

The long life of Mesolithic bone/antler projectile points from the North Sea

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In the past decades, hundreds of bone/antler points were recovered on the Dutch North Sea coast. These finds, related to the Mesolithic occupation of the now submerged Doggerland, are interpreted as arrowheads and spearheads for hunting activities based on their shape and size [1,2]. As pointed out in previous morphometric and traceology studies [3,4], some points provided evidence, such as binding impressions and adhesive remains that may be related to hafting. To further explore this issue, a sample of 17 bone/antler points with potential hafting traces were selected for a detailed examination at Delft University of Technology and Leiden University.

The tools were analysed with light microscopy to detect macro and microscopic traces of production, use and post-deposition wear. Potential hafting residues were first morphologically characterized and described through microscopy and then inspected with non-destructive and destructive chemical techniques (micro-FTIR, Raman, SEM-EDX, XRD, GC-MS). Before the points were subjected to destructive sampling, 3D models were generated to create permanent records of the objects. In addition, to create a reference collection of relevant hafting traces an experimental program was carried out on bone points.

The functional analysis of the points provided evidence of the long use-life of these tools. Reshaping, reuse, and repair attempts were documented on most of the artefacts. The fractures observed on tools' tips and bases are comparable with impact fractures generated from use as projectiles. The examination of the proximal area of the points revealed a combination of macro and microscopic traces and residues connected to different hafting designs. Based on these data, it is therefore likely that these tools were hafted with the aid of bindings and adhesives with various hafting arrangements.

The results of our comprehensive analysis that integrates examination of use-wear traces and residues – encompassing morphological and chemical identification of residues – and experiments allow us to write a complete biography of these tools and gain insights into their use-life cycle. During their long life, these points were used, reuse, curated, and rehafted many times before being discarded or lost. Their long use-life may be connected to their changing use from spear/atlatl to arrow points. In addition, material selection, e.g., human and brown bear bones [5], may also underline that these points embedded specific cultural and symbolic meaning and therefore used for a very long time by their Mesolithic owners.

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The Mousterian lithic assemblage of Galería de las Estatuas site (Sierra de Atapuerca, Spain) from a functional perspective. Preliminary results

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Galería de las Estatuas (GE) is a cave site located within the karst system of Sierra de Atapuerca (Burgos). It is a sub-horizontal gallery placed on the upper level of the Cueva Mayor-Cueva del Silo complex, close to one of the ancient entrances. It covers a 4 km long extension and it is currently sealed on the outside by sediments and speleothems silting [1]. The excavation of two pits has revealed five lithostratigraphic units which yielded evidence of Mousterian occupations with sporadic carnivore activity [2]. OSL dating has provided a chronological frame of 70-112 ka BP, placing GE sequence within marine isotope stage (MIS) 5 and the beginning of MIS 4 [3]. In 2017, a foot phalanx belonging to *Homo neanderthalensis* was recovered in the interface between lithostratigraphic units 3 and 4 (107-112 ka BP) [4]. Finally, nuclear and mitochondrial DNA from the cave sediments has been recovered, further confirming the presence of *Homo neanderthalensis* at the site [5].

To date, the lithic assemblage is composed of 558 pieces with a clear Mousterian affinity. The raw materials are mainly chert (n=464) and quartzite (n=74) but there is also presence of sandstone (n=8), limestone (n=8) and quartz (n=4). Knapping products as simple flakes (n=103), broken flakes (n=28) and flakes fragments (n=22) are the most common elements. Retouched items (n=77) are also mainly represented by several typologies as sidescrapers (n=34) with mostly Quina-type retouching, and denticulates (n= 31). There are also some notches (n=6), endscrapers (n=4) and points (n=1). Furthermore, pieces as hammerstones (n=11) and cores (n=9) have been also recovered. Cores are mainly centripetal (n=7) although Levallois knapping is quite present as well. Analysis conducted on the flakes reveals principally non-cortical striking platforms (n=117) and non-cortical dorsal surfaces (n=120) in contrast to cortical platforms and cortical surfaces. This data combined with the high exploitation of cores, suggests that early stages of knapping activity were barely present on the site.

Among the lithic assemblage, 80 tools were chosen for the functional analysis. The selection criteria considered elements as the state of preservation of the pieces or the existence of useable or retouched edges. Accordingly, both simple and retouched flakes are included on the sample. This study presents preliminary results from a small sample analysed in order to understand the use-wear features of the assemblage and determinate the feasibility of a wider study. All the lithostratigraphic units have been examined, except for unit 5, which is currently under excavation and it has not provided any lithic materials yet. The sample is composed of chert and quartzite. Some chert artefacts present a patina which complicates the use-wear identification but fortunately does not prevent it. On the other hand, some quartzites show also surface modifications on their crystals, probably linked with post-depositional alterations. The data obtained from microwear analysis suggest different movements, both longitudinal and transversal related to cutting and scraping actions, and differences on the hardness of worked material. In some artifacts clear use-wear has been documented but their weak development and the lack of association between traces have not provided detailed information about the type of use. We expect that a broader analysis will yield more accurate data about the activities developed by *Homo neanderthalensis* at the site.

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Establishing a chronology of *Homo sapiens*-specific genetic variants

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Over the last years we have come to the realization that the deep past of our species is complex and multi-faceted [1]. A fragmented fossil record and multiple admixture events with extinct human species highlight the necessity of drawing from different sources to establish a chronology of events in human evolution, and while the emergence of human ancient DNA allows for the possibility of exploring the biological foundations of *Homo sapiens*, we can now complement the fossil record with variant dating methods. Temporally-aware genomic analyses are key to not only uncover what changed in the *Homo sapiens* lineage, but also to solve the crucial questions of when and in what order.

Making use of a large-scale variant dating database, GEVA [2] and a catalog of *Homo sapiens*-specific variation [3], we present a time-sensitive approach to the study of derived variants, as well as positively selected genomic windows and introgressed alleles from Neanderthals and Denisovans. GEVA is non-parametric coalescence-based method that provides publicly available age estimates for over 45 million human variants. We show that genetic variants that are almost-fixed across human populations are distributed in two modes over time, peaking at times approximately coinciding with i) the expansion of our population after the Out-of-Africa event, and ii) the emergence of our species. We then derive trends from genetic variation time windows corresponding with milestones of evolution, such as the split with the Neanderthals and Denisovans branch. Chronologically-aware enrichments of gene ontology categories bring into prominence facial and behavioural terms in the 300-500 thousand years window, a time coinciding with the retraction of the face in early humans. Additionally, we applied a machine-learning gene expression predictor [4] to highlight which genes accumulate predicted directional expression variability in each time window. Our analysis captures variability in genes associated with dopamine and glutamate regulation at distinct times. We also propose that one of the potential strengths of this kind of temporally-aware analysis is the integration of genetic data derived from ancient DNA and verified functional associations tested in vitro studies. We offer the example of BAZ1B, a gene known to affect facial development in *Homo sapiens* [5]. Using data validated in neural crest stem cells, we show that genetic variants linked to BAZ1B validated targets span a wide temporal window, suggesting that the molecular changes that make the *Homo sapiens* face characteristic relative to extinct human species are dependent on variation that likely predates the split event.

Overall, our work highlights the mosaic-like nature of our species history and explores a temporal dimension in genotype-phenotype that is usually overlooked, yet one that is key to start facing the challenges that our current understanding of human evolution brings.

For more details about the work, you can consult the preprint: <https://www.biorxiv.org/content/10.1101/2021.01.22.427608v1>. For reproducibility purposes, the code is also available in this repository: <https://github.com/AGMAndirko/Temporal-mapping>

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Evolutionary selection and morphological integration in the foot of modern humans

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The foot is one of the skeletal structures that is composed of meristic elements. Primates display a large variety of modes of locomotion, which is also reflected in their foot morphology. Modern humans are the only obligate bipedal extant primate, and the feet have evolved to cope with both body balance and terrestrial propulsion during walking and running accurately [1]. The conversion from a prehensile foot to a stiffer propulsion lever commendable for bipedal locomotion was possible due to a series of apomorphies in the human feet. For example, the medial longitudinal and tarsal transverse arches provide the necessary stiffness for the exertion during locomotion against the ground, the fully adducted and non-opposable robust hallux enhance propulsion during the push-off phase, and the short and strait pedal phalanges offer better performance for bipedal gait, especially during running [2].

Looking at the fossil record, most of the modern human pedal apomorphies were already present at the origin of the genus *Homo*, whereas earlier hominins displayed a mosaic of human-like feet with primitive features. These derived morphological pedal adaptations for bipedalism did not appear all at once; the general trend indicates that first early hominins (i.e., *Ar. ramidus*) had stiff lateral column of the foot for bipedal locomotion. Then, with *Australopithecus*, the hallux became relatively adducted losing the climbing ability and utilizing the medial column for bipedal propulsion. Finally, selection for long-distance walking and endurance running in early *Homo* favored short and strait pedal phalanges morphologies, losing their last primitive foot grasping abilities [2-3].

Beyond the fossil record, in the last decades other evolutionary methods such as morphological integration and the estimation of different indexes of response to selection, have been applied in palaeontological studies to better understand the evolution of organisms. Integration reflects how variability between traits is organized due to developmental and functional factors, affecting also how characters evolve [4]. Broadly, integration is seen as a factor that biases the production of new phenotypes, either by selecting negatively to the fitness or by constraining the variation exposed to selection in a determined direction. On the other hand, the indexes of response to selection evaluate the ability of a population to evolve under different scenarios, like directional and stabilizing selection, or the degree of internal constraints to evolve in the direction of selection (5). Thus, the analysis of integration, and the indexes of selection at individual foot bone level, can partially explain the differential selection process of each element, which might be mainly due to functional factors.

Here, to better understand the evolution of the human foot, we evaluate the ability of the 26 skeletal elements of the modern human's foot to evolve by analyzing both the magnitudes of integration and different index of response to selection. To do so, we collected between six and 13 linear measurements on each foot skeletal element of 247 adult male and female individuals belonging to Euroamerican, Afroamerican, European, and Amerindian populations, producing a total of more than 50,500 measurements. The results revealed that distal phalanges are less integrated, more evolvable, and more flexible than proximal elements (i.e., proximal phalanges and metatarsals). Also, bones from the medial ray (e.g., hallux) show stronger integration and weaker evolvability than their counterparts from the lateral column (e.g., fifth ray), following this trend from medial to lateral positions. Among the tarsals, the talus and calcaneus, are most integrated, least evolvable, and flexible elements from that module.

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Poster Presentation Number 54, Session 2, Thursday 2:15-3:15 pm

Locomotor behaviour of Plio-Pleistocene cercopithecoids: evidence from trabecular bone properties

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Cercopithecoids are particularly abundant in the Plio-Pleistocene African fossil record and they are often found in association with early hominins. As such, cercopithecoids are studied as a “control group” for contextualizing hominin adaptations [1]. In particular, their ecological sensitivity is useful for reconstructing the palaeoenvironments of African hominin-bearing sites and modelling environmental changes. The loads experienced during locomotor activity are relevant factors in shaping the form and structure of the skeleton [2]. Following the concept of ecomorphology, we predict that variation in the trabecular bone properties at selected skeletal sites that are sensitive to locomotor activities in fossil cercopithecoids would be useful for reconstructing locomotor behaviour and therefore infer the paleohabitats. The focal point of this study is the proximal femur (i.e., femoral head) as it represents a key-anatomical region in assessing locomotor-related functional adaptations in primate bony organisation [3]. The study sample consists of three extant *Papio* femora curated at the Evolutionary Studies Institutes of the University of Witwatersrand (Johannesburg) and seven fossil femora from the southern African hominin-bearing sites of Swartkrans (Member 1) and Sterkfontein (Member 4) housed at the Ditsong National Museum of Natural History (Pretoria) and attributed to fossil cercopithecoid taxa. The sample was scanned at the micro-focus X-ray tomography facility (MIXRAD) at NECSA (Pelindaba) where spatial resolution ranged from 18 to 28 microns. Trabecular textural and structural properties (e.g., bone volume fraction, trabecular thickness, degree of anisotropy) were assessed on standardized volumes of interest placed at the centre of the femoral head, excluding the cortical shell. Degree of anisotropy (0.5) and trabecular thickness (0.3-0.5 mm) of fossil specimens fall within the range of extant specimens (0.3-0.6 and 0.4-0.5 mm respectively). However, trabecular density is lower in fossil specimens (32-45%) as compared to extant specimens (50-57%). Collectively, these results indicate that trabecular bone textural and structural properties in the femoral head of fossil cercopithecoids reflect loading associated with terrestrial quadrupedal locomotion, suggesting an open savannah type of environment. This project offers a unique opportunity to provide further insight into the fossil cercopithecoid locomotor behaviour and the palaeoenvironmental context that Plio-Pleistocene monkeys shared with contemporaneous hominins in South Africa.

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New fossil evidence for a large-bodied hominin from Early Pleistocene 'Ubeidiya, Israel

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'Ubeidiya, Israel, dated to 1.6-1.2 million years ago, is one of a few sites with evidence for the early Pleistocene dispersal out of Africa [1]. The site contains rich lithic and faunal assemblages deriving from a clear stratigraphic context. Hominin remains are scarce and limited to adult cranial fragments and three worn isolated teeth, all assigned, by default, to *Homo* (cf.) *erectus/ergaster*. Here we report a juvenile vertebra (UB-10749) from stratum II 23 uncovered in 1966, rediscovered among the faunal remains.

UB-10749 is a complete vertebral body with no arch. There are no apparent signs of taphonomic or post-mortem modifications. Vertebral superior length to dorsal height index, which separates *Homo* from *Pan* and *Australopithecus*, places UB-10749 well within the genus *Homo*. Linear measurements and geometric morphometrics analysis identify UB-10749 as pre-sacral 2 or 3 vertebra (L3-L4). A pronounced lordotic wedging, a concavity of the inferior vertebral plate, and a lateral widening towards the inferior part of the vertebra leads us to assign UB-10749 to early *Homo* sp.

Linear measurements estimate the age at death as 11-15 years, while geometric morphometric shape analysis estimates the age as 6-10 years. In contrast, the ossification of UB-10749 visible under the microscope and a μ CT scan reveals that the vertebral arch did not ossify, and that there are no signs of endplate ossification, comparable only to a 3-6 year-old modern human. It is important to note that the vertebral arch in chimpanzee ossifies at an even younger age. Thus, while the size suggests an age equivalent to a modern human adolescent, the ossification pattern corresponds to a modern human child. The discrepancy between the size and developmental age suggests that the 'Ubeidiya *Homo* displayed a different developmental pattern than modern humans. Different growth pattern for extinct hominins species was previously suggested by several studies [2-4].

We estimate that UB-10749 was 6–10 years old at death, and predict an adult size for UB-10749 upward of 180cm and 65kg. Based on these estimations, UB-10749 does not belong to small-bodied hominins such as *H. habilis* or *H. georgicus* and instead exhibits biological affinities to east African large-bodied early Pleistocene hominins, such as penecontemporaneous KNM-WT 15000.

The difference between the putative larger size of the UB-10749 with the more diminutive stature of the Dmanisi paleodeme may be reflected in the difference in lithic traditions between the two sites (Oldowan vs. Acheulean) and indicative of two distinct out-of-Africa dispersal events [5].

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Internal bone architecture in the triquetrum of extant hominids and *Homo neanderthalensis*

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Bones on the radial side of the wrist have dominated research on the evolution and functional anatomy of the hominoid carpus. However, soft and hard tissue structures at the ulnar side of the wrist, such as reduced ulna-triquetrum articulation and the Triangular Fibrocartilage Complex (TFCC), are some of the most conspicuous synapomorphies among hominoids linked to high degrees of ulna-deviation and forearm supination [1,2]. However, there is also notable variation in the bony and soft tissue anatomy of the ulnar wrist among hominoids that affects how loads are transferred from the hand to the forearm but are not clearly understood, in part because the functional morphology of the triquetrum is understudied. Here we investigate for the first time the internal trabecular bone structure of the triquetrum and test the null hypothesis that great apes will exhibit similar distributions of relative trabecular bone volume to total volume (BV/TV) and degree of anisotropy (DA).

Using a whole-bone methodology (<http://www.dr-pahr.at/medtool/>) this study quantifies BV/TV and DA in the triquetrum in *Pongo* (n=12), *Gorilla* (n=10), *Pan* (n=10) and a temporogeographically diverse sample of modern humans (n=21), in comparison to three *Homo neanderthalensis* individuals (El Sidron SD-1227, Tabun C1_1-154, and Amud 1). The distribution of BV/TV and DA values are visualised across the entire bone using Paraview (3.89.0). Low DA was identified as values equal to or less than 0.20. High BV/TV was identified as the top 20% of values for that individual's range. In line with presumed force transfer at the ulna-side wrist in hominoids [2], it is predicted that the low DA values will be present at the TFCC insertion site, with the high BV/TV at the lunate and hamate articulations.

Low DA was observed at the TFCC insertion site in 41% of *Pongo*, 100% of *Gorilla*, 90% of *Pan*, 100% of *Homo neanderthalensis*, and 76% of *Homo sapiens*. High BV/TV was observed at the hamate articulation site in 75% of *Pongo*, 90% of *Gorilla*, 70% of *Pan*, 100% of *Homo neanderthalensis* and 61% of *Homo sapiens*. High BV/TV was observed at the lunate articulation site in 91% of *Pongo*, 20% of *Gorilla*, 0% of *Pan*, 33% of *Homo neanderthalensis*, and 0.04% of *Homo sapiens*.

Overall, these results suggest relatively consistent interspecific patterns in the trabecular structure of the triquetrum which contrasts the interspecific variation reported in some previous studies, including the capitate [3]. DA predictions were supported for all species except *Pongo*, where there was only partial support. Predictions for high BV/TV at the triquetrolunate joint were broadly supported while predictions for high BV/TV at the triquetrolunate had mixed support. This pattern suggests that force transfer between the lunate and triquetrum is lower than that between the hamate and triquetrum. *Pongo* is the exception to this pattern with 91% exhibiting high BV/TV at the triquetrolunate joint, which, when combined with the DA results, may reflect a less-developed TFCC [2] and a greater reliance on the (relatively large) lunate to support ulna-side force transfer compared with other great apes. Although the Neanderthal triquetrum morphology is primitive relative to *H. sapiens* [4], all three show a BV/TV and DA pattern most similar to that of modern humans. This suggests a similar force transfer pattern at the ulna-side wrist in Neanderthals despite this primitive morphology. There is considerable debate as to whether Neanderthals utilised the same grip patterns as modern *H. sapiens* and the ulna-side wrist may shed light on the importance of carpal morphology in predicting force transfer and grip types among hominins.

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Lake-level changes and their paleo-climatic implications at the MIS12 Lower Paleolithic (Middle Pleistocene) site Marathousa 1, Greece

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The Megalopolis Basin (central Peloponnese, southern Greece) comprises complex cycles of fossil-rich detrital and lignite seams, deposited during the Middle Pleistocene. The current working hypothesis is that the sediments reflect the glacial-interglacial cycles, with the cold and dry conditions of the glacial leading to the deposition of the detrital seams and the warm and moist conditions of the interglacial resulting in the formation of the lignite seams [1,2]. Excavations at the site Marathousa 1 (MAR-1) exposed a 6-m thick profile between the two upper lignite seams, containing lithic artifacts and faunal remains (including elephant bones) with cut-marks, indicating hominin activity occurring along a paleo-shoreline ca. 444 ka ago [3, and references therein]. However, the local environmental and climatic background conditions of human presence in the area during the MIS12 glacial remain largely unknown. For a better temporal constraint on the archaeological site MAR-1 and the sedimentary units, a Bayesian age model was constructed, placing them at ~463–427 ka [4]. In order to reconstruct the paleo-environment, including paleo-lake levels and governing paleo-climatic factors, the MAR-1 sedimentary sequence was analyzed in high resolution with a multiproxy approach covering ostracods, sponge spicules, diatoms, grain sizes, total organic carbon, total inorganic carbon and conventional X-ray fluorescence analysis. Results reveal MAR-1 as a protected intermontane region, which was constantly influenced by water: at times a shallow, partly anoxic water body surrounded by reed belts; a riverine-lake deltaic system; a floodplain; or a seasonal freshwater pond. The local environment appears to react to large trends and rhythms of regional Mediterranean records, as well as directly to sea surface temperature changes in the North Atlantic. Specifically, when the sea surface temperature was high, more moisture reached the study area, and vice versa. Another source of water are the surrounding glaciers, which melted after brief warming periods in the Mediterranean during MIS12, leading to the formation of small freshwater ponds, in which the horizon containing the excavated remains was deposited. Such ponds, rich in ostracods and other microorganisms, provided mammals and hominins valuable resources, such as potable water, a wide range of plant species and hunting opportunities. Consequently, these kinds of deposits contain a high archaeological potential. The results from our study suggest that the Megalopolis Basin served as a refuge for hominins and other organisms due to its capacity to retain freshwater bodies during glacial and interglacial periods.

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Bone breakage experiments under the microscope: modelling an archeological situation in bone fragmentation at Upper Paleolithic Pavlov I site, Czech Republic

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Bone fragmentation represents a direct evidence of deliberate human activity connected to the exploitation of animal resources in the Upper Paleolithic. Specific diagnostic traces enable us to distinguish between different fragmentation agents of the biotic and abiotic origin. However, they are oriented mainly on macroscopic features (e.g., angle, outline, or surface of fracture). Every single fracture begins at a micro-level and the final differential characteristics on the macroscale result from various mechanic forces spreading in bone structure. In this contribution we used several methods of microscopy. (A) Through scanning electron microscopy (SEM) we observed irregularities in bone fracture surface. These changes tend to be noticeable especially for the helical type of fracture, of course within direct dependence on the force type causing the cortical bone failure [1]. (B) The traces after micro-cracking were documented in detail by transmitted light microscopy. Naturally, microfractures are typical diagnostic markers for other taphonomic bone alternations (e.g., burning), thus precise description of their characteristics helps to reveal the primary agent of the observed modification. Both selected methods were applied on experimental material with known fragmentation history. The first experimental set consists of bones with different stages of preservation (dried, frozen, fresh, with or without tissues) broken by the rockfall [2]. Individual specimens were chosen based on the fragmentation freshness index (FFI) [3]. The precisely selected samples with fracture surfaces (squares 1×1 cm) were studied under SEM and then subjected to histological thin section preparation and analysis. Another experimental set, which consists of fresh bones with and without periosteum intentionally broken by humans, was subjected to macroscopic evaluation, and expected outcomes with respect to acquired knowledge were considered. Finally, we discuss obtained results and potential application of used methods in relation to the archeozoological assemblage from the Upper Paleolithic site Pavlov I (Czech Republic).

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Paleoenvironmental insights by stable isotopes and phytoliths at Simbiro III Monumental Section (~1.2-1.3 Ma) (Melka Kunture, Upper Awash, Ethiopia)

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Stable isotopes and phytoliths analysis have been widely used in archaeological research, providing key information in the study of paleoclimate and paleoecology, and allowing to test hypotheses on adaptation and habitat changes in Africa during human evolution.

Here, we report on both stable isotopes (¹³C, ¹⁸O) (14 fossil teeth samples) and phytoliths (12 sediment samples) from Simbiro III Monumental Section, investigating the plants' signal and the dietary patterns of herbivores.

The so-called Monumental Section (MS) of Simbiro III is part of the Melka Kunture cluster archaeological sites on the Ethiopian highland, at ~2000 m a.s.l. The MS looks like a ~5 meters-high cliff. It includes the impressive remnant of multiple layers deposited before ~0.9 Ma and currently dated at ~1.2-1.3 Ma, and which were cut by natural erosion and left in full view. The archaeological levels investigated here are from top to bottom Levels A, B, C, and C' from MS, and Level D adjacent to MS.

Isotopic results on bulk enamel samples from the archaeological levels (except levels C and C', due to the lack of fossil faunal remains) indicate that hippopotamids, bovids, and equids were mainly grazers, consuming C₄ plants all through their lifetime. Isotopic carbon data, accordingly, point to C₄ grassland developing in the area. Intra-tooth analysis carried out on a hippo tusk indicates stable C₄ diet and water conditions during the growth of the tusk. Pleistocene hippopotamids, however, were more opportunistic than the other analyzed mammals, and also include an amount of C₃ plants in their diet. Fossil phytolith assemblages from levels B and C' are rich in grass and sedge phytoliths (60% on average). Forest indicators including conifers and woody dicots phytoliths do not exceed 20% and are particularly abundant in level B. Especially in samples from level C', diatoms of the pennate type, sponge remains, and/or *Chrysophyte* cysts were also present suggesting open or marsh wetland. In the time interval sampled here, around the MS graminoids were dominant, growing in an area seasonally underwater. Forests or woodlands including broadleaved trees and shrubs, and conifers, likely developed at some distance. The grass phytolith assemblages indicate that dominant grasses were likely mesophytic *Panicoideae* (which include many C₄ species but also species using the C₃ photosynthetic pathway), and C₃ high-elevation *Pooideae*, while xerophytic C₄ grasses were rare at Simbiro III MS.

Our results show how stable isotopes results from mammal teeth indicate a C₄ diet which is the outcome of ecological factors and behavior, including the selection of preferred plant species. Instead, phytoliths analysis allows characterizing the distribution of local plants at the time of deposit formation. Accordingly, the data are complementary to each other, allowing to reconstruct both the environment "on spot", and the vegetation landscape at a slightly larger distance.

The retrodeformation of the cranium from Steinheim an der Murr, Baden-Württemberg, Germany

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The morphological study of fossil specimens must take into consideration the effects of taphonomic processes, that may severely distort or worse remove important shape information [1]. One of the strategies used to address this issue is the restoration of the specimen to conditions approximating a state prior to the taphonomic modifications. Nowadays this can be done by applying digital tools, in a safe virtual environment [2]. Most of such software works by restoring the symmetry of the object, through mirroring or retrodeformation. The former is useful to reconstruct missing or damaged parts of specimens, however, it is prone to the generation of artefacts or morphological biases due to possible deformations present on the preserved counterpart. The retrodeformation is calculated by sampling bilateral landmarks and semi-landmarks (e.g., curves and/or surface patches). Differently from mirroring, the power of retrodeformation is limited by the preservation of portions carrying bilateral homologous points.

An interesting case-study is the cranium from Steinheim, found in 1933 near the town of Steinheim an der Murr, in Baden-Württemberg (Germany) and tentatively dated between 300 and 250 ka [3]. In addition to missing almost the entire left side of the face, Steinheim is also affected by a complex pattern of taphonomic deformations. Simple mirroring of the right side of the specimen, therefore, would lead to a biased morphology. On the other hand, retrodeformation is limited by the lack of bilateral reference points. A recent protocol [1] overcomes the latter issue by maximising the use of curves and patches of semi-landmarks during the retrodeformation. We applied this protocol to a 3D mesh of the Steinheim cranium. We sampled 52 bilateral landmarks and 8 curves of evenly spaced points on its preserved portions. The curves were computed by the function *equidistantCurve* of the R package Morpho [4]. We used the Arothron [5] and Morpho R packages to also generate a patch of 500 bilateral semi-landmarks on preserved portions of the neurocranium, the face and the palate. The retrodeformation protocol was then applied, following Schlager and colleagues [1]. The local displacement registered on the resulting reconstruction was then calculated and visualized by the function *localmeshdiff* of the Arothron R package, to assess the local taphonomic deformations on the specimen. We performed a principal component analysis on a landmark configuration built on the preserved and symmetrized portions of Steinheim and including both modern and fossil human comparative samples. Results placed the restored model of Steinheim closer to the Neanderthal cluster. The retrodeformed reconstruction, therefore, allows the assessment of several important anatomical regions, including the parietals, occipital and nasal region, helping to place Steinheim more firmly in the Neanderthal evolutionary lineage.

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The phylogenetic definition and mode of evolution of the genus *Homo* - A new conceptual approach

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No consensus exists in human evolution research regarding the definition of the genus *Homo* and its mode of evolution. Using a database of 391 craniodental characters scored on 22 hominin species from Late Miocene to Holocene, we address these two questions with a quantitative and innovative taxonomic approach that combines a tree-like Maximum Parsimony (MP) phylogenetic reconstruction protocol, and a web-like Phylogenetic Networks (PN) method [1]. Our methodological approach follows three logical steps as follows:

1. Implementation of a tree-based MP protocol with the complete dataset to select the most parsimonious tree scenario out of 16 numerical runs based on various algorithmic constraints. This scenario highlights hypothetical ancestor-descendant relationships among the 22 hominin species that serve to suggest phylogenetic definitions of the genus *Homo*.

2. Intermediate step to establish a methodological link between the MP and PN analyses. We execute an MP run based on apomorphies identified from the most parsimonious tree obtained in step 1 and generate multiple most parsimonious trees (MMPT) as input for the PN analysis. This run allows one to verify the phylogenetic signal of the most coherent scenario from step 1.

3. PN analysis based on input of MMPT from step 2 that produces a consensus tree, a consensus network and a reticulate network. From the reticulate network we infer whether or not the phylogenetic relationships among the hominin species of the dataset are of a reticulate nature or not.

Based on our MP protocol, we identify three most parsimonious *Homo* definitions based on cumulative distinguishing feature changes (apomorphies) in support of the respective hypothetical last common ancestors (LCAs). These definitions are illustrated by a novel graphical elliptic representation. We analyze the complexity of hominin evolutionary processes by means of the PN method and propose the following inferences: 1) for the late Miocene-Pliocene taxa from *Sahelanthropus tchadensis* up to *Australopithecus africanus*, the reading of the reticulate network shows no evidence of diffuse ancestral radiations but rather directional adaptive anagenetic changes with uncertain cladogeneses during this chronological interval, and 2) more importantly, we show the probable web-like reticulate mode of evolution of the genus *Homo* since it emerged 2.8 Ma ago with the survival of only one paleospecies, *Homo sapiens*. Our coherent results confirm a paradigm shift in the study of human evolution in favor of reticulation, in accord with numerous recent paleogenomic findings.

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Middle Paleolithic occupations in the Escoural Cave (southern Portugal): preliminary geoarchaeological results

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The cave of Escoural (Alentejo, southern Portugal) was accidentally discovered in 1963 as a result of quarry blasts that opened an artificial entrance to the cave. Since then, the site has been mostly known for its rich set of rock art, stylistically attributed to the Solutrean and the Aurignacian techno-complexes [1]. In the top levels of the cave, an impressively well-preserved Neolithic burial ground was almost completely excavated during the late 1960s. Between 1988 and 1992 the last series of archaeological testing occurred at the southern end of the site, revealing a different set of occupations attributed to the Middle Paleolithic, spanning close to 1.5 meters of the stratigraphy, and generically dated by U-Series to 48.900 ± 5.500 BP [2]. The excavators hypothesized that the Middle Paleolithic artifacts were deposited by colluvial processes, which originated from outside the cave. However, limited information was published about the site lithology, its archaeological assemblages and dating.

To achieve a better understanding of the formation and archaeological contents of the Middle Paleolithic deposits of Escoural, we re-investigated the southeastern chambers and the area outside its entrances. We identified and expanded previous test pits and collected new archaeological, faunal, anthracological, and micromorphological materials. This poster presents the preliminary results of the analysis of these materials.

From a geoarchaeological point of view, we were able to confirm that the sediments were accumulated by erosional processes, likely originating from upslope areas within the karst system and the above plateau, although the orientation and tilting of the piece plotted materials do not show any specific pattern. The reworking of these materials was not a continuous process, but it alternated with periods of stability, during which carbonate crusts formed, particularly in the inner part of the cave. This seems to indicate that the possibility to isolate separate Neanderthal occupations at Escoural and reconstruct their relationship with past environments is not entirely precluded. Fauna remains, composed mostly of red deer, horse, wild boar, and carnivores, are abundant, but only in the upper part of the deposit. The quartz-dominated lithic assemblages are marked by the presence of very few typical Mousterian implements, and the presence of laminar blanks. In combination with pending absolute dating results, these new data will allow to significantly advance the state of the art regarding Neanderthal occupations in a region (southern Portugal) for which there is currently little data available [3].

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Is a well-developed calcar femorale evidence of bipedal locomotion?

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The calcar femorale (CF) is an internal bony structure of the proximal femur that has been considered as functionally linked to bipedal locomotion and has recently received revived attention due to its purported presence in the early fossil hominin *Orrorin tugenensis* [1]. It is a spur of thickened bone that variably extends deep to the lesser trochanter and projects laterally and distally towards the greater trochanter [2]. Beyond its identification in recent humans [2], the potential presence of a CF among non-human primates has only been investigated in *Pan* [1] and a reportedly “strong calcar” in a Pliocene hominin identified as habitually bipedal [3].

To address this gap, we investigated the occurrence, 3D morphology and size variation of the CF using microtomography in a comparative mixed sex, adult sample of humans (n=10, including left and right femora for 5 individuals to check for bilateral asymmetry), *Pan troglodytes* (n=10), *Gorilla gorilla* (n=10), *Pongo* sp. (n=9), and *Papio ursinus* (n=5). We also investigated the development of the CF in four immature human femora (4, 6, 7 and 10 years-old). We first automatically segmented the cortex from the trabecular bone, and manually extracted the CF for 3D rendering. We measured the following variables: Periosteal-to-tip maximum length (PT MaxLength) - distance between the periosteal surface and the farthest-most point of internal extension of the CF (the tip); CF maximum length (CF MaxLength) - distance from the root to its tip (not taking into account cortical thickness); CF maximum width (CF MaxWidth) - distance between the most anterior and posterior limits of the CF root; and CF maximum vertical extension (CF MaxHeight) - distance between the lowest and the uppermost extracted slices bearing evidence of a CF. To allow for intergeneric comparisons, the body size-related superoinferior diameter of the femoral head was used to standardise all measurements.

Our results indicate that all extant adult and subadult humans, apart from one 30-49 year-old male, had a well-developed CF, with no evidence of appreciable bilateral asymmetry. Among the great apes, 6/10 *Pan* (4M, 2F) and 6/10 (4M, 2F) *Gorilla*, the latter all wild individuals, showed a distinct CF. In *Pongo*, a fully-developed CF was found only in one captive male individual and none of the *Papio* specimens showed any trace of a CF. Compared to *Pan*, extant humans had a significantly higher absolute and relative CF length, while intermediate values associated to a wide range of variation were found in *Gorilla*. When scaled to femoral head diameter, CF width did not discriminate across taxa. In the non-human great apes, the CF distal portion was commonly confined to the proximal half of the lesser trochanter compartment, while in humans it systematically extended into its lower part and was associated with significantly higher CF MaxHeight values. However, a human-like distally extended CF was also present in a female *Gorilla*.

In humans, the CF is considered to be related to the iliopsoas tendon insertion on the lesser trochanter and to weight transmission through the hip joint by providing bone stiffness and resistance to torsion in the femoral neck [4,5]. The identification of a CF in great apes, including in *Pongo*, and its morphological and dimensional variation across all taxa, including humans, provides an important new comparative context from which the functional significance of this feature is unclear. Among the investigated features, only a more vertically extended CF appears as a human autapomorphy. This comparative context of the CF should be taken into consideration when reconstructing locomotor behaviour in the hominin and primate fossil record.

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Late Pleistocene to Holocene palaeoenvironmental reconstruction and human behaviour at Iho Eleru rock shelter, Nigeria

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The Ihò Eléérú (here named Iho Eleru in its anglicised rendition, and erroneously known as “Two Eleru”) rock shelter (7°26'28.83"N, 5°7'29.16"E) is located within the hilly ancient igneous landscapes near Akure, Nigeria. It is widely known for the discovery of the only West African Pleistocene hominin fossil remains, identified as *Homo sapiens* associated with Later Stone Age (LSA) technology [1-2]. While the modern regional vegetation has been extensively modified by human activity, the environmental context of these fossils as associated with tropical rainforest has been debated [3]. Between 1964 and 1965, T. Shaw and S.G.H. Daniels conducted a series of excavations at the rock shelter [4], revealing a terminal Pleistocene to middle Holocene sequence documenting a history of recurring human occupations ranging from the LSA into the Holocene. Here, we present new findings following an expedition to the Iho Eleru rock shelter, and an inspection of the storage rooms of the Department of Archaeology and Anthropology at the University of Ibadan which took place in November 2019. During the re-analysis of the remaining assemblages excavated at Iho Eleru, J.N. Cerasoni and authors found: (1) the entirety of the excavated charcoal collection (65 bags), with samples ranging from the uppermost to the lowest excavated levels, and (2) the entirety of the vertebrate faunal assemblage (59 bags) which was originally thought to be lost and has never previously been described. The original context identification tags were intact for each bag of charcoal and faunal remains. We present new data from the analyses of these unique assemblages. Firstly, fourteen new ¹⁴C dates from charcoal and faunal bone samples were obtained, originating from consecutive archaeological layers spanning two adjacent trenches and the entire depth of the stratigraphic section where the Iho Eleru human fossil was discovered. Secondly, we present anthracological identifications from the charcoal collection, and taxonomic identification and taphonomic analysis of the Iho Eleru vertebrate faunal assemblage, making it the first West African Pleistocene faunal assemblage ever discovered and described. Finally, isotopic analyses were carried out on the faunal assemblage. We synthesise these results with climate reconstructions spanning the last 22,000 years [5] for the area surrounding Iho Eleru to reveal the consistent human habitation of a mosaic forest-savannah ecotone.

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Taphonomic approach to the faunal assemblages of the Middle Pleistocene sites of Oxígeno and Santa Elena (Manzanares Valley, Spain)

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The valleys of the Manzanares and Jarama rivers preserve one of the largest concentrations of Pleistocene sites in Europe, and feature plenty of discoveries of lithic industry and faunal remains that have taken place since 1862 [1]. The sites Oxígeno and Santa Elena are located in what is known as the Complex Terrace of Butarque (CTB) downstream from Madrid, to the last stretch of the Manzanares river, where it flows into the river Jarama. In this area the stepped terraces system disappears and gives way to the CTB, thanks to the dissolution of an underlying karst subject to a syndimentary subsidence process, which gives rise to the thickening of the alluvial deposits, which can reach several tens of meters [2]. Different numerical dates obtained in several spots of the CTB visible base suggest that the bottom of the CTB was deposited during MIS 6 or even MIS 7 [1].

The lithic series of Oxígeno (9,440 pieces) and Santa Elena (2,556 pieces), although fairly unpublished [3], have been described as Large Flake Acheulean on flint, and possible Middle Palaeolithic industries [4]. The presence of handaxes with broad bilateral and bifacial configuration, which occasionally show retouch and edges conformed with soft hammer, and among which amygdaloidal silhouettes predominate, is outstanding both in Oxígeno (4%) and in Santa Elena (6%). Trihedrals and cleavers are also present in both series. Retouched elements are more common in Oxígeno (13%) than in Santa Elena (8%), with scrapers the best represented (37% of the retouched pieces of Oxígeno and 24% of Santa Elena).

This taphonomic study, the first complete one for both collections [5], brings to light a complex taphonomic history when trying to understand these faunal accumulations. 445 fossil elements have been recorded at Oxígeno, consisting of remains of *Bison priscus*, *Bos* cf. *primigenius*, *Bos/Bison* sp., *Cervus elaphus*, *Equus caballus*, *Equus hydruntinus*, *Elephas antiquus*, *Elephas* sp., *Mammuthus* sp., *Megaloceros matritensis* and *Stephanorhinus* sp. The most commonly represented element are cranial fragments of *Elephas* sp. (24,71%); as well as teeth and mandibular fragments of *Bos* cf. *primigenius* (12,58%). With regard to Santa Elena, 130 fossil elements have been recorded, which have been identified as those of *Bos* cf. *primigenius*, *Bos/Bison* sp., *Cervus* sp., *Equus caballus*, *Equus* sp., *Elephas antiquus*, *Mammuthus* sp., *Megaloceros* sp., *Stephanorhinus hemitoechus* and *Stephanorhinus* sp. Here, the best represented elements are fragments of *Bos/Bison* sp. (25,38%) horns and of *Elephas* sp. (23,84%) tusks, although taking into consideration the number of molars and premolars, the most abundant taxon (NISP) is *Equus caballus*. Taphonomic processes of weathering, abrasion, rounding, concretion and trampling, among others, have been identified in both assemblages. The incidence of processes related to fluvial transport is higher in Oxígeno than in Santa Elena, where abrasion and rounding are virtually absent. In both sites post-cranial bones are better represented than cranial bones, and their preservation is better. Dismemberment cut marks have been identified on a humerus of *Bos* cf. *primigenius* in Santa Elena. No cut marks have been preserved in Oxígeno. However, the preservation of the bone surfaces is not good, and therefore the lack of human action cannot just be assumed. Additionally, despite carnivore remains not being identified among the fossil elements, several tooth marks of that type of animals have been recorded: small pits and scores at Oxígeno; as well as pits and furrowing on *Bos* cf. *primigenius* and *Megaloceros* sp. bones at Santa Elena. The presence of human and carnivore activity makes it even more complicated to interpret the origin of the accumulation of these faunal assemblages associated with Acheulean industries.

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Brain differences between *Homo sapiens* and Neandertals and their potential cognitive consequences

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Despite the ‘perceived wisdom’ that the only differences between *Homo sapiens* and Neandertals which resulted in the latter’s extinction was demographics [1], brain differences and their potential cognitive consequences between the two human types have either been ignored or considered inconsequential. Interestingly, demographic factors such as population density and geographical location may still be a partial function of biological factors, because as E. O. Wilson has insightfully noted, biology places a tight leash on culture. The purpose of the present paper is to summarize three major brain differences between these two groups. Bruner [2] may have been the first paleoneurologist to determine that *Homo sapiens* skulls had a clear expansion of their parietal lobes compared to Neandertals. Coolidge [3] explicated the modern cognitive functions of the parietals that included visuospatial imagining, representations of self and others, and a sense of numbers which included differentiation of 1, 2, and 3 things and small and large set discrimination. Bastir et al. [4] noted that the olfactory bulbs of *Homo sapiens* were approximately 11% larger than those of Neandertals based on the size of the cribriform plate. The cribriform plate is a sieve-like structure located in the anterior nasal cranial fossa that allows input from the olfactory epithelium in the nasal cavity directly into the olfactory bulbs. Olfaction has been shown to be critical in mate selection and immunity responses. Thus, the possibility that larger olfactory bulbs may result in finer olfactory discriminations cannot be easily dismissed, as there is some empirical evidence with modern humans that the latter is the case. Kochiyama et al. [5] and others have shown that the cerebellum to cortex ratio is larger in *Homo sapiens* than in Neandertals, and the cerebellum has been shown to have a variety of cognitive functions including insight, creative thinking, and novel problem solving in addition to its well-known role in the refinement of motor movements. Thus, although the overall brain volume of Neandertals may have been equal to or exceeded the volume of modern *Homo sapiens*, there were demonstrable brain shape and brain region differences with potential significant cognitive consequences that may have played a role in evolutionary success of *Homo sapiens* and the extinction of Neandertals.

