

## 100 years of *Homo heidelbergensis* – life and times of a controversial taxon

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**Abstract:** The hominin taxon *Homo heidelbergensis* was named 100 years ago after the discovery of the fossil mandible from Mauer, a village near Heidelberg. Middle Pleistocene specimens commonly attributed to this species show *Homo erectus*-like features, but also some modern human-like characteristics. Perhaps most importantly, they exhibit an increase in brain size and encephalization, and concomitant changes in skull shape. Throughout the last century, *H. heidelbergensis* has been the subject of controversy, with some researchers placing it within *H. erectus*, and others recognizing it as an archaic form of our own species, *H. sapiens*. More recently, it has been accepted as either the last common ancestor to both Neanderthals and modern humans, spanning Africa, Europe and perhaps Asia, or as a chronospecies of the Neanderthal lineage restricted to Europe.

**Keywords:** Middle Pleistocene, Archaic *Homo sapiens*, Accretion hypothesis, Neanderthals

### 100 Jahre *Homo heidelbergensis* – Die Biographie eines kontroversen Taxons

**Zusammenfassung:** Im Oktober 1907 wurde in einer Sandgrube bei Mauer, südöstlich von Heidelberg, ein menschlicher Unterkiefer mit ungewöhnlichen Merkmalen entdeckt. Das genaue Alter ist nach wie vor unklar, es liegt jedoch wahrscheinlich bei mindestens 500.000 Jahren. Damit handelt es sich um das älteste Menschenfossil aus Mitteleuropa. Der Unterkiefer wurde bereits im Jahr nach der Auffindung von Otto Schoetensack einer in Anlehnung an die Lage der Fundstelle bei Heidelberg als *Homo heidelbergensis* bezeichneten Menschenform zugeordnet, für die der Unterkiefer als definierendes Fossil diente. Wenn die *Homo heidelbergensis* zugeordneten Fossilien, darunter die Funde von Arago in Südfrankreich, auch ‚modern‘ anmutende Merkmale zeigen, z.B. in der Gehirngröße und -entwicklung sowie Veränderungen in der Schädelform, so sind doch deutliche Ähnlichkeiten mit *Homo erectus* unverkennbar. Während der 100 Jahre seit seiner Definition ist die Stellung von *Homo heidelbergensis* als Taxon innerhalb der Menschheitsentwicklung immer wieder kontrovers diskutiert worden. Einige Forscher ordneten diese Form innerhalb von *Homo erectus* ein, andere sahen in ihr eine archaische Ausprägung unserer eigenen Art *Homo sapiens*. In jüngerer Zeit werden Modelle favorisiert, nach denen *Homo heidelbergensis* entweder als letzter gemeinsamer Vorfahre von Neandertalern und modernen Menschen oder als auf Europa beschränkte Chronospezies der Neandertalerlinie betrachtet wird.

So sehen viele Anthropologen eine eigenständige Menschenentwicklung in Europa, die nach und nach zu der Herausbildung der Neandertaler bis hin zum klassischen Neandertaler geführt hat. Diese als *accretion*-Hypothese (wörtlich: Zuwachs-Hypothese) bezeichnete Annahme geht von einem fortschreitenden Zuwachs immer weiterer für die Neandertaler typischer Merkmale aus. Gemäß dieser Hypothese wären Mauer und vergleichbare europäische Fossilien des Mittelpleistozäns erste Vorfahren der Neandertaler, aber nicht der modernen Menschen, die sich nicht in Europa entwickelt haben. Unter den Befürwortern der *accretion*-Hypothese herrscht jedoch Unklarheit, ob die entsprechenden europäischen Fossilien zu einer eigenen Art *Homo heidelbergensis* gehören, sie also eine Chronospezies des Neandertalers repräsentieren, oder ob sie innerhalb der Art *Homo neanderthalensis* zu platzieren seien. In jedem Falle müsste man die afrikanischen Fossilien aus dem Mittelpleistozän einer wiederum eigenen Art zuordnen, für die gelegentlich der Name *Homo rhodesiensis* verwendet wird. Der letzte gemeinsame Vorfahre der Neandertaler und der modernen Menschen wäre dann in einem älteren Taxon, vielleicht *Homo erectus* im weiteren Sinne, zu suchen. In einem anderen Modell wird *Homo heidelbergensis* als ein Taxon gesehen, das sowohl die mittelpleistozänen Fossilien aus Europa als auch diejenigen aus Afrika (und vielleicht auch aus Asien) umfasst. In diesem Falle wäre *Homo heidelbergensis* der letzte gemeinsame Vorfahre sowohl der Neandertaler als auch der modernen Menschen. Dementsprechend hätte sich ein

