The Paleoarcheology of Eastern Asia
Pt. 1

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2025

CJV Commentary

- I have had my suspicions about the accuracy of Chinese hominin fossil interpretation, starting with Chinese researchers original and persistent Multiregionalist adherence (claiming that MHs arose from H. erectus in China, not Africa).
- Lack of Western access to Chinese fossils (won’t allow export; fear of black market in fossils; cultural heritage issues)
- My views may need the decolonization that is going on in paleontology!

CJV

- In 2021, Chinese researchers suggest the Denisovans were members of *Homo longi.*

- In 2024, paleoanthropologists Christopher Bae and Xiujie Wu designated the (Sh) Xujiayao hominin fossils as the holotype of the species *Homo juluensis*, and sank Denisovans into this species.

- Hoped the new book by Christopher Bea would dissuade my caution.

Warnings

- All the 94 pictures in the book are presented here; I have an additional 225 pictures. Have removed thousands of citations. Almost every finding is cited in Bea’s book. See his book if you want citation.

- This book contains a massive number of Chinese names. I apologize beforehand for slaughtering their pronunciations.

- **Q:** "ch" like in "cheese"
- **X:** "sh" like in "sheep"
- **Zh:** s "j" like in "job"
- **C:** "ts" like in "tsar"

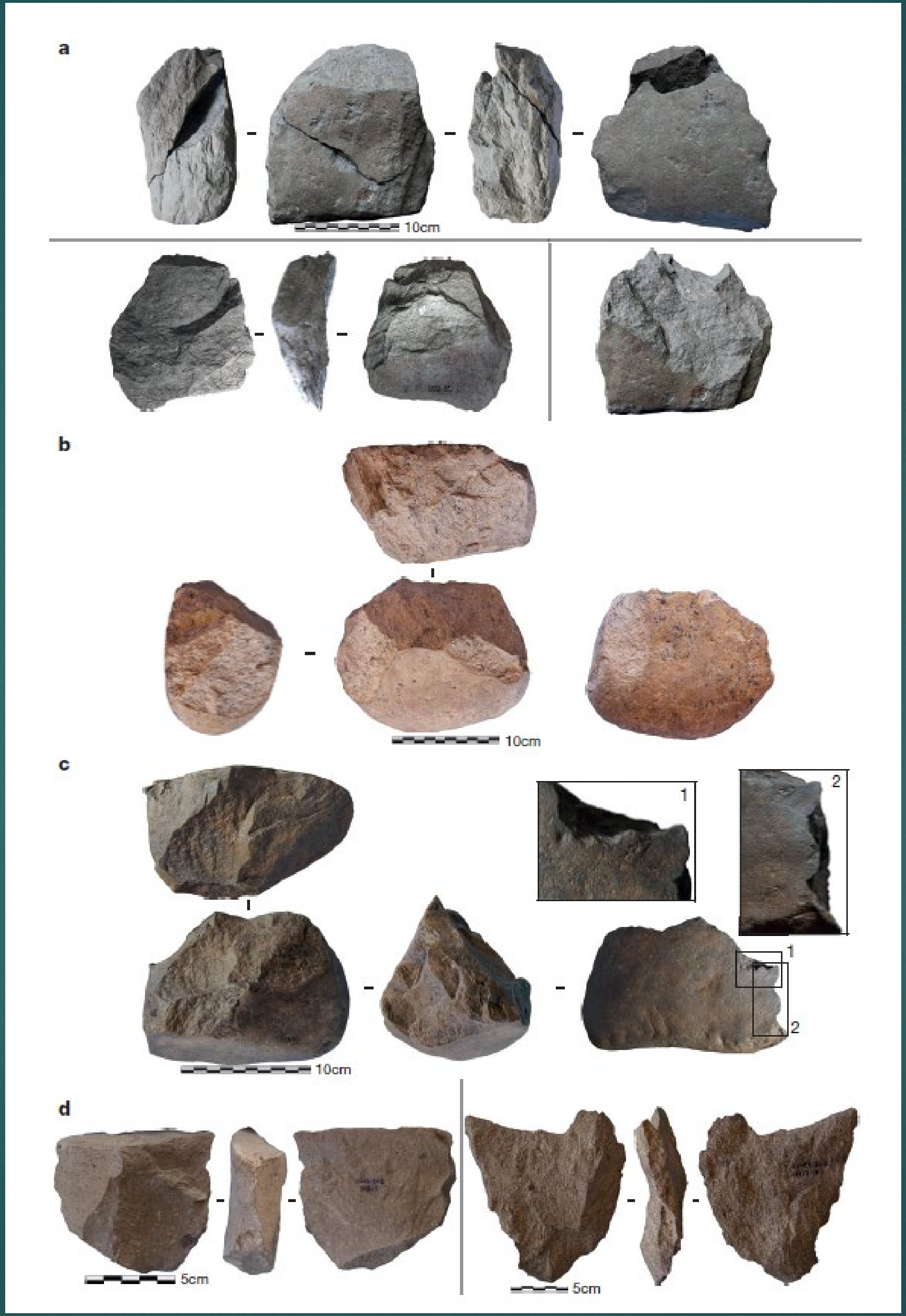
Prelude

- **CJV**: Before starting the summary of Bea’s book, I will be giving the state of Asian research before the book was published based on two recent reviews.
- This info can give a contextual background for interpreting Bea’s conclusions.

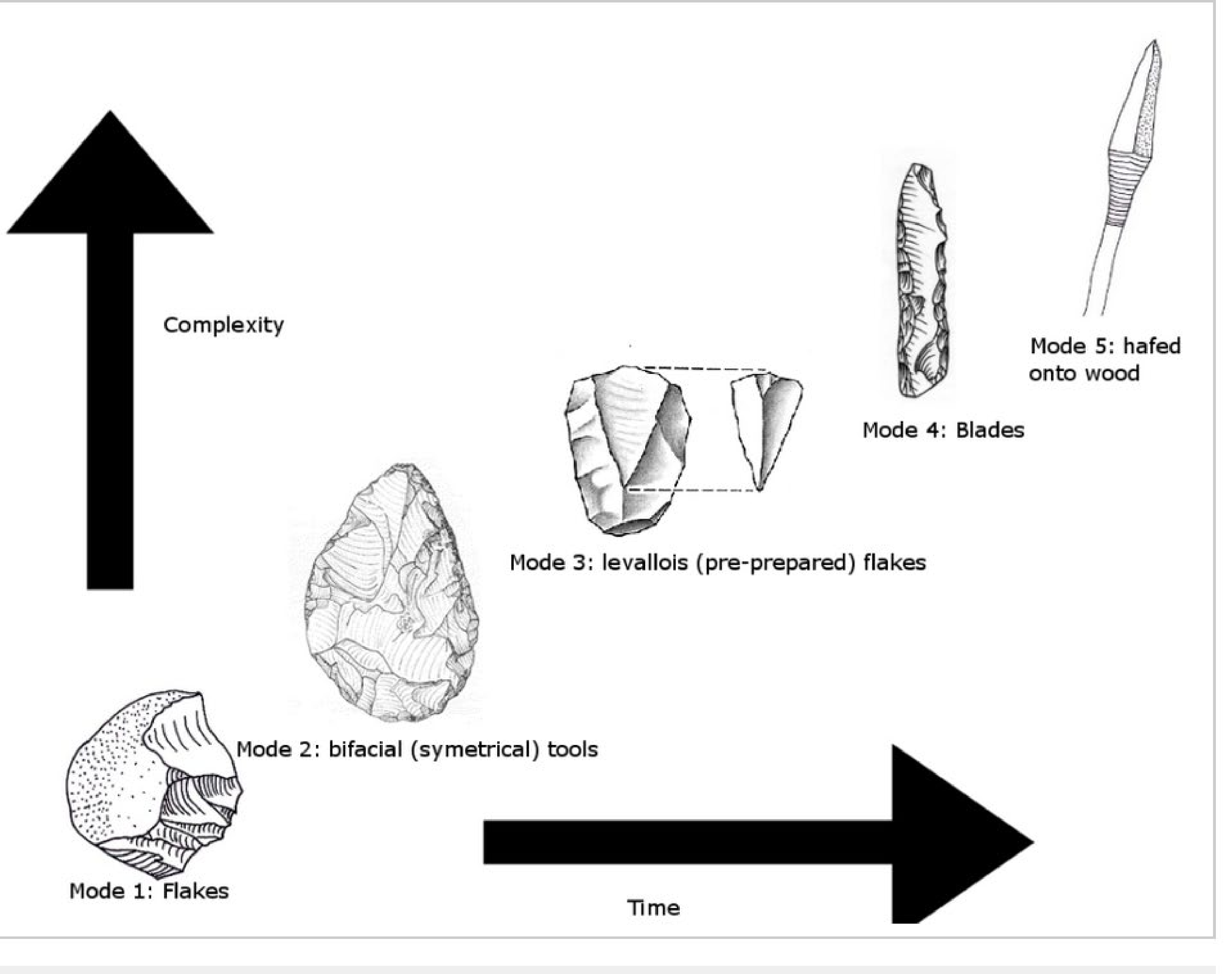
History of lithics and hominin associates

- Oldest African stone tools: 3.3 Ma, Lomekwi; predate Homo species; Australopithecus afarensis, Kenyanthropus platyops,
- Mode 1 (Oldowan) (2.9 to 1.6 Ma): Simple pebble tools and flake tools. Associated with H. habilis, P. boisei, Australopithecus garhi
- Mode 2 (Acheulean) (1.75 Ma): Marked by the development of large, bifacially worked tools, most famously the handaxe. Associated with H. erectus
- Mode 3 (Mousterian): (335 Ka): Known for the use of prepared-core technology, including the Levallois technique. Associated with Neandertals
- Lithics are used to identify which species was at a location

Lomekwi, West Turkana, 3.3 Ma Unknown hominin



Modes 1 to 5


Complexity
Mode 5: hafed onto wood
Mode 4: Blades
Mode 3: levallois (pre-prepared) flakes
Mode 2: bifacial (symetrical) tools
Mode 1: Flakes
Time

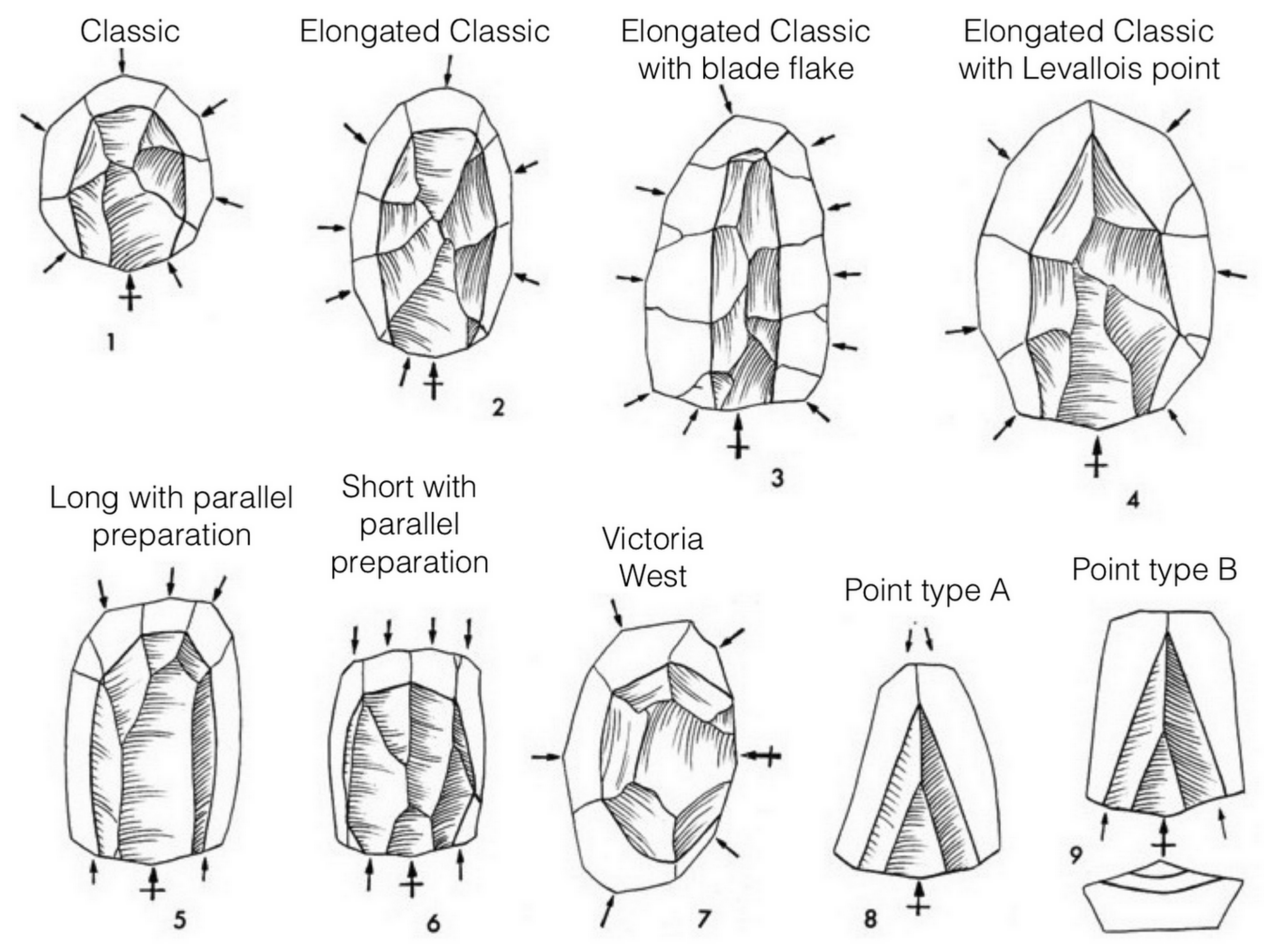
Mode 1, 2, 3

Mode 1
Oldowan

Mode 2
Acheulean

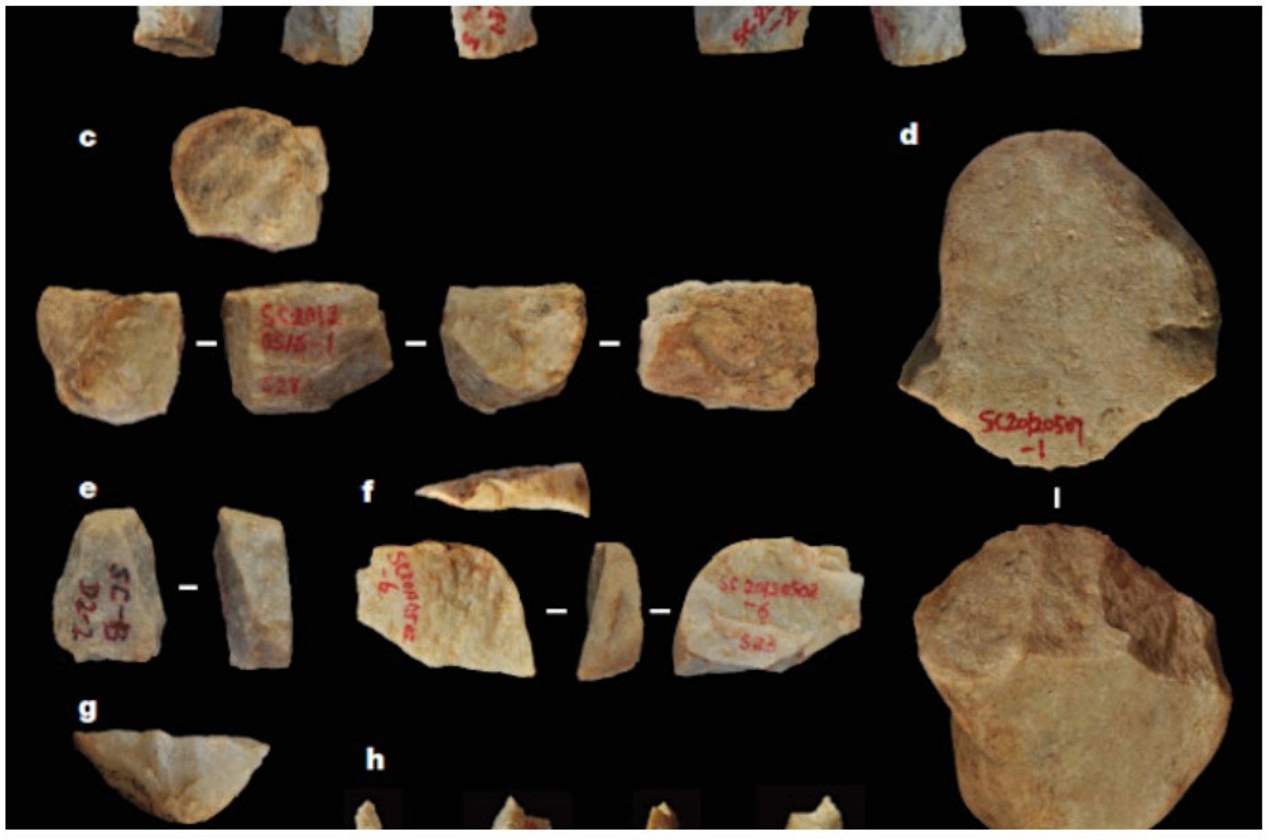
Mode 3
Middle Stone Age

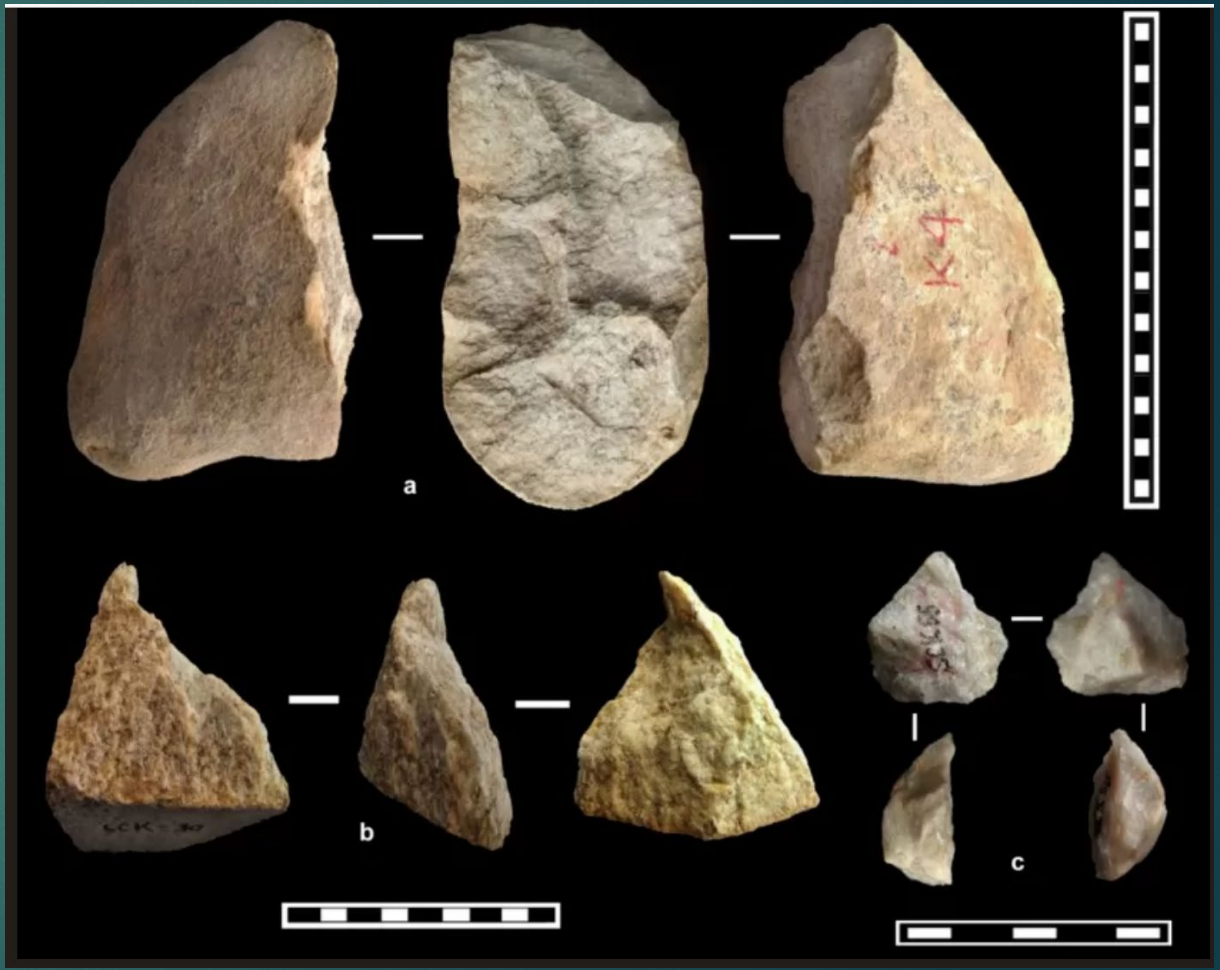
Levallois


Classic
1
Elongated Classic
2
Elongated Classic with blade flake
3
Elongated Classic with Levallois point
4
Long with parallel preparation
5
Short with parallel preparation
6
Victoria West
7
Point type A
8
Point type B
9

Original asymmetric scrappers from La Quina

What stone tradition? Shangchen, 2.1 Ma





What stone tradition?

