



DISSERTATION | DOCTORAL THESIS

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Reassessing the Middle to Upper Palaeolithic of the Crimea Peninsula and beyond using AMS radiocarbon dating and palaeoproteomics

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*Misty morning, clouds in the sky
Without warning, the wizard walks by
Casting his shadow, weaving his spell
Long grey cloak, tinkling bell*

*Never talking
Just keeps walking
Cursing his magic*

*Evil power disappears
Demons worry when the wizard is near
He turns tears into joy
Everyone's happy when the wizard walks by*

*Never talking
Just keeps walking
Spreading his magic*

*Sun is shining, clouds have gone by
All the people give a happy sigh
He has passed by, giving his sign
Left all the people feeling so fine*

*Never talking
Just keeps walking
Spreading his magic*

Black Sabbath. 1970. Song: The Wizard, Album: Black Sabbath.

To lift the spirits when things get a little tough

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‘you can do it. You can do anything’.

As we say in Yorkshire, Ta an Ta'Ra.

On to the next adventure.

List of Publications

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Manuscript II: Pigott, E, M., van der Sluis, L, G., Cooper, L., Higham, T. (2026). Glaston: The earliest *Homo sapiens* identified in the British Isles through XAD-2 pre-treatment for radiocarbon dating. *Antiquity* In Review

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Abstract

The Crimean Peninsula, situated on the edge of southeastern Europe, is the location of numerous deeply stratified, well-preserved Palaeolithic archaeological sites. The Crimean Peninsula has been considered a refugium for Neanderthals in Eurasia before they were replaced by anatomically modern humans (AMH). This understanding is primarily drawn from lithic technological analysis and radiocarbon dating. However, recent developments in radiocarbon dating have introduced improved protocols in pre-treatment chemistry (including HYP or hydroxyproline extraction, ultrafiltration, XAD-2 ion chromatography), designed to improve the accuracy of radiocarbon dating bone collagen. This has revealed that some of the previously obtained radiocarbon dates appear to be too young. The discrepancies arise primarily from sample contamination and the failure of radiocarbon chemistry approaches to remove the contamination to a sufficiently low level. To test the reliability of previous results, a critical re-evaluation is undertaken in this dissertation using bone samples from eight Middle to Upper Palaeolithic archaeological sites in the Crimean Peninsula: Starosele, Siuren I, Kabazi II, Kabazi V, Chokcurcha I, Buran Kaya III, Zaskalnaya V, Zaskalnaya VI. Another important European site: Glaston in the United Kingdom, is also analysed with improved pre-treatment protocols. There, samples were redated from previously prepared bone collagen that reveals what is likely to be the oldest evidence for *Homo sapiens* in this part of Northern Europe.

Zooarchaeology by Mass Spectrometry (ZooMS) has also been applied to five of the Crimean Palaeolithic sites, revealing subsistence strategies and a new human, named Star 1, which was mitochondrially sequenced. This revealed long-distance migration amongst Neanderthals, probably from the Russian Altai region, which occurred ~60,000 years ago.

The results of dating Palaeolithic bone from the Crimea using XAD-2 resin allowed me to test whether the Crimean Peninsula was indeed a refugium for Neanderthals, prior to their extinction. ZooMS analysis enabled further insights into hominin subsistence strategies, the reconstruction of palaeoenvironments and, crucially, the ability to recover human remains which are exceedingly rare in the world of the Palaeolithic.

Keywords: Palaeolithic, Radiocarbon dating, Palaeoproteomics, Neanderthals, Eurasia, Palaeoenvironment

Abstrakt

Die Krim, am Rande Südosteuropas gelegen, beherbergt zahlreiche tief stratifizierte, gut erhaltene paläolithische Fundstätten. Sie galt lange als Rückzugsgebiet der Neandertaler in Eurasien, bevor diese vom anatomisch modernen Menschen verdrängt wurden. Diese Annahme basiert hauptsächlich auf der Analyse lithischer Technologien und der Radiokohlenstoffdatierung. Neuere Entwicklungen in der Radiokohlenstoffdatierung haben jedoch verbesserte Protokolle in der Probenvorbereitung (HYP-Extraktion, Ultrafiltration, XAD-2-Ionenchromatographie) eingeführt, um die Genauigkeit der Radiokohlenstoffdatierung von Knochenkollagen zu verbessern. Dabei zeigte sich, dass einige der zuvor ermittelten Radiokohlenstoffdaten zu jung ausfallen. Die Diskrepanzen resultieren vor allem aus Probenverunreinigungen und der unzureichenden Entfernung dieser Verunreinigungen durch die radiokohlenstoffchemischen Methoden. Um die Zuverlässigkeit bisheriger Ergebnisse zu überprüfen, wird in dieser Dissertation eine kritische Neubewertung anhand von Knochenproben aus acht archäologischen Fundstätten des Mittel- und Jungpaläolithikums auf der Krim durchgeführt: Starosele, Siuren I, Kabazi II, Kabazi V, Chokcurcha I, Buran Kaya III, Zaskalnaya V und Zaskalnaya VI. Eine weitere wichtige Fundstätte in Eurasien wird ebenfalls mit verbesserten Vorbehandlungsprotokollen analysiert. In Glaston (Vereinigtes Königreich) wurden Proben aus bereits präpariertem Knochenkollagen neu datiert. Dies liefert die vermutlich ältesten Belege für *Homo sapiens* in diesem Teil Nordeuropas.

Die Zooarchäologie mittels Massenspektrometrie (ZooMS) wurde zudem an Proben von fünf der paläolithischen Fundstätten der Krim angewendet. Dabei wurden Subsistenzstrategien und ein neues menschliches Knochenfragment, Star 1, identifiziert, dessen Mitochondriensequenz bestimmt wurde. Dies deutet auf eine Fernwanderung von Neandertalern hin, wahrscheinlich aus der russischen Altai-Region, die vor etwa 60.000 Jahren stattfand.

Die Ergebnisse der Datierung paläolithischer Knochen von der Krim mithilfe von XAD-2-Harz erlaubten es mir zu überprüfen, ob die Krim-Halbinsel vor dem Aussterben der Neandertaler tatsächlich ein Refugium für sie war. Die ZooMS-Analyse ermöglichte weitere Einblicke in die Subsistenzstrategien der Homininen, die Rekonstruktion ihrer Paläoumwelt und, ganz entscheidend, die Bergung menschlicher Überreste, die in der Welt des Paläolithikums äußerst selten sind.

Schlüsselwörter: Paläolithikum, Radiokohlenstoffdatierung, Paläoproteomik, Neandertaler, Eurasien, Paläoumwelt

1. Chapter 1: Introduction

1.1. Structure of thesis

My PhD mainly focused on the region of the Crimean Peninsula, where I conducted detailed chronological and biomolecular analyses of bone material from eight sites. I also had the opportunity to work on material from the Middle to Upper Palaeolithic transitional phase of the British Isles. This included obtaining new dates from pre-extracted collagen samples from the Lincombian-Ranisian-Jerzmanowician (LRJ) site of Glaston in the county of Rutland. The bone samples were previously dated with the ultrafiltration pre-treatment approach and published by Cooper et al. (2011). I hydrolysed the remaining collagen samples and treated them with XAD-2 methods to further remove potential contaminants. Finally, I have also been working with bone material from Spain (see Appendix), including two key sites with Châtelperronian lithic technological assemblages: Labeko Koba and Cova Foradada. At the former site I undertook Zooarchaeology by Mass Spectrometry (ZooMS) analysis on 200 bones, which allowed a snapshot of the palaeoenvironment and subsistence strategies of the humans occupying the site. At Cova Foradada I obtained funding to explore subsistence strategies and the palaeoenvironment at the site, in the key layer IV (Châtelperronian) horizon. I conducted ZooMS analysis on 210 faunal remains and found the first possible evidence for carnivorous marine animals being predated, probably by Neanderthals. This work is ongoing and not fully reported in this dissertation, material will be processed later using ancient DNA, stable isotope analysis and radiocarbon dating to place the results from the site in a structured wider context. In summary, my PhD has aimed to further understand some key aspects of the Middle to Upper Palaeolithic transition, by targeting several key archaeological sites in three regions within Eurasia and analysing or re-analysing samples of fragmented bone, using the latest cutting-edge methods for radiocarbon dating and palaeoproteomics.

1.1.1. The Crimean Peninsula

The Crimean Peninsula contains a rich record of archaeological sites covering the transition period between the Middle to Upper Palaeolithic, broadly dating to ~55,000 – 35,000 cal BP (Davies et al., 2015; Higham et al., 2014; Hublin, 2015; Hublin et al., 2020). This transition phase is a pivotal period in human prehistory, where we see evidence of the wide expansion of *Homo sapiens*, or anatomically modern humans (AMH), the admixture of those groups with Neanderthals, and the subsequent disappearance of Neanderthals across Eurasia (Fernández-García et al., 2023). More widely, a narrower part of this time-scale (~47,000–42,000 cal BP) is recognised as a crucial phase in the biocultural transition from the Middle to

Upper Palaeolithic (Davies et al., 2015; Higham et al., 2014; Hublin, 2015; Hublin et al., 2020), coinciding with the increasing presence of *Homo sapiens* and the decline of Neanderthal populations (Hublin, 2015). The Initial Upper Palaeolithic (IUP) technocomplex plays a key role in this transition, marking profound cultural and technological shifts that are increasingly associated with derived *Homo sapiens* (Hublin et al., 2020). Over time, the IUP was replaced by fully developed Upper Palaeolithic industries (Rybin et al., 2023). Recent research suggests that AMH may have arrived in Europe earlier than previously thought, offering new insights into the timing and dynamics of this cultural and technological shift. This period is often described as a cultural revolution, characterised by significant advancements in toolmaking and changes in human lifestyles. Archaeological evidence from sites across Europe highlights this transformation, with Bacho Kiro in Bulgaria serving as a notable example. The lithic assemblage discovered there belongs to human groups that do not appear to contribute to later human populations, suggesting a complex and dynamic process of cultural and demographic change during this period (Hajdinjak et al., 2021).

The Crimean Peninsula has been suggested as being a refugium for some of the last Neanderthals of Eurasia when conditions of extreme climatic downturn in other regions made human occupation unfavourable there (Soffer, 1994; Stepanchuk, 1998; Burke, 2006; Ramírez-Pedraza et al., 2020). The evidence is based on archaeological material culture and chronometric dating. The site of Siuren I, for example, has produced radiocarbon dates from bone between 13 – 30 ka yr BP for levels F to H containing Aurignacian and Micoquian lithic remains (Demidenko & Otte, 2001; Demidenko & Noiret, 2012). The younger end of this range seems very unlikely for lithic assemblages from these industries (Demidenko & Otte, 2001).

In terms of material culture, Crimean Neanderthals have been strongly associated with the Western Crimean Mousterian (WCM) and Crimean Micoquian (CM) technocomplexes, range in age between ~100—50,000 years ago (Chabai, 2004; Chabai, Marks & Monigal, 2004). The CM is characterised by soft hammer bifacial thinning techniques used to produce bifacial tools such as Keilmessers, while unifacial tools, including side scrapers, are often made from bifacial thinning flakes (Chabai, 2004). The WCM emerged later and persisted for about 50,000 years until the end of the CM industry. Unlike the CM, the WCM is distinguished by its absence of bifacial tools and reliance on flake-based tools produced through Levallois and, later, volumetric core reduction techniques (Marks & Chabai, 2006). These kinds of lithic assemblages have been found co-mingled with Neanderthal remains at various sites including Kiik Koba, Zaskalnaya V and Zaskalnaya VI (Demidenko & Uthmeier, 2013; Chabai & Uthmeier, 2017; Stepanchuk et al., 2017), giving us a reasonably confident link between the two. The CM is conventionally linked to Neanderthals due to the discovery of Neanderthal remains at sites such as Kiik Koba (Demidenko & Uthmeier, 2013), Zaskalnaya V (Chabai and

Uthmeier, 2017), and Zaskalnaya VI (Stepanchuk et al., 2017). However, the human species associated with WCM remains uncertain due to the lack of skeletal evidence. However, we assume it to be Neanderthals.

During the Upper Palaeolithic, two lithic industries, the Aurignacian and Eastern Szeletian appear to have coexisted partially alongside CM and WCM (Chabai, 2005). The Aurignacian, known for its carinated technology, finely retouched twisted and non-twisted bladelets, micro-blades, and bone tools, is widely attributed to AMH (Demidenko & Otte, 2001). Meanwhile, the Eastern Szeletian is distinguished by bifacial leaf points, end-scrapers on flakes, geometric trapezoidal microliths, and bone tools, with radial core reduction practices but relatively infrequent blade production (Laroulandie & d'Errico, 2004; Monigal, 2004). The Aurignacian in the Crimea is tentatively associated with AMH, as suggested by a human tooth found at Siuren I (Slimak et al., 2022; Benazzi et al., 2015) and the presence of a *Homo sapiens* tooth at the site of Buran Kaya III, within the same layer as Aurignacian artefacts (Bataille et al., 2012), suggesting that this industry is linked with AMH, as it is in other European sites (Benazzi et al., 2015).

Several studies have shown that previously obtained radiocarbon dates on bulk bone have a strong tendency to be too young. At Kabazi II, for example, which has been re-dated through the hydroxyproline (HYP) pre-treatment method, previous dates were found to be underestimates of the 'true age' by over 10,000 years (Spindler et al., 2021). Throughout various Palaeolithic archaeological sites across the Crimean Peninsula, the vast majority of chronometric dates obtained in the last few decades also have the potential to be underestimates due to unremoved contamination from humic acids and other ground-based contaminants. This remains to be tested. With more advanced dating methods, more reliable chronometric dates can be produced. Reliable dating is crucial if we are to understand the biocultural transition at the heart of the Middle to Upper Palaeolithic transition, in this case in the Crimea.

Many excavated Palaeolithic archaeological sites have yielded thousands of fragmented and therefore unidentified samples that remain in storage. In this research project, I applied ZooMS to identify faunal remains, and sometimes to locate rare human remains. This has given a more complete picture of the palaeoenvironment at each site, as well yielding exciting new human remains and revealing aspects of their subsistence patterns, genetics and age.

This PhD thesis highlights the advancement of archaeological scientific techniques, and how they can further our understanding of the Middle to Upper Palaeolithic transition across Crimea and beyond. By implementing these methods and building more reliable chronologies, a key aim is to test the refugium hypothesis, which suggests that Neanderthals were occupying the

Crimean Peninsula during times of extreme unfavourable climatic periods elsewhere. This has been linked with their late survival. The Crimean sites that have been analysed within this thesis are Kabazi II, Kabazi V, Siuren I, Starosele, Chokurcha I, Buran Kaya III, Zaskalnaya V and Zaskalnaya VI (Figure 1.)



Figure 1. Map showing the Crimean Peninsula and all the sites that have been analysed in this study with different methods.

Table 1. Table presenting Crimean sites studied within this thesis, their excavations and analysis previously taken place within each site.

Site name	First excavated	Further excavations	Previous analysis	Reference
Kabazi II	1987	1994, 2000-2001	Radiocarbon dating	Bataille, (2012), Spinder et al. (2021)
Kabazi V	1986	1990, 1994 – 1996 and 2002 -2003	Radiocarbon dating and Luminescence analysis	Housley et al. (2007), Chabai et al. (2008)
Siuren I	1926 – 1929	1994 - 1997	Radiocarbon dating, Zooarchaeological analysis	Demidenko & Otte, (2001) and Massé & Patou-Mathis, (2012)
Starosel'e	1952	1993-1995	Radiocarbon dating and ESR	Burke, (2000) & Marks et al. (1997)
Chokurcha I	1927	1996-2000	Radiocarbon dating, ESR and Zooarchaeological analysis	Markova, (2004) & Patou-mathis, (2004)
Zaskalnaya V	1969 - 1994	2012 - 2013	Radiocarbon dating	Chabai & Uthmeier, (2017)
Zaskalnaya VI	1969 - 1975	1977 – 1978, 1981 -1985 and 2005	Radiocarbon dating	Stepanchuk et al. (2017) & Majkić et al. (2017)
Buran Kaya III	1990	1996 -1998, 2001, 2009 - 2011	Radiocarbon dating	Hardy, (2001) & Pean et al. (2013)

1.2.1. The Lincombian-Ranisian-Jerzmanowician (LRJ)

Another lithic technocomplex that assumes importance in the debate regarding the Middle and Upper Palaeolithic transition broadly is the Lincombian-Ranisian-Jerzmanowician (LRJ). It is not related to the Crimea geographically, rather to the northern European plain and Central Europe (Figure 2). I include it here in the thesis, because I was given the opportunity of working on a key site from this period in my dissertation, using the same methods as I applied to samples from the Crimea Peninsula.

The LRJ is distributed across a broad geographic area of roughly 1,500 km, spanning latitudes between 50° and 55°N (Hublin, 2015)(Figure 2). The assemblages associated with LRJ are notably characterised by leaf-shaped points manufactured on blades, ‘Jerzmanowice points’ and bifacial leaf points, alongside less common implements such as pointed blades, endscrapers, and burins (Flas, 2011; Demidenko and Škrdla, 2023). Sites generally date to ~40,000–45,000 years ago (Mylopotamitaki et al., 2024). Although LRJ sites are widely distributed the highest concentration is found in Britain. Jerzmanowice Cave (also known as Nietoperzowa Cave) in Poland is recognised as one of the richest LRJ sites in Europe, yielding points interpreted as projectile weapons (Wiśniewski et al., 2022).

The origins and authorship of the LRJ have long been debated. Some researchers have attributed it to Neanderthals (Jöris & Street, 2008), while others have suggested it may have been produced by both Neanderthals and *Homo sapiens* (Pettitt, 2008). Recent mitochondrial DNA analysis from Illsenhöhle, located beneath Ranis Castle in Thuringia, Germany, indicates that the LRJ there was likely associated with *Homo sapiens*. Hominin remains genetically identified as *Homo sapiens* were discovered in layers 8–9 alongside LRJ artefacts during excavations conducted between 2016 and 2022 (Mylopotamitaki et al., 2024).

The LRJ is considered to reflect a technological and cultural adaptation of *Homo sapiens* to cold, open grassland environments in Northwestern and Central Europe. Faunal remains at these sites support this interpretation, indicating cold palaeoenvironments during Marine Isotope Stage 3, with species such as woolly mammoth, woolly rhinoceros, and reindeer present (Cooper et al., 2011; Higham et al., 2011; Smith et al., 2024).

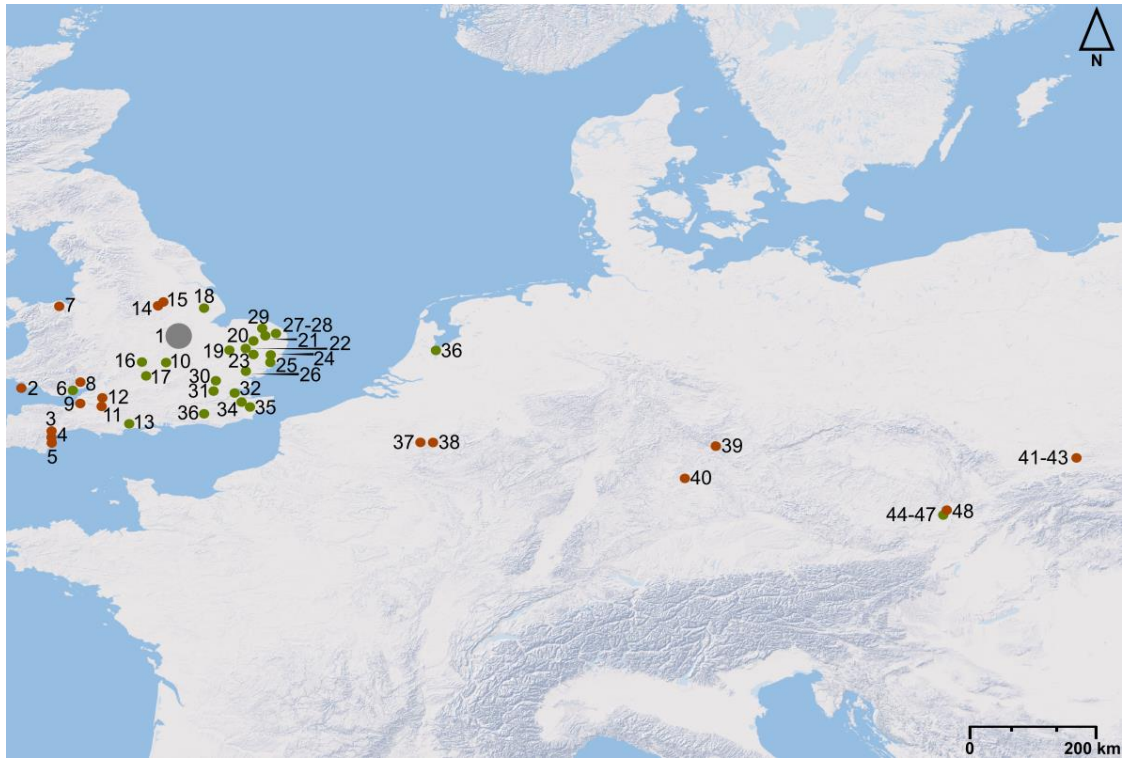


Figure 2. Map of LRJ sites within Britain and Europe (dark red/brown c represents cave sites, green open-air sites and grey represents Glaston Grange Farm). Map adapted from Jacobi, (2007); Jacobi & Higham, (2011); Rogerson & Ashley, (2013); Cooper, (2020, unpublished); Demidenko & Škrdla, (2023) and an unpublished report from L. Cooper. 1. Glaston Grange Farm; 2. Paviland; 3. Kent's Cavern; 4. Bench Quarry Tunnel Cavern; 5. Windmill Hill Cave; 6. Goldcliff; 7. Ffynnon Bueno Cave; 8. King Arthur's Cave; 9. Uphill Quarry Cave; 10. Pineham; 11. Hyaena Den; 12. Badger Hole; 13. Moordown; 14. Pin Hole; 15. Robin Hood Cave; 16. Osney Lock; 17. Sutton Courtenay; 18. Wallow Camp; 19. Hainey Hill; 20. Brandon; 21. Drayton; 22. Warren Hill; 23. Town Pit; 24. Eastall's Pit; 25. Warren Livingstone Pit (Bramford Road, Ipswich); 26. White Colne Pit I; 27. Bastwick and Colby; 28. Saxethorpe; 29. Aleysham; 30. Creffield Road; 31. Earl of Dysart's Pit; 32. Temple Mills; 33. Bapchild; 34. Conningbrook Manor Pit; 35. Beedings; 36. Aardjesberg; 37. Spy; 38. Goyet; 39. Zwergloch; 40. Ranis 2; 41. Nietoperzowa Cave; 42. Koziarnia Cave; 43. Puchacza Skala Cave; 44. Líšeň/Podolí I; 45. Líšeň I/Líšeň—Čtvrť; 46. Želešice III/Želešice-Hoynerhügel; 47. Tvarožná X, "Za školou;" 48. Pekárna Cave.

1.2.2. Archaeological background - Glaston and the LRJ

In 2000, a rescue excavation at Glaston, County of Rutland, conducted by the University of Leicester Archaeological Services (ULAS), uncovered important evidence pertaining to the British LRJ. While the site yielded archaeological material spanning the Bronze Age, Medieval, and post-Medieval periods, the team also recovered rare Palaeolithic LRJ artefacts. These included a leaf-point, a partially broken point, and associated lithic debitage, alongside faunal remains. Some of the animal bones, primarily from *Equus* specimens, showed evidence of human modification, likely for marrow extraction.

In the late 2000s, radiocarbon dating was undertaken on six faunal samples recovered within 500 mm of a leaf-point findspot (context 193) in archaeological area A (Cooper et al., 2011). The samples underwent ultrafiltration pre-treatment (Higham et al., 2006) and were dated using accelerator mass spectrometry at the Oxford Radiocarbon Accelerator Unit (ORAU). These analyses indicated that the LRJ occupation at Glaston dates to approximately 44,290–42,440 cal BP. This study within my PhD thesis focuses on evaluating the reliability of these initial radiocarbon determinations. To achieve this, the samples were re-examined employing an XAD-2 resin treatment, following the methodology outlined by van der Sluis et al. (2023).

Table 2. Table presenting Glaston, sites studied within this thesis, excavation date and analysis previously taken place.

Site Name	First Excavated	Previous analysis	Reference
Glaston	2000	Radiocarbon dating, Zooarchaeological analysis	Cooper et al. (2011)

1.3.1. Cova Foradada (pilot study)

Another site that I worked on during my thesis was in Spain at Cova Foradada (Figure 3) and this is included in the Appendices of the dissertation. The site is located 1.8 km away from the Mediterranean coastline in the Catalan region of the Iberian Peninsula. It was discovered in 1997 and partly excavated in 2013 and 2017. Cova Foradada is an important site because it is the southernmost Châtelperronian-Early Aurignacian stratified sequence ever documented in Europe (Morales et al., 2019). This is a time of transition between the Middle to Upper Palaeolithic, during which there is intense evidence of the disappearance of Neanderthals (Davies et al., 2015; Higham et al., 2014; Hublin, 2015; Hublin et al., 2020). The discussion of the Châtelperronian belonging to Neanderthals or *Homo sapiens* has been long debated, with important work on aspects of technology (Sorresi & Roussel, 2014 & Roussel et al., 2016), palaeo-anthropological remains (Bailey & Hublin, 2006) and more recently with the application of paleoproteomic and genomic studies (Welker et al., 2016). However, there is still no definite answer that is accepted by researchers.

Previous zooarchaeological analysis was undertaken on 2296 faunal remains found within layers III-V, with 348 (16.7%) being unidentifiable. As this study centres on the Châtelperronian layer of Cova Foradada, it is important to note that layer IV has the largest number of unidentifiable faunal remains (45.5%), signifying the importance of further analysis (ZooMS).

In early 2025, I carried out a pilot study of 50 bone samples at IPHES, Tarragona, Spain, which achieved a 68% success rate. From this work I managed to identify species and genus groups such as Cervidae, Bovidae, Equidae and Canidae. However, amongst these were five identifications likely to be Carnivorous marine animals, which is unusual in terms of the location and period of the site. However, as only 20 mg of bone was sampled at the institution of IPHES, no further analysis has been undertaken. Furthermore, radiocarbon dating was previously undertaken on four charcoal samples from layer four at Cova Foradada. These were dated to approximately 34 ka yr BP for layer IV and 31 ka yr BP for layer IV1, with a calibrated age of range of 42.2 to 35.7 ka cal BP for Unit IV (Morales et al., 2019). These dates may be considered too young, somewhat overlapping with the youngest boundary of the Châtelperronian, which has been proposed to be distributed across southwestern Europe between an approximate range of 45-41 cal ka BP (Higham et al., 2014; Rios-Garzier et al., 2022).

Due to the interesting results from the pilot study at Cova Foradada, I decided to write a grant proposal to perform further analyses at the site. This, and additional information on the work, is given in the Appendix.

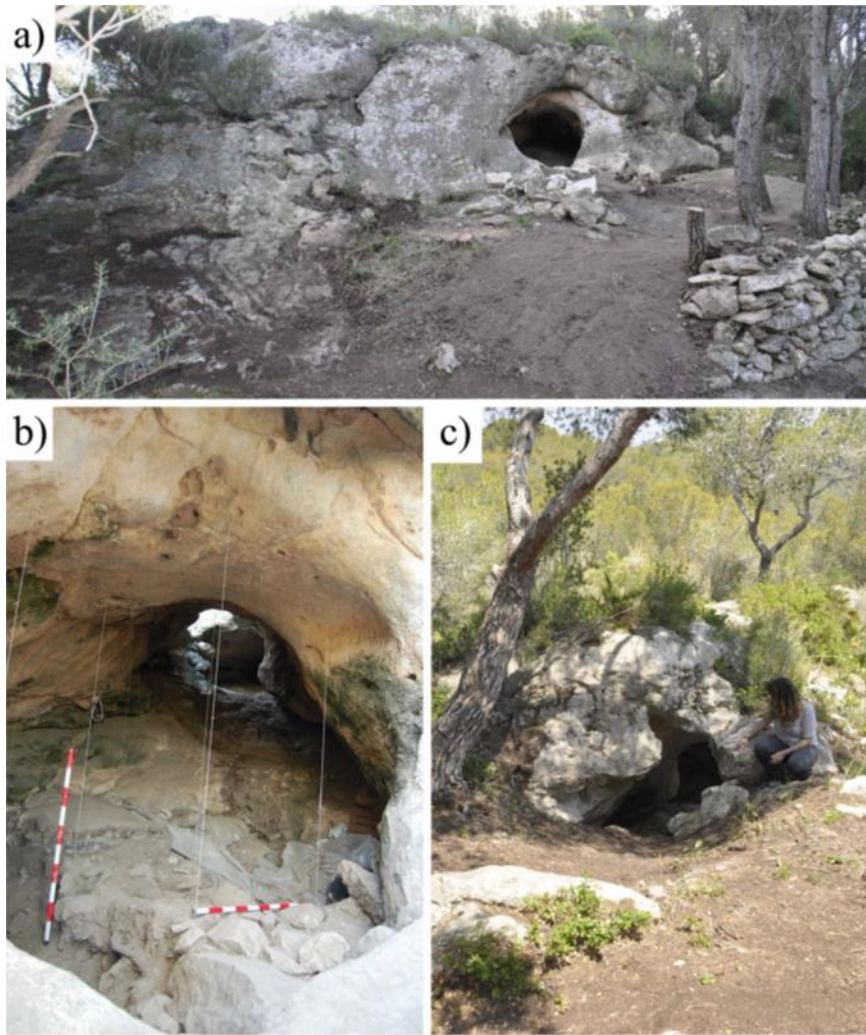


Figure 3. View of the different parts of Cova Foradada. a) General view of the Lower Entrance of the cave and external terrace prior to its excavation in 2014; b) interior of the cave from the Lower Entrance during the excavation of Layer I in 2006, the excavation hall; c) view of the Upper Entrance of the cave. From Morales et al., (2019).

1.4.1. Thesis research aims

Archaeological science can contribute significantly to our understanding of hominins and their lifeways during this key period. My work had several overarching research objectives:

1. To review and re-assess the archaeological record from the Crimean Peninsula in the light of previous radiometric analysis. A careful review and assessment of the chronologies with new calibration and Bayesian modelling is needed. This will allow us to assess whether some radiocarbon dates that were obtained are outliers or not and allow us to place the sites in context relative to the lithic techno-complexes found at the sites.
2. Obtain new radiocarbon dates from eight Crimean Middle to Upper Palaeolithic archaeological sites, to assess the reliability of previous published chronologies. This will be undertaken with more robust pre-treatment methods such as XAD-2 resin chromatography, designed to minimise contamination and produce more reliable radiocarbon dates. The resulting data will enable a critical evaluation of whether the Crimean Peninsula functioned as a refugium during the period of Neanderthal replacement by *Homo sapiens* during the Middle to Upper Palaeolithic transitional period.
3. Obtain new radiocarbon dates from eight Crimean Middle to Upper Palaeolithic archaeological sites, to assess the reliability of previous published chronologies. This will be undertaken with more robust pre-treatment methods such as XAD-2 resin chromatography, designed to minimise contamination and produce more reliable radiocarbon dates. The resulting data will enable a critical evaluation of whether the Crimean Peninsula functioned as a refugium during the period of Neanderthal replacement by *Homo sapiens* during the Middle to Upper Palaeolithic transitional period.
4. To build Bayesian models of the new results to answer the question ‘When did Neanderthals disappear from the Crimean Peninsula’? In parallel, I aim to also address the question of when early modern humans become visible in this region and consider whether the two groups were potentially contemporaneous. A robust chronology is necessary to do achieve this objective.

5. Use ZooMS at Crimean archaeological sites, as well as other sites within wider Europe, on previously unidentified fragmented bone samples. This will allow a re-assessment of the faunal material at each site and enable a further understanding of the subsistence strategies being targeted by hominins, as well as shedding light on the wider palaeoenvironmental picture. Another aim is to screen bone fragment assemblages to search for new hominin remains. If found, these can be genetically sequenced, directly dated and analysed for their stable isotopes, thereby informing us about genetic ancestry and relatedness, admixture, age, diet and more. The great rarity of human material in the Late Middle and Early Upper Palaeolithic can be addressed using the application of this method to previously excavated material.

2. Chapter 2: Methodology

Radiocarbon dating with different pre-treatment protocols, ZooMS, stable isotopes and ancient DNA methods were used across the three scientific articles. The methods are explained in detail within each, as well as in the following section with further background information.

2.1.1. Sampling: Crimean Peninsula

All faunal remains were collected during sampling trips at the University of Erlangen–Nuremberg, Germany and the National Museum of Natural History, Institute of Human Paleontology, Paris, France. The number of samples processed for ZooMS and radiocarbon dating from each site can be seen in Table 3. This does not reflect the number of samples that passed or failed, but only those that were processed. The material for radiocarbon dating was chosen specifically for any anthropogenic modifications.

Table 3. Table showing the sample material used for full ZooMS analysis (publication II and manuscript I) and radiocarbon dating across the eight Palaeolithic sites within this study and the institution they were collected and sampled from. All samples that were radiocarbon dated were also processed with ZooMS, with the majority being successful (see manuscript I, supplementary material).

Site	Typology	Level & Square No.	No. of bones - ZooMS	No. of bones - Radiocarbon	Sampled from institution
Kabazi II	Western Crimean Mousterian (WCM)	I/2	-	1	Oxford University, England
Kabazi II	Western Crimean Mousterian (WCM)	II/I	-	2	National Museum of Natural History, Paris
Kabazi II	WCM	II/2	25	2	-
Kabazi II	WCM	II/2-1	25	1	-
Kabazi II	WCM	II/3	25	2	-
Kabazi II	WCM	II/4	-	1	Oxford University, England
Kabazi II	WCM	II/5	25	1	National Museum of Natural History, Paris

Kabazi II	WCM	II/6	-	1	Oxford University, England
Kabazi II	WCM	II/8	25	7	National Museum of Natural History, Paris
Kabazi II	WCM	II/9	-	6	-
Kabazi II	WCM	II/10	-	1	Oxford University, England
Kabazi II	WCM	II/13	-	3	National Museum of Natural History, Paris
Kabazi V	Micoquian	II/4, 10D	-	1	National Museum of Natural History, Paris
Kabazi V	Micoquian	III/Ib, 7A	-	1	-
Kabazi V	Micoquian	III/2, 83	-	1	-
Kabazi V	Micoquian	III/5-2, 9-2	-	1	-
Kabazi V	Micoquian	III/5-2, 9A, 6	-	1	-
Kabazi V	Micoquian	III/5-2, 9G	20		Uni. Erlangen - Nuremburg
Kabazi V	Micoquian	III/5-3, 9, 10G	20		-
Kabazi V	Micoquian	III/5-3, 9D	20		-
Starosele	Micoquian	3a, F21	20	-	Uni. Erlangen - Nuremburg
Starosele	Micoquian	1, G20	-	4	-
Starosele	Micoquian	1, G21	-	2	-
Starosele	Micoquian	1, G21	20	1	-
Starosele	Micoquian	1, G21	-	2	National Museum of Natural History, Paris
Starosele	Micoquian	1, H21	-	1	-
Starosele	Micoquian	1, H23	20	2	Oxford University, England
Starosele	Micoquian	1, H23	-	1	National Museum of Natural History, Paris
Starosele	Micoquian	1, I22	20		Uni. Erlangen - Nuremburg

Starosele	Micoquian	1, I22	-	2	National Museum of Natural History, Paris
Starosele	Micoquian	1, I23	-	7	-
Starosele	Micoquian	1, I23	70	2	Uni. Erlangen - Nuremburg
Starosele	Micoquian	1, J22	-	1	-
Starosele	Micoquian	1, J22	-	1	National Museum of Natural History, Paris
Starosele	Micoquian	1, J23	-	2	Uni. Erlangen - Nuremburg
Starosele	Micoquian	1-2, H23	-	1	-
Starosele	Micoquian	2, G22	-	1	-
Starosele	Micoquian	3, I25	-	1	-
Chokurcha I, Unit IV	Micoquian	2, B21	-	2	National Museum of Natural History, Paris
Chokurcha I, Unit IV	Micoquian	B, B22	20	2	-
Chokurcha I, Unit IV	Micoquian	B, G21	-	1	-
Chokurcha I, Unit IV	Micoquian	B, G22	20	1	-
Chokurcha I, Unit IV	Micoquian	F, B21	-	1	-
Chokurcha I, Unit IV	Micoquian	F, G21	-	2	-
Chokurcha I, Unit IV	Micoquian	F, G22	-	4	-
Chokurcha I, Unit IV	Micoquian	I, B21	-	1	-
Chokurcha I, Unit IV	Micoquian	I, B22	-	5	-
Chokurcha I, Unit IV	Micoquian	I1, B22	13	1	-
Chokurcha I, Unit IV	Micoquian	I1, G22	-	3	-

Chokurcha I, Unit IV	Micoquian	I2, G22	-	1	-
Chokurcha I, Unit IV	Micoquian	M, B22	-	1	-
Chokurcha I, Unit IV	Micoquian	M, G22	20	1	-
Chokurcha I, Unit IV	Micoquian	Q, B21	-	1	-
Chokurcha I, Unit IV	Micoquian	Q, G22	-	1	-
Chokurcha I, Unit IV	Micoquian	Q2, G22	-	1	-
Chokurcha I, Unit IV	Micoquian	O, G22	-	1	-
Chokurcha I, Unit IV	Micoquian	S, B22	-	3	-
Chokurcha I, Unit IV	Micoquian	S, G22	-	1	-
Siuren I	Micoquian/ Aurignacian	Ga, 8D	20	-	National Museum of Natural History, Paris
Siuren I	Micoquian/ Aurignacian	Gb2, 7D	20	-	
Siuren I	Micoquian/ Aurignacian	Gb2, 8C	-	1	
Siuren I	Micoquian/ Aurignacian	Gb2, 8D	20	-	
Siuren I	Micoquian/ Aurignacian	Gc1, 6C	20	-	
Siuren I	Micoquian/ Aurignacian	Gc1, 6D	20	1	
Siuren I	Micoquian/ Aurignacian	Gc1, 7C	-	1	-
Siuren I	Micoquian/ Aurignacian	Gc1, 7C	-	1	-
Siuren I	Micoquian/ Aurignacian	Gc1, 8E	20	-	-
Siuren I	Micoquian/ Aurignacian	Gc1, 9C	-	1	-

Siuren I	Micoquian/ Aurignacian	Gc2, 6D	-	1	
Siuren I	Micoquian/ Aurignacian	Gc2, 7C	-	3	-
Siuren I	Micoquian/ Aurignacian	Gc2, 8C	-	1	
Siuren I	Micoquian/ Aurignacian	Gc2, 7D	20	-	-
Siuren I	Micoquian/ Aurignacian	Gc2a, 7D	-	1	
Siuren I	Micoquian/ Aurignacian	Gd, 6C	-	2	
Siuren I	Micoquian/ Aurignacian	Gd, 6D	-	1	-
Siuren I	Micoquian/ Aurignacian	Gd, 9E	20	-	-
Siuren I	Micoquian/ Aurignacian	H, 6D	-	1	-
Siuren I	Micoquian/ Aurignacian	H, 6E	20	1	-
Siuren I	Micoquian/ Aurignacian	H, 7C	-	2	-
Siuren I	Micoquian/ Aurignacian	H, 7D	20	4	-
Siuren I	Micoquian/ Aurignacian	H, 7E	-	2	-
Siuren I	Micoquian/ Aurignacian	H, 8C	-	1	
Siuren I	Micoquian/ Aurignacian	H, 8E	20	-	-
Buran Kaya III	Micoquian	B	-	1	Oxford University, England
Buran Kaya III	Micoquian	C, D8	-	1	-
Zaskalnaya V	Micoquian	Level II.I.Sq.18b	-	1	
Zaskalnaya VI	Micoquian	II, 30b	-	1	Oxford University, England

Zaskalnaya VI	Micoquian	IIIa, 30D	-	1	-
Total			628	126	

All bone samples were manually cleaned with air abrasion mixed with aluminium oxide powder at the Douka/Higham Lab, Department of Evolutionary Anthropology at the University of Vienna, Austria. This enabled the removal of superficial contaminants before being processed for radiocarbon dating or ZooMS analysis. On average 600 mg was taken for pre-treatment for radiocarbon dating and 25 mg for ZooMS. Stable isotopes analysis was performed on already extracted collagen (~1 mg) for radiocarbon dating.

2.1.2. Sampling: Glaston

Five bone samples from Glaston were previously radiocarbon dated with ultrafiltration, including one that was dated twice (Cooper et al., 2011). This resulted in six pre-extracted collagen samples to analyse within my thesis. All the samples were re-analysed using XAD-2 approaches with one sample being processed twice, to ensure there was no major variation. All samples were from the bone bed layer at the site, with no clear stratigraphic superposition.

2.2.1. Radiocarbon dating and stable isotope analysis

To connect human behaviour culturally with biological aspects in human evolution, one key requirement to place them in a proper context is time. The first radiocarbon dating was undertaken on a Palaeolithic archaeological site over 70 years ago (Movius, 1960) and radiocarbon continues to be the primary dating technique for the period, despite it reaching its limit as the Middle Palaeolithic comes to an end. However, some discrepancies and dating errors of thousands of years have been found from past dated sites across Eurasia. This has resulted in a large proportion of dates being underestimates of their 'true age' (~70%), due to contamination and less rigorous pre-treatment methods being used (Higham, 2011). Contamination may occur from a range of sources, including soil humates and conservation products (Devièse et al., 2021), which can include artificial carbonate, nitrate, and humic acids (Vaiglova et al., 2014). The introduction of contamination can dramatically affect the radiocarbon age, potentially by thousands of years, with only an uptake of 1-2% modern carbon (Douka & Higham, 2017). It is important to re-date samples from some archaeological sites, as they may prove key for understanding hominin interactions with other species, extinctions, and behaviours in conjunction with technological industries. However, it is sometimes very difficult to know which sites and which material require re-analysis because of potential

problems with contaminants or less than rigorous pre-treatment techniques. We suspect that in some instances bulk collagen dates from open-air sites might be more problematic, due to their exposure to soil humates and water intrusions. Over the past three decades, new pre-treatment chemistry methods have been established to improve the radiocarbon method for dating bone collagen (see Figure 4 for flowchart diagram of protocol). The new protocols which are being used more widely now include ultrafiltration, XAD-2 chromatography and the extraction of the single amino acid hydroxyproline.

2.2.2. Chemical pre-treatment and ultrafiltration for radiocarbon dating

Collagen extraction and pre-treatment of the bones was conducted at the Higham Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. Sampled bones underwent ABA (Acid-Base-Acid) treatment and ultrafiltration following Brock et al., (2010) and Higham et al. (2016). This involved a demineralisation with 0.5 M HCl three times, the first two times were for two hours and the last for ~24 hours. Then the samples were washed three times with ultrapure Milli-Q water. A base wash was then performed with 0.1 M NaOH for 30 minutes. Three more washes with Milli-Q water were then undertaken. Following this, 0.5 M HCl was added for 15-minutes to remove absorbed CO₂ from the base wash, and three Milli-Q water washes were then completed. The collagen was then gelatinised in pH3 water for 20 hours at 75°C. The gelatin was filtered with a pre-cleaned Ezeefilter, before being processed with a cleaned ultrafilter (Vivaspin® Turbo 15 30kD MWCO) and centrifuged until 1.0 mL of the >30 kD gelatin fraction remained (~20 minutes at 2700 RPM). The gelatin was then placed into a glass tube before being freeze-dried at ~18°C for 48 hours. After freeze-drying, the collagen samples were then weighed out to determine if the sample had enough yield to be further processed with XAD-2. For the comparative sample analysis within this thesis (ABA and ultrafiltration), the samples were weighed out into pre-cleaned tin capsules. Three pre-tins for the combustion were made up of 2-2.5 mg of collagen to remove memory effects and ensure the accuracy of the radiocarbon date in the AMS.

2.2.3. XAD-2

After successful ultrafiltration, further pre-treatment with the XAD-2 protocol was performed on collagen samples that had a yield higher than 3 mg. The XAD-2 method involves hydrolysis of collagen into amino acids and their recovery using ion-exchange columns (Stafford et al., 1987, 1988, 1991). The hydrolysis step is important because it effectively breaks the strong bonds between the collagen and humates where they occur. The purification process occurs through an ion-exchange column comprising a styrene-divinyl-benzene resin (XAD-2). Contaminants

such as humates and fulvic acids remain on the resin while the amino acids pass through, to be collected, deacidified and passed for AMS dating (Minami et al., 2016; van der Sluis et al., 2023). At least 3-10 mg of collagen was placed into a clean glass tube with ultrapure 6 M HCl and hydrolysed for 24 hours at 110°C. Pre-cleaned and conditioned XAD-2 columns were used to allow the passage of the hydrolysed collagen. The columns had a pre-fitted filter frit at the bottom, and a filter frit was placed above ~100 µL of XAD-2 resin. 20 washes of 1 M HCl and 10 washed of 6 M HCl were passed through the columns. The samples were then passed through the column, with one more wash of 1 mL of ultrapure 6 M HCl, to collect any leftover amino acids. The samples were then placed into a Genevac evaporator for 6-12 hours, to evaporate the remaining acid. Following this, ~100 µL of Milli-Q was placed into each tube and these were returned to the Genevac for 1-2 hours until full evaporation. After this was complete, ~200 µL of Milli-Q was placed again in each sample tube. Each sample was pipetted into a pre-cleaned tin 'boat' along with 8-10 mg of baked out Chromosorb™. Each tin boat was placed one at a time on a hot plate for the water to evaporate, before being carefully folded up into a sealed ball prior to combustion. For XAD-2 samples, phthalic acid was used for the 3 pre-tins.

2.2.4. Combustion and graphitisation

The tin capsules were combusted using an AGE3 automated graphitisation system (Ionplus AG) at VERA, University of Vienna. The AGE3 system is coupled to an elemental analyser. During combustion, carbon and nitrogen in the samples are quantitatively converted to CO₂ and N₂. Residual water vapours are removed using a chemical trap, and the gases are subsequently separated by gas chromatography. A helium gas stream carrier is used throughout this process.

The purified CO₂ is transferred to evacuated graphitisation reactors within the AGE3 system containing a pre-loaded iron catalyst (2-2.5 mg). Hydrogen is then introduced at a stoichiometric ratio of approximately 2.2:1 (H₂: CO₂), and the reduction reaction is carried out at 560 °C for approximately six hours in a closed system. This results in the graphite targets typically containing between 1 - 2 mg of carbon, depending on the sample yield (Rom et al., 1997).

2.2.5. AMS measurement

The radiocarbon measurements were carried out at VERA using accelerator mass spectrometry (AMS). Measured ¹⁴C/¹²C and ¹³C/¹²C ratios were corrected for machine background and procedural blanks, including contributions arising from chemical pre-

treatment, combustion and graphitisation. Within the Higham Lab, we used a Hollis bone standard that is from a mammoth of a known age, dating to the Middle Pleistocene, ca. 700 ka BP (De La Torre et al., 2019). Also, a VIRI standard was used of a known age whale bone recovered from Svalbard, Norway, with a consensus ^{14}C age of 8331 ± 6 radiocarbon years BP (Scott et al., 2010). Radiocarbon results were normalised to the international accepted Oxalic acid standards (Wacker et al., 2019). The stable carbon isotope ratio ($\delta^{13}\text{C}$) was determined for each graphic target from the measured $^{13}\text{C}/^{12}\text{C}$ ratio relative to the oxalic standard average, allowing for isotopic fractionation correction. Finally, $^{14}\text{C}/^{12}\text{C}$ ratios of unknown samples were calculated relative to the Oxalic acid and standards used to calculate radiocarbon ages.

2.2.6. Stable isotope analysis

As in the standard protocol here at the Higham/Douka lab, all samples were analysed for their stable carbon and nitrogen isotope content ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios). 300 μg was weighed out into a tin capsule for isotopic analysis using an elemental analyser coupled to an isotope ratio mass spectrometer (Thermo Scientific EA-Isolink with a flash 2000 coupled to a Delta V Advantage isotope ratio mass spectrometer) at the Silver Laboratory (Large-instrument Facility for Advanced Isotope Research), which is located at the Centre of Microbiology and Environmental Systems Science of the University of Vienna. The values are reported relative to the Vienna Pee Dee belemnite and atmospheric Air standard and are measured with an analytical precision of $\pm 0.1\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

2.2.7. Calibration

OxCal v. 4.4.3 software was used to calibrate the radiocarbon dates (Bronk Ramsey, 2009a&b). Calibration of the results is necessary because of variation in the production rate of the ^{14}C isotope in the troposphere (Reimer, 2022). I used the IntCal20 calibration curve, which allows an extension of a new limit of up to 55, 000 cal BP (Reimer et al., 2020).

2.2.8. Bayesian age modelling

For the analysis of the samples, Bayesian chronometric modelling was used (Bronk Ramsey, 2009a&b). The mathematical basis of the method (Figure 4 describes the equation) is based on Bayes' theorem (Bayes, 1763):

$$P(t|y) \propto p(y|t)p(t)$$

Table 4 describes the terms in the equation.

Symbol	Definition
t	Set of parameters
y	Measurements made
p(t)	Information on the parameter's measurements
p(y t)	Within a set of parameters, the likelihood of the measurements
p(t y)	The likelihood/posterior probability for a parameter with the set measurements

The equation is split into three parts. This includes the posterior information (quantitative answers), the standardised likelihood (radiocarbon date), and the prior information (generally speaking, the models built here most commonly comprises the stratigraphic position in the archaeological sequence). These connect with the equation in three different sections. These being the radiocarbon dates, the archaeology and the answer (Bayliss, 2009).

Bayesian age modelling not only allows for quantitative assessment for dates but also combines the radiocarbon calibration information with stratigraphic position and enables the inclusion of other chronometric dating methods on a unified time-scale. Furthermore, the difference for Bayesian modelling in comparison with traditional statistical assessments, is that as more prior information is known, the higher the refinement of the probability it becomes (Bayliss et al., 2007).

Posterior information is expressed as a probability. This is resolved through the method of Markov Chain Monte Carlo (MCMC), based on the so-called "Metropolis algorithm", which was first described by Metropolis et al., (1953). The method involves repeated sampling of the probability of the highest distribution, with the prior beliefs taken into account. When a confidence percentage of 95.4% is reached, it is noted as a most likely age range based on these prior beliefs. This method has been widely applied and is highly useful in archaeology and human evolution research. Improvements to the method have involved outlier detection,

the reduction of background noise and statistical variation in calibrated age ranges (Bronk Ramsey, 2017a&b).

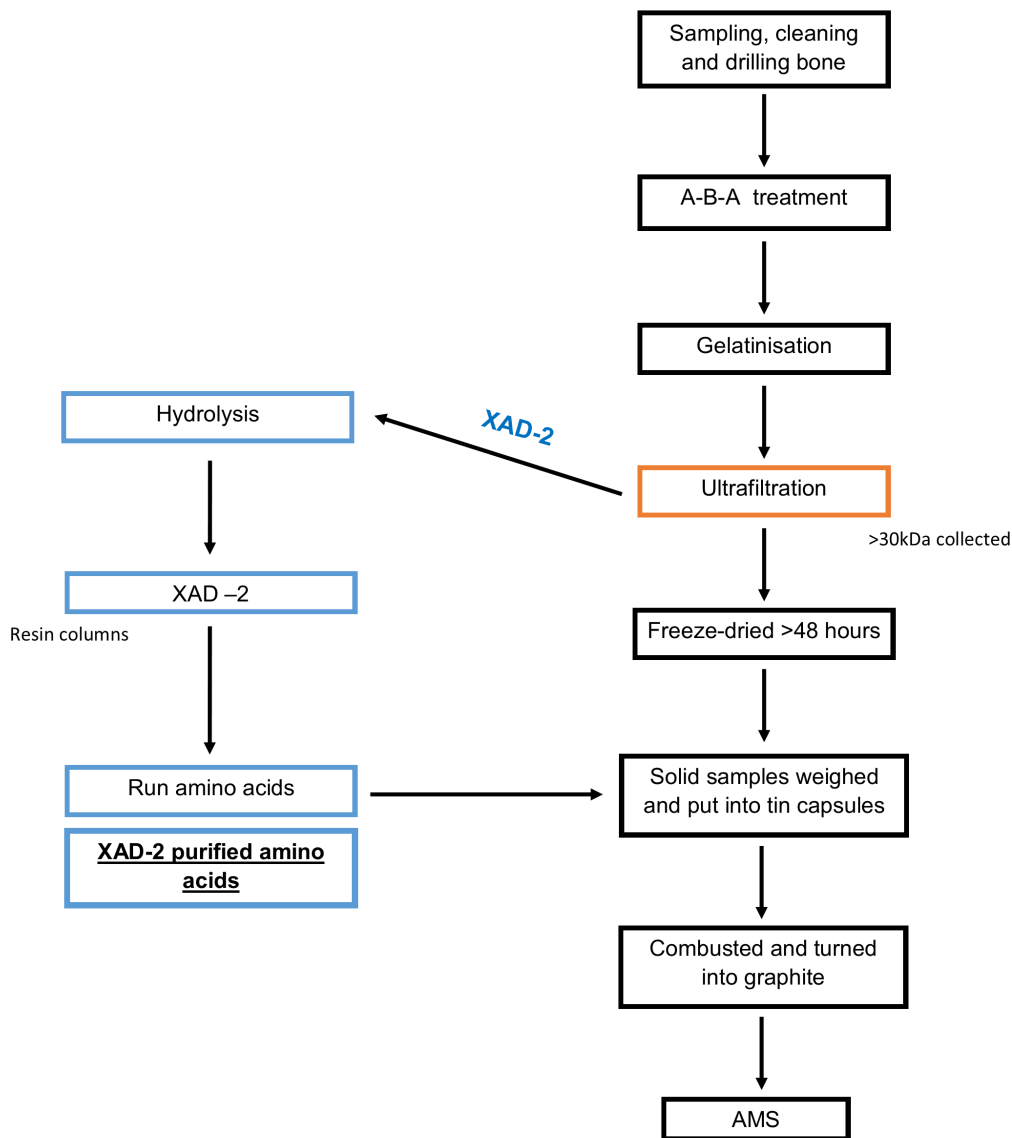


Figure 4. Laboratory and post laboratory protocol for radiocarbon dating with ultrafiltration and XAD-2.

2.3.1. ZooMS

Palaeolithic sites often contain large quantities of unidentified faunal remains that axiomatically contain potential human bone remains (Morin et al., 2017). Carnivore activity (Smith et al., 2024), anthropogenic fragmentation (Sinnet-Mathiot., 2019) and taphonomic activities (Pineda and Saladié., 2022) modify and fragment bone assemblages, hindering formal identification. ZooMS has allowed us use molecular techniques to identify bones to a species or family/genus level and thereby enhance our understanding of the palaeoenvironment of archaeological sites, including those in the Crimean Peninsula. In addition, it has been applied in several instances to screen for hominin remains, resulting in some major insights with the recovery of several important human genomes, dating evidence and more (Brown et al., 2016; Welker et al., 2016; Pigott et al., 2025).

Zooarchaeology by Mass Spectrometry (ZooMS) was first developed over 15 years ago (Buckley et al., 2009). The method enables the identification of unidentifiable bone fragments to species/genus level through collagen peptide fingerprinting. Collagen has been proved to be one of the most dominant and best-preserved biomolecules in archaeological bone. This has enabled amino-acid sequencing of species, which were previously unable to be identified via morphological analysis (Buckley, 2018). The method is also highly accessible, since it is cheap and only requires a relatively low input of labour (Richter et al., 2022).

Overall, ZooMS is a powerful tool, which is rapidly expanding in protocols and application, as well as the range of different types of material that can be analysed.

2.3.2. ZooMS sampling

ZooMS sampling was undertaken either at the institution in which the analysed material was stored or at the Douka/Higham Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. The bone samples were manually cleaned with air abrasion or shot blasting with aluminium oxide and approximately 15-25 mg of bone was clipped off or drilled for subsequent analysis.

2.3.3. Chemical pre-treatment

Bone samples from the Crimean region were processed using an acid insoluble collagen extraction protocol (Welker et al., 2015). Demineralisation was carried out for up to 48 hours with 500 µL of cold (4 °C) 0.6 M HCl, ensuring the samples were completely covered during the 48 hours and became somewhat spongy before the next step. Following demineralisation, samples were vortexed for approximately 10 seconds and centrifuged for 1 minute at 12,000

RPM. The acid was then removed, and the samples were washed two to three times with 200 μ L of 50 mM AmBiC (ammonium bicarbonate buffer, pH 8.0), with each wash followed by centrifugation and removal of the supernatant. Subsequently, 100 μ L of 50 mM AmBic was added to each sample and then incubated for 1 hour at 65 °C for gelatinisation. Half (50 μ L) of the sample was removed in case a backup was needed in the future. Enzymatic digestion was conducted by adding 1 μ L of trypsin solution (0.4 μ g; Thermo Scientific Pierce™ Trypsin Protease) to the remaining supernatant, followed by incubation at 37 °C for 18 hours. Digestion was terminated by the addition of 1 μ L of 5% trifluoroacetic acid (TFA). Peptides were purified using C18 ZipTips (Thermo Scientific Pierce™) with 50 μ L of 50% acetonitrile (ACN) in 0.5% TFA. For MALDI analysis, 0.5 μ L of calibrant (diluted 1:2) was applied to the target plate alongside 0.5 μ L of matrix solution. Sample aliquots (0.5–0.7 μ L) were mixed with an equal volume of matrix prior to spotting. Mass spectrometric analyses were performed using a Bruker Autoflex Speed MALDI-ToF/ToF instrument in linear reflector mode (Buckley et al., 2009).

A single sample from Glaston (Z04548), was prepared using the AmBiC protocol (Brown et al., 2020). This method starts from the pre-extracted collagen, which then has 100 μ L of 50 mM AmBic (ammonium bicarbonate buffer, pH 8.0) added to the sample before being incubated for 1h at 65 °C for gelatinisation (then following along the acid insoluble protocol).

2.3.4. Spectra analysis

The peptide marker (A-G) was manually inspected in mMass 5.5.0 (Strohalm et al., 2010) and compared against known peptide markers in a reference library (Welker et al., 2015). After manual taxon identification, SpecieScan software was used to confirm taxon identifications (Végh & Douka, 2024). SpecieScan is a semiautomated process using R and Python to output correlated identifications from reference databases.

3. Chapter 3: A review of the radiometric record of the Crimean Peninsula in relation to the region being an area of refugium for the last Neanderthals

3.1. Publication I

Title: The Late Middle and Early Upper Palaeolithic in Crimea (Ukraine) — A Review of the Neanderthal Refugium Hypothesis

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Significance: This article is a very important first publication for the overall thesis, as it reviews all the previous archaeological excavations and chronometric work which has been undertaken for the Crimean sites that I subsequently worked on. The review introduces the key Middle to Upper Palaeolithic sites within the Crimean Peninsula. This includes aspects of their stratigraphic context and the results of previous dating. Future work was discussed. I highlight the possibility of the area being a refugium for late Neanderthals. I conclude that, when examining the radiocarbon dates, lithic assemblages and potential for contamination, this proposition seems less likely. In summary, the publication highlights the key sites which need to be re-assessed with more modern protocols to both improve the chronometric precision and generate a more reliable temporal framework. ZooMS is referenced as a potential method of interest, since thousands of fragmented and unidentified remains from Crimean sites have been excavated but not further analysed.

Contribution: This publication is a review article providing the basis for later work involving radiocarbon dating, ZooMS, stable isotopic and ancient DNA methods. I was lead author on the publication as well as the corresponding author. I also undertook all the Bayesian modelling within the manuscript, with my supervisor guiding me with the application of OxCal.



The Late Middle and Early Upper Palaeolithic in Crimea (Ukraine)—A Review of the Neanderthal Refugium Hypothesis

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Abstract

The Crimean Peninsula contains numerous important Palaeolithic sites. It has been considered a potential Neanderthal refugium in Eurasia prior to their disappearance or assimilation, and subsequent replacement by *Homo sapiens*. This understanding is primarily drawn from lithic technological analysis and radiocarbon dating. However, recent developments in the latter suggest that many of the previously obtained radiocarbon dates from Crimean sites may be too young. The chronological sequence from the site of Kabazi II is a case in point, where differences between dates of bulk collagen and those of single amino acids range up to 10,000 radiocarbon years. These discrepancies are argued to arise from sample contamination and its lack of removal in bulk collagen dating. In this paper, we undertake a critical re-evaluation of results from seven Palaeolithic archaeological sites in the Crimean Peninsula: Kabazi II, Siuren I, Buran-Kaya III, Zaskalnaya V and Zaskalnaya VI, Kabazi V and Starosel'e. Our analysis of radiocarbon results from various sites supports the view that radiocarbon dates obtained so far tend to be too young, which has been indicated in the stratigraphy and lithic assemblages. By harnessing robust radiocarbon protocols in future chronometric work, such as the extraction of hydroxyproline, ninhydrin derivatisation or the purification of amino acids using XAD-2 resin, there is potential for constructing accurate chronologies. Furthermore, improved dating accuracy holds the promise of significant additional insights into the prehistoric sequence of the Crimean Peninsula and its potential role as a refugium for Neanderthals prior to their disappearance.

Keywords Palaeolithic archaeology · Radiocarbon dating · Middle to upper Palaeolithic transition · Micoquian · Mousterian · Aurignacian

Introduction

The Crimean Peninsula is a region rich in preserved stratified Middle and Upper Palaeolithic sites. Within the Middle Palaeolithic, two distinct lithic industries have been revealed. The Crimean Micoquian (CM) appears to be present across approximately 100,000 years (Chabai et al., 2004). This technocomplex is primarily characterised by soft hammer bifacial thinning and retouching to produce bifacial tools, amongst which *Keilmessers* are the most indicative tool forms; unifacial tools such as side scrapers are often made on bifacial thinning flakes (Chabai, 2004). The Western Crimean Mousterian (WCM) appears later and is thought to have been present over 50,000 years until the end of the CM industry. The WCM is characterised by an absence of bifacial tools and presence of tools made on flakes and from Levallois reduction processes and, in its final phase, volumetric core reduction (Marks & Chabai, 2006). The Upper Palaeolithic is represented by two lithic industries

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that appear, based on the current evidence, to have coexisted partially alongside CM and WCM (Chabai, 2005). The first of these is the Aurignacian, a technocomplex characterised by pronounced carinated technology, finely retouched twisted and non-twisted bladelets and blades as well as micro-blades and bone tools (Demidenko & Otte, 2001). The second Upper Palaeolithic technocomplex, the Eastern Szeletian, is notable for bifacial leaf points, end-scrapers on flakes, geometric trapezoidal microliths and bone tools (Laroulandie & d'Errico, 2004). This industry also exhibits radial core reduction practices, albeit with blades being a relatively infrequent component (Monigal, 2004). The CM has conventionally been attributed to Neanderthals due to the presence of Neanderthal remains in Crimean sites such as Kiik Koba (Demidenko & Uthmeier, 2013), Zaskalnaya V (Chabai & Uthmeier, 2017) and Zaskalnaya VI (Stepanchuk et al., 2017). Based on a human tooth from Siuren I, the Aurignacian in the Crimea can be tentatively linked with what we call here derived *Homo sapiens*,¹ as indeed it is across Europe (Benazzi et al., 2015; Slimak et al., 2022). The association between the WCM and one of these human species is unknown due to the lack of human remains.

Refuge

In general, the period spanning approximately 47,000–42,000 cal BP marks a pivotal juncture in the bio-cultural transition from the Middle to the Upper Palaeolithic in Eurasia (Davies et al., 2015; Higham et al., 2014; Hublin, 2015; Hublin et al., 2020). This temporal range aligns with the increasing presence of derived *Homo sapiens* and the waning of Neanderthals throughout Eurasia (Hublin, 2015). The Initial Upper Palaeolithic (IUP) assumes key importance within this transition period, ushering in significant changes in culture and technology increasingly linked with derived *Homo sapiens* (e.g. Mylopotamitaki et al., 2024). The IUP itself was then replaced by industries of the Upper Palaeolithic (Rybin et al., 2023). This can be seen in various sites across Europe, one notably being Bacho Kiro, Bulgaria. A lithic assemblage was found, which did not relate or contribute to later assemblages and populations (Hajdinjak et al., 2021).

The Crimea, like the southern Iberian Peninsula and Gibraltar, are regions with unusually recent dates for Middle Palaeolithic assemblages (Finlayson et al., 2008; Jennings

et al., 2011). Soffer (1994) suggested that the Crimea was a technological and anthropological eastern European *cul-de-sac* or refugium (Soffer, 1994; Stepanchuk, 2006; Burke, 2006, see also Ramírez-Pedraza et al., 2020). A refugium describes a region/area which supports an isolated species or community during a period where unfavourable conditions prevail elsewhere (Birks, 2015; Jones, 2021). In classical biological terms, the area must also provide sufficient temperatures to live and reproduce, and shelter against strong winds, and should have no permafrost present (Birks & Willis, 2008). Presently, the term refugium (local environment to have escaped ecological change) or refuge (general state of safety) is used in various fields and can be defined by different functions, for example macro or micro refugia (Jones, 2021). Macro refugia refers to regional refugial scales, whilst micro refers to a microclimate.

The Crimea can be defined as a macro refugium because of its large size and the fact that it is a peninsula. The region was inhabited long before the Middle to Upper Palaeolithic transition. At Kabazi II, absolute dates and palaeoenvironmental evidence show that the lowermost archaeological horizons date to Marine Isotope Stage (MIS) 5. Similarly, at Starosel'e, CM artefacts are found in the lowermost occupation from level 4, dating to between 80,000 and 77,000 uncal BP (Hardy et al., 2001; McKinney, 1998; Rink et al., 1998). The earliest layer radiocarbon dated at Starosel'e has been dated to ~42,500 ¹⁴C years BP (without ultrafiltration) (Marks et al., 1997). This date of course may be too young, given the common underestimates associated with non-ultrafiltered dates. The age of the earliest occupations of Kabazi II fall into a phase of rising sea levels which made the Crimea an island (Marks & Chabai, 2006). This suggests the presence of Neanderthals, pre-dating MIS 5, during the Saalian complex, when it was still possible to reach continental land from the Crimea. On a longer chronological perspective, the Crimea might have experienced refugial phases with human presence cut off from the mainland during interglacial periods on the one hand, and refugial phases with connectivity to the larger northern Black Sea region during glacial periods on the other. The transitional palaeoenvironment during the Middle to Upper Palaeolithic shift was characterised by colder and more arid conditions. Environmental studies based on small mammal fauna, malacofauna, pollen, pedology and large mammal fauna all indicate that the conditions during MIS 3 during both stadials and interstadials were moderate rather than severe (Markova, 2012; Ramírez-Pedraza et al., 2020).

While the idea of the Crimean Peninsula being a refugium for late surviving Neanderthals holds some merit, doubts have begun to surface regarding the chronological evidence used in its support. At the Crimean Palaeolithic site of Kabazi II, for example, AMS radiocarbon dates ranging from 40,000 to 35,000 cal BP for WCM contexts were taken

¹ The precise terms used to refer to what were previously known as 'anatomically modern humans' or *Homo sapiens* are undergoing a great deal of debate currently. Stringer (pers. comm'd in Bermúdez de Castro and Martínón-Torres, 2022) suggested that 'basal *H. sapiens*' and 'derived *H. sapiens*' might be more preferred over the more traditional 'archaic' and 'modern'. We follow this suggestion here for 'modern' humans.

as evidence for a Neanderthal presence later than the disappearance of Neanderthals elsewhere in Europe, as shown by Higham et al. (2014). Recent redating of the bones that provided these initial results suggest that they likely date to > 50,000 cal BP, much older than was first assumed (Spindler et al., 2021), casting doubt on the notion of an unusually late Neanderthal presence in the Crimea.

Other European regions, such as Iberia, Italy, Belgium and the Balkans, have also been posited as potential refugia due to their geography, which might at times have offered benefit to human groups facing progressively unfavourable climatic conditions (Bicho & Carvalho, 2022). Southern Iberia has been suggested as an optimal location for Neanderthal populations seeking to evade the more severe glacial conditions further in the north, much like a potential Crimean scenario (Chabai, 2005). Pleistocene Iberia boasted a rich biodiversity and sustained a persistence of rainfall (Jennings et al., 2011). Among the notable sites postulated as Neanderthal refugia, Gorham's Cave, Gibraltar, stands out (Finlayson et al., 2006). The cave features a Mousterian level, radiocarbon dated to between 33,000 and 23,000 cal BP (López-García et al., 2011), although the reliability of these dates has been criticised for potential contamination and uncertainties surrounding the dated charcoal remains within the stratigraphy (Zilhão & Pettitt, 2006; Higham et al., 2012). Southern Iberia is not favourable overall for the preservation of organic remains and biomolecules due to the high average temperatures. This has deleteriously affected the bone preservation at various sites. At the Palaeolithic sites of Jarama VI and Zafarraya, for example, only 27 out of 215 bones contained a nitrogen yield high enough to proceed with radiocarbon dating (Wood et al., 2013). The challenge of dating sites in southern Iberia makes it difficult to assess whether the region really was a refugium for late Neanderthals. Our view is that this remains to be demonstrated. By comparison, the Crimean Peninsula holds greater promise for reliable radiocarbon dating, due to the improved preservation of biomolecules, including collagen. At Buran Kaya III, for example, collagen yields as determined by %nitrogen was significantly better (Péan et al., 2013). However, it is important to note that collagen yield does vary between the Crimean archaeological sites. For this reason, the Crimea offers us the possibility of testing the hypothesis of whether the Neanderthal refugia hypothesis is robust or not.

Based on the interstratification of Middle and Upper Palaeolithic industries in the Buran-Kaya III sequence and the presence of Middle Palaeolithic toolkits in the two lowermost Aurignacian units of Siuren I, it seems likely there was a co-existence or periodic overlap between the two populations within the wider framework of the Middle to Upper Palaeolithic transition (Bataille, 2017; Chabai et al., 2004). This implies the co-existence of Middle and Upper Palaeolithic industries on the relatively small territory of

the Second range of Crimean Mountains. The movement of people into the Crimean would, at this time, have been facilitated due to the decreased sea levels of the Black Sea during MIS 3 and in fact during the entire last Glacial cycle (Winguth et al., 2000). The Crimea was not a peninsula at this time but part of dry land, which stretched from the Lower Danube to the Northern Caucasus and thus enabled population movements from east-to-west (Chabai et al., 2004).

Radiocarbon Dating

In assessing the veracity of late Neanderthal refugia, chronology is crucial. Bone, like all other carbonaceous materials, is prone to contamination, which can affect the reliability of radiocarbon dates unless removed. Carbon contamination may derive from human/laboratory/conservation sources, but most commonly it comes from soil organic acids, such as humic and fulvic compounds which come from the decay and degradation of plant remains (Deviese et al., 2021). When the bone is of Palaeolithic age, particularly > 30,000 years ago, errors due to contamination can be significant because of the overwhelming influence of modern sources of carbon contaminants on dating samples which are necessarily low in remaining radiocarbon. Underestimated ages resulting in dating errors of thousands of years have been found from past dated sites across Eurasia (Higham, 2019). Up to 70% of previous results are thought to be affected and usually are too young (Higham, 2011).

It is important to review and describe the various protocols for radiocarbon dating that have been applied to bone in Crimean archaeological sites over the last few decades if we are to understand the potential for errors in the corpus of dates we have currently. There are two broad methodological approaches that have previously been applied to AMS dating of bone from the Crimea. The first comprises methods used to isolate bulk type 1 mammalian collagen; the second has been to date compound-specific single or purified hydrolysed amino acids, or carboxylic carbon. The vast majority of dates in the literature fall into the first category. This paper will discuss previous radiometric analysis, which has been undertaken on the Palaeolithic sites.

Collagen is the most prominent protein within bone, comprising ~20% by weight in modern material. Collagen molecules comprise three polypeptides of alpha chains, each with approximately 1000 amino acids per alpha chain (Higham et al., 2006). Collagen is bound within a mineral matrix (hydroxyapatite). Bulk collagen dating undergoes a multi-step extraction process, which involves sequential steps of decalcification, ABA (acid-base-acid) treatment, gelatinisation and freeze-drying (Brock & Higham, 2009). The 'collagen' extracted is known widely as 'Longin' collagen after the researcher who originally published the gelatinisation method (Longin, 1971). It is the most commonly applied

method in dating bone and is essentially the precursor approach for all chemical pretreatment protocol discussed below. Data shows that, while this method can provide reliable radiocarbon dates, it is also prone to errors when bone has been contaminated with greater age, resulting in errors manifestly larger.

