



SAPIENZA
UNIVERSITÀ DI ROMA



Applying cladistics to geometric morphometrics data: a new approach to resolve the phylogeny of the genus *Homo*.

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*« La nature est un temple où de vivants piliers
Laissent parfois sortir de confuses paroles;
L'homme y passe à travers des forêts de symboles
Qui l'observent avec des regards familiers. »*

Baudelaire, Correspondances, Les Fleurs du mal (1857)

Abridged version

The study of evolution, particularly hominin evolution, has been profoundly shaped by debates surrounding the mechanisms driving species formation and the methodologies employed to reconstruct phylogenetic relationships. Understanding both evolutionary patterns and processes is essential, yet the approaches to achieving this understanding have varied considerably across time and disciplinary perspectives. An evolutionary theory, as articulated by Simpson, distinguished anagenesis, the gradual evolution of a single lineage, from cladogenesis, which involves the branching of one lineage into two, effectively representing speciation. This distinction emphasized the dual dimensions of evolutionary change: temporal continuity and lineage diversification. Subsequently, Eldredge and Gould challenged the assumption that evolutionary change occurs primarily through gradual, continuous processes, proposing instead the Punctuated Equilibrium model. This model posits that species often experience long periods of morphological stasis interrupted by relatively rapid episodes of speciation, underscoring the non-linear and episodic nature of evolutionary dynamics. These theoretical frameworks collectively highlight the importance of examining both morphological patterns and the underlying processes that generate diversity in the fossil record.

Central to evolutionary studies is the concept of species, yet its definition remains contentious, particularly when applied to fossil taxa. The Biological Species Concept (BSC) emphasizes reproductive isolation as the defining feature of a species, whereas the Phylogenetic Species Concept (PSC) identifies species as the smallest diagnosable clusters on a phylogenetic tree. The Evolutionary Species Concept (ESC) frames species as distinct evolutionary lineages, supported by multiple lines of evidence, including reproductive, morphological, and genetic traits. Although the BSC cannot be directly applied to extinct taxa because reproductive behaviour is unobservable, the ESC and PSC were developed to overcome this limitation. In practice, palaeoanthropology often relies on the morphological or Phenetic Species Concept, which defines species based on observable anatomical differences, an approach that is operationally useful, even if it does not fully capture evolutionary dynamics. As a result, studies of fossil hominins rely heavily on morphological patterns and inferred evolutionary relationships, necessitating rigorous analytical methods to distinguish between shared ancestry and convergent evolution.

Morphological analysis remains a cornerstone of evolutionary reconstruction. Traditional morphometric approaches quantify linear distances, ratios, and angles, offering insight into phenotypic variation but often neglecting the geometric relationships between traits. The emergence of geometric morphometrics (GMM) has addressed this limitation by enabling the precise quantification of shape using landmark coordinates and multivariate statistical techniques. GMM integrates biological insight with mathematical rigor, allowing researchers to capture both size and shape variation in a reproducible and statistically robust manner. In palaeoanthropology, the advent of 3D virtual models of fossil specimens has revolutionized skeletal analysis, facilitating comprehensive, reproducible studies that combine traditional morphological assessment with advanced shape analysis.

Cladistics, grounded in the principle of minimizing homoplasy to better reconstruct phylogenies, has traditionally relied on discrete characters, yet much phenotypic variation is continuous. Integrating continuous morphometric data into phylogenetic inference poses methodological challenges due to issues of landmark homology, high-dimensionality, and statistical dependence among coordinates. Early approaches often relied on distance-based or principal component analysis (PCA)-derived data, which have frequently been criticised for capturing phenetic rather than true phylogenetic signals. Recent advances employing Bayesian and likelihood-based methods have begun to allow continuous data to inform phylogenetic trees and ancestral state reconstructions, although these approaches remain computationally intensive and conceptually complex.

These methodological frameworks have been applied extensively to the study of hominin evolution, from australopiths to later *Homo* species. *Australopithecus afarensis* is widely considered a basal form, potentially ancestral to both *Paranthropus* and early *Homo*. Other australopiths, including *A. africanus* and *A. sediba*, exhibit some variably expressed derived morphologies resembling early *Homo*, reflecting the complex, non-linear pathways of hominin evolution. *Paranthropus* species demonstrate ecological and morphological diversification, with *P. aethiopicus* representing a basal East African lineage, and *P. boisei* and *P. robustus* reflecting regional adaptations. Early *Homo* exhibits branching and reticulate evolutionary patterns, with *H. habilis* and *H. rudolfensis* occupying transitional positions between australopith-grade morphologies and *Homo* phenotypes, while *H. ergaster*, *H. georgicus* and *H. erectus* illustrate early dispersals in and out of Africa. Later lineages, including *H.*

neandertalensis and *H. sapiens*, demonstrate admixture and interbreeding, emphasizing the dynamic and branching nature of hominin evolution.

The present study has two main aims: (1) to evaluate the integration of geometric morphometric data into cladistic analysis, testing whether landmark coordinates and PCA-derived datasets can recover meaningful evolutionary patterns and how these compare to traditional discrete morphological matrices; and (2) to apply these methods to the fossil record of early *Homo* and australopiths to assess their phylogenetic relationships and evolutionary patterns. By combining datasets and confronting the resulting phylogenies with ongoing debates in hominin systematics, this research aims to establish a phylogeny, clarifying the relationships among *Australopithecus*, *Paranthropus*, and early *Homo*; and assess the contributions of continuous versus discrete data.

Phylogenetic analyses in this study were conducted on 23 and 28 operational taxonomic units (OTU) under maximum parsimony, using both discrete character matrices and geometric morphometric datasets. Wagner parsimony was applied with heuristic searches employed for larger datasets to optimize computational efficiency. Consensus trees were generated when multiple most parsimonious trees (MPTs) emerged, and node support was evaluated using bootstrap analyses, with values $\geq 50\%$ indicating robust clades. Tree robustness was further assessed using standard indices, including tree length, the Consistency Index (CI), Retention Index (RI), and Rescaled Consistency Index (RC), which quantify homoplasy and overall fit. Long-branch attraction was monitored to avoid misinterpretation of convergent similarities, and careful trait selection ensured the phylogenetic relevance of included characters.

Discrete morphological data comprised 59 and 60 cranial traits, primarily from the calvarium, coded as binary or multistate characters. Complementary GMM analyses captured cranial shape using 27 anatomical landmarks and 121 to 609 semi-landmarks from 3D digital models. Landmark coordinates were aligned using Generalized Procrustes Analysis (GPA) to remove non-shape variation, with configurations projected into Kendall's shape space and analysed using PCA to identify primary axes of variation. Missing data were addressed through mirroring or thin-plate spline interpolation.

In Chapter III, three distinct data matrices were analysed: (A) discrete morphological characters; (B) PCA scores from Procrustes-aligned coordinates; and (C) raw 3D Procrustes coordinates. Phylogenetic congruence was assessed using Robinson–Foulds distances and Subtree Pruning–

Regrafting similarity scores. Results indicate that PCA-based trees improved in resolution with increasing landmark density, while raw landmark analyses consistently yielded the highest topological congruence with morphology-based reference trees. Although traditional discrete characters provided the clearest synapomorphies, GMM datasets, particularly raw landmarks, offered continuous, reproducible measures of morphological variation, reducing observer bias.

In Chapter IV, the integration of discrete and morphometric data substantially enhanced the statistical and topological outcomes of phylogenetic analyses. By combining traditional character matrices with 3D landmark data, the study was able to capture complementary aspects of cranial variation that neither approach could fully represent alone. This integration improved node support across the phylogenetic trees, resolved previously ambiguous basal polytomies, and clarified evolutionary relationships within complex taxa such as *H. erectus* sensu lato. In particular, the combined dataset revealed clearer structuring among African and Asian *H. erectus* specimens, reflecting both temporal succession and geographic differentiation. Importantly, these results highlight that discrete characters and geometric morphometric data, while differing in analytical logic, can converge on coherent evolutionary interpretations when applied within a unified framework. This underscores the value of methodological pluralism in palaeoanthropology, particularly for addressing longstanding debates about species boundaries and transitional morphologies.

Later *Homo* species, such as *H. neandertalensis* and *H. sapiens*, showed stable monophyly across datasets, consistent with both fossil and genomic evidence. However, these results are secondary to the primary focus of this analysis, clarifying the phylogenetic relationships among early *Homo* and australopiths, where the integration of geometric and discrete morphological data provides the greatest improvement in resolution.

Within early *Homo*, relationships were less stable, reflecting both genuine evolutionary diversification and incomplete fossil sampling. The position of *H. habilis* and *H. rudolfensis* remained variable across analyses, suggesting either unresolved phylogenetic signals or overlapping morphological variation within an early *Homo* grade. *H. erectus* sensu lato, by contrast, formed a more cohesive clade, with African and Asian representatives showing consistent affinities and preserving key features linking earlier and later taxa. These findings highlight that the transition from *Australopithecus* to *Homo* was not a single, abrupt event but a complex phase of diversification within which multiple lineages experimented with different adaptive strategies.

The robust australopith clade, including *Paranthropus* species, demonstrated remarkable stability across all analytical approaches. Consistent clustering of *P. aethiopicus* and *P. boisei* reinforces the interpretation of these taxa as a monophyletic group that diverged early from the *Australopithecus*–*Homo* lineage. Morphologically, they retain distinctive cranial traits, such as pronounced postorbital constriction, sagittal crest development, and robust masticatory structures, suggesting a specialized adaptive trajectory largely independent of the lineage leading to *Homo*. These findings support the notion that evolutionary divergence within the hominin clade was not uniform; some lineages, such as *Paranthropus*, pursued highly specialized adaptations, while others, including early *Homo*, exhibited greater morphological plasticity and continuity with ancestral forms. This dichotomy illustrates the interplay of ecological pressures, functional demands, and developmental constraints in shaping hominin cranial evolution.

Overall, this dissertation demonstrates that hominin cranial evolution followed a branching trajectory. It reflects a complex process, shaped by temporal overlap, geographic structure, and ecological adaptation. Integration of discrete morphological characters with quantitative 3D morphometric data provides a more nuanced and statistically robust framework for reconstructing these evolutionary relationships. By combining these approaches, the study resolves ambiguities surrounding key taxa, such as *H. erectus* and *H. habilis*, and highlights the morphological variability and phylogenetic relationships among taxa at the interface between australopiths and early *Homo*. Importantly, the research also illustrates that evolutionary ambiguity often arises from genuine biological complexity, reticulation, population overlap, and developmental plasticity, the limitations imposed by incomplete or uneven fossil sampling, rather than analytical shortcomings. By adopting an integrative, pluralistic methodology, this thesis advances a comprehensive understanding of hominin evolution, reframing it as a dynamic network of continuity and change that is best interpreted through multiple analytical dimensions. This approach provides both a methodological model for future studies and a conceptual framework for appreciating the mosaic and branching nature of human evolutionary history.

English abstract

This dissertation investigates hominin cranial evolution through an integrative analytical framework that combines discrete morphological data with geometric morphometrics (GMM) in cladistic analysis. Defining species in the fossil record remains a major challenge in palaeoanthropology, as reproductive isolation cannot be directly inferred from morphological evidence. Morphological evidence, therefore, remains the primary basis for reconstructing phylogenetic relationships, requiring rigorous methods to distinguish shared ancestry from convergent adaptation.

Traditional morphometric approaches quantify linear measurements but often overlook geometric relationships among traits. GMM addresses these limitations by capturing three-dimensional shape variation through landmark coordinates and multivariate statistical methods, providing a robust, reproducible framework for analysing cranial morphology. However, integrating continuous morphometric data into cladistic analysis presents challenges related to homology, dimensionality, and statistical dependence.

This research empirically assesses the use of GMM data in cladistics and their combination with discrete morphological matrices to clarify relationships among *Australopithecus*, *Paranthropus*, and early *Homo* taxa. Phylogenetic analyses were conducted under maximum parsimony using datasets of 23 and 28 operational taxonomic units. Robustness was assessed through bootstrap resampling and topological congruence metrics. Results demonstrate that raw landmark coordinates retain stronger phylogenetic signal than PCA-derived variables, and that integrating continuous and discrete datasets significantly improves node support and overall tree resolution.

The combined analyses resolve several key ambiguities, notably clarifying the internal structuring of *Homo erectus* sensu lato and supporting the monophyly of the robust australopiths (*Paranthropus*). Later hominins, including *Homo neandertalensis* and *H. sapiens*, display stable, well-supported clades consistent with fossil and genomic evidence.

Overall, this work demonstrates that hominin evolution followed a branching trajectory shaped by geographic differentiation, ecological adaptation, and developmental plasticity. The integration of traditional and geometric morphometric approaches provides a more nuanced and statistically rigorous framework for reconstructing the complex evolutionary history of the genus *Homo*.

French abstract

Cette thèse examine l'évolution crânienne des hominines à travers un cadre analytique intégratif combinant des données morphologiques discrètes et la morphométrie géométrique (GMM) dans une analyse cladistique. La définition des espèces dans le registre fossile demeure un défi majeur en paléanthropologie, l'isolement reproductif ne pouvant être inféré directement à partir des seules données morphologiques. L'évidence morphologique constitue donc la base principale de la reconstruction des relations phylogénétiques, ce qui nécessite des méthodes rigoureuses permettant de distinguer l'héritage commun des adaptations convergentes.

Les approches morphométriques traditionnelles quantifient des mesures linéaires, mais négligent souvent les relations géométriques entre les caractères. La morphométrie géométrique répond à ces limites en capturant la variation de forme tridimensionnelle à l'aide de coordonnées de points homologues et de méthodes statistiques multivariées, offrant ainsi un cadre robuste et reproductible pour l'analyse de la morphologie crânienne. Toutefois, l'intégration de données morphométriques continues dans les analyses cladistiques pose des difficultés liées à l'homologie, à la dimensionalité et à la dépendance statistique des variables.

Cette recherche évalue empiriquement l'utilisation des données issues de la GMM en cladistique, ainsi que leur combinaison avec des matrices morphologiques discrètes, afin de clarifier les relations phylogénétiques entre les taxons d'*Australopithecus*, de *Paranthropus* et d'*Homo* ancien. Les analyses phylogénétiques ont été conduites selon le critère de parcimonie maximale à partir de jeux de données comprenant 23 et 28 unités taxonomiques opérationnelles. La robustesse des résultats a été évaluée par rééchantillonnage Bootstrap et par des mesures de congruence topologique. Les résultats montrent que les coordonnées brutes des points de repère conservent un signal phylogénétique plus fort que les variables dérivées de l'analyse en composantes principales (ACP), et que l'intégration des données continues et discrètes améliore significativement le soutien des nœuds et la résolution globale des arbres.

Les analyses combinées permettent de résoudre plusieurs ambiguïtés majeures, notamment en clarifiant la structuration interne d'*Homo erectus* sensu lato et en soutenant la monophylie des australopithèques robustes (*Paranthropus*). Les hominines plus récents, incluant *H. neandertalensis* et *H. sapiens*, forment des clades stables et fortement soutenus, en accord avec les données fossiles et génomiques.

Dans l'ensemble, ce travail démontre que l'évolution des hominines a suivi une trajectoire ramifiée, façonnée par la différenciation géographique, l'adaptation écologique et la plasticité développementale. L'intégration des approches morphométriques traditionnelles et géométriques fournit un cadre plus nuancé et statistiquement rigoureux pour la reconstruction de l'histoire évolutive complexe du genre *Homo*.

Acknowledgments

I would first like to express my deepest gratitude to my three supervisors, Giorgio Manzi, Aurélien Mounier, and Valéry Zeitoun, for their guidance, patience, and constant support throughout my PhD. Their scientific expertise, insightful feedback, and encouragement have been invaluable during the course of this work.

I am sincerely grateful to Sapienza University of Rome for funding my PhD and to the Muséum national d'Histoire naturelle (MNHN) for hosting me as part of the cotutelle program. Both institutions have provided an inspiring and stimulating environment that made this project possible.

My heartfelt thanks also go to my colleagues at Sapienza University, Sofia, Giulia, Martina, Silvia, and all the others, and at the MNHN, particularly the UMR 7194 team and the Ph.D. students, for their warm welcome, enthusiasm, and stimulating discussions. I am especially grateful to Pierre for his invaluable help with the literature reviews and for the many engaging discussions on palaeoanthropology; to Hugo for his patient and much-needed assistance with R, which at times proved quite challenging; and to Marina for the enjoyable lunches that brought lightness to what could otherwise have been a demanding period. Their dynamism, kindness, and camaraderie made my research experience both productive and genuinely enjoyable.

I am sincerely grateful to the Willi Hennig Society for the travel award that enabled me to attend the congress and workshops in Mexico. That opportunity was not only scientifically enriching but also allowed me to meet many wonderful people and exchange ideas that deeply influenced my perspective.

My gratitude also goes to Santiago Catalano, for welcoming me into his laboratory at Miguel Lillo Institute in Argentina, for teaching me the fundamentals of coding in TNT, and to all the colleagues there who kindly made me feel at home. I would also like to thank Pablo Goloboff for kindly answering my numerous questions about TNT. Their support and patience greatly facilitated the analytical components of this work.

I would like to express my sincere gratitude to the members of my jury, Pr. José Braga, Dr. Costantino Buzy, Pr. Isabelle Rouget, Pr. Fabio Di Vincenzo and Dr. Laura Buck, for accepting to evaluate my work and for their time, insightful comments, and valuable feedback. Their expertise and perspectives have greatly contributed to improving the quality of this thesis.

A very special thanks goes to my dear friend Quentin, whose friendship has been a constant source of inspiration and support. Our countless discussions about phylogeny, taxonomy, and life in general not only enriched my thinking but also brought balance and joy to these demanding years. Our long walks and conversations were an essential part of the journey that led to the completion of this thesis, and I am deeply grateful for his presence, kindness, and insight.

Finally, I would like to express my deepest appreciation to my friends and family for their unwavering support, encouragement, and understanding throughout these years. Their presence and belief in me have been a constant source of strength and motivation.

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Introduction

This dissertation explores the integration of geometric morphometric data within a cladistic framework, with a particular focus on applications in palaeoanthropology. It seeks to determine whether and how shape data, derived from landmark configurations and principal component analyses, can improve the resolution and stability of phylogenetic hypotheses compared to traditional discrete morphological matrices. In order to properly situate this research, it is essential to first introduce the epistemological and methodological foundations underlying the main concepts addressed throughout the work. This requires a discussion of the historical development of these approaches and their place within the broader history of the discipline.

Accordingly, this introductory chapter begins by outlining the conceptual and methodological context, including key developments in phylogenetic systematics, morphometrics, and virtual anthropology. It then presents a state-of-the-art review of the tools and techniques employed in this study. Finally, the chapter concludes with a general overview of the major paleoanthropological debates concerning the genera *Paranthropus*, *Australopithecus*, and *Homo*, in order to frame the scientific questions addressed in the following chapters.

I. Phylogeny and other concepts

The processes involved in evolution have been at the centre of debates ever since Darwin published his theory of evolution in 1859 (Darwin, 1859). Simpson (1944) made a careful distinction between two types of evolutionary processes: anagenesis, evolution along a single lineage, which he considered primary, and cladogenesis, which involves the splitting of one lineage into two. Cladogenesis generally results in two distinct species where there was once just one and can therefore be thought of as broadly synonymous with speciation. After that, Eldredge and Gould (1972) saw that long-term stasis in a lineage is often followed by the sudden appearance of a new species that replaces the older one. They formulated a new theory, the theory of Punctuated Equilibrium (PE). Its true innovation was its insistence that stasis, rather than anagenesis, is the typical situation, with speciation, not gradual change, being the driving force of evolution. Up until 1972, most palaeontologists interpreted their fossils as evidence of gradual change over time. If the fossils did not show such gradual change, it was often seen as a failure to demonstrate significant change, or the lack of change was attributed to the incomplete nature of the fossil record (Groves, 2015).

I.1. Species concept

Assessing whether species can be regarded as the core units of evolution, beyond their widely accepted role in ecology, biogeography, and conservation, first requires a clear understanding of what the term “species” entails. This issue is not confined to systematics, where the concept originally developed, but has broader implications across biological research. The number of species concepts recognised in the literature varies depending on how finely distinctions are drawn between authors’ viewpoints. For instance, Harrison (1998) identifies seven species concepts, while Mayden (1997) and Hey (2001) proposed up to 24. Despite this diversity, these concepts can generally be organised into two broad categories. Some approaches define species based on reproductive separation, while others rely on different criteria independent of interbreeding. Groves (2001) described a similar distinction using the terms “theoretical” and “operational,” which also aligns with the broader contrast between pattern-based descriptions of biodiversity and process-oriented explanations of how species arise and persist.

Among these perspectives, the Biological Species Concept (BSC) has been particularly influential. Developed by figures such as Dobzhansky (1937) and Mayr (1963), it defines species primarily in

terms of reproductive isolation. In this view, a species is composed of natural populations that are capable of interbreeding but remain reproductively isolated from others. Mayr (1940) characterised species as groups of actually or potentially interbreeding populations, while, while Dobzhansky (1950) emphasised their nature as the largest reproductive communities sharing a common gene pool.

When working with animals preserved in a museum or studying the fossil record, the species criterion of the BSC, no matter how much it's modified, can at best be a rough inference and, at worst, misleading. As Nixon and Wheeler (1990) pointed out, under these conditions, all that can be observed are patterns, not processes. This issue was recognised over 30 years ago by Sokal and Crovello (1970), who rejected the BSC for this reason, and advocated for a morphological ("phenetic") species concept, as it was usable in palaeontology. It was Cracraft (1983, 1989, 1997; but also Eldredge and Cracraft, 1980) who introduced the Phylogenetic Species Concept (PSC), in which a species is defined as the smallest cluster of individuals (a population or group of populations) that is distinctly diagnosable from other such clusters. This concept is termed "phylogenetic" because species are considered the terminal points on a cladogram, making them the least inclusive phylogenetic units. Cracraft (1983) suggested that "diagnosable distinct" means having at least one diagnostic character state, while Baum (1992) and others argued that a species could be distinguished by a unique combination of traits. Under the PSC, species are considered units of genetic cohesion, not necessarily reproductive cohesion. This is because different phylogenetic species might still interbreed. The PSC is highly operational, relying on the available evidence rather than requiring extensive inference, as the BSC and its modifications do. While palaeontologists and palaeoanthropologists have little choice but to use the PSC, most researchers rely on a morphological ("phenetic") concept to produce alpha taxonomy.

In 1961, Simpson proposed the Evolutionary Species Concept (ESC): *"A lineage...evolving separately from others and with its own evolutionary role and tendencies"*. De Queiroz (2007) expanded the ESC, asserting that the core idea is simple: a species is essentially an evolutionary lineage. He argued that what have historically been referred to as "species concepts" are merely different types of evidence for the separation of lineages. Any of the properties traditionally used to define species, such as reproductive isolation, a distinct mate recognition system, diagnosability, or genetic distance, can serve as evidence for the existence of a species. Consequently, since the fundamental property that defines species is fixed heritable differences, what we have previously called the Phylogenetic

Species Concept (PSC) should, in de Queiroz's framework, be more accurately referred to as phylogenetic evidence, which takes precedence in defining species. In other words, *"a species is an evolutionary lineage and may be recognised by having fixed (absolute) heritable differences from other species"*.

I.2. Phenetics

Alongside the debates about the definition of a species, other concepts were also developed over the years. Phenetics, or numerical taxonomy, emerged in the 1950s as a method to group species based on overall similarity, particularly in observable traits like morphology, without regard to evolutionary history or phylogeny. Later, Sokal and Sneath (1963) defined numerical taxonomy as the process of quantitatively evaluating the similarity or affinity between taxonomic units and organising them into groups based on these affinities. The primary goals of numerical taxonomy are repeatability and objectivity. Repeatability aims to ensure that different taxonomists using the same methods and data achieve consistent results, eliminating biases in interpretation. Objectivity refers to minimising subjective assumptions about which traits are important or how they should be weighed, leading to classifications that are less influenced by personal biases. Despite this, researchers follow the morphological species concept: *"A species is a systematic unit which is considered a species by a competent systematist (preferably a specialist of the group)"* (Mayr, 1942, p. 115). According to Sokal and Sneath, the foundation of numerical taxonomy lies in the use of standardised methods for data analysis and classification, reducing subjectivity (Nixon, 2001).

Sokal and Sneath outlined six axioms for constructing classifications, which include the idea that the best taxonomy is based on the maximum number of characters to increase the information content, that all characters should be treated equally, and that similarity between entities is determined by comparing multiple characteristics. They emphasised that taxonomy should be empirical, with affinity estimates independent of phylogenetic considerations. In their view, alpha taxonomy focuses on constructing classifications that are not necessarily linked to evolutionary relationships, distinguishing it from methods aimed at inferring phylogenetic histories.

There are two primary approaches in phenetic analysis: clustering methods, which generate tree diagrams, and ordination methods, which plot species on multiple axes. Both methods treat all similarities equally, whether derived or primitive. Similarity coefficients, ranging from 0 (no similarity) to 1 (identical), are calculated between pairs of organisms and used to create a similarity matrix, which is then represented as a phenogram, a tree-like diagram illustrating phenetic

relationships (Choudhuri, 2014). Phenetics assumes that species with greater similarity are more likely to be related, but it does not rely on evolutionary considerations to form these groups.

This realisation led to the development of alternative methods, including phylogenetic analysis, which focuses on the reconstruction of evolutionary relationships through more rigorous methods like phylogenetic systematic.

I.3. Phylogenetic systematic

In 1950, Willi Hennig formalised phylogenetic systematics, also known as Cladistics. Over time, this approach developed into a broader research programme that has been widely adopted by evolutionary biologists seeking to understand both patterns and mechanisms of evolution. As the framework spread across disciplines, researchers began applying it with different methodological perspectives and data types, which in turn led to the emergence of a range of quantitative techniques. The validity and interpretation of these methods remain topics of ongoing discussion.

A central idea in many phylogenetic methods is the principle of parsimony (from the Latin *parcere*, meaning “to spare”), sometimes described as a preference for simplicity. This principle is often associated with the medieval philosopher William of Ockham (ca. 1285–1349), and is traditionally expressed through formulations such as *pluralitas non est ponenda sine necessitate* (“plurality should not be assumed without necessity”) and *entia non sunt multiplicanda praeter necessitatem* (“entities should not be multiplied beyond necessity”) (Folinsbee et al., 2015). In evolutionary biology, parsimony is generally used as an epistemological guideline, favouring explanations that require the fewest additional assumptions when interpreting data. This does not imply that nature itself is necessarily simple. A contrasting ontological interpretation can be traced back to Aristotle (350 BCE) who suggested that natural processes tend to operate in the most direct way possible and that, when sufficient, simpler explanations are preferable (Charlesworth, 1956). From this perspective, simplicity may be considered a property of nature itself rather than solely a methodological preference.

A major conceptual contribution of Hennig (1950, 1966) was the proposal that similarity between organisms should initially be interpreted as homology, shared traits derived from common ancestry, unless evidence suggests otherwise. This idea, later termed Hennig’s Auxiliary Principle, is closely aligned with earlier evolutionary thinking. For instance, Darwin (1859, p. 13) argued that inheritance should be regarded as the norm rather than the exception, and also noted that affinities between

groups are generally broad rather than narrowly specific (Darwin, 1872, p. 409). Within Hennig's framework, the goal is to maximise interpretations of similarity as homology while minimising explanations based on homoplasy (independent similarity). Parsimony plays a key role in this reasoning by discouraging unnecessary assumptions of repeated or independent evolutionary origins. In an idealised scenario where evolution strictly followed the simplest possible pathways, all characters would perfectly reflect true phylogenetic relationships, with no conflicting signals across traits, meaning homoplasy would be absent (Folinsbee et al., 2015).

However, Hennig's Auxiliary Principle also acknowledges that such conflicts are expected in real data. Phylogenetic analysis therefore involves selecting hypotheses that minimise assumptions of repeated evolution (homoplasy) in favour of shared ancestry (homology). In this sense, both parsimony and the Auxiliary Principle function as essential tools for reconstructing evolutionary history. If all similarities were interpreted as homoplasy, evidence for common descent, and thus evolution itself, would disappear. Consequently, phylogenetic methods must be capable of distinguishing between competing evolutionary explanations. When applied consistently, the Auxiliary Principle effectively converges with the principle of parsimony as a methodological strategy (Farris, 1983; Wiley et al., 1991). Wiley (1981; Wiley and Lieberman, 2011) summarised the foundations of phylogenetic inference in four assumptions: (1) evolution has occurred and is reflected in organismal traits; (2) species are unique combinations of ancestral, derived, and unique characters; (3) prior to analysis, the distinction between homologous and homoplastic traits is unknown; and (4) the true phylogenetic relationships and rates of divergence are also unknown (Folinsbee et al., 2015).

Modern phylogenetic reconstruction employs a variety of quantitative approaches applied to different data types. These methods are generally divided into two broad categories: parsimony-based approaches, which rely on epistemological simplicity, and likelihood-based approaches, which can be interpreted in terms of ontological assumptions about evolutionary processes.

In 1965, Camin and Sokal developed one of the earliest computer-based parsimony methods, marking a significant shift in systematic biology and challenging phenetic approaches (Sokal and Sneath, 1963). Shortly thereafter, Kluge and Farris (1969; Farris, 1970) introduced improved algorithms for identifying the most parsimonious trees from sets of possible phylogenies. Their "Wagner parsimony" method was named after W. H. Wagner, whose earlier ground plan-divergence approach (Mitchell, 1901, 1905; Wagner, 1952, 1961, 1969, 1980), provided an important

conceptual foundation. Importantly, Kluge and Farris (1969) emphasised that parsimony in this context is not a claim that evolution itself is simple, but rather a criterion for choosing among competing hypotheses. Farris further distinguished this phylogenetic approach from phenetic methods by focusing on shared derived characters and their evolutionary interpretation (see, Figure 1). Unlike earlier tree-based representations, Wagner parsimony initially generates a network that does not assume any taxon to be ancestral. Farris later proposed that such networks could be rooted post hoc, thereby converting them into phylogenetic trees by selecting a specific lineage or segment as the point of reference.

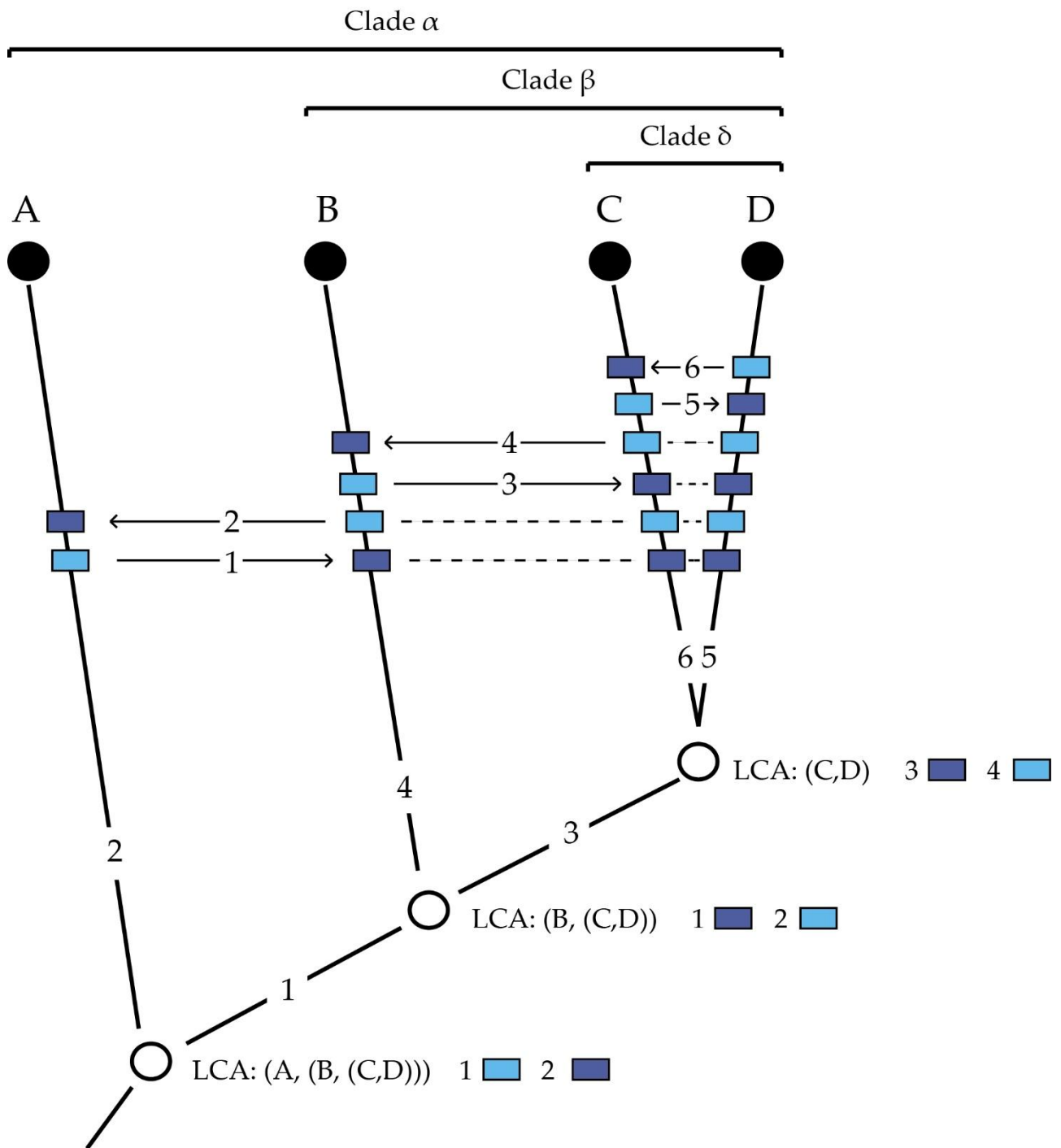


Figure 1: Schematic representation of phylogenetic systematics. The diagram illustrates the evolutionary relationships among four terminal taxa (A–D) based on six characters (1–6), each expressed in either a plesiomorphic (“primitive,” light blue) or apomorphic (“derived,” dark blue) state. Monophyletic groups are defined by shared derived characters, for instance, taxa B, C, and D share character 1, while C and D share characters 1 and 3. The morphology of ancestral nodes (last common ancestors, LCAs) can be inferred, such as the last common ancestor of taxa C and D, which exhibits character 3 in the derived state and character 4 in the primitive state. (Modified from Hennig, 1965, p. 106, Fig. 3).

I.4. Cladistic analysis in palaeoanthropology

Phylogenetic systematics has become a central tool across many domains of evolutionary biology, driving important advances in how evolutionary relationships and patterns are understood. In palaeoanthropology, however, its uptake has remained comparatively limited (Nunn, 2011). Researchers in this field have often favoured more interpretive approaches, constructing evolutionary scenarios by informally integrating temporal, geographic, and selected anatomical evidence (Strait, 2013). While such methods can be insightful, they differ fundamentally from phylogeny-based approaches, which provide a formal framework for proposing and rigorously testing evolutionary hypotheses, often generating perspectives that would not emerge from intuition alone. Although still not widely adopted, phylogenetic methods have been applied in several studies of primate evolution (e.g., Berger et al., 2010; Chamberlain and Wood, 1987; Kimbel et al., 1988, 2004; Lieberman et al., 1996; Martín-Torres et al., 2007; Strait et al., 1997; Strait and Grine, 2004; Walker et al., 1986; Wood, 1991, 1992a). For example, Kimbel et al. (2006) used phylogenetic analysis with operational taxonomic units (OTUs) based on geographical location to test the hypothesis that *Australopithecus anamensis* was the direct ancestor of *A. afarensis*. Their findings were consistent with the hypothesis of direct ancestry, supported by the temporal succession of the taxa and the absence of derived traits in *A. anamensis* that are also lacking in *A. afarensis*. In another example characterized *Homo erectus* as a geographically widespread and morphologically diverse species composed of regionally successive populations (“allotaxa”). Such propositions can be more thoroughly assessed within a phylogenetic framework, which also enables reconstruction of ancestral character states and broader interpretations of morphological change within lineages.

Applying phylogenetic approaches to the primate fossil record raises several ongoing questions. Among the most prominent are how morphological characters should be selected and defined, whether hominin evolution is better described as a gradual transformation within a single lineage (anagenesis) or as a branching process involving multiple speciation events (cladogenesis), how geometric morphometric data might be incorporated into analyses, and what role ancient DNA can play in reconstructing relationships among more recent human groups (Folinsbee et al., 2015).

The introduction of cladistic methods into the study of hominin evolution dates back to Eldredge and Tattersall (1975), who, along with collaborators, outlined a sequence of steps for phylogenetic reconstruction, from producing simple cladograms to building comprehensive evolutionary

scenarios (Delson et al., 1977; Tattersall and Eldredge, 1977). Early applications during the late 1970s and early 1980s were relatively straightforward, typically emphasizing the identification of a limited number of shared derived characters and the construction of basic branching diagrams (Andrews, 1984; Bonde, 1977; Delson, 1985; Grine et al., 1987; Lockett and Szalay, 1975; Olson, 1978; Wood et al., 1986). Despite their simplicity, these studies marked an important shift by explicitly distinguishing between derived and ancestral traits, improving methodological clarity over earlier approaches.

A major methodological advance occurred in the mid-1980s with the adoption of quantitative cladistic techniques to the study of hominin evolution. The use of computer algorithms allowed researchers to assess numerous traits and compare thousands of possible phylogenetic trees, a task that had previously been impractical. Chamberlain and Wood (1987) were among the first to apply numerical methods to analyse hominin phylogeny, followed by Stringer (1987) who focused on the genus *Homo*. Other studies of hominin and primate phylogeny employed similar techniques (Fleagle and Kay, 1987; Kay et al., 1997; Ross et al., 1998; Strait et al., 1997). The criticisms made by Trinkaus (1990) regarding the irrelevance of applying cladistics in palaeoanthropology, due to *"its biological limitations are too abundant for it to be more than a heuristic device for the preliminary ordering of complex human paleontological and neontological data"*, have slowed its application in palaeoanthropology. However, these criticisms are largely unfounded, confusing the nature of evolutionary processes with that of the scientific method on one hand, and also applying to all other methods (Tassy, 1996) then, since 1994, a significant number of new hominin fossils were discovered and new species were created (e.g., Asfaw et al., 1999; Brunet et al., 1996, 2002; Gabounia et al., 2002; Haile-Selassie et al., 2004; Leakey et al., 1995, 2001; Ward et al., 2001; White et al., 1994) that legitimates the use of cladistics. While it was believed that these discoveries would help clarify ongoing phylogenetic debates, many of these new finds (fossils and species) raised more questions than they resolved. Although each new fossil typically came with its own phylogenetic hypothesis, these often focused on relationships among only a few taxa. As a result, testing these hypotheses using cladistic methods was challenging, as they often implied specific ancestor-descendant relationships without addressing the sister-group relationships necessary for a complete analysis. Additionally, many of these fossils had not yet been fully published, and further morphological data were needed to enable more thorough and comprehensive analyses.

Key-points I.1.1

Evolutionary processes:

- Simpson (1944): distinguished between
 - Anagenesis (evolution within a lineage)
 - Cladogenesis (splitting of lineage → speciation)
- Eldredge and Gould (1972): Proposed Punctuated Equilibrium (PE) – long stasis punctuated by rapid speciation, challenging gradualism.
- Pre-1972: Fossil record often interpreted as evidence of gradual change; lack of change blamed on incompleteness of fossils.

Species concepts:

- Species = fundamental unit in ecology, conservation, and possibly evolution.
- Many definitions exist:
 - Biological Species Concept (BSC) – reproductive isolation defines species (Dobzhansky, Mayr).
 - Limitation: not applicable to fossils/museum specimens (only patterns observable).
 - Phylogenetic Species Concept (PSC) – smallest diagnosable cluster with at least one fixed heritable difference (Cracraft).
 - Highly operational, widely used in palaeontology.
 - Evolutionary Species Concept (ESC) – species as separate evolving lineages (Simpson; expanded by de Queiroz).
 - Species defined by heritable differences, with other traits as supporting evidence.
- Debate: *Pattern vs. process* → observable characteristics vs. underlying mechanisms of species formation.

Phenetics (numerical taxonomy):

- Emerged in 1950s: groups species based on overall similarity (ignoring phylogeny).
- Sokal and Sneath (1963): Six axioms for objective classification, stressing equal weighting of characters, repeatability, and independence from evolutionary assumptions.
- Methods:
 - Clustering → tree diagrams.
 - Ordination → species plotted on axes.
- Products: Phenograms (tree-like diagrams of similarity).
- Limitation: doesn't capture evolutionary relationships → led to rise of phylogenetic methods.

Phylogenetic systematics (cladistics):

- Willi Hennig (1950): Founded cladistics; emphasised homology (shared ancestry) vs. homoplasy (parallel evolution).
- Auxiliary Principle: Assume homology unless evidence suggests otherwise.
- Relies on parsimony (simplest explanation preferred).
- Key algorithms:
 - Camin and Sokal (1965): first computerised parsimony analysis.
 - Kluge and Farris (1969): Wagner parsimony → rigorous tree searches.
- Assumptions of phylogenetics: evolution occurred; species are unique trait combinations; character homology unknown prior to analysis; divergence rates unknown.
- Methods: parsimony vs. likelihood.

Cladistic analysis in palaeoanthropology:

- Adoption slower than in other evolutionary fields; many relied on intuitive methods.
- Applications:
 - Eldredge and Tattersall (1975): first hominin cladistic analysis.
 - 1980s: shift from simple cladograms → quantitative, computer-based analyses.
 - Used to test hypotheses (e.g., *A. anamensis* as ancestor of *A. afarensis*; *H. erectus* as widespread variable species).
- Key challenges:
 - Selecting appropriate morphological characters.
 - Debate: gradual lineage evolution (anagenesis) vs. branching speciation (cladogenesis).
 - Integrating geometric morphometrics and ancient DNA.
- New fossil discoveries since 1994 expanded data but often raised new questions rather than resolving debates.

Key-points I.1.2

Core concepts:

- Cladistics: A method of classifying organisms based on shared derived characters (synapomorphies) to reconstruct evolutionary relationships.
- Clade: A monophyletic group, an ancestor and *all* its descendants.
- Character: Any observable trait or feature that can vary among taxa (morphological, molecular, behavioural, etc.).
- Character state: The specific condition of a character (e.g., “presence” vs. “absence” of a trait).

Homology vs. homoplasy:

- Homology: Similarity due to *shared ancestry* (e.g., forelimbs of bats and whales).
- Homoplasy: Similarity not due to shared ancestry, but to *convergent evolution, parallelism, or reversal*.
 - Convergence: Independent evolution of similar traits in unrelated lineages.
 - Parallelism: Similar traits evolve independently in closely related lineages.
 - Reversal: Reappearance of an ancestral trait by loss of a derived condition.

Types of characters:

- Plesiomorphy: Ancestral character state (not informative for relationships).
- Apomorphy: Derived character state (evolutionary novelty).
 - Synapomorphy: Shared derived state → defines clades.
 - Autapomorphy: Unique derived state → identifies a single lineage.

Three criteria for recognizing homology:

1. Position criterion: Same relative position in structure/organism.
2. Specific quality criterion: Similarity in fine structure or details.
3. Continuity criterion: Intermediate forms or developmental/phylogenetic continuity.

Principle of parsimony:

- Parsimony: The simplest explanation (fewest evolutionary changes) is preferred.
- Used to select the *most likely* phylogenetic tree (the one minimizing total changes in character states).

Tree interpretation:

- Nodes = common ancestors
- Branches = lineages
- Rooted tree = shows direction of evolution (ancestor → descendants)
- Unrooted tree = shows relationships without ancestral direction

II. Morphometrics, geometric morphometrics and virtual anthropology

II.1. Morphometrics

Morphological data constitute a fundamental source of information across a wide range of disciplines, including the natural sciences, materials science, and engineering. In biological contexts, variation in form can reflect processes such as pathology, development, environmental adaptation, or evolutionary divergence. More broadly, differences in form often signal underlying mechanisms, whether functional specialisation, responses to selective pressures, or distinct developmental pathways. Consequently, analysing form is essential for interpreting both the causes and significance of morphological diversity (Zelditch et al., 2004).

Form is typically understood as comprising two interrelated components: size and shape. Size refers to the overall scale of an object and is quantified using measurements such as length, width, height, area, volume, or mass, often in relation to a standard reference. Shape, in contrast, captures the geometric properties of an object independent of its scale and is frequently described by comparison to reference configurations or familiar geometries. Such comparisons can help highlight key structural features, particularly when dealing with complex or unfamiliar forms.

Beginning of the 1970's, these data were analysed through methods called traditional morphometrics, also known as multivariate morphometrics (Blackith and Reyment, 1971; Marcus, 1990; Reyment, 1990), which used multivariate statistical analyses of morphological traits such as linear distances, ratios, counts, and angles. Methods like Principal Components Analysis (PCA), Canonical Variates Analysis (CVA), and discriminant function analysis were used to explore patterns of covariation, often focusing on allometry, or how shape changes with size (Jolicœur, 1963).

However, traditional morphometrics had several limitations. Size correction methods varied and often led to differing results, causing debate over best practices. Additionally, many measurements lacked anatomical homology, and geometric relationships between features were often lost (Adams et al., 2004). For example, two shapes such as an oval and a teardrop might share identical height and width values yet differ markedly in form, something that is difficult to capture with linear measurements alone. Furthermore, graphical reconstructions of shape were generally not possible

from linear data, as the spatial configuration of measurements was not preserved (Bookstein et al., 1985).

In the late 1970s and early 1980s, there was a renewed interest among researchers in graphical approaches to morphological analysis that had been prominent in earlier decades. During this period, Bookstein introduced his approach based on Cartesian transformations, providing a novel way to represent shapes mathematically (Bookstein, 1977). Meanwhile, Oxnard investigated innovative applications drawing from fields such as mathematical optics, biomechanics, and computer vision, expanding the analytical toolkit available for studying biological form (Oxnard, 1978). Additionally, Blum developed and evaluated the concept of the "medial axis," a method designed to capture the fundamental structure of shapes (Blum, 1973; Blum and Nagel, 1978). Despite the introduction of these diverse and promising graphical techniques, progress in the statistical methods used to summarise and rigorously test relationships between shape data and biological variables, traditionally framed within the narrower field of biometrics, did not advance at a comparable pace. This gap highlighted the need for integrated approaches that combined powerful visualization tools with robust quantitative analysis (Rohlf and Bookstein, 1990).

II.2. Geometric morphometrics (GMM)

A major breakthrough came with the statistical theory of shape introduced by D. Kendall and further refined by others, which enabled the integration of multivariate statistics with biologically meaningful visualisations (Bookstein, 1996; Kendall, 1977). At the heart of this framework lies a precise definition: shape refers to all the geometric information that remains once position, scale, and rotation of an object have been eliminated. This definition, foundational to modern geometric morphometrics, allows researchers to compare biological forms consistently and meaningfully. Kendall's (1981, 1984) introduction of shape manifolds changed the understanding of the geometric properties of shape and its relationship to size. His work also paved the way for developing statistical methods to summarise shape variation, describe shape transformations, and test for shape similarity. By showing that linear distance data and boundary outlines can be represented through configurations of Cartesian coordinates, Kendall's contribution bridged the gap between the three traditional approaches to morphometric analysis, highlighting their underlying unity (MacLeod, 2017). Bookstein referred to this conceptual integration as the morphometric synthesis (Bookstein, 1996), while (Rohlf and Marcus, 1993) described it as the beginning of a morphometric revolution.

In the early 1980s, researchers such as Bookstein, Goodall, and Kendall, each developed a statistical approach that fully used the information contained in sets of landmark coordinates. Although this convergence of ideas was only formally communicated to the statistical community as early as 1986, Bookstein's comprehensive treatment of the subject, *Morphometric Tools for Landmark Data*, was not published until 1991 (Bookstein, 1991). It has since become apparent that the earlier "multivariate morphometrics," which was thought to analyse distances and angles, was in fact fundamentally concerned with the analysis of landmark location data. Similarly, methods focusing on outlines were effectively summarising relationships among corresponding points analogous to landmarks, and graphical superimposition techniques were approximate visual representations of these underlying statistical concepts (Rohlf and Bookstein, 1990).

Morphometric approaches, methods quantifying shape using mathematical and statistical methods, provide a systematic and objective means of comparing biological structures, offering a level of precision not possible through visual analogy alone. While morphometric data may appear abstract, typically expressed as numerical matrices or statistical outputs, they enable reproducible and quantifiable analyses of morphological variation. In doing so, morphometrics aligns shape analysis more closely with disciplines such as geometry and statistics, without abandoning the biological questions at its core (Zelditch et al., 2004).

Therefore the "revolution" in morphometries is more a synthesis of developments in shape theory, the recognition of landmarks' coordinates as manageable data with analytical approaches using multivariate statistics. Through these revolutions, geometric morphometrics emerged as a powerful and flexible framework, allowing researchers to measure, visualise, and analyse shape with unprecedented precision. Its continued development has transformed how scientists investigate form and function, bridging the gap between biological morphology and mathematical theory.

The applicability of this theoretical model to biological research depends on how well this mathematical definition reflects the intuitive concept of shape used by biologists. Moreover, because shape and size are closely intertwined, understanding one necessitates an understanding of the other and of their interaction. Size, typically represented by centroid size in GMM, is mathematically independent of shape, though the two often covary in biological systems (Bookstein et al., 1985). Thus, while researchers may mathematically separate shape and size, their empirical relationship remains an essential subject of study (Jungers et al., 1995; Sundberg, 1989).

II.3. Virtual anthropology

Advances in computing and imaging technologies over the past two decades have further transformed morphometric analysis, particularly through the development of geometric morphometrics (GMM) and related tools. These innovations have enabled detailed, high-resolution studies of both external and internal anatomical structures. A major objective has been to capture morphological variation quantitatively while ensuring that datasets are reproducible, shareable, and suitable for complex statistical analysis (Weber, 2015). The term “virtual anthropology” (VA) was first introduced by (Weber et al., 1998), with an expanded definition later presented by Weber and Bookstein (2011). VA is referring to a multidisciplinary approach that uses digital technologies to study morphology, especially that of humans and their relatives, in three or four dimensions.

These new approaches presented new opportunities, such as easy access to spatial information. 3D methods, for instance, provide far richer spatial details than traditional 2D images or projections. VA often relies on 3D technologies for data collection, which in turn necessitates the development of algorithms capable of processing such data effectively. Many researchers contributed to their development, including Fleagle and Simons (1982), who used computed tomography (CT) to examine the long bones of an Oligocene primate; Wind (1984), who worked on the *Pithecanthropus* IV fossil from Java using 2D tomographic slices; or Conroy and Vannier (1984, 1987), who employed 3D CT data to digitally remove matrix from a fossil and investigate the cranial cavity and later, the dental development of the Taung child (Weber, 2015). Later, Zollikofer et al. (1995) virtually reconstructed Neandertals and other fossils.

A defining feature of virtual anthropology is the use of digital models rather than physical specimens. These “virtual” objects allow researchers to investigate morphology in ways that were previously impossible. For example, internal structures, such as brain cavities, sinuses, or trabecular bone, can be examined non-destructively. Digital datasets can be stored, shared, and reanalysed indefinitely, enabling broader collaboration and reproducibility. High-density spatial data also allow for more detailed and powerful quantitative analyses, while computational tools facilitate flexible visualisation and statistical modelling (Weber, 2015):

Virtual anthropology provides the technological foundation of the 21st century for working with digital replicas of specimens. This approach allows for analyses of shape and size based on a comprehensive and quantitative framework that captures the full geometry of an object. By

visualising changes in form, it enhances understanding through its intuitive nature, supports reproducible, database-driven reconstructions, and facilitates the expansion of sample sizes through data sharing.

While these innovations have significantly advanced comparative morphology, there are overlaps with other emerging digital techniques. For example, phylogeny, which rely on shared characters, would benefit greatly from integrating virtual imaging. The algorithms needed to fully integrate these two areas are still under development. However, combining these fields could give rise to a new dimension of computer-based analysis.

II.4. Geometric morphometrics in palaeoanthropology

In recent years, with the development of virtual anthropology (VA), the use of geometric morphometrics (GMM) has significantly increased in paleoanthropological research (Slice, 2005, 2007). This methodological framework focuses on the quantitative analysis of biological shapes using landmark coordinates, enabling researchers to carry out robust multivariate statistical analyses (Slice, 2007). The flexibility of GMM makes it applicable to various research areas, including functional morphology, growth and development, allometry, intraspecific and interspecific variation, and evolutionary relationships.

In some studies, GMM-derived data are directly incorporated into phylogenetic analyses during the character coding phase. For instance, Cardini and Elton (2008) employed 3D geometric morphometrics to investigate the phylogenetic signal in different cranial regions of guenon monkeys. Similarly, Gilbert (2011) applied 3D morphometric techniques to identify phylogenetically informative features in the basicranium of papionines. By accounting for allometric effects, he isolated shape differences that could be used to construct phylogenetic characters. Von Cramon-Taubadel and Smith (2012) also used GMM to explore whether different parts of the hominoid skull reliably reflect evolutionary relationships. Their analysis showed that cranial shape variation and molecular phylogenies led to consistent patterns, suggesting that geometric morphometrics can provide evolutionary insights that are complementary to those derived from genetic data.

Other research approaches involve mapping morphological shape variation onto phylogenetic trees that have been generated without shape data. This approach allows researchers to interpret morphological evolution within the context of an independent evolutionary framework (e.g., Fleagle et al., 2010; Wiley et al., 2005). For example, Wiley et al. (2005) employed 3D landmark data from

primate skulls to generate mean shape configurations associated with molecular phylogenies. However, their approach produced generalized averages rather than true reconstructions of ancestral shapes along the phylogenetic tree. These reconstructions provide valuable insights into morphological changes over time and allow for the estimation of ancestral traits at key evolutionary nodes (Nunn, 2011; Wiley et al., 2005).

The increasing availability of computational resources and advancements in statistical software have further propelled the development of geometric morphometrics.

Key-points I.2

Morphometrics – general concepts:

- Morphology provides key insights in biology, medicine, engineering, and materials science.
- Form = size + shape:
 - Size: physical dimensions (length, area, volume, etc.).
 - Shape: geometric attributes once location, scale, and rotation are removed.
- Morphological variation often reflects function, adaptation, or developmental processes.

Traditional morphometrics (1970s):

- Relied on multivariate statistics (PCA, CVA, discriminant function analysis).
- Focused on linear distances, ratios, counts, angles.
- Issues:
 - Inconsistent size correction methods.
 - Lack of anatomical homology.
 - Geometric relationships lost (linear data can't fully capture shape).
 - No graphical reconstructions possible.

Early graphical and mathematical approaches (1970s–1980s):

- Bookstein: Cartesian transformations for shape representation.
- Oxnard: Applied mathematical optics, biomechanics, computer vision.
- Blum: “Medial axis” to capture core structure of shapes.
- Progress slowed due to weak integration of visualization with robust statistical testing.

Geometric morphometrics (GMM) – revolution:

- Kendall (1977, 1980s): Statistical theory of shape; shape = geometry independent of scale, position, rotation.
- Introduced shape manifolds, allowing rigorous statistical comparisons.
- Bookstein (1991): Landmark-based analysis → comprehensive framework.
- Integration of multivariate statistics + visualization = morphometric synthesis.
- Advantages:
 - Landmarks and outlines analysed as coordinate data.
 - Shape variation and transformation testable quantitatively.
 - Bridges traditional methods into one coherent system.
- Key distinction: *size* (centroid size) is mathematically independent of shape but biologically correlated (allometry).

Virtual anthropology (VA):

- Emerged with GMM + digital imaging (CT, 3D scans).
- Definition (Weber and Bookstein, 2011): Multidisciplinary study of morphology in 3D/4D (humans + relatives).
- Key advantages:
 1. Access to internal and hidden structures (e.g., braincase, sinuses, trabeculae).
 2. Digital preservation of specimens.
 3. Dense quantitative datasets.
 4. Flexible data management, visualisation, and sharing.
 5. High reproducibility.
- Applications: early CT uses (1980s), virtual fossil reconstructions (1990s), database-driven comparative morphology today.
- Potential: integration with phylogenetics for evolutionary reconstructions (algorithms still developing).

Geometric morphometrics in palaeoanthropology:

- GMM + VA increasingly applied in paleoanthropological research.
- Applications:
 - Growth, functional morphology, variation, evolutionary relationships.
 - Direct incorporation into phylogenetic analyses (e.g., cranial studies in monkeys and papionines).
 - Mapping shape variation onto independent phylogenetic trees (ancestral reconstructions).
- Findings: cranial shapes often strongly congruent with molecular phylogenies (e.g., hominoids).
- Advancements in computational power and software have further expanded GMM's utility.

III. GMM in cladistics: controversies, what has been done and what problems remains

Cladistics is a method of phylogenetic inference that favours the hypothesis which explains the greatest number of observed similarities as inherited from a common ancestor, thereby minimizing instances of homoplasy, similarities not due to shared ancestry. Traditional cladistic analyses have predominantly relied on discrete morphological characters, considered to reflect heritable and evolutionarily informative variation.

However, a large portion of phenotypic variation in organisms is continuous rather than discrete, particularly regarding shape. Geometric morphometrics provides a powerful framework for quantifying and analysing shape through the use of landmark data. Despite its potential to enhance morphological analyses, the integration of GMM data into cladistics has remained contentious due to theoretical, methodological, and computational challenges. This approach therefore seems desirable, but many points remain under discussion.

III.1. Core controversies in using GMM data for phylogenetic inference

One of the earliest obstacles to incorporating GMM data into cladistics was the association of continuous variables with phenetics, a method that clusters taxa based on overall similarity without regard to evolutionary history. In contrast, cladistics requires that similarities be interpreted as shared derived characters (synapomorphies) explained by common descent. A more substantial concern lies in the heritability of continuous characters. It has been argued that shape, being subject to environmental influence, may not reliably reflect underlying genetic relationships (Adams et al., 2004; MacLeod et al., 2002a). However, this critique also applies to many discretized traits. In both cases, systematists rely on informed judgment to select characters deemed to reflect heritable differences. Importantly, discretizing continuous morphological variation often entails a loss of information and introduces subjective biases, as observed in other methodological approaches. Discretization can obscure gradients of similarity, enforce arbitrary thresholds between states, and reflect prior assumptions about phylogenetic relationships.

Another fundamental issue in using GMM data is the question of homology. As Bookstein (1994) pointed out, homology is a binary concept: features are either homologous or not. In contrast, shape

exists on a continuum. Determining whether shape similarity reflects shared ancestry or convergence becomes ambiguous when dealing with high-dimensional continuous data.

III.2. Proposed methods for integrating shape into phylogenetic analysis

Over the years, several methodological frameworks have been proposed to incorporate geometric morphometric data into phylogenetics.

In the early 2000, the first methods proposed were distance-based and phenetic approaches, like UPGMA and Neighbour-Joining. These methods grouped taxa according to overall morphological similarity derived from Euclidean distances between landmark configurations. However, because they are based on pairwise similarity rather than shared derived characters, they do not constitute true phylogenetic (cladistic) analyses and cannot reconstruct ancestral states (Monteiro, 2000).

Subsequent efforts focused on incorporating morphometric variables into explicitly phylogenetic frameworks. One direction involved the use of shape variables derived from thin-plate spline analysis, Partial Warp scores (Rohlf, 2002), as potential characters. While these scores capture local deformations relative to a consensus shape, they have rarely been used in cladistics due to limited biological interpretability and sensitivity to reference choice. A more explicitly phylogenetic use of morphometric data emerged with the proposal to employ Principal Component (PC) scores as continuous characters in cladistic analysis (González-José et al., 2008). Although this method provided a way to integrate high-dimensional shape data into phylogenetic trees, it was later criticized (see, Adams et al., 2011, 2013). PCA reduces high-dimensional landmark data into fewer axes of variation. However, PCA scores are statistically derived, and their use as phylogenetic characters is problematic, as they may not correspond to meaningful morphological changes.

In 2010, a new method was developed, Square-Change Parsimony on Procrustes Coordinates (Klingenberg and Gidaszewski, 2010). This method seeks the tree minimizing the sum of squared shape changes across branches. While computationally feasible, this approach lacks an explicit phylogenetic model and does not conform to the parsimony criterion as defined by Farris (1983), since it minimizes global similarity rather than homology.

With the advancements in Bayesian and Likelihood-Based methods, the incorporation of landmarks into phylogenetic analyses was developed, with several key-study:

- Revell et al. (2015): implemented in the 'phytools' R package a wide range of methods for phylogenetic analysis, focusing on phylogenetic comparative biology. These methods also assume Brownian motion and use a fixed topology to estimate ancestral states via maximum likelihood. It is limited to tree calibration scenarios and does not allow full topology search (see also, Revell, 2024).
- Parins-Fukuchi (2018): each landmark coordinate is treated as an individual continuous character assumed to evolve under Brownian motion. A Bayesian framework is used to position fossils on a known topology. This approach permits probabilistic ancestral state reconstruction but assumes specific evolutionary models.
- Zhang et al. (2024): proposes a Bayesian framework that integrates continuous shape data, molecular sequences, and tip-dating. This method accounts for covariation among characters and estimates divergence times. While promising, it is computationally intensive and requires large, integrated datasets.

III.3. Persistent challenges and open problems

Despite methodological advances, several fundamental challenges persist. Landmark-based data are inherently high-dimensional and statistically interdependent. Methods such as Procrustes superimposition introduce dependencies between landmarks, violating the assumption of character independence that underlies many phylogenetic methods (Klingenberg and Monteiro, 2005; Rohlf, 1998).

The process of aligning landmark configurations across specimens (e.g., Procrustes superimposition) can distort biologically meaningful variation. There is currently no consensus on how best to align landmark data in a phylogenetic context.

Derived variables such as PCA scores or partial warps often lack clear biological interpretation. It remains unclear whether minimizing changes in such variables reflects meaningful evolutionary processes. Moreover, current methods do not fully align with the optimality principles of cladistics, such as minimizing ad hoc hypotheses and maximizing explanatory power.

The integration of geometric morphometric data into phylogenetic analysis remains a complex and evolving frontier in systematics. While Bayesian and likelihood-based approaches offer promising avenues, they rely on strong assumptions and are computationally demanding.

Key-points I.3

Cladistics and morphology:

- Cladistics: favours hypotheses explaining similarities as inherited from a common ancestor, minimizing homoplasy.
- Traditionally relied on discrete morphological characters (binary/categorical traits).
- Challenge: much phenotypic variation is continuous (shape) → better captured by Geometric Morphometrics (GMM).

Core controversies in using GMM for cladistics:

- Association with phenetics: Continuous data risk being treated as overall similarity, not synapomorphies.
- Heritability concerns: Shape influenced by environment; reliability as genetic marker debated.
- Discretization issues: Simplifying continuous variation loses information, imposes subjective thresholds.
- Homology problem: Homology is binary, but shape is continuous → difficult to distinguish ancestry vs. convergence.

Proposed methods for integrating GMM data:

1. Distance-based (early 2000s)
 - UPGMA, Neighbour-Joining (based on Euclidean distances).
 - Weakness: phenetic, not cladistic; no ancestral state reconstruction.
2. Scores-based methods
 - Partial Warp scores (Rohlf 2002): derived from thin-plate spline analysis; criticised for lacking biological interpretability and reference-dependence.
 - PCA scores (González-José et al. 2008): reduce dimensionality; criticised (Adams et al.) for being statistical artefacts, often reproducing phenetic groupings.
3. Square-Change Parsimony (2010, Klingenberg and Gidaszewski)
 - Minimises squared shape changes across tree branches.
 - Criticism: lacks explicit phylogenetic model, minimises similarity not homology.
4. Bayesian and Likelihood-based methods
 - Revell et al. (2015): ML ancestral state estimation under Brownian motion; limited to fixed topologies.
 - Parins-Fukuchi (2019): Bayesian treatment of landmarks as continuous characters evolving under Brownian motion; positions fossils on known trees.
 - Zhang et al. (2023): Bayesian framework integrating shape data + molecular data + tip-dating; promising but computationally heavy.

Persistent challenges:

- High-dimensional, interdependent data: Landmarks not independent → violates phylogenetic assumptions.
- Alignment issues: Procrustes superimposition can distort biologically meaningful variation.
- Interpretation problems: PCA/partial warps may not reflect real evolutionary processes.
- Optimality conflict: Current GMM methods don't fully align with cladistic principles (minimising ad hoc hypotheses, maximising explanatory power).

Takeaway:

- Integrating 3D geometric morphometric data into cladistics remains difficult.
- Advances in Bayesian and likelihood frameworks are promising but rest on strong assumptions and heavy computation.
- The field is evolving, but theoretical, methodological, and interpretive challenges persist.

IV. *Paranthropus*, *Australopithecus* and *Homo*: phylogenetic hypothesis and debates

Following the conceptual and methodological background, I will now provide a general overview of key paleoanthropological debates surrounding the genera *Paranthropus*, *Australopithecus*, and *Homo*, to contextualize the scientific questions explored in the chapters that follow.

In the first half of the twentieth century, a central question in palaeoanthropology revolved around the boundary between humans and apes. Most fossil specimens could be readily assigned to one category or the other, yet some, most notably *Australopithecus*, occupied intermediate positions, challenging researchers to decide whether they should be classified as apes or as early members of the human lineage. Earlier in the twentieth century, many scholars conceived the human lineage in narrowly taxonomic terms, often recognizing only *Homo sapiens* as truly “human,” while treating other fossil forms as peripheral or pre-human stages (as discussed in Tattersall, 1999). By the mid-twentieth century, this perspective shifted with the rise of the New Darwinian Synthesis. Human evolution came to be viewed as a continuous, unbroken sequence of forms, with observed differences interpreted primarily as intraspecific variation due to geographic distribution or sexual dimorphism (Brace, 1967; Buettner-Janusch, 1966). This perspective culminated in Mayr's (1950) influential proposal to classify all fossil hominins, including both robust and gracile australopithecines, within the genus *Homo*, reducing diversity to just three species. However, this linear and simplified view began to unravel in the 1970s. Fossil discoveries at sites such as Olduvai Gorge and Koobi Fora revealed the simultaneous presence of multiple hominin lineages, while new analytical techniques highlighted that evolution was not a straightforward, linear progression (Bräuer, 1982; Eldredge and Tattersall, 1975; Howells, 1975; Leakey, 1969; Leakey and Walker, 1976; Stringer, 1974, 1978). The identification of *Australopithecus afarensis* in 1978 (Johanson et al., 1978; Johanson and White, 1979) and the subsequent discovery of the “Black Skull” (KNM-WT 17000) in Kenya (Walker et al., 1986) underscored the substantial taxonomic and phylogenetic diversity among early hominins. These findings catalysed vigorous debates throughout the 1980s (Kimbel et al., 1984; Olson, 1981; Tobias, 1980; Wood, 1988). By the same decade, discussions regarding the relationships among *Homo sapiens*, Neandertals, and *Homo erectus* further demonstrated that human evolution followed a branching, rather than a linear, trajectory, characterized by diversity and coexistence.

The mid-1970s also marked a methodological transformation with the introduction of cladistic analysis into palaeoanthropology. Previously, evolutionary scenarios were often described as linear sequences or broad narratives, with little explicit justification for proposed phylogenetic relationships. Foundational works by Eldredge and Tattersall (1975), followed by Delson et al. (1977) and Tattersall and Eldredge (1977), established a rigorous framework for hominin systematics. This approach emphasized the construction of cladograms based on shared derived characters (synapomorphies), distinguishing these from primitive retentions, rather than relying solely on overall similarity or implicit notions of evolutionary progress.

The earliest cladistic studies of hominin evolution, conducted in the late 1970s and early 1980s, were relatively simple, often analysing a small set of morphological characters and producing qualitative tree reconstructions (Andrews, 1984; Delson, 1985; Grine et al., 1987; Olson, 1978; Wood et al., 1986). Despite their limitations, these studies marked a significant advance by providing explicit morphological justifications for each phylogenetic grouping. As Tattersall (1999) emphasized, cladistics promoted a more detailed and rigorous documentation of hominin morphology, in which competing hypotheses could be tested and potentially falsified through the discovery of new characters or the re-evaluation of existing traits.

By the mid-1980s, computational approaches began to complement qualitative analyses. Quantitative methods enabled researchers to assess dozens of traits simultaneously, evaluating thousands of possible phylogenetic trees for parsimony. This provided a systematic and reproducible framework for phylogenetic inference (Chamberlain and Wood, 1987; Stringer, 1987). These methodological innovations generated a wave of new analyses which, although differing in specific outcomes, gradually converged toward a limited set of alternative hypotheses regarding the relationships among early hominins.

IV.1. *Australopithecus*

The transition from Pliocene to Pleistocene (from ~5 Ma to ~0.012 Ma) saw a remarkable diversification of hominins across Africa. The genus *Australopithecus*, first established in the 1920s (Dart, 1925), has long functioned as a central category for accommodating gracile, small-brained, bipedal apes that predate and overlap with the earliest members of *Homo*. Nevertheless, the taxonomic cohesion of this genus and its phylogenetic relationships, both to the robust australopithecids (*Paranthropus*) and to early *Homo*, remain subjects of ongoing debate (Wood and Strait, 2004). The

richness of the African fossil record, particularly in eastern and southern regions, provides unprecedented insight into early hominin evolution but also presents significant interpretive challenges.

A dedicated section will address current perspectives on the phylogenetic positions of *A. afarensis*, *A. africanus*, and the robust australopiths. These taxa are emphasized here due to their comparatively well-preserved and extensively studied fossil remains, which make them pivotal to ongoing debates within the broader context of hominin taxonomy.

A. afarensis (ca. 3.9–2.9 Ma) is widely recognized as one of the earliest well-documented hominins, with a large sample drawn from Hadar, Laetoli, and other East African sites (Johanson et al., 1978; Kimbel et al., 2004). Phylogenetically, *A. afarensis* is frequently positioned as a stem taxon from which both robust australopiths and later *Homo* species may have derived (Kimbel et al., 2004). Its early chronological range and broad geographical distribution support its candidacy as a potential last common ancestor for multiple later lineages. Yet the species exhibits substantial intraspecific variation, and uncertainties regarding sexual dimorphism complicate phylogenetic interpretation (Lockwood, 1999).

A. africanus (ca. 3.0–2.0 Ma), discovered at Taung in 1924, serves as the type species of the genus (Dart, 1925). It is generally considered a descendant of *A. afarensis*, although its exact relationship to later hominins is contested. Some analyses place *A. africanus* as basal to both robust australopiths and *Homo* (Strait and Grine, 2004), whereas others argue it represents a distinct southern African lineage, separate from the ancestors of *Homo*.

IV.2. *Paranthropus*

The robust australopiths, traditionally assigned to the genus *Paranthropus*, represent one of the most distinctive evolutionary radiations among early hominins. They are defined by extreme craniofacial adaptations for heavy mastication, including massive jaws, enlarged post-canine teeth, flaring zygomatic arches, and sagittal crests, contrasting sharply with the more generalized, gracile australopiths (Broom, 1938; Rak, 2014; Wood and Constantino, 2007). Fossils of robust australopiths are found across eastern and southern Africa, spanning approximately 2.7 to 1.2 million years ago and overlapping temporally with both gracile australopiths and early *Homo* (Wood and Strait, 2004).

The monophyly of robust australopiths is widely supported, with most analyses suggesting they arose from an *A. afarensis*-like ancestor (Strait and Grine, 2004). Nonetheless, their taxonomic status

remains debated. While initially grouped within *Australopithecus*, the designation *Paranthropus* has increasingly been used to emphasize their morphological distinctiveness (Broom, 1938; Grine, 1986). Proponents argue that their specialized adaptations and ecological divergence justify a separate genus, whereas critics maintain that splitting them exaggerates differences that could fall within the range of a single diverse genus (Wood and Strait, 2004).

The robust clade is generally recognized as comprising three species: *Paranthropus aethiopicus*, *P. boisei*, and *Paranthropus robustus*.

P. aethiopicus (ca. 2.7–2.3 Ma), the earliest known robust australopith, is typically considered the basal member of the clade and is often viewed as the ancestor of *P. boisei*, reflecting morphological continuity in eastern Africa (Strait and Grine, 2004). However, its limited fossil record complicates assessments of intraspecific variation and evolutionary trajectory.

P. boisei (ca. 2.3–1.2 Ma), the best-documented robust australopith, is widely distributed across East African sites, including Olduvai, Koobi Fora, Omo, Chesowanja, and Konso (Wood, 1991). Phylogenetically, it is generally treated as the eastern descendant of *P. aethiopicus*, forming a clade distinct from southern African *P. robustus*.

P. robustus (ca. 2.0–1.2 Ma), found in multiple South African cave sites such as Swartkrans, Drimolen, and Gondolin, is often interpreted as an independent southern radiation from an *A. africanus*-like ancestor (Rak, 2014; Strait and Grine, 2004). This suggests a degree of parallel evolution, with eastern and southern robust australopiths converging on similar cranio-dental adaptations, though some analyses propose a common robust ancestor predating 2.5 Ma.

The taxonomic distinction of *Paranthropus* remains a focal point of debate. Broom (1938) emphasized their unique morphology in establishing the genus, and supporters highlight monophyly, dietary specialization, and divergence from gracile australopiths (Grine, 1986; Wood and Constantino, 2007). Critics contend that robust forms may represent an extreme subgroup within *Australopithecus*, analogous to subspecies variation, rather than a separate genus (Wood and Strait, 2004). This debate exemplifies broader tensions in palaeoanthropology between “splitter” and “lumper” approaches to classification.

Phylogenetic analyses have produced varying interpretations. Delson et al. (1977) recovered a trifurcation between *Australopithecus*, *Paranthropus* and *Homo*. Wood (1991, 1992a), using

craniometric data, recovered *A. africanus* as the sister taxon to *Homo*, with *H. habilis* and *H. rudolfensis* forming a basal *Homo* clade. *P. boisei* and *P. robustus* were recovered as a monophyletic *Paranthropus* group, with *P. aethiopicus* described as sister to *P. boisei*. Lieberman et al. (1996) in contrast, suggested *Paranthropus* was paraphyletic: *P. robustus* and *P. boisei* remained sister taxa, but *A. africanus* appeared nested within early *Homo*, implying it could be part of the *Homo* radiation rather than a side branch.

Subsequent analyses by Strait et al. (1997) and corroborated by Kimbel et al. (2004) supported a monophyletic *Paranthropus* as sister to *Homo*. Kimbel and colleagues reported two equally parsimonious trees: one consistent with Strait et al. (1997) and another placing *A. africanus* as sister to the *Paranthropus* clade rather than directly associated with *Homo*. These divergent results underscore persistent uncertainty regarding *A. africanus*, which has variously been interpreted as close to *Homo*, as part of *Paranthropus*, or as an independent lineage.

Overall, disagreements focus on a few critical points: the monophyly versus paraphyly of *Paranthropus*, the phylogenetic position of *A. africanus*, which bears on hypotheses about the origin and adaptive trajectory of robust australopiths, and the implications of these issues for interpreting early hominin diversity and ecological variation. While *Paranthropus* is widely treated as valid in modern analyses, its precise rank remains more a matter of convention than consensus.

IV.3. Emergence of the genus *Homo*

The phylogenetic reconstruction of early hominins remains one of palaeoanthropology's most debated topics. Taxonomic status for several taxa is contentious, and evolutionary interpretations vary substantially across studies.

The genus *Australopithecus* encompasses morphologically diverse species from the Pliocene (i.e. 5.3-2.58 Ma) and Early Pleistocene (i.e. 2.58-0.78 Ma) of East and South Africa, including *A. afarensis*, *A. africanus*, *A. anamensis*, and *A. sediba* (Kimbel et al., 2004, 2006). Species delimitation within the genus is controversial due to overlapping cranial, dental, and postcranial traits as well as intraspecific variation (Reed et al., 2013). *A. sediba* exemplifies this challenge: it exhibits a mosaic of primitive and derived features, leading some researchers to interpret it as a transitional species toward *Homo*, while others view it as reflecting local adaptation or variation within *Australopithecus* (Berger et al., 2010; Kimbel and Rak, 2017; Mongle et al., 2023).

The distinction between *Australopithecus* and *Paranthropus* is similarly debated. *Paranthropus* species, *P. robustus*, *P. boisei*, and *P. aethiopicus*, are traditionally recognized for hyper-robust cranio-dental traits, including large post-canine teeth, sagittal crests, and powerful mandibular musculature (Wood and Constantino, 2007). Supporters of a separate genus emphasize these features as adaptive specializations justifying genus-level distinction (Leakey, 1959). Others adopt a “lumping” approach, treating *Paranthropus* as an extreme morphological variant within the australopith lineage rather than a distinct genus (Kimbel and Rak, 1993). Recent palaeoproteomic data suggest a close evolutionary relationship between the two genera, consistent with a sister-lineage scenario (Madupe, Koenig, et al., 2025; Madupe, Munir, et al., 2025).

Unresolved australopith taxonomy affects interpretations of early hominin evolution. The coexistence of multiple australopith species in East and South Africa indicates a branching, rather than linear, evolutionary pattern, with implications for understanding the origins of *Homo* and the placement of *Paranthropus* (Kimbel and Villmoare, 2016).

The emergence of *Homo* is closely tied to late Pliocene and early Pleistocene australopiths. Two early species, *H. habilis* and *H. rudolfensis*, highlight ongoing morphological and taxonomic debates. Some researchers propose merging the two into a single variable species, while others maintain their separation based on cranial and mandibular differences, suggesting distinct evolutionary lineages and potentially independent adaptations after diverging from australopith ancestors (Leakey et al., 1995; Spoor et al., 2015; Wood, 1992a).

Both species are crucial for understanding the australopith–*Homo* transition. Phylogenetic analyses often position *H. habilis* as a likely descendant of *A. afarensis* or *A. africanus*, whereas *H. rudolfensis* may represent a separate lineage (Spoor et al., 2015). Their coexistence with robust australopiths (*P. boisei*) underscores the complexity of early Pleistocene hominin diversity, revealing overlapping ecological niches and multiple parallel evolutionary trajectories.

Across studies, *H. habilis* and *H. rudolfensis* consistently occupy the base of the *Homo* clade, though their relationship to each other remains debated: some analyses favour a sister-taxon relationship, while others treat them as sequential branches. By contrast, relationships among later *Homo* species, particularly between *H. ergaster* and *H. sapiens*, are more consistently recovered, appearing as sister taxa.

Some authors have questioned the inclusion of *H. habilis* and *H. rudolfensis* within *Homo*, arguing that adaptive differences between early *Homo* and australopiths warrant their removal from the genus (Wood and Collard, 1999a, 1999b), though this proposal has not achieved wide acceptance. Overall, these unresolved issues highlight the challenges of reconstructing early *Homo* evolution and understanding species diversity during the Pleistocene.

IV.4. *Homo erectus* sensu lato

Homo erectus represents one of the most geographically widespread and temporally persistent hominin taxa, occupying large parts of Africa and Eurasia from approximately 2 Ma ago to less than 100 ka (Dennell and Roebroeks, 2005). This extensive distribution is associated with substantial morphological variability, which has led to persistent debates regarding taxonomy, population structure, and phylogenetic relationships. Rather than forming a single homogeneous lineage, *H. erectus* is now widely interpreted as a set of regionally differentiated populations connected by dispersal events and varying degrees of gene flow (Baab, 2011).

The classification of *H. erectus* has long been debated, particularly regarding the relationship between African and Asian fossil assemblages. A central issue concerns whether these fossils should be grouped within a single species or divided into distinct taxa. Some researchers maintain a taxonomic distinction between African and Asian forms, assigning the former to *H. ergaster* and reserving *H. erectus* sensu stricto for Asian populations (Antón, 2003; Wood and Turner, 1995). This distinction is typically based on differences in cranial morphology, such as thinner cranial vault bones, reduced postorbital constriction, and less pronounced supraorbital tori in African specimens compared to their Asian counterparts (Antón, 2003; Baab, 2011; Zeitoun, 2000).

However, other researchers have argued that these differences do not necessarily imply speciation (Bräuer, 1992; Bräuer and Mbua, 1992). Instead, they may reflect variation within a single, geographically widespread species. Lordkipanidze et al. (2013), for example, emphasized that the range of morphological variation observed across African and Asian fossils overlaps substantially, particularly when considering temporal depth and sample size. From this perspective, erectus-like hominins represent a single evolving lineage exhibiting regional variation rather than clearly bounded species (Hublin, 2014).

Recent comparative and morphometric analyses have further complicated the picture by showing that morphological variation tends to cluster geographically, without forming sharply defined

boundaries between groups (Baab, 2011). For instance, cranial vault thickness is generally greater in Asian fossils, while African specimens tend to show more gracile features; yet these traits do not covary consistently enough to define discrete taxonomic units. Similarly, facial morphology and dental characteristics exhibit patterns of regional differentiation but also display overlap distributions of traits (Rightmire, 1998a).

In response to these patterns, many researchers now favour a population-based framework, in which African and Asian assemblages are interpreted as interconnected populations within a broader evolutionary lineage (Antón et al., 2014). This approach shifts the focus away from rigid taxonomic categories and toward evolutionary processes such as dispersal, local adaptation, and demographic history.

African fossils dated between ~1.9 and 1.5 Ma, including those from Koobi Fora (Kenya) and the Nariokotome skeleton (KNM-WT 15000), are commonly attributed to *H. ergaster* (Groves and Mazak, 1975). Morphologically, these African specimens are characterized by relatively thin cranial vault bones, reduced postorbital constriction, and less massive supraorbital tori compared to many Asian fossils (Antón et al., 2014; Groves and Mazak, 1975). These populations are widely considered central to early hominin dispersals beyond Africa. Archaeological evidence supports this interpretation, particularly the emergence and spread of Acheulean lithic industries, which appear in Africa around 1.76 Ma and are often associated with *H. ergaster* populations (Lepre et al., 2011). The technological and behavioural flexibility implied by these industries may have facilitated expansion into diverse environments. However, variability within African assemblages is itself substantial. Differences in cranial morphology, size, and robusticity across sites such as Koobi Fora, Olduvai Gorge, and West Turkana suggest that early African populations were not uniform. Antón et al. (2014) argue that this variability may reflect population structuring within Africa, possibly involving ecological differentiation or partial geographic isolation. Consequently, dispersals out of Africa may have involved multiple subpopulations, rather than a single homogeneous ancestral group, contributing to the diversity observed in Eurasian *H. erectus*.

H. erectus sensu stricto is generally composed by the Indonesian and Chinese records.

The Indonesian record, particularly from the island of Java, is fundamental for understanding the long-term evolution of *H. erectus*. The first discovery of *H. erectus* was made at Trinil in the 1890s by E. Dubois, who unearthed a cranial vault and femur along the Solo River, marking the first identification of a fossil hominin outside Europe (Zeitoun, 2000). Subsequent excavations at the

Sangiran dome in central Java have yielded one of the largest fossil assemblages attributed to *H. erectus*. Sangiran fossils are characterized by thick cranial vault bones, pronounced supraorbital tori, and long, low cranial profiles. Dental remains also show distinctive features, including relatively large molars and complex enamel-dentine junction morphology (Kaifu et al., 2008; Zanolli, 2013). The Ngandong assemblage, discovered in the 1930s along the Solo River, represents a much later population, dated to approximately 117-108 ka (Rizal et al., 2020). These fossils include a series of relatively complete crania with larger endocranial volumes compared to earlier Javanese specimens, as well as some derived cranial features (Santa Luca, 1980). Nevertheless, they retain key *erectus* traits, such as thick cranial bones and pronounced brow ridges (Rizal et al., 2020). The Javanese fossil record suggests long-term regional continuity, potentially spanning over one million years. This continuity is often interpreted as evidence for sustained occupation of Southeast Asia by *H. erectus* populations, possibly with limited external input. At the same time, morphological changes observed between earlier (Sangiran, Trinil) and later (Ngandong) fossils indicate evolutionary processes occurring within the region (Antón, 2003; Kaifu, 2017; Kaifu et al., 2008).

Chinese *H. erectus* fossils represent another major regional expression of the species, with a long history of discovery and research. The most famous site, Zhoukoudian Locality 1 near Beijing, was excavated extensively during the 1920s and 1930s, leading to the identification of “*Sinanthropus pekinensis*” (Black, 1927). The Zhoukoudian fossils display a distinctive combination of features, including a long, low cranial vault, thick cranial bones, and a continuous supraorbital torus (Weidenreich, 1943). However, compared to Indonesian specimens, they often exhibit differences in cranial vault shape, facial flatness, and dental morphology, including relatively smaller teeth and different patterns of enamel thickness (Weidenreich, 1943; Xing et al., 2009).

The morphological differences between Chinese and Indonesian fossils have been interpreted in several ways. Some researchers argue that they reflect independent dispersal events into East and Southeast Asia, potentially originating from different African source populations (Dennell and Roebroeks, 2005). Others suggest that these differences arose through regional adaptation to distinct ecological conditions, such as climate and diet (Antón, 2003). A third interpretation emphasizes long-term population structure with limited gene flow, in which geographically separated populations diverged over time while retaining a shared ancestral framework (Zeitoun, 2000).

Recent syntheses increasingly favour the latter perspective, proposing that East Asia hosted multiple contemporaneous hominin populations, which may have experienced varying degrees of

interaction and isolation (Bae et al., 2017). This view is consistent with both the fossil record and emerging genetic evidence, which point to complex demographic processes shaping hominin diversity across Asia.

Early phylogenetic models of *H. erectus* were structured around a relatively linear evolutionary sequence, in which Eurasian *H. erectus* evolved from African *H. ergaster*, followed by Middle Pleistocene hominins such as *H. heidelbergensis*, ultimately leading to Neandertals and modern humans (Andrews, 1984; Mounier, 2009; Mounier et al., 2009; Rightmire, 1998b; Stringer, 2002). This framework was consistent with an expansion out of Africa and a branching model of speciation. However, this model has proven insufficient to account for the increasing complexity of the fossil record. The coexistence of morphologically distinct populations across wide geographic areas, combined with overlapping chronologies, challenges the idea of a simple ancestor–descendant sequence. For instance, Southeast Asian populations appear to persist independently over long periods, while East Asian and African populations follow different morphological trajectories (Antón, 2003; Baab, 2011).

In response, alternative models have been proposed that emphasize geographic structuring and evolutionary diversification within a widespread lineage. Particularly, Zeitoun (2000) argued that *H. erectus* should not be viewed as a single evolving species but rather as a set of regionally distinct evolutionary units. Zeitoun's analysis of Indonesian fossils highlighted discontinuities between populations such as Sangiran and Ngandong, suggesting that local evolutionary processes and possible population replacements played a significant role. More recent syntheses build on this perspective by proposing that *H. erectus* forms a spatially structured evolutionary system (e.g., Dembo et al., 2015; González-José et al., 2008; Irish and Grabowski, 2021; Ji et al., 2021; Kaifu, 2017; Ni et al., 2021). Within this framework, different populations may follow partially independent evolutionary trajectories while remaining linked through intermittent gene flow.

A key implication of this revised framework is the recognition of multiple dispersal events out of Africa, rather than a single expansion (Carotenuto et al., 2016; Lahr and Foley, 1994; Profico et al., 2023). Archaeological and fossil evidence indicates that hominins reached Eurasia as early as ~1.8–2.0 Ma, as documented at sites such as Dmanisi and in northern China (Zhu et al., 2018).

Early Southeast Asian populations, particularly those from Sangiran, are often interpreted as representing one of the earliest dispersal waves. Their relatively primitive morphology supports the

idea of an early expansion from Africa into tropical Asia. In contrast, later populations in China and possibly western Eurasia may reflect subsequent dispersals involving different source populations or more derived forms (Gilbert and Asfaw, 2008).

At the same time, certain region, like Java, appear to have experienced long-term population continuity. The sequence from Sangiran through Ngandong has often been interpreted as evidence of sustained occupation over hundreds of thousands of years (Antón, 2003). However, this interpretation remains debated. Some researchers argue for continuity with local evolution (Kaifu et al., 2008), while others, following Zeitoun (2000), suggest that morphological differences between assemblages may reflect population turnover or complex demographic histories rather than simple in situ evolution (Ni et al., 2021).

The revised dating of the Ngandong fossils to approximately 117-108 ka provides strong evidence that *H. erectus* survived much later than previously assumed (Rizal et al., 2020). This late persistence raises the possibility of temporal overlap with early *H. sapiens* populations in Southeast Asia, which are documented in the region by at least ~70-50 ka (Bae et al., 2017).

Although direct evidence of interaction between these populations remains limited, the coexistence of multiple hominin groups in Southeast Asia suggests a complex ecological and demographic context. Possible scenarios include an ecological competition for similar resources (Antón et al., 2014), niche partitioning, allowing coexistence in different environmental zones (Roberts and Stewart, 2018), or indirect interactions. Some authors have also raised the possibility of limited genetic interaction, although clear genomic evidence linking *H. erectus* directly to modern Southeast Asian populations remains scarce compared to Denisovan introgression (Jacobs et al., 2019; Reich et al., 2011).

One of the most persistent challenges in the study of *H. erectus* concerns the interpretation of its morphological variability. The wide geographic range and long temporal span of the species have produced a fossil record characterized by significant diversity in cranial and dental features. A notable example is the group of robust Javanese fossils sometimes attributed to *Meganthropus*. These specimens exhibit extremely thick mandibular corpora and large teeth, leading some researchers to propose that they represent a distinct taxon (Indriati et al., 2011; Santa Luca, 1980; Zanolli, 2013). However, others argue that they fall within the upper range of variation of *H. erectus*, particularly when considering regional adaptation and sexual dimorphism (Kaifu et al., 2005). Similarly, the

taxonomic status of the Ngandong fossils remains debated. While some authors have proposed the designation *H. soloensis*, most recent studies favour their inclusion within *H. erectus*, albeit as a late and morphologically distinctive population (Rizal et al., 2020).

The distinction between *H. ergaster* and *H. erectus* also remains unresolved. While differences in cranial morphology are often cited, these do not consistently align with clear geographic or temporal boundaries. As a result, many researchers emphasize intraspecific variation and population structure as more informative frameworks than rigid taxonomic divisions (Antón et al., 2014; Baab, 2011).

Overall, current debates highlight the difficulty of applying traditional species concepts to fossil hominins. Increasingly, *H. erectus* is understood as a variable and regionally structured set of populations. A more detailed synthesis of the current literature is provided in Gousset (2026).

IV.5. *Homo neandertalensis* and *Homo sapiens*

The evolutionary relationship between *H. neandertalensis* and *H. sapiens* has long been central to discussions on human evolution. Earlier interpretations were influenced by linear, grade-based models of evolution, in which hominin forms were often arranged along an implicit progressive sequence (Wiley and Lieberman, 2011). This perspective was progressively undermined by the development of cladistics (phylogenetic systematics), which emphasized branching patterns of descent and the identification of shared derived traits rather than perceived evolutionary “stages” (Hennig, 1966). Within this framework, Neandertals and modern humans are instead understood as sister lineages within a branching hominin phylogeny. Fossil and genetic evidence now supports a more complex scenario involving structured populations, regional differentiation, and repeated episodes of interaction between lineages (Green et al., 2010; Prüfer et al., 2014; Reich, 2018).

Neandertals emerged in Europe from Middle Pleistocene populations, including those from Sima de los Huesos and Ehringsdorf, which display a combination of archaic and derived traits. These assemblages document a gradual and regionally variable development of Neandertal morphology (Condemi, 1988; Dean et al., 1998; Hublin, 2009). The combination of derived Neandertal features with more archaic characteristics supports a pattern of regional continuity, whereby populations descended from earlier Eurasian hominins accumulated distinctive traits over time, albeit unevenly (Hublin, 2009). Morphometric analyses further indicate that Neandertals eventually occupied a

distinct morphological space within Middle Pleistocene *Homo*, while still retaining internal variability (Mounier and Mirazón Lahr, 2016).

By the Late Pleistocene, Neandertal morphology reached its most derived expression in European populations (Hublin, 2009; Trinkaus, 2006, 2011). In contrast, Near Eastern groups, such as those from Shanidar and Amud, retain the same overall morphological pattern but exhibit regional differences in craniofacial robustness and skeletal structure (Hovers et al., 1995; Trinkaus, 2011). Fossil, dating and archaeological evidence suggests that European and Near Eastern populations occupied these regions at the same times, with possible episodes of geographic overlap (Stringer, 2016; Stringer, 2006). This geographic pattern underscores the persistence of population structure and regional variability throughout Neandertal evolution. Genetic data further indicate that Late Pleistocene Neandertals were organized into relatively small and structured populations (Fabre et al., 2009), with limited gene flow and episodes of demographic contraction (Prüfer et al., 2014), a pattern that may have increased their vulnerability to environmental fluctuations and demographic pressures (Higham et al., 2014; Slimak et al., 2024).

In parallel, *H. sapiens* emerged in Africa through a long-term evolutionary process involving multiple interconnected populations rather than a single localized origin (Schlebusch et al., 2017). The subsequent expansion of *H. sapiens* into Eurasia during the Late Pleistocene brought them into contact with Neandertals (Prüfer et al., 2017). Genetic evidence demonstrates that interbreeding occurred, as non-African modern human populations retain a small but significant proportion of Neandertal ancestry (Sankararaman et al., 2016). Archaeological evidence further suggests that these interactions varied across regions and through time, potentially involving competition, niche partitioning, and limited cultural exchange (Roebroeks and Soressi, 2016; Shea, 2008).

These developments have important implications for the taxonomic status of Neandertals and modern humans. While some earlier interpretations proposed that both groups could be grouped within a single species (e.g., Ahern et al., 2002; Bonde, 1989; Campbell, 1963; Curnoe and Thorne, 2003; Dubois, 1940; Gingerich, 1979; Jelinek, 1980; Relethford, 2001; Smith and Trinkaus, 1991; Trinkaus, 1991; Wolpoff, 1980), most paleoanthropologists now support their classification as distinct species. This view is supported by both cladistic analyses of discrete morphological traits and genetic data (e.g., Hajdinjak et al., 2018; Harvati et al., 2004; Hublin, 2000; Mounier et al., 2016; Mounier and Caparros, 2015; Ni et al., 2021; Rak, 1993; White et al., 2014), despite clear evidence for

gene flow between the two groups (e.g., Fu et al., 2015; Green et al., 2010; Li et al., 2024; Mounier and Mirazón Lahr, 2019; Petr et al., 2020; Posth et al., 2017; Prüfer et al., 2017, 2021).

Alternative models, such as the “ring species” hypothesis, have been proposed to explain the gradual geographic differentiation of Neandertal traits (Voisin, 2006). According to this model, “ring species provide dramatic evidence that normal genetic divergence within one species can build up to a sufficient level to generate two species” (Ridley, 2004:388). In this framework, populations across Eurasia would have formed a continuum, with Neandertal traits becoming increasingly pronounced from east to west, eventually leading to differentiation in western Europe (Voisin, 2006). However, the idea that highly derived Neandertal populations were reproductively isolated from *H. sapiens* is not supported by current genomic evidence (e.g., Fu et al., 2015; Prüfer et al., 2017, 2021; White et al., 2014).

Overall, the relationship between *H. neandertalensis* and *H. sapiens* is best understood as a dynamic evolutionary process shaped by regional diversification, population structure, and intermittent gene flow, rather than a simple replacement scenario. A more detailed synthesis of the current literature is provided in Gousset (2026)

Key-points I.4

Australopithecus:

- *A. afarensis* is a basal species, plausibly ancestral to both robust australopiths and early *Homo*.
- *A. africanus* represents a southern African offshoot, possibly related to *A. sediba* and early *Homo*, but likely too derived to be a direct ancestor.
- *A. sediba* shows strong morphological links to *Homo*, though its direct ancestral status remains debated.
- Australopiths exhibit high morphological diversity; their phylogeny remains complex and partly unresolved.

Paranthropus:

- Likely a monophyletic clade diverging from an *A. afarensis*-like ancestor around 2.7 Ma.
- *P. aethiopicus*: basal East African form.
- *P. boisei*: hyper-robust descendant, persisted until ~1.2 Ma.
- *P. robustus*: South African form, likely evolved independently.
- Highlights the evolutionary importance of ecological flexibility.

Early Homo:

- *H. habilis* and *H. rudolfensis*: larger brains, reduced prognathism, technological innovations; show transition from australopith morphology.
- Evolutionary pattern is branching and reticulate, not strictly linear.
- Phylogenetic placement of some specimens remains debated, but overall *Homo* lineage is increasingly well resolved.

H. erectus, H. ergaster and H. georgicus:

- *H. erectus*: widespread, long-lived species; exhibits increased brain size, reduced prognathism, and robust postcranial adaptations.
- *H. ergaster*: African variant, likely ancestral to later *H. erectus* populations.
- *H. ergaster*: distinct taxon, likely ancestral to *H. erectus* sensu stricto and many later *Homo* lineages.
- *H. georgicus*: basal Eurasian form, illustrates early dispersal out of Africa.
- This group represents the first major hominin expansion beyond Africa.

H. neandertalensis and H. sapiens:

- *H. neandertalensis*: European and western Asian lineage; well-documented fossil record; genetically characterized; evidence of interbreeding with *H. sapiens* and Denisovans.
- *H. sapiens*: earliest fossils >211-255 ka in Africa; arose through a pan-African process; multiple dispersals out of Africa; admixture with Neandertals and Denisovans shaped genetic diversity.
- Early *H. sapiens* populations exhibit morphological diversity, reflecting both population structure and occasional gene flow with other hominins.

Overall:

- Hominin evolution characterized by branching lineages, regional diversity, and repeated morphological experimentation.
- Coexistence of multiple lineages and instances of parallel evolution highlight the dynamic nature of hominin adaptation.
- Flexibility and adaptability appear critical for long-term survival and evolutionary success.
- Broad patterns now allow a framework connecting australopiths to early *Homo* and ultimately to later species such as *H. heidelbergensis*, *H. neandertalensis*, and *H. sapiens*.

V. Objectives

The main objective of this dissertation is to evaluate the potential and the limitations of GMM data in phylogenetic inference, with a particular focus on hominin evolution. Despite significant theoretical and methodological advances, the integration of continuous shape data into cladistics remains controversial, especially when compared with more traditional approaches based on discrete morphological characters. By empirically testing and comparing different types of morphological evidence, this work aims to contribute both to methodological debates in systematics and to paleoanthropological discussions of hominin phylogeny.

First, I will empirically assess a single inference protocol on two different forms of GMM data, Principal Component (PC) scores and raw landmark coordinates, in order to evaluate whether phylogenetic results are sensitive to the way shape information is represented. This comparison will help assess whether commonly used data reduction techniques such as PCA preserve meaningful evolutionary signal or instead introduce biases that limit their cladistic utility. Second, I will directly compare these GMM-based results with those obtained from a traditional morphological matrix composed of discretized characters. This step will serve as a benchmark, situating the performance of continuous shape data relative to the established standard in phylogenetic studies of fossil hominins.

Third, I will apply the same inference protocol to a combined dataset integrating both landmarks and discrete morphological characters. This integrative approach will allow me to test whether shape data provide additional phylogenetic signal when analysed alongside conventional traits, or whether the two data types introduce conflict that complicates inference. Fourth, I will compare the outcomes of this combined dataset with those of the standalone morphological matrix in order to quantify the extent to which incorporating GMM data enhances phylogenetic resolution, alters tree topology, or shifts interpretations of character evolution.

Finally, beyond methodological evaluation, this dissertation seeks to engage directly with the paleoanthropological implications of the results. By confronting the recovered phylogenies with ongoing debates in hominin systematics, I aim to evaluate the degree to which alternative data sources can clarify contested evolutionary relationships. This includes assessing whether *Australopithecus afarensis* truly occupies a basal position relative to both *Paranthropus* and early *Homo*; and whether *Australopithecus africanus* represents an evolutionary side branch or retains closer ties

to the origins of *Homo*. At the same time, the analyses will address questions about the monophyly of *Paranthropus*, as well as the degree of resolution achievable for the branching versus reticulate nature of early *Homo* diversification. Finally, results will be discussed considering the broader evolutionary trajectory leading to later species such as *Homo erectus*, *H. neandertalensis*, and *H. sapiens*, with particular attention to how methodological choices shape our interpretation of morphological continuity, parallel evolution, and admixture among lineages.

In doing so, this thesis not only provides a critical test of protocols for incorporating GMM data into phylogenetics but also situates these methodological outcomes within the broader scientific dialogue on the origins and diversification of our lineage.

Chapter I – Material

This study investigates human evolution during the end of the Pliocene and the beginning of the Pleistocene (from ~5 Ma to ~0.78 Ma), with a particular emphasis on the origins of the genus *Homo*. The genus was first introduced by C. Linnaeus in 1758, in the tenth edition of his *Systema Naturae*, where he classified primates into four genera: *Homo* (humans), *Simia* (monkeys), *Lemur* (lemurs), and *Vespertilio* (bats), without distinguishing between different human populations (Linnaeus, 1758). Since Linnaeus' classification, the fossil record has grown significantly, and numerous taxonomic revisions have been proposed. However, the phylogenetic relationships among early hominin taxa remain the subject of ongoing debate, largely due to new fossil discoveries and unresolved classification criteria.

This study has two primary objectives. First, it seeks to develop and test a protocol that integrates 3D geometric morphometric data with cladistic analysis. Second, it aims to clarify the phylogenetic relationships among hominin fossils (from ~3.7 to 0.05 Ma). To achieve these goals, a comparative sample was compiled, encompassing thirty key groups across three major genera: *Paranthropus*, *Australopithecus*, and *Homo*. The sample includes specimens from a wide range of geographical regions and chronological contexts to account for intraspecific variability.

The study focuses on hominin fossils from Africa, Europe and Asia, dating from ~3.7 to ~0.05 Ma. Except for current modern humans, fossils were primarily grouped based on their geographic and chronostratigraphic context for morphological analyses. Specimens were included in the analysis if at least one observable character from the relevant calvarial zone was preserved. Juvenile specimens were generally excluded due to their lack of diagnostic adult features, apart from D2700 from Dmanisi, an important fossil from periods with limited representation. While such fossils provide crucial data, their interpretation remains complex and tentative.

Fossil ages are reported in millions of years (Ma) and thousands of years (ka). Dating methods specific to each site are also detailed.

As with the previous sample, the comparative material was selected to represent established hominin taxa. The modern human sample (n=45), though not intended to reflect the full scope of modern or ancient human variation, offers a baseline of morphological diversity across space and time (Mounier, 2009). This sample, dating roughly to the 19th century, includes individuals from Africa (n=25), Asia (n=5), Oceania (n=5), and Europe (n=5). It is further supplemented by three fossil *Homo sapiens* specimens, dated to approximately 135,000 years ago. This broad temporal and

geographical coverage mimic the type of variability commonly encountered in the fossil record and provides a comparative framework similar to the one used for Neandertals.

The Neandertal sample (n=7) includes individuals from Europe and the Near East, dating between 250 and 50 ka. In addition to the so-called “Classic Neandertals” (n=3), such as those from Monte Circeo, La Ferrassie, and La Chapelle-aux-Saints, the sample also includes specimens from Saccopastore and Ehringsdorf. Two Near Eastern individuals, from Amud and Shanidar, round out the group.

Early and Middle Pleistocene fossils were categorized by geographic region rather than taxonomic assignment to reduce bias during morphological analysis. This group comprises 23 specimens: 14 from Africa, 6 from Asia, and 3 from Europe. A brief description of these sites and fossils is provided, with further details summarized in Table 1. Additional information on the modern human series is available in Appendix 1.

In this chapter, the material will be presented grouped by operational taxonomic units (OTUs).

I. Outgroups

To implement and test phylogenetic reconstructions based on 3D geometric morphometrics, different taxa belonging to the family Hominidae Gray, 1825 (e.g., Lockwood and Tobias, 1999) were sampled and analysed. The Hominidae family includes the genera *Gorilla*, *Homo*, *Pan*, and *Pongo*. The genus *Gorilla* is divided into two species: the Western gorillas, *Gorilla gorilla* Savage and Wyman, 1847, and the Eastern gorillas, *Gorilla beringei* Matschie, 1903. The genus *Pan* is divided into two species: *Pan troglodytes* (Blumenbach, 1776) and *Pan paniscus* Schwarz, 1929. Finally, the genus *Pongo* is divided into three species: *Pongo abelii* Lesson, 1827, *Pongo pygmaeus* (Linnaeus, 1760), and *Pongo tapanuliensis* Nater et al., 2017.

Various studies, including genetic analysis, suggest that the human lineage diverged from the *Pan* lineage approximately 7 to 8 Ma (Langergraber et al., 2012), from *Gorilla* around 8–19 Ma (Glazko and Nei, 2003), and from *Pongo* around 12 to 16 Ma (Chen and Li, 2001).

While different species are described for each genus, the three OTUs of the outgroups were defined at the genus level. Each OTU is composed of three skulls, for a total of nine specimens.

In order to avoid any distortion of the results due to the presence of strongly expressed secondary sexual characters in some ape males (e.g., the sagittal crest), only female individuals were included.

II. Ingroups

The ingroup is formed by representatives of the *Homo*, *Paranthropus* and *Australopithecus* genera (see Table 1): 31 fossils and 45 modern skulls for a total of 85 specimens that are grouped into 23 OTUs for Chapter III and 28 OTUs for Chapter IV. These specimens were found across Asia, Africa and Europe (see Figure 2).



Figure 2: Repartition of the sites of the studied specimens. Colours represent the fossil specimens of different species.

II.1. *Paranthropus*

This genus was primarily described by Broom in 1938, with the discovery of the fossil TM1517. The *Paranthropus* specimens are characterized by several morphological features of the skull, such as, large and thickly enamelled post-canine teeth supported by a deep and broad mandibular corpus with tall and broad rami; zygomatic bones, extending both laterally and anteriorly; a orthognathic face and a sagittal crest (Rak, 2014). These features indicate a diet of tough, fibrous vegetation,

suggesting that *Paranthropus* specimens were highly specialized for processing hard-to-chew plant material.

In the sample, the genus *Paranthropus* is represented by three OTUs corresponding to two species: *P. boisei* and *P. aethiopicus*. Those species are still referred as both *Australopithecus* and *Paranthropus* in the literature (e.g., Constantino and Wood, 2007; Kimbel, 2015; Wood, 2011). Here, the decision to use *Paranthropus* was made to reflect phylogenetic distinctions supported by morphological and cladistic analyses, which often place these species in a monophyletic clade separate from *Australopithecus* (e.g., Mongle et al., 2019, 2023; Nevell and Wood, 2008; Strait et al., 1997). This taxonomic assignment underscores their unique evolutionary trajectory and aids in clarifying patterns of hominin diversification.

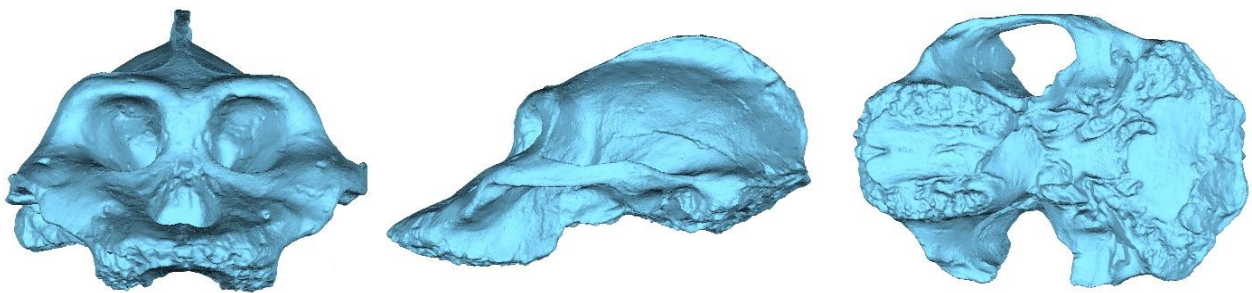


Figure 3: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Paranthropus aethiopicus* specimen, KNM-WT 17000 (original).

The species *Paranthropus aethiopicus* (Arambourg and Coppens, 1968) lived around 2.7 to 2.3 Ma in East Africa, primarily in present-day Kenya and Ethiopia. It is one of the earliest members of the genus *Paranthropus*. This hominin had a relatively small brain (about 410–450 cm³) but was distinguished by large molars, a sagittal crest, and a thick jaw, all adaptations for a diet of fibrous vegetation (Constantino, 2021). Despite its robust features, it likely shared some similarities with earlier species like *Australopithecus afarensis*.

This OTU includes one specimen: **KNM-WT 17000** (see Figure 3). This fossil was discovered in the Lokalalei Member in West Turkana in Kenya in 1985 by A. Walker and colleagues (Walker et al., 1986) and is dated 2.57–2.47 Ma (Feibel et al., 1989). This specimen is an adult cranium, missing some facial, frontal and parietal bone fragments (Walker et al., 1986). While firstly described as *Australopithecus boisei* (Leakey and Walker, 1988), this specimen was later attributed to *Paraustralopithecus aethiopicus* Arambourg and Coppens, 1968 (Kimbel et al., 1988), before being allocated to the genus *Paranthropus*.

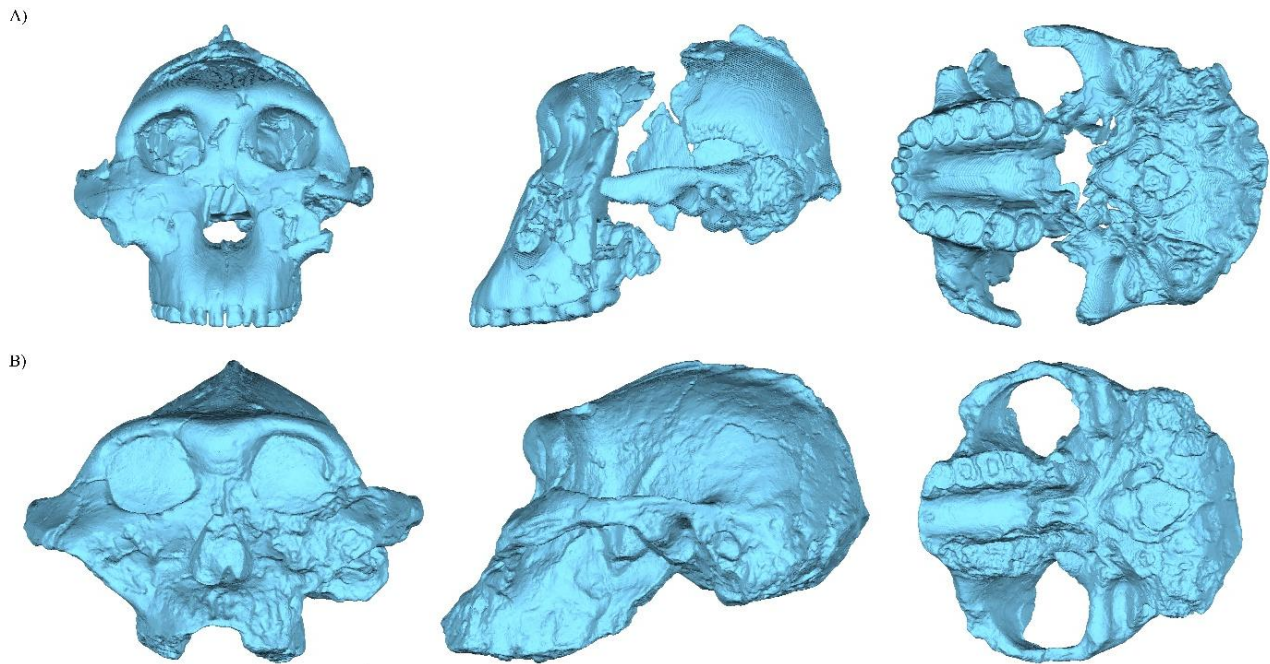


Figure 4: *Norma facialis, norma lateralis and norma basilaris of Paranthropus boisei specimens: A) OH5 (original), and B) KNM-ER 406 (original).*

Paranthropus boisei (Leakey, 1959) lived between 2.3 and 1.2 Ma in East Africa, where numerous fossil were found, especially in Tanzania, Kenya, and Ethiopia. It is one of the most famous species within the genus *Paranthropus* and is often referred to as the “hyper-robust” australopithecine due to its extreme cranial and dental traits. *P. boisei* had a massive jaw and huge molars, which, along with its sagittal crest, suggest it was highly specialized for processing tough, fibrous plant material (Wood and Constantino, 2007). Despite having a small brain (around 510 cm³), its robust cranial features set it apart from other hominins. The species is thought to have adapted to environments with abundant vegetation that required heavy mastication. Initially, *P. boisei* was thought to be a direct ancestor of modern humans due to its large teeth and jaw, but later research showed it was a side branch of the hominin family tree, having no direct descendants. It is considered to be a descendant of *Paranthropus aethiopicus*, showing further adaptations toward robust cranial features (Wood and Constantino, 2007). *Paranthropus boisei*, was primarily named *Zinjanthropus boisei* Leakey, 1959. The taxonomy was later changed to *Australopithecus boisei* (Leakey, 1959) by Tobias (1967) and *Paranthropus boisei* (Leakey, 1959) by Robinson (1960) and Constantino and Wood (2007).

The *Paranthropus boisei* OTU is composed by two specimens: OH5 and KNM-ER 406 (see Figure 4). **OH5** was discovered ~22 ft. below the upper limit of Bed I at site FLK in Olduvai Gorge in Tanzania in 1959 by M. Leakey and later described by her husband L. Leakey (Leakey, 1959). This fossil is a well-preserved cranium, dated from around 1.79 - 1.85 Ma (Hay, 1976). **KNM-ER 406** was

discovered in KBS Member in Koobi Fora Formation in Kenya in 1969, by R. Leakey and his team (Leakey et al., 1971). This specimen is dated 1.6-1.56 Ma (Feibel et al., 1989). It is an almost complete cranium, where “the mastoid processes and the right occipital condyle have been abraded” (p.2, Leakey et al., 1971).

II.2. *Australopithecus*

The genus *Australopithecus*, first described by Dart (1925), is known to have inhabited the African continent between approximately 4.2 and 1.4 Ma (e.g., Granger et al., 2015; Kimbel et al., 1994; Schwarcz et al., 1994). Fossil evidence places members of this genus in present-day South Africa, Malawi, Tanzania, Kenya, Ethiopia, and Chad, though their actual range was likely broader (e.g., Alemseged, 2023; Johanson et al., 1978; Kimbel, 2007; Kimbel et al., 1994). In the present study, *Australopithecus* is represented by four OTUs, three representing well-defined species, *A. africanus*, *A. afarensis*, and *A. sediba*, and one focusing on the Stw 53 specimen which taxonomical attribution has reached no consensus at the species level.



Figure 5: *Norma facialis*, *norma lateralis* and *norma basilaris* of Stw 53 (cast).

We decided to analyse Stw 53 in a separate OUT (see Figure 5), named after the specimen, in order to reflect the ongoing debates on this fossil taxonomic attribution. This fossil was originally attributed to *H. aff. habilis* (Hughes and Tobias, 1977), then *H. habilis* (Tobias, 1991) and later *Homo sp. nov.* (Grine et al., 1996). Other researchers attributed the fossil to the *Australopithecus* genus without specifying a species (Braga, 1998; Ferguson, 1989; Thackeray et al., 2000) and K. Kuman and R. Clarke proposed an classification within *A. africanus* (Kuman and Clarke, 2000). In 2004, S. Prat confirmed the Tobias and Hughes hypothesis and attributed the specimen to the genus *Homo* (Prat, 2004). Finally, in 2010, D. Curnoe proposed the invention of a new species, *Homo gautengensis*, making Stw 53 the holotype of this new taxon (Curnoe, 2010).

Stw 53 was discovered by A. Hughes and P. Tobias in 1976, in Member 5 of the Sterkfontein Formation in South Africa and was dated between 1.49 and 2.6 Ma (Hanon et al. 2018; Hughes and Tobias, 1977). It is a fragmented cranium, comprising the right frontal, most of both parietals and the basicranium (Hughes and Tobias, 1977). The 3D model used here was digitized by A. Mounier from a cast using the reconstruction made by Curnoe and Tobias (2006).

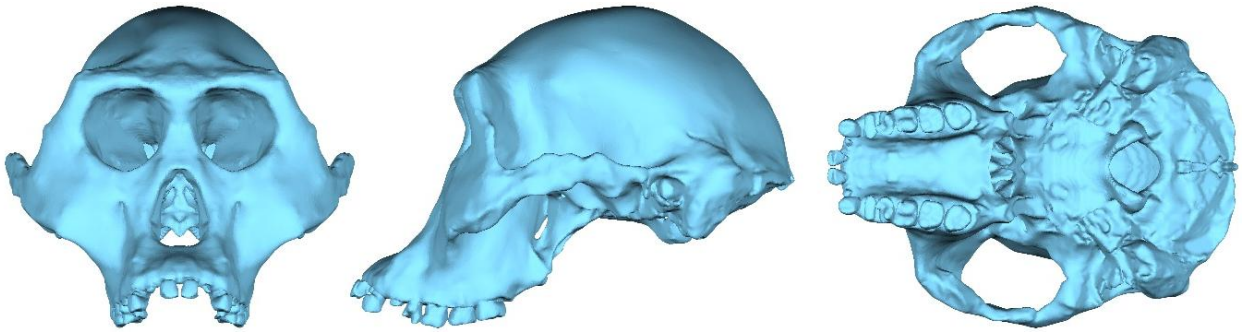


Figure 6: *Norma facialis*, *norma lateralis* and *norma basilaris* of the reconstructed *Australopithecus afarensis* specimen, A.L. 444-2.

Australopithecus afarensis Johanson et al. (1978) lived in East-Africa approximately 3.9 to 2.9 Ma during the late Pliocene. This species is considered a key ancestor in the human evolutionary lineage, as it exhibits a mix of both apelike and humanlike traits. The majority of fossils of *A. afarensis* have been found in East Africa, with important sites such as Laetoli (Tanzania) and Hadar (Ethiopia) (Kimbel et al., 2004). *A. afarensis* had a small brain (around 375–550 cm³), much like other australopithecines, but it showed evidence of bipedal locomotion, with adaptations such as a pelvis and lower limb structure suited for walking on two legs (Kimbel et al., 1994). Despite being bipedal, *A. afarensis* still had long arms, a curved finger morphology, and apelike features in the skull, indicating it still spent significant time in the trees. Its diet was likely omnivorous, including fruits, leaves, and perhaps some meat, based on dental wear and isotopic analysis. This species represents an important stage in human evolution, demonstrating a transition toward full bipedalism while retaining many primitive traits (Kimbel et al., 1994).

The *Australopithecus afarensis* OTU is formed of the skull **A.L. 444-2** (see Figure 6), discovered by Y. Rak in 1992 in Kada Hadar-2 in Hadar Formation in Ethiopia (Kimbel et al., 1994). This well-preserved skull is dated around ~3 Ma (Kimbel et al., 1994). This specimen was reconstructed virtually by Ledogar et al. (2022). There was no taxonomic revision for this fossil.

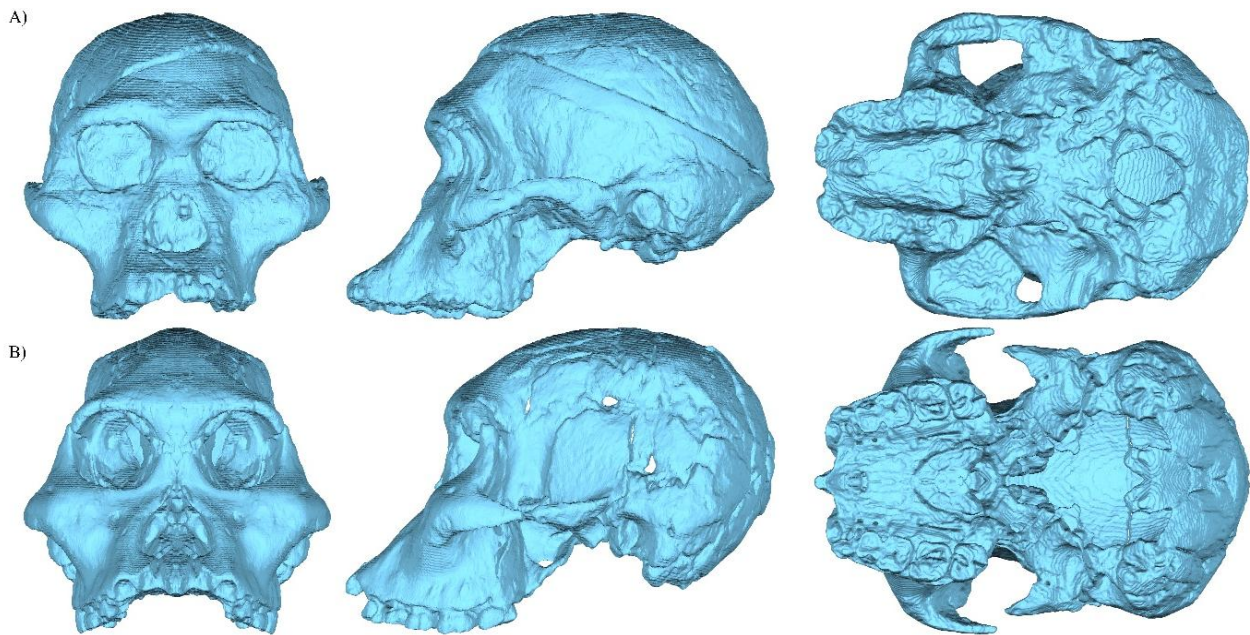


Figure 7: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Australopithecus africanus* specimens: A) Sts 5 (original), and B) Sts 71 (reconstruction).

Australopithecus africanus Dart, 1925 lived between 3.3 and 2.1 Ma in South Africa where numerous key sites such as Sterkfontein, Makapansgat, and Taung (Kimbel, 2015) have yielded fossil specimens. *Australopithecus africanus* was in many aspects similar to earlier australopithecines, with a small brain, but it also presents more advanced features in the face and dentition, suggesting a closer evolutionary link to humans. The species displayed a mix of both primitive traits (such as a somewhat projecting face and long arms) and more derived human-like characteristics, including a more rounded cranium, reduced canine teeth, and evidence of bipedal locomotion (Kimbel, 2015). *A. africanus* is believed to have been omnivorous, with a diet that included fruit, leaves, and possibly some meat, based on dental wear patterns. Though it shared many traits with earlier australopithecines, *A. africanus* is often regarded as a potential ancestor or sister species to later human species, marking a significant step in the evolution of hominins in terms of brain development, social behaviour, and locomotion (Grine, 2013). The taxonomic classification of the specimens of *Australopithecus africanus* Dart, 1925 has been the subject of significant discussion. Some researchers have identified them as *Plesianthropus transvaalensis* (Broom, 1939), while others have classified them as *A. afarensis* (Clarke, 2008). Initially, this species was thought to be the common ancestor of two later hominid groups, *A. robustus/boisei* and *Homo*, as suggested by Tobias (1980). In this sample, the *A. Africanus* OTU is composed of the specimens Sts 5 (“Mrs. Ples”) and Sts 71 (see Figure 7). Those specimens are dated from around 2.07 Ma for STS5 and 2.61-2.7 Ma for STS71 (Schwarcz et al., 1994). They were discovered in Member 4 of Sterkfontein Formation in South Africa

in 1947 by R. Broom and J. T. Robinson (Broom and Robinson, 1950). While **Sts 5** was described as a well-preserved subadult cranium (Broom and Robinson, 1950), **Sts 71** is a fragmented calvaria. It was reconstructed by tomography by Conroy et al. (2000). We used this reconstruction because it provides a more complete and anatomically coherent representation of the original specimen, allowing for more reliable comparative analyses. The tomographic reconstruction corrects for post-depositional deformation and fragmentation, enabling the extraction of consistent metric and morphological data necessary for phylogenetic interpretations.

II.3. *Homo* fossils

The genus *Homo*, originally described by Linnaeus in 1758, is composed of various species, all of which, but *Homo sapiens*, are extinct. In the present study, we defined 18 OTU in order to reflect the morphological diversity of the genus, taking into account the various taxonomical debates surrounding the definition of the species of the genus (see Appendix 1).

Homo rudolfensis (Alexeev, 1986) lived approximately 1.9 to 1.8 Ma during the early Pleistocene. The species is primarily known from fossils found at Koobi Fora in northern Kenya. *Homo rudolfensis* was initially described as a distinct species based on its larger brain size and more modern features compared to other early *Homo* species, such as *Homo habilis* (Wood, 1992a). The species is characterized by a larger brain size (approximately 750–800 cm³), which is significantly larger than that of *Homo habilis*, though still much smaller than modern humans. It also had a flat face and larger molars, with a more human-like body structure that suggests it may have been capable of more efficient bipedal locomotion (Schrenk et al., 2007). However, *H. rudolfensis* still retained some primitive features, such as a relatively small body size and long arms.

H. habilis Leakey et al., 1964 is one of the earliest species of the genus *Homo*, often regarded as a pivotal point in human evolution. It lived approximately 2.4 to 1.4 Ma. Fossils of *H. habilis* have been primarily found in East Africa, with key sites including Olduvai Gorge (Tanzania) and Koobi Fora (Kenya). The species was first described in 1964 by L. Leakey and his colleagues, based on a partial skull and hand bones from Olduvai Gorge. *Homo habilis* is characterized by its relatively small brain size (around 510–600 cm³), which is larger than that of earlier australopithecines, but smaller than that of later *Homo* species (Schrenk et al., 2007). The species also exhibits larger teeth, and a more rounded calvarium compared to earlier hominins, such as *Australopithecus*. The bipedal locomotion of *H. habilis* is evident from its pelvis and lower limb morphology, although its long arms and ape-

like proportions suggest it retained some arboreal adaptations (Ruff, 2009). One of the key features of *Homo habilis* is its association with stone tools, specifically Oldowan tools, which marks an important shift in hominin behaviour (Kimbel et al., 1996). The species is often credited with the development of simple toolmaking techniques, a significant step toward the cultural and technological advancements seen in later *Homo* species (Kimbel et al., 1996; Schrenk et al., 2007).

