Homo sapiens: Emergence of Modern Humans
Part V: The Levant
African Multiregionalism

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JULY 2021

*** Migration thru Levant

Skhul Cave, Mt. Carmel

Tabun and Skhul

Limestone, karstic, caves: open and closed at various periods; collapsed and eroded

Tabun

Skhul
~100K

Mount Carmel caves, Israel (Skhul and Tabun)

- Early hominins used Levant as an Out of Africa corridor through much of Lower Pleistocene
  - Ubeidiya at 1.4 Ma;
  - Evron Quarry at 1 Ma;
  - Gesher Benot Ya'aqov at 800 Ka
  - but hominin skeletal remains are scarce

- Often considered earliest evidence of fire at Acheulean site of Gesher Benot Ya'aqov at 730 KA (burned seeds, wood, flint)

- Mount Carmel Caves at Tabun and Skhul in 1930s: initially Tabun as Ns

Mt. Carmel, Israel: Skhul (scul) & Qafzeh (qafza)

In 1930s, English archeologist Dorothy Garrod: 10 MH skeletons, 100K; oldest human remains outside of Africa;

Skhul: early MH but with Mousterian tools

Tabun: Ns with Mousterian tools (400-500K)

Hawks: mixed population based on migration vs tools based on environment

Zuttiyeh, Arago 21, Skhul V, Shanidar 5

Zuttiyeh, Arago 21, Skhul V, Shanidar 5 (side view mirrored). Credit: 1 = Pierre-Francois

Skhul

- When and where our species left Africa is another hot topic for researchers.
- Outside of Africa, the oldest fossils of our species found so far are the Skhul/Qafzeh fossils in the Levant (where Israel is today), dating to around 100,000 years old.
- Originally thought of as a failed exodus, some believe the Skhul/Qafzeh fossils may represent a more successful distribution with stone tools on the Arabian Peninsula dating to between 100,000 and 80,000 years old.
- The location of these fossils falls in line with a Northern route out of Africa, through Egypt and Sinai.
- The other possible direction is a Southern route out of Africa through Ethiopia and the Bab el Mandeb strait across the Red Sea, following the coastline towards the Arabian Peninsular, heading to India.

Mount Carmel caves, Israel (Skhul and Tabun), MHs

- Skhul:
- modern like humans, esp. Skhul V cranium;
- but lots of morphological variation;
- Skhul 4 and 9 are much more N

- Dating: Skhul, Qafzeh, Tabun: 100-130 Ka; earlies burials of MHs at 1st 2

- But stone tools of AMHs at Skhul & Qafzeh are indistinguishable from later dated Ns (Kebara)

- Both groups did intentional burials;

Mount Carmel: (Skhul and Tabun)

- Only distinctions between MH and Ns:
  - Ns at Kebara had more points than Qafzeh;
  - more AMHs at Qafzeh and Skhul
  - more evidence of deliberate burials, and use of ochre and shells

- More MHs at Qafzeh/Skhul and more N-like Amud/Shanidar/Tabun group

- Qafzeh: 90-100 Ka; 3 burials (adult, double burial of woman and child, young boy) with perforated Glycymeris shells; have chins (unlike Skhul)

Kebara 2 skeleton: most complete N skeleto

Mount Carmel: Kebara Ns

- Kebara: 60 Ka;
  - almost complete adult N male;
  - fully modern hyoid bone;
  - head removed and replaced; complete pelvis

- Mosaics in Levant lead to conclusion that Levant Ns and early MHs were not uniquely derived;

- Supported idea that there was not complete replacement in OoA:
  - extreme variation in Skhul and Qafzeh suggests that while AMHs originated in Africa, they mixed with other populations as they spread.

Anatomically MH: Levant, 40-120K

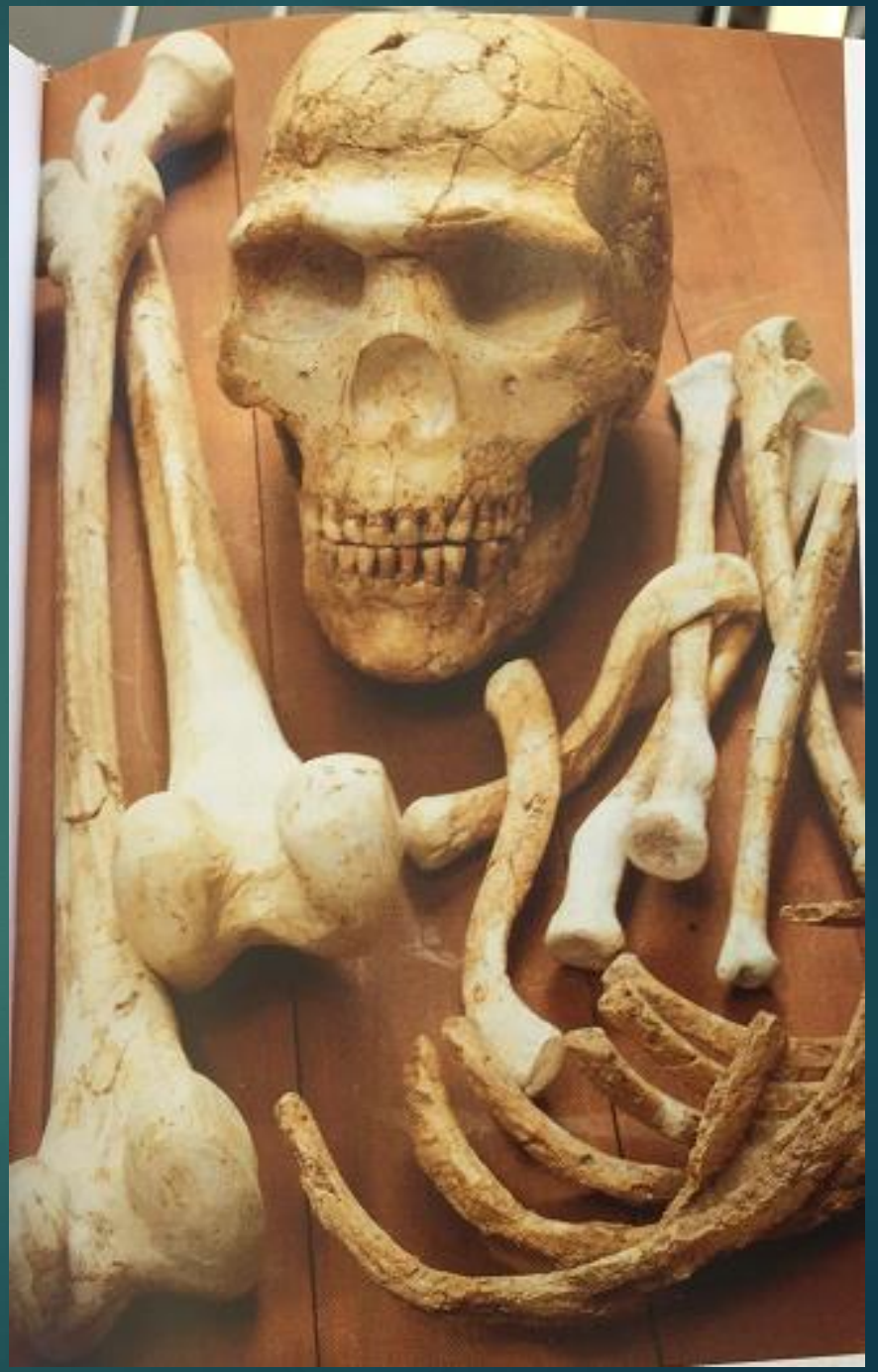
- Lots of intentional burials
- Original belief: N sites predate MH; turned out to be more complex
- question of modern human origins.
- Whether there was species replacement, or some kind of more complex population-level process, in an evolving human species.

Dating confusion

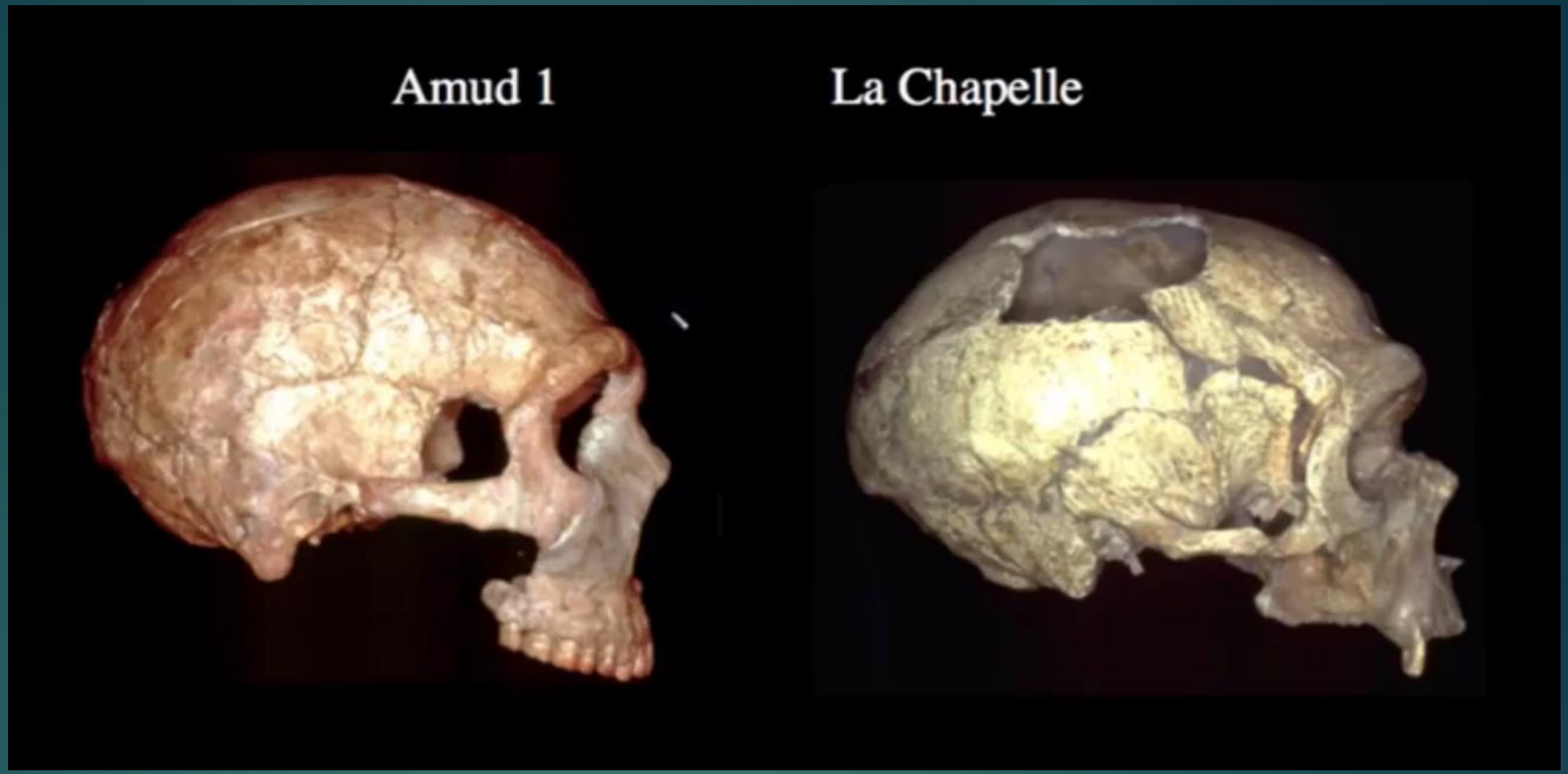
- Ns and early MHs coexisted or alternated in Eurasia for 10s of thousands of years, from before 100 Ka to 35 Ka
- At Qafzeh: MHs came first
  - early MHs (16 individuals) originally dated to 40-50 Ka are actually 90 Ka;
  - Ns at Saint-Cesaire, France dated to 35 Ka.

Skhul/Qafzeh Skull 5, 90 Ka, MH

The earliest anatomically modern humans out of Africa around 100,000 years ago, Skhul/Quafzeh Skull number 5. (Image Public Domain)

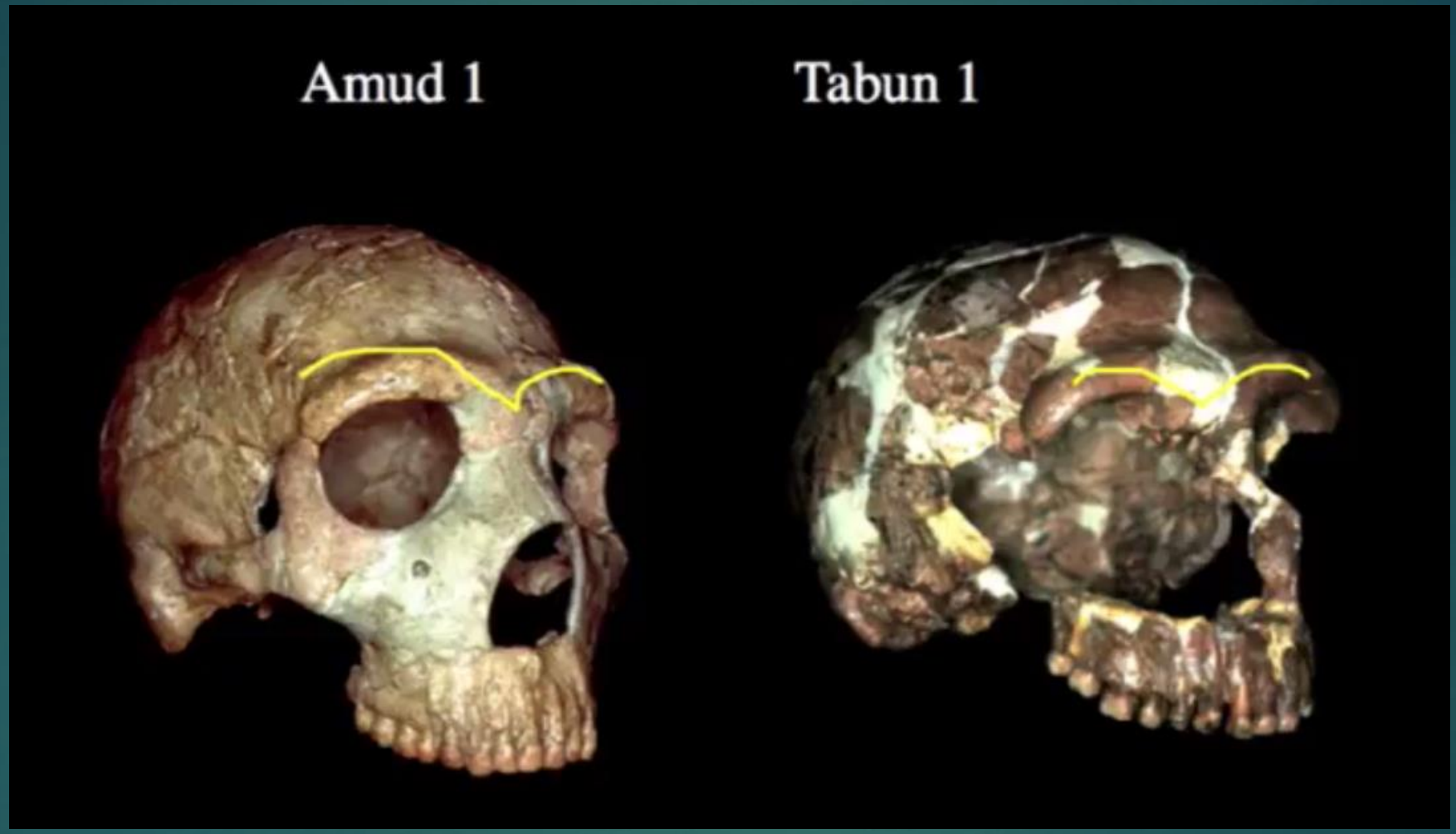


Two Ns



- Similar N features: high nasal bone, projecting brow ridges, fairly flexed occiput, large cranial vault (1600 cc)
- Amud = 40-60K

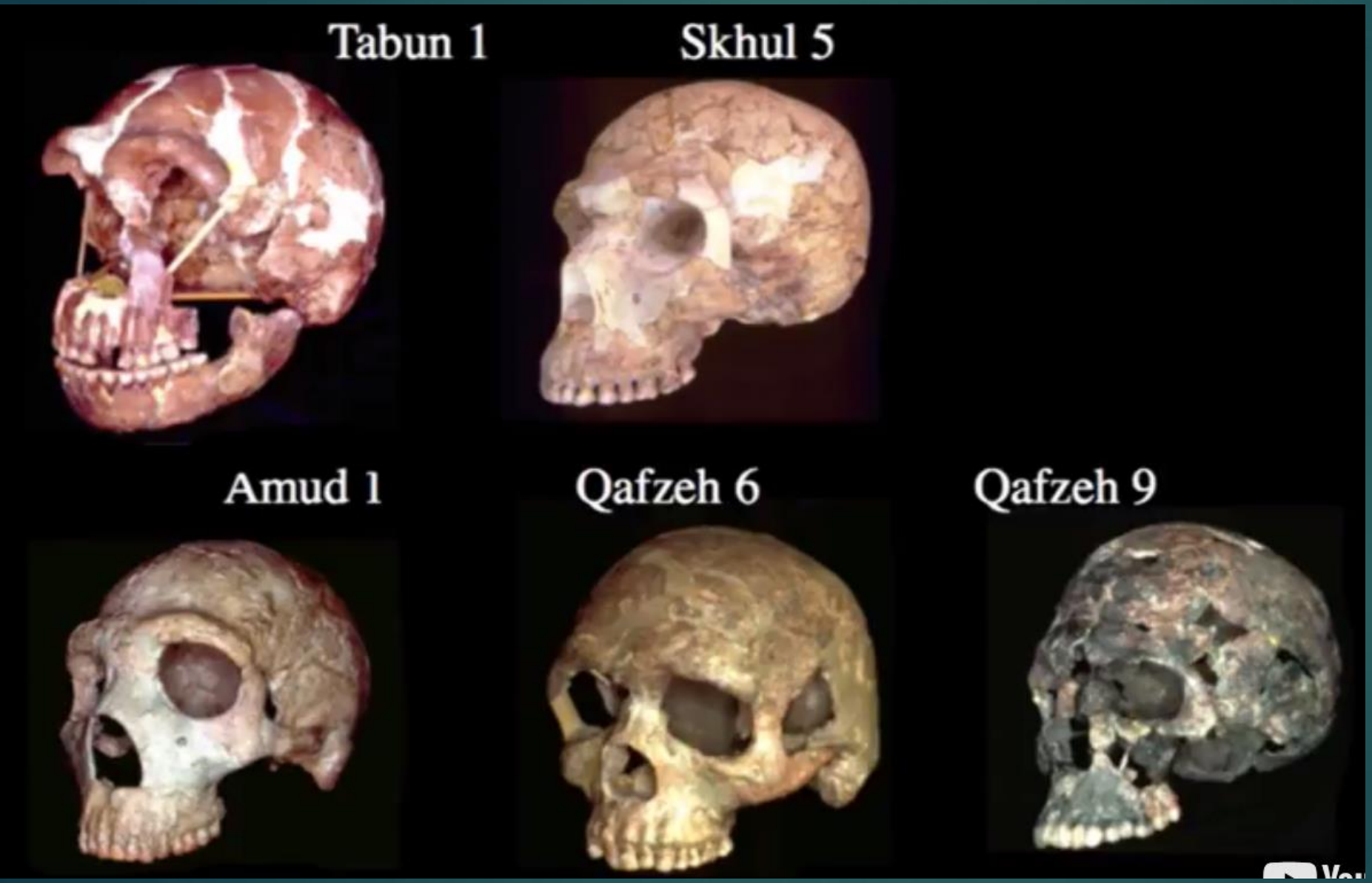
Amud & Tabun Ns



Earlier N

- double-arched, fairly projecting supraorbital torus; low frontal slope.

More complex Ns in Levant



Question of Temporal sequence:

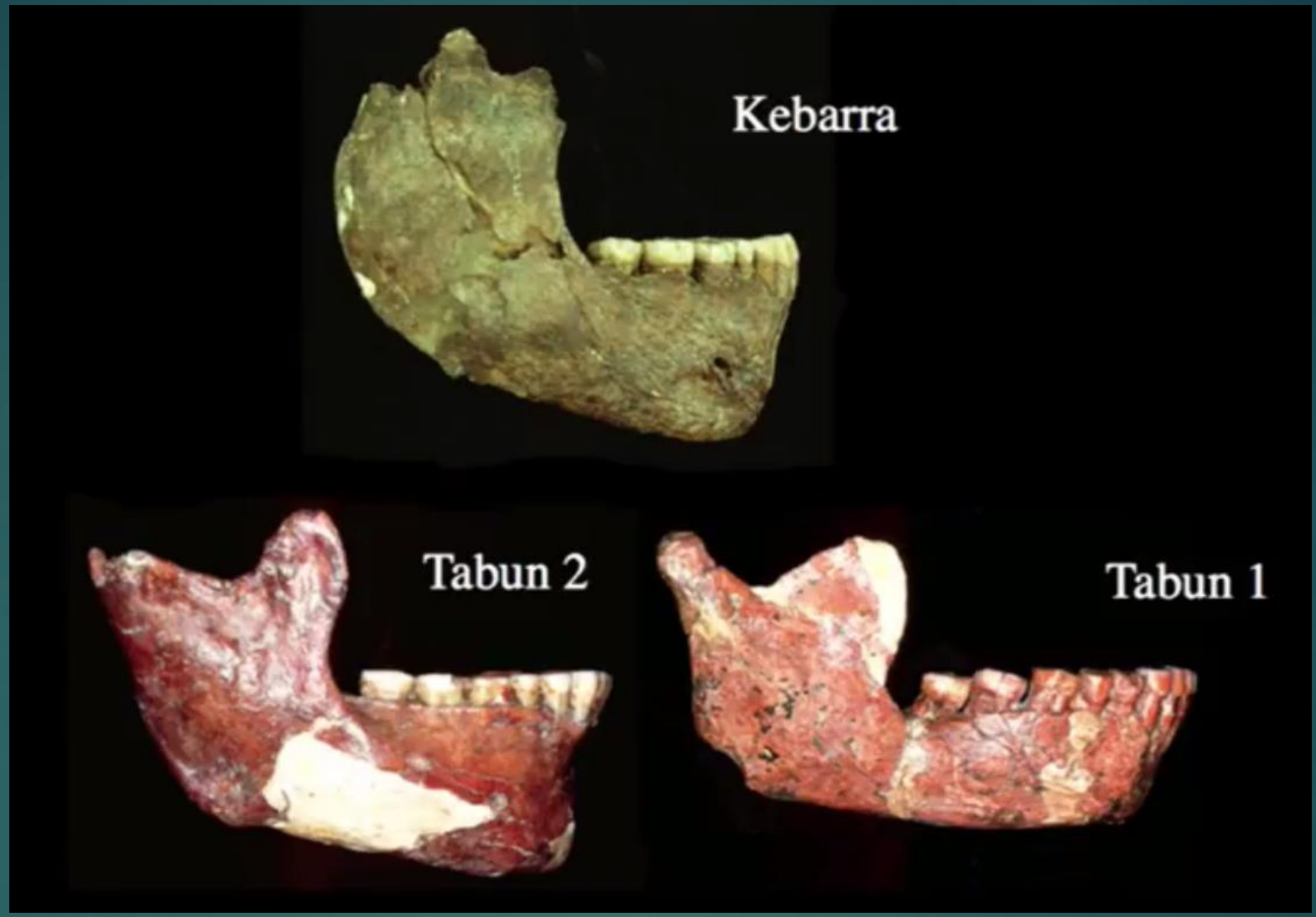
- Tabun 1 = N
- Skhul 5 = MH; browridge & projecting face;
- Amud 1 = N
- Qafzeh 6 = MH, but more primitive than Q9; more projecting zygomatic; a projecting SO torus; less rounded cranial vault.
- Qafzeh 9 = MH; slanting forehead,

Arranged based on occipital rounding: different species or populations?

- Qafzeh 5: flexed occipital (a N characteristic)
- Qafzeh 6: similar

- Qafzeh 9: rounded globular cranium, MH morphology
- Qafzeh 3 & Skhul 1 also
- Tabun 1 & Amud 1 also
- Hard to differentiate N from MH

N Mandibles



• Kebara and Tabun 1 lack chins, a classic Neanderthal trait, as is the presence of a retromolar space in Tabun 1 and Tabun 2; The coronoid process of the ascending ramus appearing above the mandibular condyle of Tabun 2 is a classic Neanderthal trait. But Tabun 2, a N, has a chin; Kebara has no retromolar space; Tabun 1 has a mandibular condyle and coronoid process of the ascending ramus that are equal in terms of the vertical height.

Origin of *H. sapiens:* Near East

- Levant: Western Asia (Skhul and Qafzeh):
  - The Levant has clearly been a conduit for ancient population movement between Africa and Eurasia.
  - Skhul fossils, comprising 10 individuals, were discovered by Ted McCown in 1931–1932 as part of a larger dig in the Mount Carmel area directed by Dorothy Garrod
  - Some of the Skhul individuals were intentionally buried; Skhul material (Skhul 2, 5 and 9) has now been dated to between approximately 100 and 130 ka

Specimens from Israel

(a) Skhul 5

(b) Qafzeh 6

- These specimens from Israel are thought to be representatives of early modern Homo sapiens.
- The vault height, forehead, and lack of prognathism are modern traits.

Levant: Qafzeh

- Qafzeh Cave excavated in 1930s and 1970s; 16 individuals;

- Vandermeersch' s monographic work demonstrated that the Skhul and Qafzeh samples shared Middle Paleolithic associations; cranial, dental and postcranial anatomy of the combined Skhul-Qafzeh sample represents an early form of *H. sapiens* sensu stricto, albeit with robust or primitive features; 90 to 120 ka

- Currently impossible to determine whether the Skhul and Qafzeh specimens represent different samples from essentially the same variable population

Dating variation

- Dating switch:
  - Originally thought NE Neandertals dated to only 50 Ka, whereas AMHs from Qafzeh and Skhul were younger and implied evolution of Ns into MHs.
  - Not true.
  - The AMHs (Qafzeh) were at 90 Ka.
  - The Kebara Ns were 100-46 Ka.
  - Some of MHs predated the Ns by 10s of thousands of years.
  - AMHs from Tabun coexisted with Ns for 50 K in Near East.
  - Killed idea that Ns evolved into MHs in Near East and that MHs coincided with technological revolution of UP, since both Ns and MHs used Mousterian.

Near East

- Two groups may have had different ecological niches based on different fauna (N = palearctic; MH = African)

- Archeological evidence indicates that transition from MP to UP industries in Levant occurred ~40 Ka, typified by less reliance on Levallois technique and more on blade and bone technology; and use of shells, art objects, red ochre, grinding tools, and hearths with encircling stones

Near East summary

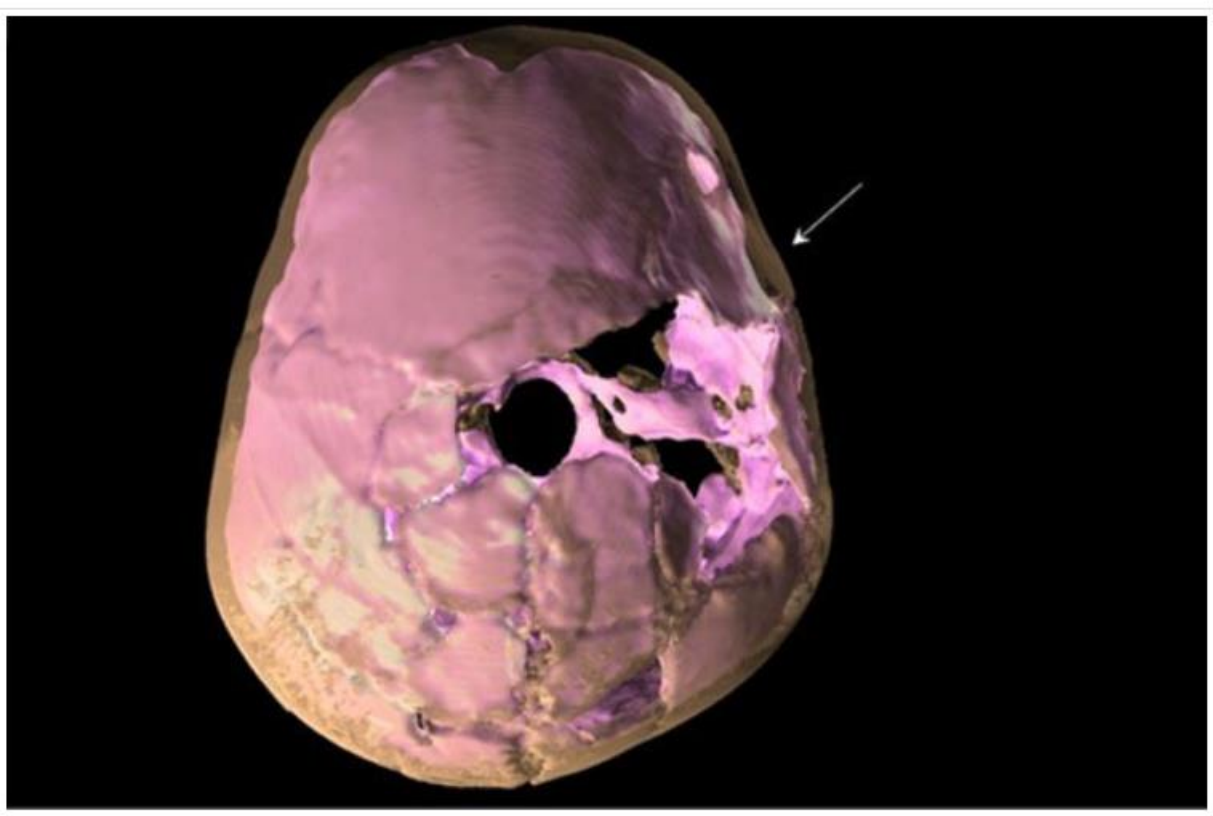
- Near-modern humans (Skhul, Qafzeh) and N (Tabun, Kebara) occupied West Asia between 130 and 40 KA

- MHs were predominant before 80 Ka, Ns after 80 Ka

- Neither group gave rise to other; AMH from Africa & Ns originated in western Europe and migrated to West Asia during opening stages of last glaciation

- Two groups were archeologically indistinct from each other.