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An analysis of morphological evolution in the hominid lower limb using methods from quantitative genetics

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Morphological differences are a common line of evidence in studies of evolutionary processes, but it is difficult to distinguish evolutionarily significant traits among the measurable morphological features. Quantitative genetics, which focuses on the evolution of continuous traits, provides mathematical frameworks for estimating the evolutionary pressures on lineages and individual traits. The application of quantitative genetics methods to phenotypic data can therefore help researchers identify potential directional selection in morphological evolution [1,2]. Lande's generalized genetic distance (GGD) is one method that can provide insight into the strength and direction of selection over evolutionary transitions and allow us to estimate whether observed morphological change is the result of directional selection on the observed trait or an indirect change influenced by selection on other traits [1,2]. These applications are especially useful in the study of evolution in the *Homo* lineage where change is often assumed to be adaptive [3,4].

This study tests for directional selection in the morphological evolution of the hominid lower limb using 45 interlandmark distances (traits) on the os coxa, femur, tibia, and fibula of *Homo sapiens* (n=35), *Pan troglodytes* (n=34), *Gorilla gorilla* (n=35), and *Pongo pygmaeus* (n=30) using Lande's GGD. Estimates of ancestral traits were calculated for three ancestral nodes: the last common ancestor (LCA) of *Pan* and *Homo*, the LCA of African apes, and the LCA of hominids, using a rapid maximum likelihood algorithm [5]. Mean estimated ancestral traits and mean traits of extant taxa were then used to calculate Lande's GGD for each evolutionary transition. Genetic drift cannot be rejected as the primary evolutionary force in the branch from the LCA of African apes to *G. gorilla*. Strong directional selection was identified in two transitions: the branch from the LCA of *Homo* and *Pan* to *H. sapiens*, and in the branch from the LCA of *Homo* and *Pan* to *P. troglodytes*. Strong stabilizing selection was identified in all other branches.

Selection gradients (representing estimated magnitude and direction of selection pressure on each trait) and selection responses (representing estimated magnitude and direction of real morphological change in trait size from ancestor to descendant) were calculated for the two branches under strong directional selection. Large selection gradients were indicated in the os coxa, tibia, and femur in the branch leading to *H. sapiens*. Decreased height of the os coxa, increased diameter of the femoral head, and elongation of the tibia were under the strongest directional selection. Large selection gradients also were indicated in all four elements on the branch leading to *P. troglodytes*. Here, increased height of the os coxa, decreased anteroposterior breadth of the acetabulum, and decreased diameter of the femoral head were under the strongest selection.

The pattern and magnitude of selection gradients were different among the lineages, indicating that they experienced unique evolutionary pressures resulting in directional selection on different morphological traits. Both lineages also showed large estimated selection responses in traits that were not estimated to be under strong directional selection, or responses to selection opposing the selective pressures on the trait. This indicates that, for these traits, the morphology of the descendant branch was not the result of direct selection. These traits included morphological features that are often assumed to be adaptive, such as the relative size of the tibial plateau in *H. sapiens*. Overall, results indicate the morphology of lower limb elements is derived in both *P. troglodytes* and *H. sapiens*, and emphasize the need to separate observed morphological change from evolutionarily significant morphological change when investigating evolutionary morphology, particularly in the *Homo* lineage.

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Ontogenesis of femoral biomechanical properties in non-human primates: study of olive baboon

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The positional repertoire of primates changes with age, from a diversified form combining several modes in infancy to a more stereotyped form in adults. It is assumed that mechanical stresses imposed by locomotion influence the cortical structure of limb bones [1]. Biomechanical properties of the bones through age should thus change in parallel with the positional repertoire [2]. In olive baboon (*Papio anubis*) the repertoire is initially dominated by grasping during the first months of life while infants are not fully independent from their mother. Around 5 months old, the locomotor autonomy is established; the repertoire becomes quickly dominated by terrestrial quadrupedalism (60.2% of locomotion), associated with other modes in variable proportions (for example climbing, leaping and bipedalism represent 27.5%, 5.4% and 1.9% of the locomotor repertoire respectively). In adults, the repertoire is much more stereotyped with an extreme predominance of terrestrial quadrupedalism, with 98.7% of the locomotor repertoire [3]. One can expect an early and quick shift in the biomechanical properties of the femur toward the adult pattern with a transitionary period from the acquirement of the locomotor autonomy in infancy. Here we evaluate this possible link through development by studying the biomechanical properties of the femur in an ontogenetic sample of olive baboons for which behavioral data are available [4].

We studied femoral cross-section geometry parameters and cortical thickness maps [5] of an osteological ontogenetic sample of 65 olive baboons from newborn to 28 years old individuals; they originate from the Primatology Station of the CNRS (Rousset-sur-Arc, France) and belonged to a single social group living in a controlled environment. We then confront the results by age classes to the available behavioral knowledge for this colony [4].

Cross-section parameters in newborns highlights a sub-symmetric longitudinal distribution of the cortical, an amount of cortical area that is higher than in later stages and associated with an antero-posteriorly oriented bending and tension rigidity. In later stages, from infancy to adulthood, the longitudinal distribution of cortical is asymmetric with a thick proximal part and a thinner distal part. The distal half of the diaphysis shows mediolateral orientation of bending and torsion rigidity, and balanced orientation in proximal half. Concerning the consensus thickness maps, newborns show a central and posterior thickness hotspot. In infants this area elongates posteriorly and the distal shaft becomes thinner. Juveniles and adults show a common cortical distribution with thin distal part and two longitudinally extended areas of high thickness in proximal posteromedial and posterolateral locations.

Our results highlight an early and rapid transition from the newborn condition to an adult-like pattern as soon as the locomotor autonomy is established. At this period, although combined with other modes such as leaping, vertical climbing and bipedalism, terrestrial quadrupedalism already represents an important component of the repertoire. Even if it is not as predominant as it is in adults, the evolution of the femoral cortical distribution reveals that the impact of quadrupedalism is already preponderant when compared to other locomotor modes from the onset of locomotor autonomy in olive baboons.

This highlights the difficulty of accounting for the diversity of the locomotor repertoire from femoral biomechanical properties and invite to caution when inferring from morphology complex behaviors such as these of primates.

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Postcanine EDJ morphology in *Homo habilis* and its implications for the evolution of early *Homo*

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A large portion of the *Homo habilis* hypodigm consists of dental remains, including the key specimens from Olduvai Gorge in Tanzania. The type specimen of the species, OH 7, includes the mandible with a nearly complete tooth row, and specimens such as OH 13 and OH 16 preserve mandibular and maxillary tooth rows. Teeth are useful in studying hominin systematics, and the outer enamel surface (OES) morphology of the *H. habilis* dentition has been studied extensively. Relatively few features of the postcanine dentition are considered distinctive in *H. habilis*, but the mandibular premolars and molars are frequently described as being buccolingually narrow [1]. Based on new microCT scans we investigate the enamel-dentine junction (EDJ) morphology of *H. habilis* postcanine teeth from Olduvai Gorge, early *Homo* specimens from Koobi Fora (Kenya), *Australopithecus afarensis*, *A. africanus*, *Homo erectus* s.l., and later *Homo* (modern humans, Neanderthals, and middle-Pleistocene *Homo*). We use geometric morphometrics to quantify EDJ shape of every postcanine tooth position for these taxa.

We find that for a number of *H. habilis* specimens, the postcanine dental morphology is very primitive. Type specimen OH 7, as well as OH 24 and several Koobi Fora specimens (KNM-ER 1802, KNM-ER 1813), show an EDJ morphology that is largely within the range of variation for *Australopithecus* and retain several primitive features. However, there are a number of features of the postcanine EDJ morphology that reliably distinguish later *Homo* from *Australopithecus*, including an increase in the height of the dentine body (defined as the distance between the cervix and marginal ridges) in all tooth positions, reduction of the talon or talonid in the premolars, and reduction in the distal aspect of the crown of the upper molars. Our findings are consistent with previous work emphasizing the generalized postcanine dentition of *H. habilis* [1]. Contrary to previous work [1,2], our EDJ shape analyses do not suggest that *H. habilis* is characterized by buccolingually narrow mandibular molars and premolars, in line with observations on the outer enamel surface [3]. However, there are some aspects of the postcanine dentition that we find to be more distinctive; for example, the maxillary third molars of *H. habilis* are distinguished from those of *Australopithecus* by the presence of a further mesially placed metacone and a mesiodistally shorter crown.

We also find variation within the *H. habilis* hypodigm. While Bed I Olduvai specimens such as OH 7 and OH 24 show a largely primitive morphology, some Bed II specimens show a more derived morphology. This is most notable in OH 16, which displays a suite of derived features, particularly in the mandibular and maxillary premolars, which show a tall dentine body and a reduced talon/talonid region; in these respects the specimen is more derived than the early African *H. erectus* sample. OH 13 is the youngest specimen assigned to *H. habilis*, and although it shows some derived aspects of postcanine morphology, other key features are more similar to Bed I specimens such as OH 7, which is consistent with the mandibular dental arcade shape [4].

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Bringing blood to the brain: how to estimate the size of the vertebral arteries in fossil specimens

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Owing to the central role of the brain in the emergence of modern human biology and behaviour, the question of how to 'feed' an evolving brain, and thus how the hominin brain vascular and metabolic system changed through time, is of particular interest [1]. In addition to the internal carotid arteries, vertebral arteries contribute significantly to the cerebral and cerebellar blood flow and, consequently, provide the brain with oxygen and glucose. Since soft tissues do not fossilize, the total encephalic arterial canal area (i.e., the areas of the carotid canal and of the transverse foramina in the cervical vertebrae) has been suggested to represent the most reliable proxy for estimating brain perfusion and metabolism in fossils [2,3]. Given the rising interest in the study of vertebral arteries in fossil hominins (e.g., [4]), here we statistically explore spatial relationships between the transverse foramina and the vertebral arteries in the cervical segment of the extant human vertebral column. Contrast computed tomography (CT) scans of the cervical regions of 11 living human individuals were collected from a South African hospital with a slice thickness varying from 0.5 to 1 mm. Cross-sectional areas of the right and left transverse foramina and the corresponding vertebral arteries were measured on each cervical vertebra from C1 to C6 within the same individuals. The cross-sectional areas of the right and left foramina and the left and right arteries range between 13.4 and 71.3 mm² (with a mean of 33.0 mm²) and between 4.5 and 29.4 mm² (with a mean of 12.1 mm²), respectively. Overall, the cross-sectional areas of the arteries represent approximately 38% of the cross-sectional areas of the transverse foramina. The two variables are significantly correlated. There are no significant differences between the cross-sectional areas of the left and right foramina nor between the cross-sectional areas of left and right arteries. Using regression analysis, we generate equations that can be subsequently used to estimate the size of the vertebral arteries in fossil specimens. By providing additional evidence of intra- and inter-individual size variation of the arteries and corresponding foramina in extant humans, our study introduces an essential database for better understanding the evolutionary story of soft tissues in the fossil record.

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Pattern and magnitude of taxonomic classification accuracy of living and fossil hominoid upper molars through landmark-based and surface-based approaches

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Teeth play a significant role in the study of diversity and evolution of living and extinct hominoids. Their exceptional preservation in the fossil record has promoted their use in taxonomic assessments. The investigation of the outer enamel surface (OES) and the enamel-dentin junction (EDJ) through different quantitative approaches, including 2D/3D landmark-based and 3D surface-based methods, has become a standardized practice in alpha taxonomy and phylogenetic reconstructions. In this regard, a central question is how efficiently the statistical methods currently available distinguish among hominoid species on the basis of dental shape data. Given the diversity of methods it is not clear which approach presents methodological advantages over others. Here we evaluate the performance of four widely used methods: 2D landmarks/semilandmarks; 3D curve and surface semilandmarks; diffeomorphic surface matching (DSM) and generalized Procrustes surface analysis (GPSA).

The sample investigated consists of 70 OES and EDJ second upper molar surfaces, obtained through micro-computed tomography, representing seven living and extinct hominoid species including: *Pan troglodytes* (n=10), *Gorilla gorilla* (n=10), and *Pongo pygmaeus* (n=10), modern humans (n=10), Neanderthals (n=10), *Australopithecus africanus* (n=10) and *Paranthropus robustus*. We used PCA as a dimension reduction technique to avoid overfitting and we explored the shape and form spaces. We used Random Forest (RF), a supervised machine learning algorithm, and size and shape variables to evaluate the pattern of classification accuracy across the methods. Three metrics were used to evaluate the magnitude of classification accuracy including average and maximum error (misclassification) rates as well as the classification error derived from the confusion matrix. We also evaluated the classification accuracy using different numbers of semilandmarks.

The results for the 2D dataset (OES form and shape spaces) showed high average and maximum error rates (lowest error rate 17%). Neanderthals and *A. africanus* presented high error rates, whereas *Gorilla* and *Pongo* presented lower error rates. The 3D semilandmark dataset (EDJ curves) for both shape and form spaces presented lower average and maximum error rates (lowest error rate 7%) than the 2D approach. *A. africanus* and Neanderthals presented high error rates (0.4-0.6), *Pongo* presented mean error rates (0.2-0.3) and *Gorilla*, *H. sapiens* and *P. robustus* were classified with complete accuracy. The total 3D dataset (EDJ curves + surface semilandmarks) presented similar average and maximum error rates per species than the curves dataset (lowest error rate 5%). The use of high numbers of semilandmarks led to similar classification error rates and provided slightly more separation between species. DSM showed the lowest error rates (4%) and the highest classification accuracy and discriminatory power, whereas GPSA presented high average and maximum error rates (lowest error rate 17%). The deformation-based methods presented different patterns of species classifications where *Pan* and *Pongo* (DSM), and Neanderthals, *Pan* and *P. robustus* (GPSA), respectively were the hardest species to be classified correctly. The inclusion of size improved the performance of most methods and increased the correct species classification rates.

The main conclusions of the present study are: 1) the 2D landmark-based approach performs relatively poorly; 2) the 3D landmark-based approaches perform well but exhibit problems with data redundancy; 3) increasing the number of landmarks does not necessarily improve classification accuracy and increases the risk of overfitting; 4) one of the deformation-based approaches DSM is the best performing method; 5) the pattern and magnitude of species classification accuracy differs between the landmark-based and deformation-based approaches and 6) with RF the inclusion of size let higher classification accuracy than shape alone.

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Modelling plant nutritional data on the South African Lowveld: Hominin dietary implications of plant nutritional variation on a proxy savanna landscape

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Diet is a key driver in human evolution, influencing an organism's physiology and social behaviour. Plant foods provided the bulk of early hominin nutrition, but plant nutritional values across savanna landscapes are highly variable, including the C4 vegetation-dominant African savanna landscapes of human evolution [1]. By ~3.5 Ma, hominins began incorporating C4 plant food resources into their diet. East African *Paranthropus* became a C4 plant specialist, while other taxa made variable use of these resources [2].

However, the nutritional profiles of potential hominin plant foods from modern savanna ecosystems, their plant community composition, and nutritional variability across time and space remain poorly understood, and empirical data on potential hominin plant food nutritional variation in models/reconstructions of early hominin diet are relatively scant. Such information can provide insights into important questions of early hominin dietary behaviour, such as questions of paranthropine dietary flexibility, whether foods with the “right” isotopic signature were nutritionally viable, questions regarding eastern and southern African *Paranthropus* isotopic differentiation, the distribution of hominin genera due to dietary constraints, and more.

This project has collected a large assemblage of plant nutritional data from the modern savanna landscape of Kruger National Park, South Africa. Investigating the nutritional properties of potential hominin plant foods (analysing protein, fibre, fat, antifeedants, energy content etc.) and the distribution of such nutrition across the South African Lowveld, we quantify dietary variability, both in terms of plant parts and plant types (forbs, sedges, grasses, leaves, stems, tubers etc.) and model the spatiotemporal distribution of such properties and plant availability across a proxy hominin landscape. We explore this variation on a regional scale by comparing to similar work conducted by our group in the Cradle of Humankind Nature Reserve, South Africa and Amboseli National Park, Kenya. Such proxy analyses allow a unique opportunity to investigate questions of resource availability and to add to debates on hominin dietary ecology.

Our results so far reveal inter-/intra- habitat and taxon nutritional variation in plant food resources across different savanna habitats. Regionally, South African Lowveld habitats are intermediate in terms of plant food palatability between the Highveld and East African savanna, with some significant differences observed. Pronounced nutritional differences indicate that C4 grasses and sedges can be highly variable. These differences may have implications for the carbon isotope ratios observed between eastern and southern African *Paranthropus*. Among our samples, while tree and forb leaves are generally higher in protein, some of the grass leaves sampled are comparable, with protein values of ~16%.

Rather than assuming causal links between environmental change and human evolutionary events, we use our collected nutritional data to build agent-based models, grounded in behavioural ecology frameworks, to understand the influence of environment more fully on hominin behaviours [3-5]. Using a hypothesized regional African landscape, we test our data, make predictions, explore hominin interactions within reconstructed environments, and begin to evaluate drivers of hominin behaviour via agent-based models with empirical data, which are lacking. Results of preliminary modelling will be presented, and potential hominin wild plant foods considered in terms of the fundamental and realised niches of early hominin species. This combined approach of collecting nutritional data and agent-based modelling, and incorporation of ecological methods and frameworks, provides a new means to test hypotheses about the underlying causes of patterns seen in the hominin fossil record.

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Evaluating the spatio-temporal proximity of Neanderthals and *Homo sapiens* at the onset of the Upper Palaeolithic in France and northern Spain.

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Recent discoveries in Bulgaria and the Czech Republic have suggested that Neanderthals and *Homo sapiens* may have co-existed on the European landmass for as long as four to six thousand years (cal) [1,2]. The widening of their temporal overlap reignites discussion concerning the potential interaction between *Homo sapiens* and Neanderthals in Europe preceding the disappearance of the latter [1]. Yet, despite a) strong evidence for their temporal co-existence at a continental scale [1,2] and b) indications of at least occasional gene-flow at the gates of Europe [3], evidence for their contemporaneity at a regional scale within Europe remains exceptionally rare [4]. In France and northern Spain, a region with one of the most well-dated archaeological records between 45 and 40 kya cal BP, Protoaurignacian assemblages attributed to *Homo sapiens* appear to swiftly ‘replace’ Neanderthal-associated Châtelperronian assemblages. However, whether these occupations were at least partly contemporaneous remains unclear. Recently, optimal linear estimation modelling (OLE) has been introduced to archaeological research from biological conservation sciences [5]. OLE is a frequentist modelling approach which uses the earliest/latest dates of an archaeological phenomenon to estimate its true chronological duration – based on the assumption that we rarely, if ever, identify the ‘first’ or ‘last’ appearance of a culture in the archaeological record. Here, we use optimal linear estimation modelling [5] and GIS-based analysis to evaluate the spatio-temporal proximity of Protoaurignacian and Châtelperronian occupations in France and northern Spain. We use a selection of modern, previously published C14 age determinations (n=56) that we calibrated using the recently operationalised IntCal20 calibration curve. The results indicate that 1) with or without modelling, the age ranges for Châtelperronian and Protoaurignacian assemblages in France and northern Spain show a substantial degree of statistical overlap between 43 and 40 thousand years ago and 2) there appears to be a geographic structuring underlying this overlap. Additionally, using a dataset of 10 directly-dated Neanderthals from western Europe, we demonstrate that the calibrated age ranges of both the Châtelperronian and the Protoaurignacian of France and northern Spain overlap significantly with at least three directly-dated late Neanderthal specimens from the region - preceding their modelled disappearance at around 40 kya cal BP. Taken together, we suggest that these observations strengthen the proposition that the archaeological features characterising the onset of the Upper Palaeolithic in western Europe may be driven by some form of interaction between different human groups.

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Isotopic calcium biogeochemistry: Application to the dietary reconstruction of middle Paleolithic Neandertals from Regourdou (Montignac, France) and Grotte du Bison (Arcy-sur-Cure, France)

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Since the first discoveries of human fossils, the nature of the relationships between hominin biological and cultural evolutions and dietary habits has been a fundamental subject of debate. The development of accurate analysis of stable isotope ratios in geochemistry, particularly due to MC-ICP-MS, has now allowed the measurement of calcium (Ca) isotopes on small samples of bones or teeth.

The Ca isotopic composition of mammals is largely defined by the Ca intake of the diet and represents an important source of information that has been unexploited. In natural conditions, the $\delta^{44/42}\text{Ca}$ value of bone and teeth varies according to dietary intake with a constant isotopic offset of about -0.57‰ [1], resulting in a difference between prey and predator close to -0.30‰ [2]. The $\delta^{44/42}\text{Ca}$ value of bone therefore has the potential to reconstruct the ecology of existing or extinct mammals.

Using a bone-muscle Ca isotopic offset determined on extant animals, we show that the $\delta^{44/42}\text{Ca}$ value of predators cannot be accounted for by the consumption of meat only, as plants and meat have indistinguishable $\delta^{44/42}\text{Ca}$ values. Mass balance calculations indicate that the low $\delta^{44/42}\text{Ca}$ values of carnivores are explained by the accidental or intentional ingestion of bone during prey consumption.

Here, we present Ca isotopes analysis of fossil bone samples of the fauna from the Regourdou (MIS 5, Dordogne, France; [3]) and La Grotte du Bison (MIS 3-4, Yonne, France; [4]) sites as well as from bone samples of 3 Neandertal individuals. Comparison between the Neanderthals of Regourdou and that of La Grotte du Bison shows a different feeding behavior. All the $\delta^{44/42}\text{Ca}$ values of Regourdou 1 Neandertal are low ($< -1.6\text{‰}$), placing this individual among carnivores, contrary to the Regourdou 2 Neandertal [5] and that of La Grotte du Bison which has values placing them with the variability of herbivores ($> -0.75\text{‰}$).

Using the bone-muscle Ca isotopic offset, we further show that the $\delta^{44/42}\text{Ca}$ value of the Regourdou 1 diet are explained by the ingestion of bone marrow containing as little as 1% trabecular bone. Our results show that the Regourdou 1 Neandertal consumed a mixture of various herbivorous prey, as well as trabecular bone, which probably occurred when marrow was ingested, by accident or intentionally. This is not the case for the Neandertal from La Grotte du Bison and Regourdou 2, for whom we have no indication of any bone consumption. Of course, our results don't exclude meat consumption by Regourdou 2 and Grotte du Bison Neandertal individuals.

The results of our Ca isotope analyses of long bones of three French Neandertals allow us to suppose the existence of different and potentially contrasted subsistence strategies between Neandertals from the same site or from different sites related to MIS 5 to MIS 3.

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Degree of trabecular bone extension into the medullary cavity of the first metacarpal in Plio-Pleistocene hominins

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The evolution of the dexterous modern human thumb has long been of interest to paleoanthropologists and palaeolithic archaeologists alike due to the thumb's critical role in producing and using stone tools. The range of thumb movements that facilitate precision grips have traditionally been inferred from first metacarpal shape in fossil hominins [1,2]. As trabecular bone is thought to (re)model in response to mechanical loading over an individual's lifetime, this internal morphology can reflect how a fossil thumb was predominantly used. For example, a recent analysis demonstrated that, compared to great apes, humans have significantly more trabecular bone directly beneath the radial aspect of both the distal and proximal articulations of the first metacarpal, consistent with differences in both external morphology and observed manipulative capabilities [3]. However, without a means to conduct robust statistical comparisons throughout the entire trabecular volume, researchers have been limited to more qualitative observations regarding differences in deeper epiphyseal trabecular structure and the degree to which the trabecular network extends into the medullary cavity.

Here we use a novel, canonical holistic morphometric analysis (cHMA) to test for significant univariate differences in relative trabecular bone density (rBV/TV) across a sample of living great apes including: modern humans (*Homo sapiens*, n=10), bonobos (*Pan paniscus*, n=10), chimpanzees (*Pan troglodytes*, n=11), gorillas (*Gorilla gorilla gorilla*, n=10) and orangutans (*Pongo* sp., n=8) as well as fossil hominins including: *Australopithecus africanus* (StW 418), *Homo* sp./*Paranthropus robustus* (SK 84), *Australopithecus sediba* (UW 88-119) and *Homo neanderthalensis* (Kebara 2). This method uses a statistical deformation model, based on the whole sample, to create a canonical shape of both the external and internal bone space (delimited by cortical bone). A regular volumetric mesh of this canonical internal space can then be deformed back to each specimen and trabecular bone density can be measured throughout this internal space using holistic morphometric analysis (HMA) in Medtool 4.5 (www.medtool.at). Since the same mesh is deformed back to each specimen, each element of this canonical mesh is a homologous data point. This canonical bone map can be used to visualise and test for significant species differences in measured trabecular variables, in this case relative BV/TV (rBV/TV) [3-5].

Results demonstrate that humans have significantly different trabecular bone distribution than in great apes across both first metacarpal epiphyses, consistent with previous results using the subarticular method [3,4]. Thus, here we focus on novel results demonstrating that humans have significantly less trabecular bone (rBV/TV) in the medullary cavity compared to all extant apes. StW 418 and SK 84, have a less-human like trabecular bone distribution, in that it extends distally from the base into the diaphysis. The trabecular distributions in UW 88-119 and especially Kebara 2, do not extend as far into the medullary cavity and are more similar to that of modern humans. We hypothesise that variation in the amount trabecular bone within the medullary cavity may partially reflect a biomechanical 'trade-off' with cortical bone morphology, at least in later *Homo*. These results highlight the need for further work on the potential biomechanical significance of trabeculae that extend into the medullary cavity and their implications for our understanding of thumb use during hominin evolution.

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On the tracks of Neandertals on the Iberian Coast. Palaeobiological analyses of the footprints from Matalascañas (Almonte, SW Spain)

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Hominin footprints represent a unique vestige giving access to brief moments of life, an unusual time scale in archaeology or palaeoanthropology. They provide information not only on the locomotor behaviour of individuals (locomotor anatomy including soft tissue, motion capture) but also on the size and composition of the groups that made them, parameters that have an important impact on the adaptive success of these groups but are unknown within the fossil record. Although footprints have great potential, their study remains a challenging task. Indeed, their morphology does not only result from the biological and biomechanical characteristics of the individuals but also from the nature of the substrate (moisture, granulometry...) in which they are made as well as from the action of taphonomic agents. Furthermore, despite the discovery of important sites in the last decade, footprints represent a relatively rare material compared to the more common skeletal remains or archaeological artifacts. This is particularly the case for footprints attributed to Neandertals known until recently from only 5 sites.

It is in this context that we report here the discovery and the study of footprints attributed to Neandertals at the Spanish site of Matalascañas.

This site is located in southwestern Spain in a coastal environment marked by strong aeolian dynamics. According to the ephemeral condition of the deposit, we conducted a fast UAV flight mission over the whole emerged layer in order to map and locate every track and footprint in the generated orthomosaic. Such aerial view has been proven as an essential document since the surface faded out just 2 weeks later. Following a field analysis, 87 footprints, mostly isolated, were identified within a surface composed of fine sand in a silty matrix, having been covered by an aeolian deposit nearly 106,000 years ago. These footprints are mostly oriented towards an adjacent surface where several animal tracks were discovered.

Particular attention was paid to the 31 longitudinally complete footprints of this ichnological assemblage in order to estimate the number of individuals that left them and their biological characteristics (stature and age class) from the footprint lengths. For this purpose, experimental data from a study carried out under the same substrate conditions as in Matalascañas were used. Statures were estimated for each footprint from linear relationships linking stature to footprint length. The stature estimates were then used to estimate an age class thanks to a model quantifying the variation of stature with age in Neandertals. Finally, a minimum number of individuals has been estimated based on the experimental knowledge of the intra-individual morphometric dispersion of footprints.

The 31 complete footprints were left by a minimum of 3 individuals representing the different age classes: a child (6-8 years old between 104-115 cm tall), an adolescent or a small adult (126-149 cm) and a tall adult (154-188 cm), probably a male based on the sexual dimorphism in the stature of Neandertals.

The discovery of the Matalascañas footprints thus completes the Neandertal ichnological record, which was relatively poor. Moreover, these footprints provide a direct view of the behaviour of a Neandertal group in a coastal plain environment; the orientation of Neandertal footprints towards animal tracks can for example be explained by a hunting or even fishing behaviour in which very young individuals took part.

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Craniovascular morphology and craniostenoses: an evolutionary perspective

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In paleoanthropology, craniovascular traits provide indirect information about the evolution of the endocranial blood flow, and supply information relevant for functional craniology and cerebral metabolism. Different vascular elements can be observed in dry skulls in form of imprints and cranial canals – middle meningeal artery, dural venous sinuses, diploic veins and emissary veins [1,2]. It was shown that craniovascular morphology has changed noticeably during human evolution [3-5]. For example, extinct human species are characterized by dolichocephalic head proportions, and a co-dominance of the anterior and posterior branches of the middle meningeal vessels [3], while modern humans display a globular braincase and a frequent dominance of the anterior branch [2]. The occipito-marginal sinus is more frequently observed in early hominins, and it was suggested that variations in this sense may be related to the anatomical modifications that accompanied the transition to the upright posture [5]. Also, the emissary foramina are in general less frequent in extinct human species than in modern humans [4], although their expression is highly variable also in modern populations [2,4]. However, it remains to be investigated whether these changes are due to evolutionary adaptations, or else to secondary structural consequence and passive physiological responses. Here, we present an analysis of the craniovascular morphology in craniostenotic skulls in order to provide some clues about the functional and structural factors that influence the prevalence and expression of these macrovascular features. In contrast to normal skulls, the craniostenotic skulls present more numerous and often larger foramina. The confluence of sinuses with persistent enlarged occipito-marginal sinuses varies between modern human populations [2], but its prevalence is higher in the craniostenotic skulls. Moreover, the dolichocephalic craniostenotic skulls display frequent dominance of posterior branches of middle meningeal artery. The craniovascular morphology is based on the relationship between hard and soft tissues and is affected by both genetic and epigenetic factors. In the case of middle meningeal artery redistribution, the vascular differences between long and short crania may be associated with different biomechanical forces that are experienced during the endocranial morphogenesis. On the other hand, the morphology of both emissary veins and dural venous sinuses is probably more influenced by their function related to the intracranial pressure maintenance and, possibly, heat management.

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Non-destructive extraction of ancient DNA from bone and tooth artefacts

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The analysis of ancient human DNA sequences from skeletal remains and sediments has made important contributions to our understanding of hominin history. Human-made artefacts, such as bone tools and perforated animal teeth, are another potential source of ancient DNA and may help to establish cultural context. In addition to identifying the source material used for artefact production, it is conceivable that DNA from the makers or users of osseous artefacts may be adsorbed to the artefact matrix. However, exploring this possibility by destructive sampling is highly problematic in most cases as it compromises the structure and surface topography of the material. To make artefacts accessible to genetic analysis we developed a non-destructive DNA extraction technique and characterized the DNA that can be recovered from artefacts.

To establish the non-destructive DNA extraction protocol, ten Pleistocene bone and tooth samples, which were similar in size and shape to material typically used for artifact production at Paleolithic sites, were submerged in reagents that have previously been used in ancient DNA extraction protocols. These included ethylenediaminetetraacetate (EDTA) [1], guanidinium thiocyanate (GTC) [2], sodium phosphate [3] and sodium hypochlorite (bleach), a reagent often used for decontamination of surfaces [3]. Quantitative 3D surface texture measurements [4] were performed before and after the treatments to monitor possible surface alterations. The results of these measurements showed that EDTA and GTC led to substantial surface alterations, whereas incubation in water, sodium phosphate and bleach did not.

Based on these results we developed a non-destructive DNA extraction method that is based on temperature-controlled release of DNA from the bone/tooth matrix using sodium phosphate buffer [5]. We then applied the method to a set of 17 bone artifacts excavated more than 30 years ago: six samples from the Magdalenian site Arudy Espalunge (France) [6] and eleven samples from the Quinçay (France) Châtelperronian layers [7]. Unfortunately, we did not recover ancient DNA in the samples from Arudy Espalunge, possibly due to unfavorable conditions for DNA preservation at the site. From two of the samples from Quinçay we were able to recover ancient mammalian DNA, which could be assigned to Cervidae and Elephantidae, consistent with the morphological identification of the source material. However, on average 92.6 % of the retrieved sequences originated from modern human contamination, hampering our ability to detect traces of ancient hominin DNA that may point to the makers/users of the artefacts.

In summary, we show that ancient DNA can be recovered from bone artefacts using a non-destructive DNA extraction protocol. Nevertheless, excavation under cleaner conditions (e.g., using gloves), and limited sub-sequent handling of the specimens during storage, are required to minimize the introduction of present-day human DNA contamination. It is conceivable that the implementation of such clean excavation and storage protocols may make it possible to isolate ancient hominin DNA from bone artefacts without causing damage to the precious material.

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What were the kids doing during the Late Pleistocene in northern Spain? Insights from activity-related dental wear

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One of the proxies used for the study of past human behavior is the analysis of the non-masticatory, cultural or activity-related dental wear, characteristic of the genus *Homo* since its appearance [1-2; and references therein]. The use of “teeth as tools” has principally been studied in permanent dentitions from adult individuals. Here, we present the results of the analysis of the non-masticatory dental wear modifications on the deciduous dentition assigned to eight Neandertal and anatomically modern human subadult individuals, from MIS 3 to late MIS 1, along the Cantabrian region (Northern Spain)[3]. The sample includes the deciduous teeth from the Mousterian levels of Axló cave (Basque Country), the Transitional Aurignacian and Gravettian from El Castillo cave (Cantabria), and Magdalenian levels from Las Caldas and Tito Bustillo (both in Asturias) and Santa Catalina (Basque Country). Although preliminary, we tentatively suggest that these eight subadults present activity-related dental wear, including cultural striations, chipped enamel, toothpicking grooves, and subvertical grooves within the interproximal contact facets, same as reported in permanent dentition (mostly adult individuals), despite the known differences between the deciduous and permanent enamel. Our results provide evidence of habitual dental hygienic practices in the form of toothpicking on a deciduous premolar, and the orientation of the cultural striations indicates a similar handedness development as in modern children. Taken together, these dental wear patterns support the initiation and participation of young individuals in group activities, as seen in the Middle Pleistocene hominins from Sima de los Huesos [4], Neandertals from Krapina [2] and El Sidrón [5], making them potential contributors to group welfare. Furthermore, the characteristics of their non-masticatory dental wear (low number and small features) could suggest that these children and juveniles could have been learning, practicing and acquiring the adult-like skills. If that is the case, the length of learning could have spanned at least childhood and juvenility, a similar length in the learning process as in modern hunter-gatherers. And, thus, their role within the group could be extrapolated as similar: learning from more experienced individuals within the group to become skilled performers.

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Using Petri nets to model the production of *Ammocharis coranica* and *Ozoroa schinzii* adhesives by Ju/'hoan hunters.

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*The concept of Chaîne opératoire (CO) allows studying traditional and prehistoric technological systems by systematically describing the raw material procurement, production, use, discard, and cultural and technological variables. However, in recent debates it is increasingly important to understand how the complexity of a technological system can change due to the interplay between these variables. CO is limited in the information that can add to this debate because generally it offers one potential state of the system. As an alternative, through petri net modelling, the states of a system can be mapped, and the possible sequences of events, and the patterns of interaction between elements and events can be analysed. Petri nets are directed, bipartite graphs with three basic elements: transitions, places, and arcs [1]. These nets can model systems such as computer networks, biological regulatory networks, and production systems, by using formal mathematical semantics. Petri nets can be presented in a graphical format that allows people unfamiliar with the mathematical notations to understand the modelled system. Petri nets also allow to study the properties of systems using systematic methods [2]. Considering current debates about the complexity of technological systems, petri nets can map the possible states that a system may reach by identifying the possibilities of the executing steps (e.g., during production), conducted in order, out of order, and/or in parallel. Usually, the more out of order/parallel steps the higher the concurrency of a system is and the larger the possible number of states that a system can reach. The number of possible states is directly informative about the behaviour of the system. Simply put, when concurrency is high, predictability is low and this may make the behaviour of a system complex. Although high concurrent systems tend to be complex, they are also flexible, allowing for changes on the spot in the execution of processes. Production process of traditional and prehistoric technological systems show the potential to be concurrent [3,4], but this property has not been formally analysed. In this pilot study, we applied a petri net approach to model and compare the production process of *Ammocharis coranica* and *Ozoroa schinzii* adhesives, based on ethnographic descriptions of traditional activities of Ju/'hoan hunters from Nyae Nyae, Namibia [5]. We compared the number of possible states in both production processes. The results suggest that the relation between the number of technological units and the behavioural complexity of the system as derived from the type of activities conducted can vary. Also, units and complexity can both influence the number of possible states and the predictability of the production processes. The Petri net models of these two ethnographic cases show order-independent and parallel activities, suggesting that concurrency may be prevalent in the production of traditional adhesive technologies.*

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The influence of hand dimensions on the pattern of fingers flexion during Lower Paleolithic stone tool manipulation

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The comfortable grasping of a tool is pivotal for both ergonomic handling and efficient tool use. It implies a secure handling, preventing the object from slipping. The hand should not experience any harmful tension nor unpleasant sensations, and the haptic process should not imply manipulative stress [1]. When studying ergonomic patterns, hand size is a major factor to be taken into consideration, because the applied forces and the contact area are related to grip diameter, and therefore hand dimensions might influence the comfort during the grasping [2]. In humans, males are able to produce greater grip force than females, and hand dimensions are very good predictors of grip strength [3]. Moreover, males display on average larger hands than females [4]. Here we study the ergonomic grasping of Lower Paleolithic stone tools. We asked 82 subjects to reach a comfortable stone tools grip, and we recorded the phalanx flexion of each finger in by using a VMG 30™ motion capture hand glove (Virtual Motion Labs®). The degree of flexion of the phalanxes are used to define the grasping patter of each participant. We also took 10 anthropometrics measures of the hand of each individual, and used them in a Principal Component Analysis on the hand dimensions. The first Principal Component represents 82% of the variance, and it is positively correlated with hand dimensions. The flexion of the first, second, and third phalanx of the little finger, the flexion of the second and third phalanx of the index finger, the flexion of the first phalanx of the middle, and the flexion of the first phalanx of the thumb show a significant correlation with the PC1 of hand dimensions, and accordingly, hand size does influence grasping pattern. Generally, individuals with larger hand need a larger degree of finger flexion to achieve a comfortable grasp. Individuals with larger hand are mainly males. Therefore, future studies will assess whether this result is due to allometric factors or if there are sexual-related difference on the manipulation of Lower Paleolithic stone tools.

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Palaeoanlaytics: data science approaches to lithic analysis

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The evolutionary sciences have been transformed by the impact of data science methods. Prevalent in genomics, these are now being extended to palaeontology and archaeology. Such approaches hold the hope of expanding the quantification of phenotypes, enhancing pattern recognition and classification, and providing the basis for much larger samples. However, while a genome can be easily reduced to a linear sequence of bases, similar approaches for phenotypes and material culture are more challenging. There are three easily identifiable problems – one, the capture of data in a form that can be quantified and information maximised, two, that the data are not a linear sequence but complex 3D objects or 2D image representations, and three, transforming these into systematic data for analysis. Here, we present the principles and preliminary results from the PALAEOLANLYTICS project that is developing machine learning and computer vision methodologies for lithic data capture and analysis.

For over one hundred years, archaeologists have recovered, recorded, photographed and drawn stone tools, and used these to build up strong models of their typologies, technologies, distributions and affinities. Much of this information is recorded in publications of greater or lesser accessibility, and large-scale, comprehensive databases are few and far between. To improve the scale and quality of these data, the PALAEOLANLYTICS Project has utilised computer vision methodologies to develop *PyLithics*, an open-source, free for use, software package to capture rapidly large volumes of these data in usable forms. *PyLithics v1.0* processes lithic artefact illustrations scanned from the literature, and has been optimised for feature extraction and measurement using a number of computer vision techniques, including pixel intensity thresholding, edge detection and segmentation, and custom template matching and image kernels.

On both conventional and modern drawings, *PyLithics v1.0* can identify and measure dorsal surface scar number, shape, size, orientation and diversity. The orientation and flaking direction of dorsal scars can also be calculated from either ripples or arrows. Complete size and shape metrics of individual scars and whole flakes can be calculated and recorded in a customisable database. The resulting data can be used for metrical analysis or for extracting features indicative of both typologies and technological processes. Data output has been optimised for machine learning algorithms and can easily be employed to explore patterns of variation within and between assemblages.

While the work is at a preliminary stage, focusing on flakes rather than complete assemblages, we describe these methods, present some initial results, and show how researchers can access it for their own drawings. We outline briefly how these can be used to enhance current approaches to prehistoric lithic analysis.

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The undescribed juvenile maxilla from Grotte des Contrebandiers, Morocco – a study on Aterian facial growth

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Late Pleistocene *Homo sapiens* fossils associated with the Aterian industry in Northern Africa can provide valuable insight into the spread of our species within and out of Africa. Aterian sites yielding human remains have been found exclusively in Morocco and include Mugharet el 'Aliya, Grotte des Pigeons (Taforalt), Dar es-Soltan II, El Harhoura I and Grotte des Contrebandiers (Temara). Both the time range and geographical proximity of these sites to Eurasia suggest that these hominins may be associated with one or several out of Africa dispersals between 120 and 50 ka. Historically, Aterian fossil remains, which are characterized by robust facial and mandibular morphology and large teeth, were sometimes considered "African Neanderthals." More recent studies, however, emphasize facial [1] and dental affinities [2] to early *H. sapiens* from the Middle East (Skhul and Qafzeh).

In this study, we quantify the shape and growth patterns of a previously undescribed juvenile maxilla from Grotte des Contrebandiers by integrating three-dimensional geometric morphometrics and bone surface histology (i.e., bone resorption and formation). The site of Grotte des Contrebandiers was first excavated by Roche in 1955. Subsequent excavations yielded a mandible and cranial fragments in the mid-1970s [3] and in 2009 a skull and partial skeleton [4] of a 7 or 8-year-old child dated to around ca. 108 ka [5].

While much of the cranium was found shattered, the maxilla remained largely intact. Following minor virtual reconstruction, three-dimensional shape data was collected in the form of landmark and semilandmark coordinates, and compared to an extensive sample of Early to Late Pleistocene juvenile and adult hominin fossils and Holocene humans. We used developmental simulations to predict adult shapes of the Contrebandiers maxilla by growing it along three ontogenetic trajectories using multivariate regression: Neanderthal, African and Middle Eastern early *H. sapiens* and Holocene *H. sapiens*. The resulting juvenile and adult shapes were plotted in principal component analyses (PCA). Finally, patterns of bone formation and resorption were mapped on the Contrebandiers maxilla and compared to Qafzeh 11, Neanderthals and Holocene *H. sapiens*.

