Neandertals and the Black Swan

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ABSTRACT

Neandertals have long been considered remarkably different from modern humans, to the point that most consider them a species apart from us. Yet, recent research shows they had many of the same cultural features used to define modernity, such as art and personal ornaments, and, while morphologically different, their behavior becomes more modern-like with each passing year. We now know they also interbred with moderns and their eastern relatives, the Denisovans. In many respects these recent discoveries were unanticipated and represent what Taleb calls *black swans*. A survey of assertions about Neandertals and the subsequent discoveries overturning them should be a lesson for paleoanthropologists when thinking and hypothesizing about their Neandertal cousins.

Taleb (2010) describes the likelihood of unlikely events happening and how it is important for economists to expect the highly improbable. He refers to these as black swans—unpredicted, unexpected, uncommon events—and black swans because the Europeans thought all swans were white until black ones were discovered in Australia. Black swan occurrences so revolutionize a *known* entity that they completely disrupt its perception. They can have devastating impacts such as the 1988 collapse of the stock market because of the failure of credit default swaps or catastrophic effects such as planes bringing down the Twin Towers. The key to black swans is that they are implausible, rare, yet inevitable happenings that forever change the worldview of a culture, whether past or present. Another factor is sample size of the known phenomena. Europe is a fairly small area of the world and the sampling of swan variation was quite limited, so it is not surprising that Europeans thought all swans were white. In general, the smaller the number of facts, the more likely black swans can swoop in and completely revamp current understanding. And, given these black swans are rare, the addition of one to a small database makes, whatever it is affecting, especially susceptible to being overturned.

The impact of a black swan can be extended to anthropological research, especially paleoanthropology, which is particularly affected by notions based on known facts and small samples. How many times in the past fifty years has the headline "New fossil overturns everything we previously knew" been applied to a newly found fossil discovery, whether a bone, tooth, tool or a gene? Milford Wolpoff once submitted a joke abstract for the American Association of Physical Anthropologists meeting titled "Phenomenal new discovery overturns all previously held theories of human evolution" (Wolpoff 1983). When they accepted the abstract he was stunned. He called me and wondered what he could say for 20 minutes. I reminded him that there was a rich database to be mined and he gave an excellent, engaging and, at times, humorous paper. He concluded his abstract by warning that "[s]ince each new critical discovery once again seems to validate the concept that the data speak for themselves, it is of some interest to carefully discern the messages that are being sent by the fossils." Wolpoff argued that new discoveries add to the continuing story of human evolution and the story is not ever over. A young scientist chairing their first session in an adjacent room was furious with Wolpoff—the laughter in Wolpoff's talk drowned out his session.

A REAL BLACK SWAN

In a very few cases, new discoveries actually do overturn everything, but this is mainly because there was an empty space; that is, no or little evidence of anything in the first place. One example is the discovery of the early *Homo* fossil KNM ER-1470 initially dated at 2.9 mya from Lake Turkana, Kenya. Its discovery stunned everyone in that no one expected a large brained *Homo* that early (Leakey 1973). It had a brain size nearly twice as large as any australopithecine and more than half the size of modern humans. A year later it was re-dated to 2.61 mya ± 0.26 Myr (Fitch et al. 1974), which was later revised to 1.82 mya ± 0.04 Myr (Curtis et al. 1975). Even if the age of KNM ER-1470 fell by more than one million years from the original estimate, it was still unexpected at 1.82 mya for such a large brained hominin. Additional scattered fossil remains were known in the area, hinting at the existence of more modern forms, but these were based mainly on reduced tooth size compared to the mega-toothed australopithecines. These fossils were mostly fit into the scenario *after* the discovery of KNM ER-1470 and, ironically, KNM ER- 1470 had a face and posterior tooth roots indicating it was megadont like australo-

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pithecines (Wolpoff 1999). But, compared to all other fossils known at that time, its large brain size represented a true black swan from the perspective of early hominin evolution. KNM ER-1470 was described as "remarkable," "exciting," "extremely exciting," "extremely interesting." In his article "Myanthropus is older than youranthropus," Krantz (1975: 179) noted the "tremendous news coverage [and the] articles centering on it in *Playboy* and *Ebony*."

There are many reasons for these fossil holes, but maybe the most important is the small samples of a long-passed living record—making any new discovery a candidate to easily overturn what was known before. New technological approaches also contribute to these holes by creating a before and after landscape of knowledge. Who in 1965 (the beginning of my college training) would have predicted retrieving DNA from Neandertals?—not even the most farsighted professionals. Self-aggrandizement is an equally important factor. There is a tendency in science to overhype any new discovery. Every scientist considers their research important (me included) and the most effective way to emphasize this is to add *the earliest, the first, a unique,* or other descriptors noting the exceptional nature of the discovery … these words also aid in getting the paper published and in receiving subsequent funding.

