Origin of Our Species

Early Humans in Britain in last 1 Ma
+
Huxley Lecture 2023
- Prof Chris Stringer
+
Multiple other lectures

Compiled by
Charles J Vella, PhD
March 2024

Final Rank Ordering of Your Interests for 2024 HE group

- 1st run: Origin of MHs = 6, Myths of HE = 4
- 2nd run: Pre-homo hominins 3, Myths 2, Fossilizations 2
-

  1 Pre-Homo hominins 222
  - 2 Great Myths of Human Evolution 1111 22
  - 3 Fossilization And Dating in Human Evolution 22
  - 4 Origin of Modern Humans - Chris Stringer 111111 2
  - 5 Any topics or books you want to review

Question

- Science Updates
- Large number of studies in last 4 months
- Question of when to present them
- Continue 1 hour update, 1 hour topic
- Or occasionally add extra 2 hour session

MtDNA puzzles

mtDNA issues

- Ron Arenson: H. heidelbergensis fits in with Neanderthals and MH - as I understand it H heidelbergensis is ancestral to Neandertals but not us.
- And that mtDNA and nDNA don’t show the same hierarchy - possibly related to the inclusion of mtDNA from MH into neandertal early on.
- As I understand it, ancestral Eve (mtDNA) and ancestral Adam (nuclear DNA) seem quite different. And the separation of MH and Denisovans appear earlier than MH and Neanderthals, yet Denisovans and Neanderthals are close cousins and their separation was quite recent.

mtDNA issues

- CJV response:
- I think I now understand your puzzlement, which was mine from the time the Sima de los Huesos mtDNA was first analyzed as being more Denisovan, but their nuclear DNA is Neandertal. Also relates to why N mtDNA turned out to be from MH. It appears that in introgressions, MtDNA can later be swapped out for a better version via natural selection.

D mt DNA

- The D mtDNA being older than the N mtDNA first came from the 2010 Krause study: "The complete mitochondrial DNA genome of an unknown hominin from southern Siberia" which compares chimps, N, D, and MH mt DNA, states: Assuming an average divergence of human and chimpanzee mtDNAs of 6 million years ago, the date of the most recent common mtDNA ancestor shared by the Denisova hominin, Neanderthals and modern humans is approximately one million years ago (mean 1,040,900 years ago; 779,300–1,313,500 years ago), or twice as deep as the most recent common mtDNA ancestor of modern humans and Neanderthals (mean 465,700 years ago; 321,200–618,000 years ago). "

mtDNA

- Although the absolute dates depend on several assumptions and are subject to uncertainty, the fact that the divergence of the Denisova hominin mtDNA is about twice as old as the divergence of Neanderthal and modern human mtDNAs is robust to most assumptions."
- Sima Ns at 430 Ka; with D mtDNA
- Rogers study: N-D split at 744 Ka; implies N-MH split was earlier
- J. Hublin, who argues that Neanderthal features emerged gradually in Europe, over an interval that began 500–600 Ka. C. Stringer would argue for earlier date.

mtDNA

- Also: "Although nuclear DNA sequences are needed to clarify definitively the relationship of the Denisova individual to present-day humans and Neanderthals, the divergence of the Denisova mtDNA lineage on the order of one million years shows that it was distinct from the initial radiation of H. erectus that first left Africa 1.9 Myr ago, and perhaps also from the taxon H. heidelbergensis, if the latter is the direct ancestor of Neanderthals.
- An unambiguous association of the Denisova mtDNA with morphologically defined hominin taxa awaits determination of mtDNA sequences from more complete skeletal remains."

CJV understanding

- Originally I took the 1-million-year-old D mtDNA as indicating it came from the 4-6% H. erectus DNA found in Ds. But Krause seems to imply that this was not the origin of the mtDNA and we still await explanation of the origin of this D mtDNA.
- My understanding is that the LCA of MH and Ns is yet to be determined. They split off from each other circa 700 Ka? (or earlier) and then Ns and Ds split later at 400-500 Ka. How you can have D mtDNA being 1 Ma old, while N mtDNA is not, is a still a puzzle to me.
- Remember that Ns got their mtDNA and Y chromosome from MHs after 300 Ka; and it still is present in the late Ns
- This is as far as I have gotten.
- Natural selection has played some interesting shifts in N, D, and MH DNA.

Prufer et al 2013

- Prufer et al. 2013 article which discusses archaic introgression into Denisovans.
- Core paragraph: "…we considered a scenario where Denisovans received gene flow from a hominin whose ancestors diverged deeply from the lineage leading to Neanderthals, Denisovans and present-day humans. We find that this scenario is consistent with the data, as also suggested by others, and estimate that 2.7-5.8%...of the Denisova genome comes from this putative archaic hominin which diverged from the other hominins 0.9-1.4 million years ago. An approximate Bayesian computation again supports the third scenario and estimates that 0.5-8% of the Denisovan genome comes from an unknown hominin which split from other hominins between 1.1 and 4 million years ago."
- This study includes famous graphic:

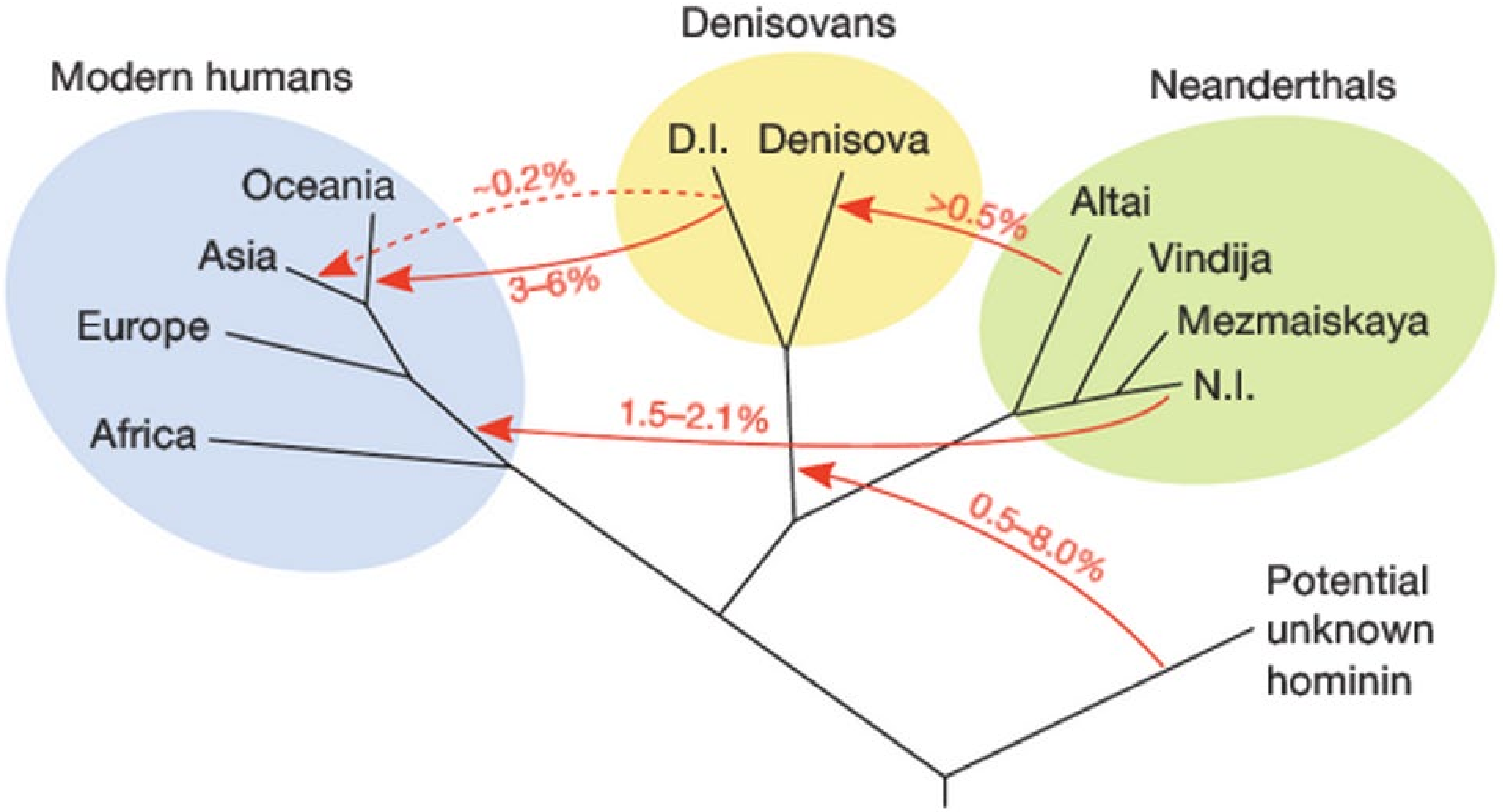

Figure 8 | A possible model of gene flow events in the Late Pleistocene. The

R. Cann 1987 study of mtDNA

- 1987, R. Cann: all current human mtDNA originated from a single population from Africa, at the time dated to between 140,000 and 200,000 years ago = today's Haplogroup L
- Mitochondrial Eve is the most recent common matrilineal ancestor for all modern humans; Mitochondrial Eve: had at least two daughters who both have unbroken *female* lineages that have survived to the present day.
- As of 2015, estimates of the age of the Y-MRCA range around 200,000 to 300,000 years ago, roughly consistent with the emergence of anatomically modern humans
- Another 2013 study (based on genome sequencing of 69 people from 9 different populations) reported the age of Mitochondrial Eve between 99 and 148 kya and that of the Y-MRCA between 120 and 156 kya.

N mtDNA

- Modern humans contributed mtDNA to the Neanderthal lineage, but not to any Denisovan mitochondrial genomes yet sequenced.

- The mtDNA sequence from the femur of a 400,000-year-old early N from the Sima de los Huesos Cave in Spain was found to be related to those of Neanderthals and Denisovans, but closer to Denisovans, and the authors posited that this mtDNA represents an archaic sequence which was subsequently lost in Neanderthals due to replacement by a modern-human-related sequence.

- Although the ancestors of Neandertals at Sima de los Huesos carry mtDNA most closely related to that of Denisovans, the mtDNA and the Y chromosome of later Neandertals are more closely related to that of modern humans.

DNA Replacements

- Neandertals and modern humans share their mtDNA and Y chromosome from ancestors who lived around 410 ka and 370 ka, respectively, which is at least 100,000 years more recent than their estimated split time.

- Alternatively, divergent mtDNA could have also resulted from the persistence of an ancient mtDNA lineage which only went extinct in modern humans and Neanderthals through genetic drift. Modern humans contributed mtDNA to the Neanderthal lineage, but not to the Denisovan mitochondrial genomes yet sequenced. The mtDNA sequence from the femur of a 400,000-year-old "*H. heidelbergensis*" from the Sima de los Huesos Cave in Spain was found to be related to those of Neanderthals and Denisovans, but closer to Denisovans, and the authors posited that this mtDNA represents an archaic sequence which was subsequently lost in Neanderthals due to replacement by a modern-human-related sequence.

MH, N, D DNA

- Denisova 3's mtDNA differs from that of modern humans by 385 bases (nucleotides) out of approximately 16,500, whereas the difference between modern humans and Neanderthals is around 202 bases. In comparison, the difference between chimpanzees and modern humans is approximately 1,462 mtDNA base pairs.
- This suggested that Denisovan mtDNA diverged from that of modern humans and Neanderthals about 1,313,500–779,300 years ago; whereas modern human and Neanderthal mtDNA diverged 618,000–321,200 years ago. Krause and colleagues then concluded that Denisovans were the descendants of an earlier migration of *H. erectus* out of Africa, completely distinct from modern humans and Neanderthals.
- However, according to the nuclear DNA (nDNA) of Denisova 3, Denisovans and Neanderthals were more closely related to each other than they were to modern humans.

Various dates for D-N split based on molecular clock

- Using the percent distance from human–chimpanzee last common ancestor, Denisovans/Neanderthals split from modern humans about 804,000 years ago
- Using a mutation rate of 1×10^{-9} or 0.5×10^{-9} per base pair (bp) per year, the Neanderthal/Denisovan split occurred around either 236–190,000 or 473–381,000 years ago respectively.
- Using 1.1×10^{-8} per generation with a new generation every 29 years, the time is 744,000 years ago.
- Using 5×10^{-10} nucleotide site per year, it is 616,000 years ago

mtDNA

- According to M. Meyer, the <u>Sima de los Huesos sample is old enough that it could represent an ancestor to both Denisovans and Neanderthals</u>.
- However, it is also possible that H. heidelbergensis is not ancestral to either group, but later interbred with the Denisovan lineage.

Sima de los Huesos

- Most importantly, the Sima de los Huesos specimen is so old that it probably predates the population split time between Denisovans and Neanderthals, which is estimated to one-half to two-thirds of the time to the split between Neanderthals and modern humans, which is estimated to be 170 to 700 Ka ago.

- The Sima de los Huesos hominins may be related to the population ancestral to both Neanderthals and Denisovans. Considering the age of the Sima de los Huesos remains and their incipient Neanderthal-like morphology, this scenario seems plausible to us, but it requires an explanation for the presence of two deeply divergent mtDNA lineages in the same archaic group, one that later recurred in Denisovans and one that became fixed in Neanderthals, respectively

Gene flow

- Another possible scenario is that gene flow from another hominin population brought the Denisova-like mtDNA into the Sima de los Huesos population or its ancestors. Such a hominin group might have also contributed mtDNA to the Denisovans in Asia.
- Based on the fossil record, more than one evolutionary lineage may have existed in Europe during the Middle Pleistocene (780-126 Ma). Several fossils have been found in Europe as well as in Africa and Asia that are close in time to Sima de los Huesos but do not exhibit clear Neanderthal traits.
- Furthermore, there may have been relict populations of still earlier hominins, notably those classified as Homo antecessor.

Have I confused you enough yet?

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Charles J Vella, PhD
2024

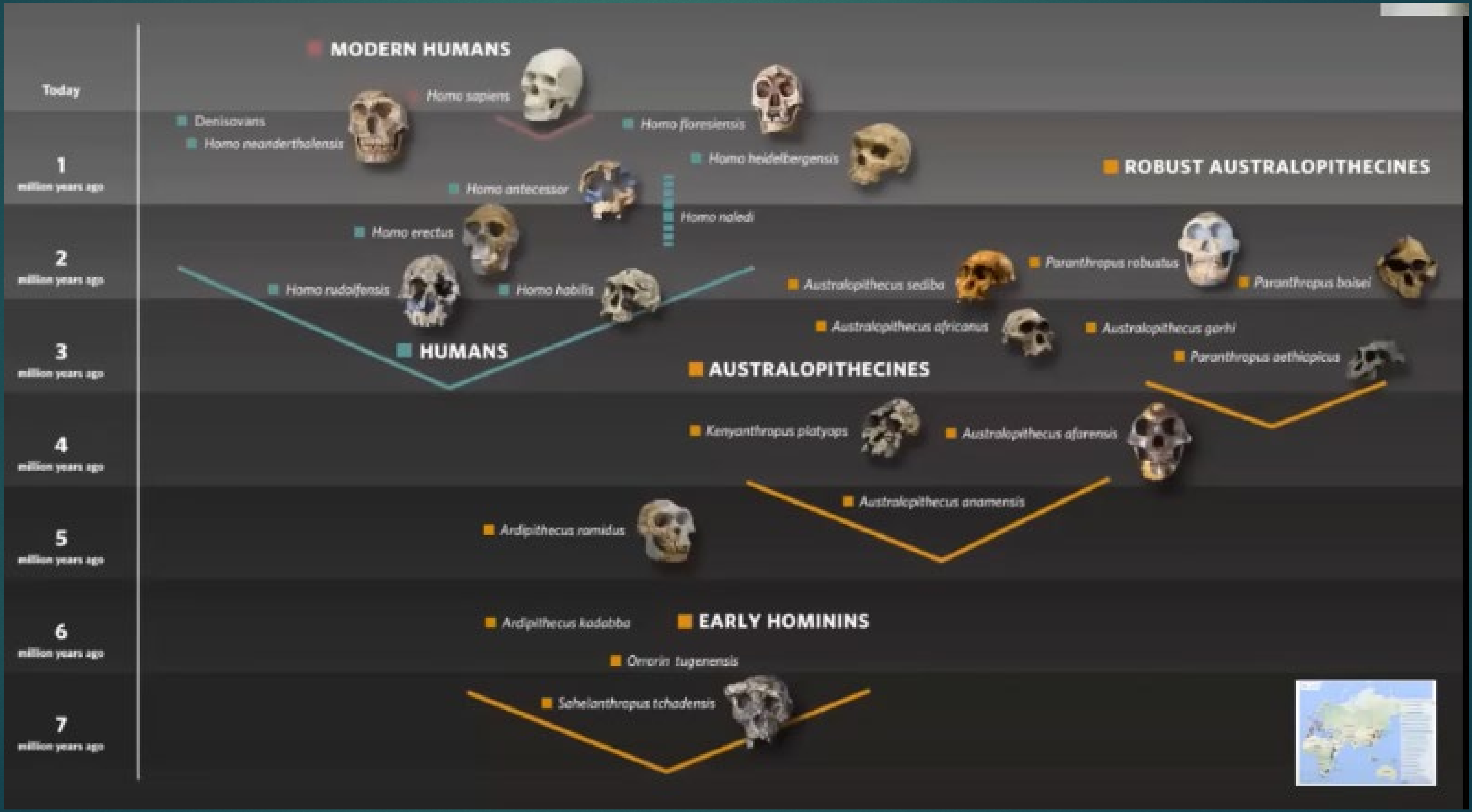
Chris Stringer

- B.Sc., University College London
- D.Sc., University of Bristol
- Ph.D. University of Bristol

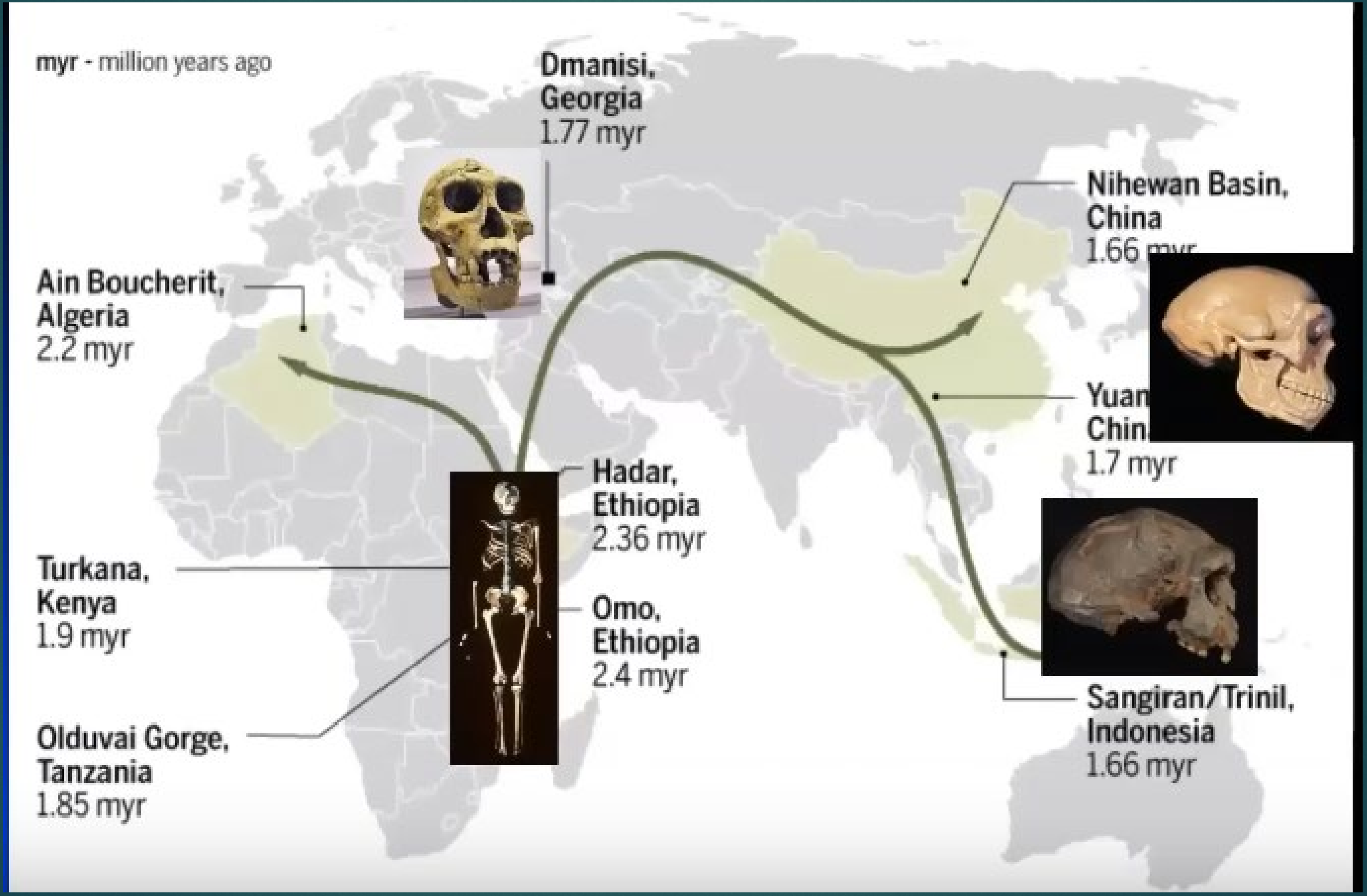
- 1973- Natural History Museum (curr. Research Leader in Human Origins)
- Director of the *Ancient Human Occupation of Britain* project (2001-2013)
- Co-Director of *the Pathways to Ancient Britain* project

- Hundreds of papers, >30,000 citation, h-index 94
  - "Origins of Modern Human Ancestry" in *Nature* (Feb.10, 2021)
- Fellow of the Royal Society

Early Humans in Britain in last 1 Ma: Springer heads the Ancient Human Occupation of Britain & Pathways to Ancient Britain Projects since 2001



Out of Africa 1 – H. erectus - 1.8 Ma?

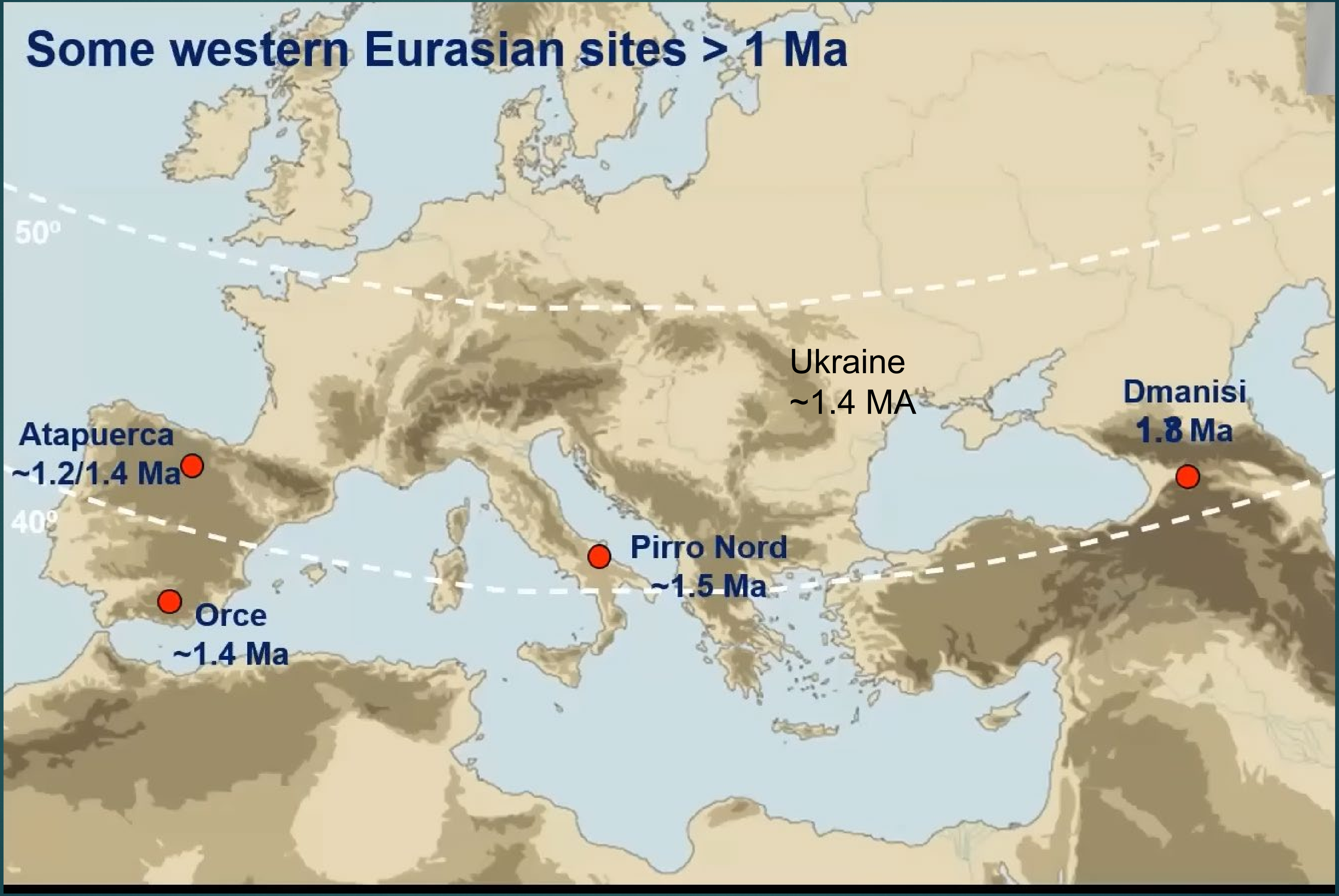


Major climate changes, esp. in last 100 Ka

You are here……

Many major and repeated climate changes in the last 2 million years

Some western Eurasian sites > 1 Ma



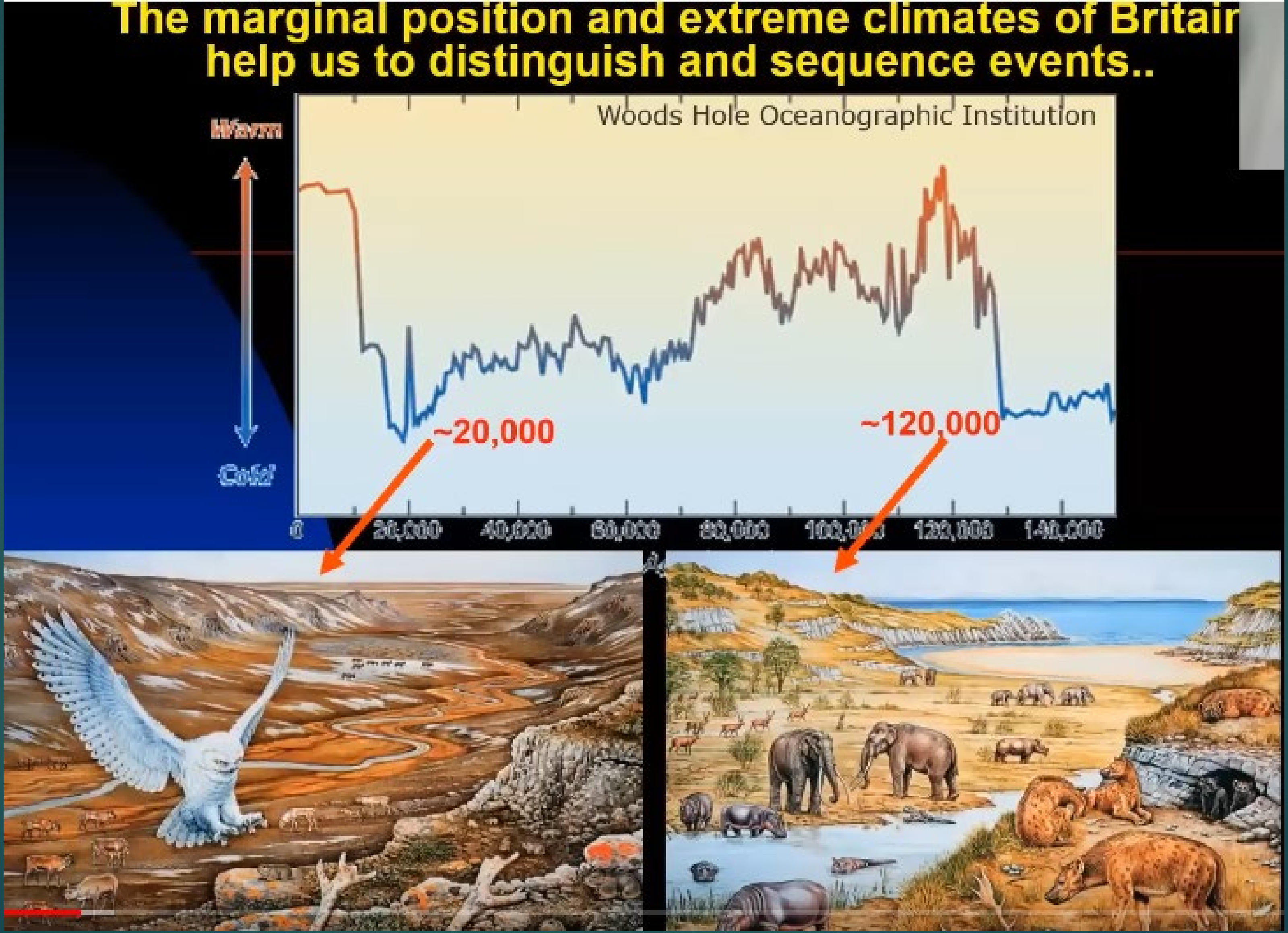
How and when did people first get to Britain? What did they need to survive?

Britain in last 1 M years

- Interglacial at 900 Ka – oldest dates of human occupation in Britain

An example of severe climate change in Britain: Three Cliffs Bay, Gower, S. Wales

No humans in Britain in either period

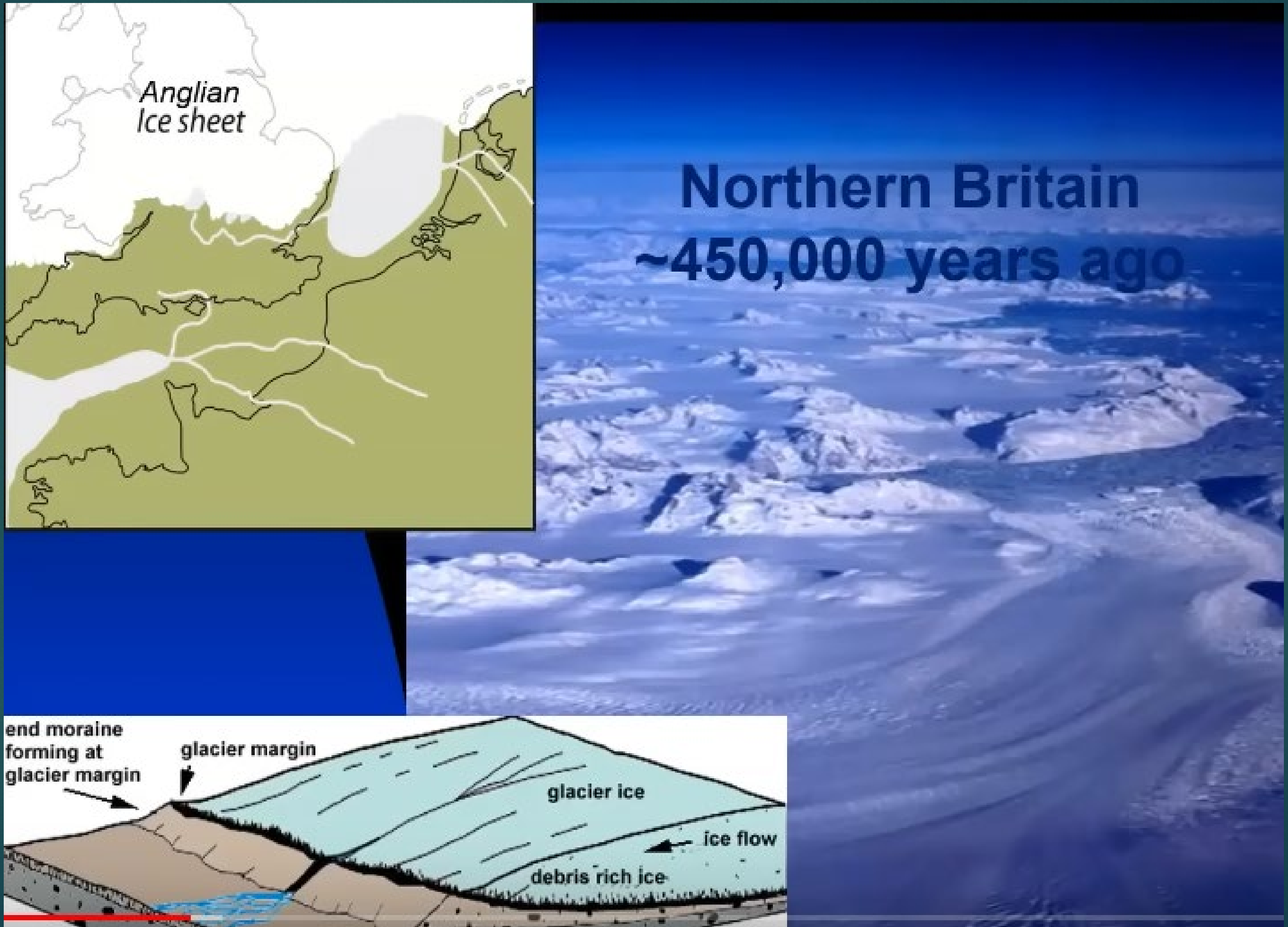


The marginal position and extreme climates of Britain help us to distinguish and sequence events..

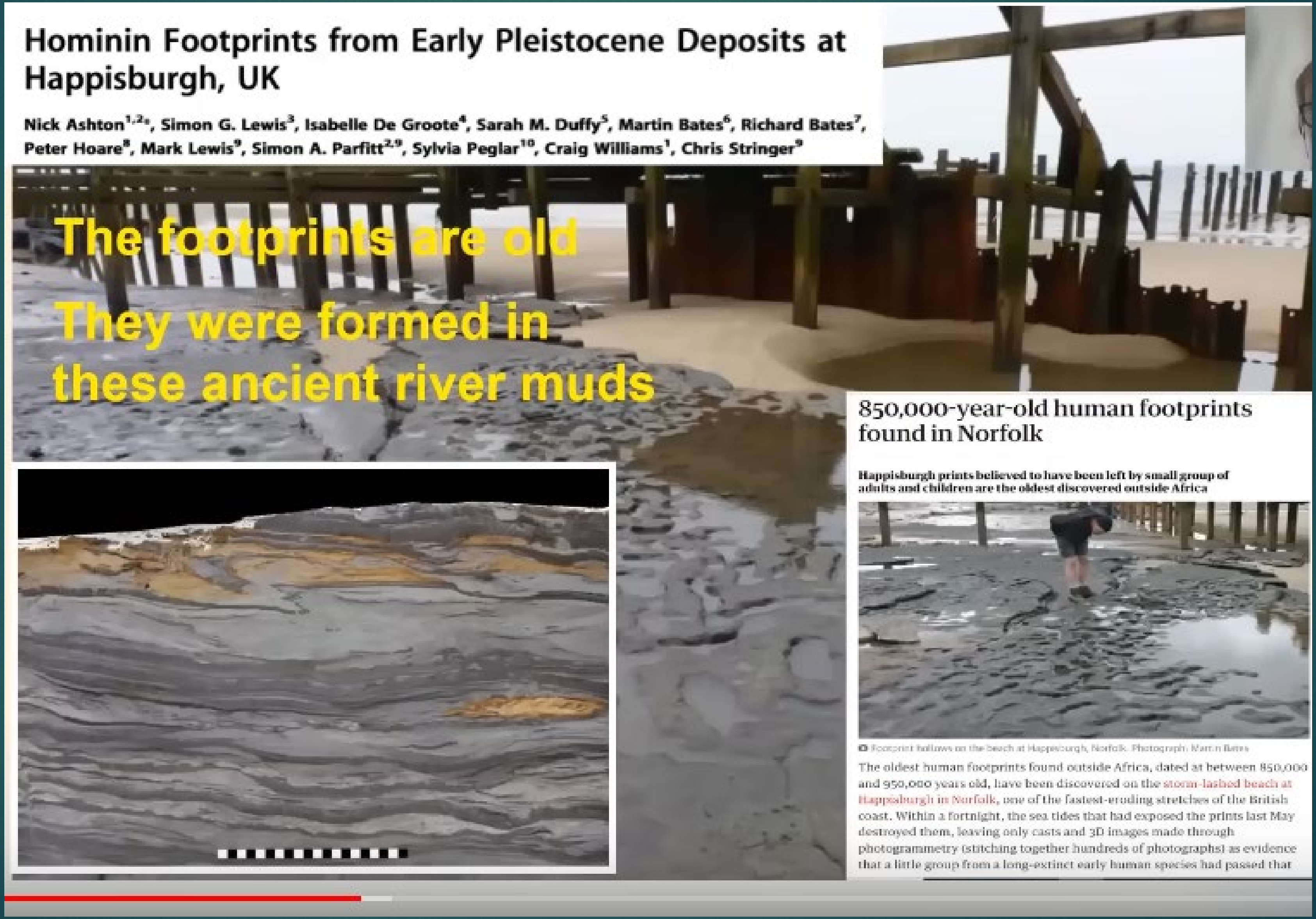
Peak of
Last
Glaciation:
Steppe-tundra;
Sea level drop

Peak of
interglacial

Repeated severe glaciations



Footprints at Happisburgh, UK – 850 Ka – along proto-river Thames



Hominin Footprints from Early Pleistocene Deposits at Happisburgh, UK

Nick Ashton[1,2*], Simon G. Lewis[3], Isabelle De Groote[4], Sarah M. Duffy[5], Martin Bates[6], Richard Bates[7], Peter Hoare[8], Mark Lewis[9], Simon A. Parfitt[2,9], Sylvia Peglar[10], Craig Williams[1], Chris Stringer[9]

The footprints are old

They were formed in these ancient river muds

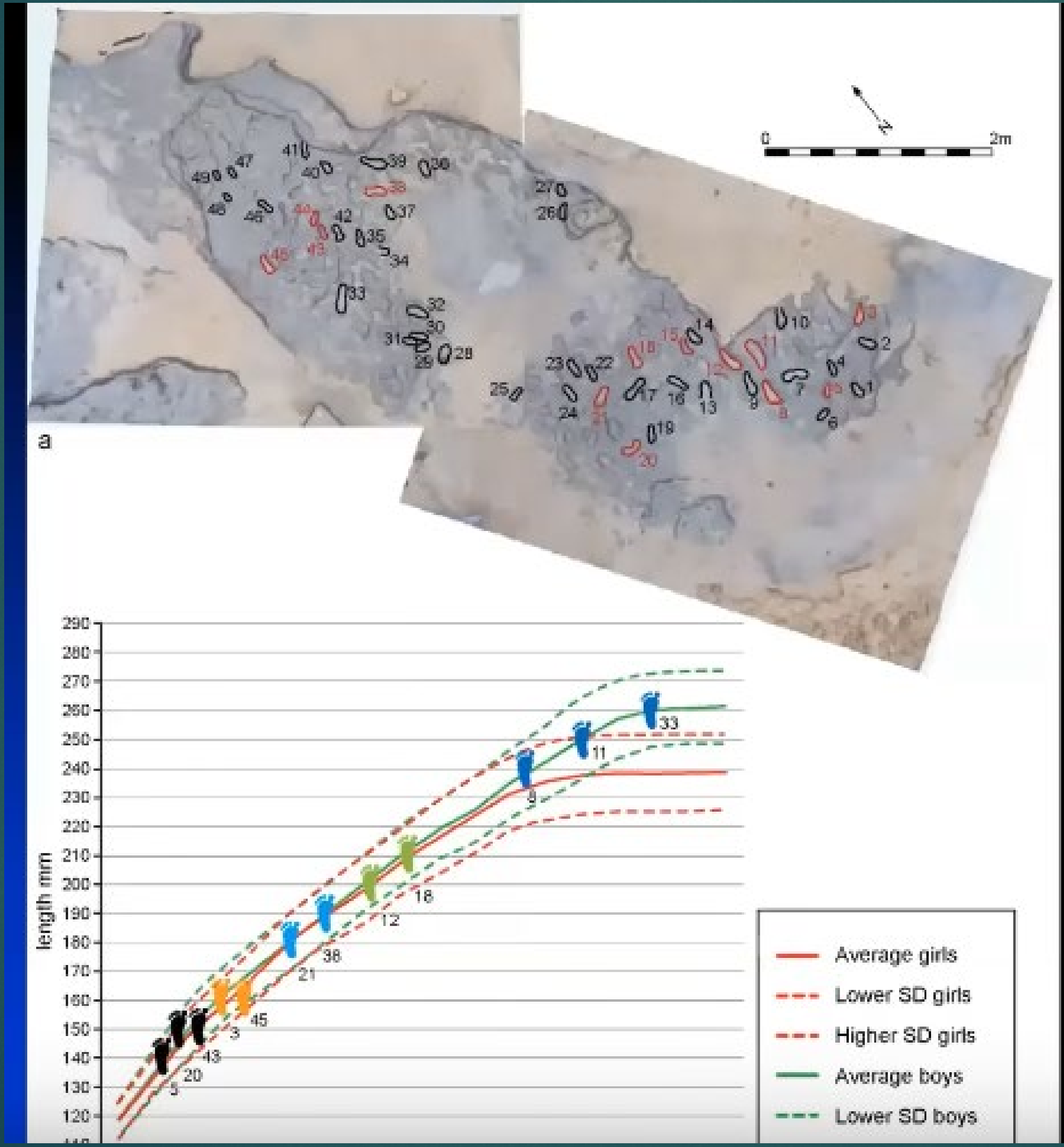
850,000-year-old human footprints found in Norfolk

Happisburgh prints believed to have been left by small group of adults and children are the oldest discovered outside Africa

Footprint hollows on the beach at Happisburgh, Norfolk. Photograph: Martin Bates

The oldest human footprints found outside Africa, dated at between 850,000 and 950,000 years old, have been discovered on the storm-lashed beach at Happisburgh in Norfolk, one of the fastest-eroding stretches of the British coast. Within a fortnight, the sea tides that had exposed the prints last May destroyed them, leaving only casts and 3D images made through photogrammetry (stitching together hundreds of photographs) as evidence that a little group from a long-extinct early human species had passed that

Oldest footprints outside of Africa – *H. antecessor or erectus*



Landbridge to Europe at 700 Ka; Acheulean tools at 600 Ka

Early Britons walked across a landbridge in warm times about 700,000 years ago

Pakefield: a 'Mediterranean' environment MIS 17

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Research

On the earliest Acheulean in Britain: first dates and *in-situ* artefacts from the MIS 15 site of Fordwich (Kent, UK)

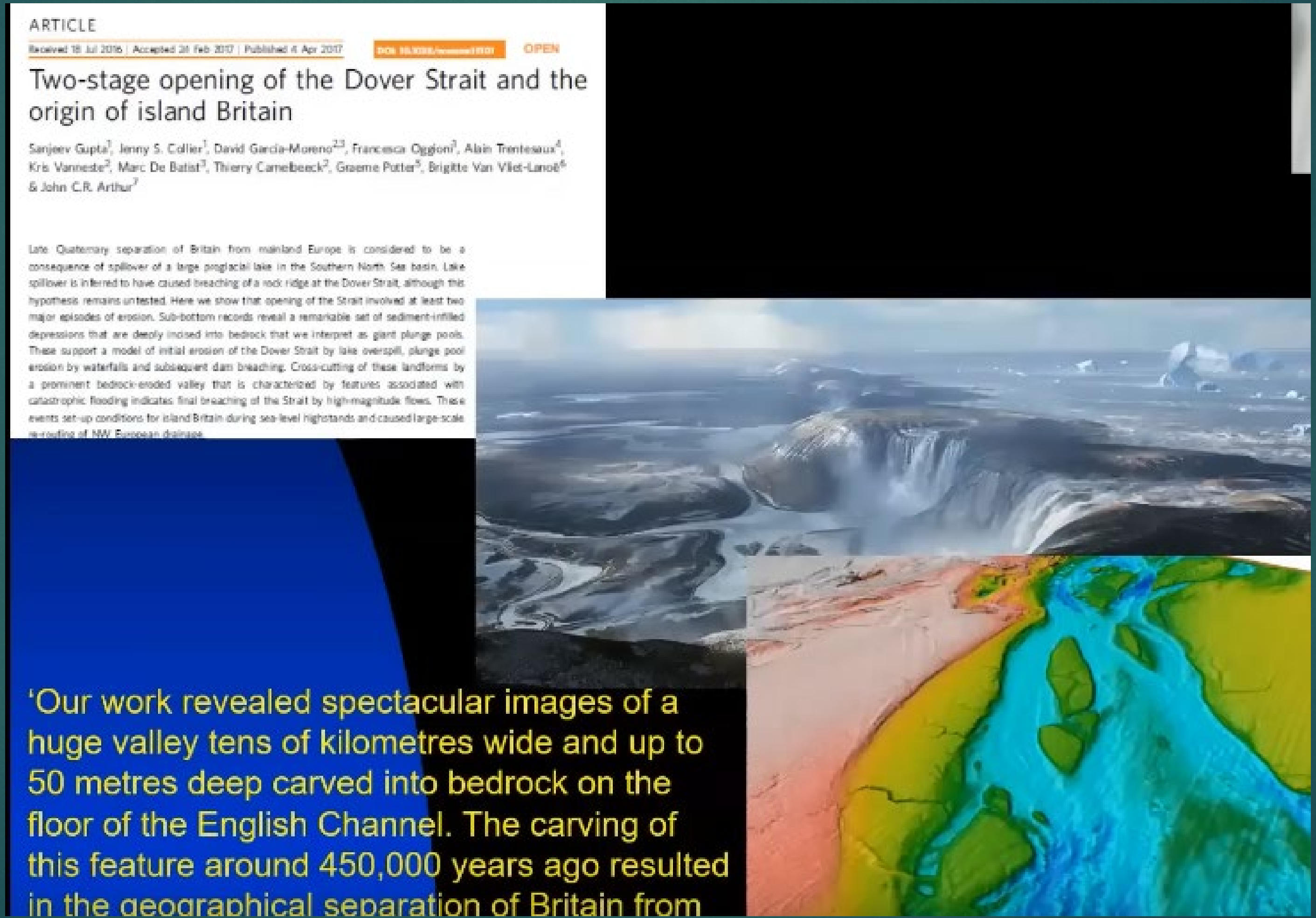
Mauer mandible, type specimen of H. heidelbergensis, 610 Ka = Same time period – possibly in Britain?

