

The meaning of Neandertal skeletal morphology

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A procedure is outlined for distinguishing among competing hypotheses for fossil morphology and then used to evaluate current views on the meaning of Neandertal skeletal morphology. Three explanations have dominated debates about the meaning of Neandertal cranial features: climatic adaptation, anterior dental loading, and genetic drift. Neither climatic adaptation nor anterior dental loading are well supported, but genetic drift is consistent with the available evidence. Climatic adaptation and activity patterns are the most discussed explanations for Neandertal postcranial features. Robust empirical relationships between climate and body form in extant humans and other endotherms currently make climatic adaptation the most plausible explanation for the wide bodies and relatively short limbs of Neandertals, and many additional postcranial features are likely secondary consequences of these overall skeletal proportions. Activity patterns may explain certain Neandertal postcranial features, but unlike the situation for climate, relationships in extant humans between morphology and activities are typically not well established. For both the cranium and the postcranium, changes in diet or activity patterns may underlie why Neandertals and Pleistocene modern humans tend to be more robust than Holocene humans.

cranium | human evolution | modern human origins | postcranium

Since the discovery of Neandertals in 1856 at the Kleine Feldhofer Grotte in the Neander Valley near Düsseldorf, Germany (1), deciphering the meaning of Neandertal skeletal morphology has fascinated scientists and the public alike. According to some early proposals, Neandertal skeletons were simply pathological modern human skeletons, but as more fossils accumulated with a consistent set of morphological features these explanations became untenable (2, 3). Although pathology cannot explain Neandertal skeletal morphology in general, pathological lesions, particularly healed traumatic injuries, are frequent on Neandertal skeletons (4).

Current evidence suggests that Neandertals last shared a common ancestor with modern humans >350,000 years ago (5–7), and fossils that are certainly classified as Neandertals are present in the fossil record by ≈130,000 years ago (8, 9) and persist until <35,000 years ago (10, 11). Separate Neandertal and modern human lineages perhaps emerged when geographic barriers produced by climate fluctuations isolated Neandertal populations in Europe from modern human populations further south (8, 12). Although Neandertals originated in Europe they later extended their geographic range into western and central Asia, ranging as far south as Israel and perhaps as far east as southern Siberia (8, 13).

My purpose is to present current views on the meaning of Neandertal skeletal morphology. Instead of a giving comprehensive review, I concentrate on aspects of Neandertal cranial and postcranial morphology that have been studied extensively using a variety of differ-

ent approaches. I begin by outlining a procedure for distinguishing among competing hypotheses for fossil morphology.

Distinguishing Among Competing Explanations

The morphology of fossil skeletons, like any aspect of the phenotype, is the product of genetic influences, environmental influences, and often interactions between the two (14). Genetic influences on skeletal morphology are ultimately the result of the adaptive (i.e., natural selection) or neutral (i.e., mutation, gene flow, genetic drift) evolutionary forces that have shaped allele frequencies in a population or species over multiple generations. There are many possible environmental influences on the phenotype (14), but dietary, locomotor, or manipulative behaviors that shape skeletal form through the mechanical loading patterns they produce over the lifetime of an individual are of particular interest to investigations of ancient skeletons (15). Therefore, the task of deciphering the meaning of Neandertal skeletal morphology can be encapsulated as finding ways to infer the evolutionary and lifetime behavioral causes of Neandertal skeletal features. This task is not straightforward, and, even when it is possible to determine whether genetic or environmental influences are primarily responsible for variation among individuals, populations, or species for a particular skeletal trait, it is still necessary to decide among competing evolutionary or lifetime behavioral explanations. With this in mind, I outline a procedure for going from a description of fossil morphology to its meaning.

Lifetime Behavior vs. Evolution. Traits produced by lifetime behaviors should typically be found on the skeletons of adults, possibly older subadults, but not the skeletons of very young individuals. Individuals so young that they have not yet done certain behaviors would not be expected to show traits that result from the mechanical loading produced by actually doing a behavior. This argument is certainly relevant to the foraging, manipulative, or mobility activities that have been proposed to explain certain Neandertal traits (16, 17). Therefore, if a trait is present on the skeletons of young Neandertals, it must either have an evolutionary explanation (i.e., be due to genetic differences shaped by natural selection or neutral evolutionary forces) or result from environmental influences unrelated to adult behaviors. An improved understanding of development often cannot help with distinguishing among possible evolutionary explanations, because neutral evolutionary forces or different natural selective pressures can act through similar developmental shifts (18), but it can help with deciding whether an evolutionary explanation is warranted or not.