Overturning old ideas and replacing them with new data is a process one could argue is just the normal, self-correcting nature of science—as new details are discovered they correct the past mistakes. But refutation of a previously assumed fact such as cold fusion, which was based on some poorly designed experiments, is different from refuting evidence that never existed in the first place. Speth (2004: 520) pointed to the weakness of these normal science arguments, using the adage, "absence of evidence does not equal evidence of absence." This is the case with the contentions about the subhumanity of Neandertals, who from their very first discovery were identified as inferior, sometimes *much* more inferior, to anatomically modern humans based on no evidence. It is a concept that continues today in much of the scientific and popular literature and in the general public perception of Neandertals. Whether it is dietary breadth, burial habits, symbolic activity, just plain coping with the environment or, as in media advertisements, offensive, stupid behavior, Neandertals, from the beginning and since then, have been considered to be massively inferior to modern *Homo sapiens*. Ironically, they survived at least twice as long as modern *sapiens*; they made it through periods colder than and warmer than Europe is today; they lived through major volcanic eruptions; and, although, they had a much less sophisticated technology than we have today, they persisted through it all. What challenge did they not survive? Until recently, it was thought to be the invasion of modern humans into Neandertal territories that caused their extinction, with modern humans ultimately replacing them without issue. Much to the initial surprise of the paleogeneticists, Neandertals bred with those invaders and left their genes in those that followed their disappearance, even into the present. With the current popularity of DNA testing, who today is not interested in their Neandertal DNA complement? So, in some respects, they are still with us today in mind, body and DNA.

NEANDERTAL FINDS, NEW INTERPRETATIONS, AND BLACK SWANS

Ever so slowly the times are changing, pushed by each new discovery of Neandertal achievements. But there is still a long road ahead for these forerunners of later Europeans. As an example, at a scientific conference in 2015, my colleagues and I presented our discovery of eight modified white-tailed eagle talons and a foot bone (Figure 1) from Krapina in Croatia (Frayer et al. 2015). Gorjanović-Kramberger, a person far ahead of his time, excavated this site more than 100 hundred years ago. He dug in levels, drew a stratigraphy of the site, wrote the level on many of the tools and animal and human bones he found, was the first to apply x-rays for studying human fossils and was the first to test the relative age of the human fossils by chemically dating the extinct animals and comparing their values to the Neandertals (Gorjanović-Kramberger 1906; Radovčić 1988). All this pioneering work is fortunate because there is nothing left of the sandstone rock shelter except the material Gorjanović-Kramberger collected.

Gorjanović-Kramberger found more than 900 Neandertal remains, several thousand stone artifacts and several more thousand animal bones. The rock shelter is dated at ~130,000 years ago, a date no one has ever questioned. It is confined to a warm period (MIS 5e) in the final glacial cycle (Würm), confirmed by ESR dates (Rink et al. 1995) and the small size of the cave bears, which are significantly larger in glacial times (Miracle 2011). There are only Neandertals at the site and only Mousterian tools; modern humans were not in the region until ~80,000 years later. Krapina has been uniformly accepted as a Neandertal site for the past 100 years.

After our talk, a member of the Neandertals are subhumans crowd suggested we radiocarbon date the talons. I replied "but they are 130,000 years old" (as most readers know, ^{14}C dating only works over the past ~40,000 years because of its short half-life). I initially missed the point because the person actually assumed the talons must be recent. Then, I pointed out the irony that no one ever questioned the age of the site until evidence of modern behavior was found in a Neandertal context. But, he was pretty certain they were not old. In the level where the talons were found, there were only Mousterian tools, a hearth, and a few Neandertal bones, but that was not enough of an association for the people who argue that Neandertals lacked complex behavior.

Another Neandertal critic argued that we were assuming ritual and ceremony, when there were other explanations, like the talons "could have been used as tools." I countered that they showed no signs of wear on the tips or other signs of being used as a tool. I also said that if these were found in an Upper Paleolithic context, people like him would be falling over each other ascribing them as distinctive evidence for uniquely modern human behavior. We also had evidence the Krapina Neandertals captured at

Figure 1. Eight talons and the first digit from Level 8 at Krapina. The talons show cut marks, heavily burnished areas, polishing on the sides of the talons and three show notches carved into the plantar border. The digit preserves at least 21 cut marks. It is uncertain how the talons were arranged—whether they were part of a necklace, bracelet, or rattle.

least three separate eagles, because of duplication of claws, and given eagles' revered place in modern groups and their less-than-ideal use as a source of food, there is no reason to assume they were anything but ornamental and had a symbolic connotation (Radovčić et al. 2015). He remained unconvinced. Such is the reaction from the front lines of the Neandertal wars one fights when the battles are over the evidence for sophisticated Neandertal behavior.

Most recently Tattersall (2019: 2) has referred to these Krapina talons (along with other examples of Neandertal art) as "a few straws in the wind," none of them sufficient to signify a cognitive revolution. No one has suggested that the new discoveries of Neandertal symbolic behavior have made this a cognitive revolution equivalent to the later Eu-

