

UNIVERSITÉ DE LA MÉDITERRANÉE
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Validité du taxon *Homo heidelbergensis* Schoetensack, 1908

T H È S E

Abstract

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VALIDITY OF THE TAXON *HOMO HEIDELBERGENSIS* SCHOETENSACK, 1908
(VALIDITE DU TAXON *HOMO HEIDELBERGENSIS* SCHOETENSACK, 1908)

In order to better understand the evolutionary context of the genus *Homo* in middle Pleistocene, I test the validity of the main debated species in middle Pleistocene *Homo heidelbergensis* Schoetensack, 1908.

Middle Pleistocene is a key period in human evolution since it witnessed the apparition of both Modern humans and Neandertals. New fossil discoveries as well as the recognition of a greater morphological diversity in the fossil record led to a reconsideration of the middle Pleistocene evolutionary context.

The species name *Homo heidelbergensis* was invented at the beginning of the century following the discovery of the Mauer mandible (Germany) (Schoetensack, 1908). Since the eighties, *Homo heidelbergensis* has been regularly used in order to accommodate most of the mid-Pleistocene hominids fossils. However, there is no consensus concerning the hominid systematic in middle Pleistocene. Indeed, the peculiar morphology of the Mauer mandible is still poorly understood and most of the important mid-Pleistocene fossils lack mandibular remains which do not allow direct comparison with the holotype of *Homo heidelbergensis*. As a result, this species is either considered as an Afro-European taxon ancestor to both Modern Humans and Neandertals (Stringer, 1983, 1985; Rightmire, 1996, 1998, 2008), or as a uniquely European species ancestor to the Neandertals only (Arsuaga et al., 1997; Mallegni et al., 2003; Bermúdez de Castro et al., 2004). The validity of the species is also often challenged (Rosas and Bermúdez de Castro, 1998; Hublin, 2001, 2009), and the 1908 diagnosis does not allow a correct attribution of new specimens to the taxon.

This work is organised in three parts. I start with the study of mandibles since the holotype of the species *Homo heidelbergensis* is a mandible. I then move to the study of the upper face and I finally turn to the calvaria. **My main objective is to see whether I can identify groups of mid-Pleistocene fossils on each cranial part and if the Mauer mandible can be included in these groups.** When this step is achieved I can redefine *Homo heidelbergensis* and propose a coherent evolutionary hypothesis concerning the systematic in middle Pleistocene.

For each cranial part, I use two different and complementary approaches on the same sample (134 fossils from Pleistocene among which 36 originals and 128 extent Humans).

The first is a morphological analysis led on 139 morphological features (mandible: 39, face: 35 and calvaria: 65). I conduct a comparative morphology analysis to better understand the morphology of the middle Pleistocene fossils. Then, I use a phenetic analysis in order to obtain specimens grouping.