Neanderthals and *H. sapiens* show distinct ontogenetic trajectories, with early *H. sapiens* from Africa and the Middle East plotting intermediate between the two in the PCAs. The shape of the juvenile Contrebandiers maxilla is most similar to the juvenile remains from Qafzeh (10, 11 and 15). Its predicted adult shapes always plot within *H. sapiens* variation - even when grown along a Neanderthal ontogenetic trajectory. However, these predicted adult shapes do not show any special affinities to Dar es Soltan II-V. Visualization of shape changes along the trajectories show subtle differences in maxillary growth between Neanderthals and early *H. sapiens*. The maxillary body becomes more inflated along the Neanderthal trajectory, whereas the lower maxilla becomes more prognathic along the early *H. sapiens* trajectory. These results are confirmed in our surface histology analysis. Like recent *H. sapiens*, both Contrebandiers and Qafzeh 11 are characterized by greater amounts of bone resorption compared to Neanderthals, indicative of their orthognathic mid-faces. This study supports previous research on Aterian facial and dental morphology linking them to both the Middle Pleistocene fossils from Jebel Irhoud and Late Pleistocene fossils from the Middle East.

This contribution is in memory of Harold L. Dibble. We would like to thank all members involved in the Contrebandiers excavations, in particular Zeljko Rezek, and all curators who gave us access to recent and fossil hominin specimens for computed tomography and analysis, as well as Heiko Temming and David Plotzki for their technical assistance.

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Studying mobility degree of extant caribou (*Rangifer tarandus*) and its application to fossil reindeer in South-Western France: an actualistic approach

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Reindeer (*Rangifer tarandus*) was one of the most important prey species for human populations in Western and Central Europe during much of the Paleolithic period, notably during the glacial periods [1]. The high frequency of reindeer remains in French sites during the Magdalenian suggests that hunter-gather groups were highly dependent on this animal resource [2]. Mobility patterns of reindeer would have affected the hunting strategies and the mobility of hunter-gatherer groups that depend on them. The question of the seasonal occupation of human territories and the seasonal behavior of reindeer remains open. Thus, many studies have focused on it, particularly during the Magdalenian. However, and despite the numerous attempts to reconstruct the migratory behavior of Paleolithic reindeer, there has yet to be a definitive model that can explain their movement patterns.

Modern ethological data indicates that reindeer herds adopt different mobility strategies or patterns that correlate with habitat type and topography [3]. Furthermore, it has been demonstrated that an animal's habitat and mobility patterns hypothetically affect bone density and limb bone morphology as has been proven in several species [4].

Therefore, the main goal of our project is to quantify the link between mobility and morphology using metacarpals, metatarsals and phalanges (because of the specialization and elongation of metapodial bones in artiodactyls, they have traditionally been used in a number of morphometric studies to assess body size, locomotor behaviour and habitat preference) from current caribou populations (migratory and sedentary settings) and to apply these results to twenty-three faunal assemblages from Upper Paleolithic archaeological sites in South-western France to reconstruct reindeer mobility. Thus, from an actualistic approach, we have successfully created a referential framework using linear measurements from metacarpals, metatarsals and phalanges of extant reindeer (caribou) in combination with Machine Learning (ML) algorithms to identify two major types of migration: the first corresponds to mobile reindeer, which cover distances greater than 200 km and the second to weakly migratory reindeer that move for distances of less than 200 km [5]. Then, this referential framework has been applied to archaeological samples from South-western France. As a result, ML analyses showed how it is possible to distinguish reindeer mobility patterns with more than 90% of accuracy depending on the skeletal part and bone type. These results will allow us to reconstruct how migratory patterns of Paleolithic reindeer affected human hunting strategies and the mobility of hunter-gatherer groups that depended on them during Magdalenian period.

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Time and space: spatial and functional analysis at Rodo (Central Portugal) Late Pleistocene open-air site

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The identification of three Prehistoric archaeological sites in the Vouga river valley - Rodo, Vau and Bispeira 8 - was the most important outcome of the archaeological works carried out in 2014/2015, in the scope of the Ribeiradio-Ermida Hydroelectric project.

The identification, excavation and study of these sites, situated halfway between Estremadura and the Côa Valley, the focal areas for the study of Upper Pleistocene in Portugal, is extremely relevant to understand raw material procurement, mobility and land use by Upper Palaeolithic hunter-gatherers. The analysis of allochthonous raw materials and spatial distribution at Vau indicates that the occupation during the Gravettian (US005) denotes characteristics of less specialized permanent residence. Rodo seems to show traces of a greater mobility which translates into ephemeral occupation sites during the Middle/Late Magdalenian and Azilian. This poster explores the spatial distribution of this kind of materials at Rodo in order to get a better understanding of the mobility during this period. The Rodo archaeological site is located on a platform, broadly corresponding to a fluvial terrace, sloped towards the current riverbed of the Vouga River, encompassing the convex sector of a meander. This platform results from the long process of river incision (the formation of different terrace levels) combined with slope erosion. A colluvial deposit (UE006) developed on top of the river terrace and packed a lithic assemblage and some stone structures that may correspond to anthropic combustion features. The top of the sequence (UE003) was disturbed by post-depositional phenomena (ravine channels, recent reforestation and road construction). Excluding some blade fragments and microlith types, possibly from Neolithic occupation, the lithic industry shows uniform techno-typological characteristics. Retouched tools are rare but flint unguiform endscrapers, marginally backed bladelets and backed curved bladelets (Azilian points) were identified. Débitage is oriented towards the production of flakes and bladelets. Cores on flake were exploited along their edges (mostly burin but also endscraper types) to produce bladelets and bipolar débitage on anvil is also frequent. Quartz, quartzite and other coarse-grained cobbles were used for expedient flake débitage or transformed into denticulates, notches or scrapers and macro-tools. According to lithic technology and radiocarbon dates (15,831-15,383 cal BP - ref. 17C/0828; 10,696-10,443 cal BP - ref. 17C/0825 and 10,252-10,177 cal BP - ref. 17C/0824) the Rodo human occupation can be attributed to Middle/Late Magdalenian and Azilian. Flint, silcrete and other hydrothermal veins, available in smaller amounts and more distinctive in terms of the reduction sequences applied, were preferentially chosen to attempt refitting. The spatial analysis of these lithic raw materials allowed to identify clusters and preferential distribution patterns. This work aims to shed light on site formation processes, stratigraphic integrity, duration of human occupations and site function and answer the following questions: are we dealing with short-term occupations or long-term residential camps? Are we dealing with a single occupation or a repeated one within the scope of the annual displacement circuit of the hunter-gatherers who lived there? Does the available information support choosing between one multi-purpose residential base camp occupied during a season of the year or one specialized camp?

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Evolutionary morphology of the European Upper and Middle Pleistocene archaic human clavicle: an ontogenetic study

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Upper Pleistocene Neandertals are characterized by absolutely and relatively long clavicles, which are related to a large thorax with broad shoulders and pelvises in turn related to medio-lateral wider bodies [1,2]. This thoracic bauplan seems to be associated with a delayed pattern of maturation of specific skeletal regions (vertebral column) rather than with the developmental pattern of the whole skeleton [3]. In contrast, previous studies have pointed out that Neandertals and modern humans (MH) differ either in the overall rate or in the duration of growth [4,5].

The Middle Pleistocene Sima de los Huesos (SH) hominins, share with Neandertals the “wider body” bauplan and many anatomical features of postcranial skeleton [2]. Among the skeletal remains unearthed from this site there are three complete clavicles belonging to three different individuals: two subadult represented by two right clavicles in different growth stages (CI-IV and CI-VI) and one adult represented by the left clavicle (CI-VII) [2]. With these specimens, the pattern of clavicle development can be explored in this sample and comparisons with Neandertals and MH performed. We seek to answer two important questions: 1) Did Neandertals and SH hominins share the same clavicular developmental pattern, as expected by their shared body bauplan? and if so, 2) Are there differences in the pattern of clavicular growth between these two archaic species and MH?

Using both, 3D geometric morphometric (3DGM) techniques and the traditional formalism (TF) for the analysis of ontogenetic allometry, we carried out a comparative analysis of the clavicular morphology during development in Neandertals and their direct ancestors (same paleodeme) as well as in modern humans. 3DGM methods were applied in a comparative framework including 92 modern human clavicles aged from birth to adulthood and the 3 complete clavicles from SH (we do not have 3D data from Neandertals). A set of 22 homologous 3D landmarks and 124 semilandmarks (located along 20 curves) were used to collect the precise morphology of these clavicles using Stratovan Checkpoint software. For the TF, we measured 23 linear variables in 252 recent adult and subadult clavicles coming from four different skeletal collections along with 13 Neandertal (6 subadult plus 7 adult) clavicles.

Comparing the SH and modern human clavicles using 3DGM we have detected non-size related shape differences related to the development of the curvatures and the relative conoid length. Similar differences are detected between Neandertal and MH clavicles through TF analysis but not between SH and Neandertals. These results support that Neandertals and SH hominins share the pattern of clavicle development which differ to that of MH. These different patterns of development seem be related to different body shape.

Differences between the SH-Neandertal paleodeme and MH are mainly due to dissociated patterns of growth allometry, which in turn are due to the different rate of growth of the conoid length of the clavicle relative to the maximum length. These archaic humans show a higher degree of negative allometry in the growth of this variable than MH.

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Comparative anatomy of the upper ribs and vertebrae of MH1 (*Australopithecus sediba*) from a 3D geometric morphometrics approach

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Our understanding of the evolution of the human thorax has largely improved during the last decade through the use of virtual anthropology and 3D geometric morphometrics. For example, recent research has produced 3D reconstructions of the thorax of adult and subadult Neanderthals [1,2], but also other fossil species such as *Homo erectus* [3]. In these studies, it was suggested that the morphology of the Neanderthal thorax, relatively deep and shorter compared to the one from modern humans, could be also retained from *H. erectus*. However, it is still debated if some features of thorax morphology from this lineage (considered as the primitive condition) could have even older roots in human evolution. In this regard, the morphology of the *Australopithecus* ribcage is important. Because of that, different hypotheses have been proposed through the study of different *Australopithecus* specimens. For example, Schmid et al. [4] proposed that the *A. sediba* thorax was largely apelike in the upper part but more human like in the lower part. However, Latimer et al. [5] in their study of the KSD-VP-1/1 *A. afarensis* proposed that this individual had a modern human-like overall thorax morphology. Limitations include of the latter's non-inclusion of intermediate species between *Australopithecus* and humans, such as *H. erectus*, due to the subadult status of specimens.

Here, we compare the best-preserved thoracic fossil remains of the MH1 *A. sediba* juvenile individual with those of adult and subadult *H. sapiens*, *P. troglodytes* and the juvenile *H. erectus* from Nariokotome. After 3D scanning of the individual fossil elements, we used a protocol of 60 semi-landmarks to quantify the 3D morphology of ribs 1-6 and a protocol of 111 semi-landmarks to quantify the 3D morphology of the T2 and T4 vertebrae from MH1. After Procrustes superimposition of the 3D coordinates, the shape data was subjected to a cluster analysis in order to explore morphological similarities between the MH1 specimen and the rest of the sample. Our results show that the upper ribs (R1 and R2) present morphological affinities with *H. erectus* from Nariokotome, whereas the rest of the upper thorax (R3-R4) are more similar to both adults and subadult *P. troglodytes*. This is caused by the reduced rib torsion of MH1 and chimpanzee ribs compared to those of *H. sapiens* and *H. erectus*. However, in the two vertebrae analyzed, we find a clear association between the *A. sediba* vertebrae and those of *H. erectus* but also to juvenile modern humans. This affinity is due to the shorter but more horizontally oriented spinous process of those groups, but also by the relatively taller vertebral body.

For the first time, we compared the 3D morphology of *A. sediba* ribs and vertebrae with those of adult and subadult current extant taxa and also with other fossil species such as *H. erectus*. We highlight here the morphological affinity of MH1 vertebrae to *H. erectus* but also to subadult *H. sapiens*. In the ribs, we observe also some similarity of the upper ribs of MH1 with *H. erectus*, whereas the ribs towards the central thorax are more ape-like because of reduced torsion. The thorax morphology of *A. sediba* was likely a mosaic of features between more ape-like ribs and a more human-like spine, with the very upper thorax (R1 and R2) probably representing a unique morphology shared by fossil hominins but not observed in humans or chimpanzees. We also propose that ontogeny plays an important role for the understanding of the spine of MH1, since our results show morphological affinities between *H. sapiens* subadults and MH1 and Nariokotome *H. erectus*, which are also subadults. Future studies should invest in efforts to reconstruct the 3D morphology of the ribcage to paint a larger picture of hominin thorax evolution.

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The manufacture of antler tools in the Magdalenian Swabian Jura: technological analysis and reconstruction of the reduction sequence

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The Magdalenian culture in the Swabian Jura is characterized by a rich archaeological record, consisting of lithic tools, faunal and human remains, evidence of symbolic behavior, secondary burials, and osseous tools. This poster shows the results of the technological analysis carried out on the 98 worked reindeer antler pieces, consisting of discarded matrices, secondary matrices, waste products, blanks, preforms, and finished tools. The assemblage comes from the sites of Hohle Fels and Brillenhöhle in the Ach Valley, and Vogelherd and Langmahdhalde in the Lone Valley. Particularly, the rich corpus of finished tools is composed of barbed points, pointed tools, beveled tools, a *baguette demi-ronde*, a polished antler piece, and a *baton percé*. The pointed tools, mainly consisting of beveled and double bevel-based points, dominate the assemblage, followed by a lower number of barbed points. The archaeological layers where the artifacts were recovered are dated to a Late Magdalenian phase, from an occupation spanning from 16.3 to 13.9 cal Kyr BP ca [1-3]. The analysis aims at understanding which technical strategies Magdalenian human groups adopted in terms of raw material management and processing for antler tool production. Furthermore, we compare our data to evaluate differences and similarities of the tool technology at the different sites and to place the antler working of the Ach and Lone valleys in a wider continental context. In our study, we analyzed the worked antler artifacts on a morphological and morphometric basis, and observed the surfaces of each artifact to assess their degree of preservation as well as to detect anthropogenic modifications related to manufacturing. The assemblage shows an overall good degree of preservation, with a few specimens displaying a sign of low-to-medium weathering, exfoliation, and corrosion. Despite these taphonomic alterations, and a quite diffused presence of manganese dioxide on a third of the assemblage, the marks ascribed to anthropogenic activity are well preserved and visible. The observation of the surfaces shows a recurrence of technological traces ascribed to the techniques of grooving, sawing, hacking, drilling, engraving, scraping, and abrading. The distribution and frequency of these techniques on specimens from different technological categories, and their location on the artifact surfaces, allowed us to infer a common raw material management and reduction sequence that Magdalenian people adopted at all the sites in our study. Further, our results fit with contemporary antler tool technology attested elsewhere in Europe [4-5], suggesting the Swabian Jura to be actively included in a common technical tradition characterizing osseous technology during the Magdalenian.

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Like two peas in a pod: lithic technology points to high similarity in the early Upper Palaeolithic

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During the last twenty years, lithic technology has acquired a prominent role in defining techno-complexes in the early Upper Palaeolithic (eUP). Four techno-complexes, with entangled, and still debated connections, are linked to the eUP: the Southern Early Ahmarian, the Northern Early Ahmarian, the Protoaurignacian, and the Early Aurignacian. Their different approach to bladelets-making, disassociated or continuous with blades-making, coupled with a typological variability, is the main argument for splitting them into different technological traditions [1,2]. The techno-typological definitions have been embraced to understand the origin and the different routes of dispersal during the eUP [3,4]. Bladelets production and typological variability have become the gold standard for understanding eUP traditions [5]. Therefore, the research is an attempt at reconstructing the design of bladelets-making in the eUP. It is a direct first-hand technological comparison between three assemblages: Al-Ansab 1, Românești-Dumbrăvița I layer GH3 and Grotta di Fumane units A1-A2. They are dated to the eUP span, ca. 43-38 ka cal BP, and encompass at least two defined techno-complexes, Southern Early Ahmarian and Protoaurignacian. Assemblages have been sampled for cores, complete, and semi-complete blanks, analysed through chaîne opératoire approach and morpho-technological attributes. Chaîne opératoire is used for defining the different knapping stages, while the attributes are a further characterisation for identifying management and primary blanks recognised in the diacritical diagrams. Bladelets are identified as <12 mm wide laminar blanks. Despite the arbitrary cut-off, metrical data are showing a natural prevalence of blanks under the established threshold. Cores' different morphologies, often cited as decisive in differentiating between technocomplexes, underlie the same focus on producing unipolar bladelets from narrow portions of the flaking surface. Bladelets are consistently identified as blanks exploiting convexities, while blades are more related to the shaping of the core convexities. Asymmetrical, twisted-in-profile blades are the most frequent blanks in management ones and are compatible with isolating narrow portions of the flaking surface. An integrated production of blade and bladelets might occur in the first stages, but bladelet production is dominant. No fundamental difference in bladelets-making strategies is detected among the three assemblages, therefore questioning former definitions of techno-complexes and their variability.

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The development of bite force resistance in modern humans and Neanderthals

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Modern human and Neanderthal faces present clear morphological differences at all ontogenetic stages. Their post-natal ontogenetic allometric trajectories diverge [1] and in both species, as the various components of the mid-face develop and grow, bone facial remodelling is thought to play a key role in adapting them to their final adult form. In modern humans, maxillary growth is characterised by bone resorption on the anterior surface, whereas in Neanderthals extensive bone deposition is the common finding [2]. This morphogenetic difference is present by approximately 5 years of age [2].

During development, crania are loaded by forces applied to the masticatory system in feeding and manipulation. These change over time, as diet (e.g., weaning) and paramasticatory behaviour change. Differences are known to exist in adults between *Homo sapiens* and Neanderthals, with *Homo sapiens* relatively more efficient at generating bite forces but less able to support the strains and deformations produced by such forces [3,4]. Differences in mid-facial form between these species might be expected to be influenced and to influence the distribution and magnitude of strains experienced during masticatory system loading. Since bone adapts to loads, such differences might underlie and contribute to the distinctive distributions of facial remodelling fields in both species and so, to differences in craniofacial growth.

The present study explores the ontogeny of modern human and Neanderthal biting resistance as a preliminary to assessing potential associations between the distributions of facial strains arising from biting and facial remodelling among hominins. Our aim is to see if any differences in strains exist during post-natal ontogeny. We test the null hypothesis that modes and magnitudes of cranial deformation do not differ between modern humans and Neanderthals at each age stage when exposed to similar constraints.

We used ontogenetic series of Neanderthals and modern humans ranging from newborn to adult. Using 44 landmarks and 201 sliding semilandmarks multivariate regressions of cranial shape on size were used to create three surfaces representing the mean infant, juvenile, and adult stages. These surfaces were converted into finite element models and constrained and loaded in a standardised way to simulate right first incisor and P4/dm2 biting. Applied forces and material properties were identical among models to control all variables except craniofacial form. We compared the resulting deformations, maps of von Mises strains and tensile and compressive strains in the maxilla.

The resulting deformations differ in both mode and magnitude between modern humans and Neanderthals. In both incisor and P4/dm2 biting simulations, modelled strains decrease between infants and adults, as is to be expected given differences in size. The infant modern human presents higher strains than the infant Neanderthal over the anterior and inferior maxilla in both biting simulations. This is reversed in the juvenile models and the strains are more similar in adults. Finally, for both biting simulations, modern humans and Neanderthals deform differently, reflecting the differences in developed strains at each age stage.

These findings reflect differences in the dynamics of facial growth between modern humans and Neanderthals. Moreover, the differences in strains in the infant, juvenile maxillae in modern humans and Neanderthals model may to some extent underlie and explain the differences in maxillary surface remodelling in these two species. Further work on a wider range of models and loading scenarios is needed to explore this issue further.

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Phylogenetic analysis of *Homo luzonensis*: taxon, characters, phylogeny and island evolution

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Homo luzonensis is a species that lived until at least 50,000 to 67,000 years ago in northern Philippines, East of the Wallace line [1]. Likely to have been isolated on Luzon Island for tens to hundreds of thousands of years, it shows both archaic features (i.e., occurring in the australopiths) and derived characters (i.e., occurring in the upper Pleistocene *Homo* species). Their archaic features could result either from a close phylogenetic relationship with the Australopithecines or the early members of the genus *Homo*. It may also result from the effects of island evolution that favored reversals (i.e., return to primitive characters), correlated with a close phylogenetic relationship with a more derived hominin species (e.g., Asian *Homo erectus*). To test these two main hypotheses, we carried out a cladistic analysis based on the dental (premolars and molars) and postcranial (hand and foot bones) remains of adult *H. luzonensis* and most of the modern and fossil species recognized in the family Hominidae. The matrix used for this analysis contains characters frequently found in paleoanthropological studies, such as frequency-defined ASUDAS characters [2], and new characters we created to describe hand and foot remains. The various trees obtained indicate that both hypotheses are possible. The phylogenetic hypotheses where *H. luzonensis* is derived from *H. erectus* are supported by higher retention index and average group support after symmetric resampling. However, those where *H. luzonensis* is basal to the whole *Homo* genus are obtained using implied weighting [3], a method whose relevance is discussed when island taxa are analyzed. Moreover, *H. luzonensis* probably had reduced body dimensions and adaptations of his locomotor repertoire which have parallels in other insular mammals [4]. Besides, the tropical forest environment present on Luzon Island [5] could have favored the selection of such features. Combining our results with the state of the art concerning the hominin fossil record in Asia, island evolution and the environmental context of *H. luzonensis*, we conclude that *H. luzonensis* most probably results from an insular evolution with an Asian *H. erectus* ancestor.

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The La Ferrassie 1 individual dated with Optically Stimulated Luminescence: at least 3 of the skeletons from the site date from the same period

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The Palaeolithic site of La Ferrassie yielded seven Neanderthal skeletons, first in the early 20th century and then in 1972. Beyond their importance for the biological identity of Neanderthals, these finds raise questions about potential funerary practices of this extinct branch in human evolution. Of the seven individuals, two were already dated thanks to recent excavations of the site: the La Ferrassie (LF) 2 individual was dated to ca. 43-45 ka by Optically Stimulated Luminescence (OSL) and radiocarbon [1], while LF 8 was dated, by radiocarbon applied to associated finds, to ca. 42-45 ka [2]. In 1909, LF 1 was found and extracted in at least two blocks of sediment for studies in Paris by M. [3]. Here we present joint chronologies for (i) the main sequence where LF2 was located thanks to sedimentological analyses, (ii) the LF8 area and (iii) a sediment lump associated with LF1. Indeed, in 2015 we could retrieve sediment, some of which was still (naturally) consolidated, from one of the sediment blocks that were transported and kept in the Musée de l'Homme, Paris. The chronology is obtained by applying BayLum [4,5] to the set of numerical ages obtained by radiocarbon and OSL, taking into account both stratigraphic constraints and shared errors across OSL ages. Despite the limited size of the sample associated with LF, 1, 271 grains gave enough light to give an exploitable OSL signal (test dose signal uncertainty >15%), of which 117 have a D0 value >100 Gy and are thus prone to measuring doses of several tens of Gy (expected dose is around 50-100 Gy). Unsurprisingly, the OSL signal for this sample is dominated by the fast component – as was previously observed for other samples from the site. The overdispersion in equivalent doses is equal to $36 \pm 3\%$, which – at this site – is consistent with values obtained for well-bleached samples. However, one difficulty in dating such sediment taken from a museum collection lies in the impossibility to measure the corresponding gamma dose rate in situ. Therefore, we tried calculating the age of LF 1 based on various assumptions to estimate the gamma dose rate.

Whereas generally the modelled chronology does not change for previously published samples – although we note a better precision, especially for OSL ages, thanks to modelling with BayLum – the age of the sediment associated with LF1 is of ca. 42-45 ka. Thus, LF 1, LF 2 and LF 8 all date from the same period – the very end of Middle Palaeolithic. This work further contributes to the study of La Ferrassie and to our understanding of Neanderthals behaviors.

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Middle Pleistocene tools and site functions: preliminary traceological analysis of the lithic assemblage from Marathousa 1 (Megalopolis, Greece)

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The lithic industries of Lower Palaeolithic Europe are characterized by a wide range of diversity. Biface assemblages stand alongside small tool assemblages and core-and-flake industries. This variability is still poorly understood, hindering the assessment of hominin techno-economical choices. Recent studies on lithic variability of the Middle Pleistocene investigate whether differences in assemblage composition is related to cultural or temporal trends, site function, or availability of raw materials. As part of this broader reassessment, we interpret the functional goals of lithic production by conducting a techno-morpho-functional study of lithics from well-dated, well-preserved and well-documented sites, to build a solid chronostratigraphic and contextual framework. It constitutes a prerequisite for conducting reliable traceological analyses.

Marathousa 1 (MAR-1; Megalopolis, Greece) meets these requirements as the only Middle Pleistocene site in Greece with archaeological and faunal remains recovered from stratified and dated contexts [1]. The archaeological layer is ca. 400-500 ka BP and is composed of a fine-grained matrix. The excavation has yielded a lithic assemblage made almost exclusively of small-sized flakes found in direct association with diverse megafauna. MAR-1 provides a rare opportunity to investigate small tool functions in a reliable framework. The excavation took place in two sections, approx. 60 m apart, areas A and B, in order to investigate the spatial distribution of the remains and the extent of the site. Area A exhibits numerous elephant bones from a largely complete single individual (*Palaeoloxodon antiquus*) with anthropogenic cut-marks and a low density of lithic finds. Area B has yielded a higher density of lithics, with a more diverse toolkit than Area A, but also additional elephant remains and other bones with cut-marks and anthropogenic modifications. The data suggest that hominins exploited an elephant carcass in Area A, whereas, in Area B a larger variety of mammals were exploited.

We present here, the results of a preliminary traceological study on a sample of 250 lithics from Area A and B from a total of 2058 artifacts. The traceological data complements previous studies on the lithic and faunal remains of MAR-1 in four aspects: taphonomy, tool and site functions and tool morphology. The analysis of post-depositional surface modifications of the artifacts confirms their exceptional state of preservation and validates the integrity of the site. The preliminary use-wear analysis on 13 artifacts yielded promising results: half of the studied pieces exhibit traces of human activity (use-wear or technological traces), which is rare for an assemblage of this age. Functional data confirms the zooarchaeological assessment that butchering activities took place at both excavation areas, and also demonstrates that plants were exploited by hominins. These new results open up the possibility that MAR-1 was not necessarily a special-purpose site for the exploitation of animal resources, but included other tasks, possibly involving to various degrees of intensity the exploitation and/or use of plants in combination with stone tool maintenance and use. Tools with use-wear traces do not show any significant standardization in terms of blank shape or edge morphology. However, more than half of the tools are backed, supporting the original identification of backing as an important technological element of tool production [2]. Finally, the functional results of lithics from MAR-1 provide new data on the function of small tools and more broadly on tool in the European Lower Palaeolithic.

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Initial Upper Palaeolithic genomes from Bacho Kiro Cave reveal recent Neandertal ancestry and links to Asia

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Modern humans started spreading across Eurasia by at least 47,000 years before present (ky BP) [1,2]. However, the genetic history of these early dispersals, the extent to which they interacted with resident archaic populations, and the extent to which they contributed to later human populations are poorly understood. Skeletal remains of modern humans from this time period are rare and there is even smaller number of individuals from whom genome-wide data are available. Among the oldest modern humans from Eurasia with genomic data are the ~40,000-year-old Oase1 individual from Romania [3] and the ~45,000-year-old Ust'-Ishim individual from Siberia [4], both of whom did not contribute considerably to later populations.

Using in-solution hybridization captures we recovered genome-wide data from five human remains found in direct association with an Initial Upper Palaeolithic (IUP) assemblage at Bacho Kiro Cave, Bulgaria [1,2]. Directly dated to between 45,930 and 42,580 cal. BP [1,2], these individuals represent the oldest Upper Palaeolithic modern humans in Europe recovered to date. Counter to what would be expected for ancient individuals from Europe, we find that the IUP Bacho Kiro Cave individuals are more related to present-day and ancient populations with East Asian ancestry than to later West Eurasians. This is consistent with the IUP archaeological assemblages found from central and eastern Europe to present-day Mongolia [5], and a putative IUP dispersal that reached from eastern Europe to East Asia.

However, populations related to the IUP Bacho Kiro Cave individuals ultimately disappeared in western Eurasia, as indicated by the fact that later individuals, including the ~35,000-year-old BK1653 individual at Bacho Kiro Cave, were closer to present-day Europeans than to ancient or present-day Asians. These results demonstrate that multiple differentially related human groups were present in Eurasia during the early Upper Palaeolithic, with IUP Bacho Kiro Cave individuals belonging to a modern human migration into Europe that was not previously known from the genetic record.

Based on the segments of Neandertal ancestry detected in their genomes, we find that all IUP Bacho Kiro Cave individuals had Neandertal ancestors only a few generations back in their family history, similar to Oase1 [3], thus suggesting that mixing between Neandertals and some of the early groups of humans in Europe could have been common. Moreover, we find almost no introgressed Neandertal DNA in the IUP Bacho Kiro Cave and Oase 1 individuals that is within previously identified parts of the human genome devoid of Neandertal ancestry (i.e., Neandertal “deserts”). This would indicate that the selection against Neandertal DNA variants occurred within just a few generations after Neandertal introgression, although additional individuals with recent Neandertal ancestry will be needed to fully resolve this question.

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Ecological diversity of *Gorilla* spp. from dental macrowear analyses

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Size and shape variation of molar crowns in primates play an important role in testing phylogenetic hypotheses and understanding how species adapted to their environment. Primate teeth have evolved to improve mechanical chewing efficiency for coping with a variety of food resources. Thus, differences in tooth structures and size reflect mechanical properties of foods that primates eat [1]. While the primary dental morphology informs us which mechanical principles, such as shear-cutting, crushing and grinding is most dominant with respect to occlusal relief, tooth wear patterns help us to reconstruct and understand individual pathways and dental contacts during the power strokes of the chewing cycles.

Gorillas are commonly considered to be folivorous primates, with a diet consisting of leaves, stems, roots and bark [2]. However, the proportion of fruit in their diet can vary significantly depending on their habitats, with the lowland gorillas (which inhabit lowland rain forests) being more frugivorous than the mountain gorillas (which live in high-altitude montane forests). The objective of this study is to analyse molar macrowear patterns in various gorilla groups to obtain information about their diets. We employed the well-established virtual Occlusal Fingerprint Analysis (OFA) [3], a quantitative approach that examines occlusal wear facets using high-resolution digital models of teeth.

In this preliminary study we analysed lower second molars of western lowland gorillas (*Gorilla gorilla gorilla*; N=21), eastern lowland gorillas (*Gorilla beringei graueri*; N=4) and mountain gorillas (*Gorilla beringei beringei*; N=2). We selected molars characterised by a degree of wear between wear stages 2 and 3 [4]. Digital 3-D models of teeth were generated using a white-light scanning system with a xy resolution of 45 µm (smartSCAN3D C-5, Breuckmann GmbH). We examined the relative surface areas and the inclination of each occlusal wear facet [3]. We also calculated the percentage of dentine exposure (PDE), by dividing the dentinal area with the 3-D occlusal surface of each molar.

The results showed no major significant differences in the occlusal wear pattern between eastern and western lowland gorillas. However, small differences were noted in buccal shearing areas, with mountain gorillas possessing slightly larger buccal shearing areas than those of lowland gorillas. Overall, the macrowear pattern of *Gorilla* is characterised by steep wear angles, and is dominated by large phase II and lingual phase I facets and by small buccal phase I facets. Interestingly, the facet inclination between wear stages two and three does not change, suggesting that their dentitions maintain mechanically efficient shear-cutting capability for processing food through time, as highlighted by other studies [5]. Similarity in molar macrowear could indicate high levels of dietary overlap between the gorillas examined in this study. It probably is related to the mastication of mechanically challenging foods, highly fibrous in nature, maybe masking wear signals associated with softer preferred diets. The presence of slightly larger buccal phase I facet in mountain gorillas suggests an increased shearing capability, which is probably associated with their more folivorous diet.

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EASY, FAST, AND CLEAR. Recognizing the role of the optical microscope for the quantification of human dental microwear

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Dental microwear analysis has a long history of use for paleodietary reconstruction. Naturally, substantial changes in the methodologies and technologies used to observe and quantify microwear have occurred. The earliest studies of human dental microwear were done with optical microscopy (OM). Their replacement by SEM (scanning electron microscopy) in the 1980's was due to a series of technical limitations of OM that included limited depth of field and problems with shiny enamel surfaces. Furthermore, much of the field of view was out of focus and only narrow bands were visible, making the analysis of dental microwear with OM less efficient in comparison to SEM. These problems were also recognized by some lithic use-wear analysts working to advance traceology. However, traceology has continued to use, advance, and adopt technological improvements to OM—often in combination with other techniques like SEM or confocal microscopy—whereas dental microwear studies have largely moved away from OM. With this in mind, we aim to evaluate the applicability of optical microscopy for dental microwear analysis by testing OM against established SEM procedures for buccal microwear analysis.

The sample analyzed consists of 18 human molars from several Holocene sites from the Iberian Peninsula: El Mirador Cave, Galls Carboners, Cova de la Guineu, and Mas Trader. After image acquisition using both OM and SEM, the total number of striations (TN) and their lengths (XT) were recorded with open-access software (ImageJ) following a standard methodology [1]. The equivalence of the magnifications between microscopes is based on a previous calibration where the size of the field of view dimensions for each acquisition system is known [2], the field of view of both microscopes are equivalent.

In most of the cases, OM records greater TN in each tooth compared to SEM. Results show that more striations are observed using OM than when analyzing the same surface with SEM. However, the central count trend is similar for both techniques, as indicated by the high correlation between microscopes by tooth for each variable. The higher mean of TN observed with the OM could be due to the imaging characteristics of this microscope, which has a better qualitative resolution and a three-dimensional appearance facilitated by improvements to extended focus.

Regarding the comparison of microscopes, the OM methodology that we propose is faster in terms of sample preparation and image acquisition, especially when compared to the use of SEM at high vacuum. The most significant advantage of the OM over SEM is probably the greater accessibility of OM for most researchers. A SEM is a large piece of equipment that is not only expensive to acquire but demands constant and expensive maintenance. In contrast, OM microscopes require much less physical space, are generally much lower in initial cost to purchase, require less maintenance, and require little in terms of associated equipment aside from a computer and a camera.

Lastly, from the point of view of the person analyzing the micrographs, the nature of the images obtained through the OM—in terms of 3D appearance, contrast, and brightness—makes it much easier to detect the striations which greatly reduces researcher eye fatigue associated with buccal microwear quantification. We can therefore conclude that OM is a consistent and user-friendly method that provides good image resolution together with a series of economic and technical advantages over SEM for buccal microwear analysis [3].

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The evolutionary enlargement of hominoid cerebellar surface area relative to the neocortex

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Recent studies have highlighted the importance of the cerebellum in humans and other fossil hominins. The cerebellum is understood to ameliorate motor functioning, memory, attention and learning in *Homo sapiens* [1], and may therefore have a notable role in the evolution of behaviours associated with humans, such as language and tool use. Congruous with this hypothesis, recent work has indicated that cerebellum surface area is much larger in humans than in macaques [2]. However, ape (i.e., non-human hominoid) cerebella share similar morphometric scaling values with *H. sapiens* in both volume [3] and neuron number [4], obscuring what can be gleaned about the function of this interspecific variation. Thus far, few studies have considered the role of cerebellar surface area towards cognitive evolution [2,5], and none have investigated the evolution of cerebellar surface area when comparing humans to other anthropoids. Here, we aimed to address the evolution of human cerebellar surface area in comparison to apes. We predicted that, in accordance with preceding literature [2,3,5], hominoid cerebella would be relatively larger in volume and surface area than those of non-Hominoidea.

In the current study, we use high-resolution histological sections of an eastern lowland gorilla (*Gorilla beringei graueri*) brain to study the cerebellum. We used the collaborative web application MicroDraw (<https://microdraw.pasteur.fr>) to delineate the molecular layer boundaries of the cerebellum and the pial surface of the cerebrum, aiming to measure and assess interspecific differences (presented within prior literature) in surface area and volume. MicroDraw allowed us to interactively annotate multiple regions and to relocate, combine, and refine them through addition or subtraction of points. Secondly, we developed a three-dimensional (3D) reconstruction of the gorilla cerebellum. This reconstruction facilitated both a direct comparison between cerebellar segmentation from high resolution histological sections and its 3D shape, and validated the structural and substructural boundaries.

When converted to length values and corrected for shrinkage during fixation, the gorilla cerebellum surface area constituted 64.4% of its neocortex, and a cerebellar volume of 14.3% of its whole brain. This exceeded prior estimations of *Macaca fascicularis* relative surface area (33%), but is surpassed by estimates of *H. sapiens* relative surface area (78%) [2]. Relative cerebellar to cerebral volume in the gorilla was comparable to hominid values from the literature. To investigate whether human values deviated from the non-human anthropoid trend, a phylogenetic generalised least squares model was used to determine the scaling relationship between cerebellum surface area and volume to cerebrum volume in non-human anthropoids when accounting for phylogeny. It was found that compared to the non-human anthropoid prediction, human cerebella had 19.3% more surface area relative to cerebral volume, but were 15.1% less voluminous relative to cerebellar surface area. Human cerebellum is thus more foliated than predicted, but, because surface area increases more rapidly than volume, requires little accommodative volumetric increase. Its volume, in fact, could be predicted by the cerebral volume of other anthropoids. Hominoid cerebella were significantly more voluminous than monkeys', in support of past work indicating a volumetric grade shift between them [3]. Subsequent comparative research into the scaling of human cerebellar surface area and volume and their possible association with cognitive divergence from other hominoids, will benefit from a phylogenetically diverse sample. Presently, we uphold the notion that enlarged cerebellar surface area is conducive to cognitive aptitude when comparing *H. sapiens*, *G. beringei graueri*, and *M. fascicularis*.

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How does hyperostosis frontalis interna affect bone cranial vault thickness and organization?

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Hyperostosis frontalis interna (HFI) is characterized by the thickening of the inner surface of the frontal bone. As there are virtually no symptoms nor medical complications associated, the diagnosis is often established by chance during imaging tests. The extent to which the bone is modified ranges from isolated, elevated bony islands (Type A) to continuous bony overgrowth (Type D) [1]. While this condition affects a large proportion of the general population (between 5 and 12%, more commonly older women), little is known about its aetiology, demographic, and evolutionary history. Interestingly, previous studies reported the presence of HFI in fossil hominins, including the *Homo erectus* specimen Sangiran 2 and the Neanderthal specimens Gibraltar 1 and Shanidar 5 [2]. Given the strong emphasis on cranial vault thickness in the diagnosis of fossil hominins (e.g., *Homo erectus*, [3]) and the possibility that this condition might bias our appreciation of the variation in past populations, in this study we provide further evidence of frontal bone thickness in extant humans by noninvasively investigating the cranial vault of pathological and non-pathological individuals. Additionally, we refine the grading system introduced by Hershkovitz et al. [1] by including measurements of bone thickness and spatial arrangement of compact and trabecular bones. We studied 18 extant human individuals from the Pretoria Bone Collection of the University of Pretoria (South Africa), including 8 individuals (5 males and 3 females) that show manifestations of HFI and 10 unaffected individuals (6 males and 4 females). Crania were scanned by microtomography at the MIXRAD facility located at the African Nuclear Corporation (Necsa) in South Africa. Frontal bone thickness variation as well as the structural organization of the cortical and trabecular bone were assessed at regular intervals along two coronal sections that document the anterior and posterior regions of the frontal bone. Preliminary results indicate that frontal bone thickness ranges from 1.62 to 24.86 mm in affected individuals and from 1.16 mm to 17.96 mm in unaffected individuals. Moreover, in affected individuals, the spongy bone represents up to 57% of the total bone area while in unaffected individuals it represents about 51% of the total bone area. Patterns of frontal bone thickness variation differ along the two sections between affected and unaffected individuals, with the former showing irregular distribution and the latter showing more homogenous distribution. Our study shows that, in addition to thickening the frontal bone, HFI also modifies bone microarchitecture, supporting previous studies of bone microstructural properties [4]. Overall, our results open interesting perspectives for future applications of the microtomographic-based assessment of bone thickness and tissue proportion and both the assessment of cranial vault thickness and the diagnosis of HFI in the fossil hominin record.

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Intensive and expedient resource extraction strategies through the flexible use of lithic bipolar methods in Early Aurignacian of Abri Pataud

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The arrival of *Homo sapiens* and subsequently the Upper Paleolithic in Western Europe is marked by the appearance of the Aurignacian industry [1]. A predecessor to the Gravettian and a successor to transitional industries like the Châtelperronian and the Middle Paleolithic Mousterian industries, the Aurignacian marks some of the earliest blade technologies in this region [1,2]. One particularity that the Aurignacian shares with other Upper Paleolithic industries is the considerable representation of lithic bipolar technology compared to prior industries.

In this paper we analyze the bipolar technology of the early Aurignacian occupations of Abri Pataud, a site well known for its Aurignacian and Gravettian occupations [3-5]. By exploring the technological, functional and cultural use of bipolar technology during the early Aurignacian occupations of the site, we aim to provide new data on how this technology contributed to the adaptation and settlement of *Homo sapiens* in this region.

Our results show patterns in terms of function and reduction intensity related to environmental adaptability and mobility patterns. The Abri Pataud Early Aurignacian initial occupation (Level 14) seems to be initially marked by a long occupation during a cold moment in which reindeer dominate in the faunal spectrum [4,5]. In this level splintered pieces dominate the range of bipolar artifacts and were used as wedges for working hard organic materials (e.g., bone and antler). While bipolar technology has a low representation in terms of overall technological spectrum, this period is marked by reutilization of blades or flakes as wedges until depletion (e.g., large fractures). Suitable blanks were being chosen most likely due to their durability for consistent and intensive reutilization in carcass processing activities (e.g., bone splintering, bone marrow extraction etc.) as a means for maximization of organic resource extraction. In subsequent levels there seems to be a succession of short-term occupations also typically dominated by reindeer [3]. This is where a shift can be noted in terms of bipolar method usage. This period is marked by wedging activities in higher frequencies than before, but with different strategies. In this period wedges were being selected from a variety of artifacts, often former tools (typically scrapers) and were used to a lesser extent, exhibiting less fragmentation and damage, meaning they were abandoned early on. In addition, and in low frequencies, expedient on anvil re-debitage (bipolar knapping) is also present with flake production as its main goal. Overall, this period is marked by fast, expedient on-the-go use of bipolar methods for achieving tasks in a quick manner, likely related to higher mobility.