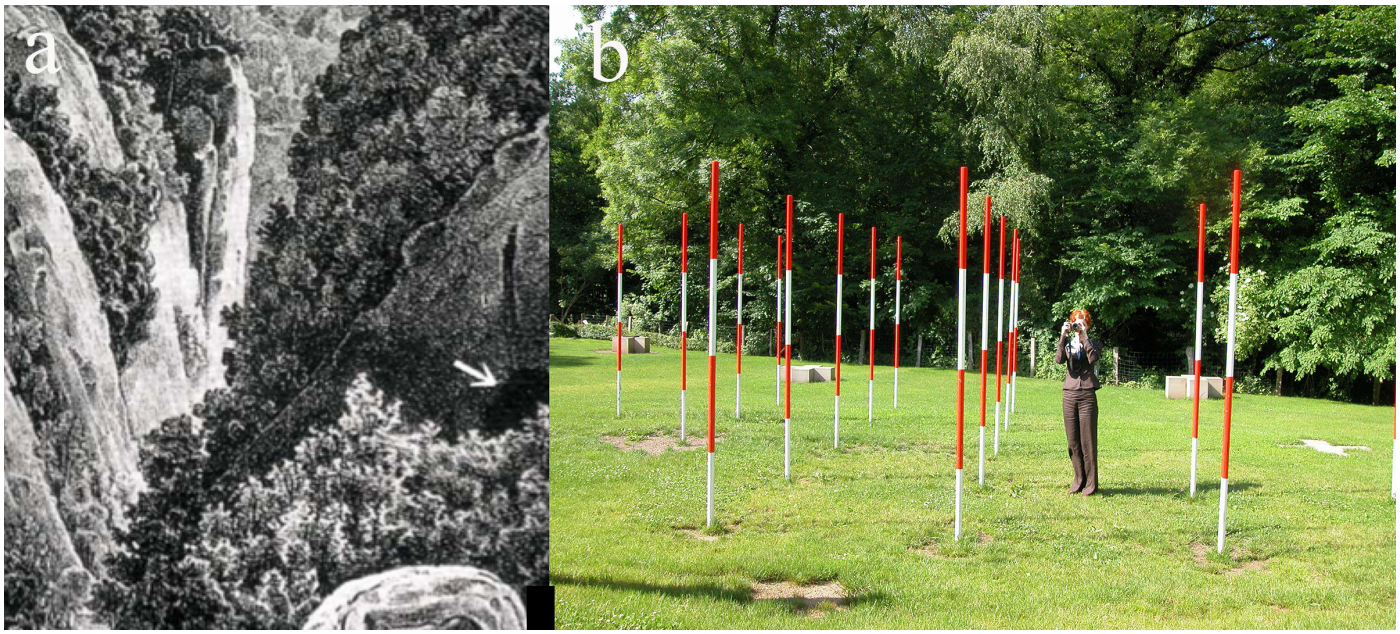


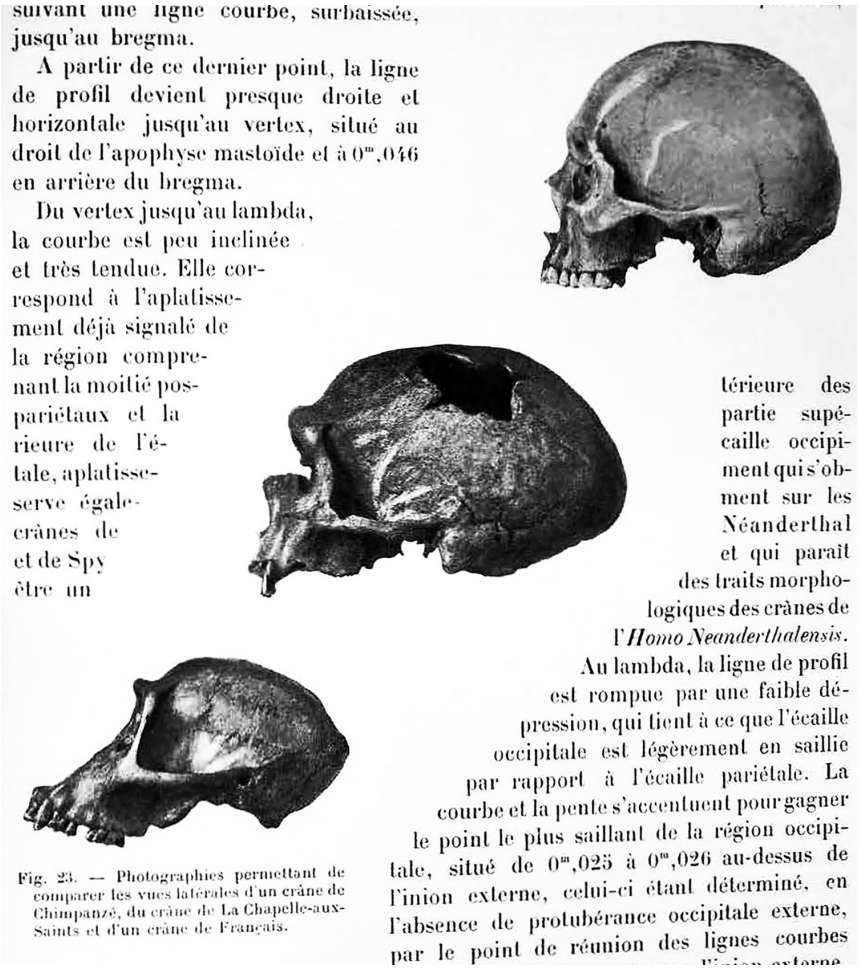
Figure 2. a) The reconstructed cave position in the Neander valley shown by the arrow. b) The area today after massive removal of limestone from the valley. The once steep, narrow valley is now flat. Posts show the vicinity where the new remains of the Feldhofer 1 skeleton were found.

ropean Upper Paleolithic, but compared to the recent past when Neandertals were thought to be bereft of any kind of symbolic behavior, it is incontestable that these finds and surely the ones awaiting discovery have made Neandertals more like us. Also, it is important to ask how much evidence for symbolism will be enough to tilt the balance? Despite some people minimizing of the importance of these eight talons, four of which show cut marks and all eight which show other non-natural modifications, they are a real black swan—fittingly in this case it was bird that sank their denialist ideas.

