



MULTIPROXY RECONSTRUCTION OF THE ECOLOGICAL CONTEXT OF THE PLIO-PLEISTOCENE TRANSITION AND EARLY MIDDLE PLEISTOCENE IN MOROCCO

Iván Ramírez Pedraza

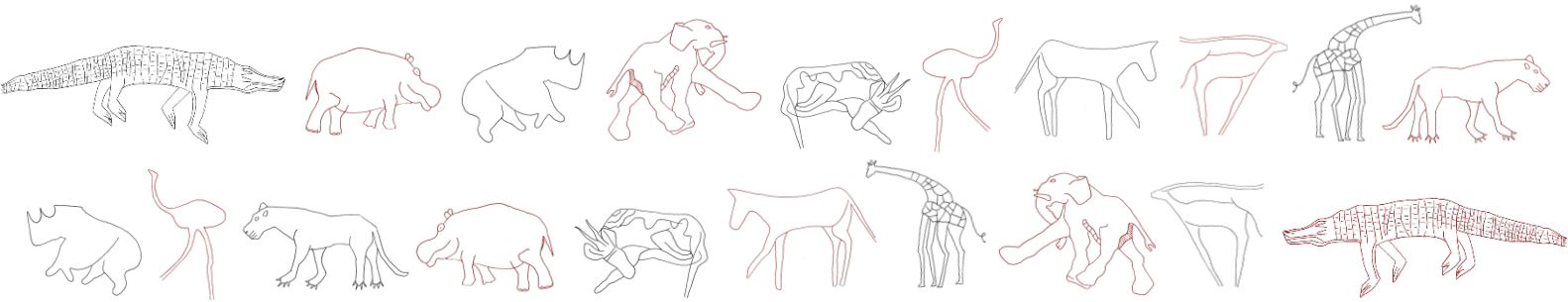
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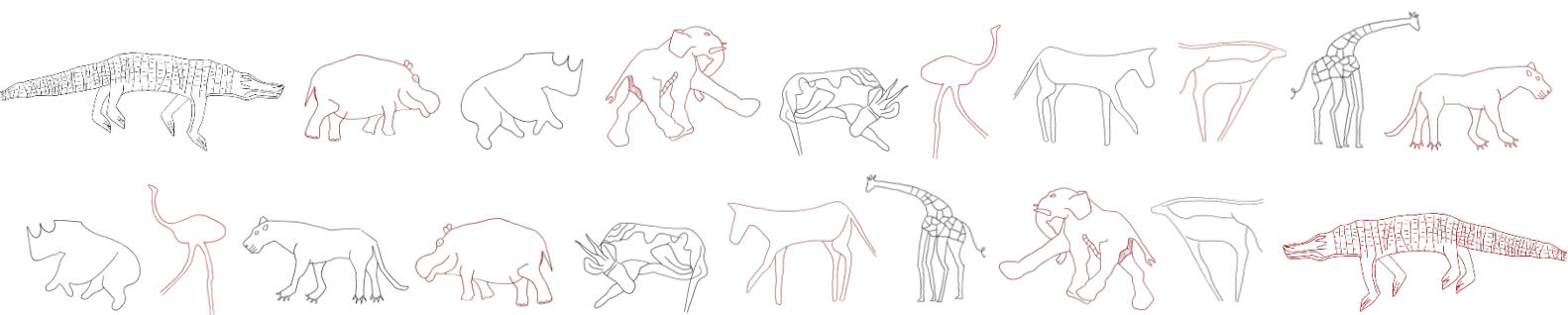


UNIVERSITAT
ROVIRA I VIRGILI



Multiproxy reconstruction of the ecological context of the Plio-Pleistocene transition and early Middle Pleistocene in Morocco

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DOCTORAL THESIS
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DOCTORAL THESIS

Supervisors:

Dr Florent Rivals

Dr Carlos Tornero



**UNIVERSITAT ROVIRA I VIRGILI
Departament d'Història i Història de l'Art**

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FAIG CONSTAR que aquest treball, titulat “Reconstrucció multiproxy del context ecològic del límit Plio-Plistocè i el Plistocè Mitjà al Marroc”, que presenta **Iván Ramírez Pedraza** per a l’obtenció del títol de Doctor, ha estat realitzat sota la meva direcció al Departament d’Història i Història de l’Art d’aquesta universitat.

HAGO CONSTAR que el presente trabajo, titulado “Reconstrucción multiproxy del contexto ecológico del límite Plio-Pleistoceno y el Pleistoceno Medio en Marruecos”, que presenta **Iván Ramírez Pedraza** para la obtención del título de Doctor, ha sido realizado bajo mi dirección en el Departamento de Historia e Historia del Arte de esta universidad.

