



**ESHE**  
*European Society  
for the Study of  
Human Evolution*



[www.eshe.eu](http://www.eshe.eu)

9<sup>TH</sup> ANNUAL MEETING OF THE

**European  
Society  
for the study of  
Human  
Evolution**

19-21 September 2019  
LIÈGE/BELGIUM



# Journal of Human Evolution



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The *Journal of Human Evolution* concentrates on publishing the highest quality papers covering all aspects of human evolution. The central focus is aimed jointly at palaeoanthropological work, covering human and primate fossils, and at comparative studies of living species, including both morphological and molecular evidence. These include descriptions of new discoveries, interpretative analyses of new and previously described material, and assessments of the phylogeny and palaeobiology of primate species.

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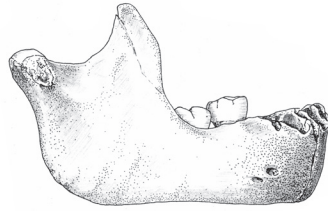
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**European Society for the study of Human Evolution**  
**ESHE**  
**9th Annual Meeting**  
**Liège, Belgium, 19th-21st September, 2019**





Cover image: Scladina mandible (Scla 4A-1 & 9): External view from the right side showing the receding symphyseal region (drawing S. Lambermont, AWEM)

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**Dear Participants of the 9th Annual Meeting of ESHE,**

**Bienvenue à Liège! Welkom aan Luik! Herzlich Willkommen in Lüttich!**

We are delighted to welcome you to the beautiful city of Liège for our 9th Annual Meeting of the European Society for the Study of Human Evolution. Belgium, and particularly the region of Liège, has historically played a key role in the early development of Palaeoanthropology. Twenty-six years before the famous Feldhofer discovery in 1856, the skull of a Neanderthal child had already been discovered by P.-C. Schmerling near Engis. The caves of Spy, Goyet, La Naulette or Scladina are known worldwide and to this day the Paleolithic sites of the Mosan Basin continues to be at the forefront of Neanderthal research. Therefore, we cannot think of a better place to celebrate the newest research and the gathering of so many scientists concerned with the study of human evolution than here in Liège.

As we open the 9th Annual ESHE meeting, we celebrate the ongoing success of the society, of which I am honoured to have been President since its creation. I would like to remind you that during this year's general assembly, we will be voting for the renewal of the board. As per the statutes of the society, the ESHE board must be re-elected every two years. All members of the society are able to vote. The success of the society means that each year we are able to present to you ever more exciting and ground-breaking research. This year, we accepted many fascinating abstracts, and as of August, have over 788 members. At this point, I would like to warmly thank our keynote speaker, Héléne Rougier, who will give us a comprehensive overview on current Neanderthal studies in Belgium.

As in previous years, we are able to encourage and support our student members to attend and participate in the conferences by providing travel grants to those presenting at this year's meeting. We also award a student poster prize, and, thanks to the kind donation by the Journal of Human Evolution, a Pecha Kucha Prize for students. The journal will also host a workshop on Friday to help young researchers get their work published. As in 2018, we are able to offer free child care, and support for parents to make it easier to attend the meeting.

The 2019 ESHE meeting is sponsored by the Agence wallonne du Patrimoine, Loterie Nationale, Ville d'Andenne, Province de Liège, University of Liège, Fédération Wallonie Bruxelles, Municipality of Liège and La Boverie, Scladina Cave Archaeological Centre, Prehistomuseum, Espace de l'Homme de Spy, Grottes des Goyet. The conference would also not be possible without the tireless efforts of our local organisers Kévin Di Modica, Grégory Abrams, Stéphane Pirson, Dominique Bonjean, Damien Flas, Veerle Rots, Pierre Noiret and our volunteers team. We are particularly grateful for Kévin Di Modica for scouting and providing us with the beautiful venues and making everything fall into place so seamlessly. Furthermore, meeting preparation and the publication of our proceedings volume has been made possible by the work of our assistant Imogen Pare and by the ESHE Board Officers and Board Members, particularly Philipp Gunz, Shannon McPherron, and Gerhard Weber. We thank you for making this year's ESHE meeting a success, and we look forward to celebrating the ESHE decade with you next year.

With best wishes,

**Jean-Jacques Hublin**

## Board Officers

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Kévin Di Modica  
Grégory Abrams  
Stéphane Pirson  
Dominique Bonjean  
Damien Flas  
Veerle Rots  
Pierre Noiret

## Thanks to

Agence wallonne du Patrimoine  
Loterie Nationale  
Ville d'Andenne  
Province de Liège  
University of Liège  
Service public de Wallonie  
Scladina Cave Archaeological Centre  
Prehistomuseum  
Espace de l'Homme de Spy  
Grottes de Goyet  
TraceoLab





### **Scladina Cave Archaeological Centre (SCAC) – Local Organizing Committee**

Scladina Cave Archaeological Centre (SCAC) is a scientific research centre located in the village of Sclayn (Municipality of Andenne), just a few hundred meters away from Scladina Cave. The centre is devoted to the study of Middle Palaeolithic settlements in Belgium and more broadly in Northwestern Europe. In Scladina Cave, the team developed the only permanent

on-field research programme

on Palaeolithic archaeology in Belgium. This programme involves fieldwork, preventive conservation, management and digitalisation of collections, as well as conference and workshop organisations or scientific publications. When studying the cave findings the team either resorts to on-site based researchers or to an ever growing collaboration network. Preventive archaeology operations related to the Prehistoric period also



SCAC team and students from international universities excavating in Scladina Cave

offer the opportunity to work with the “Agence Wallonne du Patrimoine (AWaP)”, and when studying, digitalising or preserving Palaeolithic collections the team is in close contact with other museums and public services. Overall, SCAC has created or contributed to many exhibitions and the archaeological centre has been officially recognised as a museum by the “Fédération Wallonie-Bruxelles”.

Due to its prominent position - Scladina Cave being the only Palaeolithic excavation site accessible to the general public in Belgium - the SCAC has recently launched a cultural mediation service that focusses on bringing more awareness to Palaeolithic research. The opening of a brand-new municipal museum in Andenne in early 2020 will further increase knowledge of the Scladina discoveries and establish the role of the SCAC in the public. In 1983 the archaeological centre was founded as a non-profit organisation as a result of the collaboration between the University of Liège conducting Scladina’s excavation at that time and the Municipality of Andenne owning the cave. In its current form, the SCAC directly employs 10 people thanks to multiple public contributors: “Service public de Wallonie”, Municipality of Andenne, “Fédération Wallonie-Bruxelles”, “Agence wallonne du Patrimoine” and recently the European Commission through SCAC’s participation in a H2020 funded project (grant number 665066).

### **L'Agence wallonne du Patrimoine (AWaP) – Local Organizing Committee**

The Wallonia Heritage Agency (AWaP) is a government department of Wallonia, a region in the south of Belgium. The agency was created in 2018, following the merging of the “Wallonia Heritage Institute” with the “Heritage Department of the Public Service of Wallonia”, and employs approximately 300 people, including art historians, archaeologists, architects, lawyers, technicians and office and communications staff. Ever since, it has become the principal point of contact when it comes to heritage in Wallonia.

The agency's public mission is the study, protection, promotion and conservation of Wallonian heritage, covering buildings, sites, archaeological remains, excavations etc. Integral part of this mission is a heritage awareness policy, and also the management of two Heritage Skills Centres and the development of regional monuments.

In Wallonia, most of the archaeological investigations are related to development-led archaeology. Some 100 sites are assessed or excavated each year by the government agency without subcontracting nor soliciting the private sector. Furthermore, the agency also manages the grant applications related to archaeological heritage, delivers excavation permits and accreditations for archaeological repositories, and investigates the archaeological remains discovered by accident.

For more information visit: <https://agencewallonnedupatrimoine.be/lagence-wallonne-du-patrimoine>



Left - The Neolithic Flint Mines at Spiennes (Mons, Belgium), inscribed into the list of Unesco World Heritage Sites in 2000 (Picture G. Focant; © SPW). Right – Excavations in 2018 at the Grognon, the city of Namur's historic heart, at the confluence of the Sambre and Meuse rivers (© SPW).

### **University of Liège, Prehistory Research Group – Local Organizing Committee**

Research in prehistory has a long tradition at the University of Liège and its development has been stimulated by the rich archaeological record of Wallonia with numerous well-known prehistoric sites, including caves

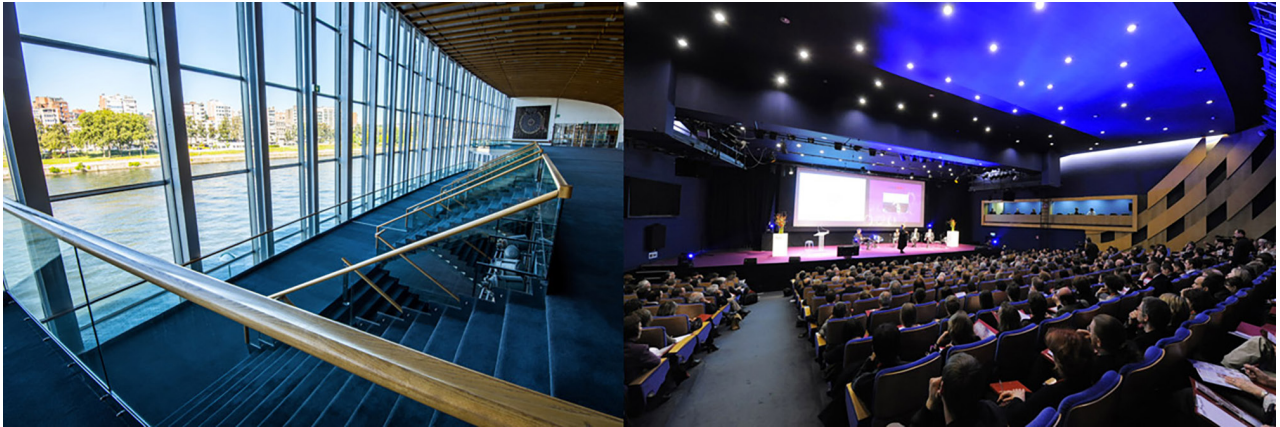
such as Spy, Goyet, Scladina, Maisières-Canal. The current Prehistory research group of Liège consists of two complementary research centres, which mainly concentrate on the Paleolithic period and are both active in Belgium and abroad, especially in France, Germany, Romania and South Africa. Prehistoric research in Liège focusses on the technological and functional analysis of stone tools by applying macroscopic (e.g., chaîne opératoire) and microscopic methods (e.g. use-wear analysis, residue analysis) and experimentation.

TraceoLab ([www.traceolab.be](http://www.traceolab.be)) is a research centre directed by V. Rots with a strong focus on functional studies of wear traces and residues on stone tools combined with systematic experimentation. The researchers are carrying out a comparative study between Neanderthals and (early) modern humans in view of a broader understanding of technological evolution and changing human behaviours. Therefore, attention is devoted to both the Middle Stone Age in Africa and to the Middle and Upper Palaeolithic period in Europe and the group is involved in different collaborative research projects in France, Germany, Italy, Ethiopia, Zambia, South Africa and Israel. The study of hafting is one of the key research topics, besides projectiles and propulsion modes, and most research is characterised by an important methodological focus. TraceoLab was created in 2012 by V. Rots, who had received an ERC starting grant in 2011 on the Evolution of Stone Tool Hafting in the Palaeolithic (EVO-HAFT). Several other research projects have developed since and TraceoLab currently houses a fully equipped microscope lab, a lab for residue extraction and processing and a lab for systematic experimentation including a set-up specifically devoted to projectiles. A further highlight is the large reference collection for wear traces related to production, use and hafting, as well as a reference collection for residues, including residues on stone tools. Projectiles form an important part of these collections.

The research group of P. Noiret primarily concentrate on the Gravettian period and is especially active in Eastern Europe, more precisely in Romania (e.g. Mitoc-Malu Galben), and in Asia (e.g. research of D. Flas). A renewed excavation project at Trou al'Wesse was launched in 2018 in collaboration with N. Zwyns (UC Davis) and will focus on both the Mousterian (Middle Palaeolithic) and Aurignacian (Upper Palaeolithic) occupations. Field work and lithic analysis play a prominent role in the group of P. Noiret. Particular attention is devoted to detailed typological and technological analyses of Upper Palaeolithic sites and to the transition between the Aurignacian and the Gravettian in view of an improved understanding of the Upper Palaeolithic traditions of Central and Eastern Europe (Aurignacian and Gravettian), in Romania and Ukraine.

### Palais des Congrès – Conference location

This year's conference will take place in the "Palais des Congrès" (Convention Centre) of Liège. The Palais is situated between the banks of the Meuse River and the Parc de la Boverie, one of the most beautiful green spaces in the city. The "Palais des Congrès" is within walking distance from the city's historical centre and the Guillemins railway station thanks to a recently built pedestrian bridge. Other undeniable assets of the site are a 4-star hotel (Vander Valke Hotel) and an on-site free parking area.



Left: Grand Foyer. Right: Auditorium

The "Palais des Congrès" is the only convention centre in Wallonia, with over 20 halls, 14 conference rooms and two sprawling terraces with breath-taking views across the river. The ESHE conference will take place in three respective spaces. The "Auditoire Reine Elisabeth", a 700 m<sup>2</sup> auditorium with a capacity of 500 seats, is reserved for oral presentations and is located next to a 1295 m<sup>2</sup> hall called the "Grand Foyer". This vast hall on the first floor of the "Palais des Congrès" offers an exceptional view over the Meuse River and the city and will serve for different purposes: the welcome desk, a presentation upload platform, the posters display and the catering services. Lastly, we will also have the "Simenon Hall" at our disposal, a 147 m<sup>2</sup> room located on the ground floor, where the childcare service will be offered by a professional company.

### Palais Provincial – Pre-registration and Opening Cocktail

Thanks to the generosity of the College of the Province of Liège, this year's pre-registration and opening cocktail will take place in the "Palais Provincial" (Provincial Palace). This prestigious building is the official residence of the Governor and House of both the Provincial College and Council. This grey limestone building combining both classic and neo-gothic elements was actually an addition to the west wing of the former Palace of the Prince-Bishops, the most important historic building in the centre of Liège.

The entire building designed by the architect Jean-Charles Delsaux is characterised by multiple but harmonious

architectural styles from the 16th, 18th and 19th centuries. On June 11, 1849, thirteen years after the approval of the law which officially established the Belgian Provinces, the first King of Belgium, Leopold I, laid the foundation stone of the Provincial Palace. The palace's small courtyard, "Cour Notger" (Notger Square), was named after the first Prince-Bishop of the city. The structural work was completed in 1853, but a few decades went by before all the decoration of the front façade were finished. This façade is decorated by sculptures, bas-reliefs and blazons inspired by the genuine or legendary history of Liège and its Principality. All works were completed in 1887. This project reflects the habit of the 19th century of building in the "old style" of the Middle Ages to suggest an ancient past of the Principality.

ESHE participants will enter the building by the main entrance of the Palace of the Prince-Bishops, located on "Place Saint-Lambert" (Saint-Lambert Square). Pre-registration will take place on the ground floor hall of the "Palais Provincial" from 15:00 to 18:00 and will be followed by a cocktail in the "Salle des Pas perdus" and "Salle du Conseil Provincial" on the first floor from 18:00 to 19:30. Drinks for the cocktail are generously offered by the Provincial College.



Left: Provincial Palace and Square Notger. Right: Ground floor of the Palais Provincial

### Salle Académique – Public Lecture

When the academic hall, also known as the "Palais de l'Université" (University Palace), was built in 1824, the building was isolated due to its parallelepiped form of 26m by 31 and its blind walls. The façade of the building consisted of a portico with eight ionic columns. The flat frieze bears a sentence in bronze letters: „UNIVERSIS DISCIPLINIS“, attributed to professor Gall. The south wall also formerly was the beginning of the chorus of a church, whose architect kept elements as an economy measure. An open gallery, supported by a double row of columns, connects the academic hall with the main wing of the former Jesuit church,



The neoclassic ceiling of the Academic Hall © ULg

built by the architect Paquay Barbière. Gardens lie on the other end of the „Jesuits“ wing, and along the river Meuse.

From 1889 to 1892, the University square (Place du 20 Août) was constructed in front of the academic hall. The peristyle of the Academic Hall, its vestibule and a part of the roof disappeared in the course of the years. The current hemicycle room in neoclassical style is made up of tiers and adorned with a walkway on two floors, with Ionic columns on the ground floor and Corinthian columns on the 1st floor. Originally, one would sit directly on the tiers; the benches were only installed later on.

In 1874, the properties commission qualified the academic hall as a damp and sad monument, going as far as foreseeing its demolition: “No one, we believe, will think to stand up for this building, whose only merit is the inscription that it bears.” The 24 January 1983, the Academic hall became a protected monument, considered the most prestigious building of the University and one of the most remarkable examples of neoclassical architecture in the country.

### **Musée de la Boverie – Closing Diner**

Inaugurated in 2016, the new museum of La Boverie promises international accessibility and culture. Located on an island formed by the Meuse and its derivation, La Boverie museum is part of a complex comprising a historical building, built in 1905 for the World’s expo, and a modern wing designed by the architect Rudy Ricciotti and the Liège-based architect firm p.HD.

La Boverie’s vocation is to become a showcase for contemporary creation, various cultural projects and the richness of historical collections. Its programme offers both international exhibitions and a new presentation

of the permanent collections of the City of Liège. One storey of La Boverie is solely reserved for showing a selected pieces from the collections of the Museum for Fine Arts of the City of Liège. Ingres, Monet, Gauguin, Picasso, Pissarro, Evenepoel, Delvaux, Magritte, and others will walk the visitor through the Renaissance to our modern days. The upper level, on the other hand, hosts large-scale temporary exhibitions,



Musée de la Boverie, main entrance

on an area of approximately 3.000 m<sup>2</sup>. These exhibitions are either organised directly by the City of Liège, or curated in collaboration with the Louvre, or other operators, for instance the National Museum of Indonesia in Jakarta. Since 2016 La Boverie museum has developed an even closer structural partnership with the prestigious Louvre Museum. The latter hereby offers artistic advice and the organisation of exhibitions of international stature. This collaboration assures a pledge of quality and confidence.

In sum, La Boverie provides a rich programme where all forms of arts allow the visitor to immerse themselves into different periods and theme. It will offer the ideal backdrop for the Closing Dinner of the conference and will hopefully add a further, colourful dimension to the ESHE conference in Liège.

The Closing Dinner will take place on Saturday, September 21st, from 19:30 - 22:30 in La Boverie, Parc de la Boverie.

## CONFERENCE PROGRAMME

### Wednesday, September 18<sup>th</sup>

15:00	<b>Pre Registration</b>	<b>Main Hall, Palais Provincial (Place Saint-Lambert 18A)</b>
18:00	<b>Welcome Drinks</b>	<b>First Floor, Palais Provincial</b>
20:00	<b>Keynote</b>	<b>Academic Hall, University of Liège (Place du 20 Août 7)</b>

## Two Centuries of Neanderthal Discoveries in Belgium

Neanderthal discoveries in Belgium played a critical role in the development of European prehistory in the 19th century. Neanderthal fossils such as those from the Betche aux Rotches at Spy have significantly contributed to shaping our understanding of Neanderthal anatomical characteristics as well as aspects of their behavior, including their cognitive and symbolic abilities. Today, Paleolithic sites in the Mosan Basin continue to be at the forefront of Neanderthal research through multidisciplinary projects involving active fieldwork and the reassessment of old collections. The use of state-of-the-art methods from various disciplines has not only resulted in new Neanderthal discoveries but has also led to advances in their biological study and that of their chronocultural and archeological context. This lecture will present an overview of the major contributions that the research on Belgian sites and fossils has made towards current issues and debates on Neanderthal studies. The presentation is in French with English slides.

### Hélène Rougier, Ph.D.

Hélène Rougier is a paleoanthropologist interested in the evolutionary dynamics of Neanderthals in the Middle and Late Pleistocene and focusses on patterns of variability and the emergence of the Neanderthal morphological pattern. Another research emphasis lies on the disappearance of Neanderthals and their relationships with early modern humans in Europe, and on the diversity of mortuary practices among Neanderthals. She has taken part in field excavations at Saint-Césaire and Le Piage, France, and Peștera cu Oase, Romania. She has also worked extensively on the re-assessment of old collections in order to verify the provenance of fossils, clarify their associated context and check for previously overlooked human remains. This has resulted in new Neanderthal and early modern human fossil discoveries. In particular, she initiated a multidisciplinary project examining the archeological collections from the Troisième caverne of Goyet, Belgium, that resulted in the discovery of the largest Neanderthal collection of Northern Europe.



Rougier is a Professor in the Department of Anthropology of California State University Northridge, USA. She received her PhD from the University of Bordeaux, France, followed by two post-docs at the Royal Belgian Institute of Natural Sciences in Brussels, and at Washington University in St. Louis.

Her publications are available on <https://csun.academia.edu/HélèneRougier>.



## Thursday, September 19<sup>th</sup>

- 08:00 Meeting Registration Palais de Congrès (Esplanade de l'Europe 2)
- 08:30 Official Meeting Opening
- 08:45 Welcome Address by the "Agence wallonne du Patrimoine"

### Session 1 • Podium

- 9:00 **Mateja Hajdinjak** - Doubling the number of high-coverage Neandertal genomes.
- 9:20 **Stéphane Peyrégne** - Analysis of Nuclear DNA Sequences from the Neandertals of Hohlenstein-Stadel and Scladina Caves.
- 9:40 **Benjamin Peter** - Gene flow between hominins was common.
- 10:00 **Benjamin Vernot** - Neandertal population histories from sediment nuclear DNA.
- 10:20 **Jean-Jacques Hublin** - Away from Denisova.

10:40-11:00 Coffee Break

### Session 2 • Pecha Kucha

- 11:00 **Rachel Sarig** - Population composition and possible origin of the Levantine Aurignacian culture: the dental evidence.
- Jonathan Haws** - Modern human dispersal into western Iberia: The Early Aurignacian of Lapa do Picareiro, Portugal.
- Nils Vanwezer** - 10,000 km and 21 flat tires: New interdisciplinary archaeological investigations of the palaeolakes and caves in the Gobi-Altai, Mongolia.

#### Questions

- 11:25 **Emily Hunter** - The effects of environmental conditions and food manipulation on masticatory requirements: how hard is it for a primate to crack a nut?
- Evie Vereeke** - An image-based approach to study hand function in primates.
- Maxine Whitfield** - A cognitive forager's landscape? The profitability of marine and subterranean foods for chacma baboons and humans in South Africa.

#### Questions

- 11:50 **Paola Cerrito** - The dentition of *Kenyanthropus platyops*: a comparative study.
- Thomas Davies** - Endostructural morphology of the *Homo naledi* mandibular premolars.
- Shara Bailey** - Rare dental trait is first morphological evidence of archaic introgression in Asian fossil record.

#### Questions

12:15-14:00 Lunch and Poster Session 1

### Session 3 • Podium

- 14:20 **Susana Carvalho** - Stone selection by Chimpanzees Reveals Parallel Patterns to Oldowan Hominins.
- 14:40 **David Braun** - Earliest known Oldowan Artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, Highlight Early Technological Diversity.
- 15:00 **Policarpo Sanchez Yustos** - Assemblage variability during the Oldowan-Acheulean transition at Olduvai Gorge (Tanzania). Techno-economic data from FLK West (Lower-Middle Bed II).
- 15:20 **Darya Presnyakova** - Lithic economy and hominin landscape use in the early Acheulean of Koobi Fora, Kenya.
- 15:40 **Ella Assaf** - Lower Paleolithic shaped stone balls were used for bone marrow extraction.

**16:00-16:20 Coffee Break**

### Session 4 • Podium

- 16:20 **Cinzia Fornai** - *Australopithecus* variability at Sterkfontein, South Africa: evidence from the pelvic remains.
- 16:40 **Nicole Webb** - KSD-VP-1/1: The „Big Man“ Just Got Bigger.
- 17:00 **Pierre Frémondrière** - Reviving australopithecine birth: contribution of numerical simulation.
- 17:20 **Nicole Grunstra** - Sexual dimorphism in the chimpanzee pelvis: Implications for understanding the human childbirth dilemma.
- 17:40 **Philipp Mitteroecker** - Biological evolution of *Homo sapiens* in response to medical and technological transitions: The shifting trade-off model.

## Friday, September 20th

### Session 5 • Podium

- 09:00 **René Bobe** - Gorongosa National Park: A new window on the late Miocene at the southern end of the African Rift Valley.
- 09:20 **Hervé Bocherens** - Isotopic tracking of the paleoecology of Late Miocene Ponginae (*Khoratpithecus*, *Sivapithecus*).
- 09:40 **Tina Lüdecke** - Is it possible to gain direct evidence of early hominin meat consumption? - A first approach using Pleistocene fossil tooth enamel nitrogen isotopic composition.
- 10:00 **A. Pascual-Garrido** - Living archaeology: Revealing plant technology in wild chimpanzees.
- 10:20 **Kate McGrath** - Facial fluctuating asymmetry tracks genomic diversity among gorilla subspecies

**10:40-11:00 Coffee Break**

## Session 6 • Pecha Kucha

- 11:00 **Cosimo Posth** - Palaeogenomic investigations at the Troisième caverne of Goyet, Belgium.  
**Elena Zavala** - Recovery of Ancient Hominin and Mammalian Mitochondrial DNA from High Resolution Screening of Pleistocene Sediments at Denisova Cave.  
**Diyendo Massilani** - Genomic analyses of the 34,000-year-old Salkhit individual from Mongolia.

### Questions

- 11:25 **Sarah Pederzani** - Contextualising Neanderthal behaviour during MIS 3 and 4 at La Ferrassie, France: Seasonal palaeotemperature reconstructions from oxygen stable isotopes.  
**Samantha Brown** - Investigation into the subsistence strategies of hominins from Denisova Cave (Russia) based on stable isotope data.  
**Virginie Sinet-Mathiot** - Using ZooMS to assess hominin subsistence behaviour during the Middle to the Upper Palaeolithic transition at Fumane (Italy).

### Questions

- 11:50 **Manuel Will** - The role of climate in the evolution of body and brain size of *Homo* in the last 2 million years.  
**Alexandra Schuh** - Neanderthal maxillary ontogeny at the micro- and macroscopic scales: an integrative approach to study facial growth.  
**Jaap Saers** - Trabecular and cortical bone structure correlate differently with terrestrial mobility in the human first metatarsal. Implications for behavioural inferences in the fossil record.

### Questions

### 12:15-14:15 Lunch

## JHE Workshop • „What is research integrity and why you should care“ (Auditorium)

## Session 7 • Podium

- 14:20 **Jérémy Dubeau** - The hominin footprints from Le Rozel (Manche, France): A snapshot to a Neandertal local group composition.  
14:40 **Juan Luis Arsuaga** - *Homo steinheimensis*, a comparison between the Steinheim skull and the Atapuerca Sima de los Huesos fossils.  
15:00 **Federica Landi** - The facial ontogeny of Neanderthals and *H. sapiens*.  
15:20 **Philipp Gunz** - *Homo heidelbergensis* is not your ancestor.  
15:40 **Sarah Freidline** - Reexamination of the Cranial and Mandibular *Homo sapiens* Fossils including a New Frontal Bone from Tam Pa Ling (Laos).

### 10:40-11:00 Coffee Break

## Session 8 • Podium

- 16:20 **Omry Barzilai** - Back to Geula Cave: New insights on the Mousterian of north Mt. Carmel, Israel.
- 16:40 **Nicolas Zwyns** - The Mousterian from Trou al'Wesse (Modave, Belgium): lithic taphonomy, measures of assemblage curation and implications for Late Neanderthal mobility patterns.
- 17:00 **Naomi Martisius** - A comparative investigation into Neanderthal bone tool manufacture and use.
- 17:20 **João Marreiros** - Functional analysis on the lithic assemblage from Layer I (the Bachokirian) at the onset of the Upper Paleolithic in Bacho Kiro cave, Bulgaria.
- 17:40 **Andrey Sinitsyn** - New reflections on the EUP and AMH dispersal in Eastern Europe.

## General Assembly • 18:10 Auditorium

Saturday, September 21st

## Session 9 • Podium

- 09:00 **Nicholas Conard** - MSA deposits at Sibudu and Umbeli Belli in KZN, South Africa document cultural change in high resolution.
- 09:20 **Will Archer** - Environmental carrying capacity, population density and the later Pleistocene expression of backed artefact manufacturing traditions.
- 09:40 **Marjolein Bosch** - Ornament or not?: Investigating perforation locations in *Tritia gibbosula* and *Columbella rustica* shells at Ksâr, Akil (Lebanon) using Micro-CT data.
- 10:00 **Ana Marin-Arroyo** - Chronology, climate and environmental conditions during the Middle to Upper Paleolithic transition in NW Spain with relevance to the debate on the disappearance of the Neanderthals.
- 10:20 **Sahra Talamo** - How to improve the radiocarbon calibration in the Middle to Upper Paleolithic - RESOLUTION for the study of human evolution.

10:40-11:00 Coffee Break

## Session 10 • Pecha Kucha

- 11:00 **Quentin Goffette** - Human exploitation of birds during the late Magdalenian at the Trou de Chaleux, Belgium.
- Mareike Stahlschmidt** - Preservation of Ancient DNA in Late Quaternary Stalagmites from Western Georgia.
- Isabella Reynard** - Bones of predation at Gorongosa National Park: insights into Plio-Pleistocene hominin resource exploitation.

Questions

- 11:25 **Guillermo Bustos-Pérez** - Degrees of rounding among lithic artifacts: experimental program and archaeological application.
- Alastair Key** - Controlled cutting tests reveal raw material optimisation in the Early Stone Age of Olduvai Gorge (Tanzania).
- Lisa Schunk** - Is a knife a knife? Testing bifacial backed knives in controlled experiments.

#### Questions

- 11:50 **Ivan Calandra** - Quantitative surface analysis: a collaborative endeavor between paleontology and archeology.
- Geeske Langejans** - A Neandertal tar-backed tool from the Dutch North Sea and Middle Paleolithic complex technology.
- N. Taipale** - Diverse means to an end: domestic tool hafting in the European Upper Palaeolithic.

#### Questions

### 12:15-14:00 Lunch and Poster Session 2

#### Session 11 • Podium

- 14:20 **Thibaut Deviese** - Dating the latest appearance of Neanderthals in Belgium.
- 14:40 **Helen Fewlass** - Radiocarbon dating small samples of Gravettian human remains from Dolni Vestonice II and Pavlov I (Czech Republic).
- 15:00 **Christoph Wißing** - When diet became diverse: Isotopic tracking of subsistence strategies among Gravettian hunters in Europe.
- 15:20 **Nicolas Bourgon** - Zinc isotopes in Late Pleistocene fossil mammal teeth as trophic level tracer.
- 15:40 **Frido Welker** - Multi-enzyme digestion of Pleistocene bone proteomes.

#### 16:00-16:20 Coffee Break

#### Session 12 • Podium

- 16:20 **Jennifer Leichtliter** - Enamel-bound stable nitrogen isotopic composition preserves trophic information in modern and fossil mammalian teeth.
- 16:40 **Clément Zanolli** - Taxonomic revision of the initial Early Pleistocene HCRP-U18-501 hominin mandible from Malawi: a tooth internal structural perspective.
- 17:00 **Tara Chapman** - The gait of *Homo naledi*.
- 17:20 **Martin Hora** - Origins of fur loss in humans: effect of gait, sweating capacity, and exposure to direct solar radiation.
- 17:40 **Michael Westaway** - Island South East Asia and its important role in hominin speciation.

#### Closing Dinner • 19:30 Musée de la Boverie

## Sunday September 22nd

### Excursion • Schedule

08:30	Departure by coach	Meeting point in Liège, Palais des Congrès
	Tour of three caves: Spy, Goyet, Scladina	
18:00	Farewell Drinks	Préhistomuseum
	Presentation of the Engis cave, activities (flint knapping, fire production etc.)	
20:00	<i>either</i> Return to Liège by coach	
	<i>or</i> Dinner at the museum (optional, costs not included)	Archéobistrot
22:30	Return to Liège	

### Excursion • The Belgian Neanderthals

This year's ESHE excursion will be devoted to Belgian Neanderthals. Ph.-Ch. Schmerling was the first to discover Neanderthal remains in the Engis cave during winter 1829-1830. He did not immediately recognise the Engis skull as belonging to a species distinct from *Homo sapiens*. However, the juxtaposition of human remains, stone tools and extinct animal species within the same karstic context led Schmerling to reject the biblical view of creation and believe in a greater antiquity of man. Schmerling's monographic publication - one of the earliest scientific research in Prehistory - was not accepted at that time, more than 20 years before the works of Darwin and Boucher de Perthes, and the eponymous discovery of the Neanderthal. In 1866, an excavation conducted in La Naulette by Ed. Dupont immensely contributed to the claim of old age for the highly controversial human type described as „Neanderthal“ ten years before: stratigraphic observations located the mandibula “similar to Neanderthal” under a thick sequence of sediments intersected with stalagmitic floors. This led the famous anthropologist P. Broca to write that this fossil constituted “the first fact providing Darwinists with anatomical evidence”. In 1885-1886, the research conducted in Spy cave by M. Lohest and M. De Puydt led to the discovery of two almost complete Neanderthal skeletons that were found in a well-controlled stratigraphic context, associated with “Mammoth age fauna” and Mousterian artefacts. These elements therefore provided the first definite evidence for the existence of prehistoric fossil humans, which differed morphologically from anatomically modern humans, and led to the final acceptance of Neanderthal man as a human type.

More recently multiple Neanderthal discoveries were reported, some directly on the field in precise stratigraphic

context (e.g. Couvin, Walou and Scladina cave) and others whilst reappraising 19th century collections (e.g. Spy and Goyet cave). This last decade, the fossils of Spy, Scladina and Goyet have been subject to intense scientific investigation and deeply enriched our knowledge on Neanderthal anatomy, behaviour, evolution and chronology.

### Scladina Cave

The discovery of numerous archaeological assemblages as well as the remains of a roughly 8-year-old Neanderthal child brought Scladina into prominence. Since 1978 the site has been excavated and studied continuously by professional archaeologists.

The stratigraphic sequence comprises ca. 150 layers, recording the climatic fluctuations of the last 200,000 years and yielding the richest palaeontological collection of Northwestern Europe. A dozen of archaeological assemblages have been identified, three of which are of outstanding significance: an early Weichselian butchery site (assemblage 5),



Scladina cave © SCAC

one of the latest occurrence of Mousterian in Northwestern Europe (assemblage 1A, around 43 ky calBP) as well as one of the earliest Upper Palaeolithic occurrences in Belgium (assemblage T, around 40 ky calBP). Since 1993, 19 teeth and bone fragments belonging to the same juvenile individual were discovered in an early Weichselian context (sedimentary complex 4A). This constitutes the most significant on-field discovery of Neanderthal remains in Belgium since Spy cave, in 1886.

### Spy Cave

This relatively small cave witnessed the excavation of tens of thousands of archaeological and paleontological objects between 1879 and 1981. No less than 14 distinct archaeological phases have been identified so far, including 10 Middle and Upper Palaeolithic assemblages. Spy, however, is mainly known as a reference site for European palaeoanthropology. As part of an interdisciplinary research conducted by geologist Maximin Lohest, archaeologist Marcel De Puydt and palaeontologist Julien Fraipont in 1886, skeletal remains were

unearthed in front of the entrance of the “Betche aux Rotches” cave. The remarkable monograph published the following year is the first-ever comprehensive analysis on Neanderthal skeletons.

### Goyet Cave

Since the 1860s Goyet cave has brought an abundant assortment of lithic artefacts, fauna remains, bone tools, ornaments and art objects from the Middle Palaeolithic to the Neolithic to light. Unfortunately, this material is deprived of reliable stratigraphic context due to both taphonomic processes and inaccuracy of the excavations. Recently, numerous human remains were discovered in the bone collections: several Neanderthals individuals from the Late Middle Palaeolithic as well as *Homo sapiens sapiens* from the Upper Paleolithic. This discovery made Goyet the largest palaeolithic human remains collection in North-West Europe and has allowed the use of recent methods to provide valuable information on the behavior and genetic history of European Paleolithic populations.



Left: Cave terrasse in Goyet © SCAC. Right: Children trying out flint knapping © Prehistomuseum

### Préhistomuseum

This museum, associated with the Ramioul Cave and located just a few kilometers away the Engis Cave, is one of the largest devoted to Prehistory in Europe. In order to provide a unique and original experience of the Prehistoric period, the museum did not confine itself to its award-winning building but also spreads over 30 hectares of land. Visitors can enjoy twelve extraordinary “experience-exhibitions” set along a discovery trail: discovering the museum exhibitions and conservation centre, prehistoric flint knapping, making ceramics in a „Neolithic“ fashion, recreating varied human locomotion on a barefoot walk path, getting to know more about human evolution through a vegetal labyrinth, or even tasting food from the past in a restaurant that cooks based on archaeological evidence and authentic recipes from historical periods.



## Posters

The two posters sessions will take place at 12:15-14:00 on Thursday, 19th and Saturday, 21st.

All posters will be on display for the entire duration of the conference.

Below the poster presentations are listed in alphabetical order.

Name	Title	Session	No.
<b>Alba, David M.</b>	A new dryopithecine mandibular fragment from the middle Miocene of Abocador de Can Mata (Vallès-Penedès Basin, NE Iberian Peninsula).	Session 1, Th. 12:15-14:00	55
<b>Albessard, Lou</b>	Trends in cerebral organisation in Upper Palaeolithic and recent humans.	Session 1, Th. 12:15-14:00	23
<b>Alichane, Hajar</b>	Comparative analysis of the enamel-dentine junction of the lower molars in the Aterian populations.	Session 1, Th. 12:15-14:00	81
<b>Arlegi, Mikel</b>	Evolutionary selection and morphological integration in the vertebral column of modern humans.	Session 2, Sa. 12:15-14:00	44
<b>Aviá, Yasmina</b>	Diet-related differences and wear effects in dental topography of first molars from papionini tribe primates.	Session 1, Th. 12:15-14:00	57
<b>Balolia, Katharine</b>	Size and shape variation among the <i>Australopithecus africanus</i> mandibular specimens from Sterkfontein and Makapansgat.	Session 1, Th. 12:15-14:00	5
<b>Barash, Alon</b>	Changes in thoracic cage morphology from birth into adulthood.	Session 2, Sa. 12:15-14:00	32
<b>Bartsch, Silvester</b>	Global or local: Where do we find ontogenetic change in hominid cranial shape?	Session 1, Th. 12:15-14:00	13
<b>Baumann, Malvina</b>	Neandertalian bone industry in Chagyrskaya (Altai, Russia).	Session 2, Sa. 12:15-14:00	114
<b>Bayle, Priscilla</b>	The Tooth Fairy collection of human deciduous teeth: learning from a documented sample of living children to understand factors related to morphology, growth, and developmental disruptions in the past.	Session 1, Th. 12:15-14:00	95
<b>Been, Ella</b>	Who's afraid of hypolordosis? Implications of Neandertal spinal posture reconstruction.	Session 2, Sa. 12:15-14:00	6
<b>Benson, Alexa</b>	Investigating palaeoclimate variability in the Western Iberian Peninsula during the last glacial period using speleothems.	Session 2, Sa. 12:15-14:00	126

## Posters

<b>Bicho, Nuno</b>	First results of a Middle Stone Age survey in the Kerma region, northern Sudan.	Session 2, Sa. 12:15-14:00	86
<b>Bocaege, Emmy</b>	Human upper incisors from the Gravettian site of Fournol (Soturac, Lot, France) show high biological variation in Upper Palaeolithic human populations.	Session 1, Th. 12:15-14:00	105
<b>Brophy, Juliet</b>	Hominin dental material from a new passage in the Rising Star Cave System, South Africa.	Session 1, Th. 12:15-14:00	79
<b>Bucchi, Ana</b>	Patterns of insertion areas in proximal phalanges of African apes and modern humans.	Session 2, Sa. 12:15-14:00	2
<b>Buck, Laura</b>	The effect of admixture on pelvic morphology.	Session 2, Sa. 12:15-14:00	26
<b>Buzi, Costantino</b>	A New Tool for Digital Alignment in Virtual Anthropology.	Session 1, Th. 12:15-14:00	15
<b>Carvalho, Milena</b>	An assessment of refugia concepts during MIS 3 in Iberia: the case from Lapa do Picareiro (Portugal).	Session 2, Sa. 12:15-14:00	124
<b>Cazenave, Marine</b>	The TM 1517 odontoskeletal assemblage from Kromdraai B, South Africa, and the maturational pattern of <i>Paranthropus robustus</i> .	Session 1, Th. 12:15-14:00	65
<b>Chappell-Smith, Kerris</b>	A Novel Social Dimension of Bipedal Behaviour and its Implications for Human Evolution: A Cross- Disciplinary and Cross-Species Investigation.	Session 2, Sa. 12:15-14:00	14
<b>Chapple, Simon</b>	Challenging the paradigm: how enamel-dentine junction variation across primates is inconsistent with current tooth crown nomenclature schemes.	Session 1, Th. 12:15-14:00	63
<b>Cofran, Zachary</b>	Virtual reappraisal of the Krapina 1 juvenile cranium.	Session 1, Th. 12:15-14:00	39
<b>Collard, Mark</b>	Back pain, vertebral shape, and the evolution of bipedalism.	Session 2, Sa. 12:15-14:00	8
<b>Coolidge, Frederick</b>	Symbolic Behavior in Planaria, Dogs, and <i>Homo sapiens</i> .	Session 1, Th. 12:15-14:00	33

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<b>David, Romain</b>	Accurately predicting head motion in fossil primates using soft-tissue information.	Session 1, Th. 12:15-14:00	45
<b>de Sousa, Alexandra A.</b>	Social factors in the evolution of the human hippocampus.	Session 1, Th. 12:15-14:00	35
<b>Dean, Christopher</b>	The distribution of zinc in modern and fossil enamel, dentine and cementum.	Session 1, Th. 12:15-14:00	87
<b>Deckers, Kim</b>	Ontogenetic changes in third metacarpal trabecular bone in western lowland ( <i>Gorilla gorilla</i> ) and mountain gorillas ( <i>Gorilla beringei</i> ).	Session 1, Th. 12:15-14:00	1
<b>del Bove, Antonietta</b>	Sexual dimorphism in the human calvarium: a Geometric Morphometric approach.	Session 1, Th. 12:15-14:00	43
<b>Devereux, Emma</b>	Plant nutritional variation across a savanna biome: Investigating hominin dietary ecology on the South African Lowveld.	Session 2, Sa. 12:15-14:00	54
<b>Di Maida, Gianpiero</b>	The DISAPALE project: 3D and lithic types of European Paleolithic.	Session 2, Sa. 12:15-14:00	80
<b>Dilena, Miguel Angel</b>	Constructive Archaeology: Restoring a Palaeolithic Excavation through a Virtual Time Machine.	Session 1, Th. 12:15-14:00	135
<b>Dogandzic, Tamara</b>	Controlled experiments on flake formation using glass and different raw materials.	Session 1, Th. 12:15-14:00	115
<b>Dolding- Smith, Jessica</b>	Evaluating the Anterior Dental Loading hypothesis in the Middle Pleistocene populations from Sima de los Huesos.	Session 1, Th. 12:15-14:00	83
<b>d'Oliveira Coelho, João</b>	A MaxEnt approach to estimate the likelihood of finding new fossil sites in Lake Turkana, Kenya, using satellite images.	Session 2, Sa. 12:15-14:00	62
<b>Fedato, Annapaola</b>	Electrodermal activity and haptic perception with Lower Paleolithic stone tools.	Session 1, Th. 12:15-14:00	109
<b>Figus, Carla</b>	The ontogeny of bipedalism: insights from trabecular changes during growth.	Session 2, Sa. 12:15-14:00	16
<b>Fiorenza, Luca</b>	Functional molar macrowear analysis in <i>Pongo pygmaeus</i> and <i>Pongo abelii</i> .	Session 1, Th. 12:15-14:00	59

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<b>Fitton, Laura</b>	Examining the relationship between tooth size and food size: the functional consequence of dental reduction during hominin evolution.	Session 1, Th. 12:15-14:00	89
<b>Foley, Robert</b>	<i>Homo naledi</i> , <i>Homo floresiensis</i> and „taxic outlieriness“: a comparative approach to odd species.	Session 1, Th. 12:15-14:00	11
<b>Fornai, Cinzia</b>	Morphological assessment of modern human upper and lower first molars.	Session 1, Th. 12:15-14:00	93
<b>Freyne, Alison</b>	New insights into historic excavations of a Later Stone Age cemetery at Grotte des Pigeons.	Session 2, Sa. 12:15-14:00	96
<b>Gallo, Giulia</b>	Differential preservation of burnt bone: Impacts on the visibility of Upper Paleolithic fire in the steppes of Mongolia.	Session 1, Th. 12:15-14:00	119
<b>Gameiro, Cristina</b>	Portela II (Leiria, Portugal): a Vale Comprido Points specialized production area in Proto-Solutrean times?	Session 2, Sa. 12:15-14:00	74
<b>García Campos, Cecilia</b>	Sexual dimorphism of the Middle Pleistocene hominins from Sima de los Huesos (Burgos, Spain): a study the enamel and dentine dimensions of the permanent canines.	Session 1, Th. 12:15-14:00	103
<b>Gellis, Jason</b>	Inferring human population history and diversity from tooth roots: the application of a phenotypic set approach to global variation.	Session 1, Th. 12:15-14:00	67
<b>González Rabanal, Borja</b>	Vascular grooves on human tibias as a proxy for Paleolithic mobility pattern inference: the case of the Lower Magdalenian „Red Lady“ of El Mirón cave (Cantabria, Northern Spain).	Session 2, Sa. 12:15-14:00	34
<b>Graham, John W.</b>	Change in the discourse: the impact of ancient DNA analysis on Neanderthal studies.	Session 2, Sa. 12:15-14:00	104
<b>Gruwier, Ben</b>	<i>Homo erectus</i> palaeoecology in Java: A study of cervid post-cranial ecomorphology.	Session 2, Sa. 12:15-14:00	60
<b>Hammond, Philippa</b>	Dynamic landscapes of fear: Effects of habitat-heterogeneity, seasonality, and predator diversity on a population of terrestrial primates ( <i>Papio ursinus</i> ).	Session 2, Sa. 12:15-14:00	132

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<b>Hanegraef, Hester</b>	Facial morphology of <i>Australopithecus afarensis</i> : exploring intraspecific variation in human evolution.	Session 1, Th. 12:15-14:00	3
<b>Harcourt- Smith, William</b>	Predicting ankle mechanics in the fossil hominin record using finite element modeling.	Session 2, Sa. 12:15-14:00	22
<b>Harvati, Katerina</b>	Marathousa 2: A new Middle Pleistocene locality in Megalopolis Basin (Greece) with evidence of human modifications on faunal remains.	Session 2, Sa. 12:15-14:00	110
<b>Heinrich, Susann</b>	A Model for Predicting the Heating Temperatures of Middle Stone Age Silcrete Artefacts Based on Non-destructive Infrared Analyses.	Session 1, Th. 12:15-14:00	123
<b>Heuzé, Yann</b>	Variation in facial skeletal shape, nasal structures, and paranasal sinuses in adults from Cambodia and France.	Session 1, Th. 12:15-14:00	17
<b>Horta, Pedro</b>	Lithic bipolar reduction strategies in the Late Stone Age site of Txina Txina, Mozambique.	Session 2, Sa. 12:15-14:00	76
<b>Jimenez, Elodie-Laure</b>	Multi-stable isotope zooarchaeological investigations at Abri du Maras: exploring the palaeoecological context of Neanderthal subsistence strategies in the Rhône Valley.	Session 2, Sa. 12:15-14:00	106
<b>Johnson, Corey</b>	Raw material impacts on lithic technology at Donggutuo, Nihewan Basin, China: Preliminary results from the 2016 excavation campaign.	Session 2, Sa. 12:15-14:00	82
<b>Karakostis, A. -F.</b>	Original experimental support for the effects of physical activity on the multivariate patterns among entheses.	Session 2, Sa. 12:15-14:00	40
<b>Kedar, Einat</b>	The Legacy of the Paranasal Sinuses.	Session 1, Th. 12:15-14:00	41
<b>Kivell, Tracy</b>	Partial hominin upper limb skeleton (KNM-ER 64062) from Ileret, Kenya (1.8 Ma).	Session 2, Sa. 12:15-14:00	28
<b>Kozowyk, Paul</b>	Understanding taphonomic and identification biases of ancient adhesives through experimentation.	Session 1, Th. 12:15-14:00	113

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<b>Krenn, Viktoria</b>	Evolution of morphological variation and sexual dimorphism of the modern human sacrum.	Session 2, Sa. 12:15-14:00	20
<b>Krüger, Susanne</b>	Diet, environment and technological performance of <i>Paranthropus boisei</i> .	Session 1, Th. 12:15-14:00	91
<b>Kubicka, Anna Maria</b>	Variation in femoral cross-sectional indicator of robusticity (J) in human populations.	Session 2, Sa. 12:15-14:00	46
<b>Lagle, Susan</b>	Comparison of faunal data and associated behavioral interpretations from Quina Mousterian contexts in southwestern France.	Session 2, Sa. 12:15-14:00	108
<b>Le Cabec, Adeline</b>	Taphonomic reassessment of the early, <i>Homo</i> mandible from Garba IVE, and questioning the diagnosis of an ancient case of amelogenesis imperfecta.	Session 1, Th. 12:15-14:00	77
<b>Le Luyer, Mona</b>	New human remains associated with Magdalenian rock art from La Marche cave (Lussac-les-Châteaux, France).	Session 1, Th. 12:15-14:00	53
<b>Le Maitre, Anne</b>	Macaque-like or baboon-like? What we learn from the bony labyrinth of <i>Paradolichopithecus</i> .	Session 1, Th. 12:15-14:00	47
<b>Libois, Timothée</b>	Investigating the Aurignacian-Gravettian „Transition“ East of the Carpathians.	Session 2, Sa. 12:15-14:00	94
<b>Limmer, Laura Sophia</b>	An outlook on new 3d methods for dental enamel hypoplasia analysis using confocal imaging profilometry.	Session 1, Th. 12:15-14:00	85
<b>Lockey, Annabelle</b>	A comprehensive metric analysis of Palaeolithic deciduous and permanent teeth.	Session 1, Th. 12:15-14:00	101
<b>Lombao, Diego</b>	A new method to infer the reduction intensity on cores and handaxes: The Volumetric Reconstruction Method (VRM).	Session 1, Th. 12:15-14:00	117
<b>López Herráez, David</b>	Reconstructing Neandertal population history by targeted enrichment of variable positions in their nuclear genomes.	Session 2, Sa. 12:15-14:00	102
<b>Lugli, Frederico</b>	Elemental imaging of human teeth by laser ablation ICP-TOF-MS: fast acquisition and high-resolution.	Session 1, Th. 12:15-14:00	75

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<b>Macho, Gabriele</b>	The partial skeleton StW 431 provides new insights into the palaeobiology of Plio-Pleistocene hominins from Sterkfontein, South Africa.	Session 1, Th. 12:15-14:00	7
<b>Mahoney, Patrick</b>	Enamel development and thickness in deciduous canines from <i>Pongo pygmaeus</i> and <i>Pan troglodytes</i> .	Session 1, Th. 12:15-14:00	61
<b>Mallol, Carolina</b>	Fire and short-term human occupations in Iberia during MIS 4: Evidence from Abric del Pastor (Alcoy, Spain).	Session 1, Th. 12:15-14:00	129
<b>Marginedas , Francesc</b>	Making skull cups: butchering traces on cannibalised human skulls from five European archaeological sites.	Session 2, Sa. 12:15-14:00	116
<b>Martelli, Sandra</b>	Postnatal developmental interactions between the hominoid cranial base, suprahyoid muscle complex and the mandibular symphysis.	Session 1, Th. 12:15-14:00	29
<b>Mateo Lomba, Paula</b>	Carcass processing with bone tools: a multidisciplinary approach.	Session 2, Sa. 12:15-14:00	112
<b>May, Hila</b>	Evidence of social support revealed by healed trauma in human foot bones from Manot Cave, an Early Upper Paleolithic site.	Session 2, Sa. 12:15-14:00	48
<b>McPherron, Shannon</b>	The Middle Stone Age Site of Negus Kabri, Asbole, Ethiopia.	Session 2, Sa. 12:15-14:00	84
<b>Mednikova, Maria</b>	Concerning body manipulation practice during the Stone Age: trepanations and ritual amputations.	Session 2, Sa. 12:15-14:00	50
<b>Menendez, Lumila</b>	Retrodeformation techniques and 3D morphometric analysis of an early Holocene South American skull (Cuncaicha, Peru).	Session 1, Th. 12:15-14:00	9
<b>Mentzer, Susan Marie</b>	A deeper look into the Mousterian Hearths at Kebara Cave, Israel.	Session 1, Th. 12:15-14:00	133
<b>Michel, Marine</b>	What about taphonomy for prehistoric stone tools? The effect of freeze and thaw cycles on use-wear and residues.	Session 1, Th. 12:15-14:00	111
<b>Monnier, Gilliane</b>	New Excavations at Crvena Stijena, Montenegro: First Results.	Session 2, Sa. 12:15-14:00	88

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<b>Mori, Tommaso</b>	Basicranial ontogeny comparison in <i>Pan troglodytes</i> and <i>Homo sapiens</i> and its use for developmental stage definition of KNM-ER42700.	Session 1, Th. 12:15-14:00	37
<b>Nava, Alessia</b>	Postnatal crown formation time of three Neanderthals deciduous teeth from Northeastern Italy.	Session 1, Th. 12:15-14:00	99
<b>Neubauer, Simon</b>	Brain lateralisation in humans and apes - insights from endocranial casts.	Session 1, Th. 12:15-14:00	21
<b>Nyssen, Pieter</b>	Studying Bone Microstructure in Primates: Shedding Light on Some Methodological Constraints.	Session 2, Sa. 12:15-14:00	4
<b>O'Mahoney, Thomas</b>	Endostructural and periosteal variation in the humerus in juvenile Pleistocene individuals.	Session 2, Sa. 12:15-14:00	24
<b>Otto, Taylor</b>	Moving Around and Settling Down - A Methodological Framework for Analyzing Hunter-Gatherer Land Use.	Session 2, Sa. 12:15-14:00	134
<b>Oxilia, Gregorio</b>	The most recent Neandertal remains in Italy.	Session 1, Th. 12:15-14:00	49
<b>Pablos Fernandez, Adrian</b>	A notch in the hallux. Presence of pseudoepiphysis in the hallucal metatarsals from Sima de los Huesos Middle Pleistocene site (Atapuerca, Burgos).	Session 2, Sa. 12:15-14:00	36
<b>Parow- Souchon, Hannah</b>	Human-environment interaction in the Upper Palaeolithic of the Southern Levant.	Session 2, Sa. 12:15-14:00	130
<b>Pearson, Alannah</b>	Temporal lobe morphology in Neanderthals and modern humans.	Session 1, Th. 12:15-14:00	25
<b>Picin, Andrea</b>	Neanderthals lithic toolkits in high mobility context: an overview from Teixoneres Cave (Spain).	Session 2, Sa. 12:15-14:00	78
<b>Pineda, Antonio</b>	Open-air sites reveal evidences about Lower Palaeolithic hominin foraging activities.	Session 2, Sa. 12:15-14:00	120
<b>Piqué- Fandiño, L.</b>	Birth seasonality in the Baka pygmies.	Session 2, Sa. 12:15-14:00	52



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<b>Pokhojaev, Ariel</b>	Temporal changes in human mandibular size and shape throughout the Terminal Pleistocene-Holocene Levant.	Session 1, Th. 12:15-14:00	71
<b>Profico, Antonio</b>	Endomaker: an algorithm for fast, accurate, fully automatic extraction of endocasts and their volumes from digital models of the skull.	Session 1, Th. 12:15-14:00	19
<b>Püschel, Thomas</b>	The biomechanical importance of the scaphoid-centrale fusion during simulated knuckle-walking and its implications for the locomotion of the last common ancestor of humans and African apes.	Session 2, Sa. 12:15-14:00	10
<b>Rampelli, Simone</b>	Unveiling traces of the Neanderthal gut microbiome by shotgun metagenomics of feces-containing sediment from El Salt (Alicante, Spain).	Session 2, Sa. 12:15-14:00	56
<b>Rathmann, Hannes</b>	Testing the utility of different ASUDAS dental trait combinations for biodistance analysis.	Session 1, Th. 12:15-14:00	69
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Abstracts  
European Society for the study of Human Evolution

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## A new dryopithecine mandibular fragment from the middle Miocene of Abocador de Can Mata (Vallè-Penedès Basin, NE Iberian Peninsula)

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A mandibular fragment with  $M_2$ – $M_3$  (IPS1826+1827) found in 1941 at Can Vila (CV), els Hostalets de Pierola (NE Iberian Peninsula), was initially assigned to *Dryopithecus fontani* but subsequently used to erect *Sivapithecus occidentalis* [1]. CV is thought to be close to, but somewhat lower stratigraphically than, the type locality of *Pierolapithecus catalaunicus* (ACM/BCV1) [2, 3], thus raising doubts about the synonymy between these taxa. Previously, '*S.*' *occidentalis* had been synonymized with either *D. fontani* or *Hispanopithecus laietanus*. However, following the description of *P. catalaunicus* it has been considered a nomen dubium [2, 4], due to the lack of *P. catalaunicus* lower molars and the record of other large-bodied hominoids (*D. fontani* and *Anoiapithecus brevirostris*) from roughly coeval ACM localities [4, 5]. Here we report a previously unpublished right mandibular fragment with  $M_2$  (IPS41734). It comes from locality ACM/BCV4, which is only minimally younger than ACM/BCV1 and CV (11.94 vs. 11.96 and ~12.0 Ma, respectively [5]). Based on outer enamel surface (OES) morphology, enamel-dentine junction (EDJ) morphology, and two-dimensional relative enamel thickness (2DRET), we compare IPS41734 with other middle Miocene dryopithecines from ACM to provide a more conclusive taxonomic assignment and reassess the taxonomic status of '*S.*' *occidentalis*. The specimens, housed at the Institut Català de Paleontologia Miquel Crusafont (ICP), were scanned using microfocus X-ray  $\mu$ CT and processed following standard methods (see [3] for details). OES comparisons were also undertaken with the holotype of *D. fontani* (HGP1) from France. IPS41734 displays a Y5 occlusal pattern with hypoconid-entoconid contact. The crown is longer than broad (breadth/length index = 9.2 mm/10.9 mm = 84%) and displays slight buccal waisting and minimal distal crown tapering (except for the protruding distolingual corner). It has a restricted distal fovea with a conspicuous hypoentocristid, a tuberculum intermedium just behind the metaconid, no patent cingulids (except for some buccal remnants), and some enamel wrinkling at the talonid basin. In OES morphology IPS41734 closely resembles the  $M_2$  of '*S.*' *occidentalis*, while comparisons with *A. brevirostris* are restricted due to the poor preservation of the holotype  $M_2$ , which displays slightly broader proportions (breadth/length index = 88%). In contrast, IPS41734 can be distinguished from the  $M_2$  of *D. fontani* by multiple features displayed by the latter: lack of hypoconid-entoconid contact, non-protruding distolingual crown corner, more distal entoconid, open distal fovea without hypoentocristid, conspicuous buccal cingulid, and broader crown proportions. EDJ morphology shows further similarities between IPS41734 and '*S.*' *occidentalis*, including a buccal cingulid much better developed than at the OES (particularly between protoconid-hypoconid and hypoconid-hypoconulid), as well as a centrally tilted and mesiodistally elongated and double metaconid dentine horn (in agreement with the twinned metaconid at the OES). Finally, 2DRET results indicate that IPS41734 (15.9) and particularly '*S.*' *occidentalis* (19.6) have thicker enamel than both *P. catalaunicus* and *A. brevirostris* (similar to orangutans), and especially *D. fontani* (more comparable to African apes) [3]. Our results allow us to discount an assignment of IPS41734 to *D. fontani* and support its conspecificity with the '*S.*' *occidentalis* holotype, but do not favor their attribution to either *P. catalaunicus* or *A. brevirostris* (in which case the species name of '*S.*' *occidentalis* would take precedence). Since additional dentognathic hominoid material from ACM combining upper and lower molars would be required to settle this issue, we provisionally leave these specimens unassigned to genus (*Dryopithecini* indet). However, ongoing 3D analyses of the internal tooth structure might throw additional light into this question in the near future.

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## Trends in cerebral organisation in Upper Palaeolithic and recent humans

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At the forefront in the history of studying fossil crania is the idea that the development of a large brain, and with it highly complex cognition, is among the major characteristics of human evolution. Thinking and behaving like extant humans is often considered to be the benchmark for “modernity”, and clues attesting to the advent of these characteristics have been looked for, both in the archaeological record and in the anatomical evolution of hominins. The study of endocasts - their volume, general morphology, convolutional patterns, and the development of cognitive areas recognised in extant humans – has been contributing information to this question since the beginnings of the field of palaeoanthropology. Within our own species, some differences are documented between the endocasts of Upper Palaeolithic samples and those of recent samples, including a 10% decrease in average volume [1], an increase in the size of the parietal lobe chord relative to frontal and occipital chords [2], and a relative increase in the importance of the cerebellum compared to the occipital lobe [3] and perhaps to the cerebrum [4]. This is sometimes interpreted in terms of cognitive evolution and linked up to the archaeological record. However, there is relatively little information available concerning endocranial variations in recent samples, or putting endocranial morphology in the context of cranio-facial morphological integration. Here, we propose to discuss this issue using data based on two complementary methods: 3D geometric morphometrics (GM) and surface deformations. GM is widely and successfully used in palaeoanthropology in order to tackle questions related to morphological variability and shape change, while analyses of surface deformations are newer to the field and offer one solution to problems arising from the lack of homologous features on some endocranial areas [5]. Combining these methods allowed us to cross-examine our results. We were able to analyse both a simplified representation of the endocast featuring landmarks of special interest (for instance on sulci representing the main divisions between the cerebral lobes), and deformations occurring over the entire surface of the endocast, including areas devoid of reproducible landmarks. The main results of these analyses are two-fold. We find that endocranial shape varies in different populations, in a similar fashion to neurocranial morphology. We also find slightly different tendencies in overall morphology and in cerebral organisation in Upper Palaeolithic *Homo sapiens* relative to recent populations. We argue that these can be linked to more globular cerebral and neurocranial morphologies in some Holocene populations.

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## Comparative analysis of the enamel-dentine junction of the lower molars in the Aterian populations

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The Aterian fossil humans are one of the richest samples of human remains associated with Middle Stone Age assemblages in Africa, but they are still poorly described [1]. Our study mainly focuses on the morphology of the enamel-dentine junction (EDJ) that was visualized by segmenting the micro tomographic scans of each molar. The sample include 155 first and second mandibular molars of recent and fossil humans. The fossil sample originates from 4 different regions: North Africa (El Harhoura 2, Dar es-Soltan 2, Contrebandiers and Jebel Irhoud), South Africa (Die Kelders and Equus), the Near East (Qafzeh and Skhul), and Neandertals from Europe. The recent *H. sapiens* sample includes molars from Holocene archaeological sites in Belgium, anatomical collections and clinical extractions. On each specimen, we digitized 3D landmarks on the tips of the dentine horns of the four primary cusps (protoconid, metaconid, entoconid and hypoconid) in Avizo. We then placed the same number of curve-semilandmarks (n=60) on the marginal ridge connecting the four dentine horns, following the protocol described by [2] using Mathematica. After semi-landmark sliding, we performed Procrustes superimposition to compute shape variables, and used centroid size as a measure for the overall size of the dentine crown. The shape data were analyzed using principal component analysis (PCA). The dental size of the Aterian sample is generally very large, reminiscent of the Near East series from Qafzeh and Skhul. Centroid sizes of M1 and M2 of recent *H. sapiens* are smaller than in fossil *H. sapiens* and Neandertals. This primarily results from a size reduction within the *H. sapiens* lineage. The molar centroid sizes are more variable in fossil *H. sapiens* than in Neandertals and recent *H. sapiens*. Fossil *H. sapiens* values overlap with those of the Neandertals, but generally display higher values. In a PCA of M1 EDJ shape, fossil *H. sapiens* and recent *H. sapiens* are similar, and neither group overlaps with Neandertals. Neandertals display different crown outlines between protoconid and metaconid than *H. sapiens*. For M1, all Aterian individuals are separated from the Neandertal distribution and cluster with recent *H. sapiens*. Whereas the shape differences between *H. sapiens* and Neandertals are consistent, but subtle for the first molar, M2 shape differences are more pronounced: generally, the EDJ crown shape of fossil *H. sapiens* are more buccally protruding than lingually. Neandertals are characterized by tall crowns compared to fossil *H. sapiens* and recent *H. sapiens*. In a PCA all but one Aterian M2 cluster with recent *H. sapiens*; the M2 of El Harhoura falls within the distribution of the Neandertals. Our findings confirm the attribution of the Aterian individuals to an early *H. sapiens* population. However, they are highly variable and retain primitive characteristics, which may explain similarities with Neandertals for some specimens.

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## Environmental carrying capacity, population density and the later Pleistocene expression of backed artefact manufacturing traditions

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As is the case today, both climate variability and population density influenced human behavioural change in the past. The mechanisms underpinning later Pleistocene human behavioural evolution, however, remain contested. Many complex behaviours evolved in Africa, but early evidence for these behaviours varies both geographically and temporally. Scientists have not been able to explain this flickering pattern, which is present even in sites and regions clearly occupied by *Homo sapiens*. Certain later Middle and Later Stone Age technologies are useful archaeological proxies for complexity, as the skills necessary for their production would have required high fidelity - potentially process-oriented - learning and cooperation. These complex behaviors are represented archaeologically by a range of technologies, as well as symbolic items such as ground or engraved organic materials (e.g. perforated and incised ostrich egg shells, bones, teeth and ochre), many of which are preserved only under favorable conditions or are constrained by available raw-materials. In Africa, the vast majority of these proxies tend to be confined to particular sub-regions or sites, making them unsuitable for broad scale quantitative models.

Backed stone artefacts are arguably one such technology that are patchy but, in terms of data spread, are spatially and temporally ubiquitous in the African later Pleistocene. In Africa, they are also widely accepted to be synonymous with skills like composite weapon design and various multi-phase lithic production processes. To explore this flickering pattern of cultural complexity, here the presence and frequency of evidence for backed stone artefact production are modelled against climate driven, time series population density estimates, in all known African Late Pleistocene archaeological sites (n=116 sites, n=409 assemblages, n=893 dates). In addition, a moving-window, site-density population estimate is included at the scale of southern Africa. Backed stone artifacts show a broad but sporadic distribution in Africa, prior to their association with *Homo sapiens* dispersing into Europe 45-40 ka. Two independent population density estimates explain this pattern, and implicate nuanced interactions between climate change and demography in the expression of cultural complexity in Pleistocene *Homo sapiens*.



## Evolutionary selection and morphological integration in the vertebral column of modern humans

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The evolution of the vertebral column in mammals is conservative with regard to the number of vertebrae in amniotes [1], and displays a clear morphological regionalization of the pre-sacral vertebral column into cervical, thoracic and lumbar regions. In contrast to the numerical constraint, the ancestral mammalian vertebral column has become morphologically more complex through time, permitting the relative independence of each region due to developmental and functional factors [2]. Modern humans display a unique mode of locomotion compared to other mammals and at the same time, a derived morphology of the pre-sacral vertebral column. Conceptually, the organization of the vertebral column can be treated either as a whole integrated structure evolutionarily dissociated from the abaxial skeleton, or as a modularized system where each morphological region is internally integrated. In the last few decades much research has been carried out analyzing patterns and magnitudes of integration and modularity in vertebrates [3]. However, only recently a few authors have paid attention to phenotypic integration in the vertebral column [4], with special interest in the cervical region of the vertebral column [5]. In this work our main objective is to quantify integration, modularity and response to selection in the pre-sacral vertebral column of modern humans. To do that 17 linear measurements were taken on each of the 24 presacral vertebrae in more than 100 individuals, producing a total of approximately 39,000 measurements. Then we quantified patterns and magnitudes of integration at regional, vertebral and intra-vertebral levels. Additionally, we calculated the ability of vertebrae to respond to selection by quantifying differences in evolvability, flexibility and constraint throughout the spine. We highlight three crucial findings in this study of the modern human spine. The first is that caudal pre-sacral vertebrae are more evolvable than those located more cranially in the vertebral column. Secondly, central thoracic vertebrae are internally the most integrated, decreasing the magnitudes of overall integration towards the most peripheral vertebrae (C1 and L5). Thirdly, correlations across vertebrae show the high influence of the *Hox* genes in vertebral interactions, subdividing the pre-sacral vertebrae into four functional and developmental modules (i.e. cervical, cranial and caudal thoracic and lumbar), in which the fewest number of interactions across vertebrae occur in the cervical region than in the thoracolumbar region. We conclude that the results obtained for the modern human pre-sacral vertebral column can be related to three main factors: body plan organization expressed by the *Hox* genes, the strong developmental constraints that determine the number of mammalian vertebrae, and, finally, the functional requirements of an adaptation to bipedal locomotion in the human lineage. Additionally, we hypothesized that the integration and evolvability patterns found in the pre-sacral vertebrae of modern humans could be similar or common to mammals due to the strong ancestral influence of the organization of the pre-sacral vertebral column. However, differences in the magnitudes of the analyzed indices between species and clades could depend on developmental and functional factors, the latter mainly related to differences in mode of locomotion.

