

Human Evolution
Interest Group
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by
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Henry the giant crocodile, who has sired 10,000 babies, celebrates 124th birthday



The Nile crocodile (*Crocodylus niloticus*) has lived at the Crocworld Conservation Centre in Scottburgh, South Africa since 1985. He was originally captured in the Okavango Delta in Botswana in 1903. [fathered over 10,000 offspring](#) with numerous partners since he arrived there almost 40 years ago.

Who Is Jonathan Meijer? The Man With 1000-3000 Kids ...

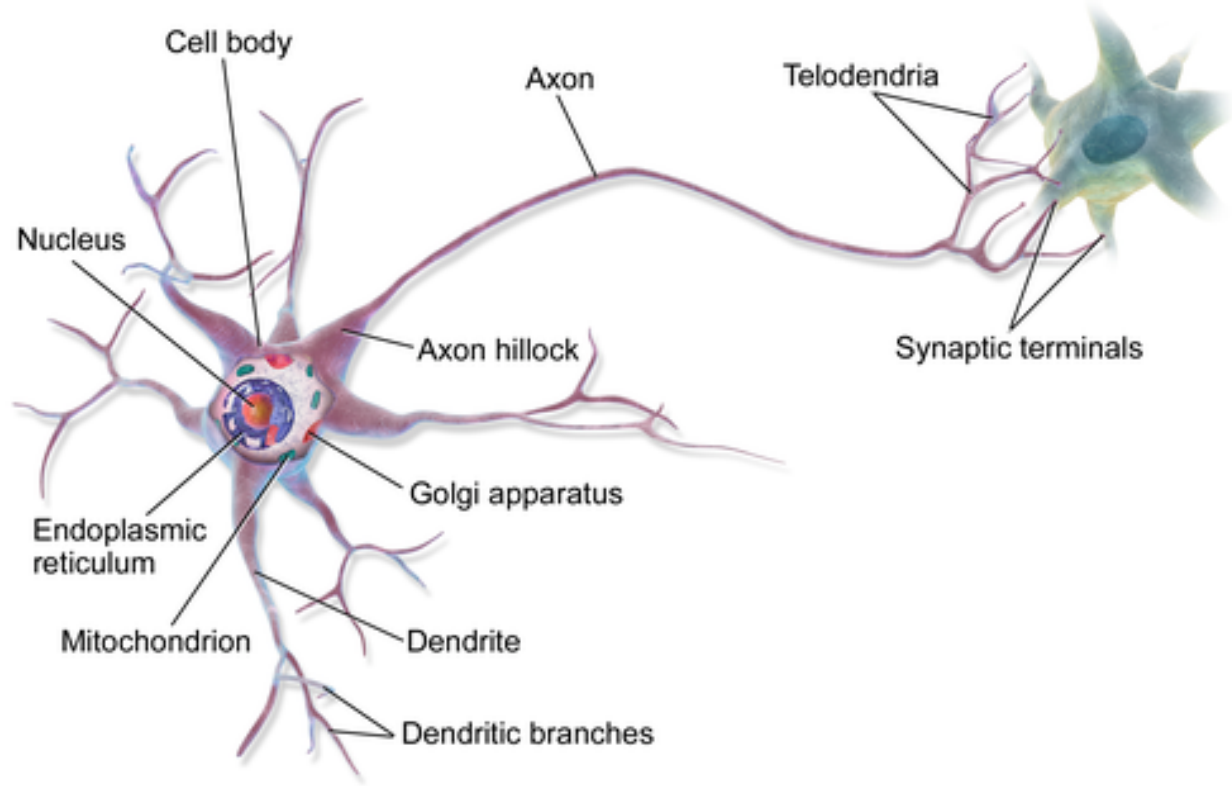
- ▶ A psychopathic serial sperm donor operating out of the Netherlands
- ▶ Netflix documentary



After 37 year hiatus, orcas are wearing dead salmon again!

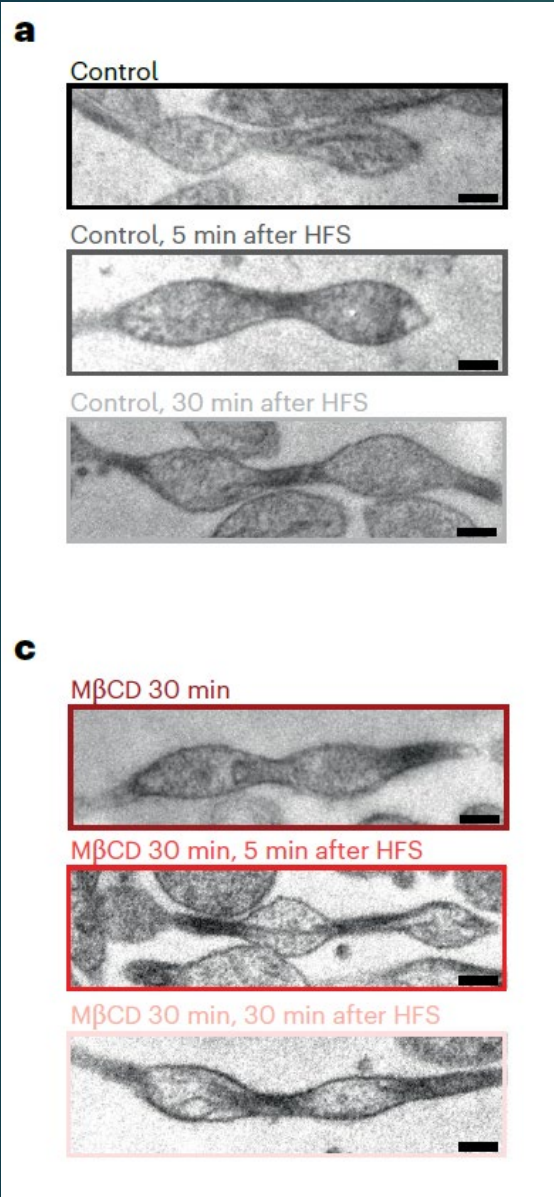


*** Neuron with classical thin axon



- Axons are ultrathin membrane cables that are specialized for the conduction of action potentials between neurons.
-
- Although their diameter is variable along their length, how their morphology is determined is unclear.

String like or pearls-on-a-string shape for axons?



- Here, we demonstrate that unmyelinated axons of the mouse central nervous system have nonsynaptic, nanoscopic varicosities ~200 nm in diameter repeatedly along their length interspersed with a thin cable ~60 nm in diameter like pearls-on-a-string.
- Unmyelinated axons = 15-20% of axons; almost all in grey matter.
- Most myelinated white matter tracts are situated subcortically,

***Science: Open-access journal eLife to lose “Impact factor”.

- ▶ Web of Science index decides to strip key metric because *eLife*'s unusual peer review doesn't meet its criteria
- ▶ The journal *eLife* will no longer receive a journal impact factor, the much-debated metric that many scientists view as a badge of quality.
- ▶ Clarivate, which operates the influential Web of Science database, said a review determined the journal's novel publishing model adopted in January 2023—which includes public peer review but no final decision on whether a manuscript is accepted or rejected—does not meet its standards for peer review.
- ▶ Many institutions evaluate their scholars for promotion based on the impact factors of journals in which they publish, and other journals that have lost their impact factor—which is based on average citations to a journal's papers—have subsequently published fewer articles

*** Dark proteome' survey reveals thousands of new human genes

- ▶ Database confirms that overlooked segments of the genome code for a multitude of tiny proteins.
- ▶ Human genome: how few genes it contained, about 20,000.
- ▶ New systematic analysis of what some call the “dark proteome” suggests scientists have missed thousands of nontraditional genes that lurk in previously overlooked stretches of the genome and make smaller than average proteins.

Genes produce proteins

- ▶ A gene is typically assumed to consist of a long protein-coding DNA sequence known as an open reading frame (ORF), which has signals telling a cell where to start and stop reading it.
- ▶ A cell transcribes the ORF sequence into messenger RNA, which travels to cellular factories called ribosomes that assemble amino acid sequences into proteins.
- ▶ An ORF qualified as a gene if it encoded a protein with 100 or more amino acids.

New genes

- ▶ But biologists have recently unearthed a plethora of so-called noncanonical ORFs, which are shorter than average.
- ▶ Yet they are often transcribed into RNA, and a method known as ribosomal profiling has shown that many of the transcribed RNAs attach to ribosomes, where they may be translated into short amino acid chains—even proteins with less than a dozen amino acids.

New miniproteins

- ▶ Many scientists disregarded these microproteins. But about 3 years ago, discovery that cancer cells contained about 550 of these microproteins.
- ▶ By 2022, the scientists had tracked down 7264 noncanonical ORFs in the human genome.
- ▶ One-quarter of those tallied made proteins, some 3000 in all.
- ▶ The newly discovered miniproteins help provide a more complete picture of the coding portion of the [human] genome

Possible biomarkers and drug targets

- ▶ One miniprotein has a critical role in medulloblastoma and may be a drug target
- ▶ Others involved in pancreatic cancer and metabolic diseases.
- ▶ Now 23,000 genes. There may be as many as 50,000.

*** Neanderthals were making hand stencil rock art more than 66,000 years ago.



Neandertals as first European artists

- ▶ Hand stencils in Maltravieso Cave are more than 66,000 years old, suggesting that Neanderthals, not modern humans, were the world's first artists.
- ▶ Stencils and prints of the human hand are some of the earliest forms of deliberately created visual artwork preserved in the archaeological record. Maltravieso Cave houses more than 60 red hand stencils, but their precise ages have remained a mystery.
- ▶ Researchers applied U-series dating to calcium carbonate crusts overlying the hand stencils in the cave's Sala de las Pinturas and Galería de la Serpiente.
- ▶ The team collected carbonate samples overlying pigment on hand stencils and performed U-series dating.

The age of hand stencils in Maltravieso cave (Extremadura, Spain) established by U-Th dating, and its implications for the early development of art – Christopher D. Standish et al., 2024

- ▶ The crust covering the hand stencils in the deepest recess of the cave dates to 66,700 years ago, suggesting that Neanderthals likely created these illustrations.
- ▶ The oldest three samples were dated 46,600, 55,240 and 66,710 years ago.
- ▶ The oldest known hand stencil art previous: Leang Timpuseng Cave on the Indonesian island of Sulawesi. A minimum age of 39,900 years. And also a 51 Ka painting of pigs.

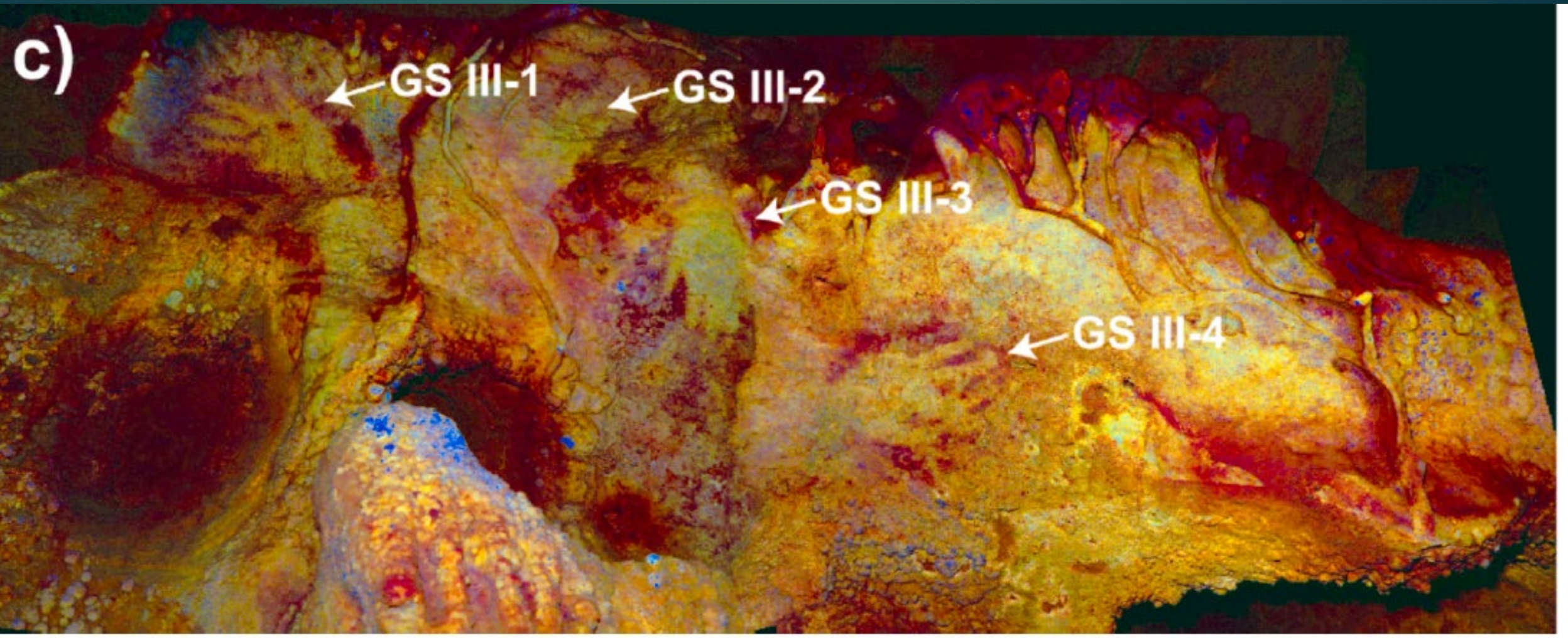
Handprints and red dots

- ▶ Handprints and footprints in mud found on the Tibetan Plateau have been dated to approximately 200,000 years ago.
- ▶ Previously, a team of researchers at the **Cave of La Pasiega**, also in Spain, used U-series dating to discover that the **iconic red dot art had to be older than 64,800 years.**
- ▶ The red dot style is found throughout ancient cave art of Spain

Handprints



Handprints



*** Enamel proteins reveal biological sex and genetic variability within southern African *Paranthropus*

- ▶ The study investigates the evolutionary relationships and genetic variability within the southern African hominin species Paranthropus robustus from the site of Swartkrans using enamel proteins from four dental specimens dated to approximately 2 Ma.
- ▶ The researchers employed mass spectrometric sequencing to analyze the enamel proteomes, enabling them to determine the biological sex of the specimens and explore intraspecific genetic diversity.
- ▶ The findings revealed significant variation within Paranthropus robustus, suggesting potential substructuring or the presence of multiple species.

Recovery of 2 Ma phylogenetically-informative genetic material in African hominins

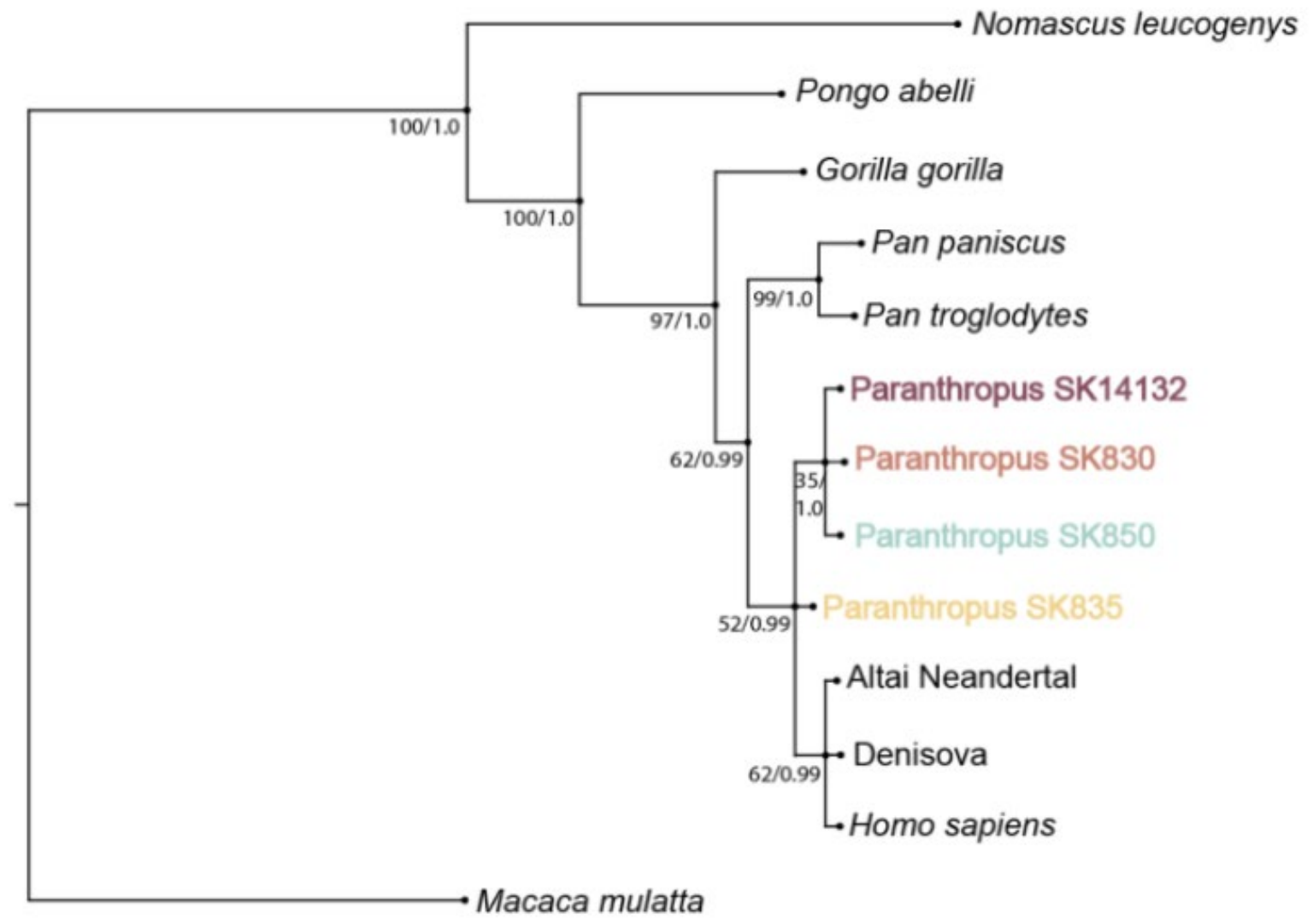
- ▶ Identification of both male and female *Paranthropus* individuals: The identification of AMELY-specific peptides and semi-quantitative MS data analysis enabled us to determine the biological sex of all the specimens.
- ▶ Our combined molecular and morphometric data also provide compelling evidence of a significant degree of variation within southern African *Paranthropus*, as previously suggested based on morphology alone. Hypothesis of two different *Paranthropus* groups

Sex by protein

- ▶ Amely protein refers to a specific variant of the amelogenin protein encoded by the AMELY gene located on the Y chromosome, which is used in forensic science to determine an individual's sex by comparing the presence and size of the AMELY gene alongside its counterpart on the X chromosome (AMELX), allowing for sex identification based on DNA analysis; essentially, if the AMELY gene is detected, the individual is male, while its absence indicates female
- ▶ Analysis of these proteins can contribute to understanding whether hominin morphological variation is due to sexual dimorphism or to taxonomic differences.
- ▶ Finally, the molecular data also confirm the taxonomic placement of *Paranthropus* within the hominin clade.

Phylogenetic analysis

A



*** The Inner Ear as a Window to the Past

- ▶ The bony labyrinth houses sensory organs that are vital for balance and spatial awareness. Variations in vestibular morphology can provide clues about habitual posture, locomotion, and environmental adaptations.
- ▶ The inner ear morphology of *P. robustus* and *A. africanus* reveals significant differences in vestibular structure.
- ▶ Vestibular system of *Paranthropus robustus* is highly derived, exhibiting features that differ markedly from both *Australopithecus africanus* and modern humans
- ▶ These features align more closely with extant great apes, suggesting functional differences in balance and head orientation.

Australopithecus africanus vs *Paranthropus robustus*, DNH 7,



2.5 Ma,
male

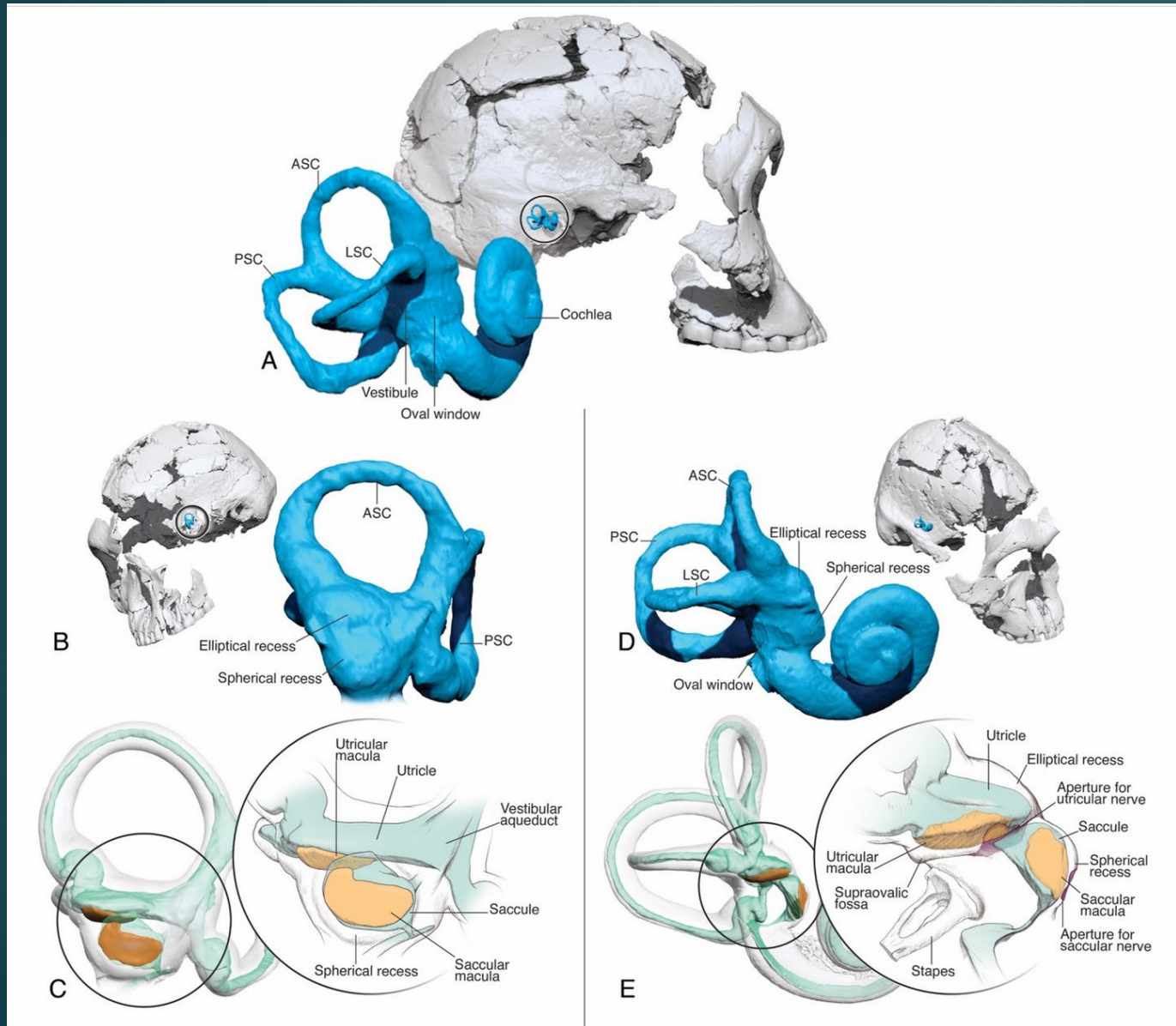


Taung child,
2.5 Ma



1.95
Ma,
female

The inner ear of *Paranthropus robustus* specimen, DNH 7, and comparisons to the modern human membranous labyrinth



A) **Right *P. robustus*, DNH 7, inner ear** in the right lateral view is shown enlarged alongside the cranium in the same orientation. B) **DNH 7:** Anteromedial view of the right labyrinth C) **Right *Homo sapiens* ear** in the anteromedial view showing the membranous labyrinth (green) inside the bony labyrinth (transparent). Otolithic organ maculae are shown in orange. D) **DNH 7: $\frac{3}{4}$** anteroanterior view of the right labyrinth. E) **Right *H. sapiens* ear** from the anteroanterior view. Insets show diagrams of membranous anatomy from the corresponding panel.

P. robustus and *A. africanus*

- ▶ The reduced saccule size could indicate limited sensitivity to vertical acceleration, possibly tied to a less arboreal lifestyle or different locomotor strategies.
- ▶ Australopithecus africanus: The Generalist
- ▶ In contrast, the vestibular system of *A. africanus* aligns more closely with that of modern humans. Its morphology suggests a greater range of movement and adaptability, supporting the view of *A. africanus* as a generalist capable of both bipedal locomotion and climbing. This flexibility likely enabled it to exploit diverse resources in varying environments, from open savannahs to forested landscapes.

P. robustus

- ▶ *P. robustus* appears to have specialized in a niche that required less dynamic movement, possibly tied to its robust cranial and dental morphology, which suggests a diet of hard, fibrous foods.
- ▶ In contrast, *A. africanus* retained the versatility of its ancestors, balancing climbing and terrestrial foraging.
- ▶ The study also has implications for the taxonomy of *Paranthropus*. The distinctive vestibular morphology strengthens the case for considering *Paranthropus* as a separate genus, distinct from *Australopithecus*

*** *Paranthropus boisei* KNM ER 406 and *Homo erectus* KNM ER 3733.



Earlier skeletal material of both species
at Koobi Fora, Kenya

Different contemporaneous hominin species at Koobi Fora

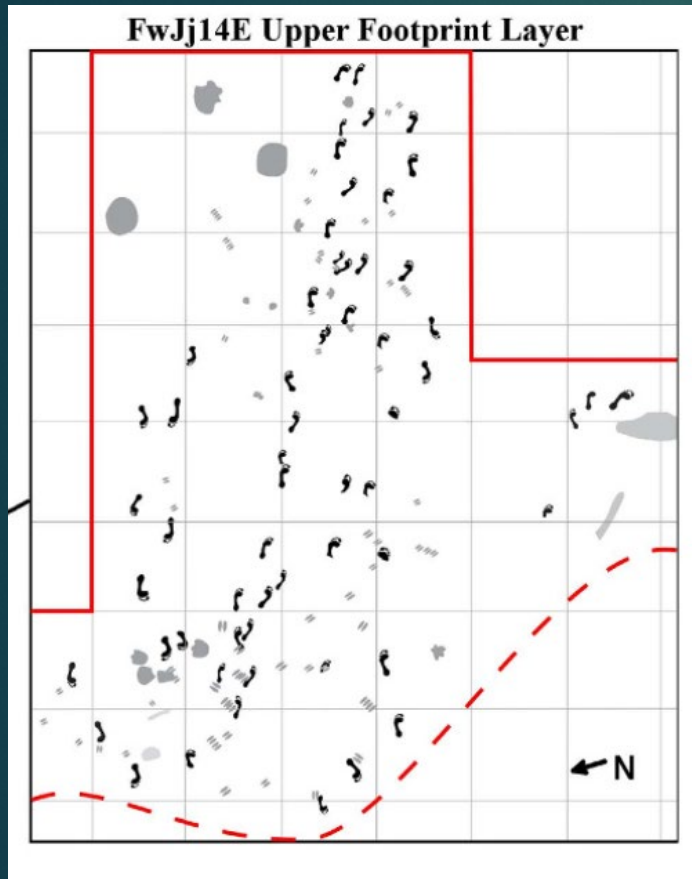
- ▶ They were radically different in shape and way of life.
- ▶ *Homo erectus* was already close to our height, although possibly with a somewhat squat body, and a brain of about 1000 cc.
- ▶ *Paranthropus*, on the other hand, showed a postcranial morphology more similar to that of *Australopithecus*, and a skull very different from that of humans, marked by a massive jaw and dentition, with a brain size of 500 cc.
- ▶ 3.66 Ma ago, *Australopithecines* from Laetoli (Tanzania) left footprints that show a similar heel strike, but a different propulsion pattern, with a somewhat flatter arch.

Most famous
fossil footprints:

Laetoli, Tanzania,
3.66 Ma ago,
Site G,
70 footprints
made by
three
A. afarensis



2nd Most famous footprints: Ileret, Kenya; 1.5 Ma; 97 footprints left by at least 20 *Homo erectus*



2016 Hatala: oldest direct evidence for modern human-like weight transfer and confirm the presence of an energy-saving longitudinally arched foot in *H. erectus*

*** Footprint evidence for locomotor diversity and shared habitats among early Pleistocene hominins -- Kevin G. Hatala, et al. 2024

- ▶ For much of the Pliocene and Pleistocene, multiple hominin species coexisted in the same regions of eastern and southern Africa.
- ▶ Report the discovery of footprints (~1.5 million years old) from Koobi Fora, Kenya, that provide the first evidence of two different patterns of Pleistocene hominin bipedalism appearing on the same footprint surface.
- ▶ New analyses show that this is observed repeatedly across multiple contemporaneous sites in the eastern Turkana Basin.