In the early 2000s, an ultrafiltration method was applied to purify bulk Longin collagen samples from Palaeolithic bone routinely dated at the Oxford Radiocarbon Accelerator Unit (Higham et al., 2006). This was based on work previously undertaken by Brown et al. (1988). Ultrafiltration is an additional step in bone pretreatment designed to separate low molecular weight (MW) components (often including organic contaminants and broken up degraded collagen) from the high MW fraction (> 30 kD), thereby isolating individual alpha chains of polypeptides which themselves weigh ~ 110 kD. This has been shown to improve the collagen quality as well as remove much of the contaminating substances that affect so many Palaeolithic samples (Higham et al., 2006). A limitation is that, in cases where the MW size of the contaminant exceeds the MW cut-off of the ultrafilter, the contamination will not be removed. This could be significant in specific cases where museum consolidants have been applied to bones or where there has been cross-linking of the collagen with organic ground acids derived for example via the Maillard reaction. This limitation aside, ultrafiltered collagen approaches are the most reliable methods for dating bulk collagen extracted from archaeological bones. Sometimes, however, more rigorous methods are required to obtain accurate dates. The most common involve hydrolysing the collagen to its constituent amino acids. Two main approaches are currently used. The first is using XAD-2 resin; the second, hydroxyproline.

The XAD-2 method revolves around the hydrolysis of collagen amino acids and their recovery using ion-exchange columns (Stafford et al., 1991). The hydrolysis step is important because it effectively breaks the strong bonds between the collagen and humates where they occur. The purification process occurs through an ion-exchange column comprising a styrene-divinyl-benzene resin, usually XAD-2. Contaminants such as humates and fulvic acids remain on the resin while the amino acids pass through, to be collected, deacidified and passed for AMS dating (Minami et al., 2016; Van der Sluis et al., 2023).

Single compound dating is a challenging but attractive approach. Rather than purifying the bulk collagen, the method focuses on extracting a single compound from the collagen amino acid pool. The most common target has been hydroxyproline (HYP) (Stafford et al., 1982; Gillespie et al., 1984). HYP serves as a valuable biomarker for mammalian collagen type 2, due to its rarity in nature, with its abundance constituting approximately ~ 10% of bone amino acids. The collagen is hydrolysed then the amino acids injected onto an

HPLC where they are separated chromatographically and the HYP collected (Devièse et al., 2017). HYP provides contaminant-free measurements, ensuring reliable and accurate results, because only the HYP is being dated (Devièse et al., 2017; Marom et al., 2012). This has resulted in several high-profile cases where previously contaminated and very valuable archaeological specimens have been reliably dated for the first time (e.g. Becerra-Valdivia et al., 2018; Devièse et al., 2019, 2021; Marom et al., 2013). Some notable exceptions have been identified, for example when samples are contaminated with amino acids from modern bone glues (see Devièse et al., 2018; Prüfer et al., 2021). In these cases, the HYP method will not discriminate the ancient from the contaminating amino acids, and only the use of ancient DNA or palaeoproteomics will enable the identification of the source of this carbon. The low proportion of HYP also means that sample size requirements are generally much higher than for other methods, with extensive lab work. This, along with the added cost, means that this method is often used only to date severely contaminated bone, or bone which is from particularly important single specimens.

The use of ninhydrin derivatisation for isolating carboxylic carbon is an alternative method first described by Nelson (1991). This method involves a chemical reaction between carboxylic batches of proteinaceous molecules and the CO₂ which is extracted from them (Tisnérat-Laborde et al., 2003). The protocol involves two treatments of ninhydrin, which removes amino acids which are weakly attached to the collagen. Acid hydrolysis and filtration is completed in between the two steps (Dumoulin et al., 2017). The method is attractive in that it is straightforward to use. It has been suggested, however, that it is not possible to exclude the inclusion of carbon derived from exogenous carboxylic groups (Hedges & Klinken, 1992).

Following these protocols, the process of dating follows the same general set of procedures, involving combustion, purification, graphitisation and usually measurement by accelerator mass spectrometry.

For each site, tables are included with previous radiometric dates, which were undertaken. The method for each date is included if this is known.

Location

The present-day Crimean Peninsula covers approximately 27,500 km², bounded by the Black Sea to the west and south, and the Azov Sea to the east. The peninsula encompasses a predominantly steppe environment, interwoven with a mountainous terrain separated into three distinct ranges. The first comprises mountains over 1000 m in elevation. This topography offered not only elevated vantage points but also an abundance of water sources, rendering it probably a favourable and stable habitat prior to the onset of

the last glacial maximum. The second range, situated more centrally within Crimea, hosts a wealth of rock shelters and a profusion of high-quality flint outcrops, distributed within an altitude range of 300–800 m above sea level (asl). The third consists of low hills with occasional rock shelters and flint outcrops (Ferring, 1998).

Materials—Archaeological Sites and Previous Radiometric Dates

This review will cover the key Middle and Early Upper Palaeolithic archaeological sites of the Crimean Peninsula, with a particular focus on the chronostratigraphy in the light of hypotheses regarding its roles as a possible refugia. Seven sites will be critically considered: Kabazi II, Siuren I, Buran-Kaya III, Zaskalnaya V, Zaskalnaya VI, Kabazi V and Starosel'e. These sites are all located within the middle mountain range of the Crimea (Fig. 1). In a broader context, the peninsula harbours an impressive array of more than 35 stratified Middle Palaeolithic sites and more than 10 Upper Palaeolithic sites (Chabai, 2005).

Of the selected archaeological sites we review here, six are rock shelters, whilst Kabazi II is an open-air site (for radiometric date ranges, see Table 1). The rockshelters are situated within Eocene nummulite limestones, some of which exhibit evidence of rock fall as discerned in the stratigraphy. Kabazi V and Siuren I are good examples. These sites contain an exceptionally good preservation of the archaeological faunal remains (Bataille, 2012; Uthmeier & Chabai, 2018), favoured by high sedimentation rates (Chabai & Uthmeier, 2017). In contrast, open-air sites present unique challenges. These sites are susceptible to erosion or disturbances due to contemporary human activities, potentially leading to the destruction of valuable deposits. Furthermore, open-air sites can deleteriously affect the preservation of

biomolecules. The downward leaching of soil organic acids can lead to problems with cross-contamination of bone and charcoal, which can make radiocarbon dating significantly more difficult (Spindler et al., 2021). Another challenge for radiocarbon dating is the often-low presence of intact collagen for dating, which may not be adequately preserved in the bone. Charcoal samples can serve as an efficient substitute if the collagen content is low. However, the efficacy of this approach hinges on the quality of charcoal preservation and the yield of viable samples, as well as the context of the material of course.

Currently, considering the absolute dates obtained so far, the sites under review here encompass a temporal range spanning from 28,000 cal BP to > 50,000 cal BP, and thus cover both late Middle and early to middle Upper Palaeolithic periods. Only Kabazi II has, in our view, undergone recent robust re-dating using the most up-to-date protocols: HYP dating. Because these dates were considerably older than expected, it is quite plausible that other sites might also contain dates which underestimate their 'true' age, because of unremoved contaminants, as there is a wide range of literature attesting to age offsets between bulk and compound-specific dating. Such offsets between dates with different sampling pretreatment have been reported from many other sites from this temporal range, some defined as 'open-air' contexts (Becerra-Valdivia et al., 2018; Bourrillon et al., 2018; Deviese et al., 2017, 2018, 2019; Dinnis et al., 2018; Kosintsev et al., 2019; Marom et al., 2013; McColl et al., 2018; Moreno-Mayar et al., 2018; Nalawade-Chavan et al., 2013; Reynolds et al., 2017; Sikora et al., 2017). It is critically important to employ refined protocols to ensure the accuracy of dating results across archaeological sites such as these.

In this review, we consider the individual sites and their chronologies based on our experience of AMS dating of

Fig. 1 Map of the Crimean Peninsula, showing the position of Siuren I, Starosel'e, Kabazi II, Kabazi V, Buran-Kaya III, Zaskalnaya V and VI. The red to brown colours represent the first and highest mountain range, which reaches elevations over 1000 m, the lighter and less frequent red to orange colour indicates the second middle mountain range; due to low elevations, the lowermost third range in the north of the middle range is almost not visible in this map. Map made with Mapbox and Topographic map (2024)



Table 1 Table of sites mentioned, lithic technological assemblage, time frame and the most recent radiocarbon dates which have been published

Site	Industry	Timeframe	Radiocarbon age	Main reference
Kabazi II	Western Crimean Mousterian	Middle Palaeolithic	> 50,000 cal BP	Spindler et al., (2021)
Siuren I	Aurignacian or Micoquian?	Upper Palaeolithic	28,000–29,000 uncal BP	Demidenko and Otte (2001) and Demidenko and Noiret (2012)
Buran Kaya III	Micoquian and Eastern Szeletian	Middle/Upper Palaeolithic	28,000–36,000 uncal BP	Péan et al., (2013)
Zaskalnaya V	Micoquian	Middle Palaeolithic	30,000–40,000 uncal BP	Chabai and Uthmeier (2017)
Zaskalnaya VI	Micoquian	Middle Palaeolithic	30,000–39,000 cal BP	Stepanchuk et al., (2017)
Kabazi V	Western Crimean Mousterian and Micoquian	Middle Palaeolithic	30,000–38,000 uncal BP	Housley et al., (2007)
Starosel'c	Micoquian	Middle Palaeolithic	Circa 42,000 uncal BP	Marks et al. (1997)

bone, and we also build Bayesian age models to explore outliers and offsets. We built Bayesian models, where appropriate, from previously published radiocarbon determinations with OxCal 4.4.3 software (Bronk Ramsey, 2009a) and the INTCAL20 calibration curve (Reimer et al., 2020).

Kabazi II

Kabazi II, part of a larger group of sites including Kabazi V, is a multi-layered open-air archaeological site situated along the right bank of the Alma River, within a forest-steppe environment (Gerasimenko, 2005; Markova, 2005). It boasts one of the most extensive and important Palaeolithic sequences in Crimea, extending from the end of the Last Interglacial period, approximately 115,000 years ago (MIS 5d), to the Late Middle Palaeolithic period, less than 50,000 years ago. Kabazi II has been subject to comprehensive analysis and research, including recent radiocarbon dating, as mentioned above, contributing to a deeper understanding of its chronology. New radiocarbon dates confirm that the site dates to more than 50,000 years ago and was not, therefore, a site of very late Neanderthal presence, as originally suspected (Spindler et al., 2021).

The stratigraphy comprises seven stratigraphical units (Fig. 2, further subdivided into 55 in situ archaeological levels (Uthmeier & Chabai, 2018). In total, 20 levels at Kabazi II relate to the WCM and 35 to the CM. Unit II includes a WCM lithic assemblage, characterised by Levallois core reduction and absence of bifacial technology (Chabai, 2005).

Faunal remains and lithics suggest that Kabazi II is an open-air kill and butchering site, most likely occupied by Neanderthals (Patou-Mathis, 1999, 2005, 2006). This inference is drawn from the analysis of the lithic assemblages and is further bolstered by Neanderthal burials at nearby sites with CM material such as Kiik-Koba at Zaskalnaya V and VI, and the absence of *H. sapiens* remains in the Crimea until the appearance of the Aurignacian.

Siuren I

Siuren I is located within the second range of the Crimean Mountains (Demidenko, 2014). It is a rock shelter at an elevation of 15 m above the Belbek River.

The site exhibits a stratigraphic sequence comprising four distinct undisturbed occupational archaeological levels of the Aurignacian (see Fig. 3), belonging to three broader

Fig. 2 Kabazi II Drawings of the western (a) and eastern (b) sections. Arabic numbers indicate lithological layers and Roman numerals indicate archaeological layers. From Uthmeier and Chabai (2018)

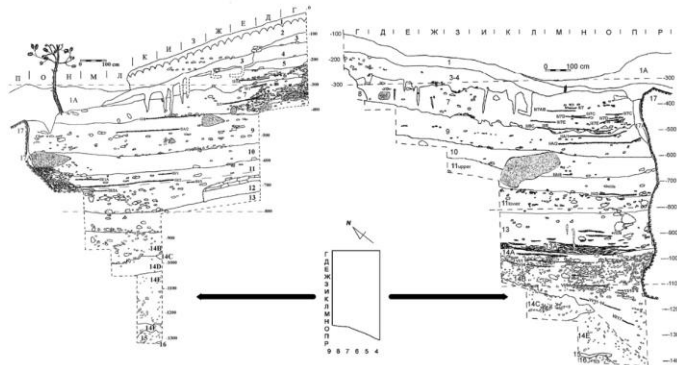
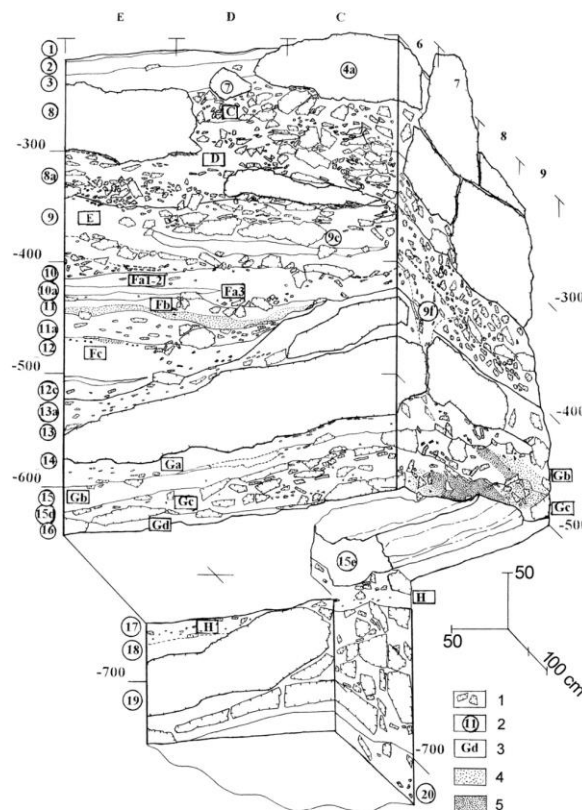


Fig. 3 Siuren I. Stratigraphy of the site. Profiles II and IV. From Chabai (2005)



archaeological units. The archaeological levels are separated by sterile rock fall sediments. In units F, G and H, Aurignacian assemblages have been uncovered with the presence of finely retouched non-geometric microlithic, e.g. Dufour bladelets, which are interpreted as being indicative of the Aurignacian and thereby probably linked with *Homo sapiens*. However, there is the intriguing possibility of an overlap with Neanderthals, as evidenced by a CM component in the Aurignacian assemblages of archaeological units G and H (Chabai, 2005; Demidenko & Otte, 2001).

The Aurignacian units at Siuren I can be subdivided into two major phases: an earlier one, encompassing unit H and G, each with several archaeological levels, and a later one, consisting mainly of levels from unit G (Demidenko & Otte, 2001). The latter is characterised by retouched bladelets with a twisted length profile (Dufour bladelets, sub-type Roc du Combe), also found in Central Europe (Chabai, 2005). The previous calibrated radiocarbon date for unit F indicates that the Aurignacian was present around 31–35,000 cal BP,

which would be very late within a European context, and might be seen perhaps as unlikely, since there is evidence for the Aurignacian being present around 43–35,000 years ago (Chu & Richter, 2020). The uncalibrated radiocarbon results are in Table 2. Units G and H can be assigned to an earlier phase of the European Aurignacian; like other Proto-Aurignacian assemblages, the main argument is the presence of retouched Dufour bladelets of the Dufour sub-type that are straight in length profile. In addition, and as already mentioned above, there are bifacial and unifacial thinning flakes, scrapers, and points typical of the CM technocomplex (Bataille, 2012; Demidenko, 2014). This Middle Palaeolithic component is often patinated, implying a longer exposure to weathering, contrasting with the Aurignacian artefacts, which are preserved with unpatinated, fresh surfaces. Around 10% of the assemblages observed in units G and H fit this pattern (Demidenko & Noiret, 2012). The presumed oldest grinding stone linked with *Homo sapiens* was also found within unit G, relating to the Aurignacian.

Table 2 Previous radiocarbon dates obtained from levels H, G and F at the site of Siuren I (Demidenko & Noiret, 2012; Demidenko & Otte, 2001). The dates are on ungulate bones. AG is the abbreviation for unfiltered gelatine and AI for ion-exchanged gelatine. The dates used in the Bayesian model are highlighted in italics

Lab no	Material	Unit	Industry	Pre-treatment method	Radiocarbon Age BP
<i>OxA-8249</i>	Bone	H	Aurignacian/Micoquian	AG	28,200 ± 440 BP
GrA-46553	Bone	H	Aurignacian/Micoquian		22,040 ± 120 BP
Beta-260924	Bone	H	Aurignacian/Micoquian		30,490 ± 220 BP
<i>OxA-5154</i>	Bone	Ga	Aurignacian/Micoquian	AI	28,450 ± 600 BP
Lv-2132	Charcoal	Ga	Aurignacian/Micoquian		250 ± 60 BP
Beta-260919	Bone	Gb1	Aurignacian/Micoquian		28,070 ± 190 BP
Beta-293363	Bone	Gb2	Aurignacian/Micoquian		13,020 ± 70 BP
Beta-293361	Bone	Gb2	Aurignacian/Micoquian		19,680 ± 100 BP
Beta-293362	Bone	Gb2	Aurignacian/Micoquian		22,220 ± 120 BP
Lv-2131	Charcoal	Fb2	Aurignacian		10,520 ± 150 BP
<i>OxA-5155</i>	Bone	Fb2	Aurignacian	AI	29,950 ± 700 BP
Beta-293364	Bone	Fb2	Aurignacian		29,540 ± 200 BP
<i>GrA-46552</i>	Bone	Fb2	Aurignacian		30,910 ± 240 BP

This suggests food was being mechanically processed at the site (Lango et al., 2021).

Archaeological units G and H hold significance for understanding the humans that once inhabited Siuren I. The combination of Upper and Middle Palaeolithic artefacts, represented by Aurignacian and CM assemblages, within one and the same in situ levels raises the possibility of a co-existence of Upper and Middle Palaeolithic humans. This could be interpreted as the periodic presence of Neanderthal visits to the site during a period when derived *Homo sapiens* were already widely spread in Europe but not perhaps occupying the Crimean Peninsula as permanently (Demidenko & Chabai, 2012a, 2012b). Alternatively, it might indicate that there were more extensive interactions between Neanderthals and derived *Homo sapiens* groups (Bataille, 2012). This underlines the complexities inherent in archaeological interpretation and the need for clearer understanding of the potential mixing of lithic assemblages at the site itself. From a methodical point of view, this might be solved through refined dating techniques to determine whether ages are mixed or consistent, more extensive refitting studies, in-depth sediment micromorphology or sediment DNA analyses.

Buran-Kaya III

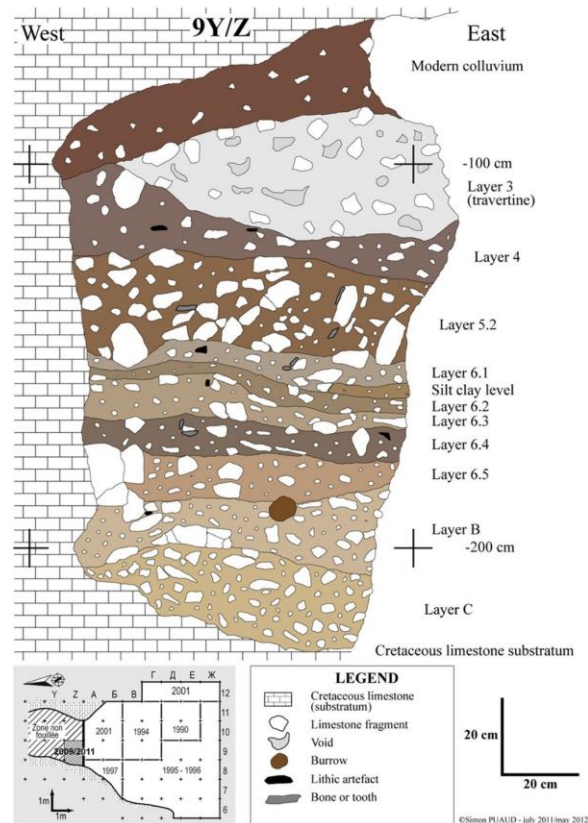
Buran-Kaya III sits within an overhanging rock shelter within a narrow valley in the second mountain range of the Crimean Peninsula (Uthmeier, 2024). The rock shelter is 5 m wide and 6 m deep, sitting 8 m above the current Burulcha river (Marks & Monigal, 2000). The rock shelter's location encompasses diverse biomes, including steppe, forests and plateau, making it potentially an ideal habitat for hominins during the Palaeolithic period. This ecological diversity

can be seen throughout the extensive stratigraphy of the site (Péan et al., 2013).

A total of 19 cultural layers have been identified at Buran-Kaya III. These layers were initially documented following the 2001 excavations, encompassing a time span ranging from the Medieval period to the Middle Palaeolithic. Subsequent excavations in 2009, as illustrated in Fig. 4, specifically focused on nine archaeological layers, which span from the Middle to the Upper Palaeolithic (Péan et al., 2013). Layers 5.2, 6.1 and 6.2 have been characterised as Gravettian, while layers 6.3, 6.4 and 6.5 are associated with the Aurignacian. Layer B has been identified as CM and Layer C as Eastern Szeletian (Péan et al., 2013; Prat et al., 2011). The available radiometric dates can be found in Table 3.

One hundred and sixty-two *Homo sapiens* remains have been discovered within the Upper Palaeolithic layer 6.1, but no evidence for intentional burial has been identified. These human remains, as evaluated through dental wear analysis, have been determined to belong to juveniles or sub-adults (Prat et al., 2011). Isotopic analysis for palaeodiet using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ has been undertaken on the human remains, which has revealed a likely high amount of mammoth and plant protein-based consumption, which indicates the environment was rich in game and nutritious plants (Drucker et al., 2017). Layer B/B1 (Demidenko, 2004; Uthmeier, 2004) shows evidence of bifacial tool production, with few cores but a rich assortment of bifacial and unifacial points attributed to the Kiik-Koba facies for the CM (Demidenko, 2004). Below this, in Layer C, an Eastern Szeletian assemblage, sometimes termed Streletskayan, has been identified, comprising bifacial foliate points, geometric trapezoidal microliths and endscrapers, as well as snapped bone tubes and handles (Monigal, 2004; Uthmeier, 2012). Residues found on these tools provide evidence of their hafted use in cutting animals and avian tissues, as well as plants (Chabai, 2005;

Fig. 4 Stratigraphic sections of Buran-Kaya III and plan of the excavations. From Péan et al. (2013) with permission



Hardy et al., 2001). Level C is conventionally attributed to the Upper Palaeolithic (Monigal, 2004), so it is interesting that layer B above signals a markedly different industry. As in the case with Siuren I, this stratigraphic position raises intriguing questions about the possibility of a coexistence of Neanderthals and Upper Palaeolithic humans not only at the site but also on Crimean Peninsula as a whole. However, interpreting this coexistence is complex due to the nature of the Eastern Szeletian, which is described as a transitional industry (Adams, 2009; Uthmeier, 2012) or an Upper Palaeolithic technocomplex (Monigal, 2004) within the archaeological record. In any case, the lack of human remains does not allow for a secure identification of the makers of this industry.

Various worked faunal remains have been discovered, some of which were modified through bone tube manufacturing (Laroulandie & d'Errico, 2004). These modifications observed in Layer C involved the use of materials from a wolf, bird and hare. One of these remains exhibits signs of

having been heated. Additionally, evidence of sawing and cutting on different bone specimens has been documented. Remains that show evidence of scraping marks evidence the use of hare (Laroulandie & d'Errico, 2004), which is highly unusual in the Crimean Middle Palaeolithic. Furthermore, it appears that humans employed a specific technology in the creation of lithic artefacts for working bone (Laroulandie & d'Errico, 2004). The archaeozoological analysis of the faunal material from Layer C suggests that not only humans, but also carnivorous animals, played a role in the formation of the faunal assemblage. This is again an exception in the Crimean Middle Palaeolithic and interpreted as indicating an ephemeral presence of humans at the site that was scavenged by carnivores afterwards. In the Aurignacian and Gravettian layers above level C, there are numerous artefacts crafted from bone, and ornaments were made from both marine and freshwater shells, mammal teeth and ivory. In the Gravettian layers, there is strong evidence of cultural ornamentation of objects, a trend that is evident not only at this site, but also

Table 3 Radiocarbon dates from Buran Kaya III, obtained using various methods (Longin collagen and ultrafiltration). Some dates are in groups (bold line and date in underscore). These groups represent a single bone which was dated using different methods. AI is the abbreviation of ion-exchanged gelatine. The dates used in the Bayesian model are highlighted in italics

Lab no	Material	Layer	Industry	Pre-treatment method	Radiocarbon Age BP	Reference
<i>OxA-6672</i>	Bone	C	Szeletian	AI	32,350 ± 700 BP	Pettit (1998)
<i>OxA-6868</i>	Bone	C	Szeletian	AI	36,700 ± 1500 BP	Péan et al. (2013)
<i>OxA-6869</i>	Bone	C	Szeletian	AI	32,200 ± 650 BP	Péan et al. (2013)
<i>GrA-47319</i>	Bone	B	Micoquian	Longin	35,590 ± 290/-270 BP	Péan et al. (2013)
<i>GifA-11218/SacA-25135</i>	Bone	B	Micoquian	Ninhydrin	36,500 ± 1200 BP	Péan et al. (2013)
<i>OxA-36921</i>	Bone	B	Micoquian	Ultrafiltration	37,700 ± 900 BP	Uthmeier (2004)
<i>OxA-6673</i>	Bone	B	Micoquian	AMS	38,840 ± 260 BP	Péan et al. (2013)
<i>OxA-6674</i>	Bone	B	Micoquian	AI	28,520 ± 460	Péan et al. (2013)
<i>OxA-6990</i>	Bone	Horizon 20	Aurignacian	AI	34,400 ± 1200 BP	Péan et al. (2013)
<i>GrA-47318</i>	Bone	6–5	Aurignacian	Longin	32,800 ± 230/-210 BP	Péan et al. (2013)
<i>GifA-11217/SacA-25134</i>	Bone	6–5	Aurignacian	Ninhydrin	35,900 ± 1100 BP	Péan et al. (2013)
<i>OxA-4128</i>	Bone	6–5	Aurignacian	AI	28,700 ± 620 BP	Hedges et al. (1996)
<i>GrA-48399</i>	Bone	6–4	Aurignacian	Longin	31,250 ± 2450/-1880 BP	Péan et al. (2013)
<i>GifA-11220/SacA-25137</i>	Bone	6–4	Aurignacian	Ninhydrin	33,350 ± 830 BP	Péan et al. (2013)
<i>OxA-13302</i>	Human bone	6–4	Aurignacian	Ultrafiltration	32,790 ± 280 BP	Higham et al., (2007)
<i>OxA-4127</i>	Bone	6–4	Aurignacian	AI	11,952 ± 130	Péan et al. (2013)
<i>OxA-4126</i>	Bone	6–3	Aurignacian	AI	11,900 ± 150 BP	Péan et al. (2013)
<i>GrA-40485</i>	Bone	6–3	Aurignacian	Longin	34,050 ± 260/-240 BP	Péan et al. (2013)
<i>GifA-80181/SacA-12260</i>	Bone	6–3	Aurignacian	Ninhydrin	34,910 ± 950 BP	Péan et al. (2013)
<i>GrA-53939</i>	Bone	6–3	Aurignacian	Longin	29,040 ± 180/-170	Péan et al. (2013)
<i>GifA-11221/SayA-25138</i>	Bone	6–3	Aurignacian	Ninhydrin	32,740 ± 780	Péan et al. (2013)
<i>GrA-50460</i>	Bone	6–2	Gravettian	Longin	29,440 ± 190 BP	Péan et al. (2013)
<i>GrA-50457</i>	Bone	6–2	Gravettian	Longin	32,450 ± 250 BP	Péan et al. (2013)
<i>OxA-6882</i>	Bone	6–2	Gravettian	AI	30,740 ± 460 BP	Mentioned by Otte (2021). Original source Pettit (1998)
<i>GrA-53942</i>	Bone	6–1	Gravettian	Longin	29,640 ± 170 BP	Péan et al. (2013)
<i>OxA-25669</i>	Bone	6–1	Gravettian	Ultrafiltration	32,200 ± 450 BP	Péan et al. (2013)
<i>GifA-10021/SacA-19018</i>	Bone	6–1	Gravettian	Ninhydrin	31,320 ± 820 BP	Péan et al. (2013)
<i>GrA-37938</i>	Human bone	6–1	Gravettian	Longin	31,900 ± 240/-220 BP	Péan et al. (2013)
<i>GifA-11216/SacA-25133</i>	Bone	6–1	Gravettian	Ninhydrin	31,530 ± 670	Péan et al. (2013)

across the Crimea and mainland Ukraine. This suggests the possibility of extensive social interactions and exchanges among Gravettian *Homo sapiens* (Yanevich, 2014).

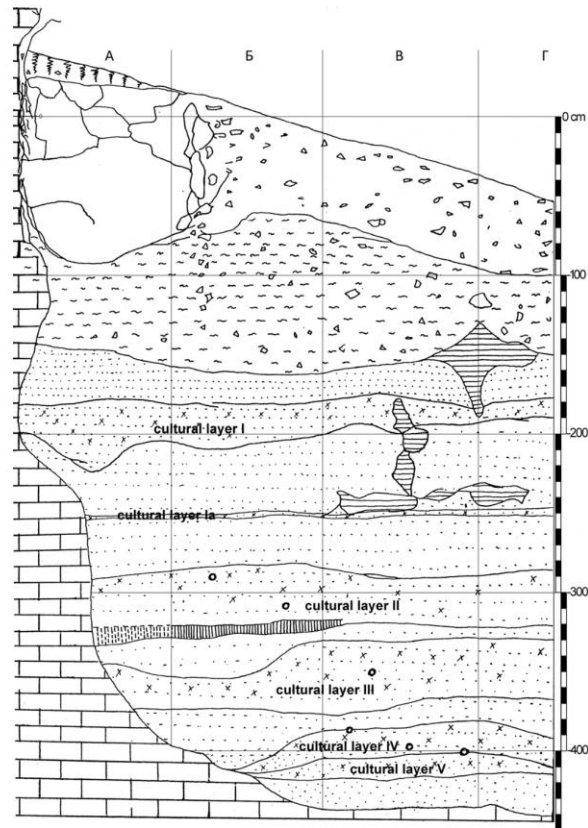
Zaskalnaya V

The rock shelter site of Zaskalnaya V is situated within a limestone cliff at the lower level of the Krasnaya Balka. The rock shelter is 60 m above the Bijuk Karasu River and faces south towards the Krasnaya Balka Valley. The reconstructed size of Zaskalnaya V, based on rockfall excavated downslope the actual rock shelter, is similar in size to Siuren I: approximately 25 m in width, 8 m in depth, and 4 m in height. High-quality flint outcrops are near the site (Chabai & Uthmeier,

2017). Zaskalnaya V has one of the most intensively occupied sequences within the Crimean Middle Palaeolithic, comprising 23 lithological layers and 87 archaeological levels, which were uncovered during the most recent excavations conducted in 2012 and 2013 (Chabai & Uthmeier, 2017). The archaeological levels were sub-divided into different groups (termed A, B, C, D) based on taphonomy and archaeological features, and cross-correlated with excavation units of Y. Kolosov concluded in 1994 (Fig. 5).

Group A consists of archaeological levels with lithic artefacts, burnt material and faunal remains. Group B comprises levels with primarily burnt material, indicating the former presence of hearths, but significant erosion makes it challenging to draw confident interpretations about precise

Fig. 5 Zaskalnaya V: drawing of Kolosov's section along square line 17 and 18. From Chabai and Uthmeier (2017), after Kolosov et al. (1997)



taphonomic processes. Group C levels are categorised by depressions within the sediment, which have been filled up with a combination of lithic artefacts, burnt material and faunal remnants. In some cases, depressions may have been used to construct a hearth or for the anthropogenic deposition of burnt remains from nearby fireplaces. However, most of the depressions and their filling are assumed to go back to natural site formation processes. Group D comprises water eroded sediments.

From top to bottom, the 87 archaeological levels of the most recent excavations were correlated to the eight 'cultural layers' defined by Y. Kolosov during his excavations, to enable comparison with older data, and labelled units I, Ia, II to VII. Across stratigraphical units I–V, a consistent pattern emerges regarding the dominant lithic tools, which are primarily scrapers. Notably, a high proportion of these scrapers are bifacially worked. Additionally, other tool types such as points, denticulates, burins and notches

were present in all levels. The lithic artefacts all show characteristics of the CM, indicating a Neanderthal occupation. This is further supported by the discovery of a Neanderthal upper deciduous molar within cultural unit IV. The tooth is currently under further analysis to isolate aDNA (Chabai & Uthmeier, 2017). A fragment of a skull of a 5- to 6-year-old child was found within unit V and a metacarpal bone of a 25-year-old woman from units II–III (Danilova, 1979a, 1979b; Kolosov, 1983; Stepanchuk, 2022). Two facies of the CM have been recognised at the site, these being the Kiik Koba (units I and IV) and Ak Kaya facies (units II, IIa and III). Both can be described as a sub-type of lithic assemblages within the CM, demonstrating either small lithic artefacts with intense reworking in the Kiik Koba Facies, or comparably large, unreduced bifacial tools in the Ak Kaya facies (Chabai & Uthmeier, 2017; Majkić et al., 2018). The uncalibrated radiometric dates can be seen in Table 4.

Table 4 Uncalibrated radiocarbon and ESR dates from Zaskalnaya V (see Chabai and Uthmeier (2017). ZR is the abbreviation for ABA charcoal. The dates used in the Bayesian model are highlighted in *italics*

Lab no	Material	Unit	Industry	Pre-treatment method	Radiocarbon Age BP	Reference
<i>Ki-10603</i>	Bone	IV	Micoquian		> 47,000 BP	Chabai and Uthmeier (2017)
<i>GrA-13916</i>	Burnt bone	IV	Micoquian		> 46,000 BP	Kolosov and Stepanchuk (2002)
ESR-EU	Tooth	IV	Micoquian	ESR mean	21,000 ± 2100 BP	Chabai and Uthmeier (2017). Original source, McKinney and Rink (1996)
ESR-LU	Tooth	IV	Micoquian	ESR mean	32,400 ± 3400 BP	Chabai and Uthmeier (2017). Original source, McKinney & Rink, 1996)
<i>OxA-35526</i>	Charcoal	III/5	Micoquian	ZR	42,700 ± 1100 BP	Chabai and Uthmeier (2017)
<i>OxA-35602</i>	Charcoal	III/5	Micoquian	ZR	32,000 ± 800 BP	Chabai and Uthmeier (2017)
<i>Ki-10603</i>	Bone	III	Micoquian		39,200 ± 520 BP	Chabai and Uthmeier (2017)
ESR-EU	Tooth	III	Micoquian	ESR mean	20,900 ± 1800 BP	Chabai and Uthmeier (2017). Original source, McKinney and Rink (1996)
ESR-LU	Tooth	III	Micoquian	ESR mean	32,000 ± 2100 BP	Chabai and Uthmeier (2017). Original source, McKinney and Rink (1996)
<i>OxA-35253</i>	Charcoal	IIA/3	Micoquian	ZR	37,350 ± 500 BP	Chabai and Uthmeier (2017)
<i>OxA-35786</i>	Bone	II/1	Micoquian	Ultrafiltration	41,600 ± 1400 BP	Chabai and Uthmeier (2017)
<i>Ki-10743</i>	Bone	II	Micoquian		31,600 ± 350 BP	Chabai and Uthmeier (2017)
ESR-EU	Tooth	II	Micoquian	ESR mean	24,900 ± 2300 BP	Chabai and Uthmeier (2017). Original source, McKinney and Rink (1996)
ESR-LU	Tooth	II	Micoquian	ESR mean	41,800 ± 3100 BP	Chabai and Uthmeier (2017). Original source, McKinney and Rink (1996)
Ki-10891	Bone	I	Micoquian		28,850 ± 400 BP	Chabai and Uthmeier (2017)
<i>Ki-10744</i>	Bone	I	Micoquian		30,080 ± 350 BP	Chabai and Uthmeier (2017)

Zaskalnaya VI

Zaskalnaya VI is a multi-layered rock shelter site, situated near to the Biyuk-Karasu river and facing south. The rock shelter is located 60 m above the river level, which is 10–12 m in width (Stepanchuk et al., 2017).

The stratigraphy unearthed by Y. Kolosov consists of at least seven archaeological cultural layers, with the lower levels being associated with MIS 5 and the upper layers (I–III) with MIS 3 (Stepanchuk et al., 2017). Also, in the light of the much higher stratigraphical resolution obtained from

the re-excavation of Kolosov's sequence at Zaskalnaya V described above, it is highly likely that each 'cultural layer' at Zaskalnaya VI also consists of several separate archaeological levels. The six cultural layers defined in Fig. 6. The radiometric dates can be seen in Table 5.

The presence of CM tools at the site provides strong evidence for Neanderthal occupation, which is strongly supported by Neanderthal remains discovered in cultural layer III and IIIa. In the latter, a triple dismembered child burial was found, indicating the possibility that Neanderthals may have practised complex burial rituals. The

Fig. 6 The section of the Western profile of the excavation area at Zaskalnaya VI, line 29/28 AK. From Chabai (2004), after Kolosov, (1986). The Roman numerals indicate the position of cultural layers. The Arabic numerals represent the lithological layers

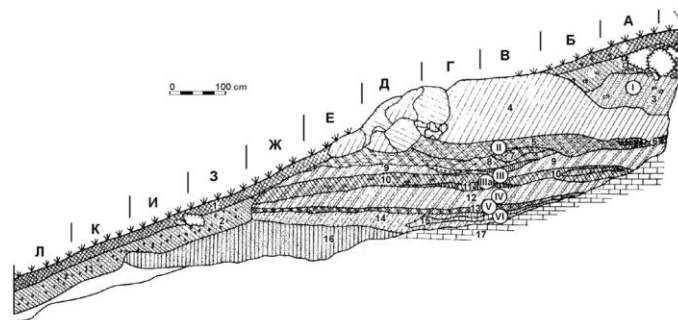


Table 5 Previous uncalibrated radiocarbon dates from Zaskalyana VI (Stepanchuk et al., 2004). The original papers in which the dates were published can be found in the reference column. The two dates which are highlighted in bold are from the same bone. Ultrafiltration was

undertaken on OxA-X-2788–9, which produced an older radiocarbon date along with an improved measurement error. AI is the abbreviation for ion-exchanged gelatine. The dates used in the Bayesian model are highlighted in *italics*

Lab no	Material	Layer	Industry	Pre-treatment method	Radiocarbon Age BP	Reference
<i>Ki-10611</i>	Bone	IV	Micoquian		> 47,000 BP	Stepanchuk et al. (2004)
<i>Ki-10610</i>	Bone	IIIa	Micoquian		39,400 ± 480 BP	Stepanchuk et al. (2004)
<i>OxA-4773</i>	Bone	IIIa	Micoquian	AI	39,100 ± 1500 BP	Hedges et al. (1996)
<i>OxA-4132</i>	Bone	III	Micoquian	AI	30,706 ± 690 BP	Hedges et al. (1996)
<i>OxA-X-2788–9</i>	Bone	III	Micoquian	Ultrafiltration	32,250 ± 400 BP	Unpublished (dates sent to process by T. Uthmeier)
<i>Ki-10609</i>	Bone	III	Micoquian		38,200 ± 410 BP	Stepanchuk et al. (2004)
<i>Ki-10894</i>	Bone	III	Micoquian		36,400 ± 450 BP	Stepanchuk et al. (2004)
<i>OxA-4772</i>	Bone	III	Micoquian	AI	35,250 ± 900 BP	Hedges et al. (1996)
<i>Ki-10608</i>	Bone	II	Micoquian		31,100 ± 490 BP	Stepanchuk et al. (2004)
<i>Ki-10893</i>	Bone	II	Micoquian		30,700 ± 450 BP	Stepanchuk et al. (2004)
<i>Ki-10607</i>	Bone	II	Micoquian		30,220 ± 400 BP	Stepanchuk et al. (2004)
<i>OxA-4131</i>	Bone	II	Micoquian	AI	30,110 ± 630 BP	Hedges et al. (1996)
<i>Ki-13376</i>	Bone	I	Micoquian		24,600 ± 170 BP	Stepanchuk (2006)
<i>Ki-13375</i>	Bone	I	Micoquian		25,200 ± 160 BP	Stepanchuk (2006)
<i>Ki-13373</i>	Bone	I	Micoquian		25,700 ± 160 BP	Stepanchuk (2006)
<i>Ki-10606</i>	Bone	I	Micoquian		24,400 ± 480 BP	Stepanchuk et al. (2004)
<i>Ki-10605</i>	Bone	I	Micoquian		22,800 ± 400 BP	Stepanchuk et al. (2004)
<i>Ki-10892</i>	Bone	I	Micoquian		22,500 ± 450 BP	Stepanchuk et al. (2004)

accumulation of features such as pits, hearths, bone fragments, charcoal and lithic artefacts across cultural layer III suggests an extended period of occupation at the site. This accumulation reflects various activities and behaviours of Neanderthals over time (Stepanchuk et al., 2017). There is also evidence that mammoth bones were brought to the camp, where they were knapped and possibly used as fuel (Fedorchenko, 2018). In total, 120 animal bones were found with splitting marks, caused by anthropogenic lithic abrasion. These abrasion marks include striking blows or negatives of previous chips (Fedorchenko, 2018).

Interestingly, the remains of a young dolphin were found, despite the coast being 50 km away from the site. The presence of marine mammal remains is taken as argument to suggest that Neanderthals were engaged in small-scale migrations and effectively exploited resources, including those from coastal areas (Stepanchuk et al., 2017). However, the lack of cut marks leaves open the possibility that scavenging birds brought the dolphin bones to the site. Traces of abraded ochre found on lithic artefacts may indicate the Neanderthals at the site were engaged in activities that may have had a symbolic or cultural significance (Stepanchuk, 2022).

Kabazi V

Kabazi V is a rock shelter situated within the second range of the Crimean Mountains and only a few hundred meters east of the open-air site of Kabazi II (Uthmeier et al., 2008). The location marks the transition into the higher mountainous terrain of the region. Within the Kabazi Mountain, it stands out as one of eight Middle Palaeolithic sites, and notably is the second deeply stratified site dating to the Upper Pleistocene period from this locale. Kabazi V is situated 120 m above the Alma River, facing south-east (Uthmeier & Chabai, 2018).

The geological genesis of the site is different from others, as the geological formation partly resulted from the effects of running water instead of being primarily caused by gelifraction of the nummulites limestone (Uthmeier & Chabai, 2018). Later, phases of rockfall and sedimentation processes relate to intense weathering of the rock shelter walls. In its final phase, the Kabazi V rock-shelter became an open-air site after the final collapse of the roof. These events, while potentially disruptive, have had a positive impact on the preservation of the site's archaeology and stratigraphy (Housley et al., 2007).

The stratigraphic sequence is 8 m deep, containing 27 lithological layers and 40 archaeological levels (Uthmeier & Chabai, 2018).

Four major archaeological units can be seen in Fig. 7. Unit III/1B represents the phase during which the site became an open-air site, due to a potential rock fall. This would have changed the dynamics of the site entirely (Uthmeier & Chabai, 2018).

Regarding Pleistocene human use, the development of Kabazi V can be divided into three major stages. The first involves the major inflow of water, which hindered any human occupation. The second stage sees the first presence of human occupation, with rock fall, sedimentation and weathering of limestone. The third stage is characterised by sedimentation accompanied by different degrees of erosion within the rock shelter; in this phase, the site was used as a residential camp. Numerous hearths with lithic scatters were found, some of them being placed towards the back of the cave (Uthmeier et al., 2008; Uthmeier & Chabai, 2018; Uthmeier & Chabai, 2018).

In addition, artificial pits are present in greater number at Kabazi V dissociated with CM occupations. Such archaeological evidence points to extensive and diverse activities at the site and the surrounding area, including the exploitation of flint outcrops for tool production. The stratigraphy

of the hearths suggest that the site was occupied multiple times during short-term occupations (Chabai & Veselsky, 2007). Radiocarbon dates from archaeological units III/1A and III/5-3B2 have suggested that the cave site was occupied at least 39,000 cal BP. Dates were obtained from a charcoal fragment and a charred bone sample (Housley et al., 2007). The charcoal sample was dated using the humic acid fraction, which is less reliable than dating the black carbon fraction. Charred bone is considered an unreliable sample type, but at Kabazi V there were few options available due to low collagen levels in bone.

Starosel'e

The site of Starosel'e is located within a steep canyon, slightly off the Churuksu river valley (Burke, 2000). At the time of its initial discovery, the site spanned a north–south distance of 40 m with a depth of approximately 1 m (Marks et al., 1997).

The initial excavation of the site was conducted in 1952 by Formosov (Hardy et al., 2001) and led to the discovery of a single occupation thought to correspond to the late Mousterian. Subsequently, between 1993 and 1995, the site was re-excavated by A. E. Marks and Y. E. Demidenko, revealing the presence of four distinct cultural archaeological

Fig. 7 Kabazi V. Drawing of the combined sections, taken from Chabai and Veselsky (2007). Arabic numerals indicate lithological layers, Roman numerals indicate archaeological levels. From Uthmeier and Chabai (2018)

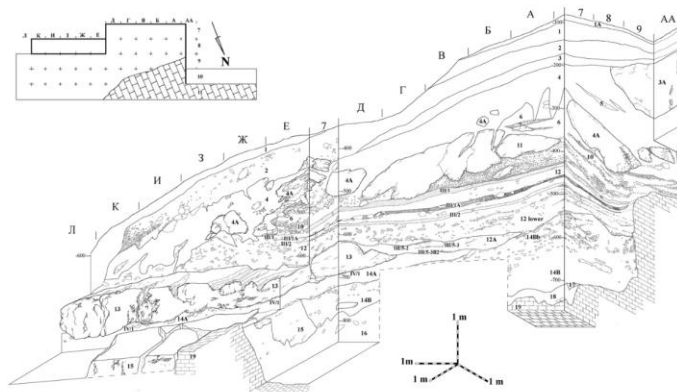
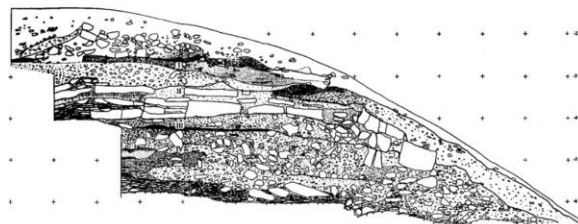


Fig. 8 East/West profile. From Marks et al. (1997)



levels (Fig. 8). These were assigned to the CM (levels 1–2 and level 4), and the Starosel'e level 3 industry. The combined AMS and ESR dates of the site range from around 100,000–40,000 uncal BP (Hardy et al., 2001; Marks et al., 1997, 1998). Level 1 has been dated to around 40,000 uncal BP (see Table 6), while level 2 has not been dated. Levels 3 and 4 are separated by a rock fall event, with level 4 representing a relatively brief occupation period, preserved by a fine clay sediment layer. This level is currently dated to around 100,000 uncal BP by radiometric dating methods (Burke, 2000; Marks et al., 1997, 1998).

Human remains, including those of a juvenile individual, were discovered at Starosel'e (Burke, 2000; Monigal et al., 1998). The juvenile remains, initially unearthed during the 1953 excavation, were considered to exhibit transitional features between Neanderthals and derived *Homo sapiens* in terms of morphology (Alexeyev, 1976), while others suggested that these characteristics were caused by hydrocephalus (Wolpoff, 1980; Spitery, 1980). The juvenile individual was estimated to be approximately 18–19 months old and was found in the southeastern quarter of the excavation. It was noted that the juvenile was discovered beneath level 1; however, it is important to mention that there are no available photographs or detailed field notes that can confirm its exact positioning of the juvenile (Marks et al., 1997). The re-excavations from 1993 to 1995 clearly showed that the so-called Starosel'e child was in fact of recent origin (18th century) and represents one out of three burial pits at the site that follow Muslim ritual practises (as demonstrated by the position of the bodies and face orientation (Monigal et al., 1998)).

The faunal assemblage at Starosel'e is dominated by *Equus hydruntinus* (horse), *Cervus* sp. (deer), various carnivores and several bird species (Burke, 1999; Hardy et al., 2001). The presence of anthropogenic cut marks on some of these remains provides strong evidence of butchering activities. The faunal remains of level 3 suggest that complete carcasses were processed at the site, rather than just specific parts. It is therefore assumed that the site served as a location for trapping animals, particularly horses, within the box canyon, possibly for mass killing. In level 2, to the contrary, faunal elements from the skulls and less meaty parts of the horse carcasses dominate. This may indicate

scavenging, probably as the result of natural events like flash flooding, which may have created opportunities for scavenging (Burke, 2000). Such natural or human-induced accumulation of horse remains could potentially explain the scarcity of other taxa in level 4 (Burke, 2000).

There is evidence for a change in the technology of lithic artefacts, whereas levels 1, 2 and 4 belong to different facies of the CM, level 3 represents an industry otherwise unknown from the Crimea termed the Starosel'e level 3 industry. One fundamental difference is the presence of bifacial tools in the levels of the CM, and the lack thereof in level 3. Furthermore, the blank production of level 3 exhibits characteristics of the discoidal method. This raises intriguing questions about possible shifts in either the site function (within the CM) or in the groups that were using the site (Burke, 2000). Feather barbs from swans, geese and ducks found at the site were at least potentially used for enhancing the stability of projectile weapons (Hardy et al., 2001). With all caution, this is interpreted as a possible hint at innovative hunting practices connected to the utilisation of the site for hunting activities.

Methods

Bayesian Age Modelling

OxCal v. 4.4.3 (Bronk Ramsey, 2009a) and INTCAL20 calibration curve (Reimer et al., 2020) were used to calibrate previous radiocarbon results. INTCAL20 the limit of 55,000 cal BP, in contrast to previous curves, contains some important updates that influence the calibration and modelling of Palaeolithic sites such as these (Reimer et al., 2020). We used Bayesian chronometric modelling to analyse previous uncalibrated dates for the sites of Siuren I, Buran Kaya III, Zaskalnaya V, Zaskalnaya VI and Starosel'e. We built age models using established methods based on building a prior framework corresponding to the site stratigraphy, using Sequence and Phase commands. All stratigraphic models used the General outlier model which allows an assessment to be made of whether individual radiocarbon dates and combined dates were outliers within the constraints of the model (Bronk Ramsey, 2009b). We set the prior sample

Table 6 Radiometric dates from Starosel'e (Marks et al., 1997). The dates used in the Bayesian model are highlighted in *italics*

Lab no	Material	Level	Industry	Pre-treatment method	Radiocarbon Age BP	Reference
U-series	Tooth	IV	Micoquian	U-series	104,000 ± 8500 BP	Marks et al. (1997)
ESR LU	Tooth	III	Micoquian	ESR	42,000 ± 4700 BP	Marks et al. (1997)
U-series	Tooth	III	Micoquian	U-series	46,000 ± 2500 BP	Marks et al. (1997)
<i>OxA-37084</i>	Bone	I	Micoquian	Ultrafiltration	43,000 ± 1700 BP	This paper
<i>OxA-37083</i>	Bone	I	Micoquian	Ultrafiltration	41,300 ± 1300 BP	This paper

outlier probability to 5%. We also used Simple outlier models to assess the statistical reproducibility of paired dates using R_Combine. The CQL code used in the models is in the Supplementary Methods along with a more detailed description of the Bayesian modelling method.

We did not construct a Bayesian model for Kabazi II, as this has already been discussed extensively by Spindler et al. (2021), nor did we build a model for Kabazi V due to the lack of chronometric data available. We feel it will be more beneficial to create a model when more data is available. In the models, we use different colours to represent the different dated technological assemblages. Gravettian is green, Aurignacian is purple, Micoquian is blue and Szeletian is red. We use grey when this is not clear. Brackets under the distributions represent the 68.2 and 95.4% probability ranges.

Results and Discussion

The Bayesian models built from the various sites are shown in Figs. 9, 10, 11, 12 and 13.

Buran Kaya III is the site with the most robust chronometric sequence in the Crimean Peninsula with several radiocarbon determinations obtained using the more reliable methodological approaches (Péan et al., 2013; Table 3 and Fig. 10). As mentioned above, previously it was suggested that Neanderthals of unit B might have inhabited the site as late as around 28.5 ka uncal BP (34.4 kcal BP). This was based on older radiocarbon pre-treatment protocols, which implies caution.

More recent dating work has shown that several dates produced in the 1990s were underestimates of the 'true age'. Péan et al. (2013), for example, redated GrA-53942, a *Saiga tatarica* bone from layer 6.1. The original result of $29,640 \pm 170$ BP was not duplicated when the same

bone was dated in Oxford using ultrafiltration. There, the result was $32,320 \pm 450$ BP (OxA_25669). Another comparison can be made between OxA-6673 ($28,840 \pm 460$ BP) and OxA-36921 ($37,700 \pm 900$ BP), another sample which underwent ultrafiltration. The substantial age shifts between the results implies that the newer ultrafiltered results are to be preferred. They also cast some doubt on samples previously dated using a simple Longin collagen approach. This cannot be the pattern in all cases, however, because Péan et al. (2013) also showed that there was agreement between some Longin treated dates and others pretreated using Ninhydrin derivatisation methods, although the comparison was helped by very imprecise Longin dates sometimes. This is not surprising, since the reliability of bone determinations depend in specific instances on the level of contamination present. In cases where contamination is low to non-existent, less robust pretreatment methods will produce accurate results. The problem is that it is difficult, if not impossible, to determine which bulk collagen determinations are accurate without redating them.

We built two Bayesian models to test the sensitivity of the posterior results to including or not some of the determinations from the site that were obtained in the 1990s. Model 1 included some of the previous Oxford dates from the unit C Szeletian (OxA-6672) (Péan et al., 2013). We gave these a 40% prior outlier value due to the potential for underestimated ages (other dates from the same period have been shown to underestimate the true age). We left out OxA-13302, as it was originally found in a supposed Mesolithic layer (after Péan et al., 2013). OxA-4126 and OxA-4127 from layer 6.1 were not included, due to their dates being extremely young compared to the other radiocarbon results. The final model contained 8 outliers, roughly 30% of the total determinations (SOM). In model 2, we left these results out completely. The results for the

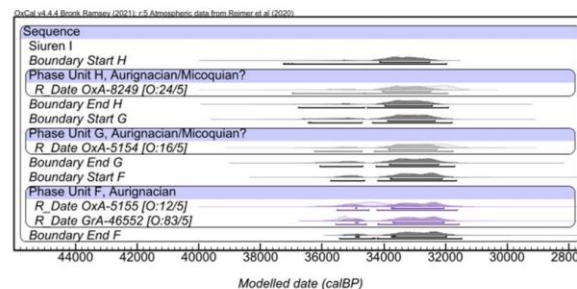


Fig. 9 A Bayesian model for the site of Siuren I. The model comprises dates primarily made at Oxford University and published in Demidenko and Otte (2001). The model comprises three archaeological units, purple representing the Aurignacian (unit F) and grey repre-

senting unit G and H, due to their mixed assemblages. Outliers can be seen within H and F. These are given in the form (O: posterior probability/prior probability) with the priors set at 0.05

Fig. 10 A Bayesian model for the site of Buran Kaya III. The model comprises seven archaeological units, green representing Gravettian, purple Aurignacian blue Micoquian and red Szeletian. The General Outlier Model shows significant outliers in every unit except horizon 20 and layer 6.4

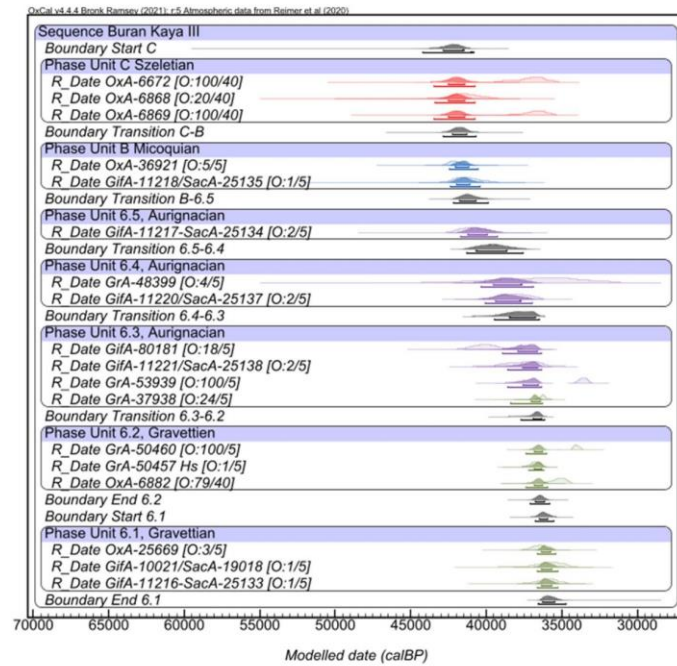
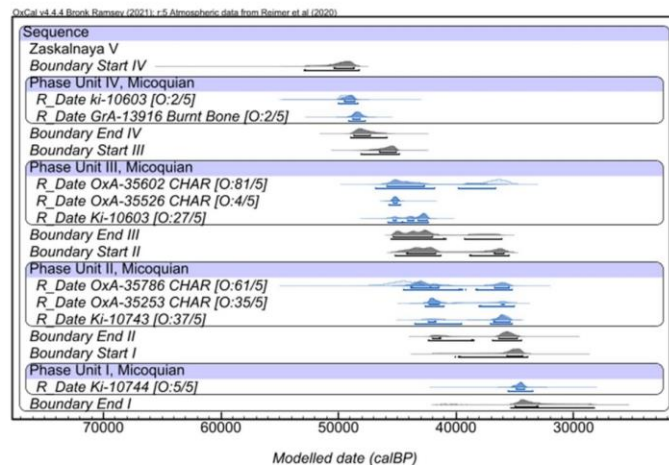


Fig. 11 A Bayesian model for the site of Zaskalnaya V. The model comprises dates primarily made at Oxford University. The model comprises four archaeological units, blue representing CM. The 'General Outlier Model' shows significant outliers in units III and II



main boundaries in both models were similar, which is not surprising given the high prior outlier probabilities we applied. We favour model 2, and this is shown in Fig. 10. The model has only 3 outliers, all downweighted by the outlier posterior percentage.

The model confirms the age of the *Homo sapiens* remains in the Gravettian layer 6.1 of Buran-Kaya III between 37 and 36.4 ka cal BP (Prat et al., 2011, 2018). For the Micoquian layer B, the model gives an age range from 42,810 to 40,870 cal BP (95.4% prob.), which compares closely

to the ages obtained for terminal Neanderthal Mousterian archaeological sites in Europe (Higham et al., 2014). For the Eastern Szeletian layer C, Buran Kaya III, the date ranges between 43 and 39 cal BP (Bataille, 2017). These more recent dates suggest that Crimea may not have served as a refugium for Neanderthals much later than 41 cal BP. In sum, Buran Kaya III challenges the idea that Crimea was a late Neanderthal refuge. However, it is important to reiterate that these interpretations are contingent upon accurate dating, and it would still be important to re-date some of the samples of faunal remains previously analysed, with newer protocols, to establish if these dates are correct and provide

more determinations for the Bayesian model. For the time being, we have the highest level of confidence in the Buran-Kaya III chronometric sequence. In Fig. 14, we summarise the date ranges for the key horizons in the model.

Suiren I presents a very different case. Layers F, G and H from the site have been previously dated by AMS (Table 2), but the results are extremely variable and young, compared with sequences like Buran-Kaya III. We suspect a combination of contamination, poor collagen preservation and post-depositional or taphonomic influences. Several dates were not included in our tentative Bayesian model (see Table 2), due to extremely young ages (e.g. Lv-2132). Previous results

Fig. 12 A Bayesian model for the site of Zaskalnaya VI. The model comprises five archaeological layers, blue representing Micoquian

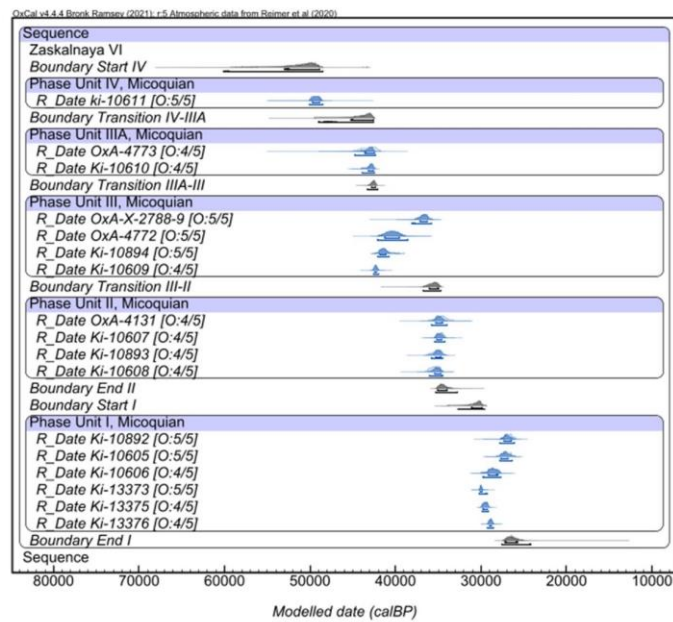


Fig. 13 A simple one phase Bayesian model for the site of Starosele. The model comprises dates measured at the University of Oxford and published in Marks et al. (1997). The model comprises one archaeological layer, representing the Micoquian

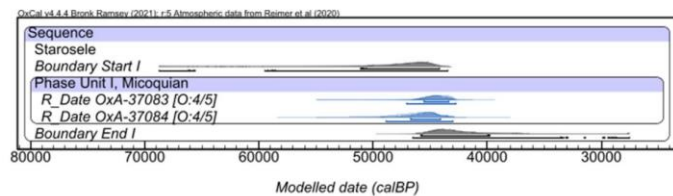
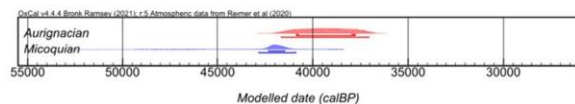


Fig. 14 Date ranges for the Aurignacian and Micoquian levels at Buran-Kaya III



indicated that Neanderthals may have been present at the site as late as 35,000–30,000 cal BP, but there are rightfully considered much too young (Demidenko, 2014). Charcoal was also used for dating in some instances, but yielded dates that were much too young and therefore no additional material was dated (Demidenko & Noiret., 2012). The dating of the Aurignacian/CM assemblages in Siuren I present at around 35,000–12,000 cal BP is obviously erroneous, since the CM has only been evident until early MIS 3 in various sites in Europe (Andreeva et al., 2022; Kozłowski, 2014; Picin et al., 2020) and probably until around 40,000 cal BP in the Crimea (Spindler et al., 2021). However, caution is required due to some dates being based on charcoal, being only reliable with pre-treatment methods such as oxidation and stepped combustion (Brock & Higham, 2009; Wood et al., 2012). It can be estimated that the previous radiocarbon dates are around 5–10,000 years too young, based on the technological assemblages present in the archaeological units alone. Early iterations of the modelling with did show high outlier probabilities and the likelihood is that the dates are most likely incorrect or unreliable. Our tentative Bayesian model includes only AMS dates that we have a degree of confidence in. Interestingly, the results appear to produce a fairly consistent pattern within which all of the dates sit with a tight wind down centred on 34–33 ka cal BP. The assessment of these archaeological layers as being more aligned with the Proto-Aurignacian is obviously chronologically at odds with this picture, given the fact that this industry is much earlier in all other parts of western Eurasia. More work is needed. This should focus on a re-dating of samples from archaeological units F, G and H utilising the latest radiocarbon protocols. Given the complexities surrounding dating bone remains from these units, it is plausible that the dates shown in our model are potentially too recent. This assessment aligns with the observations made by Demidenko (2014), highlighting the necessity for a rigorous re-analysis to provide a more precise chronology and a deeper understanding of the site's history.

Zaskalnaya V comprises archaeological units I, II, III and IV, which have previously been radiocarbon dated using bone and charcoal (see Table 4 for a complete list of ESR and uncalibrated dates). Unit I has two uncalibrated radiocarbon dates from a bulk collagen protocol, which range from 30,080 to 28,850 uncal BP. For unit II, an age range of 41,800–24,900 uncal BP (radiocarbon and ESR) was determined, and for unit III, a date range from 42,700 to 20,900 uncal BP was obtained (radiocarbon and ESR). For unit IV, an age of 47,000 to 46,000 uncal BP was calculated. Outliers can be seen within the Bayesian model for three charcoal samples within units III and II (Fig. 11). The charcoal dates should be assessed carefully. It is noteworthy that the lowermost levels of units V and VII, based on the pedogenesis of the sediments and pollen analysis,

are proposed to date within MIS 5d to MIS5a (Chabai & Uthmeier, 2006; Chabai & Uthmeier, 2017). The ESR dates should also be assessed extremely carefully, due to the large differences compared with the radiocarbon dates. This is a significant time period within the Late Pleistocene and includes multiple climatic and environmental fluctuations, so refining the dating of these layers can help place the archaeological record within this broader context. However, to obtain dates from these levels, other protocols for radiocarbon dating must be applied.

The Bayesian model results for Zaskalnaya VI can be seen in Fig. 12, for units I–IV. The site of Zaskalnaya VI has been determined as Middle Palaeolithic, relating to Micoquian (Stepanchuk et al., 2017). This alone strongly indicates that the radiocarbon dates especially from the lowermost units are extremely young to be Micoquian, and thus unlikely the technological assemblages belonging to Neanderthals. Also, it is quite interesting that the dates within this unit spread across a wide range of around 6000 years. This strongly indicates that further work needs to be undertaken on the radiocarbon analysis for this site.

Bayesian modelling was not undertaken for Kabazi V, due to the possibility of the charcoal dates being affected by contamination due to their treatment method. Dating was also attempted on four bones from the site, but these samples proved to be challenging due to low collagen yields. All four bone samples yielded less than 1% collagen. Nevertheless, two of the samples produced dates of 38,780 to 30,980 uncal BP (Housley et al., 2007).

Finally, we turn to Starosel'e, which has only two radiocarbon dates (Fig. 13), both of which were treated using ultrafiltration. Starosel'e also has some ESR dates; however, we have decided to only concentrate on the analysis of radiocarbon dates within this paper. The results from the simple Bayesian model shows a date range of 49,000 to 43,000 cal BP. Further work on this important Palaeolithic is needed, due to its significance.

Bayesian modelling is of great importance in reliably interpreting the radiocarbon and other dating chronologies in archaeology. In the Crimea, the challenge is in deciphering which of the radiocarbon dates available from the Palaeolithic sites are reliable and can be faithfully incorporated into models. No Bayesian model can compensate for problematic dates, of which there are many in this instance, as this review can show. Only Buran Kaya III has a reliable chronometric sequence. Some other sites, such as Zaskalnaya VI, have had different protocols tested on bones and some that appear reliable, but more work is needed to compare different protocols and include them in statistical analyses and Bayesian modelling.

Great caution is therefore required in the interpretation of some of the corpus of results at face value. The application of improved methods of decontaminating bones, such as

the hydroxyproline single amino acid dating (HYP), the use of XAD-2 resin approaches, or methods such as ninhydrin derivatisation dating of carboxylic carbon, offers a promising solution to obtain more accurate dates (Devi  se et al., 2017; Higham, 2019). As this review has shown, many sites likely have dates that are not accurate and almost certainly too young. There are some limitations with HYP, especially in regard to large quantities of collagen needed and lab work. However, work is currently underway to test HYP results against XAD-2. This will help us understand further how the two methods compare and then, if results are encouraging, to apply the method more widely.

The ubiquitous problem of low collagen levels in bones from Crimean sites also has implications for reliability (as collagen yields decrease so the impact of constant low-level contamination in sites increases). In the future, the use of %nitrogen or NIR approaches as a means of screening bones for their collagen yield before proceeding with full AMS dating is a valuable approach (Jacob et al., 2018; Sponheimer et al., 2019) that can save considerable time and resources. Additionally, when collagen levels are insufficient for AMS dating, alternative materials like charcoal can be considered. Charcoal is a valuable resource for dating purposes and has been found at numerous Palaeolithic sites in Crimea, including Kabazi V and Zaskalnaya V. However, the application of oxidation and stepped combustion pre-treatment method should be undertaken to ensure a complete as possible contamination removal (Brock & Higham, 2009).

Questions of a seemingly intractable nature, concerning which human groups were present through the late Palaeolithic in the Crimea, may also be addressed through a wider application of zooarchaeology by mass spectrometry (ZooMS) for screening previously excavated faunal remains. This method enables the identification of unidentifiable bone fragments to species/genus level through collagen peptide fingerprinting. By comparing the spectra of unidentifiable bones to a comprehensive database of published peptide markers, it is possible to identify those that have the characteristic marker of the Hominidae (Richter et al., 2022). ZooMS can be used to screen thousands of bone fragments and has proved to be an immensely beneficial method for identifying the species of non-diagnostic fragmented bones. It proved to be pivotal in the discovery of the Denisovans F1 hybrid ‘‘Denny’’ at Denisova Cave, Russia, for example (Brown et al., 2021). As at Denisova, a high percentage of fragmented bones in the Crimea could not be assigned to species, so ZooMS could be useful. At Suiren I, for example, a staggering 88% of fragmented bones could not be assigned to a species (Mass   & Patou-Mathis, 2009). This method opens exciting possibilities, as it may aid in the discovery of additional hominin bones, for Buran-Kaya III, or even potentially the first hominin bones, as would be the case at Suiren I. These advances in species identification techniques

continue to enrich our understanding of the past and may lead to significant discoveries in the field of palaeoanthropology. Research on this subject is currently ongoing, and we hope to share the results later this year. Similarly, the wider application of sediment DNA methods (Gelabert et al., 2021) would also provide the possibility of identifying human presence in some of the key Crimean sites.

Conclusion

The Crimean Peninsula has emerged as a profoundly significant region for understanding the process of the biocultural shift associated with the Middle to Upper Palaeolithic transition. This area holds great importance, particularly over the question of when this transition occurred in the Crimea, the extent to which Neanderthals and derived *Homo sapiens* may have overlapped with one another, and whether Neanderthals may have used the Peninsula as a refugium or not. Recent research has demonstrated that there are challenges in obtaining accurate dates, such as the case with bulk collagen extracts from Kabazi II, which yielded dates that were deemed too young. This highlights the need for more advanced and precise dating methods to sharpen the chronological lens during this key period. New radiocarbon dates have the potential to significantly contribute to our understanding of the Middle and Upper Palaeolithic technocomplexes observed in the region and their chronological relationships. Only with a strong and reliable underpinning chronology will it be possible to obtain a deeper understanding of the relationships between various hominins through this period and whether there is weight in the refugium hypothesis of late Crimean Neanderthals.

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Author Contribution Pigott, E. M1.2., Uthmeier, T3., Chabai, V4. and Higham, T.F.G1.2. Pigott wrote the main manuscript, with the main reviewer being Higham Pigott prepared all figures and tables All authors reviewed manuscript.

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Data Availability No datasets were generated or analysed during the current study.

The CQ data in the supplementary material can be used to replicate the OxCal figures.

Declarations

Conflict of Interest The authors declare no competing interests.

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The Late Middle and Early Upper Palaeolithic in Crimea (Ukraine) - A review of the Neanderthal refugium hypothesis

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Supplementary material

Methods

Bayesian age modelling

Bayesian chronometric modelling was used to create chronometric figures, presenting previous dates obtained for the Crimean sites within this publication. The software allows for statistical analysis, using OxCal software (Bronk, 2009). The mathematical basis of the model originates from Bayes' theorem (Bayes, 1763). Bayesian age modelling undertakes quantitative assessment, combined with the stratigraphic position. The difference for Bayesian modelling in comparison from traditional statistical assessment, is that the more prior information is known, the higher the refinement of the probability (Bayliss et al., 2007). The original equation from Bayes, (1763):

$$P(t|y) \propto p(y|t)p(t)$$

To simplify the equation Tab s1 describes each part of the equation.