I STATE that the present study, entitled “Multiproxy reconstruction of the ecological context of the Plio-Pleistocene transition and early Middle Pleistocene in Morocco”, presented by **Iván Ramírez Pedraza** for the award of the degree of Doctor, has been carried out under my supervision at the Department of History and History of Art of this university.

Tarragona, 30 d’agost de 2024

Els directors de la tesi doctoral
Los directores de la tesis doctoral
Doctoral Thesis Supervisors

Dr Florent Rivals

Dr Carlos Tornero

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· Abstract ·

The discovery of archaeological sites with hominin presence dated to the Early Pleistocene to the Middle Pleistocene has conferred a significant role to North Africa, especially Morocco and Algeria, integrating this territory into the global discussions of human evolution alongside eastern and southern Africa. A better understanding of the dynamics of the Green Sahara Events has allowed the identification of multiple humid episodes that could have favoured the dispersal of various species, including hominins. However, despite this diachronic occupation of the Maghreb area, there is limited knowledge about the ecological context in which these different occupations occurred.

For this thesis, various archaeological and palaeontological sites in Morocco dated to the Plio-Pleistocene transition (Guefaït-4.2 and Ahl al Oughlam) and to the early Middle Pleistocene (Oued Rabt, Grotte à Hominidés, and Grotte des Rhinocéros) have been selected, located, on the one hand, on the Atlantic coast of the present-day city of Casablanca (western Morocco), and the other hand, in the Maghreb depression of the Intra-Atlas in the Aïn Beni Mathar – Guefaït basin (eastern Morocco). This work aims to reconstruct the landscape of these sites and their surroundings and to characterise the diet of the large vertebrates.

To achieve this, different methods with different temporal resolutions have been used: dental microwear (buccal and occlusal surfaces), dental mesowear, analysis of carbon and oxygen isotopes in the dental enamel of mammals (bulk and sequential analysis of the crown), and finally, isotopic analysis of carbon of *n*-alkane chains found in plant waxes recovered from sediments.

Overall, the results indicate a predominantly arid environment in both the Plio-Pleistocene transition sites and those of the early Middle Pleistocene. On the Atlantic coast, the data show a similar pattern between 2.5, 0.77, 0.7 and 0.5 million years, with a predominance of open spaces dominated by C₃ grasslands and shrubs, where forested environments might be very residual. The type of landscape and climate are similar regardless of whether hominins are present. In eastern Morocco, during the Plio-Pleistocene, the defined landscape is much more diverse, including forests, wetlands, shrubs, and C₃ and C₄ grasslands. Considering that Guefaït-4.2 is relatively close in distance and chronology to Ain Boucherit, the oldest site with human presence in the Maghreb, we hypothesise that this diversity of habitats and resources could have favoured the occupation of the first hominins in northern Africa.

· Resumen ·

El descubrimiento de yacimientos arqueológicos con presencia antrópica con dataciones del Pleistoceno Inferior hasta el Pleistoceno Medio ha otorgado al Norte de África, especialmente a Marruecos y Argelia, un papel significativo en la evolución humana, integrando este territorio en los grandes discursos sobre la evolución de los primeros homínidos junto al este y sud del continente. A la vez, un mejor entendimiento de las dinámicas de los eventos de reverdecimiento del Sahara ha permitido identificar múltiples episodios húmedos que podrían haber favorecido la dispersión de diversidad de especies, entre ellas los homínidos. Sin embargo, a pesar de esta evidente ocupación diacrónica del área del Magreb, se conoce muy poco sobre el contexto ecológico en el que ocurrieron estas diferentes ocupaciones.

Para esta tesis, se han seleccionado varios yacimientos arqueológicos y paleontológicos marroquíes datados en el límite Plio-Pleistoceno (Guefaït-4.2 y Ahl al Oughlam) y en el Pleistoceno Medio inicial (Oued Rabt, Grotte à Hominidés y Grotte des Rhinocéros), localizados, por un lado, en la costa Atlántica de la actual ciudad de Casablanca (oeste de marruecos), y por otro, en la depresión magrebí del Intra-Atlas en la cuenca de Aïn Beni Mathar – Guefaït (este de marruecos). El objetivo de este trabajo es reconstruir el paisaje de dichos enclaves y sus alrededores y caracterizar la dieta de los mamíferos.

Para ello hemos empleado el uso de diferentes métodos con distintas resoluciones temporales: el microdesgaste dental (superficies bucal y oclusal), el mesodesgaste dental, el análisis de los isótopos de carbono y oxígeno en el esmalte dental de la fauna (*bulk* y análisis secuencial de la corona), y finalmente el análisis isotópico de carbono de las cadenas de *n*-alcanos encontrados en la cera de las plantas recuperadas de los sedimentos.