europäischer Zweig zum Neandertaler entwickelt, ein afrikanischer Zweig zum anatomisch modernen Menschen. Endgültige Einigkeit herrscht trotz der vielen Informationen, über die wir heute verfügen, auch 100 Jahre nach der Entdeckung des Heidelberger Unterkiefers, und damit des Typusfossils für das Taxon *Homo heidelbergensis*, noch nicht.

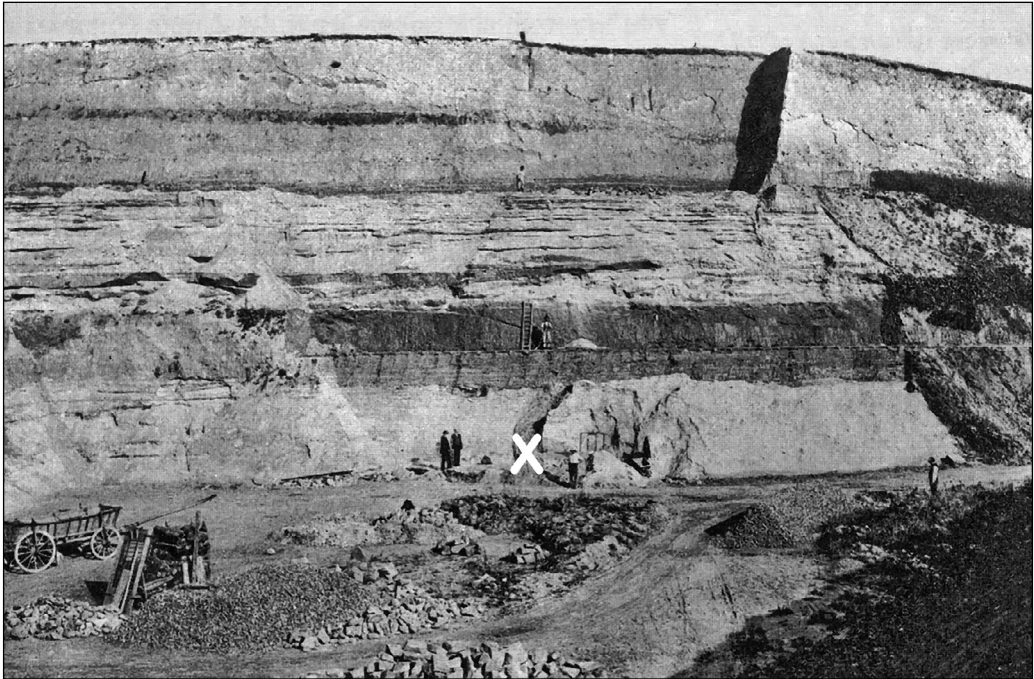
**Schlagwörter:** Mittelpleistozän, Archaischer *Homo sapiens*, *accretion*-Hypothese, Neandertaler

On October 21<sup>st</sup>, 1907, a workman discovered a fossil human mandible at a sandpit in the village Mauer, South-East of Heidelberg (Fig. 1). The jaw was recovered from the Mauer sands at a depth of more than 24 meters, in a deposit that had already yielded rich mammalian fossil fauna (Fig. 2). The importance of the discovery was recognized almost immediately and indeed marked the birth of one of the most controversial hominin taxa. *Homo heidelbergensis* was named the following year by Prof. Otto Schoetensack (Fig. 3), with the Mauer mandible as its type specimen (Schoetensack 1908).