The taxonomic status of *Homo rudolfensis* and *Homo habilis* are still debated. Some researchers consider *H. rudolfensis* a variant of *H. habilis*, while others view it as a separate species in the genus *Homo* (Stringer, 1986; Tattersall and Schwartz, 2009). The debate mainly centres around the differences in cranial features and brain size compared to other early *Homo* species, but the lack of complete fossils makes it difficult to draw definitive conclusions. For some researchers *H. habilis* is a direct ancestor of *Homo erectus*, while others suggest it may represent a distinct evolutionary branch of early *Homo*. Its exact place in human evolution remains somewhat controversial due to its mixture of primitive and derived traits. The debate surrounds three particular specimens: KNM-ER 1470, KNM-ER 1813 and OH24. Initially, KNM-ER 1470 was allocated to *Homo sp. indet.* (Leakey, 1973). It was later attributed to *H. habilis* (Leakey, 1976), *Pithecanthropus rudolfensis* (Alexeev, 1986), before being classified as *H. rudolfensis* (Groves, 1991; Wood, 1992a). KNM-ER 1813 was attributed to *A. sp. indet.* (Day et al., 1976; Leakey, 1974), before being assigned to *H. africanus* (Olson, 1978), *H. habilis* (Howell, 1978), *A. cf. africanus* (Walker, 1981), *H. antiquus* (Ferguson, 1987), *H. ergaster* (Groves, 1989), *H. habilis* (Wood, 1991). It was also described as the holotype of *H. microcranous* (Ferguson, 1995). This specimen is currently attributed to *H. habilis*. OH 24 fossil was originally attributed to *H. aff. habilis* (Leakey et al., 1971). No taxonomic revision were made (Wood, 2011). The specimens KNM-ER 1470 and KNM-ER 1813 are still in the middle of ongoing debate regarding their classification as the same or different species (Prat, 2022). KNM-ER 1470 has been identified as *H. habilis* (Walker and Leakey, 1978), *H. rudolfensis* (Alexeev, 1986; Argue, 2016; Wood, 1992b; Zeitoun, 2000), and even as an *Australopithecus* species (Walker and Leakey, 1978), with some researchers suggesting it could represent a sister group to both *H. habilis* and *H. rudolfensis* according to Groves (1989). On the other hand, the KNM-ER 1813 skull has been variously attributed to *A. africanus* (Walker and Leakey, 1978), *H. ergaster* (Groves, 1989; Groves and Mazak, 1975; Zeitoun, 2000), and *H. habilis* (Lieberman et al., 1996).



Figure 8: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo rudolfensis* specimen, KNM-ER 1470 (original).

In the present study, the *H. rudolfensis* OTU is composed of one specimen: **KNM-ER 1470** (see Figure 8). He was collected in 1972 by B. Ngeneo on the East river of Turkana Lake, in East Turkana in Kenya (Leakey, 1973). This calvarium comes from area 131 of Koobi Fora Formation, 35.5 metres below the KBS tuff of the upper Burgi Member (Wood, 2011). This specimens is dated to ~1.8 Ma (Gathogo and Brown, 2006). The fossil is a skull without the mandible and with a fragmented base (Walker, 1981).

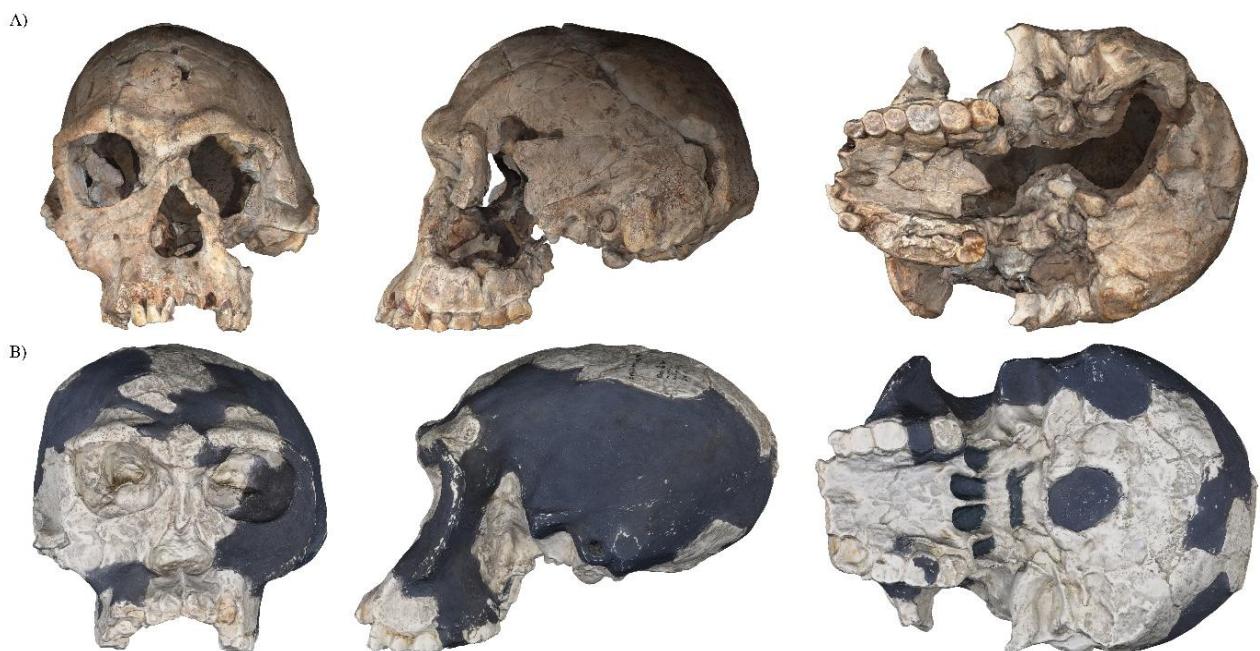


Figure 9: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo habilis* specimens: A) KNM-ER 1813 (original), and B) OH24 (original).

The OTU *H. habilis* is represented by two fossils: KNM-ER 1813 and OH24 (see Figure 9). **KNM-ER 1813** was collected in 1973 by K. Kimeu on the East river of Turkana Lake, in East Turkana in Kenya (Day et al., 1976; Leakey, 1974). This fossil comes from the Upper Burgi Member of the Koobi Fora Formation beneath the KBS tuff. This specimens is dated to >1.78 Ma (Feibel et al., 2009). This

specimen is a nearly complete cranium. **OH 24** was discovered by P. Nzube in 1968 in Bed I in Olduvai Gorge in Tanzania (Leakey et al., 1971). It is dated at around 1.8 Ma (Tamrat et al., 1995). This fossil is a distorted and fragmented cranium, but was reconstructed by Leakey et al. (1971).



Figure 10: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo georgicus* specimens: A) D2282 (original), B) 2700 (original), and C) D4500 (cast).

Homo georgicus Gabounia, de Lumley, Vekua, Lordkipanidze and de Lumley 2002 is an early human species that lived approximately 1.8 Ma. The first fossils attributed to the species were discovered in 1999 in unit Stratum B1 at the Dmanisi site in Republic of Georgia (the Caucasus region), where fossils of several individuals were found, including partial skulls, mandibles, and teeth. The discovery of *H. georgicus* has had profound implications for understanding the dispersal of early *Homo* species out of Africa. The fossils of *H. georgicus* are remarkably similar to those of *H. habilis* in terms of brain size (around 600–750 cm³) and overall morphology. However, *H. georgicus* exhibits features that are somewhat more advanced, including a more human-like face, smaller teeth, and a larger body size compared to earlier hominins like *H. habilis* (de Lumley et al., 2006). One of the most important aspects of *H. georgicus* is its role in the early human migration out of Africa. The Dmanisi site, where the fossils were found, is one of the earliest known sites outside of Africa, showing that

early humans had already begun to spread into Eurasia well before the appearance of *Homo erectus*. The taxonomic status of *H. georgicus* has been debated, with some researchers considering it a distinct species within the genus *Homo*, while others argue it might simply represent an early population of *Homo erectus*. These Dmanisi specimens were originally allocated to *H. aff. H. ergaster* (Gabounia, Vekua, and Lordkipanidze, 2000). They were later assigned to *H. erectus* (Rightmire et al., 2006) and *H. georgicus* (de Lumley et al., 2006; Gabounia et al., 2002). Their current taxonomic allocation is debated. The study of these skulls, particularly D4500, has been used to support the idea that several species or subspecies previously classified within the genus *Homo* should actually be regarded as part of a single lineage, *H. erectus* (Lordkipanidze et al., 2013). These fossil are dated around ~1.77 Ma (Gabounia, Vekua, Lordkipanidze, et al., 2000; Lordkipanidze, 1999).

H. georgicus is represented by one OTU, “Dmanisi”, composed of three specimens: D2700, D2282 and D4500 (see Figure 10). **D2700** was discovered in 2001 by G. Kiladze (Vekua et al., 2002). This fossil is a complete sub-adult cranium (de Lumley et al., 2006). **D2282** is a complete cranium, discovered in 1999 by A. Justus (Gabounia, Vekua, Lordkipanidze, et al., 2000; Lordkipanidze et al., 2013; Vekua et al., 2002). **D4500** was discovered in 2005 by L. Gabunia and D. Lordkipanidze and colleagues (Lordkipanidze et al., 2013). D4500 is a complete, but fragmented cranium.



Figure 11: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo ergaster* specimens: A) KNM-ER 3733 (original), and B) KNM-ER 3883 (original).

Homo ergaster Groves and Mazak, 1975 is a species that lived approximately 1.9 to 1.4 Ma. The fossils of *H. ergaster* have been primarily found in East Africa, particularly at sites like Koobi Fora and

Olduvai Gorge (Tattersall, 2015). *Homo ergaster* is notable for its larger brain (ranging from 600 to 910 cm³), which represents a significant increase over earlier species like *Homo habilis*. The species also displayed a more modern body shape, with longer legs, narrower hips, and smaller teeth, which suggest obligatory bipedalism and possibly more advanced tool use (Walker and Leakey, 1993). The taxonomic status of *H. ergaster* is still debated (Tattersall, 2015). Some scientists consider it a distinct species, while others argue that it represents an African variant of *Homo erectus*. The *H. ergaster* Groves and Mazak, 1975 OTU is composed of two specimens: KNM-ER 3733 and KNM-ER 3883. Originally, KNM-ER 3733 specimen was classified as *H. habilis* (T. D. White et al., 1981), but was later attributed to *H. erectus* (Grine et al., 1996; Leakey and Walker, 1985; Walker and Leakey, 1993) before being reassigned to *H. ergaster* (Groves, 1989; Tattersall, 2015). Its taxonomic allocation is still debated. On the other hand, KNM-ER 3883 was classified as *H. erectus* (Grine et al., 1996; Leakey and Walker, 1985; Walker and Leakey, 1993) before being reassigned to *H. ergaster* (Groves, 1989; Tattersall, 2015). Some researchers even suggested that those specimens might represent two different new species (Zeitoun, 2000).

KNM-ER 3733 was found in 1975 by B. Ngeneo in Koobi Fora in Kenya (Leakey, 1976; Leakey and Walker, 1985) (see Figure 11). This well-preserved cranium was discovered in area 104 of Koobi Fora, between the KBS and Koobi Fora/BBS tuffs, and is dated around ~1.6 Ma (Gathogo and Brown, 2006). **KNM-ER 3883** was discovered in 1976 by R. Leakey and M. Muluila in Koobi Fora in Kenya (Leakey and Walker, 1985). This well-preserved calvaria was discovered in area 1 of Ileret and belongs to the “Okote Member” of the Koobi Fora Formation. It is dated around ~1.6 Ma (Gathogo and Brown, 2006), though KNM-ER 3883 seems older than KNM-ER 3733 (Leakey and Walker, 1985).

Homo erectus sensu stricto (Dubois, 1893) is one of the most important and widely studied species in human evolution. It lived between 1.9 Ma and around 110 ka, making it the longest-lived species of the genus *Homo*. Fossils of *Homo erectus* have been found across Africa, and Eurasia, with notable sites such as Zhoukoudian in China, and Java in Indonesia (Antón, 2003). *Homo erectus* is known for its advanced features compared to earlier hominins. The species had a larger brain (ranging from 600 to 1,100 cm³) than previous species like *Homo habilis*, with some specimens, such as those from Zhoukoudian, showing brain sizes comparable to modern humans. The increased brain size is associated with improved cognitive abilities, suggesting *H. erectus* may have been capable of more complex behaviours, including the use of tools and the control of fire (Antón, 2002). One of the defining characteristics of *H. erectus* is its modern body proportions, which include long legs and

shorter arms, indicating better adaptation to bipedal locomotion. These anatomical features suggest that *H. erectus* was capable of long-distance walking and running, a trait that likely contributed to its ability to disperse across wide geographic regions (Antón, 2003). *Homo erectus* is also known for its association with the Acheulean tool industry, which produced bifacial hand axes and cleavers. These tools represent a significant technological development over Oldowan tools and indicate greater skill in shaping and using stone tools (Antón and Swisher, 2004; Toth and Schick, 2015).

In the present study, *Homo erectus* (Dubois, 1893) was divided into three pairs of specimens from the Sangiran, Zhoukoudian, and Ngandong sites to illustrate its temporal and geographic variability.

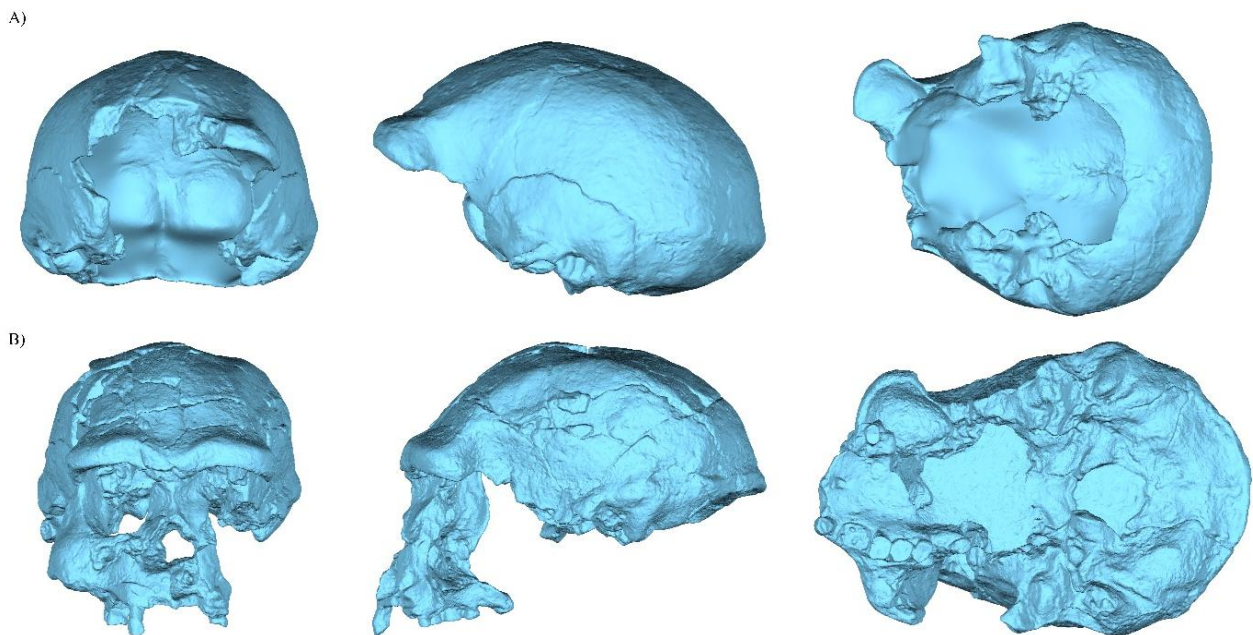


Figure 12: *Norma facialis*, *norma lateralis* and *norma basilaris* of Sangiran specimens: A) Sangiran 2 (original), and B) Sangiran 17 (original).

Two specimens come from the Sangiran locality (Java, Indonesia) and are constituting the Sangiran OTU, the skulls Sangiran 2 and Sangiran 17. The Sangiran site has been dated to between 1.02 ± 0.06 Ma and 1.51 ± 0.08 Ma (Antón, 2003; Antón and Swisher, 2004; Larick et al., 2001). Originally, these specimens were classified as *Pithecanthropus erectus* by von Koenigswald (1940) and as *Pithecanthropus erectus sensu stricto* by Weidenreich (1945). According to Jacob (1980), Sangiran 2 is a *Pithecanthropus erectus* and Sangiran 17 a *Pithecanthropus soloensis*, whereas according to Sartono (1976) they belong to *Homo palaeojavanicus sangiransis*. Sartono, in 1982, considered it to be an archaic *Homo erectus*.

Sangiran 2 was discovered in 1937 and later described by G. von Koenigswald (see Figure 12). According to the stratigraphy established by De Terra in Van Heekeren (1972), this specimen comes

from the Trinil layers of the Kabuh Formation. This fossil is a cranium missing the base and a part of the left sided frontal region. **Sangiran 17** was discovered by Mr. Tukimin on the south bank of the Putjung stream, a tributary of the Tjemoro River, this fossil is attributed to the Trinil level of the Kabuh Formation by Sartono (1971). It is known to be the most complete Javanese *H. erectus* cranium.



Figure 13: *Norma facialis*, *norma lateralis* and *norma basilaris* of Zhoukoudian specimens: A) *Sinanthropus III* (original), and B) *Sinanthropus XI* (original).

The Zhoukoudian OTU is composed of two specimens: *Sinanthropus III* and *Sinanthropus XI* (see Figure 13). The Zhoukoudian specimens are known as *Sinanthropus pekinensis* Black, 1927. This nomenclature was proposed based on a single tooth by Black and then extended to the calvarium of the *Sinanthropus III* specimen. They were later placed within the *H. sapiens* clade (Campbell, 1962; Zeitoun, 2000) but is more commonly classified as *H. erectus*. They come from the Zhoukoudian site in Hopei Province, north of Beijing (China). They were discovered by D. Black in early 1930's (Black, 1930, 1934). **Sinanthropus III** was discovered in Locus E, in a sheltered corner of the lower east cave of the Lower Fissure, while **Sinanthropus XI** come from layers 8-9 according to Pope (1992). They are both the most complete calvariae described by Weidenreich (Weidenreich, 1943; Zeitoun, 2000). They are dated between ~0.68 Ma and ~0.78 Ma (Shen et al., 2009).



Figure 14: *Norma facialis*, *norma lateralis* and *norma basilaris* of Ngandong specimens: A) Ngandong 7 (original), and B) Ngandong 14 (original).

The Ngandong OTU is composed of **Ngandong 7** and **14** (see Figure 14). These two specimens are part of a series and Ngandong 1 constitute the holotype of *Homo (Javanthropus) soloensis* Oppenoorth, 1932. Dubois (1940) did not agree with the attribution of von Koenigswald to *Pithecanthropus erectus* and used the trinomial *Homo sapiens soloensis* for the Ngandong specimens. They were later attributed to *Homo erectus* by Santa Luca (1980), late *Homo erectus* by Sartono (1982) and evolved *Homo erectus* by Lumley and Sonakia (1985). The Ngandong site was discovered by W. Oppenoorth in 1932, near the river Solo in Java (Indonesia) (Oppenoorth, 1932). This site has unearthed several specimens thought to be *Homo erectus*. These two specimens are well-preserved calvariae. The stratigraphic position of these fossils is disputed and a consensus on the dating of the site is very difficult to reach. Proposed dates range from 200 ka to 25 ka (Swisher et al., 1996; Grün and Thorne, 1997). Rizal et al. (2020) recently proposed a direct absolute dating of the Ngandong specimens between 108 and 117 ka.

Homo neandertalensis King, 1864, commonly known as Neandertals, were a species of archaic humans that lived in Europe and Western Asia between 400,000 and 40,000 years ago (Hublin, 1998). They are one of the closest extinct relatives to modern humans, with whom they shared a common ancestor approximately 600,000 years ago (Mendez et al., 2016). Neandertals are known for their distinctive robust physique, which was adapted to the cold, with features such as short, stocky bodies, large noses, and broad, muscular frames (Harvati, 2015). The Neandertal brain was comparable in size to that of modern humans, and in some cases, even larger, ranging between 1,200

to 1,750 cm³. This suggests that they had sophisticated cognitive abilities, although their brain structure was slightly different from that of modern humans, with the occipital lobe (associated with visual processing) being larger and the frontal lobe (linked to higher-order thinking) slightly smaller (Holloway, 1985). Evidence suggests that Neandertals were capable of fabricating and using tools (they are mainly associated with the Mousterian tool industry), controlling fire, and burring their dead (e.g., La Chapelle-aux-Saints and La Ferrassie), as seen in cave paintings and carvings (Harvati, 2015; Toth and Schick, 2015). Neandertals are also known for their interbreeding with anatomically modern humans (*Homo sapiens*), and some modern humans still carry traces of Neandertal DNA, around 1% to 2% in people of non-African descent (Green et al., 2010; Prüfer et al., 2014).

To reflect populations that genetic data distinguish as distinct and which come from different periods and geographic regions (Fabre et al., 2009), three OTUs were defined. The "early Neandertal" OTU includes the specimens Saccopastore 1 and Ehringsdorf H; the "Near East Neandertal" OTU consists of Amud 1 and Shanidar 1; and the "Classic Neandertal" OTU includes the specimens from Monte Circeo, La Ferrassie 1, and La Chapelle-aux-Saints.



Figure 15: *Norma facialis*, *norma lateralis* and *norma basilaris* of "Early Neandertals" specimens: A) Saccopastore 1 (cast), and B) Ehringsdorf H (cast).

The "Early Neandertal" OTU is composed of the two oldest Neandertal specimens of this sample (see Figure 15). The fossil used in this study were initially allocated to *H. neandertalensis* and *H. neandertalensis aniensis* during the 1930's (Wood, 2011).

Saccopastore 1 was discovered by A. Giovannini and V. Casorri in 1929 in a sand and gravel quarry in Rome (Italy) (Wood, 2011). The specimen is estimated to be between 130 and 250 ky (Marra et al., 2015). This fossil is a cranium missing part of the supraorbital region. He displays many Neandertal traits, but do not fully correspond to the morphological pattern of classic Neandertals. On the other hand, this skull is morphologically very close to Near Eastern Neandertals (Condemi, 1992; Sergi, 1944, 1948). **Ehringsdorf H** was discovered in between 1908 and 1928 by F. Weidenreich in the Weimar-Ehringsdorf quarry in Germany (Weidenreich, 1928). The site has been dated to at least 200 ka (Grün and Stringer, 1991). This fossil consists of a calvarium, missing the face and the base of the cranium (Street et al., 2006; Vleck, 1993). The morphology of the calvaria shows similarities with the Steinheim specimen and with other fossil individuals from the late Middle Pleistocene (e.g. La Chaise) considered by many researchers to be early representatives of Neandertals (proto-Neandertals) (Condemi, 2001; Dean et al., 1998).

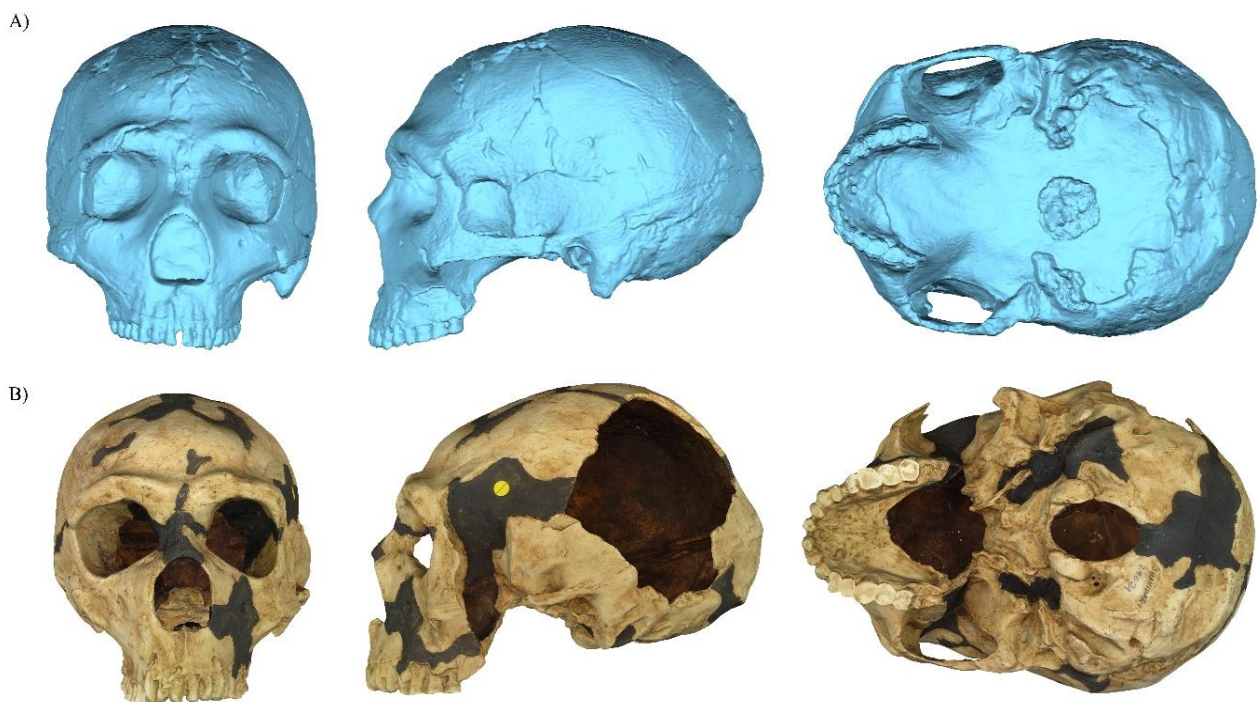


Figure 16: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Near East Neandertals” specimens: A) Amud 1 (original), and B) Shanidar 1 (original).

The “Near East Neandertal” OTU consist of two more recent fossils from Middle East: Amud 1 and Shanidar 1 (see Figure 16). Amud 1 fossil was originally assigned to *H. neandertalensis* (Hovers et al., 1995), but it was rejected by Arensburg and Belfer-Cohen (1998). Similarly, Shanidar 1 fossil was attributed to *H. sapiens neandertalensis*, before being assigned to *H. neandertalensis* (Wood, 2011).

Amud 1 was discovered on the north shore of Lake Tiberias, 500 m upstream from the Zuttiyeh cave by H. Suzuki and colleagues in 1961 in a cave (Suzuki, 1970; Vallois, 1962). The burial of this individual is located at the top of member B1 of the stratigraphy of the site Amud in Israel (Chinzei, 1970). This fossil has been dated between ~50 and ~60 ka (Grün and Stringer, 1991; Rink et al., 2013). The calvarium is complete, while the face is damaged (missing nasal bones and part of the maxilla), the mandible is complete except for the right condyle and coronoid process (Suzuki and Takai, 1970).

Shanidar 1 was discovered in 1957 by R. Solecki and his team in the Shanidar cave during a prospecting mission in northern Iraq (Mounier, 2009). The site is dated to between 60 and 80 ky (Trinkaus, 1991). This fossil present a complete cranium (Trinkaus, 1983).

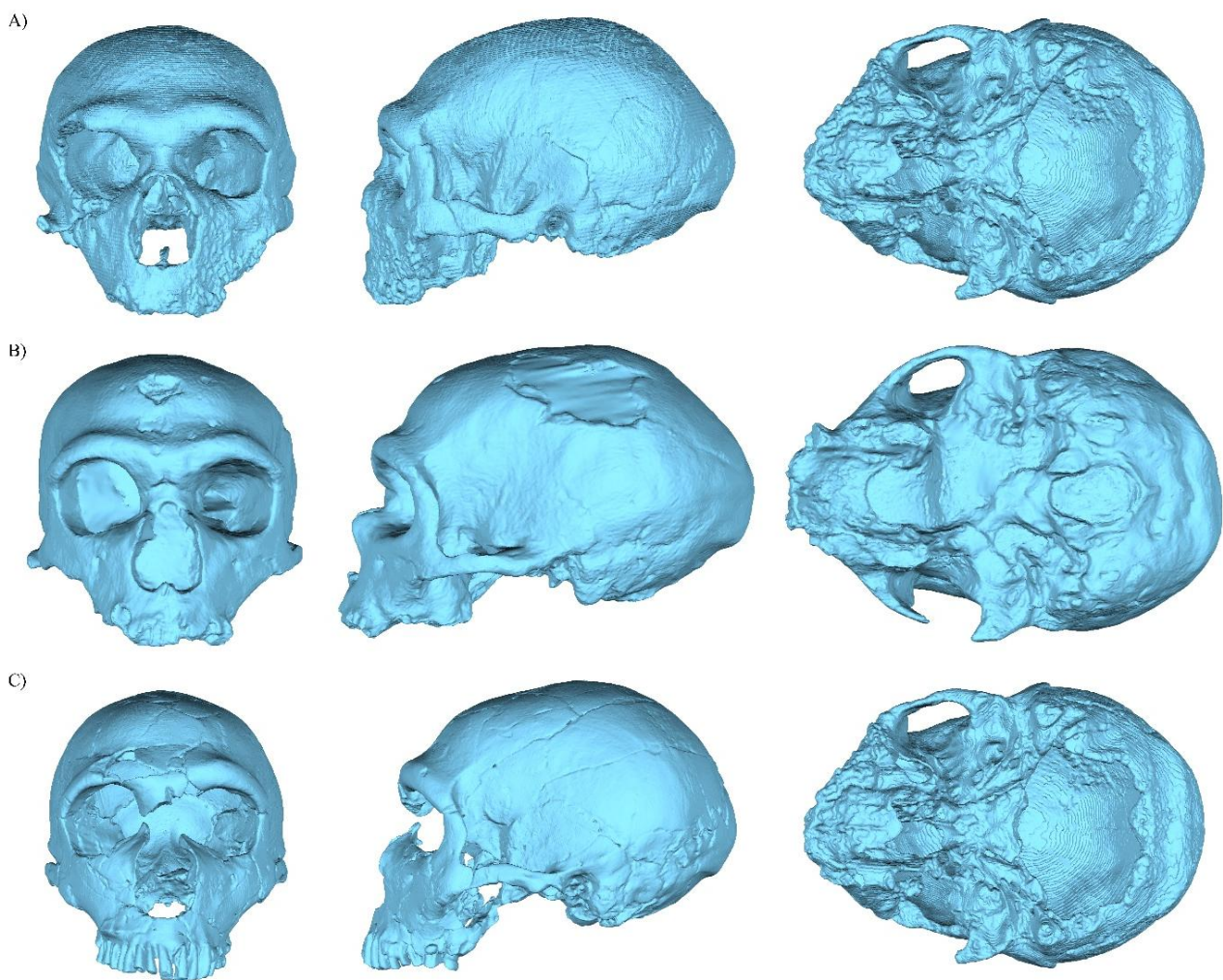


Figure 17: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Classic Neandertals” specimens: A) Monte Circeo 1 (original), B) La Chapelle-aux-saints 1 (cast), and C) La Ferrassie 1 (original).

The “Classic Neandertal” OTU include three recent European specimens: Monte Circeo 1, La Chapelle-aux-Saints, and La Ferrassie 1 (see Figure 17). The initial taxonomic allocation for all this specimen was *H. neandertalensis*, there was no taxonomic revision (Boule, 1911, 1912, 1913, 1921).

Monte Circeo 1, also known as Guattari 1, was discovered on the surface in a cave room at the Guattari site in Montecirceo in Italy during the 1940's and described by S. Sergi in 1991 (Sergi, 1991). It was dated from 52 ± 12 ky (Grün and Stringer, 1991). This fossil is a "[...] a fairly complete cranium [...]" (p. 291, Wood, 2011). It is complete except for the base of the skull and the right side of the face. **La Chapelle-aux-Saints** was discovered in 1908 by Abbés A. and J. Bouyssonie and their brother P. Bouyssonie in the cave at La Chapelle-aux-Saints (Corrèze, France) (Boule, 1911, 1912, 1913). The site is estimated by ESR at between 56 ± 4 ka and 47 ± 3 ka (Grün and Stringer, 1991). The skeleton of an elderly man was discovered during excavations and is complete, apart from the nasal bones. This fossil is a nearly complete cranium. **La Ferrassie 1** was discovered in 1909 in the rock shelter at La Ferrassie in Dordogne (France) during excavations carried out between 1905 and 1921 by D. Peyrony and L. Capitan. Absolute dating by ESR on bovid teeth from the same geological stratum as La Ferrassie 1 put the age at 55 ± 2 ky to 61 ± 5 ky (Blackwell et al., 2007). La Ferrassie 1 specimen is well preserved, with nasal bones missing, gaps in the maxillo-alveolar area and the right maxilla. The mandible is in good condition, with the right condyle absent (Boule, 1921; Heim, 1976; Peyrony and Capitan, 1909).

Homo sapiens (Linnaeus, 1758), the species to which all current modern humans belong, first appeared >235 ka in Africa, based on fossil and genetic evidence (Vidal et al., 2022). Anatomically, *Homo sapiens* is characterized by a relatively small face, large brain (averaging 1,300–1,400 cm³), and a gracile body. The cranial structure of *H. sapiens* is distinct, with a more rounded skull, a prominent chin, and smaller teeth and jaws compared to earlier species (Bräuer, 2007). Similarly to Neandertals, these anatomical features are associated with advanced cognitive abilities, which allowed our ancestors to create and manipulate tools, develop social networks, and adapt to a wide range of environments. This is reflected in the early evidence of symbolic behaviour, such as art, burials, and the possible use of spoken language that could have been inherited from the last common ancestor of *H. neandertalensis* and *H. sapiens* (Mounier, et al., 2020), which marks a clear distinction from other hominins like *H. erectus*. Fossil evidence suggests that *H. sapiens* lived alongside other hominins, such as Neandertals and Denisovans (e.g., Hawks, 2017; Hublin, 2000; Rogers et al., 2017). These interactions likely included cultural exchanges and interbreeding, contributing to the genetic diversity seen in modern human populations today (Prüfer et al., 2017).

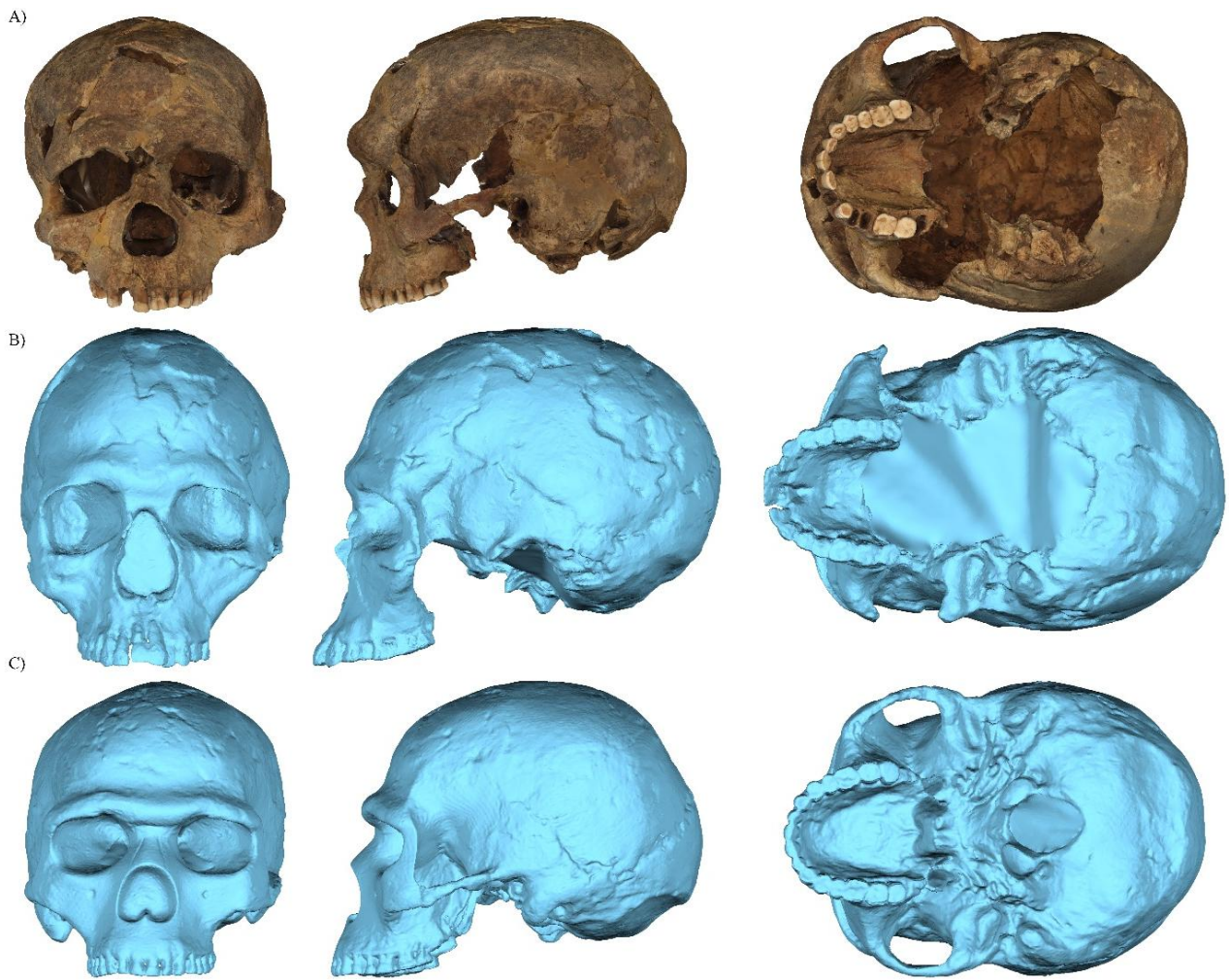


Figure 18: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Early *H. sapiens*” specimens: A) Qafzeh 6 (original), B) Qafzeh 9 (cast), and C) Skhul V (cast).

To account for variability within *H. sapiens*, the distinction of the earliest specimens from the modern human was made with the creation of one OTU “Early *H. sapiens*”. This OTU corresponds to fossil specimens of *H. sapiens*, including Qafzeh 6, Qafzeh 9, and Skhul V (see Figure 18). The initial taxonomic allocation for Qafzeh 6 and 9 was *H. sapiens*, there was no taxonomic revision (Vandermeersch, 1970, 1971, 1981). On the contrary, Skhul V was initially attributed to *Palaeoanthropus palestinensis*, a large number of taxonomical reviews were made over the years (e.g. Brothwell, 1961; Garrod and Bate, 1937; Higgs, 1961; Howell, 1957; Stewart, 1960). This fossil is now attributed to *H. sapiens*.

Qafzeh 6 was discovered in 1934 by R. Neuville and M. Stekelis in the inferior Cave of Qafzeh Site in Israel (Köppel, 1935). This specimen was dated ~100 ky (Grün et al., 2005; Grün and Stringer, 1991). It is a well-preserved, but fragmented cranium. **Qafzeh 9** was discovered in 1969 by B. Vandermeersch in the inferior Cave of Qafzeh Site in Israel (Vandermeersch, 1970). This specimen was dated ~100 ky (Grün et al., 2005; Grün and Stringer, 1991). It is a fragmentary skull. **Skhul V**

was discovered in 1932 by T. McCown and colleagues in the B layer of the Skhul Terrace in Mughareet-es-Skhul in Israel (McCown, 1932). This fossil was dated by thermoluminescence between 101 and 137 ky (Mercier et al., 1993) and is an almost complete calvarium.

II.4. Recent *Homo sapiens*

Eight additional OTUs were formed, each containing five recent individuals, to reflect the evolutionary history of human populations, as indicated by genetic diversification between different metapopulations (Mounier and Mirazón Lahr, 2016).

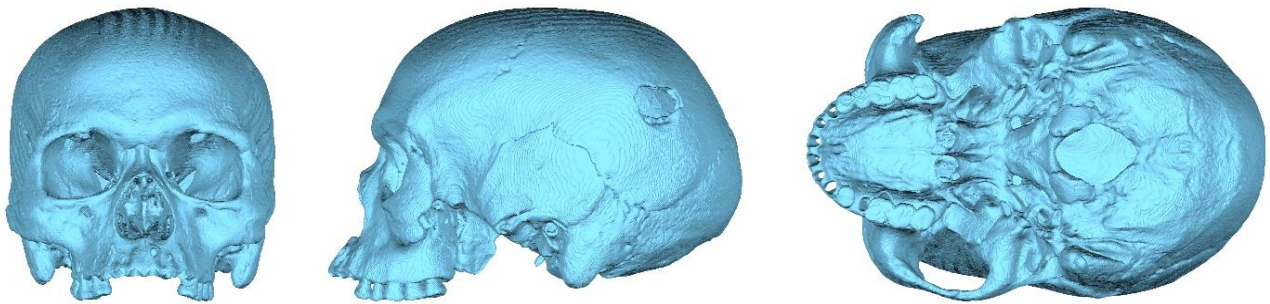


Figure 19: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of KhoiSan's specimens, Kh-1751 (original).

Five **KhoiSan** individuals from the 19th-20th century from South Africa were included (see Figure 19). They were in a satisfactory state of preservation, and age and sex were known. The sex ratio of this assemblage was balanced, with three females and two males (DC, Cambridge). These specimens were obtained through CT-scan.

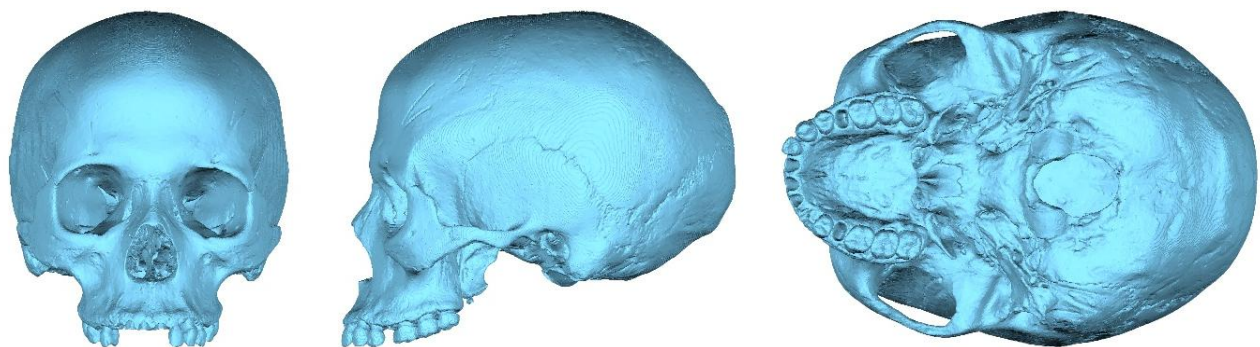


Figure 20: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Haya's specimens, AF.23.0.20 (original).

Five **Haya** individuals from the 19th-20th century from Tanzania were included (see Figure 20). They were in a satisfactory state of preservation, and age and sex were known. The sex ratio of this assemblage was balanced, with three females and two males (DC, Cambridge). These specimens were obtained through CT-scan.



Figure 21: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Kongo's specimens, AfC-9642 (original).

Five **Kongo** individuals from the 19th-20th century from Congo, Angola and Gabon were included (see Figure 21). They were in a satisfactory state of preservation, and age and sex were known for three specimens, but uncertain for two. The sex ratio of this assemblage is supposed to be balanced, with three females and two males (DC, Cambridge, and MH, Paris). Two of these specimens were obtained through CT-scan and three through photogrammetry.



Figure 22: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Mande's specimens, AfW-9543 (original).

Five **Mande** individuals from the 19th-20th century from Mali and Guinea were included (see Figure 22). They were in a satisfactory state of preservation, and age and sex were known. The sex ratio of this assemblage was unbalanced, with four females and one male (DC, Cambridge, and MH, Paris). Two of these specimens were obtained through CT-scan and three through photogrammetry.



Figure 23: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Berber's specimens, AfN-18458 (original).

Five **Berber** individuals from the 19th-20th century from Morocco were included (see Figure 23). They were in a satisfactory state of preservation, and age and sex were uncertain for all the specimens. The sex ratio of this assemblage is supposed to be balanced, with three females and two males (MH, Paris). These specimens were obtained through photogrammetry.



Figure 24: *Norma facialis, norma lateralis and norma basilaris* of one of Papu's specimens, MEL085 (original).

Five **Papu** individuals from the 19th-20th century from Papua-New-Guinea were included (see Figure 24). They were in a satisfactory state of preservation, and age and sex were known for all the specimens. The sex ratio of this assemblage was balanced, with three females and two males (DC, Cambridge). One of these specimens was obtained through CT-scan and four through photogrammetry.

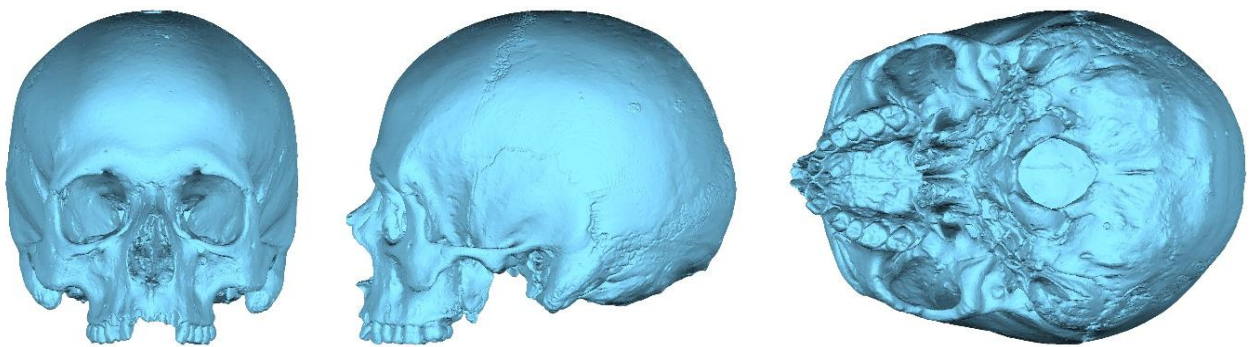


Figure 25: *Norma facialis, norma lateralis and norma basilaris* of one of French's specimens, Eu-1042 (original).

Five **French** individuals from the 19th-20th century from France were included (see Figure 25). They were in a satisfactory state of preservation, and age and sex were known for all the specimens. The sex ratio of this assemblage was balanced, with three males and two females (DC, Cambridge). These specimens were obtained through CT-scan.

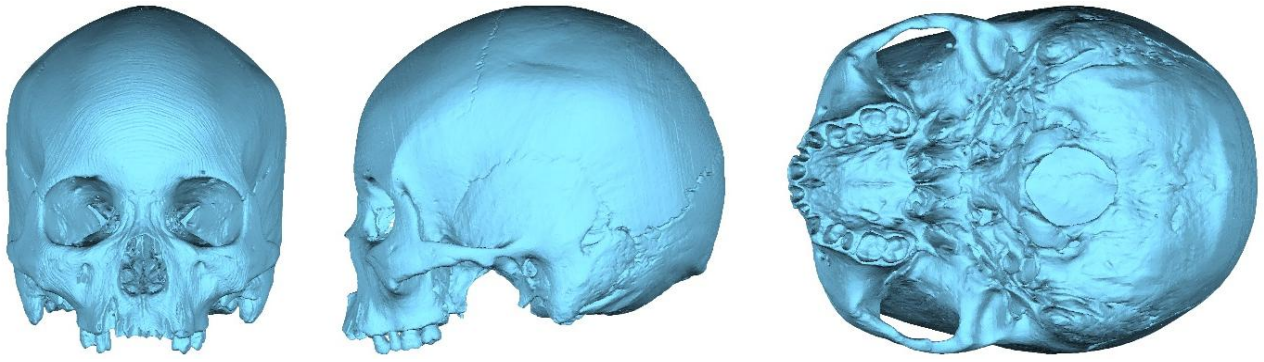


Figure 26: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Chinese's specimens, EAS-ORSA0427 (original).

Five **Chinese** individuals from the 19th-20th century from China were included (see Figure 26). They were in a satisfactory state of preservation, and age and sex were known for all the specimens. The sex ratio of this assemblage was balanced, with three males and two females (OR, Penn Museum). These specimens were obtained through CT-scan.

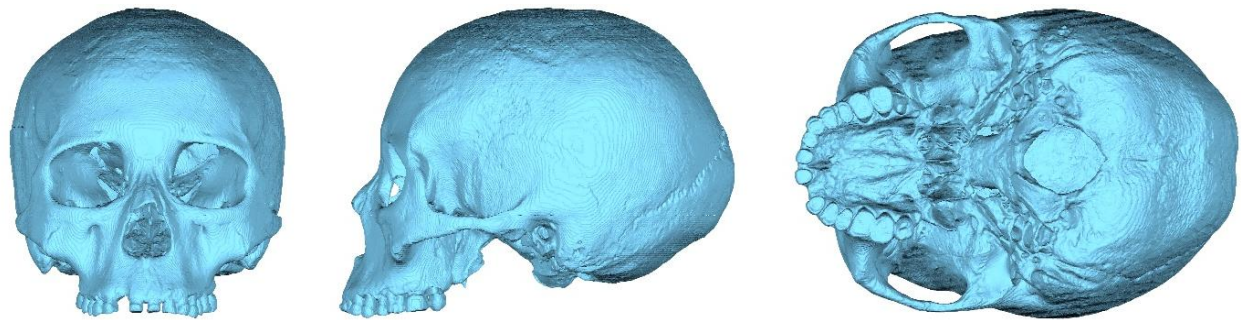


Figure 27: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Inuit's specimens, 99.1-102 (original).

Five **Inuit** individuals from the 19th-20th century from Alaska were included (see Figure 27). They were in a satisfactory state of preservation, and age and sex were known for all the specimens. The sex ratio of this assemblage was balanced, with three females and two males (AM, New-York). These specimens were obtained through CT-scan.

The cladistic analysis was conducted at the population/species level, with the shape data of specimens averaged per population/species, resulting in 23 operational taxonomic units for the analysis.

III. Collect of the 3D models

Most of the 3D models used in this study were obtained by Aurélien Mounier during previous research (e.g., Mounier et al., 2020, 2024; Mounier and Mirazón Lahr, 2016, 2019) through three distinct procedures, depending on the availability of equipment and specimens (see Table 1):

1. Medical computed tomography (CT) scans processed using Amira software (v5.5, FEI),
2. Photogrammetry conducted with Metashape software (v1.8.1),
3. 3D surface scans acquired using an optical scanner (HDI Advance, with 45 μ accuracy, LMI) and processed with Flexscan software (v3.3, LMI).

The remaining 3D models were sourced from various published studies, where different authors have made their datasets publicly available. These authors contributed specimens from their respective research, and the models were provided either as supplementary data or through collaborative access. Specifically, the specimen Sts 71 was retrieved from research works published by Ledogar et al. (2022), who included 3D models of relevant taxa in their studies. This allows for a broader representation of species within the dataset, complementing the models obtained by A. Mounier and diversifying the dataset across different methodologies and research contexts.

Photogrammetry offers a high level of accuracy, enabling the creation of reliable 3D models with an error margin comparable to that of laser surface scanning (Katz and Friess, 2014). When comparing 3D models derived from medical CT scans and laser surface scanning, both techniques yield models of similar quality (Slizewski et al., 2010).

All the figures and photos presented are original to this work.

Table 1: Summary of the specimens studied. The original specimens are presented in bold.

Specimens	Chapter		Sites	Chronology	Scanning technic*	Institution of origin**	References		
	III	IV					First taxonomic attribution	First description	Chronology
<i>Paranthropus</i>									
KNM-WT 17000		x	Lomekwi, West Turkana, Kenya	2.57 - 2.47 Ma	OP	Cast from DC	(Walker et al., 1986)	(Walker et al., 1986)	(Feibel et al., 1989)
OH5		x	Olduvai Gorge, Tanzania	1.79 - 1.85 Ma	CT	Original CT from NMK	(Leakey, 1959)	(Leakey, 1959)	(Hay, 1976)
KNM-ER 406		x	Koobi Fora, Kenya	1.7 Ma	OP	Cast from DC	(Leakey et al., 1971)	(Leakey et al., 1971)	(Feibel et al., 1989)
<i>Australopithecus</i>									
Stw 53		x	Sterkfontein, South Africa	~1.49-2.6 Ma	PH	Cast from Pretoria	(Hughes and Tobias, 1977)	(Hughes and Tobias, 1977)	(Hanon et al., 2018)
AL 444-2		x	Hadar, Ethiopia	~3 Ma	CT	Open access on the virtual anthropology portal of Vienna University	(Kimbel et al., 1994)	(Kimbel et al., 1994)	(Kimbel et al., 1994)
STS5	x	x	Sterkfontein, South Africa	2.07 Ma	CT	DNM	(Broom and Robinson, 1950)	(Broom and Robinson, 1950)	(Schwarcz et al., 1994)
STS71	x	x	Sterkfontein, South Africa	2.61 - 2.07 Ma	CT	DNM	(Broom and Robinson, 1950)	(Broom and Robinson, 1950)	(Schwarcz et al., 1994)
<i>Homo fossils</i>									
KNM-ER 1470	x	x	Koobi Fora, Kenya	~1.8 Ma	PH	NMK	(Leakey, 1973)	(Leakey, 1973)	(Gathogo and Brown, 2006)
KNM-ER 1813	x	x	Koobi Fora, Kenya	>1.78 Ma	PH	NMK	(Leakey, 1974)	(Day et al., 1976)	(Feibel et al., 2009)
OH24		x	Olduvai Gorge, Tanzania	~1.8 Ma	PH	MH	(Leakey et al., 1971)	(Leakey et al., 1971)	(Tamrat et al., 1995)
D2282	x	x	Dmanisi, Georgia	~1.77 Ma	PH	IPH	(Gabunia et al., 2000)	(Gabunia et al., 2000)	(Lordkipanidze, 1999)
D2700		x	Dmanisi, Georgia	~1.77 Ma	PH	NHM	(Vekua et al., 2002)	(Vekua et al., 2002)	(Lordkipanidze, 1999)
D4500	x	x	Dmanisi, Georgia	~1.77 Ma	PH	FD	(Lordkipanidze et al., 2013)	(Lordkipanidze et al., 2013)	(Lordkipanidze, 1999)
KNM-ER 3733	x	x	Koobi Fora, Kenya	~1.6 Ma	PH	NMK	(Leakey and Walker, 1985)	(Leakey and Walker, 1985)	(Gathogo and Brown, 2006)
KNM-ER 3883	x	x	Koobi Fora, Kenya	~1.6 Ma	PH	NMK	(Leakey and Walker, 1985)	(Leakey and Walker, 1985)	(Gathogo and Brown, 2006)

Specimens	Chapter		Sites	Chronology	Scanning technic*	Institution of origin**	References		
	III	IV					First taxonomic attribution	First description	Chronology
Sangiran 2	x	x	Sangiran, Java, Indonesia	1.02 - 1.50 Ma	CT	SFN	(Van Heekeren, 1972)	(Rightmire, 1990)	(Larick et al., 2001)
Sangiran 17	x	x	Sangiran, Java, Indonesia	1.02 - 1.50 Ma	OP	IPH	(Sartono, 1971)	(Rightmire, 1990)	(Larick et al., 2001)
Sinanthropus III	x	x	Zhoukoudian, Beijing, China	~0.68 - 0.78 Ma	PH	IPH	(Weidenreich, 1943)	(Weidenreich, 1943)	(Shen et al. 2009)
Sinanthropus XI	x	x	Zhoukoudian, Beijing, China	~0.68 - 0.78 Ma	PH	IPH	(Weidenreich, 1943)	(Weidenreich, 1943)	(Shen et al. 2009)
Ngandong 7	x	x	Ngandong, Solo River, Java, Indonesia	108 - 117 ka	PH	IPH	(Oppenoorth, 1932)	(Santa Luca, 1980)	(Rizal et al., 2020)
Ngandong 14	x	x	Ngandong, Solo River, Java, Indonesia	108 - 117 ka	PH	IPH	(Oppenoorth, 1932)	(Santa Luca, 1980)	(Rizal et al., 2020)
Saccopastore 1	x	x	Saccopastore, Italy	130-250 ka	PH	SU	(Sergi, 1944)	(Condemi, 1992)	(Marra et al., 2015)
Ehringsdorf H	x	x	Ehringsdorf, Germany	~200 ka	PH	IPH	(Weidenreich, 1928)	Street et al., 2006	(Grün and Stringer, 1991)
Amud 1	x	x	Amud, Israel	50-60 ka	OP	DC	(Suzuki, 1970)	(Suzuki, 1970)	(Rink et al., 2013)
Shanidar 1	x	x	Shanidar, Iraq	60 - 80 ka	PH	MH	(Trinkaus, 1983)	(Trinkaus, 1983)	(Trinkaus, 1991)
Monte Circeo 1	x	x	Monte Circeo, Italy	52 +/- 12 ka	CT	MP	(Sergi, 1991)	(Sergi, 1991)	(Grün and Stringer, 1991)
La Chapelle- aux-Saints	x	x	La-Chapelle- aux-Saints, France	~50 ka	CT	MH	(Boule, 1911, 1912, 1913)	(Boule, 1911, 1912, 1913)	(Grün and Stringer, 1991)
La Ferrassie 1	x	x	La Ferassie, France	53-66 ka	CT	MH	(Peyrony and Capitan, 1909)	(Heim, 1976)	(Blackwell et al., 2007)
Qafzeh6	x	x	Qafzeh, Israel	~100 ka	PH	IPH	(Köppel, 1935)	(Vandermeersch, 1981)	(Grün et al., 2005)
Qafzeh9	x	x	Qafzeh, Israel	~100 ka	OP	DC	(Vandermeersch, 1970)	(Vandermeersch, 1970)	(Grün et al., 2005)
SkhūlV	x	x	Mugharet-es- Skhul, Israel	101 - 137 ka	CT	PM	(McCown, 1932)	(McCown and Sir Keith, 1939)	(Mercier et al., 1993)

Recent *Homo sapiens*

KhoiSan (n=5)	x	x	Republic of South Africa	19-20th century	CT	DC	-	(Mounier and Mirazón Lahr, 2019)
Haya (n=5)	x	x	Tanzania	19-20th century	CT	DC	-	(Mounier and Mirazón Lahr, 2019)
Kongo (n=5)	x	x	Congo, Angola and Gabo	19-20th century	CT, PH	DC, MH	-	(Mounier and Mirazón Lahr, 2019)
Mande (n=5)	x	x	Mali, Ginea	19-20th century	CT, PH	DC, MH	-	(Mounier and Mirazón Lahr, 2019)
Berber (n=5)	x	x	Marocco	19-20th century	PH	MH	-	(Mounier et al., 2024)

Specimens	Chapter		Sites	Chronology	Scanning technic*	Institution of origin**	References		
	III	IV					First taxonomic attribution	First description	Chronology
Papu (n=5)	x	x	Papua-New-Guinea	19-20th century	CT, PH	DC	-	(Mounier and Mirazón Lahr, 2019)	
French (n=5)	x	x	France	19-20th century	CT	DC	-	(Mounier and Mirazón Lahr, 2019)	
Chinese (n=5)	x	x	China	19-20th century	CT	OR	-	(Mounier and Mirazón Lahr, 2019)	
Inuit (n=5)	x	x	Alaska	19-20th century	CT	AM	-	(Copes, 2012)	

* CT = CT-scanner; OP = optical scanner; PH = photogrammetry

** AM = American Museum of Natural History, New York; DC = Duckworth Laboratory, Cambridge; FD = Laboratoire départemental de préhistoire du Lazaret, Fort de la Drette; GPI = Geologisch-Paläontologisches Institut Ruprecht-Karls Universität Heidelberg; IPH = Institut de Paléontologie Humaine, Paris; IRSNB = Institut Royale des Sciences Naturelles de Belgique, Bruxelles; IsIPU = Istituto Italiano di Paleontologia Umana, Roma; MH = Musée de l'Homme, Paris; MNHN = Museum National d'Histoire Naturel, Paris; MP = Museo Pigorini, Roma; NHM = British Museum, Natural History Museum, London; NMK = National Museums of Kenya, Nairobi; OR = ORSA database, Penn Museum; SFN = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt; SMN = Staatliches Museum für Naturkunde, Stuttgart; SupL = Soprintendenza del Lazio, Tivoli; UA = Département de Géologie et de Géographie Physique, Université Aristote, Thessalonique; UMR = UMR 6578, Unité d'Anthropologie Bioculturelle, Marseille; UP = Università degli studi di Pisa; USap = Università La Sapienza, Roma.

Chapter II – Method

This study aims at reassessing human evolutionary patterns during the end of Pliocene (3.6 Ma to 2.58 Ma) and the early Pleistocene (2.78 Ma to 0.78 Ma) transition by focusing on the integration of 3D geometric morphometric (GMM) data into phylogenetic analysis. Since the early 2000s, methods incorporating 3D data within a cladistic framework have been under development (e.g., Catalano et al., 2010; González-José et al., 2008; MacLeod et al., 2002). Building on this foundation, this research has three core objectives: (1) to empirically test a new protocol for incorporating GMM landmark data directly into cladistic analyses and compare the outcomes of this new protocol with those generated using traditional morphological characters, (2) to explore the potential of a combined approach, integrating GMM data into a unified morphological matrix, and (3) reassess the phylogeny of hominins during the Plio-Pleistocene transition (from 5 Ma to 0.78 Ma).

To help answer these objectives, this chapter provides a comprehensive overview of the theoretical foundations and methodological approaches underpinning this study. It outlines the principles and application of cladistic analysis and geometric morphometric analysis, describes the nature and sources of the data employed, and details the specific protocols and procedures followed in conducting each type of analysis.

I. Theoretical and methodological context

I.1. Cladistics and TNT

I.1.1. Principle of Cladistics

One of the phylogenetic approaches used in systematics rely on the principle of parsimony. This principle was introduced during antiquity by Aristotle, but was formalised during the 1950's, when Hennig formalised phylogenetic systematics (Hennig, 1950). Later, Camin and Sokal (1965) introduced the first algorithm for applying the parsimony criterion to phylogenetics. They were the first to use the term “parsimony” in the context of phylogenetic inference. Shortly thereafter, Kluge and Farris (Farris, 1970; Kluge and Farris, 1969) developed a new algorithm for reconstructing phylogenetic trees and searching for the most parsimonious tree from a set of trees for a given dataset. They named their method “Wagner parsimony”.

The Wagner algorithm generates a minimum-length network, often referred to as an “unrooted tree”. To convert this network into a phylogenetic tree, it must be rooted. The inclusion of species outside the ingroup allows researchers to distinguish changes in state characters (plesiomorphies from apomorphies) and establish the direction of transformations. This opens the possibility for phylogenetic analysis to become testable, at least within the framework of Darwinian concepts. Watrous and Wheeler, (1981) built on this idea, proposing rules to determine ancestral states for each character based on comparisons with an outgroup taxon. For smaller datasets, the Branch and Bound algorithm (Hendy and Penny, 1982) guarantees finding the shortest tree, while the Exhaustive Search option evaluates all possible trees.

Cladistic analysis can yield multiple trees with the same minimal number of steps, a situation referred to as multiple most parsimonious trees (i.e., MPTs). With large data sets containing substantial homoplasy or missing data, parsimony often results in multiple MPTs. In such cases, no single preferred tree can be chosen, but consensus trees can be generated to highlight similarities in the topologies of different MPTs (Adams, 1972). Consensus trees offer a visual summary of agreements between MPTs obtained from the results of phylogenetic analysis. For those situation, bootstrap analysis can be used to estimate the degree of sampling error in the original data by constructing confidence intervals for the phylogeny, accounting for variability in the data set. Bootstrapping (Felsenstein, 1985a) creates new data sets by sampling with replacement, where some

characters are sampled more than once, while others may be excluded. Programs like TNT (Goloboff and Morales, 2023) generate a majority-rule consensus tree based on these resampled data. The frequency with which a particular group appears in the consensus tree reflects the confidence in that group's presence. Felsenstein (1985a) suggested that bootstrap values of 95% or greater indicate statistically significant support for a clade. However, there are caveats: the bootstrap cannot compare trees built from different data sets and assumes that characters are independent and evenly distributed. It measures repeatability within a single data set, not the accuracy of the phylogeny. Additionally, it can be influenced by biases like long-branch attraction (Swofford, 1998).

The long-branch attraction problem arises when convergent homoplastic changes occur more frequently than non-reversed changes in an informative part of the tree (Felsenstein, 1978). This complicates phylogenetic systematics because the convergent homoplasies are likely to be interpreted as homologies, causing taxa with these convergent "long branches" to be grouped together (Felsenstein, 1978; Hennig, 1966). Simply put, when the data misrepresents the true relationships of taxa, phylogenetic systematics (as per Hennig, 1966) may fail to accurately determine those relationships.

I.1.2. Robustness methods

To empirically test the robustness of their results, phylogeneticists developed various methods. These "goodness of fit" measures serve as indicators of internal conflict among the data (characters). One approach to measuring robustness involves evaluating how characters behave over different tree topologies (Wiley and Lieberman, 2011). The simplest summary statistic is tree length, which represents the total number of steps required to produce a given topology. Tree length is calculated by adding up the character changes across the tree (Wiley et al., 1991). Parsimony analysis aims at selecting the tree or trees with the shortest overall length, given a set of characters. Consistency indices (Kluge and Farris, 1969) attempt to quantify the amount of homoplasy within a tree. The original consistency index (CI) is the ratio of the total number of apomorphic states to the tree length. A high CI indicates minimal homoplasy (i.e., the tree length is close to the minimum number of steps), while a low CI suggests a high degree of homoplasy. This index is independent of a specific data set, enabling comparisons across different trees. However, CI is correlated with the number of OTUs (Siebert, 1992) and with the number of autapomorphies. If the number of autapomorphies is high in a tree, this index value will be high (tending towards 1), regardless of the homoplasy content of the other traits. An alternative to this index, is the retention index (RI), proposed by Farris (1989).

This new index is a measure of the relative homoplasy. It quantifies the proportion of informative variation that is effectively retained as synapomorphy on the phylogenetic tree (Goloboff, 2022b). The index is designed to yield a value of zero when the tree performs as poorly as possible for the dataset at hand. Finally, Farris (1989) proposed the rescaled consistency index (RC), an adjusted version of the CI (i.e., $CI \times RI$) that removes the influence of characters like autapomorphies, providing a relative measure of homoplasy for a particular tree. However, this index will only give the proportion of maximum observable homoplasy (Goloboff, 2022b).

I.1.3. Phylogenetic morphometrics

Although the use of geometric morphometric data in cladistic analyses remains a topic of active debate, there are currently technical tools available to test the methods applied in this study. Among the various cladistic software options, such as PAUP* and Hennig68, TNT, developed by the Willi Hennig Society, stands out as the only platform that includes an algorithm capable of handling continuous, overlapping quantitative data directly. This specialised algorithm aims at reconstructing ancestral morphologies using landmark-based shape data, with the objective of minimizing evolutionary changes across the phylogenetic tree through parsimony-based optimization (Catalano et al., 2010; Goloboff and Catalano, 2011).

The methodology adopted here follows the approach proposed by Catalano et al. (2010) and Goloboff and Catalano (2011), “Phylogenetic morphometrics”. Rather than relying on discrete traits, this method works directly with either principal component scores or raw landmark coordinates. It seeks to reduce the total displacement of landmarks between ancestral and descendant forms. To achieve this, the algorithm estimates the ancestral configurations at internal nodes of the phylogenetic tree in a way that parallels how ancestral trait states are inferred in traditional parsimony methods, which typically uses discrete character states. In this framework, ancestral shapes are treated as spatial configurations, and landmark positions are optimized as multivariate traits. The ancestral coordinates are estimated by exploring a finite set of possible positions within a grid defined by the observed variation in descendant landmarks. This estimate can be refined either by increasing the grid resolution or by re-running the procedure with a narrower grid centred around the initial estimate, thus enhancing the precision of the ancestral shape reconstruction.

Key-points II.I.1

Cladistics and Wagner parsimony:

- Cladistics, a phylogenetic approach, relies on parsimony (the principle of choosing the simplest explanation).
- Kluge and Farris (1969, 1970) developed the Wagner parsimony algorithm for reconstructing phylogenetic trees.
- Wagner algorithm generates an unrooted tree (minimum-length network). To convert it into a phylogenetic tree, an outgroup species is included to distinguish homoplasies (conflicting traits) from plesiomorphies (non-conflicting traits).
- Branch and Bound algorithm (Hendy and Penny, 1982) guarantee the shortest tree for small datasets. Exhaustive Search evaluates all possible trees.
- Large datasets often yield multiple most parsimonious trees (MPTs) due to homoplasy or missing data. Consensus trees summarize the similarities between MPTs but do not represent the actual phylogeny.

Bootstrap analysis:

- Bootstrap analysis (Felsenstein, 1985a) estimates sampling error by constructing confidence intervals for phylogenetic trees. Bootstrap values $\geq 95\%$ indicate strong support for a clade.
- Bootstrap analysis has limitations: cannot compare trees from different datasets and assumes independent, evenly distributed characters.

Long-branch attraction:

- Long-branch attraction occurs when convergent homoplastic traits lead to taxa being incorrectly grouped together. This problem can misrepresent the true evolutionary relationships.

Robustness methods:

- Goodness of fit measures help assess internal conflicts within phylogenetic data.
- Tree length: Total number of steps needed to create a topology; shorter trees are preferred.
- Consistency Index (CI) quantifies homoplasy in a tree, with high CI indicating minimal homoplasy. Retention Index (RI) quantifies the proportion of informative variation that is effectively retained as synapomorphy on the phylogenetic tree. Rescaled Consistency Index (RC) adjusts for biases like autapomorphies.

Phylogenetic morphometrics:

- TNT software is the only platform capable of handling continuous quantitative data directly for cladistic analysis.
- Catalano et al. (2010) and Goloboff and Catalano (2011) proposed phylogenetic morphometrics, which work with landmark-based shape data rather than discrete traits.
- The method aims at minimizing evolutionary change across the phylogenetic tree.
- Ancestral shapes are treated as spatial configurations with landmarks optimized as multivariate traits.
- The algorithm estimates ancestral coordinates using a grid defined by observed variation in descendant landmarks, with the option for increased precision.

I.2. Geometric morphometry

I.2.1. Principle of geometric morphometrics

Geometric morphometrics is a group of methods developed to study shape variation by analysing data derived from specific anatomical landmarks in a statistical framework. These landmarks are precise points on anatomical structures that can be consistently located across all specimens in a sample, as described by (Zelditch et al., 2004). In essence, they are corresponding reference points that can be reliably identified on each object being compared, such as specific anatomical points on skulls or mandibles (O'Higgins, 2000). The collection of these landmarks, positioned in either two or three dimensions, represents the overall form of the object. One of the key advantages of geometric morphometric methods is that they retain the spatial relationships among these points throughout the analysis, operating within a mathematical framework known as shape space (specifically, Kendall's shape space). This approach allows the shape of an object to be separated from non-shape attributes, namely, its position, orientation, and scale. Kendall (1977) defines this "shape" as the remaining geometric structure once those variables are eliminated, effectively isolating the object's morphology from its size, position and orientation. Geometric morphometrics thus enables researchers to explore and quantify these morphological differences across specimens. Moreover, it provides tools to visually represent these shape variations between individuals or groups (O'Higgins, 2000; Zelditch et al., 2004).

I.2.2. Landmarks

Traditional morphometric methods often require researchers to identify and choose which measurements to analyse in advance. If these chosen variables turn out to be poorly suited for testing the research hypothesis, their limited relevance can be overshadowed by noise from less meaningful data. In contrast, geometric morphometric techniques do not require this preliminary selection. Although the landmarks themselves must be identified beforehand, the method allows all potential shape variables derived from the spatial relationships between these landmarks to be considered in the analysis. This ensures that meaningful patterns are not masked by irrelevant measurements, as the analysis inherently determines which variables are most informative (Zelditch et al., 2004).

Bookstein (1991) introduced a classification system that categorizes landmarks into three types based on their anatomical precision and biological relevance. Type I landmarks are the most reliable; they are clearly defined by anatomical features and show strong homology across different

individuals, for example, the bregma is the point where the coronal and sagittal sutures intersect. Type II landmarks are less precise; they are located using identifiable features but also depend on less definitive characteristics such as the peak or hollow of a curve or a specific developmental feature. These points are geometrically consistent but lack strong anatomical anchors. Type III landmarks are the least reliable in terms of homology. They are defined by spatial extremes, such as the widest point of the skull (e.g., the opisthocranium), and are not associated with distinct anatomical structures. Because of their less precise definitions, Type III landmarks can vary significantly between individuals, making their interpretation more complex. Despite this limitation, they can still be valuable for capturing certain morphological traits that are not represented by the more structurally defined Type I or II landmarks (O'Higgins, 2000; Zelditch et al., 2004). Curve and surface sliding semi-landmarks are included in the Type II. They correspond to point with deficient coordinates whose location is estimated during a Procrustes superimposition, allowing the semi-landmark to slide along the curve or the surface it characterises.

I.2.3. Superimposition methods

Once the landmarks are collected, superimposition or registration methods are necessary to detect and quantify shape differences, estimate average shapes, and describe shape variation. This involves placing the landmark configurations into a common coordinate system where their shapes can be directly compared. The process requires translating, rotating, and scaling the shapes in a way that minimizes the differences between them, and therefore, isolate and remove certain variables, namely size, position, and orientation, so that the focus of analysis can be directed solely toward the shape of the specimens as defined by their landmark configurations. The quality of the superimposition depends on how these differences in landmark positions are evaluated. After alignment, any remaining variation in the landmark coordinates, called residual differences, represents true shape differences that cannot be explained by simple adjustments like translation, rotation, or scaling.

Among the superimposition methods, the most widely used are the Procrustes methods: the resistant-fit theta-rho analysis (RFTRA; Siegel and Benson, 1982) and generalised least squares Procrustes superimposition (Rohlf, 1990), also known as Generalised Procrustes Analysis (GPA). The RFTRA method employs a technique known as the "repeated medians" approach to calculate the necessary scaling and rotation for aligning one shape with another (Chapman, 1990). The procedure for determining the scaling factor is:

- a. Calculate the distances between all pairs of landmarks within each shape and then find the ratio of each corresponding pair of distances.
- b. For every landmark, compute the median of these ratios across all segments that extend from that landmark. This results in one ratio per landmark.
- c. Take the median of all the landmark-specific medians obtained in step 2. This final median represents the scaling factor, which is then applied to all coordinates of the second shape during the superimposition process.

Once the second shape has been scaled, a similar strategy is used to determine the rotation angle. This begins by calculating the angles between corresponding segments in the two shapes. Then, for each landmark, the median of these angular differences is computed, followed by the median of those medians, yielding the rotation angle (see, Zelditch et al., 2004).

This method has been considered more appropriate for phylogenetic analysis due to its robustness against the Pinocchio effect, where alignment causes the change to be spread across many landmarks, even though it actually stems from just one or a few landmarks with significant displacement (see, Goloboff, 2022b; Palci and Lee, 2019; Zelditch et al., 2004). Although this method helps to highlight the region where the effect occurs, it was not used in this study. This decision is due to the limited development of the method in software like R and TNT; for instance, TNT currently supports this approach only for two-dimensional datasets. To ensure the analyses could proceed smoothly, Generalized Procrustes Analysis was chosen instead.

I.2.4. Generalized Procrustes Analysis

Generalised Procrustes Analysis (GPA), also known as Procrustes superimposition (Goodall, 1991; Gower, 1975; Rohlf and Slice, 1990). Starting with landmark data from each individual, the geometric centre, or centroid, of each configuration is calculated. This is done by determining the average position of all landmarks, essentially locating the centre of gravity of the shape.

Afterwards, the centroid size is computed, which involves taking the square root of the sum of the squared distances from each landmark to the centroid. Although this measurement is technically independent of the object's shape, in biological specimens' size and shape may still show some correlation, as larger forms can exhibit different shapes than smaller ones (O'Higgins, 2000; Zelditch et al., 2004). Once size is quantified, it can be mathematically removed to allow for a more accurate comparison of shape alone.

GPA proceeds through three main steps:

1. Translation: Each object, in this context, each calvarium, is translated so that its centroid is positioned at the origin of the coordinate system. This is done by subtracting the centroid coordinates from each landmark's coordinates.
2. Scaling: The configurations are then standardized to a uniform size by dividing all landmark coordinates by the centroid size of the specimen.
3. Rotation: Finally, the configurations are rotated relative to one another to minimize the overall distance between corresponding landmarks. This is to achieve the best possible alignment by reducing the sum of squared distances between homologous points.

Through this process, GPA facilitates the comparison of shape while effectively controlling for non-shape variation, providing a powerful tool for morphological analysis.

Once the GPA is complete, the remaining positional differences between corresponding landmarks reflect the variation in shape between the specimens. These shape differences can be visualized and subsequently used as variables in multivariate statistical analyses.

When more than two specimens are included in the analysis, the process begins in the same way: centring and scaling each configuration. During the final step, however, the algorithm calculates a mean shape by averaging the configurations across all specimens. Through an iterative process, it then aligns each individual configuration to this average by minimizing the total squared distances between corresponding landmarks, seeking the best overall fit among all the specimens.

I.2.5. Kendall space and Principal Component Analysis

Following Procrustes alignment, each individual shape can be represented as a single point within a geometric framework known as shape space. For the GPA, this space corresponds to Kendall's shape space, which is inherently non-Euclidean. In simple configurations, such as triangles, this space can be visualized as a unit sphere. However, when dealing with configurations that include more than three landmarks in multiple dimensions (i.e., k landmarks in m dimensions), the structure of this space becomes significantly more complex, making shape analysis more challenging.

To facilitate comparison and analysis of these shapes, the data are firstly projected into a Euclidean space that is tangent to the average shape within Kendall's shape space. This tangent space serves

as a local approximation of the original non-Euclidean space, allowing for more straightforward statistical analysis.

Once in tangent space, Principal Component Analysis (PCA) can be applied to explore patterns of shape variation among the specimens. PCA helps reduce the dimensionality of the dataset while retaining the most meaningful sources of variation. It identifies principal components, orthogonal axes that capture the greatest variation in the data, thereby simplifying the interpretation of shape differences. In this context, PCA extracts eigenvectors, which correspond to the main directions of shape change across the sample, enabling a visual and quantitative assessment of shape trends.

Key-points II.I.2

Geometric morphometrics:

- A method to study shape variation using anatomical landmarks in a statistical framework. Landmarks are precise, consistent points that can be identified across specimens (e.g., skulls, mandibles).
- Shapes are analysed in a mathematical space called shape space, isolating shape from position, orientation, and scale.
- Geometric morphometrics quantifies and visualizes morphological differences between specimens.
- Landmarks allow all shape variables to be considered based on their spatial relationships. This prevents irrelevant measurements from affecting the analysis.

Types of landmarks (Bookstein, 1991):

- Type I: Highly reliable, clearly defined by anatomical features (e.g., bregma).
- Type II: Less precise, dependent on identifiable features or developmental traits.
- Type III: Least reliable, defined by spatial extremes (e.g., widest point of skull), often variable across individuals.
- Semi-landmarks: Sliding points along curves or surfaces, used for imprecise landmark definitions.

Superimposition methods:

- Align landmarks in a common coordinate system to isolate shape differences.
- Minimize differences in position, orientation, and scale.
- Procrustes methods are widely used, including:
 - Resistant-fit theta-rho analysis (RFTRA): Focuses on alignment using medians of distances and angles between corresponding landmarks.
 - Generalized Procrustes Analysis (GPA): Aligns shapes by translating, scaling, and rotating them to minimize differences in landmark positions.

Generalized Procrustes Analysis (GPA):

- Steps: Translation (centroid alignment), scaling (standardize size), and rotation (minimize distance between landmarks).
- After alignment, the remaining differences reflect true shape variation.
- The mean shape is computed when analysing multiple specimens.
- GPA enables comparison of shapes while controlling for size, position, and orientation.

Kendall's shape space and PCA:

- Shapes are represented as points in Kendall's non-Euclidean shape space.
- Data is projected into a Euclidean tangent space for easier statistical analysis.
- Principal Component Analysis (PCA) is used to reduce dimensionality and identify the most significant shape variations, simplifying interpretation.

II. Data

II.1. Morphological characters

Selecting which traits to analyse is an essential and foundational step in any phylogenetic study, and one of the most influential in shaping the final evolutionary tree. The outcome of the analysis heavily depends on the traits chosen, the way they are categorised, and their polarity, i.e., whether they are identified as ancestral or more recently evolved. Because of this, the methodology for selecting and defining traits is often a point of active and sometimes intense discussion within primate systematics, especially in studies focused on human evolution. Some researchers in palaeoanthropology question the reliability of using physical characteristics to infer evolutionary relationships. They argue that many traits might have arisen independently through convergent evolution and therefore may not accurately reflect common ancestry. Specific to hominins, several researchers have raised concerns that certain evolutionary complexities could distort the results produced by phylogenetic methods (e.g., Collard and Wood, 2000, 2001; Hawks, 2004).

Building on this methodological consideration in phylogenetic analysis, the first step involved the practical application of these principles through the careful selection and coding of morphological characters from the calvarium from existing literature. These traits were all drawn from a single anatomical region, the calvarium, which encompasses the frontal bone, both parietals, both temporals, and the occipital. Details about the selected characters and the references used can be found in the appendix. A total of 59 cranial features were chosen based on prior studies (Andrews, 1984; Antón, 2003; Barriel, 1994; Boule, 1911, 1912, 1913; Caparros, 1997; Condemi, 1992, 2001; Elyaqnine, 1995, 2001; Grimaud, 1982; Hublin, 1978, 1988; Mounier, 2009; Mounier and Caparros, 2015; Nara, 1994; Rightmire, 1990; Stringer, 1984; Suzuki and Takai, 1970; Trinkaus, 1983; Vallois, 1969; Vandermeersch, 1981; Weidenreich, 1945; Zeitoun, 2000). The selection process followed three main criteria:

1. Each trait needed to represent both general and specific morphological aspects of the targeted cranial regions.
2. The features had to be informative about evolutionary patterns connecting the various hominin populations under study.

3. The traits had to be defined in a way that allows for consistent and reproducible observations.

These selected morphological characteristics help reveal the diversity seen in modern humans while also highlighting distinctive traits of earlier hominins like *H. neandertalensis*, *H. erectus*, *Au. africanus*, and others. Each character was examined across all specimens in the dataset.

For analysis, the traits were categorized using a system that accommodated two types of morphological data. Binary traits (e.g., presence vs. absence) were coded with 1 indicating absence and 2 indicating presence. Continuous traits were divided into up to three states to reflect varying degrees of expression or morphological configurations. In this framework, state 1 typically represented the absence of a feature or a particular form, while subsequent states indicated increasing expression or alternative configurations. Due to challenges in consistently grading intermediate forms, most continuous traits were simplified into binary categories; however, in certain cases, intermediate states were necessary to adequately describe morphological variation.

No attempt was made to determine character polarity. To facilitate comparison and summarize the findings, a table was produced showing the distribution of character states across the different specimen groups (see Table 2, Figure 28, and Appendix 2 for a detailed definition of each character).

Table 2: Description of each morphological feature and character state common in all chapters; for more details see Mounier and Caparros, 2015 and Mounier et al. (2016).

Morphological features		Character states	
1	Outline of the calvarium, <i>norma occipitalis</i>	1	triangular
		2	circular
		3	pentagonal
2	Frontal cord length / parietal cord length	1	Frontal < Parietal
		2	Frontal $\approx$ Parietal
		3	Frontal > Parietal
3	Outline of the supraorbital region, <i>norma facialis</i>	1	straight
		2	convex
4	Supraorbital region: <i>sulcus supraorbitalis</i>	1	complete
		2	incomplete
		3	absent: <i>arcus superciliaris</i> and <i>supraorbitalis</i> merged
5	Projection of the supraorbital region	1	not projecting
		2	<i>arcus superciliaris</i> only
		3	whole supraorbital region
6	Post-orbital constriction (Ipc=M9/M43)	1	important (Ipc<0.75)
		2	weak (0.75 $\geq$ Ipc $\geq$ 0.85)

		3	absent ($I_{pc} > 0.85$)
7	Outline of the supraorbital region, <i>norma verticalis</i>	1	medially concave (glabella)
		2	straight
		3	convex
8	<i>Sulcus postorbitalis</i>	1	absent
		2	medially present
		3	present continue
9	<i>Tuber frontale</i>	1	absent
		2	defined, medially shifted
		3	present
10	Antero-posterior convexity of the frontal ($I_{fc} = M29 * 100 / M26$)	1	weak ($I_{fc} > 95$)
		2	intermediate ($95 > I_{fc} \geq 90$)
		3	important ($I_{fc} < 90$)
11	<i>Linea temporalis</i> development on the frontal	1	absent
		2	present, unique
		3	present, double
12	Sagittal keel on the frontal	1	absent
		2	present
13	Bregmatic eminence	1	absent
		2	present
14	Pterion (antero-lateral region of the skull formed by the junction of the frontal, the parietal, the sphenoid and the temporal)	1	spheno-parietal
		2	fronto-temporal
15	Thickening on the superior part of the coronal sutures	1	absent
		2	present
16	Sagittal keel on the bregma-lambda arch	1	absent
		2	present
17	Parasagittal hollowing on both sides of the parietal suture	1	absent
		2	present
18	Pre-lambdatic hollowing on the bregma-lambda arch	1	absent
		2	present
19	<i>Linea temporalis</i> width of the temporal band	1	absent
		2	narrow ($< 20\text{mm}$)
		3	wide ($\geq 20\text{mm}$)
20	<i>Linea temporalis</i> : position on parietal (R_{lt} = temporo-parietal suture-superior line / temporo-parietal suture-bregma)	1	high ($R_{lt} > 0.55$)
		2	medial ($0.54 > R_{lt} > 0.46$)
		3	low ($R_{lt} < 0.45$)
21	<i>Torus angularis parietalis</i>	1	absent
		2	present
22	<i>Tuber parietale</i>	1	absent
		2	present, medially shifted
		3	present, high position

23	Outline of the occipital, <i>norma lateralis</i>	1	rounded profile
		2	sharply angled
24	Outline of the <i>planum occipitale, norma lateralis</i>	1	no convexity
		2	convexity
25	Relative development: <i>planum nucale</i> (PN) / <i>planum occipitale</i> (PO)	1	PN $\geq$ PO
		2	PN<PO
26	Occipital bun	1	absent
		2	present
27	Opisthocranium relative position / inion	1	same position
		2	different position
28	<i>Processus retromastoideus</i>	1	absent
		2	present
29	Outline of the <i>planum occipitale, norma occipitalis</i>	1	triangular
		2	circular
		3	pentagonal
30	Suprainiac fossa	1	absent
		2	hollowing, weakly-delineated
		3	present
31	Suprainiac fossa: lateral edges	1	absent
		2	convergent upward
		3	parallels or arched
32	<i>Sulcus supratotalis</i>	1	absent
		2	hollowing
		3	present
33	<i>Torus occipitalis transversus</i>	1	absent
		2	present: medially protruding
		3	present: bilaterally protruding
34	<i>Torus occipitalis transversus form, norma occipitalis</i>	1	absent
		2	rectilinear
		3	convex
35	<i>Protuberantia occipitalis externa</i>	1	absent
		2	present
36	<i>Tuberculum linearum</i>	1	absent
		2	present
37	External occipital crest	1	absent
		2	present, posterior only
		3	present
38	Aligned posterior and anterior external occipital crest	1	yes
		2	no
39	Temporal squama heigh (Iet=maximal height from <i>auriculae</i>*100 / maximal width)	1	low (Iet $\leq$ 60)
		2	high (Iet > 60)
40	Outline of the anterior border of the temporal squama	1	curved or sinuous
		2	rectilinear
41	Outline of the superior border of the temporal squama	1	curved or sinuous

		2	rectilinear
42	Development of the <i>crista supramastoidea</i> at the porion	1	absent
		2	weakly marked
		3	marked
43	<i>Crista supramastoidea</i> / <i>processus zygomaticus temporalis</i>	1	not lined up
		2	lined up
44	<i>Tuberculum supramastoideum anterius</i>	1	absent
		2	present
45	Supramastoid groove (between <i>crista supramastoidea</i> and <i>crista mastoidea</i>)	1	absent
		2	present, closed anteriorly
		3	present
46	Form of the auditory meatus	1	circular
		2	elliptic
47	Position of the auditory meatus / <i>processus zygomaticus temporalis</i>	1	below
		2	intermediate
		3	lined up
48	<i>Tuberculum mastoideum anterior</i>	1	absent
		2	present
49	<i>Processus mastoideus</i> : downward development / basicranium	1	weak
		2	strong
50	Juxtamastoid ridge development / <i>processus mastoideus</i>	1	less developed
		2	as developed
		3	more developed
51	Digastric groove: presence of a bony bridge	1	no
		2	yes
52	<i>Crista occipito mastoidea</i>	1	absent
		2	present
53	Glenoid cavity depth / articular tubercle lowest point	1	shallow (<0.9 mm)
		2	deep (>0.9 mm)
54	Petro-tympanic crest orientation in relation to the sagittal plan	1	perpendicular
		2	frontward
		3	backward
55	Articular tubercle configuration	1	medio-lateral concavity
		2	antero-posterior convexity
		3	medio-lateral convexity and vertical
56	<i>Tuberculum zygomaticum anterius</i>	1	absent to weakly marked
		2	marked
57	<i>Tuberculum zygomaticum posterius</i> (post glenoid process)	1	absent to weakly marked
		2	marked

58	Tympanal contribution to the posterior wall of the glenoid cavity	1	weak
		2	important
59	Preglenoid tubercle	1	absent
		2	present

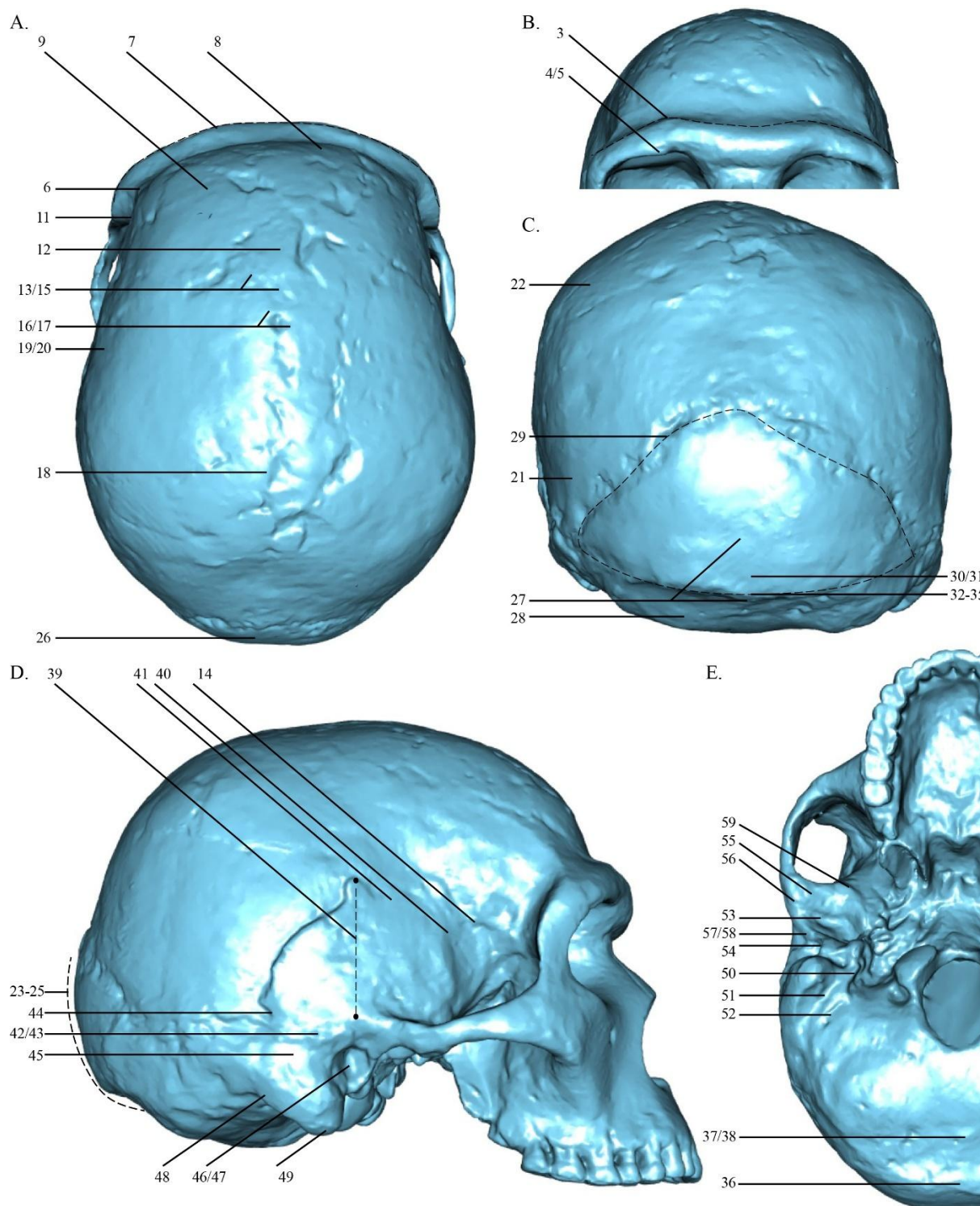


Figure 28: Position of the 59 morphological characters on the calvarium: A. *norma verticalis*; B. *norma facialis*; C. *norma occipitalis*; D. *norma lateralis*; and E. *norma basilaris*.

Key-points II.II.1

Trait selection in phylogenetic studies:

- Trait selection is a foundational and influential step in shaping phylogenetic trees.
- The outcome of analyses depends on:
 - The specific traits selected.
 - How traits are categorized.
 - The polarity assigned to traits (ancestral vs. derived).

Practical trait selection for this study:

- Focused on morphological characters from the calvarium:
 - Included the frontal, parietals, temporals, and occipital bones.
 - All traits were sourced from established literature.
- A total of 59 cranial traits were selected (see Appendix 2 for full list and references).
 - Based on studies such as Andrews (1984), Antón (2003), Boule (1911–1913), Mounier (2009), and many others.
- Three main criteria guided trait selection:
 - Traits had to represent both general and specific aspects of the calvarium.
 - They needed to be informative about evolutionary relationships among hominins.
 - Each trait had to be consistently and reproducibly observable.

Trait coding and categorization:

- Traits were categorized into two main types:
 - Binary traits: coded as 1 (absence) and 2 (presence).
 - Continuous traits: divided into up to three discrete states to capture degrees of variation.
- In this framework:
 - State 1 typically indicates absence or a baseline form.
 - State 2 and 3 reflect increasing expression or alternate configurations.
- In cases of ambiguity:
 - Traits were often simplified into binary states to ensure consistency.
 - Intermediate states were used only when necessary to describe variation accurately.

Polarity and data presentation:

- No attempt was made to determine character polarity (ancestral vs. derived).
- To support analysis and visualisation a summary table and figure were created to display the distribution of character states across the different specimen groups (see Table 2 and Figure 27).

II.2. 3D characters

The reference landmarks employed in this study were initially established in prior research (Martin and Saller, 1957). The landmarking protocol, originally developed by Mounier and Mirazón Lahr (2016, 2019) for the entire cranium, was adapted in the present analysis to focus specifically on the calvarium. Accordingly, a subset of landmarks was selected (i.e., 27 in total) (see Figure 29), and the number of semi-landmarks was systematically reduced in R, across three sub-datasets comprising 609, 320, and 141 landmarks, respectively (see Chapter II – Method / Protocols / Chapter III – Cladistics and GMM, Figure 30). The semi-landmarks were equally spaced across six patches: two on the frontal bone, two on the parietal bone, and two on the occipital bone, covering both the left and right sides.

When selecting these landmarks, an important criterion was considered: the landmarks needed to capture the overall shape of specific anatomical regions and effectively represent individual morphological variation within the sample. At the same time, a particular constraint related to the characteristics of the fossil sample also had to be addressed. For the individuals included in the study, the emphasis was placed on landmarks with strong anatomical homology. Whenever possible, Type I landmarks, those with clear and consistent anatomical definitions, were prioritized (see, Table 3), while the inclusion of Type III landmarks was minimized due to their lower reliability. Nonetheless, a few Type III landmarks were used in cases where they were the only available option to describe specific regions lacking Type I points.

Table 3: Landmarks used, their types and their definitions (see, White et al., 2011).

Name of the landmark	Type	Definition
Anterior zygomatic tubercle*	III	The most inferior point on the anterior zygomatic tubercle.
Asterion*	I	Intersection point of the lambdoid, parietomastoid, and occipitomastoid sutures.
Basion	I	The central point on the anterior margin of the foramen magnum.
Bregma	I	The ectocranial junction of the coronal and sagittal sutures.
Entoglenoid*	III	The most inferior point of the entoglenoid process.
Frontomalare*	II	The central point of the frontozygomatic suture.
Frontomalare orbital*	I	The point where the frontozygomatic suture intersects with the inner rim of the orbit.
Frontomalare temporal*	II	The point where the frontozygomatic suture crosses the temporal line (or outer orbital rim).
Glabella	III	The most anterior midline point on the frontal bone, typically above the frontonasal suture.
Hormion	I	The most posterior central point on the vomer.

Infra-temporal*	III	Highest point of the infra-temporal crest, where the temporal bone and the sphenoid meet.
Inion	I	The point at which the superior nuchal lines merge in the external occipital protuberance.
Lambda	I	The ectocranial midline point where the sagittal and lambdoid sutures meet.
Mastoïdal*	I	The most inferior point on the mastoid process.
Maximum depth of the TMJ*	III	The deepest point of the temporo-mandibular joint (TMJ).
Nasion	I	The central point where the two nasal bones meet the frontal bone.
Opisthion	I	The midline point at the posterior margin of the foramen magnum.
Porion	III	The highest point on the outer edge of the external acoustic meatus.

*Bilateral landmarks

The coordinates of the selected landmarks were recorded in three-dimensional space (X, Y, and Z axes) from 3D models of the crania using the Landmark software (IDAV, Wiley, 2005). A full list of the studied material is presented in Chapter I – Material, Table 1.

The state of preservation of the fossil specimens also influenced the landmark selection process, and the deliberate choice to avoid estimating or reconstructing missing parts of poorly preserved fossils was taken. Instead, the analysis was limited to the anatomical area with a reasonable level of integrity, the calvarium, i.e., the cranium without the facial and mandibular part, and avoided those with high uncertainty or significant reconstruction controversies. Consequently, the number of usable landmarks was significantly reduced.

Afterwards, the landmark configurations describing the samples were aligned using GPA (Goodall, 1991; Gower, 1975; Rohlf and Slice, 1990) and bilateral asymmetry was removed from the data (Klingenberg et al., 2002). To prepare the landmark data, different analysis were carried out using R 4.4.2 (R Core Team, 2024). First, an array was assembled to include all landmarks from all specimens. Missing landmarks were identified and removed, then estimated by mirroring the existing landmarks onto the other side and, when not possible, by estimating them by thin-plate-spline interpolation (i.e., TPS, Bookstein, 1989). The sliding procedure used in this study follows the method outlined in Gunz et al. (2005) and Gunz and Mitteroecker (2013) and has been applied in several prior studies (e.g., Mounier and Mirazón Lahr, 2016, 2019). The criterion used was bending energy. Second, the specimens belonging to the ingroup were aligned together, while the outgroup specimens were aligned separately. A GPA and PCA were then carried out on the complete set of specimens with “Geomorph” package (Baken et al., 2021). Third, specimens were grouped by operational taxonomic unit (OTU) and aligned separately to generate average landmark

configurations using “Rphylopars” package (Goolsby et al., 2017) in R. A second GPA and PCA were subsequently performed on these averaged OTUs.

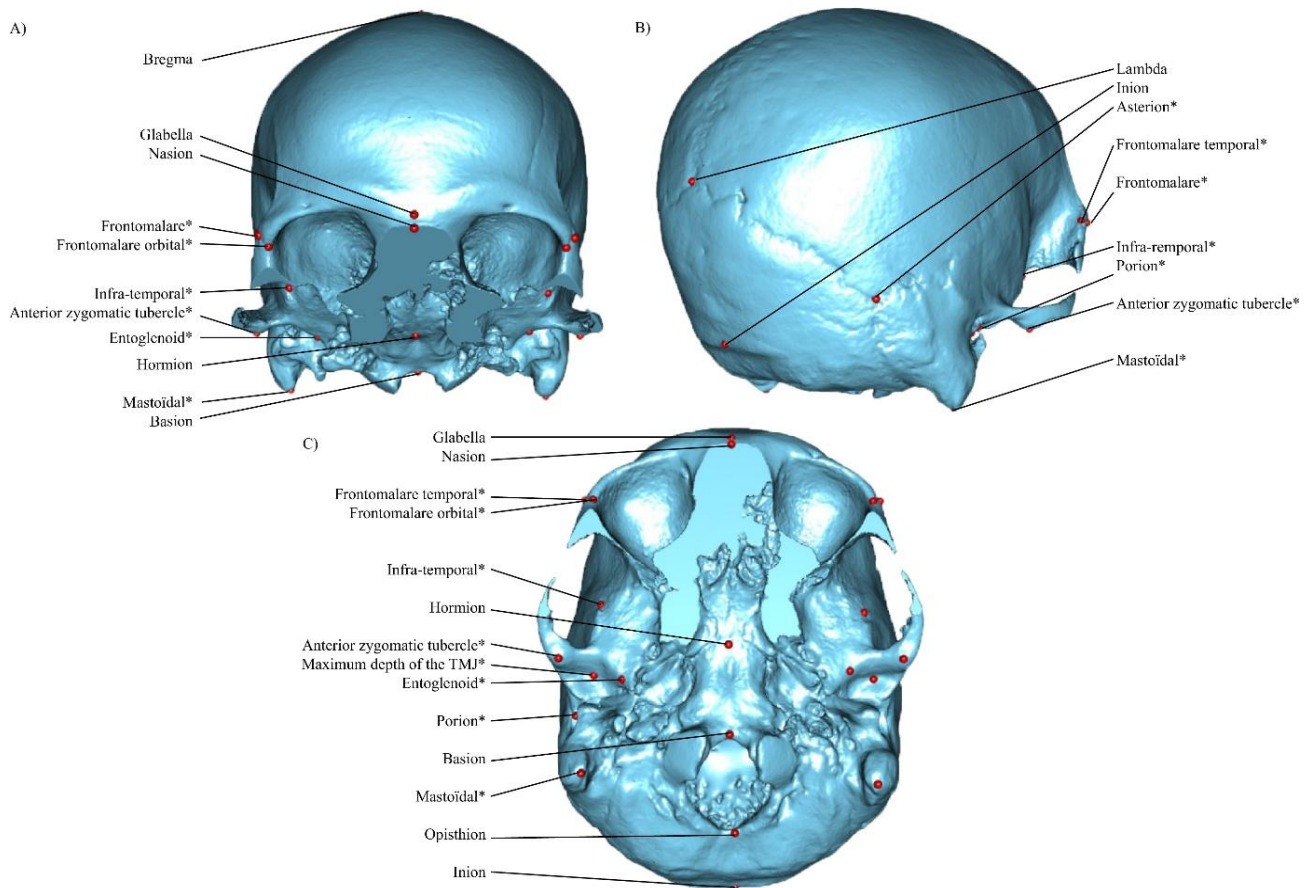


Figure 29: Position of the 27 landmarks on the calvarium: A) *norma facialis*, B) $\frac{3}{4}$ posterior view, and C) *norma basilaris*. The landmarks with an asterisk “*” are bilateral.

Key-points II.II.2

Landmark selection:

- Reference landmarks were based on previous studies (e.g., Martin and Saller, 1957; Mounier and Mirazón Lahr, 2016, 2019)
- Included both standard craniometric points and landmarks commonly used in morphometric analyses.
- Selection criteria aimed to:
 - Capture the shape of specific anatomical regions.
 - Reflect individual morphological variation within the sample.
 - Prioritize anatomical homology, especially for fossil specimens.
- Landmark types:
 - Type I landmarks were prioritized due to clear anatomical definitions.
 - Type III landmarks were used sparingly, only when necessary for describing regions lacking Type I points.

Data acquisition:

- Landmark coordinates were recorded in 3D (X, Y, Z) using Landmark software (IDAV; Wiley, 2005).
- Data were collected from 3D models of the specimens.
- Complete list of specimens is provided in Chapter I – Material, Table 1.

Landmarks and semi-landmarks:

- A total of 27 anatomical landmarks were used on the calvarium (see Figure 28).
- The number of semi-landmarks varied by analysis:
 - Ranged from 121 to 609 (see Chapter II – Method / Protocols / Chapter III – Cladistics and GMM, Figure 29).
- Handling missing data:
 - Landmarks were mirrored from the preserved side when possible.
 - When mirroring was not feasible, thin-plate spline interpolation (TPS) was applied (Bookstein, 1989).

Data processing:

- Landmark configurations were aligned using Generalized Procrustes Analysis (GPA) (Goodall, 1991; Gower, 1975; Rohlf and Slice, 1990).
- Bilateral asymmetry was removed from the dataset (Klingenberg et al., 2002).

III. Protocols

III.1. Chapter III – Cladistics and GMM

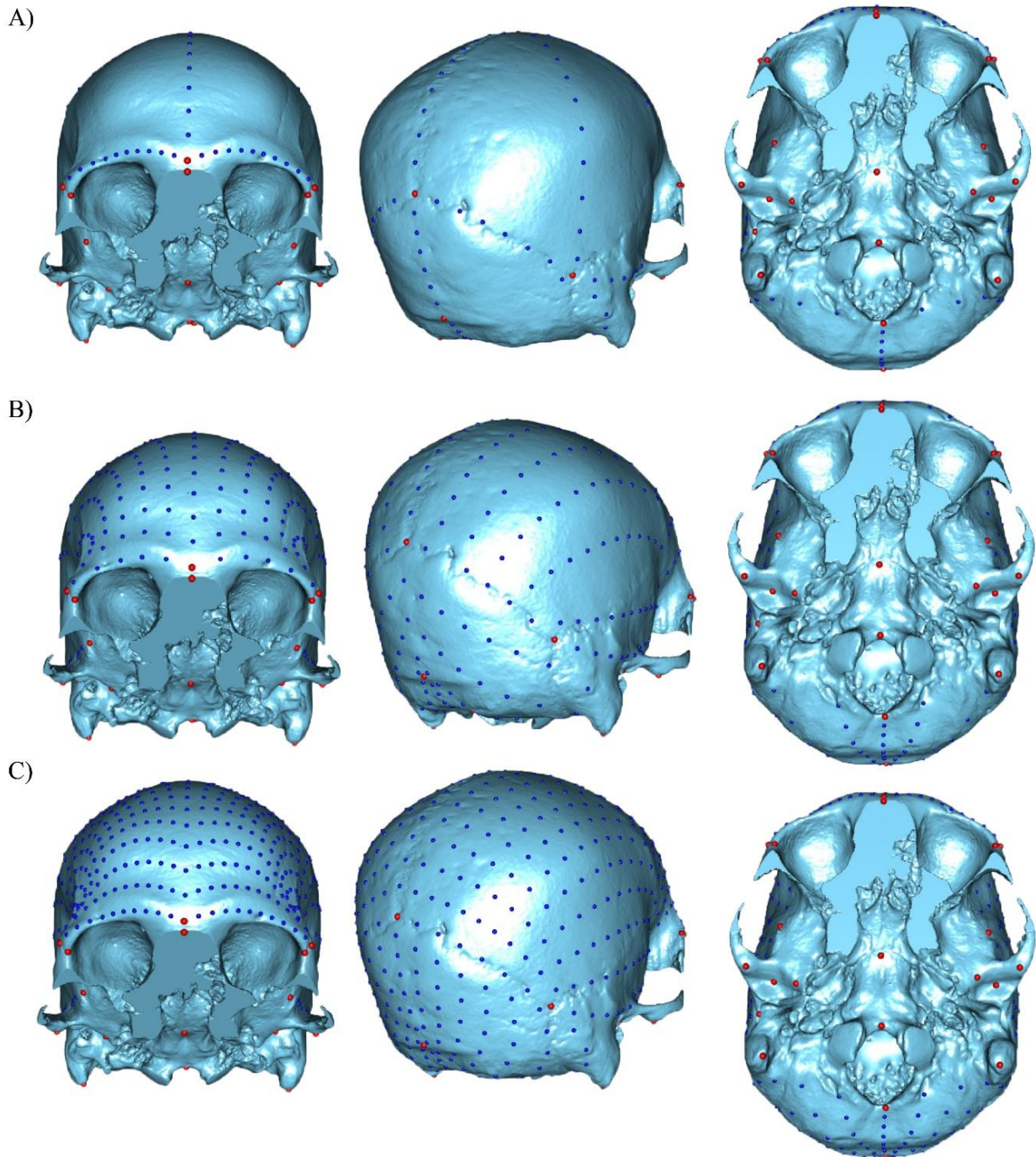


Figure 30: Position of the landmarks on the calvarium for each dataset: A) 148 landmarks; B) 347 landmarks; C) 636 landmarks. From left to right: *norma facialis*; $\frac{3}{4}$ view; and *norma basalis*.

III.1.1 Matrices

In the first set of analyses, 23 OTUs, including the three outgroup taxa (see Chapter I – Materials / Table 1 and Chapter III – Cladistics and GMM), were analysed through seven distinct matrices:

- **Morphological matrix:** Matrix A (see, Appendix 3) contained 59 morphological characters describing the morphology of the calvarium (see, Chapter II – Method / Data / Morphological Characters), coded as discrete states ranging from 1 to 3 (Table 2).
- **PC coordinates matrices,** obtained through PCA on the Procrustes residuals after aligning via GPA the 23 averaged configurations: Matrix B.1 (Appendix 4), derived from an analysis of 148 landmarks. Matrix B.2 (Appendix 5) used the PC coordinates obtained from the analysis of the 347 landmarks dataset. Finally, matrix B.3 (see Appendix 6) used the PC coordinates obtained after GPA and PCA derived from an analysis of 636 landmarks.
- **Landmarks matrices,** obtained directly from the Procrustes-aligned 3D coordinates of the landmarks averaged per OTU: Matrix C.1 (Appendix 7) was derived from an analysis of 148 landmarks, i.e., 27 landmarks and 121 semi-landmarks (see Figure 30). Matrix C.2 (Appendix 8) was derived from an analysis of 347 landmarks, i.e., 27 landmarks and 320 semi-landmarks. Finally, matrix C.3 (Appendix 9) was derived from an analysis of 636 landmarks, i.e., 27 landmarks and 609 semi-landmarks.

A technical issue arose with the variables presenting negative values, as these could not be processed by TNT version 1.6 parsimony software (Goloboff and Morales, 2023). Since the protocol involving PC coordinates resulted in negative values, ten units were added to each variable across the three matrices to enable the software to process the data correctly. To ensure that the taxonomic ordering did not influence the results, several analyses were conducted using different outgroups, with the order of taxa varied in each matrix.

III.1.2. Analyses

In each analysis, three outgroup OTUs (*Gorilla*, *Pan*, and *Pongo*) were used to root the tree and polarize the transformations of the characters. Phylogenetic analyses were performed using TNT version 1.6 parsimony software (Goloboff and Morales, 2023), which allowed for the comparison of multiple phylogenetic hypotheses and the rapid selection of the most parsimonious tree. Parsimony was chosen as the reconstruction method because it is the only approach that enables the identification and discussion of synapomorphies at each node (Matile et al., 1987).

Twenty-one parsimony phylogenetic analyses were conducted, corresponding to the analysis of the seven different matrices, with the reweighting according to three indices: the consistency index (i.e., CI), the retention index (i.e., RI) and the rescaled consistency index (i.e., RC), following the successive approximative weighting method (SAW) of Farris (1969) (see, Chapter II – Method / Protocols / Scripts). Farris proposed a method to evaluate homoplasy using trees generated from an initial set of weights. He suggested using the levels of homoplasy observed to adjust the weights assigned to the characters and then conduct a new analysis with these updated weights. This iterative process continues until the new weights match those from the previous round (Farris, 1969). However, as others, this weighting method is not without biases. Using the consistency index (CI) provides insights into the homoplasy associated with each character, i.e., a CI of 1 indicate the absence of homoplasy, while a CI of 0 represents a homoplastic character (Farris, 1983; Farris, 1989), but it diminishes the influence of multistate characters. Consequently, for a similar number of steps, binary characters tend to have a greater impact than multistate characters (Goloboff, 2022b, 2022a). To address these issues, we opted to compare the CI with the RI and RC (Farris, 1989). The RI correspond to the relative homoplasy, meaning the proportion of informative variation that is effectively retained as synapomorphy on the phylogenetic tree (Farris, 1989; Goloboff, 2022b). The RC combines the CI and RI. The RC will measure the proportion of maximum observable homoplasy and will achieve 0 when a character fits the tree as poorly as possible (Farris, 1989; Goloboff, 2022b). Given these considerations, we chose the SAW method because it helps reduce bias from homoplasy by adjusting character weights through an iterative process. This ensures that less informative characters, which may contribute to homoplasy, are given less weight, while more informative characters are prioritized (Goloboff, 2022b). Additionally, SAW offers flexibility in handling complex datasets, allowing for more accurate reflection of evolutionary relationships among OTUs. This leads to better tree resolution and reduces the effects of convergent evolution or reversals. Overall, SAW helps create a more reliable and balanced interpretation of the data, improving the robustness of the phylogenetic analysis (Farris, 1969).

After the reweighting process a subsequent tree search was run using the heuristic algorithm implemented in the software. In the presence of MPTs, the strict consensus was calculated.

In these analyses, characters were treated as unordered, and no transformation cost matrix was applied. A heuristic search algorithm was employed, which used random addition sequences (RAS) and tree bisection and reconnection (TBR) for branch swapping. This process involves splitting the

tree into subtrees, which are then rearranged and reconnected to find the most parsimonious tree with the fewest steps.

The consistency index (CI) was calculated to assess the robustness of the trees and to gauge the extent of homoplasy in each phylogeny. However, a high number of autapomorphies in a tree can artificially inflate the CI (towards 1), making it less reliable in indicating the level of homoplasy. To address this, the retention index (RI) was also calculated, representing the ratio between the maximum possible homoplasies and the observed homoplasies.

Evaluating the performance of a phylogenetic method can be challenging, as the “real” phylogeny cannot often be known. One of the approach used is based on a congruence criterion, commonly used in cladistic (Wheeler, 2001). To assess the accuracy and reliability of the GMM data, the trees obtained from matrices A and B are compared to a reference phylogeny based on an independent source of evidence. In this study the reference topology is the tree obtained from the morphological matrix (i.e., Matrix C), as molecular data are not available for most of the specimens sampled. To minimize the effect of the weighting, we compared each topology with the one derived from the same weighting (for example, the tree from matrix C from CI-weighting versus the tree from matrix A from CI-weighting). The level of concordance was then measured by calculating the number of SPR (Subtree Pruning and Regrafting) moves (Goloboff, 2007). This metric represents the inverse of the number of SPR moves needed to transform one tree into the other, divided by $T-3$, where T is the number of taxa (Goloboff, 2007). We also calculated Robinson-Foulds distances (RF, Robinson and Foulds, 1981) to further assess topological similarity. Lower SPR values and higher RF distances indicates greater dissimilarity, and therefore lower congruence, (i.e., a tree with a SPR value of 0.6 will be more congruent than one with 0.4; and a tree with a RF distance of 0.4 will be more congruent than one with 0.6).

To assess the influence of allometry on shape, a linear regression of shape coordinates was performed on centroid size using “lm()” function (Chambers, 1992) on R, and then the residuals were submitted to the same phylogenetic protocol described previously.

Finally, the robustness of the phylogenetic tree was assessed through 100 bootstrap replications, following the methodology of (Felsenstein, 1985b).

Key-points II.III.1

Matrices:

- Total OTUs: 23 from *Homo* and *Australopithecus*, including 3 outgroups (*Gorilla*, *Pan*, and *Pongo*).
- Data Type: Average calvarial morphology per OTU, based on 3D landmark data, or discrete characters.
- Matrix sets:
 - Matrix A: 59 discrete morphological characters of the calvarium, coded 1–3 (from Chapter II). Serves as a reference tree for comparison with GMM-based matrices (A and B).
 - Principal Component (PC) coordinates matrices, from PCA on Procrustes residuals:
 - B.1: 22 PC based on 148 landmarks (27 landmarks + 121 semi-landmarks).
 - B.2: 22 PC based on 347 landmarks (27 landmarks + 320 semi-landmarks).
 - B.3: 22 PC based on 636 landmarks (27 landmarks + 609 semi-landmarks).
 - Procrustes-aligned 3D coordinates:
 - C.1: 148 landmarks (27 landmarks + 121 semi-landmarks).
 - C.2: 347 landmarks (27 landmarks + 320 semi-landmarks).
 - C.3: 636 landmarks (27 landmarks + 609 semi-landmarks).
- Symmetry correction and allometry: Bilateral landmarks can cause left/right features to be overrepresented. Test of allometry through linear regression. Two version of Matrix B was made, excluding left-side landmarks after GPA and without allometry.
- Technical Adjustment: TNT software cannot handle negative values. Added 10 units to each variable in all matrices with PC coordinates to avoid processing issues.
- To avoid taxonomic order bias, analyses were run with varied outgroup placements.

Phylogenetic analyses:

- Software: TNT v1.6 (Goloboff and Morales, 2023).
- Total analyses: 21 parsimony-based analyses (Matrices A–C × 3 weighting schemes).
- Weighting schemes: Successive Approximations Weighting (SAW):
 - Method:
 - Initial unweighted analysis → calculate CI (Consistency Index), RI (Retention Index) or RC (Rescaled Consistency Index).
 - Use these to reweight characters → run analysis again.
 - Only one iteration was performed
 - Why SAW? Helps reduce bias from homoplasy. Prioritizes informative characters and down weights noisy traits.
 - CI vs RI vs RC:
 - CI = Homoplasy indicator; 1 = perfect fit, 0 = total homoplasy.
 - RI = Proportion of homoplasy, similar to the CI.
 - RC = Combines CI × RI; compensates for CI's bias against multistate characters.

Phylogenetic methodology:

- Approach: Maximum parsimony.
- Character treatment: Unordered; no transformation cost matrix applied.
- Initial Search: Heuristic algorithm with equal weighting using Random Addition Sequences (RAS) and Tree Bisection and Reconnection (TBR).
- Post-weighting search: SAW-adjusted weights used in a second heuristic search. In case of multiple most parsimonious trees (MPTs), a strict consensus tree was computed.
- Tree quality metrics:
 - CI: Indicates tree homoplasy (higher = better fit).
 - RI: Complements CI, adjusts for autapomorphies.
- Robustness and congruence assessment to evaluate reliability of GMM-based trees (Matrices A–B):
 - Bootstrap: 100 replicates following Felsenstein (1985b).
 - Reference Tree: Matrix C (discrete morphology-based).
 - Method: Compared topologies derived from the same weighting type (e.g., A-C CI-weighted trees).
 - SPR (Subtree Pruning and Regrafting) moves: Measures tree similarity.
 - RF (Robinson-Foulds) distances: Measures branch agreement.
- Interpretation:
 - RF distances: Lower values (closer to 0) = greater topological congruence.
 - SPR similarity: Higher values (closer to 1) = greater topological congruence.

III.2. Chapter IV – Morphological and 3D characters

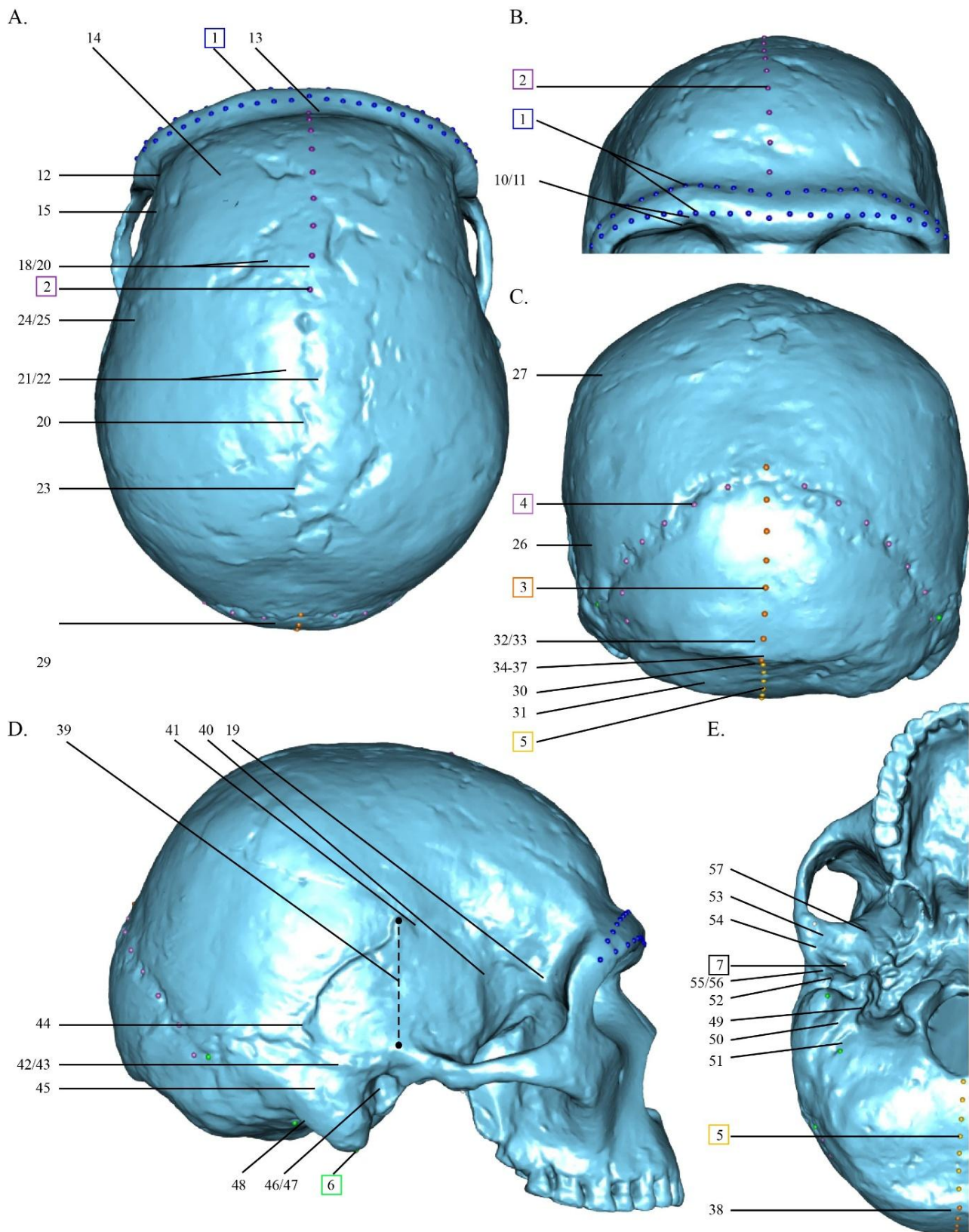


Figure 31: Position of the 57 characters on the calvarium: A) *norma verticalis*, B) *norma facialis*, C) *norma occipitalis*, D) *norma lateralis*, and E) *norma basilaris*. In the squared coloured boxes are the landmark configurations.

Table 4: Correspondences between the morphological features used in “Chapter III – Cladistics and GMM” and in “Chapter IV – Morphological and 3D characters”. The characters in light blue are the one replaced by landmark configurations in Matrix E and the character in light green was added in both matrices of Chapter IV – Morphological and 3D characters.

Character number in Chapter III	Definition/Name	Character number in Chapter IV	
		Matrix D	Matrix E
3	Outline of the supraorbital region, <i>norma facialis</i>	1	1
7	Outline of the supraorbital region, <i>norma verticalis</i>	2	2
10	Antero-posterior convexity of the frontal (Ifc=M29*100/M26)	3	3
23	Outline of the occipital, <i>norma lateralis</i>	4	4
24	Outline of the <i>planum occipitale</i> , <i>norma lateralis</i>	5	5
29	Outline of the <i>planum occipitale</i> , <i>norma occipitalis</i>	6	6
37	External occipital crest	7	7
38	Aligned posterior and anterior external occipital crest	8	8
49	<i>Processus mastoideus</i> : downward development / basicranium	9	9
53	Glenoid cavity depth / articular tubercle lowest point	10	10
1	Outline of the calvaria, <i>norma occipitalis</i>	11	11
2	Frontal cord length / parietal cord length	12	12
4	Supraorbital region: <i>sulcus supraorbitalis</i>	13	13
5	Projection of the supraorbital region	14	14
6	Post-orbital constriction (Ipc=M9/M43)	15	15
8	<i>Sulcus postorbitalis</i>	16	16
9	<i>Tuber frontale</i>	17	17
11	<i>Linea temporalis</i> development on the frontal	18	18
/	Sagittal crest	19	19
12	Sagittal keel on the frontal	20	20
13	Bregmatic eminence	21	21
14	Pterion	22	22
15	Thickening on the superior part of the coronal sutures	23	23
16	Sagittal keel on the bregma-lambda arch	24	24
17	Parasagittal hollowing on both sides of the parietal suture	25	25
18	Pre-lambdatic hollowing on the bregma-lambda arch	26	26
19	<i>Linea temporalis</i> width of the temporal band	27	27
20	<i>Linea temporalis</i> : position on parietal (Rlt = temporo-parietal suture-superior line / temporo-parietal suture-bregma)	28	28
21	<i>Torus angularis parietalis</i>	29	29
22	<i>Tuber parietale</i>	30	30
25	Relative development: planum nucale (PN) / planum occipitale (PO)	31	31
26	Occipital bun	32	32
27	Opisthocranium relative position / inion	33	33
28	<i>Processus retro mastoideus</i>	34	34
30	Suprainiac fossa	35	35
31	Suprainiac fossa: lateral edges	36	36
32	<i>Sulcus supratotalis</i>	37	37
33	<i>Torus occipitalis transversus</i>	38	38
34	<i>Torus occipitalis transversus</i> form, <i>norma occipitalis</i>	39	39
35	<i>Protuberantia occipitalis externa</i>	40	40

36	<i>Tuberculum linearum</i>	41	38
39	Temporal squama heigh (Iet=maximal height from auriculae*100 / maximal width)	42	39
40	Outline of the anterior border of the temporal squama	43	40
41	Outline of the superior border of the temporal squama	44	41
42	Development of the <i>crista supramastoidea</i> at the porion	45	42
43	<i>Crista supramastoidea</i> / <i>processus zygomaticus temporalis</i>	46	43
44	<i>Tuberculum supramastoideum anterius</i>	47	44
45	Supramastoid groove (between <i>crista supramastoidea</i> and <i>crista mastoidea</i>)	48	45
46	Form of the auditory meatus	49	46
47	Position of the auditory meatus / <i>processus zygomaticus temporalis</i>	50	47
48	<i>Tuberculum mastoideum anterius</i>	51	48
50	Juxtamastoid ridge development / <i>processus mastoideus</i>	52	49
51	Digastric groove: presence of a bony bridge	53	50
52	<i>Crista occipito mastoidea</i>	54	51
54	Petro-tympanic crest orientation in relation to the sagittal plan	55	52
55	Articular tubercle configuration	56	53
56	<i>Tuberculum zygomaticum anterius</i>	57	54
57	<i>Tuberculum zygomaticum posterius</i> (post glenoid process)	58	55
58	Tympanal contribution to the posterior wall of the glenoid cavity	59	56
59	Preglenoid tubercle	60	57

III.2.1. Matrices

In the fourth set of analyses, 30 OTUs, including the three outgroup taxa (see Chapter I – Materials / Table 1 and Chapter IV – Morphological and 3D characters), were analysed through two matrices:

- Matrix D contained 60 morphological characters describing the morphology of the calvarium (see, Table 4 and Appendix 10), coded as discrete states ranging from 1 to 3 (Table 2 and Appendix 11).
- Matrix E combine two types of data (see Table 4): morphological characters and 3D Procrustes-aligned coordinates of landmarks and semi-landmarks (post-Generalized Procrustes analysis, GPA) representing the averaged morphology of specific features of each OTU.

