

New Neandertals, Pt. 2

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+++ Neandertals 2.0
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What we will cover about Ns

Today

- N brain
- N language
- N genetic lineages
- Ns as technicians
- N hunting strategies
- N life histories
- Ns as stone artisans

Next month:

- N healthcare
- N food choices
- Home and hearth
- Ns and birds
- N Burials
- N transitional industries
- Reasons for N demise

Discussion notes

- ▶ **N** = Neandertal (new German; but *H. neanderthalensis*)
- ▶ **MH** = early modern humans = early African *sapiens*
- ▶ **Ns** (300-40 Ka) had significant variation (cranial, brain, genetic differences)
- ▶ **Early MHs** (60-20 Ka) were not anatomically identical to current MHs (larger mass; cranial, brain, genetic differences)

2016: Mask of la Roche-Cotard, also known as the "Mousterian Protofigurine", dated to 75 Ka



- Found in the entrance of the cave, a piece of flat flint that has been shaped in a way that resembles the upper part of a face.
- A piece of bone was pushed through a hole in the stone and has been interpreted as a representation of eyes. Flint flakes were wedged in to hold the bone in place. Flakes have been chipped off the block to make it more face-like.
- Found within a Mousterian layer
- OSL dating of layering = 75 Ka

2023: The earliest unambiguous Neanderthal engravings on cave walls: La Roche-Cotard, Loire Valley, France

- ▶ Report on Neanderthal engravings on a cave wall at La Roche-Cotard in central France, made more than 57 ± 3 Ka ago.
- ▶ Following human occupation, the cave was completely sealed by cold-period sediments, which prevented access until its discovery in the 19th century and first excavation in the early 20th century.
- ▶ The timing of the closure of the cave is based on 50 optically stimulated luminescence ages derived from sediment collected inside and from around the cave.

La Roche-Cotard Neandertal engravings

- ▶ Cave closure occurred significantly before the regional arrival of *H. sapiens*, and all artefacts from within the cave are typical Mousterian lithics; in Western Europe these are uniquely attributed to *H. neanderthalensis*.
- ▶ Concluded that the LRC engravings are unambiguous examples of Neanderthal abstract design.

History of La Roche-Cotard excavations

- ▶ In 1846, La Roche-Cotard cave entrance was exposed during quarrying and in 1912, the site owner Francois d'Achon excavated almost all the inner sedimentary deposits.
- ▶ Only Mousterian lithic artefacts were discovered within the cave; no later-period material was found.
- ▶ Subsequent excavation, in the 1970s and from 2008 onwards.

The walls of LRCL: finger flutings

- ▶ On the walls of LRC, the first observation of seemingly organized digital traces (finger flutings) were made during field campaigns from 1976 to 1978, and then again from 2008 (all directed by the lead author).
- ▶ In addition, sparsely occurring red ochre spots were identified.
- ▶ Other types of marks are also present: (i) traces left by animal claws, (ii) the smoothing of the very fragile wall surface presumably through repeated contact with animal fur, and (iii) numerous easily recognizable traces caused by the percussion of metal tools, from the excavation in 1912.

Neandertal Engravings

- ▶ Study uses the term “engravings” for the finger-flutings, as an “engraving” is generally defined as the deliberate removal of material carried out with a tool or a finger.
- ▶ This removal of material is neither accidental nor utilitarian, but rather that it is intentional and meticulous. In 2008, the digital traces were recognized as ancient traces.
- ▶ They were made by Neanderthals

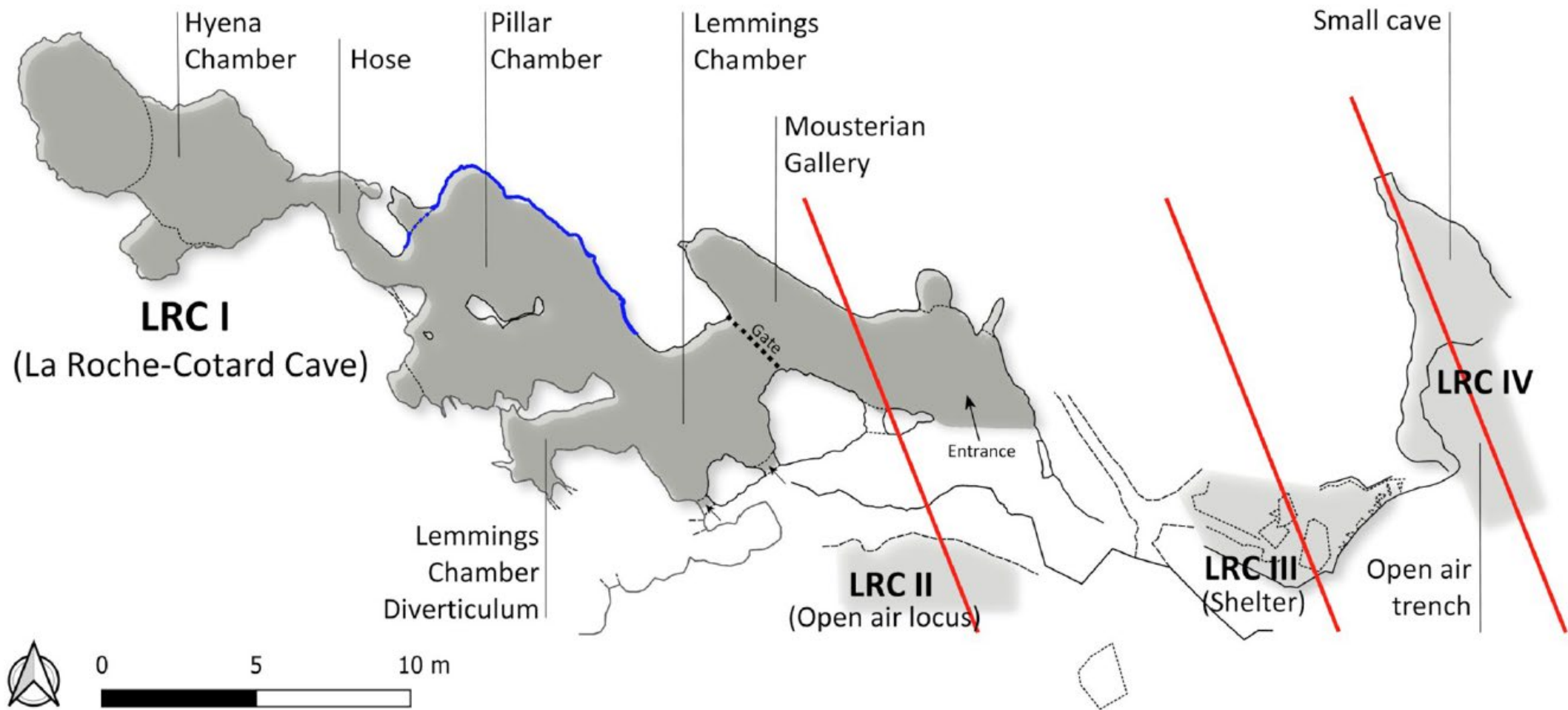
The cave

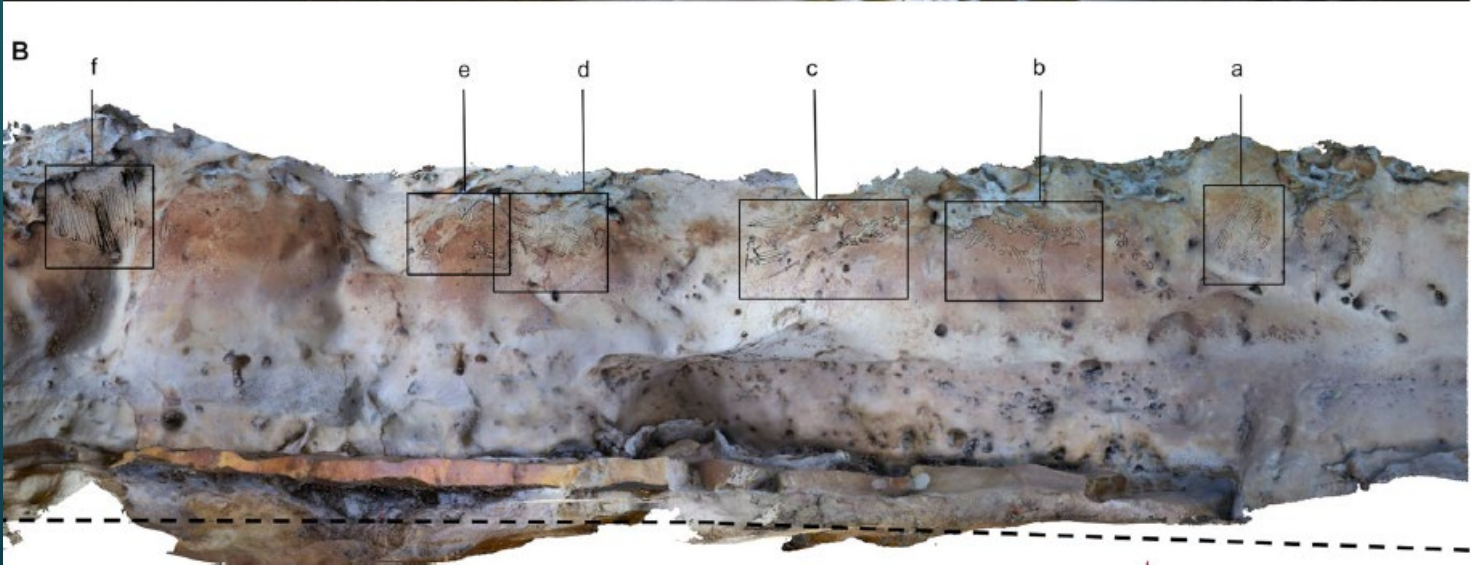
- ▶ Today, the **cave of La Roche-Cotard** comprises four main chambers extending ESE-WNW for 33 m: the Mousterian Gallery, the Lemmings Chamber, **the Pillar Chamber** and the Hyena Chamber.
- ▶ **Only Mousterian lithic artefacts were discovered**, either within or outside the cave; no later period material was found. **Bifaces and Levallois** flakes were found in the cave (LRC I).
- ▶ In addition, **engravings were made on the walls of the Pillar Chamber at LRC I**. No other, more recent occupations (until the 19th century) have left traces in the cave,

6 panels: finger traces

- ▶ First six panels (a to f) are at an average height of 1.50 to 1.70 m above the Neanderthal floor.
- ▶ The majority of the traces on these panels were made by fingers laid flat, while a few rare traces appear to have been made by a finger on edge (on the side).

A





Spatial organization of the marked panels in the Pillar Chamber.

A. View of the Pillar Chamber from the entrance, showing the location of panels with markings.

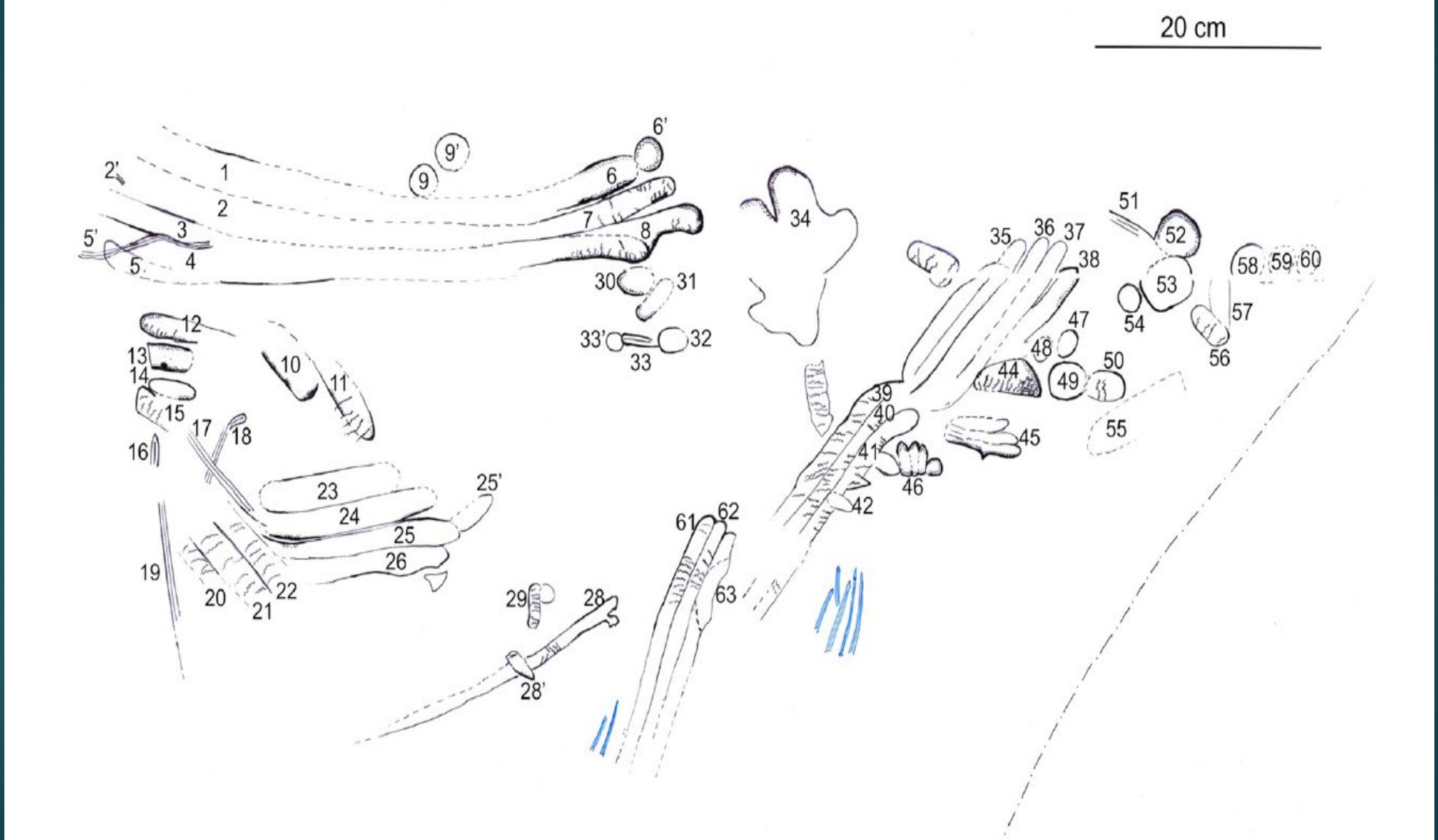
Sections and ridges of the ceiling are indicated by red lines.

Numbered panels are indicated by blue areas or arrows

Neanderthal cave engravings identified as oldest-known, more than 57,000 years old

- ▶ Markings on a cave wall in France are the oldest known engravings made by Neanderthals.
- ▶ The cave is La Roche-Cotard in the Center-Val de Loire of France, where a series of non-figurative markings on the wall are interpreted as finger-flutings, marks made by human hands.
- ▶ The researchers made a plotting analysis and used photogrammetry to create 3D models of these markings, comparing them with known and experimental human markings. Based on the shape, spacing, and arrangement of these engravings, the team concluded that they are deliberate, organized and intentional shapes created by human hands.

Linear Panel: 1.50 m long and 0.50 m high, is made up of 63 ancient anthropogenic traces

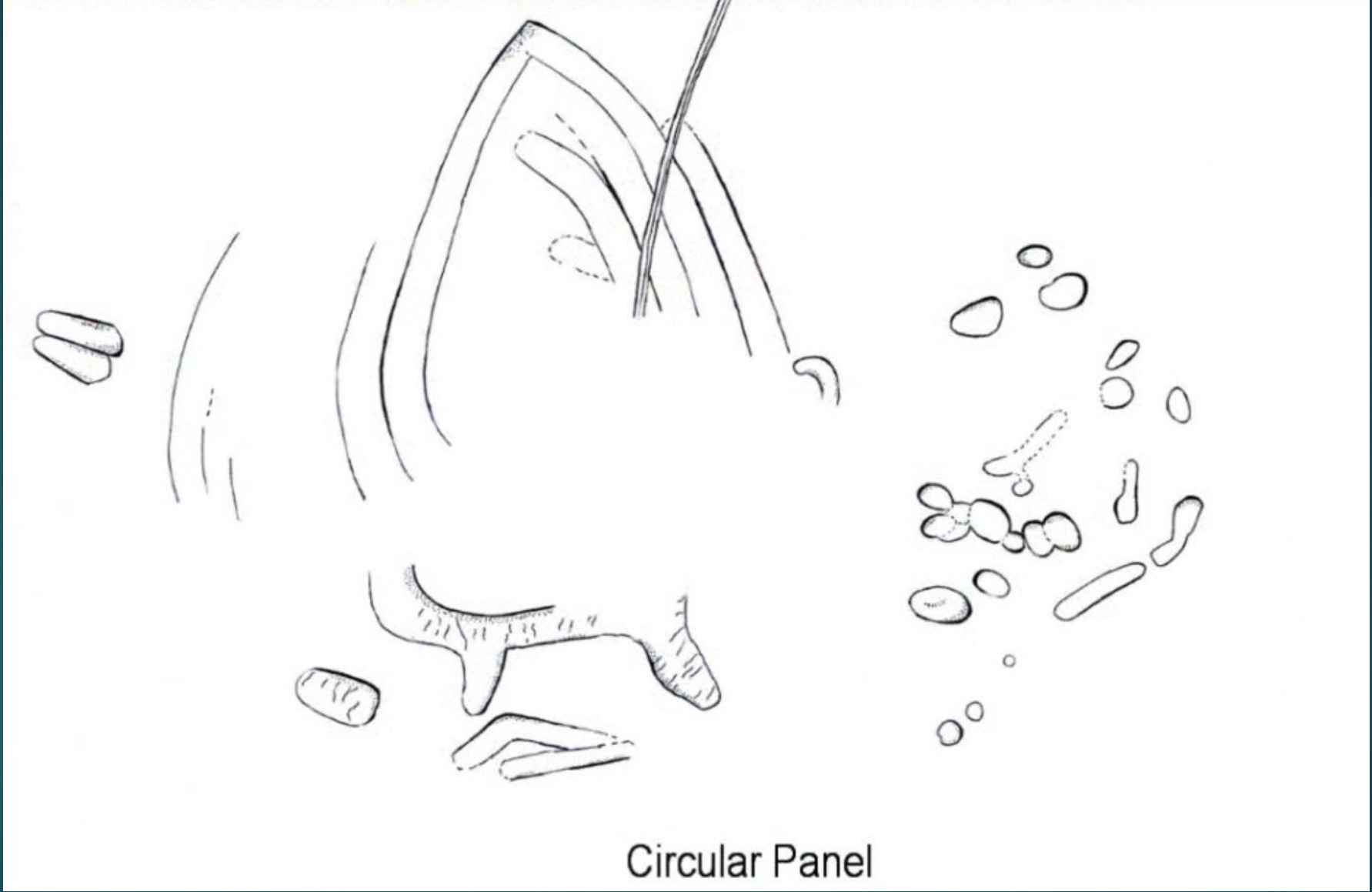


Undulated Panel



Circular Panel





Circular Panel

Triangular Panel





Triangular Panel

Dotted Panel





Dotted Panel

Dating: 57 to 75 Ka

- ▶ The team also dated cave sediments with optically-stimulated luminescence dating, determining that the cave became closed off by infilling sediment around 57,000 years ago, well before *Homo sapiens* became established in the region.
- ▶ This, combined with the fact that stone tools within the cave are only Mousterian.
- ▶ The engravings have been dated to over 57,000 years ago and, thanks to stratigraphy, probably to around 75,000 years ago, making this the oldest decorated cave in France, if not Europe.

The main decorated wall of
La Roche-Cotard cave

Dating

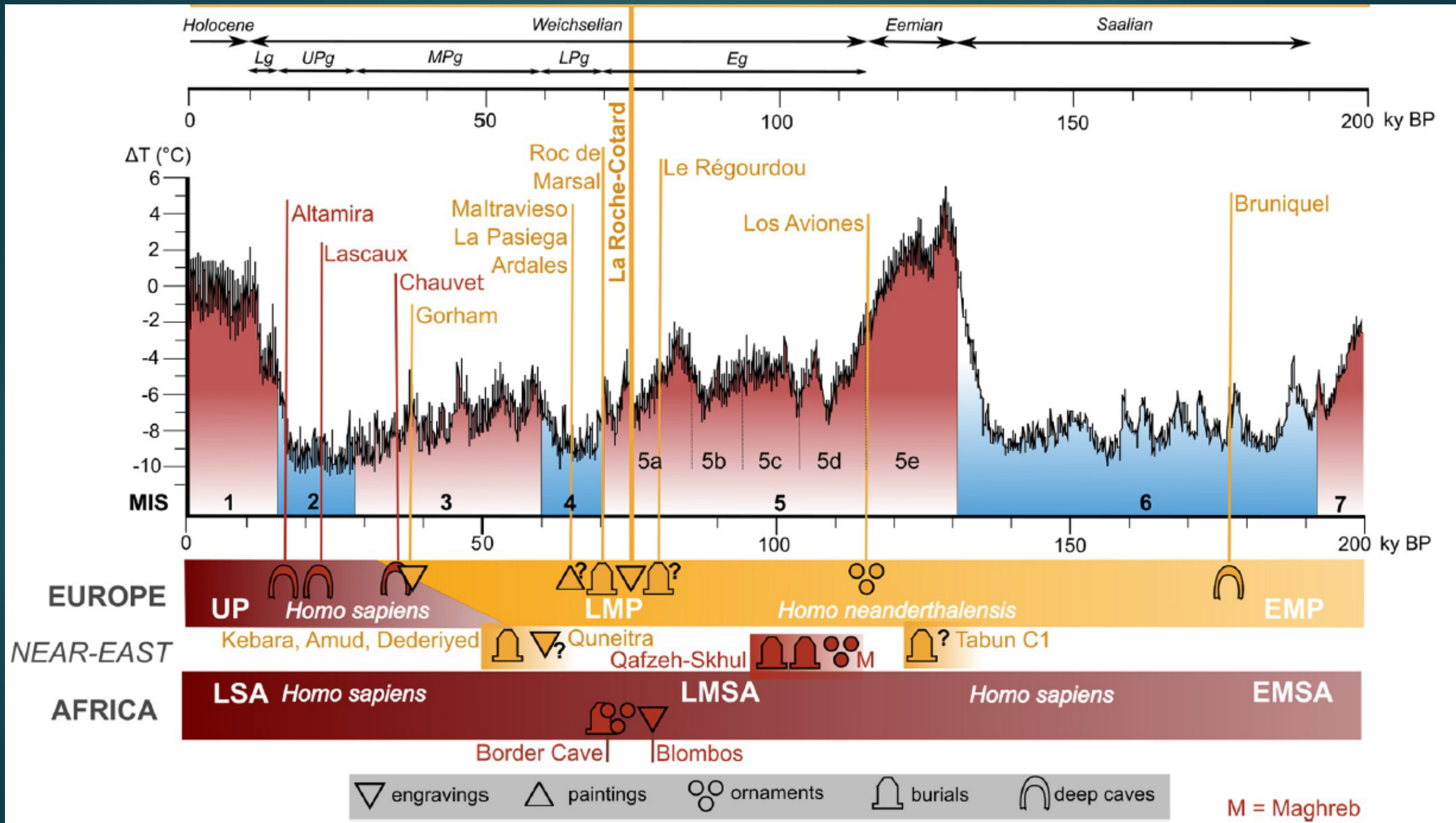
- ▶ OSL dating indicates that the sediment deposition closed the cave > 51 ka (95% CI) ago, or at 57 ± 3 ka (68% CI).
- ▶ This age makes access to the cave interior by anatomically modern humans (AMH) highly unlikely; earliest MHs in Europe at 45 ka (Bacho-Kiro)
- ▶ The non-figurative engraved marks at La Roche-Cotard are necessarily older than 57 ± 3 ka, and can be, therefore, confidently stated to be of Neanderthal origin.

A creative process

- ▶ The graphic productions identified on the walls of La Roche-Cotard demonstrate a deliberate creative process visible in the spatial arrangement of the engraved marks on the cave wall.
- ▶ There is little historical graphic evidence associated with Neanderthals, and that is mainly on mobile objects (pebbles, slabs, bones...), rather than walls.
- ▶ In contrast, the walls of La Roche-Cotard testify to something different: the frequent repetition of finger engravings, organized in space both on the wall surfaces and with respect to the cave as a whole.
- ▶ There even seems to be a progression in the complexity of these graphic entities, particularly from the first to the sixth panel.