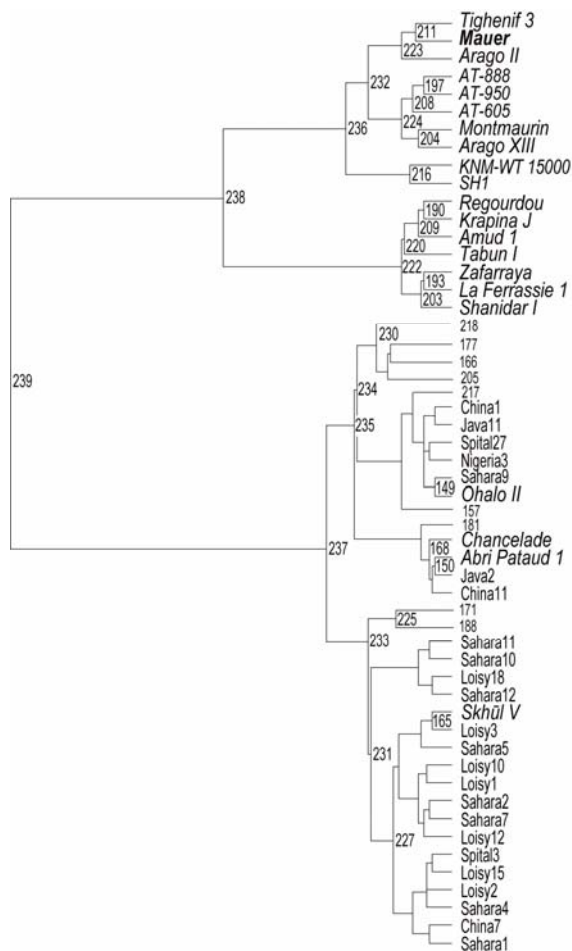


Figure 1: Phenetic analysis of mandibles: dendrogram. A middle Pleistocene specimens' cluster includes Mauer (node 232). This group contains exclusively African and European fossils. Tighenif 3 and Arago II are more similar to Mauer than the other middle Pleistocene mandibles. The Asiatic specimen SH1 (*Sinanthropus* H1.12) get more closely associated to the Early Pleistocene mandible KNM-WT 15000 (node 216). The Neandertals cluster together (node 222). Modern Humans fossils are grouped with the extent *Homo sapiens* which show a high degree of variability (node 237).

Table 1: Description of the Afro-European middle Pleistocene specimens group thanks to the most statistically significant state of traits

Morphological traits	States	T-Value	p
Afro-European middle Pleistocene group			
<i>Planum alveolare</i>	present	6.08	0.000
Symphysis : profile	receding	5.74	0.000
<i>Tuber symphyseos</i>	absent	5.74	0.000
Ascending ramus : length	wide	5.66	0.000
Lateral tubercles	absent	5.43	0.000
<i>Incurvatio mandibulae</i>	absent	5.19	0.000
<i>Fossa subcondylea</i> : size	well-developed	5.03	0.000
<i>Planum triangulare</i> : size	well-developed	4.68	0.000
Central keel	absent	4.57	0.000
Retromolar surface: orientation	horizontal	4.03	0.000
<i>Incisura submentalis</i>	present	3.91	0.000
<i>Prominentia lateralis</i> : position	M3	3.68	0.000
Mylohyoid line: orientation	parallel	3.58	0.000
<i>Fossa masseterica</i> : depth	deep	3.32	0.000
<i>Torus marginalis superius</i>	strongly marked	3.09	0.001
Mandibular notch's deepest point: position	medial	3.09	0.001
<i>Foramen mentale</i> : position	P4-M1	3.09	0.001
<i>Sulcus extramolaris</i>	large	2.90	0.002
Mylohyoid line: position at the M3 level	low	2.84	0.002
Gonion profile	truncated	2.83	0.002
<i>Foramina mentale</i> : number	multiple	2.26	0.012
<i>Prominentia lateralis</i> : relief	strong swelling	2.20	0.014
<i>Foramen mentale</i> : position	M1	2.20	0.014
<i>Fossae digastrica</i> : orientation	downward	2.08	0.019

The statistical analysis identifies which character state contributes the most to the formation of the cluster. For a significant level of 5% (i.e., $p < 0.05$) the T-Value must be ≥ 2 .

I developed a new phenetic method to perform these analyses based on statistics which have not been previously used in a systematic context (see, Mounier et al. 2009). It is

based on exploratory statistics which do not need to conform to any prior hypothesis. I use a Multiple Correspondence Analysis to quantify the morphological similarities between fossils and a hierarchical classification to obtain clusters of specimens each of which can be described thanks to statistical significant morphological traits (see the example of the mandible Figure 1 and Table 1).