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## ***Homo steinheimensis*, a comparison between the Steinheim skull and the Atapuerca Sima de los Huesos fossils**

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With the rise of the 3D Geometric Morphometrics (GMM) we often forget that, after all, GMM is about phenetics, and phenetics is not the most suitable way to make phylogenetic inferences. Cladistics is. In this paper we analyse the species *Homo steinheimensis* taking a cladistic approach. *Fortunately*, this is the only possible way to study it since the general distortion of the type specimen, the Steinheim skull, would not allow a GMM analysis. This species (created in 1936 by Berekhemer) lacks a proper diagnosis, and as such, it is not clear whether it is a valid species. However, this would not affect the cladistic analysis [1]. In the first description of the specimen, the morphology of the face was the main trait used for the phylogenetic interpretation, and this was described as sapiens-like and not Neandertal-like. Berekhemer's conclusion was that all the traits shared by Steinheim and the Neandertal specimens known to that date were plesiomorphies ("The other, Neandertal-like features of the Steinheim cranium could then perhaps be explained assuming a common ancestry with Neanderthals through an older lineage"). Today, practically nobody argues that Steinheim belongs to the Neandertal clade, as a sister group of the latter "classic" Neandertals [2]. But the remarkable "sapiens-like" morphology of the Steinheim face is either neglected or attributed to postmortem deformation. Rak considered that the Steinheim face displayed a generalized (primitive) pattern, as modern humans do, the condition from which the extended Neandertal face would arise [3]. But if this is the case, who are the pre-Steinheim fossils? The specimens attributed to *Homo tautavelensis/heidelbergensis* do not show a "sapiens-like" face. No other European Middle Pleistocene fossil show such a strong maxillary flexion. Only *Homo antecessor*, and perhaps the Zhoukoudian *Homo erectus* specimens do. Could the Steinheim facial morphology rather be the product of plastic distortion? In our analysis we did not find signs of major plastic deformation in the maxillary region, so we conclude that its facial morphology cannot be attributed to it. On the other hand, the face of Steinheim is reminiscent of the Sima de los Huesos (SH) faces, although in the latter, the morphology is more derived [4]. In the rest of the features, Steinheim is generally similar to the SH specimens, in some traits slightly more primitive, in other traits slightly more derived towards the "classic" Neandertal condition. Regarding the dentition, Steinheim shares with the SH sample the expression of classic and diagnostic Neandertal features such as rhomboidal upper molars, with large and protruding hypocones [5]. The M3 of Steinheim are remarkably reduced and the hypocone is absent, a pattern in common with the majority of the Sima de los Huesos and the Pontnewydd upper M3s. In contrast, Steinheim does not show the degree of M2 reduction displayed by the Sima de los Huesos population, although the strong postcanine reduction of the latter could be a particularity of this group (Martín-Torres et al., 2012). Our conclusion is that Steinheim and Sima de los Huesos, as well as other specimens such as Aroeira, Swanscombe and Reilingen can be classified together in a group that is cladistically intermediate between *Homo tautavelensis/heidelbergensis* and *Homo neanderthalensis*.

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## Lower Paleolithic shaped stone balls were used for bone marrow extraction

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The presence of shaped stone balls (SSBs), also known as spheroids or polyhedrons, in early Paleolithic sites has attracted scholarly attention since the pioneering work of Louis and Mary Leakey in Olduvai, Tanzania. Despite the persistent production of SSBs for two million years, their function is still unknown. We present new results on the use of ten SSBs from the Middle Pleistocene (420–200ka) Qesem Cave, Israel based on use-wear and residue analyses, accompanied by a dedicated experimental program. The use wear and residue indicate crushing of fresh bone by thrusting percussion and provide direct evidence for the repeated use of SSBs to access fat-rich bone marrow of animal prey. These traces are as yet the only (and earliest) direct evidence of the use of this type of artifact. Our study indicates that inhabitants of Qesem Cave favored the use of shaped, somewhat angular, stone balls made of calcareous rocks to crush fresh animal bones to access marrow. The presence of use wear on the Qesem SSBs highlights this preference, as shown by SSBs with a patina and even broken SSBs that were selected from outside the cave and brought in for this specific activity. Our experiments demonstrated that SSBs are indeed efficient for bone processing, providing a comfortable grip and useful active areas with a number of suitable working edges for prolonged use. The morphology of SSBs and the specific manipulation of the tools, which were possibly turned around during the use, seem to have affected the use wear distribution throughout the surface of the tool. Our analysis and experimental use of replicas support, for the first time, linking functional and morphological traits of these intriguing Paleolithic items. Furthermore, experiments suggest that the distinct spherical morphology of SSBs is a result of a complex knapping trajectory, which required careful planning and necessitated a high degree of knowhow and precision. Moreover, experiments indicate that the level of experience in bone breaking and knowledge about bone anatomy affect the processing time of the bone. We thus infer that skill and knowledge were required in selecting adequate tools and using them properly for this task. These results shed new light on the function of Paleolithic SSBs and accord well with the significance of animal fat in the caloric intake of Middle Pleistocene humans at Qesem Cave and beyond.

## Diet-related differences and wear effects in dental topography of first molars from papionini tribe primates

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Diet, a major evolutionary factor affecting primate life histories, provides significant clues to the understanding of adaptation and ecological niche separation in primates. *Papionini* tribe primates are a very successful *Cercopithecoidea* group that inhabits a very large number of environments and consume a wide range of resources. Thus, the study of dental morphological traits in extant and fossil specimens can provide clues to the interpretation of evolutionary processes as response to climatic events and dietary diversification in this monophyletic group. The aim of the present study is to create a reference model for dental topography in living *papionini* primates (family *Cercopithecidae*, subfamily *Cercopithecinae*) to infer dietary adaptations. This model will be the baseline to compare the processes of dental change that took place within the *papionini* and *hominini* lineage, as both taxa inhabited the same sites during the Plio-Pleistocene transition and faced the same climatic events. Measures of tooth crown curvature, complexity and relief have been shown to discriminate relevant aspects of dental functionally morphology in relation to dietary habits in extant primate species. The studied sample consists of high-resolution 3D dental scans of first upper and lower molars of wild *papionini* specimens (N=315) from 13 African *papionini* species of 6 different genera, with known differences in dietary preferences. A sample of 71 of non-*papionini* *Cercopithecoidea* specimens were included for comparative purposes. All the sample were scored into 5 wear categories to characterize topographic shape changes through wear stages in the extant *papionini* primates. The results obtained showed a relatively few significant effects of dental wear stages upon the topographic measurements within taxa, which suggest that differences in dental topography between taxa hold for any given stage of wear and that worn specimens can be included in the analysis to assess dietary adaptations. The *papionini* species showed greater intragroup than intergroup variability in dental topography compared to the non-*papionini* *Cercopithecoidea*. Dirichlet Normal Energy (DNE) was the topographic variable that showed the highest number of significant between-groups differences. The hard fruit eaters *Cercocebus* and *Lophocebus* showed the lowest DNE values, while *Theropithecus gelada* and *Papio anubis* showed the highest. The complexity of the occlusal surface (OPCR) showed great between-species heterogeneity, reflecting distinct topographic adaptations to food consumption within genera.

## Rare dental trait is first morphological evidence of archaic introgression in Asian fossil record

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The new Denisovan hemi-mandible from Xiahe, Tibet (1) exhibits an unusual dental trait: a three-rooted lower second molar. Three-rooted lower molars maintain both mesial and distal roots with a third accessory root on the distolingual aspect or lingually between the mesial and distal roots. The root is usually about one-third the size of the normal roots. The three-rooted lower molar may appear either unilaterally or bilaterally. When present in recent humans, the accessory third root is most commonly found on the mandibular first molar but it also may occur (less frequently) on the lower second and third molars(2). We refer to these collectively as 3RM. We surveyed the clinical, bioarchaeological and paleoanthropological literature for frequencies of the 3RM in human populations. We confirm the rarity of the 3RM outside of Asia and the New World. Within Asian-derived populations the frequency of 3RM on the first molar can exceed 40% (Aleut, Neolithic China), whereas in non-Asian derived populations the frequency of the 3RM does not exceed 3.4%. Until recently, the 3RM had not been observed to have great antiquity, nor had it been observed outside of *Homo sapiens* populations. One possible explanation for the high frequency of the anomaly in recent Asian-derived populations is that it represents a relatively recent acquisition that postdates the origin of *H. sapiens* and occurred well after their dispersal into Eurasia. However, the discovery of a 3RM in Xiahe requires us to revise this hypothesis. This individual has been identified as closely related to Denisovans and is dated to 160,000 years BP. In addition, a recently described mandible from Taiwan (Penghu 1) that is “... most likely 190K-10K” also exhibits a 3RM (3). Although the Penghu mandible’s taxonomic attribution is uncertain, similarities to the Xiahe mandible have led Chen et al (2019) to suggest that Penghu 1 may also be a Denisovan individual. The Xiahe and Penghu mandibles strongly suggest that the 3RM anomaly (a) very likely has its origin in Asia; and (b) evolved in a pre-sapiens population. Moreover, until a 3RM is found in more archaic hominins, it should be understood as a novel morphological trait that evolved in Asia and was transferred to *H. sapiens* through gene flow with Denisovans. Thus, we conclude that the 3RM is the first example of a morphological character in recent humans that can be clearly traced to this archaic admixture.

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## Size and shape variation among the *Australopithecus africanus* mandibular specimens from Sterkfontein and Makapansgat

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The number of species represented in the *Australopithecus africanus* hypodigm has long been a subject of debate, and analyses of skeletal and dental remains suggest that the specimens currently attributed to *Au. africanus* may not be taxonomically homogeneous (1-4). In this study, I investigate whether more than one species is represented in the *Au. africanus* hypodigm from Sterkfontein and Makapansgat based on mandibular corpus size and shape variation at the position of M<sub>1</sub>, using an extant hominid reference sample. I measured the size and shape of the mandibular corpus at M<sub>1</sub> in a maximum of 8 dentally mature mandibular *Au. africanus* specimens (4 specimens from Sterkfontein and 4 specimens from Makapansgat). The extant hominid comparative mandible sample consisted of 11 *Homo sapiens* specimens, 12 *Pan troglodytes* specimens, 12 *Gorilla gorilla* specimens and 11 *Pongo pygmaeus* specimens. I collected mandibular corpus size and shape data directly from 3D surface scans, employing four measures of mandibular corpus size and one measure of mandibular corpus shape. I measured mandibular corpus size and shape variation using the Coefficient of Variation (CV%). I visually represented mandibular corpus shape at M<sub>1</sub> using a Principal Components plot of PC1 and PC2, which together account for 65% of the sample variation. Results show a high degree of size variation in mandibular corpus breadth at M<sub>1</sub> within the *Au. africanus* sample, with StW 404 and StW 384 representing the smallest and largest extremes of size variation respectively. Despite the large degree of size variation observed, CV% estimates of *Au. africanus* mandibular corpus breadth variation at M<sub>1</sub> fall below the degree of size variation observed in some extant hominid taxa. By contrast, CV% estimates of *Au. africanus* mandibular corpus height variation at M<sub>1</sub>, and variation in the outline of the mandibular corpus at M<sub>1</sub>, exceeds the degree of size variation found in extant hominids, with specimens from Sterkfontein showing the smallest size values and specimens from Makapansgat showing the largest size values. Among the four specimens for which mandibular corpus shape measurements could be recorded (representing specimens from both Sterkfontein and Makapansgat), the degree of shape variation falls within the range of variation observed among extant hominid taxa. Visualisation of Principal Component scores representing mandibular corpus shape at M<sub>1</sub> shows that *Au. africanus* specimens cluster together and do not overlap with any extant hominid taxon. The findings that variation in mandibular corpus height at M<sub>1</sub> in specimens from Sterkfontein and Makapansgat exceeds the variation observed in extant hominid taxa suggests that more than one species may be represented in the *Au. africanus* hypodigm.

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## Changes in thoracic cage morphology from birth into adulthood

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Thoracic cage morphology correlates with respiration, posture and locomotion. The shape of the thoracic cage and the thoracic kyphosis (TK) changes significantly from infancy into adulthood. Few studies emphasized the rapid changes in thoracic morphology in the first two years of life, assuming the changes are related to the establishment of an erect posture. Other studies, however, pointed to puberty as a period in which the thoracic cage proportions are changing. There are contradicting evidences in current literature, regarding sexual dimorphism of the thoracic cage morphology. The main goal of the current study is to characterize the morphological changes in the thoracic cage of males and females from birth into adulthood. Material and Methods For this Cross-sectional retrospective CT study, we included chest CT scans of typically developing individuals from birth to 29 years of age, all displaying non-pathological morphology. We combined traditional length and angular measurement with 3D geometric morphometric analysis (GMA). For the traditional measurements, we used 176 chest CT scans. Measurements included manubrium level in relation to spinal level, and TK angle. For the GMA we created 50 3D models based on CT scans; 302 3D landmarks and semi-landmarks were placed on each thoracic cage. Using Procrustes method, all models were superimposed to eliminate size-related variation, thus, we observed shape differences. We then used EVAN-Tool box to preform principal component analysis (PCA). Results: Traditional measurements: TK increases significantly with age from  $24 \pm 5.6^\circ$  in infants to  $36.7 \pm 6.5^\circ$  in adults ( $p < .000$ ). Most of this change occurred in the first 5 years. We found no difference in TK between genders ( $p = .323$ ). The level of the manubrium was higher in infancy and lower in childhood and adulthood ( $p < .000$ ). The manubrium of sub adult and adult females was positioned lower than in males ( $p = .013$ ). GMA: Our results indicate that the 1st PC accounts for 52% of the total variation, while the 2nd PC accounts for 8.5% of the total variation. The 1st PC nicely separates along an age gradient. The 2nd PC separates males from females, but this becomes evident only from the onset of puberty. The shape of the thoracic cage at infancy is pyramidal (in frontal view), the ribs are horizontal. The thoracic spine is relatively straight and is mildly invaginated into thoracic cage. The position of the manubrium is high, and the sternum is aligned more horizontally than in adults. Along PC 1, 50% of the morphological changes occurred in the first 3-4 years of life. The shape of the thoracic cage in adults is barrel (in frontal view), and the ribs are antero-inferiorly inclined. The thoracic spine is kyphotic and there is marked invagination of the spine into the thoracic cage. The sternum is aligned more vertically, and the manubrium is lower. Sexual differences in adult thoracic cage are subtle and include mainly more inferiorly inclined ribs together with lower position of the manubrium in females, compared with males. Discussion: Our results clearly indicate shape differences from birth into adulthood, which are more rapid in the early years. The results of this study conform with previous publications, indicating that the establishment of an erect posture is probably a significant factor in thoracic cage morphology, thus, supporting previous publications indicating increased TK and more antero-inferiorly inclined ribs with age. Surprisingly, we also found differences in the orientation and position of the sternum, with age, which, to the best of our knowledge, have not been published before. Regarding sexual dimorphism, our study supports previous publications that have shown shape differences between males and females. These differences are subtle and they only appear with the onset of puberty. The most striking differences are shown in the position of the manubrium and the inclination of the ribs.

## Global or local: Where do we find ontogenetic change in hominid cranial shape?

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The shape of the vertebrate cranium undergoes extensive change throughout ontogenetic development and varies across individuals within and between species. However, it has scarcely been explored to what extent the individual cranial bones contribute to ontogenetic and inter-individual variation in overall cranial shape. For example, the overall shape of the brain case is likely to be developmentally constrained (i.e., canalized) owing to its functional importance in housing and protecting the brain. However, the relative contributions of the frontal, parietal, temporal and occipital bones to the brain case are less functionally important and may therefore be less constrained. In this study, we present a novel approach to the analysis of cranial shape by decomposing it into two components: The 'global' component reflects the functionally relevant features of cranial shape and captures large-scale morphological variation, which we represent by the cranial outline. The 'local' component or 'residual' shape, which captures more small-scale variation, represents the relative contribution of individual bones to overall shape. We investigated to what extent postnatal ontogenetic changes in cranial shape occur in the overall shape versus the relative contribution of individual bones, respectively. We conducted a geometric morphometric analysis of 93 midsagittal landmarks taken on CT scans in an ontogenetic sample of 84 crania of modern humans (*Homo sapiens*) and common chimpanzees (*Pan troglodytes*). We defined the outline shape by a subset of 60 landmarks and treated type 1 landmarks as sliding semilandmarks, thereby eliminating information on the delineation of bones. Residual shape was obtained by warping the full set of 93 landmarks to the mean outline shape of all specimens using thin plate spline interpolation. The variation that remains after this standardization of outline shape represents the differential contribution of the bones to the outline shape. Our results show that cranial outline shape clearly differs between species (PC 1) and along an ontogenetic trajectory (PC 2). The residual shape, by contrast, does not appear to change throughout postnatal development, although it significantly differs between *H. sapiens* and *P. troglodytes* ( $p < 0.001$ ). Residual shape differences between humans and chimpanzees are primarily driven by the relative contribution of the facial bones to overall cranial shape. In addition, we find that adult chimpanzees are more variable than adult humans, both in outline (36%) and in residual (62%) shape. These findings indicate that local shape variation, i.e. the contribution of individual bones to global shape, arises prenatally or perinatally and remains largely stable during postnatal development. Cranial outline shape, by contrast, differs between species and changes postnatally. The increased variability in residual shape may result from a relaxed canalization regime or higher genetic drift due to population substructure in chimpanzees.



## Back to Geula Cave: New insights on the Mousterian of north Mt. Carmel, Israel

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The Middle Paleolithic of Mt. Carmel has been thoroughly investigated and includes two main phases. The early phase, ca. 250-170 kya, is characterized by the production of elongated points (Abu Sif and Hummal points). The late phase, ca. 170-50 kya, is centered on manufacture of Levallois points and scrapers using various production modes (centripetal, bidirectional and unipolar). Paleoanthropological studies indicate the presence of two hominin species: archaic *Homo Sapiens* (i.e. Misliya 1, Tabun 2 and Skhul I-IX) and *Neanderthals* (i.e. Tabun 1, Kebara XII and Ein Qashish 3, at the foothills of the eastern Carmel). Absolute chronology of the hominin fossils indicates archaic *Homo Sapiens* (ca. 170-100 kya) predated *Neanderthals* (ca. 80-55 Kya). The study of the prehistory of the Carmel has been focused on cave sites located along the western escarpment of the mountain. The current paper is focused on Geula Cave located at the northern tip of Mt. Carmel, today within the boundaries of the city of Haifa. The cave comprises several chambers and segments, the remains of a larger cave system destroyed in quarrying activities before the 1940s. The cave, initially excavated between 1958-1964, contained large amounts of Upper Pleistocene faunal remains, Mousterian flint artifacts and three human bone fragments identified as archaic *Homo sapiens* [1,2]. The excavation yielded one radiocarbon date of 45 kya which was clearly insufficient to determine the chronological place of Geula's lithic industry and its hominin remains within the Carmel Middle Paleolithic sequence. In 2016 we carried out salvage excavations at the site, in three areas that were not explored previously. The new excavation revealed large amount of faunal remains, Mousterian flint artifacts and two human teeth. A study of the lithic assemblages shows consistency in technology throughout the new excavation areas, with an emphasis on Levallois production using mainly a centripetal mode, a trait that fits the late Mousterian phase of Mt. Carmel. The faunal analysis identified both intensive predator (mostly of Hyena) and human activities in the different parts of the cave. Preliminary OSL dating set the age of the human occupation at Geula to ca. 100 kya. In sum, Geula Cave is the only complex of its kind known today on the northern Mt. Carmel. Our preliminary results suggest Geula Cave should be ascribed to the later phase of the Mousterian of Mt. Carmel, chronologically corresponding to Skhul Cave. The taxonomy of the Geula inhabitants have not yet been identified.

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## Neandertalian bone industry in Chagyrskaya (Altai, Russia)

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The Anatomically Modern Human introduced in Western Eurasia a variety of artifacts made from bone material which were not only responding to technical needs but also incorporated sign function. Their functional and social specialization went hand in hand with a pronounced shaping involving different techniques and resulting in types that we may today individualize. The definition of what a bone industry should be has long been based on this combination of criteria implicitly seen as indivisible. This led to deny the existence of bone industry in the Middle Paleolithic and to include the use of bone materials in the list of the key elements of a behavioral modernity. The identification of more than 1500 bone tools in the Mousterian site of Chagyrskaya, in the Siberian Altai, changes the perspective. Excavated since 2008 by a team of the Institute of Archaeology and Ethnography (SBRAS), the cave of Chagyrskaya, a hundred km far from Denisova, has several dense Mousterian layers with Neandertal remains, dated around 50 000 - 45 000 BP. The rich lithic industry, from local raw material, does not show shortage which could justify a compensating use of bone blanks. While an abundance of bone retouchers is not surprising in a Mousterian assemblage where stone scrapers prevail, less common is the presence of borers, burnishers, intermediate tools and knives of different modules with a minimal shaping, by percussion, but taking profit of anatomical properties. Experimental replication shows not only their functional efficiency but also their particular qualities. Our results raise the question of their cultural meaning: was the use of unformal bone tools for several tasks on different materials a cultural specificity of the late local Mousterian, called the Sibiryachikha tradition, resulting from a regional adaptation in the most Eastern territory of Neandertal, or are we facing a widespread but disregarded technical practice because of inappropriate discerning criteria inherited from typological studies? A closer look at the empirical data is necessary for complementing larger scale investigations.

## The Tooth Fairy collection of human deciduous teeth: learning from a documented sample of living children to understand factors related to morphology, growth, and developmental disruptions in the past

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Teeth provide a wealth of unique information about evolutionary pathways and their underlying factors, growth and life-history schedules. For example, teeth preserve within their mineralized tissues evidence of an individual's developmental trajectory that can provide information about gestation (duration and birth), as well as the way the individual interacted with its environment (diet, stress events) [1-3]. In order to explore the variability of tooth morphology, growth, and developmental disruptions within human children, we have collected naturally exfoliated deciduous teeth from French individuals with known kinship and life-histories since 2014. By combining information obtained from different methods, the ultimate goal of our research is to understand some of the factors underlying the numerous dental changes observed between populations in recent human evolution [4-5]. The Tooth Fairy collection is composed of about 900 deciduous teeth from around a hundred of modern-day individuals belonging to 40 families. The life-history records include date and place of birth, sex, birth weight and length, weight measurements during the first six months of life, whether the child was premature or a full-term birth, delivery conditions, and dietary information including weaning age. Analyses conducted so far have focused on first and second deciduous molars. All teeth have been imaged at high-resolution using microcomputed tomography, dental impression have been taken for occlusal microwear texture analysis, and molars have been sectioned for histological and physicochemical analyses. Tooth external morphometrics, as well as dental tissue proportions and enamel thickness have been recorded on original samples and 3D virtual models, respectively. Thin sections were prepared using standard histological methods. Retzius periodicities were calculated for each section and compared to each child's birth weight. Accentuated lines were examined and only considered as such if they were visible for approximately 75% of their length from the enamel-dentine junction to the crown surface. Prenatal and postnatal areas in the enamel were analyzed by the means of Scanning Electron Microscopy coupled to an Energy Dispersive X-ray Spectroscopy (SEM-EDX) and Raman spectroscopy to see whether changes in the chemical composition (within the detection limits of these methods) can be related to stress marks, especially around the neonatal line. Furthermore, dental microwear texture analysis was performed using a confocal microscope and scale-sensitive fractal analysis. The size and shapes of facets 9 and 11 have been described and microwear measurements were calculated for three standard locations on facet 9 and one on facet 11. Our preliminary results show a range of Retzius periodicities between four to 12 days. Females tend to have a higher Retzius periodicity linked to lower birth weight while males exhibit the opposite pattern. Accentuated lines were found in the pre and postnatal enamel and matched with the individual's clinical history. Physicochemical analysis (SEM-EDX) shows progressive changes in the enamel's chemical composition. Some elements' concentrations appear to evolve continuously in a monotonic function and the slope seems to change before and around the formation of the neonatal line. Raman spectroscopy analysis can potentially give us information about the variations of intensity of phosphate pics at the neonatal line. These variations still have to be related to life-history records and characterization of enamel formation. Finally, microwear measurements varied greatly across a facet upon a tooth, and microwear texture variables correlated with facet size and shape. Results from the studies conducted on the Tooth Fairy collection will provide an integrative framework to understand some of the microevolutionary changes that occurred within human past populations.

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## Who's afraid of hypolordosis? Implications of Neandertal spinal posture reconstruction

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Neandertal spinal posture has attracted the interest of scholars for more than a 100 years. Boule [1] proposed that the La Chapelle-aux-Saints (LC) individual presented a low degree of cervical and lumbar lordosis and a hunched back, which affected much of the subsequent reconstruction. This view was contested in the '50s [2] proposing a similarity between the spinal posture of Neandertals, and that of modern humans. During the last 10 years we have found significant differences in the spine of Neandertals when compared to modern humans, including a low degree of lumbar and cervical lordoses [3]. This view has been contested by Haeusler et al. [4] based on a new reconstruction of the pelvis and spine of the LC Neandertal individual. Moreover, they have mistakenly interpreted that our model of both spinal and general body posture for Neandertals was similar to that proposed by Boule, meaning, an imbalanced spine. They have placed our study as “part of a persistent trend to view the Neandertals as less “human” than ourselves”. This is not the case, as in our view the spinal differences between Neandertals and modern humans should be understood amongst the many anatomical differences present between these two groups. These differences may have postural, biomechanical and pathological implications, without considering them as either “superior” or “inferior”. The objective of the present study is to answer two questions: first, does a hypolordotic spine require a bent over posture or can a hypolordotic spine exist in an erect posture (head above pelvis)? Second, what are the biomechanical and pathological implications of having a hypolordotic spine compared with an average or hyperlordotic spine? In this work, we have combined original data from radiographs and CT scans of over 250 individuals with published data that examined the interaction between posture, biomechanics, function and pathology. Our results indicate that the range of standing lordosis in modern humans is between 25-85° with the average lumbar lordosis (L1-S1) between 50-60°. Hypolordotic spines are those at the lower end of the range and hyperlordotic spines are those at the upper end. All of our subjects, regardless of their degree of lordosis show erect posture (head above pelvis). Individuals with hypolordotic spine show a more stable spine than those with hyperlordotic spine. They also have limited range of motion and reduced shock attenuation compared to individuals with normal or hyper-lordosis. Individuals with hypolordotic spine have stronger cervical and lumbar flexor muscles compared to extensors. Functionally, they perform better overhead activities such as throwing, compared to individuals with normal or hyperlordotic spines, and when lifting an object from the ground they prefer squatting than stooping (5). They usually present slower gait velocity and an increased ankle motion during walking compared to those with normal or hyperlordotic spines. When it comes to pathology Individuals with hypolordotic spines tend to suffer more from disc narrowing, disc degeneration and back pain compared with those with average lordosis. On the other hand, individuals with hyperlordosis suffer more from spondylolysis and spondylolisthesis compared to those with hypo or average lordosis. Conclusions: Modern humans stand erect regardless of the amount of lordosis they present - hypolordotic, average or hyperlordotic spines. This reinforces the notion that a less lordotic spine in Neandertals does not mean that they were bent over. It shows that Neandertals could have been fully erect, with small lumbar and cervical lordoses. On top of that, any spinal configuration has its advantages and disadvantages, both biomechanically, functionally, and pathologically. This means that hominins with different spinal postures might have had somewhat different movement pattern, or different pathologies compare with modern humans.

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## Investigating palaeoclimate variability in the Western Iberian Peninsula during the last glacial period using speleothems

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Climate is one of many powerful driving forces for faunal and human migration; however, with regards to the Iberian Peninsula, there are not extensive terrestrial records which limit our understanding of the palaeoenvironmental boundary conditions for early modern human (EMH)/Neanderthal occupation or migration during that last glacial period. Based on Greenland ice core data, the last glacial period encompasses a time of increased abrupt and significant climatic variability, when known bursts of migration into Iberia have been largely substantiated by marine cores, which can only provide a vague understanding of terrestrial vegetation and climate. Here, we will present a new terrestrial climate record (22-68 ka) spanning most of marine isotope stage (MIS) 3 and part of MIS 4. We use direct Uranium-series dating, stable oxygen and carbon isotopes as well as spatially-resolved trace element analysis on two speleothems (FB1102 and FB1103) from Gruta Figueira Brava, Portugal, to establish a precisely dated high-resolution palaeoclimate record. The site provides a direct link of palaeoclimate reconstruction to a place with human occupation since it is also home to a Mousterian industry, rich in denticulates, with Levallois, Discoid and Dombewa debitage. The stone tool assemblage is associated with Neanderthal remains [1]. We aim to constrain the local palaeoclimatic conditions at Gruta Figueira Brava, as well as provide a regional perspective for the western Iberian realm. Both stalagmites exhibit consistent growth, with the exception of two hiatuses (FB1103 between 45-40 ka and FB1102 between 69-63 ka, respectively). The close proximity of Figueira Brava to the coast will allow us to investigate the impact of marine events like Heinrich (H)-events, Dangaard-Oeschger Oscillations or southward movement of the polar front on the terrestrial climate and thereby assess, for example, a previously claimed relationship of H-events with the extinction of Neanderthals. With this poster, we aim to discuss the following: To what extent did the Atlantic climate affect the Iberian Peninsula? How drastic were the fluctuations in climate throughout our area of interest in the Iberian Peninsula? How do the conditions compare to records in the Mediterranean realm during the same time?

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## First results of a Middle Stone Age survey in the Kerma region, northern Sudan

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One of the primary centers for understanding the process of Anatomically Modern Human dispersal is the Nile Valley and the Coast of the Red Sea, including Sudan, Egypt, and Ethiopia (1). Nubian technology has been used as the tracer for the transit from Africa to the Arabian Peninsula (2), sometime between 150 and 60 thousand years ago. In this poster, we present the first results from a week survey in the Kerma, in the Nile Valley region in northern Sudan, just south of the Third Cataract, in January 2019. This work follows survey by MH in 2007-08 looking for Holocene human occupation in the region (3). Our survey located 16 new Middle Stone Age sites from a 60 km walk and over 100 kms drive, in two north-south transepts, respectively at 15 and 25 km east of the Nile. There seems to be various types of sites in the region: 1. The most common location is on the flat stone pavement desert directly associated to a hilly basalt outcrop, no more than 15 to 20 meters high, visible on the landscape from various km away. These are surface sites. 2. The second type of sites are small quarry locations on the top of large basalt volcanic plugs, such as the case of Jebel-el-Azrak, a 150 meters high hill, and visible from at least 15 kms away. These are circular flat areas with thousands or artifacts made in the local basalt. The circular features result from removing the big surface basalt blocks and transform them into artifacts. 3. There are also several sites located on the dunes that rest against the base of the basalt plug, some using basalt, others the local quartzite outcrop that was pushed up at the time of the basalt extrusion. Some of these may be in situ, below or inside the dunes. 4. Finally, there are various rockshelters in the landscape, formed in the local Nubian Sandstone. At least one such location has evidence of MSA lithic artifacts mixed with material of other more recent chronologies, suggesting that the site has a long sequence. All sites seem to be related to the exploitation of local raw materials, directly from basalt or quartzite primary sources, visible on the arid landscape. In the case of basalt, it seems that as one goes south, the quality of the raw material diminishes and so does the frequency of sites and artifacts on each site. The largest basalt outcrop is the volcanic plug Jebel-el-Azrak. On top of this landscape feature, there are at least five circular loci that were used to exploit the basalt. Around those loci we found various large scaled pieces, over 1 kg and at least 20 cm long, associated to removals of large flakes from the local bed rock, and thus are interpreted as wedges to crack and remove large basalt blanks used for Levallois technology, including Nubian type 2 cores, Levallois centripetal preferential cores, as well as traditional discoidal cores. All of those were also found in quartzite. The cores were used to produce Levallois flakes, blades and points. There are very few retouched tools. There are no evidence of the presence of either Nubian type 1 cores or of Khormusan technology (4). Based on the technology as well as on recent dating of the sand dunes in the region, the likely date for these assemblages is between 120 and 60 thousand years, and thus possibly a key moment and location to understand the viable routes from Africa to Arabia (5) for the Anatomically Modern Human diaspora.

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## Gorongosa National Park: A new window on the late Miocene at the southern end of the African Rift Valley

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The late Miocene was a key time in the emergence of human ancestors. Molecular and paleontological data indicate that the last common ancestor of the African apes (and humans) likely lived in the early part of the late Miocene of Africa. Likewise, the earliest species of our zoological tribe, the Hominini, first appeared in the late Miocene, during a time of atmospheric decreases in CO<sub>2</sub>, increasingly frequent fires, and perhaps the emergence of the Old World savanna paleobiome [1]. Yet this time interval remains very poorly sampled in Africa, with major chronological and geographical gaps in the distribution of fossil localities [2]. These gaps severely limit our understanding of the origin of the African apes and hominins, of the environmental and ecological conditions in which these primates first evolved, and of the range of vegetation types across the continent. Here we describe the fossil record of a new fossil site dated to the late Miocene of Africa: Gorongosa National Park, located at the southern end of the East African Rift System in Mozambique [3]. At Gorongosa, our team has discovered 8 paleontological localities in estuarine depositional environments of the lower Mazamba Formation. Abundant fossil wood at the western end of the exposures documents mesophytic species intolerant of water stress, while pedogenic carbonates are indicative of predominantly C<sub>3</sub> vegetation. Marine conditions are more prevalent toward the eastern localities (which today are more than 90 km from the coast), with abundant crustaceans, gastropods, and bivalves. Two specimens of fossil sharks constitute the first record of elasmobranchs from the African Rift Valley. Most of the localities have yielded a range of fossil mammals, including proboscideans, suids, hyracoids, and a possible anthropoid. The mammalian fauna is dominated by brachyodont species, and stable isotope analysis of dental enamel indicates that these species had a diet of C<sub>3</sub> vegetation. Thus, Gorongosa fills key gaps in our knowledge of the African late Miocene. It is the first site in the East African Rift System to provide evidence of estuarine environments; it is the first site to document late Miocene coastal forests and woodlands; and it is one of the few sites in Africa from this time period south of the equator. Gorongosa is thus the first site that can be used to test key hypotheses about the importance of coastal forests in the origin and early evolution of the Hominini [4].

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## Human upper incisors from the Gravettian site of Fournol (Soturac, Lot, France) show high biological variation in Upper Palaeolithic human populations

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The Upper Palaeolithic Gravettian period (around 29-21,000 years ago) is characterised by a cultural homogeneity in most of continental Europe. Whereas in the past, these populations were known only through individual assessments of skeletal material from a small number of sites with relatively complete, articulated individuals, the current Gravett's project aims at assessing the morphological variability of these Upper Palaeolithic populations as a whole, including isolated and fragmented remains. Here we report on a newly discovered sample of Gravettian remains from Fournol (Soturac, France). Clandestine excavations were carried out at the site between 2000 and 2005. In 2012, at least part of the illegally excavated material was seized by the Gendarmerie and acquired by the Musée National de Préhistoire. Since 2015, excavations carried out at the site by A.M. yielded numerous remains attributed to the Gravettian. Since 2015, excavations carried out at the site yielded numerous remains attributed to the Gravettian. At this point in our study, a total of 188 very fragmented skeletal human remains were identified of which 63 were isolated teeth. We matched these isolated dental remains based on developmental age, occlusal wear, comparisons of size and shape (externally and internally) as well as the occurrence of hypoplastic defects. Here, we present the results of the matching procedure and the detailed dental analysis for the upper anterior teeth of three individuals (A1, J1 and J2). We compare the dental morphometric variability of these individuals to modern human and Neanderthal samples and discuss Late Pleistocene variation in modern human populations [1-3]. Crown dimensions (mesiodistal/buccolingual dimensions, crown height) were measured to the nearest 0.1mm using a sliding calliper. For the internal structures analysis (enamel thickness and dental tissue proportions), all teeth were imaged with micro-computed tomography. Volumes were reconstructed with an isotropic voxel size of 18.21µm. After segmentation, linear, surface, and volumetric variables were digitally measured or calculated for describing 3D and 2D crown tissue proportions and enamel thickness [4]. External enamel long period lines (perikymata) were counted under a light microscope, with replicas oriented perpendicularly to the microscope's optical axis [5]. At least nine individuals were identified from the dental remains, six juveniles and three adults. All the incisors from Fournol show notably large crown sizes in relation to the modern human comparative sample, especially for the mesiodistal diameter. In terms of dental tissue proportions, the absolute values of enamel and dentine are higher than the variability recorded in modern human comparative samples. The large crown dimensions are mainly due to a higher proportion of dentine in comparison to enamel. For upper central incisors, both average and relative enamel thickness (AET and RET respectively) values fall in the range of variation of modern humans and are slightly higher compared to the values for one Neanderthal specimen. For upper lateral incisors, 3D values for AET and RET are closer to Neanderthal samples but within the lower range of variation recorded for Holocene teeth. Total perikymata counts and the percentage of perikymata present in the cervical halves of the crowns are low in comparison to published modern human ranges. The range of perikymata counts in the cervical halves falls well in the range of Neanderthals for both upper central and lateral incisors. Our data reveal an undocumented biological variation in Upper Palaeolithic human populations and suggest that there is a need for more quantitative information on Upper Pleistocene human teeth at the meso- and microstructural levels. This is crucial to fully appreciate the extent of modern human variation in dental development and in order to evaluate possible chrono-geographical trends in modern and fossil humans.

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## Isotopic tracking of the paleoecology of Late Miocene Ponginae *Khoratpithecus*, *Sivapithecus*

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*Khoratpithecus* and *Sivapithecus* are two fossil relatives of *Pongo* (orangutan) that lived in eastern Asia during the Late Miocene. To compare the lifestyle of these ponginae with that of their modern relative, carbon and oxygen isotopes in tooth enamel can be used as tracers of paleobiology. Carbon stable isotopes track the habitat of an extinct mammal through the type of plants at the basis of its foodweb, if they originate from an open or closed vegetation structure, and from which part of the canopy they come from in a forested environment. Oxygen stable isotopes reflect the origin of water (standing water or water from plants) consumed by an extinct mammal. Comparing both isotopic compositions for different taxa in a given fossil assemblage provides information about habitat use and diet partition among taxa. Serial isotopic analysis of high-crown teeth allows evaluating seasonal changes in climate and diet for the analyzed specimens. While *Sivapithecus* teeth from the Siwalik Group were already investigated through this isotopic approach [1], we present here the first isotopic data on a species of *Khoratpithecus* from the Irrawaddy Formation in Myanmar, *Khoratpithecus ayeyarwadyensis*, dated between ca. 10 and 9 Ma [2]. Carbon and oxygen isotopic abundances in fossil tooth enamel of *Khoratpithecus* and coeval large herbivorous taxa (proboscidea, giraffids, bovids, cervids, equids, rhinocerotids) from the Late Miocene Irrawaddy Formation in Myanmar (ca. 9-10 Ma) have been analyzed as bulk enamel (n=50). Herbivorous taxa allowed us to document the possible habitats available in the landscape. Moreover, serial sampling of tooth enamel from proboscidea, bovids, rhinos and giraffids (n=57) provided information about seasonality of climate and foraging of large herbivores, and therefore some insights about the environmental variability through the year also for the fossil ape. Carbon isotopic values indicate a pure C3 diet for all analyzed taxa, with some variation indicating that some taxa (rhino) were dwelling under a closed canopy, and more open environments were used by bovids. Intra-tooth isotopic variations in large herbivores indicate some seasonal variation of climate but with little influence on their feeding behavior. The relatively high oxygen isotopic values of *Khoratpithecus*, similar to those of giraffids, suggest that its food resources were obtained in the canopy rather than at ground level. A comparison with the isotopic data obtained on *Sivapithecus* and coeval large herbivores from roughly the same age in the Siwalik Group (9.3-9.2 Ma) [1] yielded a similar isotopic trophic niche for both fossil Ponginae. Pleistocene *Pongo* fossil teeth also yielded high oxygen isotopic values compared to coeval herbivores indicating the use of food resources from the canopy, in a forested environment, as shown by low carbon isotopic values in coeval herbivores and *Pongo* [3]. The fossil ponginae *Khoratpithecus* and *Sivapithecus* exhibit a similar isotopic pattern pointing to a diet coming from the canopy of a forested vegetation in an environment with some seasonal variations of precipitations, but with no significant impact on the availability of food resource. A similar ecology as Pleistocene *Pongo* is suggested by stable isotopic analysis. The isotopic data suggest an ecological continuity among the Ponginae *Sivapithecus*, *Khoratpithecus* and *Pongo* since around 10 Ma.

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## Ornament or not?: Investigating perforation locations in *Tritia gibbosula* and *Columbella rustica* shells at Ksâr 'Akil (Lebanon) using Micro-CT data

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Perforated shells are often used to study socially mediated behaviour in past hunter-gatherer groups. The assumption is that their exclusive symbolic function makes them ideally suited to investigate social networks, dispersal activity, and social interaction. Before making any statements regarding human behaviour, however, it needs to be established whether perforated shells from archaeological assemblages were used as personal ornaments. One of the key issues regarding beach-collected marine taxa is whether beached specimens were purposefully collected, e.g., preferentially selected naturally holed specimens, or whether human-made perforations may be identified. Past studies have investigated these questions by comparing datasets from modern death assemblages of shells with archaeological collections and through manufacture and use-wear analysis (e.g., 1) This study introduces a novel approach using  $\mu$ CT scans of pristine shells to create a three-dimensional model of shell thickness in two taxa that are often used in Palaeolithic personal adornments: *Tritia (Nassarius) gibbosula* and *Columbella rustica*. These models are used to map robust and fragile zones on shells of these taxa. The goal of this approach is to identify structurally weak zones that would be prone to natural perforations. Heat maps of shell thickness are then used to investigate perforation locations in modern natural death and archaeological assemblages. Our results show that in thanatocoenoses natural death assemblages, most perforations occur in structurally weak zones, and that their distribution is random. In our archaeological samples, from early Upper Palaeolithic contexts at Ksâr 'Akil, (Lebanon), we found that perforations in *T. gibbosula* mainly occur in structurally weak zones, but their distribution within these zones is not random and favours locations facilitating easy suspension (e.g., on cordage). Perforations in archaeological *C. rustica* show a more standardised profile in size, appearance and location. They further occur more commonly in robust zones contrary to our newly collected natural death assemblage of modern *C. rustica* in which, as hypothesised, natural perforations are widely distributed across structurally weak zones. This suggests that at Ksâr 'Akil, both *T. gibbosula* and *C. rustica* shells were used as beads, and that shells with conveniently located natural perforations were intentionally sought for, that humans perforated the shells themselves, or that they used a combination of both. The uniformness of perforation appearance and location in *C. rustica* is congruent with experimentally pierced datasets (e.g., 2,3) and thus may indicate intentional perforation by Ksâr 'Akil's past inhabitants. We discuss the social and behavioural implications of these perforated beads.

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## Zinc isotopes in Late Pleistocene fossil mammal teeth as trophic level tracer

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While stable carbon and nitrogen isotope ratios of collagen from bone/dentin have come to be one of the most frequently used tool in archaeology for dietary reconstruction, protein preservation limits its use [1]. Trophic level assessment of ancient mammals and hominins, older than ~100 kyr and from arid and wet tropical settings, thus currently remain mostly out of reach. However, multi-collector inductively coupled plasma mass spectrometer (MC-ICP-MS) analysis of non-traditional stable isotopes (calcium [Ca], magnesium [Mg], zinc [Zn] and strontium [Sr]) offer the potential to overcome this difficulty. Among these, isotopes of the trace element Zn (<sup>66</sup>Zn/<sup>64</sup>Zn, expressed as  $\delta^{66}\text{Zn}$  value) constitute a promising trophic level indicator [2-4]. Additionally, as Zn is incorporated as trace element in the enamel bioapatite, its potential for long-term preservation of pristine diet-related isotope compositions is inherently greater than that of collagen-bound nitrogen [5].

Here, we present the first Zn isotope dataset of fossil tooth enamel of mammals from the new Late Pleistocene (38.4 to 13.5 ka) fossil assemblage of Tam Hay Marklot cave, northeastern Laos. In order to assess the impact of post mortem taphonomic processes on the preservation of diet-related zinc isotope values, element concentration profiles were measured through in situ laser ablation analysis on cross sections of fossil mammal teeth.

The resulting  $\delta^{66}\text{Zn}$  values for the fossil mammal taxa are in agreement with expected feeding habits and previous studies [3-4]. Carnivores show the lowest, omnivores intermediate and herbivores the highest  $\delta^{66}\text{Zn}$  values, with a corresponding trophic level spacing of +0.60‰ between carnivores and herbivores and half of it (+0.30‰) between carnivores and omnivores. Additionally, Zn and trace element concentration profiles from enamel cross sections indicate minimal impact of diagenesis on the enamel, with no identifiable alteration of the biogenic Zn concentration gradients. Even under adverse tropical conditions, diet-related  $\delta^{66}\text{Zn}$  values in fossil enamel are thus preserved. Given this long-term preservation potential, Zinc stable isotopes provide a powerful and much needed tool to assess the diet and trophic relationships in past food webs, opening new research avenues to apply  $\delta^{66}\text{Zn}$  as dietary tracer for fossil hominins and animals.

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## Earliest known Oldowan Artifacts at >2.58 Ma from Ledi-Geraru, Ethiopia, Highlight Early Technological Diversity

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The manufacture of flaked stone artefacts represents a technological milestone in the human lineage. Although the earliest production of primitive stone tools, pre-dating the genus *Homo* and emphasizing percussive activities, has been reported at 3.3 million years ago (Ma) from Lomekwi, Kenya [1], the systematic production of sharp-edged stone tools is unknown prior to the 2.58-2.55 Ma Oldowan assemblages from Gona, Ethiopia [2]. The organized production of Oldowan stone artefacts is part of a suite of characteristics that is often associated with the adaptive grade shift linked to the genus *Homo* and has been shown to significantly increase processing efficiency of high-quality food items. Recent discoveries from Ledi-Geraru, Ethiopia, place the first occurrence of *Homo* ~250 thousand years earlier than the Oldowan at Gona [3]. Here, we describe a substantial assemblage of systematically flaked stone tools excavated in situ from a stratigraphically constrained context (Bokol Dora 1, BD 1 hereafter) at Ledi-Geraru bracketed between 2.61-2.58 Ma. The BD 1 assemblage currently represents the earliest evidence of hominin understanding of sequential flake removal and systematic flake production that is a characteristic of the Oldowan. Quantitative technological analyses of the BD 1 artifacts indicate that hominins had not yet mastered the skills that experimental studies have shown to be critical in the systematic production of sharp edges (e.g., location of percussion, identifying optimal platforms [4]). However, in many respects the overall technological pattern of the BD 1 assemblage most closely aligns with that of the earliest Oldowan rather than with the earlier Lomekwian or with stone tools produced by modern non-human primates. These differences reinforce current evidence that hominin flaked stone technology is distinctly different from generalized tool use, which may be a shared feature of much of the primate lineage. Thus, BD 1 is distinct from the much earlier Lomekwi 3 assemblage, which may be reflective of a more generalized primate pattern of tool use than was present in the last common ancestor shared with *Pan* [5]. Although the earliest stone tool use may have enhanced the extractive foraging abilities of members of the genus *Australopithecus* or *Kenyanthropus*, as it does in many living primates, the ability to systematically produce sharp-edged flakes at BD 1 constitutes a derived trait likely related to new foraging strategies. The BD 1 assemblage, near the origin of our genus, provides a link between behavioral adaptations—in the form of flaked stone artifacts—and the biological evolution of our ancestors.

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## Hominin dental material from a new passage in the Rising Star Cave System, South Africa

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*Homo naledi* has been described from the Dinaledi and Lesedi Chambers in the Rising Star Cave System, South Africa [1, 2]. New dental material has been recovered from a separate area in the cave system known as Grid Unit S2000W800. This area was identified in a narrow fissure 12 m southwest of the original Dinaledi Chamber excavation unit, at roughly the same elevation. The fragments were recovered as surface scatter from loose sediments of geological sub-unit 3b [3]. Six maxillary specimens are recorded, consisting of left and right deciduous second molars (ldm<sup>2</sup>, rdm<sup>2</sup>), a right permanent first incisor (RI<sup>1</sup>), a right permanent second incisor (RI<sup>2</sup>), a right permanent fourth premolar (RP<sup>4</sup>), and a right permanent first molar (RM<sup>1</sup>). These teeth likely belong to the same sub-adult individual. The deciduous molars are moderately worn but the permanent teeth are unworn suggesting they were not in occlusion at the time of death. The morphology of the new dental specimens is consistent with that of *H. naledi* from elsewhere in the Rising Star Cave system. The mesiodistal and buccolingual (or labiolingual) crown dimensions of all the new teeth fall within the range of the *H. naledi* dental sample. The incisors are similar to the Dinaledi and Lesedi fossils in that they lack prominent incisocervical crown curvature, are not shoveled, and have no prominent crests on its lingual surface. The paracone of the RP<sup>4</sup> is bigger than the protocone and the buccal grooves are weakly developed; these traits are consistent with *H. naledi*. The first molar is similar to *H. naledi* in crown outline shape, cusp areas, and in possessing small, isolated Carabelli's features that do not intersect the buccal groove. The deciduous molars are similar to each other in morphology, developmental status, and lack of a distal interproximal facet, suggesting these teeth are antimeres. Enamel chipping is also evident on these molars, something encountered in only one other deciduous *H. naledi* tooth, UW. 101-384 (rdm<sup>2</sup>), from the Dinaledi Chamber. These deciduous molars add to the already large number of *H. naledi* deciduous teeth from the cave system (n=22). The teeth from this passage provide evidence of *H. naledi* from a third locality in the Rising Star Cave system and further support a consistent morphology for *H. naledi*.

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## Investigation into the subsistence strategies of hominins from Denisova Cave (Russia) based on stable isotope data

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A growing body of biomolecular evidence is advancing our understanding of the diets of Neanderthals [1]. Little attention, however, has been paid to the dietary behaviours of Neanderthals living beyond Europe, despite the wide range of environments they are known to have inhabited throughout the Pleistocene. As a result, the diet of Neanderthals within Europe has become a proxy for the understanding of the diets of all Neanderthals. The individuals at Okladnikov Cave provide tantalizing clues on dietary variation within Northern Asia. These eastern Neanderthals display unusual bulk stable nitrogen ( $\delta^{15}\text{N}$ ) isotope values of 13.4 - 13.9‰ which are higher than those reported for western Neanderthals [2]. Denisova Cave, another important site for Pleistocene hominin groups within Northern Asia, has traditionally produced hominin fossils which have been too small for stable isotope analysis. Nevertheless, the use of peptide mass fingerprinting (ZooMS) has enabled the identification of new fossils large enough for multiple destructive analyses [3,4]. To explore dietary values within Northern Asia further, we analyse both the bulk isotope and single amino acid values for three hominins from Pleistocene contexts at Denisova Cave; Denisova 11 (layer 12) [3], Denisova 14 (layer 9.3) [4], and Denisova 15 (layer 11.4) [4]. This analysis has identified variable bulk nitrogen values for the hominins, two of which are more than 3‰ higher than Neanderthals with the most elevated trophic positions in Europe. We also analyse the bulk stable isotope values of over 200 faunal specimens which were excavated from layers 11 and 12 of the East Gallery of Denisova Cave to act as an isotopic baseline for the hominin data. These include freshwater fish and mammal species typically assumed to be favoured by Neanderthals, such as mammoths, which were taxonomically identified using ZooMS. Our results show that many of the mammals present at the site have similar isotopic values to taxa living in Europe. The discrepancy between the expected  $\delta^{15}\text{N}$  values for mammals present at Denisova Cave and the unexpectedly elevated values for the hominins highlights the need for a more regional perspective for dietary behaviours. By creating this collection of isotopic data we aim to expand the current understanding of Middle and Upper Pleistocene hominin behaviours and strategies in environments across a greater portion of their geographical range than has been traditionally considered.

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## Patterns of insertion areas in proximal phalanges of African apes and modern humans

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Here we study the insertion sites of the common flexor sheath of the hand in 30 gorillas (*Gorilla beringei* and *Gorilla gorilla*), 31 chimpanzees (*Pan troglodytes*) and 37 recent modern humans. This sheath is attached to digits 2-5 and holds the main flexor muscles of the fingers (*flexor digitorum profundus* and *flexor digitorum superficialis*). Both muscles are strongly recruited during suspension and climbing, and are slightly active during knuckle-walking [1]. Although both genera share a similar locomotor repertoire, chimpanzees spend more time in suspensory postures than gorillas [2] and they load their hand differently during travel [3][4]. We look for the skeletal traces of those differences in the sheath insertion of fingers 2-5. We also expected to find different patterns for these insertion areas in African apes and in humans as they use their hands for essentially different purposes (locomotion and manipulation in the former, and exclusively for manipulation in the latter). 3D models of phalanges were constructed through photogrammetry and a high-resolution surface scanner (Breuckmann SmartScan). The insertion sites were delimited in 3D models of proximal phalanges 2-5, and were measured in terms of surface area (mm<sup>2</sup>). Since there is a strong correlation between the size of the phalanges and the size of the insertion areas, the insertion areas were divided by the total area of the phalanx in order to size-adjust, so they would allow interpretation in terms of behavior. Each genus had a unique pattern for these insertion sites. In chimpanzees the insertions for digits 2, 3 and 4 were of the same size while the fifth was significantly smaller. In gorillas, insertions for digits 2 and 5 are similar in size, and significantly smaller than those of digits 3 and 4, which a similar conclusion as reached previously for gorillas [5]. In humans the insertions for digits 3-5 were of the same size while the second was significantly smaller. It remains to be seen whether these differences between groups correspond to functional traits.

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## The effect of admixture on pelvic morphology

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Interpreting the effects of hybridisation is critical for understanding context and processes across human evolution [1]. Yet, despite methodological advances in aDNA analysis, we are still far from understanding the importance of gene flow between different hominin lineages in determining anatomical shape, and from being able to recognise hybrids in the fossil record [2]. The effects of admixture on pelvic form are of particular interest, due to the interaction of the functional and physiological constraints of locomotion and successful parturition. The pelvis is also a region of divergent shape in *Homo sapiens* and *H. neanderthalensis*, which combined with the differently shaped crania of their foetuses, could have implications for the viability of hybrid offspring [3]. Here we use a non-human primate proxy to investigate the role of hybridisation in the evolution of the hominin pelvis. We employ a large, multigenerational sample of admixed Chinese and Indian rhesus macaques (*Macaca mulatta*) and geometric morphometric methods to investigate the morphological consequences of admixture in the pelvis. Unlike many non-human hybrid studies which focus on the first one or two generations after hybridisation [4, 5], our sample has a distribution from purebred Indian and Chinese animals to admixed individuals with very low percentages of Chinese ancestry (< 10%). This range of admixture is a better representation of what we expect in hybrid zones and in the fossil record. Our initial results show a small admixture signal in pelvic form, with sexual dimorphism as the strongest determinant of morphology. We discuss the potential effects of functional constraints on the expression of hybrid morphology in different skeletal regions and the implications of these results for ascertaining hybrid status in the human fossil record. We also provide further details about the macaque sample, from which open-source data will become available to the scientific community over the next several years.

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## **Degrees of rounding among lithic artifacts: experimental program and archaeological application**

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Many Paleolithic lithic collections are found in contexts where post-depositional alterations (such as those made by water streams or sedimentary displacement) have affected the surface of most of the lithic artifacts. A major alteration often observed is the rounding of lithic artifacts due to sedimentary abrasion. Faunal remains are usually the main source of site formation process, but in many of these archaeological sites, faunal remains are scarce. Also, post-depositional alterations may result in diachronic episodes of deposition that can make associations between lithic implements and faunal remains doubtful. This awareness of diachronic formation process has led to an increasing desire to differentiate possible deposition episodes and determine assemblage integrity. Thus, a major goal of lithic studies is to determine the degree of integrity of a lithic collection and to spatially analyze the distribution of lithic artifacts according to their degree of rounding/sedimentary abrasion. The following presentation is structured in two parts. First, insights into the experimental program undertaken to develop a methodological approach to determine degree of rounding among lithic artifacts are provided. The experimental program focused on the analysis of ridges, edges and surfaces of lithic implements and was undertaken in a sequential way to maximize information. Second, this methodological approach is employed to analyze the Middle Paleolithic lithic artifacts from the Calabazas open-air site (Madrid, Spain) and information is crossed with the spatial distribution of the lithic artifacts. Results from the experimental program are promising, showing the development of an efficient methodology to determine degree of rounding among lithic artifacts. Results from the archaeological analysis show the non-altered character of most of the lithic assemblage from Calabazas (near 60% of the lithic artifacts can be considered as fresh/non altered by rounding) although this assessment must be tempered due to the spatial distribution of lithic artifacts. Taphonomic studies on lithic industry through artifact alterations can contribute to determine assemblage integrity, deposition patterns and the asynchronous or synchronous character of an assemblage in open-air sites.

## A New Tool for Digital Alignment in Virtual Anthropology

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The study of the fossil record is fundamental to understand the evolution of morphological traits. Fossil remains often appear fragmented and/or deformed by taphonomic processes, which result in cracks, missing portions and deformation of the original morphology [1]. In paleoanthropology, cranial remains are at the same time the most informative and sometimes the most badly deformed fossil portions, often presenting themselves broken, partially incomplete, and/or distorted. It is nowadays possible to overcome some of these issues, thanks to three-dimensional imaging techniques which allow to operate on digital models of the specimens. It is possible, in particular, to virtually restore damaged remains and recover or estimate the missing information by relying on the one that is present. In this communication, we present a new semi-automatic, landmark-based alignment software, the Digital Tool for Alignment (DTA), embedded in the R package 'Arothron' [2]. DTA uses the shape information contained in a reference sample to find the best alignment solution for the disarticulated portions of a specimen [3]. We showed DTA performance on two different case-studies: a modern human skull, in which a casual disarticulation in two fragments has been simulated and a real case of a disarticulated human fossil specimen, the Amud 1 cranium (*Homo neanderthalensis*). The first case study consists of an artificially disarticulated model of a skull from a female modern human ("Bol-2548"), on which the DTA was applied using a comparative sample of 50 modern human specimens and a landmark configuration of 32 landmarks (17 on the first module and 15 on the second one). The DTA performance on "Bol-2548" was both calculated using the original complete skull and compared to 11 manual alignments. The second case-study consists on the application of DTA on the Amud 1 cranium, in which part of the facial skeleton is missing, with no recovered points of contact between the calvarium (Amud 1a) and the maxillary region (Amud 1b). We acquired two landmark sets of 16 (Amud 1a) and 17 (Amud 1b) landmarks; in addition, we defined two semi-landmark sets of 104 and 42 points respectively on Amud 1a and Amud 1b. We used separately the Neanderthal specimens Shanidar 1 and La Ferrassie 1 as reference models. The result of the DTA was compared to the original restoration of Amud 1 by Suzuki [4]. The application to the modern human case study returned a Procrustes distance between the Aligned Model (AM, built on "Bol-2548") and the Starting Model (SM, unbroken "Bol-2548") equal to 0.0046. The average Procrustes distance of the manual alignments group from the SM was twice that much, reaching 0.0110 on average (95% CI = 0.0079 - 0.0142). The range of the distances between the manual alignments and the SM was bracketed from 0.0032 to 0.0175. The mean Procrustes distances between the SM and the AMs performed on the comparative sample was 0.006. For what concerns the case study of Amud 1, the average distances between the surfaces of the SM of Amud 1 and the AM Shanidar 1 amounts to 3.44 or 5.20 mm, using only landmarks or both landmarks and semi-landmarks, respectively. Using La Ferrassie 1 as the reference model, the average distances are equal to 5.87 (landmarks) and 7.06 (landmark + semi-landmarks), respectively. The results of DTA performed on the artificial case-study (*Homo sapiens*) show that DTA works almost as well as expert-based reconstruction, which is fundamental in situations where the handling of fossil items is difficult, dangerous (because the specimen is delicate), or simply unavailable. The alignment via DTA performed on the Amud 1 cranium differs by only 3 millimetres from the original reconstruction made by Suzuki. This result confirms the usefulness of DTA as a technique for aligning broken fossil specimens.

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## Quantitative surface analysis: a collaborative endeavor between paleontology and archeology

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Dental microwear and artifact use-wear analyses have a lot in common regarding the questions they address, their developmental history and their issues. However, few paleontologists and archeologists are aware of this, and even those who are, do not take into account most of the methodological insights from the other field. On the other hand, both fields have advanced toward quantitative analysis, relying on techniques and methods developed by engineers and tribologists to quantify surfaces. The established, industrial applications are often difficult to transfer to paleontological and archeological questions, so a closer collaboration between dental wear and use-wear analysts would benefit both fields. In this communication, we briefly review the main developmental steps of both methods and, in doing so, highlight how similar their histories are. In both cases, the traditional analyses have been strongly criticized mainly because of their subjectivity and their lack of repeatability and reproducibility. Quantitative surface analyses have been proposed in response, resulting in the so-called dental microwear texture analysis (DMTA) and quantitative use-wear analysis. While DMTA is a mature method well supported within the paleontological community, quantitative use-wear analysis is still nascent and not widely recognized by archeologists. We argue that use-wear analysts could and should borrow a lot from DMTA. For example, there is every reason to believe that quantitative surface analysis can be applied to archeological objects; use-wear analysts should therefore continue to adapt it to artifacts. Additionally, a lot of parameters have been applied to quantify dental surfaces; use-wear should also apply at least all these parameters to find out the most appropriate ones. Borrowing from DMTA would allow quantitative use-wear analysis to become an established method much more quickly. Dental microwear analysts can also learn from traceology, especially regarding experiments and residue analysis. Both are routinely performed in traceological studies; as such, traceologists have a strong expertise that could benefit paleontologists. We hope that this communication will stimulate more awareness, exchanges and collaborations between paleontologists and archeologists, especially between dental microwear and use-wear analysts. At the same time, tribology must remain an integral part of DMTA and quantitative use-wear analysis, to benefit from new developments and insights into wear processes. Paleontology, archeology and the field of surface analysis as a whole would all benefit from a more intense cooperation.

## Stone selection by chimpanzees reveals parallel patterns to Oldowan Hominins

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Tool use is a feature of some members of the family hominoidea, including chimpanzees and humans. The flexible use of tools to increase dietary breadth through extractive foraging behaviour is a feature shared by humans and their closest living relatives (*Pan troglodytes*). Yet comparisons between tool use in hominins and chimpanzees is limited by archaeological palimpsests and the differences in toolkit composition. One feature that primate stone toolkits share is the selection of certain rock types based on certain variables, e.g. tool function or the target of extractive foraging. Here, we document selectivity patterns of tools used by chimpanzees to crack nuts at Bossou (Guinea) through controlled experiments that introduce raw materials unknown to this population. We test decisions made by chimpanzees when selecting hammerstones and anvils that vary in their mechanical properties - features not directly visible to the individual. These rock mechanical properties are known to influence selection patterns amongst Pleistocene hominins ~2 million years ago in East Africa. Results indicate that chimpanzees select both anvils and hammers based on a continuous variation in rock strength and hardness. Selectivity of rock types suggests that chimpanzees quickly assess the appropriate materials for each function, discriminating these 'invisible' properties. Despite the "invisible" nature of these properties, rock selection decisions converged on similar patterns across the social group quickly. This pattern of behavior may diffuse within the community through 're-use' of toolkits by younger individuals. Adults readily identified rock mechanical properties through individual learning and juveniles reuse the toolkits used by adults. These patterns of stone selection parallel what is documented for Oldowan hominins. The processes identified in this experiment may provide insights into the relatively discrete nature of hominin rock selection patterns in Plio-Pleistocene stone artifact production.

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## An assessment of refugia concepts during MIS 3 in Iberia: the case from Lapa do Picareiro (Portugal)

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Neanderthals and anatomically modern humans (AMH) adapted to a series of environmental changes during the Late Pleistocene and may have sought refugia in the southern reaches of Europe during periods of unfavorable climate in response to environmental degradation [1]. Explanatory models such as the Ebro Frontier Model propose that Neanderthals were adapted to woodland environments while AMHs preferred open landscapes [2]. This model suggests that Late Neanderthal survival in southern Iberia may have been the result of Neanderthals seeking refuge during the relatively mild conditions of MIS 3 on the peninsula. Heinrich Events, especially H4, on the other hand, may have created harsh climatic conditions that could have reduced Neanderthal populations below survival thresholds. Generally, however, assessments of refugia concepts in archaeology and other disciplines such as biogeography use the term 'refugia' too loosely, inhibiting proper assessments of refugia-based models like the Ebro Frontier Model [3] and its ecological implications. It is possible that the southern Iberian Peninsula acted as a refugium on a variety of scales, further complicating what we know about paleoecology and human-environmental interactions in the past. Was the southern Iberian Peninsula an active refugia, or locations with favorable environmental conditions and rich in resources that were actively procured or a passive refugia, defined as areas of species retention or survival relative to surrounding regions [4]? Was the southern Iberian Peninsula a macrorefugium, or large areas with favorable conditions or comprised of many microrefugia, or small areas where microclimates produced favorable conditions despite surrounding adverse environments [3]? These questions force us to rely on reconstructions of local and regional paleoenvironmental conditions to which Neanderthals and AMHs were subjected and are key to understanding whether both groups periodically sought refuge in Iberia. Here, we present a paleoenvironmental study using stable isotopes analysis of carbon and oxygen of red deer, ibex and rabbit tooth enamel from Middle and Early Upper Paleolithic levels from Lapa do Picareiro, a cave site located in Portuguese Estremadura. Picareiro sits as the highest altitude Paleolithic site in Portugal, and its well-established chronology, stratigraphic integrity, human occupations spanning the Middle to Upper Paleolithic transition, and large assemblage of zooarchaeological and paleoecological remains make it an ideal location to address the environmental adaptations of Neanderthals and AMHs. These data are then compared to other paleoenvironmental reconstructions from relative archaeological sites in southern Iberia as well as other paleoclimate indicators from Picareiro to assess what type(s) of refugia were present in central Portugal.

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## The TM 1517 odontoskeletal assemblage from Kromdraai B, South Africa, and the maturational pattern of *Paranthropus robustus*

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The holotype of *Paranthropus robustus* was discovered by R. Broom in 1938 in an outcrop of bone breccia at the cave site of Kromdraai B, in Gauteng, South Africa [1]. It consists of the left half of a cranium (TM 1517a) and an associated right mandibular corpus (TM 1517b), both bearing teeth, and of seven isolated teeth (a LLP3, a LLP4 and the series URP3-M3 labelled as TM 1517c). A few weeks later, close to the block containing the cranial remains, Broom identified four postcranial elements: the distal end of a right humerus (TM 1517g), the partial proximal end of a right ulna (TM 1517e), and two toe bones (TM 1517k and TM 1517o), all at the time attributed to the same young individual represented by the cranial remains. However, the distal foot phalanx TM 1517o was subsequently attributed to a baboon. While the holotype has been variously referred to as a 'young female', a 'young adult', as 'probably male and immature', or as a 'late adolescent', it certainly represents a dentally immature individual. Since these early descriptions, no study has explored the possibility that the associated postcranial remains preserve evidence of active bone growth or recent epiphyseal closure. Clearly, however, such information would either strengthen, or challenge the idea that the craniodental and postcranial remains belong to a single *P. robustus* individual and, importantly, might provide the first evidence about the odontoskeletal maturational pattern of this fossil taxon. Accordingly, we performed a micro-XCT-based study aimed at characterising the inner structure of the distal humerus TM 1517g, the proximal ulna TM 1517e and the distal hallucial phalanx TM 1517k. Our 2-3D analyses show that the distal humerus was likely completely fused, while the proximal ulna still displays a faint remnant of fusion, and the distal hallucial phalanx shows evidence of still growing bone. These findings, as well as the observation that the distal humerus and the proximal ulna fit anatomically and morpho-dimensionally [2], provide support for the original attribution of the cranial and the three postcranial remains from Kromdraai B to a single individual representing the *P. robustus* type specimen. Using extant human dental standards, the age at death estimate of TM 1517 is of  $16.5 \pm 3$  years if based on the LM2 (not fully closed distal apices) and LM3 root developmental stages (root formation stage between half and three-quarters completed). The skeletal age ranges between 14 and 18 years, for a male, and between 11 and 15 years, for a female individual. When a chimpanzee dental growth pattern is considered, TM 1517 fits the c. 10.5 years 'older juvenile' group [3], while chimpanzee skeletal maturity standards place it between 7.95 and 13.5 years. Interestingly, in humans fusion of the distal hallucial phalanx commonly slightly precedes that of the distal humerus. However, a sequence of distal humerus-distal hallucial phalanx-proximal ulna fusion, as displayed by TM 1517, is usually observed in *Pan*. Taken together, this new evidence for TM 1517 more closely resembles the chimpanzee condition for maturational patterning. This finding is broadly in line with the evidence observed for *Australopithecus sediba* [4] and *Homo erectus* from Nariokotome [5]. Nevertheless, since *P. robustus* seems characterised by sexual bimaturism (with the males experiencing prolonged growth), the uncertain sex attribution of TM 1517 still represents a limiting interpretative factor.

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## The dentition of *Kenyanthropus platyops*: a comparative study

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Our understanding of hominin taxonomic diversity in East Africa during the Middle Pliocene has been greatly informed by a number of discoveries over the last 20 years. Among these, the remains dated to ~3.5 Ma found in Lomekwi (Kenya) and assigned to the new genus *Kenyanthropus platyops* [1] are particularly important, as they are the only other genus, aside from *Australopithecus*, to be found in East Africa at this time. The taxonomic status and phylogenetic relationship of *K. platyops* have been debated [2]. These issues are highlighted in a recent Bayesian phylogenetic analysis [3], which shows that among the hominins species included, *K. platyops* shows the greatest disagreement between its morphological clock date (1.159 Ma) and its geological date (3.5 Ma). Presuming its geological date is secure [1] a re-examination of its morphology is warranted.

Since the original publication of *K. platyops*, a number of studies have undertaken comparative analyses of the cranial remains [4,5]. However, to our knowledge a comparative evaluation of the dental remains has not been undertaken. This is significant because dental traits, specifically reduced dental dimensions, are some of the key features driving its taxonomic assignment [1].

We performed dental occlusal area measurements and statistical multivariate analysis of dental crown outlines using geometric morphometric methods to explore and evaluate the taxonomic affinities of *K. platyops*. Our comparative sample consists of 205 permanent and deciduous postcanine teeth. All comparative fossil species are dated to between 1.6 and 3.7 Ma, from a variety of both East and South African localities. They include: *Au. Afarensis* (n=82), *Au. africanus* (n=46), *H. habilis* (n=27), *H. rudolfensis* (n=64), *Homo sp.* (n=8), *P. boisei* (n=18).

