Rethinking Neandertals

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Abstract

In this article, I first provide an overview of the Neandertals by recounting their initial discovery and subsequent interpretation by scientists and by discussing our current understanding of the temporal and geographic span of these hominins and their taxonomic affiliation. I then explore what progress we have made in our understanding of Neandertal lifeways and capabilities over the past decade in light of new technologies and changing perspectives. In the process, I consider whether these advances in knowledge qualify as so-called Black Swans, a term used in economics to describe events that are rare and unpredictable and have wide-ranging consequences, in this case for the field of paleoanthropology. Building on this discussion, I look at ongoing debates and focus on Neandertal extinction as a case study. By way of discussion and conclusion, I take a detailed look at why Neandertals continue to engender great interest, and indeed emotion, among scientists and the general public alike.

INTRODUCTION

Species: a group of individuals in which members can actually or potentially interbreed and produce fertile offspring and that is reproductively isolated from other such groups

Hominin: taxon that includes extant humans and their extinct ancestors

During a graduate seminar on Neandertals, the late Paleolithic archaeologist Prof. Harold Dibble told students assembled around a table the story of his recent trip to the barber. It was right after the release of the 1986 film *Clan of the Cave Bear*, based on the novel of the same name by Jean Auel (1980). His barber had wanted to talk about how terrible the film was. In fact, everywhere Dibble went, people wanted to share their often emotional and deep-seated opinions on whether it was a good film or a bad one, based not on plot or the acting chops of its lead, Darryl Hannah, but rather on how realistically Neandertals had been portrayed. Either they were not "human enough" or the director had gotten this species "just right." Dibble pointed out that he had not once had a similar conversation with anyone about the film *Star Wars*. Moviegoers accepted that light sabers made one long, sustained sound when in use instead of something more staccato, and that spaceships banked in space despite the lack of oxygen. Even the famed film critic Roger Ebert (1986) gave *Clan of the Cave Bear* 1.5 stars, writing that the movie "approaches those times with a modern sensibility. It shows us a woman winning respect from a patriarchal tribe, when, in reality, the [Neandertal] men would have just banged her over the head real good. It isn't grim enough about what things were probably like back then." There is a lot to unpack in Ebert's assertion about male and female roles in the Pleistocene (see Nowell & Chang 2014), but his review and Dibble's experience getting his hair cut beg the question of why the general public and even scientists have what at times appears to be an emotional connection to our extinct cousins.

In this article, I first provide an overview of the Neandertals by briefly recounting their initial discovery and subsequent interpretation by scientists. I then discuss our current understanding of the temporal and geographic span of these hominins and their taxonomic affiliation. Next, I explore what progress we have made in our understanding of Neandertal lifeways and capabilities over the past decade [what Papagianni & Morse (2015, p. 14) refer to as a "Golden Age" in Neandertal research], particularly in light of new technologies and changing perspectives. In the process, I consider whether these advances in knowledge qualify as "Black Swans" (Frayer 2019). In economics[1], a Black Swan is a term used to describe an extremely rare and unpredictable event that has severe consequences but in hindsight was foreseeable (Taleb 2010). Recently, Frayer (2019) has argued that some advances, such as the sequencing of the Neandertal genome and the discovery of a Neandertal "necklace" at the site of Krapina in Croatia (Frayer et al. 2020, Radovčić et al. 2015), are paleoanthropological Black Swans with widespread consequences for scientists' perceptions of Neandertals. Building on this analysis, I look at ongoing debates in the field using Neandertal extinction as a case study. By way of discussion and conclusion, I return to the story with which I began this article to understand why Neandertals continue to engender interest, and indeed emotion, among scientists and the general public alike.

[1]The use of the term Black Swan in economics differs from how it is understood in the philosophy of science, where it originates. In 1620, Francis Bacon argued that inductive reasoning was the basis of all scientific knowledge. According to Hakan (2022), a line in the second-century Roman poet Juvenal's *Satire VI* makes reference to a "rare bird," a black swan that was presumed not to exist. This held true for centuries, as Europeans had observed many swans, and they were all white. Then, in 1667, a Dutch explorer spotted black swans in Australia. This observation falsified the hypothesis that all swans were white (Hakan 2022) and undermined Bacon's assertion about inductive reasoning. In 1934, Karl Popper argued that science cannot prove anything through induction but only disprove it through falsification. He writes, "No matter how many instances of white swans we may have observed, this does not justify the conclusion that all swans are white" (Popper as cited in Hakan 2022, p. 1656).

WHAT'S IN A NAME?

(*a*) *Homo neanderthalensis* versus *Homo sapiens neanderthalensis*? In 1864, King published the diagnosis (official scientific description) of *Homo neanderthalensis* based on the Neanderthal 1 holotype. In his view, the fossil remains more closely resembled apes than humans, but he nonetheless included Neandertals in the genus *Homo* because he did not have a complete skull to analyze. Although it is not an official taxonomic designation, some researchers prefer *Homo sapiens neanderthalensis*, implying that Neandertals are separated from modern humans only at the subspecies level based on morphological, behavioral, and especially paleogenomic evidence. However, the evidence of interbreeding between Neanderthals and *Homo sapiens* cannot tell us if they formed one species or two. Given how closely related they are phylogenetically, it is possible that gene-level reproductive isolating mechanisms had not yet fully evolved between the two lineages (Nowell 2016). For example, all species of the genus *Canis* can interbreed and produce fertile offspring. The problem is that the commonly understood definition of "species" may not be sensitive enough to the actual complexities of biological organisms (Nowell 2016; see also discussion in Meneganzin & Bernardi 2023). (*b*) Neanderthal or Neandertal? Both spellings are correct. *Thal* is the old German word for valley, but in 1901, the valley's name was officially changed to Neander*tal*.

