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The Neanderthal cranium: functional reappraisal of a peculiar morphology

Barbara Coletti & Giorgio Manzi

Dipartimento di Biologia Ambientale, Sapienza Università di Roma, Rome, Italy
e-mail: giorgio.manzi@uniroma1.it

Neanderthals (*Homo neanderthalensis*) have long fascinated the scientific community and the general public. They were the first extinct humans to be discovered and formally named (1864), representing the European lineage of the Middle and Late Pleistocene. Over the past century and a half, thousands of fossils have come to describe an extinct species of human beings with large brains, robust bodies, and a unique craniofacial architecture. However, a unified explanation for their peculiar cranial morphology still remains elusive. In particular, the Neanderthal face – with a typically projecting midface, broad nose, and receding cheekbones – has been interpreted as an ensemble of adaptations: to cold climates, to heavy chewing, or to specific muscular demands. Similarly, their cranial base and cervical spine have often been studied separately, whereas a little consensus has been reached on how these anatomical regions functioned together.

In a recent paper we co-authored with M. Boggioni, A. Papini, A. Profico and F. Di Vincenzo (Boggioni et al. 2025), decades of detailed anatomical descriptions and a long-standing debate were reconsidered from an integrated perspective. Rather than asking what each single trait means, we asked how these traits might work as components of a morpho-functional system. This approach stems from a fundamental shift in how form and function are viewed in human evolution. Anatomical structures rarely evolve independently, as they are constrained by shared developmental pathways and mechanical interdependence. The Neanderthal lineage offers a striking case study of this principle.

By systematically reviewing the fossil evidence – from Middle Pleistocene ancestors, such as the Atapuerca-Sima de los Huesos sample, to the so-called "classic" Neanderthals of the last glaciation (*e.g.*, Di Vincenzo and Manzi 2023) – we identified a suite of traits that covaried across the cranium and cervical spine. When considered together, these traits reveal an integrated pattern, which we interpret as a morphological network shaped by both functional demands and inherited constraints. This long-term evolutionary trajectory is consistent with the "accretion model" (Dean et al. 1998; but see also Rosas et al. 2006), which envisions Neanderthal morphology as the cumulative outcome of derived features progressively fixed over successive glacial cycles, under the combined effect of both climatic stress and demographic pressure.

The focal point of our interpretation is the role that the neck may have played as a structural and functional driver in the evolution of Neanderthal cranial morphology. As a matter of fact, the cervical vertebrae of *Homo neanderthalensis* were short, wide, and robust, implying reduced flexibility and enhanced stability (Gómez-Olivencia and Arsuaga 2024): the spinous processes were elongated and horizontally oriented, the occipital region was expanded for the attachment of powerful neck muscles, and the external occipital protuberance was greatly reduced. These features – together with the peculiar morphology of the Neanderthal semicircular canals (Spoor et al. 2003; Malinzak et al. 2012) – indicate a lower degree of cervical lordosis and a diminished capacity for flexion-extension, replaced by a configuration better suited to maintaining the head in a stable position. This limited mobility likely acted as a biomechanical constraint that drove Neanderthal cranial evolution as a whole. Reduced neck flexibility would have