Our results indicate that the *K. platyops* postcanine dental dimensions are substantially less reduced than what is currently thought. We found that the measured occlusal surface areas exceeded the range for early *Homo* but were within the range of *Au. afarensis*. We note that our estimate of crown size and dimensions of the maxillary M2, which is part of the holotype KNM-WT 40000, are larger than those published. We also question the identification of KNM-WT 38337 as a permanent tooth [1]. Indeed, its crown size and morphology are more similar to that of a deciduous P4 as compared to those of *Au. afarensis*. Principal component analysis indicates that the overall molar and premolar crown outline morphology of *K. platyops* is most similar to that of *Au. afarensis*, and different from that of the East African early *Homo* specimens in our sample. Together, these findings suggest that the dental remains assigned to *K. platyops* may fit within the variation observed in the genus *Australopithecus*.

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## The gait of *Homo naledi*

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Remains of the foot, upper and lower limb, thorax and cranium of *Homo naledi* present a mosaic of primitive and *Homo*-like traits. These include curved phalanges in the hands, although a human like wrist and palm, an ape-like thorax with *Homo*-like vertebrae, and a shoulder girdle indicative of climbing competency. The individual bones of the foot and lower limbs largely seem to show an individual compatible with obligate bipedalism, although the pedal phalanges also show curvature [1,2]. Despite the remarkably voluminous assemblages, the *H. naledi* remains do not include a complete lower limb confidently ascribed to a single individual. A complete lower limb of *H. naledi* would be informative in what it could tell us regarding potential locomotion. The aim of this study was to reconstruct the lower limbs of the *H. naledi* skeleton and analyse the potential gait of *H. naledi* whilst also reviewing recent work on the functional morphology of *H. naledi* and how this pertains to inferences about bipedal locomotion.

The *H. naledi* lower limb was constructed using estimated femoral, tibial and fibular lengths from the most complete remains of *H. naledi* currently available [2,3]. Pelvis remains were too fragmented to reconstruct the pelvis. All transformations were performed in 'LhpFusionBox', which is a musculoskeletal software primarily used to analyse gait in clinical contexts, but recently adapted for paleoanthropologists [4]. Estimated lengths were used as a reference to reconstruct the individual bones by using anatomical landmarks (ALs) to scale other *H. naledi* material to the size of the estimated bones. Both a modern human model and new lower limb associations of a juvenile skeleton found in the Dinaledi chamber were used as guides to reconstruct a complete lower limb. Reconstructions of individual isolated and scaled limb and foot bones were then placed together to have a complete lower limb reconstruction taking into account ligaments, muscles and following the orientation of joint surfaces. The entire limb was then fused to a modern human walking motion to analyse potential locomotion. The reconstruction and biomechanical analysis of the *H. naledi* lower limb largely demonstrates a morphology compatible with obligate bipedalism, with a medial arch (although reduced), elongated limbs, marked bicondylar angle and joint surfaces compatible with bipedal gait. The elongation of the lower limb is generally seen as a marker of obligate bipedalism although the *H. naledi* limbs are exceptionally elongated relative to the diaphyseal diameter of the long bones and preserved joint proportions. Longer limbs are generally thought of as more energy efficient, but they also require a greater moment of inertia, which increases energy costs. Whilst the longer tibia (and leg) may have necessitated a longer swing phase, low limb mass (as evidenced by long bone gracility and small joints) may have offset this energetically. Other unique traits such as the flaring ilium, flattened femoral lower neck and overall general mix of primitive and *Homo*-like traits may not have impeded obligate bipedalism, but they may have been advantageous for climbing. Primitive traits are often thought of as vestiges of an ancient past on the way to the modern human form of obligate bipedalism, however, *Homo erectus* and other skeletons from the genus *Homo* are largely thought to be fully obligate bipedals from approximately 1.5 million years onwards, and as *H. naledi* has been dated between 335 and 236ka [5], it is therefore curious why this particular branch of the hominid tree would 'hang on' to the 'primitive traits' for at least a million years longer. It is therefore likely that this hominin engaged in both arboreal climbing and bipedal walking.

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## A novel social dimension of bipedal behaviour and its implications for human evolution: a cross-disciplinary and cross-species investigation

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Obligate bipedalism is a trait which defines humans and their ancestors, and which has intrigued scientists for centuries. Yet, there remain significant debates and gaps in understanding. It remains unclear which early advantageous function(s) of bipedalism instigated its evolution in hominins (the unknown cause of bipedalism), and how bipedalism might connect to or have facilitated the evolution of traits which emerged later in the human lineage (the unknown consequence of bipedalism).

This research considers the possibility that the solutions to these unknowns remain contested because theory and research has not adequately contemplated or investigated how the performance of bipedal behaviours was expressed above the organism-level, at the level of hominin society: that the social dimension of bipedalism has not been well-characterised. Upon examining previous works, it appears that authors hold two key types of assumption about the social variables and processes which influence, or are influenced by, bipedal behaviours. First are assumptions regarding the impact of age and sex variables: authors appear to either assume no effect ('one-size-fits-all' assumption) or assume a large effect by emphasising the role of a single age-sex category in the evolution of bipedalism ('driver-sidecar' assumption). Second, are assumptions that early bipedalism was performed in a context within which the behaviour did not affect interactions between group members, and rather was performed to benefit the individual bipedal individual ('solo-function' assumption).

It was the aim of this research to investigate if such assumptions are biased, and to assess their contribution to the persistence of unknowns. An empirical study using a primate model (the baboon, genus *Papio*) investigated the effect of age and sex on the performance of bipedal behaviours, and the presence and significance of both solitary and interactive bipedal functions (some of which have rarely, if ever, been proposed as likely functional drivers of bipedalism). The results challenged all three assumptions. All age-sex categories performed bipedal behaviours. Functions were distributed differently across age-sex categories (play was associated with infants and juveniles, foraging with adult males and infant handling with female subjects). Interactive functions of bipedalism were performed. Based on the results, a novel social dimension of bipedalism is offered, which captures how bipedal behaviours might have been performed at the level of hominin society. Interactive functions of bipedalism may hold the key to understanding how bipedalism might have facilitated the emergence of those traits of later hominin evolution which rely on social bonding to some degree. Further empirical works are called for, to test the validity of the research findings and to address the limitations of the present study.

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## Challenging the paradigm: how enamel-dentine junction variation across primates is inconsistent with current tooth crown nomenclature schemes

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Advances in imaging technology have allowed researchers to study the internal structures of teeth in high resolution and extract novel morphological data to answer long-standing questions in primate dental morphology. Additionally, recent qualitative observations of discrete trait variation at the enamel-dentine junction (EDJ) of primate molars has resulted in the recognition of dental crown features that are either unidentifiable within current systems of nomenclature, or show a greater level of complexity and variability in expression than conventional terminology presently allows [1]. Currently, observations describing this morphological complexity at the EDJ surface have been limited to hominoid molars, and it is unclear whether similar levels of variability and complexity are also present in other primate clades. Using micro-computed tomography (micro-CT) to image the EDJ surface from a taxonomically diverse sample of primate molars, this study conducted qualitative observations of discrete dental traits to examine the morphological variability and complexity of the primate tooth crown, and in doing so, investigate the suitability of current terminologies for studies of primate dental morphology and evolution.

Findings from these observations identified multiple examples of tooth crown features that were considered unidentifiable within the current systems of tooth crown nomenclature. While subtle variation was identified in crest patterning in all species studied, the majority of observed variability was in accessory cusp expression. Of particular note, the observed expression of accessory cusps along the marginal ridges of Cercopithecoidea molars demonstrates a high level of complexity exhibited through the variable presence of single and/or multiple dentine horns situated between adjacent primary cusps, as well as significant variation in their topographical positioning and developmental origin. These observations, and the difficulties faced when trying to accommodate these features within the Cope-Osborn system of nomenclature (or any of the subsequent variants), highlights both the need to revisit this long accepted component of dental morphology, and perhaps to re-consider how we identify and define a cusp. In Platyrrhine molars, accessory cusps were also observed along the marginal ridges between primary cusps, and in some cases, were of comparable size to the primary cusps. In addition to the concerns this raises regarding the confident identification and discrimination of these features in anthropological studies, these similarities in cusp size also contribute to developmental arguments regarding the status of cusps as either primary or accessory.

Overall, the findings from this study demonstrate that a greater degree of tooth crown variability and complexity exists than has been generally appreciated in primate molars. Such observations reignite concerns regarding the suitability of current systems of tooth crown nomenclature, and contribute to debates about the degree to which current models of cusp patterning (such as the patterning cascade) adequately explain primate tooth crown variation. As crown morphology is used extensively in systematics, taxonomy, and the reconstruction of the evolutionary history of primates, this has crucial implications for the confident use of these structures in future anthropological work.

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## Virtual reappraisal of the Krapina 1 juvenile cranium

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Krapina 1 (Cranium A) is a relatively complete calvaria of a child Neandertal, consisting of most of the frontal, right and left parietal, and left temporal bones. A juvenile occipital fragment (Krapina 12/Occipital 6) has also been hypothesized to belong with the cranium [1], although there are no direct contacts between the specimens. Technological advancements since the last major treatment of Krapina 1 [2] make it timely to revisit this important specimen. In this study, we use modern methods to digitally reconstruct and analyze this most complete juvenile cranium from Krapina.

Original fossils from Krapina were digitized with an Artec Spider blue light scanner, and processed into high resolution 3D surface meshes. For the Krapina 1 reconstruction, pieces that were incongruously affixed to the cranium were repositioned or removed. Krapina 12 (Occipital 6) was added to the reconstruction using the Krapina 2 juvenile cranium as a guide. Mirror-imaging allowed estimation of unilaterally missing areas. In addition to the cranial reconstruction, we used landmark-based geometric morphometrics to reconstruct the specimen's endocast and estimate endocranial volume. Finally, we assessed cranial vault thickness in Krapina 1 and other individuals from the site, which we compared with an ontogenetic series of modern human skulls derived from CT scans.

Our Krapina 1 reconstruction confirms previous observations of the specimen's notable cranial breadth [2], which is large relative to both its maximum length, and to other juvenile Neandertals. Cranial vault thickness is comparable to that of modern human juveniles with one or both of the first two permanent molars emerged. Throughout the frontal and parietals, thickness averages around 4.0 mm, but ranges from 2.5 mm (at the frontal boss and near pterion), to over 7.0 mm (at the supraorbitals, near bregma, and along the sagittal sinus). Interestingly, the Krapina 1 parietals are thickest anterior to the parietal boss, in contrast to humans and other Neandertals in whom parietal thickness is usually greatest at the eminence. The endocranial reconstruction yields a cranial capacity around 1450–1500 ml, depending on the reference endocasts used. This is larger than previous estimates, and indeed among the larger estimates of any individual from Krapina. Our virtual analysis of Krapina 1 provides new information about the developmental status of this individual, as well as the paleobiology of the Krapina Neandertals.

Davorka Radović provided access to and assistance with the Krapina fossils. Lynn Copes made publicly available her human CT datasets from the American Museum of Natural History in New York. We are very grateful for internal support from Vassar College for equipment, travel funding (Emily Ford Fund), and employment of undergraduate students through research assistantships and the Undergraduate Research Summer Institute (via the Joan E. Morgenthau Hirschhorn '45-44 Fund). Walker Kelly and Abigail Pamenter helped collect human cranial measurements.

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## Back pain, vertebral shape, and the evolution of bipedalism

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Understanding back pain is an important task. Up to two-thirds of people experience back pain at some point in their life, making it one of the commonest medical conditions. It is also one of the most serious medical conditions. Surveys indicate that it is the single greatest contributor to disability worldwide, and this has major economic impacts. US companies, for example, have been estimated to lose in excess of \$7 billion per year due to back pain among workers in the 40-65 age group alone. Given the individual and societal costs of back pain, there is a pressing need for further research on its causes.

Over the last few years, we have sought to use palaeoanthropological theory and methods to shed light on two serious spinal pathologies—vertical intervertebral disc herniation (VIDH) and spondylosis, which is a condition where a fatigue fracture causes a cleft in the neural arch. In one set of studies, we used geometric morphometrics to compare the shapes of modern human vertebrae that show evidence of VIDH with the vertebrae of healthy modern humans, chimpanzees, and orangutans. These studies revealed that the vertebrae of VIDH-afflicted modern humans are more similar to chimpanzee vertebrae than are healthy modern human vertebrae. In another study, we compared the three-dimensional shapes of the vertebrae of modern humans suffering from spondylosis with the vertebrae of healthy modern humans and great apes. The results of this study contrasted with those obtained in the VIDH-focused study. We found that the pathological modern human vertebrae were more different from the great ape vertebrae than were the healthy modern human vertebrae.

These findings can, we think, be linked to the evolution of bipedalism. It is now generally accepted that hominins are more closely related to chimpanzees and bonobos than they are to any other living species. Currently, the locomotor behaviour of the common ancestor of the hominin and chimpanzee/bonobo lineages is debated. The most frequently cited suggestion is that it was a knuckle-walker like chimpanzees and bonobos. However, it has also been argued that it was an arboreal quadrumanous climber like orangutans. Depending on which of these hypotheses is correct, the hominin lineage shifted from knuckle-walking to bipedalism or from quadrumanous climbing to bipedalism. In both cases, the demands placed on the spine would have changed. Selection can be expected to have acted to improve the ability of the vertebrae to cope with the new demands, but we can also expect vertebral shape in modern humans to be normally distributed around the optimal shape for bipedalism, with some individuals positioned towards the ancestral end of the distribution and others located at the opposite, highly derived end. Vertebral shapes at both ends of the distribution are likely to be less able to cope with the demands of bipedalism and therefore will be more frequently associated with pathologies, albeit different ones—VIDH at the ancestral end and spondylosis at the highly derived end.

## MSA deposits at Sibudu and Umbeli Belli in KZN, South Africa document cultural change in high resolution

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Since the 1980s when scholars mobilized strong arguments for the origins of modern humans in Africa, the Middle Stone Age (MSA) has been a main focus of international research in paleoanthropology. Southern Africa in particular has been a leading region for research on the MSA with many high-profile excavations yielding results that have helped to shape the debates on the origins of modern humans and innovative behaviors that are viewed by many to have triggered the expansion of populations into Eurasia.

Building on the outstanding work by Lyn Wadley's crew from 1998-2011 [1], the current team has excavated for nine seasons in the MSA deposits at Sibudu Cave in KwaZulu-Natal. Additionally, we have conducted studies of collections from the KwaZulu-Natal Museum and excavated three seasons at Umbeli Belli Rock Shelter about 100 km south of Sibudu near Scottburgh. This paper provides an overview of the results from this research and addresses multiple questions related to the nature and tempo of cultural change during the MSA of southern Africa. We consider how these results contribute to the ongoing debates about the importance of the southern African MSA for the evolution and spread of modern humans to other regions. This research has identified much cultural variability that has not previously been documented in studies of the MSA. The work also contributes to placing record from KwaZulu-Natal more firmly in middle of the discussion of human evolution in southern Africa.

Considering the sequences from Sibudu and Umbeli Belli, we have established an exceptionally detailed record of the period from about 90 to 30 ka, spanning what is often referred to as the "Pre-Still Bay" to the Final MSA [2-4]. This sequence documents rich and often exceptionally well-stratified horizons from the "Pre-Still Bay", Still Bay, Howiesons Poort, Sibudan, Late MSA and Final MSA. In this paper we examine when and why marked cultural changes are documented in this sequence using multiple lines of evidence from comparative lithic studies, techno-functional analyses of lithic and organic tools, intra-site spatial patterning, the use of ochre and other sources of information. These results do much to balance previous suggestions that the Still Bay and Howiesons Poort represent the main periods of cultural innovation during the MSA [5].

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## Symbolic Behavior in Planaria, Dogs, and *Homo sapiens*

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A common definition of a symbol or symbolism is that it is the use of a sign or mark to represent some idea, object, or relationship. Frequently, definitions of a symbol include that it is an arbitrary referent for what it actually represents, there is no resemblance between the signifier and the signified, and it must be culturally learned. Anthropologists typically invoke Charles Sanders Peirce's (1839–1914) [1] semiotic concepts of icons, indexes, and symbols to analyze parietal art, personal ornamentation, language's origins, highly ritualized burials, and other topics. It is the purpose of this paper to raise the question of when and how classical conditioning is different from these standard definitions of symbols. Classical conditioning (aka Pavlovian conditioning) is considered one of the two basic types of learning, and they are non-associative learning (habituation and sensitization) and associative learning (classical conditioning and operant conditioning) [2]. Classical conditioning's origins are attributed to the Russian physiologist Ivan Pavlov (1849-1936). Pavlov observed that dogs would salivate to the sight and smell of food. The sight and smell of food was labeled the unconditioned stimulus (UCS) and the dog's saliva was considered a reaction or reflex to the food and labeled the unconditioned response (UCR). It is important to note that the dog did not have to learn this initial UCS-UCR association as it is considered an 'innate' reflex (although the pairing was learned initially over evolutionary time and passed down through genetic memory). Pavlov then paired a neutral stimulus (NS), like the sound of a bell or a buzzer, to the UCS. Initially, the NS did not elicit any specific reaction other than an orienting response. Next, Pavlov presented the NS, followed shortly after by the UCS. With a sufficient number of pairings between the NS and the UCS, the sound of the bell alone came to elicit the dog's salivation. At that point, the original NS (the bell) is said to have become a conditioned stimulus (CS), and it now elicits the conditioned response (CR; i.e., saliva). In this example, the bell is an absolutely *arbitrary* referent of food to a dog, there is no resemblance between the sound of the bell and food, and the pairing was learned in a social context. Thus, the crux posed by this paper: how is the bell *not* a symbol of food to the dog? It is also important to note that planaria (class *Turbellaria*), with only a simple nervous system and rudimentary brain, can be classically conditioned [3]. Further, why are the words DOG, PERRO, CHIEN, or 狗 arbitrary referents to an actual dog and thus those letters "symbolize" a real dog to *Homo sapiens*, but why is a bell or a light *not* a symbol to a dog or planaria? There must be qualitative differences between the 'symbolic-ness' of a bell to a dog and the word 'dog' to *Homo sapiens*. What are those differences? Anthropologists sometimes refer to 'symbolically capable brains.' However, by the aforementioned examples, a dog's brain or a planaria's rudimentary brain are 'symbolically capable' because they are capable of learning and retaining reliable responses to arbitrary referents in their environments. Peirce's symbol semiotics appear inadequate for explicating this task. It has been suggested [4] that there is a gap between minimally symbolic cognition (perhaps like classical conditioning) and fully immersed symbolic cognition. It may be time for anthropologists to 'mind the gap' and begin to address the conceptual chasm and dilemma presented by the classical conditioning paradigm and to define more judiciously the definitions of symbols, symbolic behavior, and symbolically capable brains. The present paper will delineate some possible answers and alternatives to this dilemma from cognitive psychology and the cognitive neurosciences.

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## Accurately predicting head motion in fossil primates using soft-tissue information

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As part of the sensory organ of balance the semicircular ducts of the membranous labyrinth monitor head rotations and are crucial to gaze stabilization, motor coordination and orientation[1]. Fossils only preserve the shell of these ducts, the semicircular canals of the bony labyrinth, and their morphological features are used to infer locomotor behaviour of extinct primates, including hominins[2-4]. Here we explore how accurately such features predict finely tuned semicircular duct function. Soft-tissue ear samples of 25 extant mammal species, including 13 primates, were stained using PTA and CT-scanned to visualize membranous and bony labyrinths *in situ*[5]. Geometric morphometric methods and the Ariadne Toolbox[5] were used to analyze the morphology and function of the semicircular ducts and canals. We found that neither the shape of the semicircular canals, nor the deviation of their planes from orthogonality reliably predict any of the main functional parameters of the semicircular ducts system. As such it is unlikely that these characteristics can help infer locomotor repertoires. More meaningful information can be obtained using the radius of curvature of semicircular canals combined with body mass. However, this only predicts response speed of the duct system, but not sensitivity. Integrating evidence from the morphology of the bony labyrinth and the membranous soft-tissue in the extant sample we developed a new approach for accurately predicting semicircular duct function. This protocol estimates soft-tissue properties from measurements on the bony labyrinth, and can therefore also be applied to fossil specimens. We first use thin plate splines to warp central streamlines of the semicircular ducts system of various extant species into the semicircular canals of a fossil specimen, using equivalent landmarks placed on the bony labyrinths. Streamlines thus inferred provide accurate lengths, enclosed areas and functional planes. Additional morphological parameters of the duct system are subsequently predicted using statistical models describing interspecific relationships between bony and membranous labyrinths. These phylogenetically constrained and weight-averaged models show adjusted  $R^2$  values between 0.71 – 0.95, suggesting a particularly good fit. Finally, the morphological features of the semicircular ducts predicted for a fossil specimen are analysed using the Ariadne Toolbox. The full suite of functional parameters thus obtained provide good insight into the head motion typical for a species, and these are indicative of locomotor behaviour.

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## Endostructural morphology of the *Homo naledi* mandibular premolars

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The taxonomic position of the recently discovered species *Homo naledi* is still uncertain. One of the many distinctive aspects of the dentition of the species is the external morphology of the mandibular third premolar, which has two roots and is fully bicuspid, a configuration which is unusual for late-Middle Pleistocene *Homo*. The fourth premolar is also bicuspid, and both premolars have a notably symmetrical occlusal outline [1]. In this study, we examine the endostructural morphology of the premolar tooth crowns as the surface of the dentine crown in particular is known to carry important taxonomic information and elucidate the developmental basis of premolar crown morphology.

We use micro-tomography to image the enamel-dentine junction (EDJ) of *H. naledi* mandibular premolars from both the Dinaledi and the Lesedi chambers, and use geometric morphometrics to quantitatively compare the EDJ morphology to specimens of early *Homo*, *Paranthropus robustus*, *Australopithecus africanus*, *Homo neanderthalensis* and *Homo sapiens* (n=76). Additionally, we investigate patterns in the size relationship between the P3 and P4 among the study taxa using centroid size.

The mandibular premolar EDJ morphology of *H. naledi* from the Dinaledi Chamber is distinctive and consistent. Both the P3s and P4s display a tall well-developed metaconid and strongly developed mesial marginal ridges, while the P4 shows a relatively mesiodistally elongated crown. The P3 and P4 are distinct from a number of early *Homo* specimens. In particular, the *H. naledi* premolars can be distinguished from KNM-ER 1802 (*Homo sp.*), as well as KNM-ER 992, the type specimen of *Homo ergaster* [2]. Swartkrans *Homo* specimen SKX 21204 clusters closely with KNM-ER 992, particularly for the P4, and is also quite distinct from *H. naledi*. Premolars from the Lesedi chamber, although worn, are consistent with the morphology seen in the Dinaledi chamber, clustering closely with these *H. naledi* specimens in the geometric morphometric analysis, although they are slightly larger in size.

Finally, we find that when considering centroid size, *P. robustus* and *A. africanus* show a P4>P3 pattern, which is also found in modern humans, and in early *Homo* specimens KNM-ER 1802 and SKX 21204. In KNM-ER 992, the premolars are approximately equal in size. *H. naledi* however shows the pattern P3>P4, which is distinctive among our sample.

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## The distribution of zinc in modern and fossil enamel, dentine and cementum

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Zinc is an essential trace element involved in many physiological processes as both a catalyst in biochemical reactions, in the maintenance of protein quaternary structure and as a component of many essential enzymes [1]. In mineralised tissue formation, Zn is a component of alkaline phosphatase, carbonic anhydrase and several enzymes involved in enamel maturation. In palaeoanthropology, Zn can be informative about life history (perinatal physiology) and about diet. The presence of Zn as a trace element in bone and tooth tissues has been reported extensively in the literature [2]. Here we used synchrotron X-ray fluorescence (SXRF) of polished thin ground sections of teeth to map and quantify the distribution and concentration of Zn in enamel, dentine and cementum. Teeth were scanned with an X-ray beam monochromatised to 17.0 keV at either 10.0, 2.5 or 1.0  $\mu\text{m}$  resolution and 10 ms integration time. Our sample included extant teeth attributed to modern humans, *Pan* and *Gorilla* and fossil teeth including Neanderthals (Amud 7, dm1) and *Homo* from Skhul (Israel), *P. boisei* from Koobi Fora, and *Ekembo* from Rusinga Island, Kenya. Our aim was to address three issues relevant to the study Zn as a trace element in extant and fossil primate tooth tissues. First, we mapped and quantified the distribution of Zn in pre- and postnatal enamel and dentine to test the hypothesis that Zn distribution in dental tissues reflects rising prenatal fetal serum Zn levels in the last trimester and Zn-rich colostrum in the first postnatal days [3]. Second, we compared unerupted teeth with teeth that had been in function in the oral environment to test whether relatively high levels of Zn reported in outer enamel are likely to derive entirely from the oral environment, or if Zn may be retained during enamel maturation [4]. Third, we mapped Zn distribution and concentrations in fossil hominoid and hominin teeth from different geological contexts to identify any consistent Zn-rich regions and compare these with modern material. Our results show that prenatal dentine and the neonatal line are relatively Zn rich with concentrations reaching  $\sim 200$  ppm. Unerupted teeth, both fossil and modern, showed the same enriched levels of Zn in surface enamel reaching 400-500 ppm in some cases. In all teeth, both extant and fossil, cementum, secondary dentine and outer enamel are all consistently Zn-rich. Zn appears to be tenacious enough to resist diagenetic change over millions of years. In particular, Zn is retained in *P. boisei* cementum and secondary dentine with similar concentrations to extant teeth (140-180 ppm). The outer enamel of *Ekembo* teeth still retain Zn to an equivalent depth and concentration as extant primate material. Zinc may be present in tooth tissues for different reasons. It may accumulate in slow-forming dental tissues (such as peritubular, secondary dentine and cementum) where there is direct contact with tissue fluid. In cementum it may be adaptive and resist resorption by osteoclasts [5]. Elevated Zn levels perinatally may be incorporated into forming hydroxyapatite crystals and/or bind with components of the dentine protein matrix. Zinc in outer enamel may in part be derived from enamel proteases and be retained and sequestered after maturation [4]. The implications of our findings for studies of Zn in fossils are promising, since Zn preservation appears to be good, even in some of the older hominoid fossils.

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## Ontogenetic changes in third metacarpal trabecular bone in western lowland (*Gorilla gorilla*) and mountain gorillas (*Gorilla beringei*)

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Trabecular bone structure is influenced by joint loading during life. As such, trabecular bone is becoming a frequently used source of functional information to reconstruct locomotor behaviour in adult fossil hominins. However, trabecular bone models and remodels at a faster rate during early development (infant to adolescent stages), suggesting that adult trabecular structure may be more indicative of loading regimes during early life. Although there are some studies on human trabecular development (e.g. humerus [1], innominate [2]), little is known about trabecular ontogeny in other primates. This study investigates developmental changes in trabecular structure of the third metacarpal (Mc3) of adult and immature gorillas (n= 37), including western lowland gorillas (*Gorilla gorilla*, n=12) and Karisoke mountain gorillas (*Gorilla beringei*, n=25). The Mc3 was chosen because the third digit is typically used during all forms of terrestrial and arboreal locomotor behaviours. From microCT data, trabecular bone volume fraction (BV/TV) and degree of anisotropy (DA) were quantified using a 'whole-epiphyses' method and colour maps were generated to visualise these variables.

The study sample was divided into five age categories based on locomotor transitions [3]: (1) 0-6 months, (2) 6 months – 4 years, (3) 5 – 9 years, (4) 10 years – full epiphyseal fusion, and (5) adult. Analyses were run on the whole Mc3 bone and on the proximal and distal metaphysis/epiphysis (when present) separately. Kruskal-Wallis and post-hoc Dunn's tests were performed on the data to identify changes in BV/TV and DA throughout the entire Mc3 during ontogeny. We found no notable differences in the trabecular development between lowland and mountain gorillas, although sample sizes are small for each age category. The results demonstrate that throughout the whole Mc3 bone, BV/TV is lowest in infancy (<1 year) and increases with age, and that these values are statistically significant (p=0.008) when comparing the <5 years of age specimens to those older than 5 years. Analysis of changes in DA in the whole Mc3 across ontogeny did not provide any statistically significant results. However, colour maps generated to visualise changes at the distal metaphysis and epiphyseal head of the Mc3 show clear changes in trabecular structure occur in these regions across ontogeny.

BV/TV in just the Mc3 head and proximal metaphysis also increases with age. Gorillas <4 years of age demonstrate a palmar concentration of trabeculae in the Mc3 distal metaphysis. This higher concentration of BV/TV in the palmar region of the metaphysis persists until ±9 years of age. At 4 years of age, a similar proximal-palmar concentration of high BV/TV can also be observed in the Mc3 epiphyseal head. Between 6 – 9 years of age, BV/TV concentrations in the Mc3 head become more adult-like [4], with the highest BV/TV occurring disto-dorsally on the head. By 12 years of age, the adult pattern of BV/TV distribution is reached. DA is high in the distal metaphysis and low in the epiphysis until full fusion occurs. Once fusion is completed at age 13-15, the adult-like DA pattern is observed.

The changes in trabecular structure observed in this study are consistent with ontogenetic changes in locomotor behaviours in immature gorillas. The strongest changes in trabecular structure occur when knuckle-walking becomes more frequent, but when other arboreal behaviours are still common (± 4 years), and at 9-10 years of age when full adult-like locomotor patterns are reached. This indicates that changes in locomotion likely influence trabecular bone modelling throughout ontogeny. Future comparisons of human-like and ape-like bone development to dental development of various well-preserved juvenile hominins (e.g. *A. sediba* MH1, *A. afarensis* DIK-1/1), may provide new insights into the developmental patterns of early fossil hominins.

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## Sexual dimorphism in the human calvarium: a Geometric Morphometric approach

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In human evolution the assessment of sex in fossil specimen is performed by transposing the information relative from extant species (e.g., *Homo sapiens*, *Pan paniscus*, *Gorilla gorilla*) to extinct ones. The cranium is considered a key component in establishing others types of biological information including age, state of health and provenience and is considered the second important skeletal structure for a determination of sex after the pelvis [1]. In this communication, we analysed the human calvarium in know-sex specimens to detect which anatomical traits are more sexual dimorphic. To reach the aim of this project, we collected digital models of 165 adult specimens and on each skull we acquired 50 landmark on the entire cranial morphology. The only use of landmarks does not allow to study some anatomical traits due to lack of anatomical point. For this reason, we opted to collect also a surface patch of 500 semi-landmarks. We performed the analysis in R environment by using the Morpho, Arothron and geomorph R packages [2]–[4]. After semi-landmark placing and sliding, we split the semi-landmark configuration into three sub-regions: the entire calvarium, the frontal bone and the supraorbital torus. On each sub-region, we performed the General Procrustes Analysis (GPA) and the rotated configurations were subjected to Procrustes Anova to calculate the relation between shape and sex. Subsequently, we calculated the shape variations associated to the female and male morphology. All the sub-regions resulted related to sex variable, the R-squared from Procrustes Anova are the following 0.014, 0.024 and 0.048 for calvaria, frontal bones and supraorbital torus respectively. The shape variation associated to female morphology highlights the presence of more vertical frontal bone, short brain case and more shortening part of posterior parietal bones. On the contrary the male morphology is characterized by more horizontal profile of frontal bone, larger brain case above all in posterior part of parietal bones. In sum a geometric morphometric approach applied on the study of sexual dimorphism resulted very useful in the determination of sex because the accuracy value are higher (82% for the entire calvarium, 85% for both frontal bone and supraorbital torus) than currently (i.e., traditional) methods used to establish sex in unknown sample. Future research will be focus in the using of sex-known sample to detect sex in unknown archaeological and paleoanthropological collections.

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## Social factors in the evolution of the human hippocampus

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The hippocampus is well known for its roles in spatial navigation and memory, but it is organized into regions that have different connections and functional specializations. Notably, the cornu ammonis (CA) region CA2 has a role in social and emotional cognition, in contrast, surrounding regions CA1 and CA3 have roles in spatial cognition. [1, 2]. A further complication is that much of what we know about the function of the hippocampus comes from studies in rodents. In highly neocorticalized humans compared to rodents, the hippocampus may be important for memory but not have as prominent a role in spatial cognition [3]. Here we investigated the evolution of the hippocampus in terms of its size and its organization into regions in relation to the evolution of social and ecological variables in primates. We found that the volumes within the whole cornu ammonis coevolve with group size, while only the volumes of CA1 and the subiculum can be predicted by home range size. On the other hand, diet, expressed as a shift from folivory toward frugivory, was not related to hippocampal volume. Interestingly, CA2 was shown to exhibit phylogenetic signal (Pagel's  $\lambda$ ) only against certain measures of group size but not with ecological factors. We also found that sex differences in the hippocampus in primates are related body size sex dimorphism. This is in line with reports of sex differences in hippocampal volume in non-primates that are related to social structure and sex differences in behaviour. Given the importance of social skills in primates, it is possible that in this order, social memory (overlain onto spatial maps for navigation) has increased in dominance over spatial mapping as a hippocampal function. Given the special circuitry of the hippocampus, memories could be structured within the spatial framework of the hippocampus [4]. In fact, social memory might in part be an exaptation that reuses neural circuitry of the hippocampus for spatial maps in an ancestral mammal [5].

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## Plant nutritional variation across a savanna biome: Investigating hominin dietary ecology on the South African Lowveld

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Reconstructions of early hominin diet increasingly recognize the significance of plant foods, and their importance for hominin feeding ecology. Dental microwear and stable carbon isotope analyses have called into question many previously held assumptions regarding hominin diet. For example, *Paranthropus boisei* was formerly assumed to have subsisted on a primarily hard-object diet due to its hyperrobust craniodental morphology. However, dental microwear analyses reveal little hard object feeding for the species, and isotopic studies suggest that ~80% of its diet came from C<sub>4</sub> plant foods (mostly likely grasses and/or sedges).

Unfortunately, empirical data on the nutritional properties of wild plants growing in modern African savanna habitats are relatively scant, despite the recognition that many modern Africa savannas are roughly analogous to the landscapes inhabited by early hominins. Early hominin paleodietary reconstructions have looked to general assumptions regarding plant nutritional/abundance value within particular habitats. However, in order to accurately investigate hominin dietary ecology, and to better understand morphological and biochemical aspects of the hominin fossil record, a posteriori models of hominin dietary behaviour must be employed. Such models must incorporate data on: plant nutrition and abundance; habitat and seasonal effects; and mechanical properties. It is the goal of this project to provide such data for a South African savanna landscape.

This study is part of an ongoing research project undertaken in collaboration with the Nutritional and Isotopic Ecology Lab (NIEL) at the University of Colorado, Boulder. We will quantify dietary variability, both in terms of plant parts and specific plant types (forbs, sedges, grasses), and model the spatiotemporal distribution of plant nutritional, antifeedant, mechanical properties, and plant availability, across a savanna biome. The data generated will be used to inform debates on how such variation in wild African plant nutrition might influence early hominin feeding ecology.

Here we present crude protein and dietary fiber values for plants collected from savanna habitats (e.g., woodland, wetland, grassland) in SANParks Kruger National Park, South Africa. Though C<sub>4</sub> grasses and sedges are often regarded as offering little nutritional value, they can be highly variable. For example, while tree and forb leaves are generally higher in protein, some of the grass leaves we sampled are comparable, with protein values of ~16%.

It is interesting to assess C<sub>4</sub> differences across sites, habitats and seasons. C<sub>4</sub> resources can represent hard objects but also “low quality” grassy vegetation. Prior studies show C<sub>4</sub> resources tend to be a more stable food resource. By building a picture of C<sub>4</sub> resource availability, variation and nutrition, we can discuss such topics as the dietary ecology of East African *P. boisei*, and South African *P. robustus* who both possess adaptations and stable carbon isotope signatures suggestive of a diet dominated by C<sub>4</sub> biomass such as sedges or grasses. Grasses and sedges are often portrayed as low-nutrient foods with significant mechanical defenses against herbivory, and are generally regarded as poor dietary resources for most primates. However, empirical data to support this view is lacking. Recent studies by our group have shown that some grasses may actually have been quite high-quality resources.

We will also consider our results within the greater context of research undertaken by members of the NIEL lab over the past decade, comparing and contrasting Kruger National Park with the Cradle of Humankind Nature Reserve (Highveld, dolomitic grassland), and savanna contexts in Amboseli National Park, Kenya.

## Dating the latest appearance of Neanderthals in Belgium

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Belgium represents a key region for studying the Middle to Upper Palaeolithic transition (MUPT) in North-West Europe. This area sits at the crossroads between Palaeolithic cultural facies with influences from eastern, western and southern Europe intermingling during the Late Middle Palaeolithic and the MUPT. Until recently, a temporal gap believed to be around 4ka (ca 42-38 ky calBP) existed between the Late Mousterian and the earliest dated Aurignacian settlements in the region [1, 2]. The dates obtained on Neanderthal remains from Spy fell into this gap, making them the latest Neanderthals in the region [3]. Including the dates from Spy, a gap of two millennia remained between the dates on Neanderthals and the beginning of the Aurignacian. Based on this chronological evidence, the transition from Neanderthals to Anatomically Modern Humans (AMH) in this region was believed to have been without contact between species. AMH would have settled in an area Neanderthals abandoned long before. As part of the PalaeoChron project, we have redated the Neanderthal specimens from Spy (tooth, maxilla and scapula), Engis 2 (skull and tooth) and Fond-de-Forêt (femur), using the compound specific radiocarbon dating method in place at the Oxford Radiocarbon Accelerator Unit. This method is based on the extraction of the amino acid hydroxyproline that occurs in mammalian collagen using preparative liquid chromatography. This method is more efficient than others in eliminating modern carbon contamination such as conservation materials. In this presentation, we report the new radiocarbon dates obtained on the Belgian Neanderthal specimens. These results show how much impact sample preparation can have on the AMS measurement when specimens have been heavily preserved with conservation materials, which is often the case for human remains. These results also now place the Belgian Neanderthal remains from Spy, Engis and Fond-de-Forêt in their proper chronometric context and allow us to refine our understanding of the disappearance of Neanderthals in north-western Europe and integrate this with other evidence for the human occupation of this region during the Palaeolithic.

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## Constructive Archaeology: Restoring a Palaeolithic Excavation through a Virtual Time Machine

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Every archaeological excavation represents a destructive process. Such a demolishing experiment becomes on one side unrepeatable and irreversible, on the other side, a source of information that provides evidence [1]. To mitigate this critical archaeological paradox, employing Mixed Reality Applications (MRAs) is possible to implement innovative virtual ‘Time Machine’ tools able to restore an excavation in its entirety. 3D virtual techniques are the core of MRAs that not only superimpose but also anchor 3D models to the real world [2]. Therefore, through a mobile display, such computing approaches manage to align realistic 3D images, which represent archaeological evidence, onto the original excavated context. MRA methodology uses georeferenced coordinates retrieved in the field and stored in databases (DB) to generate automatically such volumetric 3D models. Hence, with these geo-positioned elements, MRAs can reconstruct virtually the complete set of already unearthed evidence of the site.

From this perspective, MRAs can help archaeologists to recreate the intricate Middle to Upper Palaeolithic (MP-UP) excavations, where generally, stratigraphy presents coarse-grain chronologies and diachronic evidence may superimpose [3]. For this purpose, MRAs can filter specific categories of 3D models by querying mechanisms on the DB (e.g., typology of the find, layer of origin, date of excavation, etc.), and through mobile devices in situ (smartphones and tablets), MRAs show where such virtual models were initially located to accomplish spatial correlations with the current context.

According to the previous features, the present version of MRA uses Les Cottés Palaeolithic site (France) as a study case since such excavation embraces twelve years of research and presents a complete Mousterian-Châtelperronian-Aurignacian sequence within its layers [4]. Mainly, bone and lithic elements characterise each one of those technocomplexes. Therefore, MRA enables to create at the site precise virtual distributions of retouched or heated Palaeolithic artefacts, for instance, giving a filtered panorama about what the archaeologist needs to detect three-dimensionally over the excavation’s lifetime.

On the other hand, multiple deployment platforms (i.e., Apple, Windows, and Android) could support the present MRA just by implementing slight variations. Similarly, the current MRA could easily adapt to different types of excavations by using a georeferenced-anchoring system. Lastly, researchers can place the MRA like a simulated environment anywhere, providing the possibility to experience a virtual 3D-tour around the excavated site. To conclude, MRAs employ a methodology to reconstruct the archaeological excavation digitally, demonstrating that within these virtual limits, a ‘Time Machine’ that supports a ‘Constructive Archaeology’ is eventually possible.

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## The DISAPALE project: 3D and lithic types of European Paleolithic

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“La typologie n’est plus à la mode. Pourtant, comme la prose de M. Jourdain, nous l’utilisons quotidiennement, perpétuellement”: if possible, in the twenty years elapsed from that moment in which Marcel Otte introduced a reprint of a volume about the lithic types of the Upper Paleolithic [1], typology became less *à la mode*. However, as Otte remarked, it firmly kept its role in the formation of a common vocabulary for archaeologists: despite the critics and many issues embedded in it, typology still represents an extremely valuable and irreplaceable tool for all the subjects involved in Paleolithic studies (students, researchers and enthusiasts alike). With the ambition to give to all the people interested in the subject a single place where to find the most relevant information about the typology of Paleolithic stone artifacts – that are usually scattered among several publications, many of which are since decades out-of-print –, the idea of an updated and critically engaged catalogue of lithic types was developed. At the same time, in the past years, Archaeology has experienced a turbulent and rapid change due to a so-called digital turn (e.g. [2]), that has invested every single aspects of the discipline, starting from the documentation. In planning this re-arrangement of the typological subject, it was impossible to ignore the reality of such a revolutionary turn. All these observations together, led to the conception of the DISAPALE (Digitale Sammlung Palaeolithischer Leitformen) project: a 3D digital catalogue of Paleolithic lithic types from Europe. Lithic objects from different continental collections will be scanned in 3D, organized in a catalogue according to typological categories, and finally made available for the final users on the NESPOS platform, administrated by the Neanderthal Museum. In our poster, we would like to present the DISAPALE project to an audience of experts, and by doing so, we also hope to trigger a constructive discussion on all the critical points of our project.

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## Controlled experiments on flake formation using glass and different raw materials

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Replicative knapping experiments have played an early, and crucial, role in reconstructing methods and techniques of stone tool production that may have been used in the past [1,2]. They contributed greatly to our understanding of how particular variables can be manipulated to achieve particular results. This further provided a better understanding of the knapping choices of prehistoric people, their skills, learning processes, and cultural transmission. More recently, the design of lithic experiments has been broadened to investigate these relationships in a more objective and quantitative fashion using controlled conditions for flintknapping [3-5]. Controlled experiments utilize a device with mechanical strikers to produce a flake from a core. This way it is possible to isolate the effects of a single variable on a resulting flake's formal characteristics and further examine more complex interplays of several different variables in combination. In our experimental setting it is possible to control for the following variables: core morphology by using cores that are molded to a specific size and surface morphology; exterior platform angle by cutting the platform surface to a specific angle; angle of blow by positioning the core's platform surface area relative to the angle at which the hammer strikes the core to a specific angle value; hammer material. The results obtained with this experimental setting have confirmed some conclusions drawn from replicative experiments, moreover, they have also demonstrated the importance of certain variables relative to others.

In this paper, we will present some of the main results on the formation of lithic artifacts that emerged from these experiments. More specifically, these are related to how platform depth and exterior platform angle affect blank size and shape. These two variables explain a large portion of flake size variability and their interplay to a large extent affects the shape of the resulting flake. Other variables controlled by the knapper have lesser relative importance in flake size and shape. Earlier controlled experiments in lithics that have confirmed this effect have entirely been based on glass cores. It remained unclear, however, whether different rocks fracture in the same way and if the relationships between these variables obtained on glass cores are applicable to materials that were used in the past. To address this question, a set of additional experiments was performed on four different raw materials: glass, obsidian, flint, and basalt. We examined the effects of platform depth and exterior platform angle on flake size while holding constant other variables that are known to have an effect on flake size and shape (core morphology, angle of blow, hammer type). The results show that the effects of platform depth and exterior platform angle are similar in nature and degree across different raw materials, therefore providing further corroboration of the effects of independent platform variables resulting from previous controlled experiments.

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## Evaluating the Anterior Dental Loading hypothesis in the Middle Pleistocene populations from Sima de los Huesos

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Several hypotheses have been proposed to explain the unique craniofacial morphology of Neanderthals. One of these, the anterior dental loading hypothesis, states that the repetitive and high levels of biomechanical stress placed on the Neanderthal anterior dentition from masticatory and paramasticatory use would select for facial and dental architecture to resist such loads over time. The hominins of Sima de los Huesos are considered to be closely related to the Neanderthal lineage, sharing many Neanderthal traits, such as a degree of midfacial prognathism and shovel-shaped incisors. Under the anterior dental loading hypothesis, these traits are considered evolutionary adaptations.

This study examines occlusal wear of the hominins of Sima de los Huesos ( $n = 19$ ) and compares this wear to a contemporary modern human sample from Spain ( $n = 14$ ) and previously published data on Late Pleistocene hominins (Neanderthals  $n = 21$ , Middle Palaeolithic modern humans  $n = 5$ , Upper Palaeolithic/Early Epi-Palaeolithic modern humans  $n = 26$ ). Dental wear was calculated from the ratio of enamel to exposed dentine on the first permanent molars, which was then compared to other tooth types. Damaged teeth and unworn first molars were excluded from the study.

Statistical analyses revealed that generally, the hominins of Sima de los Huesos, did not differ to any of the other hominin groups. While the upper  $I^1$  was significantly more worn in the Sima de los Huesos hominins compared to Neanderthals ( $p = 0.022$ ), this was not found in any of the modern human groups for any of their upper anterior dentition. The lower  $I_2$  was significantly more worn in the Sima de los Huesos hominins compared to the contemporary modern humans ( $p = 0.026$ ), but only when unworn teeth were included in the analyses. This study shows that overall the hominins of Sima de los Huesos were not wearing their anterior occlusal surfaces any more so than any other hominin group. Our findings do not clearly support the anterior dental loading hypothesis.

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## A MaxEnt approach to estimate the likelihood of finding new fossil sites in Lake Turkana, Kenya, using satellite images

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During the last decade new geospatial approaches aimed at identifying fossiliferous deposits have emerged [1]. Using satellite imagery and coordinates of previously known fossil localities, machine learning algorithms can be trained to mine spectral patterns associated with fossiliferous outcrops across a region [2]. Two main statistical paradigms can be used to find fossil sites from remotely sensed data. The first is supervised learning, which requires labelled landcover classes. The second is an unsupervised learning, which groups unlabelled spectral signatures into clusters. The problem of the first approach is the laborious pre-processing of the data. Supervised learning requires manual labelling of pixels or image objects with context-dependent landcover classes such as grassland, wetland, scrubland, forest, lake, or fossiliferous deposit to train the model [1,2]. The second approach does not require user-defined labels. Rather, this approach is “blind” to the target variable and there is no way to guarantee that any cluster is actually modelling fossiliferous outcrops [3,4]. Here, we provide a third (semi-supervised) solution. This approach uses a one-class classifier that only needs the coordinates of “fossiliferous deposits” as known locales. The model presumes that all unlabelled pixels derive from a mixed set (locales that may or may not have fossils). This semi-supervised approach thus directly addresses the difficulties of unsupervised and supervised approaches. A raster object of 2072 km<sup>2</sup> (pixel resolution: 30×30m) containing 7 spectral bands and a digital elevation model was cropped from open source satellite imagery (Landsat 8 and SRTM). A maximum entropy model (MaxEnt) was trained with a subset of 1864 pixels where known fossil locales are. MaxEnt is a popular machine learning algorithm, mainly used by ecologists to model species niches and distributions using occurrence data. We used coordinates provided by the PaleoTurkana Database [5] to estimate the location of fossiliferous deposits across the Koobi Fora Formation. To assess the performance of our predictions we selected a threshold value of 0.5 on a likelihood scale from 0 to 1. We tested the MaxEnt model using a test set of observations that were not used in the initial development of the model. The MaxEnt model correctly predicted the presence of fossils in 359 out of 478 localities (a 75.1% true positive rate). The threshold value can be further increased to reduce the total area that would need to be surveyed to ground truth these predictions. A possible fieldwork protocol would be to use only the highest ranked areas as potential locales for future survey. One-class predictive modelling is thus a powerful, easy to implement alternative to other strategies previously employed to identify fossiliferous outcrops.

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## **The hominin footprints from Le Rozel (Manche, France): A snapshot to a Neandertal local group composition.**

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Hominin footprints represent a unique snapshot of hominin life and open a window on the composition of the groups who made them. However, their study is complex, their morphology resulting from the combination of several factors, such as ground nature or the body features of track-makers. Moreover, footprints are relatively scarce, especially for those attributed to Neandertals since only 9 footprints, from 4 different sites, have been attributed to this taxon so far.

Here we report and study the 257 footprints of Le Rozel (Normandy, France) discovered between 2012 and 2017, that represent so far the largest ichnological assemblage most probably made by Neandertals.

The Paleolithic site from Le Rozel is located in a Weichselian paleodune. The annual excavations (Dir. D. Cliquet) have allowed identifying several stratigraphic subunits dated to 80,000 years, where the footprints are associated with an important archaeological material: Middle Paleolithic lithic industry and faunal remains (consumed or not) around structuring elements, such as hearths, anvils or knapping spots, that attest to the occupations of human groups.

We focused on a sample of 104 footprints coming from the densest stratigraphic subunit in tracks. A stature was estimated from the length of each footprint following three steps: 1) by using published osteometric data for a large sample of shod and unshod modern populations, we quantified the relationship between foot length and stature; and 2) based on experiments conducted in a substrate similar to that of Le Rozel, we measured the ratio between footprint length and foot length; 3) then, we applied this ratio to the published osteometric data (step 1) in order to obtain a relationship between footprint length and stature. The estimated statures for the Le Rozel studied sample were then associated with age classes (children, adolescents, adults) based on a model we developed from published Neandertal osteological data.

As a result, the 104 footprints correspond to statures ranging from 65.8 to 189.3 cm (mean: 125 cm). They reflect a large majority of children and adolescents (90%) and a minority of adults including at least one male. The footprints from Le Rozel thus represent a direct point of view on the composition of a Neandertal group which differs from that estimated from osteological assemblages. They also shed light on the Le Rozel archeological site by raising questions about the distribution of activities (hunting, carcass transport, butchery, tool making...) according to age classes at Le Rozel 80,000 years ago.

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## Electrodermal activity and haptic perception with Lower Paleolithic stone tools

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Parietal cortex underwent specialization during human evolution, probably associated with visuospatial functions, tool use, and body-tool integration [1]. Objects are perceived differently whether they are out of the body range, within the body range, or in contact with the body and, in this latter case, they are integrated in the body scheme [2]. During tool manipulation, the somatosensory perception is combined with motor feedbacks, and the haptic experience triggers cognitive responses that concern body cognition, visuospatial imaging and self-awareness. Preceding studies showed that stone tool manipulation exerts electrodermal reactions that are commonly used as proxies for attentional and emotional engagement [3, 4]. Such electrophysiological activation is different for different tools. Lithic tools are crucial in the interpretation of the cognitive abilities of extinct human species. In particular, the transition from Oldowan to Acheulean culture was hypothesized to be associated with relevant cognitive variations [5]. In this study, we analyze electrodermal level, electrodermal response and total manipulation time to reach a comfort position, during Lower Paleolithic tools handling in 46 right-handed adult, testing differences in the distribution between sexes and between tool typologies (chopper vs handaxes). Females show higher individual variation and, on average, higher engagement. Acheulean display less emotional engagement and required longer manipulation time. A likely interpretation of the sexual differences relies on allometric differences in hand size, and consequent higher perceptual sensibility in women's hand, due the more condensed pore density in smaller hands. We speculate that differences between choppers and handaxes can be due to increase/decrease ergonomic comfort associated with the geometric complexity of the latter group. Differences are, nonetheless, subtle, and further surveys will be dedicated to investigate specific physical or anatomical features that may influence haptic experience with Paleolithic stone tools.

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## Radiocarbon dating small samples of Gravettian human remains from Dolní Věstonice II and Pavlov I (Czech Republic)

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Dolní Věstonice II (DVII) and Pavlov I are large Gravettian sites located in the Pavlov Hills, Czech Republic. The region is famed for early examples of carved mammoth ivory and fired clay objects of human and animal figurines, notably the Venus of Věstonice. During the twentieth century several ritual human burials and numerous disarticulated human bones were excavated from DVII and Pavlov I, including the famous triple burial from DVII [1]. In the 1980s a series of associated charcoals were radiocarbon dated to *ca.* 31,000 – 29,000 cal BP [2] but direct radiocarbon dating of the precious human remains was not undertaken.

In 2013, seven of the human bones were sampled for aDNA analysis, including the three skeletons from the triple burial (DV13, DV14, DV15), two skeletons from single burials (Pav1, DV16) and two unarticulated human bones (DV42, DV43) [3]. Small amounts of bone material were left over from the aDNA sampling, providing the first opportunity to directly date the human bones.

A recent pilot study indicated that near-infrared (NIR) spectroscopy is an effective method to easily and non-destructively ascertain the level of collagen preservation in archaeological bone [4]. NIR analysis of the human bones from DVII/Pavlov I indicated that sufficient collagen was preserved for radiocarbon dating. We therefore sampled very small amounts (32-70 mg) of bone material for collagen extraction and ultrafiltration. Preservation was excellent (8-14% collagen preserved) which allowed us to date each collagen extract multiple times using the AixMICADAS with graphite targets (*ca.* 800 µg C) and the gas ion source (<100 µg C) [5]. The direct dates confirm the Gravettian origin of the human remains and indicate that several of the radiocarbon dates carried out in the 1980s on associated charcoals were likely affected by low-level contamination of modern carbon. The results add seven individuals to the small collection of reliably dated Upper-Palaeolithic humans in Europe.

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## The ontogeny of bipedalism: insights from trabecular changes during growth

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Many primates are capable of facultative upright locomotion for short periods of time, but this differs from the committed terrestrial bipedalism that is a hallmark of our species. For this reason the evolutionary acquisition of bipedal locomotion, and its relationship to our own transition from a crawling infant to striding bipedalism (5-7 years), have been topics of great interest within paleoanthropology. Research into this transition have highlighted cultural influences that change the timing of milestones (e.g., crawling and unaided walking), and others factors that affect the development of locomotion (e.g. stance, step length, and pace) [1]. In regard to ontogenetic changes in bone morphology, there are many questions about the interplay between genetic canalization and the bones biomechanical response to loading. While there is evidence for a bone functional adaption response to gait maturation, in the form of trabecular architectural (re)modelling of the femur [2], very little is known about trabecular architectural changes in the human foot during the transition from crawling to walking. In humans the morphology of the talus provides a wide range of movements during locomotion while efficiently dividing weight between its anterior and posterior parts. Being that locomotor variation arises during development [1], it is important to understand the morphological differences that coincide. To better understand the internal differences during these periods we quantified the trabecular architecture in an ontogenetic sample of 28 human tali (8 weeks – 13 years) from the known age/sex/death collection in Bologna, Italy (n = 18), and an archaeological collection from Norris Farms #36, Illinois, USA (n = 10). Tali representing five age classes (8 weeks-1 year, n = 5; 1.1-3 years, n = 9; 3.1-6 years, n = 8; 6.1-10 years, n = 3; 10.1-15 years, n = 3) were microCT scanned (20-40 µm voxel resolution) and reconstructed as 16bit tif stacks. Segmentation of the images into bone and non-bone voxels was performed using the MIA-clustering algorithm [3] with trabecular bone isolation and quantification (bone volume fraction [BV/TV], degree of anisotropy [DA], elastic modulus in gigapascals [E], thickness [TbTh], spacing [TbSp], number [TbN], total surface [TS], and total volume [TV]) performed in Medtool 4.2 (Dr. Pahr Ingenieure.e.U. [4]). Logistic regression was run in R 3.5.3 (The R Foundation for Statistical Computing, 2019) with trabecular variables as responses, and age class along with population as predictors. Significant results (p<0.05) between age class were found for E (8wk-1 and 1.1-3 years), and TS (3.1-6, 6-10, and 10.1-15 years). Among the age classes TbTh, TbSp, TS, and TV steadily increase with age. BV/TV and E are lowest for individuals in the second oldest class (14%, 6.7), and highest in the oldest class (17.9%, 10.8). For DA, the youngest class is relatively isotropic (.16), which increases towards more anisotropic trabeculae and plateaus in the older classes (.22-.23). The increase in architectural variables (TbTh, TbSp, TS, and TV), relative to age, is expected. The variables associated with fracture resistance (BV/TV and E) are at their lowest in the age class (1.1-3 years), which coincides with the developmental period when modern children begin walking unassisted. Interestingly, these preliminary results agree with a similar study on the radius [5], which suggests the ontogenetic trajectory may be similar between skeletal elements during the transition from crawling to walking. Future analyses will consider also the external morphology and cortical bone thickness, which will provide a more complete picture of these differences. These results could then be used to compare the external and internal morphologies of non-human primates and fossil taxa, which would be useful in identifying developmental milestones related to the evolutionary history of committed terrestrial bipedalism.

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## Examining the relationship between tooth size and food size: the functional consequence of dental reduction during hominin evolution

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During hominin evolution post-canine dentition has varied considerably in size. These size changes have been associated with dietary adaptations: Premolar expansion in extant primates has previously been associated with stress-resistant feeding [1], and molar size reductions between the australopithecines and *Homo* are often discussed in relation to a relaxation of masticatory requirements due to extra-oral food processing. Yet little is known regarding the functional significance of these changes in dental size. Whether larger teeth are mechanically more advantageous for small or large food breakdown, or indeed whether the smaller teeth of *Homo sapiens* are necessarily disadvantageous is not known. An improved understanding of these topics may give us a better insight into the selective pressures faced by our hominin ancestors.

To examine this relationship between tooth size and food breakdown, hypothetical dental models with increasing surface area were created, as were food replica items of varying sizes. The food replicas were crushed under compression between the models using a universal physical testing machine. To create the dental models, high resolution surface scans of the upper and lower dentition were obtained from a modern *Homo sapiens* skull. The dental rows were isometrically scaled to create three models: original (small), increased by x1.5 (medium), and increased x2 (large). The original models and hypothetical dental models were then printed in metal and attached to the physical tester. Using a 3D printer, spherical hard brittle food replicas were produced in small (10mm diameter), medium (15mm), and large (20mm) sizes. Spheres of each size were crushed between the M2 of each of the three dental models. The spheres were placed at two locations on the M2 teeth, and the peak force at initial fracture, energy required to induce fracture, and fragmentation were recorded. Given the previous association between hard object feeding and increased dental size, it was expected that the larger teeth would be the most efficient (lower force and overall energy).

Contrary to our prediction, the smaller teeth were slightly more efficient, reducing the force and energy for all sizes of food. However, compared to the effect of changes in food size and the location of the bite on the tooth, performance varied minimally between the different sizes of teeth. The results suggest that individuals could access different stress-resistant food resources by simply changing how they position a food item, but also suggest that dental reduction during human evolution may have had a relatively minor impact on the mechanical efficiency of the individual to break hard food items of varying sizes. Further consideration is now needed into how such dental reduction would impact on tooth fracture risk and dental performance with foods of different material properties and how variations in dental topography may influence food breakdown.

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## *Homo naledi*, *Homo floresiensis* and ‘taxic outlieriness’: a comparative approach to odd species.

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In the last two decades new fossils have added greatly to the diversity of the hominin lineage. While much of this has been relatively modest additions to the range of phenotypic variation, two taxa in particular have been notable for the extent to which they are outliers from the expected range – *Homo floresiensis* [1] and *H. naledi* [2]. These extinct taxa do not fit neatly into existing models of hominin evolution, being morphologically divergent from other hominins. While much has been written about their phenotypic characteristics, the focus has been on their position within hominin phylogeny and evolution. However, their discovery prompts a broader question – are they true outliers, and how common are ‘outliers’ in evolution? There is no clear word or concept in evolutionary biology for the pattern we are seeking to explore, and so we have borrowed the data science and statistics concept of ‘outlieriness’ – the state of being an outlier. The aim of identifying outliers in statistics is often to remove them or their effects; here, however, we want to use it to infer evolutionary processes. Outlieriness is used in computer science, data science, machine learning and statistics [3], but has not been employed in evolutionary biology to our knowledge, although there has been some usage in bioinformatics and systems biology [4]. We define ‘taxic outlieriness’ as the state of degree of being an outlier within a higher taxon. To explore the issue of taxic outlieriness, and the place of *Homo floresiensis* and *H. naledi* within this framework, we collected data on skull dimensions in 300 anthropoid primates. These are distributed across 30 genera, and we examined variation in outlieriness in relation to the number of species per genus, the diversity observed, and the extent to which they contained an outlier species. Measuring ‘outlieriness’ is not straightforward [5], and alternative metrics are explored. Taxic outlieriness was found to occur in a number of primate lineages, and we explored the effects of phylogeny, taxonomic unreliability, generic diversity, evolutionary age and ecology. The observed diversity of hominins is discussed in the light of these results, along with the broader evolutionary implications of this approach.

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## *Australopithecus* variability at Sterkfontein, South Africa: evidence from the pelvic remains

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The taxonomy of Southern African *Australopithecus* has been a matter of intense debate. Traditionally, all hominin fossils from Sterkfontein Member 4 (ca. 2.6 – 2.1 Ma) have been attributed to *A. africanus* despite high morphological variability in both craniodental and postcranial elements [1]. The interpretation of the Sterkfontein fossil material is complicated by its fragmentary and incomplete state of preservation and by the uncertainty surrounding its chronology. The adult specimen StW 431 and the subadult Sts 14 from Sterkfontein Member 4, presumed male and female individuals respectively, are represented by partial skeletons and preserve a fairly complete pelvis and vertebral column. For these specimens' differing pelvic reconstructions have been generated via various methods [2]. Based on their general shape and on a recent geometric morphometric analysis of the first two sacral elements [3], we previously suggested that the morphological differences between Sts 14 and StW 431 might exceed the expected range of variation for a male and female of the same species with reference to the human variation. Here, we perform new virtual reconstructions of the StW 431 and Sts 14 pelvises to elucidate key aspects of their variation. The restoration of the StW 431 hipbone was performed by virtually reassembling the preserved right and mirrored left fragments. The alignment of the elements was facilitated by several contact points and by the absence of patent asymmetry. Except for the ischiopubic ramus and the pubic body, which are not preserved, the missing parts of the hipbone were supplemented by alternatively warping the Sts 14 and A.L. 288-1 hipbones, obtaining the same outcome. The pelvic girdle could be reassembled confidently thanks to the presence of well-preserved auricular iliac and sacral surfaces. Sts 14 was restored by virtually removing the areas reconstructed by Robinson with plaster of Paris and by reassembling the fractured ischiopubic region of the right hipbone. The missing areas of the left hipbone were implemented using mirror-images of the right side. Finally, the pelvic girdle was recomposed. The sacrum was completed based on the preserved first two sacral elements. The virtual protocol was supported by manual reconstructions using 3D prints of the original fossils. The new virtual models of StW 431 and Sts 14 pelvises are generally compatible with the earlier reconstructions by Haeusler [2,4], even though in StW 431 local differences appeared with respect to the orientation of the iliac blades, and in Sts 14 the sacrum might be less curved than previously thought. Compatible with previous observations, StW 431 presents a very peculiar morphology which differs dramatically from that of *Homo* and great apes possessing extremely flared iliac blades. Moreover, the StW 431 pelvis is markedly different from Sts 14, the latter being reminiscent of the *Homo* pelvis with its more verticalized iliac blades. The StW 431 sacrum is significantly less entrapped in the pelvis than in Sts 14, implying a greater mobility of the lumbar spine. Moreover, its iliac blades are much wider and more laterally flaring. The pelvic inlet is sagittally oval in both individuals, rather than being platypelloid. Since pelvic shape reflects functional adaptation to locomotion and giving birth, it is reasonable to assume that the profound morphological differences observed between StW 431 and Sts 14 might indicate different biology and taxonomic affiliations. Our conclusions agree with the observations by Crompton et al. [5] that StW 431 might belong to a taxon other than *A. africanus*. However, further studies are needed to elucidate the relationship between StW 431 and StW 573, a specimen from Sterkfontein Member 2 attributed to *A. prometheus* that was likened to StW 431 and distinguished from Sts 14 based on some pelvic features.

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## Reexamination of the Cranial and Mandibular *Homo sapiens* Fossils including a New Frontal Bone from Tam Pa Ling (Laos)

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Tam Pa Ling (TPL) is a cave site in northeastern Laos that continues to yield new fossils attributed to *H. sapiens*. To date, they represent the earliest anatomically modern humans in mainland Southeast Asia. The cranial and mandibular fossils were excavated from different, undisturbed stratigraphic layers ranging from ca. 46 ka to more than 70 ka, and include, in chronological order, a partial cranium (TPL 1), a nearly complete mandible (TPL 2), the anterior corpus of a mandible (TPL 3), and a new, undescribed frontal (TPL 7). Previous studies show clear *H. sapiens* affinities combined with archaic features, especially in dental and mandibular proportions [1:4].

We use semilandmark geometric morphometric methods to compare the shape of the TPL cranial and mandibular remains to a large sample of fossils, including Neanderthals, early and Upper Paleolithic *H. sapiens* from Africa, the Near East and Europe, Late Pleistocene humans from Australasia, as well as a geographically diverse sample of Neolithic and recent Holocene *H. sapiens*. While geometric morphometric analyses have been done on the TPL mandibles [1:4], the frontals and maxilla have never been analyzed using these methods. Following virtual reconstruction of the fossil material, including a new reconstruction of the TPL 2 mandible, landmark and semilandmark datasets were created according to the preserved anatomical elements. For each dataset, the shape coordinates were analyzed in between-group principal component analyses and linear discriminant analyses were performed to classify each TPL fossil.

Our results are consistent with previous findings supporting clear *H. sapiens* affinities for the TPL fossils [1:4]. Within the sample, the TPL 1 maxilla and TPL 2 and 3 mandibles also show archaic features, with the TPL 1 maxilla and TPL 3 mandible classifying with Middle to Late Pleistocene early *H. sapiens* from Africa and the Near East and Upper Paleolithic humans from Africa and Europe, respectively. Whereas, the TPL 1 and 7 frontals and the TPL 2 mandible classify with the Australasian Late Pleistocene group.

The size of the maxilla and frontal are similar to other Late Pleistocene Australasian fossils, a large maxilla coupled with a small frontal bone. The TPL mandibles are extremely small compared to all other groups, and the geologically younger TPL 2 mandible is smaller and its anterior corpus is more modern than the older TPL 3 corpus. This trend in gracilization through time is not present in the frontal bones. The younger frontal (TPL 1) is larger and more archaic than the older (TPL 7).

The presence of fossil material in Southeast Asia over 70 ka implies an early dispersal of *H. sapiens* from Africa into tropical Asia. However, unlike the large and robust early *H. sapiens* frontal bones from Africa and the Near East, the TPL 7 frontal is remarkably gracile for its geological age of over 70 ka. The TPL 1 frontal dated to ca. 46 ka, on the other hand, shows a more typical Late Pleistocene Australasian morphotype and is most similar to the fossils from the sites of Kow Swamp and Lake Mungo. Morphological similarities between the TPL 1 frontal and maxilla and Amerindians suggest that they could represent the ancestral morphotype of later populations migrating to the Americas.

We would like to thank all of the curators who gave us access to recent and fossil hominin specimens for computed tomography and analysis and to Heiko Temming for his technical assistance.

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## Reviving australopithecine birth: contribution of numerical simulation.

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Paleoanthropological research on the evolution of childbirth is often hampered by three main limiting factors. First, fetal head movements are usually only deduced from static steps that explore fetopelvic relationship in three 2D planes. Second, the fetal head size as well as the exact shape of the mother's pelvis are unknown for most fossil hominins, and a large range of estimates is rarely considered. Third, the biomechanical consequences of the contact of the fetus with the mother's pelvis are often ignored. In this study, we perform dynamic finite-element simulations of childbirth to estimate delivery outcomes for multiple reconstructions of A.L. 288-1 (*Australopithecus afarensis*), Sts 14 (*A. africanus*), and MH2 (*A. sediba*) by assessing the trajectory and rotation of the fetal head, and by observing whether an arrest of the descent occurs (i.e., a dystocic birth). In our finite-element simulations, the pelvis was treated as a rigid body with the exception of two springs located at the centre of both auricular surfaces. These modelling parameters permitted the sacrum to be displaced posteriorly or anteriorly to accurately simulate the complex nutation and counter-nutation movements produced within the pelvic ring. A left occiput anterior orientation of the fetal head was chosen for the onset of the simulations, as this is the most commonly observed head presentation in modern humans. The models used the force of gravity applied on the fetal head as the power of descent. Three fetal head sizes reflecting brain weights of 110 g, 145 g, and 180 g were used to encompass the entire range of estimations reported in the literature [1, 2, 3]. Our results show that all dyads with a 110 g brain size systematically had an unproblematic birth (i.e., a eutocic birth), whereas dyads with a 180 g brain size were all dystocic. Of the eight dyads with an intermediate brain size (145 g), six had an eutocic birth. Of the eight dystocic dyads, six had an arrest of descent at the inlet level. When the parietal bosses were situated on the same side of the ischiatic level (i.e., the occiput is facing the sacrum or the symphysis), birth was retroischiatic. In all instances of eutocic birth, the fetal head passed along a straight trajectory through the birth canal. A.L. 288-1 and MH2 pelvises were dystocic or eutocic with a 145 g brain size depending on the reconstruction considered. The differences between the pelvic reconstructions significantly affected birth outcome, which emphasizes the importance of considering several possible reconstructions in the same obstetrical analysis. Finite-element simulations suggest a rotational birth process for australopithecines and an eutocic birth in most of the pelvic reconstructions combined with a 145 g brain size. Considering an adult brain size of 440-469 g, the neonatal capacity is 32% or less of the adult brain size. In non-human primates, the weight of the neonate's brain is 42% of that in adults on average, but only 29% in humans. Since the ratio of australopithecines (32%) is human-like, we propose that australopithecines might have already experienced notable fetopelvic constraints. This might have led to a certain degree of secondary altriciality in early hominins and with consequent increased degree of parental investment [2] [4].

