Spanish Journal of Palaeontology 40 (1), 97–114, 2025
https://doi.org/10.7203/sjp.30506
Sociedad Española de Paleontología ISSN 2255-0550 / eISSN 2660-9568

OPEN ACCESS RESEARCH PAPER

Mosaic evolution. An example in the origin of Neandertals

Evolución en mosaico. Un ejemplo en el origen de los neandertales

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Abstract: The emergence of Neandertal morphology (*Homo neanderthalensis*) is associated with the appearance of mosaic phenotypes in Middle Pleistocene ancestral populations. Using this case as a reference, we analyze the concept of "mosaic evolution". Mosaic evolution suggests that different traits can evolve independently, at different times, resulting in various combinations of primitive and derived traits (mosaics) in descendant species. Often, the seemingly random nature of these trait combinations is interpreted within the conceptual framework of population genetics, where the different states of anatomical traits are seen as direct expressions of allelic variants. In this paper, we propose that the appearance of these mosaics of traits in Middle Pleistocene hominins of Europe occurred within a complex network of morphogenetic interactions involving two factors that affect the organism as a whole. First, during the early part of the Middle Pleistocene, there is an increase in body size, and consequently, an increase in metabolism, which may have affected facial anatomy through the expansion of the respiratory tract. Second, the hominin lineage from which Neandertals, Denisovans, and modern humans descend experiences an increase in the size of certain brain areas, leading to changes in the anatomy of the cranial vault and the integration of anatomical systems related to the base of the skull. In this context, changes in the overall orientation of the basicranium and in the topological relationships between the midline of the skull base and the lateral portions of the skull (temporal fossae) can be explained from an organismic perspective.

Resumen: La emergencia de la morfología de los neandertales (*H. neanderthalensis*) se asocia a la aparición de fenotipos en mosaico en las poblaciones antecesoras del Pleistoceno Medio. Tomando como referencia este caso, analizamos el concepto de "evolución en mosaico". La evolución en mosaico sugiere que los diferentes caracteres de los organismos pueden evolucionar de manera independiente, en distintos momentos, dando distintas combinaciones de caracteres primitivos y derivados en las especies/organismos descendientes. Con frecuencia, el carácter aparentemente aleatorio de estos mosaicos se interpreta en el marco de la genética de poblaciones, considerando las variantes anatómicas como expresión de variantes alélicas. En este trabajo planteamos que la aparición de mosaicos de caracteres en los homininos del Pleistoceno Medio europeo tuvo lugar en el seno de una red de interacciones morfogenéticas de dos factores que afectan al organismo en su conjunto. En el primer tercio del Pleistoceno Medio se produce un incremento en el tamaño corporal y en el metabolismo con efectos sobre la anatomía de la cara a través del incremento de las vías respiratorias. Paralelamente, el linaje de homininos del que descienden neandertales, denisovanos y humanos modernos experimenta un incremento en ciertas áreas del encéfalo, provocando cambios en la anatomía de la bóveda craneana y en la integración de sistemas anatómicos relacionados con la base del cráneo. Los cambios en la orientación basicraneal y en la topología de la línea media de la base del cráneo y las porciones laterales del cráneo permiten explicar fenómenos de evolución en mosaico.

Received: 29 June 2024
Accepted: 11 October 2024
Published: 10 March 2025

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Keywords:
Human evolution
Morphological integration
Middle Pleistocene
Hominin
Neandertal

Palabras-clave:
Evolución humana
Integración morfológica
Pleistoceno Medio
Hominino
Neandertal

INTRODUCTION

It is now accepted that the human group referred to as Neandertals constitutes a distinct species (*Homo neanderthalensis*) that shares a last common ancestor (**LCA**) with the present-day human species *H. sapiens*. Recent genetic estimates place the age of this LCA between 550 and 765 ky (Hublin, 1998a; Prüfer *et al.*, 2014; Meyer *et al.*, 2016), while Gómez-Robles (2019) suggests that Neandertals and modern humans diverged before 800 ky. In a broader sense, the species *H. sapiens* and *H. neanderthalensis* represent evolutionary extremes arising respectively from the diversification of a "sapiens" clade and a "Neandertal"

clade. The discovery of their DNA has also revealed the existence of a new group of hominins, known as the Denisovans, a sister group to the Neandertals (Reich *et al.*, 2010).

Neandertals have a very characteristic phenotype. Palaeontologically, this phenotype can be traced back to around 250 ky, at which point it appears to have consolidated. Late Middle Pleistocene European fossils from around 250–200 ky, such as those from Ehringsdorf and Salzgitter-Lebenstedt (Germany), Biache-Saint-Vaast and La Chaise-Suard (France), are considered morphologically very similar to Upper Pleistocene Neandertals, with only minor morphological nuances (Arsuaga *et al.*, 1997; Dean *et al.*, 1998; Hublin, 1998a; Daura *et al.*, 2017). Hominin populations before these dates, from the central part of the Middle Pleistocene (250–450 ky), display Neandertal-derived traits inconsistently. It is common to find fossils from this period exhibiting different combinations of primitive and derived traits, identified as mosaics. Examples of these populations include those from the Sima de los Huesos in Atapuerca (Spain), Steinheim (Germany), Arago (France), among others (see Tab. 1). Further back in time, before 450 ky, human populations do not show clear Neandertal apomorphies, and there is debate over whether any of these fossils exhibit the early morphological traits that would eventually become Neandertal apomorphies. The best example is the Mauer mandible (Germany), a significant fossil as it is also the holotype of *H. heidelbergensis*. According to some researchers, the morphology of the Mauer jaw does exhibit precursor traits of the Neandertal phenotype (Rosas & Bermúdez de Castro, 1998; Mounier *et al.*, 2009; Bermúdez de Castro *et al.*, 2016; Rosas *et al.*, 2022), while others strongly deny that this fossil shows any derived traits (Tattersall, 2011).

In any case, whether or not these fossils from the early Middle Pleistocene belong to the Neandertal clade, it is accepted that the evolutionary root of Middle Pleistocene populations can be traced to the species *H. erectus* in its broadest sense, with the African representatives of this species appearing to be the most closely linked to the transitional populations of the European Middle Pleistocene (Manzi, 2016). In summary, the origin of the Neandertal phenotype can be understood as a sequence of changes in three stages: 1) a stage of clearly plesiomorphic origin; 2) intercalary populations showing combinations of apomorphies and plesiomorphies (referred to here as mosaics); and 3) the clearly derived Neandertal populations that make up *H. neanderthalensis*. The interpretation of this second, intercalary phase is an excellent example of mosaic evolution, and the difficulty in interpreting it has been one of the most persistent problems in palaeoanthropology. This is why there has been a long-standing debate about the taxonomy of Middle Pleistocene intercalary populations, with no consensus model today.

In the last decade, the idea has gained traction that several demes with distinct phylogenetic trajectories coexisted in the Middle Pleistocene of Europe (Tattersall, 2011; Stringer, 2012; Arsuaga *et al.*, 2014; Zanolli *et al.*, 2018). This perspective suggests that Europe was inhabited by populations that represent the ancestors of Neandertals, identified by the presence of clear derived traits. The paradigmatic representatives of this group are the Sima de los Huesos hominins, along with Swanscombe (England) and Aroeria (Portugal). We will refer to this group as “the Sima group”. These authors also argue that, alongside “the Sima group”, other populations coexisted in Europe that do not show Neandertal traits and, according to this hypothesis, would fall outside the Neandertal clade. Among the latter, Ceprano (Italy) and Arago (France) are the most representative examples, which we will call “the Arago group.” Apart from the identification of Neandertal apomorphies in both groups, the strongest argument put forward by proponents of this model is the supposed contemporaneity of the Sima de los Huesos and Arago hominins. The inclusion of other fossil specimens in one or the other group is dependent on the interpretation of the researchers. The best example is the Petralona skull (Greece). While some have included it in the “Sima group” (Arsuaga *et al.*, 1997), others exclude it and group it with the “Arago group” (Arsuaga *et al.*, 2014; Di Vincenzo & Manzi, 2023).