Earlier discoveries of Neandertal ornaments were met with similar skepticism. Objects of shell, bone, and teeth are found in the French Châtelperronian, the latest Mousterian industry. For these, some have suggested Neandertals were simply copying moderns who were in the area; others maintained the levels were mixed between the Mousterian (Neandertal) and Upper Paleolithic (modern) zones, so there was no evidence of advanced behavior at all. This issue still has not been resolved, but Zilhão et al. (2011) have shown there is no mixing of the other artifacts at Grotte du Renne and that the dates are correct. He and his co-authors asserted that the late Neandertals very likely made the ornaments at Arcy-sur-Cure, Grotte du Renne in France.

A similar response surfaced when cave art was attributed to Neandertals in three sites in Northern Spain (Hoffman et al. 2018a). These authors used uranium-thorium techniques to date the carbonate films covering art on cave walls and stalactites. They documented a scalariform symbol at Pasiega (64.8 kya), a hand stencil at Maltravieso (≥66.7 kya) and at Ardales, red ochre staining of cave "curtains" bracketed from 32.1–63.1 kya. Most of these dates indicate Neandertals made the art, since they are before the arrival of modern *Homo sapiens* in the area. Slimak et al. (2018) contended the dates to be no older than 47 kya, but this, of course, would not eliminate Neandertals as the artists, since it seems that moderns as represented by Aurignacian tools were not in Iberia until a few thousand years later (Cortéz-Sánchez et al. 2019). Slimak et al. (2018) also argued that the red ochre could be due to natural depositions. Hoffman et al. (2018b) argue their dates are accurate and reject the natural explanation for the red ochre at Ardales, because there is no source in the cave. While the art at these three sites is neither as extensive nor as pictorial as the later Upper Paleolithic art, it clearly documents Neandertal artistic expression and is a black swan for those like Mellars (2005) who argue for the uniqueness of Upper Paleolithic figurative art.

So, when and how did this begin with the Neandertals? The first recognized Neandertal was discovered in Germany in 1856 and it was immediately scrubbed from any kind of connection to modern Europeans. The specimen, Feldhofer 1, came from diggings in a cave by workmen and was a fairly complete skeleton, almost surely a burial. Unfortunately, the site along with the valley walls were mined away in subsequent years. Truly amazingly, sixty-two bones, some from a different individual and some fitting on to the cranium were found in excavations on the valley floor (Figure 2). These came from where workmen dumped material from the cave and included a piece from the back of the cranium and a piece of cheek bone (Schmitz et al. 2002). Both clicked into their anatomical positions, so there was no doubt about their association with the original Feldhofer 1, discovered nearly 150 years before. There is more to excavate in the area and several missing parts in the bony remains of Feldhofer 1, so eventually more of the



suivant une ligne courbe, surbaissée, jusqu'au bregma.

A partir de ce dernier point, la ligne de profil devient presque droite et horizontale jusqu'au vertex, situé au droit de l'apophyse mastoïde et à 0m,046 en arrière du bregma.

Du vertex jusqu'au lambda, la courbe est peu inclinée et très tendue. Elle correspond à l'aplatissement déjà signalé de la région comprenant la moitié postérieure des pariétaux et la partie supérieure de l'écaille occipitale, aplatissement qui s'observe également sur les crânes de Néanderthal et de Spy et qui paraît être un des traits morphologiques des crânes de l'*Homo Neanderthalensis*.

Au lambda, la ligne de profil est rompue par une faible dépression, qui tient à ce que l'écaille occipitale est légèrement en saillie par rapport à l'écaille pariétale. La courbe et la pente s'accentuent pour gagner le point le plus saillant de la région occipitale, situé de 0m,025 à 0m,026 au-dessus de l'inion externe, celui-ci étant déterminé, en l'absence de protubérance occipitale externe, par le point de réunion des lignes courbes

Fig. 23. — Photographies permettant de comparer les vues latérales d'un crâne de Chimpanzé, du crâne de La Chapelle-aux-Saints et d'un crâne de Français.

Figure 3. From Boule's description of La Chapelle-aux-Saints, which is in the middle, flanked by a chimpanzee cranium below, and a modern human above.

face and the mandible will likely be recovered.

In the first German description, Fuhlrott and Schaafhausen (1857) considered Feldhofer 1 a primitive human, but Mayer (1864: 16) later argued: "were this the skeleton of the oldest man, then the oldest man was a freak" (as quoted in Brace 1964). This has to be the all-time best quote about a new fossil. When Feldhofer 1 was described in English, King (1864: 97) followed Mayer's thinking and stressed:

> "it more closely conforms to the brain-case of the Chimpanzee --- incapable of moral and theositic conception --- a similar darkness characterized the being to which the fossil belonged."

This is despite Feldhofer 1's much bigger cranial capacity than any chimpanzee and one even exceeding many humans alive today. Later Boule (1911–13) described the La Chapelle-aux-Saints skeleton from the Corréze in France and likewise eliminated Neandertals from any kind of relationship with modern humans. In a famous comparison, he showed a modern chimpanzee, La Chapelle-aux-Saints, and a recent French cranium in lateral view to emphasize the differences. (Figure 3) The small brain size of the chimp is evident and the differences with the recent human are obvious. But, the Neandertal male did not evolve from the chimpanzee nor directly into a modern French person. There were other specimens from the early Upper Paleolithic, like Cro-Magnon 1, which would have made a more appropriate comparison, but Boule chose a fully modern specimen. It is also interesting to note that the La Chapelle-aux-Saints cranium is out of Frankfurt Horizontal in a way that underrepresents its forehead height. At about the same time the *Illustrated London News* commissioned Kupka to illustrate La Chapelle- aux-Saints, which apparently was approved by Boule (Figure 4). Kupka's famous rendition well depicts attitudes about Neandertals at that time and is strikingly different from a recent reconstruction of an Abri Fumane Neandertal from northern Italy, where evidence of feather removal from bird bones was first documented by Peresani et al. (2011). No one today, not even the Neandertalphobes, concur with Kupka's version, but few ascribe the level of humanity to Neandertals as shown in the Abri Fumane feathered Neandertal. Rimmer (no date) has done a nice photoreview of the changing perceptions of Neandertals. Despite their improved image over time, it is still derogatory to call someone a Neandertal.