Qafzeh 11: Brain damaged child, 100 Ky



24 JULY, 2014 - 14:30 APRILHOLLOWAY

New study shows brain-damaged child was well cared for 100,000 years ago

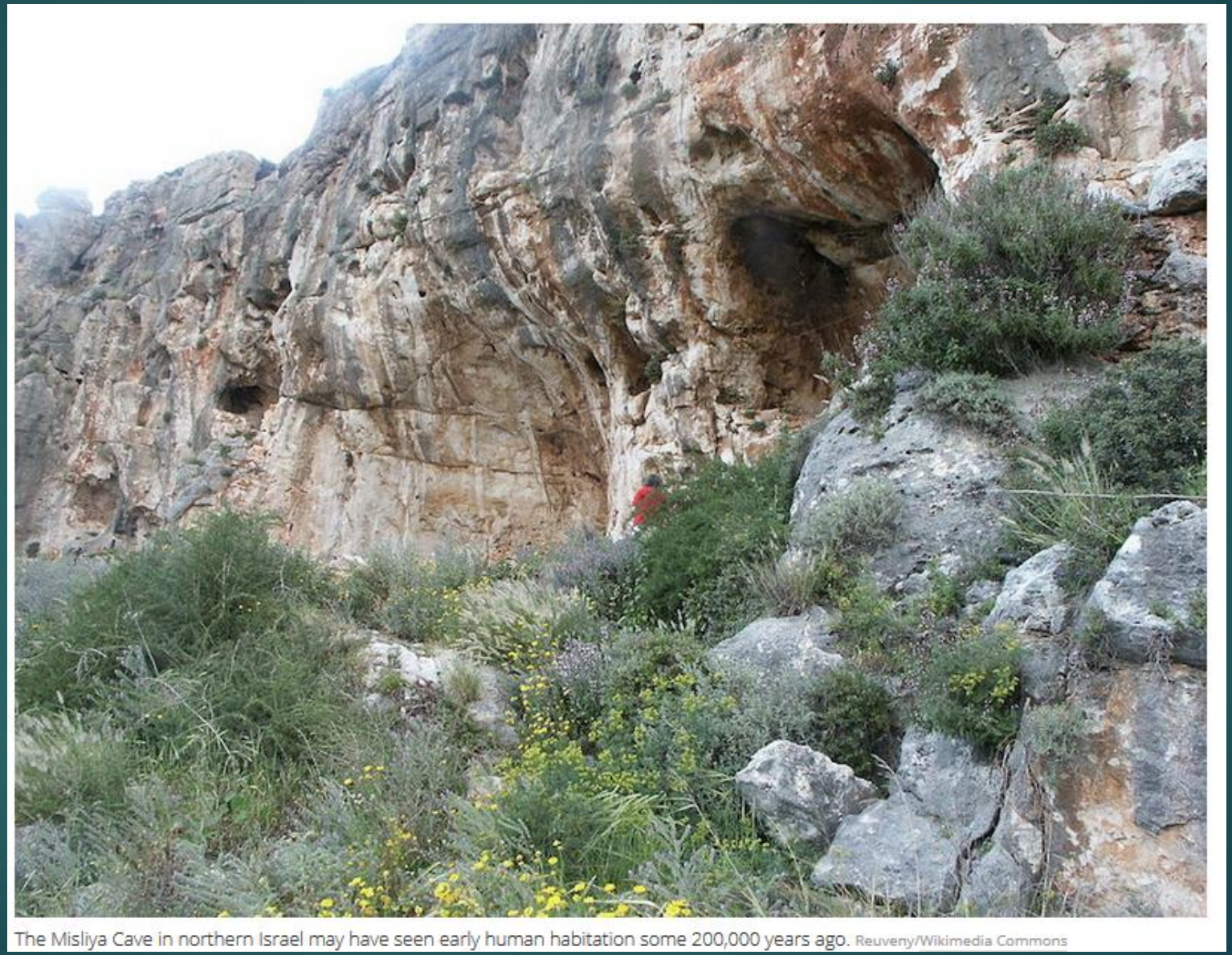
Qafzeh 11: Brain damaged child, 100 Ky

- Signs of care for a disabled person suggest that the roots of human compassion go way back
- Found with a visible fracture in the skull and a pair of deer antlers placed across the chest.
- Child suffered a blunt-force trauma at the front of the skull that created a compound fracture, with a piece of bone depressed in the skull. It wasn't clear whether child abuse or an accident caused the injury.
- In addition, tooth growth indicated that the youngster was 12 or 13 years old when he or she died, but the child's brain volume was more akin to that of a 6- or 7-year-old. Cared for for years.
- A 400 Ka fossil human from Sima de los Huesos in Spain shows signs of severe brain deformity starting at birth, but that child still lived to age 5, which mean someone cared for the child despite his or her disorder.

When did MHs leave Africa? There was more than one ‘out of Africa’ dispersal

- A new crop of discoveries, particularly from Asia, suggest that modern humans first left Africa some 200,000 years ago, taking multiple different routes.
- Misliya Cave in Israel. In 2018, archaeologists revealed that they had found a human jawbone in this cave.
- The bone—dated with three different methods in the course of a decadelong investigation—is between 177,000 and 194,000 years old, pushing back the timeline of when humans first lived here by at least 50,000 years. And older stone tools found in layers beneath the jaw suggest that humans could have been present in this area even longer.

Israeli Misliya Cave



The Misliya Cave in northern Israel may have seen early human habitation some 200,000 years ago. Reuveny/Wikimedia Commons

Misliya-1 Mandible

- One of oldest fossils of modern humans outside Africa have been discovered in Mt. Carmel, Israel: MH jaw, dubbed Misliya-1, revealing that its owner lived between 177 to 194 Ka;
- fire hearths; stone tools of Levallois technique;
- large animals;
- migration out of Africa via Nile Valley and the eastern Mediterranean coast — and not through the southern route — the Bab el Mandeb Strait, the southern coast of Saudi Arabia, the Indian subcontinent, East Asia; Israel Hershkovitz, et al., Science, 2018

- Changes our discussion of geographic boundaries and temporal timings

Oldest known human fossil outside Africa discovered in Israel

177-194 Ka

Israeli Misliya Cave half jaw: 177-194 Ka – earliest out of Africa

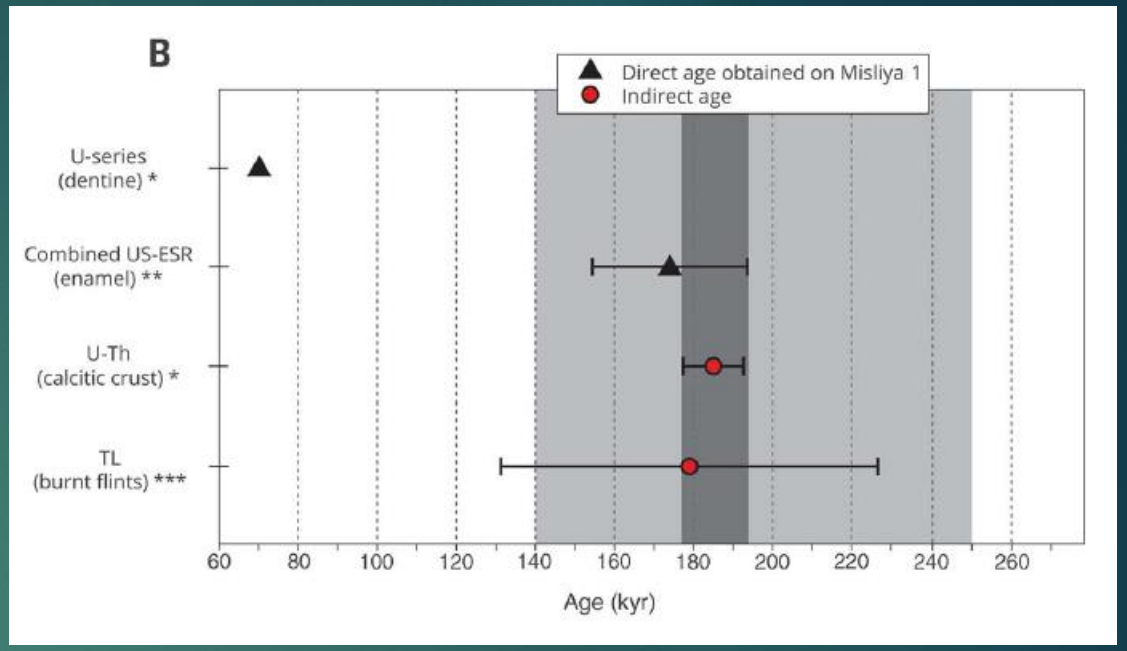
- Misliya-1 appears to represent the earliest fossil evidence of the migration of members of the *H. sapiens* out of Africa.
- Mt. Carmel, Misliya Cave, Israel
- dated teeth from the jaw and flint tools found with the remains, obtaining an average age for the specimens of about 177,000-194,000 years old.

Israel Hershkovitz, et al., Science, 2018

Israeli jaw: at least 140 ka, and most likely around 185 ka,

- Before the Misliya fossil (177-194 ka) the oldest modern human fossils outside Africa were the Qafzeh and Skhul materials (90-120 ka) and the 47 teeth from Fuyan Cave, China (80-120 ka) - which now pale in comparison to the new find!
- Misliya Cave in Mt. Carmel, Israel: Roasted hare, turtle, and ostrich eggs and 1000s of knapped stone tools from flint. One of the first modern members of our species to leave Africa.
- Its canine and other teeth resemble those of the modern humans at Skhul and Qafzeh, and it lacked features found in Neandertals.
- Found with many Levallois (Early Levantine Mousterian (Tabun D type); (i.e., ~250 to ~140 ky)) technology stone tools; dated the burned flint tools to 212 to 140 ky (179K)

Misliya Cave



Misliya-1 considerably pushes back the timing of the earliest migration of members of the H. sapiens clade out of Africa, well predating Qafzeh and Skhul in the Levant, and Daoxian and Liujiang in China

2008: Manot, Israel: Manot 1, 58 Ka

- I. Hershkovitz: Modern human skull (Manot 1) which is estimated to be 54,700 years old

- Oldest MH outside of Africa; Manot 1 is nearly 11,000 years older than the oldest early modern human remains in Europe, the skeletal remains from Bacho Kiro Cave

- First physical evidence that supports the Out of Africa theory

Barzilai, O, et al., *Nature*, January 2015

Earlier dispersals

- Out of Africa dispersals documented at
  - Misliya Cave (177 to 194 ky ago),
  - Qafzeh and Skhul Caves (90 to 120 ky ago),
  - and Manot Cave (50 to 60 ky ago)
- reflect expansions of the geographical range of H. sapiens, fluctuating in response to demographic or environmental factors
- To date, Misliya-1 appears to represent the earliest fossil evidence of the migration of members of the H. sapiens clade out of Africa. It therefore opens the door to the possibility that H. sapiens dispersal from Africa could have occurred earlier than previously thought (probably before 200 ky ago), as has been recently suggested based on genetic evidence (Hohlenstein–Stadel femur: N-MH admixture between 413 and 268 ka)

Manot Cave skull

Anthropologists discovered a 55,000-year-old skull fossil in the Manot Cave in western Galilee in 2008

Could this support recent genetic evidence that modern Homo sapiens and their Neanderthal cousins interbred, perhaps in the Middle East and most likely between 65,000 and 47,000 years ago?

From left, a Neanderthal skull, the Manot cranium and a complete modern human skull on display near the cave in Israel where the Manot cranium was found. Jim Hollander/European Pressphoto Agency

N-MH hybrid?? - distinctive bunlike shape at the base of the skull resembles modern African and European skulls but differs from other anatomically modern humans from the Levant,

Earliest displays of human adornment in the Middle Palaeolithic

- *Glycymeris* shell beads found in Middle Palaeolithic sites are understood to be artifacts collected by modern humans for symbolic use. In Misliya Cave, Israel, dated to 240–160 ka BP, *Glycymeris* shells were found that were neither perforated nor manipulated; nevertheless, transportation to the cave is regarded as symbolic.
- In about 120 ka BP at Qafzeh Cave, Israel, modern humans collected naturally perforated *Glycymeris* shells also for symbolic use. Use-wear analyses backed by experiments demonstrate that the Qafzeh shells were suspended on string, thus suggesting that the collection of perforated shells was intentional.
- The older Misliya shells join a similar finding from South Africa, while the later-dated perforated shells from Qafzeh resemble other assemblages from North Africa and the Levant, also dated to about 120 ka BP. We conclude that between 160 ka BP and 120 ka BP there was a shift from collecting complete valves to perforated ones, which reflects both the desire and the technological ability to suspend shell beads on string to be displayed on the human body

Daniella E. Bar-Yosef Mayer, et al., 2020

Multiregionalism in Africa

Genetics, archaeology, & fossils evidence

- New age of Kabwe/Broken Hill skull (300 Ka) implies *H. heidelbergensis* is too young to be ancestor of *H. sapiens;* he was a neighbor.

- If *Homo heidelbergensis* wasn't one of our recent ancestors, then who was?

- Coexistence: Multiple African hominins at 300 Ka: *H. sapiens* in Jebel Irhoud; *H. naledi* in S. Africa; *H. heidelbergensis in* Kabwe, Zambia

- Africa has a far more complex past than was previously appreciated—one rich in diversity, migration, and possibly even interbreeding with other hominin species in Africa.

Katarina Zimmer, 2020

Sparse fossil record

- Bones easily disintegrate in many parts of Africa, in acidic forest soils or dry, sun-exposed areas.

- Moreover, the continent is largely unexplored by archaeologists. While northwestern Africa and former British territories in eastern and southern Africa have a long tradition of professional archaeological research, few researchers have looked for fossils anywhere else.

- That's especially the case for the western and central parts of the continent, where preservation conditions are also poor and excavations difficult at times due to political instability.

Origins of *Homo*

- Most abundant Australopith fossils are in sediments between 3.5 million and 3.2 million years old.

- Our own genus, *Homo*, emerged from transitional ape species some 2.8 million years ago as a clan of hominins with distinctive teeth, probably adapted to an eclectic diet that allowed them to thrive in a wide range of habitats.

- But there are few sediments, let alone fossils, left behind from that time, making the birth of our genus one of the most poorly understood periods in our evolution.

Origins of *Homo*

- By around 160,000 years ago, the constellation of physical features that defines us today—such as a globular braincase and a pointed chin—had begun to emerge in ancient hominin groups represented by fossils found across Africa, i.e. Herto

- Later, some of these anatomically modern humans crossed the thin spit of land that connects Africa to Eurasia, probably on several occasions. On that new continent, they eventually met Neanderthals and Denisovans.

- Africa was this sort of leaky faucet, and hominins were just dribbling out of it all the time.

Our Origins: genetic discoveries

- Several studies of genetic variation among modern-day Khoe and San individuals, they represent our species' most genetically diverse lineage.

- The Khoe-San is thought to have split from other populations between 200,000 and 350,000 years ago, making them the most ancient population of modern humans to diverge.

- Non-Africans represent a reduced subset of the genetic diversity in Africa, who ventured out of the continent between 60,000 and 70,000 years ago.

- Some scientists see the extraordinary diversity in modern Khoe-San people as evidence that our species arose in southern Africa.

Our origins: archeology vs genetics

- Along with some archaeological evidence from the region, that challenges the long-held idea of an East African origin, which was based on the fact that many early hominin fossils were found there.
- However, trying to pinpoint the precise location of our species' origins from DNA is often criticized for the simple reason that people move around—it's not known if the populations living in one place today were there hundreds or thousands of millennia ago

Our Origins

- Scerri, Stringer, and Thompson, have recently proposed an entirely new theory of our origins:
  - that anatomically modern humans didn't arise from a single place, but gradually emerged from a web of interconnected populations sprawled across Africa—a continental gene-sharing bonanza that hominin lineages besides our own may have participated in.

- Researchers are interested in *how we evolved*: which genes gave us a selective advantage to survive in particular environments, and which ancestors contributed to our genomes?

- Unfortunately, modern African DNA is severely underrepresented in genetic research.

Our origins: Genes

- Most sequenced genomes are of European origin, with fewer than 2 percent coming from Africans.

- This dearth of African genomes is compounded by the fact that the genetic scaffold underlying some frequently studied traits such as skin pigmentation appear to be far more complex in Africans than in other populations.

- The twelve to fifteen genes [for skin pigmentation] that people cite in Eurasian populations explain less than 25 percent of the variation in Africans.

Our African Origins

- African population history consisted of large-scale migrations pulled people back and forth across the continent for thousands of years.
- People from Eurasia also migrated back to Africa.
- Where people moved, they swapped their genes with local populations, shuffling patterns of ancestry across African genomes.
- One intriguing finding: possible evidence of mixture with now-extinct, unknown groups of modern humans and other hominins: “ghost” populations that left traces in modern genomes.
- In one analysis of 15 sequenced genomes, Tishkoff’s group investigated the sources of genetic variation in three different modern African hunter-gatherer groups.

Our origins

- A handful of similar studies have also revealed traces of ghost hominins in modern African genomes, sometimes accounting for up to 10 to 20 percent of the genetic variation.

- Some research suggests that mixing took place after the ancestors of modern Eurasians left Africa, hinting that other kinds of hominins could have existed alongside *Homo sapiens* in Africa until very recently = Ten percent of the genome

- So far, the oldest human DNA found on the continent is just 15,000 years old

Genetics of Our Origins

- In 2015, harvesting of the first ancient DNA in Africa—the genome of Mota, a man who left behind 4,500-year-old remains in an Ethiopian cave.

- In the five years since that publication, researchers have published nearly 100 other full and partial ancient human sequences from Africa.

- For instance, mitochondrial DNA from the skulls of seven people who lived some 15,000 years ago in modern-day Morocco revealed that they were closely related to Natufians, hunter-gatherers who dwelled in the Near East, as well as people living south of the Sahara desert.

- This finding suggested that there were far-flung connections between North Africa, the Near East, and sub-Saharan Africa before the dawn of agriculture

Sone Genetic studies of African groups

Date (years)	Populations	Citation
110000	San versus Pygmy & West Africans	Veeramah *et al.*
110000-150000	San versus Yoruba	Gronau *et al.*
130 000	San versus Eurasians	Mallick *et al.*
100000	KhoeSan versus other Africans	Schlebusch *et al.*
150 000-20 000	Yoruba versus Europeans	Schiffels and Durbin
120000-140000	San versus Mbuti	Song *et al.*
87 000	San versus Yoruba	Mallick *et al.*
160000	Central Pygmy versus West Africans	Hsieh *et al.*
130000-140000	Central Africans versus Europeans	Lopez *et al.*
260 000-350 000	Ancient San versus	Schlebusch *et al.*

Our origins

- Analyses of ancient DNA have also helped researchers understand how ancient migrations affected the genomes of people alive today.
- One such migration is the Bantu expansion, which gradually spread West African farming practices across the continent between roughly 5,000 and 1,000 years ago.
- By comparing DNA from ancient hunter-gatherer remains in southern Africa with modern-day Khoe-San people, discovered that some Khoe-San groups carry DNA that ancient farmers brought with them.
- They also carry mixed Eurasian ancestry that had been introduced to North Africa with earlier back-migrations into the continent and eventually carried to the southernmost tip of Africa as other migrating human populations moved southward.

*** New Perspective of our origins

- The latest research suggests that *H. sapiens* emerged from groups located across Africa and that interbreeding with other human species contributed to our success.

- How did our kind come to be the last human standing?

- Recent theory favored a simple explanation:
  - *H. sapiens* arose relatively recently, in more or less its current form, in a single region of Africa and spread out from there into the rest of the Old World, supplanting the Neandertals and other archaic human species it encountered along the way.
  - There was no appreciable interspecies fraternizing, just wholesale replacement of the old guards by the clever newcomer.

*** New Perspective of our origins

- Newer theory: looks as though *H. sapiens* originated far earlier than previously thought, possibly in locations across Africa instead of a single region, and that some of its distinguishing traits—including aspects of the brain—evolved piecemeal.

- Debate about the origin of our species has traditionally focused on two competing models.

New Perspective of our origins 2

- On one side was the Recent African Origin hypothesis, championed by paleoanthropologist Christopher Stringer and others, which argues that *H. sapiens* arose in either eastern or southern Africa within the past 200,000 years and, because of its inherent superiority, subsequently replaced archaic hominin species around the globe without interbreeding with them to any significant degree.
- On the other was the Multiregional Evolution model, formulated by paleoanthropologists Milford Wolpoff, Xinzhi Wu and the late Alan Thorne, which holds that modern *H. sapiens* evolved from Neandertals and other archaic human populations like *H. erectus* throughout the Old World, which were connected through migration and mating. In this view, *H. sapiens* has far deeper roots, reaching back nearly two million years.

New Perspective of our origins

- By the early 2000s the Recent African Origin model had a wealth of evidence in its favor.
- Analyses of the DNA of living people indicated that our species originated no more than 200,000 years ago.
- The earliest known fossils attributed to our species came from two sites in Ethiopia, Omo and Herto, dated to around 195,000 and 160,000 years ago, respectively.
- And sequences of mitochondrial DNA recovered from Neandertal fossils were distinct from the mitochondrial DNA of people today—exactly as one would expect if *H. sapiens* replaced archaic human species without mating with them.

New Perspective of our origins

- Many archaeologists think that the start of a cultural phase known as the Middle Stone Age (MSA) heralded the emergence of people who were beginning to think like us. Replaced prior Acheulean style.
- The problem was that the earliest dates for the MSA were more than 250,000 years ago—far older than those for the earliest *H. sapiens* fossils at less than 200,000 years ago. Did another human species invent the MSA, or did *H. sapiens* actually evolve far earlier than the fossils seemed to indicate?
- Comparison of the Neandertal nuclear DNA with that of living people revealed that non-African people today carry DNA from Neandertals, showing that *H. sapiens* and Neandertals did interbreed after all, at least on occasion.

New Perspective of our origins

- Subsequent ancient genome studies confirmed that Neandertals contributed to the modern human gene pool, as did other archaic humans.
- Further, contrary to the notion that *H. sapiens* originated within the past 200,000 years, the ancient DNA suggested that Neandertals and *H. sapiens* diverged from their common ancestor considerably earlier than that, perhaps upward of half a million years ago. If so, *H. sapiens* might have originated more than twice as long ago as the fossil record indicated.
- In 2017, J. Hublin recovered additional fossils from the Jebel Irhoud, Morocco site, along with MSA tools. Dated to 315 Ka. The researchers had found the oldest traces of *H. sapiens* to date, as well as the oldest traces of MSA culture.

New Perspective of our origins

- Not everyone agrees that the Jebel Irhoud fossils belong to *H. sapiens*.
- Constellation of skull traits that distinguish H. sapiens from other human species did not all emerge in lockstep at the inception of our kind, as supporters of the Recent African Origin theory had supposed.
- The Moroccan fossils resemble modern humans in having a small face, for example. But the braincase is elongated like those of archaic human species rather than rounded like our own dome.
- This shape difference reflects differences in brain organization: compared with fully modern humans, the Jebel Irhoud individuals had smaller parietal lobes and a smaller cerebellum,

New Perspective of our origins

- The total *H. sapiens* package did not coalesce until sometime between 100,000 and 40,000 years ago.
- So what happened in the intervening 200,000 years or more to transform our species from run-of-the-mill hominin to world-conquering force of nature?
- How did the size and structure of early *H. sapiens* populations factor into the metamorphosis.
- Eleanor Scerri of the University of Oxford and a large interdisciplinary group of co-authors, including Stringer, make the case for what they call the African Multiregionalism model of *H. sapiens* evolution.

New Perspective of our origins

- The earliest members of our species—namely, the Jebel Irhoud fossils from Morocco, the Herto and Omo Kibish fossils from Ethiopia, and a partial skull from Florisbad, South Africa—all look far more different from one another than people today do.

- "…maybe early *H. sapiens* was just ridiculously diverse," Scerri offers.

- And maybe looking for a single point of origin for our species, as many researchers have been doing, is "a wild goose chase," she says.

New Perspective of our origins

- Scerri's theory: emergence of *H. sapiens* began to look less like a single origin story and more like a pan-African phenomenon.
- Rather than evolving as a small population in a particular region of Africa, they propose, our species emerged from a large population that was subdivided into smaller groups distributed across the vast African continent that were often semi-isolated for thousands of years at a time by distance and by ecological barriers such as deserts.
- Those bouts of solitude allowed each group to develop its own biological and technological adaptations to its own niche, be it an arid woodland or a savanna grassland, a tropical rain forest or a marine coast.
- Every so often, however, the groups came into contact with one another, allowing for both genetic and cultural exchange that fed the evolution of our lineage.

New Perspective of our origins

- Shifting climate could have fueled the fracturing and rejoining of the subpopulations.

- For instance, paleoenvironmental data have shown that every 100,000 years or so, Africa enters into a humid phase that transforms the forbidding Sahara Desert into a lush expanse of vegetation and lakes.

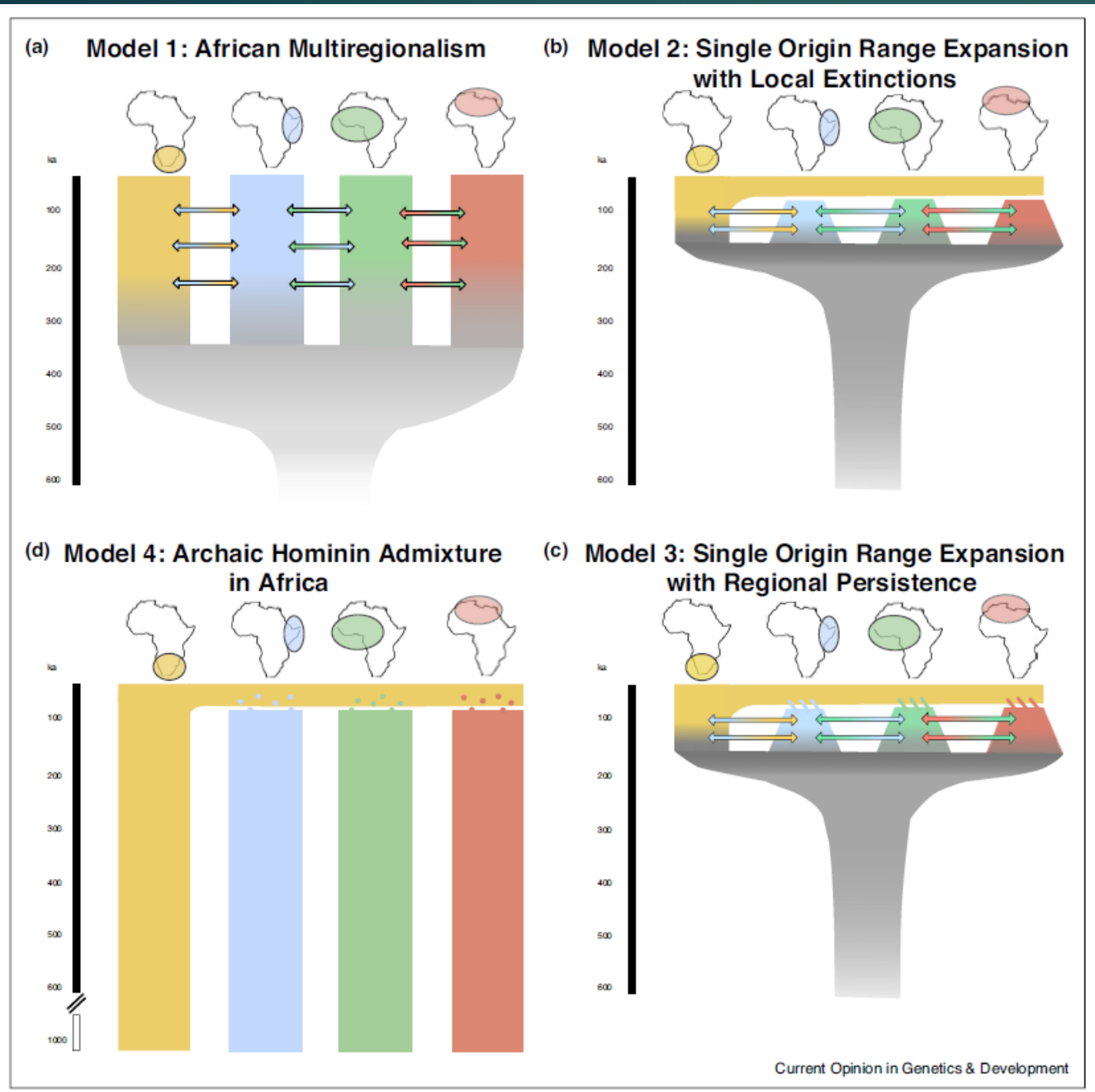
- These green Sahara episodes would have allowed populations formerly isolated by the harsh desert to link up and exchange genes and cultural traditions.

New Perspective of our origins

- This pattern would explain not only the mosaic evolution of *H. sapiens*' distinctive anatomy but also the patchwork pattern of the MSA lithic traditions

- Unlike Acheulean tools, which look mostly the same everywhere they turn up throughout the Old World, MSA tools exhibit considerable regional variation.

- Recent study by Arun Durvasula and Sriram Sankararaman, found that nearly 8 percent of the genetic ancestry of the West African Yoruba population traces back to an unknown archaic species (researchers have yet to recover DNA from any archaic African fossils for comparison).



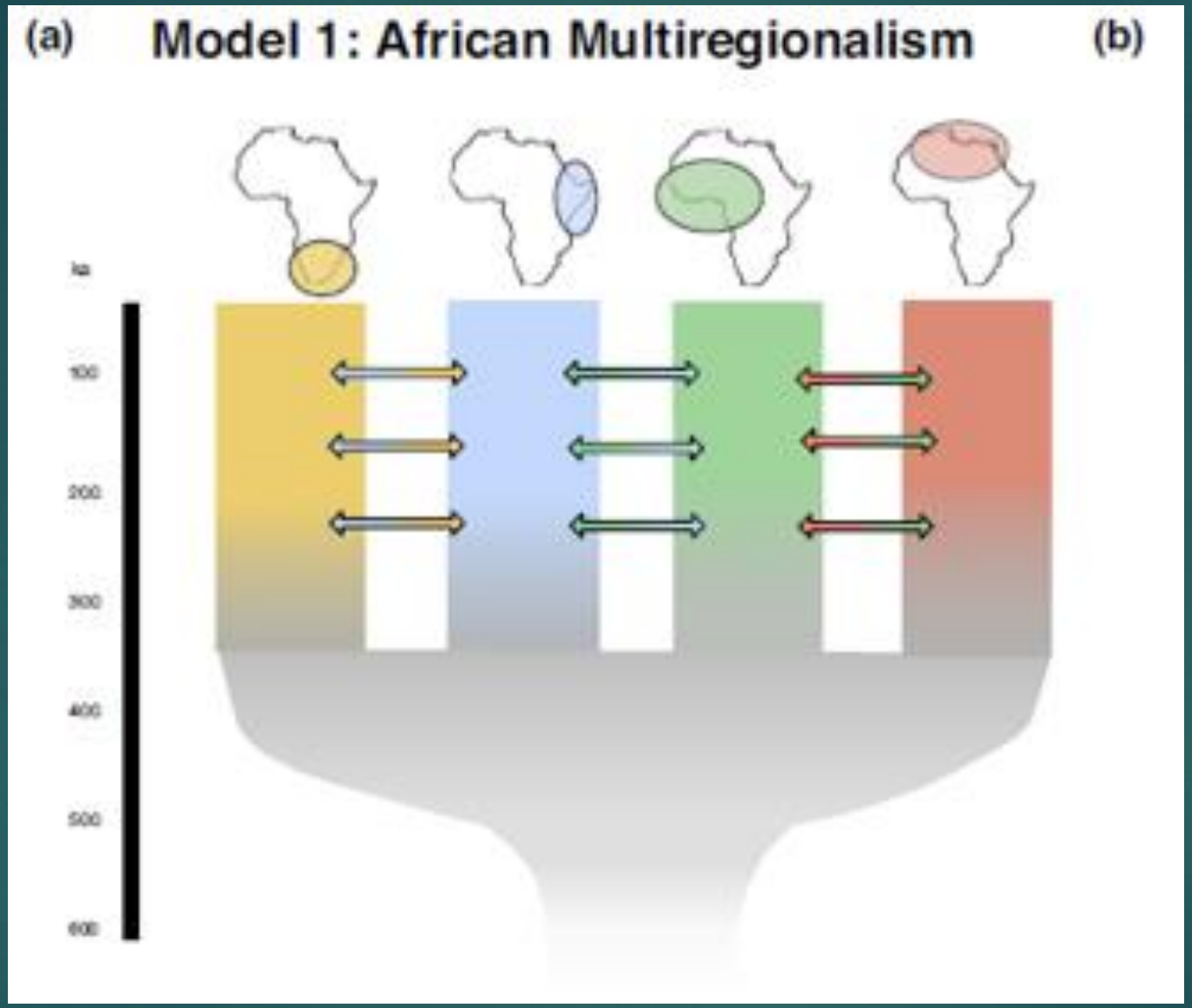
Brenna. M. Henn, et al., 2018

Clarifying distinct models of modern human origins in Africa

- Horizontal arrows indicate gene flow between regions.
- Diagonal lines or dots indicate admixture between expanding and local populations, with lines corresponding to higher gene flow than dots.

