Special Issue: What's in a Name? Late Middle and Early Late Pleistocene Hominin Systematics

Informal Nomenclature and Hominin Classification

JOHN HAWKS*

Department of Anthropology, University of Wisconsin-Madison, 1180 Observatory Drive, 5240 W. H. Sewell Social Science Building, Madison, WI 53706, USA; and, Centre for the Exploration of the Deep Human Journey, University of the Witwatersrand, SOUTH AFRICA;

corresponding author: John Hawks; jhawks@wisc.edu

submitted: 20 December 2024; revised 8 August 2025; accepted: 18 August 2025

Guest Editors: Mirjana Roksandic (Department of Anthropology, The University of Winnipeg) and Christopher J. Bae (Department of Anthropology, University of Hawai'i at Manoa)

Handling Editor in Chief: Karen Rosenberg

ABSTRACT

Many of the names used by specialists in studies of hominin evolution are outside the formal Linnaean classification governed by the International Code of Zoological Nomenclature. These names include many of the most widely used terms in the field, such as "Neanderthal" and "modern human." Although these may be considered as "informal" in comparison to Linnaean classification, such names are often used as formal units of analysis in research as well as for communication to the public. Researchers have defined more and more of these non-Linnaean names in recent years, in part connected with the greater application of genomic information to recognize ancient groups. Archaeogenomics, which encompasses many Holocene and terminal Pleistocene human populations, has naming practices that are distinct from those typical of paleoanthropology. A survey of non-Linnaean names in current use within hominin evolution research reveals four overlapping patterns of naming, which have shifted in importance over the years. These practices have a history that began in the eighteenth and nineteenth centuries with the classification of human races. While some paleoanthropologists have argued for greater application of formal Linnaean names, the flexibility of non-Linnaean nomenclature has encouraged many specialists to use them in scientific communication and public engagement.

esearchers today use an array of non-Linnaean names Researched to an arrow of prehistoric hominins. Examples include "Neanderthal," "Cro-Magnon," "robust australopith," and "hobbit," among many others. Some like "Neanderthal"—are common or vernacular names known to the public and translated across languages. But others—like "habiline"—may have been used by researchers and educators but otherwise mentioned only rarely outside of anthropological or historical writing. These are informal terms and yet they function within the science more than informal names in other taxonomic groups, such as the common names of birds. Such names for hominins are often applied formally by researchers to describe their units of analysis, from populations to putative species and higher-level groups. In the field of paleoanthropology, "Neanderthal" and "modern human" have each been used as formal units of analysis in scientific research articles and academic books more often than any Linnaean binomial

other than Homo sapiens (Figure 1). The use of such non-Linnaean names is accelerating. Specialists in human evolution have invented more new non-Linnaean names in recent years than they have diagnosed formal Linnaean taxa.

Specialists invent and use such non-Linnaean names for varied reasons. A name may apply to population-level or sample-level grouping where a Linnaean name does not fit. For example, the meaning of "modern human" for most researchers includes all living populations of *Homo sapiens* and some fossil samples while excluding fossils that a researcher might attribute to "early Homo sapiens" or some other category. Specialists sometimes use a non-Linnaean name to facilitate greater consensus than a Linnaean classification would inspire. This is one of the factors that has buoyed the term "Neanderthal" instead of the formal *Homo* neanderthalensis or H. sapiens neanderthalensis (Tattersall 2007). Increasingly, geneticists invent names for ancient hominins that may be known either from ancient DNA or

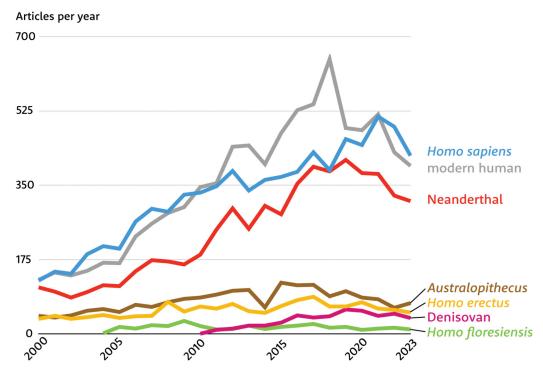


Figure 1. Scientific journal articles per year using various Linnaean and non-Linnaean names from human evolution research. Article counts across all scientific disciplines from 2000 to 2023 generated from Web of Science (Clarivate).

from population modeling. This is the origin of the terms "Denisovan" (Reich et al. 2010) and "superarchaic" (Sánchez-Quinto 2014). Scientists also invent names for ancient groups for the purposes of marketing research to the public. While some such names may be intended only for informal use, such names may later gain currency in research contexts, as happened with the name "hobbit" (Goulden 2013).

These names are outside the Linnaean classification for animals, which is codified in the International Code of Zoological Nomenclature (ICZN) and adjudicated by the International Commission on Zoological Nomenclature (1999). Names like "modern human" and "Denisovan" are not governed by any body, nor are they described in any formal code. Specialists may use them in classifications outside the ICZN, may redefine the names, or may use the same name to refer to several different things. Further, unlike Latin binomial names, non-Linnaean names can be translated or rewritten in varied world languages. Researchers rely on such names because they are useful, both for scientific work and for public communication. Flexibility is one of the most important reasons they are useful.

But flexibility comes at the risk of confusion. Publications rarely make clear why Linnaean binomials apply to some prehistoric groups and not others, or what a non-Linnaean name may signify about a group's classification. Researchers may use several partially overlapping names with uncertain boundaries between them, sometimes combining Linnaean and non-Linnaean forms such as "anatomically modern *Homo sapiens*," "modern human," and "derived *Homo sapiens*." Names matter not only for human

readers but also for metadata tools that tend to stumble in cases of unclear classification or nomenclature. As multiple-authored scientific research publications are becoming more and more the rule, it can be challenging to come to consensus within such groups about the appropriate names for ancient groups. Ancient DNA information is making important contributions to classification, but this kind of information has sometimes generated resistance and skepticism from some specialists who rely on morphological evidence for classification, leading to the formation of different kinds of classifications.

Awareness has been growing across anthropology, human biology, and human genetics that names for populations sometimes impede clear communication (Athreya and Hopkins 2021; Bae et al. 2024; Reed et al. 2023). It is therefore appropriate to take stock of names currently in use and to provide some context about why researchers choose non-Linnaean names instead of Linnaean alternatives. In this contribution I survey the application of non-Linnaean names in human evolution research. The purpose of this survey is not to provide an exhaustive historical list of every name, but instead to illustrate current applications of nomenclature and some recent trends. The addition of molecular data to the paleoanthropological record has prompted a burst of naming of ancient groups, and I consider the emergence of this trend.

The survey focuses upon English-language sources with some consideration of how names in other languages have influenced recent research. While there is a great deal of overlap across European languages in names like "Neanderthal," some names are more regionally or cultur-

ally specific and would merit broader review. The use of informal classification for humans and other hominins has been flexible and relatively non-hierarchical, transcending categories that may often be formalized. This contrasts to some degree with the discussion of informal nomenclature presented by Simpson (1961, 1963), who presented a hierarchical schema of informal and formal nomenclature. In this review I have focused on practices and history within the study of human origins and have not attempted to align or reconcile names into a single system.

PRACTICES IN ARCHAEOLOGY AND ARCHAEOGENETICS

Archaeologists, bioarchaeologists, and archaeogeneticists who study Holocene and terminal Pleistocene peoples work with a larger array of group names than paleoanthropologists do. Naming conventions that specialists apply to Holocene groups vary depending on context, period, and type of information available about the groups. Researchers who study these comparatively recent time periods may consider not only genetic and morphological information but also cultural and linguistic heritage. Cultural or linguistic information combined with genetic data links some Holocene and terminal Pleistocene groups to the historic record. Where group names or place names for groups are attested in historic records or documents, archaeologists and historians generally use those attested names. Examples include "Sumerian," "Hittite," or "Avar." The use of attested names is not without contention, since some historical records or oral traditions may derive from other cultures who misunderstood a group name, or possibly attributed a culturally inappropriate name. An example of such a name that was long used in archaeological research but later re-evaluated through consultation with descendant communities is "Anasazi" (Colwell-Chanthaphonh 2009).

In archaeological cases where no attested name is known, specialists use varied approaches to developing names. Eisenmann and coworkers (2018) reviewed current naming conventions, focusing upon the intersection between ancient DNA information and more traditional archaeological and bioarchaeological approaches. Ancient DNA research has been extraordinarily productive in the classification of Holocene bioarchaeological samples, particularly from Europe, although much less data have emerged from earlier time periods (Mallick et al. 2024). These new datasets have revealed cases of correlation between genetic clusters and archaeological traditions, but also cases of mismatch. In some cases, archaeogenetic results have revived early twentieth-century ideas about migration and movement of peoples, which were in some cases incorporated into racialized ideologies (Burmeister 2021; Feinman and Neitzel 2020; Heyd 2017). Archaeologists and geneticists perceived a need for clear naming systems apart from past systems that may be inappropriate to the complexity and dynamics that are recognized today.

Eisenmann and collaborators (2018) recognized two kinds of systems in use by current archaeogeneticists:

• "Mixed systems" in which names for geographic

- region, relative time period, subsistence practices, and names of archaeological cultures may all be used within naming conventions for ancient groups. They cite "Western European hunter-gatherers", "Bell Beaker Late Neolithic", and "Yamnaya" as examples of names used within mixed systems of nomenclature.
- "Genetic nomenclature" (referencing Fu et al. 2016) in which the name of a group is formed from the name of the archaeological site where one or more genomes characterizing the group were found.

After considering the history of naming archaeogenetic groups, Eisenmann and coworkers (2018) presented three approaches to nomenclature as possible ways of moving forward—one using a numerical system for different groups, one based on a mixture of cultural, geographic, and temporal categories, and one based on geographic-temporal names.

All three of these systems generate names that appear more like computer code than common names in some ways. For example, the mixed nomenclature would include names like *Bell_Beaker, Minoan_Odigitria, or WHG (Western European hunter-gatherers), while the geographic-temporal nomenclature would include names like North_Pontic and C_Europe_LN. A frequent element of archaeogenetic naming systems is the use of typographic conventions to designate names. Eisenmann and coworkers (2018) noted that different researchers prefer designating names with asterisks versus italic font, versus plain text. Names that include underscores and embedded abbreviations are harder for readers to parse, but they do facilitate a consistency between data tables, figures, and the text of research articles. These kinds of names find an analogy in Linnaean nomenclature, which also has typographic conventions such as setting binomial and trinomial names in italic font and mandatory capitalization rules.

