Modern Humans (equated to H. sapiens) were already taking place in the Middle East as far back as 140,000–120,000 years ago.

Conclusions: Admixtures

- The two competing models of human origins, which dominated the literature for several decades, are now defunct.

- Advances in the methods for extracting and studying ancient DNA in fossils and cave sediment, especially in the last decade, have allowed us to scratch the surface of the complex relations between human (genus Homo) populations and lineages in the Late Pleistocene of western Eurasia and beyond.

- These pioneering studies are revealing the high degree and frequency of admixture that took place between different populations and lineages. The inescapable conclusion is the realization that human populations in the Late Pleistocene of Eurasia were highly admixed.

Paradigm shift in the study of human origins

- It follows that attempts to map out “human species” interactions based on a small number of fossils, fossil sites or a larger number of archaeological sites (dominated by lithics) – the standard procedure for over three decades – can no longer be viewed with any degree of confidence.

- We are seeing a clear paradigm shift in the study of human origins.

- Historical narratives of the timing and extent of human species migrations, of Modern Human advantages over others, and indeed on the timing of extinctions, that probably did not happen, are finally giving way as the focus moves towards looking at the biology and culture of human populations and the nature of their interactions in time and space. We must now not only accept the reality of the “Neanderthal inside us” (Saraiva, 2022), but also that of “us inside the Neanderthals” (Petr et al., 2020).

The earliest basketry in southern Europe: Hunter-gatherer and farmer plant-based technology in Cueva de los Murciélagos (Albuñol)

- The burial site of Cueva de los Murciélagos in southern Iberia, uncovered during 19th-century mining activities, contained the best-preserved hunter-gatherer basketry in southern Europe, together with other unique organic artifacts associated with the first farming communities, such as sandals and a wooden hammer.
- Present 14 ^{14}C dates for the perishable artifacts (*N* = 76), situating the assemblage between c. 7500 to 4200 cal BCE.
- Used esparto grass (like Pampas grass)

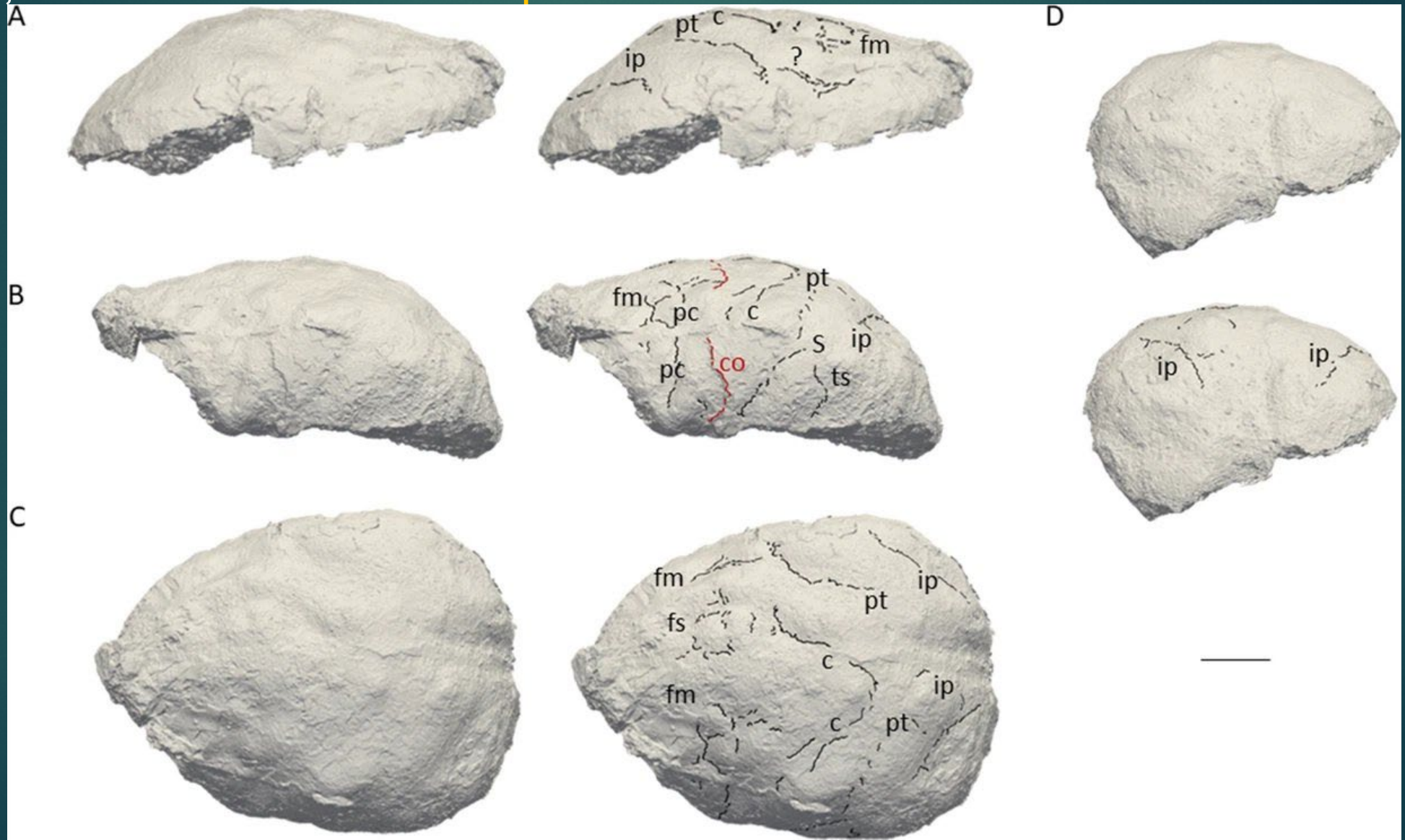
Francisco Martínez-Sevilla, et al., 2023

Mesolithic organic-based artifacts. 10-8 Ka

Neolithic organic-based artifacts. ~6500–3800

Neolithic

The endocast of ER 3732, an early *Homo* specimen dating back to about 1.9 Ma, indicates an early organization in the Broca area, associated with the speech function, with traits closer to chimpanzees than to modern humans.



ER 3732

- Field survey in the Koobi Fora area led by Richard Leakey led to the discovery of this partial cranium in 1975.
- This individual lived sometime between 2.0 and 1.87 million years ago.
- Scientists disagree about which species of hominins this skull may represent.
- Estimation of its endocranial volume of greater thaï 600 ml, within the range of sizes for known fossils attributed to Homo habilis, Homo rudolfensis, and Homo erectus. It has a less projecting and distinct supraorbital torus than most African fossils that belong to H. erectus

Broca's region in early Homo

- There are uncertainties around the derived or primitive state of the brain organization in the earliest representatives of the genus *Homo*, more particularly in key regions such as the Broca's area.

- Ponce de León et al., 2021 thoroughly examined brain endocasts of *Homo* specimens in eastern Africa and Eurasia and demonstrated that the organization of the Broca's area in the earliest representatives of the genus before 1.5 Ma was primitive. Frontal lobe expansion is the derived condition.

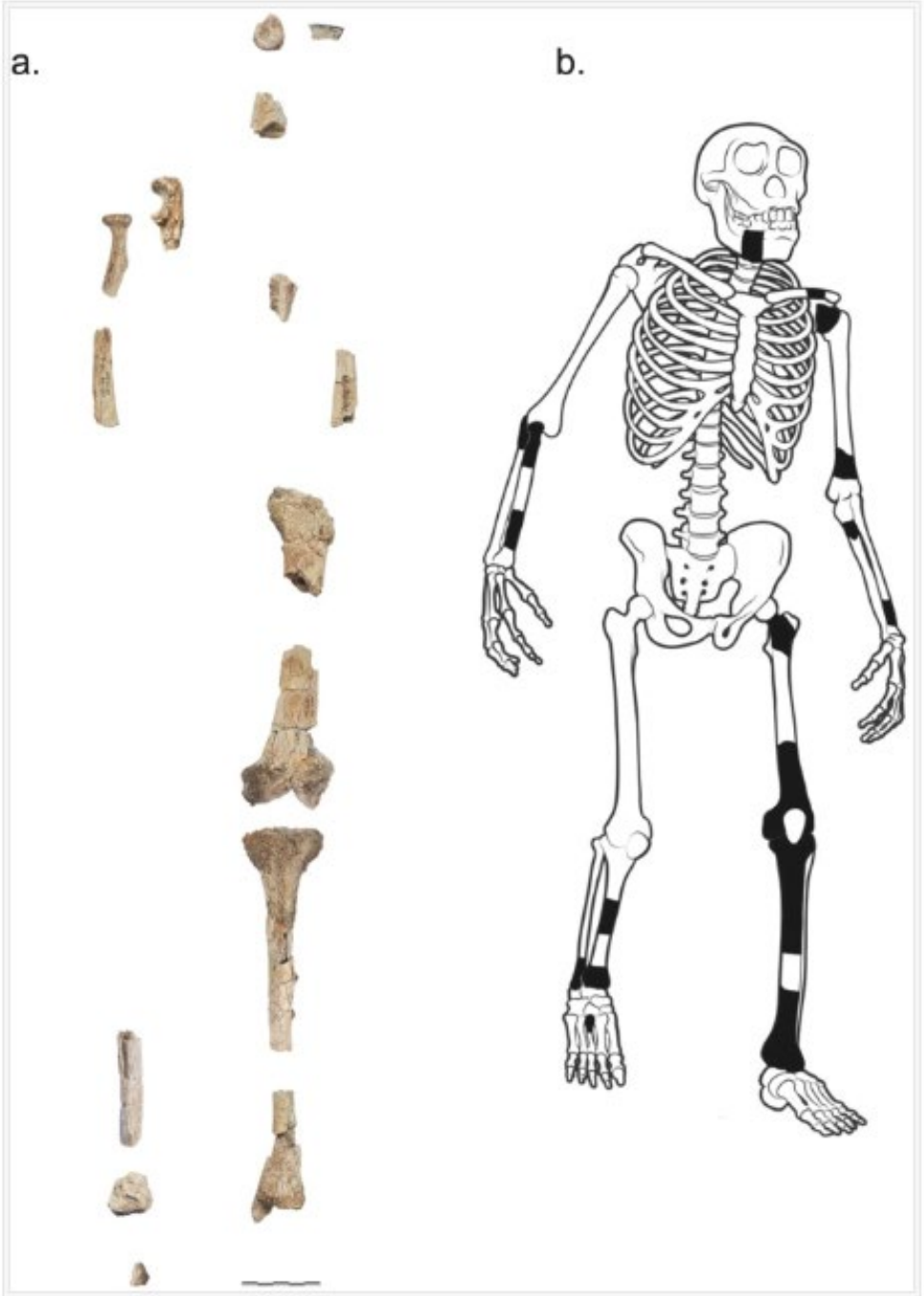
- By revisiting a particularly well-preserved fossil endocast from the Turkana basin (Kenya), here we confirm that early *Homo* in Africa had a primitive organization of the Broca's area ca. 1.9 million years ago.

1.9 Ma Homo Broca’s area

- Used the brain endocast of a ~1.9-million-year-old hominin fossil from Kenya, attributed to genus *Homo*, to show that the organization of the Broca's area in members of early *Homo* was primitive.

- Specifically, the prefrontal sulcal pattern in this early *Homo* specimen more closely resembles that of chimpanzees than of modern humans.

- Because Broca's area is associated with speech function, the **compelling** evidence from this study is relevant for understanding the timing and trajectory of evolution of speech related traits in our genus.



- KNM-ER 1500 post cranials = Paranthropus boisei

Classic P. boisei skull

KNM-ER 1500 = P. boisei, at 1.9 Ma

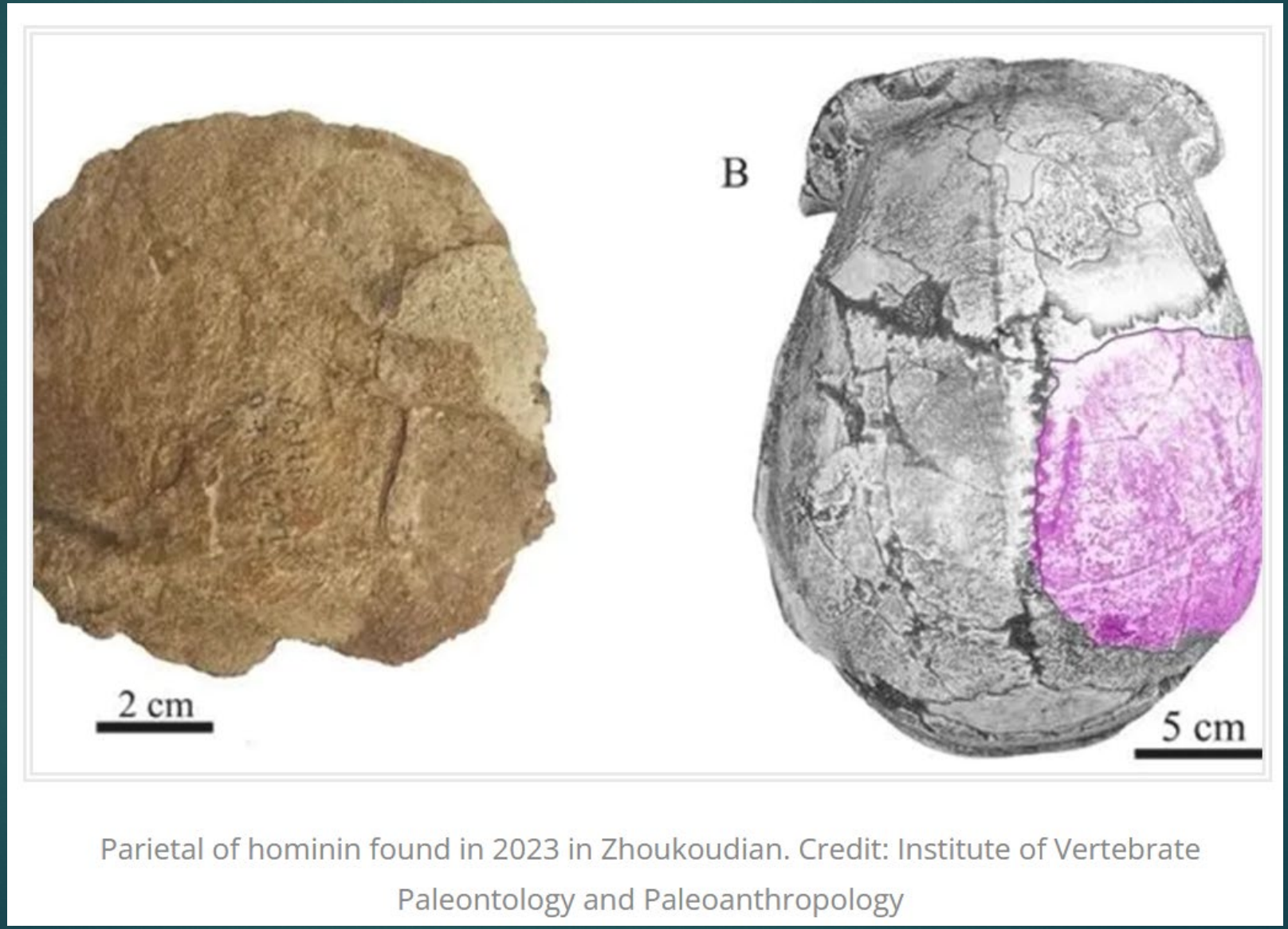
- Nearly all fossils recovered to date that are attributed to this species are craniodental remains. As a consequence, the postcranial anatomy of *P. boisei* remains poorly understood

- The mandible, radius, and femur of KNM-ER 1500 preserve morphologies that support the attribution of this specimen to *P. boisei*. The reassessment of the *KNM-ER 1500 skeleton* suggests it belonged to a female *Paranthropus boisei*. It would be a small individual, indicating the existence of sexual dimorphism in this species.

- No feature serves to align KNM-ER 1500 with *Homo* to the exclusion of *Paranthropus*.

- KNM-ER 1500 was a small-bodied individual and attributing this specimen to *P. boisei* confirms that significant postcranial-size dimorphism was present in this species.

New Zhoukoudian Parietal Bone



Parietal of hominin found in 2023 in Zhoukoudian. Credit: Institute of Vertebrate Paleontology and Paleoanthropology

First bone found at Zhoukoudian in 50 years.

- The first complete *H. erectus skull* was discovered at Zhoukoudian 92 years ago.

- The discovery of a new cranial fragment of hominin, a parietal bone, in Zhoukoudian, was announced in the press. Its thickness and size recall the *Homo erectus* specimens of that site. The last human fossil discovered there had been a tooth in 1973. Its estimated antiquity is intermediate between that of the *Homo erectus* of Zhoukoudian (about 500 ka) and the first modern humans of the place

- The Pleistocene human specimen is fully fossilized and shows a yellowish-brown color. It was excavated among a cluster of animal fossils at the site, which was first spotted in 1932 with stone tools and mammal fossils in abundance.

The Evolution of Paleolithic Hunting Weapons: A Response to Declining Prey Size

- The study of nine sites ranging from the Achelense to the Upper Palaeolithic suggests that the novelties introduced in weapons and hunting strategies were motivated by the availability and size of available prey, and are associated with an increase in cognitive capabilities in humans.

- This paper examines the hypothesis that changes in hunting weapons during the Paleolithic were a direct response to a progressive decline in prey size. The study builds upon a unified hypothesis that explains Paleolithic human evolutionary and behavioral/cultural phenomena, including improved cognitive capabilities, as adaptations to mitigate declined energetic returns due to a decline in prey size.

- Five selected case studies in Africa and Europe were analyzed to test this hypothesis, focusing on the relative presence of megaherbivores (>1000 kg) in the transition between the Acheulean/Early Stone Age and the Middle Paleolithic/Middle Stone Age.

Miki Ben-Dor & Ran Barkai, 2023

Hypothesis

- The findings indicate a decline in megaherbivores' presence and biomass contribution in the studied transition period associated with the introduction of Levallois technology.
- Reviewed the evolution of hunting weapons, including wooden-tipped and stone-tipped spears and bows and arrows.
- Analysis of tip size and breakage patterns indicate a reduction in point size over time, aligning with the declining prey size. We propose that changes in hunting weapons and strategies were driven by the practical and ontological incentives presented by the availability and size of prey. Developing smaller, more precise weapons required increased cognitive capacities, leading to the parallel evolution of human cognitive abilities.

Declining Prey size

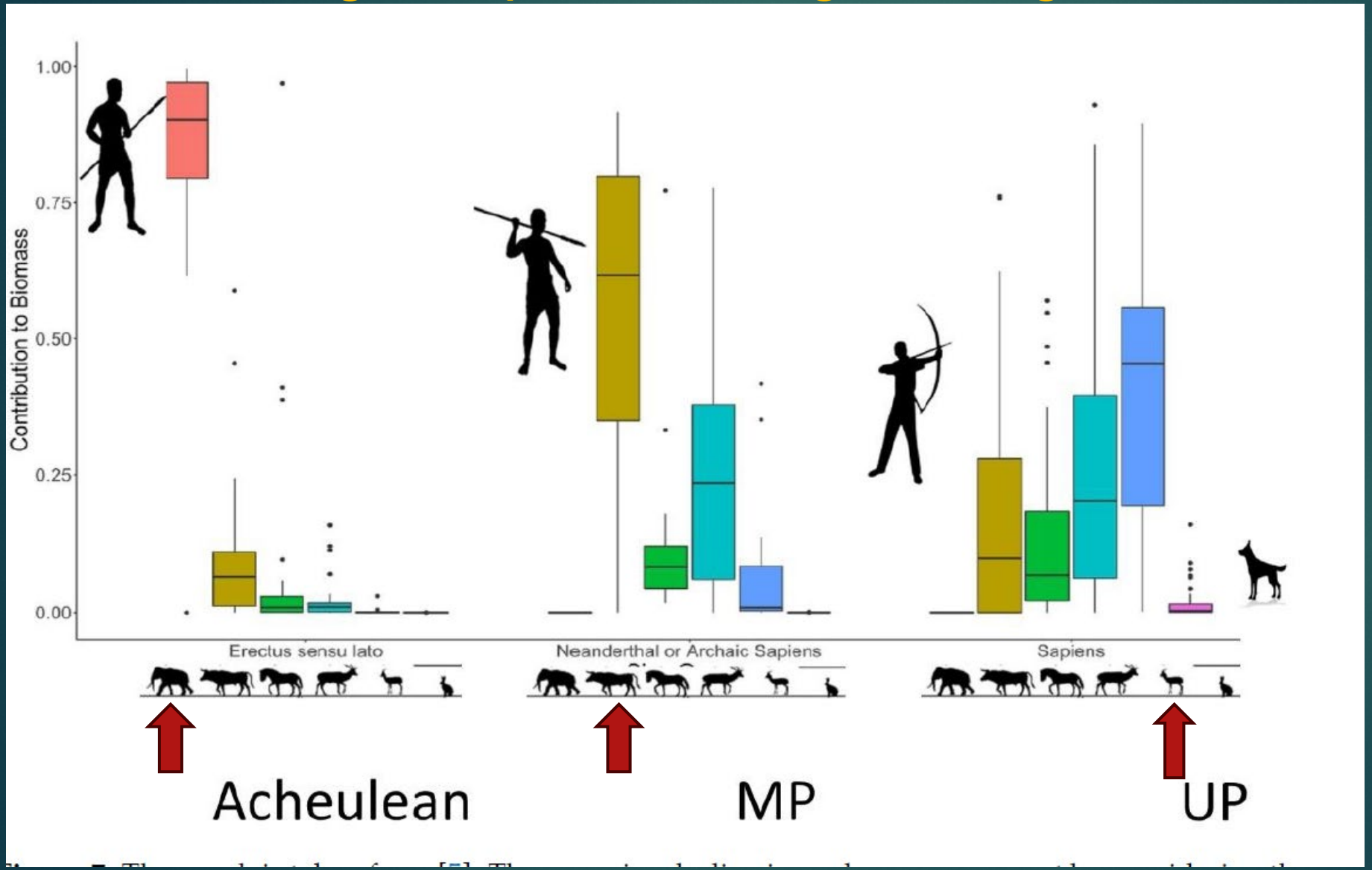
- Both methods show that megaherbivores' presence and biomass contribution declined over time in all five cases. There seems to be a clear association between megaherbivore decline and the transition between the Acheulean and the MP/MSA.

- The decline of megaherbivores was associated with an increase in Levallois-like technologies.

- In the Levant, Levallois technology at the end of the Acheulean was associated with elephant disappearance.

- In all but one case (Olorgesailie), megaherbivore declines were not directly associated with climate change.

Temporal association between the dynamics of prey size and hunting weapons' change, using data from the Levant.