WHO WERE THE NEANDERTALS?

In 1856, quarry workers at Feldhofer Cave in the Neander Valley in Germany uncovered a partial skeleton consisting of a "skull cap, right shoulder blade fragment, rib bones, two femora, three right arm bones, two left arm bones, and the ileum" (Drell 2000, p. 1). This skeleton, now known as Neanderthal 1, was not the first Neandertal ever discovered—fossils from Engis in Belgium and Forbes' Quarry in Gibraltar were found in 1830 and 1848, respectively—but it was the first extinct hominin identified as such based on fossilized skeletal remains (Roebroeks & Soressi 2016). It eventually became the holotype of the species *Homo neanderthalensis* (King 1864) (see the sidebar titled What's in a Name?), for the first time extending the genus *Homo* beyond our own species (Peeters & Zwart 2020).

In many ways, this find is what Tobias (1991) termed a "premature discovery." A discovery is considered premature if its "implications cannot be connected by a series of simple logical steps to canonical, or generally accepted knowledge" (Stent 1972, p. 84). Other examples of premature discoveries include John Frere's supposition in 1797 that flint tools he found were made by men "without the use of metals. . .from a very remote period indeed, even beyond that of the present world"; Gregor Mendel's initial discovery of the laws of inheritance in 1865; and Avery and colleagues' revelation in 1944 that DNA was the basis of heredity (as cited in Tobias 1991, pp. 371–72). In each of these cases, there were years, sometimes decades, between the initial discovery and its eventual acceptance by the scientific community. As Tobias (1991, p. 371) notes, "the degree of scepticism, even scorn, that may attend such notions, seems in keeping with the measure of their prematurity, while the amount of dissention seems to be in proportion to the margin of dissentience." One of the great stories of premature discoveries in paleoanthropology is of the Dutch physician Eugene Dubois, who in frustration buried the remains of the first known *Homo erectus* (designated *Pithecanthropus erectus* at the time) beneath the floorboards under his bed after he failed to convince his contemporaries of their significance in the early 1900s. They remained hidden until he was finally persuaded by colleagues to show them to famed biological anthropologist Aleš Hrdlička in 1922.

Holotype: a single type specimen upon which the description and name of a new species are based

When the Neander Valley material came to light in 1856, the publication of Darwin's *On the Origin of Species* was still three years away, and no other fossil hominins had been found. Instead, the framework within which scientists and others understood the diversity of life on Earth was known

as the Great Chain of Being (Bowler 1989). It was a system derived from the Ancient Greeks and developed further during the Middle Ages, when it took on Christian overtones. Within this paradigm, all "lifeforms," from minerals to plants to animals to humans and ultimately angels, were arranged hierarchically as links in a chain, each connected to the one before and after it.[2] While "higher" forms were said to have all of the attributes of those preceding them, these relationships were believed to be immutable; there was no concept of the transmutability (i.e., evolution) of species (Bowler 1989). Thus, for European scholars to imagine a world in which Neandertals could exist, they had to scaffold it onto what they already knew to be true (Crossland 2020). This meant explaining Neandertal 1 either as "antediluvian," i.e., as a creature that had lived before the Biblical flood; as a pathological human of modern origin; or in racial terms (Crossland 2020, Drell 2000). In fact, "To most researchers. . .the Neanderthal represented an ancient, inferior race of *Homo sapiens*, an extension into the past of the hierarchy of living human 'races', descending from civilized to savages" (Peeters & Zwart 2020, p. 3).

Carl Linnaeus, the Swedish botanist who in 1735 created the taxonomic system based on binomial nomenclature that we still use today, was influenced by the Great Chain of Being when he proposed that matter could be divided into Mineral, Vegetable, and Animal kingdoms. He also distinguished four types of humans: white Europeans, red Americans, yellow Asians, and black Africans (Weasel 2022). According to Weasel (2022, p. 131),

> Building on this hierarchical framework, the nineteenth century saw the rise of explicitly racist categorizations and rankings of human "types," with those with darker coloring and other phenotypic features (termed "Negro" or "Negroid") at the bottom, progressing through "Mongoloid" or "Asiatic" races to the pinnacle of "Caucasian" racial types with pale skin and a striking conformation to prevailing European beauty ideals at the top.

Neandertals both were understood within and fitted into this racist schema, and their extinction was used to further justify European imperialism. For nineteenth-century Europeans, extinction meant a failure to adapt and thrive and was a deserved consequence of evolutionary processes (Madison 2020). Thus, during the height of European imperialism, "such logic made it easier to defend the displacement, subjugation, and even extermination of human 'races' that accompanied the spread of Europeans across the globe, because these groups were seen to be doomed to extinction due to their inferiority" (Madison 2021, p. 369; see also Higgitt 2021).

It was not until other more "primitive"-looking hominins, such as *Australopithecus africanus* and *Homo erectus*, were accepted by scientists in the early twentieth century that Neandertals were broadly accepted as an extinct species of humans that were either direct ancestors of modern humans or evolutionary dead ends (Peeters & Zwart 2020). From their initial discovery until today, Neandertals have shifted between "being recognized as human or being pushed to the constitutive outside of humanness," what Drell (2000, p. 15) describes as "the oscillating dichotomy of Same and Other." I return to this observation below.