A major contributing factor to perceptions of Neandertals as dummies is the contention they lacked language. Lieberman and Crelin authored the most influential papers

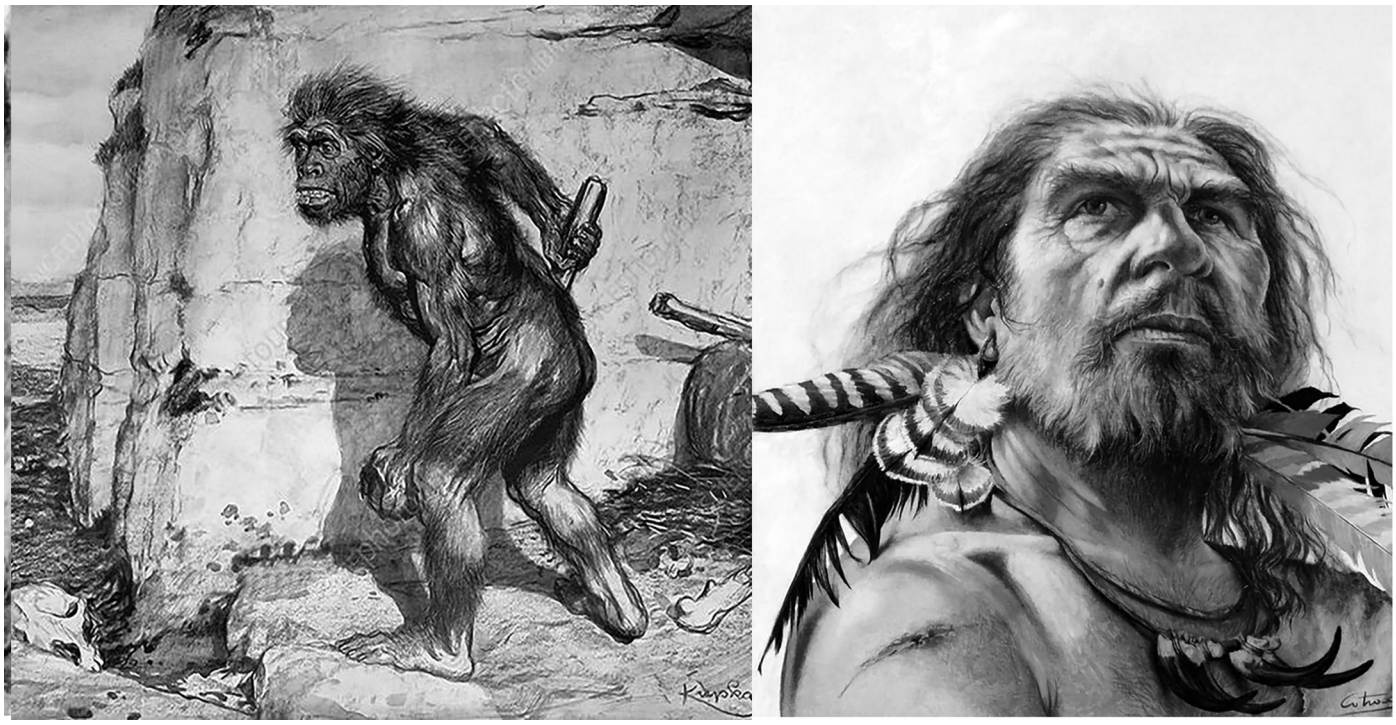


Figure 4. Kupka's reconstruction (1909) of Boule's La Chapelle-aux-Saints Neandertal compared to a more charitable version by Cutrona of a Neandertal male based on discoveries at Fumane Cave, Italy.

on this in the early 1970s. Using La Chapelle-aux-Saints as their model, they contended that this Neandertal (and by extension all Neandertals) could not produce the essential vowels *a, i* and *u,* which are found in nearly all languages (Lieberman and Crelin 1970; Lieberman et al. 1971). One of their reasons for this was a chimpanzee-like vocal space, in part defined by their high positioning of the hyoid (the bone producing the Adam's apple). Apparently, they never saw a Tarzan movie where Cheetah (the chimpanzee) made all the *a, i* and *u* vowel sounds. But there were other problems too, many other problems. In 1975, Falk showed that the position of the hyoid as reconstructed by Lieberman, Crelin and Klatt (1971) was anatomically impossible because the trachea would not be closed off in swallowing so that food would have had an equal chance of going into the lungs as into the stomach. Since the hyoid is a free-floating bone, its positioning in the throat is not defined by any hard tissue markers, like all the other bones of the skeleton. Lieberman et al. (1971) positioned a modern hyoid, (because no Neandertal hyoids were the known at the time) by the lingual tubercles and the styloid process, which was also reconstructed since both sides were broken off in La Chapelle-aux-Saints