The Mauer jaw's unusual features were described early on: the lack of a chin, and the large size of the mandible, especially the great breadth of the ascending ramus, which contrasted with the average sized dentition. Comparisons were drawn to the gorilla and the gibbon in terms of the morphology of the symphysis and the ramus, and the human character of the teeth was pointed out (Schoetensack 1908; MacCurdy 1909; Smith Woodward 1924; Howell 1960). The Mauer mandible was considered more ancient than the newly discovered Neanderthals, possibly of Middle Pleistocene or earlier age (MacCurdy



**Fig. 1:** *The Mauer mandible.*



**Fig. 2:** The stratigraphic section in the 'Grafenrain' sandpit where the Mauer jaw was discovered (see white cross). Modified after Adam 1997.

1909; Merriam 1920). Almost from the start it was thought to be either directly ancestral to, or an early representative of, the Neanderthals (MacCurdy 1909; Hooton 1932; Weidenreich 1940; Vallois 1954). Up until recently (Bermúdez de Castro et al. 1997; Manzi et al. 2001) the Mauer jaw was one of the earliest hominins known from Europe. Although its exact chronology remains unresolved, it is believed to be as old as 500 ka.

Later discoveries gradually increased the number of fossils of similar antiquity as the Mauer individual, and of fossil mandibles to which it could be compared, such as the Zhoukoudian and Ternifine *H. erectus* jaws (e.g. Black 1929; Arambourg 1954; Howell 1960). Mauer provided a natural comparison to the Piltdown jaw, announced a few years after the Mauer discovery, and the stark contrast between the two specimens was noted (MacCurdy 1913, 1924; Gregory, 1916; Smith Woodward 1924). The discovery of the Arago mandibles in the late 1960s (deLumley and deLumley 1971) was crucial: their similarity to Mauer suggested that they belonged to the same taxon. This was important in linking the lower jaw of *H. heidelbergensis* with the cranial remains recovered in Arago. The Tautavel fossils were therefore proposed as the paratype and basis for comparison for *H. heidelbergensis* (see e.g. Howell 1999; Tattersall and Schwartz 2006). From that point onwards, fossil individuals similar to the Arago remains could be considered as belonging to the same or similar populations as the Mauer mandible. This group would finally grow to include Middle Pleistocene specimens from Europe, Africa and possibly also Asia such as Arago, Petralona, Steinheim, Kabwe, Bodo, Narmada, Dali and others (Fig. 4). Such fossils show several morphological similarities to *H. erectus* (broad faces,

supraorbital tori, relatively low and long crania, heavy nuchal musculature), leading several researchers to place them within this taxon. However, they also exhibit derived cranial features (increased convexity of the frontal and parietal squama, greater arching of the temporal squama, increased height of the upper occipital scale relative to the nuchal plane, decreased total facial prognathism and decreased overall buttressing; see e.g. Rightmire 2007), suggesting affinities with later *Homo*, i.e. Neanderthals and modern people.



**Fig. 3:** Prof. Dr. Otto Schoetensack (12.06.1850 – 23.12.1912), ca. 1882. After Schoetensack and Schoetensack 1997.



**Fig. 4:** The Petralona cranium, one of the representatives of European *H. heidelbergensis*, is likely similar to what the Mauer cranium would have looked like.

