Resolving the “muddle in the middle”: The case for *Homo bodoensis* sp. nov.

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**Abstract**
Recent developments in the field of palaeoanthropology necessitate the suppression of two hominin taxa and the introduction of a new species of homins to help resolve the current nebulous state of Middle Pleistocene (Chibanian) hominin taxonomy. In particular, the poorly defined and variably understood hominin taxa *Homo heidelbergensis* (both sensu stricto and sensu lato) and *Homo rhodesiensis* need to be abandoned as they fail to reflect the full range of hominin variability in the Middle Pleistocene. Instead, we propose: (1) introduction of a new taxon, *Homo bodoensis* sp. nov., as an early Middle Pleistocene ancestor of the *Homo sapiens* lineage, with a pan-African distribution that extends into the eastern Mediterranean (Southeast Europe and the Levant); (2) that many of the fossils from Western Europe (e.g. Sima de los Huesos) currently assigned to *H. heidelbergensis* s.s. be reassigned to *Homo neanderthalensis* to reflect the early appearance of Neanderthal derived traits in the Middle Pleistocene in the region; and (3) that the Middle Pleistocene Asian fossils, particularly from China, likely represent a different lineage altogether.

**KEYWORDS**
hominin taxonomy, *Homo bodoensis*, *Homo heidelbergensis*, *Homo rhodesiensis*, Middle Pleistocene

1 | **INTRODUCTION**

In 2019, we dedicated an entire American Association of Biological Anthropology (formerly American Association of Physical Anthropology) conference session to defining *Homo heidelbergensis*. The results of the meeting were: (1) no one was happy with the taxon; (2) different people assigned different meanings to the species and included different fossils in the hypodigm; (3) ignoring this problem will not miraculously lead to a solution; and (4) that in order to better understand Middle Pleistocene hominin systematics, it was critical to clear up this “muddle in the middle.”1 Here, we propose that *H. heidelbergensis* should be abandoned altogether, as it has been poorly defined and used inconsistently. Instead, we introduce *Homo bodoensis* sp. nov. as a largely African—and likely eastern Mediterranean—taxon and argue

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that the Middle Pleistocene hominin fossils that show any derived Neanderthal traits and are traditionally assigned to *H. heidelbergensis* s.s., including the Mauer mandible, be reassigned to *Homo neanderthalensis* and considered as early Neanderthals. Taxonomic classification has a strong impact on conceptual understanding of evolution, and the taxonomic practice of reviving old names due to rules of precedence has sometimes played an important role in obfuscating our understanding of the complexity of Middle Pleistocene hominin evolution; the resurrection of *H. heidelbergensis* is a case in point. By introducing a new, properly defined species, that recognizes and systematizes some of the observed variation, we hope to contribute a foundational piece from which palaeoanthropologists can build more robust explanatory models that better describe hominin evolution during the Middle Pleistocene.

2 | A BRIEF HISTORY OF HOW HOMO HEIDELBERGENSIS MUDDLLED THE MIDDLE PLEISTOCENE

The study of human evolution in the Middle and Late Pleistocene (LP) has experienced significant advances in recent decades. We now know that the origin of *Homo sapiens* was African (possibly pan-African) and extends further back into the late Middle Pleistocene than previously thought. It is also clear that this taxon was dispersing out of Africa prior to 60 ka, likely in multiple smaller waves, with a major dispersal post-60 ka.33–11 Further, over the past two decades species assigned to the genus *Homo* (e.g., *Homo floresiensis*12, *H. naledi*,13 and *H. luzonensis*14) that were contemporary with the *H. sapiens* lineage but are considered to have played little to no role in the latter’s evolution, attest to the complexity of the later Pleistocene human evolutionary record. The Middle Pleistocene is no longer dismissed as the proverbial “muddle in the middle,”15 but is increasingly recognized as a key time frame that witnessed the appearance, on a global scale, of two critical traits of later human morphology: greater encephalization and smaller teeth, and likely the differentiation of geographic groups. The recent questioning of the validity of *H. heidelbergensis* exposes a growing malaise in lumping together observable variation that characterizes Middle Pleistocene hominins, which hinders our ability to hypothesize the scenarios for the evolution of the genus *Homo* into the LP.