Alternatively, to the aforementioned model, an earlier interpretation identifies all the populations sampled in the Middle Pleistocene of Europe as the direct ancestors of Neandertals. In other words, all these populations are involved in the “Neandertalization process” to some extent (Rosas *et al.*, 2006, 2019; Hublin, 2009), but in different ways according to two interpretations. One of them is the “accretion/coalescence model,” within the context of a metapopulation/paleodeme framework, which is the more widely accepted explanation for the evolution of large-brained hominins in Europe (Hublin, 1998b, 2009; Scerri *et al.*, 2019) and Africa (Scerri *et al.*, 2019). This family of models proposes a relatively continuous addition of new traits along evolutionary lineages within the context of population dynamics. The mosaic distribution of derived traits, where different individuals show different combinations of derived traits, has been interpreted as the result of successive independent changes accumulating in intermittently discontinuous populations that settled in European and African territories. For instance, periodic episodes of isolation and demographic crises probably resulted in genetic bottlenecks and drift effects, which, combined with local gene flow, would explain the divergence of human populations in western Eurasia (Hublin, 2009). As a biogeographical variant of this scenario, Bermúdez de Castro *et al.* (2019) suggest that different human groups from Southwest Asia arrived in Europe during the Middle Pleistocene, carrying derived traits characteristic of Late Pleistocene Neandertals (see Hershkovitz *et al.*, 2011). In both cases, it is essentially

Table 1. List of specimens used in the comparative analysis.

Specimen	Chronology	Reference	Base of the observation
Homo ergaster			
D2280	1.81 ± 0.03 My	Garcia *et al.* (2010)	Original
D2282	1.81 ± 0.03 My	id.	Original
D3444	1.81 ± 0.03 My	id.	Original
D4500	1.81 ± 0.03 My	id.	Cast
WT-15000	~1.6 My	Brown *et al.* (1985)	Cast
ER-3733	~1.63 My	Lepre & Kent (2015)	Cast
ER-3883	1.6–1.5 My	id.	Cast
ER-42700	1.55 My	Spoor *et al.* (2007)	Cast
OH 9	~1.4 My	Tamrat *et al.* (1995)	Original
Daka	~1 My	Asfaw *et al.* (2002)	Bibliography
Homo erectus			
Ngawi	100-200 ky	Antón (2002)	Cast
SambungMycan 1	40-70 ky	YokoyaMy *et al.* (2008)	Cast
Sinanthropus III	77 ± 08 ky	Shen *et al.* (2009)	Cast
Ngandong 6	117–108 ky	Rizal *et al.* (2020)	Cast
Ngandong 7	id.	id.	Cast
Ngandong 14	id.	id.	Cast
Sangiran 2	rv1.3 My	Mytsu'ura *et al.* (2020)	Cast
Sangiran 17	id.	id.	Original
Nanking	600-350 ky	Wu & Poirier (1995)	Original
African Middle Pleistocene			
Kabwe 1	299 ± 25 ky	Grün *et al.* (2020)	Original
Bodo	600 ky	Clark *et al.* (1994)	Original
Zuttiyeh	500-200 ky	Freidline *et al.* (2012)	Cast
Asian Middle Pleistocene			
Dali	~270 ky	Xiao *et al.* (2002)	Cast
Jinniushan	~260 ky	Rosenberg *et al.* (2006)	Cast, Bibliography
Harbin	146 ky	Ji *et al.* (2021)	Bibliography
European Middle Pleistocene			
Ceprano	385–430 ky	Mynzi *et al.* (2010)	Cast
Petralona	150–250 ky (?)	Grün (1996)	Virtual model, Cast
Steinheim	250 ky	Adam (1985)	Cast
Arago	450 ky	Iacumin *et al.* (1996)	Original
Swanscombe	400 ky	Bridgland (1994)	Cast
Aroeira	436-390 ky	Daura *et al.* (2017)	Bibliography
Reilingen	250-125 ky	Ziegler & Dean (1998)	Cast
SH-4, 5, 13	427 ± 12 ky	Arnold *et al.* (2014)	Cast, Bibliography
Homo neanderthalensis			
ApidiMy 1	220-130 ky (average 170 ky)	De Lumley *et al.* (2020)	Cast, Virtual model
Lazaret	190-120 ky	Michel *et al.* (2022)	Original
Eringsdorf	250-200 ky	Tattersall (2000)	Cast
Amud 1	70–50 ky	Valladas *et al.* (1999)	Cast
Gibraltar 1	95–55 ky	Nathan (2010)	Original
La Chapelle aux Saints	56–47 ky	Grün & Stringer (1991)	Original
La Ferrassie 1	54–40 ky	Guérin *et al.* (2015)	Original
La Quina H5	~40 ky	Frouin *et al.* (2017)	Cast
Le Moustier	~45 ky	Valladas *et al.* (1986)	Original
Monte Circeo I	52 ± 12 ky	Grün & Stringer (1991)	Cast
Saccopastore 1	~250 ky	Myrra *et al.* (2015)	Cast
Shanidar 1	55–45 ky	Pomeroy *et al.* (2020)	Cast
Spy 1, 2	44.2–40.6 ky	Devièse *et al.* (2021)	Original
Tabun C1	122 ± 16 ky	Grün & Stringer (2000)	Cast
El Sidrón 1, 2, 3	49 ky	Fortea *et al.* (2003)	Original

an accretional evolutionary process, shaped locally by complex dynamics of fusion-fission, extirpation, and possibly local adaptation, as interpreted within the framework of population genetics and allele frequency fluctuation.

As an alternative to the "accretion model," Rosas *et al.* (2006, 2022) propose an "organismic approach," focusing on the organizational level of the organism rather than specific traits. In contrast to a particularistic view of traits (which holds that any individual trait, especially one that can be metrically defined, could be modified by directed genomic changes), the philosophy of the organismic approach is based on evolutionary developmental biology (evo-devo). This view asserts that "characters can no longer be legitimately independently 'added to' or 'subtracted from' a phenotype; rather, changes in entire developmental cascades are likely to occur in such a way that many aspects of a phenotype are altered simultaneously" (Lovejoy, 2014). Anatomical traits are not simply the product of individual genes but emerge from the action of complex and integrated "developmental systems"

(Buchanan *et al.*, 2009) (Fig. 1). Consequently, a palaeo-evo-devo approach to the phenotypes of large-brained hominins would need to test whether deterministic evolutionary processes involve bundles of integrated traits, such as those within the craniofacial system (Rosas & Bastir, 2004; Bastir *et al.*, 2007; Bastir & Rosas, 2016; Rosas *et al.*, 2019). From this perspective, mosaics of traits do not result from the genetic determination of isolated traits, but rather from successive systemic modifications of the organism, developmentally implemented through local integration/disintegration (developmental regulation mechanisms) necessary to maintain the organism's functionality.