Controlled experiments on laboratory animals are another way to distinguish between lifetime behavioral and evolutionary explanations for morphology (19, 20). Because it is possible in the laboratory to control many variables other than the ones of interest, the results of laboratory experiments can of-

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Fig. 1. Neandertal and modern human cranial differences. On the left is a Neandertal (La Chapelle-aux-Saints). On the right is a modern human (Cro-Magnon 1). Anterior (above) and lateral (below) views. Photos courtesy of Chris Stringer and the Musée de l'Homme (Paris).

ten be interpreted unambiguously. However, it is important to be cautious when extending laboratory results outside the realm of the experiment. It is well known that the sources of variation within and between groups and for different sets of groups can be quite different (21). This means, for example, that variation in a feature could be mostly due to environmental effects for the laboratory animals within the context of the experiment, but genetic effects could be responsible for variation in the feature between different groups of the same species or between different species. The central issue is that, although interpretation of the experimental results is straightforward, determining their applicability to understanding extinct species, such as Neandertals, is more difficult.

Single Features vs. Complexes of Features.

If features vary together because of genetic, developmental, or functional links, then explaining one of them may be sufficient to explain them all. Ideally, we would like to be able to estimate the covariance among features directly from fossil specimens, but a much larger and less fragmentary Neandertal sample would be necessary to robustly estimate covariance patterns. Even so, arguments that 2 features form a complex would be weakened by finding fossil specimens that have one of the features but not the other. However, consistently finding a set of features together does not demonstrate that they all have the same explanation, because individuals of a species will share features

simply due to shared ancestry, even if the features are genetically, developmentally, and functionally unlinked.

An alternative to directly estimating covariance patterns from fossils is to study extant species, with the implicit assumption that they have similar covariance patterns to the fossil species of interest. Covariance patterns are similar across human populations (22), and although there are some important differences, African apes and humans have broadly similar covariance patterns (23–25). The sum suggests that it is reasonable to assume that Neandertals would have had similar covariance patterns to humans, at least for most features. Most important for evolutionary explanations is the within-group additive genetic covariance matrix, which can often be approximated by the within-group phenotypic covariance matrix (26, 27). Within-group additive genetic covariance is what constrains the response to natural selection or the direction of change by genetic drift (28). Within-individual covariance patterns (fluctuating asymmetry) can give insights into the covariance caused by developmental interactions (29). Analyses that combine among- and within-group variation within a species may identify covariance patterns that are not readily apparent from analyses of individual groups (30), but these associations should be interpreted cautiously, because they could be due to population history or phylogeny rather than genetic, developmental, or functional links.

Evolutionary Explanations. If an evolutionary explanation is warranted, the final step is to distinguish among possible hypotheses. One approach is to investigate whether there is an empirical relationship between the morphological feature of interest and a potential selective factor (e.g., temperature, humidity, locomotor behavior, etc.) in one or more extant species. If so, then perhaps the same relationship explains patterns of variation for the feature in the fossil record. This approach implicitly assumes that whatever factors lead to a relationship in the extant species are also important for the extinct species, and consequently, is most robust when similar relationships are found for multiple populations or species.

A second approach is to evaluate whether the form of the feature, or complex of features, observed in fossil specimens is consistent with its purported function. This approach does not attempt to directly model how natural selection would have acted; it simply evaluates the internal consistency of an adaptive hypothesis. An internally consistent adaptive hypothesis is not necessarily correct, but an inconsistent one can be rejected. Depending on the particular hypothesis, different approaches can be taken to assess consistency, but biomechanical modeling or laboratory experiments are often used (31).

Third, it is sometimes possible to distinguish among different evolutionary explanations by explicitly modeling evolutionary forces with quantitative and population genetics (18, 32). This modeling can be used to evaluate the importance of genetic drift vs. natural selection or the fit of different selective hypotheses with observed data. A strength this approach is that the dynamics of the evolutionary process are quantitatively incorporated into the testing of hypotheses (33). This additional level of quantification requires hypotheses to be specified more precisely, which can sometimes be difficult, but, in principle, it allows for more rigorous tests.

Finally, the patterning of traits in the fossil record can be used to evaluate competing evolutionary explanations. The value of this final approach and the previous one would increase substantially if we knew more about how evolutionary forces typically act over hundreds to thousands of generations.