We now know that Neandertals neither led directly to modern humans nor were an evolutionary dead end in the sense that through multiple episodes of interbreeding "remnants of Neanderthal genomes survive in every modern human population studied to date" (Chen et al. 2020, p. 677). Neandertals last shared a common ancestor with *Homo sapiens* sometime between 770,000 and 550,000 years ago (Meyer et al. 2016).[3] Whereas modern humans evolved in Africa, the line leading to Neanderthals underwent further diversification, leading to the Denisovans

[2] It is from the Great Chain of Being that we derive the phrase the "missing link."

[3] Gómez-Roble (2019) has recently proposed a time of divergence prior to 800,000 years ago based on dental evolutionary rates.

sometime before 600,000 years ago (Kubicka et al. 2022, Rogers et al. 2020). Neandertals as an identifiable lineage "began emerging in mosaic fashion in Europe before 400 ka and genetic evidence points to descent from the Sima de los Huesos population, around 430 ka" (Kubicka et al. 2022, p. 517; see also Galway-Witham et al. 2019, Meyer et al. 2016). Neandertals are known to have occupied a wide geographic area from northwestern Europe to the Levant to Central Asia and as far east as southern Siberia (Kubicka et al. 2022, Roebroeks & Soressi 2016). Although Neandertals underwent a series of replacement, contraction, and local extinction events throughout their long history, the lineage survived until approximately 52,000 years ago in the Levant (Fu et al. 2014) and 40,000 years ago in Western Europe (Devièse et al. 2020, Djakovic et al. 2022, Picin et al. 2022).

THE GOLDEN AGE

Even a cursory survey of the literature supports Papagianni & Morse's (2015, p. 14) assertion that we are experiencing a "Golden Age" in Neandertal research. This is due in large part to new fossil discoveries and improved methods for dating archaeological evidence, as well as developments in the study of ancient proteins (paleoproteomics) and ancient DNA (paleogenomics), including environmental DNA, biomolecular analyses, and X-ray microtomography and synchrotron radiation, that "have allowed the virtual reconstruction of the external morphology and internal architecture of bones and teeth" (Romagnoli et al. 2022b, p. 6). What follows is a brief overview of Neandertal research from the past 5 years, with a focus on publications from the past 24 months.

Language, Cognition, and Brain Development

Many recent studies have focused on the differences between Neandertal and modern human brains in terms of structure and development. For example, a 3D reconstruction of the Neandertal brain based on computational neuroanatomy found that Neandertals had smaller cerebellar hemispheres than *H. sapiens*. According to Kochiyama et al. (2018), these neuroanatomical differences mean Neandertals were less cognitively flexible, had greater difficulty processing language, and possessed more limited memory capacity than modern humans. In another approach to studying Neandertal brains, scientists took human stem cells and replaced their *NOVA1* genes with a Neandertal variant. *NOVA1* controls the functioning of many other genes and is important in early brain development. The modified cells grew into cortical organoids ("mini brains"). They discovered that not only did these mini brains look different (Neandertal ones were more popcorn-like in comparison to the *H. sapiens*' spherically shaped ones) but importantly their neurons fired sooner (i.e., matured much more quickly) (Trujillo et al. 2021). Similarly, Pinson and colleagues (2022) found that *H. sapiens* produce more neurons (neurogenesis) and connections between these neurons (synaptogenesis) than their Neandertal counterparts. In a study comparing genes related to emotion, self-control, and self-awareness in modern humans, Neandertals, and chimpanzees, Zwir et al. (2022, p. 354) "conclude that modern humans have more than 200 unique nonprotein-coding genes regulating co-expression of many more protein-coding genes in coordinated networks that underlie their capacities for self-awareness, creativity, prosocial behavior, and healthy longevity, which are not found in chimpanzees or Neanderthals."

In another study, Mora-Bermúdez et al. (2022, p. 1) explored "amino acid substitutions in three proteins known to have key roles in kinetochore function and chromosome segregation and to be highly expressed in the stem cells of the developing neocortex." The neocortex is greatly expanded in hominins. The neurodevelopmental program for the proliferation of cortical progenitors and the timing of differentiation are critical. Multiple neurodevelopmental disorders are associated with gene variants that disturb this timing. Mora-Bermúdez et al. (2022, p. 1)

write that their "results imply that the fidelity of chromosome segregation during neocortex development improved in modern humans after their divergence from Neanderthals." In other words, from an evolutionary perspective, *H. sapiens* found a successful developmental pattern, and genetic variants that stabilized that developmental program were selected for.

It is too soon to know if these studies will lead to a consensus on Neandertal cognition. At present, whereas some argue Neandertals did not differ significantly from *H. sapiens* (Breyl 2021, Hoffmann et al. 2018a; see also Sansalone et al. 2023), others have pointed to differences, for example, in working memory (Wynn & Coolidge 2019) and creativity (Finlayson 2009). Conversely, there is greater consensus supporting the argument that modern humans and Neandertals had similar linguistic and auditory capacities (see Dediu & Levinson 2018 for a full review of the evidence, but see Botha 2020 for a dissenting view based on his reading of the archaeological record). Auditory capacity is an important and until recently underexplored aspect of language, as communication involves both the production and the reception of the message being transmitted (Conde-Valverde et al. 2021).