African Multiregionalism, Model 1

- A form of multiregionalism that is limited to Africa: Lahr, Scerri, Stringer
- This view has been motivated by:
  - the presence of regional geographic variation in hominins in the African archaeological record by 300,000 years ago – McBrearty
  - the morphological diversity of the African fossil record between 300 000 and 100 000 years ago, and
  - the presence of modern, derived morphological features in divergent regions of Africa - Hublin
- Together, these findings inspired the hypothesis that populations across Africa were all connected to each other.
- This model states that migration across the continent is more parsimonious than independent convergence of anatomical features and archaeological innovations.


(a)
Model 1: African Multiregionalism
(b)
ka
100
200
300
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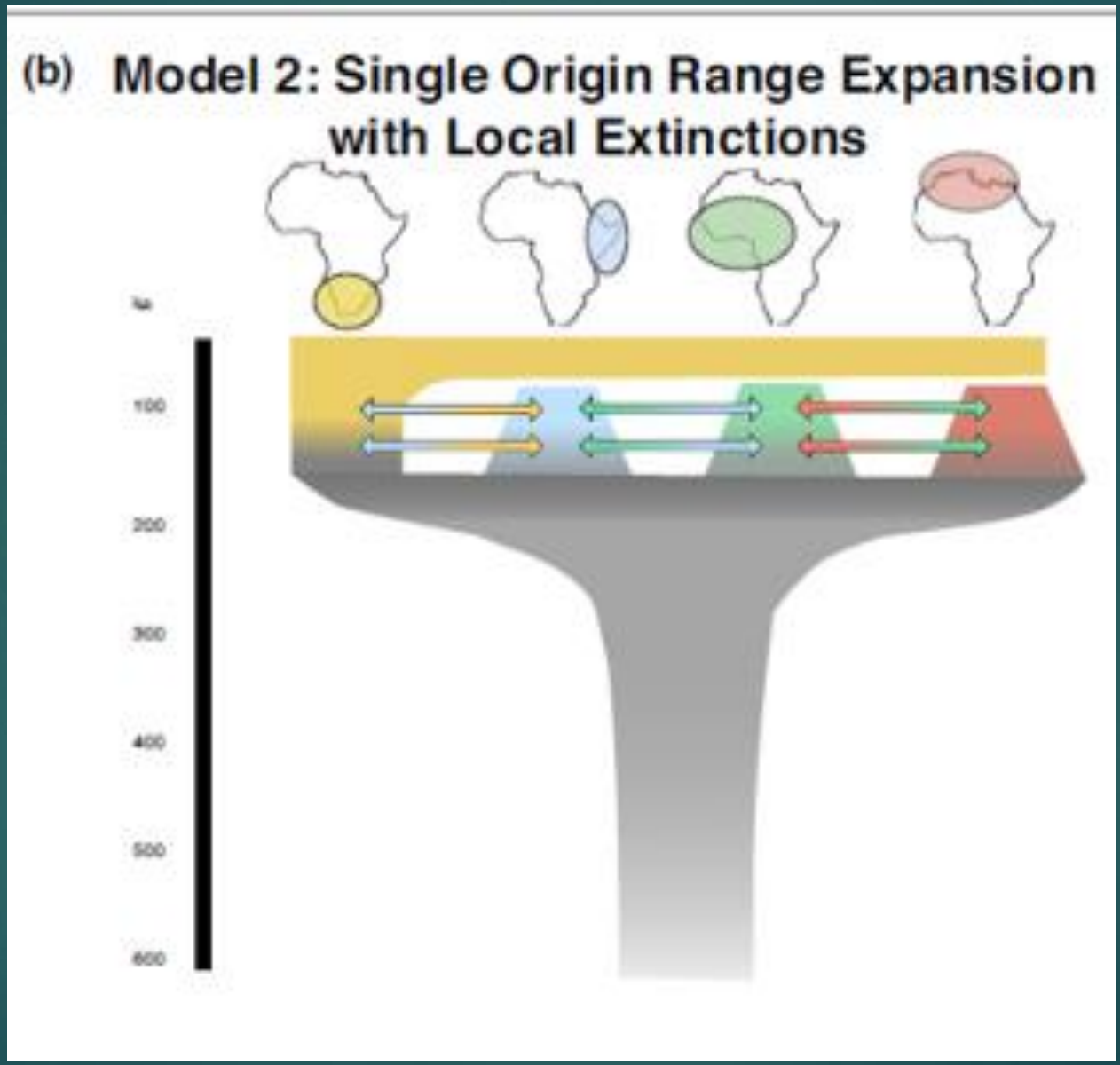
Model 1: African Multiregionalism (pan-African origins).

- Modern humans originate across Africa.
- No single region is the primary source of modern humans.
- Instead, genetic, morphological, and archaeological markers of modern humans originate in multiple regions and spread by migration between regions.
- Depending on the amount of gene flow between regions, the pan-African population is more or less structured.
- Regional structure dates back to just after the split with the evolutionary lineage leading to Neandertals.

Model 2: Single Origin, Range Expansion with Local Extinctions

- A single region is the source for modern humans within (and outside of) Africa.
- 'Near modern' human populations are present throughout Africa after 200 Ka and connected by migration between regions.
- Subsequently, a population from a single region of Africa expands across the continent. The source region is usually thought to be south or east Africa.
- The expanding population successfully outcompetes the other populations, for either biological or behavioral reasons; or alternatively it expands into the vacuum left by local population extinction due to climatic events.


(b) Model 2: Single Origin Range Expansion with Local Extinctions
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Model 2: Out of Africa model

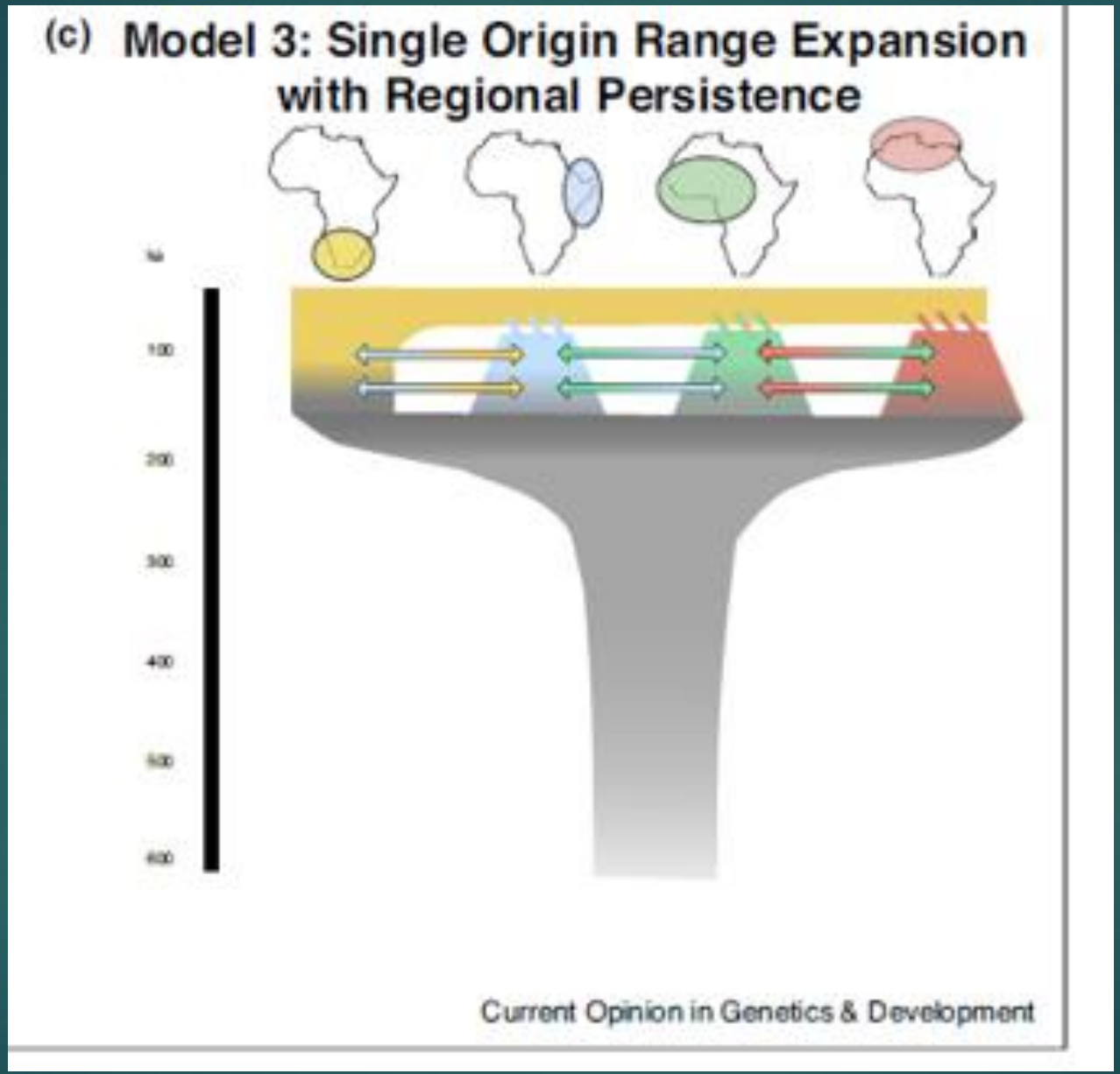
- A corollary of the Out of Africa expansion and suggests that the source of modern humans was restricted to a single region of Africa
- This population then expanded throughout Africa, either outcompeting remnant 'near modern' human groups or these other groups were extirpated due to climatic pressures.
- This view has been primarily motivated by genetic analyses but also by studies of fossils and archaeology.
- Requisite in this family of models is an explanation of why one population of 'near modern' or 'modern' humans underwent a demographic expansion while others did not.
- The Single Origin Model is often implicitly assumed in visual schematics of human origins, with an arrow originating in southern or eastern Africa leading to the Out of Africa founder event.

Model 3: Single Origin Range Expansion with Regional Persistence

- Similar to Model 2, except that rather than complete replacement there is some gene flow between the expanding and local populations. Gene flow could be high or low.

- Gives priority to a single geographic region of Africa but allows for limited gene flow between the source population expanding from a single region and the 'near modern' or 'modern' human populations local to the other regions.

- The time scale of hominin divergence and levels of gene flow are key to distinguishing Model 3 from Model 1.


(c) Model 3: Single Origin Range Expansion with Regional Persistence
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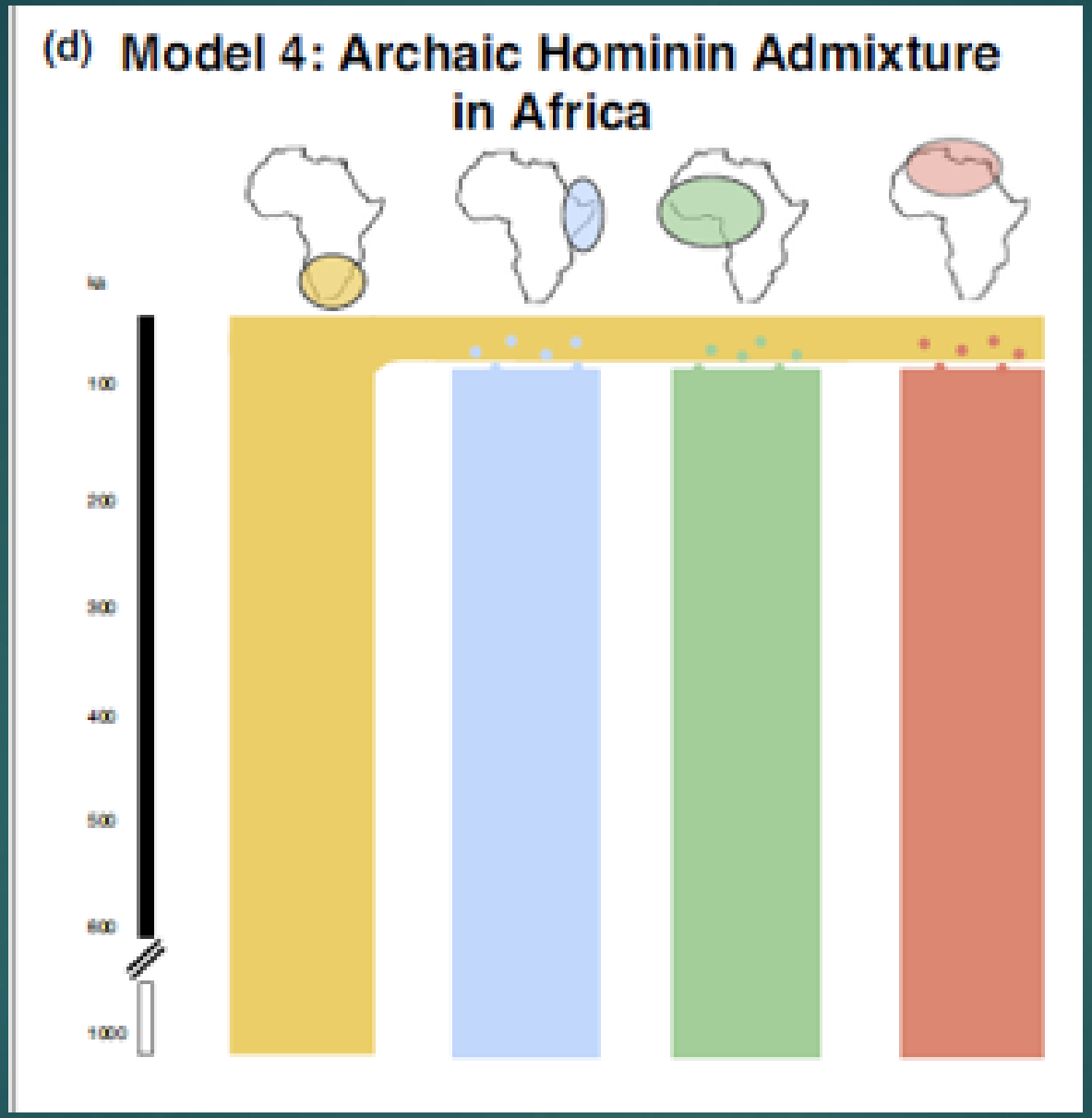
Current Opinion in Genetics & Development

Model 4: Archaic Hominin Admixture in Africa

- Modern humans evolve in Africa side by side with archaic hominins (e.g. Homo naledi).
- As modern humans expand across Africa there is gene flow between modern and archaic populations. Archaic gene flow is very low (<5%).
- 'Archaic' here refers to groups that shared a distant common ancestor with modern humans (more than 500,000 years ago and assigned to a Homo species).
- This view is often discussed in concert with African multiregionalism, but it is distinct enough conceptually to warrant a fourth model.


(d) Model 4: Archaic Hominin Admixture in Africa
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Model 4

- This view is motivated by discussions of
  - archaic admixture outside of Africa, between modern humans, Neandertals, and Denisovans,
  - patterns of variation at certain genes, and
  - fairly recent (<25 000 years ago) African fossils that appear to show morphological similarities with archaic humans.

*** *Did Our Species Evolve in Subdivided Populations across Africa?*

- 2018 Review by E. Scerri et al.: Challenges the view that our species, *Homo sapiens*, evolved within a single population and/or region of Africa.

- Anatomically varied populations pertaining to the *H. sapiens* clade lived throughout Africa.

- African archaeological record demonstrates the multiregional origin and persistence of regionally distinct Pleistocene material traditions in a variety of paleoecological settings.

Eleanor M.L. Scerri, et al., Trends in Ecology & Evolution, 2018

Scerri

- Genetic studies indicate that present-day population structure within Africa extends to deep times, paralleling a paleoenvironmental record of shifting and fractured habitable zones.

- Argue that Homo sapiens evolved within a set of interlinked groups living across Africa, whose connectivity changed through time.

- Review: we didn't evolve from a single population in a single region of Africa, but rather from separate populations across Africa that fully mixed only much later

Scerri

- Only around 300,000 years ago did early people actually begin to have features that made them look like modern humans.

- All the fossils between 300 and 100 Ka don't really look like anyone living today.

- The features that define us today, such as a small face, prominent chins, a globular skull and small teeth, were indeed present back then, but not all in a single person.

Scerri

- And these groups remained separate for a long time, because the dense forests and deserts in Africa served as formidable barriers.

- But with the occasional mixing of different groups, between 100,000 and 40,000 years ago, fossils that combine all the modern features in a single individual begin to appear.

- Evolution probably progressed at a different speed and tempo in different regions of Africa as different groups came into contact with each other at different times.

- By about 12,000 years ago, when hunting and gathering gradually shifted to agriculture, archaic features such as an elongated head and large robust faces had all but disappeared in humans,

Outstanding Questions

- In the conventional view, H. sapiens emerged in one region and/or population of Africa.

- Instead, new data suggest that a variety of transitional human groups, with a mosaic of primitive and derived features, may have lived over an extensive area from Morocco to South Africa between >300 ka and 12 ka.

- Three outstanding questions emerge from this view.

- First, within the African ‘multiregional’ paradigm, which species best fits as the ancestor(s) of H. sapiens?

Outstanding Questions

- Many aspects of the delicate H. sapiens facial shape may not be derived but instead be primitive retentions from an ancestor with a generalized facial shape.

- It seems possible that H. sapiens did not evolve from the African forms of *H. heidelbergensis* (as represented, e.g., by the Bodo skull from Ethiopia, and Broken Hill from Zambia), but from a more primitive *H. antecessor or H. erectus-like* ancestor, beginning at 0.5 Ma.

- However, hybridization during the inception of this process is also a possibility.

Outstanding Questions

- Second, how many populations, environments, and geographical areas of Africa played a role in the origins of H. sapiens?
  - Did adjoining areas of western Asia also play a part? It seems possible that early humans followed the same ecological partitioning and sub-speciation patterns that are seen among continentally distributed African mammals, many of which emerged at the same time as the genus Homo.
  - The Sahara may have played a particularly important role in this respect.
  - Other areas, such as regions of forest, may also have supported populations who remained semi-isolated from those in grasslands and savannahs.

Outstanding Questions

- Thirdly, were some of our anatomical traits inherited from transitional African forms before they became extinct?
  - H. naledi and H. heidelbergensis confirms the late survival of at least two archaic species in Africa.

- These have fueled speculations that H. sapiens may have interbred with archaic species in Africa itself..

- H. sapiens is a lineage with deep and likely diverse African roots that challenge our use of terms such as ‘archaic H. sapiens’ and ‘anatomically modern humans’.
- Need to operationalize these terms with more clearly defined traits,

Humans Didn't Evolve From a Single Ancestral Population

- Scerri: "While 'Mitochondrial Eve' was a real person, she wasn't the only ancestor around, and would not have come from the only population around." "She just happened to be the woman from which all people living today inherited their mitochondrial genetic code."

- The reality is that human ancestors were spread across Africa, segregated by diverse habitats and shifting environmental boundaries, such as forests and deserts. These prolonged periods of isolation gave rise to a surprising variety of human forms, and a diverse array of adaptive traits. When stratified groups interbred, they preserved the best characteristics that evolution had to offer.

Hublin agrees

- Jean-Jacques Hublin: “There is no Garden of Eden in Africa, because the Garden of Eden *is* Africa.”

- J. Hublin: “There is growing evidence that the emergence of so-called ‘modern humans’ did not occur in a restricted cradle in sub-Saharan Africa and at a precise point in time.”

- “Rather, it involved several populations across the continent and was a fundamentally gradual process.”

- “According to this new model, gene flow spread advantageous mutations from one population to the next when climatic conditions would allow contact between populations,” said Hublin.

*** Eleanor Scerri, 2019: Beyond multiregional and simple out-of-Africa models of human evolution

- Authors argue that a simple out-of-Africa model is also outdated, and that the current state of the evidence favors a structured African metapopulation (interrelated groups of a population) model of human origins.
- Genetic studies have repeatedly falsified classic multiregionalism.
- Neither did humans 'leave' Africa; humans expanded their range, like other mammalian species and hominins before them.
- Recent findings estimating 1.5 to 2.8% genetic contribution from Neanderthals to non-African peoples and 0.3 to 5.6% contribution from Denisovans to East Asian and Oceanian peoples do not change this.
- The remaining ~91.8 to ~98.5% of the ancestry of people not living in Africa today still derives from Africa

Scerri

- While the concepts of trees, species and hybridization have had their utility, and may still be useful, they have become constraining and sometimes misleading in the emerging picture of human evolution.
- Fossil data show that the physical features characterizing contemporary humans did not appear progressively in one region.
- Instead, they appeared across Africa in a mosaic-like fashion, emerging at different times and in different combinations with diverse ancestral features, indicating a fragmented continental-wide trend towards the modern human form.
- Similarly, the Middle Stone Age — thought by many to reflect the emergence of modern cognition — appears to have multiregional origins across Africa.
- Habitable zones radically shifted throughout deep time and connections between them repeatedly appeared and disappeared.

Metapopulation models

- These data indicate that early *H. sapiens* populations were strongly structured.

- They comprised sets of interconnected subpopulations forming a metapopulation that was distinct from other metapopulation sets corresponding to Neanderthals, Denisovans and possibly other hominin groups.

- A **metapopulation** consists of a group of spatially separated populations of the same species which interact at some level.

Metapopulation

- A metapopulation model stresses the importance of structure and connectivity within evolutionary lineages as a continuous process of oscillating fission, fusion, gene flow and local extinction.

- It can accommodate a wide range of previously hypothesized scenarios, including
  - persistent or shifting isolation,
  - ‘archaic hominin’ admixture,
  - range expansion with regional persistence, and
  - local extinction followed by recolonization from other subpopulations.

Scerri, 2019

- Structured models better explain the evolution of various derived morphological features associated with modern humans, such as a globular braincase, a small and gracile face, and a chin.

- These features first appear separately at different times in different fossils across Africa, but are only found together in the past 100 to 40,000 yr.

- A view whereby these and other derived features evolve separately in distinct subpopulations, and spread asynchronously through fluctuating gene flow, would explain the lack of sequentiality in their appearance and lessen the temptation to assign subspecies labels to different fossils.

Interpreting the African middle–late Pleistocene fossil human record

- Recent African Origin model has increasingly dominated the discussion of the evolution of H. sapiens, but with changes due to the evidence of introgression from archaic humans such as Neanderthals and Denisovans outside Africa.
- The date of origin of H. sapiens in this model has changed and is now often placed at about 200 ka, with the generally accepted first appearance of ‘anatomically modern humans’ in the form of the Omo Kibish 1 skeleton and the somewhat younger Herto material.
- Stringer diagnosing H. sapiens through a ‘working definition’ delimited by recent skeletal, and particularly, cranial variation in traits such as a domed neurocranium, reduction in facial size and projection,

Early Homo sapiens in Africa

- This array of fossils shows differing combinations of archaic and derived (recent H. sapiens-like) traits. These potential 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

Scerri

- Scerri has called this an ‘African multiregionalism’; Others (Lee Berger) have used the analogy of a braided stream for what they consider to be an open genetic network for different human lineages

- Evidence of the survival of even younger elements of archaic morphology into the late Pleistocene at sites like Eyasi, Iwo Eleru and Lukenya Hill.

- 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.

Human origins

- This would have led to the creation or removal of biogeographic barriers such as tropical rainforests and deserts—both probably largely impenetrable to early humans.

- These had direct demographic effects on human populations. For example, the middle of MIS6 (approx. 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.

Human origins

- Refugia in which populations could weather the worst of climatic downturns have been suggested as a key driver of morphological and perhaps adaptive behavioral changes in Eurasia

- In Africa climatic improvements could have been equally important in seeding denser and more networked populations, facilitating both genetic and cultural changes

Human origins: Last Common Ancestor (LCA)

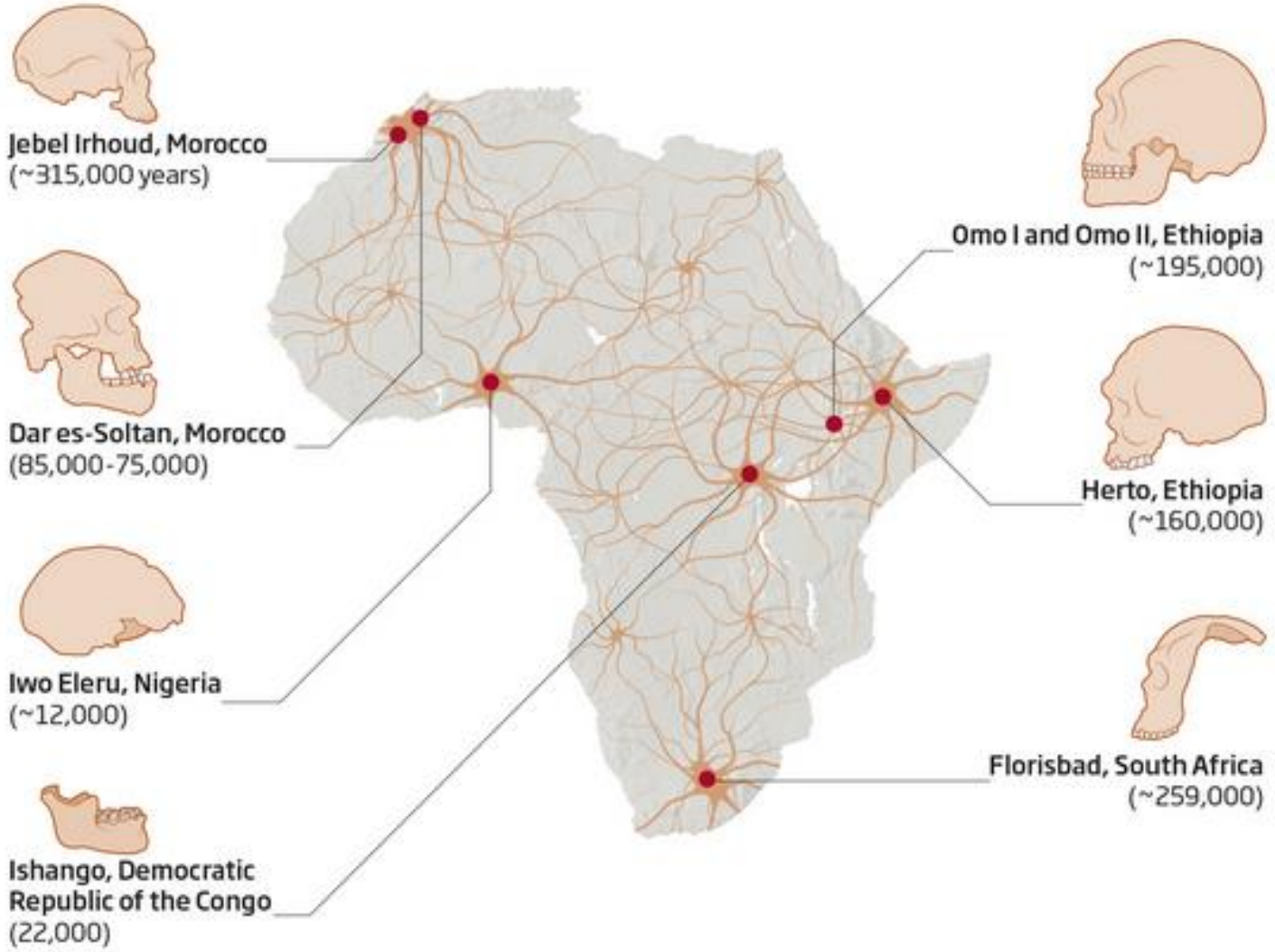
- As already mentioned, mtDNA indicates that the LCA lived approximately 400 ka, consistent with a heidelbergensis origin.

- However, the clear Neanderthal morphological and genetic affinities of the Sima fossils, now dated to at least 400 ka, suggest there was probably an evolutionary divergence well before that date.

- 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

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



Origin of our species: Scerri

Why humans were once so much more diverse

- There was extraordinary physical variation in early *H. sapiens*– greatly exceeding that in modern human populations. Our species lost the huge variety it once had.

- Mitochondrial Eve: The mitochondrial research provided a solution: any fossil older than 200,000 years must be another species.

- Middle Stone Age technology: the Middle Stone Age didn't emerge in one location at the purported dawn of humanity. Instead, there was a wholesale, continent-wide shift to this new technology around 300,000 years ago.

Eleanor Scerri, 2018

Origin of our Species 2

- Fossils found at Ishango in the Democratic Republic of the Congo, which, although dated to just 22,000 years ago, have decidedly robust, archaic features.

- Then there's the Iwo Eleru skull with an odd, elongated braincase found in southern Nigeria. It is around 12,000 years old, yet looks more like fossils dating from 100 to 300 Ka than people living today.

- New *H. sapiens* skull dated to 315,000 years ago and in Morocco. Modern faces and modern teeth, but elongated braincases.

- This anthropological bombshell has persuaded a group of 23 researchers – including Chris Stringer, Mark Thomas, Lounès Chikhi and Eleanor Scerri – that we need to radically rethink how our species emerged.

Origin of our Species 3

- Theory: diverse array of *H. sapiens* populations, displaying a mosaic of archaic and modern features, lived over an extensive geographic area from Morocco to South Africa between about 300,000 and 12,000 years ago.
- How could such widely dispersed and physically diverse populations all belong to a single species?
- One way to conceive of this is to imagine the human lineage as a river of braided streams: Although there is only one river/species, as time passes, different channels branch off and rejoin it. Just as the river's braids are separated by islands that form and are submerged, so environmental barriers kept our ancestors apart, and adapting to different conditions. This fits with emerging evidence of asynchronous changes in climate across different regions of Africa as our species began to appear.

Origin of our species

- The Sahara repeatedly greened for short periods every 100,000 years or so, while equatorial Africa underwent extended periods of drought.
- These and other similar processes across the continent would have created fluctuating barriers, shifting human populations around and modulating their degrees of isolation.
- Studies of other African mammals indicate that such conditions explain much of the physical diversity found within a species.
- “How could such wildly different individuals all belong to one species?”
- Stringer has called this new perspective “African multiregionalism”.

A Mix of subpopulations

Figure 1. Left lateral views of African and Israeli archaic and early modern *Homo sapiens* crania (replicas unless otherwise stated). Top (L to R): Florisbad, Jebel Irhoud 1, Jebel Irhoud 2 (original), Eliye Springs, Guomde (reversed), Omo 2. Bottom (L to R): Omo 1, Herto (original, reversed), Ngaloba, Singa, Skhul 5, Qafzeh 9.

Origins of our Species

- Studies have generally assumed that early *H. sapiens* exchanged genes in a random fashion, at a constant rate over time. African multiregionalism suggests otherwise.

- This would mean that the textbook view of humans originating in a single, small population is based on a misinterpretation. There is no unambiguous genetic evidence for it.

- The same goes for the idea that humans evolved in East Africa. Genetic data alone do not support any single region of Africa over any other.

- Genetic studies have identified very ancient branches in the human tree, which look like evidence that hybridization happened in Africa too.

*** R. Klein, 2019: Population structure and the evolution of Homo sapiens in Africa

- Critique of Scerri's African multiregionalism model

- A novel gene combination that additively or cumulatively enhanced cognition could explain how and why fully modern H. sapiens initiated the African LSA by 45 ka and dispersed to Europe by 44 ka.

- Genetic change is unlikely to have involved one or a few simple mutations, as I once postulated, because whole genome scans have failed to reveal any potentially relevant genes that swept to fixation in the millennia before these events.