En general, los resultados indican un ambiente predominantemente árido tanto en los yacimientos del límite Plio-Pleistoceno como los del Pleistoceno Medio inicial. En la costa atlántica los datos muestran un patrón ambiental muy similar entre 2,5, 0,77, 0.7 y 0,5 millones de años, con una predominancia de espacios abiertos dominados por pastizales y matorrales C₃, y una cobertura vegetal muy escasa. El tipo de paisaje y clima es similar independientemente de si hay presencia de homínidos o no. En el este de Marruecos durante el Plio-Pleistoceno, el paisaje definido es mucho más diverso, incluyendo bosques, humedales, matorrales y pastizales tanto C₃ como C₄. Teniendo en cuenta que Guefaït-4.2 se encuentra relativamente cerca en distancia y cronología de Ain Boucherit, yacimiento más antiguo con presencia antrópica del Magreb, planteamos la hipótesis de que esta diversidad de hábitats y recursos pudiera haber favorecido la ocupación de los primeros homínidos en el Norte de África.

· Resum ·

El descobriment de jaciments amb presència humana des del Pleistocè Inferior fins al Pleistocè Mitjà ha conferit al Nord d'Àfrica, especialment a Marroc i Algèria, un paper significatiu en l'evolució humana, integrant aquest territori als grans discursos de la evolució dels primers homínids juntament amb l'est i sud de l'Àfrica. Un millor coneixement de les dinàmiques dels esdeveniments de reverdiment del Sàhara ha permès identificar múltiples episodis humits que podrien haver afavorit la dispersió de diverses espècies, incloent els homínids. No obstant això, malgrat aquesta ocupació diacrònica de l'àrea del Magrib, existeixen molt poques dades sobre el context ecològic en què van ocórrer aquestes diferents ocupacions.

Per a aquesta tesi, s'han seleccionat diversos jaciments arqueològics i paleontològics marroquins datats en el límit Plio-Pleistocè (Guefaït-4.2 i Ahl al Oughlam) i en el Pleistocè Mitjà inicial (Oued Rabt, Grotte à Hominidés i Grotte des Rhinocéros), localitzats, d'una banda, a la costa atlàntica de l'actual ciutat de Casablanca (oest de Marroc), i d'altra banda, a la depressió magrebina de l'Intra-Atlas a la conca d'Aïn Beni Mathar – Guefaït (est del Marroc). L'objectiu d'aquest treball és reconstruir el paisatge d'aquests jaciments, i els seus voltants, i caracteritzar la dieta dels mamífers.

Per a això, s'han utilitzat diferents mètodes amb diferents resolucions temporals: microdesgast dental (superfícies bucal i oclusal), mesodesgast dental, anàlisi dels isòtops de carboni i oxigen en l'esmalt dental de la fauna (anàlisi *bulk* i seqüencial de la corona), i finalment, l'anàlisi isotòpic de carboni de les cadenes de *n*-alcans trobats a la cera de les plantes recuperades dels sediments.

En general, els resultats indiquen un ambient predominantment àrid tant en els jaciments del límit Plio-Pleistocè com en els del Pleistocè Mitjà inicial. A la costa atlàntica, no s'observen canvis ambientals entre 2,5, 0,77, 0,7 i 0,5 milions d'anys, amb una predominança d'espais oberts dominats per prats i matollar C₃, i una cobertura vegetal general molt escassa. El tipus de paisatge i clima és similar independentment de si hi ha presència d'homínids o no. A l'est de Marroc, durant el Plio-Pleistocè, el paisatge definit és molt més divers, incloent boscos, zones humides, matollar i prats tant C₃ com C₄. Tenint en compte que Guefaït-4.2 és relativament a prop en distància i cronologia de Ain Boucherit, el jaciment més antic amb presència humana al Magrib, plantegem la hipòtesi que aquesta diversitat d'hàbitats i recursos podria haver afavorit l'ocupació dels primers homínids al Nord d'Àfrica.