Our results show that *Homo sapiens* were flexibly using bipolar methods as means of resource extraction at the site. While bipolar methods were mostly used for wedging, for working hard organic materials these were used in different manners according to their needs. In the earliest occupation there is a clear choice and intensive use of wedges until depletion, with the goal of maximizing both each tool's potential and resource extraction. On the other hand, in later occupations, where mobility is constant, bipolar methods were used as a quick and expedient way of working organic materials of even producing flakes. Tools were quickly chosen, used and abandoned early on. While bipolar methods are often linked to contexts of: (1) raw material conservation, intensive resource extraction strategies, etc.; (2) or even expedient resource extraction strategies; this work shows that the understanding of the flexible advantages of these methods was present in technological traditions of Aurignacian groups. This work presents insights on how the understanding of the flexibility of the use of bipolar methods played a strategic role on the adaptation and settlement of *Homo sapiens* in Western Europe.

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Changes in settlement and technical behavior of the Upper Paleolithic occupations of Aghitu-3 Cave, Armenia

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Aghitu-3 Cave is located in southern Armenia along the Vorotan River at an elevation of 1601 m a.s.l. and represents the earliest evidence for modern human behavior in Armenia. Here, we present some conclusions from a doctoral study about the lithic artifacts from six phases of settlement represented by archaeological horizons (AH) VII, AH VI.1, AH VI.0, IIID, IIIC, and IIIB. These layers date between about 39,000 and 26,000 cal BP. Overall, obsidian occupies the largest share of the lithic assemblage with 85%, with chert next at 14.7%; the few remaining artifacts (<1%) are mainly dacite and basalt. Based on the completed technical and typological study of the cores and tools in these archaeological horizons, we are able to classify them into two main phases of settlement, early Upper Paleolithic (EUP) and middle Upper Paleolithic (MUP).

1. EUP settlement includes AH VII, VI.0 and VI.1. Although there are relatively few artifacts, their technical distinction is clear. The people who inhabited Aghitu-3 preferred rocks of a specific shape to create cores. They used a narrow-faced technique to create the cores and extract the tools. They often experienced technical problems, which led the knappers to discard the cores before they were fully used.

We observe that the cores are larger than in the younger layers of the cave. Once the knapper set up a core, he/she focused almost exclusively on the extraction of laminar blanks, including blades (width ≥ 10 mm) and bladelets (width < 10 mm). People relied most heavily on the production of bladelets, which represent up to 85% of the assemblage, which they retouched laterally. Based on an experimental study, we suggest that people used them as components of composite tools for cutting and slicing. Other types of tools include burins, drills, denticulates and splintered pieces.

2. MUP settlement includes AH IIID, IIIC and IIIB, which are the richest archaeological horizons in the cave. The people who inhabited Aghitu-3 did not show a preference for raw materials of specific shapes. We believe they collected rocks expediently and knapped cores in several different ways. We note that these cores are usually small and exhausted when compared to the EUP layers of the site. The diversity of tools is the most interesting feature of the MUP, with 1180 tools divided into 13 categories. Laterally retouched and backed bladelets are most common, and we assume they were used mainly as cutting inserts. Burins in Aghitu-3 are another important category of tools. People created many types of burins, such as dihedral burins, burins with truncation, and simple burins. The remaining types of tools include retouched bladelets, retouched flakes, end and side scrapers, notches, denticulates, drills, combination tools and splintered pieces.

When comparing knapping techniques and tool types of the EUP and MUP phases, we observe that the same technologies continued. The differences between them are not revolutionary, so we can say that they belong to one culture that prevailed throughout the sequence until about 26,000 cal BP. Based on this late date, we assume that these assemblages were not made by Neanderthals, and therefore provide the earliest evidence for modern human behavior in Armenia.

However, subtle shifts in ways of knapping, as well as in the size of cores and tools, tell us about changes in the lifeways and preferences of the first modern humans known from Armenia. We assume people used Aghitu-3 Cave for repeated, short-term stays during the EUP, but as a seasonal camp for longer stays during the MUP.

Craniofacial variation in early *Homo sapiens*

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Based on fossil and genetic data, it is likely that *Homo sapiens* originated in Africa sometime during the Middle Pleistocene, at least ~500 thousand years ago (ka). However, this estimated timing for the origin of our species coincides with the period referred to as the ‘muddle in the middle’ (~700–100 ka), characterised by much morphological diversity among *Homo* fossil crania [1,2]. This period also corresponds to emerging fossil evidence for African *Homo* specimens, including putative early *H. sapiens*, collectively displaying diagnostic modern human (MH) craniofacial traits in a mosaic fashion (i.e. with different combinations of primitive and derived characteristics), and with the full suite of MH cranial features only appearing from ~100–40 ka [1,3].

A fundamental and long-standing issue in elucidating the origin of our species remains with the lack of a field-wide consensus on a systematic morphology-based diagnostic method for attributing individual fossils to ‘*Homo sapiens*’. This is illustrated by the unusually vast morphological variation lumped under the species umbrella of *H. sapiens*, along with the absence of clear working definitions for ‘archaic’ versus ‘anatomically modern’, and where we draw the lines between ‘archaic’, ‘early’ and ‘anatomically modern’ *H. sapiens* [3]. Additionally, growing research indicates a more dynamic and complex evolutionary history of MH, beyond the classic origin and dispersal models of Multiregionalism and Out of Africa, with a polycentric origin of our species referred to as the structured African metapopulation model (or Pan-African Multiregionalism). This notion supports a more reticulate understanding of human evolution involving transient populations, population migration, fission, fusion, gene flow and local extinction [1,4,5]. This more recently accepted model is consistent with the striking craniofacial variation observed in the relevant fossil evidence which could reflect the existence of distinct craniofacial morphs as defined by their degree of anatomical modernity, or geographically and chronologically determined palaeodemes of ‘archaic/early *H. sapiens*’ across the African continent [4,5].

The present research explores craniofacial variation and mosaicism in Middle–Late Pleistocene *Homo* specimens, including putative archaic and early *H. sapiens*, across Africa in order to contribute to the ongoing debate around the diagnostic parameters for *H. sapiens* identification and to test current origin models. We test the predictions of the structured African metapopulations model in terms of craniofacial morphology and variation in palaeodemes of fossil crania from Africa and the Levant dating between ~1 million years ago and 50 ka. The current study uses a combination traditional morphometrics and qualitative trait-based morphological assessment to analyse specimens for any geographical and temporal patterning in variability of different craniofacial regions. Here, we report on morphological trends and temporospatial patterns in the available hominin fossil record, and the results of tests of the morphological evidence of palaeodemes and multiregionalism.

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Biomechanical evidence of increased thumb dexterity in 2-million-year-old thumb fossils

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The ability to efficiently produce and use tools constitutes a hallmark of human identity and a key component of bio-cultural evolution [1,2]. Increased manual dexterity has been proposed as a prerequisite for habitual tool-using behavior, both first appearing in the genus *Homo* [1,2]. However, recent discoveries cast doubt on these assumptions. Such evidence involves the discovery of possible stone tools predating the genus *Homo* (>3 million years ago) and the identification of *Australopithecus* hand skeletons bearing anatomical indications of heightened manual dexterity [2].

An important limitation of most previous research on the evolution of manual dexterity is that it did not rely on direct biomechanical assessments but instead focused on morphological comparisons across different fossil species, assuming that the dexterity of each hominin is proportional to its degree of similarity with the modern human form. Here, we overcome this problem by calculating manual dexterity across different early hominin species with an innovative integration of three-dimensional (3D) biomechanical modeling and geometric morphometrics [3]. Our approach precisely calculates joint torque (a major component of biomechanical efficiency), taking into consideration the potential effects of both 3D bone morphology and, importantly, of soft tissue. We focused on the essential muscle *opponens pollicis* and the act of thumb opposition, both crucial in human precision-grasping and tool use.

Results revealed evidence of increased thumb opposition efficiency in two fossil hominin thumb specimens from Swartkrans (South Africa), dated to approximately 2 million years ago, which are potentially associated with the genus *Homo*. In contrast, the *Australopithecus* specimens in our sample consistently presented lower levels of thumb opposition dexterity, despite their proposed tool-using manual behaviors. This was true also for *Australopithecus sediba* (also dated to approximately 2 million years ago), whose human-like relative thumb size has been proposed to indicate increased tool-using abilities. Finally, all later *Homo* (including Neanderthals and modern humans) exhibited similarly heightened thumb opposition dexterity. This was also the case for *Homo naledi*, a small-brained species that has not yet been found in association with stone tools. Overall, our findings suggest that an early emergence of thumb dexterity about 2 million years ago may have comprised a foundation for the subsequent gradual development of complex culture. The consistently high levels of thumb dexterity in recent *Homo* highlights the great importance of this evolutionary advantage for human bio-cultural evolution [3].

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Revisiting the functional morphology of the *Homo habilis* OH 7 hand

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The Olduvai Hominid (OH) 7 subadult hand fossils were used to define *Homo habilis* as a species, the genus *Homo* and our evolutionary understanding of hominin dexterity and tool use [1]. Early functional interpretations focussed on strong, curved digits indicating power-grasping abilities, but were more cautious about inferring modern human-like precision grip [2,3]. However, the presumed association of the OH 7 hand with stone tools and a *H. habilis* living site [1] has perhaps overstated its manipulative function and overshadowed its relatively poor preservation. Here we assess the morphology of the OH 7 hand bones through 3D geometric morphometrics (GM), cross-sectional geometry, and data-driven modelling to reconstruct intrinsic hand proportions. We compare the morphology of the partial scaphoid, partial trapezium and phalanges to a sample of extant great apes (*Pan*, *Gorilla*, *Pongo* and modern humans) and other fossil hominins, including australopiths, *Homo naledi*, *Homo floresiensis* and *Homo neanderthalensis*.

Curvature of the OH 7 intermediate phalanges falls within the range of adult and juvenile *Gorilla*, adult *Pan*, and *A. sediba*, but also within the highest extreme of humans. Cortical thickness maps (using Morphomap [4]) reveal that cortical bone is thicker palmarly in great apes and dorsally in humans. OH 7 shows a great ape-like pattern, with thicker palmar cortex, especially just proximal to the trochlea. Cortical analysis of the OH7 proximal and intermediate phalanges show high relative bending strength (Zpol, J), most similar to African apes and higher than that of *A. sediba*.

The principal components analysis (using Procrustes coordinates) for the trapezium shows that the OH 7 first metacarpal facet shape alone falls just outside the human range of variation, but when all facets are considered together, OH 7 falls within the human distribution. In comparison, the *H. naledi* trapezium clusters with African apes, and *A. afarensis* (AL 333) is intermediate between humans and African apes. The GM analysis of the entire scaphoid shape shows that all four reconstructions of OH 7 (which is missing its tubercle) fall out closest to humans, Neandertals and, less so, LB1, but is distinct in having a rectangular capitate facet. *H. naledi* and *A. sediba* scaphoid shape is intermediate between humans and African apes, while *Australopithecus* sp. StW 618 is *Gorilla*-like.

Based on a diverse extant primate sample of associated hand skeletons, we determined which species best predict the lengths of the phalanges preserved in OH 7, and from these models, imputed the lengths of the elements that are not preserved. The best performing models predict a thumb/third digit ratio between 48.3-49.6% in OH 7, a range that reflects a thumb longer than *Gorilla* (mean 40%), falls within the lower range of variation in modern humans (49-59%, mean 54%) but below the thumb proportions found in *A. afarensis* (estimated 52%), *A. sediba* (60%), *H. naledi* (58%).

Taken together, the OH 7 proximal and intermediate phalanges are African ape-like in their curvature and cortical robusticity, indicating powerful grasping with fingers that are capable -more so than *A. sediba*- of withstanding the high loads incurred during arboreal locomotion. In contrast, the OH 7 scaphoid is more human-like than previously appreciated [3], and both carpals are more human-like than all other fossil hominins in our sample, excluding Neandertals. The imputed hand proportions, albeit uncertain, show a relative thumb that is shorter than other fossil hominins and paired with an expansive trapezium-first metacarpal facet and broad distal pollical phalanx (but potentially lacking human-like flexor musculature [5]). Revisiting the functional morphology of OH 7 within the context of recent, more complete hominin skeletons, suggests that the *H. habilis* hand likely accommodated both locomotion and enhanced manipulation but in a different way to that of *A. sediba* and *H. naledi*.

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Keep the home fires burning - Neanderthal fuel selection as a modern cognitive process

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Neanderthals, an extinct hominin species closely related to our own species, are known to have some aspects of behavioural modernity, such as group hunting of large prey species, and construction, maintenance and use of specialist subsistence tools. What is less well understood however is their proficiency with fire, a technology common to modern humans. Some authors such as Sandgathe and Dibble suggest that Neanderthals did not frequently use fire, and indeed were not cognitively modern with regards to this technology [1]. This issue is incredibly variable across sites however, and Neanderthals, as much as modern humans, should not be seen as a species with uniform behavioural traits. In particular, the study of their fuel selection and the degree of active choice here is as yet underdeveloped. I challenge the assumption that Neanderthals did not habitually use fire, and I look to discover this missing record through fuel use. I address the degree to which Neanderthals chose specific arboreal species to optimise burning on their fires, by considering pollen and charcoal from publications on ten stratigraphic layers in five Iberian Neanderthal cave sites (c.90-40ka BP) [2-5]. These are Abric Romani, Cova del Coll Verdaguer, Cueva del Camino, El Esquilieu and Gorham's Cave. The relative proportions of genera are graphically compared in the two records to see if Neanderthals were being selective in their fuel choices compared to environmental availability, or if they conformed to Principles of Least Effort. Using statistical analysis including Welch's T-test for statistical significance, I find that certain species were selected for beyond the expectations based on pollen-derived environmental availability, and these species are commonly considered to be good fuels. Conversely, worse fuels were avoided. The conclusion that these Neanderthals selected towards (or against) a few genera for ease of harvesting and combustibility, specifically selecting for dry, dead pine branches, is supported. Other genera were used indiscriminately, suggesting that these were gathered, ad-hoc, to expediently fuel fires when preferred woods were unavailable. The implications of this research tentatively suggest that Neanderthals did actively select their fuel in Iberian contexts, suggesting a familiarity with their local environment and also with this technology. These findings challenge the 'primitive' narrative of Neanderthal lives, and suggest closer behavioural links to our own species. This also challenges Palaeolithic environmental reconstruction based on anthropogenic charcoal, if the charcoal samples are not uniform representations of past vegetation due to active selection for particular genera, or types of trees. If charcoal is to be used in this manner, then the behaviours leading to its accumulation, and subsequent taphonomic processes, must be better understood than they currently are.

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***Macaca* (Cercopithecidae, Primates) from the Middle Pleistocene of Marathousa 1 (Megalopolis basin, Greece)**

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Marathousa 1 (MAR-1), located in the Megalopolis palaeolake basin, southern Greece, preserves an exceptionally well-preserved archaeological and palaeontological assemblage. Radiometric dating, magnetostratigraphy, and geological and biochronological analyses indicate an age of 500–400 ka, and place the locality within the Marine Isotope Stage (MIS) 12 [1 and references therein], making it the oldest radiometrically dated archaeological locality currently known in Greece. The locality has yielded lithic and bone artefacts in stratigraphic and spatial association with micro- and macro-fauna (e.g., insects, ostracods, molluscs, fishes, amphibians, reptiles, birds, mammals), as well as micro- and macro-flora [1]. Notably, it preserves the skeletal remains of at least two individuals of the European straight-tusked elephant *Palaeoloxodon antiquus*, some of which preserve evidence of anthropogenic modifications. In addition to *P. antiquus*, the locality's large mammal faunal assemblage includes the beaver *Castor fiber*, the weasel *Mustela* sp., the otter *Lutra simplicidens*, the wildcat *Felis* sp., the fox *Vulpes* sp., the wolf-sized *Canis* sp., the hippo *Hippopotamus antiquus*, the large bovid *Bison* sp., and the deer *Dama* sp. and *Cervus elaphus* [2].

During the excavation campaign of 2019, a cercopithecine primate, represented by an almost complete mandible (MAR-1-9B), was discovered. The specimen preserves both rami and corpora, as well as the most of its dentition. Dental metric comparative analysis permits its attribution to the Barbary macaque *Macaca sylvanus*, a species that was geographically widely distributed in western Eurasia during the Plio-Pleistocene [3]. Three (chrono) subspecies [4] of European macaques from this period are generally recognized: *M. s. prisca* from the Pliocene, *M. s. florentina* from the Early Pleistocene, and *M. s. pliocena* from the Middle until the Late Pleistocene. The dental dimensions of MAR-1-9B fit better within the variation of *M. s. florentina* and *M. s. pliocena* rather than with the extant representative *M. s. sylvanus*. Moreover, a principal component analysis reveals a better match with *M. s. pliocena*. Since no clear-cut diagnostic criteria have been defined to differentiate these European fossil subspecies, we attribute MAR-1-9B to *M. s. cf. pliocena*, in agreement also with the chronology of the locality.

MAR-1-9B constitutes one of the very few known records of *Macaca* in the eastern sector of the peri-Mediterranean region and its first occurrence in the Middle Pleistocene of Greece. It therefore extends the chronological range of cercopithecids and documents, for the first time, the coexistence of macaques and hominins in the country. The palaeolake environment at Marathousa 1 would have offered macaques the protection and resources of the nearby woodlands, as well as access to freshwater and a variety of feeding opportunities throughout the year. Although MAR-1-9B does not show any evidence of anthropogenic or carnivore modifications, prey-predator relationships and interactions among hominins, carnivores and macaques at Marathousa 1 are likely: lithic artefacts and bones with anthropogenic modifications recovered at the site are spatially and stratigraphically associated with carnivore remains and carnivore-modified bones of their prey. In Europe, several Middle Pleistocene localities document the co-existence of macaques and hominins [3], including a few which, like Marathousa 1, have also yielded evidence of elephant butchering: e.g., Fontana Ranuccio, La Polledrara (Italy), Bilzingsleben (Germany), Ebbsfleet (United Kingdom) and Ambrona (Spain) [5]. MAR-1-9B marks the first documented such record in South-East Europe.

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A model method: measuring birch tar production complexity using Petri nets

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Advanced cognition is often recognized in the archaeological record through the presence of what are considered to be complex technologies, such as adhesives and composite tools. Birch tar production has been prominent in discussions about Neanderthal cognitive and technological capabilities in recent years. However, it is still currently debated how complex Palaeolithic tar production really was. Different possible production methods are assumed to be simpler or more complex than others, and definitions for what exactly makes birch tar complex often focus on different aspects and lack universal standards. Seemingly simple methods of producing tar have low yields, raising concerns about how effective they were in times when resource availability was scarce. However, it is possible to improve yield efficiency of these methods, and running multiple productions concurrently reduces the time investment needed. This makes them a viable choice, but at what cost to the production complexity? To answer this, we used Petri net models and pre-defined metrics to compare the complexity of a single tar production process with that of multiple concurrent production assemblies. Tar production processes were modelled as Petri nets using Snoopy 2 version 1.22 [1]. Petri nets are a formal modelling language, grounded in mathematical graph theory, that are used in process analytics [2]. A number of pre-existent metrics exist for studying the complexity of production processes using Petri nets [3]. Furthermore, process modelling has shown that the interaction between elements in a process is positively associated with a high cognitive load [4]. Preliminary results indicate that changing the number of concurrent tar production assemblies significantly alters the measured complexity. Additionally, these changes can affect the various complexity metrics in different ways. Our results demonstrate that extra care needs to be taken in how we define the complexity of tar production processes, and how we use this in discussion about Neanderthal behavioural abilities. Production complexity is highly dependent on a multitude of factors, and tar production processes may potentially be considered as both simple and complex, depending on how we look at them. Petri-nets and formal complexity metrics have proven to be a valuable method of defining tar production complexity.

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How sacralizations and lumbarizations shape the human sacrum

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Humans and great apes differ in their spinopelvic configurations, which reflects their locomotor behaviour and postural preferences. In great apes, the sacrum is often elongated to six or more vertebrae while the lumbar count is reduced to 3-4 and the last lumbar vertebra is entrapped within the pelvis, thus increasing trunk rigidity [1]. In humans, the lumbar column is longer and the lower lumbar vertebrae are more mobile, which facilitates the lumbar lordosis required for efficient upright walking [2]. Additionally, the sacrum itself consequently plays a central role given its biomechanical relevance. However, despite these functional constraints, the typical five-vertebrae configuration observed for humans is subjected to an unusually high prevalence of numeric anomalies ranging from four to six elements, with fossil evidence indicating a comparable range of variation for Neanderthals and early hominins.

Besides meristic changes that lead to additional or missing vertebrae, segmentation anomalies are primarily due to homeotic border shifts, where a vertebra transitions to the adjacent spinal region. At the lumbosacral border, such transitional vertebrae (LSTV) are common with documented frequencies of up to 35%. They either result from sacralizations, where the last lumbar vertebra is partly or fully integrated into the sacrum, or from lumbarizations, where the first element of the sacrum becomes detached and morphologically resembles a lumbar vertebra [e.g., 3,4]. Border shifts likewise occur at the sacrococcygeal junction by assimilation of the first coccygeal or detachment of the last sacral element [5]. However, inconsistencies in classification and counting methods, and the need to analyze the complete post-cervical vertebral column to distinguish between sacralizations and lumbarizations, have confounded proper investigation of LSTV thus obscuring their evolutionary and clinical significance.

Here, we establish a new method to consistently classify LSTV. Based on a sample of clinical CT data of 145 individuals aged 14 to 47 years, we assessed on the position of the hipbone relative to the first sacral vertebra (S1), and studied the morphological variation of the S1 shape by a geometric morphometric analysis (GM). LSTV were present in 27 individuals (19%). Most of them could be attributed to homeotic border shifts with 7 (5%) being sacralizations and 16 (11%) lumbarizations, while only 4 (3%) indicated meristic changes. The spatial relationship with the hipbones proved indicative of border shifts. In lumbarizations, the iliac crest was at the level of L5, whereas in sacralizations the iliac crest was parallel to L4. Similarly, the trajectory of the arcuate line showed a strong significant association with segmentation anomalies, resulting in a variable vertical of the S1 body relative to the sacral alae, which was also detected in our GM analysis. This offers novel diagnostic tools to reliably identify and distinguish sacralizations from lumbarizations that can also be applied to isolated sacra.

Our approach shows that the identification of most segmentation anomalies is possible by considering both the first and the last sacral elements. In fact, the coccyx was fused in 46 individuals (32%), frequently coupled with lumbarizations. This suggests that the genetic pathway leading to homeotic border shifts might affect several spinal regions. Thus, regardless of the ontogenetic origin of its vertebrae, the length of the sacrum seems highly conserved. Yet, the biomechanical and clinical implications of sacralizations and lumbarizations remain elusive. We therefore suggest that associations between LSTVs and lower back pain or obstetric complications be reanalysed with the consistent classification criteria proposed in this study. Further, the high prevalence of LSTV and the substantial morphological variability of the sacrum in humans and fossil hominins as well as in extant great apes might indicate that the lumbosacral spine is under continued evolution in these taxa.

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Poster Presentation Number 35, Session 2, Thursday 2:15-3:15 pm

The potential resource space for hominids in Olduvai Gorge, Middle Bed I

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The diet of hominids represents a selection of resources available and accessible in their environment. The selection process depends on individual and cultural skills of the hominins, tools and means used by them and options and limitations resulting from their behavior. In their environment, seasonal dynamics characterize the resource space. In this study, we examine the resource space and its seasonal dynamics. The resource space includes all edible resources and is divided into five groups: plants, insects, aquatic resources as well as small and large animals. The groups differ in habitat, behaviour and morphology, therefore requiring particular ways of acquisition and technology to exploit them efficiently.

Plants and insects can be generally gathered without technology, although the use of digging sticks or twigs increases efficiency. Aquatic and small animals can be caught by hand or, for instance, with a fish hook. Efficiency increases dramatically with the use of technology. To access large animals as a food resource, at least Oldowan tools are required to deflesh the carcass. To have primary access to large herbivores more sophisticated technology and cooperation between the group members are required. To exploit the different resource groups efficiently the technological level and behaviour of the hominids are decisive.

In order to address the functionality of this framework, we applied the model to the hominids in Middle Bed I at Olduvai Gorge, Tanzania. Two different species of hominids, *Paranthropus boisei* as well as of *Homo habilis* are described from these deposits. Both of the find sites are located on the eastern lake margin of paleo-lake Olduvai. The paleo-environment offers different habitats to access different food resources.

The resource lists for the five kinds of resources are based on fossil taxa and/or modern analogues. Plant taxa are derived from pollen [1] and phytolith studies [2], which are matched with present vegetation data from nearby Lake Manyara National Park. When the pollen assemblage contains e.g., *Cyperaceae*, all edible *Cyperaceae* taxa occurring in Lake Manyara NP, are considered as being part of the available resource space. Insect taxa are derived from the literature about edible insects in Tanzania [3]. Lists of aquatic animals as well as small and large vertebrates is based on the fossil record [4,5].

For each species, whether plants or animals, the following data were collected: 1. processing required, 2. seasonal dynamics, 3. nutritional content and 4. carbon isotope signal. Processing data indicate what actions are required to collect and consume the resource. This ranges from eating it raw without further processing to several sequential processing steps, which may require the application of multiple methods and technology. Although certain resources may be part of the available resource space, they can only be consumed by hominids who mastered a specific technological level.

Moreover, the presence of the five kinds of resources and/or their accessibility changes along with the seasons. Particular plant parts may be restricted to particular seasons, large mammals (may) migrate and/or insects and smaller vertebrates may be accessed easier during particular periods, e.g., when mating. This allows to address seasonal shifts in the hominid diet. Nutritional data indicates the percentage composition in which particular resource groups may be consumed in order to meet the physiological requirements of a hominid. In one of the following steps potential compositions can be compared with proxies collected from hominid fossils proper, for instance the carbon isotope signal.

In this way we analyse the available resource space of Middle Bed I and pave the way to answering crucial questions about the potential diet of *Paranthropus boisei* and *Homo habilis*.

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Cyclical trace element patterns in Pleistocene *Pongo* and *Homo erectus* on Java (Indonesia) indicate seasonal differences in dietary strategies

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The hominid fossil record from the Sangiran Dome in Java is one of the largest in Southeast Asia, with more than 200 dentognathic remains demonstrating an early expansion of *Homo erectus* onto the Sunda Shelf during the Early Pleistocene [1,2]. Recently, the large morphological variability in the Indonesian fossil assemblage was linked to an increased diversity in hominid taxa on the island of Java during the Pleistocene [2]. This diversity was possibly enhanced through the seasonal abundance of food resources coupled with ecological patterning of insular environments with limited space. In this study, fossil molar teeth of two penecontemporaneous Early Pleistocene hominids from the Sangiran Dome, namely *Homo erectus* (specimens S7-37, S7-13, F8865) and *Pongo* sp. (specimen F8864), were analyzed to reconstruct dietary strategies and ecological patterning through histologically-controlled Laser-Ablation Inductively-Coupled-Plasma Mass Spectrometry (LA-ICPMS) of dental enamel [3]. Besides the use of stable isotope ratios (e.g., $\delta^{13}\text{C}$ values) for dietary reconstructions, trace element ratios (Sr/Ca, Ba/Ca) in dental enamel are crucial for estimating trophic levels in fossil mammals [4]. Indeed, compared to dentine and bone, enamel is the most highly mineralized tissue in mammals and therefore least affected by post-mortem diagenetic alterations [5]. Sr/Ca ratios of (pre)molars of penecontemporaneous fossil mammals from the Sangiran Dome with known trophic positions, including Suidae, Felidae, Rhinocerotidae, Hippopotamidae and Cervidae, provide a trophic level framework for the hominid specimens. Trace elements such as U and Mn were utilized to evaluate the extent of post-mortem diagenetic overprint on the biogenic Sr/Ca and Ba/Ca signals [3]. *Pongo* sp. shows a herbivorous signal, whereas Sr/Ca ratios for *Homo erectus* overlap with omnivorous and carnivorous mammals. Both *Pongo* sp. and *Homo erectus* show cyclical patterns in time-resolved Sr/Ca profiles on an annual basis. The distribution pattern along the enamel dentine junction in the *Pongo* sp. molar enamel shows marked seasonal cycles with high and relatively narrow peaks of Sr/Ca and Ba/Ca ratios, reflecting the consumption of peculiar plant-based food resources probably during monsoon seasons, with low values suggesting scarce food availability during dry seasons. *Homo erectus* enamel reveals a comparatively low annual Sr/Ca intra-tooth variability, indicating that it may have been able to maintain its nutritional demands more independently from seasonal fluctuations, by exploiting the regional diversity of higher-quality food resources throughout the year.

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Evidence for habitual tool use in early hominins

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Systematic and intentional tool production and use is a central and unique component of the human niche. However, the timing and mode of its development remain poorly understood. The evidence provided by the archaeological record is equivocal, as the conclusiveness of the earliest traces of production and use of lithic products has been questioned [1]. This ambiguity is mirrored in the fossil record, as the hand anatomy of early hominins shows a mosaic of human- and ape-like features which may or may not have allowed for systematic tool-use.

To approach this topic from the standpoint of habitual activity, we use an innovative and validated approach to investigate the emergence of tool-related behaviors by analyzing muscle recruitment patterns in the human fossil record. We apply our novel Validated Entheses-based Reconstruction of Activity (V.E.R.A.) method [2] to the analysis of tool-related thumb muscle attachment proportions in early and recent modern humans, extant great apes, Neanderthals, *Homo naledi*, *Australopithecus* species and two fossil hominins from Swartkrans, South Africa. The analyzed muscles include the *opponens pollicis*, *abductor pollicis longus* and the first *dorsal interosseus*. Among these, the first *dorsal interosseus* (DI1) has been shown in electromyographic research to consistently activate during human-like stone tool use, irrespective of tool type, underlining the importance of this muscle for tool-related behaviors in general [3].

Results clearly differentiate between modern humans and extant apes, as known tool using species present a proportionally larger DI1 attachment site. Moreover, all hominin fossils, with the exception of an *Australopithecus africanus* specimen, exhibit thumb muscle use similar to that of later *Homo* and consistent with habitual tool-related behaviors. Recent studies have shown that both *Australopithecus afarensis* and *Australopithecus sediba* were characterized by low thumb opposition efficiency [4]. This combination of human-like muscle use and ape-like manual dexterity suggests that habitual tool use preceded the evolution of tool-related biomechanical adaptations of the hominin hand, potentially acting as a selective pressure on its development. Additionally, our findings underline the necessity to consider biomechanical efficiency and actual behavior as two separate concepts. In conclusion, our results indicate an early establishment of habitual tool use in human evolution, preceding an increase in manual dexterity and consistent with recent archaeological discoveries.

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Neanderthal symbolic behaviour - A 51,000 year-old engraved bone from Einhornhöhle, Germany

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For a long time, Neanderthals had been perceived as cognitively inferior to *Homo sapiens*. In recent years however, evidence has been accumulating to demonstrate sophisticated knowledge and complex social behaviour among pre-*Homo sapiens* humans including Neanderthals. This is exemplified by findings of composite tools [1] among others), by socially organised hunting campaigns inferred from wooden hunting weapons [2] and by habitual fire making [3]. Nowadays, Neanderthals are considered top predators well-capable to adapt to a range of different glacial and interglacial environments.

The capacity for symbolic behaviour in Neanderthals however remained scientifically contested. While bodily ornaments from Châtelperronian sites have been acknowledged, their association with Neanderthals and creation independently from *Homo sapiens* are debated. Recently, cave paintings and a hand stencil have been connected to Neanderthals based on Uranium-Thorium-dating [4], but are equally challenged by some researchers. In addition, a number of sites from across Eurasia have provided cut-marked raptor bones and claws or abstract line engravings on rock, bone, stone, and flint items (summary in [5]) that are viewed in a non-utilitarian context and are connected to Neanderthals.

Here, we present an engraved giant deer (*Megaloceros giganteus*) phalanx that was discovered during recent excavations at a former cave entrance of Einhornhöhle (Unicorn Cave) in the Harz Mountains, Germany [5]. The toe bone has been engraved with six incisions that form three stacked-offset chevrons as the primary line pattern. A secondary line pattern consists of four shorter lines engraved at the proximal part of the bone, perpendicular to the chevrons. The engraved item has been radiocarbon dated directly providing an age range of 47.5 to >55 ka cal BP (KIA-55192) that is in good agreement with further radiocarbon dates from the same layer. The bone was found in association with giant deer, red deer, bison, and cave bear bones whereof some show signs of human manipulation, i.e., cut marks. Typical Middle Palaeolithic finds (Levallois flakes/ cores) from inside the cave support an association with Neanderthals. Individual lines of the chevrons pattern are arranged systematically having surface angles of 90-100.5°. Our experiments with bovine phalanxes suggest the bone item was cooked for at about 2 hours before engraving. We were able to produce engravings with an appearance similar to the original item and it seems likely that the phalanx from Einhornhöhle, was engraved employing a cutting-scraping technique. In accordance with our experiments, a total carving time for the engraved item of 90 minutes can be assumed.

The incised giant deer bone is unique in the Eurasian Middle Palaeolithic context and substantially adds to the growing body of evidence for the cognitive capacity and symbolic behaviour among Neanderthals before *Homo sapiens* arrived in Europe.

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Nitrogen isotope analysis of 120,000-year-old tooth enamel from the Middle Palaeolithic Neanderthal site of Neumark-Nord 2, Germany

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Reconstructing (paleo)food webs and, in particular, the position of hominins within them, has been a long-standing focus of anthropological research. To date, however, no broadly accepted geochemical proxy exists for establishing trophic position in deep time. Although nitrogen isotope ratios ($\delta^{15}\text{N}$ values) are a commonly used tool for investigating trophic level in both modern and (paleo)archaeological contexts, the application of nitrogen isotopes to the anthropological record has largely been restricted to collagen from relatively young (<120 kya), well-preserved bone or dentine. This is because these tissues, which are porous and poorly mineralized (65% wt.), are susceptible to diagenetic alteration over time. Tooth enamel, in contrast, is highly mineralized (95% wt.), resistant to diagenetic alteration, and hence better preserved across long timescales. However, efforts to measure nitrogen isotopes in tooth enamel via traditional methods have not been feasible given the low nitrogen content of enamel (<0.01% wt.)

Here, we use a novel application of the oxidation-denitrification method [1] to measure the nitrogen isotope composition of tooth enamel ($\delta^{15}\text{N}_{\text{enamel}}$) of fossil fauna from Neumark Nord 2, a well-preserved 120,000-year-old Middle Paleolithic site in Germany. This site has yielded one of the largest and oldest $\delta^{15}\text{N}_{\text{collagen}}$ datasets yet measured [2], and thus represents a unique opportunity to compare collagen and enamel $\delta^{15}\text{N}$ values from the same taxa, a necessary step towards further validating the utility and applicability of this novel proxy. Moreover, tooth enamel is better preserved than bone collagen, allowing us to significantly expand the available nitrogen isotope dataset at this site to include more taxa and trophic levels.

In our study, we measured $\delta^{15}\text{N}_{\text{enamel}}$ values in the tooth enamel of representative herbivore (n=5), omnivore (n=1), and carnivore taxa (n=2) to reconstruct the paleoecology of the fauna at Neumark Nord 2. Our results show that herbivores have, on average, lower mean $\delta^{15}\text{N}_{\text{enamel}}$ values ($\bar{x}=5.3 \pm 0.9\text{‰}$) than omnivores ($\bar{x}=7.7 \pm 1.6\text{‰}$) and carnivores ($\bar{x}=6.6 \pm 1.8\text{‰}$). A previous study of herbivore $\delta^{15}\text{N}_{\text{collagen}}$ at Neumark Nord 2 by Britton et al., 2012 found evidence for differences in dietary behavior between bovids and equids. We found similar patterning in $\delta^{15}\text{N}_{\text{enamel}}$ values for the same taxa although the magnitude of the difference between taxa is somewhat smaller in enamel (1.2 vs. 2.0‰) compared to collagen.

This study significantly expands the existing geochemical dataset at Neumark Nord 2 allowing us to better reconstruct the paleo-food web at this important archaeological site. Further, these additional geochemical data provide us with the opportunity to evaluate anthropogenic influence on a past ecosystem prior to the arrival of anatomically modern humans in Europe.

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Childhood stress in Paleolithic hominins – Neanderthals vs. Modern Humans

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Neanderthals have long been portrayed as having led highly stressful lives when compared to modern humans. However, recent studies, particularly those focusing on skeletal trauma, are casting doubt on this traditional view [1,2]. Unfortunately, available examinations of dental enamel hypoplasia, a marker of health status and physiological stress in past populations, aimed at providing a resolution to the issue of stress in Paleolithic hominins, have resulted in conflicting conclusions [3,4]. The lack of consensus is mostly due to differences in methodologies used and limitations (in temporal and geographic range, as well as size) of samples employed. These contradictions highlight the need for a comprehensive re-evaluation of stress levels experienced by these hominins, to better understand if and how survival strategies differed between Neanderthals and Upper Paleolithic modern humans (UPMH). Here, we use an all-inclusive approach documenting all dental enamel hypoplastic defect forms in all tooth types in the largest sample of Neanderthals and UPMH examined in a single study to date. We report on childhood stress faced by these hominins and assess if and how stress levels and their patterns of ontogenetic distribution differed between taxa.

High-resolution replicas of 874 well-preserved Neanderthal and UPMH teeth (Paleoanthropological collections, University of Tübingen) from 59 western Eurasian sites dated to Marine Isotope Stages 2-8 were examined under oblique light conditions at 20x magnification. Hypoplastic incidences of all forms (pit, plane, linear) and the tooth types they occurred upon were recorded. Additionally, for linear defects, their vertical locations on dental crowns were recorded. When these locations were matched on at least two concurrently forming teeth of the same individual, linear defects were documented as systemic stress events whose timing of occurrence was assessed in terms of sequential stages of dental development [5]. Generalized linear mixed models were used to test for differences between Neanderthals and UPMH in the likelihoods of hypoplasia manifestations across and within tooth types and of stress events' occurrences across dental developmental stages.

Our results show no difference between the two hominin groups in the likelihood of teeth showing hypoplasia when all tooth types were considered in combination, indicating that Neanderthal and UPMH children experienced overall similar levels of physiological stress. However, mapping the distribution of enamel defects across tooth types, we found that, in UPMH, earlier forming permanent teeth, i.e., incisors, were more likely to present hypoplastic defects, whereas in Neanderthals, this likelihood is highest in tooth types with later crown development, particularly premolars and second molars. The distribution of matched linear defects also echoed these results. In UPMH stress events are most likely to occur early during permanent dental development, i.e., at an early stage of anterior teeth crowns' formation. In Neanderthals, on the other hand, we recorded a greater fluctuation in the likelihood of stress events occurring throughout ontogeny with two notable increases: one during the formation of both permanent premolar and second molar crowns, and another during the formation of third molars crowns. Overall, our results reveal species-specific patterns of ontogenetic stress distribution that may reflect differences in childcare behaviors between the two hominin groups. In UPMH high stress levels in children are only recorded around the time weaning is expected. After this stressful period, strategies like cooperative breeding and an extended post-weaning dependency could have allowed UPMH to reduce stress for their children. In Neanderthals, however, the recurrence of stressful episodes past weaning time suggests a different behavior, perhaps one with earlier independence and faster transition to adulthood.

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Combining cementochronology and tooth wear analyses to estimate the season of death of large sized game: the case of De Nadale Cave and San Bernardino Cave (north-east of Italy)

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Seasonal organization of activities and duration of site occupation are current concerns in archaeology. For instance, they document the choices made by the human groups during the Middle Palaeolithic concerning the exploitation and the management of the biotic resources, their settlement strategies and their mobility patterns.

In the zooarchaeological field, some valuable methods can be applied to teeth, such as the analysis of carbon and oxygen stable isotopes, the study of tooth eruption and replacement patterns, the analyses of dental micro- and mesowear and the use of the cementochronology technique. However, using one of these methods alone, may not always be reliable, since, when used independently, a certain technique may provide very low-resolution data and limited information.

To overcome the possible lack of data given by the application of a single methodology, we combined cementochronology and tooth wear analyses applying them to materials yielded by two sites in the north-east of Italy: De Nadale Cave and San Bernardino Cave. The two methods provide information about the season at death of the prey, by observing the last band of cementum deposited in the animal's teeth, and about the extent of the human occupation, through the quantification of scratches and pits on the occlusal surface. The study involved molars from large-sized game, mainly cervids and bovids, which formed the base of the subsistence of human groups at the sites.

The results underline more than one period of occupation: both at De Nadale and at San Bernardino Caves, the main mortality event for large game occurred during winter and one or more minor hunting activities were recognized during the good season.

Moreover, this contribution brings new insight into the occupational pattern in the North-east of Italy, an area rich in palaeolithic evidence, both as open-air sites and as caves and shelters used by Neanderthal foragers as part of a settlement system extended to the Euganean Hills, the Alpine foreland and the southern slope of the Alps.

Estimation of the diaphragmatic domes in KNM-WT 15000 *Homo ergaster* and Kebara 2 *Homo neanderthalensis* using a *Homo sapiens* model

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Despite its great evolutionary interest, a comparative analysis of thoracic breathing biomechanics in hominins is challenging because of the incomplete fossil record and unknown soft tissue morphology. However, some specimens, whose ribcages are well preserved, such as KNM-WT 15000 [1] and Kebara 2 [2], may allow for a first step towards determining diaphragmatic morphology in fossil *Homo* and its potential implications in the evolution of the breathing function. In this context, we estimated the 3D shape, surface and relative position of the diaphragmatic domes in KNM-WT 15000 and Kebara 2 using *H. sapiens* as a reference model in order to address the hypothesis of a powerful diaphragm in ancient hominins compared to current humans [1-4].

The comparative sample consisted of the reconstructed ribcages of KNM-WT 15000 and Kebara 2 as well as the thoraces of 18 healthy adult *H. sapiens* males CT scanned at Hospital Universitario La Paz (Madrid, Spain) in maximal forced expiration (at residual volume, RV) and inspiration (at total lung capacity, TLC). We first digitized 3D (semi)landmarks on the ribcages (N=450) and human lung diaphragmatic surfaces (N=161). Then we performed a Generalized Procrustes Analysis (GPA), selected the expiratory human ribcages with the smallest Procrustes distance to each fossil ribcage and used them within their corresponding diaphragmatic domes to estimate the (semi)landmarks corresponding to the diaphragmatic domes of KNM-WT 15000 and Kebara 2. Next, we studied the general variability in shape of the human and fossil diaphragmatic domes by a Principal Components Analysis (PCA). We also explored human ventilatory capacity, quantified as the 3D size of the space that is displaced by the diaphragmatic domes during a respiratory cycle, and studied its relationship with the morphology of the human diaphragmatic domes to approach functional interpretations in KNM-WT 15000 and Kebara 2.

