



Education and Culture

**Erasmus Mundus**

# The genus *Homo*



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# WHO WAS RELATED TO WHOM?

Fifty years ago, the introduction of *Homo habilis* shook up views of our genus, and the classification of early *Homo* is still debated.

*Australopithecus africanus*

*Australopithecus garhi*

*Australopithecus afarensis*

4 million years ago (approx.)



***Australopithecus***  
Australopiths walked upright, but were also adapted for climbing.

Fossil discovered 1974.



***Homo habilis***  
Remains of a foot and jawbone were judged too human-like for an australopith.

Fossil discovered 1964.



***Paranthropus boisei***  
Nutcracker Man, with its distinctively large jaws, is neither *Australopithecus* nor *Homo*.

Fossil discovered 1959.



**Later *Homo***  
Normal-sized later *Homo* species had larger brains, longer legs and smaller jaws.

Fossil discovered 1909.

Some would lump all early *Homo* species into *Homo erectus*; others would split some into a new non-*Homo* genus.

*Homo ergaster/erectus*

*Paranthropus boisei*

*Homo rudolfensis*

*Homo heidelbergensis*  
*Homo antecessor*

*Homo sapiens*

Denisovans

*Homo floresiensis*

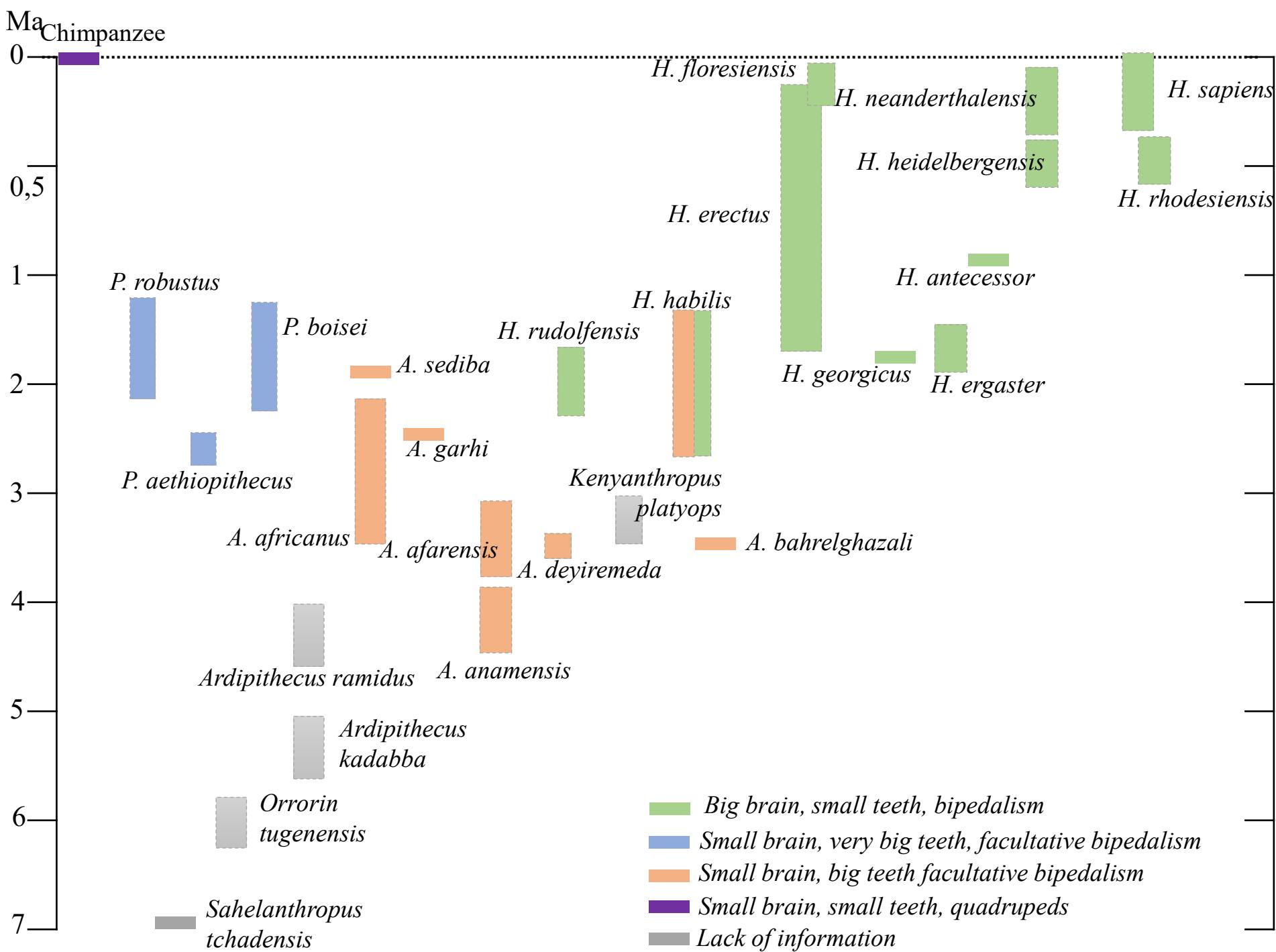
*Homo neanderthalensis*

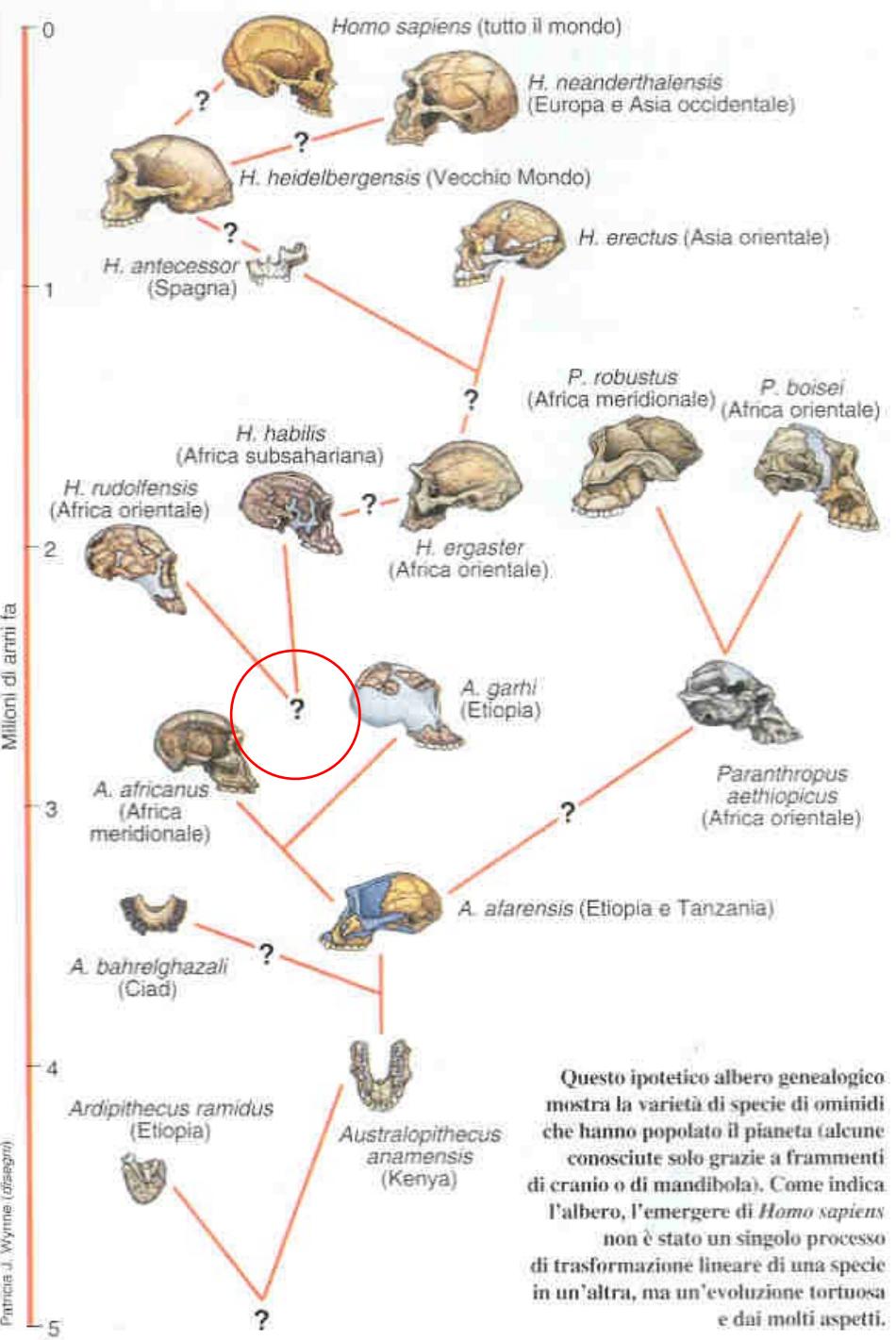
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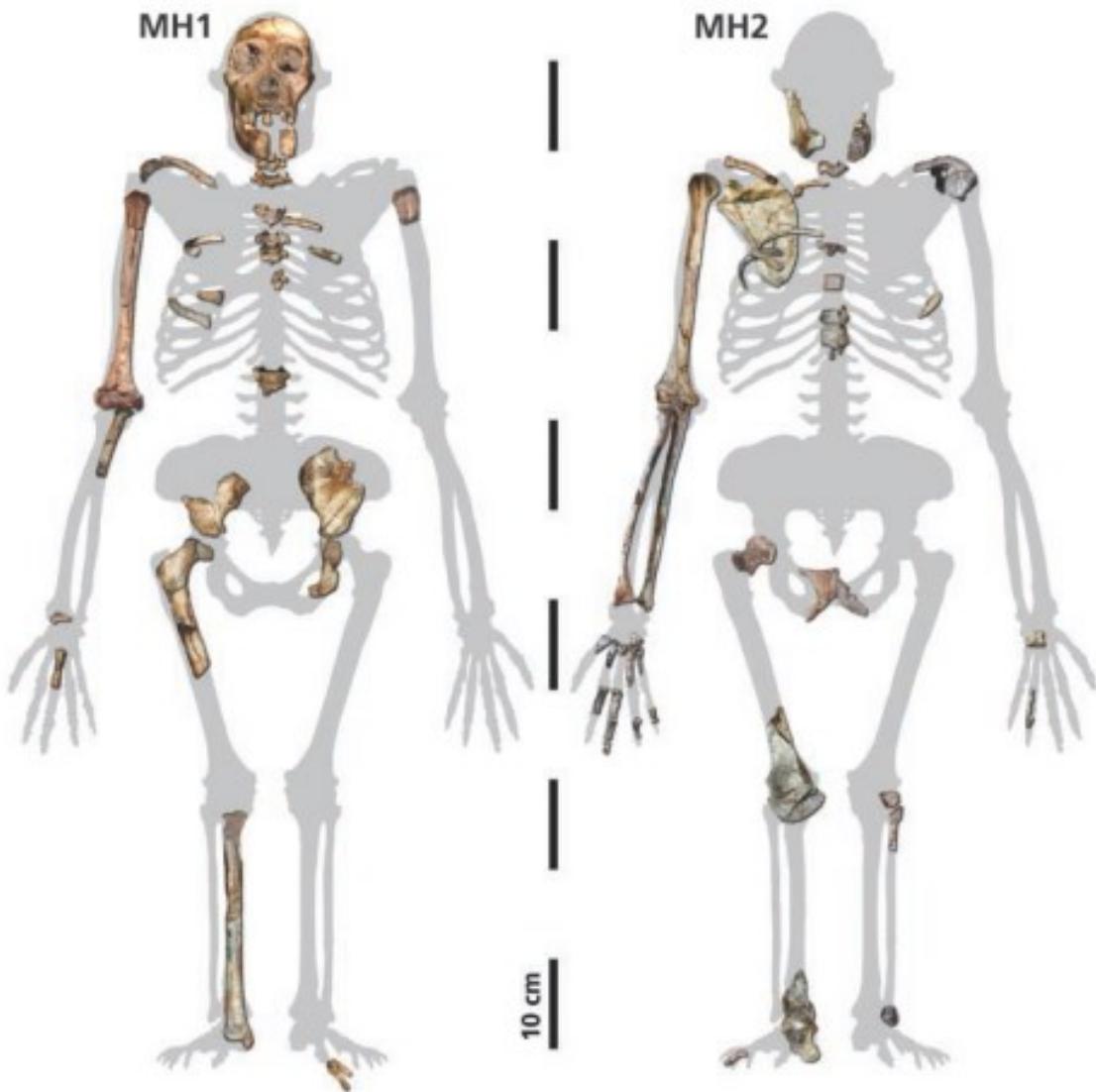
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Present





# *Australopithecus sediba*



**Fig. 2.** Associated skeletal elements of MH1 (left) and MH2 (right), in approximate anatomical position, superimposed over an illustration of an idealized *Au. africanus* skeleton (with some adjustment for differences in body proportions). The proximal right tibia of MH1 has been reconstructed from a natural cast of the proximal metaphysis.

*Au. sediba* (Malapa, South Africa)

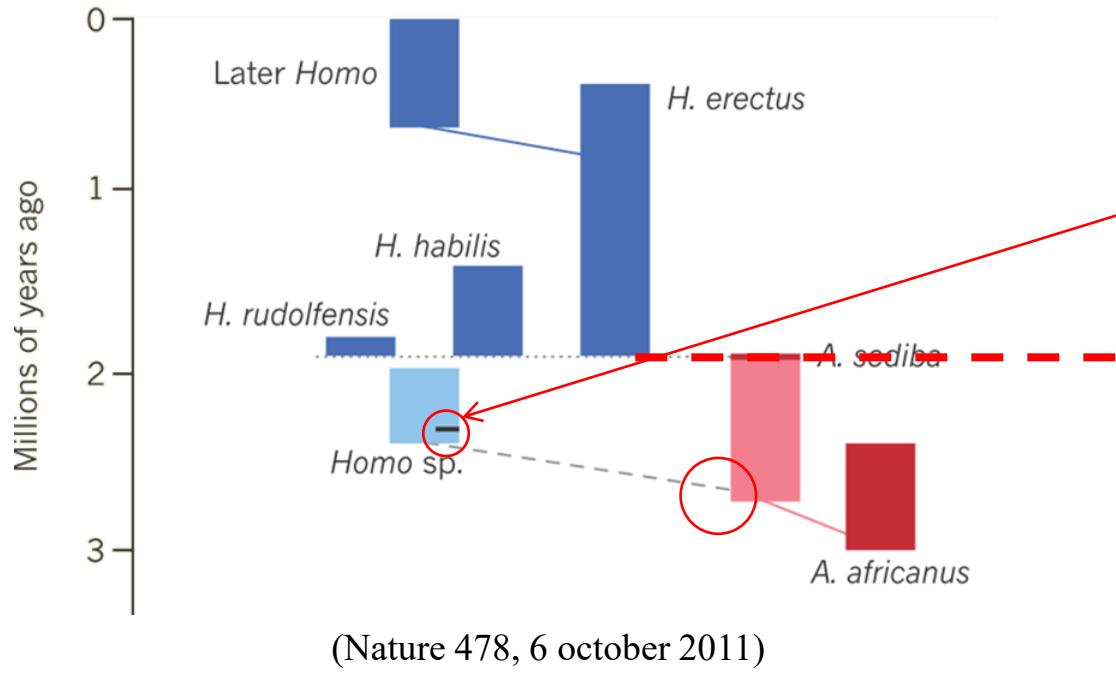
Australopiteco o *Homo* ?

Pro-Australopiteco:

- Piccolo cervello / *small brain*
- Bracci lunghi / *long arms*

Pro-Homo:

- Forma del bacino
- Articolazione dell'anca
- Pollice lungo e dita corti = mani con una manipolazione precisa
- *Shape of the pelvis and ankle joint*
- *long thumb and short finger = hands capable of precise manipulation*



Fossili frammentari generalmente attribuiti ai primi *Homo*  
*Fragmentary fossils that are generally thought to come from early Homo*



AL 666-1 (2.35 Ma, Hadar)

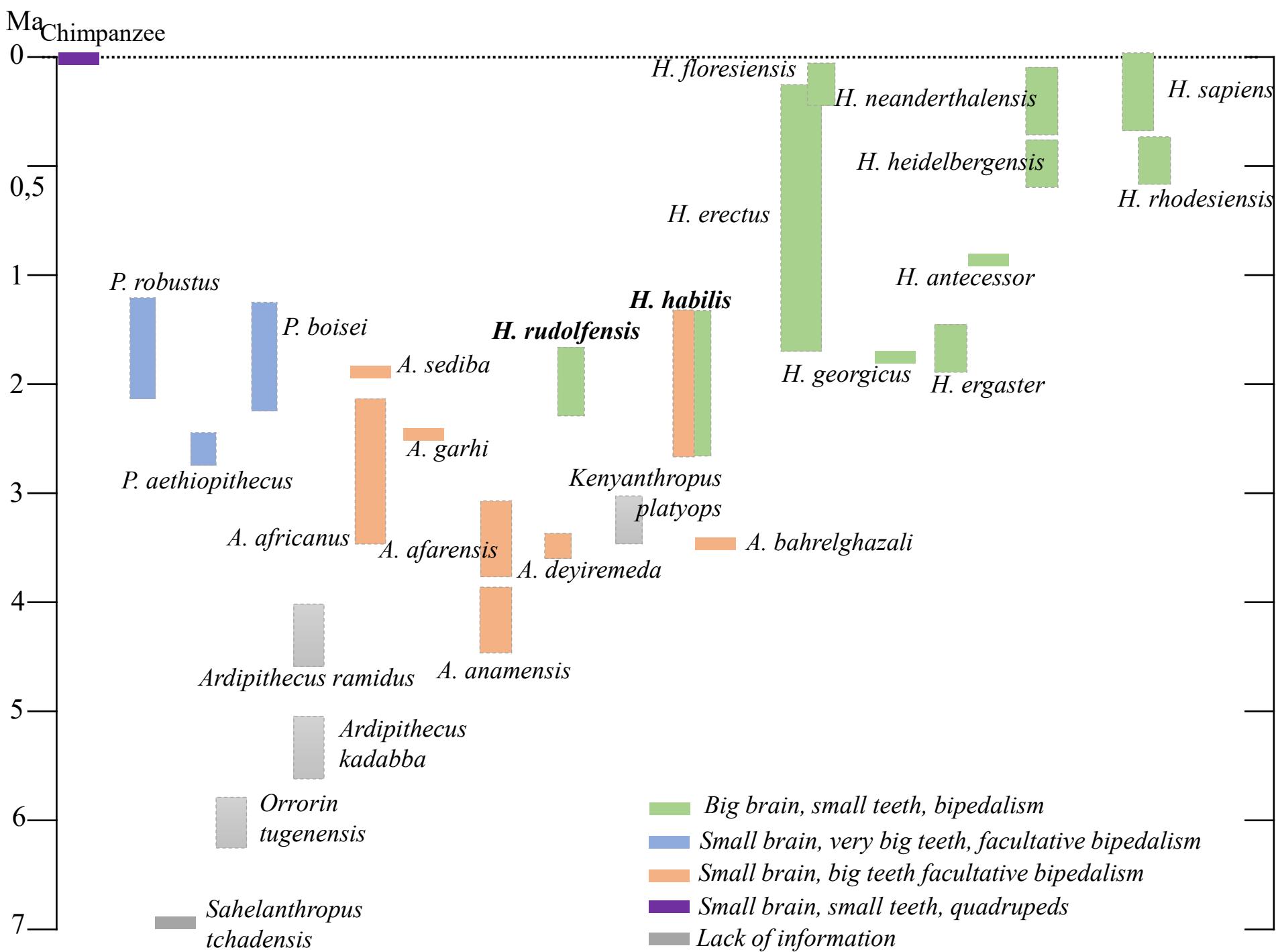
2 scenari where *A. sediba* is the ancestor of the genus *Homo*

**Scenario 1:** I fossili di Malapa sono i ultimi rappresentanti della popolazione di *A. sediba* di cui i primi rappresentanti erano ancestrali a *Homo*

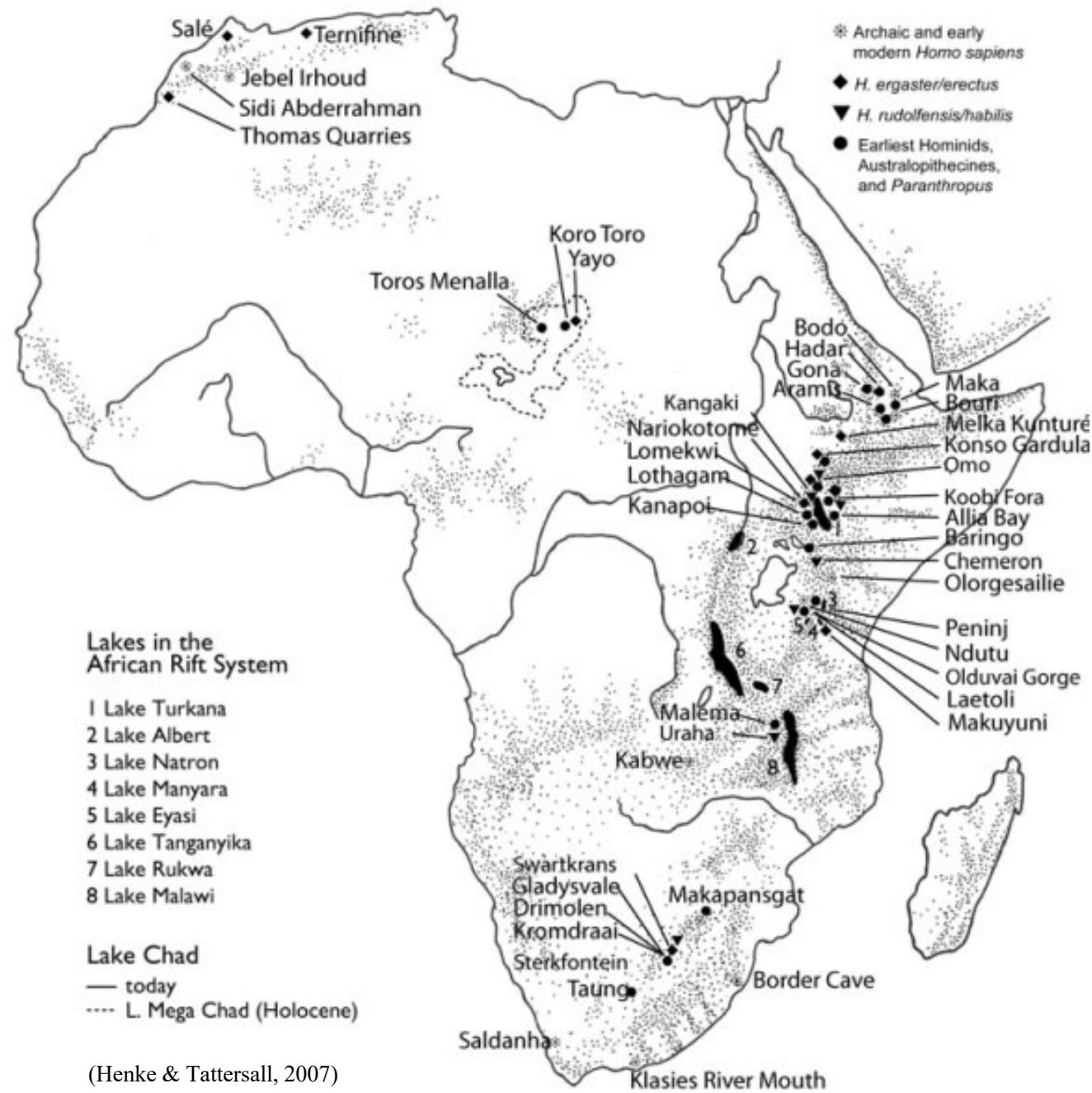
*Scenario 1: Fossils at Malapa come from a late-surviving population of A. sediba, whose earlier representatives were ancestral to Homo*

**Scenario 2:** La popolazione di *A. sediba* a Malapa era ancestrale ai primi *Homo*, implicando che i fossili datati prima di 2 Ma non possono essere attribuiti a *Homo*

*Scenario 2: the A. sediba population at Malapa was itself ancestral to early Homo which means that fossils pre-dating 2 My ago cannot be attributed to Homo*



## African early hominid sites. *Homo rudolfensis* and *Homo habilis* sites in bold



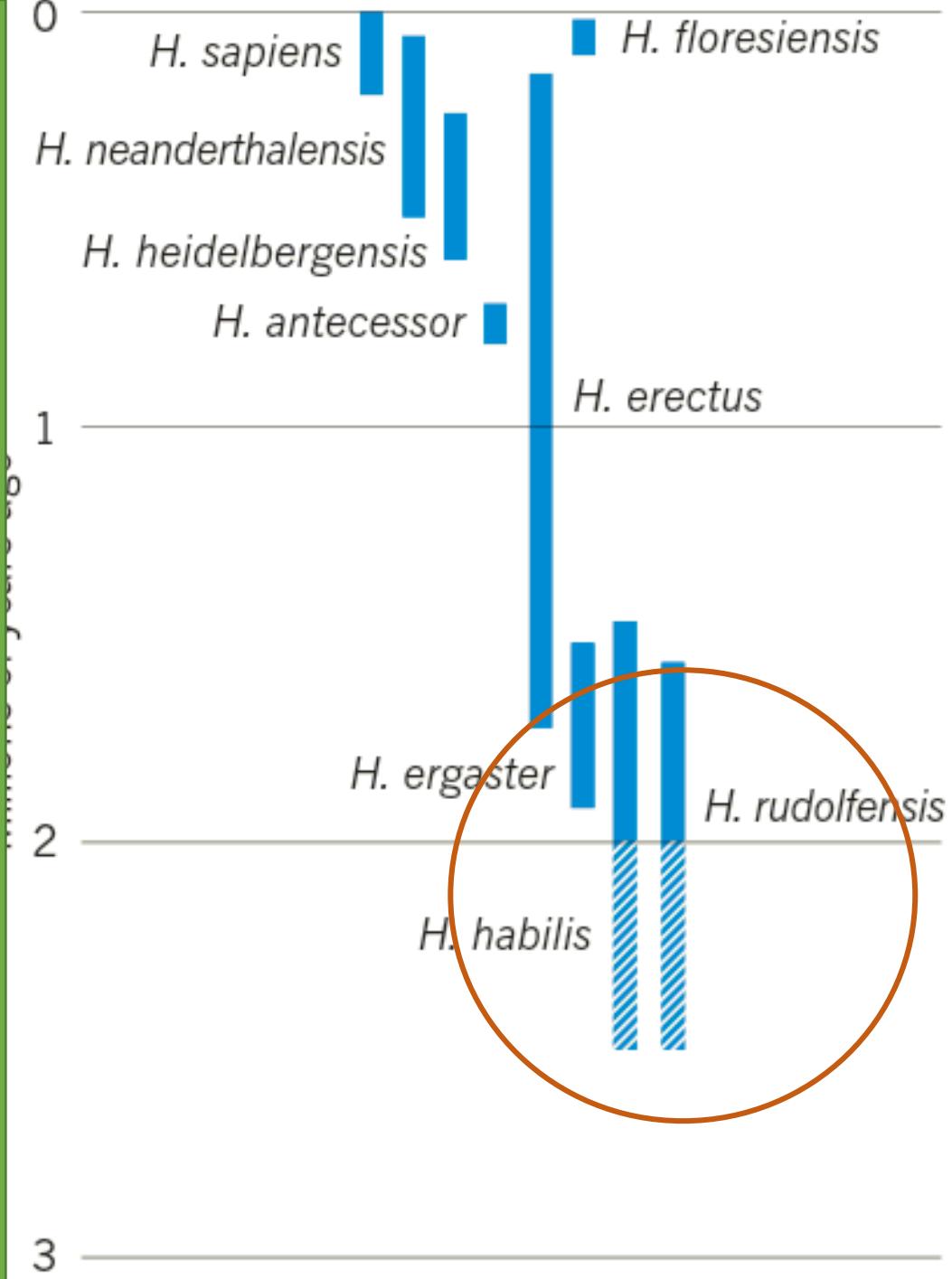
Criteri di assegnazione al genere *Homo* (Keith 1948; Tobias 1991; Wood and Collard 2001)

- Capacità cranica  $> 600\text{cm}^3$
- Capacità di parlare e di produrre industrie
- Pollice opponibile

*Hominid fossils are generally assigned to the genus Homo if they fulfill four main criteria Keith 1948; Tobias 1991; Wood and Collard 2001):*

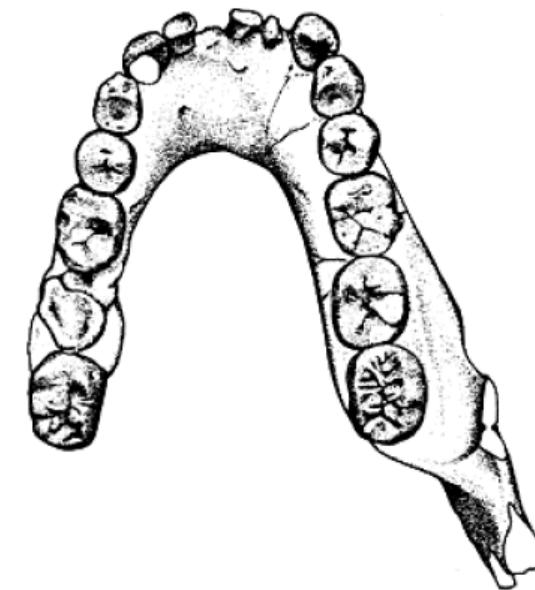
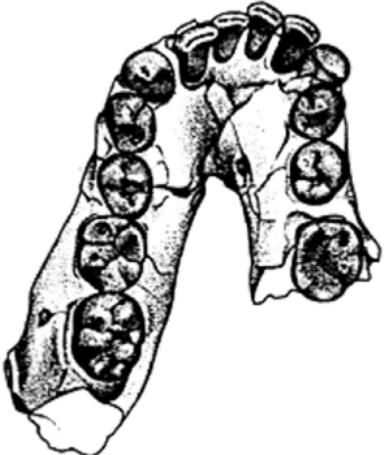
- *A brain size above 600 cm<sup>3</sup>*
- *Ability for speech and tool-making*
- *Opposable Pollux*

# *Homo habilis*



The genus *Homo*, to which modern humans (*Homo sapiens*) and several extinct species belong, most probably arose between **2 million and 3 million years ago**, but fossil evidence **before 2 million years ago** (hatched lines) is frustratingly **sparse**. New fossil discoveries from Leakey and colleagues strengthen the case for recognizing at least two evolutionary lineages at the early stages of the genus, to which the species *Homo habilis* and *Homo rudolfensis* are assigned. However, whether either of these two lineages was ancestral to *Homo erectus*, let alone to modern humans, remains uncertain.

# *Homo habilis*



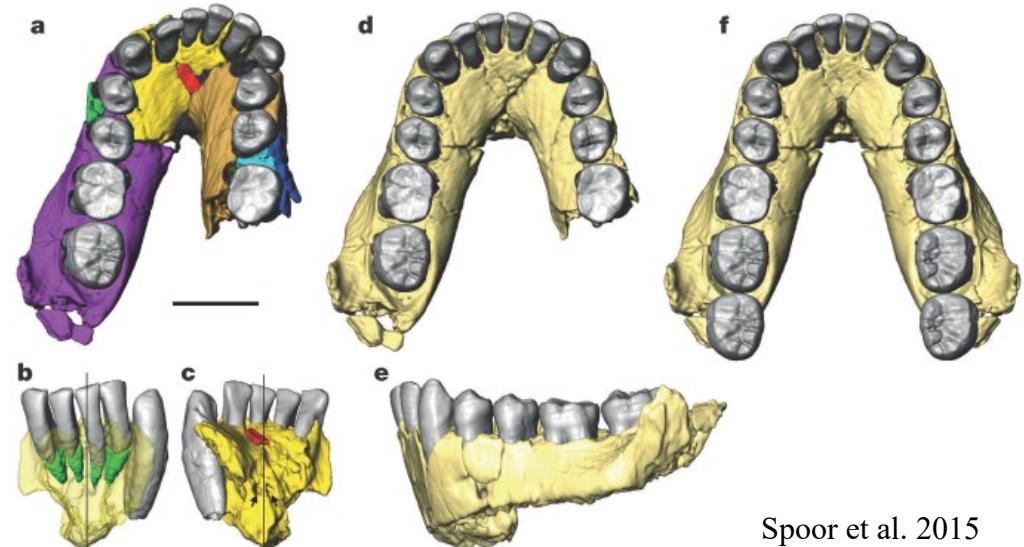
*Homo habilis* mandible OH 13 from Olduvai Gorge, Tanzania. Scale is 1cm.

OH 7: Olotipo di *H. habilis* trovato a Olduvai in 1964.

- Spessore elevato
- PM e M < *Australopithecus*
- CC (calcolato a partire di 2 parietali) = 700 ml

*OH 7: Holotype of Homo habilis from Olduvai Gorge (1964)*

- Thick jaw
- PM and M < *Australopithecus*
- CC (calculated from two parietal bones) = 700 ml

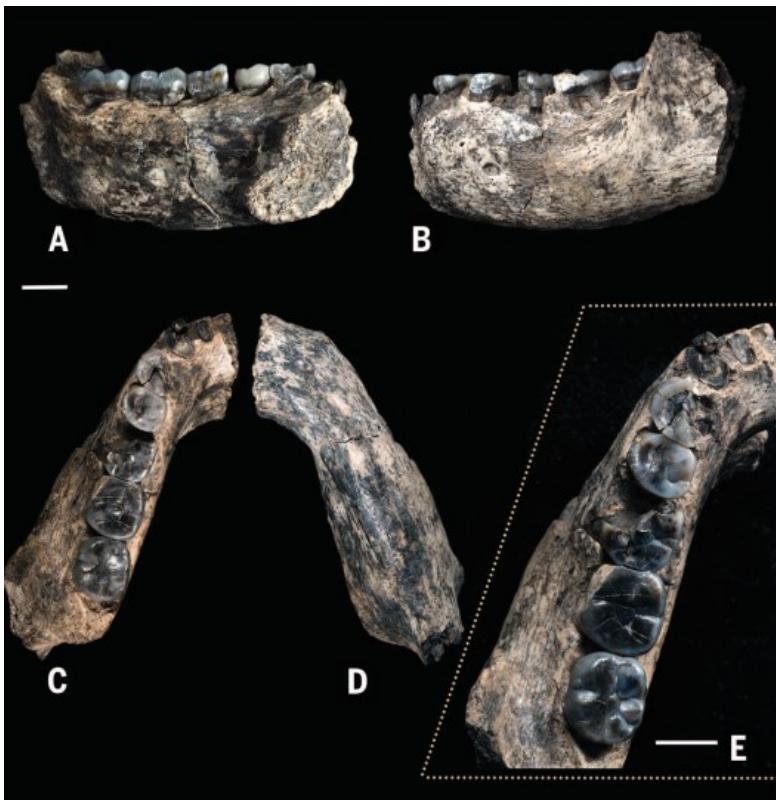


Spoor et al. 2015

# Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia

Brian Villmoare,<sup>1,4,6\*</sup> William H. Kimbel,<sup>2,\*</sup> Chalachew Seyoum,<sup>2,7</sup>  
Christopher J. Campisano,<sup>2</sup> Erin N. DiMaggio,<sup>3</sup> John Rowan,<sup>2</sup> David R. Braun,<sup>4</sup>  
J Ramón Arrowsmith,<sup>5</sup> Kaye E. Reed<sup>2</sup>

Our understanding of the origin of the genus *Homo* has been hampered by a limited fossil record in eastern Africa between 2.0 and 3.0 million years ago (Ma). Here we report the discovery of a partial hominin mandible with teeth from the Ledi-Geraru research area, Afar Regional State, Ethiopia, that establishes the presence of *Homo* at 2.80 to 2.75 Ma. This specimen combines primitive traits seen in early *Australopithecus* with derived morphology observed in later *Homo*, confirming that dentognathic departures from the australopith pattern occurred early in the *Homo* lineage. The Ledi-Geraru discovery has implications for hypotheses about the timing and place of origin of the genus *Homo*.



« The time period 2.8 to 2.5 Ma witnessed climatic shifts that are frequently hypothesized to have led to the origin of the *Homo* lineage. Although the open habitats reconstructed for the Lee Adoyta faunal assemblages provide a new window on these changes, too little is known of the pattern of hominin evolution during this period to forge causal links to specific evolutionary events. The Ledi-Geraru specimen confirms that divergence from australopith dental and mandibular anatomy was an early hallmark of the *Homo* lineage. Additional discoveries are needed to determine whether or not these dentognathic changes were accompanied by neurocranial expansion, technological innovation, or shifts in other anatomical/behavioral systems that are familiar components of the *Homo* adaptive.”