Neandertal Cranial Morphology

Numerous metric and nonmetric features typically distinguish the crania and mandibles of Neandertals from those of modern humans (30, 34–38) (Fig. 1, Table 1). Table 1 lists both uniquely derived (autapomorphic) and primitive

Table 1. Selected Neandertal cranial features

Anatomical region	Features
Cranial vault	Receding frontal squama Long, low braincase, sometimes with a posteriorly bulging occipital ("bun") Globular ("en-bombe") braincase when viewed from behind
Cranial base	Occipital torus with a suprainiac fossa above it Fairly unflexed ectobasicranium Large juxtamastoid eminence and relatively small mastoid process Tubercle on mastoid process adjacent to the external auditory meatus Anteroposteriorly elongated foramen magnum
Acoustic cavities	Large lateral, small anterior, and small and inferiorly positioned posterior semicircular canal
Facial skeleton	Pronounced, double-arched supraorbital torus Projecting midface Minimally angled zygomatic bone Absence of infraorbital concavity and canine fossa Wide, tall nasal aperture Wide, projecting nasal bridge Depressed nasal floor
Mandible	Retromolar space Inferiorly positioned and laterally expanded condyle Asymmetric sigmoid notch Large coronoid process Horizontal-oval mandibular foramen Large medial pterygoid tubercle Absence of mental eminence

(symplesiomorphic) features, because both need to be explained. The appearance of derived features in the fossil record can point to the action of directional natural selection or genetic drift, and the retention of primitive features can indicate stabilizing natural selection.

Lifetime Behavior vs. Evolution. Many distinctive Neandertal cranial features are present on the skeletons of very young individuals, suggesting that they are not the result of mechanical loading patterns produced by lifetime behaviors. Of particular interest are the features present on 2 well-preserved neonatal skeletons from Mezmaiskaya, Russian Federation and Le Moustier, France. The Neandertal features found on the Mezmaiskaya specimen include an overall cranial shape similar to that of other Neandertals, an elongated foramen magnum, a projecting midface, an inferiorly positioned posterior semicircular canal, and an inferiorly positioned mandibular condyle (39, 40). Those on Le Moustier 2 include the absence of an infraorbital concavity and nasal bones shaped like those of adult Neandertals (41). The slightly older Amud 7 skeleton from Israel also shows Neandertal cranial features, including the absence of a mental eminence, an oval foramen magnum, and an enlarged medial pterygoid tubercle (42). The general impression from these skeletons of very young

Neandertals, along with studies of older subadults (43), is that most Neandertal cranial features are present very early in development and, consequently, appear to warrant evolutionary rather than lifetime behavioral explanations. It should be pointed out, however, that most studies of subadult Neandertals have tended to focus on the Neandertal features that are present rather than providing a systematic assessment of the percentages of present vs. absent features, which may give the impression that young Neandertals look more like adult Neandertals than they actually do.

Although many cranial differences between Neandertals and modern humans are likely due to different allele frequencies at loci underlying cranial form, there is some experimental evidence that lifetime behavior differences, specifically which foods are eaten, can influence cranial form. For example, Lieberman and colleagues (20) performed laboratory experiments on rock hyraxes to investigate the effects of food processing on cranial growth and form. The maxillary molars of rock hyraxes are positioned directly beneath or behind the orbits as in humans, which may make them more appropriate models for human mechanical loading patterns than more prognathic nonhuman primates (20). The hyraxes were divided into 2 groups of 4 animals each. One group was fed cooked food, whereas the other was fed raw/dry food. The animals

raised on cooked food showed $\approx 10\%$ less growth for some facial dimensions, suggesting that diet, and perhaps other behaviors, may influence facial size (20). These results are intriguing, but unless the animals in the 2 treatment groups were specifically selected to be siblings, they could reflect genetic differences between treatment groups rather than diet. Although differences in diet do not appear to explain most cranial differences between Neandertals and contemporaneous modern humans, they could explain why the crania of Pleistocene modern humans tend to be more robust than those of Holocene humans (19, 20).

Single Features vs. Complexes of Features. On the one hand, studies of extant species have consistently demonstrated substantial integration of cranial features (31). On the other hand, the fossil record shows a certain degree of independence for the cranial features typically found in Neandertals. For example, European fossils >130,000 years old exhibit some but not all Neandertal features (8), which is not the expected pattern if all Neandertal features were part of an integrated package. This point is illustrated nicely with specimens from the Sima de los Huesos, Spain. Fossils from this site have prognathic midfaces like Neandertals and some of the associated morphological features, but they lack cranial base traits such as the mastoid tubercle or a large juxtamastoid eminence coupled with a relatively small mastoid process (44). They also lack some cranial vault traits, such as a globular shape when viewed from behind, but display others, such as an incipient suprainiac fossa (44).

Evolutionary Explanations. Three main evolutionary explanations have been proposed for Neandertal cranial morphology: adaptation to cold climates, adaptation to anterior dental loading, or genetic drift. The cold-climate hypothesis is based on the observation that the geographic range of Neandertals was centered quite far north in Europe, and except for brief warm periods, global climates were substantially cooler when Neandertals were evolving than they are today. Neandertals clearly experienced fairly cold temperatures, but this does not require that their cranial features are adaptations to these climatic conditions. Most climatic hypotheses for Neandertal cranial form focus on the nasal region and how other facial features may result from adaptations in this region (30, 36, 45, 46).