We found clear differences in diaphragmatic shape between RV and TLC and between modern humans and fossil *Homo*. The estimated diaphragmatic domes of KNM-WT 15000 and Kebara 2 show a major relative antero-posterior extension compared to expiratory and inspiratory human diaphragmatic domes in response to the pyramidal shape of their thoraces [1-3]. The surface area in Kebara 2 was significantly larger than in modern humans in response to the greater size of its lower thorax [2,3]. The juvenile *H. ergaster* specimen also showed a large surface area but it was within the upper range of adult modern males. These data support the hypothesis of a more powerful diaphragm in *H. neanderthalensis* [2-4] and possibly *H. ergaster* [1] than in modern humans. Our results further showed a subtle but significant relationship between the morphology of the diaphragmatic domes at TLC and its ventilatory capacity, which was higher in those diaphragms that, in maximum inspiration, were antero-laterally expanded and flatter. This seems coherent as it suggests that a flatter diaphragm experienced a stronger contraction at TLC than a more curved one. The antero-posterior component could be linked to an important contribution of the ribcage shape to ventilatory capacity. This study might show further that differences in lung volume are also related to differences in the morphology and size of the diaphragmatic domes. Preliminary kinematic simulations in the upper thorax of *H. ergaster* indicated a greater medio-lateral ventilatory movement than in modern humans, where ventilation was more cranio-caudally oriented [1]. A greater medio-lateral kinematic component is compatible with greater flattening of the diaphragm during inspiration. However, more complete kinematic simulations are necessary in both rib cage reconstructions to address this hypothesis.

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First enamel nitrogen isotope data of early hominins: Early Pleistocene *Australopithecus* (Sterkfontein Member 4, South Africa) did not consume significant amounts of animal resources

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Dietary change, specifically the incorporation of animal resources, is considered a key event in human evolution. However, direct evidence for the trophic behavior of our hominin ancestors remains elusive. The earliest signs of meat consumption include crude stone tools and possible cut marks on fossil bones which are older than 3 Ma. However, their origin and the assumption that *Australopithecus* shaped and used tools prior to the emergence of *Homo* are heavily debated.

Yet, meat eating has major implications for the evolution of the hominin lineage, as it is a calorie-dense, high-quality food whose consumption has been linked to brain expansion and other significant adaptations in the genus *Homo*. Moreover, the shift from a mainly vegetarian diet represents an encroachment of hominins into the large carnivore guild, presenting our ancestors with entirely new competitive pressures. A better understanding of animal resource consumption by early hominins, for example in the genus *Australopithecus*, is crucial to reconstruct the timing of changes in hominin dietary behavior and to evaluate their position in (paleo)food-webs.

Nitrogen isotope ($\delta^{15}\text{N}$) data are frequently used in conjunction with carbon isotopes ($\delta^{13}\text{C}$) to reconstruct diet because $\delta^{15}\text{N}$ values reveal information about an individual's position in the food web. $\delta^{15}\text{N}$ measured in collagen from fossil bone and dentin provide key insights into the dietary behavior of species in modern ecosystems and the recent geological past (<120 kyr). However, due to diagenetic alteration, such analyses have been limited to fossil sites with exceptional preservation. Unlike bone or dentin, organic matter in tooth enamel is protected from alteration by its highly mineralized structure, potentially preserving isotopic signals over millions of years, but low organic matter content in enamel has so far prevented nitrogen isotope analysis.

Recently, my colleagues and I developed a novel oxidation-denitrification method for analyzing the isotopic composition of mineral-bound nitrogen in ca. 5 mg enamel, which requires over 100-fold less nitrogen compared to traditional approaches. We established that enamel $\delta^{15}\text{N}$ records the isotopic composition of diet and preserves a trophic signal in a feeding experiment [1], as well as in natural ecosystems.

Here, we utilize this novel biogeochemical method to present $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ data for Sterkfontein Member 4 (ca. 2.6 to 2.2 Ma) mammalian fauna, including seven australopithecines. Results represent the first $\delta^{15}\text{N}$ data measured in any early hominin. Our data indicates a large variation in $\delta^{15}\text{N}$ values between *Australopithecus* individuals, larger than in the other primate taxa analyzed from Sterkfontein Member 4. The values however do not overlap with carnivore $\delta^{15}\text{N}$ data, pointing to a plant-based diet of these early Pleistocene hominins. Our dataset provides a first step towards better understanding the trophic behavior of early hominins.

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Tug of war

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Introduction: One Tuesday in early November of 2004, a man packed a skull into a suitcase, descended a staircase, and exited a research center in Jakarta, Indonesia. The specimen, LB1, had just been announced as a purported new hominin species, *Homo floresiensis*. [1] While the discovery team argued *H. floresiensis* was a surprising find with a unique combination of primitive and derived traits, other scientists disagreed. After transporting the specimen from the discovery team's laboratory to his own across Java, the man with the suitcase, paleoanthropologist Teuku Jacob, joined the dissenting voices, declaring that LB1 was nothing more than a diminutive modern human [2].

Jacob's actions provoked an international controversy that the press quickly termed a "tug of war," a debate encapsulating both the physical bones and the intellectual content of the interpretation. In the subsequent months, the controversy escalated as accusations amongst researchers circulated in the press, research at the field site stalled, and the bones were eventually returned to Jakarta damaged—some beyond repair. This talk asks: why did this tug of war occur?

Methods: This paper uses historical methods to establish the controversy's context, analyzing primary, archival materials including unpublished field notes and oral history interviews collected from key participants. I incorporate sources recorded in both English and Indonesian in order to broaden the range of voices represented. I structure my analysis by focusing on the history of excavations at the *H. floresiensis* field site, Liang Bua, from 1950. Tracing excavations at Liang Bua reveals a transition from a colonial endeavor to a more collaborative, international project. I therefore approach the history by interrogating the relationship between the colonial history and the science of paleoanthropology in the archipelago, following a growing recognition that the science would benefit from an increased awareness of the historical conditions of scientific practice [3].

Results: Examining the history of science at Liang Bua reveals that the "tug of war" was rooted in Indonesia's postcolonial transition, which instilled a particular set of intertwined values, excavation practices, and theories with national identity in ways that collided with the discovery of LB1. The archipelago's scientific history, I found, directly shaped the handling of LB1 by influencing the people present for the discovery, their relationship to the research, and their ideas about the prehistory of the region.

By inspecting the intersection of science and society in postcolonial Indonesia, then, we arrive at a more nuanced, inclusive understanding of the historically rooted, practical and theoretical considerations of researchers involved in the explosive controversy.

Conclusion: This new perspective on the conflict that occurred around *H. floresiensis* raises important questions about cross-cultural scientific collaborations in an uneven, global playing field. Disputes around autonomy and authority are not isolated events, but instead indicative of larger problems in a field initially built on colonial pathways and examining case studies like this one can begin to offer solutions moving forward [4]. For decades, researchers of human evolution have asked why study disciplinary history? [5] This paper argues that reflecting on the history of the discipline, far from being merely an act of storytelling, is a necessary step toward facilitating productive collaborations, increasing diversity, and reconfiguring structural imbalances in the field.

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Dental occlusal form and function in *Equus capensis*: Evaluating a controvertible taxonomic status

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The Giant Cape zebra *Equus capensis* is one of the most iconic fossil herbivore species of the South African Quaternary. It is widely believed to have persisted relatively unchanged in its morphology for the duration of its existence, that encompassed the mid-to late Pleistocene. Described as a large-bodied equid, its skeletal remains were originally regarded as distinct and readily distinguishable from those of other fossil equids, especially with respect to their large size [1]. This applied particularly to its cheek teeth, that were consistently described as large with unique occlusal enamel morphology. Palaeontologists have generally accepted the taxonomic status of *E. capensis* without question. However, in reality, its taxonomic status is far from incontrovertible as many of its definitive morphological traits are based on conjecture.

Equus capensis was originally described on the basis of a large mandible embedded in limestone that had much of its dental row obscured [2]. The rest of it was reconstructed using unassociated, usually isolated osteological elements from a variety of localities. Perhaps not surprisingly, apart from size, researchers have struggled over the years to distinguish between *E. capensis* skeletal elements and those of other fossil equids. An ancient DNA study of four *E. capensis* teeth further compounded the uncertainty around its taxonomic status by exposing a high degree of genetic similarity to *E. quagga* [3].

The present study represents the first systematic investigation of morphological traits originally used to define *E. capensis*. Specifically, it considers dental occlusal enamel form and function to help shed light on the taxonomic status of *E. capensis*. Geometric morphometrics was used to compare premolar and molar occlusal enamel pattern in *E. capensis* and a large comparative equid sample. This was followed by an evaluation of levels of enamel complexity. Next, traditional linear methods were used to compare overall occlusal dental form. Finally, mesowear analysis was used to evaluate dental function. Analyses of dental occlusal enamel form were able to distinguish *E. capensis* teeth from those of equids in the comparative sample on the basis of size, but not shape. This result is telling since the shape of dental occlusal enamel bands carries greater taxonomic significance than their size. Size is easily influenced by environmental factors and may fluctuate through time. Lastly, analyses of mesowear patterns were unable to separate *E. capensis* teeth from those of *E. quagga*, with which it is thought to have co-occurred [4]. Overall, the results of this study do not support the legitimacy of *E. capensis* as a taxon and lays the ground for additional enquiries.

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The Uluzzian techno-complex at Grotta di Castelcivita (southern Italy): production and use of stone tools

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Grotta di Castelcivita is a cave site located in southern Italy, which is characterised by a significant stratigraphy made up of several anthropogenic layers, including the Final Mousterian, the Uluzzian and the Protoaurignacian techno-complexes. Thanks to the wealth of its deposits and the presence of four Uluzzian layers, Castelcivita is crucial in helping us to understand the Middle to Upper Palaeolithic transition in southern Europe.

In this study, we present the production of stone tools in the Uluzzian occupation. This is characterised by the use of local raw material, mainly chert, available in the form of blocks. The concept of debitage mostly deals with unidirectional (employing parallel planes and semi-tourning cores) and orthogonal debitage. The cores are characterised by either no opening or just a simple opening of the striking platform (usually obtained by one stroke) and an absent or fairly accurate management of the convexities and angles of debitage. The production is aimed at obtaining small items, both flakes and blades. A prominent use of bipolar technique on anvil is attested as well. Moreover, both direct freehand percussion and bipolar technique are used in the same reduction sequence. Among the retouched tools, there is the occurrence of side-scrapers, denticulates, end-scrapers, backed pieces and lunates [1].

The straightforward manufacturing mode adopted at Castelcivita creates debitage products with unstandardised technical features and morphologies. This lack of standardisation means that it is not helpful to study the assemblage by using the typological approach or by applying strictly defined technological categories [2]. The low degree of standardization of the Uluzzian requires, instead, an inclusive analytic approach, involving the integration of techno-functional and use-wear analyses [1,3]. This approach, in fact, is not limited by the use of a priori defined categories but is conceived in order to globally understand the structure and functionality of the tools.

The sampled tools are a selection of unretouched blanks of several dimensional classes and varied technological categories (cortical, un-cortical flakes/blades and fragmented flakes) and retouched tools (side scrapers, lunates, end scrapers, backed tools, and denticulates). Specifically, our work aimed first to identify every single techno-functional unity (prehensile and transformative portions) through the techno-functional analysis [3,4] and secondly to reveal how these tools had been used employing use-wear analysis [5], that means identifying the activity involved (piercing, cutting, and scraping) and the type of material (vegetable or animal, soft or hard) on which this activity had been carried out.

Integrating these two approaches [1,3] allowed us to understand that this assemblage is not only characterised by the dominant use of the bipolar technique, which produces informal blanks. It also allowed us to ascertain that there are specific categories of retouched tools (i.e., lunates and end-scrapers), which possess specific manufacturing of both the blank and transformative portion which correspond to a specific use. Whereas the other retouched tools (e.g., side-scrapers, denticulates) and unretouched pieces do not present careful management of the morpho-volumetry of the tools. Transformative portions with similar functions can be found on different supports. The selection and use of the tool are linked to the most performative characteristics of the transformative portion.

Finally, the obtained results allowed us to observe that in the Uluzzian of Castelcivita the low degree of standardisation of product morphologies plays a key role, as it allows one to get out of schematism and select only the best-performing products for every specific objective. The strength of this kind of conceptualisation is its versatility and flexibility, without loss of efficiency of the final products.

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SUBSILIENCE Database System: an integrated bioarchaeological database

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Zooarchaeological studies need to be based on the record of faunal data by a standardised methodology to avoid intra and inter-variation among archaeological sites, regions, periods and even human error. However, software databases used by zooarchaeologists are still not normalised, leading to problematic comparisons. Moreover, databases are not adapted to integrate multiple inputs from geochemical data, such as C14, stable isotopes or proteomics. For tackling all these issues, the ERC-SUBSILIENCE project has developed a Database System for recording (1) zooarchaeological and taphonomic data on macrofaunal assemblages directly associated with (2) radiocarbon dating, (3) isotopes and proteomic analysis, applied on more than 20 Middle to Upper Palaeolithic European sites, whose study is ongoing by different scholars located in diverse regions. This database system is a multidisciplinary work designed by zooarchaeologists, biochemists, data modellers and ITs. The Database System allows (i) Working online by different people at the same time, wherever they are; (ii) Standardising the data recording to reduce inter-personal variability and to allow inter-site comparison; (iii) Fast data entry and analysis reducing recording errors with a broad graphic methodological support; (iv) Centralised database from different analytical approaches related to the same assemblage; (v) Easily analysing the zooarchaeological and isotopic data providing analytical tables, graphs and statistical tests; (vi) Facilitating training of Master, PhD and postdoc researchers thanks to a comprehensive graphic and methodological support.

The SUBSILIENCE Database System, designed to be open access, will be available through an online interactive public tool (www.subsilience.es). It was created in HTML5, Javascript and PHP, with Javascript libraries such as HighCharts for graphic representation. It is divided into two main categories: “BONES and ISOTOPES”, related to each other and directly orientated to the main project objectives: economy, climate, environment and ecological reconstructions at the Middle to Upper Palaeolithic transition along the southern European regions (Balkans, Italy, SW France and N Iberia) to test how both human species were able to adapt to different ecological niches and evaluate their resilience. Each category has one recording part to include general information, identification, and taphonomy data and one analytic part for direct statistical analysis (e.g NISP, MNE, MNI, MAU, Food Utility Index, Bayesian analysis of Skeletal profiles, etc). Apart from this, C14 data (lab code, pre-treatment, %C and %N, %yield, bone sample left) as well as stable isotopes (sample type such as collagen, enamel, dentine, Iso code, Lab information, values of each sample analysed such as $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, $\delta^{34}\text{S}$, δD , $\delta^{18}\text{O}$, $\delta^{87}\text{Sr}$) are precisely recorded. During data entry, there is an automatic verification achieved at each step to avoid personal mistakes while recording. By direct use of the proposed standardised variables and analytical methods, the compiled results from the more than 20 archaeological sites within the SUBSILIENCE project will be compared spatiotemporally and allow for observing evolutionary trends of human diet vs the particular climatic and environmental conditions at the time humans occupied those sites. Likewise, the data and results will be open access at the end of the project.

Beyond a proposal to standardise the zooarchaeological analyses, we present a multidisciplinary approach to study bioarchaeological assemblages that could be used for research groups working in any archaeological site, region and chronological period.

The role of non-formal education in teaching human evolution: An online advanced course for high school students

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The Institute of Education and Citizenship (IEC) is a non-profit organization which acts as an interface between knowledge centers, such as universities and scientific research institutes, and the population, with an emphasis on the school community. IEC facilitates knowledge transfer from universities and scientific research institutes to schools. IEC is located in a rural area, Mamarrosa (Oliveira do Bairro, Aveiro, Portugal), where the dissemination of scientific knowledge has increased due to the initiatives of IEC. In 2014, Oliveira do Bairro was recognized as European City of Scientific Culture.

IEC developed a non-formal educational program for primary, middle and high school students and teachers, designated Advanced Studies Program. The program of Advanced Studies refers to a set of activities, which includes the intensive teaching of advanced concepts in defined areas of knowledge. The IEC's Advanced Studies Program includes: 1) advanced courses, dialogue with scientists and science in action courses; 2) conferences; 3) scientific internships; and 4) school trips.

This program is unique because its activities are continuous and permanent. Each advanced course for high school students and teachers has a duration of ten weeks, three hours once a week. These advanced courses are taught by university professors and successful researchers with PhDs, from universities and scientific research institutes. Usually, these advanced courses take place at IEC and high school laboratories. However, during the current pandemic context, these advanced courses are taught online.

In order to evaluate these courses, at the beginning and the end of each course, the students answer a multiple-choice test, composed of ten questions, each one related to one of the ten sessions of the course. Moreover, at the end of each course, the students answer a satisfaction survey.

Human Evolution is an uncommon approached topic in the formal Portuguese curricula, even for high school students. And most of the subjects covered are outdated. Between January and March 2021, IEC organized an online non-formal advanced course in human evolution. This course was attended by 35 high school students, from the Escola Secundária Marques de Castilho, a school located at Águeda (Aveiro, Portugal), and was taught by five university professors and researchers of the University of Coimbra and IEC. Throughout the sessions, students attended lectures on subjects of human evolution, such as Evolutionary Biology, Primatology, Biological Anthropology, Paleoanthropology, Primate Archaeology and Prehistoric Archaeology.

The students answered correctly 48,93% of the questions at the beginning of the course, which increased to 67,14% at the end of the course. Besides that, 85,29% of the students totally agree (7/7 in a Likert scale) that professors dominated the subjects, and 64,71% of the students totally agree (7/7 in a Likert scale) that professors transmitted the subjects in a very good way. One of the students considered that he “enjoyed the course and that it helped him in developing his intellectual ability on subjects that are superficially included in lessons”. Another student considered that “in some moments, I felt I was in a university (...) there was a rich and diverse approach to the subjects (...) professors were excellent and outstanding”.

These results show that this advanced course had an impact on the high school students' knowledge concerning human evolution. We conclude that online non-formal advanced courses are an efficient strategy to teach human evolution to high school students. More investment has to be made in human evolution's formal and non-formal educational programs, in order to engage students in this topic.

Buccal dental microtexture analysis of extant primates and Pliocene *Australopithecus* from East Africa

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Reconstructing diets of extinct hominins is important to interpret the evolutionary history of our lineage. During the middle Pliocene and early Pleistocene, the diversity of local climate conditions changed gradually the East African landscape towards more open ecosystems. The early hominins *Australopithecus anamensis* and *Australopithecus afarensis* (4.15-3.04 Ma) have traditionally been proposed to show an adaptative shift from diets dominated by soft C3 fruits to more abrasive and brittle resources in relation with this climatic change [1,2].

In the present study we tested for the first time the microtexture analysis of the buccal surfaces of primates and hominins by using ISO (25178) parameters. 3D dental microtexture analysis has been demonstrated as a valuable tool for inferring the highly diversified diets of extant primates and establishing a baseline for the reconstruction of the diets of hominins. Here, we analyzed nine extant African primate species with diverse dietary regimes (*Gorilla gorilla*, *Pan troglodytes verus*, *Pan troglodytes schweinfurthii*, *Cercocebus atys*, *Chlorocebus* sp., *Papio anubis*, *Mandrillus* sp., *Colobus* sp., *Theropithecus gelada*). We performed a stepwise Discriminant Analysis to test the potential of 37 roughness parameters to predict interspecific dietary regimes. Four ISO parameters from the model (Sal, Sha, Sdv, Smr2) registered the highest discriminatory power. Results indicate that buccal microtextures can distinguish among diets characterized by different mechanical properties and are similar to previous 2D semi-automatic buccal microwear results [3,4]. Overall, *Mandrillus* tends to have an autocorrelation length (Sal) and closed dale volume (Sdv) values similar to folivorous *Colobus* and higher than the rest. Moreover, soft and hard-item frugivorous Primates (*Pan t. schweinfurthii* and *Cercocebus atys*) showed similar microtexture patterns, along with *Theropithecus gelada*, characterized by lower closed hill areas (Sha) than *Colobus*, *Chlorocebus* and *Mandrillus*. On the other hand, western lowland *Gorilla gorilla gorilla* had surfaces with the deepest valley structures (Smr2). Microtexture parameters were used to analyze the buccal surfaces of Pliocene *Australopithecus anamensis* (n=5) and *Australopithecus afarensis* (n=30) molars from East Africa. Hominin results suggest that *A. anamensis* buccal microtexture surfaces resemble those of open savanna cercopithecoids that typically include a wide variety of seasonal available plants, with the occasional consumption of hard and brittle foods. Otherwise, *Australopithecus afarensis* showed buccal microtexture surfaces resembling those of *Pan t. verus*, a species that exploit a mosaic habitat year-round. The savanna chimpanzee consumes plant species, especially fruits, from riverine forests and open ecosystems during the wet season and woodland species during the dry season [5]. Our findings support the use of buccal microtexture analysis as an important tool to analyze the variability of Primate diets.

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Initial Upper Paleolithic bone technology and ornaments at Bacho Kiro Cave (Bulgaria)

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The expansion of *Homo sapiens* and our interaction with local environments including the global replacement or absorption of local populations is a key component in understanding the behavioral evolution of our species [1]. Of special interest is the phase in the archaeological record known as the Initial Upper Paleolithic (IUP). The IUP is characterized by Levallois-like blade technologies that can co-occur with bone tools and ornaments and appear in a number of regions throughout Eurasia around 45 ka [2]. Artifacts made from hard animal materials are important components of this record and, as such, they have immense potential to contribute to our understanding of group interactions and population movements during this phase in human evolution. Bacho Kiro Cave in Bulgaria represents one of the best-preserved cases of the IUP and it includes a diverse and sizable assemblage of bone tools and ornaments. The site is a recognized point in the distribution of IUP in Europe and is directly associated with *Homo sapiens* remains dated to approximately 45 ka as well as with a large assemblage of lithics and fauna [3]. Here, we present the osseous artifacts recovered thus far from the recent excavations that began in 2016 (n=73). We assess raw material selection of the artifacts through traditional zooarchaeological methods, and in some cases using Zooarchaeology by Mass Spectrometry. We compare general artifact morphologies with known osseous tool typologies and evaluate traces of their manufacture and use using a Nikon SMZ 1000 stereomicroscope with a magnification range of 8x to 80x. This diverse assemblage includes artifact types such as awls, pendants, and beads similar to those found in previous excavations of this site [4,5] as well as artifact types not previously described. Raw material sources for the osseous artifacts are consistent with taxa found within the faunal assemblage including cervids, large bovids, and cave bear. Pendants are made primarily from carnivore teeth (n=16), especially cave bear, however a subset of pendants consists of herbivore incisors (n=9) that were processed differently than the carnivore teeth. Three beads made on ivory, bone, and sandstone were also preserved. A wide variety of bone tool morphologies (n=31) were either manufactured using formal techniques such as scraping, grinding, and grooving, or they were modified through direct and indirect percussion. Several bone objects preserve intentional subparallel incisions and/or notches (n=13), some functional and others likely decorative. When considering the Bacho Kiro Cave osseous artifact assemblage within broader IUP contexts, we see similarities across assemblages in the presence of formal artifacts, such as awls and ornaments made of varying materials, and in the traces of their production. The methods used to analyze this assemblage, applied to the material from other regions, will add immensely to our understanding of patterns of behavior and technological diversity during the IUP.

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Denisova 3 distal phalanx microanatomy: new consideration

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Recently the information on a lost distal part of Denisova 3 phalanx appeared [1]. In 2010, it was temporarily sent from Berkeley to the Institut Jacques Monod in Paris, where it was photographed, measured and genetically studied. The data from the image of the entire phalanx allowed authors to consider its morphology and to correct preliminary estimations of biological age, concluding that the epiphysis had just fused at the time of death. This means that the individual Denisova 3 (“Denisovan girl”) was an adolescent. This important contribution prompts us to reconsider the information we received earlier in 2013 in the process of scanning the remains of this phalanx by the method of X-ray microscopy, taking into account the comparative data on other adult fossils we later studied [2,3].

After sampling for DNA analysis at the Max Planck Institute for Evolutionary Anthropology we had the opportunity to scan two remaining fragments, which seem to belong to the little finger [4]. More informative could be gleaned from the comparative study of the smaller preserved part, which represents the dorsal wall of diaphysis of the phalanx. The comparison shows that the phalanx of Denisovan girl had more similarity in microstructural features with the Neanderthal women Chagyrskaya 08 and 56 than with the earlier Neanderthal Denisova 9. These samples are brought together by the small thickness of the dorsal wall, smaller sizes of osteons and Haversian canals, and, finally, traces of extensive remodelling in the perimedullary area. In contrast, the specimen Strashnaya 4 of the anatomically modern female from the same region has remarkably thicker and denser dorsal wall, and no features of bone resorption and remodelling. But the tubular bones of Strashnaya 4 and Denisovan 3 joined together by higher mineralization as was pointed for Neanderthals. It was convincingly proven that the representatives of Chagyrskaya lineage of Neanderthals had genetic contacts with Denisovans [5]. So, although external morphology convincingly shows similarity of Denisova 3 and anatomically modern humans, microstructural features can be considered as phenotypic characters that reveal the genetic relationship between populations of Denisovans and Neanderthals.

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Clavicle curvature and shoulder height in hominoids

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Shoulder height is an anthropometric measurement that quantifies the distance between the suprasternal notch and the acromioclavicular joint. Large shoulder height measurements indicate an ‘elevated shoulder’, which is a conspicuous aspect of skeletal structure that distinguishes the Hominoidea from lower primates [1]. It gives non-human apes a ‘shrugged shoulder’ appearance, and is associated with reduced mobility between the head and shoulder girdle. Humans are the only hominoids that possess a descended shoulder and a well-defined neck. Spatial and anatomical separation between the head and shoulder girdle in humans is thought to enhance the ability of these structures to rotate independently.

Thus, hominoid paleontologists are interested in detecting an elevated shoulder in Miocene species because it has implications for identifying arm-hanging and/or vertical climbing adaptations characteristic of the crown hominoid body plan [2]. Hominin paleontologists are interested in reconstructing shoulder height in Plio-Pleistocene species to pinpoint the appearance of the uniquely derived and descended shoulder, which is associated with a decreased ability to navigate arboreal habitats, and adaptation to distance running, high-speed throwing, and other behaviors [3].

Clavicle curvature is the primary line of evidence used to reconstruct shoulder height. Most recently, Carlson et al. used observations on clavicle curvature to suggest that the ‘Little Foot’ skeleton (StW 573) possessed an elevated shoulder, consistent with their locomotor interpretation emphasizing arboreal adaptation [4]. However, the presumed association between clavicle curvature and shoulder height rests on a number of weakly supported assumptions. We previously described covariation patterns between clavicle morphology and shoulder structure within humans [5]. Here, we present new data on among-hominoid variation, using morphometric data derived from radiographic images of living apes and articulated ape cadavers to test existing ideas about how isolated clavicle morphology relates to shoulder height (reviewed in [5]).

These among-hominoid comparisons are useful in disentangling independent aspects of skeletal morphology that contribute to shoulder height, including the superoinferior position of the scapula on the thorax, rib declination, and scapula shape. Our results suggest that clavicle curvature is not a reliable predictor of shoulder height. They further highlight why isolated rib and scapula morphology are likely more informative for reconstructing shoulder structure in fossil apes and hominins.

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How to identify drift vs. selection in the evolution of human morphology? The case of the human pelvis

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Identifying evolutionary drift or selection as causes of modern population differences is a classic thrust in evolutionary biology, and numerous statistical methods have been developed to this end. These methods typically test empirical phenotypic data against an idealized model of drift. Further common arguments to support adaptive claims are based on functional explanations or experiments. Only if the genetic basis of a trait is sufficiently well understood are genomic approaches to detect selection possible.

Recently, claims about neutral evolution of human traits, such as pelvic dimensions [1,2] and the shape of the enamel-dentine junction [3], were inferred from correlations between phenotypic and geographic distances and from a decline of phenotypic variance with the geographic distance from Africa (serial founder effect). Based on these approaches, several studies concluded that human pelvic form primarily evolved by neutral evolution, without considerable natural selection. This is a surprising claim given how tightly linked pelvic form is to its various, highly fitness-relevant functions, including childbirth, locomotion, thermoregulation, and pelvic floor support.

We critically reevaluate this approach and derive a set of hypotheses about phenotypic traits under drift in a geographically heterogeneous environment. We demonstrate that a correlation between phenotypic distances and geographic or genetic distances does not necessarily indicate drift because most selective factors are also geographically structured. The isolation-by-distance pattern typical of neutral genetic markers does not directly extend to phenotypic traits. Likewise, reduction of phenotypic variance with the distance from Africa is not specific to a scenario of evolutionary drift [4].

We reanalyze the data on pelvic canal dimensions collected by Betti and Manica [2] by a series of statistical approaches from quantitative genetics. The data comprise linear distance measurements and body mass estimates of 348 female skeletons from 24 populations. Genomic data from the Human Origins Database were used to compute pairwise population F_{ST} values for these populations. Our results suggest that the between-population differences in pelvic canal dimensions clearly exceed the expectations for drift derived from the within-population distributions and from neutral genetic markers (F_{ST}). Moreover, pelvic dimensions significantly correlate with minimum and maximum average temperature and with body mass. This statistical evidence of selection is in agreement with the rich gynecological and orthopedic literature that reports how small differences in pelvic form have major effects on childbirth, locomotion, and the health of the pelvic joints and the spine [4].

Clearly, the fields of evolutionary biology and anthropology share an adaptationist tradition. Too often, phenotypic differences have been interpreted as specific evolutionary adaptations without a mechanistic model or empirical evidence of fitness consequences. However, there are cases where traits are obviously the products of natural selection because variation in these traits is intimately connected with variation in fitness (reproductive success). We suggest that multiple aspects of human pelvic morphology are such traits.

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Ankle bone morphology sheds light on the locomotor repertoire diversity in early primates

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The transition from archaic primates to the first Euprimates or primates of modern aspect (adapiforms and omomyiforms) is marked by a substantial reorganization of the body plan [1]. Several ecological scenarios have been proposed to explain the adaptative morphological innovations of crown primates in association to their origin and early evolution in the arboreal environment. Hence, understanding the locomotor behaviour of early primates is of vital importance to shed light on their origins. However, all the scenarios remain disputed and either agree to an ancestral locomotor repertoire that was either cheirogaleid-like (similar to that of mouse and dwarf lemurs), vertical clinger and leaper (as observed in tarsiers and bushbabies), or lorid-like (visual predators similar to extant lorises) [2-4]. Although the morphology of the tarsus has been examined for the calcaneus and astragalus bones, the navicular remains poorly studied even if it is also an important component of the midfoot mobility. To date, an integrative study on the functional significance of this bone in a large sample of living and extinct Euprimates at the light of quantified locomotor data is currently missing. In this study, we quantitatively assessed, by means of 3D geometric morphometric analyses, the relationship between the morphology of the navicular bone and locomotion in a sample of 108 extant and fossil primate specimens. Our results prove that navicular shape is strongly influenced by size, foot type and locomotor behaviour, and hence can be used as a good proxy to predict the locomotor repertoire of extinct primates. Moreover, we reconstructed the locomotor behaviour of representatives of the major early euprimate lineages, demonstrating a diverse locomotor repertoire in early primates suggesting a rapid ecological diversification from a small-sized and active arboreal ancestral euprimate [5]. Body mass was also a significant factor that channelled such locomotor diversification, allowing some groups of early primates to depart from the ancestral euprimate condition. In conclusion, this study reveals that 1) the shape of the navicular bone is a good predictor of the locomotor behaviour and thus can be used to shed light on the locomotor repertoire of fossil primates and 2) that previous scenarios on early euprimate evolution are not mutually exclusive as early Euprimates exhibited a moderately broad locomotor diversity that allowed them to colonize diverse arboreal niches.

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Revisiting hunting efficiency: do hunting returns scale with prey body size?

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Explaining variation in hunter-gatherer livelihoods hinges on our ability to predict the tradeoffs and opportunities of pursuing different kinds of animals. This variation is important because the pursuit of animals with high social or nutritional payoffs likely played a key role in our characteristic extended juvenile periods, central place foraging, cooperative subsistence, and expansive social coordination. But which animals or types of animals were important? In archaeology, it is commonly assumed that large animals were more profitable than smaller ones because they are assumed to have provided larger amounts of food relative to the time and energy expended. Yet, ethnographic observations indicate that larger animals may not always provide higher caloric returns if the per capita costs of pursuit and processing, along with the failure rate, are taken into account [e.g., 1-3]. By ignoring these costs, we run the risk of misconstruing the role of large game hunting in our models of the evolutionary contexts of human sociality and economic variability.

To fully explore the reliability and generality of expectations about prey choice in different contexts we first assess the replicability and methodological comparability of hunting returns across a diverse, global dataset of 217 distinct post-encounter return rates for 181 terrestrial and avian prey types. In this dataset, we explore how hunting returns are mediated by variations in the costs of pursuit, capture, and processing relative to the size, energy value, proportion of adipose tissue and behavioral properties of the prey. Overall, our correlation analyses show that body size is a poor predictor of on-encounter return rate, while prey characteristics and behavior, mode of procurement, and hunting technology are better predictors.

These results have several important implications. Depending on the species that are compared, the widely used procedure of comparing small to large species can be problematic and earlier studies made on that basis may merit reanalysis for confirmation. Likewise, the practice of combining species of similar body size into single prey categories (e.g., medium-sized ungulates) may overlook important disparities in prey profitability when the species differ noticeably in terms of herding behavior, escape strategies or any other parameter that noticeably influences pursuits. For this reason, archaeologists must improve the methodologies that they use for estimating post-encounter rates. Simply assuming that body size is a robust proxy of profitability does not do proper justice to the broad range of procurement methods and contexts of encounter historically documented for most prey species.

In sum, debates about hunting and human evolution, the origins of broad-spectrum economies and the factors that drive intensification have relied extensively on ethnographic observations of the relative rankings of different prey types, coupled with the assumption that larger species typically will be higher ranked than smaller ones, especially when the latter involve fast prey. Although this assumption may be correct in some ecological contexts, our data indicate that, at a global scale, species with high fat content and low pursuit costs are more consistently higher-ranked, regardless of body size. These results thus throw into question most models of intensification that rely extensively on the assumption of a strong relationship between body size and profitability.

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Ontogeny aspects of femoral mid-neck strength in modern humans and Middle Pleistocene humans from Sima de los Huesos (Atapuerca, Spain).

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Most studies of cross-sectional geometries focus on population variation in adults, however, less is known about population variation in the lower limb robustness in subadult individuals. Moreover, while a wide variety of studies have focused on a single location of the long bone, by convention, the midshaft, less is known about changes during growth in cross-sectional geometries of the femoral mid-neck.

The characteristics of the femoral neck are highly influenced - more than the midshaft - by the hip abductor action and the bending from the hip joint force, the greatest stresses occurring in the medial mid-femoral neck region. The aim of this study is to evaluate the cross-sectional properties of the subadult femoral mid-neck in one recent and one fossil human sample.

In this work we study the ontogeny of femoral mid-neck strength of the humans from Sima de los Huesos (SH) Middle Pleistocene site (Sierra de Atapuerca, Burgos) dated to around 430 thousand years ago [1]. This site has provided, in addition to a large record of adult specimens, 90 specimens belonging to juvenile femora, representing a minimum of 14 individuals in different growth stages [2]. Six complete femora are the main objective of the present study. Cross-section slices at mid-neck were obtained through CT scans. The CT images were visualized using the Mimics™ (Materialise, NV., Belgium) software, and femoral mid-necks cross sections were subsequently imported into ImageJ to compute the cross-sectional parameters with the MomentMacro plugin. We focus on the mid-neck section total subperiosteal area (TA), cortical subperiosteal area (CA) and medullar cavity area (MA). For comparative purposes, we collected the same variables in 42 modern human subadults belonging to a medieval population from Burgos (dental aged from zero to sixteen years old). In this archaeological sample we established the growth of CA and MA relative to TA and the growth of MA relative to CA. These relative growth trajectories were assessed using log-log Reduced Major Axis (RMA) regression using PAST software. We calculated the standardized residuals of these regressions for both, the recent and SH specimens. Then, these residuals were compared between these two samples using nonparametric Kruskal-Wallis test.

Our results show that there are statistical differences between modern humans and SH hominins in all relative dimensions. SH hominins show relative to TA more CA and MA than our comparative sample. Thus, SH show more robustness than modern humans at this location of the femur during growth. This could be related to global growth acceleration, as in Neandertals [3], which would include faster endochondral bone formation that in turn would result in an increase in robustness. Our results agree with previous studies focused on cross-sectional properties of the adult and subadult femur diaphyses from SH, that compared to recent humans have relatively thick cortical bone and a relatively small medullar cavity [4, 5].

In sum, the Middle Pleistocene immature individuals from SH are relatively more robust when compared with our recent human sample, with large cross-sectional areas. These findings support the idea that differences in cross-sectional properties of femoral mid-neck between SH and modern humans are not only related to different activity patterns, but also to differences in the relative growth rate [5].

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A machine learning approach to sexual dimorphism in hominoid mandibular morphology and its application to *Paranthropus boisei*

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Sexual dimorphism remains one of the most challenging aspects when analyzing the hominin fossil record. Yet, multiple studies include attributed sex as a significant source of intraspecific variation in several taxa. Amongst early hominins, *Paranthropus boisei* has been suggested to show one of the highest degrees of sexual dimorphism in cranial and mandibular morphology. While focus has been placed on the cranial morphology of this species, the variability within the large *P. boisei* mandibular hypodigm has not been rigorously addressed, presenting an invaluable opportunity to explore the nature of sexual dimorphism in an extinct hominin species.

In this study, we use a machine learning model to predict sex in 22 mandibular fragments assigned to *P. boisei* using 3D geometric morphometric data. To do this, we first explored the accuracy of sex identification in a known-sex sample of great apes (*G. gorilla*, *G. beringei*, *P. troglodytes*, *P. pygmaeus* and *P. abelii*; set 1, n=87), in a sample of human mandibles sexed on the basis of standard cranial parameters (set 2, n = 25), as well as in the combined great ape and human sample (set 3, n = 112). Two sets of landmark atlases were used. The first consisted of 16 fixed landmarks and 387 sliding semi-landmarks placed on equidistant curves and surfaces of the entire hemimandible. The second maximized the available *P. boisei* mandibular sample. This second landmark atlas design consisted of 12 fixed landmarks and 642 sliding semi-landmarks placed on surfaces and equidistant curves of the mandibular corpus from M2 to P4. Differentiation between male and female individuals was tested using canonical variate analysis (CVA) in the three samples sets, with cross-validation scores showing a high degree of discrimination success in both the hemimandible (set 1: 96.3%; set 2: 75%; set 3: 94.9%) and corpus fragment (set 1: 97.7%; set 2: 88%; set 3: 94.6%). Visualizations of what aspects of mandibular morphology differentiated males and females in each species were rendered using thin plate spline deformations and distance heatmaps.

These comparative datasets were then used to train a semi-supervised classification model based on Gaussian finite mixture modeling, with Bayesian information criterion (BIC) used to determine the best fit. The resulting algorithms from the three datasets of the corpus fragments were then used to predict sex of individual *P. boisei* fossil mandibles, using thin plate spline warping to visualize the nature of this variation in the fossil taxon.

Despite the constraints of working with a fragment of the mandibular corpus, our results show that the shape information therein is sufficient to identify males and females to a high degree in all three datasets (great apes, humans, great apes and humans). However, the application of the algorithms derived from the different datasets to the *P. boisei* sample gives very different results. The ape-only and human-only equations fail to identify sex differences in the *P. boisei* mandible fossils, using the combined ape/human-based algorithm results in the grouping of some of the same fossils as male and others as female. Here we discuss the implications of these results for interpreting sexual dimorphism in early hominins.

Middle Palaeolithic, Upper Palaeolithic and Mesolithic flint artefacts dredged from the offshore Last Glacial Rhine-Meuse valley floor. The Maasvlakte 2 and Zandmotor sites (The Netherlands)

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The southern North Sea overlaps the northwestern limits of known Neanderthal distribution. This area was low lands for most of pre-Holocene time which explains why the seabed holds a rich archaeological and palaeontological archive, crucial to our understanding of hominin behaviour in northern latitudes. In the course of large scale coastal defence and harbour infrastructural works along the Dutch coast, sediments coming from dredging sites 10-15 km offshore are used to build new and replenish existing beaches.

By now numerous finds by a crowd of beach walking citizen scientists (>1600 lithics registered formally) provide ample evidence of Palaeolithic and Mesolithic occupation of the Last Glacial Rhine-Meuse valley, which we have systematically inventoried, described, sorted culturally and placed in reconstructed stratigraphic context. Detailed studies have focused on typo-technological characteristics of flint and other stone artefacts, raw material procurement, postdepositional surface modifications, and the integrated work allows assessing and assigning ages of the majority of finds and placing them in original geographic context.

Our poster presents the results for the two major sites Maasvlakte 2 (seaward harbour extension of the Port of Rotterdam) and Zandmotor ('Sand Engine') large scale beach nourishment, drawing from reports [1,2] commissioned by BOOR archaeological service of the municipality of Rotterdam and National Heritage Agency (RCE) respectively. Special identifications have been a handaxe made of Wommersomquartzite, transported over a distance of more than 150 km, from Maasvlakte 2 [3], and the tar-hafted Neanderthal tool from the Zandmotor dated to ~50ka BP [4]. The oldest replenished beach finds are attributed to the Acheulian, presumably c. 250-170 ka (i.e., shortly predating the Saalian glaciation in MIS 6). A considerable number of artefacts is attributed to the late Middle Palaeolithic (c. 115-40 ka; Early to Middle Weichselian, MIS 5d-MIS 3), and ascribed to several variants of the Mousterian Complex, particularly the *Moustérien de tradition acheuléenne* (MTA) and the *Moustérien type Quina*, and the *Keilmessergruppen* (KMG). Several small bifacial tools may indicate the presence of the 'Mousterian with Bifacial Tools' (MBT) [5]. A small number of artefacts probably dates to the earlier Upper Palaeolithic (Late Aurignacian and/or Early Gravettian), and Ahrensburgian and Federmessergruppen are also attested, intriguingly significantly more at Maasvlakte 2 than at Zandmotor. Mesolithic finds are numerous and at Zandmotor include Late Mesolithic core axes and trapezes, which seabed depth, valley rim setting and sea-level history constrain to be older than 6100 BCE. A few core axes from Maasvlakte 2 are older and can be attributed to the Early Mesolithic Maglemose-Duvensee group. The Upper Palaeolithic and Mesolithic finds will be studied in greater detail within the project '*Resurfacing Doggerland. Environment, humans and material culture in a postglacial drowning landscape*' funded by the Dutch Research Council.

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Hominin femur from Lusi Depression, North of Central Java: Its morphological character and taxonomical position

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Java island is known as the most prospective place in Island Southeast Asia for human paleontological study in Quaternary prehistory. This island has been formed as complexity of collision zone and glacial-interglacial processes since Plio-Pleistocene boundary around 2.4 Ma [1].