Context of site ET



Footprints

- ▶ They found that three of the isolated footprints had high arches and a heel-to-toe footfall like modern humans. These footprints were likely made by our direct ancestor H. erectus, which had a very human-like body shape and size.
- ▶ However, the trackway of a dozen footprints revealed a different pattern. These tracks were much flatter, with a deeper forefoot strike compared to the heel strike. The researchers also noticed that the big toe was somewhat spread out and not fully in line with the foot as it is in humans, suggesting that the trackmaker was likely Paranthropus boisei, a heavily built australopithecine with large jaws and a divergent big toe.
- ▶ It is likely that both hominins met there looking for water and food in a resource-rich environment. While the paranthropes had a diet based on C4 type plants (grasses and sedges), humans were omnivores, consuming vegetables and animal proteins

Sympatry: 2 hominins and a giant stork

- ▶ These data indicate a sympatric relationship between Homo erectus and Paranthropus boisei, suggesting that lake margin habitats were important to both species and highlighting the possible influence of varying levels of coexistence, competition, and niche partitioning in human evolution.
- ▶ The newly discovered Koobi Fora footprint trail is about 26 feet (8 meters) long and includes one trackway consisting of a dozen footprints made by one individual and three more footprints made by others.
- ▶ A giant extinct marabou stork (Leptoptilos falconeri) also tracked through the wet mud, which was rapidly buried and preserved.

Giant Marabou stork: also on Flores



Footprints

- ▶ Modern human footprint dataset: Deep human prints made in soft sandy mud show a high human arch even more consistently than shallow human prints. Human footprints don't show the big toe angling very far from the medial side of the print, called abduction. Maybe more important, people today don't move their big toe much from one footstep to the next.
- ▶ The **sizes of the feet varied**, but the researchers do not have enough information to determine whether the trackmakers were males, females or children.

A large *P. boisei*

- ▶ The dozen footprints were made by a *P. boisei* individual who would have worn a U.S. men's size 8.5 or women's size 10 shoe, while the isolated *H. erectus* footprints were smaller, roughly a women's size 4 to a men's size 6.
- ▶ The large HT1 prints suggested a pretty big body size for the *P. boisei* individual, at an estimated 55 kg (121 lbs) it would outweigh the largest known associated *P. boisei* skeleton

Laetoli vs Koobi Fora

- ▶ Comparison to footprints from Laetoli, Tanzania: Like the HT1 prints, the footprints from the Laetoli G1 and S1 trackways have flatter arches than humans, have big toes more abducted than humans, and abduction angles that vary from step to step.
- ▶ But the longer HT1 trackway did not fit the range of human footprints. These prints had a flatter arch, the big toes averaged higher abduction than humans, and showed a lot of variation in abduction angle from step to step. This long trackway, the team concluded, likely was made by a large *P. boisei* individual.

P. boisei and H. erectus

- ▶ Fossil footprints, unlike skeletal material, record information within extremely narrow spatiotemporal scales (e.g., tens of square meters over periods of hours to days),
- ▶ Consistently find evidence at East Turkana footprint sites for two different patterns of hominin foot kinematics. These patterns occur adjacent to each other on the same surfaces and are recorded across multiple sites.
- ▶ We hypothesize that the HT1 trackway was created by P. boisei and the isolated TS-2 tracks by H. erectus. The two individuals walked through the lake area within hours or days of each other — leaving the first direct record of different archaic hominin species coexisting in the same place. The prints preserved the height of their foot arches, the shape of their toes and their walking pattern

Sympatry at 1.5 Ma

- ▶ Snapshot of data appropriate for demonstrating sympatry (hominins sharing a space; on a scale of hours to days), showing that two different hominin taxa repeatedly crossed paths ~1.5 million years ago in lake margin environments.
- ▶ The track surface presented here is stratigraphically about 10 m below the Elomaling'a Tuff, recently dated to ~1.52 million years ago (Ma)
- ▶ On the TS-2 surface, we uncovered one continuous trackway made by a single hominin individual and three isolated hominin tracks that, based on sizes and orientations, appear to represent three additional, different individuals. The TS-2 surface also includes 61 bird, 30 bovid, and 3 equid tracks. Some of bird tracks are of giant marabou storks.
- ▶ Impressions of rippled sand, reed beds and fish nests suggest that the area was a lake shore with shallow water.



TS-2 tracks

- ▶ TS-2 surface: Animals were walking and standing in shallow water or very close to the shoreline on a wet substrate that was supportive but deformable. After tracks were formed, the surface was gently covered with fine sand and silty sand and preserved under the accumulating strata. There is no evidence for erosion into this surface, supporting continuous, rapid sediment accumulation
- ▶ Evaluation of all available evidence from ~1.4- to 1.6-Ma East Turkana sites suggests that two different patterns of locomotor kinematics are recorded on the same footprint surfaces, with some trackways indicating modern human-like locomotion and others representing a different pattern of foot motion
- ▶ The path comprises 13 footprints. The hominin that created it walked at 1.81 meters per second, similar to a modern human walking briskly. The isolated footprints belong to individuals of *H. erectus*,

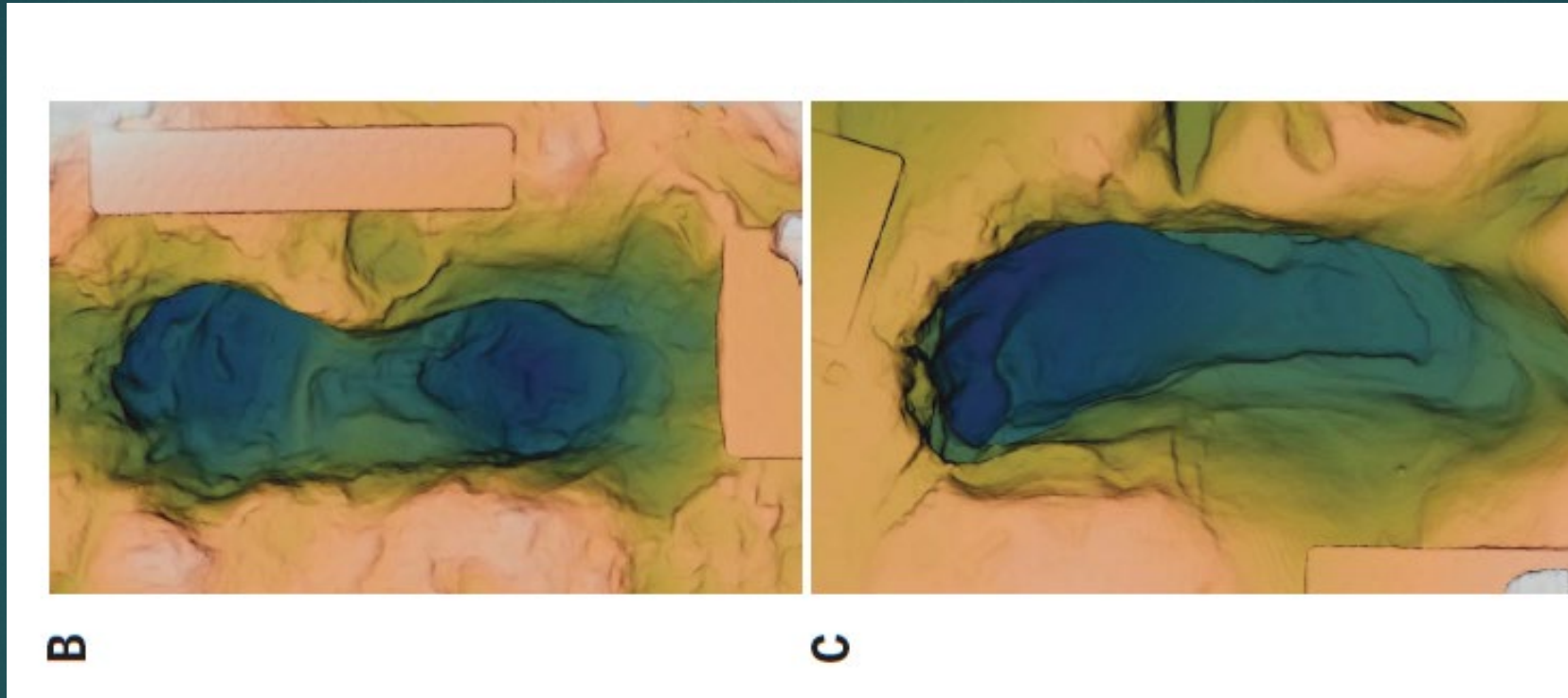
Higher arches vs big toe divergence

- ▶ Used X-ray technology to understand how foot motion affects imprints left in the mud. Compared with the continuous trail of prints, **the three isolated footprints all had higher arches, indicating that they arose from a gait more similar to that of humans today.**
- ▶ They also found that the **feet responsible for the trail of prints had a big toe with a position that changed from step to step. The toe was not as mobile as those on apes, but more varied than what is seen in modern humans**
- ▶ **A re-analysis of footprints from a site nearby showed a similar overlap of the two hominins occurring more than 100,000 years later. This suggests that the two species possibly lived alongside each other for a long time, and that they weren't in direct competition for resources**

Big toe angulation

- ▶ Propose that the TS-2 surface records the co-occurrence of two different taxa, exhibiting different foot morphology and kinematics, within the growing number of early Pleistocene track assemblages at East Turkana.
- ▶ The researchers attributed the continuous trail to an individual from the species *Paranthropus boisei*, which also seemed to walk upright. That species had a flatter foot and the position of its big toe changed from step to step. The big toe had a greater range of motion — able to angle outwards by up to 19 degrees in the right foot and nearly 16 degrees in the left foot — compared with human big toes, which extend outwards by up to about 10 degrees.
- ▶ H. erectus and P. boisei were the only two hominin species present at Koobi Fora at 1.5 Ma.

Two footprints: *H. erectus* and *P. boisei*



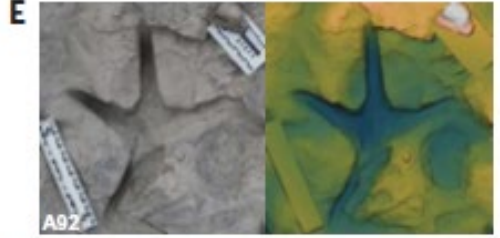
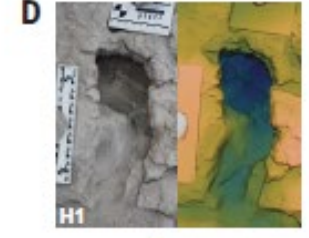
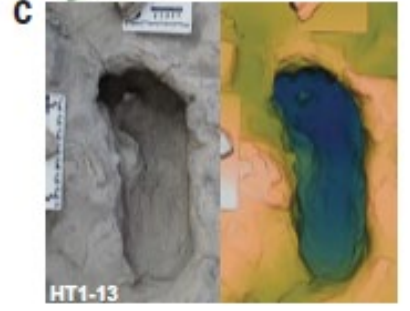
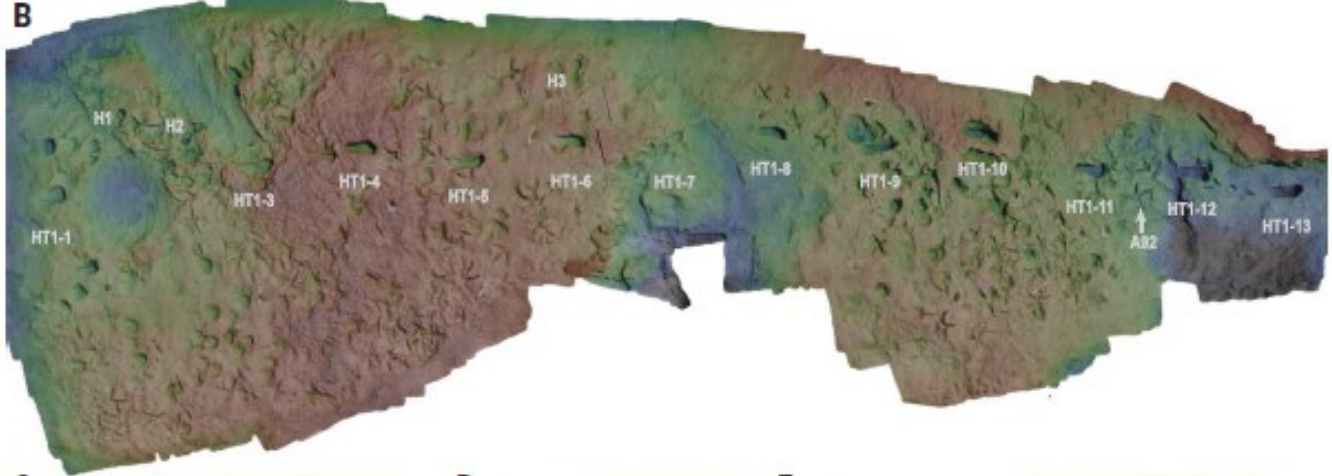
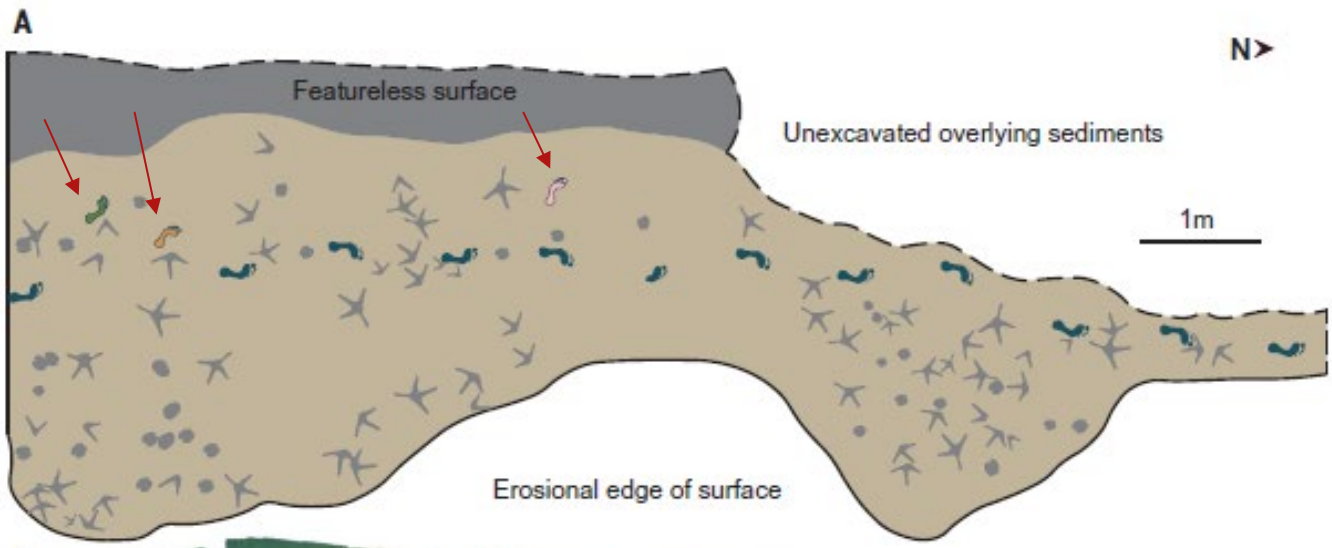
(B) *P. boisei*: Track H3, which has a RAV of 17.93 at a relative depth of 0.38.

(C) *H. erectus*: Track HT1-5, which has a RAV of 3.62 at a relative depth of 0.45.

H. erectus and P. boisei



Footprints of Homo erectus (left) and Paranthropus boisei (right). Credit: Kevin Hatala/



The TS-2 track surface and selected individual tracks. The continuous HT1 trackway appears in dark blue (*P. boisei*). Isolated tracks H1 (green), H2 (orange), and H3 (pink) are oriented nearly perpendicular to the HT1 trackway (*H. erectus*)

Geologically instantaneous

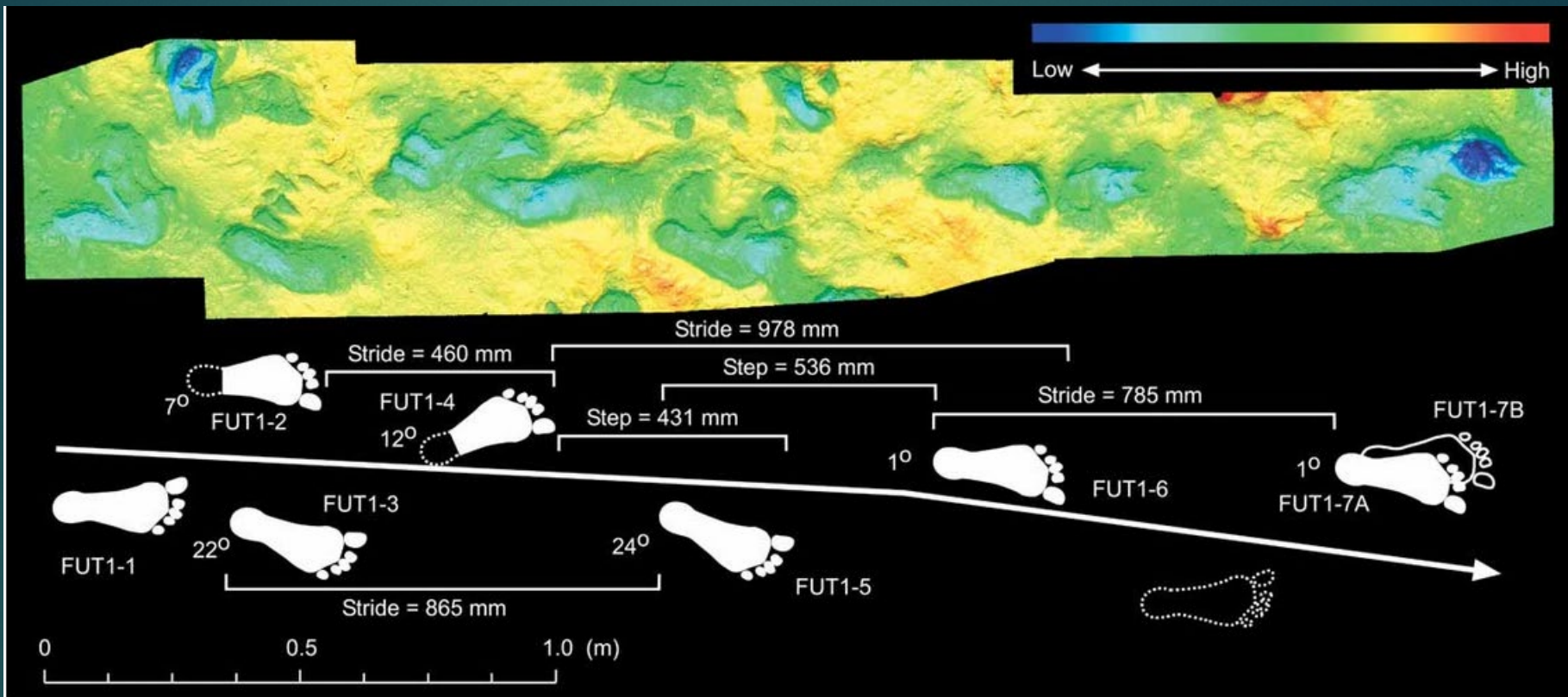
- ▶ The co-occurrence of different hominin track morphologies, and their association with other mammal and bird tracks on the TS-2 surface, was geologically instantaneous.
- ▶ The FE22 footprints are similar to those of other track-bearing deposits in Area 103 and Ileret Area 1A , which occur at different stratigraphic levels between ~1.4 and 1.6 Ma.
- ▶ Based on these data, it is clear that hominins were repeatedly visiting lake margin habitats, walking on wet substrates, wading into shallow water, and potentially interacting with other animals frequenting these environments.

Ecological sympatry

- ▶ Skeletal fossils of *H. erectus* and *P. boisei* have long been known to co-occur within the same geological members of the Koobi Fora Formation. Prior analyses have shown that fossils of one taxon or the other are more common in certain paléoenvironnements. Lake margin sediments preserve Homo and Paranthropus fossils at roughly even frequencies, suggesting that these environments may have supported ecological sympatry.
- ▶ With a sparse record of postcranial fossils that are mostly isolated, fragmentary, and/or difficult to attribute taxonomically, there is little skeletal evidence allowing direct comparisons of bipedalism in *H. erectus* and *P. boisei*.
- ▶ Fossil footprints, by contrast, provide focused in situ snapshots that allow interspecific co-occurrences and interactions to be inferred more directly.

FE22 site at Kobi Fora

- ▶ At both FE22 and at site FwJj14E near Ileret, we have documented two distinct patterns of hominin track morphology on the same footprint surfaces. We propose that these represent two different taxa, characterized by disparate foot anatomies and locomotor kinematics. This interspecific co-occurrence, within meters and hours to days of each other, implies that *H. erectus* and *P. boisei* coexisted and potentially interacted with each other in lake margin environments during the early Pleistocene.
- ▶ Furthermore, given different locations (~40 km apart) and depositional and temporal differences between sites recording these two hominin track morphologies within the same ~200,000-year time interval, evidence is provided for a sustained pattern of hominin sympatry.



Footprint trail designated as FUT1 in Bennett and coworkers (2009). As discussed below, later work showed that this includes two overlapping trackways, FUT1A and FUT1B.

By far the most extensive data came from the Upper Footprint Layer at [FwJj14E](#) in 2009 Ileret study, where at least 8 different *H. erecti* made trails. This single trail was actually two overlapping trails, made by two different individuals.

Reinterpretation of prior trackways

- ▶ Using their new approach, Hatala and coworkers revisited FwJj14E and some of the other footprint sites. Some of those prints were incompatible with human footprints, too.
- ▶ With the new data, the Upper Footprint Layer trails at Ileret now include not only *H. erectus* but also at least one *P. boisei* trackway.
- ▶ The most interesting example is the one discussed above, the FUT1 trail that in 2016 Hatala and collaborators showed was actually two overlapping trackways. Now the footprints themselves support the reinterpretation that these two overlapping trackways were made by two different species: the FUT1A trackway by *H. erectus* and the FUT1B trackway by *P. boisei*.

3 Ileret footprints were *P. boisei*

- ▶ They revised prior hypotheses by attributing tracks FUT1-6, FUT1-12, and FUT1-14 to trackway FUT1B rather than FUT1A, and we tentatively attribute that trackway to *P. boisei* given morphological similarity to the TS-2 HT1 trackway.
- ▶ Unlike the new Koobi Fora example, where the *H. erectus* prints are the isolated, **at the FwJj14E site two species made long trackways in the same direction on the same path.**

Footprint Layer at FwJj14E

- ▶ In fact, these two overlapping trackways were made by two different species: the FUT1A trackway by *H. erectus* and the FUT1B trackway by *P. boisei*.
- ▶ Unlike the new Koobi Fora example, where the *H. erectus* prints are the isolated, at the FwJj14E site two species made long trackways in the same direction on the same path.
- ▶ **John Hawks:** To me, that was a surprising twist with greater import than the new footprint site. This reinterpretation of the Ileret tracks contradicts the ideas from 2016 about a pack of male *Homo erectus* individuals moving together—at least, unless the pack included a *boisei* member. Maybe instead, a smaller *erectus* group might have followed one or more *boisei* individuals down the shoreline. Or maybe they were foraging in the same place for the same foods.

Bennett, 2009 & K. Hatala, 2016

- ▶ Carried out experiments to determine how long the footprints could have retained their shape in the sandy silt without being protected by more sediment. They found that even a day or two of exposure to the elements tended to degrade them. Each of these surfaces is a record of a fairly short time on the landscape.
- ▶ A
- ▶ t the very least, the evidence from the Ileret track surfaces of multiple *H. erectus* males walking across the same landscape, and possibly even traveling together, is consistent with a level of male–male cooperation similar to that observed in modern chimpanzees

The Koněprusy caves in the Czech Republic: 45 Ka Zlatý kůň skeletons



MH Zlatý kůň woman, in the Koněprusy caves, Czech Republic.



Zlatý kůň woman illustration based on genetic speculation



Nature, 2024: Earliest modern European genomes

- ▶ MHs from 49 to 42 Ka = 6 MH genomes from Ranis, Germany, and one from the Zlatý kůň site in the Czech Republic;
- ▶ These **linked populations**, which probably **consisted of only about 300 members** spread across Central Europe, also **shared 2.9 percent Neandertal ancestry**.
- ▶ Study: By looking at the length of the Neandertal gene segments in these human genomes, the researchers were able to gauge when Neandertal ancestry was introduced: **Longer segments are more recent additions because genetic recombination hasn't had a chance to scramble them. Shorter segments come from a more distant interbreeding event.**
- ▶ Central Europeans were removed by about 80 generations, or between 1,500 and 1,000 years, from ancestors who mixed with Neandertals.

MHs in Europe by 45 Ka

- ▶ Earlier this year, some of the same researchers showed that Ranis was inhabited by modern humans 45,000 years ago – confirming that our species had reached Europe by this time.
- ▶ Based on the length of the Neanderthal DNA segments, the team estimated the MH-N interbreeding happened between 45,000 and 49,000 years ago – and that it was the same mixing event that produced all non-Africans today. The interbreeding seems to have happened around 80 generations before the studied individuals lived.

Extinction is the norm in evolution

- ▶ Notably, there is no trace of earlier mixing with Neanderthals in modern human genomes: all the Neanderthal DNA comes from 47,000 to 40,000 years ago.
- ▶ Just as Ns went extinct circa 40-42 Ka, the implication is that the earlier modern human migrations out of Africa also went extinct.
- ▶ The genomics also shows that some of the modern human populations were shockingly small. The Ranis and Zlatý kůň individuals were quite closely related, despite being hundreds of kilometers apart.
- ▶ The Zlatý kůň woman was “either a distant cousin or a grandmother or grandchild” of the Ranis individual.

When did N and MHs mix?

Study, published Dec. 12 in the journal Nature showed that Neanderthal DNA found in all ancient and present-day non-Africans came from one "pulse" of interbreeding that happened somewhere around 45,000 to 49,000 years ago.

- ▶ There was a fifth- or sixth-degree genetic relationship between a woman from Zlatý kůň and two individuals from Ranis, meaning they all descended from the same population that moved to Europe from Africa.
- ▶ The Ranis/Zlatý kůň people split off quickly from the original population that moved out of Africa — and that the split happened shortly after the original population interbred with Neanderthals.
- ▶ This group was not the only group of that original OoA population.
- ▶ Then, the Ranis/Zlatý kůň lineage died out.

7000 years of hooking up

- ▶ The research pinpointed a pivotal period that began about 50,500 years ago and ended around 43,500 years ago. Over this 7,000-year time frame, early humans encountered Neanderthals, had sex and gave birth to children on a fairly regular basis. The height of the activity was 47,000 years ago.
- ▶ It suggested that the main wave of migration out of Africa was essentially done by 43,500 years ago because most humans outside Africa today have Neanderthal ancestry originating from this period,

All MHs over 50 Ka went extinct

- ▶ This means that "all modern human remains outside of Africa over 50,000 years old are not ancestors of modern-day people" but rather evolutionary dead-ends.
- ▶ The study underscores the **fragility of early human populations** in Ice Age Europe, whose survival depended on navigating both climatic challenges and interactions with other hominins.
- ▶ The **genomic data reveals a small, tightly connected population descended from an early wave of humans who left Africa approximately 50,000 years ago.**

Other findings

- Two of the Ilsehöhle individuals were infants. Three were male and three female. Among them was a mother and a daughter, while others were more distant relatives.
- There was a fifth- or sixth-degree genetic relationship between the individual from Zlatý kůň and two individuals from Ilsehöhle, which means that Zlatý kůň was part of the Ranis family and probably also made LRJ-type tools.
- The male Ranis13 and the female Zlatý kůň represent the oldest high-quality modern human genomes sequenced so far.
- Zlatý kůň/Ranis individuals had genetic variants associated with dark skin, dark hair and brown eyes.

Findings

- *No traces of introgression with later Neanderthals observed in other more recent sapiens have been identified in their genomes .*
- Strong selection against newly acquired Neanderthal DNA has been observed in the 100 generations following interbreeding, except for genetic variants related to skin pigmentation, the immune system, metabolism and some diseases, such as autism.

Science article: identical conclusions

- ▶ A separate study, published Friday (Dec. 13) in the journal Science, also employed genomic analysis of ancient and present-day humans to arrive a similar conclusion:
 - ▶ The vast majority of Neanderthal DNA in modern humans comes from one period of gene flow that lasted for about seven millennia, between 50,500 and 43,500 years ago.
- ▶ Found that an "extended pulse" model was the best fit for the data, meaning Neanderthals and modern humans mated over multiple generations for roughly 7,000 years.
- ▶ In the Science study, Leonardo Iasi, an evolutionary geneticist at the Max Planck Institute for Evolutionary Anthropology, led a team of researchers in combing through 334 modern-human genomes from around the world.