Life History and Social Structure

The evolution of hominin life history is characterized by a transition from an apelike pattern to a humanlike one with a concomitant extension of the dependency period. Specifically, two life history stages, childhood and adolescence,[4] were either extended or gradually inserted into the ancestral primate pattern for the first time. This extenuation of dependency in immature humans means that there is additional time to learn from the adults and peers in their lives and to practice skills needed to survive in their environment (Nowell 2016). Debate has surrounded how similar Neandertals are to *H. sapiens* in this regard.

Early growth and development. There are more immature specimens associated with Neandertals than with all other hominins other than *H. sapiens*. This is at least in part due to the fact that some Neandertals buried their dead, meaning that more of their little ones were protected from scavengers and erosional forces and thus were more likely to survive in the fossil record. Although some studies suggest that Neandertal growth and development were within the range of modern humans (see discussion and references in Nowell 2021), other research documents accelerated growth. For example, anatomical features of the brain, mandible, and thorax that distinguish Neandertals from modern humans are already present at birth (García-Martínez et al. 2020), and Neubauer & Hublin (2012) estimate that Neandertal neonates had brain sizes that slightly exceeded those of modern human neonates. This is indicative of greater prenatal brain growth than is found in humans. Postnatal brain growth in Neandertals was also more accelerated. The maturation rate of Neandertals is further supported by a recent study of the rib cages of four young Neandertals (Mezmaiskaya 1, Le Moustier 2, Dederiyeh 1, and Roc de Marsal) ranging in age from a newborn to approximately 3 years old at time of death, which demonstrate faster thoracic growth than exhibited by early modern humans (García-Martínez et al. 2020). Overall, more robust limbs and wider torsos would have made Neandertal infants appear stockier than their *H. sapiens* counterparts (García-Martínez et al. 2020; see also Nowell 2021). Similarly, using virtual histology, Mahoney and colleagues (2021) studied prenatal and early postnatal growth in five deciduous teeth from three Neandertals from the site of Krapina in Croatia. They found that the year following birth was a period of advanced somatic (bodily) growth relative to modern human infants.

[4]Although many biologists contend that adolescence is unique to humans, primatologists argue that this life history stage is shared with other primates (e.g., Sandel et al. 2023).

Sex and sexuality. A detailed analysis of Neandertals based on ethnographic data, skeletal evidence, primatology, archaeology, and paleogenetics reveals a great deal about Neandertal later maturation and reproduction. For example, Neandertals likely reached menarche earlier than *H. sapiens* (Kubicka et al. 2022, p. 542). Although exogamy and mating systems likely varied with ecological conditions, monogamy was the dominant mating strategy employed by Neandertals in harsher environments, whereas polygamy was likely more common in richer environments such as the Levant (Kubicka et al. 2022, p. 542). Data on the cephalo-pelvic relationship of Neandertals suggests that the birth process was difficult, necessitating assisted births. Births more often took place during the spring with weaning in the fall, roughly at the same age as in modern humans, although there is individual variation. Kubicka and colleagues (2022, p. 543) argue that "even with high risks of mortality during prime adulthood, elders (>40 years old) were present, meaning that intergenerational alloparenting may have been available, not only from older siblings, but also from grandparents." Neandertal grandmothers especially would have been involved in caring for their young grandchildren, allowing their adult daughters to participate in resource provisioning, including hunting. Despite care from grandmothers, some Neandertal children experienced stress related to weaning (Kubicka et al. 2022, p. 543; Nowell 2021; Rosas et al. 2006). Although not all Neandertals were inbred, most lived in smaller effective breeding populations than early *H. sapiens*. Evidence documents that they interbred with at least two other hominin populations (Denisovans and *H. sapiens*) in multiple phases over more than 150,000 years (Kubicka et al. 2022, p. 543).

Family structure. New research is providing a window into Neandertal social structure. Scientists analyzed the genetic data of 13 Neandertals from Chagyrskaya Cave and Okladnikov Cave, two Middle Paleolithic sites in the Altai Mountains (Siberia). According to Skov et al. (2022, p. 519),

> some Chagyrskaya individuals were closely related, including a father-daughter pair and a pair of second-degree relatives, indicating that at least some of the individuals lived at the same time. Up to one-third of these individuals' genomes had long segments of homozygosity, suggesting that the Chagyrskaya Neanderthals were part of a small community.

The researchers further found evidence of female exogamy. Previous research uncovered evidence of interbreeding between a Neandertal female and a Denisovan male in the genetic makeup of a young female nicknamed Deny, who died 90,000 years ago in Denisova Cave (Siberia) (Slon et al. 2018). Significant information about Neandertal social structure has also come from studies of their footprints showing that groups were composed of a mix of sexes and age classes, dominated by immature individuals (e.g., Mayoral et al. 2021).

Inbreeding, introgression, and disease. Paleogenomics is one of the fasting-growing areas of Neandertal research. Recent studies now point to interbreeding having occurred in multiple phases between 40,000 and 200,000 years ago, involving all combinations of male–female pairings between both lineages (Enard & Petrov 2018, Kubicka et al. 2022, Petr et al. 2020, Villanea & Schraiber 2019). Whereas initial studies suggested that only modern humans outside of Africa shared alleles in common with Neandertals (Green et al. 2006, 2010; see Weasel 2022 for a detailed discussion of the consequences of this misconception), Chen et al. (2020) demonstrated that all human populations have Neandertal DNA. In other studies, Churchill et al. (2022) identified the Levant as an important region for interbreeding, whereas Compton et al. (2021) explored evidence for interbreeding in Europe.