Original panels

- ▶ These traces were meticulously made only on selected surfaces and most often exploiting the shape of the cave wall.
- ▶ These figures are clearly intentional.
- ▶ The layout of these non-figurative graphic entities is an organized, deliberate composition, and is the result of a thought process giving rise to conscious design and intent.



Homo naledi: 465–610 cc:

Was a small-brained hominin the world's first gravedigger—and artist?



Lee Berger's bonanza of non-peer-reviewed publicity

- 3 non-peer reviewed preprint papers published Jun 1, 2023
- Then Netflix's "Unknown: Cave of Bones" on July 17
- And then **a book** coauthored by Berger and Hawks called "*Cave of Bones: A True Story of Discovery, Adventure, and Human Origins*," available August 8.
- Berger claims all peer reviews for publication will become public.

3 non-peer-reviewed Preprints on bioRxiv

- ▶ L.R. Berger et al. "Evidence for deliberate burial of the dead by *Homo naledi*" (2023). [10.1101/2023.06.01.543127](https://doi.org/10.1101/2023.06.01.543127)
- ▶ L.R. Berger et al. "241,000 to 335,000 years old rock engravings made by *Homo naledi* in the Rising Star cave system, South Africa" (2023). [10.1101/2023.06.01.543133](https://doi.org/10.1101/2023.06.01.543133)
- ▶ A. Fuentes et al. "Burials and engravings in a small-brained hominin, *Homo naledi*, from the late Pleistocene: contexts and evolutionary implications" (2023). [10.1101/2023.06.01.543135](https://doi.org/10.1101/2023.06.01.543135)

sideways

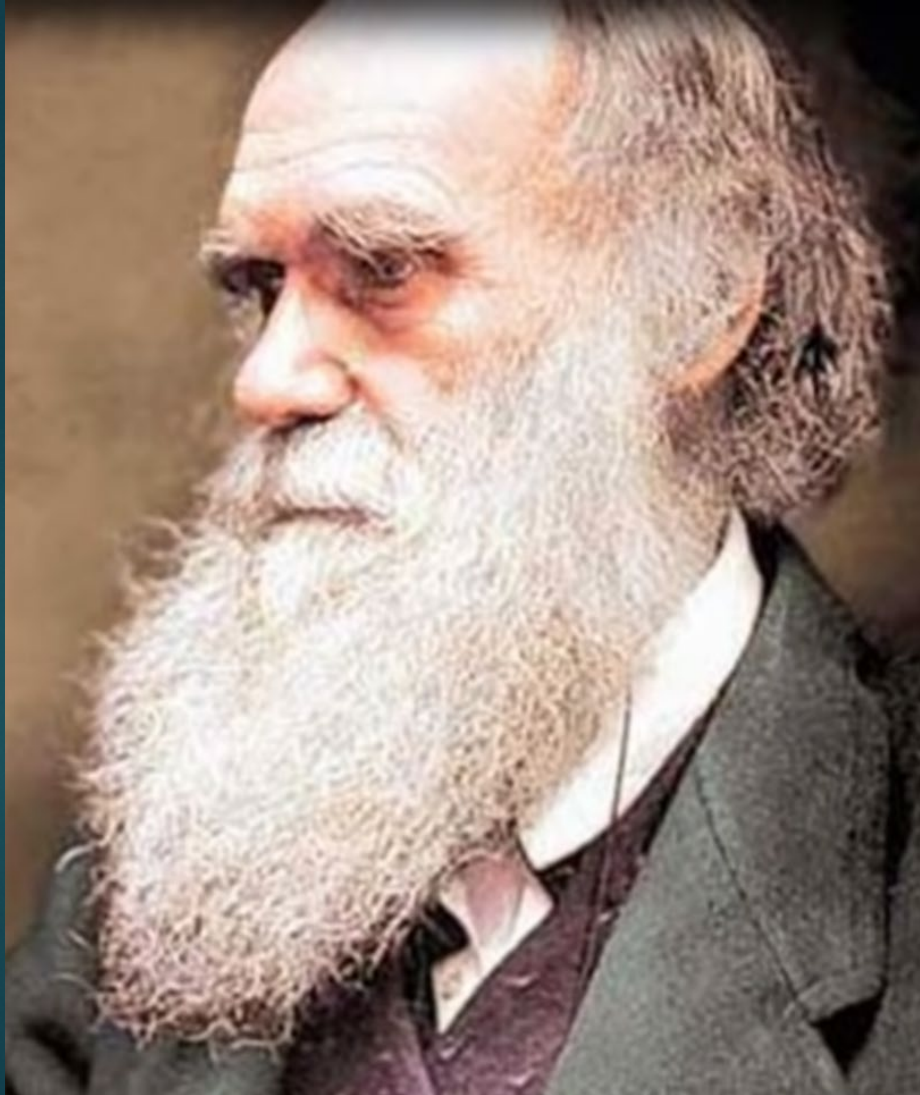




The Neandertals 2.0

- ▶ In terms of the idea of “behavioral modernity”, Neanderthals have been largely defined by what they were not (i.e., modern humans) rather than what they were—a geographically widespread, culturally sophisticated, behaviorally variable, highly adaptable, and long-lasting hominin.
- ▶ They lived for 650,000 years after separating from our last common ancestor
- ▶ They were **cognitively equivalent to early modern humans**

Only N skull Darwin ever touched



N skull that gave Ns their name: Neander 1, 1856





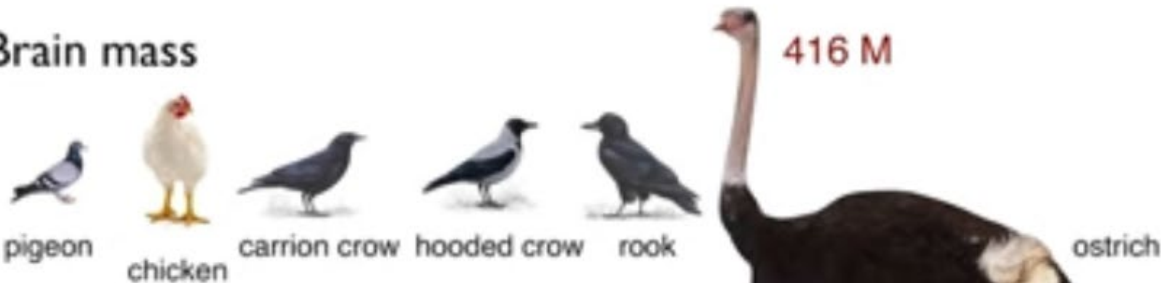
Feldhofer N skeleton: bones are very large, thicker, head of femur is very large (lots of force transmitted thru joints); bones are curved and very thick; more heavily affected by osteoarthritis. All point to their hard physical hunter gatherer lifestyle.

1007 = 1st N mtDNA = 28% base

A few comments about brains and neurons

Numbers of pallial neurons should be best predictor of behavioral flexibility

Brain mass



Pallial neurons

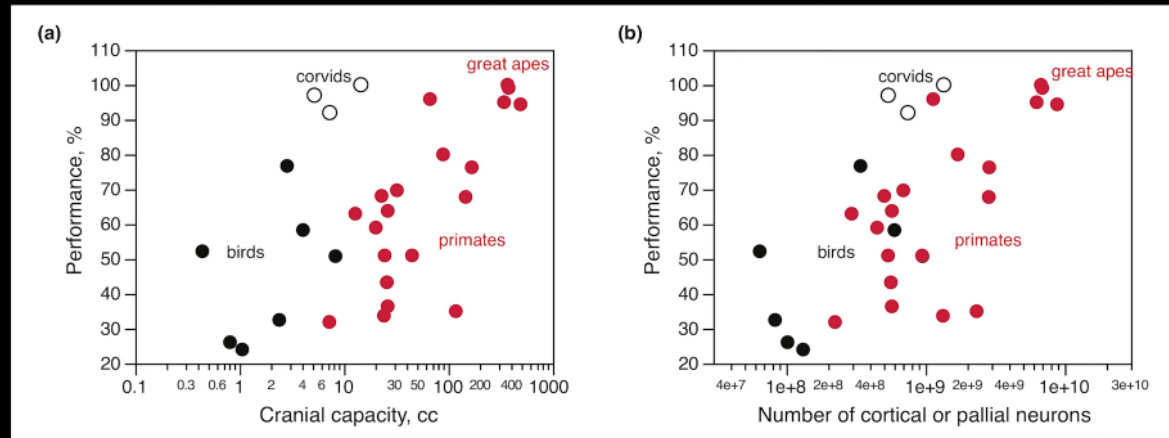


Nidopallial neurons



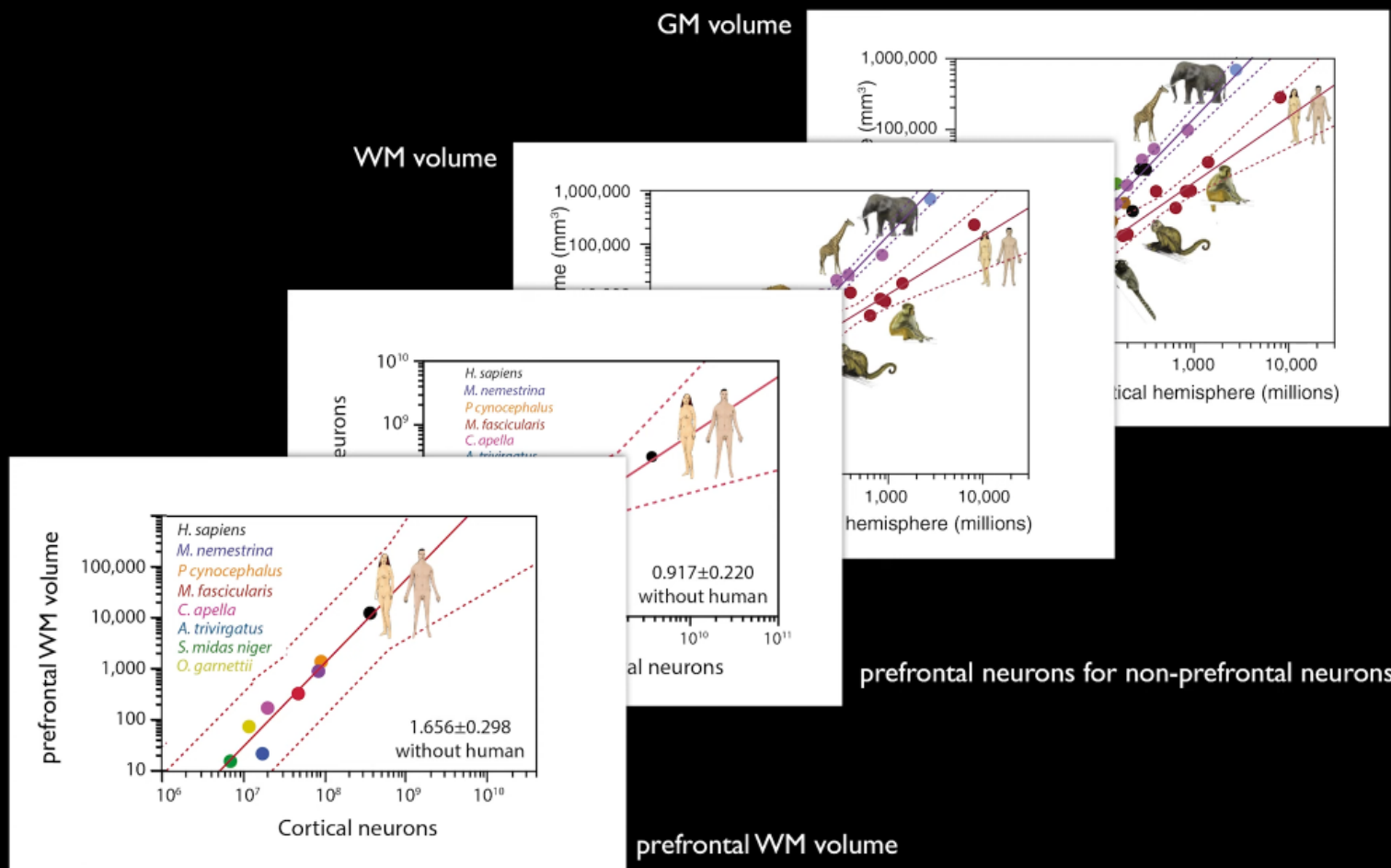
What does it matter?

Cognitive capability $\sim N_{CX}$



based on MacLean et al., 2014, and Kabadayi et al., 2016

Nothing exceptional about the human cerebral cortex



Number of neurons in prefrontal regions

BIRD NCL, primate PFC

40-50% of N_{PL}

8% of N_{CX}



Humans: ~1.3 B

542 M



Chimpanzee

300-400 M in nidop. alone



Raven



New Caledonian crow

136 M

With
Felix Ströckens,
Onur Güntürkün



Rhesus monkey

91 M



Capuchin monkey

42 M



Rock dove

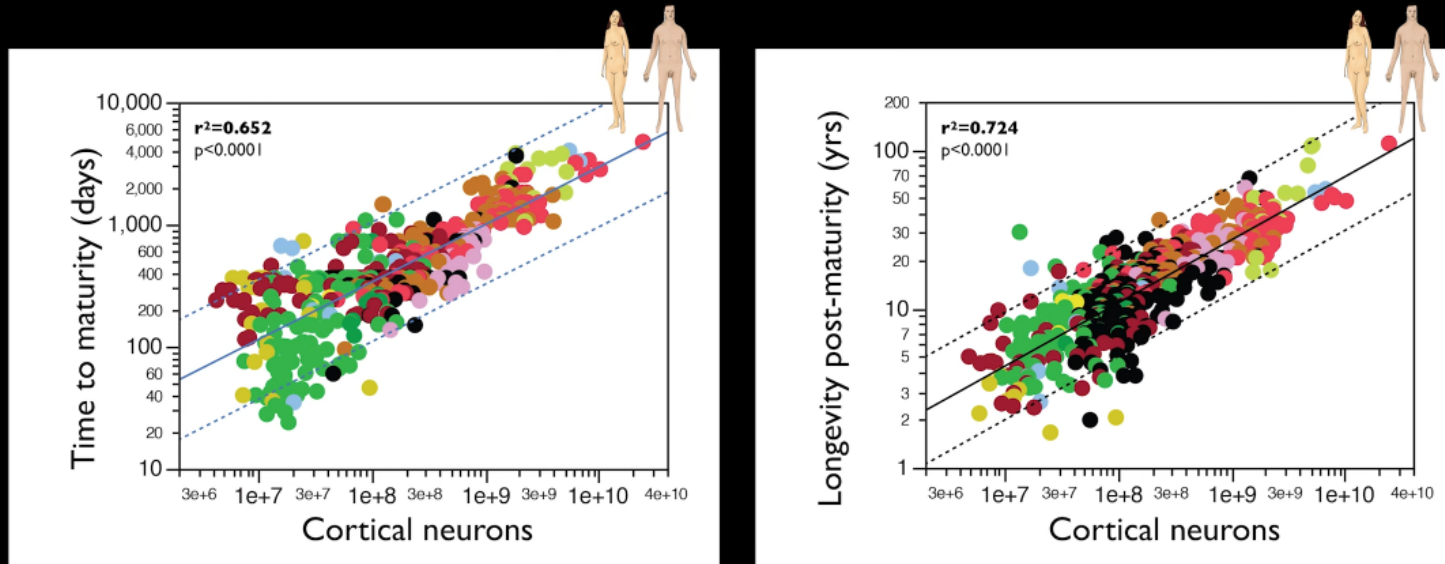
10 M



Marmoset

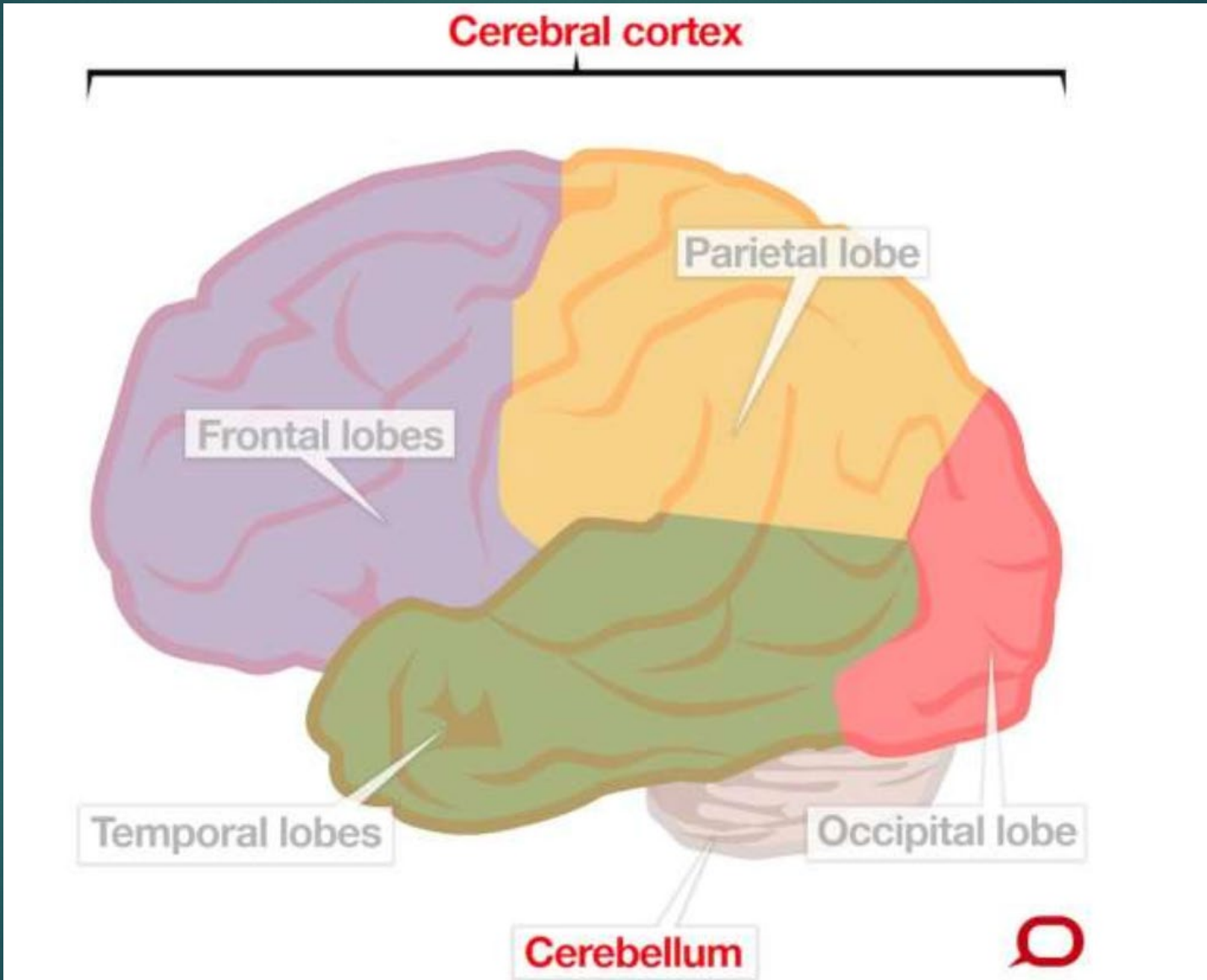
With more neurons, come slower, longer life

With more neurons comes a slower, longer life

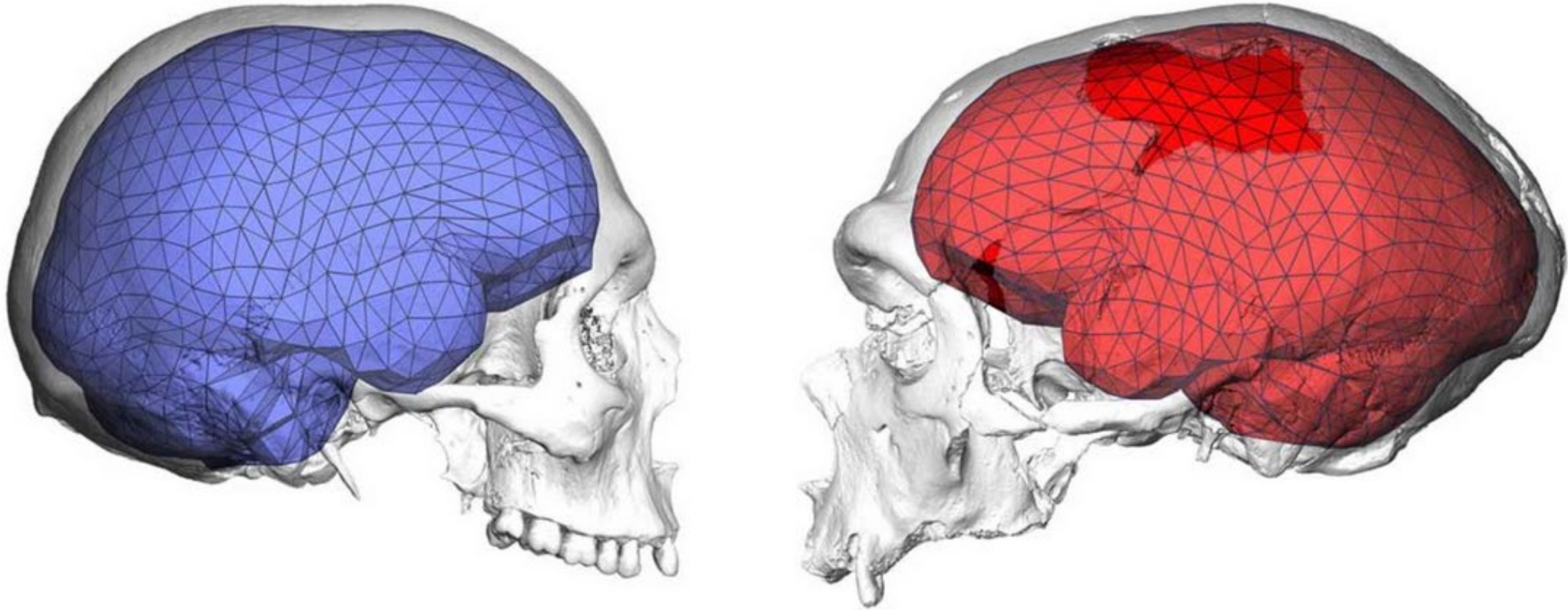


Best predictor of longer development (to sexual maturity) and of longer life is the number of cortical neurons

Evolutionary Integration of Brain lobes



Classical shape difference between MHs & Ns



Endocranial shape in a recent human (left) and La Chapelle-aux-Saints Neandertal (right). Image: Neubauer et al. 2018 (CC-BY-NC)

Skull shape is molded by brain shape



Functions of modern human brain regions

- ▶ **Human brain:** 86 B neurons, 85 B glial cells
- ▶ **Cortex:** 82% of brain mass; 16 B neurons/19% of neurons (most of any animal)
- ▶ **Prefrontal:** 8% of brain, but 1.3 B neurons: planning, executive functions, problem solving, working memory, memory retrieval, attention, flexibility
- ▶ **Posterior frontal:** voluntary motor control, speech production
- ▶ **Orbital frontal:** behavioral/emotional control
- ▶ **Temporal:** hearing, language, memory consolidation, facial recognition
- ▶ **Occipital:** Visual processing
- ▶ **Parietal:** Complex visual motor, integration of sensory info, attention, working memory; mirror neurons, intention determination
 - ▶ **Precuneus:** core of default mode network (self memory); physical sense of self, self's physical point of reference
- ▶ **Cerebellum:** 18% of brain mass; 70 B neurons/81%: movement and all of above

Unknowable facts about N brains

- ▶ We know N brain sizes (via endocranial skull sizes)
- ▶ We will never know:
 - ▶ Number of neurons in complete N brain or in their different brain regions
 - ▶ How N brains were internally organized or interconnected (what their white matter connectivity patterns were)
- ▶ Given that MHs and Ns shared same LCA (1250 cc ave), it is likely that they shared basically similar types of brains

Comparative N and MH Brain sizes

- ▶ Based on Holloway, Tattersall & Schwartz: fossil Neanderthals and African humans from the same time period had similar brain sizes.
- ▶ Study of 23 Neanderthal skulls, 40-130 Ka: endocranial volumes from 1172 to 1740 cc. Average = 1450 cc
- ▶ 60 Stone Age *Homo sapiens*: 1090 to 1775 cc.
- ▶ For **current MH**, average adult brain size is 1,349 cc based on measurements from 122 global populations compiled in the 1980s.
- ▶ Recent MHs span from 900 to 2,100 cc.
- ▶ All Ns brain volumes fall comfortably within the range of living people.