Klein, 2019: rarity of *H. sapiens* fossils

- The most striking feature of the fossil record for *H. sapiens* may be just how meager it is.
  - two skulls from Omo-Kibish, southern Ethiopia,195 ka; 1 primitive
  - one from Herto, north-eastern Ethiopia, 160 ka,
  - one from Jebel Irhoud, Morocco, 315 ka,
  - a partial skull from Florisbad, South Africa, dated 259 ka.
  - the reconstructed adult skulls # 6 & 9 from Qafzeh Cave and # 5 from Skhul Cave, Israel, 120 and 90–80 ka.
- Klein: Morphology in this sample is highly variable, but it is not geographically patterned in a way that could support application of the multiregional model

Klein: Archeology of Africa

- Stone artifact assemblages varied much more across Africa after 300–250 ka, the Middle Stone Age or MSA.
- About 80 ka, MSA people at Blombos Cave, South Africa, and at the Grotte des Pigeons, Taforalt, eastern Morocco, perforated tiny intertidal gastropod shells, perhaps for stringing as beads or pendants
- MSA people at Blombos also incised a crosshatched pattern on a lump of red pigment and they used a pigment crayon to draw a similar pattern on the surface of a stone flake MSA deposits dated to 70–60 ka at Diepkloof Rockshelter and Klipdrift Shelter, also South Africa, have provided fragments of ostrich eggshell on which patterns had been engraved. Both Diepkloof and Klipdrift may be LSA intrusions.

Klein: archeology of Africa

- The various objects are often likened to presumed “symbolic” items from the Later Stone Age (LSA) that succeeded the MSA after 50 ka. The engraved eggshell fragments provide especially compelling evidence for “symbolism,” and they so far have no counterpart in European Mousterian (Neanderthal) sites, which sometimes also contain incised pigment fragments, perforated shells, and other items like formal bone artifacts whose sporadic occurrence in MSA sites is often inferred to imply advanced cognition
- Symbolic artifacts do not occur in most MSA artifact assemblages and where they do occur, they tend to be rare. MSA pigment lumps scored and ground for powder do not qualify as symbolic, since the powder was not demonstrably used for painting, only as a bonding agent.
- But the manufacture of compound adhesives shows that MSA people shared advanced aspects of cognition with historic humans.

Klein

- Archeology does not suggest the kind of geographic population structure that would justify application of the multiregional model.
- Combined with anatomy, the archeology does show that MSA people could be considered cladistically modern, meaning that they belonged to sister lineages that shared derived morphological and behavioral characteristics with modern humans and with each other, although only one lineage is likely to have culminated in fully modern H. sapiens.
- As this dispersed from its point of origin, it may have sometimes physically replaced its sisters but it may more often have transmitted its selectively advantageous genes.

Klein: historical genetics

- Fossils and artifacts are only proxies for the genetic patterning that would conclusively demonstrate enduring population variation among African regions and continuity within each.
- Historically, the genomes of some African populations, of whom the Khoe-San of southern Africa are most often cited, exhibited remarkably low linkage disequilibrium, exceptional genetic diversity, and other features that imply especially deep (ancient) divergence.
- Time range within which the Khoe-San diverged from other Africans varies from 86–130 ka (or more) to 43–65 ka
- Deeply divergent genetic lineages underscore the likelihood that H. sapiens originated in Africa, but historically, they were limited to foraging populations in refugia, principally the Kalahari Desert and the Central African rainforest

Klein: ancient DNA

- Ancient DNA already suggested that populations with deeply divergent genomes existed not long ago in places where there was little or no trace of them historically.
- More generally, it indicates that like western Eurasia, for which aDNA research is much more advanced, Africa had a complex genomic history in which prehistoric migration, mixture, and extinction repeatedly altered the distribution of genomes.

Klein: Climatic change & population structure

- In advance, climatic change over the 300,000 years or more when H. sapiens was evolving reduces the likelihood of enduring population differences among African regions and continuity within each.

- Dramatic fluctuations in precipitation that were asynchronous between regions must have repeatedly reshuffled population structure and disrupted continuity.

- Alternating episodes of increased humidity and increased aridity famously populated and depopulated the Sahara and its borderlands.

Klein: Climatic change & population structure

- Similar shifts likewise caused humans to penetrate and then abandon the Namib Desert.
- In southwestern South Africa, where archeological research has been especially intensive, deeply stratified sites including Montagu Cave, Diepkloof Rock Shelter, Elands Bay Cave, Die Kelders Cave 1, the Klipdrift Cave complex, Blombos Cave, Nelson Bay Cave, the Pinnacle Point Caves, and the Klasies River Cave complex were abandoned for thousands, perhaps tens of thousands of years around 50–40 ka, when the LSA is thought to have replaced the MSA.

Klein: climate effect on genetics

- Pollen and algae extracted from sediments of a regional marsh imply that the occupational hiatus occurred under unusually dry circumstances following on mostly moister ones
- The periodic geographic reorganization of regional population structure must have frequently separated and then mixed previously distinct populations.
- Mixture would have produced new gene constellations, possibly including one or more in which the additive or cumulative effect of newly associated genes enhanced cognitive or communicative potential

Klein: novel genetics

- Uniquely derived cognition and communication had long been central to human evolution, which means that natural selection would strongly favor a new gene constellation that enhanced either or both.
- Subsequent mixing could have added genes that made a novel constellation even more advantageous. Behavioral or cultural feedback would have accelerated its spread until a final addition fixed it in fully modern H. sapiens.
- These may never be available, which means that a novel polygenic cluster must remain a speculative explanation for the emergence of modern human cognition.
- Still, I think its emergence accounts most economically for a significant inflection in the African archeological record 50–45 ka and the consequent spread of H. sapiens to Eurasia.

Klein: Archeology and the origin of fully modern H. sapiens

- H. sapiens spread from a circumscribed region, carried by modern H. sapiens, which replaced or interbred with its near-modern contemporaries.

- A swift spread would have produced the same result—H. sapiens everywhere—as multiregional evolution, when the underlying demographic history was far different.

- A genetic explanation for fully modern human emergence predicts a relatively abrupt appearance of its earliest widely accepted behavioral manifestation, the LSA

Klein: Conclusions

- Fossil populations of H. sapiens surely always varied in appearance and behavior across Africa, and in that sense, they were structured.
- However, there is nothing in the fossil and archeological records or in historic genetics to suggest the kind of enduring structure that encouraged Wolpoff to propose the multiregional evolution of H. sapiens across Eurasia.
- There is also nothing to suggest the degree of population continuity within African regions that Wolpoff observed in different Eurasian regions.
- In southern Africa, where archeological observations are particularly dense, they suggest regional discontinuity.

Klein: Conclusions

- As an alternative to the multiregional model for Africa, I have proposed here that population reshuffling in the face of dramatic climatic change produced novel gene constellations that occasionally included one or more in which the additive or cumulative effect of newly associated genes enhanced cognitive or communicative potential.

- Natural selection would have favored the spread of such a constellation and behavioral or cultural feedback would have accelerated its eventual fixation in the African lineage that led to fully modern H. sapiens.

Klein: Conclusions

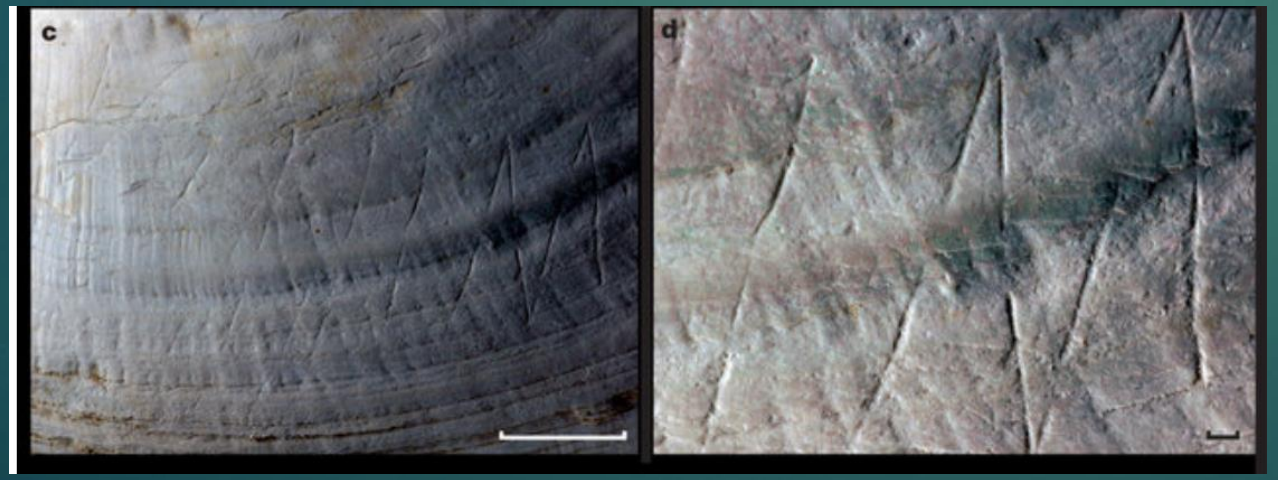
- Fully modern H. sapiens would then have dispersed rapidly across Africa, replacing other lineages or transferring its advantageous genes to them.
- In the absence of aDNA observations that could support this scenario, it may always remain speculative, but it would explain the inflection in the African archeological record marked by
  - the appearance of the LSA circa 50–45 ka,
  - its nearly simultaneous expansion to Eurasia in the form of the Upper Paleolithic,
  - and the ability of fully modern Upper Paleolithic people to swamp or replace non-modern Eurasians.

Are these all art?

Incised ochre, 75 ka at Blombos Cave

Ivory figurine, Hohle Fels, Germany, 35 Ka

Berekhat Ram figurine, 250 Ka,



Geometric engraving on mussel, 500 ka, Trinil, Java

Klein: Conclusions

- There is no theoretical reason to prefer my scenario over multiregionalism.
- However, my idea depends on an empirical issue that we should be able to resolve—do the LSA/Upper Paleolithic truly mark an inflection in the archeological record or does archeology indicate that much earlier Africans and Europeans were capable of LSA/Upper Paleolithic behaviors but expressed them more rarely or less conspicuously?
- An important corollary is the question of whether tiny naturally shaped but perforated gastropod shells that occur occasionally in MSA sites provide the same kind of evidence for ornaments or jewelry as the carefully shaped ostrich eggshell beads that occur in nearly every LSA site where preservation was suitable.

Klein: Conclusions

- Likewise, does the MSA pigment lump with the most compelling incised abstract pattern, dated roughly 75 ka at Blombos Cave, South Africa. qualify as art as unequivocally as the early Upper Paleolithic ivory figurine dated to more than 35 ka at Hohle Fels, Germany.
- To me, the answer to both questions is “No,” which is largely why I think the LSA/Upper Paleolithic represent a marked break from what went before.
- Others would answer “Yes” and some would trace art (or symbolism) even further back in time, to the volcanic tuff “figurine” dated 250–280 ka at Berekhat Ram on the Golan Heights or to a mussel valve with a proposed geometric engraving dated 500 ka from Trinil, Java

Sceptic geneticists of African multiregionalism

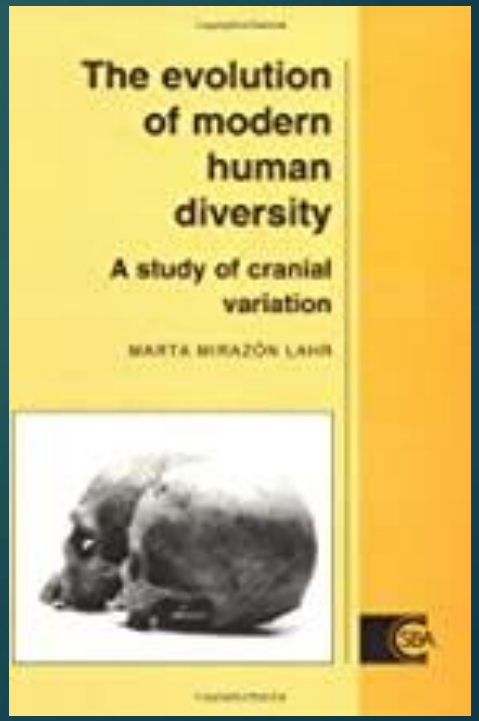
- Genetic studies of today's African populations suggest that they diverged from one another between 100,000 and 150,000 years ago—far later than the early, continent-wide origin suggested by the bones and tools.
- That deep and broad origin might be right, "but, it's not something that we geneticists have formally tested," says Brenna Henn from UC Davis. "We have discussed ways of doing that, but there's no published paper yet saying that there is deep population structure in Africa."
- But the DNA of today's Africans has been shaped by more recent population upheavals that have obscured the goings-on of 300,000 years ago.
- What's more, the studies that analyzed this modern DNA have largely relied on tree-like population models in which a single lineage grows from a single place—exactly the scenario that proponents of African multiregionalism say is wrong.

Marta Mirazon Lahr, Cambridge University

- Marta Lahr: An extended origin: Climate, populations & palimpsests in the evolution of Homo sapiens, Feb. 2021

- The Evolution of Modern Human Diversity by Marta Mirazon Lahr | May 1, 1996

- Considered the book that put the last nail in the coffin of Eurasian multiregionalism



Marta Lahr

- In the 1980s, a recent origin of Homo sapiens in Africa was proposed, leading to enormous controversy before its eventual acceptance.
- More than thirty years on, this model is now the orthodoxy.
- But is the model still valid?
- Ancient genomic and hominin fossil data have challenged the short chronology of the original model, the idea of complete replacement of archaic forms, as well as the notion of a single out of Africa dispersal of modern humans.
- Together, these lines of evidence might suggest a more prolonged process, under different climatic conditions, and possibly involving multiple populations, which may be best described as multiregional evolution at a continental level

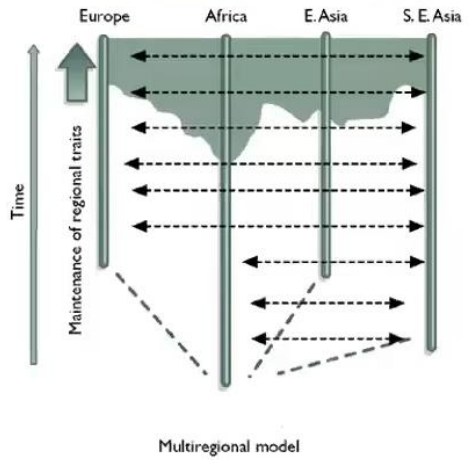
1980s: biggest debate: did we develop multiregionally or in single place

C. Stringer: first Out of Africa model

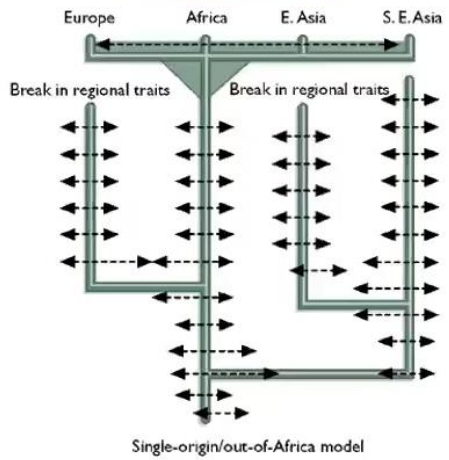
Then lot of data came in

1st two items disproved

2nd two items proven



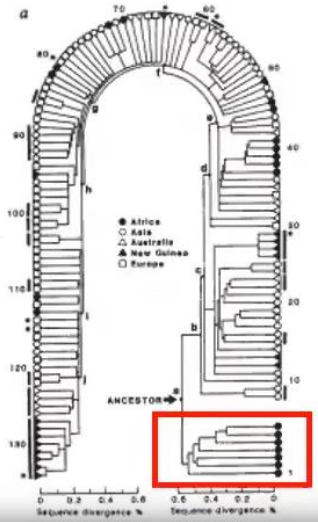
Multiregional model



Single-origin/out-of-Africa model

Late 1980s

- Asynchronicity of change
- Discontinuity in regional morphologies
- Shared derived features of all living humans
- Africa fossils of *Homo sapiens* significantly older than those from Eurasia



Africa

Cann *et al.* 1987

1990-2000: Out of Africa evidence accumulated

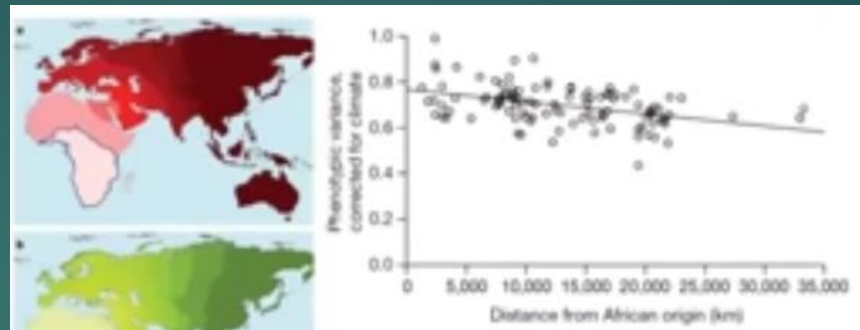
Africans had greatest genetic diversity in world

Further away from Africa, less genetic diversity

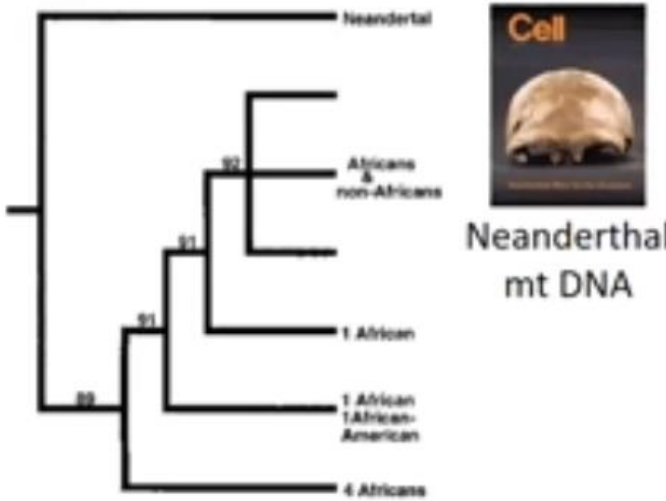
Redating of Omo & Herto to 200 and 160 Ka; distinctly MH skulls

mtDNA: Ns are a sister clade to MHs; Decreasing diversity outside Africa

Nuclear DNA: Ns and MHs are sister Clades: deeper divergence time – 37 700 Ka

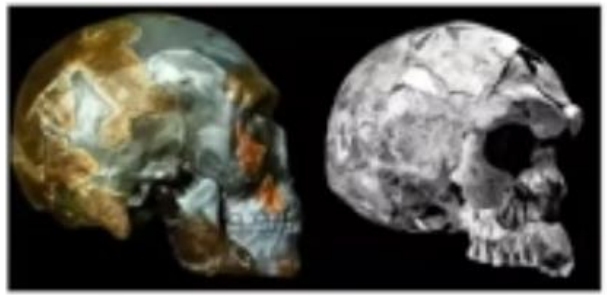


Manica *et al.* 2007.



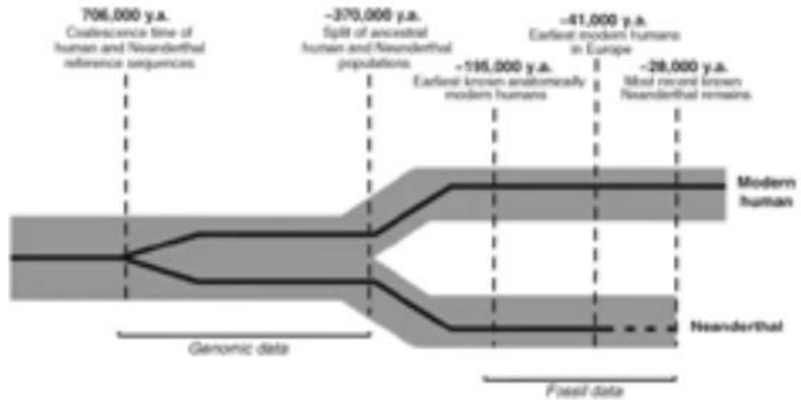
Krings et al. 1997. *Cell*

Neanderthal mt DNA



Omo Kibish, Ethiopia, 200 Ka

Herto, Ethiopia, 160 Ka

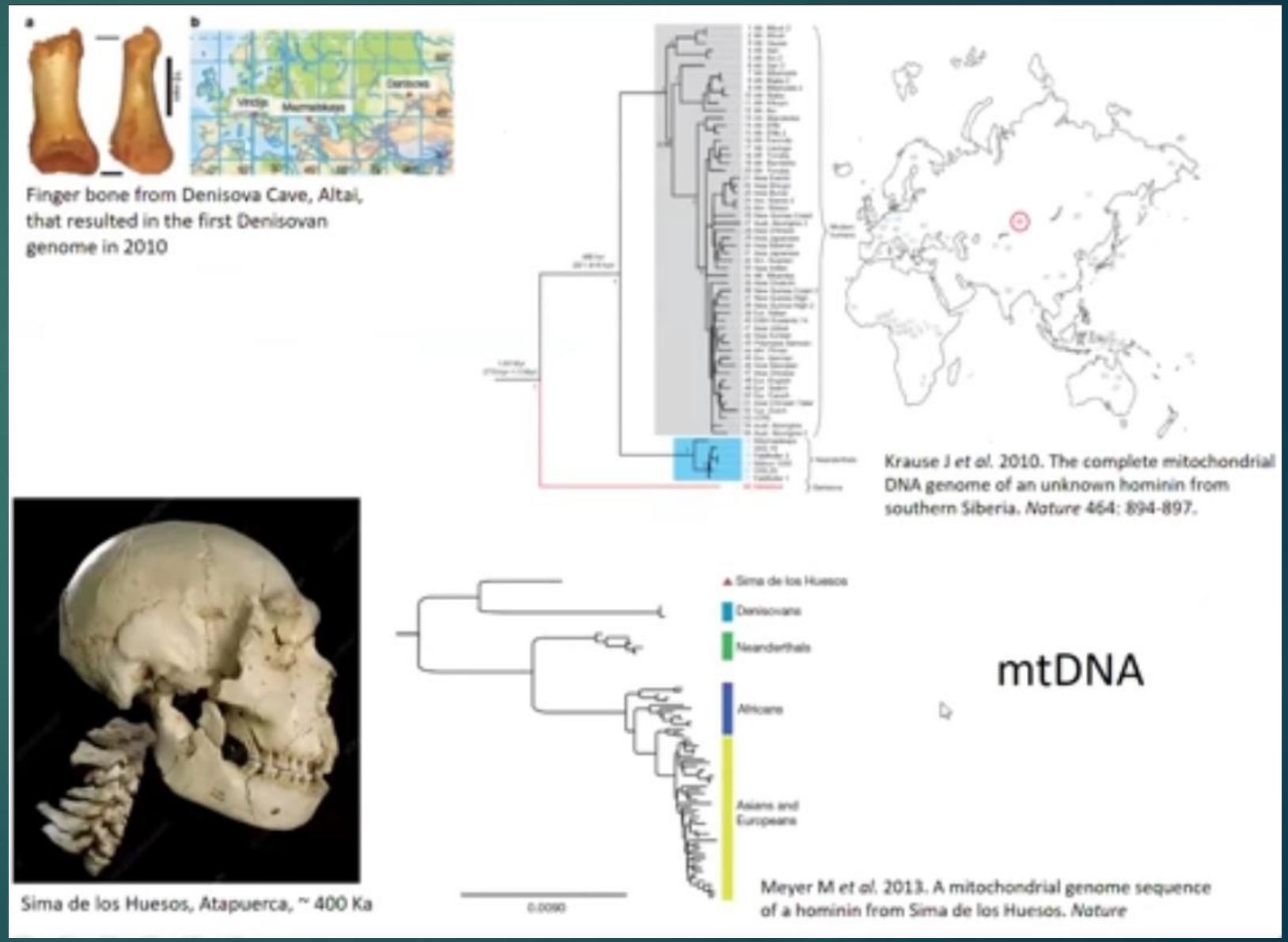


Noonan et al. 2006 Science

Neanderthal nuclear DNA

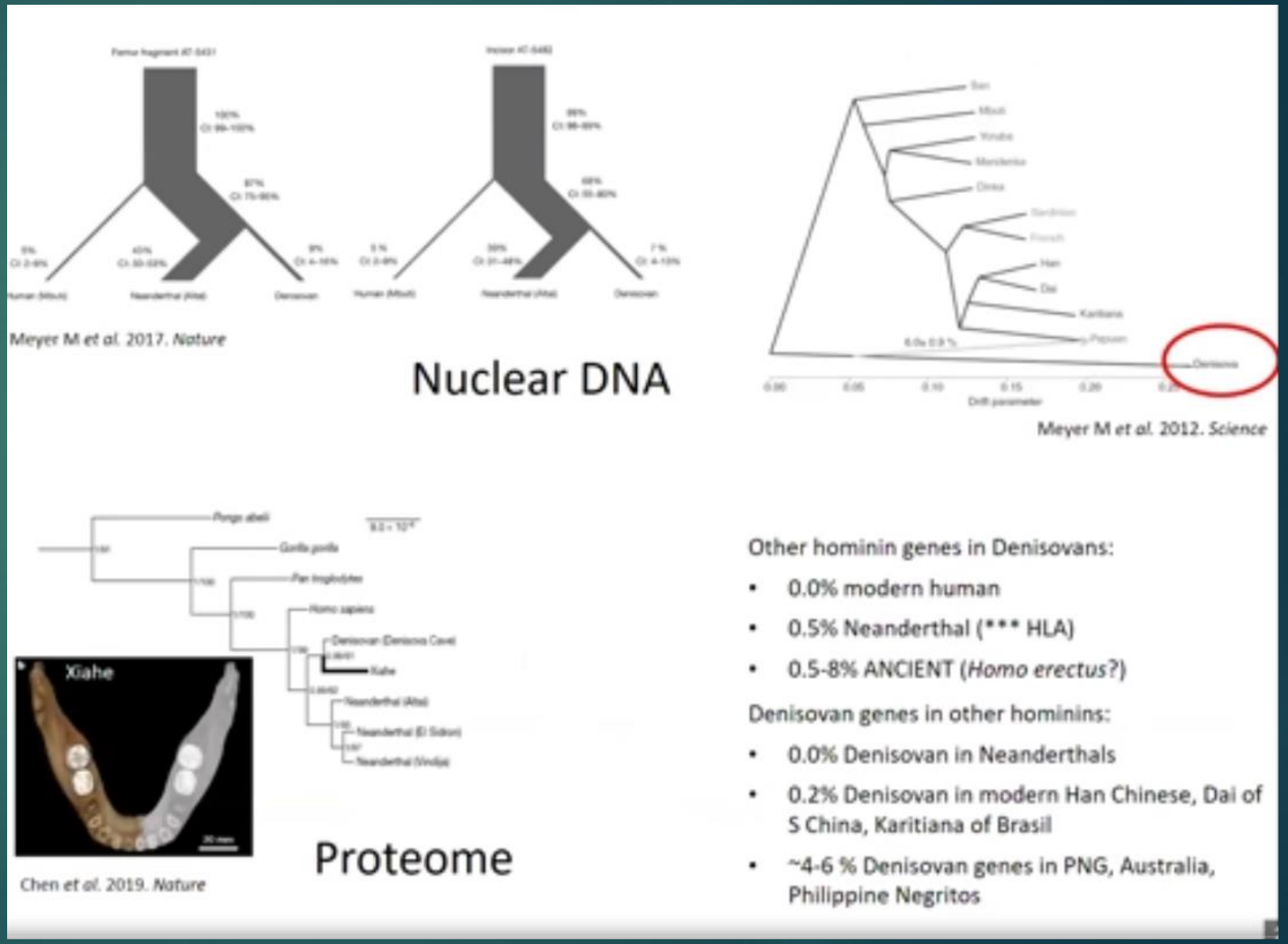
Increasing amount of ancient mtDNA discoveries

- Discovery of Denisovan DNA
- Sister clade to Ns and MHs
- Sima de los Huesos: Ns at 400 Ka



Nuclear DNA discoveries

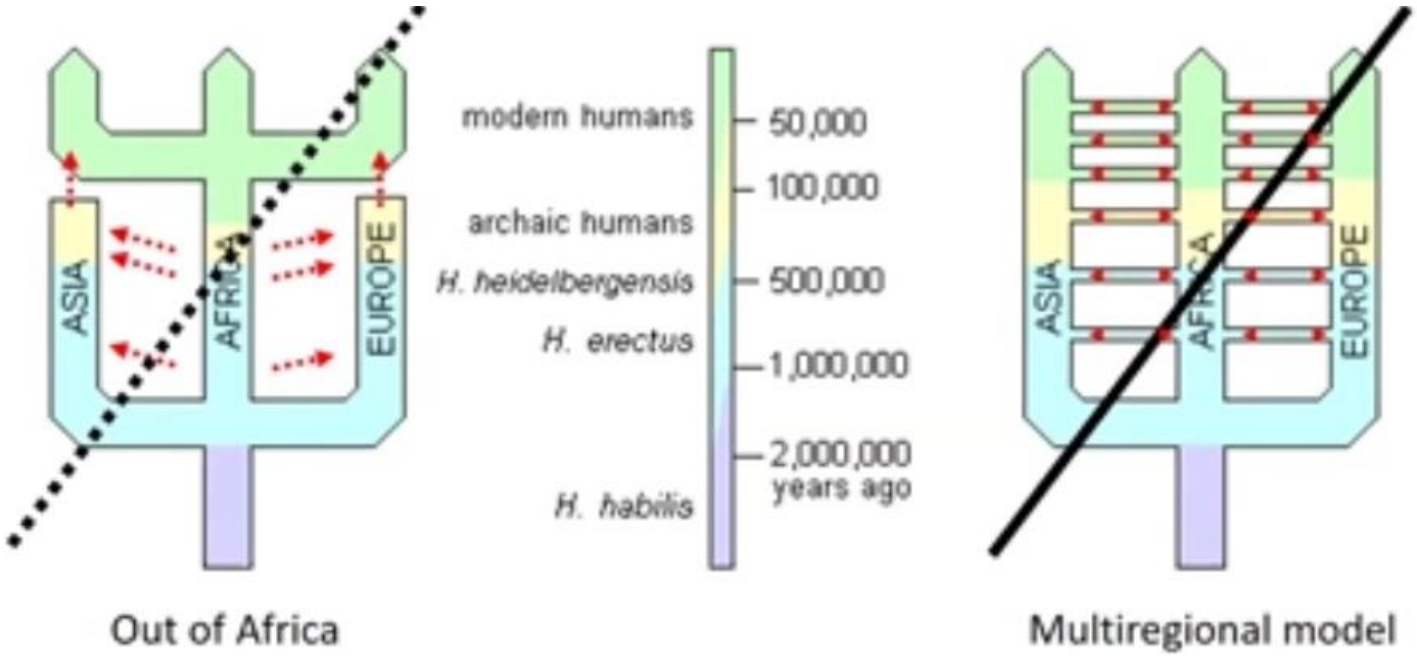
- Nuclear DNA shows that Ns and Ds share separate common ancestor from MHs
- Added evidence for this conclusion from Proteinomic data
- Evidence of MH and N genes in Ds and D genes in MHs



OoA vs Multiregional theories and data

Multiregional hypothesis with development of MH In different locations with geneflow