Boxgrove – 480 Ka

H. heidelbergensis? 800-480 Ka

?*Homo heidelbergensis* at
Boxgrove (Sussex)
~480,000 yrs

Protoglacial lake erupts creating beginning of English Channel, separating Britain from Europe ~450 Ka



ARTICLE

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OPEN

Two-stage opening of the Dover Strait and the origin of island Britain

Sanjeev Gupta[1], Jenny S. Collier[1], David Garcia-Moreno[2,3], Francesca Oggioni[1], Alain Trentesaux[4], Kris Vanneste[2], Marc De Batist[3], Thierry Camelbeeck[2], Graeme Potter[5], Brigitte Van Vliet-Lanoë[6] & John C.R. Arthur[7]

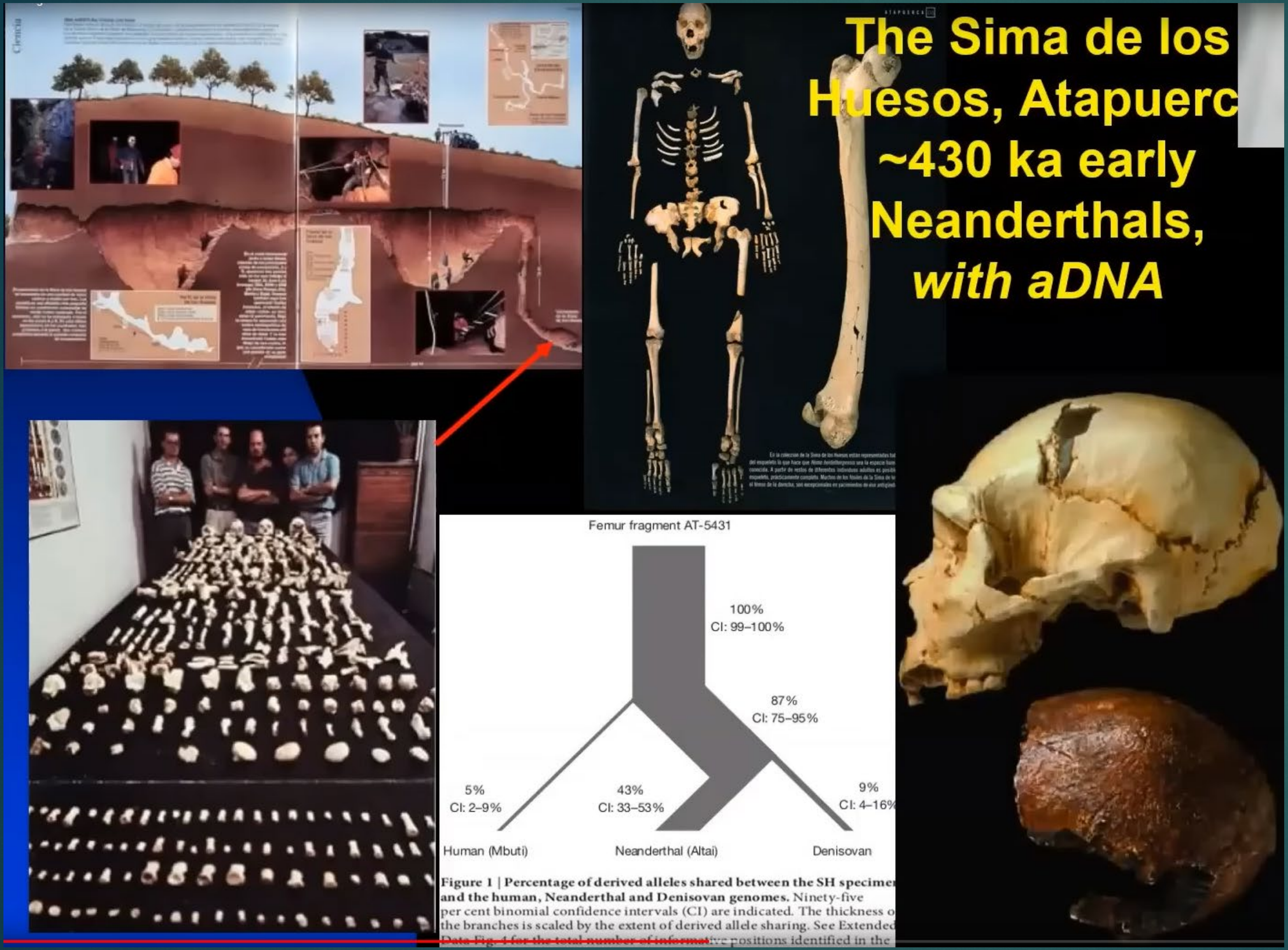
Late Quaternary separation of Britain from mainland Europe is considered to be a consequence of spillover of a large proglacial lake in the Southern North Sea basin. Lake spillover is inferred to have caused breaching of a rock ridge at the Dover Strait, although this hypothesis remains untested. Here we show that opening of the Strait involved at least two major episodes of erosion. Sub-bottom records reveal a remarkable set of sediment-infilled depressions that are deeply incised into bedrock that we interpret as giant plunge pools. These support a model of initial erosion of the Dover Strait by lake overspill, plunge pool erosion by waterfalls and subsequent dam breaching. Cross-cutting of these landforms by a prominent bedrock-eroded valley that is characterized by features associated with catastrophic flooding indicates final breaching of the Strait by high-magnitude flows. These events set-up conditions for island Britain during sea-level highstands and caused large-scale re-routing of NW European drainage.

'Our work revealed spectacular images of a huge valley tens of kilometres wide and up to 50 metres deep carved into bedrock on the floor of the English Channel. The carving of this feature around 450,000 years ago resulted in the geographical separation of Britain from

~400 Ka: 10,000 Acheulean axes at Swanscombe, with partial female skull

Swanscombe lies in the earliest post-diversion (post-Anglian) terrace of the Thames and therefore probably dates to MIS11 ~400ka

Swanscombe 1955 – John Wymer points to the location of the newly discovered right parietal, while the men in the background stand where the other two skull bones were found in 1935 and 1936 (C. Stringer, 2006.

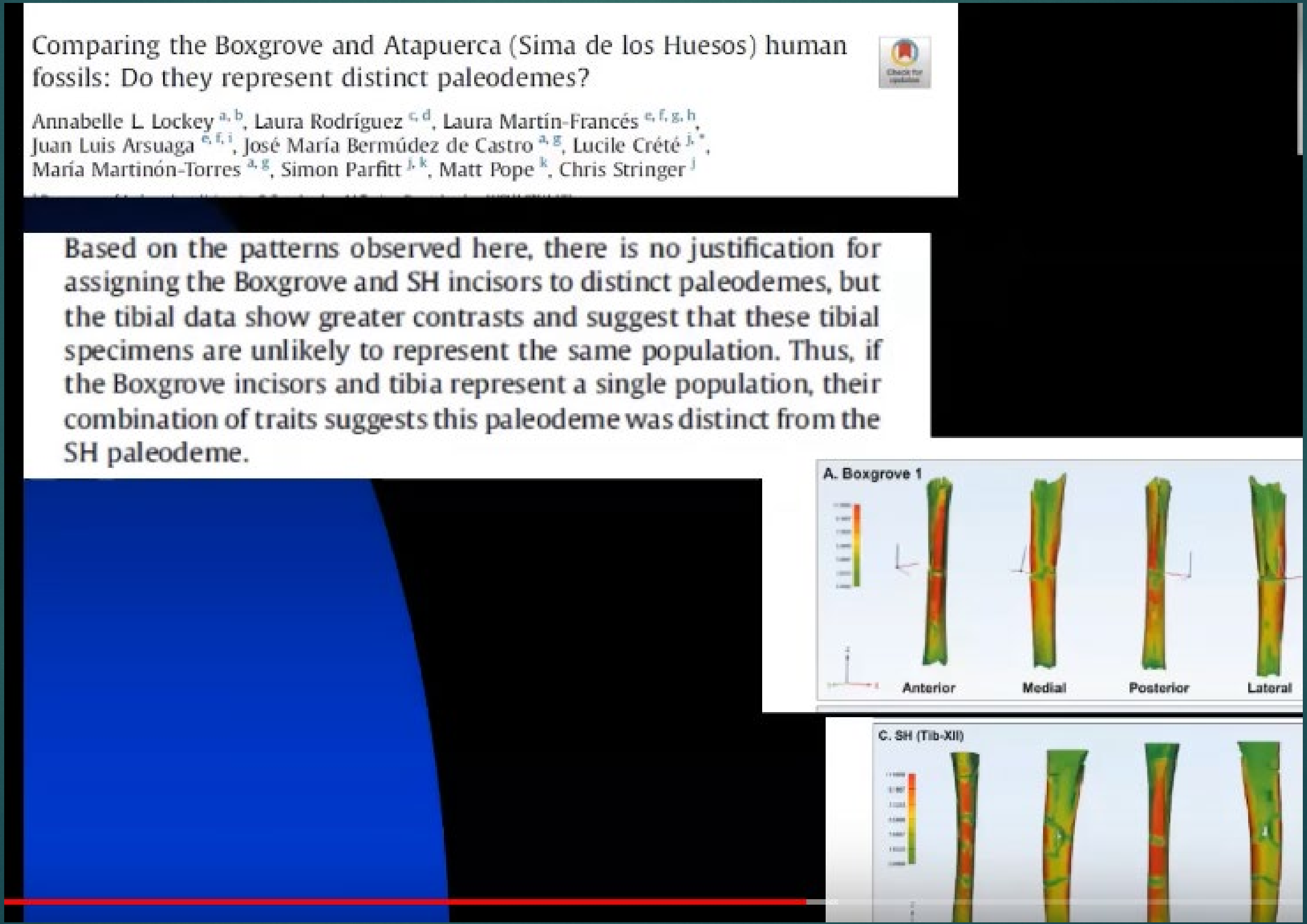


The Sima de los Huesos, Atapuerc ~430 ka early Neanderthals, *with aDNA*

Figure 1 | Percentage of derived alleles shared between the SH specime and the human, Neanderthal and Denisovan genomes. Ninety-five per cent binomial confidence intervals (CI) are indicated. The thickness o the branches is scaled by the extent of derived allele sharing. See Extended Data Fig. 4 for the total number of informative positions identified in the

Sima de los Huesos Ns are similar to Swanscombe skull – both have a suprainiac fossa

Boxgrove & Sima de los Huesos: similar but distinct populations (tibia similar, but not teeth)



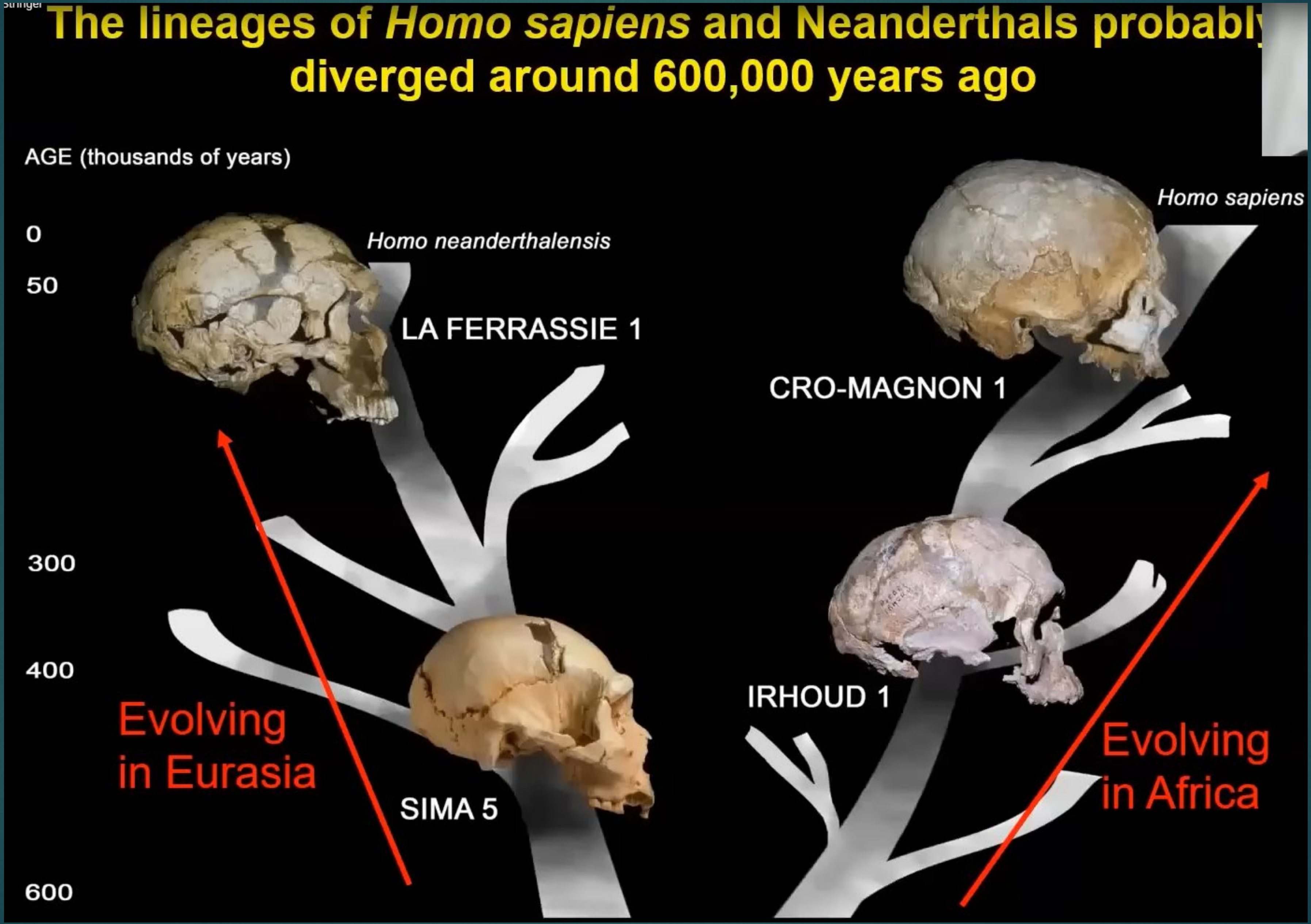
Comparing the Boxgrove and Atapuerca (Sima de los Huesos) human fossils: Do they represent distinct paleodemes?

Annabelle L. Lockey [a, b], Laura Rodríguez [c, d], Laura Martín-Francés [e, f, g, h], Juan Luis Arsuaga [e, f, i], José María Bermúdez de Castro [a, g], Lucile Crété [j, *], María Martinón-Torres [a, g], Simon Parfitt [j, k], Matt Pope [k], Chris Stringer [j]

Based on the patterns observed here, there is no justification for assigning the Boxgrove and SH incisors to distinct paleodemes, but the tibial data show greater contrasts and suggest that these tibial specimens are unlikely to represent the same population. Thus, if the Boxgrove incisors and tibia represent a single population, their combination of traits suggests this paleodeme was distinct from the SH paleodeme.

Stringer

The lineages of *Homo sapiens* and Neanderthals probabl diverged around 600,000 years ago



120-80 Ka – hippos in Thames; Britain an island; no humans

Stringer

120,000 years ago, hippos (but no humans?) were swimming in th River Thames..

Hippos and elephants were living as far North as Yorkshire, 120,000 years ago - summers were about 1° warmer, with sea levels some 5 metres higher…

Doggerland (60-8 Ka) – warming period doubled the size of England; then catastrophic release of water from a North American glacial lake and a tsunami from a submarine landslide off Norway inundated it


Doggerland fauna 60,000 year ago….

Ancient shorelines, ice sheets, and rivers are approximate.

Neandertals return to Britain at 60 Ka

Late Neanderthals in a cold Britain

Lynford Norfolk ~ 60 kya

La Cotte de St. Brelade, Jersey: teeth of 2 individuals, less than 48 Ka; hybrids

ringer

The morphology of the Late Pleistocene hominin remains from the site of La Cotte de St Brelade, Jersey (Channel Islands)

2021

Tim Compton [a,*], Matthew M. Skinner [b,c], Louise Humphrey [a], Matthew Pope [d], Martin Bates [e], Thomas W. Davies [c], Simon A. Parfitt [a,d], William P. Plummer [b], Beccy Scott [f], Andrew Shaw [g], Chris Stringer [a]

Less than 48 ka old

Figure 3. E.T. Nicolle shown standing on the level of th the ledge on which the teeth were found on the left Mollet. Reproduced with the kind permission of the So

Of the various scenarios that can be considered to explain the mix of features in the La Cotte teeth, we favor shared Neanderthal and *H. sapiens* ancestry. The likely dating of the fossils during a period of temporal overlap between these groups is consistent with

H. sapiens arrives in Britain; ~34 and ~15 Ka

Stringer

Early *H. sapiens* in Britain ~34 + ~15 ka

Paviland Cave Gower

Church Hole Creswell

Gough's Cave Somerset

R. Jacobi

captain Simon Hayward told how he became the innocent ... national drugs ring.

From RONALD RICKETTS in Stockholm

Ancient Brits ate children

What they gorged in Cheddar

THE discovery of remains from a cannibals' feast held 12,000 years ago was hailed today as the greatest find of its type in this country.

Archaeologists believe the bones and skulls discovered in caves at Cheddar, Somerset, are those of three adults and two children from the Stone Age.

The dismembered bodies had been hacked with flint knives and axes. Marks on the victims' skulls suggested the tongues and eyes had been cut out.

Victorians blasted the entrance of Gough's Cave.

One of the skulls is almost complete and fragments from another match parts of bone found 70 years ago.

Skeleton

nature ecology & evolution

Article

https://doi.org/10.1038/s41559-022-01883-z

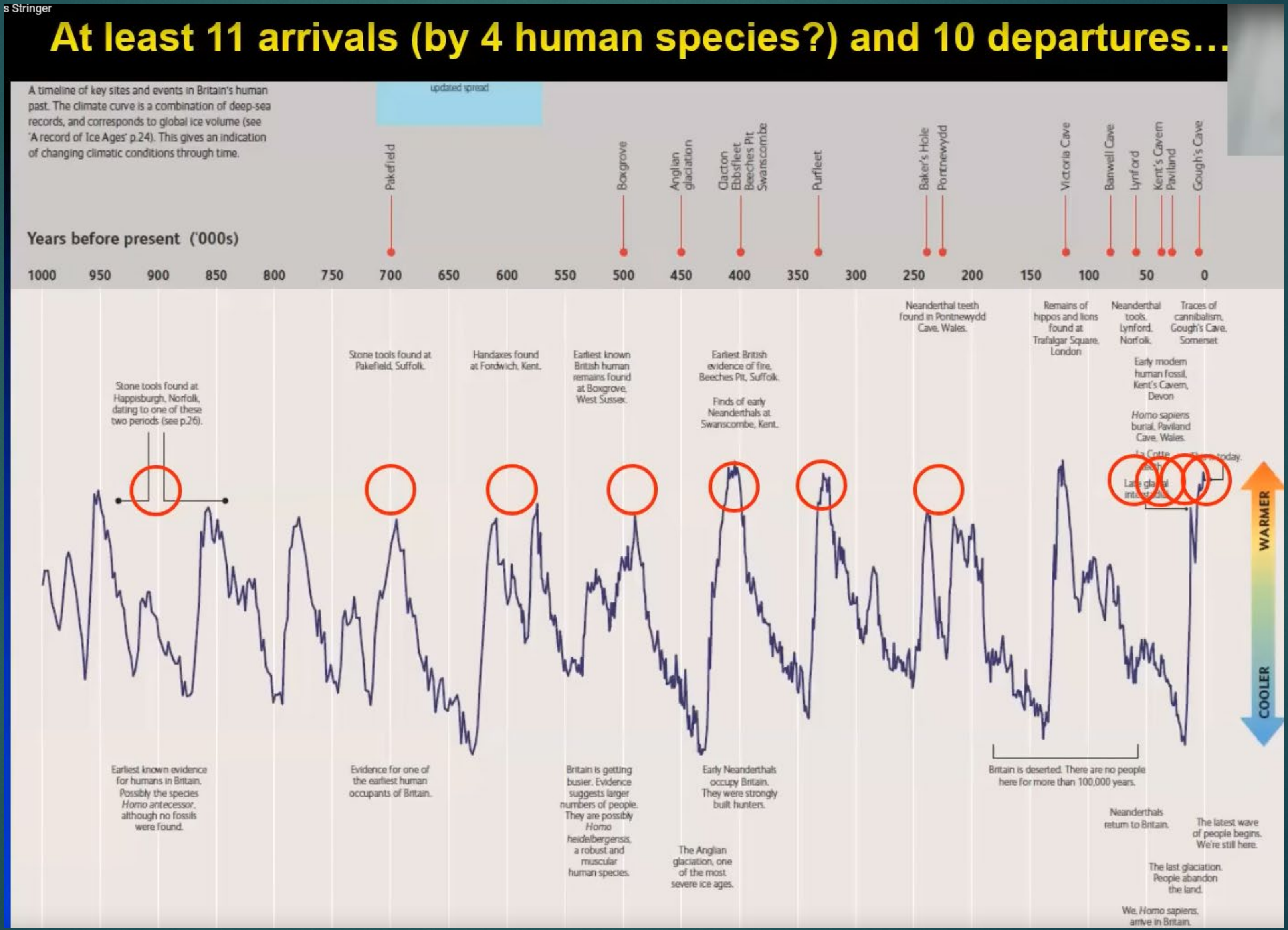
Dual ancestries and ecologies of the Late Glacial Palaeolithic in Britain

Received: 6 October 2021

Accepted: 16 August 2022

Sophy Charlton[1,2,12], Selina Brace[2,12], Mateja Hajdinjak[3,12], Rebecca Kearney[4,5], Thomas Booth[3], Hazel Reade[4], Jennifer Tripp[4,6], Kerry L. Sayle[7], Sonia B. Grimm[8], Silvia M. Bello[2], Elizabeth A. Walker[9],

In 900 K years, 11 arrivals (during interglacial periods) and 10 departures (during glacials) by 4 human species (H. antecessor, heidelbergensis, Ns, MHs)



s Stringer

At least 11 arrivals (by 4 human species?) and 10 departures…

A timeline of key sites and events in Britain's human past. The climate curve is a combination of deep-sea records, and corresponds to global ice volume (see 'A record of Ice Ages' p.24). This gives an indication of changing climatic conditions through time.

Stone tools found at Happisburgh, Norfolk, dating to one of these two periods (see p.26).

Stone tools found at Pakefield, Suffolk.

Handaxes found at Fordwich, Kent.

Earliest known British human remains found at Boxgrove, West Sussex.

Earliest British evidence of fire, Beeches Pit, Suffolk.

Finds of early Neanderthals at Swanscombe, Kent.

Neanderthal teeth found in Pontnewydd Cave, Wales.

Remains of hippos and lions found at Trafalgar Square, London

Neanderthal tools, Lynford, Norfolk.

Traces of cannibalism, Gough's Cave, Somerset

Early modern human fossil, Kent's Cavern, Devon

Homo sapiens burial, Paviland Cave, Wales.

Earliest known evidence for humans in Britain. Possibly the species *Homo antecessor*, although no fossils were found.

Evidence for one of the earliest human occupants of Britain.

Britain is getting busier. Evidence suggests larger numbers of people. They are possibly *Homo heidelbergensis*, a robust and muscular human species.

Early Neanderthals occupy Britain. They were strongly built hunters.

The Anglian glaciation, one of the most severe ice ages.

Britain is deserted. There are no people here for more than 100,000 years.

Neanderthals return to Britain.

The latest wave of people begins. We're still here.

The last glaciation. People abandon the land.

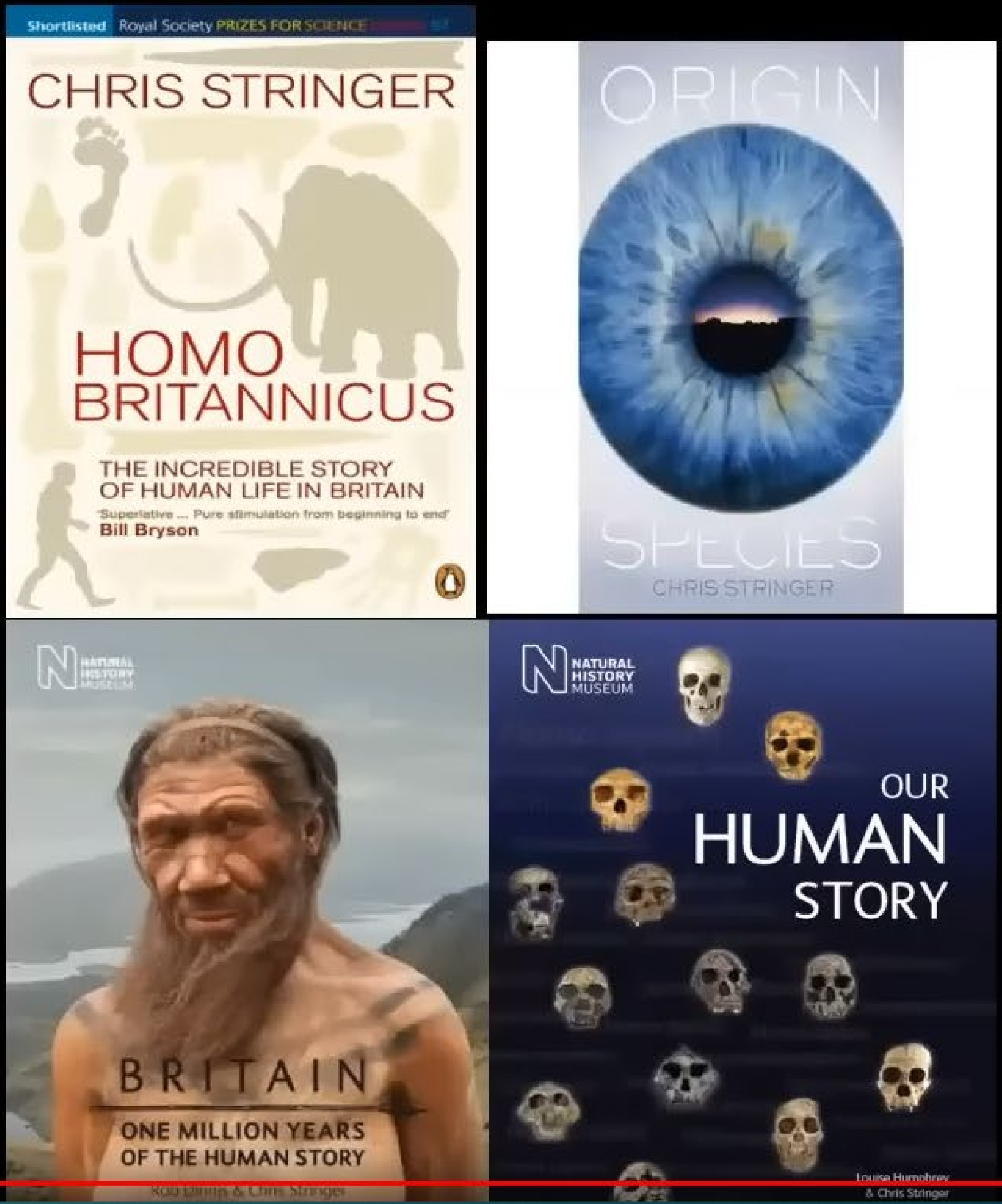
We, *Homo sapiens*, arrive in Britain.

Centre for Human Evolution Research (NHM)

AHOB
Ancient Human Occupation of Britain

PAB
PATHWAYS TO ANCIENT BRITAIN

@ChrisStringer65



Mostly Out of Africa: How, When, Where
Changing theories of Human Evolution

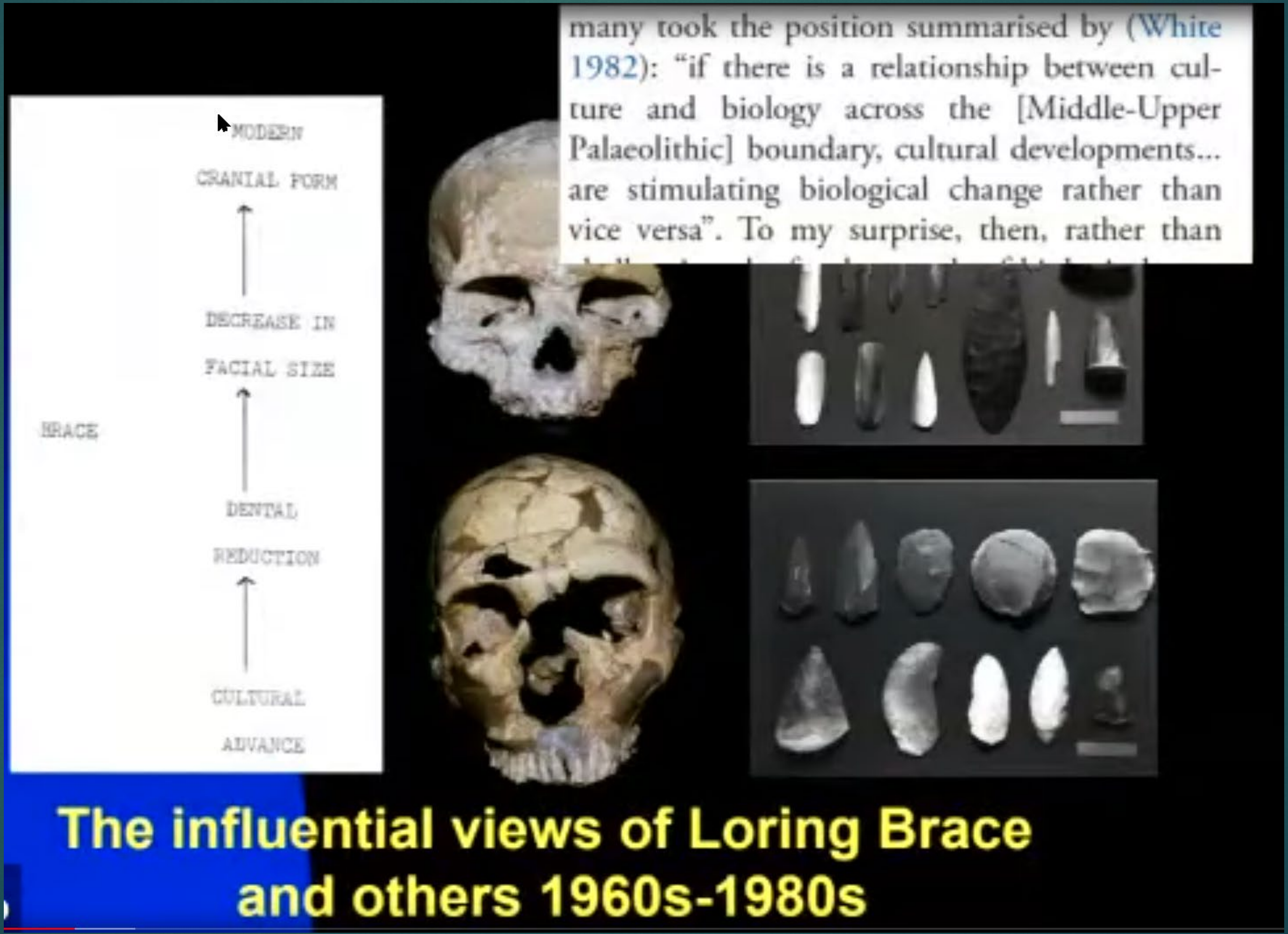
Huxley Lecture 2023

- Prof Chris Stringer

1960s: only 2 Homo species (MH, N), and a belief in a N evolutionary stage of MH origins

NHM exhibition Central Hall late 1960s

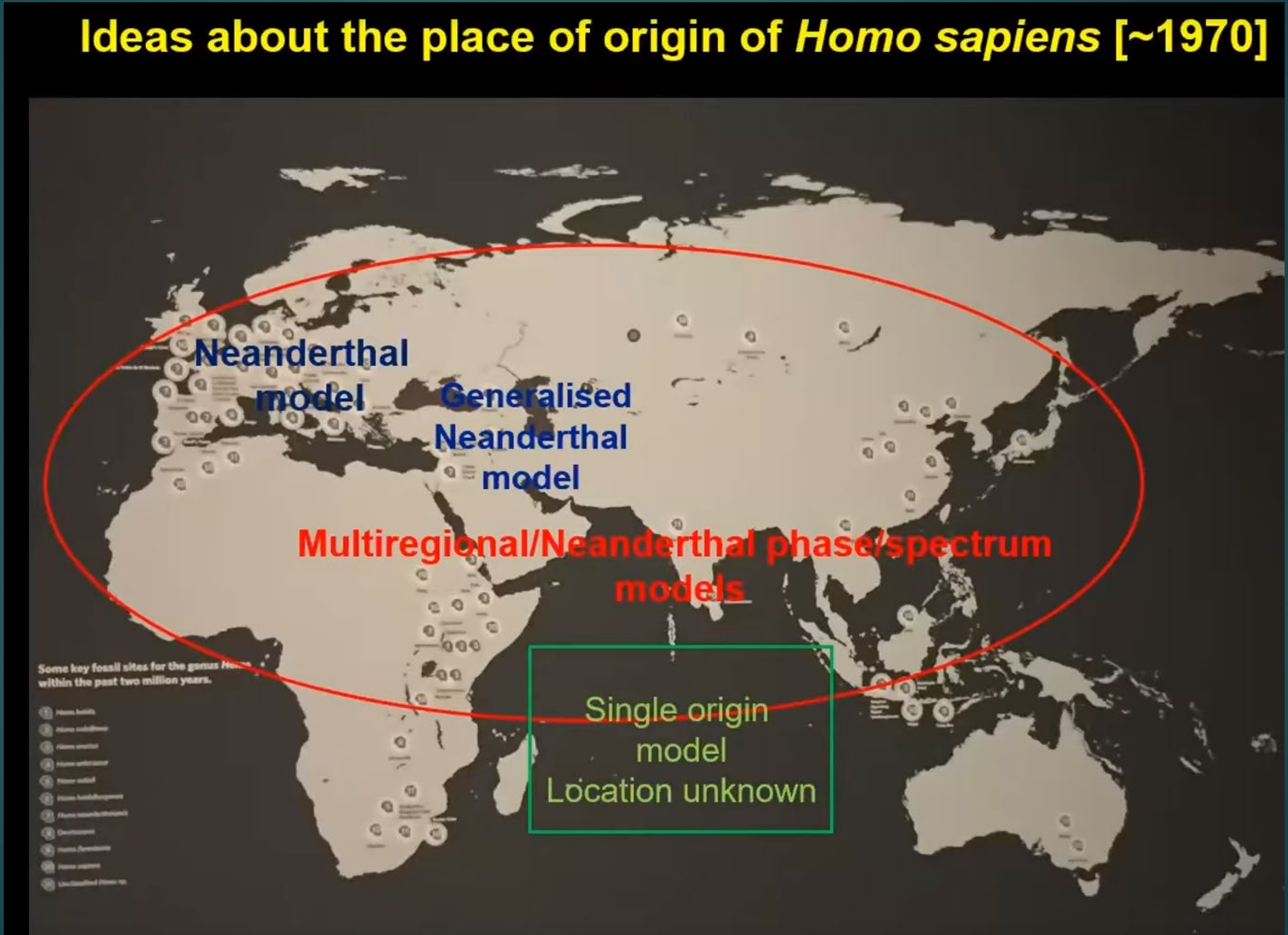
Loring Brace: Culture drove change between MP and UP



many took the position summarised by (White 1982): "if there is a relationship between culture and biology across the [Middle-Upper Palaeolithic] boundary, cultural developments... are stimulating biological change rather than vice versa". To my surprise, then, rather than

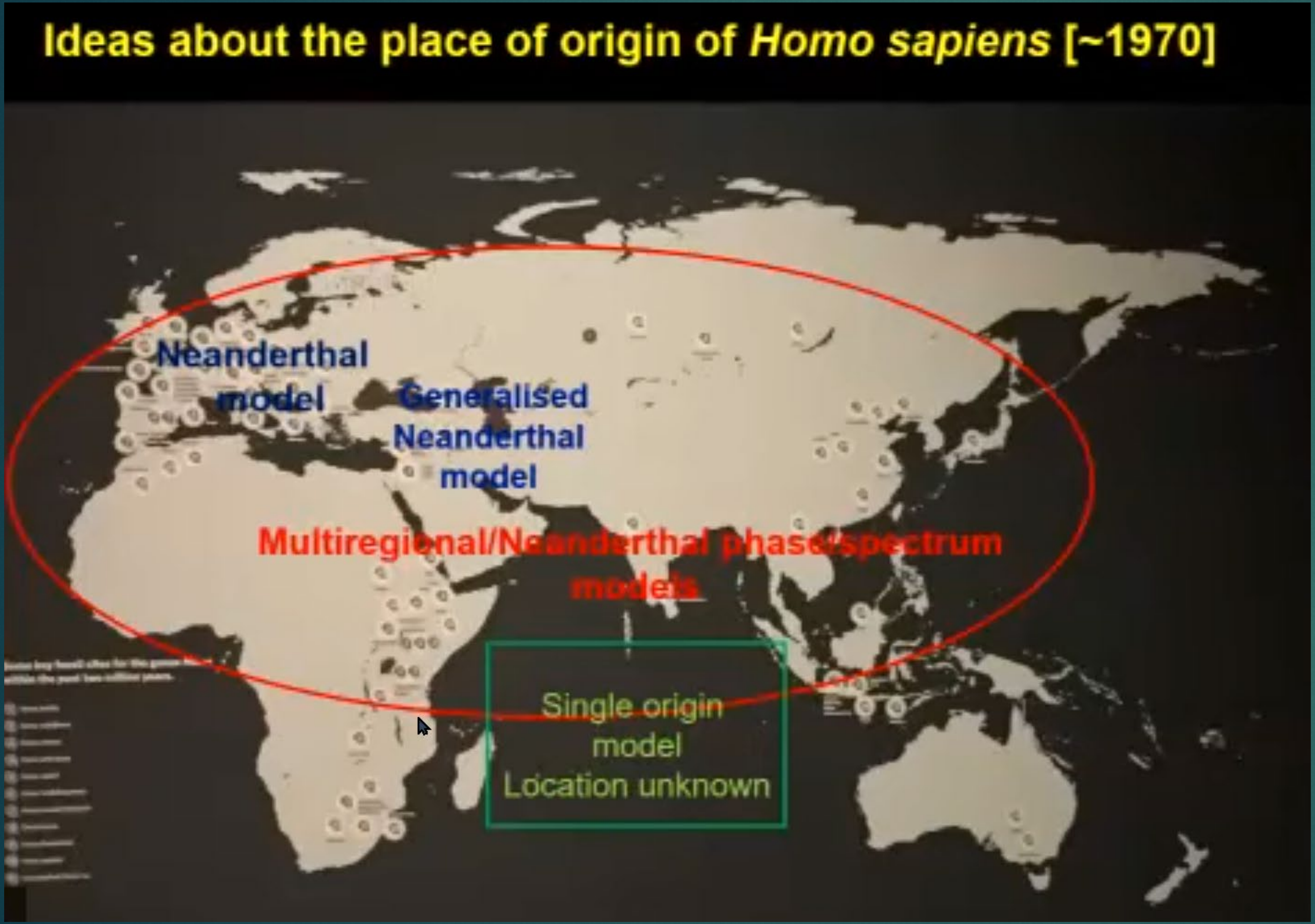
The influential views of Loring Brace and others 1960s-1980s

1970s: Noone thought Africa was MH’s place of origin



Ideas about the place of origin of *Homo sapiens* [~1970]

Place of origin of H. sapiens c. 1970s



Ideas about the place of origin of *Homo sapiens* [~1970]

“H. sapiens” included Ns, H erectus

But strict H. sapiens origin:

N model – MHs originated from Ns;

Generalized N model Clark Howells - N developed in Europe; H sapiens in Western Asia/Africa

Brace: everywhere had its N stage that became MHs

Multiregional model: Weidenreich, Coon, Wolpoff; Only 1 species (MH) for 1.5 My, all over developed from prior local forms – archaic to modern forms

Minority view, Bill House: MHs unique, originated in unknown single area

Hypotheses for human origins

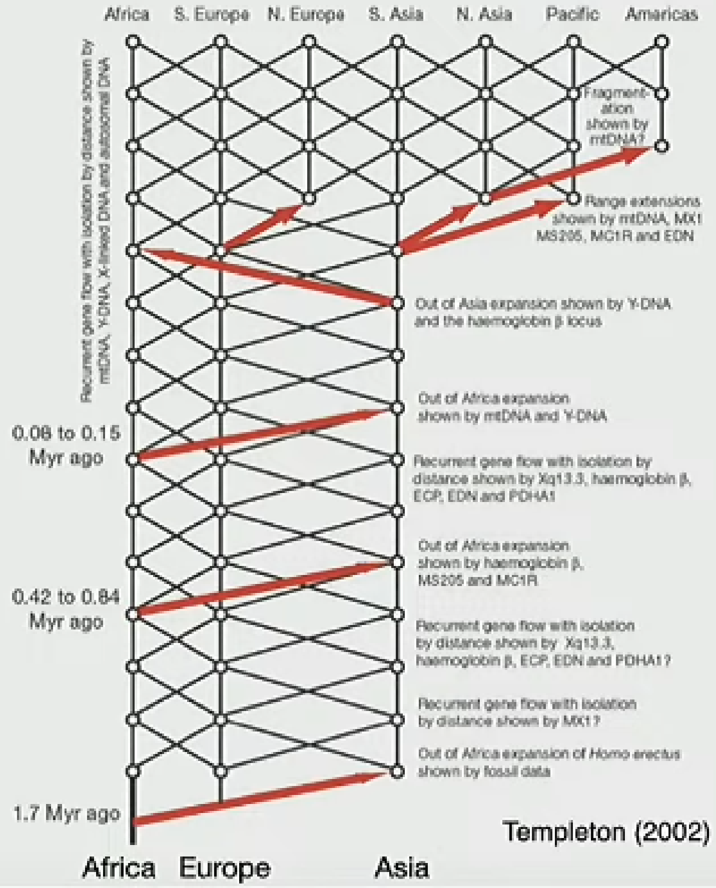
- Early debates (mid- to late-20th century) centered around the question of which model was correct:
  - Multiregional model: Humans evolved in a loosely connected manner locally across Africa and Eurasia, and evolution was largely independent for many hundreds of thousands (or millions) of years
  - Recent African origin (RAO) or Out of Africa (OoA) model: We all trace our ancestry back to a relatively recent common ancestor that lived within Africa, where our species underwent evolutionary transitions before dispersing across the globe

Stringer vs Wolpoff

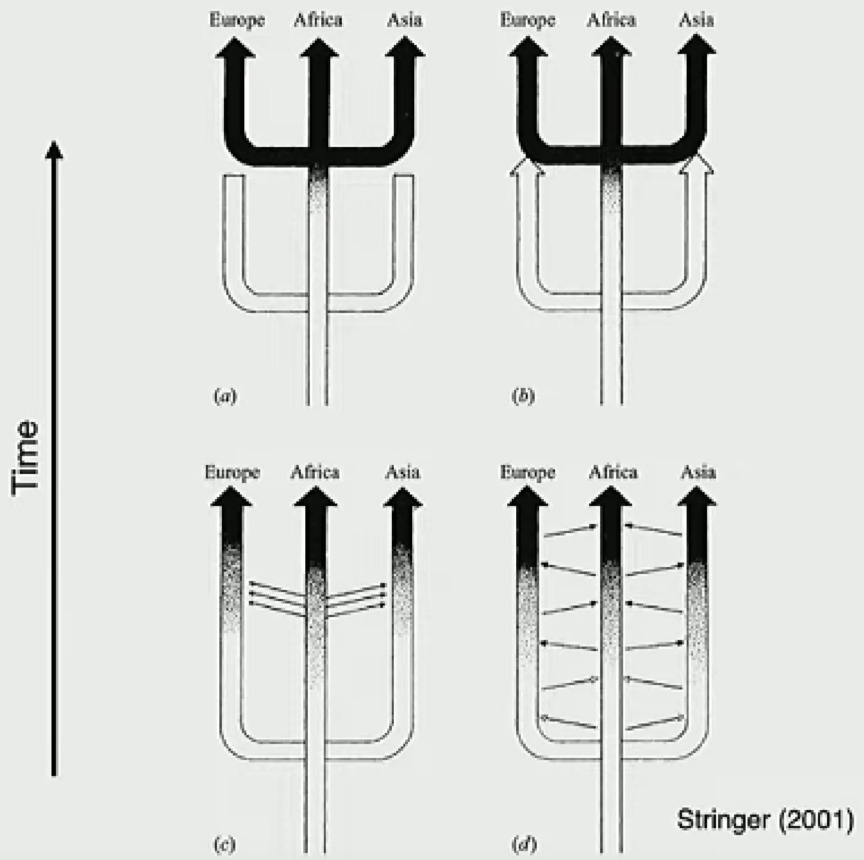
- For 27 years, Chris Stringer and Milford Wolpoff have been at odds about where and how our species was born.
- Stringer, a paleoanthropologist at the Natural History Museum in London, held that modern humans came out of Africa, spread around the world, and replaced, rather than mated with, the archaic humans they met.
- But Wolpoff, of the University of Michigan, Ann Arbor, argued that a single, worldwide species of human, including archaic forms outside of Africa, met, mingled and had offspring, and so produced *Homo sapiens*.
- The battle was long and bitter: When reviewing a manuscript in the 1980s, Wolpoff scribbled “Stringer's desperate argument” under a chart; in a 1996 book, Stringer wrote that “attention to inconvenient details has never been part of the Wolpoff style.” At one tense meeting, the pair presented opposing views in rival sessions on the same day—and Wolpoff didn't invite Stringer to the meeting's press conference. “
- It was difficult for a long time,” recalls Stringer.