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## New insights into historic excavations of a Later Stone Age cemetery at Grotte des Pigeons.

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Grotte des Pigeons, located near the village of Taforalt in north-eastern Morocco, shows evidence of human occupation from at least 110,000 yrs, intensifying at about 15,000 cal BP. This later phase of occupation is evidenced by an approximately 4 metre thick anthropogenic ashy deposit, containing large amounts of burnt snail shell and bone, referred to as the Grey Series (1). The Grey Series is also characterised by an Iberomaurusian (Later Stone Age) lithic industry. Not long after the onset of the Grey Series formation, intensive burial activity took place lasting until around 12,600 cal BP. The burials were placed towards the back of the cave, away from habitation areas, making this the earliest well dated cemetery in Africa.

The cemetery was excavated by a team led by Abbé Jean Roche from 1951-1955. Remains of adults and children were recovered in single and multiple graves designated Sepultures I-XXVIII, from spatially separate but adjacent areas designated Necropolis I and II. While there is some very limited information on funerary behaviour in Roche 1963 (2) and in the anthropological study of the skeletal remains (3), a detailed description of the cemetery in its original context was never published. More recent archaeological investigations have recovered a series of intercutting single burials in an alcove at the back of the cave referred to as Sector 10 (5).

The current study is based on previous unpublished, and partially published (4) excavation records from museum archives. These include plans of the excavation and burials, photos and crucially field notes from the excavations undertaken in 1954 and 1955. Plans were digitised, resized and oriented, and then aligned spatially using shared features and arranged into a chronological sequence. The archival research is being carried out in conjunction with a reassessment of the skeletal assemblage curated at the IPH in Paris. The integration of scaled drawings from the archive and published plans and of the cave (4) reveals the location of individual burials within Grotte des Pigeons, demonstrating a single spatially contiguous area that incorporates Necropolis I and II and the newly excavated burials from Sector 10.

Where possible, individual skeletal elements were identified on plans. In several cases skeletal elements assigned to different graves were matched based on anatomical features enabling us to reassemble elements belonging to the same individual. This information allows us to infer the relationships between and the extent of disturbance of individual burials, and partially constrain the chronological sequences of burials. Building on previous work (4), the archive data provides a basis for re-evaluating the diversity and elaboration over time of Iberomaurusian burial practice at Grotte des Pigeons.

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## Differential preservation of burnt bone: Impacts on the visibility of Upper Paleolithic fire in the steppes of Mongolia

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Burned bones can be altered by various processes before and after being buried, although the extent to which burning temperature influences bone preservation and visibility is unclear. The differential taphonomic processes which affect burnt bone, including sediment composition and water flow, are crucial to take into account when considering fire technology. Determining the fidelity of an assemblage and its relationship to the depositional context is an important step when utilizing burnt bone for analyses such as investigating if a fire is natural or anthropogenic (e.g. through the evaluation of temperature intensities, edge angularity, and dispositional reconstructions) or examining the contents or spatial features of a combustion feature. Previous research has established that increasing temperatures are positively correlated to increased fragmentation and fragility of burnt bone [1]. Other relationships between temperature intensity and changing material properties of bone are not yet well described, although experimental research has demonstrated that pH values do affect the potential for bone preservation and that bones burnt to lower temperatures are more susceptible to differing pH values [2]. Here we detail additional aspects of bone preservation through the description of bone crystallinity and structure, and a description on how heat alters bone crystalline shape and reactivity. Bone cores are heated intact to a range of temperatures between 100°C and 1200°C and analyzed through the use of Thermogravimetry and Differential Scanning Calorimetry (TGA-DSC), X-Ray Diffraction (XRD), Fourier Transform infrared spectrometry (FTIR) with Attenuated Total Reflectance (ATR) attachment, and Scanning Electron Microscopy (SEM). We find that an increase in grain size is correlated with rising temperatures, notably with the recrystallization associated with calcination which takes place in bone at temperatures of 600°C and above. This study also demonstrates that as bone porosity decreases upon heating, bioapatite hexagonal structures become more amenable to growth and less prone to dissolution. We apply the knowledge gained through the development of this experimental reference collection to the study of the Upper Paleolithic site of Tolbor-17 in the Ikh-Tulberiin-Gol (Mongolia). Although the archaeological record in the valley is particularly rich, bones and combustion features are usually poorly preserved. It is particularly important to investigate both remnants of fire in addition to the processes behind this pattern, as it is hypothesized that fire is a critical resource for human survival in the continental climate of the region. The lack of identifiable bones in this region leaves many questions open regarding the subsistence of hunter-gatherers during the Pleistocene, and it is in this context that the site of Tolbor-17 stands as an exception. With better bone preservation allowing for a significant amount of faunal material recovered, Tolbor-17 allows for the study of a ca. 35,000-30,000 year old fire in an open air context. This study shows through the use of FTIR-ATR and distribution patterns that not only do the burned bones at Tolbor-17 indicate high temperature anthropogenic fire, but also that the disproportionate amount of calcined bones resulting from that fire is a consequence of differential preservation due to biases introduced by the loess sediment matrix. Our results further suggest methodological guidelines for the study of ephemeral and altered anthropogenic combustion features and finds that this assemblage provides valuable information regarding Upper Paleolithic fire technology on the Mongolian Steppe.

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## **Portela II (Leiria, Portugal): a specialized lithic workshop for the production of Vale Comprido points in Proto-Solutrean times?**

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The severe cooling and the consequent expansion of the ice sheets during the Last Glacial Maximum (LGM), 27–19 ky ago, had a major impact on plant, animal and human populations. In Southwest Europe, a pan-European technocomplex, using bone or wood projectile points armed with lithic barbs (Gravettian), was replaced by a regional technocomplex using stone points as hunting weaponry: the Solutrean.

The origin of the Solutrean has been a central issue in the study of the European Upper Paleolithic. Different authors placed the origins of the Solutrean in Africa (Santa-Olalla and Almagro Basch saw similarities with the Aterian), France (Smith thought that Gravettian Font Robert points could be related) or Iberia (a human refuge with a milder climate, according to Strauss). Thus, this cultural change was explained by human migrations or simple adaptation to a colder environment [1].

Nevertheless, in the mid-1990s, a transition phase between the Gravettian and the Solutrean was identified in the littoral of central Portugal, Estremadura [5;3]. This phase is characterized by the presence of a particular type of stone tool: the Vale Comprido point [4]. Since then, its use as an index fossil of this phase has been successful in Spain (Peña Capón and Cueva Ambrósio) and in France (Abri Casserole and Marseillon), for example.

The Portela II archaeological site was identified in 2009, during the construction of a sewerage piping. A preventive excavation was carried out, only in the area directly affected by the works (10m<sup>2</sup>); the site is thought to extend beyond the limits of the excavated area. About 800 lithic artefacts were recovered, including 15 Vale Comprido points and a high refitting potential was identified. This poster will present the results of the technological study of the lithic assemblage. A single reduction sequence was identified: the production of elongated, naturally-pointed blanks that were subsequently transformed into Vale Comprido points, the only tools recovered at Portela II. Chippage found at the site indicates that the typical dorsal basal thinning retouch of the Vale Comprido points was performed locally.

The characteristics of this site lead us to consider a new archaeological intervention in 2020, in the scope of the PALEORES-CUE project. In fact, only the enlargement of the excavated surface can confirm whether this was a Vale Comprido points workshop or whether the previous excavation hit a specialized knapping area of the base camp. This site shows some similar features to the one excavated by M. Heleno in the 1940s at Vale Comprido Encosta, in the Rio Maior region. Current excavation methodology will clarify this issue and will enable testing the common assumption, within the Portuguese archaeological community, of Heleno's sampling bias [2].

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## Sexual dimorphism of the Middle Pleistocene hominins from Sima de los Huesos (Burgos, Spain): a study the enamel and dentine dimensions of the permanent canines

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Sexual dimorphism, as an important part of the total variation seen in populations, plays a key role in taxonomic debates. In this context, Sima de los Huesos (SH) hominins, from Sierra de Atapuerca in Spain, offer an exceptional opportunity to investigate within-population variability. For this reason, these fossil remains have been used in previous research to study sexual dimorphism during the Middle Pleistocene [1,2,3,4]. However, all these studies have had to face the same limitation: this exceptional human collection has a predominance of adolescents and prime-age adults [1]. In modern humans, most of the dimorphism in body size is generated during adolescence; nevertheless, intersexual variation in dental crown size is generated between birth and the 12th year [5]. That is why teeth, in general, and canines, in particular, are very useful in assessing sexual dimorphism in extinct populations with SH demographic characteristics. In 1993 and in 2001, Bermúdez de Castro and colleagues studied the pattern of dental size variation of the SH lower dentition [1,2]. Since then, the dental sample of the Middle Pleistocene population from Atapuerca has increased and novel imaging analytical techniques like micro-computerized tomography (micro-CT) have emerged, permitting reanalysis of this issue from a new perspective. In this study, micro-CT techniques have been applied to a sample of hominin teeth from the site of Sima de los Huesos. Dental tissue proportions of the permanent canines are here assessed with the aim of characterizing the pattern and degree of sexual dimorphism within this population. A combination of classical statistical approaches with more novel ones has allowed us not only to bolster the sex allocation of the individuals previously assigned in the literature, but also to estimate the sex of the youngest individuals, which were not assessed in previous studies. Likewise, the sex of some extensively worn canines and isolated pieces has been also estimated. As a result, the sex ratio observed in our dental sample from Sima de los Huesos population is 5:8 (Nm:Nf), showing a higher female representation. The canines of Sima de los Huesos population have, in general terms, a degree of sexual dimorphism in the permanent canines tissue proportions that is lower or similar to that of modern humans. Their mandibular canines are more dimorphic than the maxillary ones among other things, due to the marked dimorphism of their root dimensions. In light of our results, we can conclude that this European Middle Pleistocene population cannot be considered more dimorphic than modern humans, although the differences in their canine tissue proportions are enough to allow estimating the sex with a high degree of confidence. One reasonable interpretation of our results would be that the sexual dimorphism of dental tissue patterns could have already decreased during Middle Pleistocene regarding early Homo, and was maintained, to either greater or lesser extents, in subsequent groups. However, this decrease in intersexual variability may have not happened at the same time in all skeletal structures, showing a mosaic evolution of the expression of sexual dimorphism in the different bone elements. Future studies of the SH hominins, as well as other European Middle Pleistocene samples, would help to test this hypothesis.

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## **Inferring human population history and diversity from tooth roots: the application of a phenotypic set approach to global variation**

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While much of dental anthropology has focused on crown morphology (crown dimensions, cusp number, area, etc.), tooth roots are a relatively unexplored area of increasing interest. The development of advanced imaging technologies has greatly increased access to the evolutionary and adaptive information preserved in roots and has provided a rich source of additional information about the nature of human phenotypic diversity. We report here on a project to capture the structure and extent of human dental root morphological diversity. There are two elements to this. The first is to develop a comprehensive scoring system that both encompasses previous typologies and is easily expanded upon, and so captures in a semi-quantified way the nature of the dental root phenotypic set. The second is to use this system to map human tooth root variation and consider the factors that underlie this in the context of recent human evolution and diversification. Using CT scans, we investigated root and canal number, shape, and orientation, in a global sample of humans (n=947). From these data we developed a scoring system comprised of five tooth root elements (root number, canal number, canal location, root shape, canal shape). These are scored independently for each root and each tooth, and when combined provide a unique but finite set of phenotypes. Here, we present our phenotype system and the results of its application to the total phenotype space of our sample. Samples are drawn from 56 populations, distributed across 24 regions, from all inhabited continents. We investigated how variation is partitioned within and between populations and show that it has complex geographical patterns. We used the presence, absence, and frequency of traits to explore the factors underlying this, including population history and potential admixture. Results show significant differences in root and canal morphology across populations; this variation is expressed at different geographical levels - global, continental, and regional. In addition, we found significant signals of sexual dimorphism in the observed variation. Finally, we consider unusual and rare root and canal morphologies and their increased frequencies in Austronesian, Inuit, and Native American populations, as well as their presence in extinct hominin species.

## Human exploitation of birds during the late Magdalenian at the Trou de Chaleux, Belgium

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In last decades, scholars have highlighted the usefulness of birds, as part of the small game, to help understanding complex human behaviour and choices during the Prehistory. While the exploitation of birds has been documented in several sites in eastern or southern Europe, what happened in north-western Europe is still largely unknown due to a lack in the preservation and in the study of bird material. In this context, archaeological assemblages from Belgium offer a great opportunity to better understand the exploitation of birds in this part of Europe, because of the good conditions of preservation offered by its partially karstic subsoil. Here, we present the results of the study of the bird material from the largest Late Magdalenian assemblage of Belgium, the cave site of the Trou de Chaleux. Archaeological excavations at the Trou de Chaleux at the end of the 19th century yielded a vast assemblage of lithic and bone material as well as figurative art, characteristic of the Late Magdalenian. AMS dates with calibrated ages range from 15,733 cal BP to 14,134 cal BP, situating the main archaeological deposit from the Trou de Chaleux at the transition of Greenland Stadial-2 to Greenland Interstadial-1 (Bølling-Allerød Interstadial). Among the archaeozoological material, more than 500 bird bones have been isolated, which had never been studied. We performed the taxonomic and skeletal identification of the material and we examined in detail the surface of the bones in search of human modifications such as tool marks, fire traces or pigment deposits. Surface alterations were investigated based on a macro- and microscopic analysis, including an analysis of wear traces and elementary composition. More than 30 bird bones display traces of human intervention, mainly tool marks. The traces observed indicate an intense exploitation of birds for food, technical but also symbolic purposes. Ptarmigans, ducks, snowy owl and northern raven were consumed. The bones of the largest taxa such as geese, swan or loon were used as raw material to produce tubes and needles. Feathers were also extracted. Finally, talons of golden eagle, northern raven and snowy owl have been sought after for non-utilitarian purposes. The study of the bird material from the Trou de Chaleux helps precisising exploitation patterns of animal in north-western Europe and allow comparisons with other regions. The strong interest observed for geese could be a regional particularity.

## Vascular grooves on human tibias as a proxy for Paleolithic mobility pattern inference: the case of the Lower Magdalenian “Red Lady” of El Mirón cave (Cantabria, Northern Spain)

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Based on the study of the vascular grooves found on a human tibia from the “Red Lady” at El Mirón Cave, located in northern Spain, inferences about her mobility patterns are presented. The Red Lady is a Lower Magdalenian woman dated ca. 18,700 calendar years ago, with an estimated age between 35 and 40 years [1,5]. The skeletal remains were found in a disturbed primary burial from which, except the tibia (gnawed by a carnivore) and the fibulae, the long bones and cranium are missing. As part of ritual treatment, the Red Lady’s bones were coated with mineral ochre [2]. Vascular grooves are found on the inner and external table of neurocranium and the long bones shafts, such as the femur and tibia. Particularly in tibias, vascular grooves appear on the proximal and mid-shaft, where the muscular branches of the anterior tibial artery are inserted [3]. Vascular grooves appear during rapid growth periods, usually at puberty or when high levels of physical activity are undertaken. The latter is related to higher muscular tension which causes greater blood pressure and thus the creation of the vascular channels. Muscle size, sex, age and type of physical activities performed are directly related to the presence and greater or lesser frequency of thereof [4]. In studying the Red Lady, vascular grooves were scored separately, based on location on the shaft. Diagnosis was based on position, direction, linearity, margin shape and presence of absence of microstriations. Additionally, length and depth were measured, and morphology was compared with rodent marks, root marks, bacterial activity and trampling damage to maximize successful identification. Two single vascular grooves have been identified, both on the mid-shaft. They are U-shaped in cross section, with rounded borders indicating bone growth around the anterior tibial artery vessels. They appear partially covered by ochre and no signs of post-depositional erosion or microfractures have been observed. As described by [3] and [4], this woman would have had a high level of mobility during her life. In fact, previous data from the robustness and cross-sectional shape of the tibia and fibulae suggest significant physical activity related with daily activity and seasonal migration [5]. Moreover, stable isotope analysis of this individual indicates an intake of approximately 20% marine resources, so movements to the 25 km-distant Cantabrian coast can be inferred, in addition to daily moves on the steep mountain slopes surrounding the site [1]. Vascular grooves constitute a new morphological indicator with which to assess mobility patterns in past human populations. More studies are needed to highlight their future potential as an indicator of human movement and exploitation of different ecological niches among Upper Paleolithic hunter-gatherer groups from Western Europe.

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## Change in the discourse: the impact of ancient DNA analysis on Neanderthal studies

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Late Pleistocene archaeology has seen an exponential increase in publications over the past few years, particularly in studies involving Neanderthals and other extinct hominin species. To an extent this increase may be attributed to methodological advances; while there have been several innovative approaches, such as the use of stable isotopes, there is a general perception that DNA analysis has had the most significant impact on the field. Indeed, it might be claimed that it has come to occupy a central position in the discourse. This is hardly surprising given the impact of studies of mitochondrial DNA in the 1990s and the outcomes of projects such as the Human Genome Project (1990-2003), and the Neanderthal Genome Project (2006 – present) which led to the initial draft of the Neanderthal genome among other influential research papers. To date, however, there has been no wide-ranging and empirical investigation of the influence of DNA analysis on the study of *Homo neanderthalensis* although its potential importance to the field has been acknowledged for some time [1, 2] and is now even taken as a given [3]. This study presents the initial results of a text analysis of a cross-disciplinary corpus of research articles covering the period 1970-2017. A notable increase in frequency of keywords integral to DNA studies is demonstrated. Evidence is presented to support the perception that papers either directly reporting or substantially referring to the results of DNA analyses have achieved a statistically significant position in the field in terms of the number of published articles. The expansion of the influence of such studies is considered. Also shown is a highly significant difference in citations between those articles containing titular keywords linked to studies of ancient DNA, and those not. It is suggested that these phenomena signal the continuing centrality to the discourse of identifying the exact taxonomic (and hence ontological) status of *Homo neanderthalensis* and its relationship to *Homo sapiens*. This may reflect wider contemporary concerns with identity as well as perhaps a valorization of hard science in othering and ordering.

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## Sexual dimorphism in the chimpanzee pelvis: Implications for understanding the human childbirth dilemma

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The human pelvis is under antagonistic selection: Selection for a relatively narrow pelvis, often attributed to bipedal locomotion or visceral support, opposes selection for a birth canal that is wide enough to accommodate large-headed neonates. Since only women need to be able to give birth, a strong pattern of pelvic sexual dimorphism exists, with women having wider birth canals despite being on average shorter than men. Previous work has elucidated an allometric and a non-allometric component of sexual dimorphism in human pelvic shape, with the former arising due to dimorphism in stature and the latter comprising birth-relevant features [1]. In chimpanzees, where the neonate is much smaller relative to the birth canal, pelvic sexual dimorphism is not nearly as evident, and the role of body size dimorphism has been variously argued to drive or obscure pelvic dimorphism. However, most studies employ different measurements, and few have investigated sexual dimorphism in the chimpanzee pelvis in detail. We conducted a geometric morphometric analysis of the chimpanzee (*Pan troglodytes*) pelvis using a dense set of 279 3D landmarks on 20 adult females and 14 adult males. In contrast to several previous studies, we found overall pelvic shape to be significantly sexually dimorphic in chimpanzees, with males having larger and more flared ilia than females, a smaller sub-pubic angle and a superiorly narrower sacrum. We also considered the birth canal separately. The size (represented by the area of the pelvic inlet) of the birth canal was non-dimorphic between the sexes, but canal shape was clearly dimorphic, with females having a mediolaterally wider and thus rounder canal than males. Pelvic shape variation had an allometric component, which was similar for males and females, but sexual dimorphism in pelvic shape was largely unrelated to this allometric trend. The observed pattern of sexual dimorphism in the chimpanzee pelvis closely matches the pattern known in humans. Given that the chimpanzee pelvis likely poses no obstetric constraints, our findings suggest that pelvic sexual dimorphism can exist in the absence of obstetric selection and may be a shared pattern among hominids or even mammals [see also 2-4]. The current findings therefore have important implications for our understanding of the evolution of human pelvic sexual dimorphism as well as for the study of the hominin fossil record, in which the degree of sexual dimorphism and related biological aspects (e.g. cephalopelvic proportion) is a topic of debate [e.g. 5].

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## ***Homo erectus* palaeoecology in Java: A study of cervid post-cranial ecomorphology**

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This study reports on the palaeoenvironmental reconstructions of several Early to Middle Pleistocene sites from Eastern Java (Trinil, Kedung Brubus and Sangiran), based on newly developed ecomorphological methods for the cervid calcaneus and intermediate phalanx. Using a geometric morphometrics approach, 3D landmark data were collected on a sample of extant cervids of known habitat preference, to establish correlations between morphological features, locomotor behaviour and environmental parameters. These models were then applied to deer fossils from the selected hominin sites, as well as a sample of unprovenanced specimens from Java, to assess past vegetation structure and substrate type.

Our research extends the suite of ecomorphological methods available for palaeoenvironmental reconstruction of hominin sites. The morphology of the calcaneus and intermediate phalanx were found to vary with locomotor strategy and habitat along a continuum from open habitats with a dry substrate to closed habitats with a wet substrate. Furthermore, a contribution is made to our understanding of the poorly studied environments that were present in East Java during the Pleistocene. The results of Trinil were in line with earlier interpretations [1] of an open environment with some woodland cover, but with a relatively wet substrate. The results of Kedung Brubus and its associated fauna are indicative of open, but drier conditions and presumably coincided with a glacial stage where Java was connected to continental Southeast Asia, allowing increased biotic interchange with the Asian mainland [1]. The material from Sangiran is indicative of open conditions, and either more dry or wet substrates. This possibly reflects the (taxonomically) mixed or diachronic nature of the fossils from this site.

The early dispersal of *Homo erectus*, usually considered the first hominin to have expanded its biogeographic range over large parts of the Old World [2], is generally hypothesized to have been driven by either extrinsic (e.g. the expansion of open environments) or intrinsic factors (e.g. the increased capacity of *H. erectus* to adapt to variable conditions) [3]. The reported palaeoenvironmental reconstructions provide an estimate of the extent to which this species depended on a specific type of environment. The results do not contradict a scenario where *Homo erectus* was restricted to more open environments for its survival and dispersal. A degree of environmental flexibility can, nevertheless, be extrapolated from its presence in both dry and wet conditions.

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## *Homo heidelbergensis* is not your ancestor

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Genetic data suggest that *Homo sapiens* and Neanderthals evolved from a common ancestor in the Middle Pleistocene [1]. However, the morphology of this last common ancestor has remained elusive. Here we challenge the current paradigm (reviewed, e.g., in [2]) that *Homo heidelbergensis* is ancestral to both Neanderthals and *Homo sapiens*. The faces of many fossil hominins are larger and more robust than those of modern humans, and temporal trends of facial gracilization are evident in both the *Homo sapiens* and the Neanderthal lineage [3,4]. First, we therefore quantify how evolutionary changes of facial size affect facial shape. To this end we use three-dimensional geometric morphometrics based on 791 landmarks and semilandmarks to compare facial shape in a diverse sample of recent and fossil humans from Africa, Europe, and Asia (N=256). We use the residuals from multivariate regressions of facial shape on facial size to account for static allometry within each group. To reconstruct partially complete fossil specimens, we realigned displaced bone fragments based on surface or CT scans, and used mirror-imaging and thin-plate spline interpolation to estimate missing data [5].

As expected, we find that a principal component analysis (PCA) of facial shape clearly separates recent and fossil *Homo sapiens* from Neanderthals and *Homo heidelbergensis*. When allometric effects are removed by analyzing regression residuals, *Homo heidelbergensis* s.l. specimens and Neanderthals overlap completely. This indicates that allometry largely accounts for the facial shape differences between *Homo heidelbergensis* specimens Arago 21, Bodo, Kabwe, Petralona, the early Neanderthal Sima de los Huesos 5, and classic Neanderthals (Gibraltar 1, Guattari, La Chapelle-aux-Saints, La Ferrassie 1, Saint Cesaire, Shanidar 1 and 5). However, allometry does not account for the facial shape differences between these *Homo heidelbergensis* individuals and both fossil and recent *Homo sapiens*. Notably, *Homo erectus* s.l. specimens KNM-ER 3733 and Sangiran 17 and *Homo habilis* specimen KNM-ER 1813 cluster with recent and fossil *Homo sapiens* when facial size differences are accounted for.

Our findings indicate that the facial morphology of *Homo heidelbergensis* specimens Arago 21, Bodo, Kabwe, and Petralona is derived towards Neanderthals. In contrast, *Homo sapiens* retains many aspects of the more generalized, ancestral, *Homo erectus* facial shape. We suggest that whereas Neanderthals plausibly evolved from *Homo heidelbergensis* via gracilization, the last common ancestor of Neanderthals and *Homo sapiens* did not look like *Homo heidelbergensis*. Our findings therefore suggest that *Homo heidelbergensis* gave rise to Neanderthals, whereas *Homo sapiens* evolved from a more *Homo erectus*-like ancestor.

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## Doubling the number of high-coverage Neandertal genomes

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Over the last few years, the recovery and the analyses of genomes of ancient modern humans, Neandertals, and Denisovans have changed our understanding of the origins, the movements, and the relatedness of archaic and modern human populations. However, in many cases endogenous DNA represents such a small fraction of the DNA extracted from specimens that sequencing of the complete ancient genomes is economically infeasible. Thus, to date, only three Neandertal genomes have been sequenced to high coverage [1-3]. Even though Neandertal genome sequences of low coverage [4] can be used to reconstruct various aspects of Neandertal genetic history, many analyses, for example estimation of population size and levels of inbreeding, rely on the reliable diploid genotypes. Recent studies have shown that certain skeletal elements, such as the inner part of the petrous bone and the cementum layer in teeth [5 and references therein], may preserve DNA better over time. There is also evidence that the preservation of endogenous DNA may vary substantially even within a few millimeters distance in a single specimen [2, 4]. Due to the value and scarcity of ancient hominin remains, it is critical that the smallest possible amount of destructive sampling is involved in the recovery of genetic material. A usual sampling strategy typically involves taking around 50 mg of powder from a single location of a given bone or tooth. We investigated here whether taking multiple smaller samples in a step-wise manner of the Neandertal specimens from the Mezmaiskaya Cave in Russia and the Troisi eme caverne of Goyet in Belgium may improve the yield of ancient human DNA. We removed between 8.5 and 27.2 mg of bone powder from a Mezmaiskaya 1 rib fragment, between 2.5 and 35.1 mg from a Mezmaiskaya 2 skull fragment, and between 5.8 and 53.8 mg from the Goyet Q56-1 femur fragment, amounting to between 15 and 38 powder subsets per specimen and an average input of 16.6 mg of powder per extraction. Importantly, to minimize the impact of contamination, we treated each powder aliquot with 0.5% sodium hypochlorite solution prior to DNA extraction. The DNA extracts from the same specimen varied by several orders of magnitude in their proportion of endogenous DNA (between 0.07% and 54.7%), their content of nuclear genomes (between 0.01 and 78-fold coverage), as well as in the levels of present-day human contamination (0.2-50.3%). There was no significant correlation between the amount of powder used for the extraction and the overall amount of the endogenous DNA or the levels of present-day human DNA contamination. Thus, these results indicate that ancient DNA preservation varies greatly within one specimen and that the removal of multiple, small sub-samples instead of one larger sample, here coupled with a decontamination procedure, can drastically improve the likelihood of isolating large enough amounts of DNA to make whole genome sequencing feasible. This approach allowed us to identify extracts with exceptionally high endogenous DNA content and low levels of present-day human DNA contamination (<2%), enabling us to generate three additional high-coverage Neandertal genomes. The high-quality genome sequences of multiple Neandertals form a unique reference resource for the scientific community and are valuable for analyses that require reliable diploid genotypes and haplotype information. For example, these data open new opportunities to investigate Neandertal population history, to identify genetic variants that arose uniquely on the Neandertal lineage and might have changed through time, and to determine those that may underlie archaic-specific traits or adaptations.

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## Morphological assessment of modern human upper and lower first molars

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Human first permanent molars are well studied, but comprehensive investigations that elucidate 3D crown morphology variation of geographically diverse populations are lacking. The aim of the present study is to provide quantitative and qualitative data from upper and lower first molar crowns (uM1s and lM1s, respectively) for the understanding of human dental shape and size variation. Studying the outer enamel surface (OES) can be limited by various factors such as abrasion or damage. The enamel-dentin-junction (EDJ) is less affected by those factors and shows a high correspondence of features with the OES. Following previously established, non-invasive protocols [1,2], we focused both on the EDJ and the OES. This study combines 3D imaging techniques and geometric morphometric methods [3], and compares the outcome of the morphometric analyses with the results of the analysis of discrete traits scored on the EDJ.

A total of 80 molar crowns (45 uM1s and 35 lM1s) were examined. The sample consisted of populations with different geographical origin and subsistence background: Sub-Saharan Africans, Southeast Asians, Bedouins, Avars, South Americans, and Central Europeans. 3D image data were obtained at the Vienna  $\mu$ CT Lab, Austria. Four sets of landmarks were considered: EDJ occlusal surface, cervical outline, crown outline, and a dataset combining the EDJ surface with the cervical outline which represented the dentinal crown most comprehensively. Multivariate statistics were used to assess shape variance, covariance, and allometry. The discrete traits were assessed based on the Arizona State University Dental System [4].

The landmark-based analyses showed that in both upper and lower first molars, morphology did not differ significantly between modern human populations. Shape and form variation were generally high within each group, and the different populations overlapped widely. First molar crown gross morphology varied between narrow and high, and broad and low. The most distal regions of both uM1s and lM1s were more variable than the mesial regions. Molar size variation (here represented by both 2D and 3D landmark configurations) confirmed previous findings, namely Europeans possess smaller teeth than Africans and Asians. The allometric effects measured were negligible ( $\sim 4\%$ ). Similarly, we did not find an indication of molar shape sexual dimorphism. Our investigation revealed that the appearance of the cervical line (hourglass-shaped vs. oval) depended on the configuration of the root system (widely separated vs. close or fused roots, respectively). A high pairwise correlation of the occlusal surface ( $r=0.85$  for the EDJ) and dentinal crown ( $r=0.61$  for the combined dataset) were revealed between the uM1 and lM1 shape variables. These results reflect the high morphological integration of upper and lower molars, and of their occlusal aspects in particular, which in turn can be explained by a strong genetic control during odontogenesis. Few of the discrete traits considered (the anterior transverse ridge and the anterior accessory tubercles) provided population-specific frequencies. Additionally, we replicated the results of Hunter et al. [5] on the positive correlation between the intercuspal distances and Carabelli's cusp degree of expression.

In conclusion, M1s shape and form do not make it possible to attribute an individual tooth to its own population. This also means that in any comparative analyses of hominoid molars, the choice of the modern human sample would have no influence. Our results do not support a relevant effect of gene drift or diet on molar shape.

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## Dynamic landscapes of fear: Effects of habitat-heterogeneity, seasonality, and predator diversity on a population of terrestrial primates (*Papio ursinus*)

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“Evolutionary arms races” between predators and prey have shaped complex adaptations across the animal kingdom, arguably influencing some of the key behavioural transitions in human evolution. Fossil evidence indicates that a noticeable bout of carnivore extinctions that occurred between 2 and 1.5 million years ago coincides with a critical period for hominin evolution, during which a clade of species was progressively pruned down to one, *Homo ergaster/erectus*, which successfully dispersed across and out of Africa [1]. It has been suggested that the dispersal patterns and technological advances of early Homo species allowed them to hunt or outcompete East African carnivores [2], but there may have existed a converse relationship; perhaps the drastic change in predation pressure facilitated behavioural adaptations that ultimately contributed to the unique flexibility and success of *H. ergaster/erectus*? Within a framework informed by paleoanthropological research, this work employs a primate models approach [3] to explore the proximate effects of predation pressure on primate movement and behaviour in a heterogeneous and seasonal environment, seeking to fill gaps that arise from inherent limitations of fossil records. It investigates the “landscapes of fear” [4] of an extant, highly adaptive, terrestrial primate species, the Chacma baboon (*Papio ursinus*), ranging in an East African landscape analogous to the mosaic habitats occupied by hominins during the Plio-Pleistocene [5]. Gorongosa National Park, Mozambique, is an area occupied by an abundant baboon population, and of previously low, but now monitored and increasing predation pressure from several carnivorous species. Over 200 baboon troops are spread across Gorongosa’s mosaic of landscapes, resulting in varied exposure to habitat-type, water availability, inter and intra-specific competition, and predation pressure. Within this natural laboratory, longitudinal data from a 300 km<sup>2</sup> camera trap grid and GPS-collared carnivores are used to map baboons’ seasonal and diel use of the landscape in relation to habitat variation, the presence and movements of lions (*Panthera leo*), and the reintroduction of wild dogs (*Lycyaon pictus*) to the ecosystem, providing novel insight into the nuances and effects of risk on the behavioural ecology of a terrestrial primate. Preliminary results suggest that in such an environment, proximity to water is a strong predictor of animal activity, with seasonal consequences for primate-predator dynamics.

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## Facial morphology of *Australopithecus afarensis*: exploring intraspecific variation in human evolution

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The morphological variation of known species is an essential aspect that needs to be considered when attributing fossils to specific taxa. When studying human evolution, the assumed variation of extinct species is mostly inferred from samples of modern humans and great apes. However, these extant species are not necessarily representative, most obviously as they sample a much shorter time period and may well have a different pattern of sexual dimorphism. Thus, exploring the morphological variation of a well-defined early hominin species could provide an additional and improved standard. *Australopithecus afarensis* is the best candidate for such a study, because it has a densely sampled and well-preserved fossil record from eastern Africa, which represents a substantial time period (3.7-3.0 Ma). Since facial morphology typically differentiates early hominin species, this research focuses on analysing variation of the maxillae. Both adults and late juveniles, who have their third molar not yet in occlusion, were included in this study. First, the *A. afarensis* fossils were virtually reconstructed using  $\mu$ CT images, removing breakages, plastic deformation and other taphonomic distortions where necessary to recover the original morphology. Then, three-dimensional geometric morphometric analyses were used to examine the amount and nature of variation. The shape of the maxillae was captured using 65 landmarks. For comparative purposes, the nine fossil specimens of *A. afarensis* were analysed alongside 345 specimens of *Gorilla gorilla*, *Gorilla beringei*, *Pan troglodytes*, *Pan paniscus* and *Homo sapiens*, sampling large geographic areas and both sexes. Initial results show that a large amount of the morphological variation is due to allometry, and that the allometric slope differs between species. This highlights the importance of correcting for size-related shape variation while also taking phylogeny into account, in order to obtain the morphological variation that is only attributed to shape. Results of this research will provide an improved characterisation of the intraspecific morphological variation shown by *A. afarensis* maxillae, and provide a framework for species attributions of key Plio-Pleistocene hominin fossils.

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## Predicting ankle mechanics in the fossil hominin record using finite element modeling

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The majority of studies investigating the locomotor behaviour of fossil hominins focus on qualitative or quantitative assessments of bony anatomy. Predictions are then made based on inferred structure-function relationships in living primates, often drawn from field or laboratory observations on locomotor behavior. Precise biomechanical relationships between articulating elements are thus often poorly understood. One way to address this issue is through virtual modeling of the biomechanics of joint complexes critical to locomotor function. A technique that has been utilized by palaeoanthropologists in the past is Finite Element Analysis (FEA), which allows researchers to model differing loading regimes on a structure. Most FEA work to date has focused on craniofacial elements as they pertain to chewing mechanics. Here we present FEA data from the talus of modern human subjects and apply our findings to selected fossil hominin specimens.

Our sample consists of four adult human subjects (three males, one female) with a range of heights and body masses. Digital models of the talus were reconstructed from high-resolution MRI scans of the subjects, and then cleaned, smoothed and meshed using CAD software. High-speed 3D kinematics (200Hz), kinetic, and force plate (1000Hz) data were then collected from the same subjects at a wide range of walking speeds (0.72m/s-1.37m/s). We then applied these data to simulate loading regimes through the talar trochlea during the stance phase of walking. We focus here on heel-strike and the mid-stance phase of the gait cycle, and use shell-based FE models utilizing well-established material properties for bone taken from the literature.

At heel strike the highest stresses in *Homo sapiens* are located on the lateral malleolar facet, lateral posterior calcaneal facet, and the dorsal talar neck. This pattern is consistent across all individuals. When these loading regimes are applied to fossil hominin tali, with loading forces adjusted to reflect reconstructed fossil hominin body masses, we show that there is considerable variation in fossil hominin talar stress distributions. *Au. afarensis* (A.L.288) has a broadly similar pattern to that of *H. sapiens*, but those for OH 8 (*H. habilis* / *P. boisei*) and MH 2 (*Au. sediba*) are markedly different from both each other and the human sample. These findings are discussed within the broader context of fossil hominin locomotor diversity.

## Marathousa 2: A new Middle Pleistocene locality in Megalopolis Basin (Greece) with evidence of human modifications on faunal remains

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Following the discovery and excavation of the Lower Palaeolithic butchering locality Marathousa 1 (MAR-1; Megalopolis Basin, Peloponnesus, Greece) [1], conducted by the Ephoreia of Paleanthropology and Speleology, Greek Ministry of Culture in collaboration with the American School of Classical Studies at Athens, led to the discovery of a new open-air locality, Marathousa 2 (MAR-2), approximately 1.5 km eastern of MAR-1, where stratified fossils were identified on a profile of the Marathousa Member (Choremi Formation), directly below the Lignite Unit III of the Marathousa mine. Two areas were designated, both yielding so far mainly hippopotamid bones: Area A with (cervical and thoracic) vertebrae and ribs belonging to a single individual of *Hippopotamus*, as well as a mandibular fragment of a fallow deer (*Dama* sp.), and Area B, about 90 m NW, with isolated dental *Hippopotamus* specimens. The fossils in both areas occur in the same stratigraphic layer, which consists of brown, organic-rich, clayey fine sands with clay clasts. Although the vertebral plates fuse towards the end of the epiphyseal bone fusing sequence in mammals, the unfused plates of the vertebrae from Area A indicate that they belong to a juvenile-young individual. The study of the dental specimens revealed that they belong to the large-sized *Hippopotamus antiquus*. This species was present in Europe during the Early–Middle Pleistocene, and although its last occurrences are quite vague, it seems that it was replaced by the extant *H. amphibius* during the second half of the Middle Pleistocene [2]. *Hippopotamus antiquus* is already known from MAR-1, dated to between 500 and 400 ka [1], and the similar stratigraphic position of MAR-2, indicates a comparable age for the locality. *Hippopotamus antiquus* was a large-sized hippopotamid, more than twice as big as the extant *H. amphibius*, and was highly dependent on water and aquatic vegetation [3]; therefore, its presence indicates the existence of large and permanent freshwater bodies, and, together with the presence of the fallow deer, temperate climatic conditions. The good state of preservation of the MAR-2 bones allows the identification of taphonomic modifications. Of particular importance is a *Hippopotamus* thoracic vertebra, which shows striations almost at the middle of the lateral side of the spinous process. The three-dimensional virtual reconstructions of the striations with the use of a confocal microscope enabled their micromorphological study and their identification as cut marks. The presence of cut marks indicate human modification of the vertebra by means of butchering activities, possibly attributed to filleting [4]. In addition to the exploitation of straight-tusked elephants (*Palaeoloxodon antiquus*) in MAR-1 [5], MAR-2 constitutes further evidence of megafauna exploitation during the Middle Pleistocene in the Megalopolis Basin and one of the few examples of hippopotami carcass processing during the Lower Palaeolithic in Europe. As such, it contributes to the better knowledge of the food acquisition strategies and subsistence behavior of Pleistocene *Homo*, and emphasizes the need for further research in the basin.

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## Modern human dispersal into western Iberia: The Early Aurignacian of Lapa do Picareiro, Portugal

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The arrival of modern humans and associated Early Upper Paleolithic in southern and western Iberia was thought to post-date 37 ka in part due to the late survival of Neanderthals and the Middle Paleolithic [1]. The new dates from Bajondillo suggests that the Aurignacian, and modern humans, arrived in southern Iberia 43-40 ka [2]. Critics of the new interpretation point to the lack of diagnostic Aurignacian elements in the assemblage and question the association of the dated materials and lithic artifacts [3,4]. Thus, the timing of modern human arrival in Iberia, south of the Ebro, remains a disputed and contentious issue. Here we present new evidence of an early Aurignacian occupation, documenting an anatomically modern human presence in western Iberia 5,000 years earlier than previously known. Our excavation of Lapa do Picareiro has revealed 10m of sediments spanning 50,000 years of the Late Pleistocene. The cave of Lapa do Picareiro, in central Portugal, has revealed an early Aurignacian presence based on a lithic assemblage with a diagnostic carinated endscraper/core and bladelets. The artifacts are stratigraphically positioned between a Middle Paleolithic occupation dated 47-45 ka cal BP and an undiagnostic archaeological level dated 36-38 ka cal BP. The radiocarbon dates and sedimentological data from magnetic susceptibility analyses places the arrival of the Upper Paleolithic during Heinrich Event 4 [5]. The finds corroborate the idea of a much earlier penetration of southern and western Iberia by modern humans and complicate many previous scenarios. The new chronostratigraphic scenario supports a northern Iberian transfer of the Aurignacian technocomplex through Euro-Siberian ecosystems that extended along the western margin of Iberia during cold phases of the Late Pleistocene. On the other hand, the major rivers, Douro and Tejo, are also potential diffusion routes for the technocomplex since they provide direct line access to the Atlantic coast, north and south of the site. The late Neanderthal survival at the nearby site of Oliveira until ~37 ka also suggests that the two groups may have overlapped in time and/or space for several centuries or a few millennia.

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## A Model for Predicting the heating temperatures of Middle Stone Age silcrete artefacts based on non-destructive infrared analyses

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The lengths of, and numbers of hierarchical steps in stone artefact production sequences are key proxies for the evolution of cultural complexity. The heat-treatment of silcrete rocks by past hominins, to increase their knapping quality, is central to this issue. Yet conflicting views persist about the complexity of this process. On the one hand, scientists argue that silcrete heat-treatment was an elaborate, multi-level procedure involving the prolonged and indirect exposure of these rocks to heat (1, 2). Each stage of production (building a fire, burying rocks at a specific depth below the fire, maintaining prolonged insulated heat, managing gradual cooling and making standardized blanks) was reliant on the stage that came before. Such complex procedures needed to be learned to be maintained within a population, probably through high fidelity transmission mechanisms. Others argue that silcrete heat-treatment was likely far simpler, involving fewer steps (direct exposure of blanks to embers and/or flames in an open-air burning context), and that this process was managed by hominins no differently than everyday fire-related activities such as burning wood (3).

Whether heat-treated artefacts were exposed to the high temperatures and rapid increases associated with open-air fires is a key issue in this debate. We know that some archaeological silcretes fractured catastrophically during heating - implying open-fire exposure - but this could have occurred incidentally, and therefore was unrelated to intentional treatment. What is needed is a robust method to predict the heat-induced alterations of archaeological silcretes. The behavioral implications of such predictions rely on controls on [a] the minimum surface temperatures of fires in the past, [b] the sub-surface temperatures of fires exceeding these minimum temperatures and, most importantly, [c] the heating temperatures to which the silcrete artefacts were exposed.

Here we develop a model to estimate the heating temperatures of archaeological silcrete artefacts. We present the results of an experiment wherein multiple specimens of two markedly different South African silcretes were systematically heated to a controlled set of temperatures, and the infrared responses to each temperature change were quantified. Our analyses suggest that IR spectroscopy is suitable to detect subtle heat-induced changes in diverse silcretes. Both Generalized Linear Models and Machine Learning algorithms are used to make cross-validated heating temperature predictions for unknown silcrete samples. IR analysis of silcrete assemblages in combination with powerful statistical tools will be useful to assessing the heat-treatment technologies engaged by Middle Stone Age *Homo sapiens* in Africa.

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## Variation in facial skeletal shape, nasal structures, and paranasal sinuses in adults from Cambodia and France

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Recently, studies proposed to reconstruct nasal airways (NA) soft tissue (i.e. mucosa) in Neanderthals in order to simulate nasal airflows and discuss specific adaptations to cold environments in this group [1,2]. However, NA size and shape variation remains poorly described in extant species including modern humans, and so do the way NA covary with the nasal cavity (NC), paranasal sinuses, and facial skeleton morphologies [3,4]. Here, we propose to quantify the variation of these anatomical units through the study of *in vivo* CT images from adults balanced for sex living in France (N = 40) and Cambodia (N = 40). The same protocol as that described in [3,5] was used. Additionally, 23 anatomical landmarks were placed on the facial skeleton. The geometric morphometric analysis of the facial skeletal shape showed that individuals from Cambodia have a relatively wider and less prognathic face when compared to the French sample. Regarding NC proportions, individuals from Cambodia have a wider, lower, and shorter NC. However, volumes of NA, NC, and paranasal sinuses are not significantly different between the two groups except for the maxillary sinuses that are larger in individuals from France ( $p = 0.0037$ ). The study of sexual dimorphism reveals that Cambodian males have significantly larger facial skeleton, higher and wider NC than Cambodian females (no difference for NC length), as well as significantly larger NA, NC, and paranasal sinuses volumes. Sexual dimorphism is weaker in the French sample, with NC height, width, and length, as well as NA and frontal sinuses volumes that are not significantly different between males and females. NC morphology of Cambodian individuals correspond to what is expected of a population living in a warm environment, but is primarily explained by the wider and less prognathic facial skeleton of Cambodian individuals. Using larger samples than [3], we show that NA volume is larger in males than females. However, when normalizing NA volume by facial skeletal size, there is no significant differences between males and females. This study highlights the dramatic need to quantify NA morphological variation in different human populations in order to produce more robust simulations in Neanderthals.

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## Origins of fur loss in humans: effect of gait, sweating capacity, and exposure to direct solar radiation

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Loss of functional fur cover in the human lineage is usually explained as a thermoregulatory adaptation for foraging in hot open environments. Subsistence behaviors associated with two different gaits were proposed to potentially trigger the selection for fur loss: 1) walking-related gathering and small prey hunting, and 2) running-related persistence hunting and scavenging. In addition, some researchers questioned the thermoregulatory benefits of fur loss entirely. Here, we test the thermoregulatory benefits of fur loss during various subsistence behaviors in Early Pleistocene hominins using heat exchange modeling and simulations. We built models of australopithecine, *Homo habilis*, and *Homo erectus* with varying fur cover and sweating capacity. We used a heat exchange model to estimate body core temperature (°C) and relative water loss (%body mass). To evaluate the performance of the model, we first estimated the daily course in body core temperature and daily water throughput in Hadza hunter-gatherers of northern Tanzania (n = 30). The estimated body core temperature was validated against physiological ranges reported for modern humans, the estimated daily water throughput was validated against doubly labeled water data from Hadza adults. We simulated foraging in hominins in ambient conditions of the current West Turkana (daily range of air temperature 25–35 °C; daily mean relative humidity: 45%) with varying exposure to direct solar radiation and using locomotor velocities and durations reported for gathering and small prey hunting in Hadza adults, and persistence hunting in Kalahari hunters. We evaluated final body core temperature and relative water loss at the end of each simulation. Our results suggest that the thermoregulatory effect of fur loss is strongly modulated by gait, sweating capacity, and exposure to direct solar radiation. For walking hominins, fur loss resulted in increased body core temperature and increased relative water loss. The effect of fur loss on body core temperature was strongest (up to 0.5 °C difference between furred and furless model) in hominins with low sweating capacity walking under direct solar radiation but diminished to zero for hominins with high sweating capacity (regardless of exposure to direct solar radiation). In contrast, the effect of fur loss on relative water loss was strongest for walking hominins with high sweating capacity (up to 0.3 %body mass difference). For running hominins, fur loss resulted in decreased body core temperature and decreased relative water loss. The effect of fur loss on body core temperature and relative water loss was strongest (up to 1.1 °C and up to 0.5 %body mass difference) in running hominins with low sweating capacity, especially when not exposed to direct solar radiation, but diminished to zero for hominins with high sweating capacity. We conclude that fur loss would not bring thermoregulatory benefits to hominins during walking-related subsistence behaviors such as gathering and small prey hunting. Rather, our simulations support the hypothesis that human furlessness evolved as an adaptation to prolonged running in hot environments possibly associated with persistence hunting and scavenging. In addition, our data suggest that hominins would benefit from fur loss only before acquiring the sweating capacity of the modern humans.

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## Lithic bipolar reduction strategies in the Late Stone Age site of Txina Txina, Mozambique

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Southeastern Africa is often considered to be an important region for understanding the development of stone tool technologies and new adaptation strategies during the Late Pleistocene. Located between East Africa, a region well known for its long history of research spanning of all stages of Human evolution, and South Africa a likewise important region for understanding the MSA to LSA transition, despite its potential, Mozambique remains sort of a barren land when it comes to Stone Age research. In order to fill this gap, Bicho (et. al) have explored several regions of the country since 2011 including the Niassa Basin, Elephant and Limpopo rivers and the coastal setting south of Maputo (1). This has led to the discovery of over 200 Stone Age sites, with ESA, MSA and LSA occupations, some of which have been previously presented in past editions of this Conference.

Txina Txina is one of these sites, initially found in 2016 and located in the Machampane Gorge, in a small stream that runs south of the major Elephant River. Preliminary data (2) from three test pits shows that the site has a LSA occupation spanning from the Late Pleistocene to the Holocene. The lithic technology was focused on the production of flakes and bladelets through a mix of unidirectional, bipolar and centripetal strategies. Raw materials seem to be mostly local and highly variable, including rhyolites (course and fine grain), quartz (milky and hyaline), quartzite and some cherts (flint and chalcedony). Formal tools while rare are still present in all levels and these include: backed bladelets, microburins, burins, crescents, denticulates, notches and scaled pieces. Akin to other Late Pleistocene occupations throughout Southern Africa where it is considered to have been incremental for lithic miniaturization strategies (3), bipolar technology is present in the entire sequence of the site.

For this poster we present the analysis of the full bipolar assemblage following Horta et. al's methods (4). Results show several interesting patterns in regards to raw material choice, reduction strategies and function. There seems to be a deliberate choice in raw materials for bipolar reduction as quartz and chert dominate the assemblage despite the fact that there is a much wider diversity of raw materials present. Likewise, all types of bipolar artifacts can be found at the site, in the form of bipolar cores, bipolar split cobbles and scaled pieces. Overall, bipolar artifacts show smaller sizes than free-hand blanks and cores. Despite variant degrees of damage, function can be inferred for these artifacts. Bipolar knapping was likely used as an alternative to free-hand knapping for small raw material volume reduction. Small cobbles of variant knapping quality were initially split on anvil and further reduced in order to produce small flakes and bladelets. At the same time, larger free-hand struck flakes were likely used as blanks for wedging activities turning them into scaled pieces.

Our results show that modern humans at the site were strategically employing bipolar methods for several activities. Txina Txina's assemblage shows that there are underlying layers of complexity in the application of bipolar methods. This is shown by the plethora of activities carried out at the site (cobble splitting, knapping and wedging), the deliberate choice of raw materials for these activities and the understanding of how these reduction strategies can be used as a complement to the unidirectional and centripetal strategies used for larger volumes of raw material for blank production.

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## Away from Denisova

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Denisovans are an extinct sister group of Neanderthals, initially identified through the analysis of DNA of fragmentary fossils from Denisova Cave (Altai, Russia). Current genetic data suggests that they had a large geographical extension in Asia. However, although some<sup>1,2</sup> suggested that non-*erectus* and non-*sapiens* Pleistocene hominins of continental Asia might essentially be Denisovans, it has long been impossible to formally identify this group beyond the Altai.

Paleoproteomic analysis recently allowed us to assign a late Middle Pleistocene mandible from the Tibetan plateau to a Denisovan related population<sup>3</sup>. The specimen was recovered from the Baishiya Karst Cave (3280 m altitude), Xiahe county (Gansu, China), in 1980 by a local monk. The exact stratigraphic context of the discovery remains unknown, but the crust of carbonates covering the fossil yielded a U-Th date around 160 ka BP, 120 ka older than any archeological traces of human presence in the region<sup>4</sup>.

The morphology of the Xiahe mandible is reminiscent of other Eurasian Middle Pleistocene individuals. It is robust with several primitive features, including a low and thick body and a strongly receding symphyseal region. The very large size of the preserved dentition connects this fossil to the specimens from Denisova Cave. Although the third molar never developed in this individual, the dental arcade is one of the largest known in the Middle Pleistocene fossil record. Measurements of the first and second molars are in the high end of *H. erectus* and non-*erectus* Middle Pleistocene hominin ranges. A principal component analysis of the enamel-dentine junction topography groups the Xiahe M2 with other Eurasian Middle Pleistocene specimens such as Mauer and Balanica, and outside of the *H. erectus* distribution. The shape of the dental arcade, anteriorly broad and flattened, is reminiscent of Neandertals and quite distinct from that of *H. erectus*. Several dental traits connect this fossil to other Chinese hominin specimens, in particular the mandible of Penghu<sup>5</sup>.

The Xiahe discovery documents the presence of Denisovans more than 2000 km away from Denisova Cave and it yields the first substantial information on the anatomy of their masticatory system. It also elucidates the Denisovan origin of the EPAS1 allele that provides altitude adaptation to hypoxia in extant humans inhabiting the Tibetan Plateau.

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## The effects of environmental conditions and food manipulation on masticatory requirements: how hard is it for a primate to crack a nut?

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Numerous primate species rely on encapsulated seeds, which are generally considered mechanically challenging to access due to their stress-resistant structure [1]. To access these foods, certain masticatory features associated with the production of high bite force would be expected, yet recent research has suggested this may not always be the case [2]. These extreme diets and the morphology of extant primates with this feeding ecology have been used to inform predictive models of hominin diets, especially in the australopithecines [3,4]. However, when considered at a macro level, some stress-resistant objects may be less mechanically challenging to process than past measurements suggest: a seed's endocarp may have natural weak points which can be utilized by manipulating the food item, or may be weakened by environmental conditions, such as high humidity and burial on the forest floor. To investigate whether food processing activities can alter the masticatory requirements of stress-resistant food breakdown, a sample of unshelled seeds (hazel, brazil, and pecan) were crushed using a universal testing machine fitted with metal dental replicas of a primate's upper and lower dentition. Dental replicas were created from a high resolution surface scan of a wild shot male *Sapajus apella*. Force at initial fracture was recorded and compared across a series of conditions: Placing the food between P4-M1 in three different orientations relative to the natural joint between seed shell parts, and following storage in three different environmental conditions (open air, buried in dry soil for one week, buried in wet soil for one week). It was predicted that lower forces would be required to produce an initial fracture when seeds were positioned with the seed joint perpendicular to the dental row relative to other positions, and after burial in the wet soil condition. Fragmentation patterns after seed shell break were also recorded, it was predicted that fragmentation would occur along the joint in all conditions. Results found seed orientation significantly affected the force required to fracture. While the most advantageous orientation was variable between seed types, there was an orientation for each seed which required significantly less force to fracture. Environmental conditions also affected food breakdown: as predicted, across all seed types, those exposed to air rather than being buried in a soil environment required a significantly higher force to fracture. Fragmentation patterns varied both by orientation and environmental condition, but did not necessarily follow a pattern reflecting the assumption that the lines of weakness would be along the joint. These results underline the prediction that feeding behaviour and food storage likely affect the ability of an individual to access certain food resources. Primates are known to manipulate seeds before processing, and to have specific feeding behaviours for these objects, which may serve to open the seed in the most advantageous manner, lowering the required bite force. Furthermore, primates often forage in relatively humid substrates. These results suggest some "hard" foods that primates eat may not be as mechanically demanding as previously thought, and subsequently, many fossil hominins could also have accessed these stress-resistant foods by altering their food processing activities. Understanding seed fracture can inform both the relationship between primate masticatory form and function, which in turn can inform evolutionary models. Further investigations are now needed to understand the contributions of variations in dental topography and gape between primates to fracture capability.

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## Multi-stable isotope zooarchaeological investigations at Abri du Maras: exploring the palaeoecological context of Neanderthal subsistence strategies in the Rhône Valley

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In order to broaden our knowledge of Neanderthal land use and hunting behaviours, it is crucial to understand the ecology of their prey and the environments in which they lived. The isotope zooarchaeological approach utilises the anthropogenic faunal record to provide proxy data for both past environmental conditions and ecological behaviours of the different animal species exploited. Here, we present the results of a multi-isotope, multi-tissue study of ungulates remains from the Middle Palaeolithic site of Abri du Maras (Ardèche, France), providing new insights into the living landscapes of the Rhône Valley during MIS3. Bone collagen carbon and nitrogen isotope values from ungulates from Abri du Maras evidence the dietary niches of the different species exploited by Neanderthals at the site and illuminate the behaviours of now extinct species such as giant deer (*Megaloceros giganteus*). Intra-tooth strontium isotope investigations of reindeer from Level 4.2 (dated from  $42 \pm 3$  to  $55 \pm 2$  ka BP[1]) indicate likely migratory behaviour. This, combined with the fact that other fauna (e.g. horse, bison, red deer) dominate the zooarchaeological assemblage in this level, suggest that reindeer may have been hunted only opportunistically during their spring migrations. The sub-contemporaneous Level 4.1 on the other hand (dated  $40 \pm 3$  and  $46 \pm 3$  ka BP[1]), is dominated by reindeer, and suggests a seasonally restricted exploitation in Autumn[2]. However, strontium isotope data from reindeer teeth from Level 4.1 are consistent with a local range for this species during that period, and non-migratory behaviour. This may suggest the forest ecotype and is consistent with other palaeoenvironmental proxy data. In Level 4.1, the seasonal nature of reindeer exploitation, combined with their non-migratory behaviour, may be consistent with a seasonally-restricted use of the area by Neanderthals or the preferential hunting of reindeer in peak physical condition (e.g. high body fat, etc.). Thus, the integration of isotope data with the zooarchaeological analyses and other palaeoenvironmental proxy data at Abri du Maras evidence not only diversity in animal behaviour and ecology during MIS3, but also demonstrate the inter-relationships between the dynamic ecosystem and Neanderthal land use and hunting strategies.

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## Raw material impacts on lithic technology at Donggutuo, Nihewan Basin, China: Preliminary results from the 2016 excavation campaign

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With lithic and fossil bearing deposits dating to as early as 1.6 Ma [1], the Nihewan Basin (Hebei, China) is an invaluable resource for understanding hominin evolution in Asia. In particular, the ca. 1.1-million-year-old site-complex of Donggutuo has been central in discussions regarding the antiquity of hominin occupation at Nihewan and technological developments in East Asia during the Pleistocene. Since its discovery in 1981 [2], excavations at Donggutuo have established the potential the site holds for learning about Early Pleistocene hominin subsistence and technological behavior [3], and about how these behaviors were influenced by changes in the regional paleoenvironment at Nihewan [4]. In 2016, a new excavation project at Donggutuo was designed by the Institute of Vertebrate Paleontology and Paleoanthropology (Chinese Academy of Sciences) in order to investigate: 1) intra-site lithic technological variation through time; 2) the role of hominin agents in the accumulation of the lithic and faunal remains at the site; and 3) the relationship between the Nihewan paleoenvironment and hominin occupation at the site. To this end, a sample of the recently excavated lithic assemblage was studied to begin documenting the details of the reduction sequences and evaluating the impact of raw material constraints on the lithic technology from the site. Preliminary results from this study illustrate two notable features of the reduction sequences in the assemblage related to hominin raw material economy: First, the presence of cores-on-flakes and the small size of cores and flakes in the assemblage indicate reduction sequences were branching and largely resulted in the production of small flakes. Second, evidence of core volume management and simple core platform preparation in the assemblage indicate reduction sequences were also long and unconstrained by the original shape of raw material blanks [5]. When these preliminary results are considered, the close proximity of raw material sources to Donggutuo and the wide shape distribution of raw material available for selection at the site indicate that raw material distance and shape were unlikely the only factors affecting the technology of the lithic assemblage, and that the observed characteristics of the reduction sequences likely reflect other aspects of hominin raw material economy.

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## Original experimental support for the effects of physical activity on the multivariate patterns among entheses

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Reconstructing past patterns of physical activity from human skeletal remains is a central objective of the anthropological sciences. Among the skeletal traits most widely used for this purpose are muscle attachment scars on bone surfaces (entheses). The functional association relies on Wolff's law, the lifelong process of bone remodeling, and that entheses are subjected to frequent and high loads exerted during muscle-tendon unit contractions. Also, unlike muscle-tendon, the bony entheses can be preserved in the archaeological and fossil records. Despite this potential, the use of entheses as markers of occupational stress has been plagued by imprecision, methodical inconsistencies, in particular a lack of a rigorous multivariate statistical approach, and limited data for evaluating methods whilst controlling for a range of compounding variables such as ageing, body mass, and genetic variability. Moreover, a few recent experimental animal studies have even questioned the basic premise that enthesal morphology and physical activity are in fact linked. Against this backdrop, we have recently developed a new and precise multivariate method for analyzing the patterns among human hand entheses relying on high-resolution three-dimensional models [1]. This method was previously validated using a unique skeletal collection from Basel (i.e., the Basel-Spitalfriedhof collection) involving individuals with highly detailed and lifelong occupational documentation and life histories [2] and, more recently, was used to reconstruct the manual activities of Neanderthal and early modern human individuals from diverse geo-chronological contexts. Its findings were the first to reflect the latest archaeological indications on the manual behavior of these populations, contradicting a traditional viewpoint on the nature of Neanderthal manual activities [3]. Here, we further extend the application and validation of this novel approach with a blinded and controlled study of laboratory rats in which certain muscles of one lower limb were electrically stimulated [4]. MicroCT datasets representing 18 stimulated and control (contralateral) limbs were stripped of metadata and given random ID codes in Liverpool before being transferred to Tuebingen for analysis. The analysis revealed a distinct separation among that data points. Once unblinded, the separation was shown to be between stimulated lower limbs and controls. Importantly, the multivariate component explaining differences of stimulation also presented a strong statistical correlation with muscle mass as well as cortical thickness in areas of the bone subjected to biomechanical stress during muscle contraction. These results provide strong support for our novel method of reconstructing activity in the past, which can shed new light into the activities of past human populations as well as fossil hominins.

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## The Legacy of the Paranasal Sinuses

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Why do humans have large paranasal sinuses? A considerable number of explanations have been proposed over the decades for this anatomical phenomenon. None, however, have survived the critique of science. One of the most popular hypotheses suggests that the size and shape of the nasal cavity and sinuses reflect adaptations to cold climate, but ongoing efforts to test this hypothesis have yielded contradicting results. Lundberg et al. (1995)'s finding [1] that the epithelial cells covering the sinuses produce nitric oxide (NO) may be the key to this long-lasting riddle, due to the importance NO has in the human body. Nitric oxide improves oxygen intake by inducing blood vessel dilation, thus allowing longer duration of physical exertion, critical for successful hunting. Furthermore, NO is an essential element of the immune system, and serves as a local host defense. This free radical inhibits pathogens directly, and stimulates the respiratory mucosal tissue. Production of NO in high concentrations in the maxillary sinuses assists the nasal cavity in fighting viruses and bacteria, inhaled during inspiration, improving health status. During human evolution, the facial area reduced significantly and its morphology became more flattened. Nevertheless, paranasal sinuses remained relatively large. In the current research, we tested the hypothesis that following the reduction in nose size among the *Homo* lineage, paranasal sinuses compensate for the loss of respiratory tissue lining the nasal cavity by increasing the epithelial cell surface area in the maxillary sinuses. To test this hypothesis, this current study examined a sample of 50 head CT scans of modern population (aged 18-60 years). The sample included two groups: a control group (N=25), and a study group (N=25) of patients with chronic respiratory infection diseases (such as tonsillitis, otitis media, pharyngitis, laryngitis, pneumonia and tuberculosis). The triangulated mesh surface of the maxillary sinuses of each individual was reconstructed using the Philips IntelliSpace Portal software. We then calculated the maxillary sinus surface area and volume, as well as the sinus centroid size. Finally, we compared these parameters between the two groups to demonstrate the differences in sinuses characteristics between healthy individuals and those prone to suffer from infectious diseases. This research is the first step in demonstrating the significance of the paranasal sinuses for defending our health, and may elucidate the role of these enigmatic cavities in our evolutionary history.

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## Controlled cutting tests reveal raw material optimisation in the Early Stone Age of Olduvai Gorge (Tanzania)

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For >1.8 million years hominins at Olduvai Gorge were faced with a choice: whether to use lavas, quartzite or chert to produce stone tools. All three raw materials are available locally and all are suitable for stone tool production. Why Olduvai hominins preferentially chose one raw material over another in variable ways has puzzled archaeologists for >60 years. Here, we use controlled cutting tests and fracture mechanics theory to understand the raw material selection decisions of hominins throughout Olduvai's Early Stone Age sequence. We quantify the force (N), work (J) and material deformation (mm) required by each stone type when cutting soft-solid materials, before using these data to compare edge sharpness and durability. Significant differences are identified for each variable, confirming stone tool performance to be dependent on raw material selection decisions. When combined with Oldowan and Acheulean artefact data, we demonstrate that Olduvai hominins likely optimised stone tool raw material choices based on functional performance characteristics across the Early Stone Age. Doing so flexibly: preferentially choosing raw materials dependent on the sharpness and durability of their edges, alongside the loading potential and anticipated use-life of different tool forms. Hence, hominins exploited the cutting mechanics underpinning raw material performance differences to increase the efficiency and longevity of their stone tools. In this way, we demonstrate that early lithic artefacts at Olduvai Gorge were likely engineered to be functionally optimised cutting tools. When combined with earlier work, our data demonstrate that Early Stone Age hominins at multiple east African locations selected stone tool raw materials based on functional considerations. The Olduvai data, however, go further and represents previously unseen complexity in how raw material functional considerations could have been flexibly managed by multiple hominin species during the Oldowan and Acheulean.

## Partial hominin upper limb skeleton (KNM-ER 64062) from Ileret, Kenya (1.8 Ma)

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In 2013, a partial left upper limb skeleton and a relatively complete right foot (KNM-ER 64062) were recovered from the Kolom Odiet area (Area 13) near Ileret in the Turkana Basin, Kenya. The fossils derive from the KBS member and date to 1.86–1.82 Ma [1]. Here, we describe the upper limb skeleton that comprises proximal and distal elements of a left humerus, ulna and radius, as well as a complete scaphoid, proximal first metacarpal and distal second metacarpal. The trochlear notch of the proximal ulna articulates well with the humeral trochlea and all bones are consistent in size, suggesting they belong to the same individual. Preliminary analyses of some of the KNM-ER 64062 upper limb material and the foot have been previously reported as representing early *Homo* [1]. Here we present results of morphological analyses of this partial upper limb, in comparison to samples of extant hominoids and fossil hominins, including *Australopithecus*, *Paranthropus*, and early and later *Homo*.

Although the proximal humerus is fragmentary, the distal humerus has a well-preserved trochlea and capitulum. Two-dimensional landmark analyses and linear shape analyses show that the elbow morphology lacks the ape-like, deep trochlear central sulcus and narrow zona conoidea typical of *P. boisei* [2]. The lateral epicondyle is *Homo*-like in its height and degree of projection, while the more projecting medial epicondyle is similar to that of *P. boisei*. The proximal ulna has a remarkably short olecranon process and the trochlear notch appears shallow and mediolaterally broad. The articular margins of the proximal radius lack the bevelling typical of great apes, *Australopithecus* and *Paranthropus* [3], and are instead more vertical, as in *Homo*.

The well-preserved scaphoid has a long, palmarly-projecting tubercle with a flat, broad trapezoid-trapezium facet that extends to its tip. A three-dimensional geometric morphometric analysis and an analysis of articular angles and relative areas among extant humans and great apes and fossil hominins show that this scaphoid most closely resembles the morphology seen among modern humans and Neandertals as well as *Homo floresiensis* (LB1) and *Homo habilis* (OH 7). The proximal first metacarpal is more robust than that of *Pan* and similar to other hominins. A quantitative assessment of the curvature of the trapezium articular facet shows that it is strongly convex radioulnarly, like in great apes, but notably flat dorsopalmarly, like in modern humans and Neandertals. Overall, the curvature of trapezium facet is most similar to that of several Neandertal specimens, although it is comparatively much smaller in absolute size. It does not display a palmar “beak”, which is present in *Australopithecus afarensis* and *Australopithecus sediba*. The distal second metacarpal head is strongly asymmetrical like that of humans and other fossil hominins.

Overall, comparative analyses suggest that the KNM-ER 64062 partial upper limb is most aptly attributed to early *Homo*. The few elements of the hand that are preserved have morphology that is consistent with early *Homo*-like manipulative abilities, including stone tool related behaviours. The elbow morphology is best described as being unlike *P. boisei*, reflecting a reduction in the need for powerful extension (due to a short olecranon) and pronation-supination (due to non-bevelled radial head) compared to extant apes and early hominins. This early *Homo* attribution is consistent with Dmanisi-like morphology in aspects of the KNM-ER 64062 foot, as well as a mandibular dentition (KNM-ER 64060 [4]) and another partial upper limb (KNM-ER 64061), which are found in the same region but slightly earlier in time (2.03–2.02 Ma). This new partial upper limb adds substantially to our relatively limited knowledge of early *Homo* postcranial morphology in the early Pleistocene.

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## Inferring Hominin Arboreal Ecology: Evidence from Extant Sympatric Apes.

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There is vigorous debate regarding the climbing ecology of fossil hominins. Both the degree of arboreality in *Australopithecus*, and initial interpretation of *Ardipithecus* as a careful climber, remain highly contested [e.g.: 1,2,3]. Much of this debate centers on the assumed functional importance of body size and limb proportions in fossil hominins. Compared to *Australopithecus*, *Homo* is characterized by shorter arms [4]. Large body size may appear by 3-3.5 Ma in *Australopithecus* and is evident by 1.8 Ma in early *Homo erectus/ergaster* [5]. These changes in body size and proportions have been argued to reflect changes in ecology and selective pressures on terrestrial versus arboreal performance, but debate remains.