Studies by Franciscus (36) of internal nasal dimensions and Holton and Franciscus (30) of external ones fail to sup-

Table 2. Selected Neandertal postcranial features

Anatomical region	Features
General	Wide bodies with short extremities, particularly the distal limb segments Long bones tend to have bowed shafts and thick cortical bone Postcranial bones tend to be robust with rugose muscle attachments
Axial skeleton	Horizontal lower cervical spinous processes Robust, rounded rib shafts
Upper extremity	Long clavicle Wide scapula with narrow glenoid fossa and dorsal axillary sulcus Humerus with wide olecranon fossa and narrow surrounding dorsodistal pillars Ulna with high and long olecranon process and anteriorly oriented trochlear notch Radius with medially directed tuberosity and long neck Trapezium with flat first metacarpal facet Hamate with large hamulus Third metacarpal with short styloid process Subequal proximal and distal thumb phalanges Large hand distal phalangeal tubercles
Lower extremity	Wide pelvis with long, thin superior pubic ramus Femur with large articulations, rounded midshaft lacking a pilaster, and low neck-shaft angle Tibia with projecting tuberosity and absence of diaphyseal concavities Relatively symmetrical medial and lateral patellar facets Large foot distal phalangeal tubercles

port adaptation to cold climates as the primary explanation for Neandertal facial morphology. The depressed nasal floors often found in Neandertals are most common in recent humans from subSaharan Africa (36). Likewise, wide nasal apertures, which characterize Neandertals, are most frequently found in equatorial recent humans (30). Although the Neandertal nasal region, in general, does not appear to be an adaptation to cold climates, the narrow superior internal nasal dimensions, tall nasal apertures, and projecting nasal bridges of Neandertals could be, because these features are typically found in high-latitude recent humans (30). If Neandertals were adapting to the cold similarly to present-day humans, then climatic adaptation is an unlikely explanation for their cranial form.

Neandertals tend to have more worn anterior teeth than posterior ones, and their anterior teeth show a high incidence of enamel chipping, microfractures, and microstriations on the labial surfaces. Taken together, these signatures of anterior tooth use suggest that Neandertals were using their mouths like a vise. The anterior dental loading hypothesis extends this idea by proposing that Neandertal facial form, and perhaps other cranial features, are adaptations to dissipate the high mechanical loads produced by this behavior (47–52). Because Neandertal facial features ap-

pear early in development, they cannot be direct mechanical responses to anterior dental loading. They would have to be adaptations produced by natural selection after the species consistently performed this behavior for multiple generations.

One problem with the anterior dental loading hypothesis is that biomechanical modeling suggests that Neandertals were not able to produce particularly high bite forces (53, 54). Neandertal cranial form cannot be adapted to resisting high bite forces if Neandertals were incapable of producing them in the first place. O'Connor and colleagues (54) showed that, although Neandertals would have been able to produce fairly high bite forces in absolute magnitude, their bite forces would not have been unusually large for the size of their crania. Additionally, if efficiency is quantified as the ratio of bite force to muscle force, Neandertals were actually less efficient than many modern humans (54).

Neandertal and modern human populations seem to have become isolated from each other >350,000 years ago (5–7). When this occurred, Neandertals and modern humans would have diverged from each other even in the absence of natural selection through the random fluctuations in allele frequencies that happen in all real populations (i.e., populations that are not infinite in size). This process of genetic

drift could explain Neandertal cranial features. My colleagues and I (18) tested this hypothesis using predictions from quantitative and population genetics with a sample of 37 cranial measurements collected on 20 Neandertal specimens and 2,524 recent humans, and we were unable to reject it with multiple statistical tests. Subsequently, calibrated on the rate of cranial divergence among recent human populations, we estimated that Neandertals and modern humans diverged $\approx 311,000$ years ago or $\approx 435,000$ years ago, depending on assumptions about within-group variation (7). These split dates match quite closely with those derived from ancient Neandertal and extant human DNA sequences, which is the expected result if genetic drift were responsible for the cranial divergence.

Additional support for the genetic drift hypothesis comes from the fossil record. Neandertal features do not appear all at once. In fact, they seem to gradually accumulate over a period of >300,000 years (8). A similar pattern may characterize the appearance of modern human features (55), but the dating and more fragmentary nature of the African fossil record allows for other interpretations. This “accretion” of Neandertal features is exactly the expected pattern if genetic drift were responsible, and it seems less compatible with existing adaptive hypotheses such as climatic adaptation or anterior dental loading.

Neandertal Postcranial Morphology

The postcranial anatomy of Neandertals, like their cranial anatomy, distinguishes them from modern humans (34, 38, 56–59) (Table 2). As with Table 1 for cranial features, Table 2 includes both primitive and derived postcranial features.