The field of palaeoanthropology has matured substantially since *H. heidelbergensis* was proposed by Otto Schoetensack15 on the basis of the Mauer mandible. Further important discoveries have been made since the revival of the taxon in the last two decades of the 20th century.16–20 Unfortunately, in 1908, Schoetensack had no notion of the evolutionary synthesis, and cladistic methods had yet to be developed.21,22 Furthermore, the revival of the *H. heidelbergensis* taxon was rooted in the late 20th century understanding of hominin phylogeny/systematics, particularly as related to debates around the origin of modern humans.23–25 Rather than on any particular set of morphological traits, as required by the rules of zoological nomenclature.26 To further compound the problem, a mandible, without an associated cranium, was used as the holotype for the taxon, even though this bone is normally considered to be extremely plastic and may or may not reflect associated morphological changes in the crania.27 Similarities between the Mauer specimen and the Arago mandibles, which were represented by associated cranial fragments, led to the indirect reconstruction of *H. heidelbergensis*.16,28–31 The Mauer/Arago group was then linked via Petralona to the African specimens such as Kabwe 1 and Bodo, given morphological similarities in the crania.30,32 thus expanding the proposed geographic and temporal range of *H. heidelbergensis*. It was later raised as a possibility that the Chinese “archaic *H. sapiens*” fossils could also be included in *H. heidelbergensis*.33–35 (but see References 36,37). Unfortunately, revival of taxonomic names rarely produces desirable clarity (e.g., the reintroduction of *Australopithecus prometheus* Dart 194538 by Clarke and Kuman39 sparked a heated debate40–42; *H. heidelbergensis* make this taxon particularly misleading. Even to non-specialists (e.g., biologists working in other realms, Palaeolithic archaeologists, etc.) *H. heidelbergensis* represents either (and sometimes paradoxically both) the generalized Middle Pleistocene hominin, or a chronospecies of Neanderthals. Within the palaeoanthropological community, the taxon’s ambiguity has contributed to complex and sometimes hard-to-follow discussions: in a single paper, one can find numerous descriptions of the taxon with incompatible hypodigms.16,19,20,23,33–35,37,43–46 More troublingly, newly discovered Middle Pleistocene hominin fossils that cannot easily be assigned to *Homo erectus*, *H. neanderthalensis*, or early *H. sapiens*, still tend to be lumped into this one-size-fits-all taxon, often with a sensu lato qualifier to indicate a nonspecific morphology of a Middle Pleistocene hominin.35–47–50 Alternatively, they are assigned more general or descriptive names like “archaic *H. sapiens*”,51 “mid-Pleistocene Homo,”52 or “Homo sp.”53 which do little to convey their evolutionary position.

3 | HOMININ TAXONOMY AND WHY IT MATTERS

There are manyfold reasons for uncertainties in hominin taxonomy. A significant and obvious hindrance is a sparse fossil record with unequal geographic coverage, which often makes broader regional comparisons difficult. However, the theoretical underpinnings of taxonomy, and hominin taxonomy in particular, is a potentially more serious impediment54 to understanding human evolution and the place of individual fossils in it. Theoretical and methodological considerations stem from the very history of our science and therefore require a change in perspective rather than a reanalysis of currently available data.55 Genetics have added additional complexity to the issues of fossil taxonomy as some genetically well-defined populations (like the Denisovans) are poorly defined skeletally.56,57,58 “Species” is the “fundamental unit of classification recognized by the International Commission of Zoological nomenclature”58 designed within the Linnaean system of binomial taxonomy. As such, it denotes the lowest classification of organisms that form a biologically relevant group. Linnaean taxonomy, as a systematic categorization of living
beings, was developed in the 18th century prior to the development of evolutionary theory. Not surprisingly, the history of taxonomic thinking became increasingly complex as both the number of fossils and the range of variation of these fossils increased. The problem is further compounded by the need to use open nomenclature (qualifiers such as cf., aff., s.l., and s.s.)59,60 in fossil taxonomy. Furthermore, despite “many thousands of pages that have been spent arguing over species concept[s],”61 the only one that has gained widespread acceptance (at least for the sexually reproducing organisms) is Ernst Mayr’s22,62 biological species concept (BSC) that uses reproductive isolation of terminal taxa as its foundation.63 In defining fossil species, this concept is both implicit and fundamental to cladistic analysis.61