Tab s1. Symbols and definitions of the Bayesian age modelling mathematical equation

Symbol	Definition
t	Set of parameters
y	Measurements made
p(t)	Information on the parameter's measurements
p(y t)	Within a set of parameters, the likelihood of the measurements
p(t y)	The likelihood/posterior probability for a parameter with the set measurements

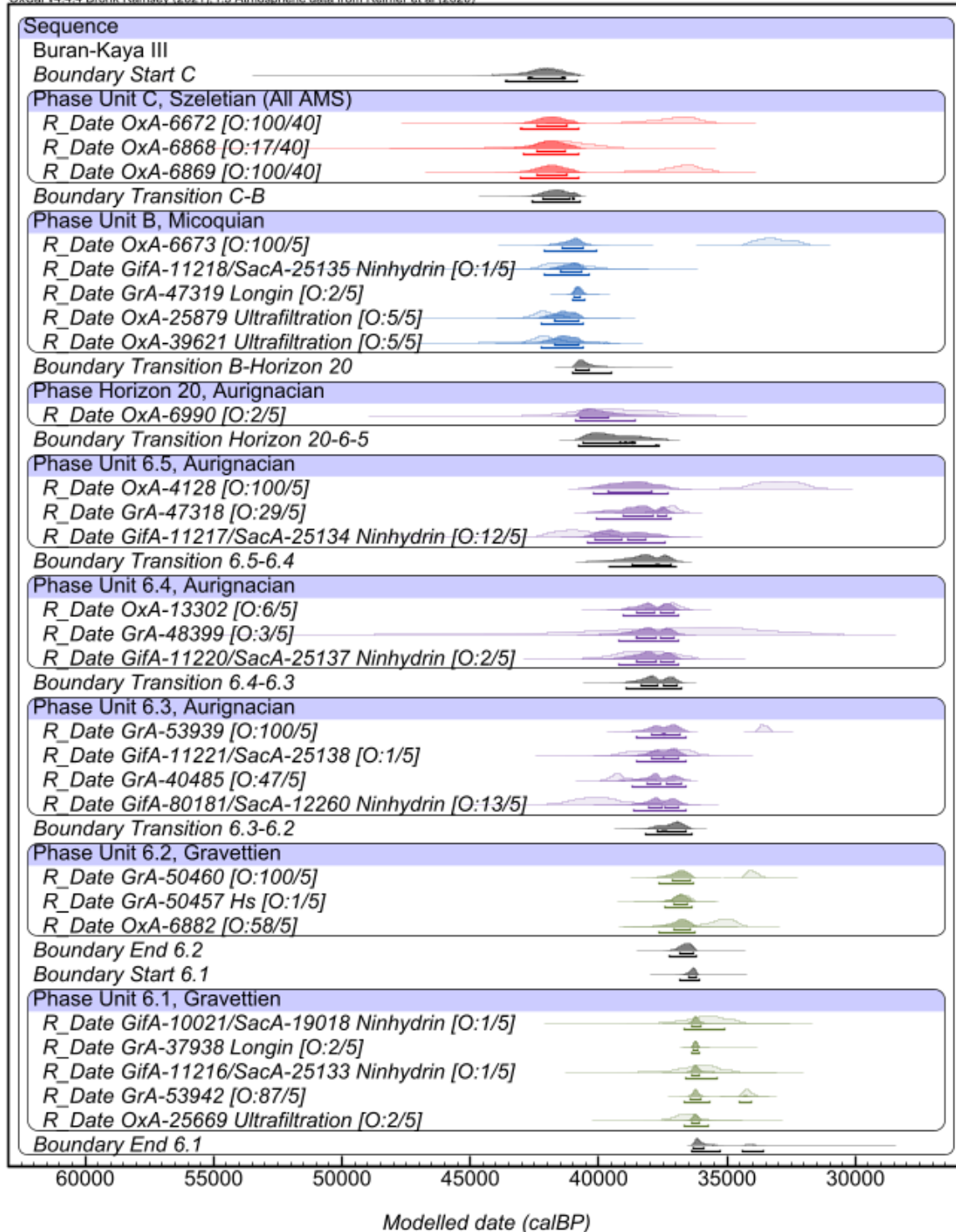
The equation combines three parts of important information. These include the posterior information (quantitative answers), standardised likelihood (radiocarbon date), and prior information (stratigraphic position in the archaeological record) within the equation (Bayliss, 2009).

Buran Kaya III

Tab s2. Radiocarbon dates from Péan et al., (2013) and Uthmeier, (2024), showing intercomparisons between the same bone, using different methods from each layer.

<u>Lab code</u>	<u>Layer</u>	<u>14C BP</u>	<u>t value</u>	<u>Chi-squared value</u>
GrA-47318	B	35,900 + 290		
GifA-11218/SacA-25135 Ninhydrin		36,500 + 1200		
OxA-36921 Ultrafiltration		37,700 + 900	3.75	5.99
GrA-47318	6.5	32,800 + 230		
GifA-11217/SacA-25134 Ninhydrin		35,900 + 1100	7.61	3.84
GrA-48399	6.4	31,250 + 2450		
GifA-11220/SacA-25137 Ninhydrin		33,350 + 830	0.66	3.84
GrA-40485	6.3	34,050 + 260		
GifA-80181/SacA-12260 Ninhydrin		34,910 + 950	0.76	3.84
GrA-53942	6.1	29,640 + 170		
OxA-25669		32,200 + 450	28.32	3.84

Tab s2 represents the comparisons of dates within each layer, for each bone, using different methods. The approach uses t and chi-squared values, to determine any significant difference. Only layer 6.1 has a significant different.



Supplementary material, Figure 1 – Overall Bayesian model of all radiometric dates for Buran Kaya III

As mentioned in the discussion section of the main publication, not all the radiometric was used within model 2 of the Bayesian model (Figure 10). This was due to some of the previous dates using older protocols or known to have discretion. We believe the radiometric dates within Figure 10 are the most reliable for Buran Kaya III.

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CQL codes

Buran-Kaya III Model 1 (Figure 1 in supplementary material)

```
Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Label("Buran-Kaya III");
    Boundary("Start C");
    Phase("Unit C, Szeletian (All AMS)")
    {
      R_Date("OxA-6672", 32350, 700)
      {
        color="#ff0000";
        Outlier("General",0.40);
      };
      R_Date("OxA-6868", 36700, 1500)
      {
        color="#ff0000";
        Outlier("General",0.40);
      };
    }
  }
}
```

```

};
R_Date("OxA-6869", 32200, 650)
{
  color="#ff0000";
  Outlier("General",0.40);
};
};
Boundary("Transition C-B");
Phase("Unit B, Micoquian")
{
  R_Date("OxA-6673", 28840, 460)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("GifA-11218/SacA-25135 Ninhydrin", 36500, 1200)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("GrA-47319 Longin", 35590, 290/270)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("OxA-25879 Ultrafiltration", 37700, 900)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("OxA-39621 Ultrafiltration", 37700, 900)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
};
};

```

```

Boundary("Transition B-Horizon 20");
Phase("Horizon 20, Aurignacian")
{
  R_Date("OxA-6990", 34400, 1200)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
};

Boundary("Transition Horizon 20-6-5");
Phase("Unit 6.5, Aurignacian")
{
  R_Date("OxA-4128", 28700, 620)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GrA-47318", 32800, 230)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GifA-11217/SacA-25134 Ninhydrin", 35900, 1100)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
};

Boundary("Transition 6.5-6.4");
Phase("Unit 6.4, Aurignacian")
{
  R_Date("OxA-13302", 32790, 280)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
};

```

```

R_Date("GrA-48399", 31250, 2450)
{
  color="#6b389e";
  Outlier("General",0.05);
};
R_Date("GifA-11220/SacA-25137 Ninhydrin", 33350, 830)
{
  color="#004aad";
  Outlier("General",0.05);
};
};
Boundary("Transition 6.4-6.3");
Phase("Unit 6.3, Aurignacian")
{
  R_Date("GrA-53939", 29040, 180/170)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GifA-11221/SacA-25138", 32740, 780)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GrA-40485", 34050, 260)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GifA-80181/SacA-12260 Ninhydrin", 34910, 950)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
};
Boundary("Transition 6.3-6.2");

```



```

Phase("Unit 6.2, Gravettien")
{
  R_Date("GrA-50460", 29440, 190)
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    Outlier("General",0.05);
  };
  R_Date("GrA-50457 Hs", 32450, 250)
  {
    color="#5d782e";
    Outlier("General",0.05);
  };
  R_Date("OxA-6882", 30740, 460)
  {
    color="#5d782e";
    Outlier("General",0.05);
  };
};
Boundary("End 6.2");
Boundary("Start 6.1");
Phase("Unit 6.1, Gravettien")
{
  R_Date("GifA-10021/SacA-19018 Ninhydrin", 31300, 820)
  {
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    Outlier("General",0.05);
  };
  R_Date("GrA-37938 Longin", 31900, 240/220)
  {
    color="#5d782e";
    Outlier("General",0.05);
  };
  R_Date("GifA-11216/SacA-25133 Ninhydrin", 31630, 670)
  {
    color="#5d782e";
    Outlier("General",0.05);
  };
};

```

```

};
R_Date("GrA-53942", 29640, 170)
{
  color="#5d782e";
  Outlier("General",0.05);
};
R_Date("OxA-25669 Ultrafiltration", 32200, 450)
{
  color="#5d782e";
  Outlier("General",0.05);
};
};
Boundary("End 6.1");
};
};

```

CQL codes

Siuren I (Figure 9 in main text of the publication)

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Label("Siuren I");
    Boundary("Start H");
    Phase("Unit H, Aurignacian/Micoquian? ")
    {
      R_Date("OxA-8249", 28200, 440)
      {
        color="#7f7f7f";
        Outlier("General",0.05);
      };
    };
  };
};

```

```

};
Boundary("End H");
Boundary("Start G");
Phase("Unit G, Aurignacian/Micoquian?")
{
  R_Date("OxA-5154", 28450, 600)
  {
    color="#7f7f7f";
    Outlier("General",0.05);
  };
};
Boundary("End G");
Boundary("Start F");
Phase("Unit F, Aurignacian")
{
  R_Date("OxA-5155", 29950, 700)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
  R_Date("GrA-46552",30910,240)
  {
    color="#6b389e";
    Outlier("General",0.05);
  };
};
Boundary("End F");
};
};

```

Buran Kaya III (Figure 10 in main text of the publication)

```
Plot()
{
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  {
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    Phase("Unit C Szeletian")
    {
      R_Date("OxA-6672", 32350, 700)
      {
        Outlier("General", 0.40);
        color="#ff0000";
      };
      R_Date("OxA-6868", 36700, 1500)
      {
        Outlier("General", 0.4);
        color="#ff0000";
      };
      R_Date("OxA-6869", 32200, 650)
      {
        Outlier("General", 0.4);
        color="#ff0000";
      };
    };
    Boundary("Transition C-B");
    Phase("Unit B Micoquian")
    {
      R_Date("OxA-36921", 37700,900)
      {
        Outlier("General", 0.05);
        color="#004aad";
      };
      R_Date("GifA-11218/SacA-25135", 36500, 1200)
      {
```

```

    Outlier("General", 0.05);
    color="#004aad";
};
};
Boundary("Transition B-6.5");
Phase("Unit 6.5, Aurignacian")
{
    R_Date("GifA-11217-SacA-25134", 35900, 1100)
    {
        Outlier("General", 0.05);
        color="#6b389e";
    };
};
Boundary("Transition 6.5-6.4");
Phase("Unit 6.4, Aurignacian")
{
    R_Date("GrA-48399", 31250, 2450)
    {
        Outlier("General", 0.05);
        color="#6b389e";
    };
    R_Date("GifA-11220/SacA-25137", 33350, 830)
    {
        Outlier("General", 0.05);
        color="#6b389e";
    };
};
Boundary("Transition 6.4-6.3");
Phase("Unit 6.3, Aurignacian")
{
    R_Date("GifA-80181", 34910, 950)
    {
        Outlier("General", 0.05);
        color="#6b389e";
    };
    R_Date("GifA-11221/SacA-25138", 32740, 780)

```



```

{
  Outlier("General", 0.05);
  color="#6b389e";
};
R_Date("GrA-53939",29040,180)
{
  Outlier("General",0.05);
  color="#6b389e";
};
R_Date("GrA-37938",31900,240)
{
  Outlier("General",0.05);
  color="#5d782e";
};
};
Boundary("Transition 6.3-6.2");
Phase("Unit 6.2, Gravettien")
{
  R_Date("GrA-50460", 29440, 190)
  {
    Outlier("General", 0.05);
    color="#5d782e";
  };
  R_Date("GrA-50457 Hs", 32450, 250)
  {
    Outlier("General", 0.05);
    color="#5d782e";
  };
  R_Date("OxA-6882", 30740, 460)
  {
    Outlier("General", 0.4);
    color="#5d782e";
  };
};
Boundary("End 6.2");
Boundary("Start 6.1");

```

```

Phase("Unit 6.1, Gravettian")
{
  R_Date("OxA-25669", 32200, 450)
  {
    Outlier("General", 0.05);
    color="#5d782e";
  };
  R_Date("GifA-10021/SacA-19018", 31300, 820)
  {
    Outlier("General", 0.05);
    color="#5d782e";
  };
  R_Date("GifA-11216-SacA-25133", 31530, 670)
  {
    Outlier("General", 0.05);
    color="#5d782e";
  };
};
Boundary("End 6.1");
};
};

```

Zaskalnaya V (Figure 11 in main text of the publication)

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General", T(5), U(0,4), "t");
    Outlier("General", 0.05);
    Label("Zaskalnaya V");
    Boundary("Start IV");
    Phase("Unit IV, Micoquian")
    {
      R_Date("ki-10603", 47000)
      {

```

```

color="#004aad";
Outlier("General",0.05);
};
R_Date("GrA-13916 Burnt Bone", 46000)
{
color="#004aad";
Outlier("General",0.05);
};
};
Boundary("End IV");
Boundary("Start III");
Phase("Unit III, Micoquian")
{
R_Date("OxA-35602 CHAR", 32000, 800)
{
color="#004aad";
};
R_Date("OxA-35526 CHAR", 42700, 100)
{
color="#004aad";
Outlier("General",0.05);
};
R_Date("Ki-10603", 39200, 520)
{
color="#004aad";
Outlier("General",0.05);
};
};
Boundary("End III");
Boundary("Start II");
Phase("Unit II, Micoquian")
{
R_Date("OxA-35786 CHAR", 41600, 1400)
{
color="#004aad";
Outlier("General",0.05);
};
};
};

```

```

};
R_Date("OxA-35253 CHAR", 37350, 500)
{
  color="#004aad";
  Outlier("General",0.05);
};
R_Date("Ki-10743", 31600, 350)
{
  color="#004aad";
  Outlier("General",0.05);
};
};
Boundary("End II");
Boundary("Start I");
Phase("Unit I, Micoquian")
{
  R_Date("Ki-10744", 30080, 350)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
};
Boundary("End I");
};
};

```

Zaskalnaya VI (Figure 12 in main text of the publication)

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Label("Zaskalnaya VI");
    Boundary("Start IV");
    Phase("Unit IV, Micoquian")
  }
}

```

```

{
  R_Date("ki-10611", 47000)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
};
Boundary("Transition IV-IIIa");
Phase("Unit IIIa, Micoquian")
{
  R_Date("OxA-4773", 39100, 1500)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-10610", 39400, 480)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
};
Boundary("Transition IIIa-III");
Phase("Unit III, Micoquian")
{
  R_Date("OxA-X-2788-9", 32250, 400)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("OxA-4772", 35250, 900)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-10894", 36400, 450)
  {

```

```

color="#004aad";
Outlier("General",0.05);
};
R_Date("Ki-10609", 38200, 410)
{
color="#004aad";
Outlier("General",0.05);
};
};
Boundary("Transition III-II");
Phase("Unit II, Micoquian")
{
R_Date("OxA-4131", 30110, 630)
{
color="#004aad";
Outlier("General",0.05);
};
R_Date("Ki-10607", 30220, 400)
{
color="#004aad";
Outlier("General",0.05);
};
R_Date("Ki-10893", 30700, 450)
{
color="#004aad";
Outlier("General",0.05);
};
R_Date("Ki-10608", 31100, 490)
{
color="#004aad";
Outlier("General",0.05);
};
};
Boundary("End II");
Boundary("Start I");
Phase("Unit I, Micoquian")

```



```

{
  R_Date("Ki-10892", 22500, 450)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-10605", 22800, 400)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-10606", 24400, 480)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-13373", 25700, 160)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-13375", 25200, 160)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
  R_Date("Ki-13376", 24600, 170)
  {
    color="#004aad";
    Outlier("General",0.05);
  };
};
Boundary("End I");
};
Sequence()
{

```

```
};  
};
```

Starosel'e (Figure 13 in main text of the publication)