Lifetime Behavior vs. Evolution. At least some Neandertal postcranial features are present on Neandertal fossils from individuals <1 year of age. For example, Mezmaiskaya has a femoral diaphysis that is long relative to the tibial diaphysis, bowed long bones, a long superior pubic ramus of the pelvis, a medially directed radial tuberosity, and a fairly robust skeleton (39, 40). Additionally, Amud 7 has a long clavicle (60), and the Kiik-Koba 2 individual from the Crimea, thought to be ≈ 3 –7 months old, has an incipient scapular dorsal axillary sulcus (61) and an opponens pollicis flange on the first metacarpal (56). However, some Neandertal postcranial features only appear later in development, including the thinness of the superior pubic ramus (62) and thick long-bone cortices (60, 63).

Numerous studies of laboratory animals, human growth series, and biomechanical models indicate that long bone cortical thickness reflects, at least in part, mechanical loading produced by locomotion and other behaviors (15, 64). These results are consistent across a variety of studies, making it likely that mechanical loading history explains a significant portion of the variation in cortical bone thickness between Neandertals and modern humans, but it is possible that at least some differences are due to genetic influences.

Single Features or Complexes of Features.

One of the foremost postcranial contrasts between Neandertals and early modern humans is in body proportions. Specifically, Neandertals have a wide pelvis, short limbs relative to trunk height, and short distal limb segments, whereas early modern humans have narrower bodies with relatively longer limbs (45, 57, 58, 65–69). These contrasts in body proportions have led multiple researchers to propose that other postcranial differences between Neandertals and modern humans are simply secondary consequences of differences in body proportions. If this proposal is correct, an explanation for Neandertal body proportions could account for many other postcranial features as well. There are few fossil individuals that preserve a large fraction of their postcranial skeleton, so, unlike the situation with cranial features, covariance patterns among postcranial features are difficult to investigate directly with the fossil record. Consequently, I focus on studies of covariance patterns based primarily on recent human samples.

Churchill (70) investigated whether upper body features typically found in Neandertals could be explained as secondary consequences of upper body size, chest shape, and robusticity. He found fairly weak correlations between upper body variables. Although a model of upper body integration fit the data better than one with no integration, the integration model explained less than half of the variance in upper body morphology. Based on these results, Churchill (70) concluded that it was unlikely that an overarching causal factor, such as body proportions, could explain Neandertal upper body morphology. This interpretation is reasonable, but it is important to note that only a fraction of the unexplained variance is likely to be the result of lifetime behavioral or evolutionary causes. Some proportion of phenotypic variance will always be due to genetic variation among individuals, microenvironmental variation, random developmental perturbations, and measurement error (14). If the variance due to these factors were to be partitioned

out, the percentage of the remaining variance explained by the integration model might be quite high.

In a study of the entire postcranial skeleton, Pearson (69) found that articular size and long bone shaft thickness relative to bone length is closely related to body proportions. Focusing more narrowly on the hip region, I (71) found that a wide pelvis relative to femur length was associated with femora with large articulations, thick and round midshafts, and low neck-shaft angles. Neandertals typically have large articulations, thick shafts, and femora with round midshafts and low neck-shaft angles, so based on the results of these 2 studies, it is plausible that many Neandertal postcranial features are best explained as secondary consequences of their body proportions. Furthermore, a wide pelvis coupled with the maintenance of a transversely oval outlet of the birth canal may explain additional Neandertal pelvic features, including why both sexes have similar superior pubic ramus lengths (72).

Evolutionary and Lifetime Behavioral Explanations.

Two main evolutionary explanations have been proposed for Neandertal postcranial morphology: adaptation to cold climates or activity patterns (either lifetime behavioral response or evolutionary adaptation). In recent humans (65–67), as in other endothermic species (73, 74), body proportions like those of Neandertals are characteristic of individuals with ancestry in cold climates. Individuals with ancestry in warm climates, in contrast, tend to have similar body proportions to the earliest modern humans (68). These robust empirical patterns suggest that Neandertal body proportions, and the covarying features discussed in the previous section, reflect adaptation to the cold climates of Pleistocene Eurasia.

The climate hypothesis is further supported by laboratory experiments. For example, Tilkens and colleagues (75) showed that human subjects with long legs relative to body mass had higher resting metabolic rates than individuals with relatively shorter limbs when sitting in an $\approx 22^\circ\text{C}$ room wearing shorts and a T-shirt. These experiments demonstrate that individuals with “warm adapted” body proportions need to expend more energy to prevent their body temperatures from dropping due to heat loss.

It could be argued that the early *Homo* pelvis from Gona, Ethiopia refutes the climate hypothesis, because it may demonstrate that a wide pelvis was the primitive condition for the genus *Homo* (76). However, showing that a morphological feature is primitive for a taxonomic group does not explain why this feature persists in some descendant taxa and not others.