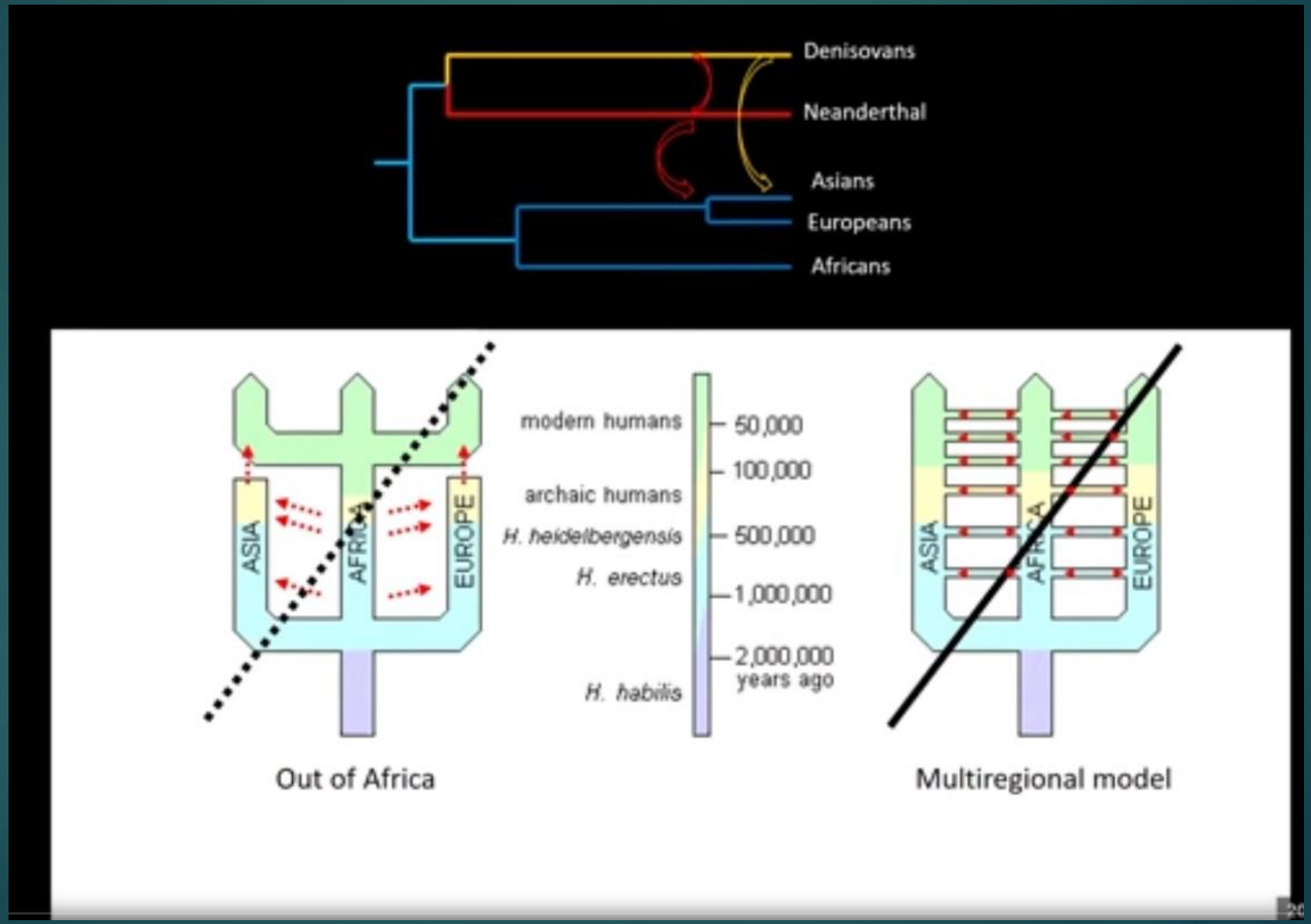
Out of Africa model: More than 1 point of contact; Assimilation more than replacement



Out of Africa

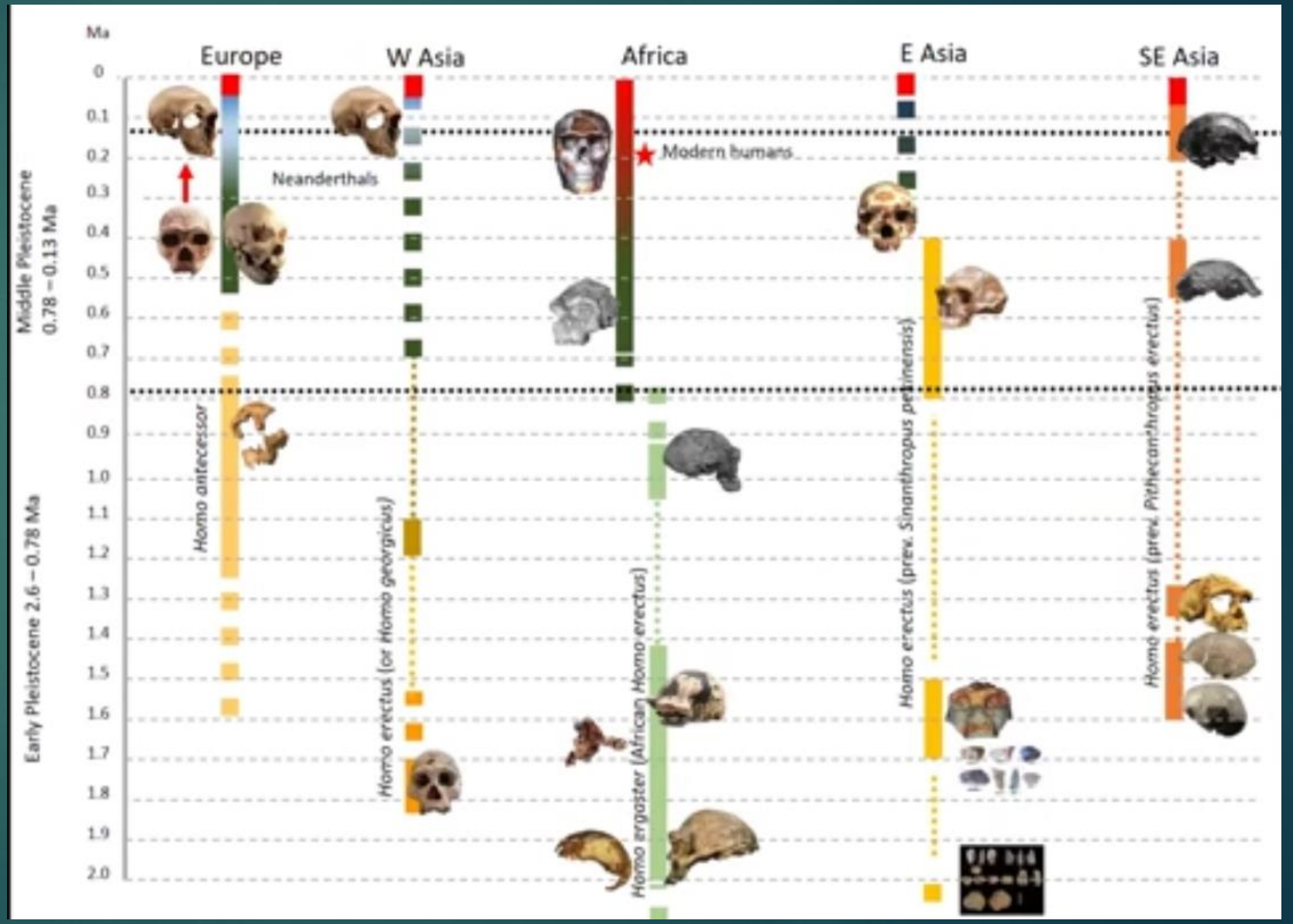
Multiregional model

There were sister clades and genetic intermixture



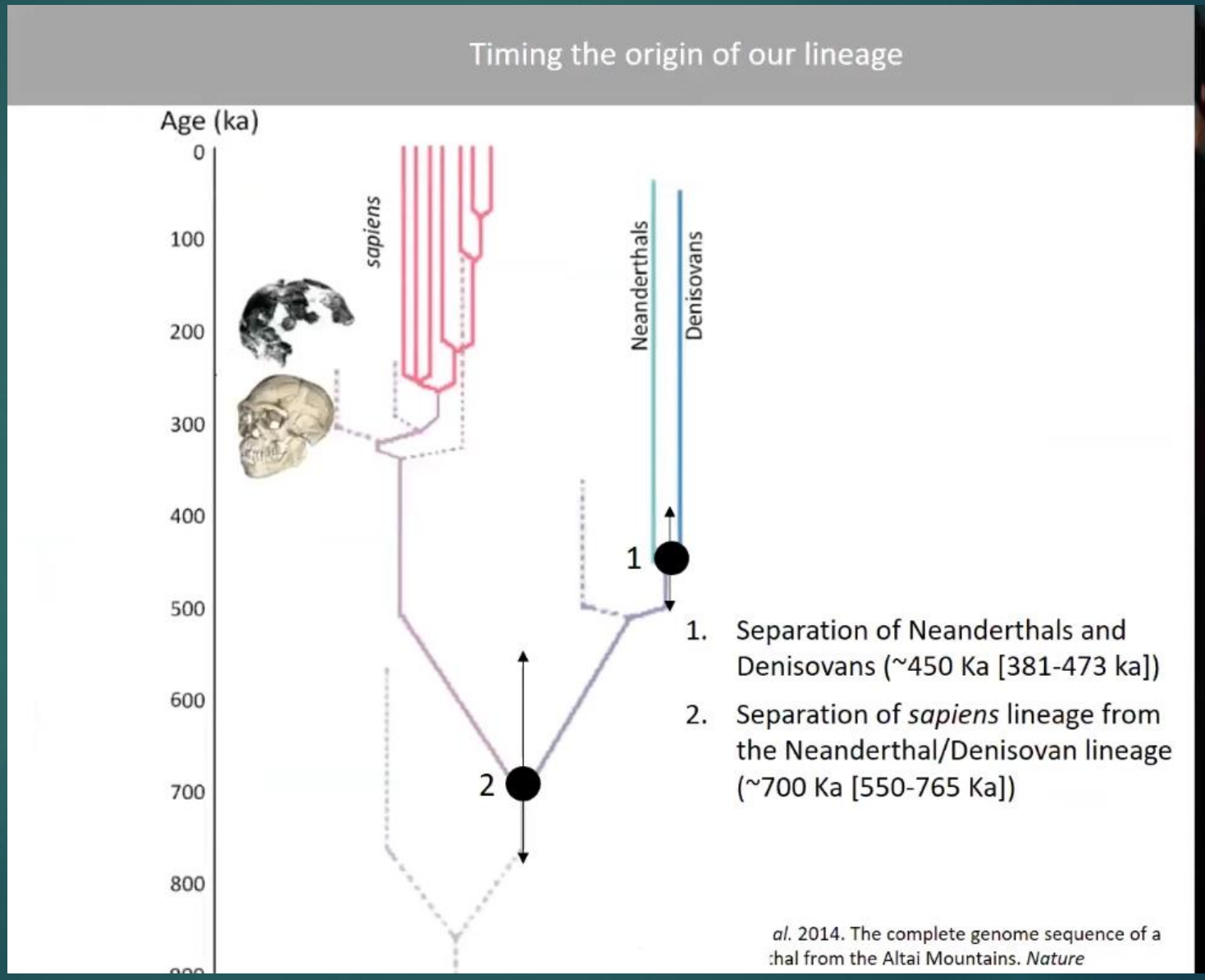
Early to Middle Pleistocene hominins

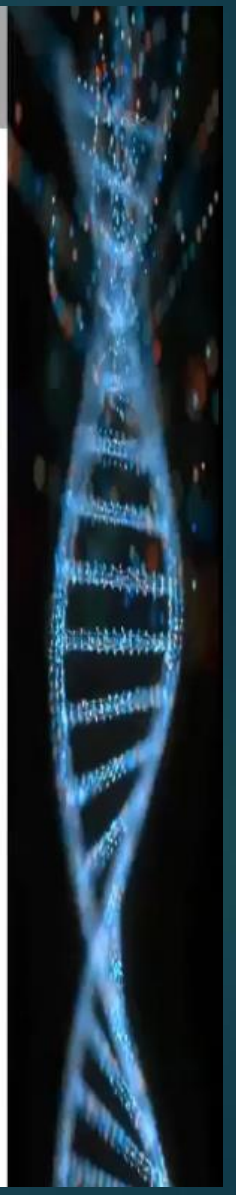
- African *H. erectus* evolves into MP hominins in Africa & Eurasia
- Development of Ns in Europe, MHs in Africa
- Asian development of different morphologies than in *H. erectus;*
- *Was this Denisovan influence?*



Origin in Africa

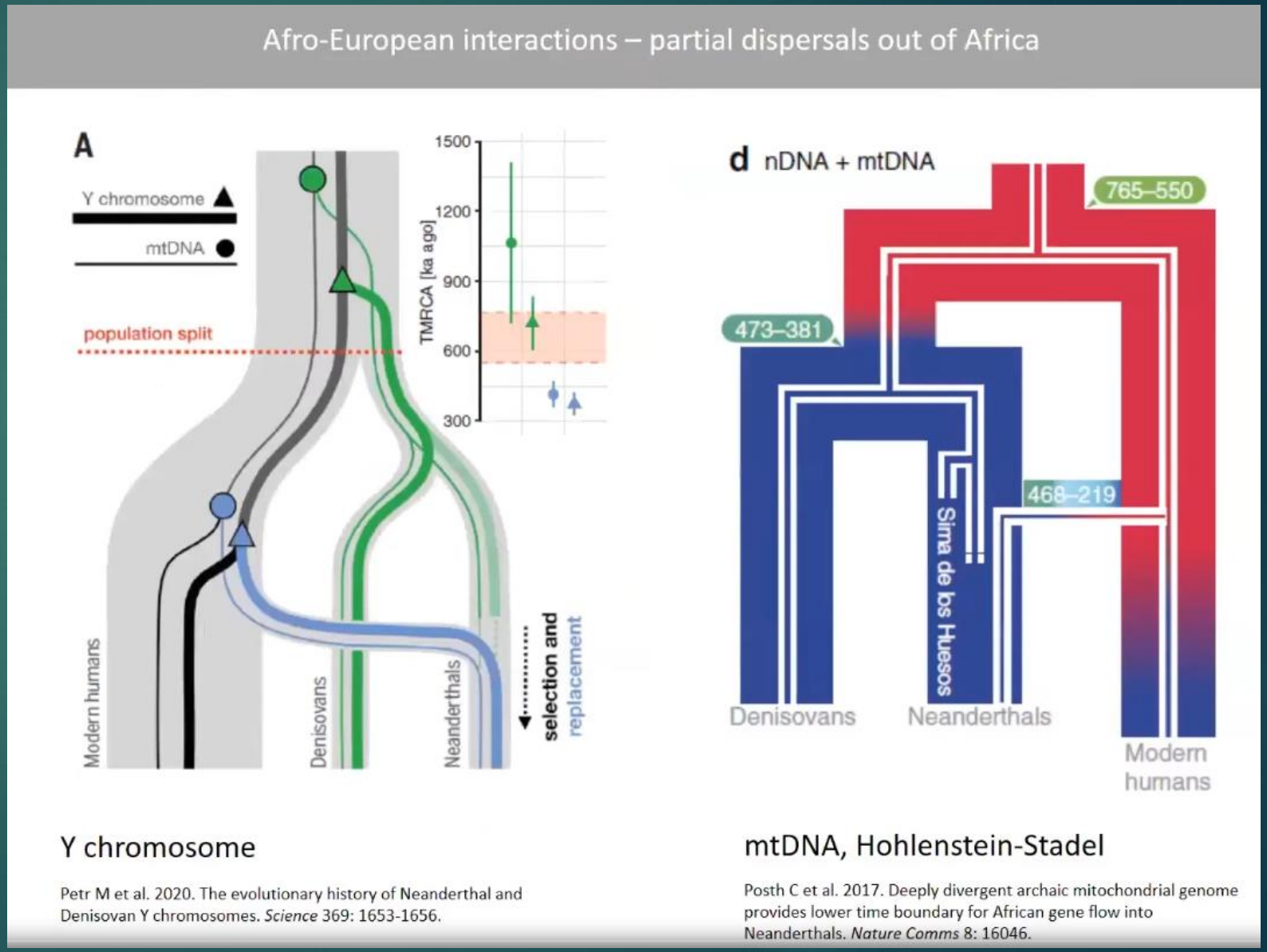
- 1 = ~450 Ka separation of N and Ds
- 2 = ~700 Ka separation of MH from N/Ds
- Not totally separate lineages since there were several gene flow events





Out of Africa: early MH dispersal into Eurasia at 300-400 Ka

- D mtDNA indicates Ds were separate group from Ns and MHs
- mtDNA and Y DNA of Ns and MHs are similar
- ~300-400 Ka MHs contacted Ns in Europe (but not Asia), after N and D split; and replaced the N mtDNA and Y chromosome with MH one



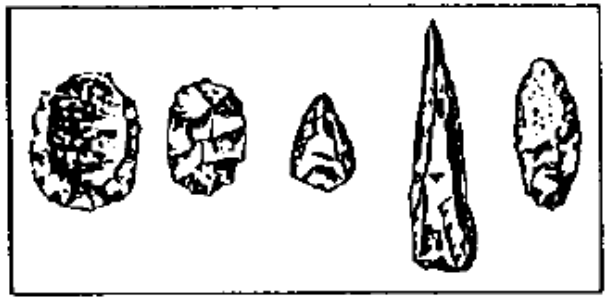
Foley & Lahr, 1997: Clark's 1969 Lithic modes classification

Time

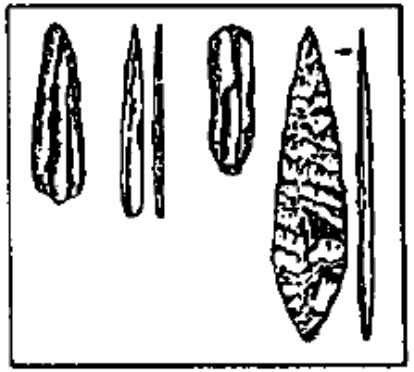
Pebble tool industries (Oldowan): simple flakes struck off pebbles, with choppers and flakes

Biface industries (Acheulean): large flakes or cores shaped on both sides to produce hand-axes.

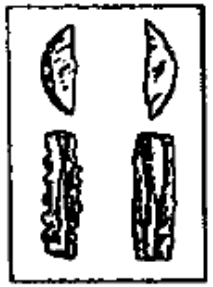
Prepared core industries (Middle Palaeolithic, Middle Stone Age): cores are prepared before the flakes are removed and then shaped.



Blade industries (Upper Palaeolithic): long thin flakes are removed and shaped into a large number of different tool types.



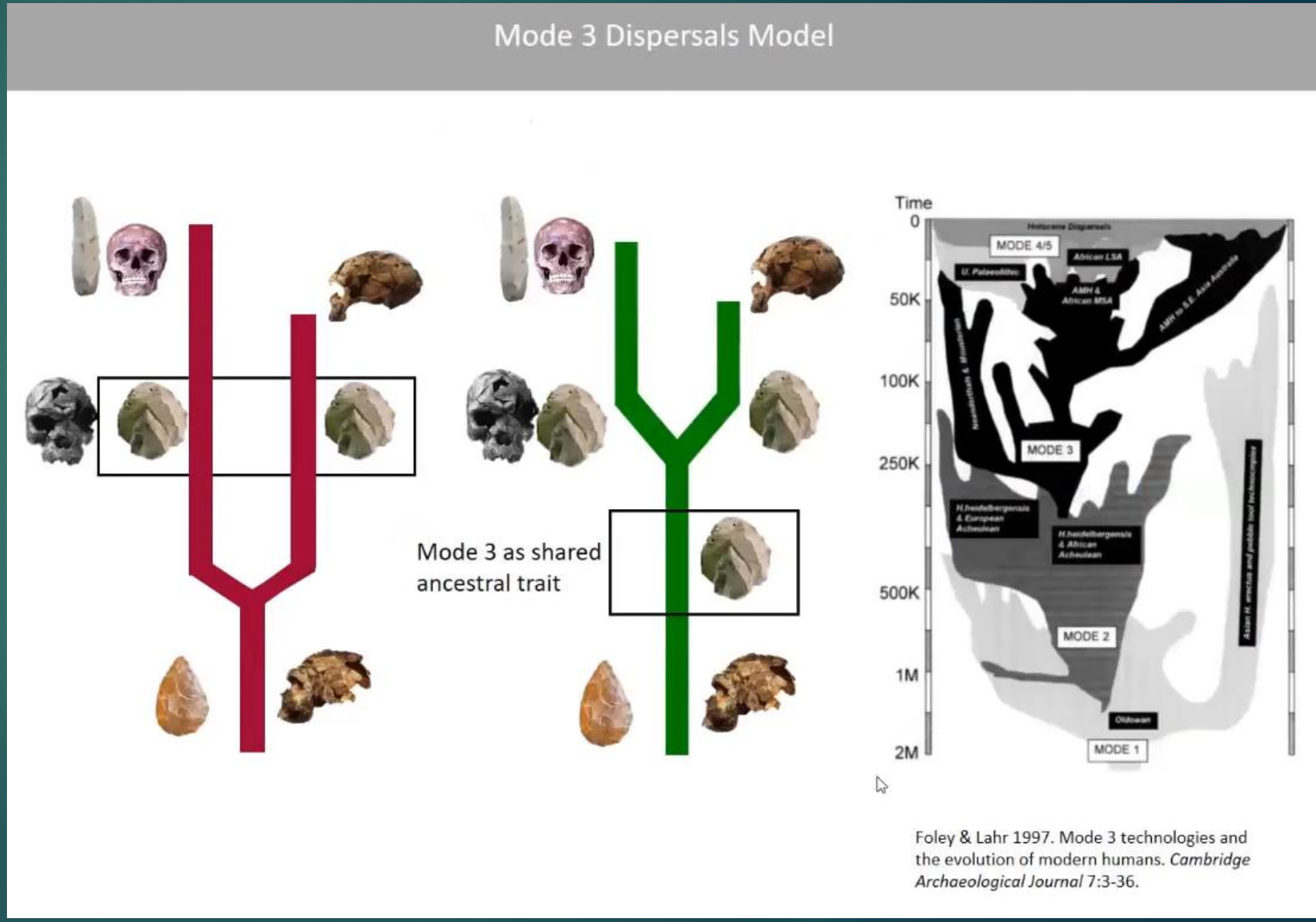
Microlithic industries: very small flakes and blades are produced and retouched and used in composite tools.



Genetics match Mode 3 tool dispersal in Europe & Africa

- European and African development of Mode 3 tools (Levallois)
  appear virtually at same time in Africa
  & in Europe -- Not independent convergent developments

- If MHs had a 300 Ka dispersal to Europe, then lithic tradition



Foley & Lahr dispersal-phylogenetic model

- The dispersal-phylogenetic model is a working premise that allows us to explore the possibility that shared technologies indicate biological populations and their movements, and that differences across time and space indicate some form of biological discontinuity.
- From the point of view of the origins of modem humans debate, the key conclusion we would draw is that the development of Middle Stone Age technologies in Africa around 250 Kyr is of greater universal significance than the origins of the Upper Palaeolithic. The former may mark a major cognitive development associated with the biological changes leading to the evolution of modem humans; the latter is merely a regional shift in behavioral patterns.
- Contrasts between the Middle and Upper Palaeolithic should not be underestimated: they represent a significant discontinuity in the archaeological record.
- But at a global scale, continuities of Mode 3 industries also occur. Rather than undermining the 'Out of Africa' model of modern human origins, these continuities in fact provide further support by solving various anomalies.

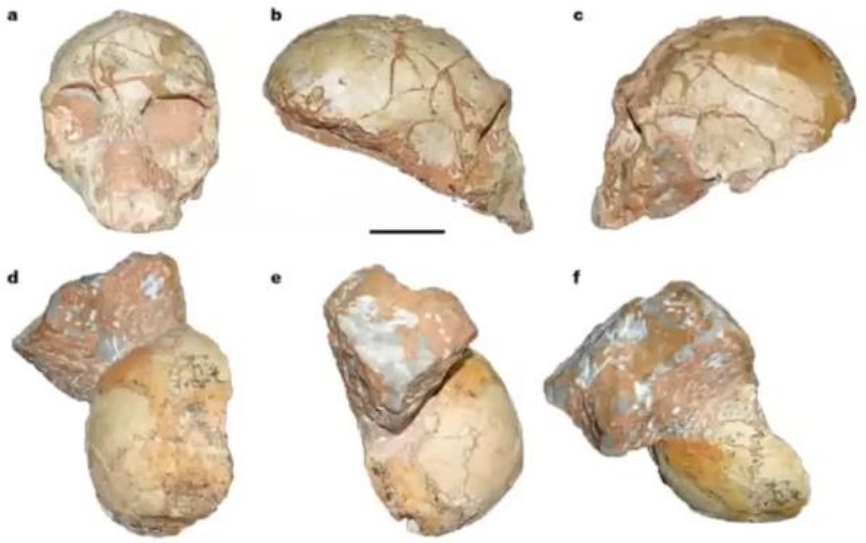
African Dispersals at 210 and 190 Ka

- Apidima, Greece: MH at 210 Ka
- Misliya, Israel at 190 Ka
- Both MH affinities

Mapping a period of multiple Afro-European contacts

ARTICLE

Apidima Cave fossils provide earliest evidence of *Homo sapiens* in Eurasia



Apidima, Greece, ~210 Ka

PALEOANTHROPOLOGY

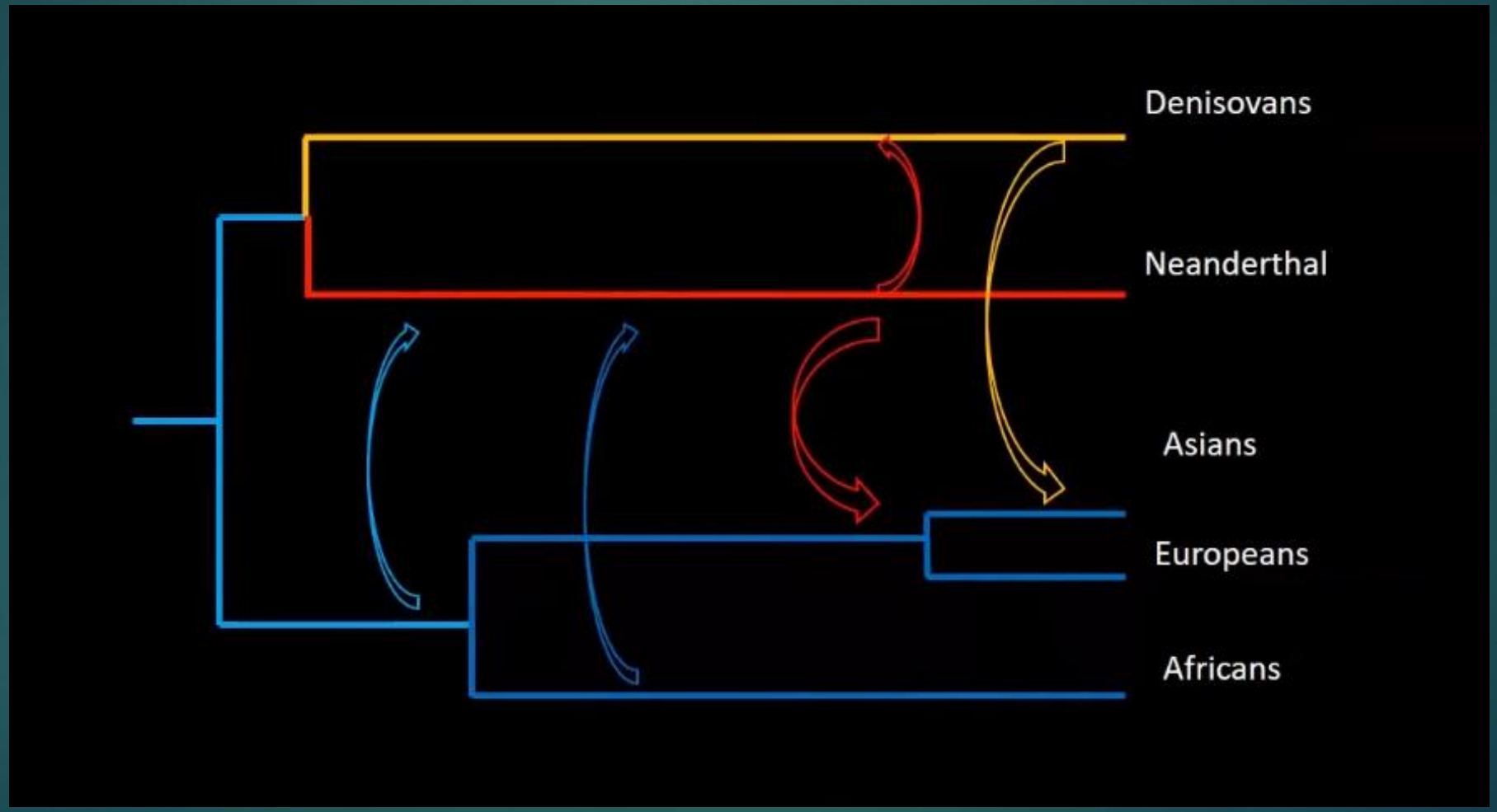
The earliest modern humans outside Africa

Israel Hershkovitz, Gerhard W. Weber, Rolf Quam, Mathieu Duval, Rainer Grün, Leslie Kinsley, Avner Ayalon, Miryam Bar-Matthews, Helene Valladas, Norbert Mercier, Juan Luis Arsuaga, Maria Martinón-Torres, José María Bermúdez de Castro, Cinzia Fornai, Laura Martín-Francés, Rachel Sarig, Hila May, Viktoria A. Krenn, Viviane Slon, Laura Rodríguez, Rebeca García, Carlos Lorenzo, Jose Miguel Carretero, Amos Frumkin, Ruth Shahack-Gross, Daniella E. Bar-Yosef Mayer, Yaming Cui, Xinzhi Wu, Natan Peled, Iris Groman-Yaroslavski, Lior Weissbrod, Reuven Yeshurun, Alexander Tsatskin, Yossi Zaidner, Mina Weinstein-Evron