# *Homo habilis*



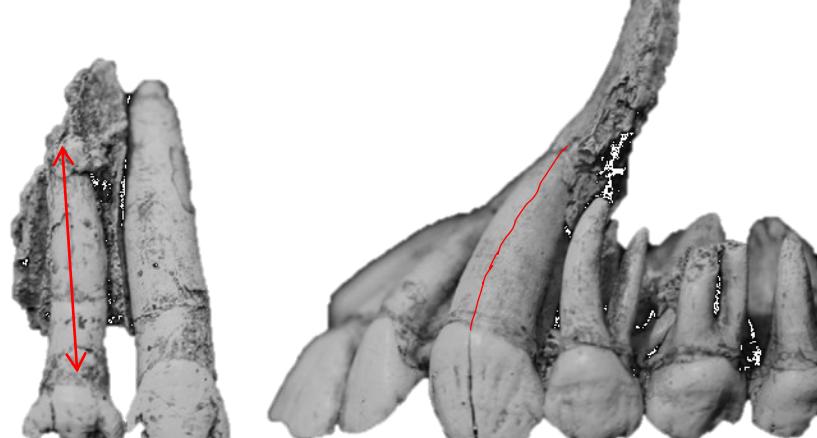
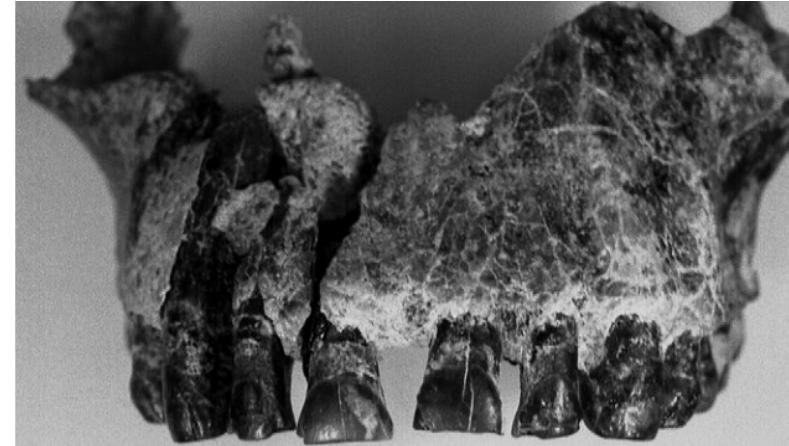
OH 65

C : Radice dritta

*C: straight root*

P3: Radice dritta e unica

*P3: Straight single root*



OH 65

StW 252 *Australopithecus*

C : Radice curva e più corta

*C: Shorter and curved root*

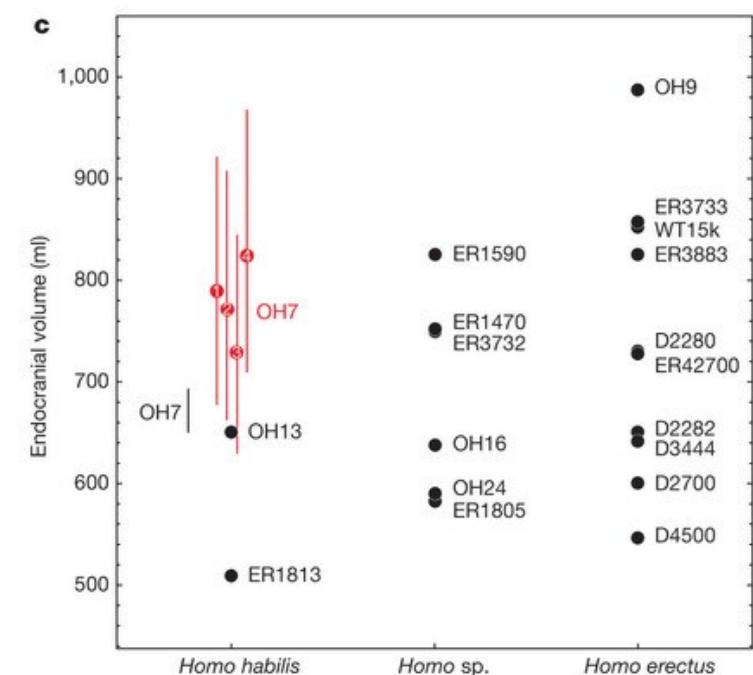
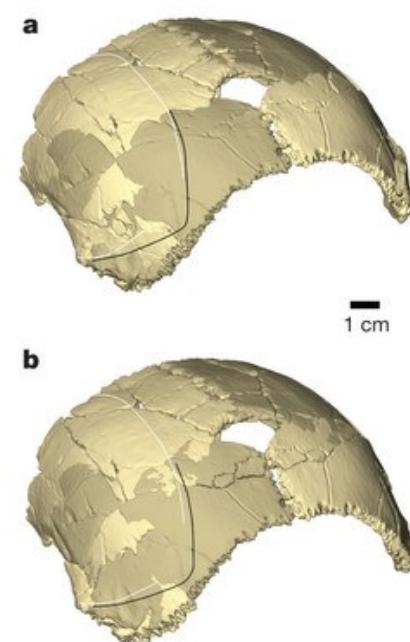
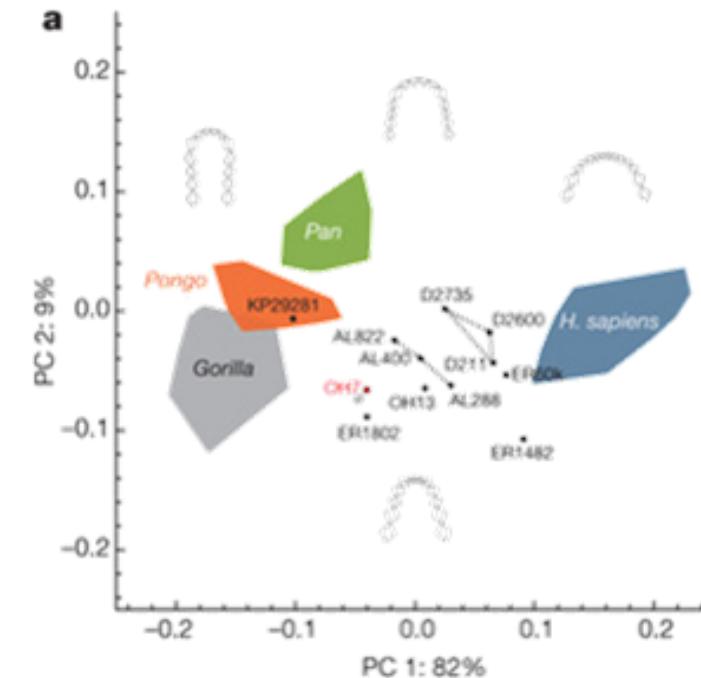
P3: Doppia radice curva

*P3: two short curved roots*

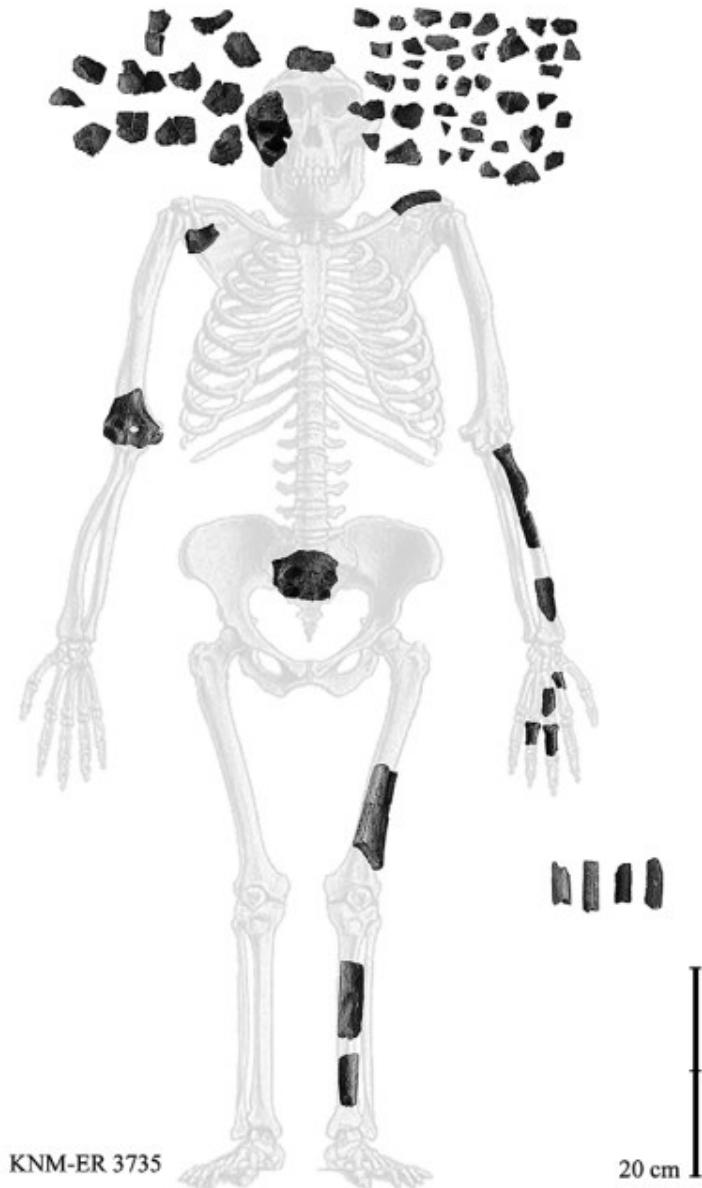
## Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*

Fred Spoor<sup>1,2\*</sup>, Philipp Gunz<sup>1\*</sup>, Simon Neubauer<sup>1</sup>, Stefanie Stelzer<sup>1</sup>, Nadia Scott<sup>1</sup>, Amandus Kwekason<sup>3</sup> & M. Christopher Dean<sup>2</sup>

OH7 = «remarkably primitive, with a long and narrow dental arcade more similar to *Australopithecus afarensis* than to the derived parabolic arcades of *Homo sapiens* or *H. erectus*. This shape variability is not consistent with a single species of early *Homo*. La forma di OH7 non concorda con un unica specie di primi *Homo*. OH 7 is incompatible with fossils assigned to *Homo rudolfensis* and with the A.L. 666-1 *Homo* maxilla. The latter is morphologically more derived than OH 7 but 500,000 years older, suggesting that the *H. habilis* lineage originated before 2.3 million years ago.



# *Homo habilis*



KNM-ER 3735

Haeusler, JHE 53(4), 2007

Mosaica di caratteri:

## Moderni:

- Gracilità dell'omero e del radio  
*Gracile humerus and radius*
- Epifisi prossimale delle falange piccole  
*Small base of the hand phalange*
- Pilastro del femore ben sviluppati  
*Well developed pilaster*
- Geometria della sezione del femore  
*Cross sectional geometry of the femur*

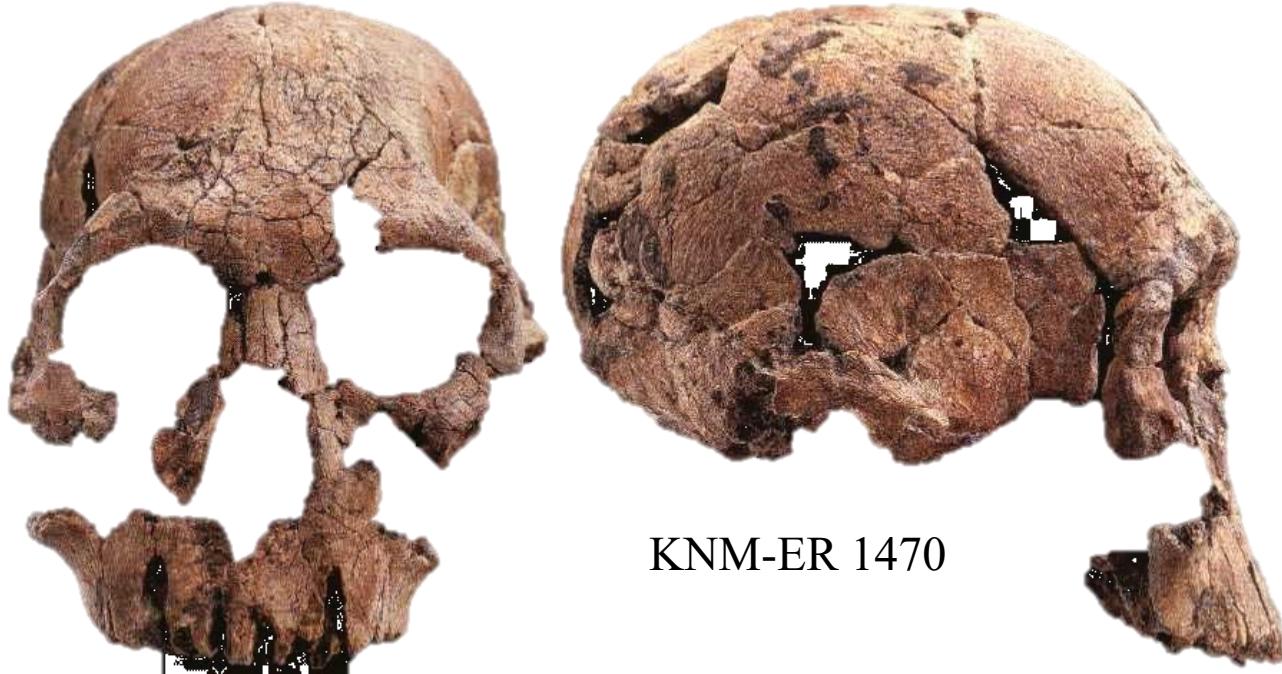
## Ancestrali (condivisi con primi ominidi):

- Sacro piccolo  
*Small sacrum*
- Diafisi delle falange robuste  
*Robust midshaft of the phalanges*

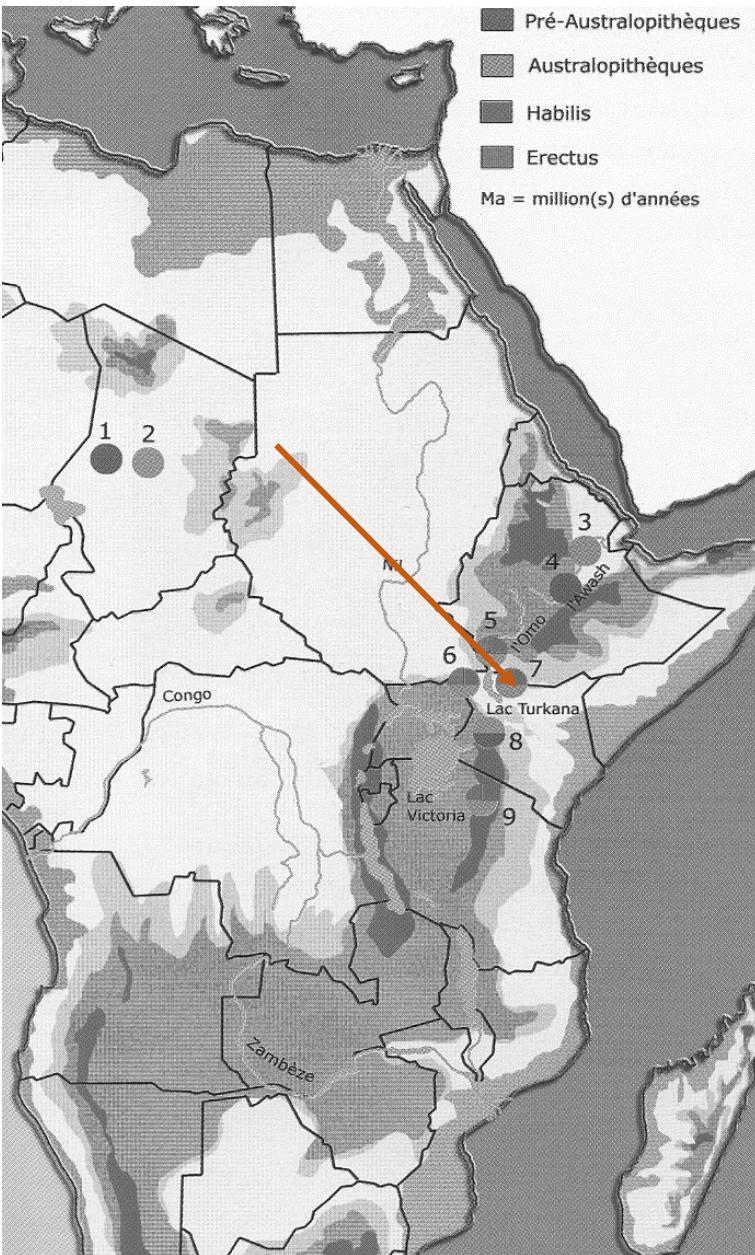
## Scimmiesche:

- Scapola robusta  
*Robust scapula*
- Avambraccio lungo  
*Long forearm*

# *Homo rudolfensis*



KNM-ER 1470





Radice dei zigomatici situati anteriormente  
*Anteriorly placed maxillary zygomatic roots*



Faccia piatta e ortognata nella regione subnasale  
*Flat and subnasally orthognathic face*

## New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*

Meave G. Leakey<sup>1,2</sup>, Fred Spoor<sup>3,4</sup>, M. Christopher Dean<sup>4</sup>, Craig S. Feibel<sup>5</sup>, Susan C. Antón<sup>6</sup>, Christopher Kiarie<sup>1</sup>  
& Louise N. Leakey<sup>1,2</sup>



Figure 1 | The KNM-ER 62000 face. a-d, Anterior (a), right lateral (b), inferior (c) and superior views (d) of the KNM-ER 62000 face. Scale bar, 3 cm.

Molari e premolari piccoli

*Small molars and premolars*

Corpo alto ma stretto mesiolateralmente

*Tall but mediolaterally narrow corpora*

The new fossils confirm the presence of two contemporary species of early *Homo*, in addition to *Homo erectus*, in the early Pleistocene of eastern Africa

KNM-ER 62000: 8 years (?)  
Crown ~ early *Homo*  
Palate shorter than Australopiths



KNM-ER 60000 (1.78-1.87 Ma) e 62003 1.90-1.95 Ma

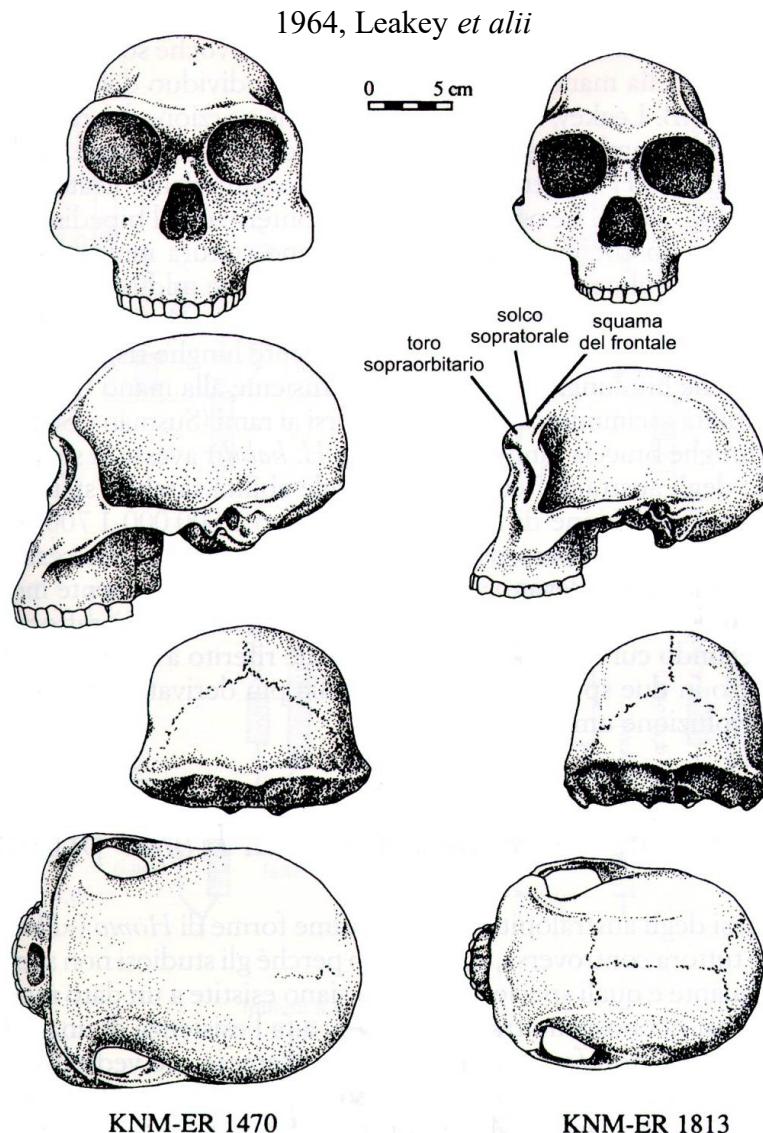
**Significant morphological differences between *H. habilis* and *H. rudolfensis***

	<i>Homo habilis</i> sensu stricto	<i>Homo rudolfensis</i>
Skull and teeth		
Absolute brain size (cm <sup>3</sup> )	An average volume of 610	An average volume of 751
Overall cranial vault morphology	Enlarged occipital contribution to the sagittal arc	Primitive condition
Endocranial morphology	Primitive sulcal pattern	Frontal lobe asymmetry
Suture pattern	Complex	Simple
Frontal	Incipient supraorbital torus	Torus absent
Parietal	Coronal > sagittal chord	Primitive condition
Face-overall	Upper face > midface breadth	Midface > upperface breadth: markedly orthognathic
Nose	Margins sharp and everted; evident nasal sill	Less everted margins; no nasal sill
Malar surface	Vertical or near vertical	Anteriorly inclined
Palate	Foreshortened	Large
Upper teeth	Probably two-rooted premolars	Premolars three-rooted; absolutely and relatively large anterior teeth
Mandibular fossa	Relatively deep	Shallow
Foramen magnum	Orientation variable	Anteriorly inclined
Mandibular corpus	Moderate relief on external surface; rounded base	Marked relief on external surface; everted base
Lower teeth	Buccolingually narrowed; postcanine crowns; reduced talonid on P <sub>4</sub> ; M <sub>3</sub> reduction; mostly single-rooted mandibular premolars	Broad postcanine crowns; relatively large P <sub>4</sub> talonid; no M <sub>3</sub> reduction; twin, platelike P <sub>4</sub> roots, and bifid, or even twin, platelike P <sub>3</sub> roots
Postcranium		
Limb proportions	Apelike	?
Forelimb robusticity	Apelike	?
Hand	Mosaic of apelike and modern humanlike features	?
Hindfoot	Retains climbing adaptations	Later <i>Homo</i> -like
Femur	Australopithecine-like	Later <i>Homo</i> -like

After Wood (1992).

*Homo rudolfensis*  
(2.5-1.6 M.a)

- Morfologia più robusta  
*Most robust morphology*
- maggiore cc (750 cm<sup>3</sup>)  
*> CC*
- faccia più robusta (larga a metà altezza e ortognata)  
*Most robust face*
- Si trova a Koobi Fora, Chemeron e Uraha
- Denti megadonti e abrasione dei denti orizzontale  
*Megadont teeth and more horizontal tooth abrasion*



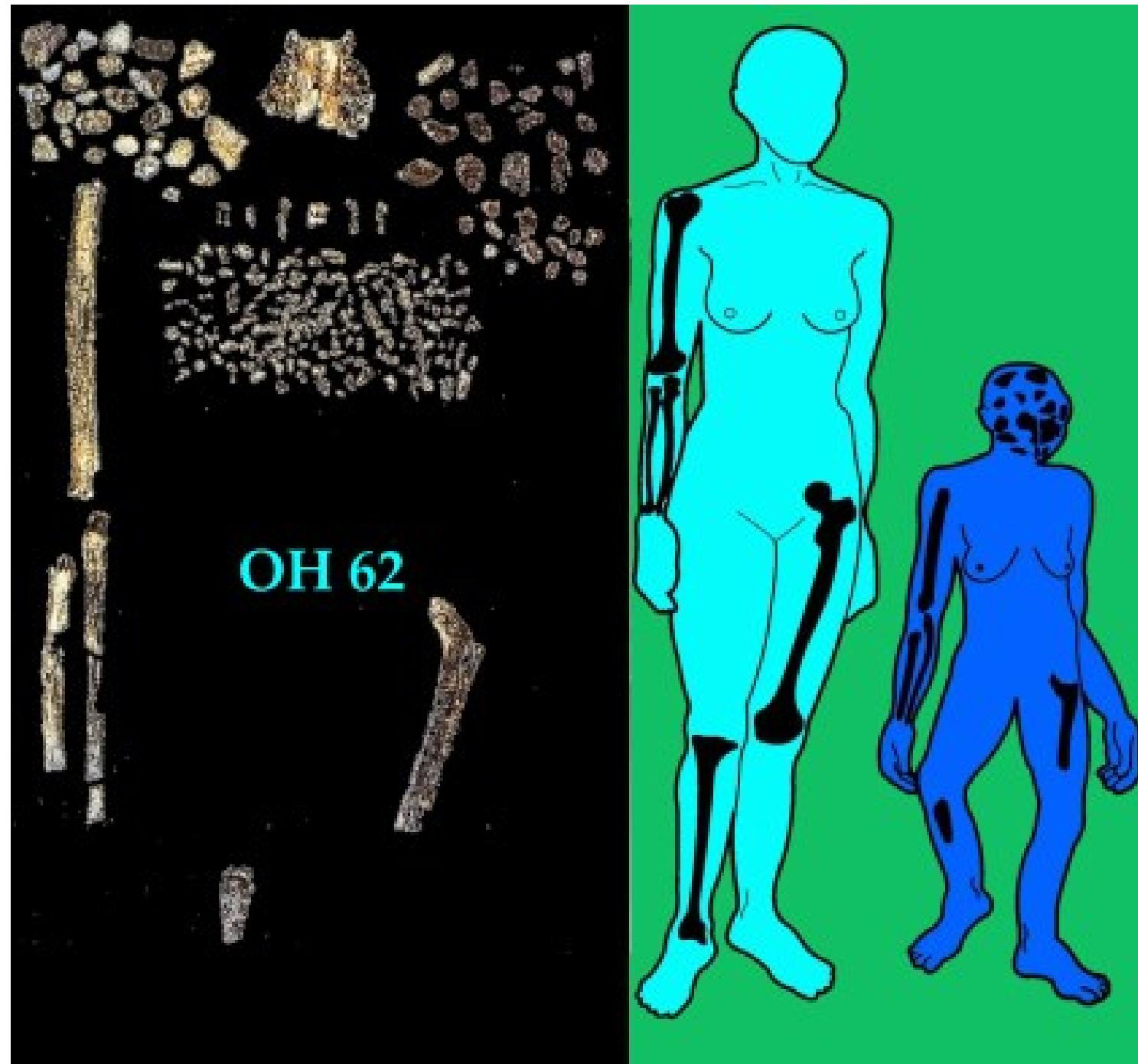
*Homo habilis*  
(2.0-1.6 M.a)

- Specie più gracile  
*More gracile*
- cervello più ridotto (610 cm<sup>3</sup>)  
*<CC*
- Si trova a Koobi Fora, Omo e Olduvai.
- Molari più gracili  
*Molars more gracile*
- Rilievo dei denti usurati più alto  
*higher relief in worn teeth*

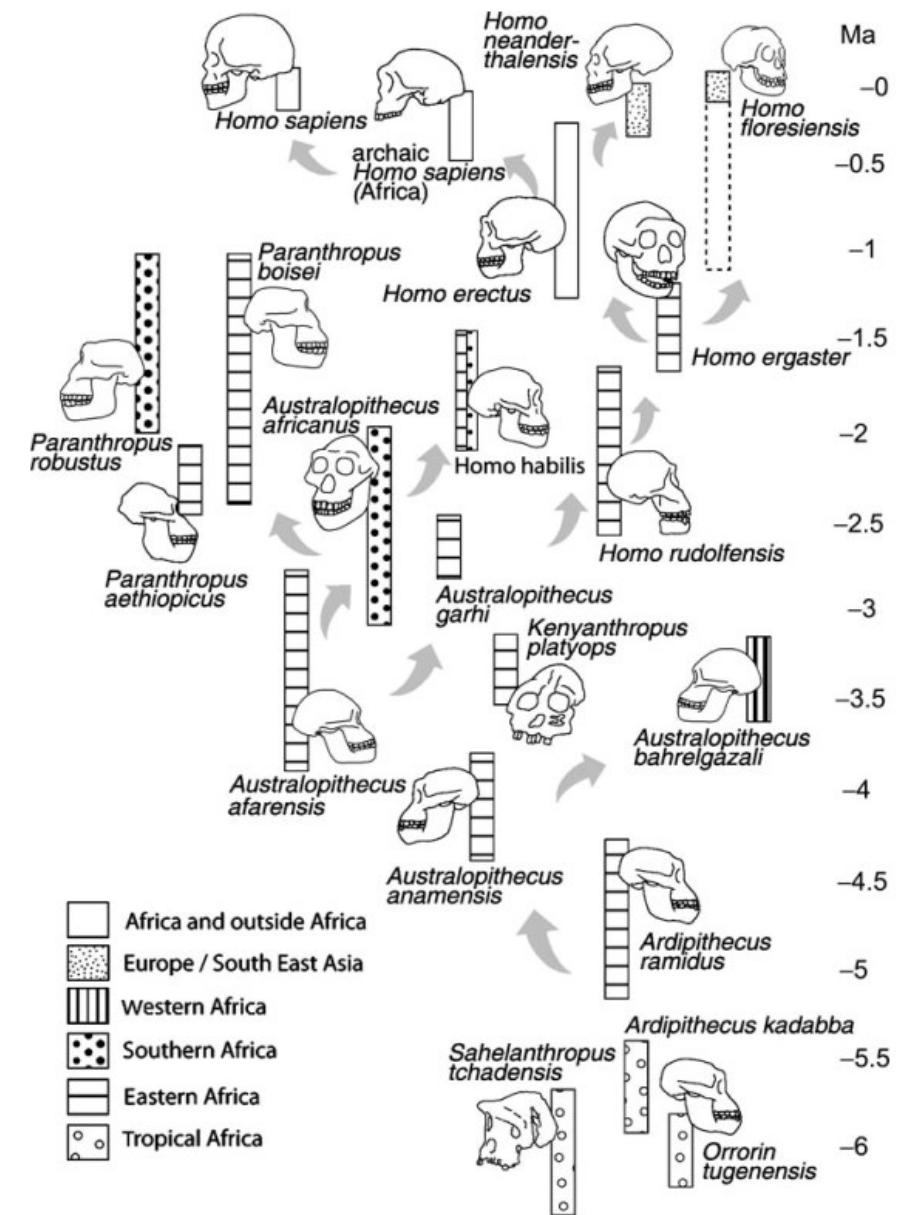
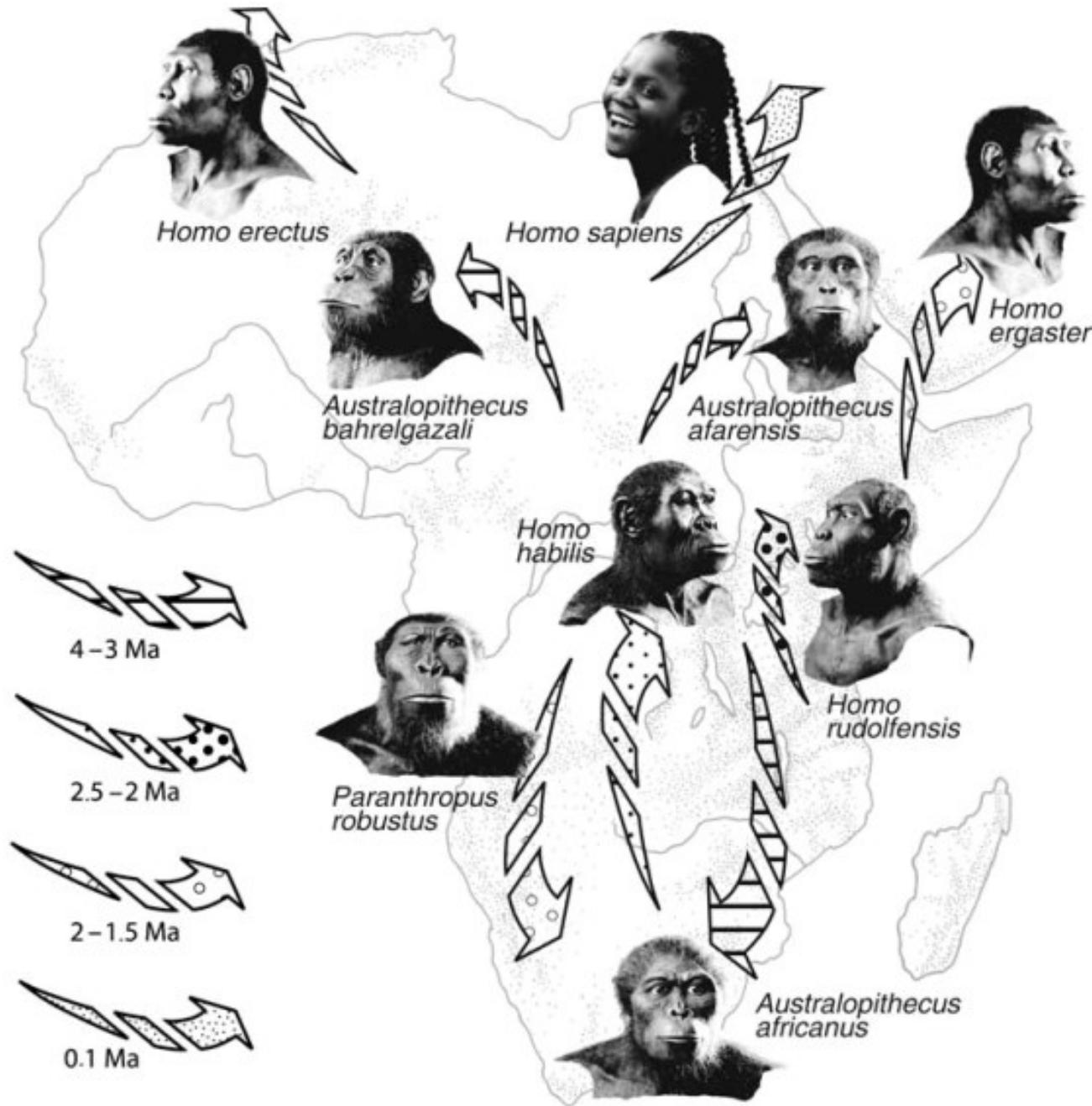
Differenze dell'usura dentaria che indicano delle differenze notevole nella dieta e l'ecologia dei primi *Homo*  
*Differences in tooth wear indicating significant differences in diet and ecology of early Homo species*

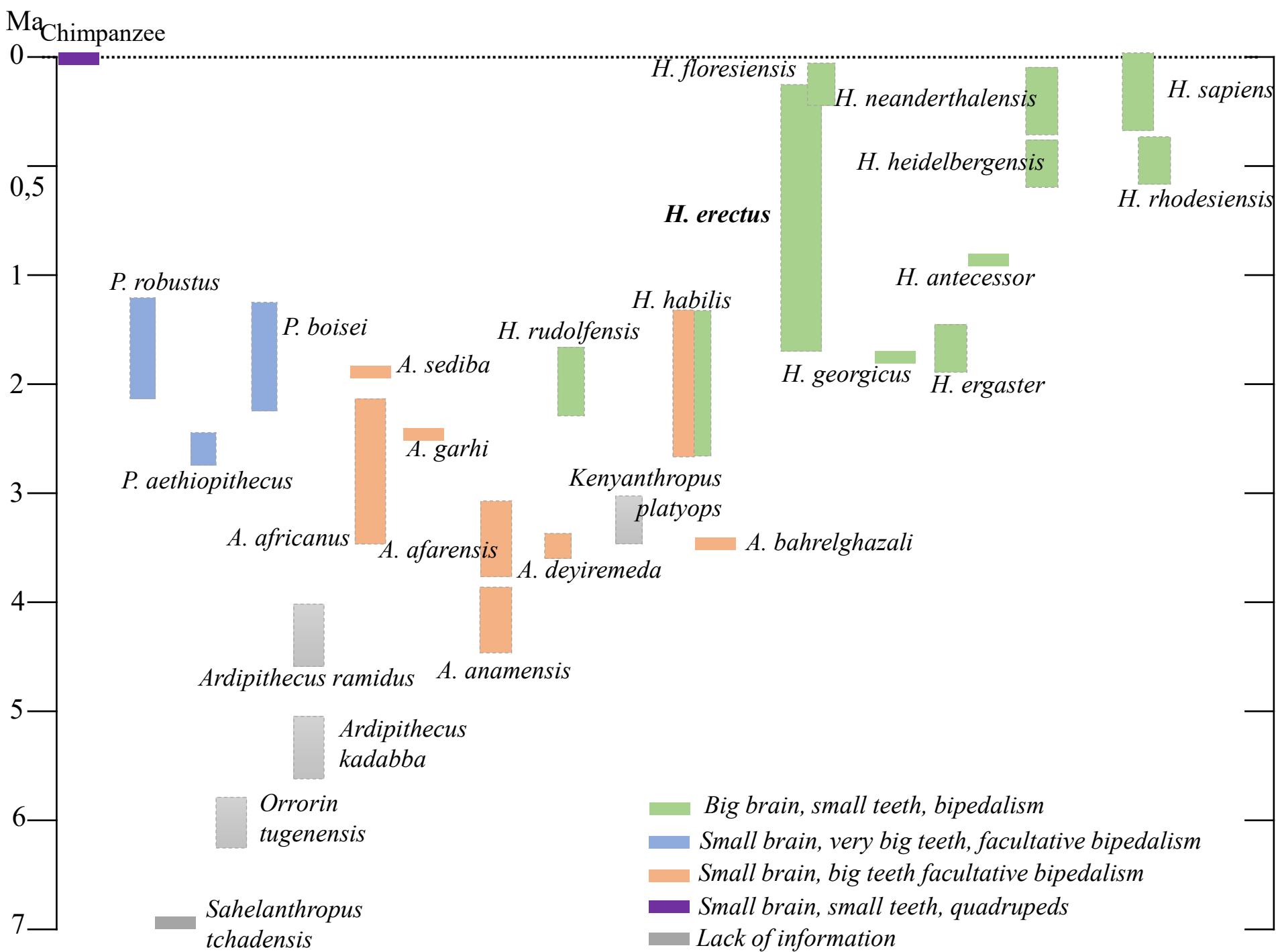
Le caratteristiche morfologiche dimostrano che i individui erano capaci di avere una bipedia efficace. Però il talus è meno umano che il resto del piede e ha una morfologia scimmiesca. La bipedia dell'*Homo habilis* può essere posizionata tra quella occasionale dei Australopitecini e quella obbligata dei *H. ergaster*.

*Efficient bipedism but the talus has ape-like morphology.*  
*The Homo habilis bipedism can be placed somewhere between the occasional one of the Australopiths and the obligatory one of H. ergaster*

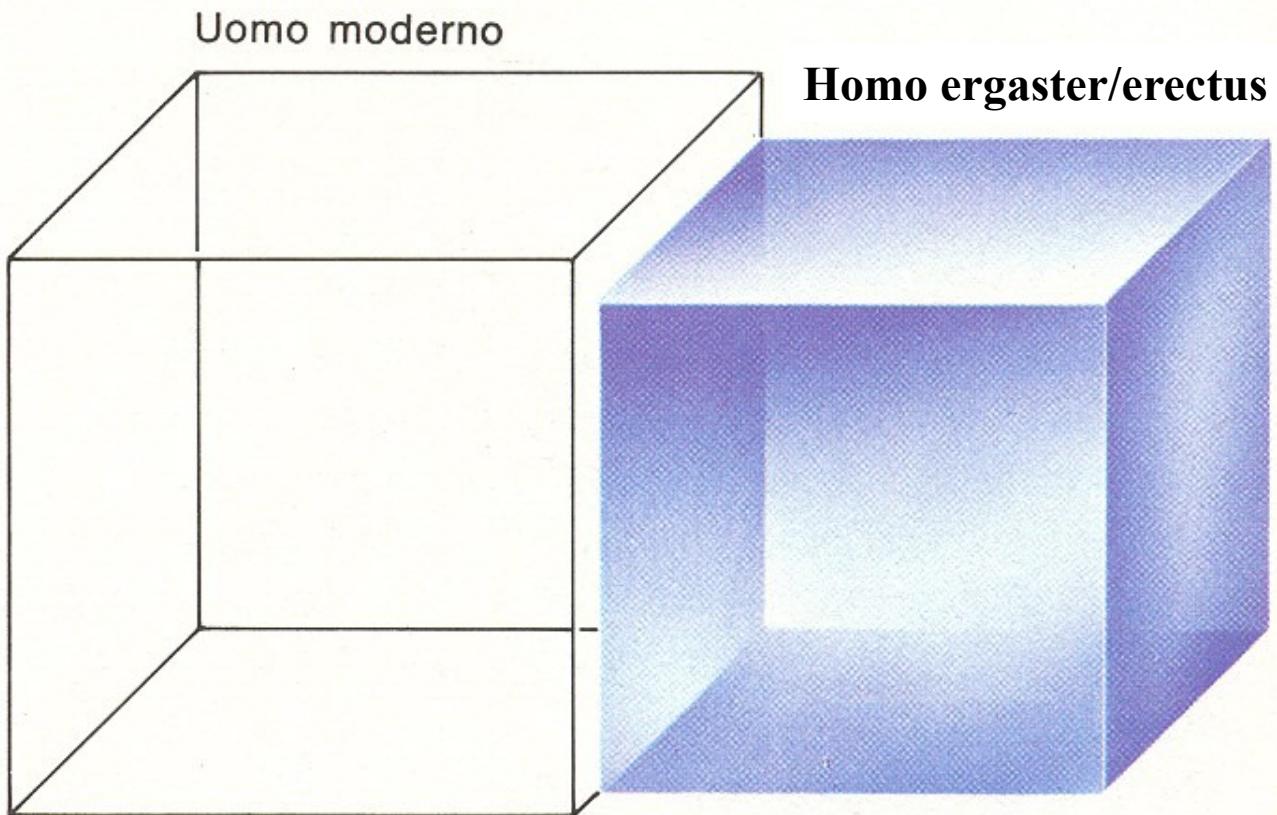


# Early hominid biogeography, dispersal and migration in Africa



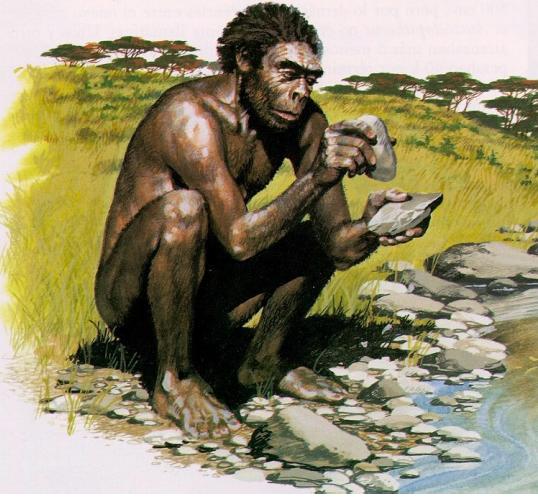


## *Homo erectus/ergaster*



Il graduale aumento nella capacità cranica degli ominidi continuò nell'*Homo erectus*, la cui media era di 950 cm<sup>3</sup>. Si verificarono anche importanti progressi sociali: la caccia fu organizzata, gli utensili divennero più vari, e nei climi più freddi venne usato il fuoco.

