Earth History and Biodiversity 7 (2026) 100036

Contents lists available at ScienceDirect

Earth History and Biodiversity

journal homepage: www.sciencedirect.com/journal/earth-history-and-biodiversity/

The Mismeasure of Neanderthals

Gabriela Amorós *, José S. Carrión *

Department of Plant Biology, Faculty of Biology, University of Murcia, Campus de Espinardo, Murcia 20100, Spain

A R T I C L E I N F O

Keywords:
Neanderthals
Paleoart
Human evolution
Paleoecology
Biodiversity
History of science

A B S T R A C T

From their nineteenth-century discovery, Neanderthals have been burdened with images of brutishness and failure—hairy, stooped figures constructed less from evidence than from Victorian prejudice, colonial ideology, and the authority of early paleoanthropology. These representations infiltrated museums, politics, and even scientific theory, sustaining the notion of Neanderthals as evolutionary dead ends. Recent advances in paleogenomics, archaeology, and paleoecology have overturned these narratives. Neanderthals are now recognised as cognitively sophisticated hominins who engaged in symbolic practices, including the use of pigments, ornaments, engravings, and cave art; who mastered fire and adhesives; who employed fibres, feathers, and shells; who cared for the sick and buried their dead; and who adapted with remarkable flexibility to landscapes ranging from Mediterranean woodlands to periglacial steppes over an exceptionally long timespan. Yet while science now acknowledges this iconographic dissonance, it remains necessary to consider how entrenched academic hierarchies, unequal funding systems, and a research culture in which the value of discoveries is often influenced as much by bibliometric performance as by novelty, disparity, or complexity, may still shape interpretations in other domains—such as the chronology of Neanderthal extinction. Paleoart is analysed here as a decisive mediator between data, culture, and consensus, and emphasis is placed on the emergence of Neanderthals as creators of distinctive aesthetic niches, as ecological actors, and as reminders that every species constitutes a unique evolutionary experiment destined for extinction. Their legacy dismantles myths of human exceptionalism and compels reflection, through the lens of deep time, on the urgent challenges of biodiversity loss and the fragile conditions of coexistence.

1. Introduction

Stephen Jay Gould's *The Mismeasure of Man* offered a powerful critique of the ways in which scientific interpretations can be shaped—consciously or unconsciously—by cultural bias. By dissecting historical episodes in the measurement of human intelligence, Gould (1981) demonstrated how supposedly objective data often reflected the prejudices and assumptions of their time. This paper takes inspiration from Gould's approach, applying it to the case of Neanderthals. Under the deliberately resonant title *The Mismeasure of Neanderthals*, we examine how cultural narratives have influenced both popular and scientific portrayals of this species.

From their earliest depictions as brutish evolutionary failures to today's more nuanced—yet still contested—images of cognitive and social sophistication, Neanderthals have never been represented in isolation from the values of the societies interpreting them (Jiménez-Arenas, 2002). More than scientific subjects, they have become cultural icons: symbols of progress and civilization, foils for defining "modernity," and versatile figures mobilized in politics, museums, literature, and film. Their enduring presence reflects not only their palaeoanthropological significance but also their symbolic power in shaping human self-understanding.

Building on this dual dimension, we adopt an interdisciplinary perspective that bridges archaeology, biology, earth sciences, history of science, and the humanities. Central to this framework is palaeoart—not merely as illustration but as a research, educational, and inclusive tool—through which we aim to reframe the fundamentally archaic concept of the Neanderthal and to promote a perception of their alterity as the outcome of an independent evolutionary trajectory.

* Corresponding authors.
E-mail addresses: gabriela.amoros@um.es (G. Amorós), carrion@um.es (J.S. Carrión).

https://doi.org/10.1016/j.hisbio.2025.100036
Received 27 September 2025; Received in revised form 13 November 2025; Accepted 22 November 2025
Available online 27 November 2025

2. The Neanderthal in outline

2.1. Discovery and early recognition

The formal recognition of *Homo neanderthalensis* began with the 1856 discovery of a partial skeleton in Germany's Neander Valley. Known as Neanderthal 1, or Feldhofer 1, these remains were the first to be identified as belonging to an extinct human species, and their announcement in 1864 marked a pivotal moment in palaeoanthropology. This discovery challenged prevailing notions of human uniqueness and initiated enduring debates about our evolutionary relationships (Trinkaus and Shipman, 1993, Carrión and Walker, 2019). Earlier fossil finds—including the Engis child in Belgium (1830) and the adult skull from Forbes' Quarry in Gibraltar (1848)—predated Feldhofer 1 but were not recognized at the time as belonging to a different human species (Harvati, 2010). Indeed, had the Gibraltar specimen been correctly interpreted, the species might today bear a different name, perhaps reflecting its southwestern European origins rather than the German valley where it was formally defined (Finlayson, 2009; Menez, 2018).

2.2. Phyletic origins and chronological framework

Neanderthals are now recognized as a deeply rooted lineage within the genus *Homo*, with evolutionary origins traceable to at least 430,000 years ago (Arsuaga et al., 2014; Meyer et al., 2016). Most scholars view them as the western Eurasian descendants of *Homo heidelbergensis* (or closely related forms; Stringer, 2012a; Roksandic et al., 2019), with a probable evolutionary origin in Eurasia rather than Africa (Stewart and Stringer, 2012; Bermúdez de Castro and Martinón-Torres, 2022). The transition from *heidelbergensis* to Neanderthal morphology appears to have been gradual, involving a mosaic of traits accumulated over hundreds of thousands of years (Bermúdez de Castro et al., 2019; Dennell et al., 2011; Rosas et al., 2022). In geochronological terms, Neanderthals span much of the Middle Pleistocene and extend into the Upper Pleistocene, roughly corresponding to Marine Isotope Stages (MIS) 12 through 3 (Rasmussen et al., 2014). Morphologically "classic" Neanderthals (Lalueza-Fox et al., 2005) are documented between ~130,000 and 38,000 years ago, with an archaeological record dominated by the Mousterian stone tool tradition (Finlayson et al., 2023). In the Levant, however, the Mousterian was produced by both Neanderthals and early *Homo sapiens*, indicating technological convergence or cultural transmission (Shea, 2003).

Late Neanderthal contexts encompass a range of so-called "transitional" industries—technocomplexes that combine elements of Middle and Upper Palaeolithic technology, sometimes attributed to Neanderthals and sometimes to *Homo sapiens* (Finlayson and Carrión, 2007; Finlayson et al., 2023). Such assignments often rely on stratigraphic associations or technotypological criteria, with relatively few cases supported by directly associated human remains. This ambiguity has fuelled long-standing debates over cultural transmission, convergence, and population replacement. Well-known examples include the Châtelperronian in western Europe and the Uluzzian in Italy—-frequently linked to *Homo sapiens* (Benazzi et al., 2011)—as well as more geographically restricted complexes such as the Bohunician (Czech Republic), Szeletian (Hungary, Slovakia), the Initial Upper Palaeolithic (IUP) sequence at Bacho Kiro Cave, the Kozarnikian (Bulgaria), and the Streletskian (Eastern Europe) (Finlayson and Carrión, 2007; Finlayson et al., 2023; Hublin et al., 2020; Fewlass et al., 2020). Recent work at Bacho Kiro has redefined the so-called "Bachokirian" as part of the broader IUP technocomplex, establishing a robust chronological and technological framework for some of the earliest *Homo sapiens* occupations in Europe (Hublin et al., 2020; Fewlass et al., 2020). The mosaic and regionally varied nature of these industries reflects the complexity of the Middle-to-Upper Palaeolithic transition, and only future research will clarify the extent to which Neanderthals themselves participated in their production.

2.3. Geographic range and environmental context

Neanderthals occupied a vast territory stretching from the Atlantic coasts of the Iberian Peninsula to the foothills of the Altai Mountains in western Siberia, and from Mediterranean regions to the periglacial margins of northern Europe (Fig. 1). Absent from North Africa but present in the Levant, some evidence and climatic modeling suggest that small groups may have reached Arctic latitudes during favorable phases (Slimak et al., 2011). This distribution formed a broad mid-latitude belt across Eurasia, encompassing habitats ranging from open steppe-tundra to temperate woodland (Carrión et al., 2026). Their disappearance from the fossil and archaeological record around 38–45 ka (Higham et al., 2014) raises questions about their extinction and about the nature of their interactions—genetic, cultural, and competitive—with anatomically modern humans.

2.4. Distinctive anatomy and functional adaptations

Adapted to the demanding climatic conditions of glacial Eurasia, Neanderthals evolved a compact, robust physique optimized for heat conservation. Adult stature generally ranged from 1.50 to 1.75 m, with body mass estimates between 64 and 82 kg. Their skeleton was powerfully built, with broad shoulders, a large thoracic cage, a wide pelvis, and relatively short, muscular limbs (Stringer and Gamble, 1996; Arsuaga, 2003). Cranially, they exhibited an elongated, low neurocranium, a receding forehead, and pronounced supraorbital ridges, contrasting with the globular vault of *H. sapiens* (Stringer, 2012b). The midface was large and projecting, allegedly coupled with a broad nasal aperture—especially in high-latitude individuals. The mandible lacked a true chin, dentition was prominent, and anterior teeth were often heavily worn from non-masticatory uses such as tool manipulation. Collectively, these traits provide insight into the interplay between environmental pressures, biomechanics, and the daily lives of Neanderthals.

3. Origins of the Neanderthal image

3.1. Caricaturing the "Primitive Brute"

The formal recognition of *Homo neanderthalensis* in 1864 took place against the backdrop of Darwin's *On the Origin of Species* (1859), when the scientific community was still negotiating the implications of evolutionary theory for human origins. Early anatomists such as William King, who proposed the species name (King, 1864), compared Neanderthal remains with both apes and modern humans, often placed Neanderthals low on a presumed evolutionary ladder. The scant fossil record—limited to specimens from the Neander Valley and Gibraltar—encouraged speculative reconstructions that exaggerated morphological differences. Features such as robust brow ridges, elongated skulls, and stout limb bones were interpreted as primitive vestiges rather than ecological adaptations (Müller and Schrenk, 2009).

In the late 19th century, these scientific framings quickly found visual expression. The first reconstruction of a Neanderthal was created by Hermann Schaaffhausen in 1888 (Fig. 2). Illustrated newspapers such as *The Illustrated London News* and *Le Petit Journal* popularized images of crouched, club-wielding Neanderthals, typically shown in violent conflict or subsistence struggle (Sommer, 2006). The first illustration of a Neanderthal in its natural environment appeared on the cover of *Harper's Weekly* in 1873, produced by Victorian illustrator Ernst Griset (Fig. 3).

At the turn of the century, museum dioramas began to consolidate the image of Neanderthals as apelike and brutish. In institutions such as the American Museum of Natural History (New York) and the Muséum national d'Histoire naturelle (Paris), they were depicted with hunched

Fig. 1. Map of Eurasia showing the extent of the known Neanderthal range (modified from https://commons.wikimedia.org/wiki/File:Range_of_Neanderthals.png, under CC BY-SA 3.0).

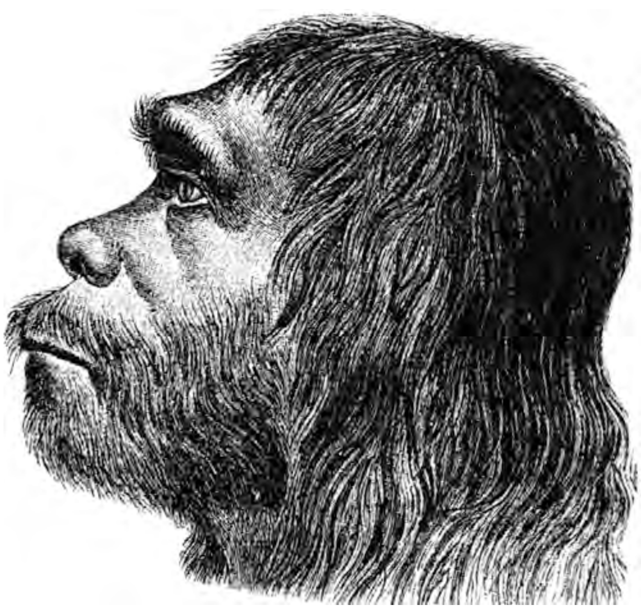

Fig. 2. *Neanderthal 1* or *Feldhofer 1* (1888), considered the first artistic reconstruction of a Neanderthal, created by Hermann Schaaffhausen, who—together with Johann Carl Fuhlrott—announced the discovery of the first *Homo neanderthalensis*. Public domain.

Fig. 3. Ernest Griset (1844–1907), *"The Neanderthal man"*, *Harper's Weekly*, July 19, 1873. Regarded as the first scientific attempt at visually reconstructing a prehistoric human. Adapted from Martínez Pulido (2016). Public domain.

postures, coarse facial features, and excessive body hair. Marcellin Boule's influential study (1908–1911) of the La Chapelle-aux-Saints skeleton reinforced this stereotype, presenting the individual as a bent-kneed, primitive figure (Boule, 1911; Madison, 2021). His interpretation inspired Charles R. Knight's famous paintings and widely circulated sculptures displayed at world fairs, which cemented the caricature of Neanderthals as intellectually limited (Hammond, 1982; Tattersall and Schwartz, 2000) (Fig. 4).

By the mid-20th century, mass exhibitions gave the Neanderthal image global visibility. In 1927, the Field Museum of Natural History in Chicago commissioned sculptor Frederick Blaschke to produce reconstructions (Amorós, 2023). Based on European specimens gathered during an expedition led by Henry Field, Blaschke created models of skulls and bodies that culminated in a diorama of a Neanderthal family, unveiled in 1929. This was the only reconstruction of its kind worldwide and achieved major popular success. However, by 1972, five of Blaschke's figures were deemed scientifically inaccurate and replaced with updated versions by museum artist Joseph Krstolich. Further modifications followed in 1985, and the dismantling of the Hall of Prehistoric Man began in 1988, marking the end of an exhibit that had shaped perceptions for more than five decades. Blaschke's reconstructions remain paradoxical: while portraying Neanderthals as apelike and savage, they also endowed them with an unsettling resemblance to contemporary psychiatric patients posed in everyday attitudes (Amorós, 2024) (Fig. 5).

3.2. The influence of social Darwinism and scientific racism

In the late 19th and early 20th centuries, evolutionary concepts were appropriated by social and political ideologies. Social Darwinism reframed natural selection to justify racial hierarchies, colonial expansion, and class divisions (Hawkins, 1997). Within this framework, Neanderthals were portrayed as evolutionary "failures," a fate to be avoided by "civilized" humanity. Scientific racism, entrenched in physical anthropology at the time, often placed Neanderthals alongside non-European peoples in typological charts (Stocking, 1987), visually relegating them to a lower rung of human development. Exhibitions at

Fig. 4. a. Neanderthal reconstruction of the La Chapelle-aux-Saints skeleton, by Fantisek Kupka, scientifically advised by Marcellin Boule for *Illustrated London News* (ILN), February 27 (Kupka, 1909). This image remained embedded in popular consciousness for decades. The ILN noted: "Our drawing can justly claim to be the first which has with scientific certainty demonstrated prehistoric man in his habits while he lived." The composition, originally titled *The Beginnings of Humanity. The Inhabitant of the La Chapelle-aux-Saints Cave during the Mousterian period*, illustrates how the press helped shape the myth of the primitive, ape-like Neanderthal. Public domain. **b.** Facial reconstruction of the Neanderthal individual *La Chapelle-aux-Saints 1*, produced by Cicero Moraes (Moraes et al., 2023). The work combines forensic facial approximation techniques with 3D cranial data, following a methodology based on anatomical landmarks, tissue depth markers, and digital sculpting protocols widely used in paleoanthropological reconstructions. The model offers a scientifically informed representation of Neanderthal facial morphology, integrating osteological evidence with comparative anatomical references. Image courtesy of Cicero Moraes.

colonial and world fairs sometimes juxtaposed reconstructions of Neanderthals with displays of Indigenous peoples, presenting both as points along a supposed scale from "savagery" to "civilization" (Blanchard, 2010). Such presentations blurred the boundaries between science and propaganda, embedding prejudiced interpretations of Neanderthals into the public imagination for decades.

From the discovery of the Feldhofer fossil onward, scientific interpretations were infused with judgments about the alleged lack of intelligence of its owner. Hermann Schaaffhausen, the first to describe it, and the Victorian naturalist Thomas Huxley went beyond anatomy to imply limited cognitive abilities. Schaaffhausen considered it unlikely that Neanderthals had mastered articulated language, suggesting instead that their sounds more closely resembled animal growls than human speech. Huxley likewise doubted that the skull could have housed anything more than "the simple mind of a savage." William King went further, claiming that the thoughts of this being had never risen above those of a brute. Other naturalists even proposed that the cranium belonged to a pathologically impaired or diseased individual (Madison, 2021).

This perspective was deeply rooted in the intellectual climate of the 19th century, when scientific attention was heavily focused on comparing human "races." During the colonial era, European naturalists classified peoples of the world within a hierarchy that placed apes at the bottom, colonized populations at an intermediate level as "inferior races," and Europeans at the top. With the advent of evolutionary theory in the 1860s, these groups came to be conceived as living stages linking primitive ancestors with the rest of the primate world, under the assumption that the biology of each "race" innately determined its cultural and intellectual potential. These "contemporary savages" thus became a window into human origins, and in this way the same racial categories used to describe living populations were projected backward in time and applied to the interpretation of Neanderthals. Assuming that Neanderthals and "contemporary savages" were biologically and culturally inferior provided Europeans with further justification for imperial expansion, reinforcing colonialism, oppression, and discrimination (Fuentes, 2021).

By the mid-20th century, excavations led by Ralph Solecki and others began to erode this stereotype. The Shanidar Cave discoveries suggested capacities for care, social organization, and symbolic behavior among Neanderthals (Solecki, 1954; Trinkaus, 1985). Nonetheless, Boule's depiction cast a long intellectual shadow (Lieberman and Edmund., 1971; Laitman et al., 1990), and only toward the close of the 20th century—bolstered by breakthroughs in archaeology and genetics—did scientific and popular narratives converge on a more complex and humanized understanding of the Neanderthal (Frayer, 2019).

4. Neanderthals in the visual arts

From their first appearance in scientific discourse, Neanderthals have been mediated to the public through visual representation. Artistic reconstructions—whether in museum dioramas, scientific illustration, or popular imagery—have played a central role in shaping perceptions of what these hominins "looked like," often with greater impact on the popular imagination than technical descriptions or skeletal remains (Sommer, 2006).

4.1. Early depictions: science meets imagination

In the late 19th and early 20th centuries, illustrators and sculptors working for museums or the illustrated press faced the challenge of reconstructing Neanderthals with little more than fragmentary fossils and prevailing scientific theories. Early works often presented them with stooped postures, protruding jaws, heavy brow ridges, and thick body hair—visual cues intended to emphasize primitiveness (Smith, 1924).

Examples include the aforementioned reconstructions by Frederick Blaschke for the Field Museum of Natural History in Chicago (Fig. 5), and illustrations published in *The Illustrated London News* (1909, 1921), as well as the sculptures displayed at the 1937 International Exhibition in Paris (Hackett and Dennell, 2003). These images were far from neutral: they were shaped by contemporary ideas about human evolution, colonial hierarchies, and the notion of a linear progression from the "primitive" to the "civilized." Particularly striking are the sculptures produced between 1909 and 1914 by Louis Mascré, under the direction of Aimé Rutot, which portrayed Neanderthals exclusively as upright apes, blurring distinctions with modern humans and erasing their individuality (Fig. 6).

Fig. 5. Reconstructions by Frederick Blaschke in 1929 for Neanderthal dioramas at the Field Museum of Natural History. **a.** Neanderthal man figure in progress (incomplete). URI: http://fm-digital-assets.fieldmuseum.org/525/789/CSA66236.jpg. **b.** Neanderthal man figure in progress (incomplete). URI: http://fm-digital-assets.fieldmuseum.org/525/790/CSA66237.jpg. **c.** Neanderthal grandmother sewing animal skin, model for Hall 38 diorama. URI: http://fm-digital-assets.fieldmuseum.org/526/767/CSA66708.jpg. **d.** Neanderthal boy model for Hall 38 exhibit diorama. URI: http://fm-digital-assets.fieldmuseum.org/525/818/CSA66833.jpg. **e.** Neanderthal man figure for Hall 38 diorama. URI: http://fm-digital-assets.fieldmuseum.org/525/806/CSA66700.jpg. © Field Museum of Natural History.