```
Plot()  
{  
  Sequence()  
  {  
    Outlier_Model("General",T(5),U(0,4),"t");  
    Label("Starosele");  
    Boundary("Start I");  
    Phase("Unit I, Micoquian")  
    {  
      R_Date("OxA-37083", 41300, 1300)  
      {  
        color="#004aad";  
        Outlier("General",0.05);  
      };  
      R_Date("OxA-37084", 43000, 1700)  
      {  
        color="#004aad";  
        Outlier("General",0.05);  
      };  
    };  
    Boundary("End I");  
  };  
};
```

4. Chapter 4: ZooMS screening reveals a new Neanderthal bone from the Crimean site of Starosele

4.1. Publication II

Title: A new late Neanderthal from Crimea reveals long-distance connections across Eurasia

Authors: Emily M. Pigott, Konstantina Cheshmedzhieva, Elke Zeller, Laura G. van der Sluis, Manasij Pal Chowdhury, Maddalena Gianni, Emese Végh, Thorsten Uthmeier, Victor Chabai, Marylène Patou-Mathis, Petra G. Šimková, Jana N. Voglmayr, Gerhard W. Weber, Ron Pinhasi, Axel Timmermann, Martin Kuhlwilm, Katerina Douka, and Tom Higham.

Status: Published

Journal: Proceedings of the National Academy of Sciences of the United States of America

Citation: Pigott, E. M., Cheshmedzhieva, K., Zeller, E., van der Sluis, L. G., Chowdhury, M. P., Gianni, M., Végh, E., Uthmeier, T., Chabai, V., Patou-Mathis, M., Šimková, P. G., Voglmayr, J. N., Weber, G. W., Pinhasi, R., Timmermann, A., Kuhlwilm, M., Douka, K., Higham, T. (2025). A new late Neanderthal from Crimea reveals long-distance connections across Eurasia. *PNAS*. Vol. 122, 45, e2518974122.

<https://doi.org/10.1073/pnas.2518974122>

Significance: The scarcity of human remains is a critical limitation in understanding more of the processes that underpin the Middle to Upper Palaeolithic transition. The Crimea is no exception. One of the main aims of my thesis was to apply ZooMS to some of the Crimean sites where we have access to fragmented bone assemblages. I eventually analysed bone material from five of the Crimean sites within this thesis. I identified a spectrum amongst the analysed bones from the site of Starosele which contained the characteristic peptide markers associated with Hominidae. The 5 cm bone was CT-scanned, radiocarbon dated, mitochondrially sequenced, morphologically assessed and analysed for its stable isotopes. We found that it contained the mtDNA sequence associated with Neanderthals and was shown to be most closely linked to Altai Neanderthals, revealing potential long-range movements of Neanderthal groups across Eurasia. We used climate modelling to understand these likely migration patterns. The bone, which we called Star 1, is the first Palaeolithic human bone to be genetically sequenced in the Crimean region.

Contribution: During the research phase of this publication, I undertook ZooMS, radiocarbon dating and prepared the collagen sample for stable isotopes. I also was the primary author for writing the publication and the leading corresponding author along with my supervisor Prof. Tom Higham.



A new late Neanderthal from Crimea reveals long-distance connections across Eurasia

Emily M. Pigott^{a,b,1,2}, Konstantina Cheshmedzhieva^{a,b,1}, Elke Zeller^c, Laura G. van der Sluis^{a,b}, Manasij Pal Chowdhury^{a,b}, Maddalena Gianni^{a,b}, Emese Véghe^{a,b}, Thorsten Uthmeier^c, Victor Chabai^d, Marylène Patou-Mathis^{e,f}, Petra G. Šimková^{a,b}, Jana N. Voglmayr^{a,b}, Gerhard W. Weber^{a,b}, Ron Pinhasi^{a,b}, Axel Timmermann^{g,h}, Martin Kuhlwilm^{a,b}, Katerina Douka^{a,b}, and Thomas Higham^{a,b,2}

Affiliations are included on p. 8.

Edited by James O'Connell, The University of Utah, Salt Lake City, UT; received July 17, 2025; accepted September 22, 2025

The Crimean Peninsula contains several important Middle and Upper Paleolithic sites, including Starosele, Kabazi II, and Siuren I. The region has been considered a potential refugium for Neanderthals before their replacement by *Homo sapiens*. However, no genetic data have been obtained from any of these late Neanderthals, some being inaccessible or badly preserved. Starosele is a notable site which has undergone excavations in recent years. We used collagen peptide mass fingerprinting (Zooarchaeology by Mass Spectrometry, ZooMS), to screen for potential human remains among thousands of fragmented bones from the site. Of the 150 bone fragments we analyzed, 97.3% had sufficient collagen preservation for taxonomic identification. Our results suggest Paleolithic humans primarily hunted horses. One ~5 cm bone fragment yielded peptide mass fingerprints matching *Hominidae*. Radiocarbon dating revealed an age range of 46 to 45,000 y old, close to the transition from the disappearance of Neanderthals to the dispersal of *H. sapiens* in western Europe. We sequenced a twofold coverage mitochondrial genome from this bone, indicating the individual belongs to the Neanderthal lineage. The mitogenome clusters with other Neanderthal mitogenomes previously generated from the Russian Altai region. Alongside this, an analysis of the lithic corpus from both regions suggests that a wider Neanderthal dispersal, linked to the Micoquian stone tool industry, occurred after ~60,000 y ago. We assessed the paleoclimate connection (temperature and precipitation) between these locations and identified a high habitat suitability corridor along 55°N, suggesting that the long-distance movement of Neanderthals would have been facilitated by periods of favorable climate.

Paleolithic archaeology | Neanderthals | paleoproteomics | radiocarbon dating | ancient DNA

The Middle to Upper Paleolithic transition marks the biocultural transformation from a Neanderthal-dominated western Eurasia to one exclusively populated by *Homo sapiens*. Documenting the precise nature and timing of this transition requires a careful analysis of the excavated remains from the numerous archaeological sites in the wider region, along with the application of the latest biomolecular and chronometric methods. Precise radiocarbon dating (1) and ancient genomics (2–4) have made significant contributions to our understanding of the disappearance of Neanderthals. However, Hominin remains are extremely rare and limit the impact of these methods.

There are currently very few known remains of late Neanderthals and early modern humans across Eurasia. A significant proportion of the faunal remains excavated at Paleolithic sites are not identifiable using traditional zooarchaeological methods (5). This is mostly due to the activity of carnivores (6), anthropogenic fragmentation (7), post-depositional movement and erosion, and taphonomic influences (8). At some sites, the proportion of unidentifiable bones is more than 95% (e.g., Denisova Cave), resulting in substantial loss of archaeological information. Collagen peptide mass fingerprinting, also known as Zooarchaeology by Mass Spectrometry (ZooMS), enables the identification of unidentifiable bone fragments to species/genus level with a high rate of throughput (9, 10). This method has allowed archaeologists to explore the full spectrum of faunal remains from archaeological contexts and in some instances to identify rare hominin bone fragments (11–14).

We used ZooMS to analyze Paleolithic bone assemblages from the Crimean site of Starosele (Fig. 1). The aims were threefold; first, to widen our understanding of the subsistence strategies of the human occupants, second, to screen bone fragments to find potential hominin bone remains which could be used for direct dating, genetic sequencing, and paleodietary analysis, and finally to determine the history of hominin occupation on the Crimean Peninsula.

Significance

The Crimean Peninsula contains key Middle to Upper Paleolithic transitional archaeological sites, including the site of Starosele, where we identified a new Neanderthal; Star 1. This study highlights the integration of Zooarchaeology by Mass Spectrometry (ZooMS), radiocarbon dating, and ancient DNA analysis to uncover rare hominin remains and enhance our understanding of late Neanderthal populations in this region. Genetically, Star 1 is closely related to Neanderthals from the Altai via its mitochondrial DNA, suggesting long-range migrations of Neanderthal groups across Eurasia. These migrations during favorable climatic conditions likely involved the spread of the Micoquian lithic tradition, indicating both cultural continuity and regional mobility during the Late Pleistocene.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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PNAS policy is to publish maps as provided by the authors.

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Published October 27, 2025.

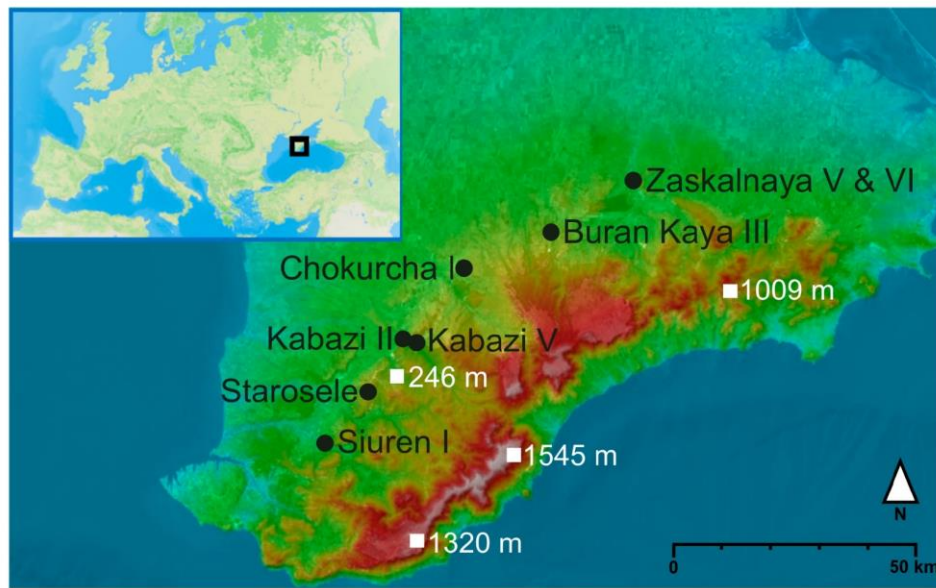


Fig. 1. The location of the sites of Starosele, Siuren I, Kabazi II, Kabazi V, and Chokurcha in the Crimean Peninsula. The red to brown colors represent the first and highest mountain range, which reaches elevations over 1,000 m, the lighter and less frequent red to orange color indicates the second middle mountain range; due to low elevations, the lowermost third range in the North of the middle range is almost not visible in this map. Map made with Mapbox and Topographic map.

Downloaded from https://www.pnas.org by 131.130.59.115 on October 29, 2025 from IP address 131.130.59.115.

The Archaeological Site of Starosele. The Crimean Peninsula contains numerous well-preserved, stratified Paleolithic sites, with many spanning within the transitional period in terms of bioculture and hominin occupations of approximately 47,000 to 42,000 cal BP (15). Based on previous radiocarbon dates, the Crimean Peninsula has been described as a refugium for late surviving Neanderthals just before their disappearance. However, new research, including radiocarbon dating using compound-specific techniques, has shown that this may need to be modified because some of the previous dates determined are, in fact, much younger in age in comparison to the compound-specific results (16).

Starosele is a rock-shelter positioned within a steep canyon (17, 18) and comprises four distinct cultural layers (19). The stratigraphy and site plan are shown in *SI Appendix, section A*. Level 2 and 3 are separated by a rockfall event, with evidence suggesting that Level 4 was briefly occupied (17). Previously, human remains within Level 1 were assumed to be Medieval Muslim burials after many decades of debate and uncertainty (20).

The Crimean Micoquian lasted from the Last Interglacial until approximately 40 kyr cal BP (21, 22). This technocomplex is characterized by soft hammer bifacial thinning and retouching, to produce bifacial tools (23). Micoquian lithic assemblages are exclusively linked with Neanderthals across Eurasia, as evidenced by the lithic assemblages co-occurring with Neanderthal remains at various sites, such as Kiik Koba (24), Zaskalnaya VI (25), Stajnia Cave (26), Mezmaiskaya (27) Chagyrskaya and Okladnikov (28, 29). In Starosele, Levels 1, 2, and 4 are assigned to the Crimean Micoquian, while Level 3 remains unassigned to a previously known lithic industry (Starosele-Level.3-Industry). Bifacial tools are present at all levels, except Level 3, which exhibits blank production methods (30). This may indicate that another group of Neanderthals was present at the site at this time. However, further analysis is needed to characterize the lithic assemblage fully.

Zooarchaeological analyses have previously been conducted at Starosele. A significant percentage of the faunal spectrum could not be identified to species through morphological inspection alone. Of the identified fauna, *Equus hydruntinus* dominates the assemblages. Level 1 comprises ~75% Equidae (19, 31). *Cervus* sp. (deer), various carnivores, and several bird species have also been identified in all levels (31, 32). Many of the faunal remains exhibit anthropogenic cut marks, indicating that butchering activities occurred at the site. Level 1 has a large assemblage of faunal material, with extensive evidence of animal butchery. However, there is also a high degree of fragmentation among the identified remains, which include *Sus* sp., *Vulpes* sp., *Ursus* sp., *Crocota* sp., *Rupicapra rupicapra*, Cervid, Elephantidae, *Bos/Bison*, and *Saiga* sp. (17).

Here we investigate the potential of the fragmented faunal assemblage for hominin bones and apply paleoproteomic analyses to unidentified fauna from Starosele. Following this, we apply DNA and radiocarbon analyses to a small number of bones.

Results

Paleoproteomics. On the basis of morphological and preservation characteristics, i.e., unburnt, sizeable bones over 2 cm long, we applied ZooMS to 150 bone fragments from all layers of Starosele. For these, we obtained 146 ZooMS identifications (97.3% success rate) (*SI Appendix, section C* and *Dataset S1*). The vast majority of these were identified as animal bones. Overall, the ZooMS results broadly confirm what was known from formal zooarchaeological analyses (17, 32) with six taxa forming the bulk of the identifications and *Equus* sp. dominating (93%). However, within Level 3, Square F21, a higher percentage of Bovidae or Cervidae/Bovidae is observed in comparison to the other stratigraphic contexts. Two faunal species were found only using ZooMS; Rhinocerotidae and *Canis lupus*. The taxonomic identifications are consistent with a classic MOIS3 paleoenvironment (33), characterized by

fluctuating warmer and colder environments during stadial and interstadial episodes (34).

Starosele Human Remains. Among the ZooMS-analyzed bones, we identified a Hominidae bone fragment (Fig. 2 *A* and *B*), which originated from Level 1 (Micoquian), Square I23 (*SI Appendix, section A*), close to previously identified human burials (see below).

We refer to this new specimen as Star 1. See *SI Appendix, section B* for stable isotope information. The ZooMS spectra for Star 1 (coded Z00113) shows the six peptide markers (A–D & F and G) associated with this Family, including 1,235.71, 1,478.74, 1,580.86, 2,115.19, 2,869.56, 2,957.68 (Fig. 3*C*) (35, 36). Peptide marker E is missing, which may be due to collagen degradation and its scarce presence in humans (12). The human bone has no

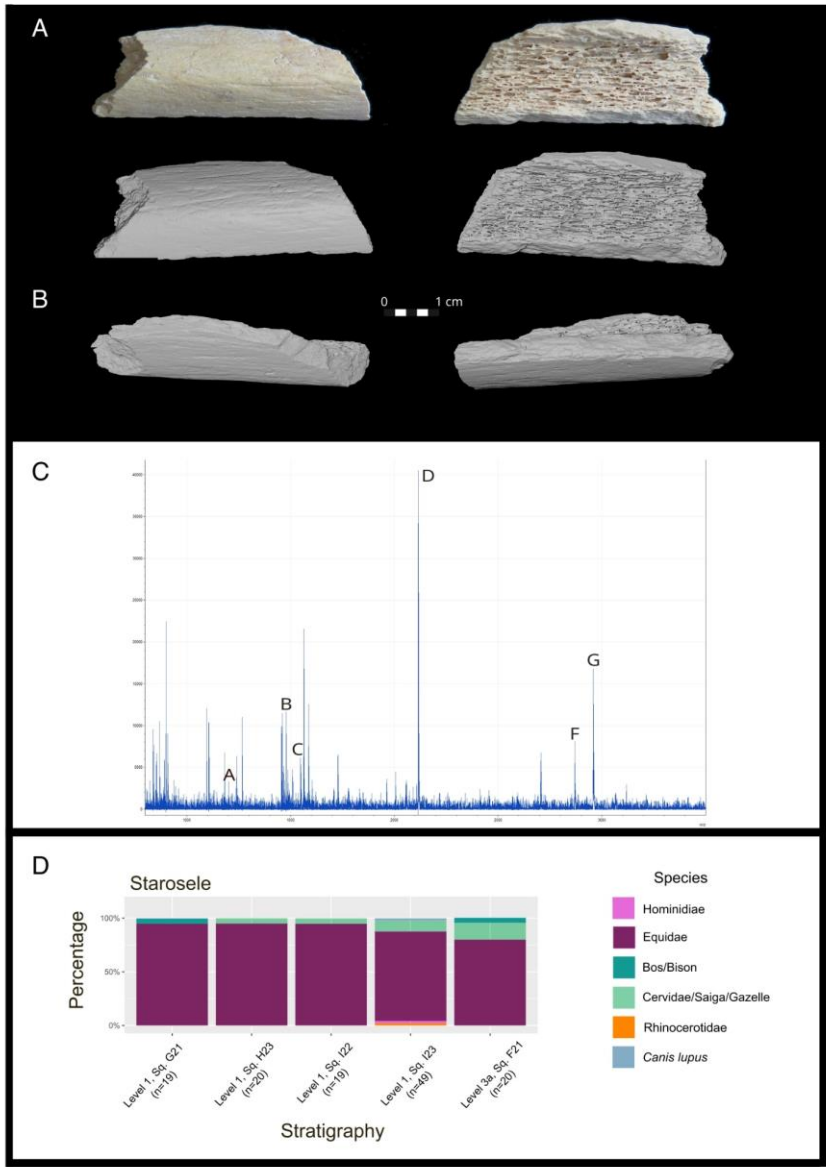


Fig. 2. (A) Photograph of the hominin bone, Star 1, from Level 1, Square I23 (Z00113) shortly after it was identified using biomolecular methods. (B) μ CT scans of the hominin bone. (C) MALDI mass spectrometry data from Z00113, Star 1. Previously published peptide markers are labeled A–D and F and G. Peptide marker E is missing. (D) Summary of the ZooMS results from Starosele plotted by the stratigraphic context and percentage. The exact percentage for each taxon can be found in *SI Appendix, section C*.

clear recognizable morphological characteristics or human-induced modifications, which is why it was overlooked during excavation and zooarchaeological analysis (Fig. 2*A*).

The fragment was microcomputed tomography (μ CT) scanned and virtually analyzed prior to any further invasive examinations. It measures 49.8 mm in maximum length and 18.8 mm in maximum width. Two relatively flat surfaces meet at an approximately orthogonal angle (Fig. 2*A* and *B*). The fragment exhibits minimal signs of fossilization and is composed primarily of cortical bone, with residual trabecular bone lining the entire inner surface. Cross-sectional measurements of the cortical bone

yielded a maximum thickness of 6.21 mm at the angled midsection. The thickness gradually decreases along both surfaces extending from the corner, with the thinnest part measuring 2.78 mm. According to Gosman et al. (2013) (37), the individual to whom this fragment belonged was likely not younger than an adolescent. The surface data can be found at the following link <https://www.virtual-anthropology.com/3d-data/free-data/>.

Based on the size, shape, and curvature of the fragment, as well as its ZooMS classification, we suggest it could only originate from a hominin femur or humerus. According to the comparative analysis we performed, the fragment most likely derives from the

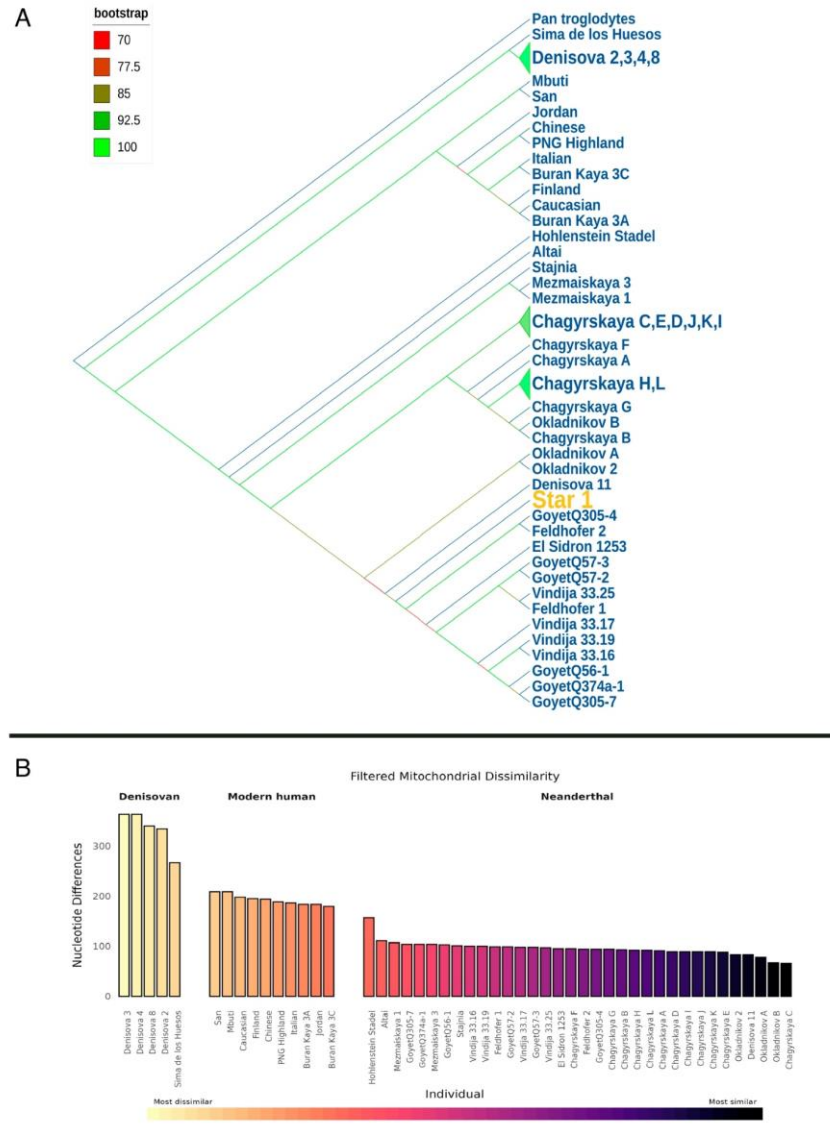


Fig. 3. (A) Phylogenetic tree of the mitochondrial genome featuring Star 1, together with other ancient hominins and modern humans. The Starosele, Star 1 branch, is highlighted in orange, and the bootstrap values are marked in a color gradient from red (minimum) to green (maximum). For the actual bootstrap values, see *SI Appendix, section D*. (B) Number of pairwise differences between Star 1 and other ancient and modern humans, sorted from most to least dissimilar.

anterior distal shaft of a femur, since it closely matches our comparable specimens in cross sectional angle, continuity of the surfaces, and cortical thickness, while it does not align with humeri with respect to these characteristics. However, it should be noted that these results are based on a small comparative sample.

Radiocarbon dating was undertaken on the bone using the standard ultrafiltration approach at the University of Vienna's Higham Lab. The result was $39,858 \pm 736$ BP (VIE-1203). The calibrated age ranges between 43,860 to 42,690 cal BP (at 68.3% prob.) and 44,390 to 42,450 cal BP (at 95.4% prob.), a result consistent with previous radiocarbon dates from Level 1 (*SI Appendix, section A*). We also treated the collagen from the bone sample following ultrafiltration with acid hydrolysis and purified the amino acids using XAD-2 resin chromatography. This resulted in a radiocarbon date of $43,212 \pm 295$ BP (VIE-1541). The calibrated age ranges between 45,910 to 45,340 cal BP (at 68.3% prob.) and 46,130 to 44,990 cal BP (at 95.4% prob.). We conclude that the XAD radiocarbon date is the most accurate of the two, as it has been shown in the past to remove environmental and museum-derived contaminants successfully and thereby yield more accurate results compared with bulk collagen determinations (38, 39).

The bone was processed for DNA extraction and sequencing and two libraries were prepared, using 40 mg (STS1.1) and 10 mg (STS1.2) of bone powder, respectively (40). One of the subsamples (STS1.2) was subjected to a bleach pretreatment (41). Two single-stranded DNA libraries were constructed using an optimal method for ancient DNA (42). Diagnostic positions for derived Neanderthal alleles compared to modern humans (43) indicated that the sample contains DNA matching the Neanderthal allele (diagnostic positions with Neanderthal reads: 10/22 for STS1.1 and 11/52 for STS1.2). Due to the extremely low endogenous DNA content in the constructed libraries (0.038% STS1.1; 0.043% STS1.2), we performed mitochondrial target enrichment, resulting in an average coverage of 2.28-fold for the mitochondrial genome.

This mitochondrial genome confirms that the bone is most consistent with belonging to the Neanderthal lineage, not modern human or Denisovan-like lineages (44–46). Although due to relatively low coverage the placement in a phylogenetic tree cannot be fully resolved, Star 1 appears basal to European Neanderthals (GoyetQ305–4/Feldhofer2), and derived to Siberian Neanderthals (Denisova 11, Okladnikov A, 2). When comparing the mtDNA sequence to complete Neanderthal mtDNA data (Fig. 3*B*), Star 1 appears most closely related to five hominins from three sites: Denisova 11, Chagyrskaya E, and Okladnikov 2, A and B (12, 47, 48). Notably, all three are in the Altai region of Russian Siberia despite being ~3,000 km distant.

Discussion

The Neanderthal bone fragment identified in this work is a key finding in the light of previous research conducted at Starosele. The site was known for many decades for the discovery of the widely cited “Starosele child” in the 1950s, originally excavated by Formozov (32). The remains, estimated to be of an 18 to 19-mo-old child, have been controversial and strongly debated. They were initially identified as a “transitional Neanderthal” or *H. sapiens* individual by Formozov and others, who saw similarities with the remains found in the Levantine site of Skhul (32). Howell agreed, comparing the Starosele child to Skhul, Qafzeh, and modern humans in Russia (49–51). Later, in the 1990s, Soffer suggested that the child was an anatomically modern human (19). Confusion regarding biological identification was mirrored by uncertainty in the age of the remains and their context, owing to excavation methods that were not of a robust nature and a lack of

photographs or detailed field notes that could confirm the exact positioning of the remains (19). New excavations by a joint Ukrainian/American team between 1993 to 1995, however, showed that it was most likely to be a much later burial, perhaps late Medieval (19). Marks and Chabai found two other burials at the site in 1993 to 1994: one infant and one adult, in squares H25 (adult) and I22 (infant). They suggested that these were probably 17/18th century Muslim burials, based on the stratigraphy of the burial pits, layout of the bodies and their direction and the typology of the ceramic pieces from the burial pits. Hence, it was inferred that the Starosele child burial was probably from a similar period (*SI Appendix, section A*) (19). No dating was performed on the new human remains, however, and while it would be interesting to demonstrate their late age, it has not been possible to do this in the current study. The most likely explanation is that the burials are late and were interred into Middle Paleolithic cultural horizons (Level 1), where the Star 1 human bone originates.

Level 1 has been dated using various methods and protocols (*SI Appendix, section A*). The calibrated ages of the latest three radiocarbon dates using the ultrafiltration protocol from Level 1 range between 47,710 to 42,490 cal BP (at 68.3% prob.) and 51,010 to 44,280 cal BP (at 95.4% prob.) (*SI Appendix, section A*). New compound specific protocols are currently being applied to date other bones.

Despite the extremely low endogenous DNA content and the lack of nuclear DNA, the 2.28-fold coverage after targeted capture shows that Star 1 did not belong to the divergent lineage of Hohlenstein Stadel (52). The sequence instead places it as being most similar to Denisova 11, Chagyrskaya E, and Okladnikov 2, A and B, which are all in the Altai region (Fig. 3). Because the genome data are incomplete, especially in parts of the D-loop and the hypervariable regions, we cannot confirm whether Star 1 can be assigned to this lineage of Siberian Neanderthals or represents a sister lineage. However, in the currently available record of Neanderthal diversity, the Siberian Neanderthals are the closest related individuals. Okladnikov and Chagyrskaya have been described as short-term, seasonal hunting camps, occupied by Neanderthals (47, 53). One suggestion, based on the close affinity of these Neanderthal mitochondrial genomes, is that they might represent an expansive movement of a Neanderthal group, most likely in an easterly direction, at some point during MIS4 ranging from ~71 to 57 ka (28).

To demonstrate further potential dispersal corridors and identify paleoclimatic and paleoenvironmental preferences, we constructed two Mahalanobis distance habitat suitability models covering the window between MIS6–MIS3, ~150 to 30,000 BP (*Methods*). This method has previously been used to explore habitat overlap between Neanderthals and Denisovans (54). Our habitat suitability models suggest that climatic conditions linking central Eurasia (Altai) and eastern Europe were most favorable during interglacial periods, supporting MIS 5e as a potentially attractive time for dispersal along this route [Fig. 4 and *SI Appendix, section F*, (55)]. We identified the most likely route between the Crimean Peninsula and Altai region along longitude 55°N (Fig. 4*A* and *E*). This dating estimate appears to fit the evidence in the Altai for the presence of Neanderthals at Denisova Cave, where genetic and chronometric evidence places them between ~130,000 to 100,000 y ago. There are hints that Neanderthals might have been present prior to this, based on mtDNA in ~170,000 y ago sediment at Denisova Cave, but no human remains of this antiquity have been found yet (56). Later, Neanderthals appear at sites such as Okladnikov Cave. The initial radiocarbon dating of Neanderthal remains there disclosed a wide range of results, including ages younger than 40,000 cal BP: Okladnikov 2, 11, and 15 have been radiocarbon dated using robust single compound hydroxyproline dating to older than 42,000 cal BP (57, 58). At other Altai sites, such as Chagyrskaya,

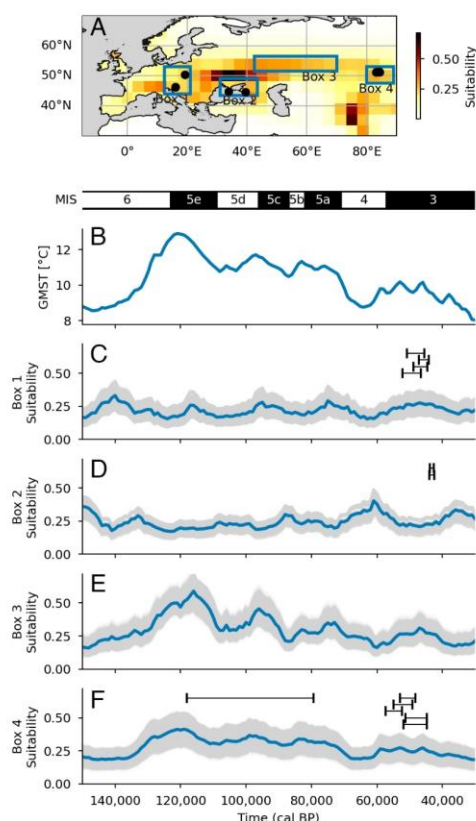


Fig. 4. Average habitat suitability of Star 1 and genetically related hominins from Croatia, Poland, the Crimean Peninsula, and Altai region (A). With time series of global mean average temperature from the 3 My transient CESM1.2 simulation (61, 62) (B), and results of the habitat suitability model over the area in Box 1, 2, 3, and 4 (C–F) where the blue line is the average suitability and the gray lines are the results of the individual models of the Monte Carlo analysis (Methods). In box 1, 2, and 4 each sample included in the primary habitat suitability model was added with the entire time uncertainty (black bars) and at the top of the timeline plots the marine isotope stages (MIS) are indicated in black and white, representing warmer and colder periods, respectively.

the most likely age of the Neanderthals is more precise and dates to between 59 and 51,000 cal BP (47). This suggests two, perhaps three, dispersals of Neanderthals from the west to the Altai at 170, 120–100, and ~60,000 cal BP. This hypothesis is supported by genetic data which suggest that the Chagyrskaya and Okladnikov Neanderthals were more closely related to the Vindija Cave 33.19 individual (59), than to the earlier Altai Neanderthal. Similarly, Denisova 11's Neanderthal mother is also genetically more closely related to European populations of Neanderthals, represented by Vindija 33.19, having 19.6% alleles present compared with 12.4% in Altai Neanderthals (60). It seems most parsimonious to conclude, therefore, that movement occurred from west to east and during times of favorable climate, particularly during MIS5e. Potential later movement, however, accounting for the Chagyrskaya and Okladnikov Neanderthals, seems more likely to have occurred during less benign climate phases, perhaps during MIS4.

In addition to the genetic links between Starosele, Chagyrskaya, and Okladnikov, these Neanderthal groups appear to have had

similar subsistence strategies, focused upon exploiting mainly horses, as well as bison and small ungulates, characteristic of steppe and piedmont environments. Sites dating to these periods have been interpreted as hunting and butchering sites focusing on large herbivores and ungulates within steppe environments (23, 63). Lithic assemblages excavated from Okladnikov, Chagyrskaya, and Starosele are also very similar, and characterized by artifacts of the Micoquian technocomplex (22, 28, 64, 65). A statistical study examining the lithic components of Micoquian assemblages from Chagyrskaya and comparing them to other Micoquian assemblages, showed that the Crimean Micoquian was significantly closer to Chagyrskaya than Denisova (64). The lithic assemblages from Chagyrskaya, in turn, compare closely to Okladnikov assemblages, being a unique variant in the Altai region, possibly representing small Neanderthal groups (63). The Neanderthals at Denisova Cave had a completely different lithic assemblage, indicating a different population of Neanderthals were present, and at a much earlier time (29, 66).

We may conclude, from the archaeological and genetic evidence, therefore, that it is likely that Neanderthals were in the Altai at two, perhaps even three, different periods. Our results show that Starosele was part of a wide-ranging dispersal network of Neanderthals, linked by genes, lithics and behavior.

Methods

Sample Selection. All faunal remains were excavated between 1993 to 1994 and sampled by EP at the University of Erlangen–Nuremberg, Germany. The samples were collected for ZooMS analysis depending on the availability and layers present at the institution. Approximately 20 to 25 bones were selected from each layer/level within different squares, when possible. Some bags containing the faunal remains had a large number of bones (50 to 100), while others contained approximately 20. A further 50 bones were sampled from Level 1, square I23, after the hominin bone was found (Table 1). Star 1 originally weighed 6.66 g, measuring a maximum 52.3 mm in length and 16.5 mm in width. In total, 26 mg was taken for ZooMS analysis, with ~900 mg taken for radiocarbon dating. Stable isotope analysis was undertaken on collagen from the radiocarbon dating preparation.

Sampling. The bone samples were manually cleaned with air abrasion mixed with aluminum oxide powder at the Douka/Higham labs, Department of Evolutionary Anthropology at the University of Vienna, Austria. This enabled the removal of superficial contaminants before sampling, with around 30 mg of bone being clipped off with clean dental pliers for ZooMS analysis. For the human bone, 26 mg was clipped for ZooMS and ~900 mg sampled for radiocarbon dating.

CT Scanning. The Star 1 hominin bone was μ CT scanned at the Vienna Micro-CT Lab with a VISCOM X8060 Scanner (39 μ m, 110 kV, 400 μ A, 1,400 ms, 0.75 mm copper filter), before further invasive sampling for dating and paleoproteomics were undertaken. For further comparative analysis a femur and humerus of one Sub-Saharan African and one European individual respectively were scanned at the same facility (63 μ m, 130 kV, 320 μ A, 1,400 ms, 0.75 mm copper filter). Additionally, scans of the Neanderthal 1 specimen from Feldhofer Grotto were provided from the Max Planck Institute for Evolutionary Anthropology Leipzig with a resolution of 91 μ m. All data were virtually analyzed and measured in the Amira 3D 2024.1 software from Thermo Fisher.

ZooMS. The ZooMS analysis was conducted at the Douka Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. Bone samples were analyzed using an acid insoluble protocol (9, 67). Following wet chemistry, the spectra were analyzed using flexAnalysis 3.4 (Brucker Daltonics) and mMass software (68). Subsequently, the spectra were compared against known peptide markers in a reference library (9). Some species/family faunal remains had already been identified from previous zoological analyses.

ZooMS analysis was undertaken using the acid insoluble collagen protocol (9). The bone specimens were first sampled using pliers, chipping off 15 to 25 mg of bone. The samples were demineralized up to 48 h with 500 μ L of cold (4 $^{\circ}$ C) 0.6 M HCl (covering the sample), until somewhat spongy. After demineralization, samples were vortexed for approximately 10 s and centrifuged for 1 min at 12 RPM. The samples then went

Table 1. Number of bones analyzed for ZooMS analysis from five different square numbers from Levels 1 and 3

Site	Typology	Level	Square	No. of bones
Starosele	Starosele-Level-3-Industry	3	F21	20
Starosele	Micoquian	1	G21	20
Starosele	Micoquian	1	H23	20
Starosele	Micoquian	1	I23	70
Starosele	Micoquian	1	I22	20

through 2 to 3 washes with 200 μ L of 50 mM AmBic, followed by centrifuging and discarding the AmBic solution. Following this, 100 μ L of 50 mM AmBic (ammonium bicarbonate buffer, pH 8.0) was inserted into each sample and then incubated for 1 h at 65 °C for gelatinization. Half (50 μ L) of the sample was removed in case a backup was needed in the future. Trypsin digestion was undertaken by inserting 1 μ L of trypsin solution 0.4 μ g (Thermo Scientific Pierce™ Trypsin Protease), which was added to each supernatant and digested for 18 h at 37 °C. The digested samples were treated with 1 μ L of 5% Trifluoroacetic Acid (TFA) to stop further enzymatic digestion. ZipTipping was performed for purification and peptide extraction, using C18 ZipTips (Thermo Scientific Pierce™ C18 Tips), using 50 μ L of 50% ACN in 0.5% TFA. A calibrant at 1:2 ratio of 0.5 μ L was added to the plate, with 0.5 μ L matrix solution. The samples (0.5 μ L) were spotted with 0.5 μ L of matrix solution. Thereafter, the processed samples were analyzed using a Bruker Autoflex Speed Matrix-Assisted Laser Desorption/Ionization Time-of-Flight (LRF MALDI ToF/ToF) mass spectrometer (69). The peptide marker (A-G) was manually inspected in mMass 5.5.0 (70).

After manual taxon identification, SpecieScan software was used to confirm taxon identifications (71). SpecieScan is a semiautomated process using R and Python to output correlated identifications from reference databases.

Radiocarbon Dating. Collagen extraction and pretreatment of the bone was conducted at the Higham Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. The human bone underwent ABA (Acid-Base-Acid) and ultrafiltration protocols (72, 73). The bone was first demineralized with 0.5 M HCl twice for 2 h and then for ~24 h. Then the sample was washed three times with ultrapure Milli-Q water. Following this, a base wash was performed with 0.1 M NaOH for 30 min. Three more washes with Milli-Q water were then undertaken, with a 15-min treatment of 0.5 M HCl, followed by three Milli-Q water washes. The collagen was then gelatinized in pH3 water for 20 h at 75 °C. The gelatin was then filtered with a precleaned Eze filter, before being ultrafiltered using a precleaned Vivaspin® Turbo 15 30 kD MWCO and centrifuged until 1.0 mL of the >30 kD gelatin fraction remained (~20 min at 2,700 RPM). The gelatin was then placed into a clean glass tube with Milli-Q water and frozen before being freeze-dried for 48 h.

After freeze-drying the collagen yielded 24 mg of collagen. A subsample of the collagen was weighed into precleaned tin capsules then combusted and graphitized using an AGE3 system, before being accelerator mass spectrometry (AMS) dated at VERA, University of Vienna.

XAD-2 resin treatment was also undertaken on a subsample of the leftover collagen (8.33 mg) after freeze-drying. This method involves hydrolysis of the collagen into amino acids and their recovery using ion-exchange columns (74). The sample was hydrolyzed for 24 h at 110 °C, in 6 M HCl. A precleaned and preconditioned XAD column was used to allow the passage of the hydrolyzed amino acids. The column had a pre-fitted filter frit at the bottom, and a filter frit was placed above ~100 μ L of XAD-2 resin. To clean the resin, 20 washes of 1 M HCl and 10 washes of 6 M HCl were passed through the column. Then the sample passed through the column, with one more wash of 1 mL of 6 M HCl, to collect any leftover amino acids. The sample was then placed into a Genevac system for 12 h, to remove the HCl acid through evaporation. ~100 μ L of Milli-Q water was placed into the tube and then placed back in the Genevac for 1.5 h until full evaporation to remove trace remnants of HCl that might otherwise interfere with the graphitization process later. Following this, ~100 μ L of Milli-Q water was placed again into the sample tube to collect the sample, before transfer of the sample into a precleaned tin boat together with precleaned chromosorb for combustion, graphitization, and AMS dating.

OxCal v. 4.4.3 software (75) and the INTCAL20 calibration curve (76) was used to calibrate the result.

Stable Isotopes. After the collagen was weighed out for radiocarbon dating, 300 μ g was weighed into a tin capsule for isotopic analysis of carbon and nitrogen by elemental analyzer-isotope ratio mass spectrometry (Thermo Scientific EA-Isolink with a Flash 2000 coupled to a Delta V Advantage isotope ratio mass spectrometer) in the Silver Laboratory (Large-Instrument Facility for Advanced Isotope Research) at the Center of Microbiology and Environmental Systems Science of the University of Vienna. Stable isotope values of all samples are measured relative to the laboratory standard alanine, which has a reproducibility of 0.07 ‰ for N and 0.1 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are reported relative to the Vienna Pee Dee belemnite and Atmospheric air standard, respectively, and are measured with an analytical precision of $\pm 0.1\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values.

DNA Extraction, Library Construction, and Target Enrichment. Ancient DNA extraction was carried out in the Pinhasi Lab, with dedicated clean-room facilities at the University of Vienna as per the protocol first described by Dabney et al. (2013) (40). Two bone powder samples were obtained using a dental drill and incubated overnight (18 h) at 37 °C on a rotation plate (800 rpm) in 1 mL of extraction buffer (final concentrations: 0.45 M Ethylenediaminetetraacetic acid, 0.25 mg/mL proteinase K). The supernatant was mixed with 13 mL of binding buffer (final concentrations: 5 M guanidine hydrochloride, 40% [v/v] isopropanol, 0.05% Tween-20, and 90 mM sodium acetate) in preassembled silica spin columns (Roche) following Korlević et al. (2015), (41). Following a 4-min centrifugation at 1,500 rpm, the columns were disassembled. The remaining spin columns were washed twice with 650 μ L of PE purification wash buffer (Qiagen; in-house) with an intermediate centrifugation step at 6,000 rpm, followed by a dry spin. DNA was eluted in 50 μ L EBT (Qiagen with 0.05% Tween-20 added) following a 5-min incubation at 37 °C and centrifugation at maximum speed for 1 min. The DNA concentrations were measured via the Qubit dsDNA DNA High Sensitivity kit. Blank samples at the beginning and the end of the batches were included to control potential cross-contamination.

Single-stranded libraries were built as per Kapp et al. (2021) (42). Based on initial DNA concentration, appropriate dilutions of single-stranded DNA binding protein (SSB), P5 and P7 adapter dilutions were prepared. 20 μ L of DNA extract were mixed with 2 μ L of the appropriate SSB dilution. The mix was incubated at 95 °C for 3 min and transferred onto an ice bath. While on ice, $\times 1$ μ L of the appropriate dilutions of P5 and P7 adapter dilutions were added together with 26 μ L of the Santa Cruz Reaction mix. An incubation at 37 °C for 45 min followed. MinElute columns and buffers from the Qiagen MinElute PCR Purification kits were used for intermediate clean-up steps. qPCR was performed on 1:40 dilution of the resulting libraries in order to estimate the number of amplification cycles to take place post unique molecular indexing (UMI). UMIs from the Ancient Meyer collection were used to double-index the samples, following an amplification with the NebNext Q5U Master Mix DNA Polymerase (NEB). Indexed libraries were pooled with other samples and submitted to the Vienna Biocenter Core Facility for Next Generation Sequencing (VBCF NGS) where the samples were sequenced on a single lane of an Illumina NovaSeq X Plus single-read mode 100 bp. For mitochondrial enrichment we used the myBaits Expert Mito kit (Arbor Biosciences), following the protocols recommended by the provider.

Bioinformatic Analysis. Standard Illumina adapters were cut with leeHom v.1.2.18 in -ancient-dna mode and filtering for sequences longer than 30 bp was performed with seqtk (77). Mapping to hg19 and Revised Cambridge reference sequences was performed with bwa aln v. 0.7.18 with ancient DNA settings (SI Appendix, section E). Unmapped reads were removed with samtools v.1.20 and PCR duplicates were filtered out with GATK MarkDuplicates v.3.1.1. Typical Ancient DNA deamination patterns were confirmed with MapDamage v.2.2.2, contamination was assessed with schmutzi v.1.5.7 and filtering out of nondeaminated reads was performed with PMDtools python3 updated version (78–80). Mitochondrial genome sequence and quality was confirmed with samtools, mosdepth, and qualimap, and visualized with BamPlotter (81–83). A consensus sequence was called with ANGSD -doFasta (SI Appendix, section E) and multiple sequence alignment including a collection of present-day humans, Neanderthals, and *Pan troglodytes* was performed via the MEGA11 in-built MUSCLE algorithm (84, 85). The phylogenetic tree was constructed with IQ-tree (SI Appendix, section E) and visualized with Interactive Tree of Life (86, 87). Pairwise nucleotide differences between Star 1 and other genomes in the alignment were calculated using a custom Python script available on the GitHub page of the project. All code used is available at https://github.com/KonstantinaChe/Star1_Neanderthal.

Table 2. Specimens and dated materials including their time uncertainty used for constructing the primary habitat suitability model

Specimen/dated material	latitude	longitude	min_age	max_age	Location	Age estimate method
Vi-33-19	46.301562	16.079687	50,901	45,561	Box 1	Age at 68.3% probability
Vi-208	46.301562	16.079687	47,256	44,126	Box 1	Age at 68.3% probability
Vi-207	46.301562	16.079687	48,904	44,579	Box 1	Age at 68.3% probability
Mammoth from layer D - same layer as the discovered Neanderthals OxA-24944	50.366	19.294	52,257	46,646	Box 1	Age at 68.3% probability
Star 1	44.75	33.92	43,858	42,695	Box 2	Age at 68.3% probability
Mezmaiskaya 2	44.5540	39.5534	43,986	42,526	Box 2	Age at 68.3% probability
Chagyrskaya Level 6a where Neanderthal remains were found	51.263299	83.091628	53,000	48,200	Box 4	Weighted arithmetic mean age from four samples
Chagyrskaya Level 6b where Neanderthal remains were found	51.263299	83.091628	55,000	49,200	Box 4	Weighted arithmetic mean age from two samples
Chagyrskaya Level 6C where Neanderthal remains were found	51.263299	83.091628	57,400	52,400	Box 4	Weighted arithmetic mean age from nine samples
Layer 7 sediment where a Neanderthal was found	51.40	84.20	51,338	44,716	Box 4	Age at 68.3% probability
Layer 7 sediment where a Neanderthal was found	51.40	84.20	51,903	44,801	Box 4	Age at 68.3% probability
Denisova 11 age estimates	51.235	84.403	118,100	79,300	Box 4	

Raw untrimmed sequencing data are available at the European Nucleotide Archive (ENA) under the accession number: PRJEB93921. All code used for data processing is available at https://github.com/KonstantinaChe/Star1_Neanderthal.

Mahalanobis Distance Habitat Suitability Modeling. Two Mahalanobis distance habitat suitability models were constructed to assess the ecological connections between three geographic regions: Croatia/Poland, the Crimean Peninsula, and the Altai region.

The primary model utilized only dated fossil data, comprising a limited dataset of 13 samples (Table 2). To assess the validity of the primary model, a second, more comprehensive model was developed. This validation model incorporated data from an extensive fossil and archaeological database (47, 48, 57, 66, 88) focused on the regions surrounding the sample locations of the primary model. The following coordinate boundaries were used for the geographical extent of these regions:

Croatia/Poland: longitude: 12.5°E–21°E, latitude: 44°N–53°N
Crimean Peninsula: longitude: 31°E–43.5°E, latitude: 43.5°N–49°N
Altai region: longitude: 80°E–89°E, latitude: 47.5°N–53°N

For both models, we employed a Monte Carlo sampling approach to address two key challenges: 1) the uneven distribution of data points at the three locations and 2) the variable temporal uncertainties associated with the data.

For each ensemble member, we randomly sampled an equal number of samples from each location to ensure balanced spatial representation. The primary model utilized two samples per location (totaling six samples per ensemble member), while the validation model used 10 samples per location (totaling 30 samples per ensemble member). Additionally, for each sample, a random age was selected from within the age uncertainty.

Sampling the data using this approach ensured that we account for the uneven sample size and varying length in age uncertainty without weighting specific locations or specimens more heavily. This sampling process was repeated 5,000 times.

For each ensemble member, we constructed habitat suitability models by extracting 1,000-y averages of annual mean temperature (T) and precipitation (P) from a 3 My quasi-transient climate simulation at a 5.75×3.75 resolution (61, 62). The extracted temperature and precipitation correspond to the nearest spatiotemporal point for each sample in the ensemble member constructed using the Monte Carlo sampling approach. Environmental conditions across the selected points were concatenated into a single matrix $C' = [T(Z'), P(Z')]$, and used to compute the mean vector $-C'$ and inverse covariance matrix Σ^{-1} of the sampled

conditions. Mahalanobis distance was then calculated across the entire climate grid using these statistics $d_M = \sqrt{(C' - C')^T \Sigma^{-1} (C' - C')}$. Suitability was derived as the exponential decay of Mahalanobis distance, i.e., $\exp(-d_M)$, where lower distances result in higher suitability.

Data, Materials, and Software Availability. Raw untrimmed sequencing data have been deposited in Star_1 Neanderthal (PRJEB93921-https://github.com/KonstantinaChe/Star1_Neanderthal) (89). Anonymized surface scan data have been deposited in Star 1 (<https://www.virtual-anthropology.com/3d-data/free-data/>) (90).

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Supporting Information for

A new late Neanderthal from Crimea reveals long distance connections across Eurasia

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SI References

Other supporting materials for this manuscript include the following:

Dataset S1 – Excel file

Supplementary information A: Site background of Starosele

Chronology of the site

The first dates published for Starosele originate from the 1956 Formozov's excavations, from Levels 1 and 2. Level 1 was found above the slabs of exfoliated limestone. Level 2 was found above and between the slabs of the exfoliated limestone (1). The site plan with the areas from different years of excavations and human remains found can be seen in Fig. S1. Level 2 has been previously dated to $36,160 \pm 1250$ BP (OxA-4133), for the deposits above the rock fall (2). Later radiocarbon dates were undertaken from the 1993 excavations from level 1 (Fig. S2), dating to $41,200 \pm 1800$ (OxA-4775) and $42,500 \pm 3600$ (OxA-4887) with ion exchange protocol (2). Further dating was undertaken by Oxford University, with a radiocarbon date of $43,000 \pm 1700$ BP (OxA-37084) and $41,300 \pm 1300$ BP (OxA-37083) (3). The overall radiocarbon dates can be seen in Table S1. These dates were undertaken with the pre-treatment method of ultrafiltration, which separates low molecular weight (MW) components from the high MW fraction (>30 kD). This has been shown to improve the collagen quality as well as remove much of the contaminating substances (4), demonstrating why there may be a difference in radiocarbon dates with different protocols. However, radiocarbon dates will be undertaken with XAD protocol, to remove any possible contamination in the bone samples. Presently, the date of the new Starosele human remains fits well with the previous ultrafiltered radiocarbon dates. The lithic industry within Level 1 has been identified as Crimean Micoquian (CM), which fits well with the human remain being categorised as derived Neanderthal within the broader context of archaeological and lithic record (5, 6).

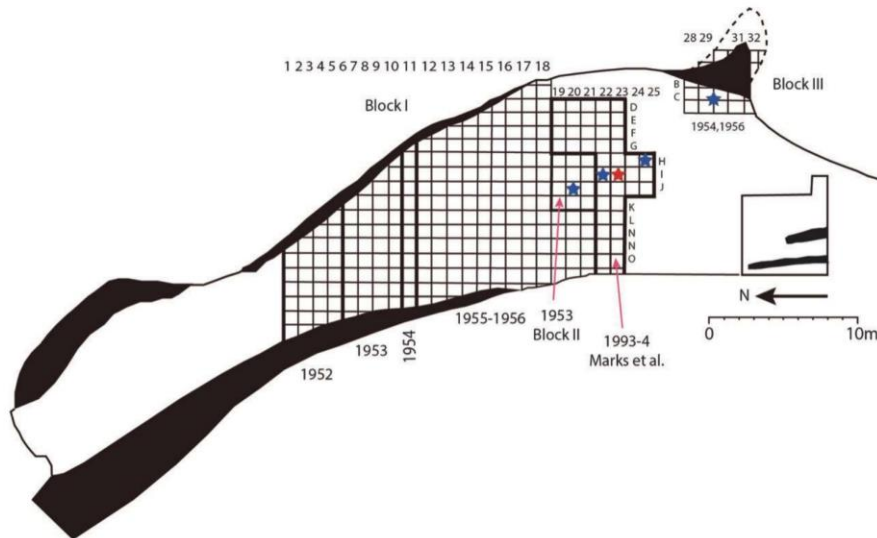


Figure S1. Excavation plan of the site of Starosele (after Marks et al., 1997, (7)). The black sections are solid rock mapped by Formozov. The thick lines denote the different excavation years undertaken by Formozov and the Joint Ukrainian/American Project (7). The blue stars indicate the position of the three previously identified burials at the site (the burial in J20 was the original child's burial), and the partial skeleton in Block III is also shown. Our new hominin bone is shown in red in square I23.

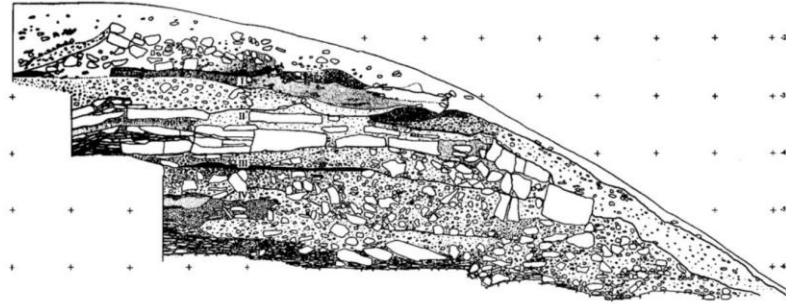


Figure S2. East/West profile at Starosele. From Marks et al. (1998), (8).

Table S1. Radiometric dates from Starosele. The dates used in the Bayesian model are highlighted in grey.

Lab No.	Material	Level	Pre-treatment method	Radiocarbon Age BP	Reference
U-series	Tooth	4	U-series	104,000 ± 8500 BP	7. Marks et al., (1997)
ESR LU	Tooth	3	ESR	42,000 ± 4700 BP	7. Marks et al., (1997)
U-series	Tooth	3	U-series	46,000 ± 2500 BP	7. Marks et al., (1997)
		Horizon 2, most likely Level 2			2. Hedges et al., (1996)
OxA-4133	Bone		Unkown	36,160 ± 1250 BP	
OxA-4775	Bone	1	Ion exchange	41,200 ± 1800 BP	2. Hedges et al., (1996)
OxA-4887	Bone	1	Ion exchange	42,500 ± 3600 BP	2. Hedges et al., (1996)
OxA-37084	Bone	1	Ultrafiltration	43,000 ± 1700 BP	3. Pigott et al., (2024)
OxA-37083	Bone	1	Ultrafiltration	41,300 ± 1300 BP	3. Pigott et al., (2024)
VIE-1203	Human bone, Star 1	1	Ultrafiltration	39,858 ± 736 BP	This paper
VIE-1541	Human bone, Star 1	1	XAD	43,212 ± 295 BP	This paper

Supplementary information B: Stable isotopes

The stable isotope measurements of Z00113/VIE 1203 yielded a $\delta^{13}\text{C}$ value of -19.3‰ and a $\delta^{15}\text{N}$ value of 13.5‰ . The carbon and nitrogen stable isotope values from this region for

humans can be compared to Buran Kaya III. The $\delta^{13}\text{C}$ ratios range from -19.4‰ to -18.8‰ and the $\delta^{15}\text{N}$ values range from 15.4‰ to 16.8‰ (9). When comparing the two sites, the stable isotope results suggest the hominin individual had a prominently carnivore diet. The $\delta^{13}\text{C}$ value indicates the individual's protein source was from a terrestrial high trophic setting. In comparison, if the food source came from a marine environment, a $\delta^{13}\text{C}$ value of around -12‰ would be expected (10). The nitrogen stable isotope value is somewhat high, which was expected when looking at Neanderthals previously found in Europe. They tend to be top-level carnivores, including a range of large herbivores in their diet (9, 11). This can also be contrasted by the ZooMS results and previous zooarchaeological findings (12, 13). Maggots may have also been a source of nutrition, resulting in a possible higher nitrogen content (14). This may have allowed for a quick source of nutrition with a lower energy cost.

Supplementary information C: ZooMS

Since 2009, ZooMS has been used on materials such as bone, antler, ivory, leather, parchment and shells, which included studies from the Palaeolithic to the Medieval period (15, 16, 17, 18, 19, 20). The abilities of ZooMS are extraordinary, allowing thousands of fragmented bones to be analysed, which have never been assigned to a species/genus previously. One phenomenal example, which has proved to be pivotal, is the discovery of the Denisovans F1 hybrid "Denny" at Denisova Cave, Russia (21). This included nearly 10,000 bones being analysed (15). Most importantly, the method only requires a small amount of collagen for the method to be successful, allowing for low levels of destruction. There are also non-destructive protocols for more delicate or highly important artefacts such as ivory (22), bone (23) and parchment (19). However, as with all methods, there are some limitations. There is a possibility there will be a lack of collagen in the sample, or gaps in the reference database (24). Also, as expected, it is not possible to analyse cremated remains that were exposed to temperatures over 155°C with the current protocols (25). Furthermore, there are new methods appearing for spectra analysis to speed up the identification process. SpeciesScan is a semi-automated process which allows for species identification (26).

Overall, ZooMS is a powerful tool, which is rapidly expanding in protocols and types of material, in which the method can be successfully harnessed.

Starosele exhibits Equidae as the most prominent identified taxon (Table. S3). The prevalence of Equidae suggests an environment characterised by possible meadow-steppe with grassland conditions, which are generally the animal's preference, during the interstadials and stadial conditions (27). Additionally, the second most prominent taxon is Cervidae/Saiga/Gazelle and Bos/Bison. It is important to note that the differentiation between Cervidae/Saiga and Gazelle was not possible for all the samples. This was due to insufficient peptide preservation during spectra analysis. The co-existence of Bovidae or Cervidae suggests the presence of slightly open-steppe and possibly forest steppe environments (28, 29). The abundance of Equidae, Cervidae, and Bovidae, suggests significant hunting activity (13). The presence of *Canis lupus* may indicate the rock shelter was used for a den, which may have been likely for various carnivorous animals, to bring their prey to a place of safety. One fragment of Rhinocerotidae was found within this study, which may indicate it was the prey of the humans occupying the rock shelter, or more likely of a wolf or hyena. We expect that if further ZooMS analysis was undertaken on a larger data set, more Rhinocerotidae faunal remains would be identified.

Table S2. The number of bone samples and their percentage within each square in Level 1 and Level 3a analysed.

Species	Level and Square number				
	L.1, Sq. G21	L.1, Sq. H23	L.1, Sq. I22	L.1, Sq. I23	L.3a, Sq. F21

Hominidae	-	-	-	2% (n=1)	-
Equidae	94.7% (n=18)	95% (n=19)	94.7% (n=18)	85.5% (n=59)	80% (n=32)
Bos/Bison	5.3% (n=1)	-	-	-	5% (n=2)
Cervidae/Saiga/Gazelle	-	5% (n=1)	5.3% (n=1)	9.1% (n=6)	15% (n=6)
Rhinocerotidae	-	-	-	1.8% (n=1)	-
<i>Canis lupus</i>	-	-	-	1.8% (n=1)	-
Number of failed samples	1	-	1	2	-
Total in number	19	20	19	69	20

ZooMS has proven to be a very powerful tool in uncovering the subsistence strategies of Hominins in the Crimean Peninsula, particularly through the identification of the Neanderthal, Star 1. The discovery of human remains in Palaeolithic archaeological assemblages is exceptionally rare, highlighting the significant impact of ZooMS as an archaeological scientific method, especially when combined with radiocarbon dating and DNA analysis.

Dataset S1 (separate file): Spectra peak markers for all faunal and hominin samples in an excel file

Supplementary information D: DNA extraction, library preparation and sequencing

Ancient DNA extraction was carried out in the dedicated clean rooms at the University of Vienna. Two samples were obtained from the ZooMS-identified bone fragment and processed following the extraction protocol described by Dabney et al. (2013) (30), with modifications from Korlević et al. (2015), (31), (full description available at the Methods section). One of the samples also underwent a bleaching pre-treatment step, as outlined in Korlević et al. (2015) (31), (see Table. S3 for details).

Two single-stranded DNA libraries were constructed following the protocol of Kapp et al. (2021) (32). MinElute columns and buffers from the Qiagen MinElute PCR Purification Kit were used for intermediate clean-up steps. Quantitative PCR (qPCR) was performed using 1 µL of the original library to estimate the number of amplification cycles required post-indexing. The libraries were then double-indexed with unique molecular identifiers and amplified using the NEBNext Q5U Master Mix DNA Polymerase (NEB). Indexed libraries were pooled with other samples and sequenced on a single lane of an Illumina NovaSeq X Plus (read mode: (single read) SR100) at the Vienna Biocentre NGS core facility.

Table S3. Screening and post-capture information about the two Star 1 libraries we use in the study.

Sample	STS1.1	STS1.2
Library Type	single-stranded	single-stranded
Bone powder input (mg)	40	10
Treatment factor	bleach	-

Endogenous DNA (%) post-screening	0.03827	0.04304
Endogenous DNA (%) post-capture	0.140	0.070
Contamination pre-PMD (%)	49	80
Contamination post-PMD (%)	0-0.5	0-1.5

Screening data revealed extremely low endogenous DNA content, hence we performed mitochondrial enrichment using the myBaits Expert Mito kit (Arbor Biosciences), following the protocols recommended by the provider.

Supplementary information E: Bioinformatic Analysis

We analyzed sequencing data from two libraries: STS1.1 (5,405,843 reads) and STS1.2 (7,655,954 reads). We used leeHom (version 1.2.18) to remove adapter sequences, and performed mapping to the human genome build hg19 using bwa aln (version 0.7.18), with ancient DNA settings. Finally, unmapped reads were removed using samtools (version 1.20), and uniquely mapped reads were retained using GATK MarkDuplicates (version 3.1.1). In both libraries, endogenous content (as uniquely mapped reads divided by all produced reads) was low: 0.038% (STS1.1) and 0.043% (STS1.2), while duplication rates were high (75.6% for STS1.1 and 31% for STS1.2). These results suggested that further sequencing would not yield sufficient genome-wide coverage for population genetic analyses. However, this initial screening data was investigated for positions where almost all modern humans carry a derived allele (>99% frequency) and the high coverage Neanderthals carry the ancestral allele (33). Reads overlapping with these positions were queried using bcftools mpileup (34), analogous to a procedure applied to identify modern human contamination in non-human primates (35).

Using these diagnostic sites, we identify 22 (STS1.1) and 55 (STS1.2) reads overlapping such positions, among which 45% (STS1.1) and 23% (STS1.2) show the Neanderthal state. These estimates are concordant with human contamination estimates using mtDNA. We concluded that the libraries likely contained small amounts of authentic Neanderthal DNA and decided to perform enrichment capture for mitochondrial sequences.

For those, adapters were trimmed from the two captured libraries using leeHom (36) with the -ancient-dna option, and sequence length was filtered using seqtk with a minimum length threshold of 30 bp (-L 30). Alignment comparisons between the revised Cambridge Reference Sequence (rCRS) and the Altai Neanderthal mitochondrial genome (37) showed that the Starosele sequences aligned more closely with the Altai reference. However, to minimize downstream bias, all subsequent analyses were conducted using the alignment to rCRS.

Reads were aligned to the rCRS using bwa aln, and only those with a mapping quality score greater than 30 were retained. Characteristic ancient DNA damage patterns were confirmed with MapDamage v2.2.2 (38). To further reduce contamination, PMDtools (39) were used to retain only reads with post-mortem damage (PMD) scores equal to or above threshold 1. This filtering step reduced contamination estimates calculated by schmutzi v.1.5.7 (40) to between 0 and 0.5%. Coverage of the merged libraries was visualized using BamPlotter (41).

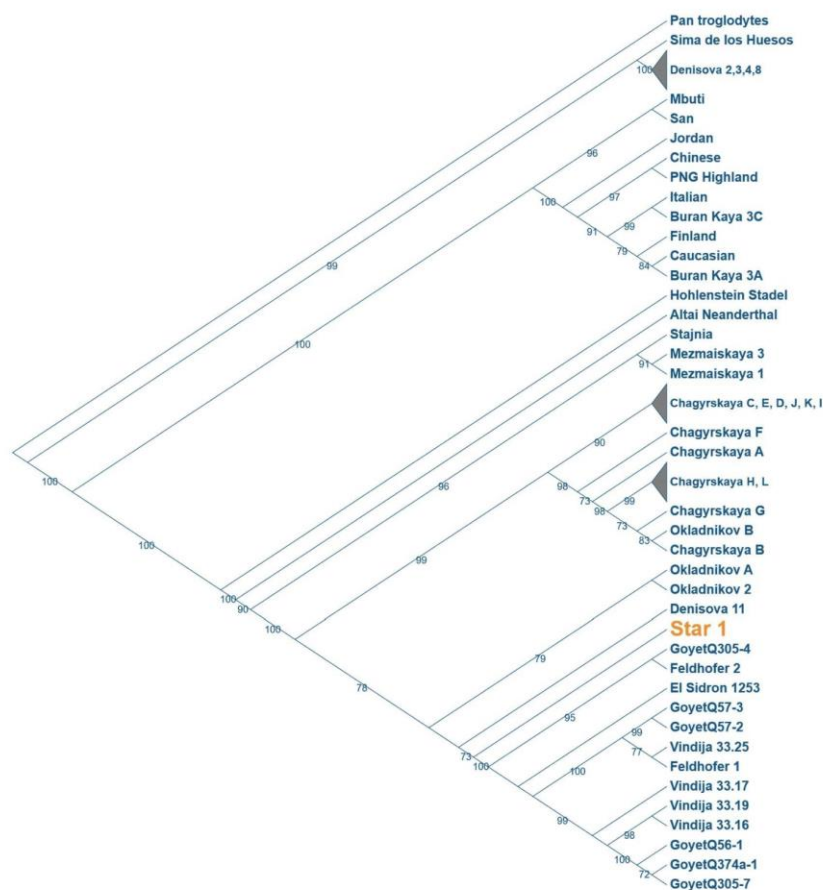


Figure S4. Phylogenetic tree featuring VIE 1203 to other ancient hominins mtDNA data. Bootstrap values are included.

Supplementary information F: Hominins in the broader picture and climate

There are currently many Micoquian sites (some which are still under discussion) known and studied in Eurasia, which can be seen in Fig. S5. Some of the main sites are highlighted within this figure, along with the Neanderthals found in the Altai region, which bears the highest genetic comparison with Star 1. The available current radiometric dates for the Altai

specimens can also be seen in Table S1. The specimens from Okladnikov went under genome capture and radiometric dating methods. Okladnikov 2 was decontaminated before mitochondrial DNA extraction and sequencing was undertaken (39). Radiocarbon dates for layer 3, range from 16,210 BP to 43,300 BP. However, the younger dates are most likely incorrect, due to stratigraphic mixing of content, causing contamination (47, 48). Okladnikov 2, 11 and 15 underwent radiocarbon dating after being treated with a single compound protocol (hydroxyproline) to eliminate any possible contamination (49, 50). Overall, the specimens should be at least 44,000 years old, based on dating at Oxford University (51). Chagyrskaya 6 is a male adult from layer 6b. The specimen was not directly dated but minerals in the sediment from layer 6 were optically dated, to around 52 kyr.

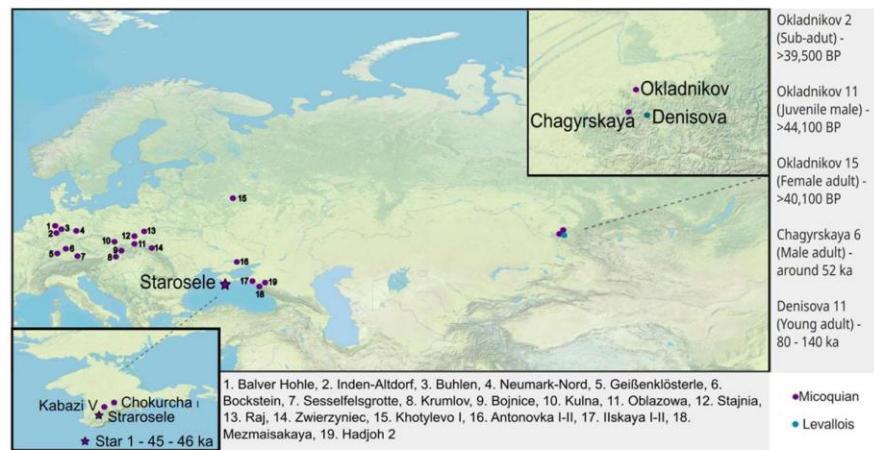


Figure S5. Map showing the location of Starosele, the Altaian sites of Okladnikov, Chagyrskaya and Denisova cluster genetically with Star 1 (more information can be found in Table S4). Key sites across Eurasia which have Micoquian lithic assemblages can be found in Table S4. Map generated with QGIS, and with HCMGIS inputs.

Table S4. Specimens closest (available data at present) related to Star 1 and their radiometric date ranges and methods

Specimen	Age at death	Level	Dated age	Lab code	Method	Reference
Starosele	?	1	42,457 cal BP	VIE 1203	Radiocarbon, Ultrafiltration	First published
Okladnikov 2	Sub-adult	3	>39,500 BP	OxA-X 2762-13	Radiocarbon, HYP	Skov et al., 2022 (51)
Okladnikov 11	Juvenile Male	2	>44,100 BP	OxA-X 2762-12	Radiocarbon, HYP	Skov et al., 2022 (51)
Okladnikov 15	Female adult	2	>40,100 BP	OxA-X 2762-20	Radiocarbon, HYP	Skov et al., 2022 (51)
Chagyrskaya 6	Male adult	6b	Around 52 kyr		Optical	Skov et al., 2022 (51)
Denisova 11	Teenager/young adult	12	80 to 140 kyr		Genomic data	Douka et al., 2019 (52)

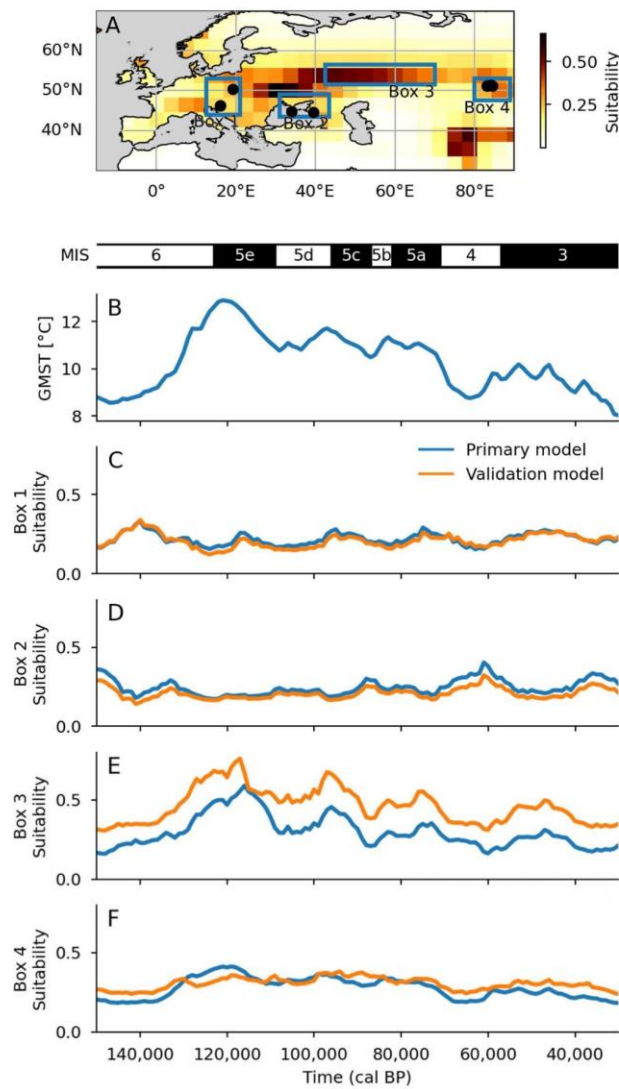


Figure S6. Average habitat suitability validation model (a). With time series of global mean average temperature from transient CESM1.2 3 million years simulation (53, 54) (b), and results of the habitat suitability calculation over the area of Box 1, 2, 3 and 4 (c-f) where the blue line is the average suitability of the primary model and orange line that of the validation model. On top of the timeline the marine isotope stages (MIS) are indicated in black and white, representing warmer and colder periods during the last glacial cycle, respectively.

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Supplementary Information, Appendix 1. ZooMS taxon identifications

Sub Sample Number	Sample Reference	Identifiable	ZooMS ID	No Total Peptide Markers Id	Alpha1 508 P1	Alpha2 978 A	Alpha2 978 +16	Alpha2 484 B	Alpha1 688	Alpha2 502 C	Alpha2 292 P2	Alpha1 220	Alpha2 793 D	Alpha2 454 E	Alpha1 586 F	Alpha1 586 +16	Alpha2 757 +16	Alpha2 757 G
Z00068.1	STAR001	Passed	Equidae	5	1105.6	1183.58		1427.73		1550.8					2883.55			
Z00069.1	STAR002	Failed		0														
Z00070.1	STAR003	Passed	Equidae	7	1105.6	1182.71		1427.72		1550.69			2144.9		2883.18		3000.32	
Z00071.1	STAR004	Passed	Equidae	9	1105.6	1182.62	1198.6	1427.73		1550.8			2145.12	2820.4	2884.48		2999.4	
Z00072.1	STAR005	Passed	Equidae	9	1105.6	1182.61	1198.6	1427.66		1550.8			2146.62	2820.4	2883.65	2899.4		
Z00073.1	STAR006	Passed	Bovidae	8	1105.6	1192.6	1208.6	1427.68		1580.8	1648.8		2131.1		2853.4			
Z00074.1	STAR007	Passed	Equidae	4		1182.6		1427.75					2145.3		2883.53			
Z00075.1	STAR008	Passed	Equidae	7	1105.6	1183.62		1427.74			1649.8		2145.59		2883.62			2983.4
Z00076.1	STAR009	Passed	Equidae	8	1105.6	1183.61		1427.78		1550.8	1649.8		2145.11	2820.4	2883.51			
Z00077.1	STAR010	Passed	Equidae	7	1105.6	1182.63	1198.6	1427.74		1550.8			2145.02		2883.45			
Z00078.1	STAR011	Passed	Equidae	6	1105.6	1182.63		1427.7		1550.8			2145.56		2883.73			
Z00079.1	STAR012	Passed	Equidae	9	1105.6	1182.66	1198.6	1427.78		1550.8			2145.17		2883.57	2899.4	3000.68	
Z00080.1	STAR013	Passed	Equidae	7	1105.6	1182.66		1427.79		1550.8	1649.8		2145.14		2883.06			
Z00081.1	STAR014	Passed	Equidae	7	1105.6	1182.08		1427.76		1550.8			2145.19		2884.76		3000.86	
Z00082.1	STAR015	Passed	Equidae	7	1105.6	1182.65	1198.6	1427.76		1550.8			2145.14		2883.49			
Z00083.1	STAR016	Passed	Equidae	7	1105.6	1182.6	1198.6	1427.71		1550.8			2145.53		2883.71			
Z00084.1	STAR017	Passed	Equidae	6	1105.6	1183.61		1427.68		1550.8			2145.47		2883.68			
Z00085.1	STAR018	Passed	Equidae	8	1105.6	1183.64	1198.6	1427.75		1550.8			2145.14		2883.56		2999.4	
Z00086.1	STAR019	Passed	Equidae	7	1105.6	1182.67		1427.79		1550.8			2145.2		2883.66		3000.77	
Z00087.1	STAR020	Passed	Equidae	8	1105.6	1183.66	1198.6	1427.7		1550.8			2145.54		2883.74	2899.4		
Z00088.1	STAR021	Passed	Equidae	7	1105.6	1183.64	1198.6	1427.71		1550.8			2145.56		2883.75			
Z00089.1	STAR022	Passed	Equidae	6	1105.6	1183.63		1427.7		1550.8			2145.53		2883.75			
Z00090.1	STAR023	Failed	Equidae	4	1105.6	1182.64		1427.75		1550.8								
Z00091.1	STAR024	Passed	Equidae	10	1105.6	1182.7		1427.81		1550.8	1649.8		2145.21	2820.4	2883.59	2899.4	3000.73	

Z00092.1	STAR025	Passed	Equidae	7	1105.6	1183.65		1427.76		1550.83			2145.14		2883.51		3000.65	
Z00093.1	STAR026	Passed	Equidae	8	1105.6	1183.65		1427.77		1550.8			2145.21		2883.77	2899.4	3000.89	
Z00094.1	STAR027	Passed	Equidae	10	1105.6	1182.66	1198.6	1427.78		1550.8	1649.8		2145.22	2820.4	2883.74		3000.88	
Z00095.1	STAR028	Passed	Equidae	10	1105.6	1183.69	1198.6	1427.8		1550.8			2145.21	2820.4	2883.58	2899.4	3000.69	
Z00096.1	STAR029	Passed	Equidae	9	1105.6	1182.61	1198.6	1427.73		1550.8	1649.8		2145.13		2883.56		3000.7	
Z00097.1	STAR030	Passed	Equidae	8	1105.6	1183.69	1198.6	1427.81		1550.8			2145.22		2883.7		3000.78	
Z00098.1	STAR031	Passed	Equidae	8	1105.6	1183.74	1198.6	1427.86		1550.8			2145.28		2883.75		3000.88	
Z00099.1	STAR032	Passed	Equidae	7	1105.6			1427.77		1550.8			2145.21	2820.4	2883.7		3000.85	
Z00100.1	STAR033	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.77		1550.8			2145.18		2883.31		3000.71	
Z00101.1	STAR034	Passed	Equidae	7	1105.6	1182.09		1427.79		1550.8			2145.2		2883.64		3000.73	
Z00102.1	STAR035	Passed	Equidae	8	1105.6	1183.66		1427.79		1550.8	1649.8		2145.21		2883.3		3000.7	
Z00103.1	STAR036	Passed	Equidae	7	1105.6	1183.68		1427.81		1550.8			2145.25		2883.64		3000.75	
Z00104.1	STAR037	Passed	Equidae	8	1105.6	1182.76		1427.88		1550.8			2145.38		2883.95	2899.4	3000.12	
Z00105.1	STAR038	Passed	Equidae	6	1105.6	1182.67		1427.77					2145.21		2883.74		3000.9	
Z00106.1	STAR039	Passed	Equidae	9	1105.6	1183.65		1427.8		1550.8	1649.8		2145.25	2820.4	2883.76		3000.91	
Z00107.1	STAR040	Passed	Saiga/Cervidae/Gazella	11	1105.6	1181.64	1198.6	1427.74		1550.76	1648.8		2131.13	2793.45	2883.58		3034.67	3018.62
Z00108.1	STAR041	Passed	Equidae	6	1105.6	1182.66		1427.76					2145.12		2883.46		3000.56	
Z00109.1	STAR042	Passed	Equidae	8	1105.6	1183.68		1427.79		1550.8			2145.21	2820.4	2883.67		3000.78	
Z00110.1	STAR043	Passed	Equidae	8	1105.6	1182.68		1427.8		1550.8	1649.8		2145.27		2883.78		3000.93	
Z00111.1	STAR044	Passed	Canidae - <i>Canis lupus</i>	8	1105.6		1226.69	1453.85		1556.8			2131.3	2820.56	2853.84	2869.4		
Z00112.1	STAR045	Passed	Saiga/Cervidae/Gazelle	8	1105.6	1180.68	1196.6	1427.75		1550.72	1648.8		2131.1					3017.55
Z00113.1	STAR046	Passed	Hominadae	8	1105.6		1235.71	1478.74		1580.86			2115.19		2869.56	2885.63		2957.68
Z00114.1	STAR047	Passed	Equidae	8	1105.6	1182.69	1198.6	1427.83		1550.8	1649.8		2145.28		2883.63			
Z00115.1	STAR048	Passed	Equidae	8	1105.6	1182.67		1427.8		1550.8			2145.36	2820.4	2884.16		2999.4	
Z00116.1	STAR049	Passed	Equidae	9	1105.6	1182.63	1198.6	1427.74		1550.8			2145.14	2820.4	2883.55		3000.65	
Z00117.1	STAR050	Passed	Saiga/Cervidae/Gazelle	10	1105.6	1180.62	1196.67	1427.84		1550.86	1648.8		2131.3		2883.75	2899.4		3034.85
Z00118.1	STAR051	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.77		1550.73			2145.13		2883.55		3000.59	
Z00119.1	STAR052	Passed	Equidae	10	1105.6	1182.64	1198.6	1427.73		1550.8	1649.8		2145.11		2883.47	2899.4	3000.62	
Z00120.1	STAR053	Passed	Equidae	8	1105.6	1183.64	1198.6	1427.75		1550.8			2145.15	2820.4	2883.5			

Z00121.1	STAR054	Passed	Equidae	8	1105.6	1182.6		1427.72		1550.8			2145.11	2820.4	2883.51		3000.63	
Z00122.1	STAR055	Passed	Equidae	8	1105.6	1182.67	1198.6	1427.76		1550.8			2145.21		2883.82		2999.4	
Z00123.1	STAR056	Passed	Equidae	10	1105.6	1182.64	1198.6	1427.75		1550.8	1649.8		2145.13	2820.4	2883.52		3000.61	
Z00124.1	STAR057	Passed	Equidae	10	1105.6	1182.66	1198.6	1427.76		1550.8	1649.8		2145.13	2820.4	2883.53		3000.62	
Z00125.1	STAR058	Passed	Equidae	10	1105.6	1182.61	1198.6	1427.69		1550.8	1649.8		2145.04	2820.4	2883.39		2999.4	
Z00126.1	STAR059	Passed	Equidae	9	1105.6	1182.66	1198.6	1427.68		1550.8			2145.14	2820.4	2883.53		3000.65	
Z00127.1	STAR060	Failed		0														
Z00128.1	STAR061	Passed	Equidae	6	1105.6	1182.6	1198.6	1427.7		1550.8					2883.4			
Z00129.1	STAR062	Passed	Equidae	7	1105.6	1182.63		1427.74		1550.8			2145.14		2883.56		3000.7	
Z00130.1	STAR063	Failed		4		1182.65		1427.77					2145.08		2883.49			
Z00131.1	STAR064	Passed	Equidae	7	1105.6	1183.64	1198.6	1427.75		1550.8			2145.12		2883.55			
Z00132.1	STAR065	Passed	Equidae	7	1105.6	1182.6		1427.7		1550.8			2145.09		2883.51		3000.63	
Z00133.1	STAR066	Passed	Equidae	10	1105.6	1182.6	1198.6	1427.7		1550.8			2145.12		2883.68	2899.4	3000.84	2983.4
Z00134.1	STAR067	Passed	Equidae	8	1105.6	1182.7	1198.6	1427.81		1550.8			2145.23		2883.63		2999.4	
Z00135.1	STAR068	Passed	Equidae	9	1105.6	1182.58		1427.67		1550.8			2145		2883.34	2899.4	2999.4	3017.74
Z00136.1	STAR069	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.72		1550.8			2145.08		2883.45	2899.4		
Z00137.1	STAR070	Passed	Equidae	7	1105.6	1182.68		1427.79		1550.8			2145.2		2883.62		2999.4	
Z00138.1	STAR071	Passed	Equidae	7	1105.6	1183.63	1198.6	1427.75		1550.8			2145.12		2883.51			
Z00139.1	STAR072	Passed	Equidae	8	1105.6	1183.63	1198.6	1427.74		1550.8			2145.11		2883.43		2999.4	
Z00140.1	STAR073	Passed	Equidae	5	1105.6	1183.6		1427.74		1550.8			2883.6					
Z00141.1	STAR074	Passed	Saiga/Cervidae /Gazelle	7	1105.6		1196.6	1427.74		1550.76			2131.1		2883.56			3018.57
Z00142.1	STAR075	Passed	Equidae	8	1105.6	1182.63		1427.74		1550.8			2145.12	2820.4	2883.49		3000.6	
Z00143.1	STAR076	Passed	Equidae	10	1105.6	1182.67	1198.6	1427.8		1550.8	1649.8		2145.19	2820.4	2883.61		2999.4	
Z00144.1	STAR077	Passed	Equidae	8	1105.6	1183.64	1198.6	1427.75		1550.8	1649.8		2145.05		2883.52			
Z00145.1	STAR078	Passed	Equidae	8	1105.6	1182.6	1198.6	1427.68		1550.8	1649.8		2145.01		2883.68			
Z00146.1	STAR079	Passed	Equidae	9	1105.6	1182.63	1198.6	1427.73		1550.8			2145.09	2820.4	2883.47		3000.55	
Z00147.1	STAR080	Passed	Equidae	9	1105.6	1182.69	1198.6	1427.81		1550.8	1649.8		2145.21		2883.64		3000.76	
Z00148.1	STAR081	Passed	Equidae	10	1105.6	1182.62	1198.6	1427.72		1550.8	1649.8		2145.08	2820.4	2883.46		3000.59	
Z00149.1	STAR082	Passed	Saiga/Cervidae/Gazelle	9	1105.6	1180.6	1196.6	1427.86		1550.91	1648.8		2131.29		2883.78	2899.4		

Z00150.1	STAR083	Passed	Equidae	10	1105.6	1182.64	1198.6	1427.75		1550.8	1649.8		2145.13	2820.4	2883.47		2999.6	
Z00151.1	STAR084	Passed	Equidae	8	1105.6	1183.63	1198.6	1427.74		1550.8			2145.09		2883.5		3000.52	
Z00152.1	STAR085	Passed	Bos/Bison	9	1105.6	1192.6	1208.6	1427.76		1580.8	1648.8		2131.15		2853.62			3034.77
Z00153.1	STAR086	Passed	Equidae	10	1105.6	1182.64	1198.6	1427.75		1550.8			2145.13	2820.4	2883.52	2899.4	3000.85	
Z00154.1	STAR087	Passed	Saiga/Cervidae/Gazelle	9	1105.6	1180.61	1196.6	1427.76		1550.8	1648.8		2131.13		2883.51			3034.61
Z00155.1	STAR088	Passed	Equidae	7	1105.6	1182.63	1198.6	1427.77		1550.8			2145.15		2883.57			
Z00156.1	STAR089	Passed	Bos/Bison	9	1105.6	1192.6	1208.6	1427.68		1580.8	1648.8		2131.07		2853.66			3033.78
Z00157.1	STAR090	Passed	Saiga/Cervidae/Gazelle	9	1105.6		1196.6	1427.73		1550.8	1648.8		2131.13		2883.76	2899.4		3034.92
Z00158.1	STAR091	Passed	Saiga/Cervidae/Gazelle	9	1105.6		1196.6	1427.8		1550.8	1648.8		2131.17		2883.57	2899.4		3034.67
Z00159.1	STAR092	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.73		1550.8			2145.11		2883.5		3000.6	
Z00160.1	STAR093	Passed	Cervidae/Saiga/Gazella	10	1105.6	1180.64	1196.6	1427.76		1550.8	1648.8		2131.15		2883.58		2999.4	3018.61
Z00161.1	STAR094	Passed	Equidae	9	1105.6	1182.64	1198.6	1427.78		1550.8			2145.2	2820.4	2883.68		3000.82	
Z00162.1	STAR095	Passed	Equidae	8	1105.6	1183.7	1198.6	1427.81		1550.8			2145.25		2883.69		3000.82	
Z00163.1	STAR096	Passed	Equidae	7	1105.6	1182.65		1427.76		1550.8			2145.16		2883.58		3000.71	
Z00164.1	STAR097	Passed	Equidae	7	1105.6	1182.64		1427.76		1550.8			2145.21		2883.74		3000.9	
Z00165.1	STAR098	Passed	Equidae	9	1105.6	1182.63	1198.6	1427.74		1550.8			2145.08	2820.4	2883.4		3000.5	
Z00166.1	STAR099	Passed	Equidae	7	1105.6	1182.65		1427.76					2145.11	2820.4	2883.45		3000.5	
Z00167.1	STAR100	Passed	Equidae	7	1105.6	1182.65		1427.76		1550.8			2145.18		2883.63		3000.77	
Z03948.1	STAR101	Passed	Equidae	9	1105.6	1182.68		1427.82		1550.88	1649.88		2145.22	2821.4	2883.52		2999.65	
Z03949.1	STAR102	Passed	Equidae	10	1105.6	1182.67	1198.7	1427.81		1550.83	1649.88		2145.22	2821.52	2883.57		2999.66	
Z03950.1	STAR103	Passed	Equidae	9	1105.6	1182.66		1427.77		1550.8	1650.83		2145.2	2821.59	2883.6		2999.72	
Z03951.1	STAR104	Passed	Equidae	10	1105.6	1182.65	1199.67	1427.79		1550.82	1650.87		2145.19	2821.4	2883.58		2999.78	
Z03952.1	STAR105	Passed	Equidae	10	1105.6	1182.66	1198.64	1427.78		1550.82	1650.87		2145.19	2821.35	2883.59		2999.77	
Z03953.1	STAR106	Passed	Equidae	10	1105.6	1182.67	1199.64	1427.83		1550.83	1649.8		2145.19	2821.5	2883.48		2999.59	
Z03954.1	STAR107	Passed	Equidae	9	1105.6	1182.63		1427.74		1550.82	1649.84		2145.09	2821.4	2883.34		3000.44	
Z03955.1	STAR108	Passed	Equidae	10	1105.6	1182.62	1198.66	1427.77		1550.84	1649.83		2145.18	2821.4	2883.53		2999.65	
Z03956.1	STAR109	Passed	Equidae	10	1105.6	1182.64	1198.72	1427.77		1550.82	1649.84		2145.28	2821.39	2883.55		3000.66	
Z03957.1	STAR110	Passed	Equidae	7	1105.6	1182.66		1427.78		1550.81			2145.2		2883.58		3000.83	
Z03958.1	STAR111	Passed	Cervus/Saiga/Gazella	10	1105.6	1180.71	1196.7	1427.79		1550.85	1648.88		2131.13		2883.48		3018.64	3034.61

Z03959.1	STAR112	Passed	Equidae	7	1105.6	1182.67		1427.82		1550.87			2145.2		2883.35		2999.57	
Z03960.1	STAR113	Passed	Equidae	9	1105.6	1182.7	1199.69	1427.85		1550.89	1650.89		2145.28		2883.66		2999.77	
Z03961.1	STAR114	Passed	Equidae	9	1105.6	1182.67		1427.79		1550.84	1649.76		2145.19	2821.48	2883.58		2999.69	
Z03962.1	STAR115	Passed	Equidae	9	1105.6	1182.67	1199.66	1427.8		1550.85	1650.85		2145.22		2883.65		2999.77	
Z03963.1	STAR116	Passed	Equidae	10	1105.6	1182.66	1198.67	1427.79		1550.83	1649.85		2145.21	2821.57	2883.64		2999.78	
Z03964.1	STAR117	Passed	Equidae	8	1105.6	1182.63	1198.64	1427.75		1550.78			2145.15		2883.57		2999.69	
Z03965.1	STAR118	Passed	Equidae	8	1105.6	1182.64	1199.63	1427.75		1550.77			2145.09		2883.36		2999.5	
Z03966.1	STAR119	Passed	Equidae	7	1105.6	1182.64		1427.76		1550.83			2145.09		2883.54		2999.63	
Z03967.1	STAR120	Passed	Equidae	8	1105.6	1182.63	1199.64	1427.75		1550.8			2145.15		2883.46		2999.56	
Z03968.1	STAR121	Passed	Equidae	7	1105.6	1182.64		1427.77		1550.82			2145.17		2883.54		3000.66	
Z03969.1	STAR122	Passed	Equidae	10	1105.6	1182.69	1198.68	1427.81		1550.85	1649.9		2145.22	2821.47	2883.58		3000.76	
Z03970.1	STAR123	Passed	Equidae	8	1105.6	1182.64		1427.77		1550.82	1650.83		2145.77		2883.52		3000.65	
Z03971.1	STAR124	Passed	Equidae	7	1105.6	1182.69		1427.79		1550.8			2145.24		2883.68		3000.83	
Z03972.1	STAR125	Passed	Saiga or Cervidae	9	1105.6	1180.71	1196.76	1427.82		1550.86	1648.97		2131.22		2883.55			3034.61
Z03973.1	STAR126	Passed	Equidae	7	1105.6	1180.66		1427.79		1550.8			2145.2		2883.63		3000.74	
Z03974.1	STAR127	Passed	Equidae	10	1105.6	1182.66	1198.63	1427.8		1550.84	1650.84		2145.21	2821.49	2883.59		3000.73	
Z03975.1	STAR128	Passed	Equidae	9	1105.6	1182.65		1427.78		1550.83	1650.82		2145.2	2821.5	2883.59		3000.73	
Z03976.1	STAR129	Passed	Equidae	9	1105.6	1182.67		1427.77		1550.78	1650.84		2145.19	2821.49	2883.55		3000.66	
Z03977.1	STAR130	Passed	Equidae	9	1105.6	1182.69		1427.83		1550.89	1650.93		2145.29	2821.61	2883.74		3000.87	
Z03978.1	STAR131	Passed	Equidae	8	1105.6	1182.67		1427.81		1550.86			2145.24		2883.73		3000.81	2984.87
Z03979.1	STAR132	Passed	Equidae	8	1105.6	1182.62		1427.74		1550.8			2145.13		2883.49		3000.65	2984.64
Z03980.1	STAR133	Passed	Equidae	10	1105.6	1182.72	1199.71	1427.86		1550.88	1650.93		2145.32		2883.76		3000.94	2984.93
Z03981.1	STAR134	Passed	Hominidae	7	1105.6	1235.69		1477.83		1580.86			2115.2		2869.61			2957.77
Z03982.1	STAR135	Passed	Equidae	9	1105.6	1182.7	1199.67	1427.85		1550.91	1650.91		2145.25		2883.63		3000.7	
Z03983.1	STAR136	Passed	Equidae	7	1105.6	1182.67		1427.8		1550.83			2145.24		2883.72		3000.85	
Z03984.1	STAR137	Passed	Equidae	9	1105.6	1182.63	1199.68	1427.81		1550.84	1650.87		2145.24		2883.59		3000.72	
Z03985.1	STAR138	Passed	Equidae	9	1105.6	1182.63		1427.76		1550.77	1650.82		2145.17		2883.58		3000.69	2984.69
Z03986.1	STAR139	Passed	Equidae	9	1105.6	1182.64	1199.64	1427.77		1550.8	1650.83		2145.18	2821.47	2883.59			
Z03987.1	STAR140	Passed	Equidae	9	1105.6	1182.65	1198.58	1427.78		1550.82	1650.85		2145.19		2883.63		3000.76	

Z03988.1	STAR141	Passed	Cervus/Saiga/Gazella	9	1105.6	1180.67	1196.69	1427.75		1550.79	1648.85		2131.13		2883.5			3033.65
Z03989.1	STAR142	Passed	Equidae	8	1105.6	1182.67		1427.83		1550.82	1650.8		2145.15		2883.58		3000.7	
Z03990.1	STAR143	Passed	Equidae	7	1105.6	1182.64		1427.76		1550.86			2145.17		2883.53		3000.66	
Z03991.1	STAR144	Passed	Equidae	7	1105.6	1182.68		1427.81		1550.86			2145.26		2883.69		3000.8	
Z03992.1	STAR145	Passed	Equidae	10	1105.6	1182.65	1198.63	1427.79		1550.82	1649.86		2145.21	2821.51	2883.61		2999.61	
Z03993.1	STAR146	Passed	Cervus/Saiga/Gazella	9	1105.6	1180.69	1197.68	1427.82		1550.85	1648.93		2131.23		2884.8			3034.81
Z03994.1	STAR147	Passed	Rhinocerotidae	7	1105.6	1182.71		1453.85		1550.89			2145.29		2869.72		3000.73	
Z03995.1	STAR148	Passed	Equidae	10	1105.6	1182.64	1198.7	1427.84		1550.86	1649.91		2145.25	2821.42	2883.56		3000.63	
Z03996.1	STAR149	Passed	Equidae	8	1105.6	1182.68		1427.81		1549.9	1649.8		2145.22		2883.5		3000.61	
Z03997.1	STAR150	Passed	Equidae	7	1105.6	1182.64		1427.78		1550.81			2145.18		2883.55		2999.63	

5. Chapter 5. Re-dating the Crimean Peninsula with XAD-2 radiocarbon dating

5.1. Manuscript I

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Significance: This manuscript includes the largest part of my work within the PhD project, undertaking an extensive amount of radiocarbon dating of Palaeolithic bone material, applying different pre-treatment methods including ABA, UF and XAD-2. The results from the XAD-2 pre-treatment method shows that this protocol eliminates contamination efficiently from Palaeolithic archaeological bones in the majority of cases, thereby enabling palaeoanthropologists to build chronometric frameworks that are trustworthy. XAD-2 results often appear thousands of years older than those generated using less robust approaches. The radiocarbon analyses I obtained, coupled with the Bayesian modelling of these and other previously determined results, strongly suggests Neanderthals were not in the Crimean Peninsula as late as once thought. Overall, this provides critical insights into the Middle to Upper Palaeolithic transition within the Crimean Peninsula and the hominin groups that inhabited the region.

To understand more about the economic basis of human subsistence, molecular methods can now be applied. ZooMS has the potential to provide new insights into the subsistence patterns of late Neanderthal and early modern human adaptation in the Crimea. I applied ZooMS at five of the sites I studied and discuss four of these in detail within the supplementary section of the manuscript.

Contribution: I am the lead author on the manuscript and undertook the radiocarbon dating of all samples within the lab (ABA, UF and XAD-2 pre-treatment methods), weighed the samples, combusted and graphitised the samples at VERA. I also constructed the Bayesian models for the manuscript. The ZooMS analysis which can be found in the main manuscript supplementary Information, was completely undertaken by myself in the Douka lab, including the chemistry and spectra analysis. I shall also be the corresponding author for the manuscript.

Reassessing the Chronology of Middle to Upper Palaeolithic Sites in the Crimean Peninsula Using XAD-2 Radiocarbon Dating

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Abstract

The Crimean Peninsula contains an important series of significant, well-preserved archaeological sites covering the Middle to Upper Palaeolithic transition. This region has been considered a potential refugium for Neanderthals before their disappearance and replacement by *Homo sapiens*. This hypothesis is supported by previous radiocarbon dates and lithic analyses. However, recent research suggests that many of the previous radiocarbon dates may be too young due to contamination. A key example of this issue can be seen at Kabazi II, where a single amino ¹⁴C protocol was used (hydroxyproline), which revealed much older ages (>10,000 years).

Several key Palaeolithic archaeological sites in the Crimean Peninsula sites are currently undergoing critical re-evaluation, including Kabazi II, Kabazi V, Siuren I, Starosel'e, Chokurcha I, Buran Kaya III, Zaskalnaya V and Zaskalnaya VI. The stratigraphy, lithic assemblages and previous radiocarbon dates from these sites suggest many of the dates are too young, except for the chronometric work already conducted on Kabazi II.

This study applies an amino acid purification method for dating bone using XAD

-2 resin. We obtained 63 new radiocarbon results from eight sites. Where possible we compared the results obtained using standard bulk collagen (gelatin) pre-treatments, ultrafiltration of collagen, and XAD-2 resin chromatography. The results indicate that radiocarbon dates tend to be older when using ultrafiltration and sometimes significantly older

when XAD-2 approaches are applied, emphasising the importance of using reliable pre-treatment methods to remove potential contamination.

Improving the chronometric accuracy for this region provides valuable insights into its potential role as a refugium for Neanderthals prior to their disappearance. The results suggest, however, that Neanderthals there were not present as recently as previously thought.

Introduction

The Crimean Peninsula contains numerous well-preserved archaeological sites dating to the Middle to Upper Palaeolithic (Figure 1), broadly 60,000—35,000 years ago. These sites are associated with both late Neanderthal and *Homo sapiens* occupations and their distinct lithic technocomplexes. Previous research has proposed that the Crimean Peninsula may have attracted humans during phases when the climate in more northerly regions was poor and therefore acted as a refugium for late Neanderthals prior to their replacement by *Homo sapiens*. This conclusion is based largely on previous radiocarbon dating and lithic analysis (Marks et al., 1997; Demidenko & Otte, 2001; Demidenko & Noiret, 2012; Housley et al., 2007; Péan et al., 2013; Stepanchuk et al., 2017; Chabai & Uthmeier, 2017). However, recent work has indicated that the previous radiocarbon pre-treatment methods applied in the dating process may not have been stringent enough to remove all potential contaminants.

It is widely known that radiocarbon ages beyond 3-5 half-lives can be significantly affected by even trace amounts of contamination (Higham et al., 2006; Higham et al., 2019; Devière et al., 2021; Spindler et al., 2021; Pigott et al., 2024). One notable recent example was the re-dating of Kabazi II using single amino acid dating of hydroxyproline, which resulted in ages that were ~10,000 years older than those obtained using bulk collagen methods (Spindler et al., 2021).

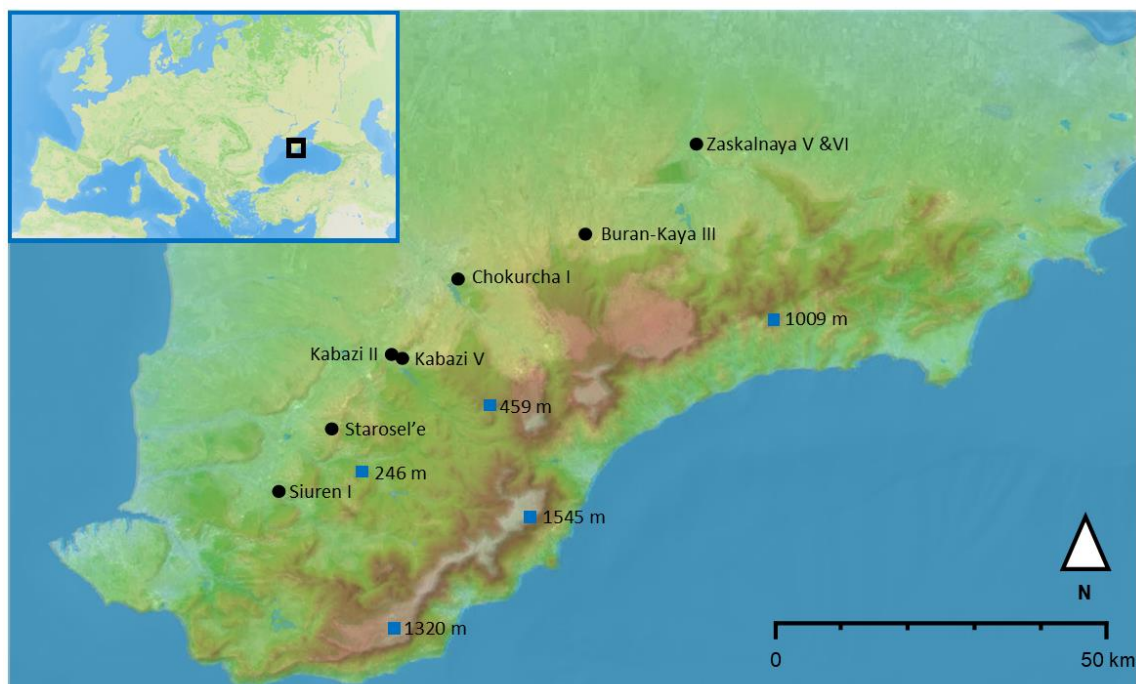