In practice, modern archaeogenetic work uses a mixed nomenclature including cultural, geographic, temporal, and specimen-centered names. There is some continuing disconnect between publications that rely on genetic data, and those that rely on archaeological or skeletal data. Work subsequent to the review by Eisenmann and coworkers (2018) has noted that archaeological taxonomies themselves are inconsistent and pose barriers for understanding the connections between biological and cultural entities in the past (Feinman and Neitzel 2020; Riede et al. 2019; Shennan 2024), and that some groups have been inappropriately divided into arbitrary chronological periods (Griffiths et al. 2023).

PATTERNS OF INFORMAL AND MIXED NOMENCLATURE IN PALEOANTHROPOLOGY

A sample of non-Linnaean names in hominin evolution research is presented in Table 1. Where possible the table includes a source either for the origination of a name or for an early occurrence that illustrates how current authors use the name in research applications. Many names have changed in meaning over time, and in such cases the early

$\mathbf{4} \bullet \textcolor{red}{PaleoAnthropology} \ 2025{:}2$

TABLE 1. EXAMPLES OF NON-LINNAEAN CLASSIFICATION TERMS IN HUMAN EVOLUTIONARY BIOLOGY.*

Name	Extent	Linnaean categories represented	Sources
Neanderthal (Neandertal, Neanderthaler, Neanderthalien)	Europe, southwest Asia, central Asia. Middle to Late Pleistocene	Homo neanderthalensis, considered by many as Homo sapiens or H. sapiens neanderthalensis	Fuhlrott 1865
classic Neanderthal	Europe, southwest Asia	Homo neanderthalensis, considered by many as Homo sapiens or H. sapiens neanderthalensis	Weidenreich 1943
progressive Neanderthal	Europe, southwest Asia	Homo neanderthalensis, considered by many as Homo sapiens or H. sapiens neanderthalensis	Weckler 1954
modern human (modern man, I'homme moderne)	Global, Late Pleistocene and Holocene	Homo sapiens	
archaic human (archaic man)	Africa, Eurasia, island southeast Asia	Homo sapiens, Homo neanderthalensis, Homo heidelbergensis, Homo helmei, Homo longi, and (for some authors) Homo erectus	Simpson 1861
Denisovan	Central Asia, southeast Asia, Middle to Late Pleistocene	Homo sapiens or Homo altaiensis, or unknown	Reich et al. 2010
D1, D2, D3 populations	Central Asia, southeast Asia, Middle to Late Pleistocene	Homo sapiens or Homo altaiensis, or unknown	Jacobs et al. 2019
Neandersovan	Eurasia, possibly Africa, Middle Pleistocene	No name yet defined	Rogers et al. 2020
australopith (australopithecine)	Africa, Pliocene and Early Pleistocene	Australopithecus, sometimes Paranthropus, Kenyanthropus	Gregory and Hellman 1938; Hallowell 1956
robust australopith (robust australopithecine)	Africa, Late Pliocene and Early Pleistocene	Paranthropus	Tobias 1963
gracile australopith (gracile australopithecine)	Pliocene, Early Pleistocene	Australopithecus africanus, Australopithecus afarensis, Australopithecus sediba	Tobias 1963
habiline	Africa, Early Pleistocene	Homo rudolfensis, Homo habilis	Tobias 1965
erectine	Africa, Asia, Early to Middle Pleistocene	Homo erectus, Homo ergaster, Homo erectus sensu lato	Sharma 1974
hobbit	island southeast Asia, Middle to Late Pleistocene	Homo floresiensis, sometimes Homo luzonensis	Meijer et al. 2010

TABLE 1. EXAMPLES OF NON-LINNAEAN CLASSIFICATION TERMS IN HUMAN EVOLUTIONARY BIOLOGY (continued).*

Name	Extent	Linnaean categories represented	Sources
chumanzee	Africa, Late Miocene	No name yet defined	Disotell 2006
ghost archaic	Africa, possibly	Homo sapiens, or unknown	Veeramah and
	Eurasia, Middle to		Hammer 2014
	Late Pleistocene		
superarchaic	Eurasia, Early to	Unknown	Sánchez-Quinto
	Middle Pleistocene		2014
ghost modern	Africa, possibly	Homo sapiens	Lipson et al.
	Eurasia, Middle to		2020
	Late Pleistocene		
Cro-Magnon	Europe, Late	Homo sapiens	Quatrefages and
	Pleistocene		Hamy 1874
Red Deer Cave	China, Late	Homo sapiens	Curnoe 2012
people	Pleistocene to		
	Holocene		
Thorin lineage	Europe, Late	Homo neanderthalensis or Homo	Slimak et al.
	Pleistocene	sapiens	2023
Skhūl/Qafzeh people	southwest Asia, Late	Homo sapiens	Smith and
	Pleistocene		Arensburg 1977
Dragon Man,	China, Middle	Homo longi	Bae et al. 2023
Longren	Pleistocene		
Juluren	China, Middle	No name yet defined, or <i>Homo</i>	Wu and Bae
	Pleistocene	sapiens	2024
Heidelbergers,	Europe, Middle	Homo heidelbergensis	Bölsche 1909
Heidelbergs	Pleistocene		

^{*}For each name the listed source is one that conveys approximately the name's current or most common meaning, which is not necessarily the first published use of the name. In some cases, the variable meanings of the name or changes over time make it more challenging to identify a source with the current meaning.

historic uses of a name may have little relevance to how researchers have applied the name recently.

Naming practices for earlier hominins differ from those applied in Holocene and terminal Pleistocene archaeogenetic contexts. Researchers do not seem to treat these two realms as connected by common principles. Still, in the Late Pleistocene, the naming practices of archaeogeneticists are increasingly relevant to paleoanthropological research. This is particularly true for skeletal material of early groups of modern humans in Eurasia. Examples of such groups are presented in Table 2. Eisenmann and coworkers (2018) did not discuss names like "Denisovan" or "Neanderthal" that pertain to earlier periods, nor have other works citing that review. Eisenmann and coworkers (2018) also did not discuss categories considered by paleogeneticists based only on inferences about admixture sources, such as "ghost populations." These have increasing importance in paleoanthropology where population studies leverage data from recent populations to understand ancestral groups.

Most of the non-Linnaean names used in hominin evolution research fall into one of the following patterns:

Names based on a discovery site or geographic region. "Neanderthal," "Denisovan," and "Cro-Magnon" are names for ancient groups that are derived from the names of the sites where remains of each group were first recognized. Recognizing discovery sites in names is so common in anthropology and archaeology that it may seem the most natural option. But such names have undergone cycles of popularity and today are used in particular contexts. Names for ancient hominin groups are not alone: names of Paleolithic archaeological industries are generally derived from the name of a type site-Oldowan (Leakey 1935) and Lomekwian (Harmand et al. 2015) are among countless examples. In Linnaean taxonomy of hominins, it has been more common to invent names based on a geographic region or political nation and rarely after a site. Australopithecus afarensis (Johanson et al. 1978), Sahelanthropus tchadensis (Brunet et al. 2002), and Homo luzonensis (Détroit et al. 2019)

TABLE 2. EXAMPLES OF NAMES FOR GROUPS USED IN ARCHAEOGENOMIC RESEARCH STUDIES.*

Name	Extent		Sources
Ancient North	Europe, Late Pleistocene	Homo sapiens	Lazaridis et al. 2014
Eurasians (ANE)	to Holocene		
Western European	Europe, Late Pleistocene	Homo sapiens	Lazaridis et al. 2014
hunter-gatherers	to Holocene		
(WHG)			
Eastern European	Europe, Late Pleistocene	Homo sapiens	Haak et al. 2014
hunter-gatherers	to Holocene		
(EHG)			
Villabruna cluster	Europe, Late Pleistocene	Homo sapiens	Fu et al. 2016
	to Holocene		
Mal'ta cluster	Siberia, Late Pleistocene	Homo sapiens	Fu et al. 2016
Věstonice cluster	Europe, Late Pleistocene	Homo sapiens	Fu et al. 2016
Goyet Q2 cluster	Europe, Late Pleistocene	Homo sapiens	Villalba-Mouco et al. 2023
Bacho Kiro IUP	Europe, Late Pleistocene	Homo sapiens	Hajdinjak et al. 2021

^{*}These names apply to Pleistocene contexts and these examples are chosen to illustrate different approaches to nomenclature rather than to be a comprehensive list.

are examples of this pattern—each of these incorporates the name of a geographic region but not a site.

Informal or non-Linnaean names based on a site name were very popular during the later nineteenth and early twentieth centuries. Many authors both within academic publications and in popular media simply added the word "Man" to the name of a site, city, or region, often using the resulting name as a racial identifier. Examples include "Peking Man," "Solo Man," "Grimaldi Man," and "Rhodesian Man." During the early twentieth century, adding "type" also signified a racial identifier, as for example "Spy type" and "Cro-Magnon type."

This way of forming names fell out of popularity in the English language in the postwar period. There were several reasons for this shift. The introduction of the Modern Synthesis into human evolution research tended to draw researchers' interest toward larger-scale groupings and away from the concept that local or regional races are sensible units of analysis. This period marked a decline of racial classification in anthropology, as described below. Many biologists of this era preferred Linnaean subspecies as a way of classifying populations, and some invented schemes attributing geographic and temporal samples to subspecies (Campbell 1965; Krantz 1980). Later, during the 1990s and early 2000s, many new hominin fossil samples represented forms of Australopithecus or other genera that were not so easily described as "people," again encouraging more formal Linnaean names.

In the last decade, names of sites and regions have been used for names of hominin groups in two contexts. For hominin samples, several names formed in Chinese languages with "rén" (人) have been added during the last

decade. Some of these are based on site, city, or regional names, such as Mengzi Ren (蒙自人). In this case the same sample of fossils were popularized in English as the "Red Deer Cave People" (Curnoe 2012) after the name of the cave site Maludong (马鹿洞).

The other context is ancient DNA. Researchers have sometimes found that genomes from a small number of individuals, either from a single site or group of sites from a similar region and time period, group together in statistical analyses. In some cases, these individuals may already be recognized within a cultural unit named by archaeologists. In Pleistocene sites genetic data are sparser, and a single site may have hominin samples from different time periods and populations. Sole genetic samples from Pleistocene sites are generally named within analyses only as individuals—examples include Goyet Q116-1 (Villalba-Mouco et al. 2023), Oase 1 (Fu et al. 2015), and Tianyuan (Yang et al. 2017). But where multiple individuals share enough genetic similarity to suggest that they represent a single ancient population, researchers have provided group names. Some of these have been recognized by site and archaeological association, such as Bacho Kiro IUP (Hajdinjak et al. 2021). In several cases, researchers have designated such groupings as "genetic clusters," naming them after the type site or type genome. Villabruna cluster (Fu et al. 2016), Mal'ta cluster (Fu et al. 2016), and Goyet Q2 cluster (Villalba-Mouco et al. 2023) are examples of this pattern.