N brain reflected larger body size

- ▶ 2013 study: **comparison of 13 N skulls to 32 human skulls (27-75 Ka)**. Study attempted to come to a “**corrected**” volume, which would account for the fact that the Neanderthals’ brains were in control of rather differently-proportioned bodies than MH brains were.
- ▶ **Size of the occipital cortex**—used for visual processing. Volume of this area is roughly proportional to the size of the animal’s eyes. N eye sockets approximate the visual cortex. N eye sockets were 20% larger than African sapiens. Due to evolution in higher latitude Europe, with poorer light conditions.

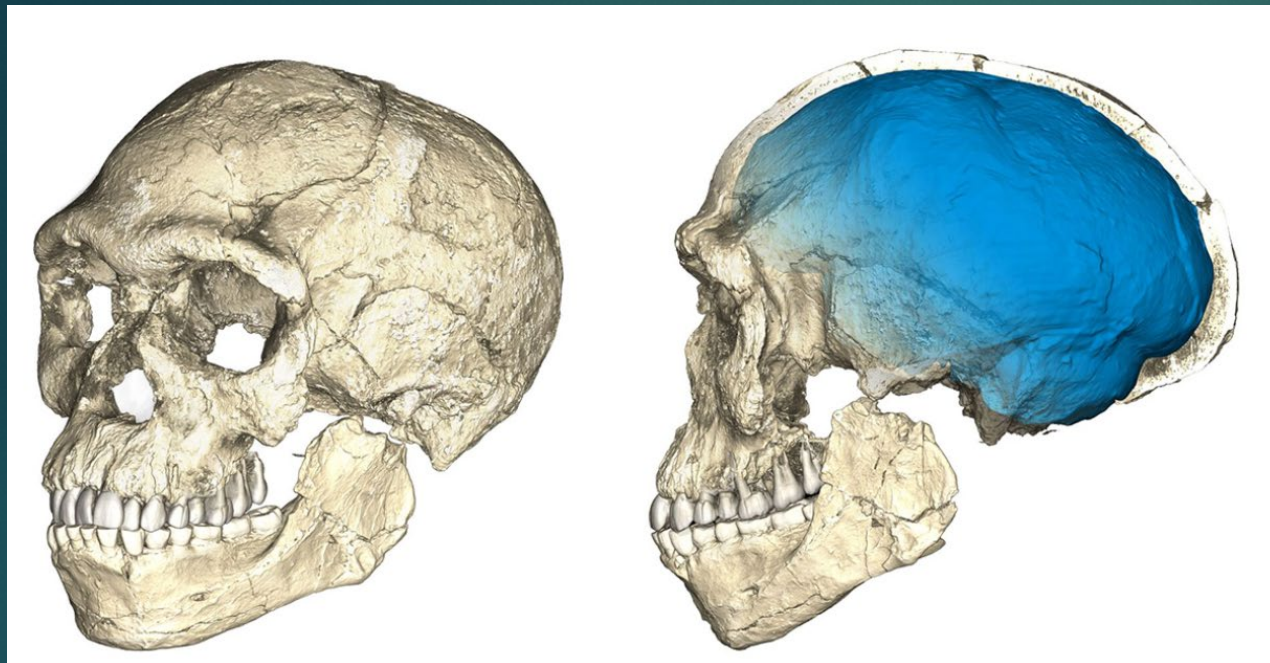
Correcting for N body mass difference

- ▶ After correcting for number of neurons devoted to body mass differences, found that the amount of brain volume left over for other tasks was **smaller for Neanderthals than for ancient *H. sapiens*.**
- ▶
- ▶ Although the average raw brain volumes of the two groups studied were practically identical (1473.84 cubic centimeters for humans versus 1473.46 for Neanderthals), the average “corrected” Neanderthal brain volume was just 1133.98 cubic centimeters, compared to 1332.41 for the humans. 200 cc difference.
- ▶ Discussed possible social cognition and coping differences
- ▶ But note that difference is still within MH brain difference range.

2018: The evolution of modern human brain shape

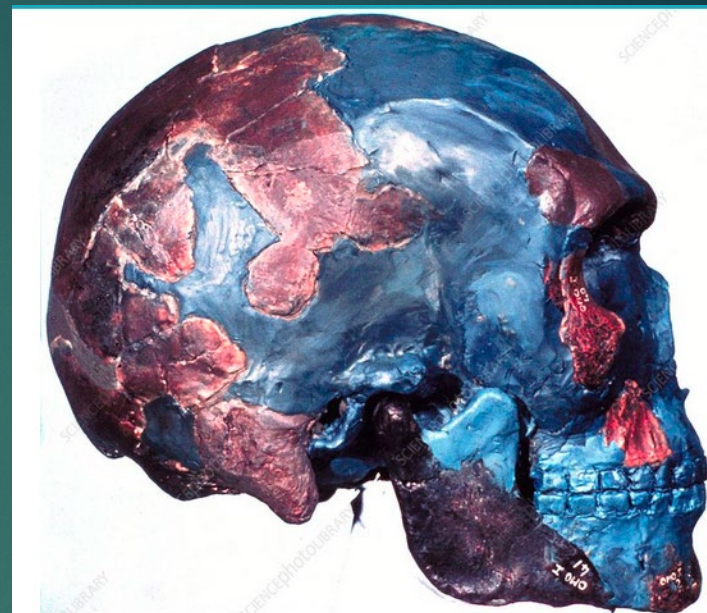
- ▶ *H. sapiens* endocasts had increasingly more modern globular shapes in accordance with their geologic age.
- ▶ Surprisingly, only fossils younger than 35,000 years show the same globular shape as present-day humans, suggesting that modern brain organization evolved sometime between about 100,000 and 35,000 years ago.
- ▶ But brain size at 300,000 years ago falls already within the range of that of present-day humans.
- ▶ So first came larger brain size, then reorganization.

Not Globular yet



Jebel Irhoud – 315 Ka

Omo 2 – 233 Ka



Current
MH

MH brain shape changes

- ▶ Changes in facial and endocranial form cannot be the driving force for globular brains: modern faces and large brains evolved long before the evolutionary brain rounding started.
- ▶ Two features of the globularization process stand out: bulging of parietal and cerebellar areas.
- ▶ The **parietal lobe** is an important hub in brain organization and involved in various integration and transformation functions.
- ▶ The **cerebellum**, in addition to motor-related functions, is associated with language, social cognition and affective processing. 84% of brains neurons

N brain: different than MH

- ▶ The mean cerebral vs. cerebellar volumes: Neandertals = 1161 cc and 149 cc, Early Humans= 1135 cc and 153 cc; MH = 1097 and 149 cc.
- ▶ No statistically significant between-group difference was detected in the total brain volume.
- ▶ NT had significantly smaller relative cerebellar volume than EH and MH.
- ▶ There were significant morphological differences in the cerebellar, parietal, occipital and medial temporal regions, but no differences in the frontal regions between NT and MH.

Cerebellum

- ▶ There is now strong evidence that the cerebellar hemispheres are important for both motor-related function and higher cognition including language, working memory, social abilities and even thought. Further, whole cerebellar size is correlated with cognitive abilities, especially in the verbal and working memory domain.
- ▶ MH had relatively larger parietal regions than the NT with significant difference, particularly in the superior medial and lateral areas.
- ▶ No differences in the relative size of the parietal region between N and EH.
- ▶ The superior medial part of the parietal lobule (the precuneus) plays important roles in highly integrated tasks, including visuo-spatial imagery, episodic memory and self-related mental representations,
- ▶ The superior lateral region is involved in integration and coordination between the self and the external space, generation of body image and sense of agency

2019 Gunz et al.: Neandertal Introgression Sheds Light on Modern Human Endocranial Globularity

- ▶ Quantified the endocranial shape differences between Neandertals and modern humans and study how Neandertal introgressed fragments affect MH phenotype. To begin identifying genes associated with variation in endocranial globularity
- ▶ Analysis of endocranial shape demonstrates that other regions beyond the cerebellum are relatively larger in modern humans than in Neandertals, including parts of the prefrontal cortex and the occipital and temporal lobes. In contrast, parietal bulging is not linked to an increased surface area, suggesting that the parietal lobe is “displaced” by reorganization of other—presumably subcortical—parts of the brain.

N genes in MHs and skull globularity

- ▶ Introgressed Neandertal alleles on chromosomes 1 and 18 are associated with reduced endocranial globularity.
- ▶ These alleles influence expression of two nearby genes, *UBR4* and *PHLPP1*, which are involved in neurogenesis and myelination
- ▶ The globular endocranial shape emerged gradually in the *Homo sapiens* lineage, evolving independently of brain size: reorganization of cerebellar and lateral parietotemporal areas was followed by continued gradual changes in the organization of cerebellar and occipital areas

Globularity is perinatal (~birth) in origin

- ▶ In present-day humans, globularity emerges during perinatal development in a period when the rapidly expanding brain is the main driver of braincase shape.
- ▶ It has therefore been proposed that globularity reflects evolutionary changes in early brain development
- ▶ The Neandertal gene haplotypes may thus be associated with developmental gene expression patterns that influence endocranial globularity through effects on neurogenesis and myelination during brain development.

Evolutionary Integration of Brain lobes

- ▶ Sansalone, 2023: This study analyzed the evolution of brain shape in primates using three-dimensional geometric morphometrics of endocasts.
- ▶ Unlike our closest living relatives, *Homo sapiens* retain high levels of covariation between cortical areas into adulthood.
- ▶ Among the other great apes, high levels of covariation are only found in immature individuals.

Similarity of MHs and Ns: integrated brain regions

- ▶ Secondly, an analysis of 400 endocasts, representing 148 extant primate species and 6 fossil hominins, shows that
 - ▶ natural selection favored a greatly integrated brain in N and MHs
- ▶ High covariation in the brain may have played a critical role in the evolution of unique cognitive capacities and complex behaviors in both modern humans and Neanderthals.

Brain integration for MHs and Ns

- ▶ Whether the brain's lobes evolved independently of each other, or whether evolutionary change in any one lobe appears to be necessarily tied to changes in others—that is, evidence the evolution of the lobes is "integrated."
- ▶ Used two methods. First analysis included 3D brain models of hundreds of living and fossil primates (monkeys and apes, as well as humans and our close fossil relatives). This allowed us to map brain evolution over time.

Brain integration for MHs and Ns

- ▶ Second digital brain data set consisted of living ape species and humans at different growth stages, allowing us to chart integration of the brain's parts in different species as they mature.
- ▶ Tracking change over deep time across dozens of primate species, we found humans had particularly high levels of brain integration, especially between the parietal and frontal lobes.
- ▶ Leading current theory of IQ = integration of prefrontal and parietal lobe interaction

Homo sapiens and Neanderthals share high cerebral cortex integration into adulthood

- ▶ Integration between these lobes was similarly high in Neanderthals too.
- ▶ In apes, such as the chimpanzee, integration between the brain's lobes is comparable to that of humans until they reach adolescence.
- ▶ At this point, integration rapidly falls away in the apes, but continues well into adulthood in humans.

Not just big brains, but highly integrated brains

- ▶ What distinguishes us from other primates is not just that our brains are *bigger*.
- ▶ The evolution of the different parts of our brain is more deeply integrated, and, unlike any other living primate, we retain this right through into adult life.
- ▶ It's increasingly clear that Neanderthals, long characterized as brutish dullards, were adaptable, capable and sophisticated people, with similarly integrated brain lobes

N brains

- ▶ Neandertal brains were similar in size to humans today.
- ▶ Two aspects of cranial vault shape explain most of the difference between endocranial surfaces in Neandertals and recent people.
 - ▶ The Neandertal cranial base is longer and less angled, giving a more elongated shape to their endocranial surface.
 - ▶ Compared to Neandertals, MHs have a bulging parietal lobe.
 - ▶ Together these two differences give humans a more compact, globular shape to their brain

2018: 3D Brain reconstruction of N brain

- ▶ Ns had:
 - ▶ smaller parietal region (most significant difference)
 - ▶ relatively smaller cerebellum (esp. right side) and a significantly larger occipital region
 - ▶ narrower orbitofrontal cortex,
 - ▶ smaller olfactory bulbs

Larger N visual cortex

- ▶ Current cranial capacity and bigger eyeballs (20% larger) correlates with increasing geographical latitude; a significant positive relationship between absolute latitude and human orbital volume, an index of eyeball size.
- ▶ Selection for larger visual systems has mitigated the effect of reduced ambient light levels
- ▶ Larger brains in coldest climates(16 cc more): modern Inuits have largest cranial capacity
- ▶ Most likely increase in visual brain areas (for visual adaptation to low light levels) accounts for most of increased brain size in Ns

N brain size = MH brain size

- ▶ Neandertal brain size is often stated as larger than MHs.
- ▶ Fossil brain size is an artifact of preservation; we having more female Ns; if you compare male Ns and MHs, less brain size difference; N brain size is equivalently as large as early MHs
- ▶ On average N brain size is comparable with MH *males* but, since it's suspected that males might be over-represented in the fossil sample, it's hard to know what this really means.
- ▶ The mean for late European Neandertals (after 96 Ka) is actually smaller (though not significantly smaller) than the Early Upper Paleolithic (EUP) mean in Europe

N brain size and body size

- ▶ All of these archaic groups do tend to have larger average cranial capacities than today's humans, but this fact reflects post-Pleistocene decreases in average body mass.
- ▶ When body size is taken into account, there is no evidence that Neandertal brains as a whole differ significantly in size from those of modern humans.
- ▶ However, early Neandertals appear to have smaller brains than the later ones.
- ▶ Most southerly Neandertals (the ones from West Asia) have the largest mean cranial capacities – the reverse of the pattern seen in modern humans.

Supposedly larger N brains: sex-biased samples

- ▶ Wragg Sykes: The apparently bigger brains of Ns are actually due to sex-biased samples due to preservation differences .
- ▶ When only males are compared, the brain size difference is much less, highlighting the probability that most complete Neanderthal skeletons belong to men.

N Brain

- ▶ **R. Holloway**, who has studied more fossil hominin endocasts than anyone else, finds nothing in Neandertal endocasts to suggest significant differences from modern humans in neural structure or function
- ▶ Neandertals exhibit a modern human pattern of hemispheric asymmetry (longer R hemisphere/shorter L hemisphere; related to handedness') (as do the Erectines) and gyrification.
- ▶ Both Ns and MHs, exhibit relatively wide frontal lobes and widening of Broca's cap (a part of the cortex associated with speech production).

N brain

- ▶ **Holloway:** N had larger occipital area, related to occipital buns; an expansion of the primary visual striate cortex, which indicates that they possessed enhanced visual and spatial abilities.
- ▶ **Conclusion:** Neandertals had a bigger visual cortex than MHs. A study of CT-generated endocasts similarly concluded that the Neandertals had a larger occipital (visual) lobe & a significantly smaller cerebellum (Kochiyama et al. 2018).
- ▶ However, the difference may be an artifact of their Neandertal sample, which includes the very small Gibraltar female. The three male Neandertals do not appear to differ markedly from the moderns.

MH brain is different

- ▶ MH brains undergo a unique postnatal growth phase, beginning shortly after birth and ending when the milk teeth start to erupt, concentrated in the parietal and orbito-frontal lobes of the cerebral cortex.
- ▶ This distinctive growth period is referred to as the “globularization phase”. It transforms the neonatal brain of modern humans, which is not dissimilar in shape to that of a Neandertal, into a shape that is markedly different – higher and more rounded than the lower, longer, broader, and less “bulging” brains of Neandertals and earlier Homo.
- ▶ This “globularization” may also be reflected in the distinctive expansion of the cerebellum and the parieto-temporal lobe in modern humans.

N brain

- ▶ After the end of the globularization phase, brain growth follows similar trajectories in both Neandertals and moderns, resulting in similar adult brain sizes.
- ▶ Modern people who carry more Neandertal genes have more Neandertal-like shapes of both the skull and brain shape.
- ▶ ** The lack of “globularity” in Neandertal brains may have been entirely compensated for by their expanded breadth.
- ▶ **We have no conclusive reason to infer inferior mental abilities from any of the distinctive features of Neandertal braincases or endocasts.

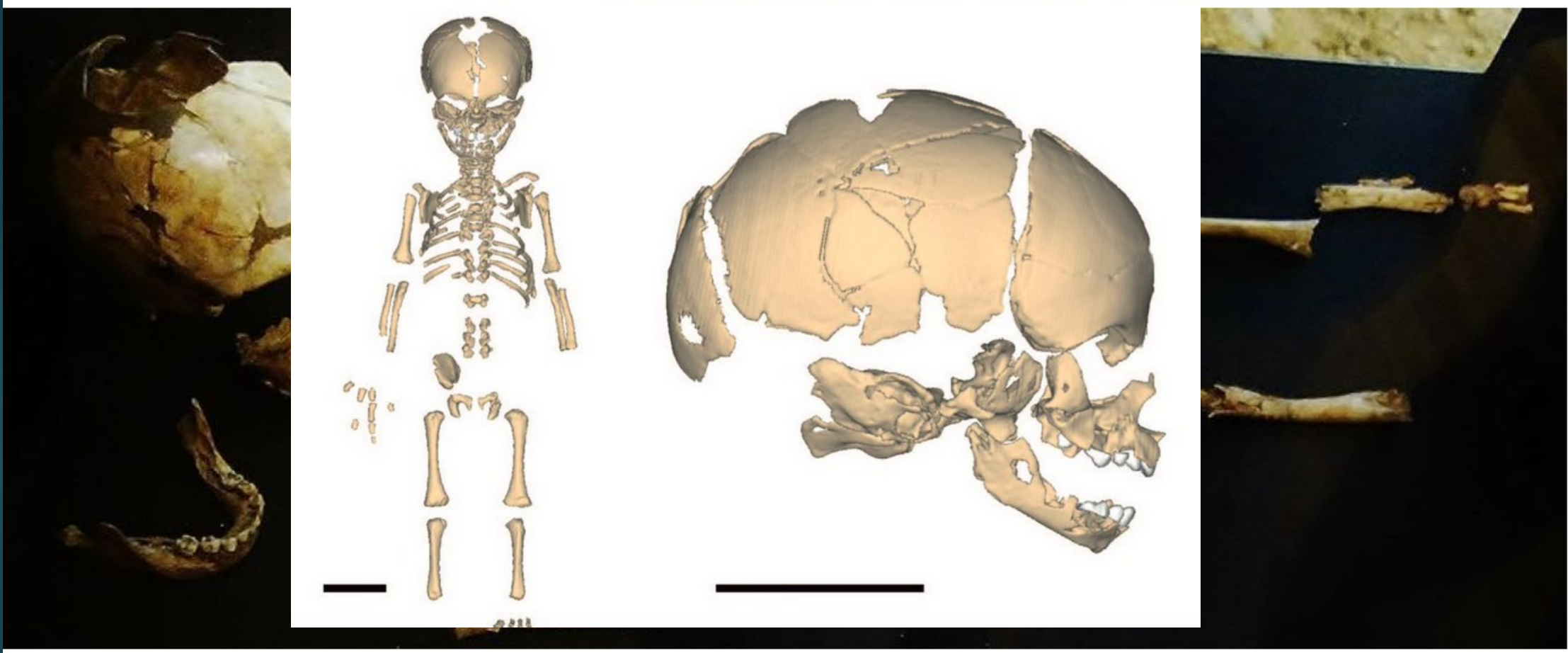
Occipital bun

- ▶ **N occipital cortex** = characteristic of only European Neandertals.
- ▶ **N occipital bun** = due to larger N occipital lobe
- ▶ **Occipital buns are also found in most of the early modern human skulls from Europe (and in a few from North Africa).** = evidence for N gene flow into early MHs

N Infants

- ▶ Neanderthal brain size at birth was similar to that in recent Homo sapiens and most likely subject to similar obstetric constraints.
- ▶ Neanderthal brain size at birth was similar as in modern humans: around 400 cc.
- ▶ Neonatal Neandertals already appear to possess the wide body, wide hips, long pubis, and robust bowed long bones of adult Neandertals. Newborn's skull shows that middle parts of their faces were already slightly pulled out, and they lacked chins
- ▶ After birth, Neanderthal brains grew faster than those of modern humans. N teeth emerged up to 4 months earlier than in MHs. Weaned at 4 m.

Le Moustier infant & Mezmaiskaya 1 infant



N and MH brain development

- ▶ Postnatal brain ontogeny was largely similar in Neanderthals and early European modern human populations.
- ▶ Evidence for similar brain development, and similar cognitive development in Neanderthals and modern humans.
- ▶ ** Similar modes of brain and cognitive development in both Neanderthals and modern humans might thus have facilitated the behavioral integration of Neanderthal–modern human offspring in their human ‘host’ groups, ultimately facilitating the introgression of Neanderthal alleles into the modern human gene pool

N DNA brain effects in MHs

- ▶ Overall brain shape doesn't matter much today. People still vary a lot in endocranial shape. Some people have wider and more rounded endocranial shape, some have longer and narrower endocasts
- ▶ **John Hawk:** If N gene can still effect MH brain shape, then the original N skull shape could not have been strongly disadvantageous in either MHs or Ns.
- ▶ The fact that current populations may still have residual echoes of the shapes of Neandertal brains suggests that they could not have worked very differently from each other.

CJV's conclusions

- ▶ At 40 Ka, Ns and MHs probably had nearly identical cognitive abilities.
- ▶ Both were highly successful in adaptations to their given environments
- ▶ Ecological variables produced variation in brain size organization.
- ▶ MHs did not develop globular brains until after 35 Ka, after Ns were gone.

Real origins of language are complex

- ▶ Forkhead Box Protein P2 (FOXP2) changes did not produce language (even in Ns), but changes in this gene system in concert with
 - ▶ changes to auditory canals,
 - ▶ communication behavior,
 - ▶ frontal and parietal lobe cortical expansion
 - ▶ enhanced neural density/connectivity,
 - ▶ increasing complexity of tool creation and manufacture,
 - ▶ in the context of increasingly complex social structures/actions,
 - ▶ all interacted to facilitate the emergence of linguistic processes/components,
 - ▶ setting the stage for the eventual emergence of full syntactic language.

N language and toolmaking

- ▶ R. Dunbar: Sociality & language increased brain size in *Homo*; suspects complex speech at 500 Ka (starting with *H. heidelbergensis*)
- ▶ Given different survival needs, it is difficult to argue that Neanderthals lacked complex linguistic codes, capable of communicating about spatial locations, hunting and gathering, fauna and flora, social relations, technologies, and so on.
- ▶ Granting Neanderthals **advanced language capacities** seems eventually to be inevitable

Language

- ▶ *Homo heidelbergensis* is thought to have been the first ancestor of modern humans not to have air sacs, which are laryngeal diverticula involved in vocalization; like those in chimps
- ▶ Ancestors such as *Australopithecus afarensis* did have air sacs, as do other great apes.
- ▶ Handedness is associated with the development of language among hominins. *Homo heidelbergensis* was right-handed.
- ▶ All successful evolutionary primate species had a successful system for communication

Language in Ns?

- ▶ Endocast of the *Kabwe Homo heidelbergensis* and *Neandertal* craniums is well within the modern range in terms of size. Their endocasts demonstrates:
 - ▶ modern pattern of left occipital and right frontal petalias: these asymmetries are connected with the presence of language functions (usually on the left side of the brain), so the lateralization evident in Neandertal endocasts hints at the presence of language.
 - ▶ Broca's area (left ventral premotor cortex) is enlarged relative to the right
 - ▶ Basicranium is more angled, a feature that has been linked to lengthening of the pharynx
 - ▶ Diameter of the hypoglossal canal is in modern range (passage in cranial base (through which pass the nerves that enervate the tongue)-enlarged canal suggest greater control of tongue

Did Neanderthals have language and speech or are these unique to modern humans?