4.2. *The rise of the "Noble Neanderthal"*

By the mid-20th century, advances in palaeoanthropology and reinterpretations of skeletal evidence began to challenge earlier caricatures. Artists such as Zdeněk Burian in Czechoslovakia and Jay Matternes in the United States produced more anatomically realistic and humanized portrayals, often situating Neanderthals in dynamic group scenes of tool-making, hunting, or social interaction (Špinar, 1972; Debus and Debus, 2002).

Burian's work, while vivid and attentive to Neanderthal intelligence and social relations, still emphasized simian features and a fierce demeanor (Fig. 7). Several decades later, in 1985, Jay Matternes produced the illustration *Marathon Man* for *National Geographic* (Amorós, 2023). This sequential composition arranged multiple *Homo* species in apparent evolutionary order, from *Australopithecus* to modern humans, including a Neanderthal figure. Crucially, Matternes highlighted the relative similarity between Neanderthals and *Homo sapiens*, suggesting less pronounced physical differences than previously assumed. While still framed by contemporary hypotheses, these works invited greater empathy, portraying Neanderthals as skilled survivors rather than evolutionary "failures."

4.3. *Contemporary visual culture: from hyperrealism to reappropriation*

In recent decades, hyperrealistic reconstructions—produced for museums, documentaries, and exhibitions—have sought to convey the

Fig. 6. Reconstructions by Louis Mascré under the direction of Aimé Rutot, Royal Institute of Natural Sciences of Belgium, Brussels. **a.** *Woman of the Neanderthal race. Descendant of earlier generations. Mousterian age.* (1909–1914). Public domain. **b.** *Man of the Neanderthal race. Descendant of earlier generations. Mousterian age.* (1909–1914). Public domain.

Fig. 7. *Neanderthal Old Man*, by Zdenek Burian. Source: http://zburian.blogspot.com/. Public domain.

individuality and humanity of Neanderthals. Artists such as Élisabeth Daynès have created life-sized silicone models with meticulous attention to skin texture, hair, and expression, often employing forensic facial reconstruction techniques (Martínez Pulido., 2016). Comparing Kupka's bust of the La Chapelle-aux-Saints Neanderthal (1909), and Daynès' (2005) version underscores how dramatically perceptions of Neanderthals have shifted and how profoundly earlier representations distorted them. More dramatically, a comparison can be made with the recent work by Cícero Moraes, who has carried out exceptional forensic work by digitally reproducing the face of the "Old Man" of La Chapelle. Using CT scans of the fossilized skull and photogrammetry, Moraes applied soft-tissue thickness markers derived from modern scans to model the facial features with striking realism (Moraes et al., 2023) (Fig. 4). The result—a Neanderthal with remarkably human-like traits and an unexpectedly "softened" appearance—helps to dispel stereotypical perceptions and emphasizes the anatomical continuity between our closest evolutionary relatives. Moraes also relies on open-source software tools, such as InVesalius and Blender, and has established himself as an international reference in digital forensic reconstruction through projects such as the *Faces of Evolution* exhibition (22 hominin faces) and numerous reconstructions of historical figures. Beyond their scientific rigor, these works carry an important pedagogical value, offering the public an accessible and visually compelling means to appreciate human evolutionary history.

These hyperrealistic works can both humanize and unsettle: the familiar gaze of a reconstructed Neanderthal blurs the line between "them" and "us." Meanwhile, contemporary art has reappropriated the Neanderthal figure in conceptual installations, political cartoons, and advertising, using it as a metaphor for resistance, lost knowledge, or societal regression. In this way, the Neanderthal continues to serve not only as a scientific subject but also as a cultural mirror, reflecting present-day anxieties and aspirations as much as prehistoric realities.

4.4. Algorithmic Neanderthals

The application of artificial intelligence (AI) and digital modeling has recently expanded the possibilities for reconstructing Neanderthal faces and bodies. Traditionally, reconstructions relied on cranial casts, forensic sculpting, and comparative anatomy, but today deep learning, 3D scanning, and genomic inference are increasingly integrated into the process (Magnani and Clindaniel., 2023). These techniques enable researchers to simulate musculature, skin texture, and pigmentation from fragmentary fossil and genetic data, producing a plurality of potential reconstructions rather than a single "definitive" face (Wroe et al., 2018). Several projects exemplify this trend: the reconstruction of *Shanidar Z*, a female Neanderthal from Iraqi Kurdistan digitally assembled from over 200 cranial fragments, or the rendering of family groups and social scenes in documentary and museum contexts (BBC/NOVA, 2023; Natural History Museum, London). The advantages of AI-based reconstructions lie in their ability to explore multiple hypotheses quickly, democratize access to paleoartistic tools, and enhance public engagement with paleoanthropological research. However, these images remain interpretive, not evidentiary: they risk naturalizing specific visual stereotypes, embedding cultural biases in apparently "objective" algorithms, and blurring the line between scientific reconstruction and artistic speculation. As such, AI contributes not only novel technical affordances but also new epistemological and ethical challenges for how Neanderthals are imagined and communicated.

5. The Neanderthal in literature

5.1. Fictional prehistory in the 19th and 20th centuries

From the late 19th century onward, Neanderthals began to appear in works of prehistoric fiction, embodying both fascination and fear. One of the earliest and most influential examples is *La Guerre du Feu* (Rosny Aîné, 1911), which cast Neanderthals as a primitive "other" locked in competition with early *Homo sapiens*, establishing a narrative template that persisted for decades. Later, William Golding's *The Inheritors* (1955) offered a more empathetic portrayal, presenting Neanderthals as gentle and intuitive beings tragically displaced by the cunning and aggression of modern humans. The late 20th century brought the commercial success of Jean M. Auel's Earth's Children series (1980–2011), in which Neanderthals are depicted with complex social lives, sophisticated skills, and deep emotional capacity—an approach that challenged lingering stereotypes. However, despite Auel's humanistic portrayal, her Neanderthals remain depicted as more bound by tradition and less inclined toward innovation than anatomically modern humans. This subtle hierarchy—emphasising emotion and community over invention—reveals that even sympathetic narratives often reproduce residual notions of evolutionary progress. Together, these fictional works shaped public perceptions of Neanderthals, oscillating between romanticization and dehumanization.

5.2. Social metaphors

Beyond entertainment, Neanderthals have served as flexible metaphors in social and political discourse. Authors have used them to explore themes of otherness, cultural survival, and the moral costs of progress. In some narratives, Neanderthals symbolize lost innocence or a more "authentic" humanity; in others, they function as cautionary figures, representing obsolescence in the face of technological or societal change. These metaphorical uses often mirror contemporary anxieties—from colonialism and racial hierarchies in early fiction to environmental degradation and species extinction in more recent works.

5.3. Children's and young adult literature

In literature aimed at younger audiences, Neanderthals are often reimagined in ways that emphasize adventure, discovery, and cross-cultural friendship. Series such as Mary Pope Osborne's *Magic Tree House* (*Sunset of the Sabertooth*, 1996) offer simplified but sympathetic portrayals, encouraging curiosity about prehistoric life while downplaying its harsher realities. These representations tend to domesticate the Neanderthal image, presenting them as approachable figures and facilitating early engagement with human evolutionary history.

In the French context, the long-running comic series *Rahan, fils des âges farouches* (Lécureux & Chéret, 1969-), which appeared in *Pif Gadget*, offers another influential popular depiction of prehistory. Its idealised protagonist —a blond, inventive *Homo sapiens* moving through a fictional Pleistocene world inhabited by dinosaurs and diverse human tribes— exemplifies the hybrid imaginaries of the 1970s–1980s. Although Neanderthals are not explicitly named, some groups encountered by Rahan clearly evoke the "primitive other," reflecting contemporaneous popular notions of human evolution and cultural hierarchy.

6. Neanderthals in film and audiovisual media

The portrayal of Neanderthals in film and audiovisual media has decisively shaped their popular image, blending scientific interpretation, artistic license, and enduring stereotypes. Their first cinematic appearances date back to the silent film era, when "prehistory" was used as an exotic and dramatic backdrop. Films such as *One Million B.C.* (Hal Roach Studios, 1940) and its famous remake *One Million Years B.C.* (Don Chaffey, 1966) relied on confrontations between primitive humans and prehistoric creatures that had never coexisted, establishing a visual canon marked by crude clothing, guttural speech, and ritual violence (Klossner, 2015).

Later productions attempted to incorporate archaeological knowledge while retaining dramatic flair. *Quest for Fire* (1981), directed by Jean-Jacques Annaud and partly inspired by Rosny Aîné's novel, sought to recreate a Palaeolithic world with relative authenticity, introducing an invented language and ethnographic references. *The Clan of the Cave Bear* (1986), directed by Michael Chapman and adapted from Jean M. Auel's novel, explored cultural and biological tensions between Neanderthals and modern humans, though it received a mixed critical reception (Auel, 1980) (Fig. 8).

A more recent and darker portrayal appears in the French horror film *Humains* (2009, dir. Pierre-Olivier Thévenin and Jacques-Olivier

Fig. 8. Poster and film still from *Quest for Fire* (1981), directed by Jean-Jacques Annaud.

Molon), in which a group of modern travellers stranded in the Alps are hunted by surviving Neanderthals. Despite its overtly fictional premise, the film reactivates long-standing tropes of the "savage ancestor" and contrasts sharply with the more humanised reconstructions seen in contemporary documentaries and paleoart.

In the realm of documentary, productions such as *Neanderthal* (BBC Studios, 2001) and *Neanderthal Code* (National Geographic Channel, 2008) combined dramatic reconstructions with expert interviews, balancing outreach and visual appeal. More recently, Neanderthals have also appeared in television series (e.g., Al-Shamahi, 2018) and video games (e.g., Panache Digital Games, 2019), ranging from humorous depictions to hyperrealistic portrayals based on forensic reconstructions. Although more firmly grounded in scientific knowledge, these contemporary adaptations continue to reproduce narrative tropes inherited from earlier decades, illustrating the persistence of a hybrid imaginary where empirical rigor coexists with fiction.

7. Political and social uses of the Neanderthal figure

The Neanderthal has been repeatedly mobilized in political and social discourse. From the late 19th century onward, colonial propaganda and scientific racism placed Neanderthals at the bottom of an alleged evolutionary hierarchy, presenting them as cautionary emblems of what "civilized" humanity should avoid becoming. Within this framework, they became a malleable metaphor for primitivism, degeneracy, and failed adaptation—concepts easily transferred to debates on race, gender, and social progress.

Scientific consensus is one matter; ensuring that such consensus permeates public understanding is quite another. Cultural narratives, sustained over generations, weave a fabric of deeply rooted assumptions. As a result, the term *Neanderthal* has often been employed pejoratively by public figures to connote primitiveness, intellectual deficiency, brutishness, or backwardness. For instance, in the United States, President Joe Biden criticized the premature lifting of COVID-19 restrictions as "Neanderthal thinking," implying irresponsibility and regression. Donald Trump likewise used the term to disparage opponents, equating their decisions with primitive thought. Such rhetorical uses are not confined to politics. A 2016 *Salon* article titled *Neanderthals for Trump: How Our Primitive Brains Are Ruining American Politics* employed the label to demean Trump's supporters, suggesting biologically archaic tendencies shape contemporary politics. In sports, footballer Zlatan Ibrahimović has also hurled "Neanderthal" as an insult, implying lack of intelligence or civility.

In recent years, however, reinterpretations of the Neanderthal figure have emerged in more positive and identity-affirming contexts. Certain social movements—linked to regional heritage, or alternative narratives of human evolution—have embraced Neanderthals as symbols of resilience, adaptability, and community spirit (Papagianni and Morse, 2013). While still rooted in cultural imagination rather than scientific fact, these reframings challenge the long-standing pejorative legacy and reflect broader negotiations over the meanings attached to the deep human past. A clear illustration of this trend can be seen in public-facing initiatives such as the "We are all Neanderthals" campaign developed by the Neanderthal Museum in Mettmann (Germany), which explicitly reclaims the figure as a positive emblem of shared ancestry. Similarly, regional heritage associations and online communities have adopted the Neanderthal image as a marker of resilience and identity, particularly within environmental and cultural-revitalisation discourses.

8. The paleokitsch of Neanderthals

Addressing the theme of Neanderthals in the arts, and drawing from aesthetic theory, we pause to highlight a phenomenon that has recurred throughout their visual history and that reflects the persistent "false measure" of *Homo neanderthalensis*: what has been termed *paleokitsch*. Any artistic representation can be situated within aesthetic discourses that broaden the ontological scope of how Neanderthals have been envisioned across the brief history of paleoart. Looking back to the Victorian era, one may ask to what extent reconstructions were shaped by the artist's psyche—infused with the ethics and morals of the time, or with *sapiens* supremacism—and to what extent they were conceived to astonish and provoke emotion. This tension has characterized paleoart in general, including Neanderthal reconstructions. It is precisely through this drive to elicit sensation in eager audiences that kitsch enters the history of paleoart. Kitsch, however, is not a distinct style; rather, it reflects the values of a given society, values to which art lends resonance (Amorós, 2024).

In this sense, Amorós and Carrión (2025) propose the concept of *paleokitsch* to encompass the diverse cases in which paleoartistic works—whether overtly pseudoscientific or produced under the auspices of science—drift into distortion. Although the meaning of kitsch is neither unidirectional nor fixed, the phenomenon typically generates an excess of sentimentality in the observer. It appeals to universal emotions such as beauty, tenderness, or nostalgia, but may also evoke vertigo and anguish, since kitsch seeks passion and spectacle (Eco, 2007), distancing itself from neutrality.

Thus, *paleokitsch* encompasses not only pseudoscientific imagery but also scientific reconstructions that, in attempting to portray past behavior, lapse into monstrosity, distorting what palaeontology has carefully reconstructed. At this juncture, we must return to the inaugural iconography of the Neanderthal man, with its fierce phenomenology: dehumanized, depicted as a being diminished by lack of intelligence, compassion, and skill. Such moralizing and reductionist imagery reflected supremacist and colonialist tendencies. According to Amorós and Carrión (2025), the Neanderthal narrative began in this way, and its iconographic origins—like those of paleoart more broadly—are fundamentally kitsch.

9. Current scientific construct

Since their discovery, representations of Neanderthals have undergone profound transformations in relation to morphology, behavior, diet, social life, and environmental settings. These portrayals have always been contingent on fragmentary or contradictory evidence, as well as on shifting theoretical frameworks. From the outset, cultural preconceptions shaped scientific narratives, ensuring that depictions of Neanderthals—whether scholarly, artistic, or popular—were never entirely free of bias. Among hominin species, they have drawn particularly sustained attention due to their close evolutionary and chronological proximity to *Homo sapiens*. Taxonomic classification has itself mirrored shifting perceptions of Neanderthal humanity. Throughout much of the twentieth century, they were frequently designated *Homo sapiens neanderthalensis*—a subspecies of modern humans—reflecting an emphasis on continuity rather than separation. The subsequent preference for *Homo neanderthalensis* as a distinct species, while grounded in anatomical and genetic evidence, also signals a conceptual turn: from kinship to otherness. These alternating labels reveal how taxonomy not only organizes biological variation but also encodes changing cultural attitudes toward human uniqueness.

It is important to recall that the very notion of prehistory as a scientific domain is itself relatively recent. Until the 19th century, inquiry into the human past was largely limited to periods with written records, while earlier epochs remained cloaked in speculation and myth. The systematic study of deep time became possible only with the consolidation of archaeology, palaeontology, and evolutionary theory, alongside discoveries of tools, fossils, and chronological frameworks that gradually established prehistory as a recognized field of knowledge (Renfrew and Bahn, 2016).

In the last two decades, however, new discoveries have radically reshaped the scientific construct of Neanderthals. Paleogenomics has revealed that they interbred with anatomically modern humans, leaving a genetic legacy that persists in present-day non-African populations

(Green et al., 2010). This finding dismantled the old view of Neanderthals as an isolated, extinct lineage, reframing them instead within a shared evolutionary history marked by admixture and interaction (Talamo et al., 2023). Archaeological evidence—such as engraved motifs at Gorham's Cave (Gibraltar) and carefully arranged stalagmites in Bruniquel Cave (France) (Fig. 9)—points to symbolic and possibly artistic behavior (Rodríguez-Vidal et al., 2014; Jaubert et al., 2016). The debate surrounding the uranium–thorium dating of Spanish cave art further illustrates the persistence of such tensions. The studies by Hoffmann et al. (2018), which attributed painted motifs from La Pasiega, Maltravieso, and Ardales to Neanderthal authorship (> 64 ka), triggered intense discussion within the European palaeoarchaeological community. While some critiques focused on analytical uncertainties or sampling protocols, the controversy also revealed deeper cultural reluctance to acknowledge Neanderthals as capable of producing symbolic or "artistic" imagery. In this sense, the scientific debate reflected not only methodological scrutiny but also the enduring struggle to reconcile empirical evidence with entrenched preconceptions about human uniqueness.

Further advances in archaeological science have demonstrated technological versatility, from Levallois and hafting techniques to the exploitation of varied ecosystems. Collectively, these findings have overturned entrenched stereotypes of Neanderthals as cognitively inferior, offering instead a portrait of adaptable and resourceful humans whose capacities substantially overlapped with our own. Recent zooarchaeological research from the Central Balkans adds further weight to this view: at Velika Balanica cave (MIS 8/7), early Neanderthals systematically exploited both red deer and ibex in rugged mountainous terrain, demonstrating planning capacities, spatial organization around hearths, and ecological flexibility beyond traditional portrayals (Milošević et al., 2025). Comparable adaptive strategies are documented at the northernmost Neanderthal sites, such as Byzovaya and Mamontova Kurya near the Arctic Circle (Slimak et al., 2011), where occupation evidence under severe glacial conditions further attests to their capacity to endure extreme cold environments through complex behavioural and technological responses.

10. Towards a more human Neanderthal

10.1. Familiar faces

Neanderthal facial morphology has often been interpreted as a textbook example of cold adaptation, with broad nasal apertures and pronounced midfacial projection viewed as evolutionary responses to glacial climates. Yet this long-standing assumption is increasingly questioned. Rae et al. (2011), using both 2D X-ray imaging and 3D CT scans, found no evidence that Neanderthal paranasal sinuses were significantly larger than those of modern humans from temperate environments. This weakens the proposed link between sinus volume and cold tolerance, pointing instead to alternative drivers such as biomechanical demands related to mastication or ecological factors unrelated to climate. More broadly, Neanderthal cranial traits diverge from the patterns observed in cold-adapted mammals, which typically display reduced prognathism (forward projection of the face) and narrower nasal passages. In contrast, Neanderthals combined midfacial prognathism with wide nasal apertures—features not easily explained by simple climatic analogies.

Recent genetic studies add another dimension. Li et al. (2023) identified novel genomic loci influencing facial shape, including a region on chromosome 1q32.3 of Neanderthal origin, associated with increased nasal height and midfacial projection. These findings suggest that aspects of Neanderthal craniofacial morphology persist in present-day populations, pointing to a subtler phenotypic divide between *Homo neanderthalensis* and *H. sapiens* than is often portrayed.

10.2. Evolutionary development and Neanderthal iconography

Comparative analyses of fossil cranial ontogenetic series and virtual reconstructions of endocranial and facial growth patterns allow us to infer that some morphological differences between Neanderthals and modern humans stem from divergences that accumulated along the pre-Neanderthal lineage since the earliest *Homo* and even further back to australopithecines and the first hominins (Huguet et al., 2025). Many of these differences can be understood within an evolutionary developmental (Evo-Devo) framework, particularly in terms of the pedomorphic—or neotenic—trajectory followed by both our species and

Fig. 9. Stalagmite ring structures from Bruniquel Cave (southwestern France), dated to ~176 ka. The photograph shows the larger circular structure and associated alignments of deliberately broken stalagmite sections arranged on the cave floor. Many fragments display evidence of heating, indicating fire use during construction. Located 336 m from the entrance, these ordered accumulations—made from selected, fractured, and transported speleothems—represent the earliest large-scale spatial arrangements attributed to Neanderthals. Image adapted under CC BY 4.0 from Jaubert et al. (2016).

Neanderthals from more "ape-like" ancestors (Zollikofer et al., 2022). This long-term trend of morphological juvenilization means that adults of derived species increasingly resemble the juveniles of their ancestral forms (Montagu, 1955; Gould, 1977; Zollikofer, 2012). Such evolutionary change is evident in cranial configuration but may also extend to genital organization and the retention of juvenile hair distribution patterns (concentrated on the head, axillae, and pubis) (Wolpoff, 2022).