Linnaean-like names. "Australopithecine" was formed with the suffix appropriate for a Linnaean subfamily, Australopithecinae (Broom 1939). Although this is not valid in current classification, many researchers and educators continue to use this name in both research and public con-

texts. "Australopith" (Hallowell 1956) is commonly used today, which is derived from *Australopithecus* but is not properly formed for any Linnaean category. "Habiline" (Tobias 1965) and "erectine" (Sharma 1974) follow the pattern of "australopithecine" but both are derived from species names and not genus names. This pattern was popular during the 1960s and 1970s, with Phillip Tobias as a particularly productive author coining them.

In the twenty-first century it has been uncommon to develop new names for ancient groups that are based on analogy with Linnaean categories. Most researchers today have much less practical familiarity with Latin and Greek languages and the use of suffixes like "-ine" and "-oid" are more likely to connote formality rather than flexibility of usage. The history of hominin classification over the last half century has moved toward the use of names derived from languages that are spoken in the geographic region where a holotype was found. Analogies to "australopith," such as "ardipith" (Lieberman 2012) have rarely caught on, although Almécija and coworkers (2021) used "kenyapith" for the corresponding Miocene ape lineage.

Another way that researchers use Linnaean-like names is when writers make colloquial use of species names "bare," without the genus name attached. The common language use of species names like "habilis," "erectus," "naledi", and "afarensis" has become almost routine in popular science writing. This usage reflects spoken language. While the abbreviation of a long genus name to a single letter may have an economy in written text, in spoken language it is much simpler to omit the genus name entirely—a speaker will tend to say simply "africanus" instead of "A. africanus." It is rare to see this formulation in articles or monographs for specialist audiences, but more and more common for authors to use bare species names in books and articles written for a wider public.

Augmented names. Many researchers identify ancient populations by modifying a Linnaean species or genus name to specify a more restricted group than encompassed by the taxon name (Table 3). An example is "anatomically modern *Homo sapiens*," which denotes today's humans around the world in addition to some Late Pleistocene and late Middle Pleistocene fossil people. A Linnaean name may be modified by adding a geographic region, time period, or anatomical trait to delimit a group.

Where "anatomically modern" represents an increased specificity compared to the Linnaean alternative, "Middle Pleistocene *Homo*" is an augmented term that reduces specificity compared to Linnaean alternatives. Most authors have used this name as a synonym for "archaic humans," meaning early Neanderthals, *Homo heidelbergensis*, and archaic humans in Africa and China, whether they are *Homo longi*, Denisovans, *Homo bodoensis*, or something else. Authors who use the term "Middle Pleistocene *Homo*" may or may not mean to include Middle Pleistocene *H. erectus*, and few mean to include *Homo naledi*. In other words, this augmented name serves as a kind of grade signifier about which there is no consensus about classification.

Names based on an informal nickname or popular name. Human origins research has always had an outsized public presence compared to other areas of biology. Researchers may have public communication goals that are facilitated by names that are more familiar or easy to use by nonspecialists. From "Mrs. Ples" and "Handy Man" to "Turkana Boy" and "Kadanuumuu," researchers for a hundred years have given nicknames to hominin fossils, species, and populations (Riel-Salvatore and Pyne 2025). Before the 1960s most popular names were derived in some way from the site name or species attribution of a fossil. But the trends in science from the 1960s onward have encouraged specialists to think of more accessible names to connect fossils to society.

Nicknames or popular names sometimes aid public dissemination of research, and under some circumstances such names take on a life within research itself. The introduction of the term "hobbit" as a vernacular term for *Homo* floresiensis is an example of this phenomenon. Upon the 2003 discovery of the LB1 skeleton, Morwood introduced "hobbit" as a nickname for the LB1 skeleton, but within a short time researchers and other writers were using "hobbit" as a vernacular name for *Homo floresiensis* (reviewed in Goulden 2013). The name now regularly appears within peer-reviewed articles as a referent for the species, including the titles of many scientific journal articles (e.g., Jungers and Baab 2009; Meijer et al. 2010; Ouwendijk et al. 2014). At the same time, some researchers have been highly critical of the use of the term "hobbit" as a reference to ancient hominins, even suggesting it may be derogatory (Forth 2005).

A more recent example is "Dragon People" (Lóng rén, 龙人) (often English-language sources translate the term as "Dragon Man"), which was presented as a vernacular name for Homo longi (Bae et al. 2023; Ni et al. 2021). This is now increasingly used in scientific work (e.g., Delson and Stringer 2022; Feng et al. 2024). The name "Red Deer Cave People" (Curnoe 2012) also originated as a vernacular name based on the English translation of the Maludong site name; as noted above most Chinese language sources have instead used the regional name (Mengzi rén 蒙自人). After it became clear that the mtDNA of Denisova 3 was different from both Neanderthal and living humans known at the time, the team of researchers began to call the individual by the name "X-Woman" (Pääbo 2014). While this name was not referenced in the publication describing the results (Krause et al. 2010), it was widely disseminated in the popular press by members of the research group (e.g., Callaway, 2010; Sample, 2010). This informal name has not subsequently been used in scientific reports other than as an element of historical or biographical reviews.

THE LEGACY OF RACE CLASSIFICATION ON TODAY'S NOMENCLATURE

Classification of hominins has its origins in pre-Darwinian natural history. The interests of early naturalists and anthropologists, who knew next to nothing about fossil hominins and comparatively little about living nonhuman

TABLE 3. MIXED LINNAEAN/NON-LINNAEAN CLASSIFICATION TERMS IN USE IN HUMAN EVOLUTIONARY BIOLOGY.

Name	Extent	Linnaean categories represented	Sources
anatomically modern Homo sapiens	Global, Late Pleistocene and Holocene	Homo sapiens, or Homo sapiens sapiens	Brose and Wolpoff 1971
archaic Homo sapiens	Africa, Eurasia, Middle and Late Pleistocene	Homo sapiens, Homo neanderthalensis, Homo longi, Homo heidelbergensis, Homo antecessor, possibly others	Howells 1974
basal Homo sapiens	Africa, Eurasia	Homo sapiens	Stringer 2022
derived Homo sapiens	Worldwide	Homo sapiens	Stringer 2022
early Homo sapiens	Africa, Eurasia, Pleistocene	Homo sapiens, or more broadly defined	Hublin et al. 2017
early Homo	Africa, Early Pleistocene	Homo habilis, Homo rudolfensis, Homo erectus, Homo ergaster, and others	Krogman 1950
Middle Pleistocene Homo	Africa, Eurasia, Middle Pleistocene	Homo antecessor, Homo erectus, Homo heidelbergensis, Homo rhodesiensis, Homo sapiens, Homo naledi, Homo longi, Homo neanderthalensis, possibly others	Athreya and Hopkins 2021
East Asian Homo erectus	China and Indonesia, Early, Middle, and Late Pleistocene	Homo erectus	Holloway 1975
Georgian Homo erectus	Georgia, Early Pleistocene	Homo erectus, or Homo georgicus	Wu et al. 2004
African Homo erectus	Africa, Early Pleistocene	Homo erectus, or Homo ergaster	Wai-Ogosu 1974
Nesher Ramla Homo	Levant, Middle Pleistocene	Homo sapiens or Homo neanderthalensis	Hershkovitz et al. 2021

primates, focused strongly upon the classification of human races. Some names still used for ancient human populations were invented within the era of race classification, including "Neanderthal" and "Cro-Magnon," which were widely understood during the late nineteenth and early twentieth centuries as race identifiers. Other similar names were invented in the early history of paleoanthropology, such as the "Furfooz race" (Broca 1878), "Grimaldi race" (Keith 1912a), or "Boskops" (FitzSimons 1915). These examples are rarely seen today, but each of these and many others had currency for a time within academic sources and popular expositions of human origins. They sometimes reemerge. For example, the notion of a Boskops race had a long twentieth-century history that bubbled up in the 1950s and then emerged once again in popular science writing of the early twenty-first century (Hawks 2008; Morris 2022).

The name "modern human" also originated in race classification. This and related terms including "modern man," "modern types," and "modern races" were used during the nineteenth and twentieth centuries in several ways. "Modern" is a chronological signifier that anthropologists and naturalists at first used in the same way that today the term "extant" is used (e.g., Morton 1839). The writers of the nineteenth century considered for the first time the question of whether ancient people must derive from races that are still extant, or instead whether they represent races no longer existing in the world. The discovery of the Neanderthal skeleton in 1856 presented naturalists with an example of an ancient individual that some argued had come from an extinct group outside the envelope of today's racial variation (e.g., Davis 1864). Some anthropologists of the time used the term "modern races" to encompass the variation of living people, which they compared as a group to ancient skeletal remains (e.g., Broca 1868). By the early twentieth century, the term "modern man" was commonly understood to refer to the racial variation of living and recent people. Keith in particular (Keith 1912a; 1912b) was influential in the use of "modern man" as an identifier within Paleolithic archaeological contexts in contrast with Neanderthals.

Various non-Linnaean classifications for human races were formulated during the eighteenth and nineteenth centuries, notably including the work of Buffon (1749) and Blumenbach (1795). Cuvier (1828) was also influential and his scheme of three major races was widely used into the twentieth century. Yet some other writers during this time favored a Linnaean classification for human races. Linnaeus himself, in the 1758 edition of his Systema Naturae, applied four names for geographic varieties of humans within his formal taxonomic hierarchy as varieties of *Homo* sapiens: Americanus, Europaeus, Asiaticus, and Afer, in addition to two non-geographic varieties, Monstrosus and Ferus. Some nineteenth-century authors followed Linnaeus in applying Latin binomials to groups that were by then considered to be races (Bory de Saint-Vincent 1827; Hoffmann 1841). Others, like Latham (1850) or Morton (1844), proposed classifications that included a mixture of non-Linnaean population names and Linnaean-like groupings with Latin or Greek endings, such as Morton's "Negroid" race. Such pseudo-Linnaean terminology lent a veneer of erudition to the construction of races by early followers of Darwin-Huxley (1870), for example, coined the terms "Australoid" and "Mongoloid" after Morton's (1844, 1849) example, which were widely used thereafter.