Multiregional model

Conceptual models



Templeton (2002)



Stringer (2001)

Until the 1980s, Multiregional model was predominant

Until the 1980s, the multiregional model appeared to be the leading hypothesis among paleoanthropologists, in which ...

·Neanderthals were the direct ancestors of present-day Europeans

·In East Asia, H. erectus or a related regional group were the direct ancestors of MHs, and likewise within Africa

·Technologies, cultures and genetics evolved locally, with only intermittent connections and exchanges between regions

1970: C. Stringer – PhD trip around Europe; saw Jebel Irhoud fossil in Paris (then dated at 40 Ka) = African N; Stringer thought it was MH

1970: Began PhD applying multivariate methods to Pleistocene crania, supervised by J. Musgrave (Bristol): a campsite in Yugoslavia August 1971

Morris 1000

Most clothes stolen later in Italy+France

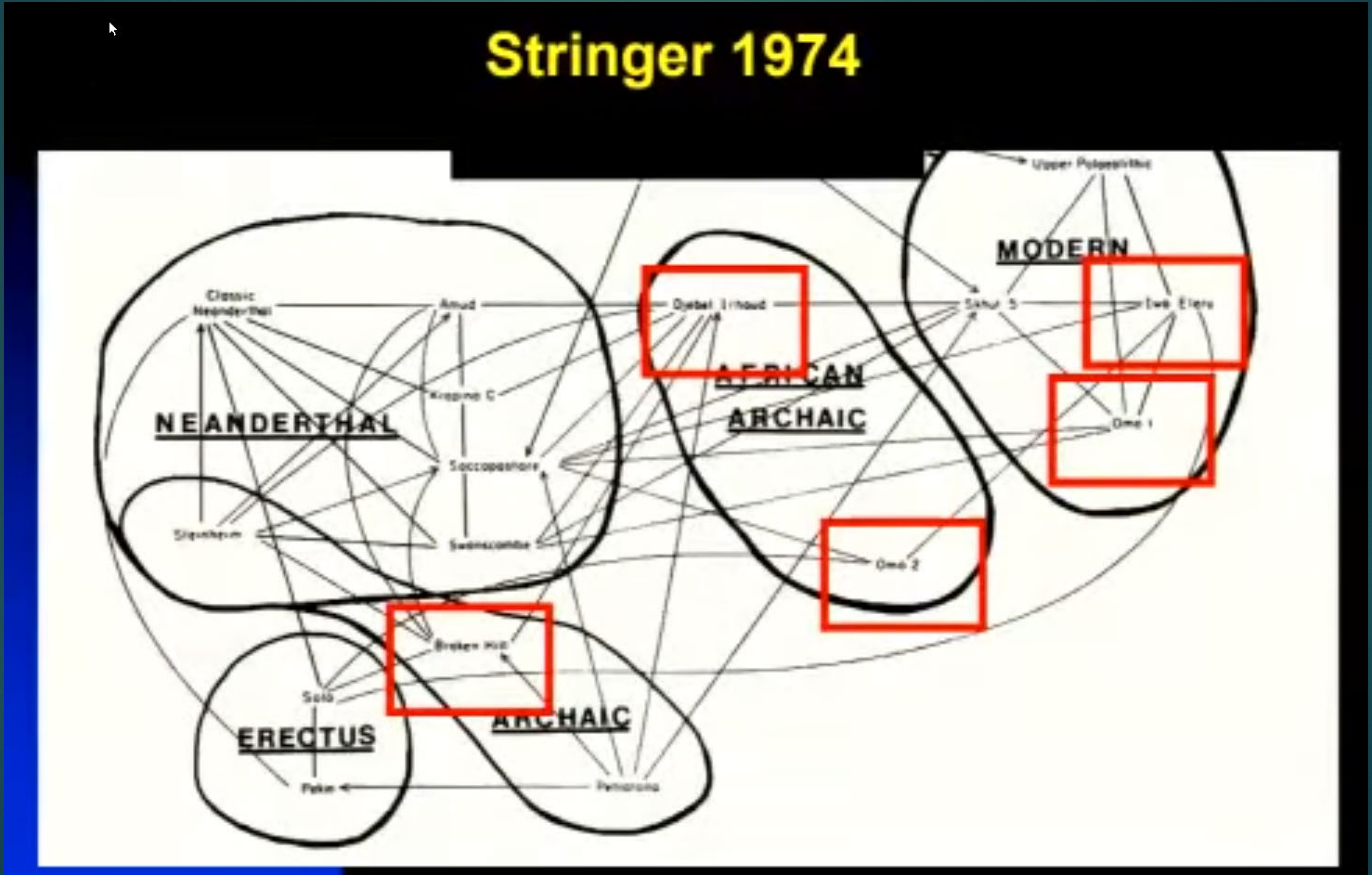
Standard ♂ look ca 1971

Measuring calipers

5000 mile drive

In Search of the Neanderthals

1974: Ns were separate species from MHs; not ancestral

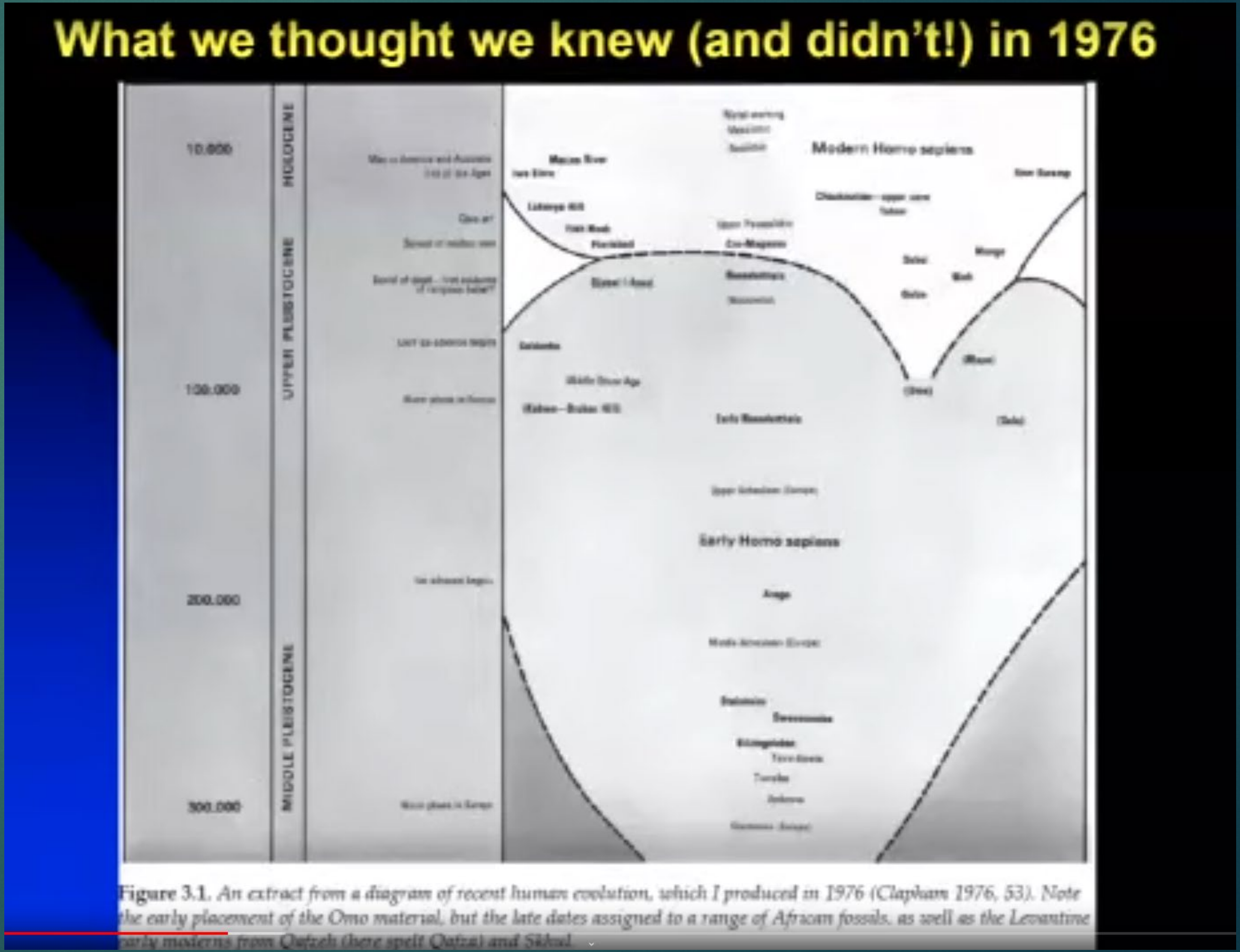


Stringer 1974

1976: only 2 species: H. sapiens & H erectus; nothing in Africa that looked like precursor to H. sapiens;

most African fossils dated to only 40-50 Ka;

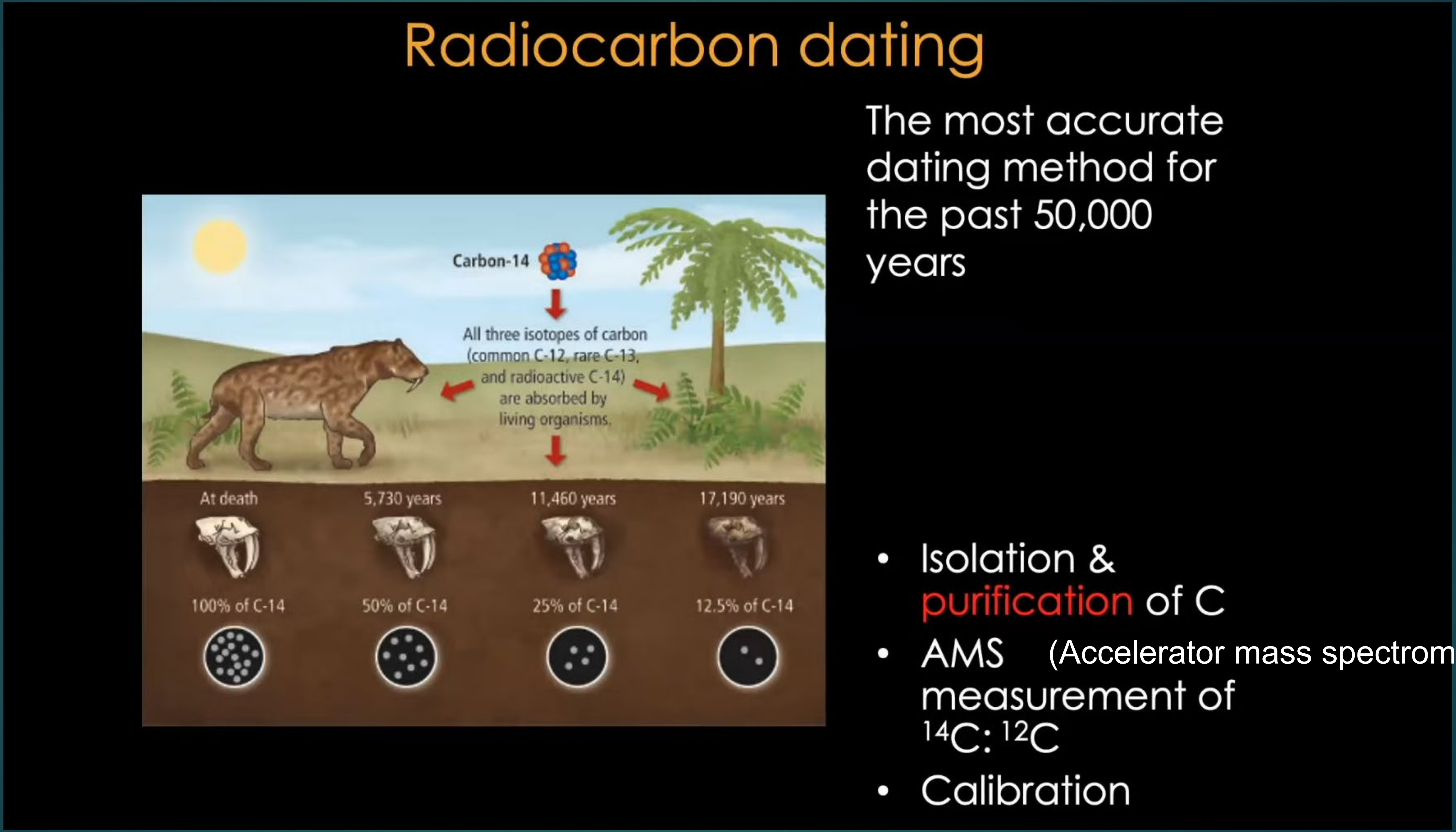
Libby got Nobel Prize in 1960 for Radiocarbon Dating



What we thought we knew (and didn't!) in 1976

Figure 3.1. *An extract from a diagram of recent human evolution, which I produced in 1976 (Clapham 1976, 53). Note the early placement of the Omo material, but the late dates assigned to a range of African fossils, as well as the Levantine early moderns from Qafzeh (here spelt Qafza) and Skhul.*

Revolution in Dating methodology



Radiocarbon dating

The most accurate dating method for the past 50,000 years

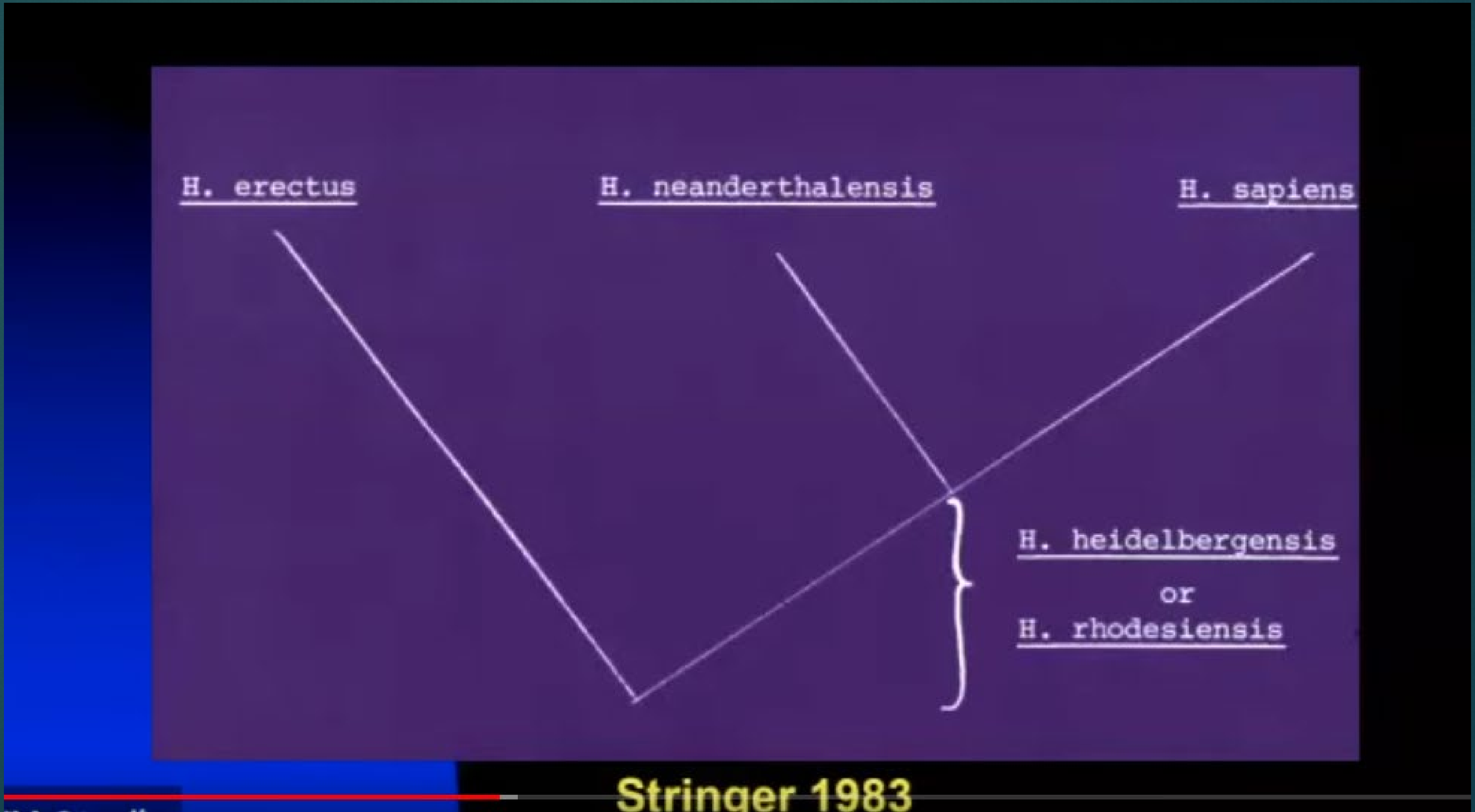
- Isolation & purification of C
- AMS (Accelerator mass spectrometry) measurement of ^{14}C: ^{12}C
- Calibration

1978

- No hints that Africa was source of Modern Humans

- Facial differences:
  - Neandertal skull vault is long and low; large brain; face is distinctive
  - MH vault is globular; small, flat face

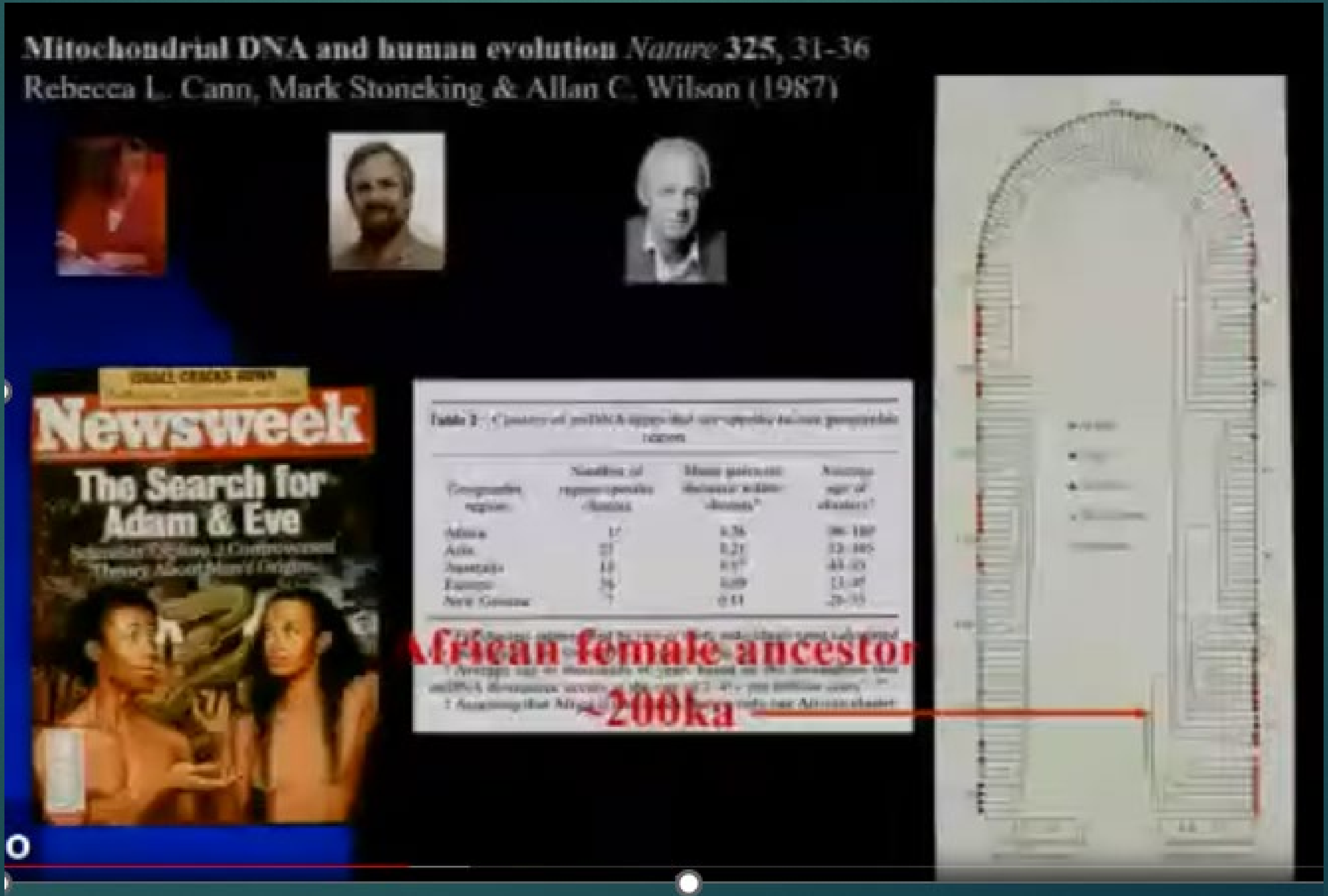
1980s: introduction of cladistics: relationships via derived features; Ns as distinct species; Stringer introduces the name H. heidelbergensis for Petralona, Broken Hill skulls



Stringer 1983

Petralona (400-200 Ka) & Broken Hill (300 Ka); prior dating at 600 Ka

1987: Mitochondrial Eve: R. Cann called her “Lucky Mother”, the one who succeeded; first genetic proof of recent African origin (RAO) for MHs



Mitochondrial DNA and human evolution *Nature* **325**, 31-36

Rebecca L. Cann, Mark Stoneking & Allan C. Wilson (1987)

Introduction of newer dating methodology

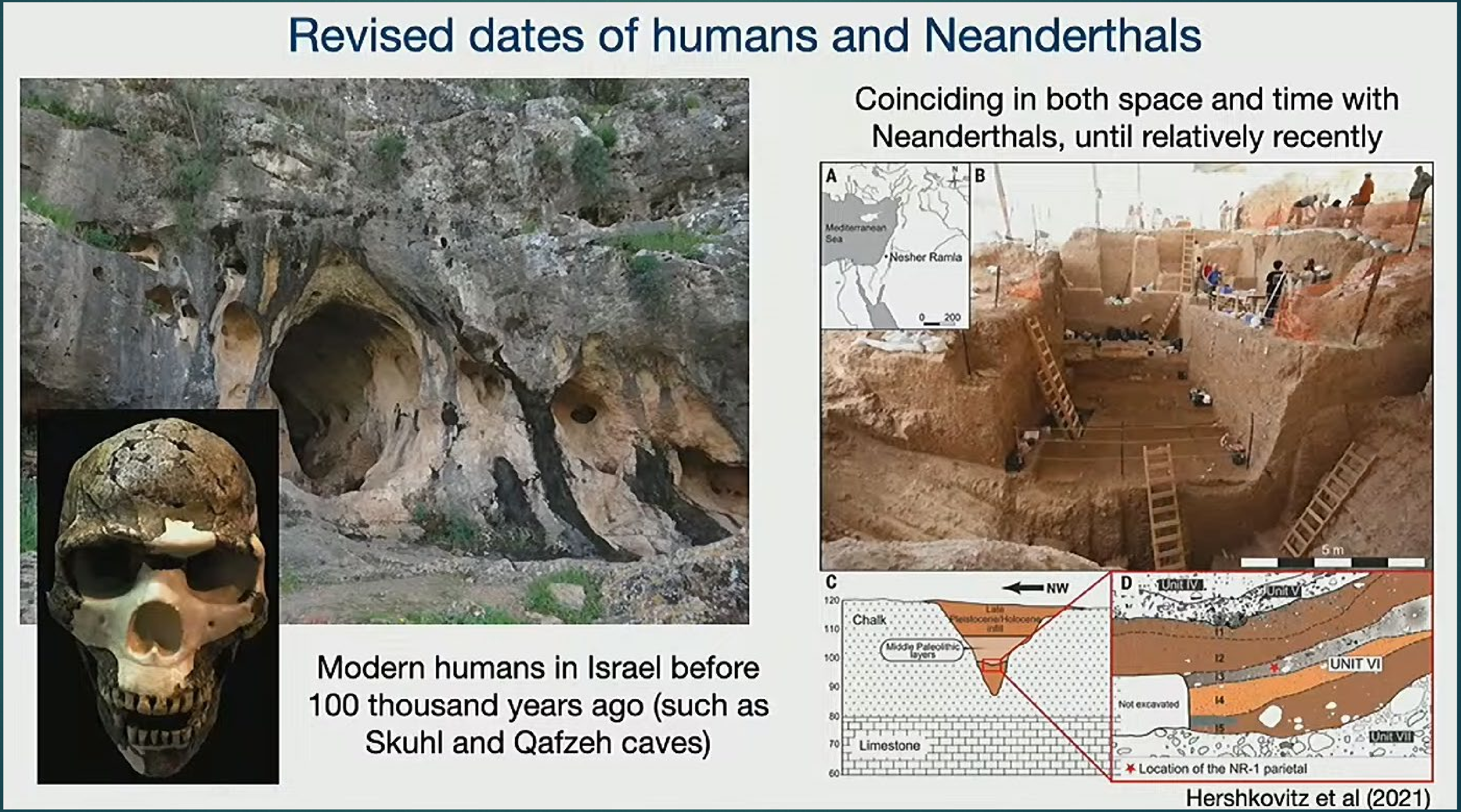
Shifts in leading hypotheses

But the 1980s and 90s, opinions began to change. This was due to vastly improved methods for dating fossil remains.

Radiocarbon dating: only works within the last 50 thousand years

New non-radiocarbon dating methods are accurate to much older times

Redating of Near East Ns and MHs: temporal alterations of 2 groups



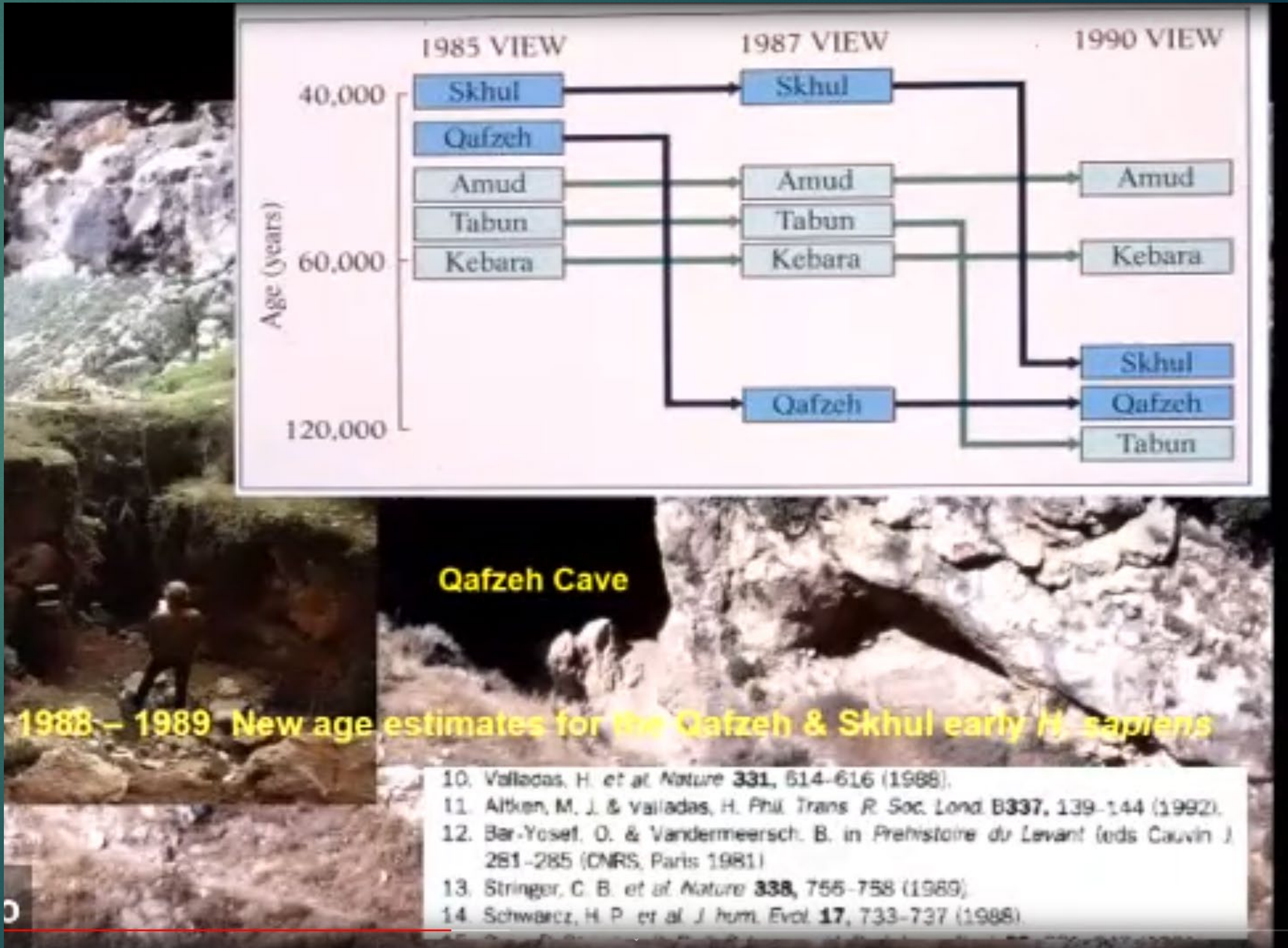
Revised dates of humans and Neanderthals

Modern humans in Israel before 100 thousand years ago (such as Skuhl and Qafzeh caves)

Coinciding in both space and time with Neanderthals, until relatively recently

Hershkovitz et al (2021)

New dating for Qafzeh/Skhul MHs: MHs originally dated to 40-50 Ka; 1988 dating ~100 Ka; prior to Ns; taken as evidence that Ns not ancestors of MHs



1988 – 1989 New age estimates for the Qafzeh & Skhul early *H. sapiens*

10. Valladas, H. *et al. Nature* **331**, 614-616 (1988).
11. Aitken, M. J. & Valladas, H. *Phil. Trans. R. Soc. Lond.* B**337**, 139-144 (1992).
12. Bar-Yosef, O. & Vandermeersch, B. in *Prehistoire du Levant* (eds Cauvin, J.) 281-285 (CNRS, Paris 1981).
13. Stringer, C. B. *et al. Nature* **338**, 756-758 (1989).
14. Schwarcz, H. P. *et al. J. hum. Evol.* **17**, 733-737 (1988).

1988: Highly controversial Stringer/Andres paper, highlighting differences b/ MR vs ROA; RAO wins

1988: My paper in *Science* with Peter Andrews

Genetic and Fossil Evidence for the Origin of Modern Humans

C. B. Stringer and P. Andrews

Tab. 3 - Predictions from models of H. sapiens origins (from Table 1 in Stringer and Andrews 1988).

ASPECT	MULTIREGIONAL EVOLUTION	RECENT AFRICAN EVOLUTION
Geographic patterning of human evolution	Continuity of pattern from Middle Pleistocene to present	Continuity of pattern only from late Pleistocene appearance of *H. sapiens* to present
	Interpopulation differences are high, greatest between each peripheral area	Interpopulation differences relatively low, greatest between African and non-African populations
	Intrapopulation variation greatest at centre of human range	Intrapopulation variation greatest in African populations
Regional continuity and the establishment of *H. sapiens*	Transitional fossils widespread	Transitional fossils restricted to Africa, population replacement elsewhere
	Modern regional characters of high antiquity at peripheries	Modern regional characters of low antiquity at peripheries (except Africa)
	No consistent temporal pattern of appearance of *H. sapiens* characters between areas	Phased establishment of *H. sapiens* suite of characters: (i) Africa, (ii) S.W. Asia, (iii) other areas
Selective and behavioural factors involved in the origin of *H. sapiens*	Factors varied and widespread, perhaps related to technology; local behavioural continuity expected	Factors special and localised in Africa; behavioural discontinuities expected outside Africa

Criticisms of this paper:

Impossible

Prescientific

Antievolutionary

Divisive

Already falsified

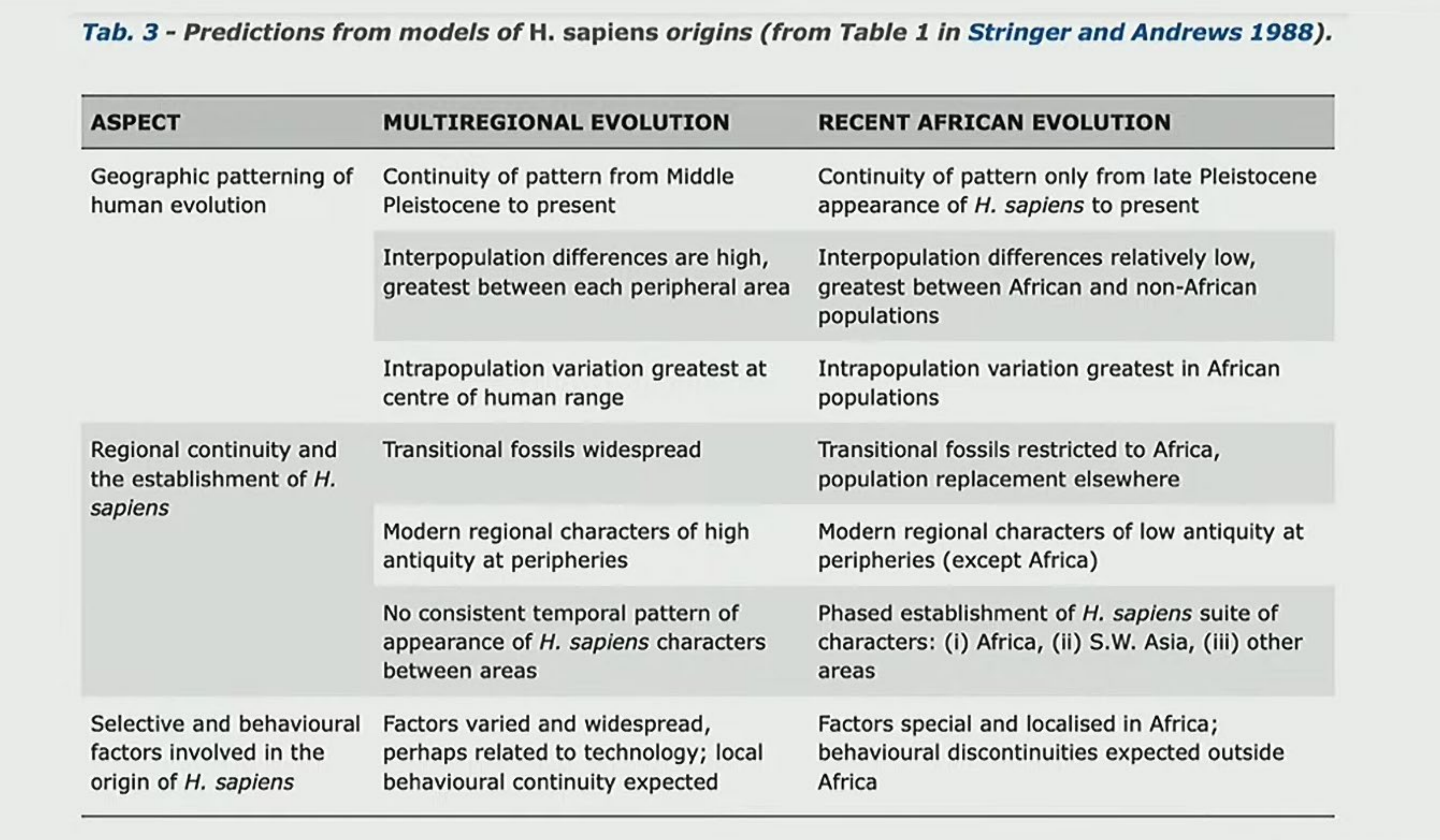
Fatally flawed

Nonsense

Great leap backward

Implying a holocaust?