Unfortunately, several problems are evident in applying BSC to fossil specimens: (1) morphological variation does not necessarily reflect reproductive isolation; (2) reproductive isolation is not absolute even in well-defined living primate and other mammal species and cross-breeding has been observed even at the genus level,64,65 and (3) as it does not include a temporal framework, BSC is ill-suited to understanding or examining evolutionary change.66 The evolutionary species concept (ESC)67 was proposed as more appropriate for the fossil record, as it requires establishing the ancestor–descendant relationship (e.g., *Australopithecus anamensis* and *A. afarensis* were proposed to represent parts of the same anagenetically evolving lineage68). However, in cases where this relationship is more tenuous, ESC can result in a circular argument. Further, while chronology is important in phylogeny, it cannot be the cornerstone of taxonomic definition, because: (1) the assessed age is subject to change with improved methods; and (2) the parent and daughter species can persist alongside each other for longer in some areas.65,69,70

Recently, Silcox61 proposed a pragmatic, purely morphological, approach to species as a “minimum diagnosable unit,” which in the case of hominins allows us to examine the global distribution of variation and possible ancestor–descendant relationships within a genus based on cladistic analysis, without assuming (or even considering) the question of reproductive isolation. Using the papionins as an analogous model, Jolly72 suggests that “any hominine species whose ancestors diverged less than 4 Ma previously may well have been able to produce hybrid offspring that could, by backcrossing, introduce alien genes with the potential of spreading if advantageous.” Despite early claims to the contrary,75,77–74 the last 10 years of ancient DNA analyses75–80 demonstrated substantial admixture among different hominin lineages. The extent and frequency of interbreeding among hominin terminal branches in the LP has been well established and recent research indicates that interbreeding can be observed in the Middle Pleistocene as well.79,81

Further issues arise from the exceptionalist nature of palaeoanthropologists’ approach to human evolution and taxonomy, compared to that of palaeontologists and evolutionary anthropologists.82,83 For instance, when it comes to hominin species, chronology (and therefore ultimately the established scenarios) play an important role in taxonomic determination, which is considered (ideally) irrelevant to the established practice of zoological nomenclature. Ultimately, we do want to understand human evolution as a process, and chronology and phylogeny play essential roles in scenario-building and determining the appropriateness (or not) of a particular classification. Further, hominins (especially the members of the genus *Homo*) represent a widely distributed polytypic taxon that displays great behavioral flexibility84–86 and occupies a “generalist specialist” niche87 that allows the members to exploit and adapt to different environmental conditions without significant alterations in morphology.

When it comes to Middle Pleistocene hominin evolution, we identify two main options, with the understanding that other possibilities may exist: (1) we could consider entire Pleistocene Homo fossils as a single lineage of *H. sapiens* with separate subspecies and/or chronospecies,88–90 or (2) we could consider the observed morphological variation as taxonomically meaningful within the “practical” species concept,61 without assuming that they were biological species and therefore not interfertile. Given that LP Neanderthals, Denisovans, and modern humans constitute sister taxa, we need to rethink the variability of the Middle Pleistocene hominin record. We find it unlikely that the observed Middle Pleistocene variability can be subsumed under a single taxon such as (nebulously defined) *H. heidelbergensis*. Middle Pleistocene hominin variation must be organized using better, more precise, and consistent criteria in defining taxa which comply at the same time with the rules of the International Code of Zoological Nomenclature (ICZN), as well as with current developments of our understanding of the process of human evolution.

4 | MOVING FORWARD

Using the problematic taxon *Homo heidelbergensis* will continue to complicate and obfuscate how we think and communicate major issues in later phases of human evolution. To help resolve these issues, we recommend the following: Suppressing the taxa *H. heidelbergensis* and *H. rhodesiensis* and introducing a new taxon *H. bodoensis*.