Blood Groups

It was presumed previously that all Neandertals had type-O blood, but scientists have confirmed that they and Denisovans were polymorphic for the ABO blood group (Condemi et al. 2021). One implication of this study is that "genetic variants in the archaic blood borne by the Neanderthals would have made them much more likely to develop hemolytic disease of the newborn (HDFN), an alloimmune condition in which a mother's immune system attacks the blood cells of her unborn fetus" (Dockrill 2021). This could result in higher infant mortality and be a factor in Neandertal extinction (see the section titled Last Hominin Standing).

Symbolic Behavior

The use of symbols is often argued to be a defining feature of *H. sapiens*. Growing evidence, however, supports the use of symbols by Neandertals in the form of personal ornaments, portable art, and spoken language (see the section titled Language, Cognition, and Brain Development) and possibly cave painting, although the latter remains somewhat controversial.

Cave art. New research has changed our understanding of Neanderthal symbolic behavior as well. Until now, although this species has been associated with pigment use, including possible body painting (Nowell & Cooke 2021 and references therein), no evidence has linked them to the production of cave art. New research suggests that Neandertals were responsible for some hand-stencils, painted lines, and dots in multiple caves in Spain (Hoffmann et al. 2018b, Pitarch Martí et al. 2021, Ramos-Muñoz et al. 2022; see also Moro Abadía & Gonzáles Morales 2010, Seghers 2018). The dates remain controversial, however, with Slimak et al. (2018) arguing the dates are younger than Hoffmann and colleagues maintain, though they nonetheless agree that Neandertals were still the only hominins in the region at the time and therefore must have created the images. Other scientists contend the dates are younger still and thus do not support Neandertal authorship of the art (Aubert et al. 2018, Pearce & Bonneau 2018, Pons-Branchu et al. 2020, White et al. 2020; but see Hoffmann et al. 2018c, 2020). At Cueva de Ardales in Málaga, Spain, Pitarch Martí et al. (2021) used optical microscopy, scanning electron microscopy with energy-dispersive X-ray spectroscopy, micro-Raman spectroscopy, and X-ray diffraction to analyze samples of red pigment dated to the Middle Paleolithic that was used to decorate speleothems. Their results suggest that Neandertals collected pigments from outside the cave to make their paints and continued to use this cave for an extended period.

More recently, archaeologists have documented the first evidence of digital tracings (or "finger flutings") made by Neandertals in soft sediments in the French cave site La Roche-Cotard 57,000 years ago (Marquet et al. 2023). This finding is significant because it extends the antiquity of digital tracings by more than 20,000 years and, for the first time, associates them with a hominin species other than *H. sapiens*. The meaning of these tracings currently remains ambiguous as the authors note that they are not necessarily symbolic in nature.

Neandertals' capacity for symbolic behavior is also supported by the recent find of a 51,000-year-old engraved giant deer phalanx found at the site of Einhornhöhle in northern Germany (Bello 2021, Leder et al. 2021). It joins other evidence of Neandertal engraving, including the "hashtag" from Gorham's cave in Gibraltar (Rodríguez-Vidal et al. 2014), the engraved cortical flint flake from Kiik-Koba (Majkić et al. 2018), and the pecked pebble from the Axlor Rockshelter in Spain (García-Diez et al. 2013), among others.[5] Macciardi & Martini (2022, p. 99) argue that engravings produced by Neandertals "all require a brain that can perceive and organize a working

[5] See Peresani et al. (2014) for a taphonomic consideration of Neandertal engravings.

space along the surface of an object, and that can manipulate those surfaces to engrave a formal representation of an abstract concept." A more controversial suggestion for Neandertal symbolic behavior is that they engaged in the nonutilitarian accumulation of large herbivore crania in Cueva Des-Cubierta (Spain) (Baquedano et al. 2023).

Palearctic: a biogeographic region that includes Europe, Asia north of the Himalayas, and Africa north of the Sahara

Culturing the body. Personal adornment and other examples of culturing the body are yet another area of symbolic behavior that has required rethinking. Items include the "Neandertal necklace" from the site of Krapina in Croatia, made from eight white-tailed eagle talons. Cut-marks, notches, and wear facets support the contention that they formed part of a single item of adornment (Frayer 2019, Frayer et al. 2020, Radovčić et al. 2015). The recovery of talons from large, powerful diurnal raptors at Neandertal sites including Combe Grenal (90,000 BP) and Les Fieux (60,000–40,000 BP), both in France, have led some researchers to speculate that the talons were worn by Neandertals and functioned in symbolic contexts (Nowell & Cooke 2021 and references therein). This necklace joins other previously known examples of personal ornaments, such as from the Châtelperronian site of Quinçay, in France, and the sites of Cueva de los Aviones and Cueva Antón, in Spain, that have yielded personal ornaments in the form of perforated, painted, and unpainted large marine bivalves (Nowell & Cooke 2021 and references therein). The remains of birds at Palearctic sites suggest ornamental feather use by Neandertals (Finlayson 2019). Cutting, peeling, and scraping marks are present on the wing bones of golden eagles, indicating the purposeful removal of large flight feathers from bird species that were unlikely to be food items. As Nowell & Cooke (2021) note, "While it is possible that the feathers were used for a number of nonsubsistence activities (e.g., lining for bedding or clothing), the use of feathers as personal ornaments is documented in many extant and historically known hunter-gatherer societies." Similar arguments have been made for remains at Fumane Cave in Italy dating to 44,000 years ago and for use of talons from large, powerful diurnal raptors as items of personal adornment in France and Croatia (Nowell & Cooke 2021 and references therein).