Multiregional Evolution vs Recent African Evolution



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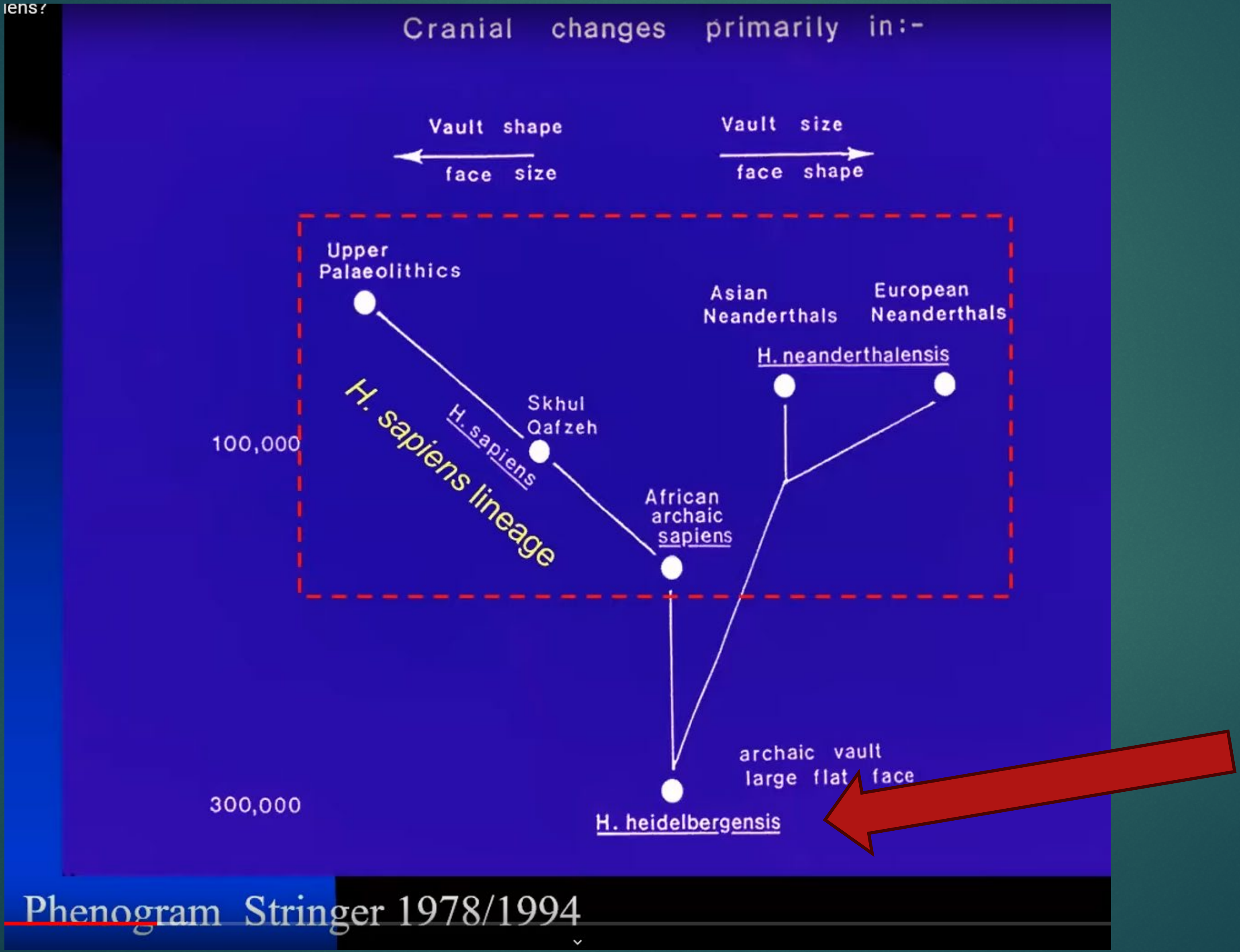
1994: more possible ancestors in Africa from new datings (Qafzeh); Ns evolved in own direction



Cranial changes primarily in:-

Phenogram Stringer 1978/1994

Stringer's original view:

In Ns, both archaic vault and faces get larger

In MHs, vault becomes globular, face smaller

No longer accepts this view

Today, only 1 modern human species; only 1 skeletal type

But stop calling Ns "archaic"

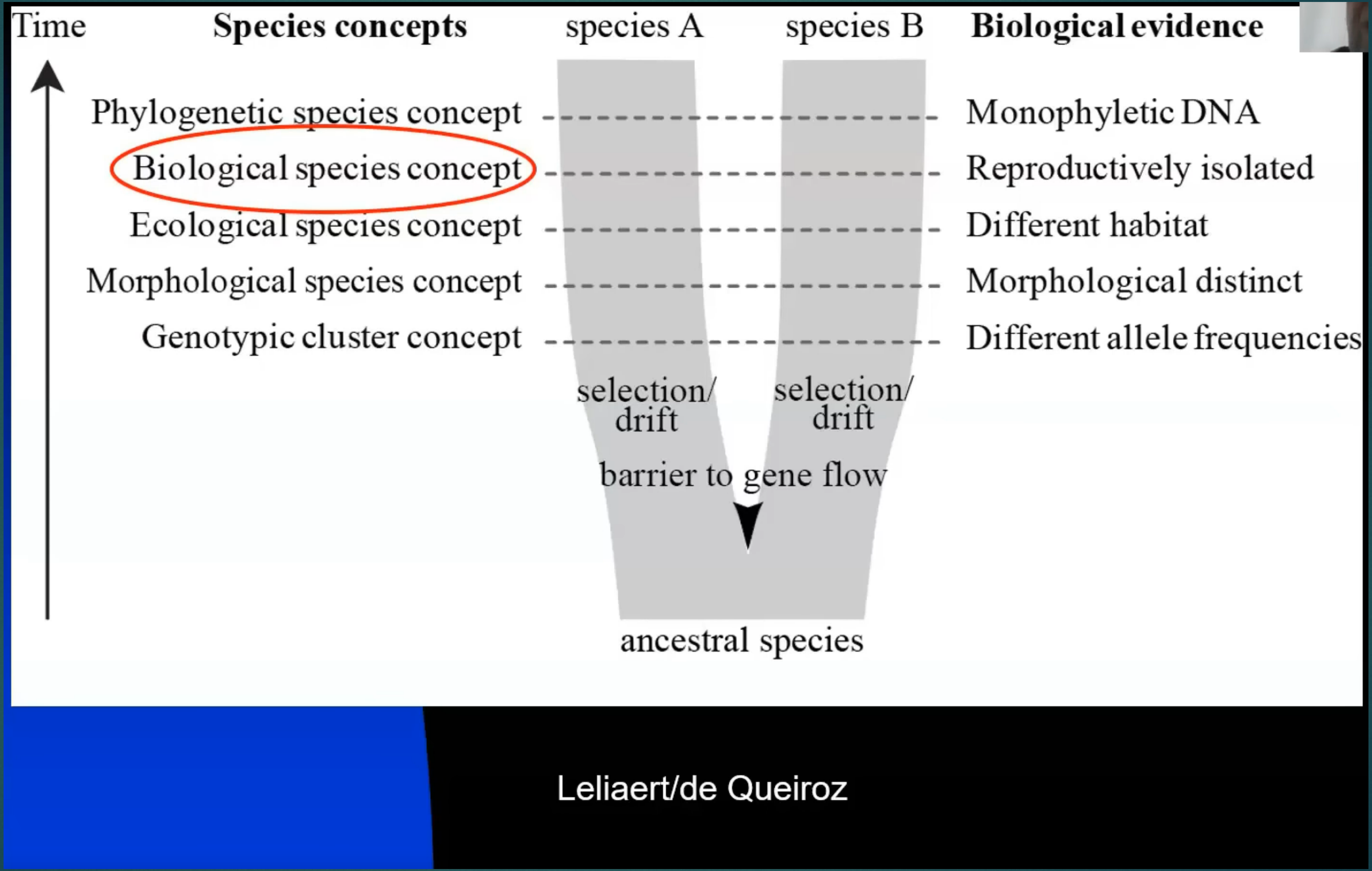
There were at least 5 kinds of humans 70,000 yrs ago

But only *1* kind of human by 30,000 yrs ago

Ns die out by 42 Ka

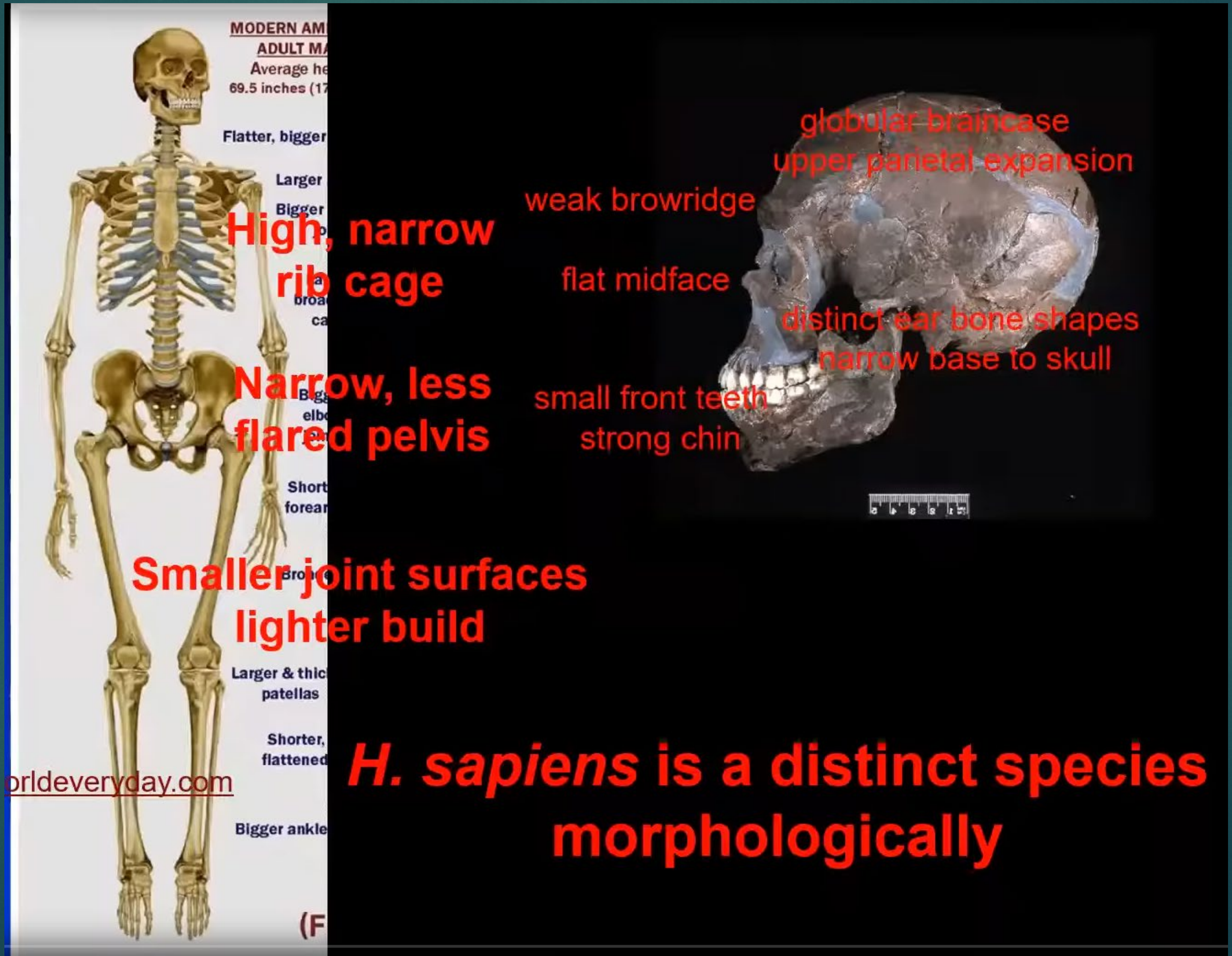
No known extinction dates for Denisovans (~25 Ka)

Species concepts



Leliaert/de Queiroz

H. sapiens is a distinct species morphologically



High, narrow rib cage

Narrow, less flared pelvis

Smaller joint surfaces lighter build

weak browridge

flat midface

small front teeth

strong chin

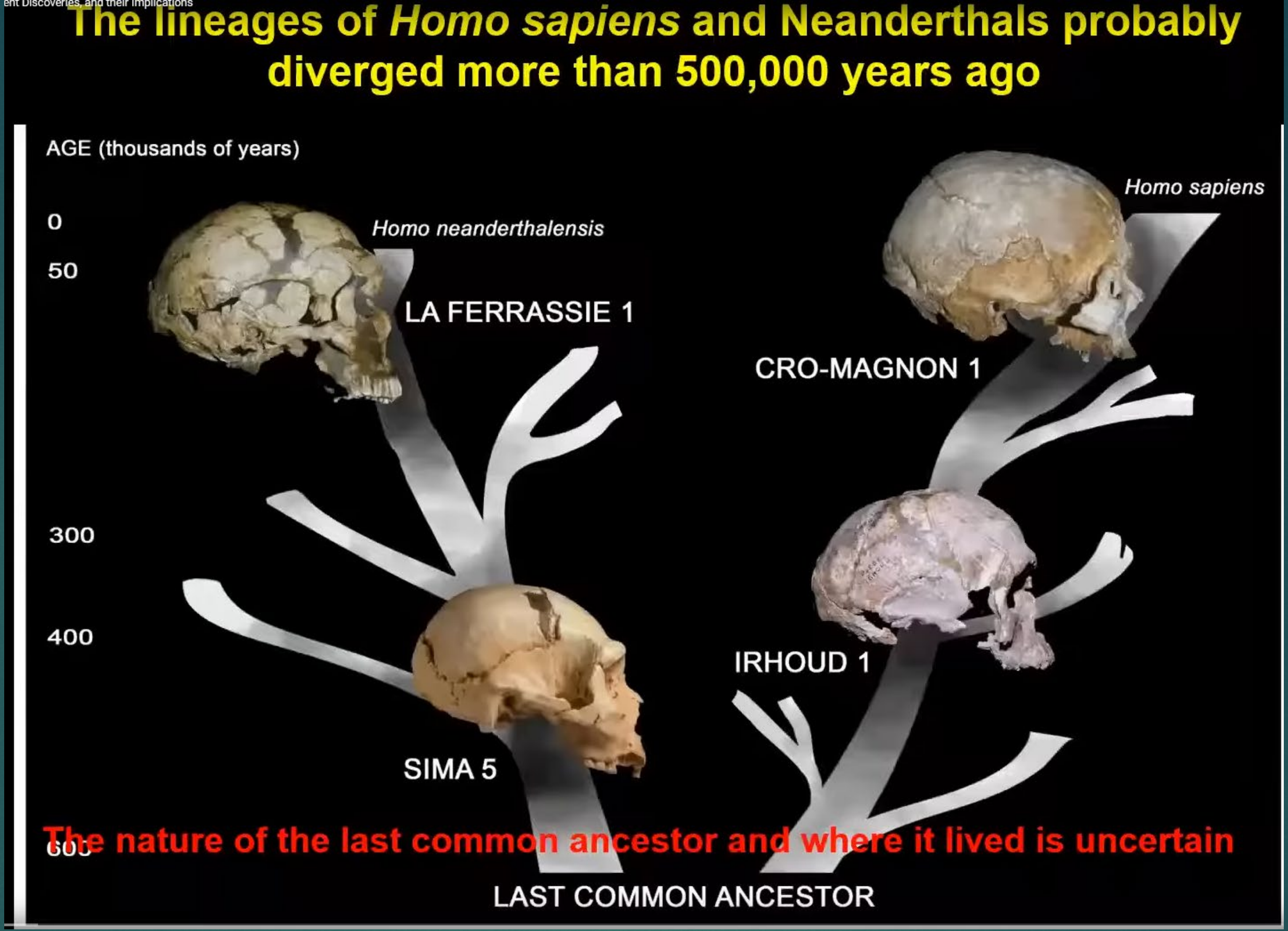
globular braincase

upper parietal expansion

distinct ear bone shapes

narrow base to skull

***H. sapiens* is a distinct species morphologically**



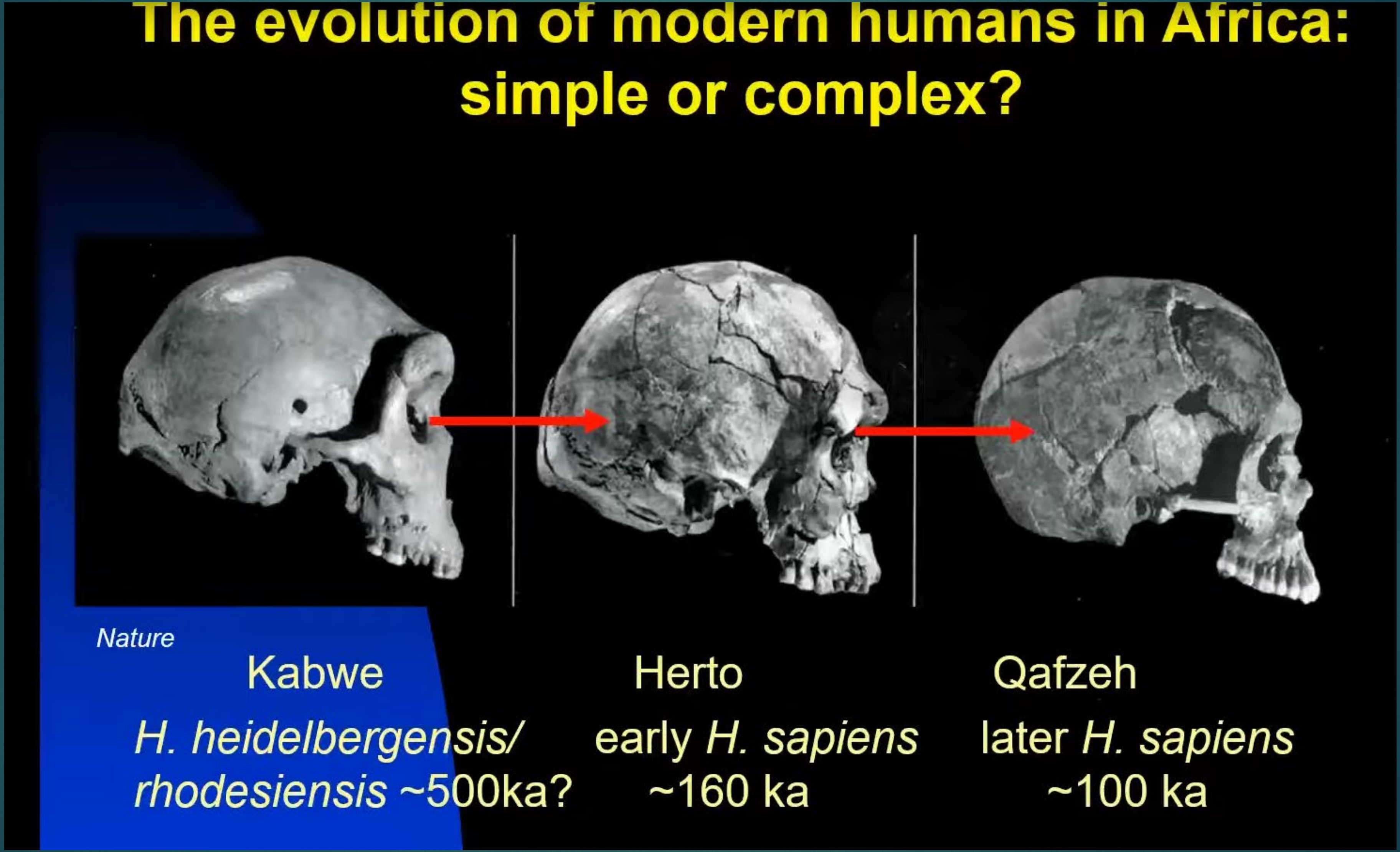
ent Discoveries, and their Implications

The lineages of *Homo sapiens* and Neanderthals probably diverged more than 500,000 years ago

The nature of the last common ancestor and where it lived is uncertain

LCA: where and when = uncertain; H. heidelbergensis?; Europe, Asia, Africa? 744 Ka?

In 2000, this was the model: Origin in East Africa



The evolution of modern humans in Africa: simple or complex?

Nature

Kabwe

H. heidelbergensis/ rhodesiensis ~500ka?

Herto

early *H. sapiens* ~160 ka

Qafzeh

later *H. sapiens* ~100 ka

2016: Chris Stringer: The origin and evolution of *Homo sapiens*

- If we restrict the use of Homo sapiens in the fossil record to specimens which share a significant number of derived features in the skeleton with extant H. sapiens,
  - the origin of our species would be placed in the African late middle Pleistocene, ~300 Ka
  - based on fossils such as Omo Kibish 1, Herto 1 and 2, and the Levantine material from Skhul and Qafzeh.

- However, genetic data suggest that we and our sister species Homo neanderthalensis shared a last common ancestor in the middle Pleistocene approximately 400–700 ka.

Chris Stringer, 2016

The origin and evolution of *Homo sapiens*

- The African fossil record will document early members of the sapiens lineage showing only some of the derived features of late members of the lineage.
- Stringer argues that human fossils such as those from Jebel Irhoud, Florisbad, Eliye Springs and Omo Kibish 2 do represent early members of the species,
    - but variation across the African later middle Pleistocene/early Middle Stone Age fossils shows that there was not a simple linear progression towards later sapiens morphology, and there was
    - chronological overlap between different ‘archaic’ and ‘modern’ morphs.

The origin and evolution of Homo sapiens

- Even in the LSA (~50 Ka) within and outside Africa, we find H. sapiens specimens which are clearly outside the range of Holocene members of the species, showing the complexity of recent human evolution.

- Extant H. sapiens share specific morphological traits: high neurocranium, rounded in lateral profile, a small face retracted under the frontal bone, a true chin even in infants, small discontinuous supraorbital tori, a lengthened post-natal growth period and life history, and a narrow trunk and pelvis

The origin and evolution of Homo sapiens

- In addition, distinctive morphologies of elements of inner ear anatomy are being increasingly well characterized in H. sapiens.
- In the cranial vault, the shape of the parietal region in H. sapiens seems particularly distinctive and makes a significant contribution to globularity in both lateral and occipital views

MHs & Ns

- A second major question concerns the mode of evolution of the species H. sapiens—whether punctuated or gradual.

- The subsequent European record had indicated a gradual accretion of further Neanderthal synapomorphies (a homologous character that originated in an ancestral species, i.e. midface pulled forward)

- A third question is the nature of the last common ancestor (LCA) of the sapiens and neanderthalensis lineages, and when that LCA lived.

H. heidelbergensis

- Since 1983, Stringer has built the case that shape resemblances between the Broken Hill and Petralona crania indicate the existence of a widespread middle Pleistocene population which can be called Homo heidelbergensis if the Mauer mandible is also included, or H. rhodesiensis (Broken Hill), if it is not.
- (In 2016) He argued that this species represents the most reasonable LCA for the neanderthalensis and sapiens lineages, with their common origin placed at about 400 ka based on the estimated mtDNA coalescence date of the two lineages; but by 2023, he no longer holds this position. Now believes H. heidelbergensis is only the ancestor of Ns, not African sapiens

The origin and evolution of Homo sapiens

- A fourth question follows from the previous ones.
- Once the Neanderthal and modern human lineages began to evolve, did more ancient (and perhaps 'ancestral') morphologies in Eurasia and Africa soon die away, or could they have persisted alongside their 'descendants' for a considerable time?
- And if the latter, was there gene exchange?

Origin of *H. sapiens*

- There is growing evidence of the survival of what could be considered as earlier middle Pleistocene morphologies (cf. *H. heidelbergensis or H. rhodesiensis*) into at least the later middle Pleistocene of Europe and Africa.
- Genetic exchanges could also have been occurring in the middle Pleistocene.

Origin of *H. sapiens*

- The fossil record in Africa is still relatively sparse and poorly dated, and is dominated by material from East Africa.
- Huge expanses of Central and West Africa were clearly inhabited during the later middle Pleistocene, (evidence of artefacts), but not a single fossil has yet been recovered to identify who those early inhabitants were.
- Thus, the available record is probably highly biased and unrepresentative of the continent as a whole.

Chris Stringer on "archaic *Homo sapiens*"

- Anatomically modern human morphology is typically seen in the high and rounded skull, the small face, the chin, the lighter-built skeleton with a narrow pelvis.
- This pattern is found in Africa back to between 150-200 ka (Herto 1 and 2, Omo I).
- Beyond 200 ka, there are specimens in the *Homo sapiens* line that do not yet show the majority of the modern features: Florisbad, Eliye Springs, Ngaloba, Jebel Irhoud.
- Different African specimens are showing different combinations of these modern human and archaic features.

Traits

- In Europe, the recent redating of the Sima de los Huesos fossils to at least 400 ka suggests that many Neanderthal features, particularly in the face, jaws and teeth, were already well developed by that time,
- An alternative model has a much older proposed LCA for the neanderthalensis and sapiens lineages, based on the 'modern' H. antecessor face from Gran Dolina, Atapuerca, dated to approximately 850 ka.
- Such a model would imply that this facial morphology was retained in the descendant sapiens lineage, but was lost in that of the Neanderthals.

Is modern face actually primitive; for both MH and Ns – we kept it, Ns more derived

Ancient faces from Spain and China – the 'modern' face is actually primitive?

nature ecology & evolution

REVIEW ARTICLE

https://doi.org/10.1038/s41559-019-0866-7

The evolutionary history of the human face

Rodrigo S. Lacruz[1,2*], Chris B. Stringer[3], William H. Kimbel[4], Bernard Wood[5], Katerina Harvati[2,6], Paul O'Higgins[7], Timothy G. Bromage[8] and Juan-Luis Arsuaga[9]

Gran Dolina (Atapuerca)
(*H. antecessor*)
~850ka

Nanjing (Hulu Cave)
~600 ka

African evolution of H. sapiens

- The fossil record available to reconstruct the evolution of H. sapiens in Africa is still relatively sparse and poorly dated, and is dominated by material from the fossiliferous sedimentary basins of Est Africa.

- The major African fossils:
- (a) North-west and North Africa: Jebel Irhoud, and some partial fossils
- (b) Southern Africa: Florisbad, Klasies River Mouth fossil
- (c) East Africa: Eliye Spring, Ngaloba Laetoli, Omo 1 & 2, Herto, Singa
- (d) Western Asia (Skhul and Qafzeh): Skhul, Qafzeh,

Interpreting the African middle–late Pleistocene fossil human record

- During the past 25 years, the Recent African Origin model has dominated discussions about the evolution of H. sapiens, but with the recent modifications to it demanded by evidence of introgression from archaic humans such as Neanderthals and Denisovans outside Africa.
- The date of origin of H. sapiens in this model has also changed in the face of new discoveries and dating work and is now often placed at about 200 ka, with the generally accepted first appearance of 'anatomically modern humans' (that is to say fossils that predominantly share the skeletal morphology of extant humans) in the form of the Omo Kibish 1 skeleton and the somewhat younger Herto material.

Pan-African evolution

- There was wide morphological variation in fossil human crania associated with early MSA archaeology in Africa, ranging from material like Florisbad and Jebel Irhoud. This array of fossils shows differing combinations of archaic and derived (recent H. sapiens-like) traits. These variations already suggest that there is probably not a simple, linear relationship between an ancestral heidelbergensis-like morphology and that of H. sapiens.

- Alternatively, as suggested by Stringer, this variation might instead reflect the coexistence of morphologically distinct populations during the later middle Pleistocene in Africa.

- Evolution may at times have progressed independently in different areas, with morphological substructure leading on to the eventual coalescence of the full suite of H. sapiens characteristics.

Not African multiregionalism; use *Pan-Africanism.*

- Stringer has called this an 'African multiregionalism', with many potentially interfertile subdivisions of the evolving sapiens species across Africa. He now calls it *Pan-Africanism.*

- Others have used the analogy of a braided stream for what they consider to be an open genetic network for different human lineages across the whole Old World, but I think the most appropriate application for this analogy is in the middle Pleistocene of Africa.

Braided Stream?

- The imperfect chronological control over the African middle Pleistocene record provides only very limited support for an ordered progression from ‘archaic sapiens’ to ‘modern sapiens’ through time.

- Instead we see morphologically varied fossils such as Broken Hill, Florisbad and Omo Kibish 1 apparently juxtaposed in close temporal proximity.

- There is also growing evidence of the survival of even younger elements of archaic morphology into the late Pleistocene at sites like Eyasi, Iho Eleru and Lukenya Hill

Climate

- While later Pleistocene Eurasia suffered both large-scale and sharp millennial-scale climatic oscillations, which were especially reflected in fluctuations of temperature, these changes in Africa were expressed much more in terms of precipitation.

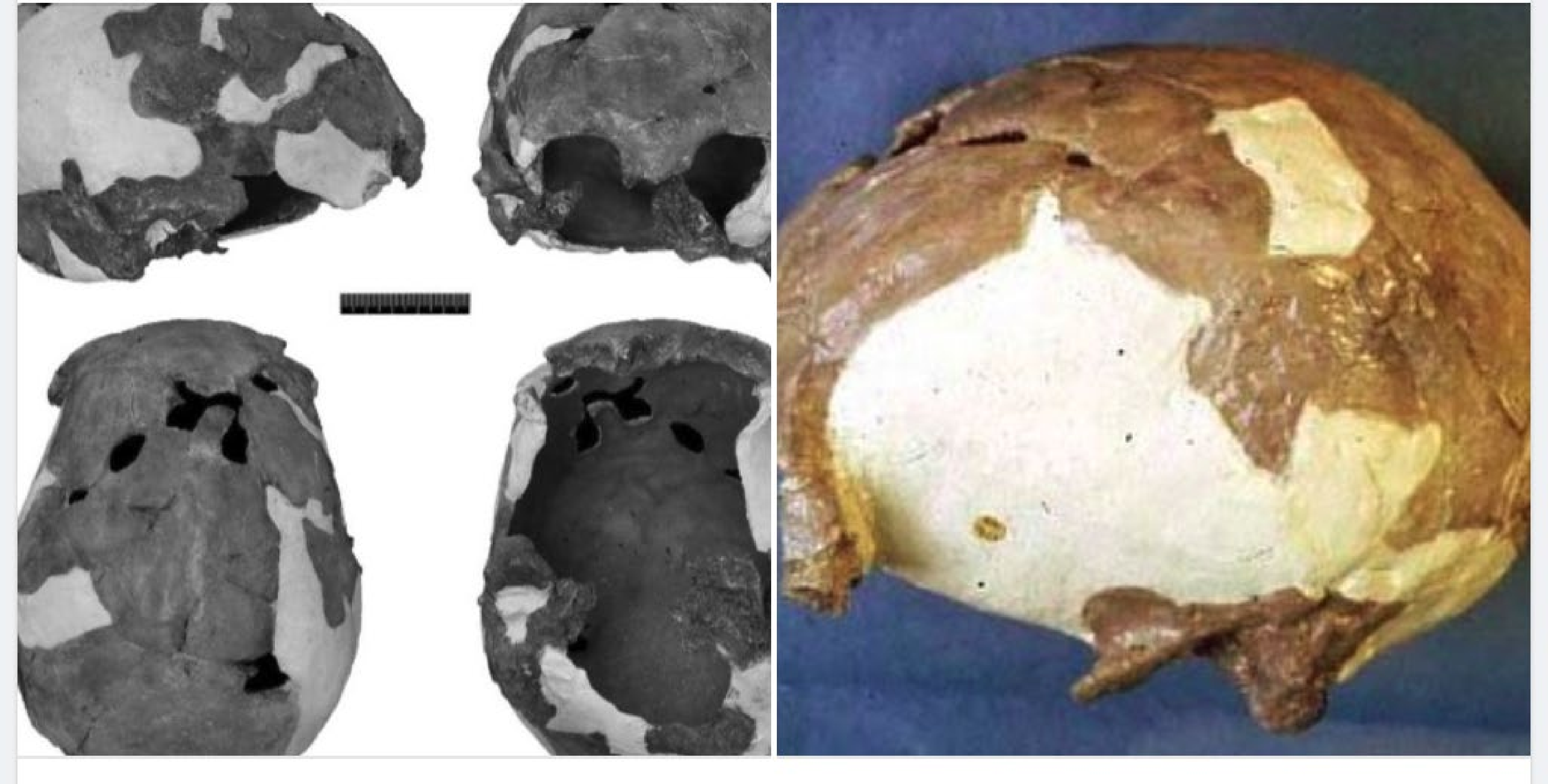
- In turn, this could have had direct demographic effects on human populations. For example, ~150 ka was predominantly arid, with the probable isolation or even extinction of small human populations across Africa. By contrast, the warmest part of MIS5 (approx. 120 ka) may have been a time of population expansions and interconnections.

Climate

- Refugia in which populations could weather the worst of climatic downturns have been suggested as a key driver of morphological and perhaps adaptive Behavioural changes in Eurasia, but in Africa climatic ameliorations could have been equally important in seeding denser and more networked populations, facilitating both genetic and cultural changes.
- The result of these processes was the composite we call modern H. sapiens, genetically, morphologically and behaviorally, but there was never a single center of origin, and despite later homogenization, some ancient substructure could have persisted

Pleistocene morphological variation across much of the African continent.

- In Stringer … e Stone Age assoc … fossil from Nigeria wa … rchaic fossils suc



- Its dating w … x. 14 ka) but also c … m recent African cra … c shape affinities to the much older Elandsfontein, Ngaloba, and Skhul and Qafzeh fossils.

Archaics

- Various specimens emphasize how little we still know about late Pleistocene morphological variation across much of the African continent.

- These fossils may indicate deep Pleistocene population substructural variation, possibly including hybridization between late H. sapiens and surviving archaic hominin lineages, variation which was subsequently lost

H. antecessor face: primitive or derived?

- Friedline et al. conducted a wide-ranging morphometric study of the faces of various fossil crania in order to better place H. antecessor developmentally and phylogenetically. They confirmed that its morphology was largely shared with H. sapiens and that this would probably have persisted into adulthood. However, they argued that this morphology was largely primitive and that it had probably evolved and re-evolved several times in human evolution, and therefore had to be used with caution phylogenetically.

- In their view, the true ‘modern’ facial morphology could only be reliably traced back to later middle Pleistocene fossils such as Jebel Irhoud 1.

H. antecessor

- But there are further relevant data. First, microscopic study of the facial growth of the immature H. antecessor fossil confirmed that it does show homologies with the maxillary developmental pattern of recent H. sapiens, a pattern argued to be derived, not primitive,

- A second study has concluded that the facial ontogeny of immature Sima de los Huesos fossils (dated approx. 400 ka) instead show homologies with later neanderthalensis specimens

Morphologies

- Moreover, using the latest estimates of the autosomal human mutation rate, the divergence date of the neanderthalensis and sapiens lineages can indeed be placed earlier, between 550 and 765 ka, which would be consistent with only the oldest suggested examples of heidelbergensis as potentially representing the LCA.

- An alternative would be to consider a H. antecessor-like morphology as more likely for the LCA of H. sapiens and H. heidelbergensis, with the heidelbergensis group exemplified by Arago, Petralona, Bodo and Broken Hill having more in common facially with the Sima fossils and subsequent Neanderthals.

Basal MH: 2017 - Jebel Irhoud new dating to 300 Ka: modern face, archaic vault

New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*

Jean-Jacques Hublin[1,2], Abdelouahed Ben-Ncer[3], Shara E. Bailey[4], Sarah E. Freidline[1], Simon Neubauer[1], Matthew M. Skinner[5], Inga Bergmann[1], Adeline Le Cabec[1], Stefano Benazzi[6], Katerina Harvati[7] & Philipp Gunz[1]

Omo Kibish 1: oldest aMH; originally dated 233 Ka; now 172 Ka

Omo Kibish 1 (Ethiopia) is currently the oldest known fossil that can fairly confidently be assigned to 'modern' *H. sapiens*

172 ka (Brown et al., 2012). Thus, the Omo I fossils have an age of at least 172 ka and, given the depositional environment of Kibish Member 1, probably closer to 196 ka. Omo I is therefore the oldest securely dated fossil evidence of anatomically modern humans

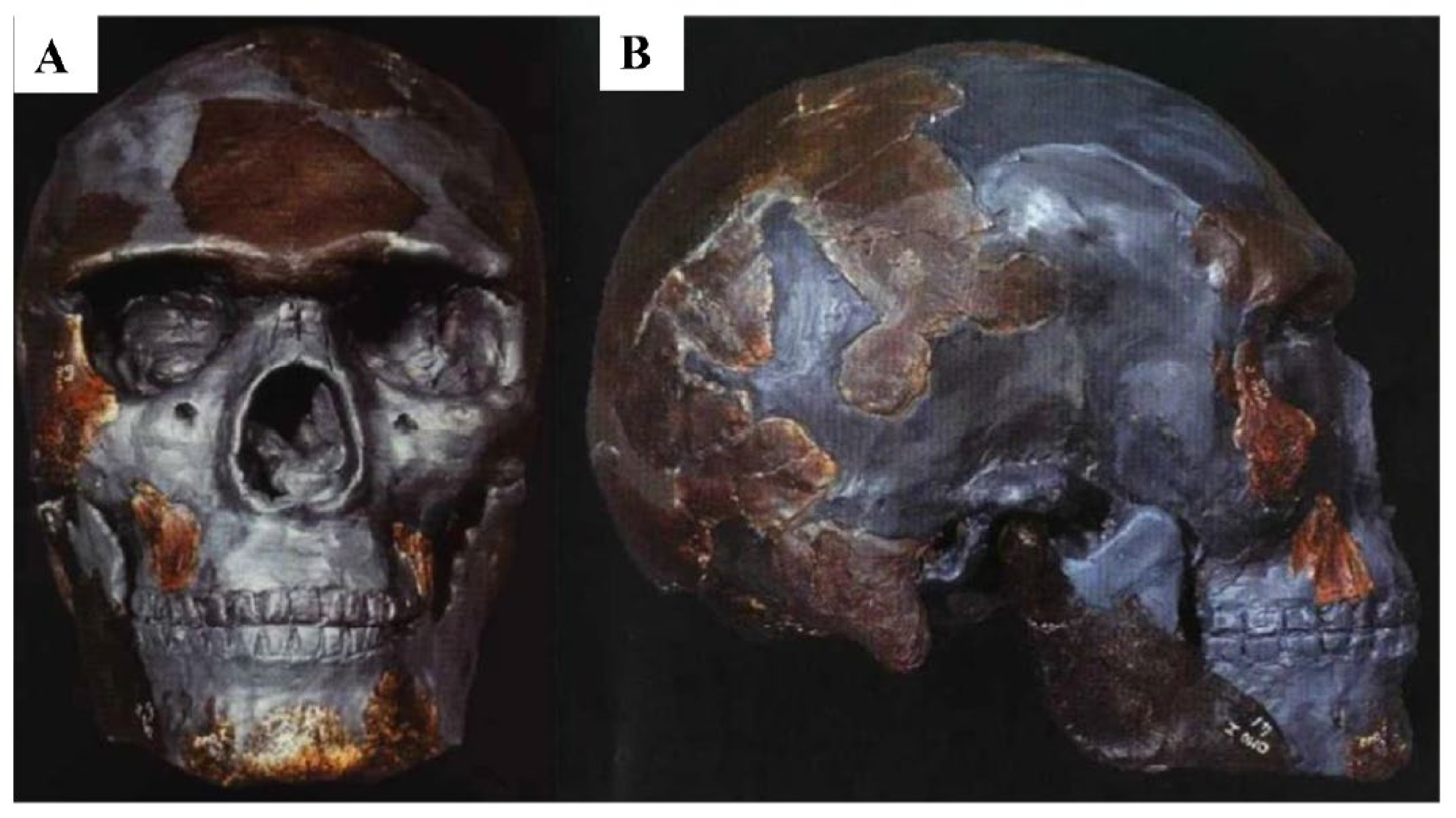
The Omo-Kibish I pelvis **(found 2001)**

Ashley S. Hammond [a,*], Danielle F. Royer [b], John G. Fleagle [c]

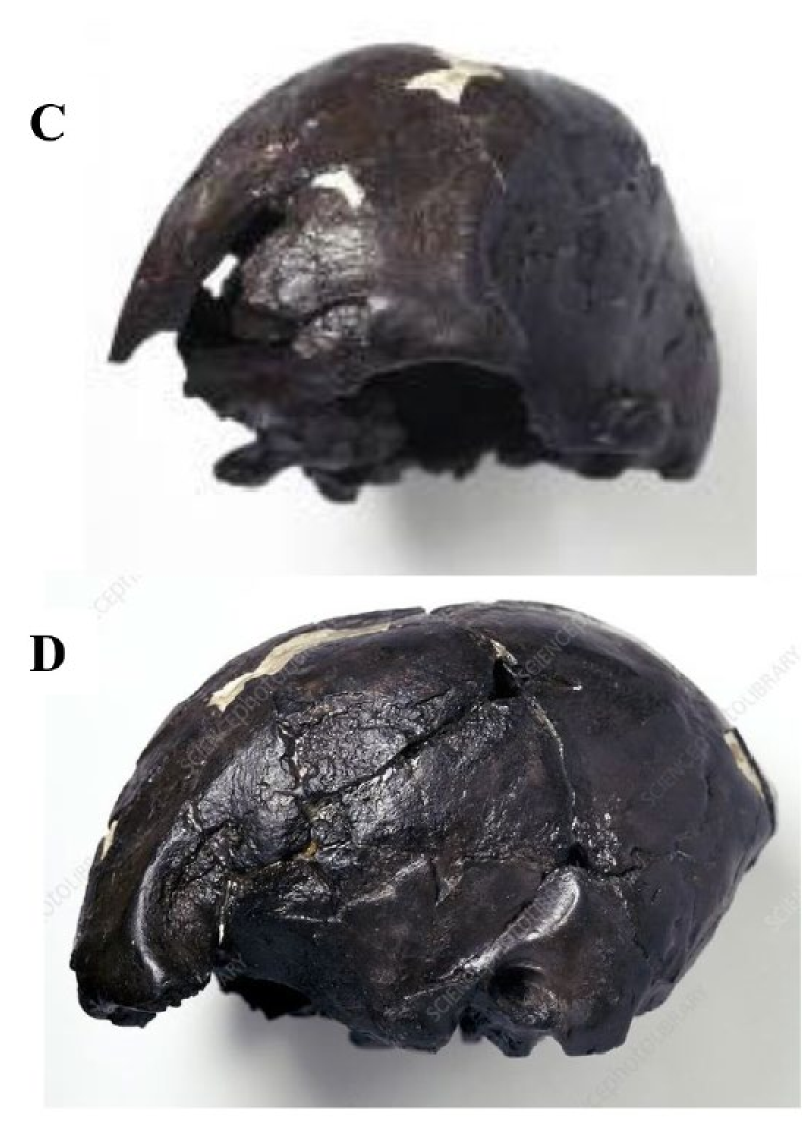
In conclusion, the Omo I hipbone is modern human in appearance. It has modern human apomorphies, including a reduced iliac tubercle (and therefore, reduced iliac pillar) and an ilium that does not appear as widely laterally flaring as earlier *Homo*. The hipbone is within the range of recent human variation for a number of features

Again, evidence that “archaic” and “modern” anatomies overlapped in Africa - found only a few km apart, these crania have both been dated to ~172 ka and are very different in cranial shape...