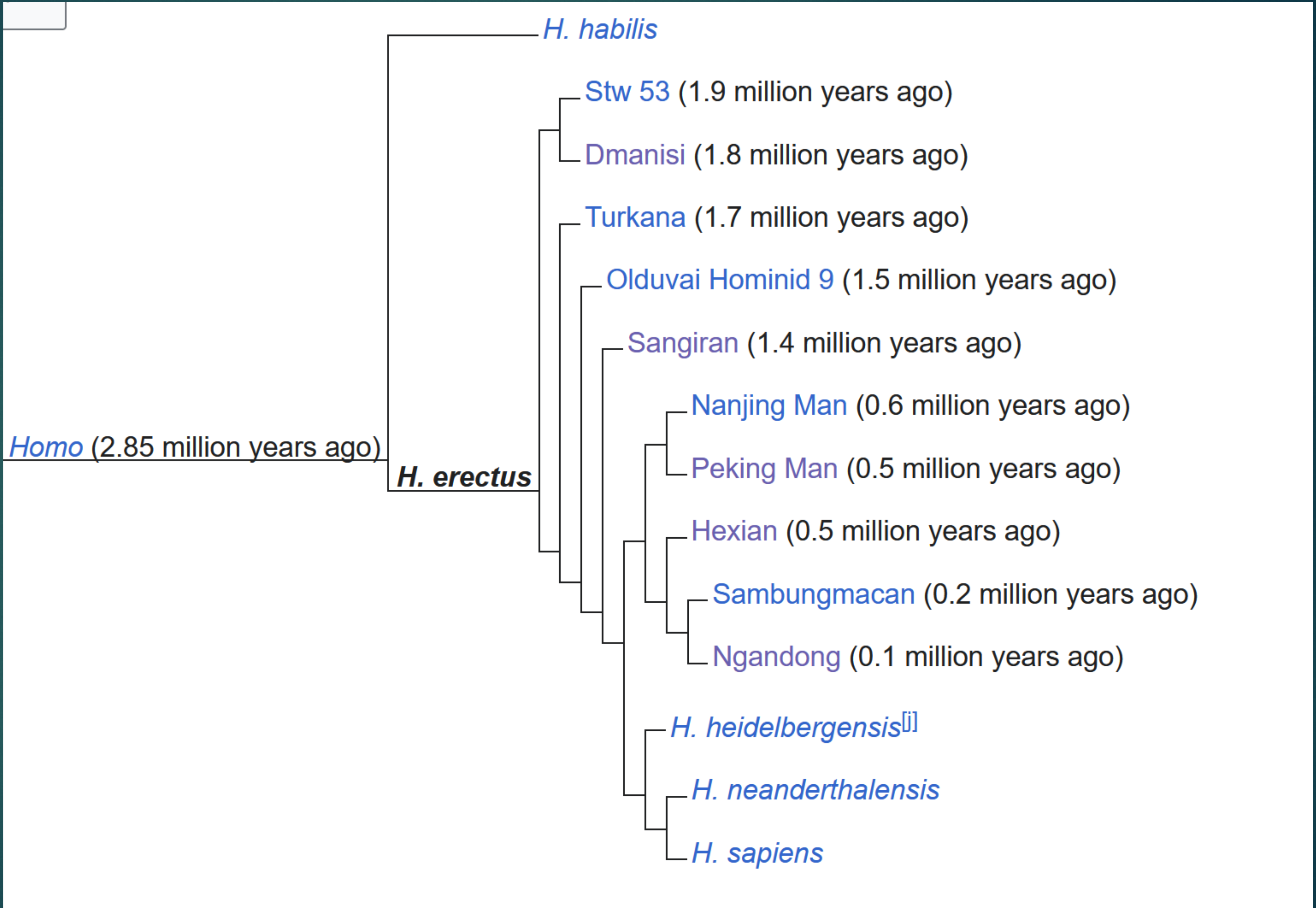
Xihoudu, 2.43 Ma

Lack of aDNA or proteomics of Chinese archaic H. sapiens

- Significant issue: lack of aDNA or protein analysis of major Asian skull species.

- Almost no aDNA of archaic H. sapiens fossils in China:
    - aDNA only from 2 fossils: Tianyuan man, Salkhit woman;
    - None of the major skulls (i.e. not from Maba, Dali, Longi, Juluensis)

Cast of characters



H. habilis

Stw 53 (1.9 million years ago)

Dmanisi (1.8 million years ago)

Turkana (1.7 million years ago)

Olduvai Hominid 9 (1.5 million years ago)

Sangiran (1.4 million years ago)

Nanjing Man (0.6 million years ago)

Peking Man (0.5 million years ago)

Hexian (0.5 million years ago)

Sambungmacan (0.2 million years ago)

Ngandong (0.1 million years ago)

H. heidelbergensis[j]

H. neanderthalensis

H. sapiens

Homo (2.85 million years ago)

H. erectus

Dating of earliest hominin discoveries relative to human origins debate

- 1 – 1856: H. neanderthalensis, Neander Valley (although 2 prior unrecognized N discoveries (Gibraltar 1 – 1848; Engis 2 – 1829)
- 2 – 1891: Java Man, H. erectus, Trinil
- 3 – 1921: Peking Man: H. erectus
- 4 - 1925: Taung child, A. africanus, S. Africa vs. "Eoanthropus dawsoni“, 1912
- 5 – 1936: Mojokerto Child, H. erectus, Indonesia
- 6 - 1959: Paranthropus boisei, Olduvai Gorge - Zinjanthropus
- 7 - 1960: Homo habilis (OH7), Olduvai Gorge
- 8 - 1964: Turkana Boy, H. erectus, Kenya
- 9 - 1972: H. rudolfensis, Kenya
- 10 -2001: Dmanisi, H. erectus?, Georgia
- 11 – 2024: H. juluensis, China

Role of racism in human origins debate

- We now accept that race is not a biological concept, but is a social construct. There are no superior races.
- The religiously based Great Chain of Being, with God at top of the ladder, and the white race just below, was clearly racist.
- Previously racist scientific theories existed.
- Racial divisions of human geographic populations
- Polygenist Racial Schemes: Johann Friedrich Blumenbach, craniometry, Louis Agassiz, Charles Pickering, Aryanism, Thomas Huxley, Paul Broca, Nazism, Carlton Coon, phrenology, eugenics, early anthropology
- The post WWII exposition of Nazi racial theories, which culminated in the Final Solution and Nazi history of genocide, created a moral revolution against racism after 1945. Culminated in UNESCO refutation of racism.

Early Chinese paleontology: CJV analysis

- The Multiregional hypothesis was first conceptualized by Franz Weidenreich in his work in 1930s in China.
- Other proponents of MR: Milford H. Wolpoff, Alan Thorne and Xinzhi (Shinji) Wu. Leading theory in 1950s by almost all paleontologists.
- Chris Stringer originated the more mainstream recent African origin theory (Out of Africa).

Multiregionalism

- In Chinese paleontology, "multiregionalism" refers to the theory that modern humans in East Asia evolved largely in situ/place from earlier hominin populations like "Peking Man" (Homo erectus pekinensis), with continuous gene flow from other regions, rather than solely originating in Africa and completely replacing existing populations - a concept <u>strongly supported by many Chinese paleontologists due to the rich fossil record found within China</u>

- Most now favor “Continuity with Hybridization”

Out of Africa

- The origin of humans in Africa was famously proposed in the 19th century by Charles Darwin. Based on the presence of chimpanzees and gorillas in Africa and on Huxley’s comparative anatomy studies that showed that modern humans and apes shared a common ancestor, Darwin argued that the ancestors of modern humans arose on African soil.
- The debate dominating much of the anthropological discourse throughout the second half of the 20th century focused on where and when archaic hominins evolved into modern Homo sapiens.
- Two main hypotheses dominated the discourse: the multiregional and the replacement hypotheses

Candelabra Versus Replacement Hypothesis

- The original multiregional model was proposed by the anthropologist Franz Weidenreich in 1946 and advocated significant gene flow among subpopulations of Homo erectus living in different parts of the globe throughout the Pleistocene, so that modern humans trace their ancestry to multiple hominin groups living in multiple regions.
- Confusingly, the term "multiregional" model often has been used synonymously with the so-called candelabra model, originally proposed by Carlton Coon in 1962. The latter theory was clearly racist.

Candelabra model

- The candelabra model hypothesizes that our early hominin ancestors, after leaving Africa 1 million years ago and migrating to other continents, independently evolved anatomically modern features.

- Under this model, the modern human form arose autonomously at multiple times and locations worldwide within the last 1 million years, so that modern non-African populations each primarily descended from separate evolutions of these Homo species. With no gene flow between groups.

- This is in contrast to the traditionally proposed multiregional model, which importantly does not propose independent parallel evolution of AMH features. Allows for gene flow.

Candelabra theory

- Candelabra theory assumes minimal gene flow: It assumes limited or no gene flow between these regional populations as they evolved separately.

- Essentially, modern humans in different parts of the world would have different, independent origins from their respective archaic Homo populations.

Evidence for MR theory

- The main fossil evidence in support of the multiregional hypotheses was the discovery of the Dali Man in China. For multiregionalists, the mixture of archaic and modern features was evidence of a midway stage between early and modern hominins

- Some genetic studies also offered support to a multiregional, inferring the origin of a few genetic loci outside of the African continent. Examples include the oldest haplotype in the human dystrophin gene, which was found to be absent in Africans, although this was later explained as resulting from adaptive introgression from Neanderthals rather than providing support for the candelabra model.

OoA model

- Opposition to the candelabra hypothesis has come from both paleontological and genetic studies.
- The replacement, or out of Africa (OoA), model proposes a single and relatively recent transition from archaic hominins to AMH in Africa, followed by a later migration to the rest of the world, replacing other extant hominin populations.
- Under this model, these hominins were driven to extinction, so that most of the genetic diversity in contemporary populations descends from a single or multiple groups of AMH who spread out of Africa sometime in the last 55–200 kya, although debate remains on the precise timings.

OoA genetic evidence

- The first genetic evidence consistent with the OoA model was provided by the study of mitochondrial DNA (mtDNA) phylogenetic trees, which identified Africa as the source of human mtDNA gene pool.

- It was shown that all mtDNA haplogroups outside of Africa can be attributed to either the M or N haplogroups, which arose around 60–65 kya in South Asia and are thought to descend from the L3 haplogroup postulated to have arisen in East Africa around 80 kya.

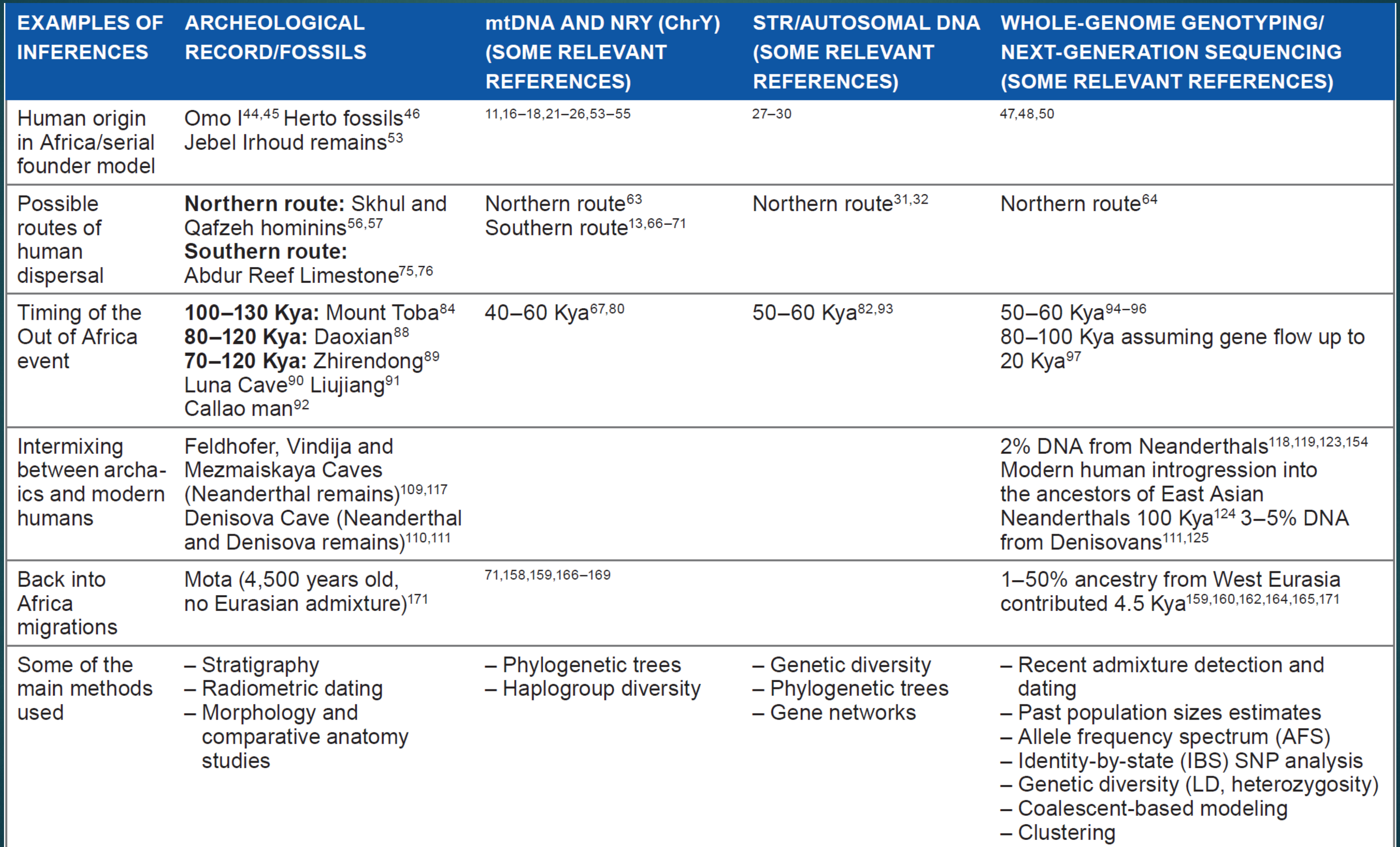
More evidence

- This was supported by further studies of mtDNA, Y chromosome, and autosomal regions that suggested the existence of a common African ancestor.

- More recently, multilocus studies of genome-wide data have demonstrated that genetic diversity decreases as a function of geographic distance from East or South Africa, for example, as shown by an approximately linear decrease in heterozygosity and increase in linkage disequilibrium (LD), a finding consistent with the OoA model.

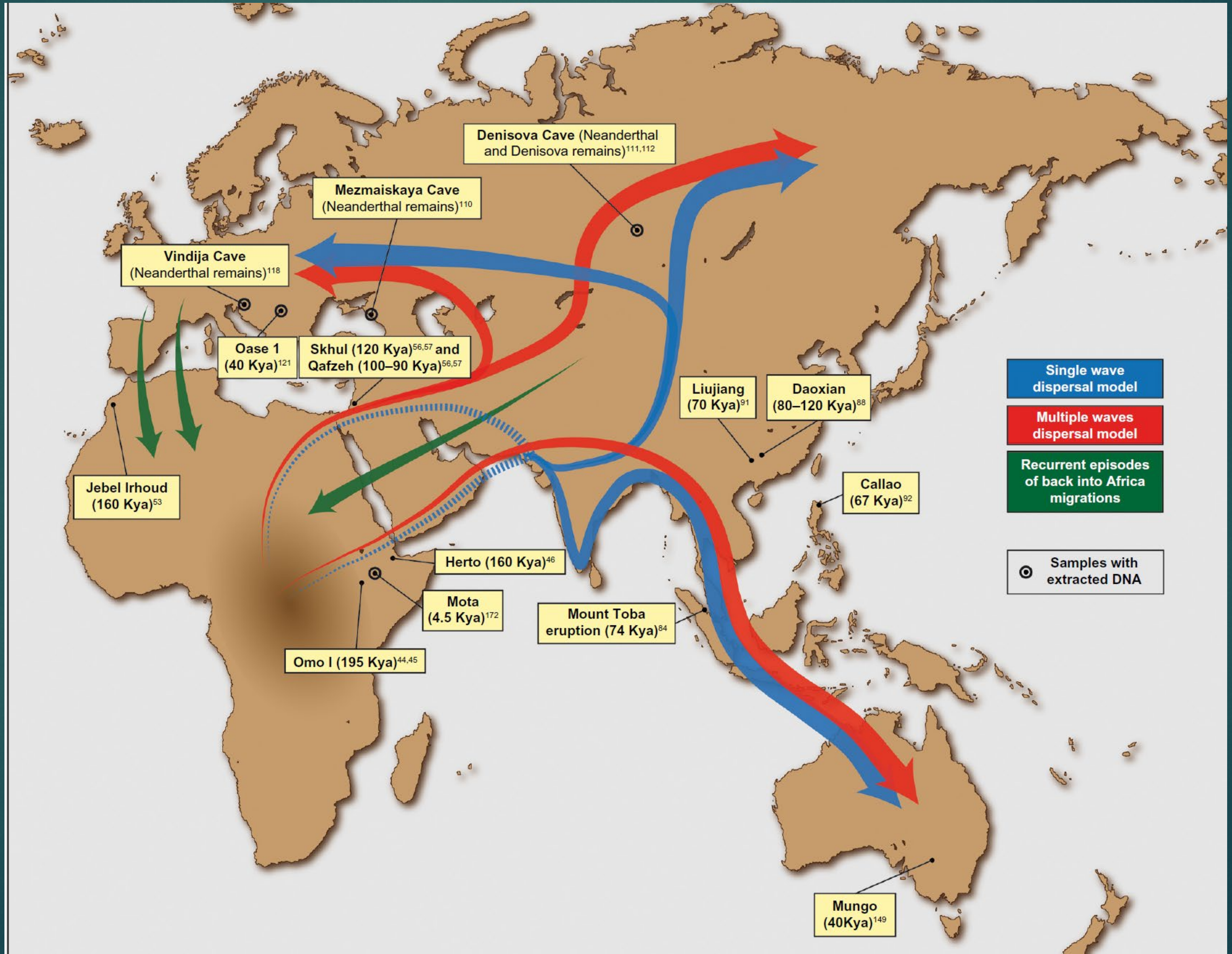
- Although the African origin of AMH is now largely accepted, debate has continued over whether the anatomically modern form first arose in East, South, or North Africa.

Most relevant studies related to the out of Africa event



EXAMPLES OF INFERENCES	ARCHEOLOGICAL RECORD/FOSSILS	mtDNA AND NRY (ChrY) (SOME RELEVANT REFERENCES)	STR/AUTOSOMAL DNA (SOME RELEVANT REFERENCES)	WHOLE-GENOME GENOTYPING/ NEXT-GENERATION SEQUENCING (SOME RELEVANT REFERENCES)
Human origin in Africa/serial founder model	Omo I[44,45] Herto fossils[46] Jebel Irhoud remains[53]	11,16–18,21–26,53–55	27–30	47,48,50
Possible routes of human dispersal	**Northern route:** Skhul and Qafzeh hominins[56,57] **Southern route:** Abdur Reef Limestone[75,76]	Northern route[63] Southern route[13,66–71]	Northern route[31,32]	Northern route[64]
Timing of the Out of Africa event	**100–130 Kya:** Mount Toba[84] **80–120 Kya:** Daoxian[88] **70–120 Kya:** Zhirendong[89] Luna Cave[90] Liujiang[91] Callao man[92]	40–60 Kya[67,80]	50–60 Kya[82,93]	50–60 Kya[94–96] 80–100 Kya assuming gene flow up to 20 Kya[97]
Intermixing between archaics and modern humans	Feldhofer, Vindija and Mezmaiskaya Caves (Neanderthal remains)[109,117] Denisova Cave (Neanderthal and Denisova remains)[110,111]			2% DNA from Neanderthals[118,119,123,154] Modern human introgression into the ancestors of East Asian Neanderthals 100 Kya[124] 3–5% DNA from Denisovans[111,125]
Back into Africa migrations	Mota (4,500 years old, no Eurasian admixture)[171]	71,158,159,166–169		1–50% ancestry from West Eurasia contributed 4.5 Kya[159,160,162,164,165,171]
Some of the main methods used	– Stratigraphy – Radiometric dating – Morphology and comparative anatomy studies	– Phylogenetic trees – Haplogroup diversity	– Genetic diversity – Phylogenetic trees – Gene networks	– Recent admixture detection and dating – Past population sizes estimates – Allele frequency spectrum (AFS) – Identity-by-state (IBS) SNP analysis – Genetic diversity (LD, heterozygosity) – Coalescent-based modeling – Clustering

Putative migration waves out of Africa and location of some of the most relevant ancient human remains and archeological sites.

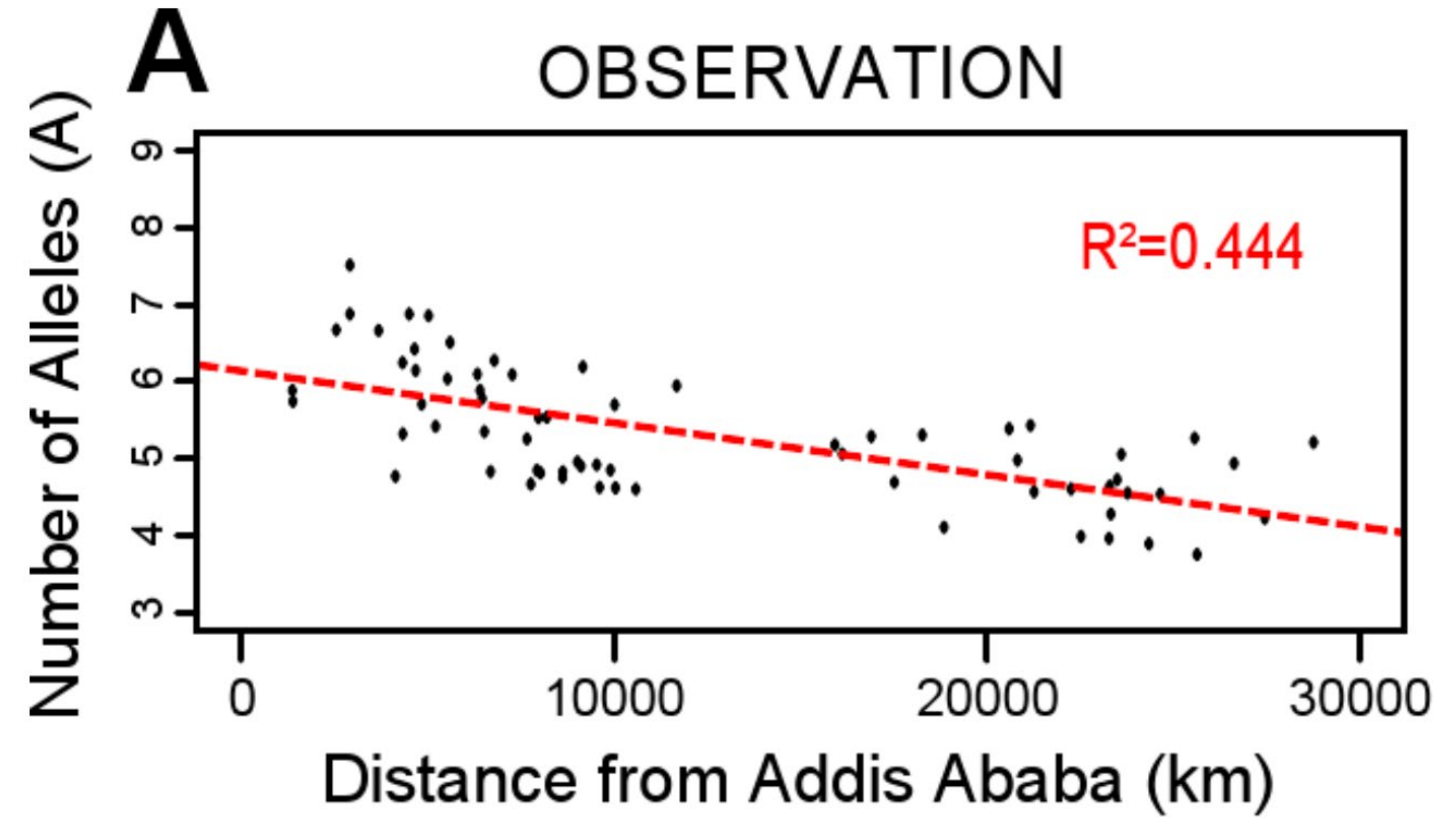


Africa is motherland

- According to a 2000 study of Y-chromosome sequence variation, human Y-chromosomes trace ancestry to Africa, and the descendants of the derived lineage left Africa and eventually were replaced by archaic human Y-chromosomes in Eurasia.

- The study also shows that a minority of contemporary populations in East Africa and the Khoisan are the descendants of the most ancestral patrilineages of anatomically modern humans that left Africa 35,000 to 89,000 years ago.