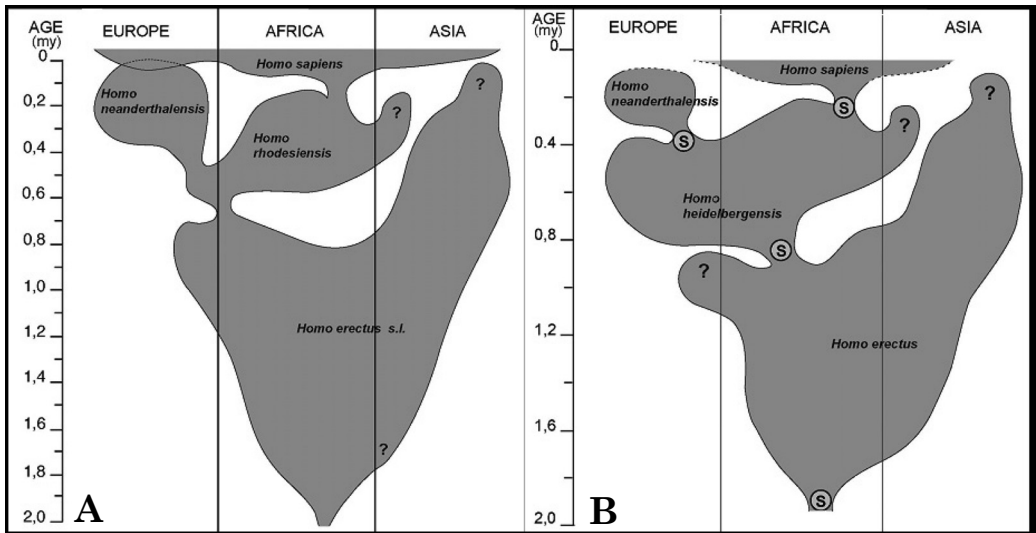
Although the number of specimens coeval and similar to the Mauer jaw had dramatically increased by the 1970s and 1980s, the classification and phylogenetic relationships of this group of fossils would not prove easy to resolve. After the extensive pruning of the nomenclature of the human evolutionary tree according to the principles of the Modern Synthesis (e.g. Evans 1945; Mayr 1963) the nomen *H. heidelbergensis* fell increasingly into disuse. An influential interpretation of the fossil record at this time saw Mauer and its European and African contemporaries as very early forms of *H. sapiens* (Stringer et al. 1979). As such they were gathered together with Neanderthals and other Middle – Late Pleistocene human forms in the same grade and collectively referred to as ‘archaic *H. sapiens*’. In this view, Mauer and the other Middle – Late Pleistocene specimens (including Neanderthals) were loosely considered as ancestral, ‘archaic’ forms, belonging to our own species (rather than to *H. erectus*) but retaining many plesiomorphic, *erectus*-like features. They were grouped together based on what was perceived to be a similar level of adaptation, or ‘grade’. This grade classification of ‘archaic *Homo sapiens*’ acknowledged affinities with later *Homo* but did not confront the thorny issue of the precise phylogenetic relationships and alpha taxonomy of these specimens.

In the last few decades the magnitude of morphological and genetic differences between Neanderthals and modern humans has become increasingly obvious (e.g. Hublin 1978; Santa Luca 1978; Tattersall 1986; Stringer and Andrews 1988; Krings et al. 1997; Harvati 2003, 2007; Harvati et al. 2004; Serre et al. 2004; Green et al. 2006). The classification of Neanderthals as ‘archaic *H. sapiens*’ therefore appears increasingly untenable, with a new consensus favoring their assignment to a distinct species, *H. neanderthalensis*. Evidence has also mounted for a recent, African origin for modern humans (e.g. Cann et al. 1987; Harpending and Relethford 1997; Harpending et al. 1998; White et al. 2003), also pointing to the exclusion of Neanderthals from the direct ancestry of our species. In this new configuration, the grade classification of Mauer and the other Middle Pleistocene human fossils has also become problematic. Nonetheless, the difficulty in the classification of the Middle Pleistocene ‘muddle in the middle’ remains, and stems

in part from the difficulty in defining *H. heidelbergensis*. Its members seem to possess a mosaic of plesiomorphic *H. erectus* features and derived later *Homo* traits (see above), as is expected for specimens evolutionary intermediate between *H. erectus* and later *Homo*. However, they lack autapomorphies, thus defying classification as a distinct species on cladistic principles.

Not only do these specimens lack their own autapomorphies, but their European representatives have been described to show ‘incipient’ Neanderthal autapomorphies to various degrees. Based on this evidence many researchers see a distinct and continuous European lineage leading to the gradual evolution of Neanderthals according to the ‘accretion’ hypothesis (Dean et al. 1998; Hublin 1998). This hypothesis postulates that Mauer and other European Middle Pleistocene forms are ancestral to Neanderthals (but not modern humans) through anagenetic evolution. Neanderthal-like features seem to appear in the European record in a mosaic fashion, as e.g. in the large assemblage from Sima de los Huesos (Atapuerca), Spain (Arsuaga et al. 1997), recently dated to up to 600 ka (Bischoff et al. 2007). Although different traits appear in different fossils, their presence suggests that the Mid-Pleistocene Europeans were early representatives of the Neanderthal lineage. According to this model, Mauer would be included in ‘Stage 1’ of the accretion process, also termed ‘early pre-Neanderthals’.