Recognizing these missing elements, Lieberman and his co-authors contended that "bony landmarks, such as the hyoid bone or styloid process which give clues to the position and shape of the upper respiratory structures are often missing" (Laitman et al. 1979: 15). Ten years later, when a Neandertal hyoid from Kebara in Israel was described (Arensburg et al. 1989), they maintained a single bone tells us nothing about the vocal tract, despite their statement a few years before. But, even more inexplicably in the same presentation at the American Association of Physical Anthropologists meeting Laitman et al. (1990: 254) claimed "suid hyoids are metrically more similar to those of modern humans than Kebara." Figure 5 shows this is obviously not the case, even without measurements. Since the Kebara discovery, more Neandertal hyoids have been found and they all resemble humans—none come close to a pig hyoid (Frayer 2017). Even a hyoid found in association with an australopithecine in Ethiopia at >3 million years ago does not resemble a pig (Alemseged et al. 2006), but it also is markedly different from a Neandertal, much more like an ape's. After this 1990 abstract, Laitman and his colleagues never published more on the Kebara hyoid as a suid and it remains a mystery why they selected an animal forbidden to all the living people of the Levant.

Another major problem was that Lieberman and Crelin only worked with a cast of La Chapelle-aux-Saints, making their anatomical reconstruction inaccurate. For example, as Burr (1976) pointed out, they included in their vocal anatomy reconstruction of La Chapelle-aux-Saints the nasal and maxillary chambers, but these do not exist in a cast. There were also problems with their modeling of palatal dimensions and the cranial base, key features of their argument. Unknown to Crelin, who did the anatomical reconstruction, much of the base of the plaster cast was fragmentary and was not put together accurately. Boule did this reconstruction and since he considered Neandertals more ape than human, he made the cranial base flat like an ape's. After the Lieberman and Crelin 1971 paper, Heim (1989) found that Boule left out a critical bone fragment of the base. He repo-

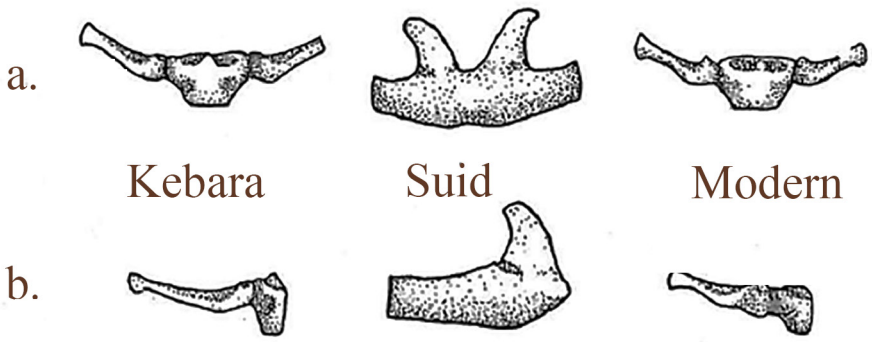


Figure 5. Line drawings of the Kebara Neandertal, a domestic pig, and a modern human hyoid in (a) lateral view and (b) anterior view. The very large lesser horns in the suid hyoid are missing in the Kebara and modern human hyoid, but if present would have been very much smaller.

sitioned it and made other adjustments to the cranial base resulting in a deep vocal tract for La Chapelle-aux-Saints just like in modern humans. This work was reviewed in Boë et al. (2002: 465) who concluded "Neandertals were not morphologically handicapped for speech."

We did some work on the cranial base comparing Neandertals with a large sample of moderns and chimpanzees, measuring the cranial base angle, a reflection of the space below the cranial base and an indication of the volume of the vocal tract (Frayer and Nicolay 2000). In this angle, the higher the number, the more arched and deeper the vocal tract. For the angle, chimpanzees ranged between 0º–31º, recent humans 31º–69º and Neandertals 38º–49º, so clearly, the Neandertals were not like chimpanzees, but completely in the modern range.

Later, Barney et al. (2012: 92) did anatomical reconstructions and computer modeling of eight adult Neandertals ("La Ferrassie, La Chapelle-aux-Saints, Gibraltar 1, Guattari, Shanidar 1, Abri Bourgeois, La Quina 9, and Regourdou, and one subadult, Le Moustier") and used the Kebara hyoid to model the vocal space. They then did acoustic modeling and produced the *a, i u* sounds of a Neandertal vocal tract. As reconstructed, contrary to earlier assertions, these are indistinguishable from modern speech. Their paper included computer reconstructions of these sounds and the Neandertal utterances of these vowels and to my ear are no different from listening to an American from Hattiesburg (MS) compared to a resident of Brooklyn (NY).

In the past few years, some paleogenetic evidence has emerged, which is the real black swan relating to language in Neandertals, since many consider genetics to be the final arbiter. Based on Neandertals from el Sidron cave in northern Spain, researchers extracted ancient nuclear DNA that revealed these Neandertals have a sequence of the FOXP2 (Forkhead box protein 2) gene found in humans, but not in apes (Krause et al. 2007). This is a complicated gene and not just related to language, but also developmental issues unrelated to language production. However, we know that people today who possess a mutated version of FOXP2 have an inability to speak like us plus a series of other abnormalities (Hurst et al. 1990). The fact that Neandertals had a modern version of the FOXP2 gene along with the anatomical evidence for speech capability precludes any argument that they lacked language ability. And, coupled with all the evidence for complex, symbolic behavior (Frayer et al. in press; Langley et al. 2008) those arguing for speechless Neandertals are swept away by several black swans.