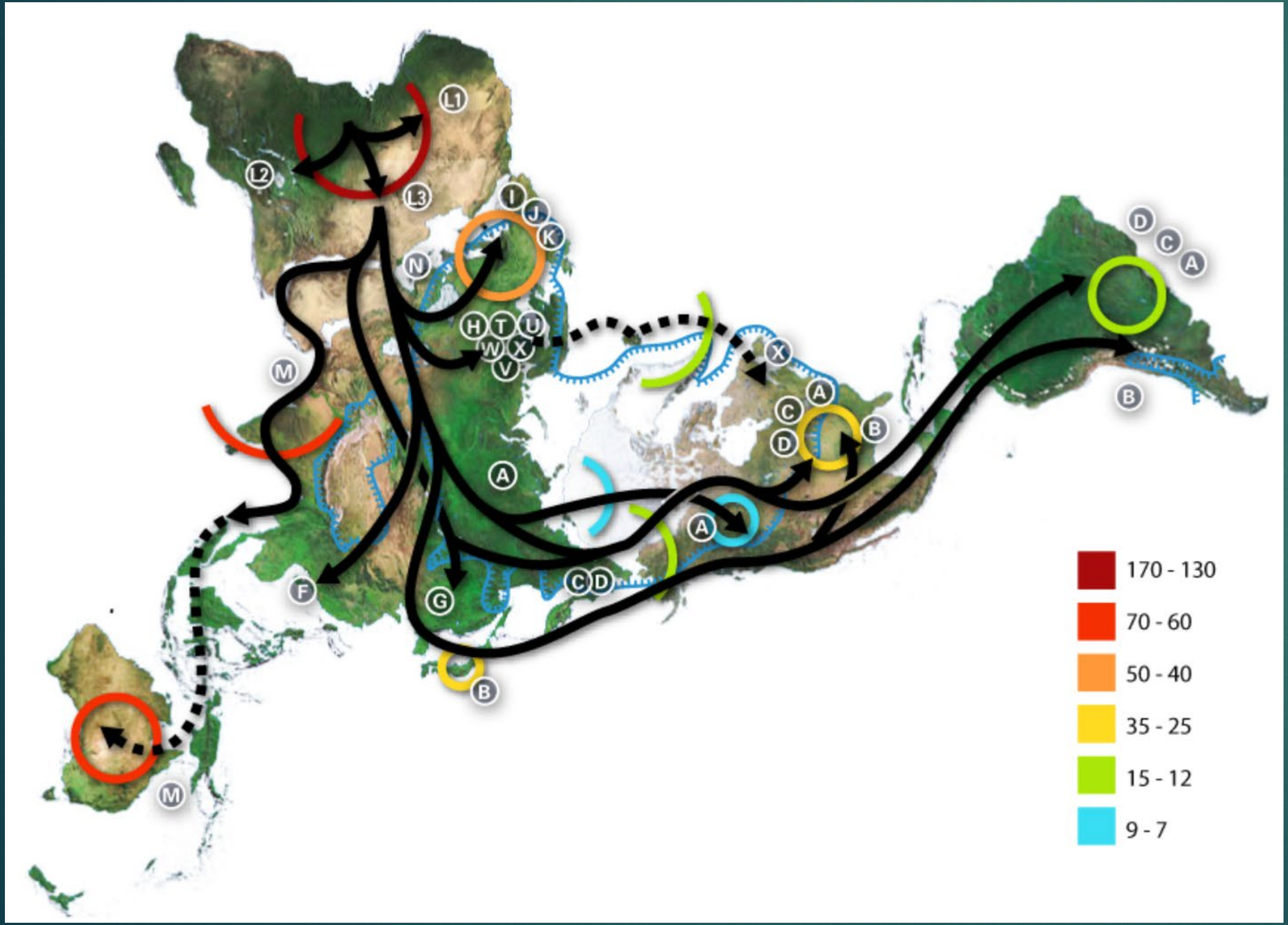
As populations are further from East Africa (represented by the city of Addis Ababa), they have declining genetic diversity as measured in average number of microsatellite repeats at each of the loci.



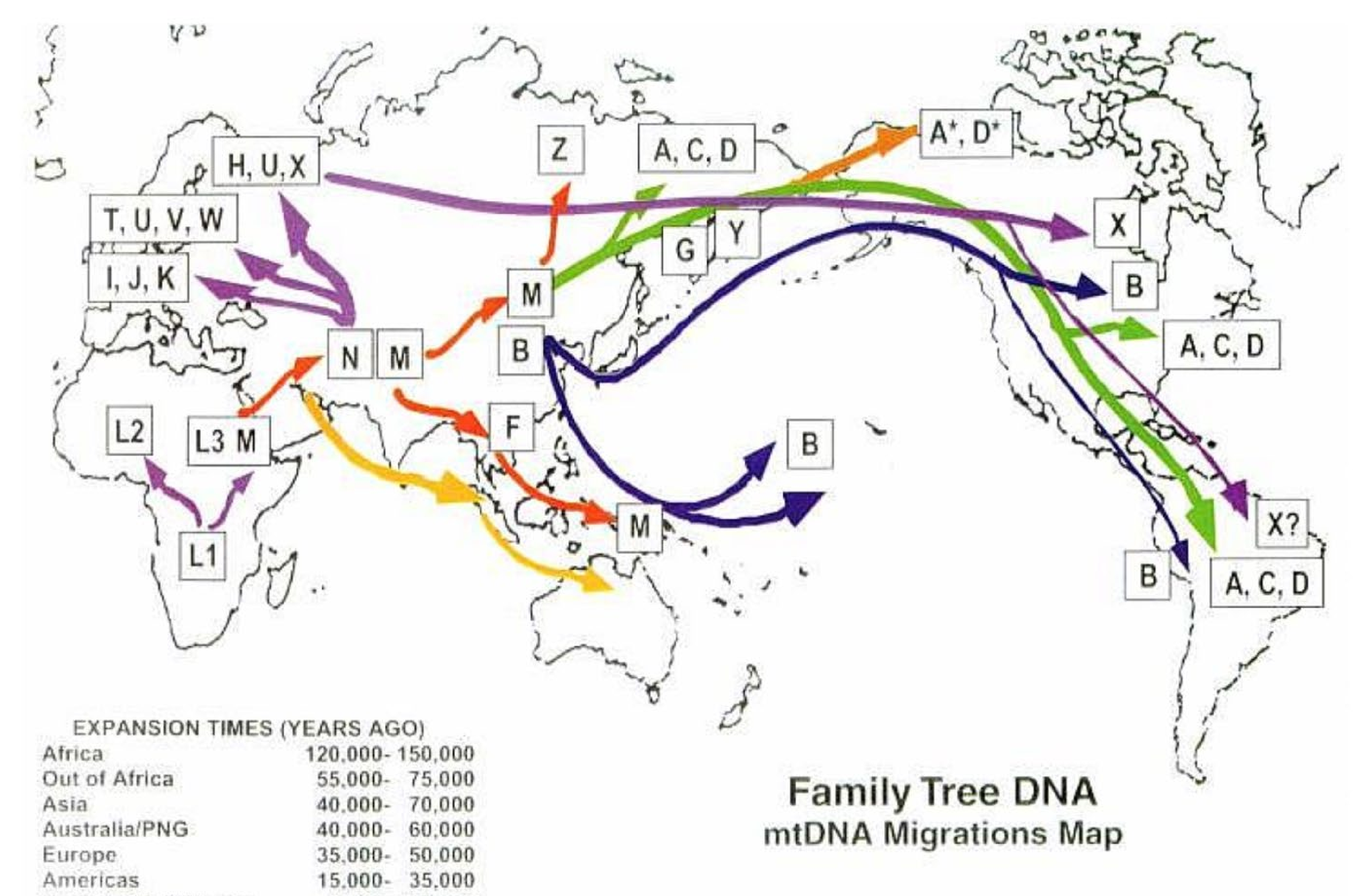
Other evidence

- Other evidence supporting the theory is that variations in skull measurements decrease with distance from Africa at the same rate as the decrease in genetic diversity.
- Human genetic diversity decreases in native populations with migratory distance from Africa, and this is thought to be due to founder effect bottlenecks during human migration, which are events that temporarily reduce population size.

Map of the migration of modern humans out of Africa, based on mitochondrial DNA. Colored rings indicate thousand years before present



The hypothetical woman at the root of all these groups (meaning just the mitochondrial DNA haplogroups; she is Haplotype L) is the matrilineal most recent common ancestor (MRCA) for all currently living humans. She is commonly called Mitochondrial Eve.



EXPANSION TIMES (YEARS AGO)

Africa	120,000- 150,000
Out of Africa	55,000- 75,000
Asia	40,000- 70,000
Australia/PNG	40,000- 60,000
Europe	35,000- 50,000
Americas	15,000- 35,000
Na-Dene/Esk/Aleuts	8,000- 10,000

Family Tree DNA
mtDNA Migrations Map

Mitochondrial DNA in Asia

- Most common mitochondrial DNA haplogroup in China is Haplogroup D, particularly the D4 subclade, which is prevalent across many regions of the country, especially in the Han Chinese population. (Also in Native Americans)
- Haplogroup B is believed to have arisen in Asia some 50,000 years before present.

Haplogroups

- The greatest variety of haplogroup B is in China. It is therefore likely that it underwent its earliest diversification in mainland East or South East Asia.
- Basal B was found in Upper Paleolithic Tianyuan man.
- Haplogroup B is now most common among populations native to Southeast Asia, as well as speakers of Sino-Tibetan languages and Austronesian languages.

Route out of Africa

- One of the most intriguing questions regarding the exit of modern humans out of Africa is which geographical route was taken.

- The consensus view is that if modern humans did exit Africa via a single dispersal, there were two possible routes (not mutually exclusive) at the time:
  - a Northern route, through Egypt and Sinai, and
  - a Southern route, through Ethiopia, the Bab el Mandeb strait, and the Arabian Peninsula.
- So far, neither archeological nor genetic evidence has been able to resolve this question with confidence.

Date of Exit

- Another key debate has focused on the precise timing of the exit of the first humans out of Africa. Currently, there are two conflicting proposals that dominate the literature, each differing by several tens of thousands of years and not mutually exclusive.
- The first claims that the Eurasian dispersal took place around 50–60 kya, reaching Australia by 45–50 kya. (Now 65 Ka)
- The second posits that there was a much earlier exodus around 100–130 kya, prior to the eruption of Mount Toba (Northern Sumatra) dated to 74 kya.

Routes

- The stone tools discovered in the archeological site Jebel Faya (present-day United Arab Emirates) and the Nubian complex of Dhofar (present-day Oman) have provided further support for an early migration via Arabia.
- More importantly, the recent discovery of 47 human teeth in the Fuyan Cave in Daoxian (Southern China), dated to 80–120 kya and unequivocally assigned to modern humans, supports the dispersal of AMH throughout Asia during the early Late Pleistocene.

Archeological evidence: AMH in East

- Other pieces of archeological evidence that may help place AMH in the Far East over 70–120 kya are
- the human remains from Zhirendong (South China),
- the teeth from Late Pleistocene Luna Cave,
- the famous Southern Chinese Liujiang skeleton, which seems to have anatomically modern features, and
- the Callao man, a human foot bone, discovered in Philippines that dates to 67 kya

Intermixing with Ns and Ds

- On their migration out of Africa, AMH were not alone, with at least two distinct groups of archaic humans inhabiting Eurasia on their arrival: the Neanderthals and Denisovans.

- Traditionally, the replacement or the OoA model assumed no intermixing between AMH leaving Africa and archaic hominins such as the Neanderthals.

- The revised replacement model, however, allows for gene flow with these archaic forms following the OoA dispersal, which is also consistent with the original multiregional model proposed by Weidenreich but still differs from the candelabra model.

Back to Africa

- Another major difficulty in using DNA from modern individuals to the study of OoA migrations is the high proportion of non-African ancestry in modern-day Africans.
- The first indicators of what is termed the “back to Africa” migrations were obtained from phylogeny and phylogeography of mtDNA haplogroups U6 and M1, which have an origin outside Africa and are currently largely distributed within North and East Africa.

Back to Africa

- There is now robust evidence for recent migrations back to Africa from non-African populations, as exemplified by high levels of non-African ancestry in present-day Horn of Africa (Ethiopia, Eritrea, Djbouti, and Somalia) and Southern Africa, where Eurasian ancestry proportions can be as high as 40%–50% in, for example, some Ethiopian populations.
- What is less clear, however, is both the number and the timing of these migrations, as there seems to be a lack of consensus among archeological, mtDNA, Y chromosome, and genomic studies.

**(Ch) Qiaomei Fu, 2013 Leipzig PhD = major Chinese geneticist

- (Ch) Dr. Qiaomei Fu: She is currently a full professor and doctoral supervisor at the Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences.

- Since 2018, has served as the deputy director of the Key Laboratory of Vertebrate Evolution and Human Origins of the Chinese Academy of Sciences.

- Her studies acquired: the first Denisovan DNA in East Asia from the sediments (“soil”) of the Tibetan Plateau, decoded the earliest modern human genome in East Asia, mapped the dynamic genetic history of early populations in China over the past 40,000 years, and proposed the selective mechanisms for East Asian-specific adaptive genes.

Continuity with hybridization

- A specific model within the multiregional framework often discussed by Chinese scientists is "Continuity with Hybridization," proposed by paleontologist Wu (Chinji) Xinzhi, which emphasizes the idea that modern humans in China evolved from local populations with some gene flow from outside regions

- Data vs MR theory:
  - Mitochondrial Eve,
  - Earliest fossils are in Africa;
  - The highest genetic diversity lies in African populations and decreasing genetic diversity further from Africa

1990s models by Aiello and Stringer

- (i) Multiregionalism denies a recent African origin for modern humans. It emphasizes the role of both genetic continuity over time and gene flow between contemporaneous populations in arguing that modern humans arose not only in Africa, but also in Europe and Asia from their Middle Pleistocene forebears. The multi-regional theory suggests that modern humans in different parts of the world evolved in different places from different populations of *Homo erectus*

- (ii) The original Recent African Origin (RAO) model argues that modern humans first arose in Africa approximately 100,000 years ago and spread from there throughout the world. Indigenous premodern populations in other areas of the world were replaced by the migrating populations, with little, if any, hybridization between the groups

1990s models

- (iii) The RAO and hybridization model is similar to the above, but allows for a greater extent of hybridization between the migrating population and the indigenous premodern populations

- (iv) The assimilation model also accepts an African origin for modern humans. However, it differs from the previous models in denying replacement, or population migration, as a major process in the appearance of modern humans. Instead, this model emphasizes the importance of gene flow, admixture, changing selection pressures, and resulting directional morphological change

History

- As recently as 1970, no paleoanthropologist that Chris Stringer was aware held the view that Africa was the evolutionary home of modern humans (as distinct from more ancient species, such as *Homo habilis* or *Homo erectus*).
- Most were multiregionalists. Or N-stage of MHs model
- Some researchers (incl. Stringer, Howells, Hublin) began to focus on Africa as the possible homeland of modern humans.

History

- By the early 1990s, the pendulum was moving in favor of Recent African Origin because fossil evidence began to be increasingly reinforced by the clear signals of mtDNA and Y-DNA in recent human samples.

- By the late 1990s, the pendulum had swung even further toward a pure RAO, with growing fossil, archaeological, and genetic data supporting this model

History

- Then came the aDNA revolution in 2010 indicating genetic introgression into MHs; reversed the pendulum swing, away from an absolute RAO.
- Now looking at a version of RAO that most closely resembles Bräuer's early formulation (out of Africa + hybridization), or perhaps a version of the assimilation model of Smith and Trinkaus, with a strong African predominance.
- If the evidence for archaic assimilation in living humans remains modest and is restricted to Africa and to the dispersal phase of modern humans from Africa, constituting less than 10% of our genome, Stringer thinks 'mostly out of Africa' is the appropriate designation.

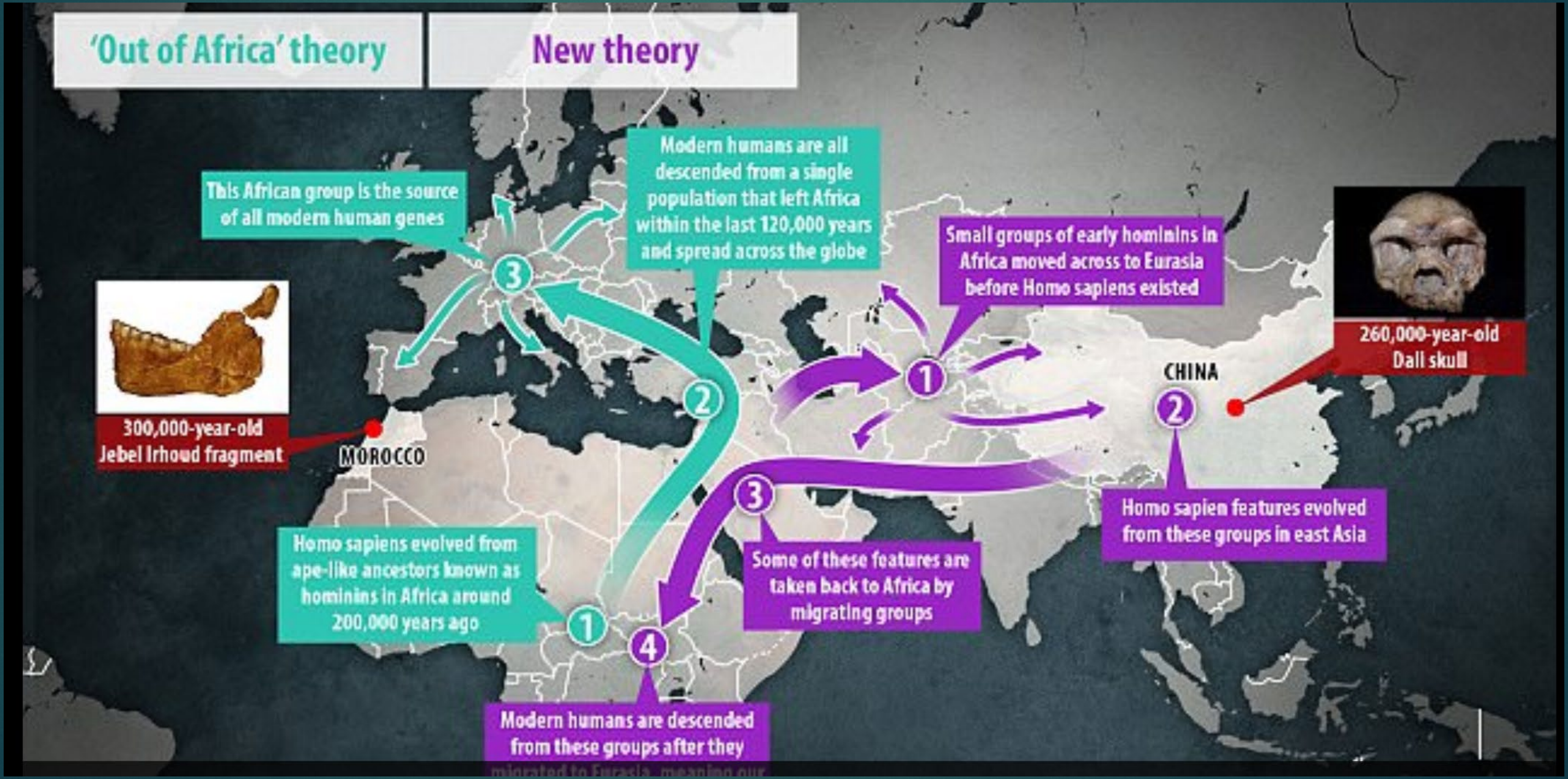
China

- Some critics argue that the strong support for multiregionalism among Chinese paleontologists might be influenced by a desire to demonstrate a long evolutionary history and indigenous origins of the modern Chinese population.

- While the "Out of Africa" hypothesis is widely accepted in the global scientific community, Chinese researchers continue to study and argue for the validity of the multiregional model based on their regional fossil evidence.

- Christopher Bae, Dept of Anthro, Univ of Hawaii: Korean professor; is the current major champion of China playing a role in the origin of modern humans.