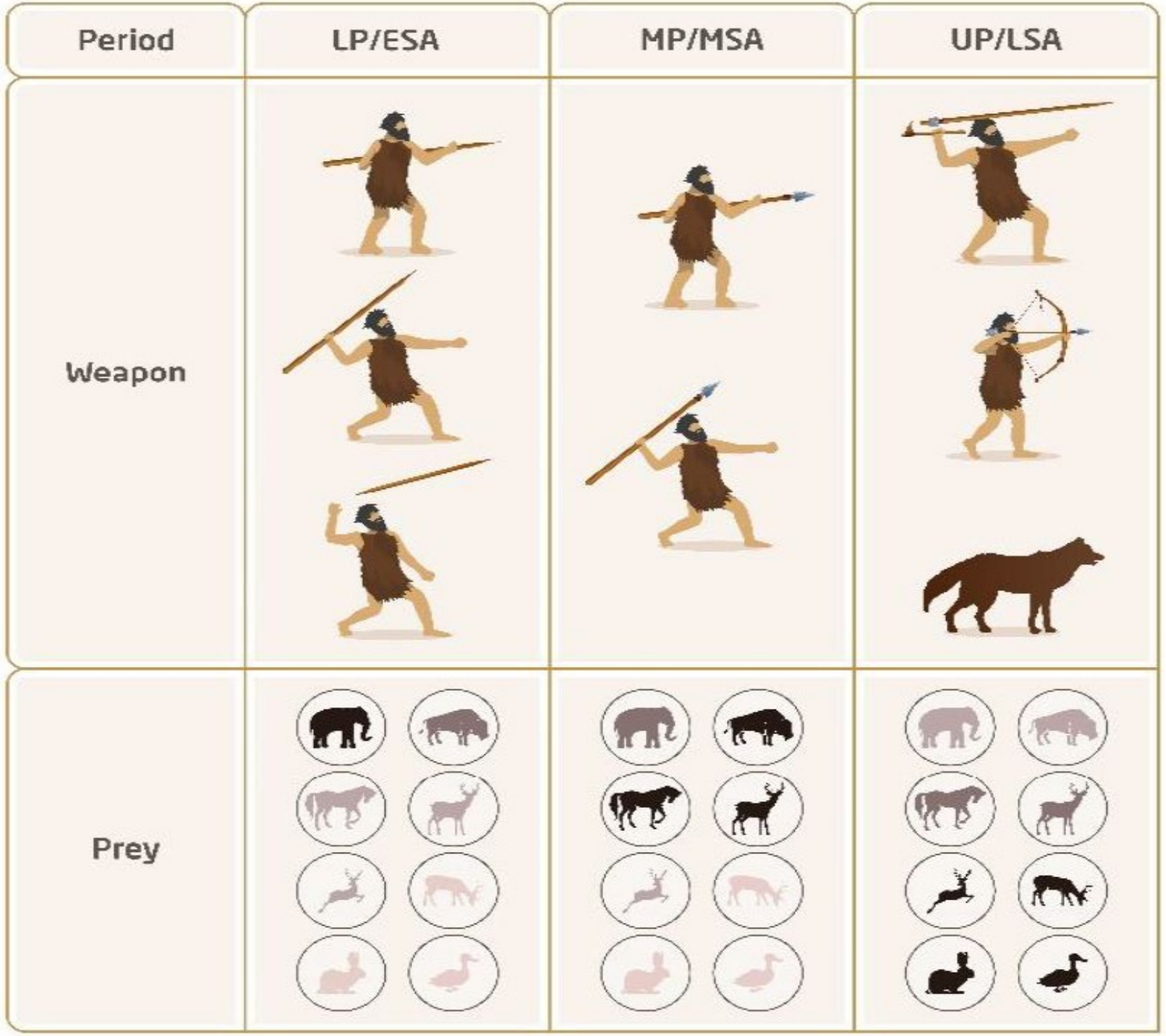


Megaherbivores dominated the Acheulean prey biomass in the Levant, whereas in the MP, Bos/bison size prey (700-1000 kg) dominated the assemblages' biomass. Later, smaller prey like gazelles provided most of the biomass in the UP. Placing the figure of the typical hunting weapon of the period next to the prey size biomass distribution demonstrates the temporal association.

Tools of the LP/MP/UP

All sizes of prey were acquired in every period

- MP/MSA appearance of hafted stone points. Stone. Tipping was used mainly in throwing spears
- Transition between MP/MSA and UP, we find a similar association. There was a decline in the size of prey in archaeological sites during this transition, and smaller stone tips = dart tips and arrowheads



Prey size & cognitive evolution

- There is strong evidence that prey size declined during UP/LSA as part of the Late Quaternary Megafaunal Extinction (52-9 Ka). The widespread usage of bows and arrows as hunting tools likely began in the Upper Paleolithic period. earliest known evidence of bow and arrow use comes from the South African site of Sibudu Cave, dating back approximately 64 Ka

- The emergence of a causal brain size—prey size (reversed) association is a key implication of the causal association between prey size decline and the development of novel hunting weapons.. As weapons become more complex, they require more cognitive ability. Additionally, tracking prey may also require enhanced cognitive abilities.

- Argue that the production of complex weapons and the employment of gradually more advanced tracking behaviors, at the cost of increasing cognitive resources, contributed to energetic savings in the increasingly longer pursuit stages of the hunt.

Conclusions

- The findings in this paper contribute to the growing body of evidence that suggests prey sizes declined during the transition between the LP, MP, and Acheulean. The decline was first associated with the appearance of spear-sized stone points, mostly made by the Levallois method.

- Later, the prey size decline known as The Late Quaternary Megafaunal Extinction was associated with the invention and adoption of complex projectile systems, trapping devices, and dog domestication.

- We hypothesized that the employment of the new weapon technology resulted in the mitigation of potential energetic cost increases with the decline in prey size. We expanded on the mechanism for the weapons to improve the energetic return from hunting smaller prey. Additionally, we discussed the emerging causal relationship between prey size decline and cognitive abilities extension.

Who were the first modern humans to settle in Europe?

- Before modern humans settled definitively in Europe, other sapiens populations left Africa for Europe beginning approximately 60,000 years ago, albeit without settling for the long term.

- This was due to a major climatic crisis 40,000 years ago, combined with a super-eruption originating from the Phlegraean Fields volcanic area near current-day Naples, subsequently precipitating a decline in ancient European populations.

- Study analyzed the genome of two skull fragments from the Buran Kaya III site in Crimea dating to 36,000 and 37,000 years ago.

Genome sequences of 36,000- to 37,000-year-old modern humans at Buran-Kaya III in Crimea

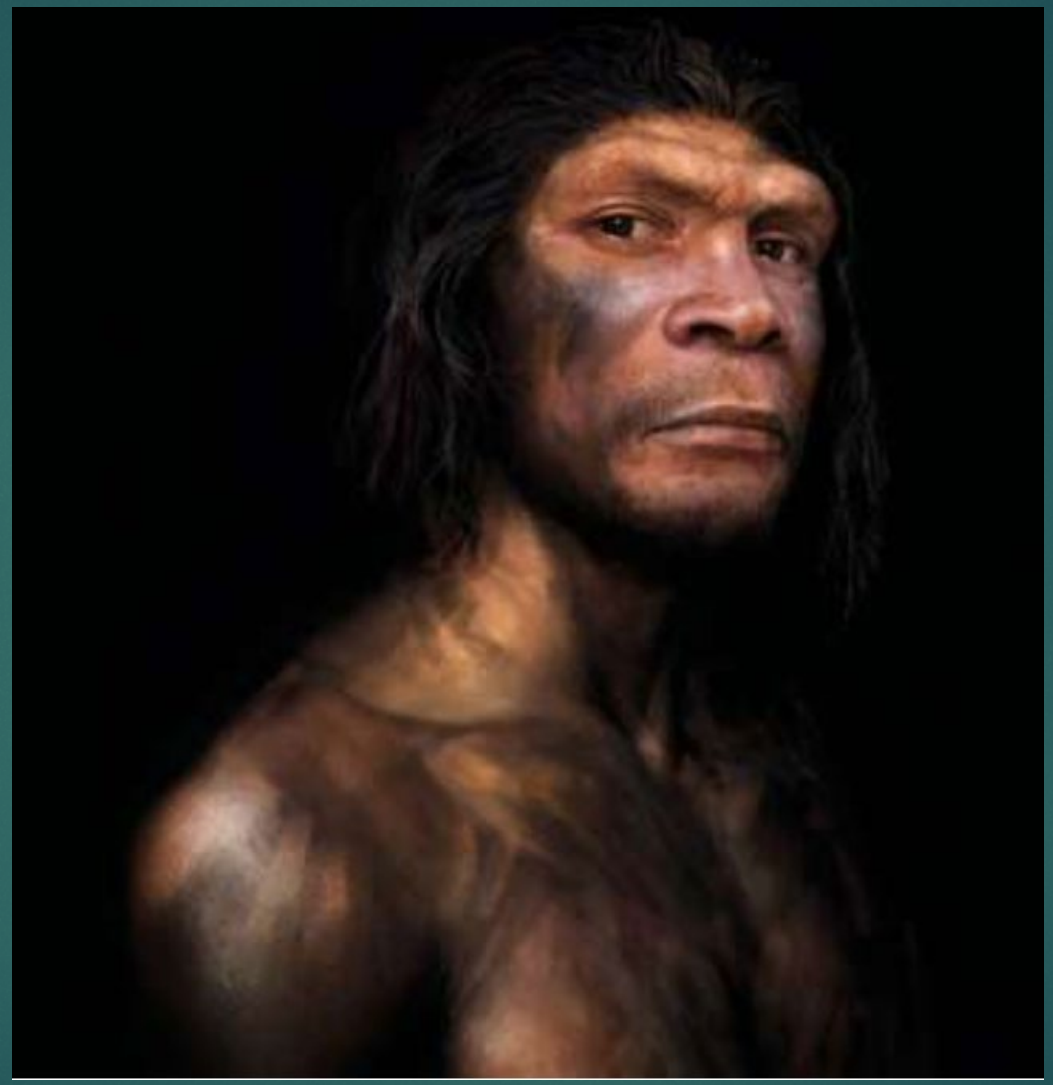
- Populations genetically related to present-day Europeans first appeared in Europe at some point after 38,000–40,000 years ago, following a cold period of severe climatic disruption. These new migrants would eventually replace the pre-existing modern human ancestries in Europe, but initial interactions between these groups are unclear due to the lack of genomic evidence from the earliest periods of the migration.

- Study describes the genomes of two 36,000–37,000-year-old individuals from Buran-Kaya III in Crimea as belonging to this newer migration. Both genomes share the highest similarity to Gravettian-associated individuals found several thousand years later in southwestern Europe.
- These genomes also revealed that the population turnover in Europe after 40,000 years ago was accompanied by admixture with pre-existing modern human populations. European ancestry before 40,000 years ago persisted not only at Buran-Kaya III but is also found in later Gravettian-associated populations of western Europe and Mesolithic Caucasus populations.

E. Andrew Bennett, et al., 2023

Some New Images of Neandertals

The exhibition "Neanderthal," which opened at the University Museum in Trondheim, Norway



Neanderthal coexistence with *Homo sapiens* in Europe was affected by herbivore carrying capacity

- During the marine isotope stage 3 (MIS3) [ca. 60–30 ka], global climatic conditions experienced rapid and severe oscillations between full glacial (stadial) and milder (interstadial) conditions.

- While some biogeographic regions served as refugia for human populations during the coldest periods of MIS3, other areas experienced harsher climatic conditions and discontinuities in the human settlement. A source-sink model has been proposed to explain these population processes of colonization, coexistence, fragmentation, isolation, and replacement.

M. Cordasco, et al., 2023

Source and sink areas

- Populations would persist in high-quality habitats (“source areas”) but could not prevail in the long term in the low-quality ones (“sink areas”).

- Neanderthals and H. sapiens had wide climatic tolerances and exploited similar trophic niches.

- Therefore, it is plausible that they would have shared the same source and sink areas, with sink areas being prone to quicker species replacement and source areas allowing a longer persistence of both human species due to the abundance and stability of their trophic (feeding and nutrition) resources.

Climate

- Combining models on the chronology of the European transition from the middle to higher palliolithic, the abundance of herbivores and the availability of plant species, it has been observed that the continental regions where the productivity of the ecosystem was low or unstable, the Neanderthals disappeared before or just after the arrival of *Homo sapiens*, while regions with high productivity and stable productivity, with an abundance of herbivores, witnessed a prolonged coexistence between the two species

- It has been proposed that climate change and the arrival of modern humans in Europe affected the disappearance of Neanderthals due to their impact on trophic resources; between 55 and 30 ka BP in each archaeological and paleontological site.

Carrying capacity of ecosystems

- This study tests whether the regional differences in the timing of the Neanderthal disappearance, the spread patterns of H. sapiens, and the temporal overlap between both human species were affected by the carrying capacity (CC) of the ecosystems that they inhabit in Europe

- Modeling shows that in continental regions where the ecosystem productivity was low or unstable, Neanderthals disappeared before or just after the arrival of Homo sapiens

High Herbivore capacity = longer N-MH overlap

- In contrast, regions with high and stable productivity witnessed a prolonged coexistence between both species. The temporal overlap between Neanderthals and H. sapiens is significantly correlated with the carrying capacity of small- and medium-sized herbivores.

- These results suggest that herbivore abundance correlated with longer coexistence between both human species.

- Has been proposed that Neanderthal populations were smaller and more isolated from one another than *H. sapiens* populations, which would imply a higher risk of demographic bottlenecks due to fluctuations in food resources

Requirements for coexistence of different species

- Although N or MHs discontinuously occupied most regions during MIS3, both human species likely coexisted in the overlapping areas
- Local spatial segregation is a common mechanism promoting coexistence among species with similar food niches by mitigating direct competition.

- Consequently, the observed temporal overlap at a regional scale does not necessarily imply coexistence at the local level.

- Even if H. sapiens and Neanderthals occupied different localities within the same regions, the overlap in this study indicates that they shared the same ecosystems and relied on their productivity

Regional variation

- On the basis of compared nucleotide diversity estimates, Neanderthal remains from central and northern Iberia dated to the MIS3 revealed more than sixfold lower diversity than Neanderthals recovered in Eastern Europe.
- Likewise, Neanderthal genetic bottlenecks or demographic vacuums have also been proposed for Northern Europe, the Carpathian region, and Central and Northern Iberia.
- In all these regions where Neanderthals experienced a loss of genetic diversity or where archaeological data suggest a demographic hiatus before the arrival of H. sapiens, the ecosystems' productivity was low or unstable during MIS3.

Herbivore availability

- These results suggest that ecosystem carrying capacity (CC = herbivore availability) and its stability throughout MIS3 could be a disruptive agent in the connectivity of Neanderthal populations rather than the appearance of H. sapiens.
- Therefore, these results cast doubt on the contention that the arrival of *H. sapiens* caused the demise of H. neanderthalensis in those regions where the Ns disappeared before or shortly after the arrival of the MHs; nonetheless, the competitive exclusion hypothesis cannot be ruled out in all regions.
- Overlap and hybrids: Analyses of H. sapiens remains from Peștera cu Oase suggest a Neanderthal ancestor four to six generations back in his family tree. An extended period of contact between H. sapiens and Neanderthals in the lower Danube Basin is also supported by the chronology of the H. sapiens remains recovered from Bacho Kiro.

Overlap and higher trophic resources

- Recent studies suggest that there was a temporal overlap between both species in France. Likewise, in the Mediterranean region of Iberia, recent discoveries suggest that Neanderthals inhabited this area at a moment when H. sapiens had already arrived in the region.

- Results obtained in this study show that in all these regions where Neanderthal genetic continuity and interbreeding with *H. sapiens* have been reported or where recent analyses suggest a longer period of contact between both human species, trophic resources were, on average, markedly higher and more stable.

Middle to Upper Paleolithic transition (MUPT)

- However, in those regions where both human species coexisted, there was substantial variation in the trophic resource availability and the temporal overlap.
- Correlation tests in this study show that the higher the CC of small- and medium-sized herbivores, the longer the temporal overlap between Neanderthals and H. sapiens.
- The regions characterized by abundant trophic resources displayed a longer temporal overlap between Ns and MHs, which would increase the potential for assimilation between both human species, while likely contributing to a direct or indirect interspecific competition.
- Trophic resources played a central role in the spatiotemporal replacement patterns of Neanderthals by H. sapiens in Europe

CC of medium-sized herbivores

- The CC of medium-sized herbivores is the only factor influencing the timing of the Neanderthal disappearance, whereas the spread of H. sapiens is also significantly affected by other components of the ecosystem's productivity, such as the CC of small-sized herbivores.

- It is worth noting that correlations do not indicate causality. The results obtained here do not indicate that herbivore CC caused the demise of Neanderthal populations nor their temporal overlap with H. sapiens.

Herbivore availability

- Large herbivores (>300 kg) have fewer natural predators, and in this study, CC of large sized ungulates is the only variable systematically uncorrelated with the temporal overlap between both human species.

- The abundance of small- and medium-sized herbivores affects the richness and stability of both Ns and MHs. Hence, herbivore CC during MIS3 likely released the trophic pressure between secondary consumers in some European regions and, therefore, could have slowed down the competitive exclusion processes, affecting the coexistence likelihood between Neanderthals and H. sapiens.

Result conclusions

- Results obtained in this study support the hypothesis that regional differences in the timing of Neanderthal disappearance, the spread patterns of H. sapiens, and the temporal coexistence between both human species were affected by trophic resource availability.

- Thus, this study shows that the ecosystem productivity and stability throughout MIS3 are fundamental for our understanding of the extinction patterns of Neanderthals, the phylogeographic structure of their last populations, and the regional differences in their period of coexistence with our species.

First identification of an evolving Middle Stone Age ochre culture at Porc-Epic Cave, Ethiopia

- Ochre gradually increases at sites from East and South Africa to become almost ubiquitous after 160 ka. The deliberate use of ochre to modify the appearance of shell beads suggests that, already at this time and probably earlier, ochre must have been involved in symbolic practices
- One of the largest known Middle Stone Age (MSA) ochre collections, from Porc-Epic Cave, Ethiopia, consisting of more than 40 kg of ochre (n = 4213 pieces), 21 ochre processing tools and two ochre-stained artefacts.
- Unveil how MSA inhabitants of Porc-Epic Cave exploited mineral resources. We show that they could predict the properties of different ochre types accessible in their environment, and gradually adapted their technology to cope with changes in raw material availability.

It has been possible to study the evolution of the use of ochre for 4500 years by humans in the Porc-Epic Cave (Ethiopia) about 40 ka, from a collection of 4213 pieces of ochre, which total 40 kg.

Forty ka ago, humans picked up and moved a wide variety of ochre types to know well, to produce dust from different textures and tones, probably adapted to different symbolic or functional activities. A type of red ochre was used specifically for symbolic purposes.

New Blombos Cave evidence supports a multistep evolutionary scenario for the culturalization of the human body

- The discovery of eye-catching unmodified shells with natural holes from 100,000 to 73,000 years ago confirms previous scant evidence that marine shells were collected, taken to the site and, in some cases, perhaps worn as personal ornaments.

- The shells were all found in the Blombos Cave, on the southern Cape of South Africa's coastline. Similar shells have been found in North Africa, other sites in South Africa and the Mediterranean Levant, which means that the argument is supported by evidence from other sites, not just Blombos Cave.

Francesco d'Errico, … Christopher Stuart Henshilwood et al., 2023

A synthesis of data on the origin of personal ornamentation

- Analyze marine gastropods from Blombos Cave dated to between 100 ka and 70 ka. Unperforated and naturally perforated shells were collected between 100 and 73 ka. A previously unrecorded gastropod species was used as bead 70 ka. Propose a multi-step scenario for the culturalization of the human body.

- The emergence of technologies to culturally modify the appearance of the human body is a debated issue, with earliest evidence consisting of perforated marine shells dated between 140 and 60 ka at archaeological sites from Africa and western Asia.

Australopithecus afarensis endocasts suggest ape-like brain organization and prolonged brain growth

- Human brains are three times larger, are organized differently, and mature for a longer period of time than those of our closest living relatives, the chimpanzees.

- Together, these characteristics are important for human cognition and social behavior, but their evolutionary origins remain unclear.

- To study brain growth and organization in the hominin species Australopithecus afarensis more than 3 Ma ago, we scanned eight fossil crania using conventional and synchrotron computed tomography. We inferred key features of brain organization from endocranial

Philipp Gunz..Dean Falk..William Kimbe, Fred Spoor, Zeresenay Alemseged et al. 2023

A. Afarensis = ape-like brain organization

- Contrary to previous claims, sulcal imprints reveal an ape-like brain organization and no features derived toward humans.

- A comparison of infant to adult endocranial volumes indicates protracted brain growth in A. afarensis, likely critical for the evolution of a long period of childhood learning in hominins.

- In contrast to African apes, the human brain growth pattern is characterized by high growth rates and protracted duration. Modern humans also give birth to relatively immature offspring who depend on caregivers for a long period of time. This provides a longer interval for cognitive development and is believed to enhance the impact of postnatal experiences on neural connectivity.

Australopithecus afarensis

- Parietal and occipital lobes differences: In all apes, a well-defined lunate sulcus approximates the rostral (anterior) boundary of the primary visual cortex (Brodmann's area 17) of the occipital lobes. Some have argued that structural changes of the brain resulted in a more posterior (human-like) placement of the lunate sulcus on endocasts of australopiths and eventually to the disappearance of a clear endocranial impression in humans.
- Hypothetically, such brain reorganization could have been linked to behaviors that were more complex than those of their great ape relatives (e.g., tool manufacture, mentalizing, and vocal communication). Unfortunately, however, the lunate sulcus typically does not reproduce well on endocranial imprints, so there is uncertainty about its position in australopiths.

A. afarensis

- There is debate whether protracted brain growth and reorganization are merely by-products of the brain size increase in the genus Homo beginning by 2 million years (Ma) ago or evolved in the genus Australopithecus roughly 1 Ma before the marked expansion of the brain.

- 1 - Is there evidence for human-like brain reorganization in A. *afarensis*?
- 2 - Was the pattern of brain growth in A. *afarensis* more similar to that of chimpanzees or that of humans?

- The beautifully preserved endocast of DIK-1-1 has an unambiguous impression of a lunate sulcus in an anterior (ape-like) position

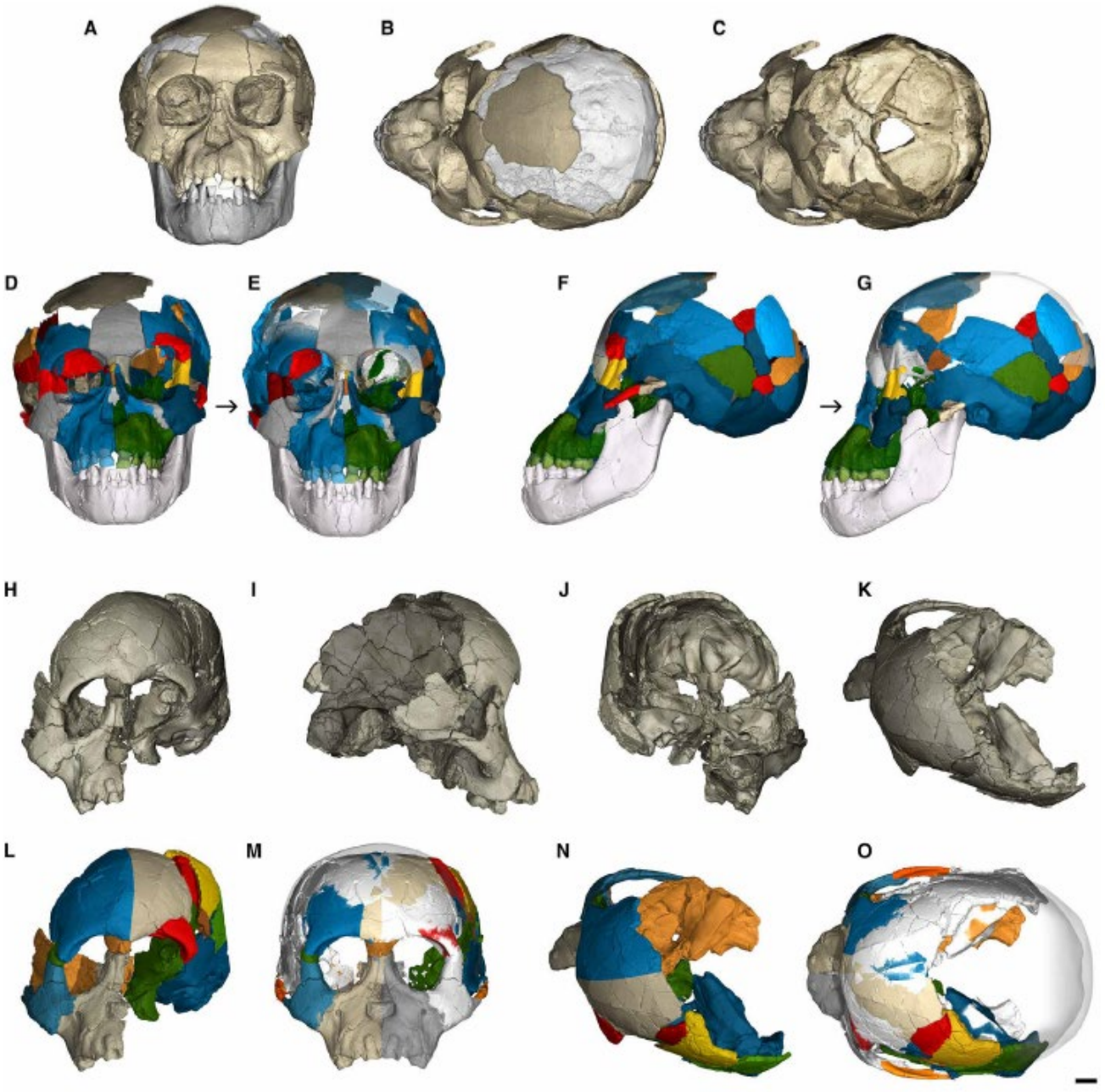


Fig. 1. Virtual reconstruction of *Australopithecus afarensis* infants from Dikika and Hadar. DIK-1-1 (**A** to **G**) and A.L. 333-105 (**H** to **O**) as preserved and reconstructed. (A) Frontal view. (B) Superior view. (C) Manual segmentation of the endocranial matrix reveals exceptional preservation of the endocranial cavity. (D to G) 3D models of the DIK-1-1 skull before (D and F) and after (E and G) virtual reconstruction in frontal and left lateral view. (H to K) Scan of the original A.L. 333-105 fossil specimen. (L) Manual segmentation. (M to O) Virtual reconstruction. The reconstructed outer shells of the braincases are shown as semitransparent surfaces. Scale bar, 1 cm.