Even if a wide pelvis was unrelated to climate in early *Homo*, climate adaptation is still the best explanation for why Neandertals maintained a wide pelvis, early modern humans living closer to the equator evolved a narrow pelvis, and recent humans who migrated to cold climates regained a wide pelvis.

Although climatic adaptation may explain Neandertal body proportions and other morphological features of their postcranium, activity patterns could be responsible for at least some postcranial features, because, as discussed above, numerous studies indicate that long bone cortical thickness reflects mechanical loading from locomotion and other behaviors. As with the cranium, activity levels may also explain why Pleistocene modern humans tend to have more robust postcrania than Holocene humans (15, 58).

Conclusions

Deciphering the meaning of Neandertal skeletal morphology is a complex endeavor that starts with determining whether a morphological feature is best considered to result from lifetime behaviors or, alternatively, from alleles passed from parents to offspring that were previously shaped by evolutionary forces. It continues with investigations of whether a feature is best explained in isolation or as part of a complex of features. It concludes with evaluating competing hypotheses using empirical studies of extant species, tests of form vs. function, modeling based on quantitative and population genetics, and documenting the patterning of features in the fossil record.

Currently, the best explanation for many Neandertal cranial features is divergence by genetic drift that began when Neandertal and modern human populations became isolated from each other $>350,000$ years ago. This explanation is supported by modeling based on quantitative and population genetics and the “accretional” appearance of Neandertal features in the fossil record. Neandertal body proportions, and likely other postcranial features, appear to be adaptations, or secondary consequences of adaptations, to the typically cold climates of Pleistocene Eurasia. However, for both the cranium and the postcranium, changes in diet or activity patterns may explain some features, and in particular, could underlie why Neandertals and Pleistocene modern humans are more robust than Holocene humans.