This "rejuvenated" morphology facilitated evolutionary innovations such as increased cranial volume and expanded prefrontal capacity (Henke and Tattersall, 2007; Ponce de León et al., 2021). Ponce de León et al. (2016) demonstrated that Neanderthals and modern humans shared broadly similar postnatal brain developmental trajectories. Although endocranial morphology exhibited species-specific differences at birth, the patterns of shape change during the crucial first two years of life were strikingly alike. This finding contradicts earlier claims that modern humans possessed a uniquely derived mode of postnatal brain development, suggesting instead that both species inherited comparable developmental mechanisms from a common ancestor. Craniofacial evidence likewise indicates that Neanderthals and modern humans did not diverge in ontogenetic trajectories after early infancy, but that major morphological distinctions were already established prenatally and in the earliest postnatal stages (Bastir et al., 2007). Additional evidence from the juvenile skeleton El Sidrón J1 further supports this view: despite subtle differences in vertebral maturation and prolonged brain growth, Neanderthal children largely followed growth rates comparable to those of modern humans, indicating that divergences reflect physiological adaptations rather than a fundamentally distinct developmental pace (Rosas et al., 2017). Together, these findings underscore that differences in cranial form after birth do not necessarily imply major cognitive distinctions, but rather reflect shared evolutionary processes subsequently modulated by craniofacial growth, physiology, and life-history factors.

On the other hand, current knowledge strongly challenges the linear evolutionary iconographies popularized in the twentieth century—such as Rudolph Zallinger's *March of Progress*—which promote an anagenetic bias inconsistent with genomic evidence for cladogenesis, reticulation, and gene flow (Gould, 2008; Lalueza-Fox, 2013; Huguet et al., 2025) (Fig. 10).

Within this context, recurrent features in artistic portrayals of Neanderthals lack scientific corroboration and often reflect deliberate or unconscious bias (Rack, 1986; Wragg and Sykes., 2020). Common tropes include excessive body hair (a plesiomorphic trait), long occipital hair emphasizing cranial elongation, overly prominent lips, a forward-shifted mandible forcing neck flexion, exaggerated supraorbital ridges, and accentuated cranial slope. Such conventions can be traced in the works of Hermann Schaaffhausen (Fig. 2), František Kupka (Fig. 4), Rudolph Zallinger (Fig. 9), Zdeněk Burian (Fig. 7), and Charles R. Knight. By contrast, Mauricio Antón situates Neanderthals within their ecological and behavioral contexts, blending scientific rigor with a naturalistic pictorial style that highlights their integration into complex environments (Fig. 11). Elisabeth Daynès, through her hyperrealist sculptural technique using silicone and anatomical modeling, conveys individuality and empathy, underscoring the humanity of these hominins (Fig. 12). Adrie and Alfons Kennis employ a dynamic mix of digital and traditional methods to capture vitality and expressiveness, presenting Neanderthals as emotionally rich and socially engaged beings (Fig. 13). Together with other artists such as Tom Björklund and Benoît Clarys, their work exemplifies a decisive shift away from caricatured

Fig. 11. Neanderthal reconstruction with shell ornaments and body paint, by Mauricio Antón (https://mauricioanton.wordpress.com/). Courtesy of the author.

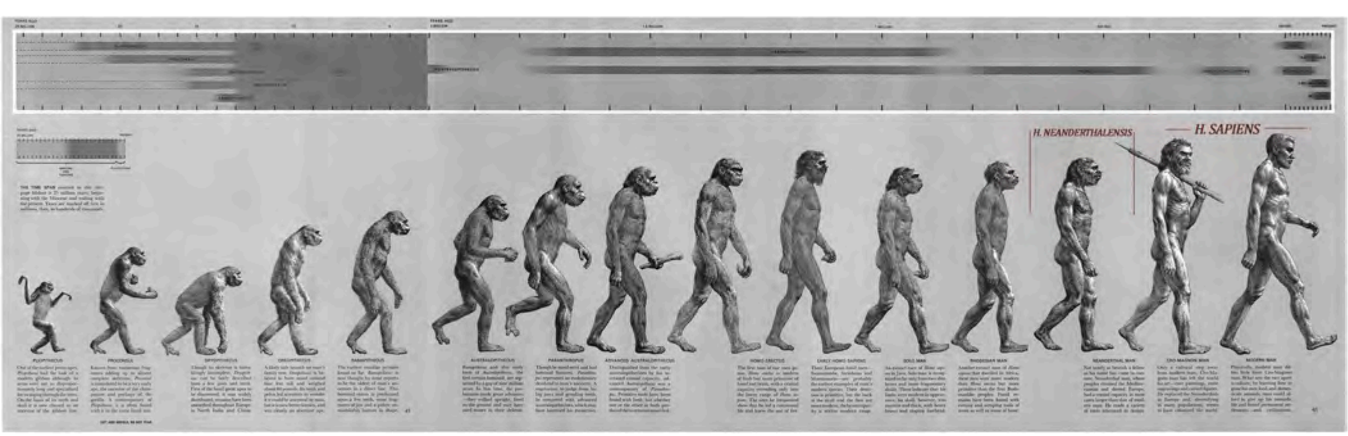

Fig. 10. The image titled *"The Road to Homo sapiens"*, though more commonly known as *"The March of Progress"*, was created by Rudolph Zallinger for the volume *Early Man* (1965), published by Time-Life Books as part of the *Life Nature Library*. Originally spanning four and a half pages and including 15 figures, only six were shown when the foldout was compressed, producing the abbreviated version that became iconic. ©Washington University in St. Louis. Source: https://sites.wustl.edu/prosper/on-the-origins-of-the-march-of-progress/.

Fig. 12. Hyper realistic sculpture of the Neanderthal male *La Ferrassie* made by Elisabeth Daynès. The La Ferrassie site (Dordogne, France) is one of the most important Neanderthal burial grounds, where several remarkably well-preserved skeletons were discovered, including adults and children. This reconstruction reflects Daynès' emphasis on individuality and empathy, situating the figure within the broader archaeological context of a population whose mortuary practices and social complexity challenge older "ape-like" representations. Courtesy Reconstruction ©Elisabeth Daynes/Photo S. Entressangle.

Fig. 13. *Homo neanderthalensis father and child* by Adrie and Alfons Kennis. The Dutch brothers are known for emphasizing vitality and sociality in their paleoart, often portraying Neanderthals in dynamic and emotionally expressive ways. This piece illustrates their characteristic style, presenting an adult and a child in a warm, lifelike manner that underscores the humanity of Neanderthal communities and contrasts sharply with older, dehumanizing depictions. ©3D model/photo by Kennis&Kennis.

primitivism toward reconstructions that foreground Neanderthal humanity. Nevertheless, outdated tropes persist, especially in certain comic book depictions—such as José Manuel Gallego, Frank Frazetta, and, to a lesser extent, Emmanuel Roudier—demonstrating the resilience of archaic visual conventions in popular culture (Fig. 14).

10.3. Beyond bones: genomics, archaeology, and the myth of sapiens exceptionalism

In the last two decades, paleogenomics has rewritten much of the story we thought we knew about the later phases of human evolution. The once-clear boundaries between *Homo sapiens*, *H. neanderthalensis*, Denisovans, and other archaic populations have blurred under the weight of new genetic evidence (Prüfer et al., 2014; Slon et al., 2018; Hajdinjak et al., 2018). Far from being isolated lineages, these groups met, interacted, and—crucially—interbred, sometimes repeatedly. Genetic traces of these encounters persist today in all non-African populations, averaging 1–4 % Neanderthal ancestry. Such findings weaken the traditional reliance on rigid morphological species concepts and recall Ernst Mayr's biological definition—reproductive isolation—as perhaps the only truly testable boundary (Mayr, 1963).

The fossil record complicates matters further. Some specimens exhibit intermediate features between modern humans and Neanderthals (Harvati et al., 2019; Higham, 2021), yet their genetic signatures remain unknown. Conversely, genetically identified hybrids often lack detailed anatomical description. Taxonomic assignments sometimes hinge on traits—such as dental morphology—shaped as much by environment as by ancestry (Ackermann et al., 2019), yet they continue to be treated as diagnostic (Bailey et al., 2009). Genomic modeling points to at least one major episode of introgression between Neanderthals and modern humans between ~370 and 100 ka (Petr et al., 2020). Fossils also reinforce the possibility of earlier contact: individuals with modern human morphology are documented at Jebel Irhoud, Morocco (~300 ka; Hublin et al., 2017), the Levant (~194–177 ka; Hershkovitz et al., 2018), and southern Greece (~210 ka; Harvati et al., 2019).

Archaeology adds another layer of complexity. In the Levant, the Mousterian tool tradition was produced by both Neanderthals and early modern humans, undermining simple links between technology and taxonomy. The makers of "transitional" industries—Bohunician, Szeletian, Uluzzian, and Châtelperronian—might be been treated as uncertain (see for discussion: Peresani et al., 2019; Finlayson et al., 2023; Higham et al., 2024). However, direct associations between Neanderthal remains and Châtelperronian layers at Saint-Césaire and at Grotte du Renne (Hublin et al., 2012; Welker et al., 2016) provide the strongest

Fig. 14. a. Neanderthal, pen and ink drawing by José Ramón Gallego. Source: http://jrgallego.blogspot.com/2012/ b. Cover illustration for the comic Neanderthal (1966, Ed. Novena Dimensión), by Frank Frazetta. Source: http://loscomicsdemachete.blogspot.com/2014/09/neanderthal-de-frank-frazetta-llega.html c. Cover illustration for the Spanish comic Neanderthal (2013, Norma Editorial), by Emmanuel Roudier. Source: http://loscomicsdemachete.blogspot.com/2014/08/neandertal-de-emmanuel-roudier.html.

evidence currently available linking this technocomplex to Neanderthals; to date, Neanderthals are the only species securely identified within these layers. Until *Homo sapiens* remains are securely documented in unambiguous Châtelperronian contexts, alternative attributions remain speculative. Even the Aurignacian in West Asia remains debated (Shea, 2016; De la Peña., 2019). Early Aurignacian sites in Iberia, such as Bajondillo Cave (Málaga), have been proposed as markers of Neanderthal extinction (Cortés-Sánchez et al., 2019), but stratigraphic problems (Anderson et al., 2019; De la Peña., 2019) and persistence of Middle Paleolithic technologies elsewhere (Slimak et al., 2022) caution against neat conclusions. Overreliance on "competitive displacement" narratives risks reviving outdated images of Neanderthals as cognitively and adaptively inferior (Finlayson, 2019).

A recent synthesis clarifies why such dichotomies collapse. Zilhão and colleagues argue that there is no one-to-one mapping between biological identity and material culture across the Middle-to-Upper Paleolithic transition: genomes varied in continuous space, while technocomplexes varied discretely (Zilhão et al., 2024). Many assemblages suffer from taphonomic and associational noise—post-depositional mixing, undated teeth, inherited charcoal—rendering taxonomic attributions to toolkits intrinsically fragile. Zilhão et al. (2024) favor an assimilation model: a millennia-long process of convergent innovation, cultural diffusion, and gene flow that culminated, after ~37 ka, in Eurasian homogenization—biological and cultural—rather than abrupt replacement.

Genomic analyses sharpen this perspective. Lalueza-Fox (2021) highlights that several Late Pleistocene modern human genomes—from Bacho Kiro (Bulgaria), Zlatý kůň (Czechia), and Oase (Romania)—carry signals of very recent Neanderthal ancestry, in some cases only four to six generations back. Rather than rare anomalies, these cases suggest that interbreeding was recurrent and systematic. Interestingly, while gene flow from Neanderthals into modern humans appears ubiquitous, reciprocal signals of admixture into late Neanderthals are absent, perhaps reflecting demographic imbalances, genetic incompatibilities, or social barriers. Together, these findings support an assimilation model in which Neanderthals were not abruptly replaced but gradually absorbed into expanding modern human populations, their genomic legacy diluted by subsequent demographic dynamics.

This debate is not purely scientific—it is cultural. For centuries, we have sought to elevate *Homo sapiens* above all others in the genus, a habit embedded in our very name: "wise human." The Enlightenment taxonomy of Carl Linnaeus, shaped by Judeo-Christian moral thought (Harari, 2015), codified the idea that our species alone possessed moral and intellectual supremacy. Early Neanderthal reconstructions—stooped, hairy, brutish—were designed as foils to highlight our supposed refinement. The more "primitive" they looked, the more exceptional we appeared.

Yet paleogenomics tells another story. Neanderthals and modern humans diverged from a common ancestor—likely *H. heidelbergensis*, and their histories remained entangled ever since (Petr et al., 2020). Genetic variants inherited from Neanderthals influence skin and hair pigmentation, immune function, metabolism, and even aspects of brain development (Zeberg et al., 2024). Some conferred adaptive advantages; others proved deleterious and were purged. Anatomically, Neanderthals exhibited longer, lower cranial vaults, midfacial projection, robust physiques, and shorter distal limbs—traits often linked to cold adaptation—but cranial capacity overlapped, and sometimes exceeded, that of modern humans. Fundamentally, their cranio-dental architecture remained strikingly similar (Reilly et al., 2022; Rosas et al., 2022).

Taken together, the evidence dismantles the myth of *sapiens* exceptionalism. What emerges is not a tale of two species divided by an unbridgeable gulf, but of close relatives bound by shared ancestry, recurrent contact, and overlapping capacities. In this light, the distinction between "us" and "them" dissolves, replaced by a more intricate truth: *Homo sapiens* is not the summit of a linear ascent, but one branch in a tangled hominin tree—different, yes, but never entirely apart.

10.4. Technology as mismeasure of progress and fitness

The conventional narrative of the Middle-to-Upper Palaeolithic shift has long been framed as a "revolution" driven by the arrival of *Homo sapiens* (Mellars, 2005). Middle Paleolithic industries, largely associated with Neanderthals, are typically characterized by flake-based production, recurrent Levallois and discoidal methods, and a relatively narrow repertoire of retouched tool types—scrapers, denticulates, and Mousterian points. By contrast, Upper Paleolithic assemblages show a striking increase in typological diversity and technological complexity: systematic blade and bladelet production, standardized projectile points, composite tools, and the use of bone, antler, and ivory, alongside ornaments and portable art (d'Errico et al., 1998; Bar-Yosef, 2002). These features have often been taken as archaeological markers of enhanced cognitive and cultural capacities in Homo sapiens. Transitional industries (such as the Châtelperronian, Uluzzian, and Szeletian) combine Mousterian features with elements associated with the early Upper Paleolithic—such as ornaments or blade production—suggesting either Neanderthal acculturation or the first dispersals of modern humans into Europe (Zilhão et al., 2024) (Fig. 15). However, direct associations between Neanderthal remains and Châtelperronian layers at Saint-Césaire and at Grotte du Renne (Hublin et al., 2012; Welker et al., 2016) demonstrate that Neanderthals themselves were responsible for at least part of this technological and symbolic repertoire. Some studies propose that early blade industries emerged in ecotonal contexts, where environmental pressures and shifting hunting strategies encouraged the proliferation of projectile weaponry (Finlayson and Carrión, 2007).

Yet a purely technocentric perspective may obscure more than it reveals. Slimak (2023), in a provocative contribution, cautions against reducing this contrast to a simplistic hierarchy of "primitive" versus "advanced." The real distinction, he argues, lies not in the number or sophistication of tool types but in the underlying logic of technological production. Whereas *sapiens* industries—such as blade and microlithic technologies—tended to display recurring patterns across vast regions, reflecting broad social networks and shared norms, Neanderthal technocomplexes often appear as localized, idiosyncratic responses to specific contexts. In this light, Neanderthal industries demonstrate inventiveness and adaptability, but limited long-distance transmission, while *Homo sapiens* industries reveal a strong orientation toward replication, standardization, and the stabilization of traditions across millennia, and across wide regions.

Thus, the so-called Upper Paleolithic "revolution" can be seen less as the sudden emergence of superior cognition and more as a shift in the ways knowledge was transmitted, codified, and perpetuated. Slimak's (2023) interpretation may not be universally accepted, but it forces critical reflection at a time when ecological and sociological change has accelerated. Our cultural baggage often conflates progress with technology (Mander, 1991). While *sapiens* technology undeniably grew in complexity, this does not necessarily equate to greater adaptive capacity.

10.5. Diet, trophic flexibility, and robustness

The Neanderthal diet offers crucial insights into their ecological niche and adaptive strategies. Once portrayed as predominantly carnivorous hunters, they are now recognized as highly flexible omnivores, capable of adjusting to the climatic and ecological variability of the Pleistocene. Metagenomic studies highlight pronounced regional variation: Iberian groups relied heavily on plants, fungi, and forest resources, while contemporaneous populations at Spy Cave (Belgium) maintained a meat-rich diet dominated by large herbivores (Weyrich et al., 2017). In Cantabrian contexts, subsistence strategies shifted dynamically in response to nutritional stress (Marín-Arroyo and Sanz-Royo, 2021) with episodes of increased reliance on lower-return prey and context-dependent shifts between montane and lowland resources.

Zooarchaeological evidence further underscores this breadth. In Gibraltar, Neanderthals exploited marine mammals (Stringer et al., 2008); in Mediterranean settings, they consumed small prey such as tortoises, lagomorphs, and birds (Blasco and Fernández Peris., 2012). Access to emergent coastal platforms facilitated the use of fish, seabirds, and shellfish (Finlayson and Carrión, 2006). At Kalamakia in Greece, faunal remains attest to the exploitation of ungulates alongside tortoises and molluscs (Harvati et al., 2013), further illustrating dietary versatility.

Microfossil and dental calculus analyses confirm the inclusion of plants in their diet. Evidence from La Quina (France) and Amud Cave (Israel) documents the consumption of cattail (*Typha*), bistort (*Polygonum*), and burdock (*Arctium*), even under glacial conditions (Hardy, 2010). At Chagyrskaya Cave (Siberia), starch grains from grasses, legumes, goosefoot, and Caryophyllaceae were identified, alongside pine and birch residues—suggesting both dietary and non-dietary uses (Salazar-García et al., 2021). Comparative studies confirm that Neanderthals and early modern humans alike exploited a wide spectrum of plant resources (Henry et al., 2014). As Fiorenza et al. (2015) note, this evidence challenges the image of Neanderthals as primarily carnivorous, revealing instead a flexible and ecologically responsive omnivory.

In colder or arid settings, where plant carbohydrates were scarce, Neanderthals relied heavily on animal-sourced carbohydrates (ACH). Glycogen stored in the organs of large mammals—such as mammoth or bison—likely buffered the risks of a protein-heavy diet (Guil-Guerrero, 2022). This dietary strategy complemented their robust physique—broad ribcage, high body mass, and stocky limbs—adaptations that supported bursts of high-intensity activity, including ambush hunting (Pomeroy, 2023).

Taken together, the emerging picture is one of ecological and physiological adaptability. Neanderthals combined a protein-rich, calorie-dense diet with the strategic use of plants and small game, supported by a metabolism tuned for high energy expenditure. Their trophic flexibility portrays them not as evolutionary specialists bound to big-game hunting, but as adaptive generalists—parallel in many respects to early *Homo sapiens*. Far from an evolutionary cul-de-sac, these strategies highlight convergent solutions to shared challenges and underscore that Neanderthals were not so different from ourselves.

10.6. Fire and glue: pyrotechnology and adhesive mastery

Archaeological evidence from Middle and Late Pleistocene contexts demonstrates that Neanderthals possessed a sophisticated command of adhesives, long-distance raw material procurement, and pyrotechnology. Early precedents extend well beyond the Late Pleistocene: tar residues on stone tools from Königsaue, Germany (~50 ka), provide the earliest direct evidence for birch-bark pitch manufacture in Europe, requiring controlled heating in oxygen-restricted conditions (Koller et al., 2001). Even earlier, bitumen residues on lithics from Campitello Quarry, Italy (~200 ka), confirm hafting technology in Europe, with chemical analyses identifying natural asphalt as the binding agent (Mazza et al., 2006). These findings establish a deep Middle Pleistocene origin for adhesive use in Europe.