Table of contents

· <i>Acknowledgment</i> ·	<i>i</i>
· <i>Abstract</i> ·	<i>iii</i>
· <i>Resumen</i> ·	<i>iv</i>
· <i>Resum</i> ·	<i>v</i>
· <i>Chapter 1: Introduction</i> ·	1
1.1. This dissertation	1
1.2. Objectives	2
1.3. Chapters Summaries	3
· <i>Chapter 2. Theoretical framework</i> ·	5
2.1. Climate changes and hominin evolution	5
2.2. The role of northern Africa in human evolution: Pliocene and Pleistocene sites.....	7
2.3. State of the art of paleoenvironmental studies in northern Africa.....	10
· <i>Chapter 3: Study region and analysed materials</i> ·	15
3.1. Eastern Morocco	15
3.1.1. Plio-Pleistocene transition site of Guefaït-4.....	15
3.1.1.1. Site description.....	15
3.1.1.2. Materials.....	18
3.1.2. Middle Pleistocene site of Oued Rabt.....	20
3.1.2.1. Site description.....	20
3.1.2.2. Material	21
3.2. Western Morocco	22
3.2.1. Plio-Pleistocene transition site of Ahl al Oughlam	22
3.2.1.1. Site description.....	22
3.2.1.2. Materials.....	24
3.2.2. Middle Pleistocene sites of Grotte à Hominidés and Grotte des Rhinocéros	25
3.2.2.1. Sites description	25
3.2.2.1.1. Grotte à Hominidés.....	25
3.2.2.1.2. Grotte des Rhinocéros	27
3.2.2.2. Materials.....	30
3.2.2.2.1. Grotte à Hominidés.....	30
3.2.2.2.1. Grotte des Rhinocéros	31

3.3. Reference collection of extant cercopithecines	32
· Chapter 4: Methods ·	35
4.1. Complementarity of selected methods	35
4.2. Enamel carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope analysis	36
4.3. Tooth wear analysis	40
4.3.1. Tooth mesowear analysis	40
4.3.2. Tooth microwear analysis	43
4.3.2.1 Occlusal low magnification microwear analysis	43
4.3.2.3 Buccal microtexture analysis	47
4.4. Plant wax biomarkers analysis	49
· Chapter 5: Results ·	55
5.1. Eastern Morocco	55
5.1.1. Paper I: Ramírez-Pedraza et al. (2024). Arid, mosaic environments during the Plio-Pleistocene transition and early hominin dispersals in northern Africa. <i>Nature Communications (Accepted)</i>	55
5.1.2. Paper II: Ramírez-Pedraza et al. (2023). Multiproxy approach to reconstruct fossil primate feeding behavior: Case study for macaque from the Plio-Pleistocene site Guefaït-4.2 (eastern Morocco). <i>Frontiers in Ecology and Evolution (Published)</i>	84
5.1.3. Oued Rabt	101
5.1.3.1. Plant wax biomarkers analysis	101
5.2. Western Morocco	104
5.2.1. Paper III: Ramírez-Pedraza et al. (2023). Palaeoecological reconstruction of Plio-Pleistocene herbivores from the Ahl al Oughlam site (Casablanca, Morocco): Insights from dental wear and stable isotopes. <i>Quaternary Science Reviews (Published)</i>	104
5.2.2. Palaeoecological reconstruction of herbivores from Grotte à Hominidés (ThI-GH) and Grotte des Rhinocéros (OHQ1-GDR)	120
5.2.2.1. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) at ThI-GH and OHQ1-GDR	120
5.2.2.2. Dental mesowear analysis at ThI-GH and OHQ1-GDR	124
5.2.2.3. Dental microwear analysis at ThI-GH and OHQ1-GDR	125
5.2.3. Paper IV: Martínez et al. (2024). Ecological context of <i>Theropithecus oswaldi</i> from the early Middle Pleistocene site of Grotte à Hominidés at Thomas Quarry I through dental microwear analysis (Casablanca, Morocco) (Under review)	128
· Chapter 6: Discussion ·	159
6.1. Enamel carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope analysis in northern Africa	159

6.2. Tooth mesowear analysis in northern Africa	162
6.3. Tooth microwear analysis in northern Africa	164
6.4. Plant wax biomarkers analysis in northern Africa	168
6.5. General comparison with ecological data from the similar chronologies in Africa and Europe.....	169
· Chapter 7: Conclusions ·	173
· References ·	177
· Appendices ·	210

· Chapter 1: Introduction ·

1.1. This dissertation

This doctoral thesis includes the study of the ecological context of five archaeological and palaeontological sites from Morocco, covering two different periods and areas. On the one hand, the early Middle Pleistocene sites Grotte à Hominidés (~0.77 Ma) and Grotte des Rhinocéros (~0.7 and ~0.5 Ma) located in the west, on the Atlantic coast near Casablanca, and the Oued Rabt (~0.5 Ma) site is located in the Aïn Beni Mathar-Guefaït area, in the East of the country, near the Algerian border. On the other hand, the Plio-Pleistocene sites of Guefaït-4.2 (~2.5 Ma) and Ahl al Oughlam (~2.5 Ma) are located in the East and West, respectively.

Over these years, I had the privilege to personally visit the sites in Morocco and sampling materials from Grotte à Hominidés and Grotte des Rhinocéros at the Thomas I Quarry in Casablanca and those from Ahl al Oughlam at the National Institute of Archaeology and Heritage (INSAP) in Rabat. We also accessed materials from level L (~1.3 Ma) in the Thomas I Quarry. However, there were very few teeth in the assemblage. Since the excavation is ongoing, sampling was postponed until more faunal remains are available. In eastern Morocco, I also participated in the excavation campaigns of 2018 and 2019 at the Guefaït-4.2 site, recovering some of the remains used in this study.