One of the major reasons for the uncertainty surrounding arboreal behavior in hominins is the lack empirical data linking anatomy to climbing performance in humans. Many human forager populations regularly climb trees, but their arboreal locomotor behavior is not well studied. This study tests whether humans and apes differ in arboreal ecology, using a comparative data set of human positional behavior in trees compared with sympatric chimpanzees and gorillas. We recorded climbing behavior and tree use in populations of chimpanzees (*Pan troglodytes troglodytes*; 22 individuals; Goualougo Triangle research site), gorillas (*Gorilla gorilla gorilla*; 19 individuals; Goualougo Triangle and Mondika research sites), and indigenous Mbendjele men (17 individuals; Makao village) in northern Republic of Congo. At two-minute intervals we recorded each subject's position, height, support diameter, and location within the tree. Among key results we find that: 1) humans spent significantly more time in the core region near the main trunk (as opposed to the peripheral branches) than apes and 2) humans spent significantly more time standing bipedally than apes. In addition, while Mbendjele men sometimes spent over an hour in the canopy, most ascents (68%) into the canopy lasted fewer than 10 minutes. We discuss implications for the ecology and evolution of fossil hominins in the context of their estimated proportions.

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## Understanding taphonomic and identification biases of ancient adhesives through experimentation

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Adhesive production is one of the earliest forms of transformative technology, predating ceramics and metallurgy by over 150,000 years. The study of adhesive use by Neandertals and early modern humans currently plays a significant role in debates about human technological and cognitive evolution [1][2]. Depending on the type of adhesive used, different production sequences were required. These can vary in complexity, and would have needed different knowledge, expertise, and resources to manufacture. However, our knowledge of this important technological development is severely hampered by poorly understood taphonomic processes, which affect the preservation and identification of adhesive materials, and leads to a research bias. Here we present the results from a three year field preservation experiment. There are two primary aims of this study: 1) To better understand the factors affecting the preservation of different adhesive types, and 2) to produce a visual reference collection of naturally weathered adhesives of known compositions to aid in future research. Flint flakes hafted with replica adhesives were left to weather naturally on and below the surface at the Leiden University Material Culture Studies experimental house at Horsterwold, the Netherlands. Materials tested include pine tar, birch tar, pine resin, beeswax, acacia gum, hide glue, bone glue, and mixtures containing ochre. Differential preservation was recorded by digitally measuring the surface area of each adhesive residue before and after the elapsed time. Residues were further assessed and photographed using stereo and metallographic optical microscopy to create a visual reference collection of naturally weathered adhesive specimens. Results show that certain adhesives preserve to a significantly higher degree than others, while some materials may be more easily overlooked or visually misdiagnosed. We must therefore be aware of both taphonomic and identification biases when discussing ancient adhesive technology. This research provides a first look that will help us understand the disparities between which adhesives were used in the past, and what we find in the archaeological record today.

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## Morphological variation and sexual dimorphism of the modern human sacrum

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Sexual dimorphism of the human pelvis has been explained by the obstetrical dilemma hypothesis as the result of antagonistic selection pressures for a narrow, biomechanically efficient pelvis in both sexes and a spacious birth canal in females. The details of how pelvic sexual dimorphism evolved are, however, largely unknown. The pattern and degree of sexual dimorphism in early hominins is obscured by geographic, temporal and taxonomical variation as well as the fragmentary condition of the fossil pelvic record [1, 2]. As part of the pelvic girdle, it is reasonable to think that the sacrum contributes to pelvic sexual dimorphism. The female sacrum is generally described as broader, shorter and more curved than in males, contributing to a wider birth canal. However, the literature provides contrasting results and it is not entirely clear which factors drive sacral variation beside sex [3, 4]. Based on linear measurements and angles as well as landmark-based data, classification accuracies for sexual determination range between 60 and 90% depending on the studied population. Here, we investigate the morphological variation of the modern human sacrum using qualitative, linear and geometric morphometric (GM) data from a worldwide sample of male and female individuals from diverse populations to account for sexual and geographical variation. Our sample comprised 150 individuals of known sex from Central Europe, South-East Asia, South America and Africa, including pygmies and Khoesan. The 3D GM analysis was based on 44 landmarks and 66 semilandmarks. Interlandmark distances were calculated to assess the classical corporo-basal index [5]. Furthermore, a qualitative sex determination was carried out by each of the co-authors and repeated three times. We observed a vast overlap of male and female sacra in the PCA plot of the GM analysis in shape space. The warps showed no sexual dimorphism in sacral curvature. Nevertheless, we confirmed a pattern in the height-to-width proportion and relative expansion of the alae. Classification accuracies for the linear measurements ranged from 50-75% and for the qualitative investigations from 65-75%. All analyses were repeated for the Central Europeans only (n=58), yielding a clearer pattern of sexual dimorphism. Males and females separated with minor overlap along PC2 and the classification accuracies increased by 10-15%, depending on the analysis. On a worldwide perspective, sexual dimorphism therefore seems to be lower than previously suggested and to be confounded by other factors, including geographical origin and body size, though regional groups such as Central Europeans remained more dimorphic. Thus, the accuracy for sex determination of the human sacrum appears to be highly population-dependent, which explains the heterogeneous outcomes reported so far. Nevertheless, the sexual dimorphism of the sacrum remains lower than demonstrated by studies of the human hipbone. Although the sacrum forms part of the birth canal, it might be under lower selective pressure than the pelvis as a whole. Perhaps, factors such as the sacro-iliac joint mobility during birth act as compensatory mechanisms, but this needs to be investigated. Learning more about modern human sexual dimorphism represents a step towards a better understanding of hominin morphology. Our outcomes suggest that sexing fossil hominin sacra remains problematic because besides taxonomy, geographic and temporal variation, it presents additional challenges for the interpretation of fossil remains.

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## Diet, environment and technological performance of *Paranthropus boisei*

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The diet of *Paranthropus boisei* is a matter of debate since the 1980s, but it is still unsolved why they needed such big teeth and jaw. In this study I want to integrate three different diet reconstruction methods (isotope signal, molar macrowear and molar microwear texture analysis) to examine the link between the environment and diet of *P. boisei* in more detail. Were *P. boisei* able to cope with the same environment all year round or were seasonal migrations required? Did they need their specialized dentognathic apparatus just as fallback strategy? Did they use tools? In order to answer these questions we have to know the resource composition of the environment. Selected habitats are analyzed with respect to the spectrum of available food resources. This analysis includes all edible terrestrial and aquatic resources and their characteristics, for instance the  $\delta^{13}\text{C}$  signal, mechanical properties, seasonal availability and nutritional content. On the other side we have the characteristics of a specific group, in this case *P. boisei*, which includes the data of the diet reconstruction methods and the technological performance. The molar macrowear and molar microwear texture analysis provide information on the mechanical properties of the food, e.g. hard and tough. With the isotope signal the proportion of different food groups to the diet can be examined. So every method provides clues about the diet composition in a specific way. Another crucial factor in the diet is technological performance of a group of hominids, because not every resource occurring in a particular environment is accessible without technology. Hunting antelopes requires for instance sophisticated equipment such as spears and many plants are toxic or at least not digestible until they are cooked. And last but not least we have to know the nutritional requirements of the group. So at the beginning we have three different datasets - a list of food resources of a specific environment and their characteristics; the diet signal of the group; and the characteristics of the group – which will be combined in the next steps. First the technological requirements of the food resources (e.g. cooking) are compared with the technological performance of the group. Every resource, which does not match, is excluded from further considerations. The second step is to compare the mechanical and chemical characteristics of the food resources with the diet signal of the group. For example, if there are very tough food resources on the list and the macro- or microwear do not indicate this kind of food they will be excluded from the diet composition. With the remaining food resources an isotope mixing model will be performed to get an idea about the possible proportions of the resources in the diet. The next step is to examine if the possible diet compositions, calculated with the isotope mixing model, fit the protein and fat requirements when they are scaled up to the daily caloric needs and how much food needs to be consumed to reach this goal. So we can see which diet composition is balanced and appears to be reasonable. For example would it be unlikely that someone eats 3 kg of termites every day. This illustrates how the approach works and in which way various methods for the reconstruction of diet are integrated. This permits to link the diet signal with specific features in the environment and the technological performance of *P. boisei*.

## Variation in femoral cross-sectional indicator of robusticity (J) in human populations

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A bone's response to mechanical loading during life and its preserved morphology after death illustrate skeletal adaptation within an individual or population. Analyses have shown that the morphology of the lower limbs differ between modern, historic, and prehistoric human populations due to activity, types of terrain, and adaptation to diverse climates. However, not all analysed populations follow this pattern. This may indicate that the trend of change in skeletal parameters is still not clear. That is why, the use of complex statistical models can be helpful interpreting the functional adaptation of the lower limbs. In addition, investigation of human populations from other regions such as Eastern Europe, Western Asia, Africa and Australia may give new information about morphological diversity. The main aim of the proposed study was to investigate variation in femoral cross-sectional indicator of robusticity (J) between human populations due to different types of economy, regions and chronological periods using a comprehensive statistical model that allows simultaneous analysis of several variables. The sample consisted of 1,981 individuals from the Early Pleistocene to modern times, aged between 16 and 87 years, with no fractures or pathological changes of the lower limbs. For each individual the following variables were collected: sex, age, date range, region, type of economy, femoral biomechanical properties (%CA, J, Ix/Iy), average slope of the terrain and body mass. The human populations came from Europe, Africa, Asia and Australia. The major part of the data came from European Data Set [1] in turn, information about Pleistocene individuals was collected from literature. The biomechanical properties of Neolithic farmers from Poland, Iran, Australian aborigines and Medieval Polish farmers were calculated using Moment Macro (v. 1.4) [2]. Generalized linear model was used to test whether the difference in the robusticity of femur were due to spatial, temporal and biological variation. In the model, difference in polar second moment of area (J) was the dependent variable and sex, age, date, region, type of economy, %CA, Ix/Iy and average slope of the terrain were independent covariates. The GLM was calculated for raw and standardized femoral biomechanical properties, respectively [3]. The model calculated for raw biomechanical properties showed that region, sex, age, %CA, Ix/Iy and some types of economy (farmers, hunter-gatherers, pastoralists, urban farmers and urban populations) explained most of the variation in the robusticity of the femur. Slightly different results were obtained for the second model which used standardized biomechanical properties. Genealogical data of the skeletal remains, sex, age, %CA, Ix/Iy and one type of economy (hunting-gathering) were significant predictor covariates. The model based on standardised biomechanical properties showed that there was a slight temporal decline in the robusticity of femur from Pleistocene to modern times. Although, this trend should be analysed with cautions due to small sample size of individuals from the older periods. Interestingly, terrain shape did not explain the variation in polar second moment of area (J) which means that individuals from mountainous terrain are not characterised by more robust femur than individuals from lowlands. Size- and not standardised femoral property showed significant differences in sex and age. In addition, the standardized robusticity of the femur was associated with hunting and gathering. It may mean that this type of economy requires more resistant lower limbs to bending and torsion than farming, pastoralism or life in urban areas. On the other hand, not standardized robusticity index also showed association with pastoralism, farming, and urban life. But, this may be a result of differences in body mass and proportions between hunter-gatherers and human populations using different types of economy.

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## Comparison of faunal data and associated behavioral interpretations from Quina Mousterian contexts in southwestern France

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In areas of southwestern France such as Charente, Charente-Maritime, and Dordogne, faunal assemblages associated with Quina Mousterian stone toolkits are often highly reindeer-dominant with the remaining portions mainly comprised of larger ungulates such as horse and aurochs/bison. Because reindeer may have been highly migratory and therefore a seasonal resource, their distinctive association with the Quina toolkit in this region has generated ideas about how reindeer-centric subsistence strategies may have impacted Neandertal mobility and thus Quina tool production and use during the Late Pleistocene [1]. Several recent studies investigating Quina-associated faunal assemblages have addressed aspects of reindeer exploitation that are relevant to these research questions, such as prey transport and processing, seasonality, and site use, contributing greatly to our understanding of Neandertal subsistence and settlement systems in cold-climate, reindeer-dominated landscapes [2,3,4,5]. This study compares published faunal data from Quina contexts at Roc de Marsal (Layer 4, Dordogne, France [2]), Les Pradelles (Layers 9-10, Charente, France [3]), Pech de l'Azé IV (Layer 4a, Dordogne, France [4]), and Chez Pinaud Jonzac (Layer 22, Charente-Maritime, France [5]) with the aim of elucidating the similarities and differences between these assemblages as well as underscoring their fundamental role in addressing broader questions regarding the relationship between subsistence, mobility, and technology. With proportions of Quina-layer reindeer at these sites ranging from around eighty to ninety percent, the published studies have primarily centered on the reindeer portions of the faunal assemblages. Though density-mediated attrition has variably affected the assemblages, complicating comparisons of skeletal part representation and prey transport, there seem to be apparent differences between study assemblages in terms of unique skeletal signatures and alignment with nutritional utility indices, which could speak to differences in subsistence behaviors and site use. All sites show some degree of intensive prey processing, though there are possible differences in butchery as indicated by cutmark locations. Interestingly, Les Pradelles (Charente) and Chez Pinaud Jonzac (Charente-Maritime) show evidence of fall and fall-early winter occupations, respectively, while moving southeastward to the Dordogne, Pech de l'Azé IV shows evidence of spring-summer occupations and Roc de Marsal shows evidence of occupations across all seasons. Additionally, all sites have high fauna-to-lithic ratios and little evidence of fire use or spatial organization, which has been interpreted in some instances as evidence of short-term and/or task-specific site use. In future work, incorporation of data from the larger ungulate portion of the Quina-associated faunal assemblages, particularly seasonality, would help better characterize overall hunting strategies and how Neandertals were using the landscape throughout the year during cold-climate periods in this region of southwestern France. Furthermore, greater integration of faunal and lithic data, such as was done for Les Pradelles, would help bolster interpretations of site use and better connect mobility-related lines of evidence from the subsistence and technology realms.

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## The facial ontogeny of Neanderthals and *H. sapiens*

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While morphological differences between *H. sapiens*, i.e. Anatomically Modern Humans, and Neanderthals are well known in adults, it is much less clear when and how they arise during ontogeny [1, 2, 3, 4]. While most workers agree that major aspects of their differences are already established in neonates, there is some disagreement about whether differences are further accentuated through divergence and changes in length of postnatal ontogenetic trajectories [5]. Beyond this, how regions of the developing cranium interact during ontogeny in both species and how they differ is limited. To address these, we carry out detailed analyses of postnatal ontogenetic changes in size and shape and of associations between craniofacial regions to test the hypotheses that ontogenetic changes in craniofacial form and interactions between regions do not differ between Neanderthals and Modern Humans. We apply geometric morphometrics to landmark data acquired on 3D surfaces of skulls of *H. sapiens* and Neanderthals (*H. sapiens* N=70, Neanderthals N=15) and compare ontogenetic trajectories and associations among developing cranial and facial regions. Multivariate regressions demonstrate that Modern Human and Neanderthal craniofacial growth and development show many similarities, with changes most marked in the anterior maxilla, nasal and zygomatico-maxillary regions. Further, major aspects of the differences between adult Modern Humans and Neanderthals are established early and are therefore already present in the youngest individuals. However, additional differences arise through differences in the degree of change in facial size and significantly divergent trajectories of scaling. In particular, Neanderthals compared to Modern Humans develop a relatively wider face at the level of the zygomatics and a relatively taller maxilla. Considering associations among craniofacial regions in Modern Humans during ontogeny, partial least squares analyses (PLS) show that in infants and juveniles the largest and most significant associations among craniofacial regions are found between the orbit, nasal cavity and maxilla, while in adults, the largest and most significant associations are located more inferiorly, between the maxilla, nasal cavity and palate. Maxillary sinus form shows absence of association with other facial regions except in the infant group where they are closely associated with the overlying maxilla, the orbits and the adjacent nasal cavity. PLS analyses of Neanderthals alone suffer from small sample size but, where significant, suggest that the interactions among cranial components are very similar to those in Modern Humans. PLS analysis of Modern Humans and Neanderthals together do not suggest otherwise. In conclusion, modern humans and Neanderthals share major aspects of craniofacial growth and development, already “in place” at birth, but there are significant differences in the details of how adult form is achieved.

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## The first Neandertal tar-backed tool from the Dutch North Sea and the evolution of complex technology

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Here we report the discovery of a 50,000-year-old birch bark tar-hafted flint tool found off the present-day coastline of the Netherlands [1]. This find is important since the conditions regulating the successful development of prehistoric complex technology are currently ill-understood [2; 3]. The technological capabilities of extinct hominin species are especially debated as they relate directly to questions of evolutionary success and extinction.

The tar object was originally deposited in the Rhine-Meuse Paleo-valley and was dredged from the North Sea floor (the Netherlands). Its origin can be securely reconstructed and matches other Dutch Middle Paleolithic North Sea finds that include a Neandertal frontal bone, fauna remains and bifaces. The tar is directly dated by <sup>14</sup>C-AMS, and analyzed using py-GC/MS, micro-CT and optical light microscopy. The object is a relatively large piece of birch tar, encompassing approximately one third of an undiagnostic flake. This find is the first from North-western Europe and complements a small set of directly dated and chemically or spectrographically identified birch tar adhesives.

combining these results and the data from other Middle Paleolithic adhesives with previously obtained experimental data, we show that Neandertals likely used a high-yield and complex tar production strategy at the northern edge of their range. The complex know-how required for this type of adhesive production was therefore maintained in small groups leading highly mobile lives. This contradicts two influential hypotheses on the necessary conditions for technological complexity to develop, namely large group size [4], and low residential mobility [5]. Our findings support the hypothesis that technological complexity is often used to mitigate ecological risk. It also suggests that more task specialization, perhaps between different genders, may have been in place than previously assumed [cf. 3]. As such this find combined with the other Middle Paleolithic birch tar adhesives technology has significant repercussions for our understanding of the versatility and complex technological adaptation of Neandertals.

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## Taphonomic reassessment of the early *Homo* mandible from Garba IVE, and questioning the diagnosis of an ancient case of *amelogenesis imperfecta*.

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MK 81 GAR IVE 0043 (henceforward GAR IVE) is a juvenile early *Homo* represented by a fragment of mandible and a partial mixed dentition. It has been unearthed at Garba IV (Melka Kunture, Upper Awash, Ethiopia), in layer E, dated to ~1.8 Ma. This is one of the very few juvenile fossils of Early Pleistocene age. It is also one of the not many hominin remains discovered during archaeological digging in association with faunal remains and lithic artefacts, namely those of the late Oldowan [1]. Following modern human standards, GAR IVE was estimated to be 2-3 years of age [2]. The specimen was recently reassessed regarding its macroscopic dental development and tooth tissue proportions [3]. This juvenile early *Homo* has been published as being affected by a group of developmental conditions known as *amelogenesis imperfecta* (AI) [4], with a prevalence ranging from 1:700 to 1:14 000 in recent modern humans. This was mainly based on the observation that pitting defects were affecting the outer enamel surface of its erupted deciduous second molar and of the partially exposed unerupted germ of its permanent first molar. Whether this juvenile was affected or not by AI may have strong implications regarding the interpretation of its dental morphology, overall development and, by extension, taxonomic status. Zilberman et al. [4] conclude that the pathology is evidence of a direct genetic link between *Homo erectus* and modern humans. Here, we re-assess the likelihood of the specimen being affected by such a genetic disorder by combining observations of its external and internal morphology using multiscale synchrotron propagation phase contrast scans acquired at the ESRF (ID19 beamline, Grenoble, France). We use 2D and 3D techniques of virtual paleohistology (e.g., [5]) to explore the outer and inner structure of GAR IVE bone and teeth. Based on the clinical literature available to describe the different forms of this disease in recent modern humans, we test whether the various criteria required to reach a diagnosis of AI can be found in GAR IVE. This concerns pitted, hypoplastic defects, but also what teeth are affected, the occurrence of taurodontism, and enamel thickness. Furthermore, a fine examination of the bone and tooth surfaces in light of the individual's young age and of the potential action of taphonomic agents leads to question the developmental origin of the defects observed on the outer surface of the exposed teeth. Taphonomic analysis of the associated faunal assemblage enabled the identification of massive bone alteration, suggesting the activity of necrophagous insects (dermestid beetles). Among other features, pupal chambers were identified in some of the faunal remains. This multidisciplinary approach provides a set of arguments to refute the hypotheses that the defects observed on the mandible were pathological, and that the GAR IVE juvenile was affected by AI.

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## Enamel-bound stable nitrogen isotopic composition preserves trophic information in modern and fossil mammalian teeth

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Stable nitrogen isotopic composition (expressed as  $\delta^{15}\text{N}$ ) is a well-established proxy for determining the dietary behavior and trophic positioning of animals in terrestrial and marine food webs. Typically, enrichment in  $^{15}\text{N}$  (i.e.  $\delta^{15}\text{N}$  of 2-3‰) is observed from diet to consumer allowing determination of an organism's trophic level. Generally, the tissues of animals which consume meat and/or protein rich resources (carnivores, insectivores, omnivores) are higher in  $\delta^{15}\text{N}$  relative to those which consume only plants (herbivores).

To date, the nitrogen isotope composition of hard tissues (e.g. bone, teeth) has only been obtained using collagen extracted from bone or dentin. However, collagen is highly susceptible to degradation and thus has poor long-term preservation potential. While nitrogen isotope composition has been measured in subfossil and fossil bones, such analyses have been limited to relatively young (typically <100 ka) and exceptionally well-preserved material. Stable carbon and oxygen isotope analyses of tooth enamel, which is more resistant to diagenetic alteration than bone, have long been used to investigate the diets of fossil organisms; however, the low organic content of tooth enamel has made nitrogen isotope analyses of enamel difficult. Here, we employ a new method to analyze the nitrogen isotope composition of intra-crystalline enamel-bound nitrogen. This method involves the oxidation of enamel-bound organic matter to nitrate followed by bacterial conversion of nitrate to  $\text{N}_2\text{O}$  and requires 200-fold less nitrogen than traditional combustion approaches (i.e.  $\sim 5$  nanomoles of N). The method is now routinely employed to study the isotopic composition of organic N bound within microfossils (e.g. foraminifera, diatoms, corals) but has not yet been widely used in studies of tooth enamel. Using this new method, we investigate the nitrogen isotope composition of enamel-bound organic matter ( $\delta^{15}\text{N}_{\text{enamel}}$ ) in modern and fossil mammalian teeth to determine if trophic information is preserved.

We show that nitrogen isotope analysis of tooth enamel organic matter is feasible and that the trophic enrichment in nitrogen isotope composition observed in other tissues is also preserved in the teeth of modern mammals. We sampled tooth enamel from herbivorous, omnivorous, and carnivorous modern African mammals from arid and semi-arid settings. The third molar was preferentially analyzed ( $\sim 3\text{-}4$  mg) in all cases to avoid any bias by potential weaning effects. To cross-validate our results,  $\delta^{15}\text{N}_{\text{enamel}}$  values obtained in this study were compared to existing  $\delta^{15}\text{N}_{\text{collagen}}$  and  $^{44}\text{Ca}/^{42}\text{Ca}$  values for the same specimens. First results show that carnivores are enriched in  $^{15}\text{N}$  relative to herbivorous taxa while omnivorous taxa have highly variable  $\delta^{15}\text{N}_{\text{enamel}}$  values.

In addition, we analyzed fossil tooth enamel of fauna from two Plio-Pleistocene hominin-bearing localities (Sterkfontein Member 4, South Africa and Chiwondo Beds, Malawi). Fossil samples were subject to a reductive-oxidative cleaning to remove exogenous organic matter and diagenetically altered matrix material. We found a trophic patterning in fossil tooth enamel which is similar to that observed in the tooth material of modern African mammals.

In conclusion, intra-crystalline enamel-bound nitrogen ( $\delta^{15}\text{N}_{\text{enamel}}$ ) represents a very promising dietary proxy applicable to deep time and opens new avenues of research for reconstructing past food webs and investigating the trophic ecology of extinct taxa. This initial dataset gives us a preliminary framework for interpreting  $\delta^{15}\text{N}_{\text{enamel}}$  values of early hominins at these fossil sites and potentially assessing the contribution of meat and/or faunivorous resources to early hominin diets.

## New human remains associated with Magdalenian rock art from La Marche cave (Lussac-Les-Châteaux, France)

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The cave of La Marche, discovered in 1937 by L. Péricard and S. Lwoff, is well known for his rock art, especially engraved blocks of animal and human figures [1-2]. During excavations in 1937-1938, L. Péricard and S. Lwoff discovered a human mandibular fragment without teeth (LC1) and an upper left third molar (LC2). A lower left third premolar (LC3) and a lower right deciduous second molar (LC4) were then found by L. Pradel in the 50s [3]. These human remains were attributed to the Middle Magdalenian [1-3]. Between 1988 and 1993, the re-evaluation of the collection (stratigraphic re-assessment and sieving of previous spoil heap) made by J. Airvaux yielded numerous new human remains: a parietal and two mandibular fragments without teeth from at least two adults, two mandibular fragments from a child and a juvenile, and 35 isolated teeth including deciduous and permanent elements [4]. The direct dating of an isolated human tooth (OxA-30980: 14 685±75 BP) is situated between 18 077 – 17 646 cal BP and confirms the attribution to the Early Middle Magdalenian [5]. In this study, we describe the Magdalenian human teeth from La Marche discovered during the re-assessment made by J. Airvaux and compare the dental morphometric variations of external and internal signatures to other Upper Paleolithic and Holocene specimens. The collection of Magdalenian teeth is composed of 49 permanent and deciduous teeth (35 isolated teeth and 14 teeth included in mandibular fragments). Among the whole sample of 49 teeth analyzed externally, 29 teeth have been microscanned for internal analysis. For the external structure, 5 variables of crown size were measured and 32 non-metrical variations were scored according to the Arizona State University Dental Anthropology System. For the examination of the internal structure, teeth were scanned using high-resolution microCT at the MRI platform (Skyscan 1076 X-ray equipment, University Montpellier 2, France). Volumes were reconstructed with an isotropic voxel size ranging from 17.93 to 36.18 µm. After segmentation, 13 linear, surface, and volumetric variables were digitally measured or calculated for describing 3D and 2D crown tissue proportions and enamel thickness, and 3D maps of topographical enamel thickness distribution were created. Based on developmental age, occlusal wear and wear facets, we have estimated that the dental remains of La Marche represent a minimum number of nine individuals, including two adults, one subadult and six immature individuals. Results show proximity in external metric analysis between specimens from La Marche and comparative Upper Paleolithic individuals. Enamel thickness and dental tissue proportions in lower first molars from La Marche are closer to those of other Magdalenian individuals than to Mesolithic, Neolithic and extant human individuals. The cave of La Marche is one of the Middle Magdalenian sites with the largest number of human remains. On the whole, the comparative analysis of the La Marche human teeth provides new paleobiological data and an exceptional insight into Middle Magdalenian populations.

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## Macaque-like or baboon-like? What we learn from the bony labyrinth of *Paradolichopithecus*.

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During the Late Pliocene – Early Pleistocene, under successively cooler climates, grasslands gained ground in Eurasia at the expense of forests. Across the continent, primates were represented by the genus *Macaca*, supposedly forest-dependent, and by large-sized papionin monkeys (*Paradolichopithecus* and *Procynocephalus*), supposedly open-dwellers. The latter two are traditionally considered as large macaques [1] but some authors proposed that they are rather close to the African baboons [2]. Post-cranial elements suggest a mainly terrestrial way of life [3] but, as their phylogenetic affinities, the ecology of these taxa remains slightly murky. In this study, we aimed at clarifying both aspects by analysing the anatomy of the bony labyrinth in the cranium LGPUT DFN3-150 of *Paradolichopithecus* from Dafnero-3 fossil site, in Northwestern Greece [2]. We used a comparative sample of 33 cercopithecines representing 13 species (9 papionini and 4 cercopithecini). We virtually extracted the bony labyrinth from  $\mu$ CT-scans and we positioned 22 landmarks [4]. After a Procrustes superimposition of the 3D landmark coordinates, we regressed the Procrustes coordinates on the log centroid size and we performed a between-species PCA on the regression residuals. Based on a molecular phylogeny of the extant species, we evaluated the phylogenetic signal in the morphology of the labyrinth, using the  $K_{mult}$  statistic [5]. We also estimated the position of the fossil specimen in the phylogenetic tree (the topology was fixed for the other species). The analyses were conducted using the R packages *geomorph*, *Morpho* and *phytools*. The allometric signal was statistically significant ( $p < 0.05$ ) in cercopithecines. The labyrinth of DFN3-150 was large, as in baboons and their closest relatives. However, because of relatively less projected semicircular canals and a less coiled and twisted cochlea, the fossil was located far below the regression line, as the two medium-sized macaque species. The first four bgPCs described 64.5 % of the total variance in labyrinth shape, and bgPC1 (28.6 %) roughly separated macaques (except the small-sized *M. fascicularis*) from the other cercopithecines. DFN3-150 grouped with two macaque species (especially *M. sylvanus*) in the shape space of the first four bgPCs, but it stayed close to papionina species (*Papio anubis* and *Mandrillus leucophaeus*). The phylogeny was reflected by the labyrinth size ( $K = 1.079$ ;  $p = 0.007$ ), and not by its shape ( $K = 0.472$ ;  $p = 0.071$ ). The fossil was placed within the baboon group when centroid size was used, whereas it grouped with macaques when only Procrustes coordinates were used for the estimation. The shape of the labyrinth in *Paradolichopithecus* corresponds either to a medium-sized, semi-arboreal macaque, or to a very large and terrestrial baboon-like monkey. Given the large body mass estimations for this species, the latter option is more likely. In this case, the *Macaca*-like shape would reflect the retention of ancestral features. This result questions the classical hypothesis of a grouping with macacina.

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## Investigating the Aurignacian-Gravettian “Transition” East of the Carpathians

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During the Upper Palaeolithic, the Aurignacian to Gravettian “transition” represents a considerable cultural change that occurred between 30.000 BP and 27.500 BP, marked by modifications in both socioeconomic behaviours and material remains, including the lithic domain. In spite of a longtime debate and an increasing interest over this last decade, this issue still lacks any explanatory consensus. Focusing on the controversial early emergence of the Gravettian in the Middle Danube region around 30.000 BP, some researchers lean towards the hypothesis of a unique origin in central Europe before its expansion, while some others favour a convergence model and the existence of different appearance centers [1]. Among the diverse European key-regions concerning that issue, the East-Carpathian area (restricted here to Western Ukraine, North-East Romania and Moldova) remains one of the least investigated, despite the presence of different sites related to final Aurignacian and early Gravettian [2]. Noticeable within these sites, Molodova V contains some of the earliest occurrences of the Gravettian in Europe in the presence of cultural layers 10 and 9 (dated around 29.000 BP) [3], making it a cornerstone in the debate. Furthermore, several east-Carpathian sites consist of secure sequences with high-resolution climatic context, allowing correlations between stratigraphies. Works by geologist P. Haesaerts have indeed highlighted the fast succession between the two technocomplexes [3], even suggesting an anteriority of the early Gravettian appearance over the last Aurignacian levels in this specific region (dated around 27.700 BP in Mitoc-Malu Galben), a fact that curiously matches a corresponding potential overlapping noticed in central Europe [4]. Most of the related lithic collections were attributed in the second half of the 20th century, but have rarely been examined else than typologically. We have then decided to lead some new researches, applying a detailed technological approach to Ukrainian (including Molodova V and Korman IV), Romanian (including Mitoc-Malu Galben) and Moldovan (including Corpaci-Mâs) assemblages. Concerning the late Aurignacian assemblages, this re-examination leads us to strengthen their attribution, as their technical system clearly correspond to the Aurignacian lithic production patterns identified throughout Europe, and despite their late dates. On the other side, the reappraisal of the Ukrainian early Gravettian sites brings new elements to refine the technological understanding of its specificities. These new results allow a re-evaluation for the emergence of the Gravettian in eastern Europe specifically, but also provide fresh reflections on the debate in its broad extent over Europe.

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## An outlook on new 3D methods for dental enamel hypoplasia analysis using confocal imaging profilometry

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Dental enamel hypoplasia, a reduction in surface enamel thickness manifested as pits, horizontal grooves, or missing enamel planes, occur on permanent and deciduous teeth. Although such defects can be caused by genetic factors, they are often linked to physiological developmental stress events, such as malnutrition and diseases, thus making their study a standard procedure when investigating the health status of ancient populations. Traditional methods employed in enamel hypoplasia studies focus on recording their presence/absence and locations on dental surfaces to reconstruct the occurrence and timing of stressful events in relation to dental developmental sequences. These assessments are generally made with the naked-eye, aided by a magnifying glass (20x). To bypass limitations of low magnifications, some studies have also employed scanning electron microscopy (SEM) to generate high magnification images. These images allow for measuring defect dimensions as well as for counting incremental growth lines within them, thus also permitting an estimation of the duration of a stress-episode [1]. Even though advantageous, enamel hypoplasia research relying on SEM faces several challenges, mostly due to light distortions caused by different projection angles on the inward slopes and depressions of enamel defects. These greatly bias results and restrict their repeatability [2]. To overcome this problem, new high-resolution imaging equipment, which can generate an accurate replication of dental surfaces and would thus allow for the objective quantification of hypoplasias, is needed. The confocal imaging profiler (CIP), a machine capable of scanning surfaces at a nano-scale resolution, provides a promising opportunity for examining enamel defects [3]. CIPs non-destructively and non-invasively collect 3-dimensional (3D) point-cloud-data from a surface and translate them into virtual high-resolution 3D topographic maps. These profilers scan at higher speeds and with higher spatial resolution than regular 3D-imaging microscopes. High spatial accuracy facilitates the quantification of incremental microstructures of bone and tooth surfaces and allows for the objective examination of surface modifications and irregularities, including hypoplasias [4]. To better evaluate the effectiveness of this 3D-imaging approach in assessing hypoplastic defects on hominin dental surfaces, we selected a sample of 25 Neanderthals and Upper Paleolithic modern humans whose teeth were previously scored for such defects using traditional techniques and re-examined them with a CIP. The presence and location of previously reported hypoplasias on high-resolution epoxy replicas of these teeth were first verified following traditional protocol, i.e., using an illuminated magnifying glass [1,5]. All teeth were then scanned using the Sensofar Plü Neox CIP at both 10x and 20x magnifications. In SensoMap software, longitudinal profiles were cut through the obtained 3D scans to examine and distinguish between regular perikymata spacing and localized enamel reductions. Our preliminary results show that using a CIP allowed for the detection of hypoplastic defects, i.e., small pits and shallow lines, that were not observable using traditional methods. As reported by McGrath et. al. (2018) in a study on great ape dentition, we conclude that small and shallow enamel defects tend to be overlooked by the traditional methods. Our study therefore further highlights the efficiency of employing CIPs in research involving hypoplasia. Using CIPs, direct measurements of defect depths and locations can be taken with high accuracy and without any optical distortion, thus eliminating observer/machine error and increasing the repeatability of results. This in turn advances objective and quantitative research in the field of dental anthropology.

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## A comprehensive metric analysis of Palaeolithic deciduous and permanent teeth

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The application of dental metric measurements is vital for understanding a wide range of intra- and inter-group variations in fossil hominins. Such measurements have been used to assess differences driven by temporal range, geographic location, sexual dimorphism, taphonomic bias, pathological conditions, but, mostly, by phylogenetic relations [4]. In relation to the latter, dental metrics have played a pivotal role in taxonomic studies of later *Homo* fossils especially in cases when teeth were found in isolation or along with only small fragmentary bone remains [e.g. 3]. However, previous studies focusing on or including metric measurements have either relied on small comparative samples or been limited to one tooth position. This is problematic since the inclusion of large samples and metric dimensions of multiple tooth types is critical for establishing and characterizing differences among taxa. Additionally, the majority of the available studies concentrate on permanent teeth with only few focusing on deciduous ones. Yet, the latter have been argued to be distinctively advantageous as they are believed to display greater morphological conservatism than permanent teeth, which potentially makes them exceptionally useful for investigating genotypes [5]. For these reasons, and to better understand dental size differences in later *Homo* species, we compiled a comprehensive database of metric measurements for all permanent (n=1870 teeth) and deciduous (n=227 teeth) teeth types. This substantial sample includes teeth of both Neanderthals (n=1000 teeth) and Upper Paleolithic modern humans (n=1097 teeth). Our aims were to: (1) characterise size differences in the various tooth types between these groups, (2) compare the patterns of differences in size across the dentitions for these two groups, and (3) assess the power of the use of metric measurements on deciduous teeth as a reliable taxonomic classification of later *Homo* taxa. Following standard methods [1], using Mitutoyo digital callipers, we recorded maximum mesiodistal and labiolingual/buccolingual dimensions from a total of 674 teeth available as high resolution dental casts at the Paleoanthropology Collections, University of Tuebingen. This data was supplemented by similar measurements available from the literature for the remaining 1423 teeth forming our sample. From these measurements, crown areas and crown indices were additionally calculated for all molars [2]. Here, we have provided one of the largest datasets of metric data ever gathered for later *Homo*. Our comprehensive analysis for every tooth position highlights the unique large size of the Neanderthals lineage permanent teeth relative to modern humans. Conversely, only the mandibular lateral incisors for the deciduous dentition stressed significantly larger dimensions in Neanderthals. With confidence, metric dimensions of permanent teeth prove to be reliable in phylogenetic classification of Neanderthal and modern human remains. This contrasts sharply with the considerable overlap in size of the respective deciduous dentition between the two hominin groups, leading to the conclusions that, overall, deciduous dental dimensions are not reliable for taxonomic distinction, at least in late *Homo* species. To conclude, this study represents a significant database for future investigations into Palaeolithic dentition, with considerable importance regarding deciduous dentition. Moreover, our provision of a reference sample for every tooth position will be especially consequential for the classification of isolated remains.

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## A new method to infer the reduction intensity on cores and handaxes: The Volumetric Reconstruction Method (VRM)

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In the last years, many researchers have developed quantitative methods to estimate the reduction intensity in stone tools, since it is a key element to understand the technological variability in archaeological assemblages, the type of occupation, mobility patterns and the management of raw materials [1]. However, most of the reduction intensity proxies applied to cores can be affected by the reduction strategies used or the original size of the blanks, making difficult the comparison among different archaeological assemblages. Here we present a new approach, the Volumetric Reconstruction Method (VRM), based on the 3D reconstruction of the original nodules. For that, according to the generations of removals and their arrangement on a blank, we added the mean platform thickness of the flakes from the assemblage to the length and width of the blank, as many times as generations identified on each section of the perimeter. Regarding the thickness, when the maximum thickness of the blank is not defined by cortical surfaces, the mean flake thickness is added to the blank's thickness following the same criteria as for length and width. Then, with the corrected values of the three dimensions, we apply the formula of the ellipsoid volume to obtain an estimated original volume. Finally, we can measure the degree of reduction (expressed as percentage of remaining volume/mass) by dividing the volume/mass of the blank by the estimated original volume/mass. To test the VRM we carried out an experiment applying four different reduction strategies (unifacial unipolar, bifacial multipolar centripetal, multifacial multipolar, and handaxes configuration) on quartzite and sandstone cobbles (n=64) from Arlanzón (Spain). Our selection comprises different sizes and shapes. Four knappers participated in the experiment. Each one freely chose the cobbles, the reduction strategy to apply to each one, and the degree of reduction. They were just asked to produce four of each strategy. 3D models of all blanks were made before and after the experiment. Our results show a very strong correlation [2] between the VRM estimated mass and the real mass of the original cobbles ( $R = 0.83$ ;  $r^2 = 0.70$ ), as well as between the real and estimated percentage of remaining mass after knapping ( $R = 0.85$ ;  $r^2 = 0.72$ ). Furthermore, we did not find statistically significant differences between the real and estimated values, both for the original mass of cobbles and for the percentage of remaining mass (ANOVA ( $p > 0.05$ ); Kolmogorov-Smirnov ( $p > 0.05$ )). In addition, we tested that the type of reduction strategy does not affect the VRM (ANOVA ( $p > 0.05$ ); Kolmogorov-Smirnov ( $p > 0.05$ )). Any reduction intensity index must fulfill some characteristics to be reliable [2]: I) Inferential power; II) Directionality; III) Comprehensiveness; IV) Sensitivity; V) Versatility; VI) Blank diversity and VII) Scale-independence. Our results show that the VRM has a high inferential power, proved by the  $r^2$  values (I), which demonstrate its unidirectional nature (II), although it is necessary to perform a sequential reduction analysis to verify this character. In addition, the VRM works correctly in cores with different degrees of reduction (III), as well as detecting small differences in the mass lost (IV). Similarly, it works correctly on different reduction strategies (V) and with very different shapes and sizes of the nodules (VI), but it must be considered that the VRM has not been tested in non-fluvial blanks, nor in cores or handaxes made on flakes. Through the VRM, direct comparisons can be made between different assemblages, since the reduction intensity can be expressed in percentage (VII) of the remaining mass. Finally, unlike other approaches [3,4], the VRM is based on the estimation of an original volume/mass, which allows also to estimate the size and the weight of the original nodule selected, both elements of major influence in the formation of lithic assemblages[5].

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## Reconstructing Neandertal population history by targeted enrichment of variable positions in their nuclear genomes

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To date, whole genome sequences have been recovered from ten Neandertal individuals [1], three of which (from Denisova Cave, Russia [2], Vindija Cave, Croatia [3], and recently from Chagyrskaya Cave, Russia [4]) were sequenced to a quality comparable to what is typically achieved for present-day genomes. Nevertheless, nuclear DNA sequences from Neandertals covering more of their geographical and temporal range are needed to better reconstruct their population history and their interactions with other hominins. To allow the efficient retrieval of genome-wide data from many Neandertal specimens where DNA preservation does not allow whole genome sequencing, we designed a DNA capture reagent targeting 718,083 single nucleotide polymorphisms (SNPs) distributed across all autosomes and the X chromosome. These SNPs are known to vary either among previously sequenced archaic genomes or among present-day African individuals. Here we describe the first application of this reagent to 20 Neandertal specimens (11 teeth and 9 bones) from Chagyrskaya Cave, which was occupied by Neandertals around the terminal phase of marine isotope stage 4, approximately 60,000 years before present [5]. Between 14 and 34 mg of material were removed from the specimens and converted into DNA libraries using the most sensitive protocols currently available. DNA preservation was characterized by direct shotgun sequencing of the libraries, as well as through enrichment of mitochondrial DNA by hybridization capture. DNA preservation and levels of contamination by microbial and present-day human DNA allowed sequencing of the genome of one specimen to high coverage (~28x) [4]. Whereas four of the remaining specimens did not contain detectable amounts of ancient nuclear nor mitochondrial DNA, we recovered varying amounts of DNA from 10 of the teeth and five of the bones. By enriching the libraries of the latter specimens using the novel capture reagent we obtained between 0.08x and 4.5x coverage of the targeted sites. Two of those 15 specimens belonged to the same Neandertal individual, and one additional specimen belonged to the same individual whose genome was sequenced to high coverage. The relationships of the individuals to each other and to other Neandertals will be discussed as well as the prospect of applying this capture reagent to the large numbers of Neandertal specimens that are not suitable for whole genome sequencing.

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## Functional molar macrowear analysis in *Pongo pygmaeus* and *Pongo abelii*

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Orangutans are found in Southeast Asian tropical rainforests of Borneo (*Pongo pygmaeus*) and Sumatra (*Pongo abelii*) and are primarily considered as frugivorous species. However, in seasonal periods when fruit availability is scarce, orangutans tend to eat fibrous and unripe fruits, leaves, nuts, bark, and in rare occasion, wood [1]. The highly seasonal environments, and fruit availability, seem to play an important evolutionary role in shaping the craniodental morphology in *Pongo* [1]. In fact, while Bornean orangutans, spend more time feeding on fallback foods (those seasonal foods with poor nutritional values and which are more difficult to digest), Sumatran populations consume more ripe fruit pulp. As a consequence, Bornean orangutans are characterised by relatively more robust mandibles, providing greater load resistance abilities to masticatory forces [2]. The aim of this study is to analyse the molar macrowear pattern of Bornean (*Pongo pygmaeus*) and Sumatran (*Pongo abelii*) orangutans, and thus investigate if there is any geographic variation in diet between the two species. We employ a well-established method known as Occlusal Fingerprint Analysis [3], that allows the three-dimensional reconstruction of the occlusal movements responsible for the formation of wear facets, those flat and polished enamel areas with well-defined borders. This approach considers the functional aspects of tooth macrowear (buccal phase I, lingual phase I and phase II facets) that occur during the sequential phases of the chewing cycle, or power stroke [4]. The sample consists of second mandibular molars (which provide a good general overview of the development of masticatory functions within a species) of *P. pygmaeus* (n = 9) and *P. abelii* (n = 8), characterised by a moderate degree of wear, between stages 2 and 3 [5]. Our results show a significant difference between Bornean and Sumatran orangutans. Specifically, *P. pygmaeus* is overall characterised by large phase II and lingual phase I facets, and minimal buccal phase I facets, while *P. abelii* shows reduced lingual phase I facets, and at the same time significantly larger buccal phase I facets. Overall, while *P. pygmaeus* is characterised by a restricted and well-defined pattern, *P. abelii* molar macrowear is considerably more variable. Some differences, although not statistically significant, have been also found in the inclination of molar wear facets, with Bornean orangutans generally showing flatter occlusal wear than those of Sumatran orangutans. This macrowear pattern variation between the two orangutan species is probably correlated with the physical and textural properties of the foods they consume. Hard and tough foods such as seeds, unripe fruits and bark, require repeated vertical mandibular movements with prominent crushing forces, which tend to obliterate molar cusp morphology, and thus reducing the molar wear angles [4, 5]. In contrast, Sumatran orangutans seem to have a greater ability to create shearing stress during mastication, probably in relation to their “softer” diet. Several studies highlighted the importance of fallback foods in the diet, ecology, and evolution of non-human primates and early hominins [1, 2]. Morphological specialisations for fallback foods may have offered the possibility to consume a wider range of foods, especially important when preferred foods are in short supply. Our preliminary study shows that the molar macrowear pattern of Bornean orangutans seems to be better adapted to eat mechanically challenging foods when preferred foods are scarce or unavailable. This method can be used to advance our understanding of the diet, ecology and evolution in extinct hominins. However, further studies will necessitate the use of a larger sample size to reconstruct the functional relationships between tooth morphology, foods mechanical properties and macrowear in orangutans and in other non-human primates.

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## Is it possible to gain direct evidence of early hominin meat consumption? - A first approach using Pleistocene fossil tooth enamel nitrogen isotopic composition

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New geochemical data from the Malawi Rift (Chiwondo Beds, Karonga Basin) fill a major spatial gap in our knowledge of African hominin adaptation. Carbon isotope ( $\delta^{13}\text{C}$ ) ratios, complemented by oxygen ( $\delta^{18}\text{O}$ ) and clumped isotope ( $\Delta^{47}$ ) data reveals an unexpected diversity in Pleistocene hominin diets in the various savanna habitats of eastern and southern Africa. Plant-based food sources of early *Homo* and *Paranthropus* living in relatively cool and wet savanna ecosystems along the western shore of paleolake Malawi contained a large fraction of  $\text{C}_3$  plant material in contrast to *P. aethiopicus* which occurred contemporaneously, but further north in the Eastern Rift and consumed a higher fraction of  $\text{C}_4$  resources. This trend towards greater  $\text{C}_4$  consumption grew more pronounced in eastern *Paranthropus* taxa (i.e. *P. boisei*) over  $\sim 2$  Ma as savannas became increasingly more open, while the genus *Homo* appears to have maintained high dietary versatility. However, southern African *P. robustus* - similar to the Malawi Rift individuals – consumed primarily  $\text{C}_3$  resources throughout the Early Pleistocene. Collectively, the new stable isotope and faunal data document that early *Homo* and *Paranthropus* were dietary opportunists able to cope with a wide range of paleohabitats, demonstrating high behavioural flexibility in the early African Pleistocene. However,  $\delta^{13}\text{C}$  data can only evaluate the plant-based component of early hominin diets, while meat-eating or omnivorous feeding behaviours cannot be distinguished with this method. Hence, important questions about Early Pleistocene hominin dietary adaptation remain:

- How much meat – compared to plant-based resources – did early hominins consume?
- Which tropic level did *Homo*, *Paranthropus* and *Australopithecus* occupy in Early Pleistocene Africa?
- Did different hominin species integrate different amounts of meat in their diets?
- How did the dietary behaviour of co-existing early Pleistocene hominins from the savannas of the Eastern Rift differ from individuals from the Cradle of Humankind in southern Africa?

These essential deficits in our knowledge can be addressed if the  $\delta^{13}\text{C}$  dataset is complemented with nitrogen isotopes ( $\delta^{15}\text{N}$ ) measurements, because the latter can inform about the individual's position in the (paleo)food chain. Until now, determination of  $\delta^{15}\text{N}$  has only been possible on (hominin) specimens younger than 100,000 years because large quantities of relatively unaltered fossil collagen were required. Here, we present a new biogeochemical method, which measures nitrogen isotope ratios with high precision on extremely small sample sizes (5 nanomoles of N), and hence permits to analyze early and mid-Pleistocene fossil (hominin) tooth enamel samples for the first time.

## Elemental imaging of human teeth by laser ablation ICP-TOF-MS: fast acquisition and high-resolution

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The distribution of trace elements in the mineralized tissue of permanent and deciduous teeth is crucial in reconstructing past human behavior and ecology. Recent work demonstrated how weaning practices and diet during infancy may be unraveled investigating chronologically-resolved thin sections of human teeth [1,2]. In addition, trace element distribution in dental tissues can decipher the health status (i.e. heavy metal intoxications) of an individual and resolve post-depositional processes (i.e. fossilization). Enamel is highly resistant to diagenesis and sequentially mineralizes over several years, recording dietary input information at high time-resolution. This tissue is thus the ideal target for trace element and isotope analysis, even if the complex process of enamel secretion and mineralization can overprint the trace element signal and great attention has to be paid in selecting the regions of interest into the crown [1]. From a methodological perspective, trace elements are commonly measured in histological sections employing in-situ and imaging techniques, such as laser ablation ICP-MS [3], electron microprobe and x-ray fluorescence. We propose here a novel workflow to map trace elements in histologically-defined sections of human teeth via LA-ICP-TOF-MS imaging [4]. The icpTOF (TOFWERK AG) combines a classical ICP-MS system with a Time-of-Flight mass analyzer and is able to acquire a complete mass spectrum in 0.03-0.05 ms for each sampling point. We analyzed thin sections from two archaeological teeth (one lower first permanent molar and one lower deciduous second molar) from the Roman Imperial necropolis of Isola Sacra (II-IV century CE, Lazio, Italy), coupling a state-of-the-art ICP-TOF-MS (icpTOF2R, TOFWERK AG, Thun, Switzerland) with a Teledyne CETAC Analyte G2 193 nm excimer laser and a low dispersion, fast-washout ablation cell (Cobalt). Teeth were embedded in EpoThin (Buehler) resin and cut using a diamond blade microtome (Leica 1600), at the Museo delle Civiltà in Rome, Italy. Final sections (~100 µm thick) were analyzed for their histomorphometric features using a polarized light microscope and chronologized counting the Retzius lines and cross striations incremental markings. Through this setup, we were able to obtain high-resolution elemental maps (pixel size ranging between 10 and 20 µm) of the dental crown and to precisely correlate chemical data with the growth patterns of the tooth. Being this technique micro-destructive for the thin section (~<1 µm ablated in depth), it is possible to re-observe the growth patterns of the enamel after ablation and, potentially, repeat the mapping on the same thin section. The two Roman teeth showed clear Pb variation through the crown, highly correlated with enamel growth trajectories, likely related to the environmental exposure to this toxic metal during the individual's lifetime. The reliability of these results is corroborated by the evidence that Pb is almost unaffected by the maturation overprint [1]. To conclude, LA-ICP-TOF-MS can either be used as a screening tool for subsequent detailed chemical and isotope mapping of the entire section of the dental crown or as an effective tool to study weaning practices, diet, environmental exposure to toxic metals, and post-depositional elemental uptake.

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## The partial skeleton StW 431 provides new insights into the palaeobiology of Plio-Pleistocene hominins from Sterkfontein, South Africa.

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In 1987/1988 Alun R. Hughes and his team discovered the hominin skeleton StW 431 from Sterkfontein Member 4. At the time of its first description in 2003, Toussaint and colleagues [1] assigned this specimen to the genus *Australopithecus* "...although there [was] little direct morphological evidence as to the species..." (p. 222). Fifteen years later, as part of their announcement of the almost complete StW 573 'Little Foot' skeleton from Sterkfontein Member 2 (3.67 ± 0.16 Ma) [2], Clarke and colleagues placed StW 431 in the *A. prometheus* hypodigm [3]. Importantly, they used aspects of StW 431 anatomy, e.g. the pelvis, which is badly crushed in StW 573, to make inferences about the positional behaviour, locomotion and palaeobiology of *A. prometheus* [3].

Here we comprehensively review and re-analyse the StW 431 morphology. Besides the pelvis, StW 431 preserves the last ten vertebrae, a rib head, and fragments of the right scapula, clavicle and elbow. Skeletal regions that can be compared to those of StW 573 'Little Foot' are therefore rather limited. However, a new reconstruction of the StW 431 pelvis suggests a different morphology and functional adaptation from that of Sts 14, a partial skeleton classically attributed to *A. africanus*. For example, the position of the sacrum within the pelvis is significantly higher positioned and the iliac blades are wider. The strong muscle markings on the iliac crests have previously been interpreted as showing a human-like development of the abdominal muscles and the *m. latissimus dorsi* [4]. Alternatively, the *m. latissimus dorsi* could also have had a much broader, chimpanzee-like origin extending to the anterior superior iliac spine. The elbow morphology, on the other hand, is comparable to that of other australopiths, both from East and South Africa. Hence, when viewed in its entirety it is clear that StW 431 is distinct from *A. africanus* sensu stricto. The fact that morphological differences between StW 431 and other postcranial fossils from Sterkfontein are generally more marked in the pelvic girdle than they are in the rest of the skeleton cautions against inferences about locomotor behaviour based on isolated skeletal elements. Evidently, Plio-Pleistocene hominins from Sterkfontein had a unique mode of locomotion and positional behaviour, but they also retained the ability to engage in arboreal activities.

On the basis of our analyses we provisionally concur with Crompton et al. [3] that StW 431 probably belongs to *A. prometheus*. Confirming this possibility is not straightforward however, as *A. prometheus* is mainly defined on the basis of craniodental traits [5]. Regardless, the distinctiveness of StW 431 from *A. africanus* throws new light on the behaviour and palaeobiology of Plio-Pleistocene hominins from South Africa, including the palaeobiogeography of early hominins.

Clarke has consistently argued that the morphology of *A. prometheus* and, by implication, StW 431 resembles that of the much younger *Paranthropus robustus* (ca. 2.1 - 0.62 Ma) and has implied an ancestor-descendent relationship between these Plio-Pleistocene South African hominins. Such a suggestion is not supported by our analyses of the postcranial skeleton. Rather, similarities in morphology could be the result of homoplasy, i.e. plastic responses of the skeleton to similar ecological conditions. Such homoplasies may have been exacerbated through niche partitioning of sympatric hominins, e.g. *A. prometheus* and *A. africanus* in case of Plio-Pleistocene hominins, and *P. robustus* and early *Homo* in case of Pleistocene hominins. Theoretical and palaeoecological considerations similarly argue against Clarke's proposition. The prevailing palaeoecological and palaeoclimatic conditions make it unlikely that *A. prometheus* and *P. robustus* are part of the same evolving lineage (e.g. anagenesis).

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## Enamel development and thickness in deciduous canines from *Pongo pygmaeus* and *Pan troglodytes*

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Tooth enamel retains an incremental growth record. Studies have drawn upon this record to reconstruct enamel growth rates for permanent teeth from extant great apes and modern humans. This research has provided an understanding of the cell mechanisms underlying enamel thickness in extant hominoids, and a basis from which to examine the evolution of these mechanisms through comparisons with fossil species. In contrast to permanent teeth, little is known about the development or thickness of great ape deciduous enamel. Here I report crown enamel extension rates, lateral enamel secretion rates, and relative enamel thickness (RET) for thin sections of a deciduous maxillary canine (dC1) from *Pongo pygmaeus* (reference number: CA28 J57-c) and a dC1 from *Pan troglodytes* (CA20A.2.36-c). Comparisons are undertaken with new developmental data and previously published RET data for modern human dC1 [1]. The trajectory of crown extension for the great ape canines differed to modern humans. Neither of the great ape canines displayed the rapid initial extension or the subsequent steep deceleration in extension rates that is characteristic of human dC1. The orangutan canine crown extended more rapidly than the canine from *Pan*. Average daily secretion rates were faster in the outer enamel of the great apes compared to humans. Secretion rates were as high as 6.00  $\mu\text{m}/\text{day}$  in the orangutan crown and may be even higher in other deciduous tooth types from *Pongo*. The RET of the great ape canines was thinner than the RET of human dC1 [1]. In conclusion, the thinly enamelled orangutan canine formed with rapid rates of secretion and a trajectory of extension that differed when compared to human deciduous canines. The rapid enamel secretion is consistent with the previously reported low Retzius periodicity [2], and short crown formation time for this dC1 from *Pongo* [3]. The thinly enameled chimpanzee canine had an enamel extension trajectory that was similar to the orangutan canine, though the extension and secretion rates were slightly slower in *Pan*.

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## Fire and short-term human occupations in Iberia during MIS 4: Evidence from Abric del Pastor (Alcoy, Spain)

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A relatively low amount of Middle Palaeolithic sites in Europe dating to MIS 4 and absence of anthropogenic fire in some of the sites brings to question the way in which this period of global cooling might have affected the Neanderthal population. The Iberian Peninsula is a key area to explore this issue, as it has been considered as a glacial refugium during critical periods of the Neanderthal time line and might therefore yield archaeological contexts in which we can explore possible changes in the behavior and settlement patterns among Neanderthal groups during MIS 4. Here we report recent data from Abric del Pastor, a small rockshelter in Alcoy (Alicante, Spain) with a stratified deposit containing Middle Palaeolithic remains. We present the results of our latest investigations at the site, which consist in: micromorphological data on site formation, absolute dates (optical stimulated luminescence and ESR/U-series) that frame the sequence within MIS4 and multi-proxy geoarchaeological evidence of in situ anthropogenic fire, including microscopic evidence of in situ combustion residues, wood ash and thermally altered sediment. We also present archaeostratigraphic evidence of recurrent, functionally diverse, short-term human occupation of the rock shelter that reveals similar settlement patterns to those documented in contexts from the following MIS 3 period. This data is complemented by a millennial scale record of past rainfall variability and local vegetation dynamics obtained through a multi-proxy paleoecological study in which we analysed sedimentary n-alkanes derived from leaf waxes, in addition to their associated carbon and hydrogen isotopic ratios ( $\delta^{13}\text{C}$  wax and  $\delta^2\text{H}$  wax), as proxies for past vegetation and rainfall variability. This was coupled with bulk organic geochemistry (TOC, %N, %S), anthracology, microfauna and macrofauna analyses as additional proxies for selected sub-units through the sequence. Our results suggest that Neanderthals occupied the Central Mediterranean coast of the Iberian Peninsula during MIS 4. These Neanderthals had activity-specific sites, were not undergoing climatic stress and were habitual fire users. Comparable high-resolution geoarchaeological data is needed for MIS 5 at a regional scale, as well as a geoarchaeological focus on the MIS 5/MIS 4 and MIS4/MIS 3 stratigraphic boundaries at different sites, which might conceal valuable paleoclimatic information and contribute to our understanding of associated human dynamics.

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## Making skull cups: butchering traces on cannibalised human skulls from five European archaeological sites

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Archaeological records of the treatment of human skulls for ceremonial or cult purposes appear at the end of Palaeolithic and are shown in different ways, being able to identify through the taphonomic modifications. According to this, the presence of skull cups (bowls from human calvaria) is currently considered evidence of ritualistic treatment of human bodies and it is found in many occasions associated to cannibalism. Prehistoric skull cups are characterized by a careful and repetitive fracture pattern and elevated frequency of cut marks. We aim to assess whether it is possible to identify a common pattern, through the cut marks disposition and frequency, in the treatment of modified skulls to produce skull-cups, by comparing evidence from different prehistoric assemblages in Europe. We compared published data and drawings of cut marks recorded on the surface of human skulls specimens from TD6.2 of Gran Dolina (1), Gough's Cave (2), Fontbrégoua (3), Herxheim (4), and El Mirador Cave (5). Cut marks were spatially plotted as polylines over the bone templates in ArcGIS, which has allowed us to evaluate their distribution and greater or lesser presence in the different views of the human skulls. In all samples except in TD6.2, it has been proposed some ritual component on the remains and perhaps of the cannibalism events. In three of the sites (Gough's, Herxheim and El Mirador) the elaboration of skull cups was recorded. The location and distribution of cut marks on the studied skulls were analysed using the ESRI ArcGIS software package. In order to statistically compare patterns among skulls of the same site and between skulls from different sites, the cut marks were digitalised on standardised templates of a skull in six side-views: anterior face; dorsal; left lateral; right lateral; superior; and inferior). Results show a high frequency and a spatial distribution with a clustered pattern of cut marks common in all the skull cups and Fontbrégoua skulls. This is particularly concerning the longitudinal cut marks located in the upper part of the skulls and superimposed or parallel to the sagittal suture. However, no parallels were observed with the treatment of *Homo antecessor* skulls. The scalping of the craniums from Gough's Cave, Fontbrégoua, Herxheim, and El Mirador may be therefore associated with the preparation of the skulls (skull cups and non-skull cups) for ritual purposes. We statistically demonstrated that on skull cups there are areas with higher concentration of cut marks, corresponding mainly to the removal of the scalp. The high frequency of cut marks can also be associated with defleshing and is found on the lateral and ventral facets of the skull. We have located patterns of spatial distribution of aggregate and regularly scattered cut marks in the skull craniums, with higher densities than in the skulls without prearranged morphology. Repetitive patterns, intended for intensive cleaning bone, have been recognised in specimens from Gough's Cave, Fontbrégoua, Herxheim, and El Mirador Cave. A methodical process has been identified in the manufacturing of the skull cups. The removal of the scalp and defleshing was meticulous and intensive according to the number of cut marks, in all skull cups and Fontbrégoua. This pattern is repeated from the Magdalenian site of Gough's Cave to the Bronze Age site of El Mirador Cave, providing further evidence of the preparation of the skulls for their possible ritualization. Intensive tissue removal can be an indicator of human cannibalism in a ritual context.

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## Chronology, climate and environmental conditions during the Middle to Upper Paleolithic transition in NW Spain with relevance to the debate on the disappearance of the Neanderthals

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Today, it is accepted that during the Middle to Upper Paleolithic transition, when Neanderthals were replaced by Anatomically Modern Humans (AMH), this was not an identical, simultaneous, continent-wide event. To what extent local and regional MIS3 climatic and environmental oscillations affected the extinction, in concert with the arrival of a new human species competing for the same resources, is still poorly understood. To do so, regional and temporal variations need to be considered to comprehend this evolutionary process. Results of a multidisciplinary pilot study, focused on radiocarbon dating, Bayesian modelling, zooarchaeology and stable isotopic analyses ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$  and  $\delta^{34}\text{S}$ ) on anthropogenically manipulated horse and red deer remains from Cantabrian Spain are presented. This region is especially relevant to investigate the causes of Neanderthal demise due to the persistence of several “Transition” sites. Recent methodological developments in radiocarbon dating [1,2] provide a temporal framework for the replacement. Here, new AMS 46 dates, in combination with other available ultrafiltered dates from the region, allowed to build up a complete Bayesian age model. According to it, the Mousterian disappeared in the region by 47.9–45.1ka cal BP, while the Châtelperronian lasted between 42.6k and 41.5ka cal BP. The Mousterian and Châtelperronian did not overlap, indicating that the latter might have been either intrusive or an offshoot of the Mousterian. The new chronology also suggests that the Aurignacian appeared between 43.3–40.5ka cal BP overlapping with the Châtelperronian and ended around 34.6–33.1ka cal BP, after the Gravettian had already been established in the region. This evidence indicates that Neanderthals and AMH co-existed for less than 1,000 years [3]. As to the palaeoenvironments experienced by both human species, multiple-isotopic analyses reveal that after the Mousterian there were a change in environment towards more open vegetation, linked to wider climatic change [4,5]. High inter-individual nitrogen ranges were observed in both herbivores during the Mousterian, Aurignacian and Gravettian, which could indicate that the animals were procured from areas isotopically different in nitrogen. However, sulphur values among sites do not suggest local variability in the hunting areas exploited. Therefore, possible explanation is that the nitrogen ranges reflect climatic fluctuations within the time of formation of the archaeological levels in question, as observed in pollen, marine and ice cores. From the subsistence point of view, the new chronology incites a reconsideration of previous zooarchaeological data available at the region.

The recently awarded and much broader ERC-funded SUBSILIENCE project aims to address further these initial results, by targeting faunal assemblages of 20 key archaeological sites located in the southern European refugia: Serbia, Croatia, Italy and Spain. By applying multidisciplinary techniques for reconstructing palaeoeconomic, palaeoclimatic and palaeoecological conditions, with high-precision chronologies, to test hypotheses of Neanderthal extinction based on the interplay of rates of climate change, modern human presence or absence and changing subsistence responses, based on correlations among these parameters.

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## Functional analysis on the lithic assemblage from Layer I (the Bachokirian) at the onset of the Upper Paleolithic in Bacho Kiro cave, Bulgaria.

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The Middle-Upper Paleolithic cave site of Bacho Kiro is well known for its so-called Bachokirian lithic industry at the base of the Upper Paleolithic chrono-stratigraphic sequence. Since its excavation in the early 80's [1], the Bachokiran has been described and interpreted as a pre-Aurignacian industry that combines some Middle Paleolithic technological features (i.e. Levallois and hard hammer percussion) with Upper Paleolithic tools types [2]. It is now understood as one of the key sites for understanding the expansion of the recently reassessed Initial Upper Paleolithic (IUP) into Eurasia [3, 4]. Although often discussed, the nature and significance of the techno-typological high variability within the IUP remains still unclear. Investigating how stone and bone tools in the IUP were used and what they were used for may help to better understand the co-existence of Middle and Upper Paleolithic technologies and typologies in the same archeological horizon. It will also help us to characterize human occupation dynamics during the onset of the IUP. Located in the Balkans, the site of Bacho Kiro represents one of the most important case studies in this discussion. Since 2015, reopened excavations have uncovered new archeological materials from two main excavation areas, Niche 1 and the Main Sector, allowing detailed examination and re-analysis of both bone and lithic assemblages from well controlled contexts. Here we present the preliminary results of lithic use-wear analysis from the Bachokirian Layer I (ex.11), uncovered on the newly excavated material. Use-wear analysis on lithic tools was carried on a sample drawn to reflect the general technological characterization of the assemblage; therefore, the selected tools for use-wear analysis include artifacts from all different technological categories, such as chips, flakes, blades and tool. Unmodified and retouched tools were also included. Our functional interpretations result from combining qualitative and quantitative analysis, and results from the lithic use-wear analysis show that evidence for tool use is mainly present on blades with unmodified and retouched edges. While unmodified blades show traces diagnostic of wood working, different types of retouched blades seem to have been designed and used intensively (e.g. long-term use) to work different materials, including bone. This is consistent with the bone tool assemblage, which includes complete tools, reworked pieces, and waste fragments. All of these components are associated with manufacture, by scraping or grinding, using lithic implements. Here we also aim to present how complementary analysis are being conducted on the rich bone industry in order to obtain a more complete understanding of site occupation and function.

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## Postnatal developmental interactions between the hominoid cranial base, suprahyoid muscle complex and the mandibular symphysis

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Postnatal development of the human mandibular symphysis is posited to link with variation in vocal tract anatomy, suprahyoid muscles and hyoid position [1]. The distinct modern human pre/postnatal globularization phase of the brain/cerebellum [2] may also contribute to this morphology. Stable neurovascular landmark configurations (LMs) of the hominoid cranial base [3] offer a reliable approach to explore 3D relationships between Foramen magnum (FM) position variation as a proxy for cerebellar expansion, the hyomandibular complex (mandible, hyoid and suprahyoid muscles) and evolutionary shape variations of the cranial base [4]. We hypothesize a postero-anterior direction of developmental events initiated by early cerebellar expansion. We measured 132 3D-(semi)landmarks describing cranial base, hyoid, mandibular and suprahyoid muscle insertion morphology in complete growth series of 57 humans and 38 chimpanzees and partial growth series of 11 gibbons, 5 gorillas and 3 orangutans. (1) Partial least square regressions (PLS) were used to assess relationships of growth patterns of the hyomandibular complex, the FM and the stable cranial base LMs: Foramen ovale (FO) Foramen rotundum (FR) and internal acoustic meatus (IAM). (2) We explored inter- and intraspecific morphology variations with General Procrustes Analysis, Principal Components Analysis and MANOVA. (1) Inter-specific PLS indicate a strong correlation (RV coeff=0.93,  $p < 0.001$ ) between stable cranial base LMs, the hyomandibular complex and FM. Intra-specific correlations are also strong (human RV coeff=0.739, chimpanzee RV coeff=0.724, both  $p < 0.001$ ) but ontogenetic variations of the FM and hyomandibular complex differ within each species: The human FM shifts downwards in relation to the cranial base and the mandibular symphysis rotates around the Foramen mentum (Fment) of the mandible. Hyoid position shifts antero-inferior relative to FR and rotates parallel to the stable LMs. The posterior digastric insertion and mastoid process shift laterally whilst the anterior digastric insertion displaces anterior to Fment. The chimpanzee FM shifts postero-superior whereas both the symphysis and Fment shift anterior relative to the cranial base. Hyoid orientation remains stable but it displaces postero-inferiorly to the cranial base. Fment and anterior digastric insertions both displace anteriorly to the stable LMs. With the exception of the specialized gibbon hyoid shape (PC3=5.4%), other apes vary like chimpanzees. (2) We observe significant variation in cranial base shape and size (PC1=40%,  $p < 0.002$ ) in very young children (<1 year) compared to older ones (>2 years). The inferior shift of the FM is accompanied by a lateral shift of the mastoid and styloid processes and the carotid canals relative to the stable cranial base LMs. In chimpanzees, the FM is the only variable neurovascular structure; styloid and mastoid processes and carotid canals retain size and shape relative to each other and to the stable LMs. The hypothesis that globularization initiates postero-anterior knock-on of developmental events seems plausible. Variation of the FM position due to cerebellar expansion, variation in inner ear position [5] and size and shape of the internal carotid arteries could influence the position of neurovascular structures of the Pars petrosus and the morphology of the tympanic plate, styloid and mastoid processes. Suprahyoid muscle insertions in turn have an effect on the hyoid position and orientation. This leads to variations in how these muscles and the tongue, anchored to the hyoid, act on the developing mandible, resulting in the uniquely modern human morphology. We consider posterior cranial base variation a good candidate to explain morphological variations of the vocal tract and mandible between humans and apes. Understanding the posterior cranial base may facilitate predictions in fossil hominins for their suprahyoid muscle configuration and hyoid position and orientation.