By the later Middle Paleolithic, these technologies were applied with remarkable precision. At Umm el Tlel (Syria), bitumen residues dated to ~71 ka—sourced from deposits over 40 km away—demonstrate not only knowledge of adhesive properties but also their deliberate incorporation into complex composite tools and long-distance provisioning systems, marking a significant expansion in the technological use of bitumen rather than the earliest chronological occurrence (Boëda et al., 2008). In Gibraltar's Vanguard Cave, a 65 ka hearth shows a multi-layered architecture deliberately designed to create anoxic, low-temperature conditions for extracting tar from resinous plants such as rockrose (Cistaceae). Experimental replication confirmed that this structure could reliably produce enough tar to haft multiple spearheads, attesting to deliberate design, environmental knowledge, and fire mastery for specific technological goals (Ochando et al., 2024).

Complementing these adhesives, Neanderthals also produced specialized bone tools previously thought to be exclusive to *Homo sapiens*. The discovery of lissoirs—polished bone implements for hide-working—in securely Neanderthal contexts predating modern human arrival in Europe points either to independent innovation or to cultural transmission from Neanderthals to incoming *Homo sapiens* (Soressi et al., 2013). Collectively, these findings reveal a technological repertoire requiring planning, material science awareness, and procedural skill—traits fully consistent with the cognitive capacities attributed to our own species.

Fig. 15. Selected lithic artefacts from the Châtelperronian assemblage at Aranbaltza II (Barrika, Basque Country, Spain), attributed to Neanderthal groups. The site provides one of the clearest Iberian examples of this transitional technocomplex. Image adapted under CC BY 4.0 from Rios-Garaizar et al. (2022).

10.7. Feathers and claws: symbolic dimensions of Neanderthal avian use

Multiple archaeological contexts demonstrate that Neanderthals systematically exploited avian species—particularly raptors and corvids—not for subsistence but for symbolic use of feathers and talons. The large-scale analysis by Finlayson et al., covering 1699 Pleistocene sites across the Palearctic, and detailed taphonomic studies at Gorham's, Vanguard, and Ibex Caves (Gibraltar), identified cut marks consistent with deliberate extraction of large flight feathers. This behaviour, observed across multiple periods, indicates a structured and repeated cultural practice rather than isolated acts, supporting the view that Neanderthal symbolic capacities paralleled those of early modern humans. Further case studies reinforce this conclusion. At Grotta di Fumane (Italy), Peresani et al. (2011) documented modifications on wing bones of lammergeier, Eurasian black vulture, golden eagle, red-footed falcon, common wood pigeon, and Alpine chough—species often non-edible—suggesting intentional feather removal (Fig. 16). Crucially, this behaviour predates modern human arrival, showing that it emerged independently among Neanderthals.

Other examples expand the scope: at Zaskalnaya VI (Crimea), Majkić et al. (2017) reported a raven bone incised with carefully spaced notches, clear evidence of symbolic marking. At Combe-Grenal and Les Fieux (France), raptor remains show patterns of modification compatible with symbolic removal of claws and feathers. A particularly compelling case comes from the Châtelperronian levels of Grotte du Renne, where a deliberately modified imperial eagle (*Aquila adalberti*) phalanx has been interpreted as a personal ornament; all these instances are reviewed in detail by Morin and Laroulandie (2012). At Krapina (Croatia), Radovčić et al. (2015), (2020) documented white-tailed eagle talons with cut marks, pigment traces, and fibre residues, interpreted as jewellery (Fig. 17).

The Iberian Peninsula has also yielded key evidence. At Cova Foradada (Spain), Rodríguez-Hidalgo et al. (2019) reported a Châtelperronian imperial eagle phalange deliberately modified as a personal ornament. This is the earliest such example in Iberia and extends the geographic range of this symbolic tradition. Its recurrence across sites and times demonstrates that the appropriation of raptor talons formed part of a durable symbolic repertoire. Together, these findings dismantle the long-standing view of purely utilitarian Neanderthal–bird interactions, revealing instead a behavioural complexity where ornamentation and symbolic expression played a recurring role.

10.8. Beyond utility: pigment and ornament use in Neanderthal societies

Archaeological evidence shows that Neanderthals systematically used pigments and ornaments, directly challenging long-held assumptions that such symbolic practices were exclusive to *Homo sapiens*. At Cueva de los Aviones and Cueva Antón (Spain), perforated shells with traces of hematite and pyrite suggest deliberate production of body ornamentation and colour symbolism more than 115 ka ago (Zilhão et al., 2010; Hoffmann et al., 2018) (Fig. 18). Similarly, ochred shells from Fumane Cave (Italy) attest to the symbolic use of mineral and faunal resources (Peresani et al., 2011). Pigments are also present at sites such as Maastricht-Belvédère (200–250 ka, Netherlands) (Roebroeks et al., 2012) and Pech de l'Azé (~51 ka, France) (d'Errico and Soressi, 2002; Heyes et al., 2016), reinforcing the idea that body painting and symbolic display formed part of Neanderthal lifeways.

Recent analytical advances have strengthened these interpretations. Geoarchaeological and geochemical studies reveal that pigment use was not opportunistic: in several Mousterian contexts, Neanderthals deliberately selected specific minerals based on colour, grain size, and physical properties, sometimes transporting them over considerable distances. At Pech de l'Azé, the consistent use of manganese dioxide blocks suggests not only symbolic applications but also possible pyrotechnological uses, as experimental work shows its capacity to facilitate fire ignition (Heyes et al., 2016). Likewise, Châtelperronian pigment assemblages reflect non-random raw material selection, pointing to established cultural preferences rather than casual use (Dayet et al., 2014).

A striking recent find from San Lázaro rock-shelter (Level H) in Central Spain provides direct evidence of symbolic marking: a leucogranite pebble with three cupules and a central ochre dot containing a fingerprint, revealed through multispectral analysis. Physico-chemical tests (XRF, SEM-EDX) confirmed deliberate pigment addition, while 3D microtopography and spatial statistics (Monte Carlo, Clark-Evans, Ripley's K) ruled out randomness. The pebble shows no functional

Fig. 16. a. A Neanderthal Man, by Mauro Cutrona. Source: https://terraeantiqvae.com/. Image courtesy of Mauro Cutrona and Marco Peresani. b. El Neandertal Emplumado, a reconstruction of a Neanderthal who lived about 50,000 years ago, created by Fabio Fogliazza. The sculpture was presented at the opening of the exhibition Cambio de imagen at the Museo de la Evolución Humana, Burgos. Source: https://www.museoevolucionhumana.com/archivos/Cambioimagen.pdf.

Fig. 17. White-tailed eagle talons from Krapina (Croatia), showing cut marks, pigment traces, and fibre residues interpreted as elements of personal adornment. These artefacts, dated to ca. 130 ka, represent some of the earliest known jewellery in human evolution. Image adapted under CC BY 4.0 from Radovčić et al. (2015).

Fig. 18. Perforated marine shells with pigment traces from Cueva de los Aviones (Cartagena, Spain), dated to > 115 ka. These objects provide some of the earliest secure evidence of symbolic behaviour in Neanderthals, demonstrating deliberate use of pigments and personal ornamentation. Image adapted under CC BY 4.0 from Hoffmann et al. (2018).

use, was transported from the Eresma river, and its configuration suggests intentional communication (possibly invoking facial pareidolia). This object—arguably a piece of non-figurative portable art—constitutes the oldest known human fingerprint associated with pigment in Europe, reinforcing the recurrence of symbolic marking in Neanderthal culture (Álvarez-Alonso et al., 2025).

While earlier discussions raised concerns about possible stratigraphic mixing at Grotte du Renne in north-central France (Higham et al., 2010; Mellars, 2010), subsequent reassessment of the site demonstrated that these concerns are unfounded (Hublin et al., 2012). Robust and stratigraphically secure evidence—further supported by biomolecular analyses identifying Neanderthal remains within Châtelperronian layers (Welker et al., 2016)—confirms that symbolic behaviours among Neanderthals were neither isolated nor ephemeral. Rather, they reflect recurrent cultural practices deeply embedded in Middle Palaeolithic societies.

10.9. Clothing and thermal protection

The widespread presence of end-scrapers, hide-processing tools, and awls in Mousterian contexts strongly suggests that Neanderthals relied extensively on animal skins for clothing and insulation. Cut-mark analyses on ungulate remains indicate systematic skinning beyond subsistence needs, pointing to deliberate hide procurement (Hoffecker, 2002; Roebroeks and Villa, 2011). While the earliest eyed needles appear later and are securely associated with *Homo sapiens*, bone awls from Neanderthal contexts imply the capacity to perforate hides and possibly produce fitted or stitched garments adapted to cold climates (Soressi et al., 2013).

Zooarchaeological and use-wear evidence reinforces this interpretation. At sites such as Abri Peyrony and Pech de l'Azé (France), bone lissoirs for hide-working provide direct evidence of leather processing (Soressi et al., 2013). Micro-wear analyses on Mousterian scrapers confirm their repeated use on soft materials consistent with hide preparation (d'Errico et al., 1998). Additionally, cut marks on carnivore remains, including hyenas, from Navalmaíllo rockshelter (Spain), suggest selective targeting for insulating furs (Moclán et al., 2024).

Complementary finds expand the picture. A three-ply cord fragment made from inner bark fibres at Abri du Maras (France) represents the earliest direct evidence of fibre technology among Neanderthals (Hardy et al., 2020). Advanced microscopy and spectroscopy confirmed deliberate fibre manipulation, showing that Neanderthals had the operational memory and planning capacity to produce cordage—likely used for fastening, stitching, or even weaving garments. Such fibre technology significantly broadened the materials available for body protection.

Palaeoenvironmental syntheses underscore that investment in clothing and shelter was central to Neanderthal resilience across diverse and often harsh climates (Hoffecker, 2002). Ethnographic parallels confirm that without protective garments, survival in periglacial settings north of ~50°N would have been impossible, even with fire and cave shelter. These settings were simply part of the northern environments Neanderthals encountered during climatic oscillations, rather than habitats they actively sought out. The evidence demonstrates that Neanderthals combined pyrotechnology, hide use, fibre-based fastening, and strategic site choice to create flexible thermal protection strategies.

Some scholars propose that *Homo sapiens* may have developed more complex tailored clothing, conferring an advantage in extreme glacial conditions (Collard et al., 2016). Yet such interpretations rest on fragmentary data and risk perpetuating narratives of Neanderthal inadequacy. As a chronospecies, Neanderthals endured multiple glacial cycles over tens of millennia, successfully inhabiting high-latitude environments long before *Homo sapiens* entered Europe. Their persistence undermines claims of a fundamental technological deficit and instead highlights their adaptive ingenuity.

10.10. Marks in the darkness: Neanderthal cave art and engravings

Uranium-thorium dating of carbonate crusts has demonstrated that cave paintings from three sites in Spain—La Pasiega (Cantabria), Maltravieso (Extremadura), and Ardales (Andalucía)—are older than 64 ka, predating the arrival of anatomically modern humans in Europe by at least 20,000 years and thus implying Neanderthal authorship (Hoffmann et al., 2018). These motifs include a red linear sign at La Pasiega, a negative hand stencil at Maltravieso, and red-painted speleothems in Ardales. Collectively, they constitute the earliest known cave art worldwide, indicating that Neanderthals engaged in symbolic expression through geometric forms and iconic imagery—challenging the long-standing view that such behaviours were exclusive to *Homo sapiens*.

Additional evidence comes from Gorham's Cave (Gibraltar), where Rodríguez-Vidal et al. (2014) reported a deeply impressed cross-hatched engraving carved into bedrock, sealed beneath an undisturbed Mousterian level and dating to more than 39 ka. Microscopic analysis and experimental replication confirm that the intersecting lines were deliberately and repeatedly incised with a lithic tool, ruling out utilitarian or accidental origins. This engraving represents the first known abstract pattern created by Neanderthals, underscoring their capacity for intentional symbolic marking in durable media (Fig. 19).

More recently, Marquet et al. (2023) documented structured, non-figurative engravings on the walls of La Roche-Cotard (Loire Valley, France), sealed beneath cold-period sediments for more than 57 ± 3 ka. Traceological, taphonomic, and experimental analyses confirm their anthropogenic origin: deliberate finger-flutings devoid of functional purpose. The associated Mousterian lithics and absence of later cultural material strongly support Neanderthal authorship, making these the earliest unambiguous engravings on cave walls attributed to this species.

From a cognitive archaeology perspective, García Capín (2025) argues that Neanderthals possessed the attentional, emotional, and causal reasoning capacities necessary to both create and interpret such non-figurative cave art. The prominence of red pigments—perceptually salient across cultures and often associated with fear and curiosity—suggests that these marks functioned not only as visual stimuli but also as indices of human presence, effectively "domesticating" the hostile cave environment.

Taken together, painted motifs in Iberia, engraved bedrock in Gibraltar, and finger-fluted walls in France demonstrate that Neanderthals repeatedly engaged in symbolic marking within deep cave contexts. Far from isolated anomalies, these examples reveal a geographically and temporally broad pattern of symbolic behaviour, undermining any sharp cognitive divide between Neanderthals and early modern humans.

Fig. 19. Abstract cross-hatched engraving carved into bedrock at Gorham's Cave (Gibraltar), overlain by undisturbed Mousterian levels dated to > 39 ka. Experimental and microscopic analyses confirm deliberate incision with a lithic tool, representing one of the earliest known examples of Neanderthal abstract marking. Image adapted under CC BY 4.0 from Rodríguez-Vidal et al. (2014).

10.11. Evidence for speech

Whether Neanderthals possessed spoken language remains a major challenge, since soft tissues such as the larynx do not fossilise. Nonetheless, anatomical evidence indicates that their vocal tract was broadly comparable to that of modern humans, and the morphology of their auditory ossicles suggests sensitivity to sound frequencies similar to our own (D'Anastasio et al., 2013). Further support comes from the Kebara 2 hyoid bone (Israel), virtually indistinguishable from that of *Homo sapiens*, implying comparable biomechanical potential for speech (Arensburg et al., 1989).

Recent bioengineering studies have refined this picture. Conde-Valverde et al. (2021) applied high-resolution CT scans to virtually reconstruct the outer and middle ear in multiple Neanderthal fossils, including specimens from La Chapelle-aux-Saints and Krapina (~130 ka), as well as Middle Pleistocene individuals from Sima de los Huesos (Atapuerca). Using auditory transmission models, they calculated sound power transmission (SPT) and occupied bandwidth (OBW), parameters linked to communication efficiency. Results revealed that Neanderthal auditory capacities fell squarely within the modern human range, extending into the higher-frequency band crucial for perceiving and producing consonants. This strongly suggests that Neanderthals not only had the anatomical potential for speech but also the auditory "hardware" to sustain communication systems as efficient as those of *Homo sapiens*.

Archaeological indicators of complex social life—coordinated hunting, symbolic ornamentation, and care for the sick—further imply that verbal language played a central role in their interactions. While the structure and richness of Neanderthal language remain unknowable, it is plausible that they were capable of transmitting complex information, supporting social cohesion, and facilitating cultural transmission in ways not unlike our own.

10.12. Ritualised funerary practices among Neanderthals

The question of whether Neanderthals engaged in intentional burial has long been contentious. While early claims were met with scepticism, systematic reassessment of site records, contextual analyses, and recent excavations now provide increasingly robust evidence that some groups deliberately interred their dead. A global review by Sala et al. (2025) identifies a suite of sites from Western Europe to Central Asia where contextual integrity, body position, and the absence of significant post-depositional disturbance collectively support intentional deposition. These behaviours appear neither isolated nor idiosyncratic, but recurrent across varied ecological and cultural settings.

One of the most compelling cases comes from La Chapelle-aux-Saints (France), where renewed excavations confirmed that an adult Neanderthal had been placed in a deliberately dug pit and rapidly covered, protecting the remains from disturbance (Rendu et al., 2013). In the Levant, Kebara Cave (Israel) yielded the skeleton of a young adult male (Kebara 2), preserved in articulation and lying in a shallow pit, while Amud Cave contained both an adult male (Amud 1) and a possible infant burial (Amud 7) interpreted as intentional interments (Tillier et al., 1991). In northern Syria, Dederiyeh Cave preserves two remarkably well-articulated infant burials (Akazawa et al., 1995).

From Shanidar Cave (Iraq), several individuals (Shanidar 1–9) were recovered in positions and contexts consistent with deliberate burial (Pomeroy et al., 2020). Shanidar 4 was famously associated with pollen clusters once interpreted as evidence for "flower burial," though later sedimentological studies have nuanced this claim. Hunt et al. (2023) showed that the pollen concentrations are better explained by burrowing rodents transporting flower heads into the sediments, rather than by deliberate funerary placement. Recent excavations revealed Shanidar Z, an articulated partial skeleton in a carefully cut depression, with sediments indicating rapid covering after deposition. Other possible burials include Tabun C1 (Israel), an adult female found in a flexed position (Grün and Stringer, 2000); Regourdou (France), where a partial skeleton was associated with stone tools and bear remains (Maureille et al., 2015); and Roc de Marsal (France), where an articulated juvenile lay in a pit cut into the sediment (Sandgathe et al., 2011).

La Ferrassie (France) stands out as one of the richest Neanderthal burial sites. Excavations uncovered at least eight individuals (LF1–LF8), including adults, children, and infants, many in excellent articulation. The best known, La Ferrassie 1, discovered in 1909, was interpreted as an intentional grave. Recent analyses confirmed the absence of carnivore damage, weathering, or trampling, and identified sediment mixing consistent with pit excavation. Several individuals share an east–west orientation, and the paired positioning of LF1 and LF2 appears deliberate, suggesting recurrent use of the shelter as a burial ground.

Although taphonomic ambiguities remain in some cases, the combination of body positioning, grave-cut features, rapid covering, and occasional associated items strongly supports intentional burial as a repeated practice. Taken together, the geographic breadth and contextual similarities challenge the notion that funerary behaviour was exclusive to *Homo sapiens*. Instead, they suggest that some Neanderthal groups engaged in formalised treatment of the dead, reflecting social bonds, group memory, and symbolic capacities comparable in scope—if not necessarily in form—to those of early modern humans.

10.13. Neanderthal therapeutic knowledge

Analyses of calcified dental plaque have provided an unexpectedly detailed window into Neanderthal diet, health, and ecological knowledge. At El Sidrón (Spain), microfossil and molecular evidence revealed the consumption of cooked plant foods, including species with medicinal properties such as *Achillea* (yarrow) and *Matricaria* (camomile), along with traces of inhaled wood smoke—clear indicators of controlled fire use and a sophisticated understanding of local flora (Hardy et al., 2012). In one individual, genomic traces of a pathogenic gut microbe were found together with plant-based compounds known for their therapeutic effects, suggesting deliberate self-medication (Buckley et al., 2013). Broader palaeobotanical and chemical evidence reinforces this interpretation, pointing to the intentional use of natural antibiotics such as *Penicillium* moulds and salicylic acid-rich bark, long before the rise of agriculture.

The medicinal interpretation, however, remains debated. Buck and Stringer (2014) have argued that non-nutritional plants found in Neanderthal calculus may instead derive from the consumption of herbivore stomach contents—a practice documented ethnographically in recent human groups—which would incidentally introduce compounds from plants such as yarrow or camomile into the Neanderthal diet. While this hypothesis does not rule out deliberate plant use, it highlights the difficulty of distinguishing intentional self-medication from incidental ingestion. Together, these contrasting perspectives underscore both the potential and the interpretive challenges of reconstructing Neanderthal pharmacological knowledge. Whether deliberate or incidental, the evidence nevertheless reveals intimate engagement with plant resources and an ecological awareness far more complex than the long-standing stereotype of Neanderthals as exclusively carnivorous hunters.

10.14. Compassion

Neanderthals have often been portrayed as brutish and violent—associated more with cannibalism, relentless hunting, and physical aggression than with care or emotional depth. Such depictions have tended to overshadow alternative perspectives on their social lives. Recent archaeological and palaeoanthropological evidence, however, challenges this stereotype, revealing that Neanderthals were capable of sustained care and compassion within their groups.

Spikins (2015) and Spikins et al. (2019) analyse cases in which individuals with severe injuries or chronic conditions appear to have been supported over long periods. The Shanidar 1 individual, for example, suffered from multiple impairments—including a withered arm, profound hearing loss, and probable blindness in one eye— conditions inferred from osteological markers such as severe degenerative joint disease, auditory canal exostoses, and traumatic injury to the left upper limb—yet survived for years, strongly implying regular assistance from companions. At La Chapelle-aux-Saints, the remains of an elderly male with advanced degenerative joint disease were found in what is interpreted as a deliberate burial; his limitations suggest that he too had been cared for despite a reduced capacity to contribute to subsistence. Such examples invite a reassessment of Neanderthal sociality. Far from embodying indifference or ruthless self-interest, their communities may have been characterised by close interpersonal bonds, resilience, and shared responsibility. Compassion, no less than strength or skill, appears to have been integral to the Neanderthal world.