A to G: DIK-1-1

H to O: AL-333

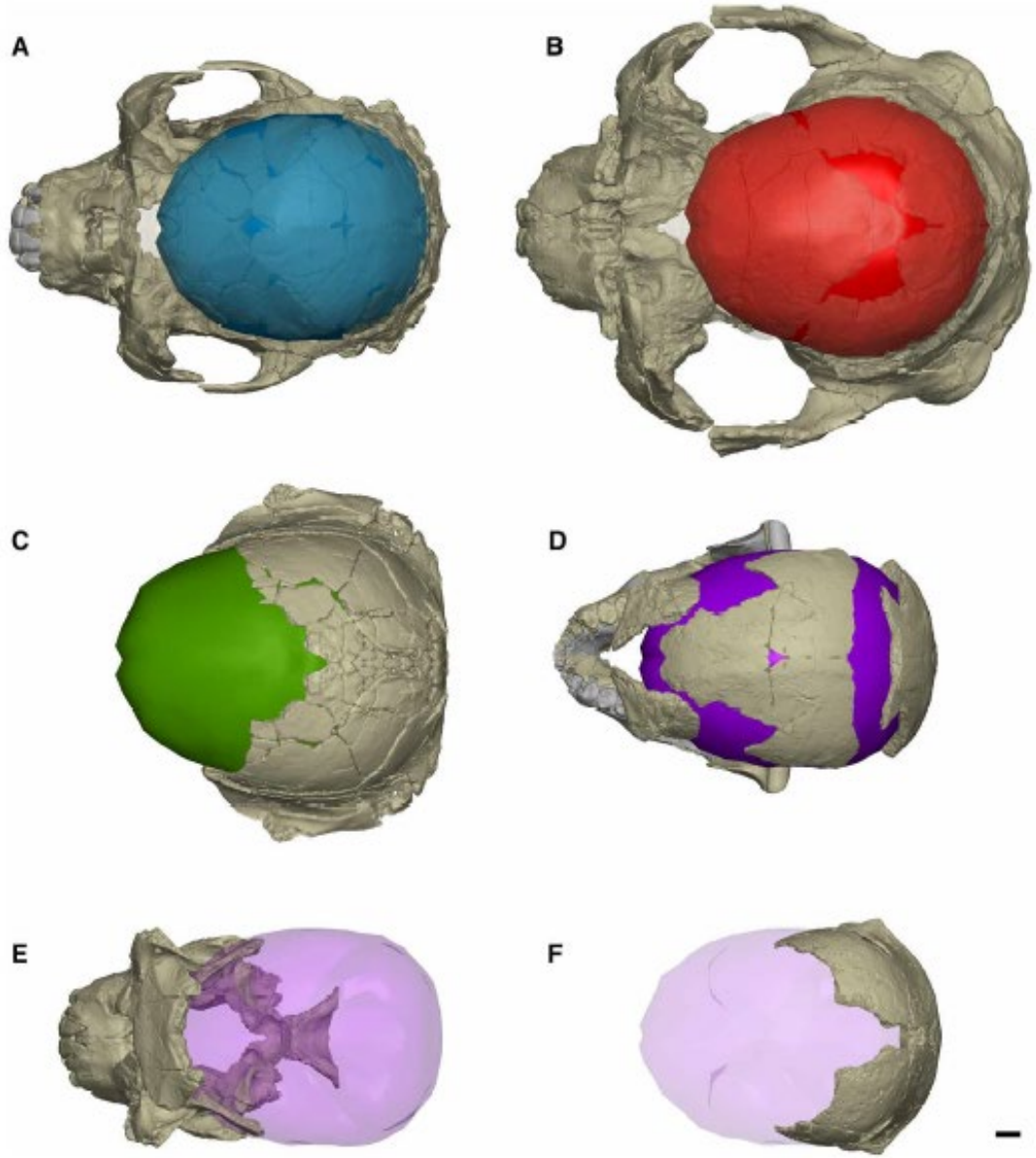


Fig. 2. Virtual reconstructions of *A. afarensis* adults. (**A**) Reconstruction of A.L. 822-1 in superior view. One of the 122 thin-plate spline (TPS)–based reconstructions of the endocast is shown in blue. (**B**) A.L. 444-2; a TPS estimation of the endocranial surface is shown in red. (**C**) A.L. 333-45; endocast in green. This endocranial reconstruction was created by scaling the endocranial surface of 444-2 based on landmarks and semilandmarks on the available morphology. (**D**) A.L. 288-1 (Lucy); endocast in purple (TPS estimation). (**E**) A.L. 417-1; the endocast of A.L. 288-1 is shown as a semitransparent surface. (**F**) A.L. 162-28; the endocast of A.L. 288-1 is shown as a semitransparent purple surface for size comparison. Scale bar, 1 cm.

Virtual reconstructions of A. *afarensis* endocasts.

(A) Reconstruction of A.L 822-1 in superior view. One of the 122 thin-plate spline (TPS)-based reconstructions of the endocast is shown in blue.

(B) A.L 444-2; a TPS estimation of the endocranial surface is shown in red.

(C) A.L 333-45; endocast in green.

(D) A.L. 288-1 (Lucy); endocast in purple

(E) A.L 41 7-1; the endocast of A.L. 288-1 is shown as a semitransparent surface.

(F) A.L 162-28; the endocast of A.L 288-1 is shown asa semitransparent purple surface for size comparison. Scale bar, 1 cm.

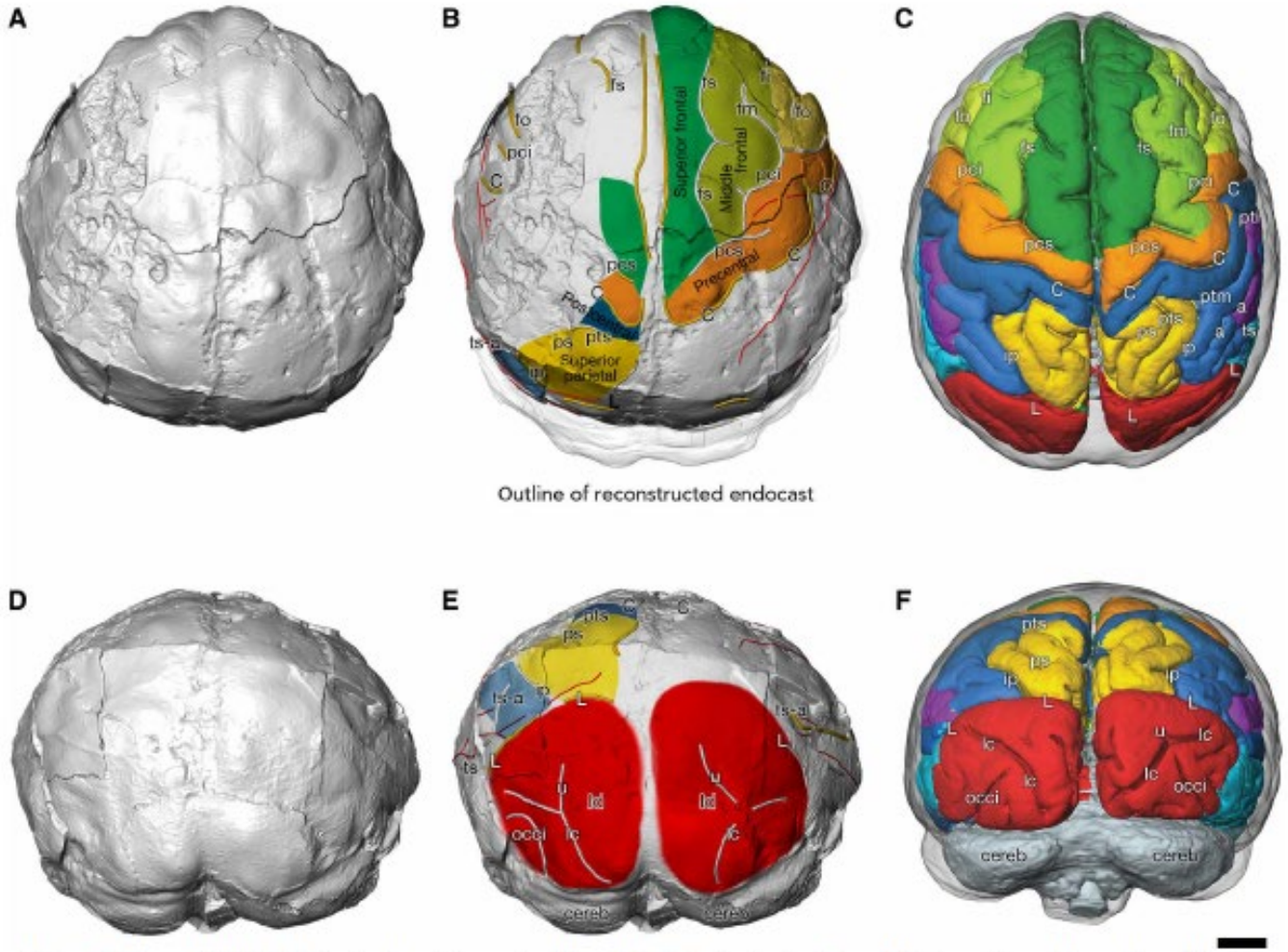


Fig. 3. Endocranial morphology of DIK-1-1. Virtual endocast in superior (**A** and **B**) and posterior view (**D** and **E**). Comparison of the endocranial surface with a juvenile chimpanzee brain (**C** and **F**) [3D model built from magnetic resonance images (MRIs)] illustrates the overall ape-like brain organization of the DIK-1-1 endocast, including an anteriorly placed lunate sulcus (L). Gyri are color-coded; sulci are labeled as in (C) and (F). Meningeal vessel impressions are shown in red. C, sulcus centralis; fs, frontalis superior; fm, frontalis medius; fi, frontalis inferior; fo, fronto-orbitalis; h, horizontal ramus of pci; ip, s. intraparietalis; pci, praecentralis inferior; pcs, praecentralis superior; ps, parietalis superior; pti, postcentralis inferior; ptm, postcentralis medius; pts, postcentralis superior; L, s. lunatus; ts, temporalis superior; ts-a, ramus temporalis superior; tm, temporalis medius; occi, occipitalis inferior; lc, s. calcarinus lateralis; u, s. calcarinus ramus superior; cereb, cerebellum; ld, lambdoidal suture. Scale bar, 1 cm.

Endocranial morphology of DIK-1-1. Virtual endocast in superior (**A** and **B**) and posterior view (**D** and **E**). Comparison of the endocranial surface with a juvenile chimpanzee brain (**C** and **F**) illustrates the overall ape-like brain organization of the DIK-1-1 endocast, including an anteriorly placed lunate sulcus (L). Gyri are color-coded; sulci are labeled as in (C) and (F). Meningeal vessel impressions are shown in red. C, sulcus centralis; fs, frontalis superior; fm, frontalis medius; fi, frontalis inferior; fo, fronto-orbitalis; h, horizontal ramus of pci; ip, s. intraparietalis; pci, praecentralis inferior; pcs, praecentralis superior; ps, parietalis superior; pti, postcentralis inferior; ptm, postcentralis medius; pts, postcentralis superior; L, s. lunatus; ts, temporalis superior; ts-a, ramus temporalis superior; tm, temporalis medius; occi, occipitalis inferior; lc, s. calcarinus lateralis; u, s. calcarinus ramus superior; cereb, cerebellum; ld, lambdoidal suture.

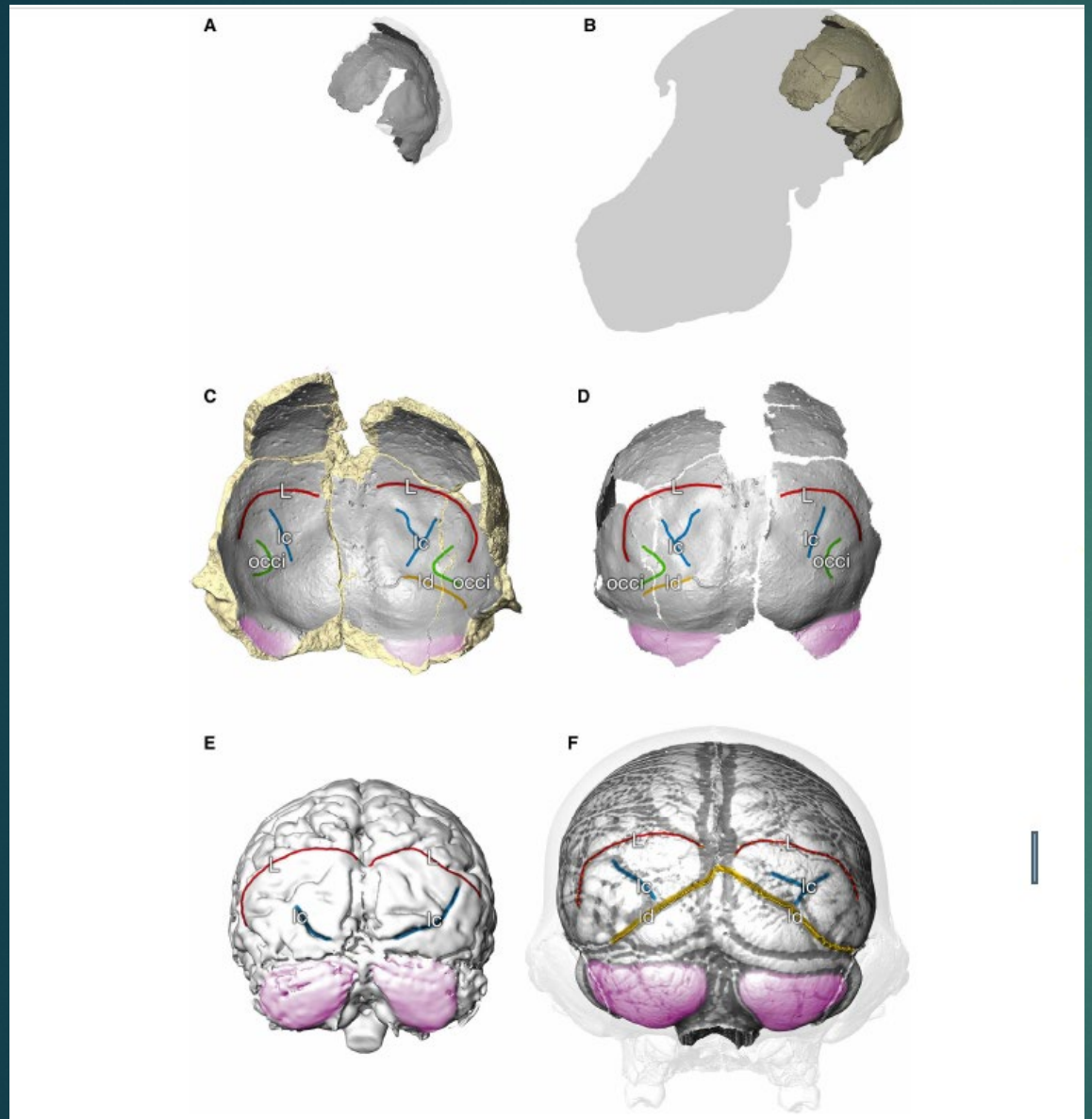


Fig. 4. Endocranial morphology of A.L. 162-28. (**A**) Comparison of the partial cranium A.L. 162-28 with the reconstructed skull A.L. 822-1 (**B**). (**C**) Anterior view of A.L. 162-28. The micro-CT data reveal a previously undetected impression of a lunate sulcus (L; red) on the left and right side. What had previously been identified as the intraparietal sulcus (ip) is an impression of the lateral calcarine sulcus (lc) on the occipital lobe. The feature previously incorrectly identified as a possible human-like lunate sulcus impression is related to the remnants of the fused lambdoidal suture (ld; yellow) and the occipital inferior sulcus (occi; green). (**D**) Posterior view of the endocranial surface of A.L. 162-28. (**E**) Posterior view of a chimpanzee brain based on an in vivo MRI scan ("Amanda" from the Yerkes National Primate Research Center). (**F**) Chimpanzee endocast based on a postmortem CT scan (*P. troglodytes verus* from the Taï forest). We superimposed a grayscale gradient based on the local curvature to visually enhance the sulcal impressions.

Endocranial morphology of A.L. 162-28.

(A) Comparison of the partial cranium AL. 162-28 with the reconstructed skull A.L. 822-1

(B) (C) Anterior view of A.L 1 62-28. The micro-CT data reveal a previously undetected impression of a lunate sulcus (L; red) on the left and right side. What had previously been identified as the intraparietal sulcus (ip) is an impression of the lateral calcarine sulcus (lc) on the occipital lobe. The feature previously incorrectly identified as a possible human-like lunate sulcus impression is related to the remnants of the fused lambdoidal suture (ld; yellow) and the occipital inferior sulcus (occi; green). (D) Posterior view of the endocranial surface of A.L 162-28.

(C) (E) Posterior view of a chimpanzee brain based on an in vivo MRI scan ("Amanda“ from the Yerkes National Primate Research Center).

(F) Chimpanzee endocast based on a postmortem CT scan *(P. troglodytes verus* from the Tal forest). We superimposed a grayscale gradient based on the local curvature to visually enhance the sulcal impressions.

Humans: High growth rate & prolonged brain growth

- Neither DIK-1-1 nor A.L. 333-105 exhibits the incipient reorganization of the inferior frontal gyrus recently described in Homo naledi. Overall, the endocasts of DIK-1-1, A.L. 162-28, and A.L. 333-105 indicate an ape-like brain organization in A. afarensis. Contrary to previous claims, we find no unambiguous indication of brain reorganization in any A. afarensis endocast that preserves detailed sulcal impressions
- Both died at ~2.5 years.
- Data indicate prolonged brain growth in A. afarensis, in that it takes longer for individuals to reach their adult EVs. Our findings therefore suggest that brain growth in A. afarensis was protracted as in modern humans. What distinguishes modern humans from A. afarensis and chimpanzees is a combination of high growth rates and prolonged brain growth.

Challenge to the central tenet of the obstetric dilemma hypothesis

- Prolonged brain growth and maturation have often been viewed as a consequence of evolutionary brain size increase in the genus Homo: a shift in life history required to evolve large adult brains despite obstetric constraints related to upright walking.
- In contrast to this view, our data from A. afarensis demonstrate that prolonged brain growth is not a mere by-product of evolutionary brain size increase. One can predict the average neonatal brain size in A. afarensis based on the statistical relationship between the brain size of newborns and adults in anthropoids. The pelvic dimensions of the small, presumed female A. afarensis specimen A.L. 288-1 (Lucy) suggest that it would have been possible to give birth to such a predicted A. afarensis neonate, potentially requiring some rotation of the fetus during parturition.

No obstetric dilemma in *A. afarensis*

- Our findings therefore challenge the central tenet of the obstetric dilemma hypothesis and suggest that obstetric constraints are not the proximate cause of the origins of prolonged brain growth in hominins. This view is in line with an earlier study that emphasized the importance of energetic constraints of the maternal metabolism on fetal growth and gestation length, suggesting that the evolution of altriciality (needing care after birth) in hominins had little to do with pelvic morphology.

- The dental development of DIK-1-1 was broadly comparable to that of P. troglodytes and therefore faster than in modern humans; but appears to have a prolonged period of brain development relative to chimpanzees.

- This indicates that the developmental pace of teeth and brain need not always be synchronized and can evolve independently, at least to some degree.

Prolonged brain growth in A. afarensis

- The fact that protracted brain growth emerged in hominins as early as 3.3 Ma ago could suggest that it characterized all of subsequent hominin evolutionary history.

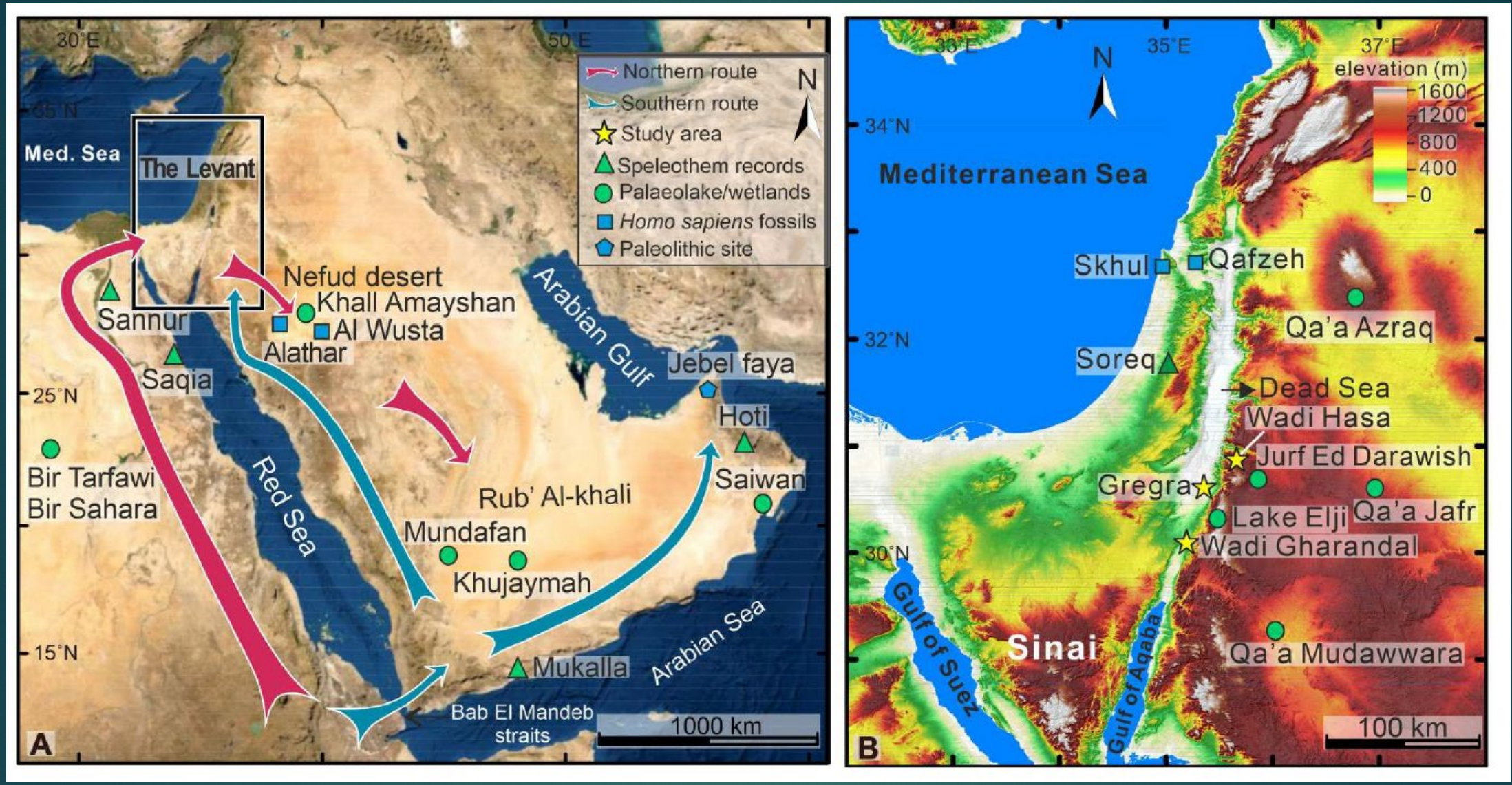
- However, it is possible that patterns of brain development varied among hominins and did not follow a linear evolutionary trajectory toward the modern human condition. Among primates in general, different rates of postnatal growth and maturation are associated with different infant-care strategies, suggesting that the extended period of brain growth in A. afarensis may have been linked to a long dependence on caregivers.