Main paleoanthropological sites were discovered in the big central depression zone along Bengawan Solo and Brantas rivers [2]. More than hundreds of *Homo erectus* individuals were recovered from those areas, but previous studies focused less on the northern depression zone along the Lusi river. Recently, Banjarejo, a paleontological site in the Lusi depression, became an important prehistoric site for Quaternary research because of its significant faunal and hominin remains.

This study describes a new finding of the hominin femur specimen from the Banjarejo site and its taxonomical position in the history of hominin evolution in the Island Southeast Asia region.

The specimen was identified by morphological and metric descriptions of the external feature of the femur. Then, comparative study to *Homo erectus* (n=2), *Homo neanderthalensis* (n=8), *Homo heidelbergensis* (n=1), prehistoric *Homo sapiens* (n=44), *Australopithecus africanus* (n=1), *Paranthropus robustus* (n=2), also non-human primate including *Pongo* (n=1), *Macaca* (n=1) and *Gibbon* (n=1) were performed.

We used bivariate and multivariate statistical analysis based on several measurements of proximal epiphysis [3] and diaphysis [4] of the femur with PAST statistical software to presents the specimen into the evolutionary perspective.

This study shows that the morphological and metric characters of Banjarejo femur specimen are placed between *Homo erectus* and prehistoric *Homo sapiens* population samples. This result could be compatible with a hypothesis that places Java as an interrogation zone between archaic hominin and anatomically modern humans in Island Southeast Asia [5]. However, further study should be addressed to investigate the hominin specimen's precise chronological and cultural context.

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Earliest western expansion of the Uluzzian groups and the late Neanderthal occupation in southern Italy

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During the Middle to Upper Palaeolithic transition, ca. 50-40 thousand years ago Europe witnessed a crucial population turnover characterized by the replacement of Neanderthals by *Homo sapiens*. In the same chronological interval, the archaeological record offers evidence of a conspicuous, although spatially and temporally differentiated, shift in material culture and technology across the continent [1] that opens critical questions about the processes underlying modern human migrations into Europe and their chronology, on the impact of a possible interaction between *Homo sapiens* and Neanderthals, and the attribution of different techno-complexes to different human groups [1-3]. In this context, the Italian Peninsula plays a pivotal role due to its geographical position, broad environmental diversity [4], and richness of archaeological evidence [1,2]. However, only a handful of Neanderthals and modern human remains dated between ~50 and ~40 ka have been found in Italy, thereby preventing a comprehensive overview of the relationship between these two species.

In this study, we show the most recent direct evidence of Neanderthal presence and the oldest date for the Uluzzian techno-complex in southwestern Italy by generating new dates and taxonomic attributions of two human teeth documented at Roccia San Sebastiano (Mondragone-Caserta, Italy) [5]. We used morphological analysis, morphometric analysis, and a variety of supervised learning algorithms (Flexible Discriminant Analysis, Multiadaptive Regression Splines, Random Forest) on the cervical and crown outlines of the two samples.

We attributed RSS1, a left second lower deciduous molar found above a level that we dated to 44,810-44,230 cal BP (1 σ), to a Neanderthal individual based on all the obtained posterior probabilities, as well as on the presence of a bucco-distal enlargement and a convex lingual side (from the occlusal view), and a complex morphology in the occlusal aspect of the EDJ (i.e., protostylid, anterior fovea and mid-trigonid crest).

The second specimen RSS2 is a left second lower deciduous molar which was found in stratigraphic continuity with a predominantly Uluzzian deposit that we dated to 42,640-42,380 cal BP (1 σ). The tooth presents with a crown outline characterised by bucco-distal narrowing, straighter lingual side, and a complex morphology in the occlusal aspect of the EDJ (i.e., crests in the mid-occlusal basin, but absence of MTC), all of which make it closer to both archaic Pleistocene and recent human samples. All supervised learning algorithms consistently attributed it to *Homo sapiens*.

Roccia San Sebastiano therefore offers direct evidence of a late presence of Neanderthals in southwestern Italy, followed by a later shift to Early Upper Palaeolithic technology compared to the Uluzzian evidence documented at Grotta del Cavallo (Puglia, Italy).

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Does stone tool ‘backing’ result in improved adhesion in hunting weaponry?

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The stone tool manufacturing technique of “backing” refers to the blunting of a flake’s edge(s) at, or near to, a 90° angle. Backed tools have a long prehistory, extending over 250 kya in sub-Saharan Africa, occurring later in Europe, Asia, and Australia. Indirect evidence from residues and micro-wear suggest that backed tools represent the earliest purported evidence for high-speed projectile weaponry. Direct evidence of backed tools embedded in human and animal bones demonstrate their use as hafted weapon components. But why blunt a sharp edge that can otherwise be used for a variety of practical tasks, such as butchery, engraving, or processing plant material? One intriguing hypothesis is that backing enabled early humans to more effectively attach (haft) stone tools to wooden or bone handles by a) providing a wider, rougher, and stronger surface area for adhesion and b) creating a blunt edge less likely to split the haft. If true, then backing represents a significant Stone Age innovation in adhesion engineering, consistent with a growing list of early human behavioral and technological innovations. Yet, the adhesion advantages of backed stone tools have never been empirically or quantitatively tested. Modern engineering experiments involving adhesion mechanics suggest an inverse relationship between surface area and the strength of a bond, especially on heterogeneous surfaces like stone. Some Stone Age humans hafted and used both backed and un-backed hunting implements for millennia in many parts of the world, suggesting effective hafting could occur with or without backing. Here we will present on a series of hunting experiments involving machine-fired arrows tipped with backed and unbacked stone implements to test the hypothesis that stone tool backing significantly increases adhesion between a stone tool and a shaft used for hunting. Regardless of whether the results support the null or the alternative hypothesis, the findings will ultimately unlock part of the answer to backed tool proliferation with extensive anthropological impact given these are the first robust, systematic tests of backing technology and adhesion.

Use of green pebbles by late Neanderthals at Fumane cave.

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Humans were constantly surrounded by colors in their existence, and we might expect colors were charged with different meanings and importance through time [1]. Also, Neanderthals collected unusual, sometimes colorful mineral materials from various sources [2]. Nonetheless, information available on the ability to collect raw materials, transport strategies, complimentary use of tools to produce and maintain tool kits made of organic or inorganic materials is still scanty for those Middle Paleolithic hunter-gatherers [3]. Excavations of the late Mousterian layers at Fumane Cave (northern Italy) have brought to light several green serpentinite pebbles characterized by naturally flat and oval shapes, smoothness and use modifications. We combined non-destructive and non-invasive analytical techniques to explore cognitive and functional criteria behind the select and use of such unique pebbles. In particular we considered the regional geographic distribution of the primary serpentinite outcrops, their areal of dispersion in the alluvial plain of the Adige River and the glacial tills, the fluvioglacial deposits of the Garda and Adige glaciers, the morphology and petrology of the pebbles as well as the analysis of diagnostic functional macro-traces and residues. The latter ones are related to bone working, an activity already documented from the presence of a bone tool in the context of the pebbles [4]. Besides the attraction for green materials, there is no evidence for the use of soft green and flat pebbles, like those from Fumane Cave, during the Middle Palaeolithic in this area. Moreover, these materials were collected by Neanderthals only from ca. 45-44 ka cal BP, despite the large availability of green serpentine pebbles in the alluvial beds near the cave during the multiple use of the cave in the Middle Palaeolithic [5]. Ultimately, we provide new data to understand the role of aesthetic and technological factors in shaping human behavioral range in the Middle Paleolithic.

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Exploring LGM subsistence in Cantabrian and Mediterranean Iberian areas: ungulates bone assemblages as nutritional and industrial resource among Solutrean groups

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The presence of human groups during the Last Glacial Maximum has been witnessed along all Iberian regions [1]. Nevertheless, the paleoenvironmental and biogeography conditions show differences, with clear influence in the settlement dynamics, subsistence strategies and social behaviour of Palaeolithic people. Under this precept, our objective is to compare at nutritional and technological level, the faunal assemblages of three archaeological sites located in two of the largest zones with Solutrean deposits, the Cantabrian and Mediterranean areas.

Cueva de Llonin (Galería sector, level IV) has interesting Solutrean deposits dated to ca. 19 Ka BP, with abundant anthropogenic evidence (lithic, fauna, hearths, parietal art), located at mid-mountain altitude of 112 m.a.s.l. and rugged orography in Asturias. Hort de Cortés-Volcán del Faro (Sector A, layers 27 to 30) is an ancient excavation in revision due to its long Upper Palaeolithic sequence, with abundant lithic and faunal remains. Currently located on the coast at 112 m.a.s.l., during the LGM it would have been in a marsh context with low-mountain ranges behind it. Les Coves de Santa Maira is a mid-mountain site in a very rugged landscape, located at a distance of 30 km from the current coastline. Its Corral del Gordo sector (layers 12 to 20) is the oldest deposit dated to ca 19 ka BP, where anthropogenic material is scarce, but the collection of personal pendants is numerous.

The results of zooarchaeological and taphonomic analysis of more than 7000 bone fragments, at nutritional terms, indicated to us that Solutrean populations carried out an intensive exploitation of medium and large-sized ungulates in both areas. Deer, Iberian ibex and chamois are the most common taxa in the anthropogenic assemblages of Llonin, with little presence of large-sized animals as horses or aurochs/bison. A similar record identified in HC-VF and Santa Maira, accompanied by a high consumption of leporids and the absent of the chamois. The butchering processes is identified by the presence of percussion marks and cut-marks, but also, through the functional analysis of 15 splintered pieces from Santa Maira, that raise the possibility of their use for fracturing long bones to obtain bone marrow [2]. Nevertheless, the anthropogenic evidences are few in Mediterranean contexts due to taphonomic alterations of bone surface. Besides, all assemblages show an intense human fragmentation, typical of harsh periods, involving different levels of taxonomic identification, higher in Llonin. The human-carnivore interactions have been attested at all sites through the recognition of dental marks and isolated carnivore bones, although with a much lower ratio than in previous periods [3]. Medium and small-sized predators, as leopards, lynx and fox, have intervened in the bone assemblages and consequently report a shared use of the cavities with human groups.

However, the use of the ungulate carcasses is not limited to the nutritional field, but also for technological and symbolic use [4]. At Llonin Cave, there is a predominance of bone over antler and teeth on a total of 69 pieces. Most of them are singularly made on bird bone tubes, but there is also an outstanding perforated scapula fragment and deer canines. Bone has also been used for awls and smoothers, while antler has been devoted for projectile points. The osseous industry in HC-VF is composed of 13 objects on antler (single beveled points, fragments of points, a chisel, and an unknown fragment) and on bone (awl, fishhook and points). With a preliminary operational schema of transformation by partition and progressive reduction of block. At Santa Maira there is no evidence of bone industry, except for a fragment close to a tip with a polygonal base and a pierced deer canine.

All previous data prove the complex exploitation of animal carcasses by Iberian Solutrean groups, with some little differences according to the biogeographical region.

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Phylogenetic ancestral character state reconstruction using maximum likelihood of hominin encephalization

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Unravelling the evolutionary pattern that characterizes hominin brain evolution is critical for understanding what is neurologically distinctive about modern humans and what cognitive underpinnings humans share with their ancestors and relatives. Studies on the evolution of human brain size have long focused on brain size and contributed to support the hypothesis of a gradual increase over human evolutionary history. Due to recent discoveries of relatively late-appearing small-brained hominin species, such as *Homo floresiensis* and *Homo naledi*, this view is no longer tenable. Here, we propose to use a phylogenetic approach to provide a robust framework for the inclusion of outliers in the study of human brain size evolution. We used brain mass, body mass, and encephalization quotients (EQ) provided in de Sousa & Cunha [1]. We tested six hypotheses based on modified phylogenetic analyses from Dembo et al. [2], and Schroeder et al. [3], with deeper nodes based on Strait & Grine [4]. Phylogenetic trees were time calibrated using stratigraphic dates obtained from Wood et al. [5], and then subjected to phylogenetically controlled statistical tests. We considered Lambda, Brownian Motion, Ornstein Uhlenbeck, and ordinary least square as candidate model structures, using Akaike information model selection criterion (AICc). Then, we investigated changes in the tempo of hominin brain evolution by subjecting the best fitting hypothesis to maximum likelihood (ML) and Markov chain Monte Carlo (MCMC) rate shift tests. Finally, we performed an ancestral character state reconstruction of absolute brain mass, EQ, and body mass in order to interpret the pattern of changes that occurred during hominin brain evolution. In the best fitting model *Homo floresiensis* is uncovered as a sister taxon of *Homo erectus sensu stricto*, supporting an Asian origin of the species. Our study supports the position that *Homo naledi* is part of a long ghost lineage that extends back to more than 2 million years ago. OLS had the least support from the AIC selection procedure, and a Brownian motion model was selected as having the best structure. Our investigation of changes in the tempo of evolutionary rate shift calculations using a ML algorithm and a MCMC algorithm showed the most commonly sampled rate shift in absolute brain size and EQ in the branch evolving crown ward to the clade encompassing *Homo*. Two more rate shifts in EQ and absolute brain size were detected in the branch leading to *Homo erectus* and to *Homo antecessor*, *Homo heidelbergensis*, *Homo neanderthalensis*, and *Homo sapiens*. Additionally, the best fitting model supports the hypothesis that *Homo naledi* and *Australopithecus sediba* are part of the genus *Homo*. The results of the ancestral character state reconstruction on brain size, body size, and EQ, show general plasticity of brain mass during the Pleistocene, with decrease in brain size in some small-brained *Homo* species along with increase in other *Homo* species. We thus conclude that a phylogenetic framework is best suited for capturing these oscillating changes during in the evolution of hominin brain size.

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At the onset of the Central European Micoquian: new archaeological and genetic data from Stajnia Cave (Poland)

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At the beginning of the Last Glacial, climatic worsening promoted environmental shifts across Eurasia and the expansion of cold adapted species from the Arctic to Central-Eastern Europe [1]. These new ecological conditions were challenging for Neanderthals of mid latitudes, causing demographic contractions and successive expansions into the regions above 48° N latitude only during climatic ameliorations. In concomitance with these environmental changes, Neanderthals of Central-Eastern Europe modified their toolkits and started to produce different types of a-/symmetric bifacial tools, foliate artefacts and bifacial scrapers. This cultural tradition, called Micoquian, diffused between Eastern France, Poland, Northern Caucasus, and Altai [2]. Despite human settlements in Central Europe being intermittent due to extreme seasonality, the Micoquian persisted up to the end of the Neanderthal' history. Adding new data from Micoquian sites is pivotal for understanding the processes of Neanderthals' adaptation to low biomass environments.

This paper presents multidisciplinary research on Stajnia Cave, a new archaeological site located in Kraków-Częstochowa Upland (Poland) [3,4]. Archaeological fieldwork at the site was carried out between 2007 and 2010. The ~1.5 m stratigraphic sequence is complicated due to post-depositional frost disturbances, partial sediment sinking, and modern distortions. The cave loam is divided into 7 lithostratigraphic units accumulated between MIS 5c and MIS 1. Radiocarbon dates on five animal bone samples reveal that layers E1, D3 and D2 are older than 49,000 years BP. The zooarchaeological analysis indicates a dominance of herbivores representative of the *Mammuthus-Coelodonta* complex, such as reindeer, steppe bison, mammoth, and woolly rhino, whereas the carnivore paleocommunity consists of weasels, cave bears, and cave hyena. The lithic assemblage is composed of bifacial artefacts and stone tools typical of the Central European Micoquian. The high fragmentation of the operative chains indicates the Neanderthal occupations were short-term. The site could have been a logistical location settled during forays into the Krakow-Czestochowa Upland.

In 2007, a Neanderthal tooth - Stajnia S5000 - was discovered in layer D2. The tooth was directly dated but the resulting age was contaminated by modern carbon, most probably caused by the presence of glue applied post-excavation. The tooth was also sampled for ancient DNA. The result reveals that the mitochondrial genome of S5000 falls close to that of Mezmaiskaya 1, a Neanderthal from the Caucasus. The molecular genetic clock was used to determine its approximate age, and after cross comparison with the archaeological record, allowed us to place the fossil at ~80,000 years BP. This indicates that the DNA from S5000 is the oldest Neanderthal DNA recovered from Poland and Central-Eastern Europe.

The technological similarities between the Micoquian assemblages in Central and Eastern Europe, and the mtDNA affinity between Poland and the Caucasus suggest a pattern of high mobility across the European Plains. The Prut and Dniester rivers were probably used as the main corridors of dispersal, facilitating seasonal forays to lower latitudes or vice versa. The persistence of the Micoquian techno-complex in South-Eastern Europe infers that this axis of mobility was also used at the beginning of MIS 3 when a Neanderthal population turnover occurred in the Northern Caucasus [5].

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Genomic analysis of Czech fossil reveals the oldest modern human skull from Europe

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Following their dispersal out of Africa, modern humans admixed with Neandertals ~60,000-50,000 years ago, and then expanded into Eurasia a few thousand years before Neandertals disappeared. The genetic composition of these first Eurasians is, so far, not well characterized since only a very limited number of individuals older than 40,000 years have been genetically analyzed. Those include Fumane 2 [1], Oase 1 [2] and Bacho Kiro Initial Upper Paleolithic individuals [3] from Europe, Tianyuan from East Asia [4] and Ust'-Ishim from Siberia [5]. However, none of the analyzed individuals is associated with an almost complete skull as is the case for Zlatý kůň, which was discovered more than 70 years ago in present-day Czechia. The age of this specimen estimated with archeological, morphological and radiocarbon dating methods is inconsistent and highly disputed. Here, we report mitochondrial DNA (mtDNA), genome-wide capture data and a ~4-fold shotgun genome generated from the temporal bone of the Zlatý kůň skull to shed light on its age and assess its genetic profile. In a phylogenetic analysis, the complete mtDNA sequence of this individual falls within mtDNA haplogroup N and exhibits a shorter branch length than Bacho Kiro individuals belonging to the same haplogroup. The nuclear genome represents a deeply divergent out-of-African lineage that did not contribute genetically to either Europeans or Asians. Moreover, it carries a similar proportion of Neandertal ancestry like other Upper Paleolithic hunter-gatherers but the length of the introgressed Neandertal blocks are longer than those observed in the 45,000-year-old Ust'-Ishim genome. This suggests that Zlatý kůň is at least as old, if not older than, as Ust'-Ishim and thus is the earliest modern human skull sequenced to date. Finally, the genetic ancestry uncovered in Zlatý kůň and in other pre-40,000-year-old modern humans largely disappeared from Europe. This provides interesting implications for a possible common demise of European early modern humans and Neandertals that requires further interdisciplinary investigations.

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Don't stop me now. How can pregnant females deal with mobility costs?

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Locomotion activities are necessary to survive in many senses because they are essential for key daily activities as foraging, offspring protection, escaping predation, mating, etc. [1]. Human pregnancy is one of the conditions that may constraint mobility in recent hunter-gatherer populations, but also in extinct hominin groups, since the increment in body mass during gestation is expected to raise locomotion costs [2]. However, other researchers highlight that in some foraging societies females maintain locomotion activities independently of the pregnancy state [3]. Different behavioural strategies and physiological mechanisms may be buffering the penalty that pregnant females experience during locomotion in those societies.

An experimental study was performed to test whether body mass affects the locomotion costs of pregnant and non-pregnant females in the same manner. The experiment was carried out at the BioEnergy Laboratory of National Research Center on Human Evolution (CENIEH, Burgos, Spain) in a sample of 42 non-pregnant and 35 pregnant females, who completed two trial rounds at their 28 and 32 gestation weeks. All the experimental procedures were approved by the Hospital Universitario de Burgos Ethical Committee (BioE6-Ref. CEIC 1595). Body mass was recorded with a digital standard scale, and body composition obtained by bioelectrical impedance analysis (BIA 101 AKERN©, Body-Gram Pro©, (v2010)). The energetic cost of locomotion (CoL) was measured by Indirect Calorimetry (Master Screen-CPX JAEGER, LabManager IntelliSupport 5.72) walking for 20 minutes, at 4 km/h, over a flat treadmill (hp COSMOS©). Body composition parameters were expressed as a percentage of body mass, and the values of all the variables measured were compared between pregnant and non-pregnant females using T-tests. A reduced major axis regression of the CoL on body mass was computed for each group (non-pregnant, 28 weeks of gestation and 32 weeks of gestation) and the slopes and intercepts of the models compared among those groups.

The results show that body mass and the percentage of fat mass are significantly higher in pregnant females. Despite pregnant females having a larger body mass, CoL is not statistically different between pregnant and non-pregnant females. Comparison of the regression lines shows that, for similar body masses, pregnant females expend less energy during walking tests than non-pregnant females. This would be caused by pregnant females having a larger proportion of passive body tissues (fat mass) for a similar body mass than non-pregnant females.

Hunter-gatherer populations adopt behavioural strategies that alleviate locomotion costs during pregnancy, like reduction of speed or distance [2]. Nonetheless, when pregnant females maintain their daily mobility [4], some physiological mechanisms may aid to reduce walking costs [5]. Thus, the differences in fat mass between pregnant and non-pregnant females detected in the studied sample, and their influence on the relationship between CoL and body mass, could constitute another trade-off that reduces locomotion costs during pregnancy. The physiological and behavioural adaptations acquired throughout human evolution are relevant to buffer the mobility demands and ensure human reproduction and survival.

We are sincerely grateful to all the volunteers who participated in this experimental study in 2016-2017. Especially, we appreciate the kind support in the recruitment of participants by Servicio de Ginecología y Obstetricia del Hospital Universitario de Burgos (HUBU) and Gerencia de Atención Primaria de la Junta de Castilla y León de Burgos (Spain), namely the midwives. Data were obtained from the EVOBREATH DataBase, managed by A. Mateos and J. Rodríguez (CENIEH).

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Feeding behavior of macaque from the Plio-Pleistocene site Guefaït-4.2 (Eastern Morocco) through dental microwear and stable isotopes

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The macaque lineage originated in Africa, dispersed across Eurasia in the Late Miocene and in eastern Asia in the Late Pliocene. In North Africa the presence of *Macaca* sp. fossils is well known during the late Miocene in Algeria, Egypt and Libya and also during the Pliocene in Tunisia and in the Early Pleistocene in Morocco [1]. The expansion of this genus is one of the most successful among primates, occupying a variety of ecological environments and geographical ranges [2]. This adaptive capacity also implies a plasticity regarding their feeding habits. However, studies that characterize the diet of fossil *Macaca* sp. are still unknown.

Guefaït-4, located in the Plio-Pleistocene basin of Aïn Beni Mathar-Guefaït (Jerada, eastern Morocco), has delivered a diverse faunal assemblage of vertebrates at the GFT-4.2 section trench (reptiles, amphibians, and both small and large mammals), including new macaque fossil remains recently published [3].

In this work, dental specimens of *Macaca* sp. from Guefaït-4.2 have been studied through dental microwear analysis under the stereomicroscope at low magnifications (35x), using the protocol established by [4] and stable isotopes (bioapatite) of tooth enamel powders following the chemical treatment protocol of [5].

The two techniques provide palaeoecological information on the feeding habits on two different timescales: the stable isotopes analysis allows us to characterize the diet the individuals had during the first years of life, while dental microwear reveals the diet from the last days/weeks of an animal's life.

Carbon isotopic results for all samples analyzed showed that the plants foraged by *Macaca* sp. were shrubs, C3-grass adapted to mild growth season and trees, which is consistent with the dental microwear pattern observed, characterized by a low number of scratches and relatively high number of pits. The bivariate distribution of the numbers of pits and scratches compared to the extant species of primates, places the specimens analysed in the browsing and leaf-dominated feeding ecospace differing from primates with a higher intake of grass such as the extant species *Theropithecus gelada*. The combination of both proxies is a key issue when there is a predominance of C3 plants in the animal's diet. In this case, the microwear indicates that this macaque fed predominantly on tree leaves at least during the days/weeks before the death of the individuals.

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An integrated information architecture for paleoanthropology

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We are rapidly approaching the centenary of Raymond Dart's 1925 landmark publication of the Taung skull which ushered in the modern era of scientific paleoanthropology as we know it today. Since then, the field has expanded rapidly with numerous fossil and archaeological discoveries. Furthermore, recent advances in geochronology, genetics, 3D imaging, paleoecology, climate modeling and other fields have prompted a deluge of data related to the primary fossil, and archaeological record. One of the major challenges facing paleoanthropology in this century will be developing systems that can synthesize diverse data from disparate sources. This synthetic effort will require greater adoption of transparent and FAIR [1] data management practices along with a fundamental shift in the epistemic culture [sensu 2] surrounding paleoanthropological research, specifically a shift from analyses organized around specific sites and projects to synthetic analyses across projects. However, data integration for the purpose of synthetic analysis requires first systematizing and aligning the data in a way that preserves the individual nuances of each project and at the same time allows for comparable and reliable integration of data within a larger framework.

In this paper we present an integrated information architecture (IIA), that comprises a conceptual framework capable of accommodating the diversity of paleoanthropological information in a consistent and comparable manner as well as an online information system to manage and disseminate the information. The conceptual framework comprises ten primary classes (Artifacts, Fossils, Rocks, Events, Locations, Contexts, Agents, Publications, Taxa and Identifications) and the principal relationships between them. Based on this framework we have developed an extensible, modular information system for paleoanthropology called the Origins Project, that currently includes over 3000 hominin fossils from over 500 locations (i.e., sites). To demonstrate the potential of this approach we have developed an online catalog of ca 166 named hominin type specimens, their associated site locations and taxonomic identifications (nomina). The catalog includes published names (valid and invalid under the ICZN) proposed in the paleoanthropological literature. Each name and associated type specimen are linked to bibliographic references, many of which point directly to full-text digital versions of the original taxonomic publications. We present an analysis of these type specimens that highlights how an integrated information infrastructure can address the challenges of hominin systematics and species delimitation [e.g., 3].

The Origins Project is developed and maintained on the Paleo Core platform using open-source software and open data standards [4]. The design, content and functionality of the application are maintained by a team of senior research scientists, graduate students and undergraduate interns and volunteers. In this way Origins serves as a powerful platform for research and also a dynamic environment for training, education and outreach.

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Beyond the EDJ: combining landmarks on the cervical line, EDJ and occlusal surface in the study of upper permanent premolars

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Dental traits are often used in paleoanthropology to infer species-specific differences that can be used to classify fossil remains. Teeth are the most abundant skeletal element in the fossil record. Their chemical and physical properties allow for a high rate of preservation in relation to bone. Nevertheless, not all teeth and overall tooth types are equally informative in attempts to classify a fossil to a known species or group. Here, we show that the combination of already established 3-dimensional landmarks on the cervical line, enamel-dentine junction (EDJ) and occlusal surface can help to increase discriminant power of shape analyses in permanent upper premolars.

Our samples comprised 43 computer tomography scans of upper third premolars and 41 scans of upper fourth premolars. Both samples consisted of Neanderthals, fossil and recent modern humans. Each tooth was segmented to virtually separate enamel and dentine at the EDJ. A set of six fixed landmarks (dentine: paracone, protocone, mesial and distal fovea; enamel: mesial and distal fovea) and 65 semi-landmarks along three curves (dentine: mesial and distal ridges, cervical line) was digitized. The combination of cervical line and EDJ allows for an indirect measure of crown height while the combination of occlusal surface and EDJ provides an indirect measure of enamel thickness. Thereby, the landmarks used on the occlusal surface were chosen so as to maximize the sample of teeth with varying degrees of dental wear that could be included in the analysis. The mesial and distal fovea or point where the central groove intersects the mesial or distal foveal grooves, respectively, are preserved even in teeth with moderate dental wear. Teeth with heavier wear are usually excluded from EDJ analyses anyway as heavy wear not only affects the enamel but extends to the dentine.

This landmark set allowed for a clear separation of groups in our data sets of upper third and upper fourth premolars. Jackknifed classification success based on the entire shape variation reached over 90 % between our samples of modern humans and Neanderthals. Neither outline analyses nor analyses based on a landmark set limited to the EDJ came close to this level of separation. Although these results should be tested with larger samples, we hope that the proposed combination of landmarks will contribute to the elucidation of isolated fossil upper premolars' taxonomic affinities in the future.

We would like to thank all institutions that provided CT scans for the underlying studies.

The late Middle Palaeolithic occupation of Abri du Maras (layer 1, Neronian, southeast France): integrating lithic analyses, ZooMS and radiocarbon dating to reconstruct Neanderthal hunting behaviour

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The exact mechanisms and dynamics of Neanderthal hunting behaviour (including prey acquisition methods and weapon technologies) remain difficult to reconstruct and continue to form a topic of debate [1]. Identifying stone-tipped hunting weapons in the archaeological record is obscured by various methodological issues [2] and in general lithic points are sparse across the European Middle Palaeolithic record. An exception is the Neronian entity in southeast France, characterised by ventrally retouched Soyons points [3]. One of the largest Neronian assemblages is layer 1 at Abri du Maras (>3,000 lithics), excavated by Gilles between 1946 and 1950 [4] and by Combier in 1958 and 1963 [5]. This study contextualises the layer 1 lithic and faunal archives to gain a better understanding of site formation, chronology, assemblage integrity and patterns of Neanderthal hunting behaviour.

The focus of our lithic analyses was on recording attributes that have been described as indicative of projectile use or hafting such as macro-traces of use (e.g., breakage patterns at the tip and macroscopic edge damage) and modifications near the proximal end of the point (e.g., basal retouch and ventral thinning). We applied this focused attribute analysis to flakes, blades and points from the Gilles collection to contextualise the morphometric and technological characteristics of the Soyons points. We found that these points were made on a variety of blank types (including Levallois, laminar and discoidal flaking techniques) and ventral retouch is present across different artefact types (including points, scrapers and denticulates). Next, we collected similar typo-technological data on a sample of blanks from the recently excavated and well-contextualised point-rich layer 4.1 of Abri du Maras (MIS-3). Although macrofractures are present, other modifications related to the use of the points as projectile tips are rare and detailed edge damage studies were obscured by the preservation state of the artefacts, with many of them being heavily desilicified.

To further assess the human behaviour at the site, Zooarchaeology by Mass Spectrometry (ZooMS) was applied to all unidentifiable fragments larger than 25mm (n: 278) from both the Gilles and Combier layer 1 collections. The resulting faunal spectrum is diverse with significant proportions of equidae, Bos/Bison, cervids and reindeer. Carnivore remains and modifications are absent while human modifications are present across species. We selected eleven bones for radiocarbon dating and five had sufficient collagen yields but returned dates younger than expected (ranging from 39,000 to 29,000 calBP). Together with an assessment of the glutamine deamidation values of the ZooMS faunal specimens, we discuss the integrity of the layer 1 material.

Finally, we place both the lithic and faunal material from Abri du Maras layer 1 in its broader regional context and discuss its relation to other Neronian assemblages and more general problematics related to studying material from old excavations. Overall, our analyses show that while we managed to obtain additional behavioural data from the Maras layer 1 collections, we also encountered contextual issues that require caution when making interpretations of Neanderthal behaviour within these upper layers.

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New insights on late Neanderthal subsistence strategies and settlement dynamics in the southern Harz, Germany

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Understanding regional patterns of subsistence strategies throughout different stages of the Middle Palaeolithic is critical to broadening our knowledge of Neanderthal lifeways. While Neanderthals inhabited a vast area within Eurasia, our focus is on the area of the Harz mountains in central Germany during early marine isotope stage 3 (MIS 3), corresponding to the late Middle Palaeolithic (~70-40 ka) [1]. This geographic area and period are poorly researched and only represented by a limited archaeological record. Einhornhöhle (Unicorn Cave) is located in the southwestern Harz and was first excavated in the early 16th century in search of alleged unicorn bones for therapeutic purposes. Despite extensive archaeological research at the site since its discovery, lithic artifacts were not found until the 1980s, providing the first evidence for the presence of archaic hominins at the cave [see review in 2]. Recent excavations at the entrance (Area 4) have uncovered a new assemblage of faunal remains bearing both hominin and carnivore modifications dating to early MIS 3.

This poster presents the results of the first zooarchaeological and taphonomic analysis of the macro-vertebrate remains from Area 4 of Einhornhöhle. Neanderthal occupation occurred in two main phases represented by the geological horizons (GH) 4 and 6. In these layers, the remains of large ungulates such as bison (*Bison* sp.), giant deer (*Megaloceros giganteus*), and red deer (*Cervus elaphus*), are more frequent and show evidence of hominin exploitation. In other layers, hominin presence is rare, while the remains of carnivores such as cave bear (*Ursus spelaeus*) and cave lion (*Panthera spelaea*) are more abundant; although, the overall frequency of faunal remains are low. Analysis of the skeletal representation of ungulates suggests that, at least during the formation of GH 4, entire carcasses were occasionally transported to the site in order to be butchered near the entrance. Furthermore, the taphonomic analysis revealed low processing intensity of these taxa. Our results indicate that late Neanderthals occupied the site sporadically, likely for brief events of butchering large ungulates, hinting at the high mobility of these late Mousterian foragers. In conclusion, Einhornhöhle represents a unique source of information for analyzing Neanderthal subsistence behavior in response to the post-1st Glacial Maximum environments of central Europe during early MIS 3.

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A 3D geometric morphometric analysis of the scapular glenoid fossa of subadult scapulae from Sima de los Huesos (Sierra de Atapuerca, Burgos, Spain)

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Sima de los Huesos (SH) is a well-known Middle Pleistocene site in which thousands of skeletal remains have been recovered. Among these fossils, around 60% correspond to postcranial bones belonging to subadult individuals (1). Thus, this sample is the most promising source of evidence for exploring the developmental aspect of the postcranial skeleton in a fossil human species. In this work, we focus in the development of the glenoid-coracoid interface of the six scapular glenoid fossae (SGF) belonging to six different subadult individuals from SH. For comparative purposes, we studied 94 modern human SGF aged from birth to 16 years old originating from two different collections. The first sample is composed of 38 SGF belonging to subadults of known sex and age at death housed in the Bocage Museum (National Museum of Natural History, Lisbon, Portugal). The second sample is composed of 51 SGF from the archaeological collection from San Pablo (Burgos) housed in the Laboratory of Human Evolution at the University of Burgos. The estimated age at death of the San Pablo individuals was based on the calcification and formation of dental crowns and roots. The mineralization stages of each tooth class were observed by CT scans and scored using the method of Moorees et al. (1963) (2). These Moorees's stages were converted into age following the adjusted data for prediction proposed by Smith (1991) (3). For the purpose of the present analysis, both Iberic samples were considered together as a single population. Individuals were sorted into four developmental groups based on the maturity of glenoid-coracoid interface.

Standardized images of SGF from San Pablo were digitized using the high accuracy structures light 3D scanner "Einscan Pro HD". Those from Lisbon collection were performed using the Laser scanner Nextengine. SGF from SH were taken from CT scans. The post-processing for all 3D models (editing, cleaning, hole-filling and smoothing) was carried out with Meshmixer (Autodesk, USA) and Meshlab. A set of 10 homologous 3D landmarks and 103 semilandmarks were measured on each of the 94 scapulae 3D models using Stratovan Checkpoint Software. Semilandmarks were located along 9 curves. In order to minimize possible shape variation, the 103 semilandmarks were slid along their correspondent curves and organized following the location of the fixed landmarks. The (semi)landmarks configurations were subjected to a generalized Procrustes analysis (GPA). Using the Procrustes coordinates of the analysis, a PCA was executed through MorphoJ software. Statistical process analysis was carried out with Past 4 software.

The analysis of PCA on the entire sample shows that 31.84% of the total variance is explained by the first two principal components. The first component (PC1) is associated with 18.31% of the variability, while PC2 explains 13.53%. PC1 accounts for the variation in the SFG shape during the developmental process. Along this axis, modern individuals are distributed consecutively, consistent with the maturation stage. In this PC, there are no differences between our comparative recent sample and the SH individuals. This, allow us to tentatively estimate a skeletal age for SH scapulae. Main differences in the SGF shape between SH and our comparative samples are related to PC2, which is accounting for variation in the angulation and torsion of the metaphyseal coracoid surface regarding glenoid surface. In general terms, the SH scapulae show more negative values corresponding with over twisted coracoid metaphyseal surface.

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Mousterian and Early Upper Paleolithic faunal and lithic assemblages from Llonin Cave (Northern Iberian Peninsula): inter-stratigraphical context, subsistence patterns, settlement dynamics and human-carnivore interactions

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Many caves and rockshelters have been repeatedly inhabited by Neanderthals and AMH in the Cantabrian region [1], alternating in some cases with carnivores [2]. This leads us to consider to what extent competition for shelter is a priority for these groups, which factors determines their interactions and their development of the occupations, as well as their patterns of exploitation of resources and their changes throughout the initial Upper Palaeolithic framed in MIS3.

Llonin Cave has a number of Middle and Upper Paleolithic occupations that makes it suitable for proving the patterns of change in a wide timeframe [3]. We have selected levels VI (Mousterian) and V (Gravettian) from the “Galería” with the aim of comparing both levels and interweaving fauna and lithic data. To do so, we have accomplished an archaeozoological and a lithic techno-typological study together with the taphonomic analysis related to each subject. Fauna from level VI had already been studied by us with a remarkably alternation between Neanderthals and carnivores [2], while level V is presented here for the first time. Lithics from both levels have been re-studied.

Data comparisons reveal that Mousterian and Gravettian patterns are not highly polarized. Faunal accumulations show the: 1. predominance of ungulates, mainly chamois and Iberian ibex with a lower representation of deer and a scant presence of Bovinae, 2. presence carnivores including wolf/dhole, fox, leopard, ursid and lynx. The carnivore-ungulate ratio is higher in the Mousterian than in the Gravettian assemblage, 3. predominance of carnivore marks (digested bones and tooth-marks mainly on caprine bones) over cut-marks and anthropic fractures (mainly on deer bones and increased in the Gravettian). Lithics engage similar dynamics with the: 1. predominance of local raw materials, namely quartzite and radiolarite, being allochthonous flints incorporated during the Gravettian (60-120 km away), 2. equilibrated technological groups regarding debris and blanks with a scarce representation of blades and bladelets; bladelets made on flint are increased in the Gravettian; cores are scant and not-exhausted in both Mousterian and Gravettian, 3. slight persistence of MP tools (namely racloirs) in the Gravettian and a presence of UP tools (namely burins, endscrapers and borers) in both levels although higher in the Gravettian, where backed bladelets and few La Gravette points are concentrated at the upper part of level V, 4. increase in intentioned fractures and splintering in the Gravettian.

Taphonomic alterations have been detected both in fauna and lithics in both levels, and they affect the stratigraphic integrity of the levels and the existence of non-polarized patterns should be therefore primarily associated with contaminations between the two levels. Regarding lithics, a radiolarite inter-stratigraphic refit points to a mixing in the intersection of the levels with a narrow vertical distance. This restricted contamination is outstripped by the presence of rounded lithics in both levels, although more intense in the Mousterian. It implies a secondary position for the Mousterian but the random distribution of these pieces in the stratigraphic and spatial development of both levels deserves further contaminations in which depositional processes would have intervened altogether with the carnivore and human activities, in a multiple and reiterative bidirectional process (i.e., non-rounded flint bladelets are likely intruded in the Mousterian; rounded bones and bones with carnivore marks would be in the Gravettian). On the other hand, Gravettian is only best isolated at the upper part of the level where a concentration of bladelet-tools is associated with slight hearths and where cave floor becomes more regular. With the available data, we seek to encapsulate the mixings for revealing the non-contaminated component of the assemblages and the duration of occupations.

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What Neanderthals and AMH ate in northern Iberia? Evaluation of the subsistence strategies and environmental exploitation during the Middle to Upper Palaeolithic transition

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Neanderthals and Anatomically Modern Humans (AMH) coincided temporarily in different regions of western Eurasia for at least 7,000 years [1]. However, after these first encounters, Neanderthals disappeared. It is widely accepted today that the Neanderthal demise was not a simultaneous Pan-European process, but it was produced with a regional and temporal variation.

Recent research in northern Spain [2] revealed the disappearance of Neanderthal populations in the Vasco-Cantabrian region around 48,000-45,000 cal BP, a few millennia earlier than in eastern and southern Iberia, around 42,000 cal BP. How climatic and environmental conditions could have affected ungulate prey and, therefore, Neanderthal and AMH subsistence strategies remain open.

We present an updated assessment of 17 key Vasco-Cantabrian sites with archaeological levels dated to the Late Middle and Early Upper Palaeolithic. For the first time, a general review of the macrofauna and taphonomic data available, combined with the most recent and reliable radiocarbon dates, provides a broad perspective on the palaeomammal community and insights about environmental and climatic indicators at the time late Neanderthals and AMH were living in the region, between 50,000 and 34,000 cal BP. Besides, this research identifies essential gaps of knowledge that prevent us from getting a complete regional understanding of the subsistence achieved by both human species and points the research line to undertake in this particular region.

In terms of subsistence, the results indicate how Neanderthals were influenced in their hunting decisions by the topographic location of each site, somewhat in contrast to the case of Aurignacian groups. This could imply longer travel times for AMH and motivated either to the biotope abundance in the site's proximity or just the preference for hunting diverse prey independent of the distance, allowing them to exploit specific distant taxa more efficiently. AMH would have relied more heavily on logistic mobility than Neanderthals, leading to greater travel distances during their expeditions which, in turn, would mean less residential mobility. Red deer is the most abundant and exploited taxa in this region. The ratio of carnivore accumulators varies through time. Combined occupations of Neanderthals and carnivores seems a common occurrence at Vasco-Cantabrian Mousterian sites, and it is relevant to discern the role of carnivores in the assemblages [3].

The ongoing ERC SUBSILIENCE project aims to complete this regional review by achieving further research by (1) analysing new sites, (2) applying taphonomic analysis to palaeontological and archaeological studied sites where it had not been applied before, and (3) undertaking stable isotopes on those mammals manipulated by both human species as part of their diet. In this way, we will obtain more zooarchaeological data and direct climatic and environmental data related to the surrounding areas where humans lived. The expected results will fulfil the lack of knowledge in the region and will determine the potential implications for regional patterns of resource exploitation, subsistence strategies and environmental–human relationships that may have been involved in the early demise of Neanderthals and the success of AMH.

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A microscopic analysis of bone development of the airo rhynch orangutan midface

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Orangutan facial architecture is strikingly different from African great apes due to facial kyphosis, the orientation of the face relative to the basicranium. The orangutan face is rotated dorsally and anteriorly, a condition called airo rhynch. In contrast, the face of African great apes, as well as many other Old World monkeys, is klinorhynch, or rotated ventrally and posteriorly. This difference in facial architecture is likely linked to modifications in bone modeling. Along with sutural growth, bone modeling is the process by which bones grow and model their shape [1]. It is represented by the simultaneous cellular activities of bone formation, which creates new bone, and bone resorption, which removes bone. The study of bone modeling can improve our understanding of the major ontogenetic changes that drove primate facial evolution.