Figure. 1 Map of the Crimean Peninsula, showing the locations of Siuren I, Starosel'e, Kabazi II, Kabazi V and Chokurcha. The red to brown colours represents the first and highest mountain range, which reaches elevations over 1000m, the lighter and less frequent red to orange colour indicates the second middle mountain range; due to low elevations, the lowermost third range in the North of the middle range is almost not visible in this map. Map made with Mapbox and Topographic map.

There are four main lithic technocomplexes in the Crimean Peninsula during the Middle to Upper Palaeolithic. In the Middle Palaeolithic, the Crimean Micoquian (CM) predominates (Monigal & Chabai, 1999; Chabai, 2004a, 2005; Demidenko & Uthmeier, 2013). Characterised by soft hammer bifacial thinning and the production of bifacial tools by retouching, it appears to date back to ~100,000 years (Chabai, 2004a). The Crimean Mousterian (WCM) variant is also present, characterised by an absence of bifacial tools, the presence of Levallois reduction processes and volumetric core reduction (Marks & Chabai, 2006). Although chronologies are challenging, it is suggested to date from around 50,000 years ago, ending co-terminously with the CM. The WCM falls within the start of the Upper Palaeolithic period, and the two lithic assemblages have been observed together whether mixed or contemporaneous is unclear. The Aurignacian technocomplex is characterised, as it is across Europe, by retouched twisted and non-twisted bladelets, as well as blades, micro blades and osseous tools (Demidenko & Otte, 2001). The fourth industry is the Eastern Szeletian, characterised by end-scrapers on flakes, bifacial leaf points and trapezoidal microliths and bone tools (Laroulandie & d'Errico, 2004). Radial core production is present, with blades being relatively infrequent (Monigal, 2004). Links between these four lithic technocomplexes and their biological makers are inferred based on the presence of Neanderthal remains at Kiik Koba, Zaskalnaya V,

Zaskalnaya VI and Starosele (Demidenko and Uthmeier, 2013; Chabai and Uthmeier, 2017; Stepanchuk et al., 2017; Pigott et al., 2025) with Middle Palaeolithic industries, and *Homo sapiens* remains at Siuren I linked with the Aurignacian technocomplex (Benazzi et al., 2015; Slimak et al., 2022). At Siuren I, bladelet technologies dominate layers G and H, linked with the Aurignacian, the only evidence for this industry in the Crimea. However, detailed studies of the lithic components in these layers indicate that around 10% are Middle Palaeolithic Micoquian tools (Chabai, 2005; Demidenko & Chabai 2012a&b). Several hypotheses have been put forward to explain this (Demidenko, 2012). It could indicate the possibility of co-existence or interactions between Neanderthals and *Homo sapiens* groups (Bataille, 2012) or reflect a palimpsest resulting from multiple repeat occupations by both. Alternatively, it might reflect more extensive taphonomic or post-depositional mixing of the archaeological sequence. Demidenko (2012) considers that 'alternating visits' by both groups might be the most parsimonious explanation.

Many Middle to Upper Palaeolithic archaeological sites in the Crimean Peninsula have been previously radiocarbon dated, but many of the results are surprisingly young, some dating to as recent as 22-29 ka BP (Demidenko & Noiret, 2012; Stepanchuk et al., 2017). Experience has shown that radiocarbon dates generated decades ago have a strong tendency to produce underestimated ages. In this paper we examine the accuracy of some of these previous legacy radiocarbon dates by redating samples of bone from several key sites, including Kabazi II, Kabazi V, Siuren I, Starosel'e, Chokurcha I, Zaskalnaya V, Zaskalnaya VI with an improved ion chromatographic method using XAD-2 resin. We compare the results with the previous corpus of radiocarbon and other dates. We also apply ZooMS, a collagen peptide mass sequencing method, to screen bones from five of the sites. We aim to identify human remains and augment the zooarchaeological analyses previously undertaken.

The archaeological sites

We analysed bone and teeth samples from Kabazi II, Kabazi V, Siuren I, Buran-Kaya III, Zaskalnaya V, Zaskalnaya VI and Starosele (Supplementary Information). All sites are rock shelters, with the exception of Kabazi II, which is an open-air site. The dominant lithic technocomplexes are Middle Palaeolithic, with the exception of Siuren I, where Units F, G and H are associated with the Protoaurignacian, probably indicating the presence of *Homo sapiens*. Also, at Buran Kaya III, there is a stratigraphic context from the Medieval period, right through to the Middle Palaeolithic. However, there is an intriguing possibility of overlap with Neanderthals, as indicated by a CM component within the Aurignacian assemblages of archaeological Units G and H (Chabai, 2005; Demidenko & Otte, 2001). The Crimean refugium model is partly based on the radiocarbon dates from Siuren I. Aurignacian industries are known Europe from approximately 43-35,000 years ago (Chu & Richter, 2020),

so a radiocarbon date of 31-35,000 cal BP, seems somewhat too young. Units G and H have produced radiocarbon dates ranging from approximately 19,680 – 30,490 uncal BP. These dates do not reflect the lithic technology present within the three units and do not compare with any other site in Europe. The reasons for these younger ages are not known but may be influenced by taphonomic processes or, more likely unremoved contamination within the bone samples coupled with poor preservation of collagen.

By comparison, Buran-Kaya III has one of the most substantial and best-preserved stratigraphic profiles in the Crimean Peninsula, ranging from the Gravettian (layer 6-1) to the Micoquian/Szeletian (Layer B-C). Various radiocarbon pre-treatment protocols have been applied to date bone across the stratigraphic profile. These include the extraction of collagen using the basic Longin method (Longin, 1971), the analysis of carboxylic carbon using ninhydrin derivatisation (Nelson, 1991), ion-exchange gelatin purification used in Oxford (coded AI) (this method was later abandoned due to possible column bleeding (Higham et al., 2006)), as well as the ultrafiltration of collagen. In this study we focused only on the Middle Palaeolithic layers of B and C. Layer B has one ultrafiltered collagen date (OxA-36921), which was dated at $37,700 \pm 900$ uncal BP (Uthmeier, 2024). This is the oldest date within layer B and C (see Supplementary Information for full tables of pre-treatment methods for each site). This indicates that perhaps more robust pre-treatment methods can have a substantial effect on the radiocarbon age.

Zaskalnaya V and Zaskalnaya VI have previously been radiocarbon dated but Bayesian modelling shows many statistically significant outliers, indicating some of the dates may be underestimates (Pigott et al., 2024). This can be seen in the lowermost units at Zaskalnaya VI, which belong to the Micoquian industry (Stepanchuk et al., 2017). Units I and II have previously produced dates ranging from 25,000 to 35,000 cal BP, dates that need to be tested for their reliability.

Kabazi V and its Micoquian technocomplex has previously proved extremely difficult to radiocarbon date, due to poor collagen preservation. Other dating methods applied, such as ESR, U-series and OSL, have produced quite divergent results. Rink et al.'s (1998) ESR results suggested quite young ages of 26 to 30 ka (Level III/1) and <41 ka for Level III/IA. Housley et al., (2007) attempted to date the site using radiocarbon. They selected material from layers III/1A, III/1, III/4-5, III/5-3B1 and IV/3, but all of the bone collagen extractions failed to yield sufficient material for dating. One charred bone sample and one piece of charcoal were dated. The charcoal sample was only dated by the humic acid component, which is less reliable and yielded an age of 31,000 ka BP, considered to be too young. Charred bone is often considered to be problematic for dating the Palaeolithic. In this case the base insoluble residue of the dated sample yielded an age of ~39,000 uncal BP (Housley et al., 2007). The few

radiometric dates suggest further work should be undertaken at the site, but this will doubtless be challenging based on previous experience. Housley et al., (2007) also attempted to date samples of burnt flint and sediment using TL and OSL methods. They obtained one measurement, which they consider a minimum age, of 81 ± 9 ka BP for layer III/1.

Starosele is notably linked with the discovery of the Starosele child which was later concluded to be a probable Medieval/Post Medieval juvenile burial (Marks et al., 1997). Only two ultrafiltrated radiocarbon dates have been obtained from Starosele, yielding dates ranging around 41-43,000 uncal BP for level 1. ESR and U-series dating has also been undertaken on levels III and IV, ranging from 42,000 to 46,000 uncal BP for level III and a date of around 104,000 for Level IV (Supplementary Information). We concentrated on level I, where three human burials were found and which should also be within the radiocarbon range.

Chokurcha is the final site we examined. Only one radiocarbon date has been obtained previously, and this came from within Unit IV–O (See supplementary Information), and dated to >45,400 uncal BP (Chabai, 2004a). We obtained new determinations from Unit IV, from various levels from the 1996-2000 excavations led by one of us (VC). Unit IV has also been assessed through zoological analysis (Patou-Mathis, 2004). Dating Unit V will allow insights into the age of the Micoquian technocomplex found there.

Table 1. Table of sites discussed in this paper and their lithic technological assemblage, time frame and the most recent radiocarbon dates which have been published. Edited from Pigott et al., (2024). Only one date has been undertaken for Chokurcha I, hence why no date range is available for this site.

Site	Industry	Timeframe	Radiocarbon age	Main Reference
Kabazi II	Western Crimean Mousterian	Middle Palaeolithic	>50,000 cal BP	Spindler et al., (2021)
Siuren I	Aurignacian/Micoquian	Upper Palaeolithic	28,000-30,000 uncal BP	Demidenko & Otte, (2001) and Demidenko & Noiret, (2012)
Buran Kaya III	Micoquian and Eastern Szeletian	Middle/Upper Palaeolithic	28,000-36,000 uncal BP	Péan et al., (2013)
Zaskalnaya V	Micoquian	Middle Palaeolithic	30,000-40,000 uncal BP	Chabai & Uthmeier, (2017)
Zaskalnaya VI	Micoquian	Middle Palaeolithic	30,000-39,000 cal BP	Stepanchuk, (2017)
Kabazi V	Western Crimean Mousterian and Micoquian	Middle Palaeolithic	30,000-38,000 uncal BP	Housley et al., (2007)
Starosele	Micoquian	Middle Palaeolithic	Level 1 ~42,000 uncal BP and 46,130 - 44,990 cal BP	Marks et al., (1997) and Pigott et al., (2025)
Chokurcha I	Micoquian	Middle Palaeolithic	Unit IV-O, >45,400 uncal BP	Chabai, (2005)

Results

New radiocarbon results are reported in Supplementary Information (Appendix 1), along with the analytical data for each determination. We assess the new results by comparing them by pre-treatment type and then build a series of Bayesian models to place the results in their proper chronometric context.

For many bones, we applied several different pre-treatment methods to determine the extent to which contaminants may have affected the results (Figure 2). Consistent results, regardless of the pre-treatment method applied, could be taken to support the idea that contamination is of limited influence. Significant variations, on the other hand, suggest contamination is significant, and one often observes the more rigorous methods often yield the oldest results because of the overwhelming influence of modern ^{14}C on the age of samples of Palaeolithic age.

We observe that the ABA pre-treatment results were mostly younger than the UF or XAD-2 pre-treatment methods, with the exception of Kabazi II and Buran-Kaya. At three sites, XAD-2-treated results produced older dates. At Zaskalanaya V, Level II, for example, the XAD-2 results were ~3000-6000 years older than the bulk collagen results. We see similar patterns at Starosele where two XAD-treated samples from one of the bones we dated resulted in the

oldest dates (Figure 2). In addition, from the same site, we dated the new Star 1 Neanderthal bone with UF and then XAD-2 treatments. The XAD radiocarbon date (VIE-1541) was ~3000 ¹⁴C years older. At Chokurcha we dated a bone from Unit IV which gave finite results for the gelatin and UF results, but a 'greater than' age for the XAD-treated sample. All other samples we dated with XAD-2 from Chokurcha (*n*=23) were beyond the radiocarbon limit except for VIE-1778 (Supplementary Information, Appendix 1). The site has one previous radiocarbon date (OxA-10877), from Unit IV-O, which resulted in an age of >45,500 BP (Chabai, 2005). Only one sample failed to produce a yield of collagen.

Buran Kaya III presents a contradictory picture. There, a bone we dated with XAD-2 from level B yielded a younger date (VIE-1539) than the ABA and UF pre-treated bones (VIE-1196 and VIE-1441). To test whether this was accurate we redated the sample again using XAD-2 and obtained a second date that agreed with the first XAD-2 result (VIE-1892).

Kabazi II has the most radiocarbon results for comparison. Previous radiocarbon dates using ion-exchanged gelatin (AI) from layers I, II/1, II/2, II/3, II/4, and II/5 produced a surprisingly young range in age of 31,550—35,100 uncal BP. Spindler et al., (2021) took seven of these previously dated bones and extracted HYP for dating. They also dated the same samples with ultrafiltration. They found differences of up to 10,000 years with HYP consistently being the oldest. We sampled and radiocarbon dated 6 of the same bones with XAD-2 resin chromatography. We compare the results with all previous results in Figure 3. In one instance (sample 14/9/II/8/8L/1988) the XAD-2 result was too young due to extremely low graphite for AMS dating, so we set this to one side. The remaining results show that while the XAD-2 determinations are consistently older than the AI and UF dates, the HYP results are older with one exception; VIE-1582, which is in statistical agreement. Further work is needed to explore which results are more reliable and why there is this variation, but we would favour the HYP results. It may be that the Kabazi II contaminant load is very high and treating the samples with additional ion exchange resin would improve the XAD-2 results. An alternative explanation might be that the background subtraction for the HYP results was greater than it ought to have been.

Several samples were not amenable to comparison because of their low collagen preservation. The bone preservation found at Siuren I was poor and the volume of failed samples high (from 27 samples only 2 results were obtained). Siuren I produced two dates within Unit H which are significantly older than a previously dated gelatin result (Figure 4b). However, caution is warranted due to the small size of the extracted collagen. The results may be minimum ages.

The bone sample pre-treated with XAD-2 from Kabazi V, Level II (VIE-1576) is a minimum age due to a very low collagen extract and a concomitant small graphite size (306 micrograms).

This result ought to, therefore, be set to one side. Kabazi V has been proven extremely difficult to date in the past due to its extremely poor collagen preservation (Housley et al., 2007).

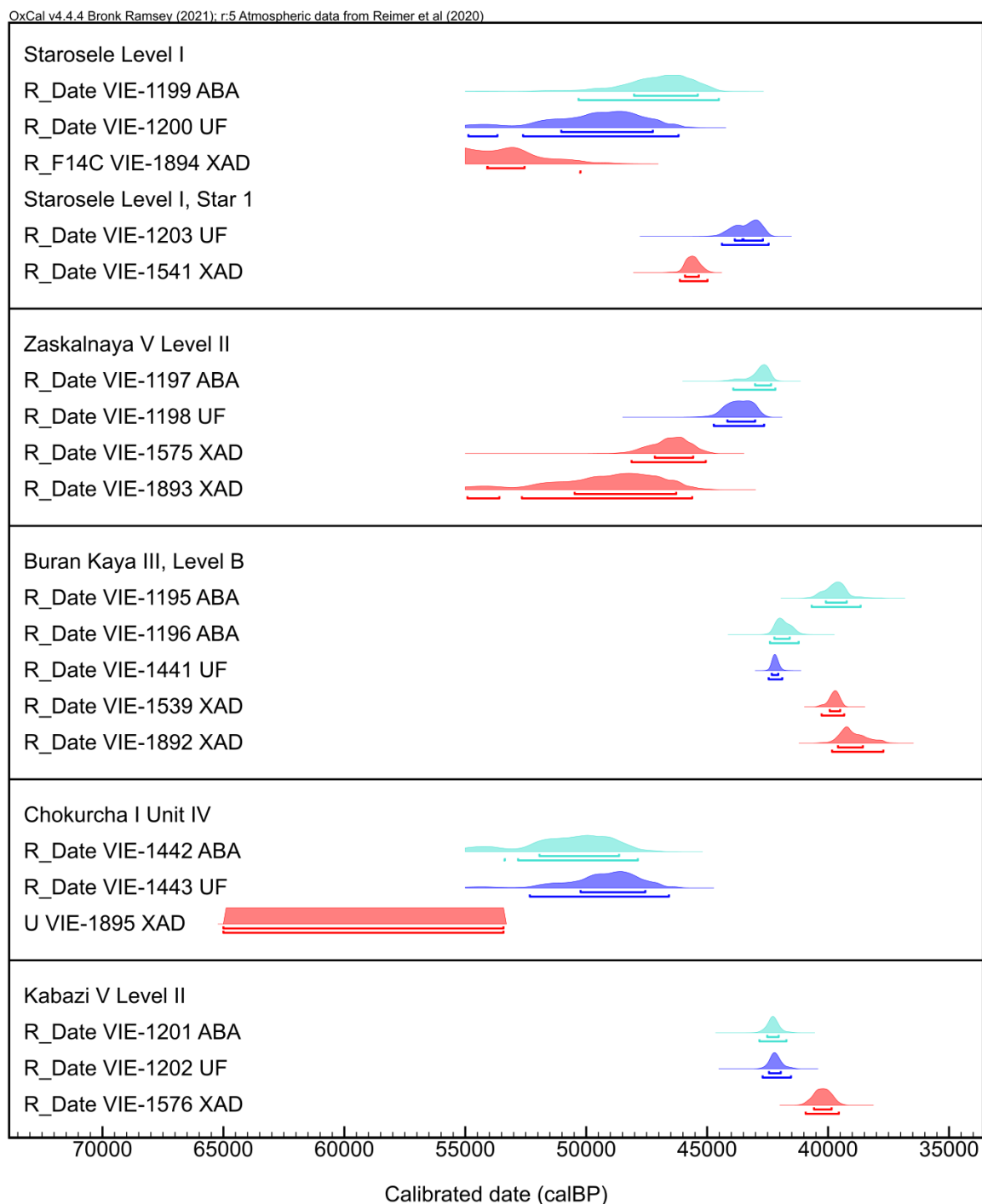


Figure 2. Comparisons made between different pre-treatment methods for the sites of Starosele (Level I), Zaskalnaya V (Level II), Buran Kaya III (Level B), Chokurcha I (Unit IV), Kabazi V (Level II). The pre-treatment methods are categorised by their pre-treatment code and colour; AI (teal), UF (blue) and XAD-2 (red). The fraction modern for the XAD-2 (red) date was used for the Chokurcha I (VIE-1895) calibration, due to the date being beyond the limit. VIE-1576 from Kabazi V had an extremely low graphite size (309 micrograms), so should be viewed as a minimum age.

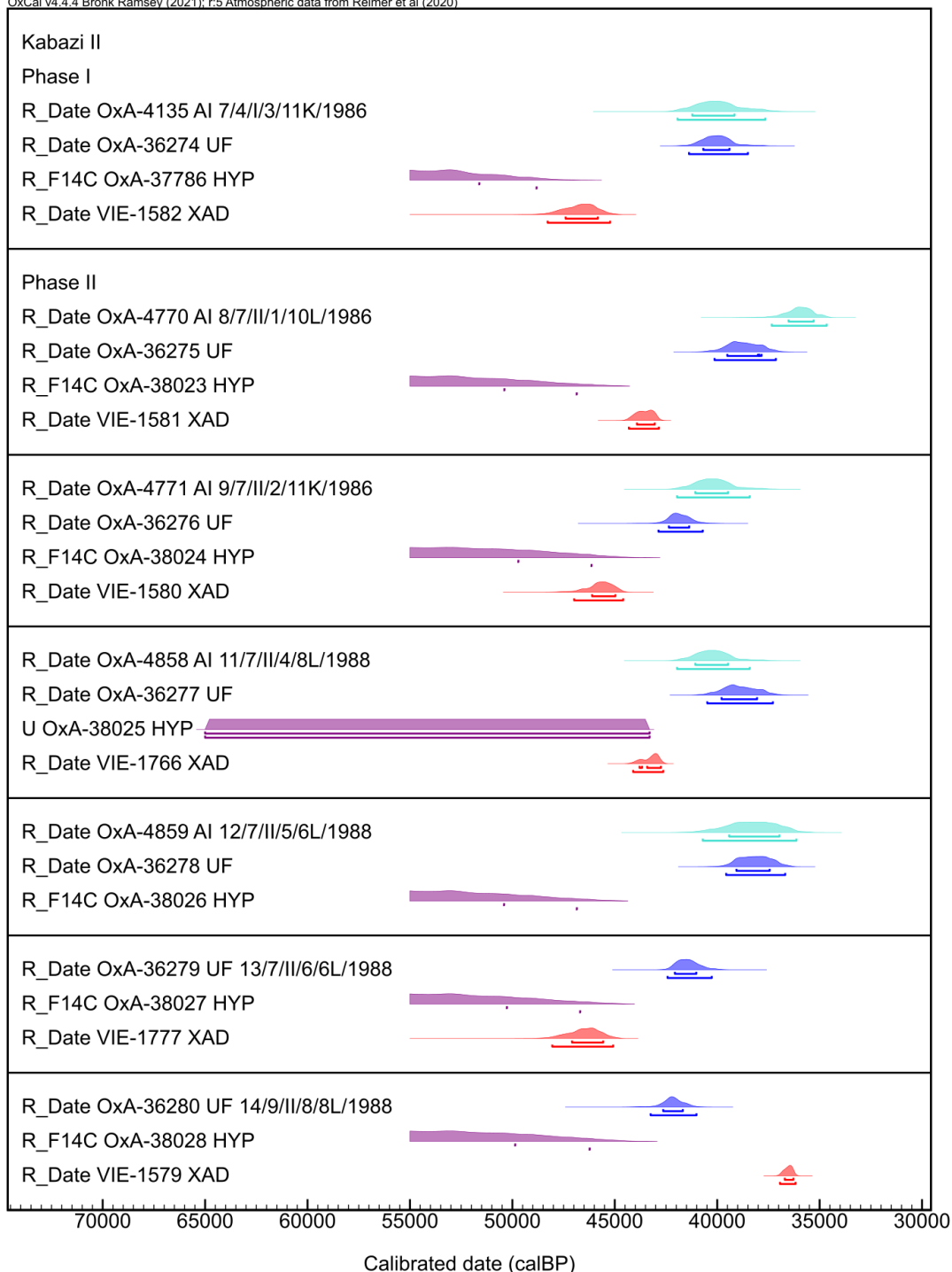


Figure 3. Comparisons made between different pre-treatment (AI (ion-exchanged gelatin), UF, HYP and XAD-2) methods from bones dated at Kabazi II (Phase I and II). The results are divided based by the same bone which was dated from each context. The pre-treatment methods are categorised by their pre-treatment code and colour; AI (teal), UF (blue), XAD-2 (red) and HYP (purple). All samples are from the same bone as outlined in Spindler et al., (2021). The fraction modern for the HYP (purple) date (OxA-38025) was used for Kabazi II, due to the dates calculated being >than ages. The result for VIE-1579 is likely to be too young due to a very small amount of measurable carbon in the graphite (615 micrograms).

Bayesian modelling

We built a series of Bayesian age models for the key sites we worked on, to place the new XAD-2 results in their proper chrono-stratigraphic context (Figures 4-5). The Starosele model (Figure 4a) contains five new XAD-treated radiocarbon dates, three of which are 'greater than' ages, ie beyond ~50,000 BP. VIE-1541 is the XAD-2 date for the Star 1 Neanderthal (Pigott et al., 2025). The results show that the end of the Micoquian sequence at Starosele ranges from 45,042 – 37,896 at 95.4% probability.

At Siuren I the picture is very complicated based, in all likelihood, on the intercalation, mixing or palimpsesting of material in the critical Micoquian and Aurignacian Units G and H, which have been held to indicate the possibility of the co-existence or periodic presence of either Neanderthals and *Homo sapiens* (Demidenko, 2012a&b; Pigott et al., 2024). New dating cannot resolve this key question of course. Despite our best attempts, we encountered very poor bone collagen preservation at the site, which necessarily limits our ability to produce a robust chronology. We included the two new XAD-2 ages in the model, along with one previously obtained bulk collagen sample (OxA-8249)(Figure 4b). However, as we stated above, despite the fact that the XAD-treated results are up to 5000 years older, we still view them as minimum ages due to their low collagen content. In terms of the Aurignacian, the results fit quite well, but they appear very young for the Micoquian technocomplex which appears to date at or close to the radiocarbon limit in other parts of Europe (see below). The older results, even with the caveats applied, tend to suggest to us that it is less likely that Neanderthals were present so late in the Crimean Peninsula as once thought.

The Zaskalnaya V model (Figure 4c) has three results in it, two of which are our new XAD-2 treated results, which are significantly older than the two bulk collagen dates we obtained above (Figure 2). The model suggests the late boundary for the Micoquian level at this site ranges from 46,812 – 42,599 (68.2% prob.) and 47,863 – 27,563 (95.4% prob.) With the long tail in the results at the higher confidence interval reflective of the lack of constraining ages in levels above the latest Micoquian.

Zaskalnaya VI produced two XAD-2-treated results within the Micoquian units II and IIIa, which are extremely similar to the previous dates which used AI pre-treatment methods. VIE-1761 yielded a large outlier probability despite the fact that it probably represents a *terminus ante quem* for the Unit IIIa material below it. This suggests these levels are probably at or prior to 45,000 cal BP in age (Figure 5a).

The Bayesian model for Buran Kaya III contains the XAD-treated results which were at odds with the other determinations run on the same bone using UF and gelatin treatment. The AI and ninhydrin results are both older and, we suggest, to be favoured. We tested the sensitivity

of model to including the XAD-2 results or not and we found that the end boundary for the Micoquian resulted in age ranges being up to 2000 years older without the new XAD-2 radiocarbon dates 42,223 – 41,337 (68.2% prob.) and 42,430 – 40,048 (95.4% prob.). With the XAD-2 radiocarbon dates the end boundary of the Micoquian date to 39,642 – 38,384 (68.2% prob.) and 40,012 – 36,656 (95.4% prob.). We conclude the model is sensitive to the inclusion of those results and suggest they be set to one side for the modelling work.

The single Kabazi V bone that was dated using XAD-2 was not accurate due to low dateable carbon. Like OxA-35786 it is probably a minimum age (Figure 4c). At Kabazi II the XAD-2 results were younger than those obtained using the HYP protocol, and for the time being we favour those, indicating an age for the Mousterian there of >45,000 cal BP after Spindler et al., (2021).

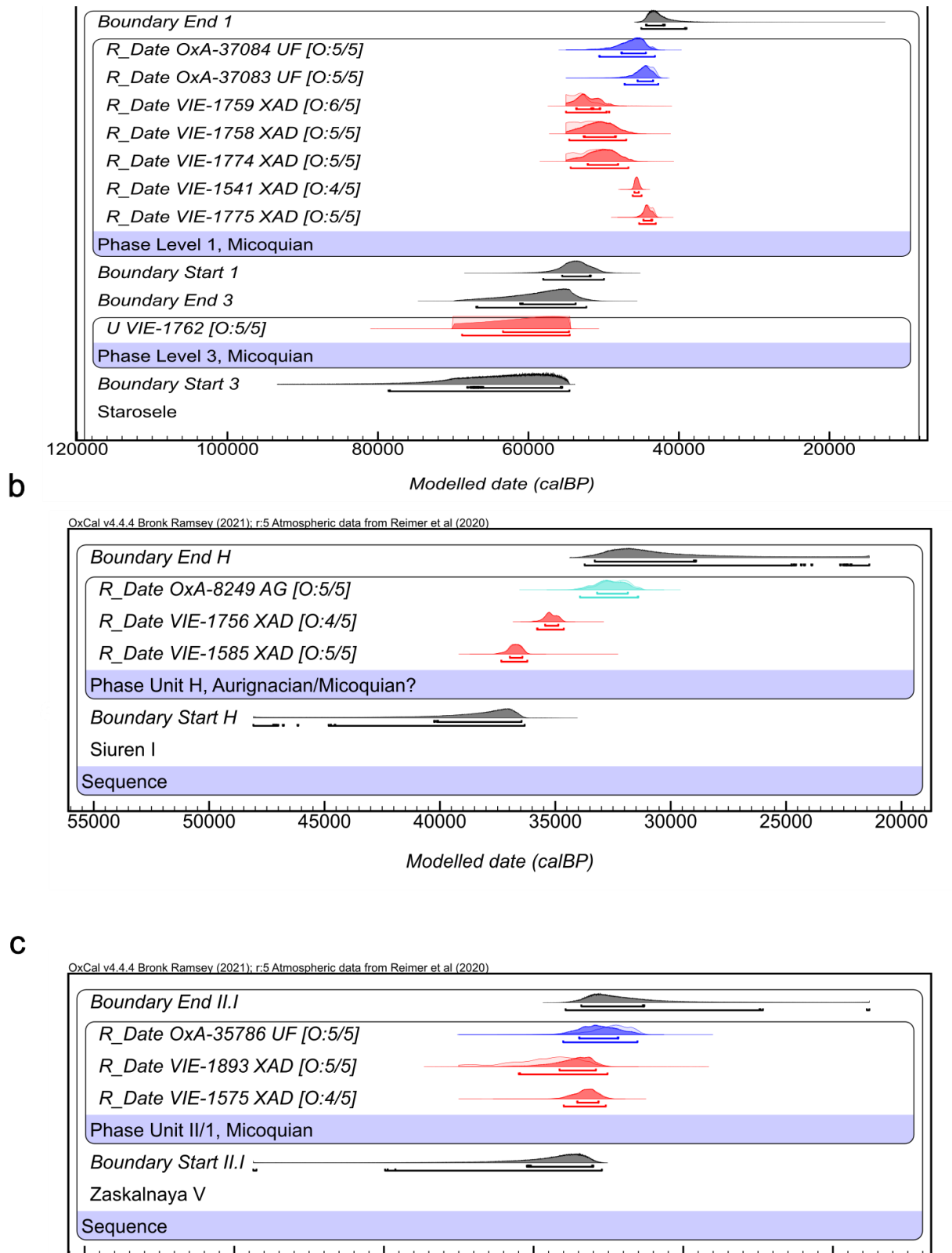


Figure 4. a. A Bayesian model for the site of Starosele, Level 1 (Micoquian). Pre-treatment method differences for Level 1 are indicated in blue which signifies UF and red for XAD-2. VIE-1774, VIE-1758 and VIE-1759 are most likely beyond the limit for radiocarbon dating. VIE-1541 is the previously identified human found using ZooMS and mitochondrially sequenced as a Neanderthal (Pigott et al., 2025). VIE-1540 was not included due to a low amount the collagen size (See appendix 1). The

General Outlier Model shows no significant outliers. b. A Bayesian model for the site of Siuren I, unit H (Aurignacian or Micoquian). Pre-treatment method differences for Unit H are indicated in teal which signifies AG and red for XAD-2. The General Outlier Model shows no significant outliers. However, the two new XAD-2 radiocarbon dates show a variation of age within Level H, which may signify a mixing of cultural material or underestimates of ages due to low amount of starting collagen before undertaking XAD-2 pre-treatment. c. A Bayesian model for the site of Zaskalnaya V, unit II.I (Micoquian). Pre-treatment methods are indicated in blue for UF and red for XAD-2. The General Outlier Model shows no significant outliers.

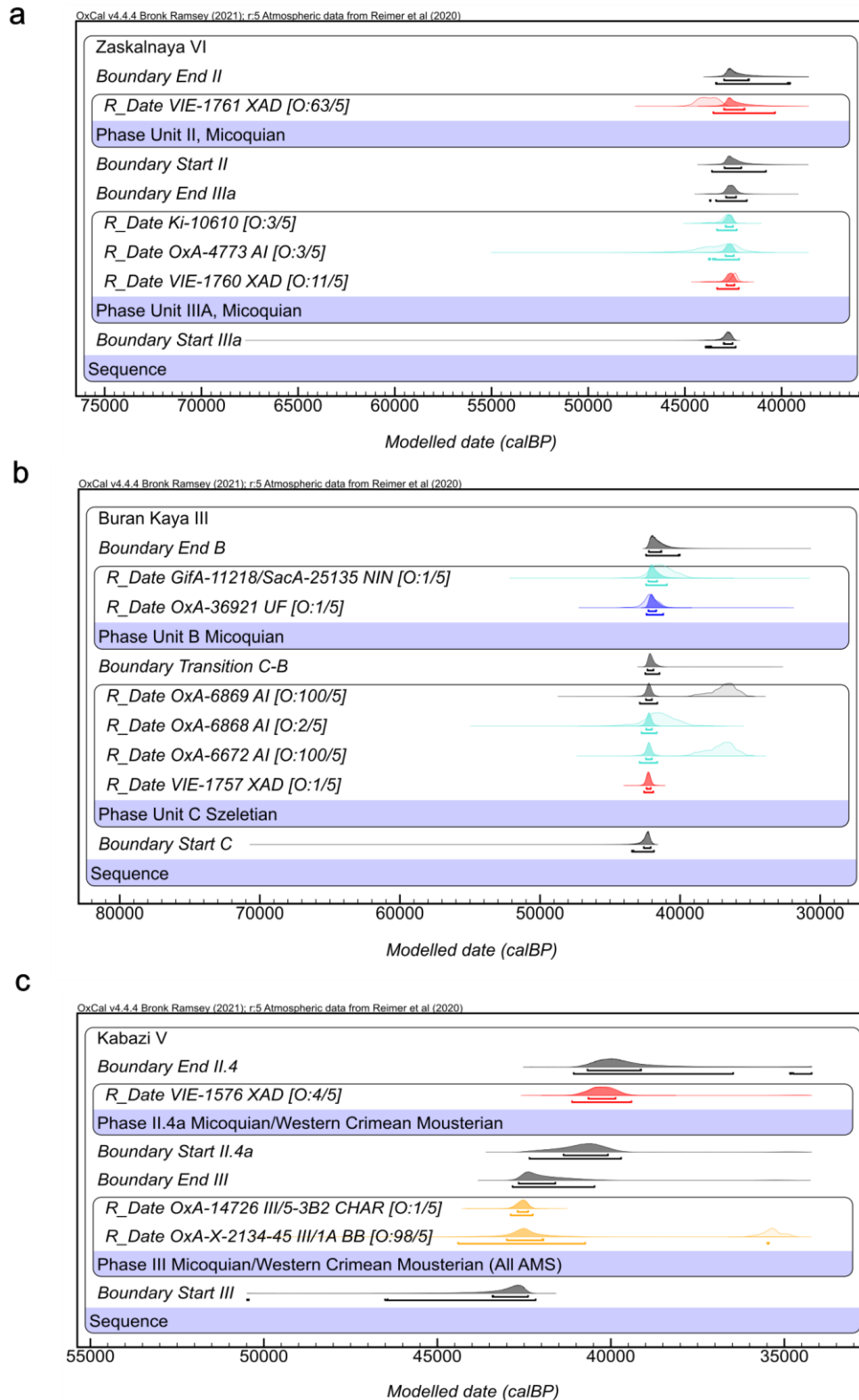


Figure 5. a. A Bayesian model for the site of Zaskalnaya VI, layer IIIa and II (Micoquian). Pre-treatment methods are AI (OxA) and ABA for the Ki result. XAD-2 is in red. The General Outlier Model shows a significant outlier for VIE-1761 in Unit II, which most likely presents the most reliable result, with the new pre-treatment method. We chose to remove the KI and AI radiocarbon dates from Unit II as we consider that they are probably minimum ages. A Bayesian model including the other precious

radiocarbon dates from Ki and Al can be found in the Supplementary Information, Figure 6. b. Bayesian model for the site of Buran Kaya III, Unit B (Szeletian) and C (Micoquian). Pre-treatment methods are Al and NIN (Ninhydrin) in teal, UF (blue) and XAD-2 (red). The `General Outlier Model` shows a significant outlier in both Unit B and C for three samples (VIE-1539, OxA-6869, OxA-6672). c. A Bayesian model for the site of Kabazi V, units II and III (Micoquian). Pre-treatment methods are categorised as charcoal (Char) and burnt bone (BB) in Yellow and XAD-2 (red). VIE-1576 is a new XAD-2 date, but ought to be viewed with caution; the collagen extract was very low - only 3.5 mg (after ultrafiltration) and the graphite carbon was 306 micrograms, so it should be viewed as a minimum age. The `General Outlier Model` shows a significant outlier for Phase III (OxA-X-2134-45), which may be a result of dating burnt bone which is difficult.

ZooMS analysis was undertaken on all samples processed for radiocarbon dating (Supplementary Information). Most of the results match with previous taxon identifications made by zooarchaeologists at sites such as Siuren I, Buran Kaya III and Chokurcha I. A selection of faunal bone remains were sampled before radiocarbon dating had taken place. This was to screen the assemblage for possible human remains and to gain insights into the palaeoenvironment and subsistence spectrum. The results from Starosele can be found in Pigott et al., (2025). The full results for Kabazi II, Kabazi V, Chokurcha I and Siuren I are in the Supplementary Information, including Appendix 2. Overall, all sites had good preservation with >75.5% of the samples yielded interpretable spectra. Most of the taxon identifications were *Equus* sp, which was consistent with previous zooarchaeological analyses. Many of the archaeological sites have yielded evidence for a reliance on horse exploitation (Burke, 1999; Hardy et al., 2001; Bataille, 2006; Péan et al., 2013; Pigott et al., 2025). The ZooMS taxonomic results from Siuren I, Layer G and H show a prominence of *Equus* sp, Cervidae and Bovidae indicating a stable palaeoenvironment. This can also be seen at Kabazi II and Kabazi V. In comparison, the ZooMS identifications at Chokurcha I show a prominence of cold adapted animals such as Elephantidae (Mammoths) and Rhinocerotidae (woolly Rhinoceros) in Unit IV, Level B, M and i1, especially in Level B, square G22. This may indicate the site was occupied more toward MIS 4, in a colder climate. It may also be interpreted that the area was used for butchering mammoths, since there is a predominance of mammoth bones found in Level B and the presence of mammoth remains in Level i1 and M.

Discussion

We examined the accuracy of previous radiocarbon dates of Crimean Palaeolithic sites containing evidence for Neanderthal lithic industries. We found that an improved ion chromatographic method using XAD-2 resin resulted in significantly older results in most instances. To explore the effect of this work on our estimates for Neanderthal disappearance

in this region, we built a series of Bayesian models using new radiocarbon dates (XAD-2) from sites within this study, including Starosele, Zaskalnaya V, Zaskalnaya VI, Buran Kaya III and Siuren I, to identify the end of the Micoquian techno complex. We can summarise the results across all sites in a single unified Bayesian model (Figure. 6a) which shows that the Micoquian ended at 73,430 to 41,050 cal BP (at 95.4% prob).

We also built a `KDE_Model` in OxCal 4.4.4 (Ramsey, 2017) to consider the broader chronological picture of the sites under study. This method utilises a kernel function, along with an associated bandwidth, to define a region over which a single observation contributes to the estimated frequency function. This approach treats the KDE-derived distribution as a prior and thereby observes the underlying distributions of the radiocarbon determinations in calibrated time using a non-parametric method. An assumption here is that the determinations reflect the presence of humans. We built three different KDE models to test the sensitivity of the results to the inclusion or exclusion of different chronometric results (Figure. 6b, c, d). We observe that our favoured model, `KDE_Model 1` in Figure. 6b based on XAD-2 and HYP results, does not show the younger tail of results that is present in the other two models that include some of the legacy and less rigorously treated results. Model 1 shows the main KDE peak at ~46,000 cal BP, with a low probability of the distribution post-dating 40,000 cal BP. This suggests that the latest Neanderthals pre-date this.

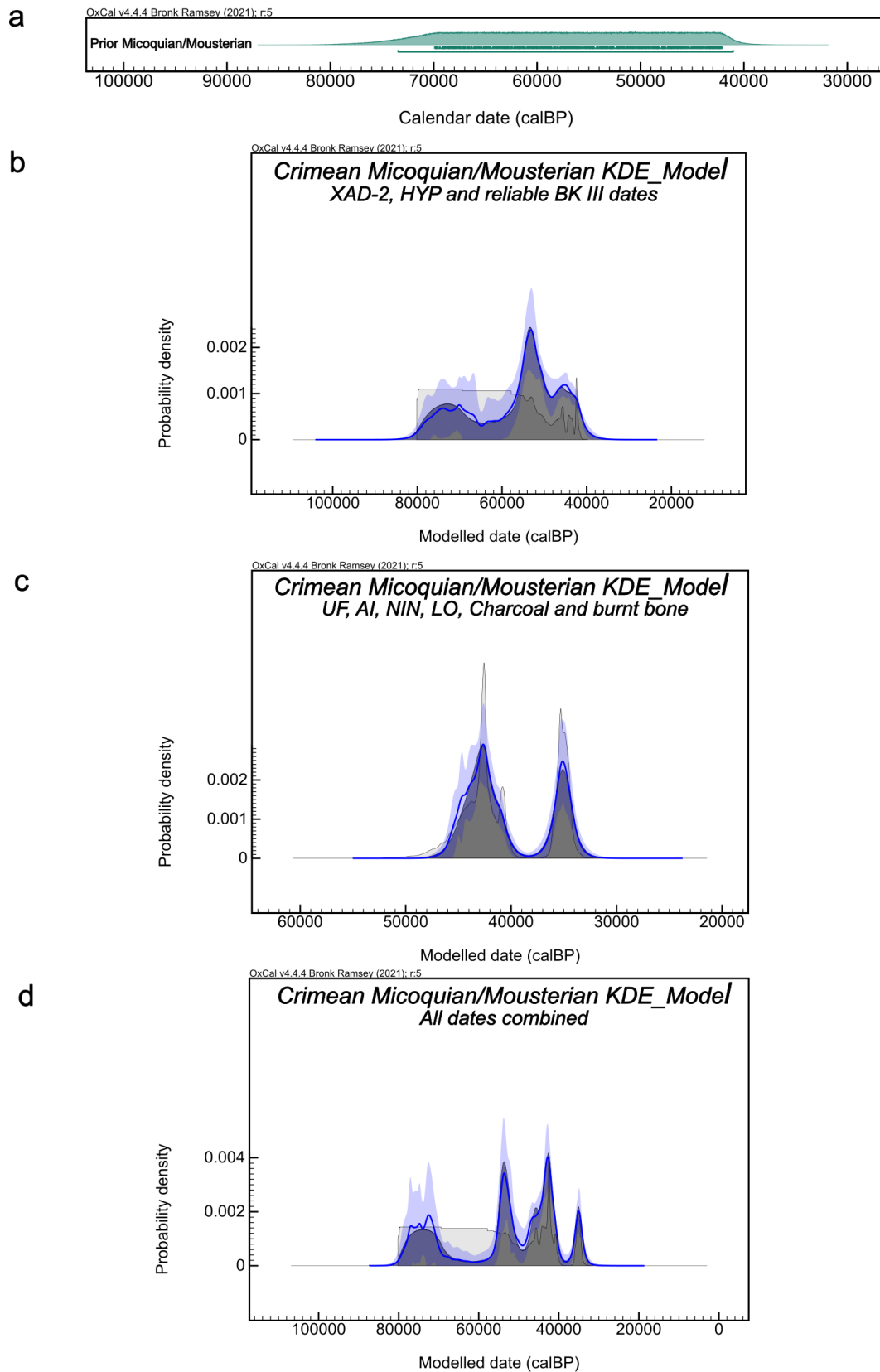


Figure 6. a. Date range for the Micoquian, using radiocarbon dates from Starosele, Zaskalnaya V, Zaskalnaya VI and Buran Kaya III (see Supplementary Information for OxCal code). We created the Bayesian model with and without Siuren I to see if there were any differences, considering Siuren I is of a younger age to the other Palaeolithic Crimean sites within this study. b. KDE model of the new

Micoquian XAD-2 dates from Starosele, Zaskalnaya V, Zaskalnaya VI and Buran Kaya III and Chokurcha I. c. KDE model of previous radiocarbon dates undertaken, using pre-treatment methods UF, AI, Longin, NIN and dates of charcoal. D. KDE_Model of the new XAD-2 radiocarbon dates and older radiocarbon dates from previous pre-treatment methods in Figure. 6c, from Starosele, Zaskalnaya V, Zaskalnaya VI, Buran Kaya III, Kabazi V and Chokurcha I (see Supplementary Information for OxCal code).

Conclusion

Palaeolithic archaeological sites have proven to be extremely difficult to radiocarbon date accurately, due to the presence of contaminants unremoved by traditional bulk collagen pretreatments in many instances (Higham, 2011; Wood et al., 2013; Higham, 2019). We have shown that pre-treating bone using XAD-2 resin chromatography can be an effective method to improve radiocarbon dating in Palaeolithic contexts, due to improved contamination removal. The new XAD-based radiocarbon dates are, in many cases, thousands of years older than previously determined and analysing the new results in a Bayesian model allowed us to calculate an end date for the Micoquian technocomplex which was significantly older than previously attested at 73,430 to 41,050 cal BP (at 95.4% prob).

The pattern of increasing ages was not a feature in all cases we re-analysed, however. In two sites, Kabazi V and Siuren I, we concluded that the poor preservation and low quality of the collagen meant that only minimum ages could be obtained. Siuren I is a key and controversial site based on several very young ages for layer G and H which appeared to support the hypothesis for a very late Neanderthal presence in the Crimean Peninsula. Our new radiocarbon campaign shed no new light on this but we suggest that the young ages are most likely due to a combination of post-depositional or taphonomic mixing of material from two temporal phases of occupation, namely the Micoquian and Aurignacian, and/or unreliable radiocarbon dates based on very low or trace collagen remaining. The late determinations from the site are at odds with the end dates for the Micoquian technocomplex outlined above, so we suggest that Siuren probably does not support late Neanderthal presence.

At Kabazi II we produced results which were probably also minimum ages based on the consistent difference between them and previously obtained results on the single amino acid hydroxyproline (Spindler et al. 2021), which, with one exception, pre-dated them. More work is needed here to understand why there was this disparity, but the most parsimonious conclusion is that some trace contaminants remained. That this was almost certainly site-specific is supported by the results obtained from the nearby site of Chokurcha I, originally dated at around 40 ka BP, but now dated by us with a large number of measurements which were

beyond the radiocarbon limit, fitting well with the estimated age of the site based on its faunal corpus (Patou-Mathis, 2004).

The disappearance of Neanderthals across Eurasia remains an intensely debated topic. A range of possible causal factors have been proposed, ranging from climatic influences, technological, cognitive and behavioural influences between Neanderthals and modern humans, as well as lower population sizes generally amongst Neanderthal groups, as shown by high coverage genomic data and runs of homozygosity along Neanderthal genomes (Wolff et al., 2010 ; Devìese et al., 2021; Vaesen et al., 2021; Skov et al., 2022; Fajardo et al., 2023; Albouy et al., 2024; Slimack et al., 2024). The question of when Neanderthals disappeared is less controversial. The largest study of Neanderthal disappearance showed that there is little to no evidence for Neanderthals being present after 41,030–39,260 cal BP (at 95.4% probability) across Europe (Higham et al., 2014; Devìese et al., 2021). Evidence for possible refugial regions include the southern Iberian Peninsula, where chronometric and lithic/archaeological evidence from Gorham's Cave, Gibraltar, has been held to represent a Neanderthal presence (Finlayson et al., 2006) as late as 28,000 years ago. This has been critiqued (Zilhão and Pettitt, 2006). Wood et al. (2010) showed that many of the legacy radiocarbon ages from the southern Iberian Peninsula were erroneously young, suggesting that the evidence was not sufficiently robust to support a model of late Neanderthal disappearance. More recently, at Lapa do Picareiro in central Portugal, an early Aurignacian occupation excavated within in a sealed stratigraphic layer was dated to 41,100—38,100 ka cal BP (Haws et al., 2020), crucially suggesting that the Ebro Frontier model of Zilhão, (2006), which argues that Neanderthals remained present in the south while early modern humans were in the northern part of the peninsula, must be false. The data we have obtained from Crimea therefore fits well within the wider picture of Neanderthal disappearance across western Eurasia, suggesting that by ~40,000 years ago the process was complete. Based on the evidence we and others have obtained (Figure 6), we reject the hypothesis of a Neanderthal refugium on the Crimean Peninsula.

Methods

Sample selection – Radiocarbon dating and ZooMS

All faunal remains were collected during sampling trips at the University of Erlangen Nuremberg, Germany, Museum of Natural history, Institute of human Palaeontology, Paris, France and samples were sent from University of Oxford, United Kingdom. All the faunal samples for Radiocarbon dating from Erlangen and Paris were specifically chosen due to evidence of anthropogenic modifications (see Supplementary Information, Figure 10). The samples from Oxford were already identified as being anthropogenically modified previously. Supplementary Information, Table 9 presents the number of bones which were selected from each site for ABA and ultrafiltration pre-treatment, before being further analysed. For ZooMS analysis the sampling was taken place depending on the availability of Layers/Levels present at the institutions from the different sites. Approximately 20-25 bones were selected from each layer/level within different squares, when possible. Some bags containing the faunal remains had a large number of bones (50-100), while others contained approximately 20. The site, layer/level and number of bones selected can be seen in Table 9, Supplementary Information.

Sampling – Radiocarbon dating and ZooMS

The faunal samples were manually cleaned with a combination of aluminium oxide powder and air abrasion at the Higham-Douka Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. This enabled the removal of superficial contaminations before sampling. Circa 600 – 900 mg of bone was drilled for each sample, depending on the size and weight of the bone for radiocarbon pre-treatment. Roughly 15 – 30 mg of bone was chipped off with dental pliers for ZooMS analysis.

Radiocarbon dating

Chemistry – Radiocarbon dating

Extraction and pre-treatment of the bone was conducted at the Higham Lab, University of Vienna, Austria. The faunal remains underwent ABA (Acid-Base-Acid) pre-treatment to extract collagen. All samples were first treated with 0.5 HCl three times for demineralisation, the first two times for two hours and the last time for ~24 hours. The samples were washed three times with ultrapure Milli-Q water. After a base wash was performed with 0.1M NaOH for 30 minutes. Three more washes with Milli-Q water were then undertaken, with a 15-minute treatment of 0.5 M hydrochloric acid. Three Milli-Q water washes were then completed again. The collagen was then gelatinised in pH3 water for 20 hours at 75°C. The gelatin was filtered with a clean Ezeefilter, before being processed with a cleaned ultrafilter (Vivaspin® Turbo 15 30kD MWCO) if there was a yield above 0.5% percent after freeze-drying. Then the samples were

centrifuged until 1.0mL of the >30 kD gelatin fraction resided (~20 minutes at 2700 RPM). The gelatin was then placed into a glass tube with Milli-Q water before being freeze-dried at ~18°C for 48 hours.

If the sample only underwent ABA and ultrafiltration, then the samples were weighed out into a clean tin capsule after freeze-drying, if there was a percentage yield above 0.5%. Three pre-tins were made up of 2-2.5 mg of collagen to ensure there is no memory effect between the dated samples during the combustion process. The sample then underwent combustion and graphitisation, before being AMS dated at the Vienna Environmental Research Accelerator (VERA), Physics Department, University of Vienna.

For samples being further processed using XAD-2 a sub-sample of collagen was taken from the freeze-dried collagen sample. For some samples, all of the collagen was needed to process with the XAD-2 protocol. Ideally, a minimum of 5 mg was used for the XAD-2 process. However, sometimes this was not possible, and 3 mg was processed. A total of 43 samples was processed with the XAD-2 protocol, with a total of 73 samples being processed including the standards for each chemistry batch (6-12). The samples were hydrolysed for 24 hours at 110°C, in 6 M HCl. Pre-cleaned and conditioned XAD-2 columns were used to allow the passage of the hydrolysed collagen. The columns had a pre-fitted filter frit at the bottom, and a filter frit was placed above ~100µL of XAD-2 resin. The resin columns were sequentially rinsed with hydrochloric acid to remove residual contaminants. Each wash consisted of passing approximately 1 mL of acid solution through the column. This included 20 washes of 1M HCl and 10 washes of 6M HCl that were passed through the columns. The samples were then passed through the columns, with one more wash of 1 mL of ultrapure 6M HCl, to collect any leftover amino acids. The samples were then placed into a Genevac centrifugal evaporator to deacidify for 12 hours and evaporate the remaining acid. ~200 µL of Milli-Q water was placed into each tube and placed in the Genevac again for 1.5 hours until full evaporation. After this was complete ~100 µL of Milli-Q water was placed again into each sample tube, before being weighed out, which allows the sample to be efficiently weighed out. The samples then went through combustion, graphitisation and processing in the AMS at VERA.

For calibration and comparing the results with previous radiocarbon dates, OxCal v. 4.4.3 software (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020) was used. We also built Bayesian age models to explore outliers and offsets, based on previous and new radiocarbon dates using `Sequence` and `Phase` commands. We used the `General outlier model` to assess whether the radiocarbon likelihoods were outliers within the constraints of the model (Bronk Ramsey, 2009). When the `General outlier model` was used, a probability of 5% was used. All the CQL code used in the models can be found in the Supplementary Information.

ZooMS

The ZooMS analysis was conducted at the Douka Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. Bone samples were analysed using an acid insoluble protocol (Welker et al., 2015, Brown et al., 2020). Following wet chemistry, the spectra were analysed using flexAnalysis 3.4 (Brucker Daltonics) and mMass software (Strohalm et al., 2008). Subsequently, the spectra were compared against known peptide markers in a reference library (Welker et al., 2015). Some species/family faunal remains had already been identified from previous zoological analyses. ZooMS analysis was undertaken using the acid insoluble collagen protocol (Welker et al., 2015).

The bone specimens were first sampled using pliers, chipping off 15 to 25 mg of bone. The samples were demineralised up to 48 h with 500 µL of cold (4 °C) 0.6 M HCl (covering the sample), until somewhat spongy. After demineralization, samples were vortexed for approximately 10 seconds and centrifuged for 1 min at 12 RPM. The samples then went through 2 to 3 washes with 200 µL of 50 mM AmBic, followed by centrifuging and discarding the AmBic solution. Following this, 100 µL of 50 mM AmBic (ammonium bicarbonate buffer, pH 8.0) was inserted into each sample and then incubated for 1h at 65 °C for gelatinization. Half (50 µL) of the sample was removed in case a backup was needed in the future. Trypsin digestion was undertaken by inserting 1 µL of trypsin solution 0.4 µg (Thermo Scientific Pierce™ Trypsin Protease), which was added to each supernatant and digested for 18 hours at 37 °C. The digested samples were treated with 1 µL of 5% Trifluoroacetic Acid (TFA) to stop further enzymatic digestion. ZipTipping was performed for purification and peptide extraction, using C18 ZipTips (Thermo Scientific Pierce™ C18 Tips), using 50 µL of 50% ACN in 0.5% TFA. A calibrant at 1:2 ratio of 0.5 µL was added to the plate, with 0.5 µL matrix solution. The samples (0.5 µL) were spotted with 0.5 µL of matrix solution. Thereafter, the processed samples were analysed using a Bruker Autoflex Speed Matrix-Assisted Laser Desorption/Ionization Time-of-Flight (LRF MALDI ToF/ToF) mass spectrometer (Buckley et al., 2009).

The peptide marker (A-G) was manually inspected in mMass 5.5.0 (Strohalm et al., 2010). After manual taxon identification, SpecieScan software was used to confirm taxon identifications (Végh & Douka, 2024). SpecieScan is a semiautomated process using R and Python to output correlated identifications from reference databases.

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Supplementary Information for Re-dating the Crimean Peninsula with XAD-2 radiocarbon dating – Manuscript I

Archaeological sites, previous radiometric dating, stratigraphic information

Kabazi II

Kabazi II is a multi-layered open-air archaeological site, featuring one of the most extensive Palaeolithic stratigraphic sequences (Figure 1) in Crimea (Markova, 2005). The site's chronology spans from the end of the Last Interglacial period, approximately 115,000 years ago (MIS 5d), to the Late Middle Palaeolithic period, less than 50,000 years ago. Kabazi II comprises seven stratigraphical units, further subdivided into 55 in situ archaeological levels (Uthmeier & Chabai, 2018). Currently, 20 levels are attributed to the Western Crimean Mousterian (WCM), and 35 levels being associated with the Crimean Micoquian (CM). The distinction lies in the absence of bifacial tool and the presence of Levallois-reduced processed flakes in a WCM assemblage (Chabai, 2005).

Kabazi II has undergone comprehensive analysis, including recent radiocarbon dating with hydroxyproline protocol (Spindler et al., 2021). The new data confirms that the site is older than 50,000 years. This indicated that Kabazi II is not a late Neanderthal site, as originally suspected (Spindler et al., 2021). Previous faunal and lithic analyses suggested that Kabazi II served as an open-air kill and butchering site, most likely associated with Neanderthals (Patou-Mathis, 1999, 2005, 2006).

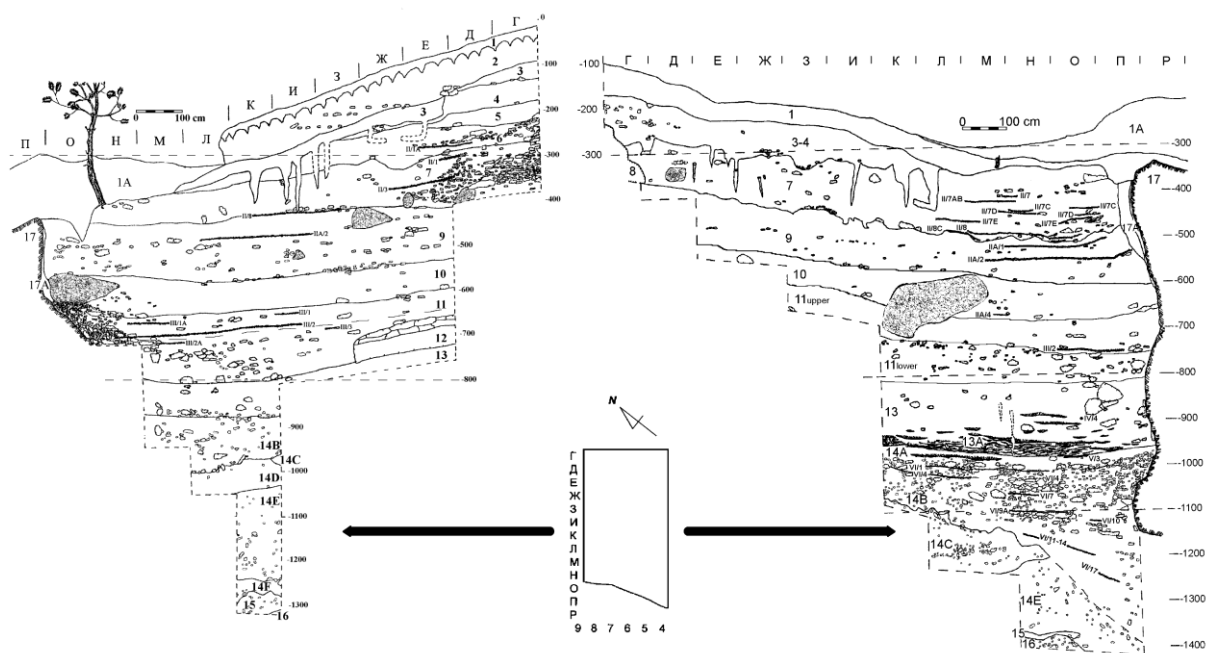


Figure. 1 Kabazi II Drawings of the western (A) and eastern (b) sections. Arabic numbers indicate lithological layers, and Roman numerals indicate archaeological layers. From Uthmeier & Chabai, (2018)

Table 1 - Previous radiocarbon dates obtained from levels I/3, II/I, II/2, II/3, II/4, II/5, II/6 and II/8 at the site of Kabazi II (Hedges et al., 1996; Chabai & Uthmeier, 2006). AI is the abbreviation for ion-exchanged gelatine, AF for ultrafiltered collagen and HYP for hydroxyproline. All dates used are from the same bone from each layer. Table modified from Spindler et al., 2021.

Lab No.	Material	Unit	Industry	Pre-treatment method	Radiocarbon Age BP
OxA-4135	Bone	I/3	Mousterian	AI	34,940 ± 1020 BP
OxA-36274	Bone			AF	34,850 ± 650 BP
OxA-37786	Bone			HYP	>46,500 BP
OxA-4770	Bone	II/I	Mousterian	AI	31,550 ± 660 BP
OxA-36275	Bone			AF	33,850 ± 550 BP
OxA-38023	Bone			HYP	>44,500
OxA-4771	Bone	II/2	Mousterian	AI	35,100 ± 850 BP
OxA-36276	Bone			AF	37,300 ± 900 BP
OxA-38024	Bone			HYP	>42,600
OxA-4858	Bone	II/4	Mousterian	AI	32,200 ± 900 BP
OxA-36277	Bone			AF	34,000 ± 600 BP
OxA-38025	Bone			HYP	>43,300
OxA-4859	Bone	II/5	Mousterian	AI	33,400 ± 1000 BP
OxA-36278	Bone			AF	36,600 ± 800 BP
OxA-38026	Bone			HYP	>44,100
OxA-36279	Bone	II/6	Mousterian	AF	36,600 ± 800 BP
OxA-38027	Bone			HYP	>44,100
OxA-36280	Bone	II/8	Mousterian	AF	37,800 ± 900 BP
OxA-38028	Bone			HYP	>43,000

Kabazi V

Kabazi V is a rock shelter located within the second range of the Crimean Mountains, near Kabazi II (Uthmeier et al., 2008). The site's stratigraphy (Figure 2) comprises 40 archaeological layers and 27 lithological layers (Uthmeier & Chabai, 2018). ZooMS analysis was conducted on layers III/5-2 and III/5-3. Previously, these layers were identified as disturbed hearths with destruction zones (Chabai and Veselsky., 2007). The site is notably a deeply stratified site, which has undergone intense weathering due to sedimentation processes and rockfall. This has subjected the rock shelter site to later become an open-air site in Unit III/1B (Uthmeier & Chabai, 2018). This may have affected the preservation of the fauna which has previously been dated.

Towards the back of the rock shelter numerous hearths with lithic scatters were found, which indicated extensive use of the rock shelter for various activities and broad exploitation of the flint outcrops for tool production. Chabai & Veselsky, (2007), have suggested the

stratigraphy of the hearths may indicate the site was occupied multiple times for short-term occupations.

Kabazi V has not been extensively dated due to poor preservation of the collagen. However, some dates were obtained with ESR and U-Th dating. Overall, the radiometric dates from level III/1 came back as 26-32 ka BP and <41 ka BP for level III/1A from the 1996/1998 excavations (Rink et al., 1998). The U-Th dates on tooth enamel came back much older in comparison to ESR, being 73.3 ± 6.0 ka BP for level III/1 (McKinney, 1998). During field work in 2004, OSL and TL dating was undertaken on Unit III, which gave radiometric dates between 60 ka and 100 ka BP, with Unit IV being around 200 ka BP (Housley et al., 2007). Radiocarbon dating was also conducted on archaeological horizons III which came back to between 30,980 – 38,780 uncal BP. These dates were undertaken on charcoal and burnt bone (Housley et al., 2007).

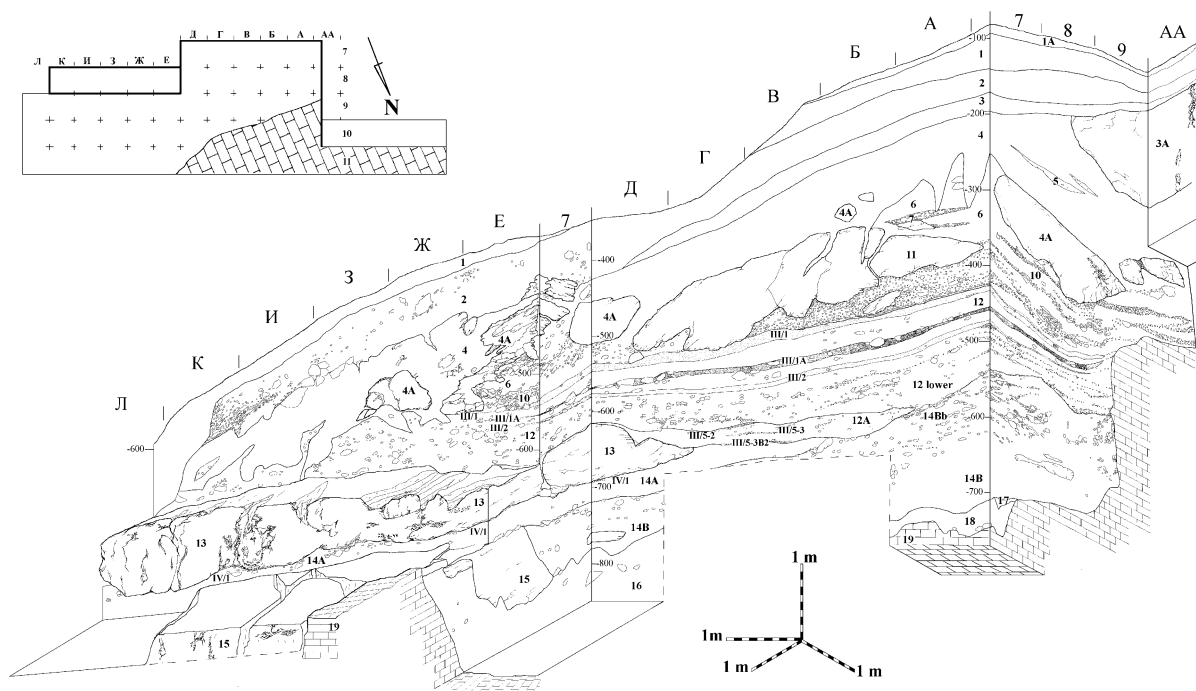


Figure. 2 Kabazi V. Drawing of the combined sections, taken from Chabai & Veselsky (2007). Arabic numerals indicate lithological layers, Roman numerals indicate archaeological levels). From Uthmeier and Chabai, (2018).

Table 2 - Previous radiocarbon dates obtained from levels III/IA and III/5B1 at the site of Kabazi V (Housley et al., 2007).

Lab No.	Material	Arch Horizon	Industry	Pre-treatment method	Radiocarbon Age BP
OxA-X-2134-45	Burnt bone	III/IA	Micoquian	Humic acids?	30,980 ± 220 BP
OxA-14726	Charcoal	III/5-3B1	Micoquian	Humin?	38,780 ± 360 BP

Starosele

Starosele is a rock shelter located within a steep canyon (Burke, 2000). At the initial time of discovery and excavation in 1952 by Formosov, the site was 40 meters north to south distance and had a depth of approximately 1 meter (Marks et al., 1997). The site is comprised of four distinct cultural archaeological layers (Figure 3) belonging to the Crimean Micoquian culture in all layers except level III, which has been suggested to belong to Starosele industry (Marks et al., 1998). Level III and IV are separated by a rockfall event, with evidence suggesting that level IV was briefly occupied (Burke, 2000).

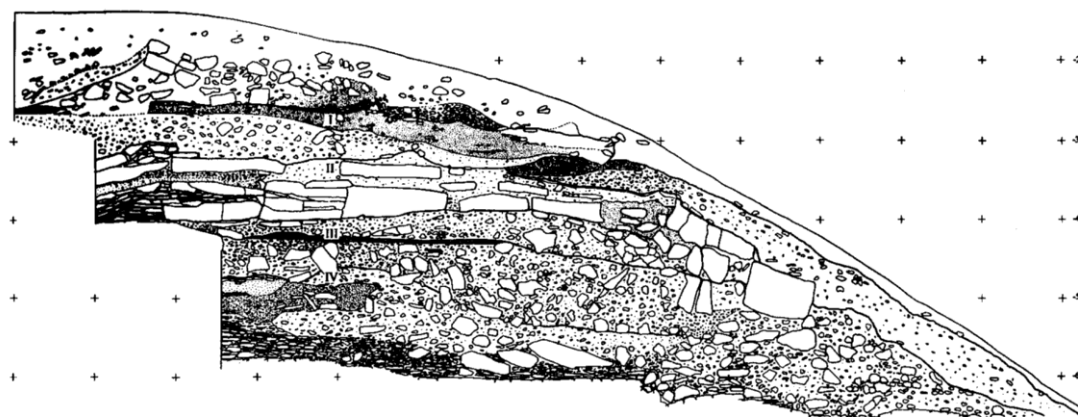


Figure. 3 East/West profile. From Marks et al., (1997).

In previous excavations by Formosov and Marks, human remains have been found within level I/proximately of level I. The first being the Starosele child which was unearthed in the 1953 excavations (Monigal et al., 1998; Burke, 2000). The individual was first considered to be a Neanderthal or a *Homo Sapiens* in terms of morphology (Alexeyev, 1976; Spitery, 1980). The juvenile individual was estimated to be 18-19 months old and was approximately found beneath level I. However, there are some discrepancies regarding the exact placement of the individual, and photographs or stratified drawings are lacking. Later the Starosele child was regarded as a late Medieval or even post-Medieval burial (Marks et al., 1997). During later excavations in 1993-1995 two more human burials were found within level I, including one infant and one adult. Because of the positioning of the bodies and direction they were facing, they were deemed to be 17/18th Muslim burials (Monigal et al., 1998; Burke, 2000; Marks et al., 1997). However, no direct dating has been performed on any of the human burials, which would be very interesting.

Notably, in 2024 (Pigott et al., 2025) a fragmented bone from a human individual was discovered with the application of Zooarchaeology by Mass Spectrometry (ZooMS). 150 bones were analysed within a study, which discovered a human remain, most likely from an adult's femur from Level I, square I23 (Figure 4). Star 1 has been radiocarbon dated with the pre-treatment method of ultrafiltration to the calibrated age of 43,860 – 42,690 cal BP (at 68.3% prob,) and 44,390 - 42,450 cal BP (at 95.4% prob.) With the pre-treatment method of XAD-2, the individual dated to 45,910 to 45,340 cal BP (at 68.3% prob,) and 46,130 to 44,990 cal BP (at 95.4% prob.) After genetic analysis the individual was concluded to being a Neanderthal species, not related to the archaic lineage from Hohlenstein Stadel. This is a very important find for Palaeolithic archaeology, showcasing the powerful technique of ZooMS and its ability to uncover human individuals from non-identifiable bones which have not been worked on for decades. Star 1 has showed that it is more closely related to Altai Neanderthals than Western Neanderthals, indicating the mass migrations by small groups across a large geographical area.

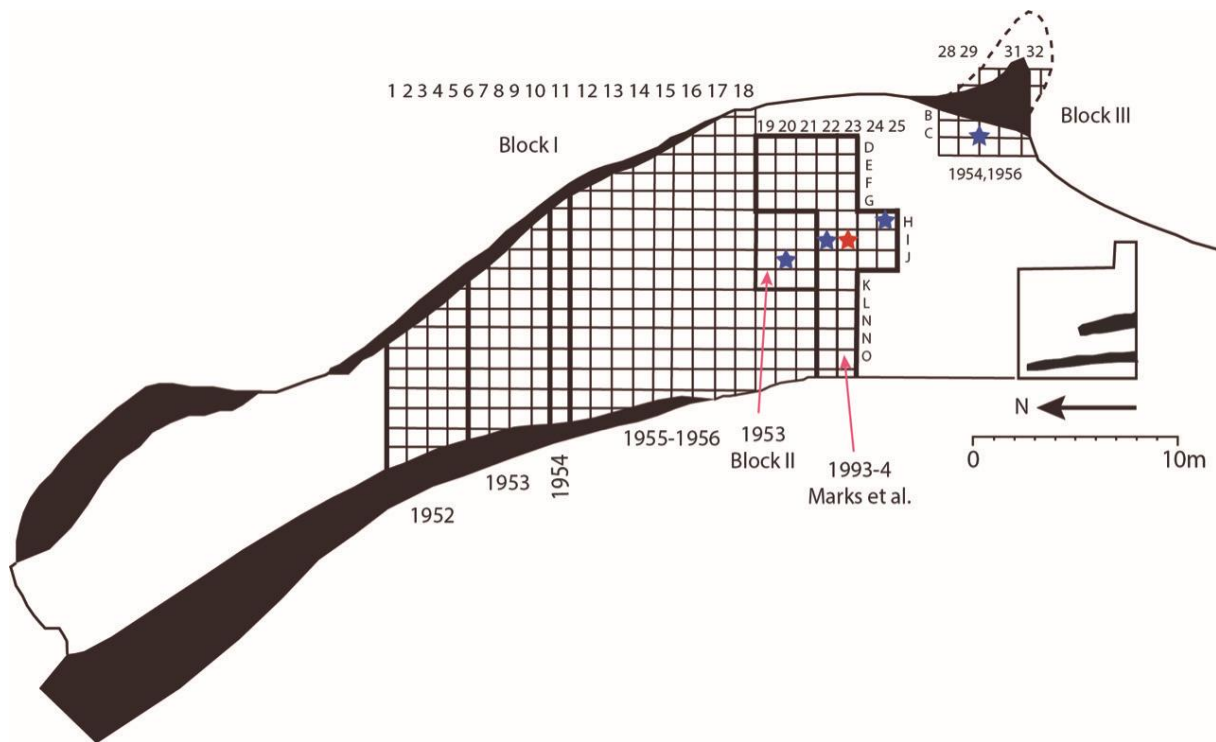


Figure 4. Excavation plan of the site of Starosele (after Marks et al., 1997). The black sections are solid rock mapped by Formozov. The thick lines denote the different excavation years undertaken by Formozov and the Joint Ukrainian/American Project (Marks et al., 1997). The blue stars indicate the position of the three previously identified burials at the site (the burial in J20 was the original child burial) and the partial skeleton in Block III is also shown. Our new hominin bone is shown in red in square I23.

Previously, a combination of AMS, ESR and U-series dating methods was applied to bone and tooth samples from Levels I, III and IV (Table 3). No dating has been undertaken within level II. The chronometric dates have revealed the site to range from 100,000 to 40,000 uncal BP (Marks et al., 1997; Marks et al., 1998; Hardy et al., 2001). Level I was previously dated to 40,000 uncal BP, Level III ranging from 42,000 to 46,000 uncal BP and Level IV to around 100,000 uncal BP.

Table 3 – Radiometric dates from Starosele (Marks et al., 1997). AF is the abbreviation for the pre-treatment method ultrafiltration. Table modified from Pigott et al., (2024).

Lab No.	Material	Level	Industry	Pre-treatment method	Radiocarbon Age BP
U-series	Tooth	IV	Micoquian	U-series	104,000 ± 8500 BP
ESR LU	Tooth	III	Micoquian	ESR	42,000 ± 4700 BP
U-series	Tooth	III	Micoquian	U-series	46,000 ± 2500 BP
OxA-37084	Bone	I	Micoquian	UF	43,000 ± 1700 BP
OxA-37083	Bone	I	Micoquian	UF	41,300 ± 1300 BP

Chokurcha I

The rock shelter is situated within a basin near the river Malyi Salgir (Markova, 2004) and was initially stratigraphically categorised into four distinct archaeological layers by N. L. Ernst during the excavation of 1928-1931 (Chabai, 2004a). Unfortunately, most of the documentation, faunal and lithic artefacts were lost during the Second World War (Chabai, 2004a). Subsequent excavations were conducted between 1996-2000 by V. Chabai with a particular focus on Unit IV including 21 archaeological horizons (A-V), due to its association Crimean Micoquian (Figure 5). Unit IV was found to be the richest in faunal remains, with limited lithic material, suggesting it may have been occupied in a single episode (Patou-Mathis 2004). The site is believed to date to MIS 3, indicating a relatively stable environment, possibly during a period of open steppe environment with cold and dry climate conditions (Markova, 2004; Patou-Mathis, 2004). One radiocarbon date (OxA-10877) was conducted on Unit IV-O, resulting in a radiocarbon age of 45,500 BP (Markova, (2004).

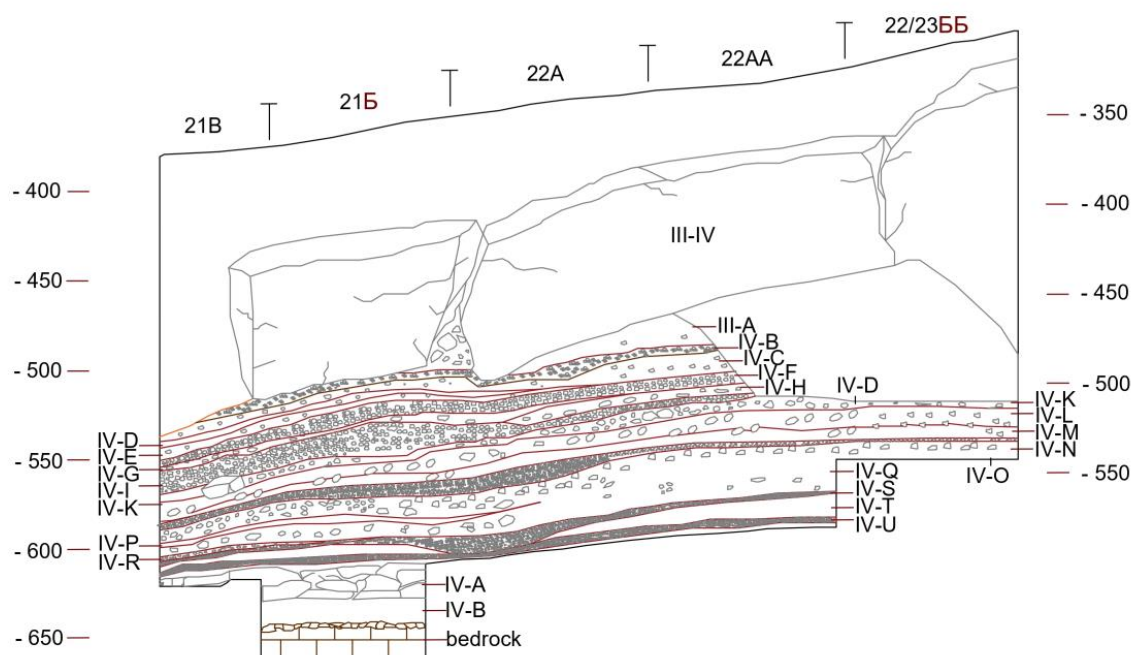


Figure 5. Chokurcha I stratigraphical section for Unit-V, excavated from 1996 to 2000. Adapted from Chabai, (2004b), p. 347. Created in AutoCad.

Buran Kaya III

Buran Kaya III is located in a narrow valley in the second mountain range as a rock shelter. This site has one of the most extensive and well-preserved stratigraphic profiles in the Crimean Peninsula, ranging from the Medieval to the Middle Palaeolithic period. Originally the site was documented as having 19 cultural layers. However, after the 2009 excavation, the team focused on nine archaeological layers (Figure 6), containing the Middle to Upper Palaeolithic (Péan et al., 2013). Layer 6.1 is particularly interesting, with 162 *Homo sapiens* remains found without burial evidence. The individuals were identified as being juveniles or sub-adults (Prat et al., 2011). Within the Palaeolithic layers (B-C), two different types of technocomplex have been found. Layer B shows evidence of bifacial and unifacial points, which have been previously attributed to Kiik-Koba for the Crimean Micoquian (Demidenko, 2004). This indicates this layer was associated with Neanderthals, due to the lithic assemblage found. In layer C, a Szeletian assemblage was found, comprising of bifacial foliate points, endscrapers and snapped bone tools (Monigal, 2004; Uthmeier, 2012). This technocomplex has been previously assigned to the Upper Palaeolithic (Monigal, 2004). This raises questions about the stratigraphy similar to what we see at Siuren I, with a complex stratigraphic profile, in relation to the lithic assemblages. This could be interpreted as coexistence between Neanderthals and *Homo sapiens*. However, this is complicated due to the Szeletian technocomplex being classed as a transitional industry (Adams, 2009; Uthmeier, 2012). No human remains have been found within these layers, so no solid conclusion is possible at this time.

Overall, the radiometric dates for Buran Kaya III are the most extensive in comparison to other Palaeolithic sites within Crimea (Table 4). However, few samples were pre-treated with more modern protocols such as ultrafiltration and XAD-2. The dates range from 32,200 to 36,700 BP, which are all younger than the oldest date (OxA-36921) within layer B, which was treated with ultrafiltration. This may indicate that further radiometric work will result in older dates especially within the Palaeolithic archaeological layers.

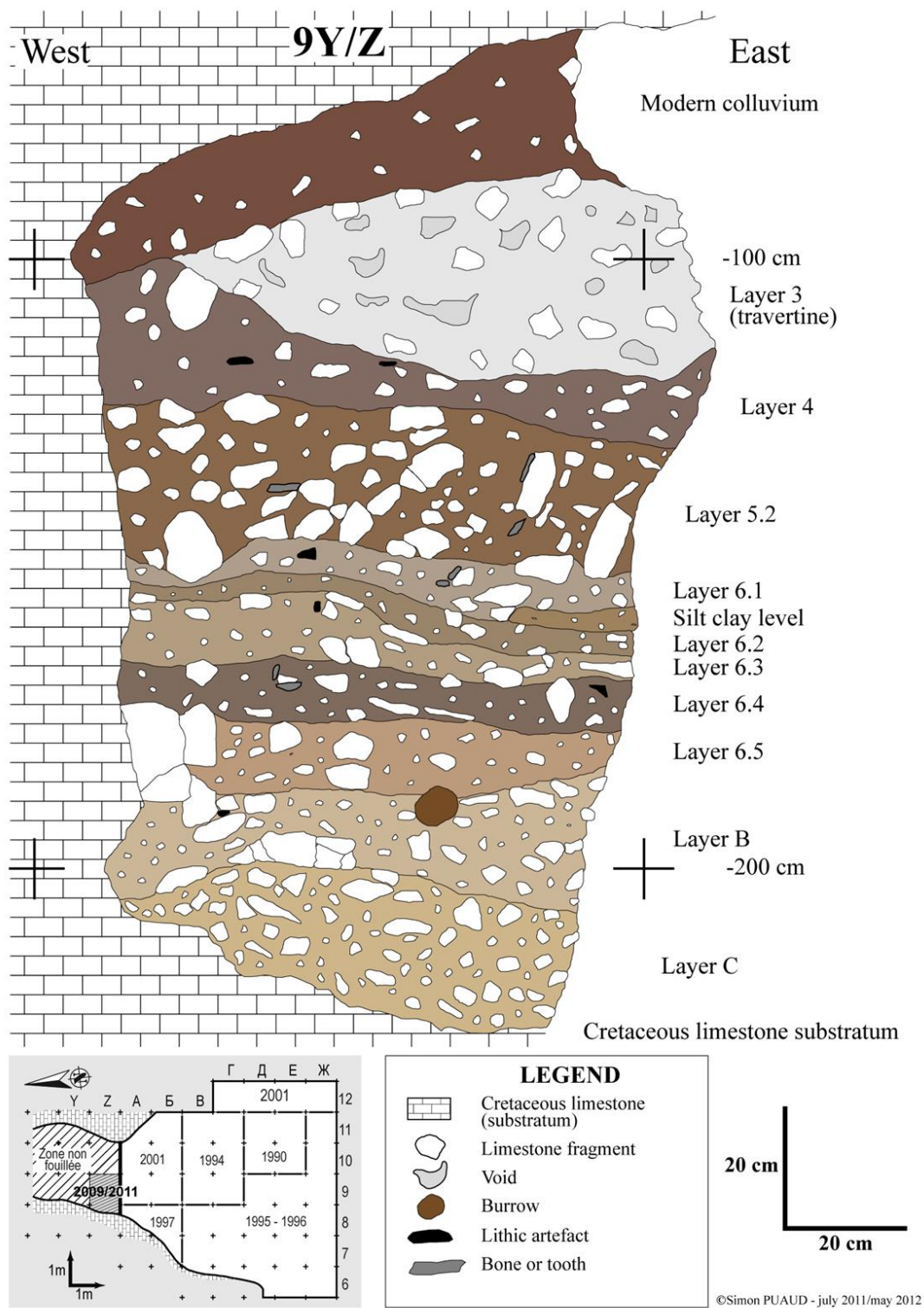


Figure. 6 Stratigraphic sections of Buran-Kaya III and plan of the excavations. From Péan et al., (2013) with permission.

Table 4 - Radiocarbon dates from Buran Kaya III, obtained using various methods (Longin collagen and ultrafiltration) from Hedges et al., (1996), Pettitt, (1998), Higham et al., (2006) and Péan et al., (2013). Some dates are in groups (bold line and date in underscore). These groups represent a single bone which was dated using different methods. AI is the abbreviation of ion-exchanged gelatine.

Lab No.	Material	Layer	Industry	Pre-treatment method	Radiocarbon Age BP
OxA-6672	Bone	C	Szeletian	AI	32,350 ± 700 BP
OxA-6868	Bone	C	Szeletian	AI	36,700 ± 1500 BP
OxA-6869	Bone	C	Szeletian	AI	32,200 ± 650 BP
<u>GrA-47319</u>	Bone	B	Micoquian	Longin	35,590 + 290/-270 BP
GifA-11218/SacA-25135	Bone	B	Micoquian	Ninhydrin	36,500 ± 1200 BP
OxA-36921	Bone	B	Micoquian	Ultrafiltration	37,700 ± 900 BP
OxA-6673	Bone	B	Micoquian	AMS	38,840 ± 260 BP
OxA-6674	Bone	B	Micoquian	AI	28,520 ± 460
OxA-6990	Bone	Horizon 20	Aurignacian	AI	34,400 ± 1200 BP
<u>GrA-47318</u>	Bone	6-5	Aurignacian	Longin	32,800 + 230/-210 BP
GifA-11217/SacA-25134	Bone	6-5	Aurignacian	Ninhydrin	35,900 ± 1100 BP
OxA-4128	Bone	6-5	Aurignacian	AI	28,700 ± 620 BP
<u>GrA-48399</u>	Bone	6-4	Aurignacian	Longin	31,250 +2450/-1880 BP
GifA-11220/SacA-25137	Bone	6-4	Aurignacian	Ninhydrin	33,350 ± 830 BP
OxA-13302	Human bone	6-4	Aurignacian	Ultrafiltration	32,790 ± 280 BP
OxA-4127	Bone	6-4	Aurignacian	AI	11,952 ± 130
OxA-4126	Bone	6-3	Aurignacian	AI	11,900 ± 150 BP
<u>GrA-40485</u>	Bone	6-3	Aurignacian	Longin	34,050 + 260/ -240 BP
GifA-80181/SacA-12260	Bone	6-3	Aurignacian	Ninhydrin	34,910 ± 950 BP
GrA-53939	Bone	6-3	Aurignacian	Longin	29,040 + 180 /-170
GifaA-11221/SayA-25138	Bone	6-3	Aurignacian	Ninhydrin	32,740 ± 780
GrA-50460	Bone	6-2	Gravettian	Longin	29,440 ± 190 BP
GrA-50457	Bone	6-2	Gravettian	Longin	32,450 ± 250 BP
OxA-6882	Bone	6-2	Gravettian	AI	30,740 ± 460 BP
<u>GrA-53942</u>	Bone	6-1	Gravettian	Longin	29,640 ± 170 BP
OxA-25669	Bone	6-1	Gravettian	Ultrafiltration	32,200 ± 450 BP
GifA-10021/SacA-19018	Bone	6-1	Gravettian	Ninhydrin	31,320 ± 820 BP
GrA-37938	Human bone	6-1	Gravettian	Longin	31,900 + 240/-220 BP
GifA-11216/SacA-25133	Bone	6-1	Gravettian	Ninhydrin	31,530 ± 670

Siuren I

Siuren I is a rock shelter situated within the second range of the Crimean Mountains (Demidenko, 2014). The site features a stratigraphic sequence consisting of four distinct undisturbed occupational units, divided by sterile rock fall sediments. Previous research indicates that the site was utilised for various activities, including tool production, butchery, and consumption (Massé & Patou-Mathus., 2009). A human tooth has been found in Unit G at Siuren I, dating to 30-28 ka BP, which also indicates this sample may be contaminated (Prat et al., 2011).

The stratigraphy of Siuren I (Figure 7) comprises three distinct archaeological units which have been separated by sterile rock fall sediments. In all archaeological units F, G, and H, the Aurignacian technocomplex has been found, indicating the presence of *Homo sapiens*. However, within units G and H, evidence of Micoquian lithic assemblages have been found, indicating a Neanderthal presence (Chabai, 2005; Demidenko & Otte, 2001).

Overall, the radiocarbon dates (Table 5) for all units are significantly too young for the Aurignacian technocomplex which is present within F, G and H. This can be especially seen within Unit F, suggesting that the Aurignacian was present between 31,000 and 35,000 cal BP. However, this appears unusually late in the broader European context, where evidence indicates that the Aurignacian tradition was active between approximately 43,000 and 35,000 years ago (Chu & Richter, 2020). The presence of both Upper and Middle Palaeolithic artefacts, specifically Aurignacian and Crimean Micoquian (CM) assemblages within the same archaeological unit suggests the potential co-existence of *Homo sapiens* and Neanderthals. One interpretation is that Neanderthals may have periodically visited the site during a time when derived *Homo sapiens* were already widespread across Europe, but not yet permanently settled in the Crimean Peninsula (Demidenko et al., 2012a, 2012b). Alternatively, this overlap may reflect more extensive interactions between Neanderthals and *Homo sapiens* groups (Bataille et al., 2012). Although, post-depositional processes may have been occurring, such as localised flooding and cryoturbation (Demidenko, 2012).

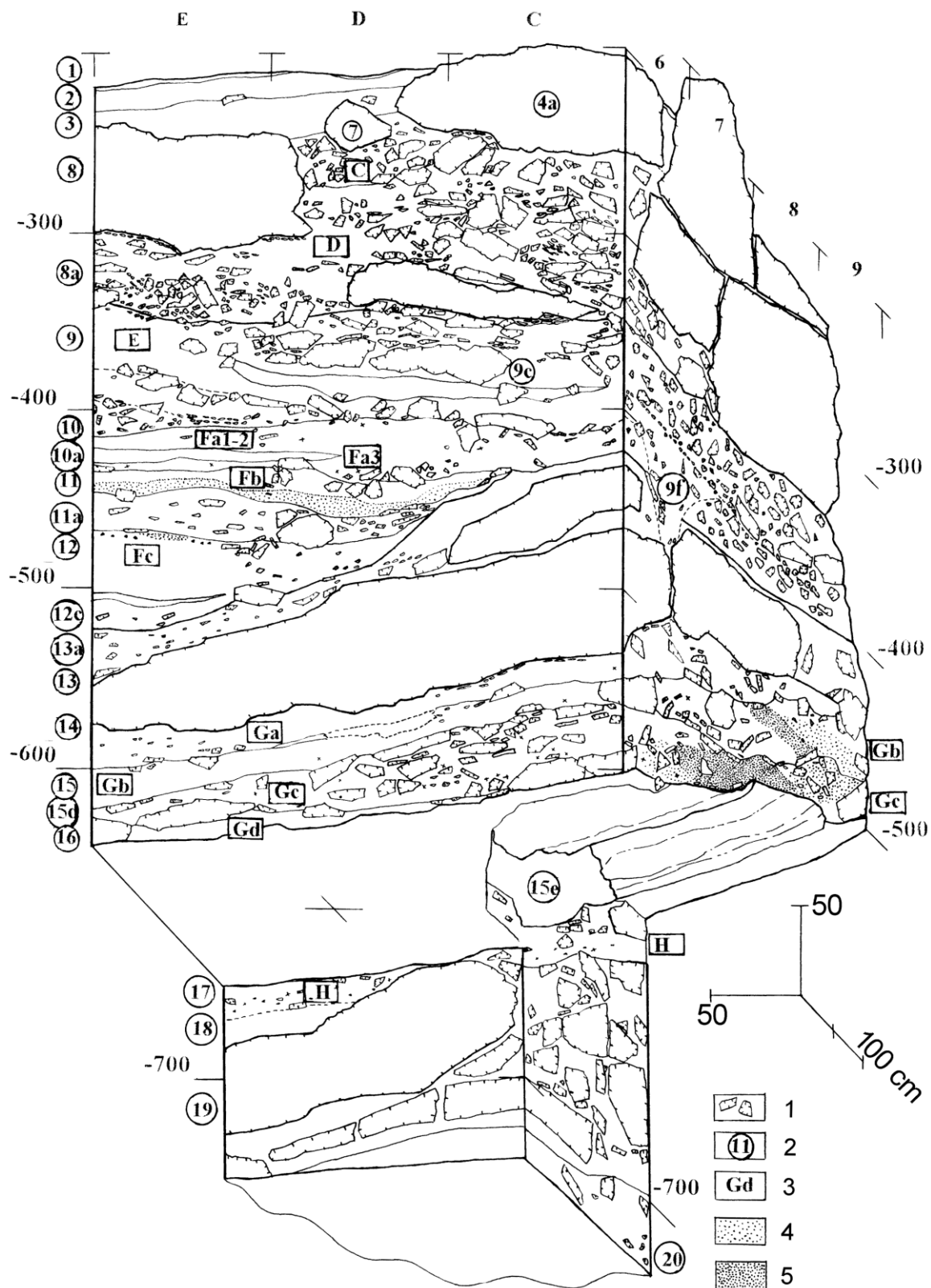


Figure. 7 Siuren 1. Stratigraphy of the site. Profiles II & IV. From Chabai (2005).

Table 5 - Previous radiocarbon dates obtained from levels H, G and F at the site of Siuren I (Demidenko & Otte, 2001; Demidenko & Noiret, 2012). The dates are on ungulate bones. AG is the abbreviation for unfiltered gelatine and AI for ion-exchanged gelatine. Table modified from Pigott et al., (2024).

Lab No.	Material	Unit	Industry	Pre-treatment method	Radiocarbon Age BP
OxA-8249	Bone	H	Aurignacian/Micoquian	AG	28,200 ± 440 BP
GrA-46553	Bone	H	Aurignacian/Micoquian		22,040 ± 120 BP
Beta-260924	Bone	H	Aurignacian/Micoquian		30,490 ± 220 BP
OxA-5154	Bone	Ga	Aurignacian/Micoquian	AI	28,450 ± 600 BP
Lv-2132	Charcoal	Ga	Aurignacian/Micoquian		250 ± 60 BP
Beta-260919	Bone	Gb1	Aurignacian/Micoquian		28,070 ± 190 BP
Beta-293363	Bone	Gb2	Aurignacian/Micoquian		13,020 ± 70 BP
Beta-293361	Bone	Gb2	Aurignacian/Micoquian		19,680 ± 100 BP
Beta-293362	Bone	Gb2	Aurignacian/Micoquian		22,220 ± 120 BP
Lv-2131	Charcoal	Fb2	Aurignacian		10,520 ± 150 BP
OxA-5155	Bone	Fb2	Aurignacian	AI	29,950 ± 700 BP
Beta-293364	Bone	Fb2	Aurignacian		29,540 ± 200 BP
GrA-46552	Bone	Fb2	Aurignacian		30,910 ± 240 BP

Zaskalnaya V

The rock shelter site of Zaskalnaya V is situated within the lower level of a limestone cliff of the Krasnaya Balka. The site was excavated from the debris of the reconstruction of the site downslope to the actual rock shelter. The stratigraphy consists of 23 lithological layers and 87 archaeological levels, which were determined in the most recent excavation in 2012-2013 (Chabai and Uthmeier, 2017). Y. Kolosov labelled the archaeological levels into units, I to VII (Figure 8) enabling a more accessible comparison with older data. Across units I-VII, a dominance of scrapers has been found, mostly bifacially worked. Additionally, across all units' tools such as points, denticulates, burins and notches were present. The lithic technocomplexes can be characterised as CM, indicating an occupation of Neanderthals at the site. This has been further evidence by a tooth (Unit IV) and fragment of a human skull (units II-III) which have been characterised as belonging to Neanderthals (Danilova, 1979a, 1979b; Kolosov, 1983; Stepanchuk, 2022). Both Zaskalnaya V and Zaskalnaya VI also have evidence of modified ochre being used symbolically throughout the stratigraphic contexts, indicating cognitive sophistication of the Neanderthals residing in the region (d'Errico et al., 2025).

Units I to IV have been defined as Micoquian through the lithic technocomplex assemblage found during excavation. However, some dates seem not to be completely reliable (Table 6). Unit I has a very young date of approximately 30,000 ka BP for Micoquian industry which seems unlikely as we see at Siuren I. Unit II has date ranges of approximately 24,000 to 41,000

kaBP which seems a wide range within one unit in this stratigraphic context. These dates have been undertaken with ESR and radiocarbon dating which may indicate why there is not a consistency with the dates. Unit III and IV are similar in age with dates ranging from approximately 20 ka to >47,000 ka BP. In all units the dates undertaken with ESR and radiocarbon dating are very different. This may indicate possible contamination is present or the samples suffer from low collagen yields.

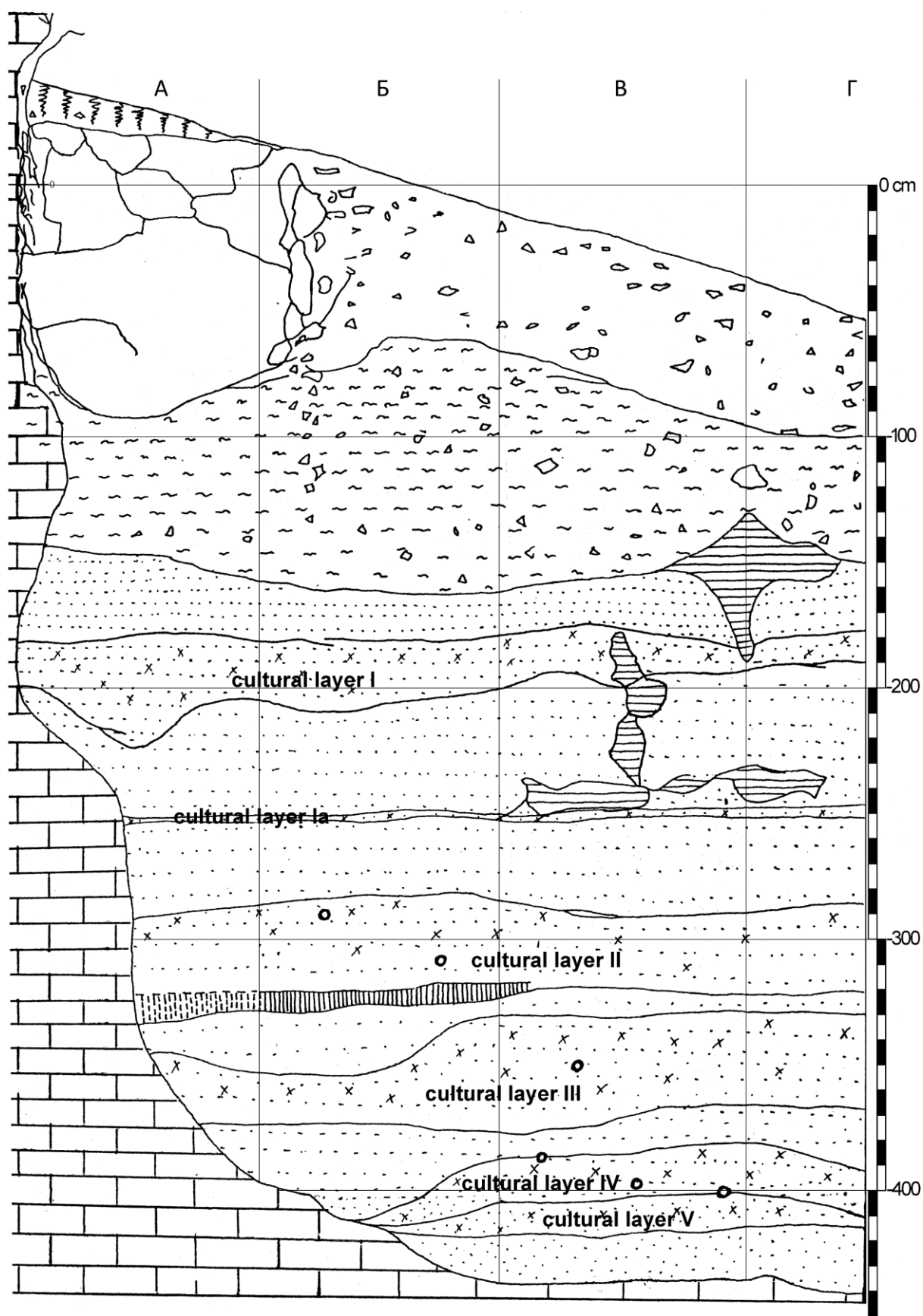


Figure. 8 Zaskalnaya V: drawing of Kolosov's section along square line 17 and 18. From Chabai & Uthmeier, (2017), after Kolosov et al., (1997)

Table 6 - Uncalibrated radiocarbon and ESR dates from Zaskalnaya V (McKinney & Rink, 1996; Kolosov & Stepanchuk, 2002; Chabai & Uthmeier, 2017). ZR is the abbreviation for ABA on charcoal. Table modified from Pigott et al., (2024).

Lab No.	Material	Unit	Industry	Pre-treatment method	Radiocarbon Age BP
Ki-10603	Bone	IV	Micoquian		>47,000 BP
GrA-13916	Burnt bone	IV	Micoquian		>46,000 BP
ESR - EU	Tooth	IV	Micoquian	ESR mean	21,000 ± 2100 BP
ESR - LU	Tooth	IV	Micoquian	ESR mean	32,400 ± 3400 BP
OxA-35526	Charcoal	III/5	Micoquian	ZR	42,700 ± 1100 BP
OxA-35602	Charcoal	III/5	Micoquian	ZR	32,000 ± 800 BP
Ki-10603	Bone	III	Micoquian		39,200 ± 520 BP
ESR -EU	Tooth	III	Micoquian	ESR mean	20,900 ± 1800 BP
ESR - LU	Tooth	III	Micoquian	ESR mean	32,000 ± 2100 BP
OxA-35253	Charcoal	IIA/3	Micoquian	ZR	37,350 ± 500 BP
OxA-35786	Bone	II/1	Micoquian	Ultrafiltration	41,600 ± 1400 BP
Ki-10743	Bone	II	Micoquian		31,600 ± 350 BP
ESR -EU	Tooth	II	Micoquian	ESR mean	24,900 ± 2300 BP
ESR -LU	Tooth	II	Micoquian	ESR mean	41,800 ± 3100 BP
Ki-10891	Bone	I	Micoquian		28,850 ± 400 BP
Ki-10744	Bone	I	Micoquian		30,080 ± 350 BP

Zaskalnaya VI

This site is a multi-layered rock shelter, which is 10-12 m in width located near Zaskalnaya V (Stepanchuk et al., 2017). The stratigraphy consists of at least seven archaeological layers (Figure 9) with the lower level being associated with MIS 5 and the layers I-III with MIS 3 (Stepanchuk et al., 2017). The site consists of Micoquian technocomplex throughout the archaeological layers, along with Neanderthal remains in layer III and IIIa. Pits, heaths and charcoal are also present within this layer, indicating an extensive period of occupation. A dolphin bone was found at the site, despite the coast being 50km away. This could be argued that small-scale migration and resource exploitation was occurring (Stepanchuk et al., 2017).

The radiocarbon dates from the site indicate they may be too young as we have seen in comparison to other sites within the area. All layers at Zaskalnaya VI have been found to have Micoquian technocomplex present. However, some dates seem extremely too young for Micoquian, thus Neanderthal occupations. This can especially be seen in layers I and II (Table 7). There is a lack of material available to date from this site currently, but dating has been undertaken on the available material.

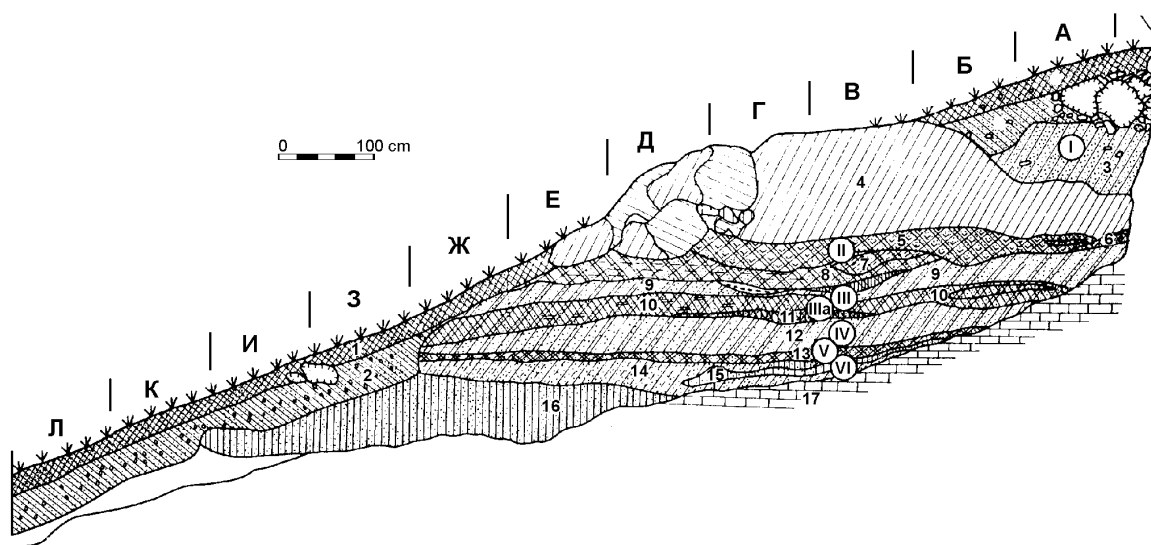


Figure 9 - The section of the Western profile of the excavation area at Zaskalnaya VI, line 29/28 AK. From Chabai, (2004a), after Kolosov, (1986). The Roman numerals indicate the position of cultural layers. The Arabic numerals represent the lithological layers.

Table 7 – Previous uncalibrated radiocarbon dates from Zaskalyana VI (Hedges et al., 1996; Stepanchuk et al., 2004). The two dates that are highlighted in bold are from the same bone. Ultrafiltration was undertaken on OxA-X-2788-9, which produced an older radiocarbon date along with an improved measurement error. AI is the abbreviation for ion-exchanged gelatine. Table modified from Pigott et al., (2024).

Lab No.	Material	Layer	Industry	Pre-treatment method	Radiocarbon Age BP
Ki-10611	Bone	IV	Micoquian		>47,000 BP
Ki-10610	Bone	IIIa	Micoquian		39,400 ± 480 BP
OxA-4773	Bone	IIIa	Micoquian	AI	39,100 ± 1500 BP
OxA-4132	Bone	III	Micoquian	AI	30,706 ± 690 BP
OxA-X-2788-9	Bone	III	Micoquian	Ultrafiltration	32,250 ± 400 BP
Ki-10609	Bone	III	Micoquian		38,200 ± 410 BP
Ki-10894	Bone	III	Micoquian		36,400 ± 450 BP
OxA-4772	Bone	III	Micoquian	AI	35,250 ± 900 BP
Ki-10608	Bone	II	Micoquian		31,100 ± 490 BP
Ki-10893	Bone	II	Micoquian		30,700 ± 450 BP
Ki-10607	Bone	II	Micoquian		30,220 ± 400 BP
OxA-4131	Bone	II	Micoquian	AI	30,110 ± 630 BP
Ki-13376	Bone	I	Micoquian		24,600 ± 170 BP
Ki-13375	Bone	I	Micoquian		25,200 ± 160 BP
Ki-13373	Bone	I	Micoquian		25,700 ± 160 BP
Ki-10606	Bone	I	Micoquian		24,400 ± 480 BP
Ki-10605	Bone	I	Micoquian		22,800 ± 400 BP
Ki-10892	Bone	I	Micoquian		22,500 ± 450 BP

Methodology

Sampling – Radiocarbon dating

All sampling was undertaken on bone samples which have evidence of anthropogenic modifications.

Table 8. This table shows the number of samples from each site which were processed with the ABA, which were anthropogenically modified. The number of bone samples which were successful with ABA pre-treatment and subsequently went through to the next stage of pre-treatment with ultrafiltration and XAD-2. Only samples that had a collagen yield of 3 mg, or more were processed with XAD-2.

*All the Chokurcha I samples were successful in ultrafiltration pre-treatment. However, we decided not to use all the bone samples for XAD-2 pre-treatment due to the age of the first 17 samples being within the upper age limit for radiocarbon dating.

Site	Number of samples which went through ABA and ultrafiltration	Number of samples which had 3mg + yield of collagen, which went through XAD pre-treatment
Kabazi II	26	9
Kabazi V	5	1
Starosel'e	32	8
Chokurcha I	34	17 *
Siuren I	28	2
Buran Kaya III	2	2
Zaskalnaya V	1	1
Zaskalnaya VI	2	2
Total	130	43

Sampling – ZooMS

The faunal remains used for ZooMS analysis were sampled at the National Museum of Natural History, Paris, France and University of Erlangen, Nuremburg, Germany. Samples were taken from unidentified bags of faunal remains from both institutions. A select number of bones were taken from each bag per level available whilst sampling to get a snapshot of the palaeoenvironment at the four archaeological sites. In the future more sampling and analysis should be undertaken to gain a further understanding of the palaeoenvironment and subsistence strategies at the four Palaeolithic archaeological sites. An overview of a selected range of bones used for sampling can be found in Figure 10.

Table 9. Sample selection of the archaeological sites and the Institution they belong too and the amount which were analysed for ZooMS

Site	Typology	Level/Layer	Square	No. of bones	Sampled from institution
Kabazi II	Western Crimean Mousterian (WCM)	II/2	-	25	National Museum of Natural History, Paris
Kabazi II	WCM	II/2-1	-	25	-
Kabazi II	WCM	II/3	-	25	-
Kabazi II	WCM	II/5	-	25	-
Kabazi II	WCM	II/8	-	25	-
Kabazi V	Micoquian	III/5-2	9G	20	Uni. Erlangen - Nuremburg
Kabazi V	Micoquian	III/5-3	9,10G	20	-
Kabazi V	Micoquian	III/5-3	9D	20	-
Chokurcha I	Micoquian	B	B22	20	National Museum of Natural History, Paris
Chokurcha I	Micoquian	B	G22	20	-
Chokurcha I	Micoquian	M	G22	20	-
Chokurcha I	Micoquian	i1	B22	13	-
Siuren I	Micoquian/Aurignacian	Ga	8D	20	National Museum of Natural History, Paris
Siuren I	Micoquian/Aurignacian	Gb2	7D	20	-
Siuren I	Micoquian/Aurignacian	Gb2	8D	20	-
Siuren I	Micoquian/Aurignacian	Gc1	6C	20	-
Siuren I	Micoquian/Aurignacian	Gc1	6D	20	-
Siuren I	Micoquian/Aurignacian	Gc1	8E	20	-
Siuren I	Micoquian/Aurignacian	Gc2	7D	20	-
Siuren I	Micoquian/Aurignacian	Gd	9E	20	-
Siuren I	Micoquian/Aurignacian	H	6E	20	-
Siuren I	Micoquian/Aurignacian	H	7D	20	-
Siuren I	Micoquian/Aurignacian	H	8E	20	-
Total				585	

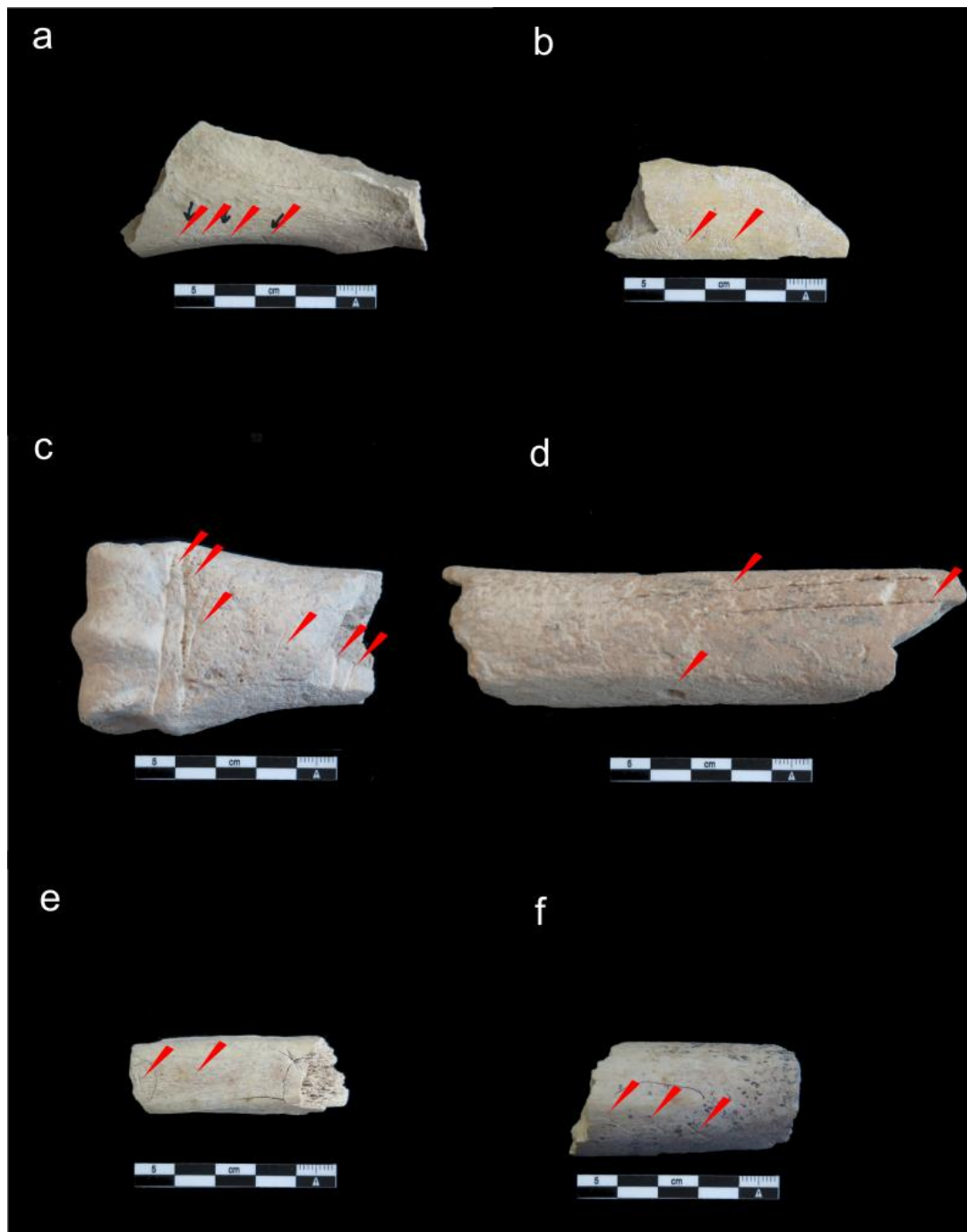


Figure 10. A selection of photos of bones sampled for radiocarbon dating with XAD-2 pre-treatment. One of the bones (a, e and f) has previous pen marker on two bones which was drawn on in the 1990's during excavations. The red arrows indicate anthropogenic modifications on the bone during butchering practices with lithic tool marks from cutting and possible perforation markings (b). a) VIE-1762 from the site of Starosele, Level I, Square I23, showing three distinctive cut marks. b) VIE-1759 from Starosele, Level I, Square H23 showing two distinctive areas of perforation. c) VIE-1542 from Kabazi II, Level II/8, Square M4, showing at least six areas of cut marks. d) VIE-1776 from Kabazi II, Level II/8, Square S0, showing two areas of fracture crack marks and one possible puncture below. e) VIE-1487 from Chokurcha I, Unit IV, Level F, Square G22, showing at least two distinct cut marks. f) VIE-1769 from Chokurcha I, Unit IV, Level S, Square B22, showing three distinct cut marks.

Supplementary for results

Radiocarbon dating

Previous radiocarbon dating was undertaken for seven samples from Kabazi II, with the pre-treatment method of hydroxyproline. These same bones were then dated with the pre-treatment method of XAD-2 and the results were compared. The EW mean values between the two methods can be seen in the Table 10. The EW mean values show that a considerable difference can be seen between the two pre-treatment methods, with only one sample not having a significant difference.

Table 10. Mean errors between the two pre-treatment methods HYP and XAD-2.

VIE Lab No.	T Value (EW mean)	N
VIE-1581	11.43	2(3.84)
VIE-1580	3.2	2(3.84)
VIE-1582	8.17	2(3.84)
VIE-1766	8.57	2(3.84)
VIE-1578	8.04	2(3.84)
VIE-1577	3.91	2(3.84)
VIE-1579	77.13	2(3.84)

Zaskalnaya VI

We performed Bayesian modelling for the new XAD-2 results from Zaskalnaya VI (VIE-1761 and VIE-1760) with the old radiocarbon dates (Figure 11). This resulted in the new XAD-2 (VIE-1761) radiocarbon date being an outlier. However, this is most likely incorrect, due to it being only one sample, against four other old pre-treatment samples. However, with XAD-2 the results are most likely correct with a lower amount of contamination in the sample affecting the radiocarbon date.

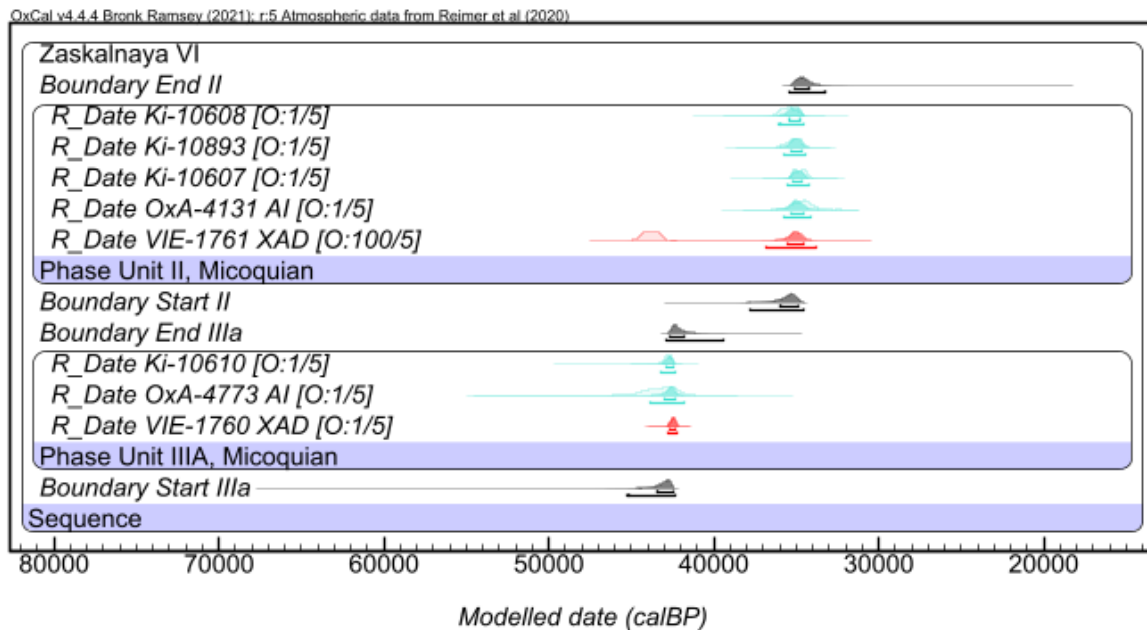


Figure 11. A Bayesian model for the site of Zaskalnaya VI, layer IIIa and II (Micoquian). Pre-treatment methods are AI and unknown pre-treatment methods, but most likely AI/AG (teal). XAD-2 is in red. The General Outlier Model shows a significant outlier for VIE-1761 in Unit II, which most likely presents the most reliable result, with the new pre-treatment method.

ZooMS

The overall ZooMS (Figure 12) results show a predominance of horse in the identified faunal remains at the five sites. This indicates a strong implication of horse hunting and butchering within the region during the occupation of archaeological sites. All sites had a relatively high Zooms success rate, although Siuren I and Kabazi II had the lowest success rate. For Kabazi II, this may be due to the site being open-air, and more susceptible to contamination. Siuren I may have had a relatively low success rate due to the geological formation of the stratigraphy, with a possible leaching effect. In total nine taxa were identified across the four sites. However, it was not possible to differentiate between two canids at Siuren I. These taxa being *Vulpes vulpes* and *Canis lupus*. It was also not possible to differentiate between *Cervus*, *Saiga* or *Gazella* across all sites. Overall, large vertebrates dominate the taxonomic results across the five sites, with *Canis lupus* and *Sus. sp* being the anomaly.

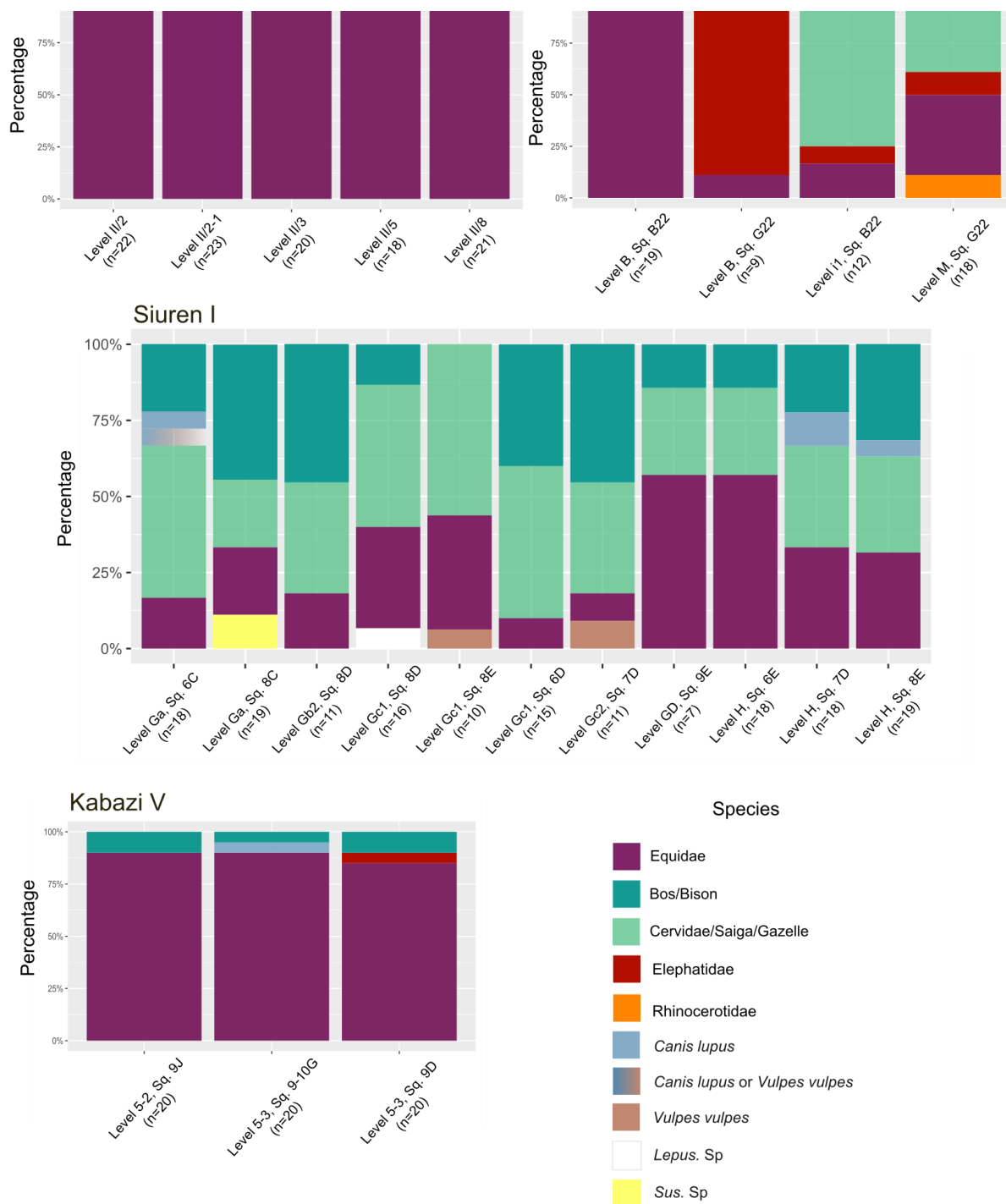


Figure 12. Overall ZooMS results for Kabazi II, Chokurcha I, Siuren I and Kabazi V against their stratigraphic context and percentage. Further details can be found in Appendix 2.

Kabazi II

Overall, 125 bones were analysed, 82.2% were successfully assigned to a species of family taxon. Unfortunately, 17.8% of the bone samples failed, possibly due to the site being open-air. Open-air sites are susceptible to downward leaching of soil organic acids and cross-contamination, which can affect the preservation of biomolecules (Spindler et al., 2021). Among the five layers sampled, Equidae comprised the largest majority, accounting for 95% or more within each layer.

Kabazi V

Out of 60 bones, there was a success rate of 93.3%, in taxonomic assignment. The majority of the assigned faunal remains belong to Equidae, with the second largest being Bovidae and Cervidae across the stratigraphic layers.

Chokurcha I

The site of Chokurcha I also exhibits a high success rate of 94.5% in taxonomic identification. The most common taxon is again Equidae, but also Elephantidae (woolly mammoth) is present across all the levels. Elephantidae is significantly prominent in Level B, square G22. This may possibly indicate that a mammoth was butchered at the site in this specific area (Square). This distribution may reflect a cooler palaeo-environment within a steppe environment. Bovidae and Cervidae are also prominent within levels i and M, suggesting a potentially slightly warmer environment.

Siuren I

Siuren I holds the largest dataset, with a success rate of 75.5% out of 220 bones. Siuren I exhibit the greatest variation within the identified taxon. Bovidae or Cervidae is the most prominent taxon within every layer, with Bovidae being the second most common. There are also two unique species which have been identified at this site, these being *Sus. sp* and *Lepus. sp*. Overall, the taxonomic distribution across all the levels and squares, indicates that the paleoenvironment was relatively stable, with grasslands and an abundance of food sources across layers G and H.

Stable isotope analysis

Stable isotope analysis was undertaken on every sample that underwent radiocarbon dating (Figure 13). This is to ensure a quality control measurement is performed and used for isotopic fractionation. Also, this gives us extra palaeoenvironmental information from each sample that was processed. All samples have relatively expected ranges of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios for their

taxonomic identification. However, one significant difference can be seen from one identification of Rhinocerotidae, which has a considerably different $\delta^{15}\text{N}$ ratio compared to the other Rhinocerotidae. This ZooMS identification is from sample VIE-1489 from the site of Chokurcha I, with a $\delta^{15}\text{N}$ value of 12.89‰ and $\delta^{13}\text{C}$ value of -18.08 ‰. In comparison the other Rhinocerotidae identification (VIE-1757) is from the site of Buran Kaya III, which has a $\delta^{15}\text{N}$ value of 5.91‰ and $\delta^{13}\text{C}$ value of -19.52 ‰. The considerable difference of stable isotope results may be due to the difference in climate. Sample VIE-1489 is from the site Chokurcha I and has a radiocarbon date that is beyond the limit. In comparisons VIE-1757 is dated to $38,017 \pm 422$ uncal BP from Buran Kaya III.

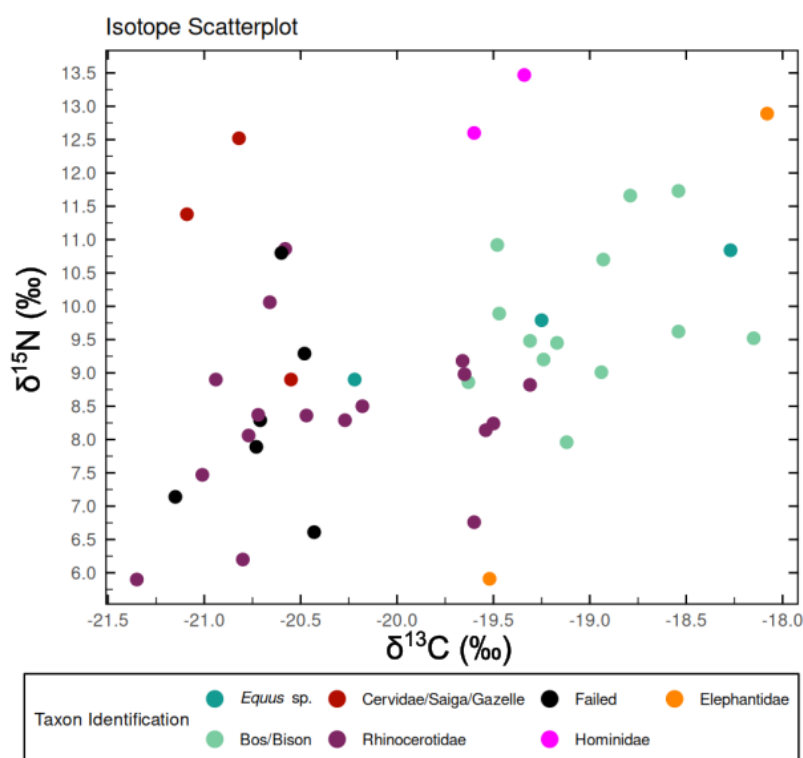


Figure 13. Carbon and nitrogen stable isotope results from all samples that were radiocarbon dated and processed with ZooMS within this paper. The black dots signify successful samples that underwent radiocarbon dating but failed for ZooMS analysis.

Supplementary for Discussion

ZooMS

This study marks the first time that ZooMS analysis has been conducted on fragmented bones from Crimean palaeolithic sites. This demonstrated the method's exceptional utility in identifying previously unidentified faunal remains.

Overall, Kabazi II and Kabazi V exhibit Equidae as the most prominently identified taxon. The prevalence of Equidae across the sites suggests an environment characterised by possible meadow-steppe, with grassland conditions. The conditions are generally Equidae's preference, during the interstadials and stadial conditions (Pawłowska, 2022). Additionally, the second most prominent taxon is Cervidae/Saiga/Gazelle. It is important to note that the differentiation between Cervidae/Saiga and Gazelle was not possible for all the samples. This was due to insufficient peptide peaks being present during spectra analysis. The presence of these family taxa indicates that the environment was predominantly steppe-like.

The co-existence of Bovidae or Cervidae suggests the presence of slightly open-steppe and possibly forest steppe environments (Julien et al., 2012). The abundance of Equidae, Cervidae, and Bovidae, suggests a significant hunting activity, as evidenced by various cut marks observed on a large number of bones from Kabazi II (Patou-Mathis, 2006). One mammoth bone was discovered in Kabazi V, within layer 5-3. This correlates to previous zooarchaeological work undertaken at Kabazi V. However, mammoth bones were previously found within layers III/1A, squares Б, (English being B) and Г (English being G) and layer and III/2, Squares 7B/7Г and 8B/8Г (English being, V/G and 8V/G). The mammoth bones were burnt, suggesting possible use of fuel (Chabai and Veselsky, 2007). However, it is worth noting that the newly identified mammoth bone used in the ZooMS analysis found within layer III/5-3, Sq. 9D, does not appear to be burnt.

Chokurcha I present a drastically different set of results, with the prominence of Elephantidae with Equidae being the second most prominent. This suggests a somewhat open-steppe environment with possibly cold and dry climate conditions (Markova, 2004; Patou-Mathis, 2004). Previously within level B, only 16.1% of the assemblage was identifiable to a taxon, indicating how fragmentary the bones from Level B. This was indicated to be related to high impact hunting on animals. Previously, mammoth remains have been identified within Level B, primarily from teeth, with a possible long bone metaphysis belonging to a juvenile mammoth or rhinoceros (Patou-Mathis, 2004). In comparison, Level I exhibits an abundance of faunal remains previously analysed, with 22.7% being identified to a taxon. Mammoth remains were reported as abundant within level I, along with one juvenile rhinoceros. In Level M, the faunal remains are also abundant with a percentage of 10.4% being previously identified as a species. Mammoth was the most abundant species previously identified from tooth and tusk fragments. Rhinoceros was also identified by two teeth (Patou-Mathis, 2004). Overall, the previous detailed analysis (Patou-Mathis, 2004), on the faunal remains is highly consistent with the ZooMS analysis within this paper. The overall faunal assemblage suggests a colder and drier climate within the palaeo-environmental record, with Levels I and M being previously assigned to a seasonal encampment. In contrast, Level B was evaluated as being shortly occupied, in a

single episode (Patou-Mathis, 2004). During the occupation of the rock shelter by humans, it is evident they used the rock shelter after hunting, for food processing and consumption. However, it is also important to note that the samples previously collected and bagged on site may only represent a very small portion of the entire assemblage. This limitation should be considered when interpreting the results, as the collected samples might not fully capture the diversity and abundance of the faunal remains at the site.

Within this study, Siuren I represents the largest assemblage for ZooMS analysis, with a total of 220 faunal remains. Siuren I exhibits the largest variation in taxa across Levels G and H, compared to the other four sites. Previously, Level G has been evaluated as being rapidly buried, which corresponds with the fragmented faunal remains found (Massé & Patou-Mathis, 2012). Across all the sub-levels of G, the previously identified taxa are very similar, except for Level Ga. No Equidae or Bovidae were previously found in Level Ga, which were identified in this study. Previously, only 12 individual faunal remains were assigned to a species. Within this study, 60 fragmented bones were analysed, with only 6 failing to be assigned to a taxon. Level H has a much higher rate of preservation than Level G. This may possibly be because of the rockfall event between Levels G and H, which may have substantially protected Level H. Overall, the ZooMS spectra results suggest that Siuren I was probably used for short intervals for butchering and skinning activities of animals. However, there is also evidence of carnivores being present in Levels G and H, which may indicate the rock shelter being used for short intervals by carnivorous animals (Massé & Patou-Mathis, 2012). The overall taxonomic results indicate a steppe environment.

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OxCal CQL Code

Figure 2

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  };
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  {
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  };
  R_Date("VIE-1198 UF",40441,769)
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  };
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  };
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    color="#0000ff";
  };
  R_Date("VIE-1539 XAD",34606,181)
  {
    color="#ff0000";
  };
  Line();
  Label("Chokurcha I Unit IV ");
```



```

R_Date("VIE-1442 ABA",47452,1168)
{
  color="#40e0d0";
};
R_Date("VIE-1443 UF",46393,1011)
{
  color="#0000ff";
};
Date("VIE-1895 XAD",(U(calBP(80000),calBP(53419))))
{
  color="#ff0000";
};
Line();
Label("Kabazi V Level II");
R_Date("VIE-1201 ABA",38017,576)
{
  color="#40e0d0";
};
R_Date("VIE-1202 UF",37811,565)
{
  color="#0000ff";
};
R_Date("VIE-1576 XAD",35066,333)
{
  color="#ff0000";
};
};