MH and Ns sympatry for 7000 years

- ▶ The genome-based estimate is consistent with archeological evidence that modern humans and Neanderthals lived side-by-side in Eurasia for between 6,000 and 7,000 years.
- ▶ Found an average date for Neanderthal-*Homo sapiens* interbreeding of about 47,000 years ago. Previous estimates for the time of interbreeding ranged from 54,000 to 41,000 years ago.
- ▶ “Extended pulse” model was the best fit for the data, meaning Neanderthals and modern humans mated over multiple generations for roughly 7,000 years

Immediately beneficial N genes

- ▶ Additionally, by scanning the genomes for regions with unexpectedly high frequencies of Neanderthal ancestry, the team identified 86 regions in the modern-human genome that suggested mating with Neanderthals conferred immediate adaptation advantages.
- ▶ Specifically, the genome regions related to skin pigmentation, metabolism and immunity had a lot of Neanderthal DNA..

N gene deserts in MHs formed very early

- ▶ They found that areas lacking any Neanderthal genes, so-called archaic or Neanderthal deserts, developed quickly after the two groups interbred, suggesting that some Neanderthal gene variants in those areas of the genome must have been lethal to modern humans.
- ▶ Early modern human samples that are older than 40,000 years already contained these deserts in their genomes.
- ▶ We find that very early modern humans from 40,000 years ago don't have any ancestry in the deserts, so these deserts may have formed very rapidly after the gene flow

*** Nature study: Earliest modern human genomes constrain timing of Neanderthal admixture -- Arev P. Sümer...J. Krause, et al., 2024

- ▶ Modern humans arrived in Europe more than 45,000 years ago, overlapping at least 5,000 years with Neanderthals. Limited genomic data from these early modern humans have shown that at least two genetically distinct groups inhabited Europe, represented by Zlatý kůň, Czechia and Bacho Kiro, Bulgaria.
- ▶ Here we deepen our understanding of early modern humans by analyzing one high-coverage genome and five low-coverage genomes from ~45,000 year-old remains from Ilsehöhle in Ranis, Germany, and a further high-coverage genome from Zlatý kůň.
- ▶ We show that distant familial relationships link the Ranis and Zlatý kůň individuals and that they were part of the same small, isolated population that represents the deepest known split from the Out-of-Africa lineage.

N-MH mix at 45-49 Ka

- ▶ Ranis genomes harbor Neanderthal segments that originate from a single admixture event shared with all non-Africans that we date to ~45,000-49,000 years ago.
- ▶ This implies that ancestors of all non-Africans sequenced to-date resided in a common population at this time, and further suggests that modern human remains older than 50,000 years from outside Africa represent different non-African populations
- ▶ However, neither study can answer a long-standing question: What did the interactions between Neanderthals and modern humans actually look like?

5 sites with genome-wide data

- ▶ To date, only five sites have yielded genome-wide data from modern humans that lived before 40 kya and thus temporally overlapped with Neanderthal. The Neanderthal ancestry in the genomes from two of these sites likely originated from just a single introgression event (i.e. an admixture with Neanderthals that may have continued over several generations) .
- ▶ However, the genomes of individuals from the other three sites showed evidence for additional, more recent Neanderthal introgression events. The high-coverage genome of the **~44 ky-old Ust'-Ishim** individual, an early inhabitant of Siberia, shows signals for such an additional introgression event around 30-50 generations before the individual lived.

Descendants in some early MHs, and none in others

- ▶ A similar analysis has shown that the ~40 ky-old Oase 1 individual from Peștera cu Oase, Romania, and four individuals dating to ~44 kya from Bacho Kiro, Bulgaria, had Neanderthal ancestors likely within the last 10-20 generations before they lived.
- ▶ In contrast, no evidence for additional admixtures have been found for the 40 ky-old Tianyuan individual from China or the Zlatý kůň individual from Czechia . Although direct radiocarbon dating yielded unreliable results for Zlatý kůň, the lengths of Neanderthal ancestry segments in the genome indicated an **age of at least 45 ky**.
- ▶ All previously mentioned individuals showed no, or at most a limited, direct contribution to the ancestry of later Out-of-Africa populations. Notably, the Zlatý kůň individual belonged to a deeply divergent population that separated from the lineage leading to non-Africans earlier than any other known ancient or present-day Out-of-Africa population and is currently the only representative of this early branch.

Small population

- ▶ 11 bone fragments that were found at Ilsenhöhle in Ranis, Germany (hereafter “Ranis”). These bone fragments were directly radiocarbon-dated to between 42,200 and 49,540 years
- ▶ Zlatý kůň and some Ranis individuals shared ancestors in their recent family history. Ranis and Zlatý kůň are thus members of the same population, which we refer to as the Zlatý kůň/Ranis population hereafter.
- ▶ Zlatý kůň/Ranis population shows no contribution to later Out-of-Africans, similar to Ust'-Ishim and Oase 1.

Multiple N introgressions

- ▶ Typical high-frequency phenotypic variants in present-day Europeans such as lactose tolerance, light pigmentation and lighter hair are absent from both the Ranis13 and Zlatý kůň genomes
- ▶ Our analyses indicate that the Zlatý kůň/Ranis population split early from the lineage leading to other non-Africans and that they left no descendants among present-day people.
- ▶ The Neanderthal DNA they carry could therefore have been introduced by a separate event from that which introduced the Neanderthal DNA identified in all present-day Out-of-Africa populations.

Ranis 13 = 43-46 Ka; N mix at 45-49 Ka

- ▶ Since the Ranis individuals carry Neanderthal ancestry from an admixture common to all non-Africans, we can combine the estimated number of generations since this event (**56-98 generations**), with an assumed generation time of 29 years and the **direct radiocarbon date of Ranis13 (43,400-46,580)** to arrive at a **revised date of the common Neanderthal admixture of 45-49 kya**
- ▶ **Ranis 6 = 2-4 yo girl & mother who was related to the Zlatý kůň woman who died 230 kilometers away; they lived within six generations of each other**
- ▶ The Ranis pair, radiocarbon dated to between 42,000 and 49,000 years ago, were likely distant cousins of the Zlatý kůň woman. Together, their DNA would **represent the earliest modern human genomes yet sequenced**.

Small populations

- ▶ Genetic homozygosity indicates only about 200 people at any given time.
- ▶ Probably lived in small, scattered bands that came together occasionally to exchange mates but ranged all across Europe, leaving distinctive, leafshaped stone tools from what is now Britain to Poland.
- ▶ Had dark skin and eyes, and lacked genes for lighter pigmentation; reflect the phenotypical characteristics of sub-Saharan African groups.”
- ▶ The new genomes confirm that close to the time these immigrants arrived in Europe, they met and mated with Neanderthals who occupied the continent.

45 Ka

- ▶ Just 80 to 100 generations, or about 2000 years, had passed since their ancestors last mated with Neanderthals.
- ▶ The result, which dovetails with a parallel study released earlier this year in a preprint and published today in Science, suggest a major episode of mixing took place some 45,000 years ago—far more recently than scientists had thought.
- ▶ Both studies show the Neanderthal DNA in all modern humans living outside of sub-Saharan Africa—resulted not from a few dalliances, but many generations of mixing.

Extinction

- ▶ The ancient family at **Zlatý kůň** and Ranis soon went extinct: these pioneers **died out about 40,000 years ago**.
- ▶ It was **a lot of small populations, facing a lot of environmental and climate change**. **Some just vanished. Neandertals included.**

45-49 KA

- ▶ The Zlatý kůň/Ranis population represents the earliest split from the Out-of-Africa population sampled to date, and our results show that this split occurred shortly after a Neanderthal introgression event that took place only ~80 generations before they lived,
- ▶ We show that this Neanderthal ancestry originates from the same admixture event that can be detected in all other non-Africans and date this event to 45-49 kya, close to or more recent than most previous estimates of 52-57 kya, 47-65 kya and 41-54 kya, in prior studies

Separate populations

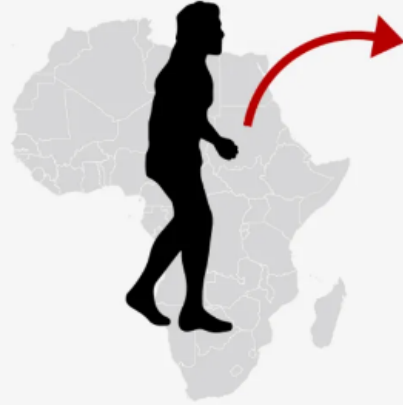
- ▶ This further implies that modern human remains and material cultures older than ~50 ky found outside of Africa would not represent this non-African population; instead they either resulted from separate Out-of-Africa migrations or they represent populations that split earlier from the ancestors of non-Africans and that were not part of the shared introgression event with Neanderthals.
- ▶ Since all populations that carry ancestry from another archaic lineage, the Denisovans, also carry Neanderthal ancestry from this shared event, we can infer that the Denisovan admixture post-dates 45-49 kya.

MHs went extinct many times early on

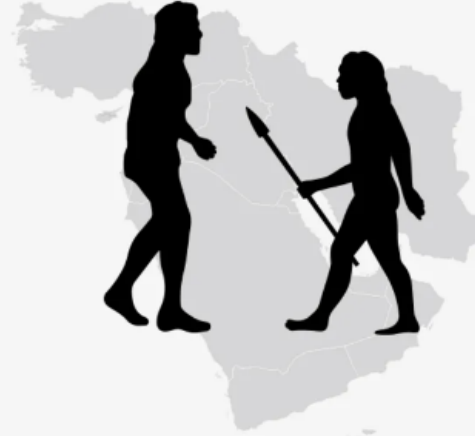
- ▶ Modern humans went extinct many times before going on to populate the world.
- ▶ While Neandertals were long seen as a species which we successfully dominated after leaving Africa, new studies show that only humans who interbred with Neanderthals went on to thrive, while other bloodlines died out.
- ▶ In fact, Neanderthal genes may have been crucial to our success by protecting us from new diseases we hadn't previously encountered.

Spread of Neanderthals and Homo sapiens

- 1** Up to **60,000 years ago** – a wave of Homo sapiens moves from Africa and spreads across globe



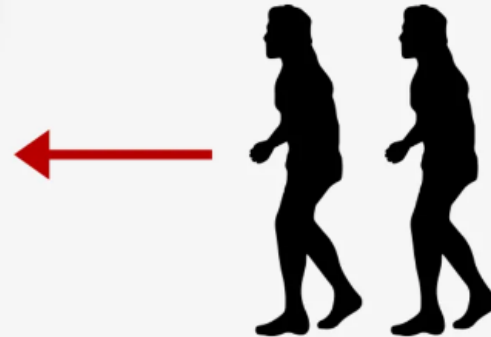
- 2** **48,000 years ago** - Homo sapiens interbreed with Neanderthals in Middle East and their offspring migrate



- 3** **40,000 years ago** – Homo sapiens, Neanderthals, and the interbred species in Europe all go extinct



- 4** New wave of interbred Homo sapiens later returns to Europe



Extinctions due to environmental factors

- ▶ Those first modern humans that had interbred with Neanderthals and lived alongside them died out completely in Europe 40,000 years ago - but not before their offspring had spread further out into the world.
- ▶ J. Krause states that these early extinctions were due to environmental factors. "Both humans and Neanderthals go extinct in Europe at this time," he said. "If we as a successful species died out in the region then it is not a big surprise that Neanderthals, who had an even smaller population went extinct."
- ▶ The climate was incredibly unstable at the time.

OoA no later than 43 Ka

- ▶ Suggests that the major migration out of Africa occurred no later than 43,500 years ago.
- ▶ Diversification of humans outside of Africa may have begun during or soon after the Neandertal gene flow, which could partially explain the different levels of Neandertal ancestry among non-African populations and also reconcile our dates with archaeological evidence for the presence of modern humans in Southeast Asia and Oceania by about 47,000 year
- ▶ Identified some Neandertal DNA regions that are present at high frequency, possibly because they were beneficial as early modern humans began to explore new environments outside of Africa. These include genes related to immune function, skin pigmentation and metabolism.

Related populations

- ▶ The Zlatý kůň/Ranis population became extinct without leaving genetic descendants in later populations.
- ▶ However, the Neanderthal DNA they carry comes from the same admixture event that gave rise to the Neanderthal DNA present in present-day non-African humans.
- ▶ This implies that, 45–49 ka ago, the Ranis. Zlatý kůň/Ranis group and the ancestors of other *early sapiens* in a “Neanderthal kingdom”, such as those from Bacho Kiro Cave (Bulgaria) and Oase (Romania), were part of a connected population that later branched off.
- ▶ On the other hand, it has been said that it would also imply that the ancestral populations of present-day humans in Asia and Oceania are later than 50 ka, since their genomes share the same introgression event, and that the interbreeding with Denisovans is also more recent, having occurred after this event.

Other possibilities

- ▶ However, it cannot be ruled out that some groups descended from the first *sapiens* in Eurasia mixed with descendants of European "hybrids" before disappearing, especially in "hot spots" such as the crossroads of the Near East.
- ▶ In Sahul, it cannot be ruled out that groups arriving before 65 ka interbred with waves after 50 ka that carried the Neanderthal introgression event.

***** Science study: Neanderthal ancestry through time: Insights from genomes of ancient and present-day humans – L. N. Jasi

- ▶ From the study of 300 genomes of modern humans from the last 45 ka, including 59 from individuals who lived between 2.2-45 ka ago and 275 from present-day humans, taking into account the amount of Neanderthal DNA present in these samples and the variation in the level of Neanderthal ancestry depending on the location and age, it has been possible to identify an important period of hybridization between both species (47 Ka ago) that lasted about 6.8 Ka. When this period ended, the amount of Neanderthal trace in the sapiens genome was approximately 5%.
- ▶ Most natural selection—positive and negative—on Neanderthal ancestry variants occurred immediately after the gene flow,

Single major admixture

- ▶ Early OoA individuals 296 MB or 34% unique N DNA.
- ▶ Most natural selection, both positive and negative, on Neandertal ancestry variants occurred immediately after the gene flow,
- ▶ *** Neandertal gene flow occurred between 321 and 950 generations before these individuals lived.
- ▶ **Single major admixture:** Infer the average generation interval as 28.4 years and the time of the shared pulse of Neandertal gene flow as 46,364 [45,682-47,045] and a duration of around 6,832 years [2,044–9,968 years].

Some Unknowns

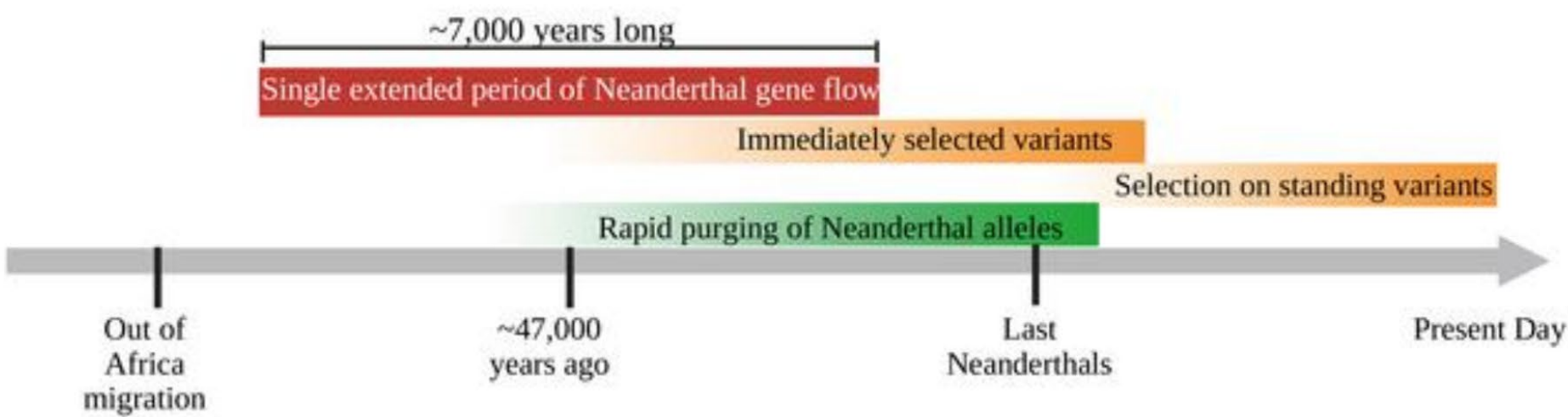
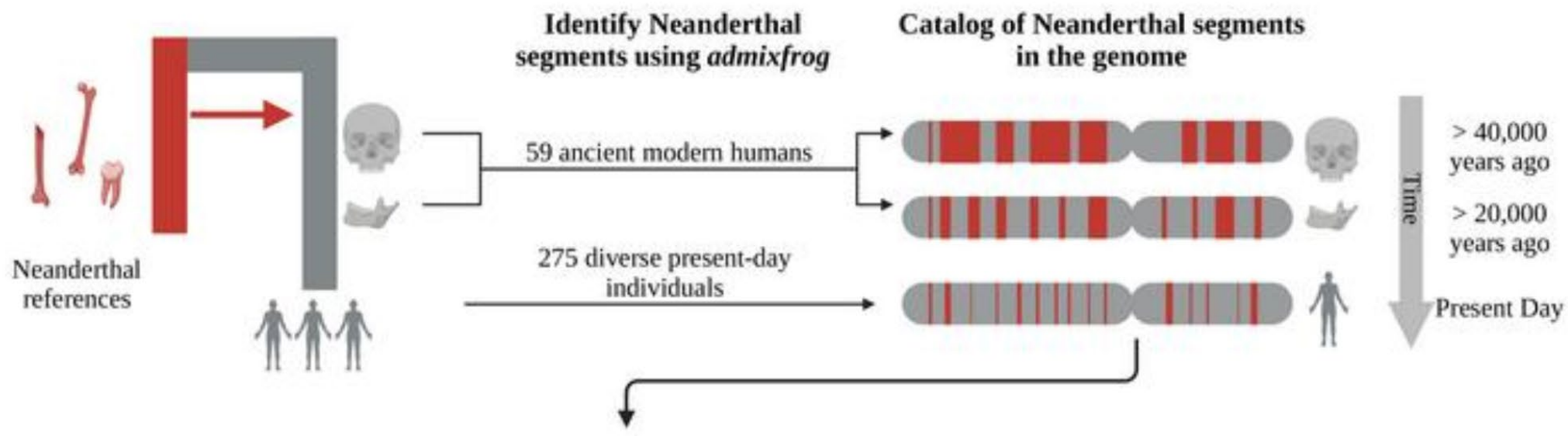
- ▶ However, there is still much scientists don't know. It's not clear why people in East Asia today have more Neanderthal ancestry than Europeans, or why Neanderthal genomes from this period show little evidence of Homo sapiens DNA.
- ▶ The family group was part of a pioneer population that eventually died out, leaving no trace of ancestry in people alive today.
- ▶ Other lineages of ancient humans also went extinct around 40,000 years ago and disappeared just like the Neanderthals ultimately did.
- ▶ These extinctions suggest that Homo sapiens did not play a role in the demise of Homo neanderthalensis.

*** Summary: Neanderthal ancestry through time: Insights from genomes of ancient and present-day humans -- Leonardo N. M. Iasi, et al., 2024

- ▶ Most non-Africans living today derive ~1 to 2% of their ancestry from Neanderthals.
- ▶ Across the genome, some genomic regions harbor a high frequency of Neanderthal variants and are identified as “candidates of adaptive introgression,” whereas others are devoid of any Neanderthal ancestry and are referred to as “deserts.”

Unique N ancestry not in MHs

- ▶ The comparison with sequenced Neanderthals, for example, Vindija, Altai, and Chagyrskaya, suggests that the gene flow occurred from a single or multiple closely related Neanderthal groups.
- ▶ By contrast, the earliest modern humans—Oase, Ust'-Ishim, Zlatý kůň, and Bacho Kiro—possess substantial unique Neanderthal ancestry and a distinct matching profile to the sequenced Neanderthals, indicating that some Neanderthal ancestry in these early individuals is not shared with modern humans after 40,000 years.



N gene flow at 47 Ka, lasting 7 K years

- ▶ Found evidence for a single extended period of Neanderthal gene flow that occurred ~47,000 years ago and lasted for ~7000 years. This is consistent with archaeological evidence for the potential overlap of early modern humans and Neanderthals in Europe.
- ▶ Finally, we examined the frequency of Neanderthal ancestry across the genome and over time. We uncovered **new candidates of adaptive introgression, including regions**
 - ▶ that were immediately adaptive for modern humans and
 - ▶ some that became adaptive more recently from introgressed standing variation.

N gene flow between 50 and 43 Ka

- ▶ Most Neanderthal deserts—on the autosomes and the X chromosome—were formed rapidly after the gene flow and were also evident in the earliest modern human genomes. Notably, the X chromosome exhibits a nonuniform and nonrandom distribution of Neanderthal ancestry, with large Neanderthal ancestry deserts overlapping previously identified signals of sweeps in non-Africans.
- ▶ We found strong support for a single extended period of Neanderthal gene flow into the common ancestors of all non-Africans that occurred between 50,500 and 43,500 years ago.
- ▶ The majority of natural selection—positive and negative—on Neanderthal ancestry happened very quickly after the gene flow and left clear signals in the genetic diversity of the earliest modern humans outside Africa.

*** Neanderthal ancestry through time: Insights from genomes of ancient and present-day humans -- Leonardo N. M. Iasi, et al., 2024

- ▶ We generated a catalog of Neanderthal ancestry segments in more than 300 genomes spanning the past 50,000 years. We examined how Neanderthal ancestry is shared among individuals over time. Our analysis revealed that the **vast majority of Neanderthal gene flow is attributable to a single, shared extended period of gene flow that occurred between 50,500 to 43,500 years ago**, as evidenced by ancestry correlation, colocalization of Neanderthal segments across individuals, and divergence from the sequenced Neanderthals. **Most natural selection—positive and negative—on Neanderthal variants occurred rapidly after the gene flow.**

Neanderthal ancestry variation in modern humans

- ▶ Using recently developed methods, we generated a **catalog of Neanderthal introgressed segments covering nearly 1.6 Gb of the human genome (1551 Mb on the autosomes and 29 Mb on the X chromosome)**.
- ▶ We found that the **vast majority of Neanderthal ancestry in modern humans is attributable to a single, shared extended period of gene flow into the common ancestors of non-Africans**, although we cannot rule out the possibility that some populations may have received minor contributions of additional Neanderthal ancestry.

East Asians have 20% more N DNA

- ▶ The earliest individuals—Oase, Ust'-Ishim, Zlaty'kun, and Bacho Kiro—possess substantial unique Neanderthal ancestry, distinct matching profiles to the sequenced Neanderthals, and the weakest correlation of introgressed segment locations with other ancient or present day individuals.
- ▶ This suggests that some Neanderthal ancestry in these early individuals is not shared with modern humans after 40,000 years. Consistent with previous studies, we found that present-day East Asians harbor ~20% more Neanderthal ancestry than West Eurasians.
- ▶ However, this difference was not observed when comparing ancient East Asians (Tianyuan and Salkhit) with pre LGM West Eurasians.

Timing of Neanderthal gene flow

- ▶ Inferred the time of the shared pulse of Neanderthal gene flow as 46,364 years ago. (45,682 to 47,045).
- ▶ Mean time of gene flow of around 47,124 years ago (46,872 to 47,404) and a duration of around 6832 years (2044 to 9968 years).

How N segments in MHs have changed thru time

- ▶ Question of how the frequency of Neanderthal variants has changed through time.
- ▶ Using Neanderthal segments in ancient and present-day individuals, we **recovered Neanderthal ancestry in 61.7% (1551 Mb) of the autosomal genome.**
- ▶ **On the X chromosome, we found Neanderthal ancestry only in 20.2% (29 of 145 Mb) of the genome. Neanderthal ancestry segments on the X chromosome have large genomic regions devoid of any Neanderthal segments.**
- ▶ We identified **86 regions (347 genes) that are at high frequency in both present-day and ancient individuals and may be candidates of immediate positive adaptation**

Beneficial N DNA

- ▶ Found that these candidate regions are enriched for pathways related to skin pigmentation, metabolism, and immunity.
- ▶ Suggesting that many of these genes may have been immediately beneficial to modern humans as they encountered new environmental pressures outside Africa.
- ▶ We found 91 candidate regions (169 genes) at high frequency in present-day individuals but not in ancient individuals, indicating that these regions may contain variants that became adaptive later on (selection on standing introgressed variation)

Deserts

- ▶ Found 32 candidate regions (102 genes) that were at high frequency in ancient individuals but not in present-day individuals. Many of these regions (~44%) are located within 1 Mb of candidate adaptive regions, suggesting that these haplotypes hitchhiked with beneficial mutations and decreased in frequency as recombination occurred.
- ▶ This indicates that the deserts formed rapidly after the initial gene flow.

N DNA depletions happened rapidly

- ▶ Found that Neanderthal ancestry on the X chromosome is substantially depleted compared with that on the autosomes, including individuals older than 30,000 years ago.
- ▶ That the depletion is present even in our earliest samples suggests that the selection on these haplotypes may have occurred rapidly during and immediately after Neanderthal gene flow.

OoA migration no later than 43,500 years ago

- ▶ The major out-of-Africa migration occurred no later than 43,500 years ago.
- ▶ Moreover, the population receiving Neanderthal ancestry might have been highly structured (a population where individuals are distinctly divided into subgroups with noticeable genetic differences) during the gene flow.
- ▶ Moreover diversification of people outside Africa may have started during or soon after the Neanderthal gene flow, which could partially explain different levels of Neanderthal ancestry among non-African populations and also reconcile our dates with archaeological evidence for the presence of modern humans in Southeast Asia and Oceania by ~47,000 years.

Positive and negative selection happened quickly

- ▶ Finally, we demonstrate that the landscape of Neanderthal ancestry across the genome was formed rapidly after the gene flow. Most natural selection—positive and negative—on the Neanderthal ancestry variants occurred within ~100 generations after the gene flow.
- ▶ Notably, we found that the depletion of Neanderthal ancestry and the strong sweeps on the X chromosomes in non-Africans occurred rapidly.
- ▶ We infer that the major Neanderthal gene flow in modern humans occurred 50,500 to 43,500 years ago, which is consistent with archaeological evidence for the overlap of modern humans and Neanderthals in Europe.

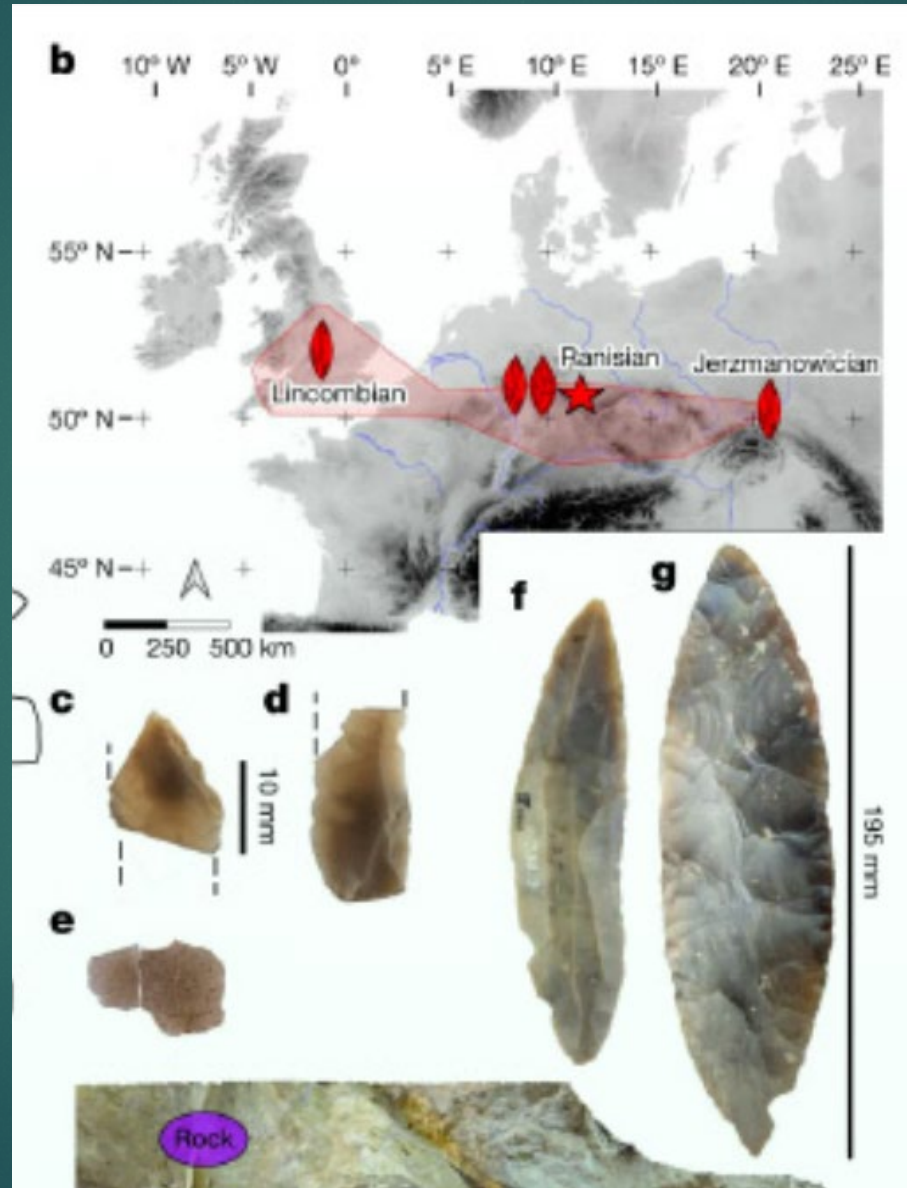
Conclusion

- ▶ These dates have several implications for the spread of humans after the out-of-Africa event.
- ▶ The timing of this gene flow into the common ancestors of non-Africans provides a lower bound on the timing of the out-of-Africa migration and settlement of regions outside Africa.
- ▶ Suggests that the major out-of-Africa migration occurred no later than 43,500 years ago. (compared to 60-50 Ka from earlier studies)
- ▶ Moreover diversification of people outside Africa may have started during or soon after the Neanderthal gene flow circa ~47,000 years.