Hershkovitz et al., *Science* 359, 456–459 (2018) 26 January 2018

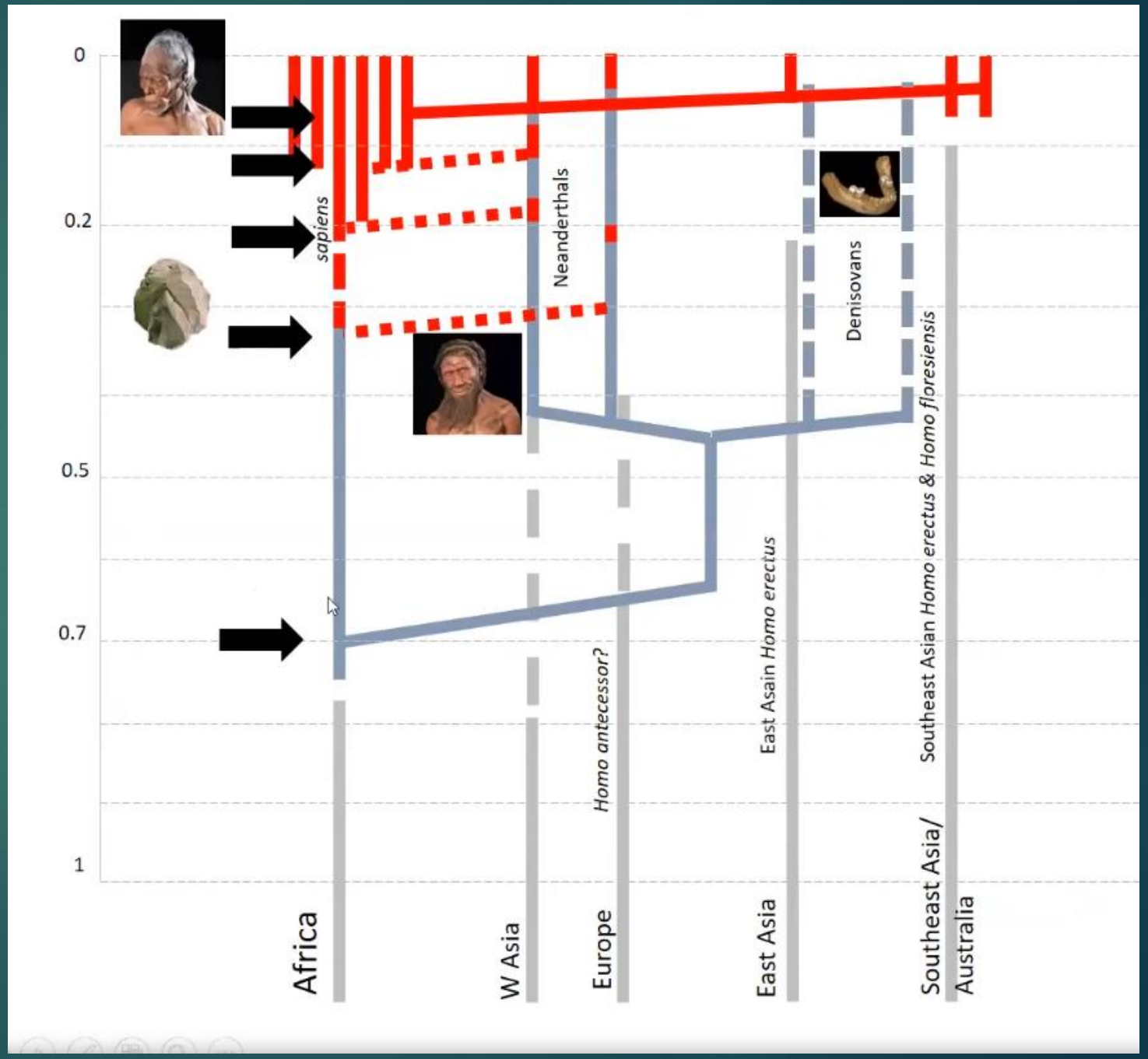
Misliya, Israel, ~190 Ka

Genetic intermixture between African MHs and Eurasian Ns and DS



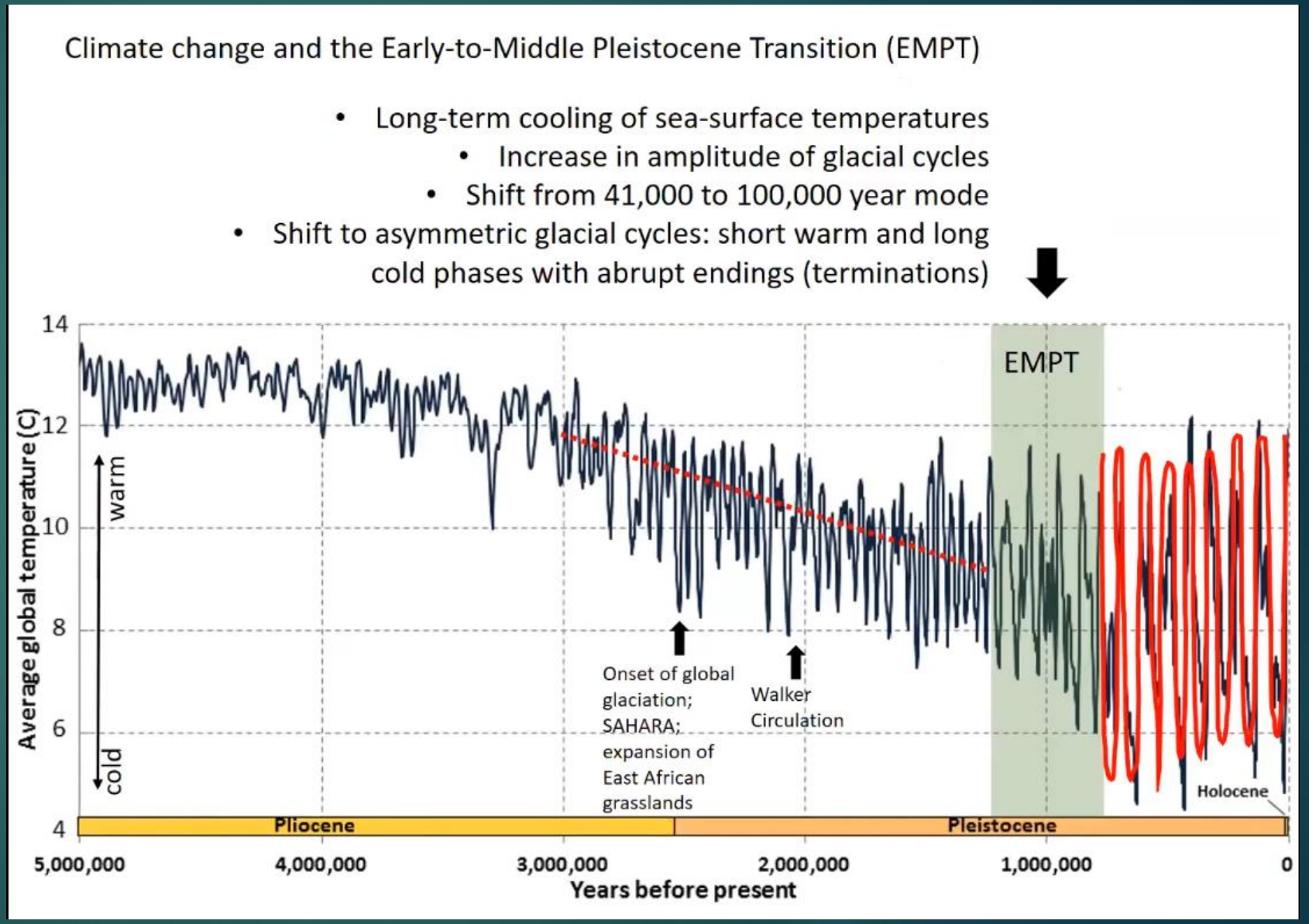
African Dispersals

- Grey = early *H. erectus* dispersals into Eurasia at 2 Ma
- Blue = MP dispersal at 700 Ka that gives rise to MHs in Africa, Ns in Western Eurasia, and Ds in Eastern Eurasia
- Red dots = DNA intermixtures in Eurasia

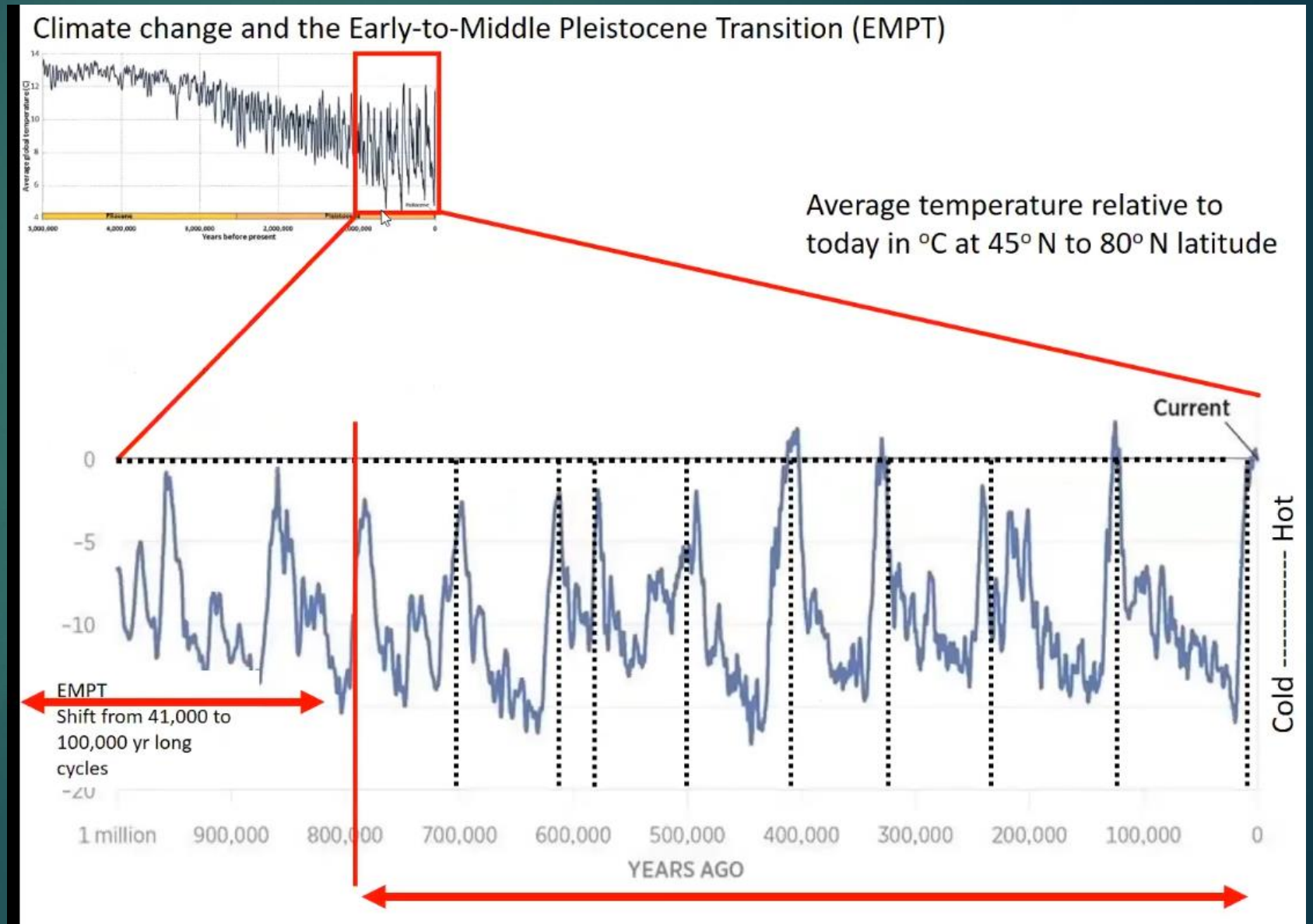


African climatic context for MH origins

- 5 M years of global climate temperature
- Climate got cooler from 5 to 1 Ma
- Major climatic instability at EP-MP transition (shift from 41 K to 100 K cycle of climate change & amplitude increase)



Early to Middle Pleistocene Climate Transition: length and amplitude change; glacial cycles and sudden heat increase (Sahara effected)



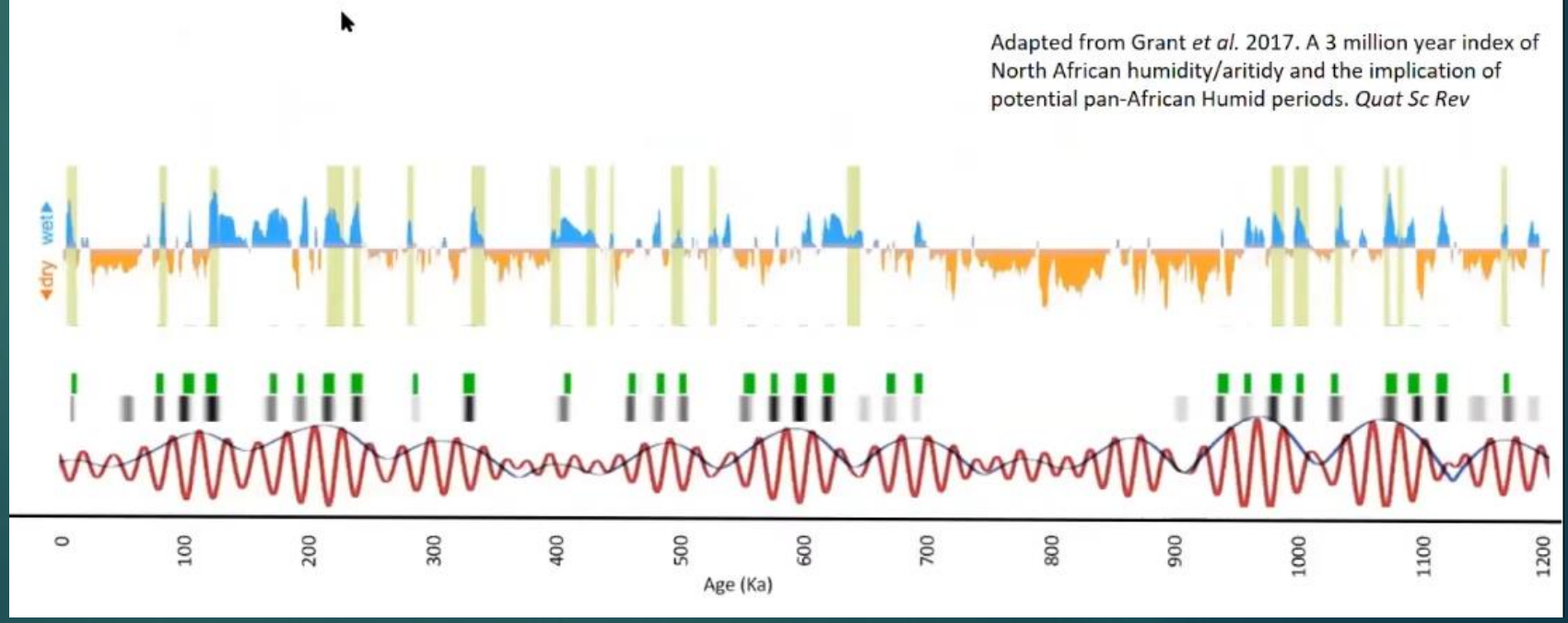
In tropics, monsoons effected: green and desert Saharas with monsoon shifts

- Yellow bars = greening of Sahara
- Dispersals during Green Sahara periods, 400 to 100 Ka

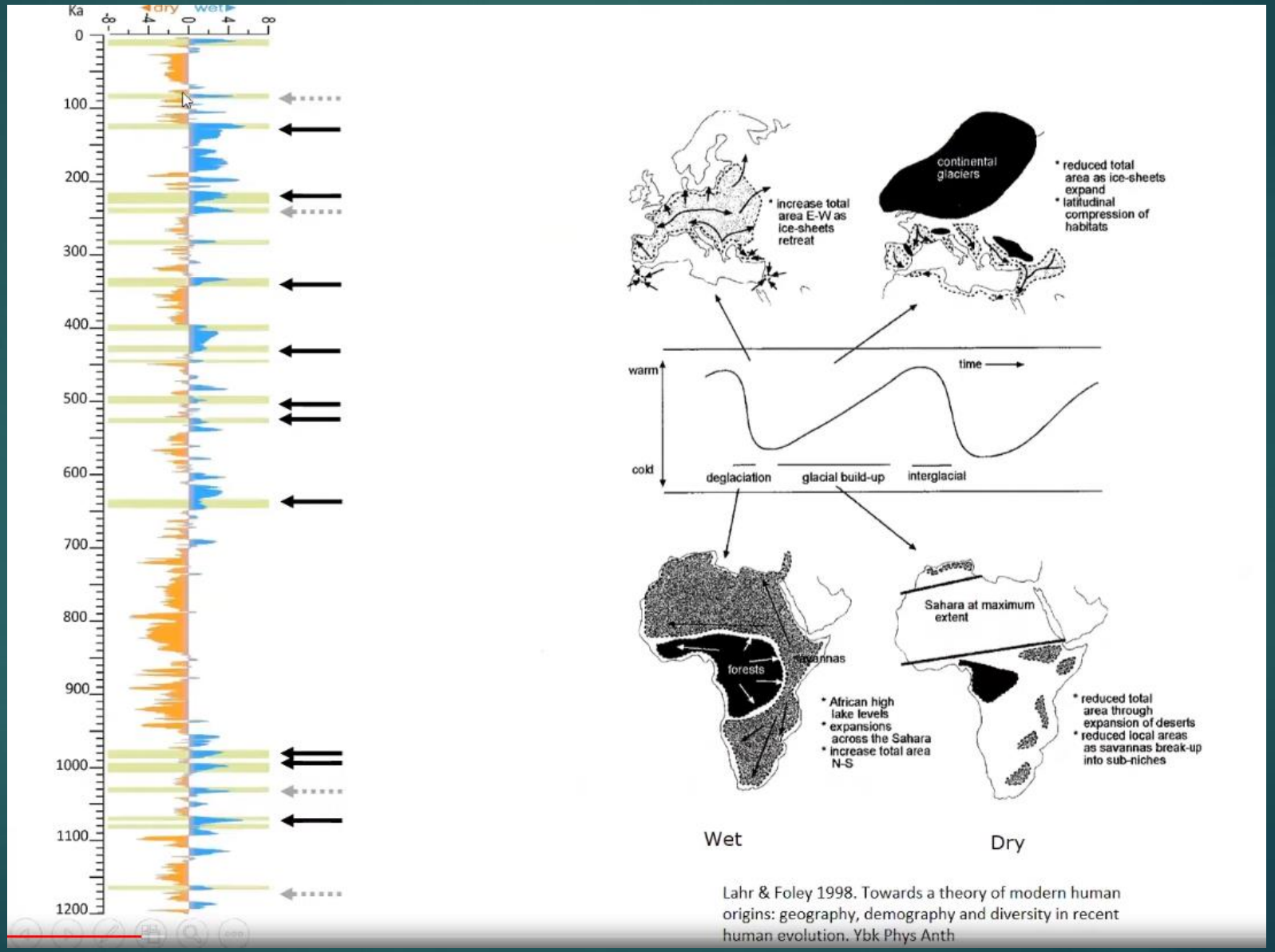
TROPICS

- Hydrological response to orbital eccentricity/precessional cycles
  - EFFECT: amplification or dampening of tropical monsoons

- **eccentricity minima**: weak monsoons at precessional timescales, increased aridity in East Africa, "Yellow Sahara" phase
- **eccentricity maxima**: increase in tropical climate variability at 100,000 and 400,000 yr cycles [independent of continental ice volume] with alternating strongest and weakest monsoons [alternating "Green Sahara" and "Desert Sahara" phases]

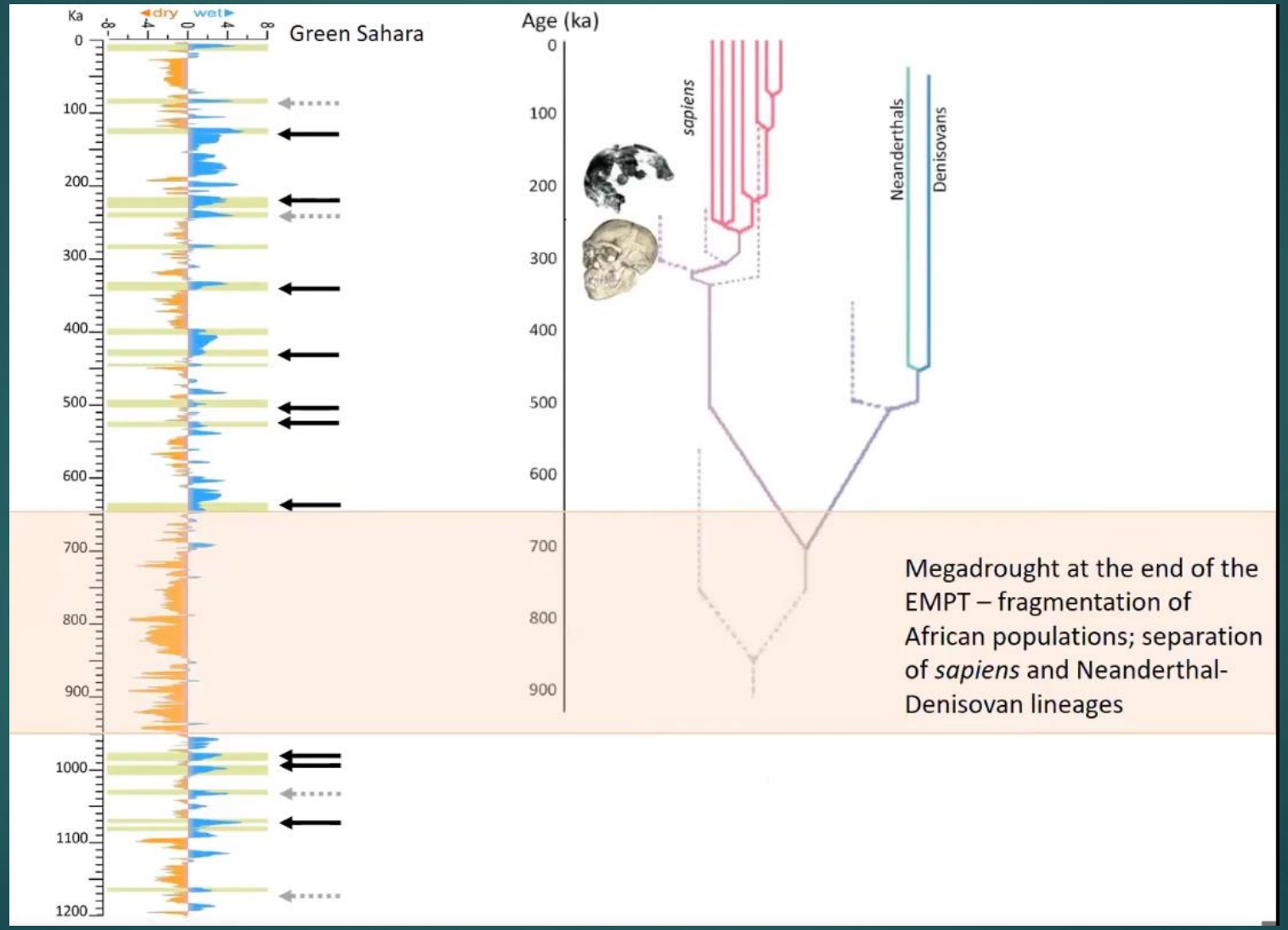


Greening and aridity of Sahara desert



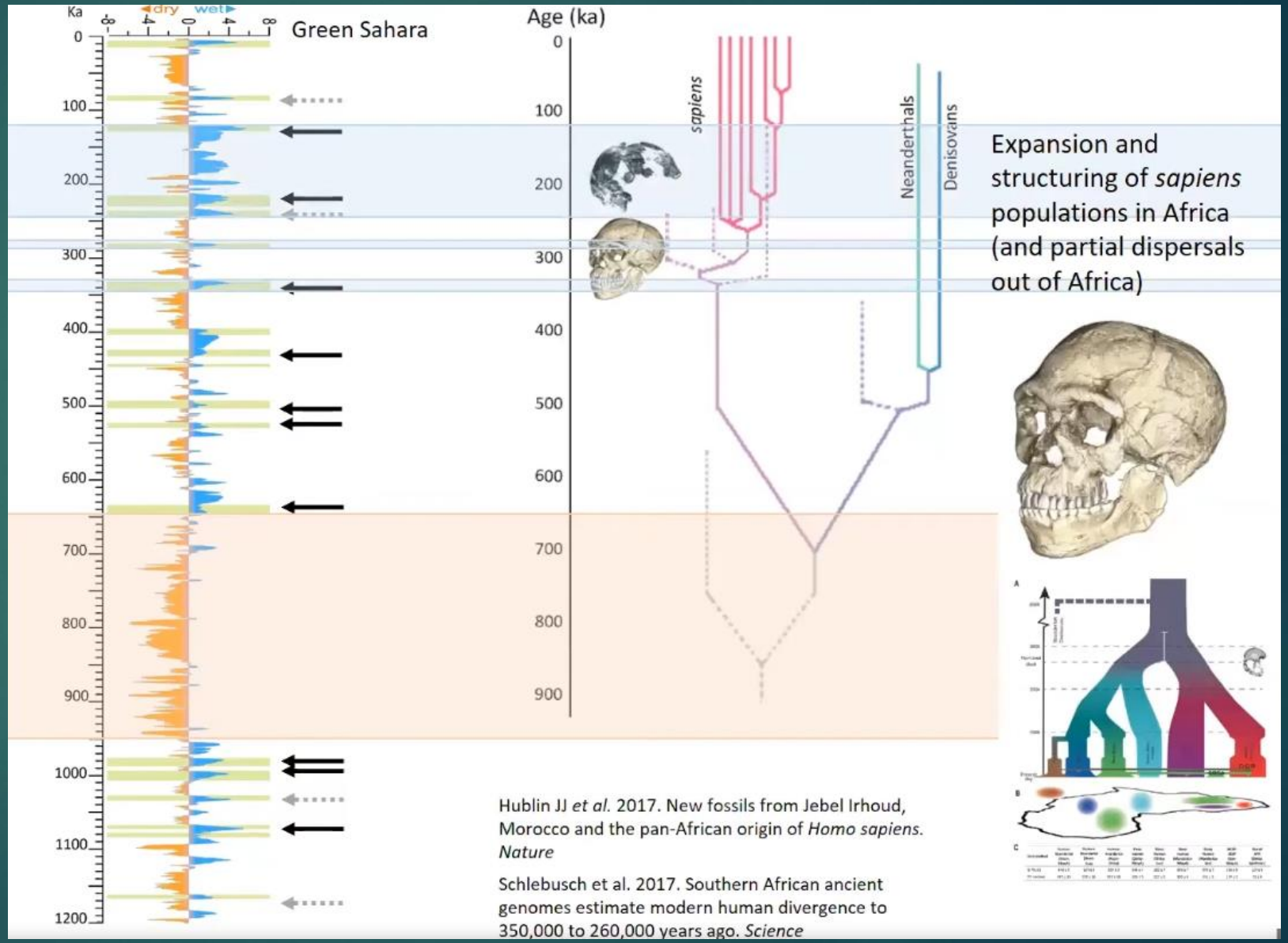
Lahr & Foley 1998. Towards a theory of modern human origins: geography, demography and diversity in recent human evolution. Ybk Phys Anth

Megadrought at 950-650 Ka: African population fragmentation; period of MH & N-D divergence

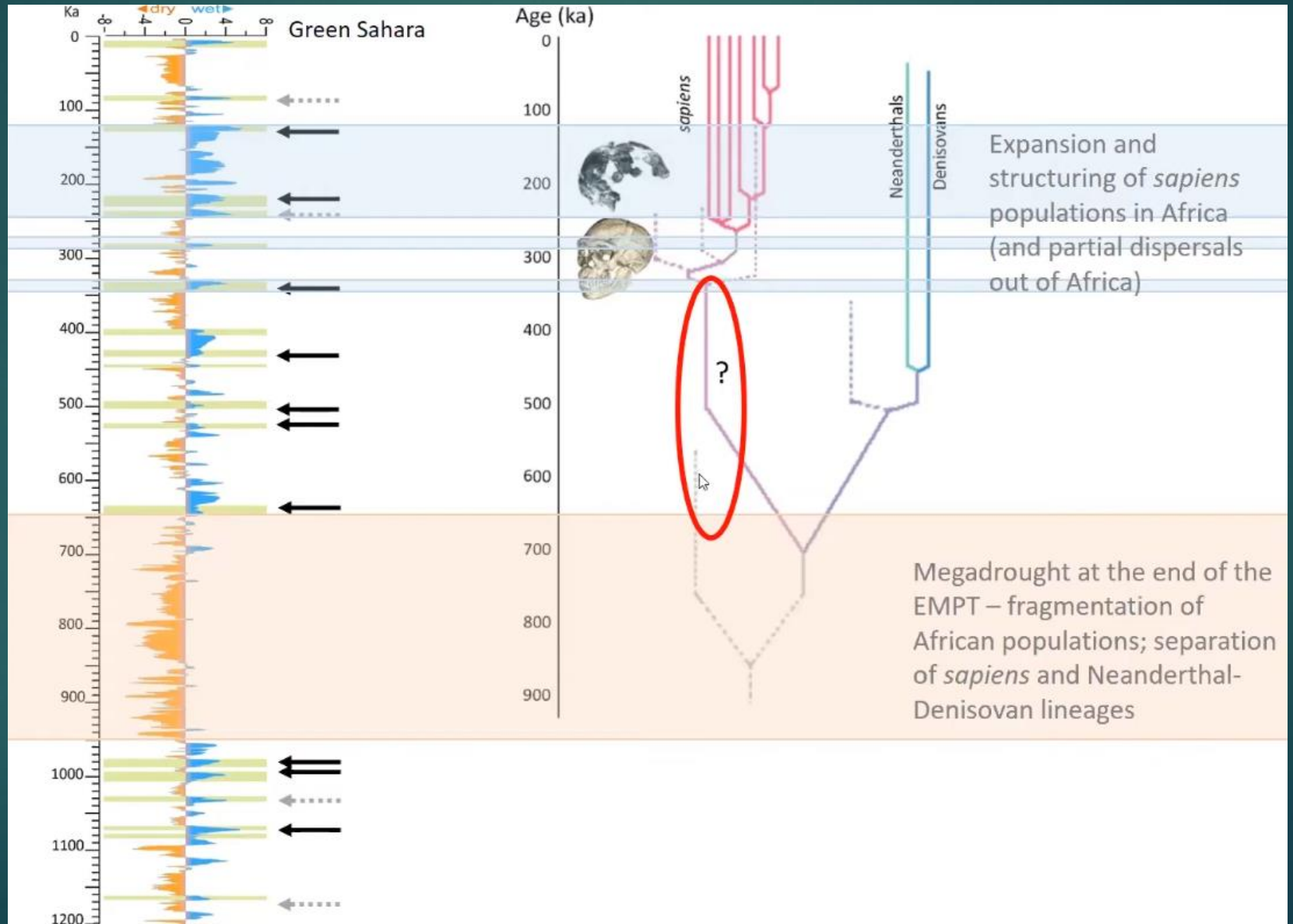


Green periods from 600 to 100 Ka: dispersal potential thru Sahara to Eurasia

- Expansion of populations within Africa
- Jebel Irhoud at 315 Ka
- Greening of Sahara:
- Occurred from south to north
- African fauna would move from South to North



What happened before early group of MHs? Conditions and selective pressures for origins.

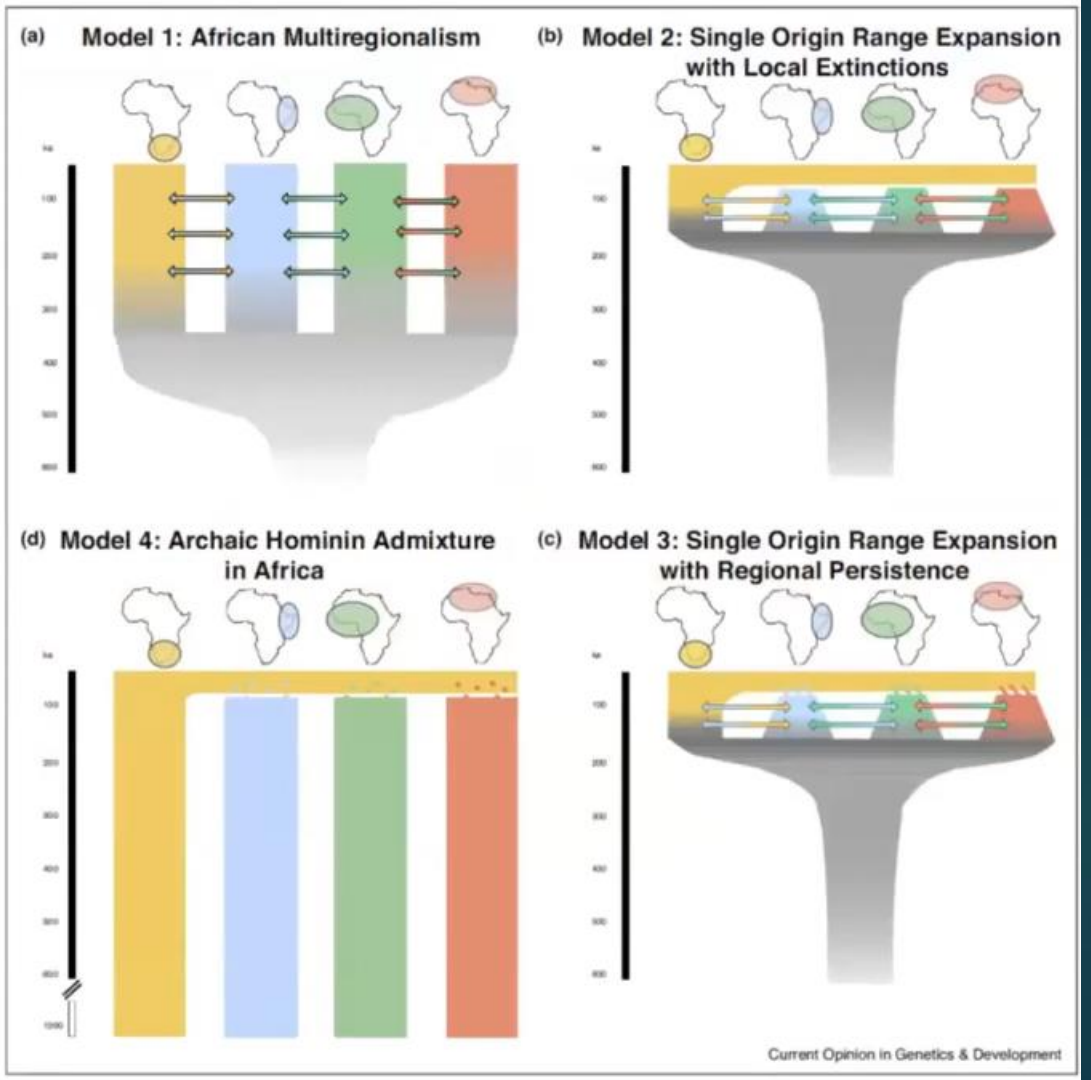


Local or Pan African?