Conceptually, we propose an alternative model that introduces additional levels of analysis: 1) the system under study is integrated into a higher system, and 2) the system under study has an internal structure, meaning that change is conditioned by the constraints derived from the interrelations between the components of that structure. In our case, the system under study is the human craniofacial system (see Bastir, 2008, 2018). The goal of this work is to clarify the conceptual foundations and the systemic model that enable us to study the phenomenon of "mosaic evolution" from a palaeo-evo-devo perspective. As already mentioned, we use data from the palaeoanthropological record to offer an explanatory framework for the development of the Neandertal phenotype. Within this framework, interpreting combinations of apomorphies in Middle Pleistocene human populations in Europe from an organicist perspective is key to understanding the complex pattern of variability observed. One of the main implications of this perspective is that the different mosaics of traits detected in various Middle Pleistocene hominin populations in Europe indicate their shared involvement in the process that led to the Neandertal phenotype.

WHAT IS MOSAIC EVOLUTION AND WHY IS IT RELEVANT?

The concept of "mosaic evolution" is fundamental to understanding the phenotypic organization of organisms and their processes of change (Raff, 1996; Bastir & Rosas, 2009). The term was proposed by Gavin de Beer (1954) in his analysis of the primitive bird *Archaeopteryx* and was later applied to the evolution of the genus *Australopithecus*. Historically, this concept has had prominent usage in the field of human evolution (Foley, 2016). In its simplest sense, mosaic evolution suggests that different characteristics in organisms may evolve independently, at different times, resulting in a pattern of morphological change in which different combinations of primitive, intermediate, and derived characteristics are seen in descendant species/organisms. These combinations are generically called "mosaics". From a fully integrated notion of shape change (a pattern of change in which mosaic evolution does not fit), the emergence of these mosaics is counterintuitive (see Fig. 2). Langdon (2016) synthesizes this particularly well: "When paleontologists compare a single ancestral species to a known descendant, there is an expectation that a fossil intermediate in time will be equally intermediate in all anatomical parts. However, these different species do not tell a simple linear story. Each body part has its own history and has evolved at a different rate and sometimes in a different direction in each species, producing unique anatomical combinations" (see Fig. 2).

This fact should not be surprising, as organisms are intrinsically heterogeneous by nature, composed of different elements, parts, and characteristics. As Gould (1977) states, "the concept of mosaic evolution dictates that organs evolve in different ways to meet varying selective pressures." The very notion of an organism

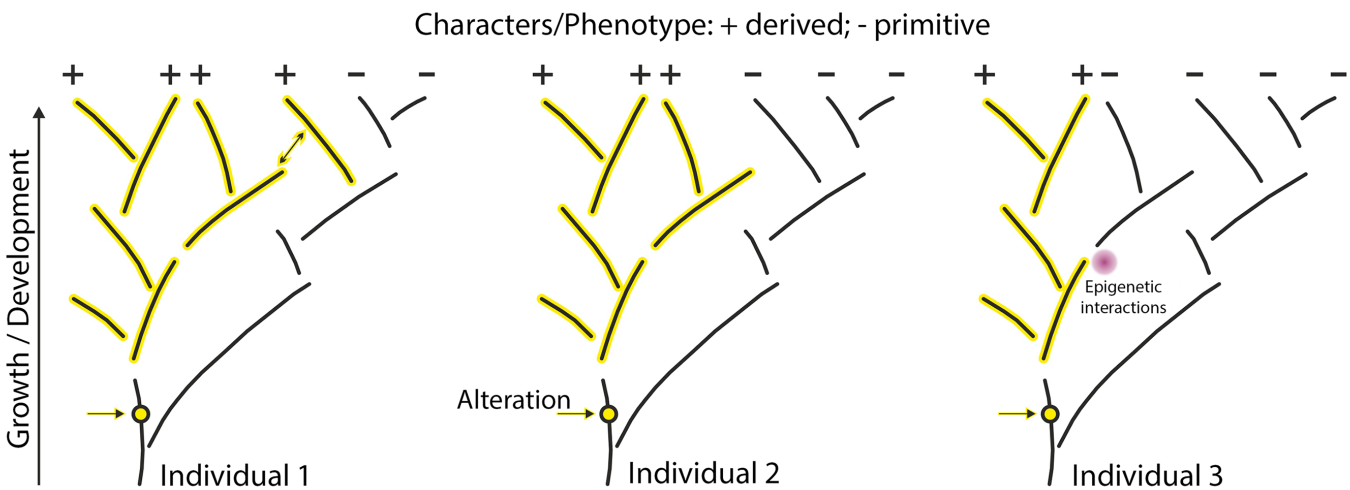


Figure 1. Diagrams illustrating individual hierarchically organized developmental trajectories. A single perturbation, shared by all individuals, produces different combinations of primitive and derived traits in the final phenotype due to pleiotropic effects under local genetic and epigenetic interactions.

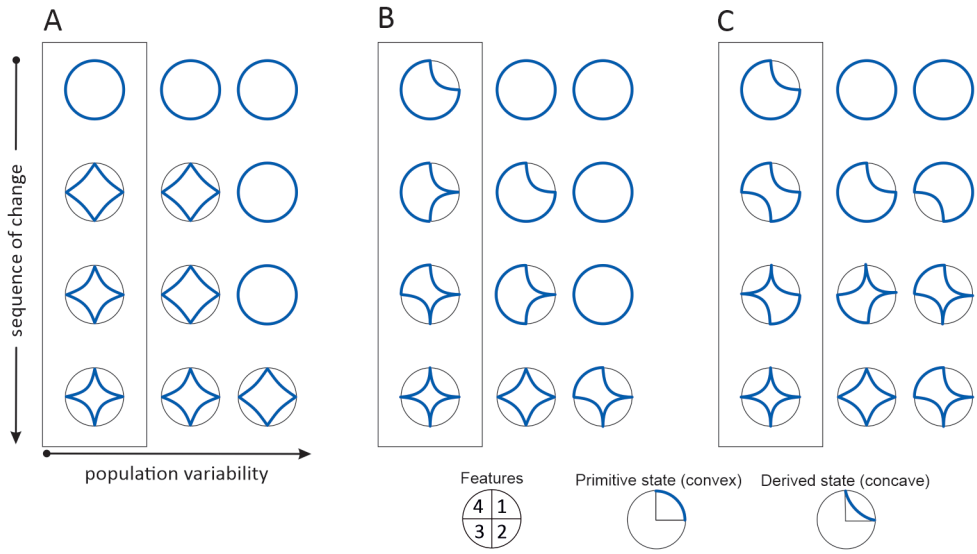


Figure 2. Diagram illustrating different modes of morphological character change. The phenotype is represented by a circle defined by four characters, each represented by the curvature—either concave or convex—of the arc in the four quadrants. A convex arc represents the primitive state, while a concave arc represents the derived state. The vertical axis shows potential variation in populations over time, while the horizontal axis shows potential variation across populations. **A,** Gradual change mode with full integration of all four characters; **B,** sequential and orderly change of characters; **C,** mosaic mode, where different characters change independently of each other, without following an orderly pattern.