Disagreements about the nature of human races influenced various nineteenth-century authors' use of nomenclature. The majority of naturalists and other authors argued for the unity of humankind, with races being varieties of a single species (e.g., Lawrence 1828; Prichard 1836). This view followed most eighteenth-century authorities including Linnaeus, Buffon, Blumenbach, and Kant (Greene 1954). But during the early nineteenth century, an opposing view developed that human races had been separately created or otherwise descended from distinct origins (e.g., Agassiz 1854; Gobineau 1853; Morton 1844; Nott 1844; Nott and Gliddon 1854), an incorrect theory known as polygenism. This latter group of authors included many who argued that the mixture of races was subject to diminished fertility or degeneration. For the most part, authors expounded these various views on the nature of human races using names that were not derived from Linnaean classification. However, some authors who argued for the specific disunity of humanity did propose species names for many human groups following Linnaean forms (e.g., Bory de St. Vincent 1827; Fischer 1829). Such formal Linnaean names for living races of humans virtually disappeared after the publication of Darwin's (1859) Origin of Species. Darwin (1859, 1873) used only non-Linnaean nomenclature for human races, as did Wallace (1864) and Haeckel (1868). Even so, the idea that race mixture was subject to diminished fertility continued among some authors into the later part of the century (e.g., Broca 1864; Knox 1862; Vogt 1864).

The discovery of the Neanderthal skeleton in 1856 presaged a new phase of classification. Anthropologists of this era began to accept that the ancient record includes human relatives much more different from living people than any of today's groups are from each other. From the naming of Homo neanderthalensis by William King (1864), there was always thereafter a strain of classification that promoted formal Linnaean names for ancient human relatives. In the period from 1890 to 1945, more than 110 Linnaean names were defined with hominin skeletal remains (Reed et al. 2023). Most of these today are considered invalid, many due to synonymy with either Homo sapiens or Homo neanderthalensis. This trend toward Latin binomials in this period did not replace the use of vernacular names. Formal Linnaean names, from *Pithecanthropus erectus* and *Sinanthropus* pekinensis to Eoanthropus dawsoni and Homo capensis, all had their vernacular equivalents—Java Man, Peking Man, Piltdown Man, and the Boskop race.

After the Second World War, systematists working in the tradition of the New Evolutionary Synthesis argued for reducing the number of formal Linnaean species and genera recognized in the human lineage. The most prominent example was Ernst Mayr, who proposed that the number of formal hominin species be reduced to three, all within the genus Homo-Homo sapiens, Homo erectus, and Homo transvaalensis (Mayr 1950). Mayr's ideas about the utility of these particular hominin species and genus names is no longer relevant to our current understanding of the hominin phylogeny, and many later authors argued that his scheme oversimplified the record known at the time. Certainly, the subsequent record of discovery and burgeoning evidence of the diversity of fossil hominins has provided abundant examples of species-level differences that substantiate a more complex tree than appreciated by Mayr at midcentury.

Meanwhile, through the same period up to the 1980s and 1990s, many anthropologists considered races as units of analysis. The names attributed to races by eighteenth-and nineteenth-century naturalists and anthropologists were widely applied in twentieth-century research. Such names as "Caucasian" (Blumenbach 1776), "Mongoloid" (Huxley 1870), "Negroid" (Morton 1844), or "Australoid" (Huxley 1870) were among the large array of names invented for the purpose of racial classification of humankind that were commonly part of twentieth-century scientific literature in human origins. Governments and scientists often imposed race classifications upon Indigenous or minoritized communities. A wide range of such racializing names were commonly used in human evolution research during the twentieth century.

To many peoples, racialized nomenclature is and was derogatory or unwelcome. It has long been recognized that racialized classification of human groups is inaccurate and may have adverse implications (Braun et al., 2007; Caulfield et al., 2009; Race, Ethnicity, and Genetics Working Group, 2005; Sankar et al., 2007). Yet the use of racialized classi-

fication and associated names has remained widespread. For example, at the time of this writing Google Scholar lists approximately 53,000 research articles published in 2022 including the name "Caucasian" and approximately 1750 including the name "Mongoloid." While a fraction of these articles are critical histories or (in the case of Caucasian) references to a geographic region, the vast majority cover subjects in human biology, genetics, or medicine. The abandonment of racialized terminology has proceeded further in human evolution, archaeology, and archaeogenomics, where such names are rarely used today, aside from the citation of historical uses of such terms. Such names have therefore not been included within Tables 1 or 2.

OPPORTUNITIES AND CHALLENGES OF DNA EVIDENCE FOR CLASSIFICATION

Names for populations identified from DNA evidence are some of the newest additions to a long tradition of non-Linnaean classification in paleoanthropology. DNA and other biomolecular lines of evidence have highlighted some challenges of communicating accurately about past hominin populations. In many cases, the ancient DNA has confirmed substantial gene flow between groups and their contribution to the genetic complement of living people (Fu et al. 2015; Green et al. 2010; Hawks et al. 2014; Reich et al. 2010; Slon et al. 2018). Older fossils sometimes preserve protein evidence, which has also begun to characterize biomolecular diversity that may not be evident from the morphology of fragmentary fossils (Madupe et al. 2023).

One challenge is finding ways to discuss genetic and morphological diversity when the connection between the two is not yet known. An example of this issue is the identity of Denisovans (Reich et al. 2010), a population identified initially on the basis of genomic data and only recently connected with fossils that preserve substantial cranial and mandibular morphological evidence (Chen et al. 2019; Fu et al. 2025; Tsutaya et al. 2025). Adding to results from ancient DNA, new modes of analysis of genomes from living people have led researchers to identify possible "ghost populations" that are ancestral to later populations but themselves not attested from ancient DNA evidence (Durvasula and Sankararaman 2020; Rogers et al. 2020). In both the cases of the Denisovans and African "ghost archaics" and "ghost moderns" (Lipson et al. 2020), it is probable that these groups identified from DNA inference will eventually be connected with one or more known fossils with identifiable morphological traits. But until such connections can be tested, researchers need clear ways to communicate about groups defined by DNA and groups defined by fossil morphology without confusing them.

A second challenge arises when a population that has previously been defined by geographic or temporal criteria is found to have unexpected genetic heterogeneity. The naming of the "Altai Neanderthal" (Prüfer et al. 2014) and the "Thorin lineage" of Neanderthals (Slimak et al. 2024) are recent examples that followed recognition of heterogeneity among Neanderthal genomes. One recent study combined ancient and modern DNA evidence for the Denisovans to

assess the structure of this ancient group of populations. Genomic segments identified as Denisovan-like within the ancestry of living research participants of the Indonesian Genome Project suggest a deep structure in comparison to the Denisova 3 genome. Jacobs and collaborators (2019) introduced a numerical scheme for the ancestral Denisovan populations: D1, D2, and D3 populations.

A third challenge is communicating about the common ancestors of genetic lineages. For example, the population ancestral to both Neanderthal and Denisovan lineages has no known fossil or genetic representatives but is inferred to have existed between around 700,000 and 500,000 years ago. Rogers and coworkers (2020) coined the portmanteau name "Neandersovan" for this common ancestral population. Disotell (2006) likewise coined the name "chumanzee" for the last common ancestor of *Homo* and *Pan*, which also has no presently known fossil representative. Such examples illustrate ways that specialists in DNA analysis have found it expedient to rely on non-Linnaean classification terms to address these communication challenges.

In 2014, Prüfer and coworkers observed that some aspects of the Denisova 3 genome suggested gene flow from a deeply diverged source population, more distantly related to the Denisovans than either Neanderthals or modern humans are. Those authors used the word "archaic" for this source population. Sánchez-Quinto (2014) introduced the term "super archaic" [sic] for this population, and that term—usually now spelled as superarchaic—has now been widely adopted (e.g., Rogers et al. 2020). Prior to 2014 this term rarely appeared in academic sources, but it was sometimes used for other concepts in historical linguistics (e.g., Frolov 1998) and in political science (e.g., Baudrillard 1989).

An additional challenge is not unique to DNA evidence but is emerging with DNA due to the high intensity of sampling from some sites. It is very common in paleoanthropology to use the name of a type site as a name for a population. This parallels the practice in archaeology to use a type site as a name for an industry or artifact type. But this practice can lead to the kind of confusion that may result from the use of a type site as the name for an ancient population given that the type site may over time have been home to *different* populations. For example, this potential confusion arose with the ancient DNA analysis of Denisova 5. This fossil is a pedal phalanx described by Mednikova (2011) and ancient DNA at high coverage from Denisova 5 was reported by Prüfer and coworkers (2014). This toe did not come from a population similar to Denisova 3 or 4; instead, the nuclear and mtDNA sequences from this specimen aligned it more closely with Neanderthals. In the publication describing the genomic results, the designation Denisova 5 was not used, and the individual was given a population-level designation—the "Altai Neanderthal" (Prüfer et al. 2014).

WHEN SHOULD NON-LINNAEAN NAMES BE FORMALIZED?

Many specialists in human evolution have favored wider application of formal Linnaean nomenclature. Instead of "Neanderthal," many favor Homo neanderthalensis (Meneganzin and Bernardi 2023; Meneganzin and Stringer 2024). Instead of "Middle Pleistocene Homo," some would offer Homo heidelbergensis (Buck and Stringer 2014), others Homo bodoensis (Roksandic et al. 2022a; 2022b). Instead of "robust australopith," many urge the wider use of Paranthropus (Wood and Schroer 2017). These three examples illustrate different kinds of challenges in classification—the first a question of species boundaries, the second a question of appropriateness of holotype specimens, the third a question of monophyly or paraphyly of a group of species. In each of these situations, there are researchers who prefer non-Linnaean alternatives. Using a Linnaean name in these contexts does not resolve the questions; it begs them. The Linnaean species or genus names presume the validity of a taxon, which may be precisely what many researchers

One of the main reasons why researchers use non-Linnaean names in paleoanthropology is to refer to groups below the species rank. Over the years some researchers have considered whether a formal Linnaean subspecies taxonomy might be appropriate for some hominin groups. Applying subspecies names to hominin groups has historical precedent. Human evolution researchers assimilated the Evolutionary Synthesis during the 1940s and 1950s, prompting the demotion of many generic and species-level Linnaean names to subspecies names. For example, Robinson (1954) simplified the classification of South African early hominins from five species and three genera down to two genera with two species, each having two subspecies. Dobzhansky (1944) suggested Homo sapiens neanderthalensis as a designation for the Neanderthals. Campbell (1963) reviewed species and genus-level taxonomic nomenclature for hominins and proposed reducing many species to subspecies including *Homo erectus pekinensis*, *Homo erectus mau*ritanicus, Homo sapiens soloensis, Homo sapiens steinheimensis, and Homo sapiens rhodesiensis. Some of these subspecies of H. sapiens were instead attributed to H. erectus by Howells (1966). Both Homo sapiens neanderthalensis and Homo sapiens sapiens were commonly used within the textbooks of the 1970s and 1980s. Groves (1989) likewise made extensive use of subspecific names as applied to variation among Middle Pleistocene fossil samples attributed to *Homo*.