*Gradual increase of cranium capacity of the hominids continue in Homo erectus (950 cc). Important social progress: organized hunting, diversification of tools*



# Comparative isotopic evidence from East Turkana supports a dietary shift within the genus *Homo*

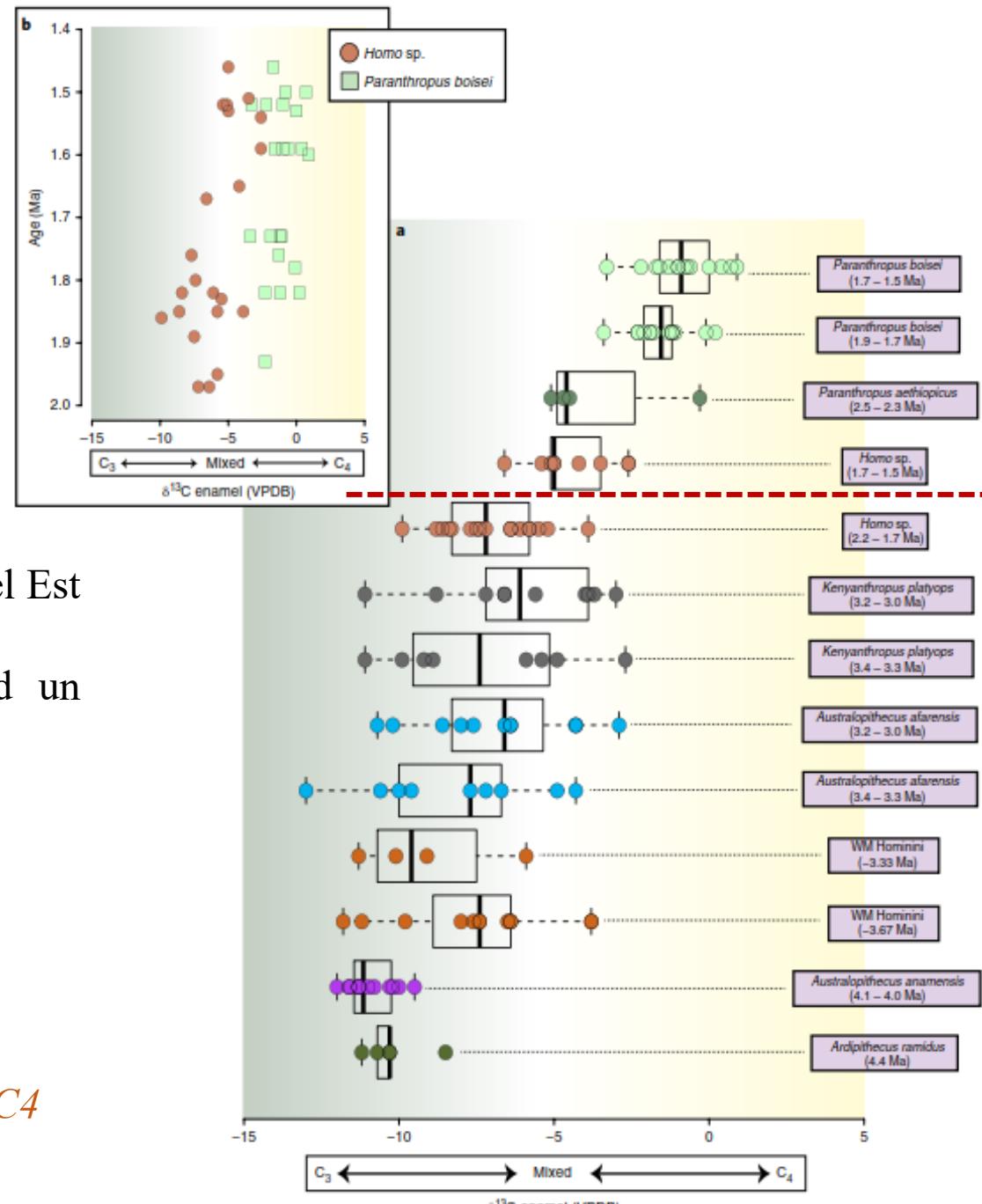
David B. Patterson<sup>1,2\*</sup>, David R. Braun<sup>2</sup>, Kayla Allen<sup>3</sup>, W. Andrew Barr<sup>2</sup>, Anna K. Behrensmeyer<sup>1,4</sup>, Maryse Biernat<sup>1,5</sup>, Sophie B. Lehmann<sup>6</sup>, Tom Maddox<sup>7</sup>, Fredrick K. Manthi<sup>8</sup>, Stephen R. Merritt<sup>9</sup>, Sarah E. Morris<sup>10</sup>, Kaedan O'Brien<sup>11</sup>, Jonathan S. Reeves<sup>12</sup>, Bernard A. Wood<sup>1,2</sup> and René Bobe<sup>13,14</sup>

Cambio significativo della dieta a -1,65 Ma in *Homo* nella regione del Est Turkana che non è correlato ad cambiamenti ambientali.

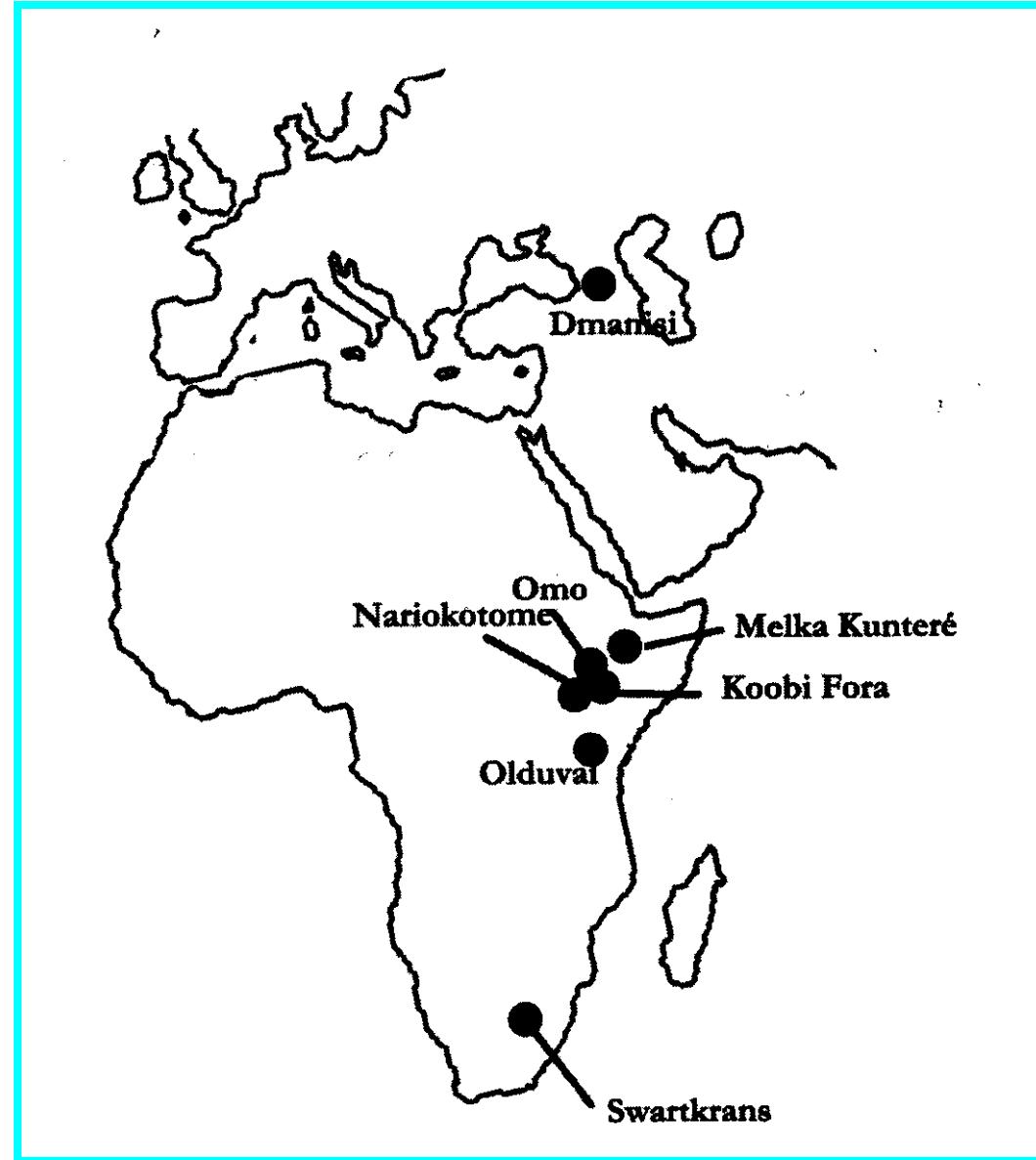
Il pattern dei post-1,65 Ma *Homo* potrebbe essere correlato ad un aumento nel consumo di carne.

*Dietary shift of the genus Homo (In East Turkana) around 1,65 Myrs ago which is not related to changes in this region vegetation and different from the patterns found in other East Turkana large mammals (including Paranthropus).*

*This shift occurred well after the first evidence of early Homo in the region and could be related to the ingestion of more animal tissues of C4 herbivores.*

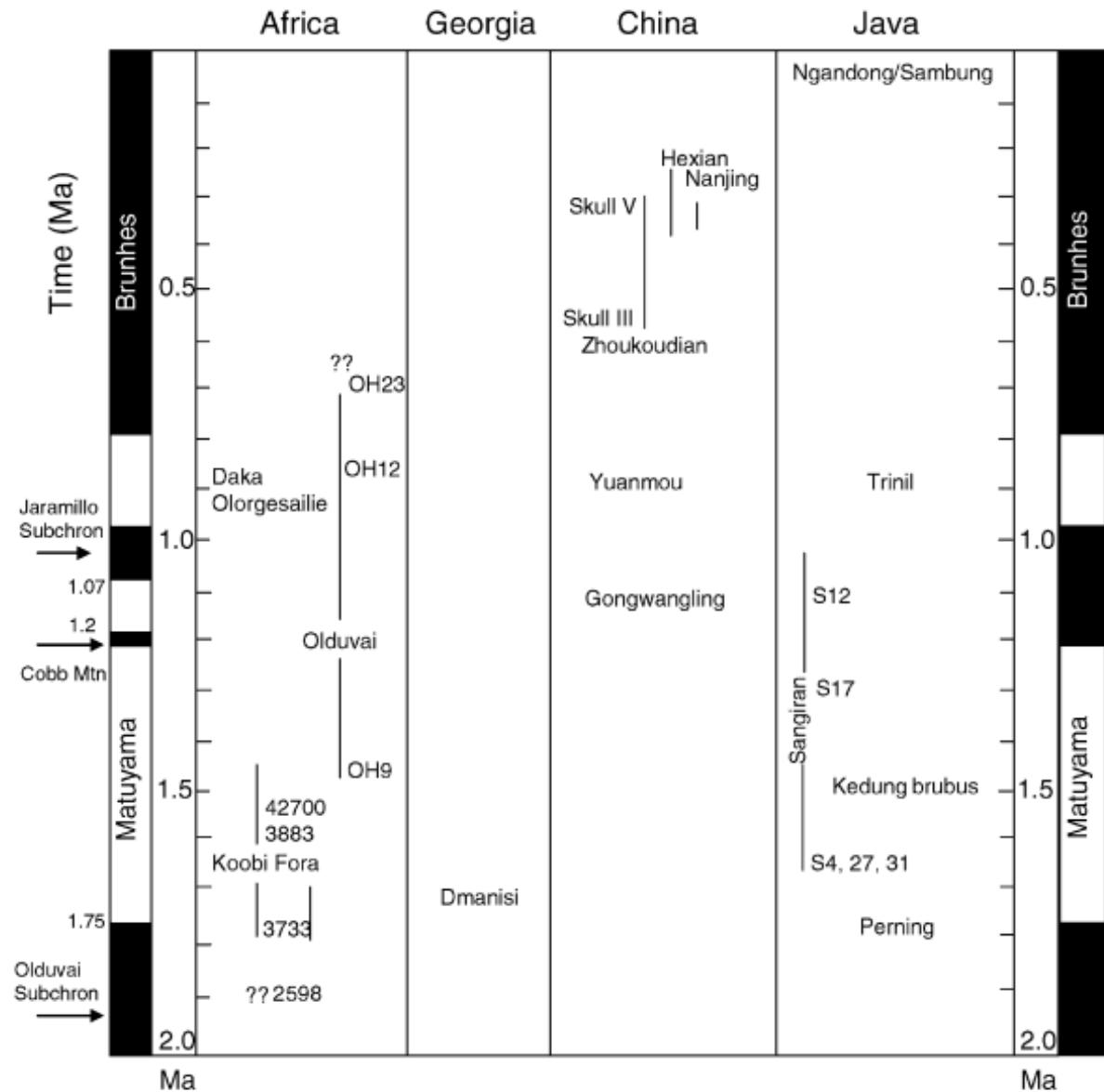


# *Homo ergaster*

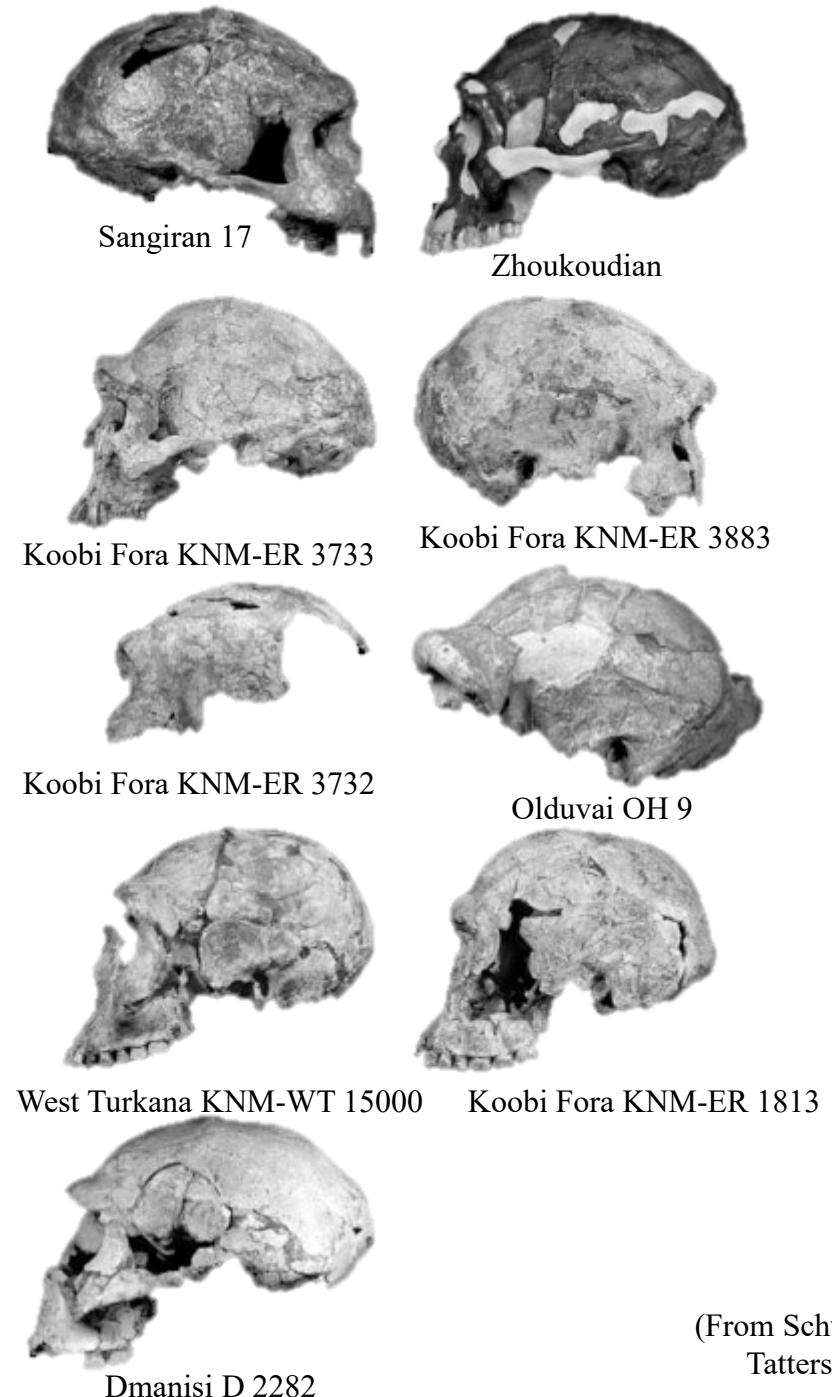


Main *Homo ergaster* sites location

### Temporal distribution of *H. erectus* sites



(Henke & Tattersall, 2007)



(From Schwartz and Tattersall, 2005)



Receding frontal  
bone

Toro sopraorbitario spesso



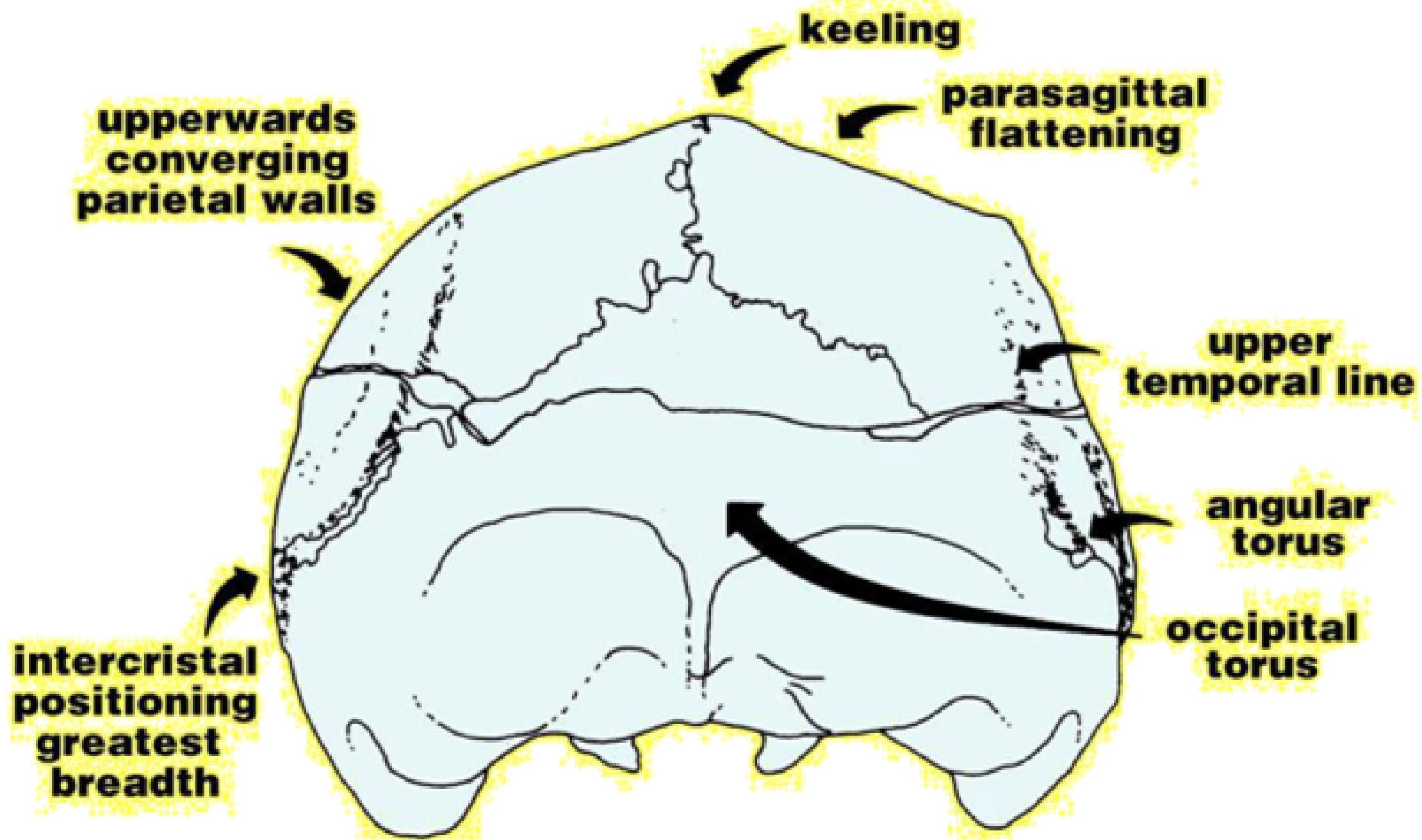
Marked temporal lines

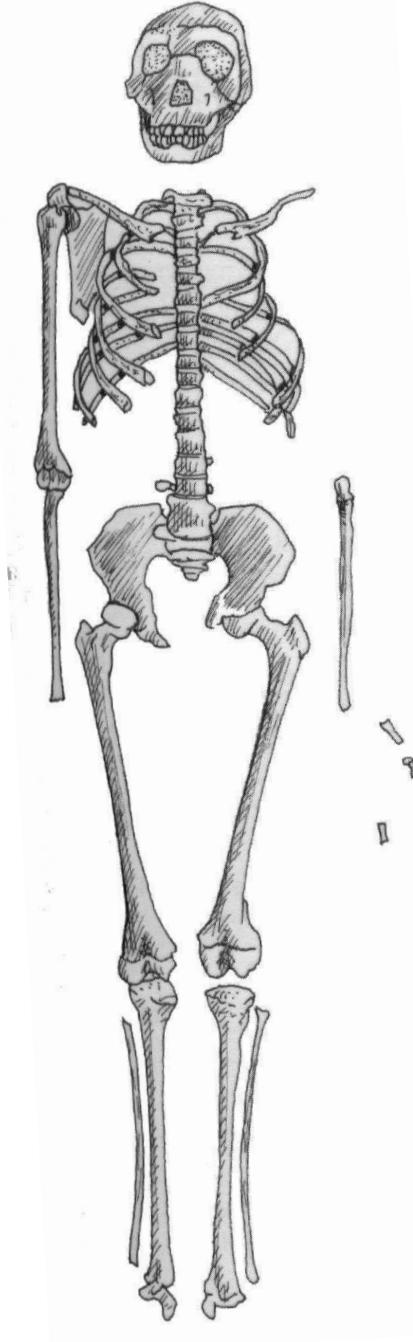


Retro-orbital shrinkage

Supraorbital sulcus

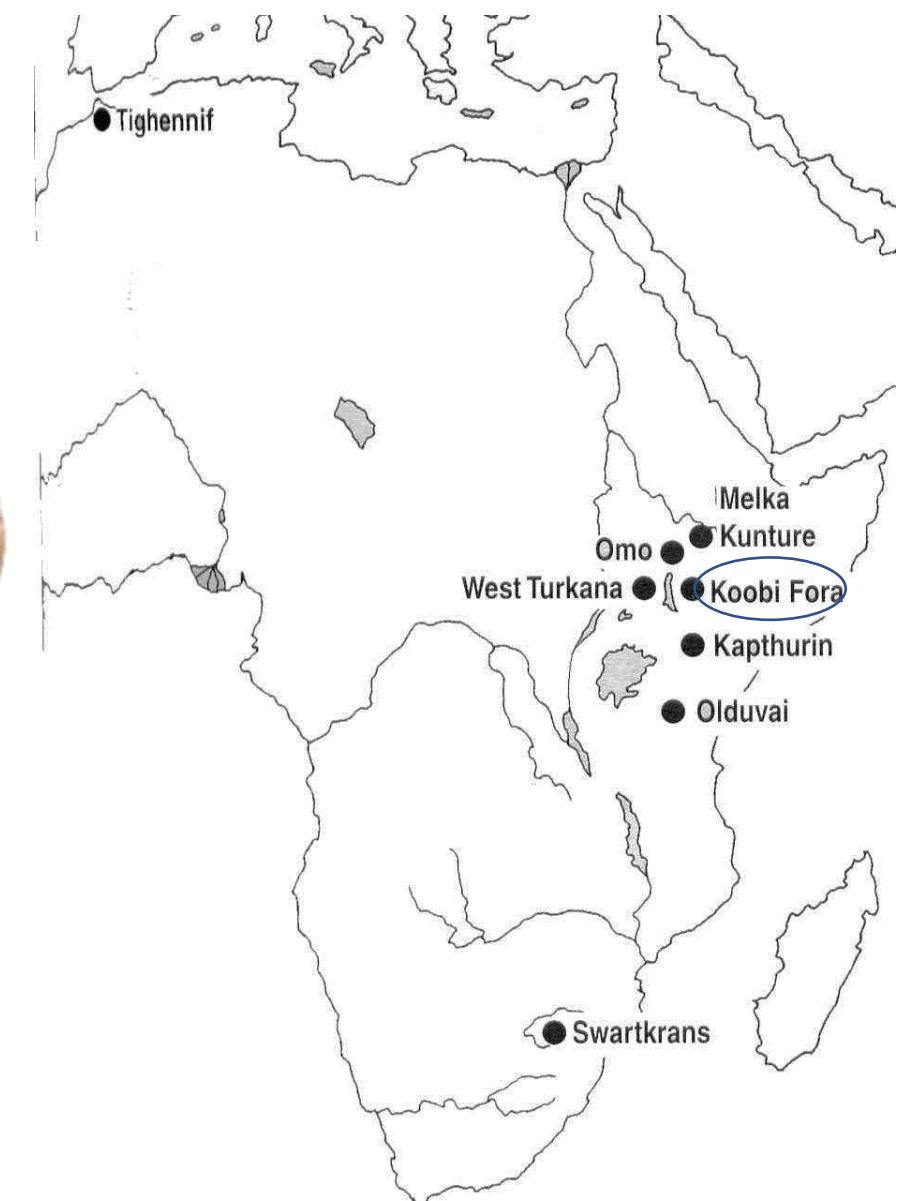
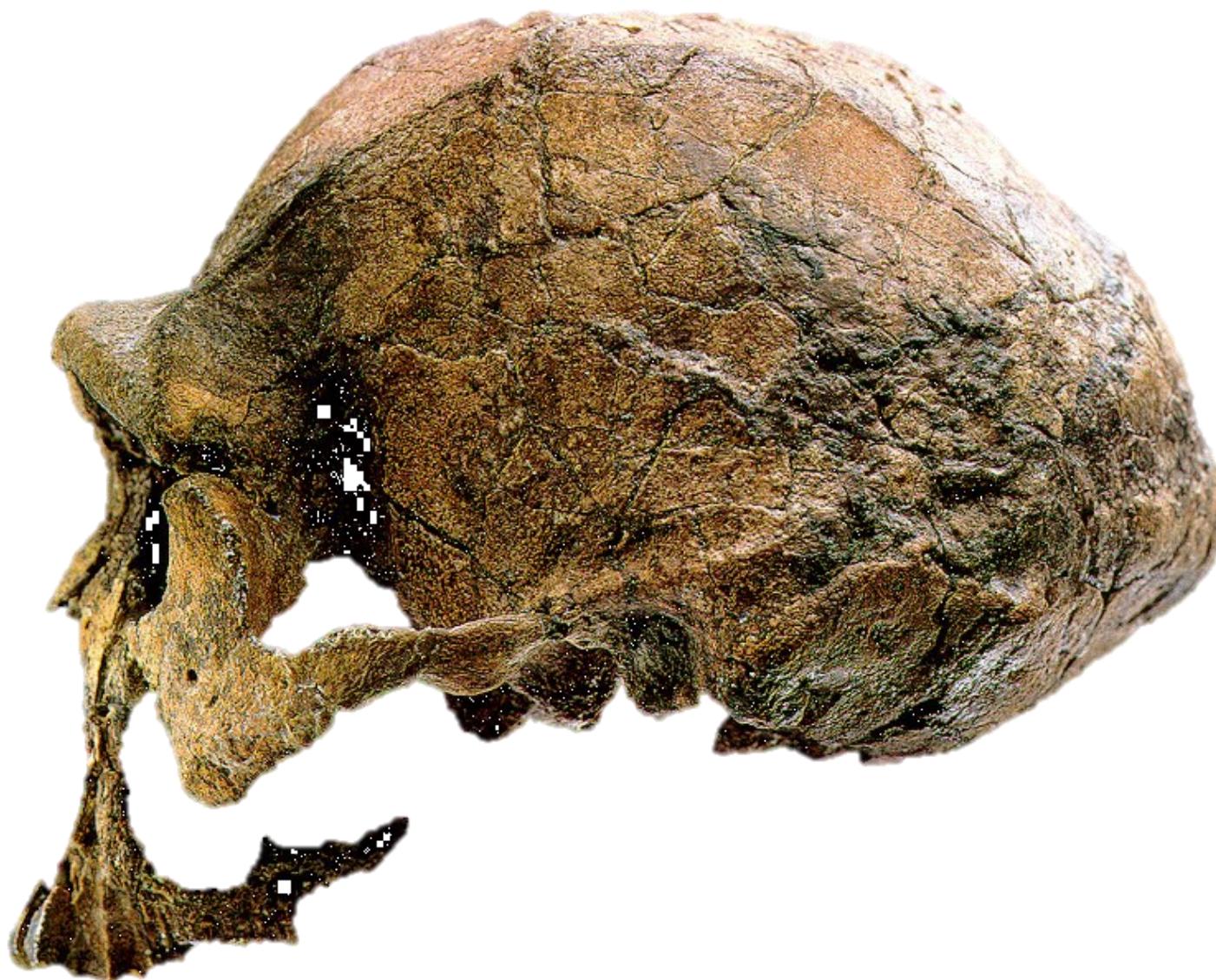
OH9, incomplete calvarium from Olduvai (shared features with Asiatic *Homo erectus*)



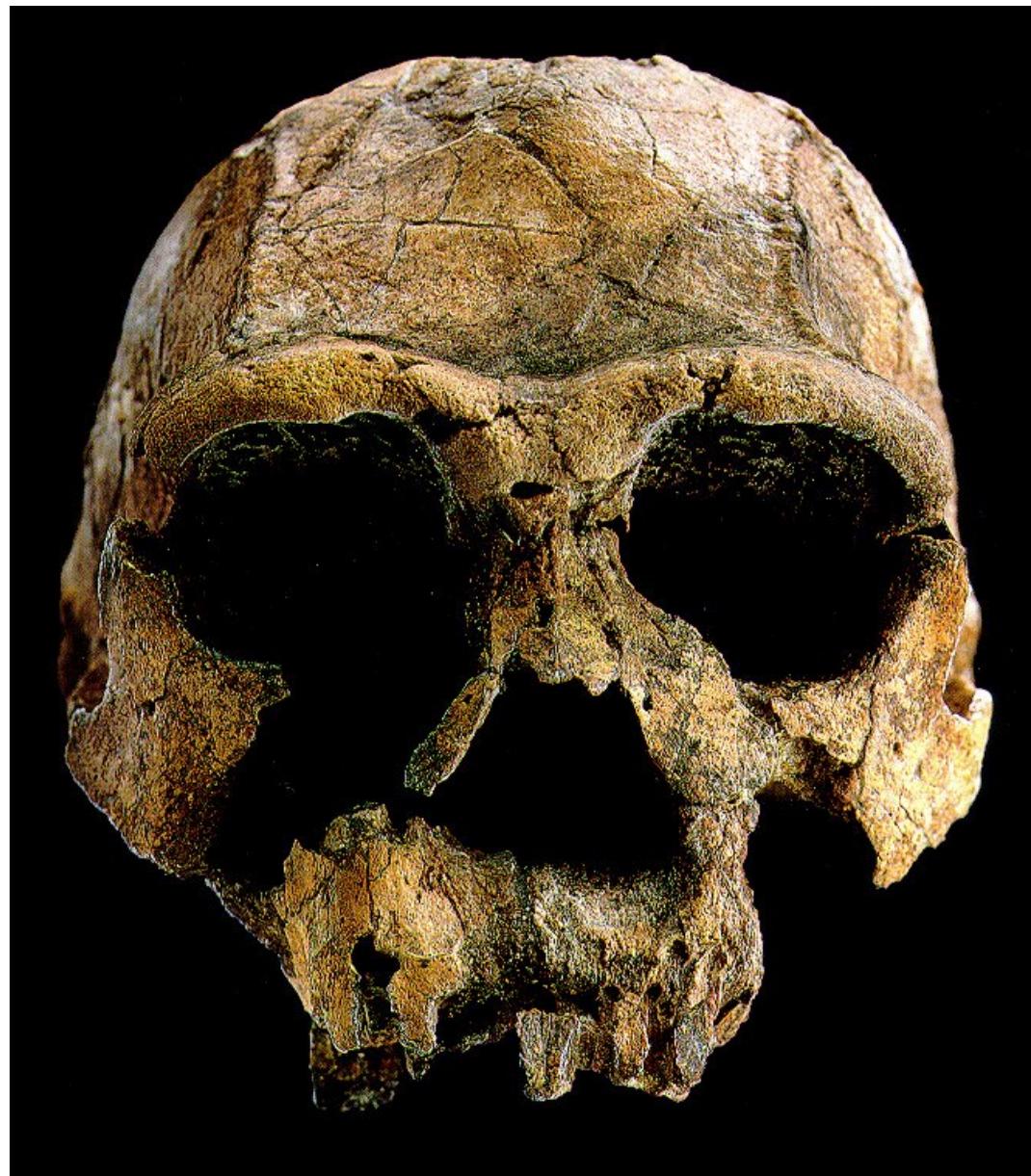


*Homo ergaster* skeleton (KNM-WT 15000) discovered at Nariokotome (Kenya) and dated to ca. 1,6 Myrs

*H. ergaster* KNM-ER 3733, Koobi Fora 1.75 MA



*H. ergaster* KNM-ER 3733, Koobi Fora 1.75 MA





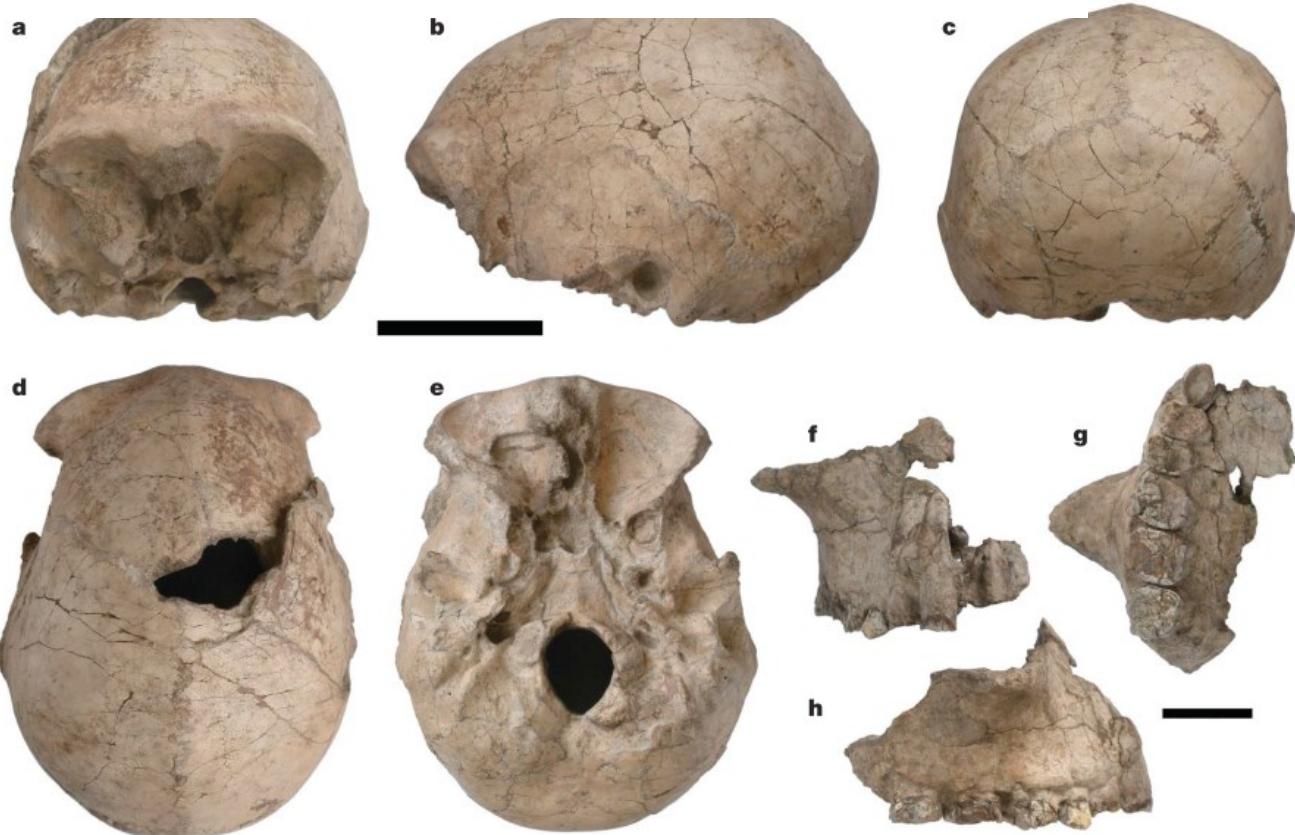
*H. ergaster*

KNM-ER 992  
1.5 Myr  
Koobi Fora  
(Kenya)

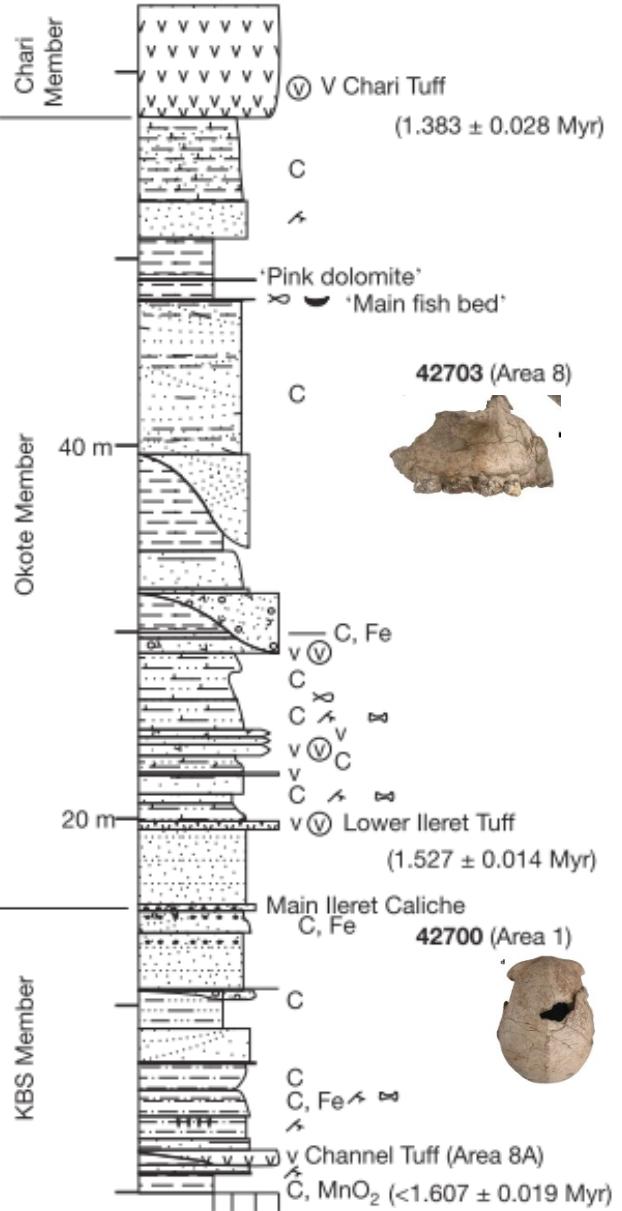
## LETTERS

## Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya

F. Spoor<sup>1</sup>, M. G. Leakey<sup>2,3</sup>, P. N. Gathogo<sup>5</sup>, F. H. Brown<sup>5</sup>, S. C. Antón<sup>6</sup>, I. McDougall<sup>7</sup>, C. Kiarie<sup>8</sup>, F. K. Manthi<sup>8</sup>  
& L. N. Leakey<sup>2,4</sup>



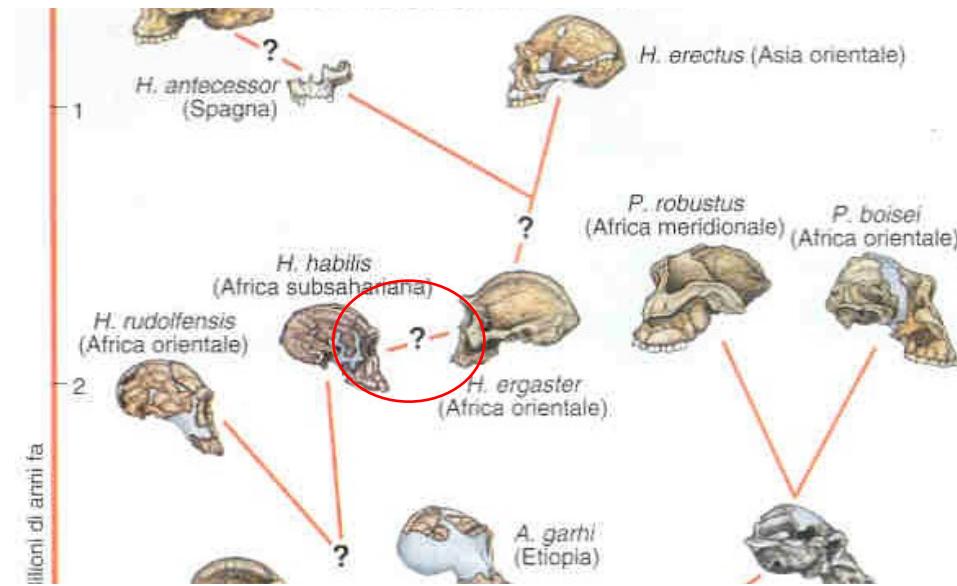
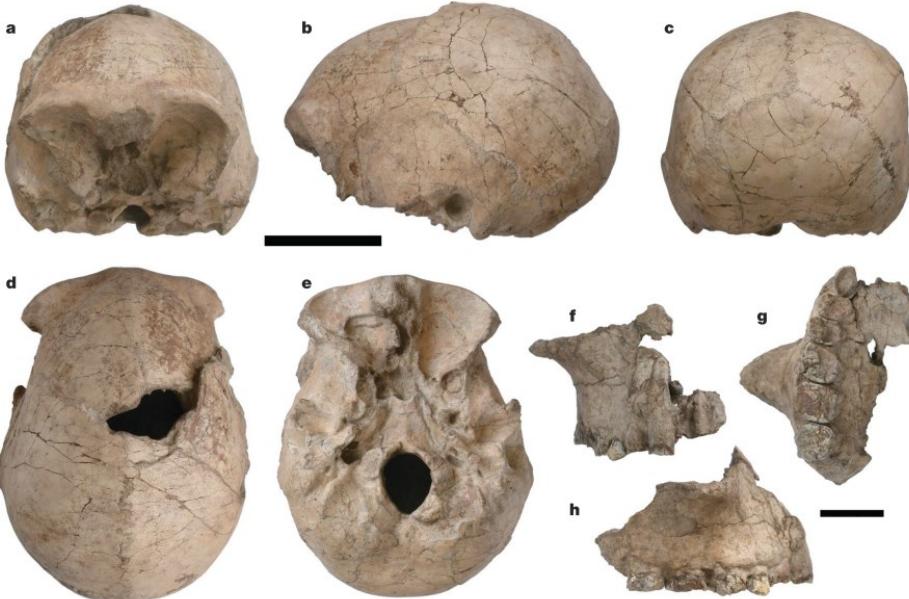
The KNM-ER 42700 calvaria (*H. erectus*) and KNM-ER 42703 partial maxilla.