```

Figure 3

```

Label("Kabazi II");
Label("Phase I");
R_Date("OxA-4135 AI 7/4/II/3/11K/1986",34940,1020)
{
  color="#40e0d0";
};
R_Date("OxA-36274 UF",34850,650)
{
  color="#0000ff";
};
R_F14C("OxA-37786 HYP",0.00114,0.00096)
{
  color="#800080";
};
R_Date("VIE-1582 XAD",44202,760)
{
  color="#ff0000";
};
Line();
Label("Phase II");
R_Date("OxA-4770 AI 8/7/II/1/10L/1986",31550,600)

```

```

{
  color="#40e0d0";
};
R_Date("OxA-36275 UF",33850,550)
{
  color="#0000ff";
};
R_F14C("OxA-38023 HYP",0.00032,0.00183)
{
  color="#800080";
};
R_Date("VIE-1581 XAD",40327,461)
{
  color="#ff0000";
};
Line();
R_Date("OxA-4771 AI 9/7/II/2/11K/1986",35100,850)
{
  color="#40e0d0";
};
R_Date("OxA-36276 UF",37300,900)
{
  color="#0000ff";
};
R_F14C("OxA-38024 HYP",0.00129,0.00183)
{
  color="#800080";
};
R_Date("VIE-1580 XAD",43179,655)
{
  color="#ff0000";
};
Line();
R_Date("OxA-4858 AI 11/7/II/4/8L/1988",35100,850)
{
  color="#40e0d0";
};
R_Date("OxA-36277 UF",34000,600)
{
  R_Date("VIE-1778 XAD",41666,547)
  {
    color="#ff0000";
  };
  color="#0000ff";
};
Date("OxA-38025 HYP",(U(calBP(80000),calBP(43300))))
{
  color="#800080";
};
R_Date("VIE-1766 XAD",39905,447);
Line();
R_Date("OxA-4859 AI 12/7/II/5/6L/1988",33400,1000)
{

```

```

    color="#40e0d0";
};
R_Date("OxA-36278 UF",33350,550)
{
    color="#0000ff";
};
R_F14C("OxA-38026 HYP",0.0001,0.0019)
{
    color="#800080";
};
Line();
color="#ff0000";
R_Date("OxA-36279 UF 13/7/II/6/6L/1988",36600,800)
{
    color="#0000ff";
};
R_F14C("OxA-38027 HYP",0.00039,0.00188)
{
    color="#800080";
};
R_Date("VIE-1777 XAD",43992,740)
{
    color="#ff0000";
};
Line();
R_Date("OxA-36280 UF 14/9/II/8/8L/1988",37800,900)
{
    color="#0000ff";
};
R_F14C("OxA-38028 HYP",0.00088,0.00193)
{
    color="#800080";
};
R_Date("VIE-1579 XAD",32189,179)
{
    color="#ff0000";
};
};

```

Figure 4a

```

Plot()
{
    Sequence()
    {
        Label("Starosele");
        Outlier_Model("General",T(5),U(0,4),"t");
        Boundary("Start 3");
        Phase("Level 3, Micoquian")
    }
}

```

```

Date("VIE-1762",U(calBP(70000),calBP(54515)))
{
  color="#ff0000";
  Outlier("General",0.05);
};
};
Boundary("End 3");
Boundary("Start 1");
Phase("Level 1, Micoquian")
{
  R_Date("VIE-1775 XAD", 41096, 651)
  {
    color="#ff0000";
    Outlier("General",0.05);
  };
  R_Date("VIE-1541 XAD", 43212, 295)
  {
    color="#ff0000";
    Outlier("General",0.05);
  };
  R_Date("VIE-1774 XAD", 47634, 2129)
  {
    color="#ff0000";
    Outlier("General",0.05);
  };
  R_Date("VIE-1758 XAD", 48671, 2719)
  {
    color="#ff0000";
    Outlier("General",0.05);
  };
  R_Date("VIE-1759 XAD", 51138, 1929)
  {
    color="#ff0000";
    Outlier("General",0.05);
  };
  R_Date("OxA-37083 UF", 41300, 1300)

```

```

{
  color="#0000ff";
  Outlier("General",0.05);
};
R_Date("OxA-37084 UF", 43000, 1700)
{
  color="#0000ff";
  Outlier("General",0.05);
};
};
Boundary("End 1");
};
};

```

Figure 4b

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Label("Siuren I");
    Boundary("Start H");
    Phase("Unit H, Aurignacian/Micoquian? ")
    {
      R_Date("VIE-1585 XAD", 32441, 229)
      {
        color="#ff0000";
        Outlier("General",0.05);
      };
      R_Date("VIE-1756 XAD", 30856, 226)
      {
        color="#ff0000";
        Outlier("General",0.05);
      };
      R_Date("OxA-8249 AG", 28200, 440)
      {
        color="#e6e6fa";
        Outlier("General",0.05);
      };
    };
    Boundary("End H");
  };
};

```

Figure 4c

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Outlier("General",0.05);
    Label("Zaskalnaya V");
    Boundary("Start II.I");
    Phase("Unit II/1, Micoquian")
    {
      R_Date("VIE-1575 XAD", 44017, 742)
      {
        color="#ff0000";
        Outlier("General",0.05);
      };
      R_Date("OxA-35786 UF", 41600, 1400)
      {
        color="#0000ff";
        Outlier("General",0.05);
      };
    };
    Boundary("End II.I");
  };
};

```

Figure 5a

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Boundary("Start IIIa");
    Phase("Unit IIIA, Micoquian")
    {
      R_Date("VIE-1760 XAD", 38457, 381)
      {
        color="#ff0000";
        Outlier("General",0.05);
      };
      R_Date("OxA-4773 AI", 39100, 1500)
      {
        color="#40e0d0";
        Outlier("General",0.05);
      };
      R_Date("Ki-10610", 39400, 480)
      {
        color="#40e0d0";
        Outlier("General",0.05);
      };
    };
    Boundary("End IIIa");
    Boundary("Start II");
  };
};

```

```

Phase("Unit II, Micoquian")
{
R_Date("VIE-1761 XAD", 40807, 609)
{
color="ff0000";
Outlier("General",0.05);
};
};
Boundary("End II")
Label("Zaskalnaya VI");
};
};

```

Figure 5b

```

Plot()
{
color="#40e0d0";
Outlier_Model("General",T(5),U(0,4),"t");
Sequence()
{
Boundary("Start C");
Phase("Unit C Szeletian")
{
R_Date("VIE-1757 XAD", 38017, 422)
{
Outlier("General",0.05);
color="ff0000";
};
R_Date("OxA-6672 AI", 32350, 700)
{
Outlier("General",0.05);
color="#40e0d0";
};
R_Date("OxA-6868 AI", 36700, 1500)
{
Outlier("General",0.05);
color="#40e0d0";
};
R_Date("OxA-6869 AI", 32200, 650)
{
Outlier("General",0.05);
};
};
Boundary("Transition C-B");
Phase("Unit B Micoquian")
{
R_Date("VIE-1892 XAD", 33992, 346)
{
Outlier("General", 0.05);
color="ff0000";
};
};
};

```



```

R_Date("VIE-1539 XAD", 34606, 181)
{
  Outlier("General", 0.05);
  color="#ff0000";
};
R_Date("OxA-36921 UF", 37700,900)
{
  Outlier("General", 0.05);
  color="#0000ff";
};
R_Date("GifA-11218/SacA-25135 NIN", 36500, 1200)
{
  Outlier("General", 0.05);
  color="#40e0d0";
};
};
Boundary("End B");
Label("Buran Kaya III");
};
};

```

Figure 5c

```

Plot()
{
  color="#40e0d0";
  Outlier_Model("General",T(5),U(0,4),"t");
  Sequence()
  {
    Boundary("Start C");
    Phase("Unit C Szeletian")
    {
      R_Date("VIE-1757 XAD", 38017, 422)
      {
        Outlier("General",0.05);
        color="#ff0000";
      };
      R_Date("OxA-6672 AI", 32350, 700)
      {
        Outlier("General",0.05);
        color="#40e0d0";
      };
      R_Date("OxA-6868 AI", 36700, 1500)
      {
        Outlier("General",0.05);
        color="#40e0d0";
      };
      R_Date("OxA-6869 AI", 32200, 650)
      {
        Outlier("General",0.05);
      };
    };
  };
};

```

```

Boundary("Transition C-B");
Phase("Unit B Micoquian")
{
  R_Date("VIE-1539 XAD", 34606, 181)
  {
    Outlier("General", 0.05);
    color="#ff0000";
  };
  R_Date("OxA-36921 UF", 37700,900)
  {
    Outlier("General", 0.05);
    color="#0000ff";
  };
  R_Date("GifA-11218/SacA-25135 NIN", 36500, 1200)
  {
    Outlier("General", 0.05);
    color="#40e0d0";
  };
};
Boundary("End B");
Label("Buran Kaya III");
};
};

```

Figure 6a

```

Plot()
{
  Sequence("Date ranges")
  {
    Boundary("Start Micoquian/Mousterian");
    Phase("Micoquian/Mousterian")
    {
      R_Date("ZASK V VIE-1575",44017,742);
      R_Date("ZASK V VIE-1893",45877,1643);
      R_Date("ZASK VI VIE-1761",40807,609);
      R_Date("ZASK VI VIE-1760",38457,381);
      R_Date("BK OxA-36921",37700,700);
      R_Date("BK GifA-11218/SacA-25135",36500,1200);
      R_Date("STAR VIE-1775",41096,651);
      Date(" STAR VIE-1894",U(calBP(80000),calBP(48100)));
      R_Date("STAR VIE-1541",43212,295);
      R_Date("STAR VIE-1774",47634,2129);
      R_Date("STAR VIE-1759",51138,1929);
      R_Date("STAR VIE-1758", 48671,2719);
      Date("STAR VIE-1762 XAD",(U(calBP(80000),calBP(54515))));
      Date("CHOK VIE-1764 XAD",(U(calBP(80000),calBP(55935))));
      Date("CHOK VIE-1488",U(calBP(80000),calBP(52351)));
      Date("CHOK VIE-1489",U(calBP(80000),calBP(47116)));
      Date("CHOK VIE-1768",U(calBP(80000),calBP(56444)));
      Date("CHOK VIE-1491",U(calBP(80000),calBP(51974)));
      R_Date("CHOK VIE-1778",44538,794);
      Date("CHOK VIE-1487",U(calBP(80000),calBP(49076)));
    }
  }
}

```

```

R_Date("CHOK VIE-1772",50858,1860);
Date("CHOK VIE-1763",U(calBP(80000),calBP(57974)));
R_Date("CHOK VIE-1444",49435,1523);
Date("CHOK VIE-1484",U(calBP(80000),calBP(51871)));
Date("CHOK VIE-1485",U(calBP(80000),calBP(49634)));
Date("CHOK VIE-1486",U(calBP(80000),calBP(47133)));
Date("CHOK VIE-1490",U(calBP(80000),calBP(69354)));
Date("CHOK VIE-1765",U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1767",U(calBP(80000),calBP(53115)));
Date("CHOK VIE-1771",U(calBP(80000),calBP(54731)));
Date("CHOK VIE-1769",U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1895",U(calBP(80000),calBP(53419)));
Date("CHOK VIE-1770",U(calBP(80000),calBP(57952)));
Date("CHOK VIE-1773",U(calBP(80000),calBP(51100)));
R_F14C("KAB II OxA-37786 HYP",0.00114,0.00096);
R_F14C("KAB II OxA-38023 HYP",0.00032,0.00183);
R_F14C("KAB II OxA-38024 HYP",0.00129,0.00183);
Date("KAB II OxA-38025",U(calBP(80000),calBP(53419)));
R_F14C("KAB II OxA-38026 HYP",0.0001,0.0019);
R_F14C("KAB II OxA-38028 HYP",0.00088,0.00193);
Date("Micoquian and Mousterian");
};
Boundary("End Start Micoquian/Mousterian");
};
};

```

For Prior boundary model for the Micoquian

```

Plot()
{
  Date(Prior("Micoquian"))
  {
    color="#147D6A";
  };
};

```

Figure 6b

```

Plot()
{
  KDE_Model("Crimean Micoquian", N(0,1), U(0,1))
  {
    R_Date("ZASK V VIE-1575",44017,742);
    R_Date("ZASK V VIE-1893",45877,1643);
    R_Date("ZASK VI VIE-1761",40807,609);
    R_Date("ZASK VI VIE-1760",38457,381);
    R_Date("BK OxA-36921",37700,700);
    R_Date("BK GifA-11218/SacA-25135",36500,1200);
    R_Date("STAR VIE-1775",41096,651);
    Date("VIE-1894",U(calBP(80000),calBP(48100)));
    R_Date("STAR VIE-1541",43212,295);
    R_Date("STAR VIE-1774",47634,2129);
    R_Date("STAR VIE-1759",51138,1929);
  };
};

```

```

R_Date("STAR VIE-1758", 48671,2719);
Date("STAR VIE-1762 XAD", (U(calBP(80000),calBP(54515))));
Date("CHOK VIE-1764 XAD", (U(calBP(80000),calBP(55935))));
  Date("CHOK VIE-1488", U(calBP(80000),calBP(52351)));
  Date("CHOK VIE-1489", U(calBP(80000),calBP(47116)));
  Date("CHOK VIE-1768", U(calBP(80000),calBP(56444)));
  Date("CHOK VIE-1491", U(calBP(80000),calBP(51974)));
  R_Date("CHOK VIE-1778", 44538,794);
  Date("CHOK VIE-1487", U(calBP(80000),calBP(49076)));
  R_Date("CHOK VIE-1772", 50858,1860);
  Date("CHOK VIE-1763", U(calBP(80000),calBP(57974)));
  R_Date("CHOK VIE-1444", 49435,1523);
  Date("CHOK VIE-1484", U(calBP(80000),calBP(51871)));
  Date("CHOK VIE-1485", U(calBP(80000),calBP(49634)));
  Date("CHOK VIE-1486", U(calBP(80000),calBP(47133)));
  Date("CHOK VIE-1490", U(calBP(80000),calBP(69354)));
  Date("CHOK VIE-1765", U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1767", U(calBP(80000),calBP(53115)));
  Date("CHOK VIE-1771", U(calBP(80000),calBP(54731)));
  Date("CHOK VIE-1769", U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1895", U(calBP(80000),calBP(53419)));
  Date("CHOK VIE-1770", U(calBP(80000),calBP(57952)));
Date("CHOK VIE-1773", U(calBP(80000),calBP(51100)));
  R_F14C("KAB II OxA-37786 HYP", 0.00114,0.00096);
  R_F14C("KAB II OxA-38023 HYP", 0.00032,0.00183);
  R_F14C("KAB II OxA-38024 HYP", 0.00129,0.00183);
  Date("KAB II OxA-38025", (U(calBP(80000),calBP(53419))));
  R_F14C("KAB II OxA-38026 HYP", 0.0001,0.0019);
  R_F14C("KAB II OxA-38028 HYP", 0.00088,0.00193);
};
};

```

Figure 6c

```

Plot()
{
  KDE_Model("Crimean Micoquian", N(0,1), U(0,1))
  {
    R_Date("KAB V OxA-X-213445 BB", 30980,220);
    R_Date("KAB V OxA-14726 CHAR", 38780,360);
    R_Date("STAR OxA-37083 UF", 41300, 1300);
    R_Date("STAR OxA-37084 UF", 43000, 1700);
    R_Date("ZASK V OxA-35786 UF", 41600, 1400);
    R_Date("ZASK VI OxA-4773 AI", 39100, 1500);
    R_Date("ZASK VI Ki-10610", 39400, 480);
    R_Date("ZASK VI OxA-4773 AI", 39100, 1500);
    R_Date("ZASK VI OxA-4131 AI", 30110, 630);
    R_Date("ZASK VI Ki-10607", 30220, 400);
    R_Date("ZASK VI Ki-10893", 30700, 450);
    R_Date("ZASK VI Ki-10608", 31100, 490);
    R_Date("BUR III OxA-36921 UF", 37700,900);
    R_Date("BUR III GifA-11218/SacA-25135 NIN", 36500, 1200);
  }
}

```

```

R_Date("BUR III Gifa-47319 LO", 35590,290);
};
};

```

Figure 6d

```

Plot()
{
  KDE_Model("Crimean Micoquian", N(0,1), U(0,1))
  {
    R_Date("KAB V OxA-X-213445 BB",30980,220);
    R_Date("KAB V OxA-14726 CHAR",38780,360);
    R_Date("STAR OxA-37083 UF", 41300, 1300);
    R_Date("STAR OxA-37084 UF", 43000, 1700);
    R_Date("ZASK V OxA-35786 UF", 41600, 1400);
    R_Date("ZASK VI OxA-4773 AI", 39100, 1500);
    R_Date("ZASK VI Ki-10610", 39400, 480);
    R_Date("ZASK VI OxA-4773 AI", 39100, 1500);
    R_Date("ZASK VI OxA-4131 AI", 30110, 630);
    R_Date("ZASK VI Ki-10607", 30220, 400);
    R_Date("ZASK VI Ki-10893", 30700, 450);
    R_Date("ZASK VI Ki-10608", 31100, 490);
    R_Date("BUR III OxA-36921 UF", 37700,900);
    R_Date("BUR III Gifa-11218/SacA-25135 NIN", 36500, 1200);
    R_Date("BUR III Gifa-47319 LO", 35590,290);
    R_Date("ZASK V VIE-1575",44017,742);
    R_Date("ZASK V VIE-1893",45877,1643);
    R_Date("ZASK VI VIE-1761",40807,609);
    R_Date("ZASK VI VIE-1760",38457,381);
    R_Date("BK OxA-36921",37700,700);
    R_Date("BK Gifa-11218/SacA-25135",36500,1200);
    R_Date("STAR VIE-1775",41096,651);
    Date("VIE-1894",U(calBP(80000),calBP(48100)));
    R_Date("STAR VIE-1541",43212,295);
    R_Date("STAR VIE-1774",47634,2129);
    R_Date("STAR VIE-1759",51138,1929);
    R_Date("STAR VIE-1758", 48671,2719);

    Date("STAR VIE-1762 XAD",(U(calBP(80000),calBP(54515))));
    Date("CHOK VIE-1764 XAD",(U(calBP(80000),calBP(55935))));
    Date("CHOK VIE-1488",U(calBP(80000),calBP(52351)));
    Date("CHOK VIE-1489",U(calBP(80000),calBP(47116)));
    Date("CHOK VIE-1768",U(calBP(80000),calBP(56444)));
    Date("CHOK VIE-1491",U(calBP(80000),calBP(51974)));
    R_Date("CHOK VIE-1778",44538,794);
    Date("CHOK VIE-1487",U(calBP(80000),calBP(49076)));
    R_Date("CHOK VIE-1772",50858,1860);
    Date("CHOK VIE-1763",U(calBP(80000),calBP(57974)));
    R_Date("CHOK VIE-1444",49435,1523);
    Date("CHOK VIE-1484",U(calBP(80000),calBP(51871)));
    Date("CHOK VIE-1485",U(calBP(80000),calBP(49634)));
    Date("CHOK VIE-1486",U(calBP(80000),calBP(47133)));
    Date("CHOK VIE-1490",U(calBP(80000),calBP(69354)));
  }
}

```

```

    Date("CHOK VIE-1765",U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1767",U(calBP(80000),calBP(53115)));
    Date("CHOK VIE-1771",U(calBP(80000),calBP(54731)));
    Date("CHOK VIE-1769",U(calBP(80000),calBP(57974)));
Date("CHOK VIE-1895",U(calBP(80000),calBP(53419)));
    Date("CHOK VIE-1770",U(calBP(80000),calBP(57952)));
Date("CHOK VIE-1773",U(calBP(80000),calBP(51100)));
    R_F14C("KAB II OxA-37786 HYP",0.00114,0.00096);
    R_F14C("KAB II OxA-38023 HYP",0.00032,0.00183);
    R_F14C("KAB II OxA-38024 HYP",0.00129,0.00183);
    Date("KAB II OxA-38025",(U(calBP(80000),calBP(53419))));
    R_F14C("KAB II OxA-38026 HYP",0.0001,0.0019);
    R_F14C("KAB II OxA-38028 HYP",0.00088,0.00193);
};
};

```

Supplementary information

OxCal Code

Figure 10

```

Plot()
{
  Sequence()
  {
    Outlier_Model("General",T(5),U(0,4),"t");
    Boundary("Start IIIa");
    Phase("Unit IIIA, Micoquian")
    {
      R_Date("VIE-1760 XAD", 38457, 381)
      {
        color="#ff0000";
        Outlier("General",0.05);
      };
      R_Date("OxA-4773 AI", 39100, 1500)
      {
        color="#40e0d0";
        Outlier("General",0.05);
      };
      R_Date("Ki-10610", 39400, 480)
      {
        color="#40e0d0";
        Outlier("General",0.05);
      };
    };
    Boundary("End IIIa");
    Boundary("Start II");
    Phase("Unit II, Micoquian")
    {
      R_Date("VIE-1761 XAD", 40807, 609)
      {
        color="#ff0000";

```

```

    Outlier("General",0.05);
};
R_Date("OxA-4131 AI", 30110, 630)
{
    color="#40e0d0";
    Outlier("General",0.07);
};
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```


Appendix 1 – New radiocarbon results, along with the taxon identification via ZooMS and stable isotope results

New radiocarbon determinations reported in this paper. Use weight is the amount of bone treated in milligrams. Yield is the amount of extracted collagen and %yield is the percent of collagen as a function of the starting weight. 'Pretreatment' denotes the pretreatment chemistry method applied. UF are samples treated using ultrafiltration of collagen. XAD is dating using XAD-2 resin. ABA is Longin collagen with gelatinisation. %C is the percentage of carbon combustion and usually averages 40-45%. CN is the CN atomic ratio and is acceptable if it ranges between 2.9—3.5. fM refers to the fraction modern carbon. Error terms are at ± 1 sigma. * denote samples dated from the same bone but using different pretreatment chemistries. Stable carbon and nitrogen isotope ratios were calculated in ‰ relative to vPDB and AIR with a mass spectrometric precision of ± 0.2 ‰ and are shown in the Supplementary Information. The collagen used for the stable isotope analysis was performed on the ABA or ultrafiltration fraction for all XAD treated samples.

VIE No.	Site	Context	ZooMS No.	ZooMS ID	Comments	Used weight	Yield	%	Pre-treatment	F14C	Error	14C	Error	D15N	D13C	C%	C/N
VIE-1585	Siuren I	LH/SQ.7e	Z01767.1	Equus sp.		646	5.72	0.9	XAD	0.01762	0.0005	32441	229	5.9	-21.35	63.43	5.14
VIE-1756	Siuren I	Level H	Z01733.1	Bos/Bison		534	3.09	0.6	XAD	0.02147	0.0006	30856	226	10.84	-18.27	43.41	3.26
VIE-1195*	Buran Kaya III	Level B	-	Cervidae/Saiga/Gazelle		984	15.06	1.5	ABA	0.01367	0.00068	34479	410	7.14	-19.6	41.79	2.78
VIE-1996*	Buran Kaya III	Level B	-	Cervidae/Saiga/Gazelle		827	47.44	1.9	ABA	0.00972	0.00064	37225	546	8.15	-18.81	30.08	3.35
VIE-1441*	Buran Kaya III	Level B	-	Cervidae/Saiga/Gazelle		820	15.68	1.9	UF	0.00908	0.00037	37771	332	9.69	-19.35	42.65	3.24
VIE-1539*	Buran Kaya III	Level B	Z01734.2	Cervidae/Saiga/Gazelle		8.23	8.23	100	XAD	0.01346	0.0003	34606	181	9.48	-19.31	33.53	3.25
VIE-1892*	Buran Kaya III	Level B	-	Cervidae/Saiga/Gazelle		760	37.7	5	XAD	0.01453	0.00061	33992	346	From	UF Fract		
VIE-1757	Buran Kaya III	Level C.Sq.D8		Rhinocerotidae		515	8.08	1.6	XAD	0.0088	0.00045	38017	422	5.91	-19.52	65.74	3.25
VIE-1758	Starosele	Level 1.Sq.H23	Z01735.1	Failed		495	18.14	3.7	XAD	0.00234	0.00067	48671	2719	7.14	-21.15	41.11	3.24
VIE-1759	Starosele	Level 1.Sq.H23	Z01737.1	Equus sp.		534	14.61	2.7	XAD	0.00172	0.00037	51138	1929	7.47	-21.01	42.37	3.32
VIE-1199*	Starosele	Level 1.2.Sq.H23	-	Equus sp.		622	8.07	1.3	ABA	0.00408	0.00061	44189	1304	8.99	-20.15	29.74	3.35

VIE-1200*	Starosele	Level 1.2.Sq.H23	-	Equus sp.		722	11.85	1.6	UF	0.00309	0.00049	46440	1389	8.82	-19.31	28.45	3.28
VIE-1540*	Starosele	Level 1.2.Sq.H23	Z01755.1	Equus sp.	530 ugC	3.2	3.5	109.4	XAD	0.01007	0.00051	36933	417	From	VIE-1200		
VIE-1894*	Starosele	Level 1.2.Sq.H23	-	Equus sp.		760	14.36	1.9	XAD	0.00129	0.00061	48100	0	From	VIE-1200		
VIE-1774	Starosele	Level I.Sq.G20	Z01751.1	Failed		540	24.24	4.5	XAD	0.00266	0.00062	47634	2129	7.89	-20.73	42.95	3.31
VIE-1203	Starosele	L1/SQ.I23	-	Hominidae		900	24	2.7	UF	0.0007	0.00061	39858	736	13.47	-19.34	45.28	3.22
VIE-1541	Starosele	L1/SQ.I23	Z00113.1	Hominidae		8.33	8.33	100	XAD	0.00461	0.00017	43212	295	From	VIE-1203		
VIE-1204	Starosele	L1/SQ.I23	-	Hominidae		573	5.89	1	UF	0.00491	0.00061	42713	1070	12.6	-19.6	44.94	3.24
VIE-1775	Starosel'e	L1.Sq.I23	Z00117.1	Cervidae/Saiga/Gazelle		912	7.86	0.9	XAD	0.006	0.00047	41096	651	9.62	-18.54	52.67	3.23
VIE-1762	Starosele	Level 3.Sq.I25	Z01752.1	Failed		521	8	1.5	XAD	0.0004	0.00037	54515	0	6.61	-20.43	57.85	3.19
VIE-1760	Zaskalnaya VI	Level IIIa.Sq.30D	Z01738.1	Failed		461	5.9	1.3	XAD	0.00833	0.00039	38457	381	8.29	-20.71	44.2	3.35
VIE-1761	Zaskalnaya VI	Level II.Sq.18b	Z01739.1	Failed		662	6.07	0.9	XAD	0.00622	0.00045	40807	609	9.29	-20.48	40.82	3.36
VIE-1997*	Zaskalnaya V	Level II.I.Sq.18b	-	Equus sp.		915	6.27	0.7	ABA	0.00773	0.00061	39061	664	8.52	-19.3	34.1	3.26
VIE-1998*	Zaskalnaya V	Level II.I.Sq.18b	-	Equus sp.		860	5.82	0.8	UF	0.00651	0.00059	40441	769	9.32	-18.9	39.43	3.25
VIE-1575*	Zaskalnaya V	Level II.I.Sq.18b	Z01756.1	Equus sp.		672	21.67	3.2	XAD	0.00417	0.00037	44017	742	8.24	-19.5	44.86	3.2
VIE-1893*	Zaskalnaya V	Level II.I.Sq.18b	-	Equus sp.		748	9.12	1.2	XAD	0.00331	0.00061	45877	1643	From	VIE-1998		
VIE-1201*	Kabazi V	Level II.4a.Sq.10D	-	Equus sp.		1027	10.9	1.1	ABA	0.0088	0.00061	38017	576	6.72	-20.45	41.02	3.11
VIE-1202*	Kabazi V	Level II.4a.Sq.10D	-	Equus sp.		572	5.04	0.9	UF	0.00903	0.00061	37811	565	From	UF		
VIE-1576*	Kabazi V	Level II.4a.Sq.10D	Z01746.1	Equus sp.		447	3.5	0.8	XAD	0.01271	0.00052	35066	333	6.76	-19.6	38.4	3.44
VIE-1584	Kabazi II	Level III/I	Z04368.1	Failed		580	3	0.5	XAD	0.01816	0.0006	32199	268	No col	remaining		
VIE-1542	Kabazi II	Level II/8. Sq.M4	Z01733.1	Cervidae/Saiga/Gazelle	253 ugC	3	3	100	XAD	0.0133	0.0004	34702	246	8.86	-19.63	26.96	3.31
VIE-1582	Kabazi II	Level I./3.Sq.11K	Prev assigned	Equus sp.		611	11.55	1.9	XAD	0.00408	0.00037	44202	760	9.18	-19.66	38.51	3.37
VIE-1581	Kabazi II	Level II/1.Sq.10L	Prev assigned	Equus sp.		712	9.96	1.4	XAD	0.0066	0.00037	40327	461	8.14	-19.54	37.49	3.38

VIE-1580	Kabazi II	Level II/2.Sq.11K	Prev assigned	Equus sp.		724	8.29	1.1	XAD	0.00463	0.00037	43179	665	8.29	-20.27	42.11	3.23
VIE-1766	Kabazi II	Level II/4.Sq.6L	Prev assigned	Equus sp.		1090	11.08	1	XAD	0.00696	0.00038	39905	447	10.06	-20.66	44.32	3.34
VIE-1579	Kabazi II	Level II/8.Sq.8L	Prev assigned	Equus sp.		540	6.07	1.1	XAD	0.01819	0.0004	32189	179	10.86	-20.58	43.43	3.23
VIE-1578	Kabazi II	Level II/5.Sq.6L	Prev assigned	Equus sp.		462	7.97	1.7	XAD	0.00559	0.00037	41666	547	8.98	-19.65	43.4	3.28
VIE-1577	Kabazi II	Level II/6.Sq.8L	Prev assigned	Equus sp.		497	9.28	1.9	XAD	0.00418	0.00037	43992	740	8.9	-20.94	41.96	3.34
VIE-1776	Kabazi II	LII/8.Sq.S0	Z04262.1	Failed		620	8.94	1.4	XAD	0.00391	0.00051	44534	1120	10.8	-20.6	41.11	3.26
VIE-1777	Kabazi II	LII/9.Sq.?	Z04296.1	Equus sp.		715	15.5	2.2	XAD	0.00517	0.00037	42296	595	6.2	-20.8	45.07	3.25
VIE-1763	Chokurcha I	Unit IV.Li.Sq.B22	Z01743.1	Cervidae/Saiga/Gazelle		573	31.16	5.4	XAD	-0.00067	0.00037	>57974	0	9.01	-18.94	48.2	3.16
VIE-1764	Chokurcha I	Unit IV.LB.Sq.G22	Z01744.1	Cervidae/Saiga/Gazelle		618	37.84	6.1	XAD	0.00011	0.00042	>55935	0	9.2	-19.24	53.93	3.06
VIE-1765	Chokurcha I	Unit IV.LM.Sq.B22	Z01745.1	Cervidae/Saiga/Gazelle		452	9.25	2	XAD	-0.0003	0.00037	>57974	0	7.96	-19.12	40.94	3.05
VIE-1484	Chokurcha I	L.I1.SQ.G22	Z04280.1	Equus sp.		675	29.83	4.4	XAD	0.00157	0.00037	51871	0	8.37	-20.72	45.93	3.21
VIE-1485	Chokurcha I	L.I1.SQ.B22	Z04281.1	Cervidae/Saiga/Gazelle		659	31.3	4.7	XAD	0.00207	0.00037	49634	0	11.73	-18.54	46.22	3.23
VIE-1486	Chokurcha I	L.I1.SQ.G22	Z04282.1	Elephantidae		653	27.29	4.2	XAD	0.00283	0.00037	47133	0	12.52	-20.82	45.15	3.2
VIE-1487	Chokurcha I	L.F.SQ.G22	Z04284.1	Elephantidae		680	15.88	2.3	XAD	0.00222	0.00037	49076	0	11.38	-21.09	40.99	3.22
VIE-1488	Chokurcha I	L.B.SQ.B22	Z04285.1	Equus sp.		760	40.52	5.3	XAD	0.00148	0.00037	52351	0	8.5	-20.18	45.61	3.22
VIE-1489	Chokurcha I	L.B.SQ.G21	Z04286.1	Rhinocerotidae		650	41.08	6.3	XAD	0.00284	0.00037	47116	0	12.89	-18.08	43.59	3.19
VIE-1490	Chokurcha I	L.I.SQ.B22	Z04287.1	Cervidae/Saiga/Gazelle		573	35.11	6.1	XAD	0.00018	0.00037	>69354	0	10.7	-18.93	47.84	3.19
VIE-1491	Chokurcha I	L.F.SQ.G22	Z04288.1	Cervidae/Saiga/Gazelle		611	34.4	5.6	XAD	0.00155	0.00041	51974	0	9.89	-19.47	47.34	3.2
VIE-1767	Chokurcha I	LM. Sq. G22	Z04303.1	Cervidae/Saiga/Gazelle		1069	50.69	4.7	XAD	0.00061	0.00037	>53115	0	9.45	-19.17	42.24	3.25
VIE-1442*	Chokurcha I	LF. Sq. G22	-	Cervidae/Saiga/Gazelle		1012	45.69	4.6	ABA	0.00272	0.00037	47452	1168	11.6	-18.69	36.58	3.29
VIE-1443*	Chokurcha I	LF. Sq. G22	-	Cervidae/Saiga/Gazelle		1060	35.22	3.3	UF	0.0031	0.00037	46393	1011	11.66	-18.79	37.23	3.25
VIE-1778*	Chokurcha I	LF. Sq. G22	Z04289.1	Cervidae/Saiga/Gazelle		6096	8.2	0.1	XAD	0.00391	0.00037	44538	794	From	VIE-1443		

VIE-1895*	Chokurcha I	LF. Sq. G22	-	Cervidae/Saiga/Gazelle		748	39.5	5.3	XAD	-0.00041	0.00061	53419	0	From	VIE-1443		
VIE-1444	Chokurcha I	Li1. Sq. G22	Z04298.1	Elephantidae		994	60.89	6.1	XAD	0.00213	0.00037	49435	1523	8.9	-20.55	42.85	3.24
VIE-1768	Chokurcha I	LB. Sq. B22	Z04304.1	Bos/Bison		893	53.5	6	XAD	0.00015	0.00037	>56444	0	9.79	-19.25	44.58	3.24
VIE-1769	Chokurcha I	LS. Sq. B22	Z04305.1	Equus sp.		731	15.11	2.1	XAD	-0.00007	0.00037	>57974	0	8.06	-20.77	42.32	3.24
VIE-1770	Chokurcha I	L2. Sq. B21	Z04306.1	Cervidae/Saiga/Gazelle		862	58.6	6.8	XAD	-0.00062	0.00037	>57952	0	10.92	-19.48	42.04	3.27
VIE-1771	Chokurcha I	LQ. Sq. B21	Z04307.1	Cervidae/Saiga/Gazelle		502	19.99	4	XAD	0.00037	0.00037	>54731	0	9.52	-18.15	43.85	3.26
VIE-1773	Chokurcha I	LS. Sq. B22	Z04309.1	Bos/Bison		574	34.15	5.9	XAD	0.00098	0.00037	>51100	0	8.9	-20.22	43.88	3.26
VIE-1772	Chokurcha I	LF. Sq. B21	Z04308.1	Equus sp.		935	39.25	4.2	XAD	0.00178	0.00037	50858	1860	8.36	-20.47	44.26	3.27