- ▶ “On the antiquity of language” - Dan Dediu & Stephen C. Levinson, 2013:
- ▶ The new data supports language and speech being old and shared with archaic humans.
- ▶ Study concludes that Neanderthals were fully articulate beings and that language evolution was gradual

On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences –

- ▶ Argue that modern language is likely an ancient feature of our genus predating at least the common ancestor of modern humans and Neandertals about 500 Ka ago.
- ▶ Neandertals linguistic capacity were closely similar to MH language.
- ▶ The idea that Ns did complex joint hunting strategies without communication and planning is untenable.

Linguistic similarities of MH and Ns

- ▶ **Ns and MHs share:**
- ▶ same FOXP2 gene – required for language production
- ▶ same HAR1 regions – genetic regions that separate MHs from chimps,
- ▶ similar vocal range
- ▶ Same auditory perception range,
- ▶ same hyoid bone – controls tongue speech capacity,
- ▶ and an enlarged vertebral canal necessary for breath control.

Language

- ▶ The auditory specializations for speech in the modern bandwidth are present,
- ▶ the morphology of the larynx looks modern,
- ▶ and air sacs have been replaced by a finely controlled pulmonic airstream mechanism for vocalization.

▶ All these changes occurred in the transition from Homo erectus to Homo heidelbergensis,

Stone knapping and language: common brain functions

- ▶ Complex toolmaking of the Mousterian kind involves hierarchical planning with recursive sub-stages which activates Broca's area just as in analogous linguistic tasks.
- ▶ The chain of fifty or so knapping actions and the motor control required to master it are not dissimilar to the complex cognition and motor control involved in language. Brain used this preexisting sequential, hierarchical function process for language use.

Language and tool making

- ▶ FMRI studies: This area is involved in both tool making ability and expressive language ability
- ▶ Study: Language seems to be a precondition for the transmission of elaborate lithic technologies:
 - ▶ Study: novices were systematically taught the simple Oldowan technology under five different conditions (reverse engineering, emulation, basic teaching, gestural teaching and spoken teaching)
 - ▶ Conclusion: Full linguistic teaching led to the most efficient technique and good tools, followed by gestural teaching.
 - ▶ Their technology and hunting tactics would have been difficult to learn and execute without language.

Cartmill and Smith on N Language functions

- ▶ 1. **Group coordination**: evolved more complicated signal systems that can produce coordinated action by a whole group. Language gives human beings the power to bend group efforts to any task.
- ▶ 2. **Representations of possibilities**: We can therefore plan our actions in advance. This feature of language makes our group coordination possible. It allows us to think in detail about our objectives before we attempt to carry them out – to model hypothetical acts in our utterances,
- ▶ 3. **Intergenerational binding**: Through language, humans can share experience and knowledge; and that each generation can build on the knowledge and skills of its predecessors.

Cartmill and Smith on N Language

- ▶ 4. **Framework of consciousness**: Language expands the scope of conceptual thought enormously by furnishing socially shared, negotiable labels for the categories of things and actions that we perceive in the world.
- ▶ **Language** has had **an overwhelming adaptive importance for modern humans**.
- ▶ As far as is presently known, no aspect of skeletal anatomy can tell us conclusively whether Neandertals – or any other ancient humans – had human-like capacities for making and using language.
- ▶ **Conversely, no skeletal evidence that we have indicates any substantial differences in language capabilities between Neandertals and modern humans**.

N language

- ▶ D. Dediu and S. Levinson (2018) adopt this position and conclude that “Neanderthals were fully articulate beings”.
- ▶ **Cartmill & Smith:** think the balance of the evidence we have supports that conclusion.
- ▶ Whether Neanderthals had any kind of language is, of course, one of the most enduring questions about them.
- ▶ Language is symbolic. If language is granted to Ns, so is symbolic ability.
- ▶ Increasing brain size is a good proxy for language evolution.
 - ▶ Sociality is highly correlated with cortex size;
 - ▶ Language is the instrument of sociality.

- ▶ **MH brains have slightly shrunk since early H. sapiens**, with no apparent shriveling in cognitive capacity.
- ▶ **Neanderthal throats** could make the same range of sounds as ours. There were perhaps some subtle differences in vowels including 'ah', but their breath control wasn't appreciably poorer, giving them the ability to utter lengthy sound combinations.
- ▶ While their **inner ear shape** was slightly different, it was similarly finely tuned to sound frequencies generated by speech.
- ▶ **If this anatomy in humans is regarded as specialized for language, then Neanderthals cannot have been that different.**

FOXP2

- ▶ 2002 study: Both MHs and Ns carry two mutations to FOXP2 not found in any other primates. Apes also have a variant.
- ▶ In modern humans, mutations of the FOXP2 gene appear to cause disorders of neurological development that result in defective abilities to articulate, analyze, and understand speech
- ▶ FOXP2 is definitely involved with cognitive and physical language capacity in living people, mainly language production, but it isn't 'the' language gene; no such thing exists.
- ▶ When it was confirmed that Neanderthals had the same FOXP2 gene as us, it was taken as strong evidence that they could 'talk'.

N *FOXP2* gene

- ▶ Today we have a lot more information about the variation of *FOXP2* but little clarity about its possible importance.
- ▶ Ns had *FOXP2* language gene (required for MH speech production): it increases the expression of 61 genes and decreases the expression of 51 genes compared with the chimp version. **Significant in brain development; severe articulation and expressive language disorder if missing**
- ▶ The ancestral *FoxP2* protein sequence from Neandertals and Denisovans is shared by many people today, who have normal speech.

N language

- ▶ Broca's area is required for both stone tool and language production.
- ▶ Complementary evidence for language comes from the fact Neanderthals seem to have had similar rates of handedness. Tooth micro-scratches and patterns of knapping on cores confirm they were dominated by right-handers, and this is also reflected in asymmetry (petalia) in one side of their brains.

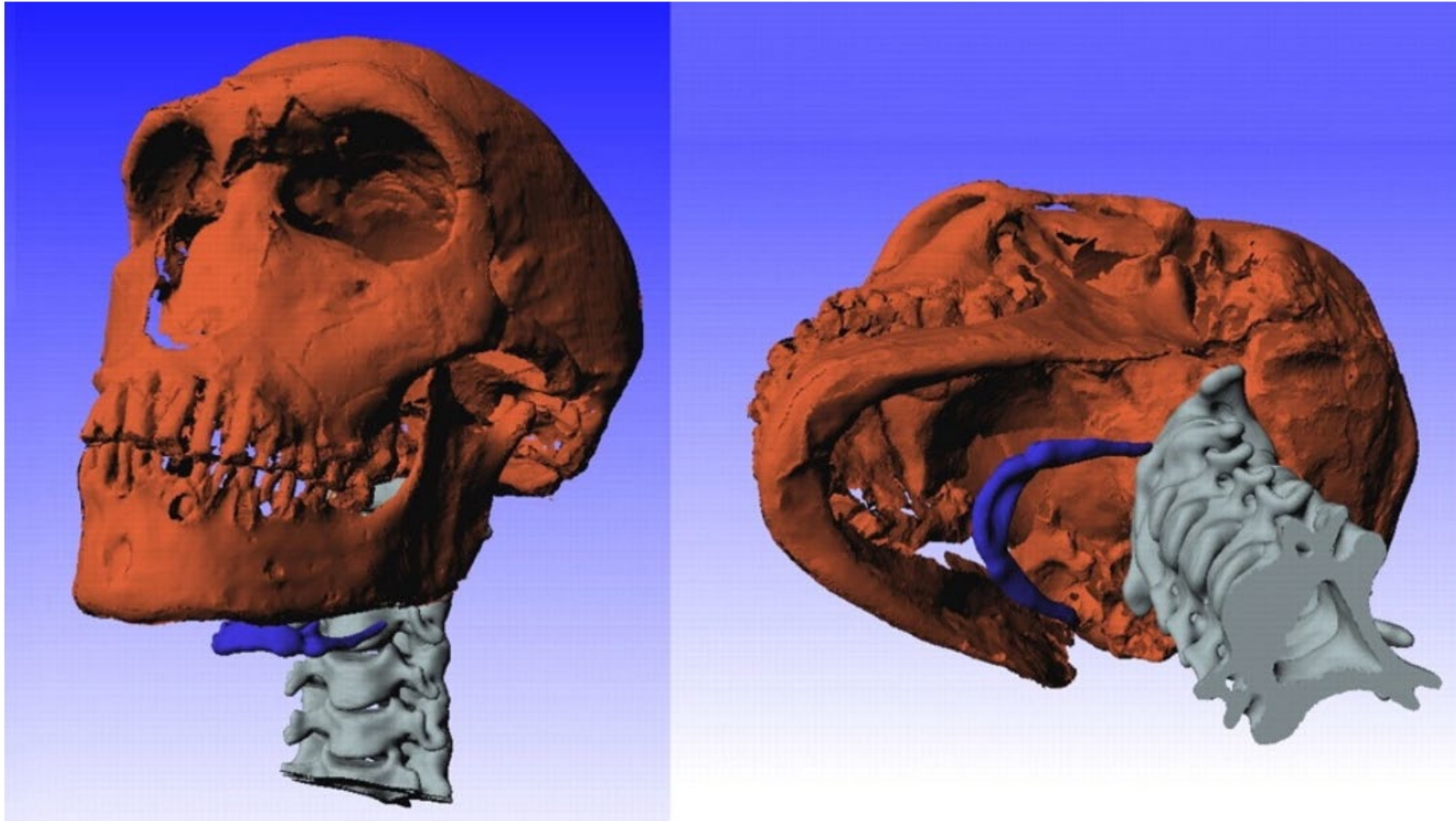
N language

- ▶ It's very likely Neanderthals spoke in some form, but about what?
- ▶ Certainly there's ample archaeological evidence that Neanderthals were organized in terms of who went where and when, so some level of communication for collaborative activity is probable.
- ▶ The complexity of their joint hunting tactics implies ability to communicate joint hunting plans.
- ▶ Current evidence about N language is ambiguous, but the evidence cannot allow us to refute it either.

Ns had language

- ▶ Ns almost certainly used some form of spoken language.
- ▶ A hyoid bone found at the Kebara site in Israel appears fully modern.
Shape and position of hyoid bone was adequate for speech.
- ▶ N vocal tract was like ours, capable of making the same sounds we make.
- ▶ Location of their tracheal anatomy suggests that they were capable of language and probably had high-pitched, raspy voices, like Julia Child.

N hyoid bone: holds up the tongue, which sits above it, and it holds up the larynx,



Models based on CT scans show where the Neanderthal hyoid (blue) likely sat.

Kebara hyoid bone



- ▶ This hyoid bone is identical to ours, thus suggesting that the Neandertals shared our capacity for language.

Hyoid bone



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

Most researchers agree Neanderthals were capable of emitting and hearing complex vocalizations.

Neandertals had
different genetic lineages

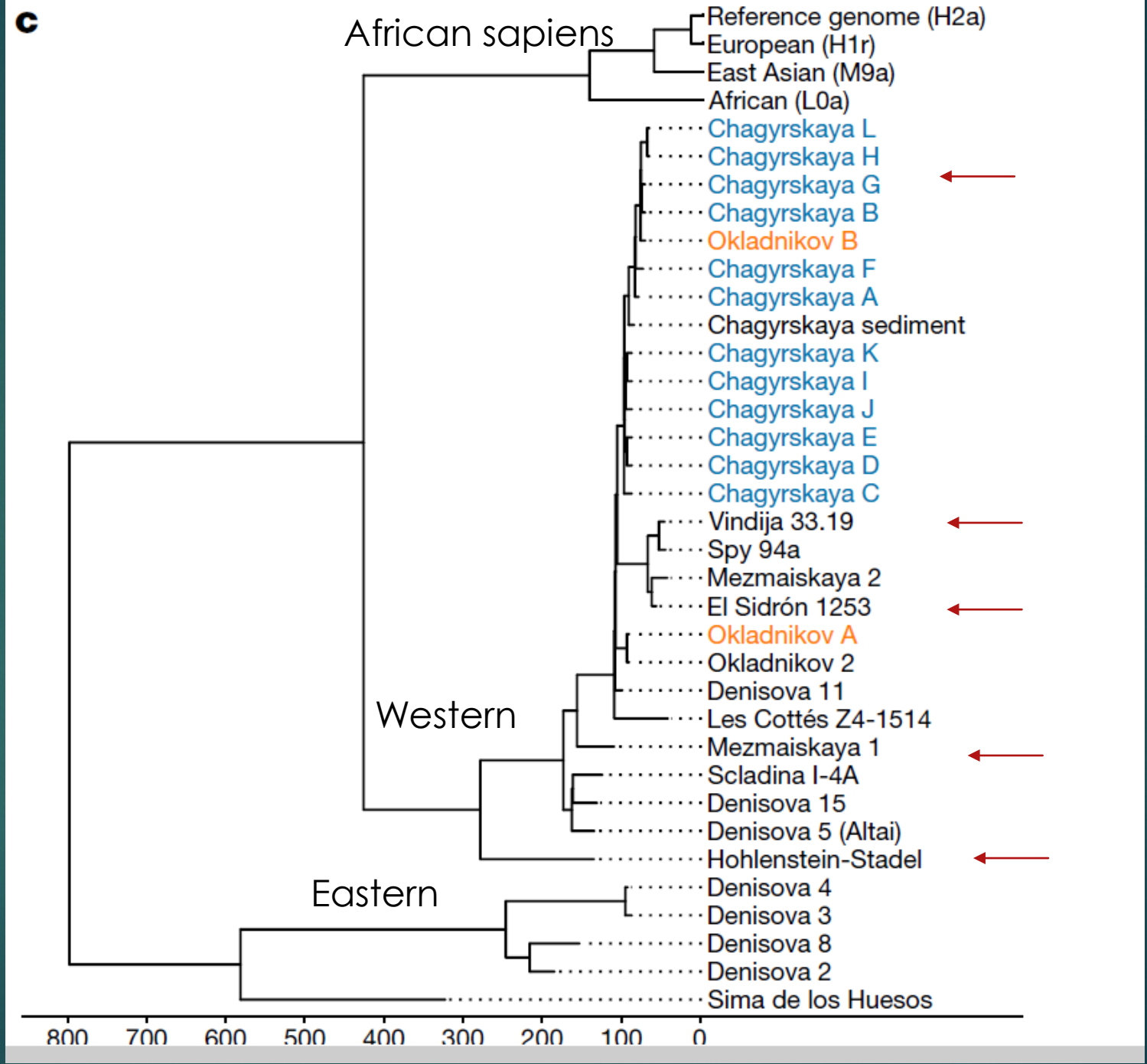
There were multiple N populations

100

- ▶ Multiple genetically distinct Neanderthal populations existed over time and space
- ▶ Genome-scale data have been reported for the skeletal remains of 22 individuals from 14 archaeological sites spanning Neanderthal history across large parts of their known geographical range, which extends as far east as the Altai Mountains in southern Siberia.
- ▶ Previous studies on the social organization of Neanderthal communities have suggested that Neanderthals probably lived in small nomadic communities.

2022:
Neanderthal
Phylogeny:
27 N genomes

Major Western
and Eastern
branches



African sapiens DNA introgression into Ns from 300 Ka onward

- ▶ Analysis suggests that the **Sapiens→Neandertal gene flow** occurred between 200-300 Ka.
- ▶ The **Neandertal mitochondrial DNA** is of African sapiens origin.
- ▶ **Neandertals were repeatedly connected to African populations in the time after 350,000 years ago.** They derive a fraction of their genetic variation from such contacts with African populations.

African sapiens introgression into Ns from 350 Ka onward

- ▶ A significant proportion of the Neanderthal genome consists of regions introgressed from ancient African sapiens.
- ▶ Estimate that 6% of the Neanderthal genome as introgressed MH DNA.
- ▶ Thus, the Neanderthal genome was likely more influenced by introgression from ancient humans (6%), than non-African human genomes are by Neanderthal introgression (2%).

Zlatý kůň and the Neandertal heritage of early Upper Paleolithic Europeans

- ▶ In Europe, the African sapiens expansion out of Africa preceded the disappearance of Neanderthals at 40 Ka by 3,000–5,000 years.
- ▶ Many early Upper Paleolithic Europeans had relatively recent Neandertal ancestry within their genomes
- ▶ The African sapiens Oase 1 carried more Neanderthal ancestry (6–9%) than other modern human genomes sequenced to date, owing to admixture with Neanderthals that occurred within the six generations before the individual lived.

N DNA in early MHs

- ▶ The Bacho Kiro, Bulgaria, MH at 46 Ka had N ancestry within 6 generations
- ▶ Zlatý kůň skeleton: discovered in 1950 in Czechia. A UP modern human. Some suggested its occipital morphology might reflect Neandertal ancestry, and noted that its cranial morphology is relatively robust for a female adult individual; dated to 45 Ka. **Had Neandertal input within 70-80 generations of her birth.**

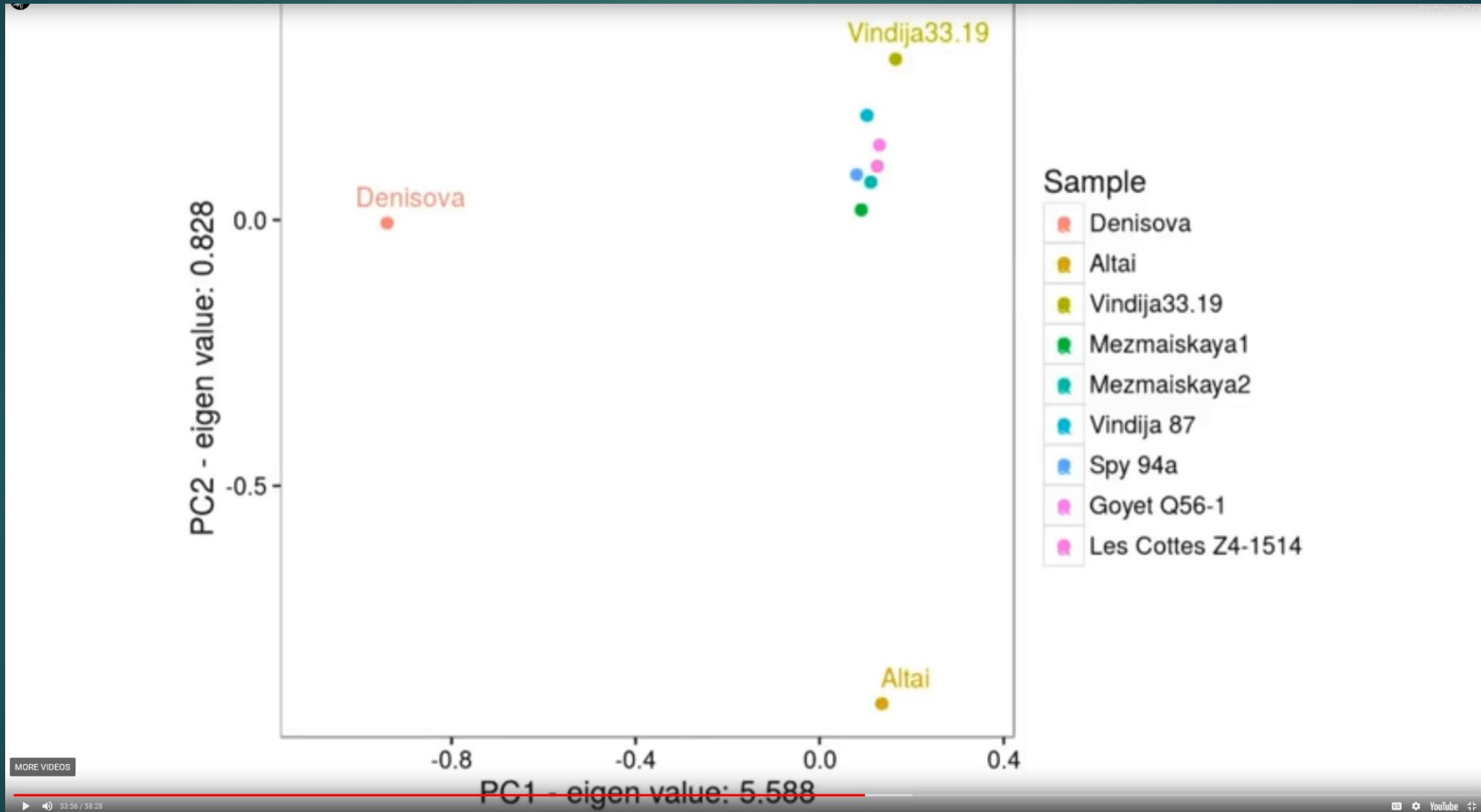
N DNA in early African sapiens

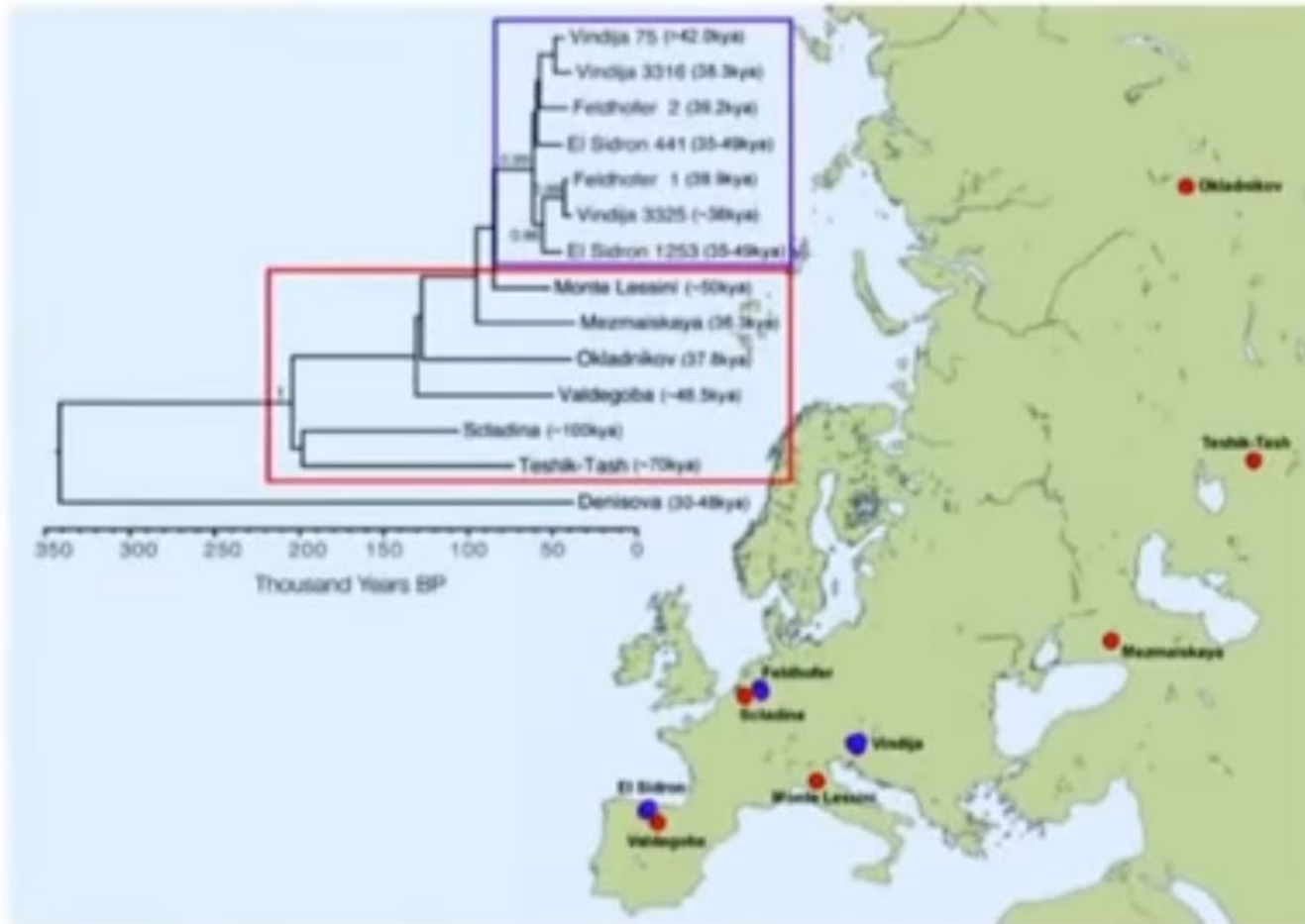
- ▶ Her genome carries ~3% Neanderthal ancestry, similar to those of other Upper Palaeolithic hunter-gatherers. **No modern descendants.**
- ▶ Her lengths of the Neanderthal DNA segments are longer than those observed in one of the oldest modern human genome, the ~45,000-year-old Ust'-Ishim individual from Siberia, suggesting that this **individual from Zlatý kůň is one of the earliest Eurasian inhabitants following the expansion out of Africa.**

Neandertal lineages

- ▶ Neandertal genetic lineages were not all identical.
- ▶ There were multiple genetic N lineages
- ▶ Remember that given repeated Glacial periods, Ns had multiple population crashes and repopulations from southern refugia.
- ▶ They were subject to repeated population turnovers.