## LETTERS

**Implications of new early *Homo* fossils from Ileret, east of Lake Turkana, Kenya**

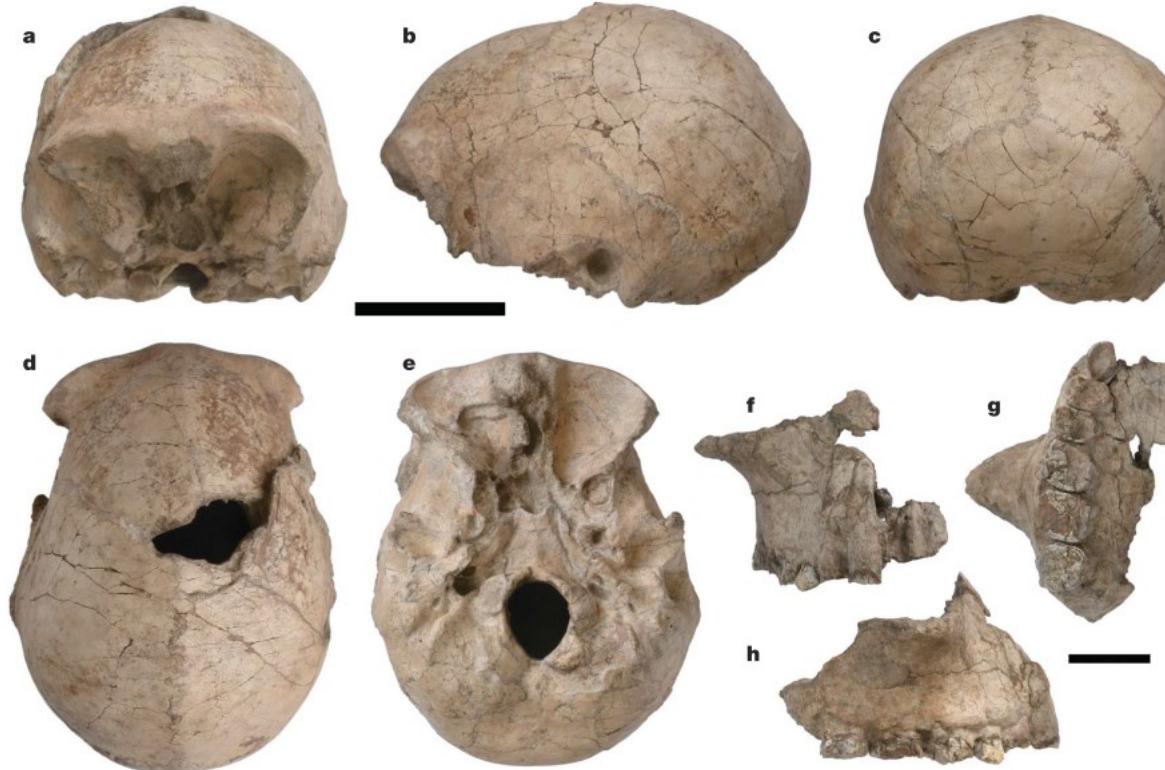
F. Spoor<sup>1</sup>, M. G. Leakey<sup>2,3</sup>, P. N. Gathogo<sup>5</sup>, F. H. Brown<sup>5</sup>, S. C. Antón<sup>6</sup>, I. McDougall<sup>7</sup>, C. Kiarie<sup>8</sup>, F. K. Manthi<sup>8</sup> & L. N. Leakey<sup>2,4</sup>



I siti in Africa orientale danno informazione sull'emergenza e l'evoluzione dei primi *Homo*.  
*Sites in eastern Africa have shed light on the emergence and early evolution of the genus Homo*

*H. habilis* e *H. erectus* sono spesso interpretati come una singola linea evolutiva anagenetica.  
*H. habilis and H. erectus, have often been interpreted as time-successive segments of a single anagenetic evolutionary lineage.*

KNM-ER  
42700  
Calvaria



KNM-ER  
42703  
Frammento di  
mascellare

Due nuovi resti cranici trovati nella formazione di Koobi Fora (Lago Turkana in Kenya) hanno cambiato le idee sul rapporto tra le specie dei primi *Homo*

*Two new cranial fossils from the Koobi Fora Formation, east of Lake Turkana in Kenya, change the knowledge about the relationship between species of early Homo.*

Il frammento di mascellare attribuito a *H. habilis* dimostra che questa specie ha sopravvissuto dopo quello che si pensava, implicando il rapporto anagenetico con *H. erectus* improbabile.

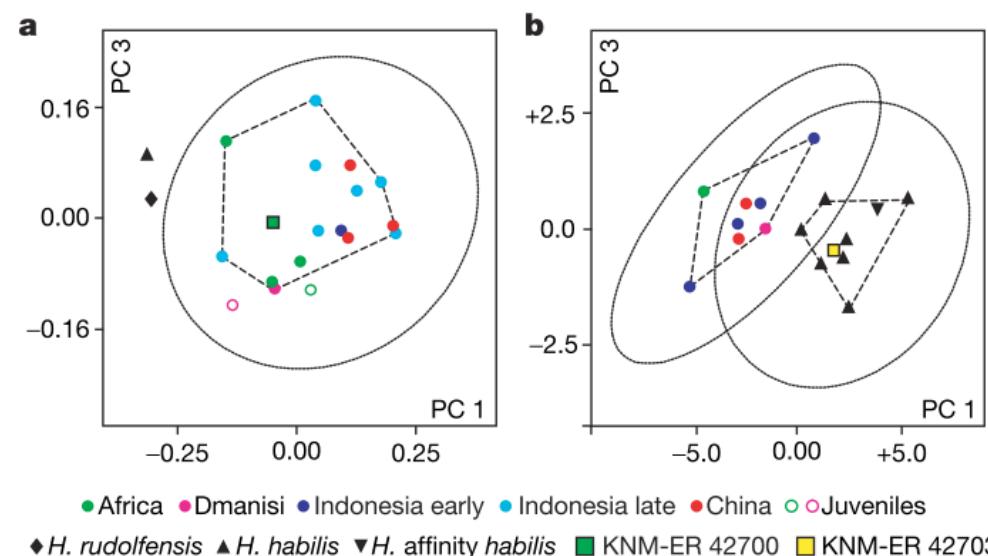
*A partial maxilla assigned to H. habilis reliably demonstrates that this species survived until later than previously recognized, making an anagenetic relationship with H. erectus unlikely.*

La scoperta di un piccolo calvario di *H. erectus* indica che questo taxa si sovrappone in taglia con *H. habilis*, e potrebbe avere dimostrato un dimorfismo sessuale marcato.

*The discovery of a particularly small calvaria of H. erectus indicates that this taxon overlapped in size with H. habilis, and may have shown marked sexual dimorphism.*

Il nuovo fossile conferma la distinzione tra *H. habilis* e *H. erectus*, indipendentemente dalla taglia generale cranica, e suggerisce che questi due taxa vivevano nella stessa area (lago) per quasi mezzo milione di anni.

*The new fossils confirm the distinctiveness of H. habilis and H. erectus, independently of overall cranial size, and suggest that these two early taxa were living broadly sympatrically in the same lake basin for almost half a million years.*



KNM-ER 42700 = *H. erectus* variability

KNM-ER 42703 (denti) = *H. habilis* variability



# Early Hominin Foot Morphology Based on 1.5-Million-Year-Old Footprints from Ileret, Kenya

Matthew R. Bennett,<sup>1\*</sup> John W.K. Harris,<sup>2</sup> Brian G. Richmond,<sup>3,4</sup> David R. Braun,<sup>5</sup> Emma Mbua,<sup>6</sup> Purity Kiura,<sup>6</sup> Daniel Olago,<sup>7</sup> Mzalendo Kibunjia,<sup>6</sup> Christine Omuroombi,<sup>7</sup> Anna K. Behrensmeyer,<sup>8</sup> David Huddart,<sup>9</sup> Silvia Gonzalez<sup>9</sup>

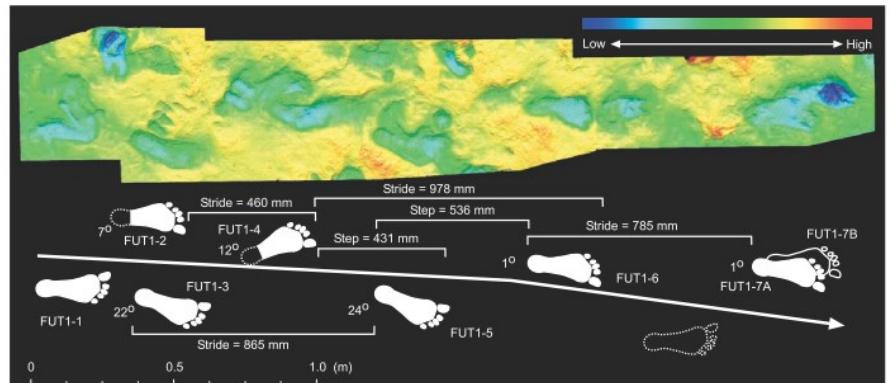


Fig. 2. Tessellated swath of optical laser scans of the main footprint trail on the upper footprint surface at FwJj14E. Color is rendered with 5-mm isopleths.

Footprints dated to 1.51-1.53 Ma

Alluce relativamente abdotto (distante) / *Relatively abducted hallux*

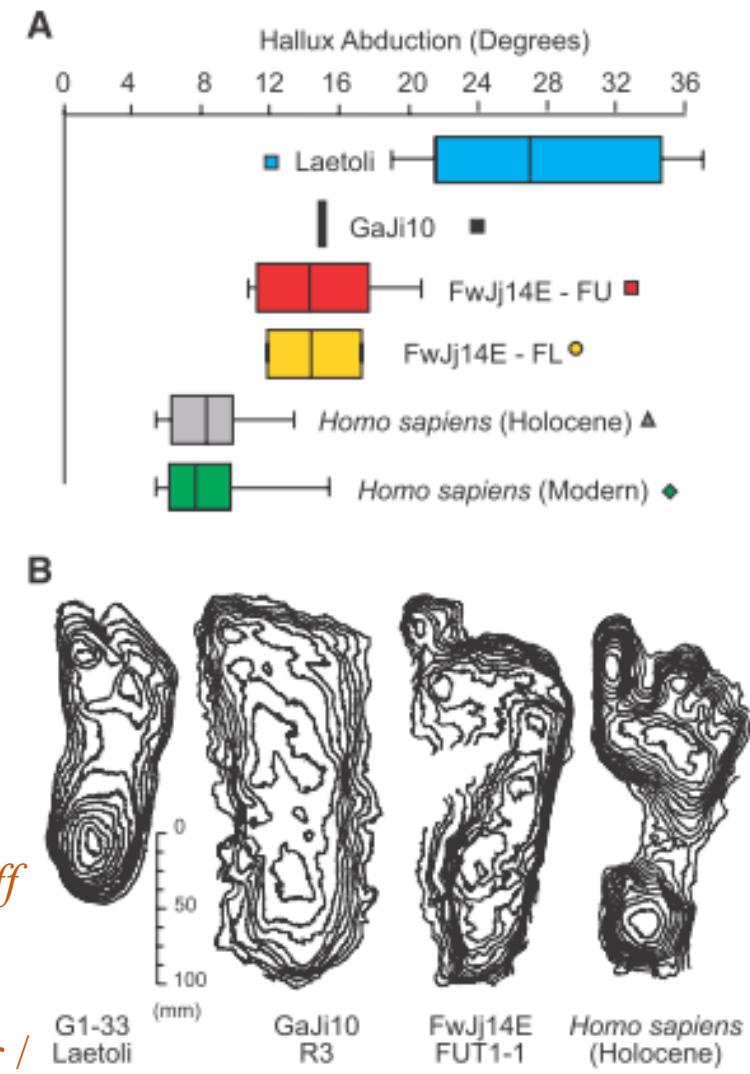
Trasferimento mediale del peso prima del push-off / *Medial weight transfer before push-off*

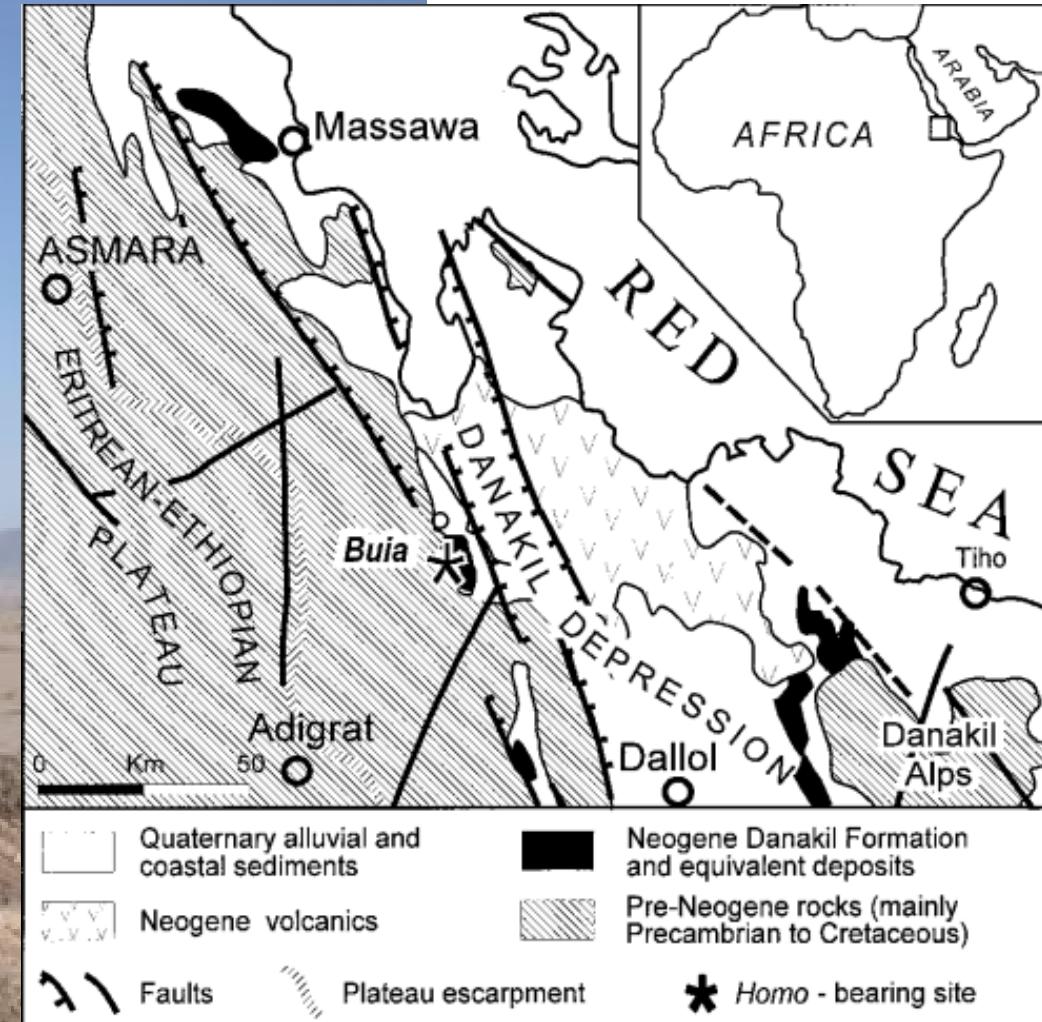
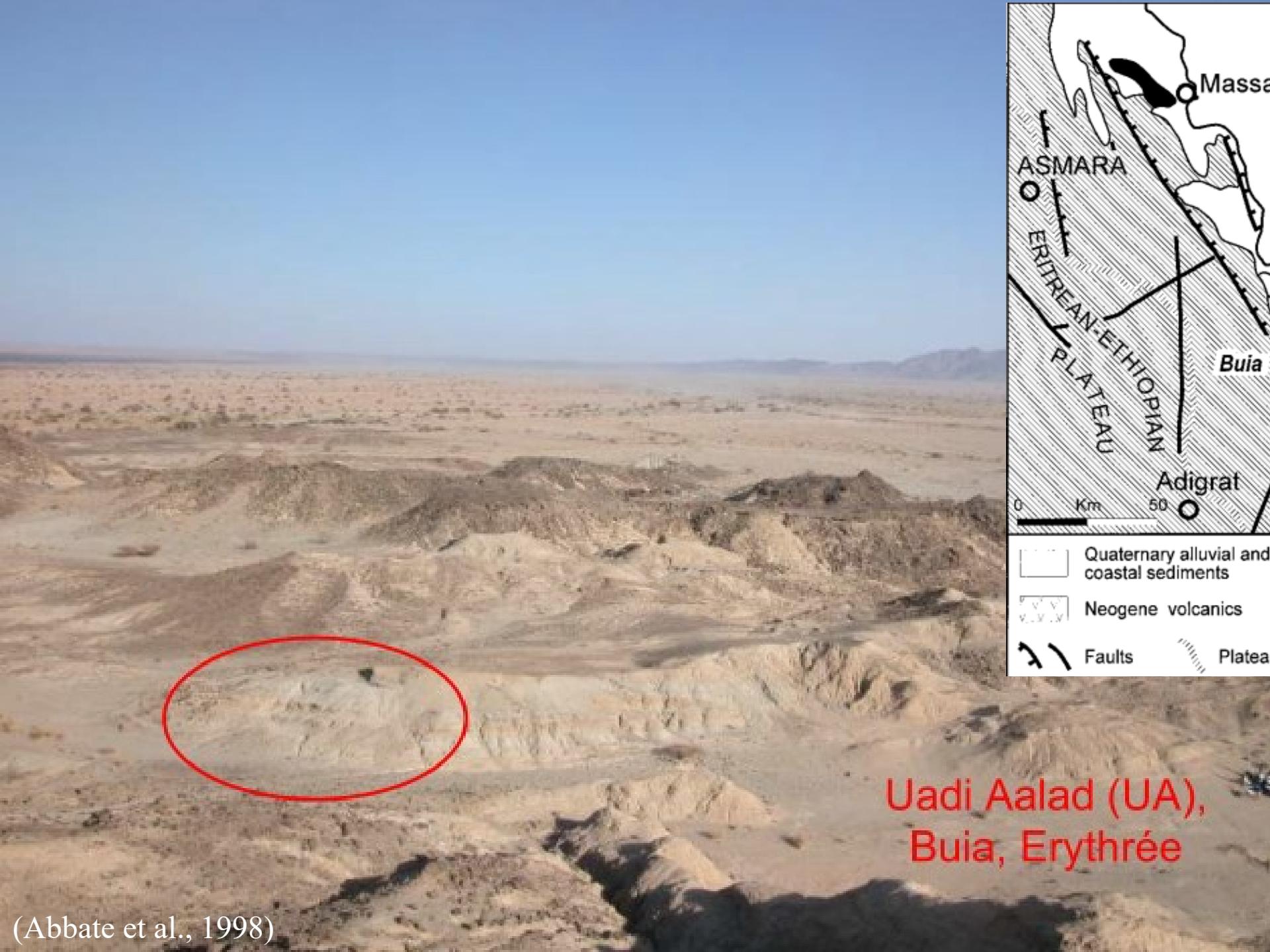
La taglia delle impronte è in accordo con la statura e la massa corporea stimata dei *ergaster/erectus*

*The size of the footprints is consistent with stature and body mass estimates for H. ergaster / erectus*

Distinti morfologicamente da Laetoli / *Morphologically distinct from laetoli (3.75 Ma)*

Dimostrano che i ominini hanno sviluppato un piede funzionalmente moderno e una locomozione bipeda / *Show that hominins had evolved an essentially modern human foot function and style of bipedal locomotion*





(Abbate et al., 1998)



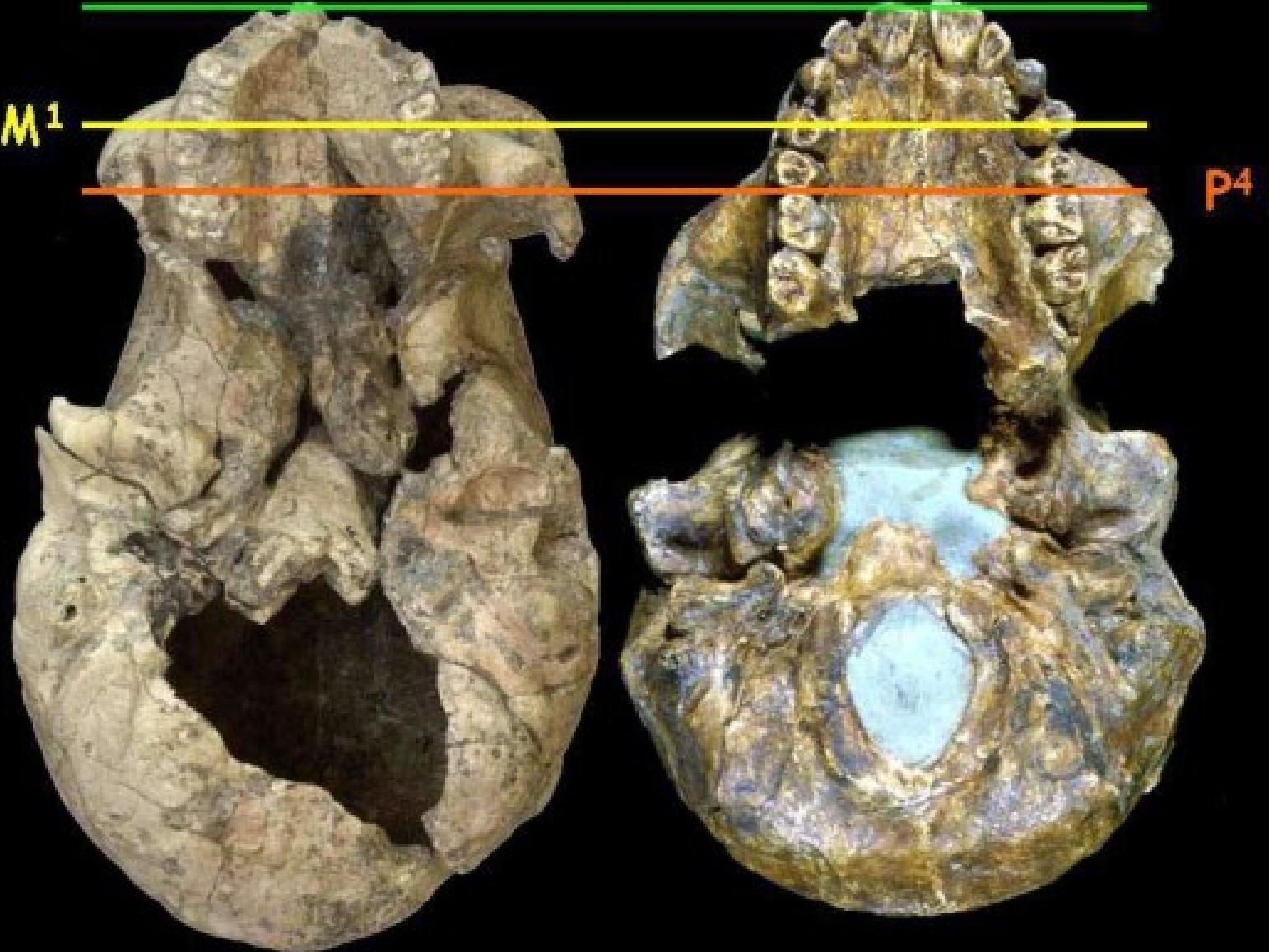
UA 31  
(Buia)

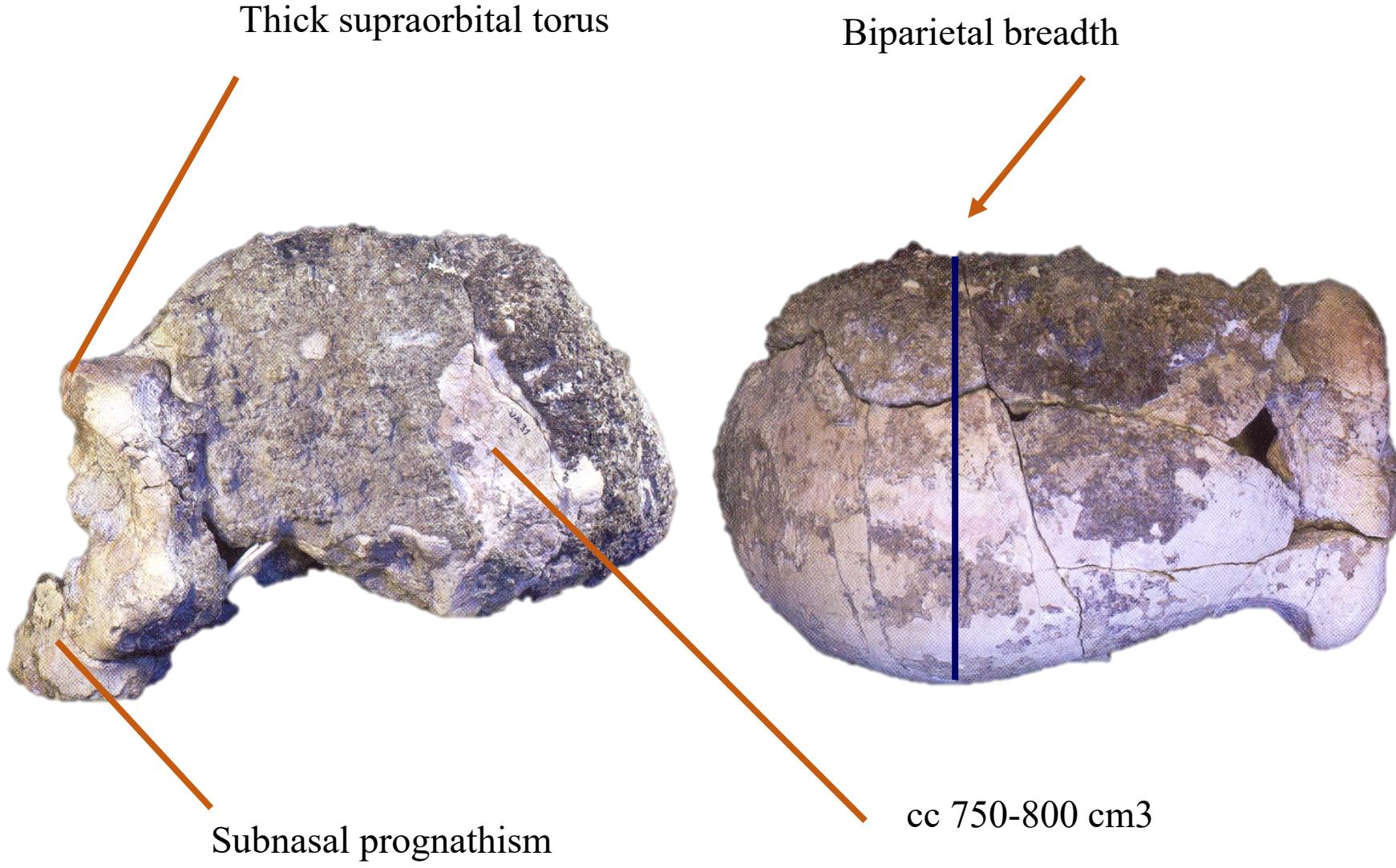
**UA 31**

**WT 15K**

**P<sup>4</sup> / M<sup>1</sup>**

**P<sup>4</sup> / M<sup>1</sup>**





Buia, UA 31, (Eritrea, 1995-97)



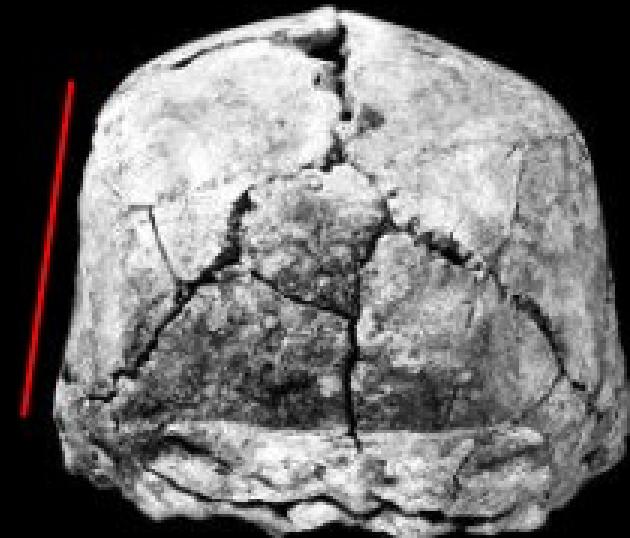
Sangiran 17



UA 31



OH 9

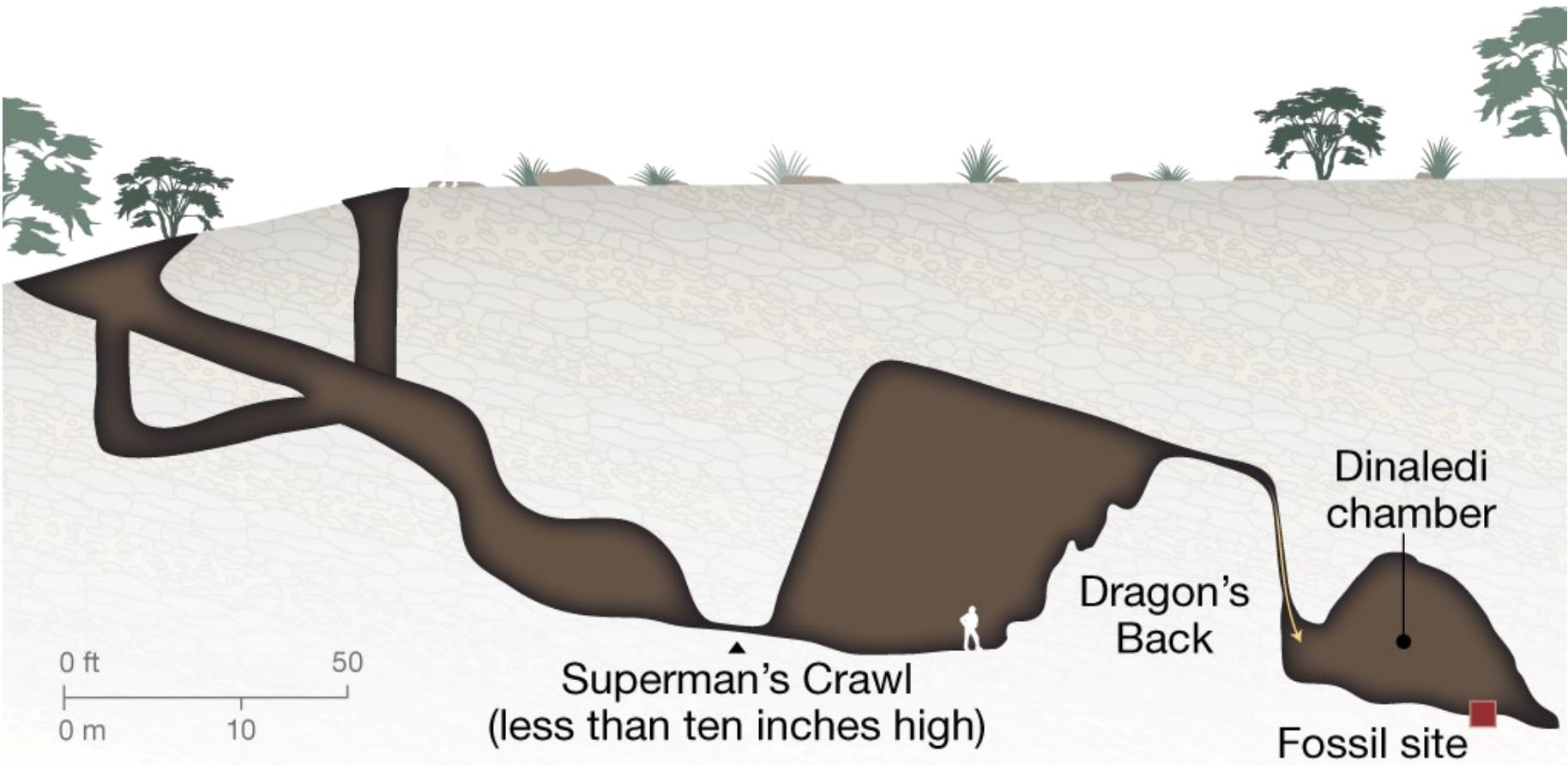


Daka

AFRICA



## *Homo naledi* 335 and 236 kya

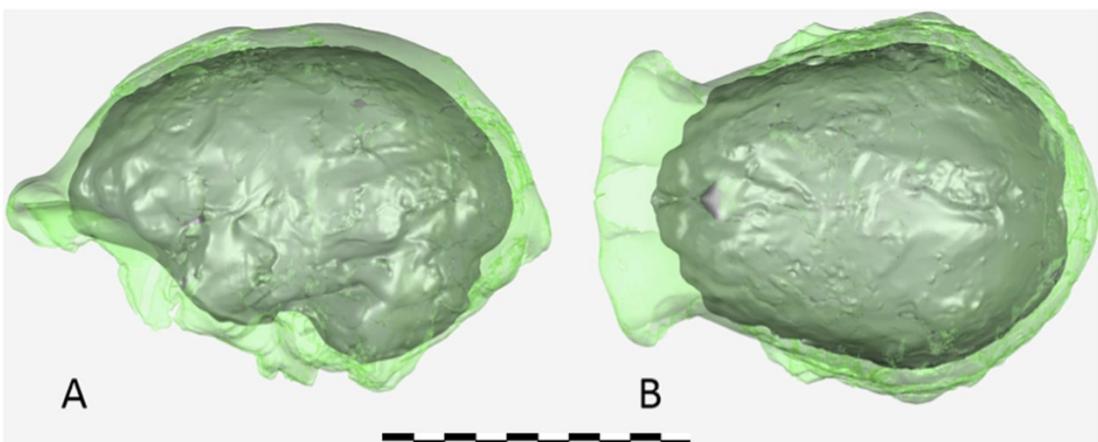




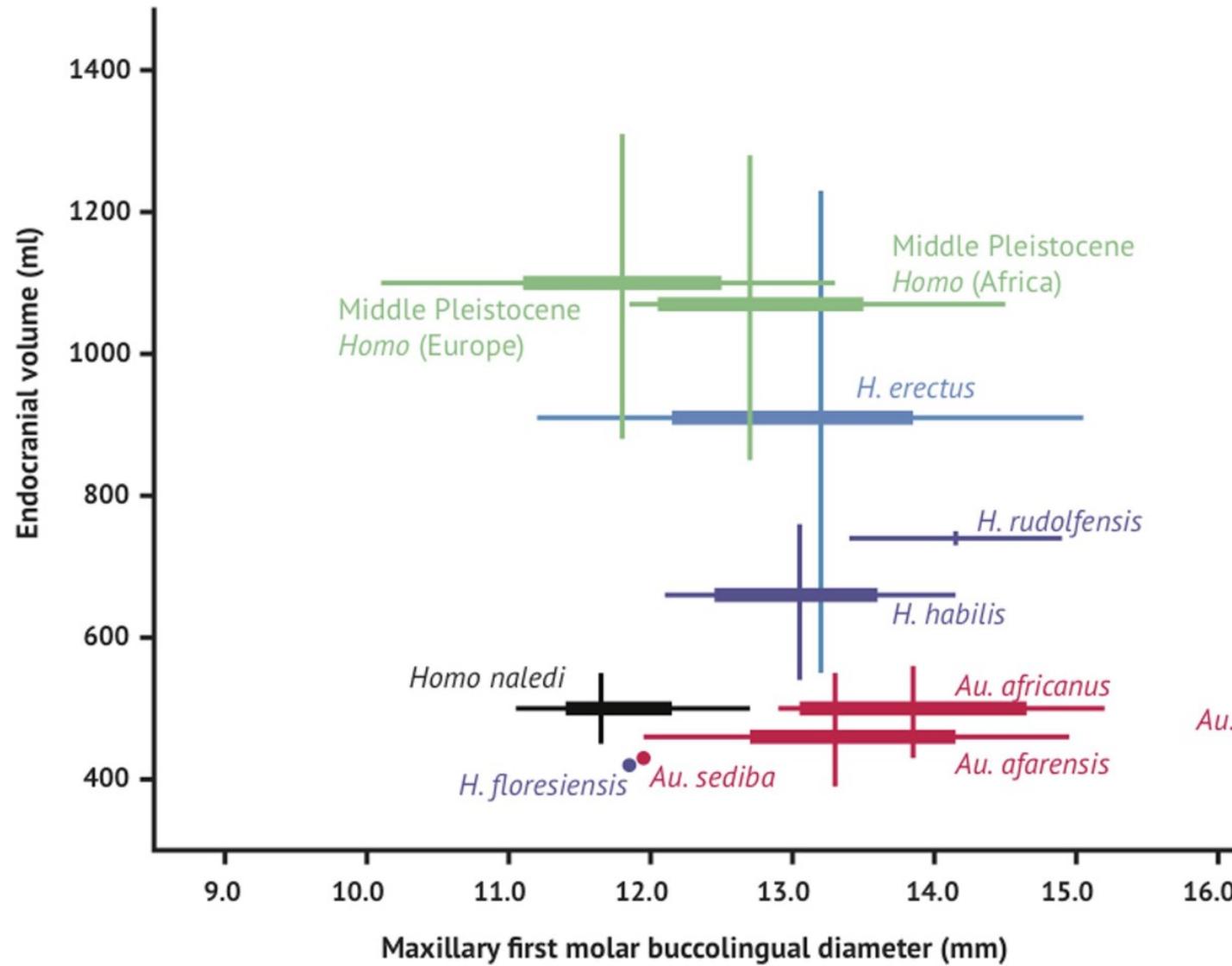


Holotype specimen of *Homo naledi*, Dinaledi  
Hominin 1 (DH1).

Virtual reconstruction of the endocranum of the larger composite cranium from DH1 and DH2 overlaid with the ectocranial surfaces.



The braincase of this composite male skull of *H. naledi* measures 560 cc less than half that of the modern human.