In this century some researchers have moved toward defining new Linnaean subspecies for fossil hominin samples. Examples of this trend include *Ardipithecus ramidus kadabba* (Haile-Selassie 2001), *Homo sapiens idaltu* (White et al. 2003), and *Paranthropus robustus ukusa* (Martin et al. 2024). In the case of *Ar. ramidus kadabba*, further research on the fossil material suggested an elevation to species rank (Haile-Selassie 2004). Another trinomial under discussion during the last few years has been *Homo sapiens daliensis* (Wu 1981). During this century some authors suggested that this subspecies should be elevated to species rank (Etler 2004). Bae and coworkers (2023) consider *H. sapiens daliensis* to have been defined conditionally and therefore unavailable (also see Reed 2025, this volume). From these examples it is apparent that while the formal Linnaean clas-

sification may have well-defined rules, subspecies names within the Linnaean classification still can suffer the same problem of instability as non-Linnaean names. Meanwhile, formal subspecies names are much less flexible than non-Linnaean names. Indeed, one reason why some authors have begun to define formal names at the subspecies rank is precisely to prevent future flexibility in nomenclature by "locking in" the formal name, in the event that later evidence supports an elevation to species rank.

Biomolecular data from ancient sites has the potential to shift taxonomic practices by providing much more detailed evidence relevant to the classification of ancient remains. The importance of such evidence is not unique to extinct populations, nor is it unique to hominins. Many taxonomists who specialize in other branches of the Tree of Life have advocated for species diagnoses based on DNA sequence information (Hongsanan et al. 2018; Palmer et al. 2022; Tautz et al. 2003; van Regenmortel and Mahy 2004) or types defined in part or whole by DNA characters (Renner 2016; Rheindt et al. 2023). Researchers working within the ICZN have applied DNA barcoding and other genetic data as part of species diagnoses for more than a decade. Under a practice known as "turbo taxonomy" (Butcher et al. 2012), many species have been diagnosed by simple publication of images of a holotype specimen, basic holotype specimen information, and a DNA barcode reference (Fernandez-Triana 2022).

It is doubtful that hominin classification requires "turbo" approaches. Nonetheless small bone fragments or sediment samples from archaeological sites sometimes represent surprisingly deep population diversity when ancient DNA is sampled (Reich et al. 2010). In light of this growing biomolecular evidence of diversity it is remarkable that scientific presentations of such data from ancient hominins have thus far been limited to non-Linnaean nomenclature.

Would it be a good idea to move toward formal Linnaean names for groups of hominins that have been defined mainly from DNA variation? The basic principle underlying Mayr's argument for taxonomic parsimony bears close consideration with respect to the nomenclature of hominins.

"The formal application of generic and specific names simulates a precision that often does not exist. To give the impression of an unjustified precision is as much of a methodological error as to make calculations to the fifth decimal when the accuracy of the original data extends only to the first decimal." (Mayr 1951: 115)

Unquestionably whole genome evidence, and even mtDNA sequences by themselves, can provide very precise genetic information about an individual. But such information from an individual requires interpretation to make inferences about the variation of a population or species. As has been evident across the last decade of discovery, these interpretations can shift markedly. The researchers who proposed the term Denisovan (Reich et al. 2010) were prescient in their choice to use a non-Linnaean term, which

has been widely adopted without substantial controversy.

CONCLUSION

Nomenclature in human evolution research must enable accurate communication among specialists in paleontology, genetics, and archaeology. In each of these fields many specialists have had substantial cross-disciplinary training and research experience and yet may have never had any formal training in biological systematics. Researchers use non-Linnaean names because they are flexible, and that flexibility has many advantages for communication. At the same time, flexibility can reduce the clarity of research, especially when research is interdisciplinary.

Classification inevitably touches upon both knowledge and uncertainty. The nomenclature of human evolution should help researchers to talk clearly about what they know, and equally clearly about what they do not yet know.

A survey of non-Linnaean names in hominin evolution research helps to illustrate that such names fulfil many different purposes. Researchers use non-Linnaean names to mark areas of uncertainty and to pave consensus across disciplinary boundaries. Most specialists work with at least some ancient populations that were not differentiated from each other at the species or subspecies level, for which Linnaean names are not appropriate. Many researchers use informal terms for fossil samples or populations when the research questions may bridge different categories of evidence. The flow of naming practices is not a one-way avenue from researchers to the public. Names that once originated for public communication often become part of research analyses.

In recent years many authors have discussed problems with formal taxonomic practices in human evolutionary biology. Challenges include the sheer proliferation of synonymous names (Reed et al. 2023), the persistence of names that may be offensive to scientists and the public due to their historical referents (Athreya and Hopkins 2021; Roksandic et al. 2022a; 2022b), and the mismatch between naming practices and diagnosis under varied species concepts (Martin et al., 2024). Due to the ICZN, paleoanthropology is stuck with many Linnaean names that reference odious historic figures, obsolete place names, or inaccurate phylogenetic understandings. The recognition of ancient populations from biomolecular evidence has joined these other problems of classification and nomenclature (Eisenmann et al. 2018).

Non-Linnaean names do not solve all these problems. Still, the flexibility of names like "Neanderthal" has enabled their meanings to shift with the times. The absence of governance has enabled researchers to ignore or discard outdated or racially charged names that no longer fit our best scientific understanding. Non-Linnaean names are a pragmatic way to classify many ancient hominin groups and are likely to remain relevant long into the future.

ACKNOWLEDGEMENTS

This article was prepared after my participation in the sym-

posium, "Meet the Chibanians: Hominin Taxonomy in the Middle and Early Late Pleistocene," organized by Mirjana Roksandic and Christopher Bae. The ideas in this contribution benefited greatly from the interactions and insights of symposium participants, and I thank them for their willingness to share and critique ideas freely.

DATA AVAILABILITY

All data used in the writing of this article are included within the article itself.



This work is distributed under the terms of a <u>Creative Commons Attribution-NonCommer-cial 4.0 Unported License</u>.

REFERENCES

Athreya, S., Hopkins, A., 2021. Conceptual issues in hominin taxonomy: *Homo heidelbergensis* and an ethnobiological reframing of species. Am. J. Phys. Anthropol. 175(S72), 4–26. https://doi.org/10.1002/ajpa.24330

Bae, C.J., Aiello, L., Hawks, J., Kaifu, Y., Lindal, J., Martinón-Torres, M., Ni, X., Posth, C.,

Radović, P., Reed, D., Schroeder, L., Schwartz, J.H., Silcox, M.T., Welker, F., Wu, X.J., Zanolli, C., Roksandic, M., 2024. Moving away from "the Muddle in the Middle" toward solving the Chibanian puzzle. Evol. Anthropol. 33(1), e22011.

Bae, C. J., Liu, W., Wu, X., Zhang, Y., Ni, X., 2023. "Dragon man" prompts rethinking of Middle Pleistocene hominin systematics in Asia. Innovation 4(6), 100527. https://doi.org/10.1016/j.xinn.2023.100527

Baudrillard, J., 1989. Politics of performance: Montand, Coluche= Le pen? New Polit. Sci. 8(1–2), 23–28.

Bellwood, P., 2017. First Islanders: Prehistory and Human Migration in Island Southeast Asia. John Wiley & Sons, New York.

Bennett, B.C., Balick, M.J., 2014. Does the name really matter? The importance of botanical nomenclature and plant taxonomy in biomedical research. J. Ethnopharmacol. 152(3), 387–392. https://doi.org/10.1016/j.jep.2013.11.042

Bennett, E.A., Crevecoeur, I., Viola, B., Derevianko, A.P., Shunkov, M.V., Grange, T., Maureille, B., Geigl, E.-M., 2019. Morphology of the Denisovan phalanx closer to modern humans than to Neanderthals. Sci. Adv. 5(9), eaaw3950. https://doi.org/10.1126/sciadv.aaw3950

Birney, E., Inouye, M., Raff, J., Rutherford, A., Scally, A., 2021. The language of race, ethnicity, and ancestry in human genetic research (arXiv:2106.10041). https://doi.org/10.48550/arXiv.2106.10041

Blumenbach, J.F., 1796. Abbildungen naturhistorischer Gegenstände. Johann Christian Dieterich, Göttingen.

Blumenbach, J.F., 1795. De generis humani varietate nativa (3rd ed.). Vandenhoek and Ruprecht, Göttingen

Bölsche, W., 1909. Der Mensch der Vorzeit. Kosmos, Gesellschaft der Naturfreunde, Stuttgart.

Bory de Saint-Vincent, J.B.G.M., 1827. L'homme (homo) essai zoologique sur le genre humain. Rey et Gravier,

Paris.

- Braun, L., Fausto-Sterling, A., Fullwiley, D., Hammonds, E.M., Nelson, A., Quivers, W., Reverby, S.M., Shields, A.E., 2007. Racial categories in medical practice: how useful are they? PLoS Medicine 4(9), e271. https://doi.org/10.1371/journal.pmed.0040271
- Broca, P., 1868. On the crania and bones of Les Eyzies; or, the ancient cave-men of Perigord. Anthropol. Rev. 6(23), 408–411. https://doi.org/10.2307/3025031
- Broca, P., 1878. Translation of the greater part of the address delivered by M. Broca, President, at the opening meeting of the French Association for the Advancement of the Sciences, at the Havre Congress, 1877. J. Anthropol. Inst. Gt. Brit. Ire. 7, 187–200. https://doi.org/10.2307/2841388
- Broom, R., 1939. On the affinities of the South African Pleistocene anthropoids. S. Afr. J. Sci. 36, 408–411.
- Buck, L.T., Stringer, C.B. (2014). *Homo heidelbergensis*. Curr. Biol. 24(6), R214–R215. https://doi.org/10.1016/j.cub.2013.12.048
- Buffon, G.-L.L., Compte de., 1749. Variétés dans l'espèce humaine. In *Histoire naturelle, générale et particulière*: Vol. III. Imprimerie Royale, Paris, pp. 371–530.
- Burmeister, S., 2021. Does the concept of genetic ancestry reinforce racism? A commentary on the discourse practice of archaeogenetics. TATuP Zeitschrift Für Technikfolgenabschätzung in Theorie Und Praxis / J. Technol. Assess. Theory Practice 30(2), 41–46. https://doi.org/10.14512/tatup.30.2.41
- Butcher, B.A., Smith, M.A., Sharkey, M.J., Quicke, D.L.J., 2012. A turbo-taxonomic study of Thai *Aleiodes* (*Aleiodes*) and *Aleiodes* (*Arcaleiodes*) (Hymenoptera: Braconidae: Rogadinae) based largely on COI barcoded specimens, with rapid descriptions of 179 new species. Zootaxa 3457(1), Article 1. https://doi.org/10.11646/zootaxa.3457.1.1
- Caldararo, N., 2016. Denisovans, Melanesians, Europeans, and Neandertals: the confusion of DNA assumptions and the biological species concept. J. Mol. Evol. 83(1), 78–87. https://doi.org/10.1007/s00239-016-9755-7
- Callaway, E., 2010. Meet X-woman: a possible new species of human. New Sci., March. https://www.newscientist.com/article/dn18699-meet-x-woman-a-possible-new-species-of-human/
- Campbell, B., 1963. Quantitative taxonomy and human evolution. In Washburn, S.L. (Ed.), Classification and Human Evolution. Routledge, New York, 50–74.
- Caulfield, T., Fullerton, S.M., Ali-Khan, S.E., Arbour, L., Burchard, E.G., Cooper, R.S., Hardy, B.-J., Harry, S., Hyde-Lay, R., Kahn, J., Kittles, R., Koenig, B.A., Lee, S.S., Malinowski, M., Ravitsky, V., Sankar, P., Scherer, S.W., Séguin, B., Shickle, D., ... Daar, A.S., 2009. Race and ancestry in biomedical research: exploring the challenges. Genome Med. 1(1), 8. https://doi.org/10.1186/gm8
- Chen, F., Welker, F., Shen, C.-C., Bailey, S.E., Bergmann, I., Davis, S., Xia, H., Wang, H., Fischer, R., Freidline, S.E., Yu, T.-L., Skinner, M.M., Stelzer, S., Dong, G., Fu,