PC map: Denisovans and Neandertals: some Ns were highly genetically divergent (Altai)

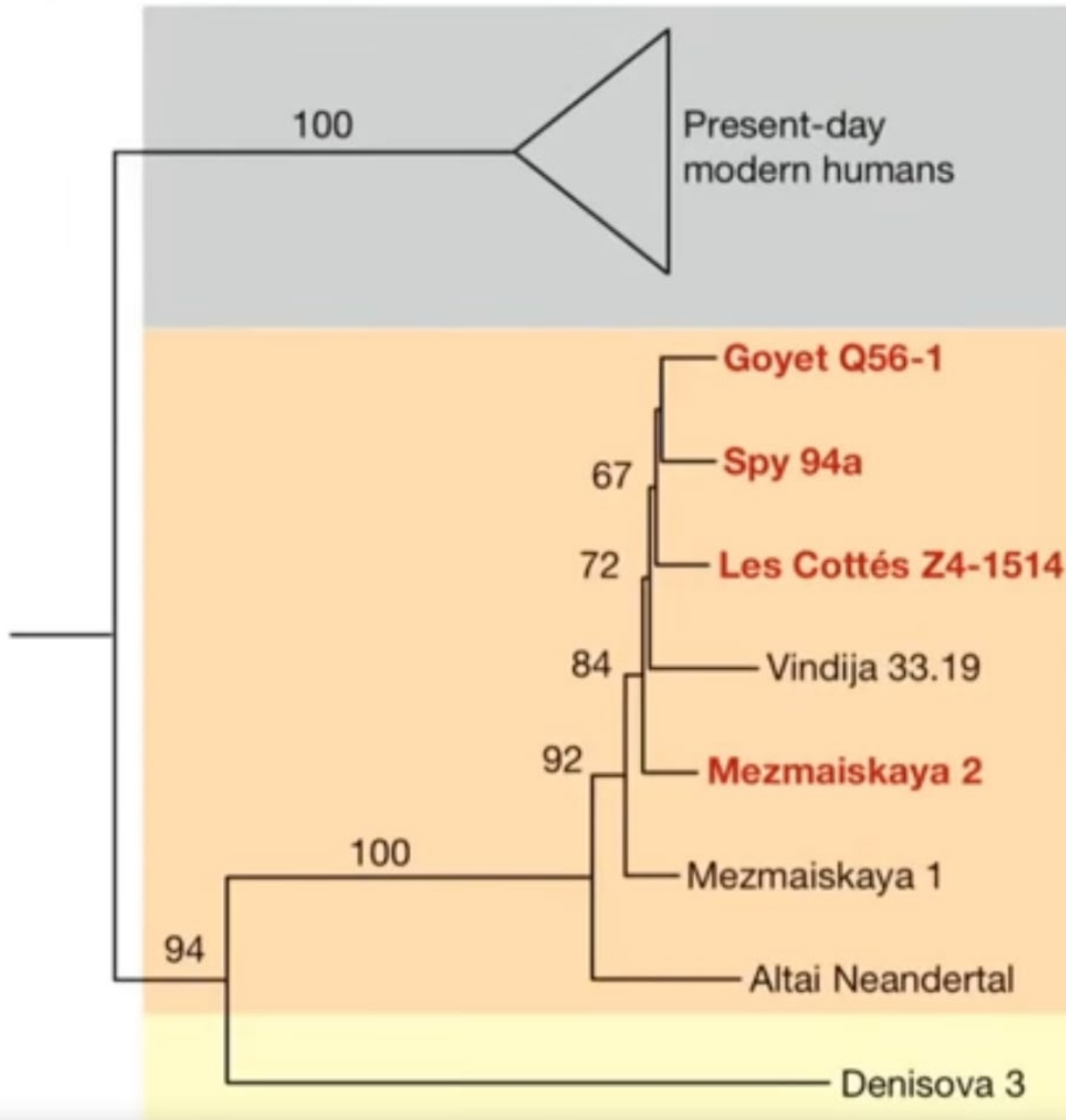




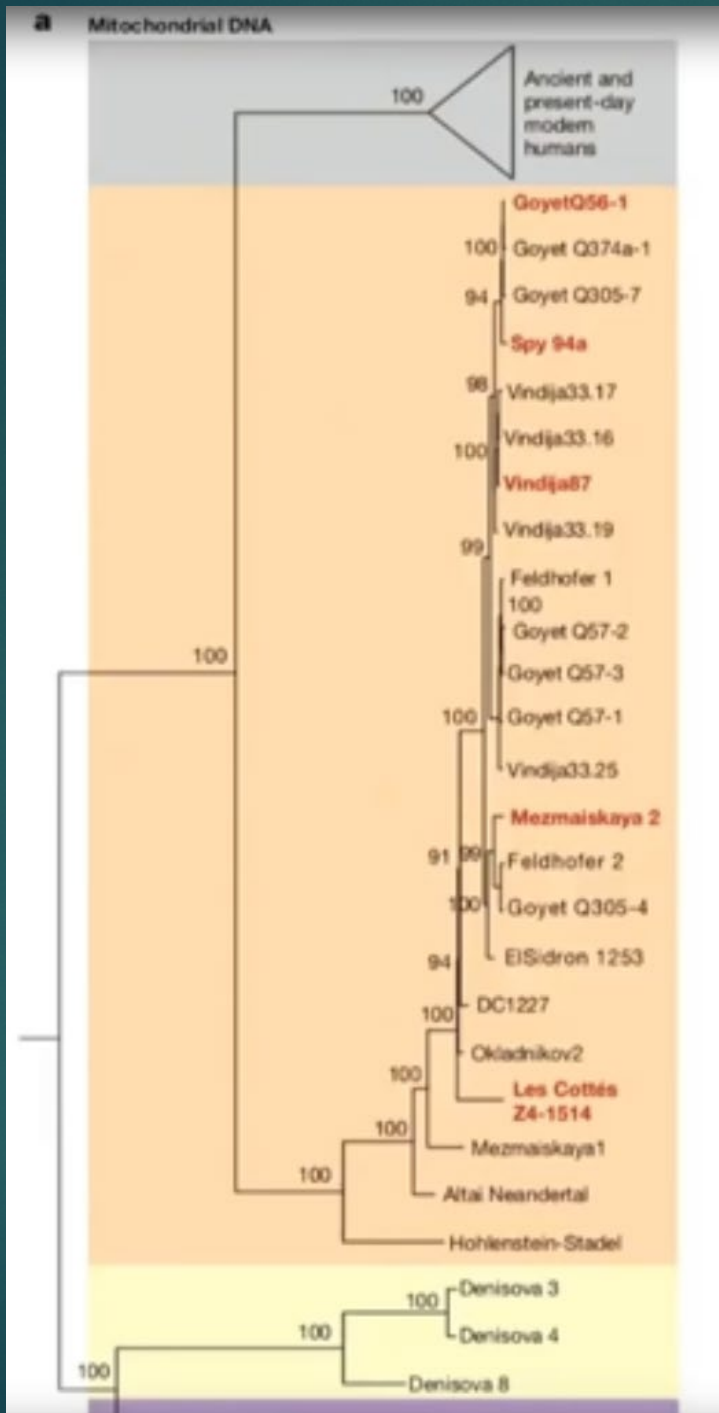
Neandertals did NOT survive, unaltered, for hundreds of thousands of years. Their population was highly dynamic and subject to continual or repeated turnover.

- Ns had more mtDNA variation than living humans have today
- Later Ns had very low genetic variability
- But earlier Ns and Ns from western Asia were much more genetically variable
- Greatest mtDNA N diversity was in the East, the Altai

C Nuclear DNA



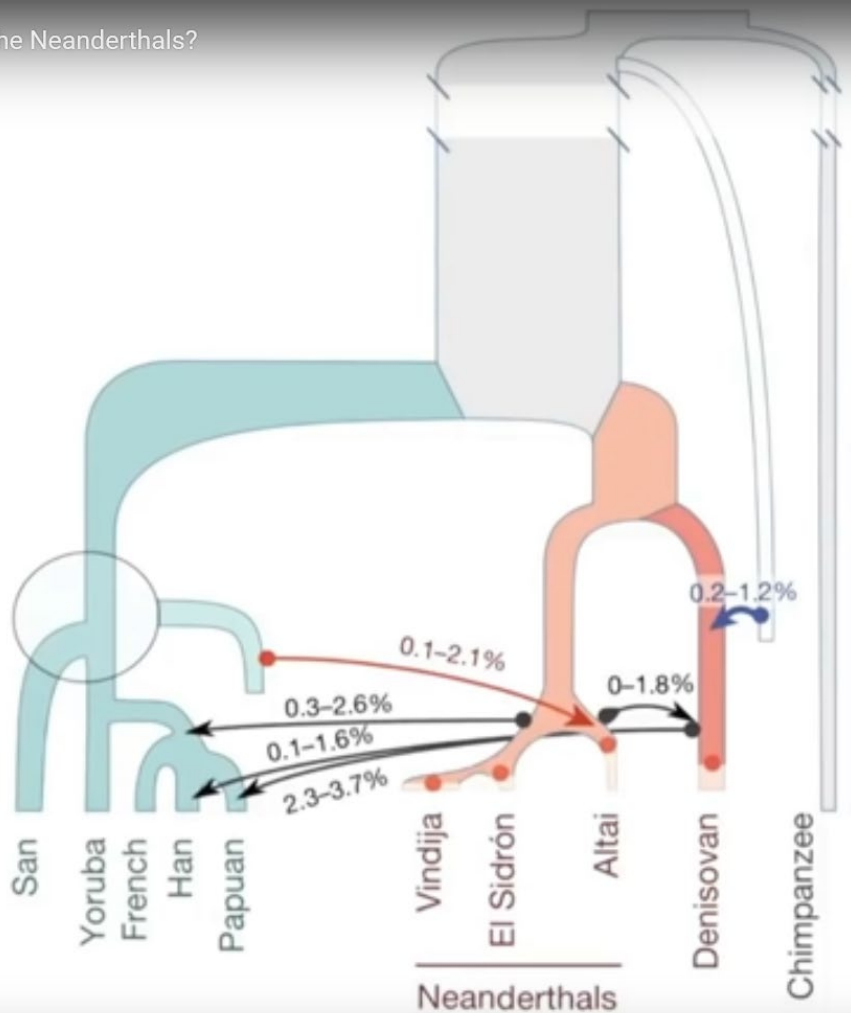
- Nuclear DNA: similar picture
- Western Ns are more similar
- Altai N is different



- **N mtDNA:**

- Western Ns are not very variable
- Earlier Ns were much more variable
- Altai and Hohlenstein-Stadel are very divergent
- Sima de los Huesos has totally different mt DNA
- There was a complete replacement of N mtDNA
- Ns were highly different from each other; different N populations

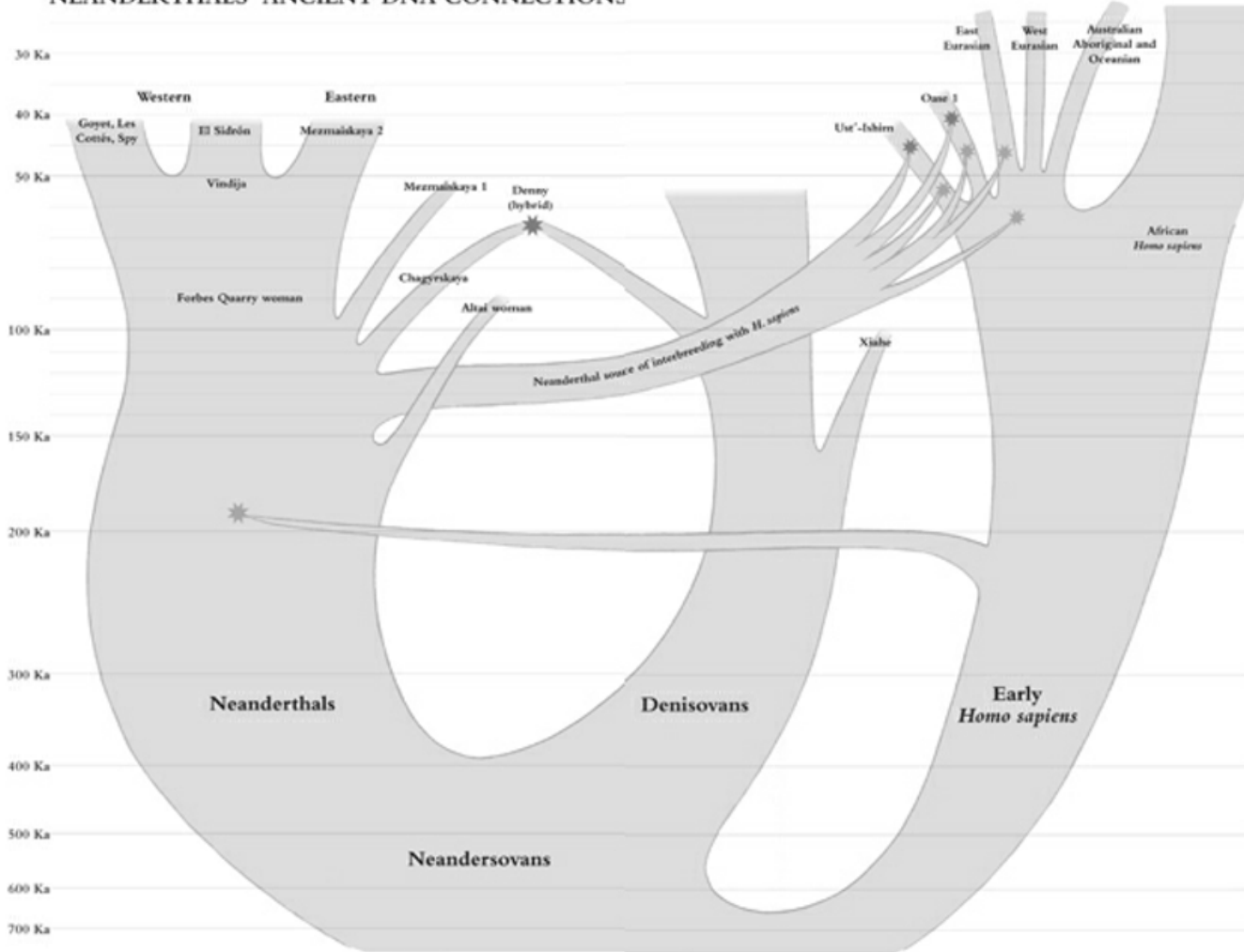
of the Neanderthals?



Kuhlwilm *et al.* 2016 *Nature* 10.1038/nature16544

- N mixtures have gone thru a succession over time
- MH input into Altai Ns ~ 100 Ka but not others
- Ns got MH DNA multiple times during their history
- Sima Ns have totally different mtDNA than any latter Ns
- Today's MH's mtDNA is the closest to Ns
- Ns had middle Pleistocene African sapiens DNA from very early
- Modern humans have African sapiens and N ancestry

NEANDERTHALS' ANCIENT DNA CONNECTIONS



N branches:

1 **Western**: Goyet, Spy, Les Combe

2 **Western**: El Sidrón, from Vindija

3 **Eastern**: Mezmaiskaya 2

4 Mezmaiskaya 1

5 Chagyrskaya

6 Altai

7 Branch that mated with MHs

2 Neandertal population divergences

- ▶ There were two distinct radiations of Neanderthal populations:
 - ▶ **Western**: Mezmaiskaya 1, Vindija 33.19, Chagyrskaya 8, and Estatuas pit II/layer 2 and pit I/layers 2 and 3 **diverged from each other ~100 to 115 ka ago**,
 - ▶ **Eastern**: Altai, HST, Scalding, and Estatuas pit I/layer 4 Neanderthals and the lineage leading to Vindija 33.19 and Chagyrskaya 8 **diverged from each other ~135 ka ago**.
- ▶ These radiation events may be associated with changes in climate and environmental conditions during the last interglacial.

4 Different N genetic lineages

▶ Western:

▶ 1- El Sidrón, Spain Neanderthals

▶ 2 - Vindija, Croatia, Neanderthals

▶ Both display significant rates of gene flow (0.3–2.6%) into MHs

▶ Eastern:

▶ 3 - Altai Neanderthal, Denisova, Siberia

▶ 4 – Mezmaiskaya 1, Caucasus Neanderthals

▶ The Altai Neanderthals separated from the El Sidrón and Vindija Neanderthals at ~110 Ka.

4 Different N genetic lineages

- ▶ El Sidrón and Vindija Neanderthals are more closely related than the Altai Neanderthal is to the Neanderthals that interbred with MHs about 47-65 Ka.
- ▶ Modern humans share more alleles with *Vindija* and *Mezmaiskaya 1* than with the Altai Neanderthal.
- ▶ Neanderthal-derived DNA in all non-Africans is more closely related to the genome from the *Mezmaiskaya* skeleton in the Caucasus than to the Altai or to the *Vindija* genome
- ▶ This shows that the introgression event from Neanderthals into OoA humans likely took place after the split of the lineage of the Altai Neanderthal from that of other Neanderthals, but before the split of the lineage of *Mezmaiskaya 1* and that of other Neanderthals

N DNA lineages: settled by 90 Ka

- ▶ There is currently:
 - ▶ no evidence for the existence of substantial genetic substructure in the Neanderthal population after ~90 Ka,
 - ▶ the time at which the “Altai-like” Neanderthals in the Altai had presumably been replaced by more “Vindija 33.19-like” Neanderthals

Regional variability in N bodies

- ▶ Sometimes regional climate might have directly influenced anatomy.
 - ▶ Southern European Neanderthals were to some degree insulated from the cold (although not always from aridity), and strikingly,
 - ▶ Ns from the Near East have larger brains, were less heavily built, & were thinner.
- ▶ But if Neanderthal physique was affected by physical activity, this difference might also be reflecting how local ecology influenced levels of mobility.

Regional variability in N bodies

- ▶ While N males from Europe had more developed lower legs, those in the Near East had stronger thighs, pointing to variation in either how much they moved around or the kind of terrain.
- ▶ In women, the difference is even greater.
- ▶ But both men and women from the Near East had beefier arms.

N teeth



Regional variability: teeth use in colder regions

- ▶ More than 40 Neanderthals at over 20 sites ranging from Wales to Iraq, clearly show that the environment affected not only what they ate, but how they used their mouths as tools.
- ▶ Those from regions or periods with more open vegetation like steppe environments had higher levels of tooth clamping.
- ▶ The most obvious reason may be that Neanderthals in colder conditions needed more clothing, and spent much more time working animal hide.

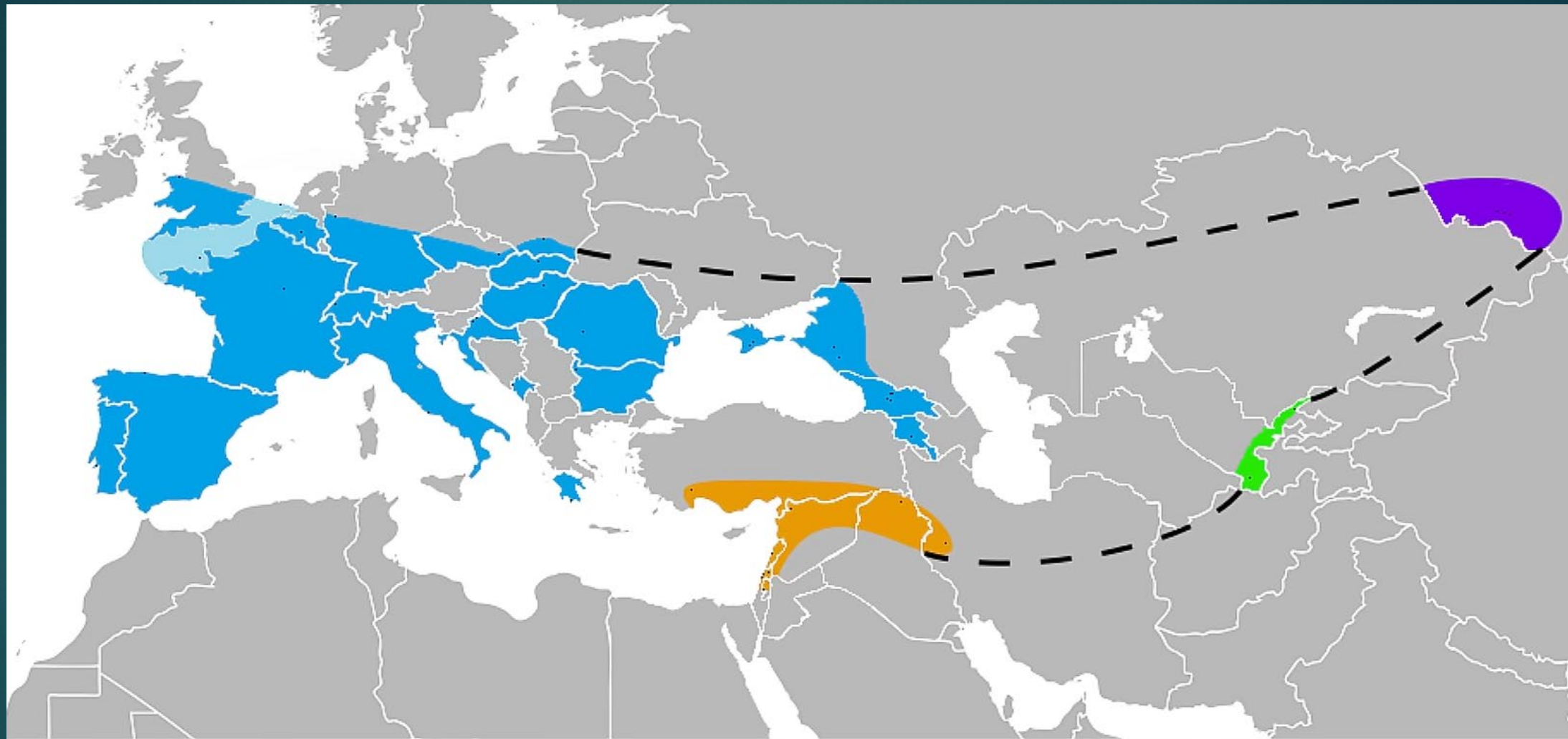
Regional variability: teeth

- ▶ Regional traditions in technology or tasks: in particular,
 - ▶ Italian Neanderthals have more teeth wear than Western Europeans.
- ▶ And strikingly, after 60 ka no Near Eastern Neanderthals display this type of teeth wear at all.
- ▶ Combined with the evidence from limbs, it suggests that those living in this warm, arid but plant-rich area hunted, foraged and processed materials in unique ways.



Locations of Neanderthal finds in Europe and the Levant.

9000 miles across N territory



**Known Neanderthal range in Europe (blue), Southwest Asia (orange),
Uzbekistan (green), and the Altai Mountains (violet)**

3 groups of Ns



N lineages

- ▶ Three geographically defined groups:
 - ▶ one in Western Europe,
 - ▶ a more southern group from an area stretching from northeastern Spain through Italy into the Balkans – had): broader and shorter faces
 - ▶ a third in Central Asia (based on samples from Okladnikov cave and Teshik Tash).
- ▶ A later study **based on nuclear DNA** also distinguished
 - ▶ **European Neandertals** (including both the Western and Southern groups) from the
 - ▶ **Altai Neandertal** from Siberia.

N lineages

- ▶ This points to two migrations of Neandertals into Siberia:
 - ▶ an earlier one represented by the Altai toe bone, and
 - ▶ a later one with European antecedents that replaced the Altai group.
- ▶ mtDNA recovered from a Neandertal femur from the Hohlenstein-Stadel cave site in Germany, which exhibits a haplotype differing from those of all other known Neandertals, thought to be an African sapiens introgression.