10.15. Ecological versatility, adaptive capacity, and resilience

Far from being passive dwellers of marginal habitats, Neanderthals emerge as highly versatile agents who actively engaged with—and in some cases reshaped—their environments. A recent synthesis of Neanderthal palaeovegetation across their range (Carrión et al., 2011) underscores their ability to thrive under diverse climatic and ecological regimes, from boreal forests and loess plains in Central and Eastern Europe to Mediterranean woodlands, steppe–tundra mosaics, and coastal refugia in Iberia and the Levant. Occupying such varied landscapes for more than 300,000 years, Neanderthals demonstrated remarkable ecological breadth, adjusting subsistence strategies and settlement patterns to the challenges of shifting glacial–interglacial cycles. A paleoartistic reconstruction of the environments in the Mid-Pleistocene Bolomor cave, performed by Gabriela Amorós, is aimed at illustrating this scenario (Fig. 19). Comparable cases are documented among Neanderthals in the Balkans (Carrión et al., 2024a), as well as within Iberia in earlier hominin taxa (Carrión et al., 2006, 2008, 2018, 2019a-c, 2024b, 2024c). This adaptive plasticity highlights their cognitive flexibility, resilience, and capacity for innovation.

Palaeoecological evidence further suggests that Neanderthals were not merely adapting to environments but were also active participants in shaping them. At Neumark-Nord (Germany), multiproxy data reveal that repeated Neanderthal occupations during the Last Interglacial coincided with persistent open clearings in otherwise forested landscapes. These openings, which endured for centuries, are associated with declines in arboreal pollen and increases in herbaceous taxa, suggesting deliberate or incidental vegetation management. Fire—used to maintain hunting grounds, encourage edible plants, or promote landscape openness—emerges as the most likely driver (Roebroeks et al., 2021). Similar patterns appear in Iberia, where palaeoecological records from Los Tollos (Carrión et al., 2024d) document recurrent fire activity, and in Megalopolis (Greece), where biomass, climate, and burning were tightly linked during the Middle Pleistocene (Kyrikou et al., 2025).

Taken together, these findings dismantle older narratives of Neanderthals as ecologically constrained hominins, revealing instead communities with the ingenuity and foresight to modify and manage their habitats. Their ability to exploit diverse biomes—from temperate forests to periglacial steppes—and to navigate profound climatic oscillations underscores their resilience as a species. By intervening in their landscapes—much like *Homo sapiens* and other keystone vertebrates—Neanderthals displayed not only adaptive strength but also ecological agency. This long-term record of versatility and landscape interaction stands as a testament to their intelligence, complexity, and enduring role in human evolutionary history.

11. The causes of Neanderthal extinction

The extinction of Neanderthals remains one of the most debated questions in palaeoanthropology, not only for its scientific implications but also for its cultural resonance. In the nineteenth century, extinction was often framed as a natural marker of progress: the inevitable outcome of evolutionary failure. Within this narrative, Neanderthals were cast as a "primitive" species, replaced by *Homo sapiens* in a teleological story that reinforced colonial ideologies of human inequality. As shown above, recent research, however, has dismantled this view, showing that Neanderthals possessed advanced cognitive, technological, and social capacities. This shift encourages us to regard them not as evolutionary dead ends but as alternative forms of humanity (Villa and Roebroeks, 2014).

Biologically, extinction is the ultimate fate of all species (Eldredge, 1995). Yet the persistence of Neanderthals over hundreds of millennia, across some of the most climatically volatile episodes of the Pleistocene, is itself a testament to their adaptability. Their disappearance around 40–38 ka, with possible late survival in Iberian refugia (Zilhão et al., 2017; Carrión et al., 2019c; Finlayson et al., 2006), coincides with profound ecological instability during Marine Isotope Stage 3. Advances in radiocarbon dating, particularly the refinement of ultrafiltration protocols (Higham et al., 2011, 2014; Devièse et al., 2017), have revised earlier claims of survival until 30 ka and established a narrower chronological window for their extinction.

No single factor can explain this outcome. Most scholars now favour a multifactorial model in which ecological stress, demographic vulnerability, and interaction with *Homo sapiens* intersected. Dansgaard–Oeschger (D–O) oscillations—millennial-scale episodes of abrupt warming—and Heinrich events—intervals of massive iceberg discharge and severe cooling—fragmented habitats, isolating Neanderthal groups into smaller populations (Hawks et al., 2000; Stewart, 2004; Finlayson, 2008; Marín-Arroyo et al., 2018). Although similar climatic pulses occurred earlier in the Pleistocene, their demographic effects were mitigated because Neanderthal ancestors occupied larger, more continuous ranges and did not yet face competition from modern humans. This demographic fragility—small, dispersed groups prone to stochastic fluctuations, inbreeding, and cultural erosion—has emerged as a central explanation. Vaesen et al. (2021), through a structured expert survey, demonstrated that a majority of specialists now regard demography as the principal driver of extinction, with climate instability, competition, and pathogens seen as secondary or compounding pressures.

The arrival of *Homo sapiens* introduced further challenges. Broader social networks, higher mobility, and technological flexibility may have given modern humans a resilience advantage in unstable environments (Timmermann, 2020). Interbreeding between the two species is well documented (Green et al., 2010; Rogers et al., 2017), yet the small proportion of Neanderthal ancestry in living humans indicates that assimilation alone cannot explain their disappearance. Catastrophic events such as the Campanian Ignimbrite eruption (~39 ka, De Vivo et al., 2001; Giaccio et al., 2017) likely intensified existing stresses but were not decisive in isolation.

Alternative perspectives stress the role of chance and dispersal dynamics. Kolodny and Feldman (2017) argue that Neanderthal replacement may be understood as a largely neutral process, driven by repeated waves of *Homo sapiens* expansion and stochastic drift rather than inevitable superiority. Such models remind us that cultural bias has often coloured interpretations, framing Neanderthal extinction as a "failure" in evolutionary competition.

In sum, Neanderthal extinction was likely the result of multiple intertwined processes rather than the simple triumph of a superior species. Their disappearance reflects the cumulative pressures of climatic instability, demographic fragility, and contact with expanding *Homo sapiens*. To interpret it solely as replacement is to oversimplify a complex history and perpetuate outdated tropes. A more balanced view recognises Neanderthals as resilient long-term survivors who thrived across diverse environments for hundreds of millennia, leaving both a genetic legacy and an archaeological record that continues to expand our understanding of humanity.

12. Closing thoughts

12.1. Old prejudices die hard

As scientists, we are often reluctant to place ourselves within the diachrony of paleoanthropology—a discipline shaped, like any other, by tradition, authority, imagination, and at times even fraud. The recent era of bibliometric obsession—hopefully now waning—has shown how citation patterns reveal the enduring power of authority and the paradigms it sustains. Foundational ideas, once endorsed by prominent figures or supported by publishers, lobbies, or funding bodies, often acquire an aura of immutability, even when contradicted by new evidence. While this dynamic is familiar across academia, openly challenging such paradigms remains professionally risky (Latour and Woolgar, 1979).

Evolutionary biology provides striking parallels. Theodosius Dobzhansky and other architects of the Modern Synthesis established an orthodoxy that sidelined alternative perspectives such as developmental biology, with adherents to the dominant view enjoying disproportionate visibility and funding (Eldredge, 1995; Bowler, 2003). Lynn Margulis's groundbreaking symbiosis hypothesis of eukaryotic origins was initially dismissed by neo-Darwinian gatekeepers, only later gaining recognition. Paleoanthropology has been no different. Louis Leakey's linear model of human evolution, positing a direct sequence from early hominins to modern humans, long overshadowed branching models that later proved more accurate (Morrell, 1995). Raymond Dart's discovery of *Australopithecus africanus* in 1924 was rejected by many European scholars who favoured Eurasian origins for humankind (Tobias, 1985). The infamous Piltdown hoax, embraced from 1912 until its exposure in 1953 (Weiner, 1955), shows how authority and desire can override evidence. Eugène Dubois's 1891 discovery of *Homo erectus* in Java likewise faced decades of dismissal before being recognised (Shipman, 2001).

Against this backdrop, it is unsurprising that Neanderthal iconography and behavioural narratives followed a similar trajectory—shaped less by evidence than by inertia, tradition, and the gravitational pull of authority. After all, humans—including both Neanderthals and modern scientists—are social animals, dependent on networks of acceptance and belonging. What may appear irrational is in fact intrinsic to community dynamics. As Robin Dennell (2001) observed, "perhaps one of the main lessons to absorb from the history of science is the danger of too many people becoming too comfortable for too long with an idea, simply because so many agree with it, and have agreed with it so often in the past."

12.2. Paleoart as consensus

Art theorist Nicolas Bourriaud reminds us that "art should not illustrate History," citing Jacques-Louis David, whose pictorial system decisively shaped the politics of his time. Form, in this case, was not subordinated to discourse but acted upon it. Transposed to Prehistory, the same principle applies: paleoart does not merely depict the past—it invents, models, and projects it *ex novo* (Amorós, 2025). Speculative reconstructions—skin, posture, gesture, hair—have profoundly shaped the discipline, conditioning hypotheses and even theories about deep humanity (Gurche, 2013). Balanced between data, inference, and imagination, paleoart functions as both a pedagogical tool and a cultural mediator, reconciling nature and culture, particularly in their entanglement with landscape (Figs. 20, 21).

For centuries, much of culture has drifted away from the natural world, once mediated through ritual and myth. John Berger warned that landscape art had died of "natural causes." Colonialism played a role in this separation: every colonial act annihilated cultures living in communion with nature, relegating them to the category of the "primitive"—as if they belonged to another time, when in reality they shared the same human present. Paleoart, too, has reflected this gesture. Instead of portraying Neanderthals and other hominins as kin, it cast them as spectres of a hostile past. Blaschke's sculptures in Chicago inspired fear (Fig. 5); the simian reconstructions of Rutot and Mascré animalised them (Fig. 6). For decades, Neanderthals were the colonial "Other"—a degraded mirror of the native.

But images change. The vibrant reconstructions of the Kennis brothers (Fig. 13) present beings who are recognisable, human, endowed with faces, dignity, and history. This transformation is not merely aesthetic but ontological. It signals a new conception of the past,

Fig. 20. Artistic reconstruction of the Bolomor Cave landscape (Valldigna Valley, Eastern Iberia) during the Middle Pleistocene. Based on detailed paleobotanical evidence, the scene emphasizes Neanderthals as active agents in a biodiverse, thermo- and meso-Mediterranean environment dominated by pine and oak woodlands. Far from the stereotype of cold-adapted hunters in desolate steppes, Neanderthals here appear integrated into a complex ecotonal setting that provided edible plants, small and large fauna, and fresh water. The depiction of daily life—an adult consuming hazelnuts, a child playing with a tortoise—highlights behavioral versatility, subsistence breadth, and ecological resilience. This paleoartistic view challenges reductionist iconographies of the "brutish Neanderthal" and instead situates them within a dynamic landscape of high biodiversity, where ecological and cultural factors intertwined. Original artwork by Gabriela Amorós (color pencils), in Amorós et al. (2021).

Fig. 21. Detail from an ongoing reconstruction of Palaeolithic landscapes in southern Iberia, depicting a Neanderthal in a karstic setting with broom thickets, junipers, and saxicolous shrubs. The wildcat and the Neanderthal are intentionally juxtaposed: the hominin's facial expression subtly mirrors that of the animal, an ecological gesture underscoring coexistence and shared habitat rather than domestication. This pictorial choice conveys tolerance and interspecies presence within a biodiverse environment. At the same time, the Neanderthal's features stand in sharp contrast to the simian caricatures of earlier centuries, presenting instead a recognizably human face engaged with its surroundings. Artwork by Gabriela Amorós.

driven not only by archaeological discoveries but also by art as a cultural force. Paleoart has colonised and decolonised in turn: fixing prejudices, dismantling them, and opening a critical space where nature, science, and culture intersect.

Artists may choose to offer nostalgic visions of a lost nature or stark proclamations before catastrophe. But at its most ambitious, paleoart becomes a conscious intervention in collective memory: a visual code that invites the observer into prehistory, urging us to reconsider our relationship with time and nature. In this sense, to return to Bourriaud, paleoart does not simply illustrate History—it transforms it. And in doing so, it transforms us, recomposing the frameworks through which we imagine the past and, ultimately, the human.

12.3. Paleoart and the ethics of conservation

In one of his appeals for a "cognitive democracy," Edgar Morin (1999) warned of a growing democratic deficit produced by the appropriation of vital problems by experts and specialists. The result, he argued, is that the expert loses the capacity to conceive the global and the fundamental, while the citizen loses the right to knowledge. Against this background, Morin suggested beginning with Voltaire and Conan Doyle, and then examining the art of the palaeontologist or prehistorian, in order to teach serendipity—the art of transforming seemingly insignificant details into clues that allow us to reconstruct entire histories. This call to broaden our interpretative frameworks invites us to reconsider Neanderthals not as marginal primitives but as protagonists of a long evolutionary adventure.

Within this perspective, the Neanderthal lineage, broadly framed between ca. 430,000 and 37,000 years ago, spanned nearly 395,000 years (Carrión et al., 2026). Paleoclimatic reconstructions suggest that roughly 72 % of this interval unfolded under glacial or stadial regimes, with only 28 % corresponding to interglacial or interstadial phases. This endurance in overwhelmingly cold and unstable environments underscores the role of refugial habitats and ecological flexibility. A parallel exercise for *Homo sapiens* highlights a similarly demanding backdrop: during their Eurasian expansion from ca. 130 ka onward, humans faced an almost equal distribution of cold versus temperate phases, while in Africa, open grass-dominated landscapes prevailed for most of the time between ~315 and 60 ka. Both species, then, evolved as survivors within recurrent ecological oscillations—yet under distinct rhythms that fostered behavioral plasticity and, in the case of *Homo sapiens*, eventual global dispersal. Such endurance was not limited to ecological adaptation; it also found expression in cultural acts that reshaped landscapes and subterranean spaces.

Among the most striking cases is Bruniquel Cave, where enigmatic constructions dated to ca. 176 ka epitomize Neanderthals as cultural agents (Jaubert et al., 2016) (Fig. 9). The deliberate arrangement of stalagmite rings deep inside a dark cave—an endeavor requiring cooperation, pyrotechnology, and spatial planning—cannot be reduced to mere utilitarian activity. Instead, it reflects a capacity to create enduring structures in spaces devoid of immediate subsistence value. Bruniquel thus stands not only as the earliest known large-scale subterranean construction in human history, but also as a material trace of Neanderthals' aesthetic and symbolic engagement with their environments, foreshadowing later traditions of cave art and ritualized space.

Bruniquel, in this sense, anticipates the ecological and symbolic engagements that paleoart seeks to recover: an art attentive not only to form, but also to the entanglement of humans with plants, animals, fungi, and microorganisms (Amorós et al., 2025). In so-called "modern societies," species and ecosystems are too often reduced to mere providers of services, stripped of intrinsic value. Yet every species represents a singular design, a historical structure that, against overwhelming odds, has endured long evolutionary odysseys to exist alongside us. To pause and admire them is not only an aesthetic act, but also an acknowledgment of their unrepeatable evolutionary histories.

Placed in this broader frame, palaeoart becomes not a nostalgic exercise but an ethical one. Today, we drive species to extinction at unprecedented rates—even erasing what we profess to value. Redirecting this course requires more than policy; it calls for a cultural transformation, a shift in perception. In this sense, paleoart may be understood as a method of survival: a creative archive that, like the fossil record itself, documents successful designs and strategies, converging into ecological achievements and long evolutionary odysseys. All of them, without exception, end in extinction. But extinction should not be judged as evolutionary failure. Rather, it reminds us of the fragility and the beauty of all living forms, and of the ethical responsibility that comes with recognizing them.

12.4. The aesthetic niche of Neanderthals

Recent work in evolutionary aesthetics challenges long-standing skepticism regarding Neanderthal sensibilities. Meneganzin and Killin (2024) argue that the archaeological record—including ornaments, pigments, engravings, and complex constructions—cannot be reduced to incidental practices or derivative borrowings from *Homo sapiens*. Instead, they propose that Neanderthals inherited a "protoaesthetic package" from common ancestors such as the makers of Acheulean handaxes, where sensitivities to symmetry, form, and design were already manifest. Against claims that Neanderthals lacked genuine aesthetic capacity, the authors show that such doubts rely on narrow, culturally loaded standards of "art" and "beauty," rooted in post-Enlightenment Western conceptions.

A broader evolutionary framework suggests that Neanderthal aesthetics were not deficient, but distinct—recognizably different from those of early *Homo sapiens*, yet no less significant. This reframing shifts the question: not whether Neanderthals matched our aesthetic benchmarks, but how they developed and inhabited their own aesthetic niches. To recognize these niches on their own terms is to open new avenues for archaeological, cognitive, and philosophical research.

As Matthew Rampley (2017) reminds us in *The Seductions of Darwin*, reducing art to adaptive explanations risks overlooking its cultural, symbolic, and ethical dimensions. Applied to the case of Neanderthals, this caution underscores that their aesthetic practices cannot be understood solely through evolutionary models of utility or fitness. Rather, they invite us to see them as intentional engagements with landscape, materiality, and coexistence, reminding us that human aesthetic experience has always been plural, contingent, and deeply ecological.

12.5. In search of the new human

The "Neanderthal question" has shifted profoundly since John Speth's (2004) heterodox essay, in which he declared—ironically—that Neanderthals had been "convicted of gross mental incompetence almost entirely on the basis of negative and missing evidence." In the decades since, research has uncovered a very different picture: Neanderthals were cognitively sophisticated, ecologically versatile, and deeply engaged with their environments. Taken together, these findings converge on the idea that we are searching not for a "primitive other," but for a *new Neanderthal*—a figure much closer to our own humanity.

Paradoxically, this forward-looking quest circles back to the origins of the species' name. The taxonomic designation *Homo neanderthalensis* means "human from the Neander Valley," the German site where the first fossil was identified in 1856. Yet the valley's name itself has deeper roots. In the seventeenth century, the Protestant theologian and hymn composer Joachim Neumann—whose surname in German signified "new man"—Hellenized his name to Neander, from the Greek *neos* (νέος, "new") and *anēr/andros* (ἀνήρ/ἀνδρός, "human being"). Etymologically, then, "Neanderthal" may be rendered as "valley of the new human."

The irony is striking: one of the last archaic human lineages bears a name that encodes novelty and renewal. In light of current scholarship, this coincidence acquires deeper resonance. As we now recognize Neanderthals as technologically inventive, cognitively sophisticated, and socially complex, we may be said to fulfill, in a sense, the destiny inscribed in their very name: discovering within an "archaic human" the true figure of the *new human*.

CRediT authorship contribution statement

Gabriela Amorós: Writing – review & editing, Writing – original draft, Software, Methodology, Investigation, Conceptualization. **José S. Carrión:** Writing – review & editing, Writing – original draft, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research has been funded by the projects HOMEDSCAPE of the Spanish Agencia Estatal de Investigación, and PID2022–136832NB-100 Fundación Séneca. Juan Manuel Jiménez-Arenas kindly reviewed an early version of the manuscript. It is an honour and a privilege to acknowledge the thoughtful comments provided by Jim Rose, Mathieu Duval and Sarah Talamo on an earlier version of this manuscript. Their observations were invaluable and have significantly improved the final text. We have learned a great deal from their feedback and, in a sense—much as with Dr. Jiménez-Arenas—their contributions make them participants in the very shaping of this article. We are grateful for the courtesy and generosity of several artists and scientists who granted permission to reproduce their works, namely Mauricio Antón, Elisabeth Daynès, the Kennis brothers, Cícero Moraes, Mauro Cutrona, and Marco Peresani.

Data availability

Data will be made available on request.

References

Ackermann, R.R., Arnold, M.L., Baiz, M.D., Cahill, J.A., Cortés-Ortiz, L., Evans, B.J., Grant, B.R., Grant, P.R., Hallgrimsson, B., Humphreys, R.A., Jolly, C.J., Malukiewicz, J., Percival, C.J., Ritzman, T.B., Roos, C., Roseman, C.C., Schroeder, L., Smith, F.H., Warren, K.A., Wayne, R.K., Zinner, D., 2019. Hybridization in human evolution: Insights from other organisms. Evolut. Anthropol. 28, 189–209.