implies structural complexity and a certain autonomy of its components (Levi-Strauss, 1973). However, the real challenge lies in determining when and how the change of these elements is established or articulated. In the mechanistic model (see Alberch, 1990), the organism is perceived as a sum of independent traits, based on the principle of "one gene, one trait." This model presents the organism as a machine, where each part or constituent has its own independent causality. Ultimately, the organism is conceived as an assemblage of parts, each created and designed independently, typically to perform a specific function. In this context, the concept of mosaic evolution is largely irrelevant, since independent changes in traits are naturally expected. However, biological nature itself contradicts the core assumptions of the mechanistic model. The complexity of organisms, with their intrinsic diversity of elements and systems, arises—emerges—through embryonic development. The origin of traits is established during cellular differentiation and embryonic morphogenesis. Starting from a single cell, it undergoes phases of cell differentiation, morphogenesis, pattern formation, growth, and maturation. Some systems arise from others through cascades of differentiation. From this perspective, at least some degree of interdependence between parts can be inferred, which is known as integration. This idea is captured in the Extended Evolutionary Synthesis (**EES**) (Laland *et al.*, 2015; Antón & Kuzawa, 2017; Müller, 2021), which provides a formal theoretical framework for the role of the organism and its development, integrating classical perspectives focused on "one gene-one trait" relationships and population genetics (see De Renzi, 2009). The key question here is how the different parts of an organism are related, what their organization is, and how they change. Between the two theoretical extremes—mechanical assembly of autonomous parts (particularism) and total integration of parts—nature moves toward intermediate solutions. We are faced with the classic structuralist problem: the relationship between the whole and the parts (Lévi-Strauss, 1973). There is a need to propose models of self-regulating systems in which the various parts maintain a balance of dependence and autonomy for proper functioning. The phenomenon of mosaic evolution reveals fundamental aspects about the very notion of organisms and their underlying structure (Levi-Strauss, 1973). For example, in a hypothetical sequence of morphological change, where at time t_0 the elements or traits co-vary together (in coordination), at time t_1 these elements or traits vary separately, and at t_2 a close co-variation occurs again, this reveals a transitional dissociation. A change in the organization of the system is therefore taking place. In the initial and final states, the number of possible combinations in the expression of traits is reduced, while in the intermediate state, the number of combinations is higher.

THE CRANIOFACIAL SYSTEM OF LARGE-BRAINED HOMININS

Two phenotypic modifications appear to occur during the transition from Lower Pleistocene and early Middle Pleistocene hominins (prior to 700 ky, classified as *H. erectus s.l.*) to Middle Pleistocene large-brained hominins (between 700 and 300 ky), whose taxonomy remains a matter of controversy (Mounier *et al.*, 2009; Stringer, 2012; Di Vincenzo &

Manzi, 2023). On the one hand, a clear increase in encephalization is observed in the genus *Homo* during the Middle Pleistocene, following a long period of stasis throughout the Lower Pleistocene (around 1800 ky) (Ruff *et al.*, 1997) (see Tab. 1). On the other hand, an increase in body mass occurred, likely associated with a corresponding increase in basal metabolism. Both modifications directly impact human cranial anatomy (Enlow, 1990; Rosas, 1998; Bastir, 2008; Lieberman, 2011). Craniofacial biology offers a robust model (Ranly, 1988; Lieberman, 2011), largely grounded in the work of Donald Enlow (see Enlow, 1990; Enlow & Hans, 1996), which integrates the two factors mentioned above. This model establishes a morpho-functional chain of causality based on the ontogenetic sequence of craniofacial system growth: brain, face, and jaw, organized in a topological influence gradient from superior to inferior. The spatiotemporal gradient of ontogenetic maturation suggests that the earliest-maturing structures (brain) will spatially influence adjacent facial structures that complete their adult morphology later. Thus, this sequence establishes a direct influence from 1) the brain to the cranial base, and 2) from the cranial base to the facial skeleton structures attached to it. This phenomenon is described in Enlow's "counterpart analysis" (Enlow *et al.*, 1969; Enlow, 1990) and has been quantitatively supported by morphometric analyses of longitudinal human craniofacial ontogeny data (Bastir & Rosas, 2006; Bastir *et al.*, 2006). All these interactions occur within a complex system that maintains morpho-functional equilibrium, with any deviations or misalignments rebalanced through "compensation mechanisms." For instance, the amount and direction of mandibular condyle growth can correct misalignments in dental occlusion (Enlow, 1990). The brain's morphological influence on the cranial base (classically analyzed using lateral 2D radiographs) has been visualized through changes in the sagittal plane of the skull, particularly via basicranial flexion (sagittal strip of the sphenoid—clivus and body—ethmoid, and central portion of the frontal bone). It is well-established that the phylogenetic enlargement of the brain in primates exerts pressure in opposite directions on both the anterior and posterior cranial bases during early ontogeny (see Fig. 3), leading to a reduction in the basicranial angle (flexion), which results in changes to the topology of the anterior and posterior cranial structures. However, in the evolution of the genus *Homo*, and possibly in earlier hominins, basicranial flexion reaches a limit (Ross & Ravosa, 1993; Ross & Henneberg, 1995), and further encephalization exerts its influence through other variables. For example, the orientation of the cranial base relative to the face becomes a highly relevant factor in evolutionary integration within the hominid head and interacts with major facial proportions (Bastir *et al.*, 2010). Additionally, it is known that brain enlargement is not isometric, as certain neural areas expand significantly more than others (Aiello & Dean, 1990; Bruner *et al.*, 2003; Bruner, 2004). The differential phylogenetic expansion of specific brain regions (frontal, temporal, and occipital lobes) exerts distinct influences on the anterior face (maxilla and mandibular arch) and the posterior face (pharyngeal space and ascending ramus).

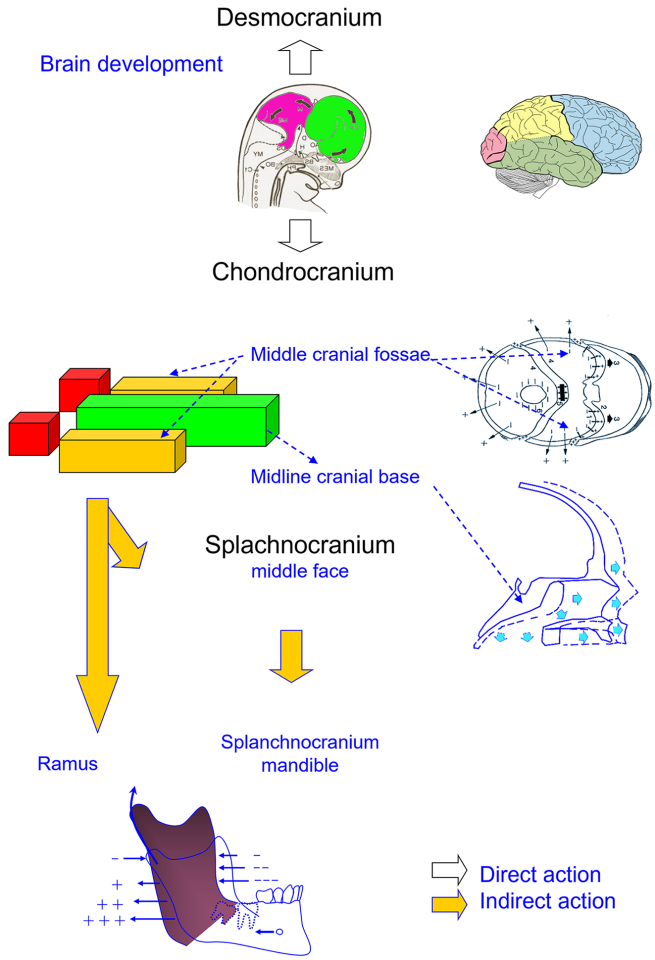


Figure 3. General scheme of the principles of craniofacial growth in humans. A key element is the influence of brain growth during embryonic phases on the different components of the head. The skull base, in turn, exerts two lines of influence: one on the posterior face and another on the anterior face. An important structural feature in craniofacial biology is the so-called posterior maxillary plane (**PM** plane), which serves as a fundamental morphogenetic boundary between the anterior and posterior faces. The anterior face lies anterior (ventral) to the PM plane, including the maxilla and its lower counterpart, the lower alveolar arch and the body of the mandible. The posterior face (dorsal) lies behind the PM plane and includes the lateral temporal fossae and the ascending ramus of the mandible.