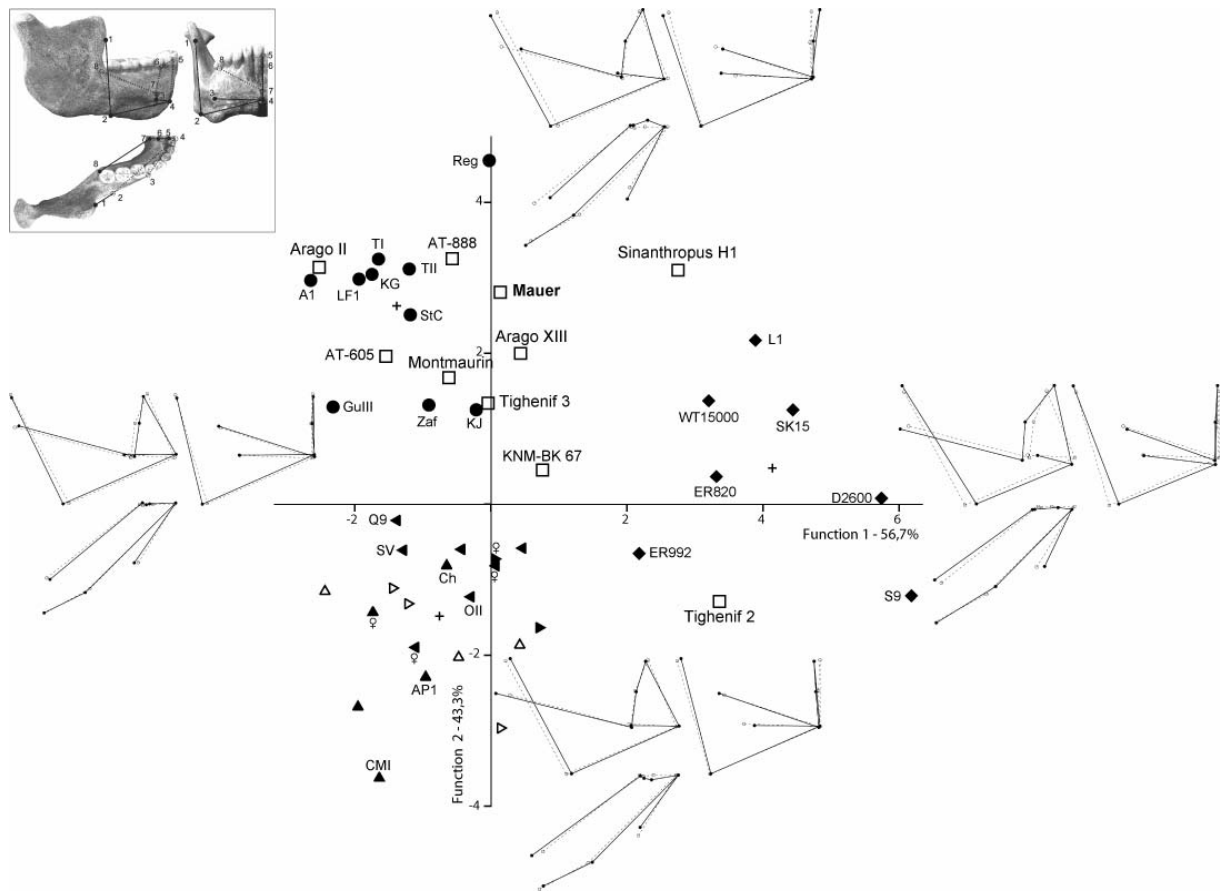


Figure 2: Canonical Variate Analysis results on mandibles. Group centroïdes: +. Modern Humans are figured by triangle (▲ Historic Europeans, △ Neolithic European, ► Historic Africans, ▷ Neolithic Africans, ◄ Asians, ♀ known female sex), ● Neandertals, ◆ Early Pleistocene, □ middle Pleistocene. Abbreviations: Modern Humans: CMI: Cro-Magnon I, AP1: Abri Pataud 1, OII: Ohalo II, Ch: Chancelade, SV: Skhūl V et Q9: Qafzeh 9; Neandertals: KG: Krapina G, KJ: Krapina J, LF1: La Ferrassie 1, Reg: Regourdou, GullI: Guattari III, StC: Saint Césaire, Zaf: Zafarraya, TI: Tabūn I, TII: Tabūn II and A1: Amud 1; Early Pleistocene: WT-15000: KNM-WT 15000, ER 820: KNM-ER 820, ER 992: KNM-ER 992, S9: Sangiran 9 et L1: Lantian 1. European specimens as well as African specimen Tighenif 3 show similarities in shape with the Neandertals.