Among those accepting the accretion hypothesis, opinions differ over the placement of these European fossils within the separate species *H. heidelbergensis* or within *H. neanderthalensis* itself (as in Fig. 5A; Hublin 1998). If the nomen *H. heidelbergensis* is retained, it can be accepted as designating a chronospecies, i.e. an arbitrary early portion



**Fig. 5:** Alternative scenarios for Middle Pleistocene human evolution. A: European Middle Pleistocene specimens are viewed as early members of the Neanderthal lineage, and assigned to *H. neanderthalensis* along with later Neanderthals (accretion hypothesis). The last common ancestor of Neanderthals and modern humans is shown here as *H. erectus* (s.l.). B: *H. heidelbergensis* is shown as a cross-continental species comprising European, African and possibly Asian Middle Pleistocene human fossils. It is shown here as the last common ancestor of Neanderthals and modern humans. Adapted from Hublin 2001.

of the Neanderthal lineage (e.g. Manzi 2004). In either case the African Mid-Pleistocene fossils would have to be assigned to yet another taxon, to which the nomen *H. rhodesiensis* could be applied, ancestral to modern people (Fig. 5A). Furthermore, the last common ancestor of all later human forms would have to be a different, older, taxon, *H. erectus sensu lato* (Fig. 5A) or possibly *H. antecessor* (Bermúdez de Castro et al. 1997).

In an alternative interpretation of the record, *H. heidelbergensis* has been viewed as a cross-continental taxon, comprising both the European and the African (and possibly also Asian) Middle Pleistocene fossil humans (Fig. 5B). This scenario emphasizes the strong morphological similarities between the European and African specimens and considers them as populations of the same species, *H. heidelbergensis*. In this view, *H. heidelbergensis* is the last common ancestor of both Neanderthals and modern humans (Fig. 5B; Rightmire 1998, 2007). This view is partly supported by metric and geometric morphometric analyses which found strong similarities among the European and the African specimens (Stringer 1974; Harvati et al. 2007; Harvati in press). The taxon's European branch is thought to have become isolated and evolved into Neanderthals, possibly in a true speciation event (as recently proposed by Rosas et al. 2006). Its African branch, on the other hand, is thought to have evolved into modern humans, either through anagenetic evolution, or also through a speciation event. Finally, a third interpretation of the fossil record sees very high levels of variability, and hence evidence for multiple taxa rather than a single evolving lineage even within the European Middle Pleistocene record (Schwartz and Tattersall 2005; Tattersall and Schwartz 2006).

Whether they represent one taxon or more, the Middle Pleistocene humans commonly placed in *H. heidelbergensis* appear to share some important trends. Perhaps most interesting is the trend for increased encephalization. Mean cranial capacity (as can be calculated based on a limited number of well-preserved specimens) is 1,206 cm<sup>3</sup>, compared with 973 cm<sup>3</sup> for the *H. erectus* mean – and well within the normal modern human range (Rightmire 2004). This increase appears to be higher than what would be predicted from gradual evolution within the *H. erectus* lineage. Furthermore, estimates of brain size relative to body mass indicate that this increase cannot be attributed greater body size alone. Larger brains and increased encephalization in turn appear to be linked with some technological advances, such as more sophisticated toolkits and hunting skills and equipment (Foley and Lahr 1997; Thieme 1997; Rightmire 2007).

In the century since the Mauer discovery, our knowledge of *H. heidelbergensis* has increased dramatically. It is now clear that they derive from the period immediately preceding the emergence of Neanderthals and of modern humans, and that they document a common trend for increased encephalization and more sophisticated behavior. As with all transitional forms, their taxonomy and precise phylogenetic relationships remain controversial and occupy a central position in the discussion on modern human origins. Intense current research on this topic and new discoveries in the field should help clarify the position of these enigmatic fossils.

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