Resource Use and Subsistence Strategies

The traditional view of Neandertals is that they were apex predators and big game hunters. This characterization remains largely true but is gradually being modified by a growing body of data on their use of plant materials for food, medicine, adhesives, and cordage. Recent studies demonstrate not only that Neandertal diets and subsistence strategies varied over time and space in relation to local environmental conditions but also that Neandertals played a role in shaping their environments.

Cordage. Neandertal use of plants is similarly more complex than once thought. The oldest evidence of cordage is now associated with Neandertals. At Abris du Maras in France, dating to 41,000–52,000 years ago, a 6.2-mm fragment of 3-ply baste fiber was found adhering to a Levallois flake (Hardy et al. 2020). As Hardy et al. (2020, p. 1) note, "Twisted fibres provide the basis for clothing, rope, bags, nets, mats, boats, etc. which, once discovered, would have become an indispensable part of daily life."

Medical use of plants. There has also been a growth in our understanding of Neandertal use of plants for medicinal purposes. Chemical compounds extracted from Neandertal dental calculus demonstrated the use of yarrow and chamomile by Neandertals at the site of El Sidrón in Spain (see discussion in Hardy 2022). At this same site, one Neandertal teen suffered from a painful dental abscess and a chronic gastrointestinal pathogen causing diarrhea (Nowell 2021, Weyrich et al. 2017). Through an analysis of his dental calculus, researchers discovered that the adolescent consumed plants that contained salicylic acid, which is a natural pain killer, similar to the active

Cumulative culture: the sum of knowledge of a community that is passed from one generation to the next

ingredients in aspirin (Barras 2017, Weyrich et al. 2017). They also found traces of the *Penicillium* fungus from which we derive penicillin. That Neandertals were cognizant of the medicinal properties of plants should not be surprising given the well-documented behavior of nonhuman primates in this regard (Hardy 2022). De la Fuente and colleagues (2022, p. 1) identified plant use "associated with antiparasitic, antibacterial, antimalarial, anti-inflammatory, insect repellent, among other properties" among 25 nonhuman primate species.

Adhesives. Botanicals can also be used for the manufacture of adhesives. Neandertal use of birch bark pitch has long been known (Koller et al. 2001), and recent experimental work (Kozowyk & Poulis 2019, Kozowyk et al. 2017) further attests to the pyrotechnical skills of Neandertals (see also Niekus et al. 2019, Nowell 2013, Wragg Sykes 2015, Zilhão 2019). Schmidt et al. (2019) initially argued that birch tar adhesives can be made simply and even accidentally and thus are not necessarily evidence of behavioral complexity. However, in a new study, these authors (Schmidt et al. 2023, p. 1) demonstrate that during the manufacturing process Neandertals "intentionally created [an] underground environment that restricted oxygen flow and remained invisible during the process." The authors argue that this technique is unlikely to have been invented spontaneously but was rather the result of improving upon earlier, simpler techniques and should be taken as evidence of cumulative culture.

Dietary use of plants. As might be expected, Neandertal diets varied depending on the environment in which they lived. A recent study documents Neandertal omnivory in Siberia (Salazar-García et al. 2021; see also Power et al. 2018 and Rampelli et al. 2021), helping to erode the stereotype of Neandertals as strict carnivores (but see Jaouen et al. 2022). Studies of the oral microbiomes of Neanderthals and modern humans document that both were able to digest starches, an adaptation missing in chimpanzees (Yates et al. 2021), confirming earlier research that identified boiled starch in Neandertal dental plaque (Henry et al. 2010). Further evidence of cooking has surfaced at the site of Shanidar in Iraq, where Neandertals cooked pulses, such as lentils, as well as nuts and grasses after soaking, pounding, and grinding them to at least partially remove any bitter taste (Kabukcu et al. 2022), and in Italy, where starch grains on grinding tools suggest that Neandertals were making flour (Mariotti Lippi et al. 2023).

Diet and sense of smell. A recent lab study explored the evolution of the hominin sense of smell using cultured odor receptors. Mammals use their sense of smell to detect danger, food, and mates, with odor receptors varying with habitat, dietary niche, and degree of sociability (de March et al. 2023). Humans, however, are most sensitive to food-based odors. Although Neandertals, Denisovans, and *H. sapiens* are highly similar in their sense of smell, Denisovans were twice as sensitive as humans to odors described as spicy, such as cloves, and they were even more strongly receptive to honey and vanilla, whereas Neandertals had reduced responses to odors perceived as green, floral, and spicy (de March et al. 2023).

Landscape modification. In the area around the 125,000-year-old site of Neumark-Nord (Germany), Roebroeks and colleagues (2021, p. 1) used high-resolution data to "identify a distinct ecological footprint of hominin activities, including fire use." Although the region is heavily forested, the site itself is in a clearing, suggesting to researchers that Neandertals intentionally removed trees to create a brighter, more open environment in which to live (Gaudzinski-Windheuser et al. 2023, Roebroeks et al. 2021); this provides some of the earliest evidence of purposeful landscape modification (see Soressi 2016 for landscape modification with a possible symbolic component).