- Alternatively, slow brain growth could also primarily represent an energetic adaptation, e.g., to less productive environments, by spreading the energetic requirements of dependent offspring over many years. In either case, the protracted brain growth in A. afarensis provided a basis for subsequent evolution of the brain and social behavior in hominins and was likely critical for the evolution of a long period of childhood learning.

Human dispersals out of Africa via the Levant

- *Homo sapiens* dispersed from Africa into Eurasia multiple times in the Middle and Late Pleistocene.
- The route, across northeastern Africa into the Levant, is a viable terrestrial corridor, as the present harsh southern Levant would probably have been savannahs and grasslands during the last interglaciation.
- Here, we document wetland sediments with luminescence ages falling in the last interglaciation in the southern Levant, showing protracted phases of moisture availability. Wetland sediments in Wadi Gharandal containing Levallois artifacts yielded an age of 84 ka.
- Findings support the growing consensus for a well-watered Jordan Rift Valley that funneled migrants into western Asia and northern Arabia.

M. Abbas, et al., 2023



Arrows indicate the suggested routes of human dispersals out of Africa.

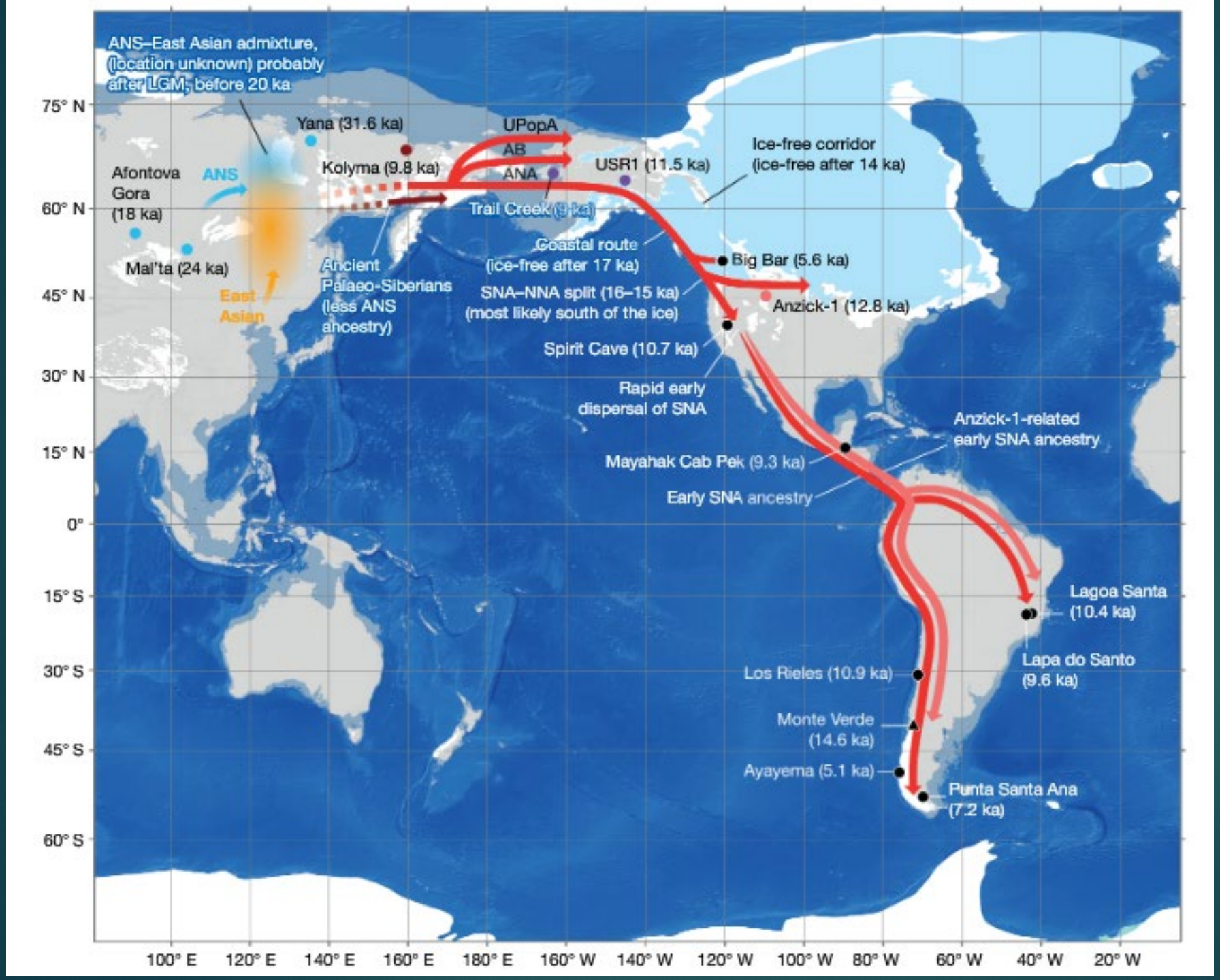
Speleothems are deposits of secondary minerals (such as calcite) that form on the ceilings, walls, and floors of caves during rainy seasons = indicate presence of water.

2 Routes North

- The geographical routes of dispersal into Eurasia have been long debated, e.g., the northern route from the Sinai Peninsula to the southern Levant then to Arabia, and the southern route via the Bab El Mandeb strait into the margins of southern Arabia. The southern route, i.e., the Red Sea crossing, is regarded as possible in glacial periods with low sea level.
- On the other hand, the dispersal via the northern corridor during ~130 to 90 ka has been considered the most viable route in MIS 5, given a growing number of archaeological and paleontological discoveries. These discoveries include hominin fossils and artifacts from the well-known caves of the Mediterranean Levant and the fossil finds, human footprints, and Middle Paleolithic artifacts from the Nefud Desert dated to between ~120 and 85 ka.
- Recent studies suggest that dispersal routes were associated with well-watered corridors that facilitated hominins to move into Eurasia. Investigations in northern, central, and southern parts of Arabia showed that these areas were habitable in MIS 5, in particular for substages MIS 5e (128 to 121 ka), 5c (104 to 97 ka), 5a (82 to 77 ka), and in MIS 3 (~54 ka), owing to climatic amelioration and enhanced humidity

The exit routes

- The present study provides a systematic luminescence chronology using quartz OSL and feldspar post–infrared-infrared–stimulated luminescence (pIR-IRSL) for three paleo-water bodies in the Jordan desert: Wadi Hasa, west-central Jordan, Gregra, and Wadi Gharandal along the Jordan River Valley.
- The luminescence ages show that Late Quaternary wetland sediments occurred in Wadi Gharandal (115 to 71 ka) with Middle Paleolithic artifacts at 84 ka, Wadi Hasa (81 to 43 Ka), and Gregra (86 to 45 Ka). Presence of water could have allowed modern humans to migrate through a green corridor from Africa to Arabia and beyond. In contrast, most of the Paleolithic finds in Arabia were associated with paleolakes and wetland deposits within endorheic basins
- Dispersals out of Africa are believed to have taken place during times of substantially increased humidity and available freshwater resources



Human dispersal and divergence into and within the Americas in the Pleistocene.

Earliest Sites In Americas

White Sands footprints redated: 21 to 23 Ka

- Migrants could have arrived earlier, 13,000 to 16,000 years ago, or perhaps more than 20,000 years ago, most likely by following routes along the Pacific Coast. Still, the bulk of archaeological evidence relates to a migration after the Last Glacial Maximum, which ended around 19,000 years ago. But some genetic modeling studies suggest that humans might have populated the Americas as long as 30,000 years ago.
- The USGS team first dated the footprints by sampling ancient ditchgrass seeds (*Ruppia cirrhosa*) from the levels just above and below them. Using radiocarbon dating, the team reached the surprising conclusion that humans had walked these shores roughly 21,130 to 22,860 years ago—thousands of years before most theories based on the archaeological record suggest that humans arrived in North America.
- New dating used: 75,000 grains of pure pollen
- Calculated when quartz grains were last exposed to daylight. Three different quartz samples produced date estimates that were indistinguishable from both the carbon-14 ages of the pollen and the radiocarbon dating ages of the seeds.= 21,000 or 23,000 years old."

Jeffrey S. Pigati, et al., 2023

White Sands NM footprints: 21-23 Ka

- **Further evidence points to footprints in New Mexico being the oldest sign of humans in Americas**

- The prints are located in the Tularosa Basin, a desert area home to the world's largest stretch of gypsum sand dunes, which cover some 275 square miles. But tens of thousands of years ago, during the last Ice Age, the ecosystem was dramatically different. Then, the basin was home to prairie-like grasslands, stands of conifer trees and a large body of water known as Lake Otero.

White Sands: woman & toddler, and sloth hunting

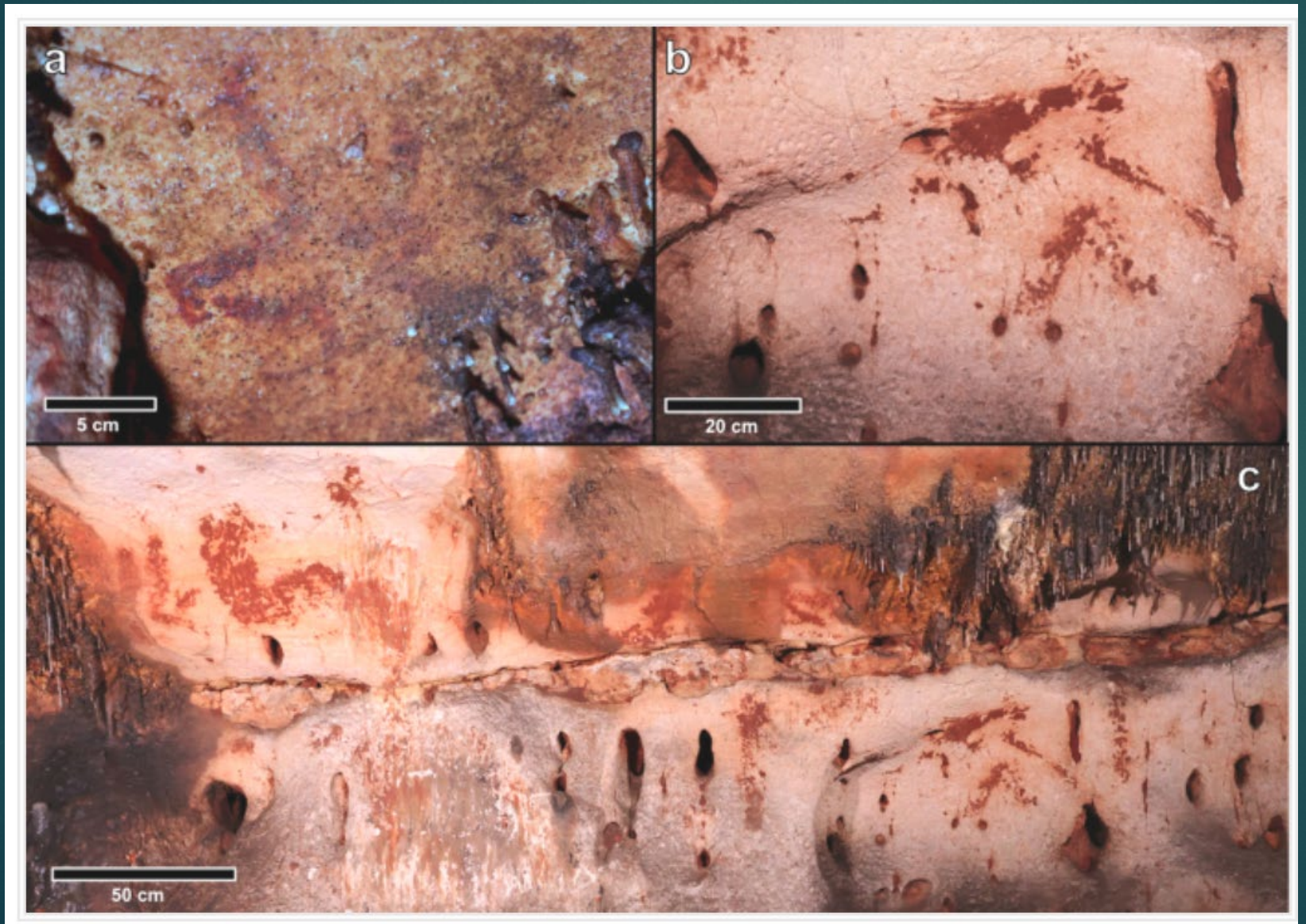
- When picking up a tired toddler on a long walk, or hunting and confronting a giant sloth, the humans walking the wetlands around a shrinking lake were simply going about their lives in prehistoric North America.
- One set of prints appears to have been made by a woman and a toddler who intermittently walked on its own and then was picked up and carried. At some places the child's little prints disappear even as the woman's prints broaden in the mud under the burden of the youngster's extra weight.
- Other tracks tell the story of a group of ancient hunters apparently stalking a giant sloth. Their prints follow the animal's prints and at times appear inside the sloth's own, as though they stepped in its tracks as they trailed it.

White Sands

Cova Dones: a major Palaeolithic cave art site in eastern Iberia

- Traditionally, the distribution of Pleistocene cave art has centered on the Franco–Cantabrian region with a ‘periphery’ including areas of southern Spain and Italy. More than 70 per cent of known Palaeolithic rock art sites are in this region; however, in recent years, there have been discoveries across Europe and discoveries outside the Franco–Cantabrian area are always relevant to enhancing knowledge of Palaeolithic symbolism.
- Along the eastern Iberian coast, cave art is rare. The Cova Dones site consists of a single-gallery cave, approximately 500m deep, that opens onto a steep canyon in the municipality of Millares . Work in 2023 allowed us to identify the site as a major Palaeolithic art sanctuary, given the quantity and variety of motifs and the richness and detail of its technical features.

With more than 110 paintings and engravings, the Palaeolithic art ensemble of Cova Dones (Valencia) has been presented, with some figures of more than 24 ka



Graphic representations in Cova Dones: (a) painted urogallo head; b) horse head made of clay; (c) panel with several motifs painted with clay, including animals and signs.

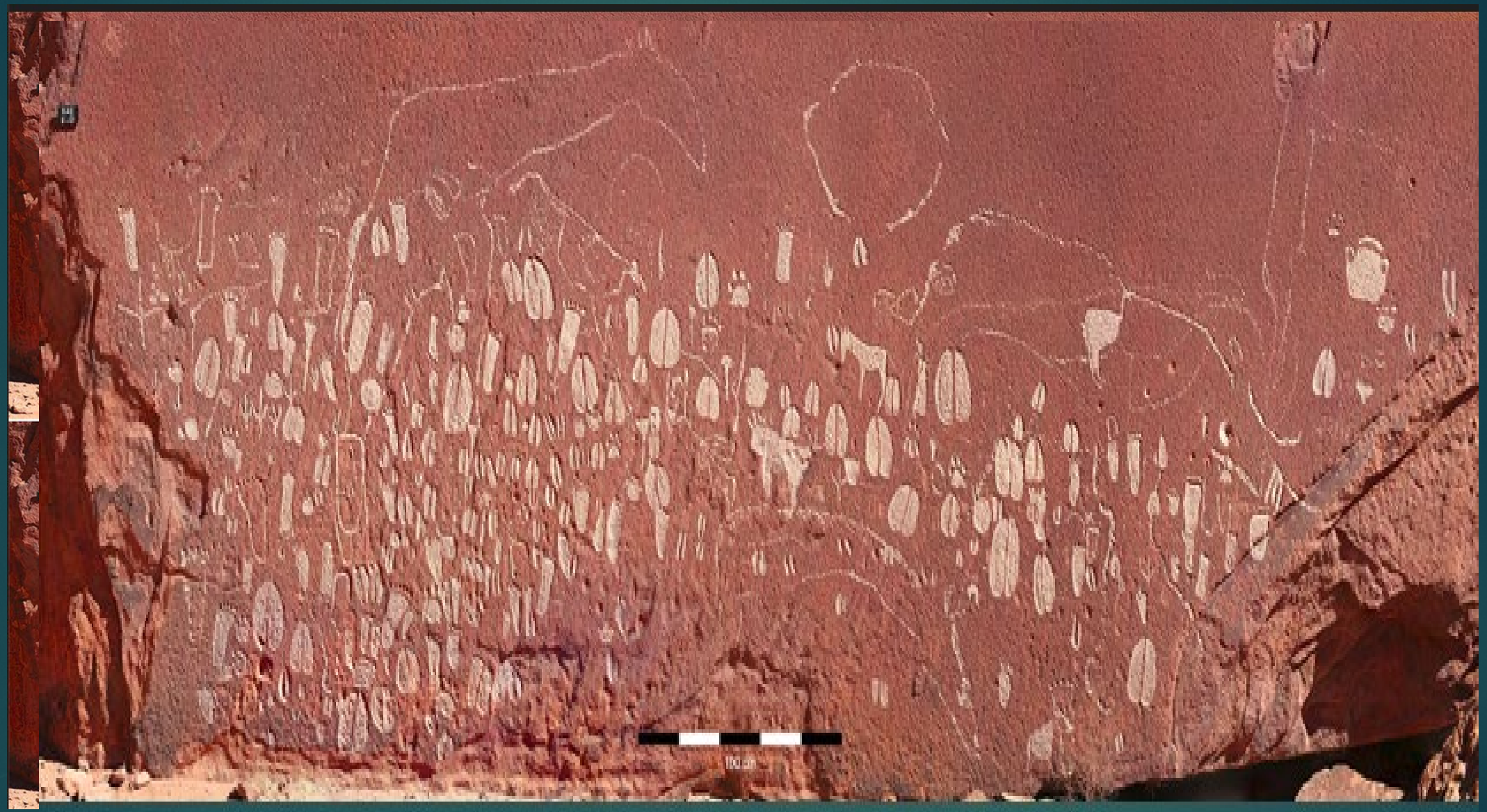
Cova Dones: 25 Ka - unique technical aspects of the rock art

- Identified more than 110 graphic units, including at least 19 zoomorphic representations, located in three different zones of the cave. Despite being deep inside the cave (the main decorated area is approximately 400m from the entrance), all zones, and the panels and figures they contain, are easily accessible without any climbing required. The depicted animals are seven horses, seven hinds (female red deer), two aurochs, a stag, and two indeterminate animals. The rest of the art consists of conventional signs (rectangles, meanders), several panels of 'macaroni' ('flutings' made with either fingers or tools dragged across a soft surface), isolated lines, and poorly preserved unidentified paintings.
- Figures shaded by scraping the *mondmilch* (a type of limestone precipitate) on the surface of the walls. In Cova Dones the entire painted corpus (>80 graphic units) is made using this technique.

Animal tracks and human footprints in prehistoric hunter-gatherer rock art of the Doro! nawas mountains (Namibia), analyzed by present-day indigenous tracking experts

- Namibia is rich in hunter-gatherer rock art from the Later Stone Age (LSA) (50-5 Ka); this is a tradition of which well-executed engravings of animal tracks in large numbers are characteristic.
- Prehistoric hunter-gatherers arguably depended for their survival on their ability to draw as much information as possible from the tracks of animals and people
- Study entailed indigenous tracking experts from the Kalahari analyzing engraved animal tracks and human footprints in a rock art region in central Western Namibia, the Doro! nawas Mountains, which is the site of recently discovered rock art.
- The experts were able to define the species, sex, age group and exact leg of the specific animal or human depicted in more than 90% of the engravings they analyzed (N = 513)
- Confirmation that indigenous knowledge has the capacity to considerably advance archaeological research.

•Tilman Lenssen-Erz, et al., 2023



Among the 513 tracks analyzed in total, the experts identified 345 quadrupeds and 62 bird tracks (407 in total from 40 different species); 20% human

In descending order of frequency, they are: giraffe, kudu, springbok, guinea fowl, white and black rhino, ostrich, oryx/gemsbok, bushpig, warthog, leopard, duiker and zebra.

Choices made

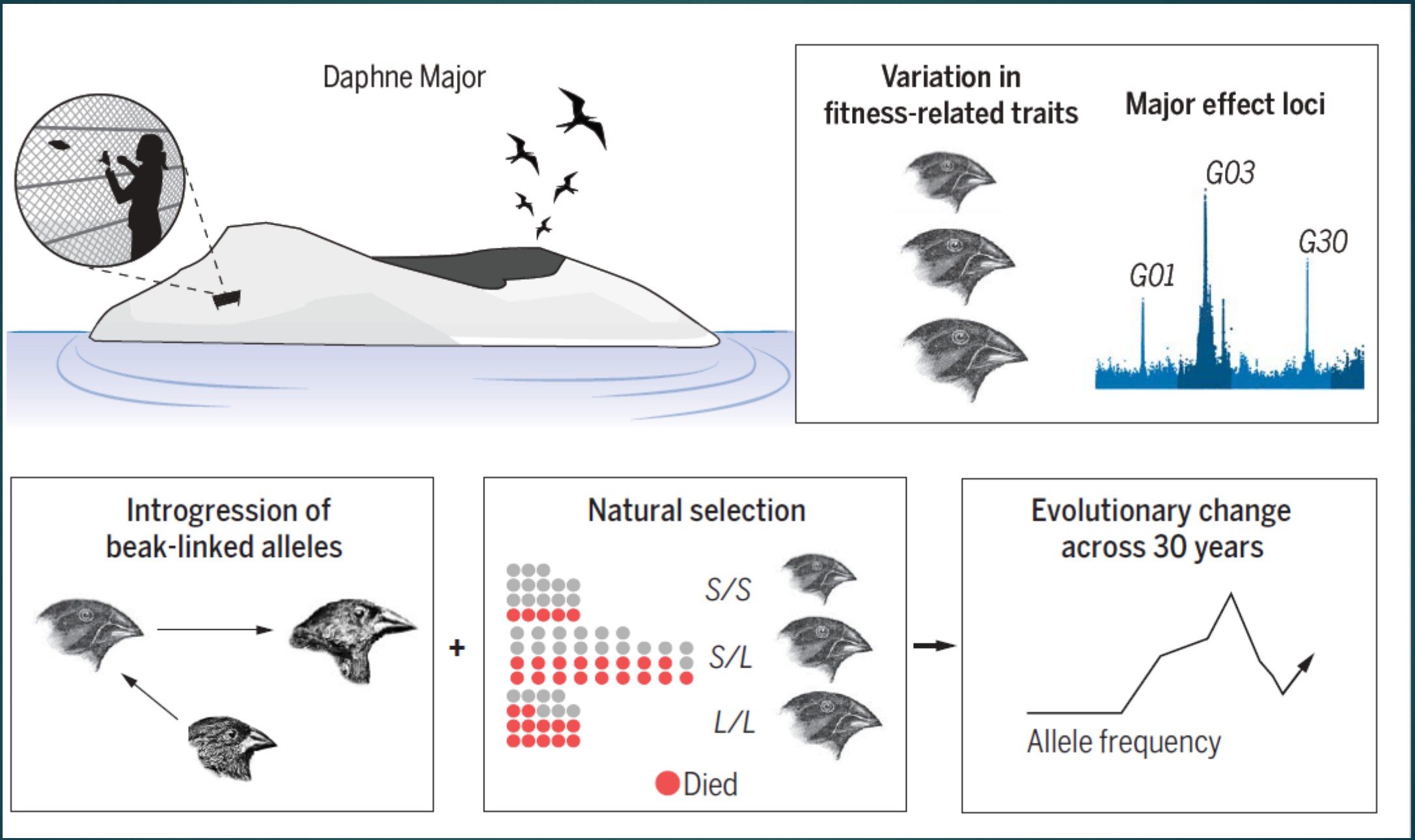
- Enables expert analysts to identify specific features such as the sex and age of the individual to whom the tracks or footprints pertain.