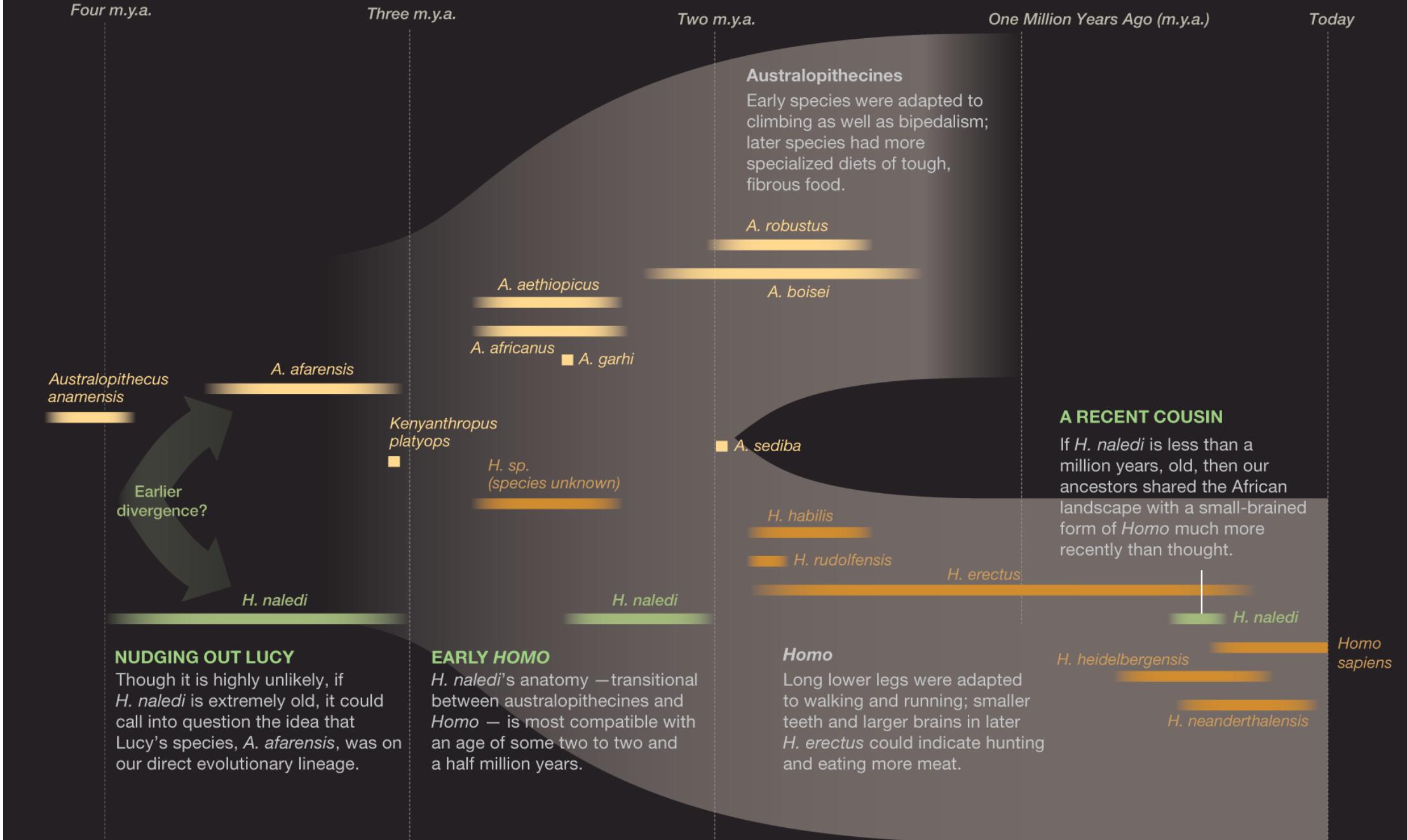


Dimensione del cervello e dei denti nei ominidi.

*H. naledi* presenta dei molari con dimensioni ridotte (confrontabili con i *Homo* successivi) e un volume endocranico relativamente piccolo (simile agli australipitecine). Il range di variazione del campione di Dinaledi è piuttosto ridotto, in particolare confrontandolo con quello dei *H. erectus* sensu lato.

*Brain size and tooth size in hominins.*

*H. naledi* occupa una posizione con dimensioni relativamente piccole dei molari (comparabili a quelli di più tardi *Homo*) e relativamente piccolo volume endocranico (comparabile agli australopithecini). Il range di variazione nel campione di Dinaledi è anche piuttosto ridotto, in particolare quando si confronta con il vasto range di variazione nell'*H. erectus* sensu lato.



## HOMO FEATURES

### Humanesque skull

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

### Versatile hands

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

### Long legs

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

### Humanlike feet

Except for the slightly curved toes, *H. naledi*'s feet are nearly indistinguishable from ours, with arches that suggest an efficient long-distance stride.

## AUSTRALOPITHECINE FEATURES

### Primitive shoulders

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

### Flared pelvis

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

### Curved fingers

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



SKELETON: STEFAN FICHTEL

SOURCES: LEE BERGER AND PETER SCHMID, UNIVERSITY OF THE WITWATERSRAND (WITS), SOUTH AFRICA; JOHN HAWKS, UNIVERSITY OF WISCONSIN-MADISON



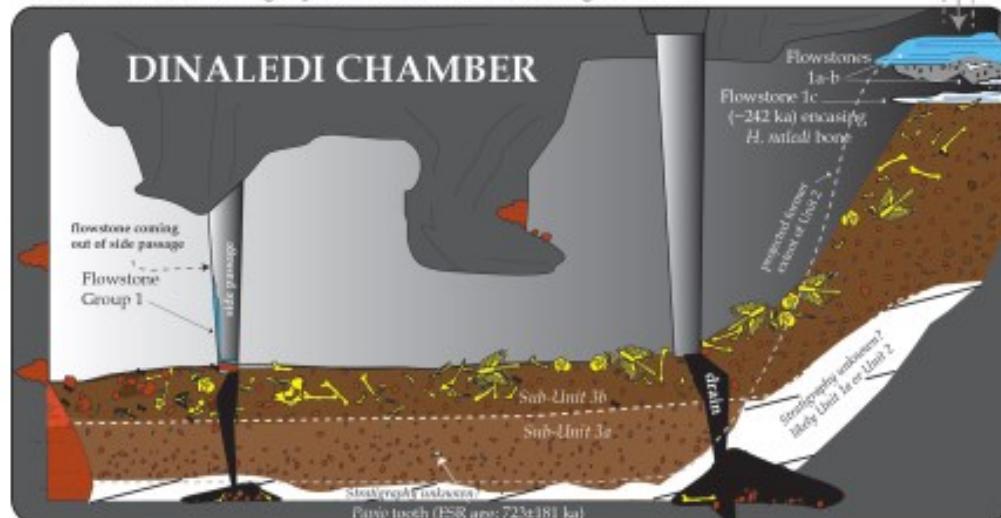
# The age of *Homo naledi* and associated sediments in the Rising Star Cave, South Africa

Paul HGM Dirks<sup>1,2\*</sup>, Eric M Roberts<sup>1,2</sup>, Hannah Hilbert-Wolf<sup>1</sup>, Jan D Kramers<sup>3</sup>, John Hawks<sup>2,4</sup>, Anthony Dosseto<sup>5</sup>, Mathieu Duval<sup>6,7</sup>, Marina Elliott<sup>2</sup>, Mary Evans<sup>8</sup>, Rainer Grün<sup>6,9</sup>, John Hellstrom<sup>10</sup>, Andy IR Herries<sup>11</sup>, Renaud Joannes-Boyau<sup>12</sup>, Tebogo V Makhubela<sup>3</sup>, Christa J Placzek<sup>1</sup>, Jessie Robbins<sup>1</sup>, Carl Spandler<sup>1</sup>, Jelle Wiersma<sup>1</sup>, Jon Woodhead<sup>10</sup>, Lee R Berger<sup>2</sup>

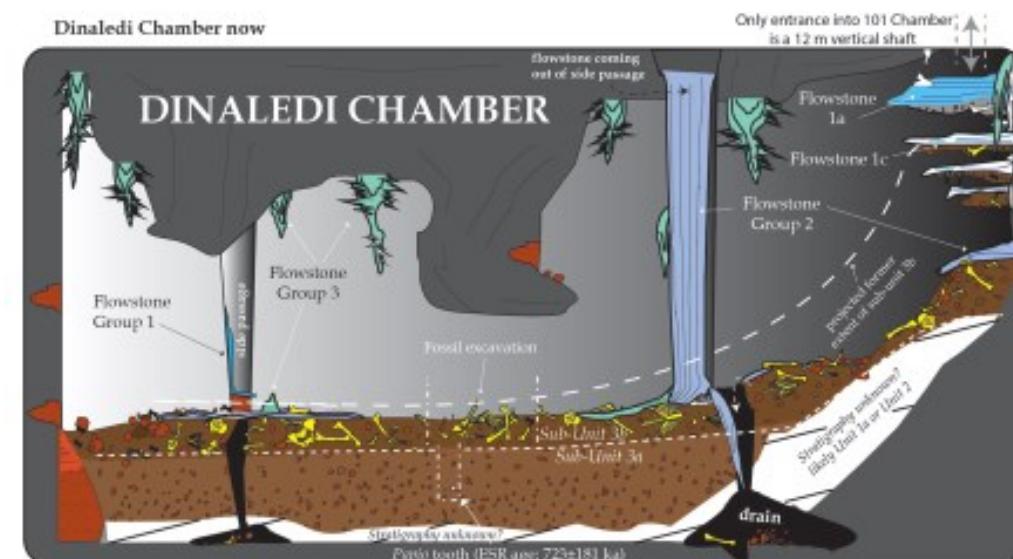
**Abstract** New ages for flowstone, sediments and fossil bones from the Dinaledi Chamber are presented. We combined optically stimulated luminescence dating of sediments with U-Th and palaeomagnetic analyses of flowstones to establish that all sediments containing *Homo naledi* fossils can be allocated to a single stratigraphic entity (sub-unit 3b), interpreted to be deposited between 236 ka and 414 ka. This result has been confirmed independently by dating three *H. naledi* teeth with combined U-series and electron spin resonance (US-ESR) dating. Two dating scenarios for the fossils were tested by varying the assumed levels of <sup>222</sup>Rn loss in the encasing sediments: a maximum age scenario provides an average age for the two least altered fossil teeth of 253 +82/-70 ka, whilst a minimum age scenario yields an average age of 200 +70/-61 ka. We consider the maximum age scenario to more closely reflect conditions in the cave, and therefore, the true age of the fossils. By combining the US-ESR maximum age estimate obtained from the teeth, with the U-Th age for the oldest flowstone overlying *Homo naledi* fossils, we have constrained the depositional age of *Homo naledi* to a period between 236 ka and 335 ka. These age results demonstrate that a morphologically primitive hominin, *Homo naledi*, survived into the later parts of the Pleistocene in Africa, and indicate a much younger age for the *Homo naledi* fossils than have previously been hypothesized based on their morphology.

DOI: 10.7554/eLife.24231.001

Dinaledi Chamber during deposition of *Homo naledi*-bearing sub-unit 3b



Dinaledi Chamber now



Stratigraphic position of flowstones and sedimentary units (not to scale- sketch only)

Sub-unit 1a: laminated maroon mudstone	Flowstone 1a	Micro-mammal fossils
Sub-unit 1b: sandy, microfossil-bearing maroon mudstone	Flowstones 1b-1e	Baboon tooth
Unit 2: mud clast breccia	Flowstone 2	Non-hominin macrofossils
Sub-Unit 3a: mud clast breccia	Flowstone 3 or undifferentiated	<i>Homo naledi</i> fossils
Sub-Unit 3b: mud clast breccia	Dolomite (cave walls)	

**"Lucy"**

*Australopithecus afarensis*

3.2 million years ago

Adult Female

3 ft 8 in

60-65 lbs

**"Turkana Boy"**

*Homo erectus*

1.6 million years ago

Adolescent Male

5 ft

110-115 lbs

**"Rising Star Hominin"**

*Homo naledi*

~300 ky

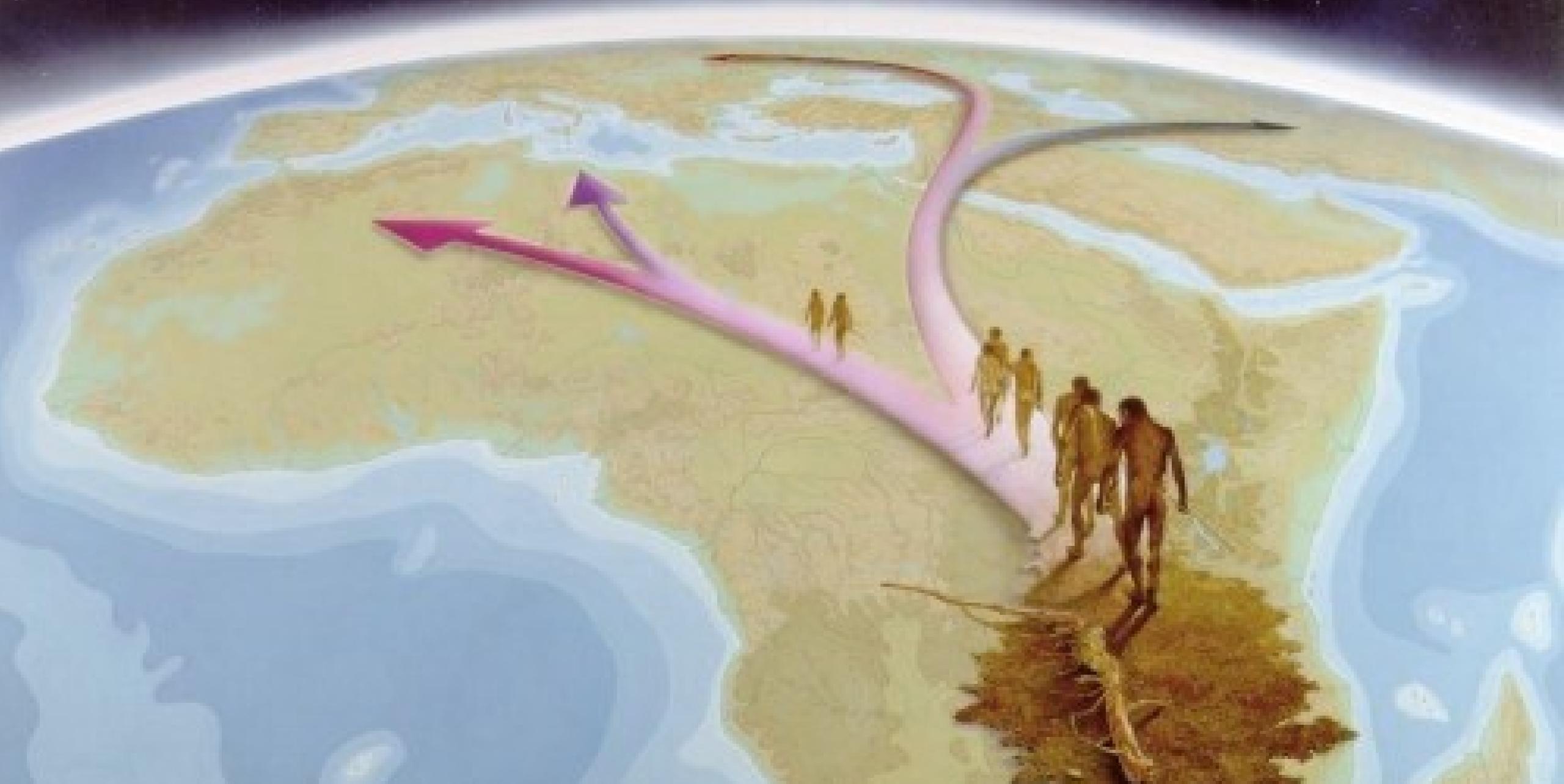
Adult Male

4 ft 10 in

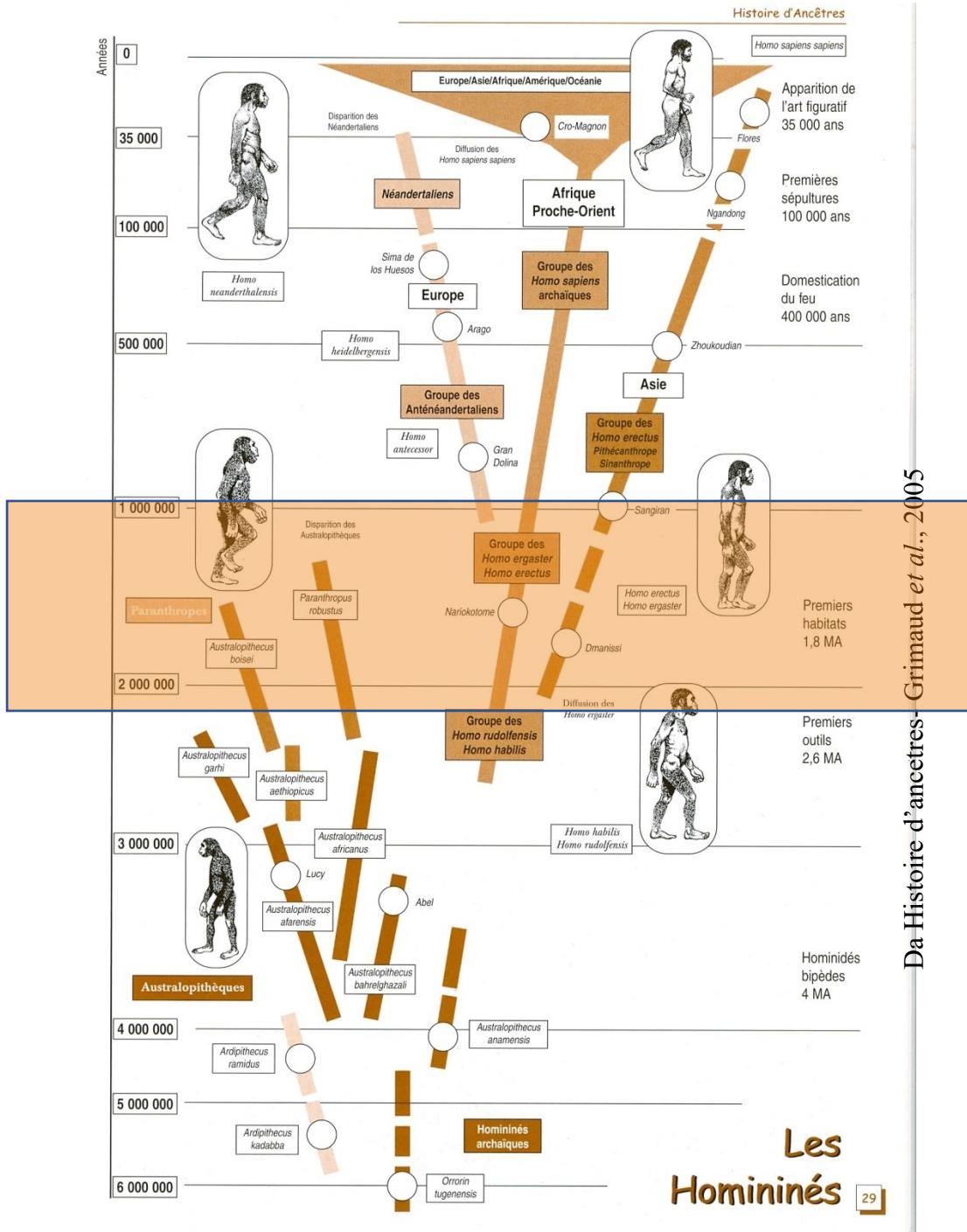
100-110 lbs

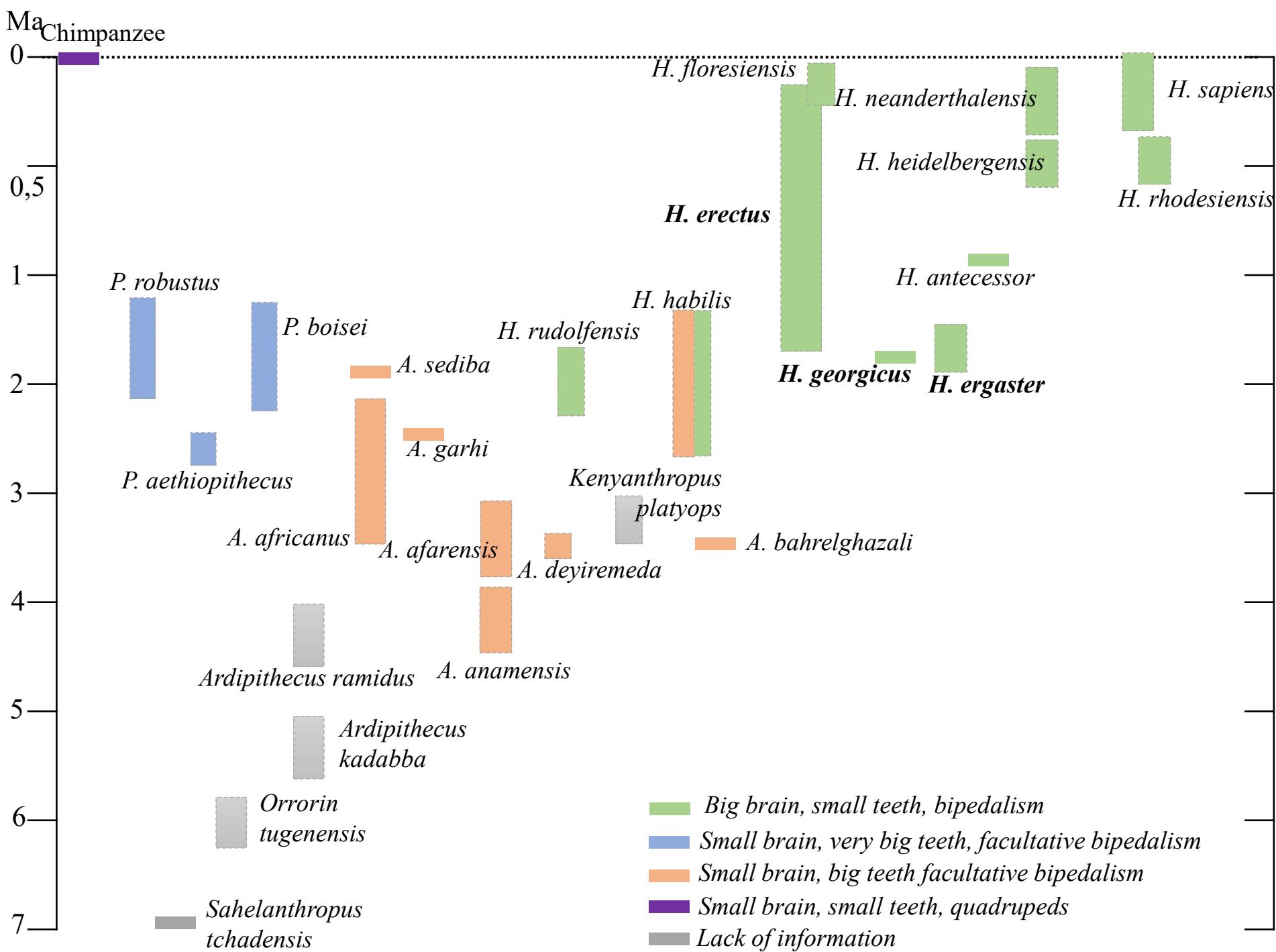


*Out of Africa.....*



# Out of Africa.....





*Out of Africa.....*

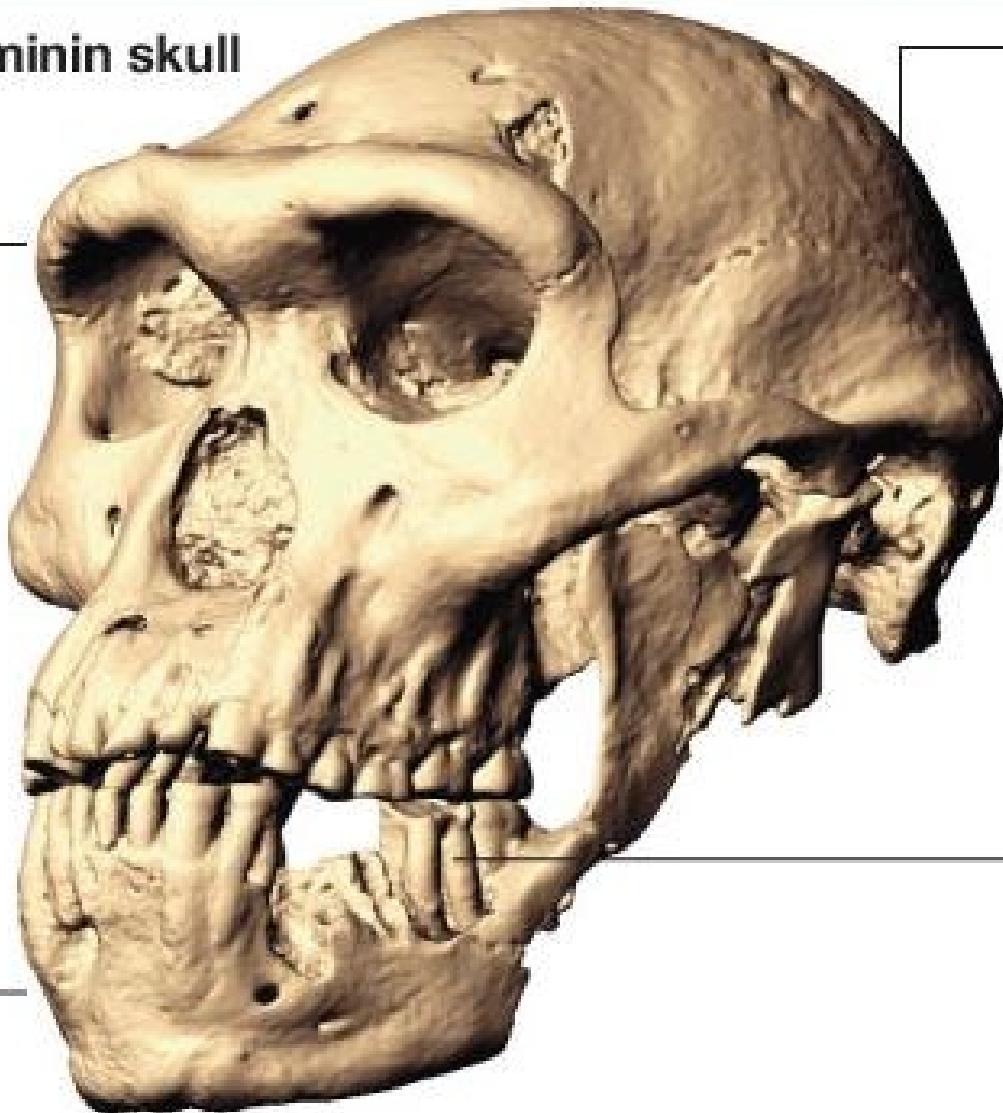


**DMANISI**  
Una nuova rivoluzione  
1.750.000 anni fa



## 1.8-million-year-old hominin skull

These features had not been observed together in an early Homo fossil until now.



**Long face**  
similar to the  
more recent  
*Homo erectus*

A small brain  
similar to the  
older *Homo  
habilis*

**Large teeth**  
similar to  
older *Homo  
rudolfensis*

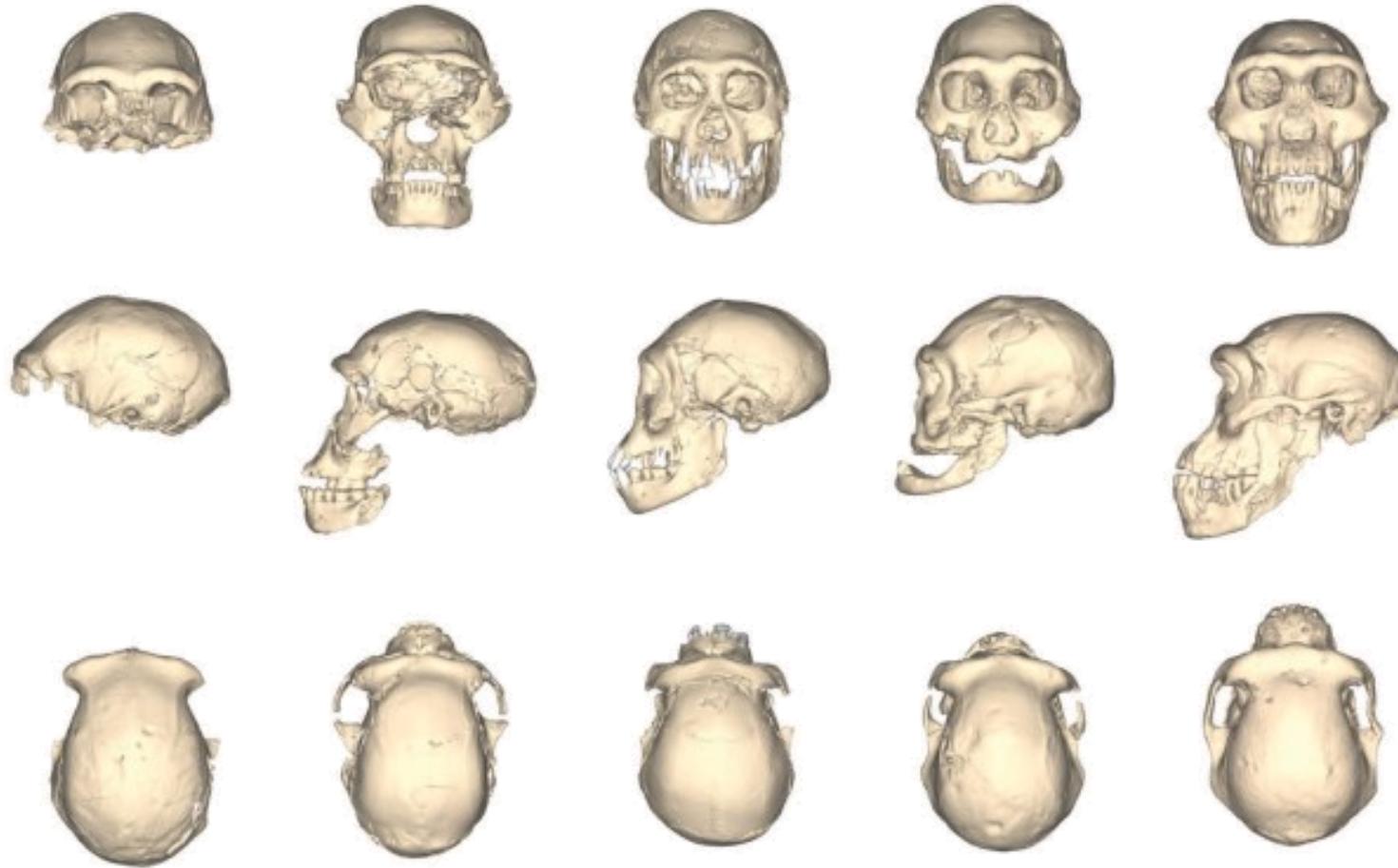
The blend of features suggests early humans were one species that had diverse facial and cranial characteristics.

SKULL IMAGE COURTESY OF M. PONCE DE LEÓN AND CH. ZOLLIKOFER,  
UNIVERSITY OF ZURICH, SWITZERLAND

NG STAFF; SOURCE: SCIENCE

# A Complete Skull from Dmanisi, Georgia, and the Evolutionary Biology of Early *Homo*

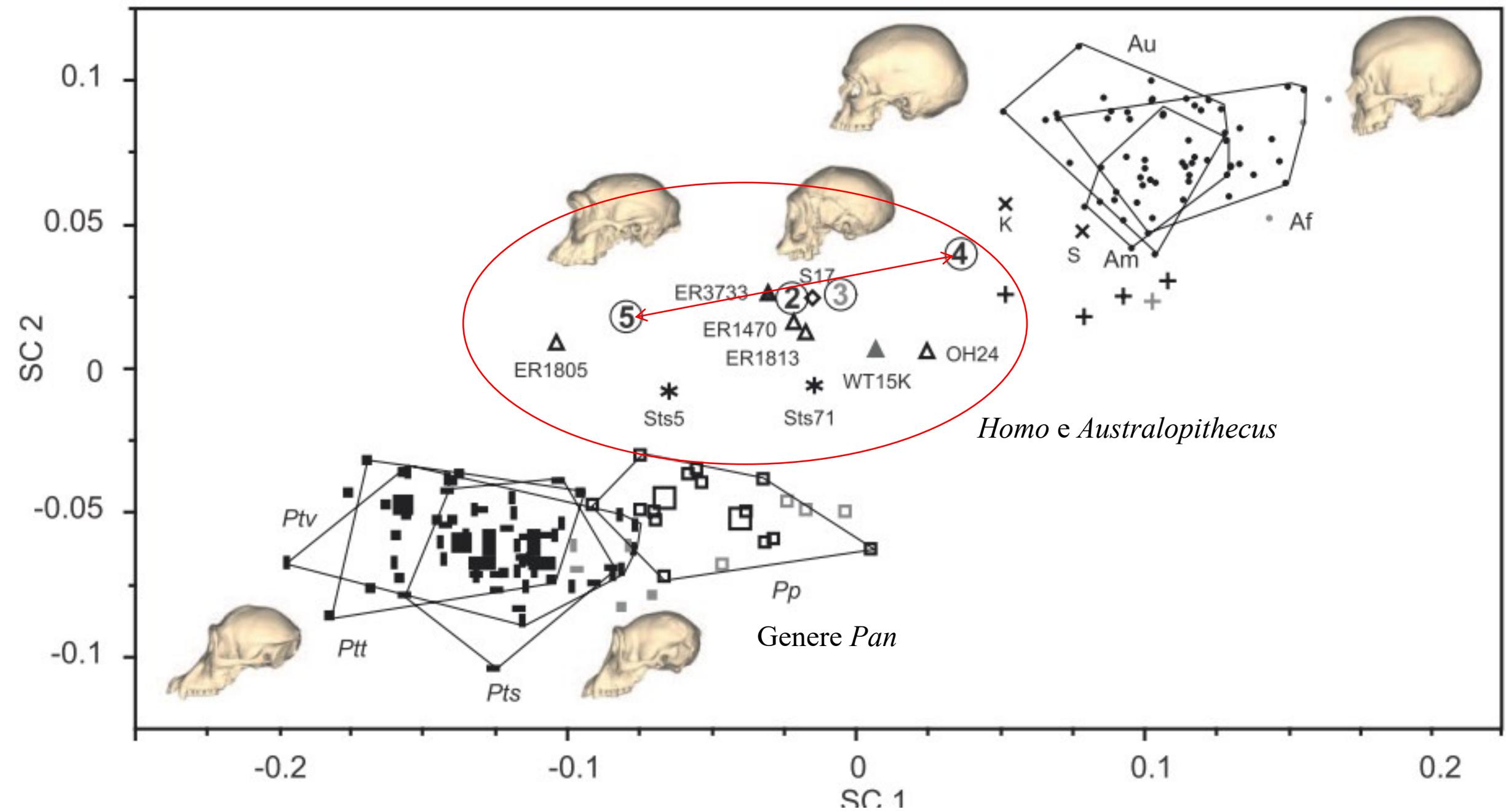
David Lordkipanidze,<sup>1,\*</sup> Marcia S. Ponce de León,<sup>2</sup> Ann Margvelashvili,<sup>1,2</sup> Yoel Rak,<sup>3</sup>  
G. Philip Rightmire,<sup>4</sup> Abesalom Vekua,<sup>1</sup> Christoph P. E. Zollikofer<sup>2,\*</sup>



Il campione di Dmanisi, che comprende ad oggi 5 crani, fornisce delle evidenze dirette di una variazione morfologica ampia all'interno e tra i primi *Homo*.

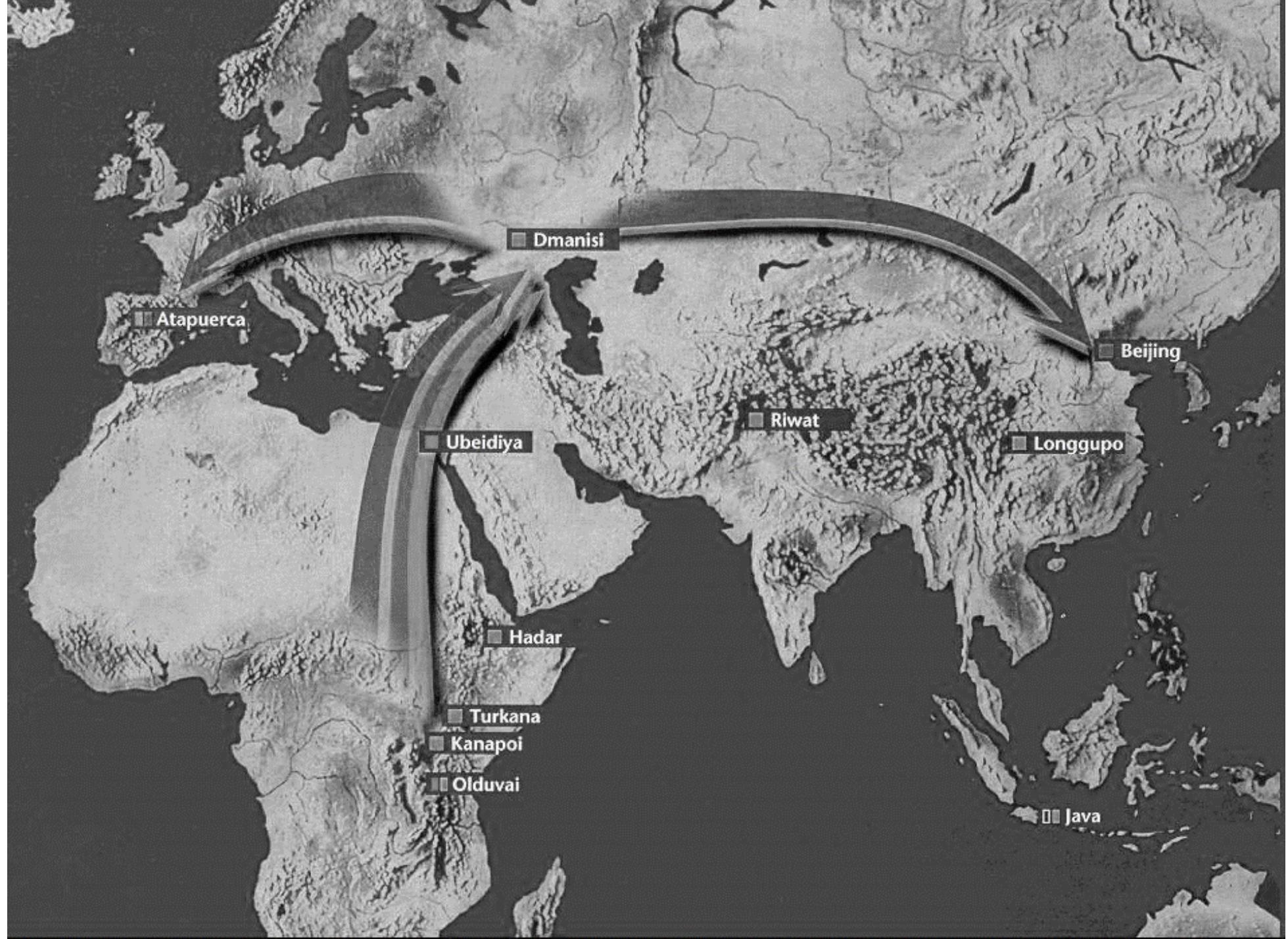
Questo suggerisce l'esistenza di una linea evolutiva unica dei primi *Homo*, con una continuità filogeographica attraverso i continenti.