*** The Lincombian-Ranisian-Jerzmanowskian period

- ▶ About 45 ka ago, *Homo sapiens* briefly inhabited the Ilsenhöhle cave in Ranis (Thuringia, Germany), and were the authors of the stone tools linked to a cultural transition period between the Middle and Upper Paleolithic known as the Lincombian-Ranisian-Jerzmanowskian (LRJ).
- ▶ These pioneering groups of modern humans adapted to the cold and a steppe and tundra landscape, competing with hyenas, cave bears and other predators for the faunal resources of the place.
- ▶ Evidence of a surprisingly early presence of *H. sapiens* in Europe, some approximately contemporary with Ranis (Bacho Kiro, Zlatý kůň, Grotta del Cavallo, Kent's Cavern, Oase, and others even older (Grotte Mandrin, 54 ka ago, and the possibilities of Banyoles, Spain, 45-66 ka ago and Apidima, Greece 211 ka ago).

Lincombian-Ranisian-Jerzmanowskian (LRJ).

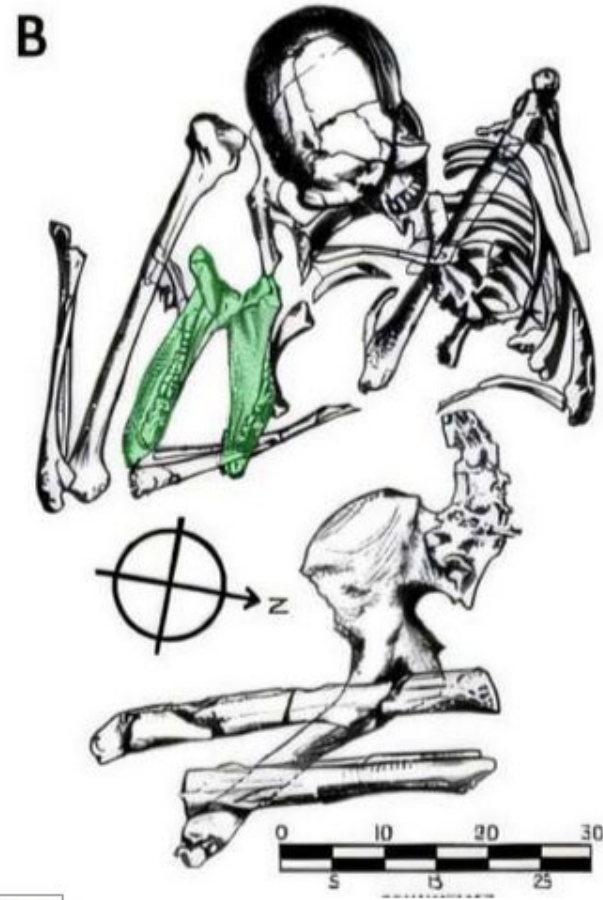
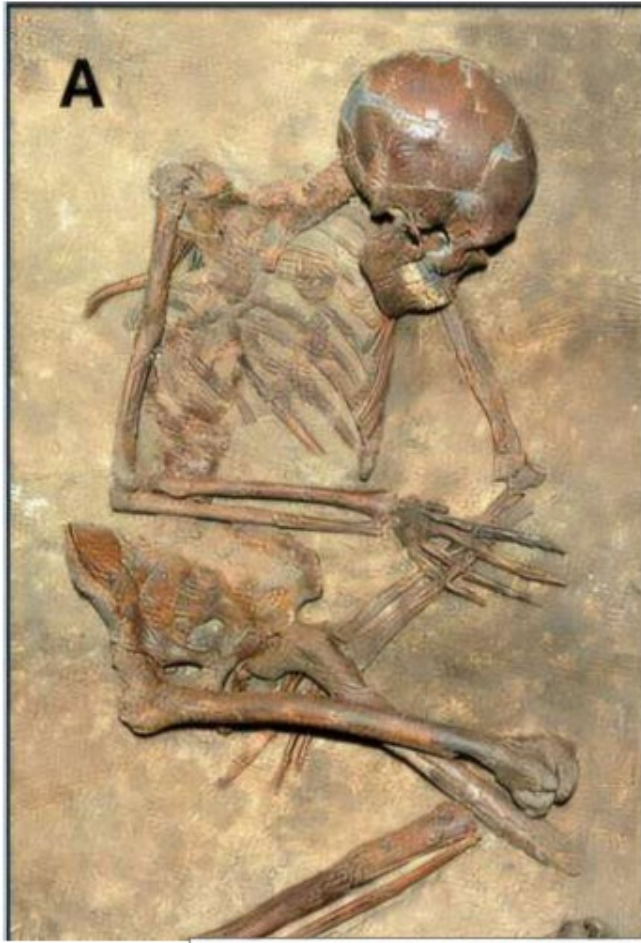


- ▶ Furthermore, the same type of stone tools found at Ranis – **Lincombian-Ranisian-Jerzmanowician (LRJ)**, characterized by long, leaf-shaped points – are also found in Ranis and Britain
- ▶ Yet Krause’s team found that the **effective population size was “about 200 individuals”**, despite them apparently spanning northern Europe.
- ▶ This LRJ culture has **left no living descendants**. Neither has the **Zlatý kůň population**.
- ▶ **Likely produced the same distinctive LRJ-style tools found at both sites**

Human bone fragment from Ilsenhöhle cave and entrance to the cave beneath Renis Castle. Tools from the LRJ culture.



*** Ancient graves reveal distinct burial practices of Neanderthals and early humans in the Levant



00 Human Evolution, Pt 5, 2024 - PowerPoint

Early Homo sapiens burial examples including a double burial from Qafzeh Ca

Ella Been & Omry Barzilai,
L'Anthropologie, 2024

A reconstruction of a burial of a Neanderthal man at La Chapelle-aux-Saints, France.



Levant: both MHs and Ns

- ▶ The *early Homo sapiens* originated from Africa whereas Neandertals arrived from Europe. In the Levant, these populations explored the same geographical niches, utilized similar resources, and may even inhabited the same caves.
- ▶ Study suggests that Neanderthals and early *H. sapiens* might have started to bury their dead at about the same time, about 90,000 to 120,000 years ago, and in the same geographical area, the Levant — the eastern Mediterranean region that today includes Israel, the Palestinian territories, Jordan, Lebanon and Syria. Scientists have long thought the Levant was a key gateway for hominins migrating out of Africa.
- ▶ While the biological and morphological evidence discriminate between the two hominin populations, the material culture does not. Middle Paleolithic Neandertals and *Homo sapiens* used the same knapping methods to make their formal stone tools (i.e., Levallois core technology). This unique scenario hypothetically proposes that the two species shared one material culture.

Burial practices

- ▶ In the current research, we examine this hypothesis through studying the burial practices of these two distinct populations and comparing biological and cultural data from primary grave contexts.
- ▶ Examined anthropological and cultural variables show similar burial behavior in some respects such as body position, gender, age at death or burial offerings/goods, but also exhibit differences in location of burials within the caves, choice of different grave goods, and special positional markers..

Burials originated in Levant?

- ▶ The analyzed data propose the two populations share some cultural behavior from the origin territory (Europe, Africa). Nevertheless, **Middle Paleolithic Levantine burials are earlier than Neandertal burials in Europe and from *Homo sapiens* burials in Africa.**
- ▶ Accordingly, we conclude the custom of human burials was innovated in the Levant from where it spread to the Neandertal territorial range in Europe.
- ▶ A compelling indicator of land ownership is evident in the widespread practice of burials by both populations. We hypothesize that the growing frequency of burials by these two populations in Western Asia is linked to the intensified competition for resources and space resulting from the arrival of these populations

17 N and 15 MH burials

- ▶ Altogether we examined 17 Neandertal burials and 15 *Homo sapiens* burials. Out of the Neandertal sample – five were babies under the age of two years, three were children and the rest were adults. The *Homo sapiens* sample included one specimen younger than two years, four children and the rest were adults.
- ▶ Neandertals and early *Homo sapiens* burial practices in the Levant region had common features but also vary from each other. The two populations buried both sexes as well as all age groups (infants, children, and adults). Previous digs found wild goat horns, red deer jaws, tortoiseshells and stone artifacts in Neanderthal burials, and deer antlers, boar jaws, seashells and the red mineral ochre with *H. sapiens* burials.
- ▶ Burial offerings/goods were also incorporated occasionally in the graves. Yet, there are few substantial differences between the two populations.

Similar and Different

- ▶ While *Homo sapiens* arrived in the region between 170,000 and 90,000 years ago and re-entered the region 55,000 years ago from Africa, Neanderthals came into the Levant from Europe around 120,000 to 55,000 years ago.
- ▶ During this time, both species suddenly began burying their dead, something neither species had done before. This suggests that burials were first innovated in the Levant before spreading or being autonomously innovated elsewhere.
- ▶ The two species are easily distinguishable based on their biology and morphology, with nearly every bone in the body being unique to either species. However, their material culture, mobility and settlement patterns are nearly indistinguishable. Despite this, it was hypothesized that the two species may have had different burial practices.

Differential burials

- ▶ While Neandertals and *Homo sapiens* share many aspects of their material culture to the level that they cannot be distinguished, when it comes to burials the picture is more complicated.
- ▶ The two species share some funerary practices such as grave goods, but they differ in the location of the graves (caves vs. cave terrace/rock shelter), usage of rocks and MLP (Neandertals) and symbolic remains near the graves (ochre and shells; *Homo sapiens*).
- ▶ These included **five Neanderthal sites**; Teshik Tash, Shanidar, Dederiyeh, Amud, Tabun, and Kebara caves, and **two Homo sapiens sites**; Skhul Cave and Qafzeh Cave.

Grave goods

- ▶ Based on the results of around 37 total confirmed burials, it was found that both Homo sapiens and Neanderthals buried their dead regardless of sex or age.
- ▶ However, Neanderthal infant burials were more common than Homo sapiens infants. Similarly, both species would sometimes include grave goods in the form of animal remains, including goat horns, deer antlers, mandibles and maxilla.

Ns buried in caves

- ▶ In the Levant during MI6-MI3, we are not aware of H. sapiens burials within caves. All of their burials are in cave entrances or in rock shelters. Neanderthals, on the other hand, bury their dead inside the caves (except for one, EQ3, which was buried in an open-air site).
- ▶ Additionally, Homo sapiens burials were very uniform, usually laid out in a flexed (fetal-like) posture. This contrasts with the Neanderthal burials, which were more varied and included individuals buried in flexed, extended (straight), and semi-flexed positions while lying on their left, back, or right.
- ▶ Furthermore, Neanderthals were more likely to include rocks in their burials, including placing a body between two large rocks as a form of positional marker or placing modified limestone pieces underneath the dead's heads as a sort of headrest.

Differences

- ▶ Similarly, some aspects of burial were practiced by Homo sapiens but not by Neanderthals, such as having burials associated with ocher and marine shells, which were completely absent in Neanderthal contexts.
- ▶ Contrary to Slimak's idea of N isolation, this is surprising because all of these small, scattered populations wouldn't be expected to share cultural practices over long stretches of space and time.
- ▶ Interestingly, the researchers also noted a burial outburst during this time. Not only did burials suddenly appear, but they occurred at a very high rate in an equally condensed region, especially compared to later burials during the MP in Africa and Europe, of which there are only three in all of Africa and 27, albeit very spatially and temporarily separated for Neanderthals in all of Europe.

Population density effects

- ▶ **An increase in population density may partly explain this sudden boom in burials.** Due to the increased humidity and, thus, a greater number of flora and fauna in the Saharo-Arabian desert around this time, Homo sapiens were attracted to the region from East Africa.
- ▶ **At the same time, melting glaciers in the Taurus and Balkan mountains opened up pathways to the south, enabling Neanderthals to enter the Levant. There, the two populations met, likely increasing population densities in the area and thus increasing demographic pressure and the presence of burials**

Sudden ending of burials

- ▶ This trend of increased burials continued in the region until they suddenly stopped around 50,000 years ago;
- ▶ The most striking thing is that in later periods, humans in the Levant did not continue the practice of burials. After the Neanderthals went extinct around 50,000 years ago, cave burials ceased until the Late Paleolithic, around 15,000 years ago, during the Natufian culture, a semi-sedentary hunter-gatherer society.

Burials as territorial markers

- ▶ Neanderthals and Homo sapiens were both semi-nomadic at the time, but they still likely came back to the same caves seasonally. Because caves were valuable shelters, burying their dead in or near these geological features may have been something like staking a claim to an area or marking territory, as the hominins competed for resources and space.
- ▶ **A cave is an asset..** Where species are meeting and interacting, they are defining boundaries.
- ▶ If both species used burials as a form of marking, that could mean the two exchanged cultural practices, or at least shared an understanding of what the graves or markers meant.

The innovation of burial actually began in the Levant.

- ▶ Many people have argued that burial periods in agricultural people have used burials to claim ownership on land. It's clearly a way of **marking the landscape**.
- ▶ **The oldest burials in the dataset from around 120,000 years ago represent the earliest possible burials from either hominin.** Believe that these burials were the first of a tradition that later radiated out of the Levant into Africa and Europe, where most burials discovered so far are more recent.
- ▶ In Africa, the oldest known *Homo sapiens* burial, a child found at Panga ya Saidi in Kenya, dates back to 78,000 years ago, while most European burials date to 60,000 years ago or less.

*** Neandertals at Gibraltar: Mediterranean Serengeti



N tech abilities

- ▶ Neanderthals were able to construct layered and complex hearths with specific technological objectives that could have included tool, medicine and/or weapon elaboration.
- ▶ At the Vanguard Cave of Gibraltar, in layers geochronologically well constrained between 67.6 ± 5.3 ka to 60.8 ± 11.0 ka, we identify for the first time a Neanderthal's specialized burning structure compatible with essential oils steam distillation from rockroses (Cistaceae) for tar production,

The pit

- Firstly, the **structure was circular**, featuring two channels and a thick wall lining, suggesting a more complex construction than a typical cooking fire pit.
- **2ndly, the hearth was dotted with chemical traces that suggest the combustion of resinous plant material.** This includes **charred wood and microscopic ash fragments**, as well as plant compounds that are often associated with the production of tar from birch bark and similar plants.
- The strands of evidence led the team to **propose that the structure was used for heating a flowering plant, rockroses (Cistaceae), under anoxic conditions by burning herbs and shrubs.**
- They even backed up their theory by building a similar structure and carrying out an experiment to see if they could cook up some birch tar.

Implications

- ▶ Distilling a small bunch of young leaves of rockrose for a reasonable period of time in a closed and almost anoxic environment enabled to produce tar that was more than enough to haft two spearheads, using only tools and materials available in the area for the period in reference.
- ▶ The process of **crafting a gooey glue-like substance from raw ingredients, and then using it to enhance complex tools, could be seen as evidence for Neanderthals possessing a high level of intelligence.**
- ▶ Evidence that **our sister species must have had some grasp of combustion and basic chemistry, not to mention a strong degree of cooperation and communication.**

*** A Neanderthal's specialized burning structure compatible with tar obtention -- Juan Ochando , et al., 2024

- ▶ Present multiproxy evidence of a new type of Neanderthal hearth discovered in Vanguard Cave (VC) (Gibraltar), which is dated 65 kyr, and associated with Middle Paleolithic stone artefacts.
- ▶ The **hearth structure** coincides with predictions from theoretical studies which require the use of heating structures for obtaining birch tar, commonly used in hafting.
- ▶ Propose that the structure was used for heating rockroses (Cistaceae) under anoxic conditions by burning herbs and shrubs, over a guano mixed with sand layer. We tested this hypothesis experimentally with success.
- ▶ The presence of levoglucosan and retene (biomarker of vascular plants) in the structure's matrix points to **combustion of higher resinous plant-derived material**.

Neandertals used tar for hafting spears

- ▶ Our results advance our understanding of Neanderthal behavior, as the ability to organize activities related with the use of fire.
- ▶ Ns made tar for “hafting” weapons — but how they succeeded was a mystery. Theoretical studies had proposed two methods by which this tar could have been made, one method was simple and of low productivity: it involved the combustion, in the open air, of birch bark.
- ▶ A second, more complex, method would have needed the anoxic heating of fragments of woody plants, such as birch; so they would exude resin but not burn.
- ▶ The findings of the 31 scientists from six countries and 15 disciplines have confirmed the Neanderthals used the complex method. It required heating plants to more than 300 degrees centigrade, a feat scientists find difficult to duplicate without a ceramic container.

Neandertals invent anoxic heating system

- ▶ **C. Finlayson:** Excavators at a cave in Gibraltar have found evidence that the species mastered a complex industrial process to make tar as an adhesive for fastening stone points to spear shafts.
- ▶ These archaic humans pioneered a system of “anoxic heating” 60,000 years ago, designing a pit on the floor of a cave in which wood was buried and heated to hundreds of degrees to make it exude resin without catching fire.
- ▶ The structure that was discovered in Vanguard Cave resembles a simple hollow in the cave sediment and its simplicity may explain why such structures may not have been recognized in the past.
- ▶ The Neanderthals had to go through a series of thought processes, choose which plants to select and work out how to extract resin without burning them

How Neanderthals used chemistry to make tools

1

The Neanderthal digs a hole and lines it with stones and woody plants

2

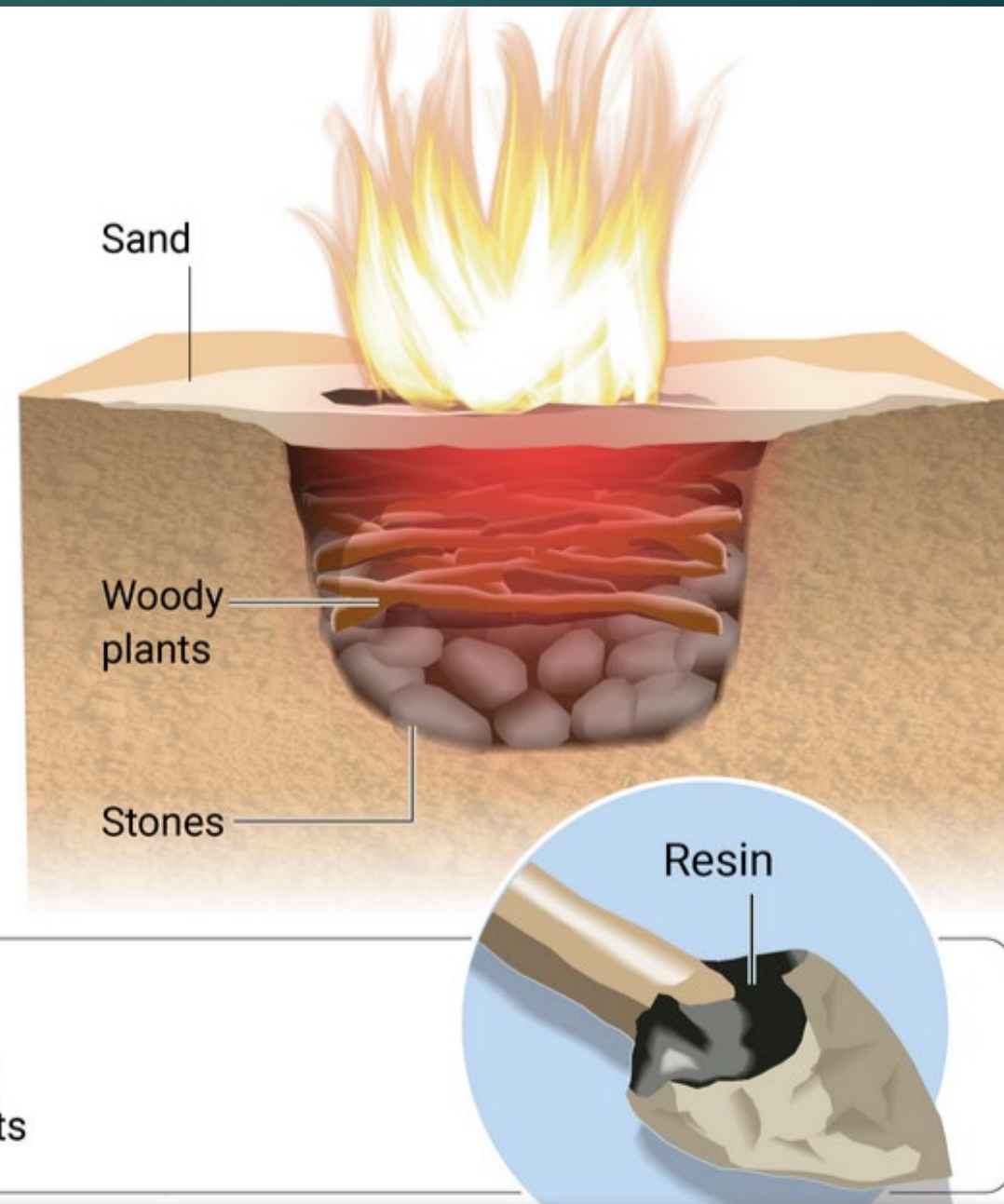
The hole is covered with guano and sand to create a primitive oven

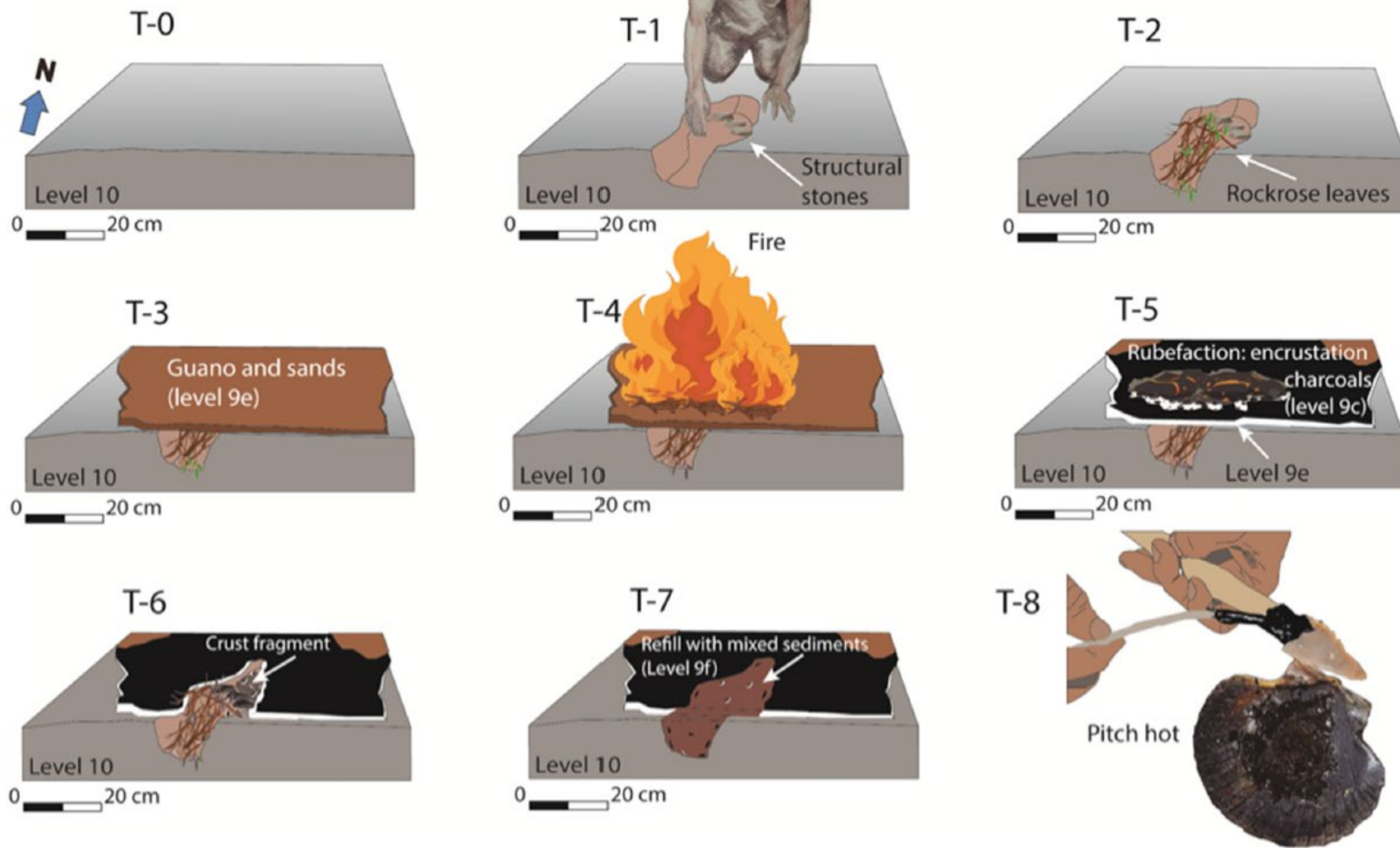
3

A fire is lit on top of the sand, heating the plants to over 315C

4

The plants release resin, which is used to attach stone blades to wooden shafts





An illustration showing how the hearth structure may have been used to create birch tar.

Experiment



Experiment 4:

- ▶ The pit structure was built by hand according to the morphology and dimensions defined by the archaeological excavations in Vanguard Cave (Layers 9 and 10).
- ▶ (a) The pit was filled entirely with ~1.9 kg of young leaves. The rockrose bundle was then sealed with a <2 cm thick layer of the same marine sand mixed with organic soil according to our interpretation for Layer 9e;
- ▶ (b) To monitor the temperatures of the fire and in the interior of the structure, an analogic pyrometer model Silex Cr-Al 48.09 mV was used. The fire was produced on the structure using wood from rock rose branches and roots, as well as grasses in the ignition process, thus simulating the interpretations made from the study of the coals found in Layer 9;
- ▶ (c) The covering crust was then broken and removed with the aid of a stick, in order to expose the mound of leaves;

Experiment 4

- ▶ (d) As the aim is to find out whether this resin could give rise to a viscous adhesive material, we reduced the labdanum placing shell containers over embers, in this way slowly heating it below the boiling point;
- ▶ (e) In order to accelerate the process of polymerization and, at the same time, produce more volume of pitch, we mixed 2–3 g of ashes;
- ▶ (f) Spearheads using the Levallois technique were produced from a flint cobble for the purpose of the experiment, while the rockrose leaves were steaming in the kiln. With the pitch still hot and elastic, it was applied to adhere the spearhead to a handle made of wild olive *Olea europaea* var. *sylvestris*;
- ▶ (g) Detail of the obtained hafted Levallois spearhead

N Tar production

- ▶ The tar pit was discovered three years ago on the floor of the Vanguard Cave in the British overseas territory of Gibraltar, but it has taken extensive testing to confirm its purpose.
- ▶ It seems, from the results obtained, that the tar was extracted from gum rockrose (*Cistus ladanifer*) instead of birch (rare in this location
- ▶ It was fortunate that the rapid advance of the sand dune 60,000 years ago facilitated the 'sealing' of the structure, with excellent preservation of pollen grains and spores, which have allowed confirmation of the ecological conditions outside the cave at the time)

*** Prey Size Decline as a Unifying Ecological Selecting Agent in Pleistocene Human Evolution - Miki Ben-Dor and Ran Barkai, 2024

- ▶ We hypothesize that megafauna extinctions throughout the Pleistocene, that led to a progressive decline in large prey availability, were a primary selecting agent in key evolutionary and cultural changes in human prehistory.
- ▶ Some changes, such as brain expansion, use of fire, developments in stone-tool technologies were uncharacteristically progressive.
- ▶ We previously hypothesized that humans specialized in acquiring large prey because of their higher foraging efficiency, high biomass density, higher fat content, and the use of less complex tools for their acquisition.

Energy costs

- ▶ Here, we argue that the need to mitigate the additional energetic cost of acquiring progressively smaller prey may have been an ecological selecting agent in adaption demonstrated in the Paleolithic archaeological record.
- ▶ We describe several potential associations between prey size decline and specific evolutionary and cultural changes that might have been driven by the need to adapt to increased energetic demands while hunting and processing smaller and smaller game.