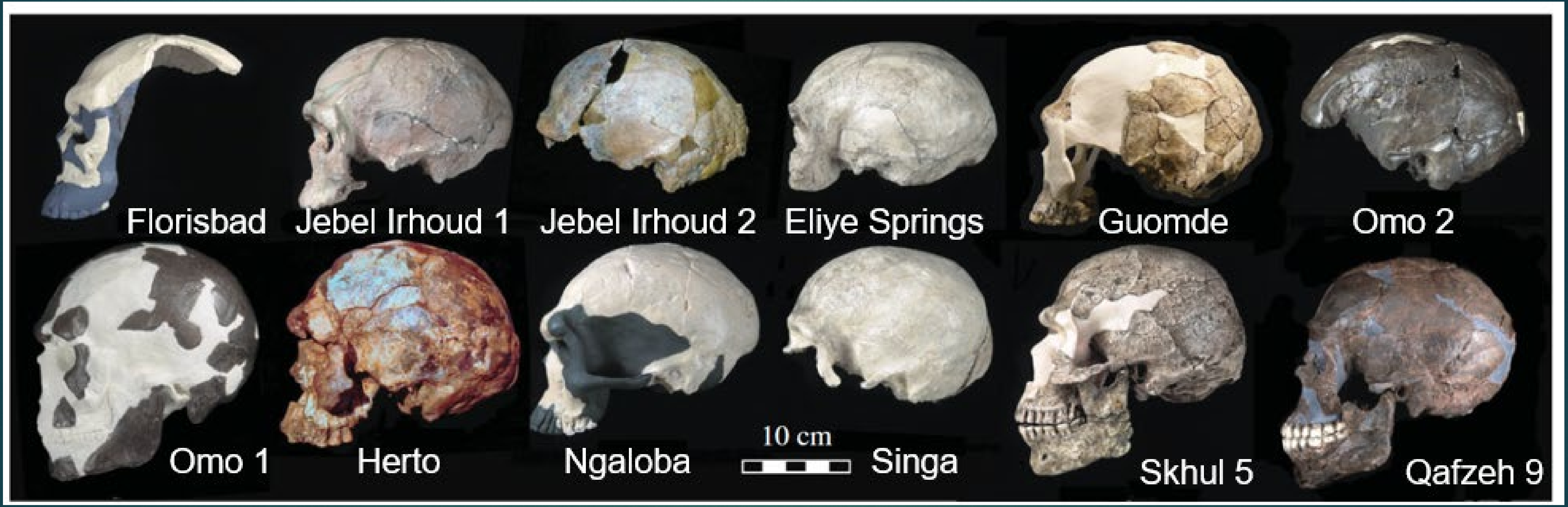
Omo Kibish human remains: Omo 1, 171 Ka



Omo 2: more archaic



African & Israeli sapiens fossils ~300-100 Ka show high variation = No clear pattern of change; even at Omo, 2 same aged distinct fossils

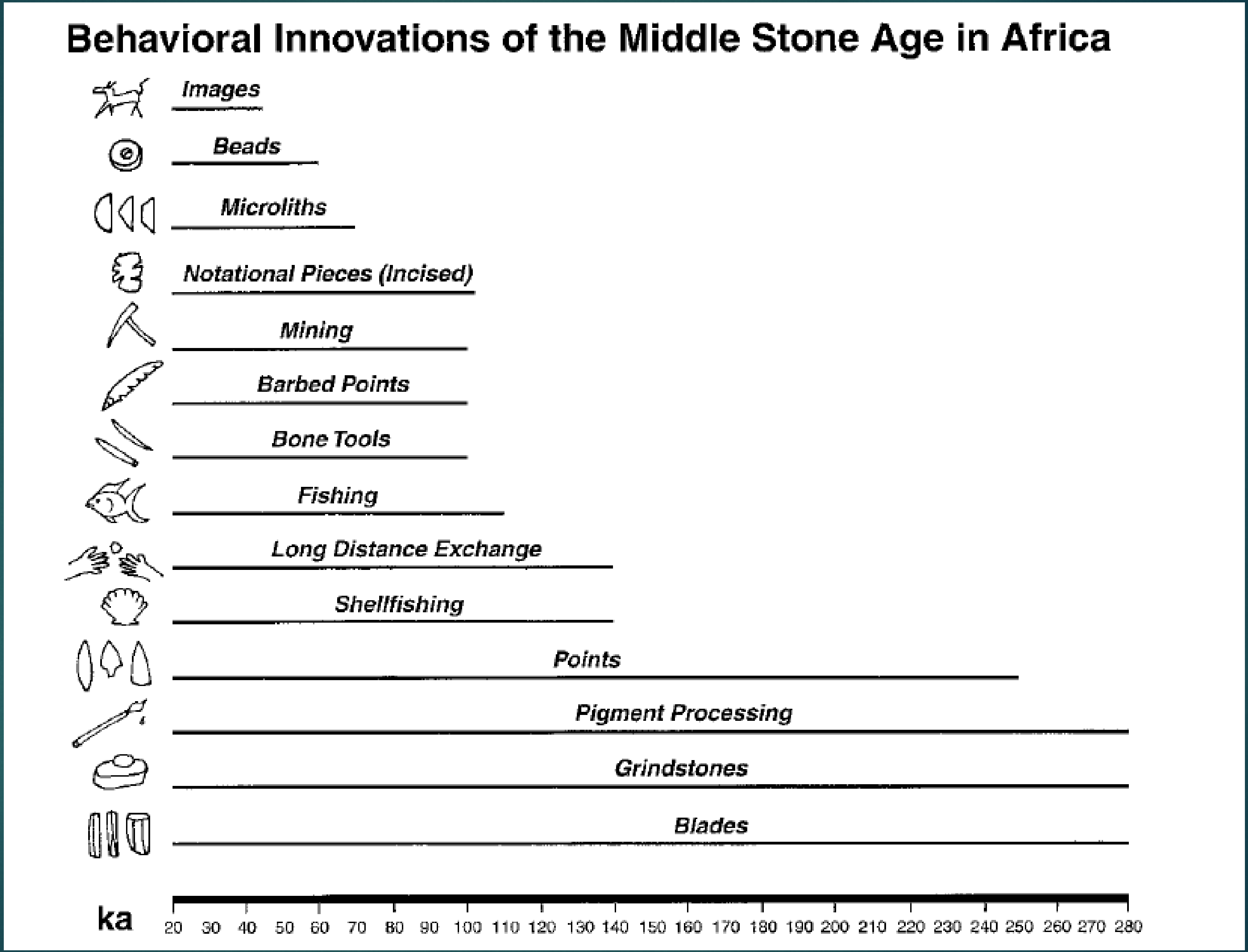


Behavioral Modernity models – See CJV Homo sapiens Pt 3 talk

Two models, 2000:

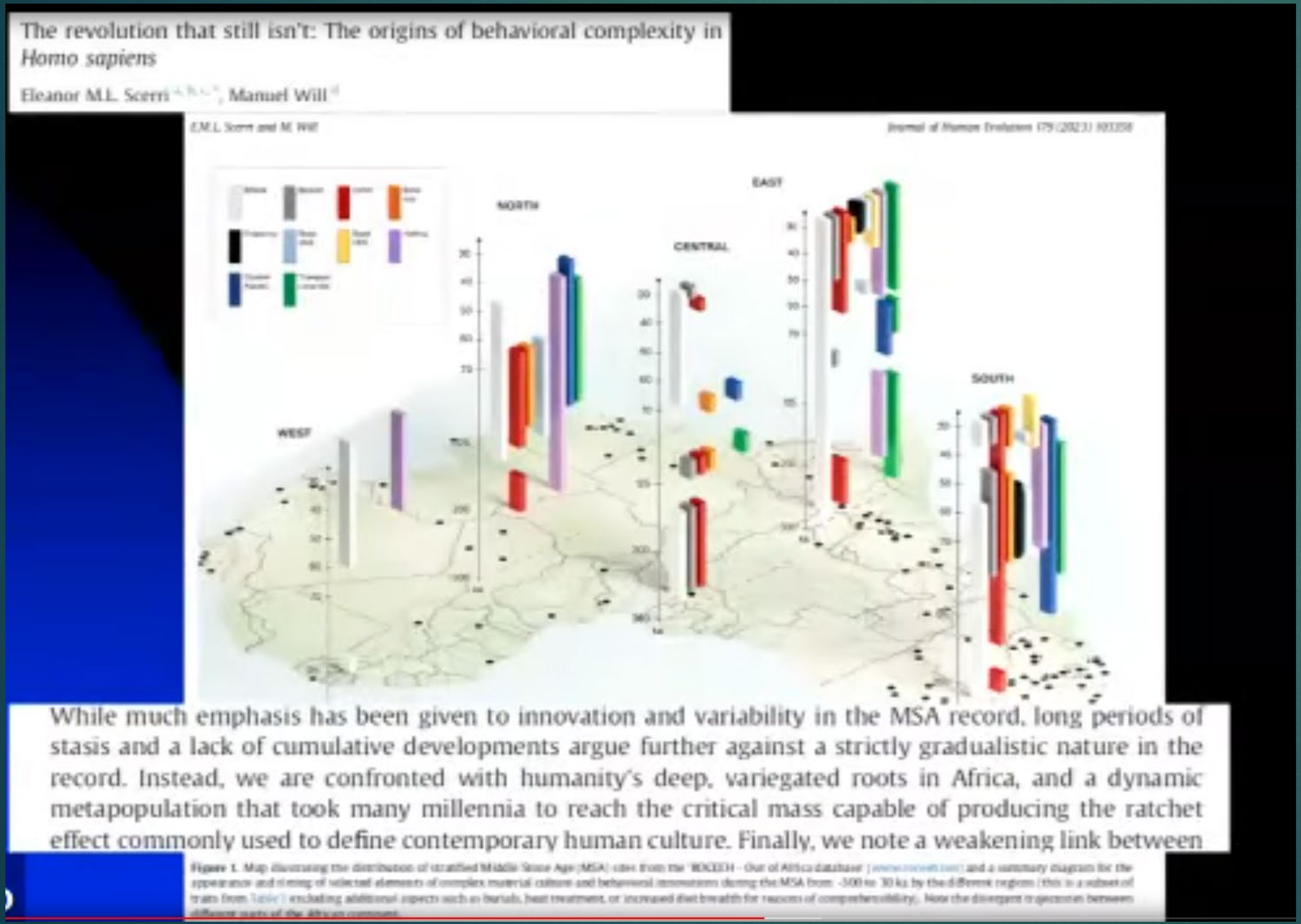
- 1. R. G. Klein, *Archeology and the evolution of human behavior*. Evol. Anthropol. 9, 17–36 (2000). = Cognitive/neuronal genetic change at 50 Ka
- 2. S. Mcbrearty, A. S. Brooks, *The revolution that wasn't: A new interpretation of the origin of modern human behavior*. J. Hum. Evol. 39, 453–563 (2000):
  - One of the most-cited papers in the history of Paleolithic archaeology. This paper argued that behavioral modernity arose in Africa over a long period of time, and that it is visible very early in the MSA archaeological record. This view challenged European-centric models for human evolution that argued for a sudden appearance of behavioral modernity in Europe during the Upper Paleolithic.

Modern behaviors and their time depths in Africa. Sally McBrearty & Alison S. Brooks.



Behavioral Innovations of the Middle Stone Age in Africa

Revolution that still isn’t (E. Scerri & M. Will, 2023): Dynamic metapopulation: multiple complex cultural patterns – beads, feathers, hafting; tech & cultures that appear, disappear, reappear



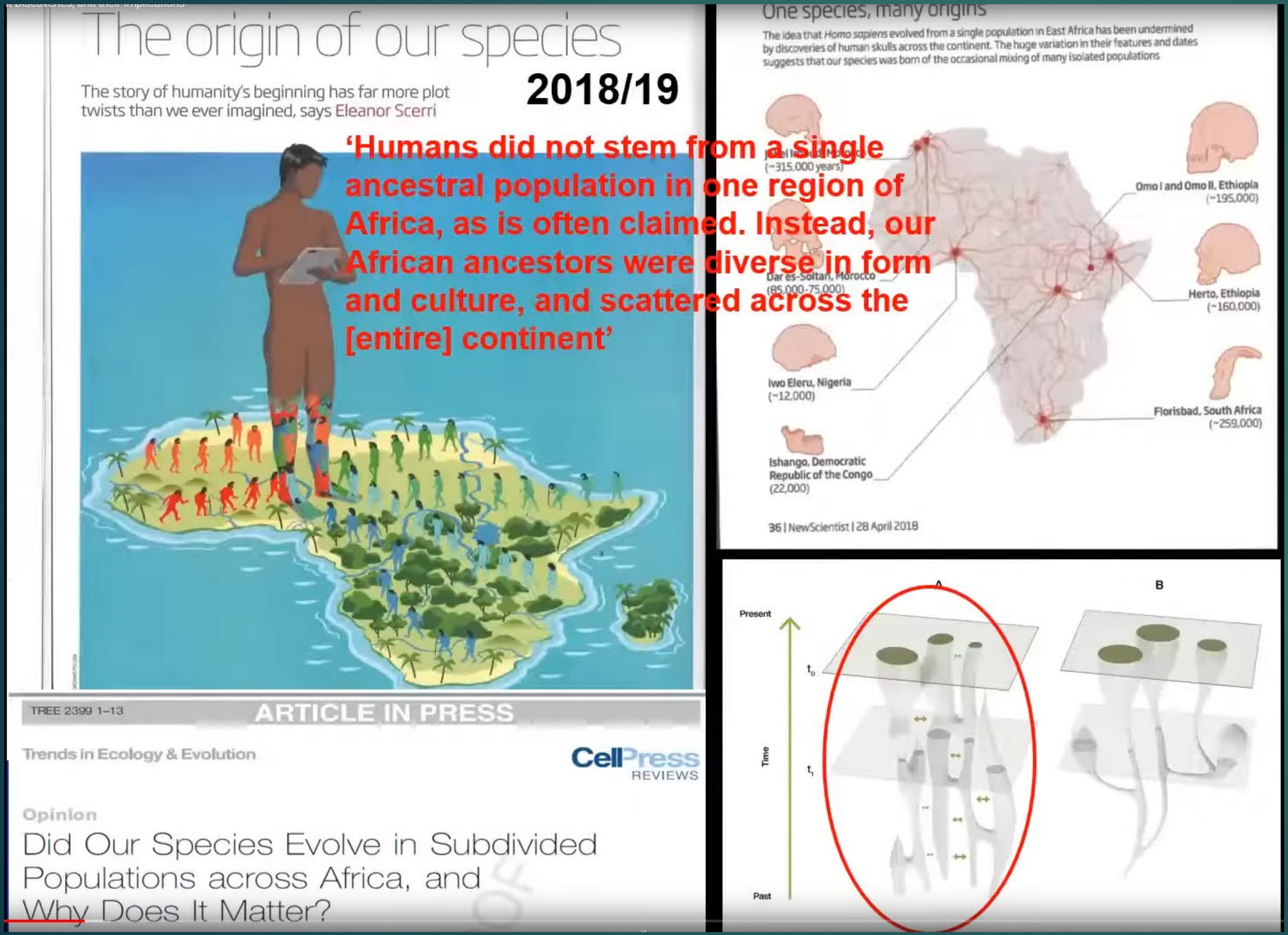
The revolution that still isn't: The origins of behavioral complexity in *Homo sapiens*

Eleanor M.L. Scerri, Manuel Will

While much emphasis has been given to innovation and variability in the MSA record, long periods of stasis and a lack of cumulative developments argue further against a strictly gradualistic nature in the record. Instead, we are confronted with humanity's deep, variegated roots in Africa, and a dynamic metapopulation that took many millennia to reach the critical mass capable of producing the ratchet effect commonly used to define contemporary human culture. Finally, we note a weakening link between

While much emphasis has been given to innovation and variability in the MSA record, long periods of stasis and a lack of cumulative developments argue further against a strictly gradualistic nature in the record. Instead, we are confronted with humanity’s deep, variegated roots in Africa, and a dynamic metapopulation that took many millennia to reach the critical mass capable of producing the ratchet effect commonly used to define contemporary human culture.

Pan African Model of H. sapiens in Africa – E. Scerri, C. Stringer



The origin of our species

The story of humanity's beginning has far more plot twists than we ever imagined, says Eleanor Scerri

2018/19

'Humans did not stem from a single ancestral population in one region of Africa, as is often claimed. Instead, our African ancestors were diverse in form and culture, and scattered across the [entire] continent'

One species, many origins

The idea that *Homo sapiens* evolved from a single population in East Africa has been undermined by discoveries of human skulls across the continent. The huge variation in their features and dates suggests that our species was born of the occasional mixing of many isolated populations

36 | NewScientist | 28 April 2018

TREE 2399 1–13

ARTICLE IN PRESS

Trends in Ecology & Evolution

CellPress REVIEWS

Opinion

Did Our Species Evolve in Subdivided Populations across Africa, and Why Does It Matter?

No single area of origin: Various regions contributed to the final pattern of H. sapiens

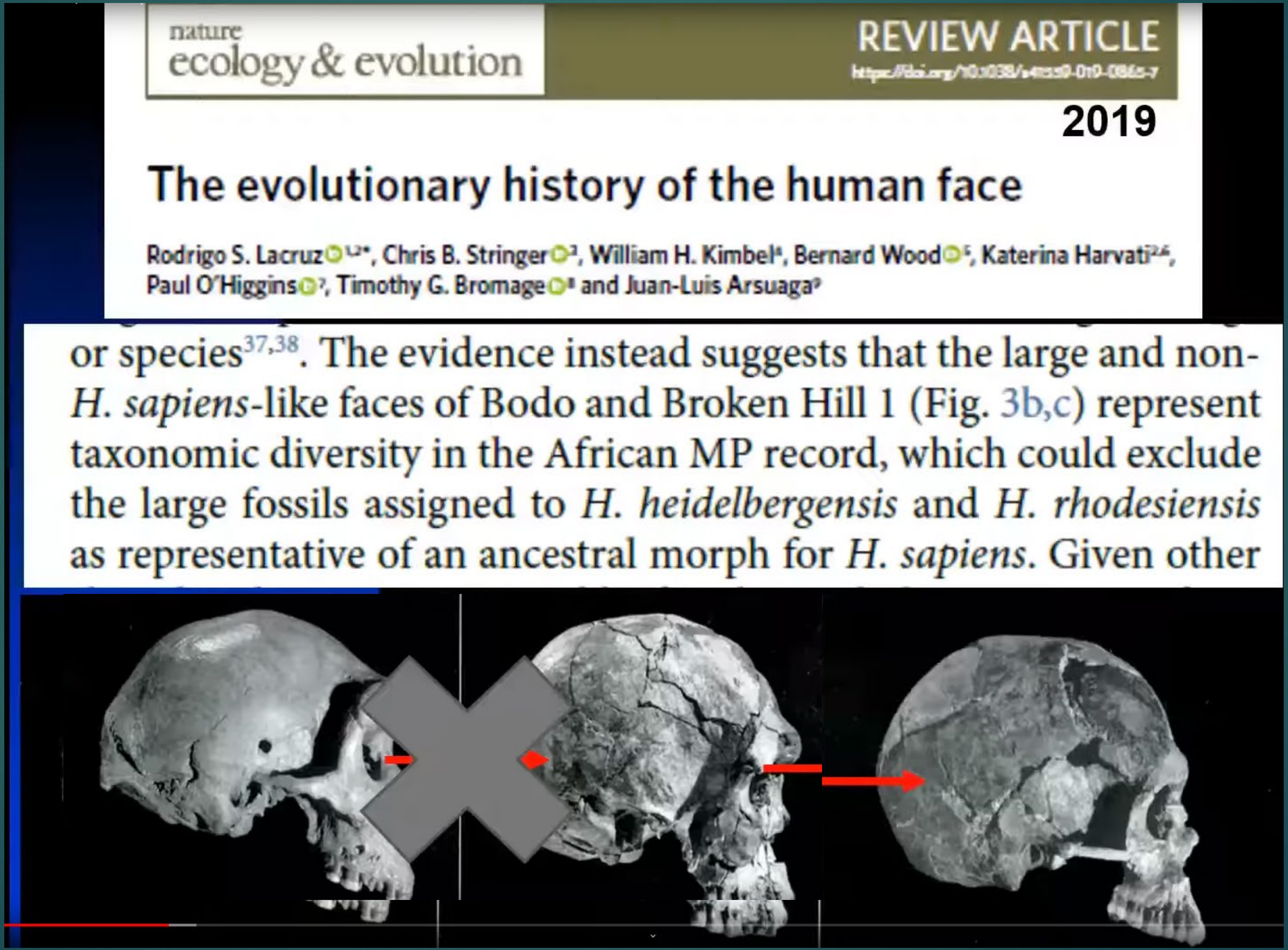
'Scerri: "Humans did not stem from a single ancestral population in one region of Africa, as is often claimed. Instead our African ancestors were diverse in form and culture, and scattered across the [entire] continent'"

Only 10% of Africa has been explored for hominin fossils

The African story gets more complex…

…and our recent fossil record comes from less than 10% of the area of Africa

Broken Hill as African pre-sapiens: Wrong model


nature ecology & evolution

REVIEW ARTICLE

https://doi.org/10.1038/s41559-019-0865-7

2019

The evolutionary history of the human face

Rodrigo S. Lacruz[1,2*], Chris B. Stringer[3], William H. Kimbel[4], Bernard Wood[5], Katerina Harvati[2,6], Paul O'Higgins[7], Timothy G. Bromage[8] and Juan-Luis Arsuaga[9]

or species[37,38]. The evidence instead suggests that the large and non-*H. sapiens*-like faces of Bodo and Broken Hill 1 (Fig. 3b,c) represent taxonomic diversity in the African MP record, which could exclude the large fossils assigned to *H. heidelbergensis* and *H. rhodesiensis* as representative of an ancestral morph for *H. sapiens*. Given other

Explosive 2020 study: Dating change of African "H. heidelbergensis/Broken Hill" from 600 Ka to <u>300 Ka</u>: not LCA of H. sapiens

Dating the skull from Broken Hill, Zambia, and its position in human evolution

2020

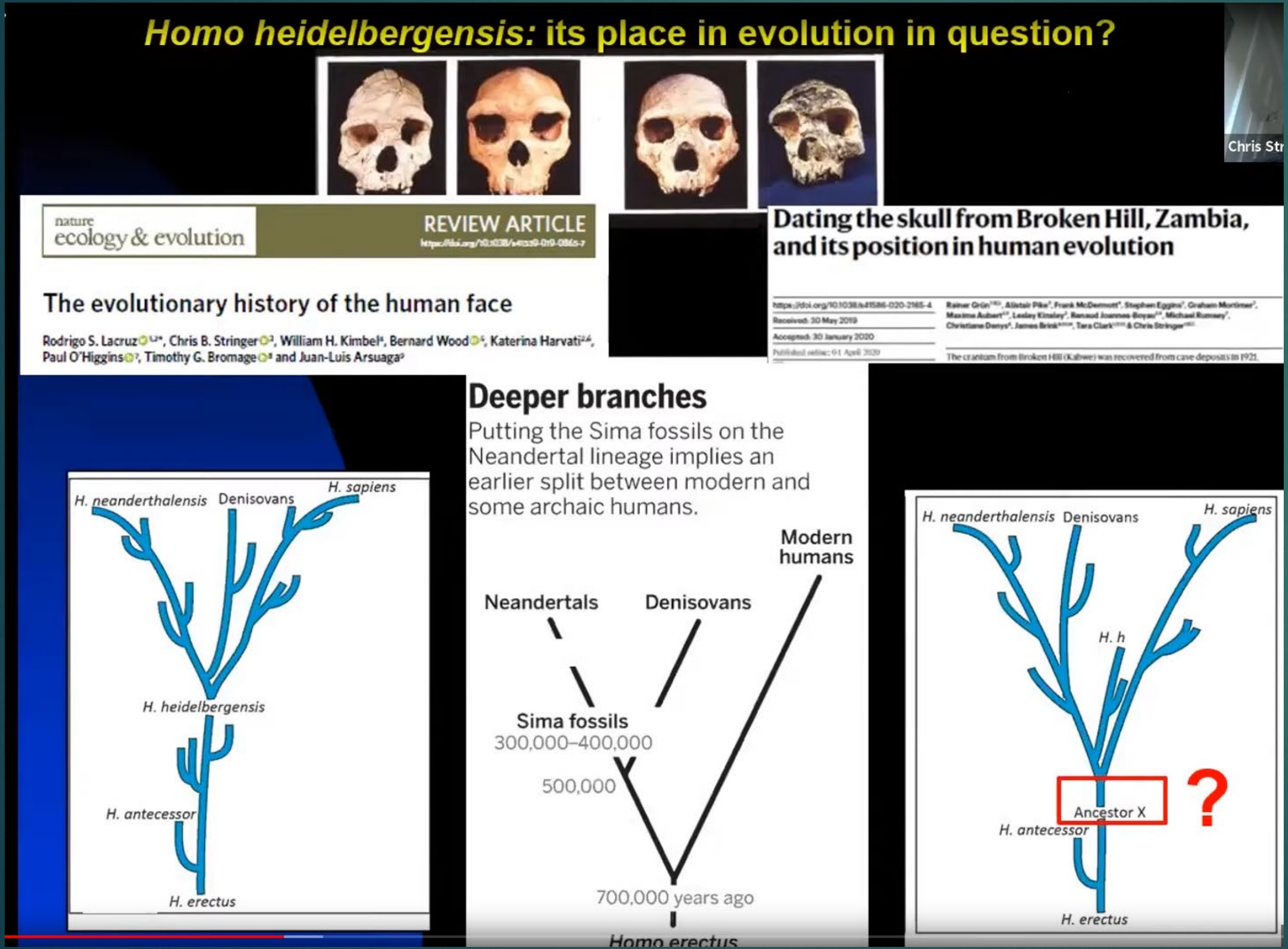
https://doi.org/10.1038/s41586-020-2165-4
Received: 30 May 2019
Accepted: 30 January 2020

Rainer Grün[1,2✉], Alistair Pike[3], Frank McDermott[4], Stephen Eggins[2], Graham Mortimer[2], Maxime Aubert[2,5], Lesley Kinsley[2], Renaud Joannes-Boyau[2,6], Michael Rumsey[7], Christiane Denys[8], James Brink[9,10], Tara Clark[1,11,12] & Chris Stringer[13✉]

The cranium from Broken Hill (Kabwe) was recovered from cave deposits in 1921,

old[5–7]—its unsystematic recovery impedes its accurate dating and placement in human evolution. Here we carried out analyses directly on the skull and found a best age estimate of 299 ± 25 thousand years (mean ± 2σ). The result suggests that later Middle Pleistocene Africa contained multiple contemporaneous hominin lineages (that is, *Homo sapiens*[8,9], *H. heidelbergensis/H. rhodesiensis* and *Homo naledi*[10,11]), similar to Eurasia, where *Homo neanderthalensis*, the Denisovans, *Homo floresiensis*, *Homo luzonensis* and perhaps also *Homo heidelbergensis* and *Homo erectus*[12] were found contemporaneously. The age estimate also raises further questions about the mode of evolution of *H. sapiens* in Africa and whether *H. heidelbergensis/H. rhodesiensis* was a direct ancestor of our species[13,14].

H. heidelbergensis?



***Homo heidelbergensis:* its place in evolution in question?**

nature ecology & evolution

REVIEW ARTICLE

https://doi.org/10.1038/s41559-019-0865-7

The evolutionary history of the human face

Rodrigo S. Lacruz, Chris B. Stringer, William H. Kimbel, Bernard Wood, Katerina Harvati, Paul O'Higgins, Timothy G. Bromage and Juan-Luis Arsuaga

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The cranium from Broken Hill (Kabwe) was recovered from cave deposits in 1921.

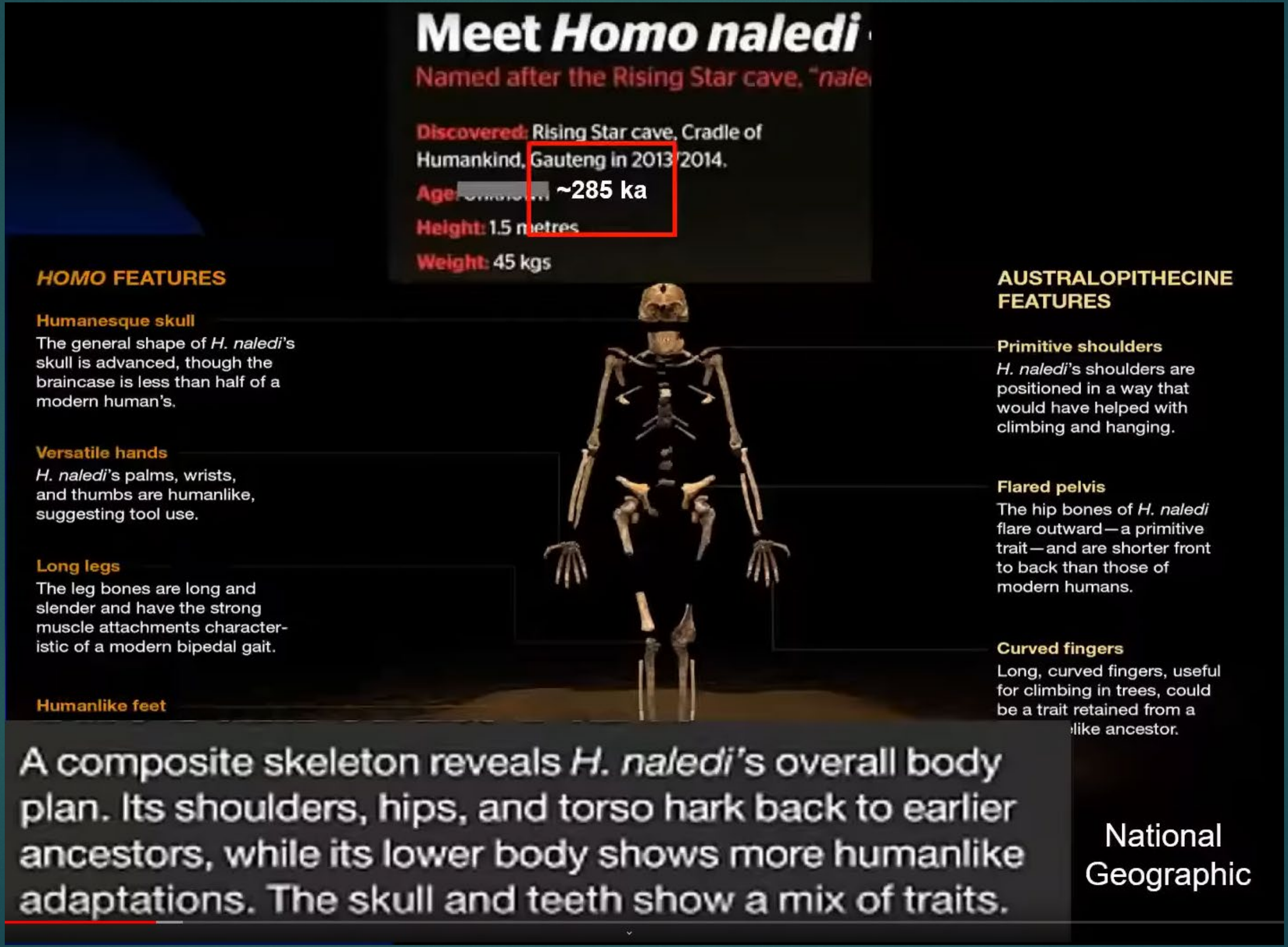
Deeper branches

Putting the Sima fossils on the Neandertal lineage implies an earlier split between modern and some archaic humans.

Broken Hill: 300 Ka – not ancestral, but contemporaneous to basal MHs

Indicates an earlier split time for MHs and Ns = >700 Ka

More complications: in S. Africa, a small brained species, 285 Ka



Meet *Homo naledi*

Named after the Rising Star cave, "*nale*

Discovered: Rising Star cave, Cradle of Humankind, Gauteng in 2013/2014.

Age: [redacted] ~285 ka

Height: 1.5 metres

Weight: 45 kgs

***HOMO* FEATURES**

Humanesque skull
The general shape of *H. naledi*'s skull is advanced, though the braincase is less than half of a modern human's.

Versatile hands
H. naledi's palms, wrists, and thumbs are humanlike, suggesting tool use.

Long legs
The leg bones are long and slender and have the strong muscle attachments characteristic of a modern bipedal gait.

Humanlike feet

AUSTRALOPITHECINE FEATURES

Primitive shoulders
H. naledi's shoulders are positioned in a way that would have helped with climbing and hanging.

Flared pelvis
The hip bones of *H. naledi* flare outward—a primitive trait—and are shorter front to back than those of modern humans.

Curved fingers
Long, curved fingers, useful for climbing in trees, could be a trait retained from a like ancestor.

A composite skeleton reveals *H. naledi*'s overall body plan. Its shoulders, hips, and torso hark back to earlier ancestors, while its lower body shows more humanlike adaptations. The skull and teeth show a mix of traits.

National Geographic

Africa at about 300,000 years: *at least* 3 species?

First forays into Europe

- Only a few years ago it was still possible to argue that even though H. sapiens began to disperse from its ancestral African homeland at least 60 ka ago, the arrival of our species in Europe took much longer, perhaps only occurring with the arrival of Aurignacian industries about 41 ka ago
- This delay was hypothesized to have been caused by the need to develop adaptations to colder European environments, or possibly because the resident human species H. neanderthalensis successfully excluded H. sapiens for many millennia.
- However, since 2019 there has been a succession of publications that demonstrate a longer-term potential co-existence of early H. sapiens and late Neanderthals not only in western Asia, as previously observed, but also in Europe. Moreover, ancient DNA evidence shows that this overlap was accompanied by multiple episodes of interbreeding

CJV’s Review of 15 known introgression events: See aDNA talks

- mtDNA Gene flow from Neanderthals
- mtDNA Gene flow from Denisovans
- 1. The most referenced introgression: 2% N DNA into MH
- 2. N DNA into Ds and vise versa
- 3. Ghost population of Archaic Hominin (*H. erectus*?) into Denisovan DNA = 2-6% of D
- 4. Archaic Asian hominin DNA into MHs
- 5. MH DNA into Ns – 200 Ka: Ns who gave us 2%, already had 3-6% of MH DNA in their DNA
- 6. N’s mtDNA inherited from MHs – 270 Ka

Genetic evidence for 15 known introgression events

- 7. MH DNA into nuclear N genome in Middle East ~100 Ka
- 8. MH DNA into Altai Ns ~100 Ka
- 9. Altai N DNA into East Asian MHs ~100 Ka
- 10. N DNA into Ds
- 11. Oase-1: early MH HG with N DNA
- 12. D DNA into MHs
- 13. Archaic hominin into MHs in Africa
- 14. Archaic DNA in the San of South Africa
- 15. Ghost lineages in 4 West African Groups

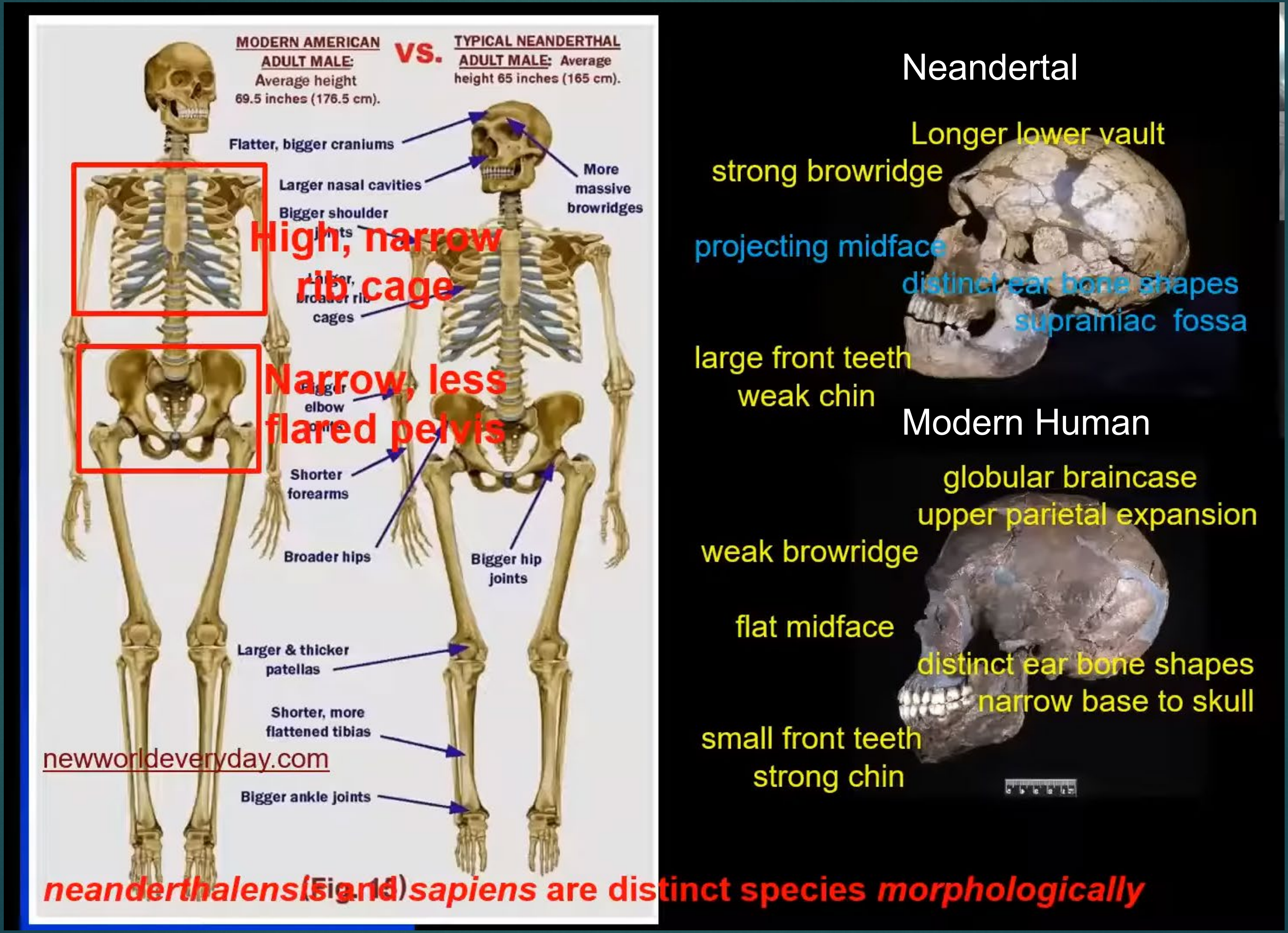
The Neanderthals – a changing image


Kupka 1909

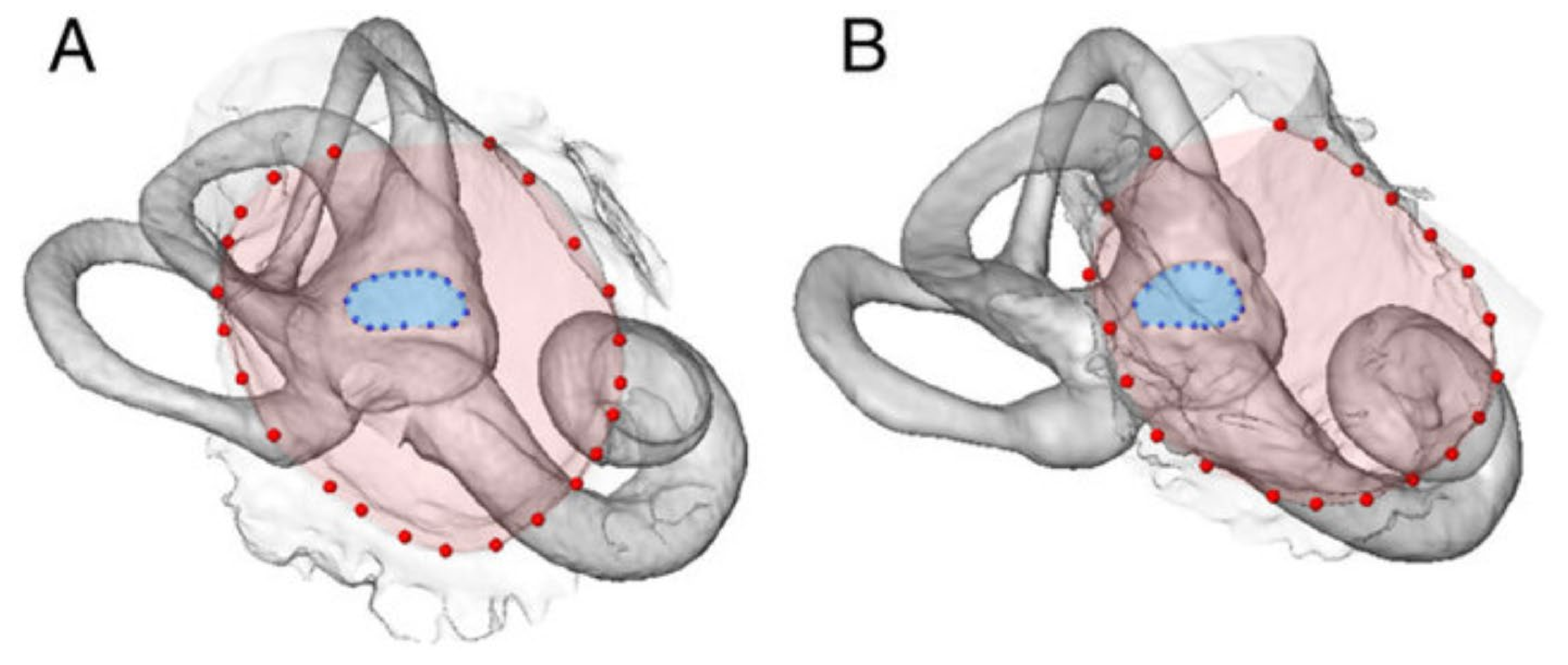

Neander Valley 1856


NHM London

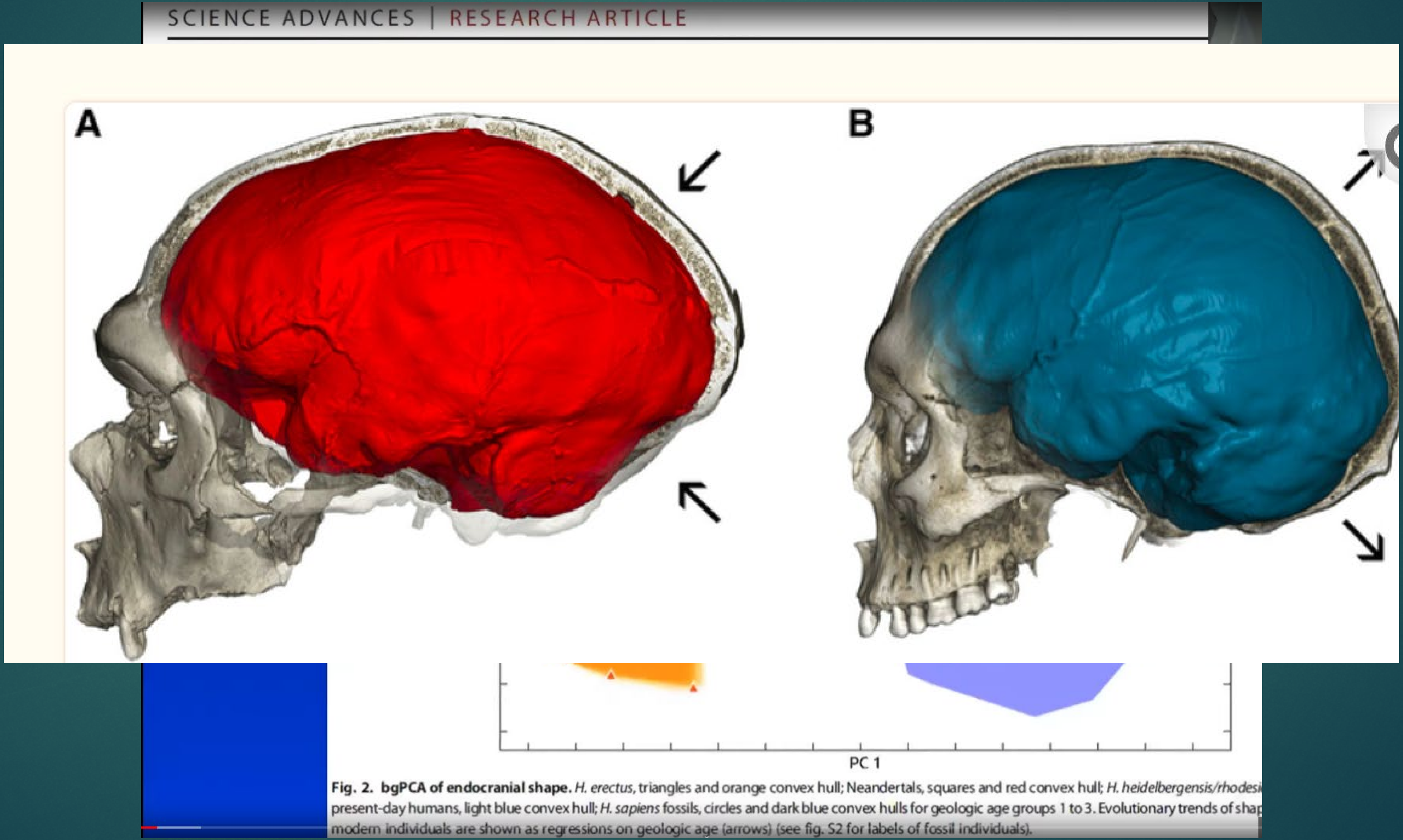
Neandertal: A different kind of human



Distinctive middle ear morphologies



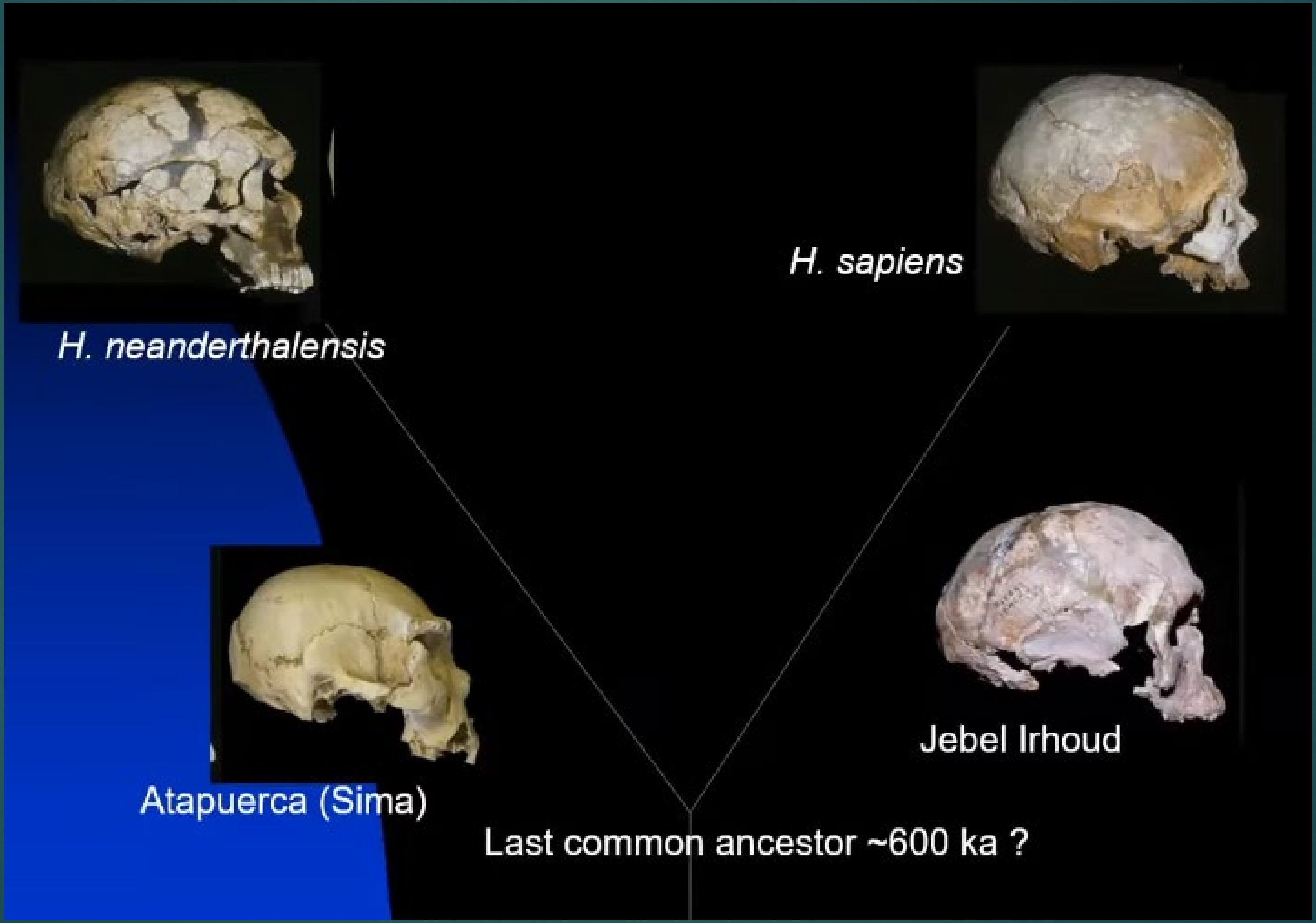
Endocast shape: distinctive N and MH brain shapes



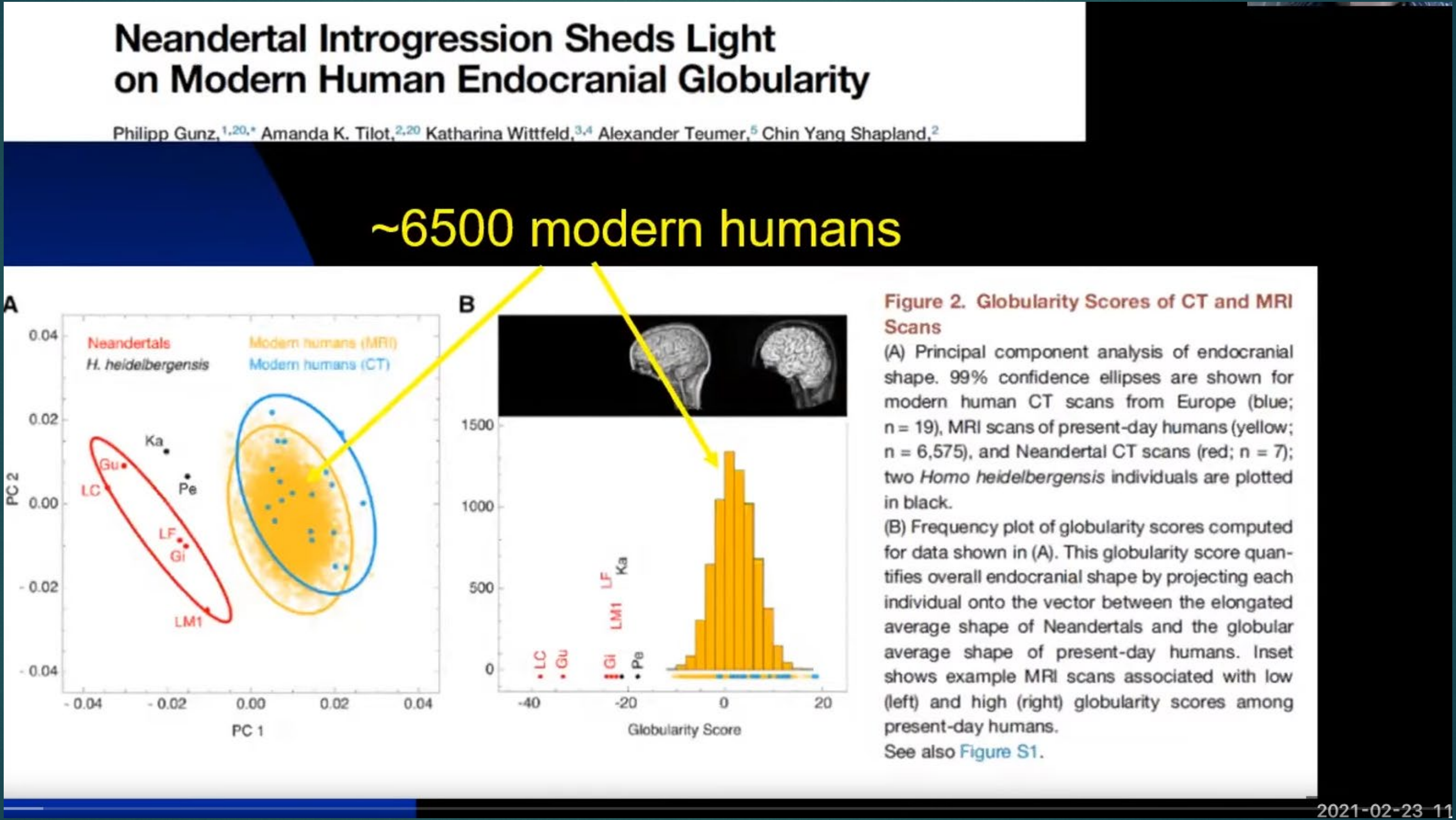
SCIENCE ADVANCES | RESEARCH ARTICLE

Fig. 2. bgPCA of endocranial shape. *H. erectus*, triangles and orange convex hull; Neandertals, squares and red convex hull; *H. heidelbergensis/rhodesi*
present-day humans, light blue convex hull; *H. sapiens* fossils, circles and dark blue convex hulls for geologic age groups 1 to 3. Evolutionary trends of shap
modern individuals are shown as regressions on geologic age (arrows) (see fig. S2 for labels of fossil individuals).