*The Dmanisi sample, which now comprises five crania, provides direct evidence for wide morphological variation within and among early Homo paleodemones. This implies the existence of a single evolving lineage of early Homo, with phylogeographic continuity across continents.*

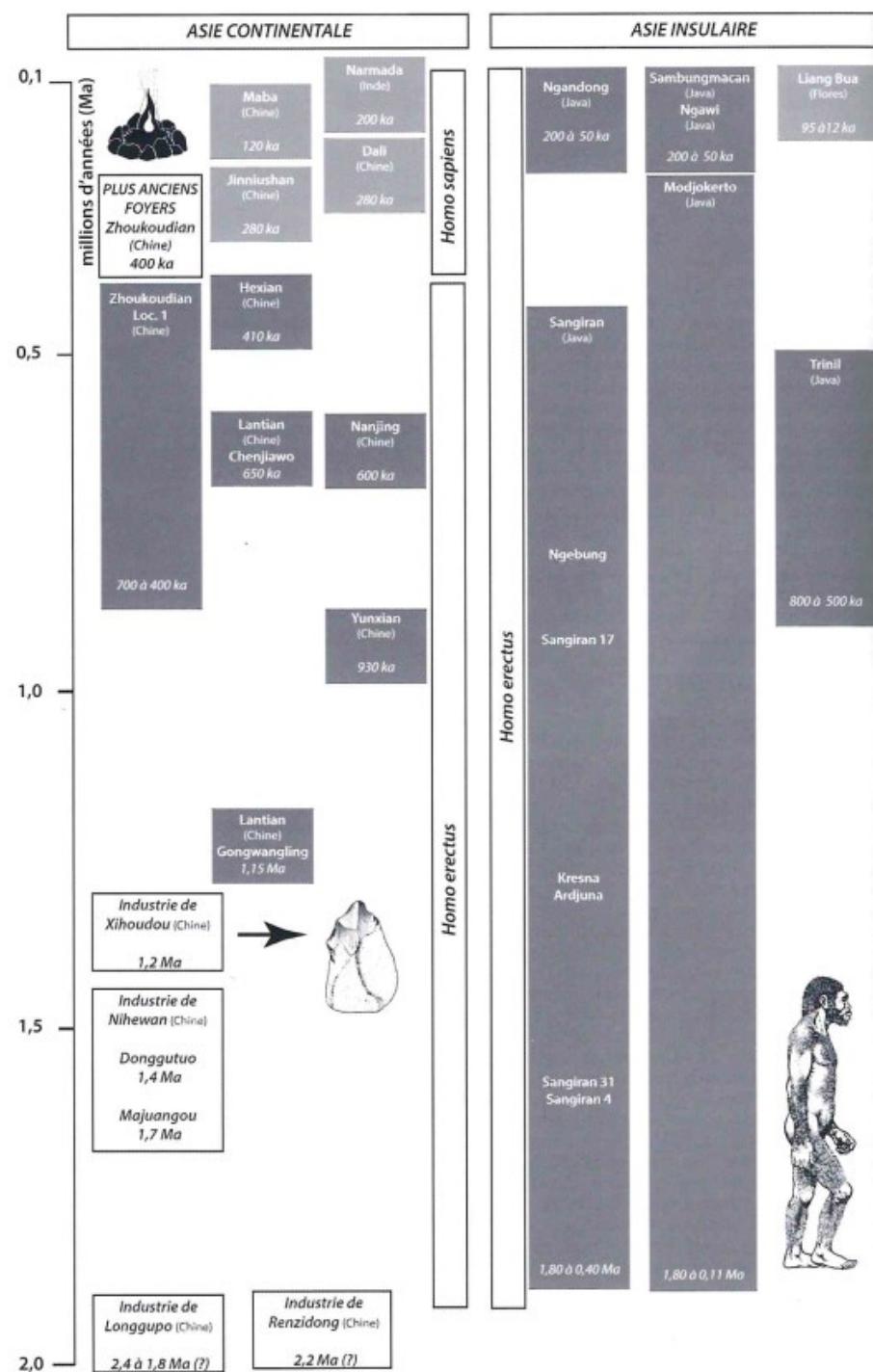


*Out of Africa.....*



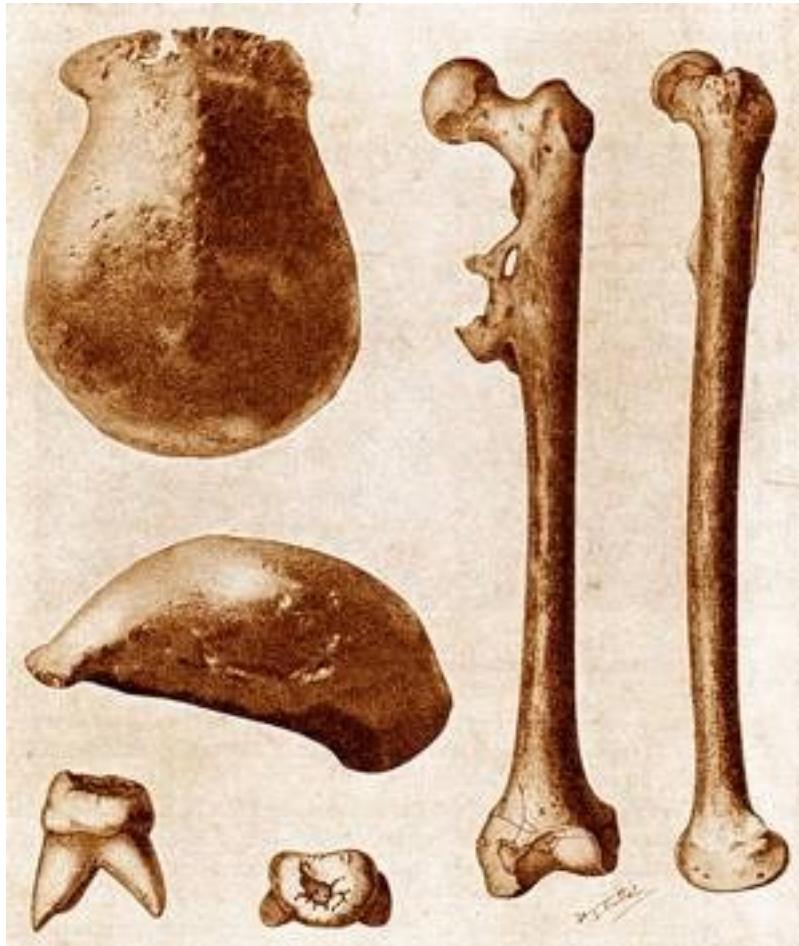


# *Out of Africa....toward Asia*



# *Out of Africa.....who?*

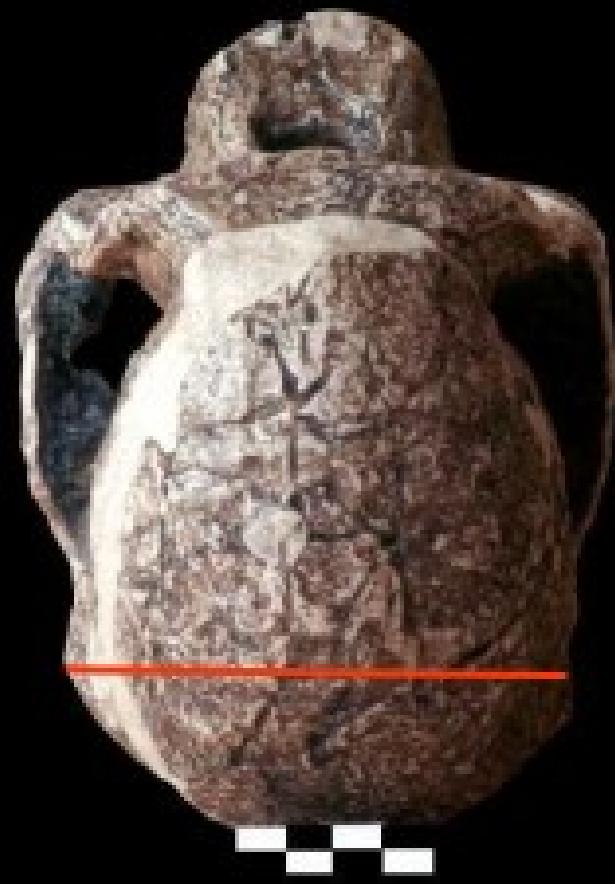
- The holotype of *Homo erectus* is the Trinil skull (Java)
- The skull from Zhoukoudian (China), Sangiran and Ngandong belongs to the same species
- ... and the African one?



Most ancient african fossil: *Homo ergaster*  
Most recent: *Homo erectus*

Larghezza cranica massima

*Maximum cranial breadth*



*Australopithecus  
africanus*



*Homo erectus*



*Homo sapiens*

Forma sfenoide: larghezza massima in posizione arretrata / *Sphenoid shape: Maximum breadth backward*

Restringimento dietro il toro sopra-orbitale / *Shrinkage retro orbital*

Parete convergente verso l'avanti: forma sfenoide  
*Wall convergent forward: sphenoidal shape*



*Australopithecus  
africanus*



*Homo erectus*

Parete convergente quasi-parallele: forma ovoidea  
*Wall almost parallel: ovoidal shape*



*Homo sapiens*

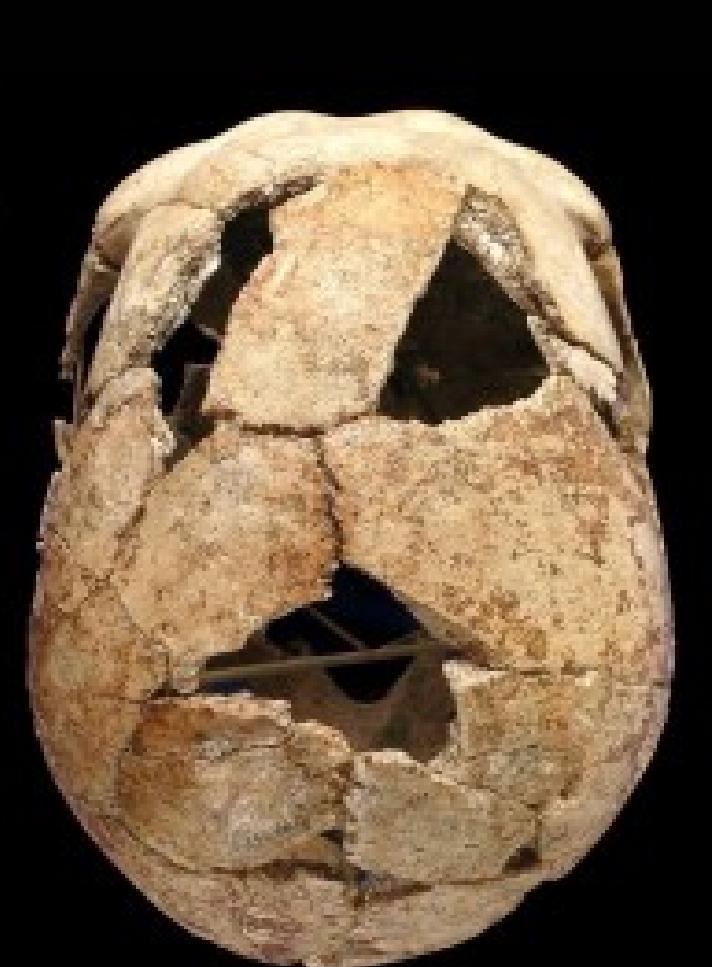
Prognatismo faciale  
*Facial prognatism*



*Australopithecus  
africanus*



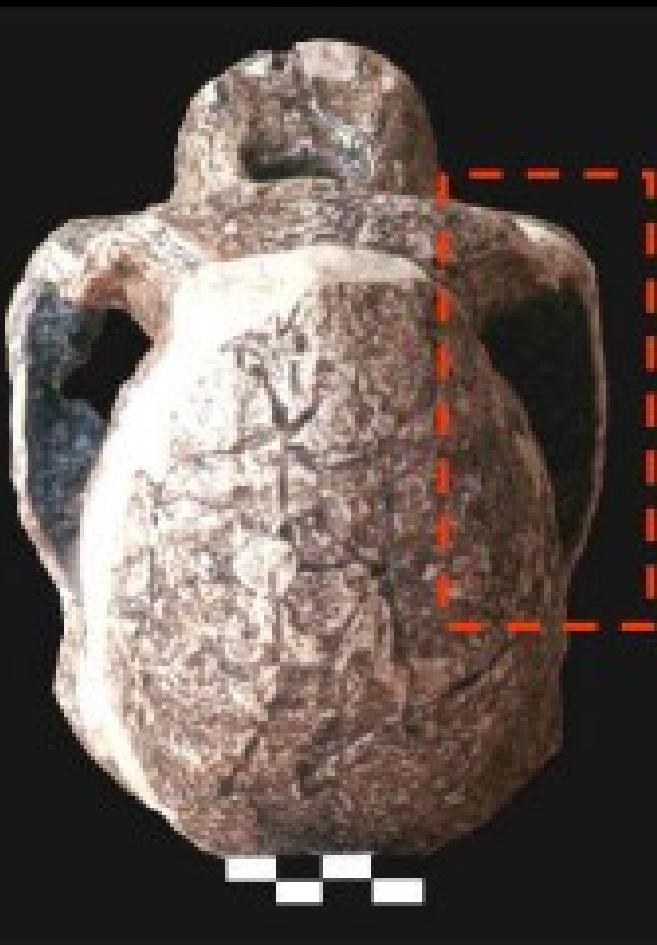
*Homo erectus*



*Homo sapiens*

Prognatismo alveolare  
*Alveolare prognathism*

Proiezione laterale dei zigomatici  
*Lateral projection of the zygomatics*



*Australopithecus  
africanus*

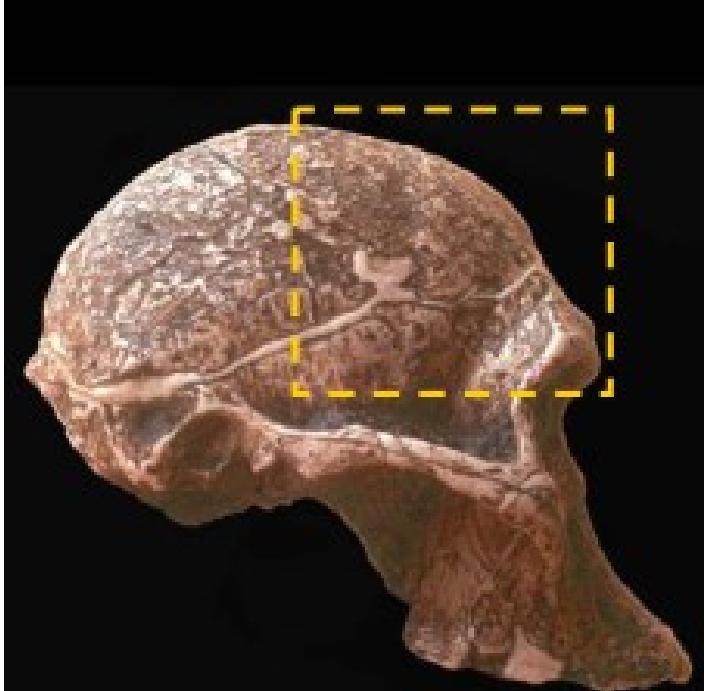


*Homo erectus*

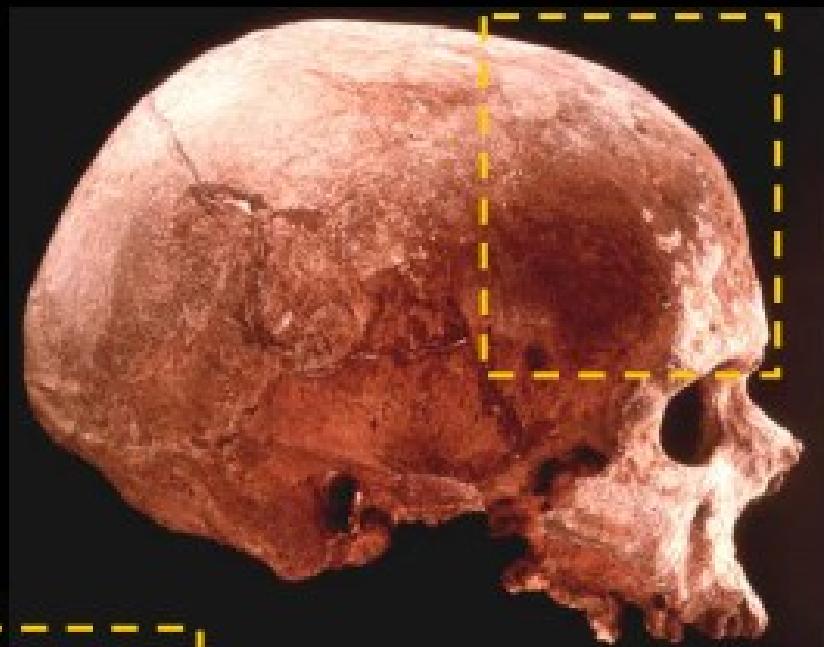


*Homo sapiens*

Osso frontale sfuggente  
*Receding frontal bone*



*Australopithecus  
africanus*



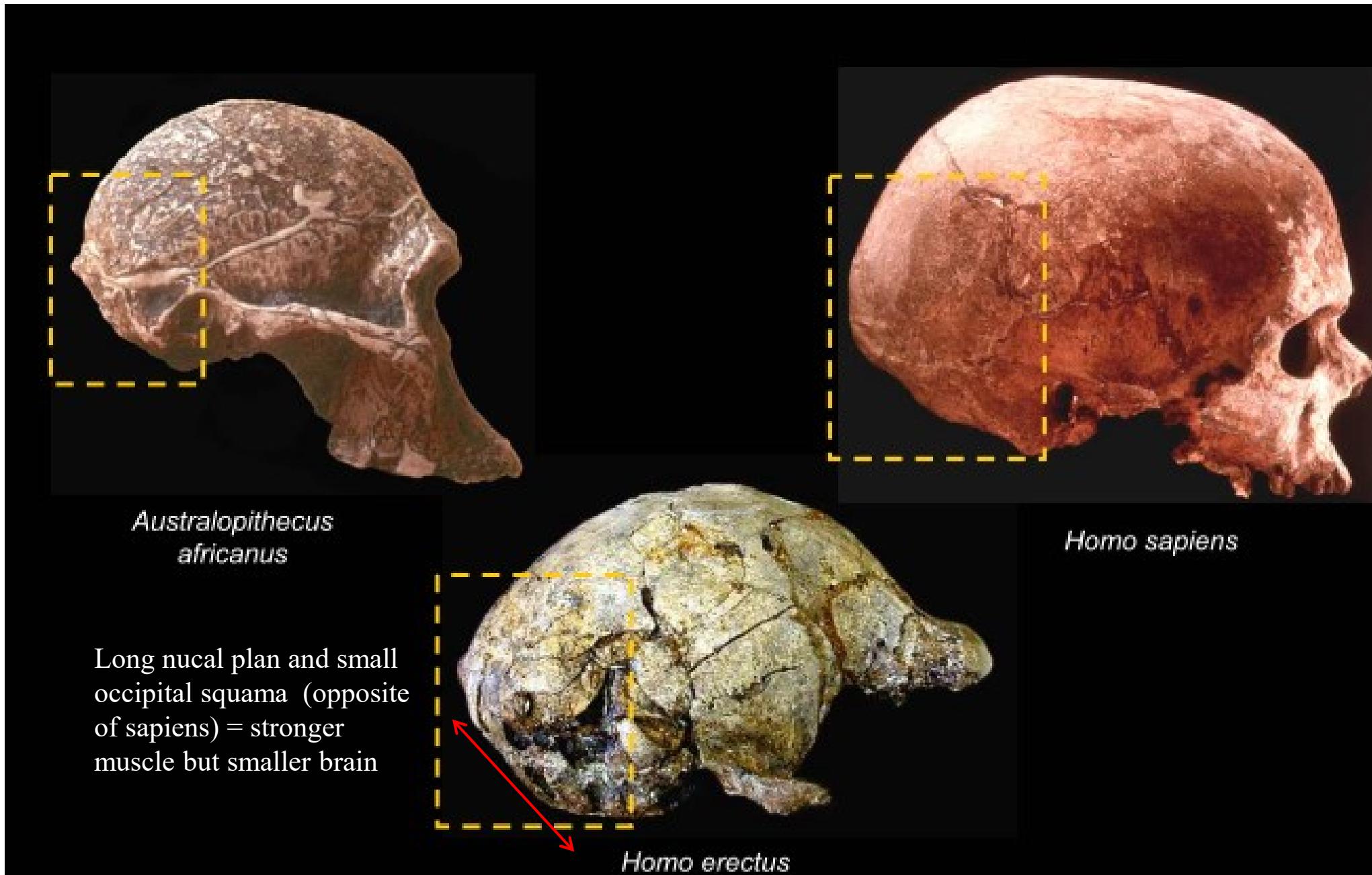
*Homo sapiens*



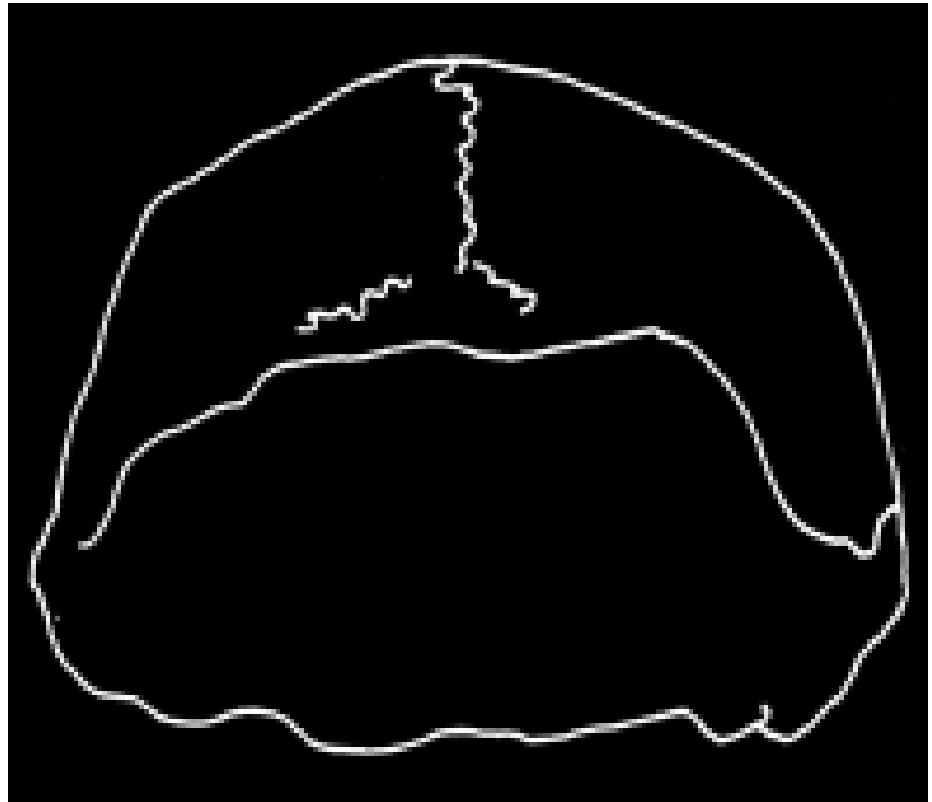
*Homo erectus*

## Forma dell'osso occipitale

### Occipital shape

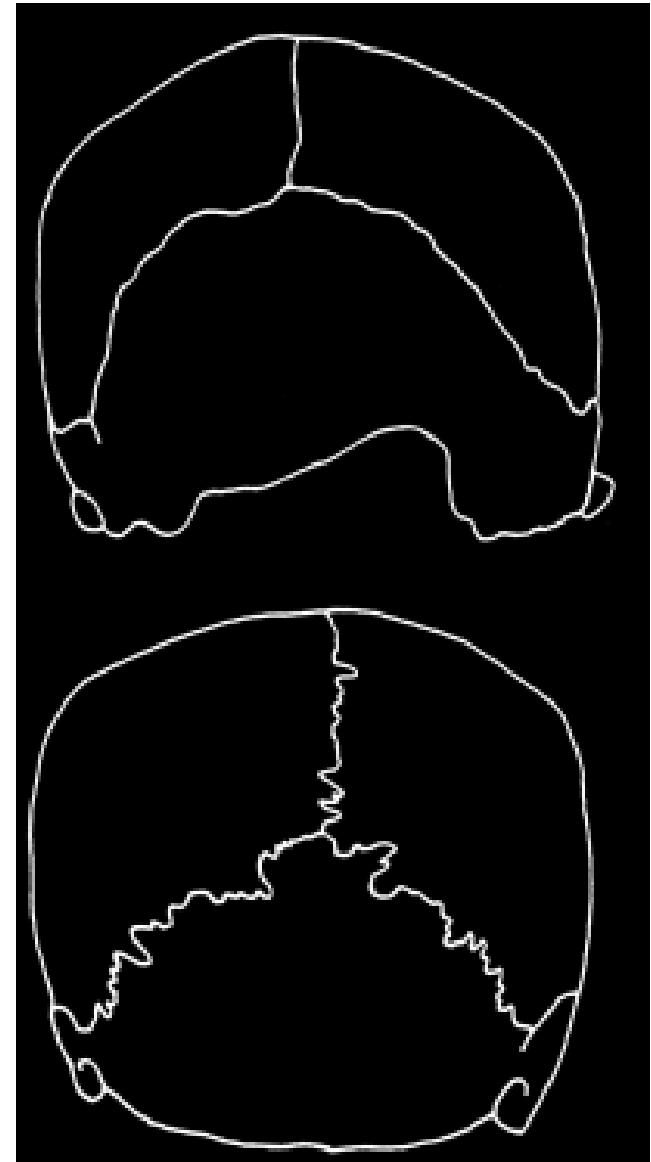


Forma del cranio in vista posteriore  
*Cranial shape in posterior view*



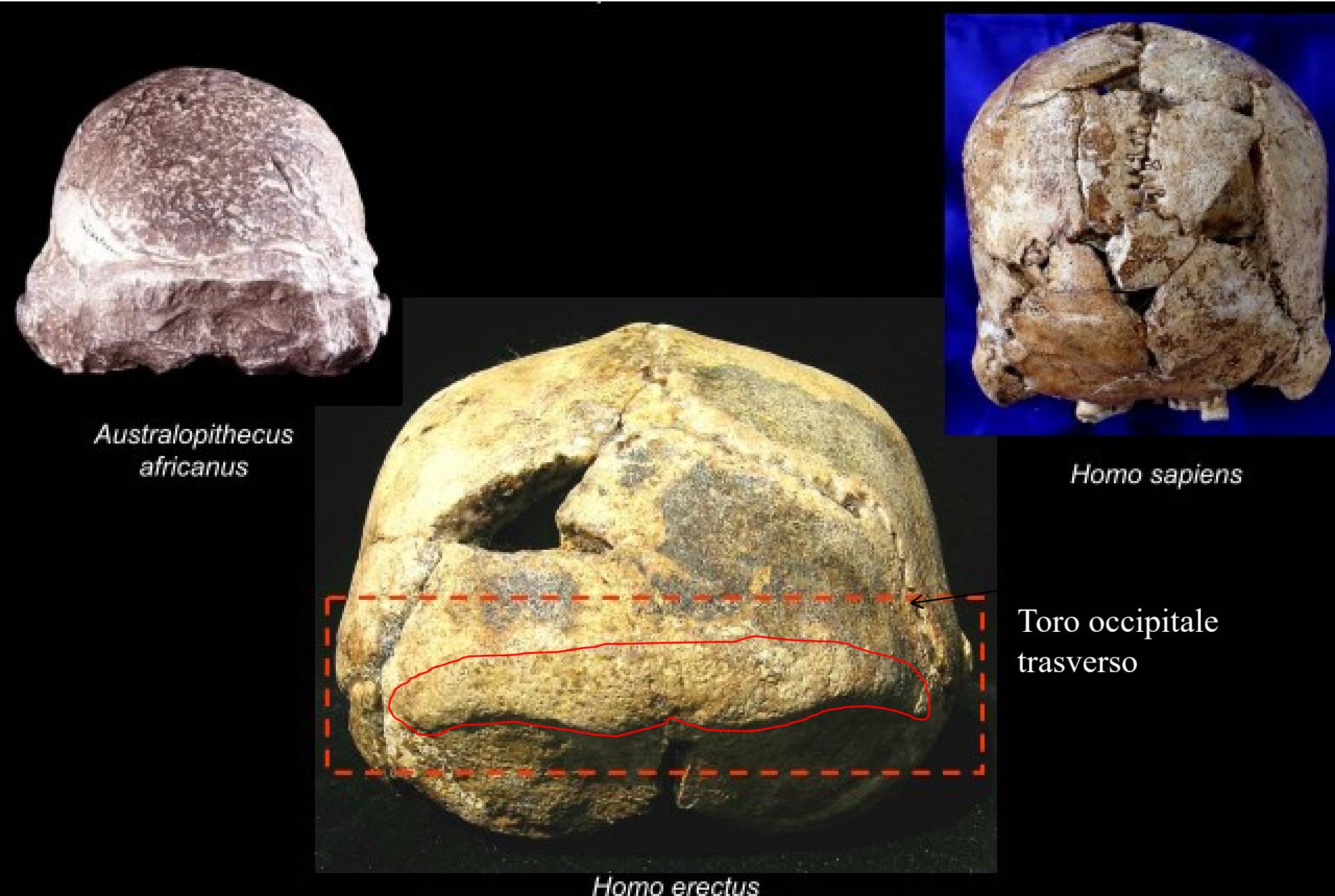
Pentagonale a parete  
convergente verso l'alto  
*Pentagonal with the wall  
convergent upward*

Bozze parietale non sviluppate  
*Undeveloped parietal bump*

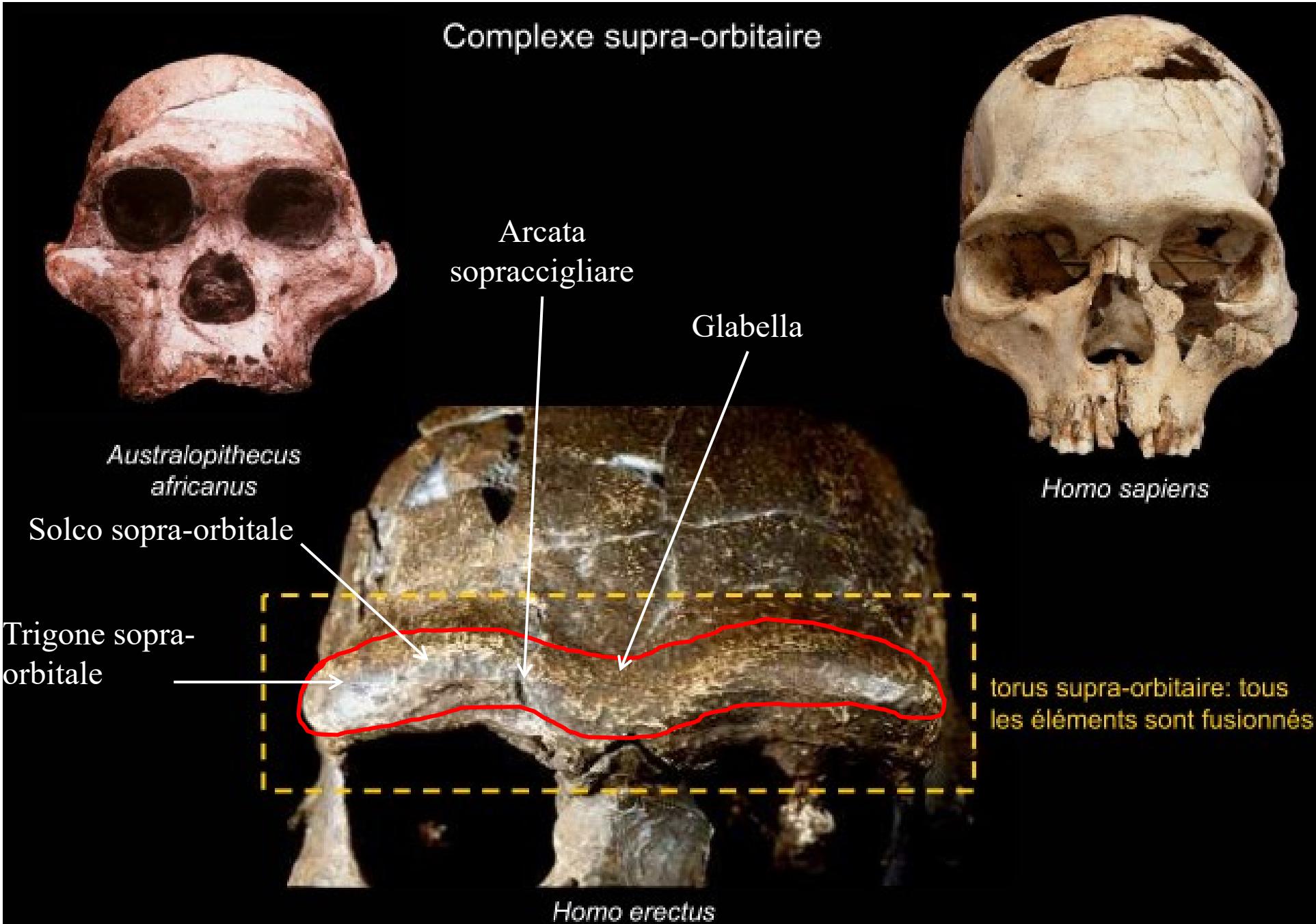


A « tetto di casa »  
(*Homo sapiens*)  
In « House roof »  
(*Homo sapiens*)

Toro occipital transverso  
*Occipital transverse torus*



## Complexe supra-orbitaire



Spazio interorbitale largo = becco encefalico / *large interorbital space = encephalic beak*

# LONGGUPO (2 Ma BP)

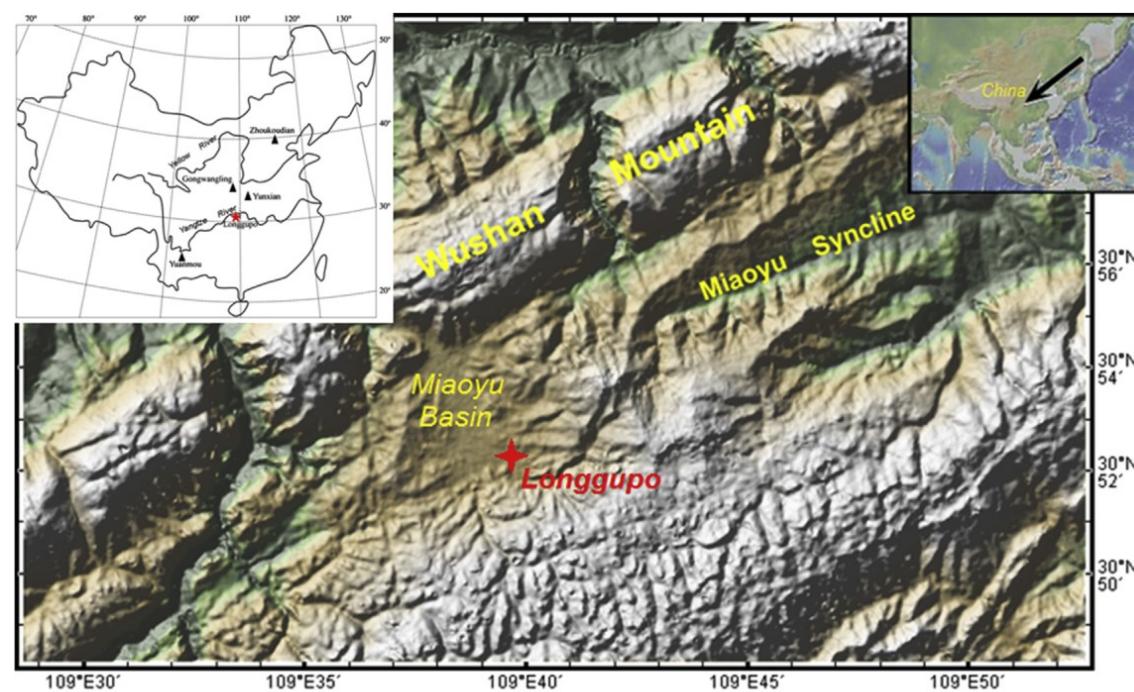
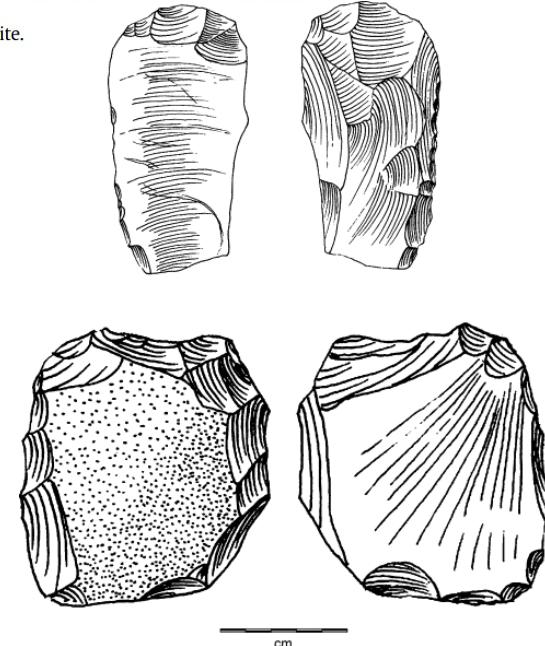


Fig. 1. Location of Longgupo site.



The earliest evidence of hominid settlement in China: Combined electron spin resonance and uranium series (ESR/U-series) dating of mammalian fossil teeth from Longgupo cave

Fei Han <sup>a,\*</sup>, Jean-Jacques Bahain <sup>b</sup>, Chenglong Deng <sup>c</sup>, Éric Boëda <sup>d,e,f</sup>, Yamei Hou <sup>e</sup>, Guangbiao Wei <sup>f</sup>, Wanbo Huang <sup>f,g</sup>, Tristan Garcia <sup>h</sup>, Qingfeng Shao <sup>i</sup>, Cunding He <sup>f</sup>, Christophe Falguères <sup>b</sup>, Pierre Voinchet <sup>b</sup>, Gongming Yin <sup>a</sup>

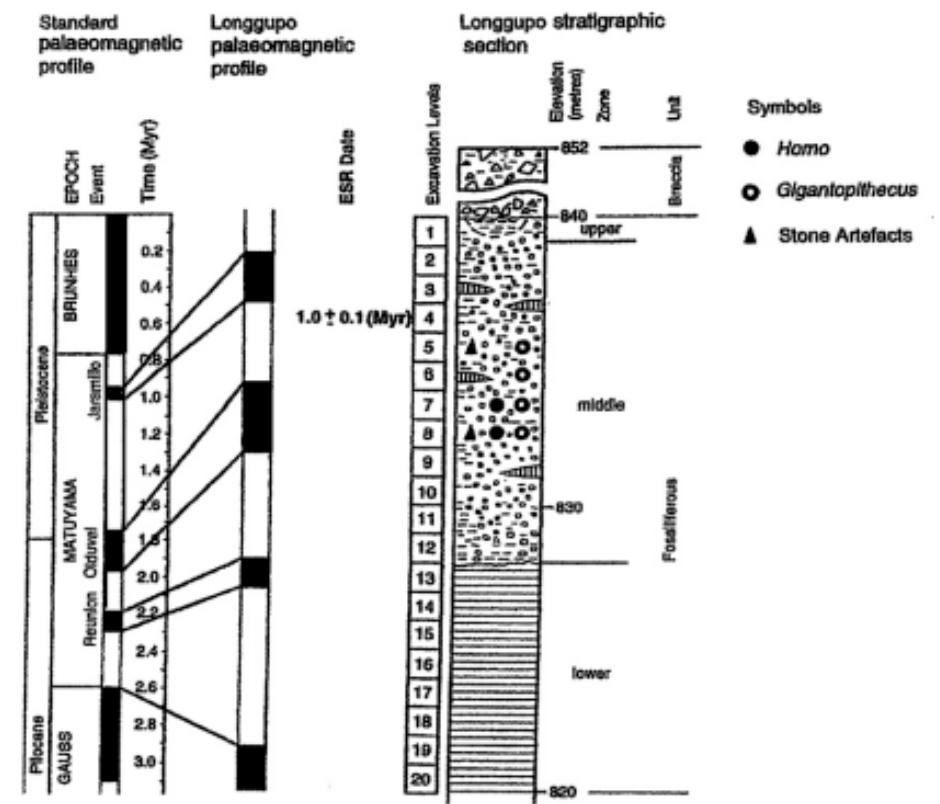
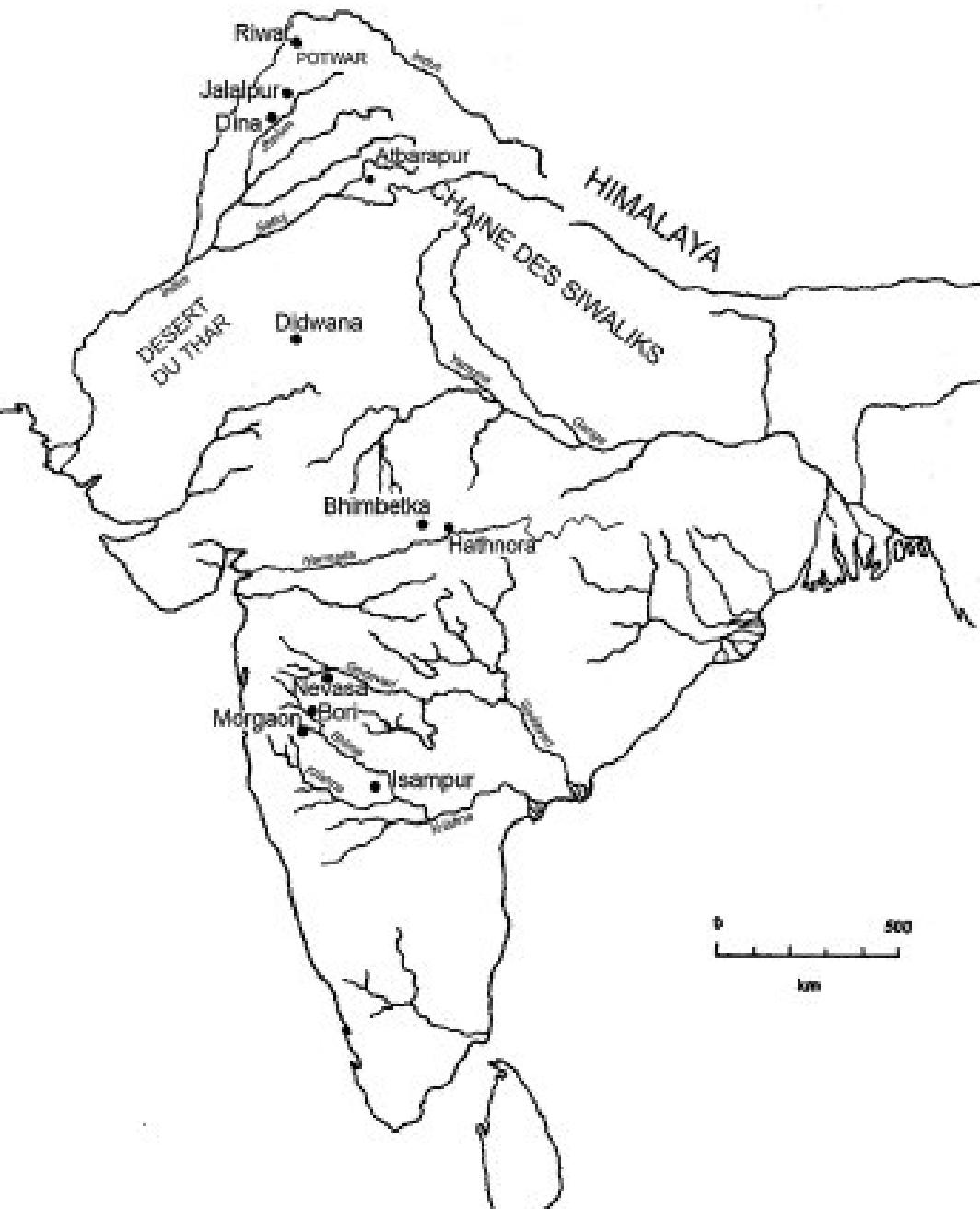


Fig. 6. Stratigraphie de la grotte Longgupo et hypothèses de datation (d'après Huang et al., 1995).  
Fig. 6. Stratigraphy of the Longgupo cave and hypotheses for datation (after Huang et al., 1995).