PALEOGENETICS AND UNANTICIPATED RESULTS

A final black swan to enter the Neandertal story is the discovery of ancient DNA and specifically ancient nuclear DNA. First off, as mentioned before, no one ever thought anyone could get DNA from Neandertal bones, but within the last few decades it has become commonplace and no one is surprised anymore. The first DNA retrieved was mitochondrial DNA (mtDNA), in part because there are many more copies of it than the DNA housed in each cell's single nucleus. The mitochondria in a cell are responsible for transforming energy, each has their own DNA inherited exclusively from the mother and there are a lot of mitochondria in every cell. This makes mtDNA easier to capture. The story begins in 1987 when Cann, Stoneking, and Wilson published results of their analysis of 147 placentas from a worldwide sample of living people. From this paper came the term "African Eve" (Lewin 1987) since they suggested all fossil populations were replaced by Africans, represented by their singular representation of mtDNA in modern people. They did not mention Neandertals, but it did not take long for paleontologists to use their arguments to push Neandertals aside. Stringer and Andrews (1988) championed the African Eve argument, claiming a wholesale replacement of all earlier resident archaic populations in Europe and Asia by the Eve people. Stringer and Andrews ended their *Science* paper with the comment "paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships will do so at their peril" (1988: 1268). This arrogance got the attention of the black swan.

There was some opposition to the implications of this Neandertal catastrophism, mainly related to Wolpoff, Wu, and Thorne's argument for multiregional evolution

(Wolpoff et al. 1984; Thorne and Wolpoff 1981). A specific critique of the Stringer and Andrews *Science* paper appeared (Wolpoff et al. 1988), followed by a more in-depth review of the issues (Frayer et al. 1993). But these arguments seemed to fall on deaf ears, especially among many geneticists who argued the morphology of fossils took second place to the genetics (e.g., Wilson and Cann 1992). There was some concern about the statistics, phylogenetic trees, and evolutionary assumptions developed from the mtDNA results (Templeton 1991, 1993), but for the most part the genetics ruled and the black swan settled in for a future flight.

Further support for lack of Neandertal contributions to modern Europeans came ten years later. Krings et al. (1997) made the breakthrough in fossils when their team sequenced Neandertal mtDNA from a section of the humerus of the Feldhofer cave Neandertal. Krings et al. (1997: 27) concluded:

> "…. although based on a single Neandertal sequence, the present results indicate that Neandertals did not contribute mtDNA to modern humans. These results do not rule out the possibility that Neandertals contributed other genes to modern humans. However, the view that Neandertals would have contributed little or nothing to the modern human gene pool is gaining support from studies of molecular genetic variation at nuclear loci in humans."

In an accompanying editorial Lindahl (1997: 1) summarized:

> "The present recovery of Neandertal DNA represents a landmark discovery, which is arguably the greatest achievement so far in the field of ancient DNA research. The mtDNA sequence data offer strong support for the displacement model, in which Neandertals did not contribute significant genetic information to modern man during their coexistence for many thousands of years in ancient Europe."

Confirmation of these results came a few years later when Serre et al. (2004) sequenced mtDNA from Neandertals in Croatia (Vindija), France (La Chapelle-aux-Saints), and Belgium (Engis) and compared it to Upper Paleolithic specimens from the Czech Republic (Mladeč) and France (Cro-Magnon, Abri Pataud and La Madeleine). They found no Neandertal mtDNA in the four Upper Paleolithic samples and concluded "while it cannot be excluded that Neandertals contributed variants at some genetic loci to contemporary humans, no positive evidence of any such contribution has yet been detected" (Serre et al. 2004: 316). Then the black swan appeared on the horizon and swept in to upset everything, much to the surprise and chagrin of a lot of the Neandertal-deniers. For example,

> "we really believed that once *Homo sapiens* evolved, they replaced all of these people around the world and didn't mate with them or incorporate any of their genes. It was a very rigid speciation event. Now what this is telling us is that our closest relatives were pretty much similar to us and it was possible to interbreed and that perhaps the speciation event wasn't quite as rigid as we thought in the past "(Long 2010: 1).

The insight came from Green et al.'s paper (2010) and based on sequencing Neandertal DNA from three bones from the late Mousterian site of Vindija cave in Croatia. They found a 1–4% frequency of unique Neandertal genes in recent, modern humans. It is important to note this research involved many of the same people who just years before had pretty much eliminated Neandertals from human ancestry based on mtDNA. And, they were surprised. In a popular account, Green (2010: 2) commented:

> "The scenario is not what most people had envisioned …We found the genetic signal of Neanderthals in all the non-African genomes, meaning that the admixture occurred early on, probably in the Middle East, and is shared with all descendants of the early humans who migrated out of Africa."

In a recent survey of ancient DNA evidence, Slatkin and Racimo (2016: 6385) concluded that:

> "[a]dmixture among archaic groups and between them and modern humans seems to have occurred whenever they came into geographic proximity. In that way, they were no different from groups of modern humans."

Neandertal DNA found in living humans was a sea change for considerations of the place of Neandertals in subsequent human evolution in Eurasia. It is appropriate here to quote again Stringer and Andrews' warning (1988: 1268) "paleoanthropologists who ignore the increasing wealth of genetic data on human population relationships will do so at their peril."