For matrix E, some morphological characters presented in “Chapter II – Method / Data / Morphological Characters” were replaced by the corresponding landmarks and semi-landmarks, for a total of 57 characters, with 50 morphological characters and 7 landmark configurations (see, Figure 31 and Table 4):

- Characters 3 and 7 (outline of the supraorbital region in *norma facialis* and *verticalis*) were replaced by a configuration of 46 landmarks (see, character 1 in Figure 31).

- Character 10 (antero-posterior convexity of the frontal) was replaced by 11 landmarks (see, character 2 in Figure 31).
- Characters 23 and 24 (outline of the occipital and the *planum occipitale* in *norma lateralis*) were replaced by 15 landmarks (see, character 3 in Figure 31).
- Character 29 (outline of the *planum occipitale* in *norma occipitalis*) was replaced by 15 landmarks (see, character 4 in Figure 31).
- Character 37 and 38 (external occipital crest and alignment of the posterior and anterior external occipital crest) were replaced by 8 landmarks (see, character 5 in Figure 31).
- Character 49 (downward development of the *processus mastoideus* in relation to the basicranium) was replaced by 6 landmarks (see, character 6 in Figure 31).
- Character 53 (the glenoid cavity depth or articular tubercle lowest point) was replaced by 4 landmarks (see, character 7 in Figure 31).

III.2.2. Analyses

As a result, four parsimony phylogenetic analyses were conducted, corresponding to the analysis of the matrices, with the weighting according to two indices: the CI and the RC, following the successive approximative weighting method (SAW) of Farris (1969) (see, Chapter II – Method / Protocols / Scripts and Chapter II – Method / Protocols / Chapter III – Cladistics and GMM).

After the reweighting process a subsequent tree search was run using the heuristic algorithm implemented in the software. In the presence of MPTs, the strict consensus was calculated.

In these analyses, characters were considered unordered, and no transformation cost matrix was used. The initial matrix analyses employed a heuristic algorithm with equal weighting, random addition sequence (RAS), and tree bisection and reconnection (TBR) for branch swapping. This method divides the tree into subtrees, rearranges, and reconnects them until the trees with the fewest steps is determined.

To assess the robustness of the tree, the CI and RI were calculated. The CI was used to indicate the degree of homoplasy in each tree. However, if a tree has a high number of autapomorphies, this index may be artificially high (closer to 1), regardless of the homoplasy content of the other traits. To address this, we also calculated the RI of each tree, which represents the ratio between the maximum and observed number of homoplasies.

To evaluate the performance of this phylogenetic method, the tree obtained from matrix E was compared to a reference phylogeny based on an independent source of evidence. In this study the reference topology is the tree obtained from the matrix D, i.e., without replacement of characters with landmark configurations, as molecular data are not available for most of the specimens sampled. To minimize the effect of the weighting, we compared each topology with the one derived from the same weighting (for example, the tree from matrix E from CI-weighting versus the tree from matrix D from CI-weighting). The level of concordance was then measured by calculating the number of SPR (Subtree Pruning and Regrafting) moves (Goloboff, 2007). This metric represents the inverse of the number of SPR moves needed to transform one tree into the other, divided by $T-2$, where T is the number of taxa (Goloboff, 2007). We also calculated Robinson-Foulds distances (RF, Robinson and Foulds, 1981) to further assess topological similarity. Higher SPR values and RF distances indicates greater dissimilarity, and therefore lower congruence, (i.e., a tree with a SPR value or RF distance of 0.4 will be more congruent than one with 0.6).

The robustness of each branch was finally assessed through 100 standard bootstrap replications (following Felsenstein, 1985a).

Key-points II.III.2

Matrices:

- Total OTUs: 28 from *Homo*, *Australopithecus* and *Paranthropus*, including 3 outgroups (*Gorilla*, *Pan*, *Pongo*).
- Data Type: Average calvarial morphology per OTU, based on 3D landmark data or discrete characters.
- Matrix sets:
 - Matrix D: 60 discrete morphological characters of the calvarium, coded 1–3 (from Chapter II). Serves as a reference tree for comparison with matrix B.
 - Matrix E:
 - Combined two data types: 50 discrete morphological characters and 7 landmark configurations (each treated as one character) derived from Procrustes-aligned 3D coordinates.
 - Morphological characters corresponding to the landmark configurations were replaced.
- To avoid taxonomic order bias, analyses were run with varied outgroup placements.

Phylogenetic analyses:

- Software: TNT v1.6 (Goloboff and Morales, 2023)
- Total analyses: Six (Matrices D–E × 3 weighting schemes)
- Weighting schemes: Successive Approximations Weighting (SAW):
 - Method:
 - Initial unweighted analysis → calculate CI (Consistency Index), RI (Retention Index) or RC (Rescaled Consistency Index).
 - Use these to reweight characters → run analysis again.
 - Only one iteration is performed.
 - Why SAW? Helps reduce bias from homoplasy. Prioritizes informative characters and down weights noisy traits.
 - CI vs RI vs RC:
 - CI = Homoplasy indicator; 1 = perfect fit, 0 = total homoplasy.
 - RI = Proportion of homoplasy, similar to the CI.
 - RC = Combines CI + RI (Retention Index); compensates for CI's bias against multistate characters.

Phylogenetic methodology:

- Approach: Maximum parsimony.
- Character treatment: Unordered; no transformation cost matrix applied.
- Initial search: Heuristic algorithm with equal weighting using Random Addition Sequences (RAS) and Tree Bisection and Reconnection (TBR).
- Post-weighting search: SAW-adjusted weights used in a second heuristic search. In case of multiple most parsimonious trees (MPTs), a strict consensus tree was computed.
- Tree quality metrics:
 - CI: Indicates tree homoplasy (higher = better fit).
 - RI: Complements CI, adjusts for autapomorphies.
- Robustness and congruence assessment to evaluate reliability of GMM-based trees (Matrix E):
 - Bootstrap: 100 replicates following Felsenstein (1985b).
 - Reference Tree: Matrix D (discrete morphology-based).
 - Method: Compared topologies derived from the same weighting type (e.g., D-E CI-weighted trees).
 - SPR (Subtree Pruning and Regrafting) moves: Measures tree similarity.
 - RF (Robinson-Foulds) distances: Measures branch agreement.
- Interpretation:
 - RF distances: Lower values (closer to 0) = greater topological congruence.
 - SPR similarity: Higher values (closer to 1) = greater topological congruence.

III.3. Scripts

To implement the protocol across all matrices, we developed a script that is structured into four distinct parts (see Figure 32):

1. *Calculation of Necessary Values*: In the first part, we calculate all the required values, such as the minimum and maximum steps for each landmark. Specifically, we determine the “real” minimum score for each landmark by running an independent search for each landmark (using the option “Settings/Landmarks/General Options/Minima for Implied Weights/Determine with tree search for each landmark”). These values were copied and included in the datafile, after the landmark coordinates (command *“usmin”*). The script then defines the necessary variables: *`lminlm`* (minimum steps per landmark), *`lmaxlm`* (maximum steps per landmark), *`CIlm`*, *`RIlm`*, *`RCIm`* (CI/RI/RC values for each landmark), *`pas\_land`* (number of steps per landmark), and *`poids`* (weight index and weight of each landmark). For morphological data, similar variables are used, replacing “lm” with “cara,” and additional variables such as *`ident`* (number of identical weights), *`poids\_pond`* (new weighted values), and *`deacc`* (deactivated characters when CI/RI/RC equals 0) are introduced.
2. *Calculation of CI/RI/RC and Weighting*: The second part of the script initiates a heuristic search with Tree Bisection and Reconnection (TBR) under equal weights. Following this initial search, a loop is opened for each iteration of the search process. Within this loop, another loop is opened for each character, where the CI/RI/RC values are calculated based on the selected index. Each character is then weighted according to the obtained CI/RI/RC values, and the weights are stored in the *`poids`* variable, considering the tree obtained in the previous iteration (or the tree obtained under equal weights if the loop is in the first iteration).
3. *Tree Reweighting and Analysis*: Finally, in the fourth part of the script, a new analysis is conducted using the reweighted characters and a heuristic algorithm with TBR.
4. *Final tree and support*: A strict consensus of the trees is calculated, followed by the computation of bootstrap values.

```

macro =;
report-;
lm f = 1;
hold 1000 / 1000;
keep 0;
tv -;

var:
    leminlm
    lemaxlm
    CIlm
    RIlm
    RCIm
    pas_land
    which
    poids [ (lmnpoints[0] + 1) ]
    ;

/*chood the number grid and the number of cell, here 5 and 1*/
lmark cel 5 nes 1;
/*choose the number of iteration and tree retained, here 2 and 2*/
mult 2 = hold 2;
tv > . ;
keep 0;
lm wts=1 0/. ;
loop 0 lmnpoints[0]
    set poids [#1] 1;
stop

/*Choose the SAW index, here CI*/
/*0 = CI, 1 = RI, 2 = RC;*/
set which 0;

/*choose the number of iteration, here only 1*/
loop=iter 0 0
    progress #iter 10 Running iteration;
    tv < . ;
    loop=cara 0 lmnpoints[0]
        set pas_land lmscore[0 0 #cara];
        set leminlm minsteps[0 #cara];
        set lemaxlm maxsteps[0 #cara];
        set pas_land 'pas_land'/'poids[#cara]';
        set lemaxlm 'lemaxlm'/'poids[#cara]';

        if ('pas_land' == 0)
            set CIlm 1;
        else
            set CIlm 'leminlm'/'pas_land';
        end;

        if ('lemaxlm'-'leminlm' == 0)
            set RIlm 1;
        else
            set RIlm ('lemaxlm'-'pas_land')/('lemaxlm'-'leminlm');
        end;

```

```

        if ('which' == 0)
            lm wts = 'CIlm' 0/#cara;
            set poids [#cara] 'CIlm';
        end

        if ('which' == 1)
            lm wts = 'RCIm' 0/#cara;
            set poids [#cara] 'RIlm';
        end

        if ('which' == 2)
            set RCIm 'CIlm'*'RIlm';
            lm wts = 'RCIm' 0/#cara;
            set poids [#cara] 'RCIm';
        end
    stop

    lm wts;
    mult 2 = hold 2;

    tv < . ;

    bb;
    nelsen*;
    tc /;
    /*choose the name of the file to save*/
    tsave * consensus_tree_lm_RI; save; tsave/;
    resample boot;
    resample poisson;
    endloop;

stop

progress/;
proc/;

```

Figure 32: TNT script to apply the SAW method to landmarks and semi-landmarks. In bold are the part that can be modified.

Chapter III – Cladistics and GMM

Over the past three decades, virtual imaging has become increasingly prevalent in non-medical fields of research, particularly in palaeontology and palaeoanthropology (e.g., Balzeau et al., 2012). This shift in methodology has coincided with the rise of geometric morphometric methods (GMM), which enable quantitative analysis to explain and visualize shape differences (i.e., form without size) that have been mathematically assessed (Adams et al., 2013; Zelditch et al., 2004). Both virtual imaging and GMM have been widely adopted by taxonomists and are now commonly used to test hypotheses concerning the classification of extinct species (e.g., Mounier, 2012; Mounier et al., 2011; Profico et al., 2016).

However, the adoption of these new tools has largely overlooked a prior advancement in taxonomy: cladistics. Cladistics revolutionized systematics by incorporating ancestor-descendant relationships into the analysis (Matile et al., 1987), a significant departure from earlier phenetic approaches that focused primarily on morphological similarities (Sneath and Sokal, 1973). While morphological data from virtual imaging and GMM can be analysed within a phenetic framework, they must be adapted for use in cladistic phylogenetic frameworks (MacLeod et al., 2002b).

The integration of GMM into cladistics is challenging due to the continuous nature of shape data, which resists discretisation into clear character states (MacLeod et al., 2002b; Thiele, 1993). Continuous traits like size or shape complicate homology assessments and tree construction (Bookstein, 1994; Pleijel, 1995a). Traditional cladistic methods, designed for discrete characters, struggle with the multidimensional data produced by landmark-based GMM (Klingenberg and Monteiro, 2005).

Despite this, identifying phylogenetic signals from geometric morphometric data has been the subject of numerous studies (Klingenberg and Gidaszewski, 2010; MacLeod et al., 2002b), and several protocols for integrating this data into cladistic frameworks have been proposed (Clouse et al., 2011; González-José et al., 2008). However, these protocols remain rare, have faced significant criticism (Adams et al., 2011; Varón-González et al., 2020). Advances in algorithms now allow for more consistent analysis (Catalano et al., 2010; Parins-Fukuchi, 2018), but theoretical disagreements remain.

This chapter explores the use of geometric morphometric data within a cladistic framework to investigate phylogenetic relationships among hominin taxa. By employing a standardised analytical protocol across different types of morphological datasets, raw landmark coordinates, principal

component scores, and traditional discrete traits, I aim at evaluating the strengths and limitations of each approach in reconstructing evolutionary relationships within the genus *Homo*. Special emphasis is placed on assessing the phylogenetic signal present in 3D shape data and how it compares to more conventional morphological characters.

While challenges remain, particularly in translating continuous variation into discrete character states, the findings highlight the potential of morphometric data to refine our understanding of hominin diversity and evolutionary history. This chapter thus offers a critical assessment of how integrating geometric morphometrics with cladistic methodology can enhance phylogenetic reconstruction in paleoanthropological research, drawing primarily on results previously published (Simon-Maciejewski et al., 2024, 2025).

I. Method

To contribute to the ongoing debate surrounding the integration of 3D morphometric data into phylogenetic reconstruction, this study develops and evaluates matrices with three distinct types of data in a strict cladistic framework. These matrices, Matrix A, B and C, are designed to combine the strengths of morphometric and cladistic approaches while addressing prior methodological concerns. The ultimate objective is to produce a phylogeny of the OTUs.

Nature of the data – To assess the performance of GMM-based phylogenetic protocols, this study compares the results obtained from two GMM matrices (Matrices B and C) with those from Matrix A, a traditional cladistic analysis based on discrete morphological traits describing the same sample.

The total sample comprises 78 specimens, including 24 fossil individuals from the genera *Australopithecus* and *Homo*, 45 recent *Homo sapiens*, and 9 outgroup specimens from *Gorilla*, *Pan*, and *Pongo* (see Table 1 in Chapter I – Material). From this dataset, 23 OTUs (including the three outgroups) were computed as the average shape of the specimens assigned to each OTU.

Table 5: Datasets used for each of the matrices.

		Number of characters		
		148 landmarks	347 landmarks	636 landmarks
Morphological matrix (see Table 2 in Chapter II – Method / Morphological characters and Appendix 3)	Matrix A	59 morphological characters.		
22 PC coordinates matrices (after GPA and PCA, see Appendices 4 – 6)	Matrix B.1	x		
	Matrix B.2		x	
	Matrix B.3			x
Landmarks matrices (Procrustes-aligned 3D coordinates, see Appendices 7 – 9)	Matrix C.1	x		
	Matrix C.2		x	
	Matrix C.3			x

Matrix A was built using 59 discrete morphological traits characterising the calvarium (see Chapter II – Method / Data / Morphological Characters and Appendices 2 and 3).

The calvarium's morphology was captured using a combination of 27 anatomical landmarks and a varying number of sliding semi-landmarks, following the method described by Bookstein (1997). Three distinct datasets were generated to describe shape variation, differing in the number of semi-

landmarks used (see Figure 30 in Chapter II – Method / Protocols / Chapter III – Cladistics and GMM):

- Dataset 1: 27 landmarks and 121 semi-landmarks
- Dataset 2: 27 landmarks and 320 semi-landmarks
- Dataset 3: 27 landmarks and 609 semi-landmarks.

These were then used to generate six different matrices (see Table 5 and Chapter II – Method / Protocols / Chapter III – Cladistics and GMM).

Matrix B uses principal component (PC) scores derived from a single Generalized Procrustes Analysis (GPA) alignment of the OTUs' 3D landmarks. By using PC coordinates from a unified GPA as cladistic characters, this matrix addresses concerns over trait non-independence and distortion introduced by multiple alignments, as often raised in previous critiques of GMM-based cladistics.

Matrix C, on the other hand, uses the raw 3D coordinates of the landmarks and semi-landmarks directly as cladistic characters. This approach bypasses PCA entirely, retaining the full dimensionality of the morphometric data and enabling a test of whether PCA reduces or alters the phylogenetic signal.

For all three matrices (A, B, and C), cladistic analyses followed the protocol defined by Mounier and Caparros (2015) and the successive approximative weighting method (SAW) of Farris (1969) (see, Chapter II – Method / Protocols / Scripts and Method / Protocols / Chapter III – Cladistics and GMM), for a total of twenty-one phylogenetic analyses, corresponding to the analysis of the seven different matrices.

The phylogenetic trees resulting from these analyses were then compared to those obtained through phenetic numerical taxonomy methods (neighbour-joining and UPGMA), applied to the same datasets. This multi-approach comparison enables a thorough evaluation of the methodological strengths and limitations of each protocol and contributes to refining the use of GMM in cladistics for more robust phylogenetic reconstructions in human evolution.

To evaluate the performance of this phylogenetic method, the trees obtained from matrices B.1, B.2, B.3, C.1, C.2 and C.3 are compared to a reference phylogeny based on an independent source of evidence. In this study the reference topology is the tree obtained from the morphological matrix

(i.e., Matrix A). The level of concordance was measured by calculating the number of SPR (Subtree Pruning and Regrafting) moves (Goloboff, 2007) and the Robinson-Foulds distances (RF, Robinson and Foulds, 1981). Higher SPR values and RF distances indicates greater dissimilarity, and therefore lower congruence, (i.e., a tree with a SPR value or RF distance of 0.4 will be more congruent than one with 0.6) (see, Chapter II – Method / Protocols / Chapter III – Cladistics and GMM).

The impact of allometry was tested through a linear regression on the PC coordinates (see, Chapter II – Method / Protocols / Chapter III – Cladistics and GMM).

Finally, the robustness of each branch was evaluated using 100 bootstrap replications, following the method outlined by Felsenstein (1985a), to assess the reliability of the phylogenetic tree (see, Chapter II – Method / Protocols / Chapter III – Cladistics and GMM).

Scripts – In this study, the software TNT is used to run the analyses. It is an interactive program, that can read command from instructions files, allowing the automatization of protocols (Goloboff et al., 2008). In order to apply this protocol to the three types of data, I developed a script (see Chapter II – Method / Protocols / Scripts) divided into five parts: first, extracting all necessary values (e.g., minimum and maximum steps); second, calculating the CI and RC of each character; third, weighting each character based on its CI, RI and RC and performing a new search with the weighted values.

Phylogenetic tree showing relationships between various hominid species and their estimated divergence times (in millions of years, My) from a common ancestor. The tree is rooted at the bottom with Pongo and branches upwards. Key nodes are labeled with letters A through M. Divergence times are indicated by numbers on the branches, with some values in green and others in red.

Species listed on the right (from top to bottom):

- Inuit
- China
- France
- Papu
- Berber
- Mandé
- Kongo
- Haya
- KhoiSan
- Skhul - Qafzeh
- Classic Neandertal
- Near East Neandertal
- Early Neandertal
- Ngandong
- Zhoukoudian
- Sangiran
- Dmanisi
- Koobi Fora - *H. ergaster*
- Koobi Fora - *H. habilis* s.l.
- A. africanus*
- Pan*
- Gorilla*
- Pongo*

Key nodes and divergence times (My):

- A**: Root node (Pongo and other hominids)
- B**: Node between *Pan* and other hominids (100 My)
- C**: Node between *Gorilla* and other hominids (61 My)
- D**: Node between *A. africanus* and other hominids (55 My)
- E**: Node between *Koobi Fora - H. ergaster* and other hominids (22 My)
- F**: Node between *Koobi Fora - H. habilis* s.l. and other hominids (83 My)
- G**: Node between *Sangiran* and other hominids (52 My)
- H**: Node between *Zhoukoudian* and other hominids (43 My)
- I**: Node between *Ngandong* and other hominids (63 My)
- J**: Node between *Skhul - Qafzeh* and other hominids (78 My)
- K**: Node between *Early Neandertal* and other hominids (42 My)
- L**: Node between *Haya* and other hominids (96 My)
- M**: Node between *Berber* and other hominids (41 My)

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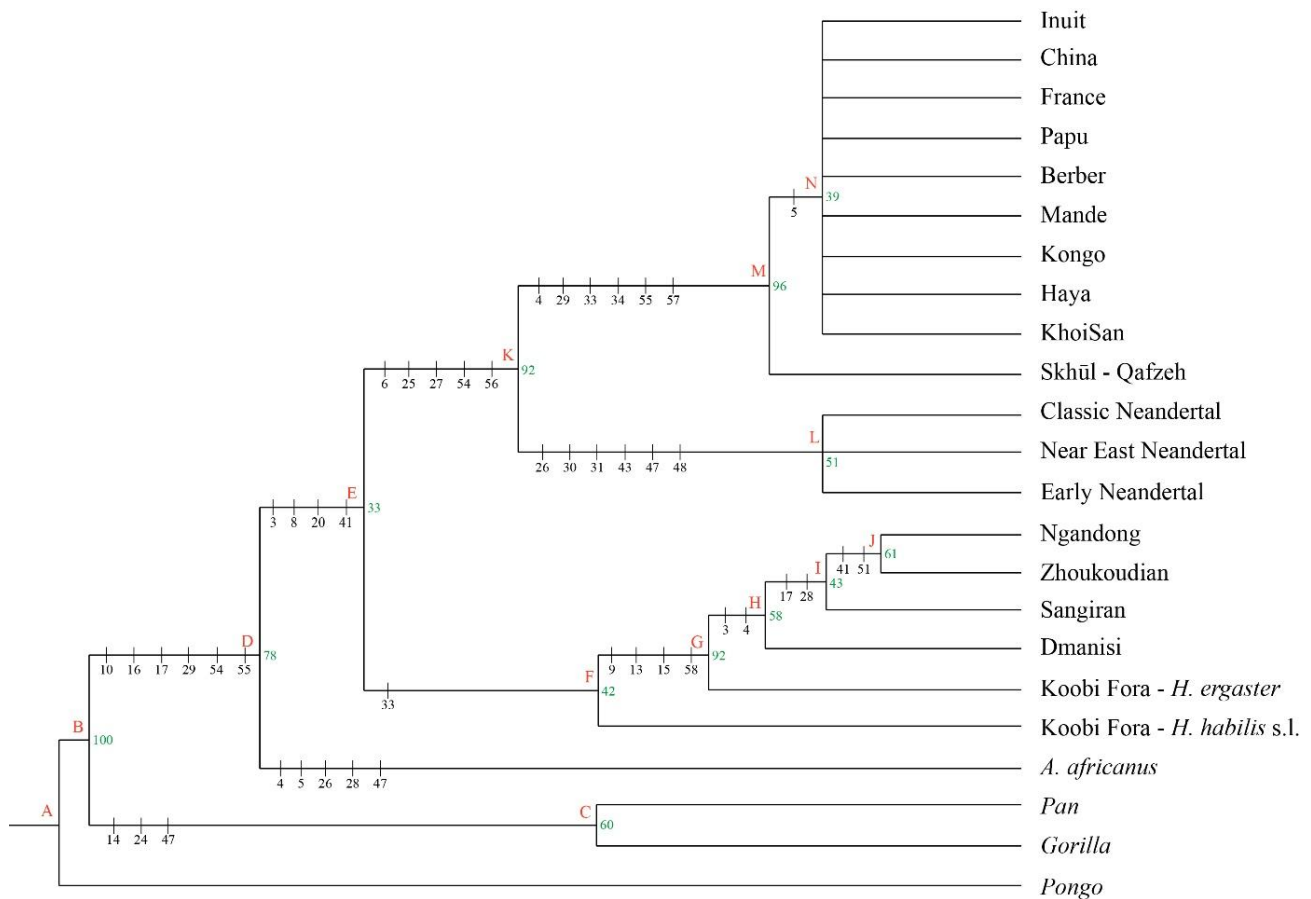


Figure 35: Unique phylogenetic tree based on the analysis of matrix A after RC-weighting (i.e., 59 morphological characters and 23 OTUs), 5327 steps (CI = 0.709 and RI = 0.886). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches, at each node, are the character number where a change in states occurred, showing synapomorphies. Red letters are used to identify each node.

The most parsimonious trees resulting from the two-step analysis of matrix A reveals several interesting trends found in the three trees (Figures 33 to 35).

In the CI-weighted and RC-weighted trees, the taxon *A. africanus* is separated from “Koobi Fora - *H. habilis* s.l.” at node E, while the RI-weighted tree presents a polytomy at node D failing to resolve the relationship of *A. africanus* in regards of the other OTUs.

In all the trees, a monophyletic group consisting of “Koobi fora – *H. habilis* s.l.”, “Koobi fora – *H. ergaster*” and the OTUs Dmanisi, Sangiran, Zhoukoudian and Ngandong can be observed at node F (CI and RC-weighting) and node E (RI-weighting), with the latter three taxa forming a terminal clade at node I (CI and RC-weighting) and node H (RI-weighting). The formation of nodes F/E and I/H is supported by bootstrap values of 39% and 38% (CI-weighting), by 22% and 43% (RI-weighting) and by 42% and 43% (RC-weighting). The Neandertals appear as a monophyletic group at node L (CI

and RC-weighting) and node K (RI-weighting), backed by a bootstrap of 72%/51% (CI/RC-weighting) and 42% (RI-weighting). At node M (CI and RC weighting) and node L (RI-weighting), which includes the OTUs representing *H. sapiens* ("Skhul - Qafzeh" along with various *H. sapiens* populations), the formation of the node is supported by a bootstrap value of 88%/96% for the CI- and RC-weighting and of 96% for the RI-weighting.

Regarding the morphological changes supporting matrix A most parsimonious trees (Figures 33 to 35; Table 6 and Appendix 12), node D is explained by characters #10, 16, 17, 29, 54 and 55 in all the weighting schemes. They corresponds to several anatomical changes; the antero-posterior convexity of the frontal (#10) changes from weak (state 1) to intermediate (state 2); the sagittal keel on the bregma-lambda arch (#16) disappears (state 1), along with the parasagittal hollowing on both sides of the parietal suture (#17, state 1), the outline of the *planum occipitale* in *norma occipitalis* becomes circular (#29, state 2), the petro-tympanic crest is now orientated backward in relation to the sagittal plan (#54, state 3), and the articular tubercle presents a medio-lateral concavity (#55, state 1).

A. africanus is supported by five autapomorphies, which correspond to different states changes in characters #4, 5, 26, 28 and 47: the *sulcus supraorbitalis* in the supraorbital region (#4) goes from absent, with the *arcus superciliaris* and *supraorbitalis* merged (state 3), to complete (state 1), the projection of the supraorbital region (#5) is only observed on the *arcus superciliaris* (state 2); the occipital bun (#26) and the *processus retromastoideus* (#28) are now present (state 2), and finally the auditory meatus is in an intermediate position in relation to the *processus zygomaticus temporalis* (#47, state 2).

In the CI-weighted and RC-weighted trees, node E is supported by a convex supraorbital region in *norma facialis* (#3, state 2), a continuous *sulcus postorbitalis* (#8, state 3), a low positioned *linea temporalis* on the parietal (#20, state 3), and curved or sinuous outline of the superior border of the temporal squama (#41, state 1).

Nodes F and I (CI and RC weighting) or E and H (RI-weighting) group together the Koobi Fora (i.e., *H. ergaster* and *H. habilis*) and Dmanisi specimens with fossils attributed to *H. erectus* (i.e., Ngandong, Zhoukoudian and Sangiran). The clades are supported respectively, by a medially protruding *torus occipitalis transversus* (#33, state 2) and by the presence of parasagittal hollowing on both sides of the parietal sutures (#17, state 2) and of a *processus retromastoideus* (#28, state 2).

The Neandertals appear as a monophyletic group from node L (CI and RC weighted tree) and K (RI-weighted tree), supported by six synapomorphies: the occipital bun is present (#26, state 2), the suprainiac fossa is present (#30, state 3), with lateral edges that are converging upward (#31, state 2), the *crista supra mastoidea* is not aligned with the *processus zygomaticus temporalis* (#43, state 1), the auditory meatus is aligned with the *processus zygomaticus temporalis* (#47, state 3), and the *tuberculum mastoideum anterior* is present (#48, state 2).

Finally, node N (CI and RC weighting) and node M (RI-weighting), which groups all *H. sapiens* OTUs (including “Skhūl - Qafzeh” and various *H. sapiens* populations), is supported by six synapomorphies. This corresponds to the presence of a complete *sulcus supraorbitalis* in the supraorbital region (#4, state 1), to a pentagonal *planum occipitale* in *norma occipitalis* (#29, state 3), to the absence of a *torus occipitalis transversus* (#33 and 34, state 1); to an antero-posterior convexity of the articular tubercle (#55, state 2), and to a weakly-marked or absent *tuberculum zygomaticum posterius* (post glenoid process, #57, state 1).

II.2. Matrix B (PC coordinates as characters)

II.2.1. General results

The morphological diversity presents in the datasets, comprising configurations of 148, 347, and 636 landmarks, was initially assessed at the level of individual specimens through Principal Component Analysis (PCA) (see Appendix 13). In the resulting morphospaces, the placement of specimens aligned well with their conventional taxonomic classifications in palaeoanthropology. When using average landmark configurations of specimens as variables for the Operational Taxonomic Units (OTUs) with the PCA, the morphospaces derived from the first three principal components revealed even more distinct taxonomic clustering than seen in the individual-level analysis (Appendix 14).

A preliminary heuristic analysis conducted on datasets B.1, B.2 and B.3 (each including 22 PCs) produced multiple phylogenetic trees (Figures 36 to 50). Among these PCs, two had a retention index (RI) above 0.4 in matrix B.1 (Figure 36), three in matrix B.2 (Figure 41), and four in matrix B.3 (Figure 46).

In analysis B.1, the heuristic analysis with CI-weighting resulted in a unique parsimonious tree. This tree had a length of 120.249 steps, with a CI of 0.479 and an RI of 0.684 (Figure 37 and Table 7). Reweighting the 22 PCs based on their RI values and re-analysing with a heuristic approach yielded

a single tree consisting of 95.286 steps (CI = 0.558, RI = 0.784; Figure 38 and Table 7). After weighting using the RC values, matrix B.1 analysis generated one tree of 53.82 steps, with a CI of 0.684 and a RI of 0.884 (Figure 39 and Table 7).

For matrix B.2, the heuristic analysis with the CI-weighting produced one parsimonious tree of 108.654 steps, with a CI of 0.486 and a RI of 0.698 (Figure 42 and Table 7). A RI-weighting analysis based on the same 22 PCs produced a unique tree of 91.428 steps (CI = 0.55, RI = 0.77; Figure 43 and Table 7). After weighting using the RC values, matrix B.2 analysis generated one tree of 50.495 steps, with a CI of 0.662 and a RI of 0.869 (Figure 44 and Table 7).

Similarly, CI-weighting analysis of matrix B.3 yielded a unique parsimonious tree of 109.843 steps, with a CI of 0.47 and RI of 0.664 (Figure 47 and Table 7). Reweighting based on RI values yielded a single tree of 83.546 steps (CI = 0.556, RI = 0.779; Figure 48 and Table 7). After weighting using the RC values, matrix B.3 analysis generated one tree of 45.433 steps, with a CI of 0.708 and a RI of 0.896 (Figure 49 and Table 7).

The CI and RI indices of the parsimony trees derived from the analyses of the three datasets are relatively high, being overall superior to 0.5 - with matrix B.3 yielding, overall, higher values - and reflect a robust phylogenetic signal (see, Table 7). We can observe that the length of the most parsimonious tree of each analysis is smaller with the RC weighting, rather than the CI and RI weighting.

Table 7: Length, consistency and retention indices of the tree for each analysis of Matrix B.

	Weighting	Length	CI value	RI value
B.1 – 22 PCs of 148lm	CI	120.249	0.479	0.684
	RI	95.286	0.558	0.784
	RC	53.82	0.684	0.884
B.2 – 22 PCs of 347lm	CI	113.37	0.48	0.675
	RI	91.428	0.55	0.77
	RC	50.495	0.662	0.869
B.3 – 22 PCs of 636lm	CI	109.843	0.47	0.664
	RI	83.546	0.556	0.779
	RC	45.433	0.708	0.896

Table 8: Topological correspondence (SPR moves and Robinson-Foulds distances) between the reference phylogeny and the trees derived from the three matrices. The average SPR similarity is 0.644 and the average RF distance is 0.515.

	Analyses	SPR similarity	RF distance
B.1 – 22 PCs of 148lm	Parsimony - CI	0.75	0.524

	Parsimony - RI	0.4	0.571
	Parsimony - RC	0.7	0.595
	NJ	0.7	0.833
	UPGMA	0.7	0.667
B.2 – 22 PCs of 347lm	Parsimony - CI	0.65	0.429
	Parsimony - RI	0.55	0.476
	Parsimony - RC	0.55	0.548
	NJ	0.6	0.833
	UPGMA	0.6	0.571
B.3 – 22 PCs of 636lm	Parsimony - CI	0.85	0.405
	Parsimony - RI	0.55	0.5
	Parsimony - RC	0.8	0.595
	NJ	0.65	0.833
	UPGMA	0.55	0.619

Among the three PC-based matrices, matrix B.3 (636 landmarks) yielded the highest topological congruence with matrix A (the character-based matrix), as measured by both Subtree Prune and Regraft (SPR) similarity and Robinson-Foulds (RF) distances (see Table 8). Specifically, SPR similarity values and RF distances for matrix B.3 were 0.85 and 0.405 under CI-weighting, 0.55 and 0.5 under RI-weighting, and 0.8 and 0.595 under RC-weighting. In contrast, matrices B.1 and B.2 showed lower congruence, with SPR similarity scores consistently below 0.75 and RF distances generally above 0.5, indicating greater topological incongruence relative to matrix A.

Across all weighting schemes, RI-weighting consistently produced the least congruent topologies, showing the lowest SPR similarity and highest RF distances for each matrix. Conversely, CI-weighting yielded the most congruent topologies, with higher SPR similarity scores and lower RF distances in each case, indicating better alignment with the morphological character-based tree.

When comparing the three PC-based matrices, B.3 (636 landmarks) outperforms B.1 and B.2 in terms of topological similarity to the reference tree, particularly under the CI-weighted scheme.

Regarding the phenetic methods, matrix B.1 produced relatively high congruence, with SPR similarity values reaching 0.7 in both the Neighbour-Joining and UPGMA trees. For RF distances, matrix B.2 performed best under UPGMA (RF = 0.571). Overall, while SPR similarity values were broadly comparable between the phenetic and parsimony-derived topologies, RF distances tended to be lower in the parsimony analyses, indicating slightly greater overall consistency with the reference topology.

The linear regression of shape (22 principal components) against centroid size revealed significant allometric effects restricted to the first three principal components (see, Appendix 15). The remaining components showed no detectable relationship with size. Following the removal of allometric signal by using the residuals from this regression in phylogenetic reconstruction, the resulting trees displayed low topological coherence and failed to recover expected evolutionary relationships. This suggests that the residualised shape data, while size-free, may lack sufficient phylogenetic signal for robust inference.

II.2.2. Matrix B.1 (22 PCs from 148 landmarks)

The most parsimonious trees derived from the two-step analysis of matrix B reveals several key patterns found in the three trees (Figures 37 - 39).

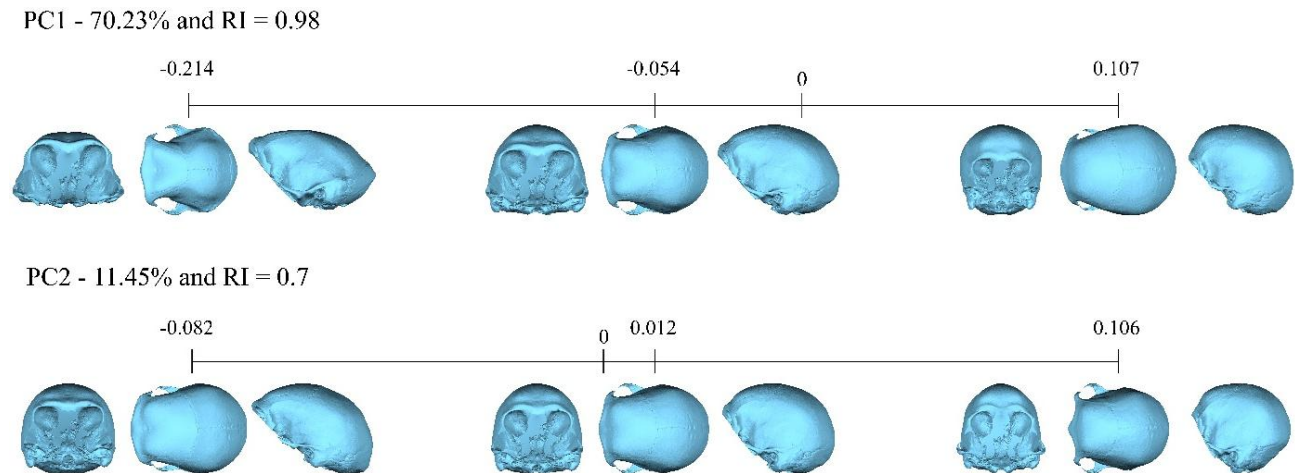


Figure 36: Cranial deformations represented by PCs obtained from the analysis of 148 landmarks. Only PCs with $RI \geq 0.5$ are shown. Values shown in percent represent variance.

Node D formation is explained by a shift from -0.122 to -0.0485 in PC1 and from 0.0225 to -0.025 in PC2 for CI and RI-weighting, from -0.122 to -0.0545 and from 0.0225 to -0.01 in PC2 for RC-weighting. The morphological changes indicated by those values are (see, Figures 36 to 39, and Appendix 16): in *norma facialis*, the *sulcus supraorbitalis* in the supraorbital region is present, but the *arcus superciliaris* and *supraorbitalis* are not merged, and the postorbital constriction is less pronounced compared to that seen in apes. In *norma lateralis*, the profile of the antero-posterior frontal bone is more convex than in apes and the transition between the *planum occipital* and *planum nucale* is rounded, in contrast to the angular transition seen in apes, with the opisthocranion positioned lower. In *norma occipitalis*, the occipital bun and the *processus retromastoideus* are also present, and the cranial outline, defined

by the position of the greatest cranial width (bi-euryon), is of triangular ('tent-like') shape (Grimaud, 1982).

Node E supports a monophyletic group comprising "Koobi Fora – *H. ergaster*", Sangiran, and Dmanisi, with the latter two forming a terminal clade at node F. Those nodes are supported by bootstrap values of 10/14/22% for node E and 26/16/29% for node F, depending on the weighting scheme (i.e., CI, RI or RC). The formation of node E is explained by shifts from -0,025 to -0,041 in PC2, from 0,003 to -0,004 in PC6 and from 0,005 to -0,002 in PC12 for the CI and RI-weighting, and from -0,01 to -0,041 in PC2 and from 0.136 to 0.001 in PC3 for the RC weighting. The formation of node F is explained by shifts from -0,041 to -0,064 in PC2, from -0,004 to -0,008 in PC6, from 0.002 to -0.002 in PC16, from 0.0001 to -0.003 in PC17 and from 0.0001 to -0.001 in PC22 for the CI and RI-weighting. For the RC-weighting the values are similar, except for PC17, where the shift goes from -0.00045 to -0.003. These changes in PC coordinates values refer to some morphological changes (see, Figures 36 and 39, and Appendix 16). At node F, in *norma verticalis*, the supraorbital profile also goes from rectilinear in "Koobi Fora – *H. ergaster*" to concave in Sangiran and Dmanisi, and in *norma lateralis*, the angle between the *planum occipital* and *planum nuchale* is more pronounced compared to the other OTUs. In *norma occipitalis*, the *processus retromastoideus* and the *torus occipitalis transversus* are present, with the later, medially protruding, and the cranial outline is triangular ('tent-like') (Grimaud, 1982), in contrast to the circular ('bomb-like') shape seen in Neandertals (Boule, 1911, 1912, 1913; Condemi, 1992; Vandermeersch, 1981).

Ngandong and the Neandertals are represented as a paraphyletic group from node G and H with the CI and RI weighting and from node I and J with the RC-weighting.

Node K in the CI and RI-weighting trees and node M in the RC weighting tree, which includes the OTUs for *H. sapiens* (i.e., "Skhül - Qafzeh" group and current populations), present bootstrap values of 50% (CI-weighting), 45% (RI-weighting) and 46% (RC-weighting) and is supported by shifts from 0,022 to 0,063 in PC1, from -0,034 to -0,0025 in PC3 and from -0,002 to 0,002 in PC10 for all the weighting schemes. In terms of morphology, the calvarium shape at this node exhibits the general characteristics of *H. sapiens* skull (see, Figures 36 to 39 and Appendix 16): in *norma facialis*, the *sulcus supraorbitalis* is present, with the *arcus superciliaris* and *arcus supraorbitalis* merged. In *norma occipitalis*, the outline of the *planum occipitale* is pentagonal, the *torus occipitalis transversus* disappears, and the cranial outline presents a pentagonal shape ('house-like') (Broca, 1868; Olivier, 1960), and the *torus occipitalis transversus* disappears. In *norma verticalis*, the profile of the supraorbital region is convex.

In *norma verticalis*, the profile of the supraorbital region is also convex. Finally, in *norma lateralis*, the convexity of the antero-posterior frontal bone is highly pronounced, and the angle between the *planum occipital* and *planum nucale* is entirely absent.

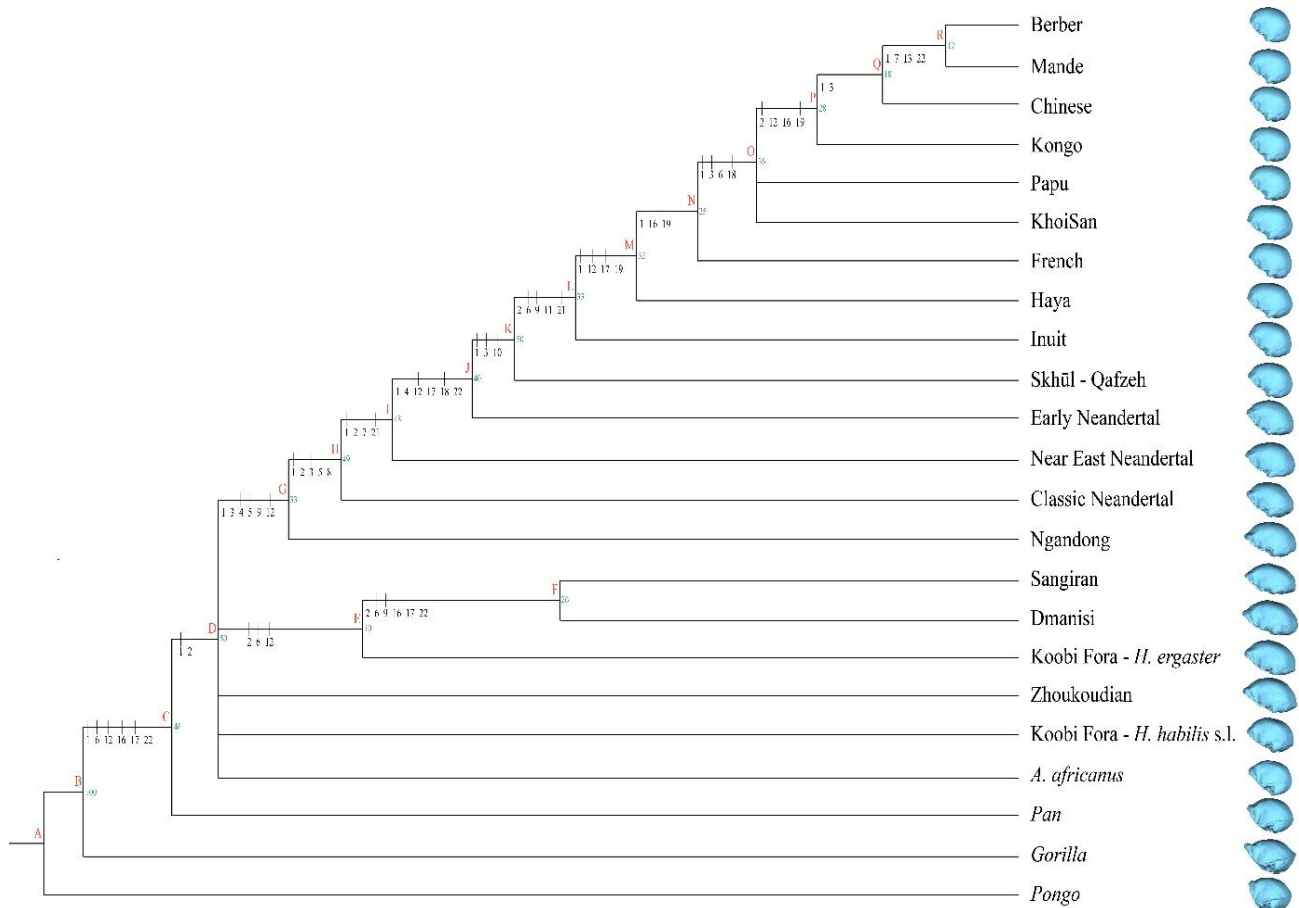


Figure 37: Unique phylogenetic tree based on the analysis of matrix B.1 after CI-weighting (i.e., 22 PC coordinates and 23 OTUs), 120.249 steps (CI = 0.479 and RI = 0.684). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the CI-weighted tree from analysis B.1, two polytomies are observed, at nodes D and O.

Node D, supported by a bootstrap value of 50%, fails to resolve the relationships among *A. africanus*, “Koobi Fora – *H. habilis* s.l.”, Zhoukoudian, the group formed by “Koobi Fora – *H. ergaster*”, Dmanisi, and Sangiran, as well as the remaining OTUs.

Node O, with a bootstrap support of 36%, is an unresolved polytomy within modern humans.

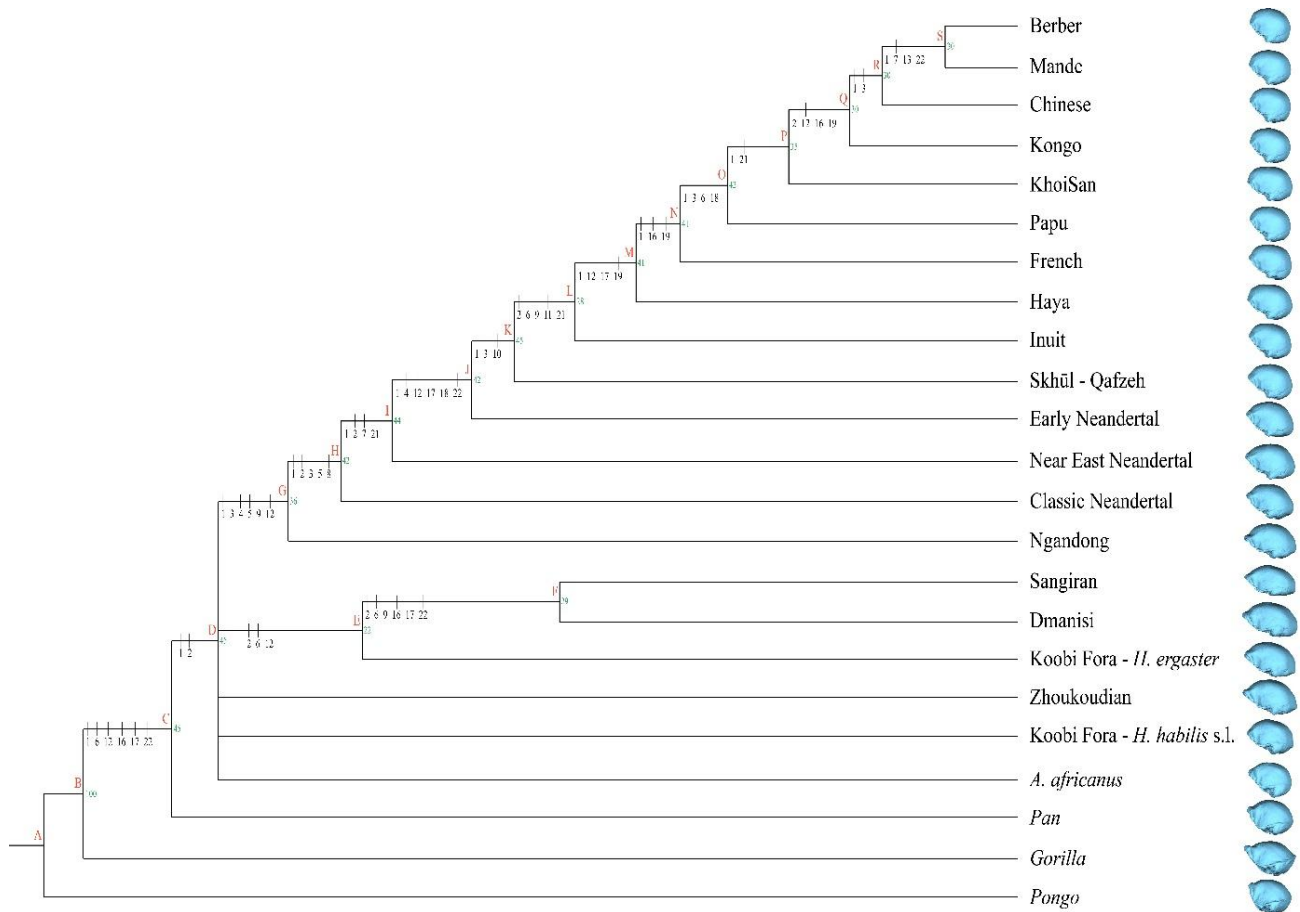


Figure 38: Unique phylogenetic tree based on the analysis of matrix B.1 after RI-weighting (i.e., 22 PC coordinates and 23 OTUs), 95.286 steps (CI = 0.558 and RI = 0.784). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the RI-weighted tree from analysis B.1, only one polytomy is observed, at node D. Compared to the CI-weighted tree, this analysis resolves the polytomy previously observed at node O.

Node O is supported by a bootstrap value of 42%, while node P, grouping the Khoisan with the Kongo, Chinese, Mande, and Berber populations, is supported by a bootstrap of 35%.

At node P, there are observable shifts in PC values: from 0.079 to 0.0825 in PC1, and from -0.001 to 0.0005 in PC21. Although these numerical changes are measurable, the corresponding morphological differences are difficult to discern (see, Figure 36).

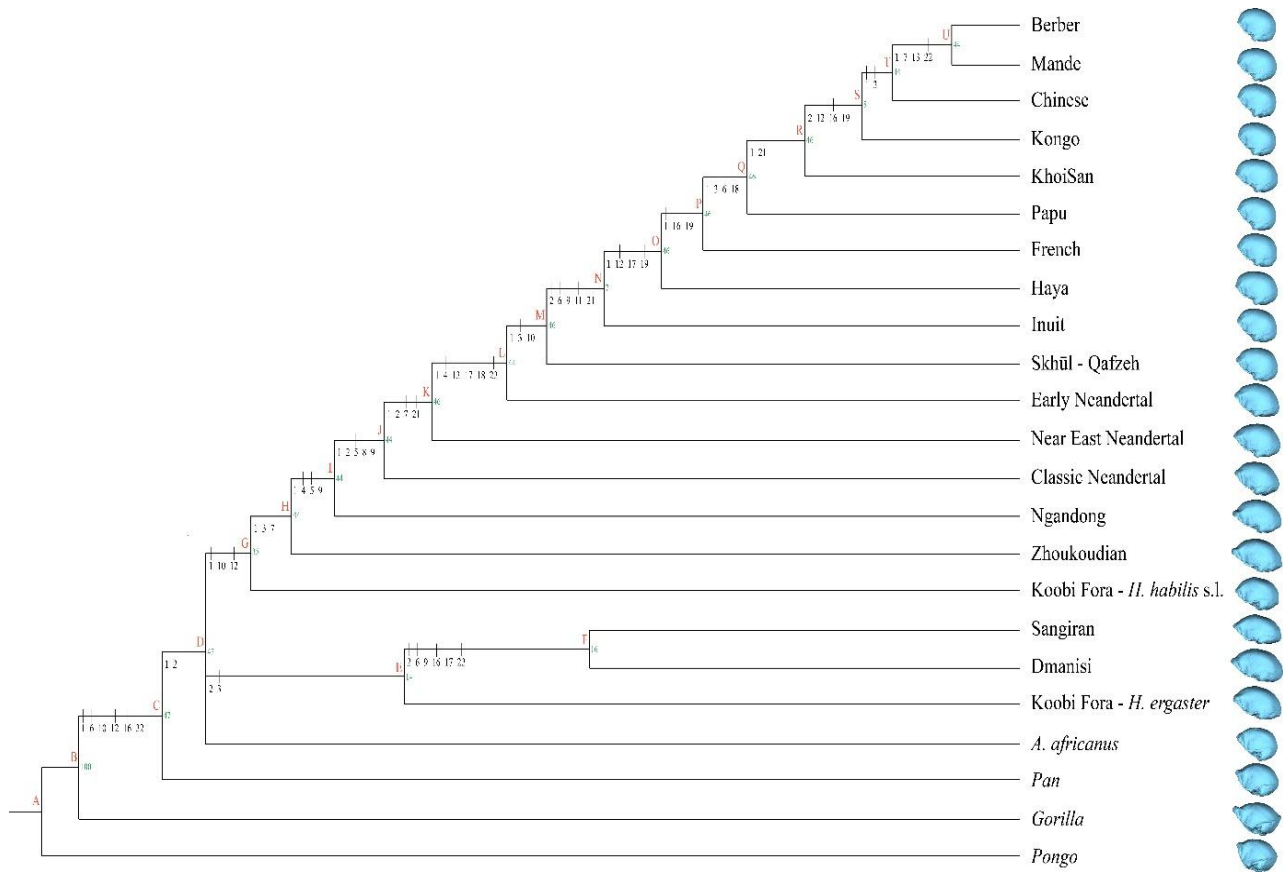


Figure 39: Unique phylogenetic tree based on the analysis of matrix B.1 after RC-weighting (i.e., 22 PC coordinates and 23 OTUs), 53.82 steps (CI = 0.684 and RI = 0.884). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the RC-weighted tree from analysis B.1, only one polytomy is observed, at node D. Node D, supported by a bootstrap value of 47%, fails to resolve the relationships among *A. africanus*, the group formed by “Koobi Fora – *H. ergaster*,” Dmanisi, and Sangiran, as well as the remaining OTUs.

In contrast to the CI- and RI-weighted trees, the relationships of “Koobi Fora – *H. habilis* s.l.” and Zhoukoudian are resolved in this analysis. “Koobi Fora – *H. habilis* s.l.” appears in node G (bootstrap = 35%), and Zhoukoudian in node H (bootstrap = 44%). Both are part of a clade that includes Ngandong, *H. neandertalensis*, and *H. sapiens*.

Node G is characterised by shifts in PC values: from -0.0545 to -0.046 in PC1, from -0.0055 to 0.001 in PC10, and from 0.001 to 0.0055 in PC12. Node H is supported by changes in PC values: from -0.046 to -0.045 in PC1, from 0.017 to -0.019 in PC3, and from 0.0075 to 0.003 in PC7.

The morphological variation along PC1 is illustrated in Figure 36; however, the remaining principal components are not displayed due to their retention indices (RI) being below 0.5.

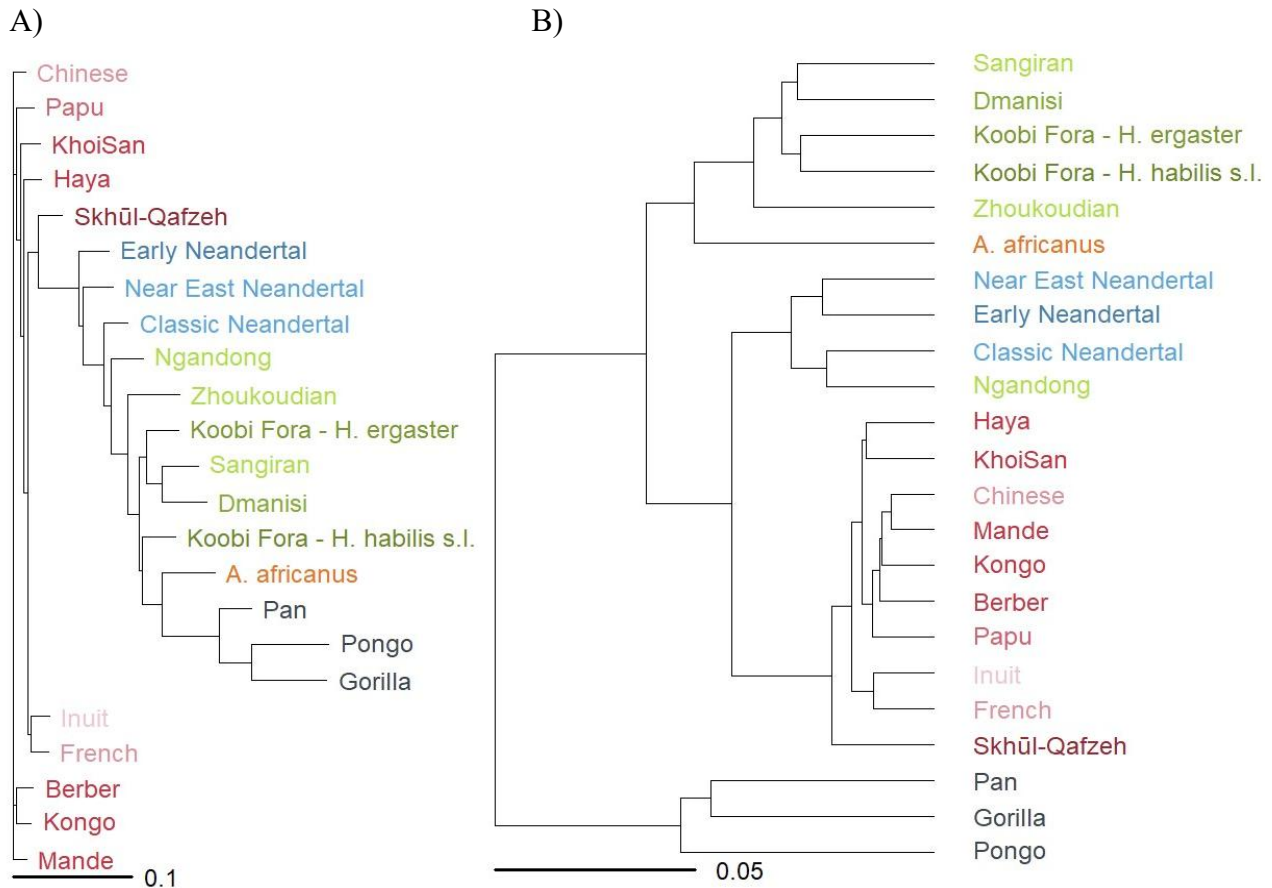


Figure 40: Distance trees based on the analysis of matrix B.1 using two phenetic methods: A) Neighbour-Joining, and B) UPGMA.

We obtained in total six phylogenetic trees –three from cladistic methods and two from phenetic approaches, neighbour-joining (NJ) and UPGMA (see Figure 40). All trees were based on the same GMM-derived datasets, allowing direct comparison of tree topologies and inferred relationships. Robinson-Foulds distances between trees are respectively 0.667 and 0.833 for NJ and UPGMA, while SPR similarity is 0.7 for both analyses, indicating high congruence based on SPR values and a low congruence based on FR distances between approaches. Overall, this suggest that cladistics perform better that phenetic approach.

Visual inspection revealed that both the cladistic and phenetic trees recovered broadly similar groupings at higher taxonomic levels, particularly clustering specimens from *H. sapiens* together with Neandertals and Ngandong at the base, and Sangiran, Dmanisi and “Koobi Fora – *H. ergaster*” consistently. However, finer-scale relationships (e.g., within-group structure) varied notably between methods.

A major point of divergence was the placement of the OTU Zhoukoudian, “Koobi Fora – *H. habilis* s.l.” and *A. africanus*, which relationships are unresolved in two of the parsimony trees, and grouped with Sangiran, Dmanisi and “Koobi Fora – *H. ergaster*” in the last cladistic tree but clustered with Sangiran, Dmanisi and “Koobi Fora – *H. ergaster*” in both NJ and UPGMA method. This discrepancy may reflect the influence of overall morphological similarity in phenetic methods, as opposed to the character-state polarity emphasized in cladistics.

II.2.3. Matrix B.2 (22 PCs from 347 landmarks)

The most parsimonious trees derived from the two-step analysis of matrix B.2 reveals several key patterns found in the three trees, similar to matrix B.1 (Figures 42 and 44).

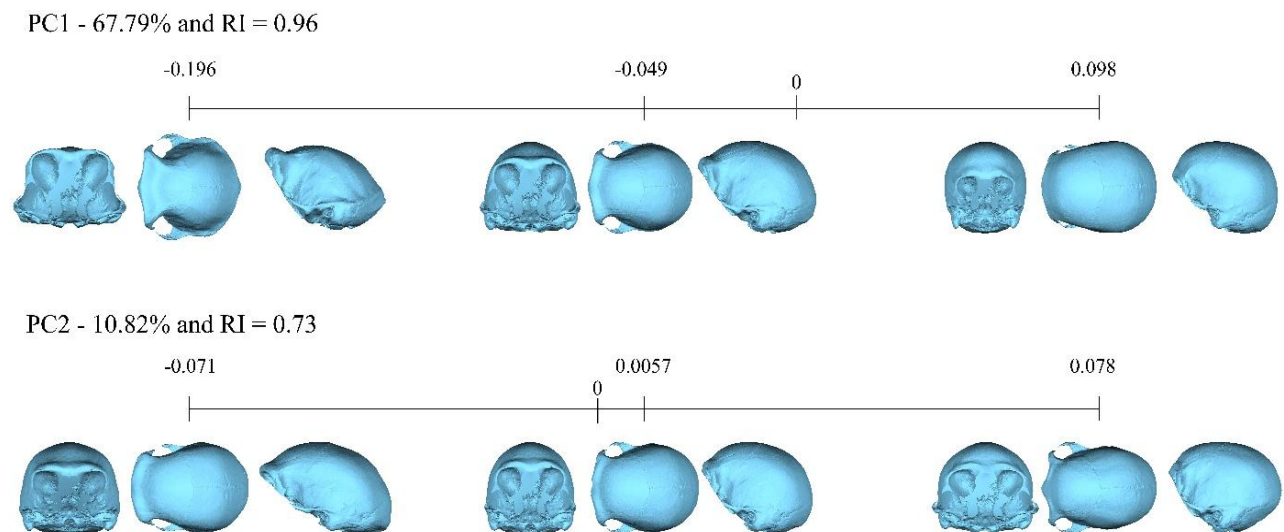


Figure 41: Cranial deformations represented by PCs obtained from the analysis of 347 landmarks. Only PCs with $RI \geq 0.5$ are shown. Values shown in percent represent variance.

Node D formation is explained by a shift from -0.016 to -0.051 in PC1 in the three weighting schemes (i.e., CI, RI and RC-weighting). This node is supported by bootstrap values of 52% for CI-weighting, 43% for RI-weighting and 47% for RC-weighting. The morphological changes indicated by those values are, for the most, similar to those observed in the analysis of the matrix B.1 (see, Figures 41 and 44, and Appendix 17): in *norma facialis*, the *sulcus supraorbitalis* in the supraorbital region is present, but the *arcus superciliaris* and *supraorbitalis* are not merged, and the postorbital constriction is less pronounced compared to that seen in apes. In *norma lateralis*, the profile of the antero-posterior frontal bone is more convex than in apes and the transition between the *planum occipital* and *planum nuchale* is rounded, with the opisthocranion positioned lower. In *norma occipitalis*, we can observe the

presence of an occipital bun and the appearance of the *processus retromastoideus*; we can also observe that the cranial outline adopts a triangular ('tent-like') shape (Grimaud, 1982).

Node F in CI and RI-weighted trees and node G in RC-weighted tree supports a monophyletic group comprising Sangiran and Dmanisi. This node is supported by bootstrap values of 36%, 38% and 37%. The formation of this node is explained by shifts from -0,033 to -0,054 in PC2 for the CI and RI-weighting and from -0.037 to -0.054 in PC2 for RC-weighting, from -0,009 to -0,005 in PC4 for the CI and RI-weighting, from -0,0005 to -0,006 in PC6, from -0,0001 to -0,008 in PC10, from -0.004 to 0.0001 in PC12 and from 0.0001 to -0.002 in PC19 in all the weighting scheme. This changes in PC coordinates values refer to the same morphological changes as those described at node F from the analysis of matrix B.1 (see, Figures 41 and 44, and Appendix 17). At node F (or G for the RC-weighting), in *norma verticalis*, the supraorbital profile also goes from rectilinear to concave in Sangiran and Dmanisi, and in *norma lateralis*, the angle between the *planum occipital* and *planum nucale* is more pronounced compared to the other OTUs. In *norma occipitalis*, the *torus occipitalis transversus* and the *processus retromastoideus* are present, and the cranial outline is triangular ('tent-like') (Grimaud, 1982), contrasting with the circular ('bomb-like') shape seen in Neandertals (Boule, 1911, 1912, 1913; Condemi, 1992; Vandermeersch, 1981). Neandertals are represented as a paraphyletic group from node H for the CI-weighted tree and node I for the RI and RC-weighted trees.

Node J for the CI-weighting, and node L for the RI and RC-weighting, includes the OTUs for *H. sapiens* (i.e., "Skhül - Qafzeh" group and current populations) and present bootstrap values of 54% (CI-weighting), 45% (RI-weighting) and 48% (RC-weighting) and is supported by shifts from 0,019 to 0,056 in PC1 for the CI-weighting, from 0.02 to 0.56 for the RI-weighting and from 0.02 to 0.0535 for the RC-weighting; from -0,0065 to -0,001 in PC2 for CI-weighting, from -0.004 to -0.001 for the RI-weighting and from -0.004 to 0.0045 for the RC-weighting; from -0.0415 to -0.003 (CI and RI-weighting) and to -0.0035 (RC-weighting) in PC3; from -0,009 to 0,002 in PC4 for the CI and RI-weighting and from -0.009 to -0.002 for the RC-weighting; from 0,004 to 0,002 in PC7 for the RI-weighting; from 0,004 to 0,002 in PC11 for the CI and RI weighting and from 0.004 to 0.0001 for the RC-weighting; from -0.001 to 0.0001 in PC18 for the CI-weighting; and from 0.0001 to 0.001 in PC21 for the CI and RI-weighting. In terms of morphology, the changes observed at this node closely resemble those described following matrix B.1 analysis (see, Figures 41 and 44 and Appendix 17): in *norma facialis*, the *sulcus supraorbitalis* is present, with the *arcus superciliaris* and *arcus supraorbitalis*

entirely merged. In *norma occipitalis*, the outline of the *planum occipitale* and the cranial outline present a pentagonal shape, and the *torus occipitalis transversus* disappears. In *norma verticalis*, the profile of the supraorbital region is also convex, and in *norma lateralis*, the convexity of the antero-posterior frontal bone and the angulation between the *planum occipital* and *planum nucale* are identical to those previously observed with matrix B.1.

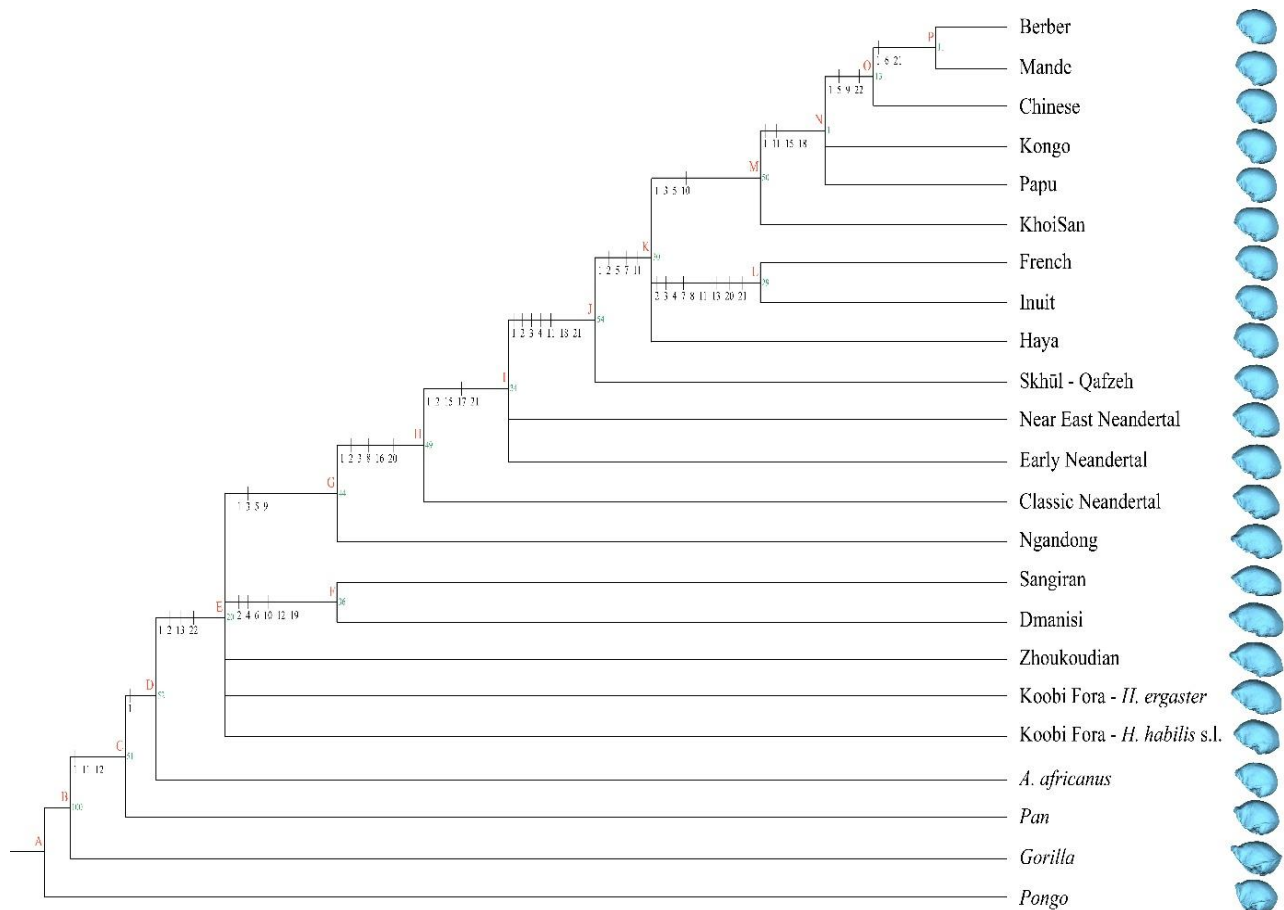


Figure 42: Unique phylogenetic tree based on the analysis of matrix B.2 after CI-weighting (i.e., 22 PC coordinates and 23 OTUs), 113.37 steps (CI = 0.48 and RI = 0.675). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the CI-weighted tree from analysis B.2, four polytomies are present at nodes E, I, K, and M.

Node E, supported by a bootstrap value of 20%, fails to resolve the relationships among “Koobi Fora – *H. habilis* s.l.”, “Koobi Fora – *H. ergaster*”, Zhoukoudian, the clade formed by Dmanisi and Sangiran, and the remaining OTUs.

Node I includes “Near East Neandertal” and “Early Neandertal,” but does not resolve the relationships between these two OTUs, nor between them and *H. sapiens*. This node is supported by a bootstrap value of 34%.

Nodes K and M represent polytomies within modern human populations. Node K (30% bootstrap) does not resolve the relationship between the Haya and other modern human groups. Node M (1% bootstrap) fails to clarify the relationships among the Papuans, the Kongo, and the clade formed by the Chinese, the Mande, and the Berber.

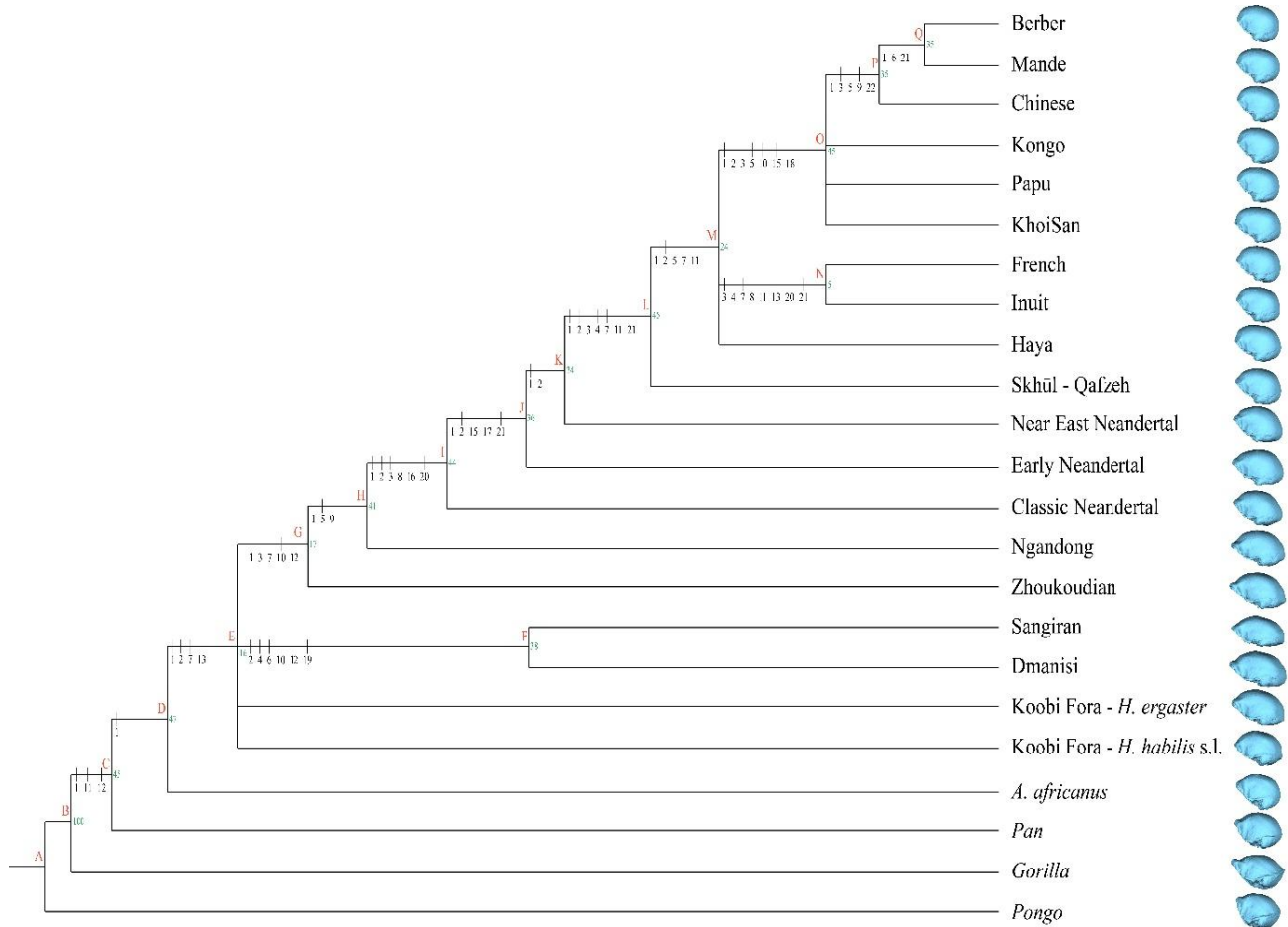


Figure 43: Unique phylogenetic tree based on the analysis of matrix B.2 after RI-weighting (i.e., 22 PC coordinates and 23 OTUs), 91.421 steps (CI = 0.55 and RI = 0.77). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the RI-weighted tree from analysis B.2, only three polytomies are observed, specifically at nodes E, M, and O. Nodes M and O occur within modern human populations.

Node E, supported by a bootstrap value of 16%, fails to resolve the relationships among “Koobi Fora – *H. habilis* s.l.”, “Koobi Fora – *H. ergaster*”, the clade formed by Dmanisi and Sangiran, and the remaining OTUs.

Unlike in the CI-weighted tree, Zhoukoudian in this analysis forms a monophyletic group at node G with Ngandong, *H. neandertalensis*, and *H. sapiens*. Node G is supported by shifts from -0.0425 to

-0.039 in PC1, from 0.01 to -0.0165 in PC3, from 0.006 to -0.009 in PC7, from -0.002 to 0.004 in PC10 and from -0.004 to -0.0055 in PC12.

Contrary to the CI-weighted tree, “Near East Neandertal” and “Early Neandertal” are resolved in this tree, with the appearance of node K. This node is supported by a bootstrap value of 34% and shifts in PC values from 0.018 to 0.020 in PC1 and from -0.009 to -0.004 in PC2. Although the morphological changes are quantifiable, they are difficult to observe.

Nodes M and O, with bootstrap supports of 24% and 45% respectively, are unresolved polytomies within modern humans. Node M is analogous to node K in the CI-weighted tree, as it does not resolve the relationship between the Haya and the rest of the modern human OTUs. Similarly, node O corresponds to node M in the CI-weighted tree, but with the addition of the Khoisan, resulting in an unresolved relationship among the Khoisan, Papuans, and Kongo relative to the clade of Chinese, Mande, and Berber individuals grouped at node M.

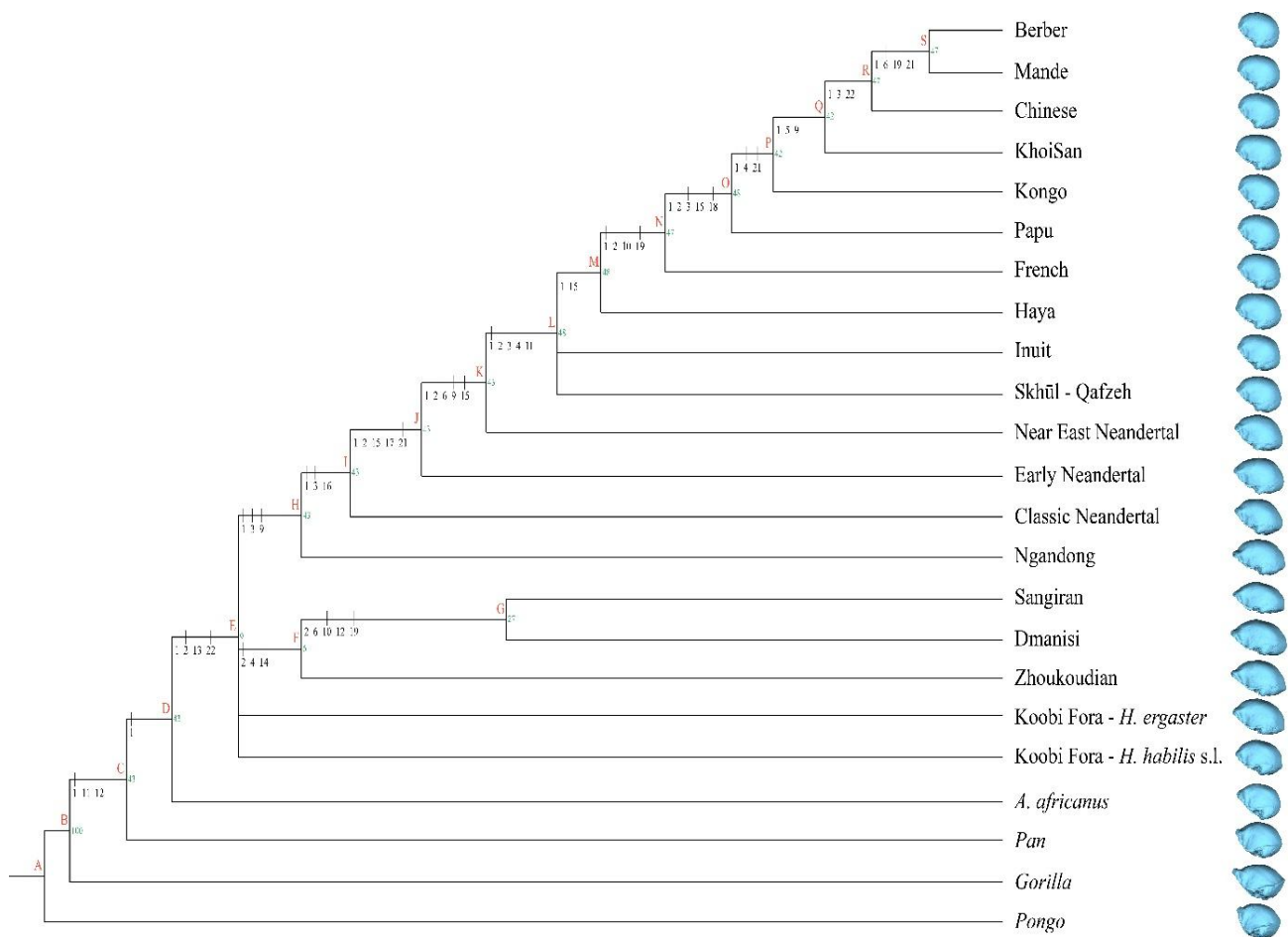


Figure 44: Unique phylogenetic tree based on the analysis of matrix B.2 after RC-weighting (i.e., 22 PC coordinates and 23 OTUs), 50.495 steps (CI = 0.662 and RI = 0.869). Values shown in green represent bootstrap

scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the RC-weighted tree from analysis B.2, only two polytomies are observed, at nodes E and L, with node L found within modern human populations.

Node E, supported by a low bootstrap value of 9%, fails to resolve the relationships among “Koobi Fora – *H. habilis* s.l.”, “Koobi Fora – *H. ergaster*”, and the clade formed by Zhoukoudian, Dmanisi, and Sangiran, as well as the remaining OTUs. Unlike in the CI- and RI-weighted trees, Zhoukoudian in this analysis groups monophyletically with Dmanisi and Sangiran at node F, albeit with limited support (bootstrap = 6%). This node is supported by PC values changing from -0.027 to -0.037 in PC2, from -0.009 to -0.002 in PC4 and from -0.0015 to 0.0005 in PC14.

Node L, supported by a bootstrap value of 48%, is an unresolved polytomy among modern humans. It fails to clarify the relationships between “Skhūl-Qafzeh,” the Inuit, and the rest of the modern human populations. This time, the rest of the modern human OTU appear well resolved (see, Figure 44 and Appendix 17).

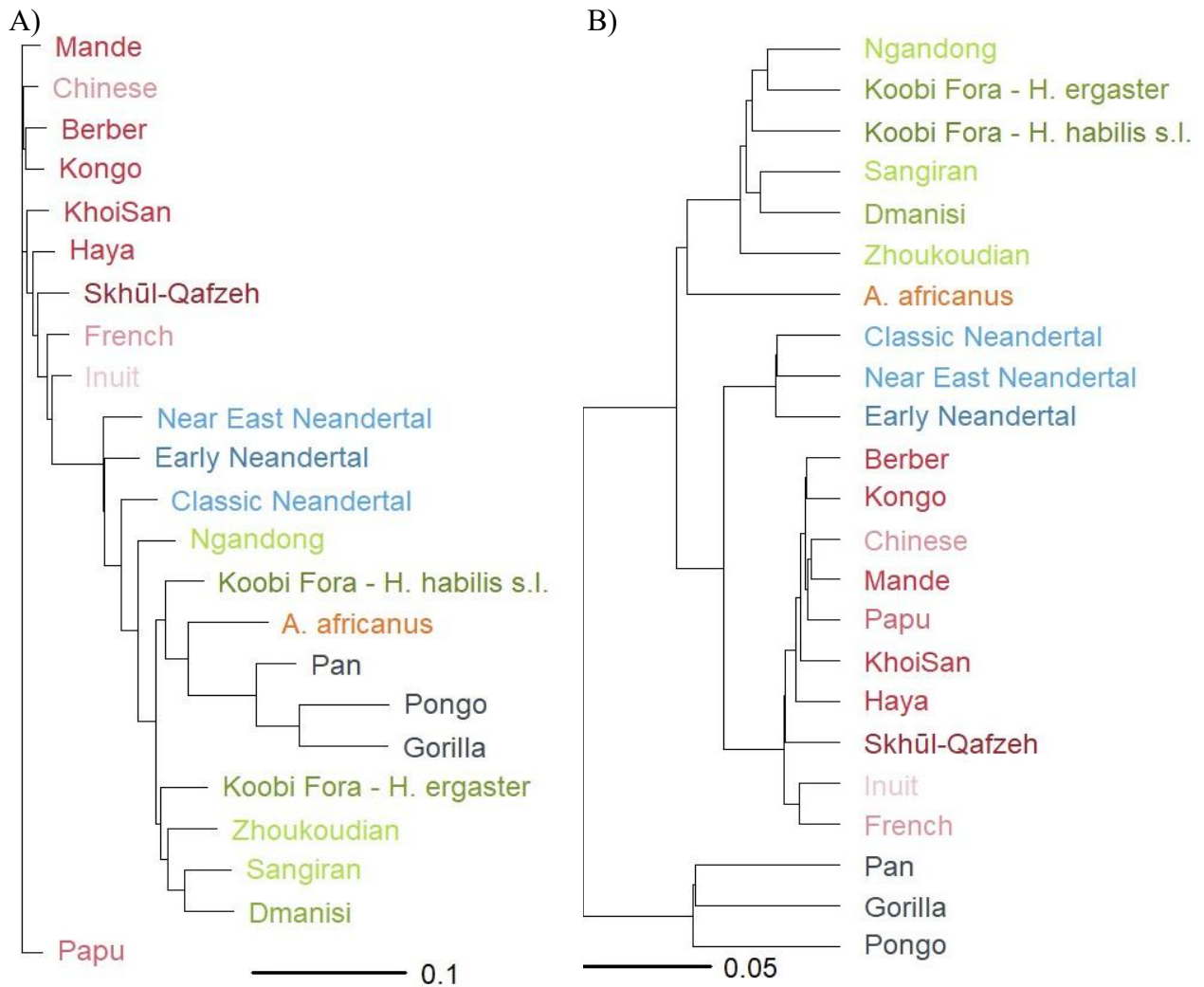


Figure 45: Distance trees based on the analysis of matrix B.2 using two phenetic methods: A) Neighbour-Joining, and B) UPGMA.

In total, six phylogenetic trees were generated: three using cladistic methods (parsimony-based) and three using phenetic approaches (Neighbour-Joining and UPGMA) (see Figure 45), all derived from identical GMM datasets. This allowed for a direct, dataset-independent comparison of tree topologies and inferred evolutionary relationships.

Across all three datasets, the resulting topologies were consistent within each method, and broadly congruent between methods. Robinson-Foulds distances are 0.833 and 0.571 for NJ and UPGMA respectively, and SPR similarity are 0.6, indicating a low degree of topological similarity for NJ approach, while the low RF distance value for UPGMA indicate a high topological congruence. Overall, this suggest that cladistics perform better that phenetic approach.

At higher taxonomic levels, both cladistic and phenetic trees consistently recovered key groupings: *H. sapiens*, Neandertals, clustered together, while Sangiran, Dmanisi, and “Koobi Fora – *H. ergaster*”

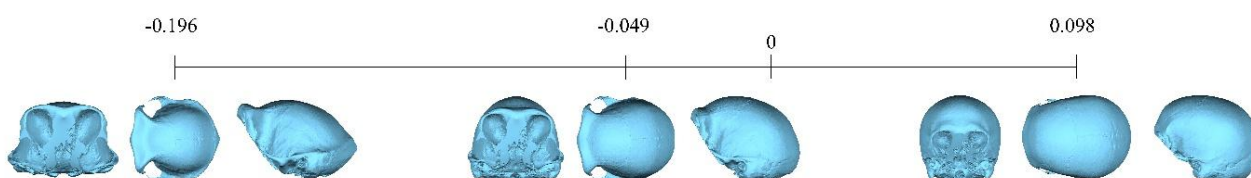
formed a separate, well-supported clade. However, some discrepancies emerged in the placement of certain OTUs. In particular, the relationships of Ngandong, Zhoukoudian, “Koobi Fora – *H. habilis* s.l.”, and *A. africanus* remained unresolved in two of the parsimony trees but were more consistently grouped with the Sangiran–Dmanisi–*H. ergaster* cluster in the third parsimony tree as well as in both phenetic trees (NJ and UPGMA).

These differences may reflect the underlying methodological assumptions of each approach. Phenetic methods, which emphasize overall morphological similarity, may be more sensitive to shape affinities captured by GMM data, while cladistic approaches prioritize shared derived character states, which can be more difficult to discern in continuous morphometric datasets. The convergence of results across different datasets and analytical methods underscores both the robustness of the major groupings and the importance of methodological pluralism in morphological phylogenetics.

II.2.4. Matrix B.3 (22 PCs from 636 landmarks)

The most parsimonious trees derived from the two-step analysis of matrix B.3 reveals several key patterns found in the three trees, similar to matrix B.1 and B.2 (Figures 47 and 49).

PC1 - 67.16% and RI = 0.96



PC2 - 10.95% and RI = 0.72

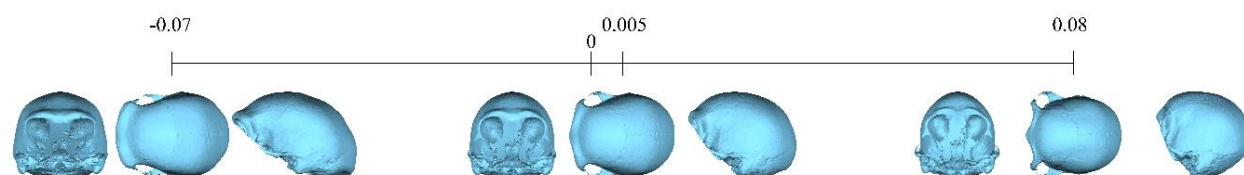


Figure 46: Cranial deformations represented by PCs obtained from the analysis of 636 landmarks. Only PCs with $RI \geq 0.5$ are shown. Values shown in percent represent variance.

Node D formation is explained by a shift from -0.099 to -0.052 in PC1 and from 0.001 to 0.0025 in PC11 in the three weighting schemes (i.e., CI, RI and RC-weighting). This node is supported by bootstrap values of 50% for CI-weighting, 52% for RI-weighting and 47% for RC-weighting. The morphological changes indicated by those values are very similar to those observed in the analysis

of the matrices B.1 and B.2 (see, Figures 46 to 49, and Appendix 18): the same less pronounced postorbital constriction in comparison to the apes. In lateral view, the profile of the antero-posterior frontal bone is more convex than in apes and the outline of the occipital bone is rounder, with the opisthocranium positioned lower. In *norma occipitalis*, we can observe the presence of an occipital bun and the appearance of the *processus retromastoideus*. Furthermore, the cranial outline becomes of triangular shape.

Node G in CI-weighted tree and node F in RI and RC-weighted trees supports a monophyletic group comprising Sangiran and Dmanisi. This node is supported by bootstrap values of 36%, 38% and 37%. The formation of this node is explained by shifts from -0,035 to -0,05 in PC2 for the CI-weighting, from -0.0325 to -0.05 for the RI-weighting and from -0.033 to -0.05 in PC2 for RC-weighting. A shift from -0,003 to 0,011 in PC3 for all the weighting schemes; from -0,009 to -0,004 in PC4 for the RI-weighting; from 0.0001 to -0.007 in PC6 for the RI-weighting and from -0.00195 to -0.007 for the RC-weighting; from 0.0025 to -0.003 in PC8 for the CI and RI-weighting and from 0.005 to -0.003 for the RC-weighting; from 0,001 to -0,011 in PC10 for the CI and RI-weighting and from -0.0005 to -0.011 for the RC-weighting; from -0.003 to -0.001 in PC12 for the CI and RI-weighting; from 0.0001 to -0.001 for PC18 in all the weighting schemes; and from 0.0001 to -0.002 in PC19 for the CI and RI-weighting and from -0.00045 to -0.002 for the RC-weighting. This node is present in all the trees of matrix B and the changes in PC coordinates values refer to the same morphological changes as those described at node F from the analysis of matrix B.1 and node F and G of matrix B.2 (see, Figures 46 to 49, and Appendix 18).

Node J for the CI-weighting, and node L for the RI and RC-weighting, includes the OTUs for *H. sapiens* (i.e., “Skhül - Qafzeh” group and current populations) and present bootstrap values of 53% (CI-weighting), 48% (RI-weighting) and 47% (RC-weighting) and is supported by shifts from 0,0175 to 0,053 in PC1 for the CI-weighting, from 0.018 to 0.515 for the RI-weighting and from 0.018 to 0.050 for the RC-weighting; from -0,007 to 0,0001 in PC2 for CI-weighting and from -0.006 to 0.0044 for the RI and RC-weighting; from -0.043 to -0.002 (CI-weighting), from -0.043 to -0.003 (RI-weighting) and to -0.004 (RC-weighting) in PC3; from -0,0085 to 0,0001 in PC4 for the CI-weighting, from -0.008 to -0.00295 for the RI-weighting and to -0.006 for the RC-weighting; from 0,0025 to 0,001 in PC11 for the CI-weighting and from 0.0025 to -0.001 for the RI and RC-weighting; and from -0.001 to 0.0001 in PC16 for all the weighting schemes. In terms of morphology, the changes observed at this node resemble those described following matrix B.1 and B.2 analyses (see, Figures 46 to 49, and Appendix

18): in *norma facialis*, the *sulcus supraorbitalis* is present, with the *arcus superciliaris* and *arcus supraorbitalis* entirely merged. In *norma occipitalis*, the outline of the *planum occipitale* and the cranial outline present a pentagonal shape, and the *torus occipitalis transversus* disappears. In *norma verticalis*, the profile of the supraorbital region is also convex, and in *norma lateralis*, the convexity of the antero-posterior frontal bone and the angulation between the *planum occipital* and *planum nucale* are identical to those previously observed with matrix B.1 and B.2.

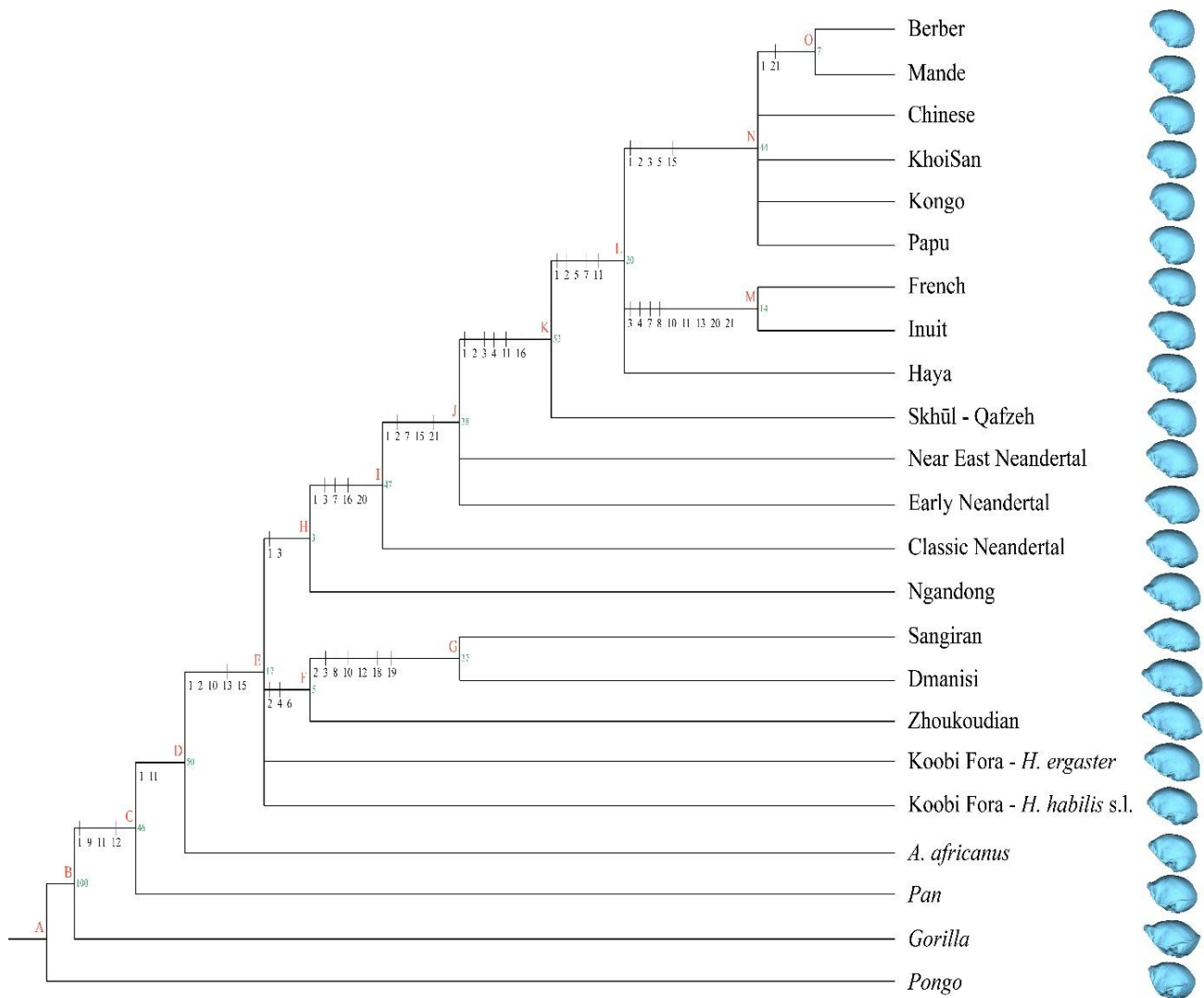


Figure 47: Unique phylogenetic tree based on the analysis of matrix B.3 after CI-weighting (i.e., 22 PC coordinates and 23 OTUs), 109.843 steps (CI = 0.47 and RI = 0.664). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the CI-weighted tree from analysis B.3, four polytomies are present at nodes E, J, L, and N. Node E, supported by a bootstrap value of 17%, fails to resolve the relationships among “Koobi Fora – *H. habilis* s.l.”, “Koobi Fora – *H. ergaster*”, the clade formed by Zhoukoudian, Dmanisi and Sangiran, and the remaining OTUs.

In this tree, Zhoukoudian is grouped with Sangiran and Dmanisi in node F (bootstrap 5%). This node is supported by shift in PC coordinates from -0.028 to -0.035 in PC2, from -0.009 to 0.0005 in PC 4 and from 0.0001 to -0.007 in PC6.

Node J includes “Near East Neandertal” and “Early Neandertal,” but does not resolve the relationships between these two OTUs, nor between them and *H. sapiens*. This node is supported by a bootstrap value of 38%.

Nodes L and N represent polytomies within modern human populations. Node L (20% bootstrap) does not resolve the relationship between the Haya and other modern human groups. Node N (44% bootstrap) fails to clarify the relationships among the Papuans, the Kongo, the Khoisan, the Chinese and the clade formed by the Mande, and the Berber.

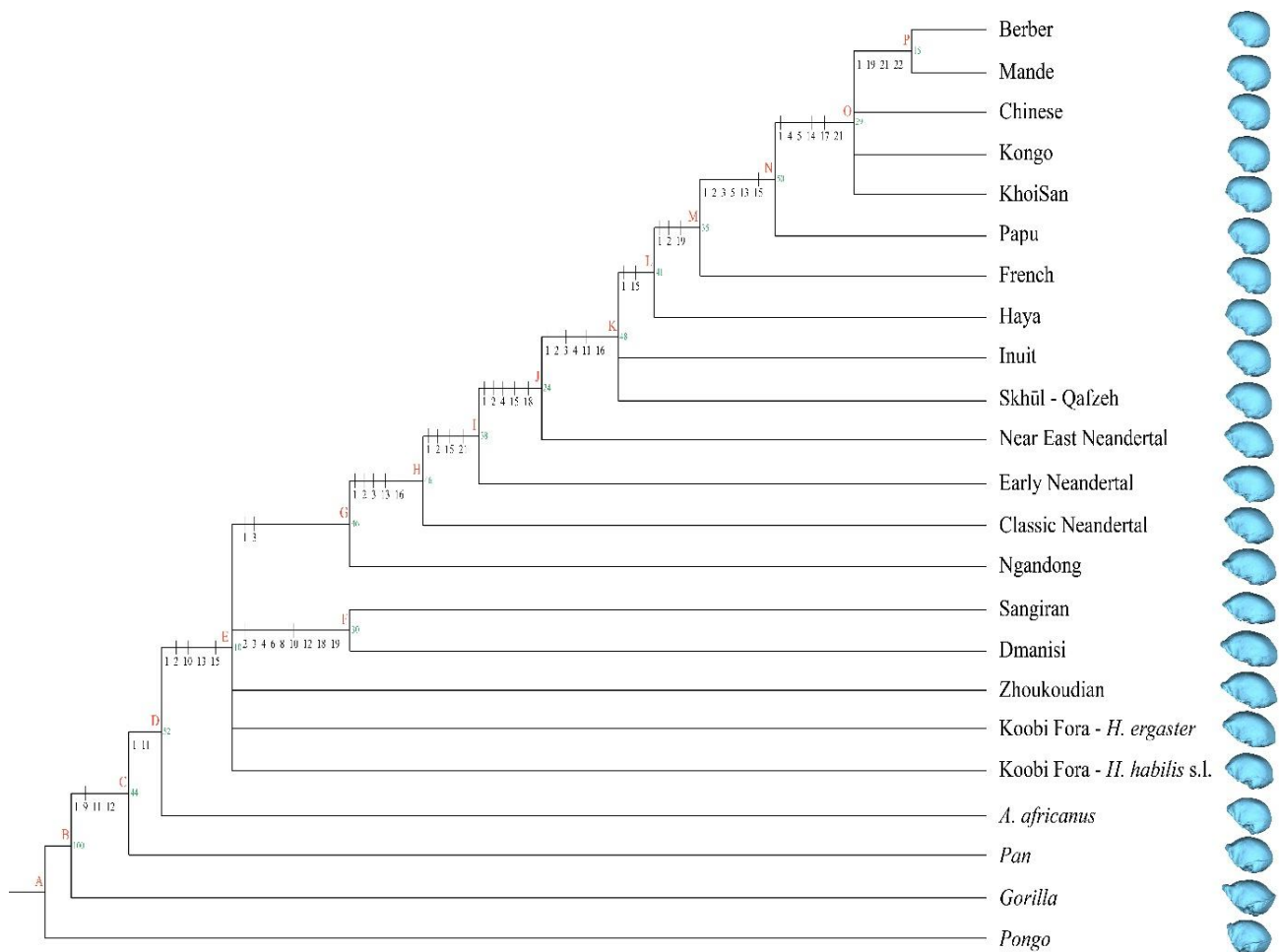


Figure 48: Unique phylogenetic tree based on the analysis of matrix B.3 after RI-weighting (i.e., 22 PC coordinates and 23 OTUs), 83.546 steps (CI = 0.556 and RI = 0.779). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the RI-weighted tree from analysis B.3, only three polytomies are present at nodes E, K, and O. Node E, supported by a bootstrap value of 10%, fails to resolve the relationships among “Koobi Fora – *H. habilis* s.l.”, “Koobi Fora – *H. ergaster*”, Zhoukoudian, the clade formed by Dmanisi and Sangiran, and the remaining OTUs. In the contrary of the CI-weighted tree, this analysis fails to resolve the position of Zhoukoudian.

Nodes K and O represent polytomies within modern human populations. Node K (48% bootstrap) does not resolve the relationship between “Skhül – Qafzeh”, the Inuit and other modern human groups. Node O (29% bootstrap) fails to clarify the relationships among the Kongo, the Khoisan, the Chinese and the clade formed by the Mande, and the Berber.

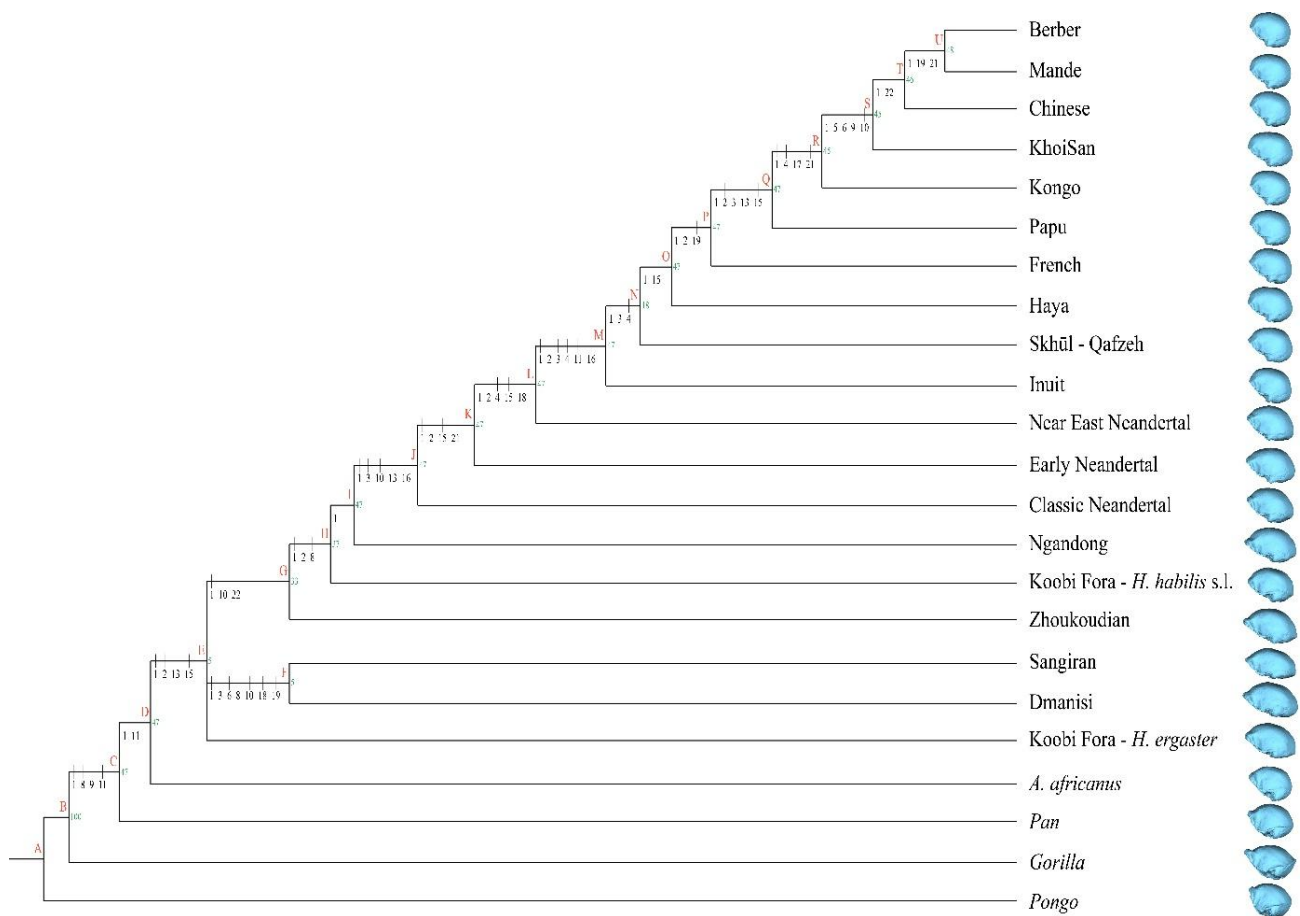


Figure 49: Unique phylogenetic tree based on the analysis of matrix B.3 after RC-weighting (i.e., 22 PC coordinates and 23 OTUs), 45.433 steps (CI = 0.708 and RI = 0.896). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches are the number of the PC changing at each node. Red letters are used to identify each node.

In the CI-weighted tree from analysis B.3, only one polytomy is present at nodes E.

Node E, supported by a bootstrap value of 5%, fails to resolve the relationships among “Koobi Fora – *H. ergaster*”, the clade formed by Dmanisi and Sangiran, and the remaining OTUs. In opposition as the previous trees, Zhoukoudian (node G) and “Koobi Fora – *H. habilis* s.l.” (node H) are grouped with the Ngandong, *H. neandertalensis* and *H. sapiens*. Node G is supported by a bootstrap value of 33% and shifts in PC coordinates from -0.046 to -0.039 for PC1, from -0.0005 to 0.008 in PC10 and from -0.001 to 0.0001 in PC22. Node H is supported by a bootstrap value of 37% and shifts in PC coordinates from -0.039 to -0.033 in PC1, from -0.033 to -0.028 in PC2 and from 0.005 to -0.0395 in PC8.

In this tree, the Inuit appear in node M (47% bootstrap), before “Skhūl – Qafzeh” and the rest of the modern human.

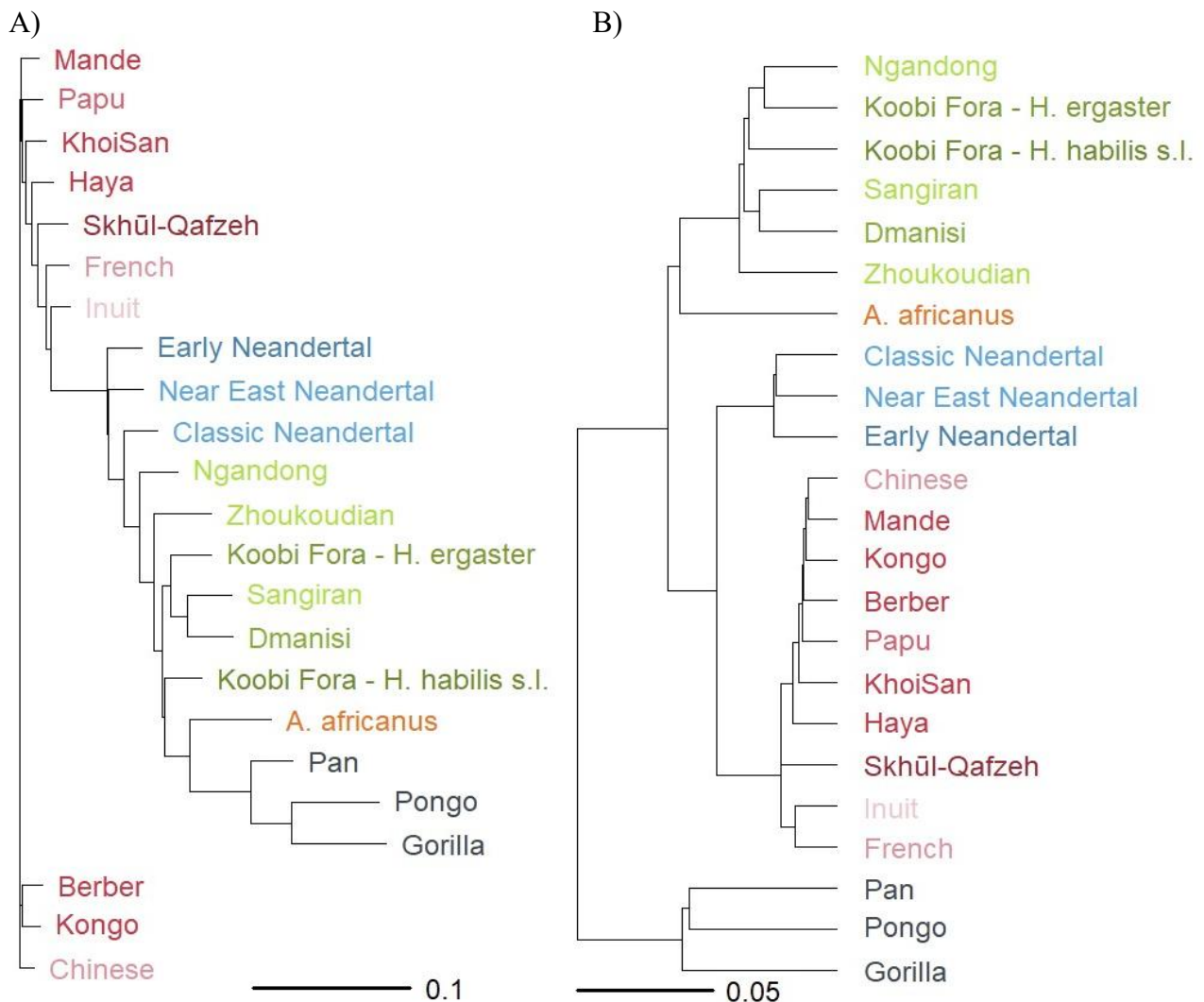


Figure 50: Distance trees based on the analysis of matrix B.3 using two phenetic methods: A) Neighbour-Joining, and B) UPGMA.

Similarly, as the previous matrices (B.1 and B.2), tree topologies were consistent across three methods (parsimony, NJ and UPGMA) (see Figure 50), allowing a coherent cross-method comparison of inferred evolutionary relationships.

Overall, the trees showed a substantial degree of topological agreement. SPR similarity is 0.65 and 0.55 for NJ and UPGMA respectively, suggesting low level of congruence, with NJ performing slightly better. Robinson-Foulds distances are 0.833 for NJ and 0.619 for UPGMA, suggesting a higher congruence of UPGMA over NJ. Overall, this suggest that cladistics perform better than phenetic approach. At broader taxonomic levels, all methods consistently recovered similar groupings, for instance, *H. sapiens* and Neandertals clustered together in all trees, while Sangiran and Dmanisi also formed a stable clade. In all tree, *A. africanus* is in basal position of the in-group.

However, certain taxa, particularly Ngandong, Zhoukoudian, “Koobi Fora – *H. habilis* s.l.”, and “Koobi Fora – *H. ergaster*”, showed variable placement. In one both phenetic trees, these taxa clustered with the Sangiran–Dmanisi–*H. ergaster* group, while in the parsimony trees, their placement varies. This pattern may reflect the differing sensitivities of each method: phenetic algorithms, which rely on overall morphological similarity, may align more closely with the shape-based affinities captured by GMM, while cladistic methods emphasize character-state changes, which can be less clearly defined in continuous morphometric data.

The consistency of major groupings across methods and datasets reinforces the robustness of the broader phylogenetic structure, while highlighting areas of uncertainty that may benefit from additional data or alternative modelling approaches.

II.3. Matrix C (3D landmark coordinates as characters)

II.3.1. General results

A preliminary heuristic analysis conducted on datasets C.1, C.2 and C.3 (including 148, 347 and 636 landmarks, respectively) produced multiple phylogenetic trees (Figures 55 – 57 and 59 – 64).

In analysis C.1, the heuristic analysis with CI-weighting resulted in a unique parsimonious tree. This tree had a length of 9.553 steps, with a CI of 0.83 and an RI of 0.818 (Figure 55 and Table 9). Reweighting the 148 landmarks based on their RI values and re-analysing with a heuristic approach yielded a single tree consisting of 9.593 steps (CI = 0.83, RI = 0.824; Figure 56 and Table 9). After

weighting using the RC values, matrix C.1 analysis generated one tree of 8.06 steps, with a CI of 0.83 and a RI of 0.756 (Figure 57 and Table 9).

For matrix C.2, the heuristic analysis with the CI-weighting produced one parsimonious tree of 13.413 steps, with a CI of 0.825 and a RI of 0.793 (Figure 59 and Table 9). A RI-weighting analysis based on the same 348 landmarks a unique tree of 13.368 steps (CI = 0.825, RI = 0.797; Figure 60 and Table 9). After weighting using the RC values, matrix C.2 analysis generated one tree of 11.153 steps, with a CI of 0.825 and a RI of 0.706 (Figure 61 and Table 9).

Similarly, CI-weighting analysis of matrix C.3 yielded a unique parsimonious tree of 17.69 steps, with a CI of 0.825 and RI of 0.792 (Figure 62 and Table 9). Reweighting based on RI values yielded a single tree of 17.567 steps (CI = 0.825, RI = 0.795; Figure 63 and Table 9). After weighting the 636 landmarks using the RC values, matrix C.3 analysis generated one tree of 14.672 steps, with a CI of 0.825 and a RI of 0.703 (Figure 64 and Table 9).

The CI and RI indices of the parsimony trees derived from the analyses of the three datasets are relatively high, being overall superior to 0.7 - with matrix C.1 yielding, overall, higher values - and reflect a robust phylogenetic signal (see, Table 9). We can observe that the length of the most parsimonious tree of each analysis is smaller with the RC weighting, rather than the CI and RI weighting.

Table 9: Length, consistency and retention indices of the tree for each analysis of Matrix C.

	Weighting	Length	CI value	RI value
C.1 – 148lm	CI	9.553	0.83	0.818
	RI	9.593	0.83	0.824
	RC	8.06	0.83	0.756
C.2 – 347lm	CI	13.413	0.825	0.793
	RI	13.368	0.825	0.797
	RC	11.153	0.825	0.706
C.3 – 636lm	CI	17.69	0.825	0.792
	RI	17.567	0.825	0.795
	RC	14.672	0.825	0.703

Table 10: Topological correspondence (SPR moves and Robinson-Foulds distances) between the reference phylogeny and the trees derived from the three matrices. The average SPR similarity is 0.75 and the average RF distance is 0.618.

	Weighting	SPR similarity	RF distance
C.1 – 148lm	CI	0.7	0.548
	RI	0.75	0.571

	RC	0.7	0.548
C.2 – 347lm	CI	0.75	0.619
	RI	0.8	0.643
	RC	0.75	0.619
C.3 – 636lm	CI	0.75	0.619
	RI	0.8	0.643
	RC	0.75	0.619

Overall, the topologies generated from landmark coordinates exhibited the highest congruence according to both SPR and RF metrics compared to the PC coordinates topologies, with SPR values exceeding 0.75 and RF distances ranging from 0.548 to 0.643 (see Table 10). Although the RF distances are slightly greater than those observed for matrix B, the SPR similarity is notably higher. The results are mitigated as the RI-weighting seems the most congruent with the SPR moves (>0.75), while the CI and RC-weighting seem more congruent with the RF distance (inferior to the RI-weighted schemes values).

II.3.2. Matrix C.1 (148 landmarks)

The most parsimonious trees, derived from the two-step analysis of matrix C.1, reveals several key patterns found in the three trees (i.e., CI-weighting, RI-weighting and RC-weighting) (Figures 55 – 57).

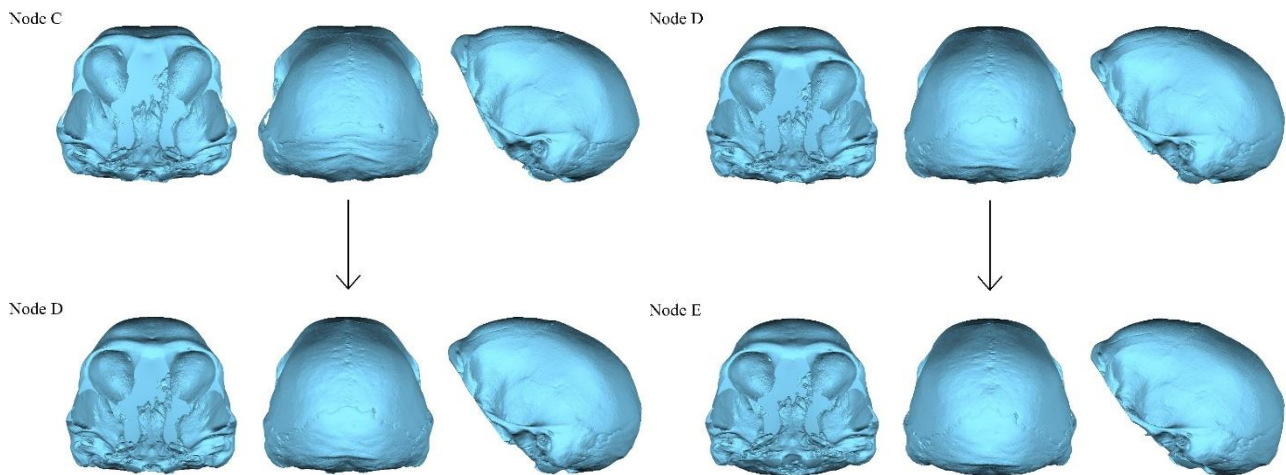


Figure 51: 3D shapes showing variation from node C to node D and node D to E.

Node D, which supports the monophyly of the in-group, is backed by a bootstrap value of 100%. There are observable changes that can be visualized through 3D shapes (see, Figure 51 and Appendix 19). Overall, in *norma facialis*, the *sulcus supraorbitalis* in the supraorbital region is present, but the *arcus superciliaris* and *supraorbitalis* are not merged, and the postorbital constriction is less pronounced compared to that seen in apes. In *norma occipitalis*, we can observe the presence of an

occipital bun and the appearance of the *processus retromastoideus*; we can also observe that the cranial outline, defined by the position of the greatest cranial width (bi-euryon), adopts a triangular ('tent-like') shape (Grimaud, 1982). In *norma lateralis*, the profile of the antero-posterior frontal bone is more convex than in apes, and the transition between the *planum occipital* and *planum nucale* is rounded, in contrast to the angular transition seen in apes, with the opisthocranium positioned lower.

At node E, "Koobi Fora – *H. habilis* s.l." is separated from the other OTUs. The morphological change at this node includes, in *norma facialis*, a less pronounced supra orbital constriction in comparison to *A. africanus*; in *norma occipitalis*, the presence of a well-defined occipital bun and *processus retromastoideus*; and in lateral view, a more convex antero-posterior profile of the frontal bone comparing to node F (see Figure 51).

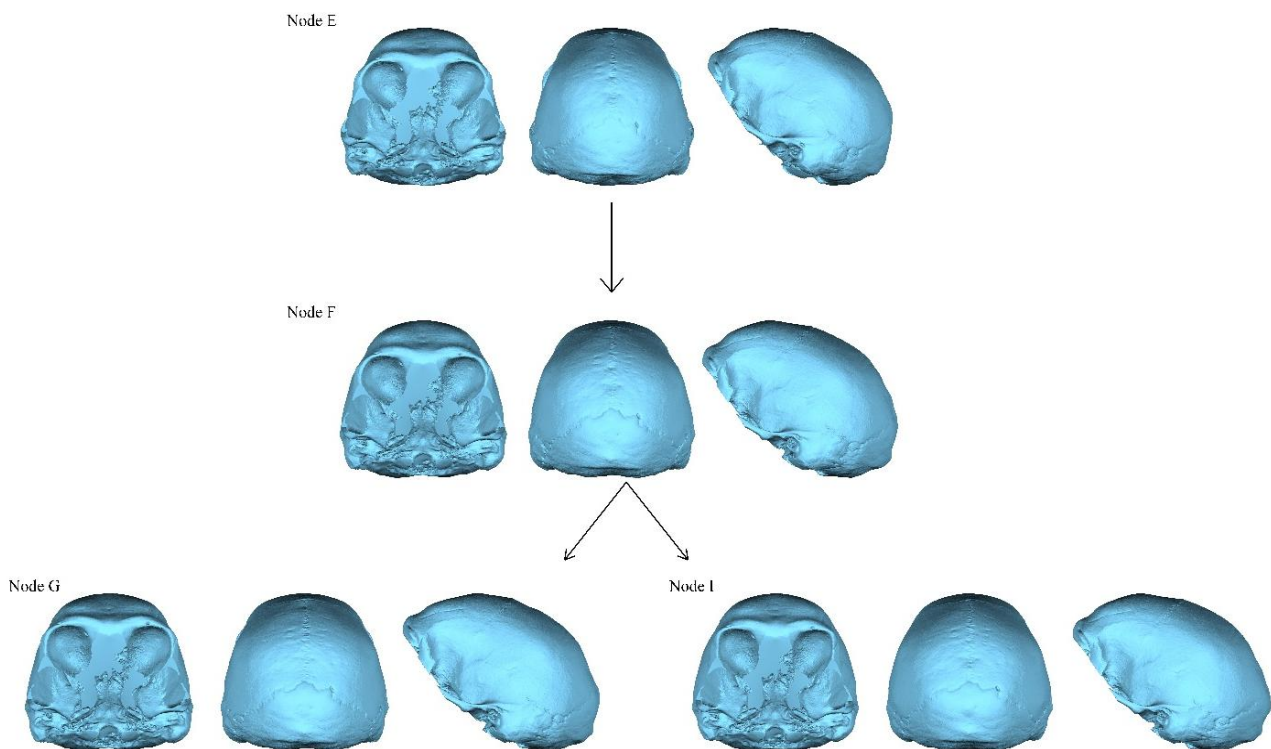


Figure 52: 3D shapes showing variation from node E to node F and node F to node G and I.

At node F, two clades are formed. The first, contains Dmanisi, Sangiran and "Koobi Fora – *H. ergaster*" (node G); while the second includes Zhoukoudian, Ngandong, the Neandertals and *H. sapiens* (node I). Morphological changes at node G includes, in *norma verticalis*, a supraorbital profile changing from medially concave at the glabella (node I) to straight; in *norma occipitalis*, the appearance of a *processus retromastoideus*, which then disappears (node I), and the presence of a triangular cranial outline, contrasting with the more, but not fully, circular shape observed at node I (see Figure 52).

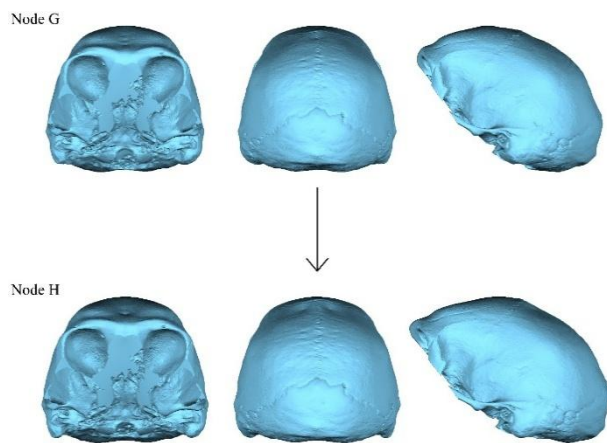


Figure 53: 3D shapes showing variation from node G to node H.

At node G, a clade is observed grouping “Koobi Fora – *H. ergaster*”, Sangiran, and Dmanisi, to the exclusion of Ngandong and Zhoukoudian. This node is supported by a bootstrap value of 72% (CI-weighting), 74% (RI-weighting) and 89% (RC-weighting). Node H, which groups Sangiran and Dmanisi, is supported by a value of 72% for CI-weighting, 76% for the RI-weighting and 91% for RC-weighting. The changes in the landmark’s coordinates (see, Appendix 19), which describe shape changes of the calvarium (see Figure 53), at node G includes, in *norma verticalis*, the transition from a rectilinear supraorbital profile to a convex one, and in *norma lateralis*, the angle between the *planum occipital* and *planum nucale* become more pronounced compared to the other OTUs. In *norma occipitalis*, the *processus retromastoideus* and the *torus occipitalis transversus* are present, with the later, medially protruding, and the cranial outline is triangular (‘tent-like’) (Grimaud, 1982), in contrast to the circular (‘bomb-like’) shape seen in Neandertals (Boule, 1911, 1912, 1913; Condemi, 1992; Vandermeersch, 1981).