Previous studies on facial bone modeling in African great apes suggest an overall similar pattern, despite some species-specific modifications, suggesting a possible shared ancestral hominid pattern [2,3]. However, this is unclear, as variation in facial bone modeling of non-human great apes has been rarely investigated with quantitative methods. Here, we contrast for the first time the maxillary patterns of bone modeling of airo rhynch and klinorhynch faces. An ontogenetic sample of 28 orangutans was compared to a sample of humans (n=59) and chimpanzees (n=33), ranging from birth to adulthood and classified into five age groups according to dental development. Bone modeling patterns were investigated on the periosteal surface and visualized as digital maps. The percentage of bone resorption was quantified for each individual using surface histology techniques. To visualize both changes in form (i.e., shape and size) and bone modeling together, semilandmark geometric morphometric techniques were employed. Mean maxillary forms were computed at each age group, and each corresponding mean bone modeling map was projected onto the latter.

Results of the surface analysis reveal that bone resorption in orangutans is located at similar locations as in chimpanzees (i.e., close to the fronto-maxillary, zygo-orbital and zygo-maxillary sutures, in the post-canine region and in the premaxilla). In young individuals, the amount of bone resorption is similar to chimpanzees of comparable ontogenetic age; however, the percentage of bone resorption rapidly decreases and becomes restricted to the sutures. During adolescence, bone formation becomes predominant in the orangutan premaxilla, while resorption is still largely present in this region in chimpanzees.

We find a shared general pattern of bone modeling between klinorhynch chimpanzees and airo rhynch orangutans. However, in contrast to klinorhynch, the development of airo rhynch is accentuated in postnatal stages by predominant bone formation. Thus, we conclude that inter-specific differences in maxillary bone modeling mostly stem from changes in timings and rates of the cellular activities. This adds to the discussion of facial bone modeling patterns of early hominins, for which clear differences between *Paranthropus* and *Australopithecus* have been found. *Paranthropus* exhibits bone resorption on the periosteal surface of the premaxilla, whereas in *Australopithecus*, this region is mainly represented by bone formation [4,5]. The results of this study suggest an ape-like maxillary bone modeling pattern in early hominins. Moreover, as in orangutans, facial prognathism in *Australopithecus* may result from low amounts of bone resorption in the premaxilla.

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Renewed excavations of Tabun Layer B: a window into the complexity of Middle Paleolithic hominin populations

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Recent paleoanthropological and genomic research has revealed the complexity of Middle Paleolithic (MP) hominin populations across Eurasia and Africa, in which current research striving to better understand their differences and similarities, as well as the nature and timing of contact between them [1]. The Levant, forming the land bridge between the continents of the Old World, constitutes a key locality in reconstructing early episodes of interactions between African and Eurasian populations. Within this framework, the significance of Tabun Cave, Mount Carmel, Israel [2,3], which forms the sole known site in the Levant that was occupied by at least two hominin populations during the MP, remains pivotal. Layer C is the principal hominin-bearing level of the three MP layers uncovered by Garrod (from bottom to top, layers D-B). The human remains include a woman's burial often defined as Neanderthal [but see 4], and a mandible, ascribed to *Homo sapiens* or archaic *Homo* [5]; and references therein]. Nonetheless, the exact stratigraphic location of the burial, whether laid at the top of Layer C or buried down from Layer B is unclear. In addition, several teeth ascribed to Neanderthals and other human bones were retrieved from Layer B.

While later excavation by Jelinek [3] provided new insights into the first half of the MP sequence, the upper part from which most hominin remains were retrieved, including the transition between layers C and B, remained unexcavated since the 1930s. Our new excavation project was initiated in 2017. Equipped with a synergy between new results, fresh from the field, and investigation of material from previous excavations at the site, we aim to trace the specific hominin populations that inhabited Tabun Cave during the second half of the MP, their chronological framework, as well as their adaptations and behavioral patterns – all with important implications for deciphering the intricate relationships and possible episodes of interactions among various hominin groups in the region.

The new excavation focuses on the inner chamber, at the very top of the stratigraphic sequence. Currently, a 2 m deep sequence was uncovered, encompassing five layers, demonstrating that what is conceived as Layer B is far from being a homogenous level. Variability is reflected in multiple aspects, including geomorphology, fauna, lithics and occurrences of burnt material. The uppermost layer preserved (Layer I) is partly cemented and includes the highest density of fauna, with only a few lithics. The underlying Layer II is composed of soft sediments and includes a high density of bones and several lithics. Layer III includes many stones of various sizes that resulted from a major episode of the expansion of the chimney that probably changed the configuration of the inner chamber from a closed to an open environment. The artifacts in this layer include primarily bones, some articulated, and stone tools and waste in small numbers. In layers IV-V lithics become more common and laminae and pockets of black, reddish and yellowish sediments within brown matrix increase gradually. Within Layer V, possibly burnt, black lumps were observed at several localities; large flint items were often found in close proximity to them.

While the research is still in progress, the series of layers identified already demonstrates the complexity of Layer B. The results show that it cannot be treated as a monolith and deposition processes, material culture, chronological framework and environmental conditions varied greatly, and should be taken into consideration when trying to grasp what Layer B represents in larger models that use this iconic site as an anchor in our investigation of human evolution and the hominins that roamed the MP Levant.

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A reliable 3D approach for identifying domestication related activities of Reindeer (*Rangifer tarandus*) based on muscle attachment sites

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Reindeer are one of the world's few semi-domesticated species and it is still unclear how and when their domestication began. Although indications of reindeer corralling date back to the 5th millennium BC [1], these can be likely regarded as hunting strategies rather than domestication attempts. The first signs of exploitation of reindeer resources and herding are dated to the Late Iron Age, as suggested by enclosure structures, bone deposits and milking evidence [2]. However, distinguishing between corralled and wild reindeer individuals has been proven challenging. In this study, we address this objective by focusing on the enthesal surfaces of reindeer specimens with documented activities [3], relying on the novel Tübingen University Validated Entheses-based Reconstruction of Activity (V.E.R.A.) method [3,5]. Entheses are defined as the areas on the bone surface where muscles or ligaments attach, and the differences in their shape and size have been linked to the habitual performance of various physical activities in both humans and animals [3,5]. Our sample consists of three modern reindeer groups that are linked to domestication activities, including 36 free-ranging (wild and undomesticated) individuals, 21 zoo (corralled) reindeer, and 8 racing reindeer associated with more specialized activities such as sleighing. We focused on various humeral and radioulnar muscles that are engaged during running and natural feeding behaviours (i.e., digging). Based on pairwise discriminant function analyses, we were able to develop equations that reached a classification rate of more than 91% for the comparison between free-ranging and zoo specimens, of 100% for the zoo versus racing group, and finally of 88% for the free-ranging versus racing group. The results of this study highlight the value of our approach for identifying domestication-related activities in archaeological contexts, proposing a new tool for identifying suspected domestication hotspots and further elucidating the interaction between humans and reindeer in the past.

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Context is Key: The case study of Umhlatuzana rockshelter, KwaZulu-Natal, South Africa

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To achieve a broader understanding of deep human history, it is crucial to define the sedimentary context in which the archaeological materials are found. The importance of comprehending the depositional history of a site and the significant role of geoarchaeology in this has long been recognized. However, many current discussions on human evolution are based on material culture, fossils, and other evidence derived from sites whose stratigraphic context has not been defined beyond a first assessment, and has not been evaluated or supported by additional analyses. Although the context of these finds in some cases is well-defined, in others our understanding of human history has been biased by problematic interpretations of the stratigraphy. Here we will discuss one such case study.

Umhlatuzana rockshelter is one of the few sites with a sequence spanning the Middle to Later Stone Age transition (~40-20 ka), making it an important site for documenting this drastic technological reorganization in southern Africa. The site was excavated in the 1980s by Jonathan Kaplan who suggested that one large-scale slumping event has impacted the integrity of the transitional MSA/LSA and the early LSA assemblages [1]. As a result, the archaeological community has been skeptical about incorporating the site's archaeological material into the general discussion on the Middle to Later Stone Age transition. In 2018, we conducted renewed excavations to clarify the site's formation processes, supported by sediment analyses, 3D spatial analyses, and soil micromorphology. Rather unexpectedly, we could not confirm Kaplan's statement that the sequence underwent any large-scale lateral sediment movement (i.e., slumping).

Here, we present our main arguments why the sediment sequence of Umhlatuzana is relatively intact and has not suffered from large-scale sediment displacement. First, analysis of the three-dimensional distribution of piece-plotted finds indicates semi-horizontal layering of archaeologically denser and more sterile zones, which would not be expected in post-depositionally translocated deposits [2]. Second, the geochemical analyses (pXRF) systematically conducted throughout the sequence reveal a smooth gradient in changes of elemental values with increasing depth for the majority of the elements [3]. In the case of large-scale sediment movement, we would expect a pattern with lateral variation in the values. Finally, we carried out micromorphological analysis in which we examined undisturbed sediment samples under a petrographic microscope. No indication for slumping was seen. Instead, we found evidence for bioturbation of the fine soil mass that did not seem to have caused significant displacement of the stone artifacts. We therefore conclude that no large-scale sediment movement has taken place in the excavated sequence of Umhlatuzana rockshelter. The understanding of the site formation processes allows us to better analyse, assess, and discuss the lithic technocomplexes of both the excavated collections shedding light on the reasons behind the Middle to Later Stone Age transition.

Umhlatuzana rockshelter is just one example in which an incorrect and weakly supported stratigraphic assessment has resulted in the discredibility of the site's collections. We anticipate that the same is true for other discredited sites. Furthermore, we expect that some sites that were initially thought to have minimal disturbance, may actually have more complex stratigraphy. Optimally, the stratigraphic evaluations of archaeological sites should always be tested using a geoarchaeological methodological approach. If this is not feasible, we recommend critically discussing existing context information of the studied material. With all the new technological advances for the study of material culture, the importance of stratigraphic provenance control is now more relevant than ever for an accurate study and interpretation of the human past.

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No sex differences during visual exploration of Lower Paleolithic tools

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Humans are specialized in eye-hand coordination and body-tool interaction through a complex visuospatial system [1]. Although manipulation has been broadly studied from an anthropological perspective, less attention has been paid to its relationship with vision. In fact, vision is the dominant source of sensory information in primates [2]. When a tool is observed, the motor areas of the brain are activated and, when grasped, it is sensed as a part of the body, with a direct influence on the neural schemes [3]. One approach to understand the underlying mechanisms behind this process is the analysis of visual attention. Attention may be influenced by “bottom up” factors such as the visual features of an image which stand out due to their sensory properties or can be directed towards regions dependent upon “top down” factors such as the importance of a feature to current task goals. On average, males and females follow distinct visual strategies. Males rely more on the general information and geometry of objects, following a bottom up strategy, while females focus more on details and characteristics, following a top down approach [4].

In this study, individuals without archaeological knowledge were asked to visually explore different stone tool replicas placed on a platform in front of them for approximately 5 seconds, including examples of worked pebbles and handaxes. Then, participants were asked to manipulate the stone tool until they reached a comfortable handle based on tactile (ergonomic) perception only. During the whole process, eye movements were recorded with a portable eye tracker. Different areas of interest based on the main tool regions were defined, namely the top, the middle region and the base, as well as cortex and knapped surface. We measured the time of fixations for each stone tool (Dwell Time, measured in milliseconds) as an indirect measure of the amount of visuospatial attention allocated by participants to distinct characteristics of the visual scene. Our results suggest that knapped areas elicit more attention than cortex. As well, the middle region triggers more attention than the top, followed by the tool base. However, we did not find any significant difference between males and females. Although visuospatial performances have been hypothesized to be involved in sexual differences associated with social roles in prehistory [5], we were not able to detect any differences at least for what concerns the variables and tools used in this survey. This study presents an empirical approach to investigate visual behaviour associated to early stone tools, providing information on the integration between brain, body and technology within an evolutionary perspective.

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Morphological variation in modern human upper premolars

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Morphological variation of human premolars is of interest within the fields of human anatomy, dental anthropology and phylogenesis [1]. While reports on the outer aspect of the teeth are abundant in the scientific literature, morphological research on 3D shape variation of premolars' crown is scarce. The examination of the enamel-dentine junction (EDJ) is advantageous with respect to the outer enamel aspect because it represents the primary developmental structures of the crown, and is worn out to a lesser degree. With this study we aim at contributing to our understanding of morphological variation of upper third and fourth premolars (UP3s and UP4s, respectively) in diverse modern human populations by using 3D imaging techniques in combination with geometric morphometrics [2]. This fundamental knowledge is crucial for the interpretation of hominin and hominoid shape variation and for taxonomic assessment.

A geographically varied sample of 74 UP3s and 73 UP4s, including African, European, South American, Southeast Asian, Oceanian, and Near Eastern specimens was considered. High-resolution scans were acquired at the Vienna micro-CT lab, and were segmented to generate 3D models for the dentinal crown and the enamel cap. Four sets of landmarks were considered [3], namely the occlusal edge of the EDJ, the cervical outline, the crown outline, and the dataset representing the entire dentinal crown combining the EDJ and the cervical outline. In both UP3s and UP4s, the fixed landmarks were set on the horn tips. In UP3s, two additional landmarks were placed at the deepest points of the mesial and distal fossae, while in the UP4s, landmarks were located at the deepest points of the mesial and distal marginal edges since the distal aspect is often represented by a flat slope rather than a depressed area. Twenty semilandmarks were used along the marginal edge. To assess shape variation within and between populations, we run a Principal Component Analysis. Two-Block Partial Least Squares analysis was used to investigate the covariation between UP3s and UP4s, as well as between data sets within tooth types. Size variation was assessed based on the natural logarithm of Centroid Sizes using a Kruskal-Wallis test.

All analyses resulted in an extensive overlap of the various populations. Along PC1 (percentage of total variance explained: UP3s = 27%; UP4s = 29%), both UP3's and UP4's dentinal crowns mainly varied between short with expanded crown base and broad, rounded occlusal aspect, or tall with reduced crown base and narrow occlusal aspect. Along PC2 (UP3s = 14%; UP4s = 18%), a relative buccal and lingual expansion of the mesial aspect of the crown base was noticeable in both P3s and P4s. We found a very high pairwise correlation ($r_1 = 0.84$) between UP3s and UP4s. The common trend of shape variation for both tooth types is to feature either a low crown with broad base and mesio-distally expanded occlusal aspect, or a tall crown with constricted base and mesio-distally narrow occlusal aspect. Low-crowned UP3s and UP4s showed tall dentinal horns, and vice versa. Oceanian individuals possessed the largest UP3s while European teeth were the smallest ($p=0.02$). However, in UP4s the smallest teeth were represented by African specimens ($p=0.02$).

This study shows that there is a broad morphological variability of modern human upper premolars shape across the world, but it is likely not associated with geographical origin and thus it is not possible to separate various populations according to their premolar shape only. The high shape correlation between UP3s and UP4s is noteworthy, considering that UP3s show prominent and steep buccal cusp and share with the canines tearing tooth function, while the UP4s' fully occluding and less sharp cusps engage more in grinding activities with the molars [4].

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Unraveling the morpho-functional traits of the Neanderthal talus

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The Neanderthal foot is mostly indistinguishable from those of *H. sapiens* in proportion and overall bone morphology, however the Neanderthal tali does have some distinctive morphological features such as a relatively larger trochlea, medial and lateral malleolar facets, broader talar head and short talar neck [1-3]. Neanderthal talar features have been interpreted as the result of the general robustness of the postcranial skeleton and/or its body mass. Alternatively, high levels of mechanical stress could have led to the development of specialized characteristics in Neanderthals, while other traits could be inherited from ancestors [1-3]. Ultimately, the interpretation of these features is still controversial. This study aims to verify if Neanderthal traits could be attributed to phylogenetic and/or behavioral factors by using an approach that combines geometric morphometrics and biomechanics of trabecular bone. External talar morphology was captured through a 3D template of 251 (semi)landmarks [4] in a sample of 10 Neanderthals and 82 *H. sapiens* (Clark Howell talus from Omo in Ethiopia, Upper Paleolithic and Holocene Hunter-gatherers, Agriculturalists, and Post-industrialists). A subsample of these tali (n=45) was selected to quantify and statistically compare site-specific bone volume fraction (BV/TV) and degree of anisotropy (DA) [5]. Ultimately, we performed a covariation analysis between point clouds of site-specific trabecular variables and surface landmark coordinates to assess if external and internal talar structures functionally adapt to the same biomechanical forces.

Results show that the external and internal talar structures do not significantly covary. The external morphology of the Neanderthal talus mixes plesiomorphic, automorphic, and functional traits. Particularly, the overall short Neanderthal talus with less inferiorly and posteriorly projecting tubercles, a more rectangular trochlea, short neck and dorsoplantarly narrow navicular facet resemble features present in Middle/early Late Pleistocene hominins, and thus they are suggestive of ancestral traits in Neanderthal tali. The broad talonavicular joint in Neanderthals may be interpreted as a mix of ancestral and functional traits, as it is similar to those of Middle/early Late Pleistocene hominins, but it also resembles those of unshod and high mobile recent hunter-gatherers. This is corroborated by the higher BV/TV in the Neanderthal talar head, suggestive of intense levels of loading, likely from high levels of mobility correlated to their presumably unshod hunter-gatherer lifestyle. Similarly, Neanderthals show an increased dorsal convexity of the trochlea, a more flared lateral and a more cupped medial malleolar facets, high BV/TV and DA along the talocrural joint. These traits are also observable in high mobile hunter-gatherer *H. sapiens* groups, suggesting that the talocrural joint is functionally constrained in both Neanderthals and *H. sapiens*. Ultimately, the Neanderthal subtalar joint shows autapomorphic features consisting in an expanded and flattened laterally posterior calcaneal facet, as well as a relatively round and joined anterior-medial calcaneal facet. These characteristics would indicate less congruent contact between the talus and calcaneus and increased subtalar instability. Furthermore, laterally flattened posterior calcaneal facet and high BV/TV and DA observed throughout the lateral side of the talus denounce increased lateral loading, suggestive of a habitually pronated foot posture that would be congruent with the hypothesized subtalar instability and lateral loading. In conclusion, this study suggests that Neanderthal tali reflect ancestral retentions, along with various adaptations to high levels

of mobility that are correlated with their presumably unshod hunter-gatherer lifestyle. Greater body mass and/ or higher mechanical stress are likely responsible for pronated foot posture during the stance phase in Neanderthals.

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Plant foods in Palaeolithic diets: nutritional relevance beyond carbohydrates

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There is ample archaeological evidence suggesting that plants were widely consumed by *Homo sapiens* during the Pleistocene [1,2]. However, most studies have considered that the main value of these plant foods lies only in the high content of available carbohydrates, particularly in underground storage organs and fruit [3,4]. Wild edible plants contain an array of other important nutrients beyond simple sugars, starch, and dietary fibre [5]. Therefore, the nutritional relevance of plant foods for hunter-gatherers could potentially be more nuanced than initially expected. To fully understand the role of plant foods on Palaeolithic diets we must therefore explore their potential value as sources of non-carbohydrate nutrients as well.

Based on published nutritional properties of wild European edible plants, we examined whether the daily nutritional requirements of a Palaeolithic *Homo sapiens* could be fulfilled based solely on a plant-based diet during different months of the year. The data regarding the nutritional values of wild plants was acquired from a nutritional composition database curated using the published nutritional values of 198 native European wild edible plant foods. These included a balanced selection of roots, stems, leaves, flowers, fruits, and seeds. We focused our analysis primarily on non-carbohydrate nutrients, including protein, fat, minerals, vitamins, and total calories. The population reference intake (PRI) values issued by the European Food Safety Association (EFSA) were used to create the estimated reference values for the daily nutritional requirements of a Palaeolithic *Homo sapiens*.

Our results indicated that plant foods contained substantial quantities of several different nutrients, enough to theoretically fulfil daily nutritional requirements throughout most of the year. During the spring, summer, and autumn months, specific combinations of leaves, seeds, fruits, and roots provide enough nutrients to fulfil daily requirements of energy, protein, fat, vitamin C, calcium, magnesium, potassium, iron, and zinc. During the winter months, most nutritional requirements can also be fulfilled solely through plant foods except for energy, fat, and zinc. Seeds and leaves were particularly nutrient rich plant parts, especially during early spring and autumn.

The nutritional relevance of plant foods extends beyond their role as sources of carbohydrates. Plants were shown to be nutritionally well-rounded foods as they are important sources of other macronutrients, vitamins, and minerals. These findings suggest that plant foods might have played a more intrinsic role in the diets of hunter-gatherers in the Pleistocene than previously thought. It is widely believed that *Homo sapiens* is a generalist omnivorous species that consumes a flexible diet in order to fulfil their nutritional requirements in variable local ecological conditions. Animal-to-plant subsistence ratios during the Palaeolithic might have fluctuated throughout the year according to the environmental availability of nutrients from specific sources, relying more heavily on plant foods during periods when their contents would have been able to sustain their daily nutritional requirements.

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The evolution of pelvic canal shape and rotational birth in humans

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The human foetus needs to rotate when passing through the tight birth canal because of the complex shape of the pelvis. In most women, the upper part, or inlet, of the birth canal has a round or mediolaterally oval shape, which is considered ideal for parturition, but it is unknown why the lower part, or outlet, of the birth canal has a pronounced anteroposteriorly oval shape. Here we show that the shape of the lower birth canal affects the ability of the pelvic floor to resist pressure exerted by the abdominal organs and the foetus.

To test our hypothesis, we created a range of 3D finite element models representing an idealised pelvic floor morphology with flat, ellipsoid and anatomically consistent sagittal profiles. The surface area of the models was kept the same, while the mediolateral diameters were varied well outside of the normal range of variation in modern women. This allowed us to include morphologies that have been removed by selection and thus are absent in modern human populations. All models were assigned material properties that were previously validated for healthy women. The same boundary conditions were applied in all finite element analyses. We found that the highest deformation, stress and strain occur in pelvic floors with a circular or mediolaterally oval shape, whereas an anteroposterior elongation increases pelvic floor stability.

This suggests that the anteroposterior oval outlet shape is an evolutionary adaptation for pelvic floor support. For the pelvic inlet, by contrast, it has long been assumed that the mediolateral dimension is constrained by the efficiency of upright locomotion. But we argue that upright stance limits the anteroposterior dimension of the inlet. A deeper inlet requires greater pelvic tilt and lumbar lordosis, which compromises spine health and the stability of upright posture. These different requirements on the pelvic inlet and outlet have led to the complex shape of the human pelvic canal and to the evolution of rotational birth.

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Functional morphology of the scaphoid of extant hominoids and fossil hominins

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The hominoid scaphoid is an integral part of the wrist bridging the proximal and distal carpal rows and helps maintain stability of the wrist joint alongside dissipating loads from the thumb during both locomotory and manipulative behaviours [1]. Variation in scaphoid morphology, including facet shape and orientation, is related to its functional role within the wrist and hand use overall, and has played a key role in hypotheses about the origin of human bipedalism and evolution of tool use. However, scaphoid morphology is irregular and complex, making it difficult to capture intra- and interspecific shape variation from linear measurements alone, potentially missing functionally-informative morphology. This study quantifies the overall morphology of the scaphoid using 3D geometric morphometrics (GM), with anatomical and sliding semi-landmarks, to assess shape differences across African apes, humans and fossil hominins. Surface models were generated from microcomputed tomography scans in a sample of *Pan troglodytes* (N=7), *Pan paniscus* (N=7), *Gorilla gorilla* (N=14), and *Homo sapiens* (N=20). Within this comparative context, we investigated the potential functional signals in scaphoid morphology in *Australopithecus sediba* (MH2), *Homo floresiensis* (LB1), *Australopithecus* sp. (StW 618), *Homo naledi* (UW 101-1726, UW 102-117R) and *Homo neanderthalensis* (Kebara 2, El Sidron SD1243 & SD258, Tabun C1). Due to slightly poorer preservation of the LB1, UW101-1726 and Tabun C1 scaphoids, multiple reconstructions of missing morphology were created in Geomagic Wrap 2021 [2], to allow for comparisons of the whole scaphoid rather than selected articular surfaces. Landmarking was done manually in Avizo 6.3 and the GM and statistical analyses were run in R using the package Morpho. Principal components analysis (PCA) using Procrustes coordinates was carried out in shape space, to quantify shape differences across species. Results of a permutational ANOVA of the extant sample reveal significant differences in shape for all pairwise comparisons, excluding bonobos and chimpanzees. The PCA yields clear separation among extant taxa; the first PC separates African apes from humans, largely reflecting the expanded trapezium-trapezoid facet in the latter, while the second PC separates *Pan* from *Gorilla*, due to a larger tubercle and more circular radial and capitate facet in the latter. When looking at the morphospace of PC1 and PC2, StW 618 falls within the *Gorilla* distribution, reflecting a more palmarly projecting tubercle (creating a deeper carpal arch) and less-expanded trapezium facet relative to other fossil hominins and humans [3]. Neandertals cluster close to extant humans, but the El Sidron specimens in particular, are distinguished by a small lunate facet. The MH2, LB1 and *H. naledi* specimens fall out as intermediate between the African ape and human distributions on PC1 and are separated from all other taxa on PC3, but each reflects a slightly different suite of scaphoid features. LB1 has a longer tubercle with a more concave trapezoid facet. *A. sediba* and *H. naledi* share greater similarity in scaphoid shape, despite temporal differences, with the trapezium facet expanding onto the tubercle and lunate facet shape but diverge in tubercle orientation and robusticity. An expanded trapezium facet allows for better force distribution on the radial side when the thumb is loaded in an abducted position [2]. This coupled with a less palmarly-oriented tubercle suggests a scaphoid morphology better adapted for tool production [3,4,5]. Each of the fossil scaphoids examined show different combinations of joint shape and orientation indicating the evolution of hominin wrist occurred in a mosaic manner in response to potentially different locomotory and manipulative capabilities.

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A 3D morphometric approach to skull integration and modularity in *Pan troglodytes* and *Homo sapiens*

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Cranial integration and modularity studies aim to analyse the covariation and interaction of the different bony structures that make up the cranium. The craniofacial morphology of Hominidae is largely variable and presents a series of integration patterns that may be due to both intraspecific and interspecific factors [1]. One of the keys to understanding the evolutionary mechanisms of our genus is to identify and quantify which integration patterns are shared and whether these can be applied to fossil species [2]. In the past decades, thanks to the application of new techniques and digital tools (mainly 3D), it has been possible to approach this problem from new perspectives. However, delving into studies about skull integration and modularity is crucial because of the complex interaction of individual bones in the integration of the whole system [3]. The aim of this work is to quantify the covariation patterns of the different cranial bones and modules of the two phylogenetically closest extant Hominidae species: *Homo sapiens* and *Pan troglodytes*. The main goal is to detect shared or species-specific integration patterns that can later be applied to extinct hominin species.

For this purpose, we conducted a Procrustes-based 3DGM study on the cranial surface of a sex-balanced sample of 40 adult individuals of both species. We have defined 6 regions -viscero-cranium, frontal, parietal, temporal, occipital and sphenoid - using 65 landmarks that collect homologous osteometric points and 367 curves, as well as 949 surface sliding semi-landmarks that detail the shape of the surface not measurable by the landmarks. To establish the integration patterns of both species and observe which of them are common and which are species-specific, we used the two-block partial least squares (PLS) method pooled by species [4]. This enabled us to obtain the RV coefficient between each bony structure and to create a covariation matrix between each 6 regions. To explore whether the observed patterns are shared or species-specific, we explored the slope of the PLS1 scores through a Bootstrap estimation of 95% confidence interval of the slope in each species [5].

The results obtained show that each of the 6 bone structures show significant covariation. The RVs range from 0.3-0.8 and each one shows a p-value of <0.0001, suggesting that the entire skull works like an integral functional system. The 30 modules tested also present significant covariations with RVs ranging between 0.3-0.7 and p-values of <0.0001. It should be noted that the full skull structures module configuration that provided the highest integration index, as suggested by previous studies, is composed by the (i) viscero-cranium and occipital block, and (ii) parietal, temporal and frontal block; with the sphenoid playing an important role in both of them. Even if this bone is placed in one block or the other, his location did not substantially alter the covariation index, but it does have an impact on the slopes that suggest shared or species-specific patterns. This 2-block modular configuration covariation seems shared by both species, thus making these shared morphological patterns very useful to explore covariation patterns in fossil human species.

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Inferring hand use in *Australopithecus sediba*: Analysis of the external and internal morphology of hominin proximal and intermediate phalanges

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The evolution of hominin hand use is characterized by a transition from locomotion to primarily dexterous hand use. However, this transition remains unclear with discoveries of hominin hand fossils evidencing a diverse range of manual behaviors. The almost complete right hand of *Australopithecus sediba* (1.98 Ma) shows a unique mix of primitive and derived morphology; an exceptionally long thumb and broad distal phalanx suggest human-like manipulative abilities, while curved phalanges and well-developed flexor sheath ridges (FSRs) on the proximal and, unusually, intermediate phalanges, suggest the continued importance of arboreality [1]. We used microCT scans to analyze the external and internal morphology of the non-pollical proximal and intermediate phalanges in *Gorilla gorilla* (N=12), *Homo sapiens* (N=14), *Pongo pygmaeus* (N=17), *Pan* sp. (N=18), and *A. sediba* (MH2). We quantified the degree of curvature via included angle [2], and variation in FSR morphology via linear measurements. We also assessed the cross-sectional cortical bone properties throughout the shaft using BoneJ [including cross-sectional area, polar section modulus (Zpol), and polar second moment of area (J)] [3] and mapped variation in cortical thickness using Morphomap [3].

Results reveal curvature in the proximal and intermediate phalanges is lowest in *Homo* followed by, in an increasing order, *Gorilla*, *Pan*, and *Pongo*. The proximal and intermediate phalanges of *A. sediba* have intermediate values of curvature, falling within the African ape range, exceeding mean values of *Gorilla* and falling below mean values of *Pan*. After controlling for size, *Gorilla* has the shortest (in length) but the most prominent (deepest) and widest FSRs and humans FSRs are short, lacking depth and width, while *Pongo* and *Pan* share morphology that is longer but intermediate in width and depth, for both proximal and intermediate phalanges. In *A. sediba*, the proximal phalanx FSRs are most similar to *Gorilla*, but longer, while the intermediate phalanges are distinct in having proximal phalanx-like morphology, such that they lack a median bar, and possessing FSRs that are deeper than the mean values of each extant species.

The cortical bone analysis indicates that *Gorilla* has the highest values across all cross-sectional properties while humans have the lowest, and *Pongo* and *Pan* are intermediate, for both the proximal and intermediate phalanges. *A. sediba* is characterized by low cross-sectional values similar to those observed in humans. Initial bone distribution analysis demonstrates that cortical bone is thicker palmarly in great apes and dorsally in humans, in both intermediate and proximal phalanges. Consistent with the human-like CSG properties, *A. sediba* also has a thicker cortex dorsally. The low CSG properties in the fingers of *A. sediba* indicate limited strength compared to great apes, which may suggest its hands were not adapted for high loads incurred upon the hand during climbing or suspension. However, this internal structure is combined with African ape-like curvature, which provides better distribution of the stress experienced during suspension [5], and prominent FSRs, which help reduce strains on the shaft of the phalanges [5]. Thus, the external morphology of the *A. sediba* phalanges indicate a hand uniquely adapted for arboreal locomotion but one that lacked the cortical robusticity of extant great apes. This suggests that either arboreal behaviors may not have constituted a large part of the *A. sediba* locomotor repertoire, or that the mechanical loads of this behavior were resisted in a manner different to great apes, or some combination of both.

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How luminescence dating highlights the earliest known prehistoric occupations of the Central Aegean (Stélida, Naxos island, Greece)

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Thanks to both archaeological study and luminescence dating conducted on Stélida (Naxos, Greece) since 2013 within the framework of the SNAP project (Stélida Naxos Archaeological Project) initiated by Tristan Carter and Dimitris Athanasoulis, the early arrival of populations during the Paleolithic to the islands of the Aegean basin and more particularly to the Cycladic islands is confirmed. This discovery challenges a long-standing dominant model that the Cycladic islands were not occupied until the Mesolithic.

First lithics discoveries in both surface and stratigraphy indicates an early occupation of the site because of the presence of Lower and Middle Paleolithic artefacts. But these discoveries need to be associated with numeric dating of the site in order to establish a clear chronological framework. Due to the a priori chronological significance and the absence of organic materials, the OSL (Optically Stimulated Luminescence) dating method was considered the most relevant approach. Despite the complex taphonomy of this sloping site (located on a hill) it was through luminescence dating that the first chronological information could be obtained, correlating with lithic tools found in the dated levels.

Due to the lack of sensitivity of quartz during luminescence measurements, a first chronological framework of the site was established by different IRSL (Infrared Stimulated Luminescence) measurements called pIRIR290 multi-grain and single-grain, on a dozen of samples of K-feldspars from three trenches (DG-A/001, DG-A/021 and SH/024), located on different parts of the hill. These measurements allowed us to obtain ages indicating the time of last exposure to light of the sediments, which means their last remobilization.

The dates of the last geological events of the dated levels, in which lithic industries were discovered, are interpreted as terminus post quem. The multi-grains and single-grains ages are in good correlation, and are also coherent stratigraphically, and thus enrich the study of the site, giving more information on its geological and archaeological history, demonstrating especially that this site experienced human occupations at least about 200,000 years ago [1].

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The human and Neanderthal first metacarpal: external shape, cross-sectional geometry and their co-variation

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Studies of fossil hominin hands are important for understanding the selective pressures that have ultimately culminated in the observed dexterity of the modern human hand [1]. However, the extent to which external morphology correlates with measures of the internal structure of hand bones, and how these in turn are related to mechanical loading during life [2], is poorly understood. Here we analyse the external shape and cross-sectional geometry of the first metacarpal (Mc1) in a sample of geographically and temporally diverse *Homo sapiens* and a *Homo neanderthalensis* specimen. The recent modern human sample (n=24) includes: pre-industrial humans from America, Australia, the Chatham Islands, and Egypt; post-industrial humans from an 18-19th Century German cemetery; and humans from the medieval shipwreck of the Mary Rose, where all individuals are assumed to be males that were melee infantry, archers, gunners or mariners [3]. The fossil *Homo sapiens* specimens (Qafzeh 9 and Arené Candide 2) and the Neanderthal specimen (Kebara 2), are all thought to have engaged in more intense manual activity than recent humans [1,4]. It is hypothesised that the pre-industrial humans, Mary Rose individuals, fossil *H. sapiens* and the Neanderthal will exhibit greater shape and cortical robusticity of the Mc1 than the post-industrial modern human group [1,3].

3D surface models and cross-sections of each Mc1 were obtained from micro computed tomography/X-ray microscopy scans. 3D anatomical and sliding semi-landmarks were used to perform a geometric morphometric (GM) analysis of Mc1 articular surface and diaphyseal shape (using the Morpho package in R). Using BoneJ, cross-sections at 33%, 50% and 66% of diaphysis length were analysed to measure cross sectional area (CSA) and the second polar moment of area (J). Principal component analysis (PCA) was carried out on both the 3D GM data and the cross-sectional geometry (CSG) variables, respectively. CSA and J were both regressed on each of the first three principal components of first metacarpal shape.

A PCA of the CSG variables revealed that among the modern human sample the Mary Rose specimens displayed the highest mean levels of CSA and J associated with high resistance to torsional deformation, and inferred intense manual loading of Mc1. The Neanderthal and fossil *H. sapiens* both closely clustered around the Mary Rose group, suggesting that these fossil individuals were all undertaking similar levels of intense manual activity, which could be driven by the frequent adoption of transverse power-grips [3]. Unexpectedly, the pre-industrial modern humans demonstrated significantly lower values of CSA and J than the Mary Rose sample, and overlapped with only some of the post-industrial modern human samples. A PCA of Mc1 shape revealed morphological similarities across the Mary Rose sample, fossil *H. sapiens*, the Kebara Neanderthal and some of the post-industrial modern humans. This group appears to share relatively robust Mc1 shafts and enlarged proximal and distal articular surfaces compared with pre-industrial modern humans. The Kebara Neanderthal was also slightly differentiated by the pronounced lateral flange associated with the *opponens pollicis* entheses. Regressions of cross-sectional geometry variables on Mc1 shape variables revealed a number of significant but relatively weak relationships (R^2 values between ~0.16-0.18), indicating a link between aspects of shaft shape and cortical bone distribution. In summary, our results provide further evidence for the impact of manipulative behaviour on thumb shape and structure [e.g., see 5], yet more investigation is needed to ascertain the exact nature of this relationship.

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Chimpanzees fail to spontaneously produce and use sharp-edged stone tools

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Human cultural evolution requires the ability to copy know-how – i.e., the ability to reproduce the behaviour and/or the outcomes of the behaviour of others. When did we start to copy know-how? One viewpoint holds that the ability to copy know-how coincides with the first sharp-edged stone tools used in our lineage. Thus, it has become of interest to determine whether techniques to produce and use sharp-edged stone tools require know-how copying or whether this know-how could have come about in other ways.

The main alternative view is that the know-how underlying these tools and their usage could have been the outcome of biologically evolved abilities (adaptations/exaptations) – with social learning merely leading to socially influenced networks (i.e., cultures) of agents who then show this know-how, but who have not copied this know-how from others. These are cultures, as social influences play a discernible role, but they are “minimal cultures”. Here, the social factor (instead of know-how copying) is socially mediated – but individual – reinnovation of said know-how.

This view requires that the know-how underlying sharp-edged stone tools can principally reoccur in the absence of social access to know-how (at least provided the internal and external conditions are suitable). And indeed, studies in the 1990s have shown that both the production and usage of sharp-edged stone tools – that is, the underlying know-how – reappears from scratch in baseline tests of task-naïve, unenculturated capuchin monkeys. What remains unknown is whether our closest living relatives – the non-human great apes – are likewise able to produce and use these tools in appropriate baseline conditions.

Here we tested – for the first time – whether non-human great apes are likewise spontaneously able to innovate the necessary know-how to produce and use sharp stone tools [1]. This required us to test apes that had not been enculturated by humans and who had not received know-how demonstrations prior to test. The previously available studies introduced stable test methods (which we copied), but they tested highly to semi-enculturated apes and they invariably tested these apes after human demonstrations had been given (and in some cases, even after physical guidance had been given). We also noted that chimpanzees have never been tested in such tasks – despite showing the highest levels of tool use of any wild ape.

And so, here we tested eleven task-naïve chimpanzees – in the absence of human demonstrations and human physical guiding, for their spontaneous reinnovation of the underlying know-how of sharp-edged stone tool production and usage. Most relevant for our results are the data from eight of our test subjects as for these we can be certain that they were unenculturated (the remaining three chimpanzees had unclear backgrounds in this respect).

All tested apes proved motivated to engage in the tasks given, but not a single chimpanzee spontaneously made or used sharp-edge stone tools. Our results stand in sharp contrast to the positive outcomes of earlier ape sharp stone tool experiments. But, again, all three apes that were previously tested (one orangutan and two bonobos) had received human enculturation (at least to some degree) and all had received human know-how demonstrations prior to their test (even, sometimes, physical guidance). We conclude that human enculturation and/or human know-how demonstrations (or physical guidance) are likely necessary before apes begin to show sharp-edged stone tool know-how. These factors were however absent in our ancestors. We conclude that sharp-edged stone tool manufacture and use know-how has likely evolved in the hominin lineage after the split between *Homo* and *Pan*. Other current projects of ours continue to aim to triangulate an answer to the question of what type(s) of evolution were responsible (cultural or biological evolution, or both, perhaps via “minimal cultural drive”).

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Notes: We are not criticising the quality of earlier studies (we indeed took over their underlying methods). We are merely highlighting that these studies answered a different question from the one that we were interested in. They answered the question what apes can do in such tasks after human enculturation and human demonstrations. Our study answered a question of spontaneous abilities.

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Aurignacian subsistence strategies at Fumane Cave between 41-37ky cal BP

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The Aurignacian dispersal to Mediterranean Europe may have followed various routes. One of those routes has been proposed to have been undertaken along the Southern Alps, possibly through the Eastern Alps and the Northern Adriatic region, around 42-41,000 cal BP, where AMH had to overcome different ecological and physical barriers. The presence of ProtoAurignacian groups is evident in the Veneto Pre-Alps, where several sites, including Fumane, Tagliente, Pàina and in the Ligurian Alps, Bombrini and Mochi reveal multiple occupations. However, despite the considerable amount of information documented for lithic and bone technology and improved sample treatments in ¹⁴C dating method, subsistence data and evaluation of human adaptation to climate change are still limited. High-resolution regional signatures are thus needed to provide insights on human-environmental interactions during the early dispersal of AMH. For this purpose, the Fumane cave, located in northeastern Italy, offers an excellent opportunity to compare two well-documented and recently dated Aurignacian units and compare them with coeval regional sites. Here, we present the new dates and the subsistence strategies achieved by those humans during the Protoaurignacian (units A2-A1) and Late Protoaurignacian (D3) at the site. Both lithic industries share a common technological background especially in bladelet production [1,2]. Although a broad spectrum of mammals is represented, alpine ibex (*Capra ibex*) and chamois (*Rupicapra rupicapra*) are the primary prey taxa, which suggest cold and dry conditions in these units. Compared to the late Mousterian context, this data reflects a decrease in woodland environments and climatic cooling [3]. The presence of newborn remains of both taxa point, at least, spring human occupations. A high frequency of anthropogenic manipulation on herbivores and even carnivores, such as *Vulpes vulpes* and *Canis lupus* is documented. These results indicate that the Fumane cave was a preferred place for a wide range of activities, including intensive exploitation of ungulate prey for meat, marrow, and fat resources and the production and maintenance of artefacts as personal ornaments, bone and lithic tools. In a regional context in Northern Italy, multi-environmental proxies (macro/micromammals, avifauna, pollen) of coeval sites show that the Early Upper Palaeolithic (Uluzzian and Aurignacian) was associated with a shift to colder and arid climatic conditions, which forced human groups to exploit open environments, alpine meadows and cliffs [4]. How these conditions affected the environment's carrying capacity, and thus the subsistence adopted by AMH will be replied with the ongoing stable isotopic analysis on mammals along the complete stratigraphic sequence. The stable isotopic results will provide a more objective palaeoecological and palaeoclimatic comparison in adaptive human strategies. Altogether, these outcomes and more to come within the ERC SUBSILIENCE project are providing new evidence about paleoeconomic strategies adopted by the early modern humans in northeast Italy.