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1. Schaffhausen H (1857) Brief communication (Translated from German). *Verhandlungen des Naturhistorischen Vereins der Preussischen Rheinlande und Westfalens* 14:50–52.
2. Stringer CB, Gamble C (1993) *In Search of the Neanderthals: Solving the Puzzle of Human Origins* (Thames and Hudson, New York).
3. Trinkaus E, Shipman P (1992) *The Neanderthals: Of Skeletons, Scientists, and Scandal* (Random House, New York).
4. Berger T, Trinkaus E (1995) Patterns of trauma among the Neanderthals. *J Archaeol Sci* 22:841–852.
5. Stringer CB, Hublin J-J (1999) New age estimates for the Swanscombe hominid, and their significance for human evolution. *J Hum Evol* 37:873–877.
6. Noonan JP, et al. (2006) Sequencing and analysis of Neanderthal genomic DNA. *Science* 314:1113–1118.
7. Weaver TD, Roseman CC, Stringer CB (2008) Close correspondence between quantitative- and molecular-genetic divergence times for Neanderthals and modern humans. *Proc Natl Acad Sci USA* 105:4645–4649.
8. Hublin J-J (1998) In *Neanderthals and Modern Humans in Western Asia*, eds Akazawa T, Aoki K, Bar-Yosef O (Plenum, New York), pp 295–310.
9. Rink WJ, Schwarcz HP, Smith FH, Radovic J (1995) ESR ages for Krapina hominids. *Nature* 378:24.
10. Hublin J-J, Barroso Ruiz C, Medina Lara P, Fontugne M, Reyss J-L (1995) The Mousterian site of Zafarraya (Andalucía, Spain): Dating and implications on the Palaeolithic peopling processes of Western Europe. *Comptes Rendus de l'Académie des Sciences Paris* 321:931–937.
11. Higham T, Bronk Ramsey C, Karavanic I, Smith FH, Trinkaus E (2006) Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neanderthals. *Proc Natl Acad Sci USA* 103:553–557.
12. Howell FC (1952) Pleistocene glacial ecology and the evolution of "classic Neanderthal man." *Southwestern J Anthropol* 8:377–410.
13. Krause J, et al. (2007) Neanderthals in central Asia and Siberia. *Nature* 449:902–904.
14. Lynch M, Walsh B (1998) *Genetics and Analysis of Quantitative Traits* (Sinauer, Sutherland, MA).
15. Ruff CB (2000) In *Biological Anthropology of the Human Skeleton*, eds Katzenberg MA, Saunders SR (Wiley-Liss, New York), 2nd Ed, pp 71–102.
16. Trinkaus E (1997) Appendicular robusticity and the paleobiology of modern human emergence. *Proc Natl Acad Sci USA* 94:13367–13373.
17. Schmitt D, Churchill SE, Hylander WL (2003) Experimental evidence concerning spear use in Neanderthals and early modern humans. *J Archaeol Sci* 30:103–114.
18. Weaver TD, Roseman CC, Stringer CB (2007) Were Neanderthal and modern human cranial differences produced by natural selection or genetic drift? *J Hum Evol* 53:135–145.
19. Lieberman DE (1996) How and why humans grow thin skulls: Experimental evidence for systemic cortical robusticity. *Am J Phys Anthropol* 101:217–236.
20. Lieberman DE, Krovitz GE, Yates FW, Devlin M, St. Claire M (2004) Effects of food processing on masticatory strain and craniofacial growth in a retrognathic face. *J Hum Evol* 46:655–677.
21. Feldman M, Lewontin RC (1975) The heritability hang-up. *Science* 190:1163–1168.
22. González-José R, Van der Molen S, Gonzales-Perez E, Hernandez M (2004) Patterns of phenotypic covariation and correlation in modern humans as viewed from morphological integration. *Am J Phys Anthropol* 123:69–77.
23. Ackermann RR (2005) Ontogenetic integration of the hominoid face. *J Hum Evol* 48:175–197.
24. Polanski JM, Franciscus RG (2006) Patterns of craniofacial integration in extant Homo, Pan, and Gorilla. *Am J Phys Anthropol* 131:38–49.
25. Ackermann RR (2009) Morphological integration and the interpretation of fossil hominin diversity. *Evol Biol* 36:149–156.
26. Cheverud JM (1988) A comparison of genetic and phenotypic correlations. *Evolution* 42:958–968.
27. Roff DA (1996) The evolution of genetic correlations: An analysis of patterns. *Evolution* 50:1392–1403.
28. Lande R (1979) Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. *Evolution* 33:402–416.
29. Klingenberg CP, Badyaev AV, Sowry SM, Beckwith NJ (2001) Inferring developmental modularity from morphological integration: Analysis of individual variation and asymmetry in bumblebee wings. *Am Nat* 157:11–23.
30. Holton NE, Franciscus RG (2008) The paradox of a wide nasal aperture in cold-adapted Neanderthals: A causal assessment. *J Hum Evol* 55:942–951.
31. Lieberman DE (2008) Speculations about the selective basis for modern human craniofacial form. *Evol Anthropol* 17:55–68.
32. Ackermann RR, Cheverud JM (2004) Detecting genetic drift versus selection in human evolution. *Proc Natl Acad Sci USA* 101:17946–17951.
33. Roseman CC (2007) Molecules versus morphology? Not for the human cranium. *Bioessays* 29:1185–1188.
34. Franciscus RG (2002) *Encyclopedia of Evolution*, ed Pagel M (Oxford Univ Press, Oxford), pp 493–497.
35. Rak Y, Ginzburg A, Geffen E (2002) Does Homo neanderthalensis play a role in modern human ancestry? The mandibular evidence. *Am J Phys Anthropol* 119:199–204.
36. Franciscus RG (2003) Internal nasal floor configuration in Homo with special reference to the evolution of Neanderthal facial form. *J Hum Evol* 44:701–729.
37. Spoor F, Hublin J-J, Braun M, Zonneveld F (2003) The bony labyrinth of Neanderthals. *J Hum Evol* 44:141–165.