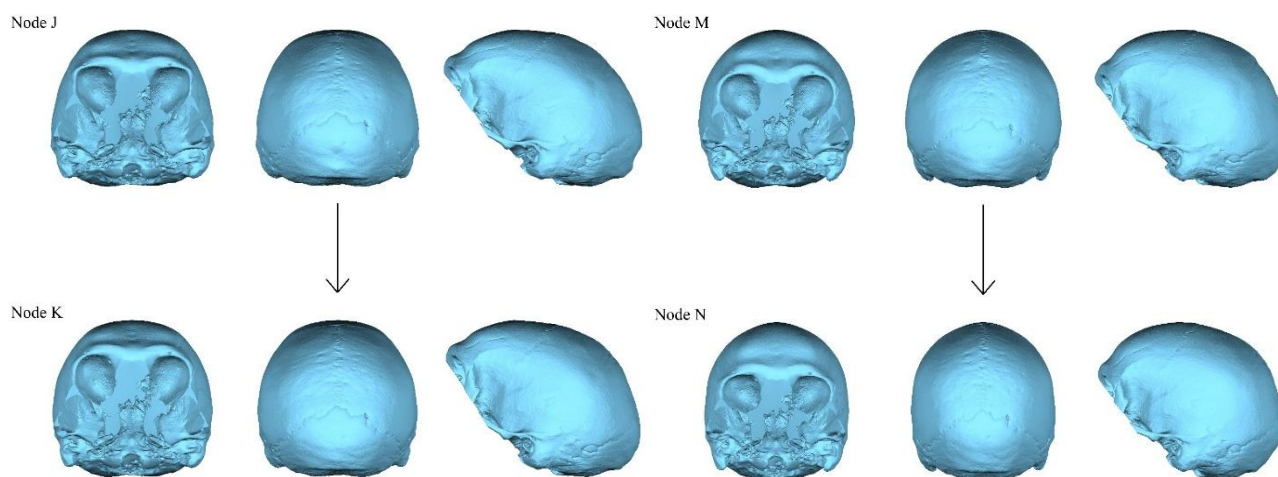


Figure 54: 3D shapes showing variation from node J to node K and node M to node N.

In those trees, Neandertals appear paraphyletic in node K, while *H. sapiens* forms a monophyletic group at node N, supported by a bootstrap value of 100% in all the weighting schemes. The calvarium shape at this node exhibits the general characteristics of *H. sapiens* skull (see, Figure 54 and Appendix 19), in *norma occipitalis*, the outline of the *planum occipitale* is pentagonal, the *torus occipitalis transversus* disappear, and the cranial outline presents a pentagonal shape (‘house-like’) (Broca, 1868; Olivier, 1960). In *norma verticalis*, the profile of the supraorbital region is convex.

Finally, in *norma lateralis*, the convexity of the antero-posterior frontal bone is highly pronounced, and the angle between the *planum occipital* and *planum nucale* is entirely absent.

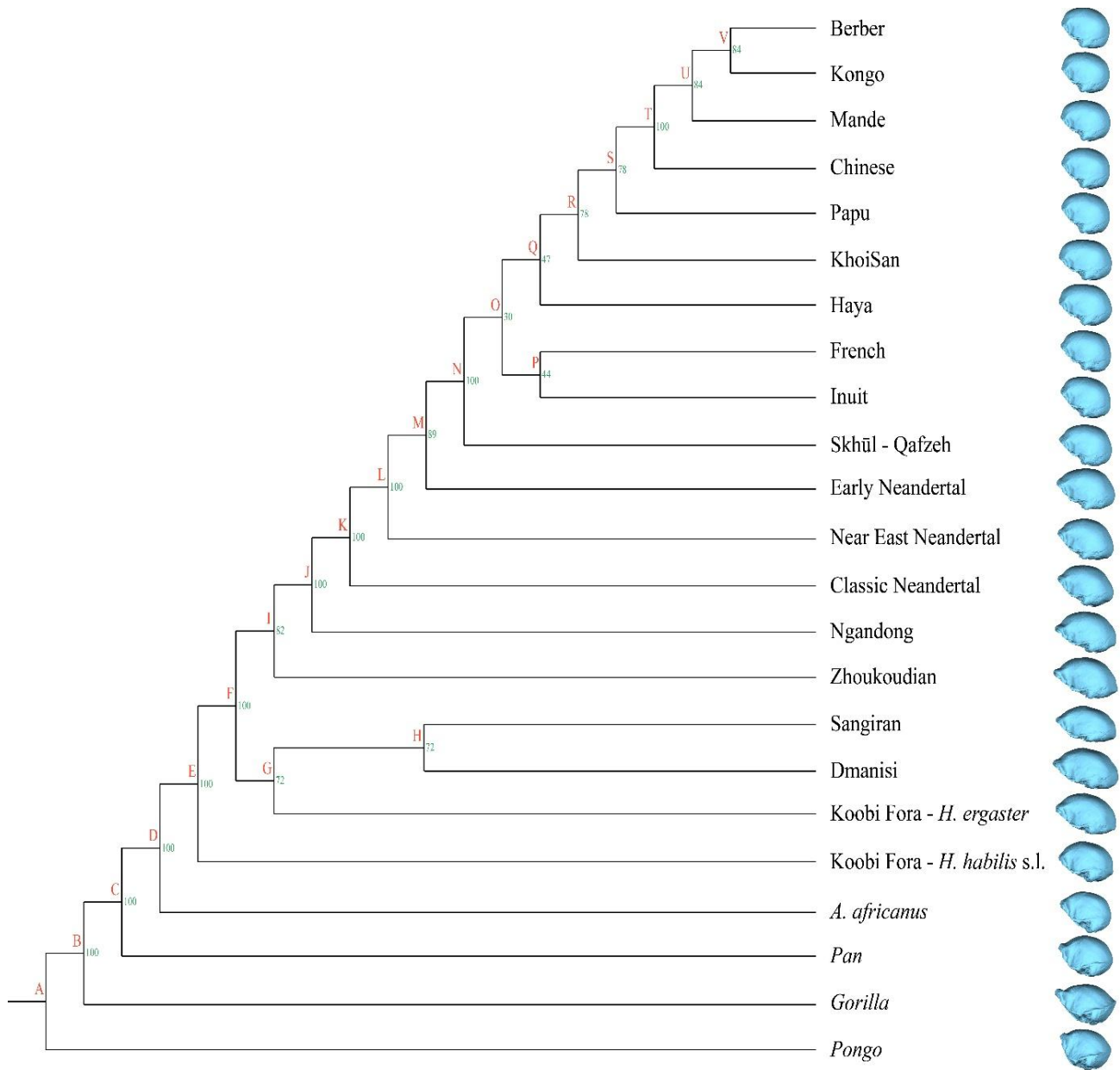


Figure 55: Unique phylogenetic tree based on the analysis of matrix C.1 after CI-weighting (i.e., 148 landmarks and 23 OTUs), 9.553 steps (CI = 0.83 and RI = 0.818). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

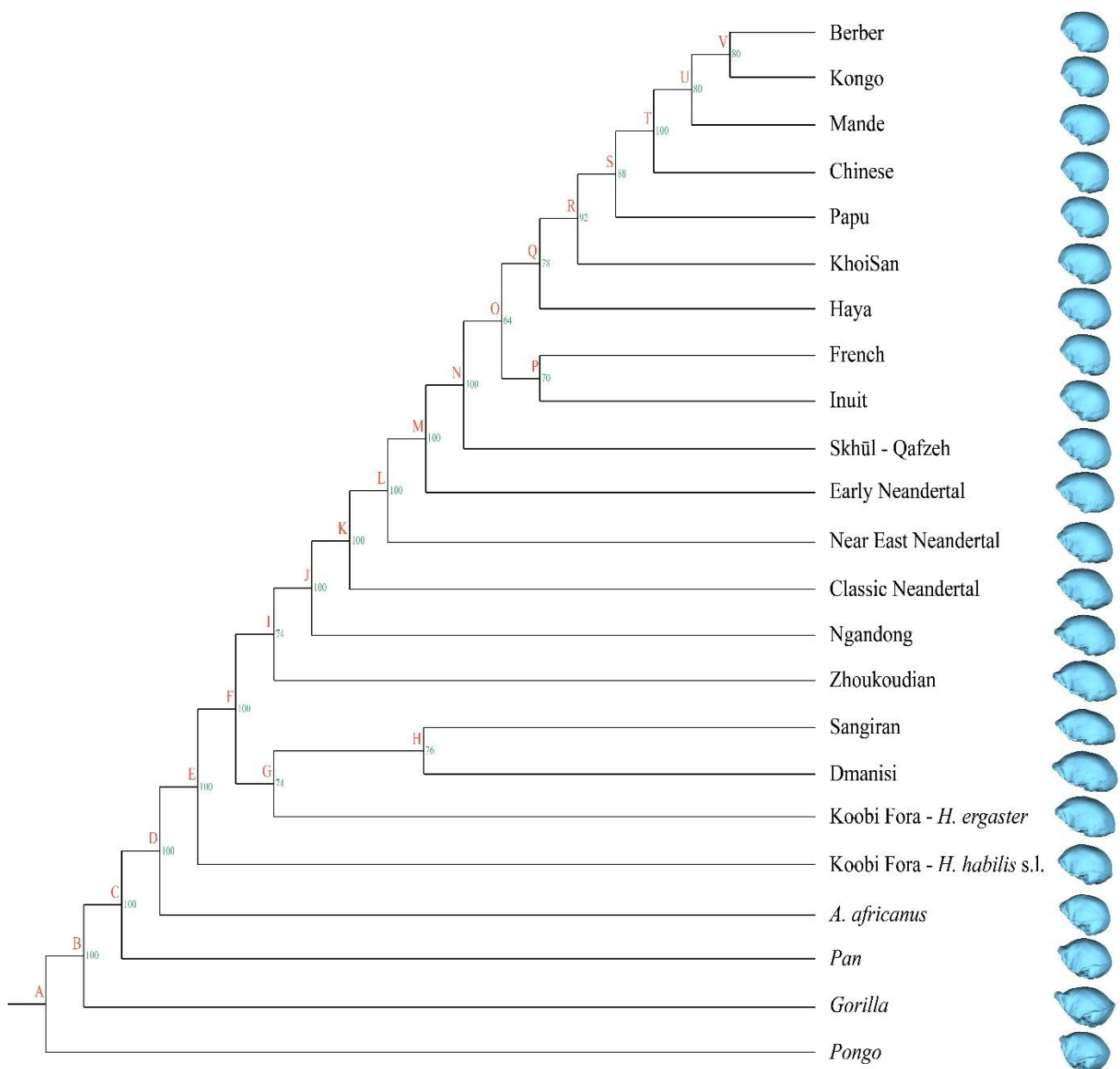


Figure 56: Unique phylogenetic tree based on the analysis of matrix C.1 after RI-weighting (i.e., 148 landmarks and 23 OTUs), 9.593 steps (CI = 0.83 and RI = 0.824). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

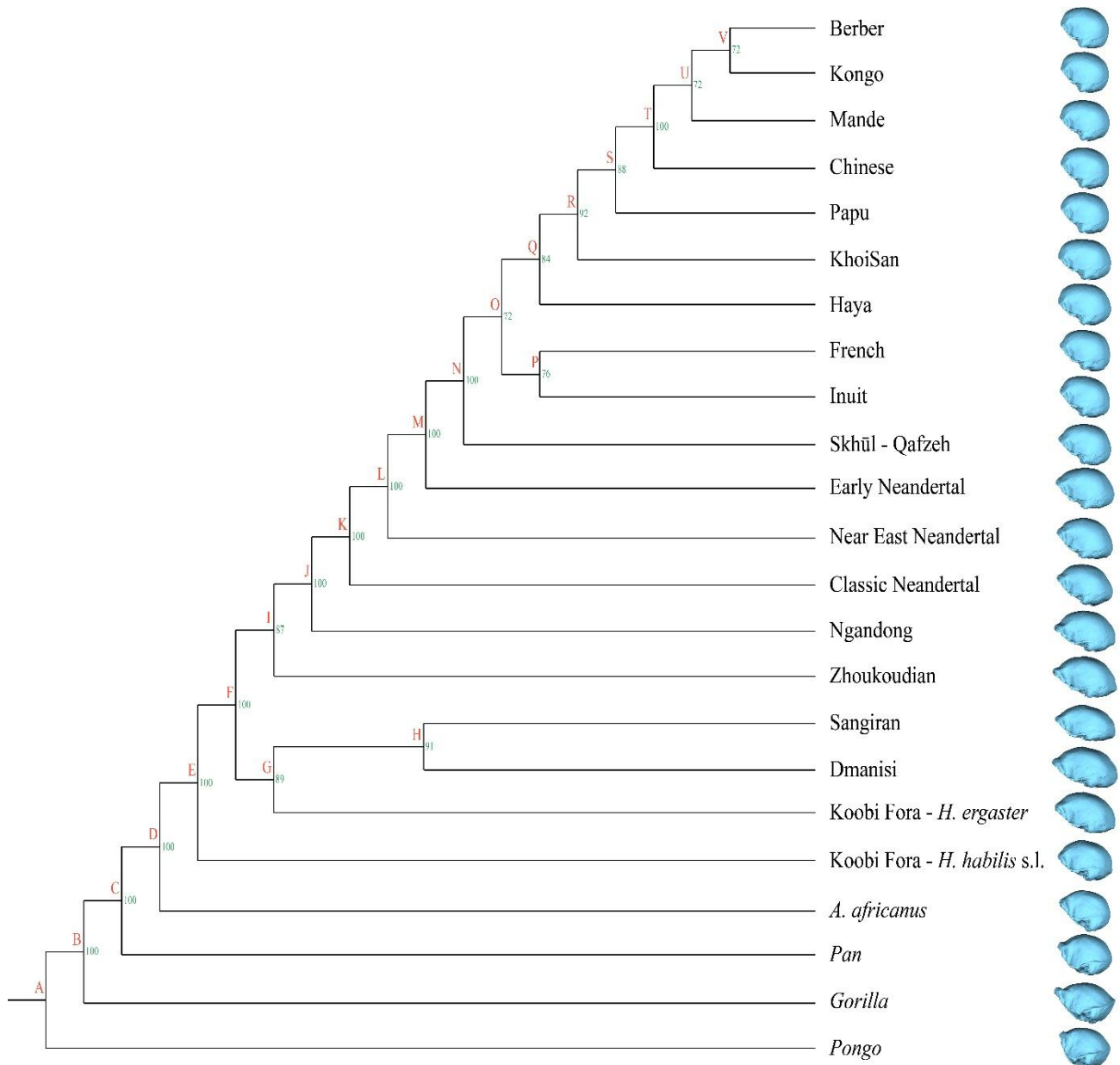


Figure 57: Unique phylogenetic tree based on the analysis of matrix C.1 after RC-weighting (i.e., 148 landmarks and 23 OTUs), 8.06 steps (CI = 0.83 and RI = 0.756). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

II.3.3. Matrix C.2 (347 landmarks)

The most parsimonious trees, derived from the two-step analysis of matrix C.2, reveals several key patterns found in all trees (i.e., CI-weighting, RI-weighting and RC-weighting) (Figures 59 – 61). Node D, which supports the monophyly of the in-group, is backed by a bootstrap value of 100% in all the weighting schemes. There are observable changes that can be visualized through 3D shapes (see, Figure 58 and Appendix 20). Overall, the morphological changes are very similar to those observed in the analysis of matrix C.1, with the exception of node F, G and I.

Similarly, at node E, “Koobi Fora – *H. habilis* s.l.” is separated from the other OTUs.

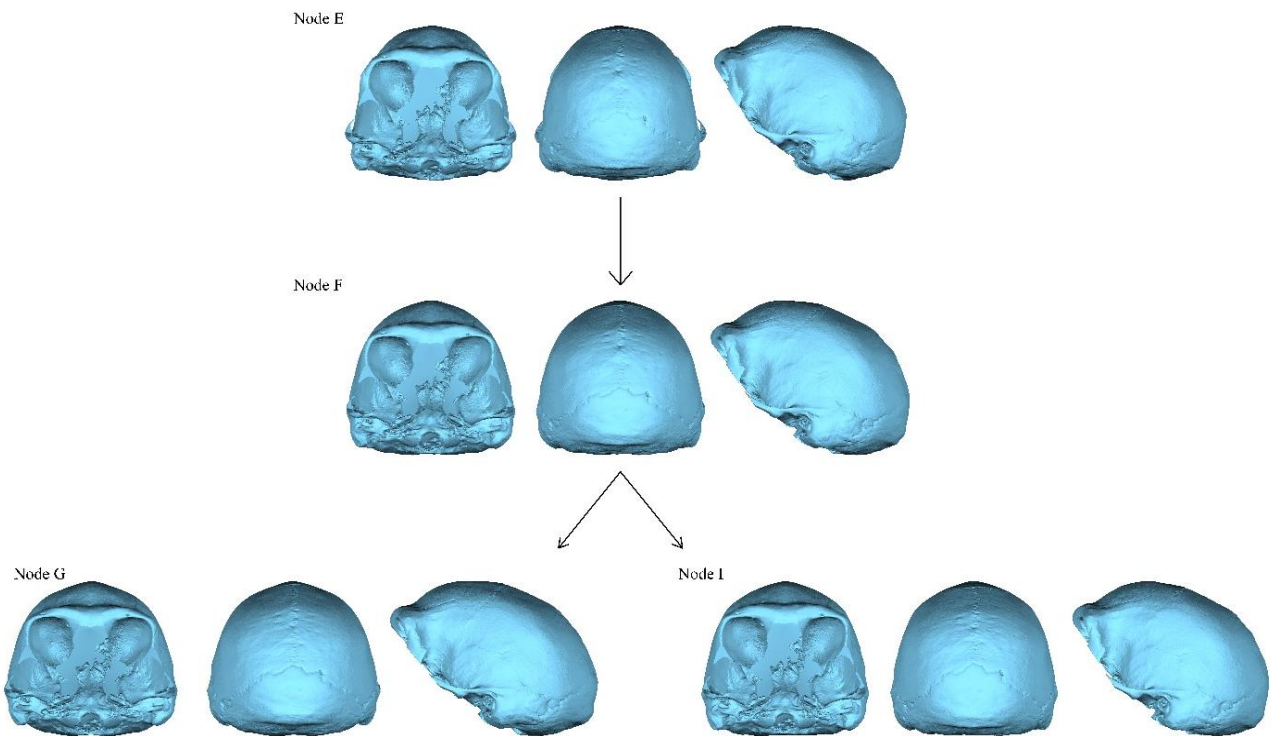


Figure 58: 3D shapes showing variation from node E to node F and node F to node G and I.

At node F, two clades are formed. The first, contains Dmanisi, Sangiran and Zhoukoudian (node G); while the second includes Ngandong, the Neandertals and *H. sapiens* (node I). Morphological changes at node F includes, in *norma verticalis*, a supraorbital profile changing from medially concave at the glabella (node E) to straight; in *norma occipitalis*, the appearance of a *processus retromastoideus*, which then disappears (node I), and the presence of a triangular cranial outline, contrasting with the more, but not fully, circular shape observed at node I (see Figure 58).

At node G, a clade is observed grouping Zhoukoudian, Sangiran, and Dmanisi, to the exclusion of Ngandong. This node is supported by a bootstrap value of 66% (CI-weighting), 82% (RI-weighting) and 88% (RC-weighting). Node H, which groups Sangiran and Dmanisi, is supported by a value of 30% for CI-weighting, 24% for the RI-weighting and 38% for RC-weighting. The changes in the landmark's coordinates (see, Appendix 20), which describe shape changes of the calvarium, at node G includes, are very similar to the C.1 analysis: in *norma verticalis*, the supraorbital profile also change from rectilinear to convex, and in *norma lateralis*, the angle between the *planum occipital* and *planum nucale* become more pronounced compared to the other OTUs. In *norma occipitalis*, the *processus retromastoideus* and the *torus occipitalis transversus* are also present, with the later, medially protruding, and the cranial outline is triangular ('tent-like') (Grimaud, 1982), in contrast to the

circular ('bomb-like') shape seen in Neandertals (Boule, 1911, 1912, 1913; Condemi, 1992; Vandermeersch, 1981).

In those trees, Neandertals appear paraphyletic in node K, while *H. sapiens* forms a monophyletic group at node N, supported by a bootstrap value of 100% in all the weighting schemes. The calvarium shape at this node exhibits the general characteristics of *H. sapiens* skull, that are also found in analysis C.1 (see, Appendix 19): in *norma occipitalis*, the cranial outline and the outline of the *planum occipitale* are both pentagonal and the *torus occipitalis transversus* disappear. In *norma verticalis*, the profile of the supraorbital region is convex. Finally, in *norma lateralis*, the convexity of the antero-posterior frontal bone is highly pronounced, and the angle between the *planum occipital* and *planum nucale* is entirely absent.

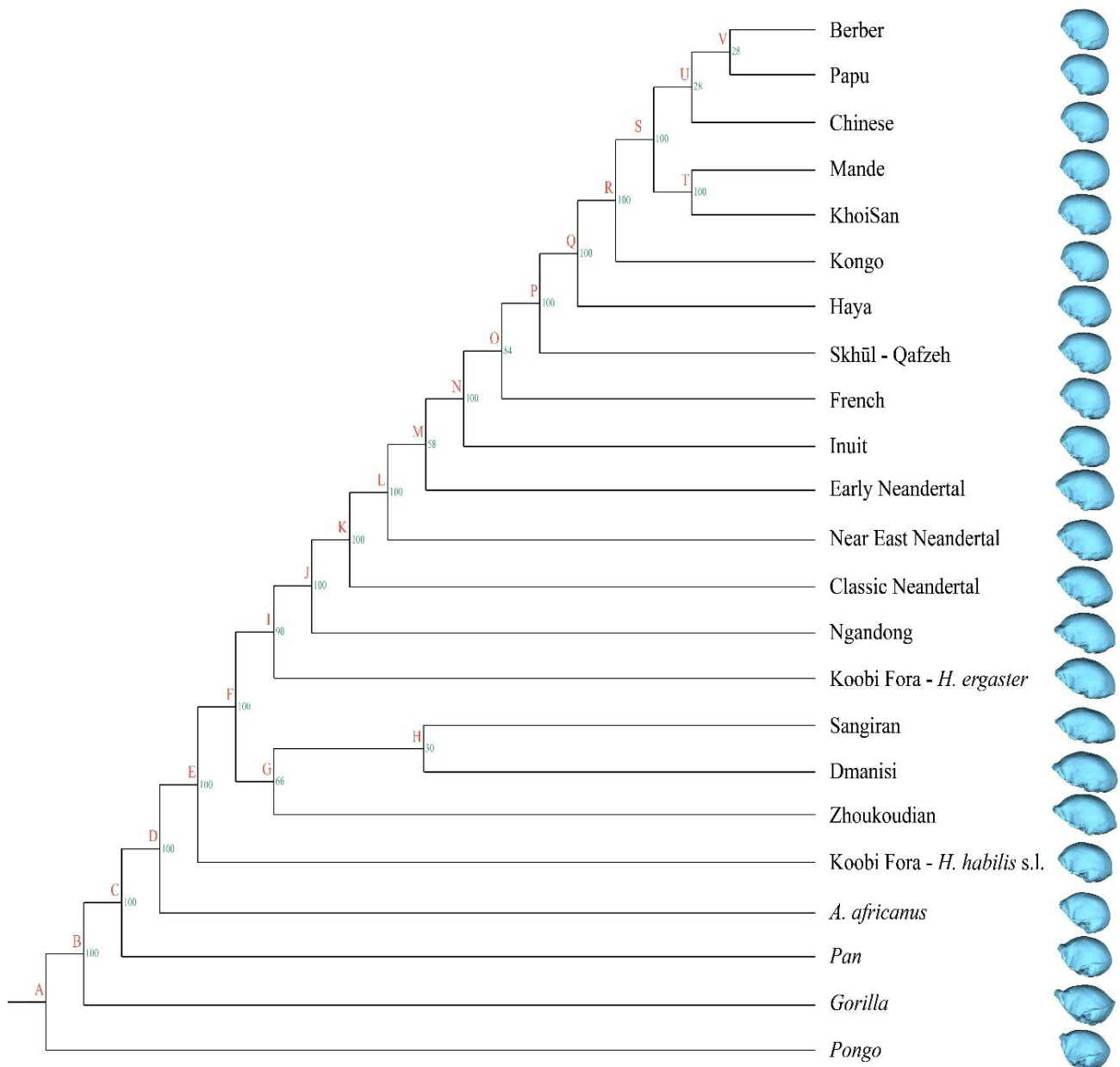


Figure 59: Unique phylogenetic tree based on the analysis of matrix C.2 after CI-weighting (i.e., 347 landmarks and 23 OTUs), 13.413 steps (CI = 0.825 and RI = 0.793). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

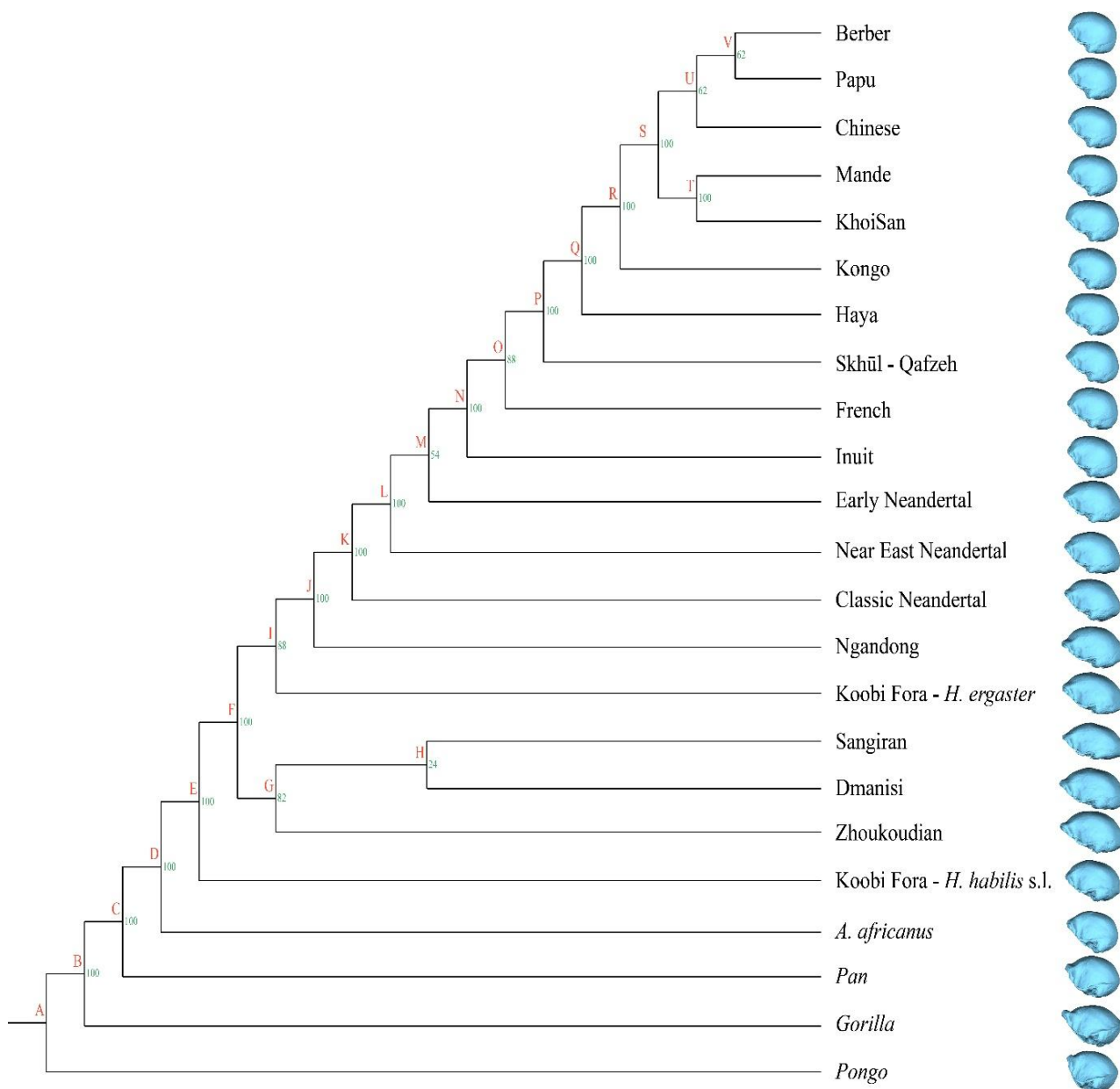


Figure 60: Unique phylogenetic tree based on the analysis of matrix C.2 after RI-weighting (i.e., 347 landmarks and 23 OTUs), 13.368 steps (CI = 0.825 and RI = 0.797). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

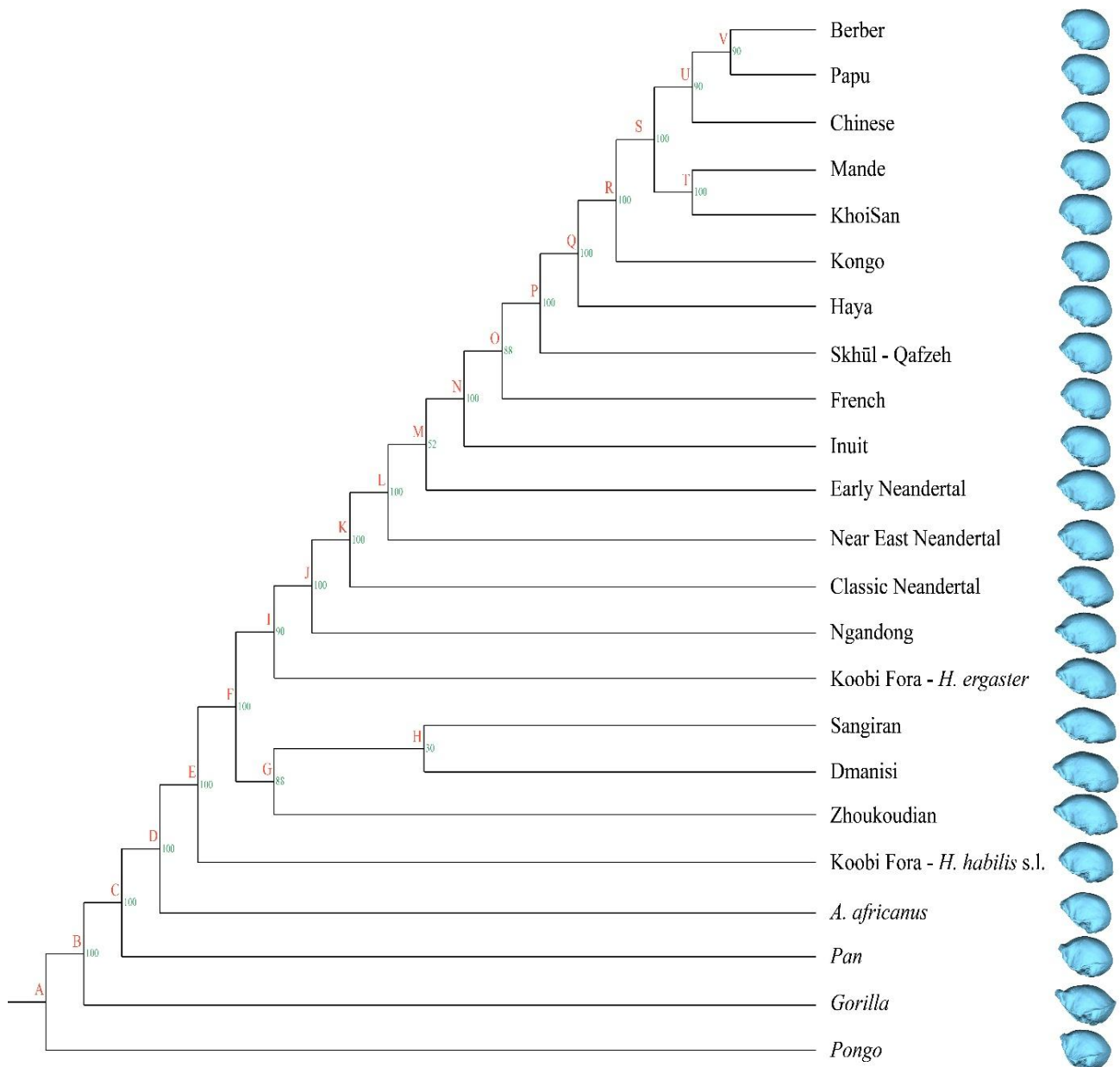


Figure 61: Unique phylogenetic tree based on the analysis of matrix C.2 after RC-weighting (i.e., 347 landmarks and 23 OTUs), 11.153 steps (CI = 0.825 and RI = 0.705). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

II.3.4. Matrix C.3 (636 landmarks)

The most parsimonious trees generated from the two-step analysis of matrix C.3 reproduces the topological structure and morphological patterns observed in the earlier C.1 and C.2 analyses, and across all weighting schemes (CI, RI, and RC) (Figures 62 – 64). Node D, supporting the monophyly of the in-group, is consistently backed by a 100% bootstrap value under all weightings. Morphological changes are also observable through 3D shape visualisations (see, Appendix 21). Overall, the morphological changes closely resemble those observed in matrices C.1 and C.2, with only minor differences at the decimal level.

Likewise, at node E, “Koobi Fora – *H. habilis* s.l.” is distinct from the other OTUs.

At node F, the same two major clades are recovered: one composed of Dmanisi, Sangiran, and Zhoukoudian (node G), and the other including Ngandong, Neandertals, and *H. sapiens* (node I). The character transformations at node F, including changes in the supraorbital profile in *norma verticalis*, the appearance and subsequent loss of the *processus retromastoideus* in *norma occipitalis*, and the transition from a triangular to a more rounded cranial outline, are consistent with those previously described.

Node G again groups Zhoukoudian, Sangiran, and Dmanisi to the exclusion of Ngandong, with comparable bootstrap support values: 30% (CI-weighting), 80% (RI-weighting), and 90% (RC-weighting). Similarly, node H (Sangiran + Dmanisi) receives lower support: 56% (CI and RI), and 66% (RC). Morphological changes in landmark coordinates at node G are also nearly identical to those seen in the C.1 and C.2 analyses, particularly in the shape of the calvarium. Notably, the supraorbital profile becomes convex in *norma verticalis*, the angle between the *planum occipitale* and *planum nuchale* increases in *norma lateralis*, and in *norma occipitalis*, both the *processus retromastoideus* and a medially projecting *torus occipitalis transversus* are present. The overall cranial outline retains the triangular or ‘tent-like’ configuration (Grimaud, 1982), contrasting with the more circular or ‘bomb-like’ morphology characteristic of Neandertals (Boule, 1911, 1912, 1913; Condemi, 1992; Vandermeersch, 1981).

As in the previous analyses, Neandertals appear paraphyletic at node K, while *H. sapiens* forms a monophyletic clade at node N, supported by 100% bootstrap values across all weighting schemes. The calvarial morphology at node N recapitulates diagnostic traits of *H. sapiens* observed in C.1 and C.2: in *norma occipitalis*, both the cranial outline and *planum occipitale* are pentagonal; the *torus occipitalis transversus* is absent; in *norma verticalis*, the supraorbital profile is convex; and in *norma lateralis*, the frontal bone exhibits pronounced antero-posterior convexity, with the angle between the *planum occipitale* and *planum nucale* completely absent.

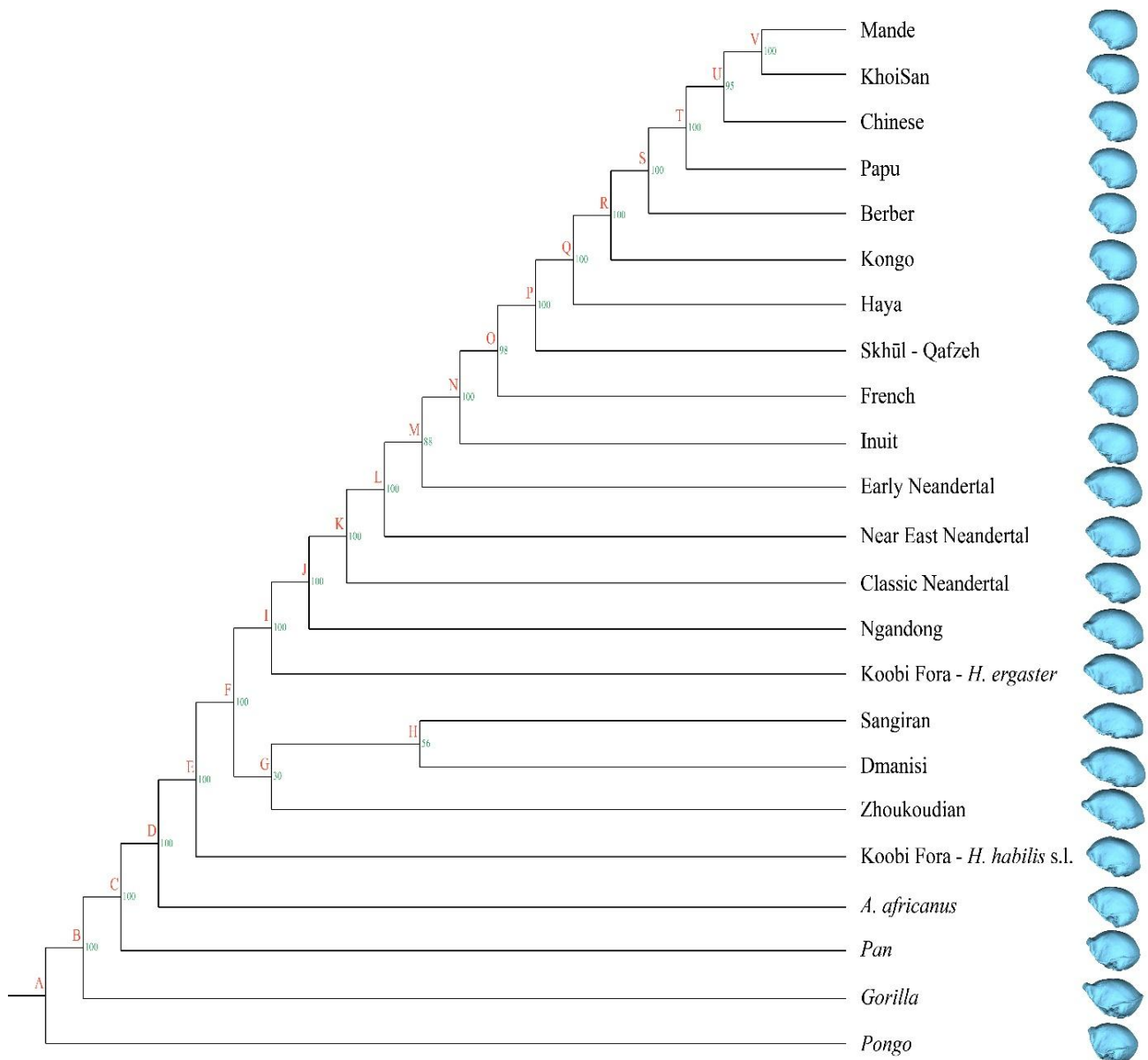


Figure 62: Unique phylogenetic tree based on the analysis of matrix C.3 after CI-weighting (i.e., 636 landmarks and 23 OTUs), 17.69 steps (CI = 0.825 and RI = 0.792). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

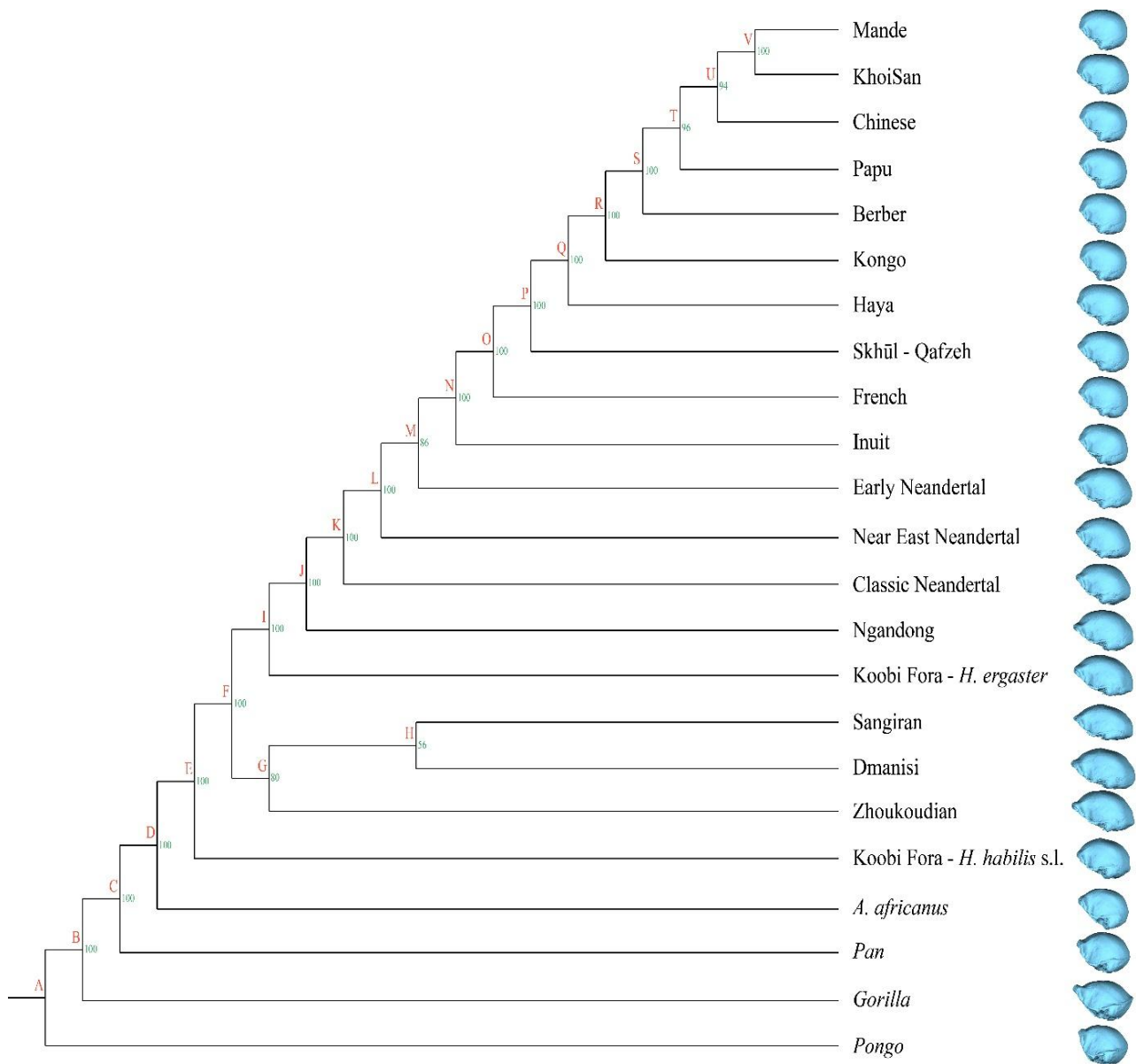


Figure 63: Unique phylogenetic tree based on the analysis of matrix C.3 after RI-weighting (i.e., 636 landmarks and 23 OTUs), 17.567 steps (CI = 0.825 and RI = 0.795). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

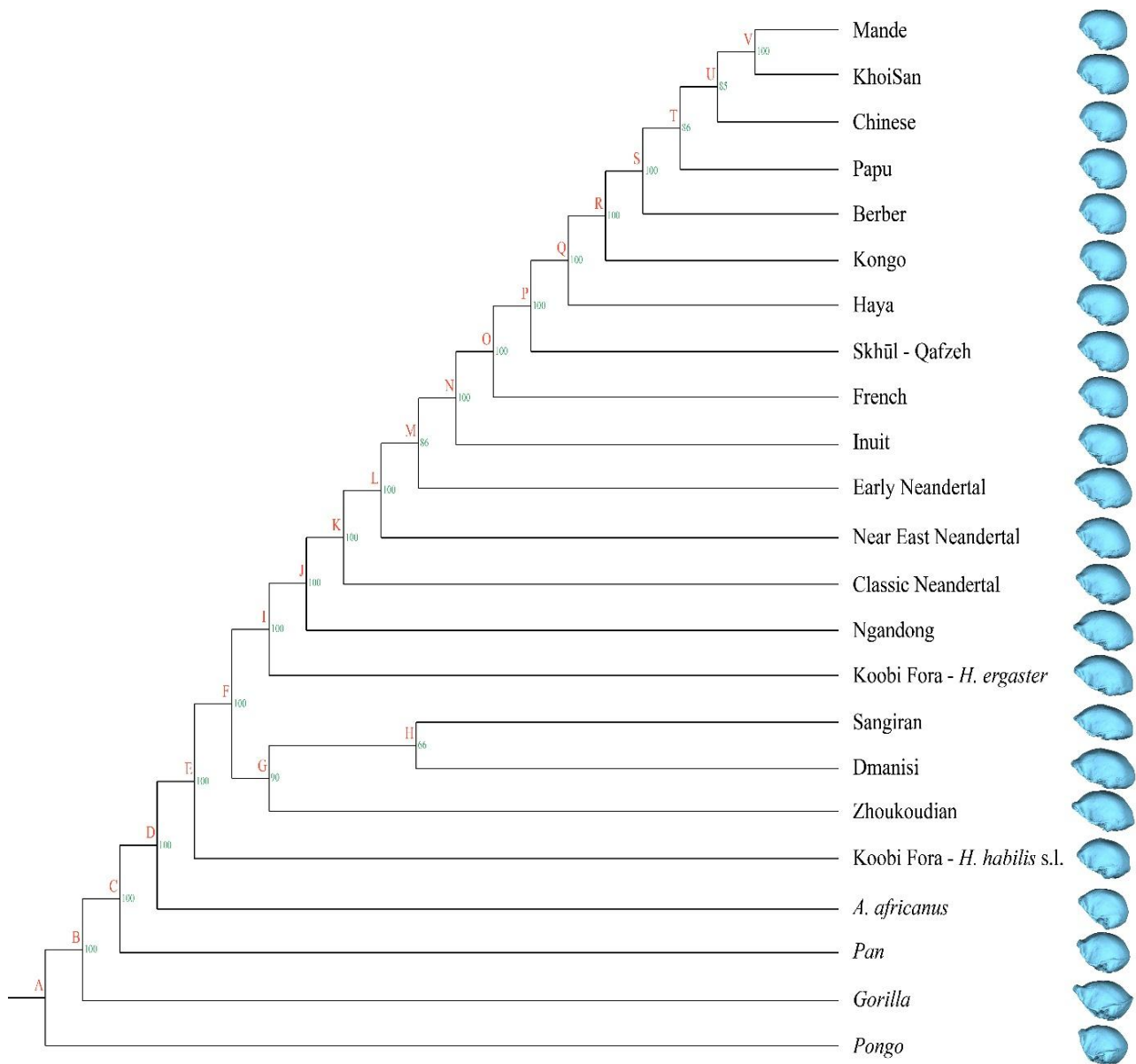


Figure 64: Unique phylogenetic tree based on the analysis of matrix C.3 after RC-weighting (i.e., 636 landmarks and 23 OTUs), 14.672 steps (CI = 0.825 and RI = 0.703). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

III. Discussion

III.1. Cladistics and 3D data

The use of geometric morphometric (GMM) data in cladistic analyses has faced several criticisms, primarily centred on two key issues. The first is the questionable reliability of phylogenetic reconstructions based on morphometric traits, particularly regarding whether landmark coordinates genuinely reflect phylogenetic signal. Some researchers argue that cladistic analyses using GMM data are no more informative than phenetic approaches, with resulting trees reflecting only superficial similarity rather than evolutionary relationships (Adams et al., 2011). Varón-González et al. (2020) also cautioned that phylogenetic inference from high-dimensional morphometric datasets may be inherently unreliable. Despite these concerns, multiple studies have demonstrated that morphometric data can indeed retain phylogenetic signal, especially when congruent with known evolutionary relationships (e.g., Catalano et al., 2015; Catalano and Torres, 2017; Perrard et al., 2016). Catalano and Torres (2017) further noted that although the overall performance of GMM data in reconstructing phylogenies was moderate, incorporating additional anatomical regions improved outcomes, reinforcing the value of morphometric traits in cladistic frameworks.

In phenetic methods like UPGMA or Neighbour-Joining, the specific definition of traits is less critical, as these approaches depend on overall distances between taxa in multivariate space (Felsenstein, 2004; Klingenberg and Gidaszewski, 2010; Swofford et al., 1996). However, cladistic methods, particularly those based on Wagner parsimony, require characters to be discrete and independent, an assumption that conflicts with the inherently interdependent nature of 3D landmark data. This poses challenges for adapting GMM datasets to traditional cladistic formats.

Nevertheless, landmark-based data still offers valuable phylogenetic insights, especially when combined with other morphological characters that help contextualize shape variation (Goloboff, 2022b). Recent work (Simon-Maciejewski et al. 2024) showed that trees generated using cladistic methods from GMM data aligned more closely with established phylogenies than those derived from phenetic analyses. In that study, phylogenies built from PCA-transformed 347-landmark datasets using UPGMA and Neighbour-Joining were inconsistent with one another and with the known evolutionary relationships. These results suggest that cladistic approaches may provide more robust and coherent clustering from GMM data than phenetic methods, as they more closely

capture the phylogenetic signal from 3D data. Wheeler (2021) also endorsed parsimony-based approaches over distance-based techniques, highlighting their capacity to reconstruct ancestral states, further supporting the preference for cladistics in the context of GMM analyses.

The second major debate surrounding the use of morphometric data in cladistics concerns character dependence. A key issue lies in how shape data should be conceptualized: as a single complex trait or as a collection of independent traits. This distinction directly affects how such data are translated into characters and states for phylogenetic analysis (Bookstein, 1991, 2002; MacLeod et al., 2002b; Monteiro, 2000; Rohlf, 1998; Zelditch et al., 2004). Importantly, this problem is not exclusive to GMM. Traditional discrete morphological traits also face challenges regarding definition and independence, as character delineation can vary across studies and establishing true independence between traits is often difficult (e.g., Hawkins et al., 1997; MacLeod et al., 2002; McCracken et al., 1999; Mounier, 2009; Pleijel, 1995; Pogue and Mickevich, 1990; Sereno, 2007; Thiele, 1993).

In this context, the TNT software developed by the Willi Hennig Society is unique in its inclusion of algorithms specifically tailored for continuous morphometric variables. These methods reconstruct ancestral morphologies directly from landmark configurations by minimizing morphological transformations across the tree (Catalano et al., 2010; Goloboff and Catalano, 2011), presenting a promising approach for integrating shape data into phylogenetic inference more effectively.

The present approach follows that of Catalano and Goloboff (2010) and Goloboff and Catalano (2011), phylogenetic morphometric, which operates on the coordinates of either the principal components or landmarks after alignment to minimize displacement between ancestors and descendants. This method estimates ancestral configurations at internal nodes in a similar way to traditional parsimony using discrete qualitative data but, in that case, each landmark coordinates are treated as a multivariate trait. The resulting ancestral patterns are composed of 3D landmark configuration which can be viewed through warping as fully rendered 3D morphologies. The ancestral position of a landmark is identified by exploring a grid of possible positions based on observed descendant landmarks, allowing for refinement through increased grid subdivisions or iterations around the initial estimation.

The primary goal of this study was to empirically test a protocol that integrates 3D data, landmark coordinates and principal component (PC) scores, and to compare the results with those obtained from the analysis of discrete morphological characters, assessing their congruence against a

phylogeny derived from an independent source of information, in this case, morphological characters. To better understand the advantages and limitations of different data types in phylogenetic analysis, we examined the specific characteristics of each of the analysed matrices.

III.2. PCs characters vs. morphological characters

As outlined in the results, a comparison of major tree statistics reveals that the most robust topology was produced by the RC-weighted tree of matrix B.3 (636 landmarks), which exhibited a short tree length (45.33), a CI of 0.708, and a RI of 0.896 (see Tables 6, 7 and 9). In contrast, the least robust tree emerged from the CI-weighted version of matrix B.1, with the longest tree length (120.25) and notably lower CI (0.479) and RI (0.684) values.

When assessing topological congruence with the morphological character-based tree (matrix A), CI-weighted schemes consistently performed best, showing higher SPR similarity scores and lower RF distances across all three PC-based matrices. Among these, matrix B.3 outperformed both B.1 and B.2, suggesting that higher landmark density enhances the recovery of topologies that more closely reflect hypothesized evolutionary relationships.

Results from phenetic analyses revealed moderate congruence. Matrix B.1 achieved relatively high SPR similarity (0.7) with both Neighbour-Joining (NJ) and UPGMA, while matrix B.2 yielded the lowest RF distance (0.571) in UPGMA. However, in direct comparison with the parsimony-based trees, phenetic methods generally returned higher RF distances, indicating lower overall agreement with the morphology-based reference tree.

Taken together, these findings indicate that denser landmark sampling (as in B.3) and CI-weighting tend to produce more stable and phylogenetically consistent trees with PC coordinates as data. Although phenetic approaches can recover meaningful morphological similarities, cladistic methods, particularly those using CI-weighting, appear better suited for reconstructing topologies congruent with established character-based hypotheses.

Phenetic methods such as Neighbour-Joining and UPGMA are widely used for their computational efficiency and visual clarity, they, nevertheless, generally performed less well than the parsimony-based approaches in this analysis. Across all datasets, phenetic trees showed higher RF distances compared to their parsimony counterparts, indicating lower overall topological congruence with the reference morphology-based tree. This supports the conclusion that cladistic methods, particularly

those using CI-weighted matrices, more accurately recover phylogenetic structure from the PC coordinates.

Interestingly, however, the UPGMA tree for matrix B.2 did show notable local congruence, recovering two separated clades for *H. sapiens* and *H. neandertalensis*, a relationship consistently affirmed in paleoanthropological studies. While this appears to support UPGMA's potential under certain conditions, it likely reflects strong morphological similarity between these taxa rather than robust phylogenetic signal. Moreover, UPGMA's underlying assumption of a constant rate of morphological change is problematic in evolutionary contexts, especially for hominins with known heterochrony and mosaic evolution.

The fact that UPGMA performed well in this limited case suggests that overall shape similarity, as captured by GMM-derived PC scores, can sometimes align with phylogenetic reconstruction. However, this result should be interpreted cautiously as it may also reflect reduced rate variation across taxa or the influence of adaptive and functionally constrained traits. In contrast, the more consistent performance of cladistic trees, especially under CI-weighting, reinforces their reliability, particularly when the goal is to recover evolutionary relationships based on character polarity and synapomorphy, rather than raw similarity.

These results also draw attention to the nature of the input data themselves, specifically, how morphometric variation is represented and encoded for phylogenetic analysis. One advantage offered by morphometric datasets is that principal components (PCs), by design, are statistically independent, addressing part of the character dependence issue. Although PCs can be challenging to interpret biologically, they provide a formal solution to the problem of non-independence. In practice, analyses based on PC scores produced slightly less coherent phylogenetic trees than those using morphological characters, suggesting that PC-based representations may offer an inadequate framework for phylogenetic coding.

Indeed, matrices B employ dimensionality reduction through PCA, transforming original variables into independent, orthogonal variables (Jolliffe, 2002). This approach addresses character dependency issues commonly associated with 3D geometric morphometric data. However, it has limitations when compared to matrix A. Unlike matrix A, it allows for ancestral shape reconstruction, but dimensionality reduction to just 22 features may distort the matrix. Results from an exploratory study showed that a smaller character set reduces the ability to account for the entire

phylogenetic history between OTUs, hence limiting the ability to discern meaningful evolutionary relationships between taxa, while limiting homoplasy (Rohlf, 2001). Another limitation is that PCA scores represent a projection of the landmarks onto a single, unidimensional value. As a result, they do not reconstruct the actual ancestral shape but instead only indicate the position where the landmarks would have been projected. Moreover, this approach shifts the analysis from being shape-based to relying on one-dimensional variables, which do not inherently provide direct insights into actual shapes (Adams et al., 2011; Catalano et al., 2010; Goloboff, 2022b; Monteiro, 2000; Zelditch et al., 2004) and might not be meaningful, as the analysis of PCA scores from GMM data rely on a phenetic analysis of overall similarity without regard to variation in individual morphological traits that represent hypotheses of primary homology (sensu de Pinna, 1991). However, our results indicate that they can still yield informative phylogenetic signal, suggesting that, despite theoretical limitations, the method may be practically effective in some contexts.

In contrast, matrix A, which uses 59 discrete morphological characters, describe less of the morphology of the calvarium but allows more straightforward discussions of synapomorphies at each node. While the characters in this matrix are morphologically separated, they are not necessarily independent, and their independence is rarely tested (e.g. McCracken et al., 1999). As with any definition of character and its various states (Pleijel, 1995a), challenges remain in character definition and states distinction, particularly with continuous variation, leading to potential loss of information when similar but not identical shapes are grouped in the same state. For instance, character 33, the *torus occipitalis transversus*, is categorized into three states: absent, present and medially protruding, and present and bilaterally protruding. In reality, the shape of this character is more nuanced and may vary between specimens included in the same OTU (Mounier, 2009). In this context, 3D geometric morphometrics (GMM) and landmark-based data offer a significant advantage, as they are less susceptible to the subjectivity and intra-/inter-observer variability often associated with the observation of qualitative characters, particularly those with vague or overlapping definitions. Because landmarks are placed based on reproducible anatomical criteria and analysed as continuous data, they allow for a more precise and standardized capture of morphological variation, reducing interpretive bias and improving replicability.

Although allometry was detected only in the first three principal components, the phylogenetic trees generated from the size-corrected residuals yielded incoherent and biologically implausible topologies (see Appendix 15). This outcome highlights a potential limitation of regressing out

allometry in geometric morphometric analyses: while intended to isolate shape variation independent of size, the process may also remove evolutionarily meaningful signal, particularly when allometric trends are themselves phylogenetically structured (Giannini, 2014; Klingenberg and Marugán-Lobón, 2013; Pélabon et al., 2014). These results underscore the need for caution when applying allometry correction prior to phylogenetic inference, especially in datasets where size and shape covary in evolutionarily informative ways.

III.3. Landmarks characters vs. morphological characters

A direct comparison between trees derived from landmark data and those based on discrete morphological characters highlights the distinct strengths and limitations of each approach. Although landmarks can be even more challenging to interpret biologically than principal components, they provide a more faithful representation of overall shape, thereby addressing some of the limitations associated with PC projections discussed earlier. In practice, however, phylogenetic analyses based on raw landmark coordinates generally yielded slightly less coherent topologies than those derived from morphological characters. Despite this, landmark data may offer a valuable alternative, or a complementary source of information, for phylogenetic inference, particularly when integrated with more interpretable character-based frameworks.

Indeed, for matrices C, the analysis requires more time and more computing resources. The nature of the data which is composed of aligned 3D coordinates allow for the reconstruction of 3D ancestral shapes at each node, providing a readily available visualisation of the morphological changes across the trees (see, Figures 51 – 54 and 58). Additionally, by using a large number of variables (i.e., 148 to 636 for matrix C compared 22 for matrix B and 59 for matrix A), it allows for a very detailed analysis of the morphological information of the OTUs. Using aligned landmark coordinates also has the advantage of resolving the discretization issues found in traditional morphological features, thereby reducing bias in state definitions and improving the quantification of shape differences. Principal component (PC) scores offer similar advantages in this regard, as they are derived from continuous variation and preserve geometric structure, although they do so through dimensionality reduction rather than direct spatial representation. However, 3D landmark coordinates are mathematically interdependent and cannot be treated as independent variables. One possible way to address this issue would be to analyse specific subsets of landmarks, such as those defining particular morphological traits or outlines (see, Chapter IV – Morphological and 3D characters). These subsets

could be conceptually comparable to individual characters and might be treated as independent units of morphological information (see, Catalano et al., 2015; Klingenberg, 2010).

IV. Conclusion

This chapter implemented a standardised cladistic protocol across three separate data matrices: one on discrete morphological traits, another on principal component (PC) scores, and a third based on aligned landmark coordinates. While the resulting phylogenetic trees differ in detail, they reveal consistent overall patterns, underscoring the usefulness of integrating 3D morphometric data into cladistic frameworks. These findings can offer insights into key debates in palaeoanthropology, including the taxonomic classification of KNM-ER 1470 and 1813, the status of *H. erectus* sensu lato, and the evolutionary relationships between *H. neandertalensis* and *H. sapiens* (see, Chapter V – Discussion).

The analysis focused exclusively on the morphology of the calvarium, and the conclusions should be approached with caution, as cladistic results are sensitive to factors such as character choice, OTU sampling, and weighting strategies (Arnold, 1981; Chamberlain and Wood, 1987). Nonetheless, applying a consistent protocol to three distinct data types produced varying yet coherent outcomes, each contributing a different viewpoint to ongoing discussions. The findings support the methodological reliability of combining GMM with cladistics, showing that 3D landmarks capture morphological variation in ways comparable to traditional comparative descriptions, and enhance phylogenetic resolution. Among the approaches tested, analyses based on principal components derived from a high number of landmarks (matrix B.3) produced consistent and congruent topologies, outperforming lower-density landmark sets and PC matrices with fewer landmarks. However, direct analyses of raw landmark coordinates (matrices C.1 to C.3) yielded even higher topological congruence, particularly under RI-weighting, based on SPR similarity scores exceeding 0.75 and moderate RF distances, suggesting that direct use of landmark data may preserve phylogenetic signal more effectively than PC-based approaches.

Despite this, parsimony analyses of discrete morphological characters still tend to produce slightly more coherent trees overall, highlighting their continued value in reconstructing evolutionary relationships grounded in synapomorphic character states. Phenetic methods, while computationally efficient and visually intuitive, generally exhibit lower congruence with reference morphologically based topologies.

Taken together, these results indicate that increasing landmark density enhances phylogenetic resolution, and that direct analysis of 3D landmarks, especially when combined with appropriate weighting schemes, can outperform PC-based analyses in recovering phylogenetically meaningful topologies. However, integrating landmark data with discrete morphological characters into a unified matrix remains essential for robust and biologically interpretable phylogenetic reconstruction in human evolution. Future research will also explore alternative weighting schemes and incorporate cost matrices to better account for the evolutionary relevance of specific character transformations.

Key-points III

Research focus and goals:

- The study tests the reliability of using 3D geometric morphometric (GMM) data, both raw landmark coordinates and principal component (PC) scores, in cladistic phylogenetic reconstruction.
- Results are compared with traditional discrete morphological character-based trees.
- The goal is to evaluate the congruence of each approach with a reference morphology-based phylogeny.

Datasets:

- Matrix A: 59 discrete morphological characters.
- Matrices B: PC scores derived from GMM (with 148, 347, and 636 landmarks).
- Matrices C: Raw aligned 3D landmark coordinates (with 148, 347, and 636 landmarks).

Principal results:

1. Cladistic trees from PCs (Matrix B)
 - CI-weighting consistently yielded the most congruent trees with reference topology.
 - Higher landmark density (B.3 with 636 landmarks) → better congruence and phylogenetic resolution.
 - PC-based trees showed lower SPR similarity and slightly higher RF distances than landmark-based trees.
2. Cladistic trees from raw landmarks (Matrix C)
 - Showed higher topological congruence with the reference tree than PC-based trees.
 - RI-weighting produced the highest SPR scores (>0.75); CI/RC better at lowering RF distances.
 - Demonstrated the best overall performance, despite high computational demands.
 - Allow ancestral shape reconstruction and avoid discretization bias.
3. Morphological characters (Matrix A)
 - Still slightly outperform GMM-based trees in topological coherence.
 - Provide interpretable synapomorphies at each node.
 - However, character subjectivity and observer bias are known issues.

Phenetic methods:

- UPGMA and Neighbour-Joining are visually intuitive and efficient.
- Performed worse than parsimony in topological congruence.
- UPGMA occasionally recovered expected clades (e.g., *H. sapiens* / *H. neandertalensis*), but may reflect overall similarity, not true phylogenetic signal.

Methodological considerations:

- PCs offer statistical independence but lack direct biological interpretability.
- Landmarks better capture shape, reduce observer bias, and provide higher spatial fidelity.
- Allometry correction removed meaningful evolutionary signal in this study.
- Landmark coordinates are mathematically dependent; possible solution: analyse subsets representing specific traits.

Conclusions:

- Direct use of 3D landmark coordinates (Matrix C) outperforms PC-based trees in phylogenetic consistency.
- PC-based trees (Matrix B.3) still perform well with higher landmark density but less so than raw landmark analyses.
- Morphological characters remain useful for interpretable phylogenetic reconstructions based on synapomorphies.
- Phenetic approaches are less reliable in this context.
- Integrated approaches combining GMM and discrete traits may offer the most robust phylogenetic reconstructions in palaeoanthropology.

**Chapter IV – Morphological and 3D
characters: An Application to the question of the
relationship between *Homo*, *Australopithecus*, and
*Paranthropus***

Building on the findings of the previous chapter, which demonstrated the value of applying a standardised cladistic approach to distinct types of 3D data, this chapter advances the analysis by integrating Procrustes-aligned landmark coordinates and traditional discrete traits into a single, combined dataset. This integrated approach allows for a more holistic assessment of hominin phylogenetic relationships by leveraging both the geometric precision of 3D morphometric data and the interpretive strengths of conventional morphological characters.

The focus here is on a newly incorporated sample of hominin specimens, whose taxonomic placement and evolutionary significance remain subjects of ongoing debate. By analysing these fossils within a unified cladistic framework, the chapter aims to explore how combining data types might enhance phylogenetic resolution and provide new insights into the evolutionary history of the genus *Homo*. Particular emphasis is placed on testing whether the integration of continuous and discrete character types improves congruence among tree topologies, clarifies relationships between established and newly added taxa, and mitigates some of the limitations associated with each data type when used in isolation.

This investigation also provides a first step toward addressing methodological challenges identified in the previous chapter, specifically, the need for unified matrices that more accurately reflect the complexity of morphological variation. The chapter will evaluate the phylogenetic signal recovered from the combined dataset, assess the impact of weighting strategies, and consider the implications of these findings for interpreting hominin diversity and evolutionary dynamics.

I. Method

To contribute to the ongoing debate surrounding the integration of 3D morphometric data into phylogenetic reconstruction, this study develops and evaluates matrices with two distinct types of data in a strict cladistic framework. These matrices, Matrix D and E, are designed to combine the strengths of morphometric and cladistic approaches while addressing prior methodological concerns. The ultimate objective is to produce the best phylogeny for the analysed OTUs.

To assess the performance of a combined GMM-based phylogenetic protocols, this study compares the results obtained from a data-combined matrix (Matrix E) with those from Matrix D, a traditional cladistic analysis based on discrete morphological traits describing the same sample. In this set of analyses, 30 OTUs, including the three outgroup taxa (see Chapter I – Materials / Table 1) were used to create two matrices:

- Matrix D contained 60 morphological characters describing the morphology of the calvarium (see, Chapter II – Method / Data / Morphological Characters and Chapter II – Method / Protocols / Chapter IV – Morphological and 3D characters), coded as discrete states ranging from 1 to 3 (Table 2).
- Matrix E combine two types of data (see Table 4 and Chapter II – Method / Protocols / Chapter IV – Morphological and 3D characters): 49 morphological characters and 7 configurations of aligned 3D coordinates of landmarks and semi-landmarks (post-Generalized Procrustes analysis, GPA) representing the averaged morphology of specific features of each OTU.

As a result, six parsimony phylogenetic analyses were conducted, corresponding to the analysis of the matrices, with the weighting according to the indices: CI, RI and RC, following the successive approximative weighting method (SAW) of Farris (1969) (see, Chapter II – Method / Protocols / Scripts and Chapter II – Method / Protocols / Chapter III – Cladistics and GMM). After the reweighting process a subsequent tree search was run using the heuristic algorithm implemented in the software. In the presence of MPTs, the strict consensus was calculated.

The initial matrix analyses employed a heuristic algorithm with equal weighting, random addition sequence (RAS), and tree bisection and reconnection (TBR) for branch swapping (see, Chapter II – Method / Protocols / Chapter IV – Morphological and 3D characters).

To assess the robustness of the tree, the CI and RI were calculated. The CI was used to indicate the degree of homoplasy in each tree. However, if a tree has a high number of autapomorphies, this index may be artificially high (closer to 1), regardless of the homoplasy content of the other traits. To address this, we also calculated the RI of each tree, which represents the ratio between the maximum and observed number of homoplasies.

As previously discussed, the tree derived from matrix D, retaining only traditional morphological characters, serves as the reference topology, given the unavailability of molecular data for most specimens. To evaluate the performance of the combined dataset in matrix E, its resulting topology was compared to that of matrix D under identical weighting conditions (e.g., CI-weighted trees compared with one another). This controlled comparison helps isolate the effect of data integration from that of weighting schemes. Topological similarity was assessed using SPR moves and RF distance, both of which quantify the degree of congruence between trees (see, Chapter II – Method / Protocols / Chapter III – Cladistics and GMM.).

The robustness of each branch was finally assessed through 100 standard bootstrap replications (following Felsenstein, 1985a).

II. Results

II.1. Matrix D (morphological characters)

II.1.1. General results

The CI-weighting heuristic analysis of matrix D results in one parsimonious tree of 7497 steps with a CI of 0.636 and a RI of 0.832 (Figure 65 and Table 11). Reweighting based on the RI values yielded a single tree of 8951 steps (CI = 0.595, RI = 0.821, Figure 66 and Table 11). With RC-weighting, the heuristic analysis of matrix D results in a unique phylogenetic tree of 5327 steps with a CI of 0.709 and a RI of 0.886 (Figure 67 and Table 11).

Table 11: Length, consistency and retention indices of the tree for each analysis of Matrix D.

	Weighting	Length	CI value	RI value
Matrix D - Morphological characters	CI	8546	0.487	0.759
	RI	11730	0.446	0.757
	RC	5372	0.539	0.824

II.1.2. CI – weighting

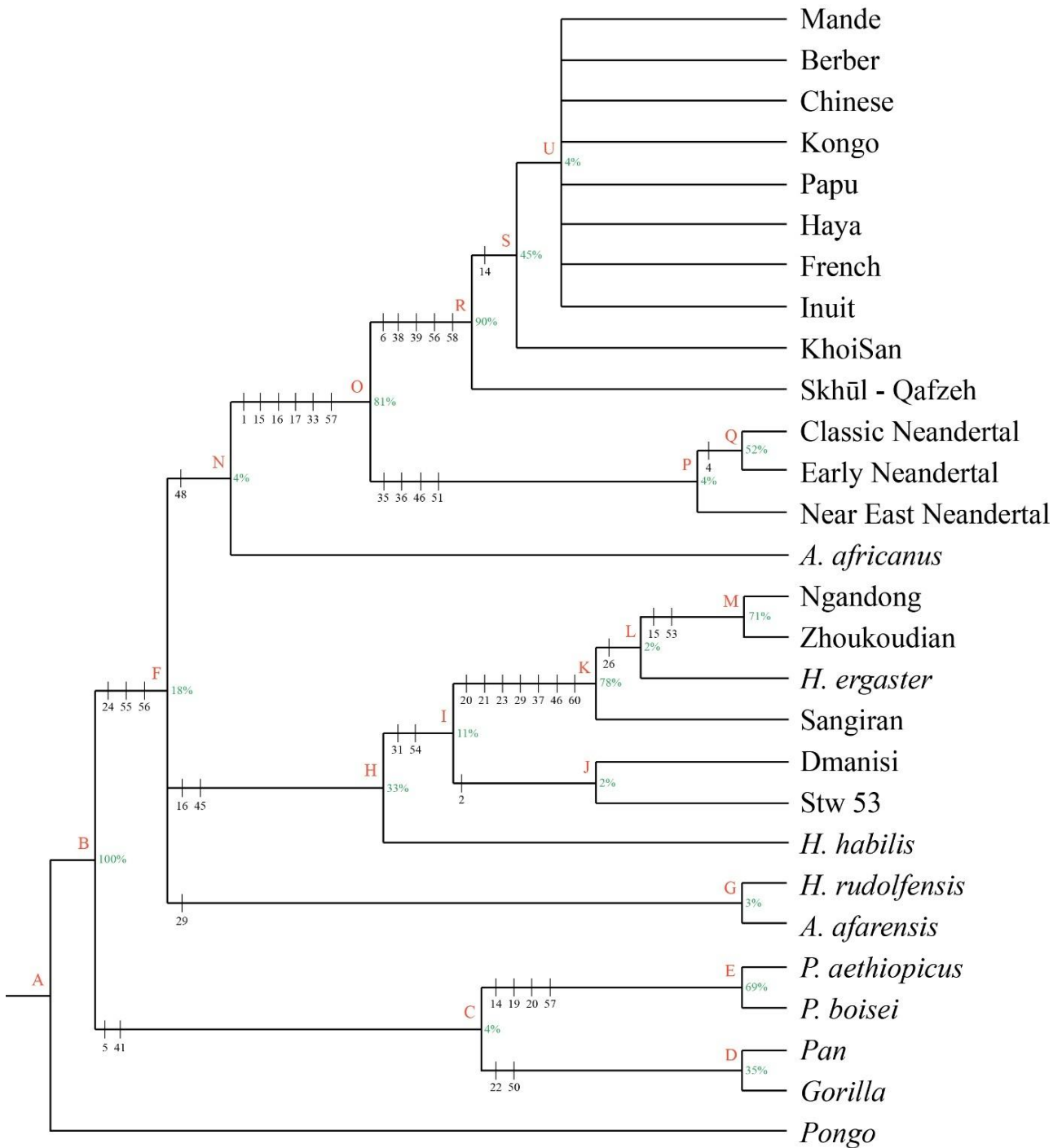


Figure 65: Unique phylogenetic tree based on the analysis of matrix D after CI-weighting (i.e., 60 morphological characters and 28 OTUs), 8546 steps (CI = 0.487 and RI = 0.759). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches, at each node, are the character number where a change in states occurred, showing synapomorphies. Red letters are used to identify each node.

In the CI-weighted analysis, two of the outgroups, *Pan* and *Gorilla*, form a clade (node D) that is grouped with *P. aethiopicus* and *P. boisei* (node E) within a larger assemblage (node C), which is

separated from the rest of the ingroup at node B. This separation is strongly supported, with node B receiving a bootstrap value of 100%. In contrast, the support values for nodes C, D, and E are substantially lower, at 4%, 35%, and 69% respectively.

Node F represents a polytomy that fails to resolve the relationships among the remaining ingroup taxa, receiving limited support (18%). Within this unresolved group, *H. rudolfensis* and *A. afarensis* form a weakly supported monophyletic grouping (node G; bootstrap 3%).

The broader clade represented by node F includes *H. habilis* (node H), the Dmanisi specimens and Stw 53 (node J), *Sangiran* (node K), *H. ergaster* (node L), and Zhoukoudian and Ngandong (node M). The Dmanisi and Stw 53 specimens form a sister group to the clade comprising Sangiran, *H. ergaster*, Zhoukoudian, and Ngandong, clustered together at node I. The bootstrap support values for these nodes vary considerably, with node H supported at 33%, node I at 11%, node J at 2%, node K at 78%, node L at 2%, and node M at 71%.

A. africanus is grouped with *H. neandertalensis* and *H. sapiens* at node N, though this association is weakly supported (bootstrap 4%). *H. neandertalensis* and *H. sapiens* are recovered as sister taxa at node O, with a higher bootstrap value of 81%. Neandertals form a well-supported monophyletic group (node P; 84%), within which “Classic Neandertals” and “Early Neandertals” form a terminal clade (node Q; 52%). Finally, node R represents the monophyletic grouping of *H. sapiens*, including the “Skhūl–Qafzeh” population in a basal position, and receives strong bootstrap support at 90%.

In terms of anatomical character support for the most parsimonious tree under CI-weighting (see Figure 65 and Appendix 22), node C is defined by the absence of convexity in the outline of the *planum occipitale* (#5, state 1) and the presence of the *tuberculum linearum* (#41, state 2). Node D, uniting *Gorilla* and *Pan*, is characterised by a fronto-temporal junction at the *pterion* (#22, state 2) and the alignment of the auditory meatus with the *processus zygomaticus temporalis* (#50, state 3). The clade *P. boisei* + *P. aethiopicus* (node E) shares four synapomorphies: a non-projecting supraorbital region (#14, state 1), a sagittal crest (#19, state 2), a sagittal keel on the frontal bone (#20, state 2), and a weak or absent *tuberculum zygomaticum anterius* (#57, state 1).

Node F, which groups australopiths and *Homo* species in a polytomy, is supported by three characters: the absence of a sagittal keel along the bregma–lambda arch (#24, state 1), antero-posterior orientation of the petro-tympanic crest relative to the sagittal plane (#55, states 2 and 3), and a medio-lateral concavity of the articular tubercle (#56, state 1). Node G, comprising *A. afarensis*

and *H. rudolfensis*, is defined by the medial placement of the *linea temporalis* on the parietal (#29, state 2).

Node H, representing *H. habilis*, is supported by the presence of a continuous *sulcus postorbitalis* (#16, state 3) and a strongly developed *crista supramastoidea* at the *porion* (#45, state 3). The clade formed at node I is characterised by a more pronounced *planum nuchale* relative to the *planum occipitale* (#31, state 1) and the presence of the *crista occipito-mastoidea* (#54, state 2). Node J (Dmanisi + Stw 53) is supported by a medially concave outline of the supraorbital region at the glabella in *norma verticalis* (#2, state 1).

The Sangiran OTU (node K) is associated with seven synapomorphies: presence of a sagittal keel on the frontal bone (#20, state 2), bregmatic eminence (#21, state 2), superior thickening of the coronal sutures (#23, state 2), *torus angularis parietalis* (#29, state 2), deep *sulcus supratoralis* (#37, state 3), *tuberculum supramastoideum anterius* (#47, state 2), and a *preglenoid tubercle* (#60, state 2). Node L (*H. ergaster*) is supported by the presence of a pre-lambdaic hollowing along the bregma–lambda arch (#26, state 2), while node M (Zhoukoudian + Ngandong) shares a weak postorbital constriction (#15, state 2) and a bony bridge across the digastric groove (#53, state 2).

Node N, grouping *A. africanus*, *H. neandertalensis*, and *H. sapiens*, is supported by the presence of a *supramastoid groove* located between the *crista supramastoidea* and *crista mastoidea* (#48, state 3). Node O, uniting Neandertals and modern humans, exhibits six synapomorphies: a convex supraorbital outline in *norma facialis* (#1, state 2), absence of postorbital constriction (#15, state 3), continuous *sulcus postorbitalis* (#16, state 3), presence of *tuber frontale* (#17, state 3), a modified relationship between the *inion* and *opisthocranium* (#33, state 2), and a reduced *tuberculum zygomaticum anterius* (#57, state 1).

The Neandertal clade (node P) is characterised by four features: presence of a *suprainiac fossa* (#35, state 3) with parallel or arched lateral borders (#36, state 2), misalignment between the *crista supramastoidea* and *processus zygomaticus temporalis* (#46, state 1), and the development of the *tuberculum mastoideum anterior* (#51, state 2). The terminal node within this group (node Q), which joins the “Classic Neandertals” and “Early Neandertals,” is supported by a single character: a sharply angled occipital outline in *norma lateralis* (#4, state 2).

Finally, the monophyly of *H. sapiens* at node R is upheld by five synapomorphies: a pentagonal outline of the *planum occipitale* in *norma occipitalis* (#6, state 3), absence of the *torus occipitalis*

transversus (#38 and #39, state 1), antero-posterior convexity of the articular tubercle (#56, state 2), and a weakly developed or absent postglenoid process (#58, state 1).

II.1.3. RI – weighting

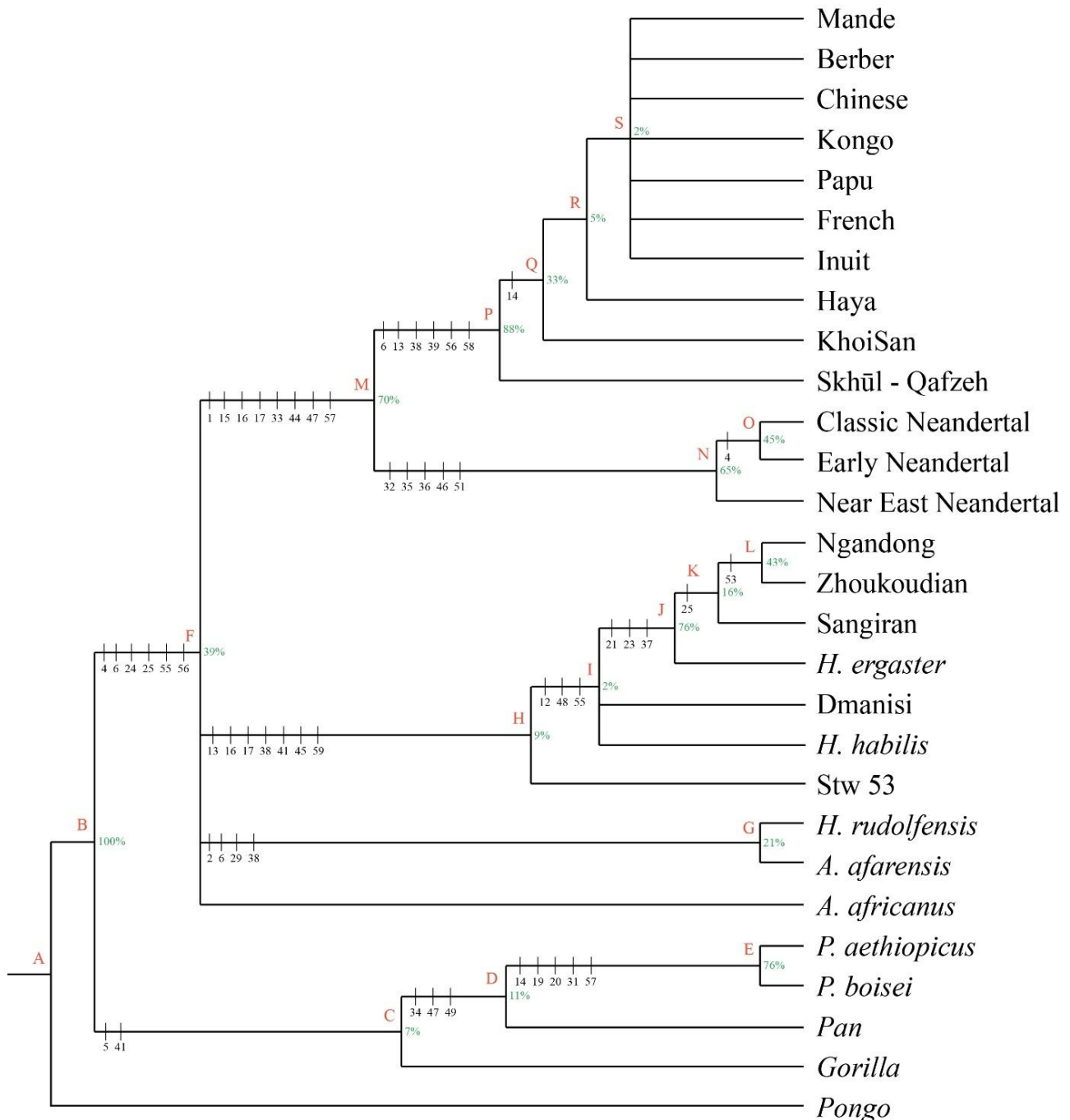


Figure 66: Unique phylogenetic tree based on the analysis of matrix D after RI-weighting (i.e., 60 morphological characters and 28 OTUs), 11730 steps (CI = 0.446 and RI = 0.757). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches, at each node, are the character number where a change in states occurred, showing synapomorphies. Red letters are used to identify each node.

In the RI-weighted analysis, the general phylogenetic structure mirrors that of the CI-weighted tree. Two outgroup taxa, *Pan* (node D) and *Gorilla* (node C), cluster with the clade *P. aethiopicus* and *P. boisei* (node E), although they do not form a monophyletic clade. Those four OTUs are separated from the rest of the ingroup at node B. This separation is strongly supported, with node B receiving a strong bootstrap value of 100%. In contrast, the internal nodes within this outgroup cluster, nodes C, D, and E, are supported to varying degrees, with bootstrap values of 7%, 11%, and 76%, respectively.

As in the CI-weighted analysis, node F represents a poorly resolved polytomy that fails to clarify the relationships among the remaining ingroup taxa, with a modest bootstrap value of 39%. Within this unresolved assemblage, *H. rudolfensis* and *A. afarensis* again form a weakly supported monophyletic group (node G; bootstrap 21%).

Node F also includes the clade comprising Stw 53 (node H), the Dmanisi specimens and *H. habilis* (node I), *H. ergaster* (node J), the Sangiran OTU (node K), and the Zhoukoudian and Ngandong specimens (node L). Notably, in this weighting scheme, the Dmanisi and Stw 53 specimens do not form a sister clade to Sangiran, *H. ergaster*, Zhoukoudian, and Ngandong, as they did in the CI-weighted analysis. Bootstrap support for these nodes varies widely: node H is supported at 2%, node I at 3%, node J at 76%, node K at 16%, and node L at 43%.

Unlike the CI-weighted analysis, *A. africanus* is not grouped with *H. neandertalensis* and *H. sapiens* but instead remains unresolved within the polytomy at node F. However, *H. neandertalensis* and *H. sapiens* continue to form a sister clade (node M), this time with a bootstrap value of 70%. Neandertals again form a monophyletic group (node N; 65%), within which “Classic Neandertals” and “Early Neandertals” are joined in a terminal clade (node O), receiving 45% bootstrap support. The *H. sapiens* species is recovered as monophyletic at node P, with the “Skhūl–Qafzeh” specimens occupying a basal position. This clade is strongly supported with a bootstrap value of 88%. While their bootstrap values are very low – 33% and 5% respectively – the KhoiSan are present in basal position of the modern human and followed by the Haya.

Regarding anatomical character support (Figure 66 and Appendix 22), many synapomorphies overlap with those from the CI-weighted tree, although several differences emerge. Node C is defined by the same two features as before: absence of convexity in the *planum occipitale* outline (#5, state 1) and presence of the *tuberculum linearum* (#41, state 2). Node D, which separates *Gorilla* and

Pan, is not associated with any synapomorphic characters. Node E (*P. boisei* + *P. aethiopicus*) shares five traits: four carried over from the CI-weighted analysis (#14, state 1; #19, state 2; #20, state 2; and #57, state 1), along with an additional feature, reduced development of the *planum nuchale* relative to the *planum occipitale* (#31, state 2).

Node F, the large polytomy uniting australopiths and *Homo* taxa, is supported by six characters. Three are shared with the CI-weighted tree (#24, state 1; #55, states 2 and 3; and #56, state 1), while three are newly observed: a rounded occipital outline in *norma lateralis* (#4, state 1), a circular outline of the *planum occipitale* in *norma occipitalis* (#6, state 2), and the absence of parasagittal hollowing on both sides of the parietal suture (#25, state 1). Node G (*A. afarensis* + *H. rudolfensis*) is defined by four synapomorphies: one also seen in the CI-weighted analysis, the medial position of the *linea temporalis* on the parietal (#29, state 2), and three additional traits: a straight supraorbital outline in *norma verticalis* (#2, state 2), a triangular outline of the *planum occipitale* in *norma occipitalis* (#6, state 1), and the presence of a medially projecting *torus occipitalis transversus* (#38, state 2).

Node H (Stw 53) is distinguished by a suite of seven characters: an incomplete *sulcus supraorbitalis* (#13, state 2), a continuous *sulcus postorbitalis* (#16, state 3), a well-defined and medially shifted *tuber frontale* (#17, state 2), a prominent and protruding *torus occipitalis transversus* (#38, state 2), presence of a *tuberculum linearum* (#41, state 2), strongly developed *crista supramastoidea* at the *porion* (#45, state 3), and a significant tympanic contribution to the posterior wall of the glenoid cavity (#59, state 2).

Node I, which groups Dmanisi, *H. habilis*, and *H. erectus* sensu lato, is characterised by three traits: a frontal chord longer than the parietal chord (#12, state 3), the presence of a closed anterior *supramastoid* groove between the *crista supramastoidea* and the *crista mastoidea* (#48, state 2), and a posteriorly oriented petro-tympanic crest in relation to the sagittal plane (#55, state 3).

Node J (*H. ergaster*) is defined by three synapomorphies: a pronounced *bregmatic eminence* (#21, state 2), thickening of the superior region of the coronal sutures (#23, state 2), and presence of a *sulcus supratoralis* (#37, state 3). The Sangiran OTU (node K) is distinguished by a single character, the presence of parasagittal hollowing on both sides of the parietal sutures (#25, state 2). Node L (Zhoukoudian + Ngandong) shares a bony bridge across the digastric groove (#53, state 2).

The clade uniting *H. neandertalensis* and *H. sapiens* (node M) is defined by nine synapomorphies. Six of these are shared with the CI-weighted analysis: a convex supraorbital outline in *norma facialis* (#1, state 2), absence of postorbital constriction (#15, state 3), presence of a continuous *sulcus postorbitalis*

(#16, state 3), *tuber frontale* (#17, state 3), different positions of the *inion* and *opisthocranium* (#33, state 2), and reduced *tuberculum zygomaticum anterius* (#57, state 1). Three additional characters support this node in the RI-weighted tree: a low position of the *linea temporalis* on the parietal (#28, state 3), a sinuous or curved outline of the superior border of the temporal squama (#44, state 1), and a strongly developed *crista supramastoidea* at the *porion* (#48, state 3).

Node N, corresponding to the Neandertal clade, is characterised by five features. Four of these, presence of a *suprainiac fossa* (#35, state 3), arched or parallel lateral borders of the fossa (#36, state 2), misalignment of the *crista supramastoidea* and *processus zygomaticus temporalis* (#46, state 1), and the presence of the *tuberculum mastoideum anterior* (#51, state 2), were also recovered in the CI-weighted tree. The fifth is the presence of an occipital bun (#32, state 2). The terminal Neandertal clade (node O), uniting “Classic Neandertals” and “Early Neandertals,” is again supported by a sharply angled occipital outline in *norma lateralis* (#4, state 2).

Lastly, *H. sapiens* is recovered as a monophyletic group at node P, supported by six synapomorphies. Five of these, pentagonal outline of the *planum occipitale* in *norma occipitalis* (#6, state 3), absence of *torus occipitalis transversus* (#38 and #39, state 1), anteroposterior convexity of the articular tubercle (#56, state 2), and a weakly developed postglenoid process (#58, state 1), are consistent with the CI-weighted results. A sixth character, newly recovered here, is the complete individualisation of the character composing the supraorbital region, including a well-defined *sulcus supraorbitalis* (#13, state 1).

II.1.4. RC – weighting

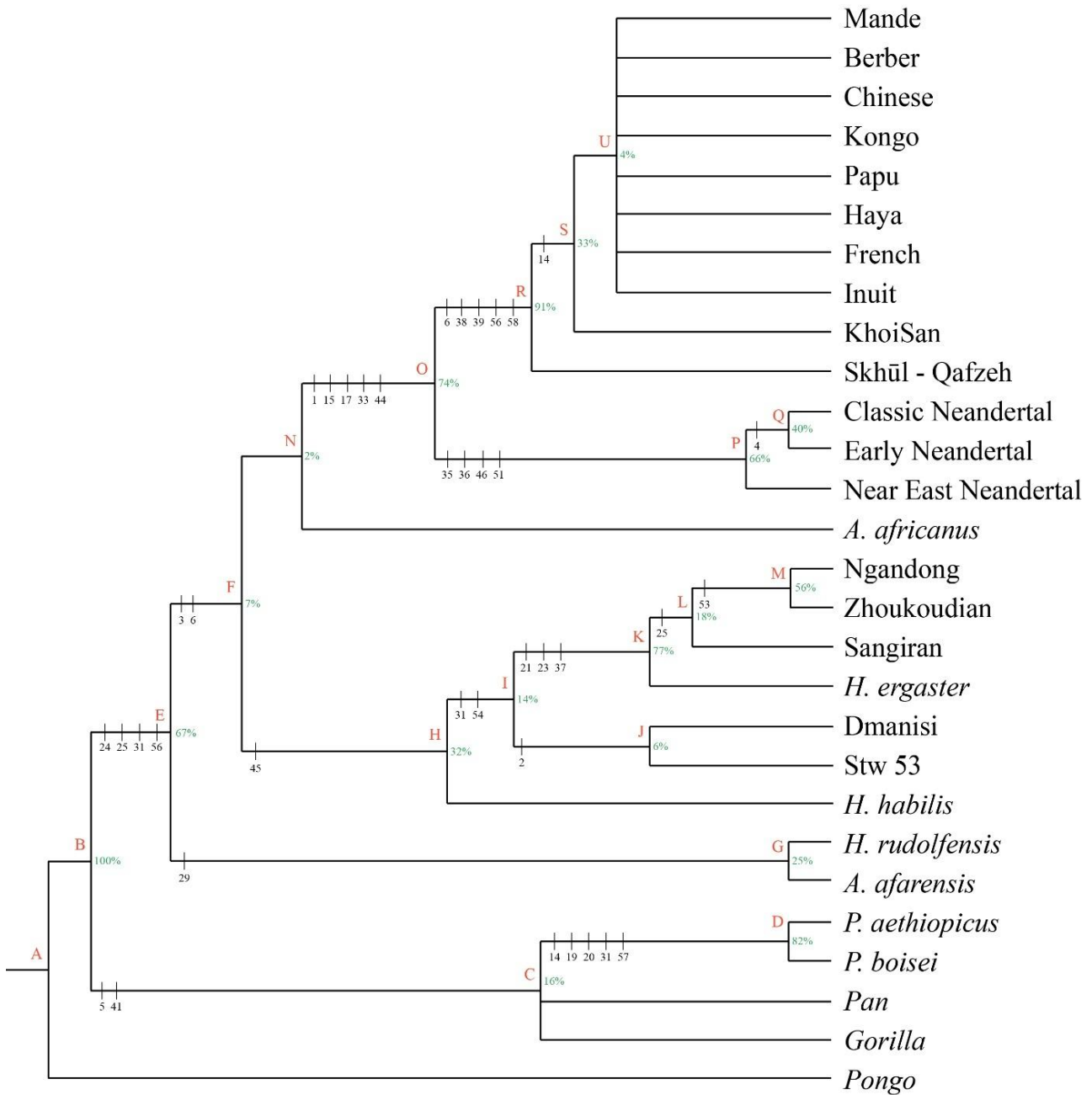


Figure 67: Unique phylogenetic tree based on the analysis of matrix D after RC-weighting (i.e., 60 morphological characters and 28 OTUs), 5372 steps (CI = 0.539 and RI = 0.824). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches, at each node, are the character number where a change in states occurred, showing synapomorphies. Red letters are used to identify each node.

In the RC-weighted analysis, the overall phylogenetic structure closely resembles that of the CI-weighted tree. *Pan* and *Gorilla* are recovered in a polytomy at node C alongside *P. aethiopicus* and *P. boisei* (node D). These four taxa are collectively separated from the ingroup at node B, which is

strongly supported with a bootstrap value of 100%. Internal support within this cluster is more variable, with node C supported at 16% and node D at 82%.

In contrast to the CI- and RI-weighted analyses, the polytomy previously present at node F is resolved here. Node E separates the clade consisting of *A. afarensis* and *H. rudolfensis* (node F) from the remaining OTUs. Bootstrap support for this bifurcation is moderate, 67% for node E and 25% for node F.

Node G further divides the dataset, separating two groups: (1) a clade comprising *H. habilis*, the Dmanisi specimens, Stw 53, and a series of *H. erectus* sensu lato specimens including *H. ergaster*, Sangiran, Zhoukoudian, and Ngandong; and (2) the clade containing *A. africanus*, *H. neandertalensis*, and *H. sapiens*. Node G, however, is weakly supported, with a bootstrap value of only 7%.

Within this framework, *H. habilis* occupies a basal position at node H (bootstrap 33%). Consistent with the CI-weighted analysis, the Dmanisi specimens and Stw 53 (node J) are recovered as sister to *H. erectus* s.l. (node I), though with very low support: 4% for node I and just 1% for node J. Within the *H. erectus* lineage, *H. ergaster* forms the basal taxon at node K (77%), followed by Sangiran at node L (18%), and finally the Zhoukoudian and Ngandong specimens grouped together at node M (56%).

A. africanus, as in the CI-weighted tree, is grouped with *H. neandertalensis* and *H. sapiens* at node N, though with minimal bootstrap support (6%). The modern human and Neandertal lineages are again recovered as sister taxa (node O), supported at 74%. Neandertals are monophyletic at node P (66%), with “Classic Neandertals” and “Early Neandertals” forming a terminal clade at node Q (40%). *H. sapiens* is recovered as a monophyletic group at node R, with the “Skhül-Qafzeh” specimens occupying a basal position within the clade. This grouping is strongly supported, with a bootstrap value of 91%.

The anatomical character support for the most parsimonious tree under RC-weighting (Figure 67 and Appendix 22) largely overlaps with the CI- and RI-weighted trees, although some differences are observed. Node C is again defined by the absence of convexity in the outline of the *planum occipitale* (#5, state 1) and the presence of the *tuberculum linearum* (#41, state 2). Node D (*P. boisei* + *P. aethiopicus*) shares five synapomorphies, all previously noted in the RI-weighted tree: non-projecting supraorbital region (#14, state 1), sagittal crest (#19, state 2), sagittal keel on the frontal (#20, state 2),

reduced development of the *planum nuchale* relative to the *planum occipitale* (#31, state 2), and a weakly marked *tuberculum zygomaticum anterius* (#57, state 1).

Node E, separating *H. rudolfensis* and *A. afarensis* from the remaining OTUs, is supported by four synapomorphies: absence of a sagittal keel on the bregma-lambda arch (#24, state 1), absence of parasagittal hollowing along the parietal suture (#25, state 1), a medio-lateral concavity of the articular tubercle (#56, state 1), and a reduced *planum nuchale* (#31, state 2). Node F, defining the *A. afarensis* + *H. rudolfensis* clade, is supported by a single character: the medial position of the *linea temporalis* on the parietal (#29, state 2), a trait shared with the CI- and RI-weighted trees.

Node G is characterised by two synapomorphies: an intermediate anteroposterior convexity of the frontal bone (#3, state 2) and a circular outline of the *planum occipitale* in *norma occipitalis* (#6, state 2). Node H (*H. habilis*) is defined by a strongly developed *crista supramastoidea* at the *porion* (#45, state 3).

Node I, separating the Dmanisi + Stw 53 clade from *H. erectus* s.l., is supported by two traits: increased development of the *planum nuchale* relative to the *planum occipitale* (#31, state 1), and the presence of the *crista occipito mastoidea* (#54, state 2). Node J (Dmanisi + Stw 53) is defined by a straight supraorbital outline in *norma verticalis* (#2, state 1).

Node K (*H. ergaster*) is again supported by three characters: pronounced bregmatic eminence (#21, state 2), thickened coronal sutures (#23, state 2), and presence of a *sulcus supratoralis* (#37, state 3). The Sangiran OTU (node L) is associated with a single feature, parasagittal hollowing on both sides of the parietal sutures (#25, state 2). Node M (*Zhoukoudian* + *Ngandong*) is defined by the presence of a bony bridge across the digastric groove (#53, state 2).

Node N, which includes *A. africanus*, is not supported by any synapomorphies. The clade uniting *H. neandertalensis* and *H. sapiens* (node O) is defined by five characters. Four are shared with the previous analyses: a convex supraorbital outline in *norma facialis* (#1, state 2), absence of postorbital constriction (#15, state 3), presence of *tuber frontale* (#17, state 3), and different positions for (#33, state 2). One additional trait is shared with the RI-weighted tree: a sinuous outline of the superior border of the temporal squama (#44, state 1).

The Neandertal clade (node P) is defined by four synapomorphies, all shared with the CI- and RI-weighted analyses: a well-developed *suprainiac fossa* (#35, state 3), parallel or arched lateral borders of

the fossa (#36, state 2), misalignment of the *crista supramastoidea* and *processus zygomaticus temporalis* (#46, state 1), and the presence of the *tuberculum mastoideum anterior* (#51, state 2). The terminal Neandertal clade (node Q), grouping the “Classic Neandertals” and “Early Neandertals,” is once again supported by a sharply angled occipital outline in *norma lateralis* (#4, state 2).

Finally, *H. sapiens* is consistently recovered as a monophyletic group at node R, supported by five synapomorphies: a pentagonal outline of the *planum occipitale* in *norma occipitalis* (#6, state 3), absence of the *torus occipitalis transversus* (#38 and #39, state 1), anteroposterior convexity of the articular tubercle (#56, state 2), and a weakly marked postglenoid process (#58, state 1). All of these traits are consistent across the CI-, RI-, and RC-weighted trees.

II.2. Matrix E (3D landmark configurations and morphological characters)

II.2.1. General results

The heuristic analysis using CI-based weighting produced a single most parsimonious tree, with a length of 6846.654 steps, a CI of 0.523, and a RI of 0.792 (Figure 68, Table 12).

The reweighting of the seven landmark configurations and 50 characters based on their RI values, followed by analysis via the heuristic method, resulted in a single tree with 9449.663 steps (CI = 0.478, RI = 0.785; Figure 82, Table 12).

Further analysis of matrix E, applying reweighting based on RC values, produced one most parsimonious tree comprising 4554.438 steps, with a CI of 0.567 and an RI of 0.842 (Figure 85, Table 12).

Across all three datasets, the resulting parsimony trees consistently exhibit moderate CI values, generally around 0.5, and relatively high RI values, all exceeding 0.7. Notably, the RC-weighted analysis yielded the highest CI and RI values, indicating a stronger phylogenetic signal (Table 12). Additionally, the tree derived from RC weighting was the shortest among the three, suggesting greater overall parsimony compared to the CI and RI-based weightings.

Table 12: Length, consistency and retention indices of the tree for each analysis of Matrix E.

	Weighting	Length	CI value	RI value
Matrix E	CI	6846.654	0.523	0.792
	RI	9449.663	0.478	0.785
	RC	4554.438	0.567	0.842

Table 13: Topological correspondence (SPR moves and Robinson-Foulds distances) between the reference phylogeny and the trees derived from the three matrices. The average SPR similarity is 1 and the average RF distance is 0.378.

	Weighting	SPR similarity	RF distance
Matrix E	CI	1	0.385
	RI	1	0.385
	RC	1	0.365

Overall, the topologies generated from the combined landmark coordinates and morphological characters exhibited high congruence according to both SPR and RF metrics, with SPR values of 1 and RF distances ranging from 0.365 to 0.385 (see Table 13). The results are mitigated as the RC-

weighting seem more congruent with the RF distance (inferior to the CI- and RI-weighted schemes values), while the SPR similarity does not change according to the weighting scheme.

II.2.2. CI – weighting

The most parsimonious trees, derived from the two-step analysis of matrix E, reveals several key patterns (Figure 68).

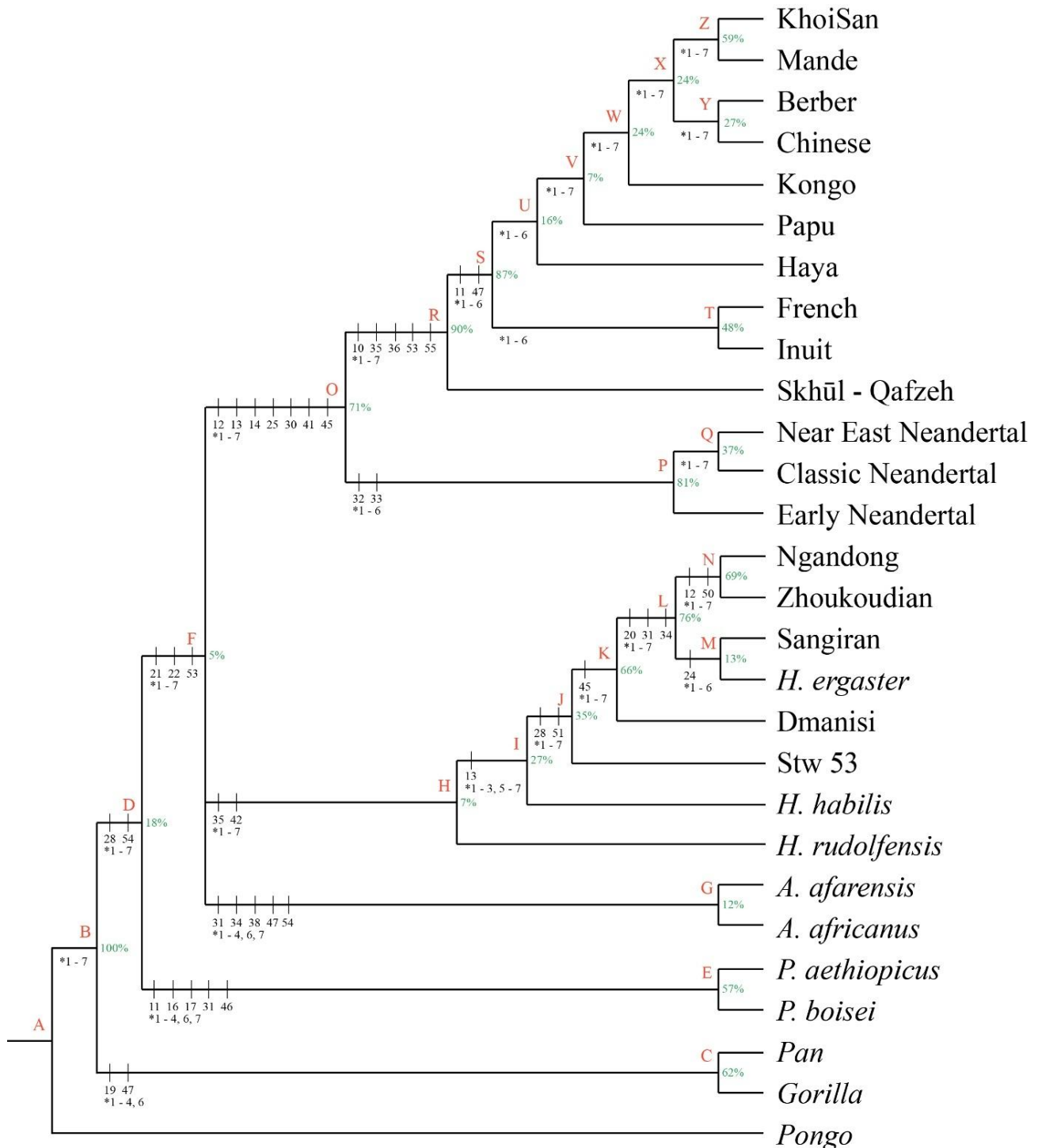
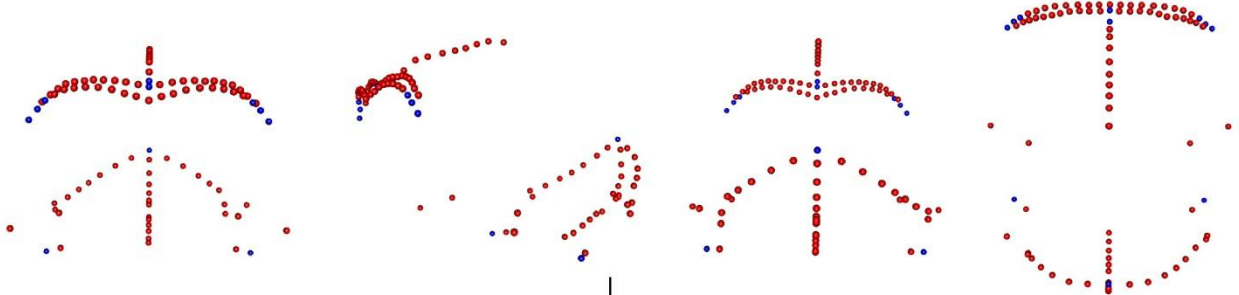


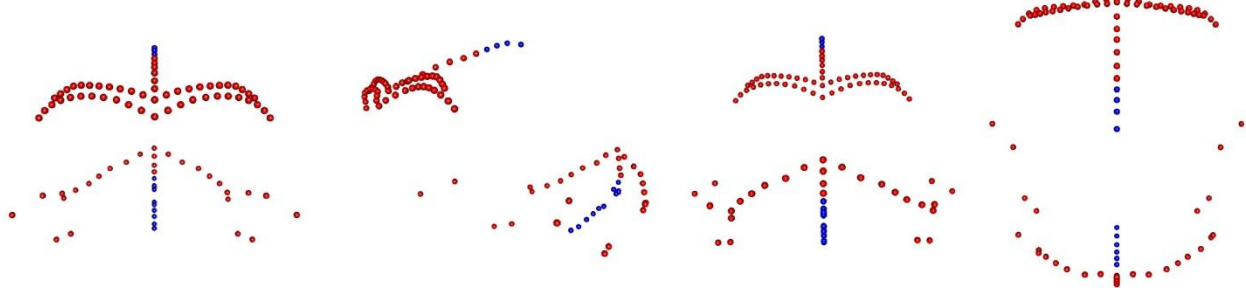
Figure 68: Unique phylogenetic tree based on the analysis of matrix E after CI-weighting (i.e., 7 landmarks configurations and 50 morphological characters and 28 OTUs), 6846.654 steps (CI = 0.523 and RI = 0.792).

Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

Node D



Node E



3D characters

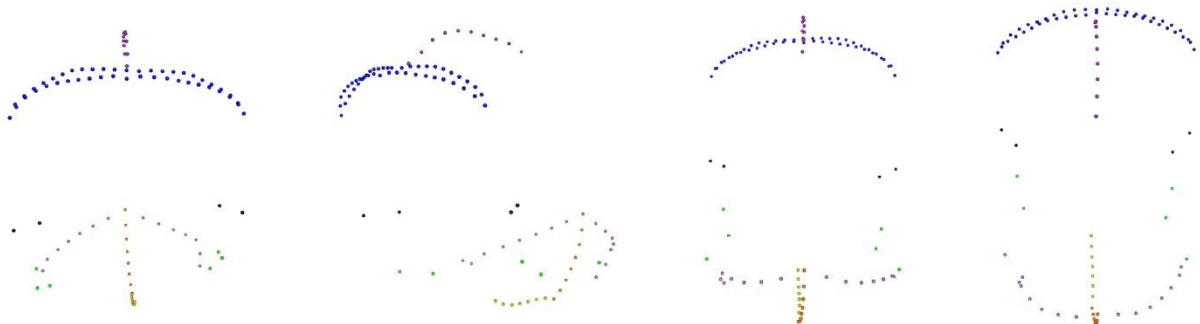


Figure 69: 3D shapes showing morphological change for the landmark configurations from node D to node E. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node D, which supports the monophyly of the in-group, is sustained by a bootstrap value of 18%. Morphological variation can be observed through the seven 3D shape configurations (see Figures 68 and 69 and Appendix 23) and two synapomorphies.

In *norma verticalis* and *norma facialis*, the supraorbital region presents a straight outline (#1). In *norma occipitalis*, both the posterior and anterior occipital crests are present and aligned (#5), while the

outline of the *planum occipitale* adopts a triangular shape (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone is slightly more convex than in apes but retains a weak convexity (#2). The transition between the *planum occipitale* and *planum nuchale* is comparable to the angular transition seen in apes (#3). Finally, the downward development of the *processus mastoideus* relative to the basicranium is similar (#6), and the glenoid cavity is slightly deeper than in apes (#7).

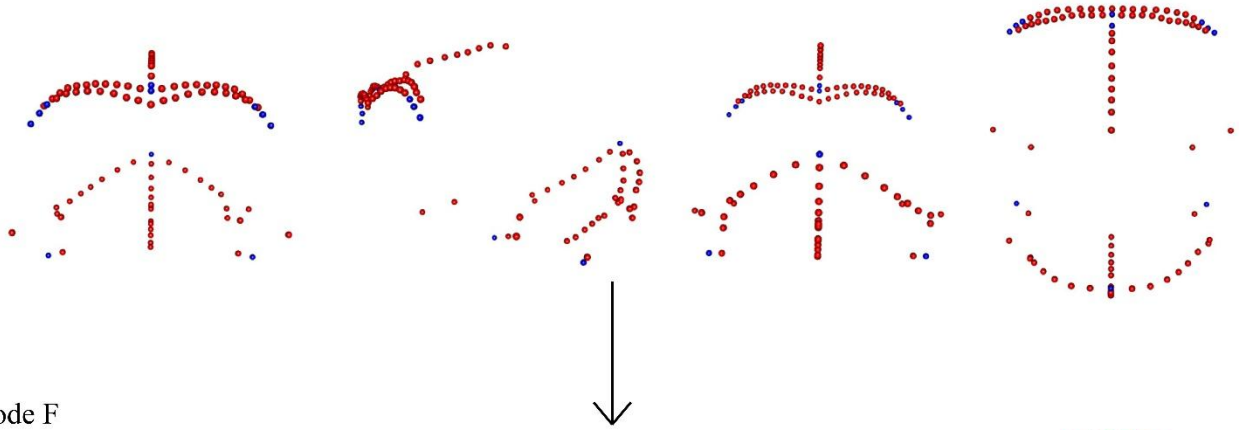
The two synapomorphies correspond to: (1) the *planum nuchale* being more developed than the *planum occipitale* (#28, state 1), which subsequently evolves into a more developed *planum occipitale* (#28, state 2), and (2) the *tuberculum zygomaticum anterius* changing from marked (#54, state 2) to absent or weakly marked (#54, state 1).

At node E, the two *Paranthropus* OTUs form a monophyletic group supported by a bootstrap value of 57%, five synapomorphies, and six landmark configurations.

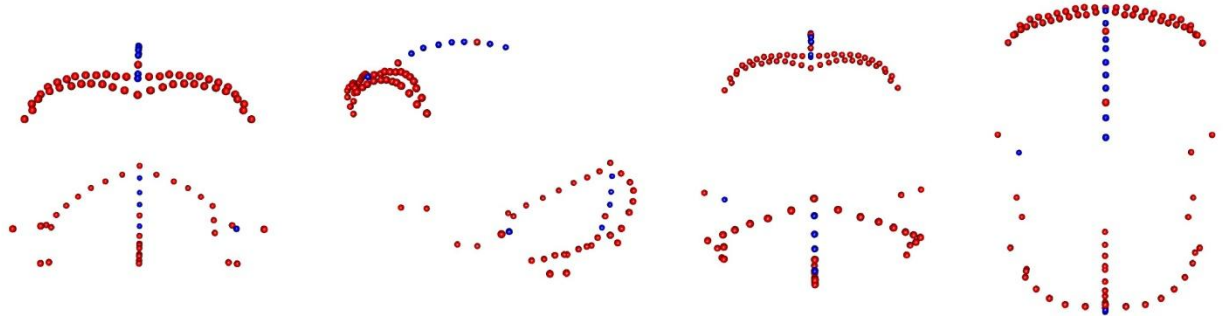
Overall, the supraorbital region changes from the straight outline observed in node D to a slightly bulged form at the glabella in *norma verticalis*, and a more rounded contour in *norma facialis* (#1). In *norma occipitalis*, the *planum occipitale* retains its triangular outline (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone becomes more convex than in node D (#2), and the transition between the *planum occipitale* and *planum nuchale* is slightly rounder (#3), contrasting with the sharper angular transition seen previously. The *processus mastoideus* exhibits a more pronounced downward development relative to the basicranium (#6), and the glenoid cavity is deeper than in node D (#7).

The five synapomorphies supporting this node include: (1) a reduction in the projection of the supraorbital region from projecting (#11, state 3) to non-projecting (#11, state 1); (2) the emergence of both a sagittal crest (#16, state 2) and a sagittal keel on the frontal bone (#17, state 2), transitioning from their previous absence (#16, state 1; #17, state 1); (3) the appearance of the *processus retromastoideus* (#31, state 2); and (4) a change in the form of the auditory meatus from circular (#46, state 1) to elliptic (#46, state 2).

Node D



Node F



3D characters

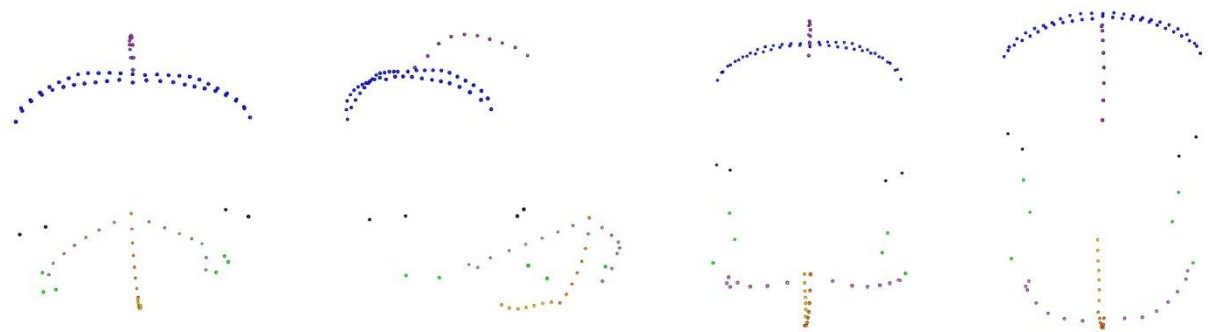


Figure 70: 3D shapes showing morphological change for the landmark configurations from node D to node F. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

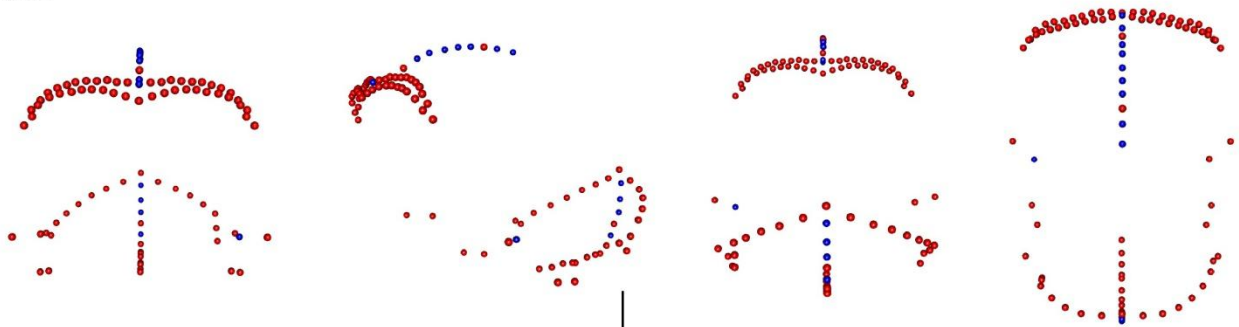
At Node F, a large polytomy is observed, failing to resolve the relationships among *Australopithecus* and the various *Homo* species. This node is supported by a bootstrap value of 5%, seven landmark configurations, and three synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital region maintains a straight outline, similar to node D (#1) (see Figure 70). In *norma occipitalis*, both the posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* outline becomes more circular than in node D (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone is more convex (#2), and the

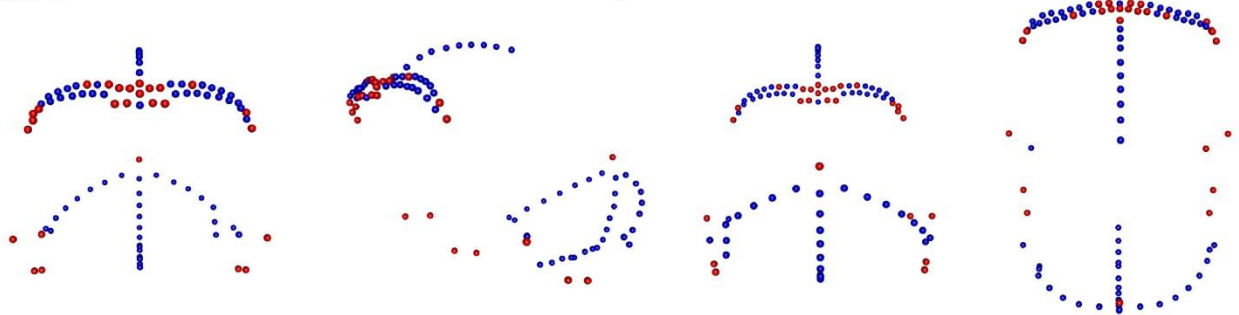
transition between the *planum occipitale* and *planum nuchale* is rounder, with a more convex *planum occipitale* (#3), contrasting with the angular transition characteristic of node D. The *processus mastoideus* shows a weak but slightly stronger downward development than in node D (#6), and the glenoid cavity is shallow (#7).

The three synapomorphies identified at this node correspond to: (1) the disappearance of the sagittal keel along the bregma–lambda arch (#21, state 1); (2) the loss of parasagittal hollowing on both sides of the parietal suture (#22, state 1); and (3) a change in the configuration of the articular tubercle, from an antero-posterior convexity (#53, state 2) to a medio-lateral concavity (#53, state 1).

Node F



Node G



3D characters

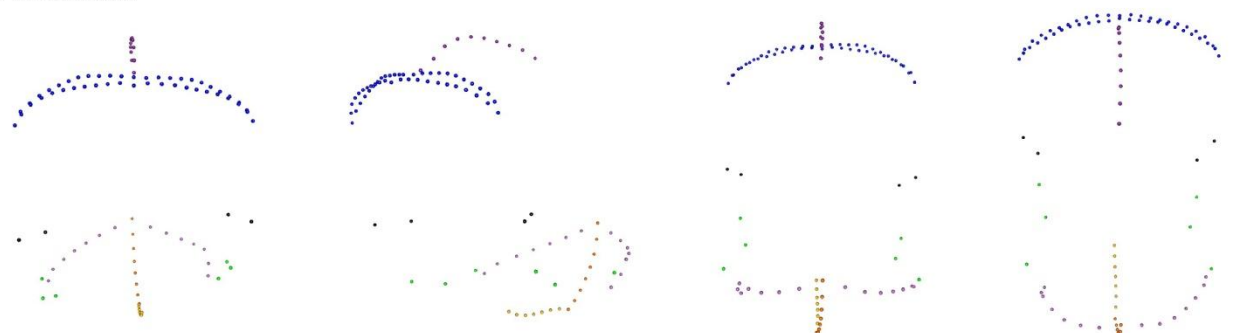


Figure 71: 3D shapes showing morphological change for the landmark configurations from node F to node G. The views are, from left to right, norma facialis, three-quarter view, norma occipitalis and norma verticalis. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a

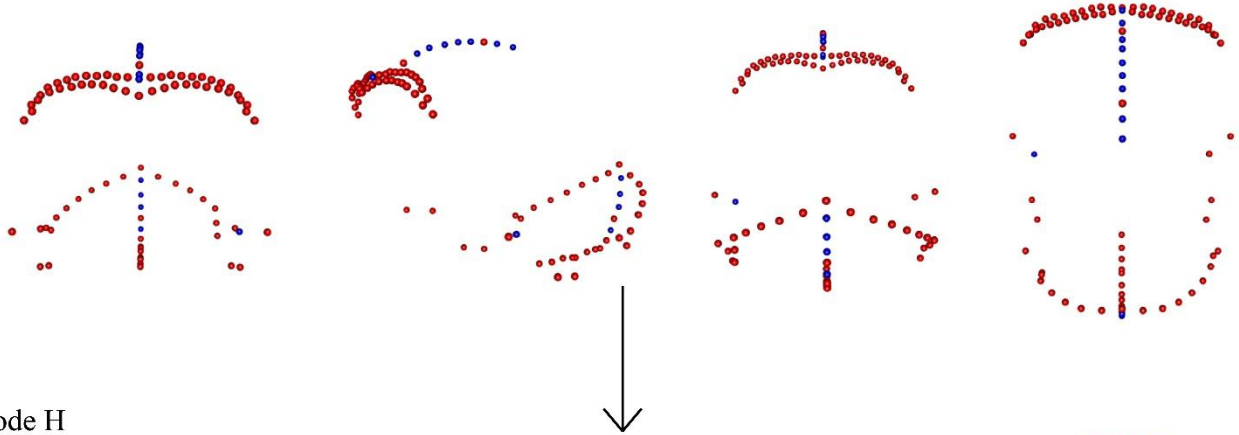
landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node G groups *A. afarensis* and *A. africanus* into a single clade, supported by a bootstrap value of 12%, five synapomorphies, and six landmark configurations (see Figure 71).

In *norma facialis* and *norma verticalis*, the outline of the supraorbital region is very similar to that of node F, though slightly straighter (#1). In *norma occipitalis*, the *planum occipitale* outline assumes a circular shape (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone displays the same convexity as in node F (#2), and the transition between the *planum occipitale* and *planum nuchale* remains identical (#3). Finally, the *processus mastoideus* exhibits a stronger downward development relative to the basicranium (#6), while the glenoid cavity is less deep than in node F (#7).

The five synapomorphies supporting this node include: (1) the presence of the *processus retromastoideus* (#31, state 2); (2) the appearance of a hollowed *sulcus supratoralis* (#34, state 2); (3) the disappearance of the *tuberculum lineare* (#38, state 1); (4) a change in the position of the auditory meatus relative to the *processus zygomaticus temporalis*, shifting from below (#47, state 1) to an intermediate position (#47, state 2); and (5) the presence of a marked *tuberculum zygomaticum anterius* (#54, state 2).

Node F



Node H

3D characters

Figure 72: 3D shapes showing morphological change for the landmark configurations from node F to node H. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

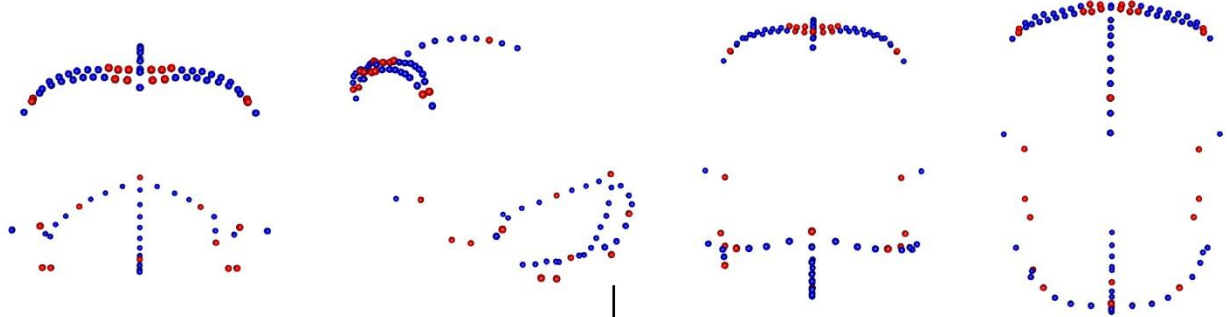
Node H groups *H. rudolfensis*, *H. habilis* (node I), Stw 53 (node J), the Dmanisi specimens (node K), and *H. erectus sensu lato* (node L). This node is supported by a bootstrap value of 7%, two synapomorphies, and seven landmark configurations (see Figure 72).