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New reconstruction of the pelvis of KNM-WT 15000 supports a wide body shape for Early African *H. erectus*

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The origin of the slender body shape of *H. sapiens* has intrigued paleoanthropologists for a long time, and several scenarios have been proposed to elucidate when and how this morphology emerged in the human lineage (1). The cylindrical thermoregulatory model supports that this body shape emerged ~2 million years ago (deep evolutionary origin) in early African *H. erectus* (namely *H. ergaster*) as an adaptation to the climate of the regions inhabited by this species. An alternative model suggests that this body shape emerged in *H. sapiens* (recent evolutionary origin), with *H. neanderthalensis* and early African *H. erectus* sharing a wide body shape consistent with high metabolic rates. A third scenario might be compatible with the two-body morphologies previously proposed as support for the existence of a great post-cranial morphological diversity in *H. erectus* (2). The well-preserved skeleton of KNM-WT 15000, a juvenile male early African *H. erectus* dated to the Lower Pleistocene (1.6 Ma), is a key fossil for understanding the origin and evolution of body shape in *Homo*. However, despite its relevance, no quantitative reconstruction of the torso of this specimen has been carried out to date. This is the aim of the current investigation. Due to the young age at death of KNM-WT 15000, 3D torso models of an ontogenetic *H. sapiens* male sample composed of 22 juveniles (7-12 y.o), 15 adolescents (13-19 y.o) and 15 adults (20-44 y.o), and 10 adult *P. troglodytes* were segmented from CT scans. One thousand and thirty (1030) landmarks and semilandmarks were measured on the resulting models to collect overall thoracic and pelvic anatomical relationships within the torso. Patterns of thoraco-pelvic morphological covariation were computed using two-block partial least squares analyses and combining the ontogenetic groups with each other and with the chimpanzee sample to assess patterns of covariation shared by these two taxa and probably maintained since the last common ancestor *Pan-Homo* (3). The statistically significant models were used to predict the pelvic morphology of KNM-WT 15000 from its previously reconstructed thoracic morphology (4). Additionally, a *H. sapiens* ontogenetic shape vector was applied to simulate the hypothetical adult pelvic morphologies. The resulting pelves were compared with previous reconstructions of *Australopithecus* and *Homo* pelves by means of principal component analysis and clustering methods based on Procrustes distances between specimens. Three models showed statistically significant (s.s) covariation: 1) adult *H. sapiens* (70% s.s covariation), 2) juveniles-adolescents-adults *H. sapiens* (90% of s.s. covariation), and 3) the latter pooled with *P. troglodytes* (90% of s.s covariation). The first two models yielded *H. sapiens*-like pelvic morphologies characterized by mediolaterally narrow pelves with vertically oriented iliac blades and short and narrow ischiopubic regions. The third model produced a pelvis with marked iliac flaring and orientation that shows affinity with the pelves of *H. neanderthalensis* and *H. heidelbergensis*, although the short and narrow ischiopubic region is indistinguishable from that of *H. sapiens*. The marked iliac flaring of the pelvis resulting from the third s.s. model is consistent with previous reconstructions (5) and shows the morphology that might most resemble KNM-WT 15000; evolutionarily, because it comes from a statistical model that overarches thoraco-pelvic covariation probably maintained in the human lineage and anatomically, because the iliac morphology and orientation are compatible with the long femoral neck of KNM-WT 15000 and its mediolaterally wide thoracic morphology, which was aligned with the pelvis. The resulting torso supports a wide (and deep) body shape for KNM-WT 15000 consistent with high body weight and metabolic rate in early African *H. erectus*. This reconstruction lays the ground for functional interpretations that must be evaluated with appropriate methods in future studies.

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The primitive morphology of the Indonesian *Homo erectus* cochlea

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Housed in the petrosal portion of the temporal bone, the inner ear bony labyrinth holds morphological information that has been used to reconstruct phylogenetic relationships, to ascertain taxonomic affinities [1], and to infer locomotor behaviors [2] and hearing capabilities [3]. Cochlear shape has been proven useful to ascertain the taxonomy and phylogeny of fossil hominins [4,5]. Based on the analysis of the cochlear morphology, previous analyses have identified patterns of shape variation among Middle and Late Pleistocene hominins. However, the use of different morphometric methods and sample compositions has prevented a comprehensive reconstruction of the evolutionary history of the inner ear in Early Pleistocene species of *Homo*. This is certainly the case for Asian *Homo erectus*, and in particular regarding the morphological characterization of cochlear shape as compared with earlier and later hominins.

Here we analyze the cochlear morphology of two Indonesian *H. erectus* individuals (Sangiran 2 and 4) by means of linear measurements and canonical variate analysis performed on shape ratios, and compare them with a sample of australopiths (n=10), South African early *Homo* (n=2), European Middle Pleistocene *Homo* (n=10), Neanderthals (n=7) and extant humans (n=10). Our results show that Indonesian *H. erectus* possesses a combination of primitive and derived features relative to Middle and Late Pleistocene *Homo*. Both specimens exhibit a large cochlear volume (larger in Sangiran 4 than in Sangiran 2) and a low number of cochlear turns, as in modern humans. Conversely, the two Sangiran specimens display a chimp-like rounded cross section and a low cochlear thickness (intermediate between chimpanzees and Pleistocene hominins). Sangiran individuals also possess low cochlear coiling height, a feature that is also shared with australopiths, indicating that Indonesian *H. erectus* retains several hominin symplesiomorphies in comparison with later occurring *Homo*. In addition, we identify an evolutionary trend from a low cochlear height in australopiths and Early and Middle Pleistocene *Homo*, towards a taller coiling in Neanderthals and modern humans. The present analysis also recovers a substantial degree of variation between the two individuals, with Sangiran 2 sharing some similarities with australopiths and Sima de los Huesos individuals and Sangiran 4 with modern humans. From a functional perspective, the low and high frequency limits inferred suggest that Indonesian *H. erectus* hearing capabilities were most similar to those of Neanderthals and modern humans, particularly in Sangiran 4, rather than those of earlier hominins.

However, the present results should be interpreted with caution, because they represent a preliminary inspection of *H. erectus* shape variation based on two specimens only. Nevertheless, the observed variability in the Sangiran individuals, together with that of early *Homo*, suggests the presence of a larger variability relative to that of later representatives of the genus. Overall, the results demonstrate that most characters found in later hominins were already present in Indonesian *H. erectus*, with the remarkable exception of Neanderthals, which show an autapomorphic condition.

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Comparison of the arm-lowering performance between *Gorilla* and *Homo*

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Comparative studies indicate that shoulder morphology is correlated with locomotor and positional behaviours within primates [1]. Non-human apes and acrobatic monkeys share certain morphological shoulder features that have traditionally been understood as arboreal adaptations (specifically, vertical climbing and/or suspension). Earlier proposals linked features like a cranially oriented scapular spine and glenoid and a projecting acromion process to greater arm abduction potential and increased arm-raising performance in non-human apes, compared to humans. However, our recent biomechanical analysis comparing glenohumeral abductors of *Homo* and *Gorilla* highlights that arm-raising performance is similar in both species [2]. Instead, some differences in skeletal structure affect the action predicted for certain muscles, such that muscles acting as abductors in humans are primarily adductors in gorillas. These results led us to further investigate a new interpretation of some long-documented morphological differences between humans and apes: namely, that these features enhance the arm-lowering, rather than the arm-raising mechanism.

Musculoskeletal models allow us to predict the performance capability of a musculoskeletal system and to quantify the impact of muscle soft tissue properties and musculoskeletal morphology. In this study, we extend the previously published musculoskeletal model of a gorilla shoulder [2] by adding glenohumeral adductor and retractor muscles, then comparing the arm-lowering performance to that of an existing human model [3]. Additionally, we compare the gorilla model predictions to shoulder kinematics reported for quadrupedal walking and vertical climbing in non-human apes [4,5].

Our results suggest that differences in shoulder configuration between *Gorilla* and *Homo* have a great impact on arm-lowering performance, and some morphological differences have greater functional consequences than others. The action of the two main arm-lowering muscles, teres major and pectoralis major, is enhanced through both greater soft tissue properties and advantageous shoulder morphology in *Gorilla* compared to *Homo*. With regard to bone morphology, a more distal insertion on the humerus especially enhances arm-lowering performance, which is further amplified by the cranially facing glenoid and elongated scapular blade. Therefore, our findings support the interpretation that gorilla-specific shoulder morphology enhances arm-lowering performance.

The arm-lowering mechanism is used during the propulsive phases of vertical climbing, suspension and quadrupedal walking of gorillas and other non-human apes [4,5]. Its importance is further supported by EMG studies that report high activity of the arm-lowering muscles during these phases. Our biomechanical analysis reveals that teres major and pectoralis major display the highest arm-lowering capabilities across glenohumeral angles used during quadrupedal walking and vertical climbing. This correlation of muscle activity, high performance capability and locomotor kinematics highlights the link between shoulder musculoskeletal morphology and function.

In conclusion, this study reveals a greater arm-lowering capability of the gorilla musculoskeletal shoulder system that is enhanced through morphological and soft-tissue properties compared to *Homo*. The correlation of enhanced arm-lowering performance capability and kinematics highlights the importance of the arm-lowering mechanism for *Gorilla* and other non-human ape locomotion. These results advance our understanding of adaptation in living apes and can improve functional interpretations of the hominin fossil record.

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Covariation of proximal finger and toe phalanges in *Homo sapiens*: a novel approach to assess covariation of serially homologous structures

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As hands and feet are serially repeated homologous elements in tetrapods [1,2], the morphology of fingers and toes is expected to covary due to a shared developmental origin [3]. Hominins and great apes have been shown to exhibit reduced integration between the limbs when compared to quadrupedal monkeys [4], which is linked to a functional differentiation between the fore- and hindlimbs in these taxa. The present study focuses on the covariation of the shape of proximal finger and toe phalanges of adult *Homo sapiens* of various phenotypes to determine whether covariation is different in the first ray relative to the others.

Proximal phalanges of 76 individuals were digitized using a NextEngine surface scanner. Landmarks were positioned on 3D surface models of the phalanges. Generalised Procrustes superimposition and two-block partial least squares analyses (PLS) were conducted. Angles of the PLS vectors were computed for each ray in the hand and the foot and compared using principal coordinate analysis (PCoA).

The novel statistical approach introduced herein is based on a PCoA of the angles between PLS axes in morphospace. The results, being graphical, are easy to interpret and provide valuable information on the nature of covariation.

Covariation between hands and feet is associated with robusticity in all five rays. The difference in PCo scores between the first and the other rays indicates that the developmental integration between the thumb and the big toe is different from that between the lateral rays of the hand and foot.

The patterns of covariation suggest the evolution of the human hand was influenced by foot evolution, but not regarding all aspects. The big toe and the thumb are less integrated with the lateral phalanges, than the lateral phalanges amongst each other. This is possibly the evolutionary consequence of differential selection pressure on the big toe relative to the other toes related to the rise of bipedalism in the human lineage. The thumb, on the other hand, was under less strong selection pressures related to the evolution of the precision grip.

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Carnivore interactions in the formation of a palimpsest using Artificial Intelligence tools: a taphonomic analysis of FLK North (Olduvai Gorge, Tanzania)

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Anthropogenic (i.e., hominin accumulated and modified) archaeofaunal assemblages are marginal in the early Pleistocene archaeological record. Most commonly, palimpsests formed by the intervention -and, sometimes, interaction- of different carnivore types and hominins have been documented in Olduvai Gorge's (Tanzania) Bed I & II sites [1]. Reconstructing the behavior of the early Pleistocene hominins of Olduvai Gorge and understanding carnivore and hominin interactions at these sites have been two of the main questions addressed in taphonomic research over years [1-3]. FLK North (FLK N) site is one of the best examples of a palimpsest at Olduvai, where felids were the main agent responsible for the accumulation of carcasses, followed by hyenids that modified intensively the assemblage, and where hominin activity was marginal [1]. In this study, we intend to test previous interpretations of the formation of FLK N using Artificial Intelligence (AI) tools to taxonomically discriminate bone surface modifications (BSM), namely, tooth marks. The objectives of this work are: 1) to test that both felids and hyenids participated in bone modification at this site, 2) to understand better the interaction between those agents, and 3) to provide new data to the existing debate on the participation of various agents in a palimpsest. Hyenids and felids modify bones differently and consequently it is possible to know which carnivore agent generates or modifies an accumulation and the order of intervention. However, it is known that under special conditions the pattern of modification of those agents can coincide and the identification made by human experts is rather limited since the anatomical location of damage can be identical. In such cases, discrimination of tooth marks according to carnivore agent could be a potential way to overcome equifinality. Recently, AI tools deployed to analyze bidimensional images of BSM have yielded high accuracy in the classification of BSM [4]. AI methods applied to different carnivores have succeeded in providing good discrimination among taxa, especially when comparing felids and hyenids, where an accuracy >90% in correctly identifying tooth marks made by hyenas and those from lions has been reported [5]. The AI analysis of carnivore BSM from FLK N has validated the results previously obtained using traditional techniques, underscoring the intensive damage of hyenas and the more discrete modification created by felids.

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A close look at artifacts' biographies: Lower Paleolithic patinated flint tools from Late Acheulean Revadim, Israel

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Lithic tools can survive time and space. This characteristic enables them to keep their biography and memory of the people who dealt with them alive. Biographical information embedded in lithic artifacts can be unraveled by examining patina of age, wear signs, and manufacturing processes they underwent during their production, use, disposal and, in the case of certain items, also during their re-collection and re-use.

Following these assumptions, flint items exhibiting modified patinated surfaces ("double patina", or post-patination flaked items) are the ideal candidates for discussing lithic recycling, stone economy, item's biography, and human choices. Different life cycles of such items are visually evident by the presence of fresh new modified surfaces alongside old patinated ones (according to color and texture differences). New modifications testify to a gap in time between the previous life cycle of the patinated flaked item and its new one. Here, we discuss the phenomenon of shaped patinated flaked items from Late Acheulean Revadim (Israel) and we reconstruct the functional aspects of their old and new life cycles. This goal is achieved by using use-wear and residue analyses and drawing on theoretical and methodological advancements in reconstructing their probable ontological/cosmological role in the worldviews of the Revadim inhabitants. The results of the functional study show that the process of choosing, collecting, and minimally shaping old patinated items was not a mere opportunistic adaptation, but rather a culturally-based behavior, most probably coupled with practical needs.

This study is significant in so far as it offers food for thought for the comprehension of different aspects of early human behavior and human adaptations, with respect to decision-making, utilitarian behavioral aspects, planning of activities, as well as perceptions on human-object relationships, human-landscape relationships, time and memory. Last but not least, this study provides a glimpse into Paleolithic recycling, attempting to explore the reasons behind a cultural behavior that is as old (and still actual) as the history of mankind.

Before and after Marine Isotopic Stage 7: the human remains from the Coupe-Gorge Cave (Montmaurin, France)

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In France, the calcareous outcrop of Montmaurin-Lespugue was well known by prehistorians from WWII. Louis Méroc carried out excavations in the cavities of the massif on the right bank of the Seygouade River from 1946 to 1961 [1]. In 1949, just after the discovery of the famous human mandible of Montmaurin, in the locality of La Niche, he brought to light abundant archaeological material from the cave of Coupe-Gorge, situated 12 meters away, roughly on the same middle karstic level, at 28 m of altitude above the modern riverbed. Apart from the faunal remains and lithic artefacts, several human remains were discovered: one right maxillary bone (bearing C, P3, P4), a fragmentary juvenile mandible (the symphysis part) and 3 isolated teeth [2,3].

Thanks to some archival documents, we were able to replace them within the stratigraphy. Moreover, in the context of new excavations (2020-2022), we have undertaken to specify the chronological framework of the stratigraphic sequence, which is about 7 m thick.

Here, we present preliminary results of the chronological attribution of these fossils as well as the morphological assessment of the remains and its comparison with other Middle Pleistocene (MP) populations and with Neanderthals.

Regarding the chronology, the mandibular fragment and the left upper P4 were discovered in Méroc's level 3z, overlying the upper stalagmitic floor (PS-1) attributed by U-series to MIS 7, whereas the right lower molar was found just below. The right maxilla and the left upper canine were located below the lower stalagmitic floor (PS-2), and are thus older than MIS 7. The morphological assessment of Coupe-Gorge dental remains identified a "classic" Neanderthal morphology showing for example a continuous middle trigonid crest and a pronounced anterior fovea in the mandibular first molar, and a strong expression of the tuberculum dentale in the maxillary canine, and bifurcated buccal essential crest in the maxillary premolars. A suite of traits also recorded in MP samples from Sima de los Huesos, Biache-Saint-Vaast and Montmaurin-La Niche. However, as the mandible from this latter site [4,5], the maxillary bone from Coupe-Gorge is not fully Neanderthal-like even if it shows a medial projection on the internal lateral wall of the nasal cavity and a bi-level nasal floor. Indeed, the surface of the maxillary bone is not totally inflated evidencing a less projected face than in "classic" Neanderthals. It suggests that the Montmaurin fossil hominins could represent a more primitive group within the MP populations.

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A tight squeeze for chimpanzees: the role of joint laxity and fetal head orientation during birth

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The assumption that great apes possess a spacious birth canal enabling a relatively easy birth is frequently contrasted with the narrower cephalopelvic fit and the accompanying elaborate, more precarious birth pattern of modern humans. The "obstetrical dilemma" hypothesis argues that this pronounced degree of birth difficulty in humans stems from an evolutionary trade-off between the reduction of the anteroposterior pelvic diameter related to bipedal locomotion and the need for the female pelvis to retain obstetrically sufficient dimensions required to give birth to large-brained infants [1]. In chimpanzees, the reported smaller cephalopelvic ratio does not seem to be attributable to a small fetal head size since their neonatal to adult head size ratio is comparable to macaques which have neonatal head sizes that exceed the pelvic canal dimensions, requiring extensive ligamentous laxity. The cephalopelvic ratio is traditionally calculated using the pelvic inlet diameters and the maximum fetal head diameters in neutral head position [2]. However, these measures are not obstetrically relevant in chimpanzees because their pelvic inlet is obliquely oriented to the birth trajectory, rendering the perpendicular diameter of the birth canal at the pelvic midplane the narrowest dimension. Additionally, the fetal head is typically flexed or extended during birth, which significantly reduces its cross-sectional area [3].

This study performed virtual simulations based on 3D models to measure the space allocated to the chimpanzee fetal head with respect to the maternal pelvis, providing a realistic approximation of soft tissue thickness between the bony pelvic wall and the skull. Our simulations included previously unaccounted for parameters like fetal head orientation and sacral nutation, i.e., the backwards rotation of the tip of the sacrum afforded by sacroiliac joint laxity. The sample consisted of 17 adult female chimpanzee pelves that were landmarked (n=104) to generate a mean female chimpanzee pelvic model that was then paired with a CT-based scan model of a newborn chimpanzee skull scaled to the mean dimensions reported by Schultz [2]. The resultant mean fetal skull and pelvic dyad were then aligned through incremental down-scaling of the pelvic canal until the skull was tightly encapsulated within the scaled-down version, centering the skull within the true midplane of the pelvic canal. In this configuration, the skull and the midplane vertices were extracted and pairwise distances between all combinations of point coordinates were performed to determine the shortest mean distances between the models at the midplane. This process was repeated iteratively using different head and sacral orientations.

Our simulations produced a mean minimum tissue thickness estimate only 1-2 mm larger than that documented in sonography-based studies of retropubic thickness in pregnant human women. Irrespective of a fully flexed or extended neck during birth, the tip of the sacrum obstructs the birth trajectory thereby requiring it to nutate posteriorly. In humans, sacroiliac joint laxity during birth affords a maximum of 20 mm of additional space which is viewed as an adaptation arising from the extraordinarily tight cephalopelvic fit. Yet, the tip of the chimpanzee sacrum must move an average of 22 mm based on our dyad simulations to avoid obstruction during birth. Our findings reveal unexpected parallels between chimpanzee and humans that challenge long-held assumptions underlying evolutionary explanations for birth difficulty in humans. Moreover, the tight cephalopelvic fit quantified for chimpanzees in this study offers a tenable explanation for the significant degree of pelvic sexual dimorphism recovered in recent 3D geometric morphometric studies [4,5]. Collectively, these similarities imply that the convoluted trajectory of the human birth canal, rather than the cephalopelvic fit, is the likely source of birth difficulty.

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Sexual dimorphism in the Middle Pleistocene brow ridge

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Middle Pleistocene hominins (MPH) (sometimes referred to as *Homo heidelbergensis*) are known for their high degree of morphological variability and mosaicism. Wolpoff [1] suggested that variability in the European MPH was likely attributable to three sources: time, sex and idiosyncrasy. When considering the broader fossil evidence of MPH from Africa, Europe and Asia, geography is an additional potential source of variability. Studies which have quantitatively explored craniofacial variation in the MPH have focused on geography and time as explanatory factors for their high variability [e.g., 2], while sexual dimorphism has been largely studied in the assemblage from Sima de los Huesos, Atapuerca [e.g., 3]. Craniofacial variation within the brow ridge of the MPH, a sexually dimorphic region, has been shown to meet the expectations of a single species [4], despite debates over the potential taxonomy and phylogeny of this group. Researchers have also estimated the sex of many MPH based on known patterns of sexual dimorphism in hominins, meaning that it is possible to explore the potential contribution of sexual dimorphism to craniofacial variation in this group.

The present study explored sexual dimorphism in size, shape, and allometry within MPH from Africa, Europe and Asia under three sex estimation schemes: the first taking sex estimates from the literature; the second and third estimating sex based on patterns of sexual dimorphism in tangent space (where the effect of size is removed) and size-free shape space (where the effects of size and allometry are removed), respectively, in a sample of modern humans of known sex. Brow ridge morphology was recorded using a configuration of 221 3D landmarks and semilandmarks across the frontal bone. Sex estimates were tested using discriminant analyses of principal components of size-free/shape variation with samples of Neanderthals and Pleistocene modern humans for whom sex had been estimated from traits other than the brow ridge, including postcrania.

Overall, sexual dimorphism, time, and geography were not found to be significantly correlated with shape for the MPH. Magnitude of dimorphism in size for the MPH was similar across all three sex estimation schemes, and comparable to values for *Homo neanderthalensis* and *Homo sapiens*. Sexual dimorphism in shape for the MPH was higher when sex was estimated using patterns of sexual dimorphism in size-free shape space, and comparable in the other two schemes. Sexual dimorphism in the size of the brow ridge was similar to that recorded for *H. neanderthalensis* and anatomically modern *H. sapiens* of known sex across all three schemes. The results of this study would therefore indicate that sexual dimorphism in the MPH brow ridge is not higher than expected for a group of hominins with hypothesised close relationships to later *Homo*, and therefore cannot explain the high degree of variation argued to be documented within the brow ridge of these hominins [5].

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Different environmental variables predict body and brain size evolution in *Homo*

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Increasing body and brain size has long been recognized to be a key macro-evolutionary pattern in the hominin lineage, particularly in the Pleistocene. Yet, the mechanisms behind these changes remain debated. Hypothesized drivers include environmental, demographic, social, dietary, and technological factors. Formal tests of these hypotheses, however, have rarely been conducted. Here, we test the influence of environmental factors on the evolution of body and brain size in the genus *Homo* over the last one million years using a large fossil dataset combined with global paleoclimatic reconstructions and formalized hypotheses tested in a quantitative statistical framework. Our body (n=204) and brain size (n=166) estimates come from individual fossils of *Homo* distributed throughout the Old World and ranging from ca. 1.0-0.01 Ma. The environmental information for each individual data point (i.e., geographical location and age of each fossil specimen) comes from a climate emulator that takes into account long-term, glacial-interglacial climate variation, caused by changes in the Earth's orbit around the sun (Milankovitch cycles) and in greenhouse gases, such as CO₂. Our results show that different environmental variables predict body and brain size in the genus *Homo* over the last 1 Ma. Temperature is a major predictor of body size variation, with larger-bodied individuals consistently occurring in colder climates. These results are in accordance with Bergmann's rule. Brain size correlates with net primary productivity of environments and long-term variability in precipitation. These variables, however, account for only small amounts of the observed variation in brain size. Other environmental factors that we test are not associated with body and brain size evolution in later *Homo*. Our work suggests that past climatic variation underlies, in part, the evolution of key biological characteristics in Pleistocene *Homo*. A significant proportion of variation remains unexplained by environmental factors, requiring further studies which incorporate tests of social, dietary and technological drivers by explicit hypotheses with statistical analyses.

Range of motion mapping of the *Australopithecus afarensis* hip joint

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Palaeoanthropologists have long debated the limb posture and, consequently, the locomotory behavior of *Australopithecus afarensis* since the discovery of the infamous, near-complete skeleton of 'Lucy' (AL-288-1) in the 1970s. Much of this debate has centered on the pelvis. The articulation and functional morphology of the AL-288-1 hip joint has been well-studied, however the exact manner in which the femur articulates with the pelvis has not been quantified, posing the question: were specific limb postures feasible? Traditionally, osteological ranges of joint motion are based upon hand or digital manipulation of two bones relative to the other to provide an estimated range of motion. Here, we use 3D models of the reconstructed AL-288-1 pelvis and femur [1] to accurately reconstruct the 3D articulation of the pelvic girdle to investigate the functional morphology and locomotory capabilities of *Australopithecus afarensis*. Anatomical and joint coordinate systems were established using the shape-fitting procedure outlined by [2] and implemented in MATLAB. Spherical shapes were fitted to the acetabulum and femoral head, and cylindrical shapes were fitted to the sacrum and femoral condyles. We did not model the distal limb. The Z axis was long-axis rotation, Y was abduction/adduction, and X was flexion/extension, with a right-handed coordinate system and X-Y-Z rotation order in Maya 2019 (Autodesk Inc., San Rafael, USA). The model was setup in the 'neutral posture' (the 'starting position'), with the hip Z-axis (i.e., the femoral long axis) perpendicular to the ground. Joint spacing was defined as the average distance between the femoral head and the acetabulum, which was established via the fitted primitive geometric shapes and thus represented the amount of cartilage in the hip, estimated to be 2.035 mm thick. A forward kinematic rig was created in Maya, which permitted rotation around the hip joint. Next, we implemented a 3D joint sampling approach in Maya, following the approach of [3,4] to estimate the 3D articulation of the femur with the pelvis in the AL-288-1 specimen. This procedure was repeated for a human and a chimpanzee individual. Each sampling approach (n=197,173 poses with three degrees of freedom per individual) reported viable and non-viable poses based upon mesh interpenetration using a Boolean operation (i.e., if the femur penetrated the pelvis then this was classed as non-viable). Poses classed as non-viable were discarded because they simply could not be possible limb postures in the AL-288-1 specimen. On the other hand, viable poses (n=32,021, with three rotational degrees of freedom) in which no mesh interpenetration was established, quantitatively report the osteological range of motion in the AL-288-1 hip joint, thus providing an insight to the functional morphology of this hominin's hip mobility. We report here the viable poses of AL-288-1 as a mapped range of motion, using an Euler cosine corrected shape space [5] in comparison to those of a human and a chimpanzee, thus demonstrating the broad repertoire of hip mobility in *Australopithecus afarensis*. We further stress the need for consideration of ligamentous restrictions on hip mobility when reconstructing joint postures in extinct taxa.

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Lower Palaeolithic and early Middle Palaeolithic in Poland: Re-assessment of the age and technological features of sites

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Little is known about the transition from the Lower to the Middle Palaeolithic in Poland. Numerous questions without answers resulted from the limited value of chronometric and archaeological data. This paper aims to present the preliminary summarization of current state of knowledge concerning chronology and technological features of finds from Poland related to this transitional period.

So far over 20 Lower Palaeolithic sites, dated to between MIS 13 and MIS 8, have been recognized in Poland. Whilst the age of the mentioned spots is mainly based on litho-stratigraphical assessments. The confrontation of the stratigraphy of the findings with the chronometric dates (OSL and U-series) or biostratigraphic records indicates that only very few sites should be correlated with the Lower Palaeolithic [1,2]. Those sites, documented in the context of fluvial and slope sediments contain scarce remains of fauna. They comprised rather small lithic inventories (<400 items) with flakes, cores, and marginal retouched tools and some might contain pseudo artefacts. Unipolar and multidirectional core reductions were recorded.

Although the total number of early Middle Palaeolithic sites is lower (~11), their cognitive value is higher. While they represent both cave and open-air sites, the former ones, including Biśnik Cave (layers 19a-14), Nietoperzowa Cave (layers 14-16) and Ciemna Cave (layers 17/IX) [3- 5] provided more reliable data concerning the age and environmental conditions of the occupation. Chronometric dates and biostratigraphic data indicate that these finds are mostly correlated with MIS 7 and MIS 6. Those small inventories (<100 items) contain traces of using several methods of Levallois system, Kombewa and discoidal methods with the domination of the unifacial tools. Only at Biśnik Cave asymmetric bifacial-backed tools were recorded which were attributed to the oldest phase of Central European Micoquian. Except for Biśnik Cave, the presence of such old bifacial tools has not been confirmed.

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Human occupation of the semi-arid grasslands in the interior of South Africa during Marine Isotope Stage 4: New archaeological and paleoecological evidence from Lovedale, Free State

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In southern Africa, Marine Isotope Stage (MIS) 4 (~71-57 ka) is a fundamental period in human evolution characterized by many cultural and technological innovations [1]. These innovations emerged against the backdrop of marked climate change that played a role in their appearance, even though climate patterns varied considerably over time across the subcontinent, with an alternation of wet and dry events at the millennial scale [2]. While the coast of southern Africa has been extensively investigated with regard to environmental variability and human paleoecology, the interior appears underrepresented within this picture. Beyond the Great Escarpment, the South African inner plateau has been investigated less intensively because of its vast extent, and as a result only a small number of known Middle Stone Age (MSA) sites reach back to MIS 4 and earlier periods [3]. This is also due to the fact that, with very few exceptions, these are all open-air sites that are not readily visible in the landscape and require large-scale surveys to be located. In addition, open-air sites are found within active sedimentary environments that may completely obliterate or obscure any trace of human occupation, making them more difficult to identify. Finally, only a fraction of the MSA sites in the interior plateau has been accurately dated and thoroughly characterized from a paleoenvironmental perspective. This paucity of evidence has hindered a proper assessment of human paleoecology and dispersal within the subcontinent, to the point that we are currently unable to formulate a narrative of local population dynamics during the MSA [4]. In this context, one particularly understudied region of the South African interior is the Free State Province of South Africa. Its Grassland Biome, today dissected by sporadic rivers and punctuated by springs and seasonally dry lakes, was characterized by exceptionally productive grasslands and wetlands throughout the Middle and Late Pleistocene, which supported large game populations and provided humans with a resource-rich environment [5]. Sites such as Florisbad, Erfkroon and Rose Cottage Cave have produced MIS 4 environmental records, although only the latter site features human occupations dated to the same period. Consequently, it is difficult to understand the cultural connections between the central interior and the coast. In order to document periods not represented at Florisbad or other archaeological landmarks in the central interior of South Africa, and thus address the lacuna regarding MIS 4 human paleoecology in the grasslands of the Free State, we focused our attention on open-air occurrences in 'dongas', a common erosional feature in local river terraces. Dongas expose Pleistocene sedimentary sequences that often contain artifacts and fossils, which become apparent in an otherwise flat landscape where buried sites are invisible to remote sensing and to the naked eye. At Lovedale, 40 km southwest of Florisbad on the left bank of the Modder River, we excavated an MSA site within a small donga. Here we show that by using a multi-analytical approach including micromorphology of sediments, phytolith analysis, infrared spectroscopy, faunal analysis and luminescence dating, we are able to reconstruct the evolution of paleoenvironments over the last ~80,000 years and to provide context for human occupation. The latter produced a poorly known lithic industry, which may be called pre-Howiesons Poort based on typological grounds, during a dry period at the onset of MIS 4. These data address crucial gaps in the paleoenvironmental record of the Free State and show the importance of the grasslands of the central interior of South Africa, a key region for human evolution at the crossroads between the coast and the Kalahari Basin.

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The structural organization of *Homo luzonensis* teeth

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The species *Homo luzonensis* has recently been described based on a set of dental and post-cranial elements found at Callao Cave (Northern Luzon, Philippines) and dated to at least 50-67 ka [1]. Seven post-canine maxillary teeth are attributed to this taxon, five of them belonging to the same individual (CCH6) and representing the holotype of *H. luzonensis*, while the isolated upper premolar CCH8 and the upper third molar CCH9 are paratypes of the species [1]. All these teeth are characterized by their small dimensions (in the inferior range or below the modern human variation) and particularly large premolars relative to the molars. A small dentition is also found in *H. floresiensis* [2], another hominin having evolved in an insular environment of Southeast Asia, while large premolars (even if to a lesser extent than in *H. luzonensis*) are also found in *H. erectus* [1]. The post-canine teeth from Callao Cave display a blend of modern-like features in the crown (with a simplified occlusal morphology) and more archaic traits in the roots (three-rooted premolars, large root volume). Postcranial bones of the hands and feet show *H. habilis*-like or australopith-like features [1,3], indicating an early origin of *H. luzonensis* and *H. floresiensis* [3], while cranial and dental morphology are more consistent with the hypothesis that they derived from Asian *H. erectus* groups [2,4]. Due to this mosaic morphology, the origin and phylogenetic relationships of both *H. luzonensis* and *H. floresiensis* are still debated. In order to test the hypothesis that *H. luzonensis* derives from *H. erectus* rather than from an earlier small-brained hominin, we analyzed the microCT record of the teeth and investigated the external and internal structure, including the enamel-dentine junction (EDJ) that is a reliable taxonomic proxy [5]. We compared these data with those available for *H. habilis/rudolfensis*, *H. erectus* s.l. (including specimens from Africa, China and Indonesia), *H. floresiensis*, Neanderthals and modern humans. We quantified tooth crown tissue proportions, explored pulp morphological variation and assessed the crown outline and EDJ shape with geometric morphometric methods (elliptical Fourier analyses for the external outline and diffeomorphic surface matching for the EDJ). Our results are relatively consistent for most tooth positions, *H. luzonensis* external crown morphology aligning more with *H. erectus* than with *H. habilis/rudolfensis*. The internal structural organization of *H. luzonensis* exhibits more affinities with that of *H. erectus* and *H. floresiensis* than with Neanderthals and modern humans (except for the M2s that show a more intermediate signal). Altogether, the analyses of the external and internal tooth structural organization of *H. luzonensis* teeth attest the validity of this taxon and highlight the taxonomic diversity of Pleistocene hominins in insular Southeast Asia. Our results suggest that both *H. floresiensis* and *H. luzonensis* likely evolved from some *H. erectus* groups that dispersed in the various islands of this region and became isolated until endemic speciation events occurred at least twice during the Pleistocene in this insular context.

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Sediment DNA identifies hominin and faunal turnovers at Denisova Cave

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The integration of ancient DNA with paleoecological studies allows us to study both the evolutionary history of humans and the environments they lived in. Currently, these studies are hampered by the rare discovery of hominin remains and the time and resources required for morphological identification of faunal remains. The discovery that DNA from Pleistocene mammals, including hominins, can be retrieved from cave sediments [1] opens up the possibility of chronological examinations of the relationship between faunal composition and hominin occupation at archaeological sites. We explore this possibility at Denisova Cave, a site in the Altai Mountains, which is thought to be a contact zone for different faunal and hominin groups. Denisova Cave is of particular interest for hominin evolutionary history due to the identification of both Neandertal and Denisovan skeletal remains at the site, as well as a bone from the offspring of a Neandertal mother and Denisovan father [2]. The site covers over 300,000 years and contains four types of archaeological assemblages [3], but no more than 15 hominin remains have been identified. Thus, the sequence in which hominins occupied the site and their association with the archaeological assemblages remains debated.

We tested 728 samples from the cave’s Pleistocene layers using a fully automated workflow for DNA extraction, library preparation and hybridization capture, for the presence of both faunal and hominin mitochondrial (mt)DNA. Ancient mammalian mtDNA was identified in 685 (94%) samples, enabling us to explore the extent to which mammalian mtDNA preservation correlates with the age and properties of the sediments it is recovered from. We identified shifts in the abundance of mtDNA from different fauna, as well as turnovers of mtDNA lineages, for example in bears and hyaenas. Ancient hominin mtDNA was identified in 175 (24%) samples. The oldest mtDNA identified was of the Denisovan type, in association with the early Middle Palaeolithic. Both Neandertal and Denisovan mtDNA was found in the middle Middle Paleolithic layers. The identification of ancient modern human mtDNA coincides with the beginning of the Initial Upper Palaeolithic – providing the first genetic evidence for modern human presence at the site. Changes in the relative proportions of DNA from various mammalian families, shifts in the presence of mtDNA from different hominin groups and other mammals appear to coincide with past climatic changes. Our study demonstrates the potential of using sediment DNA for increasing our understanding of past faunal diversity, paleoecology, and hominin occupations at archaeological sites.

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Measuring the asymmetry in long bone morphometric maps of cortical thickness: occupation-related differences in the modern human humerus

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Reconstructing the loading history in human species is crucial to understand lifestyle strategies and mobility pattern in past populations. A fundamental approach to the reconstruction of physical behaviour relies on the comparison of the differences in cortical thickness distributions among antimeres. The comparison of antimeric bones from the same individual offers the prospect of identifying asymmetry of loading and so, of activity, because genetic, systemic and environmental factors affecting bone form are the same for both sides [1]. In the present study we have tested the new *morphomapAsymmetry* function, an implementation of *morphomap* R package [2], to calculate and map asymmetry of the cortical thickness. We selected 41 male individuals and 10 female individuals from *The New Mexico Decedent Image Database* (NMDID) [3]. We chose only individuals ranging in age from 20 to 50 who have worked in the army, in building companies or at a desk. We tested the hypothesis that diaphyseal cortical thickness asymmetry is unrelated to occupation and sex. On each humerus we extracted 61 cross-sections along the diaphysis from 20% to 80% of the total biomechanical length. On each cross-section we calculated 48 equiangular semilandmarks: 24 on the periosteal and 24 on the endosteal contour, centred at the centre of gravity of the cross-section. The right humeri have been mirrored by using the function *morphomapMirror*. We measured the thickness between paired semilandmarks (periosteal and endosteal), and we built morphometric maps of cortical thickness for each individual. Eventually, we computed the difference between right and left sides and mapped the differences in morphometric maps. In this way, the diaphysis is unrolled and the differences in thickness along the direction (anterior-lateral-medial-posterior) and the longitudinal axis are reported respectively on the x and y axis. We analysed asymmetry by performing a principal component analysis on the matrices of cortical thickness of the left and right humerus. Each individual is represented by left and right morphometric maps of cortical thickness after subtracting the mean morphometric maps between sides. We calculated the pattern and magnitude of asymmetry pooled by occupation and sex. Additionally, we decomposed the total asymmetry into the “directional” and “fluctuant” components of asymmetry [4,5]. The first two PC scores account for the 33.91% of the total variance (PC1=41.05%; PC2=7.47%). PC1 is related to directional asymmetry showing a shared pattern of right-hand lateralization (except one individual left-hand lateralized). The pattern and magnitude of asymmetry among the three occupation groups are not statistically different from each other. However, the magnitude of total asymmetry is higher in army and building than desk group. The decomposition of the asymmetry into directional and fluctuant components reveals as 9.60% of the total variance is associated with directional asymmetry and 90.4% with fluctuant asymmetry. Lastly, the comparison between female and male individuals show as the pattern of asymmetry is indistinguishable. On the contrary, the magnitude of asymmetry is higher in the male subsample. The analysis of asymmetry of the cortical thickness presented here confirmed a general trend of right lateralization among the individuals belonging to the different groups of occupation. Males show a higher degree of asymmetry than females. In conclusion, these results do not falsify the hypothesis that pattern and magnitude of asymmetry differ among the occupation groups considered in this study. In perspective, recent developments in statistical analysis methods applied to the study of skeletal material show the potentiality of this approach to study the pattern of lateralization in relation to physical activity in past populations including extinct human species.

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Differences in spatial relationships of the hominoid temporal glenoid fossa and neurovascular cranial base outlets

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In hominoids, temporal glenoid fossa morphology has been demonstrated to achieve its distinct (at species-level) morphology as part of postnatal ontogenetic processes which shape their taxonomically and phylogenetically varying temporal bone [1]. Here, we contribute towards an understanding of how such differences can be assessed in the wider context of the hominoid skull morphology by studying the spatial relationships of the of adult glenoid fossa in relation to cranial base neurovascular outlets (NVOs), whose configuration can be treated as taxonomically and phylogenetically stable [2,3].

We used a 3D-geometric-morphometric approach and identified 74 3D-landmarks on the cranial base (57) and glenoid fossa (17) of a sample of 71 adult crania of *Homo sapiens*, *Pan*, *Gorilla*, *Pongo*, *Hylobatidae* and *Australopithecus africanus* (Sts5). We performed (a) General Procrustes Analysis, Principal Components Analysis and MANOVA to confirm interspecific shape variations and (b) Partial Least Square Regressions (PLS) to assess relationships of interspecific patterns of variation between the cranial base NVOs and glenoid fossa morphology.

PC1 (30.8%) summarised shape variations that separate humans from all apes. Sts5 is intermediate between the two; this is due to glenoid fossa rather than NVO morphology variation, which is more ape- than human-like. Differences between humans and all apes are due to variation in NVO and glenoid fossa morphology, the latter confirming observations made by [1]. PC2 (12.5%) separates gibbons from all other taxa due to anterior/middle cranial fossa NVOs variation between gibbons and great apes (see outcomes of b) rather than glenoid fossa variations, which are present but small.

With regards to spatial relationships, we observe porion position varying superior and entoglenoid process position varying inferior relative to NVOs, distinguishing all apes from humans. The human glenoid fossa position is relatively more lateral to the NVOs, particularly the posterior cranial fossa ones. PC2 (12.5%) separates smaller-bodied (*Hylobatidae*, *Pan*) from the large-bodied apes (*Gorilla*, *Pongo*) by exaggeration of the superior porion/inferior entoglenoid process configuration relative to the NVOs in large apes.

PLS regressions confirm these observations. Human-ape differences produce a strong correlation (RV coeff = 0.700, $p < 0.001$) between NVO pattern variation characterised by NVOs of the anterior and middle cranial fossa being stable across all taxa and the human posterior cranial fossa NVOs (carotid and hypoglossal canals) being placed relatively more antero-lateral than the ape ones. This covaries with the relatively deeper human glenoid fossa being combined with the less superior porion/inferior entoglenoid process and the opposite configuration in apes. Comparing ape taxa only and factoring in sexual dimorphism via pooled within-group analysis indicates a significant correlation (RV coeff = 0.64, $p < 0.001$) between NVO and glenoid fossa variation. Here, anterior and middle cranial fossa NVOs vary the most interspecifically and between small and large apes. This results in supero-inferior deepening and antero-posterior shortening of the middle cranial fossa, which covaries with a the ape porion/entoglenoid process configuration described above.

These results indicate a that it is possible to link outcomes of studies of the individual skull bones with species-specific NVO configurations of the cranial base. This might lead us to further explore the knock-on effects that the shift in cerebellum position and globularisation of the human cerebrum have beyond the rearrangement of some of the posterior cranial fossa NVOs such as the antero-lateral position of the carotid and hypoglossal canals observed in humans but not in other hominoids. Further studies investigating the integration of these variations in skull morphology could lead to a more refined understanding of the evolution of the hominoid skull.

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