The implementation of geometric morphometrics and 3D visualization techniques has made it possible to incorporate into this model the interactions of the lateral regions of the skull (temporal fossae and midface), which differ from those of the cranial midline (Bastir & Rosas, 2004, 2006; Bastir *et al.*, 2005; Gkantidis & Halazonetis, 2011). Specifically, the temporal lobes interact during development with the middle cranial fossa, midface, and mandible. It has been proposed

that evolutionary transformations of the middle cranial fossa have a substantial influence on craniofacial morphology (Bastir, 2008). A simple example is that when the lateral middle cranial fossae project forward, the zygomatic bones will also project forward, resulting in modifications to facial anatomy (Bastir & Rosas, 2016). In parallel, recent research on the factors influencing facial size points to the importance of the respiratory apparatus and its functional constraints on cranial airway dimensions (Rosas & Bastir, 2002; Bastir, 2008, 2019; Holton & Franciscus, 2008; Yokley, 2009; Bastir *et al.*, 2011; Bastir & Rosas, 2013). These studies support the hypothesis that the larger body mass of Middle and Late Pleistocene hominins (Ruff *et al.*, 1997; Arsuaga *et al.*, 1999; Carretero *et al.*, 2004; Churchill, 2006), along with their associated energetic demands, required larger cranial airways for oxygen delivery, which were housed in taller faces.

From a theoretical standpoint, the various factors mentioned above that potentially affect the morphological evolution of the craniofacial system introduce two key organizational elements for interpreting the phenomenon of mosaic evolution. First, the system under study is not isolated; it is integrated into other higher-level systems that influence it. Second, the system under study is highly integrated, meaning it maintains a series of internal relationships between its constituent elements that condition possible transformations (Bastir, 2008).

MATERIALS AND METHODS

The specimens directly studied are listed in Table 1. Occasionally, morphological characters of the mandible are referenced, with the sample found in Rosas *et al.* (2019, 2022). To standardize the measurement method, all encephalic volumes are taken from Holloway *et al.* (2004). Seven synthetic morphological characters (excluding the mandible) have been selected to account for much of the craniofacial morphological variation in the genus *Homo*. In order to focus on the specific evolution of Neandertals as an example of mosaic evolution, samples of *H. sapiens* have not been included in the analysis, thereby excluding features clearly derived from this species.

The morphological features considered and their states of expression are as follows:

1. Anteroposterior position of the nasion relative to the glabella. The primitive state (0) is a prominent glabella with the nasion in a clearly posterior position. The derived state (1) corresponds to the nasion in an anteroposterior position similar to that of the glabella.
2. Lateral continuity/splitting of the superciliary and supraorbital segments of the supraorbital torus, partly associated with torsion of the supraorbital torus. The primitive state (0) corresponds to a rounded and continuous supraorbital torus with no change in the orientation of its components. The derived state (1) is identified when division of the superciliary and supraorbital segments is observed. This is usually associated with some degree of torsion in the torus, where the plane of the superciliary segment has a superoposterior orientation relative to the supraorbital segment.
3. Position of the inion and the opisthocranium. The primitive state (0) is when the opisthocranium coincides with the position of the inion. The derived state (1) occurs when the opisthocranium is separated from the inion, but the maximum length of the skull is similar when measured from both points, and the occipital plane is more or less straight and vertical. The derived state (2) is when the maximum length of the skull is measured above the occipital plane, placing the opisthocranium clearly posterior to the inion.
4. Orientation of the infraorbital plane. The primitive state (0) is when this plane has a clearly coronal orientation. The derived state (1) occurs when the infraorbital plane adopts a more oblique position (tending toward a parasagittal orientation).
5. Relief of the articular eminence of the temporal bone. The primitive state (0) occurs when the anterior wall of the glenoid fossa is vertically oriented, with the angle between it and the articular eminence close to 90°. The derived state (1) is when the transition between the glenoid fossa and the articular eminence forms an inclined plane.
6. Profile of the cranial vault in posterior view. The primitive state (0) is defined by a low, pentagonal profile, with the lateral walls of the skull clearly converging toward the sagittal plane. The derived state (1) occurs when the lateral walls are parallel, and the cranial vault has a relatively greater height. The derived state (2) is when the posterior profile is clearly rounded.
7. Position of the zygomatic process in relation to the external auditory meatus. The primitive state (0) is when the zygomatic process of the temporal bone is clearly above the meatus. The derived state (1) is when the zygomatic process is at a more or less equal height to the external auditory meatus.

Morphological characters have been evaluated and compared both by individual anatomical regions and in their collective manifestation in each skull specimen. Some of the conclusions drawn have also been supported by previous results from the study of the mandible.

RESULTS

Morphological characters in the European Middle Pleistocene fossils

Table 1 shows the expression states of the selected morphological characters. In the African *H. erectus* group, it can be observed that, with a brain volume of approximately 800 cm³, morphological variability is very

low. The most variable features are the development of the occipital torus and the articular eminence. A similar pattern is seen in the Asian *H. erectus* group, where brain capacity is around 1000 cm³, though the variability is even more reduced. In Neandertals, there is a clear predominance of derived characters and significant homogeneity among individuals, associated with an average brain volume exceeding 1400 cm³. In the group of intermediate Middle Pleistocene hominins, with a brain capacity of around 1280 cm³, the pattern of variation becomes much more complex, displaying a greater number of combinations of primitive and derived traits. These data support the mosaic evolution characteristic of this transitional phase.

Focusing on European Middle Pleistocene hominins, the most primitive case is found in Ceprano, a specimen that does not show clear Neandertal features in the cranial vault, except for a slight development of the articular eminence. According to Manzi (2016), Ceprano displays a set of discrete characters partly similar to those seen in Petralona, Cranium 4 from the Sima de los Huesos (**SH**), and Arago. However, the overall shape of the calvaria does exhibit some Neandertal-like characteristics (Hautavoine *et al.*, 2024). Among the most derived forms in this group, we find the SH skulls, with some exceptions. The facial skeleton, occipital skeleton, and articular eminence are clearly derived or show intermediate expressions (mesomorphies, as defined by Arsuaga *et al.*, 1997). In this subgroup, considering the shared conserved traits, we can include Swanscombe and Aroeira. A notable combination of seemingly contrasting traits is seen in the comparison between Steinheim and Petralona. Steinheim exhibits a clearly derived occipital torus but retains a primitive (or more generalized) face, while Petralona has a primitive occipital and a more derived face. When analyzing individual anatomical regions, a gradient can be observed in the supraorbital torus, encompassing two extreme morphotypes: clear division between the superciliary and orbital segments (a Middle Pleistocene model, often accompanied by torus torsion) and continuity between these segments (the Neandertal model). Generally, the supraorbital torus is not twisted in Neandertals, although Spitery (1980) mentions that this morphology can also be found, albeit less pronounced, in this group. In our view, remnants of torus torsion can be seen in some Neandertal individuals (*e.g.*, La Chapelle-aux-Saints). The vast majority of the SH skulls present the Neandertal model, with the exception of Cranium 13, which displays a clearly twisted supraorbital torus (Arsuaga *et al.*, 2014), resembling the Middle Pleistocene model seen in Arago, Ceprano, and Petralona, which in turn are comparable to the African specimen from Kabwe. The variability detected in the SH sample is highly significant, as it links both morphotypes—this phenomenon was previously noted in the analysis of jaws (Rosas, 1997; Rosas *et al.*, 2019).