Akazawa, T., Muhesen, S., Dodo, Y., Kondo, O., Mizoguchi, Y., Abe, Y., Nishiaki, Y., Ohta, S., Oguchi, T., Haydal, J., 1995. Neanderthal infant burial from the Dederiyeh cave in Syria. PaléOrient 21 (2), 77–86.

Al-Shamahi, E. (Presenter), 2018. *The Neanderthal* [Television documentary series]. BBC Studios.

Álvarez-Alonso, D., de Andrés-Herrero, M., Díez-Herrero, A., Miralles-Mosquera, S., Sastre Barrio, M.C., Maté-González, M.Á., Nieva Gómez, E., Díaz Delgado, M.R., Ruiz Mediavilla, E., 2025. More than a fingerprint on a pebble: A pigment-marked object from San Lázaro rock-shelter in the context of Neanderthal symbolic behavior. Archaeol. Anthropol. Sci. 17, 131.

Amorós, G., 2023. *Paleoarte y naturaleza: análisis historiográfico del paisaje neandertal*. PhD Thesis, University of Murcia. ⟨http://hdl.handle.net/10201/129404⟩.

Amorós, G., 2024. *Paleoarte y paisaje: una teoría estética*. Murcia: Servicio de Publicaciones, Universidad de Murcia. https://doi.org/10.6018/editum.3108.

Amorós, G., 2025. *El paleoarte como actividad demiúrgica y heracliteana: análisis desde el marco de la Teoría Estética*. ECCE HOMO Publ. https://doi.org/10.5281/zenodo.14599428.

Amorós, G., Carrión, J., 2025. The kitsch dimension of paleoart. Arte Individuo Y. Soc. 37 (1). https://doi.org/10.5209/aris.97299.

Amorós, G., Carrión, J.S., Crivellaro, F., Marín-Arroyo, A.B., 2025. Out of the Cave: Rewilding Deep Time at the Venice Biennale. iScience 28 (9), 113392. https://doi.org/10.1016/j.isci.2025.113392.

Amorós, G., Carrión, J.S., Ochando, J., HOMOSCAPE Project Members, 2021. Paleoecology and paleoart: landscapes of the Middle Pleistocene Neanderthals in Bolomor Cave, eastern Iberia. Quat. Sci. Rev. 256, 106826.

Anderson, L., Reynolds, N., Teyssandier, N., 2019. No reliable evidence for a very early Aurignacian in Southern Iberia. Nat. Ecol. Evol. 3, 713.

Arensburg, B., Tillier, A.M., Vandermeersch, B., Duday, H., Schepartz, L.A., Rak, Y., 1989. A Middle Palaeolithic human hyoid bone. Nature 338, 758–760. https://doi.org/10.1038/338758a0.

Arsuaga, J.L., 2003. *The Neanderthal's. Necklace: In Search of the First Thinkers*. John Wiley & Sons Ltd, Chichester.

Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Gracia-Téllez, A., Sharp, W.D., Quam, R.M., Falguères, C., Pantoja-Pérez, A., Bischoff, J., Poza-Rey, E., Parés, J.M., Carretero, J.M., Demuro, M., Lorenzo, C., Sala, N., Martinón-Torres, M., García, N., Alcázar de Velasco, A., Cuenca-Bescós, G., Gómez-Olivencia, A., Moreno, D., Pablos, A., Shen, C.-C., Rodríguez, L., Ortega, A.I., García, R., Bonmatí, A., Bermúdez de Castro, J.M., Carbonell, E., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science 344, 1358–1363. https://doi.org/10.1126/science.1253958.

Auel, J.M., 1980–2011. *Earth's Children series*. Penguin Random House, New York.

Auel, J.M., 1980. *The clan of the cave bear*. Penguin Random House, New York.

Bailey, S.E., Weaver, T.D., Hublin, J.-J., 2009. Who made the Aurignacian and other early Upper Palaeolithic industries? J. Hum. Evol. 57, 11–26.

Bar-Yosef, O., 2002. The Upper Paleolithic revolution. Annu. Rev. Anthropol. 31, 363–393. https://doi.org/10.1146/annurev.anthro.31.040402.085416.

Bastir, M., O'Higgins, P., Rosas, A., 2007. Facial ontogeny in Neanderthals and modern humans. Proc. R. Soc. B Biol. Sci. 274 (1614), 1125–1132.

BBC Studios. (2001). Neanderthal [Documentary series]. BBC.

Benazzi, S., Douka, K., Fornai, C., Bauer, C.C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K., Weber, G.W., 2011. Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. Nature 479, 525–528. https://doi.org/10.1038/nature10617.

Bermúdez de Castro, J.M., Martinón-Torres, M., Martínez de Pinillos, M., García-Campos, C., Modesto-Mata, M., Martín-Francés, L., Arsuaga, J.L., 2019. Metric and morphological comparison between the Arago (France) and Atapuerca-Sima de los Huesos (Spain) dental samples, and the origin of Neanderthals. Quat. Sci. Rev. 217, 45–61. https://doi.org/10.1016/j.quascirev.2019.03.020.

Bermúdez de Castro, J.M., Martinón-Torres, M., 2022. The origin of the Homo sapiens lineage: When and where? Quat. Int. 634, 1–13. https://doi.org/10.1016/j.quaint.2022.08.001.

Blanchard, P., 2010. *Human zoos: Science and spectacle in the age of colonial empires*. Liverpool University Press.

Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quat. Int. 252, 16–31.

Boëda, É., Bonilauri, S., Connan, J., Jarvie, D., Mercier, N., Tobey, M., Valladas, H., Al Sakhel, H., 2008. New evidence for significant use of bitumen in Middle Palaeolithic technical systems at Umm el Tlel (Syria) around 70,000 BP. PaléOrient 34 (2), 67–83. https://doi.org/10.3406/paleo.2008.5253.

Boule, M., 1911. L'homme fossile de La Chapelle-aux-Saints. Ann. De. PaléOntol. 6, 1–64.

Bowler, P.J., 2003. *Evolution: The History of an Idea*. University of California Press, Berkeley.
Buckley, S., Hardy, K., Huffman, M.A., 2013. Neanderthal self-medication in context. Antiquity 87, 873–878.
Carrión, J., Amorós, G., Ochando, J., Magri, D., Marín-Arroyo, A.B., Sánchez-Giner, M.V., Amorós, A., Munuera, M., Di Rita, F., Michelangeli, F., Roksandic, M., Mihailović, D., 2024a. Welcome to the forest theatre: Unveiling a Balkan refugium through paleoart. Quat. Sci. Rev. 338, 108829. https://doi.org/10.1016/j.quascirev.2024.108829.
Carrión, J.S., Amorós, G., Sánchez-Giner, M.V., Amorós, A., Ochando, J., Munuera, M., Marín-Arroyo, A.B., Jiménez-Arenas, J.M., 2024b. Greening a lost world: Paleoartistic investigations of the early Pleistocene vegetation landscape in the first Europeans' homeland. Quat. Sci. Adv. 14, 100185.
Carrión, J.S., Amorós, G., Amorós, A., Marín-Arroyo, A.B., 2026. Beyond the cold steppes: Neanderthal landscapes and the neglect of flora. Quat. Sci. Rev., 109673 https://doi.org/10.1016/j.quascirev.2025.109673.
Carrión, J.S., Fernández, S., Fuentes, N. (Eds.), 2006. *Paleoambientes y cambio climático*. Fundación Séneca, Murcia, 258 pp.
Carrión, J.S., Fernández, S., Jiménez, J., Munuera, M., Ochando, J., Amorós, G., Ponce de León, M., Zollikofer, Ch, Martín-Lerma, I., Toro-Moyano, I., Hajdas, I., Walker, M.J., 2019a. The sequence at Carihuela Cave and its potential for research into Neanderthal ecology and the Mousterian in southern Spain. Quat. Sci. Rev. 217, 194–216. https://doi.org/10.1016/j.quascirev.2019.04.012.
Carrión, J.S., Finlayson, C., Fernández, S., Finlayson, G., Allué, E., López-Sáez, A., López-García, P., Fuentes, N., Gil, G., González-Sampériz, P., 2008. A coastal reservoir of biodiversity for Upper Pleistocene human populations: palaeoecological investigations in Gorham`s Cave (Gibraltar) in the context of the Iberian Peninsula. Quat. Sci. Rev. 27, 2118–2135. https://doi.org/10.1016/j.quascirev.2008.08.016.
Carrión, J.S., Lalueza, C., Stewart, J., 2019b. Neanderthals: ecology and evolution. Quat. Sci. Rev. 217, 1–6. https://doi.org/10.1016/j.quascirev.2019.05.008.
Carrión, J.S., Ochando, J., Fernández, S., Munuera, M., Amorós, G., Blasco, R., Rosell, J., Finlayson, S., Giles, F., Jennings, R., Finlayson, G., Giles-Pacheco, F., Rodríguez-Vidal, J., Finlayson, C., 2018. Last Neanderthals in the warmest refugium of Europe: palynological data from Vanguard Cave. Rev. Palaeobot. Palynol. 259, 63–80. https://doi.org/10.1016/j.revpalbo.2018.09.007.
Carrión, J.S., Ochando, J., Michelangeli, F., Jiménez Espejo, F., Ojeda, F., Amorós, G., Munuera, M., Marín Arroyo, A.B., González Sampériz, P., Rodríguez Vidal, J., Di Rita, F., Magri, D., 2024d. Tracing 40,000 Years of Vegetation Dynamics in the Baetic-Rifan Biodiversity Hotspot. Rev. Palaeobot. Palynol., 105202 https://doi.org/10.1016/j.revpalbo.2024.105202.
Carrión J.S., Ochando, J., Munuera, M., Casas-Gallego, M., González-Sampériz, P., López-Sáez J.A., Postigo-Mijarra, J.M., Barrón, E., Badal, E., Carrión-Marco, Y., López-Merino, L., Rubiales J.M., Burjachs, F., Fernández, S., Uzquiano, P., Jiménez-Moreno, G., Montoya, E., Amorós, G., Sánchez-Giner, M.V., Amorós, A., García-Antón, M., Gil-García, M.J., Altolaguirre, Y., Ruiz-Zapata, B., Allué, E., Morales-Molino, C., Alba Sánchez, F., Pérez-Díaz, S., Camuera, J., Ramos-Román, M.J., Aranbarri, J., Vieira, M., Vidal-Matutano, P., Peña-Chocarro, L., Anderson, S., Albert, R.M., Riera, S., Leroy, S., Fletcher, W., Gil-Romera, G., Muñoz-Sobrino, C., Gómez-Orellana, L., Iriarte-Chiapusso, M.J., Expósito, I., Rodríguez-Ariza, M.O., Martínez-Varea, C.M., López-Avilés, A., Pérez, A., Luelmo, R., Arroyo, J., Verdú, M., Di Rita, F., Magri, D., Jiménez-Espejo, F., Yll, R., Morla-Jauristi, C., Scott, L., Peñalba, C., Fierro, E., García Amorena, I., Val-Peón, C., Parra,. I., Gómez-Manzaneque, F., Figueiral, I., Michelangeli, F., Finlayson, C., Finlayson, G., Jiménez-Arenas, J.M., De la Peña, P., Marín-Arroyo, A.B., Piqué, R., Pérez-Jordá, G., Ruiz-Alonso, M., Iglesias, R., Alonso, N., Alcolea, M., Jones, S., Girona, A., Ramil-Rego, P., Roure J.M., Sánchez-Goñi M.F., Dupré, M., 2024c. *Iberian Paleoflora and Paleovegetation Series. Vol II: Pleistocene*. Ministerio de Ciencia e Innovación and Fundación Séneca, Murcia, Spain. Cartagena: Universidad Politécnica 626 p. 〈https://doi.org/10.31428/10317/16814〉.
Carrión, J.S., Rose, J., Stringer, C., 2011. Early human evolution in the Western Palaearctic: ecological scenarios. Quat. Sci. Rev. 30 (11–12), 1281–1295. https://doi.org/10.1016/j.quascirev.2011.04.003.
Carrión, J.S., Scott, L., deMenocal, P., 2019c. Paleofloras, Paleovegetation and human evolution. Rev. Palaeobot. Palynol. 267, 32–38. https://doi.org/10.1016/j.revpalbo.2019.04.006.
Carrión, J.S., Walker, M.J., 2019. Background to Neanderthal presence in Western Mediterranean Europe. Quat. Sci. Rev. 217, 7–44. https://doi.org/10.1016/j.quascirev.2018.10.011.
Collard, M., Tarle, L., Sandgathe, D., Allan, A., 2016. Faunal evidence for a difference in clothing use between Neanderthals and early modern humans in Europe. J. Anthropol. Archaeol. 44, 235–246. https://doi.org/10.1016/j.jaa.2016.07.010.
Conde-Valverde, M., Martínez, I., Quam, R.M., Rosa, M., Velez, A.D., Lorenzo, C., Jarabo, P., Bermúdez de Castro, J.M., Carbonell, E., Arsuaga, J.L., 2021. Neanderthals and Homo sapiens had similar auditory and speech capacities. Nat. Ecol. Evol. 5, 609–615. https://doi.org/10.1038/s41559-021-01391-6.
Cortés-Sánchez, M., Jiménez-Espejo, F.J., Simón-Vallejo, M.D., Stringer, C., Lozano-Francisco, M.C., García-Alix, A., Vera-Peláez, J.L., Odriozola, C.P., Riquelme-Cantal, J.A., Parrilla-Giráldez, R., Maestro-González, A., Ohkouchi, N., Morales-Muñiz, A., 2019. An early Aurignacian arrival in southwestern Europe. Nat. Ecol. Evol. 3, 207–212. https://doi.org/10.1038/s41559-018-0753-6.
D'Anastasio, R., Wroe, S., Tuniz, C., Mancini, L., Cesana, D.T., Dreossi, D., Ravichandiran, M., Attard, M., Parr, W.C.H., Agur, A., Capasso, L., 2013. Micro-biomechanics of the Kebara 2 hyoid and its implications for speech in Neanderthals. PLoS ONE 8 (12), e82261. https://doi.org/10.1371/journal.pone.0082261.
d'Errico, F., Soressi, M., 2002. Systematic use of manganese pigment by the Pech-de-l'Azé Neandertals: implications for the origin of behavioral modernity. J. Hum. Evol. 42, A13.
d`Errico, F., Zilhão, J., Julien, M., Baffier, D., Pelegrin, J., 1998. Neanderthal acculturation in Western Europe? A critical review of the evidence and its interpretation. Curr. Anthropol. 39 (. 1), S1–S44. https://doi.org/10.1086/204689.
Dayet, L., d'Errico, F., Garcia-Moreno, R., 2014. Searching for consistencies in Châtelperronian pigment use. J. Archaeol. Sci. 44, 180–193.
De la Peña, P., 2019. Dating on its own cannot resolve hominin occupation patterns. Nat. Ecol. Evol. 3, 712.
De Vivo, B., Rolandi, G., Gans, P.B., Calvert, A., Bohrson, W.A., Spera, F.J., Belkin, H.E., 2001. New constraints on the pyroclastic eruptive history of the Campanian volcanic province, Italy. Mineral. Petrol. 73, 47–65.
Debus, A., Debus, D.E., 2002. Jay Matternes: Cenozoic paleoartist. En Dinosaur memories. iUniverse, pp. 518–522.
Dennell, R., 2001. From Sangiran to Olduvai, 1937-1960 the quest for 'cen-tres' of hominid origins in Asia and Africa. In: Corbey, R., Roebroeks, Q. (Eds.), Studying Human Origins. Amsterdam University Press, pp. 145–166.
Dennell, R., Martinón-Torres, M., Bermúdez de Castro, J.M., 2011. Hominin variability, climatic instability and population demography in Middle Pleistocene Europe. Quat. Sci. Rev. 30, 1511–1524. https://doi.org/10.1016/j.quascirev.2011.03.015.
Devièse, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M., Radović, S., Procopio, N., Buckley, M., Pääbo, S., Higham, T., 2017. Direct dating of Neanderthal remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic transition. Proc. Natl. Acad. Sci. 114, 10606–10611.
Eco, U., 2007. *Historia de la fealdad*. Penguin Random House Grupo Editor.
Eldredge, N., 1995. *Reinventing Darwin: The Great Debate at the High Table of Evolutionary Theory*. John Wiley & Sons.
Fewlass, H., Talamo, S., Wacker, L., Kromer, B., Tuna, T., Fagault, Y., Bard, E., McPherron, S.P., Aldeias, V., Maria, R., Martisius, N.L., Paskulin, L., Rezek, Z., Sinet-Mathiot, V., Sirakova, S., Smith, G.M., Spasov, R., Welker, F., Sirakov, N., Tsanova, T., Hublin, J.-J., 2020. A ^{14}C chronology for the Middle to Upper Palaeolithic transition at Bacho Kiro Cave, Bulgaria. Nat. Ecol. Evol. 4, 794–801.
Finlayson, C., 2008. On the importance of coastal areas in the survival of Neanderthal populations during the Late Pleistocene. Quat. Sci. Rev. 27, 2246–2252.
Finlayson, C., 2009. *The humans who went extinct: Why Neanderthals died out and we survived*. Oxford University Press.
Finlayson, C., 2019. *The smart Neanderthal: bird catching, cave art and the cognitive revolution*. Oxford University Press, Oxford.
Finlayson, C., Carrión, J.S., 2006. Neandertales y humanos modernos en ecosistemas mediterráneos. In: Carrión García, J.S., Fernández Jiménez, S., Fuentes Molina, N. (Eds.), Paleoambientes y cambio climático. Universidad de, Murcia, Murcia, pp. 177–190.
Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol. Evol. 22, 213–222. https://doi.org/10.1016/j.tree.2007.02.001.
Finlayson, C., Pacheco, F.G., Rodríguez-Vidal, J., Fa, D.A., Gutiérrez, López, J.M., Pérez, A.S., Finlayson, G., Allué, E., Baena Preysler, J., Cáceres, I., Carrión, J.S., Fernández Jalvo, Y., Gleed-Owen, C.P., Jiménez-Espejo, F.J., López, P., López Sáez, J.A., Riquelme Cantal, J.A., Sánchez Marco, A., Guzmán, F.G., Brown, K., Fuentes, N., Valarino, C.A., Villalpando, A., Stringer, C.B., Martinez Ruiz, F., Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. Nature 443, 850–853. https://doi.org/10.1038/nature05195.
Finlayson, C., Zollikofer, C., Ponce de León, M., Finlayson, G., Carrión, J.S., Finlayson, S., Giles Guzmán, F., Shea, J., 2023. Close encounters vs. missed connections? A critical review of the evidence for Later Pleistocene hominin interactions in western Eurasia. Quat. Sci. Rev. 319, 108397. https://doi.org/10.1016/j.quascirev.2023.108307.
Fiorenza, L., Benazzi, S., Henry, A.G., Salazar-García, D.C., Blasco, R., Picin, A., Wroe, S., Kullmer, O., 2015. To meat or not to meat? New perspectives on Neanderthal ecology. Yearb. Phys. Anthropol. 156, 43–71.
Frayer, D.W., 2019. Neandertals and the Black Swan. PaleoAnthropology 2019 350–361.
Fuentes, A., 2021. A reflection on Darwin's chapter 7: on the races of man. In: DeSilva, J. (Ed.), A most Interesting Problem: What Darwin's Descentof Man Got Right and Wrong about Human Evolution. Princeton Uni-versity Press; 2021, pp. 144–161.
García Capín, M., 2025. Neanderthal cave art? A proposal from cognitive archaeology. Journal Archaeological Science Reports 61, 104904.
Giaccio, B., Hajdas, I., Isaia, R., Deino, A., Nomade, S., 2017. High-precision 14C and 40Ar/39Ar dating of the Campanian Ignimbrite (Y-5) reconciles the time-scales of climatic–cultural processes at 40 ka. Sci. Rep. 7, 45940.
Gould, S.J., 1977. *Ontogeny and Phylogeny*. Belknap Press, Cambridge, Massachusetts.
Gould, S.J., 1981. *The Mismeasure of Man*. W.W. Norton & Company, New York.
Gould, S.J., 2008. *The Structure of Evolutionary Theory*. Updated reprint edition. Harvard University Press, Cambridge, Massachusetts.
Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.-Y., Hansen, N.F., Durand, E.Y., Malaspinas, A.-S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajkovic, D., Kucan, Ž., Gušic, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Fortea, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelso, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A Draft Sequence of the Neandertal Genome. Science 328, 710–722. https://doi.org/10.1126/science.1188021.
Grün, R., Stringer, C., 2000. Tabun revisited: revised ESR chronology and new ESR and U-series analyses of dental material from Tabun C1. J. Hum. Evol. 39, 601–612.
Guil-Guerrero, J.L., 2022. Could carbohydrates from food-animals have supported a balanced diet for Neanderthals? J. Archaeol. Sci. 146, 105664.