- Q., Dong, G., Wang, J., Zhang, D., Hublin, J.-J., 2019. A late Middle Pleistocene Denisovan mandible from the Tibetan Plateau. Nature 569, Article 7756. https://doi.org/10.1038/s41586-019-1139-x
- Colwell-Chanthaphonh, C., 2009. Myth of the Anasazi: archaeological language, collaborative communities, and the contested past. Pub. Archaeol. 8(2–3), 191–207. https://doi.org/10.1179/175355309X457222
- Conard, N.J., Serangeli, J., Böhner, U., Starkovich, B.M., Miller, C.E., Urban, B., Van Kolfschoten, T., 2015. Excavations at Schöningen and paradigm shifts in human evolution. J. Hum. Evol. 89, 1–17. https://doi.org/10.1016/j.jhevol.2015.10.003
- Crawfurd, J., 1861. On the classification of the races of man. Trans. Ethnol. Soc. London 1, 354–378. https://doi.org/10.2307/3014207
- Curnoe, D., 2012, March 14. Defining 'human' new fossils provide more questions than answers. Conversation. http://theconversation.com/defining-human-new-fossils-provide-more-questions-than-answers-5847
- Davis, J.B., 1864. The Neanderthal Skull: Its Peculiar Conformation Explained Anatomically. Taylor & Francis, London.
- de Boismont, A.B., Manning, H.J., 1860. On the unity of the human species. J. Psychol. Med. Mental Pathol. (London, England: 1848) 13(20), 458–484.
- Delson, E., Stringer, C., 2022. The naming of *Homo bodoensis* by Roksandic and colleagues does not resolve issues surrounding Middle Pleistocene human evolution. Evol. Anthropol. 31(5), 233–236. https://doi.org/10.1002/evan.21950
- Derevianko, A.P., 2010. *Homo altaiensis*? Sci. First Hand 25(1), 8–10.
- Derevianko, A.P., 2011. Upper Paleolithic in Africa and Eurasia and the Formation of Man of Modern Anatomical Type. Institute of Archaeology and Ethnography of the Siberian Branch of the Russian Academy of Sciences, Novosibirsk.
- Derevianko, A.P., Shunkov, M.V., 2011. Anthropogenesis and colonization of Eurasia by archaic populations. Formation of anatomically modern human. In: Derevianko, A.P., Shunkov, M.V. (Eds.), Characteristic Features of the Middle to Upper Paleolithic Transition in Eurasia: Proceedings of the International Symposium "Characteristic features of the Middle to Upper Paleolithic Transition in Eurasia—Development of Culture and Evolution of *Homo* genus," July 4–10, 2011, Denisova Cave, Altai. Pub. Dept. of the Institute of Archaeology and Ethnography SB RAS, Novosibirsk, pp. 50–74.
- Disotell, T.R., 2006. "Chumanzee" evolution: the urge to diverge and merge. Genome Biol. 7(11), 240. https://doi.org/10.1186/gb-2006-7-11-240
- Dobzhansky, T., 1963. Genetic entities in hominid evolution. In Washburn, S.L. (Ed.), *Classification and Human Evolution*. Routledge, New York, pp. 347–362.
- Durvasula, A., Sankararaman, S., 2020. Recovering signals of ghost archaic introgression in African populations. Sci. Adv. 6(7), eaax5097. https://doi.org/10.1126/sciadv.

aax5097

- Eisenmann, S., Bánffy, E., van Dommelen, P., Hofmann, K.P., Maran, J., Lazaridis, I., Mittnik, A., McCormick, M., Krause, J., Reich, D., Stockhammer, P.W., 2018. Reconciling material cultures in archaeology with genetic data: the nomenclature of clusters emerging from archaeogenomic analysis. Sci. Rep. 8(1), 13003. https://doi.org/10.1038/s41598-018-31123-z
- Feinman, G.M., Neitzel, J.E., 2020. Excising culture history from contemporary archaeology. J. Anthropol. Archaeol. 60, 101230. https://doi.org/10.1016/j.jaa.2020.101230
- Feng, X., Lu, D., Gao, F., Fang, Q., Feng, Y., Huang, X., Tan, C., Zhou, H., Li, Q., Zhang, C., Stringer, C., Ni, X., 2024. The phylogenetic position of the Yunxian cranium elucidates the origin of Dragon Man and the Denisovans (p. 2024.05.16.594603). bioRxiv. https://doi.org/10.1101/2024.05.16.594603
- Fernandez-Triana, J.L., 2022. Turbo taxonomy approaches: lessons from the past and recommendations for the future based on the experience with Braconidae (Hymenoptera) parasitoid wasps. ZooKeys 1087, 199–220. https://doi.org/10.3897/zookeys.1087.76720
- Fischer, J.B., Fischer, J.-B., 1829. Synopsis mammalium. J. G. Cotta, Stuttgart.
- Fitzsimons, F.W., 1915. Palæolithic man in South Africa. Nature 95(2388), 615–616. https://doi.org/10.1038/095615c0
- Forth, G., 2005. Hominids, hairy hominoids and the science of humanity. Anthropol. Today 21(3), 13–17. https://doi.org/10.1111/j.0268-540X.2005.00353.x
- Frolov, S., 1998. No return for Shulammite: reflections on Cant 7, 1. Z. Alttest. Wiss. 110(2), 256.
- Fu, Q., Cao, P., Dai, Q., Bennett, E.A., Feng, X., Yang, M.A., Ping, W., Pääbo, S., Ji, Q., 2025. Denisovan mitochondrial DNA from dental calculus of the >146,000-year-old Harbin cranium. Cell 188, 3919–3929. https://doi.org/10.1016/j.cell.2025.05.040
- Fu, Q., Posth, C., Hajdinjak, M., Petr, M., Mallick, S., Fernandes, D., Furtwängler, A., Haak, W., Meyer, M., Mittnik, A., Nickel, B., Peltzer, A., Rohland, N., Slon, V., Talamo, S., Lazaridis, I., Lipson, M., Mathieson, I., Schiffels, S., ... Reich, D., 2016. The genetic history of Ice Age Europe. Nature 534(7606), 200–205. https://doi.org/10.1038/nature17993
- Fuhlrott, J.C., 1865. Der fossile mensch aus dem Neanderthal und sein verhältniss zum alter des menschengeschlechts. W. Falk & Volmer, Duisburg.
- Gee, H., 2004. Kicking the hobbit habit. Nature. https://doi.org/10.1038/news041108-4
- Gliboff, S., 2014. Ascent, descent, and divergence: Darwin and Haeckel on the human family tree. Konturen 6, 103–130. https://doi.org/10.5399/uo/konturen.7.0.3523
- Goulden, M., 2013. Hobbits, hunters and hydrology: images of a "missing link," and its scientific communication. Public Underst. Sci. 22(5), 575–589. https://doi.org/10.1177/0963662511419627
- Greene, J.C., 1954. Some early speculations on the origin of human races. Am. Anthropol. 56(1), 31–41.
- Gregory, W.K., Hellman, M., 1938. Evidence of the Aus-

- tralopithecine man-apes on the origin of man. Science 88(2296), 615–616. https://doi.org/10.1126/science.88.2296.615
- Griffiths, S., Carlin, N., Edwards, B., Overton, N., Johnston, P., Thomas, J., 2023. Events, narrative and data: why new chronologies or ethically Bayesian approaches should change how we write archaeology. J. Social Archaeol. 23(2), 173–192. https://doi.org/10.1177/14696053231153499
- Groves, C.P., 1989. A Theory of Human and Primate Evolution. Clarendon Press, Oxford.
- Hajdinjak, M., Mafessoni, F., Skov, L., Vernot, B., Hübner, A., Fu, Q., Essel, E., Nagel, S., Nickel, B., Richter, J., Moldovan, O.T., Constantin, S., Endarova, E., Zahariev, N., Spasov, R., Welker, F., Smith, G.M., Sinet-Mathiot, V., Paskulin, L., ... Pääbo, S., 2021. Initial Upper Palaeolithic humans in Europe had recent Neanderthal ancestry. Nature 592(7853), 253–257. https://doi.org/10.1038/s41586-021-03335-3
- Hall, E.R., 1946. Zoological subspecies of man at the peace table. J. Mammal. 27(4), 358–364. https://doi.org/10.2307/1375342
- Hallowell, A.I., 1956. The structural and functional dimensions of a human existence. Q. Rev. Biol. 31(2), 88–101.
- Hammer, M.F., Zegura, S.L., 2002. The human Y chromosome haplogroup tree: nomenclature and phylogeography of its major civisions. Ann. Rev. Anthropol. 31, 303–321. https://doi.org/10.1146/annurev.anthro.31.040402.085413
- Hawks, J., 2008, March 30. The "amazing" Boskops. John Hawks Weblog. https://johnhawks.net/weblog/the-amazing-boskops/
- Hebert, P.D.N., Cywinska, A., Ball, S.L., deWaard, J.R., 2003. Biological identifications through DNA barcodes. Proc. Royal Soc. B 270(1512), 313–321. https://doi.org/10.1098/rspb.2002.2218
- Heyd, V., 2017. Kossinna's smile. Antiquity 91(356), 348–359. https://doi.org/10.15184/aqy.2017.21
- Hoffmann, K.F.V., 1841. Hertha, Hand- und Hausbuch der Erd-, Länder-Völker- und Staatenkunde. Stettin'sche Buchhandlung, Ulm.
- Holloway, R.L., 2011. Early hominid endocasts: volumes, morphology, and significance for hominid evolution. In Tuttle, R.L. (Ed.), Primate Functional Morphology and Evolution. De Gruyter Mouton, Berlin, pp. 393–416. https://doi.org/10.1515/9783110803808.393
- Hongsanan, S., Jeewon, R., Purahong, W., Xie, N., Liu, J.-K., Jayawardena, R.S., Ekanayaka, A.H., Dissanayake, A., Raspé, O., Hyde, K.D., Stadler, M., Peršoh, D., 2018. Can we use environmental DNA as holotypes? Fungal Divers. 92(1), 1–30. https://doi.org/10.1007/s13225-018-0404-x
- Hooton, E.A., 1934. Apes, men and teeth. Sci. Mon. 38(1), 24–34.
- Howell, F.C., 1957. The evolutionary significance of variation and varieties of "Neanderthal" man. Q. Rev. Biol. 32(4), 330–347. https://doi.org/10.1086/401978
- Howell, F.C., 1999. Paleo-demes, species clades, and ex-