Two types of material have been used for this palaeoenvironmental reconstruction. Firstly, we examined sediments, specifically the *n*-alkanes of lipids extracted from them—a method I had the opportunity to learn during my international stay at the Max Planck Institute of Geoanthropology in Jena (Germany) under the supervision of Dr Patrick Roberts, Dr Robert Patalano, and Dr Deepak Jha. Secondly, the central focus of this thesis is the teeth of macromammals, through which we reconstructed diet and habitat using dental wear analysis and stable isotope analysis at the IPHES-CERCA institution (Tarragona, Spain). The diversity of species and the substantial volume of material were key factors in selecting these sites (excluding Oued Rabt). In addition to herbivores, which, as primary consumers, provided direct insights into the landscape, special mention should be made of the cercopithecids. For these primates, we created a reference collection of extant species for dental microwear comparison with fossils. In collaboration with researcher Dr Laura Martínez (University of Barcelona, Spain), I gained experience learning the microtexture analysis technique with the confocal microscope, gaining insights into the paleoecology of cercopithecids during the last years. This multidisciplinary approach aims to provide a more comprehensive understanding of the landscape of this North African region at different critical moments in the occupation and dispersion of hominins.

What is the rationale for this doctoral thesis?

The archaeological evidence indicates that northern Africa, mainly Morocco and Algeria, was inhabited by hominins during the Early and Middle Pleistocene, with at least well-

attested events dating approximately 2.4, 1.8, 1.7, 1.3, 0.77, 0.7, 0.5 and 0.4 million years. Currently, there is also more significant knowledge of the dynamics of multiple greening events in the Sahara, which could have facilitated the dispersion of a significant number of animal species. Additionally, large-scale global studies have increasingly established a gradual shift towards a drier climate and environmental variability during the transition from the Pliocene to the Pleistocene.

However, there is limited data on the local and regional ecological context in which these dispersions and occupations occurred in these territories, particularly for archaeological and paleontological sites. The question arises: Is there a climatic pattern for northern Africa that could have favoured different dispersion events during the Plio-Pleistocene transition to the Middle Pleistocene? Were these dispersals linked to more open and arid habitats or perhaps more closed spaces like forests? Are there similarities in the data between fossil sites on the Atlantic coast of Morocco and those further inland in the Intra-Atlas Maghrebian Depression? Are there ecological similarities between northern, eastern, southern, or Central Africa with Europe? Does the global-scale information align with the local-scale data?

Therefore, this thesis is designed to fill this knowledge gap, addressing the objectives outlined in the following section.

1.2. Objectives

The **main objective** of this thesis is to reconstruct the ecological context of early Middle Pleistocene and Plio-Pleistocene transition sites in a diachronic framework, focusing on the eastern (Aïn Beni Mathar-Guefaït) and western (Casablanca) regions of Morocco. Primarily, this involves characterising the diet and inferring the habitat of macromammal communities in northern Africa during the periods and areas mentioned.

Within this overarching goal, several **subsidiary objectives** can be identified:

- Compare palaeoecological data during the same period in different regions of Morocco (East vs. West).
- Compare palaeoecological data diachronically in western Morocco
- Integrate the collected data to reconstruct the palaeoecological context of the first hominid settlements in northern Africa.
- Compare the obtained data with those from the same chronology in other African regions, such as the central, eastern, or southern areas.
- Establish a new reference collection for low-magnification dental microwear analysis of modern cercopithecids to compare with fossil cercopithecids.

1.3. Chapters Summaries

This doctoral thesis is structured into eight chapters, including four scientific publications: two were published, one was accepted, and one is under review. Additionally, we have included unpublished results that have not yet been submitted to any journal.

Chapter 1 summarises the rationale for this thesis, introducing the research problem and the questions that led to this work. This is connected to the thesis objectives and provides an overview of each chapter's content.

Chapter 2 includes the theoretical framework of this work. Firstly, an introduction discusses the significance of theories linking hominin evolution to changes in climate and landscape. Secondly, the focus is on the study area, northern Africa, presenting the most important archaeological and palaeontological sites from the periods covered in this thesis. Lastly, the chapter presents the state of the art of the principal results on the ecological context in northern Africa during the Pleistocene and Pliocene.

Chapter 3 describes the five studied sites, including their location, characteristics, stratigraphy, chronology, previous works, and the materials analysed.

Chapter 4 provides a detailed explanation of the methodology used in the study of materials, covering enamel carbon and oxygen stable isotope analysis (bulk and sequential), tooth wear analysis (mesowear and microwear, including occlusal microwear and buccal microtexture analysis), and plant wax biomarkers analysis.