Gurche, J., 2013. *Shaping Humanity: How Science, Art, and Imagination Help Us Understand Our Origins*. Yale University Press, New Haven.
Hackett, A., Dennell, R., 2003. Neanderthals as fiction in archaeological narrative. Antiquity 77 (298), 761–769.
Hajdinjak, M., Fu, Q., Hübner, A., Petr, M., Mafessoni, F., Grote, S., Skoglund, P., Narasimham, V., Rougier, H., Crevecoeur, I., Semal, P., Soressi, M., Talamo, S., Hublin, J.-J., Gušić, I., Kućan, Ž., Rudan, P., Golovanova, L.V., Doronichev, V.B., Posth, C., Krause, J., Korlević, P., Nagel, S., Nickel, B., Slatkin, M., Patterson, N., Reich, D., Prüfer, K., Meyer, M., Pääbo, S., Kelso, J., 2018. Reconstructing the genetic history of late Neanderthals. Nature 555, 652–656. https://doi.org/10.1038/nature26151.
Hammond, M., 1982. The Expulsion of the Neanderthals from Human Ancestry: Marcellin Boule and the Social Context of Scientific Research. Soc. Stud. Sci. 12 (1), 1–036. https://doi.org/10.1177/030631282012001002.
Harari, Y.N., 2015. *Sapiens: A Brief History of Humankind*. Harper, New York.
Hardy, B.L., 2010. Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. Quat. Sci. Rev. 29 (5-6), 662–679.
Hardy, K., Buckley, S., Collins, M.J., Estalrrich, A., Brothwell, D., Copeland, L., García-Tabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Fernández Cortés, Á., Rosas, A., 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. Naturwissenschaften 99 (8), 617–626. https://doi.org/10.1007/s00114-012-0942-0.
Hardy, B.L., Moncel, M.-H., Kerfant, C., Lebon, M., Bellot-Gurlet, L., Mélard, N., 2020. Direct evidence of Neanderthal fibre technology and its cognitive and behavioral implications. Sci. Rep. 10, 4889. https://doi.org/10.1038/s41598-020-61839-w.
Harvati, K., 2010. Neanderthals. Evol. Educ. Outreach 3, 367–376.
Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, Southern Greece: The Kalamakia Middle Paleolithic cave site. J. Hum. Evol. 64 (6), 486–499. https://doi.org/10.1016/j.jhevol.2013.02.002.
Harvati, K., Röding, C., Bosman, A.M., Karakostis, F.A., Grün, R., Stringer, C., Karkanas, P., Thompson, N.C., Koutoulidis, V., Moulopoulos, L.A., Gorgoulis, V.G., Kouloukoussa, M., 2019. Apidima Cave fossils provide earliest evidence of *Homo sapiens* in Eurasia. Nature 571, 500–504.
Hawkins, M., 1997. *Social Darwinism in European and American thought, 1860–1945: Nature as model and nature as threat*. Cambridge University Press.
Hawks, J., Hunley, K., Lee, S.-H., Wolpoff, M., 2000. Population bottlenecks and Pleistocene human evolution. Mol. Biol. Evol. 17 (1), 2–22.
Henke, W., Tattersall, I., 2007. *Handbook of Paleoanthropology*. Springer, Berlin/Heidelberg/New York.
Henry, A.G., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. J. Hum. Evol. 69, 44–54. https://doi.org/10.1016/j.jhevol.2013.12.014.
Hershkovitz, I., Weber, G.W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A., Bar-Matthews, M., Valladas, H., Mercier, N., Arsuaga, J.L., Martinón-Torres, M., Bermúdez de Castro, J.M., Fornai, C., Martín-Francés, L., Sarig, R., May, H., Krenn, V.A., Slon, V., Rodríguez, L., García, R., Lorenzo, C., Carretero, J.M., Frumkin, A., Shahack-Gross, R., Bar-Yosef, O., Goder-Goldberger, M., Guérin, G., Weiner, S., David, F., Lambert, L., Jakovlić, I., Regev, L., Caracuta, V., Yeshurun, R., Barzilai, O., Ullman, M., Sandgathe, D., Mayer, D.E.B.Y., May, H., Sarig, R., Slon, V., 2018. The earliest modern humans outside Africa. Science 359, 456–459.
Heyes, P.J., Anastasakis, K., de Jong, W., van Hoesel, A., Roebroeks, W., Soressi, M., 2016. Selection and use of manganese dioxide by Neanderthals. Sci. Rep. 6, 22159. https://doi.org/10.1038/srep22159.
Higham, T., 2021. *The World Before Us: The New Science Behind Our Human Origins*. Yale University Press, New Haven.
Higham, T.F.G., Douka, K., Wood, R., Ramsey, Bronk, Brock, C., Basell, F., Camps, L., Arrizabalaga, M., Baena, A., Barroso-Ruíz, J., Bergman, C., Boitard, C., Boscato, C., Caparrós, P., Conard, M., Draily, N.J., Froment, C., Galván, A., Gambassini, B., Garcia-Moreno, P., Grimaldi, A., Haesaerts, S., Holt, P., Iriarte-Chiapusso, B., Jelinek, M.-J., Jordá Pardo, A., Maíllo-Fernández, J.F., Marom, J.-M., Maroto, A., Menéndez, J., Metz, M., Morin, L., Moroni, E., Negrino, A., Panagopoulou, F., Peresani, E., Pirson, M., de la Rasilla, S., Riel-Salvatore, M., Ronchitelli, J., Santamaria, A., Semal, D., Slimak, P., Soler, L., Soler, J., Villaluenga, N., Pinhasi, A., Jacobi, R, R., 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512, 306–309. https://doi.org/10.1038/nature13621.
Higham, T., Frouin, M., Douka, K., Ronchitelli, A., Boscato, P., Benazzi, S., Crezzini, J., Spagnolo, V., McCarty, M., Marciani, G., Falcucci, A., Rossini, M., Arrighi, S., Dominici, C., Devièse, T., Schwenninger, J.-L., Martini, I., Moroni, A., Boschin, F., 2024. Chronometric data and stratigraphic evidence support discontinuity between Neanderthals and early *Homo sapiens* in the Italian Peninsula. Nat. Commun. 15, 8016. https://doi.org/10.1038/s41467-024-49741-y.
Higham, T., Jacobi, R., Julien, M., David, F., Basell, L., Wood, R., Davies, W., Ramsey, C. B., 2010. Chronology of the Grotte du Renne (France) and implications for the context of ornaments and human remains within the Châtelperronian. Proc. Natl. Acad. Sci. U. S. A. 107, 20234–20239. https://doi.org/10.1073/pnas.1007963107.
Hoffecker, J.F., 2002. *Desolate Landscapes: Ice-Age Settlement in Eastern Europe*. Rutgers University Press, New Brunswick.
Hoffmann, D.L., Standish, C.D., García-Diez, M., Pettitt, P.B., Milton, J.A., Zilhão, J., Alcolea-González, J.J., Cantalejo-Duarte, P., Collado, H., de Balbín, R., Lorblanchet, M., Ramos-Muñoz, J., Weniger, G.-C., Pike, A.W.G., 2018. U-Th dating of carbonate crusts reveals Neandertal origin of Iberian cave art. Science 359 (6378), 912–915. https://doi.org/10.1126/science.aap7778.
Hublin, J.-J., Ben-Ncer, A., Bailey, S.E., Freidline, S.E., Neubauer, S., Skinner, M.M., Bergmann, I., Le Cabec, A., Benazzi, S., Harvati, K., Gunz, P., 2017. New fossils from Jebel Irhoud, Morocco and the pan-African origin of *Homo sapiens*. Nature 546, 289–292.
Hublin, J.-J., Sirakov, N., Aldeias, V., Bailey, S., Bard, E., Delvigne, V., Endarova, E., Fagault, Y., Fewlass, H., Hajdinjak, M., Kromer, B., Krumov, I., Marreiros, J., Martisius, N.L., Paskulin, L., Sinet-Mathiot, V., Meyer, M., Pääbo, S., Popov, V., Rezek, Z., Sirakova, S., Skinner, M.M., Smith, G.M., Spasov, R., Talamo, S., Tuna, T., Wacker, L., Welker, F., Wilcke, A., Zahariev, N., McPherron, S.P., Tsanova, T., 2020. Initial Upper Palaeolithic *Homo sapiens* from Bacho Kiro Cave, Bulgaria. Nature 581, 299–302.
Hublin, J.-J., Talamo, S., Julien, M., David, F., Connet, N., Bodu, P., Vandermeersch, B., Richards, M.P., 2012. Radiocarbon dates from the Grotte du Renne and Saint-Césaire support a Neandertal origin for the Châtelperronian. Proc. Natl. Acad. Sci. USA 109, 18743–18748.
Huguet, R., Rodríguez-Álvarez, X.P., Martinón-Torres, M., Vallverdú, J., López-García, J. M., Lozano, M., Terradillos-Bernal, M., Expósito, I., Ollé, A., Santos, E., Saladié, P., de Lombera-Hermida, A., Moreno-Ribas, E., Martín-Francés, L., Allué, E., Núñez-Lahuerta, C., van der Made, J., Galán, J., Blain, H.-A., Cáceres, I., Rodríguez-Hidalgo, A., Bargalló, A., Mosquera, M., Parés, J.M., Marín, J., Pineda, A., Lordkipanidze, D., Margveslashvili, A., Arsuaga, J.L., Carbonell, E., Bermúdez de Castro, J.M., 2025. The earliest human face of Western Europe. Nature 640, 707–713.
Hunt, C.O., Pomeroy, E., Reynolds, T., Tilby, E., Barker, G., 2023. Shanidar et ses fleurs? Reflections on the palynology of the Neanderthal 'Flower Burial' hypothesis. J. Archaeol. Sci. 159, 105822. https://doi.org/10.1016/j.jas.2023.105822.
Jaubert, J., Verheyden, S., Genty, D., Soulier, M., Cheng, H., Blamart, D., Burlet, C., Camus, H., Delaby, S., Deldicque, D., Edwards, R.L., Ferrier, C., Lacrampe-Cuyaubère, F., Lévêque, F., Maksud, F., Mora, P., Muth, X., Régnier, É., Rouzaud, J.-N., Santos, F., 2016. Early Neanderthal Constructions Deep in Bruniquel Cave in Southwestern France. Nature 534, 111–114. https://doi.org/10.1038/nature18291.
Jiménez-Arenas, J.M., 2002. The social function of the sciences in the past. Stephen Jay Gould in memoriam. Dynamis 22, 535–550.
King, W., 1864. The reputed fossil man of Neanderthal. Q. J. Sci. 1, 88–97.
Klossner, M., 2015. *Prehistoric humans in film and television: 581 dramas, comedies and documentaries, 1905–2004*. McFarland.
Koller, J., Baumer, U., Mania, D., 2001. High-tech in the Middle Palaeolithic: Neandertal-manufactured pitch identified. Eur. J. Archaeol. 4 (3), 385–397. https://doi.org/10.1177/146195710100400315.
Kolodny, O., Feldman, M.W., 2017. A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. Nat. Commun. 8, 1040.
Kupka, F., 1909. Illus. Lond. N. 312–313.
Kyrikou, S., Marinova, E., Bludau, I.J.E., Karkanas, P., Panagopoulou, E., Tourloukis, V., Junginger, A., Harvati, K., 2025. Local environment and fire history of a potential Lower Palaeolithic refugium in the Megalopolis Basin, southern Greece, during Marine Isotope Stage 12. Quat. Res. 1–20. https://doi.org/10.1017/qua.2024.59.
Laitman, Jeffrey, Jill, T., Reidenberg, S., Patrick, J., Gannon, B., Karen Landahl, Johansson, Phillip Lieberman, 1990. The Kebara hyoid: What can it tell us about the evolution of the vocal tract. Am. J. Phys. Anthropol. Abstr. 81, 254.
Lalueza-Fox, C., 2013. Paleogenomics of archaic hominins. Curr. Anthropol. 54, S146–S153.
Lalueza-Fox, C., 2021. Neanderthal assimilation? Nat. Ecol. Evol. 5, 711–712.
Lalueza-Fox, C., Sampietro, M.L., Caramelli, D., Puder, Y., Lari, M., Calafell, F., Martinez-Maza, C., Bastir, M., Fortea, J., de la Rasilla, M., Bertranpetit, J., Rosas, A., 2005. Neandertal evolutionary genetics: mitochondrial DNA data from the Iberian Peninsula. Mol. Biol. Evol. 22 (4), 1077–1081.
Latour, B., Woolgar, S., 1979. *Laboratory Life: The Construction of Scientific Facts*. Princeton University Press, New Jersey.
Li, Q., Chen, J., Faux, P., Delgado, M.E., Bonfante, B., Fuentes-Guajardo, M., Mendoza-Revilla, J., Chacón-Duque, J.C., 2023. Automatic landmarking identifies new loci associated with face morphology and implicates Neanderthal introgression in human nasal shape. Commun. Biol. 6, 481. https://doi.org/10.1038/s42003-023-04838-7.
Lieberman, Phillip, Edmund, S.Crelin, 1971. On the speech of Neandertal man. Linguist. Inq. 2, 203–222.
Madison, P., 2021. Brutish Neanderthals: History of a Merciless Characterization. Evolut. Anthropol. 30, 227–237. https://doi.org/10.1002/evan.21918.
Magnani, M., Clindaniel, J., 2023. Artificial Intelligence and Archaeological Illustration. Adv. Archaeol. Pract. 11 (4), 452–460. https://doi.org/10.1017/aap.2023.25.
Majkić, A., Evans, S., Stepanchuk, V., Tsvelykh, A., d'Errico, F., 2017. A decorated raven bone from the Zaskalnaya VI (Kolosovskaya) Neanderthal site, Crimea. PLOS ONE 12 (3), e0173435. https://doi.org/10.1371/journal.pone.0173435.
Mander, J., 1991. *In the absence of the sacred. The failed of technology and the survival of the Indian Nations*. Sierra Club Books, San Francisco.
Marín-Arroyo, A.B., Rios-Garaizar, J., Straus, L.G., Jones, J.R., de la Rasilla, M., González Morales, M.R., Richards, M., Altuna, J., Mariezkurrena, K., Ocio, D., 2018. Chronological reassessment of the Middle to Upper Paleolithic transition and early Upper Paleolithic cultures in Cantabrian Spain. PLOS ONE 13 (4), e0194708.
Marín-Arroyo, A.B., Sanz-Royo, A., 2021. What Neanderthals and AMH ate: reassessment of the subsistence across the Middle–Upper Palaeolithic transition in the Vasco-Cantabrian region of SW Europe. J. Quat. Sci. 36 (4), 597–610. https://doi.org/10.1002/jqs.3291.
Marquet, J.-C., Freiesleben, T.H., Thomsen, K.J., Murray, A.S., Calligaro, M., 2023. The earliest unambiguous Neanderthal engravings on cave walls: La Roche-Cotard, Loire Valley, France. PLOS ONE 18 (6), e0286568.
Martínez Pulido, C., 2016. Élisabeth Daynès: Fructífero encuentro entre arte y ciencia. *Mujeres con ciencia: Ciencia y Más*. ⟨https://mujeresconciencia.com/2016/03/14/elisabeth-daynes-fructifero-encuentro-entre-arte-y-ciencia/⟩.

Maureille, B., Gómez-Olivencia, A., Couture-Veschambre, C., Madelaine, S., Holliday, T., 2015. Nouveaux restes humains provenant du gisement de Regourdou (Montignac-sur-Vézère, Dordogne, France). Paleo 26, 117–138.

Mayr, E., 1963. *Species and Evolution Animal*. Belknap Press. Harvard University Press, Cambridge, Massachusetts.

Mazza, P.P.A., Martini, F., Sala, B., Magi, M., Colombini, M.P., Giachi, G., Landucci, F., Lemorini, C., Modugno, F., Ribechini, E., 2006. A new Palaeolithic discovery: Tar-hafted stone tools in a European Mid-Pleistocene bone-bearing bed. J. Archaeol. Sci. 33 (9), 1310–1318. https://doi.org/10.1016/j.jas.2006.01.006.

Mellars, P., 2005. The impossible coincidence: A single-species model for the origins of modern human behavior in Europe. Evolut. Anthropol. 14 (1), 12–27. https://doi.org/10.1002/evan.20037.

Mellars, P., 2010. Neanderthal symbolism and ornament manufacture: The bursting of a bubble? Proc. Natl. Acad. Sci. U. S. A. 107, 20147–20148. https://doi.org/10.1073/pnas.1014588107.

Meneganzin, A., Killin, A., 2024. Beyond reasonable doubt: reconsidering Neanderthal aesthetic capacity. Phenomenol. Cogn. Sci. 24, 733–765. https://doi.org/10.1007/s11097-024-10003-0.

Menez, A., 2018. *Almost Homo Calpicus: The Early History of the Gibraltar Skull*. The Gibraltar National Museum, Gibraltar.

Meyer, M., Arsuaga, J.-L., de Filippo, C., Nagel, S., Aximu-Petri, A., Nickel, B., Martínez, I., Gracia, A., Bermúdez de Castro, J.M., Carbonell, E., Viola, B., Kelso, J., Prüfer, K., Pääbo, S., 2016. Nuclear DNA sequences from the Middle Pleistocene Sima de los Huesos hominins. Nature 531, 504–507. https://doi.org/10.1038/nature17405.

Milošević, S., Dimitrijević, V., Marín-Arroyo, A.B., Plavšić-Gogić, S., Mihailović, D., 2025. Masters on the matters of ecology: Novelties in the early Neanderthal ungulate procurement and palaeoecology from MIS8/7 record of the Velika Balanica cave (Serbia). Quat. Sci. Rev. 368, 109554. https://doi.org/10.1016/j.quascirev.2025.109554.

Moclán, A., Domínguez-Rodrigo, M., Huguet, R., Pizarro-Monzo, M., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2024. Deep learning identification of anthropogenic modifications on a carnivore remain suggests use of hyena pelts by Neanderthals in the Navalmaíllo rock shelter (Pinilla del Valle, Spain). Quat. Sci. Rev. 329, 108560.

Montagu, A., 1955. *Man's Most Dangerous Myth: The Fallacy of Race*, 3rd ed. Columbia University Press, New York.

Moraes, C., Varotto, E., Portaro, C., Habicht, M.E., Torrisi, E., Vittori, V., Lambusta, L., Nuzzolese, E., Torreggiani, M., Sineo, L., Galassi, F.M., 2023. Una nuova approssimazione facciale per l'uomo de La Chapelle-aux-Saints 1. *Abissi del Tempo. La Grotta di Lamalunga, L'Uomo*, 8 Ottobre 2023 di Neanderthal. Convegno Interna Altamura 7. https://doi.org/10.13140/RG.2.2.33164.08326.

Morin, E., 1999. *La tète bien faite: Repenser la réforme, réformer la pensée*. Seuil, Paris.

Morin, E., Laroulandie, V., 2012. Presumed symbolic use of diurnal raptors by Neanderthals. PLOS ONE 7 (3), e32856. https://doi.org/10.1371/journal.pone.0032856.

Morrell, V., 1995. *Ancestral Passions: Leakey family and the quest for Humankinds Beginnings*. Simon and Schuster, New York.

Müller, S., Schrenk, F., 2009. *The Neanderthals*. Routledge.

National Geographic Channel, 2008. *Neanderthal code* [Television documentary]. National Geographic.

Ochando, J., Jiménez-Espejo, F.J., Giles-Guzmán, F., Neto de Carvalho, C., Carrión, J.S., Muñiz, F., Rubiales, J.M., Cura, P., Belo, J., Finlayson, S., Martrat, B., van Drooge, B. L., Jiménez-Moreno, G., García-Alix, A., Lozano Rodríguez, J.A., Albert, R.M., Ohkouchi, N., Ogawa, N., Suga, H., Camuera, J., Finlayson, C., the Vanguard Cave Research Team, 2024. A Neanderthal's specialised burning structure compatible with tar obtention. Quat. Sci. Rev. 346, 109025. https://doi.org/10.1016/j.quascirev.2024.109025.