- Engravers made evident and deliberate choices around the types of tracks of a particular animal they would most frequently depict. These preferences confer a specific character upon each species featured, both through the preferred direction of the tracks on the rock wall and via features such as a preference for young males among species such as bushpig and duiker or for older females in, for instance, leopard and guinea fowl.

Community-wide genome sequencing reveals 30 years of Darwin's finch evolution

- The ability of an organism to respond to shifting pressures of natural selection depends on the genetic architectures of the traits underlying adaptations.
- Examining four species of Darwin's finches from the Galápagos Islands, Enbody *et al*. identified six genetic loci with large effects on beak size that explain 59% of the total heritability in one of these species.
- Connect the incidence of droughts, which result in changes in food availability, to shifts in the allele frequency of these loci, some of which are caused by hybridization between species. This study takes advantage of 30 years of study of a classic system to elucidate the role of genetic architecture and introgression in adaptation.

Erik D. Enbody, et al., 2023


Daphne Major
Variation in fitness-related traits
Major effect loci
G03
G30
G01
Introgression of beak-linked alleles
+
Natural selection
S/S
S/L
L/L
Died
Evolutionary change across 30 years
Allele frequency

Finches: study of speciation

- Adaptive radiations are groups of organisms that have diverged ecologically from a common ancestor relatively rapidly.
- Eighteen species of Darwin's finches have evolved from a common ancestor in the last million years. They diverged in beak morphology and body size, and to a small extent, in plumage. Two evolutionary processes, natural selection and introgressive hybridization, influenced the outcomes of phenotypic evolution in this adaptive radiation.
- Whole-genome resequencing data to track evolutionary change in 3955 finches of four Geospiza species. Identified six loci that together explain as much as 45% of variation in beak size of G. fortis (medium ground finch),

Prior research

- Abrupt changes in allele frequencies at these loci in G. fortis resulted from strong natural selection during an extreme drought and explained a large part of the shift in beak size.

- Introgression of smallbeak alleles from the smaller G. fuliginosa influenced the outcome of natural selection by increasing the frequency of small alleles in G. fortis.

- In the cactus-feeding finches, we observed more gradual changes in allele frequencies over the study period resulting from introgression.

Evidence for sophisticated raw material procurement strategies during the Lower Paleolithic—Hula Valley case study

- An interesting study explores the place of origin of the raw material used in two Achelense sites in the Hula Valley: Gesher Benot Yaaqov (750 ka) and Maayan Barukh (500 ka).
- Only to produce the 3500 bifaces found in Maayan Barukh, 3.5 tons of silex were needed. The study analyzed the components of 20 bifaces (10 from each site) and found that the origin of the silex of all of them came from the Dishon Plateau, suggesting that the area served as a fountain of silex for hundreds of millennia. They also ruled out as raw material the edges of the streams that flowed into the Hula valley, because they were too small.
- Those human groups, possibly of *Homo erectus*, had high cognitive and social capacities with which they developed complex strategies for the supply of raw materials, including the displacement of 20 km and the ascension of 70-800 m, as well as the transmission of knowledge from generation to generation for many millennia

Meir Finkel, et al., 2023

Humans in transition:
The occupation of Western Europe, 600 to 400 Ka

- The Acheulean is the longest-lasting technocomplex in prehistory, and its emergence from the Oldowan is one of the major transitions in human evolution.
- It is widely agreed that the innovation of Acheulean technology represents a critical stage in early human development. Its success can be measured by its persistence over more than 1.5 Myr during the Early and Middle Pleistocene (MP), over the vast geographical area of Africa and Eurasia, and the involvement in this technocomplex of at least three hominin species, *Homo erectus, Homo heidelbergensis, and Homo neanderthalensis*.
- The Acheulean was based on the use of longer, more complex operational chains involving centripetal and recurrent knapping, which was adapted to different raw materials to create long, functional edges on a versatile tool.

Paula García-Medrano, et al., 2023

'Acheulean revolution

- The 'Acheulean revolution' was the product of two main developments:
  - 1) the production of large flakes that could be used as blanks for creating large tools;
  - 2) the existence of a 'mental template,' prior to the shaping process, an innovation derived from previous technology and essential for producing a standardized tool and the hand axe.
- It has been considered the highest reflection of human cognition during the earlier Pleistocene and had the advantage of being multifunctional and transportable with tools that could be resharpened and readapted for further use.

Emergence ca 2.0 Ma

- The emergence of the Acheulean in Africa from ca. 2.0 Ma has been suggested as a behavioral response to changing ecological conditions and associated with the evolution of *H. erectus*. In addition, the technical requirements of hand axe manufacture with improved cognitive abilities may have been dependent on the increase in brain size of H. erectus. However, the first appearance of this species with a simple core and flake technology in eastern Asia over 2 Ma raises questions about the significance of a simple association of H. erectus with hand axe technology.
- Occupation with similar core and flake technologies appears to be later in Europe, with sites such as Dmanisi in Georgia at 1.7 Ma and from 1.4 Ma further west at Pirro Nord, Orce, and Atapuerca.
- The earliest hand axe assemblages beyond Africa are currently at Ubeidiya in Israel at ca. 1.4 Ma, at Attirampakkam in southern India with average cosmogenic dates of 1.5 Ma, and in China at 0.9 Ma. Once again, there appears to be a delay in the use of this technology in Europe. La Boella (northeast Spain), dated to 0.9-1 Ma, is the oldest known Acheulean site in Europe

Dating

- This may have been a one-off innovation, but it nevertheless became more widespread from 700 to 600 Ka with an increase in the number of known sites, and especially from 500 Ka, when Europe seems to have been widely occupied. The period from 1.2 to 0.9 Ma corresponds with less stable climatic changes.
- The period after 900 Ka was controlled by episodes of 100 kyr periodicity, with longer and stable climatic intervals, progressive temperature decline and increasing aridity, greater seasonality, and increasingly specialized mammal communities, especially after 500 Ka. These environmental changes affected the survival opportunities for humans in Europe.

New Analysis of the Acheulean in Europe

- One of the most significant problems for comparing hand axe assemblages from different countries has been the various archeological traditions of lithic analysis, starting with Bordes. with different ways of categorizing or organizing information, all of which have made it very difficult to compare results.

- Thus, the first outcome of this new Acheulean project was the development of a unified protocol for technological analysis, combining technology with morphometry and statistical analysis.

- Whereas in Iberia mild climate conditions prevailed, in southern France and northeastern Italy weather conditions were more severe.

Climate effects

- Rodríguez et al. (2021) in Western Europe from MIS 14 to MIS 11: Their results show that hominins tolerated cold exposure not only during the glacial stages but also during the interglacials, with winter temperatures estimated below 0 C at many localities. They propose that MP European populations were able to endure the low temperatures of those glacial stages by combining anatomical and physiological adaptations with behavioral responses, such as the use of shelter and simple fur clothes.
- By contrast, Hosfield (2022) explores the major transformation in the hominin occupation of Europe from MIS 13 to MIS 11, pointing out that climate may only be a partial factor behind the smaller-scale occupations. The increase in hominin activity during MIS 13 contrasts with the relatively severe conditions of late MIS 13 and probably reflects significant physiological and/or behavioral adaptations. Suggests that climate only partially contributed to the reduced number of sites in northcentral Europe during MIS 13-11.

700 Ka to ca. 450 Ka.

- The climatic evidence would suggest that during this period there would have been, if not a depopulation of Europe, significant shifts in population distribution and perhaps a decrease in occupational intensity, particularly during the intense cold of MIS 12.

- From MIS 12-11, the occupation of Europe shows both an increase in the archaeological evidence and a strong adaptation to localized territories, with longer periods of continuous occupation and a greater variety of technological adaptations. Menez-Dregan I is one of the few sites with a long sequence of MP occupation from MIS 12 to MIS 5.

Cultural Mosaic Model

- Propose the 'Cultural Mosaic Model.
- Their findings suggest that the Acheulean reflects a range of expressions, which is unlikely to be caused purely by raw material constraints or functional variation, but rather reflects regional populations with different material cultures.
- Suggest that these regional signatures were maintained through stable climate, but that environmental disruption through climate change caused increased population movement, but with the benefits of increased knowledge transfer and gene exchange.

Levallois tech = end of Acheulean

- The technological innovations of the Middle Paleolithic, particularly the use of Levallois technology, are the key to understanding the end of the Acheulean.

- Recent research has established that the oldest Neanderthal fossils and the first signs of their technologies and behavior appear from MIS 11 (424-374 Ka) or possibly earlier.

- Although the earliest Levallois core technology is sporadically recorded earlier than at Orgnac 3, the transition of an interglacial or glacial period (MIS 9/8) marks the first persistent and prevalent use of Levallois technology.

Humans and Neanderthals mated 250,000 years ago, much earlier than thought

- Until now, Neanderthals and anatomically modern humans (*Homo sapiens*) were believed to have first interbred earlier than 75,000 years ago, according to a 2016 genetic analysis in the journal Nature.
- However, a new analysis, published Oct. 13 in the journal Current Biology, has revealed that one group of *Homo sapiens* from Africa interbred with Neanderthals in Eurasia around 250,000 years ago.
- Compared the genome of the 122,000-year-old “Altai Neandertal” from Siberia with those of 180 people from 12 modern sub-Saharan Africa populations. They then developed a statistical tool to uncover the origins of the Neanderthal DNA in the modern human genome.

Neither genome better than the other

- The authors found that all of the studied sub-Saharan genomes contained Neanderthal DNA, which mainly came from this 250,000-year-old human-Neanderthal interbreeding event.

- Some sub-Saharan populations also had Neanderthal DNA in up to 1.5% of their genomes, which was inherited from humans who had migrated back into Africa.

- "That means that neither one [region of DNA] is particularly better than the other, they're just bad matches for the rest of the genome," Fernando Villanea, a population geneticist at the University of Colorado Boulder. "I think that was really cool, walking away from this idea of, oh, the Neanderthals are inferior in some way, to this idea that we're just two different species and we evolve for different things in our genomes," he said.

Neandertals got as much as 6% of their genomes from Africa

- mtDNA is not all that Neandertals received from our African ancestors

- A significant proportion of the Neanderthal genome consists of regions introgressed from ancient humans. While we identified 6% of the Altai Neanderthal genome (reference N genome) as introgressed.

- Thus, the Neanderthal genome was likely more influenced by introgression from ancient humans, than non-African human genomes are by Neanderthal introgression.

- Analysis suggests that the Hum→Nea gene flow occurred between 200-300 Ka.

African DNA in Ns

- Many geneticists promoted a scenario in which gene flow between Neandertals and modern humans had been a one-way arrangement. The idea was that moderns got some DNA from Neandertals, but the Neandertals never got any from modern humans.

- The early methods applied to the Vindija low-coverage genomes could not detect "modern" genetic input into the Neanderthal population unless that modern input came from the ancestors of *some* modern populations and not others.

- The data did rule out that the Vindija Neandertals had genetic input from the immediate ancestors of living Europeans. But the analyses could not test for older introgression from African-derived populations not closely related to one living population or another.

African DNA in Ns

- African peoples are still badly underrepresented in genetic datasets.
- Turns out there was deep introgression into Neandertals from their African contemporaries.
- The African origin of Neandertal mitochondrial DNA was the first major element of our emerging understanding. Mitochondrial DNA was not alone.
- Neandertals were repeatedly connected to African populations in the time after 350,000 years ago. They derive a substantial fraction of their genetic variation from such contacts with African populations.

African DNA in Ns

- Today's populations in Africa have around one third (.03-.06 %) the Neandertal ancestry as people in Eurasia (2%).

- 2020 paper from Lu Chen provided strong evidence of the importance of gene flow from Africans into Neandertals in the period after 150,000 years ago. Differentiated 2 types of N to MH DNA: Neanderthal-to-MH introgression events that occurred after the out-of-Africa expansion (60 Ka) and MH-to-Neanderthal introgression events that occurred before the out of-Africa expansion, Both contribute to the signal of Neanderthal ancestry in sub-Saharan Africans today. Their analysis of sub-Saharan African populations was restricted to populations with largely Niger-Congo-related ancestry,

- This new 2023 paper from Hubisz (Sarah A. Tishkoff's group) is pointing to gene flow in an earlier period of time, more similar to that time when the Neandertal mtDNA introgressed.

Diverse African genomes reveal selection on ancient modern human introgressions in Neanderthals

- Neanderthals inherited at least 6% of their genome from a now-extinct lineage of early modern humans
- Prior to 60 Ka, Neanderthals carried human DNA from a much older encounter with modern humans.
- An ancient lineage of modern humans migrated to Eurasia over 250,000 years ago where they interbred with Neanderthals. Over time, these humans died out, leaving a population with predominantly Neanderthal ancestry. This group of individuals left Africa between 250,000 and 270,000 years ago
- The team arrived at this conclusion by comparing a Neanderthal genome with a diverse set of genomes from modern indigenous populations in sub-Saharan Africa.

Harris, D. N, et al., 2023

Highlights of study

- Anatomically modern human-to-Neanderthal introgression occurred 250,000 years ago (261,075 years ago (95% CI = 239,325–284,331 years ago))
- 6% of the Altai Neanderthal genome was inherited from anatomically modern humans
- Recent non-African admixture brought Neanderthal ancestry to some African groups
- Modern human alleles were deleterious to Neanderthals

2020 Chen study used genomes that shared a relatively recent common ancestry in Central and Western Africa

- Most Neanderthal-human interbreeding is thought to have occurred in Eurasia, not in Africa, Neanderthal ancestry was expected to be limited in sub-Saharan Africa; however, a recent study showed that around 0.6% of the genomes of these African populations had come from Neandertal ancestors.

- The study was unable to determine how this Neanderthal-like DNA entered these populations, whether it originated from modern humans who had migrated from Africa, interbred with Neanderthals in Eurasia, and then returned, or whether it was the result of an earlier encounter between Neanderthals and humans.

Prior studies

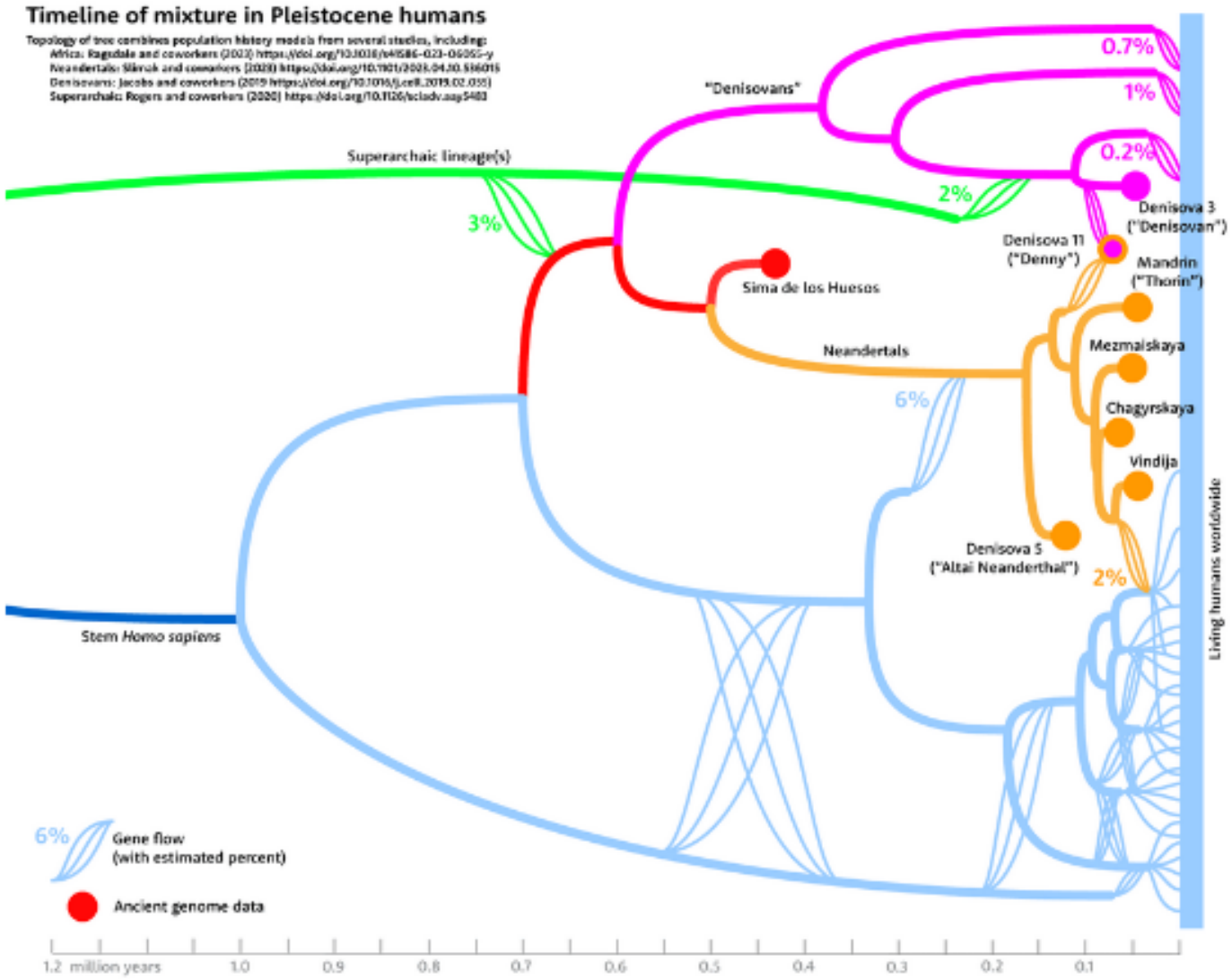
- Because the study relied on a limited number of genomes from the 1,000 Genomes Project, all of which share a relatively recent common ancestry in Central and Western Africa, it was also unclear whether Neanderthal-like DNA is widespread among sub-Saharan populations.

- Prior studies: MH DNA in Ns prior to OofA migration
- The total replacement of early Neandertal mitochondrial X (between 268 and 413 kya) and Y chromosome variation with new variants that originated in Africa.
- Comparisons of Neanderthal and AMH nuclear genomes suggested that the Altai Neanderthal, which lived 122 kya,11 has 3% AMH ancestry from interbreeding between AMHs and Ns that occurred between 200 & 300 Ka

Six percent of Neandertal ancestry was African

- In 2020, Melissa Hubisz and coworkers from Joshua Akey's research group quantified the early genetic input from Africans into Neandertals. They could show that around 3% of the Neandertal genome looked like segments from an African source and they estimated that their method could only detect around half of the ancient introgression, leading to an overall estimate around 6%.

- In their new study, Harris and coworkers were able to leverage the greater representation of present-day African variation to make a more precise estimate of ancestral African-to-Neandertal gene flow. Their estimate of 6% confirms that Hubisz and collaborators had the answer close to correct.



A network depicting the current picture of mixture among Neandertal, Denisovan, and African ancestral humans. This network focuses on ancient genomes and does not represent details of population mixture within humans of the last 50,000 years.

Denisovans

Neandertals

African sapiens

African sapiens Introgressions at ~250 Ka

- Both approaches agree that this African-to-Neandertal gene flow was underway in the time period around 250,000 years ago. This time range is also suggested by the ancient DNA data on mtDNA from early Neandertals. The data do not show whether the introgression from Africans happened in a rapid burst or many contacts over a prolonged time.
- One thing is for certain: This gene flow from an African source population shaped the evolution of Neandertals. The time period between 300,000 and 200,000 years ago was around halfway between their initial diversification from Denisovan ancestors and their last meeting with African groups. Every Neandertal sampled after this time had a mitochondrial genome derived from Africa; every individual with a Y chromosome was likewise part of an African clade. From central Asia to Iberia, the African genes spread everywhere.
- Evidence that some of the African-to-Neandertal gene flow was deleterious.

Where did N DNA come from

- To better understand how widespread these Neanderthal-like DNA regions are across sub-Saharan Africa and to elucidate their origins, Tishkoff's team leveraged a genetically diverse set of genomes of 180 individuals from 12 different populations in Cameroon, Botswana, Tanzania, and Ethiopia. For each genome, the researchers identified regions of Neanderthal-like DNA and looked for evidence of Neanderthal ancestry.
- Then, they compared the modern human genomes to a genome belonging to the Altai Neanderthal who lived approximately 120,000 years ago. For this comparison, the team developed a novel statistical method that allowed them to determine the origins of the Neanderthal-like DNA in these modern sub-Saharan populations, whether they were regions that Neanderthals inherited from modern humans or regions that modern humans inherited from Neanderthals and then brought back to Africa.

Introgression process

- First, an early migration of AMHs out of Africa led to an AMH to-Neanderthal introgression event 250 kya, creating homologous regions present in extant human populations. These introgressions were depleted from many parts of the Neanderthal genome by selection against hybrid individuals, likely through a process of incipient speciation. This left the Altai Neanderthal with 6% AMH ancestry, though earlier ancestors of the Altai Neanderthal would have had a larger proportion of AMH ancestry.
- Second, a Neanderthal-to-AMH introgression event 40 to 54 Ka introduced Neanderthal haplotypes into non-African AMH populations. Within the Neanderthal genome, MH DNA was depleted from the same regions of the AMH genome due to similar deleterious gene interactions.

Introgression

- Third, at least two subsequent recent migrations of nonsub-Saharan African AMHs into sub-Saharan Africa brought introgressed Neanderthal haplotypes to sub-Saharan African AMH populations with whom they admixed.
- They did not find any evidence that Neanderthal-derived haplotypes or Neanderthal ancestry is widely spread throughout sub-Saharan Africa as has previously been raised as a possibility
- Neanderthal homologous regions are identified in all sub-Saharan African populations: Found that all of the sub-Saharan populations contained Neanderthal-like DNA, indicating that this phenomenon is widespread.

N DNA in African populations

- In most cases, this Neanderthal-like DNA originated from an ancient lineage of African sapiens that passed their DNA on to Neanderthals when they migrated from Africa to Eurasia around 250,000 years ago. As a result of this modern human-Neanderthal interbreeding, approximately 6% (5.56%–6.83%) of the Neanderthal genome was inherited from modern humans.
- Neanderthal haplotypes in sub-Saharan Africans have multiple non-sub-Saharan sources
- In some specific sub-Saharan populations, the researchers also found evidence of Neanderthal ancestry that was introduced to these populations when humans bearing Neanderthal genes migrated back into Africa. Neanderthal ancestry in these sub-Saharan populations ranged from 0 to 1.5%, and the highest levels were observed in the Amhara from Ethiopia and Fulani from Cameroon.

MH DNA in N was deleterious & vice versa

- They found that most of the modern human DNA was in noncoding regions of the Neanderthal genome, indicating that MH gene variants were being preferentially lost from coding sections of the N genome, which suggests that having modern human genes in a Neanderthal background is detrimental to fitness.