In *norma facialis* and *norma verticalis*, the supraorbital outline is straighter than in node F and exhibits a slight medial concavity at the glabella (#1). In *norma occipitalis*, both posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* outline maintains a triangular shape (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone is more convex than in node F

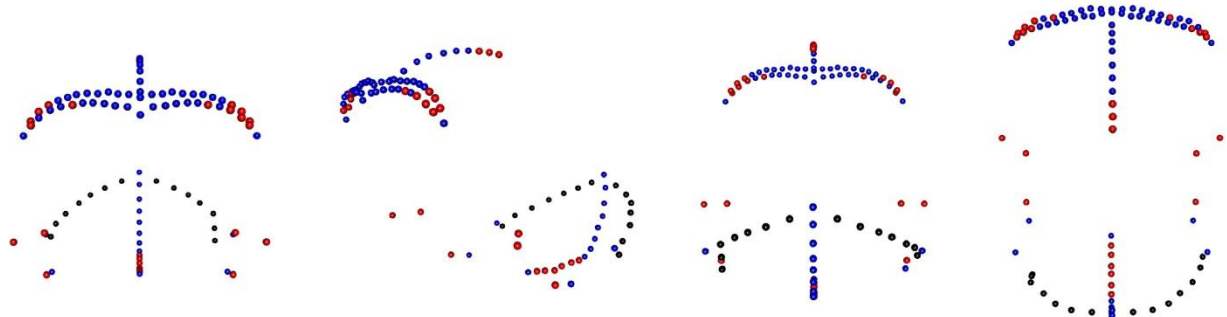
(#2), and the transition between the *planum occipitale* and *planum nuchale* is convex and rounded (#3), contrasting with the angular transition characteristic of node F. The *processus mastoideus* shows a weak downward development in relation to the basicranium (#6), and the glenoid cavity is shallower than in node F (#7).

The two synapomorphies supporting node H are: (1) a modification of the *torus occipitalis transversus* from bilaterally protruding (#35, state 3) to medially protruding (#35, state 2); and (2) a transition from a weakly marked development of the *crista supramastoidea* at the *porion* (#42, state 2) to a distinctly marked one (#42, state 3).

Node H



Node I



3D characters

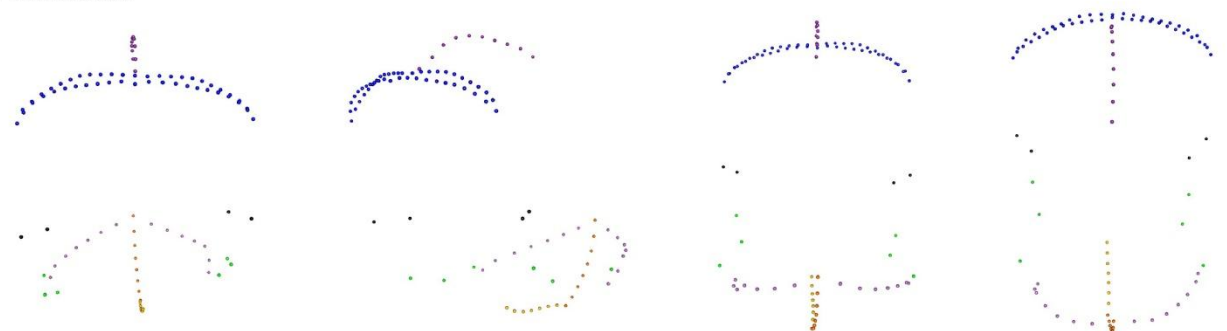


Figure 73: 3D shapes showing morphological change for the landmark configurations from node H to node I. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights

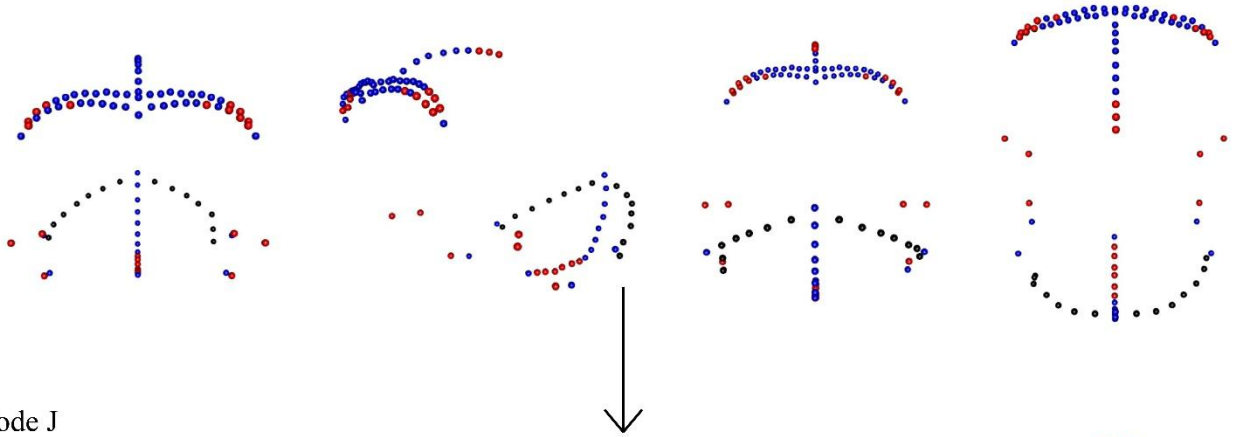
the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node I, corresponding to the *H. habilis* clade, is supported by a bootstrap value of 27%, six landmark configurations (see Figure 73), and one synapomorphy.

In *norma facialis* and *norma verticalis*, the supraorbital outline is almost identical to that of node H (#1). In *norma occipitalis*, the posterior and anterior occipital crests remain present and aligned (#5), and the *planum occipitale* retains its triangular outline (#4). In *norma lateralis*, the antero-posterior convexity of the frontal bone is slightly greater than in node H (#2), while the transition between the *planum occipitale* and *planum nuchale* remains rounded, with a gentle convexity (#3), similar to the condition in node H. The downward development of the *processus mastoideus* relative to the basicranium (#6) and the depth of the glenoid cavity (#7) are also comparable to those of node H.

The unique synapomorphy defining this node is the transition from an absent *sulcus postorbitalis* (#13, state 1) to a present and continuous one (#13, state 3).

Node I



Node J

3D characters

Figure 74: 3D shapes showing morphological change for the landmark configurations from node I to node J. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

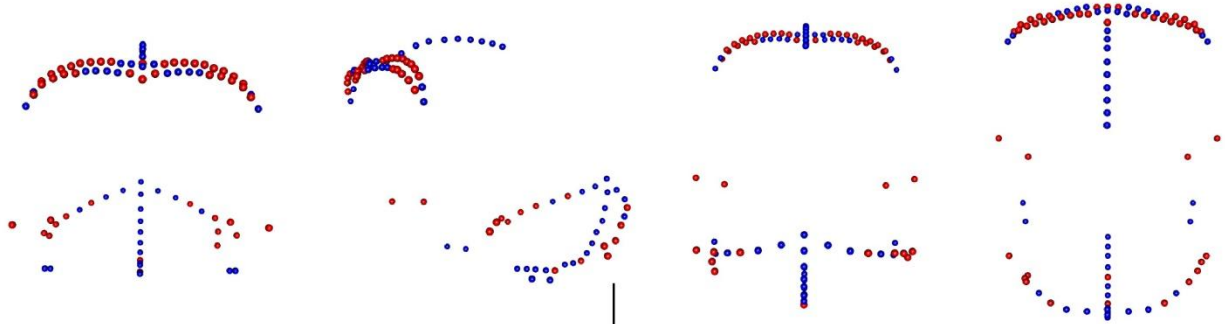
Node J is supported by a bootstrap value of 35%, two synapomorphies, and seven landmark configurations (see Figure 74).

In *norma facialis* and *norma verticalis*, the supraorbital region remains straight and medially concave at the glabella (#1). In *norma occipitalis*, both the posterior and anterior occipital crests are absent and therefore not aligned (#5), while the *planum occipitale* retains its triangular outline (#4). In *norma lateralis*, the antero-posterior convexity of the frontal bone is intermediate (#2), and the transition between the *planum occipitale* and *planum nuchale* is rounded, with a gentle convexity (#3), similar to

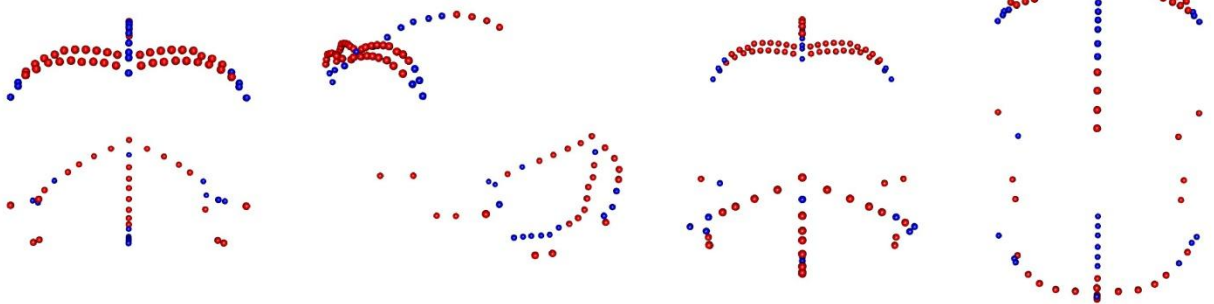
that observed in node I. The *processus mastoideus* shows a weak downward development relative to the basicranium (#6), and the glenoid cavity remains shallow (#7).

The two synapomorphies supporting this node are: (1) a more developed *planum nuchale* in comparison with the *planum occipitale* (#28, state 1); and (2) the presence of the *crista occipito-mastoidea* (#51, state 2).

Node J



Node K



3D characters

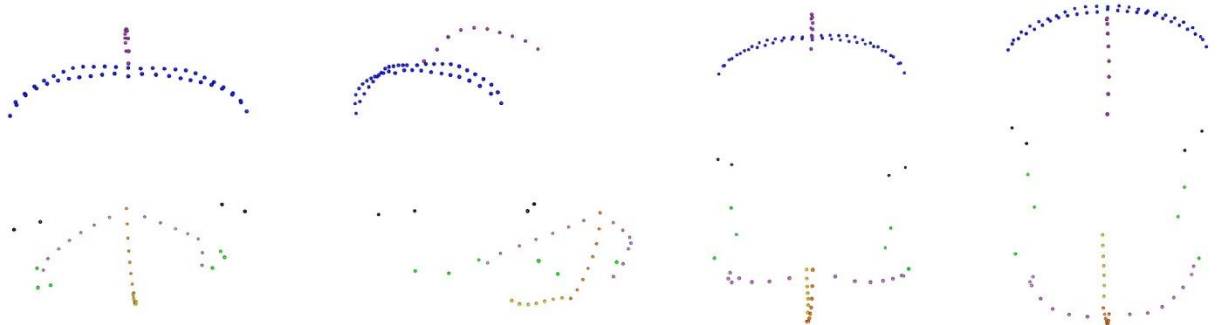


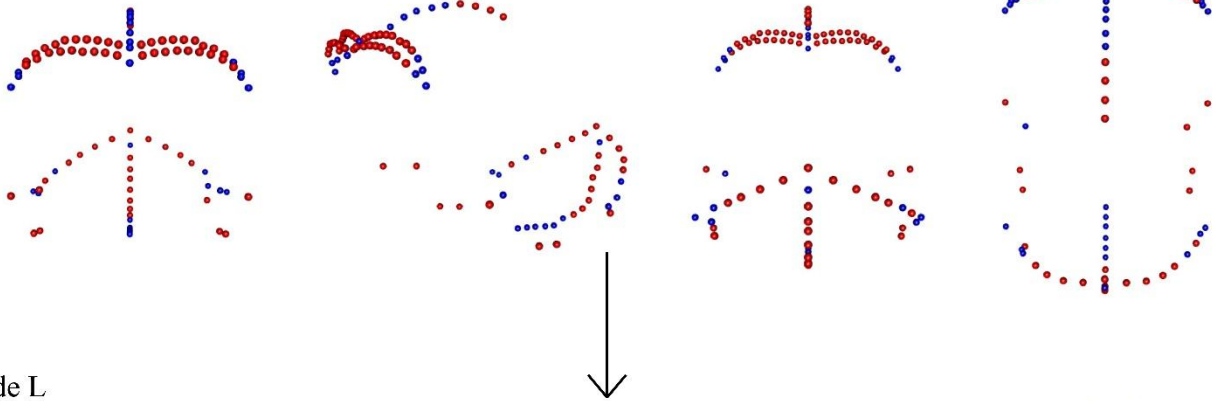
Figure 75: 3D shapes showing morphological change for the landmark configurations from node J to node K. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node K, which corresponds to the Dmanisi clade, is supported by a bootstrap value of 66%, seven landmark configurations (see Figure 75), and one synapomorphy.

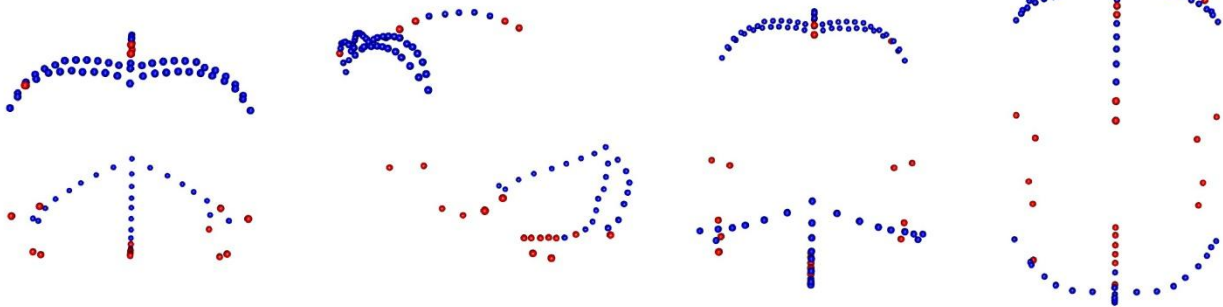
In *norma facialis* and *norma verticalis*, the supraorbital outline is more convex than in node J (#1). In *norma occipitalis*, the posterior and anterior occipital crests are present and aligned (#5), and the *planum occipitale* maintains a triangular shape, though less pronounced than in node J (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone is more convex than in node J (#2), and the transition between the *planum occipitale* and *planum nuchale* is rounded, with a slight convexity (#3), as also seen in node J. The *processus mastoideus* shows a stronger downward development relative to the basicranium (#6), and the glenoid cavity is deeper than in node J (#7).

The single synapomorphy characterizing this node is the presence of a closed anteriorly *sulcus supramastoideus* (#45, state 2).

Node K



Node L



3D characters

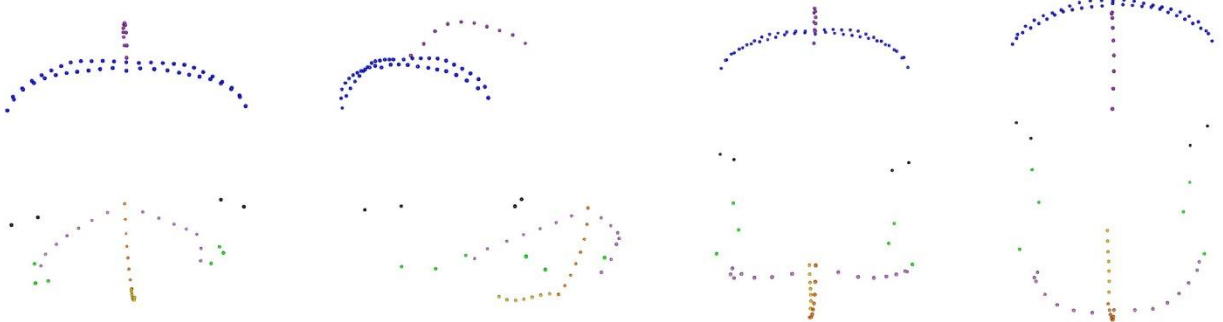


Figure 76: 3D shapes showing morphological change for the landmark configurations from node K to node L. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node L, comprising *H. ergaster*, the Sangiran specimens, Zhoukoudian, and Ngandong, is supported by a bootstrap value of 76%, seven landmark configurations (see Figure 76), and three synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline closely resembles that of node K (#1). In *norma occipitalis*, the posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* exhibits a more pronounced triangular outline than in node K (#4). In *norma lateralis*,

the antero-posterior convexity of the frontal bone is less marked (#2), and the transition between the *planum occipitale* and *planum nuchale* is less rounded than in node K (#3). The *processus mastoideus* shows a weaker downward development in relation to the basicranium (#6), while the glenoid cavity is deeper than that of node K (#7).

The three synapomorphies supporting this node are: (1) the presence of a thickening along the superior part of the coronal sutures (#20, state 2); (2) the presence of the *processus retromastoideus* (#31, state 2); and (3) the presence of a *sulcus supratoralis* (#34, state 3).

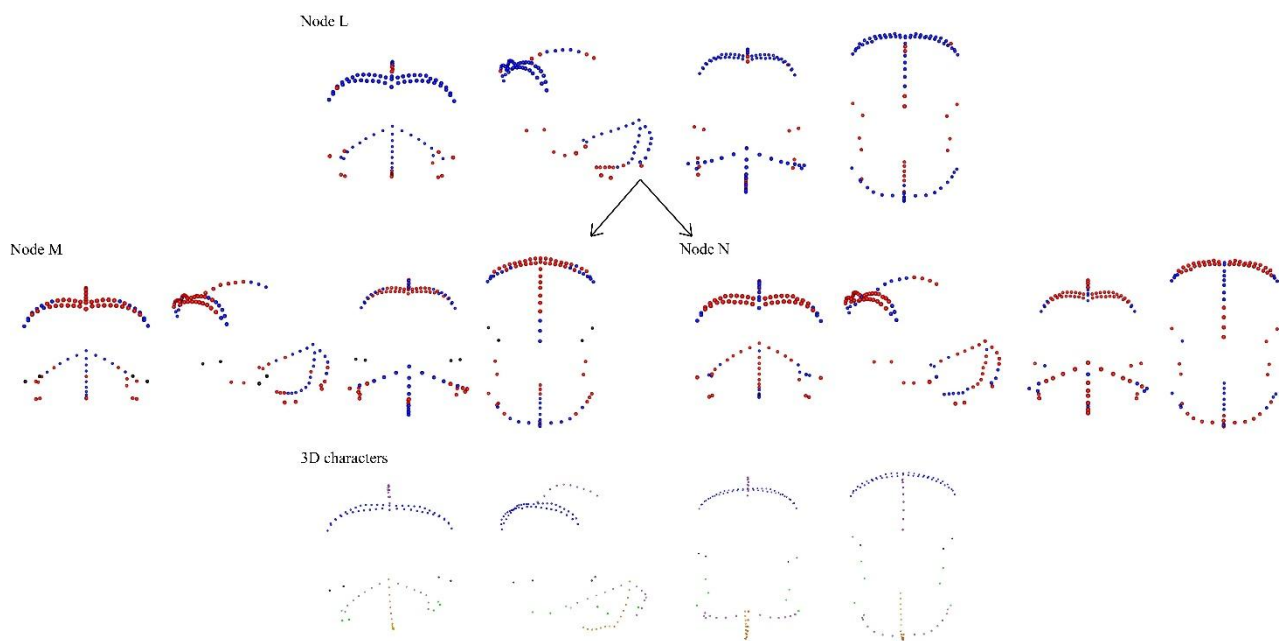


Figure 77: 3D shapes showing morphological change for the landmark configurations from node L to node M and N. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node M groups *H. ergaster* and the Sangiran specimens and is supported by a bootstrap value of 13%, six landmark configurations (see Figure 77), and one synapomorphy.

In *norma facialis* and *norma verticalis*, the supraorbital outline is convex (#1). In *norma occipitalis*, the posterior and anterior occipital crests remain present and aligned (#5), and the *planum occipitale* outline is very similar to that observed in node L (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone mirrors that of node L (#2), and the transition between the *planum occipitale* and

planum nuchale also resembles that seen in node L (#3). Finally, the downward development of the *processus mastoideus* in relation to the basicranium remains weak (#6).

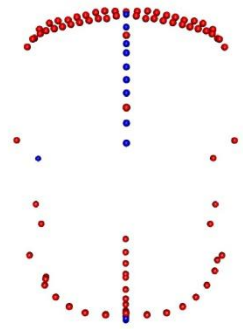
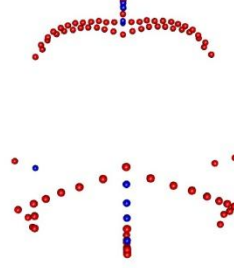
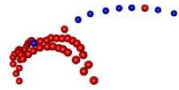
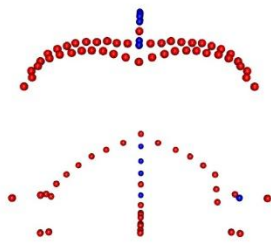
The single synapomorphy supporting this node corresponds to a change in the width of the *linea temporalis* along the parietal band, shifting from narrow (#24, state 2) to wide (#24, state 3).

Node N groups the Zhoukoudian and Ngandong specimens and is supported by a bootstrap value of 69%, seven landmark configurations, and two synapomorphies.

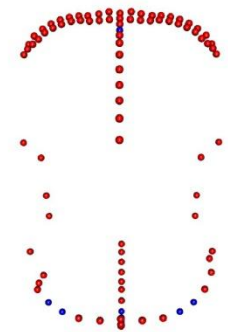
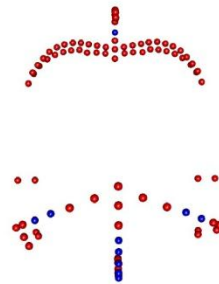
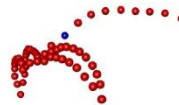
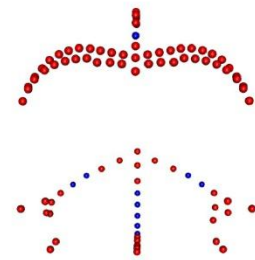
In *norma facialis* and *norma verticalis*, the supraorbital outline is straight (#1). In *norma occipitalis*, both posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* maintains a triangular shape, slightly rounder than that observed in node L (#4). In *norma lateralis*, the antero-posterior convexity of the frontal bone is greater than in node L (#2), and the transition between the *planum occipitale* and *planum nuchale* is slightly rounder (#3), contrasting with the less rounded transition of node L. The *processus mastoideus* shows a stronger downward development relative to the basicranium (#6), and the glenoid cavity is deeper than in node L (#7).

The two synapomorphies defining this node correspond to: (1) a reduction in postorbital constriction, from marked (#12, state 1) to weak (#12, state 2); and (2) the presence of a bony bridge in the digastric groove (#50, state 2).

Node F



Node O



3D characters

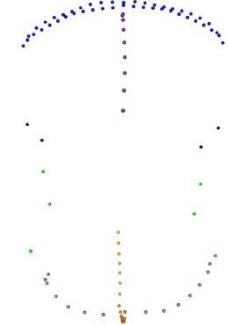
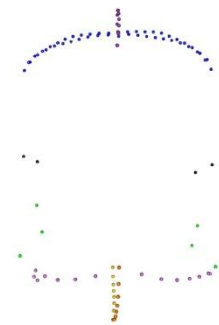
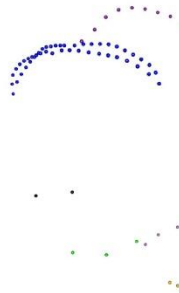
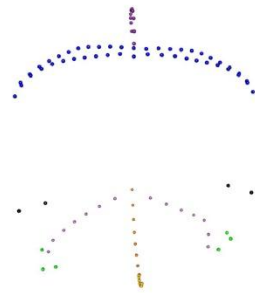


Figure 78: 3D shapes showing morphological change for the landmark configurations from node F to node O. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

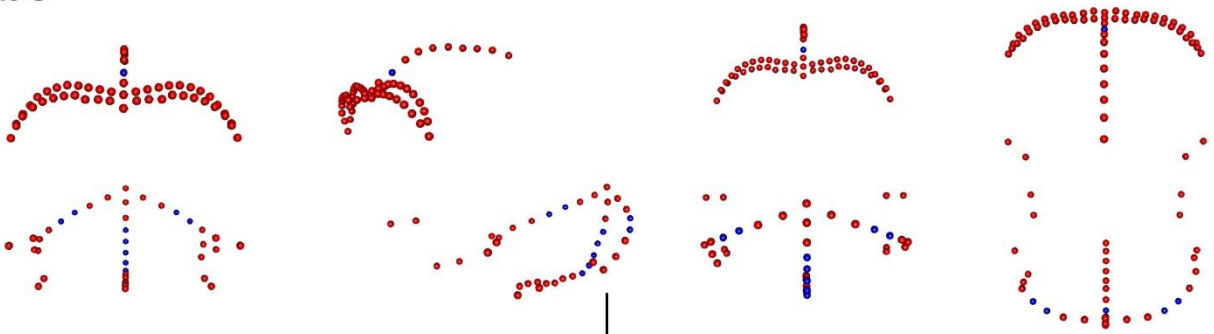
Node O groups *H. neandertalensis* and *H. sapiens* into a monophyletic clade. It is supported by a bootstrap value of 71%, seven landmark configurations (see Figure 78), and seven synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline is more convex than in node F (#1). In *norma occipitalis*, the posterior and anterior occipital crests are present but not aligned (#5), while the *planum occipitale* maintains a triangular outline (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone is more convex (#2), and the transition between the *planum occipitale* and *planum nuchale* is rounder (#3) than in node F. The *processus mastoideus* displays a stronger downward

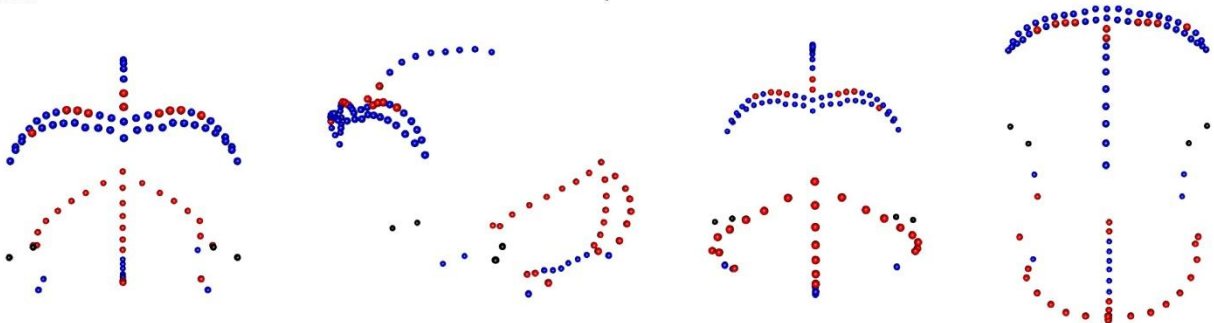
development relative to the basicranium (#6), while the glenoid cavity is shallower than in node F (#7).

The seven synapomorphies supporting node O include the absence of postorbital constriction (#12, state 3); the presence of a continuous *sulcus postorbitalis* (#13, state 3); the presence of *tuber frontale* (#14, state 3); a low position of the *linea temporalis* on the parietal (#25, state 3); a distinct relative position of the *inion* and *opisthocranium* (#30, state 2); a curved or sinuous outline of the superior border of the temporal squama (#41, state 1); and the presence of a *sulcus supramastoideus* (#45, state 3).

Node O



Node P



3D characters

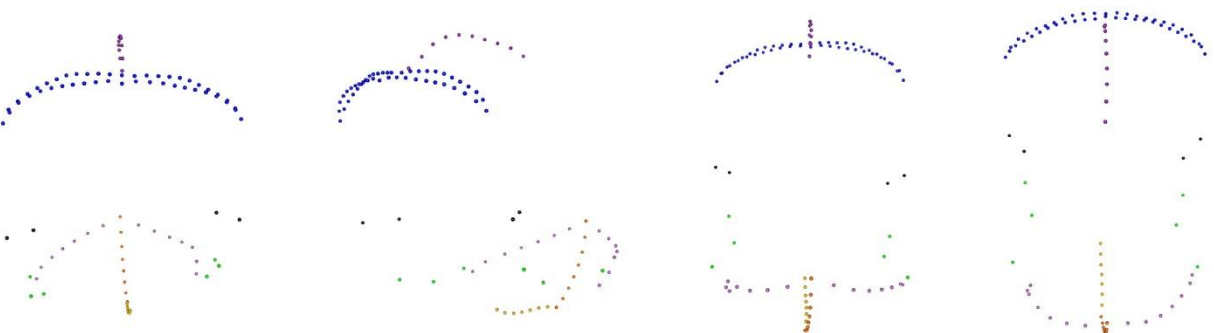


Figure 79: 3D shapes showing morphological change for the landmark configurations from node O to node P. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights

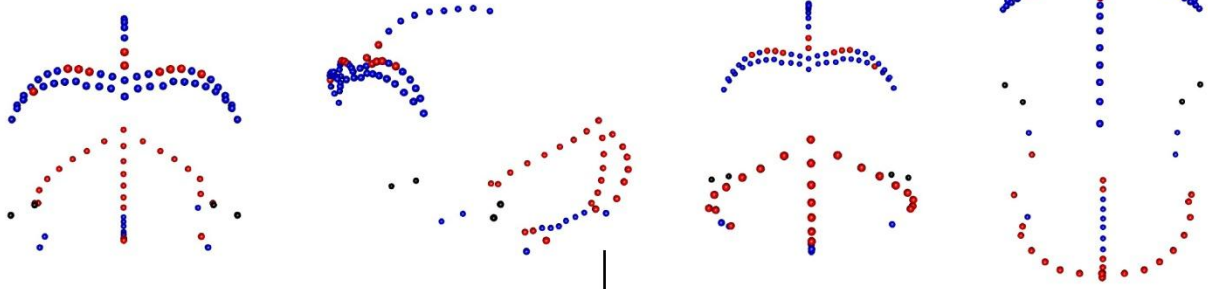
the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node P corresponds to the monophyletic grouping of *H. neandertalensis*, which includes the three OTUs “Early Neandertal,” “Classic Neandertal,” and “Near East Neandertal.” The latter two form a subclade at node Q. Node P is supported by a bootstrap value of 81%, six landmark configurations (see Figure 79), and two synapomorphies.

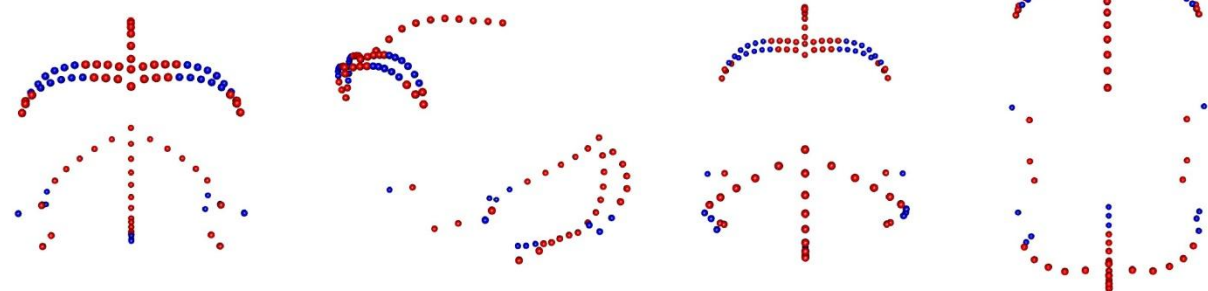
In *norma facialis* and *norma verticalis*, the outline of the supraorbital region is very similar to that observed in node O (#1). In *norma occipitalis*, both posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* adopts a more circular shape compared to node O (#4). In *norma lateralis*, the antero-posterior profile of the frontal bone exhibits the same degree of convexity as in node O (#2), but the transition between the *planum occipitale* and *planum nuchale* is rounder (#3). Finally, the *processus mastoideus* shows a slightly stronger downward development relative to the basicranium (#6).

The two synapomorphies supporting this node are: (1) the presence of a *fossa suprainiac* (#32, state 3); and (2) upward-convergent lateral edges of this fossa (#33, state 2).

Node P



Node Q



3D characters

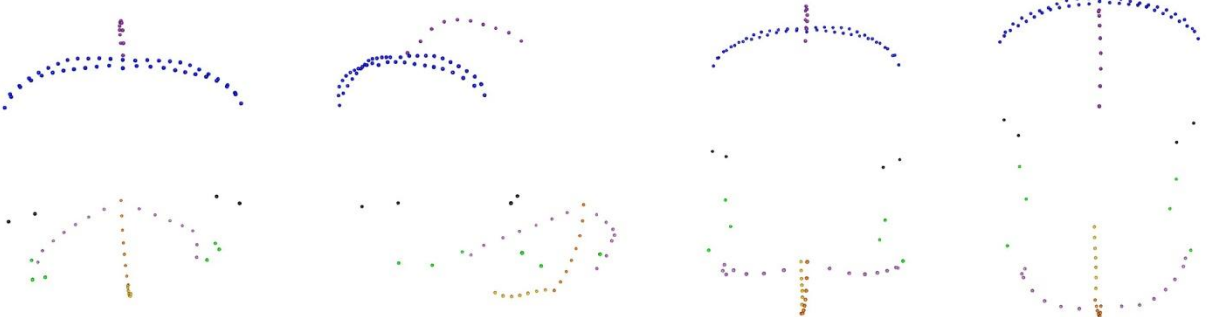


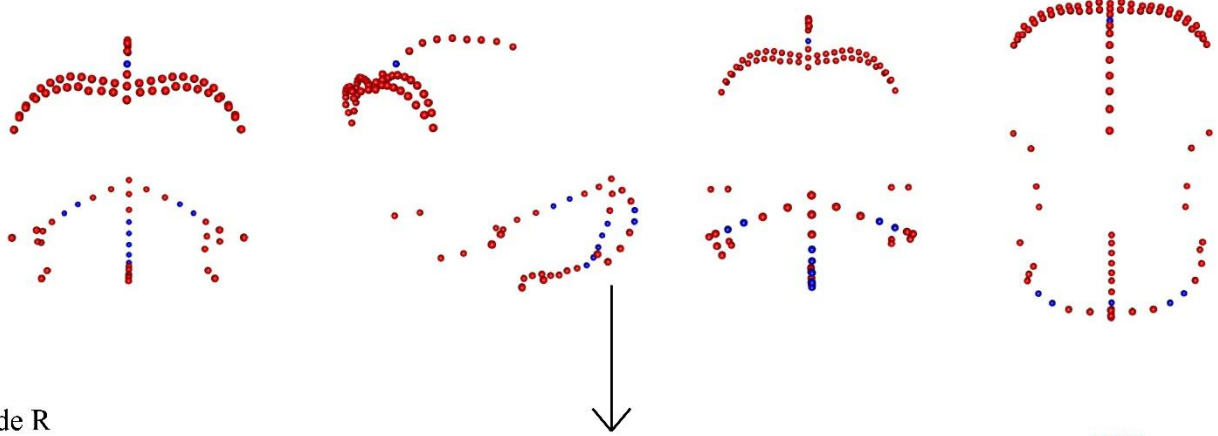
Figure 80: 3D shapes showing morphological change for the landmark configurations from node P to node Q. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node Q groups the “Classic Neandertal” and “Near East Neandertal” specimens and is supported by a bootstrap value of 37% and seven landmark configurations (see Figure 80).

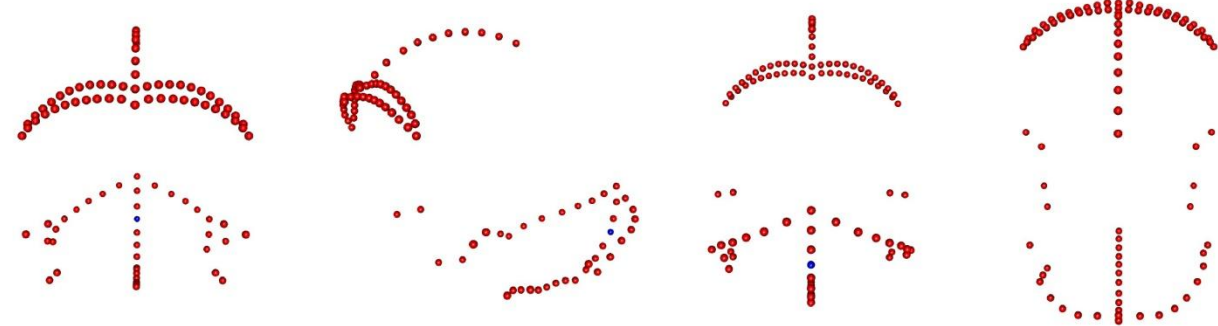
From node P to node Q, we observe six morphological changes affecting the landmark configurations. In *norma facialis* and *norma verticalis*, the supraorbital region becomes even more convex than in node P (#1). In *norma occipitalis*, both posterior and anterior occipital crests remain present but are not aligned (#5), while the *planum occipitale* assumes a more circular outline than in node P (#4). In *norma lateralis*, the antero-posterior convexity of the frontal bone is slightly reduced

(#2), and the transition between the *planum occipitale* and *planum nuchale* is smoothly rounded (#3). Finally, the *processus mastoideus* exhibits weaker downward development in relation to the basicranium (#6), and the glenoid cavity is shallower than in node P (#7).

Node O



Node R



3D characters

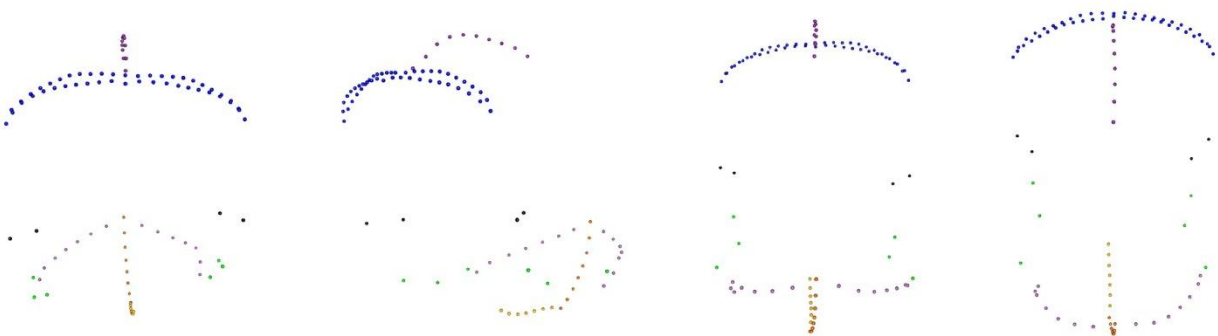


Figure 81: 3D shapes showing morphological change for the landmark configurations from node O to node R. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node R corresponds to the monophyletic clade of *H. sapiens*, supported by a bootstrap value of 90%, seven landmark configurations (see Figure 81), and five synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline is convex (#1). In *norma occipitalis*, both the posterior and anterior occipital crests are absent (#5), and the *planum occipitale* outline takes on a pentagonal shape (#4). In *norma lateralis*, the frontal bone shows strong antero-posterior convexity (#2), while the transition between the *planum occipitale* and *planum nuchale* is smooth, rounded, and convex (#3). The *processus mastoideus* exhibits strong downward development relative to the basicranium (#6), and the glenoid cavity is shallower than in node O (#7).

The five synapomorphies supporting this clade are the presence of a complete supraorbital region (#10, state 1); the absence of the *torus occipitalis transversus* (#35, state 1; #36, state 1); an antero-posterior convex configuration of the articular tubercle (#53, state 2); and an absent to weakly marked *tuberculum zygomaticum posterius* (#55, state 1).

II.2.3. RI – weighting

The RI-weighted tree largely mirrors the topology of the CI-weighted reconstruction but presents notable differences in bootstrap support and a few node-specific adjustments that affect the internal resolution of *Homo* and *Australopithecus* clades.

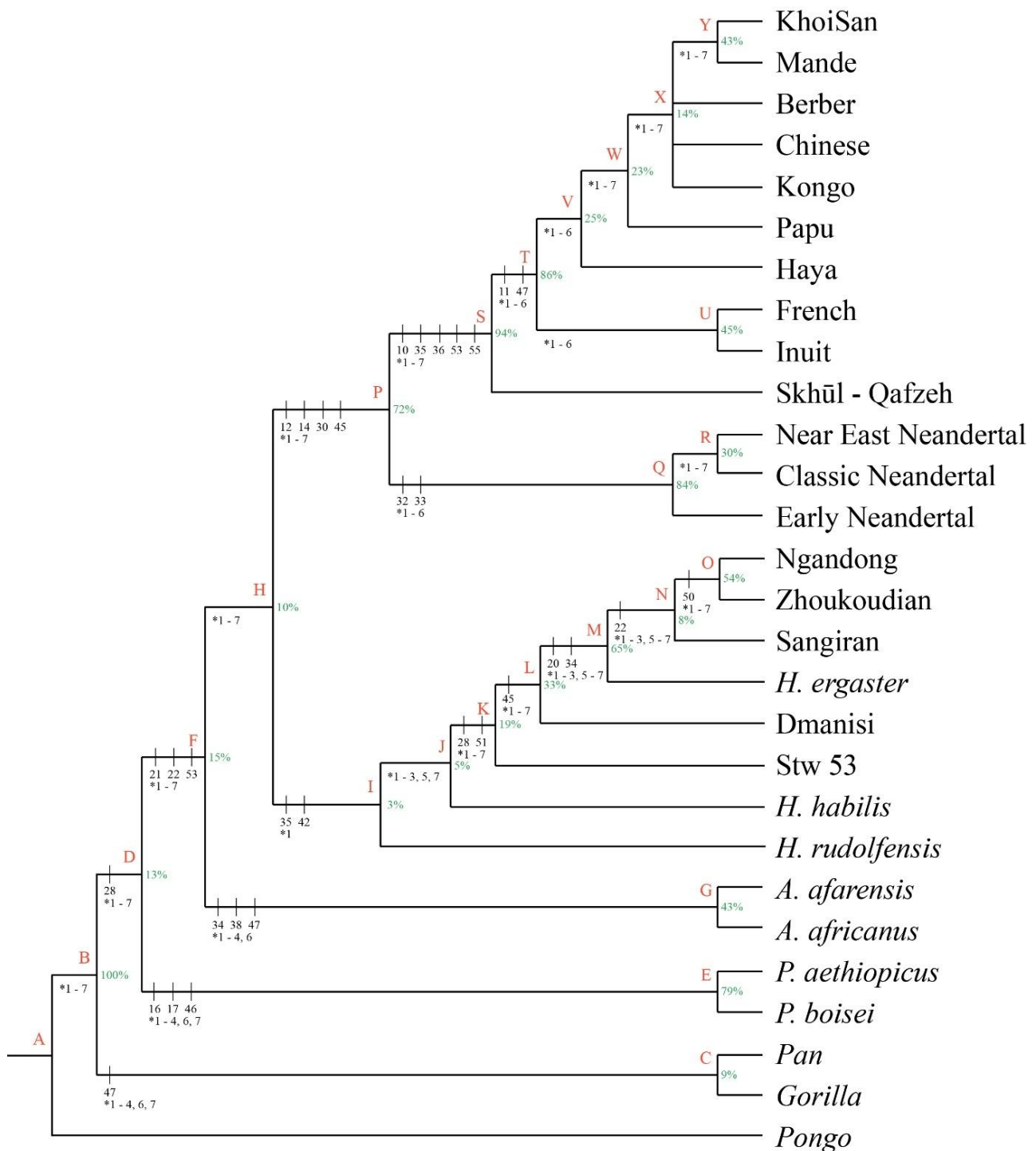


Figure 82: Unique phylogenetic tree based on the analysis of matrix E after RI-weighting (i.e., 7 landmarks configurations and 50 morphological characters and 28 OTUs), 9449.663 steps (CI = 0.478 and RI = 0.785). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

Node D supports the monophyly of the in-group, sustained by a bootstrap value of 13%. Morphological variation is illustrated by the seven 3D shape configurations (see Figures 82 – 84 and Appendix 24) and by a single synapomorphy.

Regarding 3D shape variation, the overall morphology is identical to that of the CI-weighted tree. In *norma verticalis* and *norma facialis*, the supraorbital region exhibits a straight outline (#1). In *norma occipitalis*, both posterior and anterior occipital crests are present and aligned (#5), while the *planum occipitale* adopts a triangular contour (#4). In *norma lateralis*, the frontal bone shows a slightly more convex antero-posterior profile than in apes, though convexity remains weak (#2). The transition between the *planum occipitale* and *planum nuchale* is angular, resembling the condition observed in apes (#3). The *processus mastoideus* displays a similar degree of downward development relative to the basicranium (#6), and the glenoid cavity is marginally deeper than in apes (#7).

The sole synapomorphy observed at this node corresponds to a more developed *planum nuchale* relative to the *planum occipitale* (#28, state 1), which later evolves toward the opposite condition, a more developed *planum occipitale* (#28, state 2).

Node E unites the two *Paranthropus* OTUs into the same monophyletic group, supported by an increased bootstrap value of 79%, six landmark configurations, and three synapomorphies (compared with five in the CI-weighted tree).

The 3D shape patterns remain consistent: in *norma verticalis*, the supraorbital region transitions from the straight outline of node D to a slightly bulged form at the glabella, while *norma facialis* presents a more rounded contour (#1). In *norma occipitalis*, the *planum occipitale* retains its triangular outline (#4). In *norma lateralis*, the frontal bone becomes more convex than in node D (#2), and the transition between the *planum occipitale* and *planum nuchale* appears slightly rounder (#3), contrasting with the sharper angular junction previously observed. The *processus mastoideus* displays a stronger downward projection relative to the basicranium (#6), and the glenoid cavity deepens further (#7).

The three synapomorphies supporting this node are: (1) the appearance of a sagittal crest (#16, state 2); (2) the emergence of a sagittal keel on the frontal bone (#17, state 2), both previously absent (#16, state 1; #17, state 1); and (3) a modification of the auditory meatus from circular (#46, state 1) to elliptical (#46, state 2).

Node F marks the divergence between two main lineages: on one side, the *A. afarensis*–*A. africanus* clade (node G), and on the other, a lineage encompassing *H. rudolfensis*, *H. habilis*, Stw 53, the Dmanisi fossils, *H. erectus s. l.*, *H. neandertalensis*, and *H. sapiens* (nodes H–S). This node is supported by a bootstrap value of 15%, seven landmark configurations, and three synapomorphies.

The seven landmark configurations show patterns similar to those in previous nodes (see Figure 70). In *norma facialis* and *norma verticalis*, the supraorbital region maintains a straight outline (#1). In *norma occipitalis*, both occipital crests are present and aligned (#5), while the *planum occipitale* outline becomes more circular than in node D (#4). In *norma lateralis*, the frontal bone displays a stronger antero-posterior convexity (#2), and the transition between the *planum occipitale* and *planum nuchale* is rounder and more convex (#3), contrasting with the angular condition of node D. The *processus mastoideus* exhibits a slightly more pronounced downward development (#6), and the glenoid cavity remains shallow (#7).

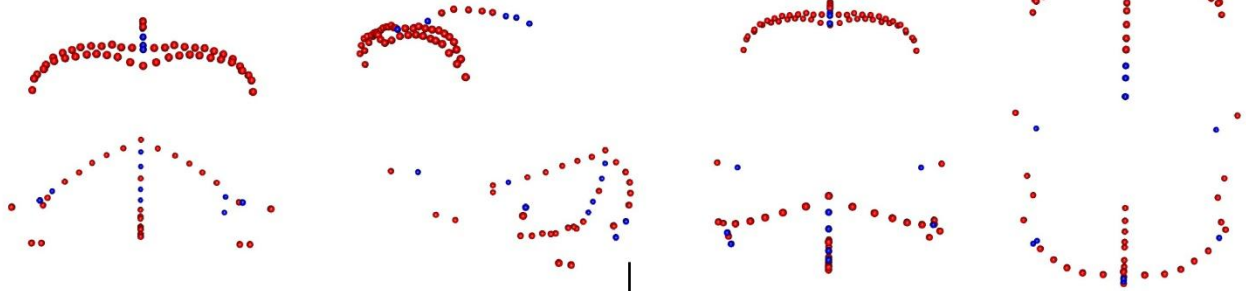
The three synapomorphies correspond to: (1) disappearance of the sagittal keel on the *bregma-lambda* arch (#21, state 1); (2) loss of parasagittal hollowing along the parietal suture (#22, state 1); and (3) a change in the articular tubercle configuration, shifting from an antero-posterior convexity (#53, state 2) to a medio-lateral concavity (#53, state 1).

Node G unites *Australopithecus afarensis* and *A. africanus* in a single clade supported by a bootstrap value of 43%, six landmark configurations, and three synapomorphies (reduced from four in the CI-weighted tree).

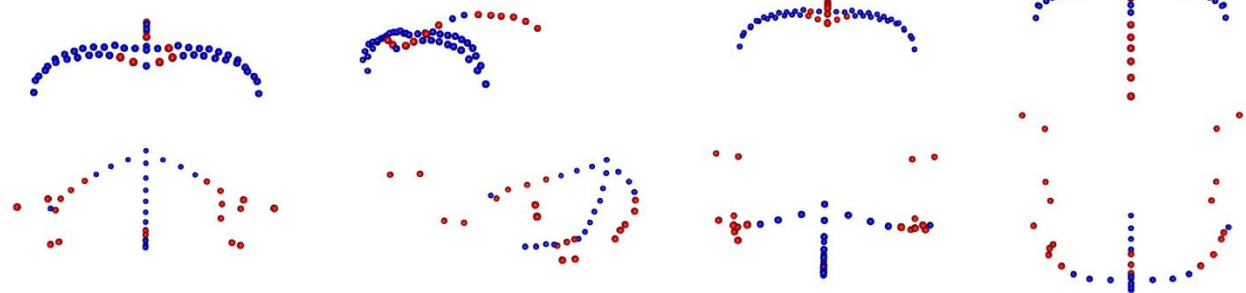
In *norma facialis* and *norma verticalis*, the supraorbital region resembles that of node F but appears slightly straighter (#1). In *norma occipitalis*, the *planum occipitale* assumes a circular outline (#4). In *norma lateralis*, the frontal bone retains the same antero-posterior convexity as in node F (#2), and the transition between the *planum occipitale* and *planum nuchale* remains unchanged (#3). The *processus mastoideus* exhibits a more marked downward projection relative to the basicranium (#6), while the glenoid cavity is shallower than in node F (#7).

The three synapomorphies supporting this clade include: (1) development of a hollowed *sulcus supratoralis* (#34, state 2); (2) loss of the *tuberculum lineare* (#38, state 1); and (3) a positional shift of the auditory meatus relative to the *processus zygomaticus temporalis*, from a lower position (#47, state 1) to an intermediate one (#47, state 2).

Node F



Node H



3D characters

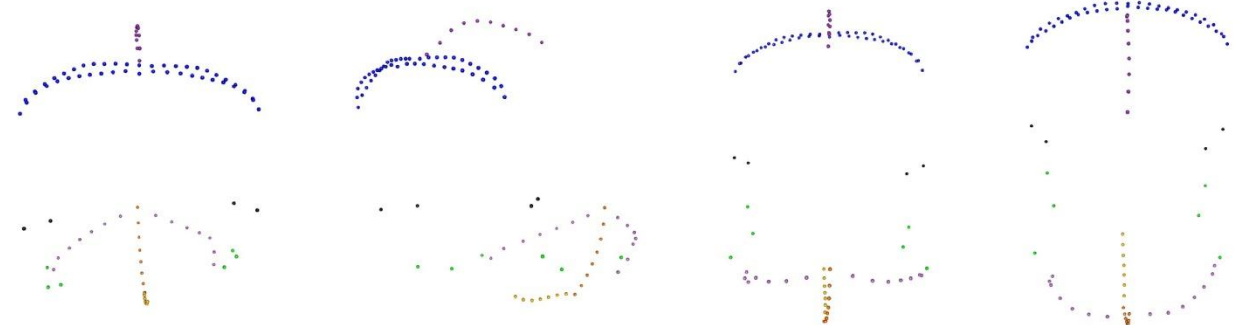


Figure 83: 3D shapes showing morphological change for the landmark configurations from node F to node H. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

Node H represents the basal divergence within *Homo*, derived from node F. It groups on one side *H. rudolfensis* (node I), *H. habilis* (node J), Stw 53 (node K), the Dmanisi fossils (node L), and *H. erectus* sensu lato (node M), and on the other side in node P, *H. neandertalensis* and *H. sapiens*. This node is supported by a bootstrap value of 10% and variation across the seven landmark configurations (see Figure 83).

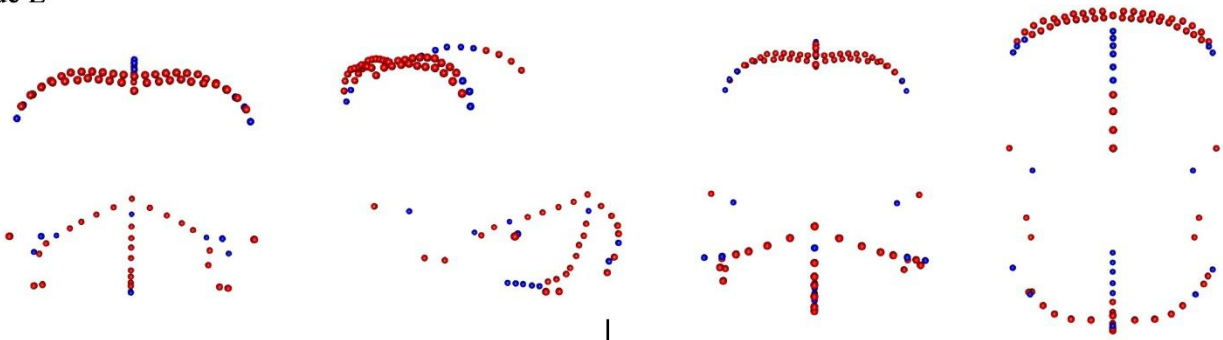
In *norma facialis* and *norma verticalis*, the supraorbital outline remains straight (#1). In *norma occipitalis*, both occipital crests are present and aligned (#5), and the *planum occipitale* outline becomes

more circular than in node F (#4). In *norma lateralis*, the frontal bone exhibits increased convexity (#2), while the transition between the *planum occipitale* and *planum nuchale* is rounder and more convex (#3). The *processus mastoideus* displays slightly stronger downward development (#6), and the glenoid cavity remains shallow (#7).

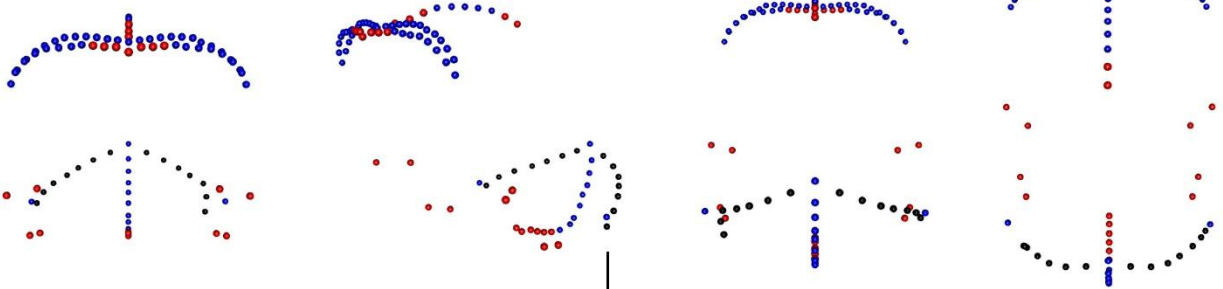
Nodes I through L correspond topologically to their equivalents in the CI-weighted analysis, with bootstrap values of 3%, 5%, 19%, and 33%, respectively.

- Node I retains the two synapomorphies (#35, state 2; #42, state 2), and one landmark change: in *norma facialis* and *norma verticalis*, the supraorbital outline becomes slightly straighter with a weak medial concavity at the glabella (#1).
- Node J preserves the same landmark changes but loses the synapomorphy recorded in the CI-weighted tree.
- Nodes K and L show identical morphological changes to their CI-weighted counterparts.

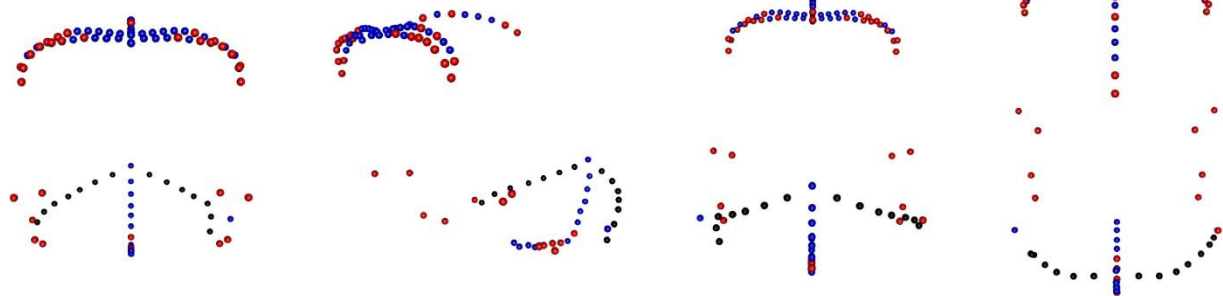
Node L



Node M



Node N



3D characters

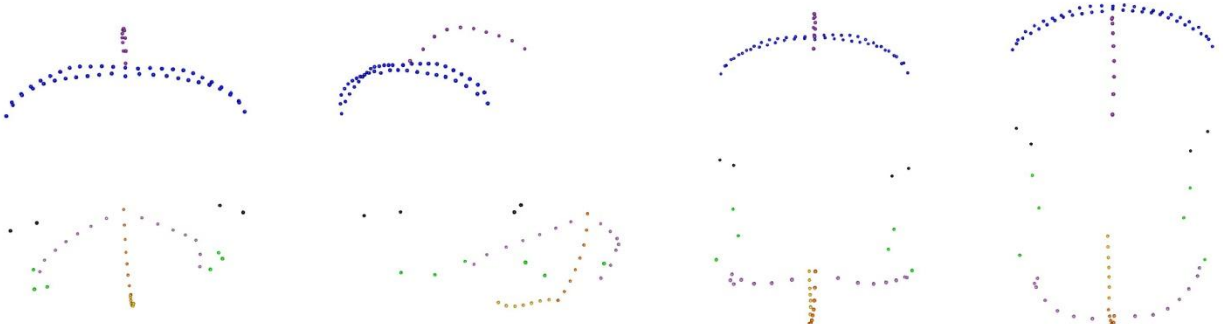


Figure 84: 3D shapes showing morphological change for the landmark configurations from node L to node M and N. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a

landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

In this RI-weighted analysis, node M represents *H. erectus sensu lato*, encompassing *H. ergaster* in a basal position, followed by the Sangiran fossils, and culminating in node O, grouping Zhoukoudian and Ngandong specimens. Node M (*H. ergaster*) is supported by a bootstrap value of 65%, six landmark configurations (see Figure 84), and two synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline closely resembles that of node L, though slightly straighter (#1). In *norma occipitalis*, only the posterior occipital crest persists (#5). In *norma lateralis*, the frontal bone maintains similar convexity (#2), and the transition between the *planum occipitale* and *planum nuchale* is marginally rounder (#3). The *processus mastoideus* exhibits pronounced downward development (#6), and the glenoid cavity is deeper than in node L (#7).

The two synapomorphies defining this node are: (1) thickening of the superior part of the coronal sutures (#20, state 2); and (2) presence of a *sulcus supratoralis* (#34, state 3).

Node N (Sangiran) is supported by a bootstrap value of 8%, six landmark configurations, and one synapomorphy. Morphologically, the supraorbital outline remains similar to node M but slightly straighter (#1); both occipital crests are aligned (#5); the frontal profile and occipital–nuchal transition are unchanged (#2, #3); the *processus mastoideus* shows weaker downward projection (#6); and the glenoid cavity is shallower (#7).

The single synapomorphy here is the development of parasagittal hollowing along the parietal suture (#22, state 2).

Node O, representing Zhoukoudian and Ngandong, forms the terminal clade of *H. erectus sensu lato*. It is supported by a bootstrap value of 54%, seven landmark configurations, and one synapomorphy. The 3D shape variation mirrors that of the CI-weighted tree: the supraorbital outline is straight (#1); both occipital crests are aligned (#5); the *planum occipitale* retains a triangular but slightly rounder shape than in node N (#4); the frontal convexity increases (#2); and the *planum occipitale–nuchale* transition becomes rounder (#3). The *processus mastoideus* shows stronger downward development (#6), and the glenoid cavity is deeper (#7).

The defining synapomorphy is the presence of a bony bridge in the digastric groove (#50, state 2).

Node P unites *H. neandertalensis* and *H. sapiens* in a monophyletic clade derived from the lineage originating at node H. This node is supported by a bootstrap value of 72%, the same seven landmark configurations as in node O of the CI-weighted tree, and four synapomorphies.

The landmark configurations mirror those previously described. In *norma facialis* and *norma verticalis*, the supraorbital outline appears more convex than in node H (#1). In *norma occipitalis*, both posterior and anterior occipital crests are present but not aligned (#5), while the *planum occipitale* retains a triangular outline (#4). In *norma lateralis*, the frontal bone shows stronger antero-posterior convexity (#2), and the transition between the *planum occipitale* and *planum nuchale* is rounder than in node H (#3). The *processus mastoideus* exhibits greater downward development relative to the basicranium (#6), while the glenoid cavity becomes shallower (#7).

The four synapomorphies supporting this node are the absence of postorbital constriction (#12, state 3); the presence of a *tuber frontale* (#14, state 3); a distinct relative positioning of the inion and opisthocranium (#30, state 2); and the presence of a *sulcus supramastoideus* (#45, state 3).

Node Q corresponds to the monophyletic grouping of *H. neandertalensis*, encompassing the three OTUs “Early Neandertal,” “Classic Neandertal,” and “Near East Neandertal.” The latter two form a subclade at node R. Node Q is supported by a bootstrap value of 84%, six landmark configurations, and two synapomorphies.

The 3D landmark configuration changes are identical to those at node P in the CI-weighted tree. In *norma facialis* and *norma verticalis*, the supraorbital outline resembles that of node P (#1). In *norma occipitalis*, both occipital crests are present and aligned (#5), while the *planum occipitale* becomes more circular compared with node P (#4). In *norma lateralis*, the frontal bone maintains the same degree of convexity (#2), but the transition between the *planum occipitale* and *planum nuchale* appears rounder (#3). Finally, the *processus mastoideus* exhibits slightly stronger downward development relative to the basicranium (#6).

The two synapomorphies defining this node are the same as those observed at node P in the CI-weighted tree: presence of a *fossa suprainiac* (#32, state 3) and upward-convergent lateral edges of that fossa (#33, state 2).

Node R groups the “Classic Neandertal” and “Near East Neandertal” specimens. It is supported by a bootstrap value of 30% and by changes in the seven landmark configurations identical to those observed at node Q in the CI-weighted tree.

Relative to node Q, this node exhibits general morphological trends: in *norma facialis* and *norma verticalis*, the supraorbital region becomes even more convex (#1). In *norma occipitalis*, both occipital crests remain present but unaligned (#5), while the *planum occipitale* assumes an even more circular outline (#4). In *norma lateralis*, the frontal bone's antero-posterior convexity is slightly reduced (#2), and the *planum occipitale*–*planum nuchale* transition is smoothly rounded (#3). The *processus mastoideus* shows weaker downward development relative to the basicranium (#6), and the glenoid cavity becomes shallower (#7).

Node S corresponds to the monophyletic clade of *H. sapiens* (node R in the CI-weighted analysis), supported by a bootstrap value of 94%, seven landmark configurations, and five synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline is distinctly convex (#1). In *norma occipitalis*, both the posterior and anterior occipital crests are absent (#5), and the *planum occipitale* assumes a pentagonal outline (#4). In *norma lateralis*, the frontal bone shows pronounced antero-posterior convexity (#2), and the transition between the *planum occipitale* and *planum nuchale* is smooth, rounded, and fully convex (#3). The *processus mastoideus* presents strong downward development relative to the basicranium (#6), while the glenoid cavity is shallower than in node O (#7).

The five synapomorphies defining this clade are identical to those from the CI-weighted analysis: presence of a complete supraorbital region (#10, state 1); absence of the *torus occipitalis transversus* (#35, state 1; #36, state 1); antero-posteriorly convex configuration of the articular tubercle (#53, state 2); and absence or weak development of the *tuberculum zygomaticum posterius* (#55, state 1).

II.2.4. RC – weighting

Compared to the CI- and RI-weighted analyses, the RC-weighted tree displays a broadly similar overall structure but introduces several notable topological adjustments. While the basal arrangement of major hominin clades remains consistent, with the in-group monophyly preserved at node D and *Paranthropus* forming a stable monophyletic group, the internal relationships within *Homo* show minor rearrangements. The positions of *H. rudolfensis* and *H. habilis* remain closely associated, as well as the placement of Stw 53 and the Dmanisi fossils, suggesting a stable branching patterns of early *Homo*. Within *H. erectus* sensu lato, the relationships among the African (*H. ergaster*), Javan (Sangiran), and Chinese (Zhoukoudian and Ngandong) specimens stay stratified as in the RI-weighted tree, forming a sequential series rather than a compact cluster, with only the inversion of

H. ergaster and Sangiran, the latter gaining a basal position. Finally, the Neandertal and modern human clades retain their monophyletic status with comparable synapomorphic support, though their connecting branch to earlier *Homo* nodes exhibits stronger resolution than in the RC-weighted topology.

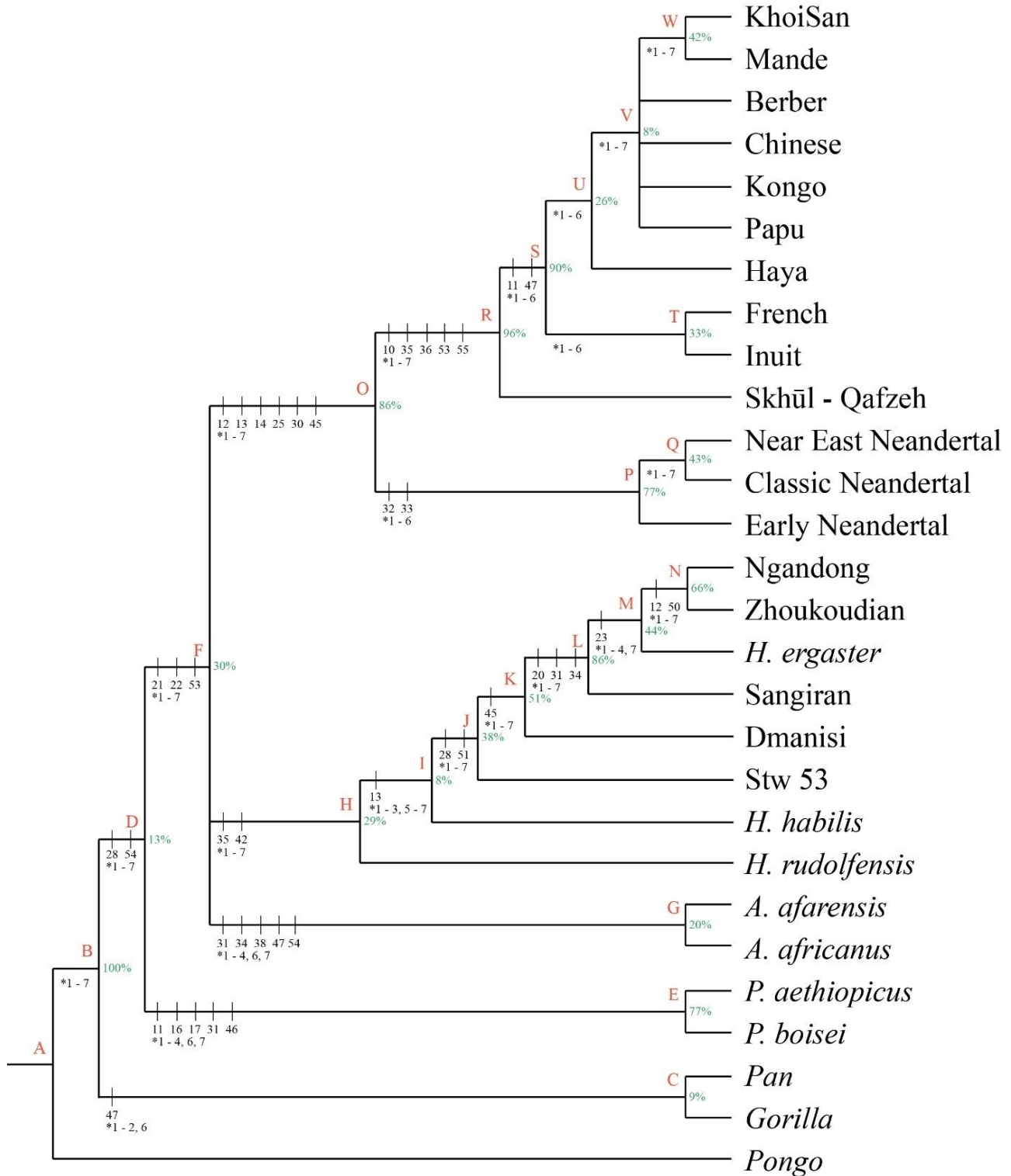


Figure 85: Unique phylogenetic tree based on the analysis of matrix E after RC-weighting (i.e., 7 landmarks configurations and 50 morphological characters and 28 OTUs), 4554.438 steps (CI = 0.567 and RI = 0.842).

Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

Node D, supporting the monophyly of the in-group, is sustained by a bootstrap value of 13%. Morphological variation is expressed across the seven 3D shape configurations (see Figures 85 - 86 and Appendix 25) and two synapomorphies, both identical to those recovered in the CI-weighted analysis.

At node E, the two *Paranthropus* OTUs form a monophyletic clade with stronger support (77%), characterized by five synapomorphies and six landmark configurations. The overall morphology mirrors that observed for node E in the CI-weighted tree, indicating stability of diagnostic cranial traits within *Paranthropus*.

Node F again reveals a large, unresolved polytomy that fails to clarify relationships among *Australopithecus* and early *Homo* taxa. It is supported by a bootstrap value of 30%, seven landmark configurations, and three synapomorphies, all identical to those in the CI-weighted topology.

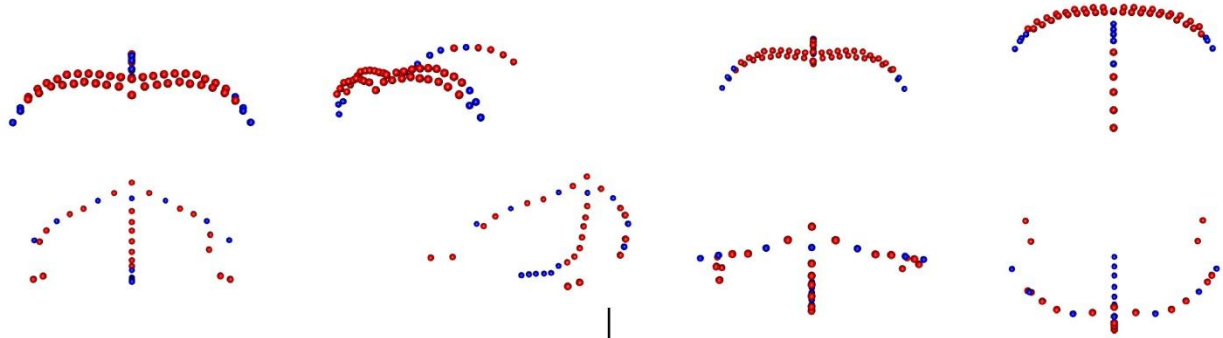
Node G groups *A. afarensis* and *A. africanus* within a single clade, supported by a bootstrap value of 26%, five synapomorphies, and six landmark configurations, all consistent with node G in the CI-weighted tree.

Node H unites *H. rudolfensis*, *H. habilis* (node I), Stw 53 (node J), the Dmanisi specimens (node K), and *H. erectus* sensu lato (node L). This node is supported by a bootstrap value of 29%, two synapomorphies, and seven landmark configurations.

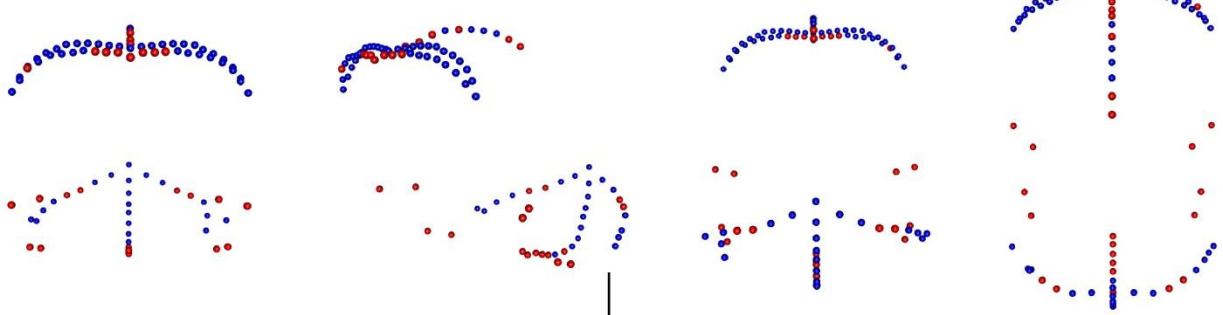
- Node I (*H. habilis*) shows a bootstrap of 8%, six landmark configurations, and one synapomorphy.
- Node J (Stw 53) reaches 38% support, with two synapomorphies and seven landmark configurations.
- Node K, corresponding to the Dmanisi clade, has a bootstrap value of 51%, seven landmark configurations, and one synapomorphy.

For all these nodes, the morphological patterns remain identical to those described in the CI-weighted analysis.

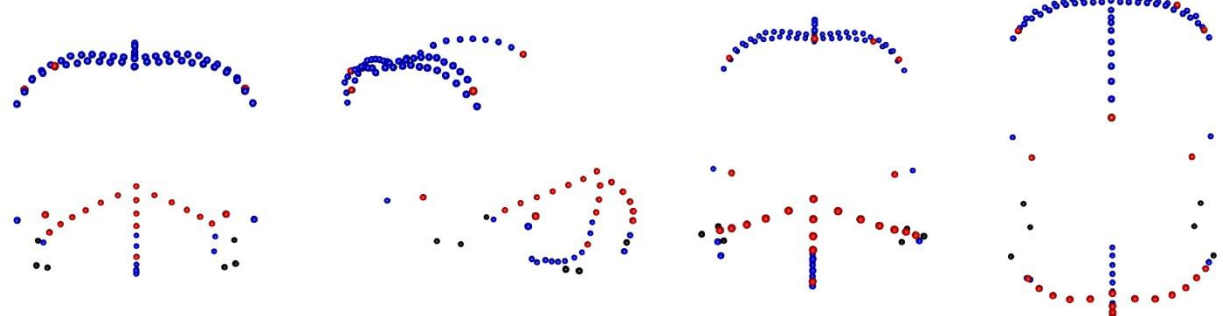
Node K



Node L



Node M



3D characters

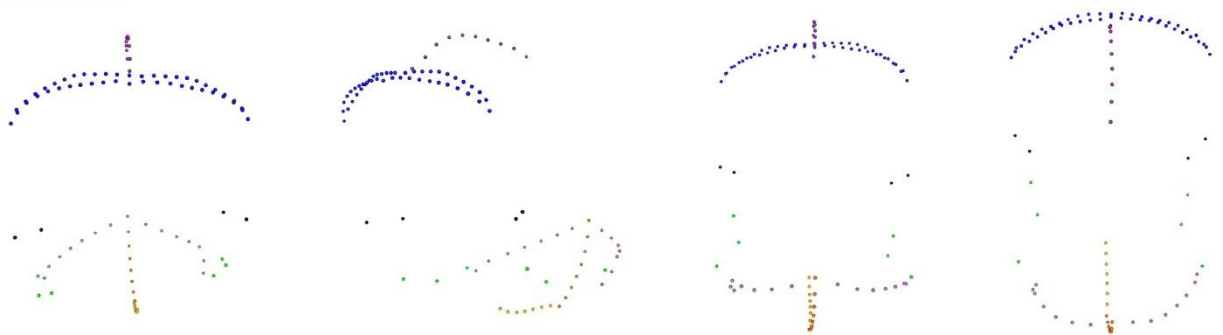


Figure 86: 3D shapes showing morphological change for the landmark configurations from node K to node L and M. The views are, from left to right, *norma facialis*, three-quarter view, *norma occipitalis* and *norma verticalis*. In the nodes, black indicates unchanged configurations, blue represents changing configurations, and red highlights the changing landmarks within each configuration. In the 3D characters, each colour represents a

landmark configuration: #1 in blue, #2 in purple, #3 in orange, #4 in pink, #5 in yellow, #6 in green and #7 in black.

In this RC-weighted reconstruction, node L represents *H. erectus sensu lato*, comprising the Sangiran fossils in a basal position, followed by *H. ergaster*, and culminating in node N, which groups the Zhoukoudian and Ngandong specimens. Node L (Sangiran) is supported by a bootstrap value of 86%, seven landmark configurations (see Figure 86), and three synapomorphies.

Morphologically, the supraorbital outline resembles that of node K but is slightly straighter (#1); both occipital crests are aligned (#5), and the *planum occipitale* retains its triangular outline (#4). The frontal profile and the *planum occipitale*–*planum nuchale* transition remain unchanged (#2, #3). The *processus mastoideus* exhibits weaker downward projection (#6), while the glenoid cavity is shallower (#7).

The three synapomorphies supporting this node are: (1) a thickening on the superior part of the coronal sutures (#20, state 2); (2) presence of the *processus retromastoideus* (#31, state 2); and (3) a *sulcus supratoralis* (#34, state 3).

Node M (*H. ergaster*) is supported by a bootstrap value of 44%, five landmark configurations, and one synapomorphy.

In *norma facialis* and *norma verticalis*, the supraorbital outline closely resembles that of node L but is slightly straighter (#1). In *norma occipitalis*, the *planum occipitale* retains its triangular shape (#4). In *norma lateralis*, the frontal bone maintains comparable convexity (#2), and the *planum occipitale*–*planum nuchale* transition appears marginally rounder (#3). The glenoid cavity is deeper than in node L (#7).

The defining synapomorphy for this node is a pre-lambdatic hollowing on the bregma–lambda arch (#23, state 2).

Node N, grouping the Zhoukoudian and Ngandong fossils, is supported by a bootstrap value of 66%, seven landmark configurations, and two synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline remains straight (#1). In *norma occipitalis*, both occipital crests are present and aligned (#5), while the *planum occipitale* adopts a slightly rounder triangular shape than in node L (#4). In *norma lateralis*, the frontal bone shows greater antero-posterior convexity (#2), and the *planum occipitale*–*planum nuchale* transition becomes

subtly rounder (#3). The *processus mastoideus* displays stronger downward projection (#6), and the glenoid cavity deepens (#7).

The two synapomorphies defining node N are: (1) reduction of postorbital constriction from marked (#12, state 1) to weak (#12, state 2); and (2) presence of a bony bridge in the digastric groove (#50, state 2).

Node O unites *Homo neandertalensis* and *H. sapiens* in a monophyletic clade supported by a bootstrap value of 86%, seven landmark configurations, and six synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline is more convex than in node F (#1). In *norma occipitalis*, the occipital crests are present but not aligned (#5), while the *planum occipitale* retains its triangular form (#4). In *norma lateralis*, the frontal profile is more convex (#2), and the *planum occipitale*–*planum nuchale* transition becomes rounder (#3). The *processus mastoideus* exhibits stronger downward development (#6), and the glenoid cavity is shallower (#7).

The synapomorphies defining node O are the absence of postorbital constriction (#12, state 3); the presence of a continuous *sulcus postorbitalis* (#13, state 3); the presence of *tuber frontale* (#14, state 3); a low position of the *linea temporalis* on the parietal (#25, state 3); distinct relative positions of the inion and opisthocranium (#30, state 2); and presence of a *sulcus supramastoideus* (#45, state 3).

Node P corresponds to the monophyletic grouping of *H. neandertalensis*, including the OTUs “Early Neandertal,” “Classic Neandertal,” and “Near East Neandertal.” The latter two form a subclade at node Q. Node P is supported by a bootstrap value of 77%, six landmark configurations, and two synapomorphies, both identical to those observed in the CI-weighted tree.

Similarly, node Q, grouping the “Classic Neandertal” and “Near East Neandertal” specimens, is supported by a bootstrap value of 43% and seven landmark configurations, reflecting general morphological trends consistent with node Q in the CI-weighted analysis.

Finally, node R, representing the monophyletic *Homo sapiens* clade, is supported by a bootstrap value of 90%, seven landmark configurations, and five synapomorphies.

In *norma facialis* and *norma verticalis*, the supraorbital outline is convex (#1). In *norma occipitalis*, both occipital crests are absent (#5), and the *planum occipitale* takes on a pentagonal outline (#4). In *norma lateralis*, the frontal bone exhibits strong antero-posterior convexity (#2), and the *planum occipitale*–

planum nuchale transition is smooth, rounded, and convex (#3). The *processus mastoideus* shows pronounced downward development (#6), while the glenoid cavity is shallower than in node O (#7).

The five synapomorphies defining this clade are the presence of a complete supraorbital region (#10, state 1); the absence of the *torus occipitalis transversus* (#35, state 1; #36, state 1); an antero-posteriorly convex configuration of the articular tubercle (#53, state 2); and an absent or weakly marked *tuberculum zygomaticum posterius* (#55, state 1).

III. Discussion

For the morphological dataset (matrix D), the most robust topology was obtained under the RC-weighting scheme, yielding a tree length of 5372, a Consistency Index (CI) of 0.539, and a Retention Index (RI) of 0.824. In contrast, the RI-weighted analysis produced the least robust topology, with the longest tree length (11,730), the lowest CI (0.446), and an RI of 0.757.

As outlined in the results, a similar pattern was observed for the combined dataset (matrix B; landmarks + morphological characters). The RC-weighted tree again produced the most robust topology, characterized by a shorter tree length (4554.438), a higher CI (0.567), and a higher RI (0.842) (see Tables 11 and 12). Conversely, the RI-weighted tree yielded the weakest result, with the longest tree length (9449.663) and comparatively lower CI (0.478) and RI (0.785) values.

When assessing topological congruence between the morphological (matrix D) and combined (matrix E) trees, the RC-weighting scheme performed best, exhibiting the lowest Robinson–Foulds (RF) distance (0.365), while Subtree Prune-and-Regraft (SPR) values remained identical across weighting schemes.

Taken together, these results indicate that the combined dataset (matrix E) yields more robust and phylogenetically stable topologies than the morphological dataset alone, especially considering they constantly have better CI and RI values. Across both datasets, RC-weighting consistently produces the most stable and internally consistent trees. Notably, in the morphological analysis, it was the only weighting scheme capable of resolving the large polytomy at the base of the ingroup, whereas in the combined analysis, only the RI-weighted tree achieved this resolution.

The comparison between the morphological-only and combined (landmark + morphological) datasets highlights both the robustness of certain phylogenetic patterns and the influence of data integration on tree topology and node support. Across all weighting schemes (CI-, RI-, and RC-weighting), the inclusion of geometric morphometric data produced a clearer and more stratified phylogenetic structure within *Homo*, while retaining the broader clade relationships identified in the morphological matrix.

In matrix D, *Pan* and *Gorilla* consistently cluster with *Paranthropus aethiopicus* and *P. boisei*, reflecting the retention of shared primitive cranial traits. However, the addition of landmark data (matrix E) reduces the instability seen in the morphological-only analyses, particularly under CI- and RI-

weighting, where bootstrap support for internal nodes within this cluster was low (<40%). In the combined dataset, the grouping of *Paranthropus* taxa remains distinct and is supported by higher consistency and rescaled consistency indices, suggesting that landmark-based shape information strengthens the phylogenetic signal for this clade.

The most striking improvement concerns the resolution of relationships among early *Homo* species. In the morphological-only trees, large unresolved polytomies persisted (e.g., node F in the CI- and RI-weighted analyses), obscuring branching order among *H. habilis*, *H. rudolfensis*, *H. ergaster*, and the Dmanisi and Sangiran specimens. In contrast, the combined analyses consistently resolved this complex into a series of nested, stratigraphically coherent clades. Under both RI- and RC-weighting, *H. ergaster* and the Asian *H. erectus* specimens (Sangiran, Zhoukoudian, Ngandong) form a cohesive, sequentially ordered lineage, while *H. habilis* and the Dmanisi fossils occupy more basal positions. This increased resolution indicates that landmark data effectively capture aspects of cranial vault and facial morphology that differentiate these taxa but were not fully represented by discrete characters alone.

The relative impact of different weighting criteria also shifts when morphometric data are included. In the morphological-only dataset, CI-weighting produced the least-resolved topology, dominated by extensive polytomies and low bootstrap support. RI-weighting introduced moderate improvements, while RC-weighting yielded the most resolved arrangement, breaking down the major polytomy and clarifying the placement of *A. afarensis* and *H. rudolfensis*. In the combined analyses, however, these differences become less pronounced. All three weighting schemes recover similar topologies, with the RC-weighted tree showing only minor refinements in the branching order within *Homo erectus* sensu lato. This convergence suggests that the addition of morphometric data reduces sensitivity to character weighting, providing a more stable phylogenetic signal across weighting criteria.

A major contrast between the morphological-only and combined analyses lies in the placement of *A. africanus*. In the morphological trees, *A. africanus* was often ambiguously positioned or even clustered with *H. neandertalensis* and *H. sapiens* (nodes N–O), reflecting shared cranial vault characteristics of limited phylogenetic relevance. In the combined analyses, *A. africanus* consistently reverts to a more basal position relative to the genus *Homo*, aligning with expectations from stratigraphic and functional morphology. This shift demonstrates that landmark data can resolve ambiguities introduced when new, and in some cases controversial, OTUs are added to the

morphology-only matrix, highlighting the strength of the combined approach in recovering true evolutionary relationships (Catalano et al., 2015).

By contrast, the *H. neandertalensis* and *H. sapiens* clade remains one of the most stable results across all datasets and weighting schemes. The addition of landmark data enhances bootstrap support and refines internal structure, notably distinguishing early and classic Neandertals and positioning the “Skhūl–Qafzeh” population basally within modern *H. sapiens*. The recurrence of these patterns under all weighting schemes underscores the robustness of the late *Homo* phylogeny and the strong morphological coherence of these groups.

Overall, the integration of landmark and discrete morphological data improves phylogenetic resolution, not only within *H. erectus* sensu lato but also among australopithecines, where it removes the previously inferred *Pan–Gorilla* + *Paranthropus* grouping, thus yielding a more plausible evolutionary signal while retaining the main clades recovered by the morphology-only matrix (Catalano et al., 2015). Landmark information contributes quantitative shape data that capture continuous variation across the cranium, particularly in the frontal, parietal, and occipital regions, thereby refining the recognition of gradual morphological trends. The reduced dependence on weighting schemes in the combined analyses suggests that morphometric data buffer the effects of homoplasy that often complicate discrete morphological datasets. Consequently, the phylogenies obtained from the combined matrices more accurately reflect evolutionary relationships within *Homo* and provide a stronger empirical foundation for interpreting morphological transitions across the Pleistocene.

IV. Conclusion

The comparative analyses of the morphological (matrix D) and combined (landmark + morphological; matrix E) datasets reveal that data integration substantially improves phylogenetic resolution and stability. Although the RC-weighting scheme consistently produced the most robust and internally coherent topologies across both datasets, the inclusion of landmark information in matrix E reduced overall tree length, increased CI and RI values, and minimized topological discrepancies between weighting methods.

In the morphological dataset, extensive polytomies and low node support values, particularly within early *Homo*, limit interpretative power. By contrast, the combined analyses resolved many of these relationships, producing a clearer hierarchical structure within *Homo erectus* sensu lato and clarifying the basal placement of *H. habilis* and *H. rudolfensis*. The integration of continuous landmark data not only enhanced the consistency of phylogenetic signal but also reduced sensitivity to weighting schemes, suggesting that morphometric characters capture complementary dimensions of cranial variation overlooked by discrete traits alone.

From an evolutionary standpoint, the combined trees present a more coherent picture of hominin diversification. The stability of the *H. neandertalensis*–*H. sapiens* clade, the reinforced distinctiveness of *Paranthropus*, and the refined branching order within early *Homo* together point a consistent hierarchical signal in the data, though cladistic analyses cannot directly resolve evolutionary tempo (e.g., Bapst, 2013).

Overall, these findings underscore the methodological advantage of integrating landmark and morphological data in phylogenetic reconstruction. The RC-weighting scheme remains the most effective approach for balancing character fit and tree resolution, but the addition of geometric morphometric information clearly enhances phylogenetic robustness and yields a more accurate reflection of evolutionary relationships within the hominin lineage.

Key-points IV

Research focus and goals:

- The study tests the combination of 3D geometric morphometric (GMM) data and morphological characters in one matrix in cladistic phylogenetic reconstruction.
- Results are compared with traditional discrete morphological character-based trees, to evaluate the congruence of this approach with a reference morphology-based phylogeny.

Datasets:

- Matrix D: 60 discrete morphological characters.
- Matrix E: Combined 3D landmark + morphological characters (7 landmark configurations and 42 morphological characters).

Tree statistics and robustness:

- Matrix D (morphological):
 - Most robust tree → RC-weighted (length = 5372; CI = 0.539; RI = 0.824)
 - Least robust tree → RI-weighted (length = 11730; CI = 0.446; RI = 0.757)
- Matrix E (combined):
 - Most robust tree → RC-weighted (length = 4554.438; CI = 0.567; RI = 0.842)
 - Least robust tree → RI-weighted (length = 9449.663; CI = 0.478; RI = 0.785)
- Topological congruence:
 - RC-weighted trees show the lowest RF distance (0.365) between matrices.
 - SPR values remained constant across weighting schemes.
- Overall: RC-weighting yields the most stable and internally consistent phylogenies in both datasets.

Morphological matrix (Matrix D):

- General pattern: *A. africanus*'s placement remained variable, but CI- and RC-weighting grouped it with *H. neandertalensis* and *H. sapiens*.
- RC-weighting resolved the basal polytomy (unlike CI and RI).
- Outgroup (*Pan*, *Gorilla*, *Paranthropus*) relationships remained stable across weightings.
- *H. neandertalensis* and *H. sapiens* consistently formed a monophyletic clade with strong bootstrap support (>80%).
- *H. sapiens* was always monophyletic, with the "Skhül-Qafzeh" specimens in a basal position.
- Synapomorphic support largely consistent across weighting schemes, but RC-weighting produced higher character fit and more coherent internal nodes.

Combined dataset (Matrix E):

- Integration of 3D landmark data enhanced tree resolution and node support.
- General pattern: large polytomy at the base of the ingroup (node F), unresolved relationships among *Australopithecus* and *Homo* species.
- Reduced overall tree length and homoplasy compared to matrix D.
- Polytomies within *Homo erectus* sensu lato largely resolved, clarifying the sequence: *H. ergaster* → Sangiran → Zhoukoudian + Ngandong.
- *H. habilis* and *H. rudolfensis* consistently occupy basal positions within *Homo*.
- Combined trees showed stronger support for major clades, notably:
 - *H. neandertalensis* + *H. sapiens* (bootstrap > 70%)
 - *H. sapiens* monophyly (bootstrap > 90%)
- Morphometric data reduced the dependency of topology on weighting scheme.

Evolutionary implications:

- Integration of landmarks and morphological data yields a more coherent evolutionary framework.
- Reinforces:
 - The monophyly of *Paranthropus*
 - The structured diversification of early *Homo*
 - The derived status and close relationship between *H. neandertalensis* and *H. sapiens*.
- Suggests gradual evolutionary diversification rather than abrupt or reticulate branching.
- Highlights the importance of combining continuous morphometric and discrete anatomical data to capture complementary phylogenetic signals.

Chapter V – Discussion

I. Cladistics and GMM

I.1. Comparative performance of different data types

The present study explored how different sources of morphological information, discrete qualitative characters, principal component (PC) scores derived from geometric morphometrics, and raw 3D landmark coordinates, perform in phylogenetic reconstruction. Each of these data types offers specific advantages and limitations in terms of analytical robustness, biological interpretability, and computational tractability.

I.1.1. Discrete morphological characters

Traditional discrete morphological characters remain the cornerstone of most phylogenetic analyses because they are easily interpretable and directly linked to observable anatomical features. Their greatest strength lies in their ability to express hypotheses of primary homology (*sensu* de Pinna, 1991), enabling explicit discussion of synapomorphies and the evolutionary transformations that define clades. This interpretability makes them invaluable for reconstructing character evolution and for correlating morphology with ecological or functional traits.

However, discrete datasets suffer from several well-known limitations. The definition and delimitation of characters and states are often subjective and can vary between researchers (Pleijel, 1995b; Sereno, 2007). The process of discretizing continuous variation inevitably entails information loss, particularly for features that change gradually rather than in distinct steps. Moreover, the assumption of character independence is rarely met or testable (Hawkins et al., 1997; McCracken et al., 1999). Many morphological traits covary due to developmental, functional, or allometric integration, which can lead to redundancy and over-representation of certain anatomical regions. In the present analysis, these issues were evident in the persistence of large polytomies in some weighting schemes and the variable resolution across nodes. Despite these challenges, the morphological dataset (matrix A of Chapter III and matrix D of Chapter IV) provided a biologically interpretable baseline for comparison with morphometric approaches.

I.1.2. Geometric morphometric data

In contrast, geometric morphometric (GMM) data capture morphological variation continuously and quantitatively, allowing for precise measurement of shape differences while minimizing observer bias (Zelditch et al., 2004). The use of landmark coordinates permits a reproducible and

standardized description of form that is less susceptible to subjective interpretation. Moreover, landmark data enable the direct 3D visualization of ancestral morphologies, offering a powerful way to assess evolutionary transformations in a geometric rather than descriptive framework (Catalano et al., 2010; Goloboff and Catalano, 2011).

Nevertheless, the use of GMM data in phylogenetics has been controversial. Critics argue that morphometric datasets often reflect overall phenetic similarity rather than true phylogenetic signal (Adams et al., 2011; Klingenberg and Gidaszewski, 2010; Varón-González et al., 2020). Because landmarks are inherently interdependent, treating them as discrete and independent characters conflicts with the assumptions of traditional cladistic methods based on parsimony (Bookstein, 1991; Monteiro, 2000; Rohlf, 1998). Despite these challenges, several studies have demonstrated that morphometric data can retain phylogenetic signal when appropriately analysed with resultant phylogenies being congruent with independent sources of evidence (Catalano et al., 2015; Catalano and Torres, 2017; Perrard et al., 2016). In this study, although landmark-based trees were slightly less coherent than those derived from discrete morphology (see, Chapter III – Cladistics and GMM), they nevertheless captured biologically meaningful relationships, particularly when combined with traditional characters (see, Chapter IV – Morphological and 3D characters).

i. Principal component-based data

Principal Component (PC) data offer a mathematical solution to some of the dependence issues inherent in landmark coordinates. Because PCs are orthogonal by construction, they represent independent axes of variation (Jolliffe, 2002), thereby reducing redundancy between variables. This property addresses one of the core criticisms of morphometric data in cladistics, namely, the violation of character independence. However, the transformation of landmarks into PC scores involves dimensional reduction, which compresses complex three-dimensional information into a limited set of one-dimensional variables. While this simplifies computation, it also sacrifices spatial context and direct biological interpretability (Adams et al., 2011; Monteiro, 2000; Zelditch et al., 2004).

In this study, analyses based on PC data (matrices B.1–B.3 of Chapter III) showed moderate congruence with the morphological reference tree. The best results were obtained from the densest landmark sampling (matrix B.3), which yielded higher consistency and retention Indices (CI = 0.708, RI = 0.896) and better topological congruence. These findings suggest that increased landmark density improves phylogenetic resolution, likely by capturing a more complete representation of

shape variation. However, PC-based trees remained less coherent overall than those from discrete or combined datasets, highlighting that while PCs mitigate dependence issues, they may inadequately model evolutionary transformations of shape.

ii. *Landmark coordinates*

Analyses based on raw landmark coordinates (matrix C of Chapter III) provided a more faithful representation of shape but also introduced computational and theoretical complexities. Because each landmark represents a coordinate in three-dimensional space, the number of variables is high, and their covariance structure is intricate. Although such datasets demand greater computational resources, they allow direct ancestral shape reconstruction at internal nodes. While PC-based matrices can perform similar analyses through an additional computational step, the dimensional reduction and subsequent reconstruction may produce less accurate or biologically realistic ancestral shapes (e.g., Klingenberg, 2016; Polly et al., 2013). The possibility of visualizing 3D ancestral forms enhances interpretability by linking topology directly to morphology. However, the interdependence of landmarks means they cannot be treated as independent characters, and their biological meaning can be ambiguous. Consistent with the approaches proposed by Catalano et al. (2015) and Klingenberg, (2010), matrix E (Chapter IV) already integrated multiple landmark configurations as distinct analytical characters. Building on this, future research could formalize landmark subsets as morphological modules, further aligning geometric precision with cladistic interpretability.

I.2. Comparative performance of different matrix types

The comparative analysis of matrix types, morphological (A and D), PC-based (B), landmark-based (C), and combined (E), demonstrated a clear hierarchy in terms of robustness, resolution, and biological coherence.

The morphological matrices (A and D) yielded well-structured trees consistent with known evolutionary relationships. However, their resolution within early *Homo* decreases when additional, debated OTUs are included, reflecting the challenges of incorporating taxa with uncertain phylogenetic positions. The PC matrices (B.1–B.3 of Chapter III) provided an objective, continuous representation of morphology, yielding results broadly comparable to those obtained with landmark configurations. Landmark-based approaches, however, retain the full geometric information and allow for analyses of morphological modules, providing additional insight into

evolutionary patterns. Although computationally demanding, the landmark matrix (C.1–C.3 of Chapter III) offered the richest anatomical detail and enabled 3D ancestral shape reconstruction. Despite this added resolution, the resulting phylogenetic trees were broadly comparable to those derived from PC-based matrices, highlighting that both approaches capture similar evolutionary signals.

The combined matrix (landmarks + morphological characters, i.e. matrix E of Chapter IV) performed best overall, yielding topologies that were both stable and congruent with independent phylogenies (e.g., Dembo et al., 2015; Mounier and Caparros, 2015; Strait and Grine, 2004; Zeitoun, 1996). Integrating GMM and discrete morphological data significantly improved resolution within *Homo* and stabilized the placement of taxa such as *A. africanus*, which shifted to a more basal position relative to *Homo* when landmark data were included. The combined analyses also showed reduced sensitivity to weighting schemes, suggesting that continuous morphometric data buffer the effects of homoplasy inherent in discrete traits. This finding supports earlier conclusions that data integration enhances phylogenetic stability (Catalano et al., 2015; Wheeler, 2021).

I.3. Effects of weighting indices

The influence of weighting schemes, consistency index (CI), retention index (RI), and rescaled consistency index (RC), was evaluated across all datasets. Each index weights characters according to phylogenetic signal, thereby modulating how conflicting signals influence topology.

Across all analyses, RC-weighting consistently produced the most robust and internally coherent topologies. RC-weighted trees exhibited shorter lengths, higher CIs and RIs, and better congruence with morphology-based reference trees. In morphological dataset, RC-weighting successfully resolved large basal polytomies that persisted under other schemes. This suggests that RC-weighting effectively balances the contribution of informative characters while minimizing the destabilizing effects of homoplasy.

RI-weighting generally produced intermediate results. It improved upon CI-weighting by retaining better resolution and higher retention indices but remained sensitive to data structure and dimensionality. In the combined dataset, RI-weighting managed to resolve the large basal polytomy present in the other schemes.

The CI-weighted trees, by contrast, were often less resolved and exhibited higher tree lengths, indicating that emphasizing raw consistency without accounting for character redundancy can over-

penalize complex datasets. Interestingly, in some cases (e.g., the *H. sapiens*–*H. neandertalensis* clade), CI-weighting recovered locally congruent topologies, suggesting that it may be useful for fine-scale relationships within morphologically cohesive groups.

An important outcome of this study is that the inclusion of morphometric data, particularly in the combined matrix, reduced the impact of weighting schemes. While the morphological-only analyses showed marked differences between CI-, RI-, and RC-weighted trees, the combined datasets converged toward similar topologies across all schemes. One possible interpretation is that continuous morphometric data provide a stabilizing effect, mitigating the influence of character weighting and yielding more reproducible phylogenetic hypotheses.

I.4. Broader implications and methodological considerations

The findings presented in this dissertation highlight the complementary nature of discrete and continuous data in phylogenetic analysis. Discrete characters remain indispensable for identifying explicit synapomorphies and testing homology hypotheses, while geometric morphometric data contribute detailed, quantitative descriptions of shape variation that enhance topological resolution and reduce observer bias. The integration of both data types yields more accurate and stable phylogenies, as continuous traits capture subtle morphological transitions that discrete coding may overlook, and discrete traits offer a framework for interpreting evolutionary relationships, but 3D landmark data can actively enhance phylogenetic resolution by representing detailed morphological variation. This is especially valuable for OTUs with uncertain positions, where landmarks compensate for incomplete understanding of their variation and help produce more reliable topologies.

From a methodological perspective, these results emphasize the importance of matching analytical approaches to data properties. Cladistic methods (particularly those based on parsimony and RC-weighting) appear more suitable for GMM data than purely phenetic methods such as UPGMA or Neighbour-Joining, which reflect overall similarity rather than shared derived features (Choudhuri, 2014). Although phenetic trees occasionally reproduce known clades due to strong morphological resemblance, such congruence should be interpreted cautiously, as it may reflect convergence or rate homogeneity rather than true phylogenetic affinity. Phenetic methods are primarily intended to capture overall similarity and are particularly useful for assessing alpha taxonomy, rather than for reconstructing evolutionary relationships.

Finally, the study underscores the need for caution in preprocessing steps such as allometry correction. Removing size effects can inadvertently eliminate evolutionarily meaningful variation when allometry itself is phylogenetically structured (Giannini, 2014; Klingenberg and Marugán-Lobón, 2013; Pélabon et al., 2014). Analyses of both raw and size-corrected data are therefore recommended to evaluate the potential impact of allometric trends on tree topology.

II. Hominin phylogeny

Building on the methodological framework and conceptual background outlined in previous chapters, this section critically examines the phylogenetic results of early hominins in the light of current paleoanthropological debates. The analyse presented here (RC-weighting tree of matrix E, Chapter IV) integrate only calvarial characters to assess relationships among *Australopithecus*, *Paranthropus*, and early *Homo*, extending to *H. erectus* sensu lato, *H. neandertalensis*, and early *H. sapiens*. By comparing the recovered the tree topology with established morphological, temporal, and geographical data, this discussion situates the results within broader evolutionary hypotheses, highlighting points of concordance, divergence, and uncertainty (see, Table 14).

II.1. *H. erectus* sensu lato, Neandertals, and early *H. sapiens*

The phylogenetic RC-weighted analysis presented in Chapter IV identify *Homo erectus* sensu lato as a widespread and internally structured lineage encompassing African (*H. ergaster*), Javan (Sangiran), and Chinese (Zhoukoudian and Ngandong) representatives. African *H. ergaster* occupies a basal position within this clade, combining moderately thick cranial vaults, pronounced supraorbital tori, and a bregmatic eminence, features also observed in Asian *H. erectus* (Antón, 2003; Rightmire, 1990). The Sangiran fossils occupy an intermediate position, exhibiting a suite of derived cranial features such as frontal sagittal keeling and parasagittal hollowing, which may represent regional or temporal morphological differentiation within the Javan lineage (Groves and Mazak, 1975; Indriati et al., 2011). The Zhoukoudian and Ngandong series are recovered as the most derived members of the clade, displaying increased cranial vault thickness, postorbital constriction reduction, and subtle neurocranial expansion, reinforcing the hypothesis of regional morphological evolution within Asia (Rightmire, 1992; Wu and Poirier, 1995). The Dmanisi specimens and Stw 53 are placed together as sister taxa or closely related to early *H. erectus* sensu lato. These fossils combine primitive cranial morphology reminiscent of *H. habilis* with derived traits shared with later *H. erectus*, supporting interpretations of acquisition of *Homo* characteristics prior to the broad geographical expansion of the genus (Lordkipanidze et al., 2013). Evolutionary implications of this topology suggest that *H. erectus* sensu lato represents a polytypic, geographically structured species, with African populations providing the morphological foundation for the dispersal into Eurasia and subsequent regional diversification. Overall, the phylogenetic pattern recovered in this analysis reinforces previous hypotheses of *H. erectus* as a chronologically and geographically extended taxon, bridging

the morphological gap between early *Homo* species such as *H. habilis*/*H. rudolfensis* and later Pleistocene hominins, including Neandertals and modern humans.

The phylogenetic analysis recovers *H. neandertalensis* as a well-supported monophyletic clade in RC-weighted tree of matrix E (Chapter IV), distinct from both earlier *Homo* species and modern humans, yet closely related to the latter. Within Neandertals, the terminal clade comprising “Classic” and “Near East” Neandertals is resolved in the combined matrix, reflecting subtle chronological and morphological differentiation across Europe and the Near East. This clade is characterised by a suite of derived cranial features, including the presence of a suprainiac fossa, upward-convergent lateral edges of the fossa, misalignment of the *crista supramastoidea* with the *processus zygomaticus temporalis*, and development of the anterior mastoid tubercle. These features correspond closely with traditional morphological diagnoses of Neandertals and corroborate previous assessments based on both discrete traits and 3D cranial morphometrics (Tattersall and Schwartz, 2006). The recovered phylogenetic structure also positions regional populations, such as the Early Neandertals, in basal position relative to the “Classic” and “Near East” forms, which aligns with paleogenetic and archaeological evidence suggesting multiple dispersals and local differentiation within the Neandertal lineage (Fabre et al., 2009; Higham et al., 2014; Stringer, 2012). Overall, the phylogenetic results support the long-standing hypothesis that Neandertals represent a coherent evolutionary lineage with strong internal morphological cohesion, yet with clear evidence of regional variation (Hublin et al., 2006; Prüfer et al., 2014).

The phylogenetic analyses recover *H. sapiens* as a strongly supported monophyletic clade, distinct from other late Pleistocene *Homo* taxa, with the “Skhül–Qafzeh” specimens occupying a basal position in most of the analyses. This basal placement reflects the retention of certain archaic cranial features relative to later Holocene populations. Key synapomorphies defining *H. sapiens* include a pentagonal outline of the *planum occipitale*, absence of the *torus occipitalis transversus*, and a smoothly convex anteroposterior profile of the articular tubercle. These features corroborate previous morphometric and qualitative assessments highlighting the combination of globular neurocranial morphology and gracile facial structures as characteristic of modern humans (Bräuer, 2007; Gunz et al., 2012). The sister-group relationship with *H. neandertalensis* reflects their close evolutionary connection during the later Middle to Upper Pleistocene, consistent with genomic evidence for shared ancestry and limited admixture events (e.g., Green et al., 2010; Hawks, 2006; Prüfer et al., 2014). Morphologically, *H. sapiens* demonstrates reduced cranial robusticity compared to

Neandertals, including less pronounced occipital and supraorbital features, a higher and more globular neurocranium, and a smoother cranial vault. These traits are associated with the expansion of braincase volume, reorganization of cranial architecture, and potentially, shifts in developmental timing (Gunz et al., 2009; Neubauer et al., 2018). The results reinforce the view of *H. sapiens* as a highly derived, cohesive evolutionary lineage, distinguished from other late Pleistocene hominins, while highlighting the early morphological diversity within the species during its initial dispersal phase.

Taken together, these results demonstrate the internal coherence of the phylogenetic framework established in this study. The congruence across the results and previous studies (e.g., Dembo et al., 2015; González-José et al., 2008; Mounier and Caparros, 2015; Ni et al., 2021; Zeitoun, 2000) provides a robust basis for broader evolutionary interpretation. This coherence validates the overall tree topology and allows the discussion to extend confidently to more fragmentary or debated taxa (e.g., *Australopithecus*, *Paranthropus*, early *Homo*), situating them within an empirically grounded and morphologically consistent evolutionary scenario for the genus *Homo*.

II.2. Early *Homo*

The phylogenetic analysis place *Homo habilis* and *H. rudolfensis* in close association within the early *Homo* speciation, yet their cranial morphology reveals distinct evolutionary patterns that directly inform long-standing debates about the emergence of the genus. *H. habilis* is recovered at the base of the *Homo* lineage, displaying a continuous *sulcus postorbitalis*, moderate frontal convexity, and a slight but marked expansion of the cranial vault relative to australopiths. These features, together with a more vertical frontal squama and reduced postorbital constriction, clearly distinguish it from *Australopithecus* and support its placement within *Homo* (Leakey et al., 1964; Ruff, 2009; Schrenk et al., 2007; Wood, 1992b). In contrast, *H. rudolfensis* exhibits a more elongated cranial vault, reduced supraorbital projection, and distinctive parietal morphology, consistent with its larger cranial capacity and broader neurocranial proportions (Schrenk et al., 2007; Wood, 1992b). These features reinforce its status as a morphologically divergent early *Homo* species rather than a variant of *H. habilis*.

These results align with previous interpretations that *H. habilis* and *H. rudolfensis* represent distinct but closely related evolutionary lineages within early *Homo*, differentiated by key cranial and mandibular features (e.g., Leakey et al., 1995; Mongle et al., 2023; Smith and Grine, 2008; Spoor et

al., 2015; Wood, 1992a). In this framework, *H. habilis* can be viewed as the earliest clearly derived *Homo*, characterized by an expansion and reorganization of the cranial vault and frontal region, while *H. rudolfensis* retains a more primitive cranial morphology (e.g., Mongle et al., 2023; Smith and Grine, 2008; Strait and Grine, 2004; Stringer, 1987). This pattern suggests that the two species may have evolved in parallel from late Pliocene australopiths, representing separate adaptive trajectories within a broader early *Homo* radiation (Spoor et al., 2015).

The coexistence of *H. habilis* and *H. rudolfensis* with robust australopiths such as *P. boisei* during the early Pleistocene underscores the taxonomic and ecological complexity of this period (Spoor et al., 2015). Their overlapping chronology and distinct cranial morphologies indicate that multiple hominin lineages presented diverse adaptations. This interpretation supports a pattern of branching evolution, where early *Homo* lineages diversified both morphologically and geographically before the appearance of *H. erectus* sensu lato (Spoor et al., 2015; Wood, 1992a; Wood and Constantino, 2007).

From a broader phylogenetic perspective, the analyses reinforce the view that *H. habilis* and *H. rudolfensis* form the basal branch of the *Homo* clade. While some authors have questioned their inclusion within the genus, arguing that their adaptive and postcranial traits still align with australopith morphologies (Wood and Collard, 1999a, 1999b), the cranial evidence presented here supports their retention within *Homo*. The combination of neurocranial expansion, reorganization of frontal and parietal regions, and reduced facial prognathism defines a morphological threshold separating them from australopiths such as *A. africanus* or *A. afarensis*.

Considering these findings, *H. habilis* and *H. rudolfensis* should be regarded as distinct, valid species representing complementary stages in the early diversification of *Homo*. *H. habilis* exhibits the foundational cranial morphology of the genus, marking a clear difference with australopith anatomy, while *H. rudolfensis* represents a lineage with slightly more derived features. Together, they capture the morphological characteristic of the early *Homo* radiation and illustrate that the emergence of our genus was not a single event but a dynamic evolutionary process encompassing multiple lineages, morphologies, and adaptive pathways (Prat, 2022; Spoor et al., 2015; Wood, 1992b).

II.3. *Australopithecus*

The phylogenetic position of the *Australopithecus* OTUs in the present analysis (RC-weighted tree of matrix E, Chapter IV) is complex and reveals nuanced relationships among early hominins. While *A. afarensis* and *A. africanus* are recovered as monophyletic, their relationships with the genus *Homo* remain unresolved, reflecting the long-standing uncertainty surrounding the transition between late australopiths and the earliest representatives of our genus (Wood, 1991, 1992b). *A. afarensis* exhibits a relatively straight supraorbital region, moderately convex frontal profile, circular or slightly triangular *planum occipitale*, and modestly developed *processus mastoideus*. These cranial features, combined with a small endocranial volume corroborate earlier morphometric assessments that place *A. afarensis* near the root of the australopith radiation (Kimbel et al., 1994, 2004). This taxon thus embodies a crucial evolutionary stage combining derived adaptations to bipedality with primitive cranial and postcranial morphologies. In the results, *A. africanus* while displaying subtle cranial modifications, including a more circular *planum occipitale*, and a slight rounding at the occipital-nuchal junction, is grouped with *A. afarensis*. This contrast with previous analyses recovering it as paraphyletic, with *A. afarensis* displaying more primitive features (e.g., Chamberlain and Wood, 1987; Mongle et al., 2023; Smith and Grine, 2008).

The position of the South African specimen Stw 53 adds further complexity to this picture. In the present analysis, Stw 53 clusters with early *Homo* specimens, including *H. habilis* and the Dmanisi fossils, supporting its interpretation as an early *Homo* representative or a transitional form (Curnoe and Tobias, 2006; Ni et al., 2021). The specimen combines *Homo*-like traits, such as a continuous *sulcus postorbitalis*, medially concave supraorbital region, and, with more primitive australopith-like features, such as parasagittal hollowing on both side of the parietal suture, narrow width of the *linea temporalis* on the temporal band and a deep glenoid cavity.

The taxonomic history of Stw 53 reflects this ambiguity. Initially described as *H. aff. habilis* (Hughes and Tobias, 1977) and later as *H. habilis* (Tobias, 1991), it has since undergone multiple reclassifications. Prat (2004) reaffirmed its placement within *Homo*, whereas Curnoe (2010) proposed its designation as the holotype of *H. gautengensis*. Our phylogenetic results, which position Stw 53 closer to early *Homo* than to *Australopithecus*, lend support to interpretations that it represents an early stage in the emergence of *Homo* cranial architecture. This conclusion aligns with Curnoe and Tobias (2006) and Grine et al. (1996), who suggested that Stw 53 documents a morphological combination between australopith and *Homo* cranial morphology.

Taken together, the combined morphological and phylogenetic evidence from *A. afarensis*, *A. africanus*, and Stw 53 indicates that these taxa occupy pivotal positions near the base of the *Homo* lineage. Their placement supports the interpretation that *A. africanus* and *A. afarensis* represents the closest australopith relative to early *Homo*. The consistent clustering of Stw 53 with early *Homo* forms, including *H. habilis* and the Dmanisi specimens, further supports its attribution to the genus *Homo*. Overall, these results refine the phylogenetic framework of early hominin evolution by reinforcing the position of the *Australopithecus* as a sister taxon to *Homo* and clarifying the transitional placement of Stw 53 within the early representatives of the genus.

II.4. *Paranthropus*

The phylogenetic analysis recovers *P. boisei* and *P. aethiopicus* as a robust and well-supported monophyletic clade, defined by a suite of cranial synapomorphies that reflect their distinctive masticatory specialization (Constantino and Wood, 2007; Walker et al., 1986). Key synapomorphies such as the presence of a sagittal crest, pronounced sagittal keel on the frontal bone, non-projecting supraorbital region, and reduced *tuberculum zygomaticum anterius* support the interpretation of these taxa as highly derived hominins adapted for intensive masticatory function. These results align with classic assessments of *P. boisei*'s "hyper-robust" cranial morphology and *P. aethiopicus*'s more primitive yet already robust cranial architecture, as discussed by Leakey and Walker (1988) and Walker et al. (1986). The retention of the *tuberculum linearum* and absence of convexity in the *planum occipitale* further distinguish this clade from both australopiths and early *Homo*, corroborating previous work suggesting that *Paranthropus* represents a highly specialized offshoot rather than a direct ancestor of *Homo* (Constantino and Wood, 2007).

Morphometric and 3D shape analyses reinforce these qualitative assessments, revealing consistent patterns across the supraorbital region, frontal convexity, and occipital–nuchal transitions. The distinct cranial profile of *Paranthropus*, characterized by a pronounced antero-posteriorly convex frontal bone and angular junction between the *planum occipitale* and *nuchale*, underscores its functional and evolutionary divergence from contemporaneous australopiths. These findings echo prior interpretations (Strait et al., 2015; Strait et al., 1997) that the genus represents a specialized lineage that radiated in parallel with early *Homo*, rather than contributing directly to the *Homo* clade. Moreover, the recovered phylogenetic separation from *A. afarensis* and *A. africanus* emphasizes that East African australopiths, including *P. aethiopicus*, do not form a transitional grade toward *Homo*, but rather reflect a side branch exhibiting convergent cranio-masticatory adaptations. In sum, the

analysis confirms the long-standing view of *Paranthropus* as a morphologically distinctive, evolutionarily specialized lineage within early hominins.

The broader phylogenetic context of *Paranthropus* remains one of the most debated questions in hominin systematics. In the present analysis, *P. aethiopicus* and *P. boisei* form a monophyletic group placed basally relative to the *Australopithecus*–*Homo* cluster. This position accords with hypotheses that interpret *Paranthropus* as an early diverging lineage that split before the last common ancestor of *Australopithecus* and *Homo*, while persisting well into the Pleistocene (Dembo et al., 2015; Mongle et al., 2023; Wood, 1991, 1992b). Notably, this phylogenetic pattern contrasts with their relatively young geological ages, as *Paranthropus* fossils postdate many specimens of *Australopithecus*, illustrating an evolutionary scenario in which an early-branching lineage persisted alongside, and even outlasted, its more derived relatives.

However, alternative reconstructions have proposed different placements. Some analyses position *Paranthropus* between *A. afarensis* and *A. africanus*, with the former occupying a more basal position, or occasionally forming a trifurcation with these taxa (e.g., Dembo et al., 2015; Lieberman et al., 1996; Mongle et al., 2023; Smith and Grine, 2008; Strait, 2001; Westergaard and Bonde, 2004; Wood, 1992b), whereas others suggest that *Paranthropus* is phylogenetically closer to *Homo* than *Australopithecus* is (e.g., Mongle et al., 2019; Strait and Grine, 2004). The present results lend support to the traditional view of *Paranthropus* as a monophyletic, highly derived clade that evolved independently from the australopith–*Homo* lineage.

Overall, the results of the present analyses reinforce the monophyly and evolutionary distinctiveness of *Paranthropus*, supporting its recognition as a specialized, non-ancestral lineage within early hominins. By consistently recovering *P. aethiopicus* and *P. boisei* as a single clade, the data clarify that these taxa do not present a transitional morphology toward *Homo* but represent a long-lived side branch. Furthermore, the basal placement of this clade relative to the *Australopithecus*–*Homo* cluster emphasizes its early divergence, while the combination of derived cranial features confirms its adaptation. These findings contribute new quantitative support from morphological and 3D analyses to longstanding debates, reconciling previous conflicting interpretations and providing a robust phylogenetic framework for situating *Paranthropus* relative to both australopiths and early members of the genus *Homo*.

Table 14: Comparative assessment of the phylogenetic placement of hominin OTUs across the literature (Introduction) and analytical results from GMM (Chapter III) and morphological and GMM (Chapter IV) cladistic analyses.

OTU	Position in past studies (see, Introduction / <i>Paranthropus</i> , <i>Australopithecus</i> and <i>Homo</i> : phylogenetic hypothesis and debates)	Position in Chapter III – Cladistics and GMM	Position in Chapter IV – Morphological and 3D characters	Agreement / Conflict
<i>A. afarensis</i>	Basal African hominin; ancestral to later <i>Homo</i>	Not included	Clusters with <i>H. rudolfensis</i> (matrix D) or <i>A. africanus</i> (matrix E)	Partial conflict – Expected basal position not consistently recovered; association with <i>H. rudolfensis</i> suggests shape convergence rather than true ancestry.
<i>A. africanus</i>	Transitional; sometimes root of <i>Homo</i>	Root of <i>Homo</i> genus (basal position of the ingroup)	Clusters with Neandertals and <i>H. sapiens</i> (matrix D) or <i>A. afarensis</i> (matrix E)	Conflict – Contradictory positions: basal in Chapter III but derived in some analyses (matrix D of chapter IV).
Stw 53	Transitional morphology; mosaic features; affiliation debated between <i>Australopithecus</i> and <i>Homo</i>	Not included	Intermediate between <i>H. habilis</i> and Dmanisi. sometimes clustered with Dmanisi (matrix D)	Agreement – Consistent with previous studies: supports hypothesis of early <i>Homo</i> attribution.
<i>H. rudolfensis</i>	Early <i>Homo</i> ; debated relationship with <i>H. habilis</i>	Not included	Clusters variably with <i>A. afarensis</i> (matrix D) or <i>H. habilis</i> (matrix E)	Partial conflict – Confirms debated affinities; unstable placement reflects persistent taxonomic ambiguity.
<i>H. habilis</i>	Basal early <i>Homo</i> ; transitional	Positioned above <i>A. africanus</i> , generally unresolved (polytomy)	Base of a new clade composing <i>Australopithecus</i> and <i>H. erectus s.l.</i> ;	Agreement – Consistent placement; corroborates previous studies and previous chapter's phylogenies.
<i>P. aethiopicus</i>	Robust australopith; early <i>Paranthropus</i>	Not included	Clusters with <i>P. boisei</i> ; basal in trees	Agreement – Reinforces monophyly of <i>Paranthropus</i> ; more derived features than <i>Homo</i> .
<i>P. boisei</i>	Derived <i>Paranthropus</i>	Not included	Clusters with <i>P. aethiopicus</i> ; basal in trees	Agreement – Reinforces monophyly of <i>Paranthropus</i> ; more derived features than <i>Homo</i> .

Dmanisi	Early European <i>H. erectus</i> ; oldest <i>Homo</i> outside Africa.	Generally grouped with Sangiran	Included within <i>H. erectus</i> s.l.; sometimes clustered with Stw 53 (matrix D)	Agreement – Confirms intermediary morphology, showing a combination of traits observed in related taxa.
Sangiran	Asian <i>H. erectus</i>	Clusters with Dmanisi, sometimes Zhoukoudian or <i>H. ergaster</i>	Part of <i>H. erectus</i> s.l.; groups with Zhoukoudian and Ngandong	Agreement – Repeated grouping with Asian <i>H. erectus</i> OTUs supports stable regional clade.
Zhoukoudian	Asian <i>H. erectus</i>	Mostly unresolved (polytomy), clusters sometimes with Sangiran/Dmanisi, sometimes with Ngandong	Part of <i>H. erectus</i> s.l.; groups with Ngandong	Agreement – Consistent regional clustering; confirms Asian continuity within <i>H. erectus</i> s.l.
Ngandong	Possibly derived; debated relation to <i>H. sapiens</i> /Denisovans	Basal position of Neandertals/ <i>H. sapiens</i>	Part of <i>H. erectus</i> s.l.; more derived; groups with Zhoukoudian	Partial conflict – Derived status confirmed, but placement differs (clustered with Neandertal– <i>sapiens</i> vs. grouped within <i>H. erectus</i>). Reflects ongoing debate on Ngandong lineage.
<i>H. ergaster</i>	African <i>H. erectus</i>	Positioned above <i>H. habilis</i> , generally unresolved (polytomy)	Basal within <i>H. erectus</i> s.l.; unresolved relationship with Sangiran	Agreement – Stable basal position within <i>H. erectus</i> s.l.; supports African origin of clade.
Early Neandertals	Europe; early stage of Neandertal evolution	Paraphyletic in GMM trees	Clustered with “Classic Neandertal” (matrix D) or in basal position of <i>H. neandertalensis</i> (matrix E); monophyly of Neandertal and sister to <i>H. sapiens</i>	Agreement – Confirms stepwise Neandertal differentiation and closeness to <i>H. sapiens</i> .
Near East Neandertal	Regional variant	Paraphyletic in GMM trees	In basal position of <i>H. neandertalensis</i> (matrix D) or clustered with “Classic Neandertal” (matrix E); monophyly of Neandertal and	Agreement – Matches previous studies: regional variation but overall Neandertal cohesion and relationship to <i>H. sapiens</i> .

			sister to <i>H. sapiens</i>	
Classic Neandertal	Later European Neandertals	Paraphyletic in GMM trees	Clustered with “Early Neandertal” (matrix D) or with “Near East Neandertal” (matrix E); monophyly of Neandertal and sister to <i>H. sapiens</i>	Agreement – Derived position consistent across analyses and with palaeogenomic evidence.
Skhūl-Qafzeh	Early <i>H. sapiens</i> ; basal populations	Sometimes basal position of <i>H. sapiens</i> , sometimes inside the modern human OTUs	Basal within <i>H. sapiens</i> clade; reflects early populations	Agreement – Repeatedly basal; consistent with early dispersal interpretation.
Modern human OTUs	Derived modern human populations, monophyletic	Sometimes monophyletic, sometimes include “Skhūl-Qafzeh”	Monophyletic; geographic substructure not observed	Agreement – Stable monophyly across analyses; supports species coherence and genomic evidence.

Key-points V

***Australopithecus* and early *Homo*:**

- *A. afarensis*: basal African hominin; clusters variably with *H. rudolfensis* (matrix D, Chapter IV) or *A. africanus* (matrix E, Chapter IV).
 - GMM alone often does not include *A. afarensis*; 3D/morphological data capture subtle cranial differences.
- *A. africanus*: transitional; basal to *Homo* in Chapter III; occasionally clusters with Neandertals and *H. sapiens*.
 - Morphological matrices detect autapomorphies that GMM might miss, influencing its placement.
- Stw 53: transitional; sometimes clusters with Dmanisi.
 - Its intermediate morphology is highlighted in 3D shape analyses.
- *H. rudolfensis*: variable placement; clusters with *A. afarensis* or *H. habilis*.
 - Differences between shape-based and discrete morphological matrices show the importance of coding subtle features.
- *H. habilis*: basal early *Homo*; bridges African *Australopithecus* and *H. erectus* s.l.
 - Consistently shows transitional features across methods; more explicit in morphological coding than in GMM alone.

***Paranthropus*:**

- *P. aethiopicus*: basal; clusters with *P. boisei*.
- *P. boisei*: derived; clusters with *P. aethiopicus*, basal in trees.
 - Robust cranial features are clearly captured in both 3D shape and traditional morphological matrices; placements are consistent.