Hunting, tools, and clothing. Recent publications in this area include the results of an actualistic study suggesting Neandertals captured birds (specifically) at night (Blanco et al. 2021; see

also Finlayson 2019). Other studies show that Neandertals employed ambush hunting rather than persistence hunting when pursuing prey, which is hypothesized to have been a crucial difference between them and modern humans, giving the latter a competitive edge (Stewart et al. 2019). Similarly, the earliest evidence for mechanically delivered projectile points in Europe is argued to be associated with modern humans, giving them an advantage over the Neandertals (Sano et al. 2019). A new study documents regular hunting (not scavenging) and butchering of adult male elephants (*Palaeoloxodon antiquus*) (Gaudzinski-Windheuser et al. 2023) at Neumark-Nord in Germany. The enormous labor involved in processing such a large animal implies Neandertals in this region lived in larger groups than previously documented for this species. Similarly, the ability to butcher and store the meat suggests a more sedentary lifestyle than normally accorded to Neandertals (Gaudzinski-Windheuser et al. 2023). Finally, increasing evidence documents that Neandertals were also able to exploit smaller prey than traditionally assumed, challenging yet another Neandertal stereotype (Nabais & Zilhão 2019), and that some of these animals were captured for their pelts, which were then made into clothing (Pelletier et al. 2019).

This brief review of just some of the new things we have learned about Neandertals in recent years begs the question of whether any of these discoveries qualify as Black Swans (Frayer 2019). As noted above, in economics, a Black Swan is an extremely rare and unpredictable event that has severe consequences but in hindsight was foreseeable (Taleb 2010). In most cases, it is too soon to know if these discoveries will have significant consequences for paleoanthropology. Many of them are interesting but are not likely to have a paradigm-shifting impact, with the exception of paleogenomic findings. Paleogenomics have revolutionized our understanding of Neandertals in terms of their relationships with other hominins and with each other, and its impact is only beginning to be felt. That said, in hindsight, interbreeding, for example, was foreseeable. When the early mitochondrial DNA studies stated unequivocally that there was no interbreeding between Neandertals and modern humans (e.g., Cann et al. 1987), many paleoanthropologists pushed back, drawing on morphological and archaeological evidence. The problem is, however, that we tended to privilege genetic data over what many scientists could see from the evidence in front of them.

LAST HOMININ STANDING

Despite real progress in our understanding of Neandertal lifeways and capabilities, as the studies above indicate, the lack of consensus on major issues means that debate continues. One of the most prolific and ongoing debates concerns the cause(s) of Neandertal extinction. Researchers have proposed a variety of hypotheses.[6] Some of these focus on diet and metabolic requirements. For example, Neandertals were too carnivorous (Pettitt 2022); they had excessive energy requirements due to their heavy frames and active lifestyles, rendering them less competitive than their more energetically efficient *H. sapiens* counterparts (Froehle & Churchill 2009); or they practiced cannibalism (for dietary or symbolic purposes; see Frayer et al. 2020, Yustos & Sainz de los Terreros 2015), which not only decimated their numbers (Agustí & Rubio-Campillo 2016) but may have resulted in the spread of transmissible spongiform encephalopathy (a rare progressive neurodegenerative disorder) (Chiarelli 2004, Cooper 2000). Others point to differences in cognition, brain growth/development, linguistic abilities, creativity, innovativeness, and/or symbolic reasoning/behavior (Finlayson 2019, Kochiyama et al. 2018). Inbreeding, possible male hybrid sterility, unsustainable demography, and corresponding lack of social networks/connectivity are another group of hypotheses for Neandertal extinction (Roebroeks & Soressi 2016; Vaesen et al. 2019, 2021). Other hypotheses center on differences in childhood, including the idea that

[6]In this list, for the sake of brevity, I am focusing on the primary proposed cause of extinction but it should be noted that many researchers argue that more than one factor was involved.

Neandertals experienced shorter childhoods with less opportunities for learning (cumulative culture), and these opportunities are key to survival in a "knowledge-rich" foraging niche (Chazan 2019; Nowell 2016, 2021). Neandertals are also said to experience higher infant mortality rates (Nowell 2021, Smith 2013, Smith et al. 2005). More recently, some researchers (e.g., Roebroeks & Soressi 2016, Stringer & Crété 2022, Villa & Roebroeks 2014) have proposed that through intensive interbreeding with *H. sapiens* ("genetic swamping"), Neandertals ceased to exist in an identifiable lineage but in some senses live on in extant humans.

Differences in technology are another hypothesized cause of Neandertal extinction. Neandertals are said to have been less pyrotechnically sophisticated (Goldfield et al. 2018). Their tools and weapons were less effective than those associated with *H. sapiens* (Marean 2015, Sano et al. 2019). They were slow to innovate and were unable to harness other species to enhance their survival; for example, they did not domesticate wolves (Shipman 2015, 2021). Competition with *H. sapiens* more generally is often listed as a cause of Neandertal extinction (e.g., Slimak et al. 2022, Timmermann 2020), along with competition with other Neandertal groups (Chang & Nowell 2020, Rios-Garaizar et al. 2022). Other researchers looked to external factors, such as climate change (Finlayson 2009, Staubwasser et al. 2018, Vahdati et al. 2022, Vernot et al. 2021; but see Columbu et al. 2020), including that driven by pole reversals in conjunction with grand solar minima (Cooper et al. 2021). Finally, many authors argue that a unique combination of factors—a perfect storm—led to Neandertal extinction, and if not for this unhappy accident, the fate of Neandertals (and presumably of humans) might have been different (Finlayson 2009, Shea 2008, Vahdati et al. 2022).