Western and central Asian Neanderthals

- ▶ Western Asian Neanderthals are known from Israel, Syria, and Iraq, while several sites in Central Asia, extending into Siberia, have also produced Neanderthal biological remains. Also from Crimean region.
- ▶ There is evidence of Neanderthal stone tool influence extending to China and North Africa.
- ▶ In Europe, Mousterian tools have to date been found only with Neanderthals. This is not the case in the Near East, and may not be the case in Central Asia

Furthest East

- ▶ Teshik Tash cave in Uzbekistan, has yielded a burial of an eight- or nine-year-old male surrounded by goat horns and skulls, and Mousterian tools
- ▶ Neandertals: inhabited parts of Siberia,
 - ▶ Okladnikov Cave in the Altai region
 - ▶ Chagyrskaya Cave in Siberia
 - ▶ Denisova Cave
 - ▶ Crimea, Mousterian-associated Neandertal remains are found at the sites of Kiik-Koba and Zaskal'naya

Costa del Neandertal

- ▶ Visions of Ns struggling thru deep snow has been a persistent view of Ns.
- ▶ The reality: Ns exhibited immense ecological adaptability. They were mostly successful in temperate climates.
- ▶ N was also a coastal forager: i.e. Gibraltar: Gorham's, Vanguard, Ibex caves;. Much of the evidence for this in other areas is now submerged.

Costa del Neanderthal

- ▶ Neanderthals, in the Alps, Carpathians and other mountain ranges were climbing at least up to 6,500 ft. Neanderthals undertook journeys over high passes in the Pyrenees, the Massif Central and other mountain ranges. Following red deer? Hibernating bears?
- ▶ Even drier environments towards Central Asia, all of which are rich in Neanderthal fossils and archaeology.
- ▶ Ecologically they could shift gear, adapting to whatever was available in the regional ecosystem, from palm dates to olives, tortoise to gazelle; even giant camels on the fringes of Arabia.
- ▶ No evidence of Ns in true wetlands

El Sidrón, Spain

- ▶ The Spanish site of El Sidrón is thought to be an accumulation of at least 12 Neanderthals including three female and three male adults, three adolescents, two juveniles and one infant.
- ▶ mtDNA indicates that the men were all closely related, but three of the four women were from outside the group.
- ▶ This suggests that Neanderthals exhibited male philopatry (stay in group they were born in) and female exogamy (join new group). At least two of the subadults share an mtDNA haplotype with one of the women, who may have been their mother.

El Sidrón, Spain

- ▶ Complete and partial mtDNA sequences from all the available individuals suggest that Neanderthals at El Sidrón formed:
 - ▶ small kinship-structured nomadic bands
 - ▶ practiced patrilocal mating behavior (outside women join the group)
 - ▶ had relatively long inter-birth intervals (ca 3 years) when compared with modern human populations

Family relationships

- ▶ Many theories have been proposed for **how reproduction was organized**.
- ▶ Male-dominated groups is one idea, supposedly backed up by the fact that **at El Sidrón, all the males were from the same genetic population**.
- ▶ In contrast, the **adult women were from two different lineages**, and researchers interpreted this **as evidence they'd joined a group based around male dominance**.
- ▶ Neanderthals probably had pair-bonding

El Sidrón Cave, Spain, 1994: *Tunnel of Bones*

- ▶ 13 people, dated 48 +/- 3 Ka :
 - ▶ 7 adults (3 males, 3 females & 1 undetermined),
 - ▶ 3 adolescents between 12 and 15 years of age (2 males, 1 female),
 - ▶ 2 juveniles between 5 and 9 years of age (1 male, 1 undetermined),
 - ▶ 1 infant
- ▶ 2017 soil sample DNA: Neandertal mtDNA
- ▶ Analysis of mitochondrial DNA supports the hypothesis that the 13 individuals represent a family group:
- ▶ Seven of the 13 individuals share the same mtDNA haplotype.

El Sidrón: genetics & patrilocality

- ▶ Nuclear DNA Genes: red hair, O & A blood group, bitter taste perception, FoxP2 (language)
- ▶ mtDNA: family related;
 - ▶ 3 males have same mtDNA;
 - ▶ 3 females had different mtDNA;
 - ▶ like modern hunter gatherers, males stay in group, females join new groups; genes moved across N populations via the women
- ▶ 2 of women directly related to children
- ▶ Familial inbreeding: caused reduced genetic diversity
- ▶ Found 17 examples of congenital anomalies

Survival cannibalism

- ▶ Although there are **no carnivore tooth marks on the bone**, the **bones are heavily fragmented and show cut marks made by stone tools**, indicating that the Neanderthals were **almost certainly killed and cannibalized** by another Neanderthal group, not by animal scavengers.
- ▶ **Cut marks, flaking, percussion pitting, conchoidal scars, and adhering flakes on the bones** all provide strong **evidence for cannibalism at El Sidrón**. Several bones have been cracked open to obtain marrow or brains.
- ▶ The bones of the Neanderthals also indicate that during their entire lives they suffered from nutritional stress, with a diet made up mostly of plants (seeds, nuts, and tubers) and some lesser quantity of meat. These data together lead researchers to believe **this family was a victim of survival cannibalism by another group, who may also have been suffering from nutritional stress.**

El Sidrón: Ns were thin on the ground

- ▶ Populations of N began to shrink;
 - ▶ climate between 50 and 30 K, varied between cold dry periods and warm wet periods
 - ▶ El Sidrón occurred in the former cold period;
 - ▶ wooded areas for ambush hunting began to shrink;
 - ▶ populations more isolated,
 - ▶ little gene flow between them,
 - ▶ suffered from genetic inbreeding

El Sidròn

- ▶ Genetically, the three adult males in the group were closely related enough to be brothers, cousins, or uncles, while the four adult females in the group came from three distinct genetic lines.
- ▶ Male-Kin bonding: it is likely that the males exchanged females with another local, slightly less closely related group.
- ▶ Mating between individuals who shared recent ancestors was fairly frequent, and possibly unavoidable, if local populations were small.

Neandertals: **patrilocality** = females move to male's family

- ▶ In contrast to the Y chromosome and nuclear DNA at El Sidrón, the **mtDNA of both males and females was relatively diverse**, implying that more female ancestors contributed to the population than males.
- ▶ That could be a founder effect, in which the initial group included fewer fertile males than females.
- ▶ Or it could reflect the nature of Neanderthal society, Either fewer men than women contributed to the next generation, or women moved more frequently between groups,
- ▶ Skov: the evidence suggests the latter.

Neandertals: patrilocality

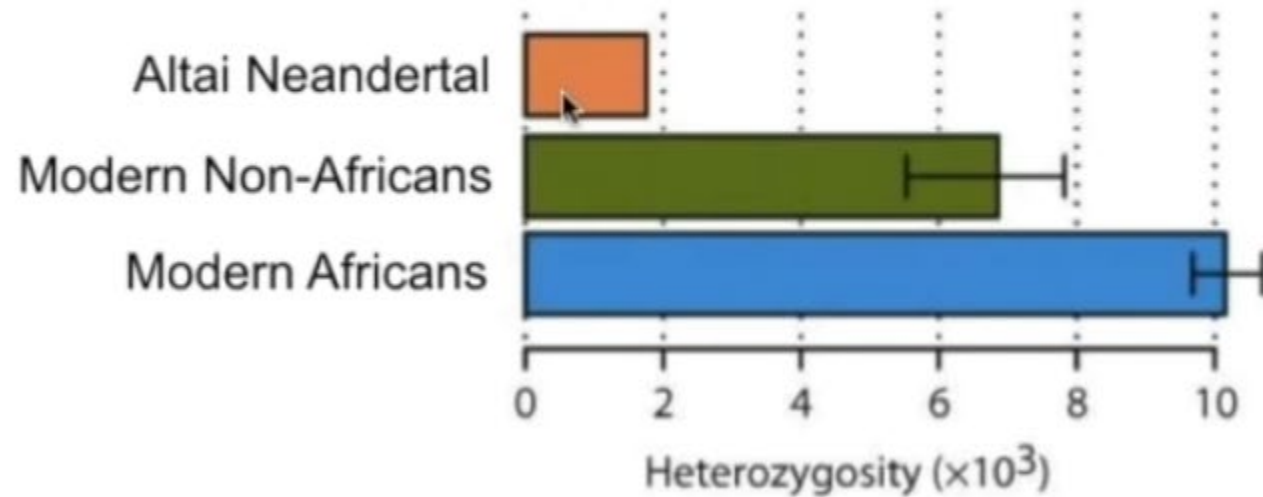
- ▶ Neanderthals lived in very small groups of 10 to 30 breeding adults, and that young females left their birth families to live with their male mates' families. Most modern human cultures are also patrilocal,
- ▶ Patrilocality may be the long term foundation of sexual gender inequality. Incoming women were relation less; lacked any social power

Denisova Neandertal clan: N brothers stuck together

- ▶ Study of the **Denisova Cave** genomes of a father and daughter and 12 of their relatives, many of whom sheltered in the same cave over less than 100 years.
- ▶ The genomes also offer clues to the social structure of a group of Neanderthals. In addition to identifying the first father-daughter pair, the genetic evidence suggests these males stayed in their family groups as adults,
- ▶ Genomes from **seven males at one site**; suggestive that they lived in small groups of closely related males.

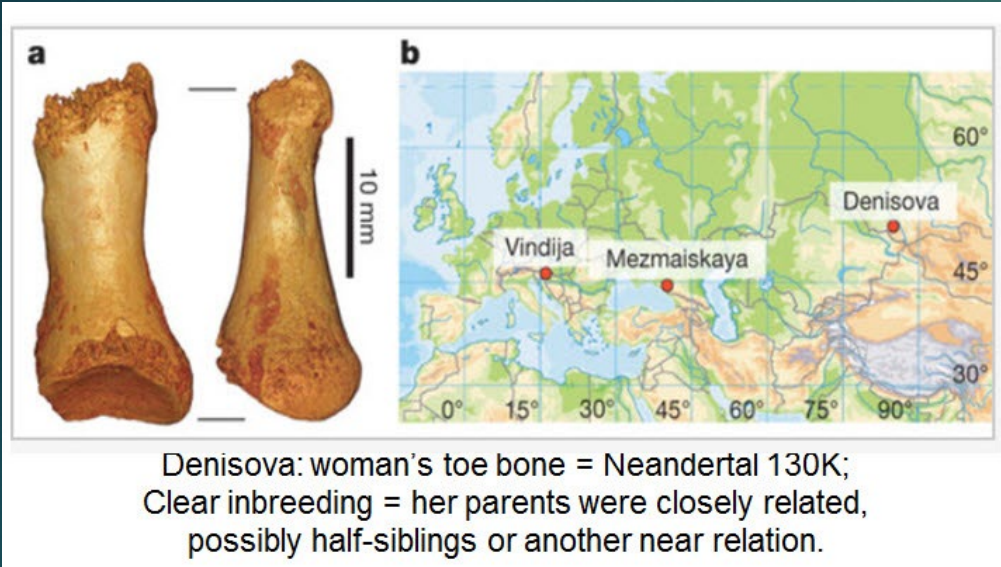
Very Low N Genetic diversity: long stretches of homozygosity; lots of inbreeding/high heterozygosity; implies closely related parents

Neandertal population history



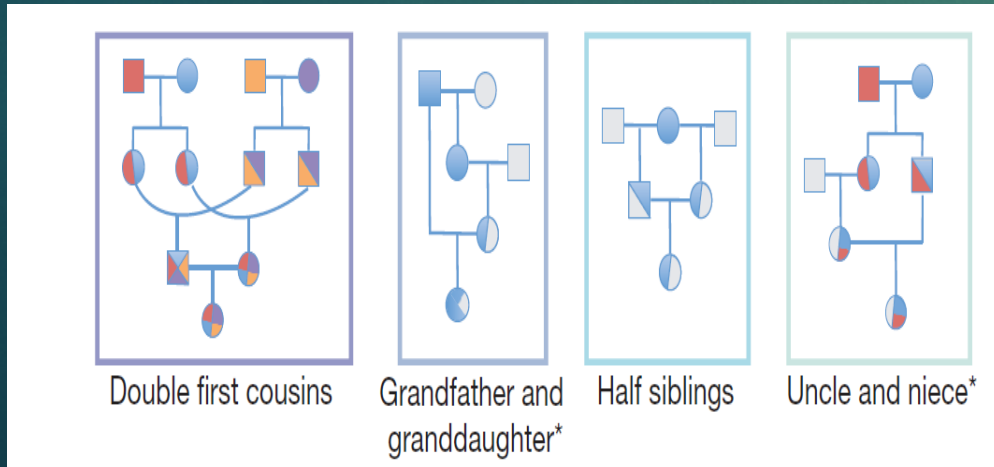
- ▣ Low genetic variability:
 - ▣ heterozygosity in Neanderthals as well as Denisovans appears to have been
 - ▣ lower than in present-day humans and is
 - ▣ among the lowest measured for any organism.

2014: One Reason for Neandertal Demise: Low population number with inbreeding



Denisova Neandertal woman toe bone:
Chromosome 21: Mom & Dad genetically related (19 Mb base pairs with no difference)

Highly inbred: equal to being =
Half siblings
Grandfather-granddaughter
Aunt-nephew
Double first cousins



Demographics

By and large Neandertal populations were small

- ▶ Small populations go extinct all the time for stochastic (random) reasons:
 - ▶ N had small group sizes,
 - ▶ Lower birth rates: If low female fertility rate, population will crash
 - ▶ Higher mortality rates,
 - ▶ Increased family inbreeding;
 - ▶ Significant decline in genetic diversity

Altai Neanderthal: lots of homozygosity

- ▶ Nuclear genomes contain a record of population history going back generations, which can be revealed by statistical analysis.
- ▶ The genome of Denisova 5, the so-called Altai Neanderthal, reveals long runs of 'homozygosity'. This is when a person inherits identical alleles on both pairs of chromosomes.
- ▶ The long sections of homozygosity on the Altai Neanderthal genome can only be explained by her parents being very close relatives: first cousins, grandfather–granddaughter, half-siblings or uncle–niece.

Altai N: high homozygosity from small population size

- ▶ Tests showed that **this homozygosity** was not due to a bottleneck, as occurs when a small group becomes isolated; it was a longer-term problem of small population size.
- ▶ In contrast, Denisovans have only a proportion of the heterozygosity of MHs (20–40 per cent), but lack the long runs of homozygosity we see in the available Neanderthal genomes.
- ▶ The most likely explanation for Denisovans is low genetic diversity in their population rather than inbreeding due to low population numbers.

Demographic history

- ▶ This information can also be used to reconstruct a demographic history.
- ▶ **Homo sapiens, Denisovan and Neanderthal population histories show dissimilar patterns to one another, with declining numbers prior to 1 million years ago, but after this, *Homo sapiens* numbers track upwards, while the two other groups decline steadily between 100,000 and 50,000 years ago towards their eventual disappearance.**
- ▶ The **MH genomes**, in contrast, show that **these groups were not nearly as inbred as the Altai Neanderthals.**

MHs = higher genetic diversity

- ▶ The African sapiens parents of Ust'-Ishim Man, for example, were completely unrelated to one another.
- ▶ At the Russian site of Sungir, where three 35,000-year-old Homo sapiens were found buried amidst great richness, analysis revealed that their degree of inbreeding was also low. They were a highly diverse genetic group with an estimated population size that was equivalent to most modern hunter-gatherer groups in places like Amazonia. This suggests that bands such as those of Ust'-Ishim and Sungir maintained strong networks of interaction with other groups and exchanged mates with them.

Homozygosity or not

- ▶ A Neanderthal from the site of Chagyrskaya, in the Altai, also had significant homozygosity.
- ▶ It appears likely that in the Altai, the Neanderthal population was particularly small.
- ▶ This might be because a **smaller founding population** moved there from the west.

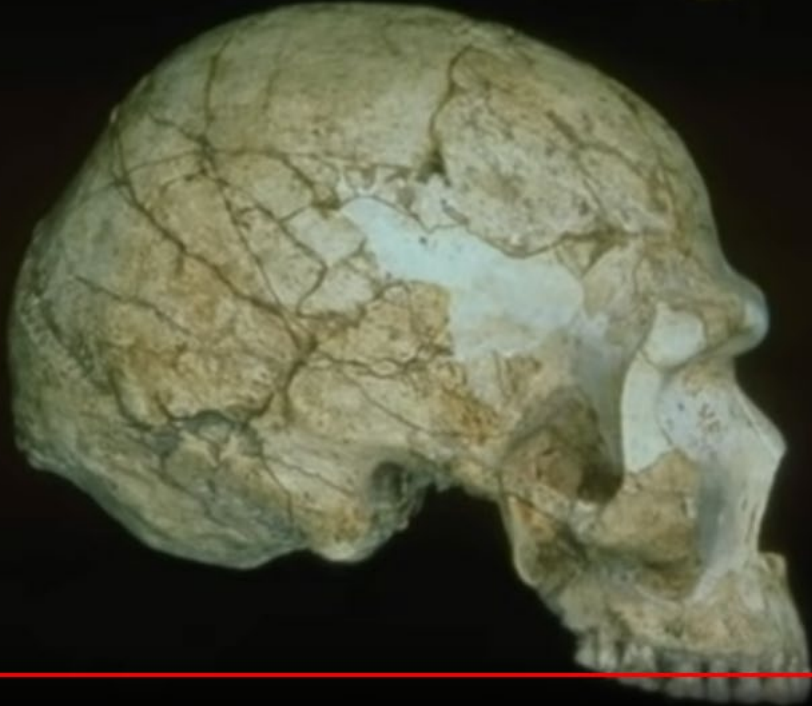
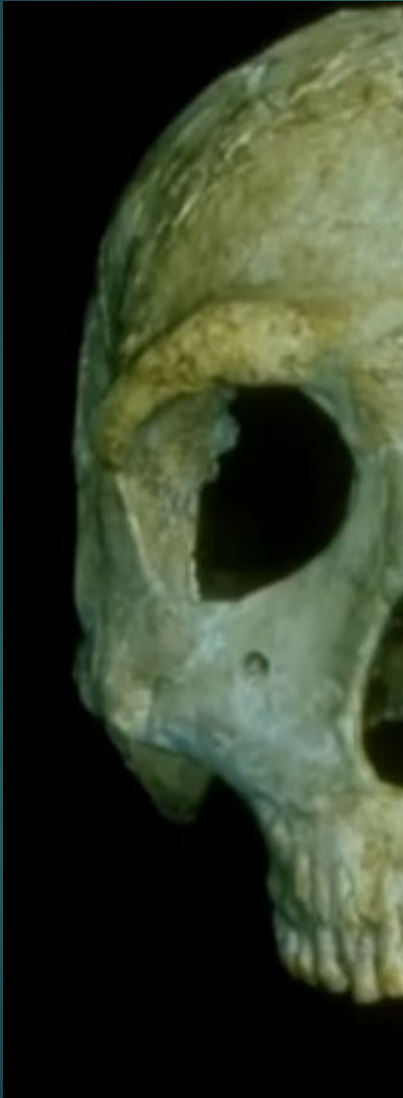
Vindija vs Chagyrskaya: less vs more homozygosity

- ▶ Perhaps this is why they failed to maintain their presence there. According to data from Chagyrskaya, Neanderthals disappeared from there around 60,000 years ago.
- ▶ The Chagyrskaya genome, dated to ~80 Ka, is more closely related to the Vindija Neandertals from Croatia than to the earlier Altai Neandertal, found only about 100 km from Chagyrskaya.
- ▶ Vindija genome, also contained low heterozygosity, although it did not have such high runs of homozygosity, suggesting that it was not as inbred as the Altai Neanderthal

Levant Ns were different

- ▶ Asian specimens: from four Mousterian sites in the Levant: Amud, Kebara, and Tabūn (all in Israel) and Dederiryeh (in Syria).
- ▶ They differ in some ways from the Neandertals of Europe.
 - ▶ The Amud 1 individual is one of the largest Neandertals known and has the largest Neandertal cranial capacity (1740 cc) on record,
 - ▶ Tabūn C1 is one of the smallest Neandertals, with a capacity of only 1271 cc.
- ▶ However, their vaults are more rounded, particularly posteriorly, and they lack occipital buns. The frontals of both skulls are quite close in form to those of early modern Near Easterners

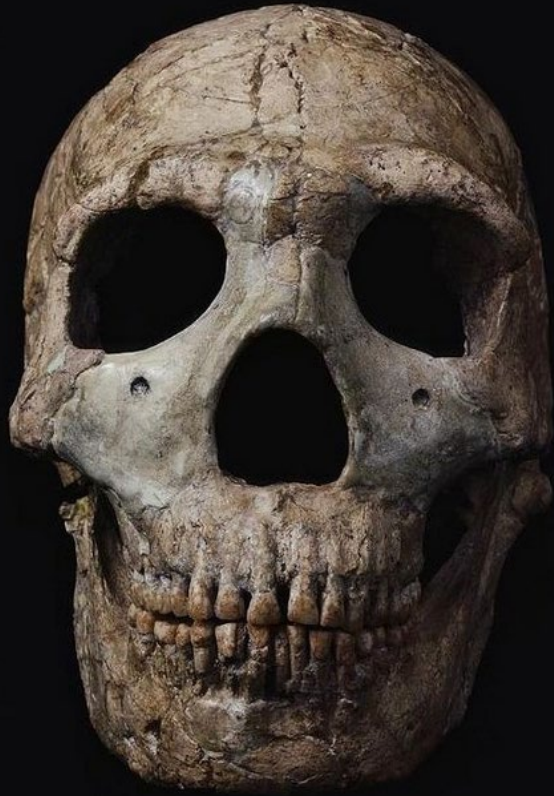
Amud N vs Skhul M



Amud vs Italian Saccopastore Ns



Amud 1 Skull - largest Neanderthal brain volume at 1736 cc+



Amud



Amud 1: 6 foot tall, no occipital bun; the least N of all the Ns; 55

Late Iberian Ns = 44 Ka

- ▶ Two relatively late Neandertals from Iberia:
 - ▶ Sima de las Palomas sample from Spain
 - ▶ Grunta de Oliveira remains from Portugal.

- ▶ The Palomas Ns were rather small-bodied.

- ▶ Some scholars have argued that the Iberian Peninsula represented the last refuge of the Neandertals – C. Finlayson = 29 Ka

Vindija, Croatia: source of original N genome

- ▶ In central Europe, the Vindija sample takes center stage in any discussion of late Neandertals. Vindija is a large cave not far from the older site of Krapina. Excavations here in the 1970s and 1980s recovered a large series of fragmentary human remains from a long stratigraphic sequence.
- ▶ Contained a cultural assemblage described as having both Upper Paleolithic and Middle Paleolithic elements.
- ▶ Although they are clearly the bones of Neandertals, they exhibit some systematic differences from other Neandertal samples.