***H. erectus sensu lato*:**

- Dmanisi: early Eurasian *H. erectus*; included in *H. erectus* s.l.; sometimes clusters with Stw 53.
- Sangiran: Asian *H. erectus*; part of *H. erectus* s.l., groups with Zhoukoudian and Ngandong.
- Zhoukoudian: Asian *H. erectus*; groups with Ngandong.
- Ngandong: more derived; groups with Zhoukoudian.
- *H. ergaster*: African *H. erectus*; basal within *H. erectus* s.l.; relationship with Sangiran unresolved.
 - GMM analyses sometimes yield paraphyletic *H. erectus* s.l., highlighting shape overlap between African and Asian populations.
 - Morphological/3D matrices resolve more nuanced relationships, detect synapomorphies, and clarify derivation and basal positions.
 - Differences between matrices illustrate the impact of coding continuous vs. discrete characters on tree topology.

Neandertals and *H. sapiens*:

- *Early, Near East, Classic Neandertals*: paraphyletic in GMM; monophyletic in morphological/3D matrices; sister group to *H. sapiens*.
- *Skhül-Qafzeh*: early *H. sapiens*; often basal within *H. sapiens* clade; sometimes grouped inside modern human OTUs.
- *Modern human OTUs*: monophyletic; geographic substructure not resolved.
 - GMM may underestimate divergence within closely related populations.

General trends and methodological implications:

- Morphological/3D matrices allow detection of discrete and subtle cranial features that GMM or morphology alone may not fully capture.
- Transitional OTUs (Stw 53, *H. habilis*, *H. rudolfensis*) show variable placements depending on method, reflecting their mosaic morphology.
- *H. erectus* s.l. demonstrates strong method-dependent variation: African vs. Asian populations are more clearly differentiated in shape-based GMM than in discrete morphological coding.
- Consistent findings across methods: monophyly of *H. sapiens*, basal positions of *Australopithecus*, and robust *Paranthropus* clustering.
- Conflicts highlight the importance of combining multiple data types for robust phylogenetic inference.

Conclusion

This dissertation sets out to evaluate how different forms of morphological information contribute to reconstructing phylogenetic relationships among fossil hominins, addressing the long-standing tension in palaeoanthropology between interpretability and precision in morphological data. By comparing discrete characters, and geometric morphometric data, as 3D coordinates or principal component variables and assessing their performance individually and in combination under multiple weighting schemes, this work sought not only to determine which data structures yields robust and biologically coherent phylogenies and to better resolve evolutionary relationships among early *Homo* and australopith species (*id est Australopithecus* and *Paranthropus*).

The analyses reveal that each data type possesses distinct strengths and limitations, and that their integration provides the most promising avenue for reconciling interpretability, reproducibility, and phylogenetic signal. Discrete morphological characters remain central to phylogenetic inference due to their historical grounding and explicit hypotheses of homology. They allow evolutionary questions to be framed in terms of trait transformations with functional and developmental significance. Yet, in any type of analysis, discretization introduces subjectivity and simplifies complex biological variation, often resulting in unresolved polytomies where morphological transitions are gradual or homoplasy is high.

Geometric morphometric data address these limitations by quantifying shape as continuous variables. Landmark coordinates and derived principal components provide a mathematically rigorous and standardized representation of form, reducing observer bias and enabling visualization of evolutionary transformations. While morphometric data alone can recover phylogenetic patterns congruent with biological expectations, they sometimes reflect overall phenetic similarity rather than shared derived characters, due to landmark interdependence influenced by integration, function, and development. Nevertheless, combining morphometric and discrete data produces trees that are both more stable and appear to reflect phylogenetic history, demonstrating the complementarity of these approaches.

Principal component (PC)-based analyses occupy a conceptual middle ground. By generating orthogonal variables, PCs mitigate interdependence but lose some spatial and biological information. PC-based trees show moderate congruence and improve with denser landmark sampling yet still underperform relative to combined datasets. This reinforces a central insight: no

single morphological representation can simultaneously maximize independence, interpretability, and completeness; phylogenetic accuracy depends on balancing these trade-offs.

A key finding concerns the stabilizing effect of data integration. When discrete characters are combined with continuous morphometric variables, resulting phylogenies exhibit reduced sensitivity to weighting differences, indicating that continuous data buffer distortions from character redundancy and homoplasy. Among weighting schemes, RC-weighting consistently performs best, balancing consistency and retention while accommodating evolutionary complexity. CI-weighting, which emphasizes raw consistency, underperforms, highlighting the limitations of strict parsimony assumptions, whereas RI-weighting benefits from morphometric integration.

These results carry conceptual significance. Morphology should not be viewed as a static record or limited to a single analytical framework. Rather, discrete and continuous datasets are complementary expressions of the same underlying signal. Discrete characters provide interpretive depth and evolutionary context, while morphometric data quantify continuous variation. Their integration reconciles these perspectives, yielding trees that are analytically robust and biologically meaningful. This framework also encourages reconsideration of character definition, suggesting that future approaches may benefit from modular descriptions that combine geometric and conceptual representation of anatomical structures.

In sum, the methodological insights of this study demonstrate that:

- Discrete data are interpretable and hypothesis-driven but constrained by subjectivity and character dependence.
- PC-based data reduce interdependence but lose spatial and biological meaning.
- Landmark data faithfully capture shape and enable 3D reconstructions but are computationally demanding and interdependent.
- Combined datasets outperform individual types, producing more stable, resolved, and biologically coherent phylogenies.
- RC-weighting optimally manages homoplasy and conflicts, while morphometric integration reduces sensitivity to weighting choices.

Overall, the analyses highlight the power of integrative morphometric–morphological approaches. By combining quantitative and qualitative data under robust weighting frameworks, researchers can generate phylogenies that are both methodologically sound and evolutionarily interpretable,

laying the groundwork for nuanced evolutionary reconstructions and future integration with genomic, ecological, and developmental data.

With each analysis a unique tree was obtained in which the phylogenetic results provided a coherent picture of hominin evolution characterized by continuity and regional differentiation. *Paranthropus* taxa occupy basal positions and emerges as a distinct, specialized clade, reflecting its unique cranial adaptations and relative evolutionary isolation. *Australopithecus*, with *A. afarensis* as an early lineage and *A. africanus* representing a derived southern branch, is generally placed at the beginning of genus *Homo*. Early *Homo* exhibits overlapping variation, with *H. habilis*, *H. rudolfensis*, and transitional specimens such as Stw 53 bridging australopiths and *H. erectus*.

H. erectus sensu lato demonstrates geographically structured diversification. African *H. ergaster* forms the basal component, while Asian populations, including Javan and Chinese specimens, represent derived regional sublineages. Morphometric and discrete data converge to show that intra-lineage variation explains much of the observed diversity, supporting a model of a dynamic, connected population network rather than multiple distinct species. The Dmanisi fossils exemplify this pattern, combining plesiomorphic and derived traits and suggesting that dispersal beyond Africa preceded the full consolidation of *H. erectus* morphology.

Later hominins, including Neandertals and modern humans, continue the pattern of continuity tempered by regional differentiation. *H. neandertalensis* is recovered as a monophyletic, well-defined clade closely related to *H. sapiens*. Morphometric analyses reveal that differences between these lineages are gradational rather than categorical, reflecting shared ancestry and divergent adaptation within a broader morphological continuum. Early *H. sapiens* specimens, such as Skhūl–Qafzeh, retain subtle archaic traits, indicating that defining modern human morphology evolved piecemeal across geographically structured populations.

Taken together, these results emphasize that morphological evolution is multidimensional and shaped by functional adaptation, developmental integration, and ecological opportunity. Quantitative shifts captured by morphometric data complement the discrete transformations encoded in traditional characters, revealing both macroevolutionary divergence and microevolutionary continuity. This integrative perspective reframes hominin evolution as a dynamic process, where morphological diversity, gene flow, and regional experimentation interact within an evolutionary continuum.

From a methodological and conceptual standpoint, the study demonstrates that ambiguity in phylogenetic reconstructions often reflects genuine evolutionary complexity, as well as differences in dataset composition, such as the inclusion of additional or poorly understood OTUs (e.g., the contrast between matrix A in Chapter III and matrix D in Chapter IV), rather than analytical failure. Poorly resolved nodes often reflect gaps in the available data, such as limited sampling or insufficient knowledge of morphological variation within fossil taxa, rather than indicating specific evolutionary processes. Future research should incorporate network approaches, Bayesian total-evidence frameworks, and morphometric integration with genomic data to capture this complexity.

Looking forward, several research directions emerge. Expanding integrated datasets across broader taxonomic and temporal scales, incorporating ecological and behavioural variables, and connecting morphological patterns to genomic and developmental data will deepen our understanding of evolutionary dynamics. Applying these frameworks beyond hominins can harmonize morphological and molecular phylogenetics across vertebrates, advancing comparative biology more broadly. Technological innovations, including 3D imaging, virtual morphology, and computational modelling, will further enhance the precision and scope of integrative analyses.

In conclusion, this dissertation demonstrates that morphology, when rigorously quantified and integrated, remains a powerful tool for reconstructing evolutionary history. Phylogenetic analyses indicate that human evolution involves branching lineages influenced by both genetic drift and selection, rather than a simple linear progression. Tree-based models remain useful for reconstructing these relationships, but resolution is limited by incomplete sampling and the variability of fossil specimens. The integrative framework developed here establishes a model for future research: one in which diverse data types, analytical methods, and conceptual perspectives coexist in dialogue, yielding phylogenetic reconstructions that are both biologically meaningful and methodologically robust. Morphology encodes history, function, and process; by synthesizing discrete and continuous data, we can begin to read that record with greater clarity, nuance, and fidelity.

The application of this work to the genera *Homo*, *Australopithecus*, and *Paranthropus* is part of the lineage of early inquiries into this question, continuing the cladistic analysis work of the first palaeoanthropologists who dared to investigate using this method. We have proposed new avenues that enrich this line of research.

Fossil evidence provides key information in the evolutionary history of early *Homo* and australopiths, capturing variation that informs phylogenetic reconstruction. Expanding the dataset with additional specimens and combining landmark and discrete data will improve resolution and provide a more robust framework for understanding morphological evolution.

References

- Adams, D. C., Cardini, A., Monteiro, L. R., O'Higgins, P., & Rohlf, F. J. (2011). Morphometrics and phylogenetics: Principal components of shape from cranial modules are neither appropriate nor effective cladistic characters. *Journal of Human Evolution*, 60(2), 240–243. <https://doi.org/10.1016/j.jhevol.2010.02.003>
- Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: Ten years of progress following the 'revolution'. *Italian Journal of Zoology*, 71(1), 5–16. <https://doi.org/10.1080/11250000409356545>
- Adams, D. C., Rohlf, F. J., & Slice, D. E. (2013). A field comes of age: Geometric morphometrics in the 21st century. *Hystrix, the Italian Journal of Mammalogy*, 24(1). <https://doi.org/10.4404/hystrix-24.1-6283>
- Adams, E. N., III. (1972). Consensus techniques and the comparison of taxonomic trees. *Systematic Biology*, 21(4), 390–397. <https://doi.org/10.1093/sysbio/21.4.390>
- Ahern, J. C. M., Lee, S.-H., & Hawks, J. D. (2002). The late Neandertal supraorbital fossils from Vindija Cave, Croatia: A biased sample? *Journal of Human Evolution*, 43(3), 419–432. <https://doi.org/10.1006/jhev.2002.0586>
- Alemseged, Z. (2023). Reappraising the palaeobiology of *Australopithecus*. *Nature*, 617(7959), 45–54. <https://doi.org/10.1038/s41586-023-05957-1>
- Alexeev, V. P. (1986). *The origin of the human race*. Progress.
- Andrews, P. (1984). An alternative interpretation of the characters used to define *Homo erectus*. *Courier Forschungsinstitut Senckenberg*, 69, 167–175.
- Antón, S. C. (2002). Evolutionary significance of cranial variation in Asian *Homo erectus*. *American Journal of Physical Anthropology*, 118(4), 301–323. <https://doi.org/10.1002/ajpa.10091>
- Antón, S. C. (2003). Natural history of *Homo erectus*. *American Journal of Physical Anthropology*, 122(S37), 126–170. <https://doi.org/10.1002/ajpa.10399>
- Antón, S. C., Potts, R., & Aiello, L. C. (2014). Evolution of early *Homo*: An integrated biological perspective. *Science*, 345(6192), 1236828. <https://doi.org/10.1126/science.1236828>
- Antón, S. C., & Swisher, C. C. (2004). Early Dispersals of *Homo* from Africa. *Annual Review of Anthropology*, 33(Volume 33, 2004), 271–296. <https://doi.org/10.1146/annurev.anthro.33.070203.144024>
- Arambourg, C., & Coppens, Y. (1968). Decouverte d'un Australophecien nouveau dans les gisements de Lomo (Ethiopie). *South African Journal of Science*, 64(2), 58.
- Arensburg, B., & Belfer-Cohen, A. (1998). Sapiens and Neandertals. In T. Akazawa, K. Aoki, & O. Bar-Yosef (Eds), *Neandertals and Modern Humans in Western Asia* (pp. 311–322). Springer US. https://doi.org/10.1007/0-306-47153-1_19
- Argue, D. (2016). *Homo rudolfensis*. In *Encyclopedia of Evolutionary Psychological Science* (Weekes-Shackelford, V., Shackelford, T., Weekes-Shackelford, V., pp. 1–4). Springer. https://doi.org/10.1007/978-3-319-16999-6_3434-2
- Arnold, E. N. (1981). Estimating phylogenies at low taxonomic levels. *Zeitschrift Fur Zoologische Systematik Und Evolutionsforschung*, 19(1), 1–35.
- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S., & Suwa, G. (1999). *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science*, 284(5414), 629–635. <https://doi.org/10.1126/science.284.5414.629>
- Baab, K. L. (2011). Cranial shape in asian *Homo erectus*: Geographic, anagenetic, and size-related variation. In C. J. Norton & D. R. Braun (Eds), *Asian Paleoanthropology: From Africa to China and Beyond* (pp. 57–79). Springer Netherlands. https://doi.org/10.1007/978-90-481-9094-2_6
- Bae, C. J., Douka, K., & Petraglia, M. D. (2017). On the origin of modern humans: Asian perspectives. *Science*, 358(6368). <https://doi.org/10.1126/science.aai9067>
- Baken, E. K., Collyer, M. L., Kaliontzopoulou, A., & Adams, D. C. (2021). geomorph v4.0 and gmShiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution*, 12(12), 2355–2363. <https://doi.org/10.1111/2041-210X.13723>

- Balzeau, A., Gilissen, E., & Grimaud-Hervé, D. (2012). Shared pattern of endocranial shape asymmetries among great apes, anatomically modern humans, and fossil hominins. *PLOS ONE*, 7(1), e29581. <https://doi.org/10.1371/journal.pone.0029581>
- Bapst, D. W. (2013). When can clades be potentially resolved with morphology? *PLOS ONE*, 8(4), e62312. <https://doi.org/10.1371/journal.pone.0062312>
- Barriel, V. (1994). *Les relations de parenté au sein des Hominoidea et la place de Pan paniscus: Comparaison et analyse méthodologique des phylogénies morphologique et moléculaire* [These de doctorat, Paris 6]. <https://theses.fr/1994PA066026>
- Baum, D. (1992). Phylogenetic species concepts. *Trends in Ecology & Evolution*, 7, 1–2.
- Berger, L. R., Ruitter, D. J. de, Churchill, S. E., Schmid, P., Carlson, K. J., Dirks, P. H. G. M., & Kibii, J. M. (2010). *Australopithecus sediba*: A new species of Homo-like australopith from South Africa. *Science*, 328(5975), 195–204. <https://doi.org/10.1126/science.1184944>
- Black, D. (1927). On the lower molar hominid tooth from the Chou Kou Tien deposit. *Paleontologica Sinica*, 7(série D), 1–28.
- Black, D. (1930). Interim report on the skull of *Sinanthropus*. *Bulletin of the Geological Society of China*, 9(1), 7–10. <https://doi.org/10.1111/j.1755-6724.1930.mp9001002.x>
- Black, D. (1934). The croonian lecture. On the discovery, morphology, and environment of *Sinanthropus pekinensis*. *Philosophical Transactions of the Royal Society of London., Series B*(223), 57–120. <https://doi.org/10.1098/rstb.1934.0003>
- Blackith, R. E., & Reyment, R. A. (1971). *Multivariate morphometrics*. Academic Press.
- Blackwell, B., Montoya, A. C., Bisson, M. S., Blisckstein, J. I. B., Skinner, A. R., & Beelitz, P. (2007). ESR dating bovid teeth from Neanderthal layer at La Ferrassie, France. *Geological Society of America Bulletin*, 39, 548.
- Blum, H. (1973). Biological shape and visual science (part I). *Journal of Theoretical Biology*, 38(2), 205–287. [https://doi.org/10.1016/0022-5193\(73\)90175-6](https://doi.org/10.1016/0022-5193(73)90175-6)
- Blum, H., & Nagel, R. N. (1978). Shape description using weighted symmetric axis features. *Pattern Recognition, The Proceedings of the IEEE Computer Society Conference*, 10(3), 167–180. [https://doi.org/10.1016/0031-3203\(78\)90025-0](https://doi.org/10.1016/0031-3203(78)90025-0)
- Bonde, N. (1977). Cladistic classification as applied to vertebrates. In M. K. Hecht, P. C. Goody, & B. M. Hecht (Eds), *Major Patterns in Vertebrate Evolution* (pp. 741–804). Springer US. https://doi.org/10.1007/978-1-4684-8851-7_26
- Bonde, N. (1989). *Erectus* and *neanderthalensis* as species or subspecies of *Homo* with a model of speciation in hominids. In *Hominidae* (E. Jiacomo, pp. 205–208). Jaca Book.
- Bookstein, F. L. (1977). *The study of shape transformation after D’Arcy Thompson*.
- Bookstein, F. L. (1989). Principal warps: Thin-plate splines and the decomposition of deformations. *IEEE Transactions on Pattern Analysis and Machine Intelligence*, 11(6), 567–585. <https://doi.org/10.1109/34.24792>
- Bookstein, F. L. (1991). *Morphometric tools for landmark data: Geometry and biology*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511573064>
- Bookstein, F. L. (1994). Can biometrical shape be a homologous character? In *Homology: The Hierarchical Basis of Comparative Biology* (Hall Brian K., pp. 197–227). Academic Press.
- Bookstein, F. L. (1996). Biometrics, biomathematics and the morphometric synthesis. *Bulletin of Mathematical Biology*, 58(2), 313–365. [https://doi.org/10.1016/0092-8240\(95\)00329-0](https://doi.org/10.1016/0092-8240(95)00329-0)
- Bookstein, F. L. (1997). Landmark methods for forms without landmarks: Morphometrics of group differences in outline shape. *Medical Image Analysis*, 1(3), 225–243. [https://doi.org/10.1016/S1361-8415\(97\)85012-8](https://doi.org/10.1016/S1361-8415(97)85012-8)
- Bookstein, F. L. (2002). Creases as morphometric characters. In *Morphology, Shape and Phylogeny* (MacLeod N., Forey P.L., editors, pp. 139–174). Taylor & Francis.

- Bookstein, F. L., Chernoff, B., Elder, R. L., Humphries, J. M. Jr., Smith, G. R., & Strauss, R. F. (1985). *Morphometrics in Evolutionary Biology*. Academy of Natural Science of Philadelphia.
- Boule, M. (1911). L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie*, 6(109–172).
- Boule, M. (1912). L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie*, 7, 105–192.
- Boule, M. (1913). L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie*, 8, 1–62.
- Boule, M. (1921). *Les Hommes Fossiles*. Mason et Cie.
- Brace, C. L. (1967). *The stages of human evolution*. Prentice Hall.
- Braga, J. (1998). Chimpanzee variation facilitates the interpretation of the incisive suture closure in South African Plio-Pleistocene hominids. *American Journal of Physical Anthropology*, 105(2), 121–135. [https://doi.org/10.1002/\(SICI\)1096-8644\(199802\)105:2%253C121::AID-AJPA2%253E3.0.CO;2-Y](https://doi.org/10.1002/(SICI)1096-8644(199802)105:2%253C121::AID-AJPA2%253E3.0.CO;2-Y)
- Bräuer, G. (1982). *Early anatomically modern man in Africa and the replacement of the Mediterranean and European Neanderthals*. *Resumé*: 112.
- Bräuer, G. (1992). Africa's place in the evolution of *Homo sapiens*. In *Continuity or Replacement. Controversies in Homo sapiens Evolution* (G. Bräuer and F.H. Smith, pp. 83–98). Balkema.
- Bräuer, G. (2007). Origin of modern humans. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 1749–1779). Springer. https://doi.org/10.1007/978-3-540-33761-4_57
- Bräuer, G., & Mbua, E. (1992). *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *Journal of Human Evolution*, 22(2), 79–108. [https://doi.org/10.1016/0047-2484\(92\)90032-5](https://doi.org/10.1016/0047-2484(92)90032-5)
- Broca, P. (1868). Sur les crânes et ossements des Eyzies. *Bulletins et Mémoires de La Société d'Anthropologie de Paris*, 30, 335–349. <https://doi.org/10.3166/bmsap-2018-0027>
- Broom, R. (1938). Further evidence on the structure of the South African Pleistocene anthropoids. *Nature*, 142(3603), 897–899. <https://doi.org/10.1038/142897a0>
- Broom, R. (1939). The dentition of the Transvaal Pleistocene anthropoids, *Plesianthropus* and *Paranthropus*. *Annals of the Transvaal Museum*, 19(3), 303–314. https://doi.org/10.10520/AJA00411752_483
- Broom, R., & Robinson, J. T. (1950). Man contemporaneous with the Sawartkrans ape-man. *American Journal of Physical Anthropology*, 8(2), 151–156. <https://doi.org/10.1002/ajpa.1330080211>
- Brothwell, D. R. (1961). The people of Mount Carmel. *Proceedings of the Prehistoric Society*, 27, 155–159. <https://doi.org/10.1017/S0079497X00016029>
- Brunet, M., Beauvillain, A., Coppens, Y., Heintz, E., Moutaye, A. H. E., & Pilbeam, D. R. (1996). *Australopithecus bahrelghazali*, une nouvelle espèce d'Hominidé ancien de la région de Koro Toro (Tchad). *Comptes Rendus de l'Académie Des Sciences - Series IIA - Earth and Planetary Science*, 322, 907–913.
- Brunet, M., Guy, F., Pilbeam, D., Mackaye, H. T., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., De Bonis, L., Coppens, Y., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., ... Zollikofer, C. (2002). A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, 418(6894), 145–151. <https://doi.org/10.1038/nature00879>
- Buettner-Janusch, J. (1966). *Origins of man*. Wiley.
- Camin, J. H., & Sokal, R. R. (1965). A method for deducing branching sequences in phylogeny. *Evolution*, 19(3), 311–326. <https://doi.org/10.2307/2406441>
- Campbell, B. (1962). The Systematics of Man. *Nature*, 194(4825), 225–232. <https://doi.org/10.1038/194225A0>
- Campbell, B. (1963). Quantitative taxonomy and human evolution. In *Classification and Human Evolution* (Washburn S.L., pp. 50–75). Taylor & Francis Group.
- Caparros, M. (1997). *Homo sapiens archaïques: Un seul ou plusieurs taxons (espèces) ? : analyse cladistique et analyse morphométrique* [These de doctorat, Paris, Muséum national d'histoire naturelle]. <https://www.theses.fr/1997MNHN0006>
- Cardini, A., & Elton, S. (2008). Does the skull carry a phylogenetic signal? Evolution and modularity in the guenons. *Biological Journal of the Linnean Society*, 93(4), 813–834. <https://doi.org/10.1111/j.1095-8312.2008.01011.x>

- Carotenuto, F., Tsikaridze, N., Rook, L., Lordkipanidze, D., Longo, L., Condemi, S., & Raia, P. (2016). Venturing out safely: The biogeography of *Homo erectus* dispersal out of Africa. *Journal of Human Evolution*, 95, 1–12. <https://doi.org/10.1016/j.jhevol.2016.02.005>
- Catalano, S. A., Ercoli, M. D., & Prevosti, F. J. (2015). The more, the better: The use of multiple landmark configurations to solve the phylogenetic relationships in musteloids. *Systematic Biology*, 64(2), 294–306. <https://doi.org/10.1093/sysbio/syu107>
- Catalano, S. A., Goloboff, P. A., & Giannini, N. P. (2010). Phylogenetic morphometrics (I): The use of landmark data in a phylogenetic framework. *Cladistics*, 26(5), 539–549. <https://doi.org/10.1111/j.1096-0031.2010.00302.x>
- Catalano, S. A., & Torres, A. (2017). Phylogenetic inference based on landmark data in 41 empirical data sets. *Zoologica Scripta*, 46(1), 1–11. <https://doi.org/10.1111/zsc.12186>
- Chamberlain, A. T., & Wood, B. A. (1987). Early hominid phylogeny. *Journal of Human Evolution*, 16(1), 119–133. [https://doi.org/10.1016/0047-2484\(87\)90063-7](https://doi.org/10.1016/0047-2484(87)90063-7)
- Chapman, R. E. (1990). Conventional procrustes approaches. In *Proceedings of the Michigan morphometrics workshop* (F. J. Rohlf and F. L. Bookstein, Vol. 2, pp. 251–267). University of Michigan Museum of Zoology.
- Charlesworth, M. J. (1956). Aristotle's Razor. *Philosophical Studies*, 6(0), 105–112. <https://doi.org/10.5840/philstudies1956606>
- Chen, F.-C., & Li, W.-H. (2001). Genomic divergences between humans and other Hominoids and the effective population size of the common ancestor of humans and chimpanzees. *The American Journal of Human Genetics*, 68(2), 444–456. <https://doi.org/10.1086/318206>
- Chinzei, K. (1970). The Amud cave site and its deposits. In *The Amud man and his cave site* (Suzuki H. and Takai F., pp. 21–52). University of Tokyo.
- Choudhuri, S. (2014). Fundamentals of Molecular Evolution. In S. Choudhuri (Ed.), *Bioinformatics for Beginners* (pp. 27–53). Academic Press. <https://doi.org/10.1016/B978-0-12-410471-6.00002-5>
- Clarke, R. J. (2008). Latest information on Sterkfontein's *Australopithecus* skeleton and a new look at *Australopithecus*: Research in action. *South African Journal of Science*, 104(11), 443–449. <https://doi.org/10.10520/EJC96745>
- Clouse, R. M., de Bivort, B. L., & Giribet, G. (2011). Phylogenetic signal in morphometric data. *Cladistics*, 27(4), 337–340. <https://doi.org/10.1111/j.1096-0031.2010.00346.x>
- Collard, M., & Wood, B. (2000). How reliable are human phylogenetic hypotheses? *Proceedings of the National Academy of Sciences*, 97(9), 5003–5006. <https://doi.org/10.1073/pnas.97.9.5003>
- Collard, M., & Wood, B. (2001). How reliable are current estimates of fossil catarrhine phylogeny? An assessment using extant great apes and Old-World monkeys. In *Phylogeny of the Neogene Hominoid Primates of Eurasia* (L. de Bonis, G. D. Koufos and P. Andrews, Vol. 2, pp. 118–150). Cambridge University Press.
- Condemi, S. (1988). Réexamen des hommes fossiles Riss-Würm de Saccopastore (Italie): Caractères archaïques et néanderthaliens. *Réexamen Des Hommes Fossiles Riss-Würm de Saccopastore (Italie): Caractères Archaïques et Néanderthaliens*, 306(7), 499–504.
- Condemi, S. (1992). *Les hommes fossiles de Saccopastore et leurs relations phylogénétiques*. CNRS Éditions.
- Condemi, S. (2001). *Les néandertaliens de La Chaise*. Comité des travaux historiques et scientifiques (CTHS).
- Conroy, G. C., Falk, D., Guyer, J., Weber, G. W., Seidler, H., & Recheis, W. (2000). Endocranial capacity in *Sts 71 (Australopithecus africanus)* by three-dimensional computed tomography. *The Anatomical Record*, 258(4), 391–396. [https://doi.org/10.1002/\(SICI\)1097-0185\(20000401\)258:4%253C391::AID-AR7%253E3.0.CO;2-R](https://doi.org/10.1002/(SICI)1097-0185(20000401)258:4%253C391::AID-AR7%253E3.0.CO;2-R)

- Conroy, G. C., & Vannier, M. W. (1984). Noninvasive three-dimensional computer imaging of matrix-filled fossil skulls by high-resolution computed tomography. *Science*, 226(4673), 456–458. <https://doi.org/10.1126/science.226.4673.456>
- Conroy, G. C., & Vannier, M. W. (1987). Dental development of the Taung skull from computerized tomography. *Nature*, 329(6140), 625–627. <https://doi.org/10.1038/329625a0>
- Constantino, P. (2021). *Paranthropus aethiopicus*. In T. K. Shackelford & V. A. Weekes-Shackelford (Eds), *Encyclopedia of Evolutionary Psychological Science* (pp. 5684–5685). Springer International Publishing. https://doi.org/10.1007/978-3-319-19650-3_3429
- Constantino, P., & Wood, B. (2007). The evolution of *Zinjanthropus boisei*. *Evolutionary Anthropology: Issues, News, and Reviews*, 16(2), 49–62. <https://doi.org/10.1002/evan.20130>
- Cracraft, J. (1983). Species concepts and speciation analysis. In R. F. Johnston (Ed.), *Current Ornithology* (Vol. 1, pp. 159–187). Springer US. https://doi.org/10.1007/978-1-4615-6781-3_6
- Cracraft, J. (1989). Speciation and its ontology: The empirical consequences of alternative species concepts for understanding patterns and processes of differentiation. In *Speciation and its Consequences* (Otte D. & Endler J.A., pp. 28–59). Sinauer Associates.
- Cracraft, J. (1997). Species concepts in systematics and conservation biology-an ornithological viewpoint. In *Species: The Units of Biodiversity*. (Claridge M.F., Dawah A.A. & Wilson M.R., pp. 325–339). Chapman and Hall.
- Curnoe, D. (2010). A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. Nov.). *HOMO*, 61(3), 151–177. <https://doi.org/10.1016/j.jchb.2010.04.002>
- Curnoe, D., & Thorne, A. (2003). Number of ancestral human species: A molecular perspective. *HOMO*, 53(3), 201–224. <https://doi.org/10.1078/0018-442X-00051>
- Curnoe, D., & Tobias, P. V. (2006). Description, new reconstruction, comparative anatomy, and classification of the Sterkfontein Stw 53 cranium, with discussions about the taxonomy of other southern African early *Homo* remains. *Journal of Human Evolution*, 50(1), 36–77. <https://doi.org/10.1016/j.jhevol.2005.07.008>
- Dart, R. A. (1925). *Australopithecus africanus* The Man-Ape of South Africa. *Nature*, 115(2884), Article 2884. <https://doi.org/10.1038/115195a0>
- Darwin, C. (1859). *On the origin of species*. John Murray.
- Darwin, C. (1872). *On the origin of species* (6th edn). John Murray.
- Day, M. H., Leakey, R. E. F., Walker, A. C., & Wood, B. A. (1976). New hominids from East Turkana, Kenya. *American Journal of Physical Anthropology*, 45(3), 369–435. <https://doi.org/10.1002/ajpa.1330450304>
- de Lumley, M.-A., Gabounia, L., Vekua, A., & Lordkipanidze, D. (2006). Les restes humains du Pliocène final et du début du Pléistocène inférieur de Dmanissi, Géorgie (1991–2000). I – Les crânes, D 2280, D 2282, D 2700. *L'Anthropologie*, 110(1), 1–110. <https://doi.org/10.1016/j.anthro.2006.02.001>
- de Pinna, M. C. C. (1991). Concepts and tests of homology in the cladistic paradigm. *Cladistics*, 7(4), 367–394. <https://doi.org/10.1111/j.1096-0031.1991.tb00045.x>
- De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic Biology*, 56(6), 879–886.
- Dean, D., Hublin, J.-J., Holloway, R., & Ziegler, R. (1998). On the phylogenetic position of the pre-Neandertal specimen from Reilingen, Germany. *Journal of Human Evolution*, 34(5), 485–508. <https://doi.org/10.1006/jhev.1998.0214>
- Delson, E. (1985). *Ancestors: The Hard Evidence*. Alan R. Liss, Inc.
- Delson, E., Eldredge, N., & Tattersall, I. (1977). Reconstruction of hominid phylogeny: A testable framework based on cladistic analysis. *Journal of Human Evolution*, 6(3), 263–278. [https://doi.org/10.1016/S0047-2484\(77\)80051-1](https://doi.org/10.1016/S0047-2484(77)80051-1)

- Dembo, M., Matzke, N. J., Mooers, A. Ø., & Collard, M. (2015). Bayesian analysis of a morphological supermatrix sheds light on controversial fossil hominin relationships. *Proceedings of the Royal Society B: Biological Sciences*, 282(1812), 20150943. <https://doi.org/10.1098/rspb.2015.0943>
- Dennell, R., & Roebroeks, W. (2005). An Asian perspective on early human dispersal from Africa. *Nature*, 438(7071), 1099–1104. <https://doi.org/10.1038/nature04259>
- Dobzhansky, T. (1937). *Genetics and the origin of species*. Columbia University Press.
- Dobzhansky, T. (1950). Mendelian populations and their evolution. *The American Naturalist*, 84(819), 401–418. <https://doi.org/10.1086/281638>
- Dubois, E. (1893). Palaeontologische onderzoekingen op Java. *Verslag van Het Mijnwezen (Batavia)*, 10, 10–14.
- Dubois, E. (1940). The fossil human remains discovered in Java by Dr. G.H.R. von Koenigswald and attributed by him to *Pithecanthropus erectus*, in reality remains of *Homo sapiens soloensis*. *Nederlandse Akademie van Wetenschappen*, 43, 841–854.
- Eldredge, N., & Cracraft, J. (1980). *Phylogenetic patterns and the evolutionary process* (Vol. 6). Columbia University Press.
- Eldredge, N., & Gould, S. J. (1972). Punctuated equilibria: An alternative to phyletic gradualism. In *Models in paleobiology* (Schopf T.J.M., pp. 83–115). Freeman Cooper & Co.
- Eldredge, N., & Tattersall, I. (1975). Evolutionary models, phylogenetic reconstruction, and another look at hominid phylogeny. *Contributions to Primatology*, 5.
- Elyaqtime, M. (1995). *Variabilité et évolution de l'os temporal chez Homo sapiens: Comparaison avec Homo erectus* [These de doctorat. Anthropologie, Bordeaux 1]. <https://theses.fr/1995BOR10582>
- Elyaqtime, M. (2001). Morphological and functional aspects of the temporal bone articular tubercle morphology in *Homo erectus* and *Homo sapiens*. *Human Evolution*, 16(3), 159–168. <https://doi.org/10.1007/BF02437410>
- Fabre, V., Condemi, S., & Degioanni, A. (2009). Genetic evidence of geographical groups among Neanderthals. *PLOS ONE*, 4(4), e5151. <https://doi.org/10.1371/journal.pone.0005151>
- Farris, J. (1983). The logical basis of phylogenetic analysis. In *Advances in Cladistics* (Platnick, N.I., and Funk, V.A., pp. 7–36). Columbia University Press.
- Farris, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology*, 18(4), 374–385. <https://doi.org/10.2307/2412182>
- Farris, J. S. (1970). Methods for Computing Wagner Trees. *Systematic Biology*, 19(1), 83–92. <https://doi.org/10.1093/sysbio/19.1.83>
- Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics: The International Journal of the Willi Hennig Society*, 5(4), 417–419. <https://doi.org/10.1111/j.1096-0031.1989.tb00573.x>
- Feibel, C. S., Brown, F. H., & McDougall, I. (1989). Stratigraphic context of fossil hominids from the Omo group deposits: Northern Turkana Basin, Kenya and Ethiopia. *American Journal of Physical Anthropology*, 78(4), 595–622. <https://doi.org/10.1002/ajpa.1330780412>
- Feibel, C. S., Lepre, C. J., & Quinn, R. L. (2009). Stratigraphy, correlation, and age estimates for fossils from Area 123, Koobi Fora. *Journal of Human Evolution*, 57(2), 112–122. <https://doi.org/10.1016/j.jhevol.2009.05.007>
- Felsenstein, J. (1978). Cases in which parsimony or compatibility methods will be positively misleading. *Systematic Biology*, 27(4), 401–410. <https://doi.org/10.1093/sysbio/27.4.401>
- Felsenstein, J. (1985a). Confidence limits on phylogenies: An approach using the bootstrap. *Evolution; International Journal of Organic Evolution*, 39(4), 783–791. <https://doi.org/10.1111/j.1558-5646.1985.tb00420.x>
- Felsenstein, J. (1985b). Phylogenies and the comparative method. *The American Naturalist*, 125(1), 1–15. <https://doi.org/10.1086/284325>
- Felsenstein, J. (2004). *Inferring Phylogenies*. Sinauer Associates.

- Ferguson, W. W. (1987). Taxonomic status of the hominine cranium KNM-ER 1813 (primates: Homininae) from the Plio/Pleistocene of Koobi Fora. *Primates*, 28(4), 423–438. <https://doi.org/10.1007/BF02380859>
- Ferguson, W. W. (1989). Reappraisal of the taxonomic status of the cranium Stw 53 from the Plio/Pleistocene of Sterkfontein, in South Africa. *Primates*, 30(1), 103–109. <https://doi.org/10.1007/BF02381216>
- Ferguson, W. W. (1995). A new species of the genus *Homo* (primates: Hominidae) from the Plio/Pleistocene of Koobi Fora, in Kenya. *Primates*, 36(1), 69–89. <https://doi.org/10.1007/BF02381916>
- Fleagle, J. G., Gilbert, C. C., & Baden, A. L. (2010). Primate cranial diversity. *American Journal of Physical Anthropology*, 142(4), 565–578. <https://doi.org/10.1002/ajpa.21272>
- Fleagle, J. G., & Kay, R. F. (1987). The phyletic position of the *Parapithecidae*. *Journal of Human Evolution*, 16(6), 483–532. [https://doi.org/10.1016/0047-2484\(87\)90036-4](https://doi.org/10.1016/0047-2484(87)90036-4)
- Fleagle, J. G., & Simons, E. L. (1982). The humerus of *Aegyptopithecus zeuxis*: A primitive anthropoid. *American Journal of Physical Anthropology*, 59(2), 175–193. <https://doi.org/10.1002/ajpa.1330590207>
- Folinsbee, K. E., Evans, D. C., Fröbisch, J., Brooks, D. R., & Tsuji, L. A. (2015). Quantitative approaches to phylogenetics. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 257–294). Springer. https://doi.org/10.1007/978-3-642-39979-4_5
- Fu, Q., Hajdinjak, M., Moldovan, O. T., Constantin, S., Mallick, S., Skoglund, P., Patterson, N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J., Reich, D., & Pääbo, S. (2015). An early modern human from Romania with a recent Neanderthal ancestor. *Nature*, 524(7564), 216–219. <https://doi.org/10.1038/nature14558>
- Gabounia, L., de Lumley, M.-A., Vekua, A., Lordkipanidze, D., & de Lumley, H. (2002). Découverte d'un nouvel hominidé à Dmanissi (Transcaucasie, Géorgie). *Comptes Rendus Palevol*, 1(4), 243–253. [https://doi.org/10.1016/S1631-0683\(02\)00032-5](https://doi.org/10.1016/S1631-0683(02)00032-5)
- Gabounia, L., Vekua, A., & Lordkipanidze, D. (2000). The environmental contexts of early human occupation of Georgia (Transcaucasia). *Journal of Human Evolution*, 38(6), 785–802. <https://doi.org/10.1006/jhev.1999.0383>
- Gabounia, L., Vekua, A., Lordkipanidze, D., Swisher, C. C., Ferring, R., Justus, A., Nioradze, M., Tvalchrelidze, M., Antón, S. C., Bosinski, G., Jöris, O., Lumley, M.-A., de Majsuradze, G., & Mouskhelishvili, A. (2000). Earliest Pleistocene Hominid cranial remains from Dmanisi, Republic of Georgia: Taxonomy, geological setting, and age. *Science*, 288(5468), 1019–1025. <https://doi.org/10.1126/science.288.5468.1019>
- Garrod, D. A. E., & Bate, D. M. A. (1937). *The Stone Age of Mount Carmel*. Clarendon Press.
- Gathogo, P. N., & Brown, F. H. (2006). Revised stratigraphy of Area 123, Koobi Fora, Kenya, and new age estimates of its fossil mammals, including hominins. *Journal of Human Evolution*, 51(5), 471–479. <https://doi.org/10.1016/j.jhevol.2006.05.005>
- Giannini, N. P. (2014). Quantitative developmental data in a phylogenetic framework. *Journal of Experimental Zoology. Part B, Molecular and Developmental Evolution*, 322(8), 558–566. <https://doi.org/10.1002/jez.b.22588>
- Gilbert, C. C. (2011). Phylogenetic analysis of the African papionin basicranium using 3-D geometric morphometrics: The need for improved methods to account for allometric effects. *American Journal of Physical Anthropology*, 144(1), 60–71. <https://doi.org/10.1002/ajpa.21370>
- Gilbert, W. H., & Asfaw, B. (2008). *Homo erectus: Pleistocene Evidence from the Middle Awash, Ethiopia* (Vol. 1). University of California Press.
- Gingerich, P. D. (1979). The stratophenetic approach to phylogeny reconstruction in vertebrate paleontology. In J. Cracraft & N. Eldredge (Eds), *Phylogenetic Analysis and Paleontology: Proceedings of a Symposium Entitled "Phylogenetic Models," Convened at the North American Paleontological Convention II, Lawrence, Kansas, August 8, 1977* (pp. 41–78). Columbia University Press. <https://doi.org/10.7312/crac92306-004>
- Glazko, G. V., & Nei, M. (2003). Estimation of divergence times for major lineages of primate species. *Molecular Biology and Evolution*, 20(3), 424–434. <https://doi.org/10.1093/molbev/msg050>

- Goloboff, P. A. (2007). Calculating SPR distances between trees. *Cladistics*, 24(4), 591–597. <https://doi.org/10.1111/j.1096-0031.2007.00189.x>
- Goloboff, P. A. (2022a). *From observations to optimal phylogenetic trees: Phylogenetic analysis of morphological data* (First edition, Vol. 1). Taylor & Francis Group.
- Goloboff, P. A. (2022b). *Refining phylogenetic analyses: Phylogenetic analysis of morphological data: Volume 2* (First Edition, Vol. 2). Taylor & Francis Group.
- Goloboff, P. A., & Catalano, S. A. (2011). Phylogenetic morphometrics (II): Algorithms for landmark optimization. *Cladistics*, 27(1), 42–51. <https://doi.org/10.1111/j.1096-0031.2010.00318.x>
- Goloboff, P. A., Farris, J. S., & Nixon, K. C. (2008). TNT, a free program for phylogenetic analysis. *Cladistics*, 24(5), 774–786. <https://doi.org/10.1111/j.1096-0031.2008.00217.x>
- Goloboff, P. A., & Morales, M. E. (2023). TNT version 1.6, with a graphical interface for MacOS and Linux, including new routines in parallel. *Cladistics*, 39(2), 144–153. <https://doi.org/10.1111/cla.12524>
- González-José, R., Escapa, I., Neves, W. A., Cúneo, R., & Pucciarelli, H. M. (2008). Cladistic analysis of continuous modularized traits provides phylogenetic signals in Homo evolution. *Nature*, 453(7196), 775–778. <https://doi.org/10.1038/nature06891>
- Goodall, C. (1991). Procrustes methods in the statistical analysis of shape. *Journal of the Royal Statistical Society: Series B (Methodological)*, 53(2), 285–321. <https://doi.org/10.1111/j.2517-6161.1991.tb01825.x>
- Goolsby, E. W., Bruggeman, J., & Ané, C. (2017). Rphylopars: Fast multivariate phylogenetic comparative methods for missing data and within-species variation. *Methods in Ecology and Evolution*, 8(1), 22–27. <https://doi.org/10.1111/2041-210X.12612>
- Gousset, P. (2026). *Phylogenetic analysis of the recent species of the genus Homo: Dispersals, evolution, extinction* [These de doctorat]. Museum National d'Histoire Naturelle.
- Gower, J. C. (1975). Generalized procrustes analysis. *Psychometrika*, 40(1), Article 1. <https://doi.org/10.1007/bf02291478>
- Granger, D. E., Gibbon, R. J., Kuman, K., Clarke, R. J., Bruxelles, L., & Caffee, M. W. (2015). New cosmogenic burial ages for Sterkfontein Member 2 *Australopithecus* and Member 5 Oldowan. *Nature*, 522(7554), 85–88. <https://doi.org/10.1038/nature14268>
- Gray, J. E. (1825). Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently appertaining to tribe. *Annals of Philosophy, London*, NS(10), 337–344.
- Green, R. E., Krause, J., Briggs, A. W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M. H.-Y., Hansen, N. F., Durand, E. Y., Malaspinas, A.-S., Jensen, J. D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H. A., ... Pääbo, S. (2010). A draft sequence of the Neandertal genome. *Science (New York, N.Y.)*, 328(5979), 710–722. <https://doi.org/10.1126/science.1188021>
- Grimaud, D. (1982). *Evolution du pariétal de l'homme fossile. Position de l'Homme de Tautavel parmi les hominidés*. [Thèse Géologie des formations sédimentaires option Préhistoire]. Université de Provence.
- Grine, F. E. (1986). Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: A quantitative analysis of permanent molar microwear. *Journal of Human Evolution*, 15(8), 783–822. [https://doi.org/10.1016/S0047-2484\(86\)80010-0](https://doi.org/10.1016/S0047-2484(86)80010-0)
- Grine, F. E. (2013). The alpha taxonomy of *Australopithecus africanus*. In K. E. Reed, J. G. Fleagle, & R. E. Leakey (Eds), *The Paleobiology of Australopithecus* (pp. 73–104). Springer Netherlands. https://doi.org/10.1007/978-94-007-5919-0_6
- Grine, F. E., Fleagle, J. G., & Martin, L. B. (1987). *Primate phylogeny*. Academic Press.
- Grine, F. E., Jungers, W. L., & Schultz, J. (1996). Phenetic affinities among early *Homo* crania from East and South Africa. *Journal of Human Evolution*, 30(3), 189–225. <https://doi.org/10.1006/jhev.1996.0019>
- Groves, C. (2015). Species concepts and speciation: Facts and fantasies. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 237–256). Springer. https://doi.org/10.1007/978-3-642-39979-4_61
- Groves, C. P. (1989). *Theory of human and primate evolution* (p. 384). Clarendon Press.

- Groves, C. P. (1991). *A Theory of Human and Primate Evolution*. Clarendon Press.
- Groves, C. P. (2001). *Primate taxonomy*. Smithsonian Institution Press.
- Groves, C. P., & Mazak, V. (1975). An approach to the taxonomy of the Hominidae: Gracile Villafranchian hominids of Africa. *Casopis pro Mineralogii a Geologii*, 20, 255–247.
- Grün, R., & Stringer, C. (1991). Electron spin resonance dating and the evolution of modern humans. *Archaeometry*, 33(2), 153–199. <https://doi.org/10.1111/j.1475-4754.1991.tb00696.x>
- Grün, R., Stringer, C., McDermott, F., Nathan, R., Porat, N., Robertson, S., Taylor, L., Mortimer, G., Eggins, S., & McCulloch, M. (2005). U-series and ESR analyses of bones and teeth relating to the human burials from Skhul. *Journal of Human Evolution*, 49(3), 316–334. <https://doi.org/10.1016/j.jhevol.2005.04.006>
- Gunz, P., & Mitteroecker, P. (2013). Semilandmarks: A method for quantifying curves and surfaces. *Hystrix, the Italian Journal of Mammalogy*, 24(1). <https://doi.org/10.4404/hystrix-24.1-6292>
- Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). Semilandmarks in three dimensions. In D. E. Slice (Ed.), *Modern Morphometrics in Physical Anthropology* (pp. 73–98). Springer US. https://doi.org/10.1007/0-387-27614-9_3
- Gunz, P., Mitteroecker, P., Neubauer, S., Weber, G. W., & Bookstein, F. L. (2009). Principles for the virtual reconstruction of hominin crania. *Journal of Human Evolution*, 57(1), 48–62. <https://doi.org/10.1016/j.jhevol.2009.04.004>
- Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., & Hublin, J.-J. (2012). A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. *Journal of Human Evolution*, 62(2), 300–313. <https://doi.org/10.1016/j.jhevol.2011.11.013>
- Haile-Selassie, Y., Suwa, G., & White, T. D. (2004). Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science*, 303(5663), 1503–1505. <https://doi.org/10.1126/science.1092978>
- Hajdinjak, M., Fu, Q., Hübner, A., Petr, M., Mafessoni, F., Grote, S., Skoglund, P., Narasimham, V., Rougier, H., Crevecoeur, I., Semal, P., Soressi, M., Talamo, S., Hublin, J.-J., Gušić, I., Kućan, Ž., Rudan, P., Golovanova, L. V., Doronichev, V. B., ... Kelso, J. (2018). Reconstructing the genetic history of late Neanderthals. *Nature*, 555(7698), Article 7698. <https://doi.org/10.1038/nature26151>
- Hanon, R., Péan, S., & Prat, S. (2018). Reassessment of anthropic modifications on the early Pleistocene hominin specimen Stw53 (Sterkfontein, South Africa). *Bulletins et Mémoires de La Société d'anthropologie de Paris*, 30, 49–58. <https://doi.org/10.3166/bmsap-2018-0013>
- Harrison, R. G. (1998). Linking evolutionary pattern and process. In *Endless forms: Species and speciation* (pp. 19–31). Oxford University Press.
- Harvati, K. (2015). Neanderthals and their contemporaries. In *Handbook of Paleoanthropology* (pp. 2243–2279). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_56
- Harvati, K., Frost, S. R., & McNulty, K. P. (2004). Neanderthal taxonomy reconsidered: Implications of 3D primate models of intra- and interspecific differences. *Proceedings of the National Academy of Sciences*, 101(5), 1147–1152. <https://doi.org/10.1073/pnas.0308085100>
- Hawkins, J. A., Hughes, C. E., & Scotland, R. W. (1997). Primary homology assessment, characters and character states. *Cladistics*, 13(3), 275–283. <https://doi.org/10.1111/j.1096-0031.1997.tb00320.x>
- Hawks, J. (2004). How much can cladistics tell us about early hominid relationships? *American Journal of Physical Anthropology*, 125(3), 207–219. <https://doi.org/10.1002/ajpa.10280>
- Hawks, J. (2006). Selection on mitochondrial DNA and the Neanderthal problem. In J.-J. Hublin, K. Harvati, & T. Harrison (Eds), *Neanderthals Revisited: New Approaches and Perspectives* (pp. 221–238). Springer Netherlands. https://doi.org/10.1007/978-1-4020-5121-0_12
- Hawks, J. (2017). Neanderthals and Denisovans as biological invaders. *Proceedings of the National Academy of Sciences of the United States of America*, 114(37), 9761–9763. <https://doi.org/10.1073/pnas.1713163114>

- Hay, R. L. (1976). The setting of the gorge and history of the geological investigations. *The Geology of Olduvai Gorge*, University of California Press, Berkeley, 25–28.
- Heim, J.-L. (1976). Les hommes fossiles de la Ferrassie. 1. Le Gisement, les squelettes adultes (crâne et squelette du tronc). *Archives de l'Institut de Paléontologie Humaine, Mémoire* 35, 331.
- Hendy, M. D., & Penny, D. (1982). Branch and bound algorithms to determine minimal evolutionary trees. *Mathematical Biosciences*, 59(2), 277–290. [https://doi.org/10.1016/0025-5564\(82\)90027-X](https://doi.org/10.1016/0025-5564(82)90027-X)
- Hennig, W. (1950). *Grundzüge einer Theorie der phylogenetischen Systematik*. Deutscher Zentralverlag. <https://cir.nii.ac.jp/crid/1130282273313290368>
- Hennig, W. (1965). Phylogenetic Systematics. *Annual Review of Entomology*, 10, 97–116. <https://doi.org/10.1146/annurev.en.10.010165.000525>
- Hennig, W. (1966). *Phylogenetic Systematics*. University of Illinois Press.
- Hey, J. (2001). The mind of the species problem. *Trends in Ecology & Evolution*, 16(7), 326–329. [https://doi.org/10.1016/S0169-5347\(01\)02145-0](https://doi.org/10.1016/S0169-5347(01)02145-0)
- Higgs, E. S. (1961). Some Pleistocene faunas of the Mediterranean coastal areas. *Proceedings of the Prehistoric Society*, 27, 144–154. <https://doi.org/10.1017/S0079497X00016017>
- Higham, T., Douka, K., Wood, R., Ramsey, C. B., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruiz, C., Bergman, C., Boitard, C., Boscato, P., Caparrós, M., Conard, N. J., Draily, C., Froment, A., Galván, B., Gambassini, P., ... Jacobi, R. (2014). The timing and spatiotemporal patterning of Neanderthal disappearance. *Nature*, 512(7514), 306–309. <https://doi.org/10.1038/nature13621>
- Holloway, R. L. (1985). The poor brain of *Homo sapiens neanderthalensis*: See what you please. *Ancestors: The Hard Evidence*, 319–324.
- Hovers, E., Rak, Y., Lavi, R., & Kimbel, W. H. (1995). Hominid remains from Amud Cave in the context of the Levantine Middle Paleolithic. *Paléorient*, 21(2), 47–61.
- Howell, F. C. (1957). The evolutionary significance of variation and varieties of 'Neanderthal' Man. *The Quarterly Review of Biology*, 32(4), 330–347. <https://doi.org/10.1086/401978>
- Howell, F. C. (1978). Overview of the Pliocene and earlier Pleistocene of the lower Omo basin, southern Ethiopia. *Early Hominids of Africa*, 85–130.
- Howells, W. W. (1975). Neanderthal man: Facts and figures. *Paleoanthropology: Morphology and Paleocology*, 389–407.
- Hublin, J.-J. (1978). Anatomie du centre de l'écaille occipitale—Le problème de l'inion. *Cahiers d'Anthropologie*, 2, 65–83.
- Hublin, J.-J. (1988). Caractères dérivés de la région occipito-mastoïdienne chez les Néandertaliens. In *L'homme de Néandertal* (Trinkaus E., Vol. 3, pp. 67–73). Université de Liège.
- Hublin, J.-J. (1998). Climatic changes, paleogeography, and the evolution of the Neandertals. In T. Akazawa, K. Aoki, & O. Bar-Yosef (Eds), *Neandertals and Modern Humans in Western Asia* (pp. 295–310). Springer US. https://doi.org/10.1007/0-306-47153-1_18
- Hublin, J.-J. (2000). Modern-nonmodern hominid interactions: A mediterranean perspective. *Modern-Nonmodern Hominid Interactions: A Mediterranean Perspective*, 157–182.
- Hublin, J.-J. (2009). The origin of Neandertals. *Proceedings of the National Academy of Sciences*, 106(38), 16022–16027. <https://doi.org/10.1073/pnas.0904119106>
- Hublin, J.-J. (2014). Paleoanthropology: *Homo erectus* and the limits of a paleontological species. *Current Biology*, 24(2), R82–R84. <https://doi.org/10.1016/j.cub.2013.12.006>
- Hublin, J.-J., Harvati, K., & Harrison, T. (Eds). (2006). *Neanderthals Revisited: New Approaches and Perspectives*. Springer Netherlands. <https://doi.org/10.1007/978-1-4020-5121-0>
- Hughes, A. R., & Tobias, P. V. (1977). A fossil skull probably of the genus *Homo* from Sterkfontein, Transvaal. *Nature*, 265(5592), 310–312. <https://doi.org/10.1038/265310a0>

- Indriati, E., Iii, C. C. S., Lepre, C., Quinn, R. L., Suriyanto, R. A., Hascaryo, A. T., Grün, R., Feibel, C. S., Pobiner, B. L., Aubert, M., Lees, W., & Antón, S. C. (2011). The age of the 20-meter Solo River Terrace, Java, Indonesia and the survival of *Homo erectus* in Asia. *PLOS ONE*, 6(6), e21562. <https://doi.org/10.1371/journal.pone.0021562>
- Irish, J. D., & Grabowski, M. (2021). Relative tooth size, Bayesian inference, and *Homo naledi*. *American Journal of Physical Anthropology*, 176(2), 262–282. <https://doi.org/10.1002/ajpa.24353>
- Jacob, T. (1980). The *Pithecanthropus* of Indonesia: Phenotype, genetics and ecology. In *Current Argument on Early Man* (Königsson L.K., pp. 170–179). Pergamon press.
- Jacobs, G. S., Hudjashov, G., Saag, L., Kusuma, P., Darusallam, C. C., Lawson, D. J., Mondal, M., Pagani, L., Ricaut, F.-X., Stoneking, M., Metspalu, M., Sudoyo, H., Lansing, J. S., & Cox, M. P. (2019). Multiple deeply divergent Denisovan ancestries in Papuans. *Cell*, 177(4), 1010-1021.e32. <https://doi.org/10.1016/j.cell.2019.02.035>
- James Rohlf, F., & Marcus, L. F. (1993). A revolution morphometrics. *Trends in Ecology & Evolution*, 8(4), 129–132. [https://doi.org/10.1016/0169-5347\(93\)90024-J](https://doi.org/10.1016/0169-5347(93)90024-J)
- Jelinek, J. (1980). European *Homo erectus* and the origin of *Homo sapiens*. *Current Arguments on Early Man*. Oxford: Pergamon, 137–144.
- Ji, Q., Wu, W., Ji, Y., Li, Q., & Ni, X. (2021). Late Middle Pleistocene Harbin cranium represents a new *Homo* species. *The Innovation*, 2(3), 100132. <https://doi.org/10.1016/j.xinn.2021.100132>
- Johanson, D. C., & White, T. D. (1979). A systematic assessment of early African hominids. *Science*, 203(4378), 321–330. <https://doi.org/10.1126/science.104384>
- Johanson, D. C., White, T. D., & Coppens, Y. (1978). A new species of the genus *Australopithecus* (Primates: Hominidae) from the Pliocene of eastern Africa. *Kirtlandia*, 28, 1–14.
- Jolicoeur, P. (1963). The multivariate generalization of the allometry equation. *Biometrics*, 19(3), 497–499. <https://doi.org/10.2307/2527939>
- Jolliffe, I. T. (2002). Principal component analysis for special types of data. In *Principal Component Analysis* (pp. 338–372). Springer-Verlag. https://doi.org/10.1007/0-387-22440-8_13
- Jungers, W. L., Falsetti, A. B., & Wall, C. E. (1995). Shape, relative size, and size-adjustments in morphometrics. *American Journal of Physical Anthropology*, 38(S21), 137–161. <https://doi.org/10.1002/ajpa.1330380608>
- Kaifu, Y. (2017). Archaic hominin populations in Asia before the arrival of modern humans: Their phylogeny and implications for the “Southern Denisovans”. *Current Anthropology*, 58(S17), S418–S433. <https://doi.org/10.1086/694318>
- Kaifu, Y., Aziz, F., Indriati, E., Jacob, T., Kurniawan, I., & Baba, H. (2008). Cranial morphology of Javanese *Homo erectus*: New evidence for continuous evolution, specialization, and terminal extinction. *Journal of Human Evolution*, 55(4), 551–580. <https://doi.org/10.1016/j.jhevol.2008.05.002>
- Kaifu, Y., Baba, H., Aziz, F., Indriati, E., Schrenk, F., & Jacob, T. (2005). Taxonomic affinities and evolutionary history of the early Pleistocene hominids of Java: Dentognathic evidence. *American Journal of Physical Anthropology*, 128(4), 709–726. <https://doi.org/10.1002/ajpa.10425>
- Katz, D., & Friess, M. (2014). Technical note: 3D from standard digital photography of human crania-a preliminary assessment. *American Journal of Physical Anthropology*, 154(1), 152–158. <https://doi.org/10.1002/ajpa.22468>
- Kay, R. F., Ross, C., & Williams, B. A. (1997). Anthropoid Origins. *Science*, 275(5301), 797–804. <https://doi.org/10.1126/science.275.5301.797>
- Kendall, D. G. (1977). The Diffusion of Shape. *Advances in Applied Probability*, 9(3), 428–430. <https://doi.org/10.2307/1426091>
- Kimbel, W. (2015). The species and diversity of australopiths. In *Handbook of Paleoanthropology, Second Edition* (pp. 2071–2105). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_61

- Kimbel, W. H. (2007). The species and diversity of australopiths. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 1539–1573). Springer. https://doi.org/10.1007/978-3-540-33761-4_50
- Kimbel, W. H., Johanson, D. C., & Rak, Y. (1994). The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature*, 368(6470), 449–451. <https://doi.org/10.1038/368449a0>
- Kimbel, W. H., Lockwood, C. A., Ward, C. V., Leakey, M. G., Rak, Y., & Johanson, D. C. (2006). Was *Australopithecus anamensis* ancestral to *A. afarensis*? A case of anagenesis in the hominin fossil record. *Journal of Human Evolution*, 51(2), 134–152. <https://doi.org/10.1016/j.jhevol.2006.02.003>
- Kimbel, W. H., & Rak, Y. (1993). The Importance of species taxa in palaeoanthropology and an argument for the phylogenetic concept of the species category. In W. H. Kimbel & L. B. Martin (Eds), *Species, Species Concepts and Primate Evolution* (pp. 461–484). Springer US. https://doi.org/10.1007/978-1-4899-3745-2_18
- Kimbel, W. H., & Rak, Y. (2017). *Australopithecus sediba* and the emergence of *Homo*: Questionable evidence from the cranium of the juvenile holotype MH 1. *Journal of Human Evolution*, 107, 94–106. <https://doi.org/10.1016/j.jhevol.2017.03.011>
- Kimbel, W. H., Rak, Y., & Johanson, D. C. (2004). *The Skull of Australopithecus afarensis*. Oxford University Press.
- Kimbel, W. H., & Villmoare, B. (2016). From *Australopithecus* to *Homo*: The transition that wasn't. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1698), 20150248. <https://doi.org/10.1098/rstb.2015.0248>
- Kimbel, W. H., Walter, R. C., Johanson, D. C., Reed, K. E., Aronson, J. L., Assefa, Z., Marean, C. W., Eck, G. G., Bobe, R., Hovers, E., Rak, Y., Vondra, C., Yemane, T., York, D., Chen, Y., Evensen, N. M., & Smith, P. E. (1996). Late Pliocene *Homo* and Oldowan Tools from the Hadar Formation (Kada Hadar Member), Ethiopia. *Journal of Human Evolution*, 31(6), 549–561. <https://doi.org/10.1006/jhevol.1996.0079>
- Kimbel, W. H., White, T. D., & Johanson, D. C. (1984). Cranial morphology of *Australopithecus afarensis*: A comparative study based on a composite reconstruction of the adult skull. *American Journal of Physical Anthropology*, 64(4), 337–388. <https://doi.org/10.1002/ajpa.1330640403>
- Kimbel, W. H., White, T. D., & Johanson, D. C. (1988). Implications of KNM-WT 17000 for the evolution of “robust” *Australopithecus*. In *Evolutionary History of the “Robust” Australopithecines* (Grine, F.E., pp. 259–268). Aldine de Gruyter.
- King, W. (1864). The reputed fossil man of the Neanderthal. *Quarterly Journal of Science*, 88–97.
- Klingenberg, C. P. (2010). Evolution and development of shape: Integrating quantitative approaches. *Nature Reviews Genetics*, 11(9), 623–635. <https://doi.org/10.1038/nrg2829>
- Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, 226(3), 113–137. <https://doi.org/10.1007/s00427-016-0539-2>
- Klingenberg, C. P., Barluenga, M., & Meyer, A. (2002). Shape analysis of symmetric structures: Quantifying variation among individuals and asymmetry. *Evolution*, 56(10), 1909–1920. <https://doi.org/10.1111/j.0014-3820.2002.tb00117.x>
- Klingenberg, C. P., & Gidaszewski, N. A. (2010). Testing and quantifying phylogenetic signals and homoplasy in morphometric data. *Systematic Biology*, 59(3), 245–261. <https://doi.org/10.1093/sysbio/syp106>
- Klingenberg, C. P., & Marugán-Lobón, J. (2013). Evolutionary covariation in geometric morphometric data: Analyzing integration, modularity, and allometry in a phylogenetic context. *Systematic Biology*, 62(4), 591–610. <https://doi.org/10.1093/sysbio/syt025>
- Klingenberg, C. P., & Monteiro, L. R. (2005). Distances and directions in multidimensional shape spaces: Implications for morphometric applications. *Systematic Biology*, 54(4), 678–688. <https://doi.org/10.1080/10635150590947258>
- Kluge, A. G., & Farris, J. S. (1969). Quantitative phyletics and the evolution of anurans. *Systematic Biology*, 18(1), 1–32. <https://doi.org/10.1093/sysbio/18.1.1>

- Koenigswald, G. H. R. von. (1940). *Neue Pithecanthropus-Funde 1936-1938: Ein Beitrag zur Kenntnis der Praehominiden*. Landsdrukkerij.
- Köppel, R. (1935). Das alter der neuentdeckten schädel von Nazareth. *Biblica*, 16(1), 58–73.
- Kuman, K., & Clarke, R. J. (2000). Stratigraphy, artefact industries and hominid associations for Sterkfontein, Member 5. *Journal of Human Evolution*, 38(6), 827–847. <https://doi.org/10.1006/jhev.1999.0392>
- Lahr, M. M., & Foley, R. (1994). Multiple dispersals and modern human origins. *Evolutionary Anthropology: Issues, News, and Reviews*, 3(2), 48–60. <https://doi.org/10.1002/evan.1360030206>
- Langergraber, K. E., Prüfer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E., Inoue-Muruyama, M., Mitani, J. C., Muller, M. N., Robbins, M. M., Schubert, G., Stoinski, T. S., Viola, B., Watts, D., Wittig, R. M., Wrangham, R. W., Zuberbühler, K., Pääbo, S., & Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier divergence times in great ape and human evolution. *Proceedings of the National Academy of Sciences*, 109(39), 15716–15721. <https://doi.org/10.1073/pnas.1211740109>
- Larick, R., Ciochon, R. L., Zaim, Y., Sudijono, Suminto, Rizal, Y., Aziz, F., Reagan, M., & Heizler, M. (2001). Early Pleistocene 40Ar/39Ar ages for Bapang Formation hominins, Central Jawa, Indonesia. *Proceedings of the National Academy of Sciences*, 98(9), 4866–4871. <https://doi.org/10.1073/pnas.081077298>
- Leakey, L. S. B. (1959). A new fossil skull from Olduvai. *Nature*, 184(4685), 491–493.
- Leakey, L. S. B., Tobias, P. V., & Napier, J. R. (1964). A new species of the genus *Homo* from Olduvai Gorge. *Nature*, 202(4927), 7–9. <https://doi.org/10.1038/202007a0>
- Leakey, M. D., Clarke, R. J., & Leakey, L. S. B. (1971). New hominid skull from Bed I, Olduvai Gorge, Tanzania. *Nature*, 232(5309), 308–312. <https://doi.org/10.1038/232308a0>
- Leakey, M. G., Feibel, C. S., McDougall, I., & Walker, A. (1995). New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, 376(6541), 565–571. <https://doi.org/10.1038/376565a0>
- Leakey, M. G., Spoor, F., Brown, F. H., Gathogo, P. N., Kiarie, C., Leakey, L. N., & McDougall, I. (2001). New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature*, 410(6827), 433–440. <https://doi.org/10.1038/35068500>
- Leakey, R. E. F. (1969). Early *Homo sapiens* remains from the Omo River region of South-west Ethiopia: Faunal remains from the Omo Valley. *Nature*, 222(5199), 1132–1133. <https://doi.org/10.1038/2221132a0>
- Leakey, R. E. F. (1973). Evidence for an advanced plio-pleistocene hominid from East Rudolf, Kenya. *Nature*, 242(5398), 447–450. <https://doi.org/10.1038/242447a0>
- Leakey, R. E. F. (1974). Further evidence of Lower Pleistocene hominids from East Rudolf, North Kenya, 1973. *Nature*, 248(5450), 653–656. <https://doi.org/10.1038/248653a0>
- Leakey, R. E. F. (1976). New hominid fossils from the Koobi Fora formation in Northern Kenya. *Nature*, 261(5561), 574–576. <https://doi.org/10.1038/261574a0>
- Leakey, R. E. F., Mungai, J. M., & Walker, A. C. (1971). New australopithecines from East Rudolf, Kenya. *American Journal of Physical Anthropology*, 35(2), 175–186. <https://doi.org/10.1002/ajpa.1330350204>
- Leakey, R. E. F., & Walker, A. (1988). New *Australopithecus boisei* specimens from east and west Lake Turkana, Kenya. *American Journal of Physical Anthropology*, 76(1), 1–24. <https://doi.org/10.1002/ajpa.1330760102>
- Leakey, R. E. F., & Walker, A. C. (1976). *Australopithecus*, *Homo erectus* and the single species hypothesis. *Nature*, 261(5561), 572–574. <https://doi.org/10.1038/261572a0>
- Leakey, R. E. F., & Walker, A. C. (1985). Further hominids from the Plio-Pleistocene of Koobi Fora, Kenya. *American Journal of Physical Anthropology*, 67(2), 135–163. <https://doi.org/10.1002/ajpa.1330670209>
- Ledogar, J. A., Senck, S., Villmoare, B. A., Smith, A. L., Weber, G. W., Richmond, B. G., Dechow, P. C., Ross, C. F., Grosse, I. R., Wright, B. W., Wang, Q., Byron, C., Benazzi, S., Carlson, K. J., Carlson, K. B., Pryor McIntosh, L. C., van Casteren, A., & Strait, D. S. (2022). Mechanical compensation in the evolution of the early hominin feeding apparatus. *Proceedings of the Royal Society B: Biological Sciences*, 289(1977), 20220711. <https://doi.org/10.1098/rspb.2022.0711>

- Lepre, C. J., Roche, H., Kent, D. V., Harmand, S., Quinn, R. L., Brugal, J.-P., Texier, P.-J., Lenoble, A., & Feibel, C. S. (2011). An earlier origin for the Acheulian. *Nature*, 477(7362), 82–85. <https://doi.org/10.1038/nature10372>
- Li, L., Comi, T. J., Bierman, R. F., & Akey, J. M. (2024). Recurrent gene flow between Neanderthals and modern humans over the past 200,000 years. *Science*, 385(6705), eadi1768. <https://doi.org/10.1126/science.adi1768>
- Lieberman, D. E., Wood, B. A., & Pilbeam, D. R. (1996). Homoplasy and early *Homo*: An analysis of the evolutionary relationships of *H. habilis* sensu stricto and *H. rudolfensis*. *Journal of Human Evolution*, 30(2), 97–120. <https://doi.org/10.1006/jhev.1996.0008>
- Linnaei, C. (1758). *Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis* (Direct. Laurentii Salvii). Holmiae: Impensis.
- Linnaei, C. (1760). *Dissertatio academica, in qua Anthropomorpha. . . Praeside. . . Carolo Linnaeo. . . Publico examini submittit Christianus E. Hoppius*: 116, 1 pl. (Vol. 6). Amoenitates Academicae.
- Lockwood, C. A. (1999). Sexual dimorphism in the face of *Australopithecus africanus*. *American Journal of Physical Anthropology*, 108(1), 97–127. [https://doi.org/10.1002/\(SICI\)1096-8644\(199901\)108:1%253C97::AID-AJPA6%253E3.0.CO;2-O](https://doi.org/10.1002/(SICI)1096-8644(199901)108:1%253C97::AID-AJPA6%253E3.0.CO;2-O)
- Lockwood, C. A., & Tobias, P. V. (1999). A large male hominin cranium from Sterkfontein, South Africa, and the status of *Australopithecus africanus*. *Journal of Human Evolution*, 36(6), 637–685. <https://doi.org/10.1006/jhev.1999.0299>
- Lordkipanidze, D. (1999). Early humans at the gate of Europe. *Evolutionary Anthropology*, 8(4).
- Lordkipanidze, D., Ponce de León, M. S., Margvelashvili, A., Rak, Y., Rightmire, G. P., Vekua, A., & Zollikofer, C. P. E. (2013). A complete skull from Dmanisi, Georgia, and the evolutionary biology of early *Homo*. *Science*, 342(6156), 326–331. <https://doi.org/10.1126/science.1238484>
- Lockett, W. P., & Szalay, F. S. (1975). *Phylogeny of the primates: A multidisciplinary approach*. Plenum.
- Lumley, H. de, & Sonakia, A. (1985). Contexte stratigraphique et archéologique de l'Homme de la Narmada, Hathnora, Madhya Pradesh, Inde. *L'Anthropologie*, 89(1), 3–12.
- MacLeod, N. (2017). Morphometrics: History, development methods and prospects. *Zoological Systematics*, 42(1), 4–33. <https://doi.org/10.1186/zs.201702>
- MacLeod, N., Forey, P. L., & Systematics Association. (2002a). *Morphology, shape and phylogeny*. Taylor & Francis.
- MacLeod, N., Forey, P. L., & Systematics Association. (2002b). Phylogenetic signals in morphometric data. In *Morphology, shape and phylogeny* (MacLeod N., Forey P.L., editors, pp. 100–138). Taylor & Francis.
- Madupe, P. P., Koenig, C., Patramanis, I., Rüther, P. L., Hlazo, N., Mackie, M., Tawane, M., Krueger, J., Taurozzi, A. J., Troché, G., Kibii, J., Pickering, R., Dickinson, M. R., Sahle, Y., Kgotleng, D., Musiba, C., Manthi, F., Bell, L., DuPlessis, M., ... Cappellini, E. (2025). Enamel proteins reveal biological sex and genetic variability in southern African Paranthropus. *Science*, 388(6750), 969–973. <https://doi.org/10.1126/science.adt9539>
- Madupe, P. P., Munir, F., Dickinson, M., Taurozzi, A. J., Mackie, M., Tawane, M., Mollereau, C., Hlazo, N., Penkman, K., Schroeder, L., Zanolli, C., Olsen, J. V., Ackermann, R. R., & Cappellini, E. (2025). Results from an *Australopithecus africanus* dental enamel fragment confirm the potential of palaeoproteomics for South African Plio-Pleistocene fossil sites. *South African Journal of Science*, 121(1/2).
- Marcus, L. F. (1990). Traditional morphometrics. In *Proceedings of the Michigan morphometrics workshop* (Rohlf F.J. & Boostkein F.L., Vol. 2, pp. 77–122). University of Michigan Museum of Zoology.
- Marra, F., Ceruleo, P., Jicha, B., Pandolfi, L., Petronio, C., & Salari, L. (2015). A new age within MIS 7 for the *Homo neanderthalensis* of Saccopastore in the glacio-eustatically forced sedimentary successions of the Aniene River Valley, Rome. *Quaternary Science Reviews*, 129, 260–274. <https://doi.org/10.1016/j.quascirev.2015.10.027>

- Martin, R., & Saller, K. (1957). *Lehrbuch der Anthropologie in Systematischer Darstellung mit Besonderer Berücksichtigung der Anthropologischen Methoden* (Vol. 1). Gustav Fischer.
- Martinón-Torres, M., Castro, J. M. B. de, Gómez-Robles, A., Arsuaga, J. L., Carbonell, E., Lordkipanidze, D., Manzi, G., & Margvelashvili, A. (2007). Dental evidence on the hominin dispersals during the Pleistocene. *Proceedings of the National Academy of Sciences*, 104(33), 13279–13282. <https://doi.org/10.1073/pnas.0706152104>
- Matile, L., Tassy, P., & Goujet, D. (1987). *Introduction à la systématique zoologique (concepts, principes, méthodes)*. Société française de systématique.
- Matschie, P. (1903). Über einen Gorilla aus Deutsch-Ostafrika. *Sitzungsberichte Des Gesellschaft Naturforschender Freude, Berlin*, 253–259.
- Mayden, R. L. (1997). A hierarchy of species concepts: The denouement in the saga of the species problem. In *Species: The units of biodiversity* (Claridge M.F., Dawah H.A. and Wilson M.R.). Chapman and Hall. <https://philpapers.org/rec/mayaho-6>
- Mayr, E. (1940). Speciation phenomena in Birds. *The American Naturalist*, 74(752), 249–278. <https://doi.org/10.1086/280892>
- Mayr, E. (1942). *Systematics and the origin of species from the viewpoint of a zoologist*. Columbia University Press.
- Mayr, E. (1950). Taxonomic categories in fossil hominids. *Cold Spring Harbor Symposia on Quantitative Biology*, 15, 109–118. <https://doi.org/10.1101/SQB.1950.015.01.013>
- Mayr, E. (1963). *Animal Species and Evolution*. Belknap Press.
- McCown, T. D. (1932). A note on the excavations and the human remains from the Mugharet Es-Sukhul (Cave of the Kids), Season of 1931. *Bull. Am. Sch. Prehist. Res.*, 8, 12–15.
- McCown, T. D., & Sir Keith, A. (1939). *The stone age of Mount Carmel. The fossil human remains from the Levallois-Mousterian*. (Vol. 2). Oxford University Press.
- McCracken, K. G., Harshman, J., McClellan, D. A., & Afton, A. D. (1999). Data set incongruence and correlated character evolution: An example of functional convergence in the hind-limbs of stiff-tail diving ducks. *Systematic Biology*, 48(4), 683–714. <https://doi.org/10.1080/106351599259979>
- Mendez, F. L., Poznik, G. D., Castellano, S., & Bustamante, C. D. (2016). The divergence of Neandertal and modern human Y chromosomes. *American Journal of Human Genetics*, 98(4), 728–734. <https://doi.org/10.1016/j.ajhg.2016.02.023>
- Mercier, N., Valladas, H., Bar-Yosef, O., Vandermeersch, B., Stringer, C., & Joron, J.-L. (1993). Thermoluminescence date for the Mousterian Burial site of Es-Skhul, Mt. Carmel. *Journal of Archaeological Science*, 20(2), 169–174. <https://doi.org/10.1006/jasc.1993.1012>
- Mitchell, P. C. (1901). On the intestinal tract of Birds. *Transactions of the Linnean Society of London*, 8, 173–275. <https://doi.org/10.1111/j.1096-3642.1896.tb03032.x>
- Mitchell, P. C. (1905). On the intestinal tract of Mammals. *The Transactions of the Zoological Society of London*, 17(5), 437–536. <https://doi.org/10.1111/j.1096-3642.1905.tb00036.x>
- Mongle, C. S., Strait, D. S., & Grine, F. E. (2019). Expanded character sampling underscores phylogenetic stability of *Ardipithecus ramidus* as a basal hominin. *Journal of Human Evolution*, 131, 28–39. <https://doi.org/10.1016/j.jhevol.2019.03.006>
- Mongle, C. S., Strait, D. S., & Grine, F. E. (2023). An updated analysis of hominin phylogeny with an emphasis on re-evaluating the phylogenetic relationships of *Australopithecus sediba*. *Journal of Human Evolution*, 175, 103311. <https://doi.org/10.1016/j.jhevol.2022.103311>
- Monteiro, L. R. (2000). Why morphometrics is special: The problem with using partial warps as characters for phylogenetic inference. *Systematic Biology*, 49(4), 796–800.
- Mounier, A. (2009). *Validité du taxon Homo heidelbergensis Schoetensack, 1908* [These de doctorat, Aix-Marseille 2]. <https://theses.fr/2009AIX20693>

- Mounier, A. (2012). The upper face of *Homo heidelbergensis* Schoetensack, 1908: Contribution of geometric morphometrics. *Bulletins et Mémoires de La Société d'anthropologie de Paris*, 24(1), 51–68. <https://doi.org/10.1007/s13219-011-0041-3>
- Mounier, A., Balzeau, A., Caparros, M., & Grimaud-Hervé, D. (2016). Brain, calvarium, cladistics: A new approach to an old question, who are modern humans and Neandertals? *Journal of Human Evolution*, 92, 22–36. <https://doi.org/10.1016/j.jhevol.2015.12.006>
- Mounier, A., & Caparros, M. (2015). The phylogenetic status of *Homo heidelbergensis* – a cladistic study of Middle Pleistocene hominins. *BMSAP*, 27(3–4), 110–134. <https://doi.org/10.1007/s13219-015-0127-4>
- Mounier, A., Condemi, S., & Manzi, G. (2011). The stem species of our species: A place for the archaic human cranium from Ceprano, Italy. *PLOS ONE*, 6(4), e18821. <https://doi.org/10.1371/journal.pone.0018821>
- Mounier, A., Heuzé, Y., Samsel, M., Vasilyev, S., Klaric, L., & Villotte, S. (2020). Gravettian cranial morphology and human group affinities during the European Upper Palaeolithic. *Scientific Reports*, 10(1), 21931. <https://doi.org/10.1038/s41598-020-78841-x>
- Mounier, A., Marchal, F., & Condemi, S. (2009). Is *Homo heidelbergensis* a distinct species? New insight on the Mauer mandible. *Journal of Human Evolution*, 56(3), 219–246. <https://doi.org/10.1016/j.jhevol.2008.12.006>
- Mounier, A., & Mirazón Lahr, M. (2016). Virtual ancestor reconstruction: Revealing the ancestor of modern humans and Neandertals. *Journal of Human Evolution*, 91, 57–72. <https://doi.org/10.1016/j.jhevol.2015.11.002>
- Mounier, A., & Mirazón Lahr, M. (2019). Deciphering African late middle Pleistocene hominin diversity and the origin of our species. *Nature Communications*, 10(1), Article 1. <https://doi.org/10.1038/s41467-019-11213-w>
- Mounier, A., Noûs, C., & Balzeau, A. (2020). Palaeoneurology and the emergence of language. *Bulletins et Mémoires de La Société d'Anthropologie de Paris*, 32(3–4), 147–157. <https://doi.org/10.3166/bmsap-2020-0098>
- Mounier, A., Villotte, S., Kacki, S., Mora, P., Espinasse, L., Dempawo, J. Z., Gerin, C., Meunier, Q., & Oslisly, R. (2024). Population affinities in pre-colonial West Africa: The case of the burial cave Iroungou (Gabon, 14th–15th century CE). *American Journal of Biological Anthropology*, 185(2), e24997. <https://doi.org/10.1002/ajpa.24997>
- Nara, T. (1994). *Étude de la variabilité de certains caractères métriques et morphologiques des Néandertaliens* [These de doctorat, Bordeaux 1]. <https://theses.fr/1994BOR10570>
- Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., Nowak, M. G., de Manuel, M., Desai, T., Groves, C., Pybus, M., Sonay, T. B., Roos, C., Lameira, A. R., Wich, S. A., Askew, J., Davila-Ross, M., Fredriksson, G., de Valles, G., Casals, F., Prado-Martinez, J., Goossens, B., ... Krützen, M. (2017). Morphometric, behavioral, and genomic evidence for a new orangutan species. *Current Biology*, 27(22), 3487–3498. <https://doi.org/10.1016/j.cub.2017.09.047>
- Neubauer, S., Hublin, J.-J., & Gunz, P. (2018). The evolution of modern human brain shape. *Science Advances*, 4(1), eaao5961. <https://doi.org/10.1126/sciadv.aao5961>
- Nevell, L., & Wood, B. (2008). Cranial base evolution within the hominin clade. *Journal of Anatomy*, 212(4), 455–468. <https://doi.org/10.1111/j.1469-7580.2008.00875.x>
- Ni, X., Ji, Q., Wu, W., Shao, Q., Ji, Y., Zhang, C., Liang, L., Ge, J., Guo, Z., Li, J., Li, Q., Grün, R., & Stringer, C. (2021). Massive cranium from Harbin in northeastern China establishes a new Middle Pleistocene human lineage. *The Innovation*, 2(3), 100130. <https://doi.org/10.1016/j.xinn.2021.100130>
- Nixon, K. C. (2001). Phylogeny. In S. A. Levin (Ed.), *Encyclopedia of Biodiversity (Second Edition)* (pp. 16–23). Academic Press. <https://doi.org/10.1016/B978-0-12-384719-5.00108-8>
- Nixon, K. C., & Wheeler, Q. D. (1990). An amplification of the phylogenetic species concept. *Cladistics*, 6(3), 211–223. <https://doi.org/10.1111/j.1096-0031.1990.tb00541.x>

- Nunn, C. L. (2011). *The comparative approach in evolutionary anthropology and biology*. University of Chicago Press.
- O'Higgins, P. (2000). The study of morphological variation in the hominid fossil record: Biology, landmarks and geometry. *The Journal of Anatomy*, 197(1), 103–120. <https://doi.org/10.1046/j.1469-7580.2000.19710103.x>
- Olivier, G. (1960). *Pratique anthropologique*. (Vigot Frères).
- Olson, T. R. (1978). Hominid phylogenetics and the existence of *Homo* in Member I of the Swartkrans formation, South Africa. *Journal of Human Evolution*, 7(2), 159–178. [https://doi.org/10.1016/S0047-2484\(78\)80008-6](https://doi.org/10.1016/S0047-2484(78)80008-6)
- Olson, T. R. (1981). Basicranial morphology of the extant hominoids and Pliocene hominids: The new material from the Hadar Formation, Ethiopia, and its significance in early human evolution and taxonomy. In *Aspects of human evolution* (Stringer C., pp. 99–128). Taylor & Francis.
- Oppenoorth W. F. F. (1932). *Homo (javanthropus) soloensis*, en Plistocene mensch van Java. *Wetenschappelijke Medische Dienst Mijnbouw Nederlandsch Indië*, 20, 49–74.
- Oxnard, C. E. (1978). One biologist's view of morphometrics. *Annual Review of Ecology and Systematics*, 9, 219–241.
- Palci, A., & Lee, M. S. Y. (2019). Geometric morphometrics, homology and cladistics: Review and recommendations. *Cladistics*, 35(2), 230–242. <https://doi.org/10.1111/cla.12340>
- Parins-Fukuchi, C. (2018). Bayesian placement of fossils on phylogenies using quantitative morphometric data. *Evolution*, 72(9), 1801–1814. <https://doi.org/10.1111/evo.13516>
- Parins-Fukuchi, C. (2018). Use of continuous traits can improve morphological phylogenetics. *Systematic Biology*, 67(2), 328–339. <https://doi.org/10.1093/sysbio/syx072>
- Pélabon, C., Firmat, C., Bolstad, G. H., Voje, K. L., Houle, D., Cassara, J., Rouzic, A. L., & Hansen, T. F. (2014). Evolution of morphological allometry. *Annals of the New York Academy of Sciences*, 1320, 58–75. <https://doi.org/10.1111/nyas.12470>
- Perrard, A., Lopez-Osorio, F., & Carpenter, J. M. (2016). Phylogeny, landmark analysis and the use of wing venation to study the evolution of social wasps (Hymenoptera: Vespidae: Vespinae). *Cladistics*, 32(4), 406–425. <https://doi.org/10.1111/cla.12138>
- Petr, M., Hajdinjak, M., Fu, Q., Essel, E., Rougier, H., Crevecoeur, I., Semal, P., Golovanova, L. V., Doronichev, V. B., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Shunkov, M. V., Kozlikin, M. B., Derevianko, A. P., Vernot, B., Meyer, M., & Kelso, J. (2020). The evolutionary history of Neanderthal and Denisovan Y chromosomes. *Science*, 369(6511), 1653–1656. <https://doi.org/10.1126/science.abb6460>
- Peyrony, D., & Capitan, L. (1909). Deux squelettes humains au milieu de foyers de l'époque Moustérienne. *Revue de l'Ecole d'Anthropologie*, 19, 402–409.
- Pleijel, F. (1995a). On character coding for phylogeny reconstruction. *Cladistics*, 11(3), 309–315. [https://doi.org/10.1016/0748-3007\(95\)90018-7](https://doi.org/10.1016/0748-3007(95)90018-7)
- Pleijel, F. (1995b). On character coding for phylogeny reconstruction. *Cladistics*, 11, 309–315.
- Pogue, M. G., & Mickevich, M. F. (1990). Character definitions and character state delineation: The bete noire of phylogenetic inference. *Cladistics*, 6(4), 319–361. <https://doi.org/10.1111/j.1096-0031.1990.tb00549.x>
- Polly, P. D., Lawing, A. M., Fabre, A.-C., & Goswami, A. (2013). Phylogenetic principal components analysis and geometric morphometrics. *Hystrix, the Italian Journal of Mammalogy*, 24(1). <https://doi.org/10.4404/hystrix-24.1-6383>
- Pope, G. G. (1992). Craniofacial evidence for the origin of modern humans in China. *American Journal of Physical Anthropology*, 35(S15), 243–298. <https://doi.org/10.1002/ajpa.1330350610>
- Posth, C., Wißing, C., Kitagawa, K., Pagani, L., van Holstein, L., Racimo, F., Wehrberger, K., Conard, N. J., Kind, C. J., Bocherens, H., & Krause, J. (2017). Deeply divergent archaic mitochondrial genome provides lower time boundary for African gene flow into Neanderthals. *Nature Communications*, 8, 16046. <https://doi.org/10.1038/ncomms16046>

- Prat, S. (2004). Les premiers représentants du genre *Homo*, en quête d'une identité. Apports de l'étude morphologique et de l'analyse cladistique. *Bulletins et mémoires de la société d'anthropologie de Paris*, 16(1–2), 17–35. <https://doi.org/10.4000/bmsap.586>
- Prat, S. (2022). Emergence of the genus *Homo*: From concept to taxonomy. *L'Anthropologie*, 126(4), 103068. <https://doi.org/10.1016/j.anthro.2022.103068>
- Principles of animal taxonomy*. (1961). Columbia University Press. <https://doi.org/10.7312/simp92414-003>
- Profico, A., Buzi, C., Di Vincenzo, F., Boggioni, M., Borsato, A., Boschian, G., Marchi, D., Micheli, M., Cecchi, J. M., Samadelli, M., Tafuri, M. A., Arsuaga, J. L., & Manzi, G. (2023). Virtual excavation and analysis of the early Neanderthal cranium from Altamura (Italy). *Communications Biology*, 6(1), Article 1. <https://doi.org/10.1038/s42003-023-04644-1>
- Profico, A., Di Vincenzo, F., Gagliardi, L., Piperno, M., & Manzi, G. (2016). Filling the gap. Human cranial remains from Gombore II (Melka Kunture, Ethiopia; ca. 850 ka) and the origin of *Homo heidelbergensis*. *Journal of Anthropological Sciences*, 94, 41–63. <https://doi.org/10.4436/JASS.94019>
- Prüfer, K., de Filippo, C., Grote, S., Mafessoni, F., Korlević, P., Hajdinjak, M., Vernot, B., Skov, L., Hsieh, P., Peyrégne, S., Reher, D., Hopfe, C., Nagel, S., Maricic, T., Fu, Q., Theunert, C., Rogers, R., Skoglund, P., Chintalapati, M., ... Pääbo, S. (2017). A high-coverage Neandertal genome from Vindija Cave in Croatia. *Science (New York, N.Y.)*, 358(6363), 655–658. <https://doi.org/10.1126/science.aao1887>
- Prüfer, K., Posth, C., Yu, H., Stoessel, A., Spyrou, M. A., Deviese, T., Mattonai, M., Ribechini, E., Higham, T., Velemínský, P., Brůžek, J., & Krause, J. (2021). A genome sequence from a modern human skull over 45,000 years old from Zlatý kůň in Czechia. *Nature Ecology & Evolution*, 5(6), 820–825. <https://doi.org/10.1038/s41559-021-01443-x>
- Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P. H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., ... Pääbo, S. (2014). The complete genome sequence of a Neanderthal from the Altai Mountains. *Nature*, 505(7481), 43–49. <https://doi.org/10.1038/nature12886>
- R Core Team. (2024). *R: A Language and Environment for Statistical Computing*. (Version 4.4.2) [R]. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rak, Y. (1993). Morphological variation in *Homo neanderthalensis* and *Homo sapiens* in the Levant. In W. H. Kimbel & L. B. Martin (Eds), *Species, Species Concepts and Primate Evolution* (pp. 523–536). Springer US. https://doi.org/10.1007/978-1-4899-3745-2_20
- Rak, Y. (2014). *The Australopithecine Face*. Academic Press.
- Reed, K. E., Fleagle, J. G., & Leakey, R. E. (Eds). (2013). *The Paleobiology of Australopithecus*. Springer Netherlands. <https://doi.org/10.1007/978-94-007-5919-0>
- Reich, D. (2018). *Who we are and how we got here: Ancient DNA and the new science of the human past*. Oxford University Press.
- Reich, D., Patterson, N., Kircher, M., Delfin, F., Nandineni, M. R., Pugach, I., Ko, A. M.-S., Ko, Y.-C., Jinam, T. A., Phipps, M. E., Saitou, N., Wollstein, A., Kayser, M., Pääbo, S., & Stoneking, M. (2011). Denisova admixture and the first modern human dispersals into Southeast Asia and Oceania. *The American Journal of Human Genetics*, 89(4), 516–528. <https://doi.org/10.1016/j.ajhg.2011.09.005>
- Relethford, J. H. (2001). Absence of regional affinities of Neandertal DNA with living humans does not reject multiregional evolution. *American Journal of Physical Anthropology*, 115(1), 95–98. <https://doi.org/10.1002/ajpa.1060>
- Revell, L. J. (2024). phytools 2.0: An updated R ecosystem for phylogenetic comparative methods (and other things). *PeerJ*, 12, e16505. <https://doi.org/10.7717/peerj.16505>
- Revell, L. J., Mahler, D. L., Reynolds, R. G., & Slater, G. J. (2015). Placing cryptic, recently extinct, or hypothesized taxa into an ultrametric phylogeny using continuous character data: A case study with the lizard *Anolis roosevelti*. *Evolution*, 69(4), 1027–1035. <https://doi.org/10.1111/evo.12628>

- Reyment, R. A. (1990). Reification of classical multivariate statistical analysis in morphometry. In *Proceedings of the Michigan Morphometrics Workshop* (Rohlf F.J. & Bookstein F.L., pp. 123–144). University of Michigan Museum of Zoology.
- Ridley, M. (2004). *Evolution*, 3rd Edition (Wiley-Blackwell). Wiley.
- Rightmire, G. P. (1990). *The evolution of Homo Erectus: Comparative anatomical studies of an extinct human species*. Cambridge University Press.
- Rightmire, G. P. (1992). *Homo erectus*: Ancestor or evolutionary side branch? *Evolutionary Anthropology: Issues, News, and Reviews*, 1(2), 43–49. <https://doi.org/10.1002/evan.1360010204>
- Rightmire, G. P. (1998a). Evidence from facial morphology for similarity of Asian and African representatives of *Homo erectus*. *American Journal of Physical Anthropology*, 106(1), 61–85. [https://doi.org/10.1002/\(SICI\)1096-8644\(199805\)106:1%253C61::AID-AJPA5%253E3.0.CO;2-G](https://doi.org/10.1002/(SICI)1096-8644(199805)106:1%253C61::AID-AJPA5%253E3.0.CO;2-G)
- Rightmire, G. P. (1998b). Human evolution in the Middle Pleistocene: The role of *Homo heidelbergensis*. *Evolutionary Anthropology: Issues, News, and Reviews*, 6(6), 218–227. [https://doi.org/10.1002/\(SICI\)1520-6505\(1998\)6:6%253C218::AID-EVAN4%253E3.0.CO;2-6](https://doi.org/10.1002/(SICI)1520-6505(1998)6:6%253C218::AID-EVAN4%253E3.0.CO;2-6)
- Rightmire, G. P., Lordkipanidze, D., & Vekua, A. (2006). Anatomical descriptions, comparative studies and evolutionary significance of the hominin skulls from Dmanisi, Republic of Georgia. *Journal of Human Evolution*, 50(2), 115–141. <https://doi.org/10.1016/j.jhevol.2005.07.009>
- Rink, W. J., Mercier, N., Mihailović, D., Morley, M. W., Thompson, J. W., & Roksandic, M. (2013). New Radiometric Ages for the BH-1 Hominin from Balanica (Serbia): Implications for Understanding the Role of the Balkans in Middle Pleistocene Human Evolution. *PLOS ONE*, 8(2), e54608. <https://doi.org/10.1371/journal.pone.0054608>
- Rizal, Y., Westaway, K. E., Zaim, Y., van den Bergh, G. D., Bettis, E. A., Morwood, M. J., Huffman, O. F., Grün, R., Joannes-Boyau, R., Bailey, R. M., Sidarto, Westaway, M. C., Kurniawan, I., Moore, M. W., Storey, M., Aziz, F., Suminto, Zhao, J., Aswan, ... Ciochon, R. L. (2020). Last appearance of *Homo erectus* at Ngandong, Java, 117,000–108,000 years ago. *Nature*, 577(7790), Article 7790. <https://doi.org/10.1038/s41586-019-1863-2>
- Roberts, P., & Stewart, B. A. (2018). Defining the ‘generalist specialist’ niche for Pleistocene *Homo sapiens*. *Nature Human Behaviour*, 2(8), 542–550. <https://doi.org/10.1038/s41562-018-0394-4>
- Robinson, D. F., & Foulds, L. R. (1981). Comparison of phylogenetic trees. *Mathematical Biosciences*, 53(1), 131–147. [https://doi.org/10.1016/0025-5564\(81\)90043-2](https://doi.org/10.1016/0025-5564(81)90043-2)
- Robinson, J. T. (1960). The affinities of the new Olduvai australopithecine. *Nature*, 186(4723), 456–458.
- Roebroeks, W., & Soressi, M. (2016). Neandertals revised. *Proceedings of the National Academy of Sciences*, 113(23), 6372–6379. <https://doi.org/10.1073/pnas.1521269113>
- Rogers, A. R., Bohlender, R. J., & Huff, C. D. (2017). Early history of Neanderthals and Denisovans. *Proceedings of the National Academy of Sciences*, 114(37), 9859–9863. <https://doi.org/10.1073/pnas.1706426114>
- Rohlf, F. J. (1990). Rotational fit (Procrustes) methods. In *Proceedings of the Michigan morphometrics workshop* (F. J. Rohlf and F. L. Bookstein, Vol. 2, pp. 227–236). University of Michigan Museum of Zoology.
- Rohlf, F. J. (1998). On applications of geometric morphometrics to studies of ontogeny and phylogeny. *Systematic Biology*, 47(1), 147–158.
- Rohlf, F. J. (2001). Comparative methods for the analysis of continuous variables: Geometric interpretations. *Evolution*, 55(11), 2143–2160. <https://doi.org/10.1111/j.0014-3820.2001.tb00731.x>
- Rohlf, F. J. (2002). Geometric morphometrics and phylogeny. In *Morphology, Shape and Phylogeny* (pp. 175–193). Taylor & Francis.
- Rohlf, F. J., & Bookstein, F. L. (1990). *Proceedings of the Michigan Morphometrics Workshop*. University of Michigan Museum of Zoology.
- Rohlf, F. J., & Slice, D. (1990). Extensions of the procrustes method for the optimal superimposition of landmarks. *Systematic Biology*, 39(1), 40–59. <https://doi.org/10.2307/2992207>

- Ross, C., Williams, B., & Kay, R. F. (1998). Phylogenetic analysis of anthropoid relationships. *Journal of Human Evolution*, 35(3), 221–307. <https://doi.org/10.1006/jhev.1998.0254>
- Ruff, C. (2009). Relative limb strength and locomotion in *Homo habilis*. *American Journal of Physical Anthropology*, 138(1), 90–100. <https://doi.org/10.1002/ajpa.20907>
- Sankararaman, S., Mallick, S., Patterson, N., & Reich, D. (2016). The combined landscape of Denisovan and Neanderthal ancestry in present-day humans. *Current Biology*, 26(9), 1241–1247. <https://doi.org/10.1016/j.cub.2016.03.037>
- Santa Luca, A. P. (1980). The Ngandong fossil hominids: A comparative study of a far eastern *Homo erectus* group. *New Haven: Yale University Publications in Anthropology*, 78.
- Sartono, S. (1976). Genesis of the Solo Terraces. *Modern Quaternary Research in Southeast Asia*, 2, 1–21.
- Sartono, S. (1982). Characteristics and chronology of early men in Java. In *Homo erectus et la place de l'Homme de Tautavel parmi les Hominidés fossiles: Prétirage* (de Lumley H., pp. 491–541). Premier Congrès International de Paléontologie Humaine.
- Savage, T. S., & Wyman, J. (1847). *Notice of the external characters and habits of Troglodytes gorilla, a new species of orang from the Gaboon River*. Little.
- Schlebusch, C. M., Malmström, H., Günther, T., Sjödin, P., Coutinho, A., Edlund, H., Munters, A. R., Vicente, M., Steyn, M., Soodyall, H., Lombard, M., & Jakobsson, M. (2017). Southern African ancient genomes estimate modern human divergence to 350,000 to 260,000 years ago. *Science*, 358(6363), 652–655. <https://doi.org/10.1126/science.aao6266>
- Schrenk, F., Kullmer, O., & Bromage, T. (2007). The earliest putative *Homo* fossils. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 1611–1631). Springer. https://doi.org/10.1007/978-3-540-33761-4_52
- Schwarcz, H. P., Grün, R., & Tobias, P. V. (1994). ESR dating studies of the australopithecine site of Sterkfontein, South Africa. *Journal of Human Evolution*, 26(3), 175–181. <https://doi.org/10.1006/jhev.1994.1010>
- Schwarz, E. (1929). Das Vorkommen des Schimpansen auf den linken Kongo-Ufer. *Revue de Zoologie et de Botanique Africaines*, 16(4), 425–426.
- Sereno, P. C. (2007). Logical basis for morphological characters in phylogenetics. *Cladistics*, 23(6), 565–587. <https://doi.org/10.1111/j.1096-0031.2007.00161.x>
- Sergi, S. (1944). Craniometria e craniografia del primo maleoantropo di Saccopastore. *Ricerche Di Morphologia*, 20–21, 733–791.
- Sergi, S. (1948). Il cranio del secondo paleontropo di Saccopastore. *Palaeontografia Italica*, 42, 25–164.
- Sergi, S. (1991). The Neandertal cranium of Monte Circe (Circeo I). In *Il cranio neandertaliano Circeo 1: Studi e documenti*. Libreria dello Stato (Piperno M. and Scichilone G., pp. 23–175). Istituto Poligrafico e Zecca dello Stato. Libreria dello Stato.
- Shea, J. J. (2008). Transitions or turnovers? Climatically forced extinctions of *Homo sapiens* and Neanderthals in the east Mediterranean Levant. *Quaternary Science Reviews, The Coastal Shelf of the Mediterranean and Beyond: Corridor and Refugium for Human Populations in the Pleistocene*, 27(23), 2253–2270. <https://doi.org/10.1016/j.quascirev.2008.08.015>
- Shen, G., Gao, X., Gao, B., & Granger, D. E. (2009). Age of Zhoukoudian *Homo erectus* determined with ²⁶Al/¹⁰Be burial dating. *Nature*, 458(7235), Article 7235. <https://doi.org/10.1038/nature07741>
- Siebert, D. J. (1992). Tree statistics; trees and confidence; consensus trees; alternatives to parsimony; character weighting; character conflict and its resolution. In P. L. Forey, C. J. Humphries, I. L. Kitching, R. W. Scotland, D. J. Siebert, & D. M. Williams (Eds), *Cladistics: A practical course in systematics* (Repr, pp. 74–75). Clarendon Press.
- Siegel, A. F., & Benson, R. H. (1982). A robust comparison of biological shapes. *Biometrics*, 38(2), 341–350. <https://doi.org/10.2307/2530448>

- Simon-Maciejewski, M., Manzi, G., Zeitoun, V., & Mounier, A. (2024). Cladistics with geometric morphometric data: The variability of the calvarium in the genus *Homo*. *Bulletins et mémoires de la Société d'Anthropologie de Paris. BMSAP*, 36(1), Article 1. <https://doi.org/10.4000/bmsap.14053>
- Simon-Maciejewski, M., Manzi, G., Zeitoun, V., & Mounier, A. (2025). Geometric morphometric data in cladistics: Comparison with phylogenies inferred from morphological data. *JASs. Journal of Anthropological Sciences*, 103, 73. <https://doi.org/10.4436/jass10307>
- Simpson, G. G. (1944). *Mode and tempo in evolution*. New York: Columbia University.
- Slice, D. E. (2005). *Modern Morphometrics in Physical Anthropology*. Kluwer Press.
- Slice, D. E. (2007). Geometric morphometrics. *Annual Review of Anthropology*, 36(Volume 36, 2007), 261–281. <https://doi.org/10.1146/annurev.anthro.34.081804.120613>
- Slimak, L., Vimala, T., Seguin-Orlando, A., Metz, L., Zanolli, C., Joannes-Boyau, R., Frouin, M., Arnold, L. J., Demuro, M., Devière, T., Comeskey, D., Buckley, M., Camus, H., Muth, X., Lewis, J. E., Bocherens, H., Yvorra, P., Tenaillon, C., Duployer, B., ... Sikora, M. (2024). Long genetic and social isolation in Neanderthals before their extinction. *Cell Genomics*, 4(9). <https://doi.org/10.1016/j.xgen.2024.100593>
- Slizewski, A., Friess, M., & Semal, P. (2010). *Surface scanning of anthropological specimens: Nominal-actual comparison with low-cost laser scanner and high-end fringe light projection surface scanning systems*.
- Smith, F. H., & Trinkaus, E. (1991). Les origines de l'homme moderne en Europe centrale: Un cas de continuité. In *Aux origines d'Homo sapiens* (Hublin J.-J. et Tillier A.M., pp. 251–290). Press Universitaires de France.
- Smith, H. F., & Grine, F. E. (2008). Cladistic analysis of early *Homo* crania from Swartkrans and Sterkfontein, South Africa. *Journal of Human Evolution*, 54(5), 684–704. <https://doi.org/10.1016/j.jhevol.2007.10.012>
- Sneath, P. H. A., & Sokal, R. R. (1973). *Numerical taxonomy. The principles and practice of numerical classification*. W. H. Freeman and Co.
- Sokal, R. R., & Crovello, T. J. (1970). The biological species concept: A critical evaluation. *The American Naturalist*, 104(936), 127–153. <https://doi.org/10.1086/282646>
- Sokal, R. R., & Sneath, P. H. (1963). *Principles of numerical taxonomy*. W.H. Freeman.
- Spoor, F., Gunz, P., Neubauer, S., Stelzer, S., Scott, N., Kwekason, A., & Dean, M. C. (2015). Reconstructed *Homo habilis* type OH 7 suggests deep-rooted species diversity in early *Homo*. *Nature*, 519(7541), 83–86. <https://doi.org/10.1038/nature14224>
- Stewart, T. D. (1960). Form of the pubic bone in Neanderthal man. *Science*, 131(3411), 1437–1438. <https://doi.org/10.1126/science.131.3411.1437>
- Strait, D., Grine, F. E., & Fleagle, J. G. (2015). Analyzing hominin phylogeny: cladistic approach. In W. Henke & I. Tattersall (Eds), *Handbook of Paleoanthropology* (pp. 1989–2014). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_58
- Strait, D. S. (2013). Human systematics. In *A Companion to Paleoanthropology* (pp. 35–54). John Wiley & Sons, Ltd. <https://doi.org/10.1002/9781118332344.ch3>
- Strait, D. S., & Grine, F. E. (2004). Inferring hominoid and early hominid phylogeny using craniodental characters: The role of fossil taxa. *Journal of Human Evolution*, 47(6), 399–452. <https://doi.org/10.1016/j.jhevol.2004.08.008>
- Strait, D. S., Grine, F. E., & Moniz, M. A. (1997). A reappraisal of early hominid phylogeny. *Journal of Human Evolution*, 32(1), 17–82. <https://doi.org/10.1006/jhev.1996.0097>
- Street, M., Terberger, T., & Orschiedt, J. (2006). A critical review of the German Paleolithic hominin record. *Journal of Human Evolution*, 51(6), 551–579. <https://doi.org/10.1016/j.jhevol.2006.04.014>
- Stringer, C. (1974). Population relationships of later Pleistocene hominids: A multivariate study of available crania. *Journal of Archaeological Science*, 1(4), 317–342. [https://doi.org/10.1016/0305-4403\(74\)90051-X](https://doi.org/10.1016/0305-4403(74)90051-X)
- Stringer, C. (1978). Some problems in Middle and Upper Pleistocene hominid relationships. *Recent Advances in Primatology*, 3, 395–418.

- Stringer, C. (1984). The definition of *Homo erectus* and the existence of the species in Africa and Europe. *Courrier Forschungsinstitut Senckenberg*, 69, 131–143.
- Stringer, C. (1986). The credibility of *Homo habilis*. In *Major topics in Primate and Human Evolution* (Wood, B., Martin, L. & Andrews, P., pp. 266–294). Cambridge University Press.
- Stringer, C. (1987). A numerical cladistic analysis for the genus *Homo*. *Journal of Human Evolution*, 16(1), 135–146. [https://doi.org/10.1016/0047-2484\(87\)90064-9](https://doi.org/10.1016/0047-2484(87)90064-9)
- Stringer, C. (2002). Modern human origins: Progress and prospects. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357(1420), 563–579. <https://doi.org/10.1098/rstb.2001.1057>
- Stringer, C. (2006). The Neanderthal-*H. sapiens* interface in Eurasia. In J.-J. Hublin, K. Harvati, & T. Harrison (Eds), *Neanderthals Revisited: New Approaches and Perspectives* (pp. 315–323). Springer Netherlands. https://doi.org/10.1007/978-1-4020-5121-0_18
- Stringer, C. (2012). The status of *Homo heidelbergensis* (Schoetensack 1908). *Evolutionary Anthropology*, 21(3), 101–107. <https://doi.org/10.1002/evan.21311>
- Stringer, C. (2016). The origin and evolution of *Homo sapiens*. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 371(1698), 20150237. <https://doi.org/10.1098/rstb.2015.0237>
- Sundberg, P. (1989). Shape and size-constrained principal components analysis. *Systematic Zoology*, 38(2), 166–168. <https://doi.org/10.2307/2992385>
- Suzuki, H. (1970). The skull of the Amud man. In *The Amud Man and His Cave Site* (Suzuki H. and Takai F., pp. 123–206). University of Tokyo.
- Suzuki, H., & Takai, F. (1970). *The Amud Man and His Cave Site*. University of Tokyo.
- Swofford, D. L. (1998). Phylogenetic analysis using parsimony (* and other methods). Ver. 4. *Sinauer, Suterland, MA*.
- Swofford, D., Olsen, G. J., Waddell, P. J., & Hillis, D. M. (1996). Phylogenetic Inference. In *Molecular Systematics, 2nd Edition* (Hillis, D.M., Moritz, C. and Mable, B.K., pp. 407–514). Sinauer Associates.
- Tamrat, E., Thouveny, N., Tai'eb, M., & Opdyke, N. D. (1995). Revised magnetostratigraphy of the Plio-Pleistocene sedimentary sequence of the Olduvai Formation (Tanzania). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 114(2), 273–283. [https://doi.org/10.1016/0031-0182\(94\)00080-R](https://doi.org/10.1016/0031-0182(94)00080-R)
- Tattersall, I. (1999). Paleoanthropology: The last half-century. *Evolutionary Anthropology*, 7, 2–16.
- Tattersall, I. (2015). *Homo ergaster* and its contemporaries. In *Handbook of Paleoanthropology* (Second, pp. 2167–2187). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-39979-4_53
- Tattersall, I., & Eldredge, N. (1977). Fact, theory, and fantasy in human paleontology. *American Scientist*, 65(2), 204–211.
- Tattersall, I., & Schwartz, J. H. (2006). The distinctiveness and systematic context of *Homo neanderthalensis*. In J.-J. Hublin, K. Harvati, & T. Harrison (Eds), *Neanderthals Revisited: New Approaches and Perspectives* (pp. 9–22). Springer Netherlands. https://doi.org/10.1007/978-1-4020-5121-0_2
- Tattersall, I., & Schwartz, J. H. (2009). Evolution of the genus *Homo*. *Annual Review of Earth and Planetary Sciences*, 37(1), 67–92. <https://doi.org/10.1146/annurev.earth.031208.100202>
- Thackeray, J. F., Loth, S. R., Swanepoel, E., Dayal, M. R., Lubbe, K., & Laing, M. (2000). Comparison of Sts 5 ('Mrs Ples') and Stw 53 ('Early Homo') from Sterkfontein, South Africa. | EBSCOhost. *South African Journal of Science*, 96(1), 21.
- Thiele, K. (1993). The Holy grail of the perfect character: The cladistic treatment of morphometric data. *Cladistics*, 9(3), 275–304. <https://doi.org/10.1111/j.1096-0031.1993.tb00226.x>
- Tobias, P. V. (1967). *The cranium and maxillary dentition of Australopithecus (Zinjanthropus) boisei* (Vol. 2). Cambridge University Press.
- Tobias, P. V. (1980). '*Australopithecus afarensis*' and *A. africanus*: Critique and alternative hypothesis. *Palaeontologica Africana*, 23, 1–17.

- Tobias, P. V. (1991). The environmental background of hominid emergence and the appearance of the genus *Homo*. *Human Evolution*, 6(2), 129–142. <https://doi.org/10.1007/BF02435613>
- Toth, N., & Schick, K. (2015). Overview of paleolithic archaeology. In *Handbook of Paleoanthropology* (pp. 1–21). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-27800-6_64-4
- Trinkaus, E. (1983). *The Shanidar Neandertals*. Academic Press.
- Trinkaus, E. (1991). *Les Hommes fossiles de la grotte de Shanidar, Irak: Évolution et continuité parmi les Hommes archaïques et tardifs du Proche-Orient*. 95(2–3), 535–572.
- Trinkaus, E. (2006). Modern human versus neandertal evolutionary distinctiveness. *Current Anthropology*, 47(4), 597–620. <https://doi.org/10.1086/504165>
- Trinkaus, E. (2011). Late neandertals and early modern humans in Europe, population dynamics and paleobiology. In S. Condemi & G.-C. Weniger (Eds), *Continuity and Discontinuity in the Peopling of Europe: One Hundred Fifty Years of Neanderthal Study* (pp. 315–329). Springer Netherlands. https://doi.org/10.1007/978-94-007-0492-3_24
- Vallois, H. V. (1962). Un nouveau Neandertaloïde en Palestine. *Anthropology*, 66, 405–406.
- Vallois, H. V. (1969). Le temporal néandertalien H27, de La Quina. Etude anthropologique. *L'Anthropologie*, 73, 365–400.
- Vandermeersch, B. (1970). Une sépulture moustérienne avec offrandes découverte dans la grotte de Qafzeh. *Comptes Rendus de l'Académie Des Sciences*, 270, 298–301.
- Vandermeersch, B. (1971). Récentes découvertes de squelettes humains à Qafzeh (Israël)-Essai d'interprétation. In *Origines de l'Homme Moderne* (Bordes, F., pp. 49–54). UNESCO.
- Vandermeersch, B. (1981). *Les Hommes de Qafzeh (Israël)* (CNRS).
- Varón-González, C., Whelan, S., & Klingenberg, C. P. (2020). Estimating phylogenies from shape and similar multidimensional data: Why it is not reliable. *Systematic Biology*, 69(5), 863–883. <https://doi.org/10.1093/sysbio/syaa003>
- Vekua, A., Lordkipanidze, D., Rightmire, G. P., Agusti, J., Ferring, R., Maisuradze, G., Mouskhelishvili, A., Nioradze, M., de Leon, M. P., Tappen, M., Tvalchrelidze, M., & Zollikofer, C. (2002). A new skull of early *Homo* from Dmanisi, Georgia. *Science*, 297(5578), 85–89. <https://doi.org/10.1126/science.1072953>
- Vidal, C. M., Lane, C. S., Asrat, A., Barfod, D. N., Mark, D. F., Tomlinson, E. L., Tadesse, A. Z., Yirgu, G., Deino, A., Hutchison, W., Mounier, A., & Oppenheimer, C. (2022). Age of the oldest known *Homo sapiens* from eastern Africa. *Nature*, 601(7894), 579–583. <https://doi.org/10.1038/s41586-021-04275-8>
- Vleck, E. (1993). *Fossile Menschenfunde von Weimar-Ehringsdorf* (Vol. 30). Konrad Theiss Verlag.
- Voisin, J. L. (2006). Speciation by distance and temporal overlap: A new approach to understanding Neanderthal evolution. In J.-J. Hublin, K. Harvati, & T. Harrison (Eds), *Neanderthals Revisited: New Approaches and Perspectives* (pp. 299–314). Springer Netherlands. https://doi.org/10.1007/978-1-4020-5121-0_17
- von Cramon-Taubadel, N., & Smith, H. F. (2012). The relative congruence of cranial and genetic estimates of hominoid taxon relationships: Implications for the reconstruction of hominin phylogeny. *Journal of Human Evolution*, 62(5), 640–653. <https://doi.org/10.1016/j.jhevol.2012.02.007>
- Wagner, W. H. (1952). The fern genus *Diellia*: Its structure, affinities and taxonomy. *University of California Publication of Botanic*, 26, 1–212.
- Wagner, W. H. (1961). Problems in the classification of ferns. *Recent Advances in Botany*, 841–844.
- Wagner, W. H. (1969). The construction of a classification. In *Systematic Biology* (pp. 67–90). National Academy of Science.
- Wagner, W. H. (1980). Origin and philosophy of the groundplan-divergence method of Cladistics. *Systematic Botany*, 5(2), 173–193. <https://doi.org/10.2307/2418624>

- Walker, A. (1981). The Koobi Fora Hominids and their bearing on the origins of the genus *Homo*. In *Homo Erectus: Papers in Honor of Davidson Black* (Sigmon, B.A. and Cybulski, J.S., pp. 193–216). University of Toronto Press.
- Walker, A., & Leakey, R. E. (1993). *The Nariokotome Homo erectus skeleton*. Harvard University Press.
- Walker, A., & Leakey, R. E. F. (1978). The hominids of east Turkana. *Scientific American*, 239(2), 54–67.
- Walker, A., Leakey, R. E., Harris, J. M., & Brown, F. H. (1986). 2.5-Myr *Australopithecus boisei* from west of Lake Turkana, Kenya. *Nature*, 322(6079), 517–522. <https://doi.org/10.1038/322517a0>
- Ward, C. V., Leakey, M. G., & Walker, A. (2001). Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution*, 41(4), 255–368. <https://doi.org/10.1006/jhev.2001.0507>
- Watrous, L. E., & Wheeler, Q. D. (1981). The out-group comparison method of character analysis. *Systematic Biology*, 30(1), 1–11. <https://doi.org/10.1093/sysbio/30.1.1>
- Weber, G. W. (2015). Virtual anthropology. *American Journal of Physical Anthropology*, 156(S59), 22–42. <https://doi.org/10.1002/ajpa.22658>
- Weber, G. W., & Bookstein, F. L. (2011). *Virtual Anthropology—A guide to a new interdisciplinary field*. Springer Vienna.
- Weber, G. W., Recheis, W., Scholze, T., & Seidler, H. (1998). Virtual anthropology (VA): Methodological aspects of linear and volume measurements—first results. *Collegium Antropologicum*, 22(2), 575–584.
- Weidenreich, F. (1928). *Der Schädel Fund von Weimar-Ehringsdorf*. Fischer-Verlag.
- Weidenreich, F. (1943). The skull of *Sinanthropus pekinensis*; a comparative study on a primitive hominid skull. *Palaeontologica Sinica*, 10, 1–485.
- Weidenreich, F. (1945). The paleolithic child from the Teshik-Tash Cave in Southern Uzbekistan (Central Asia). *American Journal of Physical Anthropology*, 3(2), 151–163. <https://doi.org/10.1002/ajpa.1330030211>
- Wheeler, W. (2001). Homology and the optimization of DNA sequence data. *Cladistics*, 17(1), S3–S11. <https://doi.org/10.1006/clad.2000.0154>
- Wheeler, W. C. (2021). Distance Wagner tree refinement as a heuristic approach to character-based initial tree construction. *Cladistics*, 37(6), 829–837. <https://doi.org/10.1111/cla.12478>
- White, S., Gowlett, J. A. J., & Grove, M. (2014). The place of the Neanderthals in hominin phylogeny. *Journal of Anthropological Archaeology*, 35, 32–50. <https://doi.org/10.1016/j.jaa.2014.04.004>
- White, T. D., Black, M. T., & Folkens, P. A. (2011). *Human Osteology*. Academic Press.
- White, T. D., Johanson, D. C., & Kimbel, W. H. (1981). *Australopithecus africanus*: Its phyletic position reconsidered. *South African Journal of Science*, 77, 445–470.
- White, T. D., Suwa, G., & Asfaw, B. (1994). *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, 371(6495), 306–312. <https://doi.org/10.1038/371306a0>
- Wiley, D. F. (2005). *Landmark* (Version 3.0) [Computer software]. University of California.
- Wiley, D. F., Amenta, N., Alcantara, D. A., Ghosh, D., Kil, Y. J., Delson, E., Harcourt-Smith, W., Rohlf, F. J., St John, K., & Hamann, B. (2005). Evolutionary morphing. *VIS 05. IEEE Visualization, 2005.*, 431–438. <https://doi.org/10.1109/VISUAL.2005.1532826>
- Wiley, E. O. (1981). *Phylogenetics: The theory and practice of phylogenetic systematics*. Wiley.
- Wiley, E. O., & Lieberman, B. S. (2011). *Phylogenetics: Theory and Practice of Phylogenetic Systematics* (2nd edn). John Wiley & Sons.
- Wiley, E. O., Siegel-Causey, D., Brooks, D. R., & Funk, V. A. (1991). The complete cladist: A primer of phylogeny procedures. *Museum of Natural History - University of Kansas - Special Publication*, 19, 1–158.
- Wind, J. (1984). Computerized X-ray tomography of fossil hominid skulls. *American Journal of Physical Anthropology*, 63(3), 265–282. <https://doi.org/10.1002/ajpa.1330630303>
- Wolpoff, M. H. (1980). Cranial remains of Middle Pleistocene European hominids. *Journal of Human Evolution*, 9(5), 339–358. [https://doi.org/10.1016/0047-2484\(80\)90047-0](https://doi.org/10.1016/0047-2484(80)90047-0)

- Wood, B. A. (1988). Are 'robust' australopithecines a monophyletic group. In *Evolutionary history of the "robust" australopithecines* (Grine F.E, pp. 269–284). Aldine de Gruyter.
- Wood, B. A. (1991). *Koobi Fora Research Project IV: Hominid Cranial Remains from Koobi Fora*. Clarendon Press.
- Wood, B. A. (1992a). Early hominid species and speciation. *Journal of Human Evolution*, 22(4), 351–365. [https://doi.org/10.1016/0047-2484\(92\)90065-H](https://doi.org/10.1016/0047-2484(92)90065-H)
- Wood, B. A. (1992b). Origin and evolution of the genus *Homo*. *Nature*, 355(6363), 783–790. <https://doi.org/10.1038/355783a0>
- Wood, B. A. (2011). *Wiley-Blackwell encyclopedia of human evolution* (Wiley-Blackwell). John Wiley & Sons.
- Wood, B. A., Martin, L., & Andrews, P. (1986). *Major topics in primate and human evolution*. Taylor & Francis.
- Wood, B., & Collard, M. (1999a). The changing face of genus *Homo*. *Evolutionary Anthropology: Issues, News, and Reviews*, 8(6), 195–207. [https://doi.org/10.1002/\(SICI\)1520-6505\(1999\)8:6%253C195::AID-EVAN1%253E3.0.CO;2-2](https://doi.org/10.1002/(SICI)1520-6505(1999)8:6%253C195::AID-EVAN1%253E3.0.CO;2-2)
- Wood, B., & Collard, M. (1999b). The Human genus. *Science*, 284(5411), 65–71. <https://doi.org/10.1126/science.284.5411.65>
- Wood, B., & Constantino, P. (2007). *Paranthropus boisei*: Fifty years of evidence and analysis. *American Journal of Physical Anthropology*, 134(S45), 106–132. <https://doi.org/10.1002/ajpa.20732>
- Wood, B., & Strait, D. (2004). Patterns of resource use in early *Homo* and *Paranthropus*. *Journal of Human Evolution*, 46(2), 119–162. <https://doi.org/10.1016/j.jhevol.2003.11.004>
- Wood, B., & Turner, A. (1995). Out of Africa and into Asia. *Nature*, 378(6554).
- Wu, H., & Poirier, F. E. (1995). *Human evolution in China: A metric description of the fossils and a review of the sites*. Oxford University Press.
- Xing, S., Zhou, M., & Liu, W. (2009). Crown morphology and variation of the lower premolars of Zhoukoudian *Homo erectus*. *Chinese Science Bulletin*, 54(21), 3905–3915. <https://doi.org/10.1007/s11434-009-0651-z>
- Zanolli, C. (2013). Additional evidence for morpho-dimensional tooth crown variation in a new Indonesian *H. erectus* sample from the Sangiran Dome (Central Java). *PLOS ONE*, 8(7), e67233. <https://doi.org/10.1371/journal.pone.0067233>
- Zeitoun, V. (1996). *Cladistique et paléanthropologie: Le cas de l'espèce Homo Erectus (Dubois, 1894)* [These de doctorat, Bordeaux 1]. <https://theses.fr/1996BOR10626>
- Zeitoun, V. (2000). Révision de l'espèce *Homo erectus* (Dubois, 1893). *Bulletins et mémoires de la Société d'Anthropologie de Paris.*, 12(1–2), Article 1–2. <https://doi.org/10.4000/bmsap.5963>
- Zeitoun, V. (2003). High occurrence of a basicranial feature in *Homo erectus*: Anatomical description of the preglenoid tubercle. *The Anatomical Record Part B: The New Anatomist*, 274B(1), 148–156. <https://doi.org/10.1002/ar.b.10028>
- Zelditch, M. L., Swiderski, D. L., & Sheets, H. D. (2004). *Geometric morphometrics for biologists. A primer*. Elsevier/Academic Press.
- Zhang, R., Drummond, A. J., & Mendes, F. K. (2024). Fast Bayesian inference of phylogenies from multiple continuous characters. *Systematic Biology*, 73(1), 102–124. <https://doi.org/10.1093/sysbio/syad067>
- Zhu, Z., Dennell, R., Huang, W., Wu, Y., Qiu, S., Yang, S., Rao, Z., Hou, Y., Xie, J., Han, J., & Ouyang, T. (2018). Hominin occupation of the Chinese Loess Plateau since about 2.1 million years ago. *Nature*, 559(7715), 608–612. <https://doi.org/10.1038/s41586-018-0299-4>
- Zollikofer, C. P., Ponce de León, M. S., Martin, R. D., & Stucki, P. (1995). Neanderthal computer skulls. *Nature*, 375(6529), 283–285.

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Figure 1: Schematic representation of phylogenetic systematics. The diagram illustrates the evolutionary relationships among four terminal taxa (A–D) based on six characters (1–6), each expressed in either a plesiomorphic (“primitive,” white) or apomorphic (“derived,” black) state. Monophyletic groups are defined by shared derived characters, for instance, taxa B, C, and D share character 1, while C and D share characters 1 and 3. The morphology of ancestral nodes (DACs) can be inferred, such as the most recent common ancestor of taxa C and D, which exhibits character 3 in the derived state and character 4 in the primitive state. (Modified from Hennig, 1965, p. 106, Fig. 3.).

Figure 2: Repartition of the sites of the studied specimens. Colours represent the fossil specimens of different species.