2018: Scerri, et al.: Pan African model

2018: Brenna Henn et al: 4 models of MH origins in Africa via genetic analysis

Scerri EML *et al* 2018. Did our species evolve in subdivided populations across Africa, and why does it matter



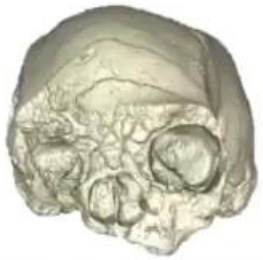
Henn BM *et al* 2018. Clarifying distinct models of modern human origins in Africa. *Current Opinion in Genetics & Development.*

Major diversity among African hominins, 400-200 Ka


Irhoud 315 Ka

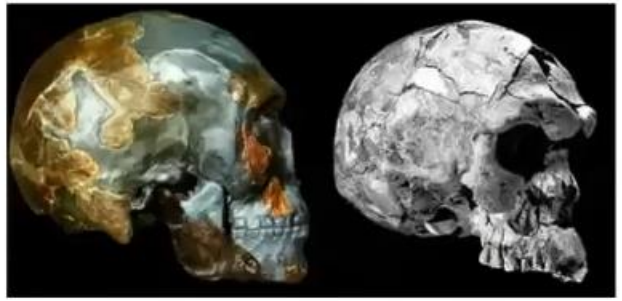

Florisbad 260 Ka


Kabwe 300 Ka


Eliye Springs 350 Ka


Ndutu 400 Ka


naledi 330-250 Ka

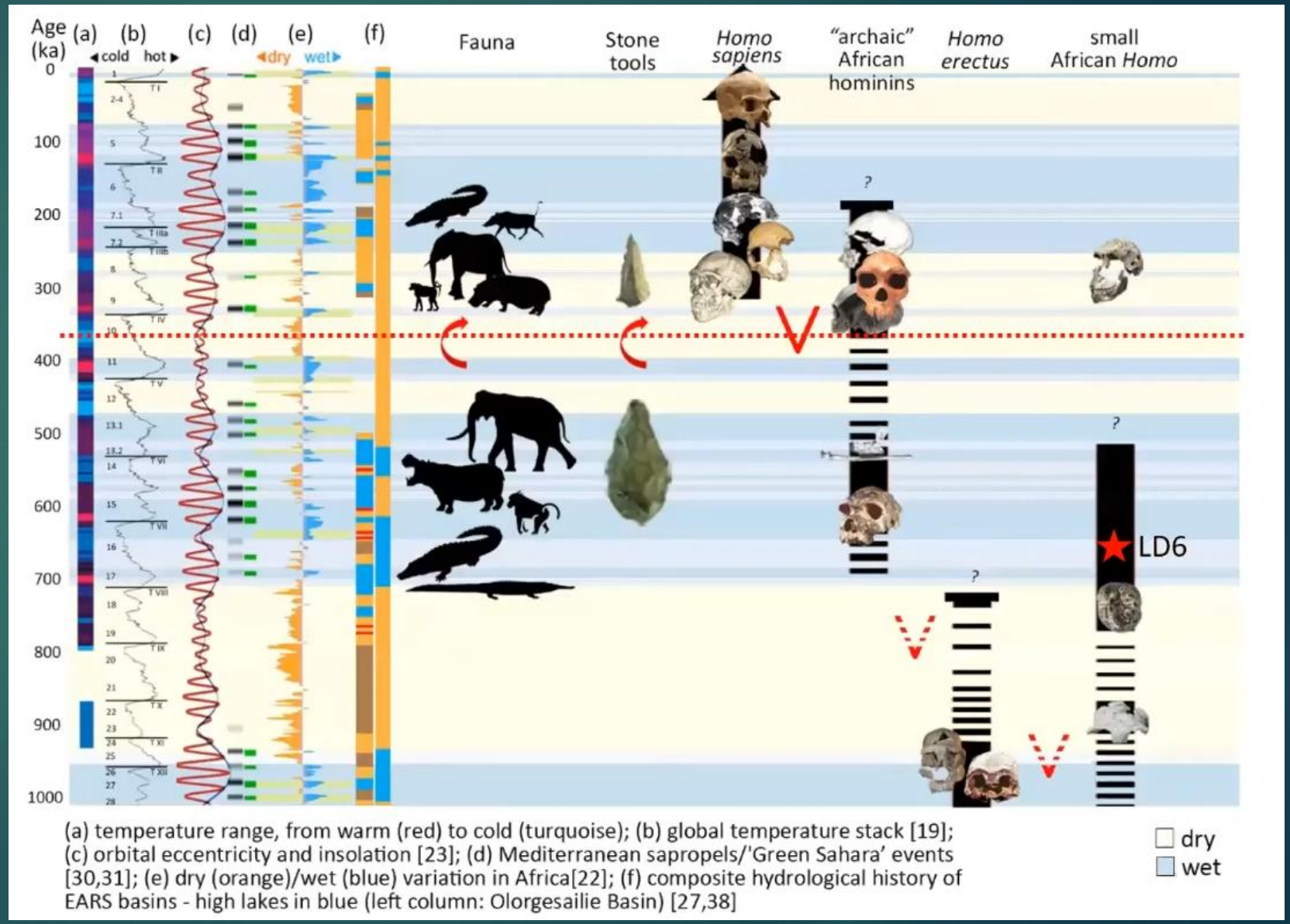

Omo Kibish, Ethiopia, 200 Ka

Herto, Ethiopia, 160 Ka

Hominin populations may have been contained in specific areas; not necessarily as a single gene pool

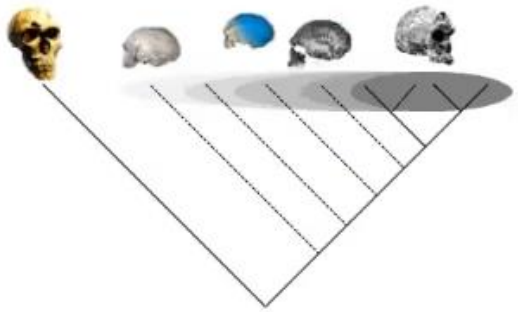
300 Ka: major MSA events

- Early period of few fossils (of small body size)
- Then archaic African hominins (Bodo, Broken Hill)
- Then *Homo sapiens emerges*
- MSA shift from Acheulean to Levallois lithics
- Faunal shift from larger to smaller species



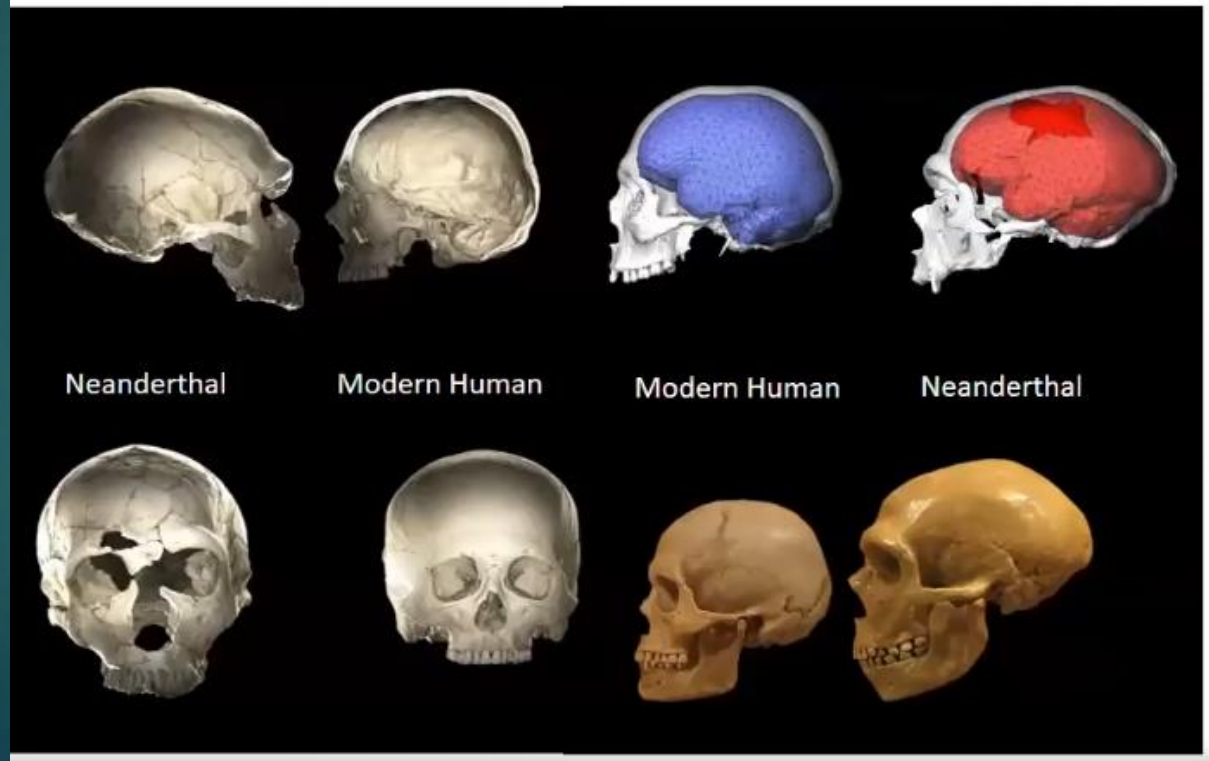
(a) temperature range, from warm (red) to cold (turquoise); (b) global temperature stack [19]; (c) orbital eccentricity and insolation [23]; (d) Mediterranean sapropels/'Green Sahara' events [30,31]; (e) dry (orange)/wet (blue) variation in Africa[22]; (f) composite hydrological history of EARS basins - high lakes in blue (left column: Olorgesailie Basin) [27,38]

Morphology of MHs



Palaeontological definition of modern humans

- Comparatively tall and narrow body
- Large brain hominin
- Tall rounded cranium*, with relatively vertical forehead
- Comparatively reduced cranial superstructures
- Small face positioned under the vault
- Mental eminence on mandible*

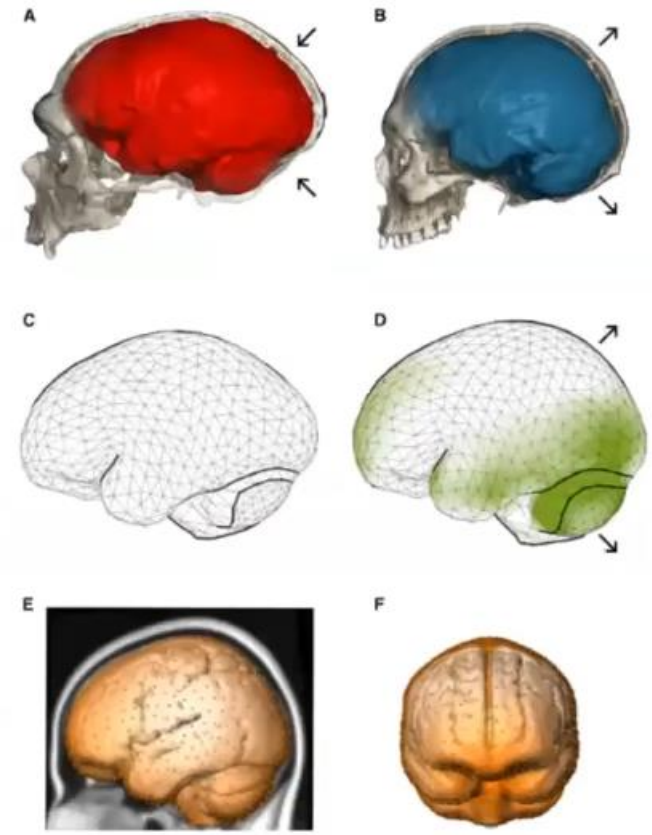


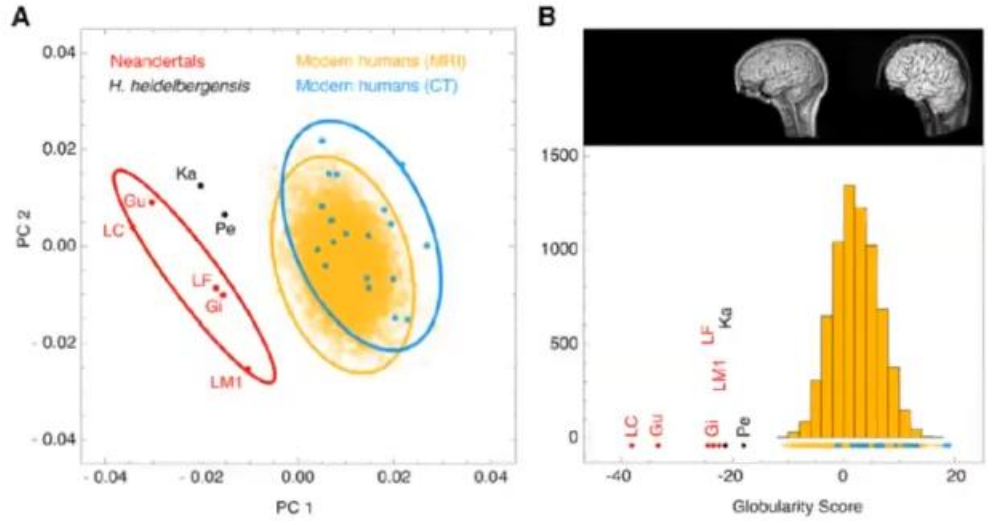
* Apomorphies of *Homo sapiens*

Globular skull: change in skull shape is part of origin of MHs

- Gunz et al., 2018: N genes associated with reduced globularity in current MH skull
- Probably affected neurogenesis in ancient MHs

- A quantitative measure of the globular modern human head
- Genetic association of values of this “index of endocranial shape” amongst Neanderthal introgressed genomic fragments in the genomes of 4468 Europeans
- Key SNPs correlations associated with reduced globularity
- Correlated SNPs: affect neural expression of 2 genes linked to neurogenesis and myelination





Gunz P *et al.* 2018. Neanderthal introgression sheds light on modern human endocranial globularity. *Curr Biol*

Unique Life History

- Increased longevity
- Sustained fetal brain growth rate
- Longer infancy and childhood
- Puberty
- Menopause

Palaeontological definition of modern humans

- Comparatively tall and narrow body
- Large brain hominin
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- Comparatively reduced cranial superstructures
- Small face positioned under the vault
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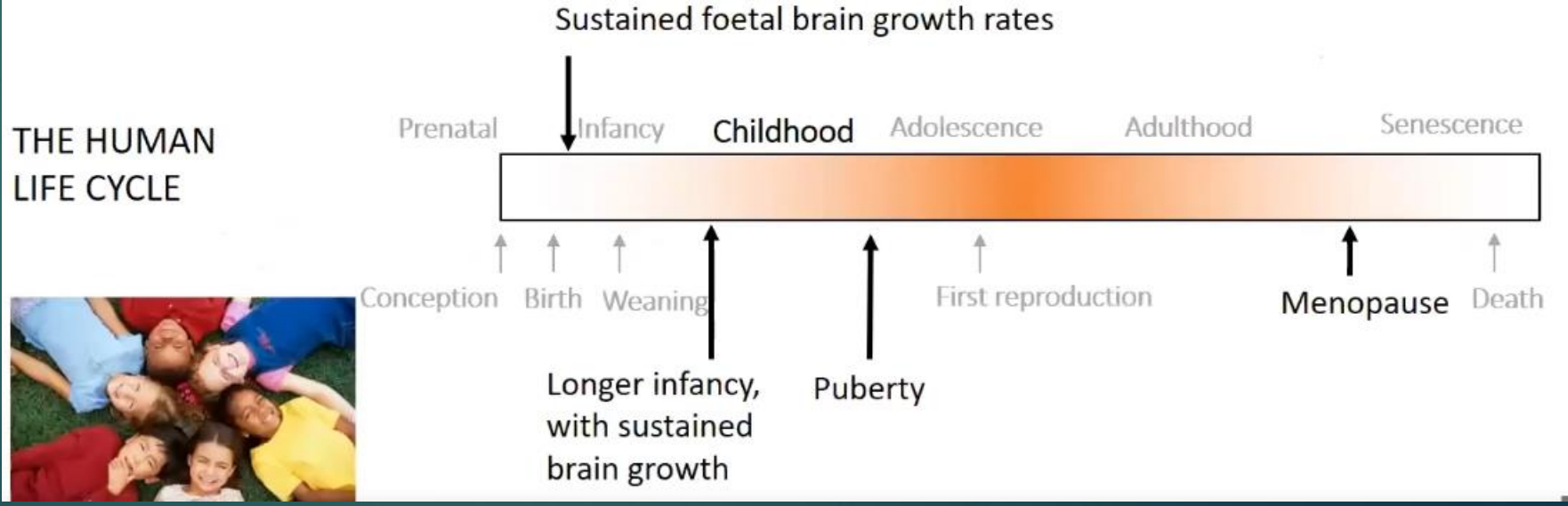
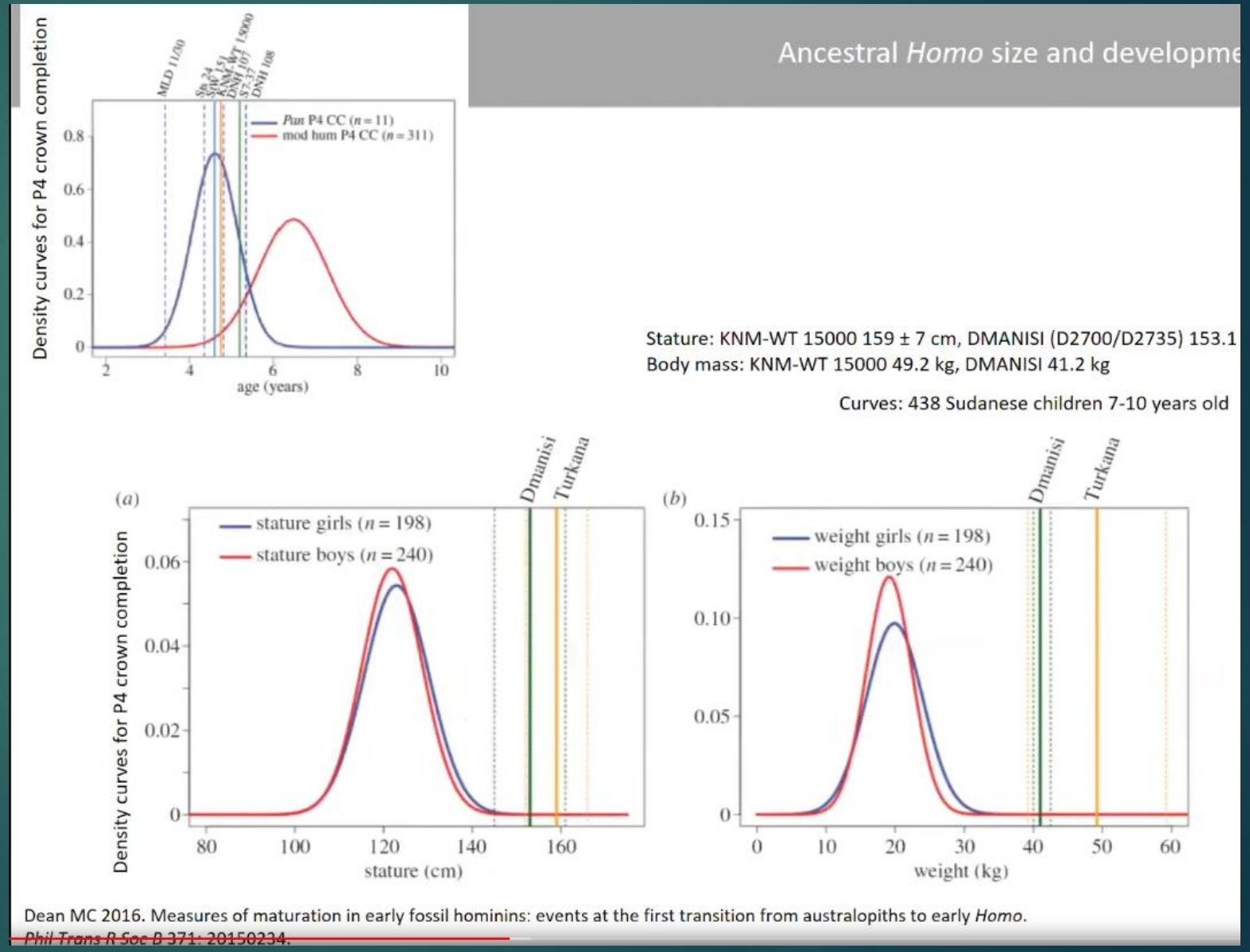
- Unique life-history*



Development of early Homo

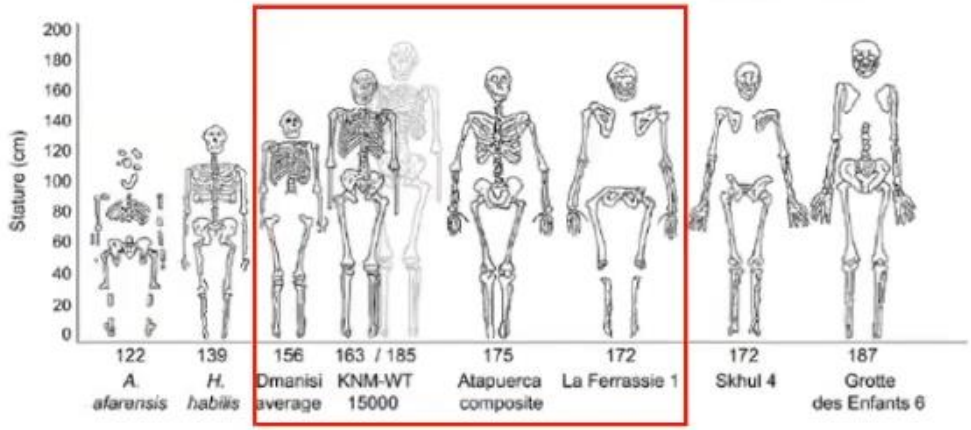
- Stature and weight growth in modern 7 to 10 year olds = slower growth rate
- 2nd molar of Dmanisi and Turkana boy: both very heavy and tall by 7-10 = faster growth rate

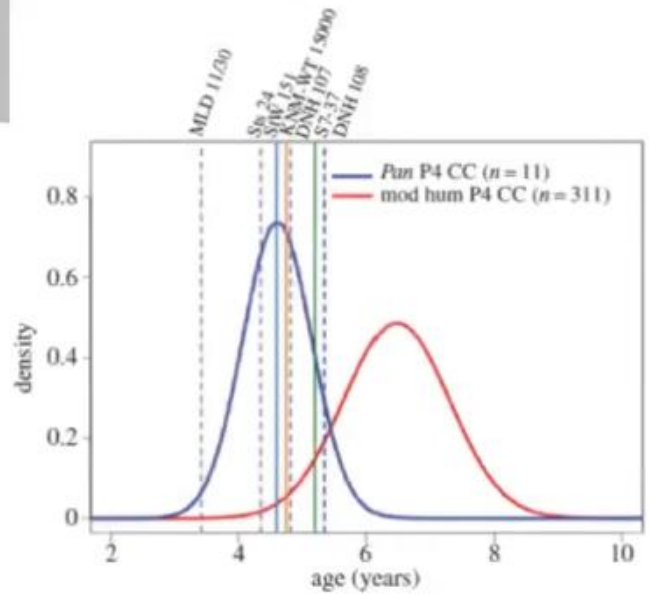


Dean MC 2016. Measures of maturation in early fossil hominins: events at the first transition from australopiths to early *Homo*. *Phil Trans R Soc B* 371: 20150234.

Ancestral life history: fast growth

Ancestral *Homo* life-history





Ancestral *Homo*: large size, encephalised, fast growth

- **Energetically very demanding** – diet shift, carnivory
- **Ecologically effective** – early independence, predator risk minimisation
- **Socially and behaviourally challenging** – likely increase role of social cohesion, provisioning, innovative solutions (cooking?)

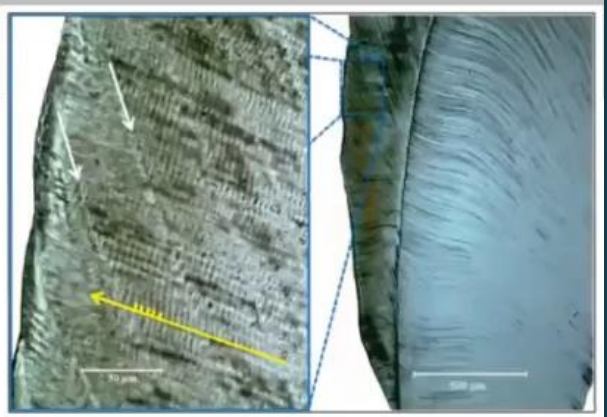
Slower, longer juvenile period

- 2020 study: MHs have unique dental growth pattern
- Based on higher energy budget and longer juvenile period and lifespan
- Dental Retzius (lines in enamel) periodicity is controlled hypothalamically

Modern human life-history :

- ❖ Relatively higher energy budget and reproductive output than apes (“fast”)
- ❖ Long juvenile period and lifespan (“slow”)

UNIQUE



Descriptive statistics of Retzius periodicity (RP) for select subsamples of our data set. Modern human data are presented separate from all other groups, because of the enormous sample size difference between them and all other groups. All values for modern humans except *n* and range are estimates drawn from 5000 bootstrapped iterations of randomly sampled geographic subsets of our overall modern human data set (see Materials and methods).

Group	*n*	Mean	Median	Mode	SD	Range	Skewness	Kurtosis
Hominids without modern humans	279	7.71	7	7	1.44	6–12	0.54	−0.57
Hominins without modern humans	71	7.51	7	7	1.29	6–12	1.31	2.00
Homo without modern humans	24	7.58	8	8	0.97	6–10	0.36	0.47
Australopiths	47	7.45	7	7	1.44	6–12	1.47	1.92
Modern humans	1194 (300 resampled)	8.04	8	8	3.03	5–12	0.16	2.35

Retzius Periodicity (RP): number of days between the deposition of successive long-period growth lines in teeth (striae of Retzius in tooth enamel)

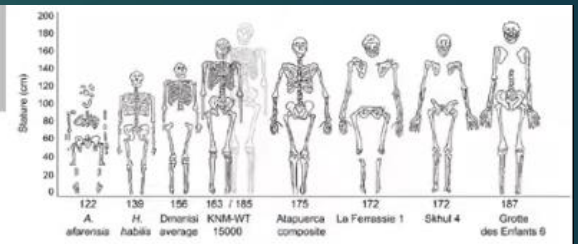
- ➢ histological manifestation of a neuroendocrine biorhythm (Havers-Halberg oscillation)
- ➢ closely related to body mass and BMR, role in regulating pace of life-history in mammals

Hogg R *et al.* 2020. A comprehensive survey of Retzius periodicities in fossil hominins and great apes. *J Hum Evol* 149: 102896

Unique human life history

- Energetically efficient
- Ecologically challenging
- Socially demanding

Unique human life-history



Homo sapiens: large size, encephalised, slow growth

- **Energetically efficient** – budgeted development through longer ontogeny
- **Ecologically challenging** – longer dependence on mother, big risk of predation
- **Socially and behaviourally very demanding** – provisioning of mothers with dependent children, social cohesion and belonging, major pressure on technological solutions, increased dependence on learning social norms and skills, increased importance of social memory

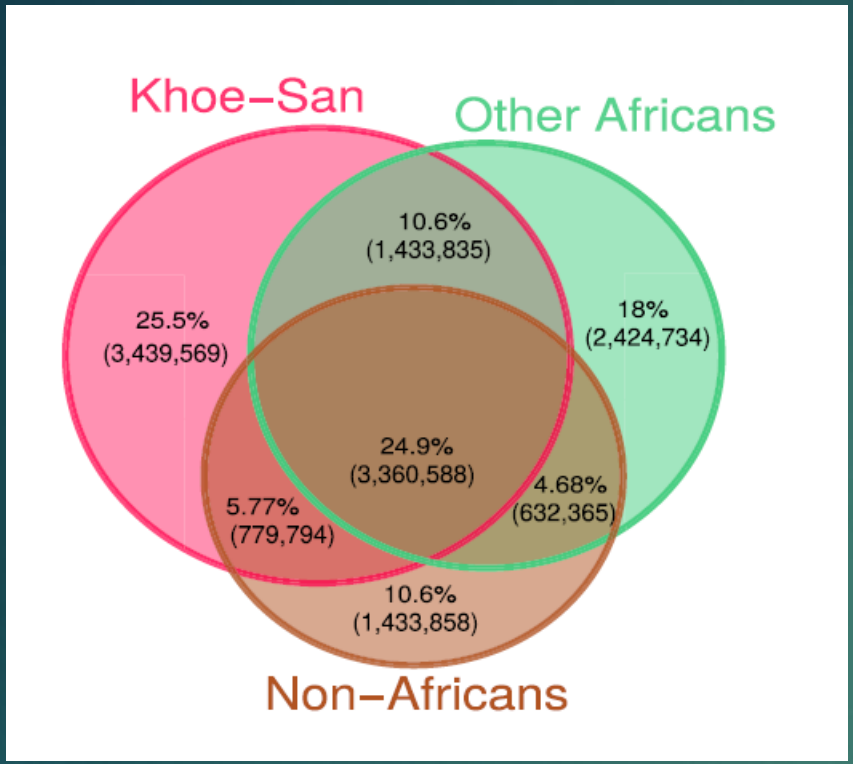
The evolution of modern human hunter-gatherer societies?