Chinese theory (in purple) which suggests our DNA did not come solely from Africa ancestors, as researchers have previously suggested (green)



This African group is the source of all modern human genes

Modern humans are all descended from a single population that left Africa within the last 120,000 years and spread across the globe

Small groups of early hominins in Africa moved across to Eurasia before Homo sapiens existed

260,000-year-old Dali skull

300,000-year-old Jebel Irhoud fragment

Homo sapien features evolved from these groups in east Asia

Some of these features are taken back to Africa by migrating groups

Homo sapiens evolved from ape-like ancestors known as hominins in Africa around 200,000 years ago

Modern humans are descended from these groups after they migrated to Eurasia, meaning our

Chinese MR theory

Out of Africa Theory

1 Homo sapiens evolved from ape-like ancestors known as hominins in Africa around 200,000 years ago

2 Modem humans are all descended from a single population that left Africa within the last 120,000 years and spread across the globe

3 This African group Is the source of all modern human genes

- Chinese MR theory
- 1 Small groups of early hominins In Africa moved across to Eurasia before Homo sapiens existed
- 2 Homo sapiens features evolved from these groups in east Asia
- 3 Some of these features are taken back to Africa by migrating groups
- 4 Modem humans are descended from these later African groups

Chinese MR theory

- Dali skull is similar to the Jebel Irhoud H. sapiens fossil.
- This suggests modern humans aren't descended solely from African ancestors
- Instead, some early humans migrated to Eurasia before Homo sapiens existed
- Here they evolved some modern human traits, and then moved back to Africa

Chinese MR theory 2

- In Africa the Asian early humans interbred with native populations

- The intermixing eventually led to Homo sapiens, which spread around the world

- Modern human DNA therefore came from both African and Eurasian ancestors

*** Where do the Dmanisi hominins fit on the human evolutionary tree?

Debbie Argue, José María Bermúdez de Castro, Michael S. Y. Lee, Maria Martinón-Torres. 2025

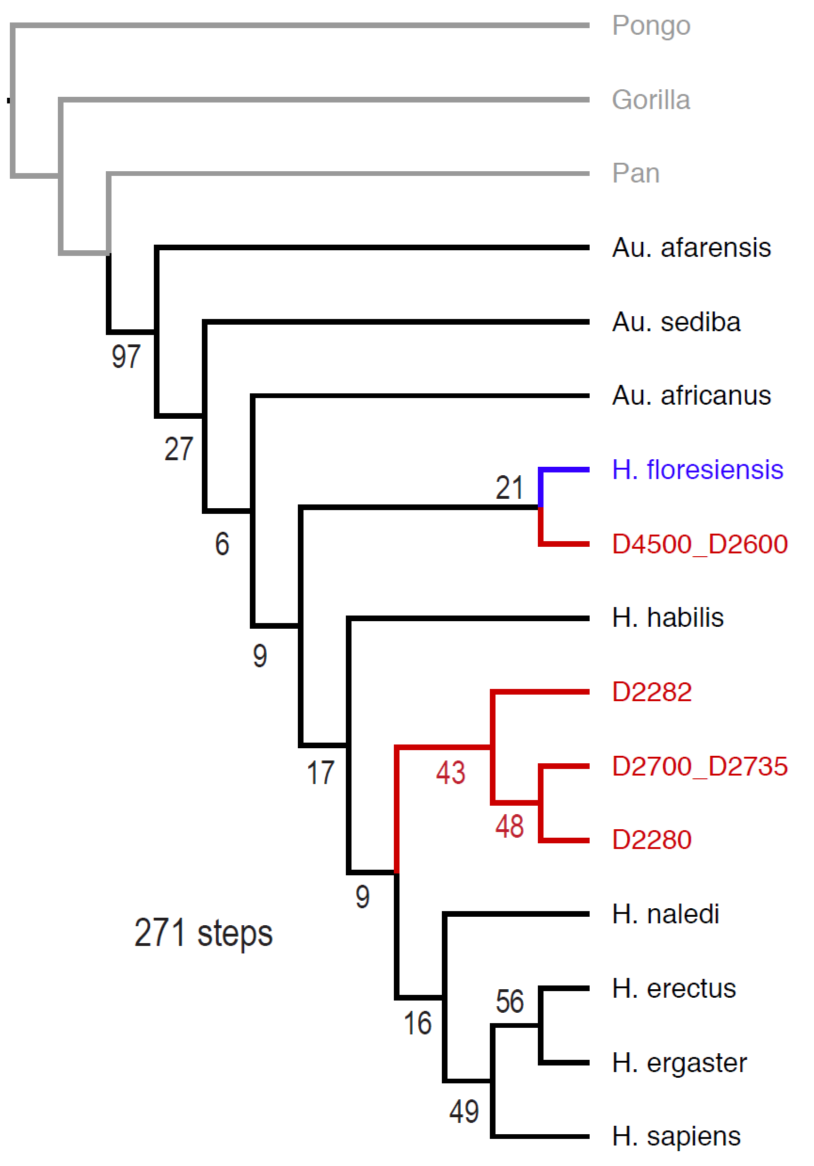
Dmanisi hominins are not H. erectus

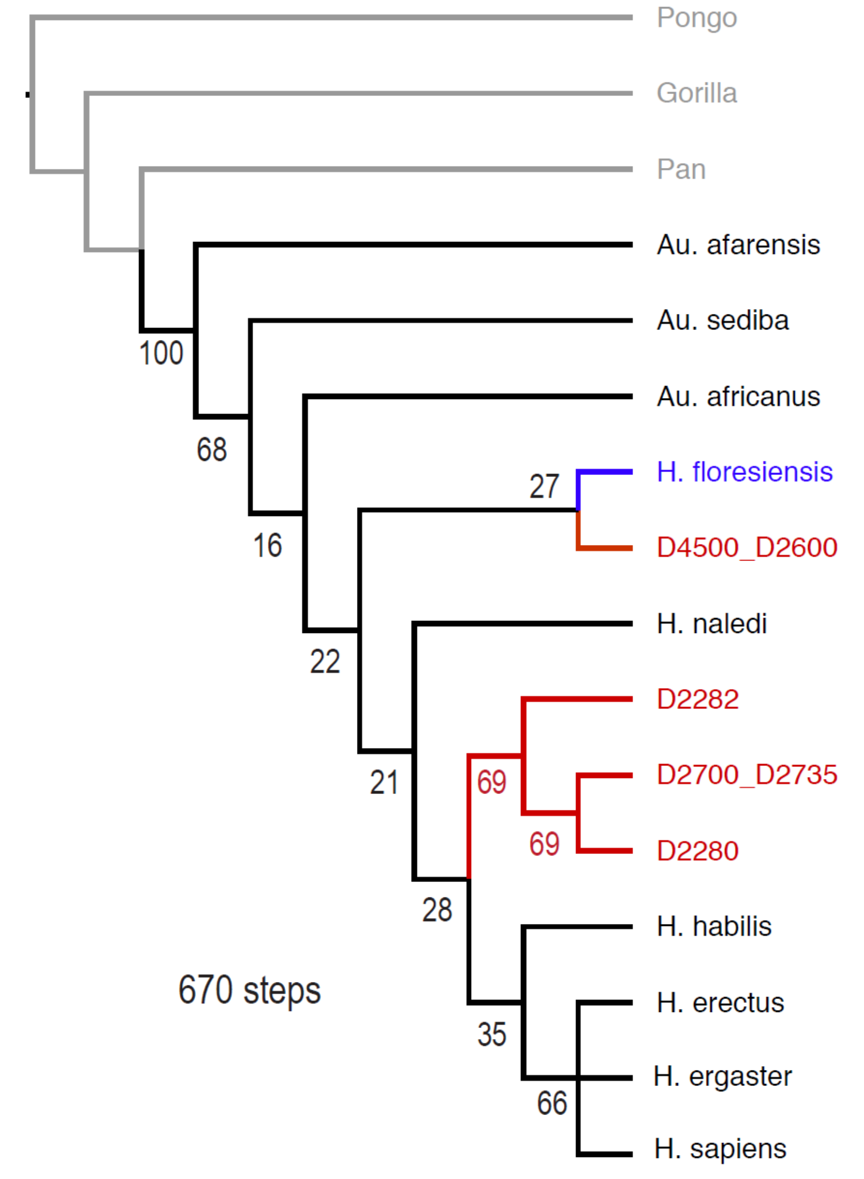
- *** We propose that
  - the Dmanisi hominins are not Homo erectus, and
  - that two species are represented among the assemblage:
  - one comprises Homo georgicus and the other an as yet unnamed species.
- Our review of the dating of the Dmanisi site leads us to propose that:
  - Homo georgicus was probably present by 1.8 Ma and
  - that the other hominins recovered from the Dmanisi excavations accumulated at some time or times during the reverse polarity of 1.07 Ma and 1.77 Ma. The specific, individual, ages of these hominins remain unknown.

Two species

- We propose that the most parsimonious hypothesis for the Dmanisi hominins is that two species are present among the assemblage: Homo georgicus comprising Skull 5, D4500, and an un-named species comprising the other Dmanisi hominins: D2280, D2282, D2700 and D3444.
- The alternative hypothesis, that the assemblage comprises a single species, requires substantial paradigm shifts in our definition of Homo.
- We surmise that the first hominin species at Dmanisi was H. georgicus (Skull 5, D4500), and that the species was probably present by 1.8 Ma.
- The other hominins, D2280, D2282, D2700 and D3444, accumulated at some time or times during the reverse polarity of 1.07 Ma and 1.77 Ma.

2 of 4 phylogenetic trees





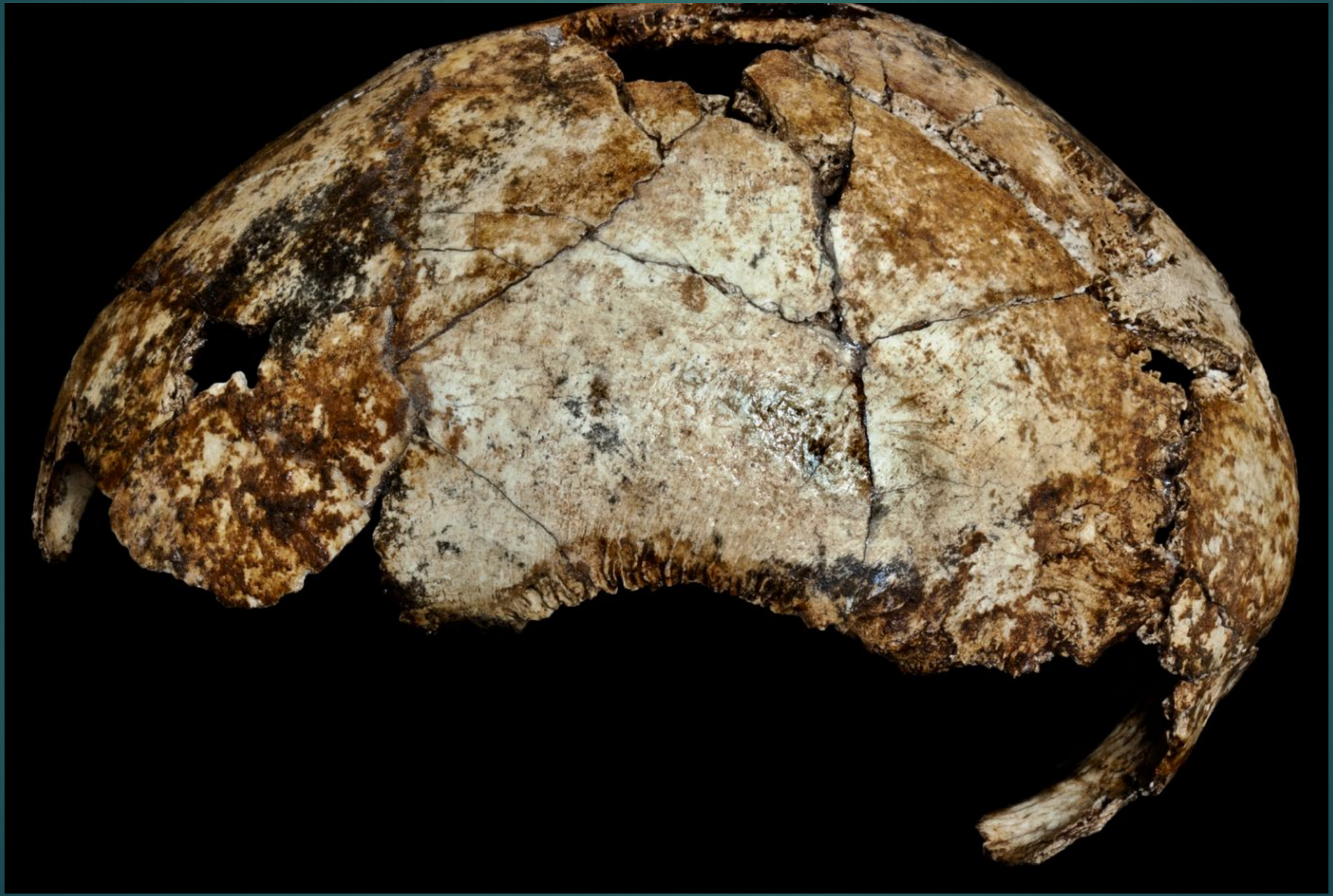
** East and Southeast Asian hominin dispersal and evolution: A review -- Rikai Sawafuji et al. 2024

- Excellent Review of Homo evolution and dispersal within EA/SEA:

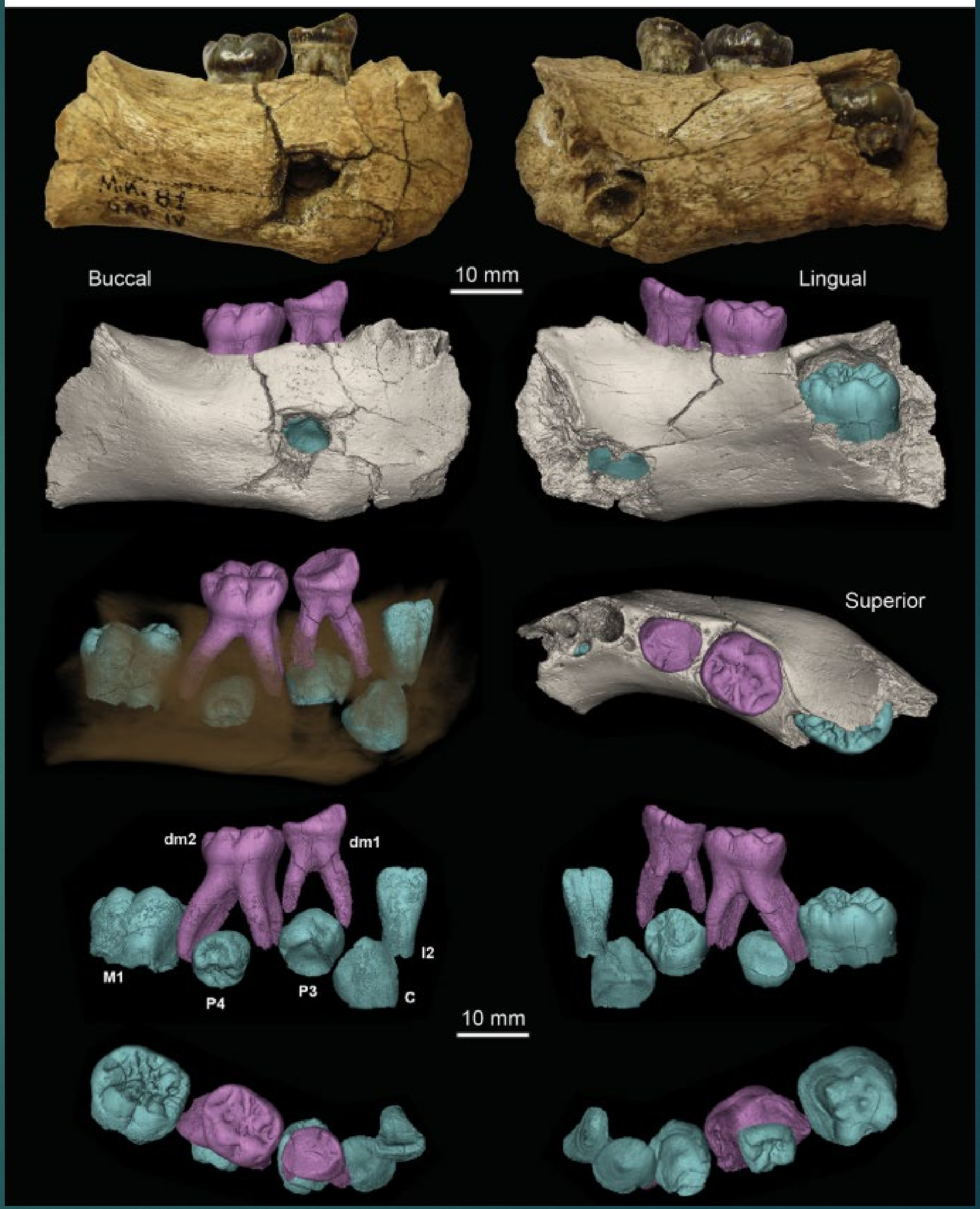
- Homo erectus: is currently recognized as the first hominin to spread out of Africa and is thought to have migrated eastward across Eurasia and then southward into Southeast Asia.

- Some of the earliest fossils of H. erectus are the ~2.04 Ma cranium found at Drimolen, South Africa and ~2 Ma mandible at Melka Kunture, Ethiopia, while the earliest generally accepted evidence of their presence out of Africa was discovered at Dmanisi, Georgia, and dated to ~1.8 Ma.

H. erectus, DNH 134 : Drimolen, S. Africa -- ~2.04 Ma

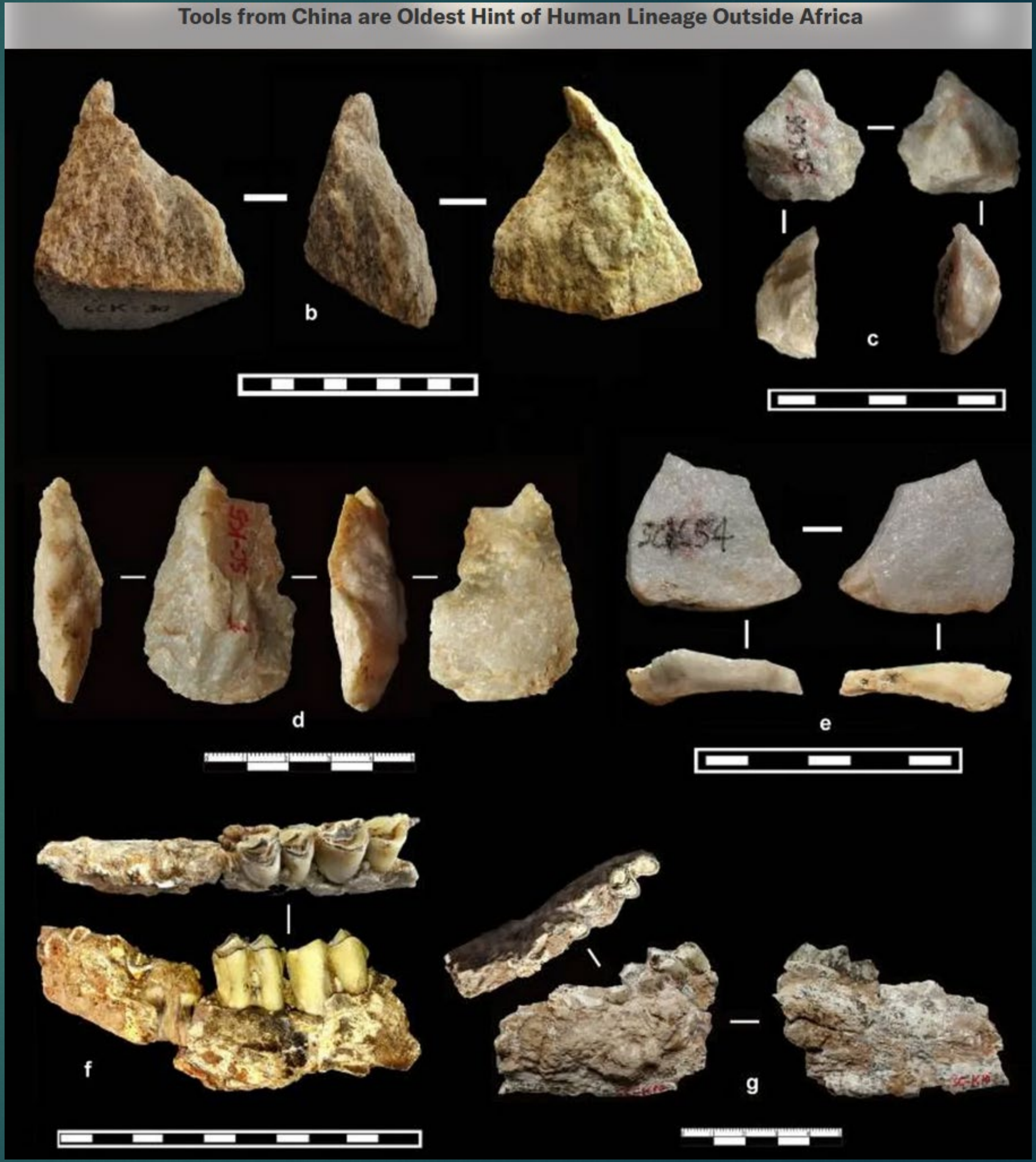


~2 Ma mandible at Melka Kunture, Ethiopia

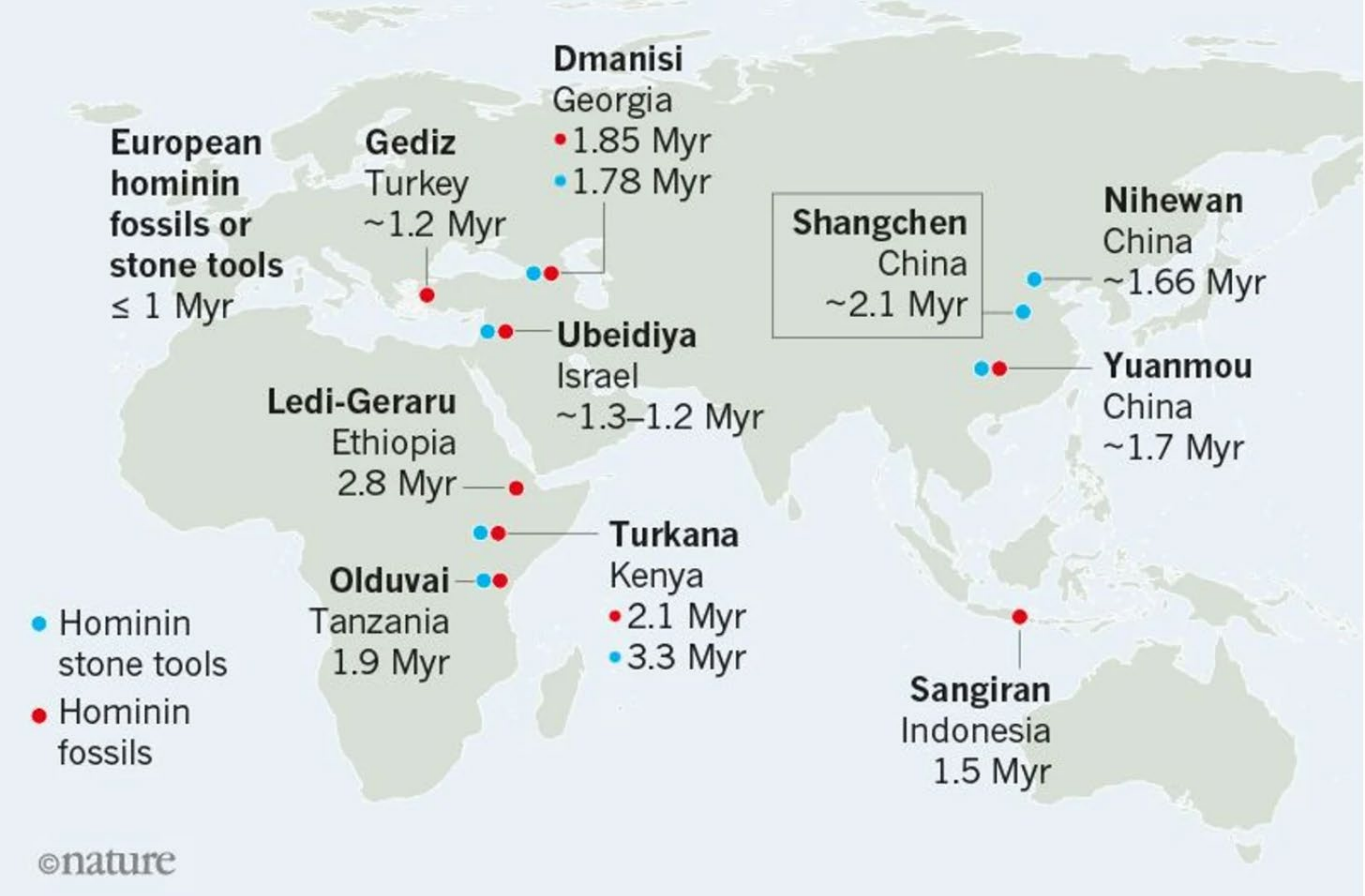


- In China, recent findings have suggested an earlier hominin presence although the evidence is scarce and primarily based on stone tools found at Shangchen, dated to ~2.1 Ma, and on hominin teeth dated between 2.42–1.8 Ma at Jianshi-Longgu Cave.

- These findings, which might predate the Dmanisi fossils, suggest the intriguing possibility that either H. erectus or another hominin arrived in China earlier than the time of Dmanisi.



