

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 sub-Saharan 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 ≈311,000 years ago or ≈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).

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