38. Trinkaus E (2006) Modern human versus Neanderthal evolutionary distinctiveness. *Curr Anthropol* 47:597–620.
39. Golovanova LV, Hoeffcker JF, Kharitonov VM, Romanova G (1999) Mezmaiskaya Cave: A Neanderthal occupation in the northern Caucasus. *Curr Anthropol* 40:77–86.
40. Ponce de León M, et al. (2008) Neanderthal brain size at birth provides insights into the evolution of human life history. *Proc Natl Acad Sci USA* 105:13764–13768.
41. Maureille B (2002) A lost Neanderthal neonate found. *Nature* 419:33–34.
42. Rak Y, Kimbel WH, Hovers E (1994) A Neanderthal infant from Amud Cave, Israel. *J Hum Evol* 26:313–324.
43. Ponce de León MS, Zollikofer CPE (2001) Neanderthal cranial ontogeny and its implications for late hominid diversity. *Nature* 412:534–538.
44. Arsuaga JL, Martínez I, Gracia A, Lorenzo C (1997) The Sima de los Huesos crania (Sierra de Atapuerca, Spain). A comparative study. *J Hum Evol* 33:219–281.
45. Coon CS (1962) *The Origin of Races* (Alfred A. Knopf, New York).
46. Sergi S (1958) In *Hundert Jahr Neanderthaler*, ed von Koenigswald GHR (Kemink en Zoon, Utrecht), pp 38–51.
47. Brace CL (1964) The fate of the "classic" Neanderthals: A consideration of hominid catastrophism. *Curr Anthropol* 5:3–43.
48. Demes B (1987) Another look at an old face: Biomechanics of the Neanderthal facial skeleton reconsidered. *J Hum Evol* 16:297–303.
49. Rak Y (1986) The Neanderthal: A new look at an old face. *J Hum Evol* 15:151–164.
50. Smith FH, Paquette SP (1989) In *The Emergence of Modern Humans: Biocultural Adaptations in the Later Pleistocene*, ed Trinkaus E (Cambridge Univ Press, Cambridge, UK), pp 181–210.
51. Spencer MA, Demes B (1993) Biomechanical analysis of masticatory system configuration in Neanderthals and Nuits. *Am J Phys Anthropol* 91:1–20.
52. Trinkaus E (1987) The Neanderthal face: Evolutionary and functional perspectives on a recent hominid face. *J Hum Evol* 16:429–443.
53. Antón SC (1994) In *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*, eds Corruccini RS, Ciochon RL (Prentice Hall, Englewood Cliffs, NJ), pp 677–695.
54. O'Connor CF, Franciscus RG, Holton NE (2005) Bite force production capability and efficiency in Neanderthals and modern humans. *Am J Phys Anthropol* 127:129–151.
55. Brüer G (2008) The origin of modern anatomy: By speciation or intraspecific evolution? *Evol Anthropol* 17:22–37.
56. Trinkaus E (1983) In *The Mousterian Legacy: Human Biocultural Change in the Upper Pleistocene*, ed Trinkaus E (British Archaeological Reports International, Oxford), Vol 164, pp 165–200.
57. Holliday TW (1997) Postcranial evidence of cold adaptation in European Neanderthals. *Am J Phys Anthropol* 104:245–258.
58. Pearson OM (2000) Postcranial remains and the origins of modern humans. *Evol Anthropol* 9:229–247.
59. Yokley TR, Churchill SE (2006) Archaic and modern human distal humeral morphology. *J Hum Evol* 51:603–616.
60. Odwak H (2000) Long bone robusticity and claviculo-humeral proportions of the Amud 7 Neanderthal baby. *Am J Phys Anthropol* 30 (Suppl):241.
61. Trinkaus E (2008) Kiik-Koba and Neanderthal axillary border ontogeny. *Anthropol Sci* 116:231–236.
62. Tompkins RL, Trinkaus E (1987) La Ferrassie 6 and the development of Neanderthal pubic morphology. *Am J Phys Anthropol* 73:233–239.
63. Cowgill LW, Trinkaus E, Zeder MA (2007) Shanidar 10: A Middle Paleolithic immature distal lower limb from Shanidar Cave, Iraqi Kurdistan. *J Hum Evol* 53:213–223.
64. Carter DR, Beaupré GS (2001) *Skeletal Function and Form: Mechanobiology of Skeletal Development, Aging, and Regeneration* (Cambridge Univ Press, Cambridge, UK).
65. Trinkaus E (1981) In *Aspects of human evolution, Symposia of the society for the study of human biology*, ed Stringer CB (Taylor and Francis, London), Vol 21, pp 187–224.
66. Ruff CB (1994) Morphological adaptation to climate in modern and fossil hominids. *Yearbook Phys Anthropol* 37:65–107.
67. Holliday TW (1997) Body proportions in Late Pleistocene Europe and modern human origins. *J Hum Evol* 32:423–447.
68. Holliday TW (2000) Evolution at the crossroads: Modern human emergence in Western Asia. *Am Anthropol* 102:54–68.
69. Pearson OM (2000) Activity, climate, and postcranial robusticity. *Curr Anthropol* 41:569–607.
70. Churchill SE (1996) Particulate versus integrated evolution of the upper body in Late Pleistocene humans: A test of two models. *Am J Phys Anthropol* 100:559–583.
71. Weaver TD (2003) The shape of the Neanderthal femur is primarily the consequence of a hyperpolar body form. *Proc Natl Acad Sci USA* 100(12):6926–6929.
72. Weaver TD, Hublin J-J (2009) Neanderthal birth canal shape and the evolution of human childbirth. *Proc Natl Acad Sci USA* 106:8151–8156.
73. Ashton KG, Tracy MC, de Queiroz A (2000) Is Bergmann's rule valid for mammals? *Am Nat* 156:390–415.
74. Freckleton RP, Harvey PH, Pagel M (2003) Bergmann's rule and body size in mammals. *Am Nat* 161:821–825.
75. Tilkens MJ, Wall-Scheffler CM, Weaver TD, Steudel-Numbers K (2007) The effects of body proportions on thermoregulation: An experimental assessment of Allen's rule. *J Hum Evol* 53:286–291.
76. Simpson SW, et al. (2008) A female Homo erectus pelvis from Gona, Ethiopia. *Science* 322:1089–1092.