- tinctions in the Pleistocene hominin record. J. Anthropol. Res. 55(2), 191–243. https://doi.org/10.1086/jar.55.2.3631209
- Howells, W.W., 1974. Neanderthals: names, hypotheses, and scientific method. Am. Anthropol. 76(1), 24–38. https://doi.org/10.1525/aa.1974.76.1.02a00040
- Howells, W.W., 1980. *Homo erectus* who, when and where: a survey. Am. J. Phys. Anthropol. 23(S1), 1–23. https://doi.org/10.1002/ajpa.1330230503
- Huxley, T.H., 1870. On the geographical distribution of the chief modifications of mankind. J. Ethnol. Soc. London (1869-1870), 2(4), 404–412. https://doi.org/10.2307/3014371
- Jacobs, G.S., Hudjashov, G., Saag, L., Kusuma, P., Darusallam, C.C., Lawson, D.J., Mondal, M., Pagani, L., Ricaut, F.-X., Stoneking, M., Metspalu, M., Sudoyo, H., Lansing, J.S., Cox, M.P., 2019. Multiple deeply divergent Denisovan ancestries in Papuans. Cell 177(4), 1010-1021.e32. https://doi.org/10.1016/j.cell.2019.02.035
- Ji, Q., Wu, W., Ji, Y., Li, Q., Ni, X., 2021. Late Middle Pleistocene Harbin cranium represents a new *Homo* species. Innovation 2(3), 100132. https://doi.org/10.1016/j.xinn.2021.100132
- Jungers, W., Baab, K., 2009. The geometry of hobbits: *Homo floresiensis* and human evolution. Significance 6(4), 159–164. https://doi.org/10.1111/j.1740-9713.2009.00389.x
- Keith, A., 1912a. Ancient Types of Man. Harper, London. Keith, A., 1912b. Certain phases in the evolution of man. Br. Med. J. 1(2674), 734–737.
- Krantz, G.S., 1993. The subspecies of *Homo erectus*. Hum. Evol. 8(4), 275–279. https://doi.org/10.1007/BF02438117
- Krause, J., Fu, Q., Good, J.M., Viola, B., Shunkov, M.V., Derevianko, A.P., Pääbo, S., 2010. The complete mitochondrial DNA genome of an unknown hominin from southern Siberia. Nature 464(7290), 894–897. https://doi.org/10.1038/nature08976
- Krogman, W.M., 1950. Concluding remarks of the chairman. Cold Spring Harb. Symp. Quant. Biol. 15, 119–121. https://doi.org/10.1101/SQB.1950.015.01.014
- Lawrence, S.W., 1828. Lectures on Physiology, Zoology, and the Natural History of Man: Delivered at the Royal College of Surgeons. Foote and Brown, London.
- Leakey, L.S.B., 1935. The Stone Age Races of Kenya. Oxford University Press, H. Milford, Oxford.
- Lieberman, D.E., 2012. Those feet in ancient times. Nature 483(7391), 550–551. https://doi.org/10.1038/483550a
- Linnaeus, C., 1758. Systema Naturae (10th ed.). Laurentius Salvius, Stockholm.
- Lurie, E., 1954. Louis Agassiz and the Races of Man. Isis 45(3), 227–242.
- Mallick, S., Micco, A., Mah, M., Ringbauer, H., Lazaridis, I., Olalde, I., Patterson, N., Reich, D., 2024. The Allen Ancient DNA Resource (AADR) a curated compendium of ancient human genomes. Sci. Data 11(1), 182. https://doi.org/10.1038/s41597-024-03031-7
- Marks, J., 2019. Naming the sacred ancestors: taxonomic reification and Pleistocene genomic narratives. In Porr, M., Matthews, J. (Eds.), Interrogating Human Origins:

- Decolonisation and the Deep Human Past. Routledge, New York.
- Martin, J.M., Leece, A.B., Baker, S.E., Herries, A.I.R., Strait, D.S., 2024. A lineage perspective on hominin taxonomy and evolution. Evol. Anthropol. 33(2), e22018. https://doi.org/10.1002/evan.22018
- Mayr, E., 1963. The taxonomic evaluation of fossil hominids. In Washburn, S.L. (Ed.), Classification and Human Evolution. Routledge, New York, pp. 332–346.
- Mednikova, M., 2011. A proximal pedal phalanx of a hominid from Denisova Cave, the Altai. Archaeol. Ethnogr. Anthropol. Eurasia 1, 129–138.
- Mednikova, M.B., 2011. A proximal pedal phalanx of a Paleolithic hominin from Denisova cave, Altai. Archaeol. Ethnogr. Anthropol. Eurasia 39(1), 129–138. https://doi.org/10.1016/j.aeae.2011.06.017
- Mednikova, M.B., Dobrovolskaya, M.V., Viola, B., Lavrenyuk, A.V., Kazansky, P.R., Shklover, V.Y., Shunkov, M.V., Derevianko, A.P., 2013. A micro computerized tomography (X-RAY MICROSCOPY) of the hand phalanx of the Denisova Girl*. Archaeol. Ethnogr. Anthropol. Eurasia 41(3), 120–125. https://doi.org/10.1016/j.aeae.2014.03.015
- Meijer, H.J.M., van den Hoek Ostende, L.W., van den Bergh, G.D., de Vos, J., 2010. The fellowship of the hobbit: the fauna surrounding *Homo floresiensis*. J. Biogeogr. 37(6), 995–1006. https://doi.org/10.1111/j.1365-2699.2010.02308.x
- Meneganzin, A., Bernardi, M., 2023. Were Neanderthals and *Homo sapiens* 'good species'? Quatern. Sci. Rev. 303, 107975. https://doi.org/10.1016/j.quascirev.2023.107975
- Morris, A.G., 2022. Bones and Bodies: How South African Scientists Studied Race. NYU Press, New York.
- Morton, S.G. 1844. Crania Aegyptiaca: Or, Observations on Egyptian Ethnography, Derived from Anatomy, History, and the Monuments. J. Pennington, Philadelphia.
- Morton, S.G., Combe, G., 1839. Crania Americana; Or, A Comparative View of the Skulls of Various Aboriginal Nations of North and South America: To which is Prefixed an Essay on the Varieties of the Human Species. J. Dobson, Philadelphia.
- National Academies of Sciences, Engineering, and Medicine; Division of Behavioral and Social Sciences and Education; Health and Medicine Division; Committee on Population; Board on Health Sciences Policy; Committee on the Use of Race, Ethnicity, and Ancestry as Population Descriptors in Genomics Research, 2023. Using Population Descriptors in Genetics and Genomics Research: A New Framework for an Evolving Field. National Academies Press (US), Washington, D.C. http://www.ncbi.nlm.nih.gov/books/NBK589855/
- Ni, X., Ji, Q., Wu, W., Shao, Q., Ji, Y., Zhang, C., Liang, L., Ge, J., Guo, Z., Li, J., Li, Q., Grün, R., Stringer, C., 2021. Massive cranium from Harbin in northeastern China establishes a new Middle Pleistocene human lineage. Innovation, 2(3), 100130. https://doi.org/10.1016/j.xinn.2021.100130
- Nott, J.C., 1844. Two Lectures on the Natural History of the

- Caucasian and Negro Races. Dade and Thompson, Mobile.
- Nott, J.C., Gliddon, G.R., 1854. Types of Mankind: Or, Ethnological Researches, Based Upon the Ancient Monuments, Paintings, Sculptures, and Crania of Races, and Upon Their Natural, Geographical, Philological and Biblical History. Lippincott, Grambo & Company, Philadelphia.
- Ouwendijk, E.M., Due, R.A., Locatelli, E., Jatmiko, Ostende, L.W.V.D.H., 2014. Bat cave and Hobbit hole, microbats of Liang Bua (Flores, Indonesia). Alcheringa 38(3), 422–433. https://doi.org/10.1080/03115518.2014.889545
- Pääbo, S., 2014. Neanderthal Man: In Search of Lost Genomes. Basic Books, New York.
- Palmer, M., Sutcliffe, I., Venter, S.N., Hedlund, B.P., 2022. It is time for a new type of type to facilitate naming the microbial world. New Microbes New Infect. 47, 100991. https://doi.org/10.1016/j.nmni.2022.100991
- Peschel, O., 1876. The Races of Man: And Their Geographical Distribution. Henry S. King, London.
- Peyrégne, S., Slon, V., Kelso, J., 2024. More than a decade of genetic research on the Denisovans. Nat. Rev. Genet. 25(2), 83–103. https://doi.org/10.1038/s41576-023-00643-4
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., ... Pääbo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505(7481), 43–49. https://doi.org/10.1038/nature12886
- Quatrefages, A. de, Hamy, E.-T., 1874. La race de Cro-Magnon dans l'espace et dans le temps. Bull. Mém. Soc. Anthropol. Paris 9(1), 260–266. https://doi.org/10.3406/bmsap.1874.3048
- Race, Ethnicity, and Genetics Working Group, 2005. The use of racial, ethnic, and ancestral categories in human genetics research. Am. J. Hum. Genet. 77(4), 519–532. https://doi.org/10.1086/491747
- Reed, D.N., 2025. Nomenclature and Taxonomy of Chibanian Hominins. PaleoAnthropology 2025:2.
- Reed, D.N., Raney, E., Johnson, J., Jackson, H., Virabalin, N., Mbonu, N., 2023. Hominin nomenclature and the importance of information systems for managing complexity in paleoanthropology. J. Hum. Evol. 175, 103308. https://doi.org/10.1016/j.jhevol.2022.103308
- Reich, D., Patterson, N., Kircher, M., Delfin, F., Nandineni, M.R., Pugach, I., Ko, A.M.-S., Ko, Y.-C., Jinam, T.A., Phipps, M.E., Saitou, N., Wollstein, A., Kayser, M., Pääbo, S., Stoneking, M., 2011. Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. Am. J. Hum. Genet. 89(4), 516–528. https://doi.org/10.1016/j.ajhg.2011.09.005
- Renner, S.S., 2016. A return to Linnaeus's focus on diagnosis, not description: the use of DNA characters in the formal naming of species. Syst. Biol. 65(6), 1085–1095. https://doi.org/10.1093/sysbio/syw032