Decline in prey size as evolutionary driver

- ▶ Our unifying hypothesis suggests one evolutionary driver for many key physiological and cultural phenomena in human prehistory—the decline in prey size.
- ▶ Here, we provided preliminary support for our contention that humans were hypercarnivores during most of the Pleistocene, starting with H. erectus and ending just before the end of the Pleistocene, possibly in the Neolithic.
- ▶ The decline in prey size itself is well-documented

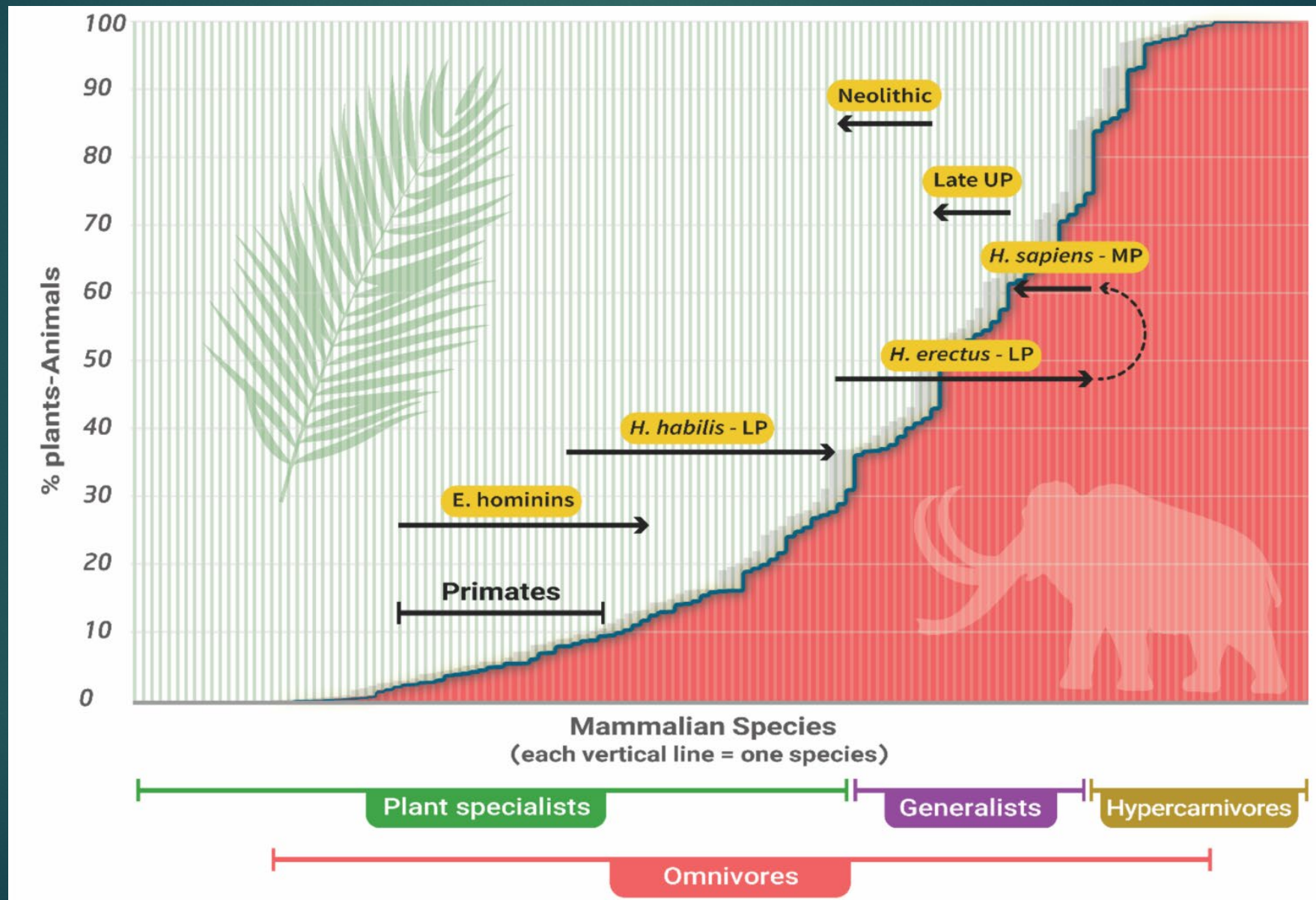
Large prey decline

- ▶ The effect of megafauna extinctions on humans has been seldom discussed.
- ▶ The genus Homo underwent an extensive set of physiological, cultural, and behavioral changes during the Pleistocene (roughly 2.6 Ma to 11.7 Ka). At the end of this period, humans had established themselves as a species of unprecedented ecological dominance.
- ▶ Most notable among these changes was the directional increase in brain volume in the lineages leading to *H. sapiens*, the habitual use of fire, periodical change of stone-tool technologies, big-game hunting, resource intensification, food production, and animal and plant domestication.

Large prey decline

- ▶ We hypothesize that large prey's declining availability was a prominent agent of selection in human evolution and cultural change.
- ▶ We argue that H. erectus evolved to become a carnivore, specializing in large prey beginning 2 million years ago.
- ▶ Later, as prey size declined, humans adapted to acquire and consume smaller and smaller prey while adapting to maintain a constrained bioenergetic budget.

Proposed evolution of the human trophic level during the Pleistocene.



Humans are carnivores

- ▶ The review finds support for the notion that **humans were carnivores starting from H. erectus**. Comparison with other social carnivores indicates that carnivorous humans would have been hypercarnivores, consuming over ~70% of their calories from animal sources. **A trend of declining trophic level (an increase in the plant component of the diet) is evident** at the end of the MSA in Africa and the Upper Paleolithic (UP) period, and especially towards the end of the UP in the rest of the old world
- ▶ The late **UP technology of bows and arrows, dogs, and grinding stones can be explained by the need to hunt smaller, fleeing animals and obtain an additional portion of the energy from plants** at acceptable energetic costs.

Reasons for hunting Megafauna

- ▶ Megafauna had **High Relative Biomass** – lots of meat
- ▶ **Do not attempt to escape**—Easier Tracking and Less Complex Hunting Tools
- ▶ Larger Prey Contains **Higher Body Fat Levels**
- ▶ Larger Animals Provide a **Higher Energetic Return**
- ▶ **Evidence for specialization in large prey hunting starting with H. erectus**

Homo erectus hunted elephants

- ▶ Based on current evidence, **Homo erectus is believed to have hunted large animals, with fossil records indicating they consumed medium to large sized prey like bovines and elephants, suggesting they developed predatory behavior and coordinated hunting strategies; however, some debate remains regarding whether they were primarily hunters or scavengers of large carcasses**
- ▶ Archaeological sites show butchered remains of large animals with cut marks, indicating consumption of meat from these animals

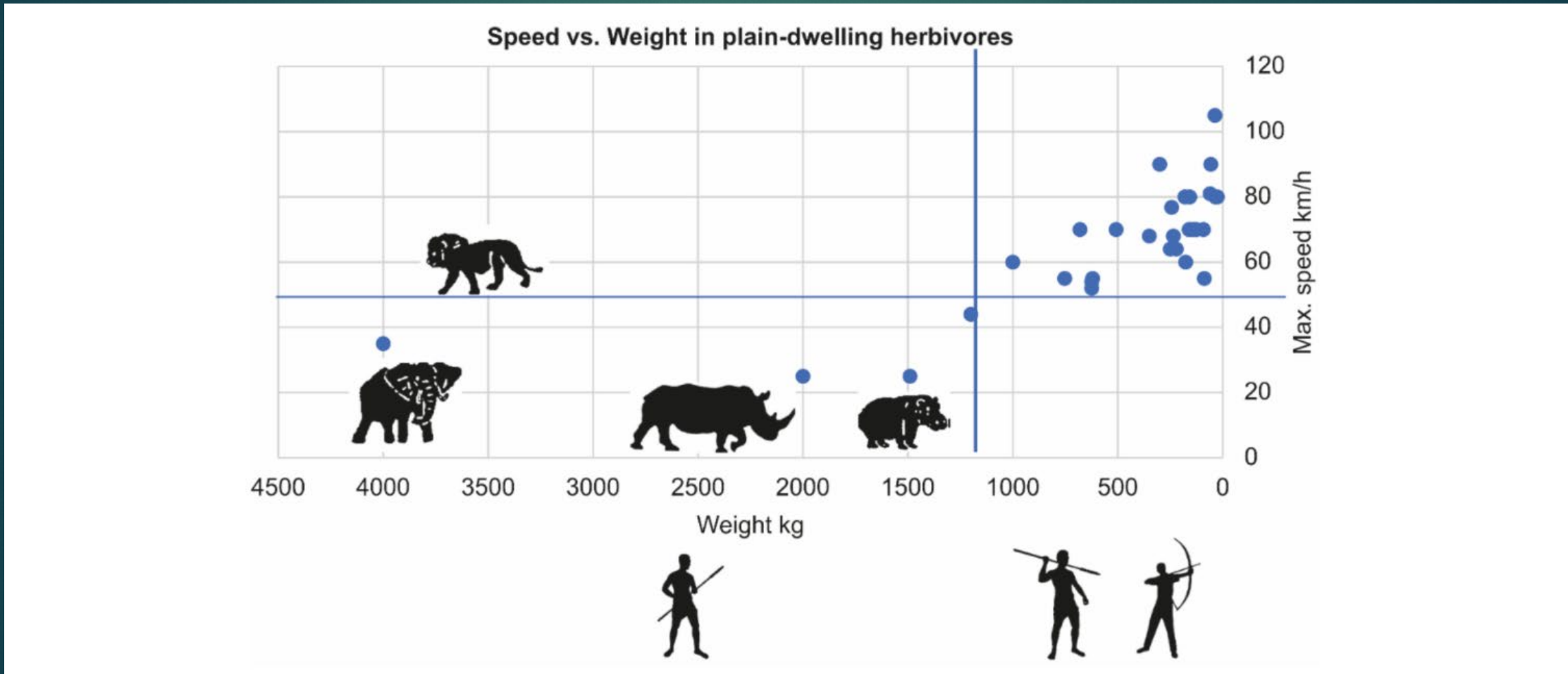
Anthropogenic Contribution to Prey Size Decline

- ▶ Preference for hunting prime-adult animals has been identified as beginning 400 Kya and perhaps 800 Kya, or even 1.8 Mya.
- ▶ This phenomenon, which is unique among predators, is also prevalent in Neandertals' faunal assemblages throughout their wide-ranging habitat.
- ▶ Immature animals invest resources in growth at the expense of fat reserves. Consequently, during most of the year, prime-adult animals will have a higher fat content than immature animals.

The Decline in Prey Size as an Agent of Selection

- ▶ Given the significant difference in energetic return per hour between smaller and larger prey acquisition, human survival must have depended on adaptations that would mitigate the additional energetic cost of replacing the acquisition of extinct larger animals with smaller ones.
- ▶ Thus, we view the progressive decline in prey size as an evolutionary selecting agent.

Hunting methods as a function of prey weight and maximum speed.
Megaherbivores (>1000 kg) are slower than a lion; do not rely on escape as a predation prevention strategy.



*** The Evolution of Paleolithic Hunting Weapons: A Response to Declining Prey Size - Miki Ben-Dor and Ran Barkai, 2024

- ▶ 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

Smaller weapons required for smaller prey

- ▶ The findings indicate a decline in megaherbivores' presence and biomass contribution in the studied transition period associated with the introduction of Levallois technology.
- ▶ 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 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.

Shift in weapon size

- ▶ In this paper, we test a sub-hypothesis that the evolution of hunting weapons during the Paleolithic era was a direct response to a progressive decline in prey size.
- ▶ Smaller, precision-focused weapons were required to replace large, strength-based weapons.
- ▶ The sub-hypothesis proposes that larger, heavier weapons, such as thrusting spears, which would have been effective for large prey like megaherbivores, became less useful as their abundance decreased. As a result, there was a shift towards more lethal and precise hunting tools for use vs smaller prey.

Decline in prey weight

- ▶ It began with an average prey weight of three tons in the Lower Paleolithic Acheulean and ended with an average of 50 kg in the Epi-Paleolithic Natufian.
- ▶ However, our hypothesis attempts to explain the implications of size decline, not its causes. It is not dependent on the reasons for this decline. Cause may have been US.

Earliest spears

- ▶ A wooden spear from Clacton, dated to 427 Ka, and wooden spears and hunting sticks from Schoningen, dated to 330 Ka, are the earliest archaeological evidence for hunting weapons.
- ▶ The undisputed second stage of weapon evolution was wooden spear stone-tipping. The stone-tipping of spears may have begun as early as 500 Ka. However, stone tipping became prevalent in archaeological sites during the MP/MSA, beginning at 300 Ka.

Projectiles and traps

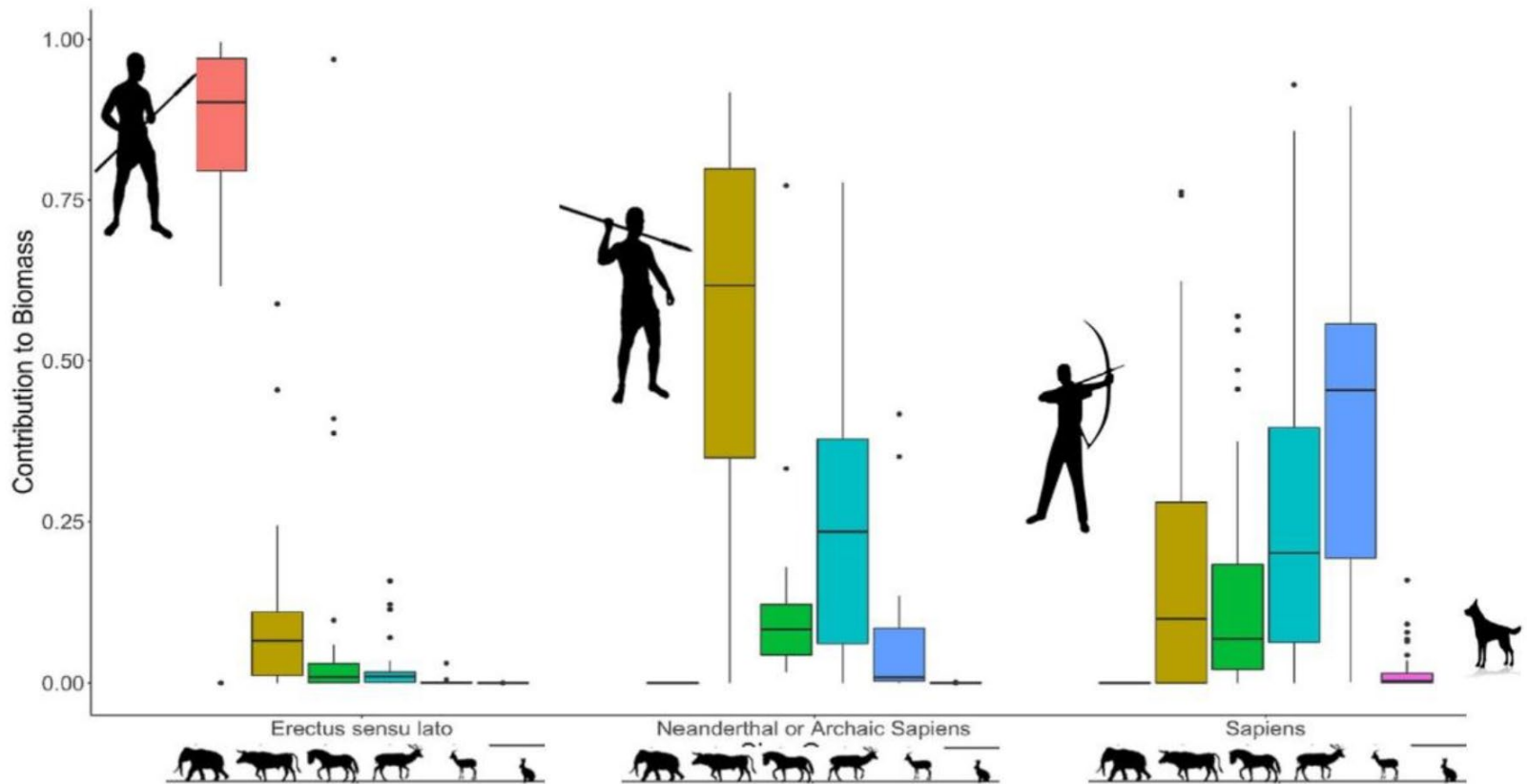
- ▶ The third wave of hunting weapons inventions was mechanically projected weaponry systems, such as bows and arrows and spear throwers, and darts, which may have originated 100–64 ka in Africa.
- ▶ Were only widely used during the UP/Late Stone Age (LSA) in Africa and the Old World.
- ▶ Other inventions include the domestication of dogs for use as hunter assistants in the middle to late UP and the use of traps to capture small game.

Hunting techniques

- ▶ Different hunting weapons were used with different hunting methods to capture different kinds of prey. In many cases, weapons and methods were associated with prey size though bows and arrows were used for hunting a wide range of prey sizes.
- ▶ A decline in megafauna presence in the Late Pleistocene is also accepted
- ▶ The chronological evolution of hunting weapons is widely accepted, namely:
 - ▶ wooden tools in the Lower Paleolithic,
 - ▶ stone-tipped spears in the MP/MSA, and
 - ▶ bows and atlatls mainly in the UP/LSA..

Decline and Levallois technology

- ▶ There seems to be a clear association between megaherbivore decline and the transition between the Acheulean and the MP/MSA (300 Ka) in the cases where the data spanned 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.









Acheulean

MP

UP

The prey size decline is made more apparent by considering the prey biomass as documented for the Paleolithic 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.

Period	LP/ESA	MP/MSA	UP/LSA
Weapon			
Prey			

A graphic description of the main premise of the paper—**In each period, the weapons were adapted to energetically efficiently hunting the dominant size prey of that period.**

Each period is depicted with its typical hunting weapons and dominant prey in terms of potential caloric contribution (in darker colors). All sizes of prey were acquired in every period

Tipping Spears with Stone Points

- ▶ At geographically widespread archaeological sites, this paper shows a decline in megaherbivore abundance between the Acheulean and MP/MSA periods. There is clear evidence for the MP/MSA appearance of hafted stone points.
- ▶ Determine a temporal correlation between the decline in megaherbivore presence and the appearance of hafted stone points. There is convincing evidence that hafted points were used in hunting proboscideans in North America and Europe, though their use has not been unanimously accepted. Stone-tipped spears may be more effective than wooden-tipped spears in hunting proboscideans under certain circumstances.
- ▶ Still, in America, stone point size declined with prey size

Complex weapons

- ▶ There is strong evidence that prey size declined during UP/LSA as part of the Late Quaternary Megafaunal Extinction.
- ▶ The widespread usage of bows and arrows as hunting tools likely began in the Upper Paleolithic period. The earliest known evidence of bow and arrow use comes from the South African site of Sibudu Cave, where researchers discovered small, pointed pieces of stone that could have been used as arrowheads, dating back approximately 64,000 years ago.
- ▶ A review of experimental and ethnographic literature concludes that humans traded wound areas for accuracy by switching to bows and arrows from spears. Small animals are as fast or faster than large escaping animals.

Animal speeds and arrow accuracy

- ▶ For example, the African elephant has a maximum speed of 35 km/h, whereas the Zebra is 70 km/h, and the Impala is 90 km/h. At the same time, the target organs (mostly the heart and lungs are smaller than those of large animals. At the same time, the depth of penetration and the wound size required to subdue the animal also decline.
- ▶ Arrows travel almost three times faster than spears. The increased arrow speed enables better aiming as the trajectory is flattened (more accurate placement). Thus, the bow provides better accuracy at the cost of a smaller wound area.
- ▶ To summarize, the main energetic savings from the transition to spear-throwers and bows and arrows may have come, as is the case with the transition from wooden to stone-tipped spears, from the increased success rate and the reduced pursuit cost when hunting small animals.

Dogs

- ▶ The domestication of dogs is another technology that can reduce the costs of pursuing small prey.
- ▶ Dog domestication occurred during the UP when prey size continued to decline as megafauna became extinct. Ethnographic evidence shows that dogs are predominantly used for hunting small prey. During small game hunting, dogs do part of the pursuit and sometimes assist in the search, saving energy.

Prey Size Decline and the Evolution of Cognition

- ▶ 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.
- ▶ Human biological and cultural evolution is closely linked to technological innovations. As weapons become more complex, they require more cognitive ability.
- ▶ Additionally, tracking prey may also require enhanced cognitive abilities. As noted, a key difference in energy expenditure between disadvantaging megaherbivores and ambush hunting smaller prey is that disadvantaging saves pursuit.
- ▶ In contrast, ambush hunting with a spear or bow and arrow is associated with a longer pursuit of the smaller and faster prey.
- ▶ As far as we could ascertain, none of the past literature discusses a unifying ecological driver for weapon technology evolution or the need for enhanced cognitive capability for the tracking stage of smaller prey

Weapons, tracking, pursuit, and cognition

- ▶ We 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.
- ▶ We can thus infer that prey size decline and the resulting need to mitigate the additional energetic expenses imposed by the decline were, at least partly, driving human cognition evolution

Conclusions

- ▶ Prey sizes declined during the transition between the LP, ESA, 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 (129 Ka) 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. Additionally, we discussed the emerging causal relationship between prey size decline and cognitive abilities extension.

Chinese paleontology: CJV analysis

- ▶ The **Multiregional hypothesis** was first conceptualized by Franz **Weidenreich** in his work in 1930s in China. Others related: Milford H. **Wolpoff**, Alan **Thorne** and Xinzhi Wu. **Chris Stringer** originated the more mainstream recent **African origin theory (Out of Africa)**.
- ▶ In Chinese paleontology, "multiregionalism" refers to the theory that modern humans in East Asia evolved largely in situ from earlier hominin populations like "Peking Man" (*Homo erectus pekinensis*), with continuous gene flow from other regions, rather than solely originating in Africa and completely replacing existing **populations** - a concept strongly supported by many Chinese paleontologists due to the rich fossil record found within China
- ▶ A specific model within the multiregional framework often discussed by Chinese scientists is "**Continuity with Hybridization**," proposed by paleontologist Wu Xinzhi, which emphasizes the idea that **modern humans in China evolved from local populations with some gene flow from outside regions**

China

- ▶ **Data vs MR theory:** Mitochondrial Eve, earliest fossils in Africa
- ▶ Some critics argue that the **strong support for multiregionalism among Chinese paleontologists** might be influenced by a desire to demonstrate a long evolutionary history and indigenous origins of the modern Chinese population
- ▶ While the "Out of Africa" hypothesis is widely accepted in the global scientific community, **Chinese researchers** continue to study and argue for the validity of the multiregional model based on their regional fossil evidence
- ▶ **Christopher Bae**, Dept of Anthro, Univ of Hawaii: Korean professor; current **major champion of China as original origin of humanity**

Those Chinese Skulls....What is going on in Chinese paleontology?

- ▶ **Dragon Man** joins a number of early human remains uncovered in China that have proven difficult to categorize.
- ▶ These include remains from Dali, Jinniushan, Hualongdong, and the Xiahe jawbone from the Tibetan Plateau.
- ▶ There has been a fierce debate about whether these remains represent primitive examples of Homo sapiens, Neanderthals, Denisovans, or something else entirely.



A



B



C



D



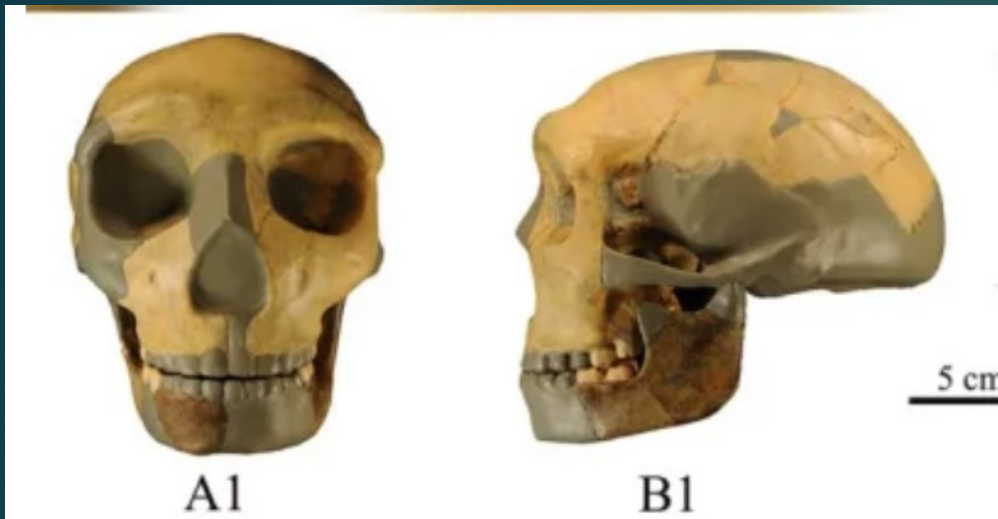
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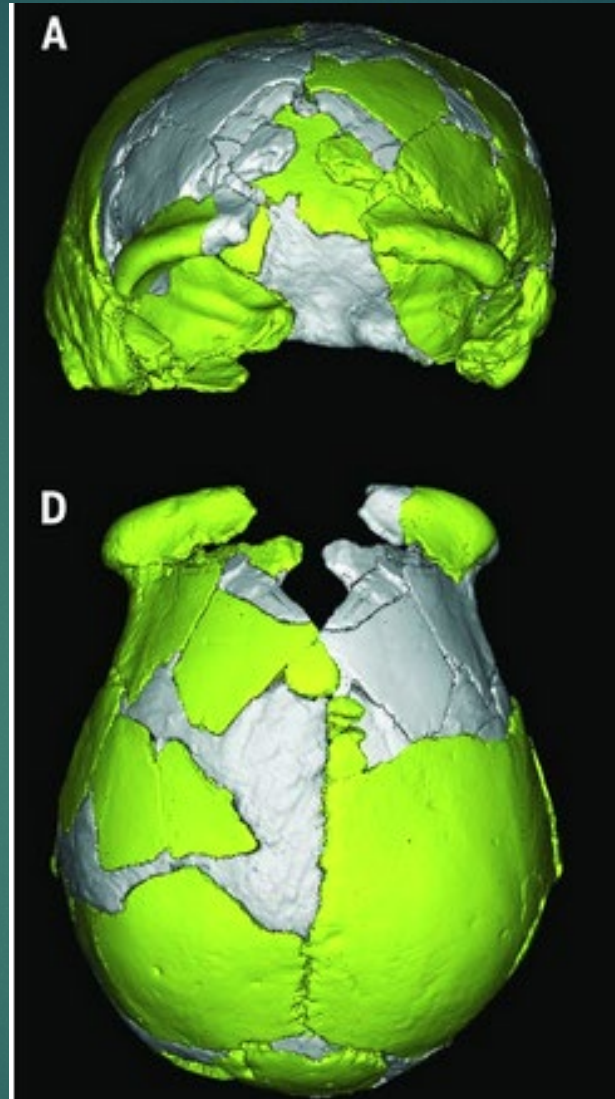
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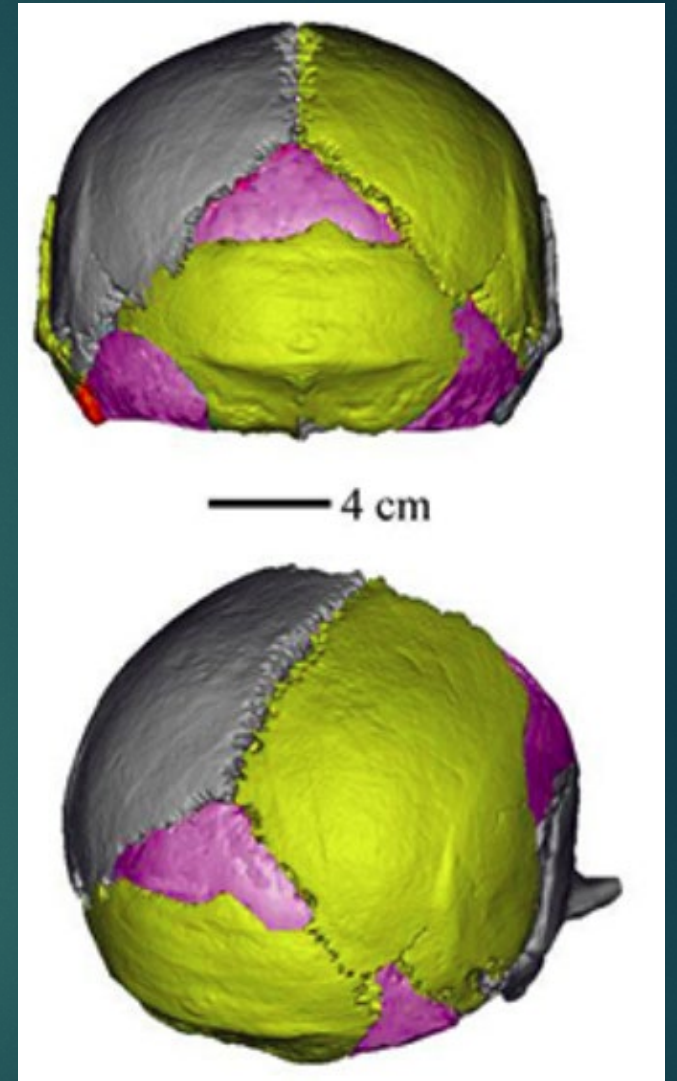
A. Hualong Cave;
B. Peking Man,
Zhoukoudian;
C. Nanjing Homo
erectus;
D. Dali Man;
E. Jinniushan;
F. Maba Man



HLD6: Hualong



Xuchang 1 cranium.