An oblique (parasagittal) orientation of the infraorbital plane is derived in most cases from the Middle Pleistocene (**MP**). For example, Arago 21 exhibits midfacial prognathism similar to that of SH5, a particularly distinctive Neandertal trait. Similarly, the morphology of Petralona's face is reminiscent of Neandertals, although its midfacial projection is less pronounced. In fact, according to Stringer and Gamble (1993), the Neandertal from Saccopastore 2 represents a reduced version of the Petralona face. Spitery (1982) related Arago 21 and Petralona to Neandertals based on the morphology of the maxilla. Moreover, in the European MP fossil record, transitional examples between the "generalized" face and Neandertal morphologies can be observed in Steinheim and AT-404 (Arsuaga *et al.*, 1997). This spectrum of variation appears to be linked to size. A similar pattern can be seen in the external configuration of the occipital bone and the *torus occipitalis*. The shape of the Neandertal occipital torus is considered clearly apomorphic (centered, straight, and with two lateral projections), associated with a marked suprainiac fossa. This configuration and/or transitional morphologies can be observed in Steinheim, Swanscombe, and SH. Larger individuals such as Ceprano and Petralona show a more primitive occipital. The variation in features associated with the temporal bone follows a seemingly more random pattern. For instance, the Neandertal glenoid fossa is flat, although Martínez and Arsuaga (1997) consider it secondarily derived. A low articular eminence is found in most Middle Pleistocene specimens, except in Aroeira and Reilingen. The mastoid processes in Neandertal temporal bones are greatly reduced, a feature observed only in Steinheim and Aroeira, while in other cases, they are larger. In Neandertals, the zygomatic process of the temporal bone is at the same level as the external auditory meatus. This derived feature is also found in Petralona and possibly in Aroeira.

In summary, certain features allow for the connection of two hypothetical phylogenetically distinct groups coexisting in the MP of Europe. One of the clearest examples is the torsion of the supraorbital torus, a trait common to the Ceprano group, which differentiates it from the morphology of the Sima group, which is closer to that of the Neandertals (continuous and rounded torus). Cranium 13 is crucial in this discussion, as it illustrates how—within the morphological variability of the Sima de los Huesos—we find examples that correspond to the Ceprano group. Even clearer examples are found in the morphology of the jaw (Rosas *et al.*, 2019).

DISCUSSION

The palaeontological record indicates that the first manifestations of Neandertal apomorphies in the skull of Europe's Middle Pleistocene populations appear in the occipital bone, although the dentition also shows early signs of change (Martinón-Torres *et al.*, 2007;

Zanolli *et al.*, 2018). These morphological changes are accompanied by modifications associated with an anterior projection of the facial skeleton in the sagittal plane, as well as a flattening of the temporal glenoid fossa. Arsuaga *et al.* (2014) argue that these initial modifications in the Neandertal lineage are concentrated in the dentition, maxilla, mandible, and glenoid fossa, and together they respond to masticatory specialization, while the cranial vault retains a primitive structure. This interpretation, however, does not take into account that the posterior half of the vault (the occipital and parietal bones) is one of the first anatomical regions to change, whose relationship with the masticatory system is difficult to establish. We argue that the causes of morphological changes in the craniofacial system of the Neandertal lineage are not directly related to the masticatory system. Certainly, many of the derived features are related to it, but their causation must be sought in the reorganization of the skull under the combined effects of an increase in brain size and a relative increase in the volume of the respiratory tract, especially the nasal cavity (Rosas *et al.*, 2006; Bastir, 2008).

Effects of Encephalization

Throughout the evolutionary sequence under study (*H. erectus s.l.* – Middle Pleistocene – Neandertals), the most striking variable is the increase in brain volume (Hawks & Wolpoff, 2001; Holloway *et al.*, 2004). This expansion significantly alters various morphological characteristics of the skull vault, particularly the posterior profile, which evolves from a low pentagonal to a high pentagonal shape (see Tab. 2). The occipital curves change, the opisthocranium unfolds from the inion, and the articular eminence becomes flattened. These features are likely associated with volumetric growth in the parietal, occipital, and temporal lobes, while the frontal lobes remain relatively stable. In other words, during the early and middle thirds of the Middle Pleistocene, encephalization is primarily driven by an increase in the postero-lateral regions of the brain (*e.g.*, Ceprano, Petralona). This growth in lateral brain areas has a differential impact on the configuration of the skull base's components (Bastir, 2008; Bastir *et al.*, 2011; Bastir & Rosas, 2016). It is hypothesized that higher degrees of encephalization lead to greater effects on the topology of the temporal fossae, further dissociating the sagittal basicranium from the lateral parts (middle cranial fossa). In more advanced phases of the Neandertalization process, a posterior relocation of the glenoid fossae occurs, already identified by Arsuaga *et al.* (1997) in the SH sample, and this is linked to the posterior positioning of the greater wings of the sphenoid (Bastir & Rosas, 2016). This suggests that the spatial position and shape of the temporomandibular joint are closely related to the evolutionary reorganization of the skull base, possibly driven by the enlargement of certain neural areas. In parallel, Bastir and Rosas (2016) argue that the midfacial projection of Neandertals is due to the anterior placement of the sphenoid body in relation to the retracted sphenoidal wings, the zygomatic arch, and possibly the mandibular branches (Bastir & Rosas, 2005). This configuration provides the cranial base support ("sphenoid wing retraction") for the Neandertal "zygomatic retraction" proposed by Trinkaus (1987). Additionally, Bastir and Rosas (2016) identify a close correlation between the anterior-posterior displacement of the midline and lateral parts of the skull base and the elongation of the skull: the further the midline shifts forward (and the lateral parts of the basicranium retract), the more elongated the skull becomes. This increase in dolichocephaly undoubtedly influences the morphological configuration of other systems, especially the occipital region. This helps explain why modifications to the occipital torus are among the earliest morphological changes observed in the fossil record, such as in the Swanscombe specimen.

Effects of Body Size

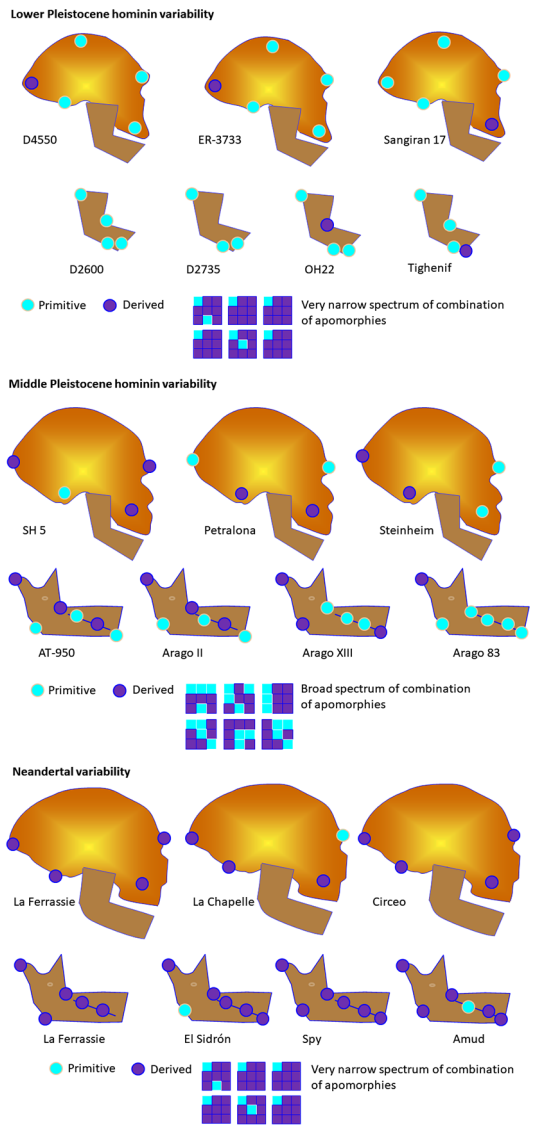
The increase in body size observed in Middle Pleistocene populations (Ruff *et al.*, 1997), associated with a rise in basal metabolism, influences the relative enlargement of the respiratory tract and its consequent effect on the nasal cavity. The expansion of the nasal cavity correlates with a vertical upward shift of the midline of the anterior cranial base, altering the anatomy of the central facial region (Bastir & Rosas, 2016; Fig. 5). Although further study is needed, it is likely that this factor influences variations in the glabellar depression and/or the relative position of the nasion (whether depressed or not) in relation to the glabella. In Middle Pleistocene populations, an allometric mandibular gradient has been identified (Rosas, 1997), indicating that certain derived traits become more pronounced with increased body size. A clear example of this can be seen in the size of the retromolar space (Rosas, 1997, 1998). This makes sense when considering that these derived traits (such as the retromolar space) are linked to a relatively larger nasal cavity and its corresponding anterior and superior displacement, which causes the separation between the anterior and posterior parts of the face (see Fig. 3) and the development of the retromolar space (Fig. 5). In other regions of the skull, we observe that smaller, less robust individuals (*e.g.*, Steinheim) exhibit less developed occipital tori along with less expanded (inflated) faces, representing a facial phenotype associated with the primitive (or generalized) stage. Conversely, larger and more robust individuals (*e.g.*, Ceprano, Petralona, SH cranium 4) show more developed occipital tori, which correspond to more inflated faces (*e.g.*, Petralona).