Tools from China are Oldest Hint of Human Lineage Outside Africa


Dmanisi
Georgia
● 1.85 Myr
● 1.78 Myr
European hominin fossils or stone tools
≤ 1 Myr
Gediz
Turkey
~1.2 Myr
Shangchen
China
~2.1 Myr
Nihewan
China
~1.66 Myr
Ubeidiya
Israel
~1.3–1.2 Myr
Yuanmou
China
~1.7 Myr
Ledi-Geraru
Ethiopia
2.8 Myr
Turkana
Kenya
● 2.1 Myr
● 3.3 Myr
Olduvai
Tanzania
1.9 Myr
● Hominin stone tools
● Hominin fossils
Sangiran
Indonesia
1.5 Myr

©nature

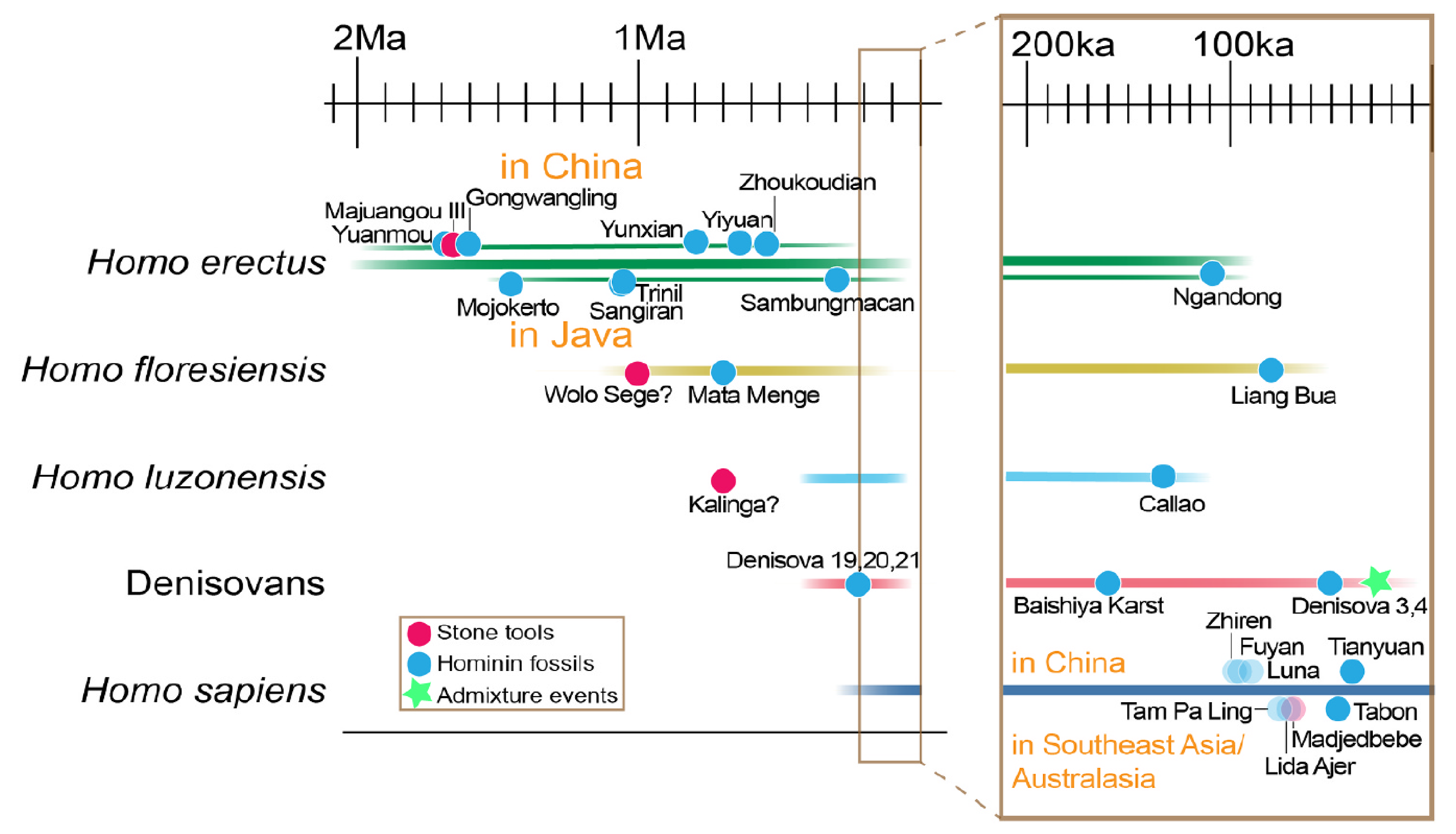
Chinese fossil locations prior to 1 Million Years Ago

Location	Age (Ma)	
Masol, India	2.6	
Longgupo, China	2.5-2.0	
Xihoudu, China	2.43	
Renzidong, China	2.4-2.0	
Shangchen, China	2.12-1.26	
Longgudong/ Jianshi, China	-2.01 -1.87	Hominin fossils
Dmanisi, Georgia	1.8-1.76	Hominin fossils
Yuanmou, China	1.72	Hominin fossils
Majuanguo III/Goudi, China	1.66	
Gongwangling, China	1.65-1.54	Hominin fossils

Eastern Asia

Majuanguo II, China	1.64	
Majuanguo I, China	1.55	
Modjokerto, Indonesia	1.49	Hominin fossils
Sangiran, Indonesia	<1.45 -0.79	Hominin fossils
Xiaochangliang, China	1.36	
Dachangliang/Xiantai, China	1.48	
Majuanguo, Banshan, China	1.32	
Donggutuo, China	1.1	
Cenjiawan, China	1.1	

Chronology of the genus Homo in EA/SEA.

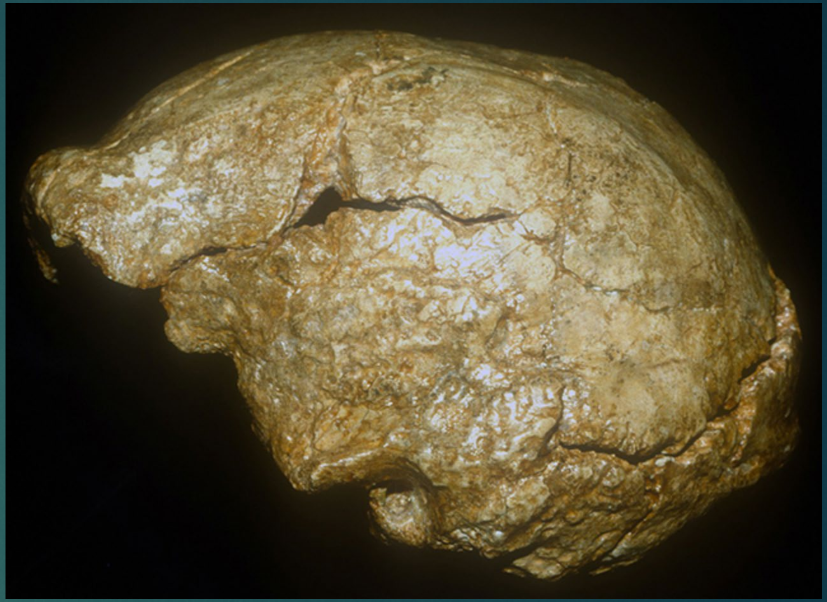


H. erectus in China: 5 pre 1.6 Ma sites

- Fossils and lithics of likely H. erectus found in China include:
  - ~1.66 Ma stone tools from Majuangou III in the Nihewan Basin and
  - 1.7–1.6 Ma stone tools from Shangshazui, and
  - a ~1.63 Ma cranium from Lantian-Gongwangling, near Shang Chen.
- Two ~1.7 Ma incisors have also been found in Yuanmou, South China. The conservative age of the emergence of H. erectus in China is about 1.7–1.6 Ma.
- *** In the context of the Middle Pleistocene period, Zhoukoudian Locality 1 yielded a significant discovery comprising six intact crania, fragments of limb bones, and over 100 teeth, dated to 780 to 300 Ka.

Yunxian, Yiyuan, and Hexian fossils

Hexian



- Other fossil finds in China include those at
  - Yunxian, dated to ~ 800 Ka, and
  - Yiyuan, dated to ~64 Ka, and
  - Hexian in southern China, with an estimated age of 410 Ka.

- *** Observation of morphological differences between the Hexian fossil and H. erectus specimens from northern China, suggesting that it could be a Denisovan or even a potentially distinct lineage. Current understanding places the disappearance of H. erectus in China at 500 to 300 Ka.

H. erectus in Java

- In Java, Indonesia, the history of H. erectus spans a considerable time frame, ranging from 1.5 Ma to as recent as 0.1 Ma.
- The earliest evidence in this region is represented by the Mojokerto child's cranium, dated between 1.49–1.43 Ma, representing the oldest fossil discovery in Java so far.

H. erectus in Java: last dates

- Sangiran and Trinil, dated between 1.3–0.8 Ma, are among the most prominent sites in Java.
- The first appearance of hominins in Sangiran is estimated at around 1.3 Ma, while the latest remains from this site are dated to 0.79 Ma.
- Other sites include
  - Sambungmacan (probably late Middle Pleistocene but no secure dating has been reported),
  - Ngawi (undated) and
  - Ngandong (0.1 Ma).
- However, recent revisions have pushed this date further back, suggesting a range of 117–108 ka.

Hobbits: Homo floresiensis and Homo luzonensis

- Flores has at least 14 individuals, are exemplified by the well-preserved partial skeleton of an adult female, known as LB1. The individual was approximately 1 m tall, and having a small cranial capacity of ~426 cc. This small size is hypothesized to be a result of insular dwarfism, potentially evolving from H. erectus.
- The fossils of H. floresiensis have been dated from >100–~60 ka, while associated stone tools extend the occupation period of these hominins to ~190–50 ka.

Flores

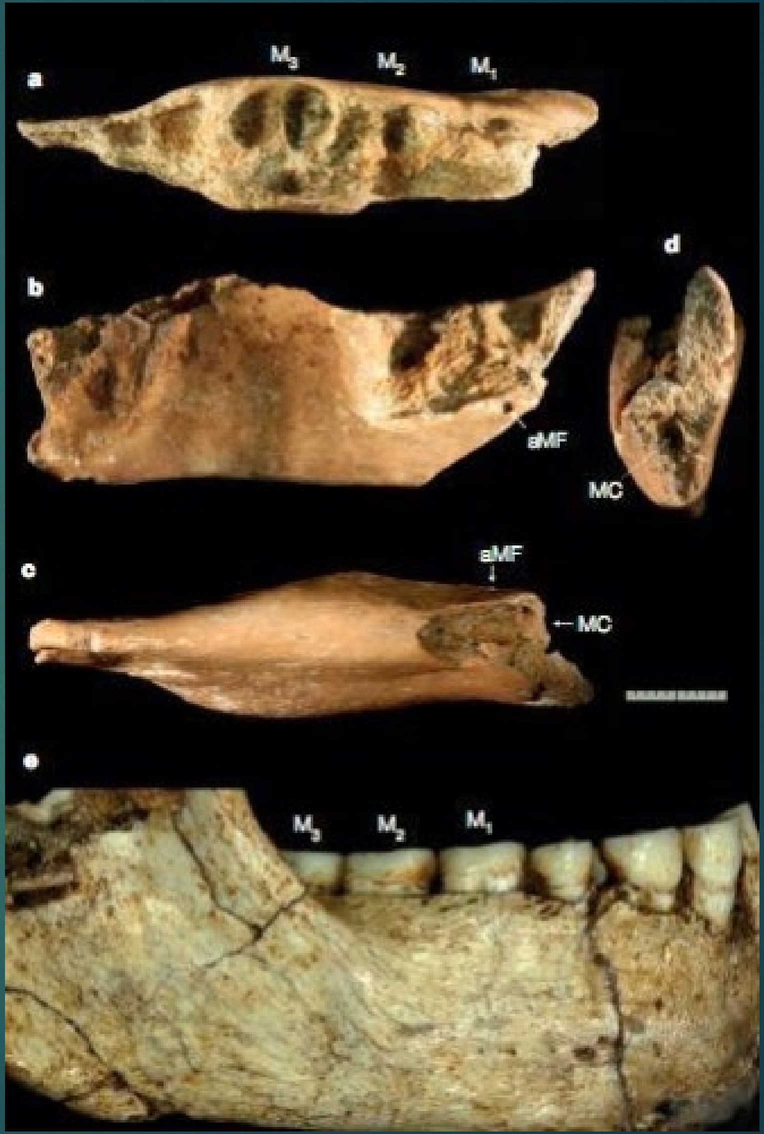
- Earlier evidence of hominin activity on Flores comes from the discovery of stone artifacts in the layers of Wolo Sege in the Soa Basin in central Flores, dated to more than 1 Ma, indicating an earlier arrival of hominins on the island.

- Additionally, a 700 Ka mandible and teeth resembling those of H. floresiensis were found at Mata Menge in the Soa Basin also on the island of Flores.

- This discovery suggests that the process of insular dwarfism, leading to the unique characteristics of H. floresiensis, might have been ongoing or fully expressed by that time

H. floresiensis vs MH skull

Mata Menge vs. Hobbit jaw



H. luzonensis

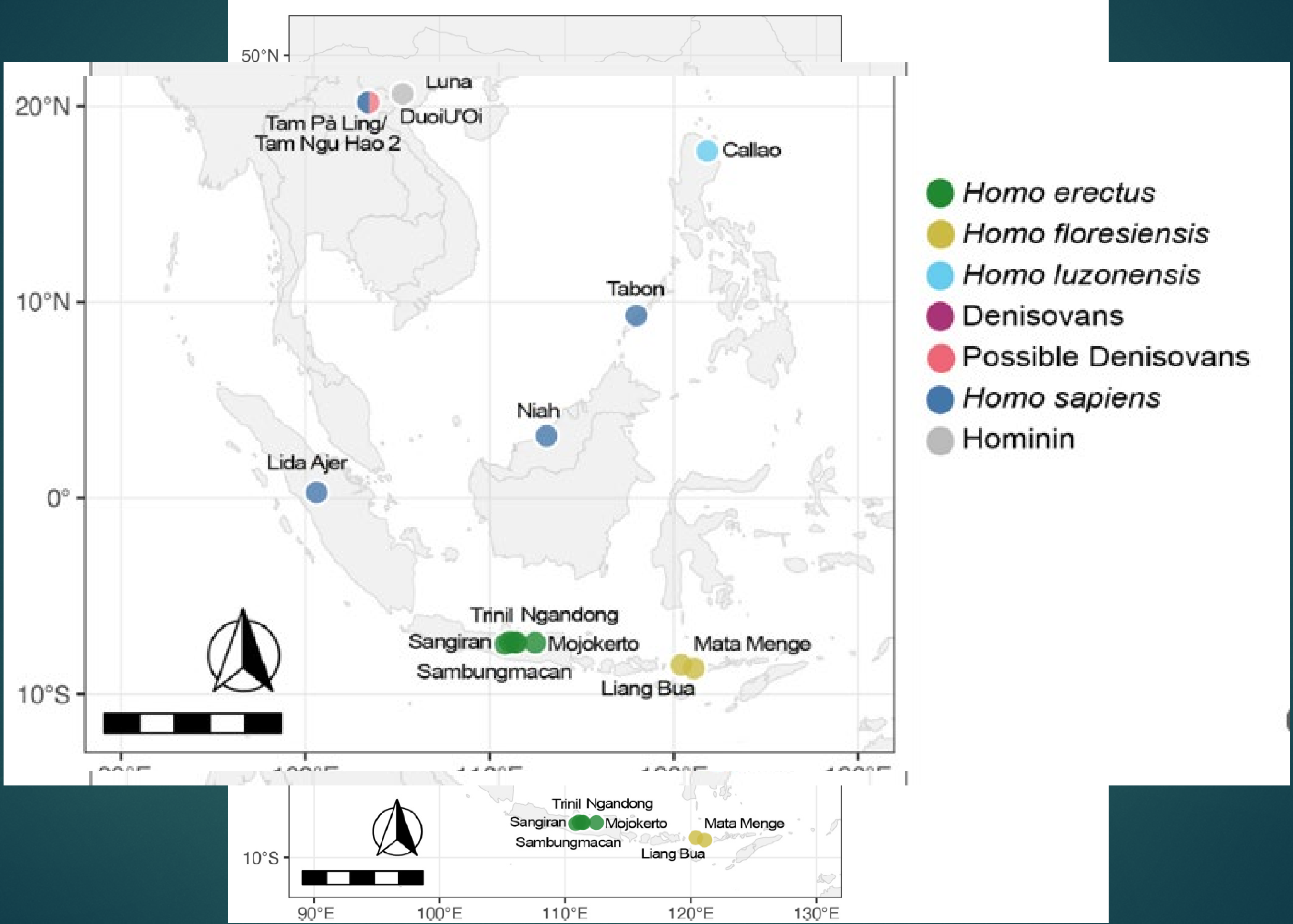
- H. luzonensis is the hominin discovered in Callao Cave on the island of Luzon, reported to be ~134 ka.

- The size of the molars is small compared to other hominins, a feature similar to H. sapiens and H. floresiensis, while the finger and toe bones are elongated and curved, a feature similar to australopithecines.

- Thus, their morphology demonstrates a unique mosaic of primitive and derived features.

H. luzonensis

- Stone tools and cut-marked animal bones have been found on the same island at 700 Ka, suggesting the much earlier presence of a hominin.
- The phylogeny of H. luzonensis is uncertain, but a study suggests that this hominin, like H. floresiensis, might be a descendant of H. erectus.
- On Sulawesi, about 300 km north of Flores across the sea, stone tools dated between 200 and 100 ka, were found, suggesting that an unknown hominin lineage also inhabited this island

50°N
20°N
10°N
0°
10°S
Luna
Tam Pà Ling/
Tam Ngu Hao 2
DuoiU'Oi
Callao
Tabon
Niah
Lida Ajer
Trinil
Ngandong
Sangiran
Mojokerto
Sambungmacan
Mata Menge
Liang Bua
● *Homo erectus*
● *Homo floresiensis*
● *Homo luzonensis*
● Denisovans
● Possible Denisovans
● *Homo sapiens*
● Hominin
Trinil
Ngandong
Sangiran
Mojokerto
Sambungmacan
Mata Menge
Liang Bua
10°S
90°E
100°E
110°E
120°E
130°E

Denisovans

- Ancient DNA analysis from a small phalanx found in Denisova Cave in Siberia was first to reveal the existence of a new archaic hominin group, which was named Denisovans.
- Genetic analysis suggests that the common ancestor of Neanderthals and Denisovans diverged from the ancestor of H. sapiens 700-500 Ka and then the Denisovan lineage diverged from the ancestor of Neanderthals earlier than 400 Ka

Denisovans

- It has been shown that the genetic contribution of Denisovans to modern humans is particularly high (>5%) among people from the Philippines, Melanesia and Australia.
- Genome analysis from modern Asian people suggested that there have been multiple interbreeding events between Denisovans and H. sapiens, and one or more of them occurred on the eastern side of the Wallace line about 30 Ka.

Denisovans

- Denisovans have yet to be reported as a new species because of the lack of information on their morphology.

- Only several pieces of bone from Denisova Cave can confidently been assigned to Denisovans at present, but a mandible from Baishiya Karst Cave on the Tibetan Plateau in Xiahe, China shows proteomic affinities to them.

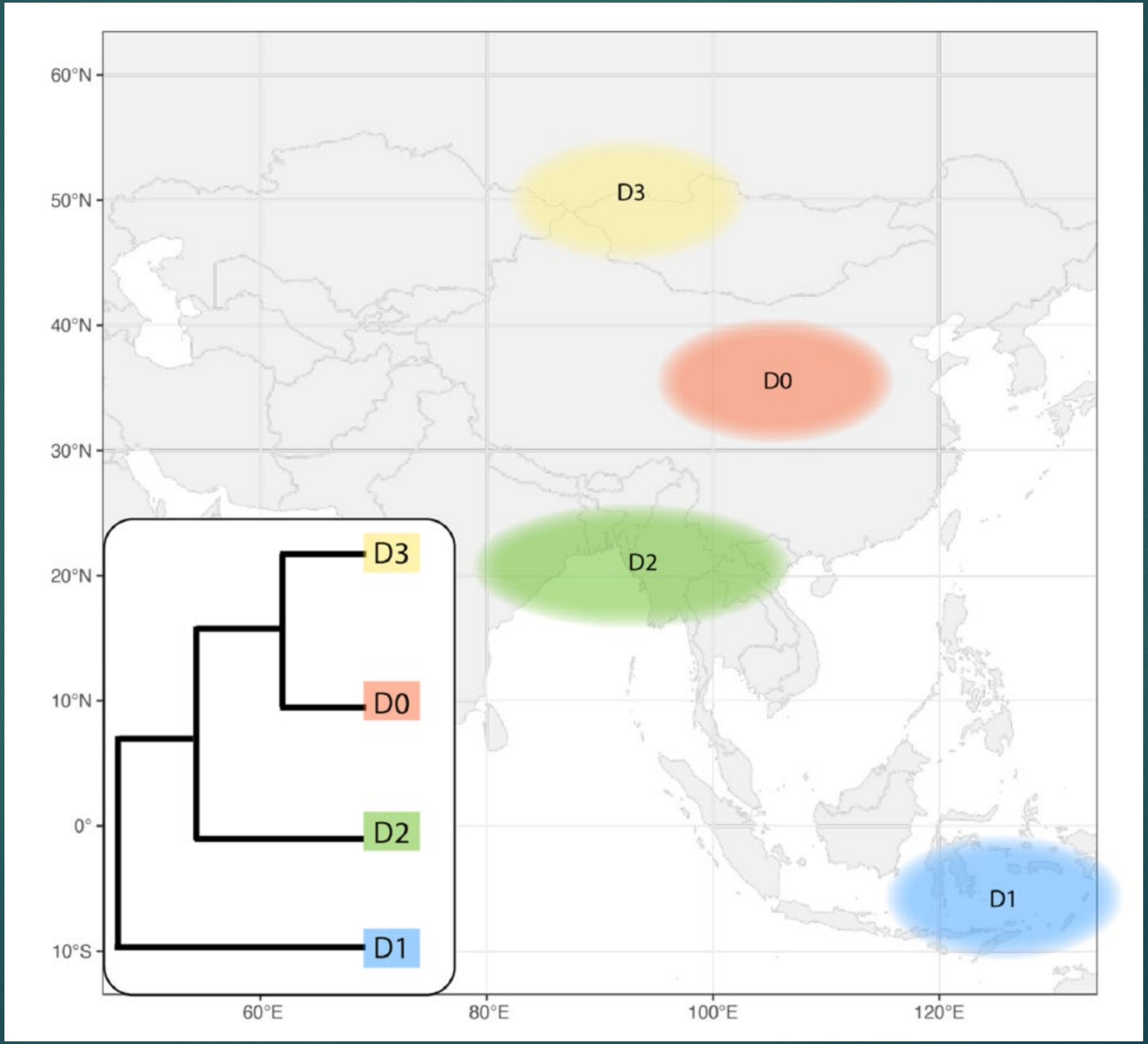
Denisovans

- The morphology of a molar from Tam Ngu Hao 2 Cave in Laos represents a Denisovan, yet there is also a slight morphological affinity with Neanderthals, and the biomolecular evidence was inconclusive
- Denisovans are hominins whose existence has been revealed mainly through ancient DNA analysis, and there is a possibility that some of the existing unclassified fossils are Denisovans.
- Denisovans inhabited Denisova Cave as far back as 200 ka, with the most recent occupation reported to be 76–52 ka.