# RIWAT 1,9 Ma BP



Available online at [www.sciencedirect.com](http://www.sciencedirect.com)



C. R. Palevol 5 (2006) 359–369



Paléontologie humaine et Préhistoire

## Les premiers peuplements d'Asie du Sud : vestiges culturels

Claire Gaillard

UMR 5198 du CNRS, département de préhistoire du Muséum national d'histoire naturelle,  
Institut de paléontologie humaine, 1, rue René-Panhard, 75013 Paris, France

Reçu le 22 novembre 2004 ; accepté après révision le 19 septembre 2005

Disponible sur internet le 28 novembre 2005

Invitation du Comité éditorial



ISAMPUR 1 Ma BP

## Java

Modjokerto 1,8-0,4 Ma

Sangiran 1,8-0,4 Ma

(Sangiran 4, 31, Ardjuna, Kresna, Sangiran17, Ngebung)

Trinil 0,8-0,5 Ma



## China

Lantian - Gongwangling 1,15 Ma

Yunxian 0,93 Ma

Zhoukoudian loc. 1 0,7-0,4 Ma

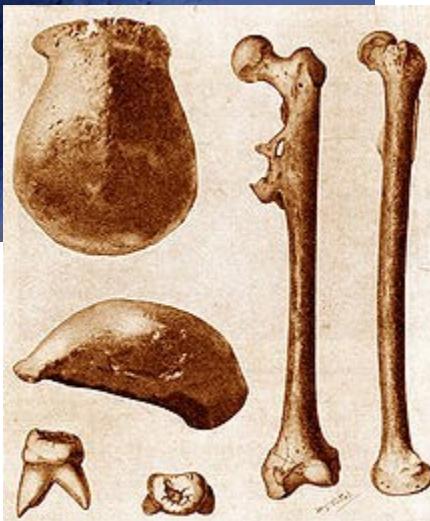
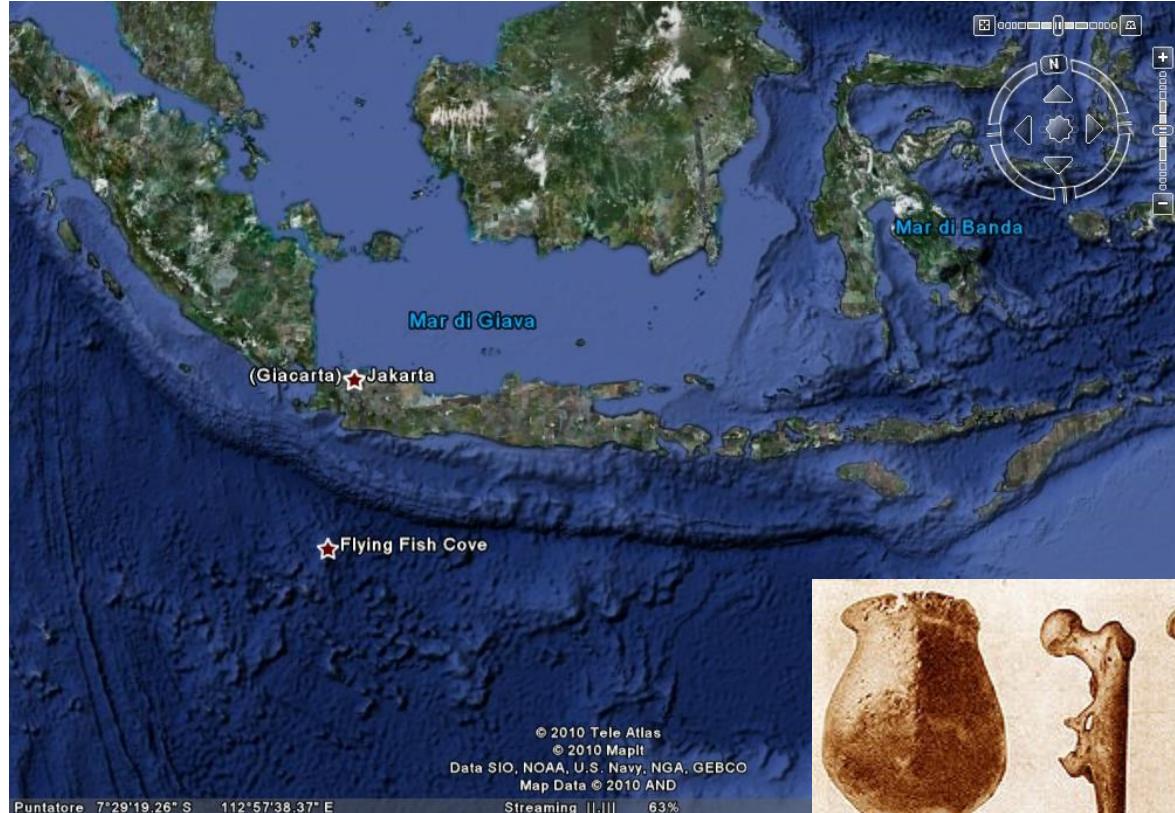
Lantian – Chenjiawo 0,65 Ma

Nanjing 0,6 Ma

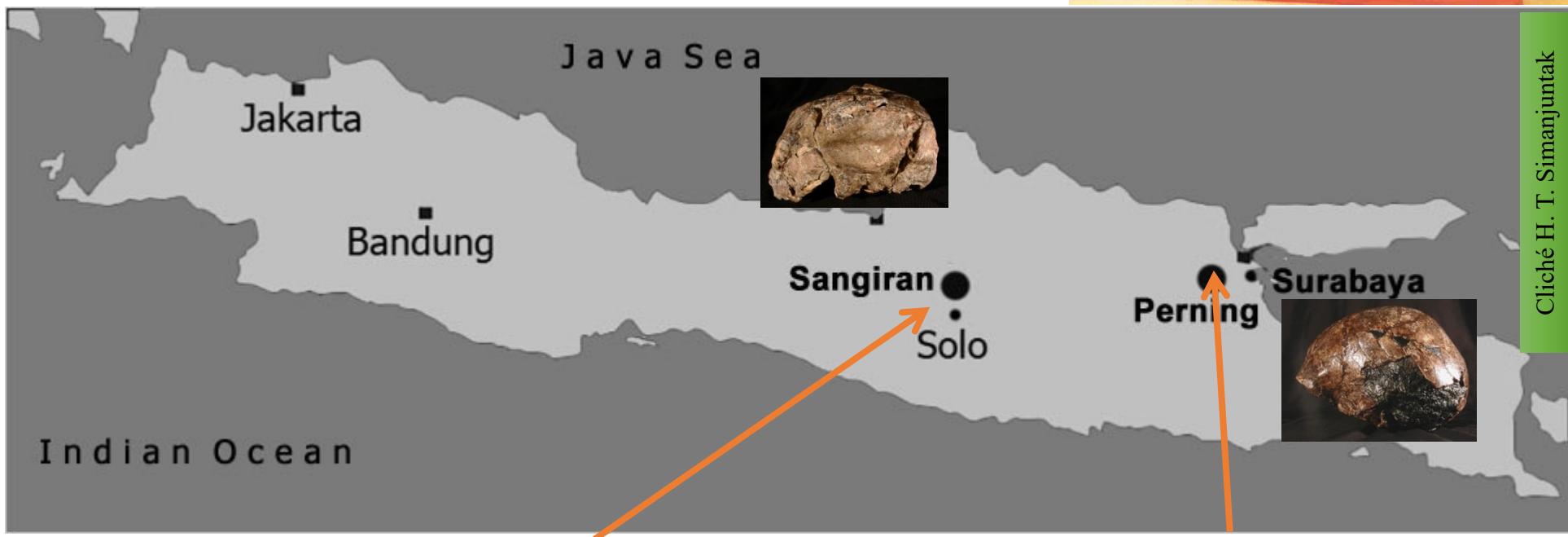
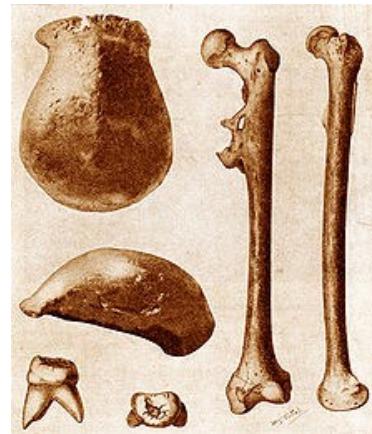
Hexian 0,41 Ma



# *Homo erectus* à Java (*Pithecanthropus*)



# *Homo erectus* à Java (*Pithecanthropus*)



$1.6 \pm 0.04$  mya (Jacob & Curtis 1971)

$1.66 \pm 0.04$  mya (Swisher *et al* 1994)

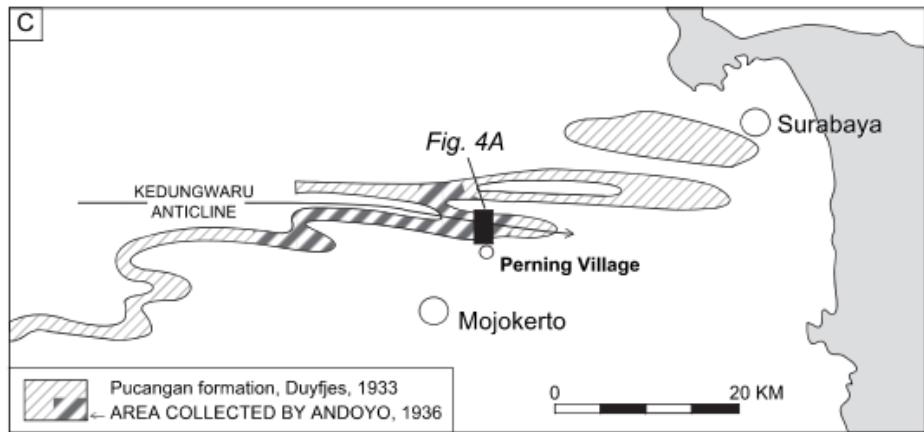
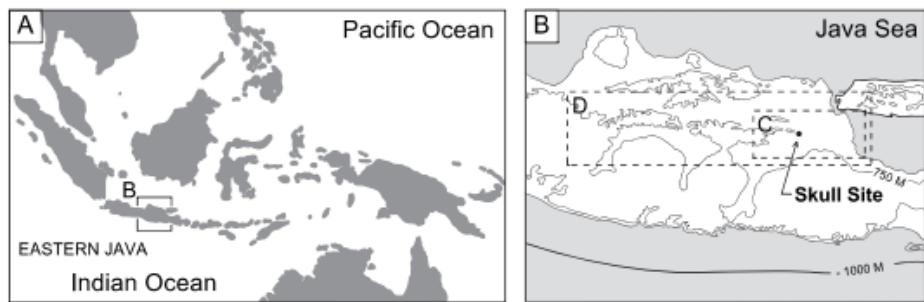
1.64-1.67 mya: Kalibeng-Pucangan (Sémah 2000)

$1.66 \pm 0.04$  mya: Lowest Pucangan: (Widiasmoro 2001).

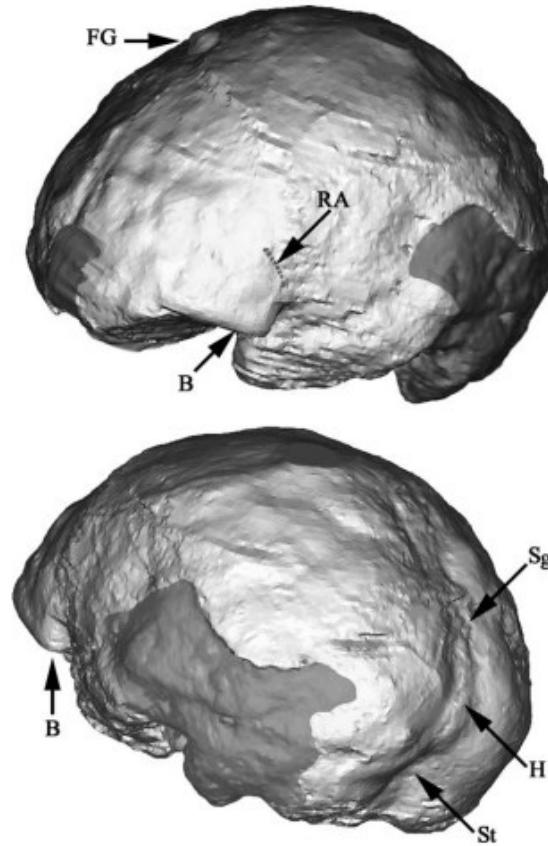
$1.9 \pm 0.5$  mya (Jacob & Curtis 1971)

$1.81 \pm 0.04$  mya (Swisher *et al* 1994).

# Mojokerto, 1.9 Myr

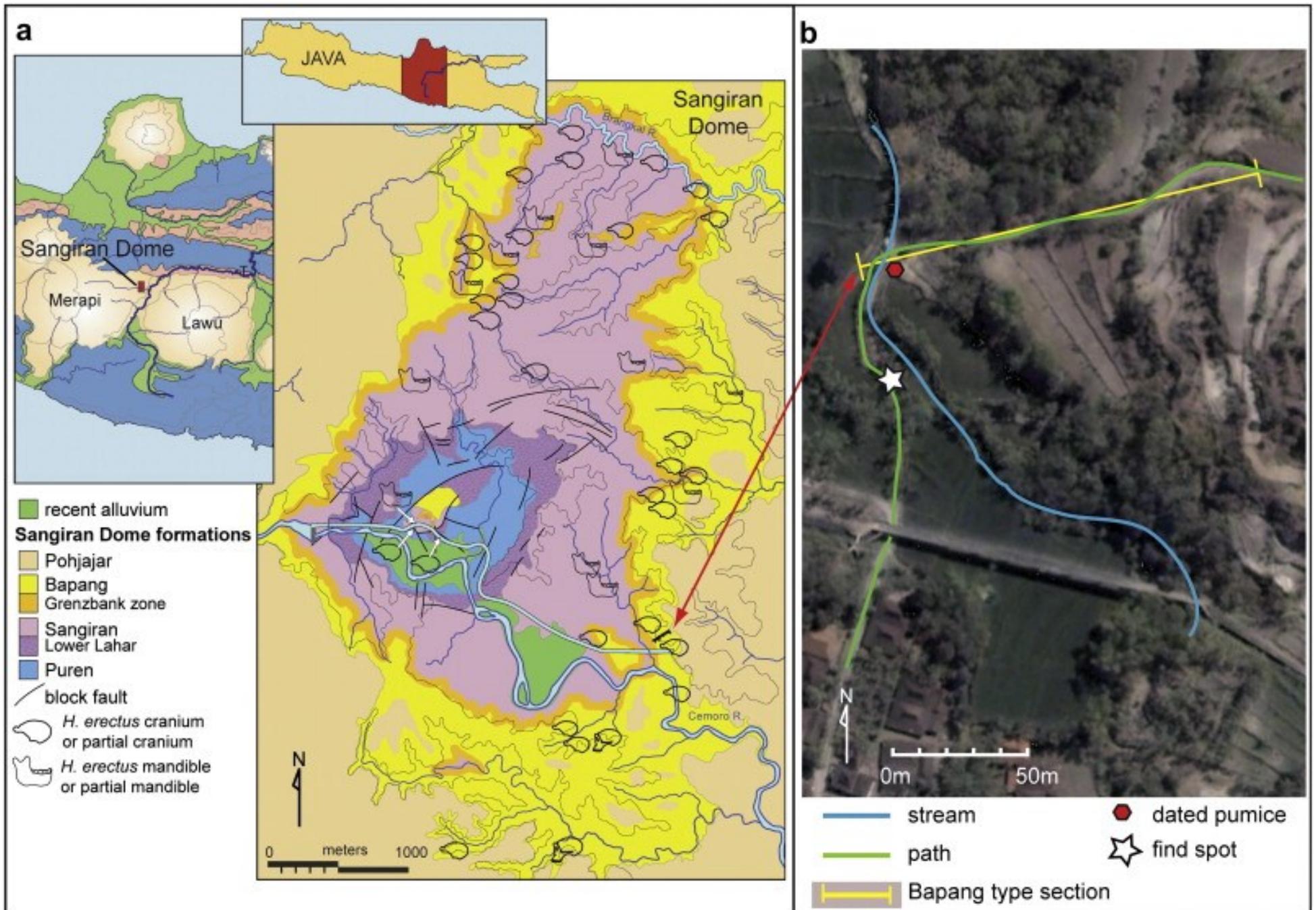


Photographs of Mojokerto child skull. A) left lateral view B) compared with 1.5 years old modern-child skull



Visualization of Mojokerto endocast (Balzeau, 2005)

# Sangiran, Java, Indonesia





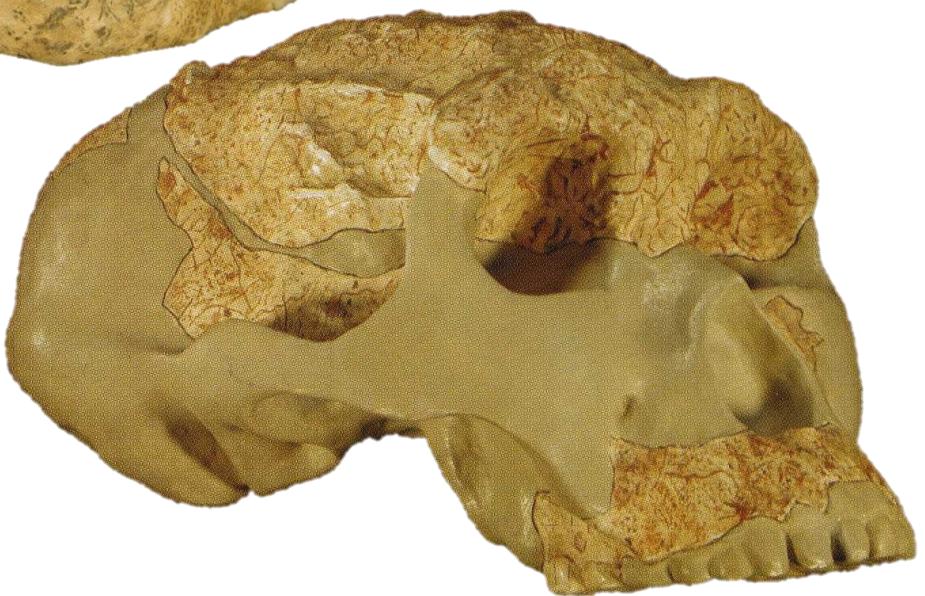
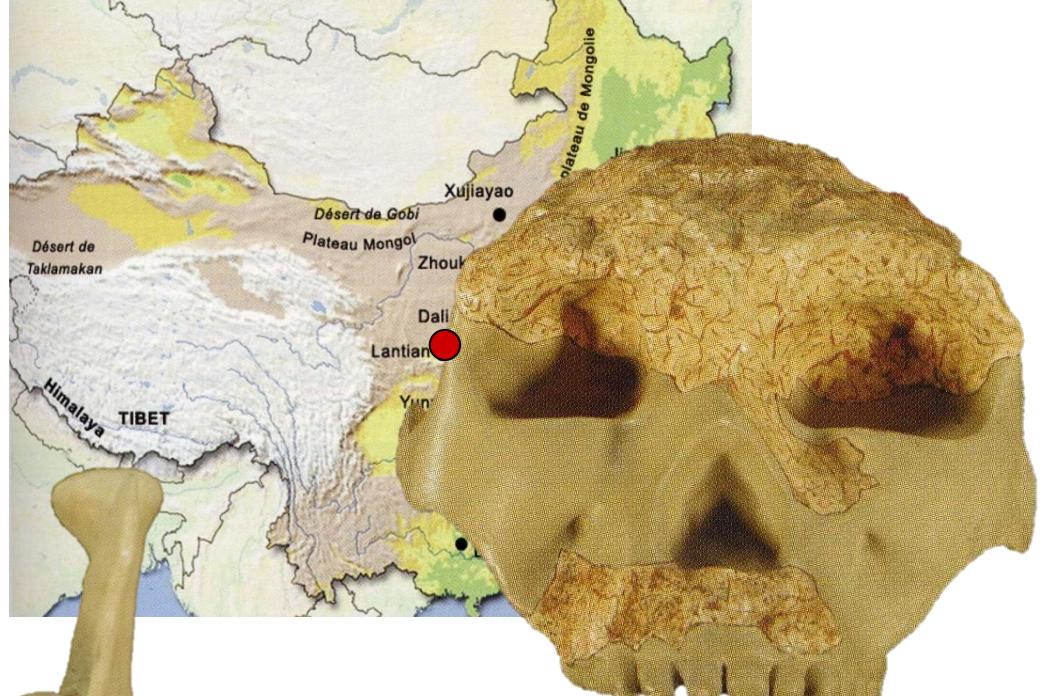
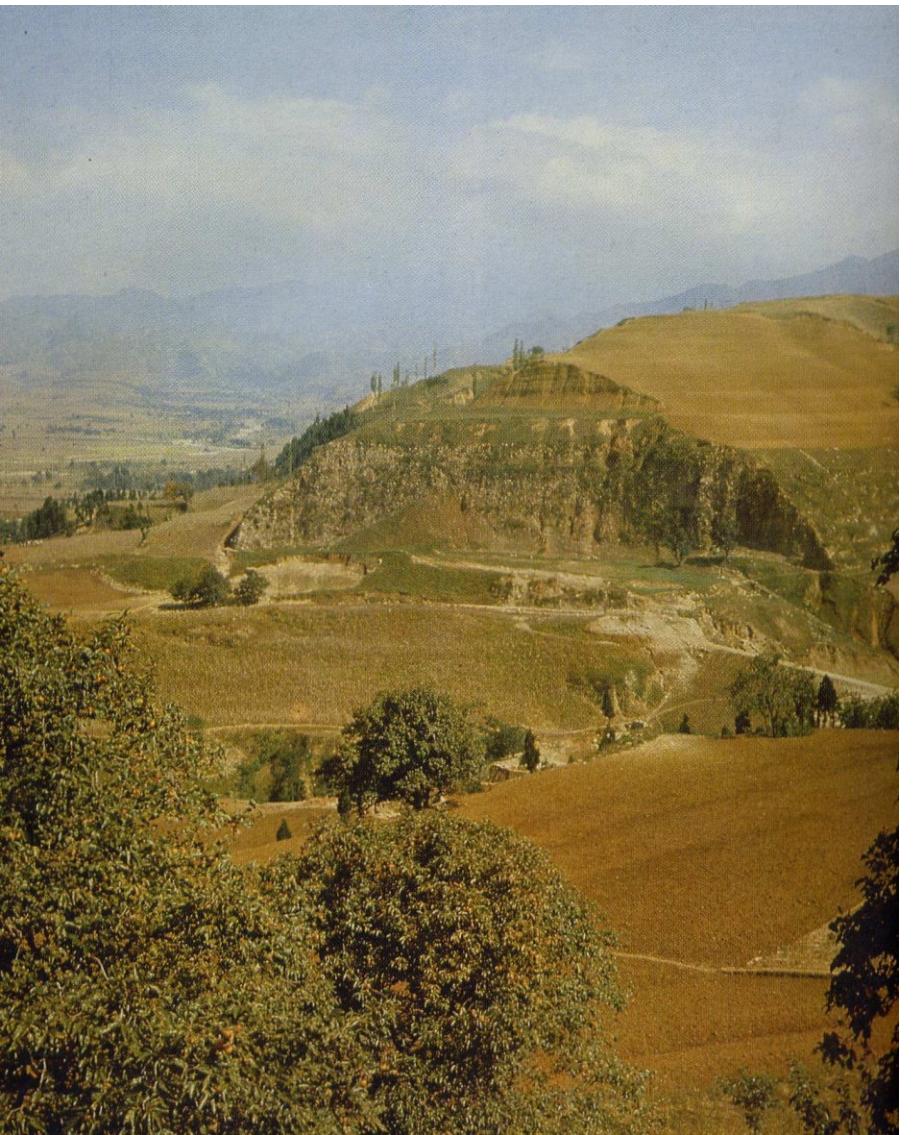
Sangiran 2



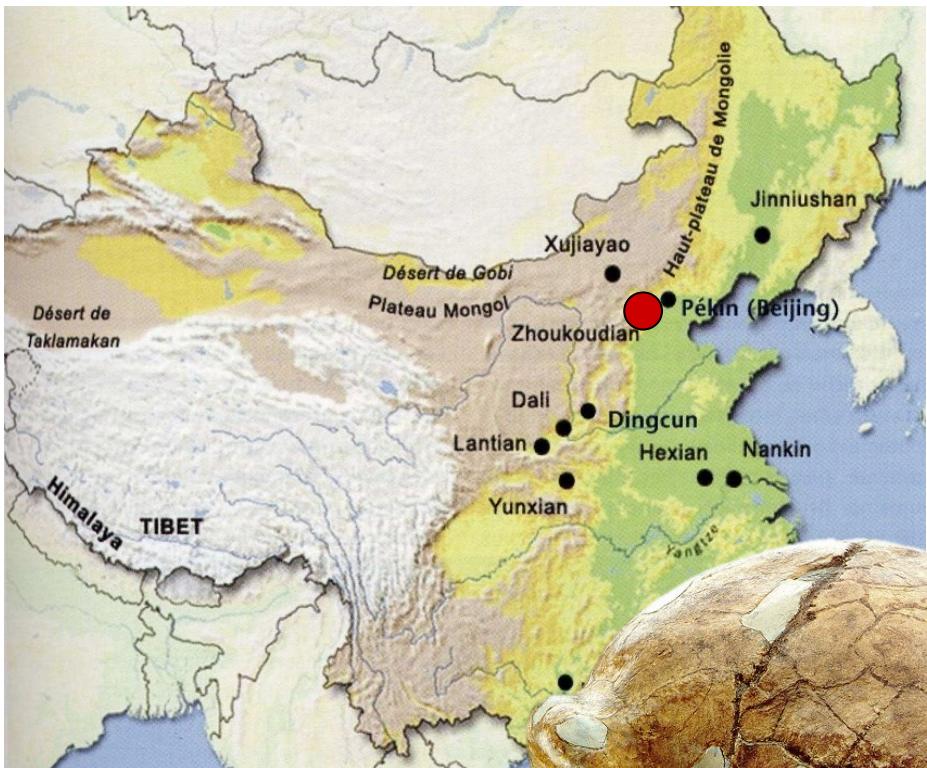
Sangiran 38

# *Out of Africa....toward Asia*

## LANTIAN

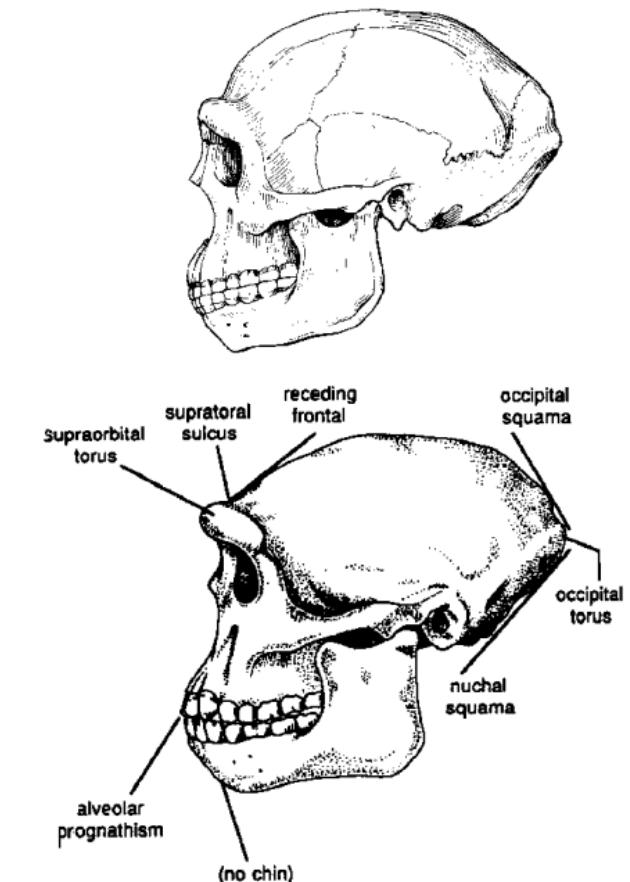


# *Out of Africa....toward Asia*



## ZHOUKOUDIAN

La località 1 è stata datata tra 600.000 e 200.000 anni BP. Si tratta di un insediamento in grotta.



Confronto tra Sangiran 4 (basso) e Zhoukoudian



## A geometric morphometric study of a Middle Pleistocene cranium from Hexian, China



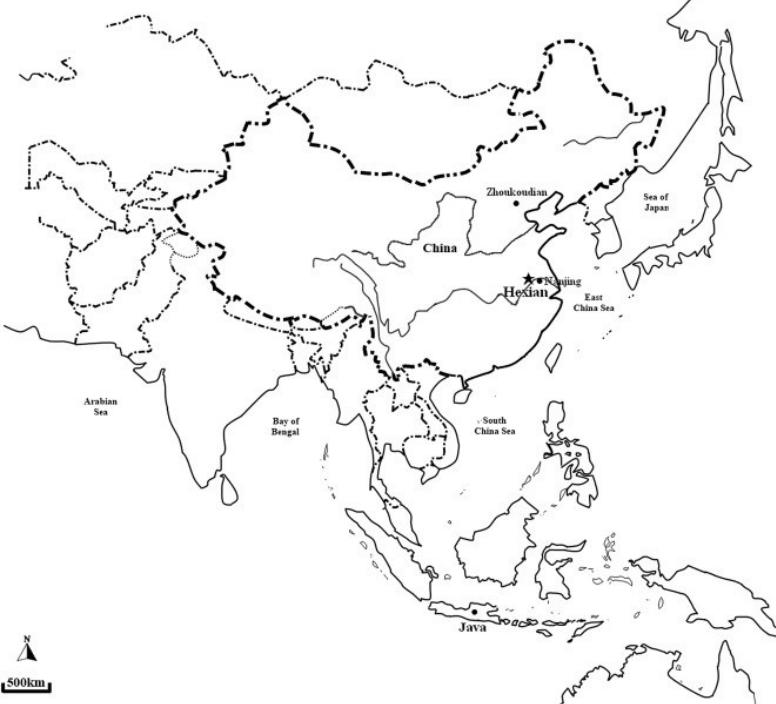
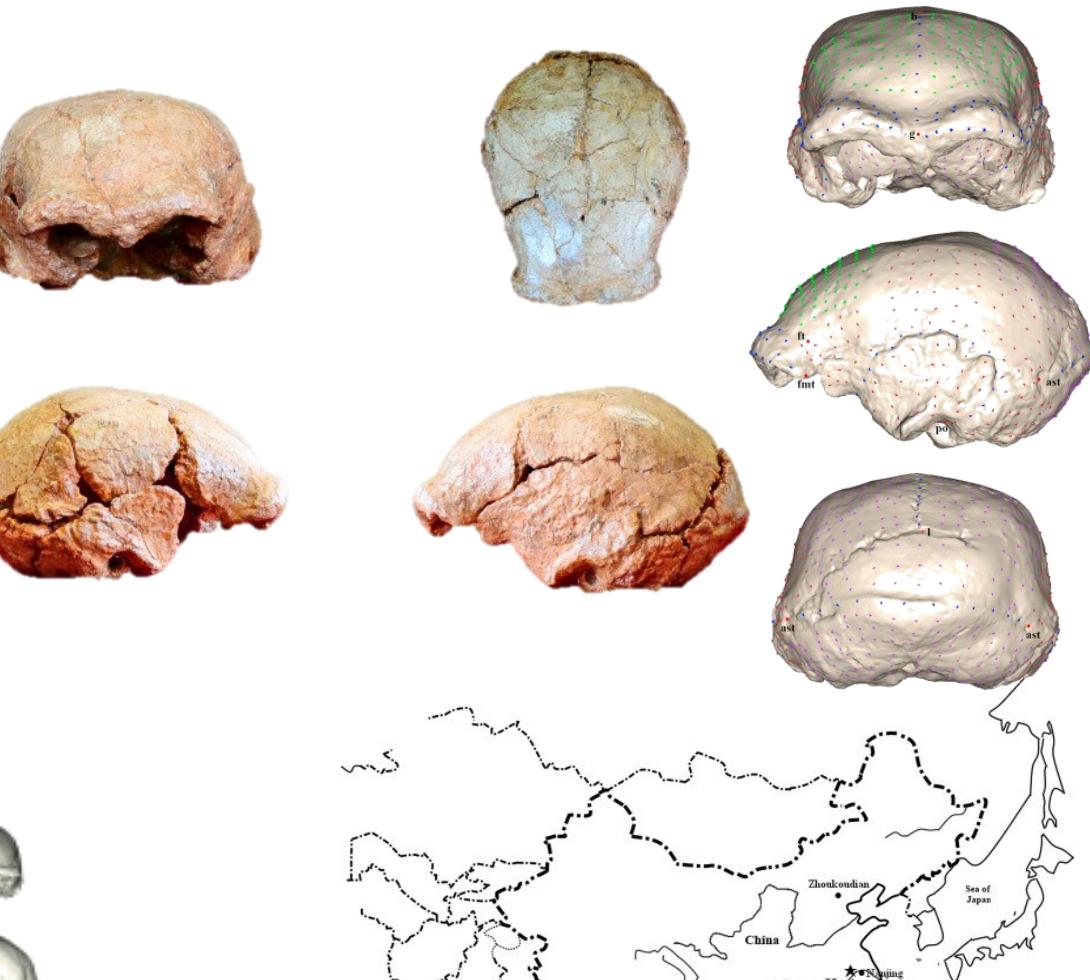
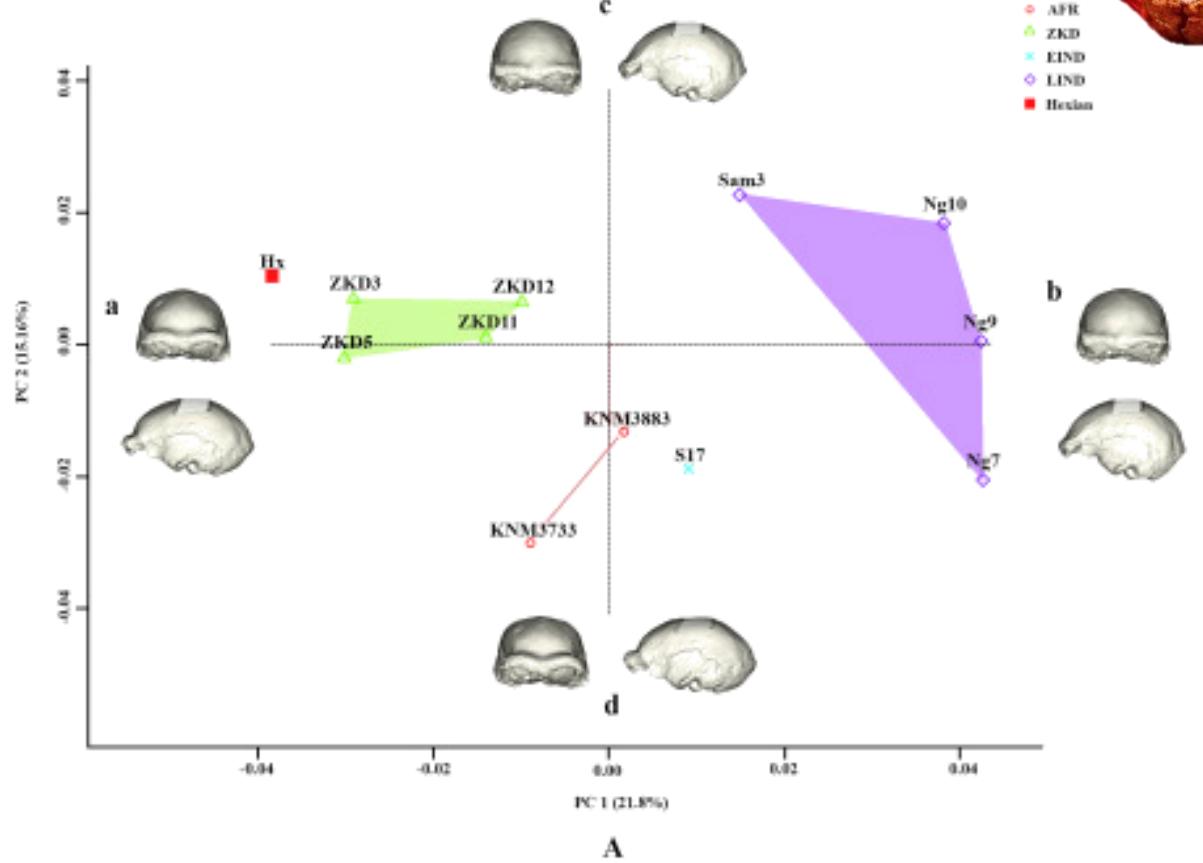
Yaming Cui <sup>a,b,\*</sup>, Xinzhí Wu <sup>a</sup>

<sup>a</sup> Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing 100044, China

<sup>b</sup> University of the Chinese Academy of Sciences, Beijing 100049, China

150 and 412 ka

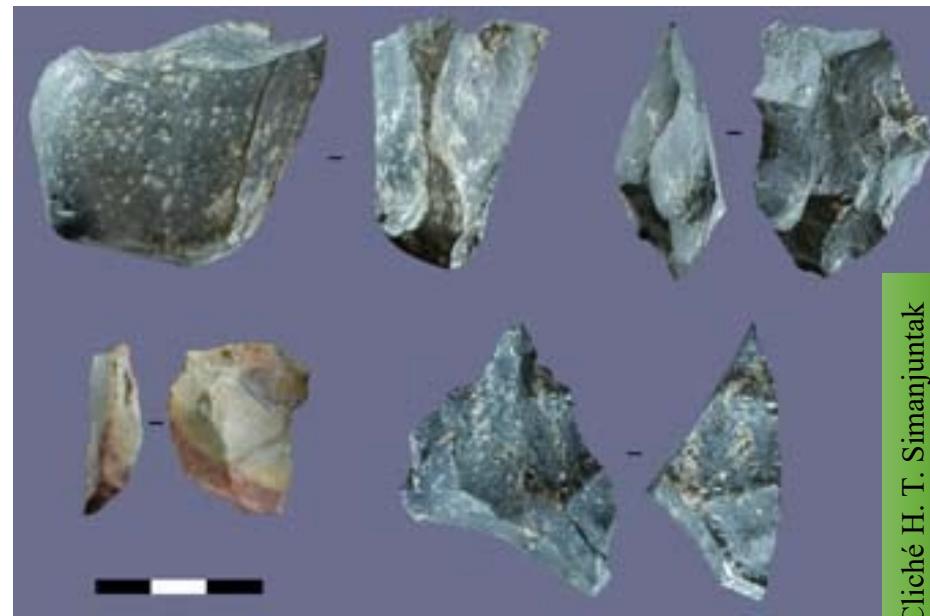
### Regional variation in Asian *H. erectus*



# Soa Bassin, Flores



Lithic artifacts discovery at the open sites of Mata menge, Tangitallo, etc associated with Stegodon, komodo dragon, rat and various other taxa from layers dated to c.800,000 BP (Morwood *et al.* 1997-1999).