Basal and derived Ns and MHs



Globular skull shape of MHs based on CT endocranial data



Neandertal Introgression Sheds Light on Modern Human Endocranial Globularity

Philipp Gunz,[1,20,*] Amanda K. Tilot,[2,20] Katharina Wittfeld,[3,4] Alexander Teumer,[5] Chin Yang Shapland,[2]

~6500 modern humans

Figure 2. Globularity Scores of CT and MRI Scans

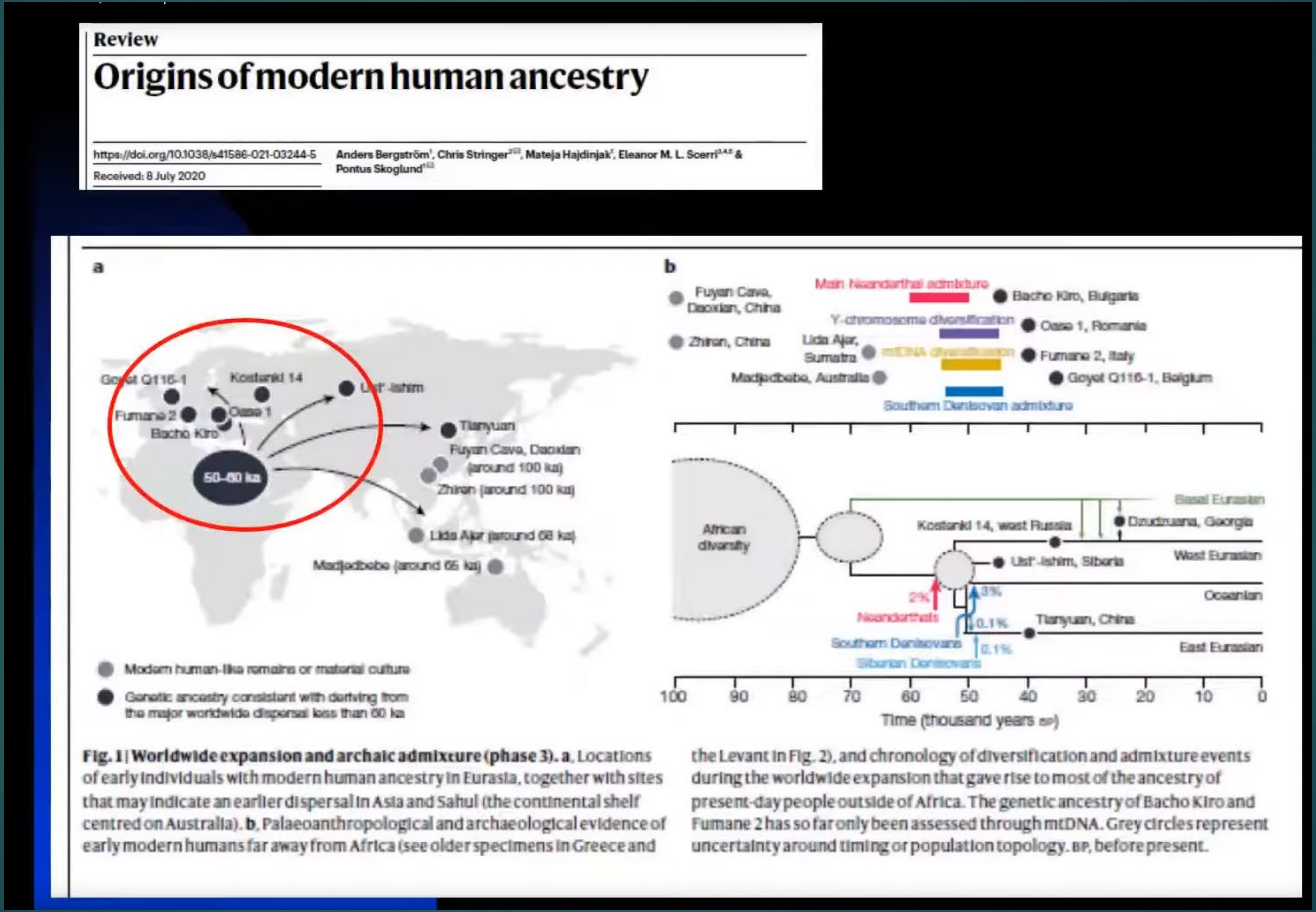
(A) Principal component analysis of endocranial shape. 99% confidence ellipses are shown for modern human CT scans from Europe (blue; n = 19), MRI scans of present-day humans (yellow; n = 6,575), and Neandertal CT scans (red; n = 7); two *Homo heidelbergensis* individuals are plotted in black.

(B) Frequency plot of globularity scores computed for data shown in (A). This globularity score quantifies overall endocranial shape by projecting each individual onto the vector between the elongated average shape of Neandertals and the globular average shape of present-day humans. Inset shows example MRI scans associated with low (left) and high (right) globularity scores among present-day humans.

See also Figure S1.

2021-02-23 11

MH genetics leave Africa



Review

Origins of modern human ancestry

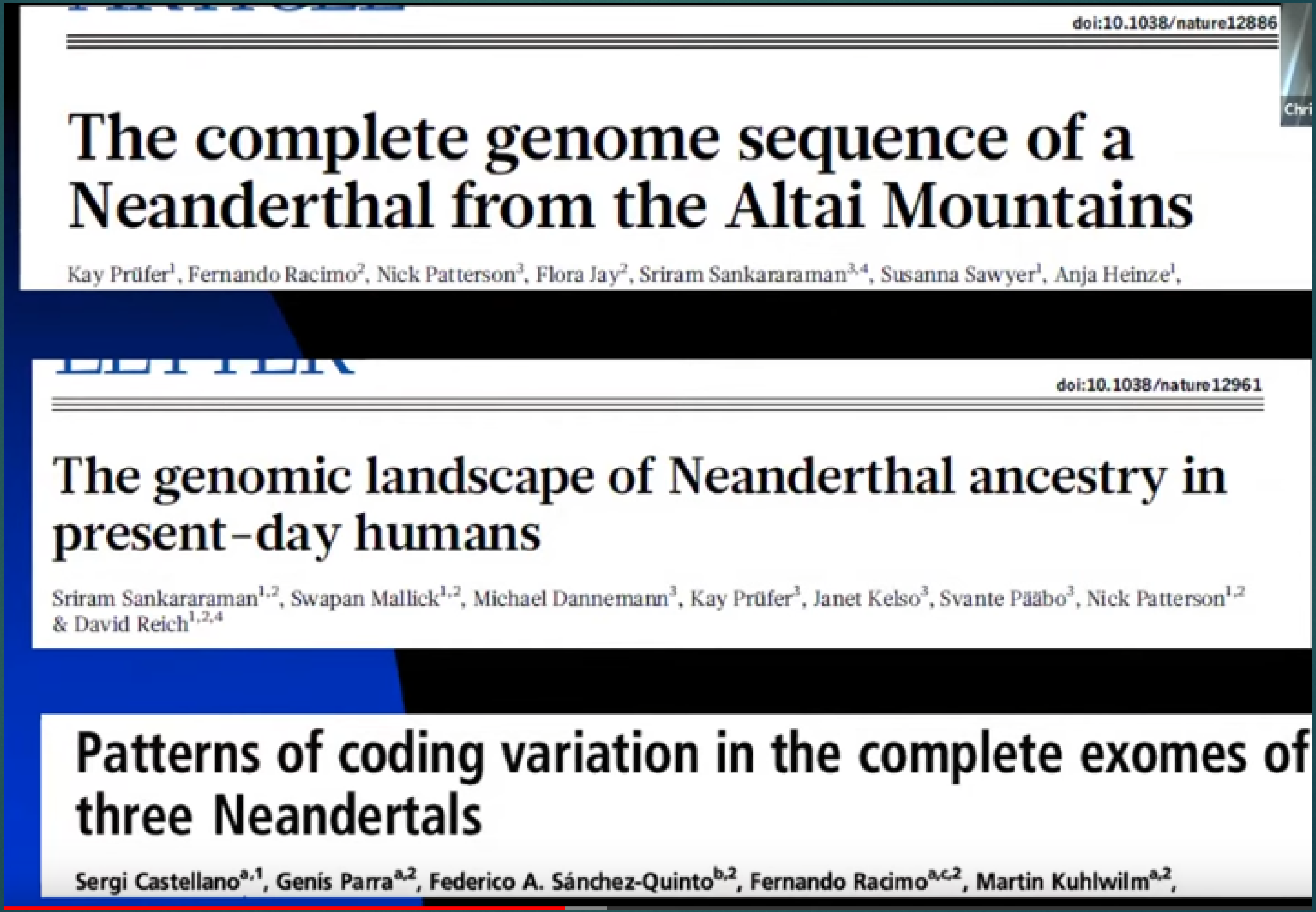
https://doi.org/10.1038/s41586-021-03244-5

Received: 8 July 2020

Anders Bergström[1], Chris Stringer[2]✉, Mateja Hajdinjak[1], Eleanor M. L. Scerri[3,4,5] & Pontus Skoglund[1]✉

Fig. 1 | Worldwide expansion and archaic admixture (phase 3). a, Locations of early individuals with modern human ancestry in Eurasia, together with sites that may indicate an earlier dispersal in Asia and Sahul (the continental shelf centred on Australia). **b**, Palaeoanthropological and archaeological evidence of early modern humans far away from Africa (see older specimens in Greece and the Levant in Fig. 2), and chronology of diversification and admixture events during the worldwide expansion that gave rise to most of the ancestry of present-day people outside of Africa. The genetic ancestry of Bacho Kiro and Fumane 2 has so far only been assessed through mtDNA. Grey circles represent uncertainty around timing or population topology. BP, before present.

aDNA revolution starts in 2010



doi:10.1038/nature12886

The complete genome sequence of a Neanderthal from the Altai Mountains

Kay Prüfer[1], Fernando Racimo[2], Nick Patterson[3], Flora Jay[2], Sriram Sankararaman[3,4], Susanna Sawyer[1], Anja Heinze[1],

doi:10.1038/nature12961

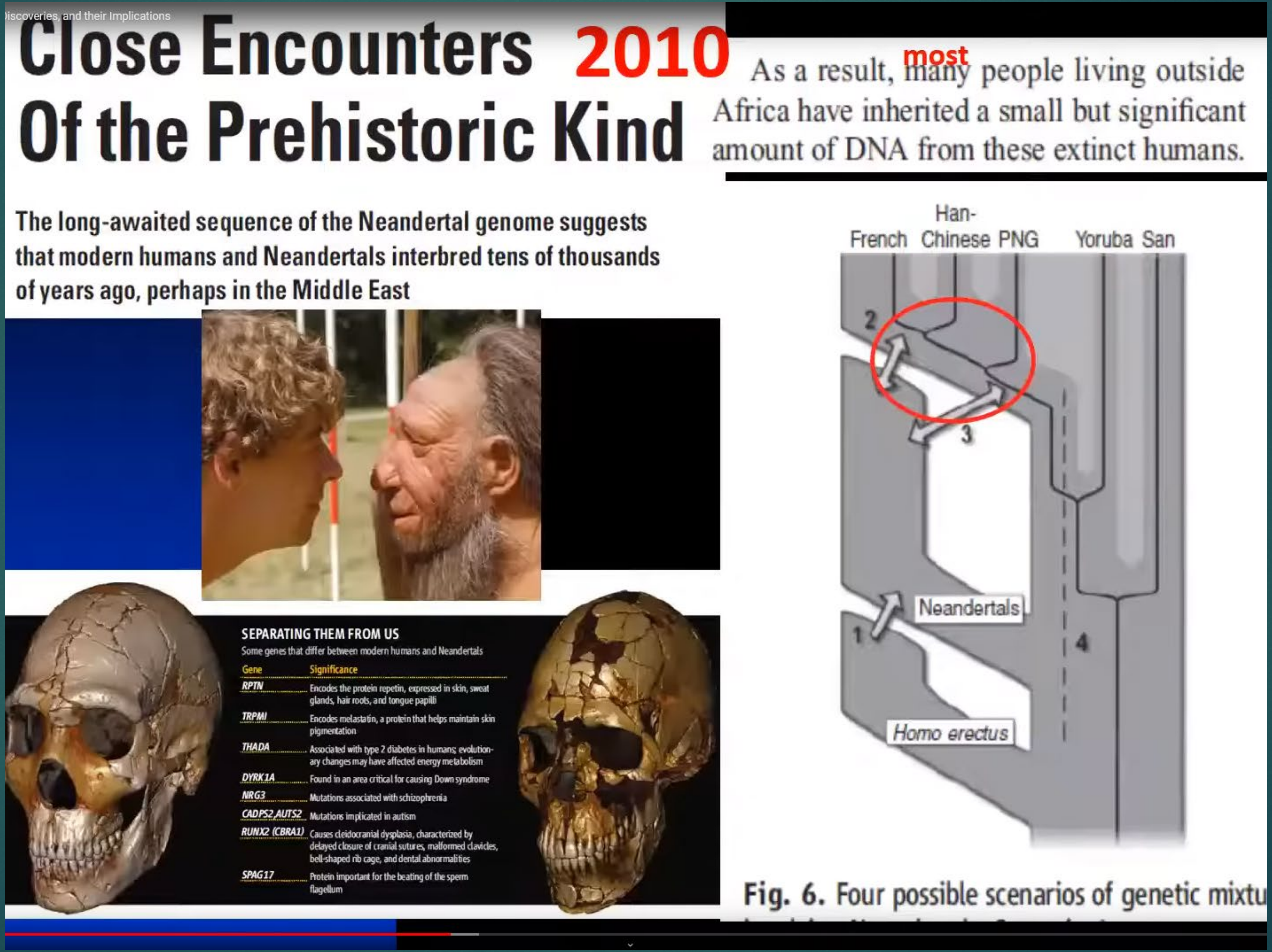
The genomic landscape of Neanderthal ancestry in present-day humans

Sriram Sankararaman[1,2], Swapan Mallick[1,2], Michael Dannemann[3], Kay Prüfer[3], Janet Kelso[3], Svante Pääbo[3], Nick Patterson[1,2] & David Reich[1,2,4]

Patterns of coding variation in the complete exomes of three Neandertals

Sergi Castellano[a,1], Genís Parra[a,2], Federico A. Sánchez-Quinto[b,2], Fernando Racimo[a,c,2], Martin Kuhlwilm[a,2],

2010: 1-2% N DNA in MHs



Close Encounters Of the Prehistoric Kind 2010

The long-awaited sequence of the Neandertal genome suggests that modern humans and Neandertals interbred tens of thousands of years ago, perhaps in the Middle East

SEPARATING THEM FROM US

Some genes that differ between modern humans and Neandertals

Gene	Significance
RPTN	Encodes the protein repetin, expressed in skin, sweat glands, hair roots, and tongue papilli
TRPMI	Encodes melastatin, a protein that helps maintain skin pigmentation
THADA	Associated with type 2 diabetes in humans; evolutionary changes may have affected energy metabolism
DYRK1A	Found in an area critical for causing Down syndrome
NRG3	Mutations associated with schizophrenia
CADPS2,AUTS2	Mutations implicated in autism
RUNX2 (CBRA1)	Causes cleidocranial dysplasia, characterized by delayed closure of cranial sutures, malformed clavicles, bell-shaped rib cage, and dental abnormalities
SPAG17	Protein important for the beating of the sperm flagellum

As a result, most many people living outside Africa have inherited a small but significant amount of DNA from these extinct humans.

Fig. 6. Four possible scenarios of genetic mixtu

How did introgressions happen?

Chimpanzees expand their territory by attacking and killing neighbours

A study has proved for the first time that groups of aggressive chimpanzees invade the territory of their neighbours in order to acquire more resources or mates

Chimpanzees cooperate to acquire new territory, killing indi
Photograph: Michael S. Lewis/Corbis

Gangs of chimpanzees carry out violent attacks o
groups in order to secure more resources or mate
has found.

Capturing females?

Napoleon Chagnon provoked uproar with his account of life in an Amazon community. His latest work has reopened the debate

ritual dance: their defenders say they are being depicted as
their land. Photograph: Leo Ramirez/Getty

scientific arguments in recent times: are the
mazon rainforest a symbol of how to live in peace
remnants of humanity's brutal early history?

Opportunistic pairings?

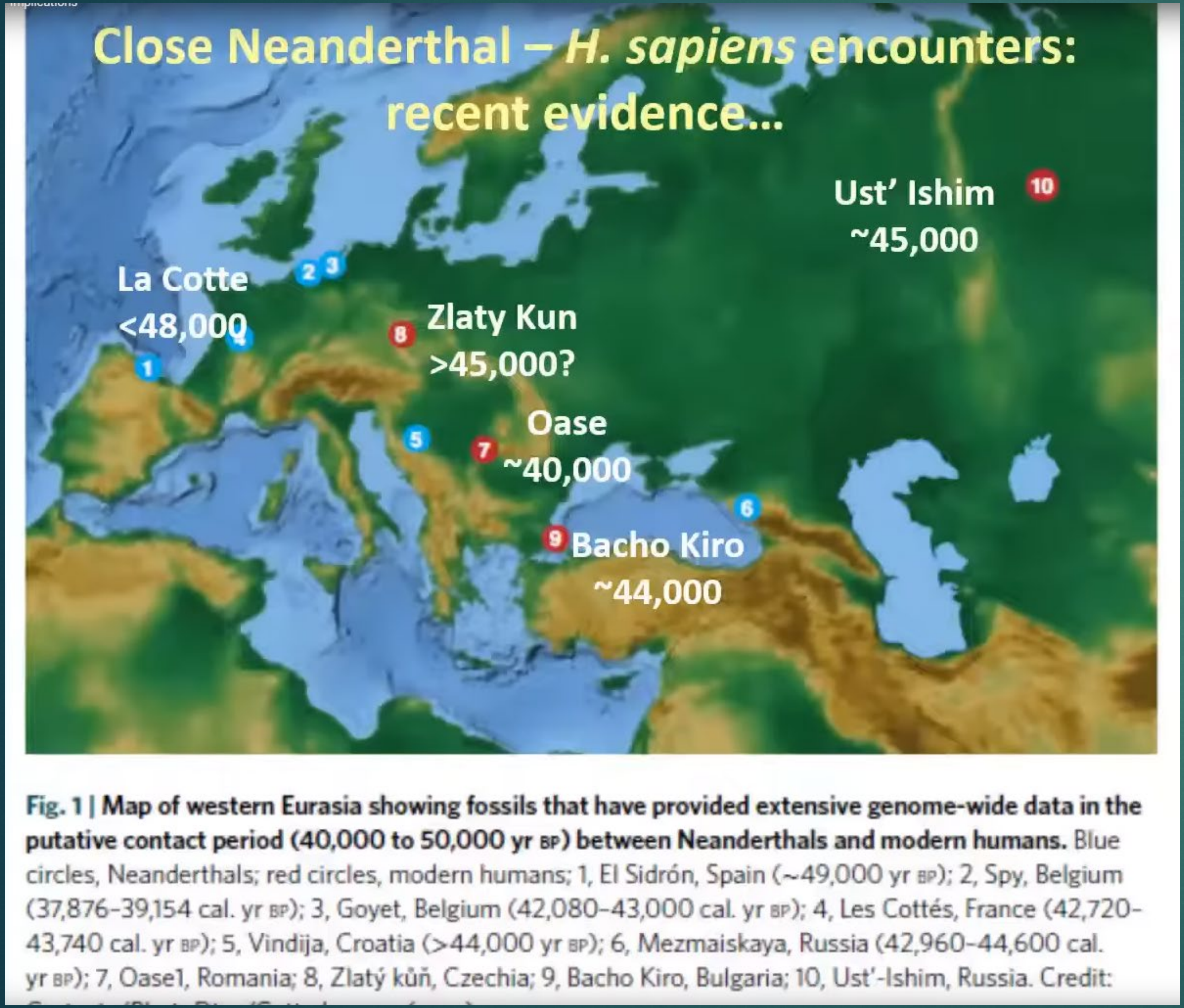
How did the interbreeding actually happen?

Peaceful exchanges or absorption?

Adopting orphans?

- Capturing females
- Opportunistic pairings
- Peaceful exchanges on absorption
- Adopting orphans

All early MHs in Europe had N DNA



Close Neanderthal – *H. sapiens* encounters: recent evidence...

Fig. 1 | Map of western Eurasia showing fossils that have provided extensive genome-wide data in the putative contact period (40,000 to 50,000 yr BP) between Neanderthals and modern humans. Blue circles, Neanderthals; red circles, modern humans; 1, El Sidrón, Spain (~49,000 yr BP); 2, Spy, Belgium (37,876–39,154 cal. yr BP); 3, Goyet, Belgium (42,080–43,000 cal. yr BP); 4, Les Cottés, France (42,720–43,740 cal. yr BP); 5, Vindija, Croatia (>44,000 yr BP); 6, Mezmaiskaya, Russia (42,960–44,600 cal. yr BP); 7, Oase1, Romania; 8, Zlatý kůň, Czechia; 9, Bacho Kiro, Bulgaria; 10, Ust'-Ishim, Russia. Credit:

Blue circles. Neanderthals; red circles, modern humans;
1, El Sidrón, Spain (~49 Ka);
2, Spy, Belgium (37-39 Ka;
3, Goyet, Belgium (42-43 Ka);
4, Les Cottés, France (43 Ka);
5, Vindija, Croatia (44 Ka);
6, Mezmaiskaya, Russia (43-45 Ka);
7, Oase I, Romania (40 Ka)
8, Zlaty Kun, Czechia (45 Ka)
9, Bacho Kiro, Bulgaria (44 Ka)
10, Ust'-Ishim, Russia (45 Ka)

CJV: Earliest *H. sapiens, Ns*

- 765–550 Ka: MH-N split
- 415 KA: earliest Ns at Sima de los Huesos, Spain
- 315 Ka: Jebel Irhoud, Morocco
- 300 Ka: Kabwe/Broken Hill, Zambia (H. rhodesiensis); not 600 Ka or H. heidelbergensis
- 259 Ka?: Florisbad, South Africa
- 171 Ka: Omo, Ethiopia
- 160 Ka: Herto, Ethiopia
- 90 Ka: Skhul, Israel

Sima de los Huesos
Cranium 5

Jebel Irhoud, H. sapiens

Kabwe/Broken Hill

Omo 1, H. sapiens

Herto

Skhul, Israel

Florisbad

Apidima

Zlat-ka, Czech

List of earliest *H sapiens* in Europe

- 270 Ka: Hohlenstein–Stadel, Germany (N femur with sapiens mtDNA)
- 210 Ka: Apidima, Greece
- 60 Ka: estimated N-MH interbreeding in Western Eurasia (Near East); consistent with introgressed modern human genes in a 50 Ka-old Neandertal from the Altai Mountains of Siberia
- 54 Ka: Mandrin Grotto, France: a MH tooth; then again at 45 Ka

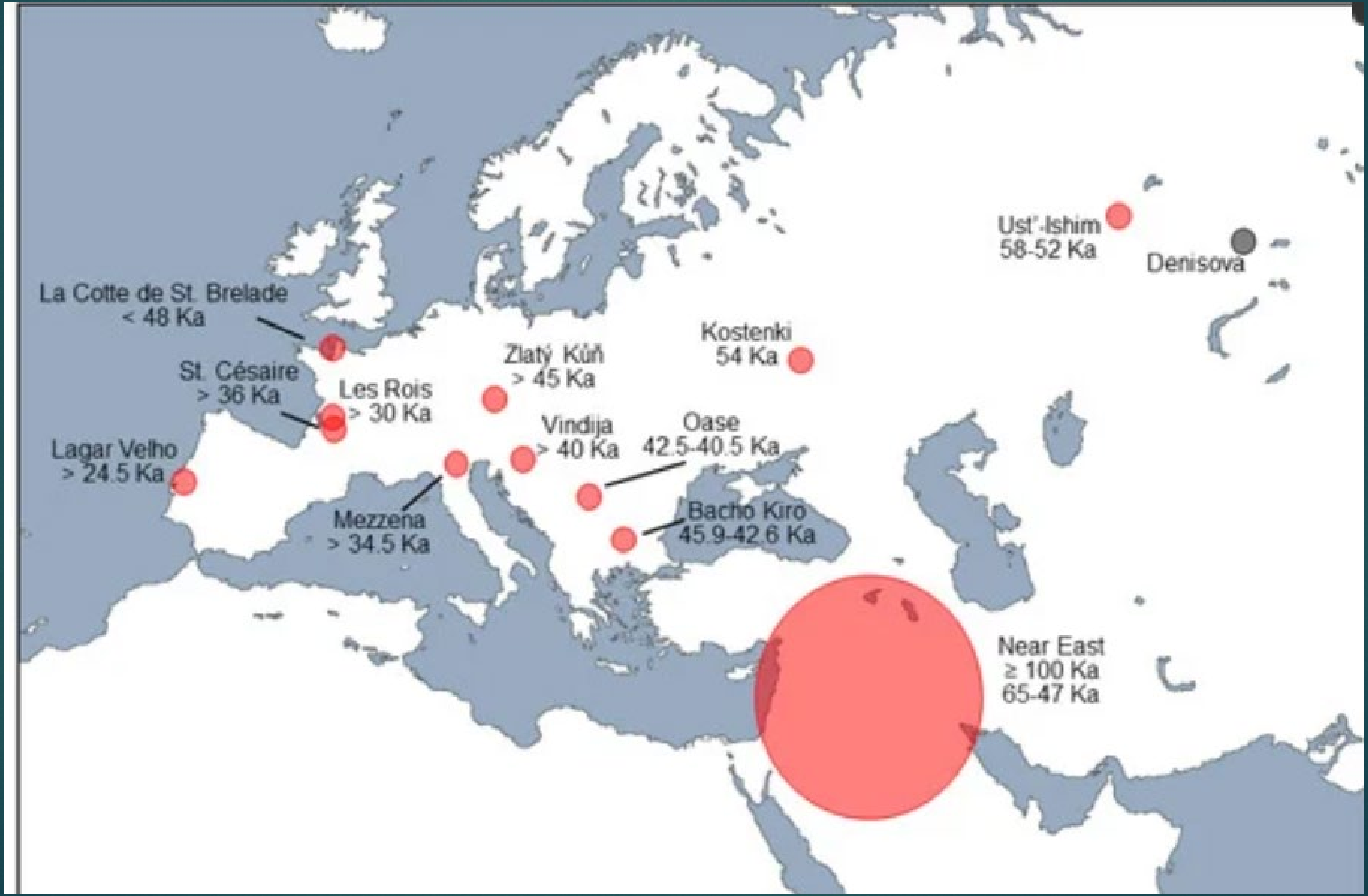
List of earliest *H sapiens* in Europe

- Earliest credible evidence H. sapiens stone tools found in South-Central Europe (Bohunician industry): Brno-Bohunice and Stránská skála (Moravia) (48 Ka), Bacho Kiro and Temnata Cave (Bulgaria), Dzierzyslaw (Poland)
- 45 Ka: Ranis, Germany: 10 bones -- – (no later European descendants) (N % untested)
- 45 Ka: Zlat-ka (Czech Republic) (3% N)

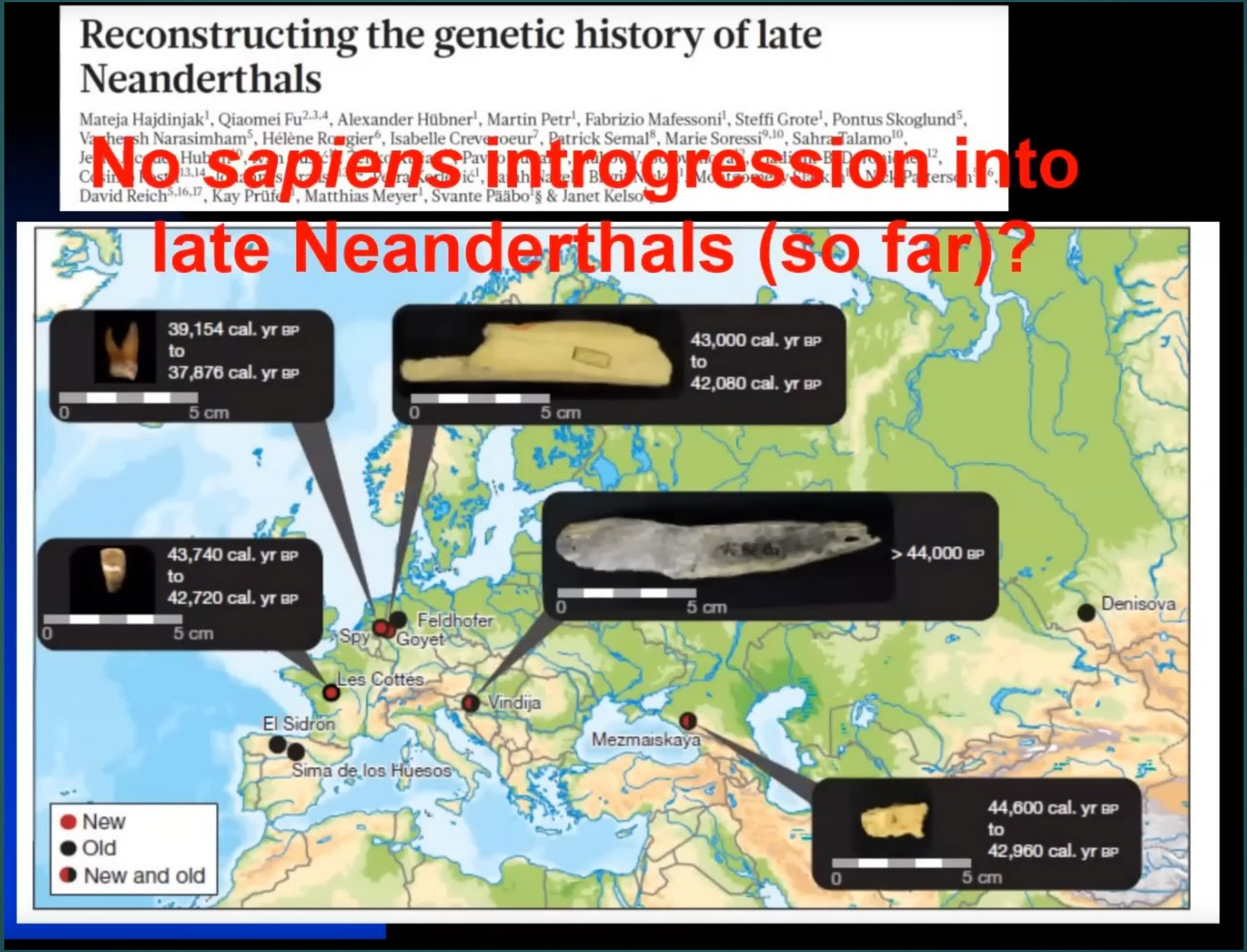
List of earliest *H sapiens* in Europe

- 45 Ka: Bacho Kiro cave, Bulgaria (3% N) ++ (had European descendants)
- 45 Ka: Ust’-Ishim, Siberia (3% N) --
- 44-42: Kent’s Cave, Britain
- 42 Ka: Peştera cu Oase, Romania (6% N) --
- 40 Ka: Tianyuan, China ++
- 39-36 Ka: Kostenki 14, Russia (?% N) ++
- 38-36 Ka: Buran-Kaya, Crimea ++
- 30 Ka: Sungir, Russia (3% N) ++

Map of western Eurasia showing areas and estimated dates of possible Neandertal–modern human hybridization (in red) based on fossil samples from indicated sites.



But surprisingly, no sapiens DNA in late Ns

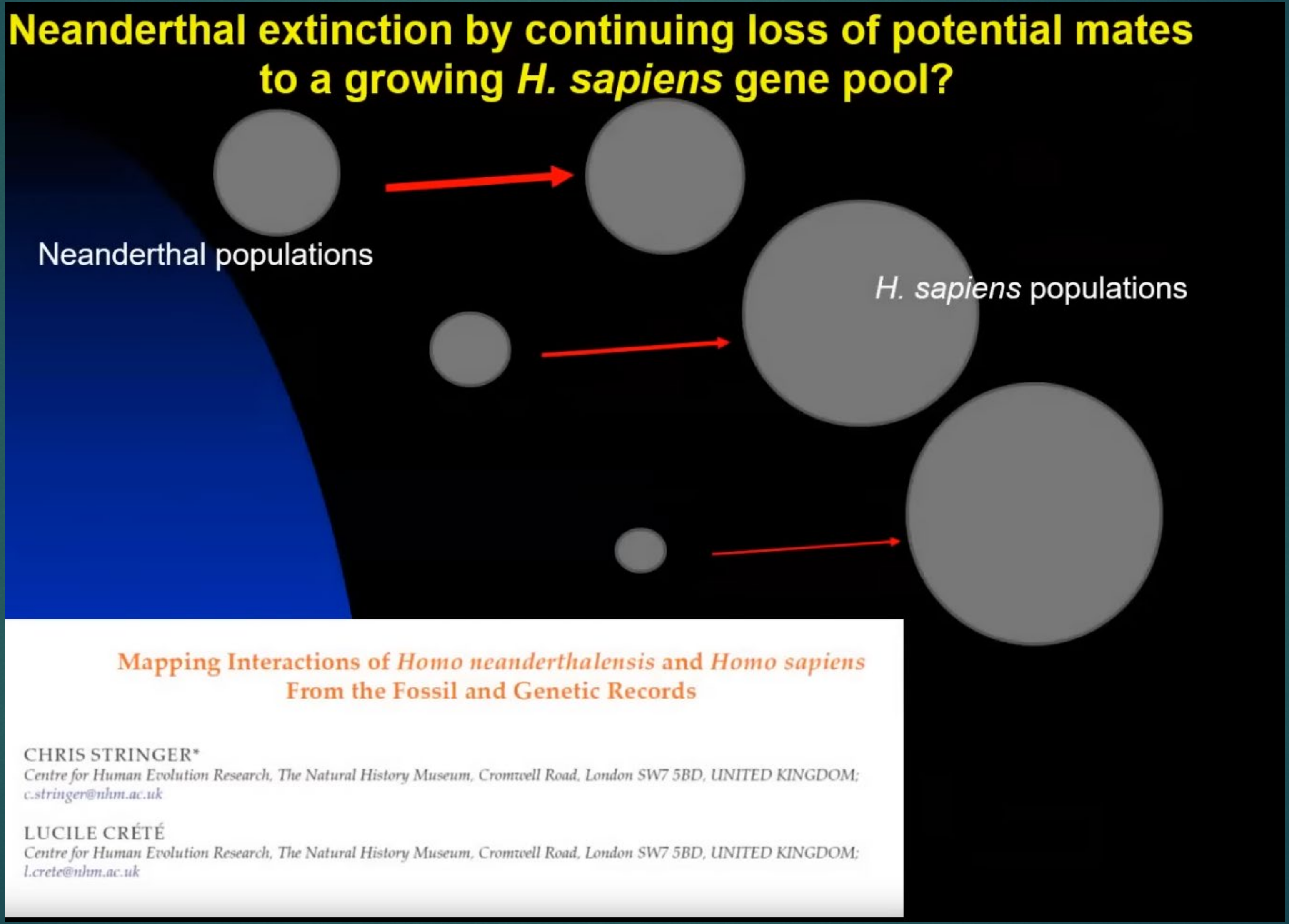


Reconstructing the genetic history of late Neanderthals

Mateja Hajdinjak[1], Qiaomei Fu[2,3,4], Alexander Hübner[1], Martin Petr[1], Fabrizio Mafessoni[1], Steffi Grote[1], Pontus Skoglund[5], Vagheesh Narasimham[5], Hélène Rougier[6], Isabelle Crevecoeur[7], Patrick Semal[8], Marie Soressi[9,10], Sahra Talamo[10], Je[illegible] Hub[illegible] Pav[illegible] [12], C[illegible] [13,14] [illegible] ić[1], [illegible] Patterson[illegible], David Reich[5,16,17], Kay Prüfer[1], Matthias Meyer[1], Svante Pääbo[1]§ & Janet Kelso[1]

No *sapiens* introgression into late Neanderthals (so far)?

One way gene flow from N to MH: would lead to N decline



Neanderthal extinction by continuing loss of potential mates to a growing *H. sapiens* gene pool?