- Rheindt, F.E., Bouchard, P., Pyle, R.L., Welter-Schultes, F., Aescht, E., Ahyong, S.T., Ballerio, A., Bourgoin, T., Ceríaco, L.M.P., Dmitriev, D., Evenhuis, N., Grygier, M.J., Harvey, M.S., Kottelat, M., Kluge, N., Krell, F.-T., Kojima, J., Kullander, S.O., Lucinda, P., ... Pape, T., 2023. Tightening the requirements for species diagnoses would help integrate DNA-based descriptions in taxonomic practice. PLoS Biology, 21(8), e3002251. https://doi.org/10.1371/journal.pbio.3002251
- Riede, F., Hoggard, C., Shennan, S., 2019. Reconciling material cultures in archaeology with genetic data requires robust cultural evolutionary taxonomies. Palgrave Comm. 5(1), 1–9. https://doi.org/10.1057/s41599-019-0260-7
- Roberts, R., (2004, October 28). Villagers speak of the small, hairy Ebu Gogo. The Telegraph (UK).
- Rogers, A.R., Harris, N.S., Achenbach, A.A., 2020. Nean-derthal-Denisovan ancestors interbred with a distantly related hominin. Sci. Adv. 6(8), eaay5483. https://doi.org/10.1126/sciadv.aay5483
- Roksandic, M., Radović, P., Wu, X.-J., Bae, C.J., 2022a. *Homo bodoensis* and why it matters. Evol. Anthropol. 31(5), 240–244. https://doi.org/10.1002/evan.21954
- Roksandic, M., Radović, P., Wu, X.-J., Bae, C.J., 2022b. Resolving the "muddle in the middle": the case for *Homo bodoensis* sp. nov. Evol. Anthropol. 31(1), 20–29. https://doi.org/10.1002/evan.21929
- Sample, I., 2010, March 24. New species of human ancestor found in Siberia. The Guardian. https://www.the-guardian.com/science/2010/mar/24/new-human-species-siberia
- Sanchez-Quinto, F., 2014. Addressing Neandertal Evolutionary Genetics at Three Different Resolution Levels: Admixture with Modern Humans, Demography and Social Structure. Ph.D. Dissertation. Universitat Pompeu Fabra.
- Sankar, P., Cho, M.K., Mountain, J., 2007. Race and ethnicity in genetic research. Am. J. Med. Genet. A 143A(9), 961–970. https://doi.org/10.1002/ajmg.a.31575
- Sawyer, S., Renaud, G., Viola, B., Hublin, J.-J., Gansauge, M.-T., Shunkov, M.V., Derevianko, A.P., Prüfer, K., Kelso, J., Pääbo, S., 2015. Nuclear and mitochondrial DNA sequences from two Denisovan individuals. Proc. Nat. Acad. Sci. U.S.A. 112(51), 15696–15700. https://doi.org/10.1073/pnas.1519905112
- Sharma, A., 1974. Comment on Darwin's Apes, Dental Apes, and the Descent of Man: normal science in evolutionary anthropology. Curr. Anthropol. 15(4), 408–410. https://doi.org/10.1086/201494
- Shennan, S., 2024. Population, culture history, and the dynamics of change in European prehistory. J. R. Anthropol. Inst. 30, 1085–1101. https://doi.org/10.1111/1467-9655.14153
- Simpson, G.G., 1961. Principles of Animal Taxonomy (1st ed.). Columbia University Press, New York.
- Simpson, G.G., 1963. The meaning of taxonomic statements. In: Washburn, S.L. (Ed.), Classification and Human Evolution. Routledge, New York, pp. 1–31.

- Simpson, S.J.Y., 1861. Archaeology: Its Past and Its Future Work. Neill, Edinburgh.
- Slimak, L., Vimala, T., Seguin-Orlando, A., Metz, L., Zanolli, C., Joannes-Boyau, R., Frouin, M., Arnold, L. J., Demuro, M., Devièse, T., Comeskey, D., Buckley, M., Camus, H., Muth, X., Lewis, J.E., Bocherens, H., Yvorra, P., Tenailleau, C., Duployer, B., ... Sikora, M., 2024. Long genetic and social isolation in Neanderthals before their extinction. Cell Genom. 4(9), 100593. https://doi.org/10.1016/j.xgen.2024.100593
- Smith, C.H., Kneeland, S., 1855. The Natural History of the Human Species: Its Typical Forms, Primeval Distribution, Filiations, and Migrations ... Gould and Lincoln, Boston.
- Smith, P., Arensburg, B., 1977. A Mousterian Skeleton from Kebara Cave. Eretz-Israel 1977, 164-176.
- Stiles, C.W., Hassall, A., 1925. Key-Catalogue of the Protozoa Reported for Man. U.S. Government Printing Office, Washington, D.C.
- Stringer, C., 2022. The development of ideas about a recent African origin for *Homo sapiens*. J. Anthropol. Sci. 100, 5–18. https://doi.org/10.4436/jass.10009
- Stringer, C., Crété, L., 2022. Mapping Interactions of *H. neanderthalensis* and *Homo sapiens* from the fossil and genetic records. PaleoAnthropology 2022:2, 401–412. https://doi.org/10.48738/2022.iss2.130
- Tattersall, I., 2006. Neanderthal skeletal structure and the place of *Homo neanderthalensis* in European hominid phylogeny. Hum. Evol. 21(3), 269–274. https://doi.org/10.1007/s11598-006-9026-5
- Tautz, D., Arctander, P., Minelli, A., Thomas, R.H., Vogler, A.P., (2003. A plea for DNA taxonomy. Trends Ecol. Evol. 18(2), 70–74. https://doi.org/10.1016/S0169-5347(02)00041-1
- Tobias, P.V., 1963. Cranial capacity of *Zinjanthropus* and other australopithecines. Nature 197(4869), 743–746. https://doi.org/10.1038/197743a0
- Tobias, P.V., 1965. Early man in East Africa. Sci. 149(3679), 22–33. https://doi.org/10.1126/science.149.3679.22
- Tobias, P.V., 1966. The distinctiveness of *Homo habilis*. Nature 209(5027), 953–957. https://doi.org/10.1038/209953a0
- Tsutaya, T., Sawafuji, R., Taurozzi, A.J., Fagernäs, Z., Patramanis, I., Troché, G., Mackie, M., Gakuhari, T., Oota, H., Tsai, C.-H., Olsen, J. V., Kaifu, Y., Chang, C.-H., Cappellini, E., Welker, F., 2025. A male Denisovan mandible from Pleistocene Taiwan. Science 388(6743), 176–180. https://doi.org/10.1126/science.ads3888
- van Regenmortel, M.H.V., Mahy, B.W.J., 2004. Emerging issues in virus taxonomy. Emerg. Infect. Dis. 10(1), 8–13.

- https://doi.org/10.3201/eid1001.030279
- Veeramah, K.R., Hammer, M.F., 2014. The impact of whole-genome sequencing on the reconstruction of human population history. Nat. Rev. Genet. 15(3), 149–162. https://doi.org/10.1038/nrg3625
- Villalba-Mouco, V., van de Loosdrecht, M.S., Rohrlach, A.B., Fewlass, H., Talamo, S., Yu, H., Aron, F., Lalueza-Fox, C., Cabello, L., Cantalejo Duarte, P., Ramos-Muñoz, J., Posth, C., Krause, J., Weniger, G.-C., Haak, W., 2023. A 23,000-year-old southern Iberian individual links human groups that lived in Western Europe before and after the Last Glacial Maximum. Nat. Ecol. Evol. 7(4), 597–609. https://doi.org/10.1038/s41559-023-01987-0
- Viola, B., Markin, S.V., Zenin, A., Shunkov, M.V., Derevianko, A.P., 2011. Late Pleistocene hominins from the Altai Mountains, Russia. In: Derevianko, A.P., Shunkov, M.V. (Eds.), Characteristic Features of the Middle to Upper Paleolithic Transition in Eurasia: Proceedings of the International Symposium "Characteristic features of the Middle to Upper Paleolithic transition in Eurasia—Development of culture and evolution of *Homo* genus", July 4-10, 2011, Denisova Cave, Altai. Pub. Dept. of the Institute of Archaeology and Ethnography SB RAS, Novosibirsk, pp. 207–213.
- Wai-Ogosu, B., 1974. Pleistocene man in Africa with special reference to West Africa. J. Hist. Soc. Nigeria 7(2), 357–368.
- Walker, J., Clinnick, D., White, M., 2021. We are not alone: William King and the naming of the Neanderthals. Am. Anthropol. 123(4), 805–818. https://doi.org/10.1111/aman.13654
- Weckler, J.E., 1954. The relationships between Neanderthal man and *Homo sapiens*. Am. Anthropol. 56(6), 1003–1025.
- Weidenreich, F., 1943. The "Neanderthal Man" and the ancestors of "Homo sapiens." Am. Anthropol. 45(1), 39–48.
- Wood, B., Schroer, K., 2017. *Paranthropus*: where do things stand? In Marom, A., Hovers, E. (Eds.), Human Paleontology and Prehistory: Contributions in Honor of Yoel Rak. Springer International Publishing, Cham, pp. 95–107. https://doi.org/10.1007/978-3-319-46646-0_8
- Wu, L., Zhang, Y., Wu, X., 2005. Middle Pleistocene human cranium from Tangshan (Nanjing), southeast China: a new reconstruction and comparisons with *Homo erectus* from Eurasia and Africa. Am. J. Phys. Anthropol. 127(3), 253–262. https://doi.org/10.1002/ajpa.20066
- Young, R.J.C., 2005. Colonial Desire: Hybridity in Theory, Culture and Race. Routledge, New York.