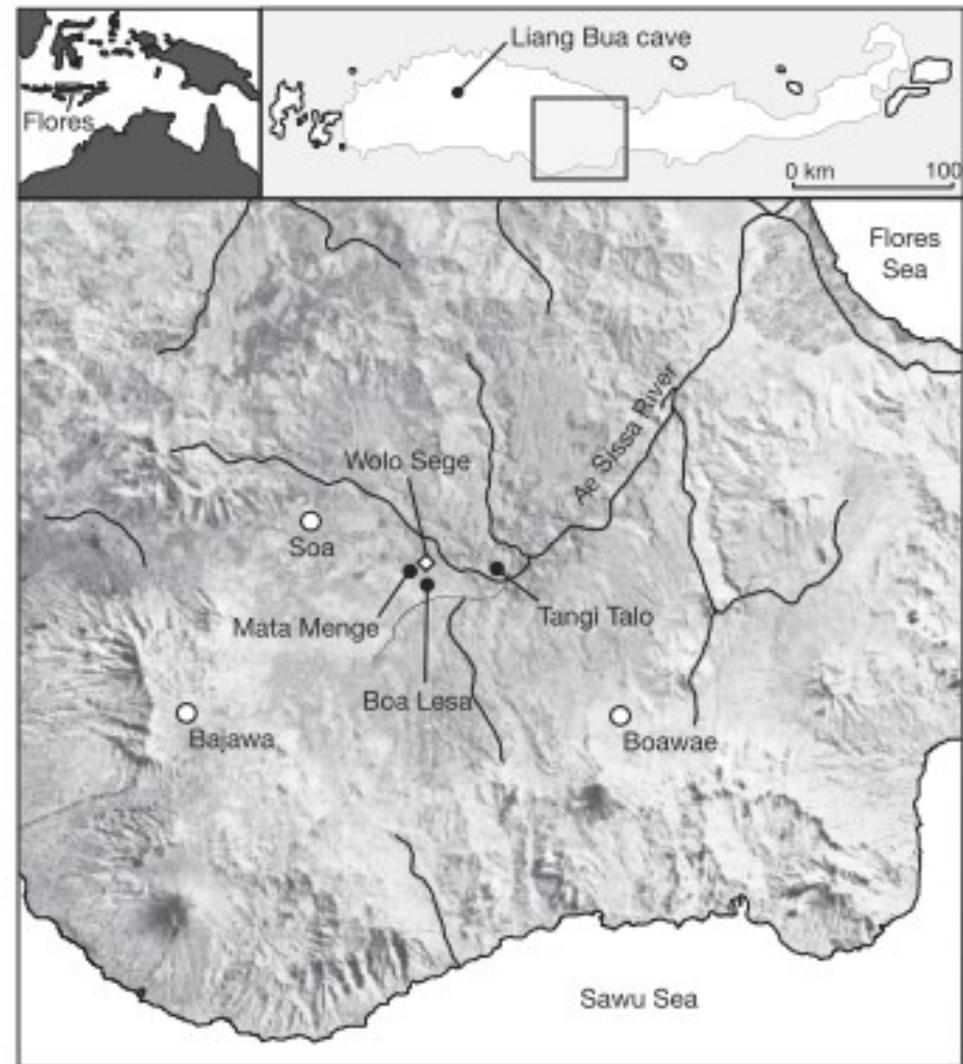
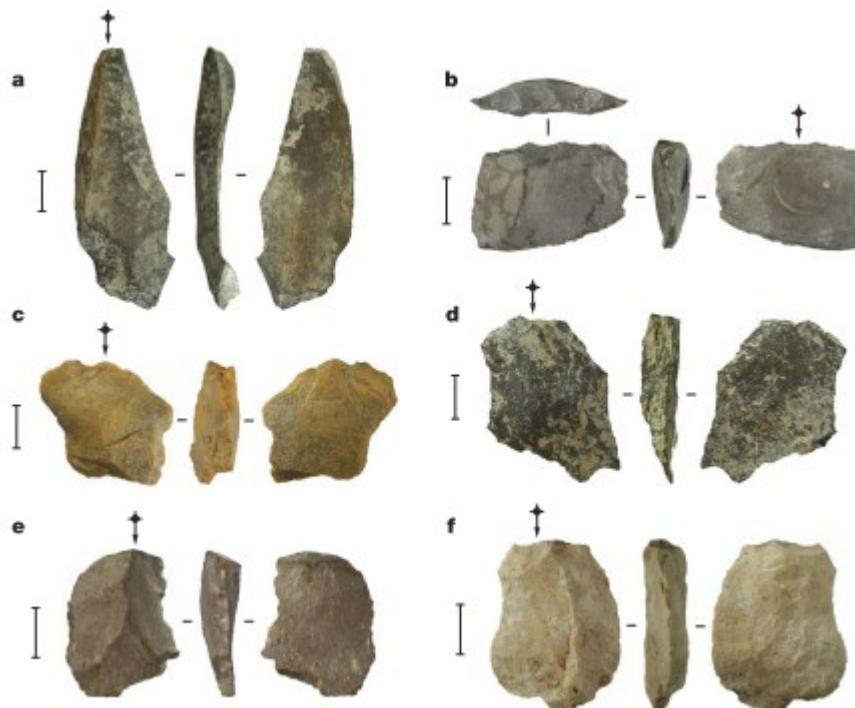


Cliché H. T. Simanjuntak

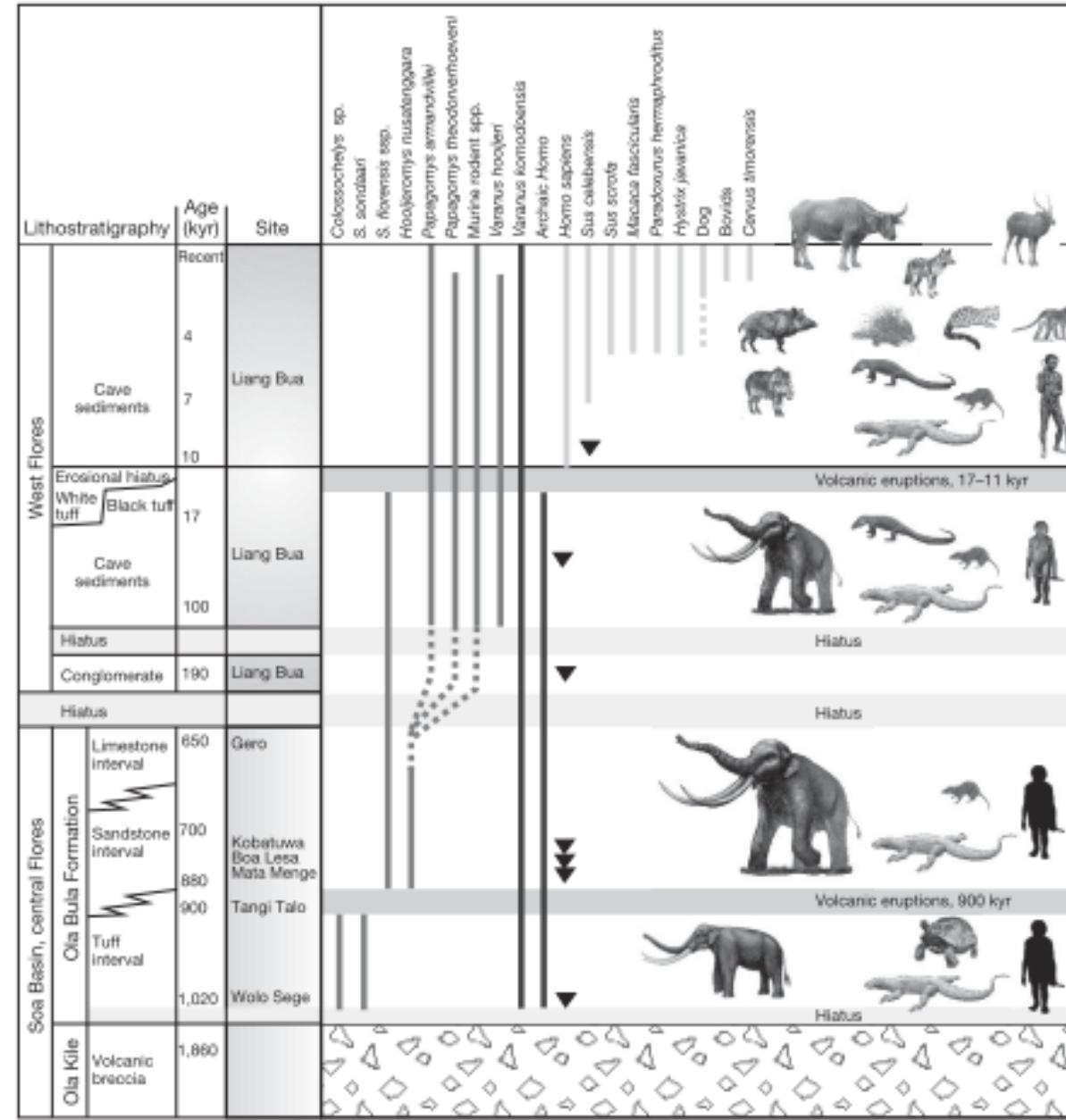
## LETTERS

## Hominins on Flores, Indonesia, by one million years ago

Adam Brumm<sup>1</sup>, Gitte M. Jensen<sup>2</sup>, Gert D. van den Bergh<sup>1,3</sup>, Michael J. Morwood<sup>1</sup>, Iwan Kurniawan<sup>4</sup>, Fachroel Aziz<sup>4</sup> & Michael Storey<sup>2</sup>



**Figure 1 | Map of Flores showing the location of Wolo Sege.** Also shown are other key early- or middle-Pleistocene archaeological and palaeontological localities in the Soa Basin mentioned in the text, and the late-Pleistocene Liang Bua cave in western Flores. (Base maps courtesy of D. Hobbs.)



# A new small-bodied hominin from the Late Pleistocene of Flores, Indonesia

P. Brown<sup>1</sup>, T. Sutikna<sup>2</sup>, M. J. Morwood<sup>1</sup>, R. P. Soejono<sup>2</sup>, Jatmiko<sup>2</sup>, E. Wayhu Sapomo<sup>2</sup> & Rokus Awe Due<sup>2</sup>

<sup>1</sup>Archaeology & Palaeoanthropology, School of Human & Environmental Studies, University of New England, Armidale, New South Wales 2351, Australia

<sup>2</sup>Indonesian Centre for Archaeology, Jl. Raya Condet Pejaten No. 4, Jakarta 12001, Indonesia

Currently, it is widely accepted that only one hominin genus, *Homo*, was present in Pleistocene Asia, represented by two species, *Homo erectus* and *Homo sapiens*. Both species are characterized by greater brain size, increased body height and smaller teeth relative to Pliocene *Australopithecus* in Africa. Here we report the discovery, from the Late Pleistocene of Flores, Indonesia, of an adult hominin with stature and endocranial volume approximating 1 m and 380 cm<sup>3</sup>, respectively—equal to the smallest-known australopithecines. The combination of primitive and derived features assigns this hominin to a new species, *Homo floresiensis*. The most likely explanation for its existence on Flores is long-term isolation, with subsequent endemic dwarfing, of an ancestral *H. erectus* population. Importantly, *H. floresiensis* shows that the genus *Homo* is morphologically more varied and flexible in its adaptive responses than previously thought.

## Description of *Homo floresiensis*

Order Primates Linnaeus, 1758

Suborder Anthropoidea Mivart, 1864

Superfamily Hominoidea Gray, 1825

Family Hominidae Gray, 1825

Tribe Hominini Gray, 1825

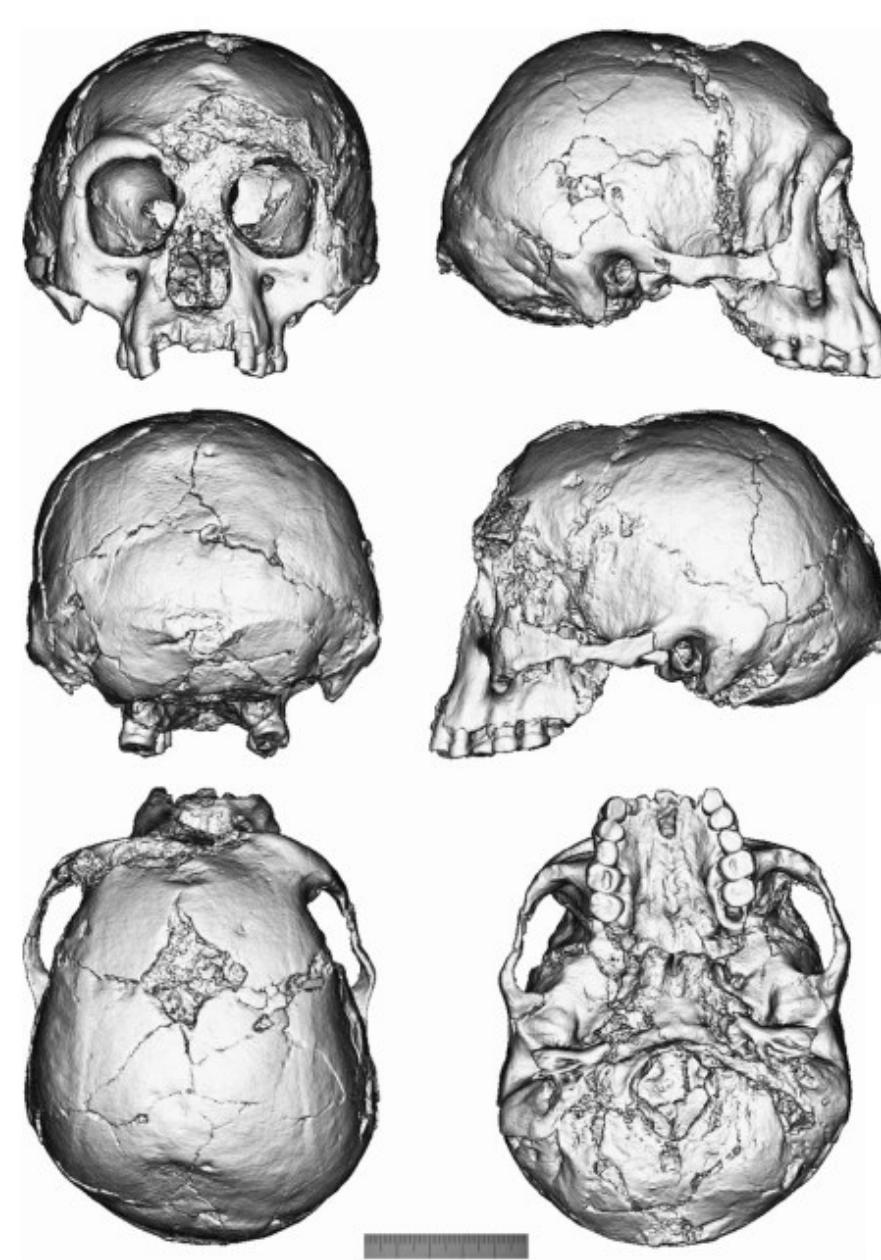
Genus *Homo* Linnaeus, 1758

*Homo floresiensis* sp. nov.

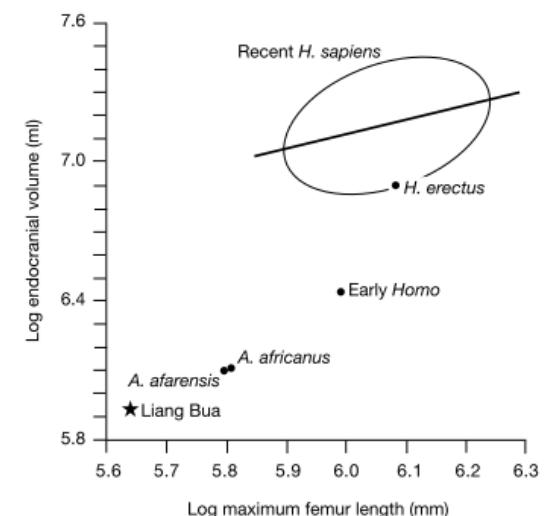
**Horizon.** The type specimen LB1 was found at a depth of 5.9 m in Sector VII of the excavation at Liang Bua. It is associated with calibrated accelerator mass spectrometry (AMS) dates of approximately 18 kyr and bracketed by luminescence dates of  $35 \pm 4$  kyr and  $14 \pm 2$  kyr. The referred isolated left  $P_3$  (LB2) was recovered just below a disconformity at 4.7 m in Sector IV, and bracketed by a U-series date of  $37.7 \pm 0.2$  kyr on flowstone, and 20 cm above an electron-spin resonance (ESR)/U-series date of  $74^{+14}_{-12}$  kyr on a *Stegodon* molar.



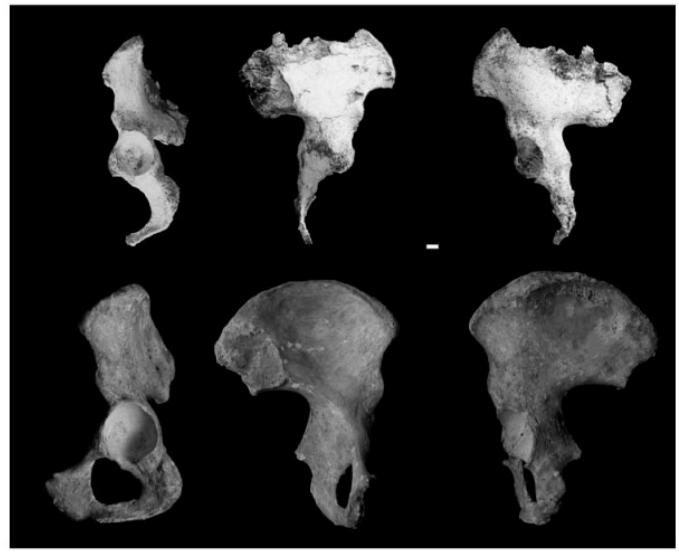
Kaifu, 2011



**Figure 2.** Surface rendered CT images of LB1/1. The orientations and scale same as in Fig. 1.



**Figure 3** Relationship between endocranial volume and femur length in LB1, *A. afarensis*, *A. africanus*, early *Homo* sp., *H. erectus* and modern *H. sapiens*. Modern human data, with least squares regression line and 95% confidence ellipse, from a global sample of 155 individuals collected by P.B. Details of the hominin samples are in the Supplementary Information.



**Figure 6** Comparison of the left innominate from LB1 with a modern adult female *H. sapiens*. Lateral (external), and medial and lateral views of maximum iliac breadth. The pubic region of LB1 is not preserved and the iliac crest is incomplete. Scale bar, 1 cm.



**Figure 7** Anterior and posterior views of the LB1 right femur and tibia, with cross-sections of the femur neck and midshaft, and tibia midshaft. The anterior surfaces of the medial and lateral condyles of the femur are not preserved. With the exception of the medial malleolus, the tibia is complete and undistorted. Scale bar, 1 cm.

LB1: Mosaica di caratteri primitivi, unici e derivati mai visti in altri ominidi: volume endocranico piccolo e statura = australopitecini

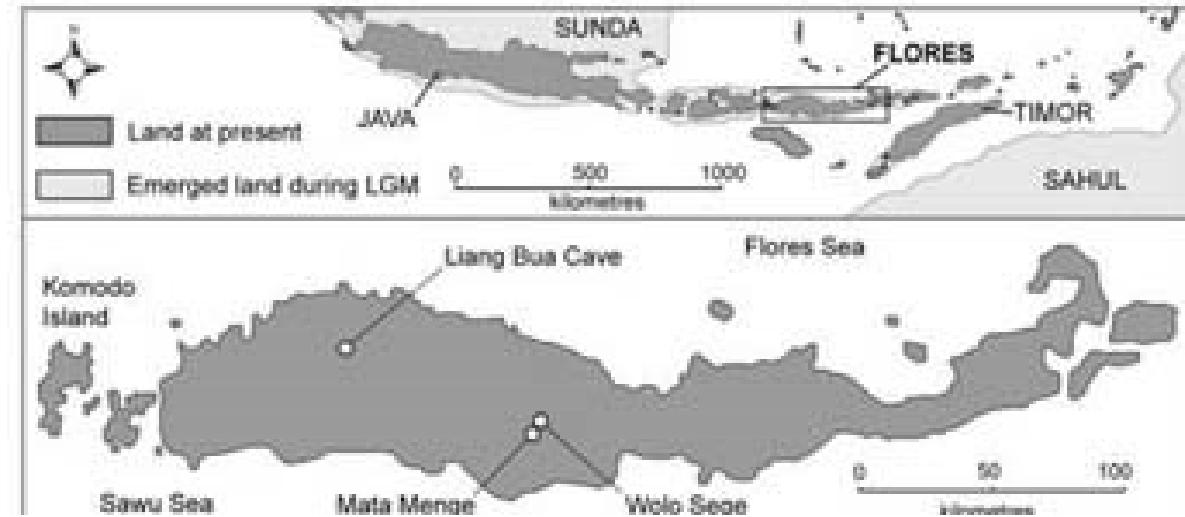
Ma non condivide con questo genere altri caratteri come le dimensione dentale, il prognatismo facciale accentuato che sono più simili ad altre specie del genere *Homo*

*LB1 has the small endocranial volume and stature evident in early australopithecines, it does not have the great postcanine tooth size, deep prognathic facial skeleton and masticatory adaptations common to members of this genus. Instead, the facial and dental proportions, postcranial anatomy consistent with human-like obligate bipedalism.*

## *Homo floresiensis*-like fossils from the early Middle Pleistocene of Flores

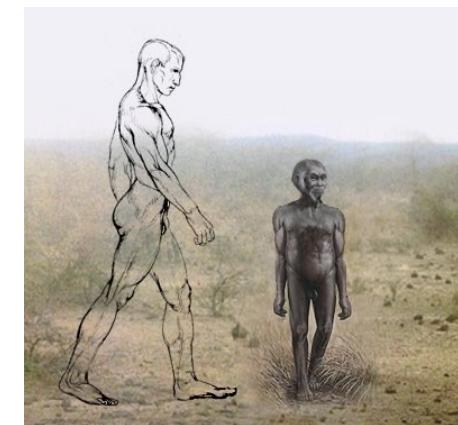
Gerrit D. van den Bergh<sup>1\*</sup>, Yousuke Kaifu<sup>2\*</sup>, Iwan Kurniawan<sup>3</sup>, Reiko T. Kono<sup>2</sup>, Adam Brumm<sup>4,5</sup>, Erick Setiyabudi<sup>3</sup>, Fachroel Aziz<sup>2</sup> & Michael J. Morwood<sup>1,‡</sup>

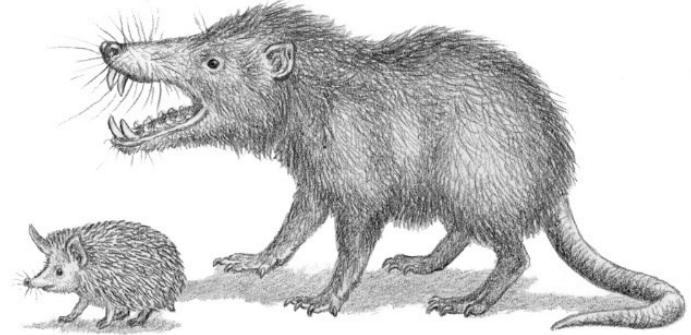
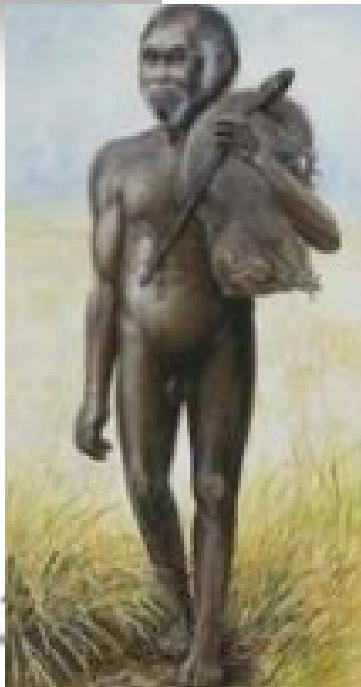
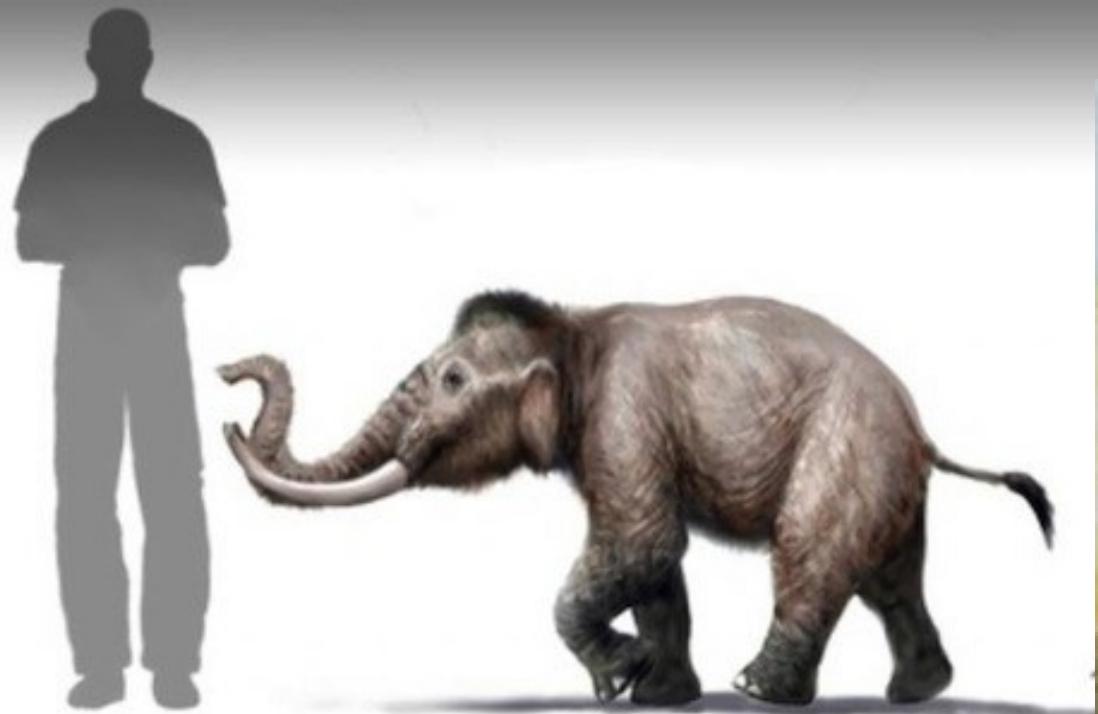
0,7 Ma



The Mata Menge are derived compared with *Australopitecus* and *H. habilis*, and so tend to support the view that *H. florensiensis* is a dwarfed descendent of early Asian *H. erectus*.

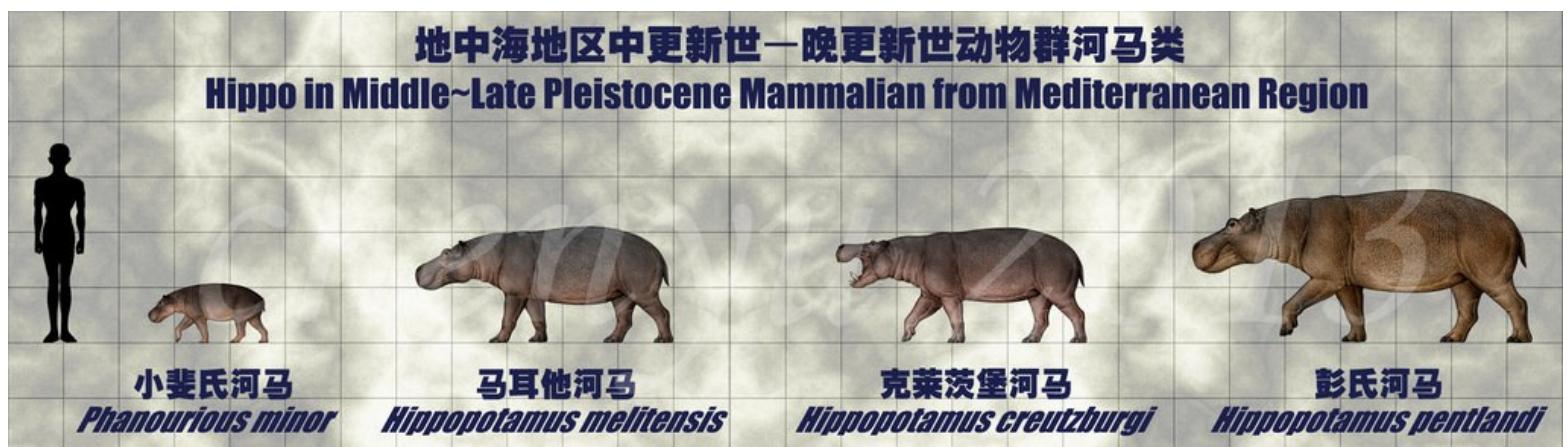
Hominins on Flores has acquired extremely small body size and other morphological traits specific to *H. florensiensis* at an unexpectedly early time





**Insular endemism:**  
Limited resources  
Absence of large predators  
Genetic drift

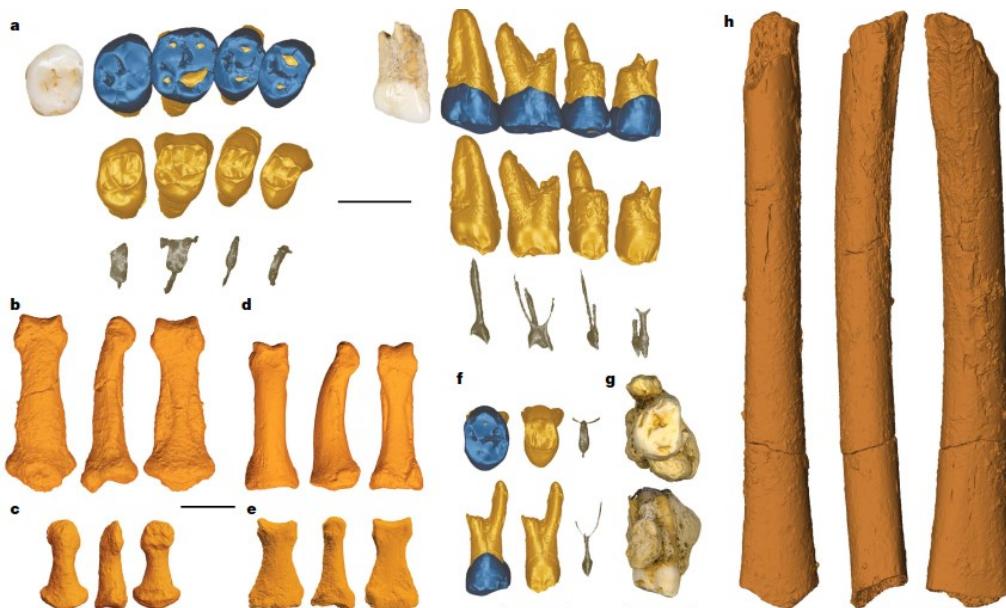
« the smallest become large and the largest become small »



# A new species of *Homo* from the Late Pleistocene of the Philippines

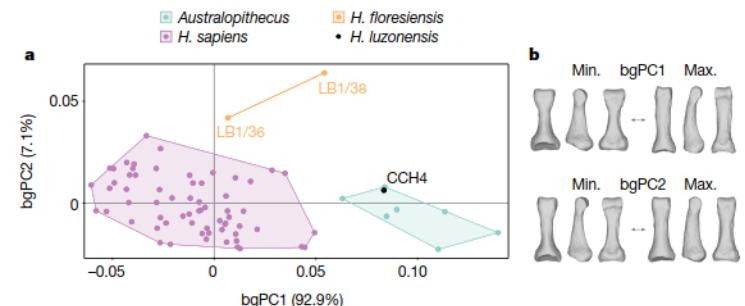
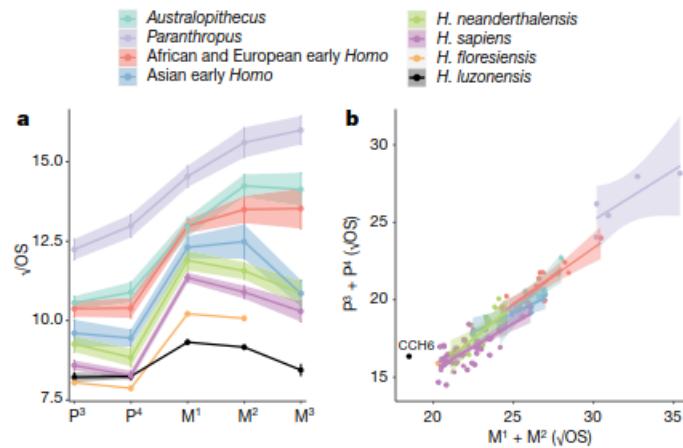
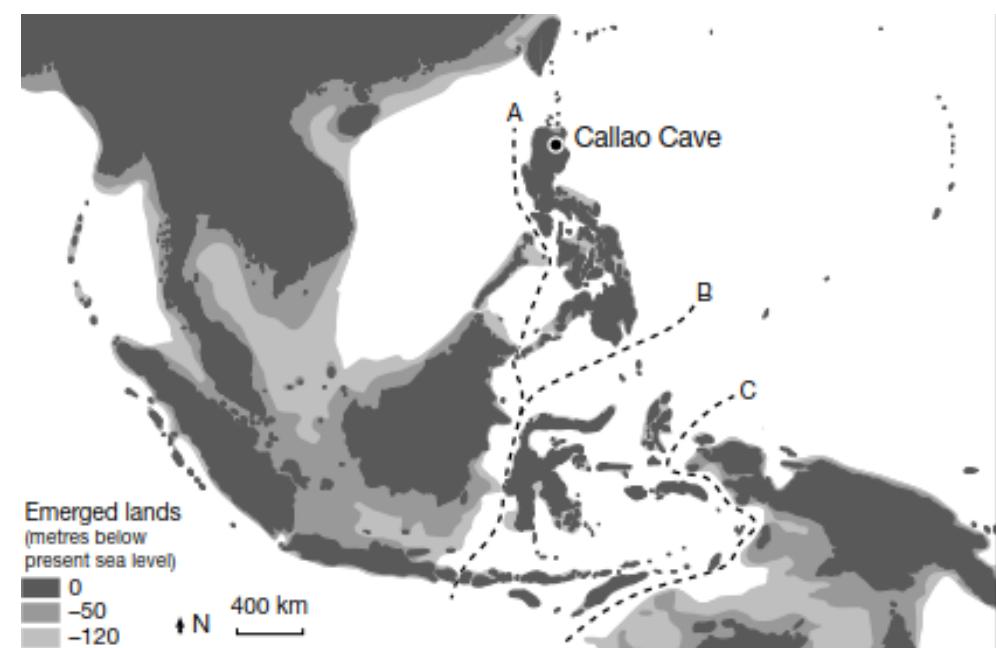
Florent Détroit<sup>1\*</sup>, Armand Salvador Mijares<sup>2,3\*</sup>, Julien Corny<sup>1</sup>, Guillaume Daver<sup>4</sup>, Clément Zanolli<sup>5,6</sup>, Eusebio Dizon<sup>3</sup>, Emil Robles<sup>2</sup>, Rainer Grün<sup>7,8</sup> & Philip J. Piper<sup>3,9</sup>

A hominin third metatarsal discovered in 2007 in Callao Cave (Northern Luzon, the Philippines) and dated to 67 thousand years ago provided the earliest direct evidence of a human presence in the Philippines. Analysis of this foot bone suggested that it belonged to the genus *Homo*, but to which species was unclear. Here we report the discovery of twelve additional hominin elements that represent at least three individuals that were found in the same stratigraphic layer of Callao Cave as the previously discovered metatarsal. These specimens display a combination of primitive and derived morphological features that is different from the combination of features found in other species in the genus *Homo* (including *Homo floresiensis* and *Homo sapiens*) and warrants their attribution to a new species, which we name *Homo luzonensis*. The presence of another and previously unknown hominin species east of the Wallace Line during the Late Pleistocene epoch underscores the importance of island Southeast Asia in the evolution of the genus *Homo*.



**Fig. 2 | Fossil remains of *H. luzonensis* from Late Pleistocene sediments at Callao Cave.** **a**, Holotype CCH6: postcanine maxillary teeth in occlusal (left) and buccal (right) aspects, with three-dimensional rendering of enamel (dark blue), dentine and cement (light brown), and pulp cavity (dark grey) for CCH6-b–CCH6-e. **b**, Intermediate manual phalanx CCH2 dorsal, lateral and palmar aspects. **c**, Distal manual phalanx CCH5 dorsal, lateral/medial and palmar aspects. **d**, Proximal pedal phalanx

CCH4 (dorsal, lateral and plantar aspects). **e**, Intermediate pedal phalanx CCH3 (dorsal, medial and plantar aspects). **f**, Left P<sup>3</sup> or P<sup>4</sup> CCH8: occlusal (top) and buccal (bottom) aspects, with three-dimensional rendering of enamel, dentine and cement, and pulp cavity. **g**, Right M<sup>3</sup> CCH9: occlusal (top) and buccal (bottom) aspects. **h**, Juvenile femoral shaft CCH7 (anterior, lateral and posterior aspects). Scale bars, 10 mm (**a–g**) and 20 mm (**h**); additional views are shown in Extended Data Figs. 1, 5, 7–10.



# Earliest known hominin activity in the Philippines by 709 thousand years ago

T. Ingicco<sup>1,2,3,4\*</sup>, G. D. van den Bergh<sup>5</sup>, C. Jago-on<sup>6</sup>, J.-J. Bahain<sup>1,2,3,4</sup>, M. G. Chacón<sup>1,2,3,4,7,8</sup>, N. Amano<sup>9</sup>, H. Forestier<sup>1,2,3,4</sup>, C. King<sup>6</sup>, K. Manalo<sup>10</sup>, S. Nomade<sup>11,12,13</sup>, A. Pereira<sup>1,2,3,4,11,12,13,14,15</sup>, M. C. Reyes<sup>6,10\*</sup>, A.-M. Sémaï<sup>1,2,3,4,16</sup>, Q. Shao<sup>17</sup>, P. Voinchet<sup>1,2,3,4</sup>, C. Falguères<sup>1,2,3,4</sup>, P. C. H. Albers<sup>18</sup>, M. Lising<sup>6,19</sup>, G. Lytras<sup>20</sup>, D. Yurnaldi<sup>21</sup>, P. Rochette<sup>22,23,24,25,26</sup>, A. Bautista<sup>6</sup> & J. de Vos<sup>18</sup>