Xujiayao Man



Dragon man: from Harbin; *H. longi*

Big skulls = 1700 cc

Deformed Yunxian 1



Two nearly complete, but heavily deformed and broken skulls were discovered in Xuetangliangzi, in 1989 and 1990.

These finds were called "Yunxian Man", after the name of the local district at the time. These were given collection numbers EV 9001 and EV 9002 and are sometimes referred to as "Yunxian 1" and "Yunxian 2".

Complaints of lack of scientific accessibility.

Yunxian 2



The two skulls bear similarities to Dali Man, but are significantly **older**. Adjacent animal fossils allowed their age to be narrowed down to 600 to 400 Ka.

It's classifications have included: *H. erectus*, *H. heidelbergensis*, Denisovan.

Yunxian 2

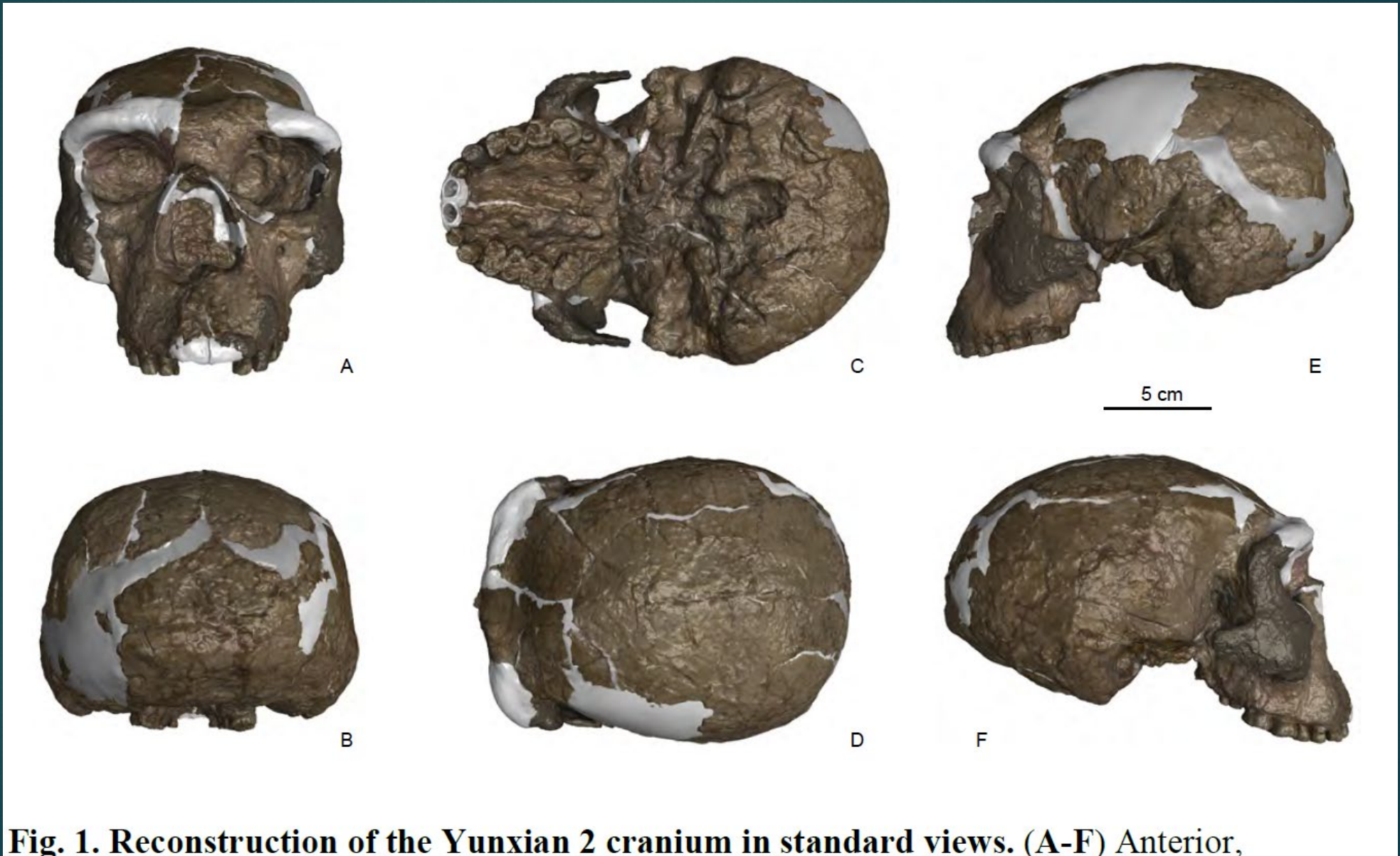


Fig. 1. Reconstruction of the Yunxian 2 cranium in standard views. (A-F) Anterior,

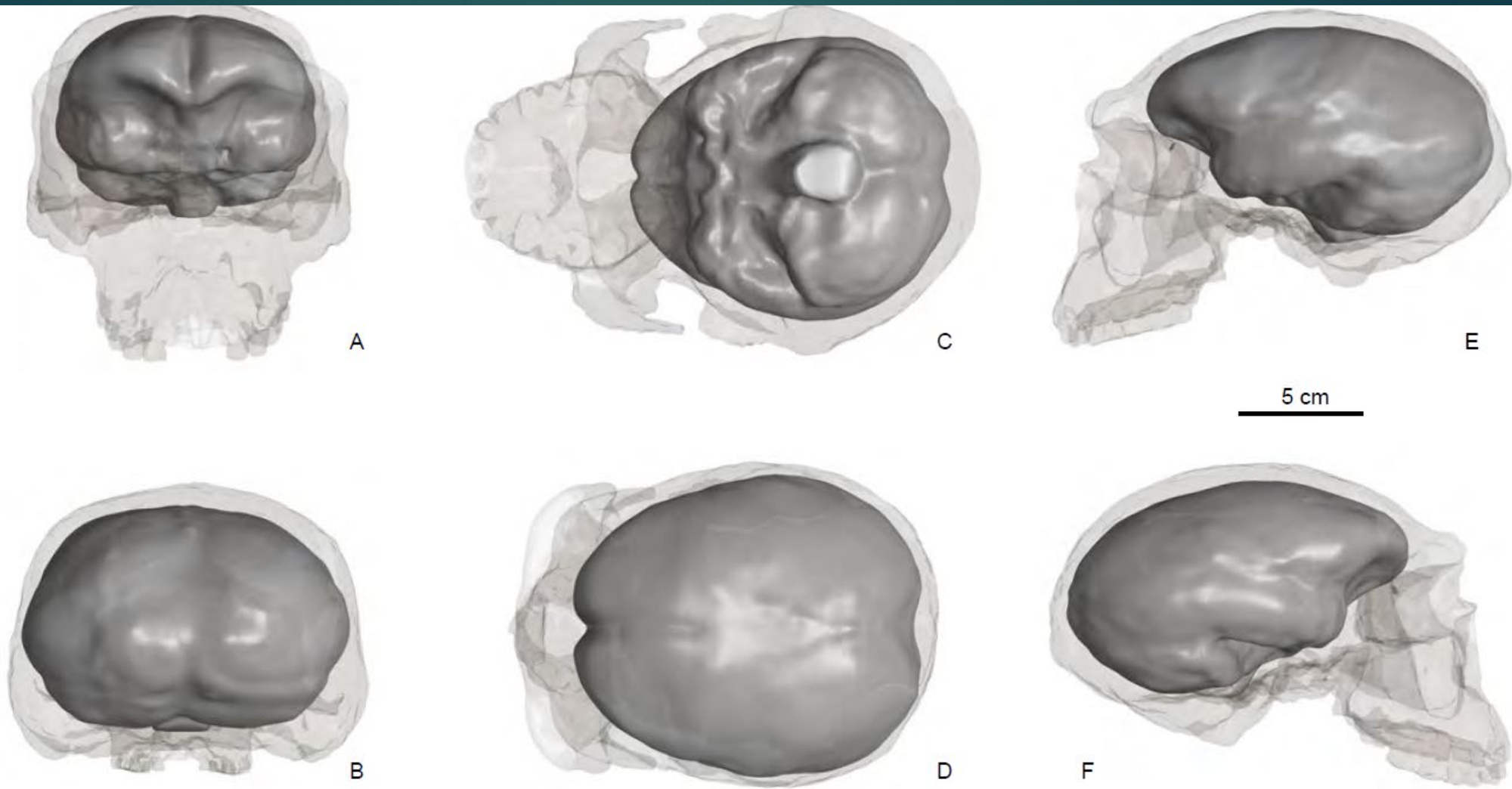


Fig. 2. Reconstruction of the endocranial cast of Yunxian 2. (A-F) Anterior, posterior, inferior, superior, left and right views. Scale bar indicates 5 cm.

*** The phylogenetic position of the Yunxian cranium elucidates the origin of Dragon Man and the Denisovans - Xiaobo Feng, et al., 2023

- ▶ The findings by X. Feng—published on the non-peer-reviewed pre-print server *bioRxiv*—claim that this ‘Yunxian 2’ skull just might be of the same lineage as the Dragon Man, and potentially one of the last common ancestors of *H. sapiens*.
- ▶ Restored and reconstructed the distorted Yunxian 2 cranium using new technology. The results show that this cranium displays mosaic features of plesiomorphy and apomorphy. Phylogenetic analyses and Bayesian tip-dating including the reconstructed Yunxian 2 suggest that it is an early member of the Asian ‘Dragon Man’ lineage, which probably includes the Denisovans, and is the sister group of the *Homo sapiens* lineage.

Yunxian 2 as distinct taxa

- ▶ Both the *H. sapiens* and Dragon Man lineages had deep roots extending beyond the Middle Pleistocene, and the basal position of the Yunxian fossil cranium suggests it represents a population lying close to the last common ancestor of the two lineages
- ▶ Overall, the Yunxian cranium shows a **distinctive combination of traits, and probably represents an additional species of Homo** from other designated human taxa such as *H. erectus*, *H. sapiens*, *H. neanderthalensis*, *H. heidelbergensis/rhodesiensis*, *H. antecessor* and *H. longi*.

Phylogenetic Analysis

- ▶ The reconstructed Yunxian 2 provides new anatomical details for systematic comparison, inferring phylogenetic position, and testing phylogenetic models for the genus Homo in general.
- ▶ Our 30 phylogenetic analyses were based on an updated data matrix containing 61 Homo OTUs (closely related) and 649 discrete and continuous characters. We added H. naledi, H. floresiensis, Penghu, Xujiayao, Denisovans, and Yunxian 2.
- ▶ Parsimony analysis and Bayesian inference show that H. sapiens, H. neanderthalensis, Asian H. erectus and those Middle Pleistocene hominins traditionally referred to H. heidelbergensis (including Bodo and Kabwe) are all monophyletic groups (descending from 1 ancestor).

Dragon Man lineage

- ▶ Most Asian Middle Pleistocene hominins, often previously referred to as "archaic Homo sapiens" including Dali, Jinniushan, Xujiayao, Hualongdong, group together with the Xiahe and Penghu mandibles to form a monophyletic group.
- ▶ These Asian Middle Pleistocene hominins are joined by the European H. antecessor. Together they form the sister group of a monophyletic H. sapiens clade.

Dragon Man lineage

- ▶ Here we call this whole sister group of *H. sapiens* the Dragon Man lineage, because *H. longi* is within this monophyletic group, although it forms a smaller monophyletic group with Yunxian and Dali. Yunxian has the oldest age within the Dragon Man lineage but is not the most basal fossil in our phylogenetic analyses.
- ▶ Analyses place Xuchang with the *H. neanderthalensis* monophyletic group as the earliest divergent branch.

H. floresiensis and naledi

- ▶ H. floresiensis is the sister clade to the Indian Narmada, Both taxa form the sister clade of Asian H. erectus.
- ▶ Such a result supports a previous hypothesis that H. floresiensis arose from a dwarfed population of early Asian H. erectus in an insular environment.
- ▶ H. naledi shows both primitive and derived features, and its phylogenetic position is still uncertain. In our analysis, H. naledi belongs to a distinct clade nested between African and Asian H. erectus.

Revised age of H. sapiens

- ▶ Previous estimates of the divergence time between H. neanderthalensis and H. sapiens are about 500-700 Ka.
- ▶ However, a recent study based on the tree sequence of a large number of ancient genomes with 3589 samples to constrain the dating relationships revealed a much deeper ancestry in H. sapiens.
- ▶ The oldest ancestral haplotypes are about 2 Ma and geographically located in Africa.

Origin dates

- ▶ Our Bayesian tip-dating analysis also revealed that the diversification of Homo and the origin of H. sapiens have much greater time depths.
- ▶ The origin of the Dragon Man lineage can be inferred to be about 1.13 Ma, probably slightly older than the Yunxian fossils.
- ▶ The origin of the H. sapiens lineage is estimated to be about 0.93 Ma, also close to the age of Yunxian.
- ▶ The divergence between the Dragon Man lineage and the H. sapiens lineage is about 1.16 Ma.

Lineage dates

- ▶ The monophyletic H. neanderthalensis lineage, widely thought to be sister to H. sapiens, diverged from the Dragon Man and H. sapiens lineages at about 1.27 Ma.
- ▶ Given its geological age of 0.94-1.10 Ma, Yunxian is close to the theoretical origin time of the lineages of Dragon Man and H. sapiens.
- ▶ Our reconstruction of Yunxian 2 shows that this fossil human has mosaic features of plesiomorphies, as seen in H. erectus, and apomorphies, as seen in Dragon Man and H. sapiens. It is reasonable to conclude that Yunxian is morphologically and chronologically close to the last common ancestor of the lineages of H. sapiens and Dragon Man.

Julurens: a new cousin for Denisovans and Neanderthals

- ▶ John Hawks analysis:
- ▶ A new study suggests that the Middle Pleistocene record in China includes more groups than have previously been recognized.
- ▶ The human evolution record of China and mainland southeast Asia has seen a lot of action during the last decade. Some European and American archaeologists of the 1980s held a stereotype that China had been a Pleistocene backwater, a place where *Homo erectus* hung on later than other places using only simplistic chopping tools. But that stereotype was based on poor evidence and a lack of familiarity with research that was happening in China.

Chinese scientific opinions

- ▶ Chinese scientists like Xinzhi Wu and Lanpo Jia documented ways that the Middle Pleistocene fossils did not seem to fit the distinctions once drawn among *Homo erectus*, Neanderthals, and recent humans.
- ▶ Those ideas contributed to the idea of Multiregional Evolution, which saw genetic exchanges between regions and continuity within regions as two aspects of a network of populations spanning Africa and Eurasia
- ▶ Wu wrote about the evolution of these populations as a river network with divergence and merging of streams.(a la Berger)

Middle
Pleistocene =
2.6 M to
126 Ka –

35 Chinese
sites



Middle Pleistocene and early Late Pleistocene sites in eastern Asia and the surrounding region. Light blue offshore areas are less than 120 meter depth and would have been dry land during glacial maximums.

New evidence – but no Chinese Denisovan data

- ▶ A better chronology has come from methodological innovations in cosmogenic burial aging, combined U-series-ESR, and optically stimulated luminescence (OSL) dating.
- ▶ Especially important is the previously-unknown diversity represented at Denisova Cave. But the anatomical variation of the so-called Denisovans is mostly unknown, while direct DNA evidence has so far eluded researchers working with fossils of Middle Pleistocene age in China.
- ▶ This has left some researchers and the media asking: Which fossils will turn out to be the real Denisovans?

Julurens—a name that means “big heads”.

- ▶ But many scientists don't subscribe to the idea that the fossil record of China should be understood through an Altai (Denisovan) lens .
- ▶ A new article from Xiujie Wu and Christopher Bae presents a new look at some fossils of the later Middle Pleistocene. They focus on fossil samples from Xujiayao in north China and Xuchang in central China.
- ▶ These fossils, which date to between 220,000 and 100,000 years ago, contrast with the so-called “Dragon Man” skull from Harbin and other similar remains.
- ▶ Wu and Bae suggest that the Xujiayao and Xuchang fossils may be something different and call them the **Julurens**—a name that means “big heads”.

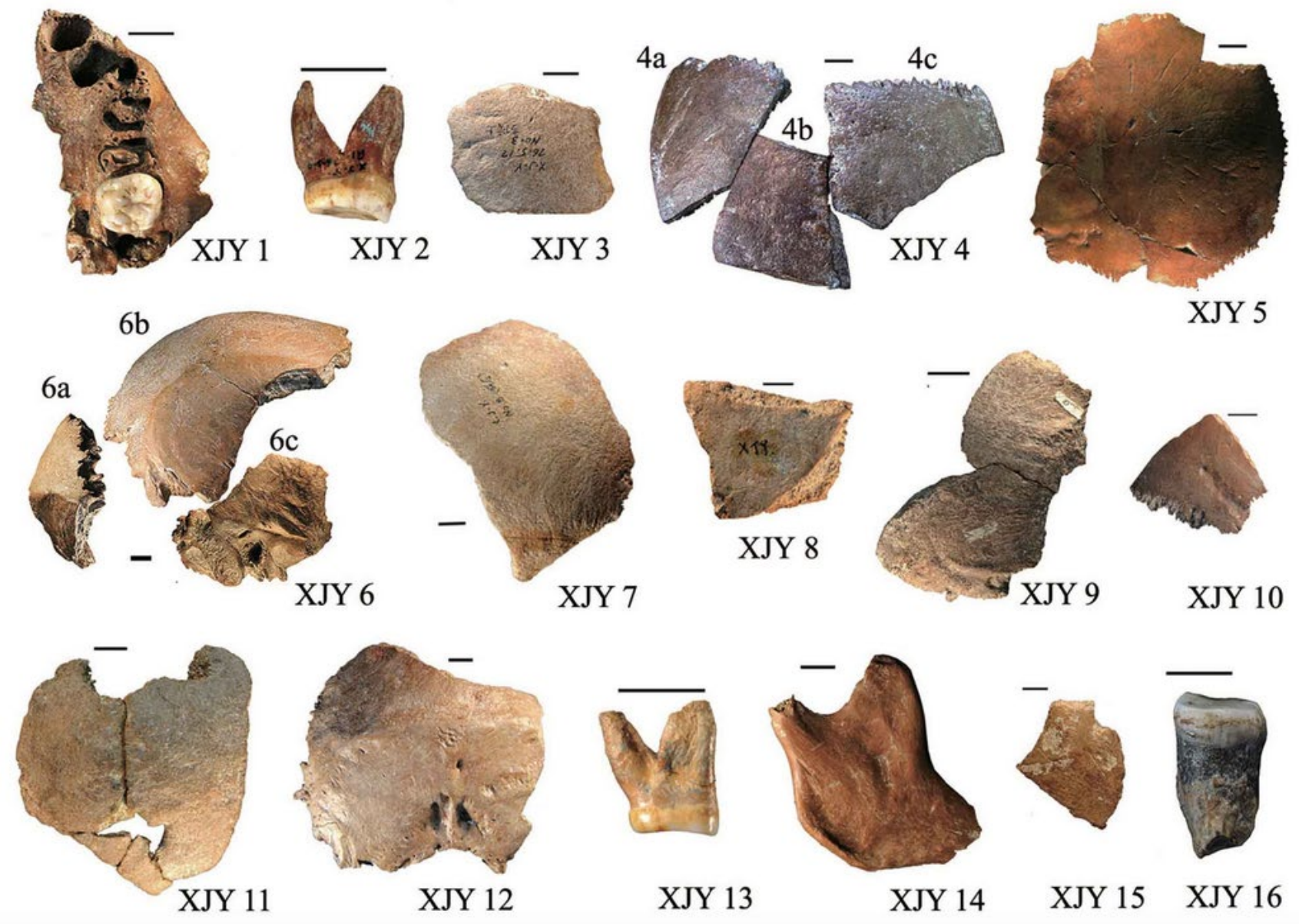


Immediate area around the Xujiayao fossil site. Image: Tu and coworkers (2015), edited to

Xujiayao [Shiji'ay'ao]

- ▶ The Xujiayao site is in northern China, within the geological area known as the **Nihewan Basin**. Near the Xujiayao villages lie exposed more than 20 meters of Pleistocene sediments including archaeological and fossil material in several places.
- ▶ The hominin site was first identified in 1974 and excavations during the remainder of the 1970s uncovered more than 10,000 stone artifacts and twenty-one hominin fossils, all fragments of skull or teeth. These come from the later part of the Middle Pleistocene between 250,000 and 130,000 years ago.

16 Xujiayao fossils

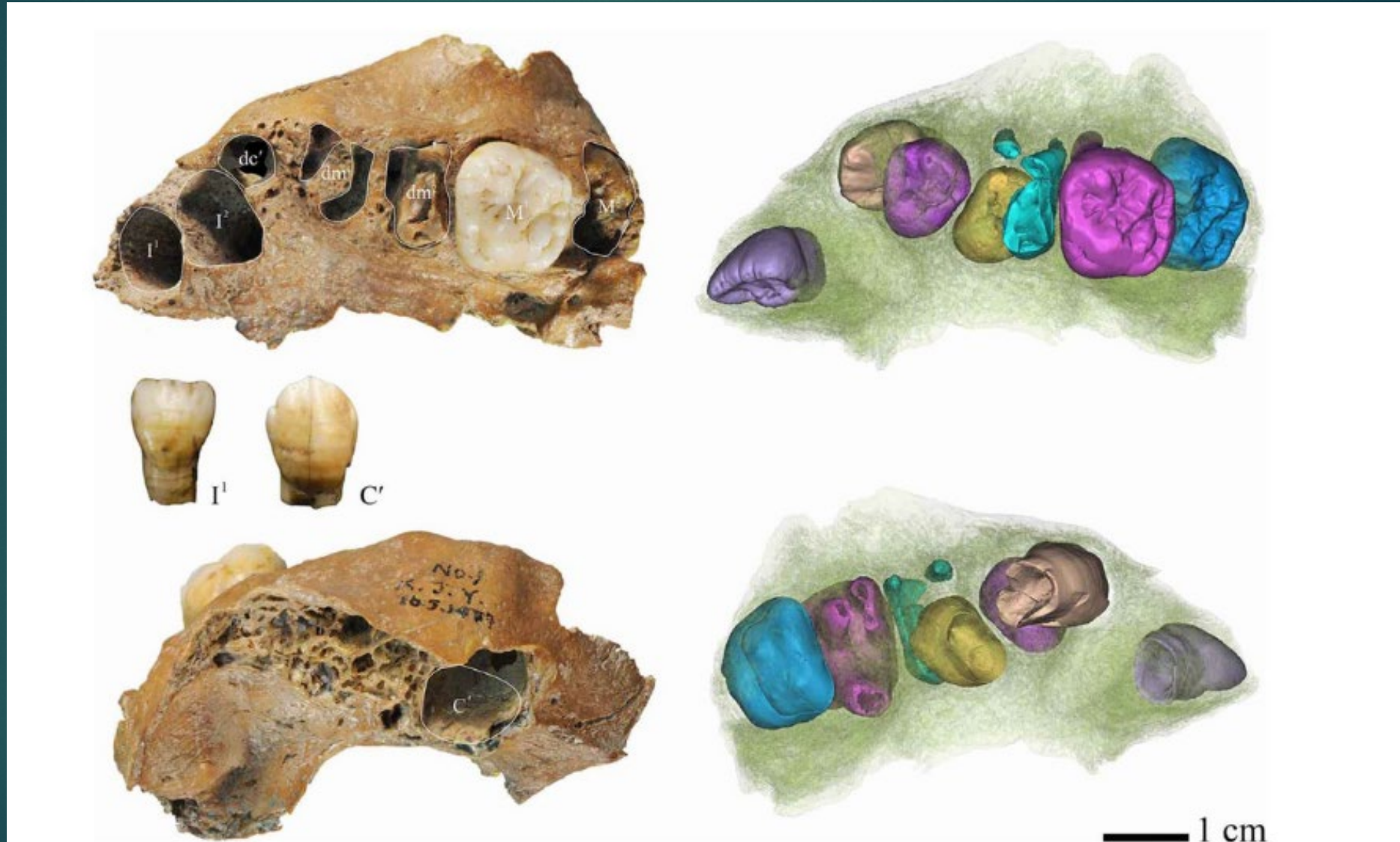


Fossils from Xujiayao. Image from Xiujie Wu (2024)

Xujiayao 6 = 1700 cc

- ▶ Wu and Bae review these fossils. The **most complete of the skulls is Xujiayao 6, which has large parts of both parietal bones and conjoining occipital**, the three parts unearthed in three different field seasons at the site.
- ▶ What remains is enough to give an idea of the size of the skull and shape of the back part of it. **The skull was big: With an estimated volume of 1700 cc, it is the largest known for any hominin of its time.**
- ▶ While the brain was larger than those of most recent people, the skull was shaped very differently from them: markedly wider at its base, and limited in skull height. Other cranial bones from the site represent at least 10 individuals in total, but are all fragments. The vault fragments also reflect **large cranial size with bones generally thicker than in recent human skulls.**

Xujiayao mandible

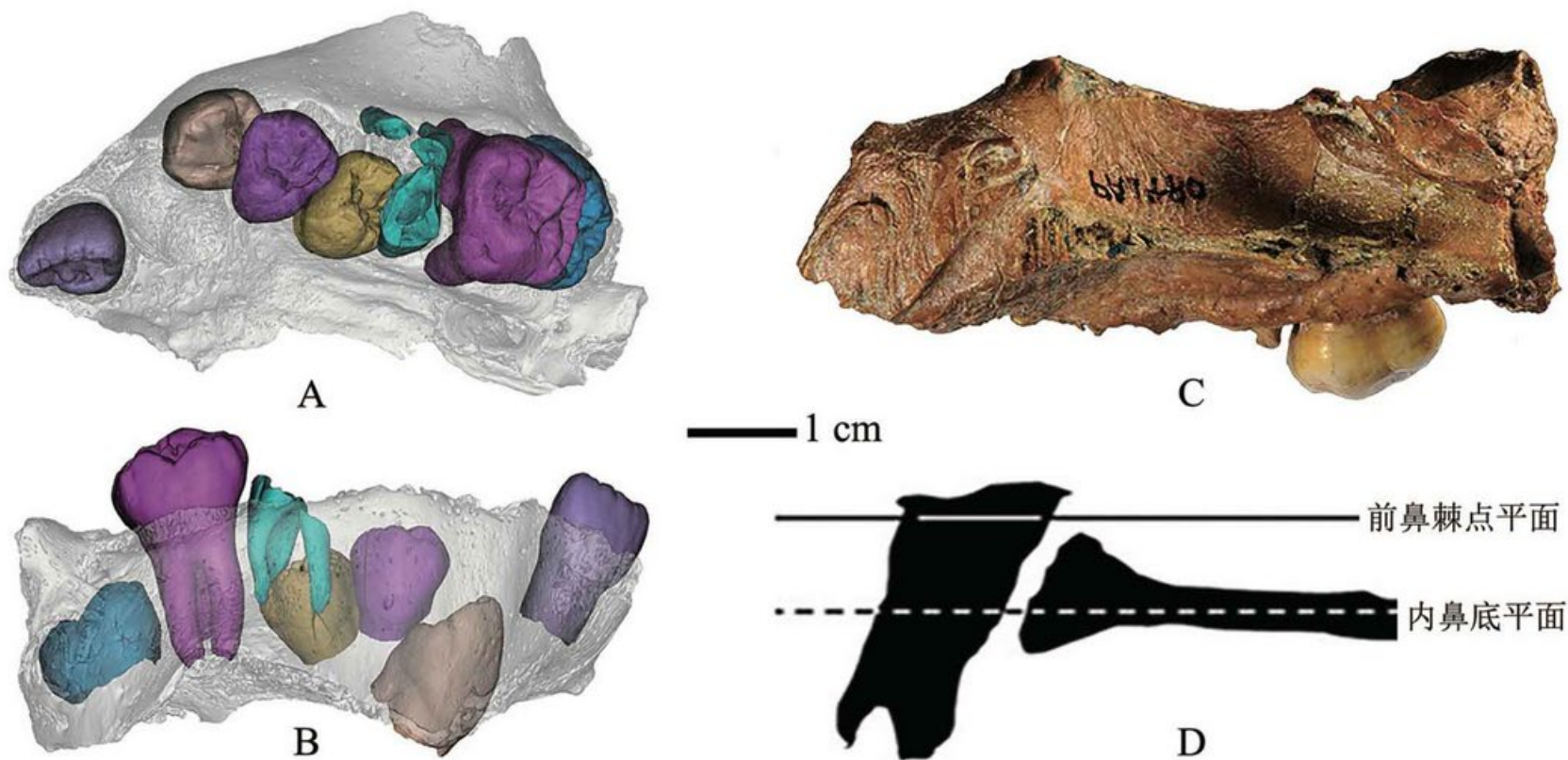


Xujiayao 1 maxilla and associated teeth. Image: Song Xing and coworkers (2019)

Xujiayao 1

- ▶ **Xujiayao 1 is the left side of a child's upper jaw**, preserving many of the permanent teeth within it. Three other isolated teeth of other individuals add to the dental picture.
- ▶ The **shovel-shaped incisor is a link to much earlier teeth from Zhoukoudian**, although Wu and Bae mention that the **crown's curved shape resembles the shape of some Neanderthal incisors**. All the teeth are big, the premolars have **asymmetrical outlines**, the first molar is not square but has a trapezoid-like shape with a narrower distal end, and the molar roots diverge markedly.
- ▶ Dental development of this child was on schedule with recent humans, the earliest known fossil in China to show this pattern.