Appendix 2 – Peptide peak markers determinations

Results from ZooMS analysis undertaken within this manuscript from Kabazi V, Chokurcha I, Kabazi II and Siuren I. Also, the peptide markers are included for the ZooMS analysis undertaken on all samples which were radiocarbon dated from

Sub Sample Number	Site	Identifiable	ZooMS ID	No Total Peptide Markers Id	Alpha1 508 P1	Alpha2 978 A	Alpha2 978 +16	Alpha2 484 B	Alpha1 688	Alpha2 502 C	Alpha2 292 P2	Alpha1 220	Alpha2 793 D	Alpha2 454 E	Alpha1 586 F	Alpha1 586 +16	Alpha2 757 +16	Alpha2 757 G	Other Peaks
Z00168.1	Kabazi V	Passed	Equidae	6	1105.6	1882.63		1427.75					2145.12		2883.48		3000.59		
Z00169.1	Kabazi V	Passed	Equidae	8	1105.6	1882.64	1198.6	1427.76		1550.8			2145.15		2883.51		3000.63		
Z00170.1	Kabazi V	Passed	Equidae	7	1105.6	1182.63		1427.76		1550.8			2145.27		2883.93		2999.4		
Z00171.1	Kabazi V	Passed	Equidae	9	1105.6	1182.68	1198.6	1427.79		1550.8	1649.8		2145.22		2883.66		3000.78		
Z00172.1	Kabazi V	Passed	Equidae	8	1105.6	1183.68	1198.6	1427.77		1550.8			2145.26		2883.74		3000.82		
Z00173.1	Kabazi V	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.73		1550.8			2145.15		2883.62		3000.72		
Z00174.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.78		1550.8			2145.18		2883.62		3000.75		
Z00175.1	Kabazi V	Passed	Bos/Bison	8	1105.6		1208.6	1427.76		1580.8	1648.8		2131.19		2853.72			3034.89	
Z00176.1	Kabazi V	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.73		1580.8			2145.16		2883.69		3000.84		
Z00177.1	Kabazi V	Passed	Equidae	7	1105.6	1182.65		1427.74		1550.8			2145.08		2883.4		3000.5		
Z00178.1	Kabazi V	Passed	Equidae	8	1105.6	1183.64	1198.6	1427.75		1550.8			2145.16		2883.59		3000.74		
Z00179.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.78		1550.8			2145.222		2883.68		3000.81		
Z00180.1	Kabazi V	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.73		1550.8			2145.11		2883.47		3000.59		
Z00181.1	Kabazi V	Passed	Equidae	7	1105.6	1182.67	1198.6	1427.82		1550.8			2145.34		2883.98				
Z00182.1	Kabazi V	Passed	Equidae	7	1105.6	1182.65	1198.6	1427.78		1550.8			2145.29		2883.96				
Z00183.1	Kabazi V	Passed	Equidae	7	1105.6	1883.67	1198.6	1427.78		1550.8			2145.19		2883.65				
Z00184.1	Kabazi V	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.74		1550.8			2145.14		2883.56		3000.69		
Z00185.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.78		1550.8			2145.22		2883.69		3000.82		
Z00186.1	Kabazi V	Passed	Equidae	9	1105.6	1182.67	1198.6	1427.79		1550.8	1648.8		2145.2		2883.66		3000.77		
Z00187.1	Kabazi V	Passed	Bos/Bison	7	1105.6	1192.6	1209.71	1427.77		1580.8			2131.15					3034.74	
Z00188.1	Kabazi V	Passed	Equidae	8	1105.6	1183.65	1198.6	1427.77		1550.8			2145.21		2883.77		3000.9		

Z00189.1	Kabazi V	Passed	Equidae	7	1105.6	1182.69		1427.8		1550.8			2145.16		2883.54		3000.59		
Z00190.1	Kabazi V	Passed	Equidae	6	1105.6	1183.64		1427.76		1550.8			2145.16		2883.51				
Z00191.1	Kabazi V	Passed	Equidae	10	1105.6	1182.66	1198.6	1427.78		1550.8	1649.8		2145.2		2883.69	2899.4	3000.81		
Z00192.1	Kabazi V	Passed	Equidae	8	1105.6	1183.66	1198.6	1427.79		1550.8			2145.19		2883.56		3000.64		
Z00193.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.78		1550.8			2145.18		2883.55		3000.68		
Z00194.1	Kabazi V	Passed	Equidae	7	1105.6	1182.63	1198.6	1427.75		1550.8			2145.25		2883.94				
Z00195.1	Kabazi V	Passed	Equidae	9	1105.6	1182.63	1198.6	1427.75		1550.8	1649.8		2145.14		2883.57		3000.65		
Z00196.1	Kabazi V	Passed	Equidae	8	1105.6	1182.69	1198.6	1427.82		1550.8			2145.28		2883.75		3000.87		
Z00197.1	Kabazi V	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.76		1550.8			2145.19		2883.64		3000.81		
Z00198.1	Kabazi V	Passed	Equidae	7	1105.6	1182.65		1427.77		1550.8			2145.18		2883.61		3000.73		
Z00199.1	Kabazi V	Passed	Canidae - <i>Canis lupus</i>	6	1105.6		1226.6	1453.81					2131.24		2853.8	2869.4			
Z00200.1	Kabazi V	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.75		1550.8			2145.2		2883.74		3000.73		
Z00201.1	Kabazi V	Passed	Equidae	7	1105.6	1182.63		1427.74		1550.8			2145.09		2883.41		3000.49		
Z00202.1	Kabazi V	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.74		1550.8			2145.08		2883.37		3000.49		
Z00203.1	Kabazi V	Passed	Bos/Bison	9	1105.6	1192.6	1208.6	1427.76		1580.8	1648.8		2131.17		2853.64			3033.79	
Z00204.1	Kabazi V	Passed	Equidae	8	1105.6	1183.66	1198.6	1427.77		1550.8			2145.16		2883.53		3000.63		
Z00205.1	Kabazi V	Passed	Equidae	10	1105.6	1182.65	1198.6	1427.76		1550.8	1649.8		2145.18		2883.61	2899.4	3000.72		
Z00206.1	Kabazi V	Passed	Equidae	7	1105.6	1182.71	1198.6	1427.83		1550.8			2145.23		2883.65				
Z00207.1	Kabazi V	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.77		1550.8			2145.21		2883.7		3000.82		
Z00208.1	Kabazi V	Passed	Equidae	9	1105.6	1182.61	1198.6	1427.68		1550.8			2145.1		2883.49	2899.4	3000.62		
Z00209.1	Kabazi V	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.76		1550.8			2145.16		2883.56		3000.67		
Z00210.1	Kabazi V	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.76		1550.8			2145.16		2883.54		3000.65		
Z00211.1	Kabazi V	Passed	Bos/Bison	10	1105.6	1192.6	1208.6	1427.75		1580.8	1648.8		2131.12		2853.49	2869.4		3034.59	
Z00212.1	Kabazi V	Passed	Equidae	8	1105.6	1182.67	1198.6	1427.77		1550.8			2145.19		2883.65		3000.79		
Z00213.1	Kabazi V	Passed	Equidae	7	1105.6	1182.67		1427.79		1550.8			2145.21		2883.68		3000.81		
Z00214.1	Kabazi V	Passed	Elephantidae - Mammoth	7	1105.6			1453.72		1579.8			2115.12		2853.4		3015.4	2999.67	
Z00215.1	Kabazi V	Passed	Bos/Bison	10	1105.6	1192.6	1208.69	1427.69		1580.8	1648.8		2131.04		2853.44	2869.4		3034.59	
Z00216.1	Kabazi V	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.76		1550.8			2145.16		2883.57		3000.7		

Z00217.1	Kabazi V	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.73		1550.8	1649.8		2145.08		2883.43				
Z00218.1	Kabazi V	Passed	Equidae	6	1105.6	1182.72		1427.82		1550.8			2145.23		2883.64				
Z00219.1	Kabazi V	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.76		1550.8			2145.16		2883.57		3000.7		
Z00220.1	Kabazi V	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.75		1550.8			2145.12		2883.43		3000.51		
Z00221.1	Kabazi V	Passed	Equidae	10	1105.6	1182.64	1198.6	1427.76		1550.8	1649.8		2145.15		2883.52	2899.4	3000.63		
Z00222.1	Kabazi V	Passed	Equidae	10	1105.6	1182.66	1198.6	1427.78		1550.8	1649.8		2145.16		2883.55	2899.4	3000.59		
Z00223.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.78		1550.8			2145.17		2883.53		3000.65		
Z00224.1	Kabazi V	Passed	Equidae	7	1105.6	1182.67		1427.79		1550.8			2145.21		2883.68		3000.79		
Z00225.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.77		1550.8			2145.18		2883.63		3000.74		
Z00226.1	Kabazi V	Passed	Equidae	8	1105.6	1182.66		1427.78		1550.8			2145.2		2883.64	2899.4	3000.79		
Z00227.1	Kabazi V	Passed	Equidae	9	1105.6	1183.63	1198.6	1427.74		1550.8	1649.8		2145.16		2883.69		3000.82		
Z00228.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.77		1579.8			2115.13		2853.4		3016.54		
Z00229.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.8		1579.8			2115.2						
Z00230.1	Chokurcha I	Passed	Elephantidae - Mammoth	5	1105.6			1453.76		1579.8			2115.11				3016.58		
Z00231.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.72		1579.8			2115.07		2853.4		3016.61		
Z00232.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.76		1579.8			2115.12		2853.4		3016.63		
Z00233.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.75		1579.8			2115.12		2853.4		3016.62		
Z00234.1	Chokurcha I	Passed	Elephantidae - Mammoth	5	1105.6			1453.76					2115.11		2853.4		3016.61		
Z00235.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.77		1579.8			2115.1		2853.4		3016.74		
Z00236.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.77		1579.8			2115.14		2853.4		3016.73		
Z00237.1	Chokurcha I	Passed	Elephantidae - Mammoth	7	1105.6		1161.6	1453.79		1579.8			2115.16		2853.4		3016.75		
Z00238.1	Chokurcha I	Passed	Elephantidae - Mammoth	7	1105.6			1453.74		1579.8			2115.11	2808.4	2853.52		3016.64		
Z00239.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.78					2115.16	2808.4	2853.4		3016.75		
Z00240.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.75					2115.14				3015.83		

Z00241.1	Chokurcha I	Passed	Elephatidae - Mammoth	6	1105.6			1453.8					2115.16	2808.4	2853.4		3016.64		
Z00242.1	Chokurcha I	Passed	Elephatidae - Mammoth	4	1105.6			1453.77					2115.14				3016.67		
Z00243.1	Chokurcha I	Passed	Elephatidae - Mammoth	4	1105.6			1453.7					2115.05				3016.58		
Z00244.1	Chokurcha I	Passed	Elephatidae - Mammoth	4	1105.6			1453.77					2115.14				3016.64		
Z00245.1	Chokurcha I	Passed	Elephatidae - Mammoth	7	1105.6			1453.79		1579.8			2115.15	2808.4	2853.4		3016.65		
Z00246.1	Chokurcha I	Failed		0															
Z00247.1	Chokurcha I	Passed	Elephatidae - Mammoth	6	1105.6			1453.75					2115.12	2808.4	2853.4		3016.73		
Z00248.1	Chokurcha I	Passed	Elephatidae - Mammoth	7	1105.6			1453.78		1579.8			2115.16	2808.4	2853.4		3016.73		
Z00249.1	Chokurcha I	Passed	Rhinocerotidae	8	1105.6	1182.66	1198.6	1453.79		1550.8			2145.19	2869.4	2869.61				
Z00250.1	Chokurcha I	Passed	Saiga/Cervidae/Gazlle	6	1105.6	1180.65		1427.75					2131.12		2883.55			3034.69	
Z00251.1	Chokurcha I	Passed	Equidae	8	1105.6	1182.65		1427.77		1550.8			2145.15	2820.4	2883.4		2999.49		
Z00252.1	Chokurcha I	Passed	Equidae	7	1105.6	1182.6		1453.69		1550.8			2114.21		2883.58		3013.17		
Z00253.1	Chokurcha I	Passed	Equidae	5	1105.6	1182.64	1198.67	1427.68		1550.58									
Z00254.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	6	1105.6	1180.69	1196.7	1427.73		1550.68	1648.8								
Z00255.1	Chokurcha I	Failed		2	1105.6			1453.67											
Z00256.1	Chokurcha I	Passed	Equidae	5	1105.6	1182.74	1199.75	1427.95		1550.8									
Z00257.1	Chokurcha I	Passed	Equidae	7	1105.6	1182.78	1198.82	1428.01		1550.8			2145.03	2820.4					
Z00258.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	5	1105.6	1180.77	1196.68	1427.95		1550.99									
Z00259.1	Chokurcha I	Passed	Equidae	10	1105.6	1182.64	1198.64	1427.76		1550.79	1649.82		2145.2	2821.72	2883.83		3000.99		
Z00260.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	10	1105.6	1180.64	1196.65	1427.73		1550.76	1648.82		2131.09		2883.5		3018.42	3034.52	
Z00261.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	9	1105.6	1180.65	1196.66	1427.76			1648.83		2131.12		2883.5		3018.58	3034.58	

Z00262.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	6	1105.6	1180.6	1196.65	1427.61		1550.59	1648.55								
Z00263.1	Chokurcha I	Failed		3	1105.6			1453.69					2115.45						
Z00264.1	Chokurcha I	Passed	Elephantidae - Mammoth	7	1105.6			1453.71		1580.81			2115.23	2809.67	2853.8	3015.98			
Z00265.1	Chokurcha I	Passed	Equidae	8	1105.6	1182.63	1198.62	1427.67		1551.77			2145.19	2820.62		2999.9			
Z00266.1	Chokurcha I	Passed	Rhinocerotidae	5	1105.6		1198.88	1454		1551.02								2983.76	
Z00267.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	6	1105.6	1180.78	1196.79	1427.98		1550								3017.6	
Z00268.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.94		1579.8			2115.1						
Z00269.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.99		1580.06			2115						
Z00270.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.79					2115.24					3016.03	
Z00271.1	Chokurcha I	Failed		2											2883.59			3000.74	
Z00272.1	Chokurcha I	Failed		2											2883.68			3000.81	
Z00273.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.6			1453.64					2115.11					3000.59	
Z00274.1	Chokurcha I	Passed	Equidae	6	1105.6	1182.66	1199.64	1427.68		1550.8	1649.8								
Z00275.1	Chokurcha I	Failed		2	1105.6			1453.76											
Z00276.1	Chokurcha I	Failed		3	1105.6			1453.92		1579.8									
Z00277.1	Chokurcha I	Passed	Elephantidae - Mammoth	7	1105.6			1453.7		1580.83			2115.81		2853.71			3015.93	2999.92
Z00278.1	Chokurcha I	Failed		3	1105.61			1427.72					2131.01						
Z00279.1	Chokurcha I	Passed	Elephantidae - Mammoth	4	1105.63			1453.69		1579.99			2115.39						
Z00280.1	Chokurcha I	Failed		2	1105.6			1453.98											
Z00281.1	Chokurcha I	Failed		3	1105.6			1454.01					2115.03						
Z00282.1	Chokurcha I	Failed		2				1428					2131.03						

Z00283.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.71		1580.81			2131.03		2853.82		3016.02		
Z00284.1	Chokurcha I	Passed	Elephantidae - Mammoth	6	1105.6			1453.79					2115.16		2853.49		3015.6	2999.6	
Z00285.1	Chokurcha I	Failed		1													3000.64		
Z00286.1	Chokurcha I	Failed		1				1453.69											
Z00287.1	Chokurcha I	Failed		3				1453.72		1580.6			2135.03						
Z00288.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	7	1105.6		1196.6	1427.77		1550.8	1648.8		2131.21		2883.9				
Z00289.1	Chokurcha I	Passed	Bovidae or Cervidae	5	1105.6	1180.65		1427.74					2131.18		2883.87				
Z00290.1	Chokurcha I	Passed	Bovidae or Cervidae	6	1105.63	1180.68	1196.68	1427.94		1550.63	1648.61								
Z00291.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	6	1105.66	1180.79	1196.79	1428		1550.05			2131.02						
Z00292.1	Chokurcha I	Failed		3	1105.6			1453.97										3015.3	
Z00293.1	Chokurcha I	Passed	Bovidae or Cervidae	5	1105.6	1181.83	1196.8	1427.97			1649.09								
Z00294.1	Chokurcha I	Passed	Equidae	7	1105.6	1182.67	1198.6	1427.71		1550.8			2145.1		2883.4				
Z00295.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	9	1105.6	1180.64	1196.65	1427.74		1550.78	1648.85		2131.2		2883.86			3018.9	
Z00296.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	8	1105.6	1181.72	1196.69	1427.7		1550.83	1648.9		2131.18		2883.54				
Z00297.1	Chokurcha I	Passed	Cervidae/Saiga/Gazella	6	1105.6	1180.71	1196.67	1427.7		1550.63	1648.6								
Z00298.1	Chokurcha I	Passed	Elephantidae - Mammoth	5	1105.6			1453.81					2115.26		2853.8	2869.82			
Z00299.1	Chokurcha I	Passed	Equidae	10	1105.6	1182.64	1198.65	1427.75		1550.8	1650.79		2145.8		2883.76	2821.67	3000.92		
Z00300.1	Chokurcha I	Passed	Bovidae or Cervidae	4	1105.6	1180.77	1196.79	1427.96											
Z00301.1	Kabazi II	Passed	Equidae	6	1105.62	1182.66		1427.78					2145.27		2883.91		3000.04		
Z00302.1	Kabazi II	Passed	Equidae	5	1105.68	1182.65	1199.81	1427.73		1551.07									
Z00303.1	Kabazi II	Passed	Equidae	6	1105.66	1182.63		1427.78		1550.99			2145.19		2883.66				
Z00304.1	Kabazi II	Passed	Cervidae/Saiga/Gazella	5	1105.6			1427.98			1648.8		2131.1					3059.4	

Z00305.1	Kabazi II	Passed	Equidae	6	1105.65	1182.74		1427.97		1550.03	1649.05					3000.74			
Z00306.1	Kabazi II	Failed		0															
Z00307.1	Kabazi II	Passed	Equidae	5	1105.6	1182.7		1427.71					2145.1			2899.4			
Z01345.1	Kabazi II	Passed	Equidae	4	1105.6	1182.79		1427.99					2145						
Z01346.1	Kabazi II	Passed	Equidae	6	1105.6	1182.76		1427.99					2145.99		2883.57		3000.7		
Z01347.1	Kabazi II	Passed	Equidae	4	1105.65			1427.81					2145.31		2883.76				
Z01348.1	Kabazi II	Passed	Equidae	7	1105.59	1182.79	1199.61	1428		1550.76			2145.05		2883.74				
Z01349.1	Kabazi II	Passed	Equidae	5	1105.68	1182.78		1427.94		1551.03			2145.02						
Z01350.1	Kabazi II	Failed		0															
Z01351.1	Kabazi II	Passed	Equidae	8	1105.61	1182.65	1199.64	1427.77		1550.8			2145.19		2883.65		3000.76		
Z01352.1	Kabazi II	Failed		0															
Z01353.1	Kabazi II	Failed		2		1182.67		1427.71											
Z01354.1	Kabazi II	Passed	Equidae	4	1105.66	1182.75	1199.76	1427.97											
Z01355.1	Kabazi II	Passed	Equidae	4	1105.66	1182.74		1427.96		1551									
Z01356.1	Kabazi II	Passed	Equidae	5	1105.68	1182.75	1199.79	1427.96		1551.03									
Z01357.1	Kabazi II	Passed	Equidae	7	1105.61	1182.78		1428		1550.81			2145		2883.84		3000.95		
Z01358.1	Kabazi II	Passed	Equidae	7	1105.58	1182.65		1427.79		1550.75			2145.27		2883.84		3000.95		
Z01359.1	Kabazi II	Passed	Equidae	6	1105.6	1182.61	1199.74	1427.74		1550.97			2145.15						
Z01360.1	Kabazi II	Passed	Equidae	5	1105.62	1182.74	1199.65	1427.96		1550.65									
Z01361.1	Kabazi II	Passed	Equidae	4	1105.6	1182.68		1427.7		1550.62									
Z01362.1	Kabazi II	Passed	Equidae	4	1105.6	1182.64		1427.68		1551.01									
Z01363.1	Kabazi II	Failed		0															
Z01364.1	Kabazi II	Failed		2		1182.73		1427.97											
Z01365.1	Kabazi II	Passed	Equidae	4	1105.6	1182.74		1427.96		1551									
Z01366.1	Kabazi II	Passed	Equidae	5	1105.63	1182.72	1199.74	1427.94		1550.96									
Z01367.1	Kabazi II	Passed	Equidae	4	1105.6			1427.7		1550.8	1649.8								
Z01368.1	Kabazi II	Passed	Equidae	5	1105.66	1182.73		1427.98		1551							2999.69		
Z01369.1	Kabazi II	Passed	Equidae	6	1105.68	1182.77	1199.79	1427.99		1551.03			2145.01						
Z01370.1	Kabazi II	Passed	Equidae	5	1105.6			1427.76					2145.1		2883.81		2999.4		

Z01371.1	Kabazi II	Passed	Equidae	4	1105.68	1182.76		1427.98		1551.01								
Z01372.1	Kabazi II	Passed	Equidae	4	1105.6	1182.71		1427.92		1550.94								
Z01373.1	Kabazi II	Failed		0														
Z01374.1	Kabazi II	Passed	Equidae	6	1105.6	1182.62		1427.74		1550.8			2145.15		2883.6			
Z01375.1	Kabazi II	Failed		0														
Z01376.1	Kabazi II	Passed	Equidae	5	1105.6	1182.64		1427.71		1550.65	1648.8							
Z01377.1	Kabazi II	Failed		0														
Z01378.1	Kabazi II	Failed		0														
Z01379.1	Kabazi II	Failed		0														
Z01380.1	Kabazi II	Passed	Equidae	5	1105.65	1182.75	1198.75	1427.96		1550.03								
Z01381.1	Kabazi II	Passed	Equidae	4		1182.64		1427.78		1550.8					2883.52			
Z01382.1	Kabazi II	Passed	Equidae	4	1105.6	1182.52		1427.61							2883.62			
Z01383.1	Kabazi II	Passed	Equidae	6	1105.6	1182.6		1427.73		1550.8			2145.01		2883.22			
Z01384.1	Kabazi II	Passed	Equidae	5	1105.6	1182.62		1427.71					2145.15		2883.16			
Z01385.1	Kabazi II	Passed	Equidae	4	1105.6	1182.64		1427.77					2145.17					
Z01386.1	Kabazi II	Passed	Equidae	5	1105.6	1182.64		1427.79					2145.19		2883.6			
Z01387.1	Kabazi II	Passed	Equidae	8	1105.6	1182.6	1198.6	1427.72		1550.8	1649.8		2145.09		2883.5			
Z01388.1	Kabazi II	Passed	Equidae	9	1105.6	1882.61	1198.6	1427.71		1550.8	1649.8		2145.04		2883.33		3000.78	
Z01389.1	Kabazi II	Passed	Equidae	7	1105.6	1182.62	1198.6	1427.72		1550.8	1649.8				2883.4			
Z01390.1	Kabazi II	Passed	Equidae	9	1105.6	1182.63	1198.6	1427.73		1550.8	1649.8		2145.07		2883.39		2999.4	
Z01391.1	Kabazi II	Passed	Equidae	8	1105.6	1182.83	1198.6	1427.72		1550.8	1649.8		2145.07		2883.39			
Z01392.1	Kabazi II	Passed	Equidae	7	1105.6	1182.6	1198.6	1427.72		1550.8			2145.19		2883.82			
Z01393.1	Kabazi II	Passed	Equidae	7	1105.6	1182.56	1198.6	1427.65		1550.8			2145.07		2883.7			
Z01394.1	Kabazi II	Passed	Equidae	7	1105.6	1883.51		1427.59		1550.8	1649.8		2145.01		2883.58			
Z01395.1	Kabazi II	Passed	Equidae	7	1105.6	1182.67	1198.6	1427.75		1550.8			2145.01		2883.22			
Z01396.1	Kabazi II	Passed	Equidae	6	1105.6	1183.58	1198.6	1427.66		1550.8					2883.09			
Z01397.1	Kabazi II	Failed		0														
Z01398.1	Kabazi II	Passed	Equidae	5	1105.6	1182.63		1427.74					2145.08		2883.57			
Z01399.1	Kabazi II	Passed	Equidae	8	1105.6	1182.61	1198.6	1427.72		1550.8	1649.8		2145.04		2883.35			

Z01400.1	Kabazi II	Passed	Equidae	4		1182.65		1427.76					2145.18		2883.54				
Z01401.1	Kabazi II	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.73		1550.8	1649.8		2145.08		2883.4				
Z01402.1	Kabazi II	Failed		0															
Z01403.1	Kabazi II	Passed	Equidae	8	1105.6	1182.62	1198.6	1427.74		1550.8	1649.8		2146.13		2883.41				
Z01404.1	Kabazi II	Passed	Equidae	5	1105.6	1182.68		1427.8		1550.83					2883.52				
Z01405.1	Kabazi II	Passed	Equidae	7	1105.6	1182.59		1427.66		1550.8	1649.8		2145.09		2883.68				
Z01406.1	Kabazi II	Passed	Equidae	7	1105.6	1182.66	1198.6	1427.74		1550.8			2146.12		2883.55				
Z01407.1	Kabazi II	Passed	Equidae	6	1105.6	1182.64	1198.6	1427.71		1550.8	1649.8								
Z01408.1	Kabazi II	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.77		1550.8	1649.8				2883.54		3000.62		
Z01409.1	Kabazi II	Passed	Equidae	8	1105.6	1182.58	1198.6	1427.66		1550.8	1649.8		2145.1		2883.11				
Z01410.1	Kabazi II	Passed	Equidae	5	1105.6	1182.65		1427.76		1550.8			2145.14						
Z01411.1	Kabazi II	Passed	Equidae	4	1105.6	1182.67		1427.78							2883.59				
Z01412.1	Kabazi II	Passed	Equidae	4	1105.6	1182.66		1427.79		1550.83									
Z01413.1	Kabazi II	Failed		0															
Z01414.1	Kabazi II	Failed		0															
Z01415.1	Kabazi II	Passed	Equidae	9	1105.6	1882.63	1198.6	1427.75		1550.8	1649.8		2145.33		2883.4		3000.89		
Z01416.1	Kabazi II	Passed	Equidae	5	1105.6	1182.7		1427.83					2145.21		2883.67				
Z01417.1	Kabazi II	Failed		0															
Z01418.1	Kabazi II	Passed	Equidae	8	1105.6	1182.51	1198.6	1427.59		1550.8			2145		2883.57		3000.72		
Z01419.1	Kabazi II	Passed	Equidae	7	1105.6	1182.61		1427.7		1550.8			2145.1		2883.18		3000.65		
Z01420.1	Kabazi II	Passed	Equidae	8	1105.6	1182.68	1198.6	1427.78		1550.8			2145.18		2883.58		2999.69		
Z01421.1	Kabazi II	Passed	Equidae	5	1105.6	1882.67		1427.78					2145.14		2883.54				
Z01422.1	Kabazi II	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.76		1550.8			2145.18		2883.59		3000.73		
Z01423.1	Kabazi II	Passed	Equidae	5	1105.6	1182.64		1427.78					2145.24		2883.59				
Z01424.1	Kabazi II	Failed		0															
Z01425.1	Kabazi II	Passed	Equidae	9	1105.6	1182.67	1198.6	1427.77		1550.8	1649.8		2145.14		2883.47		3000.73		
Z01426.1	Kabazi II	Passed	Equidae	5	1105.6	1182.66		1427.79					2145.18		2883.55				
Z01427.1	Kabazi II	Passed	Equidae	5	1105.6	1182.69		1427.83					2145.25		2883.38				
Z01428.1	Kabazi II	Passed	Equidae	4	1105.6	1182.63		1427.76							2884.4				

Z01429.1	Kabazi II	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.76		1550.8	1649.8		2145.12		2883.55				
Z01430.1	Kabazi II	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.79		1550.8	1649.8		2145.17		2883.67				
Z01431.1	Kabazi II	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.76		1550.8	1649.8		2145.19		2883.56				
Z01432.1	Kabazi II	Passed	Equidae	4	1105.6	1182.65		1427.77							2883.53				
Z01433.1	Kabazi II	Passed	Equidae	4	1105.6	1182.65		1427.77							2883.69				
Z01434.1	Kabazi II	Passed	Equidae	6	1105.6	1182.67		1427.79					2145.24		2883.74		3000.73		
Z01435.1	Kabazi II	Passed	Equidae	7	1105.6	1182.66		1427.77		1550.8	1649.8		2145.16		2883.61				
Z01436.1	Kabazi II	Failed		0															
Z01437.1	Kabazi II	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.81		1550.8	1649.8		2145.15		2883.45				
Z01438.1	Kabazi II	Passed	Equidae	5	1105.6	1182.65		1427.77		1550.8			2145.19						
Z01439.1	Kabazi II	Passed	Equidae	8	1105.6	1182.69	1198.6	1427.83		1550.8			2145.24		2883.52		3000.69		
Z01440.1	Kabazi II	Passed	Equidae	8	1105.6	1182.69	1198.6	1427.81		1550.8			2145.19		2883.48		3000.51		
Z01441.1	Kabazi II	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.78		1550.8	1649.8		2145.14		2883.58				
Z01442.1	Kabazi II	Passed	Equidae	8	1105.6	1182.66	1198.6	1427.79		1550.8	1649.8		2145.18		2883.57				
Z01443.1	Kabazi II	Passed	Equidae	7	1105.6	1182.68		1427.79		1550.8	1649.8		2145.17		2883.63				
Z01444.1	Kabazi II	Failed		0															
Z01445.1	Kabazi II	Passed	Equidae	8	1105.6	1182.68		1427.79		1550.8	1649.8		2145.2		2883.62		3000.74		
Z01446.1	Kabazi II	Passed	Equidae	5	1105.6	1182.68		1427.79		1550.8			2145.21						
Z01447.1	Kabazi II	Passed	Equidae	8	1105.6	1182.64		1427.77		1550.8	1649.8		2145.13		2883.39		3000.5		
Z01448.1	Kabazi II	Passed	Equidae	7	1105.6	1182.63	1198.6	1427.76		1550.8			2145.14		2883.58				
Z01449.1	Kabazi II	Passed	Equidae	8	1105.6	1182.71	1198.6	1427.84		1550.8	1649.8		2145.25				2999.5		
Z01450.1	Kabazi II	Passed	Equidae	8	1105.6	1183.63	1198.6	1427.76		1550.8	1649.8		2145.13		2883.41				
Z01451.1	Kabazi II	Failed		0															
Z01452.1	Kabazi II	Failed		0															
Z01453.1	Kabazi II	Passed	Equidae	8	1105.6	1182.65	1198.6	1427.76		1550.8	1649.8		2145.14		2883.14				
Z01454.1	Kabazi II	Passed	Equidae	8	1105.6	1182.63	1198.6	1427.75		1550.8	1649.8		2145.07		2882.57				
Z01455.1	Kabazi II	Passed	Equidae	4	1105.6	1182.63		1427.76		1550.74									
Z01456.1	Kabazi II	Passed	Equidae	9	1105.6	1182.66	1198.6	1427.78		1550.8	1649.8		2145.21		2883.71		3000.8		
Z01457.1	Kabazi II	Passed	Equidae	5	1105.6	1182.66		1427.78					2145.17		2883.69				

Z01458.1	Kabazi II	Passed	Equidae	6	1105.6	1182.65	1198.6	1427.78		1550.8					2883.6				
Z01459.1	Kabazi II	Passed	Equidae	7	1105.6	1182.65	1198.6	1427.78		1550.8			2145.15		2883.4				
Z01460.1	Kabazi II	Passed	Equidae	7	1105.6	1182.65	1198.6	1427.8		1550.8			2145.17		2883.46				
Z01461.1	Kabazi II	Passed	Equidae	5	1105.6	1182.66		1427.8					2145.82		2882.45				
Z01462.1	Kabazi II	Passed	Equidae	8	1105.6	1182.64	1198.6	1427.77		1550.8	1649.8		2145.23		2883.44				
Z01463.1	Siuren I	Passed	Equidae	8	1105.6	1182.67	1198.6	1427.79		1550.8	1649.8		2145.19		2883.6				
Z01464.1	Siuren I	Passed	Cervidae/Saiga/Gazella	10	1105.6		1196.6	1427.71		1550.8	1648.8		2131.07	2792.4	2883.46		2899.4	3018.5	
Z01465.1	Siuren I	Passed	Equidae	8	1105.6	1182.67	1198.6	1427.8		1550.8			2145.25		2883.59		3000.77		
Z01466.1	Siuren I	Passed	Equidae	5	1105.6	1182.63		1427.76		1550.78					2883.52				
Z01467.1	Siuren I	Passed	Cervidae/Saiga/Gazella	5	1105.6	1181.56		1427.75			1648.5		2131.09						
Z01468.1	Siuren I	Passed	<i>Canis lupus</i>	6	1105.6		1227.64	1453.79		1566.79			2131.15		2853.64				
Z01469.1	Siuren I	Passed	Cervidae/Saiga/Gazella	7	1105.6		1196.6	1427.76		1550.8	1648.8		2131.16		2883.59				
Z01470.1	Siuren I	Failed		0															
Z01471.1	Siuren I	Passed	Equidae	6	1105.6	1182.65		1427.78					2145.12		2883.41		3000.36		
Z01472.1	Siuren I	Failed		0															
Z01473.1	Siuren I	Passed	<i>Canis lupus</i>	6	1105.6			1453.78		1566.8			2131.27		2853.56		2999.63		
Z01474.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1180.64		1427.8		1550.8	1648.8		2131.21		2883.64	2899.4		3033.4	
Z01475.1	Siuren I	Passed	Bos/Bison	8	1105.6		1208.6	1427.73		1550.8	1648.8		2131.19		2853.59			3033.4	
Z01476.1	Siuren I	Passed	Bos/Bison	4	1105.6			1427.8					2131.19		2853.55				
Z01477.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.69	1427.78		1580.83			2131.12		2853.65			3034.65	
Z01478.1	Siuren I	Passed	Equidae	6	1105.6	1182.1		1427.79		1550.8			2146.12		2883.4				
Z01479.1	Siuren I	Passed	Bos/Bison	8	1105.6		1208.6	1427.78		1580.8	1648.8		2131.2		2853.62			3034.79	
Z01480.1	Siuren I	Passed	Equidae	5	1105.6	1182.6		1427.7		1550.8					2883.4				
Z01481.1	Siuren I	Passed	Cervus/Saiga/Gazella	5	1105.6	1181.62		1427.78			1648.8		2131.13						
Z01482.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.63		1427.72		1550.74	1648.8		2131.13		2883.65				
Z01483.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.6	1427.74		1580.8	1648.8		2131.16		2853.61				
Z01484.1	Siuren I	Passed	Equidae	7	1105.6	1182.7		1427.82		1550.8			2145.24		2883.67		3000.73		
Z01485.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1181.73		1427.82		1550.8	1648.8		2131.31		2883.68				
Z01486.1	Siuren I	Passed	Bos/Bison	6	1105.6			1427.74		1580.8	1648.8		2131.11		2853.51				

Z01487.1	Siuren I	Passed	Bos/Bison	5	1105.6			1427.8		1550.8			2131.19		2853.55				
Z01488.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.74		1550.8			2131.17						
Z01489.1	Siuren I	Passed	Equidae	5	1105.6	1182.66		1427.79		1550.8			2146.12						
Z01490.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1181.64		1427.76		1550.79	1648.8		2131.15		2883.61				
Z01491.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1181.61	1196.7	1427.71		1550.73	1648.8		2131.11		2883.57	2899.4			
Z01492.1	Siuren I	Passed	Bos/Bison	5	1105.6			1427.75					2131.16	1580.8	2853.59				
Z01493.1	Siuren I	Failed		0															
Z01494.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6	1181.72		1427.74					2131.09						
Z01495.1	Siuren I	Passed	Equidae	5	1105.6	1182.62		1427.74					2146.13		2883.41				
Z01496.1	Siuren I	Passed	Bos/Bison	7	1105.6		1209.72	1427.79		1580.8	1648.8		2131.21		2853.43				
Z01497.1	Siuren I	Passed	<i>Canis lupus</i>	6	1105.6	1227.61		1453.74					2131.11		2853.51	2869.4			
Z01498.1	Siuren I	Passed	Equidae	7	1105.6	1182.6		1427.82		1550.8			2145.25		2883.69		3000.8		
Z01499.1	Siuren I	Passed	Equidae	5	1105.6	1182.66		1427.78		1550.8			2145.19						
Z01500.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1181.72	1196.6	1427.82		1550.83	1648.8		2131.2		2883.59				
Z01501.1	Siuren I	Passed	Equidae	7	1105.6	1182.65		1427.78		1550.8	1648.8		2131.18		2883.64				
Z01502.1	Siuren I	Passed	Bos/Bison	8	1105.6		1208.72	1427.78		1580.8	1648.8		2131.19		2853.66			3034.82	
Z01503.1	Siuren I	Passed	Cervus/Saiga/Gazella	10	1105.6	1181.69	1196.6	1427.77		1550.8	1648.8		2131.18		2883.63	2899.4		3034.78	
Z01504.1	Siuren I	Passed	<i>Canis lupus</i>	7	1105.6		1227.72	1453.85					2131.26		2853.73	2869.4		2999.4	
Z01505.1	Siuren I	Passed	Bos/Bison	7	1105.6		1209.71	1427.77			1648.8		2131.17		2853.58			3034.72	
Z01506.1	Siuren I	Passed	<i>Canis lupus</i>	5	1105.6			1453.82					2131.2		2853.64		3000.76		
Z01507.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.68		1427.75		1550.8	1648.8		2131.17		2883.69			3034.88	
Z01508.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.56	1196.6	1427.78		1550.81	1648.8		2131.19		2883.63				
Z01509.1	Siuren I	Failed	Cervus/Saiga/Gazella	10	1105.6	1181.73	1196.6	1427.87		1550.92	1648.8		2131.3		2883.81	2899.4		3034.98	
Z01510.1	Siuren I	Passed	Bos/Bison	10	1105.6		1208.73	1427.77		1580.8	1648.8		2131.16	2792.4	2853.59	2869.4		3033.76	
Z01511.1	Siuren I	Failed		0															
Z01512.1	Siuren I	Passed	Equidae	8	1105.6	1182.55	1198.6	1427.82		1550.8			2145.2		2883.6		3000.72		
Z01513.1	Siuren I	Passed	Bos/Bison	7	1105.6		1209.72	1427.78			1648.8		2131.17		2853.61			3034.76	
Z01514.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.8					2131.19		2883.62				
Z01515.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1181.73		1427.8		1580.8	1648.8		2131.2		2883.65	2899.4		3034.74	

Z01516.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1181.73		1427.8		1580.8	1648.8		2131.2		2883.65	2899.4		3034.74	
Z01517.1	Siuren I	Passed	Equidae	7	1105.6	1182.65		1427.77		1550.8			2145.21		2883.7		3000.83		
Z01518.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.72		1427.8					2131.22		2883.76			3034.93	
Z01519.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.72	1427.78			1648.8		2131.22		2853.63			3034.84	
Z01520.1	Siuren I	Failed		0															
Z01521.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.59		1427.72		1550.75	1648.8		2131.1		2883.54			3034.67	
Z01522.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.63		1427.78		1550.87	1648.8		2131.18		2883.64			3034.76	
Z01523.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.62		1427.78		1550.78	1648.8		2131.15		2883.58			3034.7	
Z01524.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1180.6	1196.6	1427.74		1550.77	1648.8		2131.12		2883.55			3034.69	
Z01525.1	Siuren I	Passed	<i>Canis lupus</i>	5	1105.6			1453.82					2131.77		2853.4	2869.4			
Z01526.1	Siuren I	Failed		0															
Z01527.1	Siuren I	Passed	Bos/Bison	6	1105.6		1208.6	1427.72		1580.8			2131.12		2883.62				
Z01528.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.58		1427.69					2131.07		2883.56			3034.72	
Z01529.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.63		1427.74		1550.8			2131.13		2883.63				
Z01530.1	Siuren I	Passed	Cervus/Saiga/Gazella	5		1180.66		1427.79					2131.19		2883.62			3034.75	
Z01531.1	Siuren I	Passed	Equidae	4	1105.6	1182.66		1427.74							2884.53				
Z01532.1	Siuren I	Passed	Equidae	4	1105.6			1427.75		1550.73					2884.57				
Z01533.1	Siuren I	Passed	Equidae	5	1105.6	1182.63		1427.76					2145.16		2883.61				
Z01534.1	Siuren I	Failed		0															
Z01535.1	Siuren I	Passed	Bos/Bison	7	1105.6		1209.7	1427.77		1580.8	1648.8		2131.19		2853.69				
Z01536.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.7		1427.8		1550.8	1648.8		2131.21		2883.58			3034.75	
Z01537.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.58	1196.6	1427.72		1550.76			2131.12		2883.62				
Z01538.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1181.64		1427.71		1550.73			2131.12		2883.6			3034.75	
Z01539.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.7	1427.73			1648.8		2131.13		2853.59			3034.78	
Z01540.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1181.56		1427.67		1550.69			2131.1		2883.38			3034.51	
Z01541.1	Siuren I	Passed	<i>Canis lupus</i> or <i>Vulpes vulpes</i>	10	1105.6		1227.6	1453.7		1566.75			2131.08	2820.32	2853.47	2869.46	3000.02		1548.76 a2 889
Z01542.1	Siuren I	Passed	Bos/Bison	7	1105.6		1209.7	1427.76		1580.8	1648.8		2131.15		2853.64				
Z01543.1	Siuren I	Passed	Equidae	6	1105.6	1182.61		1427.72		1550.8			2145.12		2883.6				

Z01544.1	Siuren I	Passed	Cervus/Saiga/Gazella	5	1105.6	1181.57		1427.69		1550.72			2131.06					
Z01545.1	Siuren I	Failed		0														
Z01546.1	Siuren I	Passed	Equidae	5	1105.6	1182.63		1427.76		1550.8				2883.62				
Z01547.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.7		1550.8			2131.1					
Z01548.1	Siuren I	Failed		0														
Z01549.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6			1427.78		1550.8	1648.8		2131.17		2883.57			
Z01550.1	Siuren I	Passed	Equidae	6	1105.6	1882.64		1427.76		1550.8			2145.19		2883.73			
Z01551.1	Siuren I	Passed	Equidae	6	1105.6	1182.6		1427.67		1550.69			2131.06		2883.71			
Z01552.1	Siuren I	Passed	Cervus/Saiga/Gazella	10	1105.6	1181.64	1196.6	1427.74		1550.77	1648.8		2131.16		2883.68	2899.4		3034.81
Z01553.1	Siuren I	Failed		0														
Z01554.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1181.63	1196.6	1427.73		1550.8			2131.15		2883.65			
Z01555.1	Siuren I	Passed	Equidae	5	1105.6	1182.64		1427.75		1550.8					2883.67			
Z01556.1	Siuren I	Passed	Equidae	6	1105.6	1182.61		1427.7		1550.8			2145.09		2883.57			
Z01557.1	Siuren I	Failed		0														
Z01558.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1180.6		1427.74		1550.75	1648.8				2883.52			
Z01559.1	Siuren I	Passed	<i>Vulpes vulpes</i>	8	1105.6	1211.69		1453.73		1566.8			2131.17		2853.63		3000.81	1548.8 - a2 899
Z01560.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.56		1427.77		1550.84	1648.8		2131.73		2884.52			
Z01561.1	Siuren I	Passed	Cervus/Saiga/Gazella	10	1105.6	1180.59	1196.6	1427.72		1550.75	1648.8		2131.12		2883.64	2899.4		3034.79
Z01562.1	Siuren I	Passed	Cervus/Saiga/Gazella	9	1105.6	1181.62	1196.6	1427.73		1550.74	1648.8		2131.13		2883.63	2899.4		
Z01563.1	Siuren I	Passed	<i>Lepus</i> sp.	6	1105.6			1453.74		1566.73			2129.1		2883.67	2899.4		
Z01564.1	Siuren I	Failed	Equidae	5	1105.6	1182.6		1427.68		1550.7					2883.42			
Z01565.1	Siuren I	Passed	Bos/Bison	9	1105.6	1180.58	1208.6	1427.75		1580.8	1648.8		2131.18		2853.4		3018.77	
Z01566.1	Siuren I	Failed		3				1427.75		1550.78					2883.61			
Z01567.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1181.69	1196.65	1427.79		1550.8	1648.8		2131.18		2883.6			
Z01568.1	Siuren I	Passed	Equidae	4	1105.6	1182.6		1427.76		1550.86								
Z01569.1	Siuren I	Failed		0														
Z01570.1	Siuren I	Failed		0														
Z01571.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.62	1196.6	1427.71		1550.8	1648.8			2131.03	2883.4			

Z01572.1	Siuren I	Passed	Cervus/Saiga/Gazella	8	1105.6	1180.63	1196.6	1427.7		1550.8	1648.8			2131.01	2883.39				
Z01573.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.63		1427.74		1550.8				2131.51	2884.71				
Z01574.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.66	1196.6	1427.79		1550.8				2131.54					
Z01575.1	Siuren I	Passed	Bos/Bison	8	1105.6		1208.67	1427.75		1580.84	1648.8			2131.47	2854.63			3034.54	
Z01576.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6		1196.6	1427.76		1550.8	1648.8			2131.19	2883.76				
Z01577.1	Siuren I	Failed	Equidae	2		1182.21								2146.13					
Z01578.1	Siuren I	Failed		0															
Z01579.1	Siuren I	Passed	Equidae	5	1105.6	1182.65		1427.74		1550.8					2884.46				
Z01580.1	Siuren I	Passed	Equidae	4	1105.6	1182.6		1427.7		1550.8									
Z01581.1	Siuren I	Failed		2	1105.6									2132.27					
Z01582.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.61		1427.73		1550.8	1648.8			2131.05	2883.43				
Z01583.1	Siuren I	Failed		0															
Z01584.1	Siuren I	Failed		1				1427.7											
Z01585.1	Siuren I	Failed		0															
Z01586.1	Siuren I	Failed		1				1427.7											
Z01587.1	Siuren I	Failed		0															
Z01588.1	Siuren I	Failed		0															
Z01589.1	Siuren I	Failed		0															
Z01590.1	Siuren I	Failed		2		1180.14								2132.28					
Z01591.1	Siuren I	Passed	Equidae	5	1105.6	1182.63		1427.81		1550.92				2132.03					
Z01592.1	Siuren I	Passed	Bos/Bison	6	1105.6		1209.67	1427.72		1580.8	1648.8				2853.42				
Z01593.1	Siuren I	Failed		0															
Z01594.1	Siuren I	Passed	Cervus/Saiga/Gazella	5	1105.6		1196.6	1427.71		1550.8					2882.35				
Z01595.1	Siuren I	Failed		0															
Z01596.1	Siuren I	Passed	Equidae	4	1105.6	1182.6		1427.7		1550.8									
Z01597.1	Siuren I	Failed		0															
Z01598.1	Siuren I	Passed	Equidae	5	1105.61	1182.64	1199.61	1427.78		1550.83									
Z01599.1	Siuren I	Failed		1										2132.31					
Z01600.1	Siuren I	Passed	Equidae	6	1105.6	1182.63		1427.75		1550.8				2145.16	2883.73				

Z01601.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6	1180.22	1196.24							2132.36					
Z01602.1	Siuren I	Failed		0															
Z01603.1	Siuren I	Passed	Equidae	5	1105.6	1182.6		1427.78		1550.87			2131.98						
Z01604.1	Siuren I	Passed	Bos/Bison	5	1105.6		1209.71	1427.79					2131.48		2854.03				
Z01605.1	Siuren I	Failed		1	1105.6														
Z01606.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6		1196.6	1427.71		1550.8	1648.8				2882.38				
Z01607.1	Siuren I	Passed	Bos/Bison	6	1105.6		1209.68	1427.73		1580.8	1648.8				2853.27				
Z01608.1	Siuren I	Failed		0															
Z01609.1	Siuren I	Failed		0															
Z01610.1	Siuren I	Passed	Bos/Bison	6	1105.6		1208.6	1427.7		1580.8	1648.8		2132.27						
Z01611.1	Siuren I	Failed		0															
Z01612.1	Siuren I	Passed	Bos/Bison	4	1105.6		1208.6	1427.78		1580.8									
Z01613.1	Siuren I	Passed	Cervus/Saiga/Gazella	5	1105.6	1180.03	1196.06	1428.91					2132.24						
Z01614.1	Siuren I	Failed		2	1105.6								2132.19						
Z01615.1	Siuren I	Failed		2									2132.33		2883.42				
Z01616.1	Siuren I	Failed		0															
Z01617.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1180.61	1196.6	1427.76		1550.8	1648.8								
Z01618.1	Siuren I	Failed		2	1105.6	1180.61													
Z01619.1	Siuren I	Failed		2				1453.83		1566.91									
Z01620.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.71	1196.7	1427.77		1550.79	1648.82				2883.12				
Z01621.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.63	1197.68	1427.78		1550.85			2131.09		2883.19				
Z01622.1	Siuren I	Failed		1	1105.6														
Z01623.1	Siuren I	Passed	Equidae	4	1105.6	1182.64		1427.81		1550.88									
Z01624.1	Siuren I	Failed		0															
Z01625.1	Siuren I	Passed	Bos/Bison	6	1105.6	1192.08	1208.12	1428.89					2132.19		2873.44				
Z01626.1	Siuren I	Failed		2	1105.6	1180.19													
Z01627.1	Siuren I	Failed		2	1105.6								2132.37						
Z01628.1	Siuren I	Failed		3	1105.6	1180.18	1196.19												
Z01629.1	Siuren I	Failed		1			1196.2												

Z01630.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1180.71	1196.7	1427.77		1550.79					2883.12				
Z01631.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.63	1197.68	1427.78		1550.85			2131.09		2883.19				
Z01632.1	Siuren I	Failed		3		1180.17	1196.22						2132.3						
Z01633.1	Siuren I	Failed		2	1105.6		1196.6												
Z01634.1	Siuren I	Passed	Bos/Bison	5	1105.6		1208.77	1427.77		1580.8					2853.4				
Z01635.1	Siuren I	Passed	Bos/Bison	6	1105.6	1192.2	1208.27	1427.7		1580.8			2132.31						
Z01636.1	Siuren I	Failed		3	1105.6	1180.09							2132.2						
Z01637.1	Siuren I	Failed		2	1105.6								2131.2						
Z01638.1	Siuren I	Failed		2						1566.95			2132.25						
Z01639.1	Siuren I	Passed	Bos/Bison	4	1105.6	1192.6	1208.6						2131.1						
Z01640.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.56	1196.6	1427.71		1550.78			2131.59		2884.28				
Z01641.1	Siuren I	Passed	Bos/Bison	4	1105.6		1208.6	1427.7		1580.8									
Z01642.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1180.71	1196.7	1427.77		1550.79					2883.12				
Z01643.1	Siuren I	Passed	Bos/Bison	5	1105.6	1196.66	1208.6	1427.75		1550.77									
Z01644.1	Siuren I	Passed	Bos/Bison	6	1105.6		1208.72	1427.76		1580.77			2131.03		2853.13				
Z01645.1	Siuren I	Failed		0															
Z01646.1	Siuren I	Failed		0															
Z01647.1	Siuren I	Failed		3	1105.6		1209.28						2132.34						
Z01648.1	Siuren I	Passed	Cervus/Saiga/Gazella	4		1180.14		1196.16		1551.53			2132.16						
Z01649.1	Siuren I	Failed		2	1105.6								2132.2						
Z01650.1	Siuren I	Failed		2	1105.6								2132.25						
Z01651.1	Siuren I	Failed		2	1105.6		1196.6												
Z01652.1	Siuren I	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.15	1196.17	1427.7		1550.8	1648.8		2132.28						
Z01653.1	Siuren I	Failed		3	1105.6	1180.6							2131.1						
Z01654.1	Siuren I	Passed	Equidae	5	1105.6	1182.65	1198.64	1427.74		1550.73									
Z01655.1	Siuren I	Passed	Equidae	6	1105.6	1182.65	1198.62	1427.75		1550.74					2883.2				
Z01656.1	Siuren I	Failed		3	1105.24	1192.19							2132.24						
Z01657.1	Siuren I	Passed	Bos/Bison	6	1105.6		1209.64	1427.62		1580.71	1648.8				2853.79				
Z01658.3	Siuren I	Passed	<i>Sus domesticus</i>	7	1105.59	1180.68	1197.61	1453.72		1550.73			2131.08		2883.53				

Z01659.1	Siuren I	Failed		0														
Z01660.1	Siuren I	Failed		0														
Z01661.1	Siuren I	Passed	Bos/Bison	5	1105.6		1209.68	1427.76					2132.2		2854.71			
Z01662.1	Siuren I	Failed		0														
Z01663.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.6	1427.75		1580.77	1648.8		2131.1		2853.55			
Z01664.1	Siuren I	Passed	Bos/Bison	5	1105.6		1209.72	1427.78					2132.2		2854.6			
Z01665.1	Siuren I	Failed		0														
Z01666.1	Siuren I	Passed	Bos/Bison	5	1105.6		1209.68	1427.76					2132.2		2854.71			
Z01667.1	Siuren I	Failed		3	1105.6			1427.73		1550.74								
Z01668.1	Siuren I	Failed		2		1196.69		1427.73										
Z01669.1	Siuren I	Failed		0														
Z01670.1	Siuren I	Failed		3	1105.6			1427.69							2883.53			
Z01671.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.68		1427.74			1648.8		2131				3034.25	
Z01672.1	Siuren I	Passed	Equidae	4	1105.6			1427.7					2145.1		2883.4			
Z01673.1	Siuren I	Passed	Bos/Bison	6	1105.6		1208.72	1427.81			1648.8		2131.3		2853.64			
Z01674.1	Siuren I	Failed		0														
Z01675.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.76					2131.1		2883.55			
Z01676.1	Siuren I	Failed		0														
Z01677.1	Siuren I	Passed	Bos/Bison	4	1105.6		1208.72	1427.79					2131.2					
Z01678.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.79					2131.2				3034.49	
Z01679.1	Siuren I	Passed	Equidae	4	1105.6	1182.6		1427.76							2883.42			
Z01680.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1180.6		1427.77		1550.83			2131.2		2883.61			
Z01681.1	Siuren I	Failed		0														
Z01682.1	Siuren I	Failed		3	1105.6	1196.73		1427.7										
Bone samples which were radiocarbon dated and processed with ZooMS																		
Z00117.1	Starosele	Passed	Cervus/Saiga/Gazella	10	1105.6	1180.62	1196.67	1427.84		1550.86	1648.8		2131.3		2899.4		3034.85	
Z01730.1	Starosele	Passed	Equidae	4	1105.6			1427.75					2145.11				3000.62	
Z01731.1	Starosele	Failed		0														

Z01732.1	Starosele	Passed	Equidae	4	1105.6			1427.72					2145.13		2883.55				
Z01733.1	Siuren I	Passed	Cervus/Saiga/Gazella	5	1105.6			1427.73					2131.13		2883.63			3034.79	
Z01734.1	Buran Kaya III	Passed	Cervus/Saiga/Gazella	5	1105.6			1427.76		1550.3	1648.8				2883.58				
Z01734.2	Buran Kaya III	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.67		1427.77		1550.77			2131.09					3033.68	
Z01735.1	Buran Kaya III	Passed	Rhinocertoidae	5	1105.6			1453.77					2145.21		2869.69		3000.87		
Z01736.1	Starosele	Failed		3	1105.6			1427.94		1551.07									
Z01737.1	Starosele	Passed	Equidae	4	1105.6			1427.81					2145.19		2883.51				
Z01738.1	Zaskalnaya VI	Failed		0															
Z01739.1	Zaskalnaya VI	Failed		0															
Z01740.1	Zaskalnaya VI	Failed		0															
Z01740.2	Zaskalnaya VI	Passed	Cervus/Saiga/Gazella	7	1105.6	1180.61		1427.73		1550.76			2131.12		2883.58			3034.54	
Z01741.1	Starosele	Failed		3	1105.6			1427.8		1550.8									
Z01742.1	Starosele	Passed	Equidae	5	1105.6			1427.82					2145.16	2820.4	2883.33				
Z01743.1	Chokurcha I	Passed	Cervus/Saiga/Gazella	6	1105.6		1197.59	1427.75			1648.8		2131.11					3033.75	
Z01744.1	Chokurcha I	Passed	Cervus/Saiga/Gazella	5	1105.6			1427.85			1648.8		2131.09					3034.17	
Z01745.1	Chokurcha I	Passed	Cervus/Saiga/Gazella	5	1105.6			1427.73			1648.8		2131.15					3034.7	
Z01746.1	Kabazi V	Passed	Equidae	4	1105.6			1427.77					2145.21		2883.62				
Z01747.1	Starosele	Passed	Equidae	4	1105.6			1427.78					2145.22				3000.83		
Z01748.1	Kabazi II	Failed		3	1105.6			1427.76					2145.12						
Z01749.1	Siuren I	Passed	Equidae	4	1105.6			1427.77		1550.8					2883.64				
Z01750.1	Siuren I	Failed		0															
Z01751.1	Starosele	Failed		0															
Z01752.1	Kabazi II	Failed		0															
Z01753.1	Kabazi II	Failed		0															
Z01754.1	Siuren I	Failed		0															

Z01755.1	Starosele	Passed	Equidae	5	1105.6			1427.77					2145.17	2821.53	2883.63				
Z01756.1	Zaskalnaya VI	Passed	Equidae	4	1105.6			1427.7		1550.8				2820.4					
Z01757.1	Kabazi II	Failed		0															
Z01758.1	Kabazi II	Failed		0															
Z01759.1	Siuren I	Failed		0															
Z01760.1	Siuren I	Failed		0															
Z01761.1	Siuren I	Failed		0															
Z01762.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6		1197.65	1427.74		1550.76			2131.09		2883.59				
Z01763.1	Siuren I	Failed		0															
Z01764.1	Siuren I	Failed		0															
Z01765.1	Siuren I	Failed		0															
Z01766.1	Siuren I	Failed		0															
Z01767.1	Siuren I	Passed	Equidae	4	1105.6		1198.75	1427.84					2145.12						
Z01768.1	Siuren I	Failed		0															
Z01769.1	Starosele	Passed	Equidae	5	1105.6	1182.72		1427.86		1550.8			2145.24						
Z01770.1	Siuren I	Failed		0															
Z01771.1	Siuren I	Failed		0															
Z01772.1	Siuren I	Passed	Cervus/Saiga/Gazella	4	1105.6			1427.86		1550.88			2131.21						
Z01773.1	Kabazi II	Passed	Equidae	6	1105.6	1182.62		1427.77					2145.1		2883.94		2999.9		
Z01774.1	Siuren I	Failed		0															
Z01775.1	Siuren I	Failed		0															
Z01776.1	Siuren I	Passed	Cervus/Saiga/Gazella	6	1105.6	1181.66		1427.75		1550.75			2131.1					3033.87	
Z04254.1	Starosele	Failed		0															
Z04255.1	Starosele	Passed	Bovidae or Cervidae	5		1181.56		1427.65		1550.7				2131				3034.59	
Z04256.1	Starosele	Failed		0															
Z04257.1	Starosele	Passed	Bovidae or Cervidae	3		1181.65		1427.85					2131.13						
Z04258.1	Starosele	Passed	Bovidae or Cervidae	3				1427					2131.09					3034.49	
Z04259.1	Kabazi II	Passed	Saiga or Cervidae	5		1196.61		1427.78					2131.15		2883.61			3033.82	

Z04260.1	Siuren I	Passed	Bovidae or Cervidae	4		1180.7		1427.76					2131.14					3034.69	
Z04261.1	Kabazi II	Passed	Equidae	4		1182.62		1427.76		1550.82			2145.17						
Z04262.1	Kabazi II	Failed		0															
Z04263.1	Kabazi II	Passed	Saiga or Cervidae	5		1181.61		1427.75					2131.11		2883.54			3034.55	
Z04264.1	Kabazi II	Passed	Bovidae or Cervidae	4		1181.67		1427.8					2131.18					3034.55	
Z04265.1	Kabazi II	Failed		0															
Z04266.1	Kabazi II	Passed	Equidae	4		1182.68		1427.78					2145.21		2883.68				
Z04267.1	Kabazi II	Passed	Equidae	5		1182.72		1427.85		1550.89			2145.23		2883.66				
Z04268.1	Kabazi II	Passed	Bovidae or Cervidae	3		1196.7		1427.76					2131.23						
Z04269.1	Kabazi II	Passed	Equidae	2				1427.76					2145.13						
Z04270.1	Siuren I	Passed	Saiga or Cervidae	5		1180.64		1427.74		1550.75			2131.12					3034.17	
Z04271.1	Siuren I	Passed	Bovidae or Cervidae	5		1180.62		1427.74					2131.14		2883.45			3018.48	
Z04272.1	Siuren I	Passed	Bovidae or Cervidae	5		1180.27		1427.78					2131.15		2883.57			3033.76	
Z04273.1	Siuren I	Passed	Equidae	3		1182.66		1427.79					2145.2						
Z04278.1	Siuren I	Passed	Bos/Bison	7	1105.6		1208.72	1427.78			1648.86		2131.2		2853.61			3033.73	
Z04279.1	Siuren I	Passed	Equidae	7	1105.59	1182.6		1427.76		1550.8			2145.2		2883.61		2999.76		
Z04280.1	Chokurcha I	Passed	Equidae	5	1105.63	1182.7		1427.78		1550.71			2145						
Z04281.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	5	1105.6		1197.52	1427.74		1550.7			2131						
Z04282.1	Chokurcha I	Passed	Elephantidae	9	1105.62		1162.61	1453.8		1580.85			2115.2	2809.49	2853.6		3015.76	3000.76	
Z04283.1	Chokurcha I	Passed	Bos/Bison	8	1105.63	1192.68	1208.72	1427.79		1580.85	1648.91		2131.22		2853.67				
Z04284.1	Chokurcha I	Passed	Elephantidae	9	1105.61		1162.66	1453.78		1580.79			2115.17	2809.46	2853.55		3015.71	3000.67	
Z04285.1	Chokurcha I	Passed	Equidae	7	1105.6	1182.63	1198.63	1427.74		1550.79			2145.14				2999.67		
Z04286.1	Chokurcha I	Passed	Rhinocerotidae	4	1105.45			1453.58					2146.56				2999.14		
Z04287.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	10	1105.63	1182.6	1196.69	1427.79		1550.7	1648.89		2131.17		2883.55		3018.56	3033.64	
Z04288.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.55	1181.59	1196.62	1427.7		1550.72	1648.8		2131.03					3033.49	

Z04289.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	7	1105.61		1197.65	1427.75		1550.76	1648.86		2131.14					3034.66	
Z04290.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.6	1181.68	1197.65	1427.74		1550.77	1648.83		2131.12					3033.64	
Z04291.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	6	1105.58			1427.72		1550.77	1648.81		2131.09					3034.62	
Z04292.1	Chokurcha I	Passed	Equidae	8	1105.59	1182.63	1199.61	1427.75			1650.78		2145.15		2884.59		2999.61		
Z04293.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.61	1181.66	1197.66	1427.76		1550.77	1648.86		2131.15					3034.69	
Z04294.1	Chokurcha I	Passed	Elephantidae	7	1105.58		1162.63	1453.74		1580.77			2115.11				3000.67	3015.61	
Z04295.1	Chokurcha I	Passed	Elephantidae	8	1105.58			1453.75		1579.8			2115.15	2809.39	2853.49		2999.68	3015.69	
Z04296.1	Chokurcha I	Passed	Bos/Bison	8	1105.58		1208.7	1427.74			1648.83		2131.14		2853.51		3018.62	3033.64	
Z04297.1	Chokurcha I	Passed	Equidae	7	1105.6	1182.61		1427.74		1550.72			2145.13		2883.5		2999.63		
Z04298.1	Chokurcha I	Passed	Elephantidae	4	1105.47			1453.59		1580.58								3015.12	
Z04299.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.54	1181.57	1196.6	1427.68		1550.7	1648.75		2131.01					3033.45	
Z04300.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	9	1105.56	1180.64	1196.6	1427.71			1648.79		2131.06		2883.47		3018.5	3033.55	
Z04301.1	Kabazi V	Passed	Equidae	5	1105.58	1182.65		1427.74					2145.08				2999.46		
Z04302.1	Kabazi V	Passed	Equidae	5	1105.56			1427.72					2145.08		2883.42		2999.51		
Z04303.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.53	1181.6		1427.67		1550.71	1648.75				2883.27		3018.36	3033.4	
Z04304.1	Chokurcha I	Passed	Bos/Bison	8	1105.62		1208.74	1427.79		1550.85	1648.9		2131.23		2853.65			3033.77	
Z04305.1	Chokurcha I	Passed	Equidae	6	1105.58	1182.6		1427.74					2145.17		2884.67		2999.72		
Z04306.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	8	1105.58	1181.62	1196.64	1427.72		1550.74	1648.81		2131.1					3033.67	
Z04307.1	Chokurcha I	Passed	Cervidae/Saiga/Gazelle	7	1105.61		1196.69	1427.79		1550.8	1648.87		2131.16					3034.58	
Z04308.1	Chokurcha I	Passed	Equidae	5	1105.64	1182.65		1427.79					2145.23				2999.76		
Z04309.1	Chokurcha I	Passed	Bos/Bison	7	1105.61		1208.75	1427.81		1550.85	1648.89		2131.17					3033.65	
Z04310.1	Kabazi V	Passed	Equidae	5	1105.63	1182.65		1427.78		1550.82			2146.19						

6. Chapter 6. Re-dating Glaston with XAD-2

6.1. Manuscript II

Title: Glaston: The earliest *Homo sapiens* identified in the British Isles through XAD-2 pre-treatment for radiocarbon dating

Authors: Emily M. Pigott, Laura van der Sluis, Lynden Cooper, Tom Higham.

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Significance: This article explores a key LRJ archaeological site in United Kingdom. Glaston, which was previously dated using ultrafiltration methods, was re-dated with an XAD-2 pre-treatment protocol. This revealed that the initial bulk collagen dates were almost certainly only partially de-contaminated. The results suggest that, if we assume the LRJ is linked with *Homo sapiens*, that these represent the earliest evidence for this species in the British Isles. The results underscore once more the critical importance of the applying the most robust pre-treatment methods for dating important Palaeolithic archaeological material. A more thorough chronological framework allows us to further understand the wider climatic and environmental context of early *Homo sapiens* dispersals, their behavioural adaptation and the relationship of different lithic assemblages to one another.

Contribution: I was the lead author on the publication, undertook the pre-treatment work using XAD-2 on the previously extracted collagen samples. I combusted, graphitised and pressed the samples before they were processed in the AMS. I also conducted the ZooMS analysis on one bone and undertook the spectra analysis. I was also the corresponding author for the publication.

Title Page

New radiocarbon dates from Glaston reveal evidence for the earliest *Homo sapiens* in Britain

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New radiocarbon dates from Glaston reveal evidence for the earliest *Homo sapiens* in Britain

Keywords: Palaeolithic archaeology, *Homo sapiens*, radiocarbon dating, XAD-2 resin

Abstract

Glaston is an Early Upper Palaeolithic site containing evidence for the Lincombian-Ranisian-Jerzmanowician (LRJ) lithic techno-complex. Archaeologists have been unsure whether the LRJ was authored by late Neanderthals or *Homo sapiens*, but recent work at the site of Ranis (Germany) links it to *Homo sapiens* through ancient DNA. At Glaston, previous ultrafiltered radiocarbon dates span from 42,930–41,780 cal BP. Glaston is an open-air site, which can increase the chance of radiocarbon contamination. We therefore re-dated remaining collagen using XAD-2 ion chromatography, which suggest Glaston was occupied between 45,490—43,540 cal BP, making the likely *Homo sapiens* occupants the earliest in Britain.

Introduction

The Lincombian-Ranisian-Jerzmanowician (LRJ) lithic techno-complex has been seen as Early Upper Palaeolithic, and sometimes as a transitional Middle to Upper Palaeolithic stone tool industry, found mainly in northwestern and Central Europe. It is characterised by leaf-points made on blades, sometimes termed 'blade-points' to distinguish them from fully bifacial leaf-point forms. The geographical distribution of the LRJ extends over ~1,500 km, with a latitudinal range between 50 and 55°N (Hublin 2015). Sites of this technocomplex date to around 40–45,000 years ago (Myopotamitaki *et al.* 2024), but chronological control is often lacking because many sites were either excavated many years ago and reliable contextual information is difficult to ascertain. This in turn has led to major uncertainties, and therefore debate, regarding the authorship of the LRJ. Some have suggested it belongs to Neanderthals (Jöris and Street, 2008), while others think both Neanderthals and *Homo sapiens* may have authored LRJ implements (Pettitt 2008). Recently, new mitochondrial DNA evidence from the Illsenhöhle, beneath the castle of Ranis in Thuringia, Germany, has shown that the LRJ techno-complex probably belongs to *Homo sapiens*. This is evidenced within layers 8–9, in which hominin remains identified genetically as *Homo sapiens* were found co-mingled with LRJ lithic artefacts during excavations between 2016 and 2022 (Myopotamitaki *et al.* 2024).

Although LRJ sites are widely distributed across Britain, Germany, Poland, the Netherlands, Czechia and Belgium (**Figure 1**), Britain contains the greatest concentration of sites. The most notable of these is the rich site of Beedings, comprising blade leaf points found in what

was interpreted to be a former hunting camp (Jacobi 2007). The leaf-points found at Beedings can

be compared with the LRJ cave sites of Spy and Goyet (Flas 2013). Other sites such as Kents Cavern and Robin Hood's Cave also contain evidence of LRJ tools, albeit in fewer numbers (Jacobi and Higham 2009; 2010). The LRJ techno-complex also includes so-called Jerzmanowice points and bifacial leaf points, as well as some less common tools such as pointed blades, endscrapers and burins (Flas 2011; Demidenko and Škrdlá 2023). The site of Jerzmanowice Cave (also known as Nietoperzowa Cave) is known for being one of the richest LRJ assemblages in Europe, including points that were used as projectile weapons (Wiśniewski *et al.* 2022). The LRJ is thought to reflect a technological and cultural adaption of *Homo sapiens* to cold, open grassland landscapes across northwestern and Central Europe. The faunal species present at many sites are adapted to the cold palaeoenvironments of MIS 3 (Smith *et al.* 2024), including species such as woolly mammoth, woolly rhinoceros and reindeer (Cooper *et al.* 2011; Higham *et al.* 2011; Smith *et al.* 2024).

In 2000, a rescue excavation revealed important evidence related to the British LRJ at a site in the village of Glaston, in the county of Rutland. The site was excavated by a team from University of Leicester Archaeological Services (ULAS). Along with archaeological evidence dating to the Bronze Age, Medieval and post-Medieval periods, the team uncovered, by chance, rare LRJ Palaeolithic tools, including a leaf-point, a partially broken point, and some related lithic debitage, along with associated faunal remains. The latter included some that had been modified by humans. These *Equus* bones had been broken and smashed, presumably for removing fat-rich marrow. Radiocarbon dating was undertaken on six faunal remains (see **Table 1**) found within 500 mm (laterally) of a leaf-point findspot (context 193) in archaeological area A (Cooper *et al.* 2011). The samples were pre-treated with ultrafiltration (Brock *et al.* 2010; Higham *et al.* 2006) and AMS dated at the Oxford Radiocarbon Accelerator Unit (ORAU). The results suggested that the LRJ at the site dated to between 42,930-41,780 cal BP with IntCal09 and (43,975-40,071 cal BP) with IntCal20 (Reimer *et al.* 2009; Reimer *et al.* 2020).

In this paper, we focus on the reliability of this initial set of radiocarbon determinations and test them using a robust ion chromatography treatment with XAD-2 resin (van der Sluis *et al.* 2023).