The second approach is a geometric morphometrics analysis based on 30 landmarks (i.e., mandible: 8, face: 8 and calvaria: 14) which provides a test of the newly identified species based on the global morphology of the fossils. I perform a General Procrustes Analysis and a Principal Component Analysis to emphasize the intrinsic shape differences between specimens. Then, a Canonical Variate Analysis is used to amplify the differences between

Modern Humans, Neandertals and Early Pleistocene specimens. Mid-Pleistocene fossils position is calculated afterward in relation to the differences observed between the three previous groups (see example of the mandible, Figure 2).

Results from the morphological analyses led on the mandible, upper face and calvaria support the existence of a middle Pleistocene taxon different from *Homo sapiens*, *Homo neanderthalensis* and *Homo erectus* s.l. It can be defined by a list of morphological features that are found among European and African mid-Pleistocene fossils. The Mauer mandible is part of this taxon, and based on the International Zoological Nomenclature Code, the most appropriate species name is *Homo heidelbergensis* Schoetensack, 1908.

Geometric morphometrics analyses show that **shapes of African and European middle Pleistocene fossils are similar to each other.** They also show **important similarities with the shape of Neandertals.**

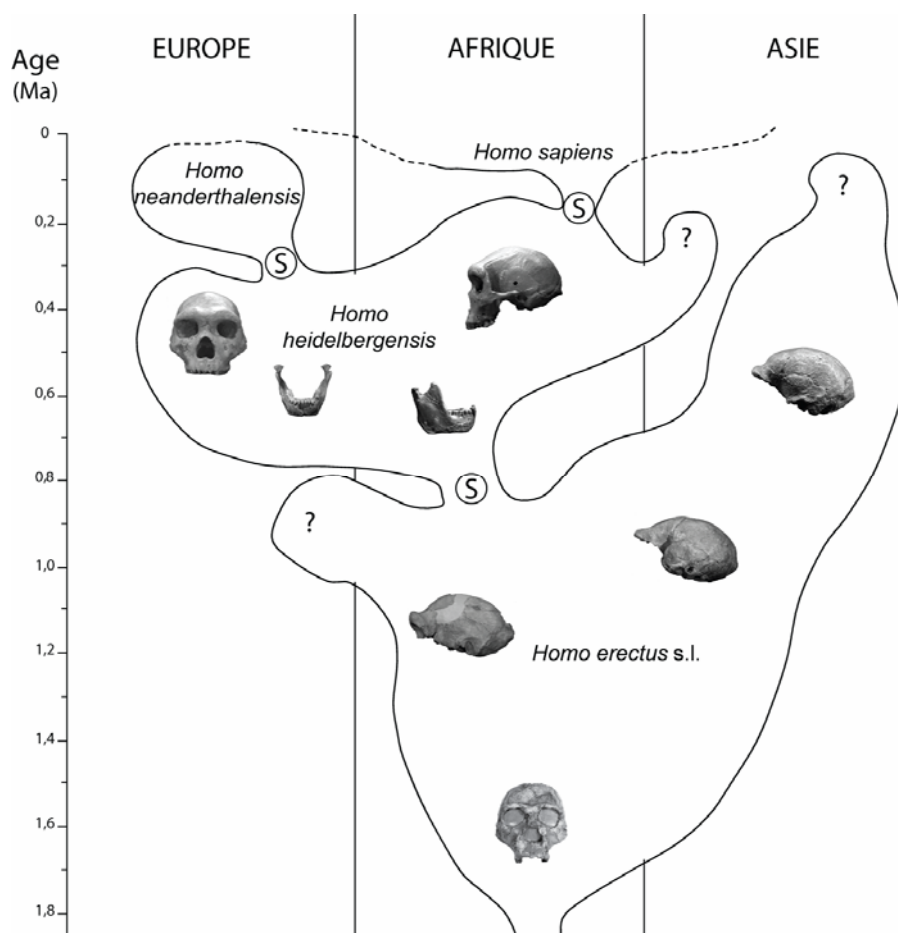


Figure 3: Evolutionary hypothesis supported by the main results of this study: *Homo heidelbergensis* is an Afro-European species last common ancestor of Modern Humans and Neandertals.