Xujiayao 1 maxilla.



Xujiayao 1 maxilla. The left panels show microCT segmentation of the permanent tooth crowns within the maxilla. Image: Xiujie Wu (2024)

Xujiayao fossil fragments: not erecti

- ▶ Other fossils provide some valuable hints. Xujiayao 14 is a wide and fairly short mandibular ramus, with an asymmetrical mandibular notch. Xujiayao 11 preserves parts of the parietal bones.
- ▶ Over the decades since these fossils were unearthed, their fragmented state limited the kinds of conclusions that researchers could draw. Early studies by Lanpo Jia and coworkers, and by Maolin Wu, made clear that the remains did not belong to a Zhoukoudian-like *Homo erectus*, at the same time underlining their differences from recent people.

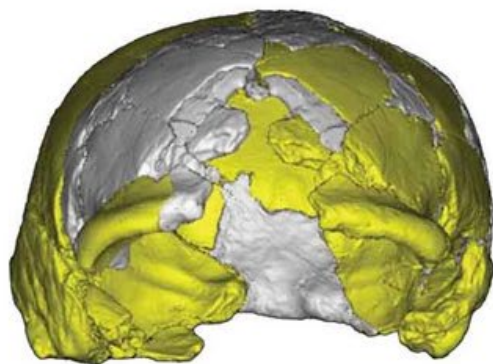
Xuchang

- ▶ Xuchang county is in Henan Province and the fossil skulls numbered as Xuchang 1 and 2 come from an open-air site inside of the town of Lingjing. Artifacts and fossil bone were noticed from the site during the 1960s, and systematic investigation started after 2005.
- ▶ Archaeologists found fragments of at least four ancient human skulls broken and scattered across a horizontal level, layer 11 at the site, determined by OSL to be between 125,000 and 105,000 years old. At that age, the Xuchang skulls are probably close to 100,000 years later than the Xujiayao fossils.

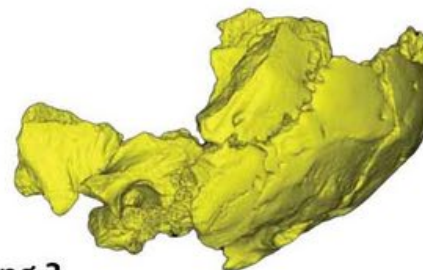
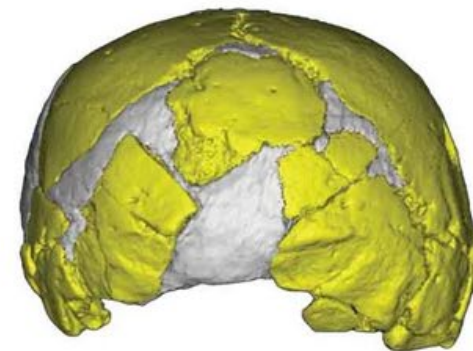
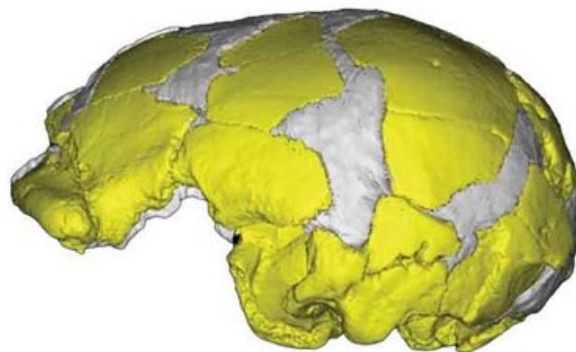
Xuchang was simultaneous with Ns and MHs

- ▶ In western Eurasia at around the same time lived the Neanderthals from Krapina, Croatia, and the early modern human fossils from Skhūl and Qafzeh, Israel. To the south, the large collection of fossil skulls from Ngandong, Indonesia, also lived around this same time.
- ▶ Xuchang 1, which is the most complete of the skulls, has an endocranial volume around 1800 cc.
- ▶ That's the size of the largest-known Neanderthal skulls and larger than most living people.
- ▶ Xuchang 2 is less complete, preserving only the back of the skull, and it is somewhat smaller in size, closer to average for a living person or Neanderthal.

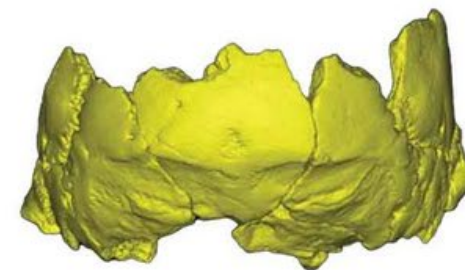
Xuchang1 and 2



Xuchang 1



Xuchang 2



Skulls reconstructed from Lingjing site. Xuchang 1 is at top and Xuchang 2 at bottom. Images from Li

Neanderthal features

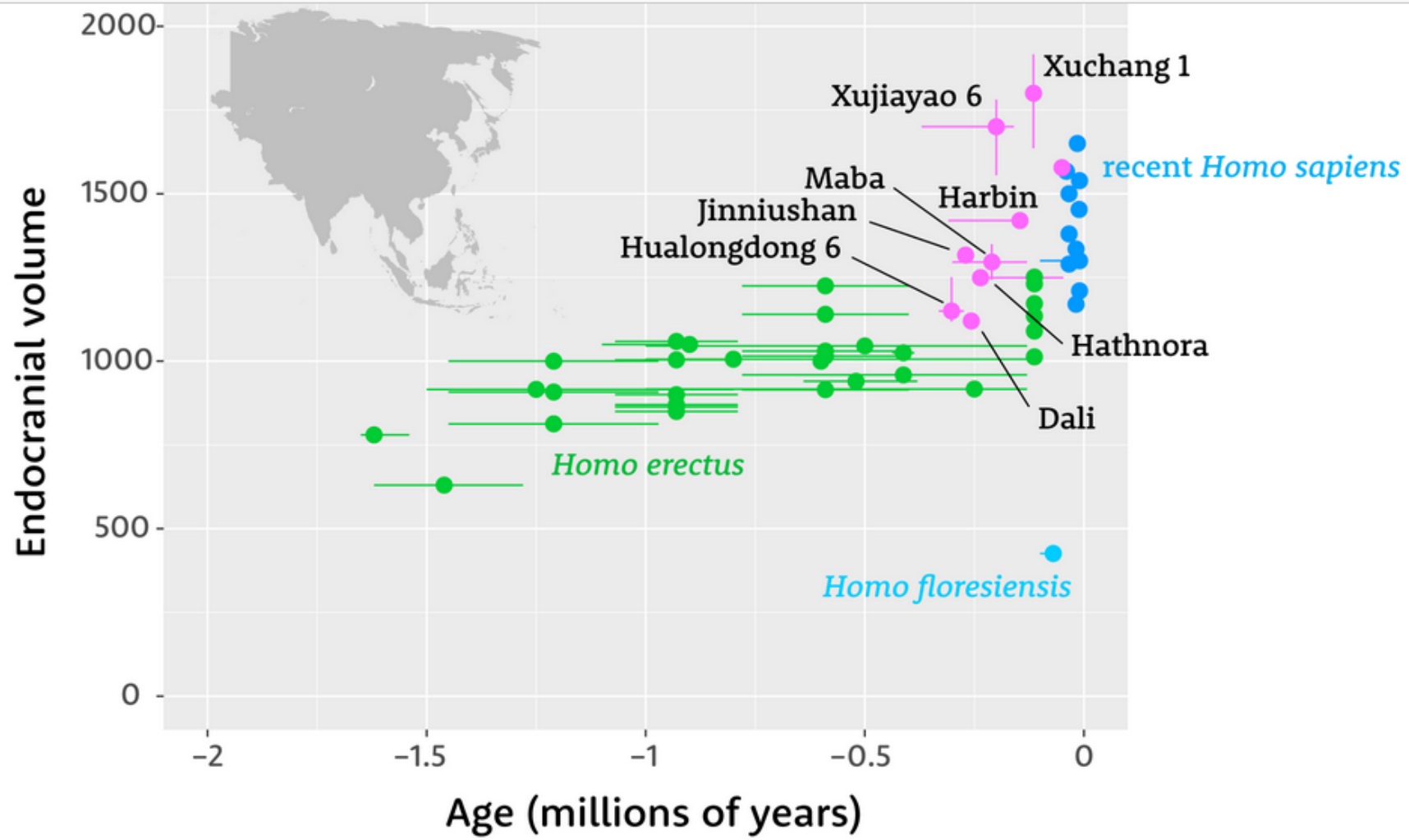
- ▶ Both are widest closer to the base and do not have the high, rounded shape of recent humans.
- ▶ Still, the back of the Xuchang 2 skull is more similar in shape to Neanderthal and modern human crania than earlier Chinese Middle Pleistocene fossils,
- ▶ The description of the Xuchang skulls emphasized some similarities with Neanderthals. Xuchang 2 has a small depression at the back of its skull, just above the main attachment area of the neck muscles, which is called a suprainiac fossa, a common N skull feature.

Xuchang skull features

- ▶ The study also points to some internal features of the semicircular canals; a pattern evident in most Neandertals and known elsewhere only in the early Late Pleistocene eastern Asian Xujiayao 15 temporal bone.
- ▶ The study of the Xuchang crania did not include the Dali skull, for example, and the Xuchang skulls do fall within the variation of recent people in their semicircular canal properties.

Julurens and Dragon People

- ▶ The evidence from Xujiayao and Xuchang has its limits. Between them, the sites present only partial evidence from the face or mandible and none from the postcranial skeleton. Different parts of different fossils don't make for easy comparisons.
- ▶ Sorting out the relationships requires us to consider which traits are **derived**, and may therefore provide evidence of a uniquely shared evolutionary history.



Endocranial volumes of fossils from south, southeast, and eastern Asia

Endocranial volumes of fossils from south, southeast, and eastern Asia, plotted with the range of estimated geological age for each fossil. The late *H. erectus* sample includes the Ngandong fossils from Indonesia.

Similarities & differences

- ▶ They could not easily ascribe the Xujiayao pattern of features to the same group as most other Chinese Middle Pleistocene fossils.
- ▶ They found that the traits that seem to connect the Xujiayao and Xuchang fossils to the other Middle Pleistocene crania from the region, including the Dali, Hualongdong, Jinniushan, and Harbin skulls, mostly are also found more broadly in later *H. erectus* and archaic humans from other regions.
- ▶ At the same time, the Xujiayao and Xuchang fossils share some traits that have been interpreted as derived in Neanderthals, which are not in other fossils from eastern Asia. And although the brain sizes of Hualongdong, Dali, Jinniushan, and Harbin have a bigger average than *H. erectus* (and in fact are similar to recent humans), the volumes of the Xujiayao 6 and Xuchang 1 skulls are bigger still.

Xujiayao and Denisovans

- ▶ One small group of fossils did impress Wu and Bae as possibly similar to the Xujiayao teeth and mandible fragment: the fossils identified as Denisovans.
- ▶ Wu and Bae recognize that these Denisovan-identified fossils include some large and complex molars like the Xujiayao teeth, and the Xiahe mandible overlaps in morphology with the Xujiayao 14 mandible fragment.
- ▶ To this group they add the Penghu 1 mandible, dredged from the Taiwan Strait, the identity and exact age of which remains unknown.

Gene flow hybridization?

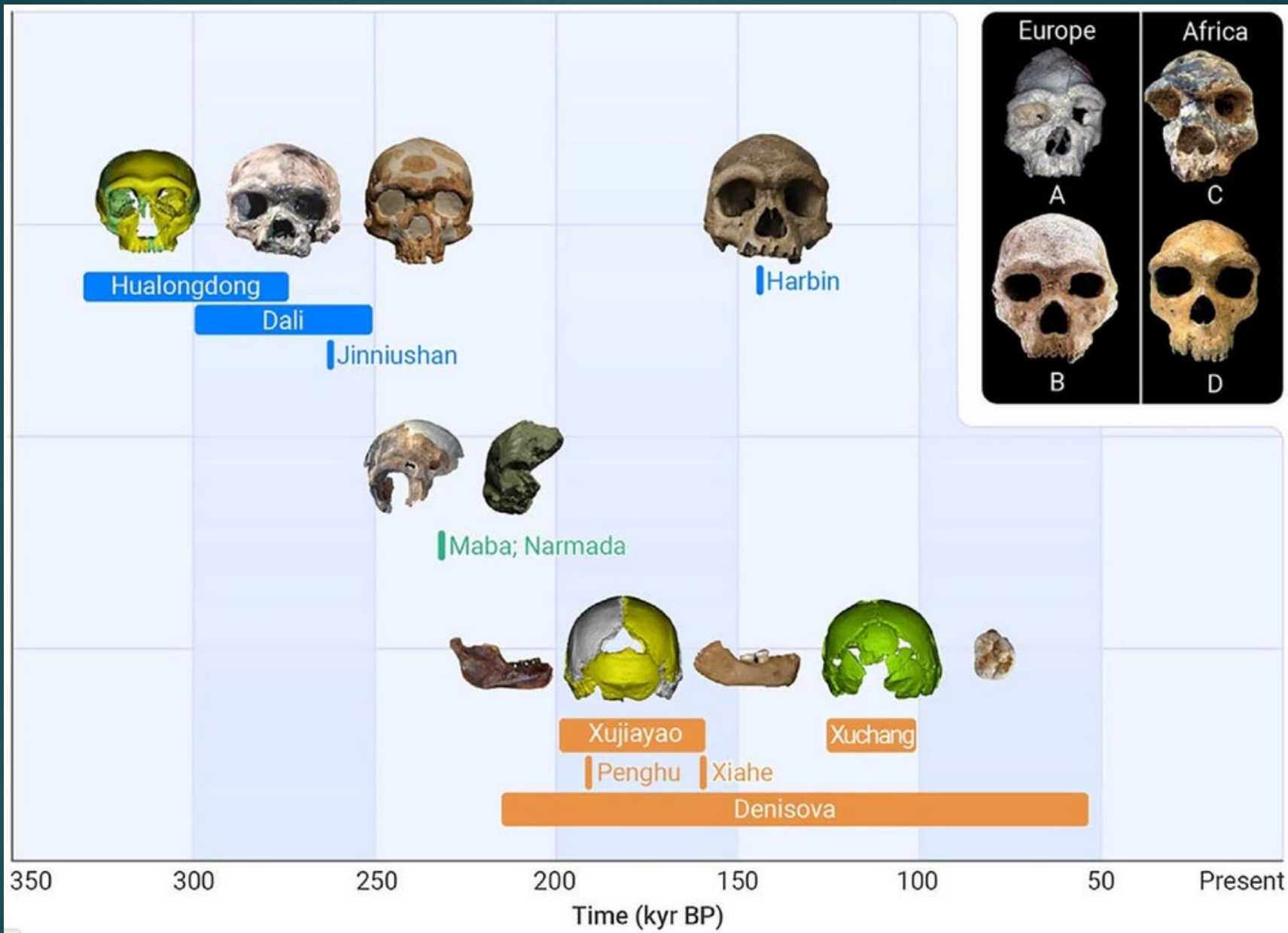
- ▶ Wu and Bae are not proposing that this group was isolated or different at a species level from the others.
- ▶ They instead consider that the pattern of morphology may result from genetic exchanges both among groups within China and with other regions further afield.
- ▶ “It is quite possible that this population represents gene flow between Asian H. erectus, and possibly H. antecessor, H. bodoensis, and/or early Neanderthals, supporting the idea of continuity with hybridization as a major force shaping human evolution in eastern Asia during the late Middle and early Late Pleistocene.” —
Xiujie Wu and Christopher Bae

Chinese MP fossils are not one group

- ▶ Article published last year by Bae, Wu, and other colleagues in *The Innovation*. In that paper, Bae and his collaborators recount the “push, primarily by Western paleoanthropologists” to assign much of the Middle Pleistocene hominin fossil record into a single group, which many would name *Homo heidelbergensis*.
- ▶ But in their piece, they argue that the Chinese record does not fit well into such a framework. They discuss some of the weaknesses of this idea, and defend the idea that the Harbin skull and possibly others represent a different population, which they recognize as *Homo longi*—the so-called Dragon Man.

Differences

- ▶ At the same time, these researchers recognize that H. longi may not include every fossil.
- ▶ They distinguish Xujiayao and Xuchang, grouping these with the Denisova and related fossils in the same way that Wu and Bae propose in their newer study.
- ▶ They also distinguish the partial skull from Maba, which fits neither of the other groups well but has some similarities with the partial skull from the Hathnora site on the Narmada River, India.



Timeline and morphological groupings considered by Christopher Bae and coworkers (2023)

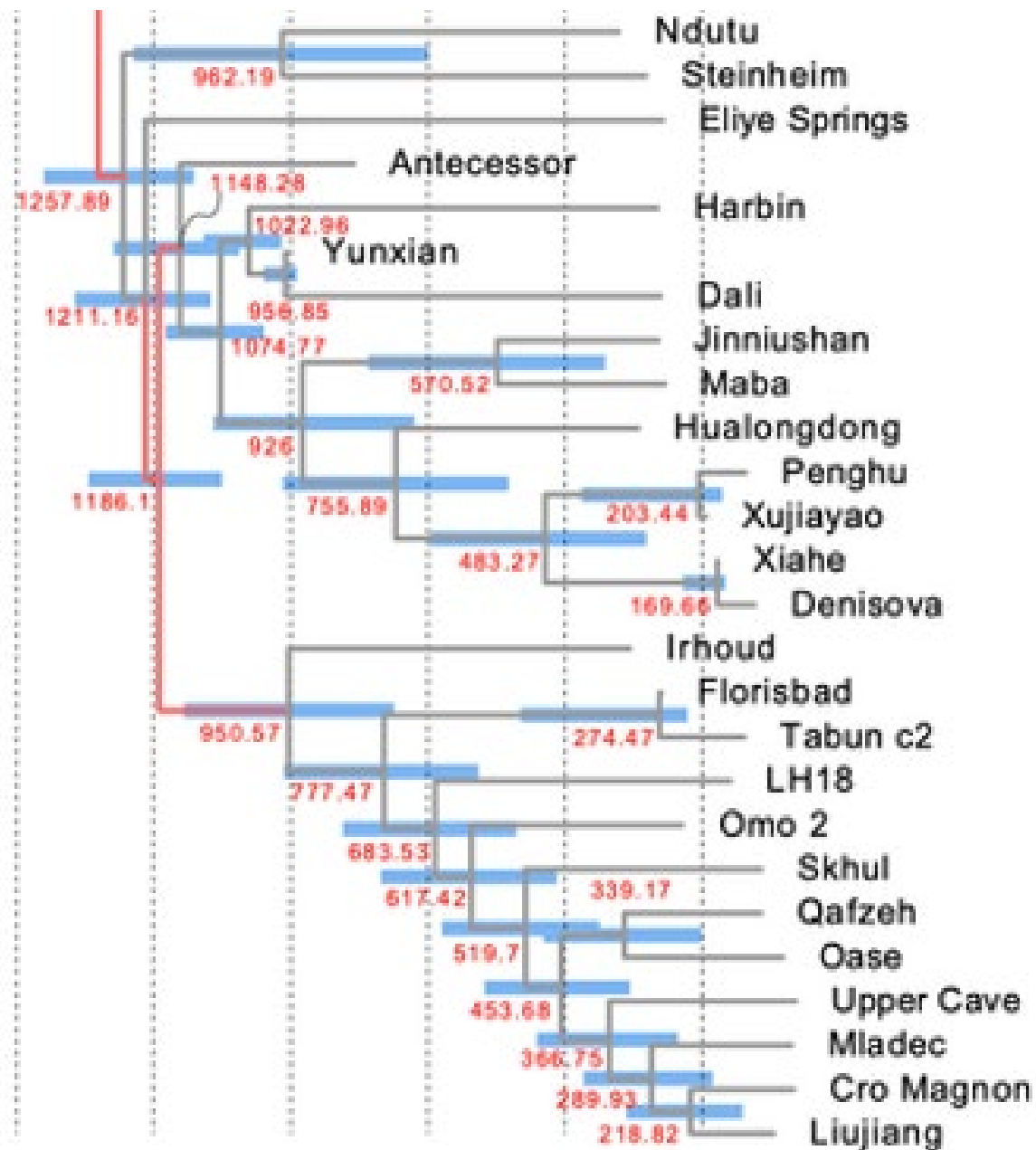
Chinese fossils as distinct group

- ▶ Hawks' opinion: Bae and collaborators have a good case for distinguishing the Chinese fossil record from the fossils from Africa and western Eurasia across this time. Focusing closely on possible groupings or differences within the record from China is a good idea. The Xujiayao and Harbin fossils may overlap in age but differ in morphology, and they may well reflect different ancestry patterns.
- ▶ In a new preprint, Xiaobo Feng and coworkers consider the relationships of many of these fossils. The aim of the study is to contextualize a new reconstruction of the Yunxian 2 cranium, usually attributed to *Homo erectus*. In the view of Feng and collaborators, Yunxian 2 may be more closely connected with *Homo longi* and not *H. erectus*.

Groupings

- ▶ Their analysis is similar to the earlier study by Xijun Ni and coworkers that supported the *Homo longi* diagnosis, using derived traits to generate a phylogeny of individual fossils.
- ▶ The Xuchang 1 fossil is placed with Neanderthals in the analysis, which counts against the idea of a Juluren group.
- ▶ But Xujiayao does cluster with Denisova, Xiahe, and Penghu, all four nested within a group that includes other Middle Pleistocene fossils from China.

2843



Dragon Man Lineage

Homo sapiens

Hawks opinion

- ▶ Hawks likes their analysis because the placement of a fossil on the tree depends on the derived traits it shares with other fossils, and that's exactly the evidence that matters.
- ▶ Still, the tree does not admit for the possibility of gene flow, and that's a significant drawback.
- ▶ If the fossils belong to a reticulate network of populations, the tree won't necessarily reflect their relationships accurately.

2 possible groupings

- ▶ Without taking the tree entirely at face value, **Hawks suggest two ways of looking at the Xujiayao-Xiahe-Denisova group.**
- ▶ If the Harbin skull defines the Dragon People, then all the later Middle Pleistocene fossils might belong to that group, with the Julurens nested a subgroup within it.
- ▶ Or the Dragon People might only include the Harbin, Dali, Maba, Jinniushan, and Hualongdong fossils, with Julurens considered separately.

Denisovans

- ▶ *** If the Xujiayao group includes Denisova Cave fossils and the Xiahe mandible, probably most people wonder why this group needs a different name. **Why would the name of this group not just be “Denisovans”?**
- ▶ It is true that species names must follow certain strict rules, including the **rule of priority**. **If two groups of fossils with different names are shown to belong to the same species, the earlier name is the one that should be used.**
- ▶ But a name like “Denisovan” is not a species name.

The Denisovans

- ▶ The name “Denisovan” was coined by David Reich and collaborators in 2010 when they realized that the Denisova 3 genome represented a group deeply diverged from Neanderthal genomes known at that time.
- ▶ The parallel between “Neanderthal”—named for the first place a Neanderthal fossil was recognized as a different group from recent humans—and “Denisovan” was deliberate.
- ▶ At the same time, Reich and coworkers demonstrated the presence of Denisova 3-like ancestry in the genomes of living people in Papua. Later research showed that similar ancestry was very widespread at a low level across Asia and a higher level in island southeast Asia and Australia.

Timeline of mixture in Pleistocene humans

Topology of tree combines population history models from several studies, including:
 Africa: Ragsdale and coworkers (2023) <https://doi.org/10.1038/s41586-023-06055-y>
 Neandertals: Slimak and coworkers (2023) <https://doi.org/10.1101/2023.04.10.536015>
 Denisovans: Jacobs and coworkers (2019) <https://doi.org/10.1016/j.cell.2019.02.035>
 Superarchaic: Rogers and coworkers (2020) <https://doi.org/10.1126/sciadv.aay5483>

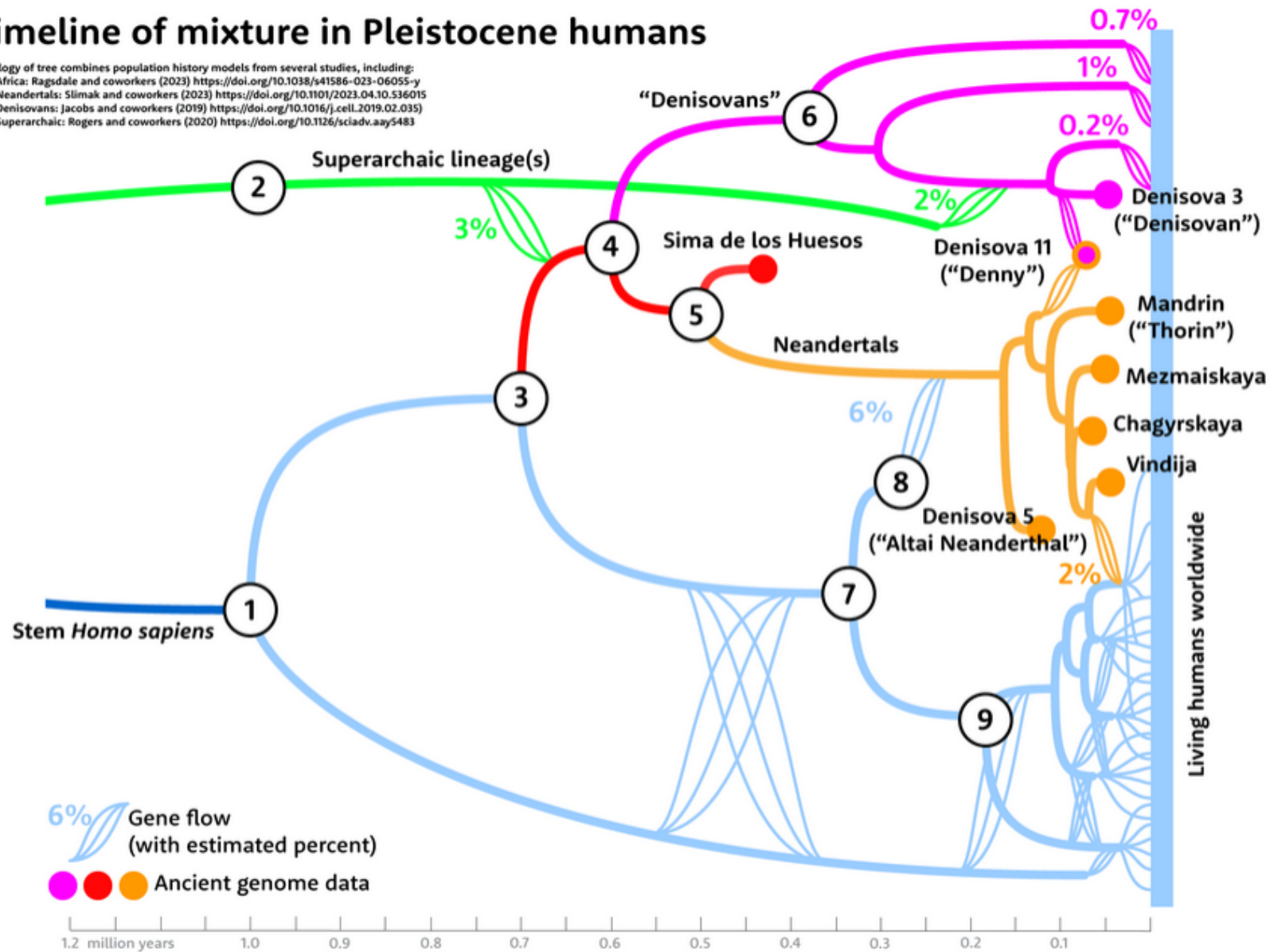


Diagram showing recent estimates of population mixture among Pleistocene human groups. The deep divergence among “Denisovan” lineages follows the analysis of Jacobs and coworkers (2019).

Neandertal divergences

- ▶ Since 2010, our understanding has deepened.
- ▶ The group we call Neanderthals was a deeply structured group of lineages. Early representatives like the sample from Sima de los Huesos, Spain, lacked ancestry inputs from Africa that were important to the makeup of later groups.
- ▶ The Denisova 5 “Altai Neanderthal” genome came from a lineage strongly diverged from later Neandertals both in Europe and Central Asia.
- ▶ Last year, Ludovic Slimak and coworkers released information about the “Thorin” Neanderthal individual from Mandrin, France, a fossil from another deeply diverged lineage.

Divergent Denisovan groups

- ▶ What we have been calling “Denisovans” was even more deeply structured than Neanderthals.
- ▶ Denisovan-like people mixed with early modern people who dispersed into island Southeast Asia. Those D groups had diverged from the ancestors of the central Asian D group as early as 350,000 years ago.
- ▶ The central Asian group itself mixed with some Neanderthals and also with the ancestors of east Asian people. This branch also received some input from another deeply-diverged “superarchaic” group, themselves neither Neanderthals nor Denisovans.
- ▶ This is a complicated picture with many groups, mixing at different times and places.