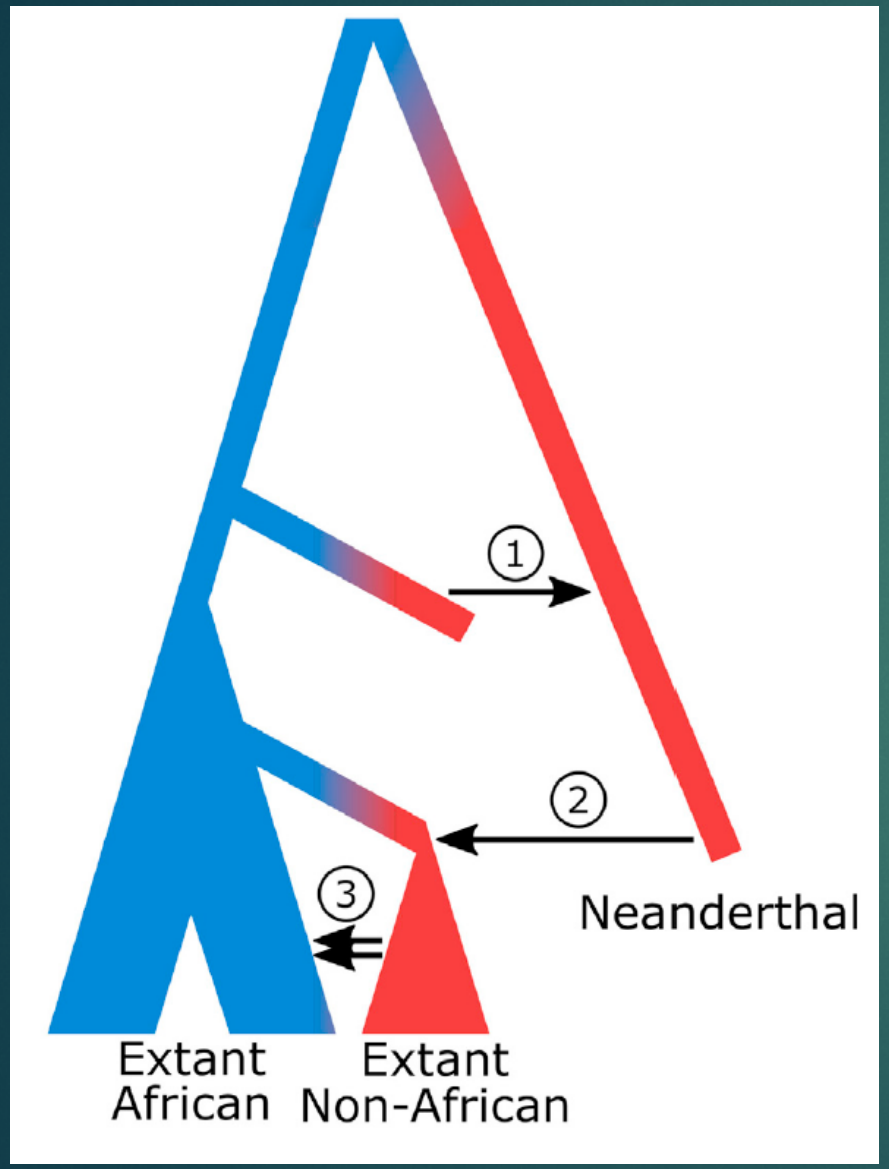
- These results are consistent with a model of speciation beginning through the accumulation of epistatic (deleterious) effects that disfavor heterospecific allele combinations and are not consistent with the hypothesis that archaic deserts found in modern human populations are caused by direct selection against universally deleterious Neanderthal alleles.

Incipient speciation

- Suggests that natural selection against hybrid individuals may have been broadly based and actively removed MH ancestry from many functional regions of the Neanderthal genome.

- This is similar to what is seen in modern humans, where natural selection has slowly been removing Neanderthal genes from modern human populations. So a Neanderthal allele might work great in Neanderthals, but you plop it into a modern human genome and it causes problems. Both modern humans and Neanderthals slowly rid themselves of the alleles of the other group

- In the almost 500,000 years between the ancestors of Neanderthals splitting off from the ancestors of modern humans and these other modern humans being reintroduced to Neanderthal populations, we had become such different organisms that, although we were still able to interbreed quite readily, the hybrids didn't work so well, which means we were very far along the path to becoming distinct species.



Three evolutionary N-MH events:
Portions in blue represent lineages located within Africa and portions in red represent lineages outside of Africa.
(1) Early migrations of AMHs from Africa that introgressed into Neanderthals - generated 6% AMH introgressed regions in Neanderthals.

(2) Following the out-of-Africa expansion, Neanderthals introgressed into non-Africans, which generated 2% Neanderthal introgressed regions in all extant non-Africans.

(3) Recent migrations from multiple non-African populations back into Africa introduced N DNA into some extant sub-Saharan African populations.

Abstract

- Comparisons of Neanderthal genomes to anatomically modern human (AMH) genomes show a history of Neanderthal-to-AMH introgression stemming from interbreeding after the migration of AMHs from Africa to Eurasia. All non-sub-Saharan African AMHs have genomic regions genetically similar to Neanderthals that descend from this introgression.

- Regions of the genome with Neanderthal similarities have also been identified in sub-Saharan African populations, but their origins have been unclear.

Abstract 2

- Analyzed a dataset of high-coverage, whole-genome sequences from 180 individuals from 12 diverse sub-Saharan African populations.

- In sub-Saharan African populations with non-sub-Saharan African ancestry, as much as 1% of their genomes can be attributed to Neanderthal sequence introduced by recent migration, and subsequent admixture, of AMH populations originating from the Levant and North Africa.

6% MH DNA in Ns from 250 Ka

- However, most Neanderthal homologous regions in sub-Saharan African populations originate from migration of AMH populations from Africa to Eurasia ~250 kya, and subsequent admixture with Neanderthals, resulting in ~6% AMH ancestry in Neanderthals.
- These results indicate that there have been multiple migration events of AMHs out of Africa and that Neanderthal and AMH gene flow has been bi-directional.
- Observing that genomic regions where AMHs show a depletion of Neanderthal introgression are also regions where Neanderthal genomes show a depletion of AMH introgression points to deleterious interactions between introgressed variants and background genomes in both groups—a hallmark of incipient speciation.

What introgression deserts are

▶ An introgression desert is a region of a chromosome that has an unusually low fraction of Neandertal or Denisovan derived sequence variants in a sample of living MHs, when compared to the average across the entire genome. The genetic ancestry that any living person has from these source populations is slight—around 2% for Neandertal ancestry—and this means that any one person's genome may include many regions of a million base pairs or more where this ancestry is absent. When we line up many people's genomes, these regions tend to be a random scatter. But not entirely. Looking at thousands of people, there are some parts of chromosomes where almost nobody has any Neandertal ancestry. These areas are the introgression deserts.

▶ The most studied cases are on the X chromosome. The X has much less introgression than the autosomes and some extended regions of the X seem to have little or no Neandertal ancestry at all.

John Hawks, 2023

Introgression deserts

- It's not yet entirely clear how much these Neandertal introgression deserts are also Denisovan introgression deserts.
- Across Icelandic genomes, there is some overlap in chromosome regions that underrepresent Denisova-like ancestry and Neandertal ancestry. This overlap provides some basis for thinking that introgression from both ancient groups might follow similar dynamics in later populations
- Geneticists have proposed several ideas about the introgression deserts.
  - The first idea, soon after the X chromosome Neandertal ancestry deficit was first identified, was that Neandertals and modern individuals may have faced incompatibilities when they mated. In this scenario, certain gene variants from Neandertals would have very low fertility in hybrid individuals, possibly even causing sterility in one sex. The phenomenon of hybrid incompatibility has been observed in many sister species of mammals.

Genetic Load theory

- Two more current hypotheses involve more subtle aspects of natural selection on introgressed genes, operating over more generations.

- One is **genetic load**, a phenomenon in which a population becomes more and more saddled with slightly deleterious genetic variants. Neandertal population structure = small local populations with high inbreeding . With smaller population numbers, natural selection would have been less effective against slightly deleterious genetic variation in the Neandertal population. Over thousands of generations, the Neandertals may have accumulated thousands of slightly deleterious gene variants. The early modern people who inherited these slightly deleterious variants belonged to a growing population, in which purifying selection became more effective.

- Children with the slightly deleterious Neandertal variants would have been a little less likely to survive and have children of their own. Over hundreds of generations, parts of the genome with the most deleterious variants ended up with much less Neandertal ancestry, some with none at all = deserts.

Genetic load not just in Ns

- Still, genetic load would not have been unique to Neandertals. The ancestral African population may have been a bit larger than the overall Neandertal population, but it also was organized into regional groups with relatively high inbreeding compared to recent times.

- The founder population that left Africa and encountered Neandertals was especially small and constrained in variation. In some parts of the genome, we might expect to see Neandertal genes actually *increase* in the subsequent population because of the founder population's genetic load.

Epistasis theory

- The alternative hypothesis is **genetic epistasis**. No gene works in isolation, all genes must work in a context determined by many other genes across the entire genome. If a gene is taken out of one population and placed into another, it may interact in unexpected ways with its new genetic background. Introgressed genes from a population that first separated more than 20,000 generations in the past might sometimes have deleterious effects, resulting in their loss over time.

- The two hypotheses are not mutually exclusive.
  - Some introgressed segments might be slightly deleterious in modern populations because they were already slightly deleterious in Neandertals—that's the genetic load hypothesis.
  - Others might be slightly deleterious in modern populations because they don't work the same as they did in Neandertals—that's the epistasis hypothesis.

Harris study = evidence for epistasis

- One way to test the difference is to look at gene flow in the opposite direction: What happened to genes that originated in African populations and introgressed into Neandertals?

- New Harris study did exactly that. They considered areas of chromosomes where Neandertal introgression is low or absent in today's people, and they looked at the same regions in Neandertals.

- What they found is that the 6% African-to-Neandertal introgression is reduced by around half in these introgression deserts. They interpret this observation as evidence of epistasis. Neandertal genes in these regions do not work as well in today's genetic background; early African genes in the same regions did not work as well in the Neandertal genetic background.

J. Hawks comment

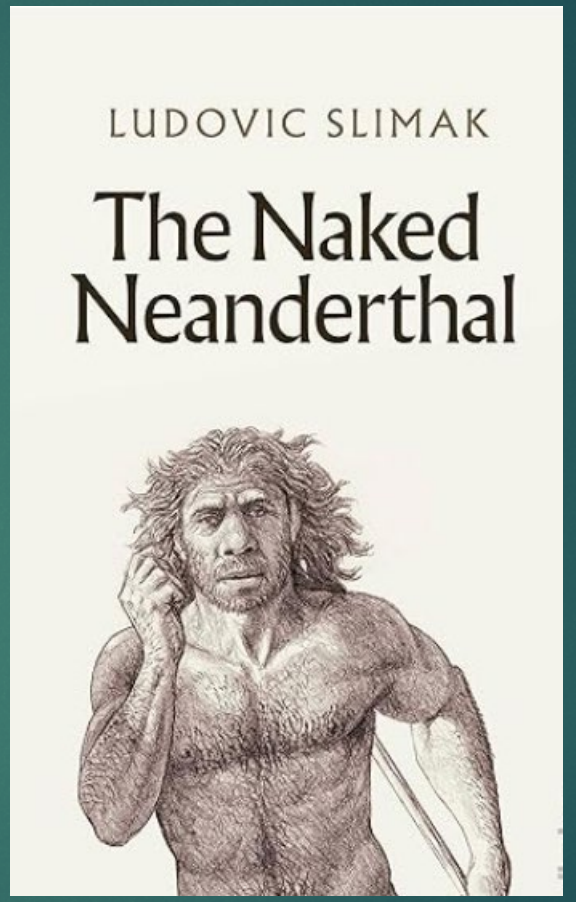
- On the other hand, the African source population for this ancient introgression was also likely to have been small in numbers. To Hawks this suggests that genetic load may have mattered reciprocally in both ancient populations.

- The fact that the same regions seem to have had more slightly deleterious introgressed variants in both directions may tell us more about the strength of purifying selection in these regions, rather than the mechanism by which variants became deleterious.

Ludovic Slimak
3 Studies
2023

The Naked Neanderthal by Ludovic Slimak, 2022

- Ludovic Slimak has been a paleoanthropologist for 30 years at the University of Toulouse in France and director of the Grotte Mandrin research project.
- His work focuses on the last Neanderthal societies, and he is the author of several hundred scientific studies on these populations.
- He has excavated at Mandrin Grotto since 1998.



Third Time's the Charm --Sapiens From the Levant Made Three Attempts to Settle in Europe: a review

- Humans from the Levant migrated to Europe in three waves starting 54,000 years ago, but it took more than 10,000 years to conquer the continent

- Thrice Homo sapiens from the Levant migrated to Europe. Twice they were forced back – either due to lack of numbers, inability to adapt to the region's Ice Age climate or resistance from the indigenous Neanderthals. Only on their third attempt, some 42,000 years ago, did sapiens succeed in establishing a permanent presence in Europe, finally wresting the continent from the Neanderthals.

- That's the conclusion of a new study that compared flint tools found in a cave in Lebanon with artifacts unearthed across Europe to identify three distinct waves of sapiens migrations starting more than 54,000 years ago.

A. David, 2023

Related to prior study of Mandrin, France, humans at 54 Ka

- Analysis based on lithic similarities: There are striking parallels between the tools belonging to three distinct Upper Paleolithic phases found at Ksar Akil, a prehistoric rock shelter just north of Beirut, and their contemporary equivalents in Europe
- The earliest anatomically modern human remains outside the continent have been found in Israel's Manot Cave and date to 55,000 years ago.
- Most scholars believed the earliest appearance of modern humans in Europe happened at least 10,000 years later, as evidenced by sapiens sites in Bulgaria and southern Italy that date to around 45,000 years ago.
- And then there is the headscratcher of how and why humans, having just expanded into the Near East, suddenly appeared in the Rhone Valley of southern France 54,000 years ago without leaving any traces between the two regions (a problem for this theory).

Ksar Akil, Lebanon, lithics

- The puzzle is compounded by two problems: 50,000 years is roughly the upper limit for using radiocarbon dating, so employing this method to date early Upper Paleolithic sites doesn't always produce precise results.

- Also, sapiens and Neanderthals often made the same tools and since human remains are relatively rare it can be difficult to assign a site to one species or the other based only on artifacts.

- The choice of Ksar Akil in Lebanon as a comparison point was made because the site tells the story of human habitation of the Levant through dozens of archaeological layers starting with the Middle Paleolithic occupation associated with Neanderthals and on into the arrival and subsequent development of sapiens stone tool cultures in the Upper Paleolithic (accompanied by a few human remains).

Ksar Akil, Lebanon

- “What we see at Ksar Akil and throughout the eastern Mediterranean in the Upper Paleolithic is something that is very continuous, very likely the same society and the same population gradually evolving throughout the millennia,” L. Slimak explains.

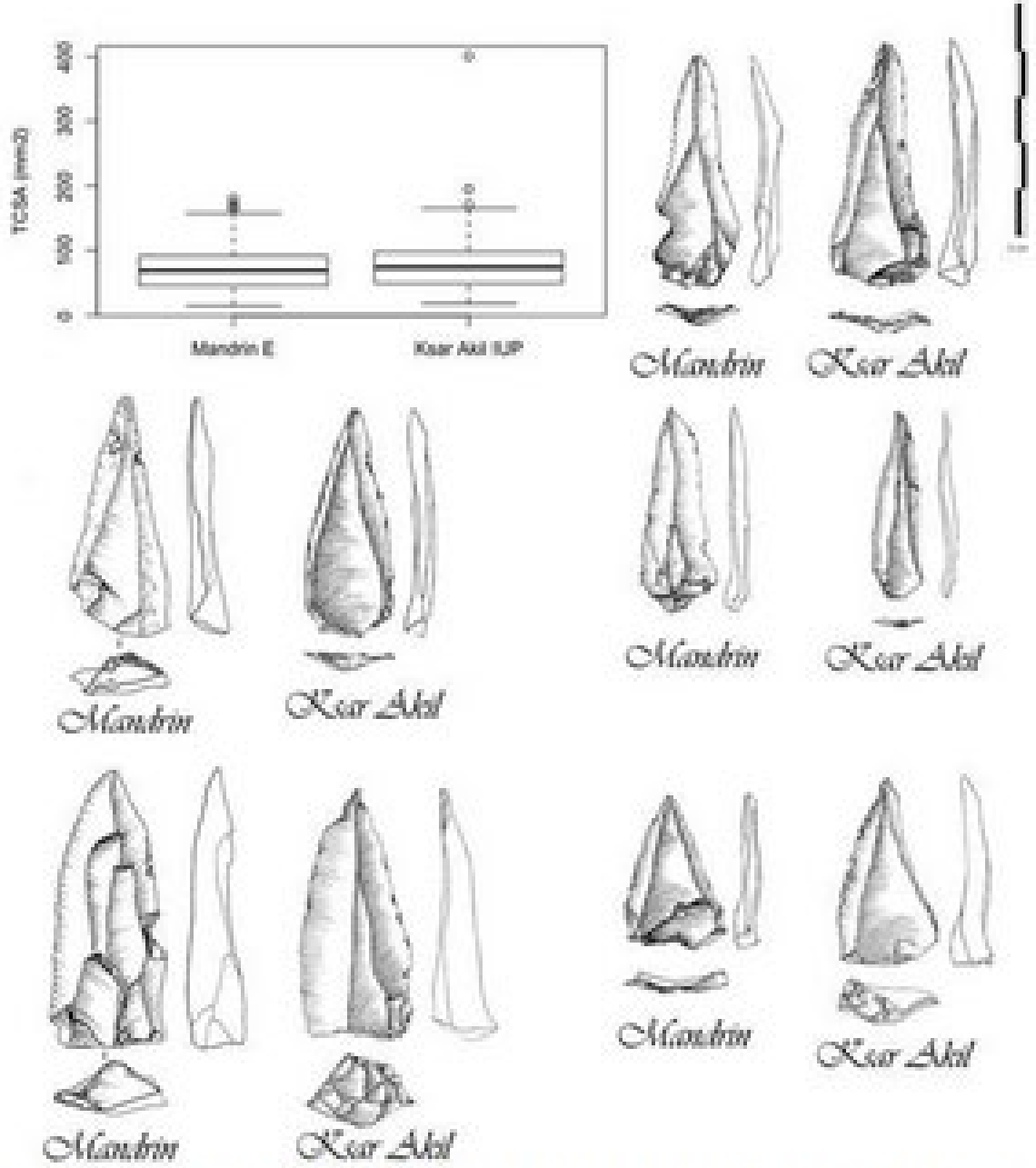
- His analysis starts with artifacts belonging to the Initial Upper Paleolithic, a technological complex that is believed to mark the arrival of sapiens from Africa in the Levant and is characterized by the use of light, very standardized points that could be mounted on javelins or arrows.

Same lithic types at both Ksar Akil and Mandrin Cave

- These artifacts are found at Ksar Akil, although they are dated to only around 46,000 years ago, and even earlier at sites like Boker Tachtit, in Israel's Negev desert, at around 50,000 years ago.

- These weapons are thought to have given sapiens a competitive edge over the heavier spearpoints of the Neanderthals, allowing our ancestors to hunt prey at a greater range.

- And lo and behold, those same projectiles are associated with the brief occupation by sapiens of Mandrin Cave 54,000 years ago, and are also found in a few sites in eastern Europe.



Comparison of flint points found at Grotte Mandrin (Mediterranean France) and Kaar Akil (Lebanon), separated by 3000km. Credit: Drawings and measurements of points: Laure Metz

Time discrepancy

- Because they haven't been compared carefully and are located in such distant regions, researchers call these stone tool cultures by different names: Initial Upper Paleolithic in the Levant, Neronian in France, Bohunician in eastern Europe – but they are all the same thing, and represent the first wave of sapiens colonization in Europe, according to Slimak.

- Issue?: By the way, the fact that the human occupation of Mandrin (54,000 years ago) is dated a bit earlier than the first IUP tools in Israel (50,000 years ago) doesn't detract from the narrative that the first sapiens came to Europe from the Levant. He puts the discrepancy down to the difficulties of using radiocarbon dating for this period.

By boat?

- One possibility is that we simply haven't discovered intermediate sites, which were likely located along the coast and may have been covered by the rise of sea levels since the end of the Ice Age.

- Another hypothesis, which Slimak favors to explain the colony in the Rhone Valley, is that sapiens had already mastered the ability to navigate the seas and reached the coast of France by boat.

- This is not as far-fetched as it may sound, as there is little doubt that humans, tens of thousands of years ago, must have reached Australia by some form of vessel since that landmass was never connected to Eurasia by any land bridge. In the Mediterranean, there is evidence that even pre-sapiens hominins, like Homo erectus, may have reached the Aegean Islands presumably by raft already half a million years ago.

3 attempts to reach Europe:

Slimak reports on evidence of strikingly similar tools in France and the Mediterranean in three distinct periods, attesting to three distinct waves of early sapiens migrations from the Levant to Europe: The image shows the technical traditions of each of the three migrations:

1) 54,000 years ago
2) 45,000 years ago
3) 42,000 years ago

Ksar Akil phase II. Early Upper Paleolithic II - Southern Early Ahmarian/Protoaurignacian.
1-8: Williams et Bergman 2010. Layers XI and Xc. 9-11: Bergman 1988. Layers XIII-XI.
Rectilinear bladelets from unipolar convergent flakings retouched by ahern or pointing retouches.

First Wave: Seeking N brides

- The first wave of sapiens colonization in Europe was short-lived – in Mandrin it lasted just around 40 years. They likely reproduced there (one tooth of a sapiens child was found in the cave) but may have had insufficient numbers to hold on in the long term.

- “My guess would be the two populations were so divergent that the fertility was very partial, and in the first two waves the attempt to build social networks with the locals didn’t work out,” Slimak says.

2nd wave: controversial

- The second wave of migration that the archaeologist identifies occurred around 45,000 years ago.

- This wave is marked by an evolution of the IUP which produced two-sided knapped points found at Ksar Akil, at the sapiens site of Bacho Kiro Cave in Bulgaria as well as at sites in southwestern France and northern Spain.

- This part of his narrative may be the most controversial among researchers. The sites in Spain and France he refers to contain few human remains and the Chatelperronian lithic industry

2nd wave failed

- Many researchers believe that the Chatelperronian was a Neanderthal industry, possibly influenced by sapiens technology.

- This of course clashes with Slimak's analysis that sees parallels between this western European stone tool culture and the artifacts at Ksar Akil.

- Be that as it may, this second wave of sapiens colonization also failed to establish a permanent presence in Europe.

The final third wave

- It was only around 42,000 years ago that a third wave of sapiens from the Levant managed to colonize the entire continent, roughly at the same time when the final decline and extinction of the Neanderthals occurred. This wave would birth Europe's earliest human culture, the Aurignacian.

- Again Slimak identifies parallels between stone tools at Ksar Akil and sapiens artifacts found in Europe: long, thin blades that are the hallmark of the Aurignacians.

- The third wave was much larger than the previous ones and sapiens ultimately overwhelmed the Neanderthals.

Critiques: no intermediate lithic sites

- Other researchers are even more cautious about the existence of the two early migration waves identified by Slimak:

- "Although the similarities between stone tools are clear, it is always difficult to draw direct parallels and suggest migrations on the basis of lithic data alone – especially given the absence of similar sites between the Levant and western Europe," says Yossi Zaidner.

- Ultimately, it seems everyone agrees that the narrative of humanity's dispersal through Europe is much more complicated than just that of a single arrival and a rapid expansion 42,000 years ago.

- "The early arrival in Mandrin is probably just the tip of the iceberg," Slimak concludes

2022 study: Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France

- Hominin fossil from Grotte Mandrin in France reveals the earliest known presence of modern humans in Europe was between 56,800 and 51,700 years ago.
- This early modern human incursion in the Rhône Valley is associated with technologies unknown in any industry of that age outside Africa or the Levant.
- Mandrin documents the first alternating occupation of Neanderthals and modern humans, with a modern human fossil and associated Neronian lithic industry found stratigraphically between layers containing Neanderthal remains associated with Mousterian industries.
- We document at least four alternating phases of replacement of Ns & MHs.

Ludovic Slimak, et al., 2022

Mandrin, France: 4 phases

- Around Mandrin from MIS 5 up to ~54 ka (Mandrin layers J to F):
  - a modern human incursion at around 54 ka (56.8 to 51.7 ka; Mandrin E)
  - followed by Neanderthal reoccupations (Mandrin D-C2-C1-B3-B2),
  - a second modern human phase from ~44.1 ka to 41.5 ka (Mandrin B1) onward.
  - This succession also represents the first known archeological evidence in Europe for the interstratification of a modern human occupation between those of Neanderthals (Mandrin E versus Mandrin F and Mandrin D).

Mandrin: rapid replacement

- No tech exchange over time: no obvious processes of cultural exchange in terms of technical traditions either between the different Neanderthal groups or between modern human and Neanderthal populations, a situation congruent with a scenario of rapid replacement processes with no major interactions.

- Both populations replaced each other rapidly or even abruptly, at least twice, in the same territory.