Results are presented in **Chapter 5**, divided into two parts for eastern and western Morocco. For the East, Paper I focuses on the ecological context of Guefaït-4.2 (~2.5 Ma) (dental wear, stable isotopes, and plant wax biomarkers). Paper II explores the palaeoecology of one of the species from Guefaït-4.2, *Macaca cf. sylvanus*, using dental microwear and stable isotopes. The chapter concludes with the results (not submitted) of plant wax biomarkers from the Oued Rabt site (~0.5 Ma).

In the western part, results (Paper III) on the ecological context of Ahl al Oughlam (~2.5 Ma) based on dental wear and stable isotopes are presented first. Subsequently, the results (not submitted) of dental wear and stable isotopes from Grotte à Hominidés (~0.77 Ma) and Grotte des Rhinocéros (~0.7 and ~0.5 Ma) are discussed. Finally, similar to the approach with *M. cf. sylvanus* from GFT-4.2, an in-depth analysis of the diet and habitat of *Theropithecus oswaldi* from Grotte à Hominidés is presented, focusing on dental microwear.

Chapter 6 comprises the discussion, structured into five sections where all the results from each of the methods used (stable isotopes, mesowear, microwear, and plant wax biomarkers) are synthesised. Additionally, the ecological context is compared with other contemporaneous sites analysed in Africa and Europe.

Chapter 7 outlines the main conclusions drawn from this work, aligning with the thematic lines that constitute the objectives of this doctoral thesis.

Finally, after the **references**, the **appendices** include the supplementary materials from the results.

· Chapter 2. Theoretical framework ·

2.1. Climate changes and hominin evolution

Climate and landscape changes and their influence on the evolution and development of Pliocene and Pleistocene mammals, particularly hominins, have been the subject of extensive debates (Menocal, 1995; Cerling et al., 1997; Reed, 1997; Cerling et al., 2011; Potts, 1998, 2013; Kingston, 2007; Maslin et al., 2015; Faith et al., 2021; Patalano et al., 2021a; Bobe and Reynolds, 2022). Throughout the 20th century, various hypotheses emerged connecting critical aspects of human evolution, such as speciation, extinction, dispersals, and morphological or behavioural changes, to environmental changes (Dart, 1925; Washburn, 1960; Vrba, 1985; Coppens, 1994; Potts, 1996, 1998; Maslin et al., 2014, 2015; Patalano et al., 2021a). One of the most impactful, partly due to being among the earliest, was the "savannah hypothesis" developed by Raymond Dart in 1925 following the discovery of *Australopithecus africanus* in southern Africa. He proposed that a shift from a closed, wooded habitat to an open one, like the savannah, favoured the emergence of bipedalism, tool use, and encephalisation (Dart, 1925; Washburn, 1960). Along similar lines is the "East side story" hypothesis, linking a specific habitat, the emergence of the savannah in the Great Rift Valley, as a key factor in the separation between *Pan* and *Homo* from their common ancestor and the origin of bipedalism (Coppens, 1994). Other hypotheses, like the "Turnover pulse" (Vrba, 1985), "Variability selection" (Potts, 1996), and "Pulsed climate variability" (Maslin et al., 2014) with different nuances, connect phases of relatively rapid climatic changes, such as transitioning from a wet to an arid environment, with significant effects on the evolution and adaptation of various mammalian lineages. The majority of these hypotheses on human evolution and the environment-hominin relationship originated in a scientific context that lasted over 50 years, during which only the species *Australopithecus africanus* (Dart, 1925) and *Australopithecus afarensis* (Day et al., 1980) were known, dated between 4 and 2.5 million years ago and located in southern Africa and eastern Africa, respectively.

In recent years, primarily due to the proliferation of multiproxy research applied to reconstruct ecological contexts, the landscape defined for these early hominins has become increasingly "complex". Concepts and hypotheses seeking simplification, such as specific habitats or drastic climate changes, have given way to heterogeneity, mosaic landscapes, or microhabitats to highlight the significant role played by the adaptive capacity of these hominins, especially the genus *Homo*, in contexts dominated by ecological diversity (Kingston, 2007; Potts et al., 2020; Faith et al., 2021; Patalano et al., 2021a; Foister et al., 2023; Peppe et al., 2023; Zeller et al., 2023).