Distribution of Denisovans

- Mitochondrial DNA (mtDNA) analysis of Denisovans indicates that their occupation at Denisova Cave was not continuous. Fragments of Neanderthal bones have also been found in Denisova Cave, and ancient DNA analysis has revealed a first-generation offspring, Denny, from a Neanderthal mother and a Denisovan father.
- In Baishiya Karst Cave, where the ~160 ka probable Denisovan mandible was reportedly found, ancient sedimentary DNA also shows Denisovan presence in layers corresponding to 100–60 ka.
- One of the questions about Denisovans is their geographical distribution. Currently, they have only been identified at Denisova Cave, on the Tibetan Plateau, and possibly also in Laos.

Potential distribution of Denisovan lineages and their phylogenetic relationship. <u>4 D lineages</u>



4 lineages of Denisovans: D0, D1, D2, and D3

- Genomic analysis of modern humans suggests that there were at least three admixture events, one in Papua, one in East Asia, and one in South or Southeast Asia.

- For this reason, it has been proposed that Denisovans may have inhabited a broad area of Asia. This hypothesis is criticized for lacking fossil evidence.

- Genomic studies have reported that there are at least four lineages of Denisovans: D0, D1, D2, and D3. Of these, only D3 has a known correspondence between fossil and genomic information, corresponding to the specimen Denisova 3 in Siberia.

D1, D2, D3

- The other lineages might have had different morphological characteristics, evolutionarily related to D3 with different affinities, and occupied different parts of Asia and Oceania: high-affinity D0 in East Asia, low-affinity D1 probably close to Papua, and intermediate-affinity D2 in South or Southeast Asia

- Each lineage has interbred with humans at least once, except D3, whose genetic contribution is not found in modern humans.

- Other studies showed that Denisovans interbred with a super-archaic hominin group, possibly H. erectus, more than 225 ka. This might have happened twice, once with the common ancestor of Denisovans and Neanderthals, and once after Denisovans diverged

4 lineages

- The following hypothesis about the dispersal of the Denisovans can be deduced: The common ancestor of Denisovans and Neanderthals which occupied around the Middle East interbred with a super-archaic hominin, and afterwards the Denisovan ancestors diverged from the Neanderthal ancestral group and moved into Asia.
  - Some of them spread towards Papua and settled in Island Southeast Asia (D1).

4 lineages

- Another group remained in South or Southeast Asia (D2), and from there, another group moved further north into East Asia (D0, D3). During the early phase of this migration, they encountered a super-archaic hominin population and interbred. The D0 group settled somewhere in East Asia.
- The D3 group reached the Altai in Siberia (D3), where they met and interbred with Neanderthals. It is important to note that this only reflects the history of the Denisovan population that interbred with modern humans. If there were other populations that went extinct without any admixture, analysis of modern human genomes would not provide any information about these.

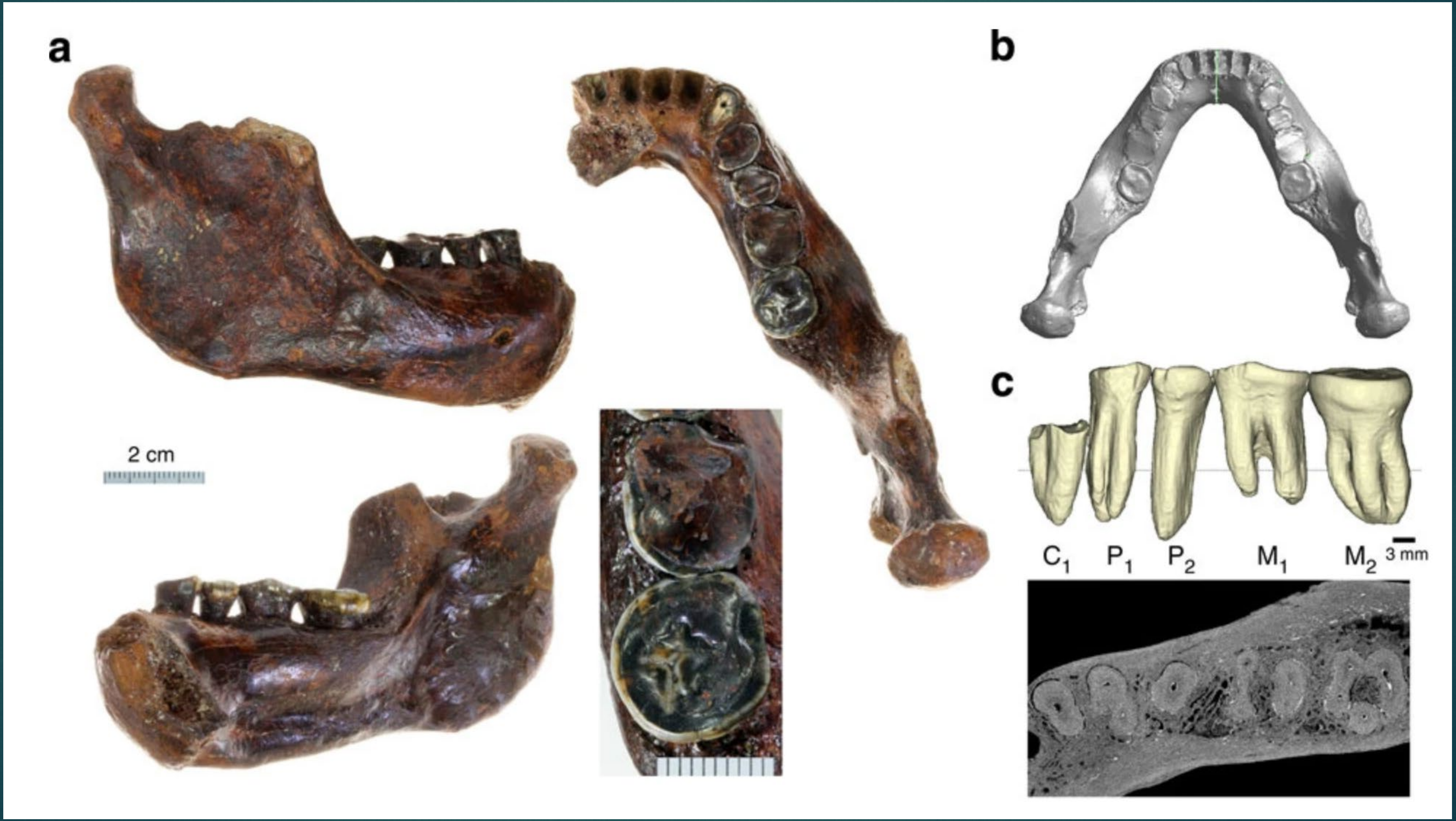
Fossils of unknown phylogenetic relationship in east Asia

- Following the appearance of H. erectus, hominin fossils of ambiguous taxonomic groups have been found, particularly in China during the Middle to Late Pleistocene.
- Some researchers call these hominins H. heidelbergensis, archaic H. sapiens, late archaic humans, or late archaic Homo.
- The morphology of these fossils is diverse and probably includes multiple lineages. Some have both primitive and derived morphological features. These fossils have been excavated from a wide variety of sites, and estimating their phylogeny from their morphology is challenging. There are some specimens that may be Denisovans.

Hominin fossils of ambiguous taxonomic group

- One example of these fossils is a cranium found from Xuchang-Lingjing dated between 125–105 ka, which has been reported to resemble Neanderthals or Denisovans.
-
- A >148 ka skull from Harbin, northern China, was proposed as a new species, H. longi, and the morphological characteristics of this individual are considered to be closely related to Denisovans.
- The putative Denisovan mandible from Xiahe is similar to fossils from Penghu (~190–10 ka) in Taiwan and from Xujiayao (~370-100 Ka) in the Nihewa Basin, China.

Penghu mandible



Penghu & Oase 1

- The morphology of the Penghu fossil is also similar to the fossil mandible from Hexian, southern China, dated to ~410 ka. Some of the morphological diversity of the fossils might be attributed to admixture.
- Given that admixture occurred many times between Neanderthals and humans, or Denisovans and humans, it is plausible that admixture occurred frequently when different hominins were contemporaneously occupying geographically close areas.
- A notable example beyond Asia is Oase 1, a modern human mandible. This fossil has been claimed to be morphologically a mosaic of modern human and Neandertal, and genomic analyses later revealed that this individual had a Neanderthal ancestor 4–6 generations previously.

Interbreeding

- There is a possibility that such interbreeding occurred between Denisovans and super-archaic hominin like H. erectus, potentially influencing their morphological traits.
- Some of them may also be affected by admixture between super-archaic hominins such as H. erectus. It is likely that the late archaic Homo consists of different taxonomic groups, some of which may be new species that have not yet been described.
- It is difficult to classify these fossils based on morphology alone, and phylogenetic relationships should be resolved using a combination of morphological and biomolecular techniques such as aDNA and proteins.

Homo sapiens: groups with no descendants

- H. sapiens appeared in Africa by at least 300 ka and subsequently spread out of Africa, with one of the earliest findings being a cranium from Apidima Cave in Greece dated to ~210 ka.
- Several human fossils have also been found in the Levant, including a ~152 ka maxilla from Misliya Cave in Israel, and 120–90 ka skulls from Skhul and Qafzeh Cave in Israel.
- These fossils support that humans expanded their habitats outside Africa earlier than 100 ka multiple times, although genetic studies support that these dispersals had no or little genetic contribution to later modern humans.

Migrants without descendants

- Populations out of Africa before 55 ka seemingly went extinct and were completely replaced by populations spreading in later dispersals.

- This is supported by analyses of mitochondrial and Y-chromosomal DNA of modern and ancient humans, indicating that the non-African human populations began to spread around the world less than 55 ka, based on the divergence time of these uniparental haplogroups.

- Evidence of MHs in China: A mandible and two teeth dated to ~100 ka from Zhiren Cave and 47 teeth dated between ~120–60 ka from Fuyan Cave have been identified as modern humans.

Homo sapiens in East Asia

- There are also reports of H. sapiens fossils before 55 ka from other sites such as Luna Cave, Liujiang-Tongtianyan Cave, Xianren Cave, and Huanglong Cave.

- In Southeast Asia, fossils were found at Tam P`a Ling in northern Laos, near China, some of which dated to earlier than 70 ka. Other evidence from Southeast Asia includes two ~73–63 ka teeth from Lida Ajer in Indonesia and ~65 ka stone tools including ground stone axe heads from Madjedbebe in Australia.

- The early dispersal into EA/SEA prior to 55 ka has been a subject of intense debate over the past decade, with two major concerns surrounding the findings.

Fossil dating debates

- The first concern involves the dating of fossils.
- Radiocarbon dating, with an upper limit of around 55 ka, is unsuitable for examining human migrations in Asia beyond this timeframe. For estimating the age of older fossils, methods such as Uranium-series, Electron Spin Resonance (ESR), and luminescence dating are employed, and these techniques are often used to date the layer in which a fossil was found.

- This approach raises questions not only about the precision of the dating but also regarding the correlation between the age of the layer and the actual age of the fossil.

Dating of fossils, not sediments

- Kaifu et al. (2022) reported the intrusion of recent human remains into older stratigraphic levels in cave sediments, emphasizing the need for direct dating of hominin specimens and taphonomic assessment.

- The second concerns the morphological classification of fossils. Given that Denisovans had already dispersed across EA/SEA before the arrival of modern humans, and may have been present up until 30–25 ka, fossils and stone tools dated before 55 ka might be attributable to Denisovans or to H. sapiens.

- Most fossils attributed to the early dispersal are teeth or fragments of bones, which frequently complicates precise taxonomic assignment of these specimens.

Other sites after 55 ka

- The later dispersal into Asia after 55 ka is confirmed by both fossil evidence and genetic information.

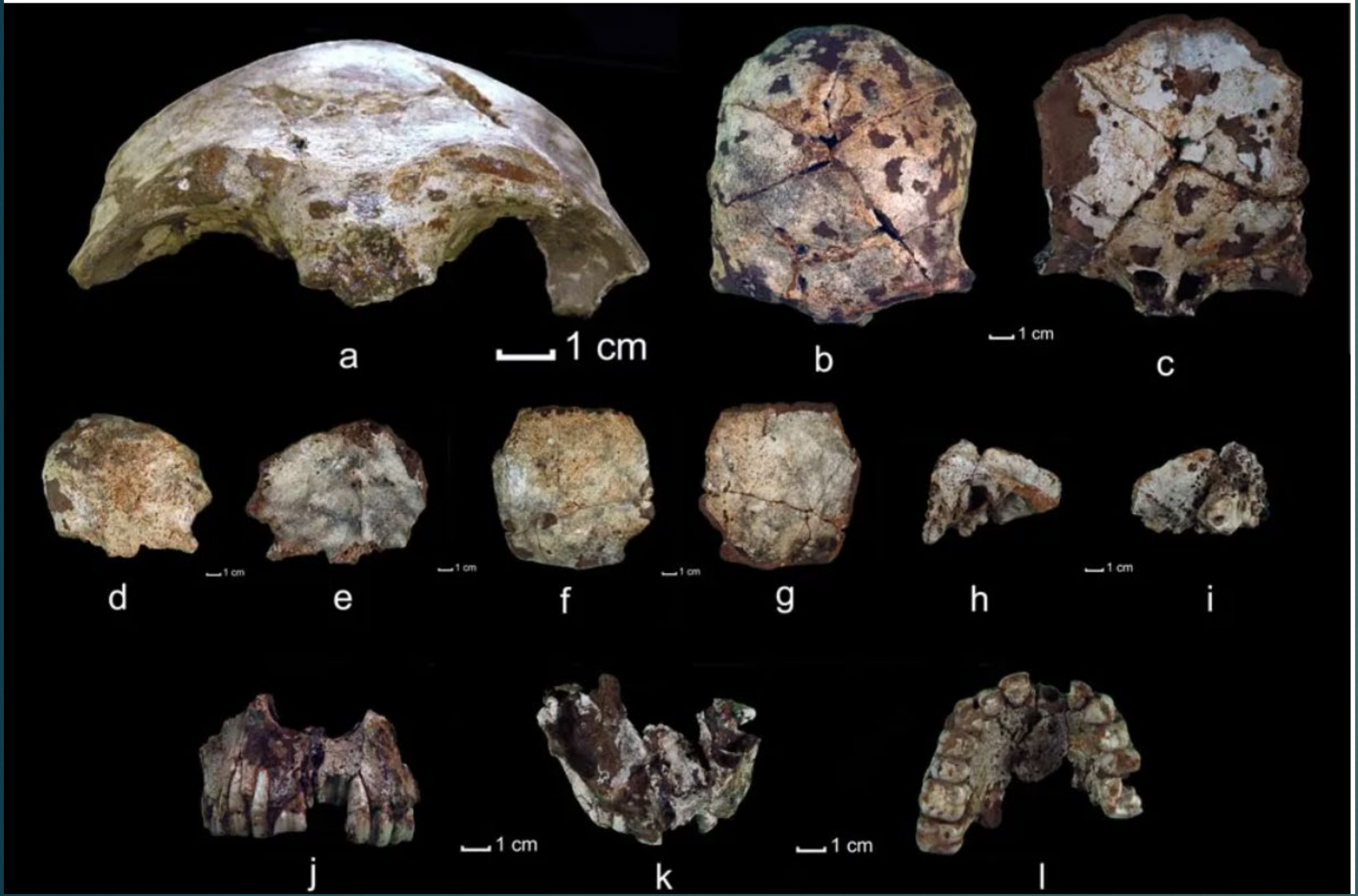
- In northern China, a mandible and postcranial bones dated between 42–39 ka have been recovered from Tianyuan Cave. Ancient DNA analysis revealed that the specimen is genetically closely related to modern human populations in East Asia and the Americas and that they had already interbred with Neanderthals and Denisovans.

- In southern China, modern human fossils dated between 44–38.5 ka have been found at Qilinshan in Lanbin.

Other sites: evidence of complex migrations

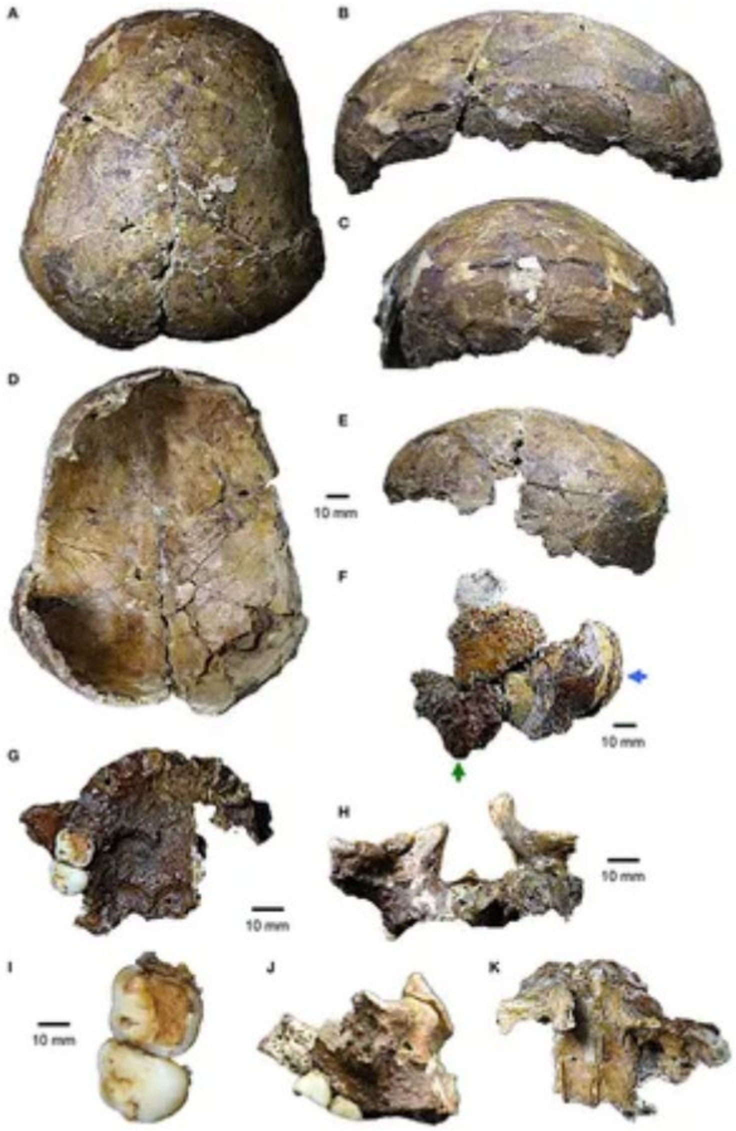
- In Southeast Asia, a skull and a mandible dated to ~46 ka have been excavated from Tam P`a Ling in northern Laos, although there are also older H. sapiens remains from the site.
- The Niah Deep Skull from Niah Cave in Borneo has been dated between ~45–39 ka,
- A tibia fragment dated to 47 ka was found in Tabon Cave in Palawan, the Philippines.
- This accumulating evidence of the early and late dispersals underscores the complexity and dynamism of migration patterns.

Tam P`a Ling



Niah Deep Skull from Niah Cave in Borneo

Figure 1



Diverse hominin dispersal and extinctions

- How the different hominins dispersed and why they went extinct still remain unclear.
- From current fossil records and genetic evidence, one plausible and coherent scenario of hominin dispersal is the following:
- H. erectus emerged in Africa and expanded into the Eurasian continent around 2 Ma, later occupying Europe, East Asia (China) and Southeast Asia (Java).
- Subsequently, the common ancestor of H. sapiens, Neanderthals and Denisovans split into two groups:
- one was in Africa (later leading to H. sapiens) and
- the other settled around the Middle East at some point.

Ns and Ds

- The latter interbred with a super-archaic hominin group (possibly H. erectus) around 700–600 ka.
- The Eurasian hominin group then split into two groups:
  - One settled in the West (Europe and Western Asia) leading to Neanderthals,
  - while the other settled in Asia leading to Denisovans. Denisovans interbred with H. erectus in Eurasia, occupying their niche.

Denisovans

- At some point, Denisovans also expanded into East and Southeast Asia, where the groups diverged into different subgroups (D0, D1, D2, D3).
- Meanwhile, H. erectus may have become extinct around 400 ka in East Asia and 100 ka in Southeast Asia.
- Denisovans reached the Altai region, eventually meeting and interbreeding with Neanderthals several times around 140–80 ka.
- Meanwhile, some H. sapiens left Africa before 200 ka. This initial migration was unsuccessful, but interbreeding with Neanderthals at this time left traces in their genome.

Successful migrants

- There were several subsequent out-of-Africa events, which might have reached Asia, but the populations that led to our ancestors left Africa around 55 ka. They interbred with Neanderthals in West Asia and with Denisovans in EA/SEA.
- Note that we consider the super-archaic hominin contributing to the Denisovan genome to be H. erectus.
- While there is a possibility that hominins other than H. erectus and Denisovans migrated into Asia or evolved from H. erectus, this is not considered here due to the lack of evidence.

Assimilation Scenario Hypothesis

- A commonly proposed explanations for the extinction of hominins are environmental changes and competition for ecological niches with other hominins.
- Recently, it has been proposed that repeated interbreeding between Neanderthals and humans led to their assimilation.

Assimilation

- Given the fact that there were multiple admixtures among the various hominins from genetic evidence, assimilation might have contributed to the extinction of some of hominins in Asia as well.

- This hypothesis assumes that when different hominins met, interbreeding occurred and the smaller group was absorbed into the larger group.

- As a result, there were various interactions and interbreeding among different hominins, ultimately leading to Homo sapiens being the sole surviving species.

Assimilation

- The geographical conditions of EA/SEA, with its many islands and mountains hindering movements, may have provided a suitable environment for diverse hominins to evolve and thrive.
- This also implies that EA/SEA, which various hominins occupied, is an ideal location for testing this possibility.
- For example, considering the admixture between Denisovans and super-archaic hominins, the extinction of H. erectus might be explained by the interbreeding and assimilation with Denisovans. Verifying this hypothesis requires additional fossil records, which are scarce in Asia

Ancient DNA often doesn’t preserve

- In essence, ancient genomics has revolutionized our comprehension of the intricate tapestry of human ancestry, unravelling a more detailed and interconnected narrative of our past.
- However, there is a strong geographical bias in these ancient genomes, which leaves EA/SEA underrepresented (as well as Africa).
- This is likely a consequence of few fossil findings as well as poor molecular preservation of these fossils which especially pronounced in hot and humid environments where bones often degrade and disappear and at times combined with acidic soils.

Ancient proteomics

- In this regard, we believe that ancient proteomics and sedimentary ancient DNA (sedaDNA) analysis can serve as an alternative method to investigate the ancient hominins of EA/SEA in place where fossils are absent or poorly preserved

- Ancient proteomics, or palaeoproteomics, has attracted attention as an alternative biomolecular method to reconstruct phylogeny. Proteins are sometimes preserved in calcified tissues older than 1 million years where ancient DNA is not preserved.