Jaw of horse with arrowhead of modern human in 54,000-year-old modern human layer Credit: Ludovic Slimak

Arrowheads found at the grotto from the earliest modern human layer compared with 1 euro penny (top) and with a bigger point (bottom) Credit: Laure Metz and Ludovic Slimak

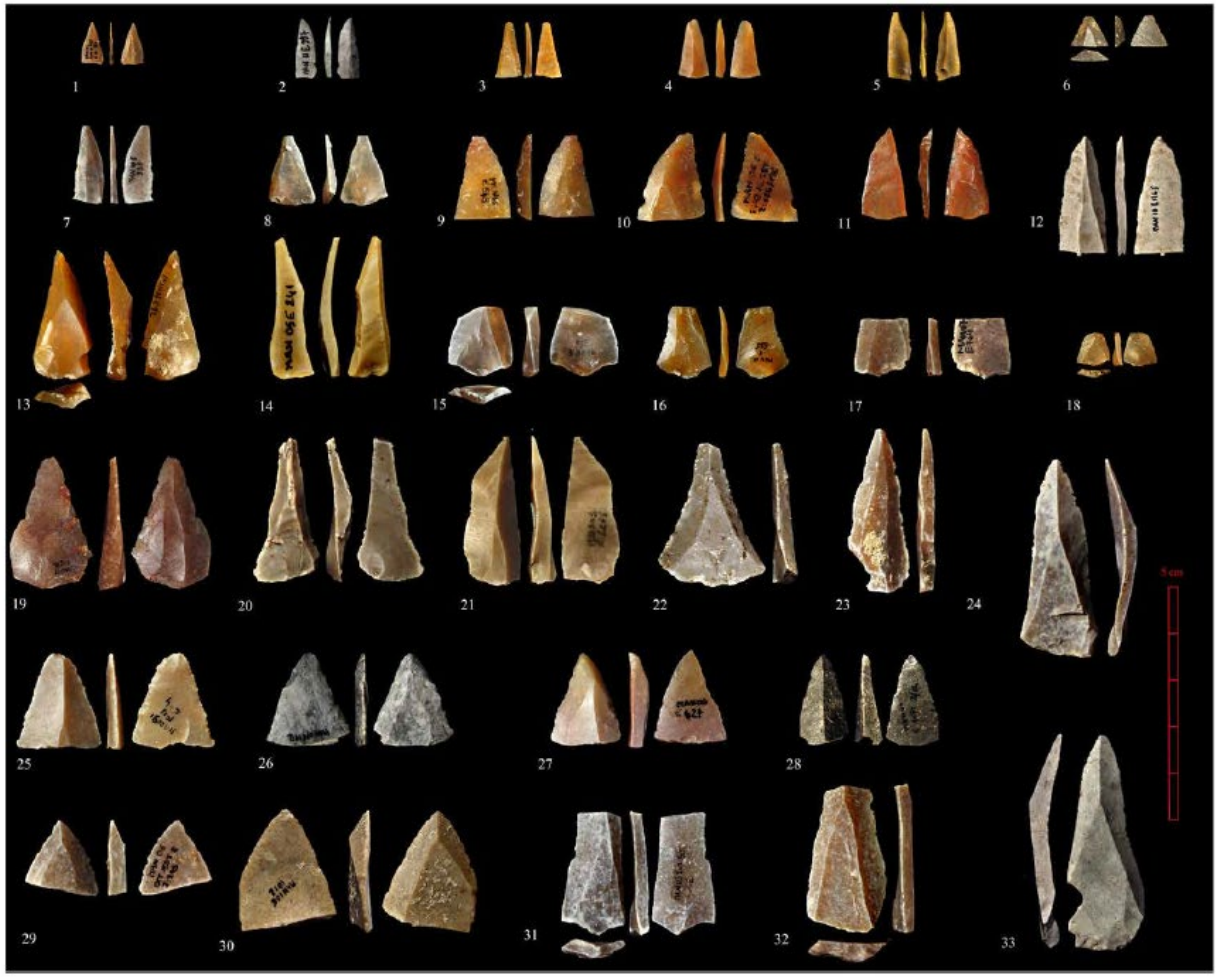


Fig. 2. Neronian points from Mandrin layer E. Micro- and nanopoints (numbers 1 to 23), pointed micropoint (number 10), and points (numbers 24 to 33).

These points represent a substantial technological difference from all of the Mousterian industries in the Mandrin sequence.

Named the “Neronian” [after the Grotte de Néron site].

Until now, the Neronian industry had not been documented anywhere as early as at Mandrin, and its makers had not been identified.

Single evidence for MH origin of arrow points:
1 molar = MH

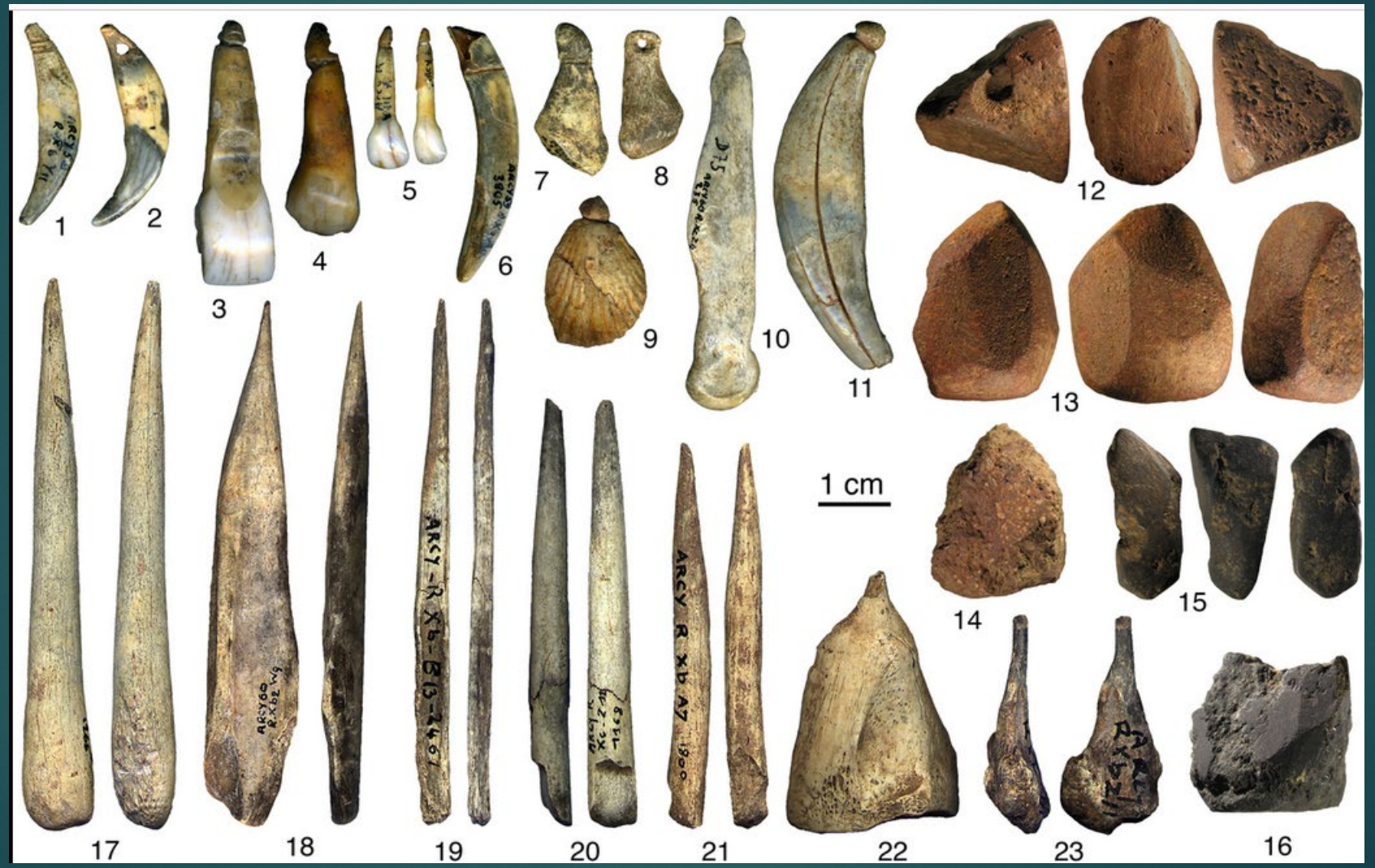
MH layer Mandrin E: arrow points and 1 MH tooth

- Layer E tooth: a deciduous maxillary second molar crown; The single tooth Man12 E 1300 specimen from layer E is unequivocally classified as an Upper Pleistocene modern human; based on morphological analysis, not aDNA.

- Teeth from layers F, D, and C are classified as Neanderthals

- Note: Ancient DNA analyses were initially carried out on fossil horse teeth excavated from throughout the stratigraphic sequence to assess the level of DNA preservation, and whether destructive attempts to recover DNA from the hominin remains to identify the population affiliation of these individuals would be warranted. However, the overall poor preservation signal from the horse material cautioned against sampling hominin remains at this time.

Châtelperronian tools and jewelry: ultimately proved to be N?



MH layer Mandrin E: arrow points and 1 tooth

- CJV: a note of caution – this study's conclusions based on 3 assumptions:
  - A single molar is concluded to be MH based on PCI morphological analysis
  - Arrowheads are assumed to be MH because they are different from N Mousterian tools above and below layer E
  - No known history of Ns making arrowheads
- They opted not to do aDNA testing of the "MH" molar in layer E because tested equid teeth from other layers were too fragile
- No sediment DNA done
- CJV: what if molar is not MH; or that there was a gifted N who created these tools just as Ns may have created Châtelperronian material

2023: Europe's first humans hunted with bows and arrows

- New 2023 study: A cave site in France holds hundreds of tiny stone points, alongside remains thought to belong to *Homo sapiens*.
- A 54,000-year-old cave site in southern France holds hundreds of tiny stone points, which researchers say closely resemble other known arrowheads — replicas that they tested on dead goats.
- The discovery suggests that the first *Homo sapiens* to reach Europe hunted with bows and arrows.
- But it also raises the question of why Neanderthals — which occupied the Grotte Mandrin rock shelter in the Rhône Valley before and after *Homo sapiens* — never adopted these superior weapons.

L. Metz, et al., 2023

Mandrin

- In 2022, researchers excavating Grotte Mandrin claimed that the site held the earliest known evidence of *Homo sapiens* in Europe
- Among the tools were hundreds of tiny points, many of which were as small as 1 centimeter wide, weighed only a few grams and were nearly identical in shape and size. Some contained similar fractures and other damage at their tips, which could have been created by high-velocity impact.
- The researchers made dozens of replica points from flint found near the rock shelter, and fashioned them into bows and arrows using wood and other materials. They also made thrusting spears and spear-thrower darts. They used the weapons to stab or shoot at dead goats.

Mandrin

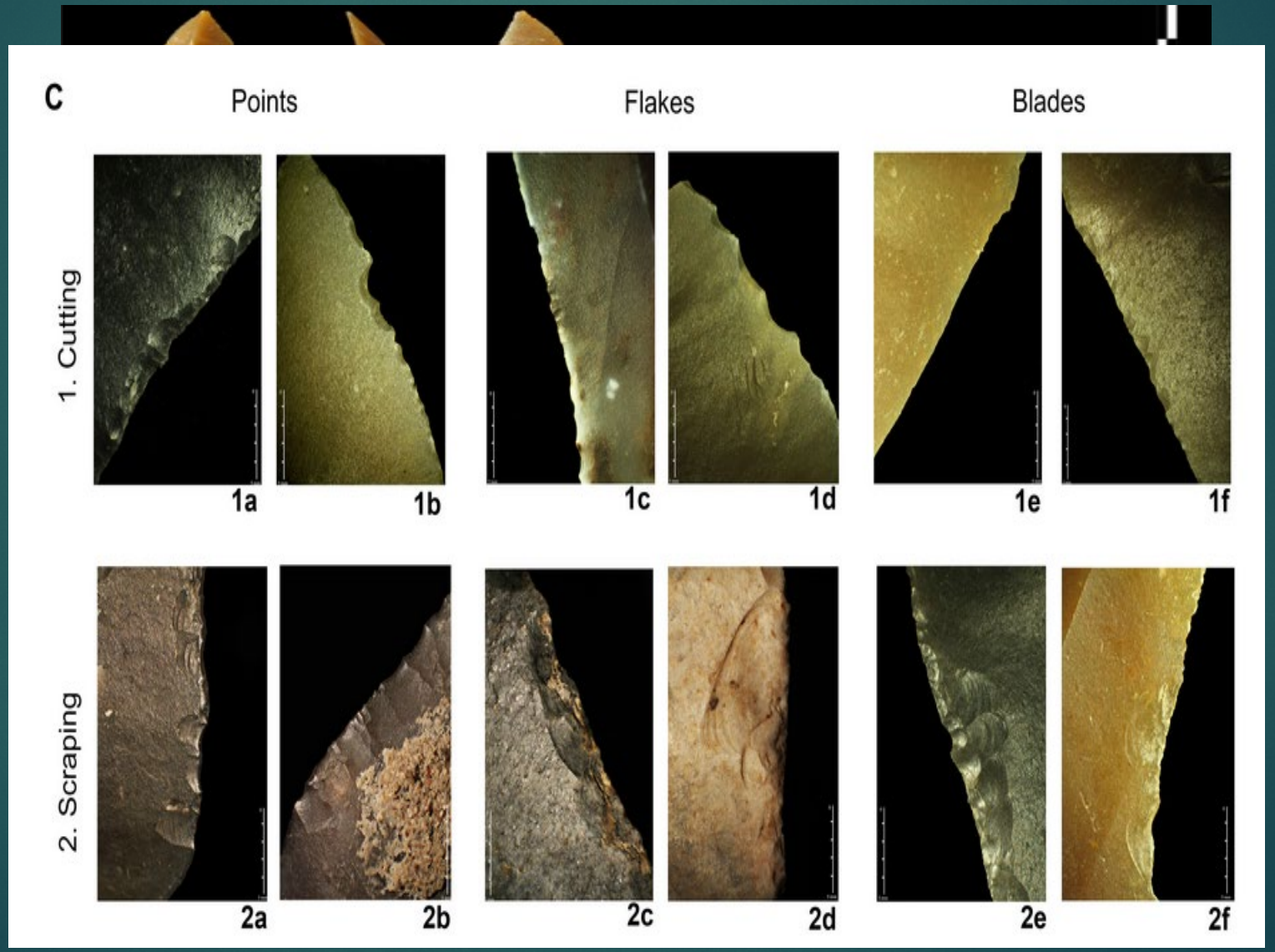
- Found a horse femur with damage consistent with a stone point
- Above and below Grotte Mandrin's layer E, researchers have found Neanderthal teeth and DNA, and Mousterian tools.
- Slimak's team contends that layer E represents an early but short-lived incursion of *Homo sapiens* into Neanderthal territory, more than 10,000 years before the species permanently settled in Europe.
- Not all archaeologists agree.
- If *Homo sapiens* did make the stone points in layer E, it's not clear why Neanderthals in the region and elsewhere did not pick up bow-and-arrow technology.

Bow-and-arrow, technology of the first modern humans in Europe 54,000 years ago at Mandrin, France

- Consensus in archaeology has posited that mechanically propelled weapons, such as bow-and-arrow or spear-thrower-and-dart combinations, appeared abruptly in the Eurasian record with the arrival of anatomically and behaviorally modern humans and the Upper Paleolithic (UP) after 45,000 to 42,000 years (ka) ago, while evidence for weapon use during the preceding Middle Paleolithic (MP) in Eurasia remains sparse.
- The ballistic features of MP points suggest that they were used on hand-cast spears, whereas UP lithic weapons are focused on microlithic technologies commonly interpreted as mechanically propelled projectiles.
- Present the earliest evidence for mechanically propelled projectile technology in Eurasia from Layer E of Grotte Mandrin 54 ka ago in Mediterranean France, demonstrated via use-wear and impact damage analyses.

L. Metz, et al., 2023

Arrow tips? At Mandrin, France, 54 Ka



Grotte Mandrin

- Grotte Mandrin is a vaulted rock shelter directly overlooking the middle valley of the Rhône River.
- Mandrin records a reference archaeological succession, for it contains all of the phases currently known for the last Neanderthal societies, right up to the emergence of the UP.
- Each archaeological layer has yielded a rich lithic industry and paleontological remains.
- Layer E yielded 2267 lithic elements attributed to the Neronian, a "culture" entirely oriented toward the production of standardized Levallois points. Quantitatively, blades, bladelets, and a variety of points represent 75% of all lithics found

Tiny points

- For almost 40% of them, = less than 10 mm in maximum diameter. This diameter of 10 mm represents an important boundary. Ethnographic stone weapons whose shafts' maximum diameter is below 10 mm are exclusively from bow technologies.

- These tiny points of less than 10-mm breadth and that are distally armed are for the use of bow-and-arrow technology at the exclusion of any other delivery system

Arrows

- These results give solid evidence of the use of the bow and arrow within the smallest Neronian points, while the largest Mandrin E points = used with a spear-thrower, but these large points could ballistically be also delivered by bow.

- More generally in sub-Saharan Africa, there is strong evidence for the combination of bow and javelin hunting by 70 to 58 ka ago

Mandrin

- At Mandrin, functional analyses of all the MP layers before and after Layer E demonstrate a lack of the advanced technologies documented in Layer E.

- Document here that this earliest migration of humans into Neanderthal territories is associated with the mastery of bow.

- We also show that these highly controlled technologies were unknown locally among Neanderthals groups like elsewhere in Eurasia.

The three waves: Rethinking the structure of the first Upper Paleolithic in Western Eurasia – L. Slimak, 2023

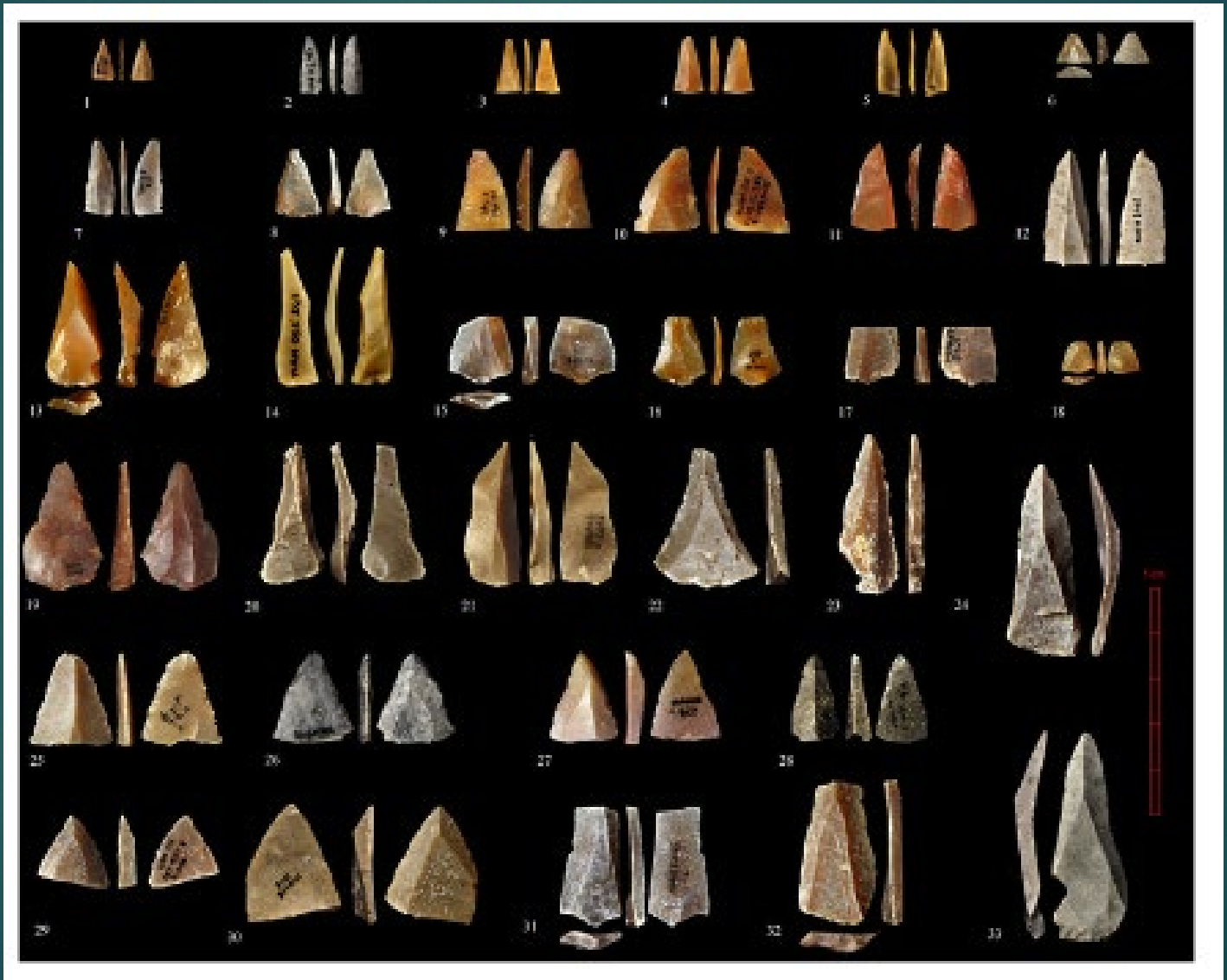
- The Neronian is a lithic tradition recognized in the Middle Rhône Valley of Mediterranean France now directly linked to *Homo sapiens* and securely dated to 54 Ka, pushing back the arrival of modern humans in Europe by 10 ka.

- This incursion of modern humans into Neandertal territory and the relationships evoked between the Neronian and the Levantine Initial Upper Paleolithic (IUP) question the validity of concepts that define the first *H. sapiens* migrations and the very nature of the first Upper Paleolithic in western Eurasia.

Three waves

- Direct comparative analyses between lithic technology from Grotte Mandrin and East Mediterranean archeological sequences, especially Ksar Akil, suggest that the three key phases of the earliest Levantine Upper Paleolithic have very precise technical and chronological counterparts in Western Europe, recognized from the Rhône Valley to Franco-Cantabria.

Neronian industry



Mandrin, France: Rethinking of the origin of the upper paleolithic: A Mediterranean odyssey

- These trans-Mediterranean technical connections suggest three distinct waves of *H. sapiens* expansion into Europe between 55–42 ka. These elements support an original thesis on the origin, structure, and evolution of the first moments of the Upper Paleolithic in Europe tracing parallel archaeological changes in the East Mediterranean region and Europe.

- The recent attribution of the Neronian industry to *Homo sapiens* at around the 54th millennium (56.8–51.7 ka) at Grotte Mandrin in France not only indicates a 10,000-year push back of the arrival modern humans in Europe, but also concrete evidence of interactions between Neanderthals and modern populations are demonstrated in a specific territory.

Mandrin, France

- Evidence: E level of the sequence that has a tooth and micropoints called Neronian, dated at 56.8-51.7 ka, between Mousterian levels that preceded and succeeded it.

- Slimak, 2023 study: concludes that they indicate the existence of three different waves of modern humans inside Europe, based on lithic similarities of Ksar Akil and Mandrin..

Three different waves of modern humans inside Europe

- Ksar Akil sequence in Lebanon, MP to UP: unity between the European Protoaurignacian and the Levantine Early Ahmarian

- The sequence of Ksar Akil allows us to document the precise technical emergence of industries identical to the Protoaurignacian of Europe (SEA), a development that can be broken down into three successive technical stages resulting from a progressive evolution of the technical systems of the first Levantine UP; IUP/ NEA/ SEA.