This paradigm shift regarding the predominant type of landscape defined for these early hominins has been accompanied by progressive palaeoanthropological discoveries from the late 20th century to the early 21st century (Gibbons, 2002). In a relatively short period,

numerous new hominin species were described in Africa: *Australopithecus garhi* (2.6 - 2.5 Ma; Asfaw et al., 1999), *Australopithecus deyiremeda* (3.5 - 3.3 Ma; Haile-Selassie et al., 2015), *Kenyanthropus platyops* (3.5 Ma; Leakey et al., 2001), *Australopithecus bahrelghazali* (3.5 Ma; Brunet et al., 1995; Lebatard et al., 2008), *Australopithecus anamensis* (4.1 - 3.9 Ma; Leakey et al., 1995), *Ardipithecus ramidus ramidus* (4.4 Ma; White et al., 1994), *Ardipithecus ramidus kadabba* (5.8 - 5.2 Ma; Haile-Selassie, 2001), *Orrorin tugenensis* (6 Ma; Senut et al., 2001), and *Sahelanthropus tchadensis* (7.2 - 6-8 Ma; Brunet et al., 2002; Lebatard et al., 2008).

The oldest presence of hominins extends from 7 to 4 Ma. Despite the majority of the species mentioned above being discovered in eastern Africa (Kenya and Ethiopia), for the first time, two species were described far from southern Africa and the Great Rift Valley, namely *Australopithecus bahrelghazali* and *Sahelanthropus tchadensis*, bipedal around 7 Ma (Guy et al., 2022), both found in Central Africa (Chad). Beyond the palaeoanthropological data classifying the mentioned species within the hominin lineage (Robson and Wood, 2008), the presence of lithic tools, as well as the discovery of butchery marks on fossils, are other pieces of evidence considered in the archaeological record to determine the presence of hominins.

The use of tools has traditionally been linked to the genus *Homo* (Leakey et al., 1964; Harris, 1983). However, the appearance of tools in contexts associated with other hominins such as *Paranthropus* (Plummer et al., 2023) or *Australopithecus* (McPherron et al., 2010) raises doubts about that direct relationship. It is also true that chronological proposals regarding the origin of the genus *Homo* are extending further back in time. According to the description of a jaw discovered in Ethiopia, it dates back to 2.8 Ma (Villmoare et al., 2015), even older (approx. 3.3 Ma) if we consider the study by Püschel et al. (2021) based on estimates of evolutionary divergence.

Regardless of the species responsible for making these tools, the reality is that, to date, the oldest ones are found in eastern Africa (de la Torre, 2011; Key and Proffitt, 2023). In the Lomekwi 3 (3.3 Ma; Harmand et al., 2015) and Nyayanga (3 Ma; Plummer et al., 2023) sites in Kenya, and in Gona (2.6 Ma; Semaw et al., 2003) and Ledi-Geraru (2.6 Ma; Braun et al., 2019) in Ethiopia. Although more recent, the first evidence of tools in southern Africa appears at 2.2 Ma in the Sterkfontein site (Granger et al., 2015).

In northern Africa, the study area of this thesis, sites such as Ain Hanech (Sahnouni and De Heinzelin, 1998; Sahnouni et al., 2012; Duval et al., 2023), El Kherba (1.7 Ma; Sahnouni et al., 2012, 2017), and Ain Boucherit (2.4-1.9 Ma; Sahnouni et al., 2018; Duval et al., 2021; Cáceres et al., 2023) with Oldowan lithic industry and evidence of animal carcass exploitation are also present.

This ancient presence of hominins in previously underexplored regions of Africa, such as the central and northern areas, has significantly expanded research into human evolution. The new evidence has prompted the scientific community to reevaluate the origins of early hominins from a more comprehensive Pan-African perspective (Brunet et al., 1995, 2005; Sahnouni et al., 2018). This new perspective, involving the entire African continent,

is also applicable to the origin of *Homo sapiens* with the discovery of the oldest fossils of our species, dated to approximately 0.3 Ma at the Jebel Irhoud site in Morocco (Hublin et al., 2017).

2.2. The role of northern Africa in human evolution: Pliocene and Pleistocene sites

The information regarding the dynamics of dispersals and occupations of mammals in northern Africa from the Early Pleistocene is quite limited (Lahr, 2010). Despite being part of the African continent, this territory is geographically close to the Iberian Peninsula latitudinally and considerably distant from the Great Rift Valley (over 5000 km) or Chad (2500 km). The Maghreb is "bounded" by two major geographical barriers: the Mediterranean Sea to the north, separating it from the Iberian Peninsula, and the Sahara Desert to the South, separating it from Sub-Saharan Africa. Regarding connections between the Maghreb and the South of the Iberian Peninsula, one hypothesis suggests the possibility that different groups of mammals, including hominins, could have crossed the Strait of Gibraltar or the Alborán Sea due to the short distance and potential sea level fluctuations at certain times (Gibert et al., 2003, 2016; García-Nos et al., 2019). However, there is no correlation between the archaeological record on both sides during the Pleistocene (Hublin et al., 2017; Tafelmaier et al., 2017; Sahnouni et al., 2018).