Methods

Radiocarbon dating

We obtained the excess collagen from seven samples from the ORAU archives, and these were then processed at the Higham Lab, in the Department of Evolutionary Anthropology, University of Vienna, using the method originally outlined by Stafford *et al.* (1987, 1988, 1991). Around 8 mg of collagen from each sample was used for the XAD process. The collagen was hydrolysed for 24 hours at 110°C in 6 M ultrapure HCl. Pre-cleaned and conditioned XAD columns were used in the ion-exchange process. The columns had a pre-fitted filter frit at the bottom, and a filter frit was placed above ~100µL of XAD-2 resin. Columns were cleaned with 20 washes of 1M HCl and preconditioned by letting 10 washes of 6M HCl pass through the columns. The samples were then passed through the columns, with one more wash of 1 mL of 6M HCl, to collect any leftover amino acids from the resin. The samples were then placed into the Genevac for 12 hours, to evaporate the remaining acid. ~100 µL of Milli-Q water was placed into each tube and these then placed back in the Genevac for 1.5 hours until full evaporation. Following this ~100 µL of Milli-Q was used to rinse each sample tube, and the liquid containing the amino acids loaded into a pre-cleaned tin boat. The treated amino acids were combusted, graphitised and AMS dated at the Vienna Environmental Research Accelerator (VERA), University of Vienna.

For calibration and modelling we used OxCal v. 4.4.3 software (Bronk Ramsey 2009) and the IntCal20 calibration curve (Reimer *et al.* 2020).

ZooMS

ZooMS analysis was undertaken on a single sample (Z04548) at the Douka Lab, Department of Evolutionary Anthropology, University of Vienna, Austria. Some species/family faunal remains such as mammoth and *Equus*. sp have had already been identified from previous zoological analyses (Cooper *et al.* 2011). The collagen was analysed using an AmBiC protocol (Brown *et al.* 2020). Following wet chemistry, the spectrum was analysed using flexAnalysis 3.4 (Brucker Daltonics) and mMass software (Strohalm *et al.* 2008). Subsequently, the spectrum was compared against known peptide markers in a reference library (Welker *et al.* 2015).

The collagen sample had 100 µL of 50 mM AmBic (ammonium bicarbonate buffer, pH 8.0) inserted and was then incubated for 1 hour at 65 °C for gelatinisation. Half (50 µL) of the sample was removed and kept as a backup. Trypsin digestion was undertaken by inserting 1 µL of trypsin solution 0.4 µg (Thermo Scientific Pierce™ Trypsin Protease), which was added to the supernatant and digested for 18 hours at 37 °C. The digested sample was treated with 1 µL of 5% TFA to stop further enzymatic digestion. ZipTipping was performed for purification and

peptide extraction, using C18 ZipTips (Thermo Scientific Pierce™ C18 Tips), using 50 mL of 50% ACN in 0.5% TFA. A calibrant at 1:2 ratio of 0.7 µL was added to the plate, with 0.7 µL matrix solution. The sample (0.7 µL) was spotted with 0.7 µL of matrix solution. Thereafter, the processed sample was analysed using a Bruker Autoflex Speed LRF MALDI ToF/ToF mass spectrometer (Buckley *et al.* 2009). The peptide marker (A-G) was manually inspected in mMass 5.5.0 (Strohalm *et al.* 2010).

Results

The XAD-treated conventional radiocarbon ages were all significantly older than the previous ultrafiltration results (**Table 1**). This is generally held to mean a more successful removal of potential trace carbon contaminants. We observe that the C/N_{atomic} ratios from the ultrafiltered results, while all falling within the range of 2.9-3.5, are all on the higher end of the spectrum, ranging up to 3.4 (Devièse *et al.* 2019). This may indicate contamination present within the faunal remains, although C/N_{atomic} ratios are not greatly sensitive to the presence of non-collagenous contaminants. Following calibration, we see that the XAD-2 dates were ~1000-3000 thousand years older than the initial results (**Figure 2**).

We built a Bayesian chronometric model for Glaston using OxCal 4.4. This is a simple model since we do not have any informative priors or relative stratigraphic information. We assume a single phase of activity in the model. We used the `Date` command to determine the overall span of occupation time at the site and combined the determinations we obtained from the same bone in `R_Combine`. The model results are shown in **Figure 3**.

The Bayesian model contained no outliers of significance. We calculated a span for the total occupation of the site ranging between 45,490—43,540 cal BP (95.4% probability). Interestingly, the previous determinations of Cooper *et al.* were modelled using the same approach, but with the IntCal09 curve (Reimer *et al.* 2009), and this resulted in an age range for the overall span of 44.3–42.5 kyr cal BP, broadly comparable to our new modelled estimate. The reason for the much greater disparity between the results now is due to the updates to the IntCal20 calibration curve. While IntCal09 had sparse data beyond 40,000 cal BP, and a heavy reliance on marine records, resulting in greater uncertainty and smoothing, IntCal20 has many new higher precision datasets including floating tree-rings, and an improved statistical treatment of uncertainties (Reimer *et al.* 2020). The result is that the Cooper *et al.* (2012) `Date` range, when re-calibrated using IntCal20, is placed at 42,930—41,780 cal BP (95.4% prob.),

while the data we obtained sit significantly earlier at 45,490—43,540 cal BP (95.4% prob.) (**Figure 4**).

One of the previous faunal samples was not identifiable to taxon (OxA-21308), so we used Zooarchaeology by Mass Spectrometry (ZooMS) to identify it. It comprises three known peptide peaks characterising Rhinocerotidae, so is most likely a woolly rhinoceros, *Coelodonta antiquitatis*. A minimum number of 5 fragments of Rhinocerotidae was previously found at the site, with evidence of the majority being chewed and cracked by hyenas (Cooper *et al.* 2011).

Discussion

Caution is needed when interpreting human presence based on an association between dated faunal remains and stone tools, particularly at a site like Glaston where these tools are limited to a single whole example and a fragmented piece of leaf point. If we assume that the LRJ is linked only with *Homo sapiens*, then this documents the oldest dated modern human presence in Britain. There are no other sites there which directly link the LRJ techno-complex with *Homo sapiens*.

It is tempting to compare our new results with the other notable early *Homo sapiens* remains in Britain, namely the Kents Cavern maxilla (KC4), which was dated with reference to faunal remains in close association to between 44.2 – 41.5 kyr cal BP (Higham *et al.* 2011). This date range has been critically viewed by some researchers, who question the stratigraphic integrity of the remains based on their early excavation and the possibility of post-depositional movement (see discussion in Proctor *et al.* 2017). Another site near to Kents Cavern, Bench Quarry Tunnel, has also been radiocarbon dated. There, a hyena (*C. crocuta*) right dentary was dated twice at 36,800±450 BP and 37,500 ± 900 BP (Jacobi and Higham 2011) (**Table 2**). The dentary was found in contact with a blade leaf-point. At Pin Hole (Derbyshire) and Badger Hole (Somerset), similar dates on bones found in very close proximity to blade leaf points were obtained (Jacobi and Higham 2011) (**Table 2**). One wonders whether, with more robust pretreatment chemistry, these dates would also result in even older ages.

When we compare the Glaston results to other LRJ sites across Europe (**Figure 5**) we observe a degree of similarity. The Glaston results are similar in age to Ranis. Humans appear to have been at Ranis during a significant cold period, as evidenced by ecological indicators and oxygen stable isotope analyses of faunal remains (Pederzani *et al.* 2023). Many cold-adapted species are present, such as horse, woolly mammoth, woolly rhinoceros and reindeer (Smith *et al.*

2023). Glaston has revealed a similar range of cold-adapted fauna, such as woolly mammoth, woolly rhinoceros and horse (Cooper *et al.* 2011). This is consistent with our Bayesian model results (**Figure 3**). When we plotted the posterior ranges of our Bayesian model against the NGRIP $\delta^{18}\text{O}$ record, synchrotronised to IntCal20 via the GICC05 record and the $^{10}\text{Be}/^{14}\text{C}$ comparison therein, this shows that the site dates securely within the GS12 stadial.

At Koziarnia Cave in the east of Europe, environmental proxies indicated humans occupied the site within a cold climatic episode, with the disappearance of Jerzmanowician occupation happening during a subsequent warming episode (Berto *et al.* 2021), but we are cautious regarding this conclusion and the dating of the site. The bulk of the radiocarbon determinations from the Jerzmanowician levels were obtained on charcoal, and there is no information given as to whether these were treated with a reliable ABOx-type chemistry (Kot *et al.* 2021). Several studies have shown that this is often required to obtain accurate results for charcoal samples dating beyond ~20 ka BP (Brock and Higham 2009; Higham *et al.* 2009; Douka *et al.* 2010; Wood *et al.*, 2012; Douka and Higham, 2017). The Koziarnia results for the Jerzmanowician assemblage of layers F and H are $33,100 \pm 1200$ BP and $33,320 \pm 480$ BP (Kot *et al.* 2021). An age for the Jerzmanowician after 40,000 cal BP now appears to be rather late and it clearly needs to be tested. A similar age can be seen at Nietoperzowa Cave, within the LRJ layers of 5b and 6, from an anthropogenically modified mammoth bone, dating to $32,500 \pm 400$ BP (Nadachowski *et al.* 2011) and $38,160 \pm 1250$ BP on a charcoal sample (Kot *et al.* 2021). These dates currently represent the youngest phase of the Jerzmanowician in Europe, with an indication of humans occupying Nietoperzowa at two different time frames. The earlier date for layer 6 at Nietoperzowa is more consistent with radiocarbon dates for LRJ sites within Britain. A re-analysis of the bone and charcoal radiocarbon results with more recent pretreatment protocols is needed, before we can draw firm conclusions.

Ancient genomics has revealed some key insights into who these human groups were in western Eurasia during this important period. Ancient DNA results from Bacho Kiro have provided evidence for the connection between early modern humans with the IUP techno-complex there but with quite recent Neanderthal ancestry. The Bacho Kiro individuals had Neanderthal ancestry less than six generations prior in one instance, while two others revealed intervals of ten and seventeen generations back, respectively (Hajdinjak *et al.* 2021). Intriguingly, the Zlatý kůň female individual, found in the Koněprusy caves in Czechia, was shown to probably belong to a different population than the Bacho Kiro population, and she differed in that she yielded 3.2% Neanderthal ancestry in her genome with an estimated age (based on Bayesian tip dating)

of >45,000 cal BP (Prüfer *et al.* 2021). The Ranis genomes, meanwhile, showed that they were most closely linked with Zlatý kůň, with genetic links between two Ranis individuals to Zlatý kůň present at a level of a fifth- or sixth-degree relative. This suggests that there were probably three genetically distinguishable groups of humans present in Europe (Sumer *et al.* 2024): two modern human groups and one Neanderthal group. The latest chronological estimates for these sites and humans are shown in **Figure 5**.

Conclusion

The new radiocarbon dates we obtained have shown that Glaston is the oldest occupied site of *Homo sapiens* in Britain. We hypothesise that the open-air nature of the site might have resulted in additional contamination for the bulk collagen samples extracted from the skeletal remains. This appears to have been more successfully removed using hydrolysis of the collagen and the subsequent purification of the amino acids using XAD-2 resin. We suggest that other LRJ sites might similarly benefit from re-dating with more robust pre-treatment methods, producing more accurate radiocarbon dates.

Across Europe there are a substantial number of LRJ sites, especially in Britain. A common feature is that they seem to have been occupied during cold climates, suggesting that these humans were already adapted to these challenging conditions with a toolkit that enabled them to survive and disperse in open, steppe-like landscapes. The IUP people at Bacho Kiro were also present in colder, stadial conditions, despite belonging to a genetically different human group and wielding different technologies. Additional biomolecular work at other sites may unravel more regarding the increasingly complex and interwoven stories of the people who occupied these regions 46-45,000 years ago.

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Table 1. Radiocarbon results for the bones dated using ultrafiltration (OxA) and XAD-2 resin (VIE). The OxA results are from Cooper et al. (2011). The symbol * denotes that the same bone was used for all the measurements. A new taxon identification was determined from a previously unidentified bone sample (VIE-1779). The new taxon identification of Z04548 can be seen in bold, as Rhinocerotidae.

Sample number	Species	Radiocarbon age BP	F ¹⁴ C and error	Start weight	Yield (mg)	% Yield	%C	δ ¹³ C (‰)	δ ¹⁵ N (‰)	C/N	%N
OxA-21308	Gnawed diaphyseal frag.	35610 ± 300	0.01188 ± 0.00044	1006.2	51.8	5.1	44.2	18.5	5.0	3.4	0.6
Z04548	Rhinocerotidae										
VIE-1779		40308 ± 460	0.00662 ± 0.00037	-	-	-	-	-	-	-	-
OxA-21309	<i>Coelodonta antiqutatis</i> gnawed midshaft r. humerus	38120 ± 360	0.00869 ± 0.00039	1010.7	70	6.9	42.8	19.9	4.3	3.3	1.3
VIE-1780	-	42033 ± 574	0.00534 ± 0.00037	-	-	-	-	-	-	-	-
OxA-21310	<i>Coelodonta antiqutatis</i> gnawed midshaft l. Humerus	38800 ± 390	0.00798 ± 0.00039	1007.2	74.95	7.4	42.4	19.7	4.2	3.3	1.2
VIE-1781	-	41677 ± 548	0.00558 ± 0.00037	-	-	-	-	-	-	-	-
OxA-21311*	<i>Equus ferus</i> 1 st phalange	37380 ± 350	0.00953 ± 0.00042	1003	43.32	4.3	42.5	20.6	3.9	3.3	0.7
VIE-1782*	-	42263 ± 591	0.00519 ± 0.00037	-	-	-	-	-	-	-	-
OxA-21312*	-	38610 ± 400	0.00818 ± 0.00041	1000	43.02	4.3	42.3	20.5	4.1	3.3	
VIE-1783*	-	41394 ± 528	0.00578 ± 0.00037	-	-	-	-	-	-	-	-
VIE-1784*	-	40734 ± 577	0.00628 ± 0.00044	-	-	-	-	-	-	-	-
OxA-22149	<i>Coelodonta antiqutatis</i> gnawed midshaft l. tibia	38400 ± 900	0.00837 ± 0.0009	610	30.2	5.0	46.1	20.3	4.3	3.2	0.6
VIE-1785	-	40534 ± 473	0.00644 ± 0.00037	-	-	-	-	-	-	-	-

Table 2. LRI sites within Britain which have been dated with radiocarbon.

Site	Key finds	Dating	Age	Reference
Gilston (Grange Farm, Rutland)	Leaf point, blade technology, horse dominated fauna	Radiocarbon dating (XAD-2)	45,189–43,244 cal BP (95.4% prob)	This paper.
Pin Hole Cave (Creswell Crags, Derbyshire)	Blade-point, found in the eastern passage. Dated by association with a <i>C. crocuta</i> pre-maxilla the sediment attached to which had an impression of the end of the broken blade-point.	Radiocarbon dating	37800 ± 1600 BP	Jacobi et al., (2006)
Robin Hood Cave (Derbyshire)	LRI-type with blade and full bifacial leaf points, burins and a dominance of horse	Radiocarbon dating (ultrafiltration)	>38,500 ka Cal BP	Jacobi et al., (2006)
Badger Hole, Wookey Hole, Somerset	Dated <i>E. ferus</i> bone found near to a blade leaf-point	Radiocarbon dating (ultrafiltration)	36,000 ± 450 BP	Jacobi and Higham (2011)
Bench Quarry tunnel, Brixham, Devon	Dated <i>C. crocuta</i> right dentary found in contact with a blade leaf-point	Radiocarbon dating (ultrafiltration)	36,800 ± 450 BP 37,500 ± 900 BP	Jacobi and Higham (2011)
Kents Cavern (Torquay, Devon)	Leaf points and blade technology, horse dominated fauna	Radiocarbon dating (ultrafiltration) of bones above and below the KC4 maxilla	~ 44,180–41,530 cal BP (95.4% prob)	Curran & Jacobi, (2011); Higham et al., (2011)

Figure captions

Figure 1. a) Map of LRJ sites within Britain and Europe (dark red/brown c represents cave sites, green open-air sites and grey represents Glaston Grange Farm). Map adapted from Flas (2011) and Demidenko & Škrdlá, (2023). 1. Glaston Grange Farm; 2. Paviland; 3. Bench Quarry Tunnel Cavern; 4. Windmill Hill Cave; 5. Kent's Cavern; 6. Goldcliff; 7. Ffynnon Bueno Cave; 8. King Arthur's Cave; 9. Uphill Quarry Cave; 10. Soldier's Hole; 11. Hyaena Den; 12. Badger Hole; 13. Moordown; 14. Pin Hole; 15. Robin Hood Cave; 16. Osney Lock; 17. Sutton Courtenay; 18. Wallow Camp; 19. Hainey Hill; 20. Brandon; 21. Drayton; 22. Warren Hill; 23. Town Pit; 24. Eastall's Pit; 25. Bramford Road Pit; 26. White Colne Pit I; 27. Creffield Road; 28. Earl of Dysart's Pit; 29. Temple Mills; 30. Beedings; 31. Bapchild; 32. Conningbrook Manor Pit; 33. Aardjesberg; 34. Spy; 35. Goyet; 36. Zwergloch; 37. Ranis 2; 38. Nietoperzowa Cave; 39. Koziarnia Cave; 40. Puchacza Skała Cave; 41. Líšeň/Podolí I; 42. Líšeň I/Líšeň—Čtvrť; 43. Želešice III/Želešice-Hoynerhügel; 44. Tvarožná X, "Za školou;" 45. Pekárna Cave. B) map of the excavations at Glaston. C) Leaf point excavated from the site.

Fig 2. OxCal calibration results for the six bones from Glaston. Blue outlines represent the dates from previous ultrafiltration pre-treatment (OxA). Red indicates the new XAD results. XAD pre-treatment was undertaken on the collagen extracted with the ultrafiltration method. Previously both OxA-21311 and OxA-21312 were duplicated by the Oxford radiocarbon lab, University of Oxford. We also dated the collagen from OxA-21312 twice with XAD and combined the results (VIE-1783 – 1784).

Figure 3. A Bayesian model comprising the new XAD results from seven samples processed (**Full data in ST.2**). The General Outlier Model we used to show outliers of significance in all units. Outliers are shown in the diagram in the form [O:4/5], in which 4 is the posterior outlier result and 5 is the prior. The * symbolises the same faunal remain dated. We followed Cooper et al. (2012) in placing the result for AIC A54 (OxA-21308) outside the Phase in the model. Code is in the Supplementary Information. The NGRIP data is shown above which synchronises the $^{10}\text{Be}/^{14}\text{C}$ records of IntCal20 and GICC05 (based on Adolphi and Muscheler, 2016; Adolphi *et al.* 2018; Andersen *et al.* 2004; Andersen *et al.* 2006; Bronk Ramsey *et al.* 2014; Rasmussen *et al.* 2006; Rasumssen *et al.* 2008; Svensson *et al.* 2006; Svensson *et al.* 2008). The NGRIP data is shown with 1 sigma envelope.

Figure 4. Bayesian model-based Date ranges from Glaston using the two datasets produced by Cooper et al. (2012) and this paper, showing the difference between the two.

Figure 5. Plot of the radiocarbon age and Date ranges calculated for sites dating to the IUP and transitional phase of the Early Upper Palaeolithic in western Eurasia. The new XAD results from Glaston and directly dated *Homo sapiens* from Ranis (LR) are shown in green, along with other LRJ sites, Bacho Kiro (IUP) is shown in red and Zlatý kůň (the date is based on estimates based on genomic data) and Ust’Ishim are in purple, with no associated archaeology (Prüfer *et al.* 2021; Mylopotamitaki *et al.* Supplementary material. 2024).

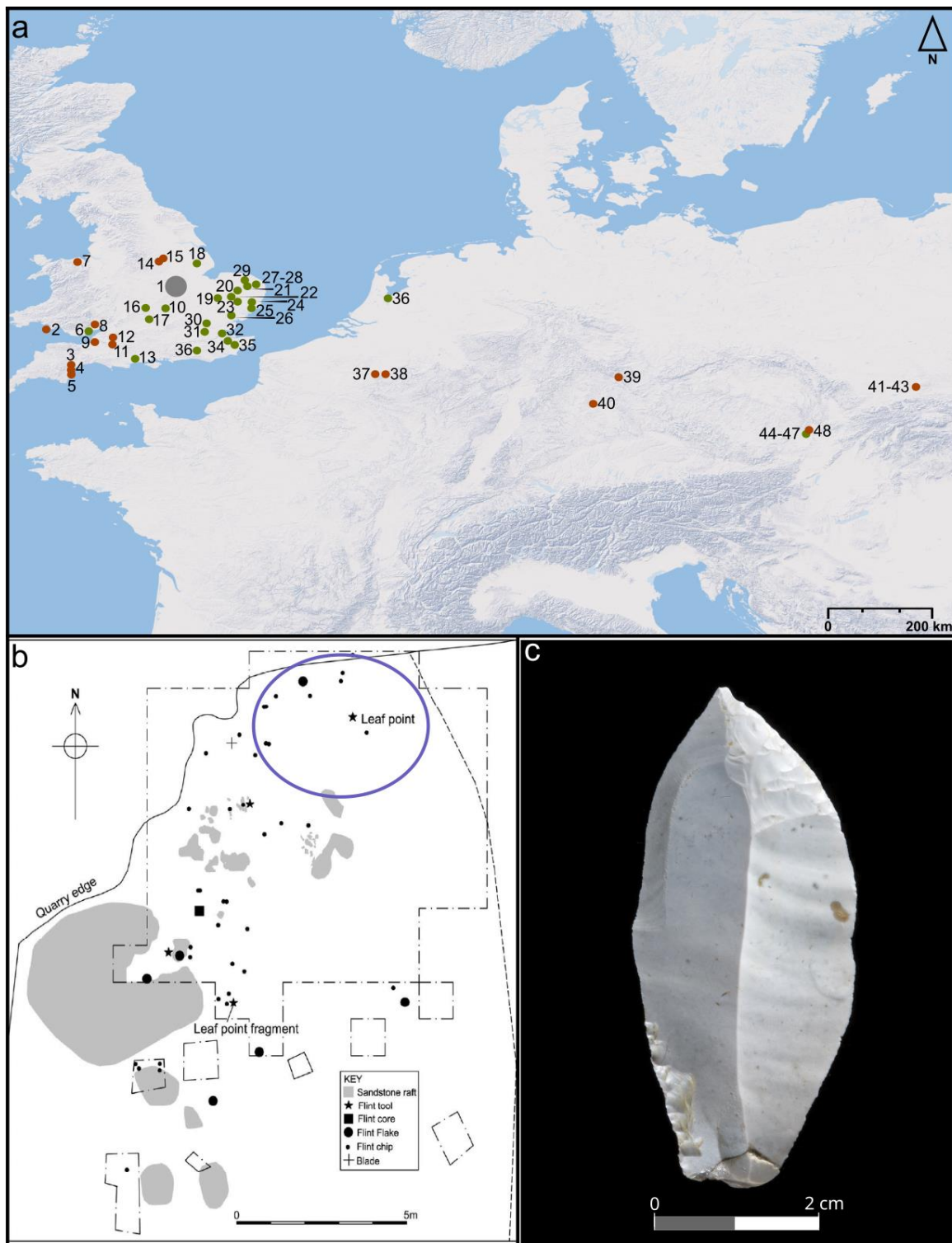


Figure 1.

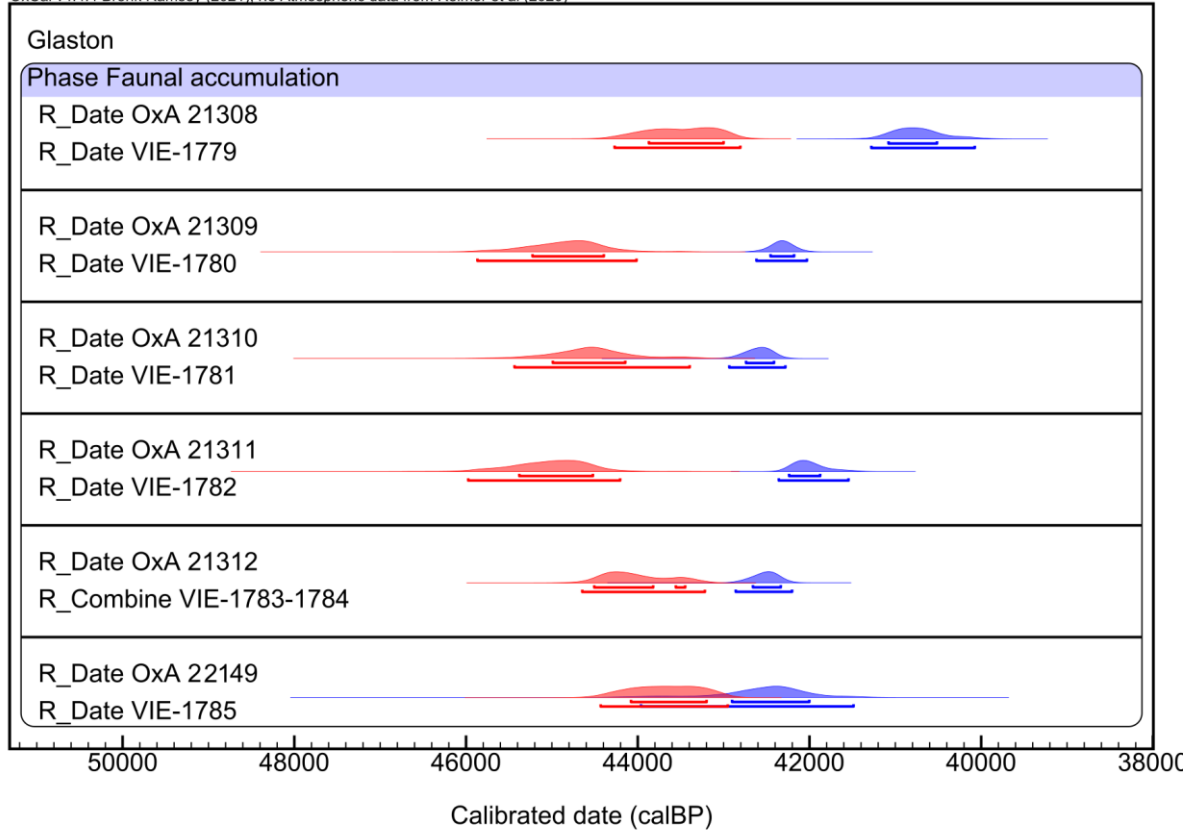


Figure 2.

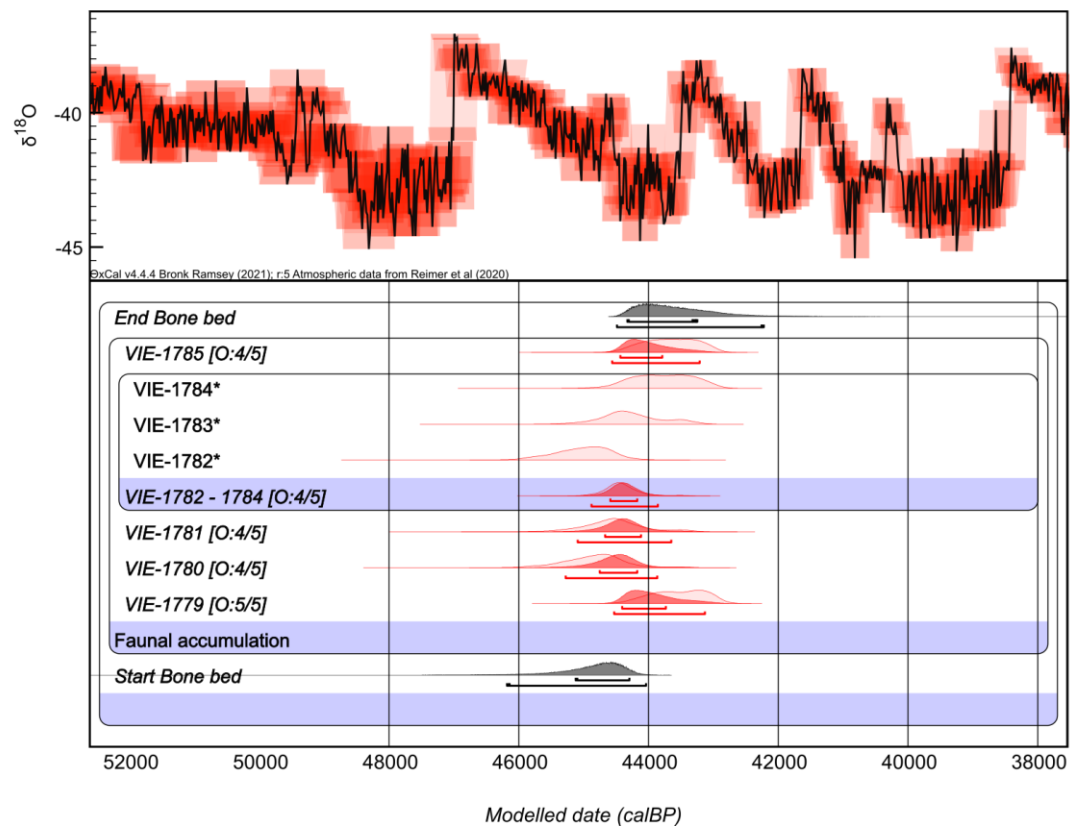


Figure 3.

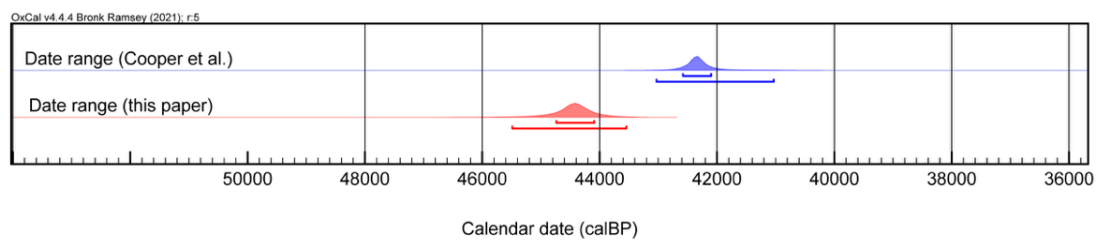


Figure 4.

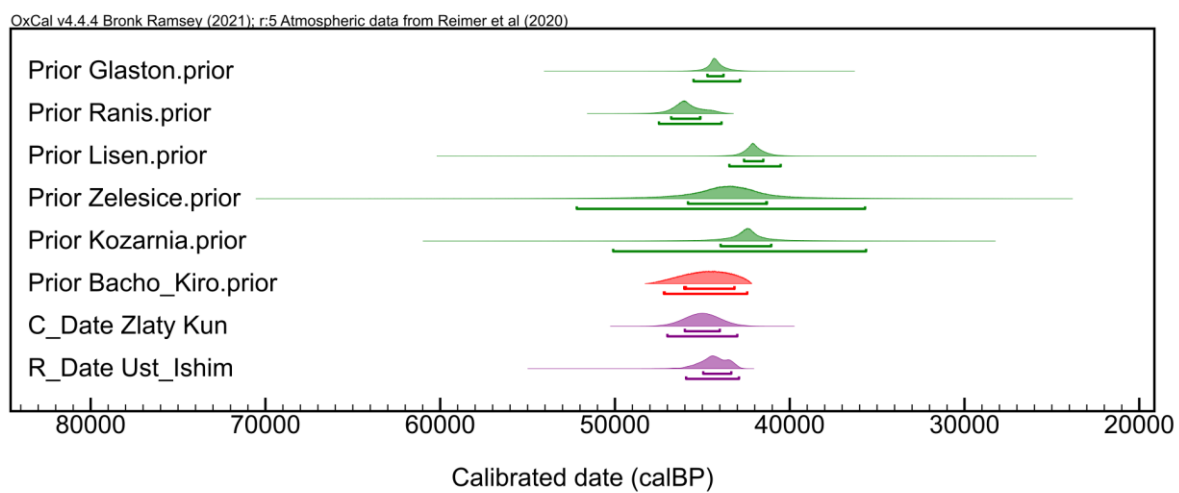


Figure 5.

New radiocarbon dates from Glaston reveal evidence for the earliest *Homo sapiens* in Britain

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Supplementary Information

ZooMS

One faunal remain from the previously radiocarbon dated samples had no taxonomic identification from its morphological analyses. We processed this sample (OxA-21308) with ZooMS (Z04548) at the Douka Lab, Department of Evolutionary Anthropology, University of Vienna. The peptide coverage is not high, however, there were three peptide markers which narrowed the taxonomic identification to the family classification of Rhinocerotidae (**Figure S1 and Table 1**) and Tapiridae. Since there is no known Tapiridae in England at any time, we can safely say the taxonomic identification is Rhinocerotidae. Most likely being woolly rhinoceros, *Coelodonta antiquitatis*, since this species was previously found by zooarchaeologists at the site and is representative of the cold environment for the time of occupation (Cooper *et al.* 2011).

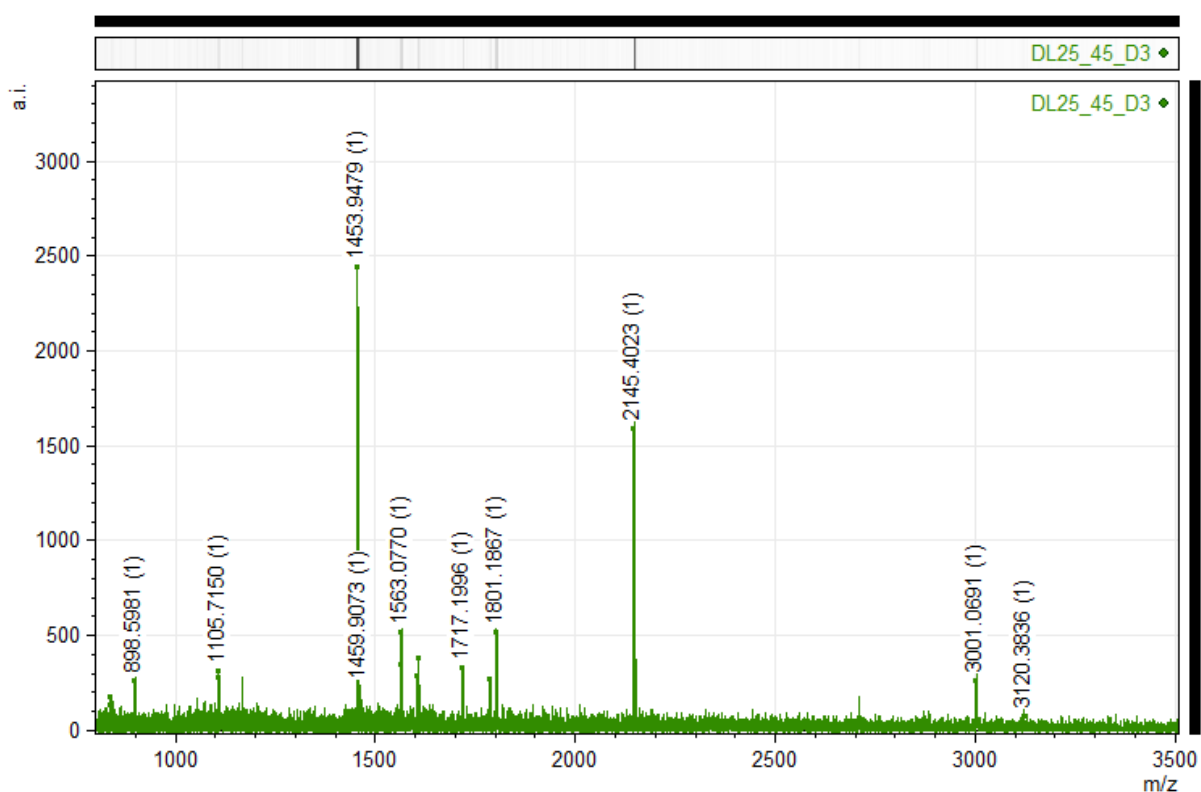


Figure S1. ZooMS taxon identification of Z04548, which was previously not identified from OxA-21308, with the new XAD radiocarbon lab number of VIE-1779.

Table S1. Peptide peak identifications of Z04548, including 3 peaks which have clearly identified the faunal remain being classed as a Rhinocerotidae.

Lab No.	ZooMS ID	No Total Peptides	Alpha1 508 p	Alpha2 484 B	Alpha2 793 D
Z04548	Rhinocerotidae	3	1105.71	1453.94	2145.4

OxCal CQL code

Figure 3

Plot()

```
{
  Outlier_Model("SSimple",N(0,2),0,"s");
  Outlier_Model("General",T(5),U(0,4),"t");
  Sequence()
  {
    Boundary("Start Bone bed");
    Phase("Faunal accumulation")
    {
      R_Date("VIE-1780", 42033, 574)
      {
        Outlier("General",0.05);
        color="#ff0000";
      };
      R_Date("VIE-1781", 41677, 548)
      {
        Outlier("General",0.05);
```

```

color="#ff0000";

};

R_Combine("VIE-1782 - 1784")

{

  Outlier("General",0.05);

  R_Date("VIE-1782*", 42263, 591)

  {

    Outlier("SSimple",0.05);

    color="#ff0000";

  };

  R_Date("VIE-1783*", 41394, 528)

  {

    Outlier("SSimple",0.05);

    color="#ff0000";

  };

  R_Date("VIE-1784*", 40734, 577)

  {

    Outlier("SSimple",0.05);

    color="#ff0000";

  };

};

R_Date("VIE-1785", 40534, 473)

{

  Outlier("General",0.05);

  color="#ff0000";

```

```
};  
  
Date("Glaston LRJ Date");  
  
};  
  
Boundary("End Bone bed");  
  
R_Date("VIE-1779", 40308, 460)  
  
{  
  
  Outlier("General",0.05);  
  
  color="#ff0000";  
  
};  
  
};  
  
};
```

Table S2: Bayesian model unmodelled and modelled results and 68.2 and 95.4% probability. Model code is above.

Name	Unmodelled (BP)				Modelled (BP)				Convergence
	<i>From</i> 68.3% <i>prob.</i>	<i>To</i> 68.3% <i>prob.</i>	<i>From</i> 95.4% <i>prob.</i>	<i>To</i> 95.4% <i>prob.</i>	<i>From</i> 68.3% <i>prob.</i>	<i>To</i> 68.3% <i>prob.</i>	<i>From</i> 95.4% <i>prob.</i>	<i>To</i> 95.4% <i>prob.</i>	
VIE-1779	43910	43030	44310	42840	43730	42950	44110	42800	99.6
<i>End Bone bed</i>									
VIE-1785	44060	43170	44420	42930	44530	44040	44700	43590	99.8
VIE-1784*	44250	43260	44620	42920					
VIE-1783*	44810	43880	45120	43220					
VIE-1782*	45380	44510	45980	44200					
VIE-1782 - 1784	44680	44210	45020	43850	44620	44250	44860	44000	99.9
VIE-1781	44990	44130	45430	43380	44690	44220	45080	43910	99.9
VIE-1780	45230	44390	45870	44010	44760	44260	45230	44020	99.8
<i>Faunal accumulation</i>									
<i>Start Bone bed</i>									
					45100	44320	46380	44130	96

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7. Chapter 7. Discussion

7.1. The Crimean Peninsula

Palaeolithic archaeological materials have long proven challenging to date accurately using radiocarbon methods, largely due to the pervasive presence of contamination within burial and depositional environments, particularly from humic acids. This thesis has demonstrated that the application of XAD-2 pre-treatment for radiocarbon analysis can substantially alter the resulting ages of some Palaeolithic samples, highlighting the significant impact of residual contamination on previously published chronologies. Improving the reliability of radiocarbon chronologies is essential for refining interpretations of late Neanderthal and early *Homo sapiens* populations, their technological traditions, and the timing of the Middle to Upper Palaeolithic transition, both within the Crimean Peninsula and across Eurasia.

This thesis has sought to test the hypothesis that the Crimean Peninsula acted as a refugium for Neanderthals prior to their eventual disappearance from Eurasia. The thesis was divided into four parts, the first of which comprised a review of key Crimean Middle to Upper Palaeolithic archaeological sites and their chronological record. This allowed me to gain a deep understanding of the lithic and faunal findings at each of the sites as well as the chronological records. Subsequently, I undertook extensive radiocarbon dating with pre-treatment methods such as ultrafiltration and XAD-2 to test the extent to which contamination within the bone samples was removed. In some instances, I found significant differences between these methods at different sites. This can be seen especially at Starosele and Siuren I. Taken together, the results suggest that the Crimean Peninsula was most likely not a refugium for Neanderthals at the late date previously inferred (around 28 uncal BP) (Demidenko & Otte, 2001). This repeats a pattern that has been seen in other contexts in Europe and Eurasia (e.g. Wood et al., 2013 in the Iberian Peninsula).

The application of XAD-2 collagen purification to Crimean samples represents a critical reassessment of one of the key regions linking eastern European and Near Eastern dispersal corridors. The results presented in this thesis demonstrate that XAD-2 treated samples consistently yield more reliable and, in several cases, systematically older ages than previously published determinations. This pattern reinforces growing evidence that contamination by exogenous factors has played a significant role in artificially extending the apparent antiquity of some early Upper Palaeolithic assemblages. The XAD-2 pre-treatment method allowed a further understanding of the actual radiocarbon dates at the various Crimean sites. One of the most dramatic differences in dates was from Chokurcha I. It was previously thought that Chokurcha, Unit IV dated to around 45 ka BP (Chabai et al., 2004). However, the new radiocarbon dates with XAD-2 pre-treatment have revealed ages beyond

the radiocarbon limit of 50-55,000 BP. The ZooMS results from the same layers indicate a cold steppe environment predominated (Markova, 2004; Patou-Mathis, 2004).

At present, a direct comparison between the HYP and XAD-2 pre-treatment methods has only been possible at Kabazi II, owing to limitations in the availability of comparable datasets. I observed some variation in the radiocarbon results between the two methods. Statistical analyses indicate differences between samples and pre-treatment methods in all cases, except VIE-1580 from Level II/2. This may suggest that the effects of pre-treatment may vary depending on sample preservation and depositional context. Further systematic comparison of pre-treatment protocols at this site is therefore required to better characterise their respective impacts on radiocarbon age determinations. More work is needed to test the reasons for the small differences at this site.

Siuren I was previously interpreted as yielding an uncalibrated age of $28,200 \pm 440$ BP, making it the youngest known Neanderthal site in the Crimean Peninsula. However, new XAD-2 treated dates from samples VIE-1585 (37,350–36,200 cal BP at 95.4% probability) and VIE-1756 (35,780–34,630 cal BP at 95.4% probability) indicate that the site is approximately 5,000 years older than previously thought. These results suggest that Neanderthals associated with Micoquian techno-complexes were no longer present in Crimea as late as earlier chronologies had implied.

In contrast, other sites included in this study, such as Zaskalnaya VI, show no significant changes in radiocarbon age following re-dating. This may suggest minimal contamination within this rock shelter context, demonstrating that the effects of more robust pre-treatment methods are not uniform across sites.

During ZooMS analysis on fragmented, previously unidentified remains from Starosele, Siuren I, Chokurcha I, Kabazi II and Kabazi V, I was extremely lucky to find two human remains at Starosele. These were both found within level I, Square I23. Each was processed further for radiocarbon dating and stable isotopes analysis. One of these bones, now known as Star 1, was analysed genetically. Its mitogenome revealed the Neanderthal-type and a subsequent analysis showed that the sequence was most closely linked with Neanderthals from the Altai region. This provided further evidence linking Neanderthal groups with their characteristic Micoquian lithic assemblages across wide tracts of Eurasia. Climate modelling was applied to understand the most likely migration pathways involved. Synthesising the revised Crimean data with evidence from western Europe supports a model of Neanderthal dispersal, characterised by episodic advances made in conjunction with phases of climate stability. Migration patterns inferred from my second publication within this thesis challenge the timeline of mass migrations across a large area across Eurasia and raise the possibility

of Neanderthal groups moving on perhaps three different occasions. Sadly, the second human bone identified via ZooMS failed to yield sufficiently good coverage aDNA.

7.2. Glaston, United Kingdom

Glaston was included in this PhD thesis as a further case study attesting to the importance of checking and re-checking existing bulk collagen dates from archaeological sites from the Middle and early Upper Palaeolithic using more rigorous methods. At the heart of the Glaston case is the assumption that modern humans are the authors of the LRJ. The cultural attribution of the (LRJ) techno-complex and whether it relates to Neanderthals or *Homo sapiens* has long been debated (Jöris & Street, 2008; Pettitt, 2008) (see manuscript II). Recent mitochondrial DNA results from the Illsenhöhle cave complex beneath Ranis Castle in Thuringia, Germany strongly suggest now that *Homo sapiens* are the prime authors (Mylopotamitaki et al., 2024).

Up until now, no human remains have been found at any of the numerous LRJ sites within the British Isles. At Glaston, a leaf-point and a partially broken point were found alongside faunal remains, some of which were humanly modified. The re-dating of previously treated collagen using XAD-2 resulted in significantly older dates and suggests that Glaston may comprise the oldest evidence for *Homo sapiens* in Britain, dating to 45,490 – 43,540 cal BP. The LRJ techno-complex is widely interpreted as representing a technological and cultural adaptation of *Homo sapiens* to cold, open grassland environments across North-western and Central Europe. The faunal assemblages associated with LRJ sites further support this interpretation, indicating occupation during cold climatic conditions within Marine Isotope Stage 3 (Smith et al., 2024). It is important to note that inferring human presence based on an association between dated faunal remains and lithic artefacts must be approached with caution, particularly at sites such as Glaston where the lithic assemblage is limited.

7.3. Future directions

Several avenues for future research can be proposed to more fully characterise and explore the Palaeolithic record across Eurasia:

Expanded radiocarbon re-dating

Many Crimean sites still rely on legacy radiocarbon dates produced with outdated pre-treatment methods. Systematic re-dating using XAD-2, HYP, or other more robust collagen purification techniques across a wider range of sites, layers, and faunal samples would refine regional chronologies and clarify occupational phases by hominins. My work is just a start in this endeavour.

Integrated Biomolecular Analyses

Further application of ZooMS, stable isotope analysis, and ancient DNA on fragmented and previously unidentifiable remains could be crucial in identifying additional hominin material, provide a stronger understanding of the subsistence strategies and possibly mobility patterns of the hominin groups within some regions.

Building on the Star 1 success, mitochondrial and nuclear DNA sequencing of Neanderthal and *Homo sapiens* remains from Crimea and other regions could broaden our understanding of cultural connections between different groups as well as revealing evidence for the authorship of different lithic industries and shed light on the question of whether more than one group of humans were occupying the same site or horizon. The application of sediment DNA may provide further indications of human presence within some layers at archaeological sites. The application of these methods at Denisova cave in Russian Siberia enabled the recovery of nuclear and mtDNA in sediments dating back more than 150,000 years ago (Zavala et al., 2021). Applying these methods to Crimean sites, while challenging due to less amenable palaeoclimatic and thermal histories, would be an exciting new application to contribute to some of these seemingly intractable issues in the Palaeolithic.

Expanded Zooarchaeological and Palaeoenvironmental Studies

Detailed re-analysis of faunal assemblages using modern ZooMS and stable isotope analysis has the potential to improve understanding of site formation processes, subsistence strategies, and human environment interactions.

Collaboration with palaeoclimatologists (see publication II) to apply high-resolution climate modelling could refine correlations between occupation phases and climatic fluctuations. This could allow further interpretations of settlement patterns and windows of enhanced mobility by hominins across Eurasia.

Technological and Behavioural Studies of Lithic Assemblages

Comparative techno-typological studies of Micoquian and other lithic assemblages could clarify cultural variability and technological continuity across the peninsula, linking Crimea more clearly to eastern European and Near Eastern dispersal corridors.

Functional analyses (e.g., use-wear, residue studies) could provide direct evidence for tool use and site function, complementing chronological and palaeoenvironmental data.

Inter-regional Comparisons

Future work should integrate Crimean data into broader Eurasian frameworks, comparing chronologies, lithic technologies, and genetic information with sites in Eastern Europe, the Caucasus, and the Near East. This may allow for further understanding of the hypotheses of refugia, migration routes and interactions between the last Neanderthals and early *Homo sapiens* across Eurasia.

8. Conclusion

This thesis has demonstrated that the application of advanced radiocarbon pre-treatment methods has the potential to fundamentally reshape our understanding of Palaeolithic chronologies and hominin presence across Eurasia. 63 new AMS radiocarbon dates from eight sites across the Crimean Peninsula enabled the testing of the proposition that Neanderthals survived later than in other areas of Eurasia in a refugium. The results, and the Bayesian models I built, show that Neanderthals associated with Micoquian techno-complexes were not present in Crimea as late as previously suggested (see manuscript I). Figure 6 of manuscript I clearly summarises the results of this work. This shows that, in contrast to previous interpretations that the Micoquian ended at around 40 ka cal BP (Chabai, 1998; Chabai, 2005; Pigott et al., 2024), the final Micoquian model boundary is older and dates to 73,430 to 41,050 cal BP (at 95.4% prob). This suggests that the Crimean Peninsula was not a refugium for Neanderthals. Instead, it shows once again the pervasive effects of underestimated radiocarbon dates due to unremoved contamination and the challenge of dealing with legacy data in this field.

Improvements in the pre-treatment chemistry of samples for dating is mirrored in improved approaches for extracting ancient biomolecules from bone. The application of ZooMS, the recovery of new hominin remains and the identification of genus and species information from fragmented assemblages demonstrates the emerging power of these approaches. Alongside climate modelling (see Publication II), this contributes to an emerging paradigm of wide-ranging movements of this hominin group during the Middle Palaeolithic, in contrast to what many previous researchers suspected.

Extending this methodological framework beyond Crimea, the application of XAD-2 pre-treatment at Glaston in the United Kingdom demonstrates the broader relevance of these approaches. The earliest securely dated evidence for *Homo sapiens* presence in the British Isles was obtained, contingent on a robust association between LRJ lithic technology and anatomically modern humans. Collectively, this thesis underscores the critical importance of re-analysing previously excavated Palaeolithic sites using modern analytical techniques. Improved chronological resolution is essential for refining interpretations of Neanderthal and *Homo sapiens* dispersal, technological traditions, and the timing and nature of the Middle to Upper Palaeolithic transition across Europe and beyond.

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10. Chapter 10. Appendix

10.1. Cova Foradada

During my thesis project across the three years, I have been involved in other research projects, primarily with ZooMS analysis in Spain.

Cova Foradada - HEAS Seed Grant

Investigating the Châtelperronian of Cova Foradada using palaeoproteomics, radiocarbon dating, ancient DNA and stable isotopes

During the pilot study of ZooMS analysis on 50 faunal remains from Cova Foradada, Level IV, with a 68% rate. Amongst the results, there was an interesting find of possible carnivorous marine animals (Figure 1). From these interesting results, I decided to apply for the HEAS Seed grant to investigate the faunal material at the site further.

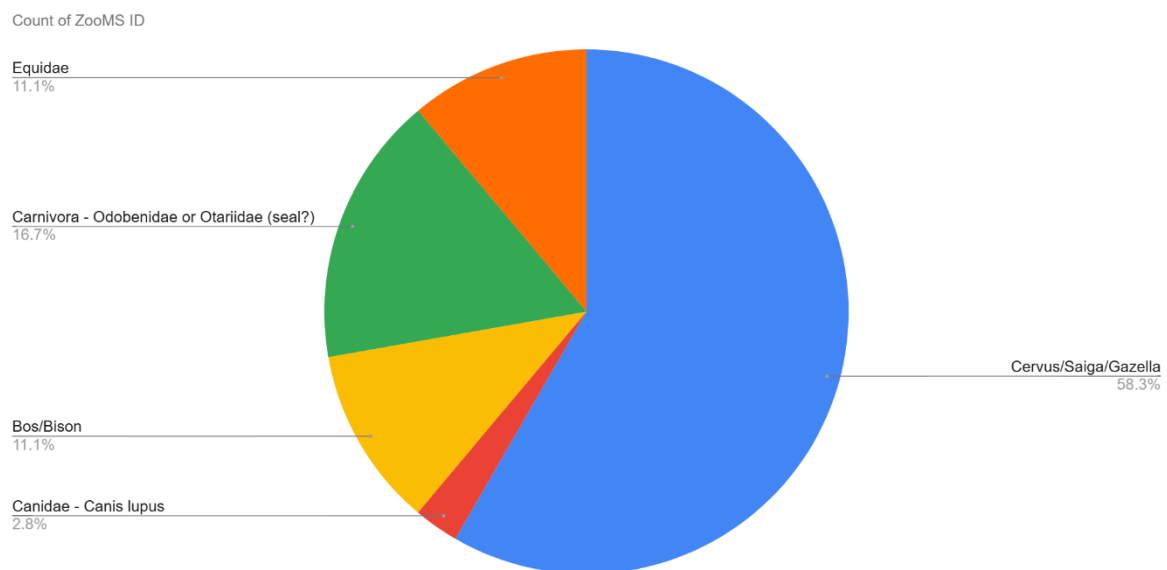


Figure 1. Taxonomic identifications from the pilot study of Cova Foradada, Level IV, using ZooMS analysis on 50 faunal samples.

In October 2025 we put in a proposal to HEAS for a Seed Grant proposition for ZooMS analysis on faunal samples from the site of Cova Foradada, which was successful.

Main applicant: Emily Pigott (PhD candidate, Department of Evolutionary Anthropology, University of Vienna).

Co-applicants: Professor. Tom Higham (University of Vienna, Department of Evolutionary Anthropology), Associate Professor. Katerina Douka (University of Vienna, Department of Evolutionary Anthropology), Associate Professor. Pere Gelabert (University of Vienna, Department of Evolutionary Anthropology), and Associate Professor. Peter Steier (University of Vienna, Faculty of Physics).

Objectives

- Sample 160 more faunal remains from Layer IV/IV.1/IV.2/IIIc (20 mg each sample) from IPHES, Tarragona
- Conduct ZooMS analysis on all samples
- Stable isotope analysis on all carnivorous marine identifications
- Radiocarbon date 5-7 new dates within layer IV
- Ancient DNA analysis on 2/3 carnivores' marine identifications

Significance to my current research

My current PhD project is centred on the Middle to Upper Palaeolithic transition period of the Crimean Peninsula. I have been using radiocarbon dating and ZooMS analysis to further understand the disappearance of Neanderthals within this region. By acquiring this HEAS Seed Grant, it will allow me to further explore a late Neanderthal site within a different region of Europe, falling under the wider scope of my research. We aim to undertake a sampling of 160 bones for a multi-disciplinary analysis, primarily using ZooMS to identify unidentifiable faunal remains. Five carnivore marine taxon identifications were previously determined, which we would like to re-sample and undertake ZooMS, radiocarbon dating (possibly with XAD-2 pre-treatment), stable isotopes and ancient DNA. These new findings are extremely important as no carnivore marine animals have been found this far north in the Iberian Peninsula within the Palaeolithic before. Carnivores' marine animals have been found in the extreme South of Iberian Peninsula, such as monk seals from the Epipalaeolithic site of Nerja Cave (Morales et al., 2019), seals and dolphins from the Middle-Upper Palaeolithic site of Vanguard and the Upper Palaeolithic site of Gorham's cave (Stringer et al., 2008). This makes the new findings at Cova Foradada extremely interesting.

Current results

ZooMS analysis has been completed on the 160 bones; 78 from Level IV, 41 from Level IV.1, 21 from Level IV.2 and 20 from the Aurignacian Level of IIIc. Overall, the results showed a success rate of 56.9%, with the highest rate of success being from Level IV (55%) and the lowest from Level IV.2 (23.8%). Five possible carnivorous marine animals were previously identified from Level IV. Within this new analysis, 5.7% (Figure 2) of the taxonomic

identifications were found to be possible from carnivores' marine animals. However, we must take these taxonomic identifications with great caution, as only three to four peptide markers were identified for these faunal remains. The other taxonomic identifications indicate a somewhat stable environment.

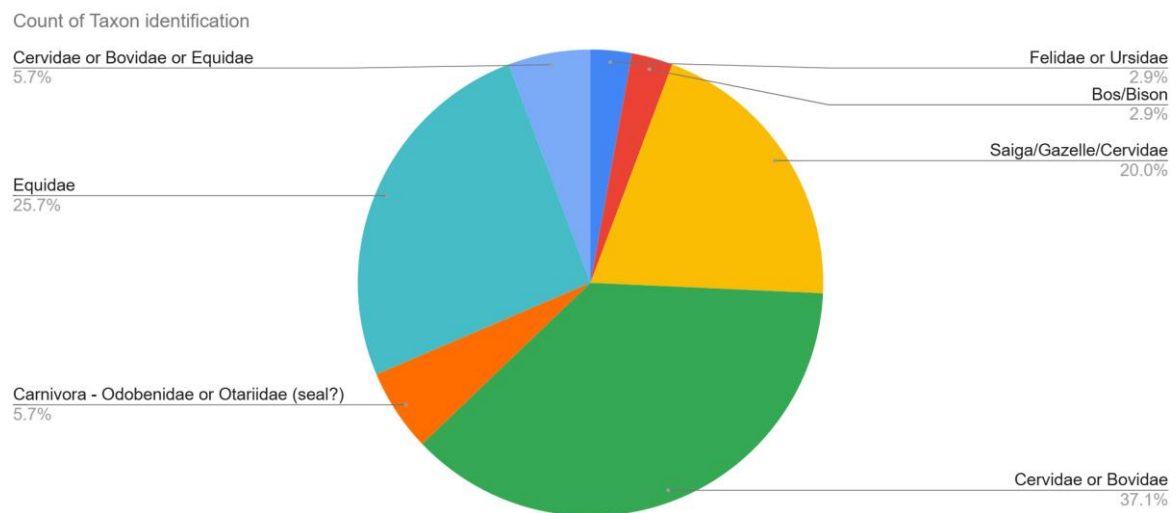


Figure 2. Taxon identifications of Level IV.

A similar group of taxon identifications was recognised from Level IV.1. A percentage of 22.2% was identified from some type of carnivorous marine animals (Figure 3). Five of the previous identified possible carnivorous marine animals were analysed with ZooMS again from the pilot study to see if the same result was achieved. Two of them came back as a type of carnivorous marine animal, the third being some sort of carnivorous mammal, the fourth coming back as Rodentia (extremely degraded peptide markers) and the fifth failing. However, again, these identifications have to be taken with great caution before further analysis is undertaken with different methods.

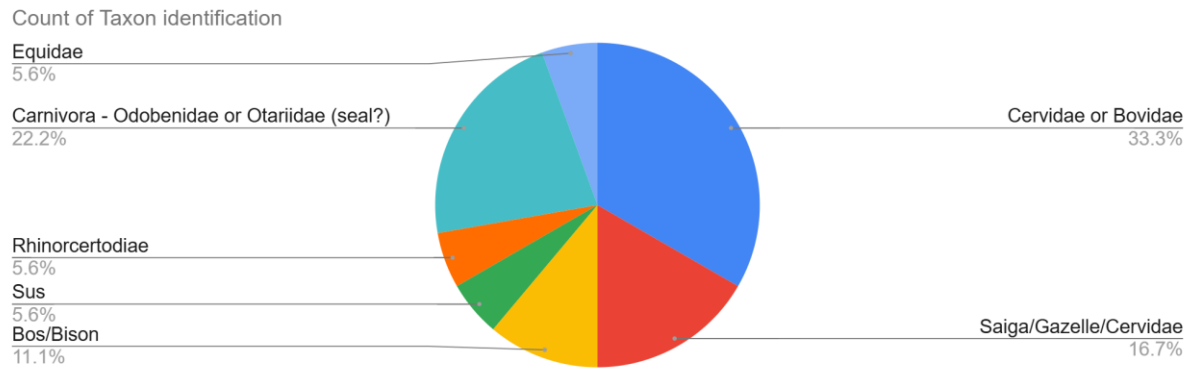


Figure 3. Taxon identifications of Level IV.1

From Level IV.2 and IIIc, only three taxon identifications were observed, being Cervidae or Bovidae, Saiga/Cervidae/Gazelle or Bos/Bison (Figure 3-4). This indicates a relatively stable environment, most likely in an open steppe.

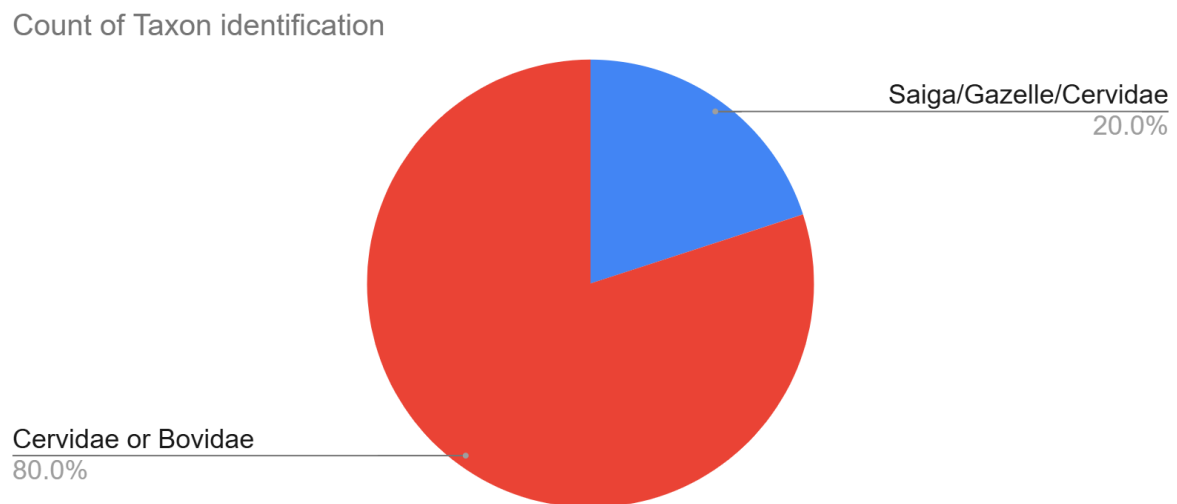


Figure 3. Taxon identifications of Level IV.2

Count of Taxon identification

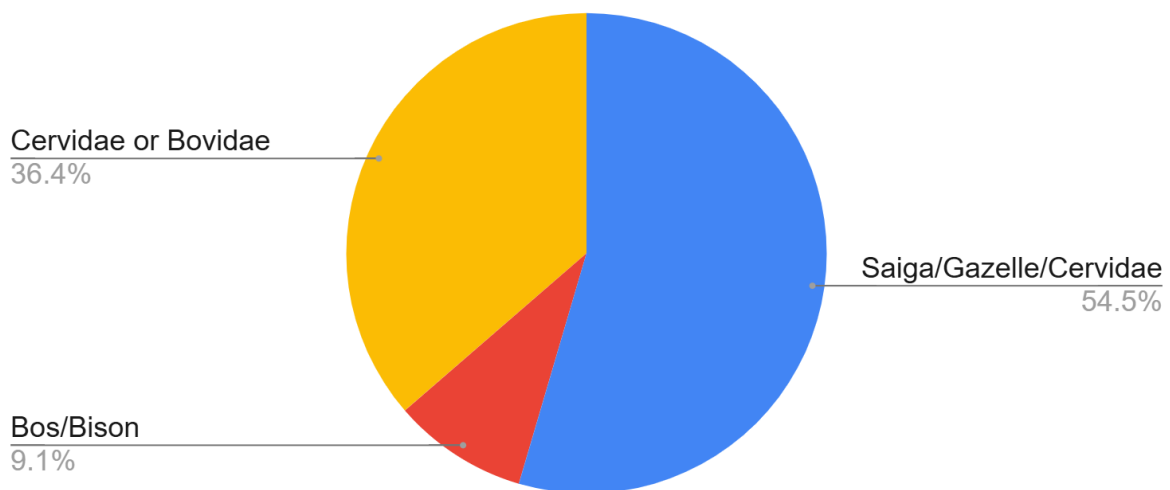


Figure 4. Taxon identifications of Level IIIc

Further work will be undertaken on the possible carnivorous marine animals from Levels IV and IV.1. This includes re-spotting these samples and re-analysing the peptide markers again. Also, all samples will be analysed using a somewhat automatic method through species scan (Végh & Douka 2024). This will allow a comparison between manual and semi-automated methods. Furthermore, stable isotope analysis will be undertaken on the possible carnivorous marine animals; to absolutely identify if they are marine mammals, before being possibly processed for ancient DNA. Radiocarbon dating, possibly with the pre-treatment of XAD-2 will then be undertaken on selected bones within Level IV to re-asertain the chronological position of the Châtelperronian at Cova Foradada, with minimal contamination influence (XAD-2).

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10.2. Labeko Koba

At the start of my PhD project, I was also involved in the project of Labeko Koba with my supervisor Prof. Tom Higham and Prof. Alvaro Arrizabalaga, who is based at the University of the Basque Country. I performed ZooMS analysis on 200 bones, with the intention of undertaking ZooMS analysis on a further 800 bones further into my PhD project. However, it proved difficult and time-consuming to obtain the essential permits to perform this analysis, which is why no further work has been taken by myself on this project.

The collapsed Upper Palaeolithic cave site of Labeko Koba, located in the Basque Country is in the south-western region of Gipuzkoa and underwent excavation between 1987 and 1988. The site has been dated to around 36,000 – 44,000 cal BP, across levels IV and IX via radiocarbon dating at Oxford University (Wood et al., 2014). The site comprises nine archaeological levels (Figure 1). Level IX (Figure 2) holds particular significance, due to its abundant faunal and lithic assemblage, which is exclusively attributed to the Châtelperronian industry, represented by 62 lithic artifacts (Wood et al., 2014). Notably, level VIII, located directly above IX is completely sterile, which has contributed to the exceptional preservation of level IX (Altuna & Mariezkurrena, 2000). Level IX has been divided into two distinct sections. The lower contains a combination of both lithics and animal bones, while the upper primarily consists of faunal remains, with only a limited number of lithic artefacts (Arrizabalaga, 2000).



Figure 1. State of the excavation before undertaking the final phase of the work (bands). From (Arrizabalaga, 2000, p.34).

The Châtelperronian is interpreted by many as being the last known lithic industry made by Neanderthals in France and Northern Spain prior to their extinction (Soressi & Rousset, 2020). It is believed to have originated prior to the final Mousterian and preceded the appearance of all Aurignacian assemblages. However, while there is a high probability of this sequence, it is not considered an absolute certainty (Wood et al., 2014). The link between the Châtelperronian and Neanderthals has also been a subject of vigorous debate at various archaeological sites. Most notably, recent findings at the Grotte du Renne (Arcy-sur-Cure) in France has raised questions. There, the co-mingling of Neanderthal remains alongside items of Upper Palaeolithic ornaments and jewellery usually attributed to anatomically modern humans (AMH) has been debated, with some suggesting that taphonomic movement is the cause for the material being found together, and others arguing that there is no evidence for this. Recently, a potential neonatal AMH bone was reported to have come from within a Châtelperronian layer (Gicqueau et al., 2023). This might suggest that the site was occupied by more than one type of hominin, but it raises again the important and challenging issue of linking a biological species to an archaeological technocomplex.

A pilot study of 200 bone for ZooMS analysis was requested with the heritage government body in the Basque country, to identify unidentified bones from the Châtelperronian level at Lebeko Koba.

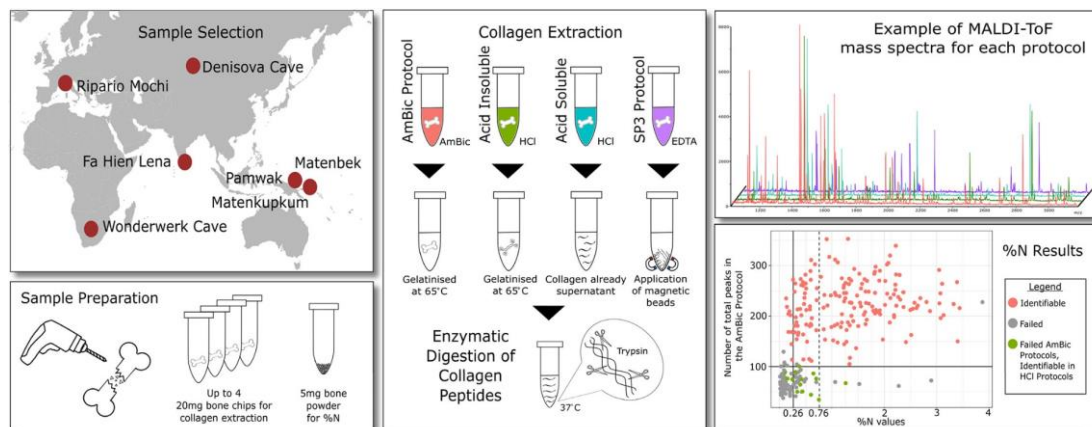


Figure 2. ZooMS standard protocol. From Wang et al. (2021)

Results

Out of 200 bones which was analysed with ZooMS, a high percentage of 84.3% of faunal remains were successful. This shows that Lebeko Koba has a high preservation percentage at the site, which may also be reflected by previous radiocarbon dating at the site. Radiocarbon dating has been undertaken on 18 faunal samples, across archaeological levels IV throughout to IX, using ultrafiltration at the University of Oxford (Wood et al., 2014). This has resulted in a robust chronology.

The overall taxon identifications from the pilot study of faunal remains indicates a somewhat stable environment (Figure 3). This is represented by all taxon identifications, which are usually found in open steppe environment.

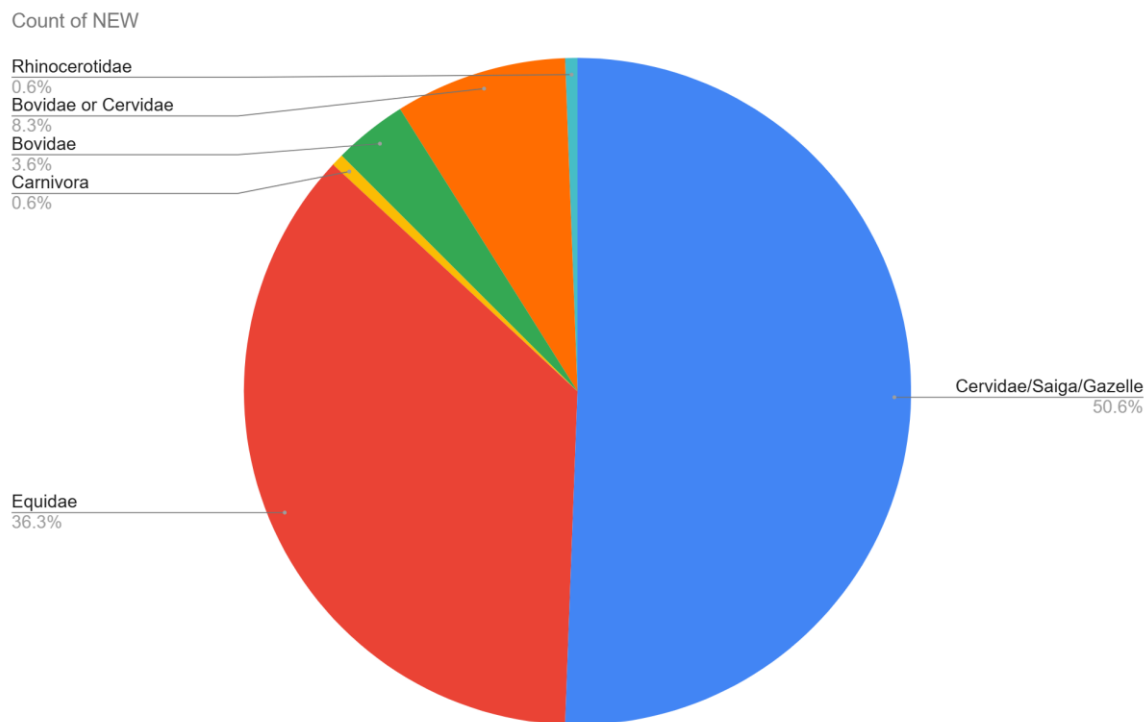


Figure 3. Overall results for taxon identifications from Labeko Koba.

Future work

A project permit has been sent to the heritage government in the Basque country to ask for permission to do a further analysis at the site. Within Level IX, there is still a considerable number of fragmented materials, which has never been able to be identified up to this presence date. A suggested number of 800 more bones was recommended for further analysis, with only 20 mg taken from each bone. However, we are still waiting for the results if this will be accepted by the Basque heritage government agency for sampling and analysis.

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