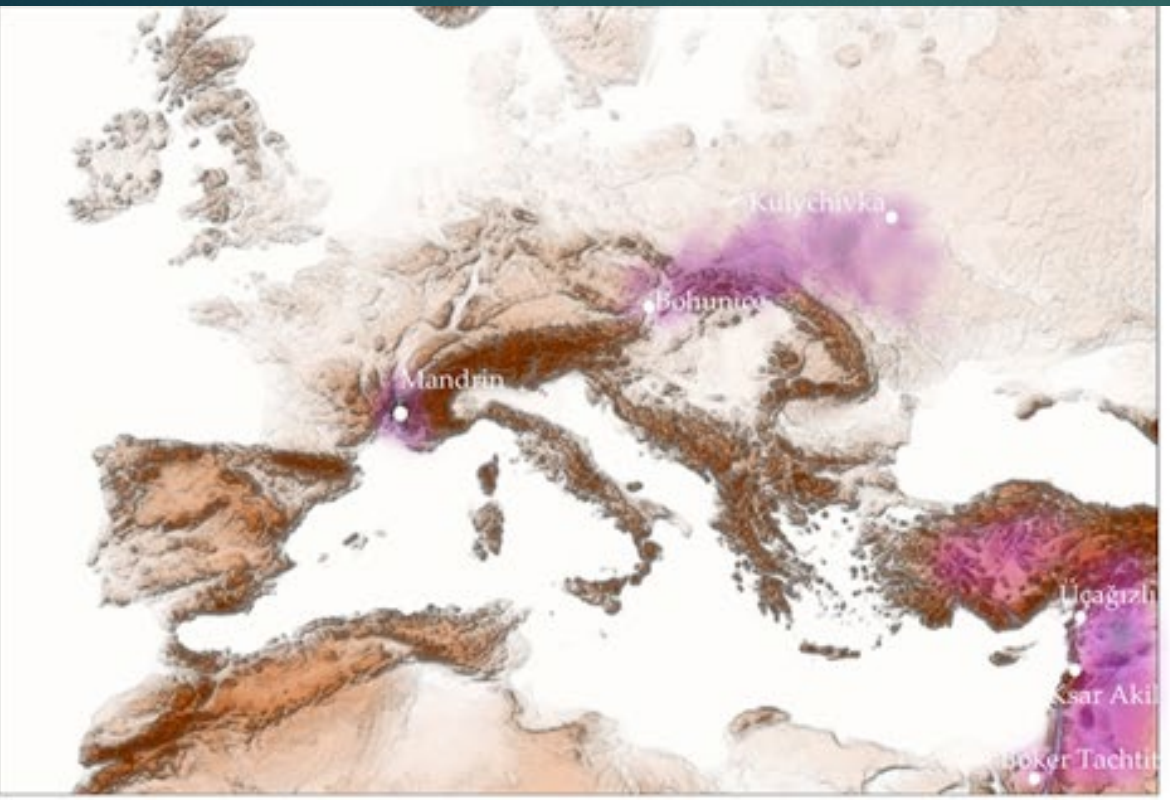
Ksar Akil = Mandrin

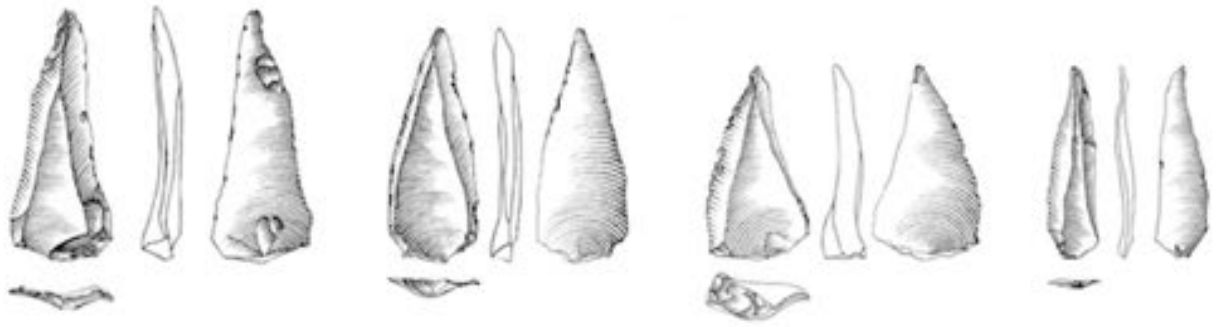
- These successions in the stratigraphy have remarkable parallels with the western end of Europe with the Neronian/Châtelperronian/Protoaurignacian triptych.

- Three phases of the first Levantine Upper Paleolithic find a strict corollary across Europe

- From the Ksar Akil sequence, three phases of the first Levantine Upper Paleolithic are proposed that are analogous to the three industries associated with such waves in Western Europe:

1st wave: Initial Upper Paleolithic

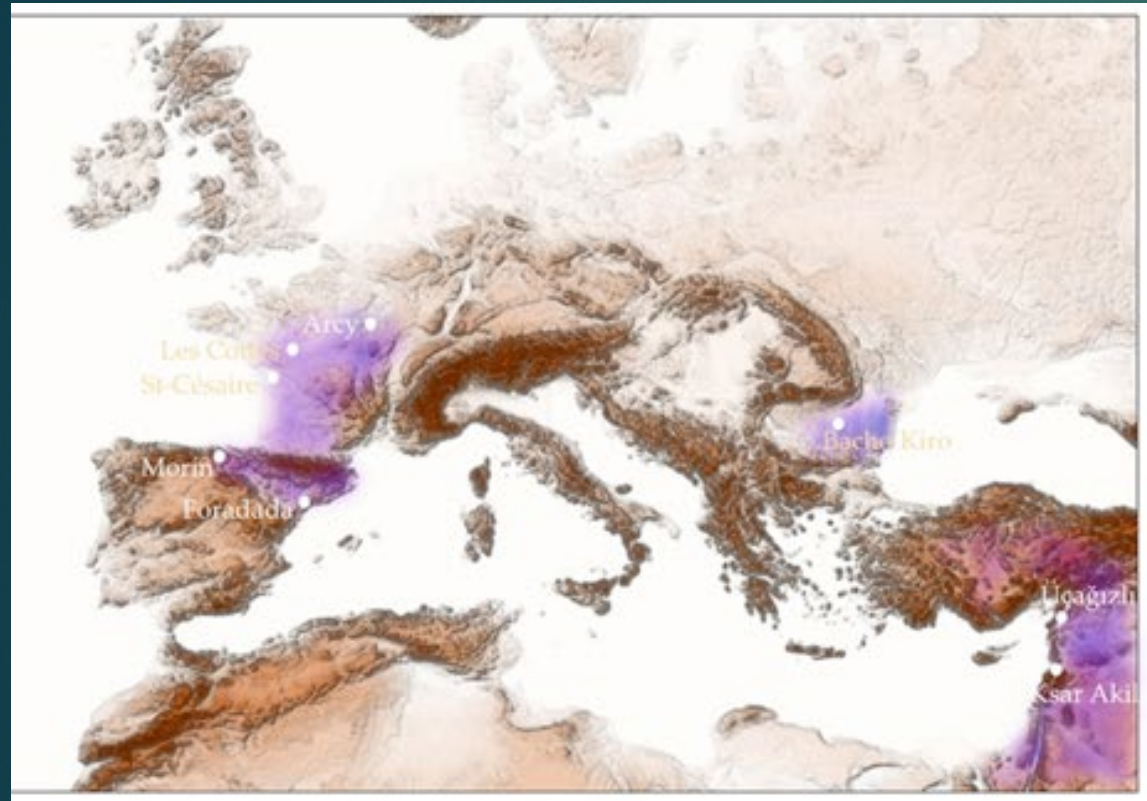


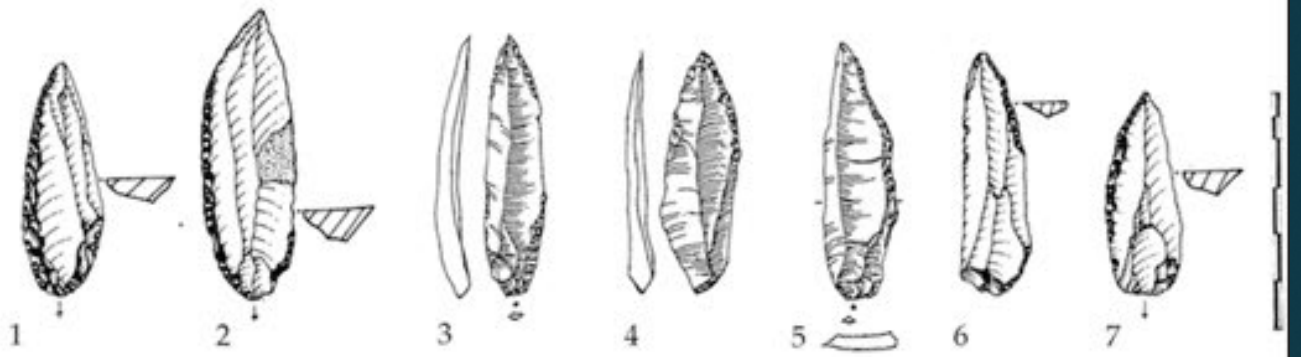


Ksar Akil phase I. Initial Upper Paleolithic/Neronian
Collections Ewing 1947-1948, Layers XXV-XXII.
Points and micropoints. Drawings Laure Metz.

1 - The first phase (Initial Upper Paleolithic, IUP) occurred in the 50 to 60 ka range. It would be equivalent to the aforementioned sapiens populations that settled for a brief period of time in "Neanderthal territory", and left the Mandrin cave Neronian (points and micropoints) and very little other evidence.

2nd wave: Early Upper Paleolithic I, EUP I, or Northern Early Ahmariense, NEA

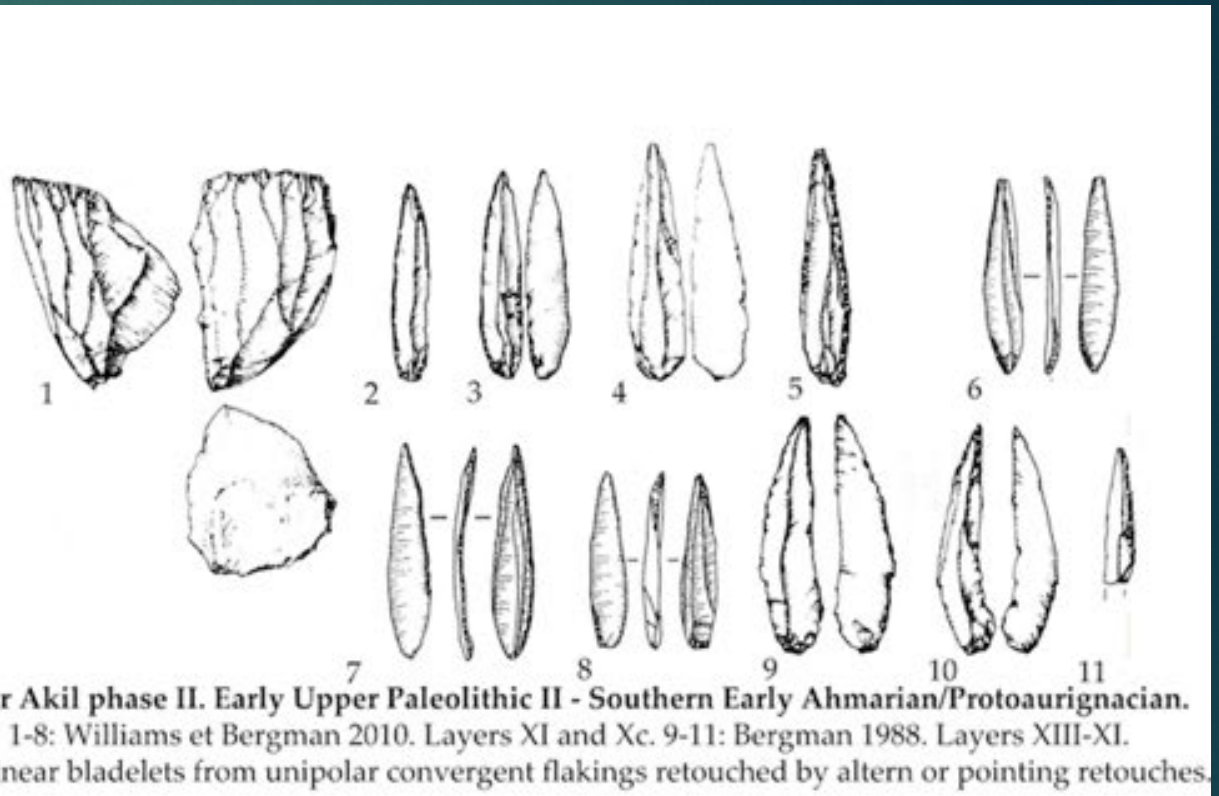




Ksar Akil phase II. Early Upper Paleolithic I - Northern Early Ahmarian/Châtelperronian
1-5: Ohnuma et Bergman 1990. Couches XVII et XVI. 6-7: Azoury 1986. Couche XVI.
Backed points on bipolar little blades

2 - The second phase (Early Upper Paleolithic I, EUP I, or Northern Early Ahmariense, NEA) would correspond to the Châtelperronian culture developed around 45 ka on the Atlantic coast of France and, on the Iberian Peninsula, the Cantabrian coast and the north of the Mediterranean area. But it is not observed in the Rhone Valley.

3rd wave: Early Upper Paleolithic II, EUP II, or Southern Early Ahmariense, SEA



Ksar Akil phase II. Early Upper Paleolithic II - Southern Early Ahmarian/Protoaurignacian.
1-8: Williams et Bergman 2010. Layers XI and Xc. 9-11: Bergman 1988. Layers XIII-XI.
Rectilinear bladelets from unipolar convergent flakings retouched by altern or pointing retouches.

3 - The third phase (Early Upper Paleolithic II, EUP II, or Southern Early Ahmariense, SEA) would correspond in Europe to the proto-Aurignacian industry of about 42 ka. This is a much more marked and recognizable expansion throughout western Europe to the Levant, leading to further cultural unification of the various sapiens populations across western Eurasia.

From colonization to relations with the Neandertals

- Three phases from the beginning of the Upper Paleolithic can be interpreted as three distinct migratory waves of biologically modern populations that systematically had their origin within the Mediterranean Levant.

- Lithics are archaeological signature of three distinct migratory phases, all likely stemming from the same Levantine cultural substrate.

Neronian sapiens

- Possible links between these waves with the gradual replacement of the last Neanderthals are proposed:
- The Neronian sapiens showed a mastery of both banks of the Rhône river and knowledge of all siliceous resources in a relatively large area, suggesting close relationships with Neanderthal aboriginal groups or isolated individuals of this species who would have prior knowledge of the territory. Rhône was one of the main migratory arteries of Western Europe
- In the second phase, there seems to be a rejection or resistance from the Neanderthals that occupied the Rhone Valley to the sapiens that spread through Atlantic, continental and Mediterranean territories.
- The Proto-Aurignacian marks the complete replacement of Neanderthals by sapiens, throughout a gradual process that would last up to 12 ka in areas such as the Rhône Valley.

N-MH overlap in Eurasia: 1400 to 2900 years

- Optimal linear estimation models predict 1400–2900 years of overlap between *Homo sapiens* and Neandertals prior to their disappearance from France and northern Spain -- Igor Djakovic, et al., 2022

- Neanderthals and modern humans coexisted in a period of 1,400 to 2,900 years in the region corresponding to present-day France and northern Spain. This conclusion has been reached using statistical models of the probability of crosses from the dating of 56 objects attributed to both species, from 17 sites, and 10 Neanderthal specimens from that region

N-MH overlap and Mandrin Cave

- Archaeologically, the first part of this period—the Middle to Upper Palaeolithic transition—is characterized by so-called ‘Initial Upper Palaeolithic’ assemblages (e.g. Bacho Kiro) which are increasingly interpreted as representing an initial, possibly unsuccessful migration of AMH into Europe occurring around 47–44 kya cal BP.

- The term ‘unsuccessful’ has been used as these initial groups appear to have left no visible genetic contributions to present-day populations in Europe.

- Recently published evidence from Grotte Mandrin, south-eastern France, may however extend this initial migration to as far back as ~ 54,000 years ago. At this site, a deciduous molar attributed to Homo sapiens was recovered from an archaeological layer bearing a distinctive IUP-type stone tool industry and dating to somewhere between 58 and 51,000 years ago.

Early MHs in Europe

- If confirmed with additional evidence, this would constitute a significant shift in perspective—placing AMHs in far western Europe upwards of 12,000 years earlier than previously thought.

- Interestingly, there is no evidence of AMH occupation in any region of France for upwards of 12–14,000 years following the disappearance of the Neronian industry—which in fact seems to represent a brief, geographically restricted technological entity.

Final migration = 42 Ka

- Instead, until ~ 42,000 years ago, the archaeological record of France appears to be characterized exclusively by Neandertal remains and cultural material.
- The evidence from Grotte Mandrin may in fact lend strength to the idea that this initial period of AMH presence in Europe consisted primarily of small scale, unsuccessful migrations—without persistent co-existence between incoming AMHs and Neandertals.
- The onset of the Aurignacian complex (sensu lato) across Europe at around 42 kya cal BP is widely accepted as reflecting a second, more successful migration of AMH groups into Europe's western extensions, and may signal the first major and persistent phase of European colonization by our species.

Transitional stratigraphy

- In many regions, Protoaurignacian and Early Aurignacian assemblages appear to rapidly replace so-called 'transitional' stone tool industries (e.g. Uluzzian, Châtelperronian, Lincombian-Ranisian-Jerzmanowician), some of which are considered to be products of Neandertals

- At present, the Châtelperronian industry of France and northern Spain shows the strongest association between one of Europe's 'transitional' industries and Neandertal fossil remains. Neandertal remains have been recovered from stratigraphic layers containing Châtelperronian artefacts at the two key French sites of Saint-Cesaire and Grotte du Renne.

The great debate

- However, the validity of these CP associations is heavily debated, and consensus regarding both the makers of this industry and the reliability of the Neandertal associations is not unanimous.

- Nonetheless, despite ongoing discussion, a Neandertal authorship for this industry remains the most parsimonious and well-accepted model. The principle reason for this is that, debates aside, the only human remains to as of yet be recovered from stratigraphic layers containing Châtelperronian artefacts are those of Neandertals.
- Bayesian modelling of radiocarbon ages for Protoaurignacian and Châtelperronian assemblages in this region has already indicated that these occupations may have co-existed for upwards of 1600 years

Overlap

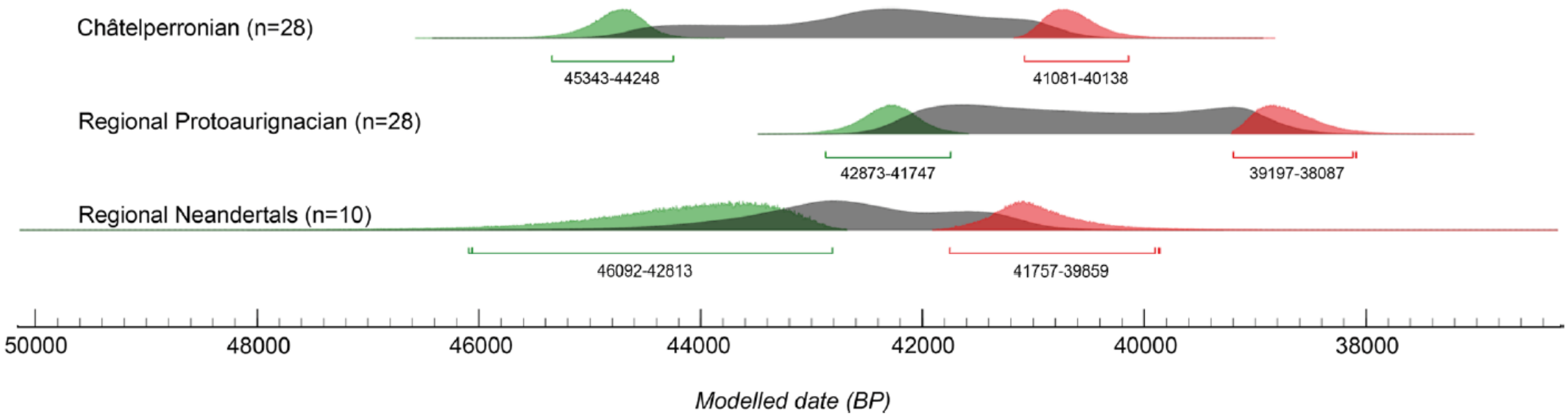
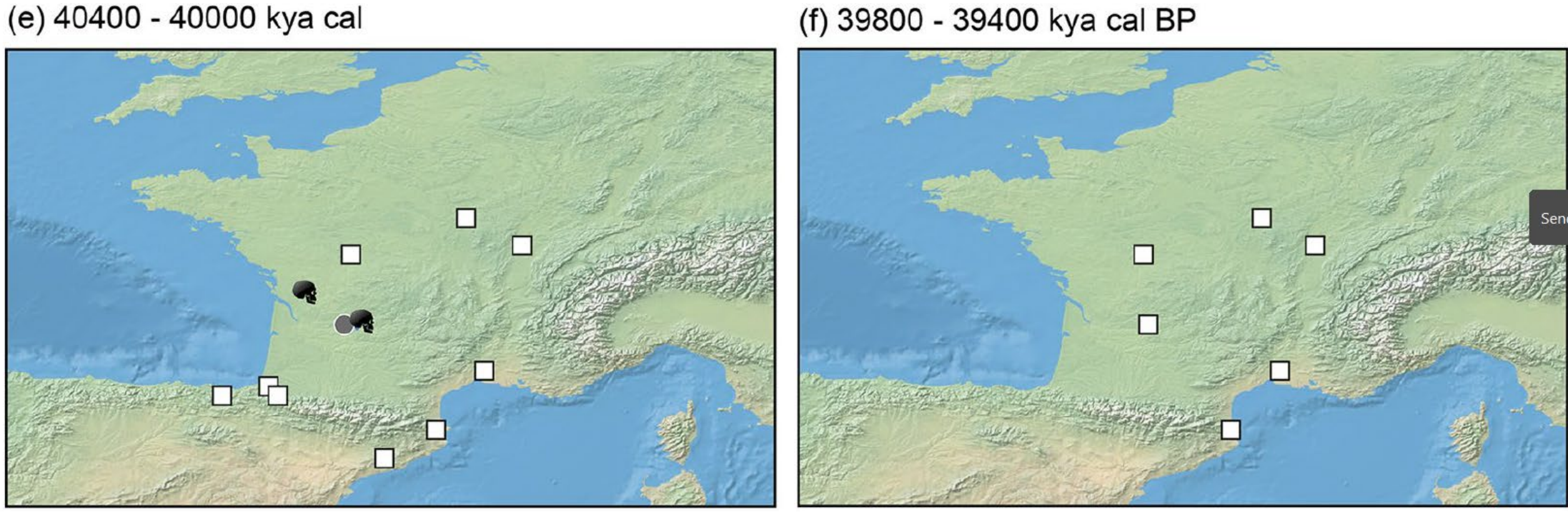


Figure 2. Kernel Density Estimation plots and Bayesian start/end date probabilities summarising the distribution of the aggregated calibrated radiocarbon ages for (**a**) the Châtelperronian assemblages (n = 28), (**b**) the Protoaurignacian assemblages (n = 28), and (**c**) the directly-dated late Neandertals (n = 10) included in this

Geographic appearance of dated occurrences for the Châtelperronian (grey circles), Protoaurignacian (white squares), and directly-dated Neandertals (black skulls) in the study region between 43,400 (a) and 39,400 (f) years cal BP



Modeling

- Combined, modelling suggests the Protoaurignacian to have emerged around 1399–2196 and 2375–2855 years before Neandertals and the Châtelperronian industry (respectively) disappeared from the region.

- Based on OLE modelling of their respective ‘origination’ and ‘extinction’ dates, the Protoaurignacian potentially appeared around 1400–2900 years before Neandertals and the Châtelperronian industry disappeared from France and northern Spain.

- This is largely consistent with previous estimates, and reaffirms the duration of co-existence between these groups during the early western European Upper Palaeolithic

MH-N co-existence

- Modelling predicts the appearance of *Homo sapiens* and the Protoaurignacian in France and northern Spain at 42.3 to 42.7 Ka, and the 'extinction' of the Châtelperronian and regional Neandertals at 40 and 40.9 Ka respectively—suggesting a possible overlap of around 1400 to 2800 years between these human groups in the region.

- Additionally, this chronological overlap appears to be geographically structured, with the Protoaurignacian following a south to north pattern of appearance.

- Taken together, these observations strengthen the proposition that the initial Upper Paleolithic in this region likely involved a period of co-existence between Neandertals and *Homo sapiens*. The precise nature of this co-existence, however, remains to be resolved