The morphological interplay between the effects of increased encephalization and larger body/energy size explains much of the variation (mosaic patterns) detected in the Middle Pleistocene (in this discussion,

Table 2. Character states of the specimens used in the analysis.

Specimen	Cranial capacity (cm3)	Position of the nasion relative to the glabella. Sunken: 0; same level: 1	Torsion of the supraorbital torus. No torsion: 0; torsioned: 1	Degree of development of the occipital torus. Prominent (primitive): 0; medium: 1; slight (derived): 2	Orientation of the infraorbital plane. Coronal (primitive): 0; oblique or parasagittal: 1	Articular eminence. Inclined septum: 0; vertical septum: 1	Posterior view profile. Low pentagonal (primitive): 0; high pentagonal: 1; rounded (bulging): 2	Position of the zygomatic process in relation to the external auditory meatus. Below: 0; at the same level: 1
African *H. erectus s.l.*								
D2280	650	1	0	0		1	0	0
D2282	780		0	0	0	0	0	0
D3444	625	0	0	1	0	1	0	0
D4500	546	0	0	1	0	0	0	0
WT-15000	900			0	0	0	0	0
ER-3733	848	0	0	1	0	0	0	0
ER-3883	804	0	0	0		1	0	0
ER-42700	691		0	2		1	0	0
OH-9	1067	0	1	0		1	0	0
Daka	995	0	1	1		1	1	0
Asian *H. erectus s.l.*								
Ngawi	870	0	0	0		1	0	0
Sambungmacan 1	1035		0	1		1	0	1
Zhoukoudian I	1225	0	0	0	0	1	0	0
Ngandong 7 (Solo VI)	1013	0	0	0		1	0	
Ngandong 10 (Solo IX)	1135		0	0		1	0	1
Ngandong 12 (Solo XI)	1090	0	0	0		1	0	1
Sangiran 2	813		0	0		1	0	1
Sangiran 17	1004		1	0	1	1	0	1
Nanking 1	1000	0	0	0	0			
African Middle Pleistocene								
Kabwe	1325	0	1	2	1	1	1	0
Bodo	1250	0	1		1	0		
Gawis		1	0	1		0	1	0
Zuttiyeh		1	1					
Asian Middle Pleistocene								
Dali	1120	0	1	2	0	0	1	1
Jinniushan	1390	0	0	2	0	0	1	0
Harbin	1420	0	1	2	0	0	2	1
European Middle Pleistocene								
Ceprano	1165	0	1	0		1	1	0
Petralona	1230	0	1	1	1	0		1
Steinheim	1200	0	0	2	0	1	1	0
Arago	1166	0	1		1			
Swanscombe	1325			2			1	
Aroeira		1	0			1	1	1
Reilingen	1430			1		1	1	0
Bilzingsleben		1						
SH-4	1390		0	2		0	1	0
SH-5	1125	1	0	2	1	0	1	0
SH-13	1436	0	1	1		0	1	0
Neandertals								
Apidima 1	1230	1	0		1		2	1
Lazaret	1250	1						
Ehringsdorf	1450		0	2		0	2	0
Amud	1740	1	0	2	1	1	2	0
Gibraltar	1200	1	0	2	1	1	2	1
La Chapelle	1625	0	1	2	1	0	2	1
La Ferrassie 1	1640	1	0	2	1	0	2	1
La Quina 5	1172	1	1	2		0	2	1
Feldofer	1525	1						1
Le Moustier	1565	1	0	2		1	2	1
Guatari 1	1360	1	0	2	1	0	2	1
Saccopastore 1	1245			2	1	1	2	1
Shanidar 1	1600	1	0	2	1	0	2	1
Spy I	1305	1	0	1		1	2	1
Spy II	1553		0	2		1	2	1
Tabun 1	1271		0	2	1	1	2	1

we have not considered the possible impact of dental size). For instance, Petralona shares similarities with SH in terms of the articular eminence, the oblique orientation of the infraorbital plane, and the anteriorly flattened maxilla. However, it differs from SH in the anatomy of the supraorbital and occipital tori, both of which are primitive in Petralona. This demonstrates that the occipital can vary without affecting the face (*e.g.*, Steinheim), and that occipital variation can occur independently of frontal changes (*e.g.*, Petralona). Nevertheless, it is important to note that the variation observed in the SH population, which is largely linked to allometric factors (Rosas & Bastir, 2004), may help explain at least part of the differences observed when comparing isolated specimens. Several phylogenetically significant traits may be directly related to size. On one hand, the relatively concave infraorbital surface (canine fossa) in the AT-404 maxilla and cranium 6 (adolescent) (Arsuaga *et al.*, 1997) is associated with relatively gracile individuals. On the other hand, primitive traits such as the *torus angularis* in cranium 4 and the torsion of the supraorbital torus in cranium 13 (as previously noted) (Arsuaga *et al.*, 2014) are found in more robust individuals.