1. The taxon *H. heidelbergensis* should be suppressed

   The taxon *H. heidelbergensis* sensu stricto should be suppressed altogether and those fossils reassigned to *H. neanderthalensis* in light of recent genetic and/or morphological data. Supporting this argument is the recent consensus that the Sima de los Huesos hominins should be considered as early members of the Neanderthal lineage.8,27,46,91,92 Dating to at least 430 ka or Marine isotope stage 12.93,94 the Sima hominin fossils already show hyper-derived dentition,8 as well as a number of Neanderthal derived traits in cranial and mandibular morphology.91 The Arago hominins and other Middle Pleistocene Western European hominins show variable but ubiquitous derived Neanderthal traits.95 As such, there is no need to introduce another species with the same morphology, in turn, making *H. heidelbergensis* a junior synonym to *H. neanderthalensis* and therefore redundant. In particular, if Mauer, as is currently considered, displays some derived Neanderthal traits47,96 at 609 ± 40 ka,97 it could
represent an early specimen within the Neanderthal lineage. Recognition of the Western European Middle Pleistocene specimens as *H. neanderthalensis*,\(^9\) does not preclude, however, the presence of other taxa in Europe (e.g., *H. antecessor* and possibly others).\(^{46}\)

The assignment of the Asian, particularly Chinese, archaic hominins into *H. heidelbergensis* should be abandoned (contra tentative suggestions by References 31,33,99). A number of researchers familiar with the Chinese record have never felt comfortable assigning the Chinese fossils into *H. heidelbergensis*.\(^{36,37,100}\) For instance, comparisons of maximum and minimum frontal breadths on a range of fossils from Europe, Africa, and China showed that hominins like Petralona, Bodo, and Kabwe cluster relatively close together and well away from the Chinese fossils.\(^{101}\) In perhaps the most comprehensive comparative study of nonmetric traits, Wu\(^{100,102,103}\) (see also References 36,104) identified the following features that differ between Middle Pleistocene hominins from the western and eastern parts of the Old World: “frontosphenoidal process of the zygomatic bone; upper facial height; maxillary shovel-shaped incisors; Inca bones; M3 agenesis” and the nasal saddle.\(^{77}\) For the most part, Chinese mid-Pleistocene *Homo* do fall away from their western penecontemporaneous counterparts (e.g., *H. bodoensis*, *H. neanderthalensis*). The picture of Middle Pleistocene hominin variability in Asia is much more complex than originally anticipated, with the possibility of multiple lineages being present in the region at the same time, some that may have yet to be identified.\(^{5,105,106}\)

*H. heidelbergensis* sensu lato should be abandoned as well since it commonly includes all nonspecific Middle Pleistocene hominins, an approach that is not particularly informative. This taxon was previously considered as the most recent common ancestor (MRCA) of LP hominins, or minimally, the common ancestor of the African and European lineages (i.e., *H. sapiens* and Neanderthals, respectively). Since the MRCA of the modern human and Neanderthal lineages has been pushed further back in time toward the late Early Pleistocene or very early Middle Pleistocene,\(^8\) the specimens currently assigned to *H. heidelbergensis* sensu lato cannot be considered representatives of the MRCA. This is a particularly pertinent point given that the split between African and Eurasian hominins has been recently proposed to be earlier than the split between the Denisovan and Neanderthal lineages.\(^3\) As such, *H. heidelbergensis* sensu lato can no longer be considered the root of all African and European hominin lineages.

If the MRCA appears in the late Early Pleistocene or very early Middle Pleistocene, then none of the regional geographic variants (African, European, or Asian) from the Middle Pleistocene can serve as the MRCA of all three. There does exist a likely candidate however, that dates to the late Early Pleistocene. The tantalizing cranial fragments (a partial left parietal MK1 and the right portion of a frontal bone MK2) from Gombore II, Melka Kunture (Ethiopia), dated to \(\sim 850 \text{ ka}\), were interpreted by Profico et al.\(^{107}\) as a possible ancestral form to the African Middle Pleistocene specimens. Given the estimated cranial capacity of 1080 \(\text{cm}^3\) the MK hominin could represent the MRCA for all Middle Pleistocene lineages that share an enlarged cranial capacity as one of its core traits. The MK cranial remains are generally considered to exhibit an “archaic” morphology. Signs of encephalization—enlarged braincase and more vertical parietal walls—coupled with a primitive morphology, are also observed in older East African specimens such as Daka and Buia.\(^{107}\) Based on the current fossil record, this suggests East Africa around 1 Ma as the most likely region for the appearance of the MRCA of later Middle Pleistocene and LP hominins.