Mapping Interactions of *Homo neanderthalensis* and *Homo sapiens* From the Fossil and Genetic Records

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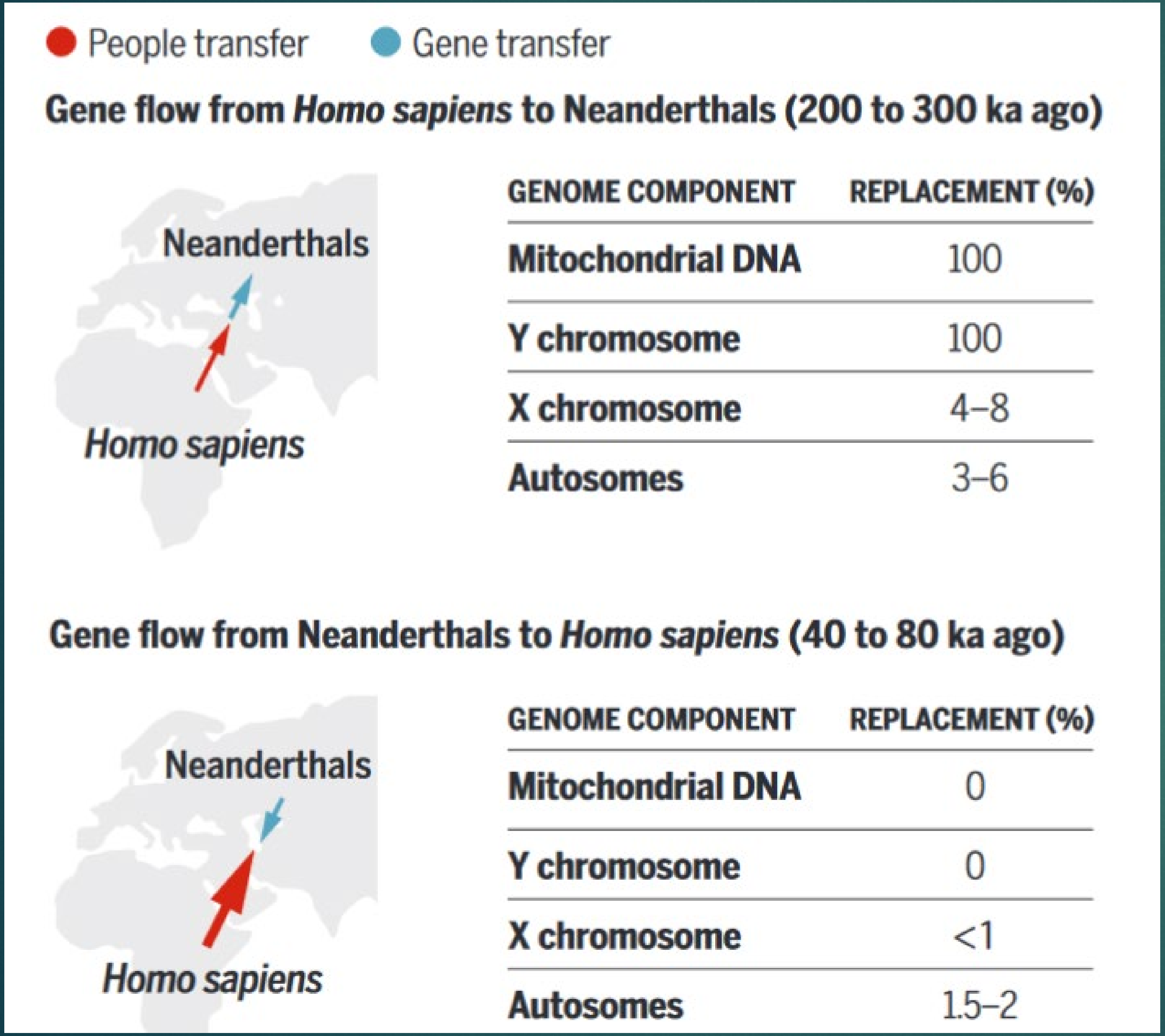
The last pieces of a puzzling early meeting: Y chromosomes transferred from H sapiens to Neanderthals between 350,000 to 150,000 years ago

- All sequenced Neanderthal mitochondria are much more similar to the human mitochondrion than either are to the Denisovan mitochondrion, suggesting a total replacement of this organelle and evidence that H. sapiens females contributed to gene flow; dated to 300 to 150 Ka
- This gene flow event is shared among all sequenced Neanderthals
- Petr, et al., 2020: 3 N males, 2 D males: mirror exactly the findings from the mitochondrion study—complete replacement of Neanderthal Y chromosomes (and no replacement of Denisovan Y chromosomes) with H. sapiens Y chromosomes
- It unequivocally shows that both male and female H. sapiens contributed to gene flow, suggesting that both H. sapiens and Neanderthal populations accepted children of mixed heritage

Mikkel Heide Schierup, 2020



🟥 People transfer 🟦 Gene transfer

Gene flow from *Homo sapiens* to Neanderthals (200 to 300 ka ago)

GENOME COMPONENT	REPLACEMENT (%)
Mitochondrial DNA	100
Y chromosome	100
X chromosome	4–8
Autosomes	3–6

Gene flow from Neanderthals to *Homo sapiens* (40 to 80 ka ago)

GENOME COMPONENT	REPLACEMENT (%)
Mitochondrial DNA	0
Y chromosome	0
X chromosome	<1
Autosomes	1.5–2

Reason for MH Y chromosome replacement in Ns: accumulations of deleterious variants on the Neanderthal Y chromosome caused it to have a lower fitness than the H. sapiens Y chromosome.

Petr, et al., 2020

- Sequencing Y chromosomes from two Denisovans and three Neanderthals shows that the Y chromosomes of Denisovans split around 700 thousand years ago from a lineage shared by Neanderthals and modern human Y chromosomes, which diverged from each other around 370 thousand years ago.
- Evidence indicates replacement of both the mitochondrial and Y chromosomal gene pools in late Neanderthals.
- This replacement is plausible if the low effective population size of Neanderthals resulted in an increased negative genetic load in Neanderthals relative to modern humans.

MHs mt and Y DNA replaced N versions

- Autosomal genomes show that Neanderthals and Denisovans are sister groups that split from modern humans between 550 and 765 Ka ago.
- By contrast, the mtDNAs of Neanderthals and modern humans are more similar to one another [TMRCA of 360 to 468 ka ago] than to the mtDNAs of Denisovans.
- Notably, ~400-ka-old early Neanderthals from Sima de los Huesos were shown to carry mitochondrial genomes related to Denisovan mtDNAs. This suggests that Neanderthals originally carried a Denisovan-like mtDNA, which was later completely replaced through ancient gene flow from an early lineage related to modern humans

6% of N DNA is from MHs

- 2023 Sarah Tishkoff study: Neanderthals inherited at least 6% of their genome from a now-extinct lineage of early modern humans.

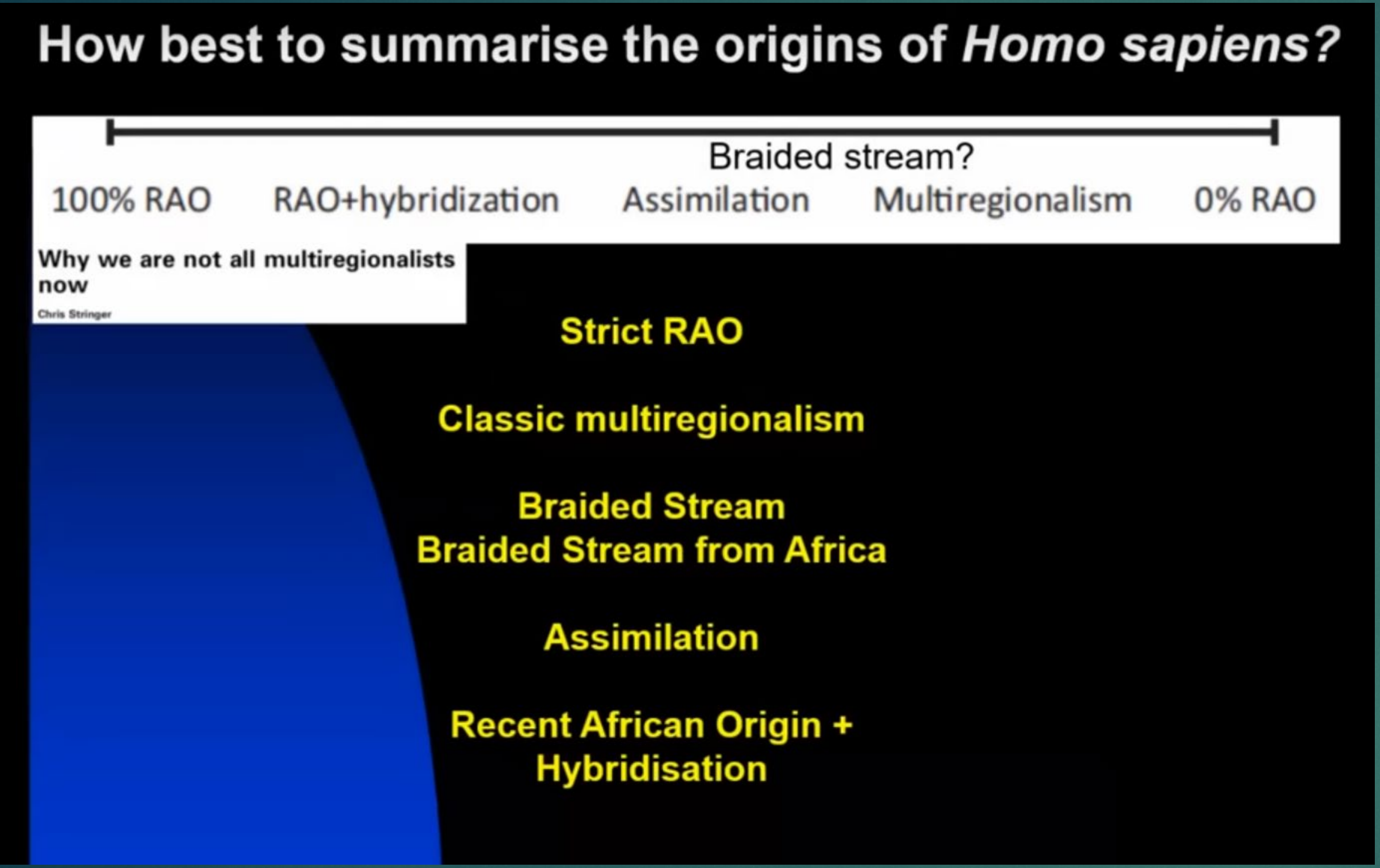
- All of the sub-Saharan populations contained Neanderthal-like DNA, indicating that this phenomenon is widespread.

- In most cases, <u>this Neanderthal-like DNA originated from an ancient lineage of modern humans that passed their DNA on to Neanderthals when they migrated from Africa to Eurasia around 250,000 years ago</u>. As a result of this modern human-Neanderthal interbreeding, approximately 6% of the Neanderthal genome was inherited from modern humans.

N DNA in MHs and MH DNA in Ns is deleterious

- There is also evidence of Neanderthal ancestry that was introduced to these populations when modern humans bearing Neanderthal genes migrated back into Africa. Neanderthal ancestry in these sub-Saharan populations ranged from 0 to 1.5%, and the highest levels were observed in the Amhara from Ethiopia and Fulani from Cameroon.

- Most of the modern human DNA was in noncoding regions of the Neanderthal genome, indicating that modern human gene variants were being preferentially lost from coding sections of the genome, which suggests that having modern human genes in a Neanderthal background is detrimental to N fitness. Both modern humans and Neanderthals slowly rid themselves of the alleles of the other group.



How best to summarise the origins of *Homo sapiens?*

Braided stream?

100% RAO RAO+hybridization Assimilation Multiregionalism 0% RAO

Why we are not all multiregionalists now

Chris Stringer

Strict RAO

Classic multiregionalism

Braided Stream
Braided Stream from Africa

Assimilation

Recent African Origin +
Hybridisation

RAO: Recent African Origin – strict version no longer tenable

Multiregionalism: Wolpoff; falsified – Chinese local H. erectus did not evolve into MHs

Assimilation: Fred Smith & E. Trinkaus

RAO+ Hybridization: G. Bauer

Braided stream model: only braided stream from Africa

RAO+ hybridization: most evidence

The Persian Plateau served as Hub for Homo sapiens after the main Out of Africa dispersal - Leonardo Vallini, et al., 2024

- A new study combining genetic, paleoecological, and archaeological evidence has unveiled the Persian Plateau as a pivotal geographic location serving as a hub for Homo sapiens during the early stages of their migration out of Africa.
- Homo sapiens spread out of Africa between ~70-60 Ka ago. However, it appears that once outside of Africa, human populations did not expand across all of Eurasia until ~45 kya.
- The geographic whereabouts of these early settlers in the timeframe between ~70-60 to 45 kya has been difficult to reconcile.
- Study combined genetic evidence and palaeoecological models to infer the geographic location that acted as the Hub for our species during the early phases of colonization of Eurasia. Leveraging on available genomic evidence we show that populations from the Persian Plateau carry an ancestry component that closely matches the population that settled the Hub outside Africa.

Persian plateau unveiled as crucial hub for early human migration out of Africa

Pebdeh Cave located in the southern Zagros Mountains. Pebdeh was occupied by hunter-gatherers as early as 42,000 years ago. Credit: Mohammad Javad Shoaee

Persian Plateau

- With the paleoclimatic data available to date, we built ecological models showing that the Persian Plateau was suitable for human occupation and that it could sustain a larger population compared to other West Asian regions, strengthening this claim.

- The geographically widespread and stable colonization of Eurasia appears to have occurred at ~45 kya through multiple population expansions associated with a variety of stone tool technologies.

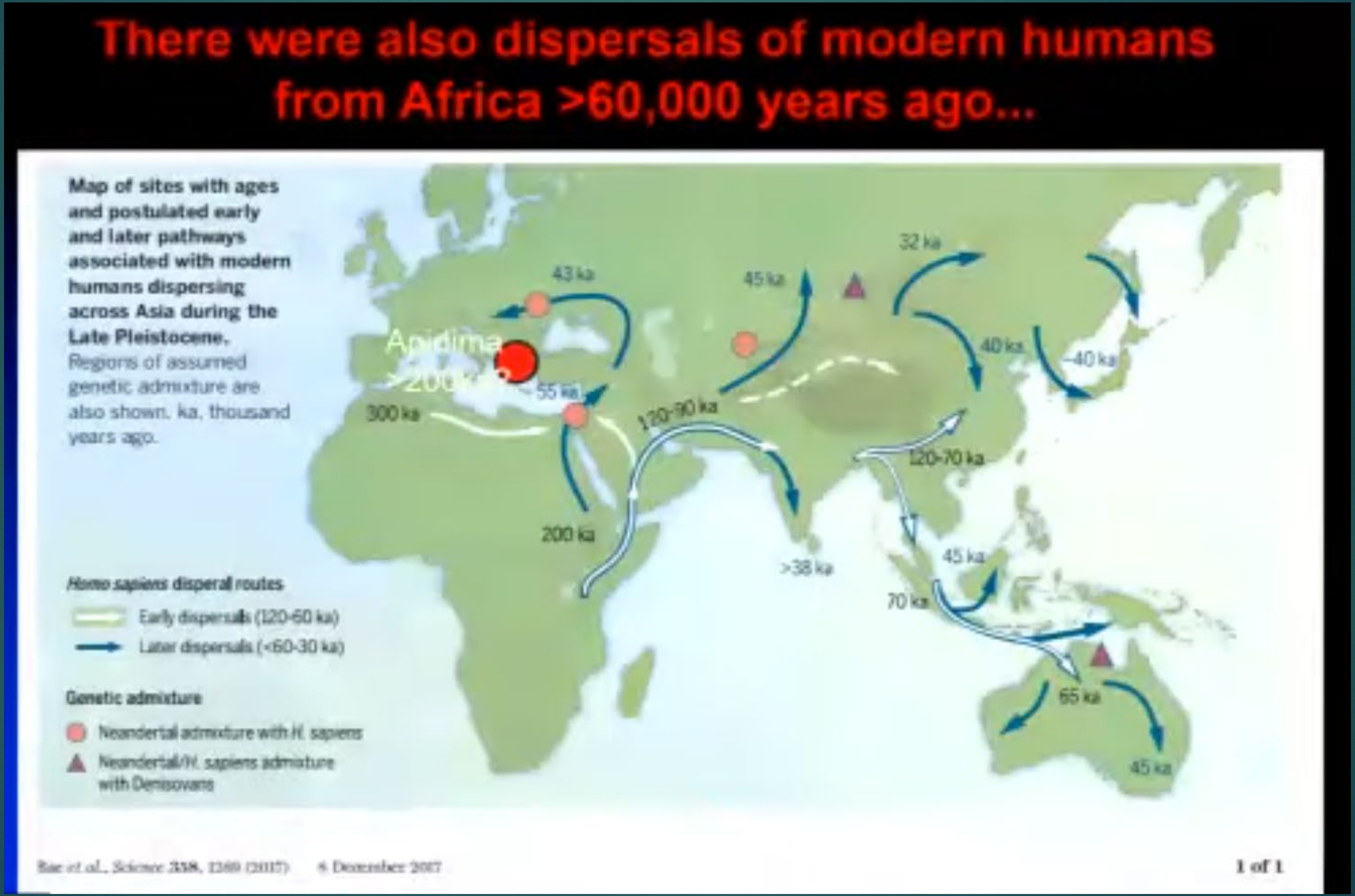
- Earlier incursions into Europe have been recorded, however, they failed to leave a significant contribution to later populations.

The Hub

- A chronological gap of ~20 ky between the Out of Africa migration (~70–60 kya) and the stable colonization (~45 kya) of West and East Eurasia can be identified, for which the geographic location and genetic features of this population are poorly known.

- On the basis of genetic and archaeological evidence, it has been suggested that the Eurasian population that formed the first stable deme outside Africa after ~70–60 kya can be characterized as a Hub population, from which multiple population waves emanated to colonies Eurasia.

Early dispersals of MHs: Australia 65 Ka



There were also dispersals of modern humans from Africa >60,000 years ago...

Map of sites with ages and postulated early and later pathways associated with modern humans dispersing across Asia during the Late Pleistocene. Regions of assumed genetic admixture are also shown. ka, thousand years ago.

Homo sapiens disperal routes

- Early dispersals (120-60 ka)
- Later dispersals (<60-30 ka)

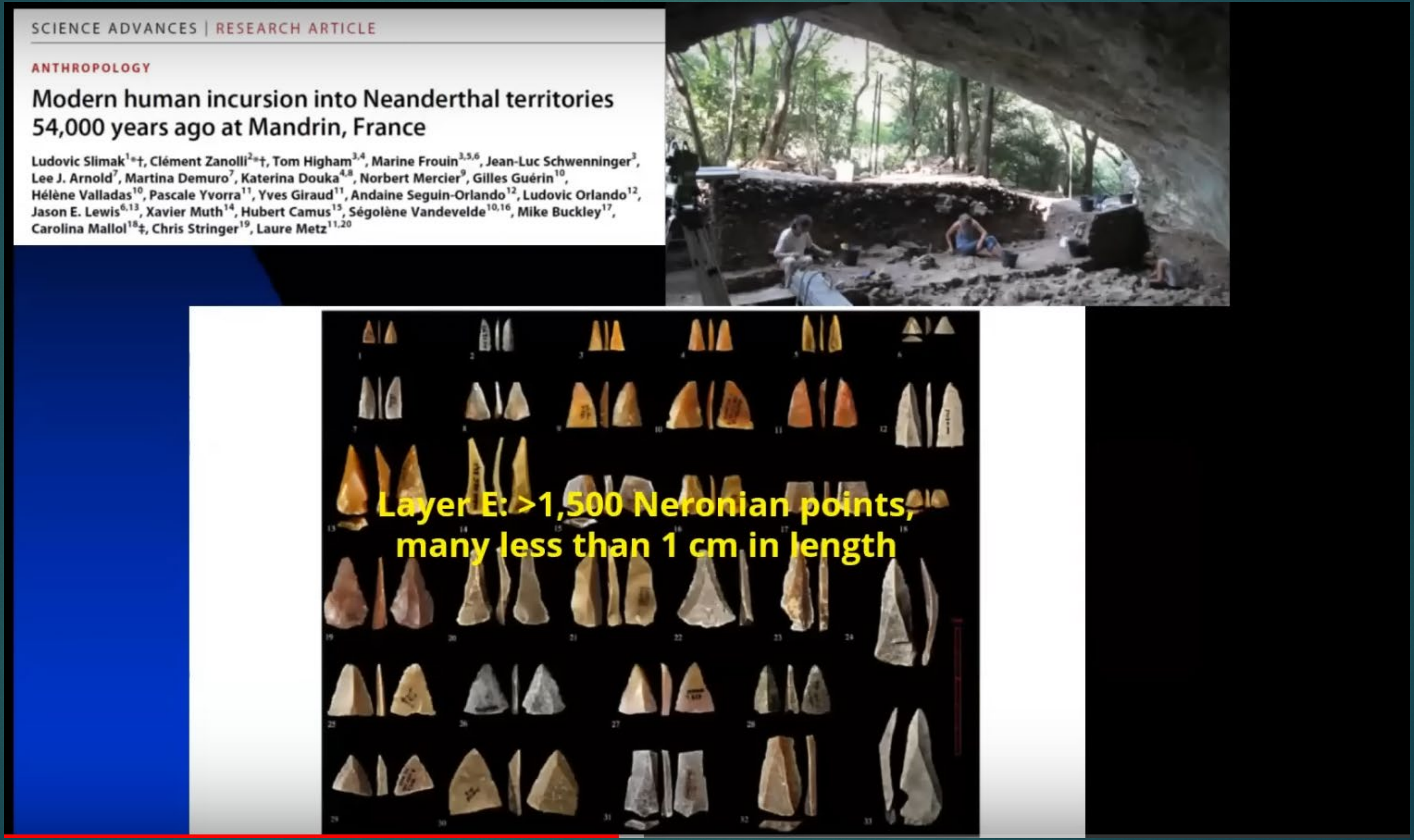
Genetic admixture

- ● Neandertal admixture with *H. sapiens*
- ▲ Neandertal/*H. sapiens* admixture with Denisovans

Bae *et al.*, *Science* 358, 1269 (2017)   8 December 2017

1 of 1

L. Slimak: Mandrin, France at 54 Ka: 1500 Neronian points



SCIENCE ADVANCES | RESEARCH ARTICLE

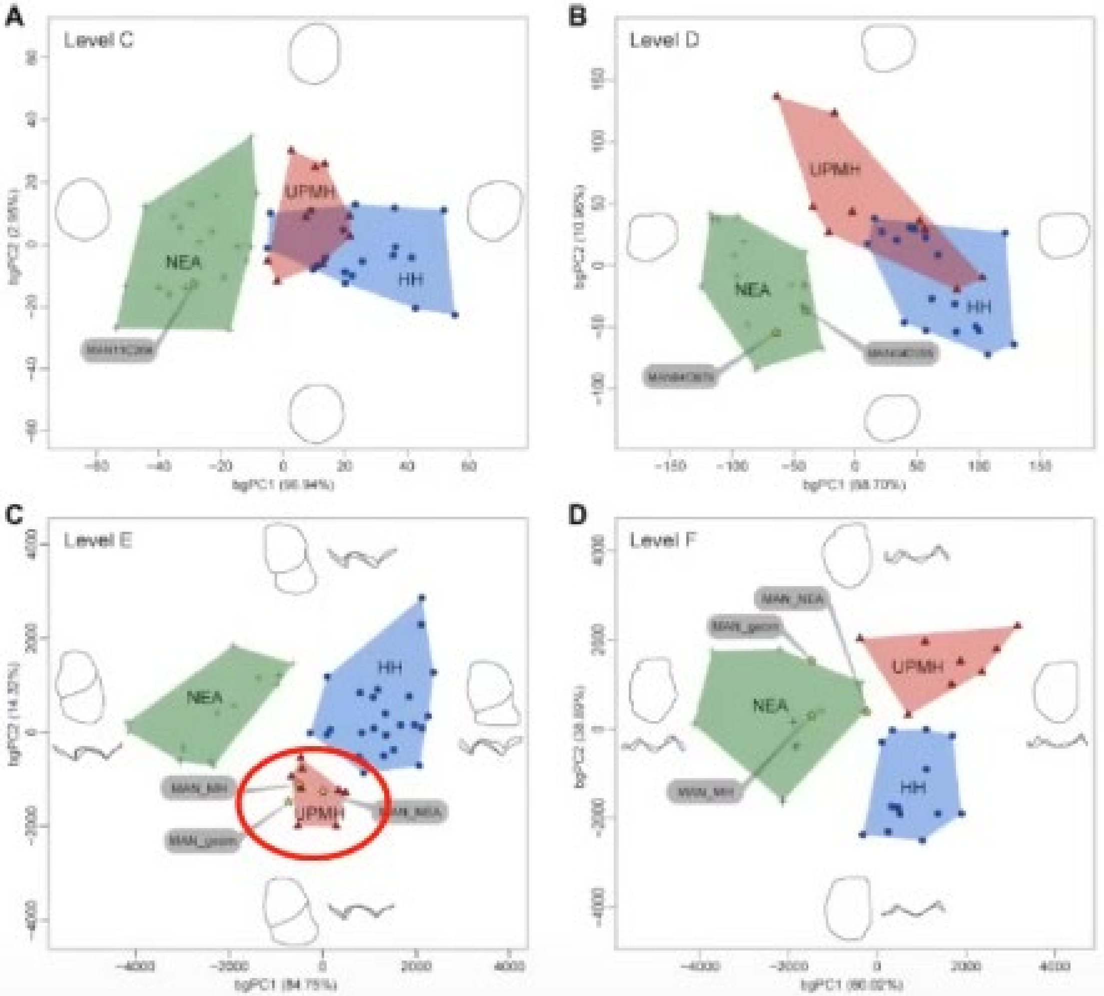
ANTHROPOLOGY

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

Ludovic Slimak[1]*†, Clément Zanolli[2]*†, Tom Higham[3,4], Marine Frouin[3,5,6], Jean-Luc Schwenninger[3], Lee J. Arnold[7], Martina Demuro[7], Katerina Douka[4,8], Norbert Mercier[9], Gilles Guérin[10], Hélène Valladas[10], Pascale Yvorra[11], Yves Giraud[11], Andaine Seguin-Orlando[12], Ludovic Orlando[12], Jason E. Lewis[6,13], Xavier Muth[14], Hubert Camus[15], Ségolène Vandevelde[10,16], Mike Buckley[17], Carolina Mallol[18]‡, Chris Stringer[19], Laure Metz[11,20]

Layer E: >1,500 Neronian points, many less than 1 cm in length

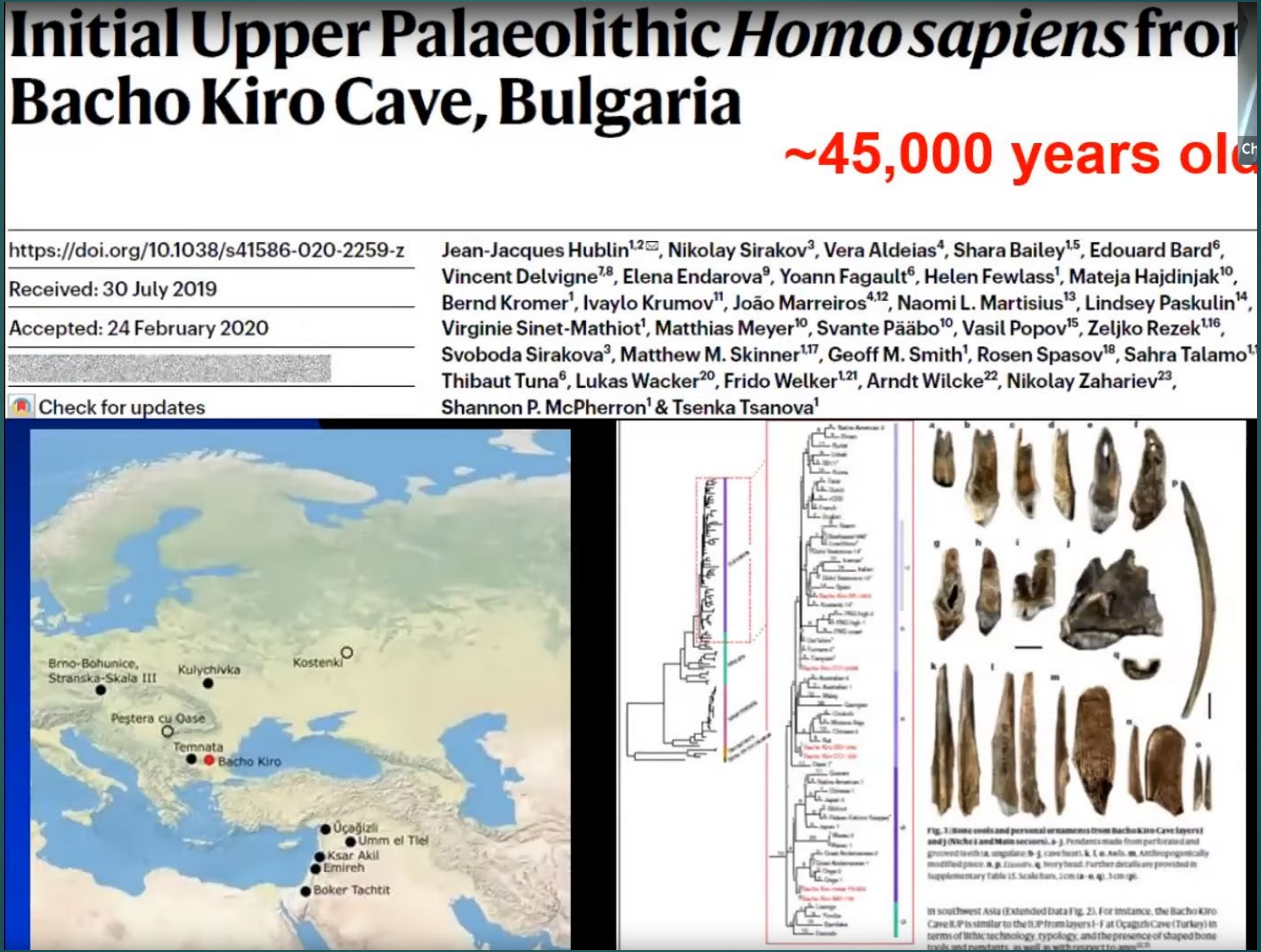
Mandrin: One tooth in layer E is MH (by morphology, not DNA); all others are N



Layer E decid. molar

Fig. 6. Geometric morphometric analyses of the crown outline and EDJ shape. (**A** and **B**) Between-group principal components analyses (bgPCA) based on the two-dimensional (2D) landmarks Procrustes-registered shape coordinates of the crown outline of the deciduous lower second molar (Ldm2) Man11 C 204 from layer C (A) and of the deciduous upper second molars (Udm2) Man04 D 395 and Man04 D 679 from layer D (B) compared with fossil and extant hominins. (**C** and **D**) bgPCA based on

Early MHs in Europe at 45 Ka



Initial Upper Palaeolithic *Homo sapiens* fro
Bacho Kiro Cave, Bulgaria

~45,000 years ol

https://doi.org/10.1038/s41586-020-2259-z

Received: 30 July 2019

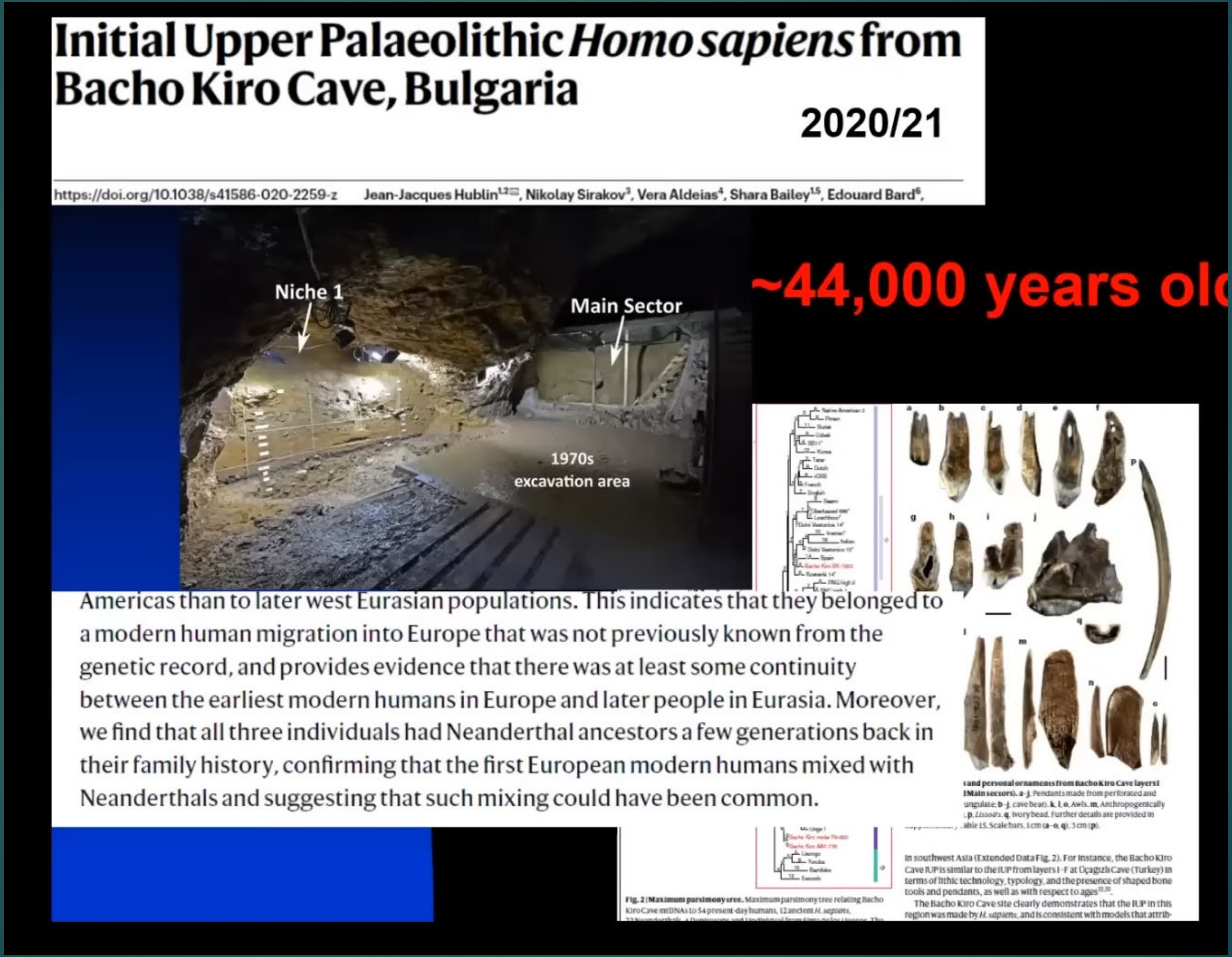
Accepted: 24 February 2020

[redacted]

Check for updates

Jean-Jacques Hublin[1,2]✉, Nikolay Sirakov[3], Vera Aldeias[4], Shara Bailey[1,5], Edouard Bard[6], Vincent Delvigne[7,8], Elena Endarova[9], Yoann Fagault[6], Helen Fewlass[1], Mateja Hajdinjak[10], Bernd Kromer[1], Ivaylo Krumov[11], João Marreiros[4,12], Naomi L. Martisius[13], Lindsey Paskulin[14], Virginie Sinet-Mathiot[1], Matthias Meyer[10], Svante Pääbo[10], Vasil Popov[15], Zeljko Rezek[1,16], Svoboda Sirakova[3], Matthew M. Skinner[1,17], Geoff M. Smith[1], Rosen Spasov[18], Sahra Talamo[1], Thibaut Tuna[6], Lukas Wacker[20], Frido Welker[1,21], Arndt Wilcke[22], Nikolay Zahariev[23], Shannon P. McPherron[1] & Tsenka Tsanova[1]

Bacho Kiro at 44 Ka



Initial Upper Palaeolithic *Homo sapiens* from Bacho Kiro Cave, Bulgaria

2020/21

https://doi.org/10.1038/s41586-020-2259-z Jean-Jacques Hublin[1,2], Nikolay Sirakov[3], Vera Aldeias[4], Shara Bailey[1,5], Edouard Bard[6],

~44,000 years ol

Americas than to later west Eurasian populations. This indicates that they belonged to a modern human migration into Europe that was not previously known from the genetic record, and provides evidence that there was at least some continuity between the earliest modern humans in Europe and later people in Eurasia. Moreover, we find that all three individuals had Neanderthal ancestors a few generations back in their family history, confirming that the first European modern humans mixed with Neanderthals and suggesting that such mixing could have been common.

s and personal ornaments from Bacho Kiro Cave layers I I Main sectors). a–j, Pendants made from perforated and ungulate; b–j, cave bear). k, l, o, Awls. m, Anthropogenically , p, *Lissoirs*. q, Ivory bead. Further details are provided in able 15. Scale bars, 1 cm (a–o, q), 3 cm (p).

Fig. 2 | Maximum parsimony tree. Maximum parsimony tree relating Bacho Kiro Cave mtDNAs to 54 present-day humans, 12 ancient *H. sapiens*,

in southwest Asia (Extended Data Fig. 2). For instance, the Bacho Kiro Cave IUP is similar to the IUP from layers I–F at Üçağızlı Cave (Turkey) in terms of lithic technology, typology, and the presence of shaped bone tools and pendants, as well as with respect to ages[illegible].

The Bacho Kiro Cave site clearly demonstrates that the IUP in this region was made by *H. sapiens*, and is consistent with models that attrib-

Initial Upper Palaeolithic humans in Europe had recent Neanderthal ancestry - 2021

- Modern humans appeared in Europe by at least 45,000 years ago, but the extent of their interactions with Neanderthals, who disappeared by about 40,000 years ago, and their relationship to the broader expansion of modern humans outside Africa are poorly understood.

- Here we present genome-wide data from three individuals dated to between 45,930 and 42,580 years ago from Bacho Kiro Cave, Bulgaria. They are the earliest Late Pleistocene modern humans known to have been recovered in Europe so far, and were found in association with an Initial Upper Palaeolithic artefact assemblage.

Mateja Hajdinjak, et al., 2021

Bacho Kiro

- Unlike two fossils of similar ages from Romania and Siberia who did not contribute detectably to later populations, Bacho Kiro individuals are more closely related to present-day and ancient populations in East Asia and the Americas than to later west Eurasian populations
- This indicates that they belonged to a modern human migration into Europe that was not previously known from the genetic record, and provides evidence that there was at least. some continuity between the earliest modern humans in Europe and later people in Eurasia
- Moreover, we find that all three individuals had Neanderthal ancestors a few generations back in their family history, confirming that the first European modern humans mixed with Neanderthals and suggesting that such mixing could have been common.

Archaeological sites that have yielded genetic data and/or IUP assemblages. Sites with modern human genome-wide data older than 40 kyr bp

1, Bacho Kiro Cave; 2, Ust'Ishim; 3, Peştera cu Oase; 4, Tianyuan Cave; 5, 6, Kostenki14 (Markina Gora) and Kostenki12 (Vokovskaya); 7, Troisème Caverne of Goyet; 8, Sunghir; 9, Peştera Muierilor; 10, Grotta Paglicci; 11, Peştera Cioclovina Uscată; 12, Krems Wachtberg; 13, Yana RHS; 14, 15, Dolní Věstonice and Pavlov; 16, Grotta del Cavallo; 17, Kents Cavern; 18, Grotta di Fumane; 19, Brno-Bohunice; 20, Stánska Skála III; 21, Temnata; 22, Kulychivka; 23, Korolevo 1 and 2; 24, Shlyakh; 25, 26, Üçagizli and Kanal Cave; 27, Um el'Tlel; 28, Jerf Ajlah; 29, Yabrud II; 30–32, Antelias; Abou Halka and Ksar Akil; 33–35, Emireh, El Wad and Raqefet; 36, Boker Tachtit; 37, Denisova Cave; 38, Kara-Bom; 39, Ust-Karakol 1; 40, Kara-Tenesh; 41, Makarvo IV; 42, Kamenka A–C; 43, Khotyk; 44, Podzvonkaya; 45, 46, Tolbor4 and Tolbor16; 47, Tsangan-Agui; 48–50, Suindonggou1, 2 and 9

Europe at 47 Ka

- The transition between the Middle and Upper Palaeolithic periods in Europe, which started about 47 ka, overlapped with the spread of modern humans and the disappearance of Neanderthals, which occurred by about 42 ka.
- Analyses of the genomes of Neanderthals and modern humans have shown that gene flow occurred between the two hominin groups approximately 60–50 ka, probably in southwestern Asia. However, owing to the scarcity of modern human remains from Eurasia that are older than 40 kyr, genome-wide data are available for only three individuals of this age.

- For example, whereas the roughly 42,000 to 37,000-year-old ‘Oase1’ individual from Romania and the roughly 45,000-year-old ‘Ust’Ishim’ individual from Siberia do not show specific genetic relationships to subsequent Eurasian populations, the ~40,000-year-old ‘Tianyuan’ individual from China contributed to the genetic ancestry of ancient and present-day East Asian populations.

- Another open question is the extent to which modern humans mixed with Neanderthals when they spread across Europe and Asia.

- Direct evidence of local interbreeding exists only for the Oase1 individual, who had a recent Neanderthal ancestor in his family history.

Bacho Kiro

- Here, we analyze genome-wide data from human specimens found in direct association with an Initial Upper Palaeolithic (IUP) assemblage of artefacts in Bacho Kiro Cave, Bulgaria

- it is debated whether the IUP represents a dispersal of modern humans across middle-latitude Eurasia, the diffusion of certain technological ideas, instances of independent invention, or a combination of some or all of these.

- The IUP is contemporaneous with late Neanderthal sites in central and western Europe and precedes later Upper Palaeolithic techno-complexes in Europe, such as the Protoaurignacian and the Aurignacian, by several thousand years.

Bacho Kiro and Oase1

- Five human specimens were recovered from Bacho Kiro Cave in recent excavations. They consist of a lower molar and four bone fragments. They have been directly radiocarbon-dated to between 45,930 and 42,580 Ka, and their mitochondrial genomes are of the modern human type, suggesting that they are the oldest Upper Palaeolithic modern humans that have been recovered in Europe (in 2021).
- Produced additional data from a mandible that was found outside any archaeological context in Peştera cu Oase, Romania (referred to as 'Oase1'). The mandible was directly dated to about 42–37 ka, although this may be an underestimate as the dating was performed before recent technical improvements

Related to East Asians

- When comparing the Bacho Kiro Cave individuals to present-day populations, we found that the IUP individuals share more alleles with present-day populations from East Asia, Central Asia and the Americas than with populations from western Eurasia. And with the roughly 40,000-year-old Tianyuan individual from China.

- All IUP Bacho Kiro Cave individuals had recent Neanderthal ancestors in their immediate family histories (6-7 generations back).
- We found that the IUP individuals carried 3.8%, and 3.4% Neanderthal DNA, respectively. This is more than the average of 1.9% found in other ancient or present-day humans, except for the Oase1 individual, who had a close Neanderthal relative (6.4%). More similar to the Vindija 33 and Chagyrskaya Neanderthals than to the Altai Neanderthal

Conclusions

- Selection against Neanderthal DNA variants occurred within a few generations.

- In conclusion, the Bacho Kiro Cave genomes show that several distinct modern human populations existed during the early Upper Palaeolithic in Eurasia. Some of these populations, represented by the Oase1 and Ust’Ishim individuals, show no detectable affinities to later populations, whereas groups related to the IUP Bacho Kiro Cave individuals contributed to later populations with Asian ancestry as well as some western Eurasian humans such as the GoyetQ116-1 individual in Belgium.