- Phylogenetically informative protein sequences are retrieved even from a specimen dated to 1.9 Ma in southern China (from a Gigantopithecus blacki molar found in Chuifeng Cave) and to 2.0 Ma in South Africa suggesting that this method might also illuminate hominin evolution in EA/SEA.

Protein analysis examples

- A mandible from the Baishiya Karst Cave was identified as a probable Denisovan by ancient proteomic analysis of dentin and even showed an amino acid polymorphism that was never found in humans, Neanderthals, and Altai Denisovan.
- Proteomic analysis of tooth enamel from H. antecessor, dated between ~949–772 ka, has also been performed and revealed that it is a sister group to H. sapiens, Neanderthals, and Denisovans.
- Since amelogenin in tooth enamel differs in sequence between the X and Y chromosomes, the biological sex of ancient specimens can be determined by retrieving the peptide sequence of amelogenin.

Ancient proteomic analysis is promising but not without its limitations

- One such limitation is that it is not always possible to identify the taxon at a desired level using proteomics. This is partly because codon (DNA component that codes for an amino acid) degeneracy means that different DNA sequences can code for the same protein sequences, reducing the ability of proteomics to distinguish between closely related species.

- Additionally, most tissues only express a small subset of the entire proteome of the organism. In contrast, DNA analysis includes non-coding regions, offering a more complete set of genetic information and a higher resolution for phylogenetic studies.

Limits of protein analysis

- These limitations are exemplified in instances where hominin peptides are indistinguishable.
- While ancient DNA analysis currently provides more detailed insights into phylogenetic relationships and species diversity, ongoing advancements in extraction methods and data analysis algorhythmic pipelines are expected to enhance the capabilities and resolution of ancient proteomic analysis

Sedimentary DNA – up to 2 Ma

- The analysis of environmental DNA (eDNA) has increasingly become a standard tool for revealing organismal diversity in various environments and materials, such as seawater, lakes, sediments and faces. Among these, sedaDNA has proven to be a powerful tool for reconstructing paleoenvironments and ecosystems of the past, even in deposits without fossils.
- This relates to the fact that throughout its life, the organism leaves traces in the environment as DNA and that these molecules can be protected and preserved. More recently, genome-wide analysis of hominins has also been performed on sedaDNA, and its survival in other organisms has been pushed back to 2 million years.

SedaDNA

- In the field of paleoanthropology, sedaDNA from caves has been used to reveal not just the paleoenvironment but also the presence of diverse hominins.
- A significant achievement was the discovery of ancient mtDNA of both Neanderthals and Denisovans in sediment samples from Denisova Cave.
- Denisovan mtDNA was also found in Baishiya Karst Cave on the Tibetan Plateau, indicating their presence at approximately 100–60 ka.

aDNA

- Hominin DNA can be obtained even from sites without fossils, as well as co-existence information about the sites they were in.

- DNA from archaeological sediments indicates not only their existence but also how long they lived there, in combination with dating methods from the sediments

SedaDNA

- There are three main topics where sedaDNA can tell us about paleoanthropology:
- 1. Phylogeny and population structure of hominins. Hominin DNA from sediments reveals the history of evolution and dispersal in addition to demography and admixture events.
- For example, sedaDNA has provided insights into the migration patterns of Neanderthals and revealed a population replacement.

Molecular dating

- 2. Molecular dating. This is a method of inferring when a lineage or population diverged from others using the molecular clock. It is mainly used in this field to determine which lineage a hominin belongs to and how old it is by comparing the DNA sequence extracted from the sediment with the known sequences of other hominins and modern humans.
- It provides a means of obtaining a rough age estimate from the genome and assessing the presence of disturbances or intrusions, allowing it to complement conventional dating methods such as radiocarbon, OSL and U/Th series. Several studies have compared ages using conventional dating with molecular dating and confirmed their consistency. This method is applicable to all taxa in principle.

SedaDNA

- 3. Paleoenvironment. Animal and plant DNA from sediments can also tell us about the environment that hominins have adapted to.

- For example, sedaDNA helps us to infer whether the environment was suitable for humans. It can also demonstrate how people exploited and affected their environment. By combining other methods such as pollen, macrofossils and lipid analysis, it is possible to gain a deeper insight into hominins and the environment they lived in.

Conclusion: Hope for a Denisovan cranium

- Since a Denisovan cranium has yet to be identified, which has hindered morphological comparison with other fossils during the Middle to Late Pleistocene, a cranium certificated by biomolecular methods could be a key specimen for unveiling the muddle of the existing unclassified fossils.

- Proteomic analysis of hominin fossils and sedaDNA analysis at hominin sites will also elucidate the evolutionary history and admixture events of the genus Homo in EA/SEA

*** Human Evolution in Asia: Taking Stock and Looking Forward

-- Sang-Hee Lee and Autumn Hudock, 2021

- In the history of modern paleoanthropology, Asia occupied a marginal space in the second half of the twentieth century, secondary to the attention given to Europe and Africa.

- The attention it did receive was shaped by Eurocentrism and colonialism.

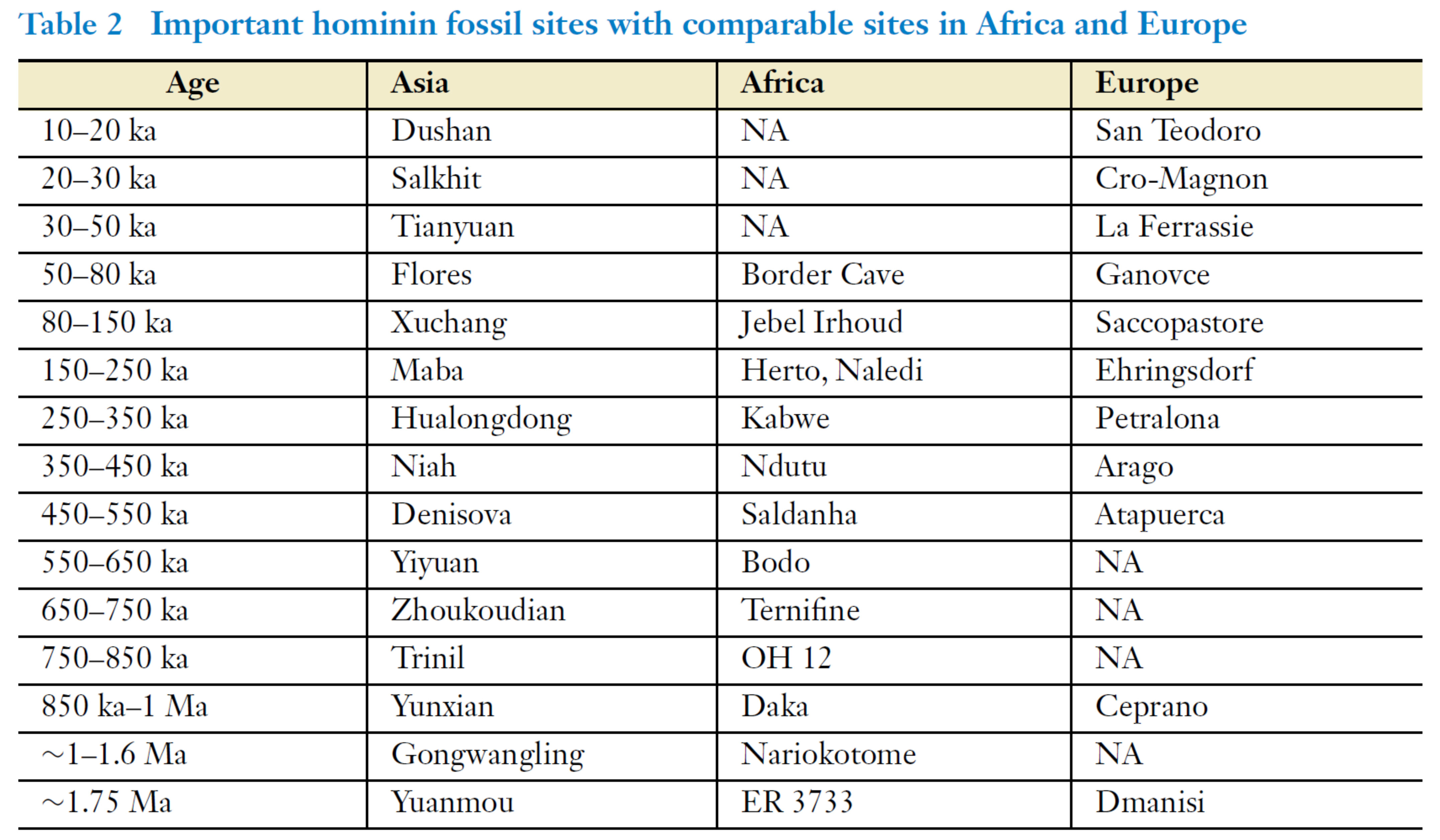


Table 2 Important hominin fossil sites with comparable sites in Africa and Europe

Age	Asia	Africa	Europe
10–20 ka	Dushan	NA	San Teodoro
20–30 ka	Salkhit	NA	Cro-Magnon
30–50 ka	Tianyuan	NA	La Ferrassie
50–80 ka	Flores	Border Cave	Ganovce
80–150 ka	Xuchang	Jebel Irhoud	Saccopastore
150–250 ka	Maba	Herto, Naledi	Ehringsdorf
250–350 ka	Hualongdong	Kabwe	Petralona
350–450 ka	Niah	Ndutu	Arago
450–550 ka	Denisova	Saldanha	Atapuerca
550–650 ka	Yiyuan	Bodo	NA
650–750 ka	Zhoukoudian	Ternifine	NA
750–850 ka	Trinil	OH 12	NA
850 ka–1 Ma	Yunxian	Daka	Ceprano
~1–1.6 Ma	Gongwangling	Nariokotome	NA
~1.75 Ma	Yuanmou	ER 3733	Dmanisi

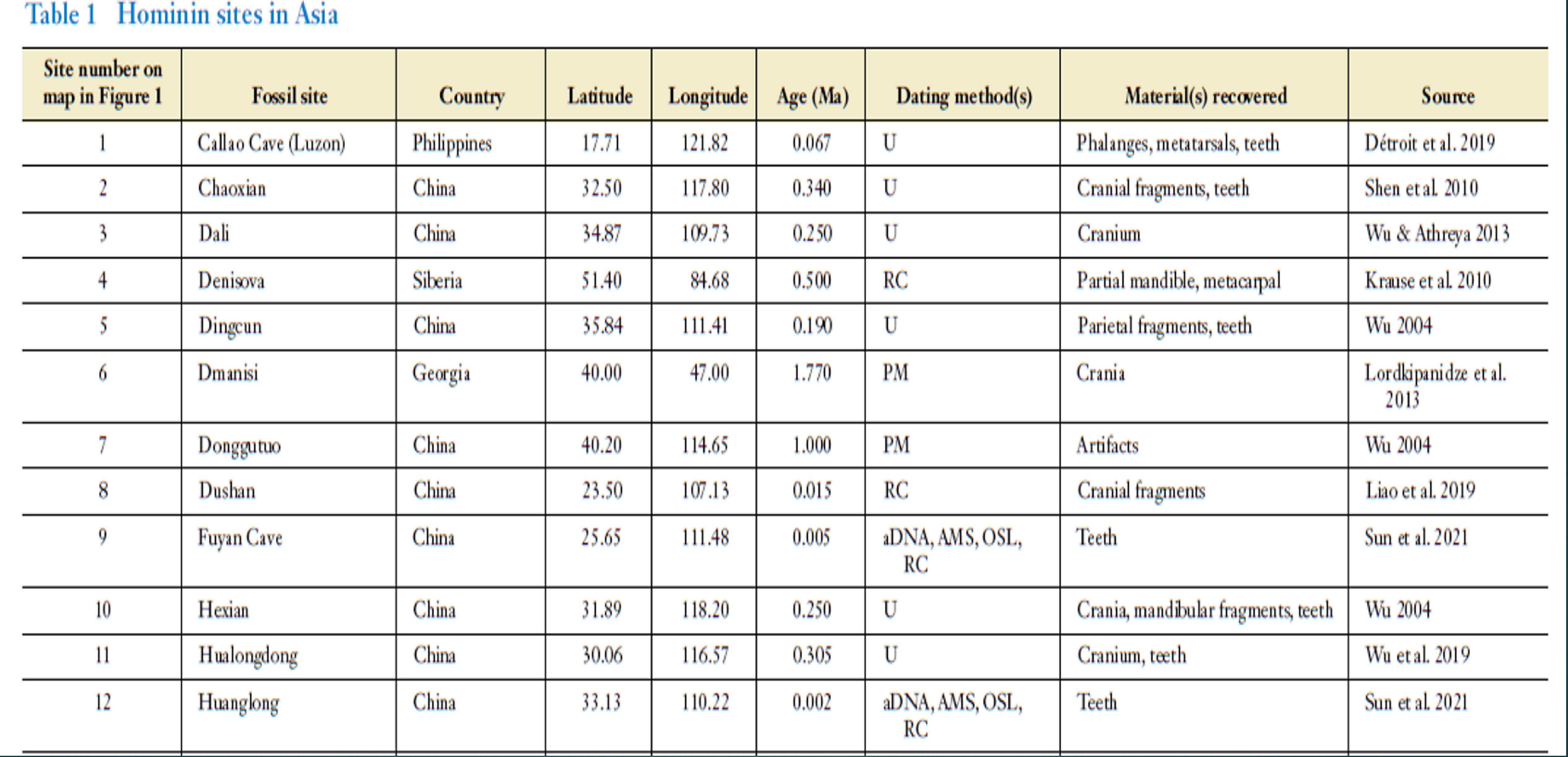
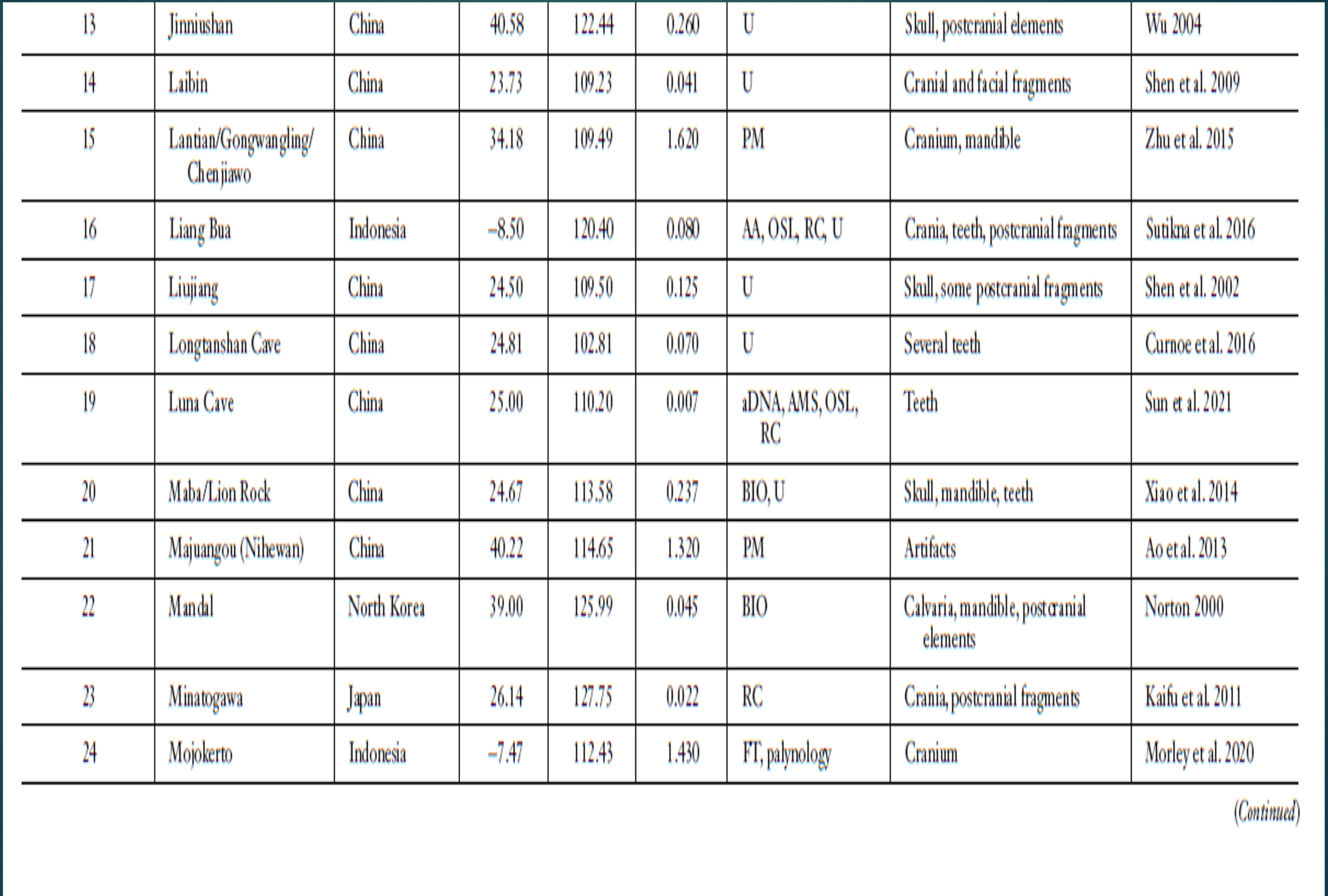


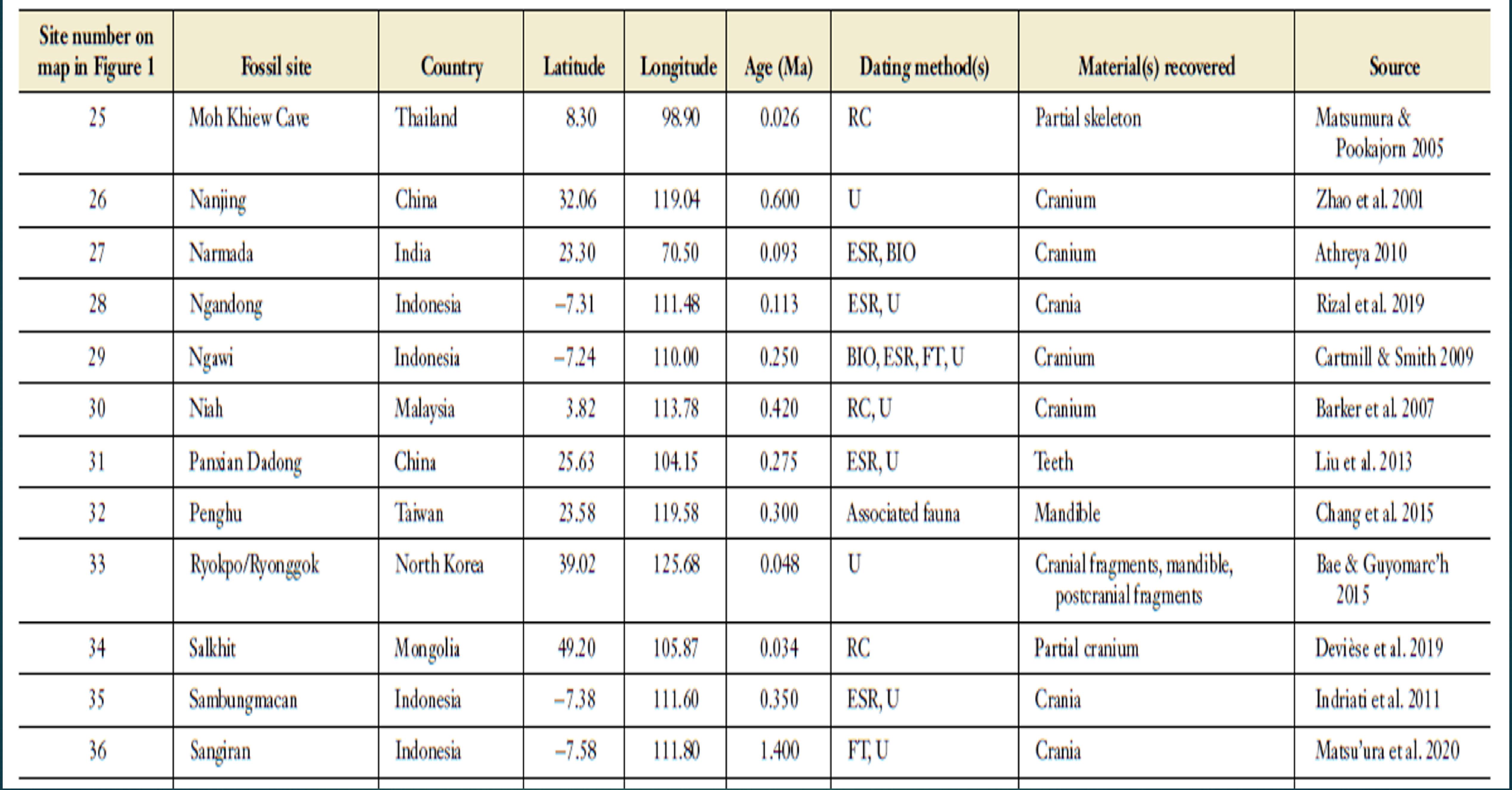
Table 1 Hominin sites in Asia

Site number on map in Figure 1	Fossil site	Country	Latitude	Longitude	Age (Ma)	Dating method(s)	Material(s) recovered	Source
1	Callao Cave (Luzon)	Philippines	17.71	121.82	0.067	U	Phalanges, metatarsals, teeth	Détroit et al. 2019
2	Chaoxian	China	32.50	117.80	0.340	U	Cranial fragments, teeth	Shen et al. 2010
3	Dali	China	34.87	109.73	0.250	U	Cranium	Wu & Athreya 2013
4	Denisova	Siberia	51.40	84.68	0.500	RC	Partial mandible, metacarpal	Krause et al. 2010
5	Dingcun	China	35.84	111.41	0.190	U	Parietal fragments, teeth	Wu 2004
6	Dmanisi	Georgia	40.00	47.00	1.770	PM	Crania	Lordkipanidze et al. 2013
7	Donggutuo	China	40.20	114.65	1.000	PM	Artifacts	Wu 2004
8	Dushan	China	23.50	107.13	0.015	RC	Cranial fragments	Liao et al. 2019
9	Fuyan Cave	China	25.65	111.48	0.005	aDNA, AMS, OSL, RC	Teeth	Sun et al. 2021
10	Hexian	China	31.89	118.20	0.250	U	Crania, mandibular fragments, teeth	Wu 2004
11	Hualongdong	China	30.06	116.57	0.305	U	Cranium, teeth	Wu et al. 2019
12	Huanglong	China	33.13	110.22	0.002	aDNA, AMS, OSL, RC	Teeth	Sun et al. 2021