2. The taxon *H. rhodesiensis* should be suppressed

*H. rhodesiensis* Woodward 1921\(^{108}\) never gained a wide usage in palaeoanthropology. Indeed, a quick search on the Web of Science provides 274 direct mentions of *H. heidelbergensis* while only 17 hits for *H. rhodesiensis*. In our opinion, there are two primary reasons for this: (1) the taxon is poorly defined and variably understood and used; and (2) the taxon name is associated with sociopolitical baggage that our scientific community is trying to dissociate itself from. We elaborate further below.

*H. rhodesiensis* has come to carry very different meanings. For instance, some see it as an African Middle Pleistocene taxon that parallels *H. heidelbergensis* sensu stricto in Europe, and that eventually gave rise to *H. sapiens* in Africa.\(^{16,109}\) Alternatively, it has, at times, been considered as the MRCA to all LP hominin lineages, ancestral to both *H. sapiens* and Neanderthals.\(^{27,35,110}\) It may be argued that if this taxon was considered as a Middle Pleistocene ancestor to the *H. sapiens* lineage exclusively, then we only need to redefine its hypodigm according to our current understanding. However, because this taxon has been defined in multiple ways it is impossible to dissociate it from these various definitions; thus, continuing to use *H. rhodesiensis* creates unnecessary confusion. It may be argued that Arthur Smith Woodward’s morphological description of *H. rhodesiensis*,\(^{108}\) which centered on its differences from Neanderthals complied with the nomenclature practice for pre-1931 taxonomic names. However, the later resurrection of the taxon was based on similarities of the holotype Kabwe 1 with Petralona, first noted by Stringer,\(^{111}\) and more recently by Fries.\(^{112}\) Including Kabwe and Petralona in the same hypodigm resulted in an Afro-European taxon. Paralleling the usage of *H. heidelbergensis* sensu lato for an Afro-European MRCA, this lumping together of Middle Pleistocene specimens is contradicted by observed Neanderthal traits in Petralona and the early appearance of the Eurasian dental pattern.\(^{113}\)

At least part of the reason why *H. rhodesiensis* never became widely used by palaeoanthropologists stems from its pernicious political baggage. The name is associated with Cecil Rhodes and English mining colonialism and its abhorrent practices used by this self-proclaimed owner of “Rhodesia” on local indigenous populations.\(^{114}\) While these considerations are not at the root of our rejection of the name, they are not minor and should not be ignored. Discussions of hominin taxonomy cannot operate in a social void.\(^{115}\) It requires a judicious evaluation of the social message that names are sending, as they have implications for our understanding of the process in the evolution of our own species. Decolonizing palaeoanthropology is an important task\(^{116}\) that needs to take precedence over rigid taxonomic rules. The unfortunate reticence of ICZN to allow for a name change is best exemplified by *Anophthalmus hitleri* Scheibell 1937\(^{117}\)—a carabid beetle found only in five caves in Slovenia—named as a dedication
to Adolf Hitler. This was an honor that was not lost on either the infamous German Chancellor or the collectors of his memorabilia, who have pushed the beetle *A. hitleri* to the brink of extinction by illegal collecting. Despite this, its taxonomic name remains valid under the rules of ICZN. There are growing criticisms of this traditional rigidity of naming rules in biology, as they are (nor they should be) neither neutral nor absolute.

3. Introducing a new hominin taxon

We propose that, in addition to suppressing these two taxa, we need to add a new hominin taxon that is clearly defined following ICZN rules and does not carry any social-political baggage. This taxon would have originated from the MRCA of European, Asian, and African Middle Pleistocene taxa sometime before the split of Eurasian taxa into Neanderthals and Denisovans and would represent the Middle Pleistocene ancestor of *H. sapiens*.

Here we introduce a new Middle Pleistocene (i.e., Chibanian Age/Stage, 774–129 ka) hominin species that represents the direct ancestor of *H. sapiens* (Figure 1). We propose that this new species be based on the Bodo skull and thus be named *Homo bodoensis*.

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 bodoensis* sp. nov.

Etymology: The name *bodoensis* refers to the site of Bodo D’ar where the fossil specimen Bodo 1 was discovered.