Vindija: different N morphology

- ▶ Vindija sample differs from earlier Neandertals and resembles early modern Europeans.
- ▶ Has a higher forehead than most Neandertals. A partial braincase from Vindija seems to show other “progressive” features – that is, a more rounded vault and less postorbital constriction – not seen in the Krapina material
- ▶ The browridges of the adults are thinner and less projecting than those of other Neandertals.
- ▶ A pattern of facial reduction is seen throughout the Vindija sample,

Gene flow at Mezmaiskaya Cave

- ▶ The most easterly of the possible late Neandertal sites is Mezmaiskaya Cave in the northern Caucasus. Skeleton of an infant (0–7 months of age), which is now dated to ≤ 43.2 Kya.
- ▶ Also a **one- to two-year-old infant** from the slightly younger Level 2 at the site.
- ▶ Facial reduction and other transitional features seen in many of these late Neandertals may reflect gene flow coming in from more modern populations elsewhere,

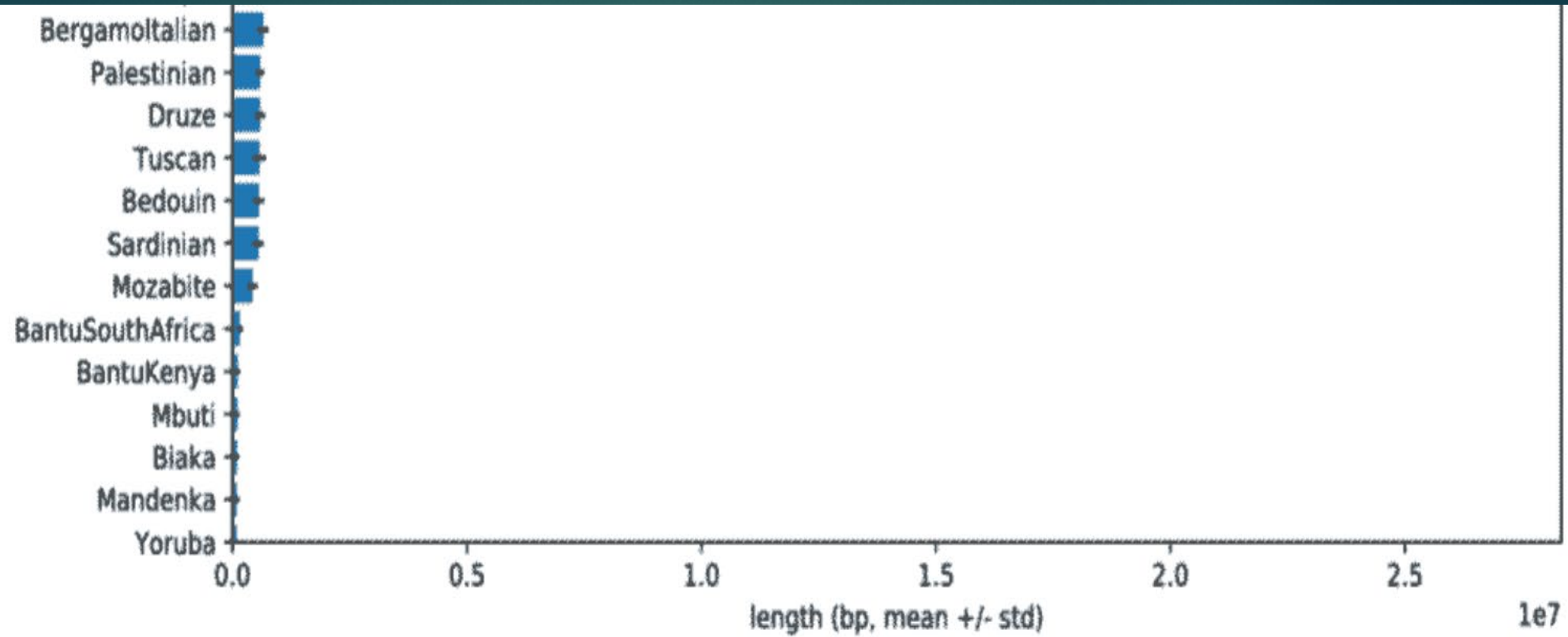
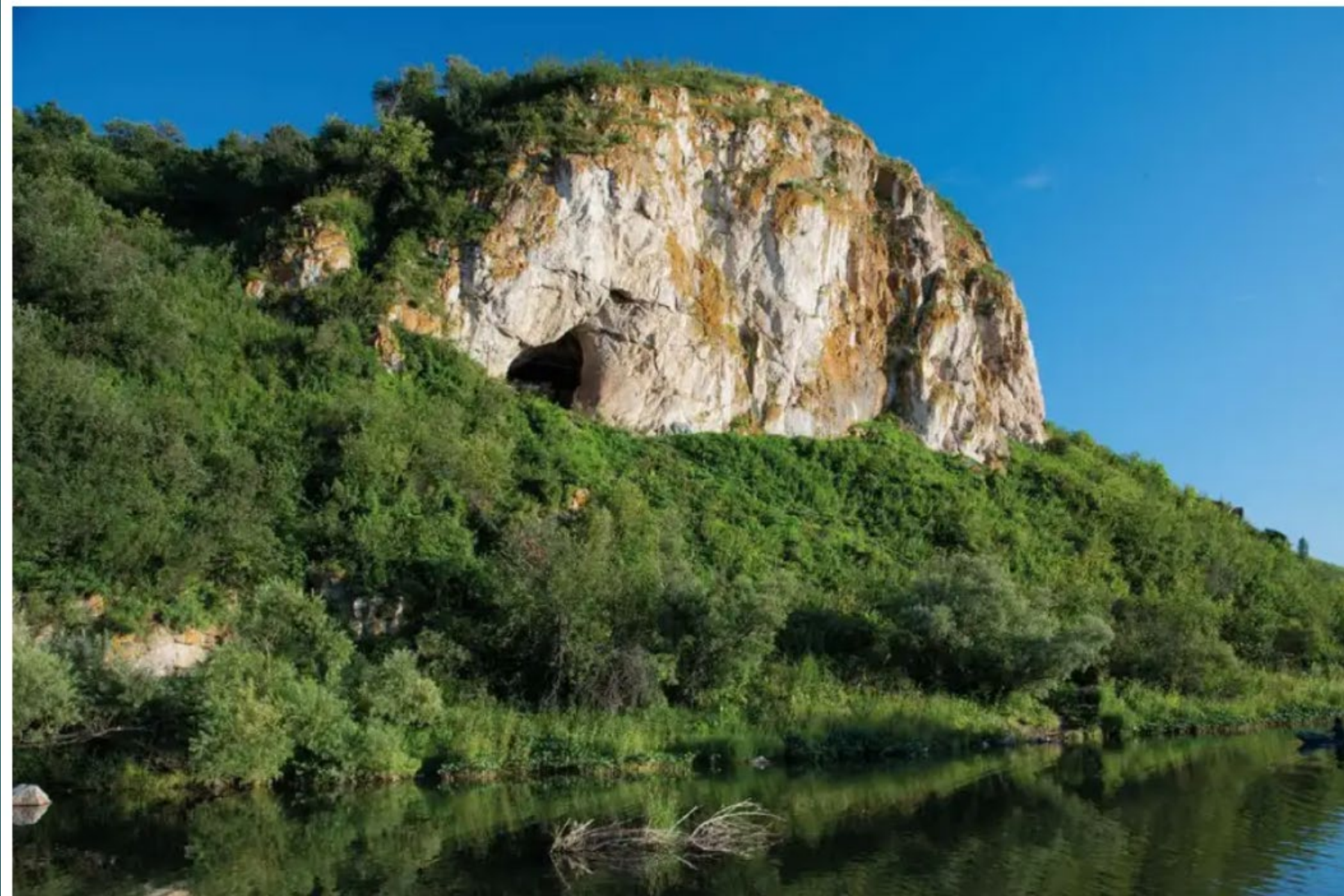


Figure S17B from Bergström et al. 2020, showing the amount of genomic sequence inferred to represent Denisovan ancestry in lots of populations. `

Chagyrskaya cave in Siberia



First Known Family of Neanderthals Found in Russian Cave

- ▶ 2022 - Skov et al. Study: Analyzing fossils from Chagyrskaya cave in Russia, found one of the first known Neanderthal family: a father, his teenage daughter and others who were probably close cousins, found alongside stone tools and butchered bison bones.
- ▶ The family, part of a band of 11 Neanderthals found together in the cave, most likely died together, possibly from starvation.

Chagyrskaya Cave

- ▶ Hunted migrating bison, retreated to Chagyrskaya Cave to enjoy their spoils.
- ▶ Their living space was cramped, but occupation was probably only seasonal.
- ▶ 90,000 stone artefacts and butchered bison bones have been found in this cave, along with the largest collection of Neanderthal remains known for north Asia.
- ▶ The DNA also reveals a very high level of inbreeding, suggesting that the Neanderthal population in the area was very small.

Ns at Chagyrskaya cave

- ▶ Inbreeding may be a result of being **an isolated group on the edge of the range of Neanderthals**, rather than being true of Neanderthals generally.
- ▶ Low Y chromosome diversity. Suggests patrilocality
- ▶ Same as at the El Sidrón site in northern Spain and at Denisova Cave.

Inbred Ns

- ▶ The Chagyrskaya genomes, like that of an earlier Neanderthal from Denisova, contain signatures of inbreeding,
- ▶ 30% of these individuals' genomes had long segments of homozygosity, suggesting that the Chagyrskaya Neanderthals were part of a small, inbred, community.
- ▶ This genetic data provides a detailed documentation of the social organization of an isolated Neanderthal community at the easternmost extent of their known range.

Chagyrskaya

- ▶ The best-fitting scenario assumes a community size of 20 individuals, with 60–100% of the females being migrants from another community.
- ▶ But at least some females remained with the group they were born in.
- ▶ Unresolved: whether this is simply a far east isolated group or typical of all Ns

Lineages

- ▶ There was a fairly rapid expansion of Neanderthals around 100 to 115 Ka.
- ▶ Unlike the Altai Ns, both the late European Neanderthals and the Chagyrskaya and Okladnikov Neanderthals are descendants of this population, which includes El Sidrón and Vindija
- ▶ They are more similar to El Sidrón than to the geographically closer Mezmaiskaya 2

N lineages

- ▶ A common observation of all these studies was that **Neanderthal mtDNA sequences were similar to each other—suggesting a general low diversity—and different to any reported modern human mtDNA.**
- ▶ Some studies began analyzing a **possible phylogeographic structure; the basal sequences in the phylogenetic trees were from the easternmost Neanderthals (located in Central Asia) or from the oldest ones (Valdegoba and Scladina).**
- ▶ This seems to support an **east–west genetic cline and also the existence of temporal bottlenecks that shaped the mtDNA diversity.**

N variation

- ▶ The variation among Neanderthals was approximately one-third of that estimated for present-day humans worldwide, suggesting a female effective population size of less than 3500 individuals
- ▶ Most recent common ancestor (MRCA) of the Neanderthal samples analyzed was estimated to have lived approximately 110,000 years ago

Western Ns = low mtDNA variation & extinction

- ▶ Later western European Neanderthals (~50 Ka) constitute a tightly defined group with low mitochondrial genetic variation in comparison with both eastern and older (more than 50 Ka) European Neanderthals.
- ▶ Eastern and western Neanderthals seem to have diverged approximately 55–70 Ka ago, followed by an extinction of western Neanderthals throughout most of their range and a subsequent recolonization of the region

3 genomes

- ▶ **Three Neanderthal genomes:** Vindija, Croatia (44 Ka), El Sidròn, Spain (49 Ka), and the Altai genome
- ▶ The **average heterozygosity among the three Neanderthals was ~30% of current MHs**; they have **longer runs of homozygosity** than modern humans
- ▶ This suggests that Neanderthals lived in **small and relatively isolated populations**,
- ▶ A **low population size over a long time would reduce the efficacy of purifying selection and contribute to a larger fraction of likely deleterious alleles**, particularly at low frequency

N mtDNA: not necessarily homogenous

- ▶ Initially the mtDNA showed that Neanderthal populations were **small and homogenous**; individuals dating around 50 to 40 ka from Spain, Germany and Croatia were genetically very similar.
- ▶ But with more data, glimpses of regional genetic diversity emerged.
- ▶ Descendants from deep population branches were still surviving scattered across western Eurasia by 50 to 40 ka.



N mtDNA: lots of differences

- ▶ The Teshik-Tash child in Uzbekistan, for example, was shown to be connected to European lineages, while even farther east at Okladnikov Cave in the Altai region of Siberia, another child's mtDNA held a bigger surprise.
- ▶ But at some point there had been one or more massive upheavals. Some of the Spanish and French Neanderthals turned out to have mtDNA more like the Okladnikov child's than a lineage centered on El Sidrón, Feldhofer and Vindija.
- ▶ And the reverse is true: the Mezmaiskaya 1 baby in Russia, thousands of kilometers from Europe, is closer to Italian Neanderthals than to the Okladnikov child, next door

Denisova Cave: Altai Neanderthal

- ▶ A sample extracted from D5, a toe bone, provided the first 'high-coverage' Neanderthal nuclear genome: our introduction to the recipe for another kind of human.
- ▶ Dubbed 'the Altai Neanderthal', the toe had belonged to a woman who died around 90 ka., from a lineage that had diverged from other Ns ~ 40,000 or 50,000 years before.
- ▶ The mtDNA of Okladnikov, geographically nearest to her, was not closest genetically, but was more genetically close to the newborn baby from Mezmaiskaya, in the Caucasus thousands of kilometers west.

Two N branches: Eastern and western

- ▶ These results have revealed a deep structure within the Eurasian Neanderthal population as a whole.
- ▶ Two main branches split, then remained isolated in Europe and Asia for millennia.
- ▶ The Eastern Altai woman's descendants disappeared and later were replaced by the European branch.
- ▶ Just as with the mtDNA in Europe, it seems that at a regional scale, multiple nuclear DNA lineages existed that were either contemporary but not mixing much, or quite rapidly replaced each other.

Lineages

- ▶ All this implies that there were continental-scale movements of lineages, certainly towards the east, but also perhaps in the other direction.
- ▶ This was likely to be an incremental process rather than a migration, but the fact that it happened at all points to enormous, long-term upheavals.
- ▶ For any region, we can't assume continuity between early Neanderthals pre-MIS 5 (180 Ka), and those afterwards.

3 N Clades

- ▶ Research on Neanderthal mtDNA has provided a shifting picture of N population demography, with early results indicating low diversity, but with some large-scale geographic structure
- ▶ There appeared to be three clades c. 50 Ka, with a west-east separation and an additional Italian group.
- ▶ More recent analysis of a new individual from the easternmost site of Mezmaiskaya, places it within the western clade, suggesting that at least for mtDNA, late Neanderthals were even less genetically diverse.
- ▶ This would seem to suggest a bottleneck after MIS4 (71 Ka) and implies regular gene flow in that population, rather than the high local genetic diversity which might be expected if models of socially exclusive local Neanderthal groups were correct.

Forbes Quarry skull

- ▶ Forbes Quarry skull: a female; her nuclear DNA was equally close to Chagyrskaya Ns in Russia and the Vindija Ns in Croatia. This makes her part of the population ancestral to them both.
- ▶ Her DNA was still different to the Altai branch, indicating that the split from the eastern cousins was probably ~170 to 130 ka.
- ▶ Neanderthals were shifting technologically and culturally during MIS 5 (130-80 Ka), which is also when we see some mtDNA sub-populations emerge.
- ▶ And after the deep freeze of MIS 4 (71-57 Ka), Neanderthals in Europe were certainly expanding their range, leading to the recolonization of Western Europe. Perhaps some of these movements were echoed in a diaspora towards the east.

Lineages

- ▶ Forbes Quarry N is genetically more similar to Ns in Belgium and in Germany, and in Russia (Mezmaiskaya 1), than to the El Sidrón Spanish and other younger Neanderthals from Europe and western Asia. Forbes Quarry N predates these latter Neanderthals.
- ▶ The genetically most divergent Neanderthal lineage known to date is represented by the Altai Neanderthal (Denisova 5) from Denisova and is one of the eastern-most Neanderthal specimens found.
- ▶ All other Neanderthal individuals are more closely related to the Vindija individual from Croatia.

Hybrids from N men and MH women

- ▶ Nobody today has mitochondrial DNA like that in Neanderthals and, since it's passed only maternally, this implies that interbreeding was more often between N men and MH women.

MH & N Interbreeding

- ▶ The higher amounts of Neanderthal DNA in some people today probably comes from extra hybridizing episodes within some of those lineages, which then passed into Asia and beyond.
- ▶ We also now know that interactions potentially happened closer to Europe.
- ▶ Peștera cu Oase, Romania, between 42 and 37 ka. His genetic ancestry was about 6-8 per cent Neanderthal. This means he had a Neanderthal ancestor within just four to six generations.
- ▶ And just like 'Ust-Ishim, the Oase man's heritage also appears to contain multiple interbreeding phases, with another around 2 millennia before his death.

Interbreeding

- ▶ Taken together, there are at least three and potentially six periods since 200 ka when Neanderthals made babies with us.
- ▶ Contact and hybridizing happened a lot more often than we'll probably ever know.
- ▶ One odd pattern sticks out, however. No late Neanderthals show any genetic input from H. sapiens.

N-MH interbreeding

- ▶ To account for the number of interbreeding episodes and the percentages of surviving DNA in us, there could have been hundreds of individual sexual encounters and resulting hybrids; perhaps more.
- ▶ There are hints in the DNA that couplings might have involved more Neanderthal men with African sapiens women than the reverse, but other explanations for the data are possible.

Pleistocene hook-ups

200

- ▶ In theorizing the social contexts behind all this, there's been a tendency to assume rape as a primary mechanism; an unpleasant residue from the days when prehistorians and the public regarded Neanderthals as more beast than potential beloved.
- ▶ Chimpanzee males will engage in coercive sex, but not with unknown females (whom they prefer to kill).
- ▶ It's possible some of our Neanderthal inheritance may derive from non-consensual circumstances, but xenophobia rather than xenophilia needn't be the default assumption.
- ▶ Pleistocene hook-ups may just as plausibly have been more similar to how bonobos deal with unfamiliar faces. Bonobos are fundamentally friendlier.

Pleistocene hook-ups

- ▶ They're more open to positive interactions with other groups, and moreover territorial border patrols and killings of non-group members are unknown.
- ▶ We should perhaps ask why the idea of enthusiastic partners driven by desire and even emotional attachment is regarded as more of a fairy tale than other explanations.
- ▶ However they were conceived, hybrid children were raised to survive. Presumably more often than not, infants stayed with their mothers, and they were fed, cleaned, kept warm; loved. These babies of mixed heritage grew up, understood the cultures they were born into, and went on to have children of their own.

Low N populations?

- ▶ Some early *H. sapiens* genes should have moved into Neanderthals too.
- ▶ But no late Neanderthal genomes show any *H. sapiens* input.
- ▶ Larger numbers of genetic samples have dramatically altered the view that Neanderthals were defined by a tiny meta-population.
- ▶ Some initial analyses suggested far lower genetic diversity than living *H. sapiens*.
- ▶ Theories implicating inbreeding in their disappearance emerged.

Inbreeding

- ▶ At Denisova, the Altai Neanderthal woman's parents must have been **one of the following**: double first cousins (sharing both sets of grandparents), an aunt with a nephew, a grandparent with grandchild, or even half-siblings.
- ▶ By many cultural definitions, **that's more like incest than inbreeding.**
- ▶ Further analysis of her DNA **also found relatively close, if less extreme, relationships between her ancestors over many generations.**

Inbreeding: not at Vindija

- ▶ A similarly small genetic population was initially indicated at El Sidrón.
- ▶ High-coverage genome from Vindija showed that it didn't have significant markers for inbreeding in previous generations, and that her parents were not close relations.
- ▶ This means that inbreeding being the norm for Neanderthals, where inbreeding and even incest was happening, it was probably about lack of choice rather than preference.

Ns may not have been shrinking

- ▶ The **Vindija genome also revealed that not all late Neanderthal populations were shrinking**, and population estimates for early Neanderthals would double if the H_öhlenstein-Stadel mtDNA is not an import from extremely ancient interbreeding with *H. sapiens*.
- ▶ The very latest studies have revealed further complexity.
- ▶ In 2020 a **high-coverage genome from Chagyrskaya, Siberia, didn't show inbreeding between parents**, but came from a reproductive population just as small as the relatively nearby Altai woman's, averaging about 60 individuals for many generations.

MH social networks

- ▶ In stark contrast, the earliest *H. sapiens* genome from Ust'-Ishim has more diverse DNA than any Neanderthal sampled so far.
- ▶ This implies that the interconnectedness of *H. sapiens*' social networks may well have been different right from the start.

Abric Romani, Iberia: a Neandertal rock shelter



Abric Romani, Iberia

200

- ▶ 27 calcium carbonate layers over 12 sediment layers, covering 40,000 years:
 - ▶ hundreds of hearths,
 - ▶ many 10s of thousands of artifacts, bones, and wood –
 - ▶ Even 2 likely wooden platters
- ▶ 2011: a wooden cleaver shaped tool, dated to 56 Ka



Remarkable travertine cast from Abric Romaní, revealing the shape of a wooden tool.

To see a world in a hafted tool: birch pitch composite technology, cognition and memory in Neanderthals

- ▶ **Neanderthal composite technology**: includes both the earliest known multi-component artefacts in the archaeological record, and the first truly synthetic material.
- ▶ **Composite technology**: stone tip, haft, glue adhesive (birch bark tar – various locations and times) (pine resin mixed with beeswax in Italy); requires multiple sources, multiple places, multiple times – and planning; or how to teach those skills
- ▶ **Klg of material properties and quality** – pick hardest wood for fire hardened digging sticks in forests

Ns as technicians

- ▶ Joinings: Ns were carpenters and pioneered composite tools, allowing modular repair
- ▶ Composite tools are example of multistage processes requiring foresight/planning. And normal frontal lobe functioning.
- ▶ Built spears: stone tips and handle or haft; with bindings of sinew, tendons, or plant fiber. And glue.
- ▶ And also used tar for binding. And 50 ka bitumen (natural asphalt) in Romania and at El Sidròn.

Composite tools

- ▶ Composite tools (i.e. stone point attached to wooden spear via tar, plant string, etc., in a multistep process) in themselves also imply cognitive capacity to plan, design and anticipate.
- ▶ They bring together multiple episodes of material sourcing and manufacture for each constituent part, even before their assembly. Handles were likely much longer-lived, and far-travelled.
- ▶ Chemical analysis of the El Sidrón 1 adult male found traces of bitumen in his calculus. The only likely explanation is using his mouth in composite tool manufacture or repair, boosted by the presence of intense chipping on his teeth and plant residues.

Composite tools and tar

- ▶ Birch tar drops can form fortuitously from bark in campfires, but to gain useable amounts Neanderthals needed to maintain careful control of the fire's temperature for extended periods.
- ▶ Moreover, the chemical purity of the North Sea tar used by Ns supports the idea that **by 50 ka**, Neanderthals had significantly finessed their technique.
- ▶ Neanderthals also aimed to improve the natural quality of pine resin by adding beeswax, which indicates the cognitive complexity equivalent to the plant gum and mineral hafting recipes known from early H. sapiens sites in southern Africa.

Inter-generational learning in Ns

- ▶ Inter-generational learning is vital for maintenance of cultural traditions, which for Neanderthals are discernible beyond the obvious lithic techno-complexes.
- ▶ The central Mediterranean shell-knapping tradition or birch tar technology extending across tens of millennia and three regions in Europe are other examples.
- ▶ Schöningen horse hunting implies cultural traditions. Time and time again the
 - ▶ hunters returned to exactly the same part of the lakeshore,
 - ▶ chose the same tree species for their almost identically made spears and
 - ▶ used only particular parts of the horses they killed as tools.

Birch tar



Neandertals invented or discovered glue: oldest synthetic substance



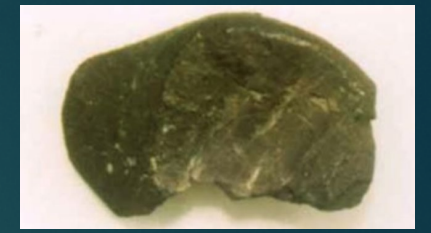
1963: German Mine: birch bark glue with a N fingerprint

Original theory: complex anaerobic production of pitch glue from birch bark

Neanderthals Were Mixing Tar 200,000 Years Ago

- ▶ Learning to extract tar from tree bark was one of humanity's earliest technological achievements.
- ▶ Adhesives fixed stone blades neatly onto wooden handles for use as a spear, an axe, or a hoe; and this was crucial when manufacturing compound tools with two or more pieces.
- ▶ Found ancient beads of tar dating back as far as 200,000 years in Italy, Germany, and other European locations.
- ▶ Neanderthals were distilling tar for tool-making long before there was evidence of *Homo sapiens* manufacturing tar

Birch-bark pitch technology, 70 Ka



- ▶ Some wooden tools (including thrusting spears) tipped with stone points:
 - ▶ manufacture of birch-bark pitch at a Neanderthal site at Konigsaeue, Germany, at 80 Ka, used to affix stone points or blades to hafts of wood, antler, or bone; adhesive for composite tools
- ▶ From 200 kya, European Neandertals used fire to synthesize pitch from bark, through a process that involved dry distillation in the absence of oxygen and within a temperature interval of 340°C–400°C
- ▶ Neandertals used fire to heat-treat existing natural materials, such as bitumen for hafting purposes. This is clear from 70,000-y-old tools with traces of bitumen on their surfaces.