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## A comparative investigation into Neandertal bone tool manufacture and use

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The discovery that Neandertals made specialized bone tools [1], previously thought restricted to modern humans, adds to a list of behaviors that both Neandertals and modern humans exhibited. Five nearly identical shaped and worn rib fragments interpreted to be *lissoirs* (a term that means “smoothers” from the French typology), have been found in three separate archaeological deposits at two late Middle Paleolithic sites in southwest France, Pech-de-l’Azé I and Abri Peyrony. Similar bone tools have been found in a wide variety of contexts across time and space and are even used by craftspeople today. Modern *lissoirs* are used for working leather, and because the bone tools in the Paleolithic show similar morphologies and wear signatures to the modern tools, it has been proposed that the Paleolithic *lissoirs* were also for working animal skins. Little research has focused on the various aspects of Paleolithic *lissoir* manufacture and use [2]. Here, I seek to form a higher-resolution picture of Paleolithic *lissoir* technology by comparing the variation and standardization of the Middle Paleolithic *lissoirs* to those of the Upper Paleolithic.

A comparative approach is key for assessing whether or not the technologies in the different time periods and regions are similar in terms of manufacture and use. I accomplish this using complementary qualitative and quantitative methods at both macro- and microscopic scales. The artifacts in this study span a temporal range from the late Middle Paleolithic to the early Aurignacian and through the final Gravettian, and they originate from sites in France (n=217) and Russia (n=6). The microscopic analyses confirm that the Middle Paleolithic *lissoirs* are formal bone tools due to the presence of manufacturing traces on all five artifacts. Additional evidence comes from a comparison of the Middle Paleolithic *lissoirs* to unmodified ribs preserved in the same layers, which show distinctive surface textures. Upper Paleolithic *lissoirs* are typically made on split ribs and smoothed on all surfaces. Conversely, Middle Paleolithic tools are made on unsplit ribs, a variation only represented in approximately 6% of the Upper Paleolithic examples. Techniques for shaping are consistent between Middle Paleolithic and Upper Paleolithic *lissoirs* and include scraping and grinding. Material wear is similar on a macroscopic scale, while microscopic wear across all artifacts is somewhat variable, but generally indicates use on a soft, supple material such as animal skin. The results indicate that while Middle and Upper Paleolithic *lissoirs* were used in similar ways, manufacturing procedures were sometimes different. Generally, Middle Paleolithic *lissoirs* were expediently made with little investment in the production process. In contrast, Upper Paleolithic *lissoirs* are often highly processed. This comparative approach lends nuance to our understanding of the behavioral diversity in Neandertals and Upper Paleolithic human groups.

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## Genomic analyses of the 34,000-year-old Salkhit individual from Mongolia.

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In recent years, the sequencing of many ancient early modern human genomes from West Eurasia has provided insights into the human population history in Europe [1]. In contrast, only four genomes from early modern humans in Siberia and one in East Asia have been generated, which limits our grasp of the genetic history of early East Eurasians [1]. Here, we present the genomic analyses of a hominin skull cap discovered in 2006 during mining operations in the Salkhit Valley, Northeastern Mongolia [2]. To our knowledge, the specimen remains the only Pleistocene hominin found so far in the country. Discovered outside any archeological context, the age and the ancestry of the specimen have been debated since its discovery and the presence of peculiar morphological features has led to potential affiliation to archaic hominin groups [3], [4]. We used a compound-specific radiocarbon dating approach to determine the age of the Salkhit individual to 34,950 - 33,900 Cal. BP (at 95% probability), placing the specimen in the Mongolian Early Upper Paleolithic period. We also determined its complete mitochondrial genome (mtDNA) and showed that it belongs to the modern human haplogroup N which is widespread in Eurasia today [5]. Nuclear analyses of the specimen show that the Salkhit individual was a female modern human. To investigate her relatedness to archaic hominin and ancient and present day modern humans, we used hybridization capture of 3.9 million single nucleotide polymorphisms across the nuclear genome. We use  $f_3$  and  $D$  statistics to show that she was closely related to the 40,000-year-old Tianyuan individual from China but shares more alleles with Western and North-Eastern Eurasians than does the Tianyuan individual. Using an admixture graph, the Salkhit individual is positioned as an ancient East Asian with some genetic contribution from West Eurasian. This scenario underlies an unexpected genetic link between East and West Eurasians after their major split. Using a new method to identify archaic introgressed DNA in ancient genome data, we estimate Neandertal ancestry in the Salkhit individual to ~2%, and show that this ancestry is contained in longer DNA tracks than those of present-day Eurasians – as expected given the age of the specimen. We also show that approximately 0.2-0.3% of the Salkhit genome is derived from Denisovans and identified longer tracts (>0.2 cM) of Denisovan ancestry in the Salkhit and other ancient East Eurasians genomes than in present-day East Eurasians genomes. This is the first evidence of Denisovan ancestry in Upper Pleistocene modern humans in East Eurasia. It is in sharp contrast to West Eurasia where we found no evidence for Denisovan introgression at the same resolution in early or later modern humans. The genome of the Salkhit individual provides further evidence for a complex population history of Pleistocene modern humans across Eurasia involving population substructure, migration and admixture. Those results emphasize the mosaic of events that shaped the genetic landscape of modern human since the Upper Pleistocene.

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## Carcass processing with bone tools: a multidisciplinary approach

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Strategies of anthropic exploitation of animal carcasses are in close relation with human evolution. Animals constitute a nutritional source -meat, marrow and fat- and they also provide other organic elements as hide, bones, horns, antlers, etc. Bones have been used as technological raw materials since the Early Pleistocene in Africa and since the Middle Pleistocene in Europe and Asia [1, 2]. According to previous studies, large taxa bones are chosen in order to shape tools in some sites and they may be related to *in situ* butchering [3]. Nevertheless, the identification of bone artefacts is usually problematic due to the characteristics of the assemblage and the presence of other agents -carnivores, trampling, etc.- that create pseudo-tools. In many cases, the criteria of identification of bone tools in Middle Pleistocene sites is not clearly defined.

An experimental protocol was designed in order to explore this issue and develop an interdisciplinary methodology for the recognition of unmodified and retouched bone tools. The first step was the anthropic bone breakage of green bovid bones. The technique used was direct percussion on an anvil with two different quartzite percussors: a hammerstone and a chopper. The aim was, first the nutritional marrow obtention and second, the technological exploitation of resulting long bones fragments. Then, after the marrow's removal, some of the obtained shaft fragments were used unmodified in skinning, defleshing and disarticulation activities on a red deer. Others were retouched by direct percussion with a quartzite hammerstone and then used for the same activities. Selection criteria were related to variables as size and morphology of the tool and the working edge. Bone tools produced diverse degree of success in the different activities involved in carcass processing. Skinning and disarticulation were proved as difficult tasks, but we obtained appropriate results on defleshing and filleting with both simple and retouched bone tools.

This faunal assemblage -including unmodified and retouched bone tools, bone fragments resulted of bone breakage and butchered red deer bones- is being studied with an interdisciplinary approach involving zooarchaeology and taphonomy, prehistoric technology and traceology. Data about selection criteria of experimental bones used as tools, such as dimensions and morphology, is going to be convenient in the identification of archaeological bone artefacts. Thus, the created reference collection is used to establish clear criteria for the characterization of anthropic bone breakage, as well as the resulting bone tools -simple or retouched- and the presence of bone artefacts in osseous assemblages from European Middle Pleistocene sites. Results will increase our current knowledge on the early Palaeolithic bone tool use and on the hominins' subsistence strategies.

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## Evidence of social support revealed by healed trauma in human foot bones from Manot Cave, an Early Upper Paleolithic site

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Recent archaeological excavations at Manot Cave, an Early Upper Paleolithic (EUP) site in the Western Galilee, Israel, retrieved the remains of a partial left foot of a young adult, including the talus, the calcaneus, the cuboid and the first, second and fifth metatarsals. A healed fracture was observed on the second metatarsal. The pedal bones are dated to 38 and 34 kya. These bones most likely originated from a burial that partially slid down the talus, as all bones are from the left side, and all demonstrate a similar color and taphonomic condition. Additional artifacts in close proximity to the bones include marine mollusks, [two Cowries shells (*Erosaria* sp. and *Zanaria pyrum*) and *Columbella rustica*], and a large number of flint tools (including four el-Wad points, two of which were made on non-local flint). The aims of the current study were to morphologically and metrically characterize the EUP foot bones, and to investigate their population affiliations (Neanderthals vs. AMH and modern humans). Additionally,  $\mu$ CT images were used to verify a suspected injury of the second metatarsal and to identify the type of and likely cause of the injury. The shape and size of the Manot pedal bones indicate an overall modern morphology for all elements, however several Neanderthal-like characteristics were also noted. Imaging analysis confirmed the existence of a healed traumatic fracture of the second metatarsal with the plantar third of the base misaligned with the shaft, and a fracture line on the lateral side. Furthermore, a bone flake on the dorsomedial side of the shaft indicated forced contact with the hallux. These features are consistent with a fracture known as 'Lisfranc's fracture,' most probably caused by an impact to the dorsum of the foot. This injury usually leads to ligamentous instability and collapse of the transverse and longitudinal arches, causing severe walking difficulties. Full recovery requires rest and immobility for several weeks. As suggested by previous studies examining healed trauma in prehistoric individuals, the long-term survival of individuals with limited mobility required a supportive social system [1]. Accordingly, the survival of this individual indicates a supportive community at Manot Cave.

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## Facial fluctuating asymmetry tracks genomic diversity among gorilla subspecies

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Facial fluctuating asymmetry (FA) is the non-directional deviation from bilateral symmetry in the facial skeleton. It is interpreted as an indicator of developmental instability, including exposure to environmental stressors and/or inbreeding. Genomic analyses show that mountain gorillas exhibit tracts of homozygosity indicative of recent and extensive inbreeding, exceeding that observed in all other gorilla subspecies, including closely related grauer gorillas and even the most inbred human populations [1]. Here, we use geometric morphometric techniques to assess intra- and interspecific variation in facial asymmetry among three gorilla taxa (Virunga mountain gorillas – *Gorilla beringei beringei*; grauer gorillas – *G. beringei graueri*; western lowland gorillas – *G. gorilla gorilla*). We test whether mountain gorillas exhibit higher levels of facial FA compared to other taxa, reflecting genetic instability in the population. We used Viewbox 4 software (dHAL) to place 156 homologous landmarks and curve semilandmarks on 48 3D models of crania derived from computed tomography and surface (laser and white structured light) scans. MorphoJ was used to conduct separate Procrustes ANOVAs by taxon and sex, with the factor “individual” reflecting symmetric variation; the factor “side” reflecting directional asymmetry (DA; consistent variation in one direction); and the interaction between “individual x side” reflecting FA [2,3]. The effect of error was minimized via repeated measurements of all individuals, calculated as the residual variation in the Procrustes ANOVAs. We found that symmetric variation, DA, and FA are significant in all three taxa ( $p < 0.001$ ). We followed Gomez-Robles et al. [4] to assess the proportion of shape variation explained by each variable among species and sexes. Symmetric variation explains the highest proportion of the total variation in the sample, while FA explains the highest proportion of asymmetric variation. As predicted, mountain gorillas have the highest proportion of FA among gorillas – more than twice as much as western lowland gorillas – explaining 14.6% of total variation vs. 11.6% in grauer gorillas and 5.8% in western lowland gorillas. In the principal component analysis of the asymmetric component of shape variation, we find that the range of variation in mountain gorillas envelopes that of the other two taxa. The facial regions with the most extreme asymmetry are the brow and the lower face, similar to the pattern that was previously reported for grauer gorillas [5]. In the intraspecific comparison, females have a somewhat higher proportion of FA compared to males in the combined species sample (11.1% vs. 8.1%, respectively), while males exhibit a higher proportion of DA compared to females (3.2% and 1.2%, respectively). It’s worth noting that while highly significant, the proportion of variation explained by DA is comparable to that explained by measurement error (ranging from 1.8-3.4% in all analyses). The pattern reported here tracks what is known about gorilla genomic diversity: mountain gorillas, with a current population size of about 1000 individuals, show the highest degree of facial FA among great apes, followed by grauer gorillas, and finally western lowland gorillas. It is not yet clear to what extent environmental conditions might contribute to these results, as gorilla subspecies live in divergent habitats and exhibit different life history strategies. Future work will expand the sample to include other gorilla populations, and in documented samples like the Virunga mountain gorillas, incorporate associated health, behavior, and climate data to assess the relationships among environmental conditions, facial asymmetry, and fitness outcomes.

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## The Middle Stone Age Site of Negus Kabri, Asbole, Ethiopia

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This paper describes the excavation, stratigraphic context, and lithic assemblage of a new Early Middle Stone Site from Negus Kabri. Negus Kabri was discovered and excavated as part of the Asbole Research Project in the Afar region of eastern Ethiopia. The site consists of a single artifact horizon rich in lithics but with poor faunal preservation. The geological context of the deposit plus site formation data based on artifact breakage, edge damage, artifact orientations, and the ratio of large to small finds all suggest an intact deposit near the top of the Busidima Formation at the Bironita-Duma Ridge. Stratigraphically the deposits lie approximately 1m above a plateau-forming gravel, which in turn lies just above the widespread Bironita Tuff (0.64 Ma). The artifact horizon also lies 10 meters below a local tephra layer, which we call the Negus Kabri Tuff and which yielded an  $^{40}\text{Ar}/^{39}\text{Ar}$  date of  $144 \pm 23$  ka. The assemblage consists of over 3500 artifacts (> 25mm) of which over 3000 are flakes and flake fragments. The cores (N = 56) are highly standardized and dominated by centripetal Levallois technology with a few discoidal cores, cores on flakes and other miscellaneous forms. Similarly, the flakes are dominated by Levallois and discoidal technologies with some blade forms and also some bifacial thinning flakes on obsidian. The flakes tend to be broad and not elongated. Typologically, points are the most common group of retouched artifacts, and these are made preferentially on Levallois flakes. The raw materials consist of coarse grained volcanics, some cryptocrystalline silicates, and fewer obsidian artifacts. The former are available today in the plateau forming gravels. Based on cortex measures, the complete reduction sequence appears to be present for the coarsed grained volcanics. Again based on cortex measures, the other types of stone appear to have been imported already reduced. This interpretation is supported as well by the blank to tool and blank to core ratios which vary greatly by raw material type. For instance, the blank to tool ratio is seven times greater in the coarse materials than in obsidian suggesting the import of completed tool forms in obsidian. As Levallois and point technologies have long been considered a defining aspect of the Middle Stone Age in eastern Africa, this, along with the age bracket, place Negus Kabri comfortably in the known Middle Stone Age variability of the region. Negus Kabri thus adds to the relatively sparse dataset of Early Middle Stone Age sites in eastern Africa.

## Concerning body manipulation practice during the Stone Age: trepanations and ritual amputations

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The practice of surgical body manipulations can be traced to the Palaeolithic, Mesolithic and Neolithic ages. The earliest case seems to be the Upper Palaeolithic symbolic trepanation from Telmanovskaya site (Kostenki 8) in European Russia. The fragment of skull was discovered by expedition of A. N. Rogachev (Leningrad Branch of Institute of Archaeology AS USSR) in 1959. Human fragmentary remains were found in the 2nd cultural layer of the Western dwelling. Special attention should be devoted to the cranial fragment of adult individual (male?) pasted together from 3 pieces by restorers. Its maximal length was 83 mm, width 58 mm. In the central part of the frontal bone is presented a lesion with diameter about 10 mm. Digital microfocus radiological examination supports hypothesis of complete healing of bone tissue. During the Mesolithic age surgical operations could be used for passage rites as proven by the case of woman 24-25 years buried the Mursak-Koba site (Crimea peninsula, excavated by S. N. Bibikov, A. N. Zhirov, 1936). New radiological study confirms, that both little toes were amputated on her hands when she was teenager. Then around 20 years old (being married?) she got an external, "symbolic" trepanation in the posterior part of the left parietal bone. The osteological collection from the Museum of Man in Paris still has no analogies in the Old World regarding the representation of ancient trepanations. New description of skulls with traces of intravital trepanations was provided [1]. Two categories of objects from the Neolithic collection were described: trepanned skulls and bone plates (rondelles), which represent practice in Lozere and Paris regions. We have evidence of a large group of people, who lived their lives after a most severe surgical intervention, which could have led to their disability. Most likely these operations affected only the skull, as brain operations were not yet performed at this time. But especially, given the size of trepanations, the risk of complications was enormous. Bleeding from the venous sinus, diploe bleeding, infection, meningocele, cognitive deviations in case of an operator error - this is a list of dangers, the empirical knowledge of which did not stop the Late Neolithic inhabitants of France from trepanning. It is a very special model of behavior, which could become a connecting thread from childhood (or adolescence), including burial and the use of plates made from skulls of successfully trepanned people.

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## Retrodeformation techniques and 3D morphometric analysis of an early Holocene South American skull (Cuncaicha, Peru).

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As a consequence of the taphonomic history, many fossils and relevant specimens present missing parts and post-depositional alterations. For that reason, in spite of the great effort invested in their recovery and preservation during the archaeological excavations, they are left out from the morphometric analysis. Therefore, they cannot be used for discussing human variability and evolutionary processes. This is especially the case for South America, where the early Holocene specimens are scarce, and some of them are incomplete and/or present some changes as a result of post-depositional alterations. We present here the first virtual reconstruction of an early Holocene South American skull that was recovered from the excavations at Cuncaicha rock shelter in the south of Peru (9240-8770 calibrated years BP) [1]. The skull is composed of 20 fragments that were scanned in the Paleoanthropology Department at the University of Tübingen. A virtual anatomical reconstruction was conducted by using Avizo and including skull reference models from the Andes. As the cranial vault presents a strong alteration resulting in a lateral distortion that affects the whole vault shape, retrodeformation techniques were applied for modeling post-depositional changes [2]. In spite of the large degree of completeness of the skull (approx. 80%), there are some missing parts that were estimated by mirroring them from the opposite preserved side of the skull. This allowed conducting 3D morphometric analysis from the whole skull by comparing it with other early and late Holocene specimens from South America (N=500), by taking into account the symmetric component only. Shape changes were studied by running between-groups Principal Component Analysis. The results are discussed together with a previous 2D morphometric study of the facial variation that allowed establishing associations with specimens from Lagoa Santa in Brazil, supporting previous claims of morphological similarities among the early settlers of the continent [3]. Such craniofacial patterns were interpreted as the retention of some ancestral features among some of the early South American populations.

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## A deeper look into the Mousterian Hearths at Kebara Cave, Israel

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Aspects of use and control of fire by Neanderthals has generated heated discussions [1]. A crucial aspect to our understanding of Neanderthal pyrotechnology is understanding the features related to fires that they left behind, including intact hearths and associated combustion residues that may have been modified syndepositionally by maintenance activities but also by post-depositional reworking and chemical alteration. We may study burnt objects from a site (bone, lithics) but to obtain a more complete understanding of Neanderthal 'fire use', we must study in detail the primary/primeval aspects of Neanderthal pyrotechnology, the deposits themselves at a microstratigraphic scale [2]. At the site of Kebara Cave, hearths and burned residues have been previously studied at the microstratigraphic scale using micromorphology and phytolith analyses [3], but direct links to concurrent macroscopic analyses, including identification of diagenetic minerals using FTIR have until recently been limited. This study links the macroscopic to microscopic records by applying  $\mu$ -XRF and  $\mu$ -FTIR directly to micromorphological samples to characterize the lithologies, composition, mineralogy, and structure of hearths. The work focuses on samples collected in 2006 after the main excavations (1982-1990) in order to evaluate their depositional and post-depositional histories and their reflection on Neanderthal and modern human fire-making and use practices.

The site of Kebara, located along the western side of Mt. Carmel, ~30 km south of Haifa, Israel, is formed in a Cretaceous limestone reef complex at an elevation of ~60 m asl. Excavations from the 1930s to 1990s exposed deposits with Natufian, Kebaran, Upper and Middle Palaeolithic (UP, MP) implements, and a Neanderthal skeleton. Burnt Mousterian flints yielded thermoluminescence (TL) dates between 48000 and 60000 BP, whereas numerous radiocarbon dates point to the transition from Middle to Upper Palaeolithic between 49/48 and 47/46 k radiocarbon calibrated years before present [3].

Samples for this study were collected from MP and UP hearths in various locations and layers in the cave, and include single hearth structures, thin superposed/stacked hearths, and ashy layered dumped hearth materials. They were removed as intact blocks that were dried and impregnated with polyester resin, from which petrographic thin sections (50x75 mm) were made.

The integrated microscopic results show that broad spatial patterns in the chemical alteration of the deposits are generally confirmed; however, several samples show evidence of multiple phases of alteration that indicate shifting chemical environments. For example, dahllite precipitation in voids parallel observations previously made at Tabun Cave, which suggest that at both sites, cycles of renewed phosphatization may have occurred several millennia after the initially more "severe" diagenetic alteration. Bands and areas that appear uniformly white in the field also contain multiple phases of diagenesis. The work also provides new information about the dark, organic-rich layers, some of which form the basal portions of hearth sequences. These layers are enriched in copper and in some cases may be associated with magnesium. Some dark layers exhibit evidence of phosphatization prior to the deposition of overlying ashes.

The combined use of microstratigraphic documentation in the field, micromorphology,  $\mu$ -XRF and  $\mu$ -FTIR is a robust approach for deconstructing chemical partitioning within the thin section, which ultimately may reflect on human activities that previously were not visible in the field or using only a petrographic microscope.

Alexander von Humboldt Society, Deutsche Forschungsgemeinschaft, US National Science Foundation, Matthias Czechowski

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## What about taphonomy for prehistoric stone tools? The effect of freeze and thaw cycles on use-wear and residues

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Archaeological sites are submitted to various taphonomic processes that have been studied mainly in order to understand the formation processes of sites, modifications in the spatial distribution of lithic artefacts or bone materials at particular sites, or preservation of bones and other organic material. Post-depositional phenomena may however also modify stone tools, altering their surface and edges and thus affecting the functional wear that may be present [1]. Alterations of stone tools have been observed since the beginning of use-wear analysis. Indeed, alterations are known to possibly cover, destroy or mimic use-wear traces, thereby hampering a reliable functional study and a loss of essential information [2]. Some time periods and regions prove to be more affected by alterations than others, while experiences have also shown that raw materials tend to react differently to specific taphonomic processes [3]. An improved understanding of functional data, in particular for Palaeolithic archaeological assemblages, requires a better comprehension of alteration phenomena in order to strengthen interpretations of altered assemblages or even render their functional data accessible. This study focuses on alterations produced by repeated freeze and thaw cycles which are frequently attested on Upper Palaeolithic sites in Europe. Thanks to a climate chamber, we succeeded in the reproduction of natural freeze and thaw cycles. Flint tools, used on wood, meat, bone and hide were buried in water-saturated loess and submitted to repeated temperature fluctuations between -20°C and 20°C. Tools were excavated after 50 cycles. We obtained an alteration polish which is frequently observed on prehistoric stone tools [4, 5] and which may hinder use-wear traces. The process also transformed and/or detached residues from the tool surface. In some cases, the residues proved to protect the flint surface against alterations. The results of this methodological study support the relevance of further explorations of how freeze-thaw cycles affect and possibly transform use-wear traces and residues. An improved understanding of these alterations not only improves present-day use-wear and residue methodologies, but also paves the way for functional analyses of altered archaeological assemblages that are now often considered as having little potential for functional studies.

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## Biological evolution of *Homo sapiens* in response to medical and technological transitions: The shifting trade-off model

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Throughout the history and prehistory of *Homo sapiens*, cultural transitions repeatedly altered lifestyle, the conditions of survival and reproduction as well as the modes of biocultural inheritance. Cultural changes thus have been important drivers of biological evolution in our species [1]. With the advancement of agriculture, housing, medicine, and other technologies, natural selection has been continually reduced. Has this also reduced evolutionary change in our lineage? Do humans still evolve in modern industrial societies, and if so, can we predict how human biology evolved in the last centuries or will continue to evolve? It is tempting to assume that evolutionary change in humans has reduced or even stopped as a result of reduced natural selection. For instance, David Attenborough claimed that "... we've stopped evolving ... as soon as we started being able to rear 95–99% of our babies that are born." [2]. I will show that this is not true: by shifting existing fitness trade-offs, reduced selection pressures have even triggered new evolutionary changes. Many anatomical, physiological, and behavioral traits evolved by trading off fitness for different functions or life stages. The resulting "evolutionary compromises" optimize average fitness in a population and may entail individuals that appear to be maladapted for one or more of the involved functions. A typical example is pelvic form: a wide pelvis is beneficial for childbirth but detrimental for pelvic floor stability; human pelvic form thus evolved as a compromise that trades off these two opposed selective forces [3]. Drawing from epidemiological and genomic data, I also show how such trade-off dynamics underlie the evolution of sickle cell disease and autoimmune disorders in humans. In modern societies, such opposed selective forces have been differently relaxed by technological or medical advances; this, in turn, has disrupted the evolutionary equilibria and triggered novel evolutionary changes [4]. I will outline this theory and use it to show how medical treatment of obstructed labor, anemia, and autoimmune disorders has evolutionarily affected human childbirth, sickle cell disease, and immune function. Furthermore, I will extend this theory to the trade-off between ecological and social selection. In particular, I show how the antagonism of ecological and sexual selection has determined the evolution of sexual dimorphism in human stature. Using global demographic and biometric data, I demonstrate how the relaxation of ecological selection has altered the pattern of sexual dimorphism in human body height. Outside of biology and medicine, researchers from various disciplines are wary of evolutionary considerations of human biology and health owing to possible linkages to racist or eugenic standpoints [5]. At the end of my talk, I will thus briefly discuss ethical and political challenges involved in these studies and address the question whether the human evolution community should engage more in studies of modern human dynamics and evolutionary medicine.

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## New Excavations at Crvena Stijena, Montenegro: First Results

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Crvena Stijena ('Red Rock') is a rock shelter in Montenegro with an exceptionally long and well-preserved sequence of archaeological deposits spanning the Middle Paleolithic to the Bronze Age. It is located in the Dinaric Alps in the southwestern part of the country, 700 meters a.s.l. and 32 km from the present-day Adriatic coastline. Half of the sequence (10 meters in depth) is older than 40 kya, as it is capped by the well-dated Y5 tephra attributed to the Campanian Ignimbrite eruption [1]. The site was excavated in the 1950s and 60s, during which a deep sounding was placed through the Paleolithic deposits. The resulting lithic collections have made Crvena Stijena a type-site for the southern Balkans [2]. Subsequent excavations by Whallon and colleagues [3] from 2004-2015 produced the first extensive absolute chronology for the site, assessed the stratified hearths and macrobotanical remains, and documented the extensive faunal record [4]. In 2017, a new collaboration was formed between the University of Minnesota, the Center for Conservation and Archaeology (Ministry of Culture), Montenegro, and the National Museum of Montenegro. The goal of this project is to excavate the Middle Paleolithic levels in order to characterize Neanderthal behavior, particularly with regards to pyrotechnology. We are testing the controversial hypothesis [5] that Neanderthals used fire only when it was available in their environment. We are applying a number of analytical techniques to reconstruct pyrotechnological behaviors, such as micromorphology, mineralogical analysis of sediments and heat-altered artifacts, and archaeomagnetic analysis of combustion features. Paleoenvironmental reconstruction is based upon faunal analysis, phytolith analysis, biomarker analysis from sediments, and charcoal analysis. Preliminary results from micromorphology indicate that the combustion features in the lower layers (e.g. XXIV) are in situ and well preserved. They are composed almost entirely of fragmented, burnt bone; wood ash; and charcoal. FTIR analyses support the identification of wood ash in the combustion features and demonstrate that some of the calcined bones were heated above 500° C. Analysis of lipid biomarkers from the same combustion features suggests that terrestrial plants are the main source of the charred matter. Anthracological analyses show that the charcoal is dominated by *Pinus nigra-sylvestris* (Black Scots Pine). The overall species composition of the charcoal indicates that the wood comes from cryophilous pine forests, typical of mid-altitude Mediterranean mountain pine forests. Analysis of the fauna shows extensive evidence of human interaction, with moderate to high frequencies of cut-marks on a wide range of skeletal parts and on all of the main ungulate taxa. The ungulate fraction, dominated by red deer, is remarkably consistent throughout the sequence. This suggests either that local ecological conditions were stable through time, or that the layers accumulated fairly quickly. We are thus beginning to refine our understanding of local environmental conditions during the time of occupation of the site, and of Neanderthals' responses to these conditions. The multi-analytical approach to the archaeological record that we have deployed will allow us to document Neanderthal pyrotechnological behavior within its ecological context, and develop a better understanding of the interaction between fire use and variation in site function as reconstructed from the lithic economy and faunal exploitation domains.

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## Basiscranial ontogeny comparison in *Pan troglodytes* and *Homo sapiens* and its use for developmental stage definition of KNM-ER42700

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*Homo erectus sensu lato* is the earliest fossil human species that shows modern human body proportions, an increase of brain size, as well as various other derived features. Its vast time range and geographic distribution have been linked with its observed high morphological variability. This variability, however, has also been interpreted in terms of taxonomic diversity, with some authors proposing the presence of two species. Understanding the factors that affect this variation, including geography, time, sexual dimorphism and developmental changes, is therefore imperative for the interpretation of the *Homo erectus* hypodigm. A case in point is the specimen KNM-ER 42700, whose taxonomy has been highly debated over the past years [1-2-3-5]. Recently a new reconstruction of the specimen was made[4]. One of the conclusive hypotheses that the authors suggested, after analyzing the endocranial shape of this fossil, is that this individual had a probable age at death between Mojokerto and KNM-WT 15000. In this study we aim to develop a comparative basis for assessing the developmental stage of KNM-ER 42700 based on the ontogenetic pattern of the ectocranial surface of the basicranium in modern humans and chimpanzees. A total of 33 landmarks were collected from an ontogenetic sample of modern humans (80), chimpanzees (51), and twelve individuals classified as *Homo erectus sensu lato*. Ontogenetic trajectories were analyzed, and common aspects were extracted for the purpose of discriminating age groups. A regression of size on the extracted shape variables was used to investigate common ontogenetic allometry. The basicranial development of chimpanzees and humans follows different trajectories; however, similarities are also present. The common shape component of development extracted can be used to define age groups in both chimpanzees and modern humans. The extracted shape component presents a similar ontogenetic and static-allometric pattern in these two species. The developmental stage of *Homo erectus sensu lato* specimens was attributed following these common traits. Developmental stages of *Homo erectus sensu lato* were correctly assigned for the specimens of known developmental stage. The component used for assessing developmental stage has an ontogenetic allometric component. However, this shape component can discriminate age group irrespective of size and is no longer related to size when static allometry is considered. Adult *Homo erectus sensu lato* specimens were attributed to the adult category. KNM-WT 15000 fell with the late juvenile age group, while D2700 plotted in the region of overlap between the juvenile and adult age groups and Mojokerto with the younger age groups, as predicted by their known developmental stages. KNM-ER42700 fell within the adult variability despite its incompletely fused sphenio-occipital synchondrosis. Our results indicate that KNM-ER42700 already attained an adult basicranial morphology. Thus, suggesting that its overall cranial morphology probably was not influenced by a very young developmental stage as previously hypothesized.

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## Postnatal crown formation time of three Neanderthals deciduous teeth from Northeastern Italy

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Differences in time of dental growth between Neanderthals and modern humans, as a proxy for ontogenetic diversity, have been subject of intense debate [1] in the past decades using morphology, classic histology and virtual histology. Particular attention has been paid to the permanent dentition while much less data is available for high resolution histomorphometry of Neanderthal deciduous dental crowns. Here we present preliminary results of the histomorphometrical analysis of three deciduous Neanderthal tooth crowns from the same geographic area of Northeastern Italy, spanning chronologically between 70 and 40 ka BP. De Nadale 1 is a lower right deciduous first molar exfoliated crown, from the De Nadale Late Middle Palaeolithic cave located in the Berici Hills (Vicenza, Northeastern Italy) with a minimum age of 70.2 ka BP [2]. Fumane 1 is a lower left deciduous second molar exfoliated crown, from the Mousterian levels of the Fumane cave in the Lessini Mountains (Verona, Northeastern Italy) dated before 47.6 ka cal BP [3]. Broion 1 is a still unreported upper deciduous left canine, possibly exfoliated, from the final Mousterian deposits of Riparo Broion (Vicenza, Northeastern Italy), preliminarily dated before 40 ka BP. The three sites are situated within a ~55 km radius of each other. Sectioning, imaging and enamel histological analyses were conducted at Museo delle Civiltà (Rome). Teeth were embedded in clean EpoThin (Buehler) resin, cut using a Low Speed Isomet microtome (Buehler) with water as lubricant and polished using 1 µm diamond paste (DP-Suspension M, Struers). Final sections were 200-250 µm thick to allow both transmitted light investigation and future LA-ICPMS chemical analysis. All the crowns are worn, making precise prenatal and total crown formation time estimates difficult. However, the neonatal line is present in all the three specimens, thus allowing a precise estimate of the postnatal crown formation time. Preliminary assessment of the enamel daily secretion rates was performed and shown to be very similar to the data reported in literature [4] for modern humans. The postnatal crown formation time of the deciduous first molar De Nadale 1 lies within the modern human variability, while the deciduous canine Broion 1 and the second deciduous molar Fumane 1 show a consistently shorter postnatal crown formation time when compared with the known archaeological [5] and modern [4] human range of variability. Despite the small sample size, the results of this study suggest there may be significant differences in some deciduous total crown formation times between Neanderthals and modern humans that may in the future contribute to the ongoing debate about ontogenetic diversity.

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## Brain lateralisation in humans and apes – insights from endocranial casts

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Brain lateralisation is commonly interpreted as crucial for human brain function and cognition. Several evolutionary hypotheses have linked human brain asymmetry to handedness, tool use, and language, and brain lateralisation for sensorimotor functions is widely assumed to provide increased neural capacity, key to the evolution of higher cognitive abilities in the human lineage. However, as comparative studies among primates are rare, it is not known which aspects of lateralisation are really uniquely human. Here, we quantify aspects of brain shape asymmetry based on endocranial imprints of the braincase in humans, chimpanzees, gorillas, and orangutans. Due to the tight interactions between the brain, connective tissues (meninges), and neurocranial bones during growth, such endocasts closely reflect the size and outer shape of the brain, including the magnitude and pattern of brain asymmetry. We use computed tomography scans of 228 individuals to generate digital endocasts and to measure 935 three-dimensional landmarks and sliding semilandmarks for a geometric morphometrics analysis. Importantly, our methodological approach neither requires the specification of an anatomical midplane (which itself can be asymmetric), nor an orientation or mapping to any reference system. We show that the average pattern and magnitude of shape asymmetry is shared across humans and non-human apes. Most individuals of the analysed taxa display a combination of a left occipital and right frontal petalia (protrusions of the cerebral cortex into the internal table of cranial bone), as previously described for humans. Additionally, this directional asymmetry pattern is associated with differential projections of the temporal poles and cerebellar lobes. Our results emphasize the need to disentangle shape asymmetry from absolute size differences, which might have concealed the shared asymmetry pattern among hominids in earlier studies. Individual variation in endocranial asymmetry around this average pattern is pervasive and most pronounced in humans. Chimpanzees show a reduced magnitude of both symmetric and asymmetric shape variation, which challenges interpretations of human “uniqueness” inferred from a comparison with chimpanzees only. Humans, however, have a weakened and decoupled pattern of directional asymmetry compared to non-human apes, the opposite of what we expected. Based on these findings, it is important to note that a left occipital petalia combined with a right frontal petalia found on a fossil hominin endocast does not necessarily imply a modern human pattern of brain lateralisation. Intriguingly, our findings suggest that instead of a unique spatial asymmetry pattern with strong directionality, humans display a uniquely variable and decoupled pattern of – otherwise conserved – endocranial asymmetry. This likely reflects increased functional and developmental modularization of the human brain.

## Studying bone microstructure in primates: shedding light on some methodological constraints

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Behaviour does not fossilise, yet, with the help of advanced imaging techniques, such as  $\mu$ CT, we could reconstruct the locomotor behaviour of extinct species. This approach is based on the complex relationship between mechanical loading and bone microstructural adaptations observed in extant primates, yet progress in this field is still hampered by methodological constraints and a lack of a golden standard. Advances occur iteratively as each new study addresses the flaws of earlier protocols. Small methodological studies could accelerate this process. Our study focusses on methodological influences on the quantification of bone parameters. We obtained  $\mu$ CT data for the third metacarpal (MC3) and capitate of 9 bonobos (*Pan paniscus*), 5 gibbons (*Hylobates lar*) and 2 gorillas (*Gorilla gorilla*). Rather than using a cylindrical volume of interest (VOI), we used an in-house developed computer routine to isolate the entire trabecular region. Following a protocol based on the 'whole-epiphysis method', we limited the 'length' of the MC3 epiphyseal VOIs at the cut-off point where the epiphysis transitions into the diaphysis [1]. The images were then converted from grayscale to binary by choosing a segmentation threshold for each bone. Using CTAn software, we quantified the microstructure of the entire capitate and both epiphyses of the MC3. We found that several relevant architectural parameters, such as degree of anisotropy (DA), bone volume fraction (BV/TV), trabecular number (Tb.N) and trabecular thickness (Tb.Th), were sensitive to methodological constraints. The whole-epiphysis method was created as an alternative to using a simple VOI, as it was found that the size and location of these VOIs could influence the measured bone parameters, obscuring functionally relevant variation and inhibiting interstudy comparison [2]. However, we found that constraints in the whole-epiphysis method could similarly limit comparison between studies and between and within species. In this method, the cut-off point is determined by the external bone shape, without considering the presence of a region containing both trabecular structures and a medullary cavity (low Tb.N, low BV/TV, high DA). To qualitatively assess the influence of the cut-off point on the data, we varied the length of the distal epiphysis of a *Pan* MC3 and confirmed that increasing the VOI length decreases the Tb.N and BV/TV and increases the DA. Scan resolution is another influence that could greatly impede interstudy comparisons. During the segmentation process, pixels on the bone interface that partially contain bone are either considered bone or not-bone. At lower resolutions, these 'partial pixels' greatly affect smaller architectural features such as thin trabeculae, intertrabecular spaces and pores. To investigate this effect, we scanned a gorilla capitate at 20 $\mu$ m and resized the image to 40 $\mu$ m, 60 $\mu$ m and 80 $\mu$ m, to obtain four scan resolutions. Prior studies have described how a lower resolution decreases the Tb.N and increases the Tb.Th and DA by preferentially eroding the trabeculae that are not aligned with the loading direction [3][4] (these thinner structures are more affected by partial pixels). We were able to confirm this, but found that the Tb.Th is increased by an additional thickening effect, likely the deletion of pores and intertrabecular spaces. We also found that the effect of resolution on BV/TV was determined by the difference in sensitivity with which Tb.Th and Tb.N increase and decrease, respectively, as BV/TV is proportional to these parameters. Understanding the methodological influences on bone microstructural analysis allows researchers to make more informed choices and provides a more solid basis for functional interpretations. Until there is a uniform standard, more small-scale methodological studies are needed to bring us closer to our goal of using fossil remains to ascertain the locomotor behaviour of extinct species.

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## Endostructural and periosteal variation in the humerus in juvenile Pleistocene individuals

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Neanderthal humeri are characterised as exhibiting considerable bilateral asymmetry, which is thought to reflect adaptation to uni-manual tasks such as hide scraping [1], even though broad trends of cross-sectional geometry are considered to be comparable with Upper Palaeolithic individuals. Juvenile remains however often exhibit considerable robusticity, though much of this is thought to relate to greater body mass [2]. It can be said that Neanderthal arms seem to have grown at a faster rate than those of modern humans [2]. This presentation is a progress report on a project to characterise this phenomenon throughout ontogeny using a whole bone approach, including data on specimens (Elesivichi, Kostenki 12 and Jebel Irhoud 4) which have not previously had their internal morphology examined in detail. CT and microCT scans of the humerus from Middle and Upper Palaeolithic juvenile hominins (n=14) were segmented through a machine-learning approach using the Weka segmentation toolbox in ImageJ [3]. Two of the humeri (Irhoud 4 and Weimar Ehringsdorf G6) were both partially covered in breccia and also required extensive virtual re-alignment of fragments in Avizo after segmentation due to crushing during fossilisation and manual reconstruction artefacts. The cortical bone was then manually separated from the trabecular bone for subsequent analyses, due to the irregular nature of this during growth. Variation in endostructural and periosteal growth of the humerus was characterised from CT and microCT scans using a whole bone approach, known as morphometric mapping [4]. Briefly, using a custom Matlab script, properties of cortical thickness and periosteal curvature are automatically extracted at a high density from every cross section between the 20-80% margins. These are then unwrapped into false colour maps which are then compared using conventional multivariate statistics. Cortical bone thickness and cross-sectional properties (including J, I<sub>max</sub>/I<sub>min</sub> and %Cortical Area) along the length of the shaft were compared with a sample of Holocene individuals as a baseline. It was found that Neanderthal endostructural properties mainly aligned with modern human individuals who were older dentally, suggesting a more rapid development. Upper Palaeolithic individuals were more in line with Holocene individuals. Of particular interest are Weimar Ehringsdorf G6 and Irhoud 4, which both exhibit massively thick cortices along the entire shaft. Elliptical Fourier descriptors of the external periosteal contours (following the methodology in [4]) were compared with Holocene Agrarian groups (n=95 individuals) and Terminal Pleistocene individuals from Tavoralt and Afalou Bou-Rhumel (n=18) using Principal components Analysis and Discriminant Function Analysis. It was found that Neanderthals occupied a different portion of shape space. This suggested a slightly modified growth trajectory in our Neanderthal sample. Upper Palaeolithic individuals aligned more closely with later Pleistocene individuals. This was confirmed through a phenotypic trajectory analysis, using the methodology outlined in [5], which demonstrated that Neanderthals, agrarian groups and hunter-gatherers all followed different growth trajectories, both in terms of direction and size. Future work will concentrate on augmenting our Palaeolithic sample to see if the tendencies discussed here are truly reflective of broader trends.

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## **Moving around and settling down – a methodological framework for analyzing hunter-gatherer land use**

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Modelling land use has always been a challenge to archaeologists examining prehistoric hunter-gatherer lifeways. The complex relationships between subsistence, culture and environment are eagerly discussed and modeled individually, but seldom are all these concepts brought together in a comprehensive characterization of hunter-gatherer land use. Such a characterization is, however, necessary in order to compare elements such as settlement pattern and mobility for prehistoric societies over temporal and regional borders. In the framework of the Collaborative Research Centre 806 of the University of Cologne, this project was initiated to set up a multi-proxy methodology for comprehensive, reproducible characterizations of pre-agricultural land use strategies. Based on Binfordian and Optimal Foraging theories, this contribution describes how the multitude of different archaeological and spatial analytical methods can be applied to archaeological datasets. We present a roadmap showing how to analyze, infer and predict certain concepts of hunter-gatherer land use, such as mobility or procurement strategy. This allows us to discuss how the input data – site locations, assemblage data, environmental data – not only directly determines the types of analyses that can be undertaken, but also how the reliability of the results changes throughout different modelling steps. After presenting the analyses we can apply to each different kind of dataset, we assess the quality of this roadmap, pointing out the ways biases in the input data can influence the analysis result and the interpretations drawn from them. Such an approach not only leaves us with clear-cut expectations for hunter-gatherer land use, but also allows us to judge the reliability of these expectations and therefore enables comparisons to other prehistoric societies. By examining land use using such a framework, we will be able to piece together the multifaceted picture of a crucial and, until now, rather enigmatic aspect of hunter-gatherer lifeways.

## The most recent Neandertal remains in Italy

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Italy preserves several archaeological sites with deposits dated to the Middle-to-Upper Paleolithic transition, and for this reason, it plays an important role in understanding the biocultural processes that characterized the disappearance of the Neandertal and the success of the newcomers modern humans. However, any conclusive statements is hampered by the paucity of well-preserved human remains dated to the transitional period. Indeed, as far as Italy is concerned, between 50-40 thousands years ago (kyr), only five human teeth have been discovered: one Neandertal and two modern human teeth respectively from the final Mousterian and the Uluzzian deposits of Grotta del Cavallo (Lecce); two modern human teeth from Riparo Bombrini (Ventimiglia) and Grotta di Fumane (Verona), respectively. In this study we present two new human deciduous teeth retrieved from the deposits of Riparo Broion (Longare, Vicenza) and Roccia San Sebastiano (Mondragone, Caserta). Specifically, the tooth from Riparo Broion, hereafter called Broion 1, was retrieved from layer 11 top, square AA3a. Radiocarbon dating is in progress, but layer 11, attributed to a final Mousterian, is below the Uluzzian layer Ig, recently dated ~40 kyr BP [1]. The tooth from Roccia San Sebastiano [2], hereafter called San Sebastiano 1, comes from layer 34, sector E14-E15. Radiocarbon dating of the entire stratigraphy is in progress, but preliminary evidence based on the archaeological sequence and lithic assemblages, suggests that layer 34 includes a final Mousterian lithic production. High-resolution microCT images of the teeth were obtained by Xalt micro-CT scanner, and three-dimensional digitals models were reconstructed using semiautomatic segmentation. Both teeth were morphologically described and morphometrically analysed using crown diameter measurements. Moreover, for San Sebastiano 1 we investigated the crown and cervical outlines and lateral enamel thickness. The results were compared with a sample of Neandertal, Upper Paleolithic modern human (UPMH) and recent modern human (RMH) teeth collected from the scientific literature. In terms of morphology, Broion 1 is a upper left deciduous canine with a strong buccal bulging of the crown and a concave lingual side with a cervical eminence. As far as San Sebastiano 1 is concerned, the tooth is a lower left second deciduous molar characterized by an enlargement of the bucco-distal side of the crown, and an anterior fovea bordered distally by a mid-trigonid crest. Overall, morphological description and morphometric analysis align both teeth to Neandertal. Archaeological information and paleoanthropological analysis point out that the Neandertal teeth Broion 1 and San Sebastiano 1 represent, along with the deciduous tooth Cavallo D (from the final Mousterian deposit of Grotta del Cavallo) [3], the most recent Neandertal remains in Italy currently known.

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## A notch in the hallux. Presence of pseudoepiphysis in the hallucal metatarsals from Sima de los Huesos Middle Pleistocene site (Atapuerca, Burgos)

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The presence of pseudoepiphysis in the non-epiphyseal end is a commonly reported trait in the hallucal metatarsals in recent populations. It is habitually represented by notches or clefts in the distal end of hallucal metatarsals, or in the proximal ones of the lateral metatarsals [1, 2]. This kind of non-metric structures generally has no influence over the longitudinal growth of the bone because they are remnants of a physeal structure, mostly incapable of producing longitudinal growth of the bone, due to the penetration of bone tissue through the physeal cartilage up to the epiphyses [2]. Sometimes this is related to pathological conditions, but frequently is clear that these structures represent normal stages in the physeal invasion of the primary centre into the head hallucal metatarsals as an isolated bone variant in healthy children [1]. The notches normally appear between the ages of 3 and 4 years and the final disappearance of these notches is related to the formation of the adult morphology of the metatarsals that occurs at around 15-16 years old. They can remain potentially identifiable until the completion of fusion of the cartilage and subsequent disappearance of the pseudoepiphysis due to alignment with the rest of the bone forming a completely normal adult morphology [1]. The presence of pseudoepiphysis in different consanguine individuals [3], suggests this character as a possible epigenetic trait. In the Middle Pleistocene site of Sima de los Huesos (SH) nearly 7,000 human fossil fragments, belonging to at least 28 individuals, have been recovered up to date. Using a variety of techniques, the hominin-bearing layer could be assigned to a period around 430 thousand years ago. Morphologically, these fossils represent an ancestral European population that evolved into the Neandertals [4]. From this sample, five immature hallucal metatarsals have been recovered. Two of them (AT-863 – left and AT-977 – right) display a physeal notch in the dorsal area of the non-epiphyseal distal end, i.e. pseudoepiphysis. They belonged to different individuals due to the different morphology and general size inside the variation of SH. The morphology of the proximal metaphysis of these two first metatarsals with a centrally located raised mound on the metaphyseal surface of the diaphysis suggests a biological age around of 12 years old for these two individuals. In recent populations the presence of pseudoepiphysis in the hallucal metatarsal is relatively frequent and it could be considered an epigenetic non-pathological trait. In our comparative samples (Hamann-Todd Osteological collection – recent, and San Pablo Medieval collection) the presence of pseudoepiphysis is identified in one of 14 and in eight of 15 individuals respectively. This study offers the first, and oldest, evidence of presence of pseudoepiphysis in the hominin fossil record. The existence of pseudoepiphysis in two of five different immature individuals in the SH sample, and the inexistence of this trait in the hominin fossil record, takes us to propose this character as a non-metric or epigenetic trait in this Middle Pleistocene as proposed by Manzi et al. [5] for the SH crania, suggesting all the individuals in SH could belong to a single biological population with phenetic relationships between and/or within populations.

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## Human-environment interaction in the Upper Palaeolithic of the Southern Levant

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Human adaptation to the environment and the resulting settlement patterns are a major point in the understanding of hunter-gatherer economy and subsistence, and rarely more so, than in environments including different ecotones as the Southern Levant. For the timeframe of the Upper Palaeolithic the results of a geoarchaeological study are presented investigating these processes on two different scale levels. A dataset of 129 inventories of published Upper Palaeolithic sites from the Southern Levant is used to model the settlement patterns. As an essential source-critical step an evaluation of the preservational conditions for Late Pleistocene sites is conducted through the analysis of geomorphological maps. Geomorphological and climatic results are used to reconstruct the Late Pleistocene Levantine environment, which presents itself as dominated by rising water tables and abundant fluvial sedimentation. The spatial distribution of the sites is mapped in relation to the major resources (water and raw material) to understand guiding factors in site locality choice. The Late Pleistocene Levantine environment is thus argued to be characterised by a mosaic landscape of patches with high resource availability and areas with resource depletion. Multivariate statistical evaluation is used to test the explanatory value of different environmental factors on the variability in the archaeological dataset. Particularities in site locality choice for the different cultural units are highlighted. The settlement patterns of Pleistocene hunter-gatherers are reconstructed and evaluated through an assessment of the different inventories in terms of the representation of the operational chains, the diversity of the tool assemblages, the working time invested in the production of the lithic assemblages, the caloric yield of the faunal inventories and tool curation. In general, the Upper Palaeolithic of the Levant is characterised by a stable residential mobility system adapted to the patchy but abundant distribution of resources. Only at the beginning and end of the analysed timeframe a specialisation of the inventories is notable. A stable use of the environment can be contrasted to a highly dynamic cultural development as reconstructed from sites from the Wadi Sabra in Southern Jordan. In the Wadi Sabra sites, the reconstruction of operational chains can highlight a potential knowledge transfer of carinated technology leading to increasing techno-typological variability in Post-Aurignacian industries.

## Living archaeology: Revealing plant technology in wild chimpanzees

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Archaeological evidence of how early humans selected and used raw materials for stone tools informs us about the evolutionary origins of human technology. However, organic materials, especially from plants, that likely were used by our ancestors hardly ever preserve. Thus, significant amounts of information about the origins of human technology remains invisible in the archaeological record. Studies of chimpanzee technology can provide valuable comparative insights. This study pioneers the use of traditional archaeological methods to study the use of plants associated to termite-fishing technology in three different populations of wild chimpanzees living in environments equivalent to early hominin habitats. Source plant species, raw material types, and locations relative to targeted termite mounds were recorded for populations at Gombe, Issa, and Mahale in west Tanzania. Results show that: a) chimpanzees selected particular plant species and tool materials for the manufacture of their tools; b) some source species were exploited at all three sites, perhaps for their especially suitable physical properties, like bark that is easy to peel off; c) chimpanzees living in a drier more open environment travelled almost double the distance to obtain their tool material and utilized sources more intensively, and d) the sourcing of tool material by chimpanzees leaves a scar on the source plant that can be studied well beyond the time of use. That populations selected different raw materials, despite similar raw materials available, may reflect cultural differences between chimpanzee groups. This study highlights how archaeological methods can reveal "invisible" aspects of technological behaviours. Albeit the "archaeology of the perishable" is still in its infancy, it may ultimately improve reconstructions of organic-based tool use in our ancestors.

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## Temporal lobe morphology in Neanderthals and modern humans

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Paleoneurological investigations into *Homo neanderthalensis* have largely been confined to the cranial vault with the cranial base often highly fragmentary or incomplete, limiting interpretations of the temporal lobes. Tentative interpretations from fragmentary basicrania, extrapolation and comparison with extant *Homo sapiens* suggest *H. neanderthalensis* possessed a temporal lobe that was wider but not longer than *H. sapiens*. The temporal lobe occupies the bony region of the basicranium, the middle cranial fossa, with the close spatial proximity of the fossa and temporal lobe reciprocally influenced by changes to basicranial size and shape. Description of sulcal imprints preserved on the surface of the fossa note the difference between *H. sapiens* and *H. neanderthalensis*, specifically the position of the inferior temporal sulcus and fusiform gyrus, corresponding to superolateral expansion of the temporal lobe in *H. sapiens*. In this study, Computed tomography (CT) scans were used to generate 3D digital crania in five specimens from *H. neanderthalensis* (La Chapelle aux saints 1, La Ferrassie 1, La Quina 5, Tabun 1, Gibraltar 1) and a comparative sample of extant *H. sapiens* (n = 40). Three linear dimensions were digitally measured on the endocranial surface of the fossa, approximating temporal lobe boundaries. We examined fossa dimensions relative to cranial length and width in the five fossil specimens of *H. neanderthalensis* and the average values for extant *H. sapiens*. Comparisons of relative fossa proportions indicate our results agree with previous findings that *H. neanderthalensis* had relatively wider temporal lobe (mediolaterally) not relatively longer (antero-posteriorly) compared to *H. sapiens*. Despite the limitations of small fossil sample size preventing statistical analyses, these results agree with previous findings that compared to *H. sapiens*, the temporal lobe in *H. neanderthalensis* was relatively wider but not longer.

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## Contextualising Neanderthal behaviour during MIS 3 and 4 at La Ferrassie, France: Seasonal palaeotemperature reconstructions from oxygen stable isotopes

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Exploration of the relationship between paleoclimate and hominin behaviour is central to Palaeolithic Archaeology and the study of past human lifeways. In particular, past climatic conditions have featured heavily in discussion around hominin adaptive behaviours. However, the palaeoclimate record for MIS 3 and 4 remains sparse for much of Europe and is almost exclusively derived from broad regional or global scale proxies, which can be difficult to correlate directly to hominin activity records at individual sites. Palaeotemperature information gleaned from oxygen isotopic analyses of faunal remains provides an opportunity to gain insights into sub-annual resolution seasonal temperature cycles on a smaller, more local level that, significantly, can be linked directly to archaeological contexts. Here we present high resolution seasonal temperature data to contextualize Neanderthal activity during MIS 3 and 4 at the site of La Ferrassie, southwest France. Summer and winter palaeotemperatures are obtained from oxygen isotope analyses of sequential enamel samples from *Bos/Bison* (aurochs/bison) teeth from Layers 2 (MIS 4), 5A and 5B (MIS 3). Carbon and nitrogen isotope ratios of bone collagen from Layer 2 through 5B are used to corroborate diachronic trends seen in the  $\delta^{18}\text{O}$  data. Oxygen isotope results indicate mild interstadial conditions in all analysed layers, with pronounced diachronic changes in seasonality (summer to winter temperature difference). We observe warm temperatures, moderate seasonality and increased forest cover for Layers 5A and 5B, which most likely date to Greenland Interstadial 12, matching results from other records showing a pronounced warm phase in southwest France during this time. We observe a cooling trend in summer and winter conditions from Layer 5A to 5B. In the lithic technology, these layers show a shift towards increasing numbers of discoidal flakes at the expense of Levallois flakes and faceted platforms. Whether this shift in technology is related to changes in mobility as a response to changing environmental conditions (e.g. [1]) is a point to be further investigated. At the same time, despite geological features such as cryoturbation indicating cold conditions during the formation of Layer 2, stable isotope results do not indicate overall cold conditions or prevalence of sub-zero winter temperatures. We interpret these discrepancies as potentially inherent differences between anthropogenic and non-anthropogenic markers of climatic conditions that may indicate preferential use of the site during warm phases of the Layer 2 formation time in MIS 4, but further exploration of this issue is necessary.

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## Gene flow between hominins was common

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In recent years, genetic data has been generated from an increasing number of Neandertal, Denisovan and early modern human specimens. Because of meiotic recombination, each individual's genome is a mosaic of its ancestors', and the length and frequency of these ancestry tracts is highly informative about a population's gene flow history: the longer an introgressed tract, the more recent the gene flow. Here, I am presenting results from a newly developed Empirical Bayes method to identify these ancestry tracts from ancient DNA. In contrast to methods developed for the same purpose in modern DNA, my approach explicitly models that ancient DNA is sparse, and frequently contaminated. Formally, I use a Hidden-Markov-Model along an individual's genome. The hidden states reflect the ancestry at a particular region in the genome, and I link sequencing read data to the hidden states by combining a genotype likelihood model (to allow for contamination) with a modified Balding-Nichols model (to allow for genetic drift and uncertainty in ancestry). Using simulations, I find that the method remains accurate at coverages as low as 0.1x and empirically I find introgressed Neandertal tracts in the 0.3x Denisova 2 genome with a contamination rate of 85% [1]. Applying this model to all published low-coverage Denisovan genomes reveals that the two oldest individuals (Denisova 2 and Denisova 8)[1,2] have 12% and 10% Neandertal ancestry, respectively. This ancestry is found in genomic tracts of up to 20,000,000 base pair length, strongly suggesting that this Neandertal ancestry is less than 30 generations old. The tract locations are not overlapping more than expected by chance, which indicates that the introgression events were distinct, which is consistent with dating results placing these specimens several tens of thousands of years apart[3]. Also adding Denisova 11 (confirmed as an F1-offspring with this method), I find that all Denisovans that are dated to be older than 90,000 years old have a substantial number of recent Neandertal ancestors, suggesting that Neandertals and Denisovans interacted recurrently for several tens of thousands of years. In addition, I find tracts of Denisovan ancestry in a high-coverage Neandertal (Denisova 5), showing that offspring was fertile in both directions. However, as I do not find evidence of gene flow in a much younger Denisovan specimen (Denisova 4), this gene flow might not have been persistent. In modern humans, the comparatively large number of genotyped specimens from Western Eurasia allows me to use my method to improve the timing of the gene flow from Neandertals into early modern humans: As expected, Neandertal ancestry tracts are commonly shared between individuals, and become shorter over time. Modelling this decay using a Bayesian mixture model allows me to estimate the distribution of times when Neandertal ancestry entered the modern human population. I find that the introgression history can be broadly subdivided into three distinct phases: In a first phase, up to until 55 kya ago, low levels of gene flow are present. The majority of Neandertal ancestry entered the modern human population in the relatively short second phase, between 48kya and 55kya. The final phase is gene-flow events private to modern humans in Europe, and ends at around 40kya. Overall, I show that gene flow between modern humans, Neandertals and Denisovans was frequent, but not ubiquitous. While Denisovans and Neandertals interacted for tens of thousands of years, the impact on later Neandertal and Denisovan genetic diversity appears minimal. On the other hand, the inferred timing of gene flow, and the absence of evidence for gene flow from modern humans into Neandertals is consistent with a model where the origin of modern human Neandertal ancestry is largely due to the range expansion of modern humans into Eurasia, with a partial absorption of the (likely smaller) local Neandertal population [4].

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## Analysis of Nuclear DNA Sequences from the Neandertals of Hohlenstein-Stadel and Scladina Caves

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The recent recovery of the mitochondrial genome from an early European Neandertal from Hohlenstein-Stadel Cave (*HST*) in Germany revealed that it shared a most recent common ancestor with other Neandertal mitochondrial genomes around 270,000 years ago. This is the deepest divergence between Neandertal mitochondrial genomes observed to date [1]. We have retrieved nuclear DNA sequences from *HST*, as well as from another early Neandertal found in Scladina Cave in Belgium, both dated to around 120,000 years ago [1, 2]. We show that both individuals are genetically closer to later Neandertals who lived in Europe until their disappearance - about 40,000 years ago - than to a roughly contemporaneous Neandertal from Denisova Cave in the Altai Mountains, Siberia. Moreover, the *HST* and Scladina individuals are also closer to Neandertals who later occupied the Altai region, suggesting that the Neandertals that migrated to Siberia between 120,000 and 90,000 years ago [3] were closely related to the *HST* and Scladina Neandertals. Their population split times from this genetically closer group of European and Asian Neandertals suggest that late Neandertals traced at least part of their ancestry back to Neandertals who predated them in Europe by at least 80,000 years. The old mitochondrial common ancestor of *HST* with other Neandertals is incompatible with *HST*'s close relationship to these Neandertals based on his nuclear sequences and the estimated long-term small population size of Neandertals. Instead, this mitochondrial genome may represent ancestry from an isolated Neandertal population, suggesting the existence of deep population substructure among Neandertals. An alternative explanation may be the replacement of the mitochondrial DNA in Neandertals by gene flow from a source related to early modern humans [1, 4] more recently than 270,000 years ago. If several mitochondrial lineages were introduced into Neandertal populations by such gene flow, then the deeply divergent mitochondrial genome in *HST* may represent a remnant of this introgressing population.

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## Neanderthals lithic toolkits in high mobility context: an overview from Teixoneres Cave (Spain)

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Studies on lifestyle of modern hunter-gatherers have provided pivotal insights on the human land use and the strategies applied for the acquisition of resources [1]. Climatic and ecological settings are two of the main causes influencing the productivity of the environment and, therefore, the mobility and dispersal of foragers groups. Generally, in territories with relative scarce biotic resources hunter-gatherers tends to move frequently whereas, in plentiful environments, they are less mobile and tend to camp near ecotones where resources from several habitats can be gathered at the same time [1]. In hunter-gatherers, carrying capacities are limited and the patchy distribution of food sources affects greatly the composition of the toolkit. In high mobility context, the personal gear of foragers groups should emphasize portability and limit the material waste. Several researches investigated the patterns of artefacts mobility and transport during the Middle Paleolithic [2][3]. These data indicate that, within retouched tools, flakes and cores were also moved from the place of production showing a high flexibility in how Neanderthals organize their technology during the displacements across the territory, and minimize the risk of shortage of lithic gears. Generally, these transported artefacts are isolate items or stone tools produced in allochthonous raw materials. However, the recurrent use of local and semi-local raw materials by Neanderthals could hamper the accurate identification of the toolkit composition because some transported items could be interpreted as part of the knapping events carried out at the site. This paper aims to explore the Neanderthals mobile toolkits from unit III of Teixoneres Cave (Moià, Spain), radiocarbon dated from >51,000 to 44,210 cal. BP (68.2%) [4]. Multidisciplinary studies on the archaeological record indicate that Neanderthals settlements at the site were of short-term and space out by the visiting of carnivores, mostly hyenas [5]. Preliminary surveys of the raw material distributions indicates the presence of cobbles of quartzite, sandstone and quartz found in secondary context in the nearby Mal stream, whereas outcrops of chert, limestone, hornfels and quartzite are found in primary and secondary positions at ~ 10-15 km east of the site. Other sources of quartz and chert in secondary contexts are located at ~ 8 km south and at ~ 15 km northwest of the cave. The technological analysis on the lithic assemblages of unit IIIa and IIIb reveals the use of two main strategies. Prepared core technologies and curated artefacts are common in chert and metamorphic rocks whereas the local quartz nodules are exploited opportunistically using the *tranche de saucisson* method. These different approaches in the reduction of the raw materials allow a clear differentiation between the artefacts of the mobile toolkit and the lithic items used during the domestic activities. The reconstruction of the operative chains in chert and metamorphic rocks reveal the transport at the site of flakes, retouched tools and configured cores that were used on site for short knapping sequences. The amount of cortical items is very low suggesting that the early phases of core configurations occurred in other locations. This pattern in raw material transport and exploitation is very different from the neighboring Middle Paleolithic sites where bigger amounts of chert nodules are transported inside the natural shelters. The study evidences also the production of pointed blanks on local quartz and the frequent import of Mousterian points and convergent tools. These latter artefacts are rare in the Northeast of the Iberian Peninsula indicating an extended network with groups from the northern Pyrenees and southern France.

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## Open-air sites reveal evidences about Lower Palaeolithic hominin foraging activities

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Pleistocene fossil concentrations excavated in open-air contexts are usually the result of the participation of one or various processes or agents (either physical or biological) involved in the transport and accumulation of several remains in a specific place, until forming archaeological deposits. In some open-air sites, however, we do not find a main actor in the accumulation of the remains and the formation of the deposits. These palimpsests could be the result of the successive accumulation of multiple independent events, which contribute to the deposition of different materials in a greater or less amount of time. The late Early Pleistocene site of Baranc de la Boella (Tarragona) and the late Middle Pleistocene site of Torralba (Soria) are two Iberian archaeological sites which formation seems to be the result of this type of accumulation processes. These archaeological sites have different taphonomic histories, although they share palaeoecological and taphonomic features, such as its formation in fluvio-deltaic contexts, the evidences of carnivore activity or the identification of the presence of hominin populations through the abundant lithic stone tools recovered, although the evidences of anthropization of faunal remains is scarce or practically null. Taphonomic analyses suggest that we are in front of discrete occupations in these sites, in which hominins would not have played a main role in the formation of osteological accumulations. We propose that these deposits do not correspond to places of activity of the Lower Paleolithic hominin populations, but could correspond to places of transit where they would have transited. These areas would be part of the wide territory of domination, control and use that these hominins populations would have exploited within their foraging strategies and different activities of acquisition of resources. These evidences would highlight the importance of patterns of mobility (both at a regional and macro-regional scale) and use of the landscape that these hominins would have during their foraging activities since Lower Pleistocene chronologies.

## Birth seasonality in the Baka pygmies

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There are evidences on marked birth seasonality in several populations across the world. However, fewer studies focus on birth seasonality of smaller hunter-gatherer population. The aim of this study is to characterise the seasonal pattern of births in a hunter-gatherer pygmy group, the Baka, living in southeast Cameroon. A secondary aim is to determine the factors that drive the fluctuations in the birth rate of this population. Data on births has been collected through continuous field studies from 2007 to 2018 and comprises written birth records from 1980 to 1982 and from 1987 to present, a total of 1067 registered births. Meteorological data has been provided by the World Meteorological Organization. Birth peaks are found in May and October, with their respective conception peaks in August and January. The seasonal pattern found has no statistical significance, despite presenting amplitude values higher than 15%. Two environmental factors are often associated with birth rate in foraging and agricultural societies, temperature and rainfall. Although it appears to be a relation between births and temperatures in the Baka, the oscillation of this weather variable throughout the year is so small that it cannot be considered as a driving factor for birth patterns. There are two rainfall peaks: May and September-October. These months correspond with the months of more births and less conceptions. Similar birth patterns, and an association with rainfall, have been also observed in other populations, such as in Ngisonyoka population in Kenya [3], in Tanzania [2] or Lese farmers and Efe pygmies in Democratic Republic of Congo [1]. Even so, the advanced factors that relate rainfall and conception and births in other populations, such as farming seasons, food scarce or worsening of health, often cannot be applied for our study sample [4]. Other cultural factors, like marriages or holidays, which can drive seasonality of births in other populations are also ruled out as a main factor for birth pattern in the Baka pygmies. Instead we propose 3 nonexclusive hypotheses to explain the relation observed between rainfall and birth seasonality: - Activity: during rainy seasons Baka tend to live in nearby forest. They are more likely to spend more hours of the day transporting the gathers and hunts to the village, instead of having more leisure time. - Nutritional status: the primordial carbohydrates source of Baka is wild yam *Dioscorea spp.*. During dry season its reserves are at maximum, which could provide an improved nutritional status that could translate to higher conception frequency. - Convenient timing: it is probably more convenient and comfortable for Baka women to give birth in nearby camps, or at the village during rainy seasons, rather than in further camps in drier seasons. Studies characterising birth seasonality in hunter-gatherer groups are highly insufficient, especially for comparison. It is interesting to note that the Efe pygmies did not present seasonality in births [1], while having a similar lifestyle to the Baka. Possible differences in growth pattern, in childcare [4], as well as diverse climatic conditions, could possibly explain these differences.