Figure 3: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Paranthropus aethiopicus* specimen, KNM-WT 17000 (original).

Figure 4: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Paranthropus boisei* specimens: A) OH5 (original), and B) KNM-ER 406 (original).

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Figure 7: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Australopithecus africanus* specimens: A) Sts 5 (original), and B) Sts 71 (reconstruction).

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Figure 9: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo habilis* specimens: A) KNM-ER 1813 (original), and B) OH24 (original).

Figure 10: *Norma facialis*, *norma lateralis* and *norma basilaris* of *Homo georgicus* specimens: A) D2282 (original), B) 2700 (original), and C) D4500 (cast).

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Figure 14: *Norma facialis*, *norma lateralis* and *norma basilaris* of Ngandong specimens: A) Ngandong 7 (original), and B) Ngandong 14 (original).

Figure 15: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Early Neandertals” specimens: A) Saccopastore 1 (cast), and B) Ehringsdorf H (cast).

Figure 16: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Near East Neandertals” specimens: A) Amud 1 (original), and B) Shanidar 1 (original).

Figure 17: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Classic Neandertals” specimens: A) Monte Circeo 1 (original), B) La Chapelle-aux-saints 1 (cast), and C) La Ferrassie 1 (original).

Figure 18: *Norma facialis*, *norma lateralis* and *norma basilaris* of “Early *H. sapiens*” specimens: A) Qafzeh 6 (original), B) Qafzeh 9 (cast), and C) Skhül V (cast).

Figure 19: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of KhoiSan’s specimens, Kh-1751 (original).

Figure 20: *Norma facialis*, *norma lateralis* and *norma basilaris* of one of Haya’s specimens, AF.23.0.20 (original).

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Figure 28: Position of the 59 morphological characters on the calvarium: A. *norma verticalis* B. *norma facialis*; C. *norma occipitalis*; D. *norma lateralis*, and E. *norma basilaris*.

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Figure 31: Position of the 57 characters on the calvarium: A) *norma verticalis*, B) *norma facialis*, C) *norma occipitalis*, D) *norma lateralis*, and E) *norma basilaris*. In the squared coloured boxes are the landmark configurations.

Figure 32: TNT script to apply the SAW method to landmarks and semi-landmarks. In bold are the part that can be modified.

Figure 33: Unique phylogenetic tree based on the analysis of matrix A after CI-weighting (i.e., 59 morphological characters and 23 OTUs), 7497 steps (CI = 0.636 and RI = 0.832). Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Values shown under the branches, at each node, are

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Values shown in green represent bootstrap scores in percentage (%) after 100 replications. Red letters are used to identify each node.

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SAPIENZA
UNIVERSITÀ DI ROMA



Applying cladistics to geometric morphometrics data: a new approach to resolve the phylogeny of the genus *Homo*.

Appendices

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A.A. 2022-2025 (Ciclo 38°)

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Appendix 1: Summary of the operational taxonomic units (OTU) used in the study.

	Current taxonomic attribution	N	Specimens	OTU and specimens of Chapter III	OTU and specimens of Chapter IV	Chronology	Site	Sexe	Scanning technic*	
Outgroups	Gorilla	3		Gorilla	Gorilla					
			Gorilla5	x	x	19-20th century	-	F	OP	
			Gorilla11	x	x	19-20th century	-	F	OP	
				Gorilla12	x	x	19-20th century	-	F	OP
	Pongo	3		Pongo	Pongo					
			Pongo2	x	x	19-20th century	-	F	OP	
			Pongo3	x	x	19-20th century	-	F	OP	
				Pongo6	x	x	19-20th century	-	F	OP
	Pan	3		Pan	Pan					
			Pan1	x	x	19-20th century	-	F	OP	
			Pan6	x	x	19-20th century	-	F	OP	
				Pan10	x	x	19-20th century	-	F	OP
Ingroups										
Paranthropus	P. aethiopicus	1		-	P. aethiopicus					
			KNM-WT 17000		x	2.57 - 2.47 Ma	Lomekwi, West Turkana, Kenya	M	OP	
		P. boisei	2		-	P. boisei				
	OH5			x	1.79 - 1.85 Ma	Olduvai Gorge, Tanzania	M	CT		
			KNM-ER 406		x	1.7 Ma	Koobi Fora, Kenya	M	OP	
Australopithecus	A. sp.	1		-	Stw 53					
			Stw 53		x	~3.67 Ma	Sterkfontein, South Africa	?	PH	
	A. afarensis	1		-	A. afarensis					
			AL 444-2		x	~3 Ma	Hadar, Ethiopia	M	Open access on the virtual anthropology portal of Vienna University	
	A. africanus	2		A. africanus	A. africanus					
			STS5	x	x	2.07 Ma	Sterkfontein, South Africa	F		CT
			STS71	x	x	2.61 - 2.07 Ma	Sterkfontein, South Africa	M	CT	

References first taxonomic attribution	References description	References chronology	Institution** (obtained by AM)
-	-	-	DC
-	-	-	DC
-	-	-	DC
-	-	-	DC
-	-	-	DC
-	-	-	DC
-	-	-	DC
-	-	-	DC
(Walker et al., 1986)	(Walker et al., 1986)	(Feibel et al., 1989)	?
(Leakey, 1959)	(Leakey, 1959)	(Hay 1976)	?
(Leakey et al., 1971)	(Leakey et al., 1971)	(Feibel et al., 1989)	?
(Hughes and Tobias, 1977)	(Hughes and Tobias, 1977)	(Granger et al., 2015)	?
(Kimbel et al., 1994)	(Kimbel et al., 1994)	(Kimbel et al., 1994)	?
(Broom and Robinson, 1950)	(Broom and Robinson, 1950)	(Schwarcz et al., 1994)	DNM
(Broom and Robinson, 1950)	(Broom and Robinson, 1950)	(Schwarcz et al., 1994)	DNM

	Current taxonomic attribution	N	Specimens	OTU and specimens of Chapter III	OTU and specimens of Chapter IV	Chronology	Site	Sexe	Scanning technic*	
<i>H. habilis sensu lato</i>	<i>H. rudolfensis</i>	1		Koobi Fora - <i>H. habilis s.l</i>	<i>H. rudolfensis</i>					
			KNM-ER 1470	x	x	~1.8 Ma	Koobi Fora, Kenya	M	PH	
	<i>H. habilis</i>	2			<i>H. habilis</i>					
			KNM-ER 1813 OH24	x	x	>1.78 Ma	Koobi Fora, Kenya	F	PH	
	<i>H. georgicus</i>	3		<i>H. georgicus</i>	Dminisi					
			D2282	x	x	~1.77 Ma	Dmanisi, Georgia	F	PH	
			D2700		x	~1.77 Ma	Dmanisi, Georgia	?	PH	
			D4500	x	x	~1.77 Ma	Dmanisi, Georgia	M	PH	
	<i>H. erectus s.l.</i>	<i>H. ergaster</i>	2		Koobi Fora - <i>H. ergaster</i>	<i>H. ergaster</i>				
				KNM-ER 3733	x	x	~1.6 Ma	Koobi Fora, Kenya	F	PH
			KNM-ER 3883	x	x	~1.6 Ma	Koobi Fora, Kenya	M	PH	
<i>H. erectus</i>		6		Sangiran	Sangiran					
			Sangiran 2	x	x	1.02 - 1.50 Ma	Sangiran, Java, Indonesia	F	CT	
			Sangiran 17	x	x	1.02 - 1.50 Ma	Sangiran, Java, Indonesia	M	OP	
				Zhoukoudian	Zhoukoudian					
			Sinanthropus III	x	x	~0.68 - 0.78 Ma	Zhoukoudian, Beijing, China	F	PH	
			Sinanthropus XI	x	x	~0.68 - 0.78 Ma	Zhoukoudian, Beijing, China	?	PH	
				Ngandong	Ngandong					
	Ngandong 7	x	x	108 - 117 ka	Ngandong, Solo River, Java, Indonesia	M	PH			
	Ngandong 14	x	x	108 - 117 ka	Ngandong, Solo River, Java, Indonesia	?	PH			
<i>H. neanderthalensis</i>	2		Early Neandertal	Early Neandertal						
			Saccopastore 1	x	x	130-250 ka	Saccopastore, Italy	F	PH	
			Ehringsdorf H	x	x	~200 ka	Ehringsdorf, Germany	M	PH	
	2		Near East Neandertal	Near East Neandertal						
			Amud 1	x	x	50-60 ka	Amud, Israel	M	OP	
		Shanidar 1	x	x	60 - 80 ka	Shanidar, Iraq	M	PH		

References first taxonomic attribution	References description	References chronology	Institution** (obtained by AM)
(Leakey, 1973)	(Leakey, 1973)	(Gathogo and Brown, 2006)	NMK
(Leakey, 1974)	(Day et al., 1976)	(Feibel et al., 2009)	NMK
(Leakey et al., 1971)	(Leakey et al., 1971)	(Tamrat et al., 1995)	UMR
(Gabunia et al., 2000)	(Gabunia et al., 2000)	(Lordkipanidze, 1999)	IPH
(Vekua et al., 2002)	(Vekua et al., 2002)	(Lordkipanidze, 1999)	NMH
(Lordkipanidze et al., 2013)	(Lordkipanidze et al., 2013)	(Lordkipanidze, 1999)	FD
(Leakey and Walker, 1985)	(Leakey and Walker, 1985)	(Gathogo and Brown, 2006)	NMK
(Leakey and Walker, 1985)	(Leakey and Walker, 1985)	(Gathogo and Brown, 2006)	NMK
(Van Heekeren, 1972)	(Rightmire, 1990)	(Larick et al., 2001)	SFN
(Sartono, 1971)	(Rightmire, 1990)	(Larick et al., 2001)	IPH
(Weidenreich, 1943)	(Weidenreich, 1943)	(Shen et al. 2009)	IPH
(Weidenreich, 1943)	(Weidenreich, 1943)	(Shen et al. 2009)	IPH
(Oppenoorth, 1932)	(Santa Luca, 1980)	(Rizal et al., 2020)	IPH
(Oppenoorth, 1932)	(Santa Luca, 1980)	(Rizal et al., 2020)	IPH
(Sergi, 1944)	(Condemi, 1992a)	(Marra et al., 2015)	SU
(Weidenreich, 1928)	Street et al., 2006	(Grün and Stringer, 1991)	IPH
(Suzuki, 1970)	(Suzuki, 1970)	(Rink et al., 2013)	DC
(Trinkaus, 1983)	(Trinkaus, 1983)	(Trinkaus, 1991)	MH

	Current taxonomic attribution	N	Specimens	OTU and specimens of Chapter III	OTU and specimens of Chapter IV	Chronology	Site	Sexe	Scanning technic*
<i>H. neanderthalensis</i>		3		Classic Neandertal	Classic Neandertal				
			Monte Circeo 1	x	x	52 +/- 12 ka	Monte Circeo, Italy	?	CT
			La Chapelle-aux-Saints	x	x	~50 ka	La-Chapelle-aux-Saints, France	M	CT
<i>H. sapiens</i>			La Ferrassie 1	x	x	53-66 ka	La Ferrassie, France	M	CT
		3		Skhül - Qafzeh	Skhül - Qafzeh				
			Qafzeh6	x	x	~100 ka	Qafzeh, Israel	M	PH
			Qafzeh9	x	x	~100 ka	Qafzeh, Israel	F	OP
			SkhülV			101 - 137 ka	Mugharet-es-Skhul, Israel	M	CT
	KhoiSan	5		KhoiSan	KhoiSan				
			Kh-1738	x	x	19-20th century	Republic of South Africa	F	CT
			Kh-1751	x	x	19-20th century	Republic of South Africa	M	CT
			Kh-3731	x	x	19-20th century	Republic of South Africa	M	CT
			Kh-3732	x	x	19-20th century	Republic of South Africa	F	CT
			Kh-5051	x	x	19-20th century	Republic of South Africa	F	CT
	Haya	5		Haya	Haya				
			AF.23.0.20	x	x	19-20th century	Tanzania	F	CT
			AF.23.0.23	x	x	19-20th century	Tanzania	F	CT
			AF.23.0.109	x	x	19-20th century	Tanzania	M	CT
			AF.23.0.110	x	x	19-20th century	Tanzania	M	CT
			AF.23.0.112	x	x	19-20th century	Tanzania	F	CT
	Kongo (Central Afric)	5		Kongo	Kongo				
			AfC-1730	x	x	19-20th century	Congo	M	CT
			AfC-1777	x	x	19-20th century	Congo	M	CT
			AfC-4974	x	x	19-20th century	Angola	F	PH
			AfC-9639	x	x	19-20th century	Gabon	F?	PH
			AfC-9642	x	x	19-20th century	Gabon	F?	PH

References first taxonomic attribution	References description	References chronology	Institution** (obtained by AM)
(Sergi, 1991)	(Sergi, 1991)	(Grün and Stringer, 1991)	MP
(Boule, 1911, 1912, 1913)	(Boule, 1911, 1912, 1913)	(Grün and Stringer, 1991)	MH
(Peyrony and Capitan, 1909)	(Heim, 1976)	(Blackwell et al., 2007)	MH
(Köppel, 1935)	(Vandermeersch, 1981)	(Grün et al., 2005)	IPH
(Vandermeersch, 1970)	(Vandermeersch, 1970)	(Grün et al., 2005)	DC
(McCown, 1932)	(McCown and Sir Keith, 1939)	(Mercier et al., 1993)	PM
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	-	MH
-	-	-	MH
-	-	-	MH

	Current taxonomic attribution	N	Specimens	OTU and specimens of Chapter III	OTU and specimens of Chapter IV	Chronology	Site	Sexe	Scanning technic*
<i>H. sapiens</i>	Mande (West Africa)	5		Mande	Mande				
			AfW-5419	x	x	19-20th century	Mali	F	CT
			AfW-6089	x	x	19-20th century	Mali	F	CT
			AfW-9539	x	x	19-20th century	Guinea	F	PH
			AfW-9543	x	x	19-20th century	Guinea	M	PH
			AfW-9544	x	x	19-20th century	Guinea	F	PH
	Berber (North Africa)	5		Berber	Berber				
			AfN-18458	x	x	19-20th century	Marocco	F?	PH
			AfN-18459	x	x	19-20th century	Marocco	F?	PH
			AfN-18460	x	x	19-20th century	Marocco	M?	PH
			AfN-18464	x	x	19-20th century	Marocco	F?	PH
			AfN-18465	x	x	19-20th century	Marocco	M?	PH
	Papu (Oceania)	5		Papu	Papu				
			MEL076	x	x	19-20th century	Papua-New-Guinea	F	PH
			MEL084	x	x	19-20th century	Papua-New-Guinea	M	PH
			MEL085	x	x	19-20th century	Papua-New-Guinea	M	PH
			MEL104	x	x	19-20th century	Papua-New-Guinea	F	CT
			MEL130	x	x	19-20th century	Papua-New-Guinea	F	PH
	French (Europa)	5		French	French				
			Eu.24.00.1	x	x	19-20th century	France	M	CT
			Eu-1036	x	x	19-20th century	France	F	CT
			Eu-1042	x	x	19-20th century	France	M	CT
			Eu-1051	x	x	19-20th century	France	M	CT
			Eu-1065	x	x	19-20th century	France	F	CT
	Chinese (Asia)	5		Chinese	Chinese				
			EAS-ORSA0427	x	x	19-20th century	China	M	CT
			EAS-ORSA0550	x	x	19-20th century	China	F	CT
			EAS-ORSA0669	x	x	19-20th century	China	M	CT
			EAS-ORSA0670	x	x	19-20th century	China	F	CT
			EAS-ORSA1858	x	x	19-20th century	China	M	CT

References first taxonomic attribution	References description	References chronology	Institution** (obtained by AM)
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	-	MH
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	DC
-	-	(Mounier & Mirazón Lahr, 2019)	OR
-	-	(Mounier & Mirazón Lahr, 2019)	OR
-	-	(Mounier & Mirazón Lahr, 2019)	OR
-	-	(Mounier & Mirazón Lahr, 2019)	OR
-	-	(Mounier & Mirazón Lahr, 2019)	OR

	Current taxonomic attribution	N	Specimens	OTU and specimens of Chapter III	OTU and specimens of Chapter IV	Chronology	Site	Sexe	Scanning technic*
<i>H. sapiens</i>	Inuit (America)	5		Inuit	Inuit				
			99.1-102	x	x	19-20th century	Alaska	F	CT
			99.1-103	x	x	19-20th century	Alaska	M	CT
			99.1-161	x	x	19-20th century	Alaska	F	CT
			99.1-168	x	x	19-20th century	Alaska	F	CT
			99.1-196	x	x	19-20th century	Alaska	M	CT

References first taxonomic attribution References description References chronology Institution (obtained by AM)**

-	-	(Copes, 2012)	AM
-	-	(Copes, 2012)	AM
-	-	(Copes, 2012)	AM
-	-	(Copes, 2012)	AM
-	-	(Copes, 2012)	AM

* CT = CT-scanner ; OP = optical scanner ; PH = photogrammetry

** AM = American Museum of Natural History, New York; DC = Duckworth Laboratory, Cambridge; FD : Laboratoire départemental de préhistoire du Lazaret, Fort de la Drette ; GPI : Geologisch-Paläontologisches Institut Ruprecht-Karls Universität Heidelberg ; IPH : Institut de Paléontologie Humaine, Paris ; IRSNB : Institut Royal des Sciences Naturelles de Belgique, Bruxelles ; ISIPU : Istituto Italiano di Paleontologia Umana, Roma ; MH : Musée de l'Homme, Paris ; MNHN : Museum National d'Histoire Naturel, Paris ; MP : Museo Pigorini, Roma ; NHM : British Museum, Natural History Museum, London ; NMK = National Museums of Kenya, Nairobi; OR = ORSA database, Penn Museum; SFN : Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt ; SMN : Staatliches Museum für Naturkunde, Stuttgart ; SupL : Suprintendenza del Lazio, Tivoli ; UA : Département de Géologie et de Géographie Physique, Université Aristote, Thessalonique ; UMR : UMR 6578, Unité d'Anthropologie Bioculturelle, Marseille ; UP : Università degli studi di Pisa ; USap : Università La Sapienza, Roma.

Appendix 2: Morphological characters of the calvarium

The description of the morphological characters (i.e. Appendix 2) is modified from [Mounier and Caparros 2025](#). Figures presenting the characters and observation protocols can be found in [Appendix A](#) of Mounier and Caparros 2025.

Outline of the calvarium in *norma occipitalis*:

The cranium outline in *norma occipitalis* is commonly used to characterise fossil specimens. For example, the Neandertal calvarium displays a distinct circular pattern (form “en bombe”, Boule, 1911, 1912, 1913; Vandermeersch, 1981; Condemi, 1992) while the calvariae attributed to *H. erectus* s.l. typically show a triangular shape in *norma occipitalis* (Grimaud, 1982). Modern humans calvariae are usually described as pentagonal (Broca, 1868; Olivier, 1960). The definitions of these three character states are based on the position of the largest cranial distance (euryon).

Three states:

- 1: triangular
- 2: circular
- 3: pentagonal

Character number:

- Chapter III: #1
- Chapter IV: #11 in Matrix A and #8 in Matrix B

Frontal cord length (M29) relative to parietal cord length (M30):

The cords M29 and M30 are defined based on Martin and Saller (1957).

Three states:

- 1: the frontal chord length is inferior to parietal chord length ($M29/M30 \leq 0.98$)
- 2: the frontal chord length is equal to parietal chord length ($0.98 < M29/M30 < 1.02$)
- 3: the frontal chord length is superior to parietal chord length ($M29/M30 \geq 1.02$)

Character number:

- Chapter III: #2
- Chapter IV: #12 in Matrix A and #9 in Matrix B

Outline of the supraorbital region in *norma facialis*:

Two states:

- 1: the anterior border of the supra-orbital region is straight

2: the anterior border of the supra-orbital region is convex

Character number:

- Chapter III: #3
- Chapter IV: #1 in Matrix A and #1 in Matrix B

The supra-orbital region consists of several complex morphological structures. Schwalbe (1901) identified two main components: the *arcus supraciliaris* and the *arcus supraorbitalis* which can either be merged or separated by the *sulcus supraorbitalis*. Cunningham (1908) recognised the *trigonum supraorbitale* and classified the variation of the supra-orbital region into four main morphological types. Santa Luca (1980) described the median part of the supra-orbital region as having a *torus glabellaris*. Spiteri (1984) characterized the supra-orbital region as comprising a medial structure (glabella) and two lateral supra-orbital tori. His description of the supra-orbital torus is associated with the *sulcus supraorbitalis*, which originates from the frontal notch and extends obliquely along the antero-superior surface of the supra-orbital region. These features have been used in various ways to describe the range of morphologies observed in the hominin fossil record (Caparros, 1997; Nara, 1994; Suzuki and Takai, 1970; Zeitoun, 2000, 1996).

Supraorbital region and presence of a *sulcus supraorbitalis*:

According to some authors (Condemi, 1992; Cunningham, 1908; Heim, 1974), the three structures of the supra-orbital region (*arcus supraorbitalis*, *arcus supraciliaris* and *trigonum supraorbitale*) are always merged in classic Neandertals, while in modern humans, they are clearly individualized, with a distinct *sulcus supraorbitalis* separating the *arcus supraorbitalis* and *arcus supraciliaris*.

Three states:

- 1: presence of a *sulcus supraorbitalis*
- 2: presence of an incomplete *sulcus supraorbitalis*; the supra-orbital trigon is merged posteriorly with the *arcus superciliaris*
- 3: absence of a *sulcus supraorbitalis*

Character number:

- Chapter III: #4
- Chapter IV: #13 in Matrix A and #10 in Matrix B

Projection of the supraorbital region:

Three states:

- 1: the supraorbital region is not projecting
- 2: only the *arcus superciliaris* is projecting
- 3: the whole supraorbital region is projecting

Character number:

- Chapter III: #5
- Chapter IV: #14 in Matrix A and #11 in Matrix B

Post-orbital constriction (Ipc=M9/M43):

The post-orbital constriction is sometimes used to define *H. erectus* s.l. (Rightmire, 1990). Here, we estimate the post-orbital constriction using the post-orbital constriction index (Ipc), defined as follows: $Ipc = M9/M43$. M9 represents the minimal length of the frontal, and M43 refers to the total length of the post-orbital region (Martin and Saller, 1957).

Three states:

- 1: the post-orbital constriction is important: $Ipc < 0,75$
- 2: the post-orbital constriction is weak: $0,75 \geq Ipc \geq 0,85$
- 3: the post-orbital constriction is absent: $Ipc > 0,85$

Character number:

- Chapter III: #6
- Chapter IV: #15 in Matrix A and #12 in Matrix B

Outline of the supraorbital region in *norma verticalis*:

Three states:

- 1: the supraorbital region is medially concave at the glabella
- 2: the supraorbital region is straight
- 3: the supraorbital region is convex

Character number:

- Chapter III: #7
- Chapter IV: #2 in Matrix A and #1 in Matrix B

***Sulcus postorbitalis*:**

Posterior to the supra-orbital region, a post-orbital sulcus can be observed in most fossil specimens. The *sulcus postorbitalis* may be continuous, extending across the entire supra-orbital region, or it may be restricted to the medial part of the supra-orbital region (glabella). The presence of a *sulcus postorbitalis* is often considered characteristic of *H. erectus* s.l., although the definition of this character remains unclear (Antón, 2003). Neandertals also exhibits a more or less continuous sulcus (Condemi, 1992).

Three states:

- 1: *sulcus postorbitalis* absent

2: *sulcus postorbitalis* medially present at the glabella

3: *sulcus postorbitalis* present and continuous

Character number:

- Chapter III: #8
- Chapter IV: #16 in Matrix A and #13 in Matrix B

Tuber frontale:

According to Stringer, Hublin and Vandermeersch (1984), a *tuber frontale* associated with a high and rounded frontal bone may be considered as a modern human derived feature. Lieberman (1995) described modern humans' *tuber frontale* as resulting from the antero-posterior extension of the brain during growth. However, this character is difficult to observe due to its considerable morphological variation among Pleistocene hominin fossils (Caparros, 1997; Mounier, 2009). Here we are using three states to represent the morphological variation of the *tuber frontale*.

Three states:

1: absence of a *tuber frontale*

2: presence of a low individualised and medially shifted *tuber frontale*

3: presence of individualised *tuber frontale* that cover the entire anterior part of the frontal bone

Character number:

- Chapter III: #9
- Chapter IV: #17 in Matrix A and #14 in Matrix B

Antero-posterior convexity of the frontal:

The antero-posterior convexity of the frontal is estimated using the Icf index defined as follows: $M29 \times 100 / M26$. M29 is the nasio-bregma chord and M26 is the nasio-bregma arc (Martin and Saller, 1957).

Trois états :

1: weak convexity: $Icf \geq 95$

2: intermediate convexity: $95 > Icf \geq 90$

3: important convexity: $Icf < 90$

Character number:

- Chapter III: #10
- Chapter IV: #3 in Matrix A and #2 in Matrix B

***Linea temporalis* development on the frontal:**

Three states:

- 1: absence of *linea temporalis*
- 2: presence of unique *linea temporalis*
- 3: presence of double *linea temporalis*

Character number:

- Chapter III: #11
- Chapter IV: #18 in Matrix A and #15 in Matrix B

Fossil hominins often display various superstructures on their calvarium. Some of these, particularly those located on the frontal and parietal bones, are considered derived features of *H. erectus* s.s. (Andrews, 1984; Antón, 2003; Clark, 1978; Hublin, 1986; Stringer, 1984). We acknowledge that some of these calvarial superstructures may be developmentally correlated (Stringer, 1991, 1984). To better account for the morphological variation in the fossil record, we have observed and coded the sagittal keel on the frontal, the bregmatic eminence, and the thickening of the superior part of the coronal sutures separately.

Sagittal crest:

The sagittal crest is a dorsal bony ridge that courses craniocaudal over the calvarium of the skull, serving as an attachment site for muscles (Owen, 1835).

Two states:

- 1: absence of a sagittal crest
- 2: presence of a sagittal crest

Character number:

- Chapter III: #11
- Chapter IV: #19 in Matrix A and #16 in Matrix B

Sagittal keel on the frontal:

A thickening of the frontal bone in its medial part (on the metopic suture) is considered to be a *H. erectus* s.l. derived feature (Clark, 1978; Rightmire, 1990) and more specifically of the Asian specimens (Andrews, 1984; Stringer, 1984). However, this inference has been questioned (Bräuer, 1992; Caparros, 1997), and particularly Bräuer and Mbua (1992) classify the character as a shared primitive feature.

Two states:

- 1: absence of a sagittal keel on the frontal
- 2: presence of a sagittal keel on the frontal

Character number:

- Chapter III: #12
- Chapter IV: #20 in Matrix A and #17 in Matrix B

Bregmatic eminence:

Two states:

- 1: absence of bregmatic eminence
- 2: presence of bregmatic eminence

Character number:

- Chapter III: #13
- Chapter IV: #21 in Matrix A and #18 in Matrix B

Pterion in *norma lateralis*:

The pterion represents the suture position in the antero-lateral region of the skull formed by the junction of the frontal, the parietal, the sphenoid and the temporal (Barriel, 1994).

Two states:

- 1: the suture is of spheno-parietal type
- 2: the suture is of fronto-temporal type

Character number:

- Chapter III: #14
- Chapter IV: #22 in Matrix A and #19 in Matrix B

Thickening on the superior part of the coronal sutures:

The upper coronal reinforcement refers to the bony reinforcement at the upper part of the coronal sutures, which can be seen in certain fossil specimens (Mounier, 2009). It is typically associated with the bregmatic eminence but can also occur in isolation.

Two states:

- 1: absence of bone thickening on the superior part of the coronal sutures
- 2: presence of bone thickening on the superior part of the coronal sutures

Character number:

- Chapter III: #15
- Chapter IV: #23 in Matrix A and #20 in Matrix B

Sagittal keel on the bregma-lambda arch:

The sagittal keel is a thickening of the bone at the level of the bi-parietal suture.

Two states:

- 1: absence of a sagittal keel on the bregma-lambda arch
- 2: presence of a sagittal keel on the bregma-lambda arch

Character number:

- Chapter III: #16
- Chapter IV: #24 in Matrix A and #21 in Matrix B

Parasagittal hollowing on both sides of the parietal suture:

Two states:

- 1: absence of a hollowing
- 2: presence of a hollowing

Character number:

- Chapter III: #17
- Chapter IV: #25 in Matrix A and #22 in Matrix B

Pre-lambdatic hollowing on the bregma-lambda arch:

A pre-lambdatic hollowing on the bregma-lambda arc was described by Weidenreich (1943) on the *Sinanthropus* specimens.

Two states:

- 1: absence of a hollowing on the posterior part of the bregma-lambda arch
- 2: presence of a hollowing on the posterior part of the bregma-lambda arch

Character number:

- Chapter III: #16
- Chapter IV: #26 in Matrix A and #23 in Matrix B

The configuration and position of the *linea temporalis* on the parietal are commonly used to describe fossils of the genus *Homo* (de Lumley et al., 2006; Grimaud, 1982; Prat, 2004; Zeitoun, 2000). To better account for the morphological variation of this anatomical structure, we used two features.

***Linea temporalis* width of the temporal band:**

Three states:

- 1: the *linea temporalis* are not visible on the parietal bone
- 2: the band formed by the *linea temporalis* is narrow (≤ 20 mm in its widest part)
- 3: the band formed by the *linea temporalis* is wide (> 20 mm in its widest part)

Character number:

- Chapter III: #19
- Chapter IV: #27 in Matrix A and #24 in Matrix B

Position of the superior *linea temporalis* on the parietal:

We estimated the position of the *linea temporalis* on the parietal by measuring on the arc asterion-bregma, the distance between the temporo-parietal suture and the superior temporal line (Dt) and the distance between the temporo-parietal suture and the bregma (Db), and computed the index $Rlt = Dt/Db$. This character exhibits significant variability in the fossil sample studied (Mounier, 2009).

Three states:

- 1: the superior *linea temporalis* is in high position ($Rlt > 0,55$)
- 2: the superior *linea temporalis* is in medial position ($0,54 > Rlt > 0,46$)
- 3: the *linea temporalis* is in low position ($Rlt < 0,45$)

Character number:

- Chapter III: #20
- Chapter IV: #28 in Matrix A and #25 in Matrix B

***Torus angularis parietalis*:**

The *torus angularis parietalis* was first described by Weidenreich (1943) as a rounded bulge on the parietal surface located at the angle of the lambdoid and parieto-mastoid sutures. It is often considered specific to *H. erectus* s.l. (Andrews, 1984; Rightmire, 1990), but is frequently absent in African specimens (Antón, 2003; Stringer, 1991, 1984).

Two states:

- 1: absence of a rounded bulge at the angle of the lamdoid and parieto-mastoid sutures.
- 2: presence of a rounded bulge at the angle of the lamdoid and parieto-mastoid sutures.

Character number:

- Chapter III: #21
- Chapter IV: #29 in Matrix A and #26 in Matrix B

Tuber parietale:

Krukoff (1967) defined the *tuber parietale* as the exocranial point that forms the summit of a pyramid, with its base being a triangle defined by bregma, lambda, and the fronto-parietal (i.e., the *parietum*). When the *tuber parietale* are not well-defined, the *parietum* corresponds to the maximum curvature of the bone. Well-defined *tuber parietale* are considered specific to *H. sapiens* (Grimaud, 1982).

Three states:

- 1: absent, the *parietum* corresponds to the maximum curvature of the bone
- 2: presence of *tuber parietale* medially shifted on the parietal
- 3: presence of *tuber parietale* in a high position on the parietal

Character number:

- Chapter III: #22
- Chapter IV: #30 in Matrix A and #27 in Matrix B

Outline of the occipital in *norma lateralis*:

Estimating the curvature of the occipital bone is challenging (Piveteau, 1970; Vandermeersch, 1981). A sharply angled occipital is sometimes considered a specific feature of *H. erectus* s.l. (Rightmire, 1990; Stringer, 1984), while modern humans typically have a rounded occipital (Vandermeersch, 1981). In Neandertals, the presence of an occipital bun may obscure this feature, but they generally exhibit an angled occipital (Condemi, 1992; Vandermeersch, 1981).

Two states:

- 1: rounded profile
- 2: sharply angled

Character number:

- Chapter III: #23
- Chapter IV: #4 in Matrix A and #3 in Matrix B

Outline of the *planum occipitale* in *norma lateralis*:

The *planum occipitale* is defined by the position of the inion, located at the junction of the superior nuchal lines and the medio-sagittal plane (i.e., precisely on the *tuberculum linearum*) (Hublin, 1986; Hublin, 1978a; Martin and Saller, 1957). A strong convexity of the *planum occipitale* may be more characteristic to *H. neanderthalensis* (Hublin, 1988), potentially linked to the presence of an occipital bun (see #26).

Two states:

1: *no convexity*

2: *convexity*

Character number:

- Chapter III: #24
- Chapter IV: #5 in Matrix A and #3 in Matrix B

Relative development of the *planum nucale* (PN) and the *planum occipitale* (PO):

A shorter *planum occipitale* in relation to the *planum nucale* can be observed on the Asian *H. erectus* specimens. This morphology is not typically found in African *H. erectus* specimens and is absent in *H. sapiens* and *H. neanderthalensis* (Stringer, 1991, 1984).

Two states:

1: *planum nucale* is bigger or equal to the *planum occipitale* (PN $\ge$ PO)

2: *planum nucale* is shorter than the *planum occipitale* (PN<PO)

Character number:

- Chapter III: #25
- Chapter IV: #31 in Matrix A and #28 in Matrix B

Occipital bun:

Trinkaus and Lemay (1982) defined this anatomical structure as being “a posterior projection of the occipital squama which is evenly rounded in norma lateralis and slightly compressed in a craniocaudal direction” (p. 27). Boule (1913, 1912, 1911) was the first to describe this structure in the La Chapelle-aux-Saints specimen, and the occipital bun is generally considered a Neandertal synapomorphy (Hublin, 1978b; Wolpoff, 1980). However, the occipital bun can also be observed in some anatomically modern humans (Smith and Trinkaus, 1991; Trinkaus, 2007; Trinkaus and Lemay, 1982).

Two states:

1: absence of occipital bun

2: presence of occipital bun

Character number:

- Chapter III: #26
- Chapter IV: #32 in Matrix A and #29 in Matrix B

Opisthocranium relative position in relation to inion:

The inion and the opisthocranium are generally located at the same position on *H. erectus* s.l. specimens. However, this is not always the case, and this morphology is not considered specific to *H. erectus* s.l. populations (Andrews, 1984; Stringer, 1984). According to Hublin (1986), in early *Homo* specimens, the opisthocranium is situated at the highest point of the occipital torus, just above the inion. In such cases, we considered the opisthocranium and inion to be located at the same position.

Two states:

- 1: inion and opisthocranium have the same position
- 2: inion and opisthocranium are at different position

Character number:

- Chapter III: #27
- Chapter IV: #33 in Matrix A and #30 in Matrix B

Processus retromastoideus:

The *processus retromastoideus* is located halfway between the inion and the *processus mastoideus* and serves as the insertion point for the *m. obliquus capiti superior*. More specifically, the *processus retromastoideus* is a protuberance on the *planum nuchale*, where the occipital torus meets the inferior nuchal lines (Santa Luca, 1980). Weidenreich observed it on the Ngandong specimens (Weidenreich, 1951).

Two states:

- 1: absence of the *processus retromastoideus*
- 2: presence of the *processus retromastoideus*

Character number:

- Chapter III: #28
- Chapter IV: #34 in Matrix A and #31 in Matrix B

Outline of the *planum occipitale* in *norma occipitalis*:

A triangular outline on the superior part of the occipital bone is often considered as characteristic of early *Homo* specimens, especially *H. erectus* s.l. (Nara, 1994), while modern humans and Neandertals typically exhibit a more rounded or pentagonal outline.

Three states:

- 1: *planum occipitale* is triangulaire in *norma occipitalis*
- 2: *planum occipitale* is circular in *norma occipitalis*

3: *planum occipitale* is pentagonal in *norma occipitalis*

Character number:

- Chapter III: #29
- Chapter IV: #6 in Matrix A and #4 in Matrix B

The suprainiac fossa is regarded as a distinct trait of Neandertals (Hublin, 1988; Rougier and Balzeau, 2007; Stringer et al., 1984). It is situated above the occipital torus and may, on rare occasions, be found in modern human specimens (Hublin, 1988).

Suprainiac fossa:

Three states:

- 1: absence of the suprainiac fossa
- 2: presence of a hollowing, weakly delineated over the torus occipital
- 3: presence of a well-defined suprainiac fossa

Character number:

- Chapter III: #30
- Chapter IV: #35 in Matrix A and #32 in Matrix B

Configuration of the lateral edges of the suprainiac fossa:

Three states:

- 1: absence of suprainiac fossa
- 2: the lateral edges of the fossa are convergent upward
- 3: the lateral edges of the fossa are parallel or arched

Character number:

- Chapter III: #31
- Chapter IV: #36 in Matrix A and #33 in Matrix B

The *torus occipitalis transversus* is regularly used in the definition of *H. erectus* s.l. (Hublin, 1986; Rightmire, 1990; Stringer, 1991, 1984; Wood, 1984), although its morphological definition is sometimes unclear. Stringer (l. 56, 1991) refers to a “strong torus occipitalis”, Rightmire (l. 189, 1990) notes that the “morphology of the transverse torus of the occiput is distinctive, as noted by Wood (1984) and others, although there is a good deal of variation.” Hublin’s definition of the torus in *H. erectus* is clearer (l. 180, Hublin, 1986): “A strong occipital torus develops between the asterion, joining the torus angularis, the supramastoid crests and the occipito-mastoid crests. It is a thickening of the external table of the occipital between the superior nuchal lines and the suprema nuchal lines forming a sulcus supratoralis. Its maximum development is in the median area, above the tuberculum linearum”, as for Neandertals (l. 69, Hublin, 1988): “Comparé à celui des *Homo erectus asiaticus*, ce torus

occipital est faiblement développé, si l'on tient compte des mesures d'épaisseur (Hublin, 1978). (...) Latéralement il s'étend rarement au-delà de l'insertion des m. semispinalis capitis (Spy 2). (...) Dans sa partie médiane, sous la fosse sus-iniaque, le torus est lui-même déprimé et ses points de développement maximal sont situés latéralement. Ainsi en vue inférieure le torus présente une saillie bilatérale et non une saillie maximale médiane comme c'est habituellement le cas". The *torus occipitalis transversus* is usually outlined by the *sulcus supratoralis*. While not always present, its morphology can vary significantly. Condemi (1992) explains that the *sulcus supratoralis* marks the occipital bun in Neandertals, being distinctly defined laterally, but less pronounced medially. We used three distinct morphological features to more accurately describe the variation in the *torus occipitalis transversus*.

***Sulcus supratoralis* development:**

Three states:

- 1: absence of the *sulcus supratoralis*
- 2: presence of a hollow around the supra-toral torus
- 3: presence of a deep *sulcus supratoralis*

Character number:

- Chapter III: #32
- Chapter IV: #37 in Matrix A and #34 in Matrix B

***Torus occipitalis transversus* development:**

Three states:

- 1: absence of the *torus occipitalis transversus*
- 2: the torus is present and medially protruding
- 3: the torus is present and bilaterally protruding

Character number:

- Chapter III: #33
- Chapter IV: #38 in Matrix A and #35 in Matrix B

Torus occipitalis transversus, form in norma occipitalis:

In classic Neandertals, the *torus occipitalis transversus* is typically straight when viewed in *norma occipitalis* (Condemi, 1992). The torus form is usually more variable in older hominins.

Three states:

- 1: absence of torus
- 2: the torus is present and rectilinear
- 3: the torus is present and convex

Character number:

- Chapter III: #34
- Chapter IV: #39 in Matrix A and #36 in Matrix B

De Stefano and Hauser (1989) defined the *protuberantia occipitalis externa* (external occipital protuberance) as formed by the convergence of the highest nuchal lines at the top and the superior nuchal lines at the bottom. Hublin (1978b, 1988) considers the absence of the occipital protuberance an archaic trait, commonly seen in Neandertals, whereas modern humans generally exhibit this protuberance. The *tuberculum linearum*, where the superior nuchal lines meet, forms a faintly defined triangular tubercle. The presence of a *tuberculum linearum* is variable, but it is not associated with the external occipital protuberance.

***Protuberantia occipitalis externa* (external occipital protuberance):**

Two states:

- 1: absence of the *protuberantia occipitalis externa*
- 2: presence of the *protuberantia occipitalis externa*

Character number:

- Chapter III: #35
- Chapter IV: #40 in Matrix A and #37 in Matrix B

***Tuberculum linearum*:**

Two states:

- 1: absence of the *tuberculum linearum*
- 2: présence of the *tuberculum linearum*

Character number:

- Chapter III: #36
- Chapter IV: #41 in Matrix A and #38 in Matrix B

The external occipital crest is typically weakly defined in classic Neandertals, with its expression showing variability among European Middle Pleistocene hominins, similar to modern humans (Condemi, 2001). The development of the posterior and anterior portions of the crest, separated by the inferior nuchal line, is often uneven. Classic Neandertals commonly display an asymmetry in the development of the posterior and anterior parts of the external occipital crest (Condemi, 1992).

External occipital crest development:

Three states:

- 1: absence of external occipital crest

2: external occipital crest is present posteriorly

3: external occipital crest is present

Character number:

- Chapter III: #37
- Chapter IV: #7 in Matrix A and #5 in Matrix B

Aligned posterior and anterior parts of the external occipital crest:

Two states:

1: the posterior and anterior parts are aligned

2: the posterior and anterior parts are not aligned

Character number:

- Chapter III: #38
- Chapter IV: #8 in Matrix A and #5 in Matrix B

Temporal squama height:

Vallois (1969) was the first to describe a low temporal squama in Neandertals. This observation was later noted in numerous older specimens, particularly in *H. erectus* s.l. fossils. This feature is often considered characteristic of the most ancient hominins (Andrews, 1984; Condemi, 1988; Hublin, 1986; Stringer, 1984). Caparros (1997) pointed out that a low temporal squama can also be found in some Anatomically Modern Humans (AMHs). To assess the height of the temporal squama, we employed the method initially defined by Schultz (1915) and then used by Vallois (1969) in the study of the temporal bone from La Quina H27. For a specimen oriented in the Frankfurt plane, the maximal height (H) of the squama from the auriculae is divided by the maximal width of the squama (L) to calculate the index Iet, i.e., $Iet = (H \times 100) / L$.

Two states:

1: low temporal squama: $Iet \leq 60$

2: high temporal squama: $Iet > 60$

Character number:

- Chapter III: #39
- Chapter IV: #42 in Matrix A and #39 in Matrix B

The outline of the temporal squama is generally more curved in AMHs than in older hominins or in Neandertals (Vallois, 1969). However, this is not always the case, as some Neandertals exhibit a curved outline of the temporal squama (Condemi, 1988). In *H. erectus* specimens, the temporal squama is often described as low with a triangular outline (Elyaqnine, 1995; Rightmire, 1990; Weidenreich, 1943).

Outline of the anterior border of the temporal squama:

Two states:

- 1: curved or sinuous
- 2: rectilinear

Character number:

- Chapter III: #40
- Chapter IV: #43 in Matrix A and #40 in Matrix B

Outline of the superior border of the temporal squama:

Two states:

- 1: curved or sinuous
- 2: rectilinear

Character number:

- Chapter III: #41
- Chapter IV: #44 in Matrix A and #41 in Matrix B

A well-developed *crista supramastoidea*, along with a *tuberculum supramastoideum anterius*, can be observed in Neandertal fossils as well as in Middle and Early Pleistocene hominins (Andrews, 1984; Condemi, 1988; Vallois, 1969).

Development of the *crista supramastoidea* at the porion:

Three states:

- 1: *crista supramastoidea* absent
- 2: *crista supramastoidea* weakly developed
- 3: *crista supramastoidea* marked

Character number:

- Chapter III: #42
- Chapter IV: #45 in Matrix A and #42 in Matrix B

Relative orientation of the *crista supramastoidea* and the *processus zygomaticus ossis temporalis* (zygomatic process of the temporal bone):

Two states:

- 1: the *crista supramastoidea* and the *processus zygomaticus ossis temporalis* are not lined up
- 2: the *crista supramastoidea* and the *processus zygomaticus ossis temporalis* are lined up

Character number:

- Chapter III: #43
- Chapter IV: #46 in Matrix A and #43 in Matrix B

Tuberculum supramastoideum anterius:

Posteriorly to the *crista supramastoidea*, a tubercle (*tuberculum supramastoideum anterius*) is sometimes observed, with its development abruptly ending at the parieto-temporal suture (Hublin, 1978).

Two states:

- 1: absence of *tuberculum supramastoideum anterius*
- 2: presence of *tuberculum supramastoideum anterius*

Character number:

- Chapter III: #44
- Chapter IV: #47 in Matrix A and #44 in Matrix B

Weidenreich (1943) noted the presence of a supramastoid groove between the *crista supramastoidea* and the *crista mastoidea* in *Sinanthropus* fossils, while this groove was absent in the Ngandong specimens. According to Stringer (1984), the *crista supramastoidea* and the *crista mastoidea* are fused in the Asians *H. erectus*.

Supramastoid groove between the *crista supramastoidea* and the *crista mastoidea*:

Three states:

- 1: absent
- 2: present, but closed anteriorly
- 3: present

Character number:

- Chapter III: #45
- Chapter IV: #48 in Matrix A and #45 in Matrix B

Form of the external auditory meatus:

The auditory meatus is generally elliptic in AMHs. Elyaqtime (1995) suggests that hominins of the Neandertal lineage evolved from an elliptical shape to a more circular form, as seen in classic Neandertals.

Two states:

- 1: the auditory meatus is circular
- 2: the auditory meatus is elliptic

Character number:

- Chapter III: #46
- Chapter IV: #49 in Matrix A and #46 in Matrix B

Position of the auditory meatus in relation to the *processus zygomaticus temporalis*:

Many researchers argue that the position of the auditory meatus is distinctive in Neandertals, where it occupies a 'high' position. It is located above the glenoid cavity, aligning with the *processus zygomaticus temporalis* (Condemi, 1988; Elyaqine, 1995; Nara, 1994; Vallois, 1969).

Three states:

- 1: the auditory meatus is below the zygomatic process
- 2: the auditory meatus is in an intermediate position in relation to the zygomatic process
- 3: the auditory meatus is lined up with the zygomatic process

Character number:

- Chapter III: #47
- Chapter IV: #50 in Matrix A and #47 in Matrix B

The *processus mastoidus* (mastoid process) is generally weakly developed in *H. erectus* s.l. and *H. neanderthalensis* (Condemi, 1988; Delson et al., 1977; Macintosh and Larnach, 1972; Vallois, 1969). However, this feature is variable, even among *H. erectus* s.l. specimens. Additionally, a poorly developed mastoid process can also be observed in Early Pleistocene specimens (Hublin, 1986). We recorded the downward development of the *processus mastoidus* in relation to the petrous part of the temporal bone in lateral view. The presence of a tubercle (*tuberculum mastoideum anterior*) on the anterior border of the mastoid process, just behind the external auditory meatus, can be considered a Neandertal trait (Condemi, 1988; Elyaqine, 1995; Hublin, 1978b).

***Tuberculum mastoideum anterior*:**

Two states:

- 1: absence of the *tuberculum mastoideum anterior*
- 2: presence of the *tuberculum mastoideum anterior*

Character number:

- Chapter III: #48
- Chapter IV: #51 in Matrix A and #48 in Matrix B

Downward development of the *processus mastoidus* in relation to the petrous part of the temporal bone:

Two states:

1: weak

2: strong

Character number:

- Chapter III: #49
- Chapter IV: #9 in Matrix A and #6 in Matrix B

Juxtamastoid ridge development in relation to the *processus mastoidus*:

Hublin (1978) described the juxtamastoid ridge as forming the medial edge of the digastric groove, generally located along the occipitomastoid suture. The juxtamastoid ridge is particularly prominent in Neandertals, though it can occasionally be observed in AMHs (Hublin, 1988). Some researchers suggest that a juxtamastoid ridge that is more prominently developed downward than the *processus mastoidus* should be considered a Neandertal trait (Condemi, 1988; Elyaqine, 1995).

Three states:

1: less developed

2: as developed

3: more developed

Character number:

- Chapter III: #50
- Chapter IV: #52 in Matrix A and #49 in Matrix B

Presence of a bony bridge over the anterior part of the digastric groove:

Vallois (1969) described a bony bridge over the digastric groove, which separates its posterior and anterior parts, as a characteristic feature of Neandertals. However, this morphology has also been observed in some specimens from Zhoukoudian and Sangiran (Condemi, 1988). In fact, the morphology of the digastric groove can be variable in AMHs, Neandertals or Asians *H. erectus* s.l. (Condemi, 1988; Weidenreich, 1943).

Two states:

1: absent

2: present

Character number:

- Chapter III: #51
- Chapter IV: #53 in Matrix A and #50 in Matrix B

Crista occipitomastoidea (occipitomastoid crest):

The occipitomastoid suture in *Sinanthropus* hominins shows a crest formed by the fusion of the *linea musculus obliquus capitis superior* and the juxtamastoid groove (Rightmire, 1990; Weidenreich, 1943). This structure has also been observed in most other Asian *H. erectus* fossils (Hublin, 1986).

Two states:

- 1: absent
- 2: present

Character number:

- Chapter III: #52
- Chapter IV: #54 in Matrix A and #51 in Matrix B

According to Condemi (1988), the morphology of the glenoid cavity is one of the few traits that can be considered characteristic of the Neandertal temporal bone: "*La cavité est très étendue, large, peu profonde et mal délimitée avec vers l'avant un tubercule temporal (tuberculum articulare) peu saillant. Si la présence d'un tubercule zygomatique postérieure n'est pas propre aux Néandertaliens, en revanche, sa participation au versant postérieure de la cavité glénoïde ne se retrouve que sur ces fossiles würmiens.*" (l. 51, Condemi, 1988). A narrow glenoid cavity in its medial part is considered more characteristic of *H. erectus* s.l. by Rightmire (1990). However, Hublin (1986) argued that the morphological variability of the glenoid cavity is too significant and that its taxonomic value should be considered with caution.

Glenoid cavity depth in relation to the articular tubercle lowest point:

Two states:

- 1: shallow (<0.9 mm)
- 2: deep (>0.9 mm)

Character number:

- Chapter III: #53
- Chapter IV: #10 in Matrix A and #7 in Matrix B

Petro-tympanic crest orientation in relation to the sagittal plane:

Three states:

- 1: the crest is perpendicular to the sagittal plane

2: the crest is frontward to the sagittal plane

3: the crest is backward to the sagittal plane

Character number:

- Chapter III: #54
- Chapter IV: #55 in Matrix A and #52 in Matrix B

Articular tubercle configuration:

According to Elyaqine (2001, 1995), the articular tubercle is typically concave medio-laterally in Neandertals, whereas it is convex antero-posteriorly in AMHs. Older hominins exhibit greater variability in the configuration of their articular tubercle.

Three states:

1: the articular tubercle shows a pronounced medio-lateral concavity

2: the articular tubercle shows an antero-posterior convexity which can be associated with a medio-lateral concavity

3: the articular tubercle is concave medio-laterally and vertical

Character number:

- Chapter III: #55
- Chapter IV: #56 in Matrix A and #53 in Matrix B

On the inferior aspect of the zygomatic process, the glenoid cavity is bordered by two other tubercles: anteriorly, the *tuberculum zygomaticum anterius*, and posteriorly, the *tuberculum zygomaticum posterius*. Vallois (1969) described the *tuberculum zygomaticum anterius* as being prominently pronounced and thick in Neandertals, although less protruding than in modern humans. In contrast, the *tuberculum zygomaticum posterius* is considered more pronounced in Neandertals than in modern humans. While Vallois suggested these morphological features were specific to Neandertals, Condemi (1988) pointed out that a well-developed *tuberculum zygomaticum posterius* can also be seen in older fossils.

Tuberculum zygomaticum anterius:

Two states:

1: the *tuberculum zygomaticum anterius* is absent to weakly marked

2: the *tuberculum zygomaticum anterius* is marked

Character number:

- Chapter III: #56
- Chapter IV: #57 in Matrix A and #54 in Matrix B

Tuberculum zygomaticum posterius:

Two states:

- 1: the *tuberculum zygomaticum posterius* is absent to weakly marked
- 2: the *tuberculum zygomaticum posterius* is marked

Character number:

- Chapter III: #57
- Chapter IV: #58 in Matrix A and #55 in Matrix B

Tympanal contribution to the posterior wall of the glenoid cavity:

In Neandertals and older hominins, when well-developed, the *tuberculum zygomaticum posterius* can significantly contribute to the posterior wall of the glenoid cavity. This morphology is not typically found in modern humans (Andrews, 1984; Condemi, 1988; Hublin, 1986; Stringer, 1984; Vallois, 1969).

Two states:

- 1: tympanal contribution to the posterior wall of the glenoid cavity is relatively weak
- 2: tympanal contribution to the posterior wall of the glenoid cavity is important

Character number:

- Chapter III: #58
- Chapter IV: #59 in Matrix A and #56 in Matrix B

Presence of a preglenoid tubercle:

Two states:

- 1: absence of a preglenoid tubercle
- 2: presence of a preglenoid tubercle

Character number:

- Chapter III: #59
- Chapter IV: #60 in Matrix A and #57 in Matrix B

References:

- Andrews, P., 1984. An alternative interpretation of the characters used to define *Homo erectus*. *Courier Forschungsinstitut Senckenberg* 69, 167–175.
- Antón, S.C., 2003. Natural history of *Homo erectus*. *American Journal of Physical Anthropology* 122, 126–170. <https://doi.org/10.1002/ajpa.10399>
- Barriel, V., 1994. Les relations de parenté au sein des Hominoidea et la place de *Pan paniscus* : comparaison et analyse méthodologique des phylogénies morphologique et moléculaire (These de doctorat). Paris 6.
- Boule, M., 1913. L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie* 8, 1–62.
- Boule, M., 1912. L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie* 7, 105–192.
- Boule, M., 1911. L'homme fossile de La Chapelle-aux-Saints. *Annales de Paléontologie* 6.
- Bräuer, G., 1992. Africa's Place in the Evolution of *Homo sapiens*, in: *Continuity or Replacement. Controversies in Homo Sapiens Evolution*. Balkema, Rotterdam, pp. 83–98.
- Bräuer, G., Mbua, E., 1992. *Homo erectus* features used in cladistics and their variability in Asian and African hominids. *Journal of Human Evolution* 22, 79–108. [https://doi.org/10.1016/0047-2484\(92\)90032-5](https://doi.org/10.1016/0047-2484(92)90032-5)
- Broca, P., 1868. Sur les crânes et ossements des Eyzies. *BMSAP* 30, 335–349. <https://doi.org/10.3166/bmsap-2018-0027>
- Caparros, M., 1997. *Homo sapiens* archaïques : un seul ou plusieurs taxons (espèces) ? : analyse cladistique et analyse morphométrique (These de doctorat). Paris, Muséum national d'histoire naturelle.
- Clark, W.E.L.G., 1978. *The Fossil Evidence for Human Evolution: an Introduction to the Study of Paleoanthropology*. University of Chicago Press, Chicago.
- Condemi, S., 2001. Les néandertaliens de La Chaise. Comité des travaux historiques et scientifiques (CTHS), Paris.
- Condemi, S., 1992. Les Hommes fossiles de Saccopastore et leurs relations phylogénétiques., CNRS. ed. Paris.
- Condemi, S., 1988. Caracteres plesiomorphes et apomorphes de l'os temporal des neanderthaliens europeens würmiens, in: *L'Anatomie*. Université de Liège, Liège, pp. 49–52.
- Cunningham, D.J., 1908. The Evolution of the Eyebrow Region of the Forehead, with Special Reference to the Excessive Supraorbital Development in the Neanderthal Race. *Transactions of The Royal Society of Edinburgh* 46, 283–311. <https://doi.org/10.1017/S0080456800002763>
- de Lumley, M.-A., Gabounia, L., Vekua, A., Lordkipanidze, D., 2006. Les restes humains du Pliocène final et du début du Pléistocène inférieur de Dmanissi, Géorgie (1991–2000). I – Les crânes, D 2280, D 2282, D 2700. *L'Anthropologie* 110, 1–110. <https://doi.org/10.1016/j.anthro.2006.02.001>
- De Stefano, G.F., Hauser, G., 1989. Epigenetic variants of the human skull. *Schweizerbart, Stuttgart*.
- Delson, E., Eldredge, N., Tattersall, I., 1977. Reconstruction of hominid phylogeny: A testable framework based on cladistic analysis. *Journal of Human Evolution* 6, 263–278. [https://doi.org/10.1016/S0047-2484\(77\)80051-1](https://doi.org/10.1016/S0047-2484(77)80051-1)
- Elyaqnine, M., 2001. Morphological and functional aspects of the temporal bone articular tubercle morphology in *Homo erectus* and *Homo sapiens*. *Hum. Evol.* 16, 159–168. <https://doi.org/10.1007/BF02437410>
- Elyaqnine, M., 1995. Variabilité et évolution de l'os temporal chez *Homo sapiens* : comparaison avec *Homo erectus* (These de doctorat. Anthropologie). Bordeaux 1, Bordeaux.
- Grimaud, D., 1982. Evolution du pariétal de l'homme fossile. Position de l'Homme de Tautavel parmi les hominidés. (Thèse Géologie des formations sédimentaires option Préhistoire). Université de Provence, Aix-Marseille.

- Heim, J.L., 1974. Les Hommes fossiles de La Ferrassie (Dordogne) et le problème de la définition des Néandertaliens classiques. *L'Anthropologie* 78, 321–379.
- Hublin, J.J., 1988. Caractères dérivés de la région occipito-mastoïdienne chez les Néandertaliens, in: *L'homme de Néandertal*. Université de Liège, Liège, pp. 67–73.
- Hublin, J.-J., 1986. Some comments on the diagnostic features of *Homo erectus*, in: *Fossil Man. New Facts - New Ideas*. Anthropos, pp. 175–187.
- Hublin, J.-J., 1978a. Anatomie du centre de l'écaille occipitale - Le problème de l'inion. *Cahiers d'Anthropologie* 2, 65–83.
- Hublin, J.-J., 1978b. Quelques caractères apomorphes du crâne néandertalien et leur interprétation phylogénique. *Comptes Rendus de l'Académie des Sciences de Paris - Série D* 287, 923–926.
- Hublin, J.J., 1978. Le torus occipital transverse et les structures associées. Evolution dans le genre *Homo*. (These de doctorat). Paris IV: Université de Pierre et Marie Curie, Paris.
- Krukoff, S., 1967. Séparation de l'euryon et de la bosse pariétale et agrandissement transversal du crâne en fonction de la position de cette bosse chez l'homme et le chimpanzé. *Comptes Rendus de l'Académie des Sciences* 265, 1492–1495.
- Lieberman, D.E., 1995. Testing hypotheses about recent human evolution from skulls: Integrating morphology, function, development, and phylogeny. *Current Anthropology* 36, 159–197. <https://doi.org/10.1086/204348>
- Macintosh, N.W.G., Larnach, S.L., 1972. The Persistence of "Homo Erectus" Traits in Australian Aboriginal Crania. *Archaeology & Physical Anthropology in Oceania* 7, 1–7.
- Martin, R., Saller, K., 1957. *Lehrbuch der Anthropologie in Systematischer Darstellung mit Besonderer Berücksichtigung der Anthropologischen Methoden*, G.F. Verlag. ed. Jena, Stuttgart.
- Mounier, A., 2009. Validité du taxon *Homo heidelbergensis* Schoetensack, 1908 (These de doctorat). Aix-Marseille 2.
- Nara, T., 1994. Étude de la variabilité de certains caractères métriques et morphologiques des Néandertaliens (These de doctorat). Bordeaux 1, Bordeaux.
- Olivier, G., 1960. *Pratique anthropologique*, Vigot Frères. ed. Paris.
- Owen, R., 1835. XXXIX. On the Osteology of the Chimpanzee and Orang Utan. *The Transactions of the Zoological Society of London* 1, 343–379. <https://doi.org/10.1111/j.1096-3642.1835.tb00635.x>
- Piveteau, J., 1970. Les grottes de la Chaise (Charente): paléontologie humaine I. L'homme de l'abri Suard. *Annales de Paléontologie (Vertébrés)* 56, 175–225.
- Prat, S., 2004. Les premiers représentants du genre *Homo*, en quête d'une identité. Apports de l'étude morphologique et de l'analyse cladistique. *BMSAP* 16, 17–35. <https://doi.org/10.4000/bmsap.586>
- Rightmire, G.P., 1990. *The Evolution of Homo Erectus: Comparative Anatomical Studies of an Extinct Human Species*. Cambridge University Press.
- Rougier, H., Balzeau, A., 2007. La fosse sus-iniaque est-elle une autapomorphie des Néandertaliens? Analyse comparatives de ses caractéristiques morphologiques externes et internes. *BMSAP* 19, 287.
- Santa Luca, A.P., 1980. The Ngandong fossil hominids: a comparative study of a far eastern *Homo erectus* group. New Haven: Yale University Publications in Anthropology 78.
- Schultz, A., 1915. Form, Größe und Lage der Squama temporalis des Menschen. *Zeitschrift für Morphologie und Anthropologie* 19, 353–380.
- Schwalbe, G., 1901. Der Neanderthalschädel. *Bonner Jahrbücher* 106, 1–71.
- Smith, F.H., Trinkaus, E., 1991. Les origines de l'homme moderne en Europe centrale : un cas de continuité, in: *Aux Origines d'Homo Sapiens*. Press Universitaires de France, Paris, pp. 251–290.
- Spitery, J., 1984. L'os frontal des hominidés fossiles, *Géologie des formations sédimentaires*. ed. Université de Provence, Aix-Marseille.

- Stringer, C.B., 1991. Homo erectus et « Homo sapiens archaïque ». Peut-on définir Homo erectus ?, in: Aux Origines d'Homo Sapiens. Press Universitaire de France, Paris, pp. 49–74.
- Stringer, C.B., 1984. The definition of Homo erectus and the existence of the species in Africa and Europe. Courier Forschungsinstitut Senckenberg 69, 131–143.
- Stringer, C.B., Hublin, J.-J., Vandermeersch, B., 1984. The origin of anatomically modern humans in Western Europe, in: The Origins Of Modern Humans: A World Survey of the Fossil Evidence. Alan R. Liss, New-York, pp. 51–135.
- Suzuki, H., Takai, F., 1970. The Amud man and his cave site, 1. ed. ed. The Univ. of Tokyo, Tokyo.
- Trinkaus, E., 2007. European early modern humans and the fate of the Neandertals. Proceedings of the National Academy of Sciences 104, 7367–7372. <https://doi.org/10.1073/pnas.0702214104>
- Trinkaus, E., Lemay, M., 1982. Occipital bunning among later pleistocene hominids. American Journal of Physical Anthropology 57, 27–35. <https://doi.org/10.1002/ajpa.1330570106>
- Vallois, H.V., 1969. Le temporal néandertalien H27, de La Quina. Etude anthropologique. L'Anthropologie 73, 365–400.
- Vandermeersch, B., 1981. Les Hommes de Qafzeh (Israël), CNRS. ed. Paris.
- Weidenreich, F., 1951. Morphology of Solo man. Anthropological papers of the AMNH 43, 205–290.
- Weidenreich, F., 1943. The skull of Sinanthropus pekinensis ; a comparative study on a primitive hominid skull. Palaeontologica. Sinica 10, 1–485.
- Wolpoff, M.H., 1980. Paleoanthropology, Knopf, Alfred A. ed. New York, NY.
- Wood, B.A., 1984. The origin of Homo erectus. Courier Forschungsinstitut Senckenberg 69, 99–111.
- Zeitoun, V., 2000. Révision de l'espèce Homo erectus (Dubois, 1893). BMSAP 12, 1–200. <https://doi.org/10.4000/bmsap.5963>
- Zeitoun, V., 1996. Cladistique et paléoanthropologie : le cas de l'espèce Homo Erectus (Dubois, 1894) (These de doctorat). Bordeaux 1.

Appendix 3: Matrix of the 59 discrete morphological characters for Chapter III

Character number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>Pongo</i>	1	1	1	3	3	1	3	1	1	1	3	1	1	1	1	2	2	1	3	2
<i>Gorilla</i>	1	1	1	3	3	1	2	1	1	1	2	1	1	2	1	2	2	1	2	1
<i>Pan</i>	1	1	2	3	3	1	3	3	1	1	2	1	1	2	2	2	2	2	2	2
<i>A. africanus</i>	1	1	1	1	2	1	3	1	1	2	2	1	1	1	1	1	1	1	2	2
Koobi Fora - <i>H. habilis s.l.</i>	1	[13]	2	[23]	3	1	2	[13]	[13]	[23]	2	1	1	1	1	1	1	1	[23]	1
Dmanisi	1	[2-]	1	2	3	1	[13]	3	2	[2-]	2	[12]	[12]	1	2	[12]	1	1	2	[23]
Koobi Fora - <i>H. ergaster</i>	1	3	2	3	3	1	[23]	3	2	[12]	2	[12]	2	1	2	[12]	1	2	3	3
Sangiran	1	[3-]	[2-]	[3-]	3	[12]	[3-]	3	2	[2-]	3	2	2	1	2	[12]	2	1	3	[12]
Zhoukoudian	1	[13]	[12]	2	3	2	2	3	[23]	[23]	2	2	2	1	2	2	2	2	2	1
Ngandong	1	3	1	[23]	3	[23]	[12]	3	2	2	2	2	2	1	2	2	2	[12]	2	3
Near East Neandertal	2	[13]	2	2	3	3	3	3	3	[23]	2	1	1	1	1	1	[12]	[12]	2	3
Early Neandertal	2	3	[2-]	[2-]	3	3	[3-]	[3-]	3	[23]	2	1	1	1	1	[12]	[12]	[12]	2	3
Classic Neandertal	2	[13]	2	3	3	3	3	3	3	[13]	2	1	1	1	1	[12]	[12]	2	[23]	3
Skhül - Qafzeh	3	[13]	[12]	[12]	[23]	3	3	[123]	3	[12]	2	1	1	1	1	[12-]	[12]	[12]	2	3
KhoiSan	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	[12]	1	2	3
Haya	3	1	2	1	1	3	3	3	3	3	1	1	1	1	1	1	2	1	2	3
Kongo	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Mande	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Berber	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Papu	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
French	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Chinese	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Inuit	3	1	2	1	1	3	3	3	3	3	2	1	1	1	1	1	1	1	2	3
Percentage of missing data per character	0	8,696	8,696	8,696	0	0	8,696	4,348	0	8,696	0	0	0	0	0	4,348	0	0	0	0

Character number	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40
<i>Pongo</i>	1	2	2	2	1	1	1	1	1	[23]	2	[12]	3	[23]	2	1	[23]	1	1	2
<i>Gorilla</i>	1	1	2	1	1	1	1	1	1	1	1	3	3	3	1	2	3	1	1	2
<i>Pan</i>	1	1	1	1	1	1	2	2	1	1	1	1	3	3	1	2	3	1	1	2
<i>A. africanus</i>	1	1	1	2	[12]	2	1	2	2	1	1	2	3	2	1	1	3	1	1	2
Koobi Fora - <i>H. habilis</i> s.l.	[12]	[13]	[12]	[12]	[2-]	1	1	[1-]	1	1	1	[12]	2	2	[1-]	[2-]	[3-]	[1-]	1	2
Dmanisi	[12]	1	2	2	[1-]	[12]	[12]	1	[12]	1	1	2	2	2	1	[12]	[3-]	[1-]	1	1
Koobi Fora - <i>H. ergaster</i>	[12]	1	2	[12]	[12]	1	[12]	[12]	[12]	1	1	[23]	2	[23]	1	2	[23]	[1-]	2	2
Sangiran	2	1	2	1	1	1	1	2	[12]	1	1	[23]	2	2	1	[12]	[3-]	[1-]	1	[12]
Zhoukoudian	2	1	2	[12]	1	1	1	[12]	[12]	1	1	3	2	2	1	[12]	[13]	1	1	2
Ngandong	2	1	2	[12]	[12]	1	1	2	[23]	1	1	[23]	2	3	2	2	2	1	1	2
Near East Neandertal	1	1	1	2	2	2	2	[12]	2	3	2	2	3	2	1	1	[13]	1	[12]	[2-]
Early Neandertal	[12]	1	2	2	2	[12]	2	[2-]	[2-]	3	2	1	3	2	1	[12]	3	[12]	[12]	[12]
Classic Neandertal	1	1	2	2	2	2	2	1	2	3	3	[12]	3	2	1	1	[123]	[2-]	[12]	[12]
Skhül - Qafzeh	1	[123]	1	[12]	2	1	2	[12]	3	1	1	[12]	1	1	[12]	[12]	[1-]	[12-]	2	[12-]
Khoisan	1	2	1	2	2	1	2	1	[23]	1	1	1	1	1	2	2	3	1	[12]	1
Haya	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Kongo	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Mande	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Berber	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Papu	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
French	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Chinese	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Inuit	1	2	1	2	2	1	2	1	3	1	1	1	1	1	2	2	3	1	2	1
Percentage of missing data per character	0	0	0	0	8,696	0	0	8,696	4,348	0	0	0	0	0	4,348	4,348	17,39	26,09	0	8,696

Character number	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	Percentage of missing data per OTU
<i>Pongo</i>	2	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	0
<i>Gorilla</i>	2	2	2	1	3	1	3	1	1	1	1	1	2	1	2	2	2	1	1	0
<i>Pan</i>	2	2	2	2	1	2	3	1	1	1	1	1	1	1	2	2	2	1	1	0
<i>A. africanus</i>	2	2	2	1	3	1	2	1	1	1	1	1	1	3	[13]	2	2	1	1	0
Koobi Fora - <i>H. habilis</i> s.l.	1	3	2	[12]	[2-]	[1-]	[1-]	[2-]	[1-]	[2-]	[2-]	[1-]	1	[23]	1	[1-]	2	1	1	23,72881356
Dmanisi	1	3	2	[12]	2	1	1	1	[2-]	[2-]	[12]	[1-]	[12]	[13]	[13]	[12]	[2-]	2	[12]	15,25423729
Koobi Fora - <i>H. ergaster</i>	2	2	2	[12]	2	2	1	[12]	[12]	[12]	1	[1-]	[12]	3	1	2	[12]	2	[12]	3,389830508
Sangiran	1	3	[12]	2	[12]	1	[12]	[12]	[1-]	[1-]	1	[2-]	[12]	3	1	[12]	[12]	2	2	16,94915254
Zhoukoudian	2	3	[2-]	2	[23]	[12]	1	1	1	[12]	2	2	2	3	3	[1-]	2	[12]	2	3,389830508
Ngandong	2	3	[2-]	2	[23]	[12]	1	[12]	2	1	2	2	2	3	[13]	[1-]	[1-]	2	2	5,084745763
Near East Neandertal	1	2	1	1	3	[12]	[23]	2	2	[1-]	1	[1-]	1	1	1	1	2	1	[1-]	6,779661017
Early Neandertal	1	[12]	[12]	2	3	[12]	[2-]	[12]	[1-]	[1-]	[2-]	[1-]	[12]	2	1	1	[12]	[1-]	1	20,33898305
Classic Neandertal	1	[13]	1	[12]	3	[12]	3	2	1	[13]	[12]	1	1	2	1	2	[12]	1	1	1,694915254
Skhül - Qafzeh	1	[12]	[12]	1	3	[12]	1	1	[2-]	[1-]	[12-]	[1-]	2	[12]	2	[12]	1	2	1	13,55932203
Khoisan	[12]	2	2	1	[13]	[12]	[12]	1	2	1	1	1	2	2	2	1	1	1	1	0
Haya	1	2	2	1	3	2	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Kongo	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Mande	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Berber	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Papu	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
French	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Chinese	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Inuit	1	2	2	1	3	1	2	1	2	1	1	1	1	2	2	1	1	1	1	0
Percentage of missing data per character	0	0	8,696	0	4,348	4,35	8,696	4,35	21,74	26,09	13	30,43	0	0	0	13,04	8,696	4,348	4,348	

Appendix 4: Table of the 22 PCs coordinates obtained from 148 landmarks (Matrix B.1, Chapter III)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
<i>Pongo</i>	-0,1745168642717500	0,0989085494367004	-0,0331211352294307	-0,0114325885220108	0,0250909641780002	-0,0136726222030106	0,0067633522663009
<i>Gorilla</i>	-0,1997599485655200	0,0110092199094005	0,0086576771553002	0,0197726340544992	-0,0412423736218006	-0,0102692122649994	-0,0191900646305001
<i>Pan</i>	-0,1211783023720300	0,0348391617971995	0,0260398083359998	-0,0116409096790395	-0,0229838173211601	0,0276439202178000	0,0250703830363008
<i>A. africanus</i>	-0,0574851659696201	0,0056332690899996	0,0825663962754000	0,0051996019290002	0,0291451658578996	0,0128924666376005	-0,0235207040360503
<i>Koobi Fora - H. habilis s.l.</i>	-0,0459890301159103	-0,0244974969793699	0,0261208687311996	-0,0071724939263405	0,0176052528794006	-0,0181550354569797	0,0124018425290000
<i>Koobi Fora - H. ergaster</i>	-0,0501760844188404	-0,0406872925788893	-0,0001801131190202	0,0240452898824000	0,0060839484330995	-0,0032053923927808	0,0097454685430005
Dmanisi	-0,0755996375571506	-0,0634365095370608	0,0034121200633006	-0,0052471929426901	0,0137695870590004	-0,0072991950691197	0,0104625402214999
Ngandong	-0,0141546126391106	-0,0350022041089897	-0,0035430419611906	0,0265232117539007	0,0050380827170997	0,0030320966867006	0,0039899972345001
Sangiran	-0,0499248798321794	-0,0729956408066599	-0,0065205751397599	-0,0311425360751798	-0,0142887219029397	-0,0085473119460993	0,0004694387287003
Zhoukoudian	-0,0449552356809804	-0,0244311458125797	-0,0434489203608504	-0,0345811010478894	0,0084008435377996	0,0091029113494994	-0,0230627204466600
Early Neandertal	0,0227436649393002	0,0008312267045003	-0,0351177832856493	0,0027244865353993	0,0127537014622998	0,0342561756222004	-0,0002047373560696
Near East							
Neandertal	0,0217949163096005	0,0037689213801997	-0,0499569037620606	0,0235621329160995	-0,0009803253193095	0,0035334561243996	-0,0111948227019898
Classic							
Neandertal	-0,0051218266462101	-0,0201362316645302	-0,0311207267198306	0,0179509971012006	0,0024488970421004	0,0039930138374995	0,0035410405334009
Skhül - Qafzeh	0,0642050909176994	-0,0090086104488893	0,0134648355431999	0,0014167188039007	-0,0071002176058208	0,0145859793918994	0,0078259587515994
KhoiSan	0,0835895785603000	0,0018288756693998	0,0018178956458996	-0,0132496048257895	-0,0051979097374506	-0,0024656569943904	0,0002822700911995
Haya	0,0700170567084992	0,0114839534791003	-0,0026154176901603	-0,0068876635557107	-0,0128539428247905	-0,0054498639319505	-0,0014098172920392
Kongo	0,0826552398300997	0,0247958518139004	0,0030879779132995	-0,0022143163005897	-0,0090162894260502	-0,0036616074371292	0,0040803729212993
Mande	0,0943505239101992	0,0179336482771006	0,0093632837049995	-0,0095708516152193	-0,0114939490219204	-0,0047869114010108	-0,0023703226884102
Berber	0,0940258494591006	0,0243841292589000	0,0072336773828994	0,0021764620006994	0,0007755018030000	-0,0028350750329800	-0,0020591689437097
Papu	0,0799704261448007	0,0116991132187003	0,0218697713017004	-0,0027606493308294	-0,0036923984334898	0,0029091873731009	-0,0061946414749095
French	0,0743502984147000	0,0119351533918000	-0,0062767908334909	0,0073352404529992	0,0080343980494000	-0,0092770210392903	0,0087040052397001
Chinese	0,0887684657899008	0,0159578229313002	0,0094859502436009	-0,0061824184935500	-0,0026763946431405	-0,0069133990019807	-0,0018366159425103
Inuit	0,0623904770849997	0,0151862355786001	-0,0012188541952494	0,0113755508847007	0,0023799968387994	-0,0154109030691405	-0,0022930545837596

	PC8	PC9	PC10	PC11	PC12	PC13	PC14
<i>Pongo</i>	0,0041590151212994	-0,0090943729792894	0,0001107938344997	-0,0017002995476503	-0,0043733150126801	-0,0017490072349506	0,0035128373793008
<i>Gorilla</i>	-0,0087709826428792	-0,0005863536723094	0,0058691231304007	-0,0002996503428996	-0,0053571827711103	0,0023091532569008	-0,0020346387222094
<i>Pan</i>	0,0068421833752002	0,0069955212512998	-0,0031282145233096	0,0042789523561009	0,0084488074076994	0,0006376219867992	-0,0017687521199097
<i>A. africanus</i>	0,0047929877575008	-0,00357842192223505	-0,0063185886279502	0,0014009495425995	0,0019772175844999	0,0011446820861991	0,0018679253354001
<i>Koobi Fora - H. habilis s.l.</i>	-0,0204762418852305	0,0059445430867005	0,0010559287138996	-0,0145015154298793	0,0060901200345001	-0,0059230427676997	-0,0052265923320096
<i>Koobi Fora - H. ergaster</i>	0,0118537477460006	0,0240300199867001	-0,0073799425861196	-0,0034371519048992	-0,0129669990942105	-0,0011931987671208	0,0023113545251992
Dmanisi	-0,0144095076846398	-0,0021908547938008	0,0023372083051001	0,0229046662767995	0,0010133095876999	0,0032253126708994	0,0017525563612004
Ngandong	0,0180066555124991	-0,0139200755951698	0,0162069648596006	-0,0011195516982401	0,0063092145036006	-0,0064516651052404	-0,0062282925370294
Sangiran	0,0138218435204003	-0,0160914177344793	-0,0137199585143595	-0,0070384803101007	-0,0042764697810291	-0,0012825739618307	-0,0000215867744604
Zhoukoudian	0,0060343774454008	0,0190547973683994	0,0119633221644992	-0,0010810998097792	0,0057790927764998	0,0005575552986006	0,0007181629261002
Early Neandertal	-0,0137067682659708	-0,0057511879006107	-0,0016128357872294	-0,0023800318392109	-0,0130560691825305	0,0005786522158004	-0,0091121606157092
Near East							
Neandertal	-0,0039405943480997	-0,0007796095295394	-0,0159484768885498	0,0059098912457998	0,0078164399463994	-0,0093957945662400	0,0040953334878005
Classic							
Neandertal	-0,0055562714650304	-0,0066370302224996	-0,0030739975340506	-0,0103351382859707	0,0120965287120995	0,0150024262529005	0,0040552948749006
Skhül - Qafzeh	-0,0061532757998304	-0,0037000240342309	0,0127165922468002	-0,0073810993205594	-0,0050378650069405	-0,0050706526631696	0,0143612782588001
Khoisan	0,0004767892281006	-0,0063528545579192	0,0019719943749994	0,0057851158227997	-0,0095360467821308	0,0028264112923999	-0,0004100847771191
Haya	-0,0040335641103706	-0,0003605668124305	0,0003048512487993	0,0057803348400007	0,0069025132660006	-0,0076963012563596	-0,0002078943338208
Kongo	-0,0021712623609904	0,0097932122447002	-0,0045325682167707	-0,0011107112390008	0,0024082487214994	0,0012508838717995	-0,0013713977608294
Mande	-0,0053236951010796	-0,0009306198020607	0,0003075633057996	-0,0005850186101508	-0,0027570532098800	-0,0008748344746596	-0,0014257697176099
Berber	0,0069844441533000	0,0032032992479003	-0,0028711168343492	0,0002129057622007	0,0041929654857995	0,0004149734317007	-0,0053405340352501
Papu	-0,0044201059133595	-0,0031188454909703	-0,0027428582780900	-0,0009766601965300	-0,0015607093778005	-0,0009352976569907	0,0020532033536007
French	0,0116320106572001	0,0006274506232007	0,0037885571298002	0,0059847118101004	-0,0019930402588599	0,0037779722439009	0,0007609705044995
Chinese	0,0040523288130991	-0,0007516203283693	0,0004861924006008	-0,0016544211551093	0,0016547074258000	0,0060319246861003	-0,0003166529719891
Inuit	0,0003058862473999	0,0041950115670009	0,0042094660760004	0,0013433020336997	-0,0037744149748402	0,0028147991602001	-0,0020245603089197

	PC15	PC16	PC17	PC18	PC19	PC20	PC21
<i>Pongo</i>	-0,0021858090815297	-0,0005018233888396	-0,0008192484044898	0,0015941999802998	0,0001638474806001	-0,0006015813311997	-0,0001802814850809
<i>Gorilla</i>	0,0008443721317999	-0,0017463665617505	-0,0000918709383093	-0,0012527871726107	0,0017194593747991	0,0003301006882008	0,0005997335131003
<i>Pan</i>	0,0033654095166007	0,0022427352405998	0,0012121087845998	-0,0001349110506297	-0,0013167531817793	-0,0000446113529993	-0,0005088621787905
<i>A. africanus</i>	-0,0020194291778104	0,0013149137752002	-0,0001218698351995	-0,0016621853423597	-0,0010949910507794	0,0009485149050992	0,0006485602952999
<i>Koobi Fora - H. habilis s.l.</i>	0,0035394028914997	0,0012124537920002	0,0021460698899993	-0,0008509085882693	0,0013502298362997	0,0008848740231997	0,0006216233621004
<i>Koobi Fora - H. ergaster</i>	-0,0038656654978109	0,0005934280784992	0,0014687767677994	0,0017678491145006	0,0007528000282999	-0,0017734209250992	0,0000031319224991
Dmanisi	-0,0002950142988301	-0,0028873146071504	-0,0024500394109506	0,0018469732311992	-0,0002866276461209	-0,0007600175901707	-0,0000430344455893
Ngandong	-0,0018229439893407	-0,0003361967678899	0,0005407991202002	0,0036380153816005	-0,0007244413604504	0,0007983703194991	-0,0002238010971798
Sangiran	0,0007227098742995	-0,0010563775219197	-0,0020477952022393	-0,0020039875441107	-0,0012861570312701	0,0002062272551004	-0,0003988239243604
Zhoukoudian	0,0009943585464995	0,0001917971906007	0,0003756369233994	0,0002961424273007	0,0003120871778997	0,0004612204977992	-0,0004305572759105
Early Neandertal	-0,0008610284212498	-0,0021104896068103	-0,0000073819634405	-0,0024013570834391	-0,0007357571144393	-0,0005208819633502	0,0002411825962003
Near East							
Neandertal	0,0055903557310995	0,0007099756403992	0,0014148869487993	0,0010749833875998	-0,0008394632194708	0,0012547711401005	0,0009864161694004
Classic							
Neandertal	-0,0038155704711294	0,0029205944964001	0,0000747806779007	-0,0000210856463596	0,0010113348839997	-0,0004077754702791	-0,0006577437015292
Skhül - Qafzeh	0,0018265171159992	-0,0008821467112394	-0,0035470415534995	-0,0012861841750507	-0,0002645394808098	-0,0002705712947293	0,0011193002900001
Khoisan	0,0008714652927004	0,0111862303976000	0,0029547454749999	0,0032528168311998	0,0037179106177998	0,0019820422311003	0,0018986137254995
Haya	-0,0101159836357496	0,0031874519964994	0,0024450290458002	-0,0054141147845499	0,0003474758484998	-0,0031635349652301	-0,0000518582137996
Kongo	-0,0057274621307997	-0,0032062288535499	-0,0041312166588003	0,0021577519248996	-0,0014594098998000	0,0053087685083995	0,0006261509841998
Mande	-0,0037023674200807	-0,0032174373245795	0,0001455039881009	0,0033023131797005	-0,0029541312134995	0,0006892283405993	-0,0007578835251003
Berber	0,0032132363605992	-0,0006563227584095	-0,0088156399482404	0,0001904509233999	0,0056784155495002	-0,0031393249504195	0,0010319346982008
Papu	0,0023095698333009	-0,0028257775283898	0,0033209122633000	0,0039003914353994	0,0036260223595992	-0,0010597806085997	-0,0051164540413105
French	0,0029628292401007	-0,0049662334810208	0,0035781027447008	-0,0078204224777299	0,0031023314608003	0,0030759663790008	-0,0004979550966606
Chinese	0,0031320059523008	-0,0057346051459195	0,0055127061341000	0,0024039697012004	-0,0034400292045405	-0,0033505162291707	0,0034344455456008
Inuit	0,0050390416376001	0,0065677396494994	-0,0031579548485201	-0,0025779136533295	-0,0073796142151608	-0,0008480676066700	-0,0023438381167100

PC22

<i>Pongo</i>	-0,0001896258841096
<i>Gorilla</i>	-0,0001849790682709
<i>Pan</i>	0,0004652493930006
<i>A. africanus</i>	0,0003268833256005
<i>Koobi Fora - H. habilis s.l.</i>	0,0002216506072994
<i>Koobi Fora - H. ergaster</i>	0,0003531200487004
Dmanisi	-0,0001942253032396
Ngandong	-0,0003416698953504
Sangiran	-0,0003740139056294
Zhoukoudian	0,0001720632459001
Early Neandertal	-0,0005272709098101
Near East Neandertal	0,0005403800345007
Classic Neandertal	0,0007116731050001
Skhūl - Qafzeh	-0,0001794554853394
Khoisan	-0,0000213861160105
Haya	-0,0008785891221503
Kongo	-0,0029689455488509
Mande	0,0054313679161009
Berber	0,0007225387644993
Papu	-0,0018563333898793
French	0,0010523615954003
Chinese	-0,0015625838014799
Inuit	-0,0007182096057701

Appendix 5: Table of the 22 PCs coordinates obtained from 347 landmarks (Matrix B.2, Chapter III)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
<i>Pongo</i>	-0,16489276678506900	0,07502437995309920	-0,04347626850215040	-0,01431309592861930	-0,02115851619504030	0,00074545064500065	0,01451464982189950
<i>Gorilla</i>	-0,18194369386105100	0,00808716189460057	0,01308519243660020	0,03240411159059950	0,01824022230530000	0,03056299954340070	-0,00881201984126001
<i>Pan</i>	-0,10538554258302900	0,04125254760099930	0,01006954276160070	0,01940220936170080	0,01249726771069960	-0,04049304825137060	-0,00854646875166054
<i>A. africanus</i>	-0,05014195788434960	0,01706521072729930	0,08678443228219910	-0,03685731224602050	-0,00682724975420967	0,00667826295750018	-0,01576917820307950
<i>Koobi Fora - H. habilis s.l.</i>	-0,03538301408707060	-0,01680778762782960	0,03137562772120010	-0,00861965504440931	-0,00176130505066041	0,00002201484599951	0,02466461036789980
<i>Koobi Fora - H. ergaster</i>	-0,04302913302901960	-0,03277374295485020	-0,00091059576704922	-0,01643690529141930	0,01977628528019970	-0,00161435736356985	0,01128872927020020
Dmanisi	-0,05910354662029070	-0,05334680906048920	0,01176147376510000	-0,00444731058881054	-0,00122363369647971	-0,00904632868435051	0,00680410265749920
Ngandong	-0,01547898560741070	-0,03222665486154950	-0,01063051408599060	-0,01156493765259010	0,02203875524480030	-0,00204384253559020	-0,00812829831717998
Sangiran	-0,04028427700295010	-0,06701243672148930	0,01097925324079970	0,02349281841770080	-0,01774027300769990	-0,00570775221405917	0,00632394681380077
Zhoukoudian	-0,03882607228272940	-0,03691440982476910	-0,02128764825124920	0,00147795363990078	-0,04051781614077930	0,00273630255130008	-0,01263666967751930
Early Neandertal	0,01868013671220050	-0,00820396324609085	-0,04101264637258950	-0,01727377300299970	-0,00465147719133086	-0,00922938329734002	-0,01976412444846080
Near East Neandertal	0,02005391572309990	-0,00304072277316081	-0,05162271205272970	-0,00848483788355914	0,00838935268810026	0,01589813797050080	-0,01006425001784980
Classic Neandertal	-0,00154501439187982	-0,02070739438321920	-0,04056866516743970	-0,00806408151898985	0,01408374846280050	-0,00029824957844049	0,00338967062429951
Skhül - Qafzeh	0,05638822266480050	-0,00003023072389929	0,00855617365809991	0,00217924012240012	0,00887921830710070	-0,00813915612753924	-0,00729283716498053
Khoisan	0,07537072972369960	0,00407496280450026	0,00629973326000055	0,01082586188389990	-0,00901964913524012	-0,00245553009809996	-0,00003224708697935
Haya	0,06252113431570020	0,01050462445009970	-0,00270527967260037	0,01688115702710040	0,00033895851430010	0,00308952492689940	-0,00043141113716949
Kongo	0,07329301906430000	0,02283885947869990	0,00034393822719991	0,00934387304399920	0,00147856275069991	0,00127856489010014	0,00403016617100072
Mande	0,08390593610119980	0,01631323033270070	0,01069154119520020	0,01536937180950030	-0,00544309599766990	0,00362081670630054	-0,00105930956135936
Berber	0,08238697327679920	0,02230652755219960	0,00799596153619930	-0,00251045087473933	-0,00152805147799029	0,00376819573619969	0,00143682953680013
Papu	0,07046097861510070	0,01608934397800080	0,02077019511479960	0,00358879479080088	-0,00052455765072956	0,00285201999889928	-0,00450898539951972
French	0,06458450307719940	0,01117601763539970	-0,01335162357107040	-0,00705672604656016	0,00695503054629931	-0,00526739188384084	0,00909857010250015
Chinese	0,07709782644050020	0,01510145166700030	0,01002321741989930	0,00655260505219957	-0,00574962408028945	0,00228476034379987	0,00485095690030057
Inuit	0,05127062842029950	0,01122983410270000	-0,00317032917600990	-0,00588891066125008	0,00346784756779961	0,01075798891820060	0,01064356734070060

	PC8	PC9	PC10	PC11	PC12	PC13	PC14
<i>Pongo</i>	0,00447255350560027	0,00976784352610061	-0,00159349965468003	-0,00248128249429946	0,00042326800780046	-0,00421903109599953	0,00238385896379967
<i>Gorilla</i>	0,00089256482420019	-0,00145432955548053	0,00391306009320047	-0,00220565652849913	0,00588183924399921	0,00261939604610006	-0,00036402097384070
<i>Pan</i>	-0,00684439351242006	-0,00678211941012030	-0,00236505169013945	0,00243116513239983	-0,00407920558587982	0,00236889823949937	-0,00205225837681056
<i>A. africanus</i>	0,00027033137589960	0,00185682503630069	-0,00683055168715008	0,00196028832790063	-0,00304437509137045	0,00303600354870071	0,00119891176090015
<i>Koobi Fora - H. habilis s.l.</i>	0,01107708938859990	-0,00477784021122041	0,01451338808499970	0,01107156299480040	-0,00372820265980955	-0,00170023176526968	-0,00433327385285054
<i>Koobi Fora - H. ergaster</i>	-0,02366398296308070	-0,00465595315434975	-0,00148429058616983	0,00501571096740072	0,00872507743079964	-0,00576394317744011	-0,00100553002899062
Dmanisi	0,01682683948179960	-0,01680032953493080	-0,00723430247152912	-0,01590753455526080	0,00168624262290074	-0,00275952412997071	0,00179064594069978
Ngandong	-0,00052162954511914	0,02002270522769930	0,00845171054460003	-0,01012264024836010	-0,01085632046940970	-0,00339475522411981	-0,00411175554869914
Sangiran	-0,00127030278222939	0,01832562117470000	-0,01361014267464000	0,00749035119529928	0,00093813519069919	-0,00011558320128913	0,00050333907550026
Zhoukoudian	-0,01659884343276020	-0,00977038866776958	0,01202413812790050	-0,00202370709761013	-0,00525606073455975	0,00234009776010069	0,00124034699219955
Early Neandertal	0,01221520240379980	0,00141068778169995	0,00363569341399916	0,00455948515629956	0,01467439143809910	0,00129365067600062	-0,00724922353277968
Near East							
Neandertal	0,00049624554210048	-0,00910977302947025	-0,01333585435835080	0,00599821167440062	-0,00812838461125054	-0,00758329688778048	0,00103673223910050
Classic							
Neandertal	0,00887155285039931	-0,00029733600154991	-0,00107295024345078	0,00964299029030080	-0,00438694159345054	0,01393200275570020	0,00532738913489972
Skhül - Qafzeh	0,00257490735680044	0,00419580537280062	0,01233840096390000	0,00200434725529952	0,00479814689940028	-0,00587534710117943	0,01329684863480020
Khoisan	0,00258516613370041	0,00539293924970075	-0,00223443200206042	-0,00625197074196038	0,00578276950900047	-0,00050455911019043	-0,00153421720695945
Haya	0,00614465529089969	-0,00375891871813039	0,00236424477449937	-0,00157992573594967	-0,00872440801112084	-0,00096154639729917	-0,00339344474659953
Kongo	-0,00225544525548926	-0,00619192094024079	-0,00115342219920045	0,00465713581560045	-0,00126328896334016	-0,00278414572860974	-0,00140359044637073
Mande	0,00429716118379986	0,00035896846070038	0,00226505275090005	0,00075012640109939	0,00074118888779928	-0,00317270971653016	-0,00060335286648972
Berber	-0,00642031528090037	0,00126704220109985	-0,00220419286083917	0,00072438026020016	-0,00113491526787080	0,00030548488759941	-0,00348526417415940
Papu	0,00414535099520030	-0,00116105742194961	-0,00230915739997073	0,00349900358330046	0,00148641349159995	-0,00244078611815013	0,00094881290420013
French	-0,00765045997622948	0,00134637734119991	-0,00188083365572034	-0,01098226542934990	0,00047617791359933	0,00458699154090070	0,00223638827699979
Chinese	-0,00239284052149991	0,00197754130300076	-0,00292064310407980	-0,00131341023080012	0,00077762206890064	0,00354292814139967	0,00142658470659995
Inuit	-0,00725140706301985	-0,00116239002957919	0,00072363583410073	-0,00693636599235958	0,00421083028330038	0,00725000605789994	-0,00185392687509989

	PC15	PC16	PC17	PC18	PC19	PC20	PC21
<i>Pongo</i>	-0,00181637401503032	-0,00115518877698051	0,00068505773280059	-0,00026611565887080	-0,00047669911215031	-0,00073204475071087	-0,00029682616212945
<i>Gorilla</i>	-0,00032856227909051	0,00141770515720019	-0,00124362066176964	0,00158925722050007	0,00036652499860068	0,00025781255829926	0,00044939419709955
<i>Pan</i>	0,00299878798369946	0,00135241870199998	0,00085642224740035	-0,00098575747867002	0,00028610247830052	0,00029958390570073	-0,00028712721772983
<i>A. africanus</i>	-0,00011912307996020	-0,00306987405885017	-0,00045797881062981	0,00012940036189946	-0,00009612096386924	0,00104198709490078	0,00054748483059974
<i>Koobi Fora - H. habilis s.l.</i>	0,00427236533579922	0,00271616431919952	-0,00121530547892057	0,00084154271119985	0,00204966708350085	0,00094095628490010	0,00050986030199951
<i>Koobi Fora - H. ergaster</i>	-0,00404874691427004	-0,00386420833097922	0,00118795793069992	-0,00006353148256011	0,00119795448039994	-0,00132756478683049	-0,00013039732981923
Dmanisi	-0,00226523522663946	0,00154141282069986	0,00104060353850066	-0,00010591004578053	-0,00199390930595023	-0,00054301100436938	-0,00012204522199077
Ngandong	-0,00236084688669003	0,00213486946710084	0,00164090434370046	-0,00185832660720919	0,00001468420239981	0,00030862111099950	-0,00032390473099042
Sangiran	0,00230335966340078	-0,00065418006911067	-0,00248068052304973	-0,00029020238135047	-0,00182361920970919	0,00014906150840055	-0,00020118165119065
Zhoukoudian	-0,00076594280296938	0,00079448487359990	0,00047074369400058	0,00018743275530042	0,00062391086660085	0,00001916952959924	-0,00045359469963024
Early Neandertal	0,00010279520659928	-0,00009972087604027	-0,00319145650898989	-0,00055674169978026	-0,00075013138098079	-0,00004559343052080	0,00072708811570088
Near East							
Neandertal	0,00634349789180000	0,00218128093539960	-0,00018055676511963	-0,00049936743443979	0,00165300600039942	0,00128135481790004	0,00059260515529935
Classic							
Neandertal	-0,00423705064594948	-0,00140901160946960	0,00354926532540034	0,00150477924369952	0,00029124953220006	-0,00012102903635913	-0,00077704129638079
Skhül - Qafzeh	0,00376517392430031	-0,00054311149663988	-0,00008396184423987	0,00021257468529967	-0,00230117921192985	-0,00041764462653937	0,00111359617890017
KhoiSan	0,00253279207350054	-0,00265673283585954	0,00860172579110063	0,00381988437360015	0,00552939517159956	0,00133205122780033	0,00134564776439916
Haya	0,00006366799630086	-0,01059501186724000	-0,00295065219937918	0,00033524167029952	-0,00060670396172036	-0,00372098566714030	0,00145202527439992
Kongo	-0,00679324883092036	-0,00079024667020988	0,00084297366699992	-0,00138585790939061	-0,00334366186494073	0,00358706228820083	0,00144417429389954
Mande	-0,00371826008655063	-0,00127005153117921	-0,00035285345011005	-0,00117950398161071	-0,00077646241575913	0,00360928325580012	-0,00357308152032942
Berber	0,00015246361940058	0,00622019837670074	0,00196259655970010	0,00747797673320072	-0,00547599705103963	-0,00248072341504013	0,00025209902070067
Papu	-0,00175448355616048	0,00316347409419926	-0,00052390156636051	-0,00154078108560007	0,00369022869240077	-0,00402026994622062	-0,00428856007689937
French	0,00106000332369938	-0,00002148249826028	-0,00922265691960966	0,00442150029149957	0,00279660898499934	0,00207244474590063	-0,00050957042349076
Chinese	-0,00412538821817954	0,00612004078580064	-0,00150908722556942	-0,00583963702536039	0,00261108258139942	-0,00151553853432063	0,00392704231640018
Inuit	0,00873835552389934	-0,00151322891113992	0,00257446112339998	-0,00594785725605007	-0,00346593059471978	0,00002501686969936	-0,00139768711892074

	PC22
<i>Pongo</i>	-0,00001770151171954
<i>Gorilla</i>	0,00023477398729987
<i>Pan</i>	-0,00035871453913927
<i>A. africanus</i>	-0,00013470623544087
<i>Koobi Fora - H. habilis s.l.</i>	0,00003541040909916
<i>Koobi Fora - H. ergaster</i>	-0,00108146715320068
Dmanisi	-0,00014671656744980
Ngandong	0,00044693521989991
Sangiran	0,00053080506480008
Zhoukoudian	0,00033808751060072
Early Neandertal	0,00006027324049995
Near East Neandertal	-0,00053806029002956
Classic Neandertal	-0,00037066535766961
Skhūl - Qafzeh	0,00008161555970077
Khoisan	0,00044903735049928
Haya	-0,00052754082678952
Kongo	0,00404170352740074
Mande	-0,00406333897056932
Berber	-0,00103069246656950
Papu	0,00260310151070087
French	0,00080154762160056
Chinese	-0,00192872862820082
Inuit	0,00057504154469967

Appendix 6: Table of the 22 PCs coordinates obtained from 636 landmarks (Matrix B.3, Chapter III)

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
<i>Pongo</i>	-0,1523323700320400	0,0747171795221995	-0,0447926483628596	-0,0137706936713204	-0,0227399965005599	-0,0033715663835494	0,0121750198795993
<i>Gorilla</i>	-0,1786325978175200	0,0076838694354997	0,0125838701461998	0,0311239281606994	0,0102850616947006	0,0325976562505996	-0,0087848075260304
<i>Pan</i>	-0,0982061013287208	0,0448364703619006	0,0091556809914000	0,0191282860156008	0,0252724832922997	-0,0345649165175299	-0,0038614136206103
<i>A. africanus</i>	-0,0518055502972992	0,0180940081496992	0,0853717829110003	-0,0380078010741691	-0,0085335263289892	0,0040983607407998	-0,0132897880016998
<i>Koobi Fora - H. habilis s.l.</i>	-0,0327985509836193	-0,0184086667942598	0,0323810634856994	-0,0088080077667794	-0,0013526160792292	0,0002293542002008	0,0159547549123999
<i>Koobi Fora - H. ergaster</i>	-0,0453099180778498	-0,0327953510540198	-0,0025361852721400	-0,0154611433054104	0,0183323654469998	0,0020944405153998	0,0191878050368999
Dmanisi	-0,0593312525475902	-0,0497679663138602	0,0110655065259007	-0,0030649060539592	0,0022088580284994	-0,0066814223927700	-0,0037000586872296
Ngandong	-0,0181466761225604	-0,0318506619634906	-0,0127755333628095	-0,0132589745498493	0,0201383917807991	0,0008959901802008	-0,0038657213687401
Sangiran	-0,0423217886298399	-0,0630967252551908	0,0151658514438999	0,0222015715880008	-0,0174014837480900	-0,0119428882781296	0,0089719603241001
Zhoukoudian	-0,0384082546366304	-0,0343571351383591	-0,0183947663475994	0,0059497629302001	-0,0369807762277397	-0,0063399985178094	-0,0068655006248797
Early Neandertal	0,0176939265874996	-0,0078518199000204	-0,0431477011010504	-0,0173525479539602	-0,0027560130301403	-0,0110178833438503	-0,0217764300409602
Near East							
Neandertal Classic	0,0183261280033999	-0,0055264830555508	-0,0516163331079493	-0,0070532064026292	0,0028708515225997	0,0166145423223991	-0,0098520551440906
Neandertal	-0,0009186791202200	-0,0234152073514196	-0,0415541286145604	-0,0087074813415207	0,0118752250051006	0,0021670404639007	0,0005351361847001
Skhül - Qafzeh	0,0534836636415008	0,0008101100684001	0,0083955040850992	0,0000987705909008	0,0118126160882994	-0,0068984093629201	-0,0083598945912602
KhoiSan	0,0730593856866992	0,0049232525456002	0,0071721381484995	0,0100176195038006	-0,0085618679645698	-0,0043334982212198	-0,0007927692499994
Haya	0,0619151711556007	0,0094478188779998	-0,0015089940220197	0,0166826106207001	0,0006534604940995	0,0041316546556995	-0,0034202842177002
Kongo	0,0728221029034000	0,0203863121165000	0,0011094107040996	0,0096316022848999	0,0018887964178003	0,0021533646257002	0,0033173227348993
Mande	0,0820778599742997	0,0151642148238000	0,0118344897976002	0,0149066572069003	-0,0050335689198100	0,0018895209849994	-0,0034653427567104
Berber	0,0807477597575001	0,0211265778889000	0,0079596201062007	-0,0021033302877100	-0,0021011309698800	0,0041983809580994	0,0047511433067005
Papu	0,0674039155656008	0,0152490526206002	0,0208521671961996	0,0031064937933998	-0,0006235235057606	0,0027083138405999	-0,0057379604088101
French	0,0642140647737008	0,0109228330196007	-0,0142417486762696	-0,0063637007538002	0,0074772784558999	-0,0020458767562701	0,0120012727897993
Chinese	0,0758600953672008	0,0139015745587994	0,0110369216146005	0,0069017845857999	-0,0060546914382194	0,0016481032419993	0,0055862591696005
Inuit	0,0506076661775001	0,0098067428366004	-0,0035159682890509	-0,0057972941197892	-0,0006761935139998	0,0117697367934007	0,0112913519000006

	PC8	PC9	PC10	PC11	PC12	PC13	PC14
<i>Pongo</i>	-0,0094262192396908	0,0056043656010001	-0,0013606251909906	-0,0013224961660505	-0,0007015471269103	-0,0038955607720599	-0,0020919941184108
<i>Gorilla</i>	0,0001579494501005	0,0023348911467007	0,0013397403736999	-0,0013730381159292	0,0060329782486992	0,0026555855636996	-0,0004133147746206
<i>Pan</i>	0,0093108207718995	-0,0053915092692503	-0,0011721292854308	0,0017431895866995	-0,0034613470618403	0,0021256127513993	0,0023387755687008
<i>A. africanus</i>	0,0058140239866997	0,0013262005002002	-0,0054095765212594	0,0032223760671002	-0,0034486875780608	0,0029170861332997	-0,0000663318377203
<i>Koobi Fora - H. habilis s.l.</i>	-0,0164862381618907	-0,0073034114962205	0,0169225067288004	0,0053527216357008	-0,0025848037662009	-0,0006931384311102	0,0024224946911993
<i>Koobi Fora - H. ergaster</i>	0,0166613218205001	-0,0036957180346793	0,0010068864204005	0,0033237620341993	0,0095787659899997	-0,0059985997018899	0,0015068788373007
Dmanisi	-0,0142381944786401	-0,0169873779953402	-0,0101255860661098	-0,0137745688826492	-0,0000384500359107	-0,0033944877492793	-0,0016711515338308
Ngandong	0,0006228147816998	0,0217950985799007	0,0053552839731008	-0,0095185181279707	-0,0092433728463597	-0,0034119781917106	0,0029676025712000
Sangiran	-0,0027415154970907	0,0134125576569009	-0,0110907796125694	0,0099319871189003	-0,0007406911314707	-0,0004945615702496	-0,0001349199026794
Zhoukoudian	0,0204456325619002	-0,0058078898876008	0,0117356806032003	-0,0050979321039293	-0,0025092652995600	0,0027052394011999	-0,0014379272949707
Early Neandertal	-0,0075900053462199	0,0020822080151994	0,0019465010689004	0,0027942605620996	0,0135153198586995	0,0013790643924008	0,0059394261154999
Near East							
Neandertal	0,0062031300796992	-0,0081255790667392	-0,0076340429916808	0,0077944440481002	-0,0086582189800701	-0,0077486498833501	-0,0010136683614395
Classic							
Neandertal	-0,0072056852635907	-0,0031529784425093	-0,0009762674541793	0,0096157355517992	-0,0048712037232992	0,0128566807262995	-0,0026601530422106
Skhül - Qafzeh	-0,0018664718778005	0,0048967643660003	0,0095829452396998	0,0013487273193995	0,0051336648496001	-0,0028651018619392	-0,0122041675492195
Khoisan	-0,0037163107642506	0,0051884206077997	-0,0045714131941903	-0,0039092179994107	0,0044518256694008	-0,0005350995959397	0,0020085299599995
Haya	-0,0045339720674207	-0,0028331836419895	0,0048537302225995	-0,0028169819194108	-0,0084004662747308	0,0010261628262001	0,0036306098857004
Kongo	0,0014641253592007	-0,0062395626236604	0,0014197911078995	0,0032432990605003	-0,0004105353591601	-0,0040740210730199	0,0021444067931000
Mande	-0,0043813596806608	0,0007740654256008	0,0028557645226996	-0,0002037965003492	0,0008013455595002	-0,0027550051563505	0,0008998529285993
Berber	0,0055094943146994	0,0005295467084991	-0,0020140024744304	0,0006094123093998	-0,0008726413706803	-0,0006413753538492	0,0028954312333003
Papu	-0,0023233867848909	-0,0007173652880894	-0,0014753493922992	0,0035889903483000	0,0007865544657992	-0,0033016762814508	-0,0012861561693391
French	0,0039132834121993	0,0010298061613003	-0,0049705518346404	-0,0085710786287194	-0,0000737885278195	0,0051008973214994	-0,0046278249454392
Chinese	0,0005675237127996	0,0017571374481005	-0,0040075051935897	-0,0000377923875501	0,0014332102400001	0,0014298639878998	-0,0022053883922393
Inuit	0,0038392389108992	-0,0004764864709994	-0,0022110010496501	-0,0059434848101105	0,0042813542002005	0,0076130625183009	0,0030589893374007

	PC15	PC16	PC17	PC18	PC19	PC20	PC21
<i>Pongo</i>	-0,0013916518798496	0,0015328491255993	0,001023633266001	-0,0005768512821103	-0,0005157478734805	0,0006951020117008	-0,0003538489212591
<i>Gorilla</i>	-0,0003817859648994	-0,0012439759095599	-0,0009895521511307	0,0017134492970001	-0,0000480335287492	-0,0002546312637204	0,0003974156583002
<i>Pan</i>	0,0026554045442992	-0,0017199560519003	0,0002435882067999	-0,0007583928409396	0,0006584908182994	-0,0003196162059194	-0,0001717196006705
<i>A. africanus</i>	-0,0009069282619301	0,0026777382273995	-0,0002868413990296	0,0000398577506999	-0,0001203106003995	-0,0008980130495608	0,0005665601196991
<i>Koobi Fora - H. habilis s.l.</i>	0,0042948148521997	-0,0031706394403201	-0,0017417747688899	0,0014474529479003	0,0016474817951000	-0,0010002956562207	0,0005965630739002
<i>Koobi Fora - H. ergaster</i>	-0,0032437992621599	0,0040491588980007	0,0010601368450001	0,0003325609889000	0,0013015446282996	0,0014186743990994	-0,0004046160831308
Dmanisi	-0,0014269714437294	-0,0010114194729898	0,0012832939706993	-0,0007442071340993	-0,0016009927382292	0,0006266707824008	-0,0002210694789806
Ngandong	-0,0019181906684107	-0,0025579348156803	0,0011302135022007	-0,0012592894722605	0,0003050008258008	-0,0003925233263509	-0,0001188982020093
Sangiran	0,0019195186365995	0,0013502454882008	-0,0026632113675493	-0,0007954813010898	-0,0018964487084698	-0,0002279247105594	-0,0001377497007002
Zhoukoudian	-0,0010022975293698	-0,0012803680887394	0,0007257356846004	0,0003298640815999	0,0005207086155004	-0,0000462520103408	-0,0003529965359608
Early Neandertal	0,0000264720641994	-0,0005172374628000	-0,0042061259335409	0,0001169562523007	-0,0004042633941399	0,0001286720832994	0,0006484511800000
Near East							
Neandertal	0,0063158363889997	-0,0010655132089905	-0,0008362071417807	-0,0001912093570695	0,0015007299735004	-0,0013058912843906	0,0006173514520000
Classic							
Neandertal	-0,0049920211431296	0,0003145979041008	0,0047059795953004	0,0008873827332003	0,0000405154460008	0,0002404382384995	-0,0007888378531398
Skhül - Qafzeh	0,0037160701311993	0,0019705676133004	0,0016235039516008	-0,0012232816313400	-0,0027334682394908	0,0005585578464995	0,0008193859755998
Khoisan	0,0032368179418008	0,0023799240880997	0,0083393150861006	0,0048146065403003	0,0043336583664999	-0,0010931122536899	0,0015242272512008
Haya	-0,0002358795606607	0,0094208658931994	-0,0030482845773392	-0,0002788497115809	-0,0002084991318103	0,0037487586902998	0,0011552744590002
Kongo	-0,0067331016761294	0,0007325410049006	0,0009297709123999	-0,0019278096861601	-0,0031586830180803	-0,0034921571964599	0,0019754829455003
Mande	-0,0033913458333306	0,0010488027344007	0,0000149247130992	-0,0008200866614096	-0,0003127895058892	-0,0035002323737192	-0,0035798704850798
Berber	0,0010784583104009	-0,0056519082755706	0,0014696416091997	0,0055576145092999	-0,0063686697351209	0,0028464840395994	-0,0002384990108393
Papu	-0,0011756672677095	-0,0023206573577799	-0,0008445239491905	-0,0005517552774101	0,0037548573113000	0,0031442625911993	-0,0038347658766504
French	0,0002005553452999	0,0008911713046000	-0,0081132117197793	0,0048999883231993	0,0013556461766999	-0,0022606802173293	-0,0001975710621096
Chinese	-0,0044564381184706	-0,0063498781901394	-0,0016295353017100	-0,0042644660146003	0,0034816148482992	0,0018736300945008	0,0031701351541997
Inuit	0,0078121303948997	0,0005210259927004	0,0018095309063000	-0,0067480530543005	-0,0015323423313607	-0,0004899212288105	-0,0010704044587104

	PC22
<i>Pongo</i>	-0,0000070282789597
<i>Gorilla</i>	0,0002152215940008
<i>Pan</i>	-0,0002697187620306
<i>A. africanus</i>	-0,0002943047739397
<i>Koobi Fora - H. habilis s.l.</i>	0,0000325249502993
<i>Koobi Fora - H. ergaster</i>	-0,0009609213723305
Dmanisi	-0,0001270903640194
Ngandong	0,0004362738111006
Sangiran	0,0004081596171002
Zhoukoudian	0,0003986984985005
Early Neandertal	0,0000061621796998
Near East Neandertal	-0,0006779389906804
Classic Neandertal	-0,0001719414513595
Skhül - Qafzeh	-0,0000860180379707
Khoisan	0,0003432720549004
Haya	-0,0005662016375005
Kongo	0,0032320163142998
Mande	-0,0036115086042994
Berber	-0,0007960728617995
Papu	0,0031253426710993
French	0,0007400686082004
Chinese	-0,0020073820927102
Inuit	0,0006383869285003

Appendix 7: Table of the 148 landmarks coordinates (Matrix C.1, Chapter III).

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 8: Table of the 347 landmarks coordinates (Matrix C.2, Chapter III).

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 9: Table of the 636 landmarks coordinates (Matrix C.3, Chapter III).