Holotype: Bodo 1, a partial cranium of an adult (presumably male) individual, preserving the face and the anterior braincase, found in autumn 1976 by Alemayehu Asfaw, Paul Whitehead and other members of the Rift Valley Research Mission in Ethiopia headed by Jon Kalb. The specimen is currently curated in the National Museum of Ethiopia in Addis Ababa, Ethiopia. *H. bodoensis* has been deposited in the ZooBank database (http://zoobank.org/) with Life Science Identifier urn:lsid:zoobank.org:act:50AC3EA4-82E0-4AAD-BCDA-6DE6055888A7.

Description (modified from References 20,30,123,125): Bodo 1 comprises a damaged facial skeleton, partial neurocranium, and basicranium anterior to the basion of a single individual, reconstructed from dozens of individual bone fragments (Figure 2). Aside from the fact that the lateral portion of the right maxilla, the right zygomatic bone, and the left temporal process are missing, the face is generally well preserved. The palate is missing the portion posterior to the P4, and except for some small fragments of the right molar roots, the teeth are not preserved, and the alveolar processes show damage. The neurocranium preserves an almost complete frontal bone, the sphenoid, parts of the left temporal and both parietals, and the right portion of the occipital bone. The basicranial portion includes the partially preserved left mandibular fossa and articular eminence, the basioccipital, and the petrous portion of the temporal bone. The face is strikingly massive, with large rectangular orbits and a very broad interorbital region, a wide nasal root and aperture, a deep and robust left zygomatic, and a broad and deep palate. Though projecting and heavily built, the supraorbital tori are arched, segmented (i.e., divided into medial and lateral segments), and attenuated laterally; they do not form a continuous bony shelf but are rather separated by a prominent glabellar region, behind which is a flattened plane (rather than a sulcus). There is a distinct sagittal keeling in the frontal view, especially in the bregmatic region of the vault. The maxillary sinus is expanded, and there is no canine fossa. The frontal sinuses are also extensive and asymmetrical (the right sinus is larger). In lateral view, the skull is long and low, and the frontal presents a low and flattened profile. There is a prominent parietal angular torus, and the temporal squama is high and arched. The anterior nasal aperture is almost vertical in the lateral projection. In the superior view, the skull presents a
**FIGURE 2** *Homo bodoensis* sp. nov. holotype partial cranium Bodo 1 (Middle Awash, Ethiopia). Frontal (a), left lateral (b), superior (c) inferior (d) views. Scale bar: 5 cm. Source: Original photos Copyright © Jeffrey H. Schwartz

piriform shape, broadening posteriorly from the noticeable postorbital constriction. In the inferior view, the large incisive foramen is placed anterior on the hard palate, the mandibular fossa is shallow, and the preserved part of the articular eminence is flat; the petrous portion of the temporal is placed in such a way that the foramen lacerum displays a crevice-like configuration. The endocranial capacity was estimated to ~1250 cm³ (i.e., between ~1200 and 1325 cm³). The series of cut marks situated on the facial and posterior parietal regions were interpreted as intentional postmortem defleshing.

**Type locality:** Bodo D’ar, the Middle Awash research area, Afar Depression, the northwestern part of the former Hararghe Province, Ethiopia.

**Geological age and stratigraphic position:** Upper Bodo Sand Unit. Dated to ca. 600 ka by laser-fusion ⁴⁰Ar/³⁹Ar technique (0.64 ± 0.03 Ma), biostratigraphy and tephrochronology.

**Archaeological context:** The specimen is associated with an Acheulean stone tool assemblage.

**Species diagnosis:** The species is diagnosed by a unique combination of cranial traits. The Bodo specimen has already been described as showing a mix of *H. erectus*-like and *H. sapiens*-like features. The species is similar to *H. erectus* in having: a robustly built midface; total facial prognathism; projecting tori and a flattened low frontal squama; sagittal keeling; a low vault profile; a prominent parietal angular torus; thick vault bones; no foramen lacerum is observable—it is presented as a narrow crevice. These traits can be linked to the retention of the general cranial structure from *H. erectus*. Traits similar to other Middle Pleistocene and later hominin taxa include: increased cranial capacity and associated traits (broader frontal and mid-vault, reduced postorbital constriction, signs of parietal bossing, high and arched temporal squama), a vertical (rather than forward sloping) nasal margin, and the position of the incisive canal in front of the hard palate. Excessively thick and projecting, but segmented brow ridges, with the incipient division of the brow at mid-orbit and attenuated laterally may be considered a distinctive trait of the species.