Interpretation of the mosaic pattern in the evolutionary process

Within a conceptual framework consistent with population genetics, in which morphological traits reflect genetic alleles, two interpretative approaches can be identified. On the one hand, when faced with a heterogeneous mix of phenotypic combinations (mosaics), it has been argued that in a sequence of anagenetic change, if the traits are relatively independent, they may undergo different rates of change (either through selection or genetic drift). As a result, heterogeneous patterns of change may arise in the intermediate stages of the process (Arsuaga *et al.*, 1997). On the other hand, some authors interpret the different expressions of population marker traits as a product of complex population dynamics, such as isolation, admixture, and replacements, in a system of "sources" and "sinks" (Dennell *et al.*, 2011; Daura *et al.*, 2017; Bermúdez de Castro *et al.*, 2019). A prime example of this can be seen in the comparison between the population of the Sima de los Huesos at Atapuerca, which shows a long series of Neandertal apomorphies (Bermúdez de Castro & Nicolás, 1995; Arsuaga *et al.*, 1997; Rosas, 1997, 2001; Martinón-Torres *et al.*, 2007), and the Arago sample, which presents fewer derived traits. The chronological overlap between these two

Figure 4. Scheme illustrating the pattern of morphological change under study. **A,** General model of the morphological variability observed in hominins classified as *H. erectus s.l.* The top line highlights some representative cranial features (occipital shape, vault height, frontal projection, and prognathism). The middle line shows mandibular features (condyle, anterior-posterior relationship of the body and ramus, anterior marginal tubercle, and the external anatomy of the symphysis). The bottom line presents a diagram visualizing the frequency and distribution of primitive and derived traits. This model depicts an essentially primitive morphological scheme for the genus *Homo*, with occasional appearances of derived trait states; **B,** general model of the morphological variability observed in European Middle Pleistocene hominins. The top line highlights some cranial features (occipital shape, mastoid process size, glabella shape, and mid-facial prognathism). The middle line shows mandibular features (condyle, gonion profile, anterior-posterior relationship of the body and ramus, mylohyoid line shape, and external anatomy of the symphysis). The bottom line presents a diagram visualizing the frequency and distribution of primitive and derived traits. This model exhibits high morphological diversity, defined by individual combinations of primitive and derived trait expressions; **C,** general model of the morphological variability observed in Neandertal populations (late Middle Pleistocene and Upper Pleistocene). The top line highlights some cranial features (occipital shape, mastoid process size, glabella shape, and mid-facial prognathism). The middle line shows mandibular features (condyle, gonion profile, anterior-posterior relationship of the body and ramus, mylohyoid line shape, and external anatomy of the symphysis). The bottom line presents a diagram visualizing the frequency and distribution of primitive and derived traits. This model reveals a clear predominance of derived traits in various craniofacial subsystems.

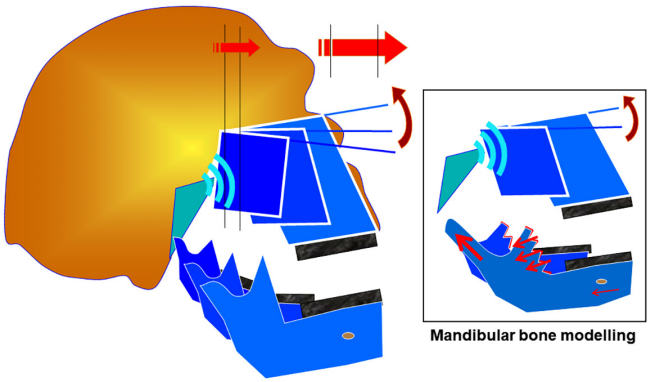


Figure 5. Schematic representation of the effects on the craniofacial system due to an increase in facial skeleton size, resulting from the overall growth of the organism. The midline at the base of the skull (sphenoid body shown in red) increases in its anteroposterior (horizontal) dimension, shifting the face anteriorly (horizontal blue arrows). This shift leads to an increased width of the posterior face, which directly affects the width of the ascending ramus of the mandible. In turn, the enlargement of the nasal cavity, in line with the overall body size increase, has two immediate consequences. First, the alveolar arch (dentition) shifts forward. Second, there is an anterosuperior tilting of the midface (maxilla) (ascending blue arrows). In response, the mandible must adapt to these changes to maintain morphofunctional balance (including occlusion, swallowing, and phonation, among others). The adjustment of mandibular morphology to the rest of the system is achieved through complex three-dimensional processes of bone deposition and resorption (modeling), which result in the emergence of derived traits in Neanderthal lineage, such as the retromolar space and posterior positioning of the mental foramen, among others.

samples, both dated to 430 ky, with Arago showing fewer derived traits, has been interpreted as evidence of phylogenetic heterogeneity among European Middle Pleistocene populations (Bermúdez de Castro *et al.*, 2019). This suggests that more than one evolutionary lineage could have coexisted in Europe during the Middle Pleistocene (Manzi *et al.*, 2010; Arsuaga *et al.*, 2014). However, while the cranial remains of Arago retain primitive traits, it is noteworthy that the Arago 21 face is inflated, and the Arago 2 mandible features a mental foramen located at the level of M1 and a wide retromolar space (Aguirre & de Lumley, 1977; Mounier *et al.*, 2009; Rosas, 2001; Bermúdez de Castro *et al.*, 2016), all set within a primitive mandibular architecture with a very wide ascending ramus and a deep submental notch, both features reminiscent of the Mauer mandible (Rosas *et al.*, 2019). Furthermore, a key point raised by Rosas (2022) is that all Arago mandibles display a typically Neandertal trait: the divided condyle (Rosas, 2001) (see Fig. 4). This body of evidence suggests that both populations were directly involved in the evolutionary process leading to Neandertals. At the same time, it cannot be ruled out that the Sima de los Huesos sample is not as old as previously published (see Tab. 1), and that the difference in the evolutionary stages between the Arago and SH samples (the latter with a greater number of Neandertal apomorphies) might reflect different phases in the evolution of the same lineage.

We support the hypothesis that these mosaics of traits emerged within the context of a complex evolutionary process, influenced by various interacting developmental factors. One key factor is the dissociation of the sagittal cranial base from the lateral parts (middle cranial fossa), driven by the process of encephalization. Another is the impact of increased body size. This mosaic evolution can only be observed through the phenotypic changes we see, and any inference of causal factors remains highly indirect. Advances in methodologies, such as predictive geometric morphometrics, combined with insights from craniofacial and developmental biology, along with a more robust theoretical framework, will improve our understanding of the mechanisms of human evolution. However, we must always recognize the ongoing need for new fossil discoveries to expand the scope of our observations and analyses.

CONCLUSIONS

The overcoming of ecological and physiological constraints that kept brain size within limited bounds—without exceeding 1000 cm³ during the early phases of genus *Homo* evolution—led to a new diversification of human lineages and the emergence of new biological forms during the Middle Pleistocene. The biocultural development of hominins during this period, exemplified by the domestication of fire (which allowed for an expanded nutritional spectrum and improved nutrient digestibility), the adoption of new forms of social organization (*e.g.*, hunting strategies), the expansion of the Acheulean tradition, and the emergence of symbolism, resulted in a broadening of the human ecological niche (Paige & Perreault, 2024). The combination of these factors created a scenario of multiple influences and niche constructions, resulting in various combinations of primitive and derived traits (*i.e.*, mosaics), which, in some cases, complicates the interpretation of the phylogenetic process, such as the emergence of Neandertals. We argue that interpreting these trait mosaics from an organismic perspective is key to understanding this phenomenon. We propose an alternative model that introduces new levels of analysis: (1) the system under study is integrated into a larger framework, and (2) the system under study has an internal structure, meaning that change is conditioned by a set of factors derived from the interrelationships among its structural components.

Author Contributions. AR conceived the study. All authors contributed to writing the manuscript and analyzing the data.

Competing Interests. The authors declare no competing interests.

Funding. This research was funded by the Ministry of Science and Innovation of Spain through projects PID2021-122356NB-I00 (to AR) and PID2020-115854GB-I00 (to MB).

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Acknowledgements. This work is dedicated to Prof. Miquel De Renzi, a mentor and guide in exploring alternative approaches to understanding morphological evolution, beyond the externalist orthodoxy of neo-Darwinism. We are grateful to the editors of this special volume, dedicated to Miquel De Renzi, for their efforts in making this publication possible. Special thanks to Enrique Peñalver, Diego Rasskin, and an anonymous referee for their insightful suggestions and corrections. Our thanks to Carlos Martínez-Pérez and the entire SJP editorial team.

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