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 10: Matrix of the 60 discrete morphological characters for matrix D, Chapter IV

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>Pongo</i>	1	3	1	2	2	1	[23]	1	1	1	1	1	3	3	1
<i>Gorilla</i>	1	2	1	2	1	1	3	1	1	2	1	1	3	3	1
<i>Pan</i>	2	3	1	1	1	1	3	1	1	1	1	1	3	3	1
<i>P. boisei</i>	2	3	1	2	1	1	2	2	[12]	2	1	3	3	1	1
<i>P. aethiopicus</i>	1	2	1	2	1	1	1	1	1	2	1	2	3	1	1
Stw 53	1	1	[2-]	1	2	2	-	-	1	1	1	1	2	3	1
<i>A. africanus</i>	1	3	2	1	2	2	3	1	1	1	1	1	1	2	1
<i>A. afarensis</i>	1	2	1	2	1	1	1	1	2	1	1	1	3	1	1
<i>H. habilis</i>	[12]	2	2	[12]	[12]	[1-]	[13]	[1-]	[1-]	1	1	3	[23]	3	1
<i>H. rudolfensis</i>	2	2	3	1	2	1	-	-	-	1	1	1	3	3	1
Dmanisi	[12]	[13]	[-2]	[12]	[12]	[12]	[-23]	[-12]	[-2]	[12]	1	[2-]	2	[23]	1
<i>H. ergaster</i>	2	[23]	[12]	2	[12]	[12]	[23]	[1-]	[12]	[12]	1	3	3	3	1
Sangiran	[2-]	[3-]	[2-]	2	1	[12]	[3-]	[1-]	[1-]	[12]	1	[3-]	[3-]	3	[12]
Zhoukoudian	[12]	2	[23]	2	[12]	[12]	[13]	1	1	2	1	[13]	2	3	2
Ngandong	1	[12]	2	2	[12]	[23]	2	1	2	2	1	3	[23]	3	[23]
Near East Neandertal	2	3	[23]	1	2	2	[13]	1	2	1	2	[13]	2	3	3
Early Neandertal	[2-]	[3-]	[23]	2	2	[2-]	3	[12]	[1-]	[12]	2	3	[2-]	3	3
Classic Neandertal	2	3	[13]	2	2	2	[123]	[2-]	1	1	2	[13]	3	3	3
Skhūl - Qafzeh	[12]	3	[12]	1	[12]	3	[1-]	[12-]	[2-]	2	3	[13]	[12]	[23]	3
KhoiSan	2	3	3	1	2	[23]	3	1	2	2	3	1	1	1	3
Haya	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Kongo	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Mande	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Berber	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Papu	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
French	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Chinese	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3
Inuit	2	3	3	1	2	3	3	1	2	1	3	1	1	1	3

Percentage of missing
data per character

6,66666667 6,66666667 6,66666667 6,66666667 6,66666667 13,33333333 23,33333333 33,33333333 30 3,33333333 0 6,66666667 6,66666667 0 0

	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
<i>Pongo</i>	1	1	3	1	1	1	1	1	2	2	1	3	2	1	2
<i>Gorilla</i>	1	1	2	1	1	1	2	1	2	2	1	2	1	1	1
<i>Pan</i>	3	1	2	1	1	1	2	2	2	2	2	2	2	1	1
<i>P. boisei</i>	1	1	2	2	2	1	1	1	2	2	1	2	1	1	1
<i>P. aethiopicus</i>	1	1	2	2	2	1	1	1	2	2	2	2	1	1	1
Stw 53	3	2	2	1	1	1	-	-	-	-	-	2	1	1	1
<i>A. africanus</i>	1	1	2	1	1	1	1	1	1	1	1	2	2	1	1
<i>A. afarensis</i>	1	1	2	1	1	1	1	1	1	1	1	2	2	2	1
<i>H. habilis</i>	3	[12]	[2-]	1	1	1	1	1	1	[1-]	1	[2-]	[13]	[1-]	[1-]
<i>H. rudolfensis</i>	1	1	2	1	1	1	1	1	1	1	1	3	1	2	3
Dmanisi	3	[12]	2	1	[12]	[12]	1	1	[12]	[12]	1	2	[123]	[12]	1
<i>H. ergaster</i>	3	2	2	1	[12]	2	1	2	[12]	1	2	3	3	[12]	1
Sangiran	3	2	3	1	2	2	1	2	[12]	2	1	3	[12]	2	1
Zhoukoudian	3	[23]	2	1	2	2	1	2	2	2	2	2	1	2	1
Ngandong	3	2	2	1	2	2	1	2	2	2	[12]	2	3	2	1
Near East Neandertal	3	3	2	1	1	1	1	1	1	[12]	[12]	2	3	1	1
Early Neandertal	[3-]	3	2	1	1	1	1	1	[12]	[12]	[12]	2	3	[12]	1
Classic Neandertal	3	3	2	1	1	1	1	1	[12]	[12]	2	[23]	3	1	1
Skhūl - Qafzeh	[123]	3	2	1	1	1	1	1	[12-]	[12]	[12]	2	3	1	[123]
KhoiSan	3	3	2	1	1	1	1	1	1	[12]	1	2	3	1	2
Haya	3	3	1	1	1	1	1	1	1	2	1	2	3	1	2
Kongo	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Mande	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Berber	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Papu	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
French	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Chinese	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Inuit	3	3	2	1	1	1	1	1	1	1	1	2	3	1	2
Percentage of missing data per character	3,33333333	0	3,33333333	0	0	0	3,33333333	3,33333333	13,33333333	13,33333333	10	3,33333333	3,33333333	6,66666667	6,66666667

	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
<i>Pongo</i>	1	1	1	1	[23]	2	[12]	3	[23]	2	1	1	2	2	1
<i>Gorilla</i>	1	1	1	1	1	1	3	3	3	1	2	1	2	2	2
<i>Pan</i>	1	1	2	2	1	1	1	3	3	1	2	1	2	2	2
<i>P. boisei</i>	2	1	1	2	[13]	[13]	1	3	3	1	2	1	2	[12]	[23]
<i>P. aethiopicus</i>	2	1	1	2	2	2	1	3	2	1	2	1	2	2	2
Stw 53	1	1	2	1	1	1	1	2	2	1	2	1	-	-	3
<i>A. africanus</i>	[12]	2	1	2	1	1	2	3	2	1	1	1	2	2	2
<i>A. afarensis</i>	2	1	1	2	2	2	2	2	2	1	1	1	-	-	2
<i>H. habilis</i>	2	1	[12]	1	1	1	[2-]	2	[2-]	[1-]	[2-]	[12]	2	[1-]	3
<i>H. rudolfensis</i>	-	1	1	-	1	1	1	2	2	-	-	1	2	1	3
Dmanisi	[-12]	[12]	[12]	1	1	1	[12]	[12]	[12]	1	[12]	[12]	1	[12]	[13]
<i>H. ergaster</i>	[12]	1	[12]	[12]	1	1	[23]	2	[23]	1	2	2	2	2	2
Sangiran	1	1	1	2	1	1	[23]	2	2	1	[12]	1	[12]	1	3
Zhoukoudian	1	1	1	[12]	1	1	3	2	2	1	[12]	1	2	2	3
Ngandong	[12]	1	1	2	1	1	[23]	2	3	2	2	1	2	2	3
Near East Neandertal	2	2	2	[12]	3	2	2	3	2	1	1	[12]	[2-]	1	2
Early Neandertal	2	[12]	2	[2-]	3	2	1	3	2	1	[12]	[12]	[12]	1	[12]
Classic Neandertal	2	2	2	1	3	3	[12]	3	2	1	1	[12]	[12]	1	[13]
Skhūl - Qafzeh	2	1	2	[12]	1	1	[12]	1	1	[12]	[12]	2	[12-]	1	[12]
KhoiSan	2	1	2	1	1	1	1	1	1	2	2	[12]	1	[12]	2
Haya	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Kongo	2	1	2	1	1	1	[12]	1	1	2	2	2	1	1	2
Mande	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Berber	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Papu	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
French	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Chinese	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Inuit	2	1	2	1	1	1	1	1	1	2	2	2	1	1	2
Percentage of missing data per character	10	6,66666667	6,66666667	13,33333333	6,66666667	6,66666667	10	6,66666667	10	13,33333333	13,33333333	3,33333333	16,66666667	13,33333333	0

	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	Percentage of missing data per OTU
<i>Pongo</i>	1	1	1	1	1	1	1	1	1	1	2	2	2	1	1	0
<i>Gorilla</i>	2	1	3	1	3	1	1	1	1	1	2	2	2	1	1	0
<i>Pan</i>	2	2	1	2	3	1	1	1	1	1	2	2	2	1	1	0
<i>P. boisei</i>	2	[12]	[13]	2	1	2	1	[12]	1	[23]	3	1	[12]	1	1	0
<i>P. aethiopicus</i>	2	2	1	2	1	1	1	1	1	1	2	1	2	2	1	0
Stw 53	2	1	1	1	1	2	2	1	2	2	3	1	1	2	1	15
<i>A. africanus</i>	2	1	3	1	2	1	1	1	1	3	[13]	2	2	1	1	0
<i>A. afarensis</i>	2	1	1	1	2	1	2	2	1	2	1	2	1	1	1	3,333333333
<i>H. habilis</i>	2	[12]	[2-]	[12]	1	[2-]	[2-]	[2-]	1	[13]	[13]	1	[12]	[12]	1	28,33333333
<i>H. rudolfensis</i>	2	2	-	-	-	-	-	-	-	2	1	-	2	1	1	25
Dmanisi	2	[12]	2	[12]	1	1	[-2]	[12]	[-1]	[13]	[13]	[12]	[-2]	2	[12]	15
<i>H. ergaster</i>	2	[12]	2	2	1	[12]	[12]	1	[1-]	3	1	2	[12]	2	[12]	3,333333333
Sangiran	[12]	2	[12]	1	[12]	[12]	[1-]	1	[2-]	3	1	[12]	[12]	2	2	16,66666667
Zhoukoudian	[2-]	2	[23]	[12]	1	1	[12]	2	2	3	3	[1-]	2	[12]	2	3,333333333
Ngandong	[2-]	2	[23]	[12]	1	[12]	1	2	2	3	[13]	[1-]	[1-]	2	2	5
Near East Neandertal	1	1	3	[12]	[23]	2	[1-]	1	[1-]	1	1	1	2	1	[1-]	6,666666667
Early Neandertal	[12]	2	3	[12]	[2-]	[12]	[1-]	[2-]	[1-]	2	1	1	[12]	[1-]	1	20
Classic Neandertal	1	[12]	3	[12]	3	2	[13]	[12]	1	2	1	2	[12]	1	1	1,666666667
Skhül - Qafzeh	[12]	1	3	[12]	1	1	[1-]	[12-]	[1-]	[12]	2	[12]	1	2	1	13,33333333
Khoisan	2	1	[13]	[12]	[12]	1	1	1	1	2	2	1	1	1	1	0
Haya	2	1	3	2	2	1	1	1	1	2	2	1	1	1	1	0
Kongo	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Mande	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Berber	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Papu	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
French	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Chinese	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Inuit	2	1	3	1	2	1	1	1	1	2	2	1	1	1	1	0
Percentage of missing data per character	6,66666 667	3,33333 333	10	6,66666 667	10	13,3333 333	36,6666 667	20	33,3333 333	3,33333 333	3,33333 333	13,3333 333	10	6,66666 667	6,66666 667	

Appendix 11: Combined matrix of the 7 landmarks configurations and 50 discrete morphological characters (matrix E, Chapter IV)

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 12: Synapomorphies et autapomorphies of Matrix A of Chapter III, according to the weighting

	CI-weighting		Near East Neandertal				
	Character	Previous state	New state				
<i>Pongo</i>					Char. 4	3	2
					Char. 54	2	1
<i>Gorilla</i>	No autapomorphies			Early Neandertal			
	Char. 7	3	2		No autapomorphies		
	Char. 20	2	1	Classic Neandertal			
	Char. 53	1	2				
<i>Pan</i>					Char. 31	2	3
	Char. 3	1	2		Char. 56	1	2
	Char. 8	1	3	Skhūl - Qafzeh			
	Char. 15	1	2		Char. 58	1	2
	Char. 18	1	2	KhoiSan			
	Char. 27	1	2		No autapomorphies		
	Char. 28	1	2	Haya			
	Char. 44	1	2		Char. 11	2	1
	Char. 46	1	2		Char. 17	1	2
<i>A. africanus</i>					Char. 46	1	2
	Char. 4	3	1	Kongo			
	Char. 5	3	2		No autapomorphies		
	Char. 26	1	2	Mande			
	Char. 28	1	2		No autapomorphies		
	Char. 47	1	2	Berber			
Koobi Fora - <i>H. habilis</i> s.l.					No autapomorphies		
				Papu			
	Char. 20	3	1		No autapomorphies		
	Char. 29	2	1	France			
Dmanisi					No autapomorphies		
	Char. 40	2	1	China			
Koobi Fora - <i>H. ergaster</i>					No autapomorphies		
				Inuit			
	Char. 18	1	2		No autapomorphies		
	Char. 19	2	3				
	Char. 39	1	2	Node C			
	Char. 41	1	2		Char. 14	1	2
	Char. 46	1	2		Char. 24	2	1
					Char. 47	1	3
Sangiran				Node B			
	Char. 11	2	3		No autapomorphies		
	Char. 19	2	3	Node D			
Zhoukoudian					Char. 10	1	2
	No autapomorphies				Char. 16	2	1
Ngandong					Char. 17	2	1
	Char. 34	2	3		Char. 29	1	2
	Char. 35	1	2		Char. 54	1	3
	Char. 37	3	2		Char. 55	2	1

CI-weighting			
	Character	Previous state	New state
Node F			
	Char. 33	3	2
Node E			
	Char. 3	1	2
	Char. 8	1	3
	Char. 20	2	3
	Char. 41	2	1
Node H			
	Char. 3	2	1
	Char. 4	3	2
Node G			
	Char. 9	1 or 3	2
	Char. 13	1	2
	Char. 15	1	2
	Char. 58	1	2
Node I			
	Char. 17	1	2
	Char. 28	1	2
Node J			
	Char. 41	1	2
	Char. 51	1	2
Node L			
	Char. 26	1	2
	Char. 30	1	3
	Char. 31	1	2
	Char. 43	2	1
	Char. 47	1	3
	Char. 48	1	2
Node K			
	Char. 6	1	3
	Char. 25	1	2
	Char. 27	1	2
	Char. 54	3	2
	Char. 56	2	1
Node M			
	Char. 4	3	1
	Char. 29	2	3
	Char. 33	3	1
	Char. 34	2	1
	Char. 55	1	2
	Char. 57	2	1
Node N			
	Char. 5	3	1

RI-weighting				Neandertal			
	Character	Previous state	New state		Char. 4	3	2
Pongo					Char. 54	2	1
	No autapomorphies			Early Neandertal			
Gorilla					No autapomorphies		
	Char. 7	3	2	Classic Neandertal			
	Char. 20	2	1				
Pan	Char. 53	1	2		Char. 31	2	3
					Char. 56	1	2
	Char. 3	1	2	Skhūl - Qafzeh			
	Char. 8	1	3		Char. 58	1	2
	Char. 15	1	2	KhoiSan			
	Char. 18	1	2		No autapomorphies		
	Char. 27	1	2	Haya			
	Char. 28	1	2		Char. 11	2	1
	Char. 44	1	2		Char. 17	1	2
	Char. 46	1	2		Char. 46	1	2
A. africanus				Kongo			
	Char. 4	3	1		No autapomorphies		
	Char. 5	3	2	Mande			
	Char. 26	1	2		No autapomorphies		
	Char. 28	1	2	Berber			
Koobi Fora - H. habilis s.l.	Char. 47	1	2		No autapomorphies		
				Papu			
					No autapomorphies		
Koobi Fora - H. ergaster	Char. 20	3	1	France			
	Char. 29	2	1		No autapomorphies		
Dmanisi				China			
	Char. 40	2	1		No autapomorphies		
Koobi Fora - H. ergaster				Inuit			
					No autapomorphies		
	Char. 18	1	2				
	Char. 19	2	3	Node C			
	Char. 39	1	2		Char. 14	1	2
	Char. 41	1	2		Char. 24	2	1
Sangiran	Char. 46	1	2		Char. 47	1	3
				Node B			
					No autapomorphies		
Sangiran	Char. 11	2	3				
	Char. 19	2	3	Node D			
Zhoukoudian					Char. 10	1	2
	No autapomorphies				Char. 16	2	1
Ngandong					Char. 17	2	1
					Char. 29	1	2
	Char. 34	2	3		Char. 54	1	3
	Char. 35	1	2		Char. 55	2	1
	Char. 37	3	2				
Near East							

RI-weighting			
	Character	Previous state	New state
Node F			
	Char. 33	3	2
Node E			
	Char. 3	1	2
	Char. 8	1	3
	Char. 20	2	3
	Char. 41	2	1
Node H			
	Char. 3	2	1
Node G			
	Char. 9	1 or 3	2
	Char. 13	1	2
	Char. 15	1	2
	Char. 58	1	2
Node I			
	Char. 17	1	2
	Char. 28	1	2
Node J			
	Char. 51	1	2
Node L			
	Char. 26	1	2
	Char. 30	1	3
	Char. 31	1	2
	Char. 43	2	1
	Char. 47	1	3
	Char. 48	1	2
Node K			
	Char. 6	1	3
	Char. 9	1	3
	Char. 25	1	2
	Char. 27	1	2
	Char. 54	3	2
	Char. 56	2	1
Node M			
	Char. 4	3	1
	Char. 29	2	3
	Char. 33	3	1
	Char. 34	2	1
	Char. 55	1	2
	Char. 57	2	1
Node N			
	Char. 5	3	1

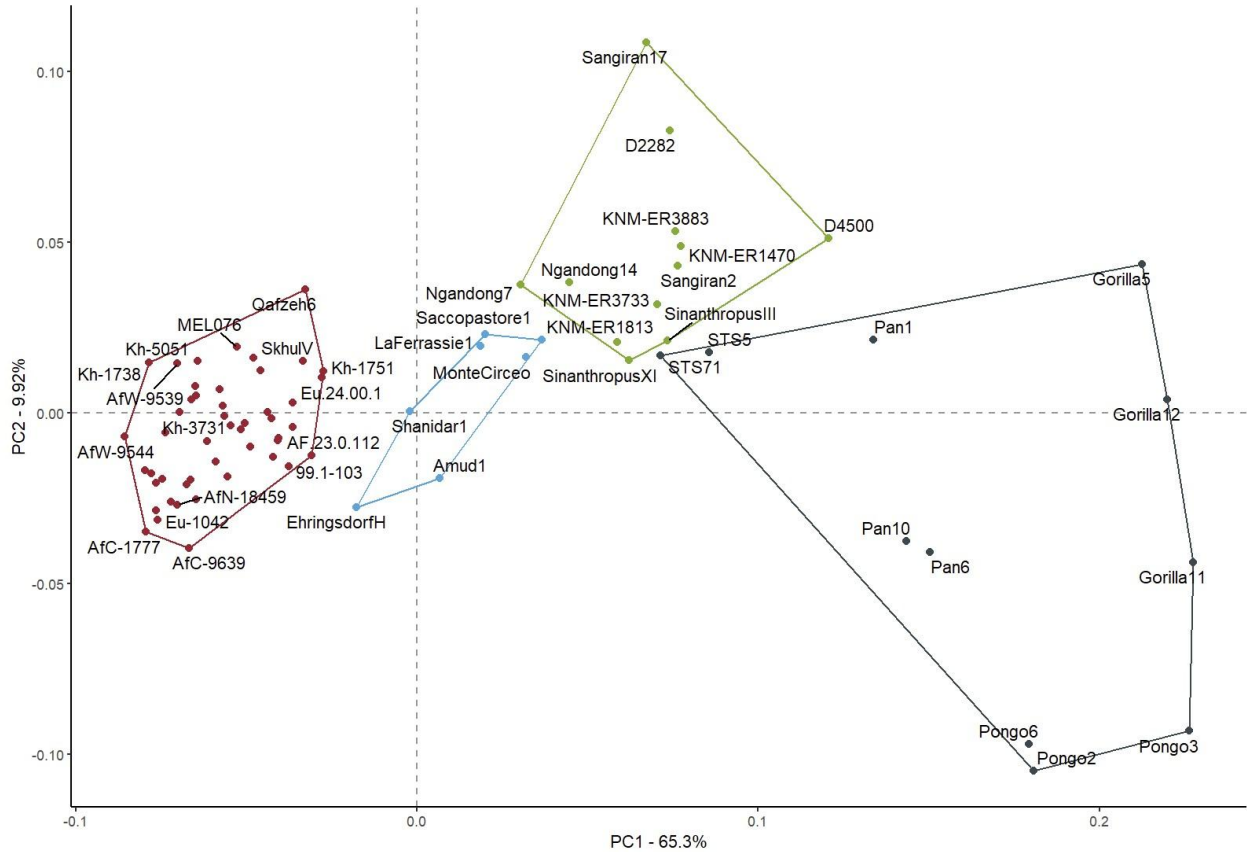
	RC-weighting			Classic Neandertal			
	Character	Previous state	New state				
<i>Pongo</i>					Char. 31	2	3
					Char. 56	1	2
	No autapomorphies			Skhūl - Qafzeh			
<i>Gorilla</i>					Char. 58	1	2
	Char. 7	3	2	KhoiSan			
	Char. 20	2	1		No autapomorphies		
	Char. 53	1	2	Haya			
<i>Pan</i>					Char. 17	1	2
	Char. 3	1	2	Kongo			
	Char. 8	1	3		No autapomorphies		
	Char. 15	1	2	Mande			
	Char. 27	1	2		No autapomorphies		
	Char. 28	1	2	Berber			
	Char. 44	1	2		No autapomorphies		
<i>A. africanus</i>				Papu			
	Char. 4	3	1		No autapomorphies		
	Char. 5	3	2	France			
	Char. 26	1	2		No autapomorphies		
	Char. 28	1	2	China			
	Char. 47	1	2		No autapomorphies		
Koobi Fora - <i>H. habilis</i> s.l.				Inuit			
					No autapomorphies		
	Char. 20	3	1				
	Char. 29	2	1	Node C			
Dmanisi					Char. 14	1	2
					Char. 24	2	1
	Char. 40	2	1		Char. 47	1	3
Koobi Fora - <i>H. ergaster</i>				Node B			
	Char. 39	1	2		No autapomorphies		
	Char. 41	1	2	Node D			
Sangiran					Char. 10	1	2
	No autapomorphies				Char. 16	2	1
Zhoukoudian					Char. 17	2	1
	No autapomorphies				Char. 29	1	2
Ngandong					Char. 54	1	3
	Char. 34	2	3		Char. 55	2	1
	Char. 35	1	2	Node F			
	Char. 37	3	2		Char. 33	3	2
Near East Neandertal				Node E			
					Char. 3	1	2
	Char. 4	3	2		Char. 8	1	3
	Char. 54	2	1		Char. 20	2	3
Early Neandertal					Char. 41	2	1
	No autapomorphies						

RC-weighting

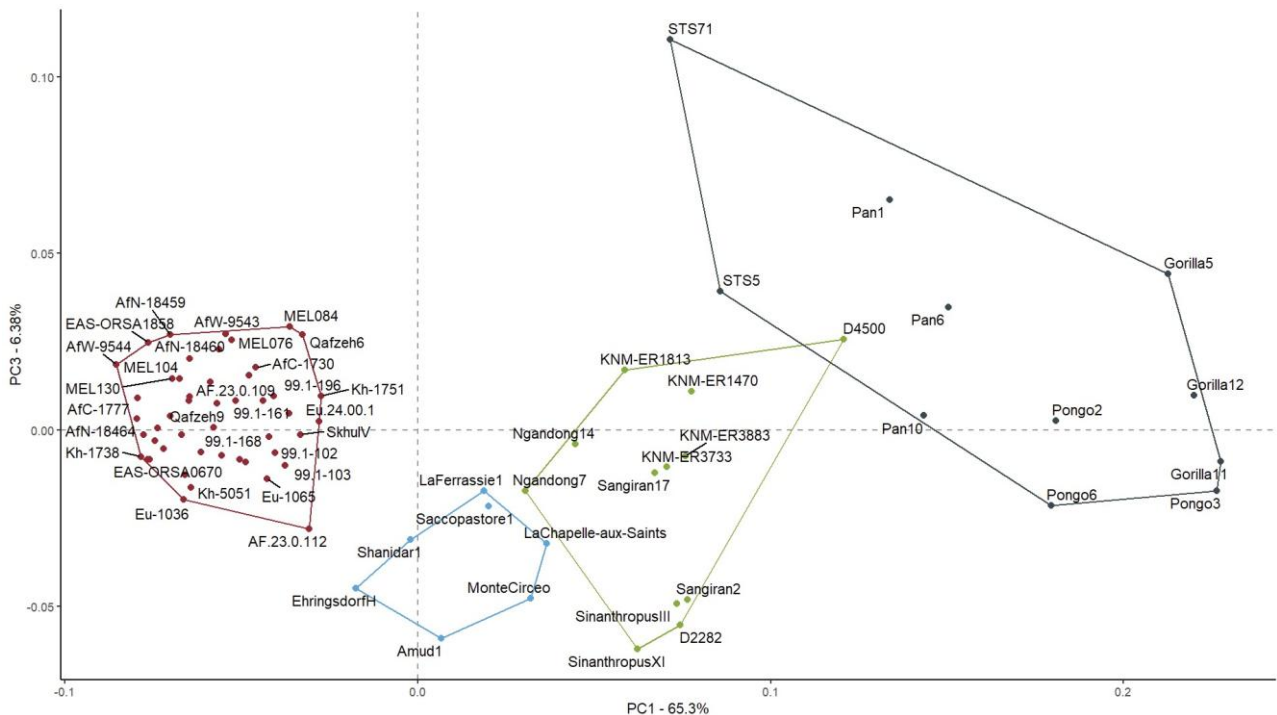
	Character	Previous state	New state
Node H			
	Char. 3	2	1
	Char. 4	3	2
Node G			
	Char. 9	1 or 3	2
	Char. 13	1	2
	Char. 15	1	2
	Char. 58	1	2
Node I			
	Char. 17	1	2
	Char. 28	1	2
Node J			
	Char. 41	1	2
	Char. 51	1	2
Node L			
	Char. 26	1	2
	Char. 30	1	3
	Char. 31	1	2
	Char. 43	2	1
	Char. 47	1	3
	Char. 48	1	2
Node K			
	Char. 6	1	3
	Char. 25	1	2
	Char. 27	1	2
	Char. 54	3	2
	Char. 56	2	1
Node M			
	Char. 4	3	1
	Char. 29	2	3
	Char. 33	3	1
	Char. 34	2	1
	Char. 55	1	2
	Char. 57	2	1
Node N			
	Char. 5	3	1

Appendix 13: Morphospaces of the specimens of Chapter III based on: A) Matrix B.1 (148 landmarks dataset); B) Matrix B.2 (347 landmarks dataset); and 3) Matrix B.3 (347 landmarks dataset).

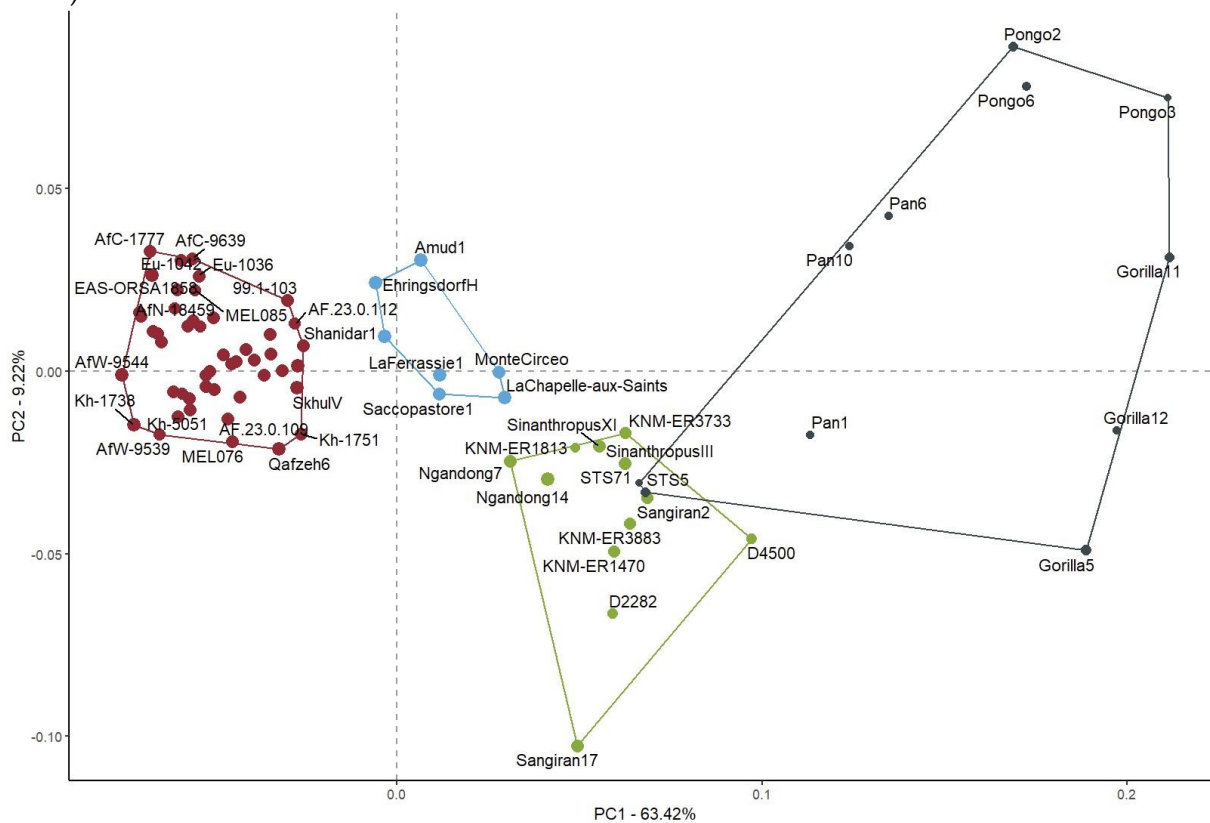
1) PC1 – PC2



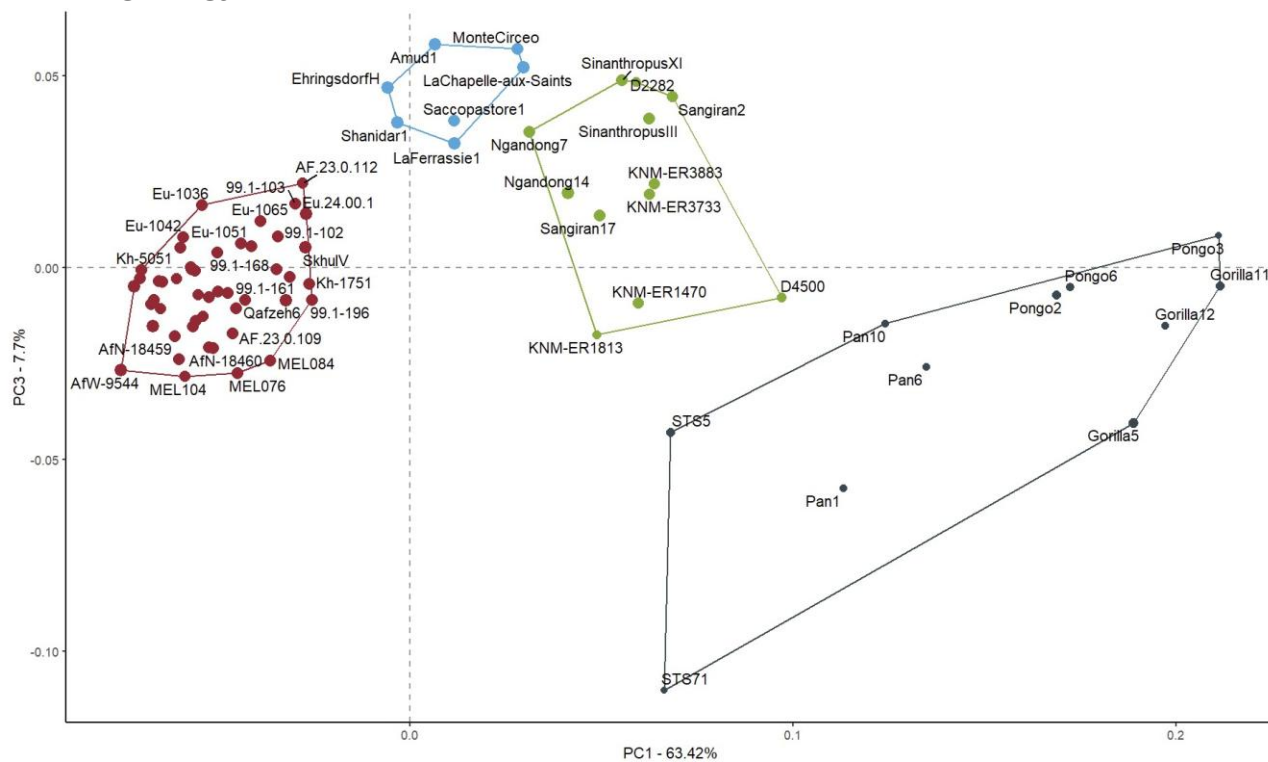
PC1 – PC3



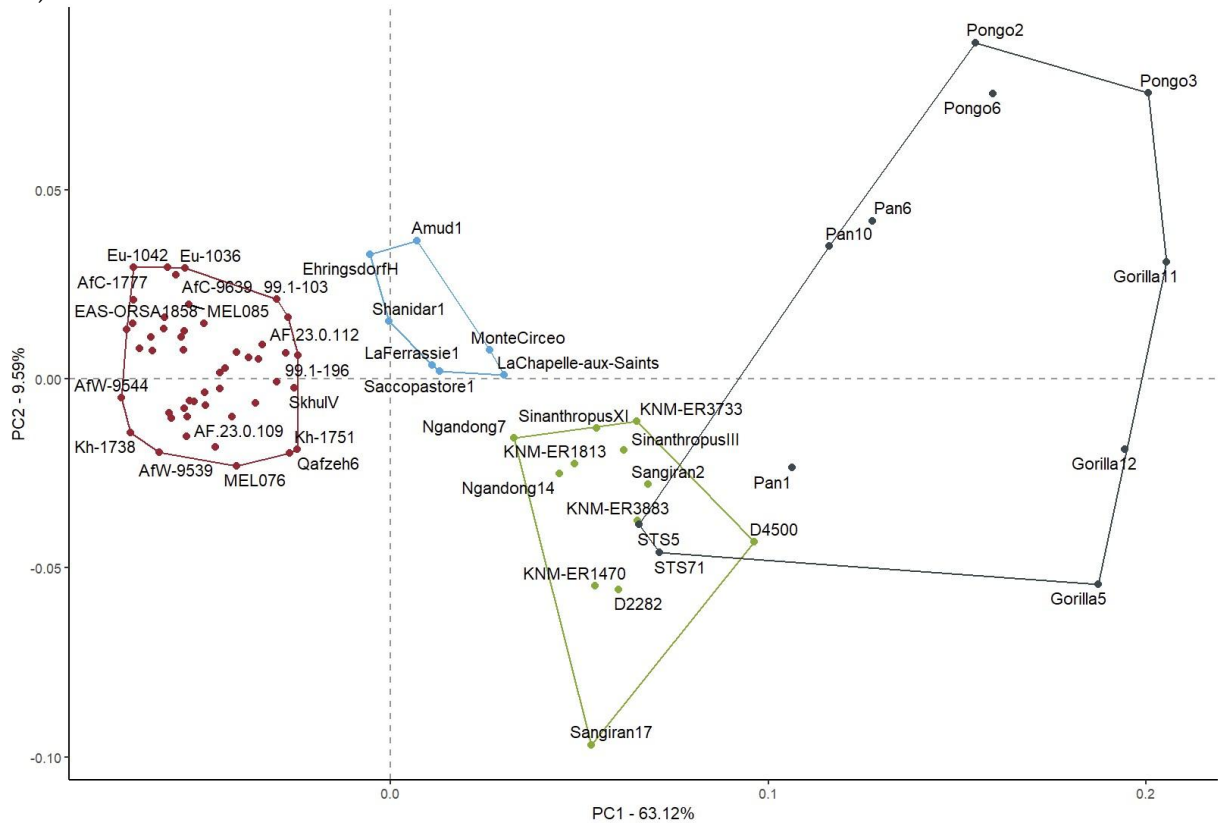
2) PC1 – PC2



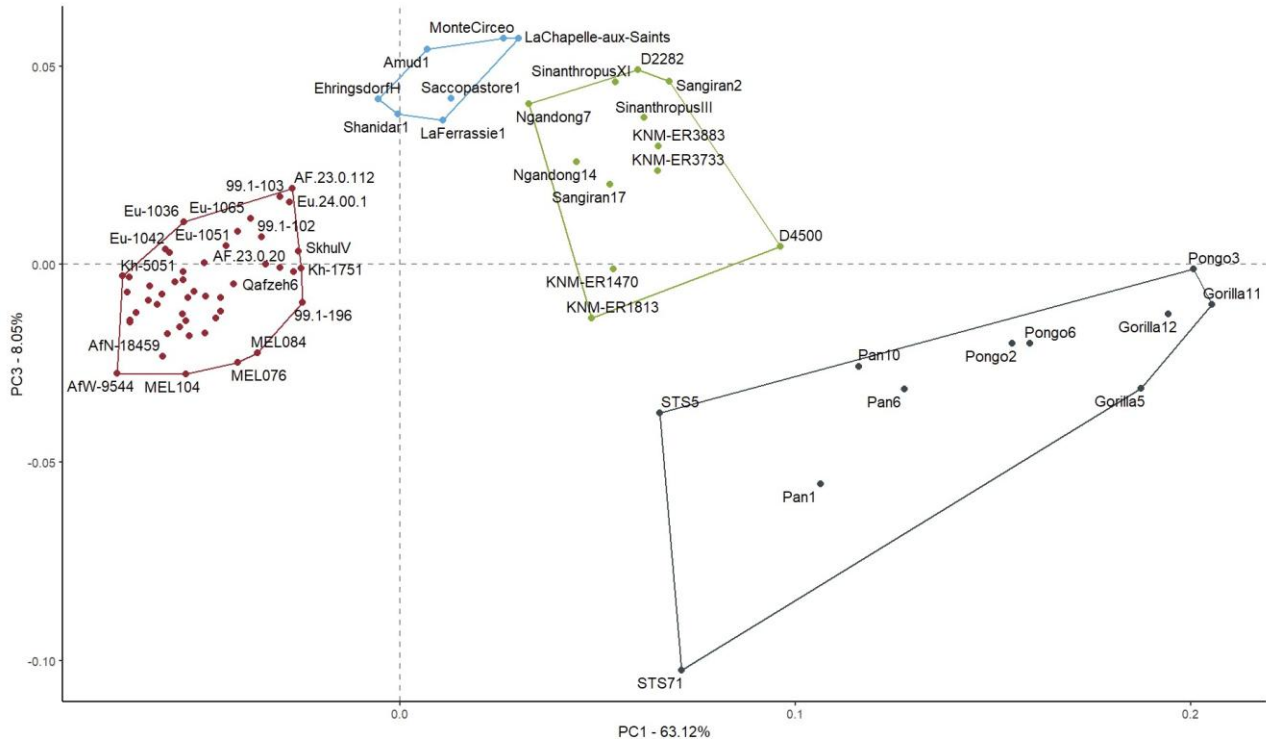
PC1 – PC3



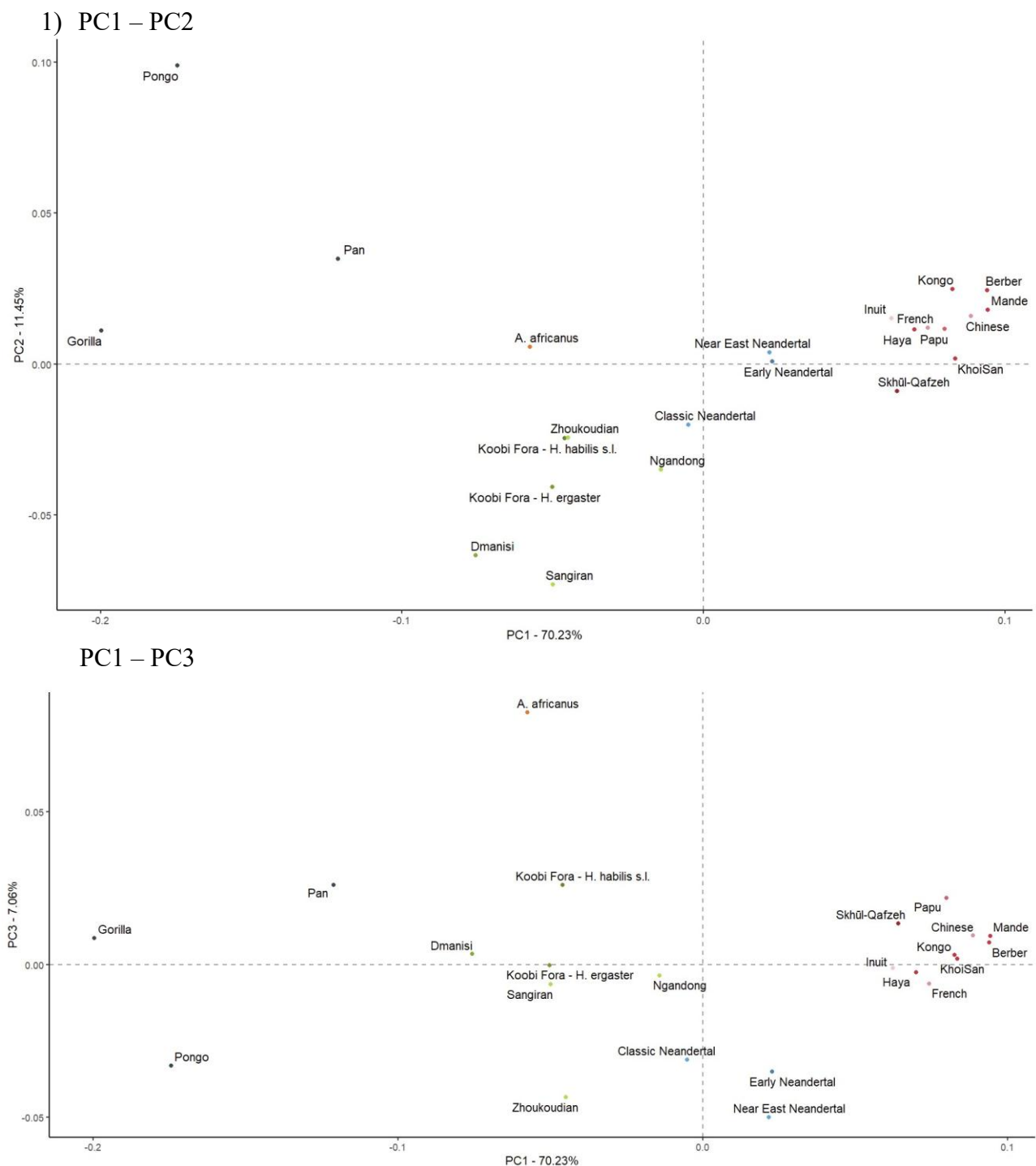
3) PC1 – PC2



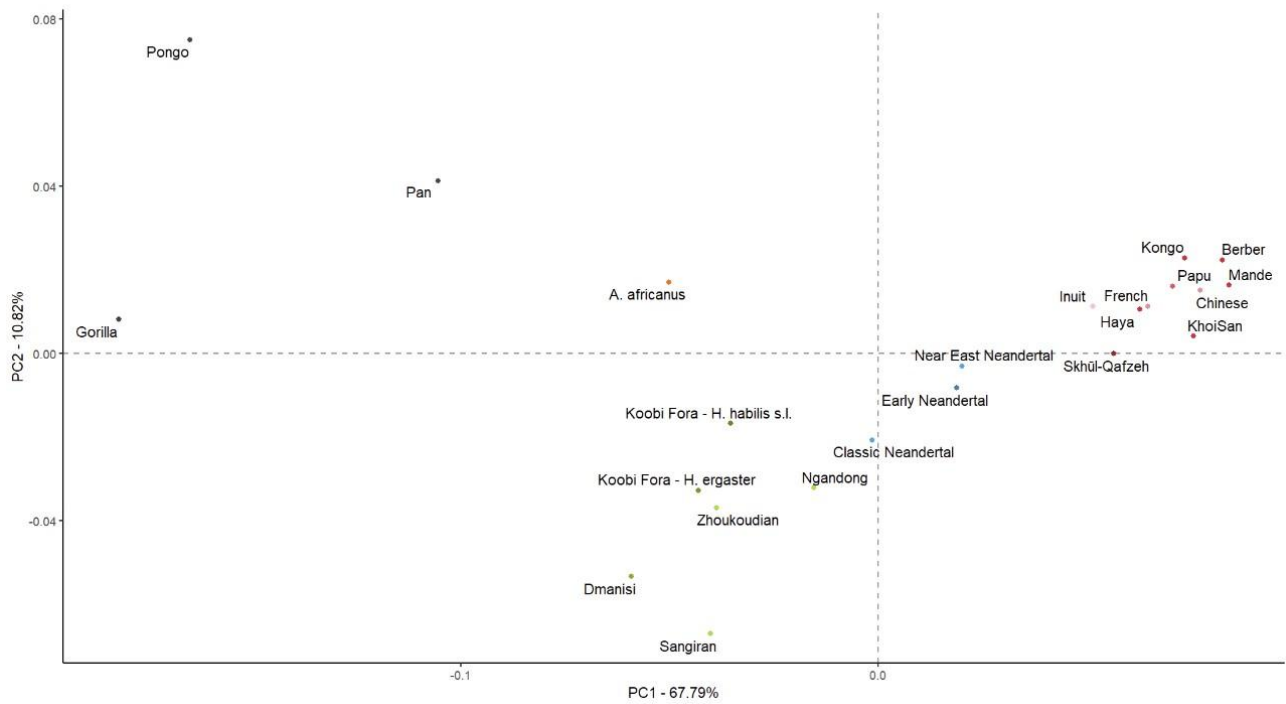
PC1 – PC3



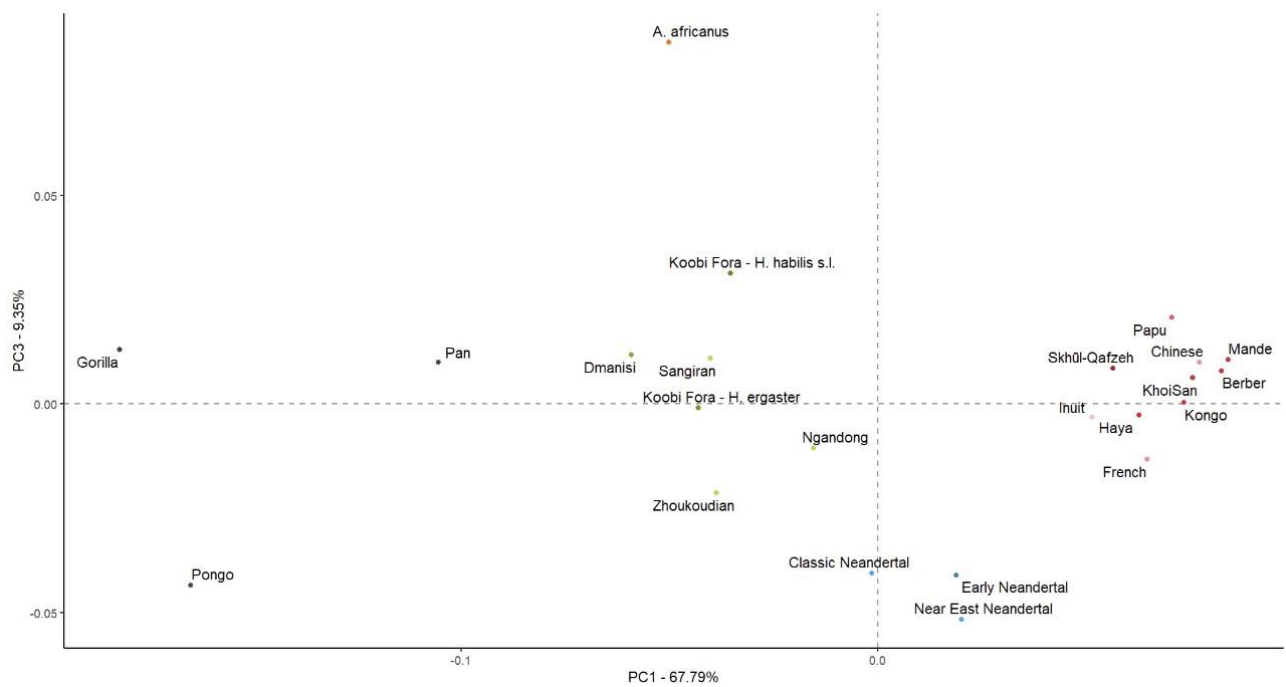
Appendix 14: Morphospaces of the 23 OTUs of Chapter III based on: A) Matrix B.1 (148 landmarks dataset); B) Matrix B.2 (347 landmarks dataset); and 3) Matrix B.3 (347 landmarks dataset).



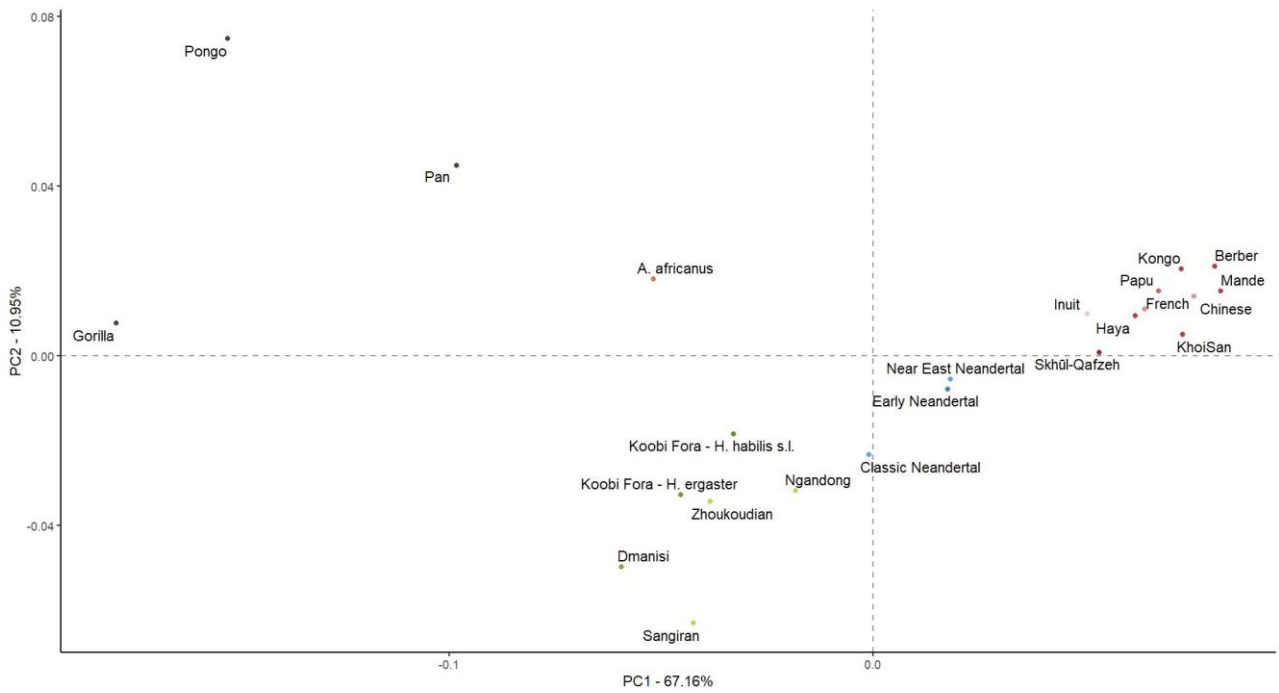
2) PC1 – PC2



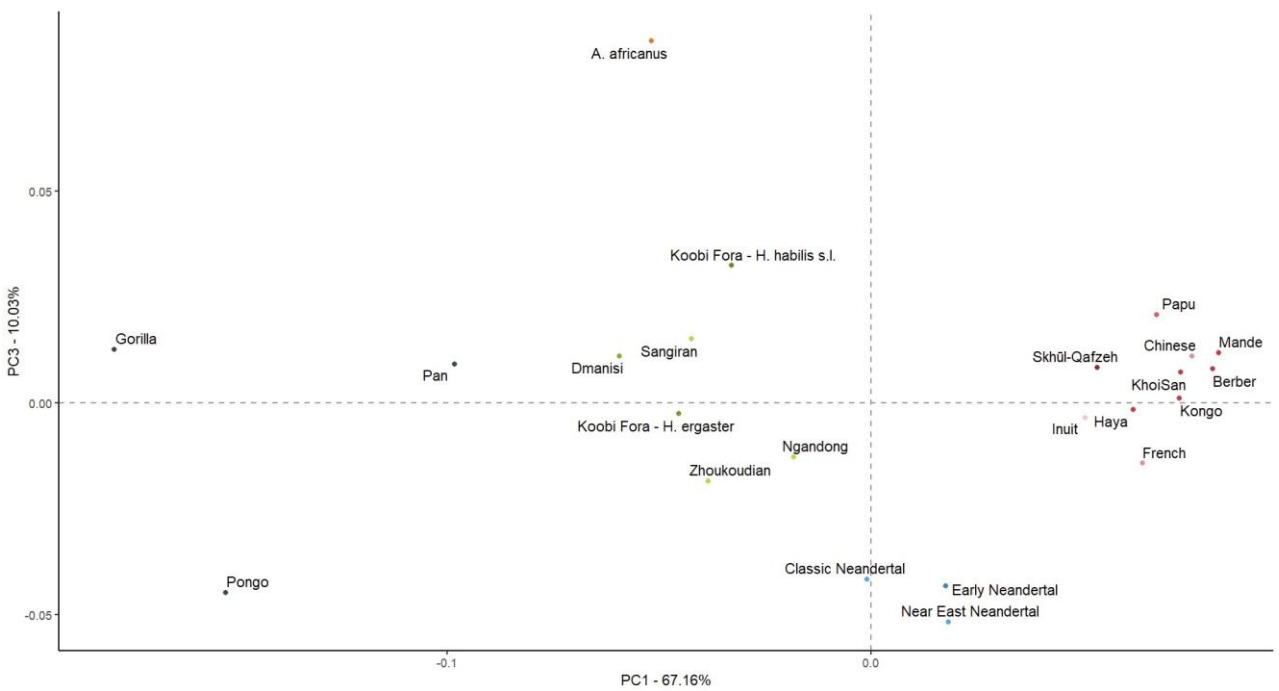
PC1 – PC3



3) PC1 – PC2



PC1 – PC3



Appendix 15: Allometric results for each PCs of matrix B.2 of Chapter III (22 PCs on 347 landmarks): 1) R report; and 2) Phylogenetic tree obtained from the residuals.

1) R report

Response PC1 :

Call:

```
lm(formula = PC1 ~ MeansCS)
```

Residuals:

Min	1Q	Median	3Q	Max
-0.08985	-0.04403	0.01765	0.04061	0.06966

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-4.790e-01	8.377e-02	-5.718	1.12e-05 ***
MeansCS	3.485e-04	6.048e-05	5.762	1.02e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.04978 on 21 degrees of freedom

Multiple R-squared: 0.6126, Adjusted R-squared: 0.5941

F-statistic: 33.2 on 1 and 21 DF, p-value: 1.016e-05

Response PC2 :

Call:

```
lm(formula = PC2 ~ MeansCS)
```

Residuals:

Min	1Q	Median	3Q	Max
-0.058652	-0.021779	0.009527	0.018788	0.053954

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	8.641e-02	5.030e-02	1.718	0.1005
MeansCS	-6.287e-05	3.632e-05	-1.731	0.0981 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.02989 on 21 degrees of freedom

Multiple R-squared: 0.1249, Adjusted R-squared: 0.08322

F-statistic: 2.997 on 1 and 21 DF, p-value: 0.09808

Response PC3 :

Call:

```
lm(formula = PC3 ~ MeansCS)
```

Residuals:

Min	1Q	Median	3Q	Max
-0.064373	-0.011364	0.003864	0.014588	0.067297

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	8.570e-02	4.628e-02	1.852	0.0782 .
MeansCS	-6.236e-05	3.342e-05	-1.866	0.0761 .

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
Residual standard error: 0.0275 on 21 degrees of freedom
Multiple R-squared: 0.1422, Adjusted R-squared: 0.1014
F-statistic: 3.482 on 1 and 21 DF, p-value: 0.07606

Response PC4 :

Call:

lm(formula = PC4 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.033696	-0.009779	-0.003517	0.009004	0.035077

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.390e-02	2.670e-02	-0.521	0.608
MeansCS	1.012e-05	1.928e-05	0.525	0.605

Residual standard error: 0.01586 on 21 degrees of freedom
Multiple R-squared: 0.01295, Adjusted R-squared: -0.03406
F-statistic: 0.2755 on 1 and 21 DF, p-value: 0.6052

Response PC5 :

Call:

lm(formula = PC5 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.040437	-0.005414	-0.000230	0.009182	0.022178

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.167e-03	2.434e-02	0.171	0.866
MeansCS	-3.032e-06	1.758e-05	-0.173	0.865

Residual standard error: 0.01446 on 21 degrees of freedom
Multiple R-squared: 0.001416, Adjusted R-squared: -0.04614
F-statistic: 0.02977 on 1 and 21 DF, p-value: 0.8647

Response PC6 :

Call:

lm(formula = PC6 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.037487	-0.004485	0.001619	0.003107	0.032776

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.151e-02	2.111e-02	-0.545	0.591
MeansCS	8.377e-06	1.525e-05	0.549	0.588

Residual standard error: 0.01255 on 21 degrees of freedom
Multiple R-squared: 0.01417, Adjusted R-squared: -0.03277
F-statistic: 0.3019 on 1 and 21 DF, p-value: 0.5885

Response PC7 :

Call:

lm(formula = PC7 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max

-0.0184066 -0.0081365 0.0006615 0.0070969 0.0229729

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) 1.100e-02 1.811e-02 0.607 0.550

MeansCS -8.000e-06 1.307e-05 -0.612 0.547

Residual standard error: 0.01076 on 21 degrees of freedom

Multiple R-squared: 0.01752, Adjusted R-squared: -0.02926

F-statistic: 0.3746 on 1 and 21 DF, p-value: 0.5471

Response PC8 :

Call:

lm(formula = PC8 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.022775 -0.003875 0.001602 0.004795 0.016826

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) -8.008e-03 1.543e-02 -0.519 0.609

MeansCS 5.827e-06 1.114e-05 0.523 0.606

Residual standard error: 0.00917 on 21 degrees of freedom

Multiple R-squared: 0.01285, Adjusted R-squared: -0.03415

F-statistic: 0.2735 on 1 and 21 DF, p-value: 0.6065

Response PC9 :

Call:

lm(formula = PC9 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.0168011 -0.0041253 -0.0005349 0.0023226 0.0198633

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) -4.782e-03 1.419e-02 -0.337 0.739

MeansCS 3.479e-06 1.024e-05 0.340 0.737

Residual standard error: 0.008429 on 21 degrees of freedom

Multiple R-squared: 0.005466, Adjusted R-squared: -0.04189

F-statistic: 0.1154 on 1 and 21 DF, p-value: 0.7374

Response PC10 :

Call:

lm(formula = PC10 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.013177 -0.002673 -0.001678 0.002880 0.013825

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) 4.475e-03 1.225e-02 0.365 0.719

MeansCS -3.256e-06 8.848e-06 -0.368 0.717

Residual standard error: 0.007282 on 21 degrees of freedom

Multiple R-squared: 0.006407, Adjusted R-squared: -0.04091

F-statistic: 0.1354 on 1 and 21 DF, p-value: 0.7166

Response PC11 :

Call:

lm(formula = PC11 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0159074	-0.0025930	0.0008072	0.0047318	0.0108955

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.144e-03	1.152e-02	0.099	0.922
MeansCS	-8.325e-07	8.320e-06	-0.100	0.921

Residual standard error: 0.006847 on 21 degrees of freedom
Multiple R-squared: 0.0004766, Adjusted R-squared: -0.04712
F-statistic: 0.01001 on 1 and 21 DF, p-value: 0.9212

Response PC12 :

Call:

lm(formula = PC12 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0109176	-0.0035226	0.0006714	0.0028839	0.0144476

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.837e-03	1.010e-02	-0.182	0.857
MeansCS	1.337e-06	7.291e-06	0.183	0.856

Residual standard error: 0.006001 on 21 degrees of freedom
Multiple R-squared: 0.001598, Adjusted R-squared: -0.04595
F-statistic: 0.03361 on 1 and 21 DF, p-value: 0.8563

Response PC13 :

Call:

lm(formula = PC13 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0074942	-0.0029567	-0.0004647	0.0024252	0.0139794

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	6.311e-04	8.204e-03	0.077	0.939
MeansCS	-4.592e-07	5.924e-06	-0.078	0.939

Residual standard error: 0.004875 on 21 degrees of freedom
Multiple R-squared: 0.0002861, Adjusted R-squared: -0.04732
F-statistic: 0.00601 on 1 and 21 DF, p-value: 0.9389

Response PC14 :

Call:

lm(formula = PC14 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0076272	-0.0018981	0.0002071	0.0015199	0.0129247

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-3.062e-03	6.854e-03	-0.447	0.660
MeansCS	2.228e-06	4.949e-06	0.450	0.657

Residual standard error: 0.004073 on 21 degrees of freedom
Multiple R-squared: 0.009559, Adjusted R-squared: -0.03761
F-statistic: 0.2027 on 1 and 21 DF, p-value: 0.6572

Response PC15 :

Call:

lm(formula = PC15 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0069105	-0.0023343	-0.0000538	0.0023167	0.0086493

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.269e-03	6.355e-03	-0.200	0.844
MeansCS	9.231e-07	4.588e-06	0.201	0.842

Residual standard error: 0.003776 on 21 degrees of freedom
Multiple R-squared: 0.001924, Adjusted R-squared: -0.0456
F-statistic: 0.04047 on 1 and 21 DF, p-value: 0.8425

Response PC16 :

Call:

lm(formula = PC16 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0106682	-0.0013896	-0.0002177	0.0018241	0.0061511

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-9.553e-04	5.940e-03	-0.161	0.874
MeansCS	6.951e-07	4.289e-06	0.162	0.873

Residual standard error: 0.00353 on 21 degrees of freedom
Multiple R-squared: 0.001249, Adjusted R-squared: -0.04631
F-statistic: 0.02627 on 1 and 21 DF, p-value: 0.8728

Response PC17 :

Call:

lm(formula = PC17 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0092017	-0.0013097	-0.0000276	0.0010886	0.0086310

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.638e-04	5.451e-03	0.085	0.933
MeansCS	-3.374e-07	3.936e-06	-0.086	0.932

Residual standard error: 0.003239 on 21 degrees of freedom
Multiple R-squared: 0.0003499, Adjusted R-squared: -0.04725
F-statistic: 0.00735 on 1 and 21 DF, p-value: 0.9325

Response PC18 :

Call:

lm(formula = PC18 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0059006	-0.0011604	-0.0001382	0.0005624	0.0075267

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) 6.727e-04 4.871e-03 0.138 0.891

MeansCS -4.895e-07 3.517e-06 -0.139 0.891

Residual standard error: 0.002894 on 21 degrees of freedom

Multiple R-squared: 0.0009215, Adjusted R-squared: -0.04665

F-statistic: 0.01937 on 1 and 21 DF, p-value: 0.8906

Response PC19 :

Call:

lm(formula = PC19 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.0053010 -0.0013280 -0.0003451 0.0013036 0.0056820

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) 2.418e-03 4.241e-03 0.570 0.575

MeansCS -1.759e-06 3.062e-06 -0.575 0.572

Residual standard error: 0.00252 on 21 degrees of freedom

Multiple R-squared: 0.01548, Adjusted R-squared: -0.0314

F-statistic: 0.3301 on 1 and 21 DF, p-value: 0.5717

Response PC20 :

Call:

lm(formula = PC20 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.0039687 -0.0007264 0.0000762 0.0008524 0.0036545

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) 7.294e-04 3.220e-03 0.227 0.823

MeansCS -5.308e-07 2.325e-06 -0.228 0.822

Residual standard error: 0.001914 on 21 degrees of freedom

Multiple R-squared: 0.002475, Adjusted R-squared: -0.04503

F-statistic: 0.0521 on 1 and 21 DF, p-value: 0.8217

Response PC21 :

Call:

lm(formula = PC21 ~ MeansCS)

Residuals:

Min 1Q Median 3Q Max

-0.0043138 -0.0003982 -0.0000908 0.0006558 0.0039064

Coefficients:

Estimate Std. Error t value Pr(>|t|)

(Intercept) -3.567e-04 2.817e-03 -0.127 0.9

MeansCS 2.595e-07 2.034e-06 0.128 0.9

Residual standard error: 0.001674 on 21 degrees of freedom

Multiple R-squared: 0.0007745, Adjusted R-squared: -0.04681

F-statistic: 0.01628 on 1 and 21 DF, p-value: 0.8997

Response PC22 :

Call:

lm(formula = PC22 ~ MeansCS)

Residuals:

Min	1Q	Median	3Q	Max
-0.0041048	-0.0005549	0.0001822	0.0003982	0.0039129

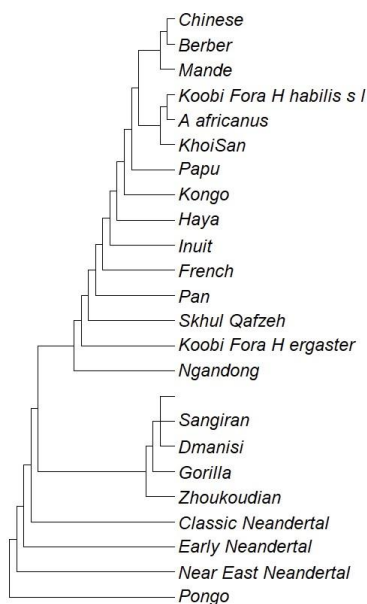
Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	-1.394e-03	2.533e-03	-0.550	0.588
MeansCS	1.014e-06	1.829e-06	0.554	0.585

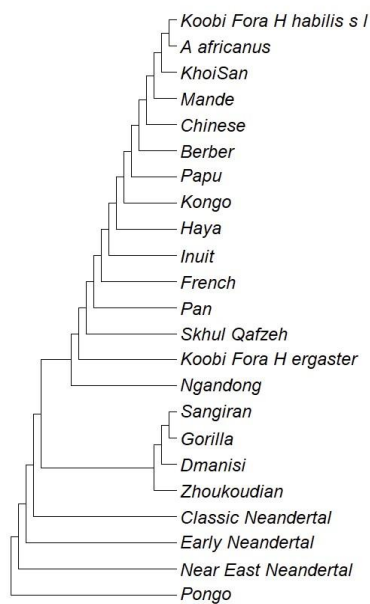
Residual standard error: 0.001505 on 21 degrees of freedom
Multiple R-squared: 0.01442, Adjusted R-squared: -0.03251
F-statistic: 0.3073 on 1 and 21 DF, p-value: 0.5852

2) Phylogenetic tree from the residuals

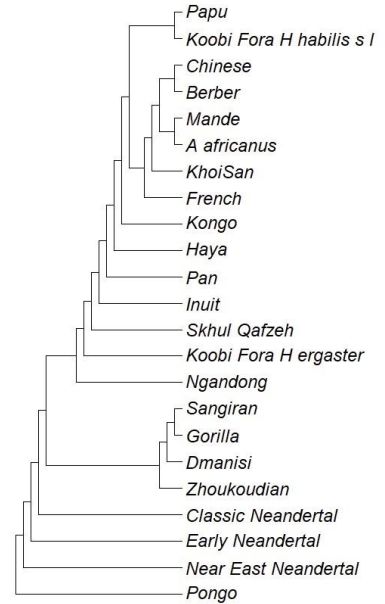
CI



RI



RC



Appendix 16: PC coordinates from each node for Matrix B.1 (Chapter III), depending of the weighting.

CI – weighting

	1	2	3	4	5	6	7
Node A	-0.174516864271748	0.0989085494367306	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0136726222030088	0.0067633522662689
Node B	-0.174516864271748	0.0989085494367306	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0136726222030088	0.0067633522662689
Node C	-0.121178302372032	0.022924190853292	-0.0331211352294343	-0.0114325885220126	0.02509096417797	0.0276439202177716	0.0067633522662689
Node D	-0.0480825572673744	-0.0244974969793681	0.036169050629189	-0.00620984343451703	0.00724239598543619	0.0276439202177716	0.0067633522662689
Node E	-0.0480825572673744	-0.0406872925788893	0.036169050629189	-0.00620984343451703	0.00724239598543619	-0.00320539239277728	0.0067633522662689
Node F	-0.0480825572673744	-0.0634365095370626	0.036169050629189	-0.00620984343451703	0.00724239598543619	-0.00792325350760947	0.0067633522662689
Node G	-0.0141546126391106	-0.0244974969793681	-0.0035430419611906	0.0179509971011651	0.00503808271709794	0.0276439202177716	0.00398999723453208
Node H	-0.00512182664621186	-0.0201362316645337	-0.0311207267198323	0.0179509971011651	0.00244889704212703	0.0276439202177716	0.00354104053340087
Node I	0.0217949163095632	0.000831226704532284	-0.0311207267198323	0.0179509971011651	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node J	0.0227436649393109	0.000831226704532284	-0.0331192550027417	0.00272448653542945	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node K	0.0642050909177048	0.000831226704532284	-0.00191713594270837	0.00272448653542945	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node L	0.0632977840013744	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node M	0.0700170567084868	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node N	0.0743502984147248	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node O	0.0813128329874502	0.0114839534791429	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node P	0.0813128329874502	0.0169457356042031	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node Q	0.0887684657899293	0.0169457356042031	0.00835981381326256	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.0018366159425085
Node R	0.0941881866846579	0.0169457356042031	0.00835981381326256	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.00221474581605818

	8	9	10	11	12	13	14
Node A	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318
Node B	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318
Node C	0.0041590151212727	-0.000586353672311191	0.000110793834503298	0.004278952356076	-0.00437331501267835	-0.00174900723495242	0.00351283737931318
Node D	0.0041590151212727	0.00267909470719374	0.000110793834503298	0.004278952356076	0.00550538167556702	0.00114468208623286	0.00351283737931318
Node E	0.0041590151212727	0.00118306058217854	0.000110793834503298	0.004278952356076	-0.00114962609825753	0.00114468208623286	0.00351283737931318
Node F	0.0041590151212727	-0.00219085479379721	0.000110793834503298	0.004278952356076	-0.00114962609825753	0.00114468208623286	0.00351283737931318
Node G	0.0041590151212727	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318
Node H	-0.00474843290656679	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318
Node I	-0.00474843290656679	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318
Node J	-0.00474843290656679	-0.00595933703682405	-0.00161283578722937	0.004278952356076	-0.00351297730446731	0.00114468208623286	0.00351283737931318
Node K	-0.00474843290656679	-0.00370002403423086	0.00225715866238474	-0.00280594304202353	-0.00351297730446731	0.00114468208623286	0.00351283737931318
Node L	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00351297730446731	0.00114468208623286	0.00351283737931318
Node M	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318
Node N	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318
Node O	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318
Node P	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00125088387175865	0.00351283737931318
Node Q	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00125088387175865	0.00351283737931318
Node R	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.000414973431736243	0.00351283737931318

	15	16	17	18	19	20	21
Node A	-0.00218580908153498	0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node B	-0.00218580908153498	0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node C	-0.00218580908153498	0.00224273524058383	0.00121210878456246	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node D	-0.00218580908153498	0.00224273524058383	0.00121210878456246	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node E	-0.00218580908153498	0.000593428078483171	0.00121210878456246	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node F	-0.00218580908153498	-0.00197184606453504	-0.00224891730659493	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node G	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node H	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node I	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node J	-0.00218580908153498	0.00224273524058383	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node K	-0.00218580908153498	0.00115265264264153	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node L	-0.00218580908153498	0.00115265264264153	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	-0.0000518582138013812
Node M	-0.00218580908153498	0.00115265264264153	0.00244502904576116	-0.00399601421894147	0.000347475848462508	-0.000601581331196144	-0.0000518582138013812
Node N	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	-0.00399601421894147	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node O	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	0.00310365339717755	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node P	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00310365339717755	-0.00145940989980353	-0.000601581331196144	-0.0000518582138013812
Node Q	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00310365339717755	-0.00145940989980353	-0.000601581331196144	-0.0000518582138013812
Node R	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00310365339717755	-0.00145940989980353	-0.000601581331196144	-0.0000518582138013812

Node A -0.000189625884109645
Node B -0.000189625884109645
Node C 0.000465249392963329
Node D 0.000465249392963329
Node E 0.000465249392963329
Node F -0.000284119604435418
Node G 0.000465249392963329
Node H 0.000465249392963329
Node I 0.000465249392963329
Node J -0.000527270909813637
Node K -0.000527270909813637
Node L -0.000527270909813637
Node M -0.000527270909813637
Node N -0.000527270909813637
Node O -0.000527270909813637
Node P -0.000527270909813637
Node Q -0.000527270909813637
Node R 0.000722538764504677

RI – weighting

	1	2	3	4	5	6	7
Node A	-0.174516864271748	0.0989085494367306	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0136726222030088	0.0067633522662689
Node B	-0.174516864271748	0.0989085494367306	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0136726222030088	0.0067633522662689
Node C	-0.121178302372032	0.022924190853292	-0.0331211352294343	-0.0114325885220126	0.02509096417797	0.0276439202177716	0.0067633522662689
Node D	-0.0480825572673744	-0.0244974969793681	0.036169050629189	-0.00620984343451703	0.00724239598543619	0.0276439202177716	0.0067633522662689
Node E	-0.0480825572673744	-0.0406872925788893	0.036169050629189	-0.00620984343451703	0.00724239598543619	-0.00320539239277728	0.0067633522662689
Node F	-0.0480825572673744	-0.0634365095370626	0.036169050629189	-0.00620984343451703	0.00724239598543619	-0.00792325350760947	0.0067633522662689
Node G	-0.0141546126391106	-0.0244974969793681	-0.0035430419611906	0.0179509971011651	0.00503808271709794	0.0276439202177716	0.00398999723453208
Node H	-0.00512182664621186	-0.0201362316645337	-0.0311207267198323	0.0179509971011651	0.00244889704212703	0.0276439202177716	0.00354104053340087
Node I	0.0217949163095632	0.000831226704532284	-0.0311207267198323	0.0179509971011651	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node J	0.0227436649393109	0.000831226704532284	-0.0331192550027417	0.00272448653542945	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node K	0.0642050909177048	0.000831226704532284	-0.00191713594270837	0.00272448653542945	0.00244889704212703	0.00905971775816994	-0.000204737356074958
Node L	0.0642050909177048	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node M	0.0700170567084868	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node N	0.0743502984147248	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node O	0.0799704261447527	0.0114839534791429	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node P	0.0831224091952336	0.0114839534791429	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node Q	0.0831224091952336	0.0169457356042031	0.00308797791327109	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node R	0.0887684657899008	0.0169457356042031	0.00835981381326256	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node S	0.0941881866846579	0.0169457356042031	0.00835981381326256	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.00221474581605818

		8	9	10	11	12	13	14
Node A	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318	
Node B	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318	
Node C	0.0041590151212727	-0.000586353672311191	0.000110793834503298	0.004278952356076	-0.00437331501267835	-0.00174900723495242	0.00351283737931318	
Node D	0.0041590151212727	0.00267909470719374	0.000110793834503298	0.004278952356076	0.00550538167556702	0.00114468208623286	0.00351283737931318	
Node E	0.0041590151212727	0.00118306058217854	0.000110793834503298	0.004278952356076	-0.00114962609825753	0.00114468208623286	0.00351283737931318	
Node F	0.0041590151212727	-0.00219085479379721	0.000110793834503298	0.004278952356076	-0.00114962609825753	0.00114468208623286	0.00351283737931318	
Node G	0.0041590151212727	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318	
Node H	-0.00474843290656679	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318	
Node I	-0.00474843290656679	-0.00595933703682405	0.000110793834503298	0.004278952356076	0.00630921450357391	0.00114468208623286	0.00351283737931318	
Node J	-0.00474843290656679	-0.00595933703682405	-0.00161283578722937	0.004278952356076	-0.00351297730446731	0.00114468208623286	0.00351283737931318	
Node K	-0.00474843290656679	-0.00370002403423086	0.00225715866238474	-0.00280594304202353	-0.00351297730446731	0.00114468208623286	0.00351283737931318	
Node L	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00351297730446731	0.00114468208623286	0.00351283737931318	
Node M	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318	
Node N	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318	
Node O	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318	
Node P	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	0.00114468208623286	0.00351283737931318	
Node Q	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00114468208623286	0.00351283737931318	
Node R	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00114468208623286	0.00351283737931318	
Node S	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.000414973431736243	0.00351283737931318	

	15	16	17	18	19	20	21
Node A	-0.00218580908153498	0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node B	-0.00218580908153498	0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node C	-0.00218580908153498	0.00224273524058383	0.00121210878456246	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node D	-0.00218580908153498	0.00224273524058383	0.00121210878456246	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node E	-0.00218580908153498	0.000593428078483171	0.00121210878456246	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node F	-0.00218580908153498	-0.00197184606453504	-0.00224891730659493	0.000296142427270496	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node G	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node H	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node I	-0.00218580908153498	0.00224273524058383	0.00121210878456246	-0.0000210856463631615	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node J	-0.00218580908153498	0.00224273524058383	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node K	-0.00218580908153498	0.00115265264264153	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	0.00098641616935069
Node L	-0.00218580908153498	0.00115265264264153	-7.38196344407527E-06	-0.0018437706292449	-0.000735757114442848	-0.000601581331196144	-0.0000518582138013812
Node M	-0.00218580908153498	0.00115265264264153	0.00244502904576116	-0.0018437706292449	0.000347475848462508	-0.000601581331196144	-0.0000518582138013812
Node N	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	-0.0018437706292449	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node O	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	0.0027052843780524	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node P	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	0.0027052843780524	0.00310233146080563	-0.000601581331196144	0.00126238235485587
Node Q	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.0027052843780524	-0.00145940989980353	-0.000601581331196144	0.00126238235485587
Node R	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.0027052843780524	-0.00145940989980353	-0.000601581331196144	0.00126238235485587
Node S	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.0027052843780524	-0.00145940989980353	-0.000601581331196144	0.00126238235485587

Node A -0.000189625884109645
Node B -0.000189625884109645
Node C 0.000465249392963329
Node D 0.000465249392963329
Node E 0.000465249392963329
Node F -0.000284119604435418
Node G 0.000465249392963329
Node H 0.000465249392963329
Node I 0.000465249392963329
Node J -0.000527270909813637
Node K -0.000527270909813637
Node L -0.000527270909813637
Node M -0.000527270909813637
Node N -0.000527270909813637
Node O -0.000527270909813637
Node P -0.000527270909813637
Node Q -0.000527270909810085
Node R -0.000527270909810085
Node S 0.000722538764504677

RC – weighting

	1	2	3	4	5	6	7
Node A	-0.174516864271748	0.0989085494367306	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0136726222030088	0.0067633522662689
Node B	-0.174516864271748	0.022924190853292	-0.0331211352294343	-0.0114325885220126	0.02509096417797	-0.0102692122649994	0.0067633522662689
Node C	-0.121178302372032	0.022924190853292	0.0173487427456216	-0.0114325885220126	0.02509096417797	-0.0000866478530205939	0.0067633522662689
Node D	-0.0538306251942302	-0.00943211394468513	0.0173487427456216	-0.0114325885220126	0.02509096417797	-0.0000866478530205939	0.0067633522662689
Node E	-0.0538306251942302	-0.0406872925788893	0.00161600347214019	-0.0114325885220126	0.02509096417797	-0.00320539239277728	0.0067633522662689
Node F	-0.0538306251942302	-0.0634365095370626	0.00161600347214019	-0.0114325885220126	0.02509096417797	-0.00729919506911969	0.0067633522662689
Node G	-0.0459890301159085	-0.00943211394468513	0.0173487427456216	-0.00620984343451703	0.02509096417797	-0.0000866478530205939	0.0067633522662689
Node H	-0.0449552356809786	-0.0244311458125779	-0.0173318843405106	-0.00620984343451703	0.00671946312742833	-0.0000866478530205939	0.00398999723453208
Node I	-0.0141546126391052	-0.0244311458125779	-0.0173318843405106	0.0179509971011651	0.00503808271709794	-0.0000866478530205939	0.00398999723453208
Node J	-0.00512182664621186	-0.0201362316645337	-0.0173318843405106	0.0179509971011651	0.00244889704212703	0.00928949661471989	0.00398999723453208
Node K	0.0217949163095632	0.000831226704532284	-0.0331192550027417	0.0179509971011651	0.00244889704212703	0.00928949661471989	-0.000204737356074958
Node L	0.0227436649393109	0.000831226704532284	-0.0331192550027417	0.00272448653542945	0.00244889704212703	0.00928949661470035	-0.000204737356074958
Node M	0.0632977840013744	0.000831226704532284	-0.00191713594270837	0.00272448653542945	0.00244889704212703	0.00928949661471989	-0.000204737356074958
Node N	0.0632977840013744	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node O	0.0700170567084868	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node P	0.0743502984147248	0.0114839534791429	-0.00191713594270837	0.00272448653542945	0.00244889704212703	-0.00544986393195224	-0.000204737356074958
Node Q	0.0799704261447527	0.0114839534791429	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node R	0.0831224091952336	0.0114839534791429	0.00245293677960134	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node S	0.0831224091952336	0.0169457356042031	0.00308797791327109	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.000204737356074958
Node T	0.0887684657899293	0.0169457356042031	0.00829848054391746	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.0018366159425085
Node U	0.0941881866846579	0.0169457356042031	0.00829848054391746	0.00272448653542945	0.00244889704212703	-0.00306363221575801	-0.00221474581605818

		8	9	10	11	12	13	14
Node A	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318	
Node B	0.0041590151212727	-0.000586353672311191	0.000110793834503298	-0.0017002995476485	-0.00437331501267835	-0.00174900723495242	0.00351283737931318	
Node C	0.0041590151212727	-0.000586353672311191	-0.00312821452331313	-0.0017002995476485	0.00197721758451763	-0.00174900723495242	0.00351283737931318	
Node D	0.0041590151212727	0.00267909470719374	-0.00312821452331313	-0.0017002995476485	0.00197721758449987	-0.00174900723495242	0.00351283737931318	
Node E	0.0041590151212727	0.00267909470719374	-0.00312821452331313	-0.0017002995476485	0.00197721758451763	-0.00174900723495242	0.00351283737931318	
Node F	0.0041590151212727	-0.00219085479379721	-0.00312821452331313	-0.0017002995476485	0.00197721758451763	-0.00174900723495242	0.00351283737931318	
Node G	0.0041590151212727	0.00267909470719374	0.00105592871391202	-0.0017002995476485	0.00604415364003152	-0.00174900723495242	0.00351283737931318	
Node H	0.0041590151212727	0.00267909470719374	0.00105592871391202	-0.0017002995476485	0.00604415364003152	-0.00174900723495242	0.00351283737931318	
Node I	0.0041590151212727	-0.00516852712836524	0.00105592871391202	-0.0017002995476485	0.00604415364003152	-0.00174900723495242	0.00351283737931318	
Node J	-0.00474843290656679	-0.00516852712836524	-0.00234341666063642	-0.0017002995476485	0.00604415364003152	-0.00174900723495242	0.00351283737931318	
Node K	-0.00474843290656679	-0.00516852712836524	-0.00234341666063642	-0.0017002995476485	0.00693029679323764	-0.00174900723495242	0.00351283737931318	
Node L	-0.00474843290656679	-0.00516852712836524	-0.00161283578722937	-0.0017002995476485	-0.00440613999088768	-0.00174900723495242	0.00351283737931318	
Node M	-0.00474843290656679	-0.00370002403423086	0.00225715866238474	-0.0017002995476485	-0.00440613999088768	-0.00174900723495242	0.00351283737931318	
Node N	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00377441497483844	-0.00174900723495242	0.00351283737931318	
Node O	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	-0.00174900723495064	0.00351283737931318	
Node P	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	-0.00174900723495064	0.00351283737931318	
Node Q	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	-0.00174900723495064	0.00351283737931318	
Node R	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	-0.00199304025886171	-0.00174900723495064	0.00351283737931318	
Node S	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00125088387175865	0.00351283737931318	
Node T	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.00125088387175865	0.00351283737931318	
Node U	-0.00474843290656679	-0.000360566812434016	0.00225715866238474	0.0013433020336997	0.0016547074257538	0.000414973431736243	0.00351283737931318	

	15	16	17	18	19	20	21
Node A	-0.00218580908153498	-0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node B	-0.00218580908153498	-0.000501823388836087	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node C	-0.00218580908153498	0.00131491377519133	-0.000819248404487993	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node D	-0.00218580908153498	0.00131491377519133	-0.000121869835197685	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node E	-0.00218580908153498	0.000593428078483171	-0.000121869835197685	-0.000121869835197685	-0.000121869835197685	-0.000121869835197685	-0.000121869835197685
Node F	-0.00218580908153498	-0.00105637752192322	-0.00224891730659493	-0.000121869835197685	-0.000121869835197685	-0.000121869835197685	-0.000121869835197685
Node G	-0.00218580908153498	0.00131491377519133	-0.000121869835197685	0.00159419998029087	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node H	-0.00218580908153498	0.00131491377519133	0.000375636923443778	0.000137528390453667	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node I	-0.00218580908153498	0.00131491377519133	0.000375636923443778	0.000137528390453667	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node J	-0.00218580908153498	0.00131491377519133	0.0000747806778740312	0.000137528390453667	0.000163847480601831	-0.000601581331196144	-0.00018028148507554
Node K	-0.00218580908153498	0.00131491377519133	0.0000747806778740312	0.000137528390453667	0.000163847480601831	-0.000601581331196144	0.00098641616935069
Node L	-0.00218580908153498	0.00131491377519133	-7.38196344407527E-06	-0.0018437706292449	0.000163847480601831	-0.000601581331196144	0.00098641616935069
Node M	-0.00218580908153498	0.00115265264264153	-7.38196344407527E-06	-0.0018437706292449	0.000163847480601831	-0.000601581331196144	0.00098641616935069
Node N	-0.00218580908153498	0.00115265264264153	-0.00158266840598209	-0.00399601421894147	-0.000264539480813397	-0.000601581331196144	-0.0000518582138013812
Node O	-0.00218580908153498	0.00115265264264153	0.00244502904576116	-0.00399601421894147	0.000347475848462508	-0.000601581331196144	-0.0000518582138013812
Node P	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	-0.00399601421894147	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node Q	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	0.00302907168014244	0.00310233146080563	-0.000601581331196144	-0.0000518582138013812
Node R	-0.00218580908153498	-0.00282577752839153	0.00244502904576116	0.00302907168014244	0.00310233146080563	-0.000601581331196144	0.00126238235485587
Node S	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00302907168014244	-0.00145940989980353	-0.000601581331196144	0.00126238235485587
Node T	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00302907168014244	-0.00145940989980353	-0.000601581331196144	0.00126238235485587
Node U	-0.00218580908153498	-0.00320622885354993	0.00244502904576116	0.00302907168014244	-0.00145940989980353	-0.000601581331196144	0.00126238235485587

Node A	-0.000189625884109645
Node B	-0.000189625884109645
Node C	0.000326883325618255
Node D	0.000326883325618255
Node E	0.000326883325618255
Node F	-0.000284119604435418
Node G	0.000326883325618255
Node H	0.000326883325618255
Node I	0.000326883325618255
Node J	0.000326883325618255
Node K	0.000326883325618255
Node L	-0.000527270909813637
Node M	-0.000527270909813637
Node N	-0.000527270909813637
Node O	-0.000527270909813637
Node P	-0.000527270909813637
Node Q	-0.000527270909813637
Node R	-0.000527270909813637
Node S	-0.000527270909813637
Node T	-0.000527270909813637
Node U	0.000722538764504677

Appendix 17: PC coordinates from each node for Matrix B.2 (Chapter III), depending of the weighting.

CI- weighting

	1	2	3	4	5	6	7
Node A	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node B	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node C	-0.105385542583033	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node D	-0.0501419578843532	0.017065210727333	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node E	-0.0395551746428389	-0.0327737429548538	0.00457947349728016	-0.00861965504441109	-0.00176130505066041	0.000745450645032619	0.0112887292702322
Node F	-0.0395551746428389	-0.0533468090604892	0.00457947349728016	-0.00444731058881409	-0.00122363369648326	-0.00570775221406272	0.00680410265749387
Node G	-0.0154789856074107	-0.0327737429548538	-0.0106305140859888	-0.00861965504441109	0.0112365505754468	0.000745450645032619	-0.00812829831718354
Node H	-0.00154501439188159	-0.0207073943832246	-0.040568665167438	-0.00861965504441109	0.0112365505754468	0.000745450645032619	-0.00812829831718354
Node I	0.019367026217644	-0.00562234300962494	-0.040568665167438	-0.00861965504441109	0.0112365505754468	0.000745450645032619	-0.00812829831718354
Node J	0.0563882226648431	-0.0000302307238975175	-0.00270527967260037	0.00217924012242143	0.00887921830705984	0.000745450645032619	-0.00729283716497875
Node K	0.062521134315654	0.0105046244500588	-0.00270527967260037	0.00217924012242143	0.00190340304105341	0.000745450645032619	-0.000431411137173043
Node L	0.062521134315654	0.0112029258690942	-0.00317032917600635	-0.00588891066125008	0.00190340304105341	0.000745450645032619	0.00909857010248771
Node M	0.0753707297237316	0.0105046244500588	0.00629973325999167	0.00217924012242143	-0.000524557650729562	0.000745450645032619	-0.000431411137173043
Node N	0.0732930190642911	0.0160893439780239	0.00629973325999167	0.00217924012242143	-0.000524557650729562	0.000745450645032619	-0.000431411137173043
Node O	0.077097826440454	0.0160893439780239	0.00629973325999167	0.00217924012242143	-0.00424025718531773	0.00228476034377501	-0.000431411137173043
Node P	0.0823869732768223	0.0160893439780239	0.00629973325999167	0.00217924012242143	-0.00424025718531773	0.00369450622128653	-0.000431411137173043

	8	9	10	11	12	13	14
Node A	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	-0.00421903109599597	0.00238385896382276
Node B	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	0.00261939604612849	0.00238385896382276
Node C	0.00447255350560916	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00407920558587804	0.00236889823946385	0.00238385896382276
Node D	0.00447255350560916	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00407920558587804	0.00236889823946385	0.00238385896382276
Node E	0.00447255350560916	-0.00477784021121685	-0.00148429058617339	0.00219572673016977	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node F	0.00447255350560916	-0.00477784021121685	-0.00723430247153445	0.00219572673016977	0.00093813519073116	-0.000907907483281178	0.00238385896382276
Node G	0.00447255350560916	-0.000297336001548132	-0.00148429058617339	0.00219572673016977	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node H	0.00257490735676136	-0.000297336001548132	-0.00148429058617339	0.00219572673016977	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node I	0.00257490735676136	-0.000297336001548132	-0.00148429058617339	0.00455948515630666	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node J	0.00257490735676136	-0.000297336001548132	-0.00148429058617339	0.00200434725532439	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node K	0.00257490735676136	-0.000297336001548132	-0.00148429058617339	-0.00157992573595322	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node L	-0.00745093351962289	-0.000297336001548132	-0.00148429058617339	-0.00693636599236314	-0.00407920558587804	0.00458699154088649	0.00238385896382276
Node M	0.00257490735676136	-0.000297336001548132	-0.00223443200205509	-0.00157992573595322	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node N	0.00257490735676136	-0.00116105742195316	-0.00223443200205509	0.00219207122099441	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node O	0.00257490735676136	0.00120118398823621	-0.00223443200205509	0.00219207122099441	-0.00407920558587804	-0.000907907483281178	0.00238385896382276
Node P	0.00257490735676136	0.00120118398823621	-0.00223443200205509	0.00219207122099441	-0.00407920558587804	-0.000907907483281178	0.00238385896382276

	15	16	17	18	19	20	21
Node A	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node B	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node C	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node D	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node E	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.0000635314825618849	0.000286102478293415	0.000940956284868122	-0.000296826162129449
Node F	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.00010591004577698	-0.0019087642578306	0.000940956284868122	-0.000296826162129449
Node G	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.0000635314825618849	0.000286102478293415	0.000940956284868122	-0.000296826162129449
Node H	-0.00181637401503032	-0.0000997208760420421	0.000685057732788152	-0.0000635314825618849	0.000286102478293415	-0.00012102903635558	-0.000296826162129449
Node I	0.000581399265133342	-0.0000997208760420421	-0.000180556765119633	-0.000556741699783814	0.000286102478293415	-0.00012102903635558	0.000659846635535644
Node J	0.000581399265133342	-0.0000997208760420421	-0.000180556765119633	0.000212574685333422	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node K	0.000581399265133342	-0.0000997208760420421	-0.000180556765119633	0.000212574685333422	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node L	0.000581399265133342	-0.0000997208760420421	-0.000180556765119633	0.000212574685333422	0.000286102478293415	0.0000250168696691588	-0.000509570423490757
Node M	0.000581399265133342	-0.0000997208760420421	-0.000180556765119633	0.000212574685333422	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node N	-0.00293993588717001	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node O	-0.00293993588717001	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node P	-0.00293993588717001	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.000252099020746854

Node A -0.0000177015117195367
Node B -0.0000177015117195367
Node C -0.0000177015117195367
Node D -0.0000177015117195367
Node E 0.0000354104090654062
Node F 0.0000354104090654062
Node G 0.0000354104090654062
Node H 0.0000354104090654062
Node I 0.0000354104090654062
Node J 0.0000354104090654062
Node K 0.0000354104090654062
Node L 0.0000354104090654062
Node M 0.0000354104090654062
Node N 0.0000354104090654062
Node O -0.00192872862819549
Node P -0.00192872862819549

RI – weighting

	1	2	3	4	5	6	7
Node A	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node B	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node C	-0.105385542583033	0.0750243799531045	0.0100695427616095	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	-0.00854646875165521
Node D	-0.0501419578843532	0.017065210727333	0.0100695427616095	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	-0.00854646875165521
Node E	-0.0416567050159866	-0.0327737429548538	0.0100695427616095	-0.00861965504441109	-0.00176130505066041	0.000745450645032619	0.00656402473565798
Node F	-0.0416567050159866	-0.0533468090604892	0.0109792532408441	-0.00444731058881409	-0.00176130505066041	-0.00570775221406272	0.00656402473565798
Node G	-0.0388260722827276	-0.0327737429548538	-0.0159590811686208	-0.00861965504441109	-0.00176130505066041	0.00273630255134982	-0.00812829831718354
Node H	-0.0154789856074107	-0.0327737429548538	-0.0159590811686208	-0.00861965504441109	0.0112365505754468	0.00273630255134982	-0.00812829831718354
Node I	-0.00154501439188159	-0.0207073943832246	-0.040568665167438	-0.00861965504441109	0.0112365505754468	0.00273630255134982	-0.00812829831718354
Node J	0.0186801367121614	-0.00820396324609085	-0.040568665167438	-0.00861965504441109	0.0112365505754468	0.00273630255134982	-0.00812829831718354
Node K	0.0200539157231283	-0.00304072277315903	-0.040568665167438	-0.00861965504441109	0.00838935268812158	0.00273630255134982	-0.00812829831718354
Node L	0.0563882226648431	-0.0000302307238975175	-0.00270527967260037	0.00217924012242143	0.00838935268812158	0.00273630255134982	-0.00729283716497875
Node M	0.062521134315654	0.0105046244500588	-0.00270527967260037	0.00217924012242143	0.00190340304105341	0.00273630255134982	-0.000431411137173043
Node N	0.062521134315654	0.0105046244500588	-0.00317032917600635	-0.00588891066125008	0.00190340304105341	0.00273630255134982	0.00909857010248771
Node O	0.0732930190642911	0.0155953978225121	0.00629973325999167	0.00217924012242143	-0.000524557650729562	0.00273630255134982	-0.000431411137173043
Node P	0.077097826440454	0.0155953978225121	0.00934375136571219	0.00217924012242143	-0.00348557373783187	0.00273630255134982	-0.000431411137173043
Node Q	0.0823869732768223	0.0155953978225121	0.00934375136571219	0.00217924012242143	-0.00348557373783187	0.00369450622128653	-0.000431411137173043

	8	9	10	11	12	13	14
Node A	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	-0.00421903109599597	0.00238385896382276
Node B	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	0.00261939604612849	0.00238385896382276
Node C	0.00447255350560916	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00304437509137223	0.00261939604612849	0.00238385896382276
Node D	0.000270331375885391	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00304437509137223	0.00261939604612849	0.00238385896382276
Node E	0.000270331375885391	-0.00477784021121685	-0.00159349965468003	0.00219572673016977	-0.00304437509137223	-0.000907907483281178	0.00238385896382276
Node F	0.000270331375885391	-0.00477784021121685	-0.00723430247153445	0.00219572673016977	0.00093813519073116	-0.000907907483281178	0.00238385896382276
Node G	0.000270331375885391	-0.00477784021121685	0.00342910544495112	0.00219572673016977	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node H	0.000270331375885391	-0.000297336001548132	0.00342910544495112	0.00219572673016977	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node I	0.00572323010355902	-0.000297336001548132	0.00342910544495112	0.00219572673016977	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node J	0.00572323010355902	-0.000297336001548132	0.00342910544495112	0.00455948515630666	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node K	0.00572323010355902	-0.000297336001548132	0.00342910544495112	0.00455948515630666	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node L	0.00257490735676136	-0.000297336001548132	0.00342910544495112	0.00200434725532439	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node M	0.00257490735676136	-0.000297336001548132	0.00236424477450115	-0.0000351396915316826	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node N	-0.00745093351962289	-0.000297336001548132	0.00236424477450115	-0.00693636599236314	-0.00482150116400604	0.00458699154088649	0.00238385896382276
Node O	0.00257490735676136	-0.000297336001548132	-0.00227179470101113	-0.0000351396915316826	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node P	0.00257490735676136	0.000813005330877914	-0.00227179470101113	-0.0000351396915316826	-0.00482150116400604	-0.000907907483281178	0.00238385896382276
Node Q	0.00257490735676136	0.000813005330877914	-0.00227179470101113	-0.0000351396915316826	-0.00482150116400604	-0.000907907483281178	0.00238385896382276

	15	16	17	18	19	20	21
Node A	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node B	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node C	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node D	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node E	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	0.000940956284868122	-0.000296826162129449
Node F	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.0019087642578306	0.000940956284868122	-0.000296826162129449
Node G	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	0.000286102478293415	0.0000191695296063443	-0.000296826162129449
Node H	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	0.000286102478293415	0.0000191695296063443	-0.000296826162129449
Node I	-0.00181637401503032	-0.0000997208760420421	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.00012102903635558	-0.000296826162129449
Node J	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.00012102903635558	0.00072708811573996
Node K	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.00012102903635558	0.00072708811573996
Node L	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node M	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node N	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	0.0000250168696691588	-0.000509570423490757
Node O	-0.0017544835561587	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node P	-0.0017544835561587	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.00111359617890372
Node Q	-0.0017544835561587	-0.0000997208760420421	-0.000180556765119633	-0.00146331949749268	0.000286102478293415	-0.00012102903635558	0.000252099020746854

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Node A -0.0000177015117195367
Node B -0.0000177015117195367
Node C -0.0000177015117195367
Node D -0.0000177015117195367
Node E 0.0000354104090654062
Node F 0.0000354104090654062
Node G 0.0000354104090654062
Node H 0.0000354104090654062
Node I 0.0000354104090654062
Node J 0.0000354104090654062
Node K 0.0000354104090654062
Node L 0.0000354104090654062
Node M 0.0000354104090654062
Node N 0.0000354104090654062
Node O 0.0000354104090654062
Node P -0.00103069246656595
Node Q -0.00103069246656595

RC – weighting

	1	2	3	4	5	6	7
Node A	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node B	-0.164892766785073	0.0750243799531045	-0.0434762685021468	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node C	-0.105385542583033	0.0750243799531045	0.00457947349728016	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node D	-0.0501419578843532	0.017065210727333	0.00457947349728016	-0.0143130959286157	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node E	-0.0278816313051813	-0.0267405686690392	0.00457947349728016	-0.00861965504441109	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node F	-0.0278816313051813	-0.0369144098247745	0.00457947349728016	-0.00148467847445843	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node G	-0.0278816313051813	-0.0533468090604892	0.00457947349728016	-0.00148467847445843	-0.0211585161950385	-0.00570775221406272	0.01451464982188
Node H	-0.0154789856074107	-0.0267405686690392	-0.0106305140859888	-0.00861965504441109	-0.0211585161950385	0.000745450645032619	0.01451464982188
Node I	-0.00154501439188159	-0.0207073943832246	-0.040568665167438	-0.00861965504441109	-0.0211585161950385	-0.000298249578442267	0.01451464982188
Node J	0.0186801367121614	-0.00820396324609085	-0.040568665167438	-0.00861965504441109	-0.0211585161950385	-0.000298249578442267	0.01451464982188
Node K	0.0200539157231283	-0.00304072277315903	-0.040568665167438	-0.00861965504441109	-0.0211585161950385	0.00232189686596129	0.01451464982188
Node L	0.0538294255425633	0.00559980168942431	-0.00293780442430247	-0.00185483526941432	-0.0211585161950385	0.00232189686596129	0.01451464982188
Node M	0.062521134315654	0.0105046244500588	-0.00293780442430247	-0.00185483526941432	-0.0211585161950385	0.00232189686596129	0.01451464982188
Node N	0.0645845030772421	0.0111760176354423	-0.00293780442430247	-0.00185483526941432	-0.0211585161950385	0.00232189686596129	0.01451464982188
Node O	0.0704609786150598	0.0160893439780239	0.00332183574360023	0.00358879479080443	0.00047700255000116	0.00232189686596129	0.01451464982188
Node P	0.0732930190642911	0.0160893439780239	0.00332183574360023	0.00794823904813668	0.00047700255000116	0.00232189686596129	0.01451464982188
Node Q	0.0753707297237316	0.0160893439780239	0.00629973325999167	0.00794823904813668	-0.00574962408028767	0.00232189686596129	0.01451464982188
Node R	0.077097826440454	0.0160893439780239	0.00934375136571219	0.00794823904813668	-0.00574962408028767	0.00232189686596129	0.01451464982188
Node S	0.0823869732768223	0.0160893439780239	0.00934375136571219	0.00794823904813668	-0.00574962408028767	0.00369450622128653	0.01451464982188

	8	9	10	11	12	13	14
Node A	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	-0.00421903109599597	0.00238385896382276
Node B	0.00447255350560916	0.00976784352614146	-0.00159349965468003	-0.00248128249430124	0.000423268007798683	0.00261939604612849	-0.000364020973844248
Node C	0.00447255350560916	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	0.00261939604612849	-0.000364020973844248
Node D	0.00447255350560916	0.00976784352614146	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	0.00261939604612849	-0.000364020973844248
Node E	0.00447255350560916	-0.00477784021121685	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node F	0.00447255350560916	-0.00477784021121685	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	-0.000907907483281178	0.00114699250806716
Node G	0.00447255350560916	-0.00477784021121685	-0.00723430247153445	0.00219572673016977	0.00093813519073116	-0.000907907483281178	0.00114699250806716
Node H	0.00447255350560916	-0.000297336001548132	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node I	0.00447255350560916	-0.000297336001548132	-0.00159349965468003	0.00219572673016977	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node J	0.00447255350560916	-0.000297336001548132	-0.00159349965468003	0.00455948515630666	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node K	0.00447255350560916	-0.00116239002958096	-0.00159349965468003	0.00455948515630666	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node L	0.00447255350560916	-0.00116239002958096	0.000723635834086522	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node M	0.00447255350560916	-0.00116239002958096	0.000723635834086522	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node N	0.00447255350560916	-0.00116239002958096	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node O	0.00447255350560916	-0.00116239002958096	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node P	0.00447255350560916	-0.00116239002958096	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node Q	0.00447255350560916	0.00197754130295458	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node R	0.00447255350560916	0.00197754130295458	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921
Node S	0.00447255350560916	0.00197754130295458	-0.00188083365571856	0.000212210759684694	-0.00356179033862603	-0.000907907483281178	-0.00068477550141921

	15	16	17	18	19	20	21
Node A	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node B	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	-0.000476699112150314	-0.000732044750705541	-0.000296826162129449
Node C	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node D	-0.00181637401503032	-0.00115518877697518	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node E	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node F	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node G	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	-0.0019087642578306	-0.000732044750705541	-0.000296826162129449
Node H	-0.00181637401503032	0.000794484873640755	0.000685057732788152	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node I	-0.00181637401503032	-0.0000997208760420421	0.000685057732800587	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	-0.000296826162129449
Node J	0.000102795206563755	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	0.00072708811573996
Node K	0.00376517392431097	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	0.00072708811573996
Node L	0.00376517392431097	-0.0000997208760420421	-0.000180556765119633	-0.000266115658865473	0.000286102478293415	-0.000732044750705541	0.00072708811573996
Node M	0.00056183566001522	-0.0000997208760402657	-0.000180556765119633	-0.000266115658865473	-0.000606703961722133	-0.000732044750705541	0.00072708811573996
Node N	0.00056183566001522	-0.0000997208760402657	-0.000180556765119633	-0.000266115658865473	0.00279660898497625	-0.000732044750705541	0.00072708811573996
Node O	-0.0017544835561587	-0.0000997208760402657	-0.000180556765119633	-0.0015407810855983	0.00279660898497625	-0.000732044750705541	0.00072708811573996
Node P	-0.0017544835561587	-0.0000997208760402657	-0.000180556765119633	-0.0015407810855983	0.00279660898497625	-0.000732044750705541	0.00144417429392618
Node Q	-0.0017544835561587	-0.0000997208760402657	-0.000180556765119633	-0.0015407810855983	0.00279660898497625	-0.000732044750705541	0.00144417429392618
Node R	-0.0017544835561587	-0.0000997208760402657	-0.000180556765119633	-0.0015407810855983	0.00279660898497625	-0.000732044750705541	0.00144417429392618
Node S	-0.0017544835561587	-0.0000997208760402657	-0.000180556765119633	-0.0015407810855983	-0.000776462415760903	-0.000732044750705541	0.000252099020746854

Node A -0.0000177015117195367
Node B -0.0000177015117195367
Node C -0.0000177015117195367
Node D -0.0000177015117195367
Node E 0.0000354104090654062
Node F 0.0000354104090654062
Node G 0.0000354104090654062
Node H 0.0000354104090654062
Node I 0.0000354104090654062
Node J 0.0000354104090654062
Node K 0.0000354104090654062
Node L 0.0000354104090654062
Node M 0.0000354104090654062
Node N 0.0000354104090654062
Node O 0.0000354104090654062
Node P 0.0000354104090654062
Node Q 0.0000354104090654062
Node R -0.00192872862819549
Node S -0.00192872862819549

Appendix 18: PC coordinates from each node for Matrix B.3 (Chapter III), depending of the weighting.

CI – weighting

	1	2	3	4	5	6	7
Node A	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node B	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node C	-0.0982061013287243	0.0747171795221924	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	-0.00386141362061387
Node D	-0.0518055502972992	0.0180940081497187	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	-0.00386141362061387
Node E	-0.0403650216332334	-0.0276329346574578	0.00330974785961402	-0.00880800776677937	0.00220885802845139	0.000229354200214971	-0.00386141362061387
Node F	-0.0403650216332334	-0.0343571351383645	0.00330974785961402	0.00144242843811782	0.00220885802845139	-0.00633999851780942	-0.00386141362061387
Node G	-0.0403650216332334	-0.0497679663138566	0.0110655065258936	0.00144242843811782	0.00220885802845139	-0.00633999851780942	-0.00386141362061387
Node H	-0.018146676122555	-0.0276329346574578	-0.0127755333628112	-0.00880800776677937	0.00287085152261213	0.000229354200214971	-0.00386141362061387
Node I	-0.000918679120223587	-0.0234152073514213	-0.0415541286145622	-0.00880800776677937	0.00287085152261213	0.000229354200214971	-0.00386141362061387
Node J	0.0180100272954338	-0.0066891514777847	-0.0415541286145622	-0.00880800776677937	0.00287085152261213	0.000229354200214971	-0.00910597486767273
Node K	0.0534836636415275	0.000810110068389491	-0.00150899402201787	0.0000987705909416547	0.00287085152261213	0.000229354200214971	-0.00835989459125663
Node L	0.0619151711556061	0.00944781887796964	-0.00150899402201787	0.0000987705909416547	0.000653460494099534	0.000229354200214971	-0.00342028421769847
Node M	0.0619151711556061	0.00944781887796964	-0.00351596828905265	-0.00579729411978747	0.000653460494099534	0.000229354200214971	0.0112913519000326
Node N	0.0729407442950372	0.0145328946912997	0.00717213814849771	0.0000987705909416547	-0.0013623272378247	0.000229354200214971	-0.00342028421769847
Node O	0.0807477597574522	0.0145328946912997	0.00717213814849771	0.0000987705909416547	-0.0013623272378247	0.000229354200214971	-0.00342028421769847

	8	9	10	11	12	13	14
Node A	-0.00942621923969433	0.0056043656009539	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	-0.00389556077205988	-0.00209199411840544
Node B	0.00298598671838235	0.00233489114665453	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	0.00265558556369605	-0.00209199411840544
Node C	0.00298598671838235	-0.00118475876725199	-0.00136062519099411	0.00174318958665154	-0.00301674567212729	0.002125612751394	-0.00209199411840544
Node D	0.00298598671838235	-0.00118475876725199	-0.00136062519099411	0.00248278282685632	-0.00258480376619552	0.00291708613334407	-0.00209199411840544
Node E	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00248278282685632	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node F	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00248278282685632	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node G	-0.00274151549709245	-0.00118475876725199	-0.0101255860661134	0.00248278282685632	-0.000389570583690713	-0.000693138431108409	-0.00209199411840544
Node H	0.000622814781667813	-0.00118475876725199	0.00100688642035784	0.00248278282685632	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node I	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	0.00248278282685632	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node J	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	0.00248278282685632	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node K	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	0.00134872731936575	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node L	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	-0.00142738715348401	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node M	0.00387626116151729	-0.00118475876725199	-0.00221100104965366	-0.00594348481011231	-0.00258480376619552	0.00510089732149055	-0.00209199411840544
Node N	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	-0.00142738715348401	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node O	-0.00186647187779698	-0.00118475876725199	0.00100688642035784	-0.00142738715348401	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544

	15	16	17	18	19	20	21
Node A	-0.0013916518798478	0.00153284912557261	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node B	-0.0013916518798478	-0.00124397590956349	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	-0.00025463126372216	-0.000353848921259114
Node C	-0.0013916518798478	-0.00171995605189501	0.00102363332658051	-0.000576851282108493	0.000658490818315371	-0.000319616205922912	-0.000353848921259114
Node D	-0.000906928261930062	-0.00171995605189501	0.00102363332658051	0.0000398577506697251	0.000658490818315371	-0.000898013049557278	-0.000353848921259114
Node E	-0.00142697144373116	-0.00171995605189501	0.00102363332658051	0.0000398577506697251	0.000658490818315371	-0.000898013049557278	-0.000353848921259114
Node F	-0.00142697144373116	-0.00128036808873944	0.00102363332658051	0.0000398577506697251	0.000658490818315371	-0.0000462520103354791	-0.000353848921259114
Node G	-0.00142697144373116	-0.00101141947298977	0.00102363332658051	-0.000769844217595406	-0.00174872072334509	-0.0000462520103354791	-0.000353848921259114
Node H	-0.00142697144373116	-0.00171995605189501	0.00102363332658051	0.0000398577506697251	0.000658490818315371	-0.000392523326349092	-0.000353848921259114
Node I	-0.00142697144373116	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	-0.000353848921259114
Node J	0.0000264720642384475	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	0.000632901315974266
Node K	0.0000264720642384475	0.000706098648683096	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	0.000632901315974266
Node L	0.0000264720642384475	0.000706098648683096	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	0.000632901315974266
Node M	0.0000264720642384475	0.000706098648683096	0.00102363332658051	0.0000398577506697251	0.000658490818315371	-0.000489921228814083	-0.000197571062113155
Node N	-0.0011756672677059	0.000706098648683096	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	0.000632901315974266
Node O	-0.0011756672677059	0.000706098648683096	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000240438238478191	-0.000238499010839277

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Node A -0.0000070282789597087
Node B -0.0000070282789597087
Node C -0.0000070282789597087
Node D -0.0000070282789597087
Node E -0.0000070282789597087
Node F -0.0000070282789597087
Node G -0.0000070282789597087
Node H -0.0000070282789597087
Node I -0.0000070282789597087
Node J -0.0000070282789597087
Node K -0.0000070282789597087
Node L -0.0000070282789597087
Node M -0.0000070282789597087
Node N -0.0000070282789597087
Node O -0.0000070282789597087

RI – weighting

	1	2	3	4	5	6	7
Node A	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node B	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node C	-0.0982061013287243	0.0747171795221995	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node D	-0.0518055502972992	0.0180940081497187	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node E	-0.0403650216332334	-0.0323230065087561	0.00330974785961402	-0.00880800776677937	-0.0227399965005617	0.000229354200214971	0.0121750198795958
Node F	-0.0403650216332334	-0.0497679663138566	0.0110655065258936	-0.0030649060539627	-0.0227399965005617	-0.00668142239277003	0.0121750198795958
Node G	-0.018146676122555	-0.0323230065087561	-0.0127755333628112	-0.00880800776677937	-0.0227399965005617	0.000229354200214971	0.0121750198795958
Node H	-0.000918679120223587	-0.0234152073514213	-0.0415541286145622	-0.00880800776677937	-0.0227399965005617	0.000229354200214971	0.0121750198795958
Node I	0.0176939265874783	-0.00785181990002215	-0.0415541286145622	-0.00880800776677937	-0.0227399965005617	0.000229354200214971	0.0121750198795958
Node J	0.0183261280033893	-0.00552648305554726	-0.0415541286145622	-0.00705320640262741	0.00176215600835583	0.000229354200214971	0.0121750198795958
Node K	0.0520456649095209	0.00530842645250473	0.00344325503152731	-0.00284926176442291	0.00176215600835583	0.000229354200214971	0.0121750198795958
Node L	0.0619151711556061	0.00944781887796964	0.00344325503152731	-0.00284926176442291	0.00176215600835583	0.000229354200214971	0.0121750198795958
Node M	0.064214064773731	0.0109228330195847	-0.00251248115553437	-0.00284926176442291	0.00176215600835583	0.000229354200214971	0.0121750198795958
Node N	0.0674039155655635	0.0145753135897309	0.00717213814849771	0.00310649379343531	-0.000623523505764112	0.000229354200214971	0.0121750198795958
Node O	0.0730593856867063	0.0145753135897309	0.00717213814849771	0.00826669343533837	-0.00356734994484675	0.000229354200214971	0.0121750198795958
Node P	0.0807477597574522	0.0145753135897309	0.00717213814849771	0.00826669343533837	-0.00356734994484675	0.000229354200214971	0.0121750198795958

	8	9	10	11	12	13	14
Node A	-0.00942621923969433	0.0056043656009539	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	-0.00389556077205988	-0.00209199411840544
Node B	0.00298598671838235	0.00233489114665453	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	0.00265558556369605	-0.00209199411840544
Node C	0.00298598671838235	-0.00118475876725199	-0.00136062519099411	0.00174318958665154	-0.00346134706183676	0.002125612751394	-0.00209199411840544
Node D	0.00298598671838235	-0.00118475876725199	-0.00136062519099411	0.00322237606706288	-0.00346134706183676	0.00291708613334407	-0.00209199411840544
Node E	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00322237606706288	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node F	-0.00274151549709245	-0.00118475876725199	-0.0101255860661134	0.00322237606706288	-0.000389570583690713	-0.000693138431108409	-0.00209199411840544
Node G	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00322237606706288	-0.00258480376619552	-0.000693138431108409	-0.00209199411840544
Node H	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00322237606706288	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node I	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00322237606706288	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node J	0.00298598671838235	-0.00118475876725199	0.00100688642035784	0.00322237606706288	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node K	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node L	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node M	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	0.00137906439239011	-0.00209199411840544
Node N	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	-0.000535099595937893	-0.00128615616933914
Node O	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	-0.000535099595937893	0.00189764208096932
Node P	0.00298598671838235	-0.00118475876725199	0.00100688642035784	-0.000734127300024312	-0.00258480376619552	-0.000535099595937893	0.00189764208096932

	15	16	17	18	19	20	21
Node A	-0.0013916518798478	0.00153284912557261	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node B	-0.000381785964895798	-0.00124397590956349	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node C	-0.000381785964895798	-0.00171995605189501	0.00102363332658051	-0.000576851282108493	0.000658490818315371	0.000695102011734505	-0.000353848921259114
Node D	-0.000906928261930062	-0.00171995605189501	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000695102011734505	-0.000353848921259114
Node E	-0.00100229752936976	-0.00128036808873944	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000695102011734505	-0.000353848921259114
Node F	-0.00100229752936976	-0.00128036808873944	0.00102363332658051	-0.000769844217595406	-0.00174872072334509	0.000695102011734505	-0.000353848921259114
Node G	-0.00100229752936976	-0.00128036808873944	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000695102011734505	-0.000353848921259114
Node H	-0.00100229752936976	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000695102011734505	-0.000353848921259114
Node I	0.0000264720642384475	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	0.000658490818315371	0.000695102011734505	0.000648451179952048
Node J	0.00371607013117981	-0.000517237462803521	0.00102363332658051	-0.00019120935707484	0.000658490818315371	0.000695102011734505	0.000648451179952048
Node K	0.00371607013117981	0.000521025992744839	0.00102363332658051	-0.00019120935707484	0.000658490818315371	0.000695102011734505	0.000648451179952048
Node L	-0.0000176621076839467	0.000521025992744839	0.00102363332658051	-0.00019120935707484	-0.000208499131806761	0.000695102011734505	0.000648451179952048
Node M	-0.0000176621076839467	0.000521025992744839	0.00102363332658051	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.000648451179952048
Node N	-0.0011756672677059	0.000521025992744839	-0.000844523949185216	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.000648451179952048
Node O	-0.0011756672677059	0.000521025992744839	0.000929770912414085	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.00197548294545236
Node P	-0.0011756672677059	0.000521025992744839	0.000929770912414085	-0.00019120935707484	-0.000312789505890976	0.000695102011734505	-0.000238499010839277

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Node A	-0.0000070282789597087
Node B	-0.0000070282789597087
Node C	-0.0000070282789597087
Node D	-0.0000070282789597087
Node E	-0.0000070282789597087
Node F	-0.0000070282789597087
Node G	-0.0000070282789597087
Node H	-0.0000070282789597087
Node I	-0.0000070282789597087
Node J	-0.0000070282789597087
Node K	-0.0000070282789597087
Node L	-0.0000070282789597087
Node M	0.000740068608154232
Node N	0.000740068608154232
Node O	0.000740068608154232
Node P	-0.000796072861801278

RC – weighting

	1	2	3	4	5	6	7
Node A	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node B	-0.152332370032042	0.0747171795221924	-0.0447926483628596	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node C	-0.0982061013287243	0.0747171795221924	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node D	-0.0518055502972992	0.0180940081497187	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node E	-0.0453099180778498	-0.0327953510540198	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node F	-0.0453099180778498	-0.0497679663138566	0.0110655065258936	-0.0137706936713169	-0.0227399965005617	-0.00668142239277181	0.0121750198795958
Node G	-0.0384082546366304	-0.0327953510540198	0.00330974785961402	-0.0137706936713169	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node H	-0.0327985509836228	-0.0276329346574578	0.00330974785961402	-0.00880800776677937	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node I	-0.018146676122555	-0.0276329346574578	-0.012775533628112	-0.00880800776677937	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node J	-0.000918679120223587	-0.0234152073514213	-0.0415541286145622	-0.00880800776677937	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node K	0.0176939265874783	-0.00785181990002215	-0.0415541286145622	-0.00880800776677937	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node L	0.0183261280033893	-0.00552648305554726	-0.0415541286145622	-0.00705320640262741	-0.0227399965005617	-0.00337156638354941	0.0121750198795958
Node M	0.0506076661775161	0.00530842645250473	-0.00351596828905265	-0.00579729411978747	0.000606301451888669	-0.00337156638354941	0.0121750198795958
Node N	0.0534836636415275	0.00530842645250473	-0.00150899402201787	0.0000987705909416547	0.000606301451888669	-0.00337156638354941	0.0121750198795958
Node O	0.0619151711556061	0.00944781887796964	-0.00150899402201787	0.0000987705909416547	0.000606301451888669	-0.00337156638354941	0.0121750198795958
Node P	0.064214064773731	0.0109228330195847	-0.00150899402201787	0.0000987705909416547	0.000606301451888669	-0.00337156638354941	0.0121750198795958
Node Q	0.0674039155655635	0.0145753135897309	0.00453451540513683	0.00310649379343531	0.000606301451888669	-0.00337156638354941	0.0121750198795958
Node R	0.072822102903368	0.0145753135897309	0.00453451540513683	0.00826669343533837	0.000606301451888669	0.00270831384057857	0.0121750198795958
Node S	0.0730593856867063	0.0145753135897309	0.00453451540513683	0.00826669343533837	-0.00554413017901823	0.00164810324203124	0.0121750198795958
Node T	0.0758600953672204	0.0145753135897309	0.00453451540513683	0.00826669343533837	-0.00554413017901823	0.00164810324203124	0.0121750198795958
Node U	0.0807477597574522	0.0145753135897309	0.00453451540513683	0.00826669343533837	-0.00554413017901823	0.00164810324203124	0.0121750198795958

	8	9	10	11	12	13	14
Node A	-0.00942621923969433	0.0056043656009539	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	-0.00389556077205988	-0.00209199411840544
Node B	0.000157949450063199	0.00233489114665453	-0.00136062519099411	-0.00132249616604874	-0.000701547126913837	0.00265558556369605	-0.00209199411840544
Node C	0.00581402398669972	-0.00118475876725199	-0.00136062519099411	0.00174318958665154	-0.000701547126913837	0.002125612751394	-0.00209199411840544
Node D	0.00581402398669972	-0.00118475876725199	-0.00136062519099411	0.00248278282685632	-0.000701547126913837	0.00291708613334407	-0.00209199411840544
Node E	0.00581402398669972	-0.00118475876725199	-0.00136062519099411	0.00248278282685632	-0.000701547126913837	-0.000693138431108409	-0.00209199411840544
Node F	-0.00274151549709245	-0.00118475876725199	-0.0106081828393414	0.00248278282685632	-0.000701547126913837	-0.000693138431108409	-0.00209199411840544
Node G	0.00581402398669972	-0.00118475876725199	0.00854548228816654	0.00248278282685632	-0.000701547126913837	-0.000693138431108409	-0.00209199411840544
Node H	-0.00329143524096231	-0.00118475876725199	0.00854548228816654	0.00248278282685632	-0.000701547126913837	-0.000693138431108409	-0.00209199411840544
Node I	-0.00329143524096231	-0.00118475876725199	0.00535528397313989	0.00248278282685632	-0.000701547126913837	-0.000693138431108409	-0.00209199411840544
Node J	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	0.00248278282685632	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node K	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	0.00248278282685632	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node L	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	0.00248278282685632	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node M	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	-0.000734127300024312	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node N	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	-0.000734127300024312	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node O	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	-0.000734127300024312	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node P	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	-0.000734127300024312	-0.000701547126913837	0.00137906439239011	-0.00209199411840544
Node Q	-0.00329143524096231	-0.00118475876725199	0.000485116807372066	-0.000734127300024312	-0.000701547126913837	-0.00197152581765359	-0.00209199411840544
Node R	-0.00329143524096231	-0.000717365288087635	-0.00147534939230098	-0.000734127300024312	-0.000701547126913837	-0.00197152581765359	-0.00209199411840544
Node S	-0.00329143524096231	-0.00224121258775511	-0.00329270783430857	-0.000734127300024312	-0.000701547126913837	-0.00197152581765359	-0.00209199411840544
Node T	-0.00329143524096231	-0.00224121258775511	-0.00329270783430857	-0.000734127300024312	-0.000701547126913837	-0.00197152581765359	-0.00209199411840544
Node U	-0.00329143524096231	-0.00224121258775511	-0.00329270783430857	-0.000734127300024312	-0.000701547126913837	-0.00197152581765359	-0.00209199411840544

	15	16	17	18	19	20	21
Node A	-0.0013916518798478	0.00153284912557261	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node B	-0.000381785964895798	0.00153284912557261	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node C	-0.000381785964895798	0.00153284912557261	0.00102363332658051	-0.000576851282108493	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node D	-0.000906928261930062	0.00153284912557261	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node E	-0.00100229752936976	0.00153284912557261	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node F	-0.00100229752936976	0.00153284912557261	0.00102363332658051	-0.000769844217595406	-0.00174872072334509	0.000695102011734505	-0.000353848921259114
Node G	-0.00100229752936976	0.00153284912557261	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node H	-0.00100229752936976	0.00153284912557261	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node I	-0.00100229752936976	-0.00181172401233454	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node J	-0.00100229752936976	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	-0.000353848921259114
Node K	0.0000264720642384475	-0.000517237462803521	0.00102363332658051	0.0000398577506697251	-0.000515747873476968	0.000695102011734505	0.000648451179952048
Node L	0.00501595326009152	-0.000517237462803521	0.00102363332658051	-0.00019120935707484	-0.000515747873476968	0.000695102011734505	0.000648451179952048
Node M	0.00501595326009152	0.000521025992744839	0.00102363332658051	-0.00019120935707484	-0.000515747873476968	0.000695102011734505	0.000648451179952048
Node N	0.00371607013117981	0.000521025992744839	0.00102363332658051	-0.00019120935707484	-0.000515747873476968	0.000695102011734505	0.000648451179952048
Node O	-0.000235879560662511	0.000521025992744839	0.00102363332658051	-0.00019120935707484	-0.000515747873476968	0.000695102011734505	0.000648451179952048
Node P	-0.000235879560662511	0.000521025992744839	0.00102363332658051	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.000648451179952048
Node Q	-0.0011756672677059	0.000521025992744839	-0.000844523949185216	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.000648451179952048
Node R	-0.0011756672677059	0.000521025992744839	0.0000149247131329133	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.00197548294545236
Node S	-0.0011756672677059	0.000521025992744839	0.0000149247131329133	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.00197548294545236
Node T	-0.0011756672677059	0.000521025992744839	0.0000149247131329133	-0.00019120935707484	0.00135564617666795	0.000695102011734505	0.00197548294545236
Node U	-0.0011756672677059	0.000521025992744839	0.0000149247131329133	-0.00019120935707484	-0.000312789505890976	0.000695102011734505	-0.000238499010839277

Node A -0.0000070282789597087
Node B -0.0000070282789597087
Node C -0.0000070282789597087
Node D -0.0000070282789597087
Node E -0.0000070282789597087
Node F -0.0000070282789597087
Node G 0.000398698498484507
Node H 0.000398698498484507
Node I 0.000398698498484507
Node J 0.000398698498484507
Node K 0.000398698498484507
Node L 0.000398698498484507
Node M 0.000398698498484507
Node N 0.000398698498484507
Node O 0.000398698498484507
Node P 0.000398698498484507
Node Q 0.000398698498484507
Node R 0.000398698498484507
Node S 0.000398698498484507
Node T -0.00140172747725664
Node U -0.00140172747725664

Appendix 19: Landmarks coordinates at each node for Matrix C.1 (Chapter III), according to the weighting.

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 20: Landmarks coordinates at each node for Matrix C.2 (Chapter III), according to the weighting.

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 21: Landmarks coordinates at each node for Matrix C.3 (Chapter III), according to the weighting

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 22: Synapomorphies et autapomorphies of Matrix D of Chapter IV, according to the weighting.

CI-weighting					Char. 47	1	2
	Character	Previous state	New state	Dmanisi			
<i>Pongo</i>	No autapomorphies			<i>H. ergaster</i>	No autapomorphies		
<i>Gorilla</i>	Char. 37	1	3		Char. 1	1	2
	Char. 48	1	3		Char. 42	1	2
					Char. 45	3	2
<i>Pan</i>	Char. 1	1	2	Sangiran	Char. 18	2	3
	Char. 4	2	1	Zhoukoudian	No autapomorphies		
	Char. 16	1	3	Ngandong	Char. 7	3	2
	Char. 23	1	2		Char. 9	1	2
	Char. 26	1	2		Char. 39	2	3
	Char. 33	1	2		Char. 40	1	2
<i>P. boisei</i>	Char. 1	1	2	Near East			
	Char. 8	1	2	Neandertal	Char. 37	1	2
	Char. 51	1	2		Char. 55	2	1
	Char. 55	1 2 ou 3					
	Char. 56	2	3	Early Neandertal	No autapomorphies		
<i>P. aethiopicus</i>	Char. 26	1	2	Classic			
	Char. 35	1	2	Neandertal	Char. 36	2	3
	Char. 36	1	2		Char. 57	1	2
	Char. 59	1	2				
Stw 53	Char. 51	1	2	Skhūl - Qafzeh	Char. 59	1	2
	Char. 55	3	2	KhoiSan	No autapomorphies		
<i>A. africanus</i>	Char. 14	3	2	Haya	Char. 18	2	1
	Char. 37	1	2		Char. 25	1	2
<i>A. afarensis</i>	Char. 5	2	1		Char. 49	1	2
	Char. 14	3	1	Kongo	No autapomorphies		
	Char. 35	1	2		No autapomorphies		
	Char. 36	1	2	Mande	No autapomorphies		
	Char. 37	1	2		No autapomorphies		
	Char. 58	2	1	Berber	No autapomorphies		
<i>H. habilis</i>	No autapomorphies			Papu	No autapomorphies		
<i>H. rudolfensis</i>	Char. 1	1	2	French	No autapomorphies		
	Char. 27	2	3		No autapomorphies		
	Char. 30	1	3	Chinese	No autapomorphies		
	Char. 45	2	3		No autapomorphies		

CI-weighting							
	Character	Previous state	New state		Char. 29	1	2
Inuit					Char. 37	1	3
	No autapomorphies				Char. 47	1	2
Node B				Node L	Char. 60	1	2
	No autapomorphies				Char. 26	1	2
Node C				Node M			
	Char. 5	2	1		Char. 15	1	2
	Char. 41	1	2		Char. 53	1	2
Node D				Node N			
	Char. 22	1	2		Char. 48	1	2
	Char. 50	1	3	Node O			
Node E					Char. 1	1	3
	Char. 14	3	1		Char. 15	1	3
	Char. 19	1	2		Char. 16	1	3
	Char. 20	1	2		Char. 17	1	3
	Char. 57	2	1		Char. 33	1	2
Node F					Char. 57	2	1
	Char. 24	2	1	Node P			
	Char. 55	1 2 ou 3			Char. 35	1	3
	Char. 56	2	1		Char. 36	1	2
Node G					Char. 46	2	1
	Char. 29	1	2		Char. 51	1	2
Node H				Node Q			
	Char. 16	1	3		Char. 4	1	2
	Char. 45	2	3	Node R			
Node I					Char. 6	2	3
	Char. 31	2	1		Char. 38	3	1
	Char. 54	1	2		Char. 39	2	1
Node J					Char. 56	1	2
	Char. 2	2	1		Char. 58	2	1
Node K				Node S			
	Char. 20	1	2		Char. 14	3	1
	Char. 21	1	2	Node T			
	Char. 23	1	2		No synapomorphies		

RI-weighting				<i>H. habilis</i>			
	Character	Previous state	New state		No autapomorphies		
<i>Pongo</i>	No autapomorphies			<i>H. rudolfensis</i>	Char. 1	1	2
<i>Gorilla</i>					Char. 27	2	3
	Char. 2	3	2		Char. 30	1	3
	Char. 37	1	3		Char. 45	2	3
	Char. 48	1	3		Char. 47	1	2
<i>Pan</i>				Dmanisi	Char. 43	2	1
	Char. 4	2	1	<i>H. ergaster</i>			
	Char. 16	1	3		Char. 1	1	2
	Char. 23	1	2		Char. 13	2	3
	Char. 33	1	2		Char. 28	1	3
<i>P. boisei</i>					Char. 42	1	2
	Char. 8	1	2		Char. 45	3	2
	Char. 51	1	2		Char. 49	1	2
	Char. 55	1 2 ou 3					
	Char. 56	2	3	Sangiran	Char. 44	2	1
<i>P. aethiopicus</i>				Zhoukoudian	No autapomorphies		
	Char. 2	3	2				
	Char. 35	1	2	Ngandong			
	Char. 36	1	2		Char. 9	1	2
	Char. 39	3	2		Char. 28	1	3
	Char. 59	1	2		Char. 39	2	3
Stw 53					Char. 40	1	2
	Char. 33	1	2	Near East			
	Char. 51	1	2	Neandertal			
	Char. 56	1	3		Char. 13	3	2
	Char. 58	2	1		Char. 37	1	2
<i>A. africanus</i>					Char. 55	2	1
	Char. 13	3	1	Early Neandertal	No autapomorphies		
	Char. 14	3	2				
	Char. 32	1	2	Classic			
	Char. 34	1	2	Neandertal			
	Char. 37	1	2		Char. 36	2	3
	Char. 48	1	3		Char. 57	1	2
	Char. 55	2	3	Skhūl - Qafzeh			
<i>A. afarensis</i>					Char. 59	1	2
	Char. 4	1	2	KhoiSan	No autapomorphies		
	Char. 5	2	1				
	Char. 14	3	1	Haya			
	Char. 35	1	2		Char. 25	1	2
	Char. 36	1	2		Char. 49	1	2
	Char. 37	1	2				
	Char. 58	2	1				

RI-weighting							
	Character	Previous state	New state				
Kongo	No autapomorphies				Char. 38	3	2
					Char. 41	1	2
Mande	No autapomorphies			Node I	Char. 45	2	3
					Char. 59	1	2
Berber	No autapomorphies				Char. 12	1	3
					Char. 48	1	2
Papu	No autapomorphies			Node J	Char. 55	2	3
					Char. 21	1	2
French	No autapomorphies				Char. 23	1	2
					Char. 37	1	3
Chinese	No autapomorphies			Node K			
					Char. 24	1	2
Inuit	No autapomorphies			Node L	Char. 53	1	2
Node B	No autapomorphies			Node M	Char. 1	1	2
					Char. 15	1	3
Node C	Char. 5	2	1		Char. 16	1	3
					Char. 17	1	3
Node D	Char. 41	1	2		Char. 28	1 ou 2	3
					Char. 33	1	2
	Char. 34	1	2		Char. 44	2	1
					Char. 47	1	3
	Char. 47	1	2		Char. 57	2	1
Node E	Char. 49	1	2				
	Char. 14	3	1	Node N	Char. 32	1	2
					Char. 35	1	3
	Char. 19	1	2		Char. 36	1	2
					Char. 46	2	1
	Char. 20	1	2		Char. 51	1	2
	Char. 31	1	2	Node O	Char. 4	1	2
Node F	Char. 57	2	1		Char. 6	2	3
					Char. 13	3	1
	Char. 4	2	1	Node P	Char. 38	3	1
					Char. 39	2	1
	Char. 6	1	2		Char. 56	1	2
					Char. 58	2	1
	Char. 24	2	1				
	Char. 25	2	1	Node Q	Char. 14	3	1
	Char. 55	1	2				
Node G	Char. 56	2	1				
	Char. 2	3	2	Node R	No synapomorphies		
	Char. 6	2	1				
	Char. 29	1	2	Node S	No synapomorphies		
Node H	Char. 37	3	2				
	Char. 13	3	2				
	Char. 16	1	3				
	Char. 17	1	2				

RC-weighting					Char. 47	1	2
	Character	Previous state	New state	Dmanisi			
<i>Pongo</i>	No autapomorphies				No autapomorphies		
<i>Gorilla</i>				<i>H. ergaster</i>	Char. 1	1	2
	Char. 37	1	3		Char. 28	1	3
	Char. 48	1	3		Char. 42	1	2
<i>Pan</i>					Char. 45	3	2
	Char. 1	1	2		Char. 49	1	2
	Char. 4	2	1	Sangiran			
	Char. 16	1	3		Char. 44	2	1
	Char. 23	1	2	Zhoukoudian			
	Char. 33	1	2		No autapomorphies		
<i>P. boisei</i>				Ngandong			
	Char. 1	1	2		Char. 9	1	2
	Char. 8	1	2		Char. 28	1	3
	Char. 51	1	2		Char. 39	2	3
	Char. 55	1 2 ou 3			Char. 40	1	2
	Char. 56	2	3	Near East			
<i>P. aethiopicus</i>				Neandertal			
	Char. 35	1	2		Char. 37	1	2
	Char. 36	1	2		Char. 55	2	1
	Char. 39	3	2	Early Neandertal			
	Char. 59	1	2		No autapomorphies		
Stw 53				Classic Neandertal			
	Char. 51	1	2		Char. 36	2	3
	Char. 55	3	2		Char. 57	1	2
<i>A. africanus</i>				Skhül - Qafzeh			
	Char. 14	3	2		Char. 59	1	2
	Char. 37	1	2	KhoiSan			
<i>A. afarensis</i>					No autapomorphies		
	Char. 5	2	1	Haya			
	Char. 14	3	1		Char. 25	1	2
	Char. 35	1	2		Char. 49	1	2
	Char. 36	1	2	Kongo			
	Char. 37	1	2		No autapomorphies		
	Char. 58	2	1	Mande			
<i>H. habilis</i>					No autapomorphies		
	No autapomorphies			Berber			
<i>H. rudolfensis</i>					No autapomorphies		
	Char. 1	1	2	Papu			
	Char. 3	1	3		No autapomorphies		
	Char. 27	2	3	French			
	Char. 30	1	3		No autapomorphies		
	Char. 45	2	3				

RC-weighting							
	Character	Previous state	New state				
Chinese				Node K	Char. 20	1	2
					Char. 23	1	2
	No autapomorphies				Char. 37	1	3
Inuit				Node L			
	No autapomorphies				Char. 25	1	2
Node B				Node M			
	No autapomorphies				Char. 53	1	2
Node C				Node N			
	Char. 5	2	1		No synapomorphies		
	Char. 41	1	2	Node O			
Node D					Char. 1	1	3
	Char. 14	3	1		Char. 15	1	3
	Char. 19	1	2		Char. 17	1	3
	Char. 20	1	2		Char. 33	1	2
	Char. 31	1	2		Char. 44	2	1
	Char. 57	2	1	Node P			
Node E					Char. 35	1	3
	Char. 24	2	1		Char. 36	1	2
	Char. 25	2	1		Char. 46	2	1
	Char. 31	1	2		Char. 51	1	2
	Char. 56	2	1	Node Q			
Node F					Char. 4	1	2
	Char. 29	1	2	Node R			
Node G					Char. 6	2	3
	Char. 3	1	2		Char. 38	3	1
	Char. 6	1	2		Char. 39	2	1
Node H					Char. 56	1	2
	Char. 45	2	3		Char. 58	2	1
Node I				Node S			
	Char. 31	2	1		Char. 14	3	1
	Char. 54	1	2	Node T			
Node J					No synapomorphies		
	Char. 2	2	1				

Appendix 23: Synapomorphies et autapomorphies of the CI-weighted Matrix E of Chapter IV.

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 24: Synapomorphies et autapomorphies of the RI-weighted Matrix E of Chapter IV.

This appendix can be found in this drive: [PhD - Appendices](#)

Appendix 25: Synapomorphies et autapomorphies of the RC-weighted Matrix E of Chapter IV.

This appendix can be found in this drive: [PhD - Appendices](#)