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## Temporal changes in human mandibular size and shape throughout the Terminal Pleistocene-Holocene Levant

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The transition to food production, exploitation of 'secondary' products (e.g., milk), and advances in cookware technology have affected all aspects of human life. It has been hypothesized that the impact of dietary changes, particularly, the decreased functional demands on the masticatory apparatus due to developments in food preparation techniques and softening of the food resulted in a reduction of alveolar bone size and changes in mandibular shape [1-3]. Previous studies have supported this hypothesis by demonstrating that mandibular shape is associated with masticatory muscle cross-sectional area (CSA, a surrogate for muscle force) [2,3]. Accordingly, larger CSAs are associated with a wider, more trapezoidal ramus, massive coronoid, rectangular body and a more curved basal arch. Whereas mandibles with small CSA are characterized by a tall and narrow ramus (more like a parallelogram) with a pointed coronoid, triangular body and a more triangular basal arch [3]. It has been shown previously that agriculturalists (softer diet) had relatively short and broad mandibles with a tall, angled ramus and coronoid process, whereas hunter-gatherer populations (harder diet) have relatively long and narrow mandibles with a short, upright ramus and coronoid process [4]. In the present study, we aimed to focus on subtle temporal morphological changes of the mandible during the terminal Pleistocene-Holocene Levant and examine whether they were associated with reduced loadings on the masticatory system. By using a three-dimensional geometric morphometric (GM) approach we examined the mandibular shape of four Levantine prehistoric populations: Natufian hunter-gatherers (14,900-11,750 cal BP; n=10), Pre-pottery Neolithic early farmers (12,175-8,450 cal BP; n=6), Chalcolithic farmers (6,500-5,500 cal BP; n=9), Roman-Byzantine (n=16), and a modern population (n=63). Changes in mandibular form and shape were analyzed using the Procrustes-based geometric morphometric method. Univariate and multivariate analyses were carried out to examine differences in size and shape between the studied populations. Our results reveal considerable temporal changes in mandibular shape throughout the Holocene Levant, mainly between the pre-agricultural population (the Natufian) and the succeeding ones, and between the post-industrial population (the Modern) and the pre-industrial populations. We have followed changes in mandibular size and shape during the entire Holocene, including modern populations, in a restricted geographical region. A tendency for a reduction in mandibular size was identified between the pre-agricultural population and the farmers. Most regions of the mandible underwent shape changes. These results are supported by previous studies demonstrating similar variations in mandibular shape between hunter-gatherers and farmers in other geographical regions [4,5]. In conclusion, substantial changes in mandibular shape occurred throughout the Holocene Levant, especially following the agricultural revolution. These changes can be explained by the "masticatory-functional hypothesis".

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## Palaeogenomic investigations at the Troisième caverne of Goyet, Belgium

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The main excavations at the Troisième caverne of Goyet in Belgium were conducted by Edouard Dupont in 1868 who identified Palaeolithic human occupations later attributed to the Middle and Upper Palaeolithic. These are represented by an archaeological record that spans the Mousterian, Lincombian-Ranisian-Jerzmanowician, Aurignacian, Gravettian, and Magdalenian, and then extends into the Neolithic and historic periods. Due to the lack of detailed documentation of the excavated materials, their association to a specific chronocultural context has been challenging. Morphometric and taphonomic analyses, combined with direct radiocarbon dating as well as isotopic and genetic analyses, were used to assign human remains to either late Neanderthals or ancient modern humans from different chronocultural groups. In 2016 the first palaeogenetic investigation of Neanderthal specimens from Goyet was published [1]. Taxonomic assignment was confirmed by performing hybridization capture of the mitochondrial DNA (mtDNA) and later inspecting diagnostic mutations at nucleotide positions that distinguish modern humans from Neanderthals. Moreover, a phylogenetic reconstruction placed seven nearly complete mtDNA sequences from Goyet within the diversity of late Neanderthal mtDNA. An around two-fold coverage nuclear genome was later sequenced from one of those individuals (Goyet Q56-1) [2], revealing a high genetic similarity to other late Neanderthals that is well correlated to their geographical distance. Analyzing modern human remains retrieved at Goyet, mtDNA genomes were initially reported for two specimens directly dated to the Aurignacian, five to the Gravettian, and one to the Magdalenian [3]. Aurignacian-related individuals were particularly intriguing as they were found to carry mtDNA haplogroup M, which is almost entirely absent in present-day Europeans. For Gravettian- to Magdalenian-related individuals, the shift from U2/U5 to U8 haplogroups was detected locally - as in other regions of Central Europe - likely influenced by the genetic bottleneck during the Last Glacial Maximum (LGM). Furthermore, nuclear sequences of five modern human individuals from Goyet were produced through genome-wide targeted enrichment [4] revealing local replacement between Aurignacian- and Gravettian-related populations. However, the genetic component associated with a 35,000-year-old individual (Goyet Q116-1) reappeared after the LGM, first in Spain and then in other European regions including in a Magdalenian-related individual from Goyet (Goyet Q-2). This individual was later found to be the best proxy for a genetic component that was largely displaced in Europe from around 14,000 years ago onwards while surviving in high proportion among Mesolithic individuals from Iberia [5]. Here we present new palaeogenetic data of Neanderthal and modern human individuals from this iconic site. First, we expand the molecular taxonomic identifications with three additional Neanderthal specimens and reconstruct their partial mtDNA genomes. Those confirm the general picture of a limited genetic diversity for late Neanderthals, which is also apparent among the Goyet Neanderthals. Second, working on modern human remains, we produced new mtDNA and nuclear data from four Gravettian specimens. They belong to mtDNA haplogroups U2 and U5, further extending the observation of both mtDNA types being largely present in pre-LGM Europe. Moreover, their nuclear genomes provide additional evidence for the genetic affinity between Gravettian-related groups across Europe, from the present-day regions of the Czech Republic to Belgium and Southern Italy. In conclusion, the deep temporal range covered by the human remains from the Troisième caverne of Goyet provides the unique opportunity to describe within a single archaeological site the major genetic transformations that took place in Europe throughout the Middle and Upper Palaeolithic.

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## Lithic economy and hominin landscape use in the early Acheulean of Koobi Fora, Kenya

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The emergence of the Acheulean is understood to mark a key adaptive shift in several dimensions of hominin behaviour. This shift is represented archaeologically by evidence for the expansion of hominin foraging ranges involving increased mobility and tool transport distances, variability in strategies of stone raw material procurement and use and increased spatial and temporal depths of planning in the organization of stone tool production. Very little archaeological data, however, has been published to support these inferences for Acheulean sites older than 1 Ma (hereafter Early Acheulean sites). This may be due to a host of factors including (1) the paucity of localities that are geologically suitable to investigate Early Acheulean landscape use and (2) the emphasis in Early Acheulean studies on the origins and production patterns of large bifacial cutting tools (hereafter 'LCTs'), the marker of the Acheulean techno-complex. We need to understand how early Acheulean hominins organized and economized their technology on a landscape scale, to make quantitative assessments about how shifts in hominin cognition are manifested archaeologically. Very few contexts exist that are conducive to such studies. One of these is a set of spatially separated semi-contemporaneous early Acheulean (~1.4 Ma) sites in Koobi Fora, east Turkana, Kenya, consisting of the localities of FxJj65, FxJj63, FxJj37 and FxJj21. The expansive lateral exposures of fluvial sediments, as well as the associated tephrostratigraphy of the Koobi Fora Formation provide the landscape context that enables these comparative analyses. Here I present analyses of variability within and between the stone artefact assemblages at the Early Acheulean localities of FxJj65, FxJj63, FxJj37 and FxJj21, focusing on two quantitative proxies for hominin landscape use. Namely, (1) variation in LCT manufacture and maintenance patterns across the landscape based on 3D Geometric Morphometrics ('3DGM') [1] and (2) geographic variation in Early Acheulean flake production and discard patterns based on a logistic predictive model [2]. One trajectory of changes in LCT size and shape is present across all four localities, implicating a single system of lithic economy for early Acheulean LCT production at Koobi Fora. This reduction trajectory is differentially represented among the four sites, which implies a spatially structured fragmentation of LCT manufacture and maintenance patterns across the landscape [3]. The flake analyses provide an independent perspective on Acheulean hominin landscape use, and imply a depth of planning in early Acheulean hominins wherein technological activities were undertaken in substantial anticipation of future needs.

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## **Endomaker: an algorithm for fast, accurate, fully automatic extraction of endocasts and their volumes from digital models of the skull**

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Reproducing cranial endocasts is the main goal for researchers interested in vertebrate brain evolution. Recent developments in 3D digital modelling enabled to overcome the complex and somewhat risky manual production of physical casts. Yet, even the most recent, cutting-edge methods still require somewhat long processing times and usually cannot deal with complex-shaped endocranial cavities. These problems limit both the statistical power and phylogenetic scope of brain shape and size evolutionary investigations. To fix these problems, we developed *endomaker*, a fully automatic tool for extracting endocasts from digital models of the skull and calculate their volume by using an innovative automatic voxel-based method. We compared *endomaker* to manual segmentation and other endocast producing software and illustrate how to apply the tool on vertebrate skulls widely differing in size and shape. In this communication, we show the versatility of *endomaker* by applying it on different shaped, different sized primate skulls including a modern human and a human fossil specimen (Petralona, *Homo heidelbergensis*). Our results show how the surface of the endocast obtained via *endomaker* fits the endocranial surface of the skull much more precisely than the one obtained with other software. Endocranial volume estimates under *endomaker* are as precise as with the use of other sophisticated approaches. Crucially, both endocast production and its volume estimation are indefinitely faster under *endomaker*. Besides being faster and more precise than competing software, *endomaker* is versatile enough that it works with disparate file formats such as .stl, .ply, or .obj and on all operating systems. This is favourable since digital models come into different forms and must be translated into a suitable format prior to use with any software other than *endomaker*. With that, *endomaker* is the first software ever capable to process single-handedly entire libraries of skull meshes and their endocranial volume estimates in a few minutes, with minimal user preparation. *endomaker* and example data are fully available in the Arothron R package.

## **The biomechanical importance of the scaphoid-centrale fusion during simulated knuckle-walking and its implications for the locomotion of the last common ancestor of humans and African apes**

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Bipedalism with an upright posture is one of the main defining traits of the earliest hominins. This locomotor behavior prominently contrasts with those observed in other African apes, which mostly exhibit diversified quadrupedal locomotor behaviors. Using the extant great apes as analogs, numerous different locomotor modes have been proposed to characterize the ancestral condition prior to the adoption of the strict bipedal locomotion seen in the human lineage. Among the ancestral proposed locomotor modes, knuckle-walking, a characteristic terrestrial quadrupedal locomotion exhibit by African apes, has played a central role. This is because it represents the most parsimonious of the alternative hypotheses since both chimpanzees and gorillas exhibit this locomotor behavior. The knuckle-walking hypothesis states that the last common ancestor (LCA) of gorillas, chimpanzees, and humans exhibited this locomotor mode, whereas vertical climbing, a common behavior observed in all of the extant apes, would be considered ancestral to knuckle-walking. Nonetheless, both phyletic and functional analyses of the earliest hominin fossils suggest that hominin bipedality might have evolved from a locomotor mode that does not have a modern analog among the great apes (i.e., careful climbing, clambering, and bridging). In addition, some authors point out that knuckle-walking could have evolved independently in the African great apes, which would imply a homoplastic evolution of this locomotor behavior in chimpanzees and gorillas. Other studies have argued the opposite by pointing out that the observed differences in knuckle-walking between these two genera can be explained by differences in positional behavior, kinematics, and the biomechanics of weight-bearing, without implying two independent origins of knuckle-walking. Due to the importance of this matter, several studies have focused on the analysis of the hominoid wrist because it represents the key anatomical location that could help to elucidate the locomotor mode of the LCA. Among the scarce osteological synapomorphies of humans and African apes, the fusion of the os centrale to the scaphoid in the wrist has been long recognized. The scaphoid-centrale fusion in the African hominoid carpus has been interpreted as a functional adaptation to the stresses exerted on this joint during quadrupedal locomotion, particularly accentuated in knuckle-walking. The functional hypothesis has led to the suggestion that the fusion is evidence for a knuckle-walking common ancestor of the hominine clade. However, the exact functional significance of scaphoid-centrale fusion remains unclear. We address this question by carrying out finite element simulations of the hominoid wrist during knuckle-walking. We virtually generated fused and unfused morphologies of our hominoid sample depending on the species to compare biomechanical performance. The unfused morphologies comprised three bony elements (i.e., capitate, scaphoid, and centrale) connected by the scaphocentralecapitate ligament, whereas the fused morphology involved the scaphoid (or fused scaphoid-centrale) and capitate connected by the scapho-capitate ligament. A structural static analysis was performed to evaluate the biomechanical behavior of the scaphoid, capitate, and centrale during the stance phase of knuckle-walking using finite element analysis. We tested the hypothesis that fused scaphoid-centrale morphologies better withstand the loads derived from a knuckle-walking scenario. The obtained results show that indeed fused morphologies better resist the loads derived from knuckle-walking, particularly in the Homininae. Hence, these results support the biomechanical aspect that is required to relate the fusion of scaphoid and the centrale as an adaptation for knuckle-walking.

## Unveiling traces of the Neanderthal gut microbiome by shotgun metagenomics of feces-containing sediment from El Salt (Alicante, Spain)

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A wealth of data is being accumulated showing that the gut microbiome has co-evolved with humans through the fulfillment of strategic roles for our biology [1]. However, most studies on putative ancestral microbiome traits have been limited to inferences from contemporary populations adhering to traditional subsistence strategies [2,3], and little or no information on the symbiotic gut-microbial communities of ancient humans is available. To bridge this gap, here we characterized seven sediment samples from stratigraphic unit X of El Salt Middle Paleolithic open-air site (Alicante, Spain), which has yielded Neanderthal fossil remains and a rich sequence of well-preserved human occupation deposits dating to MIS 3, around 50 kya. Previous work on these samples showed presence of several millimetric phosphatic coprolites and fecal lipid biomarkers, such as coprostanol and 5 $\beta$ -stigmastanol, with proportions strongly suggesting a human origin [4]. Ancient DNA was extracted from this material and subjected to shotgun Illumina sequencing, resulting in >90 M high-quality paired-end sequences. Based on our findings, bacterial species belonging to families known to be part of a putatively core human gut microbiome are variably represented across the site layers. Interestingly, these include several members of *Lachnospiraceae* and *Ruminococcaceae*, which are well-known short-chain fatty acid producers in modern human guts and have been repeatedly proposed as biomarkers of a healthy gut microbiome. By reconstructing ancient bacterial profiles from El Salt Neanderthal feces-containing sediment, we propose the existence of a core human intestinal microbiome with recognizable coherence between Neanderthals and modern humans, which may help elucidate ancient human dietary and behavioral patterns as they relate to an association with the environment. The identification of ancient microbial gut constituents could provide information about evolutionary symbioses that are crucial to development of healthy metabolic and immunological functions. Further analyses of other Neanderthal *in situ* occupation sedimentary contexts are necessary to corroborate and expand our results. This study shows the high potential of combining multidisciplinary biomolecular and ge archaeological approaches to the investigation of Paleolithic sites to advance our understanding of human biological and cultural evolution.

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## Testing the utility of different ASUDAS dental trait combinations for biodistance analysis

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In archaeological and paleontological contexts, dental morphology is widely used for biodistance analysis in order to reconstruct modern human population history [1] and hominin phylogenies [2]. Dental variation is routinely characterized using non-metric traits with reference to the Arizona State University Dental Anthropology System (ASUDAS) [3]. This system catalogues a large number of standardized crown and root shape variants that are thought to evolve in a neutral genetic manner. However, there is disagreement on whether certain traits preserve neutral genetic signatures to a greater degree than other traits [4]. For this reason, identifying traits and trait combinations that are most useful for reconstructing neutral genetic affinities is of utmost importance for future dental biodistance research. Here, we systematically test the utility of different dental trait combinations by quantifying the correlation between neutral genomic markers and dental morphological variation in modern human populations. Specifically, we assess the utility of a particular trait combination by estimating dental distance values (Euclidean squared) between 20 worldwide populations, and by comparing them to neutral genetic distance values (Delta-mu squared) among the same, or closely matched, populations. Our analysis, based on 27 ASUDAS dental traits for more than 30,000 individuals and 645 microsatellite loci for 4,391 individuals, tests the differential correlation of 134,217,727 possible dental trait combinations. Our results show that different traits and trait combinations are differentially correlated with neutral genomic variation (with a range from  $r = -0.11$  to  $r = 0.79$ ). In general, increasing the number of traits leads to a logarithmic increase in the correlation between genomic and dental distances until it reaches a plateau at approximately  $r = 0.5$ . At the same time, increasing the number of traits reduces the variance of dental distance estimates. These findings support the claim that dental distances based on many traits are, in general, more robust than those based on only a few traits [5]. Nevertheless, we found that the highest correlations between genomic and dental variation were achieved by using a rather limited number of specific and highly diagnostic traits (from 7 to 14). We argue that these traits should be prioritized in future dental biodistance analyses, when possible. Our results serve to develop accurate inferences about neutral genetic relationships among modern human populations with the use of dental non-metric traits. They have implications for drawing interpretations from the archaeological and fossil records, as well as for the evolutionary mechanisms responsible for human dental morphological diversity.

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## Fire on the rocks - establishing prehistoric heating of non-flint rocks through feldspar luminescence analysis (pIRIR)

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Throughout (pre)history, non-flint rocks have been used in combination with fire to structure fireplaces, to retain heat, to boil liquids and prepare food. They constitute an important find category for the reconstruction of past fire functions, potentially providing insights into aspects of fire-related human behaviour that cannot be obtained from other fire proxies. Thus far the identification of heated non-flint rocks in archaeological contexts largely depends on visual (macroscopic) assessment, using criteria widely assumed to be diagnostic for thermal alteration. However, visual identification can be subject to observer bias, and some heat-induced traces can be quite difficult to distinguish from other types of weathering. This can particularly be an issue for older sites where non-flint rocks occur in small numbers (as opposed to e.g. Holocene North American sites with large piles fire-cracked rocks) and where those rocks may have been used for other, non-fire-related, tasks as well. Here we present feldspar luminescence analysis as an objective way to identify heated non-flint rocks and as a way to test whether macroscopic assessment provides a reliable indication of former heating. For this purpose, non-flint manuports with and without inferred macroscopic traces of heating, originating from the Last Interglacial, Middle Palaeolithic site Neumark-Nord 2 (Germany), were submitted to feldspar luminescence analysis (pIRIR) and results compared to the visual assessment. In addition, the feasibility of the method was tested by analysing heated and unheated experimental pieces. Feldspar luminescence analysis was applied to a cross-section of different rock types from the Neumark-Nord 2 assemblage. From each stone a core was taken and divided into slices, after which at least one sample from the outside and one sample from the centre of the stone was analysed to obtain a heating-depth-profile. This allowed distinction between optical resetting (of the outer part) and thermal resetting (of the inner part of the stone). Results show good agreement between macroscopic traces and luminescence signals for the (presumed) unheated pieces. However, visual assessment of heat alteration overestimated the actual amount of heated non-flint rocks. Luminescence analysis has so far identified two heated rocks at Neumark-Nord 2, making them (to our knowledge) the oldest unambiguously heated stones at a Palaeolithic site. Despite the variety of rock types tested, the low sample size per rock type, and some methodological constraints, this preliminary study demonstrates the potential of luminescence analyses in the identification of heated rocks—and their prehistoric applications like hot-stone cooking. The study also warns against the use of macroscopic assessment and the use of inferred diagnostic criteria without further confirmation by independent, quantitative methods.

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## **Bones of predation at Gorongosa National Park: insights into Plio-Pleistocene hominin resource exploitation**

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A major problem in the archaeology of early hominins is the inference of foraging and dietary patterns from faunal remains. For example, the shift in early hominin diets from one largely based on fruits, nuts, and various forms of vegetation to one that included a significant component of animal resources has been inferred from the characteristics of archaeological bone assemblages: skeletal element representation, bone surface modification, animal tooth marks, stone-tool cut marks, etc. But the problem of equifinality – with different processes leading to similar patterns – makes these inferences problematic [1]. Here we present the first results obtained from the application of a novel set of methodologies that combines ethological and taphonomic data to study predation events on the floodplains of Gorongosa National Park, Mozambique. The geographic location of Gorongosa in the East African Rift System and its complex vegetation mosaic offer a unique environmental and ecological analogue for the context of the earliest Plio-Pleistocene archaeological sites in eastern Africa. The lead author collected data over 18 days directly documenting 7 predation events and following the fates of 11 mammal carcasses. Our results show that carrion was available from cranial contents and metapodials of fresh carcasses shortly after carnivore feeding, and that bone marrow remained relatively unexploited. Our analysis of bone surface modification highlights the ambiguity of attributing some types of bone surface marks exclusively to hominin tool use. We remark on the importance of studying overlooked species in the context of carcass modification and consumption, emphasizing the role vultures, marabou storks, and crocodiles. Furthermore, ethological data in the form of systematic scans of the Gorongosa floodplain revealed patterns of primate behaviour in relation to predators and carcasses. Baboons tended to avoid “zones of risk”, i.e. areas where carcasses or predators were in close proximity. The baboon avoidance of carcasses points to an awareness of the dangers in terms of possible predator confrontation, but also of the risk of disease. We suggest, as others have done [2], that bone marrow was a resource likely to have been exploited by hominins as a relatively hygienic and reliable source of fat and energy. To test this conclusion, we encourage the collection of experimental data over longer time scales, and the use of microscopic analysis of marks made by vultures, marabou storks, and crocodiles. This study shows that the combination of direct ethological observations and taphonomic methods in the analysis of modern bone assemblages may provide fresh insights into the behaviour of early hominins and other vertebrates in the consumption of animal resources.

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## First observations on some traits of the oral cavity in the Neanderthal from Altamura

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The Murgia plateau (Apulia, southern Italy) is a geographic area rich of karstic formations such as dolines, blind valleys and caves. One of these formation is the Lamalunga cave, part of a wider karstic complex. During a speleological survey in 1993, in a small chamber, delimited by speleothemes, speleologists found a hominin specimen with the skull stuck in the walls of the chamber and other bones laying on the ground and covered by calcareous concretions. Anthropologists visited the cave in the following years and revealed that the specimen, most likely in primary deposition, preserves most of the bones in excellent state and probably represents one of the most complete fossil hominins in Europe. Observations of the skeletal features suggested the presence of mixed archaic and Neanderthal derived traits, placing the specimen in the variability of the European Late-Middle Pleistocene. A few years ago, the extraction of a scapula fragment, allowed the conduction on new analysis that on the one hand confirmed the attribution to the Neanderthal hypodigm (morphometric analysis and ancient DNA), and on the other, dated the specimen between  $130.1 \pm 1.9$  ka and  $172 \pm 15$  ka. Recently, in the context of a broader project financed by the PRIN program of the Italian government, it has been possible taking more precise observations on several features of the specimen. In this work, we present preliminary observations on the dentition and the oral cavity of the Neanderthal from Altamura, made possible also by the use of a fiberscope, which allowed observing some hidden parts of the mandible and of the palate. The dentition of the specimen is almost complete, except for two teeth (upper right P3 and upper left M1) lost in vitam and four teeth (lower right I1 and P3 and lower left I1 and I2) lost post-mortem. Dental wear is marked. The inversion of the compensation curve of Wilson in M1s and M2s is clear, supporting the hypothesis that the individual is an adult. The general state of the periodontal bone is difficult to assess because it is covered by a calcite layer; however, no periodontal pockets are visible, except in correspondence of one of the lost teeth. Therefore, the high extent of root exposure might be related to bone resorption and/or compensative eruption linked to the marked dental wear. A frontal x-ray image on the skull revealed the presence of a periapical lesion in the upper right central incisor. Some features we observed, i.e. taurodontism and the presence of a retromolar space confirm, along with the cranial general morphology and the morphometric analysis of the scapula, the attribution to the Neanderthal hypodigm. Also, a well-developed palatine torus is documented, a feature whose occurrence in Neanderthals, to the best of our knowledge, has not been described so far.

## Cardiac output and metabolic levels in human evolution

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The metabolic rate of modern humans is larger than that from great apes, and it has been hypothesized that this metabolic increase would be related to the expensive growth of our larger brain, and to the features of our modern life history, with new growth stages, high reproductive success and longevity [1]. We propose that an increase in the metabolic rate of the organism would be related to an increase in its total blood supply. In evolutionary biology, the distal blood supply of specific organs like the brain or limbs has been studied in different species in relation to growth, maintenance or locomotion. We propose to turn this perspective around and study the total proximal blood supply within human evolution. This supply is the cardiac output, the product of the amount of blood pumped from a ventricle in a single heartbeat and the number of heart beats per minute. There are several techniques for its measurement, and the determination of the diameter of the aorta is considered one of them. The impression left by the aorta on the vertebral bodies (aortic impression or AI) was measured through surface area bilateral asymmetry on processed photographs (Adobe Photoshop CS6, ImageJ) of vertebrae of modern humans (N=48), chimpanzees (N=10), gorillas (N=5) and orangutan (N=3) specimens, including one Neandertal and one *H. erectus* individuals. Body weight and aortic root diameter (sinus of Val-salva) data from living samples of humans (N=1132) and great apes (chimpanzees, N= 87, gorillas, N=51) were also gathered and compared. Significant asymmetry towards a smaller left area of the vertebral surface was observed in modern human females and males (segments T7-L2 and T5-T11, respectively), while in the great ape sample no significant asymmetry was observed, although due to the limited sample size our results are preliminary. Asymmetry values were significantly larger in modern humans in comparison with great apes for the segment T6-T11. The pattern of asymmetry observed in modern humans fits the known trajectory of the descending aorta (DAo), confirming that the vertebral asymmetry is caused by this artery. The presence of the AI in modern humans and its absence in great apes could be explained by different factors, including a closer spatial association between the DAo and the vertebral bodies in modern humans due to differences resulting from thorax size and shape in great apes, and/or an increase in the blood flow or diameter of the DAo in modern humans. With regard to the latter explanation, it has been assumed that measurements of external arterial dimensions can indicate the rate of blood flow within them [2], and data from living modern humans and great apes indicate that in modern humans the aortic root is larger than in chimpanzees and similar to gorillas, with significantly larger body weights. The relation of body weight and aortic root is similar to the relation between total energy expenditure and fat free mass, and to the relation between basal metabolic rate and body mass in humans and great apes that reflect the raised metabolic activity of modern humans [1]. In this proposed scenario, large brained hominins with a growth pattern and a life history pattern similar to modern humans, such as Neandertals [3], would also present an AI. The T6-T7 thoracic vertebra from a young adult Neandertal from El Sidrón site [4] presents a clear AI, while a preliminary study of published photographs of the thoraco-lumbar spine of KNM WT 15000 [5] would indicate that no AI is present in this young *H. erectus*. Our results support the hypothesis that the appearance of the modern human life history and our larger brains would be linked to a change in the cardiovascular system that would have allowed for an increase in the cardiac output of the organism.

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## Lithic technology as evidence for higher order intentionality and Theory of Mind

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Theory of mind (ToM) is one's ability to imagine another's thoughts. It is an ability that modern humans rely on continually like even driving an automobile in traffic. ToM is a recursive ability; one's thoughts could include an understanding of what others know about one's thoughts. This recursiveness yields increasingly inclusive 'orders of intentionality.' First order intentionality is Mary's own mental state: "I am angry"; in second order intentionality, John knows that Mary is angry; in third order, Mary knows that John knows that Mary is angry, and so on. Modern adults regularly handle four orders of intentionality and sometimes five. Unique among primates, most humans are conscious of possessing a full theory of mind; even at their best, great apes are "just able to achieve second order intentionality" in some circumstances [1, 2]. In the present paper, we propose to use features of the archaeological record to trace the evolution of this important ability. Oldowan stone tools may provide the earliest ToM clues. These hominin stone knappers struck sharp flakes from stone cores and used the flakes to butcher scavenged carcasses. The intentional manufacture of these flakes via percussion indicates an egocentric, goal directed activity that may have required some concept of self [3]. A model [4] was proposed for the evolution of teaching in which orders of intentionality played a key role. It was suggested that novice knappers learned through demonstration, a form of teaching that requires advanced ToM because the demonstrator must understand the novice's ignorance and desire to learn. Others [5] suggest that veridical copying, in which the novice attended to the motor procedures of a knowledgeable individual and duplicates those procedures, would be sufficient. This would have required only chimpanzee-level perspective taking, i.e., an ability to imagine what another sees. This is not full ToM, let alone the 3rd order intentionality that [4] envision. The teardrop-shaped Acheulean handaxe, with its large geographic and temporal distribution, may suggest a standardization of conceptualization, that in turn, required that Acheulean knappers to have had a collective understanding of both the handaxe's purpose and the manufacturing process. Such a shared intention would implicate second order intentionality. Further, the pervasiveness of Acheulean material culture indicates a kind of group or social knowledge – widespread replication of teardrop-shaped tools necessitates transmission of knowledge across time and space. Indeed, social learning must have been present, likely in the form of imitation. Other work [2, 3] focuses not on social learning, but on identity development. This model incorporates the perspective of embodied/extended cognition, in particular the role that material culture plays in communicating information about identity. When evidence suggests that a stone knapper attempted to manipulate how he or she was seen (and the tools assessed) by others, then 3rd order intentionality was likely in play. In particular, gigantic handaxes may have gone beyond the purely functional and may indicate social signaling. The neuroaesthetic implications of 'overdetermined' handaxes also corroborates this assessment. Overdetermination occurs when handaxe makers paid more attention to appearance (including bilateral symmetry or even intentional asymmetry like S-twists) than was necessary for function. This was almost certainly done to impress others. To produce a display object, the maker clearly knew that others would not only see it, but would judge it, and took this external perspective into account when making the artifact. And it was not just 'others see me,' it must have included what others knew about what the maker knew, something similar to: "I alter what I do because you know the prototype against which I must conform my efforts", and we are proposing that it serves as good evidence for 3rd order intentionality.

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## Morphometric variation of the cerebellar area in modern humans and chimpanzees

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Some modern human higher cognitive functions, e.g. language, have recently been attributed to the cerebellum. However, it is unclear when during hominin evolution these higher cognitive functions were acquired. Inferences about the evolution of hominin cognitive function can only be based on indirect evidence, such as fossil endocasts, which represent the imprint of the brain and surrounding meninges on the endocranium, and the comparison of extant species. Therefore, there is considerable debate about whether the morphology of brain components evolved according to natural selection for functional optimization, or whether developmental constraints of conserved neurogenetic scheduling cause a predictable external morphology, with changes in function being achieved purely by internal reorganization [1,2]. Here, we aim to test whether the endocranial morphology of the modern human cerebellar area is the result of developmental constraints on evolution or whether, alternatively, it has been affected by natural selection for functional optimization. If cerebellar shape is ontogenetically constrained, adult shape can be predicted by its size. An allometric relationship in adults would suggest evolution along developmental constraints, whereas the lack of an allometric relationship would point to natural selection for functional optimization. Furthermore, shared ontogenetic shape trajectories among modern humans and chimpanzees, as well as ontogenetic shape changes mirroring adult interspecific shape differences, would also be consistent with ontogenetic constraints on cerebellar evolution. In contrast, no shared ontogenetic trajectories or differences in the ontogenetic shape changes compared to the adult interspecific shape differences would suggest evolution affected by natural selection for functional optimization. We tested these hypotheses using geometric morphometrics based on a sample of virtual endocasts from 61 modern humans and 94 chimpanzees. A set of 109 landmarks and semi-landmarks was digitized on the posterior cranial fossa of each individual. Individuals were assigned to four dental age groups based on the development of their maxillary dentition, ranging from complete deciduous dentition, erupted first molar, erupted second molar to erupted third molar. First, results show that adult size is significantly associated with adult shape which is consistent with ontogenetic constraints on cerebellar evolution. However, size only predicts a small percentage of adult cerebellar shape (4.99 % and 7.69 % of variance explained in modern humans and chimpanzees, respectively). Second, the late ontogenetic shape trajectories between modern humans and chimpanzees differ and thereby suggest evolution affected by natural selection for functional optimization. Nevertheless, chimpanzee development appears to mirror evolutionary shape changes, reflecting a shift in proportions between the anterior part of the posterior cranial fossa relative to the posterior expansion of the lateral cerebellar hemispheres. This pattern is also seen in the interspecific, as well as intraspecific, shape differences between modern human and chimpanzee adults. In hominin evolution, the posterior expansion of the lateral cerebellar hemispheres is proposed to be associated with higher cognitive functions, especially language [3,4] and a larger capacity for cognitive information processing [5]. As neither hypothesis could be completely rejected, the observed shift in proportions could indicate an evolutionarily conserved developmental pattern enhanced by natural selection for functional optimization.

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## Paleo-anthropological explorations in Equatorial Guinea (West Central Africa). The estuary of the Muni River.

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It is well known the dearth of paleoanthropological record in Central and West Africa, being the fossils of Iwo Eleru (Nigeria, 16-11 Ka) and those of Ishango (Democratic Republic of the Congo, 20 Ka) the most outstanding. In order to try to complete this gap in the human fossil record in Africa, a project of archaeo-paleontological surveys has been undertaken in Equatorial Guinea territories (latitudes 4 ° N and 2 ° S, and longitudes 5 ° and 12 ° E), an ideal place to this aim by its geographical position and its ecological context [1, 2]. There are two main objectives pursued. On the one hand, the search for fossils of hominids that help us to understand the divergence and evolution in the lineage of the great African apes: gorillas, chimpanzees and hominins. On the other hand, the investigation of the conservation patterns of early human occupations of the African rainforests. We present here the results of the year 2017 campaign, carried out in the estuary of the Muni River (continental region of Equatorial Guinea), and composed by the concurrence of several rivers: Mandyani and Congüe by the North, and the Mitong and Utanboni by the East. Previously, as the result of the 2014 campaign, 8 new surface sites in the Niefang region were found with diagnostic archaeological materials from the Middle Stone Age (MSA), characterized by polyhedral quartzite and flint cores, flakes from core preparation and bifacial reduction [4]. These sites are located in the surroundings of Mosumu, an area previously studied [5], which confirms the presence of archaeological deposits of the MSA. Subsequent works by Alejandro Terrazas and his team from the UNAM verify these findings. The fieldwork methodology includes the location on a geological map of places and areas with sediments of age and sedimentary conditions that seem favourable a priori for the conservation of fossils. Once *in situ*, an exhaustive and systemic examination of clearings and slopes, as a result of roads and forest tracks, is carried out the systematic monitoring of clearings and slopes of roads and forest tracks. A total of 50 outcrops were detected with GPS geolocation, which were sampled, photographed and annotated as Muni Point, with successive numbering. The 8 routes followed were subsequently projected onto maps. The most outstanding places in relation to Quaternary sediments correspond to the location Muni 19, where the contact of the Cretaceous with Pleistocene detrital sediments is appreciated. Besides, in Muni 14, we found lithic tools next to charcoal remains. A clear example of the so-called stone lines was seen in Muni 24, where materials corresponding to very crude stone manufacturing industries were collected. Those tools are similar to those previously referenced by Claretian scholars in the colonial period. In Muni 28 we find clear terrace sediments that contrast with the surrounding lateritic soils. Finally, in Muni 39 flint flakes of clear human manufacture were collected. In the vicinity fragments of ceramics were also found, although their synchronic association of both types of elements is uncertain. As for Miocene sediments, these emerge in the form of terraces at points Muni 18, 43 and 44, on road slopes, located on the edge of the granitic craton that connects to Monte Mitra and Monte Allén natural reserves. Those Miocene sediments, despite being favourable paleontologically facies, no presence of macrofossils was detected [2]. Surveys carried out in the Rio Muni estuary in 2017 confirm the abundance of lateritic soils, with little stratigraphic development. However, prehistoric occupations of low intensity, possibly of the MSA, were detected although their attribution is still uncertain. The presence of lithic instruments on fluvial terraces, including large-scale elements on flakes and almond-shaped bifacial tools expands the technical repertoire of the continental region of Equatorial Guinea previously described [3, 4].

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## New Neandertal remains from Trou Magrite, Belgium

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Trou Magrite is a cave site located at Pont-à-Lesse in the Lesse Valley, commune of Dinant, Belgium. It has been known since E. Dupont conducted excavations at the site in 1867 [1]. The most recent fieldwork was done by L. Straus and M. Otte in 1991-92 [2]. Trou Magrite yielded rich lithic assemblages, osseous artifacts, mobiliary art, and numerous faunal remains. Several human remains were also recovered and identified as Palaeolithic humans by E. Dupont but have been only partially published thus far. The archaeological record covers a broad time range spanning from the Middle and Upper Palaeolithic to the Mesolithic, Neolithic, and Iron Age. An important Middle Palaeolithic collection is present, probably representing several occupation phases during the Late Pleistocene [2]. Unfortunately, although E. Dupont conducted excavations that can be characterized as modern for that time, the materials from the different so-called “fauna-bearing levels” that he defined in the field were mixed post-excavation [3]. In 2015, we initiated a multidisciplinary re-assessment of the human and faunal collections from Trou Magrite in order to update the inventory of human remains already identified, check for the presence of human remains that may have been previously overlooked, and verify their chronocultural context. We revised the already known human collection, conducted a systematic sorting of the faunal material, and combined the use of morphometrics, taphonomy, stable isotopes, dating, and genetic analyses to perform taxonomic and chronocultural identifications. Here we present two previously unidentified Neandertal fossils that we isolated from the Trou Magrite faunal material excavated by E. Dupont in the 19th century. They represent two different individuals: an adult/adolescent, represented by an upper right permanent canine, and a neonate, represented by the diaphysis of a left femur. Whereas no endogenous DNA was recovered from the tooth, the palaeogenetic analyses of the neonate femur confirmed its Neandertal status and indicate its sex to be male. We will present the biological characteristics and mitochondrial DNA phylogenetic position of the Trou Magrite Neandertals, in particular with regard to the other Northern European Neandertals. Our project adds Trou Magrite to the list of Belgian sites that have yielded Neandertal fossils and helps to emphasize the importance of the Mosan Basin in Neandertal studies.

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## Identification of a Middle Aurignacian layer at Les Cottés (Vienne, France) and evidence for apprenticeship in a lithic dumping area

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Les Cottés cave located in the Center-West part of France (Vienne), is one of the rare Palaeolithic sites which contains a stratigraphical and chronological sequence from the Middle to Upper Paleolithic transition [1, 2]. Seven layers attributed to three main cultural units, with well preserved lithics and faunal remains, are identified through the sequence located in front of the cave: Mousterian (US 08), Châtelperronian (US 06), Protoaurignacian (US 04lower), Early Aurignacian (US 04upper and US 03), Middle Aurignacian (US 02) and indeterminate Upper Palaeolithic (US 01) [3]. The Les Cottés chrono-cultural sequence allows a detailed analysis of technical behaviors for each unit as sterile layers often separate them, which limits taphonomical issues.

Here, we will focus on US 02, which sealed the entire sequence. US 01, above, revealed less than one hundred lithics and is spatially restricted to 2 square meters. An updated typo-technological analysis, based on the study of 3 129 lithics allows us to classify US 02 as a Middle Aurignacian. Only known in a handful of sites from South-West France [e.g. 4], the Middle Aurignacian, considered as a short event, is chronologically situated between the Early Aurignacian and Recent/Evolved Aurignacian. Its technical features are as follows: abundance of end-nosed scrapers, rare retouched bladelets, few Aurignacian retouched blades as well as absence of busqued burins or carinated burins. The technology for blade production is similar to what is known for the Early Aurignacian. The US 02, not only Middle Aurignacian, shows evidence for different *savoir-faire* in the process for blade and bladelet production: experienced and inexperienced knappers did contribute to the lithic assemblage from US 02. These evidences (mainly cores with obvious technical mistakes) are associated in a dumping area, where broken blades, discarded cores and discarded stone-tools are found. The last stratigraphical Aurignacian layer, US 02, from Les Cottés cave provides: 1. evidence for a short event attributed to the Middle Aurignacian techno-complex, 2. evidence for use of the site by individuals of different age classes and their equal contribution to the lithic assemblage and 3. evidence for the use of Les Cottés cave entrance as a dumping area.

Fieldworks at Les Cottés are funded by the French Ministère de la Culture, DRAC-SRA Poitou-Charentes and the Max Planck Society (Germany). Fieldworks are supervised by Prof. Marie Soressi (Leiden University).

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## **Trabecular and cortical bone structure correlate differently with terrestrial mobility in the human first metatarsal. Implications for behavioural inferences in the fossil record**

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Numerous studies have demonstrated the plasticity of both cortical and trabecular bone structure in response to mechanical loading throughout life. We examined variation in cortical and trabecular bone structure in the first metatarsal of four modern human populations to assess how both tissues correlate with terrestrial mobility level. We compare two mobile populations (Black Earth n=13, Jebel Moya n=10) to two sedentary populations (Kerma n=9, St. Johns n=16). First metatarsals were  $\mu$ CT-scanned and we calculated the ratio of maximum to minimum second moment of area ( $I_x/I_y$ ), cross-sectional area (CSA), and polar section modulus ( $Z_{pol}$ ) at 5% increments along the cortical shaft. Trabecular bone volume fraction (BV/TV), trabecular thickness, and degree of anisotropy (DA) were calculated in two volumes of interest (VOIs) in the head and two in the base. Biomechanical properties were standardized for variation in body mass where necessary. Trabecular bone volume fraction strongly correlates to terrestrial mobility with mobile populations possessing significantly greater BV/TV throughout the four VOIs with no effect on the degree of anisotropy. Cortical bone properties do not strongly correspond to inferred terrestrial mobility in the four populations. The only significant difference is that the Jebel Moya sample has significantly greater cross-sectional area of the shaft between 40 and 60 percent bone length than Kerma. The only significant correlations between cortical and trabecular bone properties were between mean trabecular thickness and CSA and  $Z_{pol}$ . No significant correlations were found between cortical properties between 40 and 60 percent bone length and trabecular structure in pooled and individual populations. Several mechanisms potentially underlie the absence of significant correlations between both tissues. Trabecular and cortical bone remodel in response to different magnitudes/frequencies of loading, with trabecular bone responsive to substantially lower strains at high frequencies. Cortical bone remodeling dramatically reduces after the adolescent growth spurt whereas trabecular structure remodels at a higher rate throughout adulthood. As such, it is possible that cortical bone represents loading during adolescence whereas trabecular bone may indicate activity levels closer to death. Sex differences in the norms of reaction to loading in cortical bone may also contribute, as males show greater variation than females in cortical but not trabecular bone. These results suggest that first metatarsal trabecular structure may be a strong proxy for population-wide mobility levels in past populations. Surprisingly, no significant correlations were found between trabecular and cortical bone properties, despite both tissues being experimentally shown to adapt to mechanical loading. Tightly controlled experimental work is required to investigate potential differences in cortical and trabecular bone biology and their responsiveness to loading. Further investigations on the patterns of covariation between cortical and trabecular bone biomechanical properties in living individuals may provide further insights.

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## And the winter arrived further south. Paleoecology during the transition between the Middle and Upper Paleolithic in central Iberia

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The environmental conditions that existed during the period between 45 and 30 ka are of vital importance for addressing the transition between the Middle and Upper Paleolithic. The current archaeological evidence points to a hiatus of Paleolithic populations in Central Iberia coinciding with the mid part of Marine Isotope Stage 3 (MIS 3), between 42 and 28 cal kyr BP [1]. This break in the archaeological record makes the paleoecological approach to this critical period difficult in this region. Here we present a new cave site, Portalón del Tejadilla (PT), which is located in Segovia, central Iberia on the southern edge of the northern Castilian Plateau. The main objective of this work is to provide new information about the paleoecology of Central Iberia during the coldest episodes of the Late Pleistocene. To that end, in this paper we present a description of the PT site including: i) the stratigraphy and geochronology of the fossiliferous deposits; ii) the analysis of the systematic paleontology of the micro and macromammals; iii) the description of the lithic artifacts; and iv) the taphonomic study of the faunal association. The detailed analysis of the faunal assemblages allowed us to document an association dominated by equids (*Equus ferus* and *Equus hydruntinus*) and hyenas (*Crocuta crocuta*) in addition with cold-adapted species such as woolly rhinoceros (*Coelodonta antiquitatis*) and giant deer (*Megaloceros giganteus*) in a hyena den site context. The radiocarbon ages obtained through ultrafiltration indicate an age between ~34.2 and 40.4 ka for the deposit, which corresponds to the MIS 3 and includes the extremely cold Heinrich 4 event (H4). Some lithic remains compatible with the Middle Palaeolithic techno-complex have been recovered. The paleoecological inference derived from the faunal assemblage suggest extreme dry and cold climatic conditions and an open environment, compatible with the steppe-dominated environment of the Eurasian steppe-tundra ecosystems further south than previously expected in the Iberian Peninsula. This site together with our previous research in the area [2] document a climatic deterioration (colder and dryer) during the mid-part of MIS 3 in Central Iberia which could have had significant repercussions on the Neandertal and anatomically modern human (AMH) populations. Portalón del Tejadilla fills the temporal gap of the transition from the Middle to the Upper Paleolithic and provides valuable paleoecological information about this crucial period. Further excavations in this area could broaden our understanding of the Paleolithic human presence in this barren region in the interior of the Iberian Peninsula during this crucial period for the human past.

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## Assemblage variability during the Oldowan-Acheulean transition at Olduvai Gorge (Tanzania). Techno-economic data from FLK West (Lower-Middle Bed II).

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A long-held consensus view among archaeologists is that the Acheulean emerged abruptly in East Africa after a temporally rapid transition from the Oldowan [1]. The inter-assemblage variability documented during the Oldowan-Acheulean transition has traditionally been ordered according to the absence/presence and frequency of handaxes and other LCTs [2]. The Bed II archaeological record at Olduvai has become the referential frame to explain cultural change and variation during this period. The emergence of the Acheulean at the Gorge was dated ~1.5 Ma and placed within Upper-Middle Bed II for many decades, being coincident with the absence of *H. habilis* remains and Oldowan assemblages which could suggest an abrupt bio-cultural replacement. However, the current discovery of FLK West has provided a new and more complex picture for the Oldowan-Acheulean transition. This ~1.68 Mya site located within Lower-Middle Bed II has become the earliest Acheulean evidence at Olduvai [3]. Equally important is the fact that FLK West is the earliest site in the archaeological record where lithic assemblages with differences in the absence/presence and frequency of LCTs are interstratified in the same sequence. Therefore, it constitutes an exceptional opportunity to assess the main factors that drove inter-assemblage variability during the Oldowan-Acheulean transition. With this objective, we have carried out a detailed techno-economic analysis in order to identify the most significant similarities and differences among the six lithic assemblages unearthed in the FLK West fluvial sequence [4]. Similarities noted in terms of raw material selection, flaking reduction and flake retouching behaviour evidence homogeneous technical decisions and cognitive skills. Differences registered in the absence/presence and frequency of LCTs likely respond to occupation differences (e.g. short-term stay vs longer-term stay; low impact vs higher impact occupation) and, in turn, the type and number of subsistence activities carried out on-site. Consequently, the most parsimonious hypothesis is that a same hominin group or taxon (i.e. *H. erectus*) knapped all assemblages. However, it is necessary to bear in mind that other hominin taxa with different cognitive skills and potentially stone tool-makers (*H. habilis* and *P. boisei*) inhabited the Olduvai basin during Lower-Middle Bed II. Accordingly, two different and complementary scenarios may explain the inter-assemblage variability documented during the Oldowan-Acheulean transition in Middle Bed II: (i) handaxe and non-handaxe bearing assemblages could be performed by the same group or taxon; (ii) non-handaxe bearing assemblages could be performed by different hominin groups or taxa. The main consequence resulted from this new picture is that the Oldowan-Acheulean transition is a complex, additive and accumulative process rather than a simple and abrupt bio-cultural replacement one.

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## Population composition and possible origin of the Levantine Aurignacian culture: the dental evidence

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Who were the Levantine Aurignacians? The considerable resemblance between the Levantine and European Aurignacian cultures led to the hypothesis that its presence in the former is due to migration of people from Europe [1]. Until very recently, the scanty human remains from this time period from the Levant limited the investigation of this matter. The current study is based on the dental remains discovered at Manot Cave (MC), Western Galilee, Israel. The cave contains evidence for human occupation during the Early Upper Paleolithic period (46-33 ka) in the form of Early Ahmarian (~46-42 ka) and Levantine Aurignacian (~39-34 ka) [2]. Six teeth (three deciduous and three permanent) were found in the cave, four of which could be thoroughly analyzed qualitatively and quantitatively. Traditional and geometric morphometric methods were used to compare the Manot teeth to a large *Homo* dental sample, including Early and Middle Pleistocene *Homo*, Neanderthals and recent modern humans. The landmark configurations represented the occlusal aspect of the dentinal crown, and the cervical and crown outlines [3,4] additionally the dental diameters were considered along with dental features such as discrete traits and taurodontism. For two of the teeth the occlusal aspect could not be considered because of the advanced degree of wear. Interestingly, the Manot dental remains variously displayed modern human and Neanderthal traits. In particular, the results showed that the upper first premolar (MC-9 P<sup>3</sup>) is very probably modern human, but the attribution of the upper deciduous second molar (MC-10 dm<sup>2</sup>) and the upper second permanent molar (MC-8 M<sup>2</sup>) to modern humans is more uncertain. The lower second deciduous molar (MC-7 dm<sup>2</sup>) might represent a Neanderthal individual. Based on these outcomes, the Levantine Aurignacian culture could be associated with either modern humans, or some kind of local or foreign hybrid population of Neanderthals and modern humans. Whether the Aurignacian evidence at Manot Cave represented a local Levantine population or a human group descendant from outside the Levant, remains a matter of debate.

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## Neanderthal maxillary ontogeny at the micro- and macroscopic scales: an integrative approach to study facial growth

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Many facial features that distinguish Neanderthals from anatomically modern humans are located on the maxilla. In Neanderthals, the maxillary body is inflated and the nasal aperture is more projecting, resulting in their unique mid-facial prognathism. Previous studies have shown that Neanderthal facial morphology differs from *H. sapiens* already at birth and throughout ontogeny [1, 2]. However, little is known about the microscopic processes underlying the development of these facial features and how they relate to large-scale morphological shape changes during ontogeny. Bone modeling is the microscopic process by which bones grow in size and model their shape [3] by simultaneously forming and resorbing bone surfaces at different locations. Unlike in *H. sapiens*, the Neanderthal maxillary surface has been shown to be mainly bone forming during ontogeny, possibly explaining their prognathic midfaces compared to modern humans [4]. Here we present new bone modeling data on four additional Neanderthal maxillae: Le Moustier 2 (neonate), Roc de Marsal (~3 years), Engis 2 (3 years) and Scladina (8 years). We also analyzed the bone modeling patterns in a large ontogenetic sample of *H. sapiens* maxillae (n = 128) from diverse ethnic origins (European, Inuit and KhoiSan) in order to better understand intraspecific variability and interpret the Neanderthal bone modeling pattern in a broad, comparative context. We applied a new, integrative approach combining surface histology and semilandmark geometric morphometrics [5]. In doing so, bone modeling patterns were analyzed using confocal microscopy, resorption was quantified and digital maps were made to visualize bone modeling patterns. Additionally, landmarks and semilandmarks were applied to three-dimensional surface models of the same individuals in order to quantify and visualize maxillary growth. In *H. sapiens* the overall pattern of bone resorption is similar in all ethnic groups, however subtle differences are present already in the youngest individuals. In particular, the Inuit bone modeling pattern consistently shows more resorption in the anterior maxilla throughout ontogeny, suggesting that the bone modeling pattern is constant throughout life in a given group. Consistent with previous findings [4], we show that the Neanderthal maxilla is largely bone forming. However, we find bone resorption located around the canine root, a pattern never observed before. At the macroscopic level, this corresponds to a forward growth in the anterior maxilla, a backward displacement in the postcanine region and an elongation of the maxillary root. This pattern differs from *H. sapiens* in which forward growth is concentrated in the superior maxilla, backward displacement largely occurs in the canine fossa and the maxillary root curvature becomes more accentuated. With the addition of new specimens from early ontogenetic stages, we are able to bring new insights into the complexity of maxillary ontogeny in Neanderthals by giving detailed information on both micro- and macroscopic developmental patterns. Our holistic approach gives complementary results between morphological changes and bone modeling patterns during ontogeny. We show that both species-specific morphology and bone modeling patterns are established in the maxilla in early ontogeny and maintained into adulthood. These findings suggest that robust predictions about facial growth can be made in fossil species whose sample size is limited. Applying this integrative approach to other facial components as well as other extant and extinct species will improve our knowledge of hominin facial ontogeny.

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## Is a knife a knife? Testing bifacial backed knives in controlled experiments

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Experiments are indispensable to address the relationship between the morphological design of stone tools and their use. In the case of the Central and Eastern European Late Middle Palaeolithic bifacial backed knives (hereafter *Keilmesser*), tool morphology seems to play a key role [1]. The asymmetric *Keilmesser* is produced in a highly standardised mode, displaying a single active edge located opposite to a blunt back, resulting in the tool's wedge-shaped section. The active edge itself is often composed of sections of significantly varying edge angles. *Keilmesser* function, however, remains entirely speculative but has been inferred from tool morphology and their well-documented production sequences, assuming repeated phases of re-sharpening and re-use. Only morpho-technological analyses combined with controlled experiments and use-wear analyses can lead to a substantial understanding of the function(s) of *Keilmesser*. Therefore, two of the largest and most prominent *Keilmesser*-assemblages in Central Europe, Balver Höhle [2],[3] and Buhlen [4], both located in Germany, serve as case studies. The study presented here is a sequential, controlled experiment with the aim to test 'cutting' as one potential function for *Keilmesser*. In this first experiment, we address functional aspects such as performance, efficiency and durability. To test this, we produced morphologically standardised samples made of the lithic raw materials encountered in the archaeological context of both sites – silicified schist and flint. These standard samples were cut bifacially and were produced with different edge angles. The choice of edge angles was based on all the measurements obtained from the archaeological material. To do so, we applied a new quantitative approach to characterise the active edge: an algorithm-based, semi-automated method to calculate angles along the edge at predefined steps from 3D models. Experiments were conducted with an industrial material teststand (Inotec-AP SmartTester) to mimic cutting movements under controlled conditions, including contact angles, cutting length, force, velocity, acceleration and the number of strokes in combination with selected contact materials. This experimental setup provides us with quantitative data about e.g. penetration depth, friction, loss of material from the tool as well as the contact material and edge angle changes. The obtained data reflect tool performance and efficiency for each combination of raw material and edge angle for a defined cutting movement. Furthermore, it is also possible to quantify edge durability. This will allow an improved understanding why Neanderthals chose this specific tool morphology including the edge angle and at what stage in the *chaîne opératoire* further reduction and/or resharpening became necessary. In the next step, these results will be combined with qualitative and quantitative use-wear analyses. Our approach will bring the functional inferences from the experimental setup together with data independently obtained from the archaeological material. Given this, we aim for a holistic understanding of the underlying tool concept and manufacturing strategy of *Keilmesser*.

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## Where are the hearths? Experimental geoarchaeological investigations of fire visibility in the Lower Palaeolithic of NW Europe

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During the NW European Lower Palaeolithic (c. 1 ma - 300 ka BP), archaeological evidence for hominin fire use is sparse, with just a handful of sites providing evidence for the control of fire occurring towards the end of the period (c. 400-300 ka BP). Regardless of the many benefits of controlled fire use (e.g. warmth, light, cooking, protection from predators, communication, niche construction), it has also been suggested that even Neanderthals were not obligate fire users, with varying interpretations of the Middle Palaeolithic evidence for fire use pre-60 ka BP. A lack of evidence for fire use can be considered from a number of perspectives: a genuine absence; a reflection of past methodological limitations; location bias; and/or preservation bias. The investigation of potential evidence for hominin fire use at individual sites has been a recent focus for experimental work, providing a more detailed understanding of fire use at particular locations [1][2][3]. However, the nature of fire visibility in the wider archaeological record, including an improved understanding of the effects of small controlled fires built on different types of substrates, and the factors controlling the preservation of fire residues is essential for our knowledge of the earliest hominins in this region. The aim of this research is, therefore, to investigate how differences in sediment type affect the visibility of fire features, and discuss what short-term field experiments can tell us about the preservation and visibility of these features in the archaeological record. Results from ongoing experimental work utilising both macro- and microscopic analyses (micromorphology, magnetic susceptibility and anhysteretic remanence magnetisation, observations of changes in lithic debitage buried at different depths and lateral extents) from small (50-70 cm) controlled fires of around 2 hours duration indicate clear differences in the visibility of fires depending on a) underlying sediment type, and b) fuel load. The results of these ongoing experiments will be discussed in the context of the lack of evidence for fire-related behaviours in the Lower and Middle Palaeolithic of North West Europe.

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## Revisiting Umhlatuzana Rock Shelter, KwaZulu-Natal, South Africa: First geoarchaeological results

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Umhlatuzana is one of the few sites with deposits spanning the Middle to Later Stone Age transition (~40–30 ka). It is thus crucial that this site is considered when documenting the development of modern human behaviour in southern Africa during Marine Isotope Stages 3 and 2. The site was excavated in the 1980s by Jonathan Kaplan. The stratigraphy of the Pleistocene part of the sequence proved difficult to discern, and the deposits showed poor preservation of organic remains, including charcoal. Kaplan [1] suggested that sediment movement may have impacted the integrity of the Middle and early Later Stone Age assemblage. Due to the questionable stratigraphic integrity of Umhlatuzana, the scientific community has been sceptical about incorporating the site's archaeological material into the general discussion on the Middle to Later Stone Age transition. In 2018, we initiated a high-resolution geoarchaeological study of the site to clarify the site formation processes of the stratigraphic sequence, aiming at the Pleistocene deposits. We excavated a small (0.75 m<sup>2</sup>) area, piece-plotting all finds in excess of 2 cm. We excavated following the natural stratigraphy and used artificial spits of 1–2 cm in thicker layers. We also took samples for OSL dating, micromorphology, phytolith analysis, and bulk sediment samples for sedimentological, geochemical, and mineralogical analyses. We present our field observations of the stratigraphy, complemented with the results of the sedimentological (particle size analysis) and geochemical (pH, loss on ignition) analyses of the sediments. We also present the analysis of the vertical distribution of piece-plotted finds. The granulometry results indicate a similar sediment texture is present throughout the sequence, confirming field observations of a consistent sedimentological environment characterised by *in-situ* weathering and aeolian sediment input. The results of loss on ignition analysis reveal a paucity of organic content in the sediments presumed to be of Pleistocene age. pH analysis demonstrate lateral changes in the Pleistocene deposits, as well as much higher values in Holocene combustion features. More fine-grained analyses will be performed to determine if acidity/alkalinity can explain patterns in the preservation of organic materials across the sequence. Analysis of the piece plotted finds demonstrates semi-horizontal layering of archaeologically denser and more sterile zones. This contradicts the initial suggestions of large scale post-depositional sediment movement. Additional geoarchaeological analyses are underway to address outstanding questions on the stratigraphic integrity of the site. With a clearer stratigraphic understanding of the site, we will be able to study the archaeological materials, assess the representativeness of the existing collections, and shed light onto the reasons behind the Middle to Later Stone Age transition.

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## Form influence on electrodermal activity during stone tool manipulation

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Humans evolved a particular cognitive relationship with objects and technology, through specialized parietal areas which are associated with tool use and body-tool integration [1]. When an object is positioned within the visual range and enters the peri-personal personal space, it represents a potential tool, being further integrated into the body scheme when handled [2]. Handling involves somatosensory perception through the skin surface and a dynamic touch based on the proprioceptive response of the whole body [3]. In this sense, tools participate to the cognitive process altering the perception of the body and activating special neural functions. Recent analysis demonstrated that handling Paleolithic stone tools does influence the emotional and attentional engagement as measured through electrodermal activity, with differences associated with tool typology [4, 5]. In this survey, we tested the correlation between electrodermal activity (electrodermal level: EDL; electrodermal response: EDR), manipulation time, and stone tool geometry. Tool form was quantified by geometric morphometrics, through 30 equally-spaced landmarks in 2 dimensions, using an experimental sample of choppers, handaxes and flakes. Coordinates were registered through Procrustes superimposition, although size was not normalized, as to evaluate the overall geometry of the tool (size and shape). The first shape component (78%) is associated with size and elongation, separating the tool types although with an area of morphological overlap. The second component (15%) is common to all tool typologies, and it is associated with the degree of elongation without size changes. PC1 is correlated with EDL and TMT ( $p < 0.05$ ,  $R = -0.8$  and  $0.8$  respectively), while PC2 is related with EDR ( $p < 0.05$ ,  $R = 0.6$ ). Namely, attention and manipulation time does increase with large and elongated tools, while arousal is specifically related to elongation. We conclude that size and widening cause higher attentional and arousal engagement in contrast to small and elongated tools. It remains to be evaluated whether such physiological reaction is due to grasping difficulties, and to what extent it may depend on the different grasping modalities (power vs precision grip).

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## Using ZooMS to assess hominin subsistence behaviour during the Middle to the Upper Palaeolithic transition at Fumane (Italy)

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Pleistocene faunal assemblages are often highly fragmented, either due to taphonomic or to anthropological processes, preventing any taxonomic identification based on morphology through traditional methods [1]. This creates a potential bias in the analysis of hominin behaviour. It results in the inevitable exclusion of a vast quantity of archaeologically valuable data, but also a problematic assignment to body size classes subject to highly variable categorization. However, bone fragmentation can still be very informative, especially regarding subsistence patterns and butchery practices. Collagen type 1 (COL1) peptide mass fingerprinting through ZooMS (Zooarchaeology by Mass Spectrometry) [2] has previously focused on ecological purposes with the improvement of the faunal spectrum or the identification of additional hominin specimens in Pleistocene contexts. However, its potential to investigate hominin subsistence behaviour and faunal carcass processing based on unidentifiable bone fragments has been, largely, unexplored. In this study, we integrate complementary data sets from zooarchaeology and ZooMS to analyse bone assemblages from the final Mousterian (layer A4) and Uluzzian (layer A3) contexts at Fumane cave (Italy) [3, 4]. Thus, we investigate the relationship between faunal composition and bone fragmentation by using untargeted ZooMS analysis correlated with traditional zooarchaeology. At Fumane, we have identified a large frequency difference between the morphologically identified assemblage and the ZooMS assemblage for a particular species within the same archaeological unit. This significant difference in species abundance is marked by a six fold-increase in the quantity of *Bos/Bison* remains in the molecularly-identified component. Comparisons of different classes of surface modifications demonstrate that such fragmentation relates specifically to hominin carcass processing behaviour [5]. High frequencies of percussion marks suggest that these bone specimens have been intentionally more fragmented by human activity than other taxa in order to extract marrow from long bones. Thus, the application of ZooMS to these taxonomically unidentifiable bone specimens gives a more informative picture about carcass processing at Fumane but also allows for a clearer picture of species composition and a more secure assignment to body size class.

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## New reflections on the EUP and AMH dispersal in Eastern Europe.

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The re-dating of sites and re-examination of artifact collections provide a basis for new reflections of the pattern of the earliest Upper Paleolithic (EUP) and related dispersal of Anatomically Modern Humans (AMH) in Eastern Europe.

Pre-Aurignacian assemblages of the East European EUP include six cultural units: (1) Streletskian, traditionally distinguished as a local transitional cultural unity [1]; (2) Levallois-derived entity or Emiro-Bohunician technocomplex [2]; (3) Zaozerian as a local cultural unit with curved backed pieces [3]. (4) Spitsyean as a regional East European culture or a local variety of Protoaurignacian [4]; (5) Cultural layer IVb at Kostenki 14 [5]; (6) cultural layer C at Buran Kaya 3.

The first two traditionally considered as transitional cultures containing a Middle Paleolithic component. The Spitsyean and cultural layer IVb of Kostenki 14 are fully developed Upper Paleolithic, associated with the skeletal remains (teeth) of modern humans.

Nowhere else in Europe pre-Aurignacian assemblages exhibit such diverse cultural traditions. Their chronology, classification, and role in the spread of the EUP and AMH remain open for discussion and are the subject of this review. The earliest Upper Paleolithic complexes at Kostenki are the most representative, most reliably dated, and yield the most archaeological material. The earliest Aurignacian is dated to 40 ka (cal) based on samples from the cultural layer in volcanic ash (LVA) at Kostenki 14. Others cultural units considered here are older, possibly overlapping with the Aurignacian at the younger end of their (uncertain) temporal boundaries.

Only the Streletskian is represented at numerous sites: five at Kostenki (K1-V, K6, K11-V, K12-III, Borshchevo 5-IV), and Sungir, Garchi 1, Nepriakhino, Vys outside the Kostenki group. The dating of the Streletskian falls between 45 ka (cal) for the cultural layer V of Kostenki 1 and 34 ka (cal) at Sungir, Vys and Garchi 1 with the likelihood that the latter will be revised downward. The Streletskian traditionally has been considered the most ancient UP and new dates confirm it with the unresolved problem of its upper temporal boundary.

All other cultural unities are represented by single sites. The bases for its cultural affiliation are the single features: microblades with rectilinear profile for the proto-Aurignacian identification; curved backed pieces for the separation of the Zaozerian as particular cultural unity; bifacial leaf-points for the attributions of the cultural layer C at Buran Kaya 3, etc. Along with well-defined cultural diagnostics, all cultural units of the East European EUP exhibit a number of similar cross-cultural indicators.

Two patterns of adaptation can be reconstructed on the basis of the raw material procurement for the pre-Aurignacian traditions at Kostenki. The Streletskian and IVb cultural layer of Kostenki 14 are characterized by the use of all available varieties of raw material with the predominance of local materials. The Spitsyean, by contrast, reflects predominance of imported black Cretaceous flint, the nearest outcrops of which are at least 150 km from Kostenki.

The current situation in classification the East European pre-Aurignacian assemblages leads to the problem: in what extent criteria for the cultural identification of the Western European Paleolithic can be used for the cultural differentiation of the Eastern European ones.

Two general models for the pre-Aurignacian EUP of Eastern Europe remain under consideration: (1) within the context of the Out-of-Africa dispersal, as a pioneer waves of the populations with unformed cultural traditions and different patterns of adaptations, and/or (2) outside of migrations concept as a consequence of the trial-and-error method in the process of search the optimal models of adaptation to local conditions and environments.

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## The utility of manganese dioxide as a Palaeolithic tinder enhancer supported by actualistic fire-making experiments

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The collection of the black minerals comprised primarily of manganese dioxide ( $MnO_2$ ) by Neandertals during the late Middle Palaeolithic in France is a known archaeological phenomenon, with some of these blocks exhibiting evidence of having been abraded to produce powder [1,2]. This has generally been interpreted as resulting from the production of black pigment that may have been applied to the body as a form of symbolic expression [3]. However, Heyes and colleagues [4] demonstrate that  $MnO_2$  can reduce the auto-ignition temperature of wood by upwards of  $100^\circ C$  and suggest that this special pyrotechnic property of powdered  $MnO_2$  may have been appreciated by Neandertals. Specifically, they suggest that the addition of  $MnO_2$  to tinder materials may have aided in fire-making. Recent findings suggesting that late Neandertals were producing fire by artificial means as early as 50,000 years ago lend credence to this hypothesis [4]. The purpose of the study described here is to test the utility of  $MnO_2$  as a tinder enhancer during actualistic fire-making experiments. The flint-and-pyrite fire-making method was employed to produce sparks that were directed onto different types of tinder, both with and without added  $MnO_2$ , to determine if and the degree to which this material improves the ability of the tinders to capture sparks, allowing them to propagate into a glowing ember. The initial results of this study lend support to the hypothesis of Heyes and colleagues by demonstrating that  $MnO_2$  improves the spark capturing efficiency of tinder material over untreated tinder, thereby reducing the time and energy required to produce fire using the percussive fire-making method. However, it was also observed that the incorporation of pyrite dust into the untreated tinder over the course of the experiments appeared to improve its ability to capture sparks, lending to the idea that pyrite powder added to tinder prior to making fire could also expedite the process and largely negate the need for collecting  $MnO_2$  for this purpose.

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## Cultural interactions. Differentiating convergence from influence in the material culture record

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Ancient DNA studies have shown interbreeding in between fossil hominin populations – something that material culture studies and studies of ancient human anatomy failed to do in a convincing manner for decades. However, beyond tracking fingerprints of interbreeding, genetic studies do not help us understand how interactions between ancient hominins unfolded. The nature of the interactions remains unknown. Genes can be acquired via peaceful as well as non-peaceful ways, are transmitted via biological processes that were not under human control until very recently and they don't have to be transmitted across generations — they can be selected against and lost. Genes are only rarely entering the fossil record and likely enter in a different location than where they were originally acquired. On the other hand, artefacts are created in a cultural context that was socially mediated and susceptible to influences from outside. Manufacturing processes are controlled by humans. Technological analysis as well as recent developments in 3D geometric morphometric methodologies enable researchers to reconstruct manufacturing processes and end-products in much higher detail. Artefacts are usually found in abundance at excavated sites and are often discovered in the location where they have been abandoned by ancient humans. Yet, material culture studies are not often used to reconstruct interactions during the Pleistocene. Studying cultural exchanges processes has always been a challenge in prehistoric archaeology. How to distinguish changes due to contact from changes arising independently, in other words: how do we set aside influence from convergence? It is traditionally thought that the archaeological record lacks chronological resolution to discuss influence. When two objects are found in an archaeological layer, how can we tell if they were deposited on the same day, same month, or even the same year? In this paper, building especially upon G. Tostevin's work [1] and other's, we will argue that we can overcome what is seen as a lack of chronological resolution by checking how many design options are available and contrast what option was taken with the number of available options. If they were 20 different options available to obtain the same product, and the same option was used by broadly contemporaneous people at places that can be geographically connected, influence will be much more likely than convergence. We will argue that a detailed reconstruction of the manufacturing processes and the shape of the end-product combined with an exploration of the options available via modelling and experimental archaeology will be a powerful instrument to identify influences. With this, we hope to work toward a better understanding of the nature of hominin interactions in the Pleistocene archaeological record.