This representative but not exhaustive review of the literature on Neandertal extinction seems to suggest that this is an area of intense interest among paleoanthropologists, but is it so very different from research into the demise of other hominins? A simple survey of publications available on Google Scholar illustrates this research trend clearly (**Table 1**). Search terms related to hominin extinction were typed into Google Scholar, and the number of publications directly related to those terms appearing on the first five pages of results were tallied. Searches were run using both the "since 2018" and "anytime" (i.e., all results regardless of date or the absence of an associated date) filters. A search on "*Australopithecus* extinction" resulted in one publication in the past five years and four overall, whereas "*Homo erectus* extinction" returned three and five publications, respectively. By contrast, the same search run on "Neandertal extinction" resulted in 29 papers since 2018 and 44 overall. The question is why there is such a difference in research intensity between Neandertals and other hominins. Is it perhaps because the notion of an "unhappy accident" is unsettling? Do we have an uneasy sense that if things had been different this could have easily been our fate? As Conard (2022, p. xv) notes, "Our current situation of being the last hominin standing is clearly the exception in our evolutionary history." In the following section, I explore our often complex relationship with the Neandertals in more detail.

Table 1 A survey of hominin extinction publications listed on the first five pages of Google Scholar using the "since 2018" and "anytime" filters[a]

Filter	Neanderthal extinction	Neandertal extinction	*Homo erectus* extinction	*Australopithecus* extinction
Anytime	40	44	5	4
Since 2018	25	29[b]	3	1

[a]The results clearly show that Neandertal extinction is an area of research intensity relative to research into the demise of other hominins (search run on January 2, 2023).

[b]Please note: One article duplicated three times was counted only once.

CONCLUSION: INHABITING THE UNCANNY VALLEY

In 1998, biological anthropologist Philip Lieberman remarked that he had "been accused of being racist for saying the Neandertals couldn't speak like us" (quoted in Holden 1998, p. 1456). Two decades later, another biological anthropologist, David Frayer (2019, p. 358), commenting on a recent genetic study, wrote,

> . . .[they] never considered possible detrimental genetic defects in recent humans inherited from Upper Paleolithic ancestors, so to me this sounds more like Neandertal racism and prehistoric miscegenation than science. For example, substitute "Negro" for Neandertal and "White" for modern. . .it is typical of the Neandertal deniers to deprecate and discredit them whether symbolically, linguistically, archaeologically, or genetically.

The phrase "deniers" is one often used in association with the Holocaust, climate change, or more recently vaccine efficacy. It is not one we are accustomed to reading in relation to hominins. Similarly, to uncritically apply sociologically defined racial categories and the historically situated experience of living within their boundaries to a lineage that died out 40,000 years ago is equally jarring and problematic. Conversely, White supremacists proudly proclaim their Neandertal heritage as detected through home DNA testing kits like those provided by the biotech company 23andMe, based on the erroneous assumption that people of African descent have no Neandertal heritage (Chang & Nowell 2020, Harmon 2018, Keel 2017, Reeve 2016, Zhang 2016; see excellent discussions in Hawks 2021 and Weasel 2022). The question is why the Neandertal debate from their initial discovery until today has taken on this tone. The answer is related to the human search for meaning and identity.

One of the primary goals of paleoanthropology for scientists and in the eyes of the public is to explore what it means to be "human." This has meant defining and redefining what is unique or special about our species. In this politically charged context, Neandertals are the "quintessential scientific other" (Weasel 2022), the "losers" in the human story of struggle and competition (Peeters & Zwart 2020), the markers of the boundary between human and nonhuman (Weasel 2022), the "familiar strangers and arbiters of who and what counts as 'human'" (Weasel 2022; see also Peeters & Zwart 2020), the "humans manqué" (Holden 1998), a mirror that we hold up to ourselves (Conard 2022, Peeters & Zwart 2020, Tattersall 2002), and even an alternate way of being human (Clive Gamble, quoted in Holden 1998). In aesthetics, the uncanny valley is the relationship between an object's resemblance to a human being and humans' reactions to it (usually uneasiness and revulsion)—a relationship exploited effectively in the film *Blade Runner* (1982). Drawing on the work of Morton (2018), Peeters & Zwart (2020, p. 33) write, "Emphasising difference implies pushing Neanderthals into this valley. Appreciating Neanderthal existence as a human lifeform, accepting and embracing their uneasy, strange familiarity, their ambiguity, means making the valley a bit shallower."

Romagnoli et al. (2022b, p. 8) write that research in the twenty-first century "has shown the behavioural and cognitive complexity of Neanderthal groups, their great capacity for adaptation and resilience across Eurasia and their complex genetic history." Based on the research presented here, this assessment is certainly true. But based on the results of many of these same studies, it does not make Neandertals identical to modern humans. As Peeters & Zwart (2020, pp. 5–6) cogently write,

> What is at issue is not whether Neanderthals should be defined in terms of difference or sameness, but rather the dualistic construction of human and nonhuman as such. We will be unable to understand Neanderthals in terms of their humanity as long as our conceptualisation of humanity is grounded in the desire to find a defining difference between us and them.

Perhaps more than a century and a half after Neandertals' discovery, we can finally move beyond this simplistic dualism, this need to define ourselves in the context of what we are not.

We can finally study Neandertals for who they were then, not who we are now. Perhaps this will allow the rest of us to simply read a magazine the next time we have our hair cut.

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