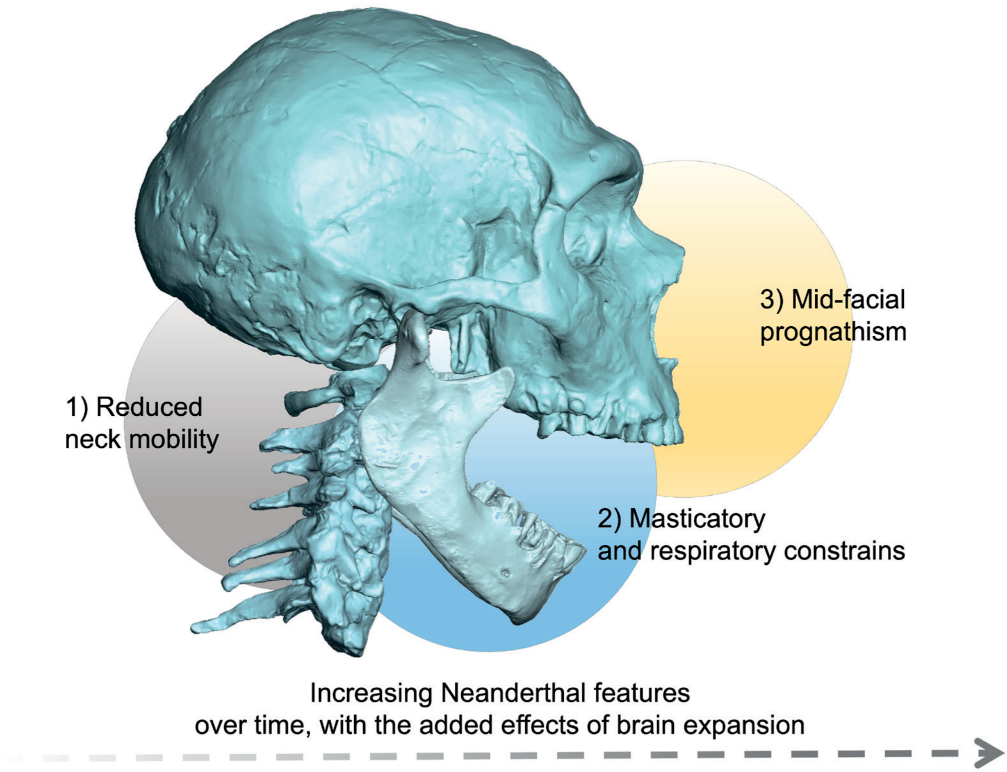

***Fig. 1** – Schematic representation of the "morpho-functional cascade" discussed in the text.*

required compensatory adjustments in the occipital bone, cranial base, mandible, and facial skeleton. Over time, such interdependent changes produced what we describe as a morpho-functional cascade (Fig. 1): a sequence of correlated transformations radiating from the cervical spine to the entire cranium, where the occipital bone became distinctive, the cranial base angle wider, and the mandibular morphology peculiar, while both the mandible and the midface were projected forward.

This framework also offers insight into broader aspects of Neanderthal biology, ecology and behaviour. A strong, stable neck-head system would have been advantageous for short-range, high-intensity activities – such as thrusting spears or close-contact hunting – as also supported by the archaeological evidence (Churchill 2014). By contrast, our species *Homo sapiens*, with a more flexible cervical column and a lighter cranial structure, appears better adapted for endurance running and long-distance foraging. The differences between the two species may therefore reflect divergent evolutionary trade-offs: Neanderthals optimized for power and stability, modern humans for efficiency and mobility.

The implications extend beyond biomechanics. Integrating the neck into discussions of cranial evolution reframes several issues. For instance, mid-facial prognathism – long explained as an adaptation to cold air or as a by-product of anterior dental loading – can instead be viewed as part of an overall cranio-cervical reorganization. Similarly, the morphology of the nasal cavity (Buzi et al. 2025), the orientation of the zygomatic arches, and the pattern of mandibular muscle insertions all appear consistent with a system designed to balance powerful masticatory forces with postural stability. In this view, Neanderthal anatomy embodies a functional logic, rather than a series of isolated features.

This integrative approach also provides a refined understanding of the evolutionary tempo and mode of the Neanderthal lineage. Many of the traits discussed here – including the structure of the cervical vertebrae, the orientation of the occipital plane, and the architecture of the mandible – first appear in European populations of the Middle Pleistocene, well before the emergence of the more derived Neanderthals of the last glaciation. These early manifestations suggest that the morpho-functional system observed in later forms resulted from long-term processes beginning around 400,000 years ago or even earlier (*e.g.*, Di Vincenzo and Manzi 2023). Repeated glacial cycles likely amplified this trend, reinforcing a body plan suited to cold and demanding environments.

These considerations also align with further evidence linking Neanderthal cranio-cervical evolution to broader functional domains such as posture, strength, and thermoregulation. From a biomechanical perspective, the Neanderthal cranio-cervical configuration represents a lever system optimized for stability and control rather than flexibility. The occipito-cervical junction functioned as a first-class lever balancing the posterior nuchal musculature against the anterior facial mass, while the mandible acted as a third-class lever integrated into the same system. Coordination between these mechanical subsystems ensured physiological mouth opening and efficient respiration. Functional coupling between the head and neck minimized the need for large mandibular excursions, preserving airway patency and reducing stress on the neurovascular bundle during mouth opening.

At the same time, this robust neck morphology may have been intertwined with a thermoregulatory strategy, shaped by cold and energetically demanding environments. The short, broad neck minimized exposed surface area and heat loss, while dense cervical and trunk musculature functioned both as heat generator and insulators. In this context, we hypothesize that brown adipose tissue (BAT) may have played a role in both Neanderthal thermogenesis and neck morphology. If present and functionally active, BAT could have contributed to metabolic heat production through uncoupled mitochondrial activity mediated by UCP1, providing additional level of thermal regulation without muscular shivering. The vascular geometry of the cervical region, characterized by short arteries and dense venous networks, may likewise have reduced heat loss through major blood vessels, contributing to overall thermal efficiency.

Taken together, these elements reinforce an integrative morpho-functional interpretation of Neanderthal anatomy: a system in which posture, strength, respiration, and thermal efficiency operated as interdependent components of a single adaptive design. Structural constraints did not merely limit evolutionary pathways, but actively shaped them, channelling Neanderthal evolution toward a robust, energetically efficient, and thermally buffered organism well adapted to the cold and demanding environments of the Pleistocene in Western Eurasia.

In conclusion (see Fig. 1), the massive body plan that emerged along the Neanderthal lineage, in response to marked climatic fluctuations, involved a neck firmly integrated into the thorax, with reduced mobility along the sagittal plane. Such a structural rigidity acted as a biomechanical constraint influencing head posture and the shape of the cranial base (1). Compensatory adjustments in the mandible followed, leading to its anterior displacement and reorientation, together with modifications of the masticatory apparatus as a whole (2). The face subsequently adapted to the forward-shifted dental arcades, establishing the characteristic mid-facial prognathism (3). These changes, combined with additional brain expansion, further shaped the cranial vault and face, contributing to the emergence of the definitive Neanderthal morphology.

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