Terminological difficulties

- ▶ These networks of relationships pose communication challenges beyond the scope of today's terminology.
- ▶ Using “Neanderthal” for every fossil that the term has come to encompass is conveying the appearance of solidity, when in fact those groups had many inflows and outflows, and were never more than a loose network.
- ▶ By coining names like “Thorin lineage” and “Altai Neanderthals”, researchers are moving beyond the limitations of the 170-year-old name. The Sima de los Huesos sample, maybe together with Arago, deserves its own name within this network.
- ▶ We need to be able to talk about much more focused groupings.

Denisovans

- ▶ What's true of “Neanderthal” is doubly so for “Denisovan”.
- ▶ So far scientists cannot assess the anatomy of Denisova-like groups of island southeast Asia. But these populations were certainly far from the ecological and climatic conditions of the Altai or Tibetan plateau.
- ▶ Calling them all “Denisovans” may say something true about their deep common ancestry but obscures the long histories that gave rise to their variation, their diverse mixtures, and their cultures.

Denisovans

- ▶ Since the discovery of the Denisova 3 genome, the media in Europe and the U.S. have framed the study of this group as a whodunnit.
- ▶ Geneticists keep hoping to identify the first Denisovan skull.
- ▶ Hawks has had some interesting conversations with colleagues in China who put this notion of mystery on its head.
- ▶ Their question is not which fossils will be revealed as Denisovans, but instead which known fossil groups may at last provide the real identity of this unknown genome.

Denisovans and Chinese fossils

- ▶ The Denisovan name, from this point of view, is a concept that exists only because of a current absence of correlation with the fossil record.
- ▶ The Denisova 3 genome may find many different patterns of connections within the network. There's a chance that the name **Denisovan** itself may be replaced by *Homo longi* or some other name.
- ▶ Hawks is not sure that the Juluren idea will be exactly right. But it does give an alternative that may prove useful in thinking about the place of Xujiayao and possibly Xuchang within this network

Julurens

- ▶ The Xujiayao sample represents people who lived long before Denisova 3, who made very different artifacts and experienced different ecological conditions.
- ▶ It's very plausible that the groups were relatives but they were as different as the Altai Neanderthals and Thorin lineage.
- ▶ A different name within a broader grouping seems entirely reasonable, even if they were related within a tree.
- ▶ A different name will be even more valuable if, as Wu and Bae suggest, the Xujiayao and Xuchang fossils do indeed reflect a mixture of ancestry from Neanderthals, earlier Chinese Middle Pleistocene people, and possibly others.
- ▶ Julurens. You may find the name grows on you.

Homo
juluensis
Locations



Big head, big teeth, big implications: early hominid from China stirs new species debate

- ▶ Scientists make their case for classifying an extinct group that lived in northern China until 120,000 years ago as a separate species
- ▶ Sometime between 200,000 and 160,000 years ago, a group of early hominids lived in northern China. They were skilled, organized hunters, having mastered primitive tools and weapons similar to spears that they used to kill wild horses. They not only ate the meat, bone marrow and cartilage, but even made clothing from the animal hides to help them survive the harsh winters.
- ▶ The sturdy individuals also had a distinctive physical feature – relatively large heads with low, wide skulls that accommodated sizeable teeth.
- ▶ “That is a very substantial difference between modern Homo sapiens, Neanderthal and this new proposed species,” said Christopher Bae.
- ▶ Dubbed the ancient group Homo juluensis – a new species. *Ju lu* means huge head in Chinese.

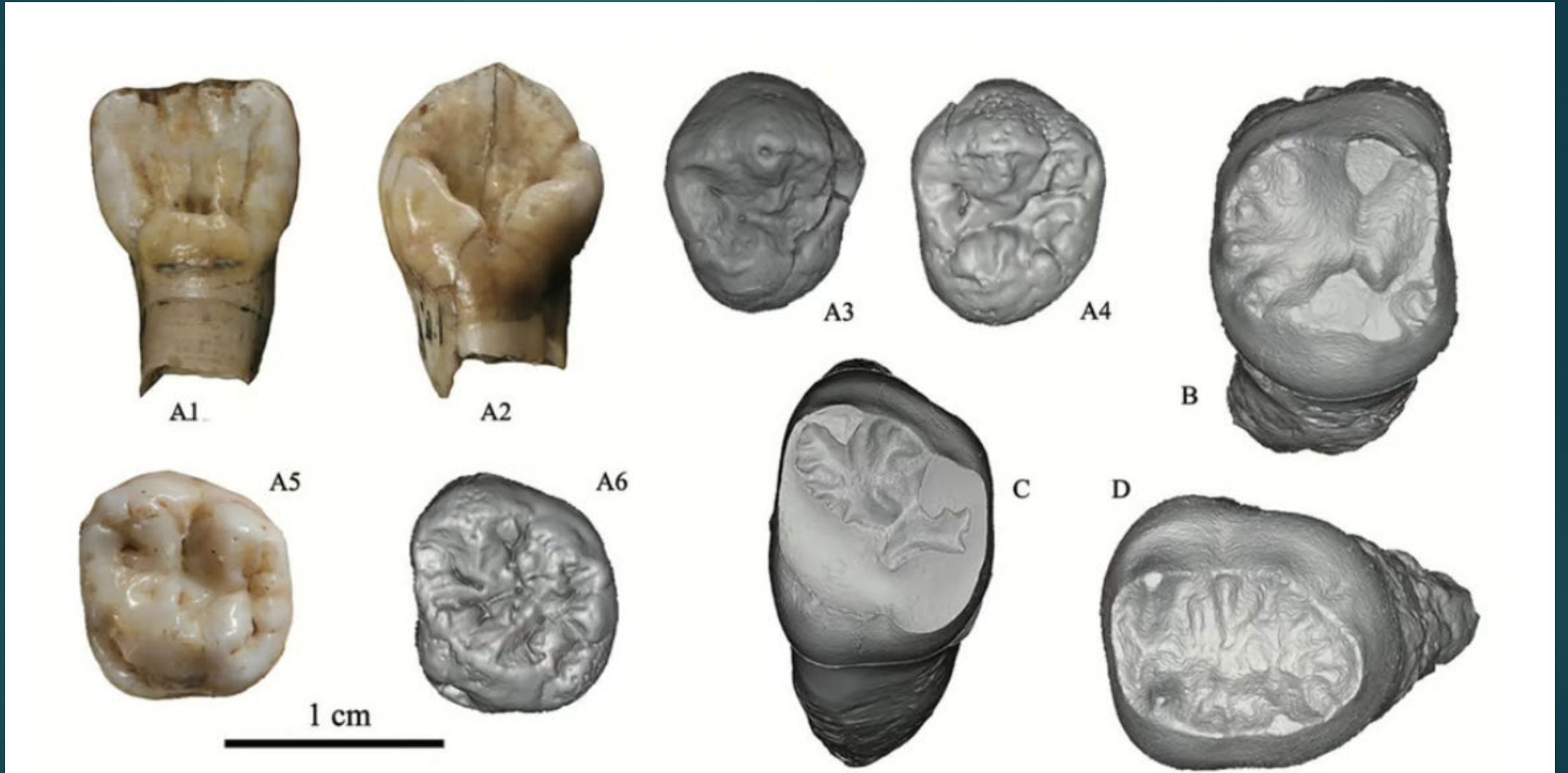
H. juluensis had very large brain and teeth

- ▶ The average cranial capacity: Homo sapiens = 1,350 cc; Neanderthals = 1,450 cubic centimeters. Homo juluensis - 1,700 to 1,800 cc. Homo juluensis skulls measured between 103 and 109 cubic inches (Ns= 88 cubic inches and MHs = 82 cubic inches).
- ▶ The teeth of Homo juluensis were very large. The teeth, they believe, have similarities to those of the Denisovans,
- ▶ They have proposed that Denisova be assigned to the new species, Homo juluensis. The idea has caused a stir among researchers, especially in the West.

Making sense of eastern Asian Late Quaternary hominin variability

- ▶ The *Homo juluensis* fossils were excavated in the late 1970s at a site known as *Xujiayao* on the border between the provinces of Shanxi and Hebei. *Fossils from Xuchang* in the central province of Henan were also considered the same species.
- ▶ Wu said fossils from *Xujiayao* and *Xuchang* shared the same inner ear system, which helps an individual to maintain balance.

The nine Xujiayao teeth fossils used in the study



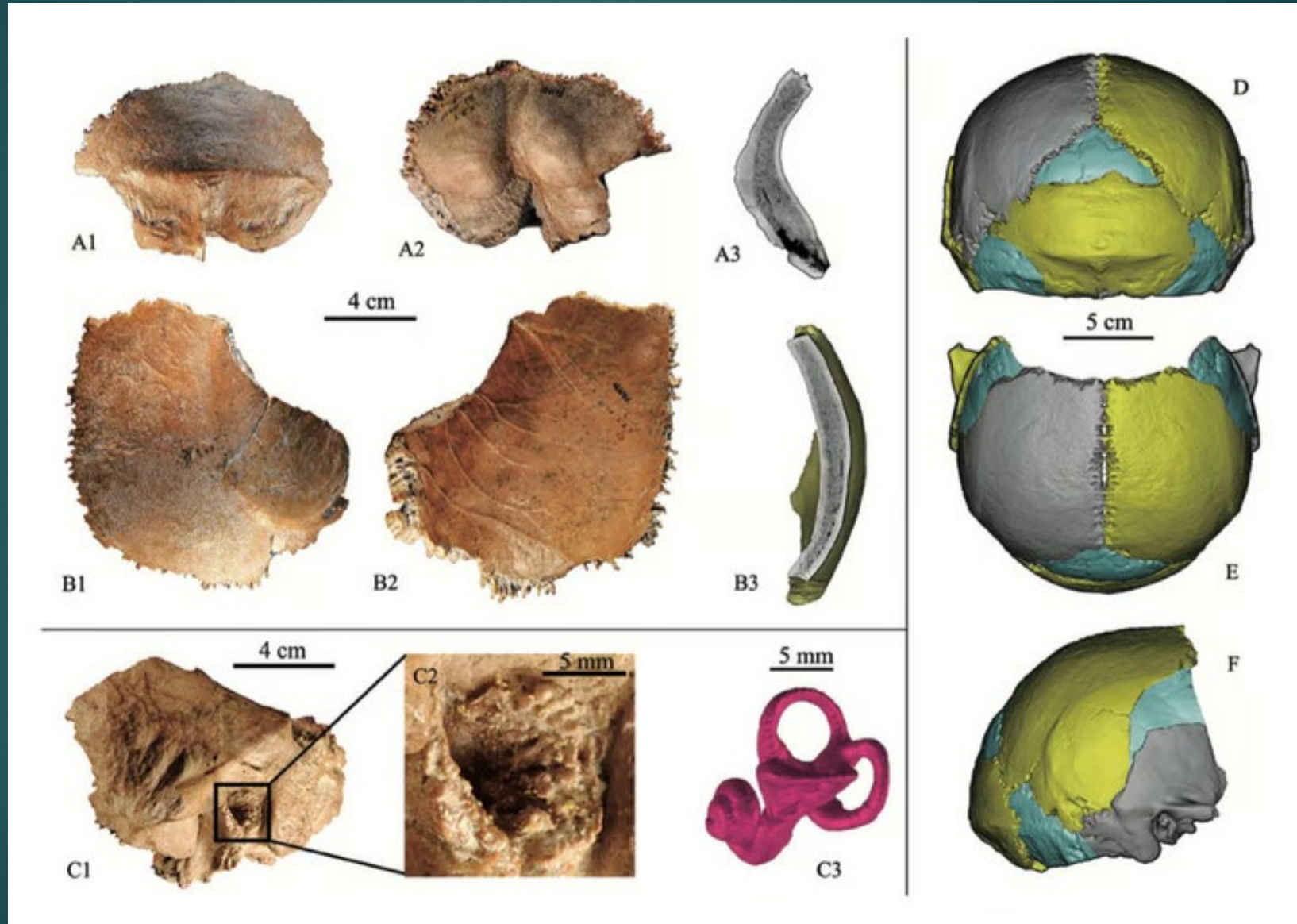
H. juluensis of Xujiayao and Denisovans

- ▶ In Xujiayao, researchers not only unearthed bone fragments from 16 individuals, they also discovered thousands of artefacts, stone tools and animal bones, all of which pointed to a horse kill site.
- ▶ Homo juluensis began to disappear as they integrated with the earliest modern humans who arrived in China about 120,000 years ago.
- ▶ Bae and Wu think Denisovans should be included in Homo juluensis because of matching teeth traits. One of the things that always stood out about the Denisova molars was that they were quite large. The molars from Xujiayao from our type specimen are also quite large.

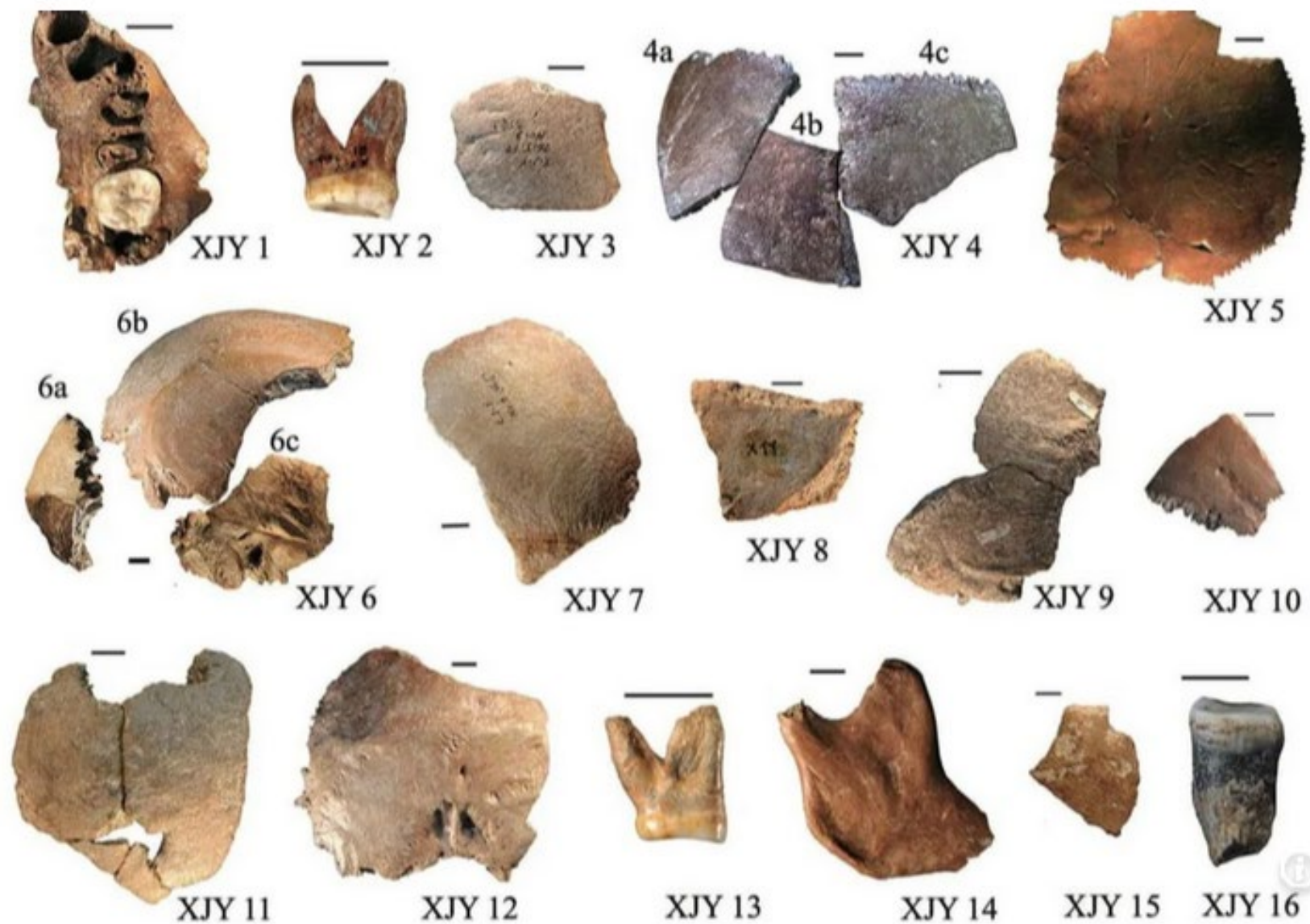
*** Denisovans

- ▶ Bae said their proposal was likely to be debated by paleoanthropologists because “a lot of Westerners said that the Chinese fossils should be called Denisova, not the other way around”.
- ▶ But Wu and Bae argue that Denisova is the name of a general population – not of a species – and should be assigned to a species if it could be confirmed.

Fossil fragments from Xujiayao and a virtual reconstruction of a cranium.



16 individuals at Xujiayao



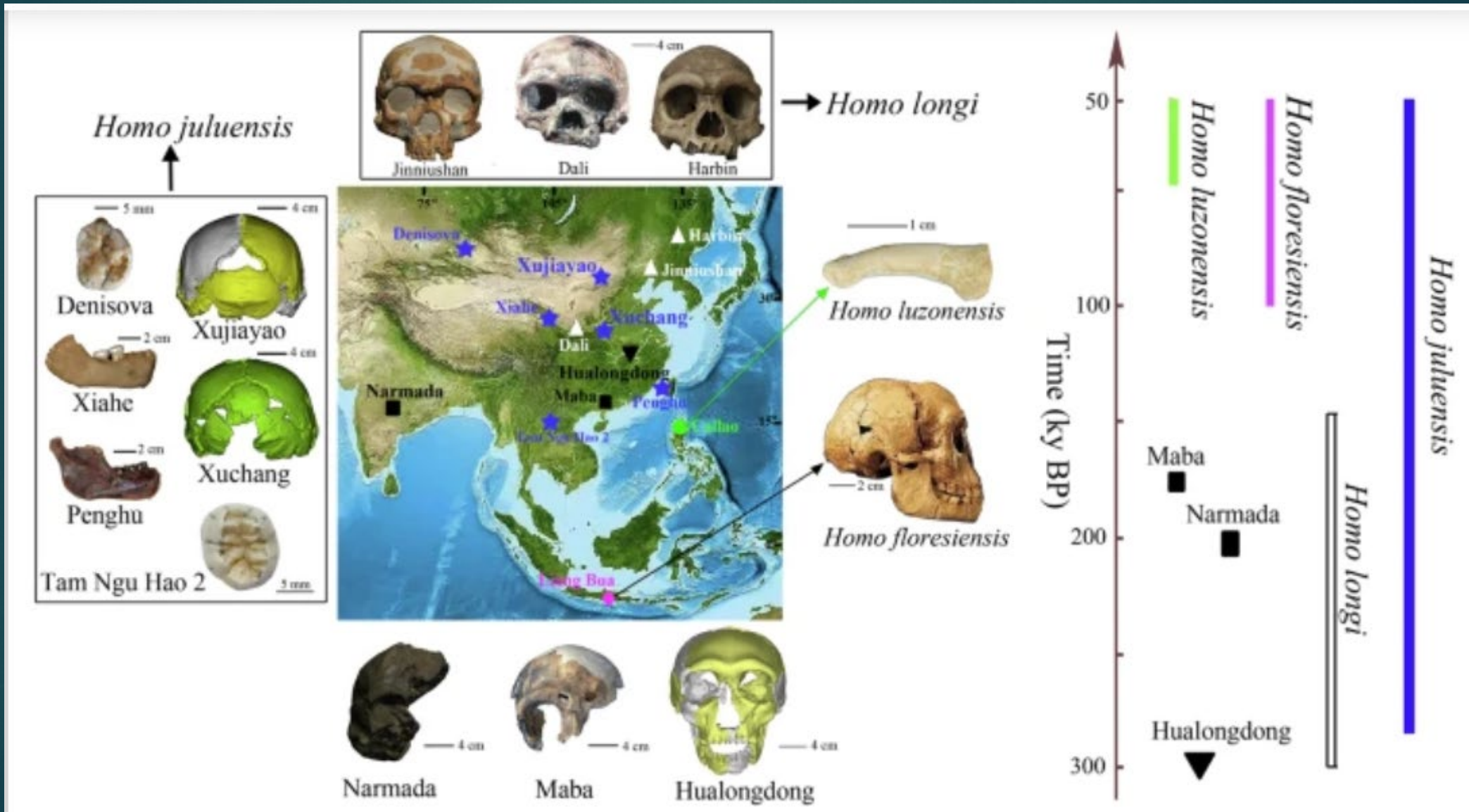
Decolonization of fossils

- ▶ Bae said it was important to “decolonize our field for Asian paleoanthropology to stand on its own” and “eventually for the name *juluensis* to be accepted”.

*** Making sense of eastern Asian Late Quaternary hominin variability – Christopher Bae & X. Wu, 2024

- ▶ When compared to other paleontological disciplines, the field of Late Quaternary (~300,000–~50,000 years BP) paleoanthropology has lagged far behind in synthesizing the degree of morphological variability in the hominin fossil record.
- ▶ It is now evident that morphological diversity among Late Quaternary hominin fossils from eastern Asia (East and Southeast Asia all-inclusive) is greater than has been expected. Indeed, there are now a number of new eastern Asian hominin taxa that have been proposed over the past several years reflecting not only a growing hominin fossil record but a greater appreciation for the degree of complexity that is present.
- ▶ This hominin variability is likely the result of a combination of dispersals and introgression that occurred throughout the Late Quaternary, rather than a single dispersal and complete replacement event.

Primary Late Quaternary (~300,000–~50,000 years BP) hominin taxa from eastern Asia.



Type specimens

- ▶ Type specimens and sites for the four hominin species discussed here: *H. floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*
- ▶ *Homo juluensis* (blue five-pointed stars) includes Xujiayao, Xuchang, Xiahe, Penghu, Denisova, and Tam Ngu Hao 2; *Homo longi* (white triangles) includes Harbin, Dali, and Jinniushan; *Homo floresiensis* (pink diamond) includes Liang Bua; *Homo luzonensis* (green circle) includes Callao.

- ▶ Although elsewhere we had tentatively grouped **Hualongdong** (black inverted triangle) with the *H. longi* fossils, we keep it separate for now pending further ongoing investigation.
- ▶ In many studies, **Maba and Narmada** (black squares) have been grouped together to form a separate population. It may be possible following further analyses that these latter fossils may be included in the broader *H. neanderthalensis* species or assigned a new taxonomic name altogether.

Lumping trend

- ▶ **Nowadays, paleoanthropologists tend to lump rather than split the Late Quaternary hominin fossils.** In general, lumpers tend to emphasize similarities between fossils, focusing on intra-specific variation around a mean, while splitters emphasize differences in fossils, using these to identify different species. This may be partially due to efforts by scientists beginning in the 1950s, particularly from discussions resulting from the 1950 Cold Spring Harbor Symposium, to be more conservative and lump hominin fossils into broader more inclusive categories.
- ▶ This latter push could be related to the realization that many of the earlier proposed distinct species in fact exhibit overlapping morphologies and lack the presence of unique traits that would clearly distinguish them into separate taxa.

Lumping in China and Multiregionalism

- ▶ The Late Quaternary record of China may be a good example of this conservative lumping.
- ▶ Since the 1920s with the formal introduction of *Sinanthropus pekinensis* (later, along with *Pithecanthropus erectus*, collapsed into *Homo erectus*) and the formal designation of *Homo longi* in 2021, all (>100 sites) Late Quaternary hominin fossils in China were considered to either represent *H. erectus* or modern *H. sapiens*.
- ▶ These data were then used to form the foundation of one of the primary traditional modern human origins models, “multiregional evolution”. In the multiregional model, through gene flow between populations, *H. erectus* was considered to have evolved in situ into archaic *H. sapiens* (Middle Pleistocene “non-*Homo erectus*”), which eventually evolved into modern *H. sapiens*.

Versus Out of Africa

- ▶ In China, this was always interpreted to mean that modern Chinese people today could trace their ancestry directly back to at least Zhoukoudian Locality 1 Homo erectus, if not to the earliest appearance of hominins in China during the Early Pleistocene.
- ▶ The other primary traditional modern human origins model, generally referred to as the “Out of Africa” or the “replacement” model posits that modern humans dispersed out of Africa and replaced all indigenous populations with no genetic contribution to living peoples.
- ▶ Based on current data, it now appears that a combination of both models is the most parsimonious way to explain the origin of modern humans, where modern humans dispersed out of Africa in multiple waves and interacted with the smaller indigenous populations regularly. In other words, modern humans across Eurasia likely arose as a result of a combination of dispersals and introgression events

Late Quaternary (300-50 Ka) species

- ▶ Thanks largely to a growing hominin fossil record, the field of Late Quaternary eastern Asian paleoanthropology is in the midst of significant and important change that is contributing tremendously to how we view and are refining these evolutionary models.
- ▶ In particular, the field received a jolt two decades ago with the publication of the diminutive *Homo floresiensis* fossils from the island of Flores in Indonesia in 2004. More recently, another diminutive species, *Homo luzonensis*, from the island of Luzon in the Philippines was added as a new hominin taxon. In China, *Homo longi* was presented following an analysis of the Harbin fossil. Fossils like *Dali and Jinniushan* may be tentatively included in *H. longi* as well, though we await further comparative analyses.
- ▶ Most recently, after a detailed study of the *Xujiayao and Xuchang* fossils, we have added *Homo juluensis* to these discussions. Importantly, we have assigned the enigmatic Denisova, along with the Xiahe and Penghu fossils, to *H. juluensis* based on comparative study of the present dentognathic remains.

Laos and China

- ▶ We assign Tam Ngu Hao 2 (Laos) tooth shares traits with Denisova, in *H. juluensis*.
- ▶ Further, the Maba (southeastern China) and Narmada (India) fossils have been grouped together in various studies, though these fossils have yet to receive a formal taxonomic name. **Maba and Narmada may ultimately find their way to be included in the broader *H. neanderthalensis* species**, particularly given early suggestions that Maba was a Neanderthal.
- ▶ These recent research initiatives in China, and broader eastern Asia, are showing clearly that multiple hominin lineages were present during the Late Quaternary.

Late Quaternary species identified in eastern Asia: *Homo floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*.

Species	Type Specimen/ Location	Year of Discovery	Year New Species Name Assigned	Chronometric Age	Hominin Fossils	Archeology	Paleontology
<i>Homo floresiensis</i>	LB1/ Indonesia	2003	2004	190–50 ka	Assorted cranial, dentognathic, and postcranial remains	Assorted Late Pleistocene stone tools	Assorted Oriental faunas
<i>Homo luzonensis</i>	CCH6/ Philippines	2007	2019	67–50 ka	Assorted cranial, dentognathic, and postcranial remains	Assorted Late Pleistocene stone tools	Assorted Oriental faunas
<i>Homo longi</i>	Harbin/ China	1933	2021	309–138 ka	Cranium	None reported	Assorted Palearctic faunas
<i>Homo juluensis</i>	Xujiayao/ China	1976-1979	2024	200–160 ka	Assorted cranial and dentognathic remains	Assorted Early Paleolithic stone tools	Assorted Palearctic faunas

All the new Chinese fossils

- ▶ Eastern Asian hominin fossils are not only increasing in number thanks to new discoveries, but that a greater degree of morphological variation is present than originally assumed or anticipated.
- ▶ This is likely the reason why the number of recent newly proposed Late Quaternary hominin taxa in Asia is higher ($n = 4$) than Europe and Africa combined ($n = 1$: *H. naledi*).

New complexity

- ▶ There has been the discovery and identification of new hominin fossils that are only adding to this complexity. A good example of **new hominin fossils** is from the **Hualongdong site in central-eastern China**. The Hualongdong fossils date to the late Middle Pleistocene (~300,000 years BP) and display a mosaic of characteristics that cannot be easily fitted into any one lineage. In this case, Hualongdong does not fit neatly into *H. juluensis* or *H. longi* and certainly not into *H. floresiensis* or *H. luzonensis*; a good example in fact of the intricacy of the human evolutionary record.

Complexity abounds

- ▶ It is quite clear now that there are a number of distinct morphologically different hominin populations present in East and Southeast Asia that are penecontemporaneous, some that now have new specific names: *Homo floresiensis*; *H. luzonensis*; *H. longi*; *H. juluensis*, with others yet to appear.
- ▶ The eastern Asian hominin fossil record is an excellent example of how unilineal models of evolution, such as traditional multiregionalism, cannot adequately explain the complexity in the paleoanthropological record, particularly during the Late Quaternary.
- ▶ If anything, the eastern Asian record is prompting us to recognize just how complex human evolution is more generally and really forcing us to revise and rethink our interpretations of various evolutionary models to better match the growing fossil record.

C. Bae

- ▶ This cross-disciplinary teamwork has laid a foundation for further exploration.
- ▶ The research team emphasized the need for additional studies to confirm *Homo juluensis* as a distinct species and clarify its relationship to other hominins like the Denisovans.