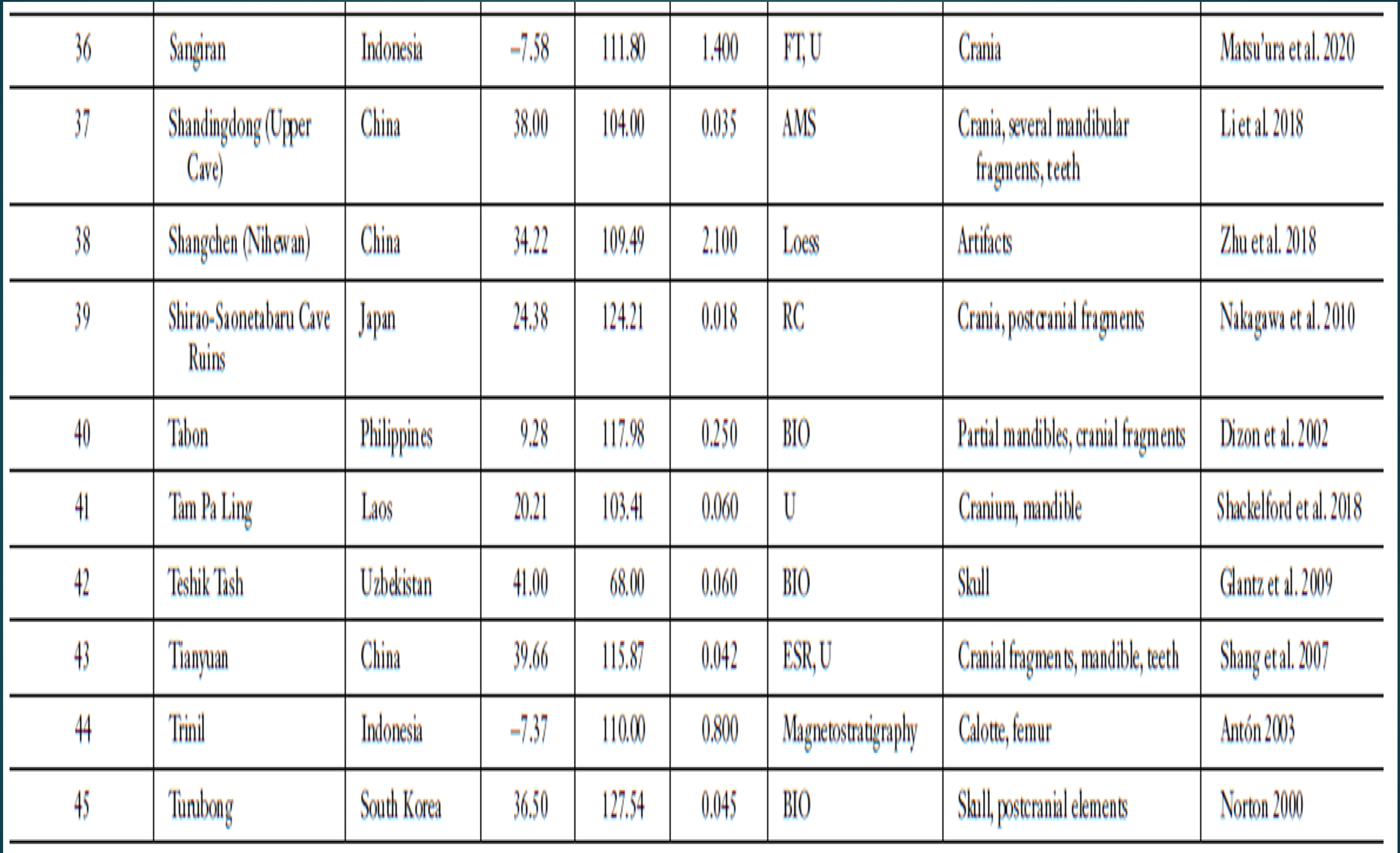


13	Jinniushan	China	40.58	122.44	0.260	U	Skull, postcranial elements	Wu 2004
14	Laibin	China	23.73	109.23	0.041	U	Cranial and facial fragments	Shen et al. 2009
15	Lantian/Gongwangling/ Chenjiawo	China	34.18	109.49	1.620	PM	Cranium, mandible	Zhu et al. 2015
16	Liang Bua	Indonesia	–8.50	120.40	0.080	AA, OSL, RC, U	Crania, teeth, postcranial fragments	Sutikna et al. 2016
17	Liujiang	China	24.50	109.50	0.125	U	Skull, some postcranial fragments	Shen et al. 2002
18	Longtanshan Cave	China	24.81	102.81	0.070	U	Several teeth	Curnoe et al. 2016
19	Luna Cave	China	25.00	110.20	0.007	aDNA, AMS, OSL, RC	Teeth	Sun et al. 2021
20	Maba/Lion Rock	China	24.67	113.58	0.237	BIO, U	Skull, mandible, teeth	Xiao et al. 2014
21	Majuangou (Nihewan)	China	40.22	114.65	1.320	PM	Artifacts	Ao et al. 2013
22	Mandal	North Korea	39.00	125.99	0.045	BIO	Calvaria, mandible, postcranial elements	Norton 2000
23	Minatogawa	Japan	26.14	127.75	0.022	RC	Crania, postcranial fragments	Kaifu et al. 2011
24	Mojokerto	Indonesia	–7.47	112.43	1.430	FT, palynology	Cranium	Morley et al. 2020

(Continued)



Site number on map in Figure 1	Fossil site	Country	Latitude	Longitude	Age (Ma)	Dating method(s)	Material(s) recovered	Source
25	Moh Khiew Cave	Thailand	8.30	98.90	0.026	RC	Partial skeleton	Matsumura & Pookajorn 2005
26	Nanjing	China	32.06	119.04	0.600	U	Cranium	Zhao et al. 2001
27	Narmada	India	23.30	70.50	0.093	ESR, BIO	Cranium	Athreya 2010
28	Ngandong	Indonesia	−7.31	111.48	0.113	ESR, U	Crania	Rizal et al. 2019
29	Ngawi	Indonesia	−7.24	110.00	0.250	BIO, ESR, FT, U	Cranium	Cartmill & Smith 2009
30	Niah	Malaysia	3.82	113.78	0.420	RC, U	Cranium	Barker et al. 2007
31	Panxian Dadong	China	25.63	104.15	0.275	ESR, U	Teeth	Liu et al. 2013
32	Penghu	Taiwan	23.58	119.58	0.300	Associated fauna	Mandible	Chang et al. 2015
33	Ryokpo/Ryonggok	North Korea	39.02	125.68	0.048	U	Cranial fragments, mandible, postcranial fragments	Bae & Guyomarc'h 2015
34	Salkhit	Mongolia	49.20	105.87	0.034	RC	Partial cranium	Devièse et al. 2019
35	Sambungmacan	Indonesia	−7.38	111.60	0.350	ESR, U	Crania	Indriati et al. 2011
36	Sangiran	Indonesia	−7.58	111.80	1.400	FT, U	Crania	Matsu'ura et al. 2020



36	Sangiran	Indonesia	−7.58	111.80	1.400	FT, U	Crania	Matsu'ura et al. 2020
37	Shandingdong (Upper Cave)	China	38.00	104.00	0.035	AMS	Crania, several mandibular fragments, teeth	Li et al. 2018
38	Shangchen (Nihewan)	China	34.22	109.49	2.100	Loess	Artifacts	Zhu et al. 2018
39	Shirao-Saonetabaru Cave Ruins	Japan	24.38	124.21	0.018	RC	Crania, postcranial fragments	Nakagawa et al. 2010
40	Tabon	Philippines	9.28	117.98	0.250	BIO	Partial mandibles, cranial fragments	Dizon et al. 2002
41	Tam Pa Ling	Laos	20.21	103.41	0.060	U	Cranium, mandible	Shackelford et al. 2018
42	Teshik Tash	Uzbekistan	41.00	68.00	0.060	BIO	Skull	Glantz et al. 2009
43	Tianyuan	China	39.66	115.87	0.042	ESR, U	Cranial fragments, mandible, teeth	Shang et al. 2007
44	Trinil	Indonesia	−7.37	110.00	0.800	Magnetostratigraphy	Calotte, femur	Antón 2003
45	Turubong	South Korea	36.50	127.54	0.045	BIO	Skull, postcranial elements	Norton 2000

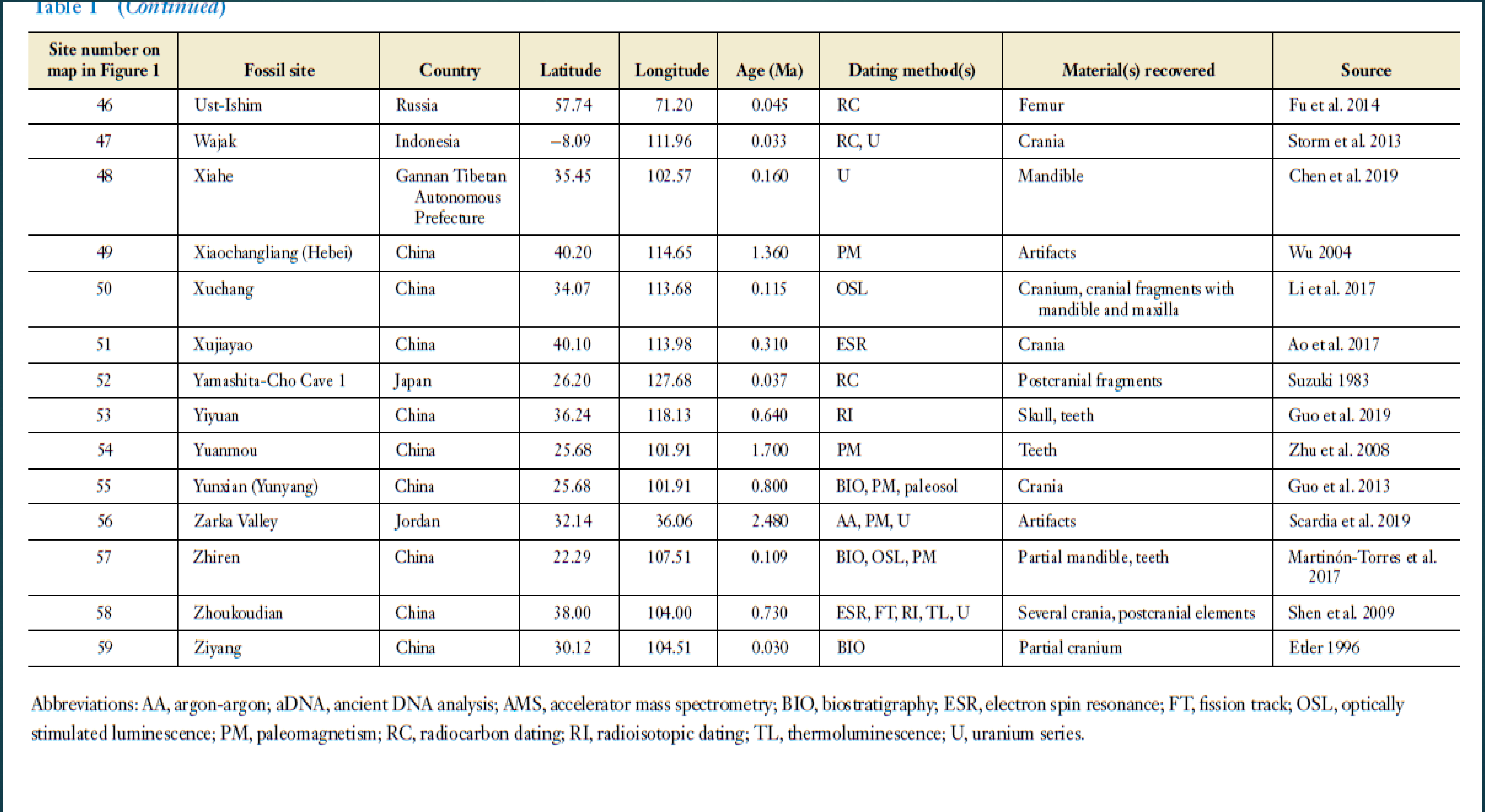


Table 1 (Continued)

Site number on map in Figure 1	Fossil site	Country	Latitude	Longitude	Age (Ma)	Dating method(s)	Material(s) recovered	Source
46	Ust-Ishim	Russia	57.74	71.20	0.045	RC	Femur	Fu et al. 2014
47	Wajak	Indonesia	−8.09	111.96	0.033	RC, U	Crania	Storm et al. 2013
48	Xiahe	Gannan Tibetan Autonomous Prefecture	35.45	102.57	0.160	U	Mandible	Chen et al. 2019
49	Xiaochangliang (Hebei)	China	40.20	114.65	1.360	PM	Artifacts	Wu 2004
50	Xuchang	China	34.07	113.68	0.115	OSL	Cranium, cranial fragments with mandible and maxilla	Li et al. 2017
51	Xujiayao	China	40.10	113.98	0.310	ESR	Crania	Ao et al. 2017
52	Yamashita-Cho Cave 1	Japan	26.20	127.68	0.037	RC	Postcranial fragments	Suzuki 1983
53	Yiyuan	China	36.24	118.13	0.640	RI	Skull, teeth	Guo et al. 2019
54	Yuanmou	China	25.68	101.91	1.700	PM	Teeth	Zhu et al. 2008
55	Yunxian (Yunyang)	China	25.68	101.91	0.800	BIO, PM, paleosol	Crania	Guo et al. 2013
56	Zarka Valley	Jordan	32.14	36.06	2.480	AA, PM, U	Artifacts	Scardia et al. 2019
57	Zhiren	China	22.29	107.51	0.109	BIO, OSL, PM	Partial mandible, teeth	Martinón-Torres et al. 2017
58	Zhoukoudian	China	38.00	104.00	0.730	ESR, FT, RI, TL, U	Several crania, postcranial elements	Shen et al. 2009
59	Ziyang	China	30.12	104.51	0.030	BIO	Partial cranium	Etler 1996

Abbreviations: AA, argon-argon; aDNA, ancient DNA analysis; AMS, accelerator mass spectrometry; BIO, biostratigraphy; ESR, electron spin resonance; FT, fission track; OSL, optically stimulated luminescence; PM, paleomagnetism; RC, radiocarbon dating; RI, radioisotopic dating; TL, thermoluminescence; U, uranium series.

History of theoretical dispute

- The fossil record from Asia has long been explained by continuity from earlier hominins to modern humans.
- The predominant view of continuity among the paleoanthropologists in Asia and the United States persisted through the 1990s;
- Tension began to develop when the idea of a recent African origin of modern humans as a new species, Homo sapiens, and the ensuing complete replacement of indigenous archaic humans increasingly gained support particularly among the geneticists in Europe and the United States.

History of theoretical dispute

- Genetics and morphology were often described as depicting different pictures of human evolution, with genetics supporting discontinuity and morphology supporting continuity.
- The development in genomics that took place in the twenty-first century brought forward the important role played by the concepts of introgression and admixture between ancient populations in shaping recent human evolution.

Hominins lived in Asia for almost 2 million years

- The first evidence of hominins in Asia, either fossil or archaeology, may date to as early as two million years ago.

- The earliest evidence for a hominin presence in Asia comes from archaeological sites in northern China without hominin fossils:
  - the Nihewan Basin sites such as Majuangou dated 1.32–1.66 Ma and
  - Shangchen dated 2.1 Ma based on loess.

Tool traditions in Asia

- Stone tools found from these early archaeological sites are Mode 1, chopper-chopping tool industry, using quartz as the material.

- Mode 1 chopper-chopping tools are associated with processing bones for marrow from a scavenging adaptation, in contrast to Mode 2 handaxes, which are associated with butchering and processing meat from big-game hunting.

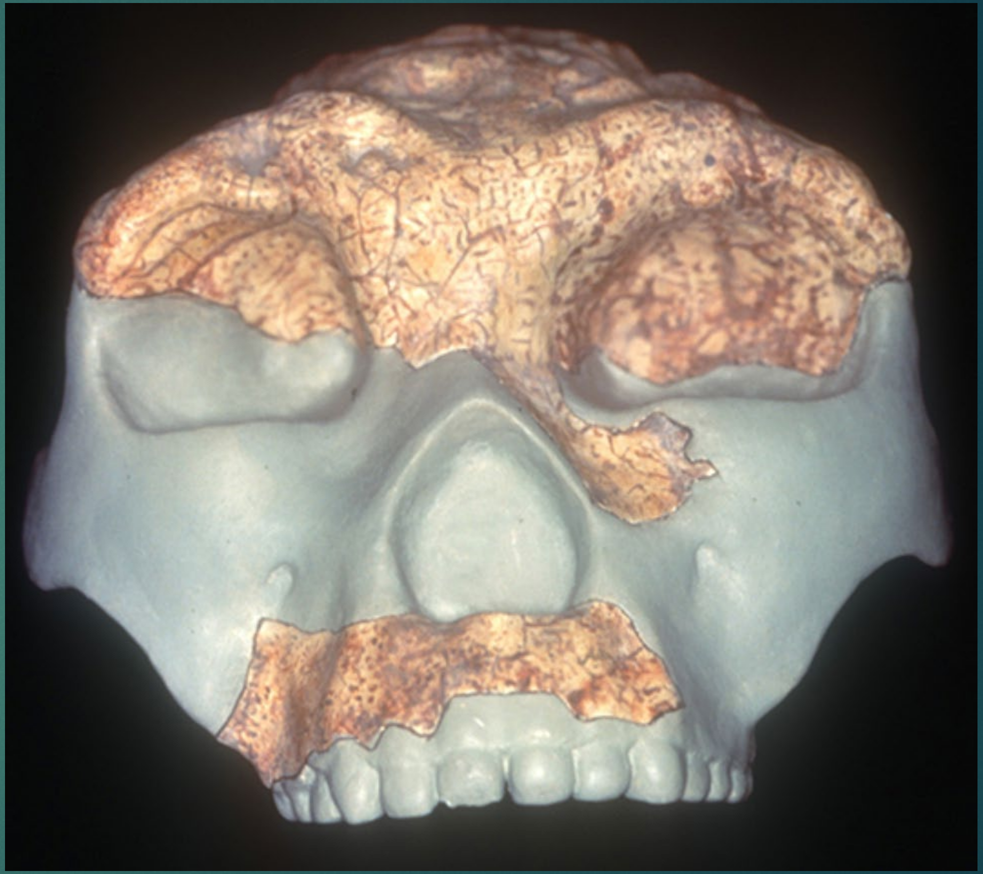
- Mode 1 technology continued in Asia for a long time, even after Modes 2 and 3 tools were made.

No hominins, only tools

- Although no hominin fossil has been discovered in the archaeological sites discussed above, Gongwangling, Shaanxi (Site 15), a fossil hominin site, is in the vicinity of Shangchen, dated to 1.62 Ma based on the paleomagnetic dating of loess-paleosol sequences. The new name given at first, Sinanthropus lantianensis, does not signify a new species.

- The Gongwangling cranium shows traits consistent with the later Homo erectus specimens in Asia—namely, a long and low frontal, thick supraorbital torus, and thick cranial bones. The cranial capacity estimated at 780 cc is similar to that of Dmanisi, Georgia (Site 6), with cranial capacity estimates in the range of 546–730 cc.

Gongwangling cranium



Yuanmou: shovel shaped incisors, 1.7 Ma

- Early fossils:
- The two incisors from Yuanmou, Yunnan (Site 54), are dated to the Early Pleistocene, at 1.7 Ma based on magnetostratigraphy.
- The Yuanmou incisors have shovel shaping, a trait found in high frequency among fossil hominins in Asia and among populations in this region today.
- It is also notable that this incisor morphology is found in hominins from Africa of earlier and comparable dates, such as KNM-ER 1590B and KNM-WT 15000. This may be an example of a trait that originated in Africa that then became a regionally predominant trait in Asia.

Other sites at 1 to 2 Ma

- In addition to the early dates of Yuanmou and Gongwangling, other sites in the region provide further evidence for hominin habitation dating more than one million years ago with Xiaochangliang, Hebei (Site 49), at 1.36 Ma, and Donggutuo (Site 7) at around 1 Ma.
- Archaeological evidence from West Asia such as Zarka Valley (Site 56), Jordan, dated with stone tools at 2.48 Ma using paleomagnetic, argon, and uranium dating methods,
- ** And the Shangchen stone tools dated to 2.1 Ma strengthen the model of early dispersal out of Africa

Asian Origins Model

- As Pliocene (<2.6 Ma) hominins are found only in Africa, and as the earliest fossil members of the genus Homo are found in Africa, hominin dispersal from Africa into Eurasia is the reasonable and widely accepted hypothesis.
- An alternative to this dispersal model is the Asian origins model, arguing for an even earlier hominin dispersal out of Africa and into Eurasia, possibly an australopithecine, from which Homo erectus originated, which in turn spread throughout Eurasia and ultimately back to Africa.

No support for Asian origins model

- ** While the Early Pleistocene (later than 2.6 Ma) presence of hominins in Asia supports the model of early dispersal of hominins into Eurasia, it does not hold enough weight to support the Asian origins model.
- Australopithecines being adapted to savanna and woodlands and using stone tools are minimally compatible with the Asian origins model.
- CJV: No evidence of pre H. erectus hominins have ever been found in Asia. At least yet.

No evidence for Asian origins model

- If the dispersing hominins originated in Africa, and if dispersal was rapid (considering that the earliest hominin appeared in Asia not long after Homo erectus appeared in Africa), the earliest hominins should be similar to one another, and all similar to the early Homo in Africa.

No evidence for australopiths outside of Africa

- However, if they are different, this would be more compatible with a different and much earlier lineage out of Africa, in the Early Pleistocene and even terminal Pliocene, with more time to diversify.
- *** As there is no validated presence of australopithecines outside of Africa, there is not much support for the Asian origins model.

3. Continuity of regional traits: ancestry or gene flow

- Homo erectus is the hominin species that is first known to have inhabited Asia and also the first hominin fossil found in Asia, with the discovery from Trinil (Site 44) in 1891.
- Hominin fossils and archaeological materials found in Zhoukoudian during the 1920s and 1930s form the basis of what we understand to be Homo erectus morphology: thick cranial bones, thick torus around the cranium (supraorbital, angular, and occipital torus), sagittal keel, low forehead, and postorbital constriction.

Zhoukoudian

- The hominin fossils from Zhoukoudian were first announced as Sinanthropus pekinensis (Black 1927). Because they were similar to those from Indonesia that were called Pithecanthropus erectus.
- The Sinanthropus pekinensis fossils were merged into Pithecanthropus erectus (Weidenreich 1943), which in turn was later changed to Homo erectus (Mayr 1950).
- The dating of the hominin activity in the Zhoukoudian (Site 58) cave as yielded various results: from 800 ka to 400 ka and from 578 ka to 230 ka.

Numerous names – ultimately, all H. erectus

- Fossils in Asia have been given various names, especially the discoveries made during the early years of paleoanthropology:
  - Pithecanthropus modjokertensis,
  - Pithecanthropus erectus,
  - Pithecanthropus robustus,
  - Pithecanthropus dubius,
  - Meganthropus palaeojavanicus,
  - Javanthropus soloensis,
  - Sinanthropus pekinensis, and
  - Sinanthropus lantianensis.

Naming issues, but ultimately all H. erectus

- Although these names take the binomial format of a genus and a species name, they were not given as a biological classification at the level of species, but rather as referents of different fossil samples.

- Early scholars such as Weidenreich had already recognized the morphological similarities shared by hominin fossils in Asia, although Mayr is credited for subsuming all the fossil materials from Asia under a single species, Homo erectus (Mayr 1950).