- Role of kin and non-kin
- Family units, foraging units, social units – multilevel societies
- Shared social norms, social identities, and social histories

Migliano AB *et al.* 2017. Characterization of hunter-gatherer networks and implications for cumulative culture. *Nature Hum Behav*

Marta Lahr: MHs were cheaper to produce

- *H. erectus* & N larger rib data implying larger lungs & more energetic needs (20% more Ox need); if size reached by age 10, size of adults
- Life hx variables of MHs indicate that comparatively they produce a body that was cheaper (body with less energetic needs; more energetically efficient body):
  - Grow more slowly
  - Were lighter in weight
  - Cost less during growth
  - Less relative provisioning of children
  - At cost of more complex society – social networks are primary characteristic of MHs
  - Leading to alternative behavior and neurology
  - Social hypothesis of brain development (R. Dunbar)



- The genetic diversity among the Khoe-San is the greatest among all human groups across the world, which, in part, is explained by relatively recent (pre-colonial) admixture
- All human groups, including the Khoe-San, showed a reduction in Ne (between 1/3 and 1/10) between 100 and 20 ka

- Khoe-San Genomes Reveal Unique Variation and Confirm the Deepest Population Divergence in *Homo sapiens* by Carina M Schlebusch, et al., 2020:
- Khoe-San have 25% unique gene variants;
- Khoe-San group harbors the greatest level of diversity across the globe;
- All human groups show a reduction in effective population size commencing around the time of the Out-of-Africa migrations, which coincides with changes in the paleoclimate records, changes that potentially impacted all

Population size

- Lahr: African hominin populations were never very large; nowhere near larger Holocene population sizes

- All our data from genetics:
- Multiple population bottlenecks:

- All human groups were inferred to have had an Ne of 30,000 about 300 ka, with a reduction in estimated effective size starting around 150–100 ka. Non-African populations reached a lowest level (Ne ~2,000) in the bottleneck around 80 ka, coinciding with the Homo sapiens Out-of-Africa migration event. Surprisingly, most African populations also showed a reduction in estimated Ne during this period, reaching an Ne of 10,000

Population size

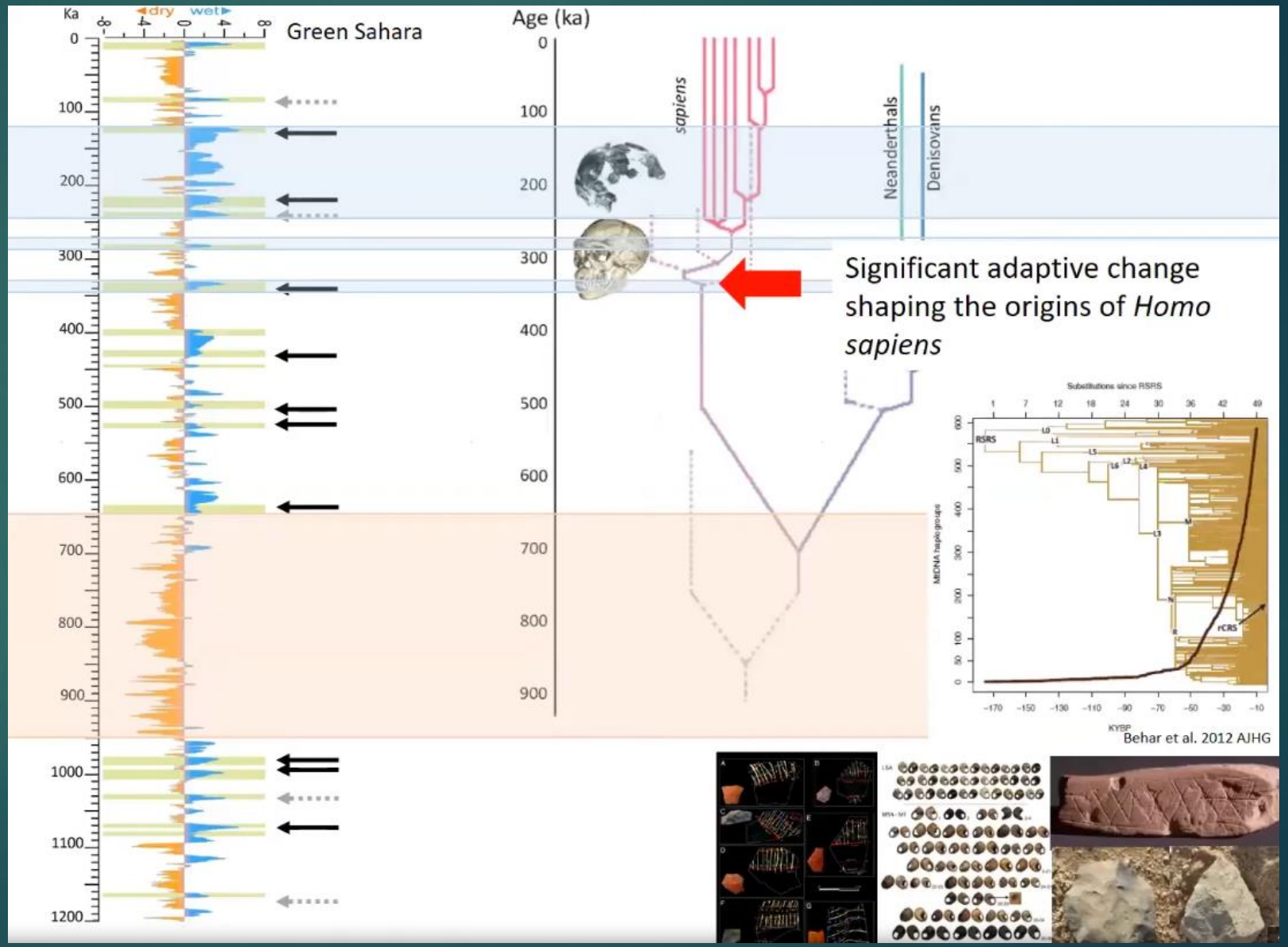
- ~60 Ka in Africa
- work on the Lake Malawi core indicates severe drought and low-lake stage occurring between109 and 92 ka when the area is also shifting from leaf- to grass-dominated vegetation; shift to colder temperatures, causing population reduction and dispersal out of Africa
- ~12-10 Ka in Europe (Iberia – haplogroup replacements)
- population increasing in concomitance with wetter climatic conditions.
- Among the most selected for genes are those that serve immunity, both in Africa & Eurasia.

N genetics

- New research:
- Genetic analysis indicates large expansion of Ns, even into Siberia
- Then large genetic collapse; could not sustain expansion
- Loss of genetic diversity; inbred populations
- 2 N fossils in Siberia from different periods were more closely related to Western Ns than to each other; very unstable demography

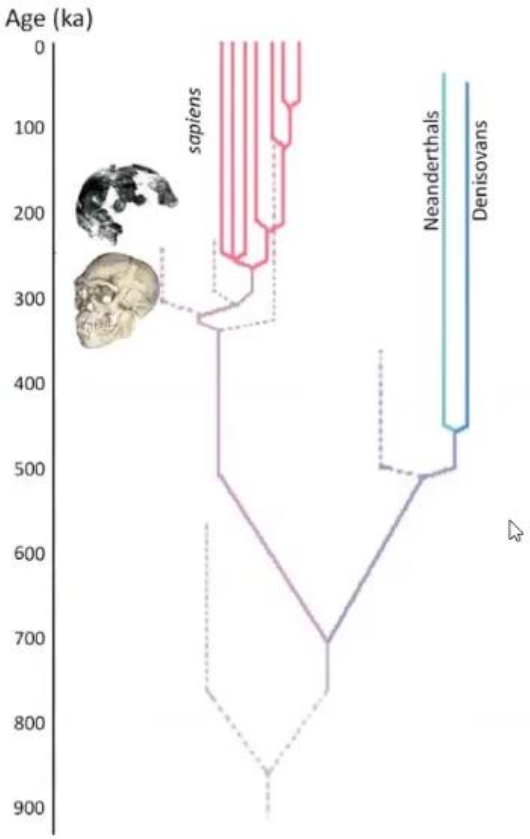
Significant adaptive change ~300 Ka = MH origin

- Significant demographic change after 300 Ka
- Beginnings of greater innovations in S Africa



Issues

Major outstanding issues



Who was the last common ancestor of MHs, Ns, and Ds (HND)?

Megadrought = 900-700 Ka

Probably between 900-700 Ka

- Period of extreme aridity in Africa: population fragmentation
- A time when the human/Neanderthal/Denisovan lineage co-existed with another hominin in Africa
  - North vs sub-Saharan Africa?
  - *Homo antecessor* ?

Mounier A & Mirazon Lahr M 2016. Virtual ancestor reconstruction: revealing the ancestor of modern humans and Neandertals. JHE

African fossils from this period: too few, each different

Where were the ancestors of Ns/Ds before they split?

- Model 1 = LCA of Ns/Ds in Africa, 700-450 Ka; split during OoA dispersal
- Some African archaics may be closer to Ns/Ds

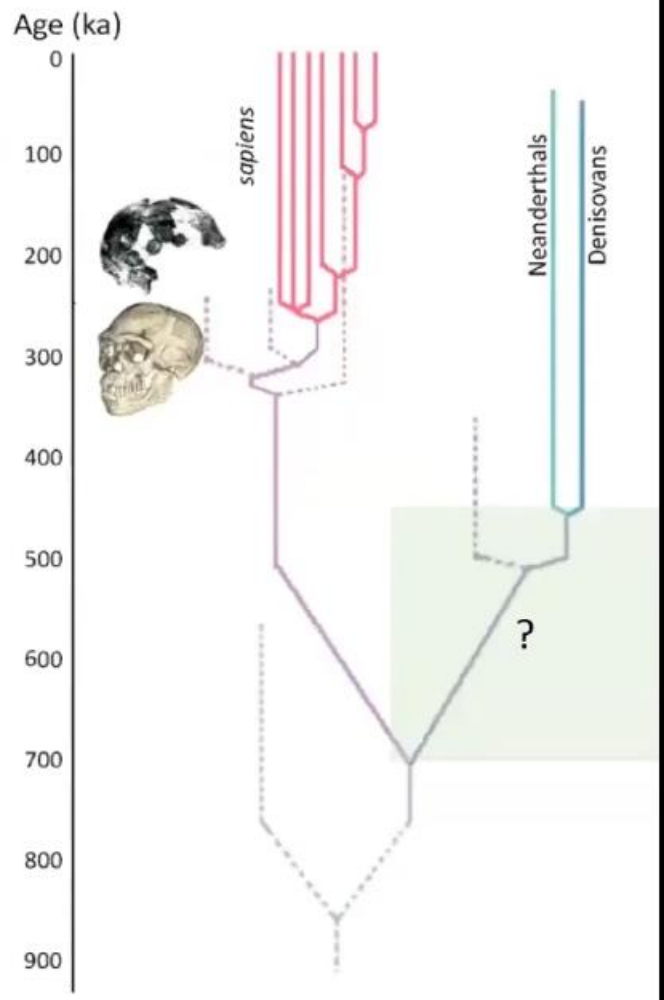
- Model 2 = LCA after OoA dispersal in Eurasia;
- Eurasian fossils may be LCA

MODEL 1: Neanderthal and Denisovan lineages separate during the process of out-of-Africa dispersal

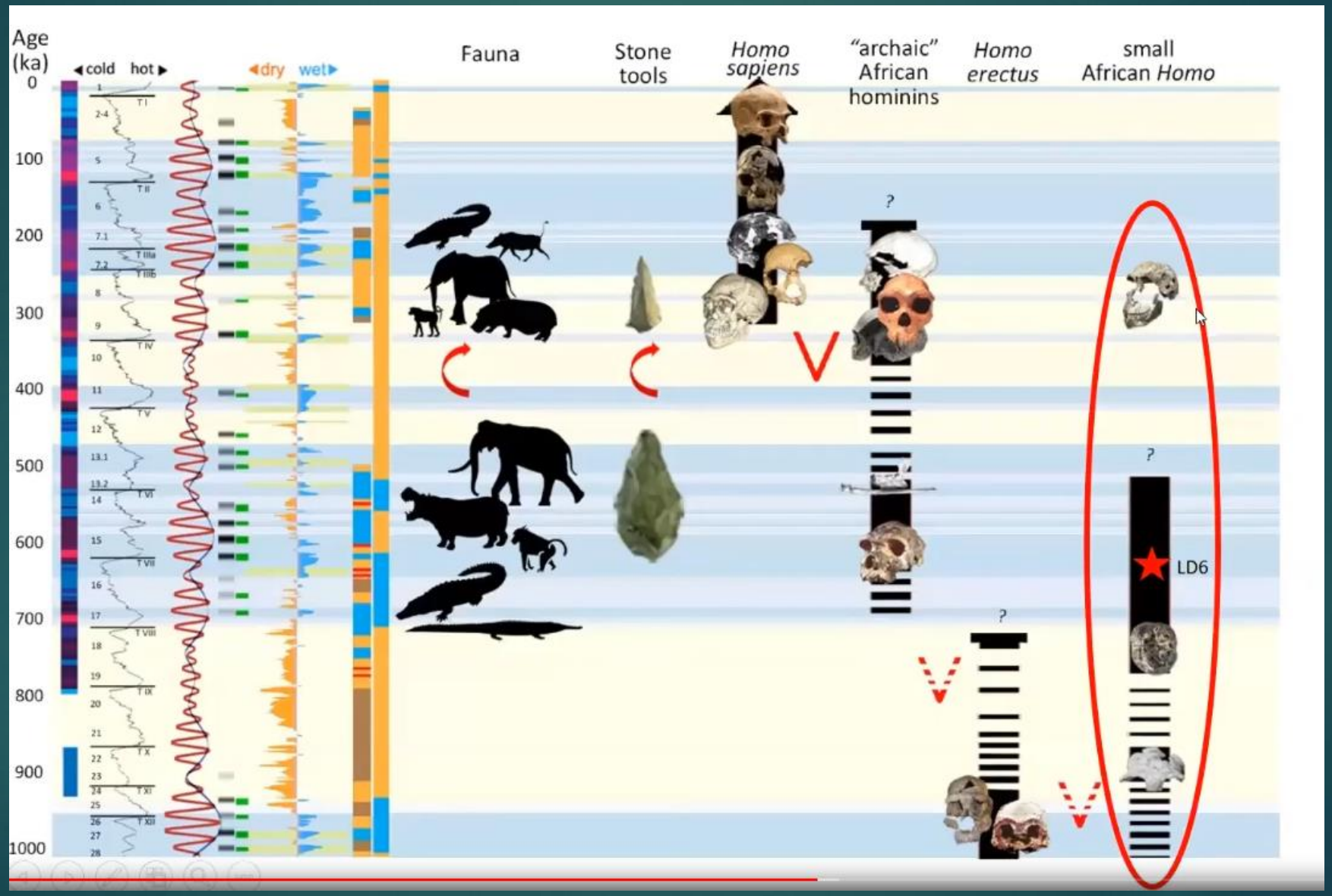
- ❑ time of split = time of dispersal out of Africa
- ❑ Implies that ancestor of NEA-DEN lived in Africa between 700 and 450 Ka
  - ➢ Too late to fit the fossil record? Earliest ages (Ceprano, Sima) ~430 Ka; Petralona?
  - ➢ Implies the rich, African looking (full of cleavers, absent in Europe) Acheulean at GBY was an earlier (limited?) dispersal

MODEL 2: Neanderthal and Denisovan lineages separate in Eurasia some time after the out of Africa dispersal

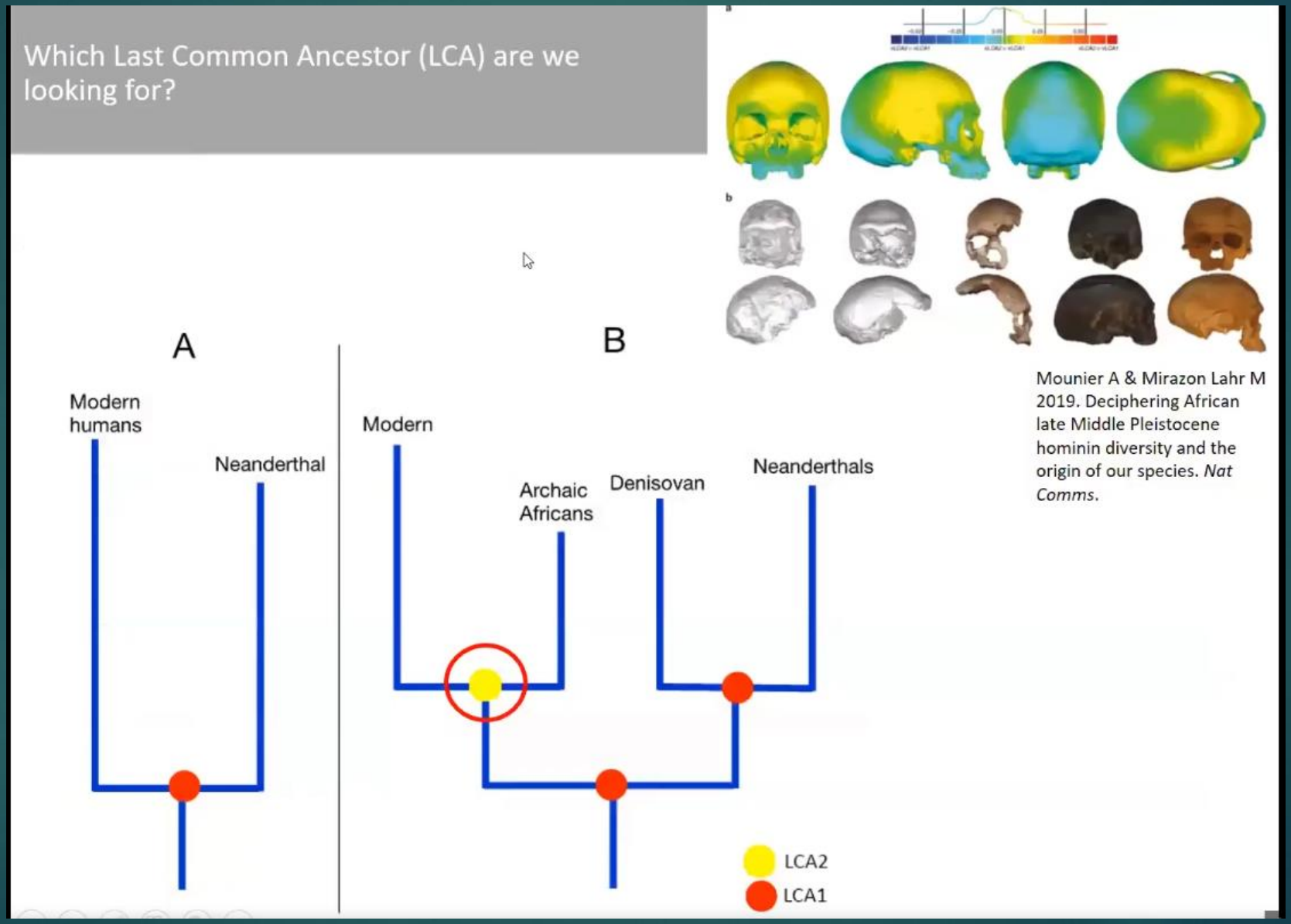
- ❑ time of dispersal out of Africa much before split NEA x DEN
- ❑ Implies that ancestor of NEA-DEN lived somewhere in Eurasia between 700 and 450 Ka
  - ➢ What Eurasian fossils match the LCA of NEA & DEN?
  - ➢ Earliest "non-*erectus*" fossils in China ~350 Ka – where were the Denisovans before?



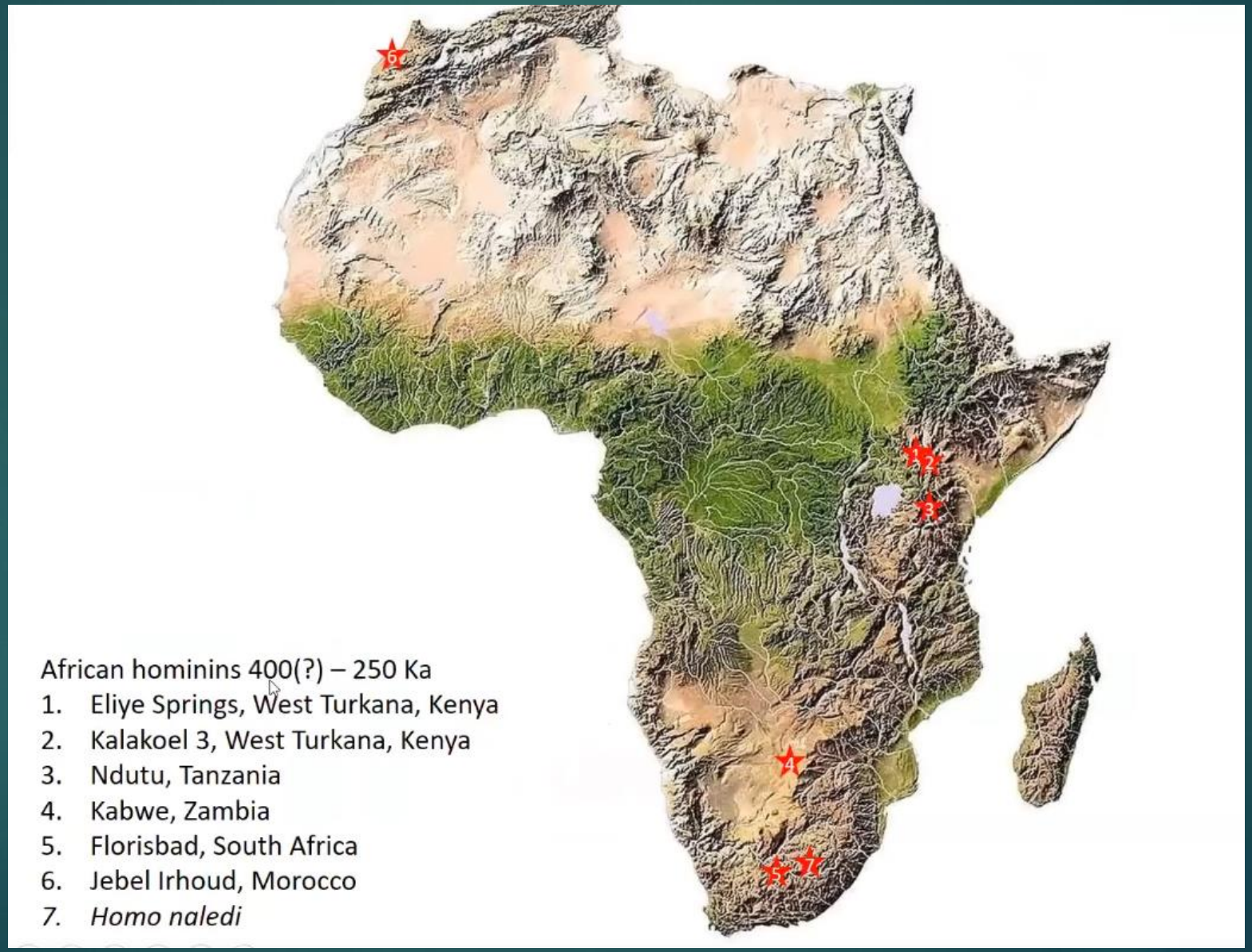
What was the adaptive niche of African small-bodied *Homo*?



Which LCA are we looking for?



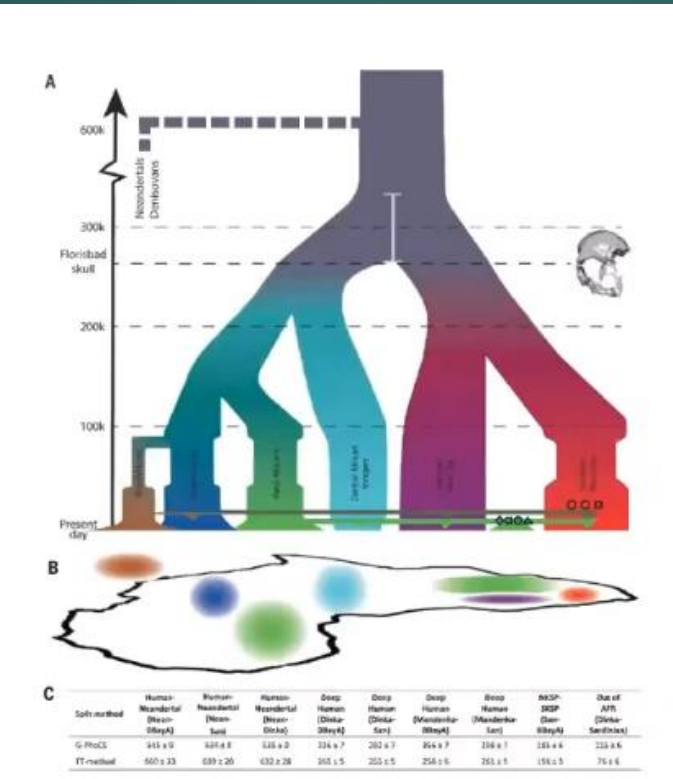
African hominins 400-250 Ka: very incomplete fossil record



How deep is the population structure of African Homo sapiens? Unresolved yet.

- Schlebusch et al., 2017: earliest population divergence: deep structure – 350-260 Ka

- B. Henn et al., 2018: not so deep – 140-110 Ka: correlates with fossil record



Schlebusch et al. 2017. Southern African ancient genomes estimate modern human divergence to 350,000 to 260,000 years ago. *Science*

Table 1

Genetic estimates of the earliest population divergence among humans

Date (years)	Populations	Citation
110 000	San versus Pygmy & West Africans	Veeramah *et al.* [60]
110 000–150 000[a,b]	San versus Yoruba	Gronau *et al.* [20]
130 000	San versus Eurasians	Mallick *et al.* [46]
100 000	KhoeSan versus other Africans	Schlebusch *et al.* [61]
150 000–20 000	Yoruba versus Europeans	Schiffels and Durbin [50]
120 000–140 000	San versus Mbuti	Song *et al.* [58••]
87 000	San versus Yoruba	Mallick *et al.* [46]
160 000	Central Pygmy versus West Africans	Hsieh *et al.* [55]
130 000–140 000	Central Africans versus Europeans	Lopez *et al.* [62]
260 000–350 000	ancient San versus East Africans	Schlebusch *et al.* [40]

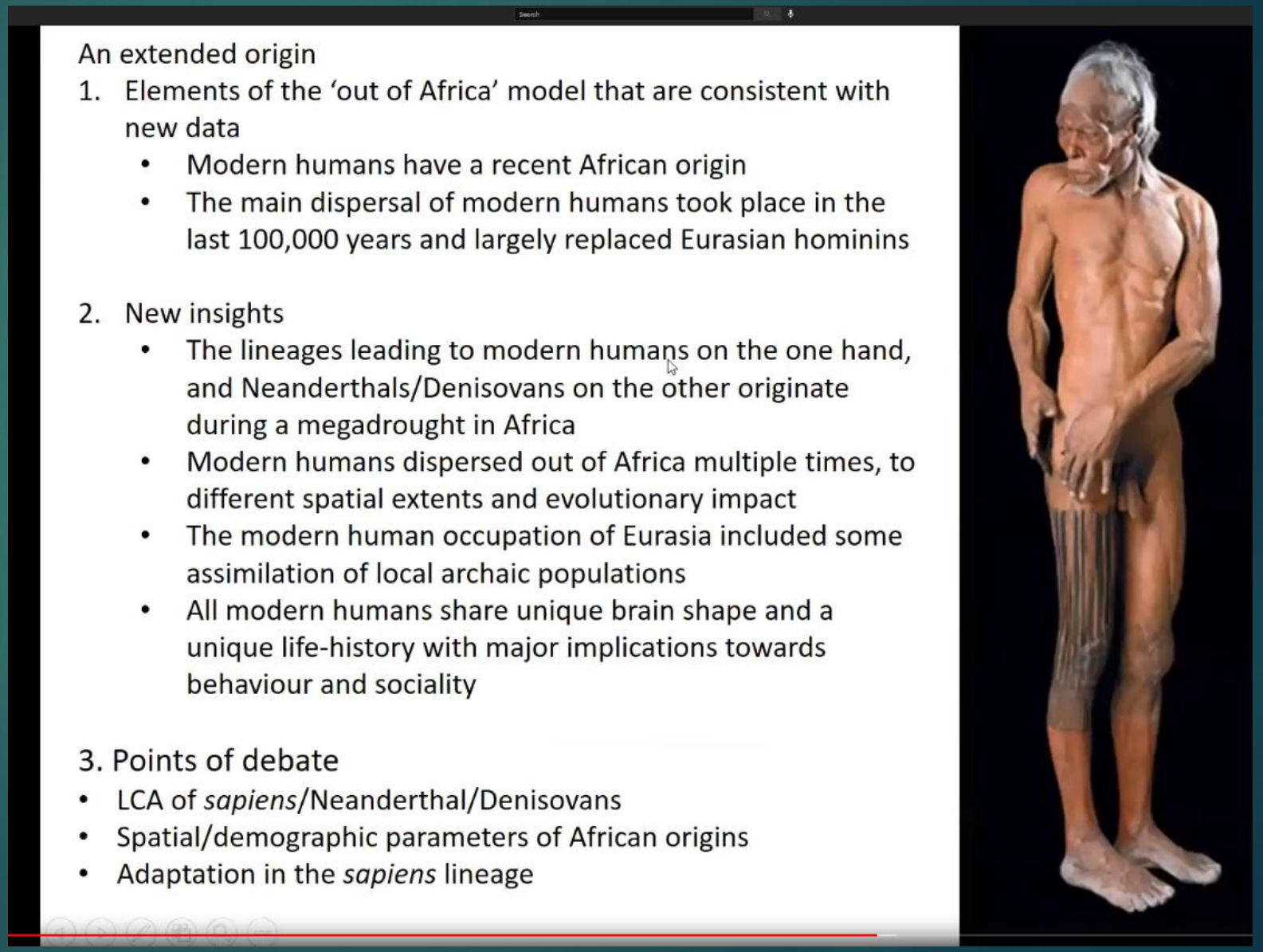
[a] Ranges here do not represent confidence intervals, but variation either in the initial versus midpoint estimate of the cross-coalescence rate; or variation between demographic inference methods.
[b] Dates do not incorporate uncertainty in mutation rate except for Ref. [20].

Henn BM et al 2018. Clarifying distinct models of modern human origins in Africa. *Current Opinion in Genetics & Development.*

An extended origin

- 1. MHS = recent African origin with deep structure; dispersal in last 100 Ka with replacement of Eurasian hominins

- 2. A. Origins of MHs & Ns/Ds during megadrought
- B. Multiple African dispersals
- C. Occupation of Eurasia included assimilation of local populations
- D. MHs have globular brain shape and unique life hx



H. Sapiens and ghost species: "*Lord of the Rings*-type world," with "many hominin populations."

- Genetic analysis of modern humans, our ancestors who lived in Africa thousands of years ago got it on with early hominin species that weren't Homo sapiens. Possibility that interbreeding wasn't just a random occurrence — but the *norm*.

- In July, Gokcumen et al.: a protein in the saliva of people from sub-Saharan Africa indicates that they carry genetic evidence of an unknown hominin ancestor.

H. Sapiens and ghost species

- Study compared saliva proteins of primates and humans. Typically, these proteins look very similar. That's why it was startling when they discovered that one protein from the sub-Saharan African population was revealed to be very different in size than the others
- This protein, known as MUC7, is thought to be the result of genetic material left over from mating between *Homo sapiens* and a 'ghost' species as recently as 150,000 years ago.
- Gokcumen believes this mysterious species was confined to Africa and split from *Homo sapiens*' evolutionary path around three million years ago.
- This study is further proof that we, in Gokcumen's polite words, "absorbed different populations that lived around us"

H. Sapiens and ghost species

- There's observable evidence that other, smaller populations made their way into our modern human gene pool.

- This unknown human relative could be a species that has been discovered, such as a subspecies of *Homo erectus*, or an undiscovered hominin.

- Compared them to equivalent MUC7 genes in Ns and Ds— they found that *those* genes more closely matched the genetics of modern humans than the Sub-Saharan version

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