Thus, *Homo heidelbergensis* is supported as a valid taxon. We support the Afro-European hypothesis for *Homo heidelbergensis* (i.e., Afro-European taxon ancestor to Neandertals and *Homo sapiens*) (Figure 3). I propose a revision of the diagnosis of *Homo heidelbergensis* Schoetensack, 1908 (Figures 4a and 4b and Tables 2a and 2b).

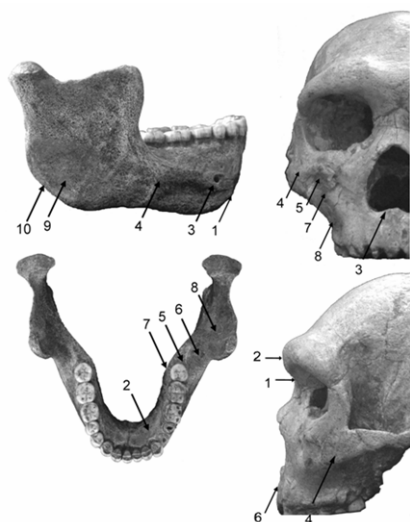


Figure 4a: Morphological features of the revised diagnosis of *Homo heidelbergensis* Schoetensack, 1908. See details in Table 2a.

Table 2a: Diagnosis features of *Homo heidelbergensis* on the face

Traits	Mandible	Upper Face
1	receding symphysis without chin with an <i>incisura submentalis</i>	deeply inserted nasion, large inter-orbital space
2	<i>planum alveolare</i> present	superior orbital rim anteriorly positioned
3	posteriorly positioned <i>foramina mentale</i>	pre-nasal fossa
4	posteriorly positioned <i>prominentia lateralis</i>	weakly curved zygomatic between the body and the temporal process of the bone
5	horizontal retromolar surface	infra-orbital foramen in a low position
6	wide <i>sulcus extramolaris</i>	long nasoalveolar clivus
7	parallel and low mylohyoid line	<i>incurvatio horizontalis</i> and <i>sagittalis</i> weakly marked
8	long ascending ramus width	<i>incurvatio inframalaris frontalis</i> weakly marked
9	deep <i>fossa masseterica</i>	-
10	truncated gonion	-

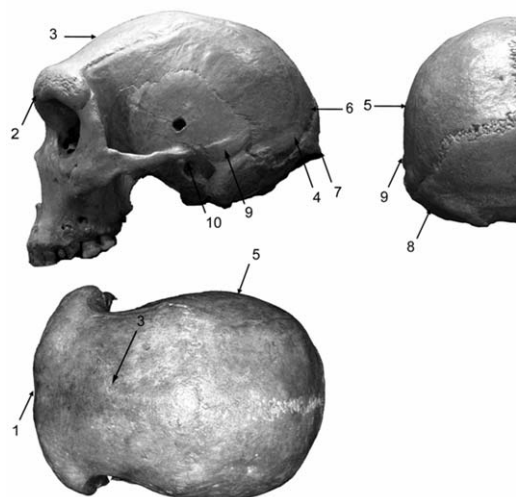


Figure 4b: Morphological features of the revised diagnosis of *Homo heidelbergensis* Schoetensack, 1908. See details in Table 2b.

Table 2b: Diagnosis features of *Homo heidelbergensis* on the calvaria

Traits	Calvaria
1	supra-orbital region medially concave
2	incomplete <i>sulcus supratoralis</i>
3	sagittal keel and frontal tuber weakly marked and medially positioned
4	<i>torus angularis parietalis</i>
5	parietal tubers defined and medially positioned
6	occipital bun
7	medially protruding <i>torus occipitalis transversus</i> :
8	<i>processus retromastoideus</i>
9	<i>crista supramastoidea</i> well-marked and continues with the <i>processus ossis temporalis</i>
10	Intermediate position of the external auditory relative to the <i>processus ossis temporalis</i>

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