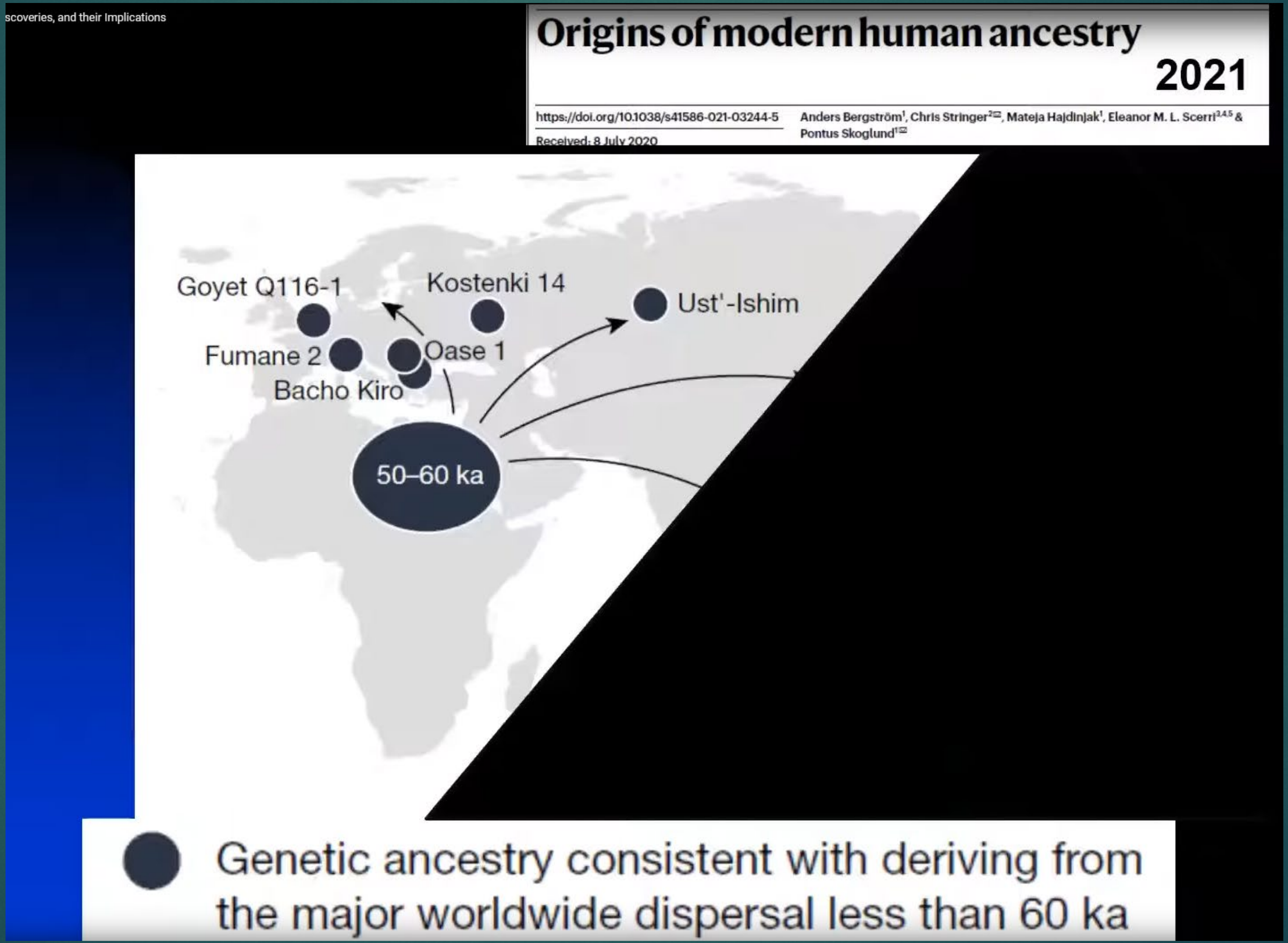
Genetics

- Eventually populations related to the IUP Bacho Kiro Cave individuals disappeared in western Eurasia without leaving a detectable genetic contribution to later populations.

- Finally, it is striking that all four of the European individuals who overlapped in time with late Neanderthals and from whom genome-wide data have been retrieved had close Neanderthal relatives in their family histories.

- This suggests that mixing between Neanderthals and the first modern humans that arrived into Europe was perhaps more common than is often assumed.

Modern immigration with common genetic ancestry less than 60 Ka



scoveries, and their Implications

Origins of modern human ancestry

2021

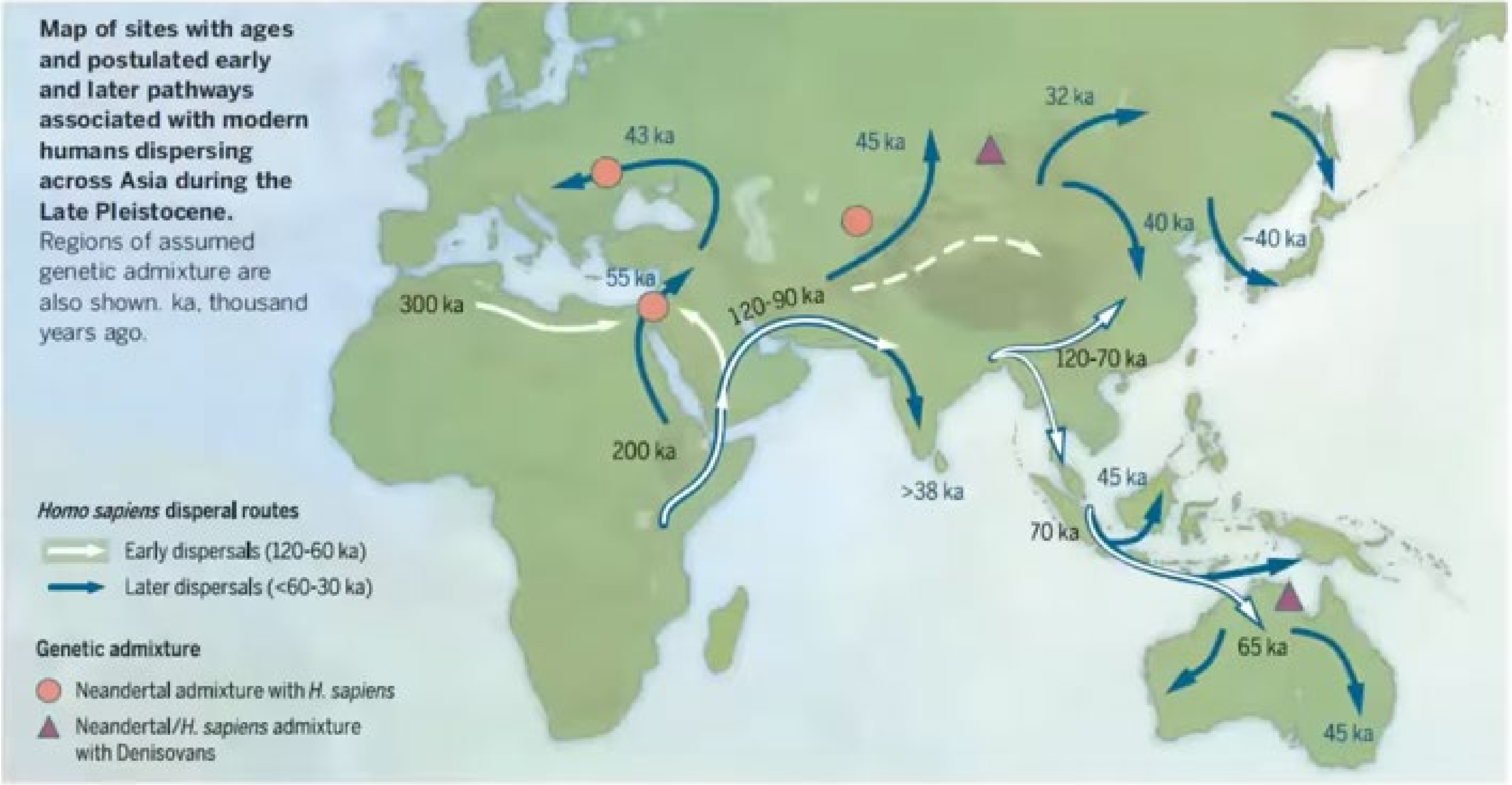
https://doi.org/10.1038/s41586-021-03244-5

Received: 8 July 2020

Anders Bergström[1], Chris Stringer[2], Mateja Hajdinjak[1], Eleanor M. L. Scerri[3,4,5] & Pontus Skoglund[1]

● Genetic ancestry consistent with deriving from the major worldwide dispersal less than 60 ka

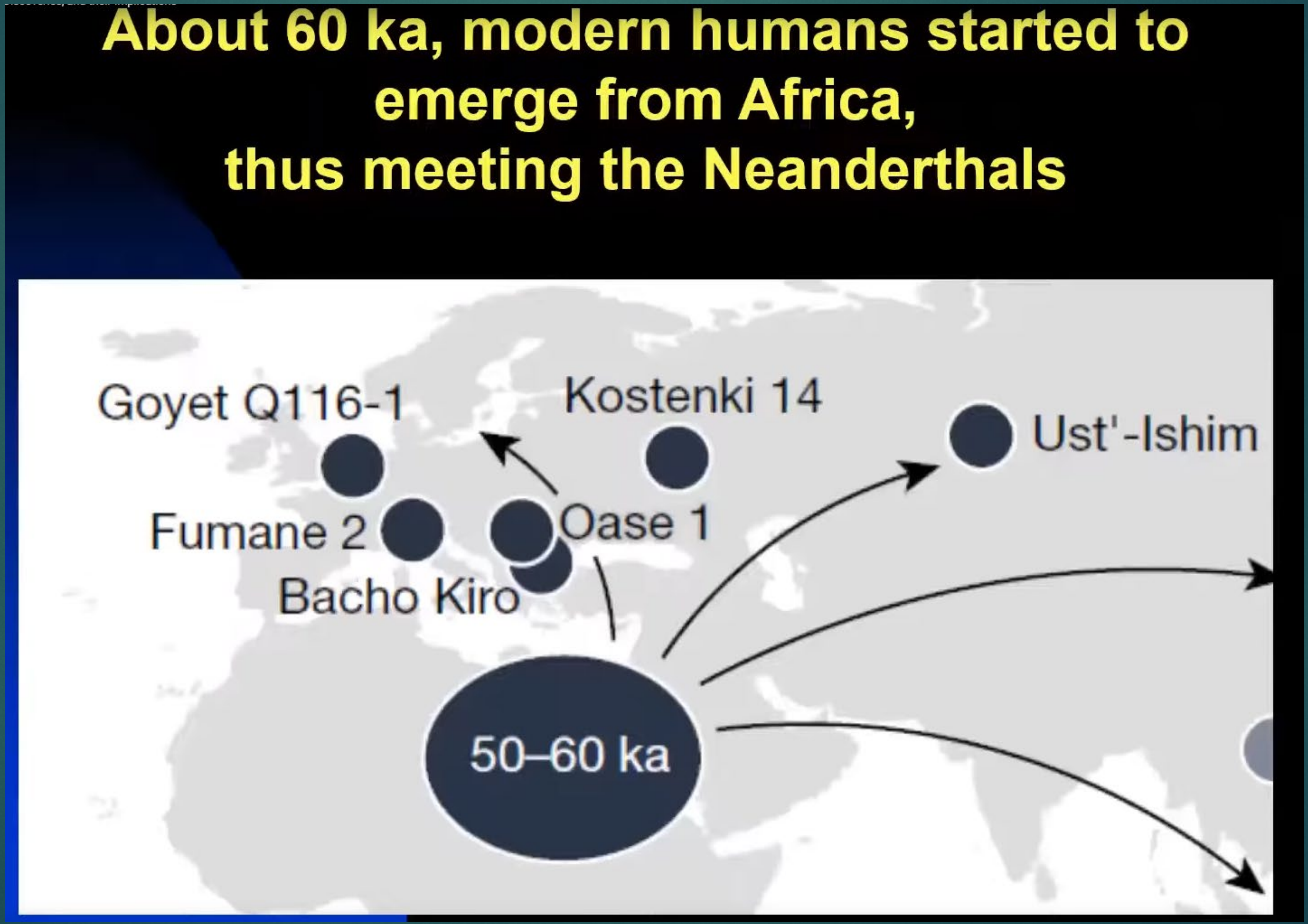
There were also dispersals of modern humans from Africa >60,000 years ago...



Map of sites with ages and postulated early and later pathways associated with modern humans dispersing across Asia during the Late Pleistocene. Regions of assumed genetic admixture are also shown. ka, thousand years ago.

Bae *et al.*, *Science* 358, 1269 (2017) 8 December 2017

Encountering Ns in Europe



About 60 ka, modern humans started to emerge from Africa,
thus meeting the Neanderthals

In 2000, Stringer thought interbreeding was rare & we'd never find evidence of it. But we did in 2010.

Chris Stringer on Human Evolution, Recent Discoveries, and their Implications

Interbreeding with Neanderthals?

If there was any interbreeding it was thought that it was on such a small scale we would find no trace of it today.

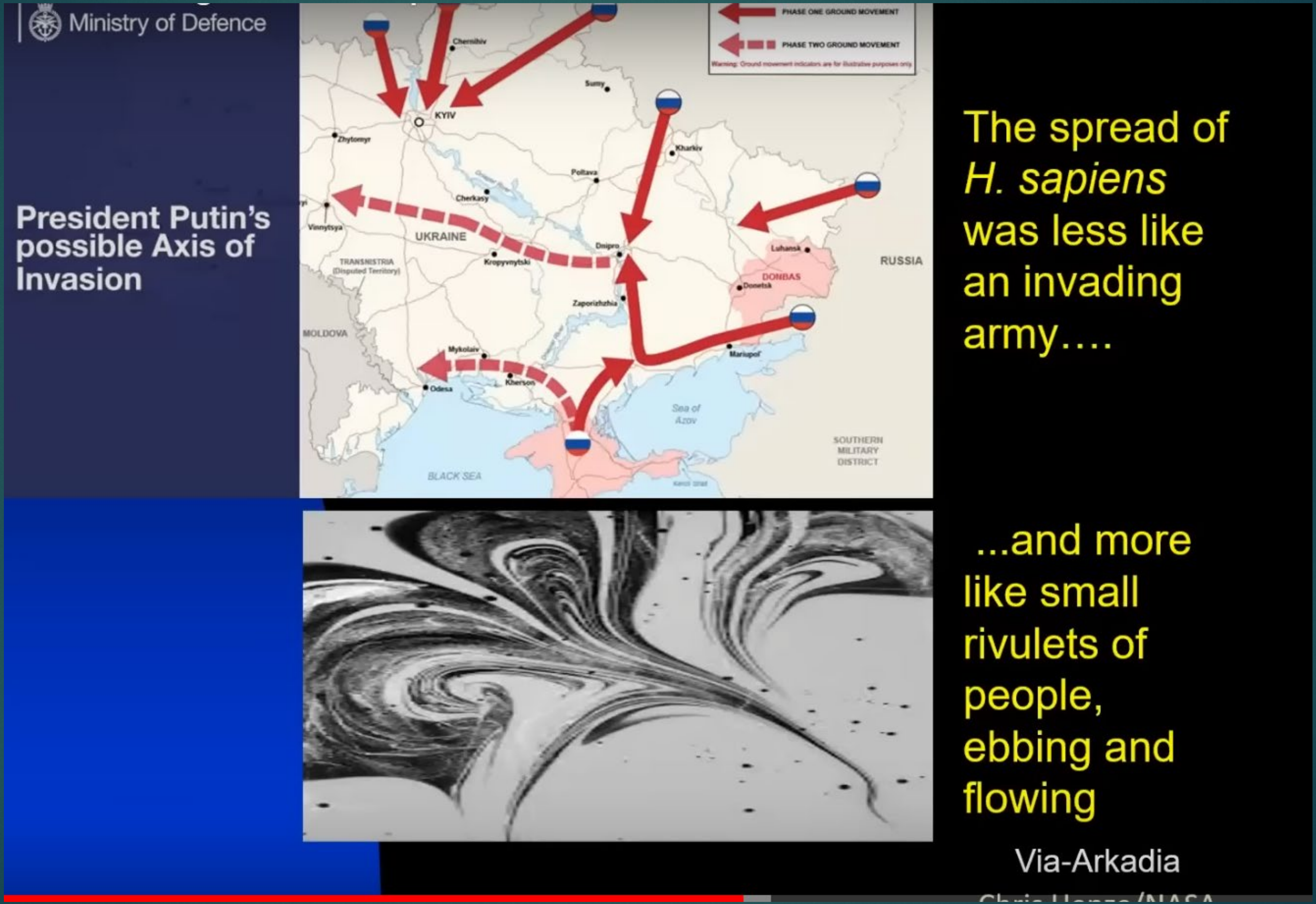
The Controversial Lapedo Child – A eanderthal / Human Hybrid?

26 Ka

Early MHs with N DNA

Close Neanderthal – *H. sapiens* encounters:
some of the recent evidence…

Mapping Interactions of *Homo neanderthalensis* and *Homo sapiens*
From the Fossil and Genetic Records



President Putin's possible Axis of Invasion

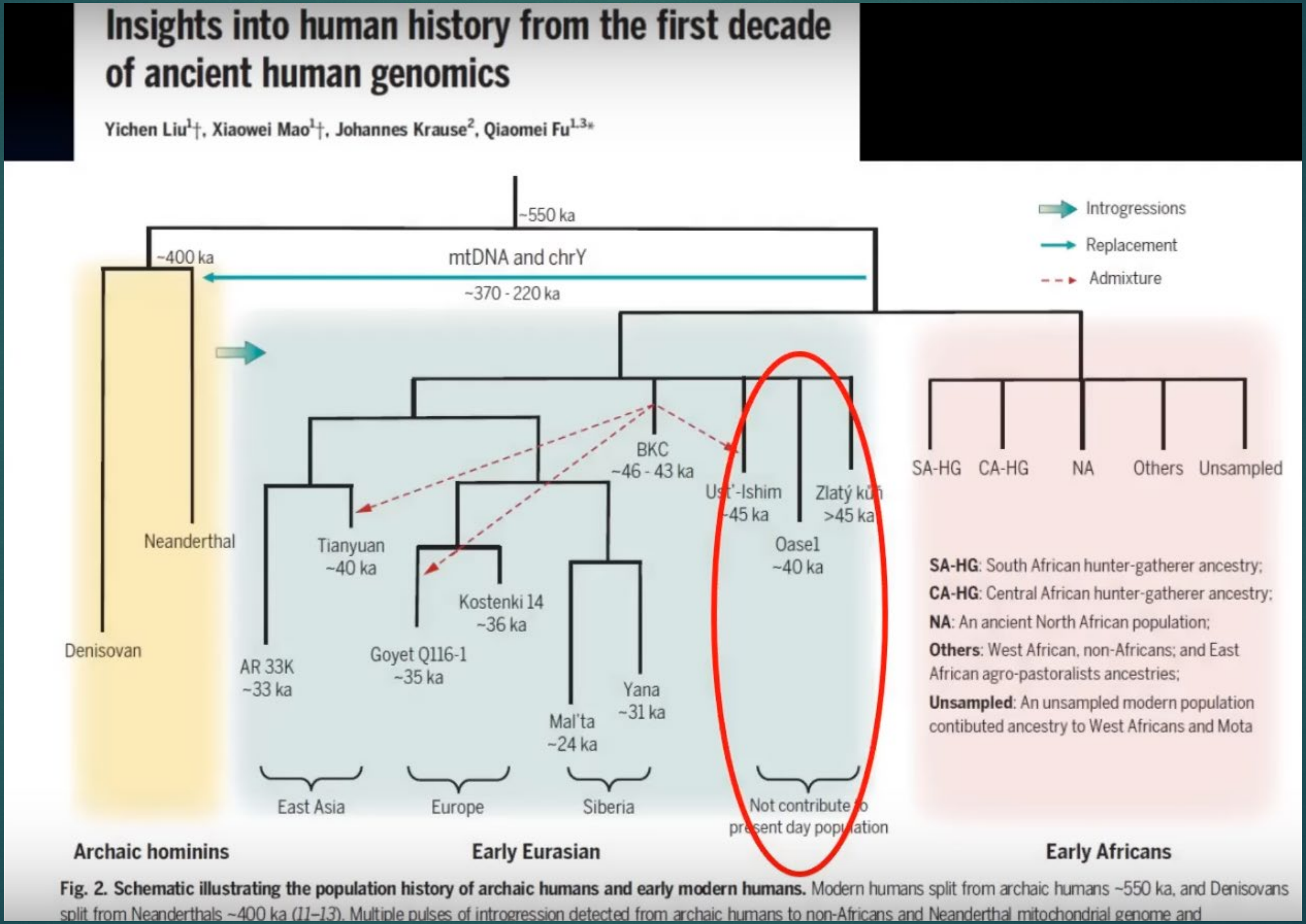
The spread of *H. sapiens* was less like an invading army….

...and more like small rivulets of people, ebbing and flowing

Via-Arkadia

Chris Henze/NASA

Lost lineages of early European MHs

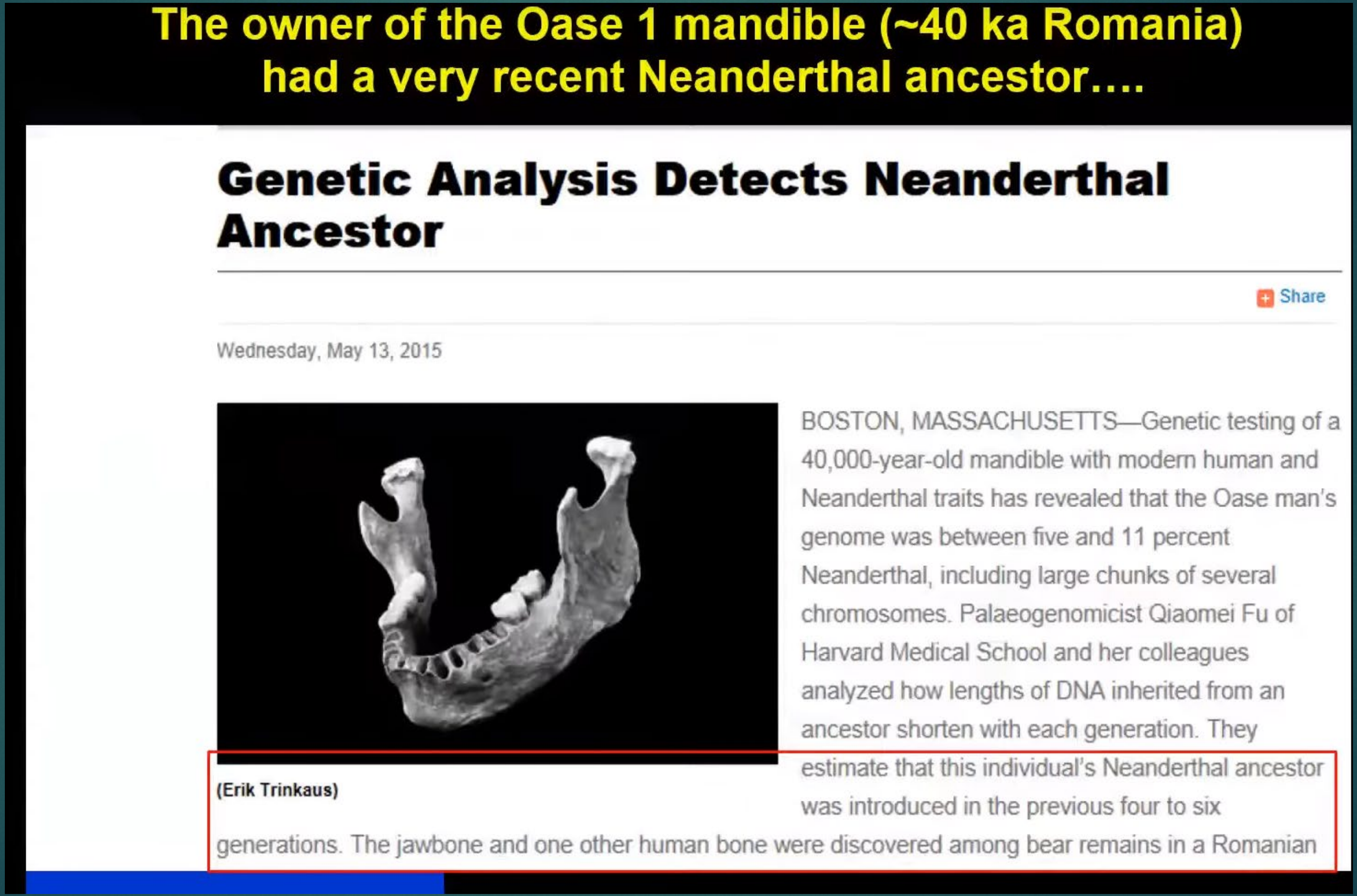


Insights into human history from the first decade of ancient human genomics

Yichen Liu[1]†, Xiaowei Mao[1]†, Johannes Krause[2], Qiaomei Fu[1,3]*

Fig. 2. Schematic illustrating the population history of archaic humans and early modern humans. Modern humans split from archaic humans ~550 ka, and Denisovans split from Neanderthals ~400 ka (*11–13*). Multiple pulses of introgression detected from archaic humans to non-Africans and Neanderthal mitochondrial genome and

Oase 1 MH had N GGGGGG grandfather (9%) despite a strong chin



The owner of the Oase 1 mandible (~40 ka Romania) had a very recent Neanderthal ancestor….

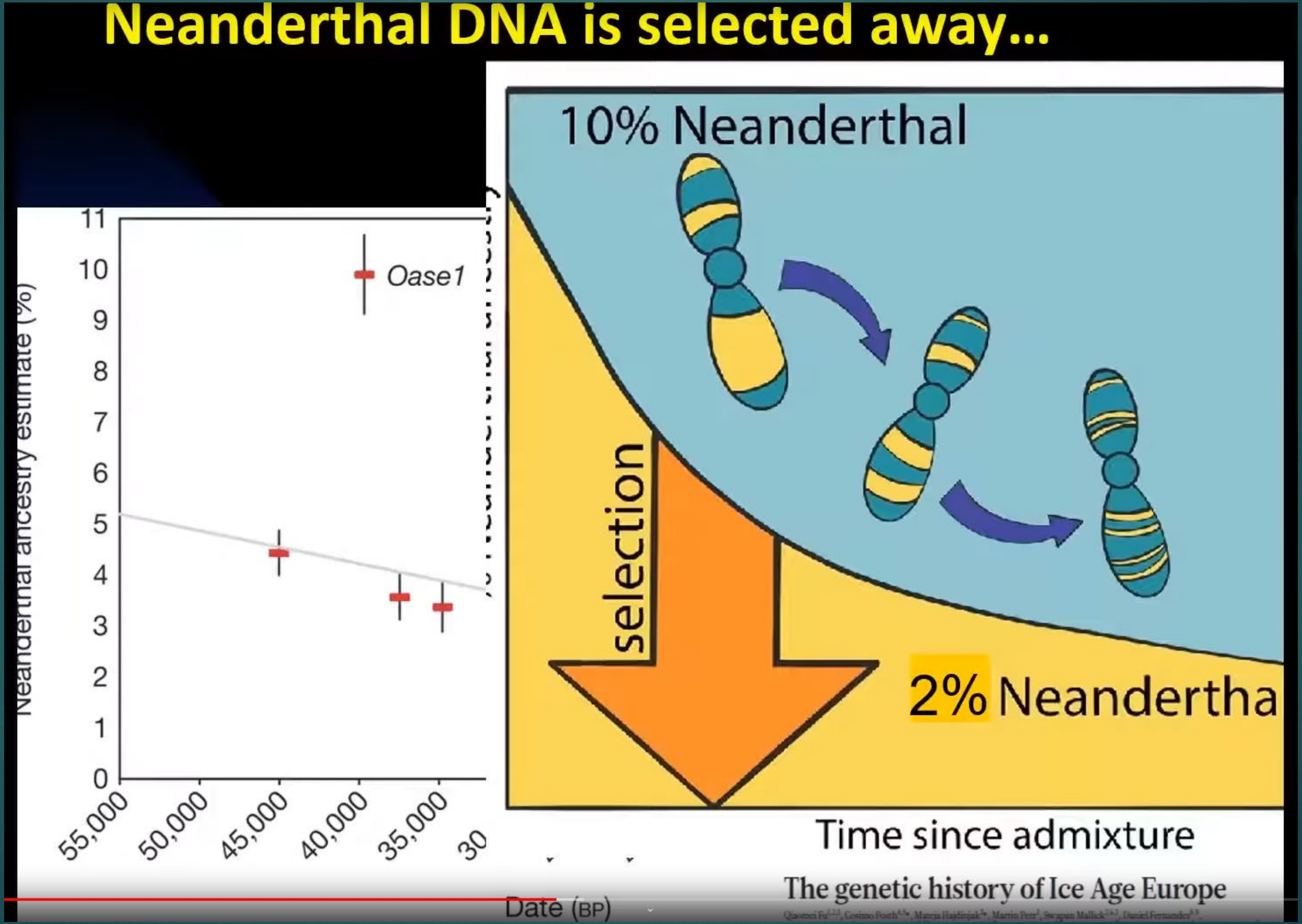
Genetic Analysis Detects Neanderthal Ancestor

Wednesday, May 13, 2015

(Erik Trinkaus)

BOSTON, MASSACHUSETTS—Genetic testing of a 40,000-year-old mandible with modern human and Neanderthal traits has revealed that the Oase man's genome was between five and 11 percent Neanderthal, including large chunks of several chromosomes. Palaeogenomicist Qiaomei Fu of Harvard Medical School and her colleagues analyzed how lengths of DNA inherited from an ancestor shorten with each generation. They estimate that this individual's Neanderthal ancestor was introduced in the previous four to six generations. The jawbone and one other human bone were discovered among bear remains in a Romanian

N Dna was negatively selected in MHs (as was MH DNA in N)



Neanderthal DNA is selected away...

The genetic history of Ice Age Europe

In Australia at 65 Ka (tools & pigment use) + critique (45 ka)

Human occupation of northern Australia by 65,000 years ago

2015

Chris Clarkson[1], Zenobia Jacobs[2,3], Ben Marwick[3,4], Richard Fullagar[3], Lynley Wallis[5], Mike Smith[6], Richard G. Roberts[2,3],

Madjedbebe rockshelter

When did *Homo sapiens* first reach Southeast Asia and Sahul?

2018

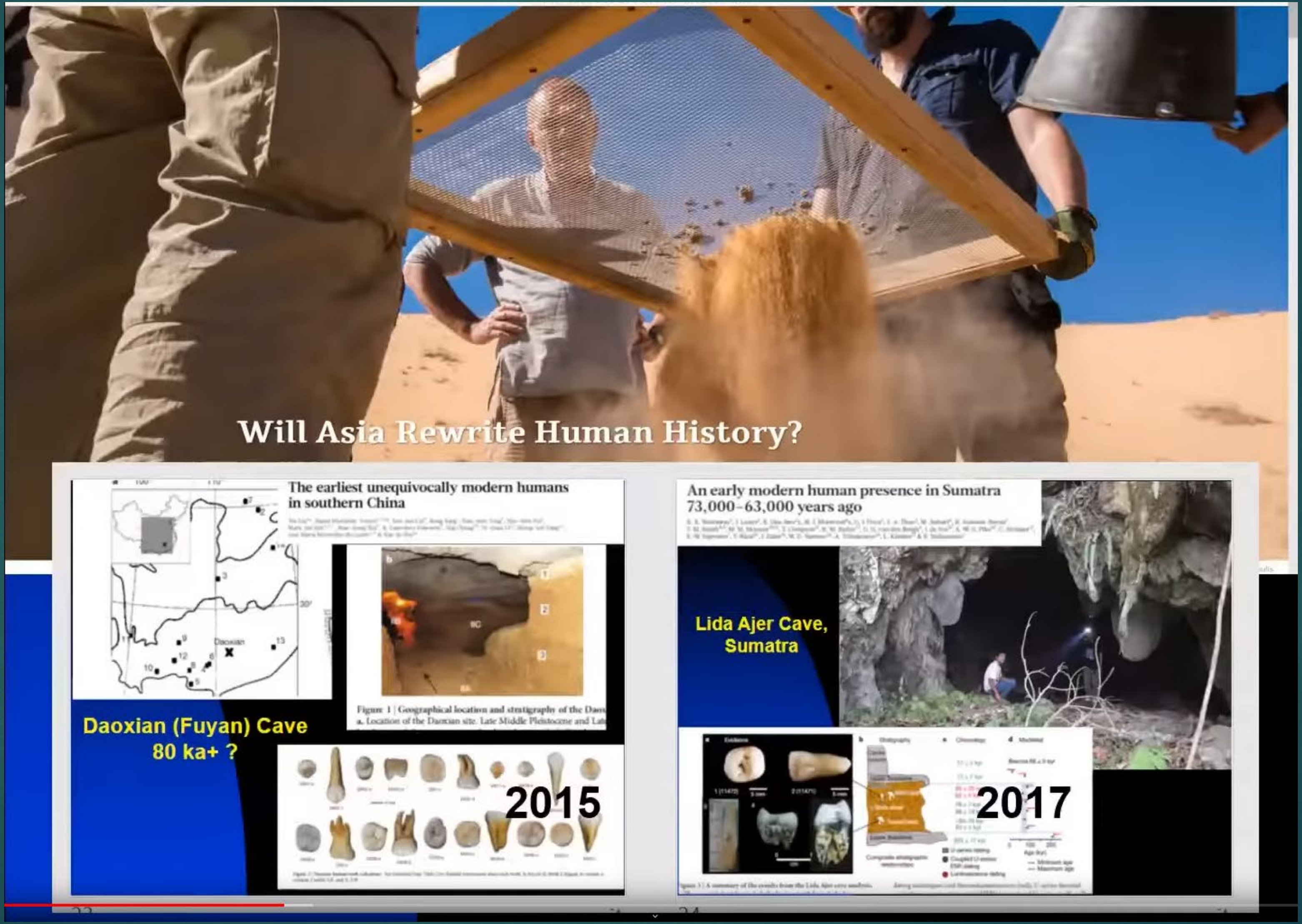
James F. O'Connell[a,1], Jim Allen[b], Martin A. J. Williams[c], Alan N. Williams[d,e], Chris S. M. Turney[f,g], Nigel A. Spooner[h,i], Johan Kamminga[j], Graham Brown[k,l,m], and Alan Cooper[g,n]

Edited by Richard G. Klein, Stanford University, Stanford, CA, and approved July 5, 2018 (received for review May 31, 2018)

Anatomically modern humans (*Homo sapiens*, AMH) began spreading across Eurasia from Africa and adjacent Southwest Asia about 50,000–55,000 years ago (*ca.* 50–55 ka). Some have argued that human genetic, fossil, and archaeological data indicate one or more prior dispersals, possibly as early as 120 ka. A recently reported age estimate of 65 ka for Madjedbebe, an archaeological site in northern Sahul (Pleistocene Australia–New Guinea), if correct, offers what might be the strongest support yet presented for a pre-55-ka African AMH exodus. We review evidence for AMH arrival on an arc spanning South China through Sahul and then evaluate data from Madjedbebe. We find that an age estimate of >50 ka for this site is unlikely to be valid. While AMH may have moved far beyond Africa well before 50–55 ka, data from the region of interest offered in support of this idea are not compelling.

Figure 3 | Bayesian model of the single-grain OSL ages. Ages have been

MHs in China at 80 Ka



Will Asia Rewrite Human History?

The earliest unequivocally modern humans in southern China

Figure 1 | Geographical location and stratigraphy of the Dao
a. Location of the Daoxian site. Late Middle Pleistocene and Lat

Daoxian (Fuyan) Cave
80 ka+ ?

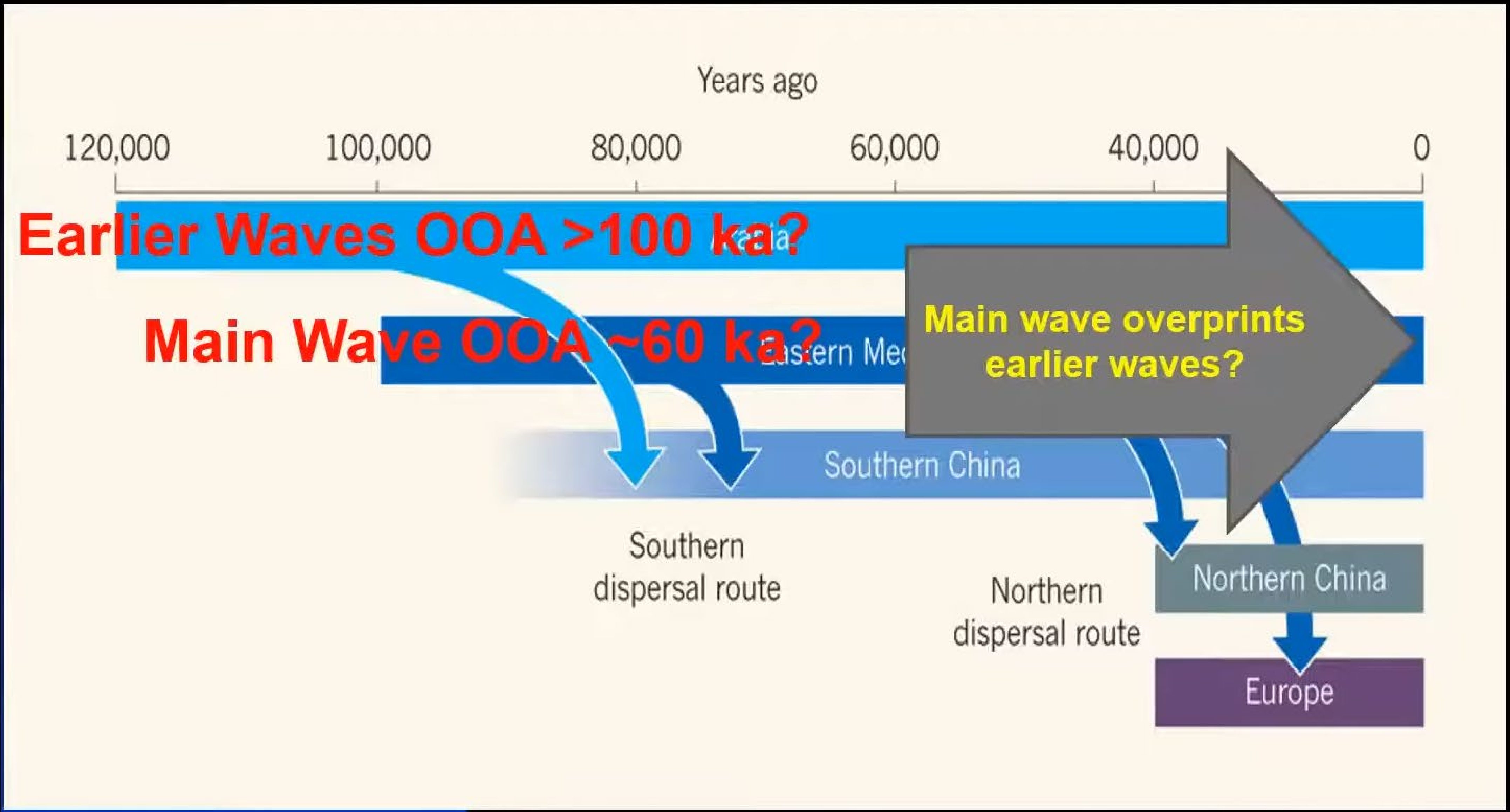
2015

An early modern human presence in Sumatra 73,000–63,000 years ago

Lida Ajer Cave,
Sumatra

igure 3 | A summary of the results from the Lida Ajer cave analysis.

2017



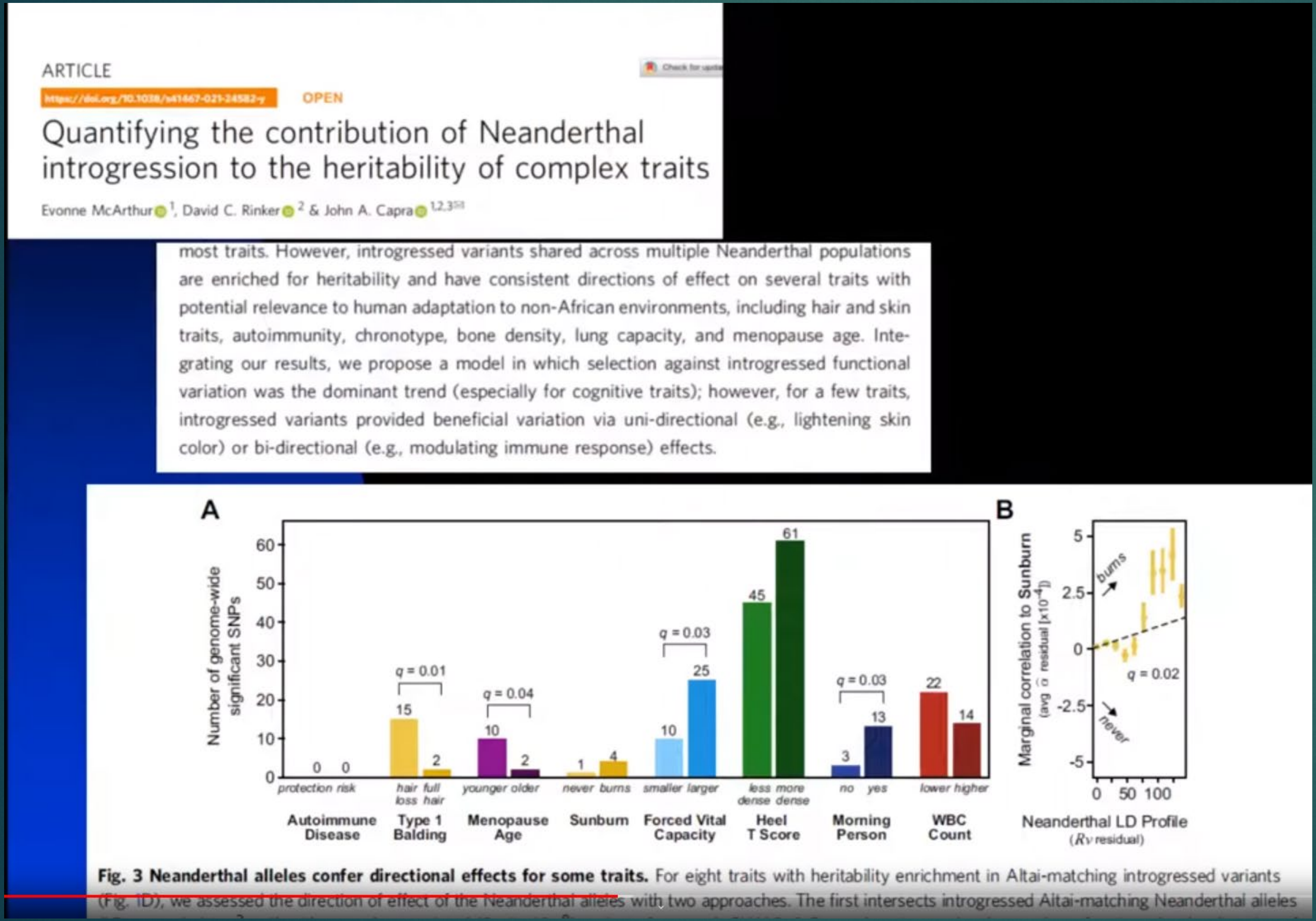
Earlier Waves OOA >100 ka?

Main Wave OOA ~60 ka?

Main wave overprints earlier waves?

Dennell 2015

N DNA in current MHs is still active.



ARTICLE

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Quantifying the contribution of Neanderthal introgression to the heritability of complex traits

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most traits. However, introgressed variants shared across multiple Neanderthal populations are enriched for heritability and have consistent directions of effect on several traits with potential relevance to human adaptation to non-African environments, including hair and skin traits, autoimmunity, chronotype, bone density, lung capacity, and menopause age. Integrating our results, we propose a model in which selection against introgressed functional variation was the dominant trend (especially for cognitive traits); however, for a few traits, introgressed variants provided beneficial variation via uni-directional (e.g., lightening skin color) or bi-directional (e.g., modulating immune response) effects.

Fig. 3 Neanderthal alleles confer directional effects for some traits. For eight traits with heritability enrichment in Altai-matching introgressed variants (Fig. 1D), we assessed the direction of effect of the Neanderthal alleles with two approaches. The first intersects introgressed Altai-matching Neanderthal alleles

Neanderthal DNA in us appears to be associated with:

Immune systems
metabolism of fats and
starches
keratin (skin and hair)
thromboses
Crohn's disease
lupus
biliary cirrhosis
rheumatoid arthritis
schizophrenia
addictive behavior
type 1 balding
susceptibility to COVID
Menopause age
Morning person
chronotype