**Comparisons:** In comparison to *H. erectus*, *H. bodoensis* differs by the increased cranial capacity (intermediate between *H. erectus* and *H. sapiens*) and a suite of associated derived traits: the curvature of the temporal squama; broader mid-vault; signs of parietal bossing; and relatively broad frontal bone where the maximal cranial breadth lies above the lower third of the skull in posterior view, with more vertical parietal walls.

Increased cranial capacity is shared among most of the Middle Pleistocene hominins (excluding *H. naledi* and island isolates of Southeast Asia such as *H. floresiensis*). This trait is presumably already under selection in the MRCA in the latter portion of the Early Pleistocene. Other features are not shared with Middle Pleistocene hominins such as *H. neanderthalensis*, late *H. erectus*, and potentially other Asian groups yet to be systematized. The species differs from *H. neanderthalensis* as it does not show any of the Neanderthal-specific morphology associated with midfacial prognathism and neurocranial shape. It also differs in the particular form of the brow ridges, which are smoothly continuous and double-arched in *H. neanderthalensis*.

*H. bodoensis* lacks a number of the *H. sapiens* specific features—warranting a separate species designation. This is contrary to what is observed in *H. neanderthalensis* where the autapomorphies emerge early in the Middle Pleistocene. However, all of the later *H. sapiens* specific features can be derived from traits present in *H. bodoensis*, including the massive but segmented (divided into lateral and medial parts) browridges.

**Hypodigm:** In addition to the holotype Bodo 1, the hypodigm is based on the sufficiently preserved cranial specimens with the exclusion of isolated mandibles and includes at a minimum: Kabwe 1 (Broken Hill), Ndutu, Saldanha (Elandsfontein), Ngloba (LH 18), and potentially Salé in Africa. Kabwe 1 could represent a late survivor of the taxon. Some Middle Pleistocene specimens from Europe (e.g., Ceprano calvarium, Kabwe 1) could be included in this group as well. Locations, dating, previous taxonomic designations, and references for the included specimens are provided in the Table S1.

**Distribution:** The species had a pan-African distribution with the peripheral range extending into the eastern Mediterranean (Southeast Europe and the Levant) from which it could have contributed to the repopulation of Europe (and possibly Central and East Asian) demographic sinks after the glaciations.

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Here, we present *H. bodoensis* as a new species and suggest that it is ancestral to *H. sapiens*. However, our new species is not to be
considered the MRCA of Eurasian (Neanderthals, Denisovans) and African (H. *sapiens*) hominins. As schematically presented in Figure 1, *H. bodoensis* separated from the Eurasian groups before the split of the Eurasian forms into Neanderthals, Denisovans, and possibly other groups. While essentially an African species, *H. bodoensis* may have played a role in the evolutionary history of the Levant and Europe. In particular, Middle Pleistocene specimens from the two regions (mostly concentrated in the eastern Mediterranean), which do not demonstrate any Neanderthal traits, such as Mala Balanica (Serbia) and some specimens from the Levant such as Hazorea and Nadaouiyeh Aïn Askar (for review see Reference 46) could be considered as *H. bodoensis*. We did not include them in the *H. bodoensis* hypodigm at this stage, because these fossils are too fragmentary. However, the species was potentially present in Europe during the Middle Pleistocene (as evidenced by the Ceprano specimen) and may have contributed to a mixed morphology seen in Arago, Petralona, and possibly other fossils in Western Europe.

The newly defined species *H. bodoensis*, described on the basis of the Bodo 1 specimen has clear advantages: (1) it recognizes the variability and geographic distribution of Middle Eastern hominins; and (2) it describes the unique morphology of the African Middle Pleistocene hominins that extends into the eastern Mediterranean that is distinct from *H. neanderthalensis* and pre-dates the appearance of *H. sapiens*. While not a true species in the strict biological sense (since there is strong and growing evidence of migrations as well as gene flow between these diverged groups) this newly defined taxon cuts through the obfuscating and inconsistent use of improperly named and defined Middle Pleistocene hominins in Europe and Africa and should facilitate more consistent and meaningful discussions around these various topics presented here.

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