Easier tar production in 3 hours from birch bark near stone

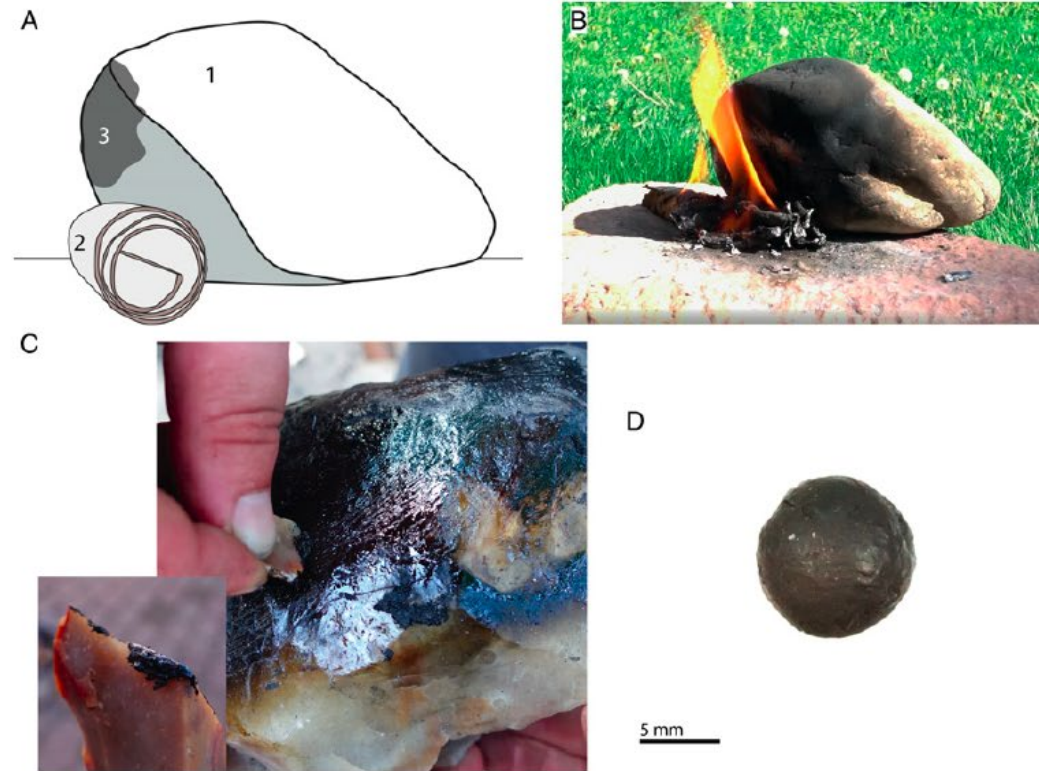


Fig. 1. Experimental birch tar making with the condensation technique. (A) Schematic drawing of the experimental setup: a cobble (1) with an inclined surface overhanging a piece of birch bark (2) is used as support for the condensation of birch tar directly above the burning bark (3). (B) Photo taken during experimentation using the setup shown in A. (C) Photo of the cobble surface where tar can be scraped off and the stone tool used for scraping. (D) Photo of a 0.62-g piece of tar produced in a single 3-h session (including bark collection).

Original discovery of tar by N may have involved this method; the application of tar for hafting purposes requires more complex excavation

Scientific parsimony: You can produce tar glue easily

- ▶ Patrick Schmidt, et al., 2019: demonstrate that recognizable amounts of birch tar were likely a relatively frequent byproduct of burning birch bark (a natural tinder) under common, i.e., aerobic, conditions.
- ▶ When birch bark burns close to a vertical to subvertical hard surface, such as an adjacent stone, birch tar is naturally deposited and can be easily scraped off the surface.
- ▶ Thus, the presence of birch tar alone cannot indicate the presence of modern cognition and/or cultural behaviors in Neanderthals.

Use of Tar in composite tools

- ▶ In the 1970s archaeologists excavating another German brown coal mine at Königsau found two small black lumps from a lakeside occupation, dating around 85 to 74 ka.
- ▶ One had certainly been part of a composite tool: three surfaces bore imprints of a lithic tool, a wooden surface and the unmistakable whorls from a partial Neanderthal fingerprint.
- ▶ It was only in 2001 that chemical analysis identified unique biomarkers from birch trees; specifically, tar derived by cooking the bark in low-oxygen conditions.
- ▶ Today at least two other examples of Neanderthal-made birch tar are known. One was dredged from under the North Sea, before being picked up on an artificial Netherlands beach. A sizeable lump of birch tar still half-covering a flint flake, it was directly dated to around 50 ka. And in Italy between 200-300 Ka.

Birch-tar from Germany with fingerprint



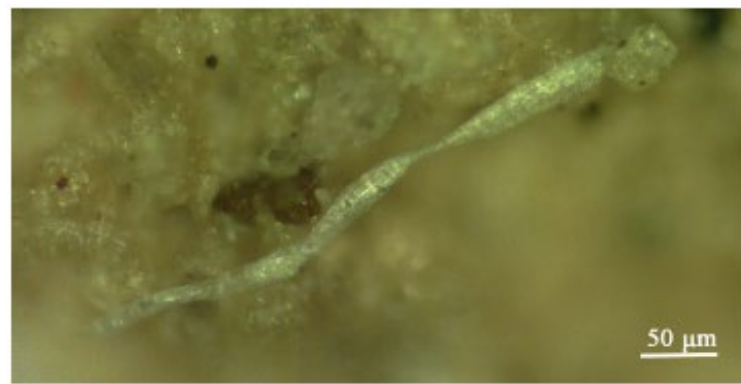
Birch-tar piece from Königsau, Germany. The impressions of wood (bottom) and stone (middle) implements, and a Neanderthal fingerprint (top), are visible.

Neandertal spears

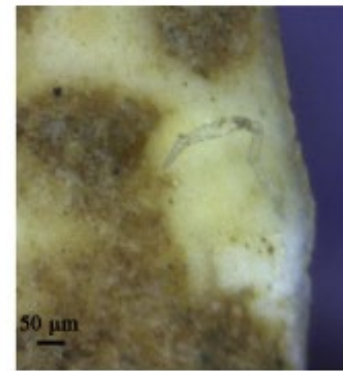
- ▶ Used large bayonet style spears
- ▶ Ns had stronger muscles in one arm than the other (evidence of 2 handed thrust)

N creation of Thread

Twisted Fibers: Abri du Maras



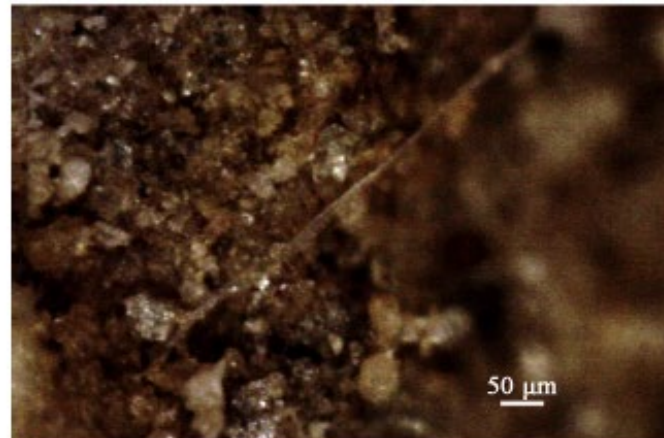
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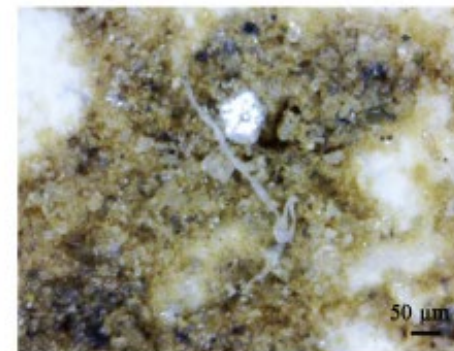
B



C



D



E

Fig. 6. Twisted fibers: A) photomosaic of twisted vessel element (N6 583) O.M. 100 \times ; B) twisted plant fiber (I7 66) O.M. 225 \times ; C) photomosaic of twisted plant fiber (F6 13) O.M. 485 \times , left edge disappears below chalcedony film; D) twisted plant fiber (L6 164) O.M. 225 \times ; E) twisted plant fiber (J6 36) O.M. 225 \times .

Abri du Maras: Thread

- ▶ Until recently, there was no evidence that Neanderthals made any kind of cord, but that changed in 2020 with the announcement of an astonishing find at Abri du Maras.
- ▶ Hidden on the underside of a flake was a natural encrustation containing a 0.2 in-long twist of plant fiber, either made from pine or juniper bark, or potentially the roots of these species.
- ▶ Furthermore, it's extremely fine: equivalent to threads in a hand-woven linen scarf.

N = Oldest Handmade String



3D microscope photos of cord fragment. (Hardy et al., Scientific Reports, 2020)

6.2 millimeter (0.24 inch) fiber fragment which is dated to ~41-52 Ka – so quite a bit older than the previous record holder, a 19,000-year-old fragment found in Israel.

N Twisted Cord: clear evidence of multistep process

- ▶ The excavated fragment of cord was derived from the inner bark of a conifer or evergreen tree, such as a pine or juniper. Ns had extensive knowledge of the growth and seasonality of these trees
- ▶ It was composed a classic three-ply thread fibers plied together: numerous fibers twisted counterclockwise, in an “S-twist,” to make yarn; and then three strands of yarn twisted in the opposite direction, clockwise with a “Z-twist,” to make cord.
- ▶ Lengths of cord could have been combined into larger structures such as bags, mats, nets, fabric, baskets, snares and even boats.

N Twisted Cord: requires complex cognition

- ▶ Cordage production entails context sensitive operational memory to keep track of each operation
- ▶ Demonstrates an 'infinite use of finite means' (like language) and requires a cognitive complexity similar to that required by human language.
- ▶ Dr. Hardy noted the cognitive parallels. "I can't have a sentence without words, and I can't have words without the individual sounds that carry meaning," he said. "So I can't have a rope or a cord or a bag or a net without the other steps along the way. **Cognitively, they are us,**" Dr. Hardy said.
- ▶ The production of cordage is complex and requires detailed knowledge of plants, seasonality, planning, etc.

N use of bone tools

N tools

- ▶ Cartmill & Smith: Neandertals were not limited in their capacity for technological innovation.
- ▶ For most of the past hundred years, our knowledge about the behavior of Neandertals was based almost solely on the stone tools they left behind.
- ▶ A single, well-crafted wooden spear is known from the Mousterian site of Lehringen, Germany, and two wooden “shovels” plus other indications of wood use are known from Abric Romani, Spain.
- ▶ The well-made spears from the pre-Mousterian site of Schöningen in Germany are strong evidence that such things were made during the Mousterian as well.

N bone technology

- ▶ Although bone is plentiful in some Neandertal sites and used pieces of bone are not rare, skillfully shaped bone tools are not common in Mousterian contexts.
- ▶ A few bone tools, including a bone point and implements (retouchers) used to do fine retouch work on stone tools, are found in Middle Paleolithic levels in southwestern Germany.
- ▶ Lissoirs: There are four carefully shaped bone tools that are identical in form and characteristics to later tools made by modern humans in the Aurignacian that were used to work hides.

Bone tech

- ▶ All these IUP bone occurrences fall toward the end of the Neandertal time span. They could reflect influence – or even manufacture – by modern humans.
- ▶ But the Pech-de-l'Azé I and Abri Peyrony tools are potentially earlier than the presence of modern humans.
- ▶ That Neandertals were making bone tools prior to the arrival of modern humans is also indicated by a multipurpose bone tool found at the site of the Grotte du Bison at Arcy-sur-Cure in France. This tool was excavated from a Mousterian occupation in association with Neandertal teeth

Szeletian bone points

- ▶ There are also **sites in Central Europe** broadly contemporaneous with the **Bohunician** (48-40 Ka) that **yield bone artifacts**.
- ▶ Many of them are classified as **Szeletian**, an industry that is most closely associated with a group of caves in the Bükk Mountains of Hungary, but is represented at sites in Moravia and southern Poland as well.
- ▶ The assemblages contain leaf-shaped stone points, bone points, side-scrapers, and others.

Szeletian bone points

- ▶ Despite the ambiguity of the skeletal remains and the presence of bone points, the **Szeletian is widely assumed to be the product of local Neanderthals.**
- ▶ The assumption is based on the fact that typical Middle Paleolithic artifacts are also found in the assemblages and the pattern appears to be analogous to that of the Châtelperronian, a group of assemblages from the Franco-Cantabrian region that contain a mixture of Middle and Upper Paleolithic artifacts and are associated with Neanderthal remains.

Bone tools

- ▶ For decades the orthodoxy claimed that antler, ivory or bone tools were virtually absent from the Middle Palaeolithic, such that they became markers for the emergence of 'modern' *H. sapiens* behavior.
- ▶ The Neanderthals emerged from a Lower Palaeolithic world where animal remains were already entangled with the production of lithics
- ▶ Their forebears clearly understood the utility of bone or antler hammers for the shallow flaking techniques needed to make bifaces.
- ▶ Mostly used for final shaping, retouching and resharpening of tools, in some sites they're extraordinarily numerous, yet absent in others.

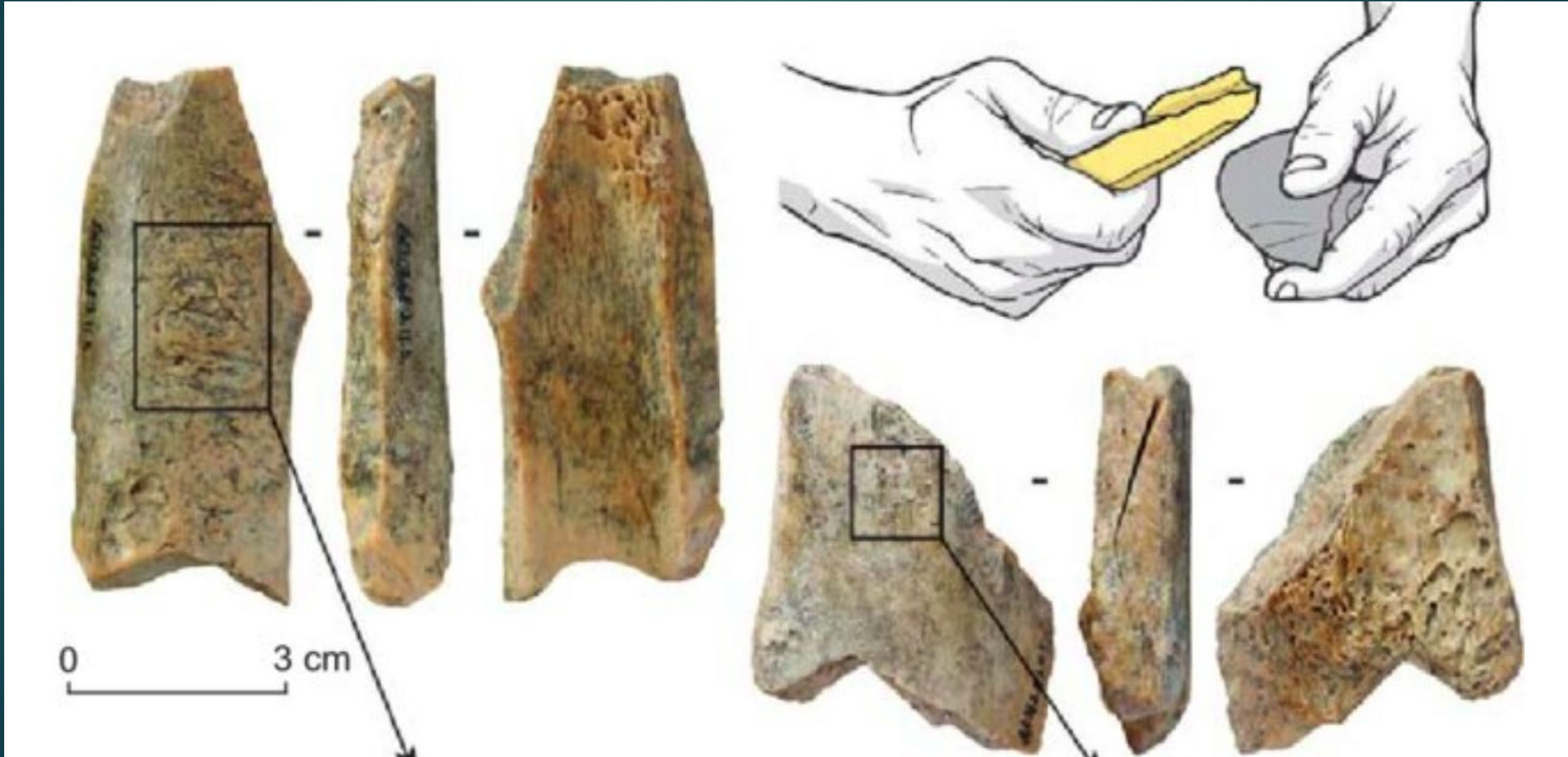
Schöningen bone hammers

- ▶ Outstanding evidence of the ascent of bone tools comes from the Spear Horizon at Schöningen.
- ▶ From an area of just 50 m² there were 15 massive bone hammers, some of which bore damage showing they'd also been used to smash other bones for their marrow (many of which had previously themselves been used to resharpen lithics).
- ▶ Neanderthals at Schöningen were obviously using large bones.

Retouchers

- ▶ At Schöningen horse carcasses were available in abundance, and their lower limb bones were definitely preferred for tools, especially multi-use objects. Bone shafts are perfect for spreading percussive energy.
- ▶ At **Les Pradelles, France:** Quina layers dating between 80 and 50 ka has so far identified some 700 retouchers. Two-thirds come from just one assemblage, where they're twice as common as lithics.
- ▶ Ns preferred specific bone types: bison bone over deer & aurochs over roe deer for retouchers. Or occasionally a saber tooth cat forelimb at Schöningen.

Bone retouchers from Denisova Cave

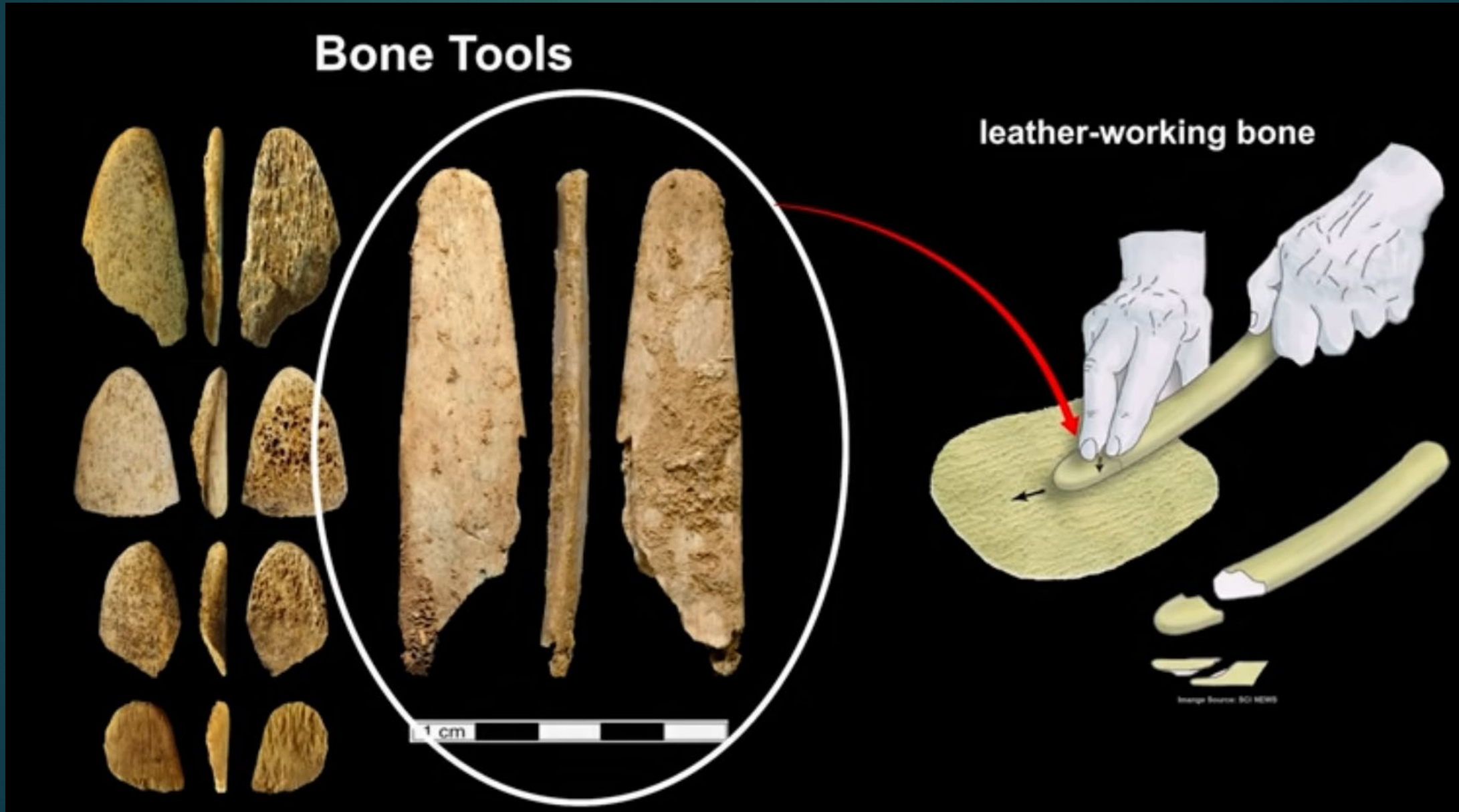


Neandertals made the first specialized bone tools in Europe

= Lissoirs

- ▶ If that's not convincing, then in addition to the **use-wear on lithics** from many sites is a recently discovered class of shaped bone tools, **lissoirs**.
- ▶ Made from rib ends, Neanderthals carved the bone to narrow it and form a standardized, symmetrical round tip.
- ▶ So far there are only five known examples, but they come from two sites: one from Pech de l'Azé, and four from Abri Peyrony, just 22 mi. away, where they're in different layers: one with bifaces, and another Discoid.

Bone lissoirs: only bison ribs, not nearby deer



Lissoirs

- ▶ They're all broken, but a nearly identical, complete object found in 1907 at La Quina may show their original form: it's strongly curved, and the opposite end was left unaltered.
- ▶ These tools are virtual clones of things called 'lissoirs' - smoothers - which are not only found in later H. sapiens cultures, but still used today to soften and burnish animal skins.
- ▶ Given how discriminating Neanderthals were about the animals and body parts their retouchers came from, it's perhaps not surprising they weren't just selecting ribs for lissoirs, but also by species. Collagen analysis found that all the surviving objects are either bison or aurochs, and strikingly, three are from a layer at Abri Peyrony that's 90 per cent reindeer.

N invention of bone 'lissoirs' for leather working; 51 Ka



Four views of the most complete lissoir found during excavations at the Neanderthal site of Abri Peyrony in France. Photograph: Abri Peyrony/Pech-de-l'Azé I Projects

The slender, curved implements called "lissoirs" were shaped from bison ribs and likely used to work animal hides to make them softer, tougher and more waterproof. Similar tools are still in use by leather workers today,

Found the first large piece of a lissoir at a cave called Pech-de-l'Azé I on a tributary of the Dordogne in southwest France, dated to 51 Ka;

Ns were excellent judges of quality.

- ▶ N concern for selection and quality was evident in all their raw materials.
- ▶ In Belgium, took only 4 longest shards from smashed bear femur.
- ▶ At Schöningen, took 75% of bone tools from left side of horses (easier to hold if right-handed?)
- ▶ One remaining puzzle exists. While individual retouchers were more intensively used in some techno-complexes, especially Quina, there's no obvious explanation for why some sites have huge numbers but others hardly any.
- ▶ Ns were choosing bone types for specific tasks.

Ns traveled extensively

- ▶ Many of the things Neanderthals made moved considerable distances.
- ▶ Tree ring data shows that the Schöningen spruce spears certainly weren't carved by the lake but were felled in summer at higher altitude (probably in the nearby Harz Mountains).
- ▶ So far there's no hard data that bone tools were transported, but considering Neanderthals would have needed to resharpen lithics while on the move, they probably were.

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