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## Preservation of Ancient DNA in Late Quaternary Stalagmites from Western Georgia

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Ancient DNA (aDNA) is a rich source of information for archaeological and anthropological research with paleogenetic studies retrieving their information mainly from animal and human bones. Recent research has explored further paleogenetic archives, such as archaeological sediments [1] and speleothems [2, 3]. Speleothems have several potential benefits as a paleogenetic archive. First, speleothems can form closed systems, limiting the effect of leaching through layers, and may be securely dated with U-series. Secondly, preservation conditions for DNA are ideal inside the stalagmites and especially for those located deeper inside caves, where temperatures are relatively stable and no light enters the cave. Thirdly, ancient DNA in speleothems can provide information on plants and animals including humans in caves where no other material evidence is left due to taphonomy or anthropogenic removal processes. Lastly, aDNA in speleothems presents a direct link between the archaeological record and paleoenvironmental data retrieved from the speleothems. Two recent studies reported on the recovery of aDNA from stalagmites [2] and 'popcorn' calcite [3]. Zepeda Mendoza et al retrieved aDNA of marine, terrestrial and cave taxa from Holocene 'popcorn' calcite from an unusual dolerite granite gneiss cave in Sweden. Our study [2] focused on the analysis of stalagmites from a limestone hosted cave, which are commonly used for paleoclimatic reconstructions. We sampled two stalagmites from a cave in Western Georgia, Solkota Cave, and almost all samples gave aDNA reads, with typical deamination of cytosine at the terminal ends. The samples yielded aDNA from mammals (bear, roe deer, horseshoe bat) as well as plants (chestnut, hazelnut, flax) and we were able to date some of the aDNA bearing stalagmite layers to between ~ 84 ka and ~ 56 ka BP with the U-series dating method. The formation history of aDNA preserved inside speleothems - DNA source, DNA adsorption, transport (agent), deposition, speleothem formation as well as preservation conditions - is, however, still an open question and greatly impacts the interpretation of these new data. We propose three different formation models for DNA preserved in speleothems: 1) Transport of DNA from the soil cover above the epikarst dissolved in water travelling through the epikarst into the cave; 2) Adsorption of DNA to sediments and their incorporation into the speleothem; 3) Direct contact of the organism with the speleothem and transfer of their DNA. A combination of these models is also possible and the effects of speleothem formation on DNA preservation must also be considered. Reconstructing the formation history of aDNA embedded in speleothems will provide us with the contextual information necessary for interpreting the archaeological and paleoenvironmental meaning of this aDNA data.

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## Digitization of an Upper Palaeolithic double infant burial from Krems-Wachtberg

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In 2005, an Upper Palaeolithic double infant burial was discovered at the Gravettian site of Krems-Wachtberg, Krems/Danube, Lower Austria [1]. Interred with ivory beads and embedded in red ochre, the infants, identified as neonates, were covered and protected by a mammoth scapula accounting for the remarkable preservation state of the find. Originally, the burial was recovered as a block and initially stored at a climate-controlled storage facility at the Natural History Museum Vienna. In 2015, the skeletal remains were carefully excavated from the block. During this excavation, we continuously generated structured-light 3D surface scans to document each step of the bones' exposure. Here, we share the first results of an interdisciplinary effort to digitize the bones, and to archive and share the data that were assembled during the excavations, as well as the data that are produced throughout this work. To digitize the individual bones after excavation, we use a SkyScan microCT-scanner at the Division of Biomechanics of the Core Facility Campus Krems, Austria. Using the surface scans made during the excavation of the bones, we are able to reconstruct the position the remains were found in. Here, we concentrate on one of the infants (individual 2) and restore the find position of sixteen preserved carpals, metacarpals, and phalanges of its left hand as well as the cranium. Since the latter is fragmented and collapsed in part we reconstruct its anatomical shape using geometric morphometrics. The resulting data will be made available in an open-source database that will be structured for different target groups ranging from interested non-specialists to experts in the fields of archaeology and palaeoanthropology. The Krems-Wachtberg double infant burial provides the rare occasion for studying both neonate anatomy and cultural behavior of early modern humans. Moreover, since it allows for ontogenetic and phylogenetic comparisons with other subadult early modern humans or Neandertal infants, digitization and reconstruction of the skeletons will set the basis for future research.

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## Biomechanical properties of the femur during locomotor development in modern humans

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The femur is a weight bearing bone which undergoes major shape transformations in early childhood. Using an engineering beam model, previous work has demonstrated that the femoral midshaft shifts from a mediolateral to anteroposterior reinforcement throughout ontogeny indicating a transition between toddling and mature bipedal gait [1]. Albeit partial and more variable, the femur is also loaded prior to the onset of independent walking during pre-ambulatory behaviours such as crawling [2]. This study aims to further explore these locomotory transitions in terms of timing and how such behaviours may manifest differently along the length of the developing diaphysis. Cross-sectional geometric properties were calculated from the femur of 110 documented subadults from 18th and 19th century London [3,4]. Age at death was determined from coffin plates and death certificates and ranged from neonate to 8.5 years old. Each femur was micro CT scanned and orientated to the same anatomical reference system and 2D TIFF images were extracted at 35%, 50% and 65% from the distal end based on the total intermetaphyseal length. The 2D cross-sections were imported into FIJI where EPmacroJ [5] was used to define endosteal and periosteal contours and extract a range of cross-sectional metrics including cortical and medullary area, second moment of area and orientation of maximum bending rigidity. The results indicate clear biomechanical differences between the distal, middle and proximal aspects of the femoral diaphysis in response to varying locomotor stages. Most striking of these is the ratio of cortical area to medullary area, which at the 35% cross-section location demonstrates a sharp decline from birth where the femur is unloaded, followed by a steady increase from mid-infancy. Segmented regression analysis indicates an inflection point at 7 months, which coincides with the time frame during which modern children display crawling, standing and cruising behaviours [2]. Coupled with an increase in both cortical and medullary areas, the results suggest that existing and newly deposited bone is distributed away from the centroid therefore providing a mechanically advantageous structure for weight bearing activities. This research has important implications for the reconstruction of infant locomotory behaviour in past populations, including in the fossil record.

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## Diverse means to an end: domestic tool hafting in the European Upper Palaeolithic

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Human technologies have traditionally been assumed to become more and more complex over time. In the recent years, this fundamental assumption has been called into question because of the absence of sufficient supportive data and straightforward ways of measuring complexity, and other concepts, such as diversity or adaptivity, have been proposed as alternatives for approaching technology and its evolution [1]. While the theoretical and conceptual debate is ongoing, it is evident that we lack concrete and detailed data on the design and use of various types of tools in the past. For the Palaeolithic, a wealth of research has been devoted to the development of stone tool knapping. Yet, our knowledge of tool hafting and overall tool design remains limited, especially for the Upper Palaeolithic. This means that it is difficult to estimate how much skill or time the manufacturing of a given tool took in its entirety, or how varied the strategies of coping with a particular task were. It also means that linking technological change to twists and turns in human biological evolution and examining potential causalities between the two is, in many cases, impossible. In this contribution, we provide a set of such missing data on technology, focusing on the younger part of the European Upper Palaeolithic. We build on earlier work on Middle Palaeolithic assemblages, which bear evidence that stone tool hafting developed early, at latest by c. 250 kya, and was quickly applied also to tools for which hafting is not a prerequisite of use (e.g., butchering knives vs projectiles) [2]. If hafting was an innovation that gradually spread and became more frequent over time, we could assume that by the time period under study here (beginning c. 30 kya), it would have been a dominant practice for various tool categories. Our dataset, which includes c. 580 scrapers and burins from the Gravettian and Magdalenian occupations of three Upper Palaeolithic sites, Hohle Fels (Germany), Abri Pataud (France), and Maisières-Canal (Belgium), shows that this is not the case. While hafting of domestic tools, particularly scrapers, was a well-established and wide-spread practice at latest by the time of the oldest occupations examined here, nothing in our dataset suggests that the frequency of hafted domestic tools would have systematically increased over time even though the necessary know-how was clearly available. The assemblages include considerable numbers of hand-held tools. Whereas hafting of scrapers is frequent, hafting of burins is an anomaly that, interestingly enough, occurs in our study only in an assemblage that is among the oldest ones analysed. The whole dataset witnesses the use of hand-held and hafted domestic tools side by side. On the basis of these observations, we argue that in the Upper Palaeolithic, hafting was a choice that was made flexibly and depending on the situation, and the variability within and between the assemblages is best explained by a combination of factors, including raw material economy and task-specific requirements. Our results imply that to be understood in meaningful evolutionary terms, stone tool hafting needs to be considered in the context of other technological strategies, site use, environmental factors, and social organisation, including the division of labour. The variability we observe calls for studies that build on solid functional results and avoid oversimplifications in understanding the evolution of tool design and technology. To fully understand the diversity and flexibility our dataset suggests, future studies should preferably aim at collaborations between different specialists so that tool manufacture and use can be examined in relation to patterns in biological and cultural evolution as well as changing environmental and social settings.

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## How to improve the radiocarbon calibration in the Middle to Upper Paleolithic - RESOLUTION for the study of human evolution

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It is proven that Neandertals lived in Europe for more than 200,000 years and that they disappeared around 37,000 cal BP (calendar years Before Present) [1]. It is proven that *Homo sapiens* invaded Europe, met our closest relatives (Neandertals) and shared with them the same territories, part of their time (usually referred to as the transitional period), and genes [2]. What remains unknown to a substantial degree is: to what extent late Neandertal innovations were influenced by incoming *Homo sapiens*, how frequently one group encountered the other, and the region by region timing of the spread of *Homo sapiens* and the demise of Neandertals. Solving this conundrum is a crucial issue in Human Evolution [3-5] and chronology plays a pivotal role, with radiocarbon representing the backbone of chronological reconstructions for the time up to 50,000 years ago (50 ka BP). So far these topics are still highly debated due to two important factors: 1) The resolution of the calibration curve is still not accurate enough in the Middle to Upper Palaeolithic period. 2) The error range, which always occurs with the <sup>14</sup>C date, for this time period has a wide confidence interval. The calibration of radiocarbon ages for the Middle to Upper Palaeolithic events is based on the IntCal13 curve, which is the best dataset so far. Although IntCal13 allows us to calibrate back to 50,000 years BP the underlying low-resolution datasets, between 15,000 to 50,000 years ago, differ up to 2000 years depending on the archive used (terrestrial or marine). Such a wide confidence interval leaves substantial room for inaccuracies in absolute age estimates and ambiguities in chronological interpretation, creating competing scenarios and different hypotheses in human evolution. Here I will present the latest news in the field of radiocarbon, the RESOLUTION project. The results of this work will be of pivotal importance to improve European prehistory and will be crucial for interpreting the relationship between the different unique human species in Eurasia.

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## Subsistence strategies during Cantabrian Aurignacian: new data from La Viña rock shelter (Asturias, Spain)

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The Aurignacian has been considered generally the techno-complex that reflects the spread of Anatomically Modern Humans through western Eurasia. Therefore, determining the timing of its appearance is a key topic in the current debates of the demise of Neandertal populations and their replacement by AMHs. Recently, several chronological data have been published for the appearance of this early Upper Palaeolithic culture in the Iberian Peninsula [1, 2]. Apart from radiocarbon dating, other archaeological approaches such as the study of subsistence strategies allow to analyse both populations' behaviour during the Middle to Upper Palaeolithic transition. In Cantabrian Spain, recent synthesis about the palaeoeconomic behaviour during Aurignacian [3, 4] established a continuity of human subsistence during the MP-UP transition based on the exploitation of red deer, with a smaller representation of equids and bovines. Nevertheless, the chronological reassessment of this transitional period in Cantabrian Region [1] might challenge some of the previous subsistence interpretations [4] and reveals the necessity to re-evaluate some of the archaeozoological studies, as well as to include new sites with stable and well-dated stratigraphic sequences. Here the archaeozoological and taphonomic analysis of the macromammal remains from western sector-Level XIII (Early Aurignacian) of La Viña rock shelter (Asturias, Spain) are presented. The animal remains were anatomically and taxonomically identified and different taphonomic (biostratinomic and diagenetic) alterations were determined on the bones surface. The high fragmentation of the sample along with other bone surface modifications (cut marks, marrow extraction breakage, impact notches and traces of burning) indicate clearly the anthropogenic origin of the assemblage. A prey ranking dominated by red deer and chamois, followed by limited horse and Spanish ibex is visible. Moreover, the assemblage has been intensely modified by taphonomic processes characteristic of a rock shelter such as a high level of weathering and mineral manganese coatings. The high relevance of chamois shows that La Viña rock shelter does not follow strictly the general subsistence patterns established for this period, although the identified taxa is coherent with the site location in a valley close to a mountainous area. These results correlate with the other subsistence data from the Aurignacian and Mousterian levels [5] reflecting similar strategies by the hunter-gatherer groups that inhabited the site during the MP-UP transition. This study also contributes to increase the palaeoeconomic information about Cantabrian Aurignacian that is relatively scarce, in comparison to the large amount of information for the Solutrean and Magdalenian.

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## A new predictive method for quantitative 3D reconstruction of lumbar spine morphology in extinct hominins

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The human lumbar spine is composed of five lumbar vertebrae each being separated by an intervertebral disc. The articulation of these structures composes the lumbar lordosis, a ventrally convex sagittal spinal curvature that is developed secondarily to an orthograde posture of the trunk. The lumbar lordosis is thus involved in the evolution of locomotion, with a crucial role in the emergence of bipedalism in hominins. The lumbar lordosis has been assessed following different methods, e.g. by quantifying the lumbar vertebrae body wedging, the orientation of the inferior articular processes in relation to the orientation of the superior endplate of each vertebra, the correlation between the lumbar lordosis angle (LA) and the pelvic incidence [1], and the correlation between the LA and the segmental lordosis angle L4-S1 [2]. Some of these methods are dependent on the presence of anatomical structures such as the intervertebral disc or intact pelvic materials that are not usually well-preserved in the fossil record, which makes the reconstruction of the lumbar lordosis in hominins difficult. Here we assessed the morphological covariation between individual lumbar vertebrae and the entire lumbar spine [3,4], and we utilized this covariation to reconstruct the fossil lumbar spine of the Early Pleistocene juvenile *H. ergaster* KNM-WT 15000 and of the Late Pleistocene Neanderthal adult specimens Kebara 2, Shanidar 3 and La Chapelle-aux-Saints 1. For this purpose, we segmented Computed Tomography data of N=44 adults and N=32 juveniles (7-12 years old) and we measured 730 (semi-)landmarks on the resulting 3D virtual models. This allowed us to collect the 3D morphology of key anatomical features that have been proposed as related to the lumbar lordosis, i.e. the anterior pillar with the vertebral bodies and the intervertebral discs, and the posterior pillar with the processes, laminae and pedicles. The configurations were translated and rotated, but not scaled, in order to keep all the information of shape predictions influenced by size. We used the Partial Least Squares (PLS) method to calculate covariation models between each isolated vertebra and the whole lumbar spine within adults (for the Neanderthals lumbar spine predictions) and juveniles (for the KNM-WT 15000 lumbar spine prediction). The PLS predictions were performed from the isolated vertebrae that yielded the highest percentage of covariation with the whole lumbar spine (best predictive model). These predictions were cross-validated for the quantification of the prediction error. We measured the LA of the lumbar spine predictions following [1]. Results showed that covariation decreases as the lumbar vertebral level increases in both adults and juveniles, with L1 being the best predictor vertebra. We therefore used this vertebra to predict the lumbar spine morphology of the Neanderthal specimens. However, since L1 is incomplete in KNM-WT 15000, we used L4 as predictor for this specimen. When we projected our predictions onto a shape space principal component analysis, Neanderthal fossils fell within the adult human variability both in 3D morphology and LA, but below the human mean (LA in human adults ranges from 30 to 79 degrees, mean 51.5 degrees  $\pm$  11 [1]). The Kebara 2 and Shanidar 3 specimens showed the least lordotic lumbar spine predictions (LA= $\sim$ 42 degrees) and La Chapelle-aux-Saints 1 has the most lordotic lumbar spine prediction (LA= $\sim$ 48 degrees) among Neanderthals. KNM-WT 15000 falls within the human range variability but shows a lordotic angle (LA= $\sim$ 52-54 degrees) above the juvenile human mean (LA 8-10 years old= 37 degrees  $\pm$  7, LA 11-13 years old= 39 degrees  $\pm$  9 [5]). This is the first comprehensive study that assesses the quantitative 3D reconstruction of fossil lumbar spines using 3D geometric morphometric techniques. Our results reveal the potential of this predictive method to reconstruct the lumbar lordosis in extinct hominins.

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## Trabecular structure of the third metatarsal head distinguishes between a grasping and non-grasping foot

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The human foot is unique compared to that of other extant apes in its adaptations for bipedal locomotion. At the metatarsophalangeal joint, bipedal locomotion in humans is associated with a high degree of dorsiflexion at toe-off and this more extreme joint position is reflected in the external morphology of the metatarsal head and base of the proximal pedal phalanx. These morphological features related to dorsiflexion of the toes have been used to determine human-like foot loading in fossil hominins, including dorsal doming of the metatarsal head and the presence of an associated sulcus, and dorsal canting of the proximal pedal phalangeal base [1]. However, the loading regime of the metatarsophalangeal joint in fossil hominins remains uncertain, due to the presence of more primitive traits, for example relatively long, highly curved proximal phalanges [2], morphologies that are also present among more recent hominins belonging to the genus *Homo* [3]. Phalanges with such a morphology indicate the potential importance of arboreal locomotion, using the foot to grasp branches for stability when navigating unstable arboreal supports. As the internal structure of bone adapts during an individual's lifetime, it can provide additional information about loading of the metatarsophalangeal joints [4]. As such, trabecular structure of the third metatarsal head may provide signals of human-like toe off and of an ape-like grasping foot. To explore the relationship between locomotor behaviour and internal bone structure, we quantified trabecular bone of the third metatarsal head of *Homo sapiens* (n = 7), *Pan troglodytes* (n = 7) and *Pongo pygmaeus* (n = 4). Using medtool software ([www.dr-pahr.at/medtool](http://www.dr-pahr.at/medtool)), 3D morphometric maps of the distribution of bone volume fraction (BV/TV) were generated, and BV/TV and degree of anisotropy (DA) were quantified. Results reveal that the trabecular bone structure of the third metatarsal head discriminates among bipedal humans, arboreal/terrestrial chimpanzees and arboreal orangutans. The distribution of BV/TV reflects loading of the human metatarsal head in dorsiflexion during toe-off and does not indicate loading of the plantar surface. In chimpanzees, in contrast to humans, a localisation of BV/TV across the entire surface of the metatarsal head suggests loading throughout the range of dorso-to-plantar flexion, likely due to a combination of terrestrial and arboreal locomotor modes. In orangutans, the region of highest BV/TV is located on the plantar surface, reflecting frequent use of the foot to grasp arboreal substrates. The human metatarsal head is characterised by a high DA reflecting the stereotypical loading regime of this joint during bipedal locomotion. As is characteristic of trabecular architecture across the skeleton of sedentary human populations, the human metatarsal head has a low BV/TV [5]. This human-typical signal may be due to lower overall activity levels. As the internal bone structure of the third metatarsal head reflects locomotor behaviour among these three extant taxa, it may further inform interpretations of foot use, both during toe-off and grasping, among early hominins.

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## Sedimentary DNA Analysis from FAY-NE1 Jebel Faya, UAE

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We report on the first ancient sedimentary DNA analysis from the FAY-NE1 rock shelter at Jebel Faya, Sharjah, UAE. The Jebel Faya rock-shelter (FAY-NE1) is the oldest stratified site in Southern Arabia (1). The site contains a 5m deep sequence of archaeological levels from the Palaeolithic to the Iron Age. The work of Armitage et al (1) and Bretzke et al (2) indicate that FAY-NE1 occupation was linked to periods of increased freshwater availability punctuated by lack of occupation during dry periods. The application of sedimentary DNA analysis promises to dramatically increase our understanding of human occupation of FAY-NE1 and Southern Arabia. The Neolithic levels comprise approximately 1m of sediment and are sealed off from the Palaeolithic layers by a dense sand layer. The layer has been dated to 9,500 BP and contains a rich archaeological assemblage (3). The Neolithic occupation of Jebel Faya is the first reoccupation of the site since the 'Assemblage A' Palaeolithic layers dated to 40 Kyr. In 2018 sediment samples were taken from the Neolithic levels of FAY-NE1. Sediments can yield ancient DNA from eukaryotes, prokaryotes and viruses and as such can provide a wide range of data about human ecology and promise to greatly enhance our understanding human-environment interaction. Two sets of samples were collected for analysis: set one were taken from the Eastern section of Trench 4 and set two were taken from the Southern section of Trench 37. Samples were collected horizontally across the sections and control samples from the exposed surface of the shelter and additional controls derived from the archaeological layers directly above and below the targeted Neolithic levels. To minimise the risk of contamination by modern DNA a custom developed sample contamination prevention protocol was followed during sampling activities. Sediments were processed in the dedicated ancient DNA laboratory at the Institute of Genomics at the University of Tartu following published protocols (5 & 6).

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## Fundamental Fats – Experimental research into the use of molecular biomarkers for investigating (prehistoric) combustion features

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The controlled use of fire is arguably one of the greatest achievements of humankind. Fire provides warmth, light, the ability to cook and protection from predators and insects. However, the research into the evolutionary history of fire is far from clear and has seen a lot of debate over recent years. To gain a proper understanding of the ways in which Palaeolithic hunter-gatherers used fire, the evidence that is left behind has to be carefully investigated. Lenses of heat-altered sediments, associated with combustion features, offer a rare opportunity to investigate the function of specific fireplaces by applying residue analysis, as known for the study of ceramics. Residue analysis uses molecular biomarkers to identify the organic substances preserved either as amorphous residues or as absorbed molecules [1]. Unfortunately, the (post-)depositional processes affecting this residual organic matter in fireplaces are poorly understood [2] [3]. Previous attempts have been undertaken to experimentally investigate the deposition of organic matter in combustion features [4], but these were never performed under controlled conditions that properly assess the molecules released from the combustion (i.e. heating under oxygen-rich conditions) of organic materials in a fireplace.

This study is the first controlled, laboratory-based investigation of the deposition of organic matter in the sediment below fireplaces with the goals of 1. identifying molecular compounds that can be used to reconstruct heated organic materials; 2. investigating the penetration depth of the identified compounds; and 3. devising a sampling strategy that can be applied in the excavation of combustion features at (Palaeolithic) archaeological sites. To investigate the molecular signatures of several suggested fuels, four materials were heated above a layer of sand in a Carbolite tube oven to 200, 300 and 500 °C in aerobic (i.e. oxygen-rich) conditions. These materials were bone (bovine femur), birch wood (*Betula pendula*, as representative of deciduous wood), pine wood (*Pinus sylvestris*, as representative of coniferous wood), and bone marrow (bovine femur, sans bone). Marrow was included as a separated category to identify what the organic signature of bone looks like when marrow had been extracted from bone for consumption prior to heating. Sediment samples of these experiments were analysed for their organic content using gas chromatography (GC), gas chromatography-mass spectrometry (GC-MS) and pyrolysis-GC-MS. Subsamples were taken for each centimetre of depth, of which the C/N levels were determined to investigate the penetration depth of the deposited organic matter.

Initial results of these experiments indicate that molecular biomarkers can be used to distinguish between animal (bone) and plant (birch and pinewood) resources used as fuel. However, these distinctions can only be made at low temperatures (200 °C). At higher temperatures, these materials combust completely and leave no recognisable traces in the sediments below the combustion features. This suggests that organic matter will only be recognisable with the abovementioned methods in areas of the fireplace where temperatures remained low (e.g. on the peripheries or at larger depths). Future studies should focus on extending the knowledge of depositional patterns of different organic materials by performing additional experiments. This will enable the identification of different materials. Furthermore, the effects of post-depositional processes should also be investigated to create an understanding of which biomarkers can be expected after extended periods of time. For now, this initial study supports the notion that the use of molecular biomarkers in the investigation of fire use has great potential and can possibly help resolve long-held debates in Palaeolithic archaeology by identifying organic materials that are otherwise invisible to archaeologists.

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## Are patterns of diversification scale-free? A multi-order analysis of correlates of subspecies formation.

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The factors underlying the rate of lineage diversification are a topic of interest across evolutionary biology. In addition to the obvious extrinsic factors, a number of intrinsic ones that predispose lineages to diversify regardless of extrinsic context have been identified in mammals, including small body size, faster life histories, and ecological specialisation [1, 2, 3]. However, what is not known is whether these factors are scale-free: that is, whether the same or different factors influence the rate of formation of subspecies as they do species. Here, we address this question by comparing the number of subspecies across pairs of sister clades, for Primates and three other mammalian orders. Since subspecies represent genetically and spatially distinct intraspecific populations, the approach we take here is to compare numbers of subspecies ('subspecies richness') between 386 primate, carnivore, cetacean, and artiodactyl species, each of which is one of a pair of sister species. We examined whether, within the 193 pairs, asymmetries between species' body mass, age at female maturity, dietary diversity and time since divergence (TSD) correlate with asymmetrical subspecies richness. If such correlated asymmetries are evident, this implies a relationship between the trait of interest and the likelihood of a species to fragment into distinct, isolated populations. Comparisons between sister species, as opposed to whole-phylogeny approaches, do not suffer from the confounding effects of phylogenetic nonindependence. Moreover, they will yield the clearest signals of relationships and trends in the factors that shape sub-species richness and whether these are the same as for species richness. In all four orders, subspecies richness differs between sister species in a large proportion of total pairs. In the Primate order as a whole, per-pair differences in subspecies richness are independent of TSD. This implies many sister species do not share a common rate of subspecies formation and extinction 'inherited' from their last common ancestor, and further, that differences in their intrinsic characteristics might account for these asymmetries. This pattern is mirrored in artiodactyl and cetacean species, but not in carnivores, where longer TSD correlates weakly with increased differences in subspecies richness between sister species. Within the Primate order, however, there is heterogeneity: the data suggest a weakly negative relationship between TSD and pairwise difference in subspecies richness in the Atelidae and Indriidae, contrasted by a weakly positive relationship between TSD and pairwise difference in subspecies richness in the Hylobatidae, Cebidae, Pitheciidae, and Lemuridae. Correlations between the intrinsic traits (body size, female life history and dietary diversity) and subspecies richness show a mosaic pattern across the four orders. In Primates, subspecies richness does not correlate with body mass or dietary diversity, but is significantly higher in species with slower life histories relative to their sister species. This relationship is especially pronounced in pairs where age at female maturity differs by more than 30% between the sister species. This pattern is surprising given previously documented associations between "fast" life histories and high species richness in other mammals [4]. In contrast, artiodactyl subspecies richness follows the species-level pattern, implying a scale free evolutionary process operates for that order. In carnivores, none of the three intrinsic traits of interest correlate with subspecies richness. In cetaceans, higher subspecies richness is associated with faster life histories in half of the pairs, with the other half showing the opposite pattern. We discuss the implications of this approach and these results in terms of how macro- and microevolutionary processes are related, and how and why primates may differ from the other orders.

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## 10,000 km and 21 flat tires: New interdisciplinary archaeological investigations of the palaeolakes and caves in the Gobi-Altai, Mongolia

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Mongolia lies in a critical place for understanding the relationship of climate variability and its connection to hominin dispersals and interactions in northern latitudes. Previous fieldwork has demonstrated the occurrence of plentiful surface sites of Palaeolithic age. However, there is a dearth of stratified archaeological sites, particularly in the southern regions of the Mongolia, including the Gobi Desert. Though it lacks stratigraphic context, the Salkhit fossil has recently been dated to ~34.4 ka cal BP, and it has been identified as *Homo sapiens* on the basis of mtDNA [1]. This demonstrates a potential for fossil preservation in the region. The relatively few stratified archaeological sites in Mongolia are mostly located in northern major river valleys [2] and in caves in the south in the Gobi-Altai [3]. Though surface sites have indicated that Palaeolithic hominins were once widespread across the region, little information is available about their depositional and environmental contexts. Yet, climate reconstructions and palaeolake investigations indicate frequent wet and warm periods during Marine Isotope Stages 5, 3, 1 [4], and favourable conditions for mammals and hominins. Because Mongolia plays a critical role in understanding dispersal processes and hominin adaptations to northern zones, a new interdisciplinary archaeological field project has been launched in the Gobi-Altai region, with the aim to investigate caves and palaeolakes. At the outset of the project, a GIS study was initiated, with the aim to investigate potential routes of hominin movements across northern Asia in the Late Pleistocene [5]. Satellite imagery and digital palaeolake level reconstructions provided targeted survey areas for both environmental and archaeological investigations. Ground-truthing fieldwork has demonstrated the presence of caves throughout the Gobi-Altai Mountains and a multitude of palaeolake features throughout the basin-range topography. The survey indicated that many of the caves were small, with little sedimentation. One speleothem was found and some caves contained Holocene artefacts with associated environmental information. Survey of targeted palaeolakes revealed the presence of lithic artefacts with Middle Palaeolithic to Holocene typologies, in association with relict palaeolake landforms. One of these contained human remains and associated palaeoenvironmental data. The project has revealed a long record of human occupation in the region beside palaeolakes, which suggest that warmer and wetter periods provided favourable environmental settings for hunter-gatherers. Future fieldwork aims to hone in on locating and dating these palaeolakes and archaeology in tandem, allowing us to assess dispersals and human adaptations to fluctuating environmental conditions in northern latitudes.

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## Novel strategies for the morphological analysis of cancellous bone: implications for human evolutionary studies

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The morphological design of cancellous bone helps dissipating forces transmitted by the overlying cortical bone. In addition, trabecular tissue is responsive to variations in nature, direction, frequency, and magnitude of load throughout life and therefore reflects directly how a joint or bone was used [1]. Such plasticity has been considered by physical anthropologists. Studies of extant primates have attempted to identify behavioural signals in trabecular structure and revealed variations in accordance with habitual mechanical loading during locomotion in humans and other anthropoid primates [2]. Trabecular bone has also been considered for reconstructing the behaviour of fossil and extant hominoids [2]. Other studies focused on the biomechanical role of cancellous bone in responding to masticatory stress [3]. Another interesting point is the remodelling of cancellous bone in response to stressful conditions. Trabecular morphology in the mandible and long bones has been observed to vary considerably in response to circumstances altering hormone balance [4] or nutrient intake [5]. Therefore, cancellous bone is of great interest in the study of human evolution for addressing functional and biological questions. Although the advent of micro-Computed Tomography ( $\mu$ CT) and digital manipulation software increased the research opportunities, the morphological characterisation of cancellous structures remains to be expanded. Because of its inherent complexity, cancellous bone sets serious obstacles to morphological analysis. As of today, studies relied mostly on bone volume fraction, trabecular thickness and orientation, and large amount of information is potentially hiding behind such apparently inextricable complexity. In addition, as most studies rely on the traditional approach based on the analysis of small subsamples of the cancellous area of interest, there exist intrinsic ambiguities in defining homology between trabecular regions in intra- and inter-specific studies. In addition, these subsamples bear only local information and do not account for three-dimensional variations of the trabecular properties across the bone. Summarising, the study of cancellous bone is limited by (I) the lack of viable proxies for morphological characterisation and (II) the difficulties encountered in choosing the regions to be analysed. Here we describe methodological strategies conceived to overcome these limitations. First, we introduce a protocol for the semi-automatic isolation of cancellous bone in  $\mu$ CT data. This procedure relies on the combination of image processing operators (“Dilation” and “Erosion”) into a sequential workflow. The protocol results in the separation of cortical, cancellous bone and the intermingled voids, each as a three-dimensional volume encompassing the whole skeletal element under study. Following, we present a set of variables calculated on the “morphological skeleton” of the trabecular structure. Morphological skeletons are thinned, simplified structures representing the minimal descriptor of complex shapes and are obtained through a process usually referred to as “skeletonisation”. The nodes and branches of the skeleton are used to calculate a set of descriptors characterising the morphological complexity of the structure: trabecular spatial density, connectivity, length, thickness, tortuosity and fractal dimension. The biological meaning of the descriptors was tested on a sample of cancellous bone of the mandibular condyle in hominoids. The results show that the descriptors behave as good proxies of morphological complexity of trabecular structures. In addition, the measures are consistent within each species, therefore demonstrating the feasibility of using these descriptors for addressing functional and biological questions in human evolution.

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## An image-based approach to study hand function in primates

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Humans are characterized by a high manual dexterity, which is for a large part due to our relatively long and highly mobile thumb. This high mobility is linked to the saddle-shaped basal thumb joint which functions as a universal joint with two degrees of freedom. Advanced manipulative capabilities and high thumb mobility are, however, also observed in some non-human primates with a different configuration of the basal thumb joint. Members of the genus *Pan*, the closest extant relatives of humans, use complex grip types, such as power grips and modified precision grips, and are capable of tool use [1]. In our study, we focus on the basal thumb or trapeziometacarpal (TMC) joint in bonobos (*Pan paniscus*, n=5), and compare it to the functional anatomy of the TMC joint of gibbons (Family Hylobatidae, n=7) and humans (*Homo sapiens*, n=5). We acquired CT-scans of primate cadaveric hands in different functional positions (thumb ab/adduction, flexion/extension) and grip types (power and precision grips) using a translucent rig. In addition, we obtained microCT-scans of the first metacarpal and trapezium of these specimens. 3D reconstructions were made of the thumb in the different positions using dedicated image processing software (Mimics, Materialise, Leuven). A kinematic analysis of the TMC joint was done using the CT-based reconstructions of the thumb bones using custom-written Python-code. MicroCT images were used to obtain high-resolution meshes of the trapezium and first metacarpal, allowing finite-element analysis of the joint contact forces. Finally, we also performed detailed dissections of the muscles and ligaments surrounding the TMC joint in all specimens. The kinematic analysis showed that the range of motion at the TMC joint is very similar between bonobos and humans, yet humans are characterized by a higher degree of thumb extension which could not be explained by differences in joint curvature[2]. Detailed study of the surrounding ligaments indicated that the volar ligaments are more well-developed in bonobos compared to humans, which might constrain metacarpal extension. In contrast to bonobos and humans, gibbons have a ball-and-socket-shaped TMC joint. This, together with the deep digit I-II cleft, gives the short gibbon thumb a higher range of motion in all three planes compared to bonobos and humans. Remarkably, the ligamentous constraints are very similar to those observed in bonobos and humans, with a marked pollical oblique ligament which likely restricts axial rotation of the first metacarpal. Studying how different skeletal configurations relate to thumb, and ultimately hand, function in extant primates can provide an effective means to establish form-function relationships that can aid the interpretation of fossil primate remains. Importantly, properties of the surrounding soft-tissue should not be overlooked as joint function cannot be explained by bone morphology alone.

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## Neandertal population histories from sediment nuclear DNA

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The study of hominin history has progressed through both archaeological and genetic insights. In recent years, ancient DNA sequencing from fossils has allowed the association of genetic populations with specific places in time and space. However, many archaeological sites lack associated hominin fossils, frustrating genetic analyses. Even when fossils are found, they often do not cover the full time-span of a site, or sampling them for DNA may not be possible. Recent work has demonstrated the sequencing of mammalian and hominin mitochondrial DNA (mtDNA) from sediment samples [1]. However, mtDNA provides limited data for the resolution of population relationships. Here we present targeted enrichment and sequencing of hominin nuclear DNA from sediments. Of particular concern is the mixture of hominin and non-hominin (faunal) DNA present in the majority of sedimentary deposits. With this in mind, we produced a set of probes targeting 1.7 million informative SNPs in the nuclear genome - specifically at loci with high genomic divergence in a set of 15 eutherian mammals. We then developed an approach to evaluate the extent of microbial and faunal DNA in our data, along with statistical methods to account for such non-hominin DNA. We applied these methods to sediment samples from Galería de las Estatuas [2], a site in northern Spain, and Denisova [3] and Chagyrskaya [4] caves, in the Altai Mountains in southern Siberia. In total, we identified and sequenced Neandertal nuclear DNA from approximately 30 sediment samples, in stratigraphic layers spanning 55kya - 130kya. We then placed each sample on a Neandertal phylogenetic tree, as defined by three high-coverage Neandertal genomes, and for each sample inferred the most likely Neandertal lineage, and a divergence date from that lineage. In some instances we are able to demonstrate population transitions within a single cave, and associate these changes with specific layers. In others, all layers are associated with a single Neandertal lineage, suggesting a more homogenous occupation. This work demonstrates that detailed genetic analyses may be possible from many more archaeological sites than was previously thought, and is particularly encouraging for time-series studies of single sites, or for sites with a sparse fossil record.

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## Survival of late Pleistocene hunter-gatherer ancestry in the Iberian Peninsula

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The Iberian Peninsula in Southwestern Europe formed a periglacial refugium for Pleistocene hunter-gatherers (HG) during the Last Glacial Maximum (LGM) [1], which served as a potential source for the re-peopling of northern latitudes [2]. After 14,000 years ago, following the warming interstadial Bølling/Allerød, the genetic signature present in Europe was dominated by ancestry associated with the individual from Villabruna, generally called Western HG (WHG). This cluster had largely replaced the earlier El Mirón genetic cluster, comprised of 19,000-15,000-year-old individuals from Central and Western Europe associated with the Magdalenian culture [2]. However, little is known about the genetic diversity of the HG in the Southern European refugia. We aimed to further refine the HG genetic structure in the Iberian Peninsula during the Upper Paleolithic and Mesolithic, and to characterise the HG ancestry sources that contributed genetically to Neolithic groups. We successfully generated autosomal genome-wide data and mitochondrial genomes of 10 new individuals from key sites in the Iberian Peninsula ranging from 13,000–6,000 calibrated years before present (years cal BP) and dating to the Late Upper Paleolithic (n = 2), Mesolithic (n = 1), Early Neolithic (n = 4), and Middle Neolithic (n = 3). We furthermore improved the sequencing depth of one Upper Paleolithic individual from the Troisième caverne of Goyet (Belgium) dated to 15,000 years cal BP and associated with the Magdalenian culture [2,3]. Our results highlight the late survival of another Paleolithic lineage in Iberia, previously reported in Magdalenian individuals. We show that all Iberian HG, including the oldest individual from El Mirón (~18,600 yrs cal BP), carry dual ancestry from both WHG and Magdalenian-associated individuals. Thus, our results suggest a connection between refugia earlier than 14,000 yrs cal BP, resulting in a genetic ancestry that survived in later Iberian HG. Our new genomic data from Iberian Early and Middle Neolithic individuals show that the dual Iberian HG genomic legacy pertains in the peninsula, thereby serving as a genetic tracer and suggesting that expanding farmers mixed with HG locally.

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## New chronological constraints for the Lower Palaeolithic site of Cueva Negra del Estrecho del Río Quípar, Caravaca de la Cruz, Murcia, Spain: Preliminary ESR dating of the late Early Pleistocene fauna

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Combined uranium-series electron spin resonance dating is being applied currently to a series of fossil herbivore teeth (*Equus cf. altidens* and *Stephanorhinus* sp.) from several stratigraphical units of the final Early Pleistocene 5 m-deep sedimentary sequence at the Palaeolithic site of Cueva Negra del Estrecho del Río Quípar, which is situated in the Segura drainage basin, in southeastern Spain. The tooth samples first were pre-screened using high-resolution laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS). Interestingly, these uranium-series analyses showed no evidence of uranium leaching from the dental tissues, thus suggesting the suitability of the samples for ESR dating. A mean apparent U-series age of  $300 \pm 112$  ka was derived from all dental tissues sampled ( $n=78$ ). This must be regarded as a *minimum* age constraint for these fossil teeth, as uranium uptake may be delayed significantly after death of an organism. Combined uranium-series and electron spin resonance age results are obtained using both the US (U-series) and CSUS (Closed system U-series) uptake models [1]. The latter typically provides a *maximum* age constraint for a given sample. For instance, a preliminary initial result points to a CSUS-ESR age of  $890 \pm 136$  ka (*ca.* 0.89 Ma) for equid tooth CN-1511 from Cueva Negra. The chronology of the site is supported by two independent methods [2]. Magnetostratigraphical findings imply correlation of the entire sedimentary infilling with the Matuyama Chron, and therefore an inferred age  $>0.78$  Ma. Biochronological considerations are consistent with a final Early Pleistocene age because the palaeontological assemblage includes both characteristic large fauna (e.g., the cervids *Dama cf. vallonnetensis* and *Megaloceros novocarthaginiensis*) and small mammals (*Iberomys huescarensis*, *Mimomys savini*, *Pliomys episcopalis*, *Prolagus calpensis*, *Stenocranius gregaloides*, *Terricola arvalidens*, *Victoriamys chalinei*). The fossils occur throughout a 5 m-deep undisturbed sedimentary sequence which was deposited by intermittent fluviolacustrine alluviation, during a short period of geological time [3] (plausibly MIS-21, *ca.* 0.87-0.81 Ma), and has provided pollen typical of temperate environmental conditions. Consequently, magnetostratigraphy, biochronology and numerical dating consistently support a late Early Pleistocene age for Cueva Negra, most likely between *ca.* 1.03 and 0.78 Ma when considering the 1-sigma upper range of the preliminary CSUS-ESR age available for CN-1511. Ongoing combined U-series/ESR dating of other fossil teeth will enable further definition of chronological constraints. Excavation at Cueva Negra has uncovered a bifacially-flaked Acheulian handaxe, a complex industry of small artefacts, including flakes removed by repetitive flaking of small cores and pieces with retouched edges, as well as evidence of combustion in a deep level [4]. There are no hominin fossils (anterior teeth of a small *Ursus deningeri*, perhaps a female, were mistaken for Neanderthal teeth and wrongly appear as such in some publications). Given contemporaneity of the Cueva Negra sedimentary deposits with *Homo antecessor*, dated to *ca.* 0.95-0.78 Ma [5] at the Gran Dolina in the Sierra de Atapuerca in northern Spain, an intriguing question is whether we owe the Palaeolithic assemblage and combustion at Cueva Negra to that hominin species.

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## KSD-VP-1/1: the “Big Man” just got bigger

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The 3.6 Ma old *Australopithecus afarensis* skeleton KSD-VP-1/1 known as “Kadanuumuu” from Woranso-Mille, Ethiopia [1], is pivotal for evaluating morphological variation and sexual dimorphism within the East African australopithecines given its relative completeness and large body size. Its robustness in combination with a narrow greater sciatic notch suggest that KSD-VP-1/1 was probably male [1]. The diameter of its hip joint previously generated a body mass estimate of 59.5 kg, which is nearly double that of the 28.9 kg calculated for the supposed female *A. afarensis* specimen A.L. 288-1 [2]. Here, we reassess the morphological variation and sexual dimorphism within *A. afarensis* based on our novel reconstruction of the KSD-VP-1/1 hipbone. We performed a 3D geometric morphometric analysis based on 24 homologous landmarks with a sample of pelves from extant humans (n=60), chimpanzees (*Pan troglodytes*; n=35), gorillas (*Gorilla gorilla*, *G. beringei*; n=45) and orangutans (*Pongo pygmaeus*; n=30), as well as restored hipbones of A.L. 288-1 (*A. afarensis*) [3], Sts 14 [3] and StW 431 (both *A. africanus*), and MH2 (*A. sediba*) [4]. Our reconstruction of the KSD-VP-1/1 hipbone was done by virtually reassembling the individual pieces of the fractured specimen after removing the adhering matrix. Then, we utilized landmark registration methods coupled with thin-plate spline-based warping of A.L. 288-1 to estimate the missing regions of the hipbone such as the iliac crest, the ischiopubic ramus and the pubic symphyseal body. Additionally, least squares best-fit regions were fitted to the undistorted sections of the acetabulum to estimate acetabular size. Using published regression equations [2], we predicted a femoral head diameter of 40.9 mm, which translated into a body mass range of 64-68 kg. These values are slightly larger than those previously published [2], thereby confirming the enormous body size variation within these early hominins. The principal component analysis of the Procrustes shape coordinates for the hipbone landmark configurations showed that KSD-VP-1/1 was closer to Sts 14 (*A. africanus*) rather than A.L. 288-1 (*A. afarensis*). This trend was maintained even when size-adjusted residuals were plotted to control for allometric influences on the shape data. Humans and australopithecines had different trajectories when residual shape components were compared to the common allometric component, suggestive of unique scaling trends for each group, even among different reconstructions of the same specimen (Procrustes ANOVA;  $P < 0.01$ ). This adds to our previous geometric morphometric analysis of the KSD-VP-1/1 sacrum [5], which demonstrated the presence of a surprisingly narrow, and likely primitive, shape of the sacroiliac joint that distinguished it from that of A.L. 288-1 and Sts 14. Procrustes distance-based pairwise permutations confirmed this morphological disparity with differences between KSD-VP-1/1 and A.L. 288-1 exceeding 98% of pairwise comparisons within modern humans. Thus, our reconstruction and geometric morphometric analysis of the KSD-VP-1/1 hipbone contextualizes its unique morphological variation and its large body size relative to other australopithecines. These findings highlight the morphological heterogeneity within the *A. afarensis* hypodigm. The peculiar shape of the KSD-VP-1/1 sacroiliac joint in combination with the robustness of the pelvis itself suggest possible functional and taxonomic diversity within the East African australopithecines that further research will need to elucidate.

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## Multi-enzyme digestion of Pleistocene bone proteomes

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The study of ancient proteins, or palaeoproteomics, has recently seen its first Pleistocene applications to human origin studies. These range from the identification of faunal complexes associated with hominin occupancy through Zooarchaeology by Mass Spectrometry screening (ZoomS; [1]) to studying hominin phylogeny based on ancient protein sequence data [2]. The latter provides a second biomolecular method to study the phylogenetic relationships between hominin individuals and populations, in addition to the now well-established ancient DNA methods. The success of a phylogenetic study of ancient protein sequence data relies on two aspects. First, the number of identified ancient proteins. Second, the amino acid sequence coverage obtained for each of these proteins. It is therefore highly beneficial to maximise these aspects, especially when aiming to assess the phylogenetic relationship between closely related species, i.e. hominins. Normally, ancient protein workflows utilise only a single protease, trypsin. It is known from studies on modern samples that the use of alternative or additional proteases significantly increases proteome recovery and/or sequence coverage [3]. Although a small number of ancient protein studies have utilised non-trypsin proteases [4], their general performance across different states of preservation has not been explored. We present a direct comparison of several proteases using Late Pleistocene bone specimens. First, we obtain Equidae bone proteomes in different states of degradation using six different proteases in parallel. We observe that each of these proteases provides access to different sequence regions, and in some cases entirely different proteins. Second, we obtain bone proteomes from a Neanderthal specimen identified through ZoomS at the Neanderthal type site, the Kleine Feldhofer Grotte (Germany [5]). We observe that the use of alternative proteases or multiple parallel digestions using several proteases has a significant impact on the recovery of single amino acid polymorphisms (SAPs) within Hominidae. Our research therefore indicates that in addition to trypsin, other proteases can be successfully incorporated into (existing) palaeoproteomic workflows to significantly increase the phylogenetic potential of ancient skeletal proteomes.

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## Island South East Asia and its important role in hominin speciation

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Island Southeast Asia has in more recent decades been viewed by palaeoanthropologists primarily as a destination for migrating hominins—initially *Homo erectus* and later *Homo sapiens*. Traditionally palaeoanthropologists have considered Africa and Europe as more significant in the evolution of new hominin species. In this paper, we suggest that in light of recent discoveries it is time to revisit this approach. The results of recent phylogenetic analyses of *Homo floresiensis* (1) and the discovery of *Homo luzonensis* (2) raise the possibility that Island South East Asia was a centre of hominin speciation. Genetic data from contemporary *H. sapiens* from Sahul (Australia and New Guinea) indicate an unusually high level of hybridization with Denisovans, with suggestions that two distinct Denisovan lineages were located in Island South East Asia. One of these lineages appears to be situated east of the Wallace Line and possibly even in Sahul (3). The suggestion that archaic hominins may have reached Sahul is highly significant, however, it is currently not supported by any fossil or archaeological evidence. Recent genomic evidence therefore supports the idea that Island South East Asia may have acted as a hybrid zone for hominins with evidence now being detected for admixture between two distinct Denisovan lineages as well a smaller admixture signature of ~1% that has tentatively been accredited to *Homo erectus* (3). With evidence now suggesting that four archaic hominins may have been contemporaneous in Island South East Asia, (*H. erectus*, *H. floresiensis*, *H. luzonensis* and the Denisovans) it would appear that the region had greater hominin diversity than Europe or Africa during the late Pleistocene. Further research is urgently required to refine our understanding of the age of some of the hominins (for example the age of *H. erectus* continues to be contentious, see 4), but by and large evidence for introgression indicates that these hominins did overlap with *H. sapiens*. Support for the idea that Island South East Asia was a centre of hominin speciation and hybridization is provided by the many plants and non-hominin animals in the Wallacean region that exhibit high levels of endemism. This change in perspective in relation to our understanding of hominin evolution in Island South East Asia has a number of significant implications for our understanding of human evolution in more general terms, and we will end by outlining the most important of these implications.

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## A cognitive forager's landscape? The profitability of marine and subterranean foods for chacma baboons and humans in South Africa

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The Cape south coast of South Africa has yielded the earliest archaeological evidence for behavioural and cognitive modernity in humans dating back to 100 ka, and this evidence overlaps with the earliest evidence for intertidal foraging of shellfish. One explanation for this overlap involves the high levels of brain-specific nutrients in the marine foods and a foraging environment that selected for cognitive foragers. Some argue that the lack of Oldowan lithic material, contrasted with the abundant Acheulian presence in the Cape Floristic Region (CFR), can be attributed to the advanced cognition that hominin foragers would have required to take advantage of the main sources of carbohydrates, fats and protein in the CFR – namely the underground storage organs of geophytic plants and marine intertidal foods. To date, we have only been able to speculate on the cognitive requirements for exploiting these resource bases, as the only return rate data available comes from human foragers. In this study, I identify three levels of cognition involved in exploiting intertidal and subterranean CFR foods most optimally: sensorimotor intelligence for extractive foraging; spatio-temporal intelligence for tracking patchily distributed hotspots, complex phenological patterns as well as tidal patterns; and exploitation intelligence involving collection, processing, preservation and storage strategies. I present data investigating the first level in a non-human primate model for earlier hominins, the chacma baboon (*Papio ursinus*).

I compare caloric gains within a given time period for these resources between humans (measured directly) and baboons (modelled). To calculate caloric return from shellfish for baboons, I collected the discarded shells after marine-foraging events, and used allometric relationships between shell length and caloric content to calculate the total caloric gain at a troop level, which I then divided by the total number of sub-adult and adult baboons present to estimate individual return. I compare baboon data to published human data from the same region. To calculate return rates from underground storage organs (USOs) of geophytic plants, I analysed footage of digging in baboons, and calculated digging times for successful and unsuccessful digging events. Using this data, I modelled potential return within a given time frame, incorporating the average mass and caloric content of corms from the same geophytic species. Along with an assistant, I conducted human digging experiments to allow for comparisons of success and return in a given time period in the same region between humans and baboons. Under ideal tidal and weather conditions, baboons met only ~1-2% of daily energy requirements through marine foraging. Individual humans, under ideal conditions and in the same region, could collect 100-126% of their daily energy requirements in an hour [1]. In rocky sandstone fynbos, adult female baboons and humans exhibited a success rate of 52% and 56% respectively when digging for USOs, and successful digs took on average 4.2 min and 11.7 min respectively to complete. In this habitat, baboons were thus more efficient USO foragers than humans. Since 50% of human foraging bouts for USOs in different habitat types in the same region yielded 100% of human daily energetic requirements within two hours [2], it is likely that this resource base is equally profitable for baboons. These data provide the first glimpse into the differences in potential profitability of two important resource bases during the cognitive phases associated with human evolution, and highlight potential reasons for these differences.

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## The role of climate in the evolution of body and brain size of *Homo* in the last 2 million years

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Body and brain size are two central determinants of a species' biology and adaptive strategy. Recent years have seen an increase in estimates for brain and body size in the genus *Homo*, with a focus on understanding their temporal, taxonomic and spatial evolution [1-3]. A key open question concerns the causal mechanisms behind the massive increase in body mass and brain volume within the human lineage from the Early to Late Pleistocene. Various hypotheses have been put forward, many invoking climatic and ecological driving forces, though cultural, technological and demographic factors have also been suggested [4, 5]. Here we provide the first explicit quantitative testing of climatic hypotheses for the evolution of brain and body size. Previous studies have relied on MIS stages or global mean temperatures (i.e. from  $\delta^{18}\text{O}$  curves) as ecological proxies [e.g. 4, 5]. Instead, we apply a newly developed method that uses an emulator of a Global Circulation Model to reconstruct local climatic conditions (on a grid of  $\sim 1^\circ$  latitude by  $1^\circ$  longitude). This approach provides various climatic variables (e.g. temperature, precipitation) based on the specific geographical coordinates and age of the fossil specimen under consideration. Here we focus on the relationship of body and brain size with mean annual temperature at the fossil location and contrast this with global mean temperature. Our anthropological data consists of  $n=324$  estimates of body mass [1] and  $n=215$  brain size estimates across *Homo* from 2.0 Mya to 10 kya, including taxonomic assessment. Thinning of data was performed to avoid having too many estimates from the same location/time. We resampled the dataset 100 times, only taking one measurement for any combination of location and time, with results being minimally affected by the subset of data used. For brain size, our baseline models find a steady increase through time with a clear association with taxonomy, roughly explaining  $\sim 75\%$  of variation over the last 2 Myr. This increase is well explained by mean global temperature, but time is an equally good predictor. Thus, it is not possible to disentangle the effect of climate using global estimates, as the world has cooled down over the last 2 Myr years. When using mean annual temperature of the location of the fossil, explanatory power goes down to  $\sim 25\%$ . Using local temperatures in combination with taxonomy does not lead to any improvement in our ability to explain brain size compared to using taxonomy alone. With regard to body size, taxonomy itself explain 40% of the observed variance in our model whereas global annual mean temperature and time perform worse ( $\sim 15-20\%$ ). Using local temperature as predictor of body size again does not yield better results ( $\sim 10-15\%$  of explained variance). However, using local temperature within each taxonomic unit leads to  $\sim 45-50\%$  explained variance, with body size increasing with colder temperatures among all taxa, though the strength of the effect varies across taxonomic units. Our analyses of a large database of *Homo* specimens with detailed quantitative climate variables find no evidence for a significant effect of local temperature on brain size. Yet, we do find evidence for Bergmann's rule operating on body size within taxonomic units (e.g. Neanderthals; *Homo sapiens*). Yet, the largest changes in body size are still observed between taxonomic units. This study underlines the necessity to reconstruct quantitative localized climate variables for individual fossils, with global mean temperature bearing little meaningfulness from a biological point of view, as temperature has changed in different ways across different locations. Future models will incorporate additional variables (e.g. precipitation) and measures of the magnitude of climatic change over time (i.e. velocity) and test in how far other ecological aspects and their interaction might influence the evolution of body and brain size in *Homo*.

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## Revisiting the bent-hip bent-knee hypothesis: Variation in hallucal abduction in the modern human foot is dependent on limb posture

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Hominin fossil trackways are commonly used to infer the locomotory behaviour of the track-makers [1], yet the relationship between movement and the foot's interaction with the underlying substrate remains poorly understood, inhibiting a comprehensive reconstruction of evolutionary locomotion [2,3]. To determine the relationship between track morphology, limb kinematics and substrate mechanics, this study employed 3D motion capture systems to characterize movement (hip, knee and ankle) in modern humans across a range of substrates and limb postures. Forty participants walked across three different substrates of varying compliance with an erect limb (the typical modern human gait) and with bent-hip bent-knee (BHBK) posture. A reflective marker-set was placed onto the lower limb bony landmarks to capture joint movements across each 12m long trackway. Joint angles were statistically compared using MANOVAs between each of the substrates and limb postures. Limb movement was compared with footprint shapes and patterns to identify the influence of kinematics and substrate on the resulting track morphology. Hallucal abduction for all tracks was measured and a generalised linear model was used to infer modular movement within the foot. Finally, the height and volume of the midfoot arches were statistically compared to determine if limb posture can be identified from footprint shapes. Variable depth distributions and under-represented midfoot shapes were identified when moving with BHBK posture in comparison to an erect limb posture. Hallucal abduction was determined to be variable within an individual when moving across substrates of differing compliancy, and was significantly correlated with increasing knee angle. The ability to abduct the hallux has only been reported in pathological individuals to date [4], and this is the first study whereby it has been demonstrated that modern humans have the ability to slightly abduct the hallux (3-5° per participant) for efficient substrate navigation. Using an experimental approach, this study has demonstrated two key variables that affect track morphology: substrate compliance and lower limb posture. The morphologies from the BHBK experimental trials on the looser sediment were found to be consistent with the Laetoli footprints, both of which were created on a substrate of similar compliance. This suggests that the Laetoli track-maker may have employed a slightly more flexed limb than modern humans. This finding was supported by the increase in hallucal abduction when traversing across a looser sediment, which likely promoted stability during movement. Importantly, limb posture was reconstructed from experimental track morphology, offering further insights into the functional morphology of fossil footprints.

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## When diet became diverse: Isotopic tracking of subsistence strategies among Gravettian hunters in Europe

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Subsistence strategies are key paleoecological features of Paleolithic hunter-gatherers and their deeper understanding provides critical insights into essential aspects of human evolution. In this study, we discuss new collagen stable isotopic values (C, N, S) representing seven Gravettian individuals from the Troisi me caverne of Goyet in Belgium. The dietary strategies of the Gravettian humans from Goyet are in line with the general trends observed among Western European Gravettian populations. These populations show both a low intake of mammoth and a high consumption of other terrestrial mammals as well as aquatic resources, such as at the sites Arene Candide and La Rochette. This is different for more eastern Gravettian hunter-gatherers, for example in Kostenki, Brno-Francouzsk a, Mal'ta, P redmost ı, and Doln ı V estonice where the dietary contribution of mammoth meat was significantly higher. The stable isotopic data of the Gravettian humans from Goyet indicate that their dietary ecology was essentially based on terrestrial resources like reindeer, horse, and, to a lesser extent, mammoth. However, they yielded  $\delta^{15}\text{N}$  values that are substantially lower than those of the earlier modern humans and Neandertals from the same site [1-2]. We hypothesize that the Gravettian humans had much less mammoth in their diet than all earlier humans from the same region. It was previously shown that in northwestern Europe a decline of mammoth, a key prey species, could already be detected at the onset of the Upper Paleolithic [2]. This trend appears to continue into the Gravettian, despite the persistence of the typical mammoth ecological niche, which is represented by a grassland with high  $\delta^{15}\text{N}$  values. Interestingly, through isotopic analysis, we are able to track the spread of the horse from the local ecosystem (represented by specimens from Walou Cave, Belgium) into this niche now under-occupied by the mammoth. Radiocarbon dates obtained from several mammoth skeletal remains from the Troisi me caverne of Goyet showed that this megaherbivore was indeed part of the ecosystem during pre-LGM periods. However, from the Gravettian in Goyet and the surrounding region we have only one mammoth specimen represented by a long bone, and interestingly, its sulphur isotopic signal indicates that this individual was not of local origin. We propose that the local mammoth population was under intensive hunting pressure or may even have been no longer present in the region. Instead, single individuals from other regions may have made it into the area and ended up as prey animals. While the  $\delta^{15}\text{N}$  values of all Goyet Gravettian humans are relatively homogeneous, their  $\delta^{13}\text{C}$  values are variable. This indicates significant dietary differences among the seven individuals, an observation that has not been described before for hunter-gatherers pre-dating the Gravettian. The human  $\delta^{34}\text{S}$  values also support substantial differences in life mobility history between different individuals, which were not observed for the Goyet Neandertals. The result that different members of the same chrono-group had various individual mobility histories has implications for land use procurement strategies of those hunter-gatherer groups. In conclusion, our new isotopic results demonstrate a broad ecological flexibility among Gravettian humans, which can be seen in different human ecosystem interactions across Europe. The Goyet individuals contribute substantially to a more complete understanding of hunter-gatherer's ecology during this particular phase of the European Late Pleistocene. Our study shows that the Gravettian cannot be depicted as a uniform entity from an ecological perspective. It instead indicates that during this period, and not earlier, both inter- and intra-group diversity in subsistence strategies can be tracked through stable isotopic analysis.

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## Reconstructing the Homininae: a subspecies approach

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What was the nature of the Last Common Ancestors (LCA) of both the African great apes and humans and of chimpanzees and humans has been a major research topic for decades. While many studies have sought to describe these ancestral species with reference to living apes, few have done so with the aid of formal phylogenetic methods. Additionally, these studies tend to ignore or simplify the considerable phenotypic variation exhibited by these animals. While some of that variation is within sub-species, much is between sub-species, and it is that level that we exploit and develop for the first time in this paper to reconstruct LCAs. In addition, we use data from several domains, to maximise the sources of information used, providing a more complete reconstruction. Bayesian phylogenetic inference techniques and full-genome mtDNA sequences were used to estimate a subspecies level Maximum Clade Credibility (MCC) tree for the Homininae (African great apes and humans). The MCC tree was used to implement ASRs for sixteen continuous traits known to vary between great ape subspecies. Phylogenetic signal was consistently higher for all trait domains when measured on a subspecies rather than species tree for traits that were found to be phylogenetically significant, suggesting that much of the observed phenotypic variation is phylogenetically structured at the subspecies level. This finding supports the use of subspecies level data when applying phylogenetic comparative methods to African great apes. For those traits where phylogenetic signal was both high and significant, we can be more confident in our interpretations of the estimated ancestral values. These traits include male body size ( $\chi^2 = 10.75$ ,  $df = 1$ ,  $p$ -value  $< 0.01$ ), female body size ( $\chi^2 = 5.92$ ,  $df = 1$ ,  $p$ -value  $< 0.01$ ), community size ( $\chi^2 = 5.94$ ,  $df = 1$ ,  $p$ -value  $< 0.01$ ), gestation length ( $\chi^2 = 4.64$ ,  $df = 1$ ,  $p$ -value = 0.03), and geographic range ( $\chi^2 = 7.42$ ,  $df = 1$ ,  $p$ -value  $< 0.01$ ). Our reconstruction of these traits predicts an evolutionary scenario in which considerable change occurred along the branch connecting the LCA of humans, chimpanzees, bonobos and gorillas to the LCA of humans, chimpanzees and bonobos. Thus, while our ancestral state estimates corroborate previous findings that the LCA of humans, chimpanzees and bonobos was a chimp-like animal, they also suggest that the LCA of the Homininae was an animal unlike any extant African great ape.



## Taxonomic revision of the initial Early Pleistocene HCRP-U18-501 hominin mandible from Malawi: a tooth internal structural perspective

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The adult hominin mandible HCRP-U18-501 (= UR 501) was found in 1991/92 in the stratigraphic Unit 3A of the Chiwondo Beds, at the Uraha site (Karonga Basin, Northern Malawi Rift) [1]. This stratigraphic level is biochronologically constrained to an age of 2.3-2.5 Ma [2]. The fossil is represented by two joining parts of the corpus broken behind the M2s on both sides and preserves the left and right P3-M2. The size of the mandible, its symphyseal shape, the anteroposteriorly elongated dental arcade, and external tooth morphology show remarkable similarities with the specimen KNM-ER 1802 from Koobi Fora (Kenya), which is regarded as *Homo cf. habilis*, as well as with OH 7, holotype of *H. habilis* [3]. The recently described specimen KNM-ER 64060, preserving the mandibular dentition of an adult individual, also exhibits tooth morphological traits and dimensions comparable to the Malawi mandible [4]. In addition, the plate-like premolar roots and some microanatomical tooth features of UR 501 recall those of *Paranthropus*, but are also present in some East African specimens commonly referred to *H. rudolfensis* and *H. habilis*. At the Malema and Mwenirondo localities in Malawi, two additional fossil specimens attributed to *P. boisei* and *Homo rudolfensis*, respectively, were also discovered in levels of the Chiwondo Beds penecontemporaneous to the Unit 3A. Recent isotopic analyses of these hominins show that these hominins relied mainly on C3 resources exploited in a wooded savanna environment under relatively cool and wet conditions [5]. Considering the relevance of UR 501 for the emergence of the genus *Homo* and by taking into account the new likely paleoenvironmental scenario, the mosaic signal of its external morphology makes the interpretation of this relevant fossil more challenging. We analyzed the internal structural organization of UR 501 premolars and molars (i.e., tissue proportions, enamel thickness distribution, enamel-dentine junction [EDJ] and root morphology) and compared it with the features displayed by some Early Pleistocene tooth specimens from Africa and Asia unambiguously representing *Homo*, as well as with the patterns respectively expressed by South African *Australopithecus* and *Paranthropus*. While in UR 501 crown tissue proportions show thick enamel, thus overlapping the ranges of *Australopithecus*, *Paranthropus* and *Homo*, the presence of an extended buccal cingulum at the EDJ level and overall root morphology more closely resemble the australopithecine condition. Geometric morphometric analyses of the molar EDJ discriminate the genera *Homo*, *Australopithecus* and *Paranthropus*. In this context, the Malawi specimen falls close to or within the variation range expressed by *Australopithecus* and clearly sets apart from *Homo* and *Paranthropus*. Altogether, these results suggest that UR 501 may be more closely related to the australopithecines than to *Homo*. The apparent mixture of australopithecine and *Homo* features in this southeastern African specimen highlights the complex phylogenetic and biogeographic history of early *Homo* and fuels the discussion about the emergence of our own genus.

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## Recovery of Ancient Hominin and Mammalian Mitochondrial DNA from High Resolution Screening of Pleistocene Sediments at Denisova Cave

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The analysis of ancient DNA sequences has become an important tool for reconstructing the evolutionary history of humans and other species. It has recently been shown that DNA from Pleistocene hominins can be retrieved not only from their skeletal remains, but also from cave sediments [1]. Therefore, through high resolution sediment sampling in the stratigraphy it may be possible to determine the sequence and timing of hominin occupations at archaeological sites. We explore this possibility at Denisova Cave, a site in the Altai Mountains in Southern Siberia, where remains of Denisovans, Neandertals and a first-generation offspring of parents from these two groups have been found. A total of 728 sediment samples were collected from the Pleistocene layers of each of the three chambers in the cave, spanning a time period of less than 36 thousand years ago to over 287 thousand years ago [2]. Aliquots of 50mg of sediment from each of the collected samples were processed using a fully automated workflow for DNA extraction [3], single-stranded library preparation [4] and hybridization capture [5]. Samples were initially enriched for mammalian mitochondrial DNA in order to establish the preservation of ancient DNA in different areas of the cave. Ninety-four percent of the samples were positive for ancient mammalian DNA. A variety of taxa were identified including hyena, bovids, cervids, canids and ursids. Large scale changes in the fauna observed in the sediment DNA correspond well with zooarcheological records in all three chambers. Next, the samples were enriched for hominin mitochondrial DNA. Twenty-two percent of the samples were positive for the preservation of ancient hominin DNA. These positive samples were spread across all three chambers and many parts of the stratigraphy. A comparison of previously sequenced archaic and modern hominin mitochondrial genomes was used to identify diagnostic positions for different hominin groups (modern human, Neandertal, Denisovan and the Sima de los Huesos hominin). These diagnostic positions allowed hominin mtDNA sequences from sixty-eight percent of the positive samples to be assigned to a specific hominin group. A comparison between the skeletal and sediment records will be discussed.

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## The Mousterian from Trou al'Wesse (Modave, Belgium): lithic taphonomy, measures of assemblage curation and implications for Late Neanderthal mobility patterns

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With a rich concentration of human and cultural remains, Belgium stands out as a promising region to investigate Neanderthal lifeways in the northern latitudes. The region, however, is investigated intensively since the onset of our discipline and there are only a few sequences left that can be excavated with modern standards. In this context, the cave of Trou Al'Wesse (TAW) (province of Liège, Belgium, 5.294° E, 50.421°N) is unique in Belgium in possessing a largely unexcavated stratified sequence spanning the Marine Isotopic Stage 3 to the Holocene, including Mousterian and Aurignacian occupations. It offers a rare opportunity to obtain detailed behavioral, climatic and paleoenvironmental data in a region where *H. sapiens* seem to arrive later than in most other parts of Europe. Neanderthals seem to have disappeared from Northwestern Europe by ca. 40 ka cal BP [1] and in Belgium, following an elusive occurrence of transitional assemblages (Spy Cave, Goyet Cave) for which the makers are still unknown [2], full-fledged Upper Paleolithic occurs only ca. 39 ka cal BP. So while potential *H. sapiens* settlements start to be documented in Europe at the beginning of the Greenland Interstadial 12 [3], there might still have been Neanderthal populations left in Belgium and what happened to them is unclear. TAW provides an unparalleled opportunity to address this question.

Although the TAW Mousterian has been known since the 19th century, only a small sample (N=45) of the lithic material remains from was excavated prior to 1988. Between 1988 and 2001, the University of Liège and the local association *Les chercheurs de la Wallonie* excavated the TAW. A Mousterian assemblage was collected from a test pit underneath the cave drip line and another one from a small area on the slope fronting the cave. The former established the stratigraphic position of the material in the sedimentary Unit 17, latter sub-divided into 3 sub-units, 17a, 17b and 17c. The lithic assemblage (N=730), which includes denticulate and large side-scrapers, comprises a combination of fairly well preserved artifacts with a material heavily damaged. Differences in preservation casted doubts on the integrity of the assemblage and thus provides a warning for time averaging [4]. Starting from 2003, Rebecca Miller excavated the site until she passed away, in 2017. She reached the Mousterian layer in 2015 and 2016 and in 2018, an international team under the field direction of D. Flas and N. Zwyns completed her work on the terrace.

With ca. 3,000 artifacts and including the thin fraction, the sample gathered between 2015 and 2018 is currently the best candidate to obtain quantitative data on the TAW Mousterian and to address three main questions. How many assemblages are there? How do depositional and diagenetic processes affect them? What can we say about the human settlements? Here, we distinguish at least two assemblages based on their position in sedimentary Unit 17b and 17c and their location on the terrace. Using an attribute analyses and spatial distribution, we show different impacts of post-depositional processes on the lithic material in the two layers. While at least part of the assemblage from 17b is significantly affected by mechanical reworking, edge damage and patina, 17c is much better preserved. This is intriguing since Unit 17b has recently yielded Neanderthal mtDNA preserved in the sediment [5]. After a taphonomic assessment, we look at the structure of the assemblages in an attempt to address issues of assemblage curations. Considering hunter-gatherers ecological models, the lithics and the available paleoenvironmental data, we discuss issues of site function, settlement patterns and Neanderthal mobility. In a region where most of Middle Paleolithic data comes from 18th/19th century excavation, the TAW assemblage offers a rare opportunity for a quantitative examination of Neanderthal lifeways before their disappearance from the record.

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