Ancient paleogenetic findings continue to provide wondrous, amazing results, giving perspectives never anticipated twenty years ago. At el Sidrón in northern Spain twelve Neandertal individuals have produced mtDNA and DNA, and, in addition to the FOXP2 data discussed above, we know from the site that Neandertals here had light skin color and red hair (Lalueza et al. 2007), were blood type O (Lalueza et al. 2008), tasted bitterness in foods (Lalueza et al. 2009) and, most interesting of all, practiced patrilocal residence patterns (Lalueza et al. 2011). For the latter, genetic variation shows that among the twelve individuals all three females come from different mtDNA types, while all six males are from the same mtDNA lineage. The remaining three individuals were unsexed, but come from two different mtDNA types, one like the males, the other two like one of the females—her likely offspring. For el Sidrón, this means that males stayed within the group and females came from outside—a residence pattern paralleling most modern hunter-gatherer groups. But, since population densities were likely low as was the effective breeding size, outbreeding was not enough to offset inbreeding. Thus, Rios et al. have published skeletal evidence for inbreeding at the site, documenting 17 congenital anomalies ranging from a retained deciduous canine, sagittal clefts on cervical vertebrae to a tripartite patella (Rios et al. 2019: 1). None of these traits are fatal and some, such as retention of a deciduous tooth, are not uncommon in panmixic groups.

Other remarkable discoveries include the finding by Slon et al. (2017) of human mtDNA fragments mixed with

other segments of vertebrate mtDNA in Pleistocene sediments from four Neandertal and two Denisovan sites in Europe and Siberia. So far, just sequences of mtDNA come from the soil. Begging the question what is next? Ancient nuclear DNA sequences from feces (apparently we already have a stool specimen [Sistiaga et al. 2014]) or other body detritus? Maybe it will be Neandertal fingerprints on stone tools? We already know from dental calculus the wide variety of items they put in their mouths (Hardy 2018; Hardy et al. 2018) and the great variety of residues they were processing, which were left on cutting edges of stone tools (Hardy and Moncel 2011), so save your "that's preposterous laugh." In a second study by Slon et al. (2018) DNA from a segment of a long bone from Denisova cave showed two X chromosomes, indicating the bone was from a female and, based on the bone thickness, it is thought she was a subadult. But, incredibly, the DNA results indicate she had a Neandertal mother and a Denisovan father. Previously it was thought there was some gene flow between the two groups, but that a Neandertal never saw a Denisovan. The black swan flew in and now we know the two groups met directly and had at least one sexual encounter and left at least one offspring. There are very likely more. It is important to recognize that this was probably *not* a lone, wandering Neandertal female, but a member of a Neandertal group that met a Denisovan group and exchanged mates. Slon et al. (2018: 116) concluded that:

> "mixing among archaic and modern hominin groups may have been frequent when they met [but] their zones of overlap may have been restricted in space and time. This, as well as possibly reduced fitness of individuals of mixed ancestry, may explain why Neanderthals and Denisovans remained genetically distinct."

They do not give references for "possibly reduced fitness of mixed ancestry," but presumably they are referring to Simonti et al. (2016) who found detrimental Neandertal genes ranging from physiological to psychological disorders in moderns. Slon et al. (2018) 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 important to consider that Neandertals had these so-called defective alleles for tens of thousands years before they encountered Denisovans or moderns and they worked just fine in them. Rather than calling them defective Neandertal genes, one could argue the Denisovans and moderns were the defective ones. Yet, it is typical of the Neandertal deniers to deprecate and discredit them, whether symbolically, linguistically, archaeologically, or genetically.

Some have explained the genetic load carried by Neandertals was protected in their expression by their low effective population size (Juric et al. 2016). These defective alleles then become expressed and selected against in the much larger effective population size of the modern invaders they interbred with. While Neandertals likely lived in low population densities and had low effective population size, they did so for several hundred thousand years and persisted with these defective alleles. From el Sidrón, we also know that they practiced patrilocal residence patterns (Lalueza et al. 2011), males getting female partners from outside the group, so some amount of gene flow occurred, reducing the effects of inbreeding, contra the assumptions of Harris and Nielson (2016). Those that account for Neandertal extinction by their small effective breeding size and inbreeding, ignore the fact that they lasted in Europe and the Near East for tens of millennia and, moreover, seem to have spread as far east as Siberia to mate with Denisovans.

SURELY THERE IS MORE TO COME

For research on Neandertals there are many black swans swimming in the paleoanthropology pond just waiting to take off and fly in to surprise everyone. There are still many issues to work on and not all of them are solutions paleogeneticists can solve. Some questions are: (1) a better understanding about dietary diversity in Neandertals, (2) the meaning of tool type variation over place and time, (3) birthing patterns and the effect of dietary and weaning stresses on fetal and infant Neandertals, (4) more details about Neandertal aging and demographics, (5) a better understanding of genetic diversity across time and space, (6) the relationship between European and Asian Neandertals and the Denisovans, (7) mtDNA and ancient DNA extraction from more Upper Paleolithic specimens with comparisons to Neandertals; and, (8) why, after 200,000+ years in Eurasia, Neandertals disappeared. These and other issues still unanticipated by paleoanthropologists lie ahead for those who work on Neandertals. Any one of these can embellish the current picture of Neandertals and their relationship to our more immediate Upper Paleolithic ancestors and us. Hopefully before then paleoanthropologists will be careful about their pronouncements of perceived and imagined inadequacies of their Neandertal cousins. Otherwise, they may be attacked by black swans, just waiting to swoop in to muddy the evolutionary waters.

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