Papagianni, D., Morse, M.A., 2013. *The Neanderthals rediscovered: How modern science is rewriting their story*. Thames & Hudson.

Peresani, M., Bertola, S., Delpiano, D., Benazzi, S., Romandini, M., 2019. The Uluzzian in the north of Italy: Insights around the new evidence at Riparo Broion. Archaeol. Anthropol. Sci. 11, 3503–3536.

Peresani, M., Fiore, I., Gala, M., Romandini, M., Tagliacozzo, A., 2011. Late Neandertals and the intentional removal of feathers as evidenced from bird bone taphonomy at Fumane Cave 44 ky B.P., Italy. Proc. Natl. Acad. Sci. U. S. A. 108, 3888–3893. https://doi.org/10.1073/pnas.1016212108.

Petr, M., Hajdinjak, M., Fu, Q., Essel, E., Rougier, H., Crevecoeur, I., Semal, P., Golovanova, L.V., Doronichev, V.B., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Shunkov, M.V., Kozlikin, M.B., Derevianko, A.P., Vernot, B., Meyer, M., Kelso, J., 2020. The evolutionary history of Neanderthal and Denisovan Y chromosomes. Science 369, 1653–1656.

Pomeroy, E., 2023. The different adaptive trajectories in Neanderthals and *Homo sapiens* and their implications for contemporary human physiological variation. Comp. Biochem. Physiol. Part A 280, 111420. https://doi.org/10.1016/j.cbpa.2023.111420.

Pomeroy, E., Hunt, C.O., Reynolds, T., Abdulmutalb, D., Asouti, E., Bennett, P., Bosch, M., Burke, A., Farr, L., Foley, R., French, C., Frumkin, A., Goldberg, P., Hill, E., Kabukcu, C., Lahr, M.M., Lane, R., Marean, C., Maureille, B., Mutri, G., Miller, C.E., Mustafa, K.A., Nymark, A., Pettitt, P., Sala, N., Sandgathe, D., Stringer, C., Tilby, E., Barker, G., 2020. Issues of theory and method in the analysis of Paleolithic mortuary behavior: a view from Shanidar Cave. Evolut. Anthropol. Issues N. Rev. 29, 263–279.

Ponce de León, M.S., Bienvenu, T., Akazawa, T., Zollikofer, C.P.E., 2016. Brain development is similar in Neanderthals and modern humans. Curr. Biol. 26 (14), R641–R666. https://doi.org/10.1016/j.cub.2016.06.022.

Ponce de León, M.S., Bienvenu, T., Marom, A., Engel, S., Tafforeau, P., Alatorre Warren, J.L., Lordkipanidze, D., Kurniawan, I., Murti, D.B., Suriyanto, R.A., Koesbardiati, T., Zollikofer, C.P.E., 2021. The primitive brain of early *Homo*. Science 372 (6538), 165–171. https://doi.org/10.1126/science.aaz0032.

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., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Pääbo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505, 43–49.

Rack, H., 1986. Comparative morphology of the Neandertal thorax. In: Else, J.G., Lee, P. C. (Eds.), Primate Evolution. Cambridge University Press, Cambridge, pp. 439–449.

Radovčić, D., Birarda, G., Oros Sršen, A., Vaccari, L., Radovčić, J., Frayer, D.W., 2020. Surface analysis of an eagle talon from Krapina. Sci. Rep. 10, 6329.

Radovčić, D., Oros Sršen, A., Radovčić, J., Frayer, D.W., 2015. Evidence for Neandertal jewelry: Modified white-tailed eagle claws at Krapina. PLOS ONE 10 (3), e0119802. https://doi.org/10.1371/journal.pone.0119802.

Rae, T.C., Koppe, T., Stringer, C.B., 2011. The Neanderthal face is not cold adapted. J. Hum. Evol. 60, 234–239.

Rampley, M., 2017. *The Seductions of Darwin: Art, Evolution, Neuroscience*. Penn State University Press, University Park.

Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B., Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek, W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson, A.M., Vallelonga, P., Winstrup, M., 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy. Quat. Sci. Rev. 106, 14–28. https://doi.org/10.1016/j.quascirev.2014.09.007.

Reilly, P.F., Tjahjadi, A., Miller, S.L., Akey, J.M., Tucci, S., 2022. The contribution of Neanderthal introgression to modern human traits. Curr. Biol. 32 (18), R970–R983.

Rendu, W., Beauval, C., Crevecoeur, I., Bayle, P., Balzeau, A., Bismuth, T., Bourguignon, L., Delfour, G., Faivre, J.-P., Lacrampe-Cuyaubère, F., Tavormina, C., Todisco, D., Turq, A., Maureille, B., 2013. Evidence supporting an intentional Neandertal burial at La Chapelle-aux-Saints. Proc. Natl. Acad. Sci. USA 111, 81–86. https://doi.org/10.1073/pnas.1316780110.

Renfrew, C., Bahn, P., 2016. *Archaeology: Theories, Methods and Practice*. 7th ed. Thames & Hudson, London.

Rios-Garaizar, J., Iriarte, E., Arnold, L.J., Sánchez-Romero, L., Marín-Arroyo, A.B., San Emeterio, A., Gómez-Olivencia, A., Pérez-Garrido, C., Demuro, M., Campaña, I., Bourguignon, L., Benito-Calvo, A., Iriarte, M.J., Aranburu, A., Arranz-Otaegi, A., Garate, D., Silva-Gago, M., Lahaye, C., Ortega, I., 2022. The intrusive nature of the Châtelperronian in the Iberian Peninsula. PLOS ONE 17 (3), e0265219.

Rodríguez-Vidal, J., d'Errico, F., Giles Pacheco, F., Blasco, R., Rosell, J., Jennings, R.P., Queffelec, A., Finlayson, G., Fa, D.A., Gutiérrez López, J.M., Carrión, J.S., Negro, J. J., Finlayson, S., Cáceres, L.M., Bernal, M.A., Fernández Jiménez, S., Finlayson, C., 2014. A rock engraving made by Neanderthals in Gibraltar. Proc. Natl. Acad. Sci. USA 111 (37), 13301–13306. https://doi.org/10.1073/pnas.1411529111.

Rodríguez-Hidalgo, A., Morales, J.I., Cebrià, A., Courtenay, L.A., Fernández-Marchena, J. L., García-Argudo, G., Marín, J., Saladié, P., Soto, M., Tejero, J.-M., Fullola, J.-M., 2019. The Châtelperronian Neanderthals of Cova Foradada (Calafell, Spain) used imperial eagle phalanges for symbolic purposes. Sci. Adv. 5 (11), eaax1984. https://doi.org/10.1126/sciadv.aax1984.

Roebroeks, W., MacDonald, K., Scherjon, F., Bakels, C., Kindler, L., Nikulina, A., Pop, E., Gaudzinski-Windheuser, S., 2021. Landscape modification by Last Interglacial Neanderthals. Sci. Adv. 7 (51), eabj5567. https://doi.org/10.1126/sciadv.abj5567.

Roebroeks, W., Sier, M.J., Nielsen, T.K., De Loecker, D., Parés, J.M., Arps, C.E.S., Mücher, H.J., 2012. Use of red ochre by early Neandertals. Proc. Natl. Acad. Sci. U. S. A. 109, 1889–1894. https://doi.org/10.1073/pnas.1112261109.

Roebroeks, W., Villa, P., 2011. On the earliest evidence for habitual use of fire in Europe. Proc. Natl. Acad. Sci. U. S. A. 108, 5209–5214. https://doi.org/10.1073/pnas.1018116108.

Rogers, R.L., Bohlender, R.J., Huff, C.D., 2017. Early history of Neanderthals and Denisovans. Proc. Natl. Acad. Sci. 114, 9859–9863.

Roksandic, M., Radović, P., Wu, X., Bae, C., 2019. *Homo heidelbergensis*: What do we need to set the question of the validity of this taxon to rest. Am. J. Phys. Anthropol. 168 (S68), 207.

Rosas, A., Bastir, M., García-Tabernero, A., 2022. Neanderthals: Anatomy, genes, and evolution, In: Editor(s): Francesca Romagnoli, Florent Rivals, Stefano Benazzi. Updat. Neanderthals 71–87 (Academic Press, Pages).

Rosas, A., Ríos, L., Estalrrich, A., Liversidge, H., García-Tabernero, A., Huguet, R., Cardoso, H., Bastir, M., Lalueza-Fox, C., de la Rasilla, M., Dean, C., 2017. The growth pattern of Neandertals, reconstructed from a juvenile skeleton from El Sidrón (Spain). Science 357 (6357), 1282–1287.

Rosny Aîné, J.-H., 1911. La Guerre du Feu. Librairie Plon.

Sala, N., Téllez, E., Arteaga-Brieba, A., Rodríguez-Iglesias, D., Rodríguez-Almagro, M., Pantoja-Pérez, A., Grabbe, J., Pablos, A., 2025. Iberian Neandertal fossils: Exploring funerary practices in a paleoclimatic context. Journal Archaeological Science Reports 66, 105316. https://doi.org/10.1016/j.jasrep.2025.105316.

Salazar-García, D.C., Power, R.C., Rudaya, N., Kolobova, K., Markin, S., Krivoshapkin, A., Henry, A.G., Richards, M.P., Viola, B., 2021. Dietary evidence from Central Asian Neanderthals: A combined isotope and plant microremains approach at Chagyrskaya Cave (Altai, Russia). J. Hum. Evol. 156, 102985.

Sandgathe, D.M., Dibble, H.L., Goldberg, P., McPherron, S.P., 2011. The Roc de Marsal Neandertal child: A reassessment of its status as a deliberate burial. J. Hum. Evol. 61 (3), 243–253. https://doi.org/10.1016/j.jhevol.2011.04.003.

Shea, J.J., 2003. Neandertals, competition, and the origin of modern human behavior in the Levant. Evolut. Anthropol. 12 (4), 173–187. https://doi.org/10.1002/evan.10101.
Shea, J.J., 2016. *Stone Tools in Human Evolution: Behavioral Differences among Technological Primates*. Cambridge University Press, Cambridge.
Shipman, P., 2001. *The Man Who Found the Missing Link*. Simon and Schuster, New York.
Slimak, L., 2023. *The Naked Neanderthal: A New Understanding of the Human Creature*. Allen Lane, London.
Slimak, L., Svendsen, J.I., Mangerud, J., Plisson, H., Heggen, H.P., Brugère, A., Pavlov, P. Y., 2011. Late Mousterian persistence near the arctic circle. Science 332 (6031), 841–845. https://doi.org/10.1126/science.1203866.
Slimak, L., Zanolli, C., Higham, T., Frouin, M., Schwenninger, J.-L., Arnold, L.J., Demuro, M., Douka, K., Mercier, N., Guérin, G., Valladas, H., Yvorra, P., Giraud, Y., Seguin-Orlando, A., Orlando, L., Lewis, J.E., Muth, X., Camus, H., Vandevelde, S., Buckley, M., Mallol, C., Stringer, C., Metz, L., 2022. Modern human incursion into Neanderthal territories 54,000 years ago at Mandrin, France. Sci. Adv. 8, eabj9496.
Slon, V., Mafessoni, F., Vernot, B., de Filippo, C., Grote, S., Viola, B., Hajdinjak, M., Peyrégne, S., Nagel, S., Brown, S., Douka, K., Higham, T., Kozlikin, M.B., Shunkov, M.V., Derevianko, A.P., Kelso, J., Meyer, M., Prüfer, K., Pääbo, S., 2018. The genome of the offspring of a Neanderthal mother and a Denisovan father. Nature 561, 113–116.
Smith, G.E., 1924. *The Evolution of Man: Essays*. Oxford University Press.
Solecki, R.S., 1954. Shanidar Cave, a Paleolithic site in northern Iraq. KIP Articles: ⟨https://digitalcommons.usf.edu/kip_articles/4774⟩.
Sommer, M., 2006. Mirror, Mirror on the Wall: Neanderthal as Image and 'Distortion' in Early 20th-Century French Science and Press. Soc. Stud. Sci. 36 (2), 207–240. https://doi.org/10.1177/0306312706054527.
Soressi, M., McPherron, S.P., Lenoir, M., Dogandžić, T., Goldberg, P., Jacobs, Z., Maigrot, Y., Martisius, N.L., Miller, C.E., Rendu, W., Richards, M., Skinner, M.M., Steele, T.E., Talamo, S., Texier, J.-P., 2013. Neandertals made the first specialized bone tools in Europe. Proc. Natl. Acad. Sci. USA 110 (35), 14186–14190. https://doi.org/10.1073/pnas.1302730110.
Speth, J.D., 2004. News Flash: Negative evidence convicts Neanderthals of gross mental incompetence. World Archaeol. 36 (4), 519–526.
Spikins, P., 2015. *How Compassion Made Us Human: The Evolutionary Origins of Tenderness, Trust and Morality*. Pen & Sword History, Barnsley.
Spikins, P., Needham, A., Wright, B., Dytham, C., Gatta, M., Hitchens, G., 2019. Living to fight another day: The ecological and evolutionary significance of Neanderthal healthcare. Quat. Sci. Rev. 217, 98–118. https://doi.org/10.1016/j.quascirev.2018.08.011.
Špinar, Z.V., 1972. Life before man (Illustrations by Z. Burian, under the direction of J. Augusta, Z. V. Špinar and V. Mazák). Thames and Hudson.
Stewart, J.R., 2004. Neanderthal–modern human competition? A comparison between the mammals associated with Middle and Upper Palaeolithic industries in Europe during OIS 3. Int. J. Osteoarchaeol. 14 (3–4), 178–189.
Stewart, J.R., Stringer, C.B., 2012. Human evolution out of Africa: the role of refugia and climate change. Science 335 (6074), 1317–1321. https://doi.org/10.1126/science.1215627.
Stocking, G.W., 1987. *Victorian anthropology*. Free Press.
Stringer, C., 2012b. The Origin of Our Species. Penguin Books, London.
Stringer, C., 2012a. The status of *Homo heidelbergensis* (Schoetensack 1908). Evolut. Anthropol. 21, 101–107. https://doi.org/10.1002/evan.21311.
Stringer, C., 2014. Why we are not all multiregionalists now. Trends Ecol. Evol. 29, 248–251.
Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R. C., Rhodes, E.J., Currant, A.P., Rodríguez-Vidal, J., Giles-Pacheco, F., Riquelme-Cantal, J.A., 2008. Neanderthal exploitation of marine mammals in Gibraltar. Proc. Natl. Acad. Sci. 105 (38), 14319–14324. https://doi.org/10.1073/pnas.0805474105.
Stringer, C., Gamble, C., 1996. *In Search of the Neanderthals: Solving the Puzzle of Human Origins*. Thames & Hudson, London.
Talamo, S., Kromer, B., Richards, M.P., Wacker, L., 2023. Back to the future: The advantage of studying key events in human evolution using a new high resolution radiocarbon method. PLOS ONE 18 (2), e0280598. https://doi.org/10.1371/journal.pone.0280598.
Tattersall, I., Schwartz, J.H., 2000. *Extinct humans*. Westview Press.
Tillier, A.M., Arensburg, B., Vandermeersch, B., Rak, Y., 1991. L'apport de Kébara à la palethnologie funéraire des Néandertaliens du Proche-Orient. In: Bar Yosef, O., Vandermeersch, B. (Eds.), Le Squelette Moustérien De Kébara 2. Cahiers de Paléoanthropologie, Paris, pp. 89–95.
Timmermann, A., 2020. Quantifying the potential causes of Neanderthal extinction: Abrupt climate change versus competition and interbreeding. Quat. Sci. Rev. 238, 106331. https://doi.org/10.1016/j.quascirev.2020.106331.
Tobias, P.V., 1985. The life and times of Emeritus Professor Raymond A. Dart. SA Med. J. 67, 134–138.
Trinkaus, E., 1985. Pathology and posture of the La Chapelle-aux-Saints Neandertal. Am. J. Phys. Anthropol. 67, 19–41.
Trinkaus, E., Shipman, P., 1993. *The Neandertals: Changing the Image of Mankind*. A. Knopf, New York.
Vaesen, K., Dusseldorp, G.L., Brandt, M.J., 2021. An emerging consensus in palaeoanthropology: Demography was the main factor responsible for the disappearance of Neanderthals. Sci. Rep. 11 (1), 4925. https://doi.org/10.1038/s41598-021-84410-7.
Villa, P., Roebroeks, W., 2014. Neandertal demise: an archaeological analysis ofthe modern human superiority complex. PLoS One 9 (4), e96424.
Weiner, J.S., 1955. The Piltdown forgery. Oxford University Press, Oxford.
Welker, F., Hajdinjak, M., Talamo, S., Jaouen, K., Dannemann, M., David, F., Julien, M., Meyer, M., Kelso, J., Barnes, I., Brace, S., Kamminga, P., Fischer, R., Kessler, B.M., Stewart, J.R., Pääbo, S., Collins, M.J., Hublin, J.-J., 2016. Palaeoproteomic evidence identifies archaic hominins associated with the Châtelperronian at the Grotte du Renne. Proc. Natl. Acad. Sci. USA 113, 11162–11167.
Weyrich, L.S., Duchene, S., Soubrier, J., Arriola, L., Llamas, B., Breen, J., Morris, A.G., Alt, K.W., Caramelli, D., Dresely, V., Farrell, M., Farrer, A.G., Francken, M., Gully, N., Haak, W., Hardy, K., Harvati, K., Held, P., Holmes, E.C., Cooper, A., 2017. Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. Nature 544, 357–361. https://doi.org/10.1038/nature21674.
Wolpoff, M.H., 2022. A moving target: Legacy review of The Mismeasure of Man. By Stephen Jay Gould, 1981. Am. J. Biol. Anthropol. https://doi.org/10.1002/ajpa.24608.
Wragg Sykes, R., 2020. *Kindred: Neanderthal Life, Love, Death and Art*. Bloomsbury Sigma, London.
Wroe, S., Parr, W.C., Ledogar, J.A., Bourke, J., Evans, S.P., Fiorenza, L., Benazzi, S., Hublin, J.J., Stringer, C., Kullmer, O., Curry, M., Rae, T.C., Yokley, T.R., 2018. Computer simulations show that Neanderthal facial morphology represents adaptation to cold and high energy demands, but not heavy biting. Proc. Biol. Sci. 285 (1876), 20180085. https://doi.org/10.1098/rspb.2018.0085.
Zeberg, H., Jakobsson, M., Pääbo, S., 2024. The genetic changes that shaped Neandertals, Denisovans, and modern humans. Cell 187, 1047–1058.
Zilhão, J., Anesin, D., Aubry, T., Badal, E., Cabanes, D., Kehl, M., Klasen, N., Lucena, A., Martín-Lerma, I., Martínez, S., Matias, H., Susini, D., Steier, P., Wild, E.A., Angelucci, D.E., Villaverde, V., Zapata, J., 2017. Precise dating of the Middle-to-Upper Paleolithic transition in Murcia (Spain) supports late Neanderthal persistence in Iberia. Heliyon 3, e00435. https://doi.org/10.1016/j.heliyon.2017.e00435.
Zilhão, J., Angelucci, D.E., Badal-García, E., d'Errico, F., Daniel, F., Dayet, L., Douka, K., Higham, T.F.G., Martínez-Sánchez, M.J., Montes-Bernárdez, R., Murcia-Mascarós, S., Pérez-Sirvent, C., Roldán-García, C., Vanhaeren, M., Villaverde, V., Wood, R., Zapata, J., 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proc. Natl. Acad. Sci. USA 107 (3), 1023–1028. https://doi.org/10.1073/pnas.0914088107.
Zilhão, J., d'Errico, F., Banks, W.E., Teyssandier, N., 2024. A Data-Driven Paradigm Shift for the Middle-to-Upper Palaeolithic Transition and the Neandertal Debate. Quat. Environ. Hum. 2 (6), 100037. https://doi.org/10.1016/j.qeh.2024.100037.
Zollikofer, C.P.E., 2012. Evolution of hominin cranial ontogeny. Prog. Brain Res. 195, 273–292. https://doi.org/10.1016/B978-0-444-53860-4.00013-1.
Zollikofer, C.P.E., Bienvenu, T., Beyene, Y., Suwa, G., Asfaw, B., White, T.D., Ponce de León, M.S., 2022. Endocranial ontogeny and evolution in early *Homo sapiens*: The evidence from Herto, Ethiopia. Proc. Natl. Acad. Sci. 119 (32), e2123553119. https://doi.org/10.1073/pnas.2123553119.