In the case of early hominins, the oldest evidence on the Iberian Peninsula is found in the Barranco León and Fuente Nueva-3 sites in Orce (Granada), dating back to ~1.4 Ma (Toro-Moyano et al., 2013; Palmqvist et al., 2022). Furthermore, the Sima del Elefante site in the Sierra de Atapuerca in Burgos, with a similar chronology, provides evidence of the presence of early hominins (Carbonell et al., 2008). On the other hand, the oldest occupations outside of Africa seem to follow the Levantine corridor, as demonstrated by the 1.85 Ma *Homo* fossils from the Dmanisi site in Georgia (Gabunia and Vekua, 1995; Ferring et al., 2011) or the 2.1 Ma lithic tools discovered at the Shangchen site in China (Zhu et al., 2018). In this context, considering the current data, the dynamics of the Maghreb appear to have more remarkable similarities with what happened in eastern Africa, not only due to the ancient presence of hominins around 2.44 Ma in Algeria but also because of the similarity in fauna between these points in Africa (Geraads, 2010). But then, what role did the Sahara Desert play during the Pleistocene and Pliocene?

The origin of this desert dates back to at least the early Miocene, around 11 - 7 Ma (Schuster et al., 2006; Zhang et al., 2014; Crocker et al., 2022). For a considerable period, the Sahara was regarded as a barrier that impeded the northward dispersal of numerous mammal species, including hominins. This view was supported by fossil evidence from the 19th and 20th centuries, indicating different dynamics in the occupation of these territories by hominins between eastern Africa and the North. However, the notion that the Sahara was not always as warm and dry as the current desert has been known since the 19th century, thanks to the fieldwork conducted by Henri Duveyrier with the Tuareg people in the north (Duveyrier, 1864). It was not until the late 20th century and the early

21st century that more precise knowledge about the Sahara dynamics and greening events emerged. These phases involved periods when the Sahara was humid and covered with lakes, rivers, and vegetation. These events occurred from approximately 8 Ma to the Holocene, making it plausible for a greater diversity of mammal species to traverse this territory (Larrasoña et al., 2003, 2013; Griffin, 2006; Osborne et al., 2008; Castañeda et al., 2009; Drake et al., 2011; Larrasoña, 2021; Armstrong et al., 2023). This improved understanding of the Sahara's humid events was accompanied by archaeological discoveries confirming the diachronic presence of hominins in the Maghreb since the Early Pleistocene.

The first archaeological and palaeontological works in northern Africa were conducted in the late 19th and early 20th centuries. Among the pioneers, Philippe Thomas, a geologist and palaeontologist (Thomas, 1880, 1884, 1886), and Nicolas Auguste Pomel, a botanist and palaeontologist, stand out. Working primarily in Tunisia and Algeria marked a turning point in describing fossil vertebrates in northern Africa. Pomel was particularly prolific, publishing over 100 articles on fossil vertebrates from northern Africa, including a series of monographic palaeontological volumes (Monographies de la Carte Géologique de l'Algérie) published between 1893 and 1897. Some species defined in this African zone bear his name, such as *Hipparion pomeli* or *Giraffa pomeli*.

Although somewhat later, another prominent figure in palaeontology and palaeoanthropology in northern Africa (Tunisia, Algeria, and Morocco) is Camille Arambourg (Coppens, 1979; Hadjouis, 2010), who reviewed and expanded upon the work on fossil vertebrates by Thomas and Pomel (Arambourg, 1959, 1970, 1979). In addition to working in the Omo Valley (Ethiopia), recovering remains and defining the species *Paranthropus aethiopicus*, Arambourg, along with Robert Hoffstetter, discovered the oldest human remains in northern Africa (Arambourg and Hoffstetter, 1954, 1963; Arambourg, 1955). These mandibles, attributed to *Homo erectus* and dating back to approximately 1 Ma, were recovered during archaeological excavations in 1954 and 1955 in the Muaska province west of Algeria at the Tighennif site (also known as Palikao or Ternifine). They are associated with thousands of Acheulean lithic tools and multiple faunal taxa (Pomel, 1878; Arambourg and Hoffstetter, 1954, 1963; Geraads et al., 1986; Bocherens et al., 1996; Geraads, 2016; Van der Made et al., 2021). In the 1950s, a human femur was also found in the Moroccan site of Ain Maarouf, located about 250 km East of Casablanca and near the town of El Hajeb (Geraads et al., 1992; Geraads and Amani, 1997). Although there are no absolute datings, as is the case with Tighennif, the biochronology and faunal associations of both sites seem to indicate a similar chronology, ranging from the Early Pleistocene to the late Middle Pleistocene (Geraads, 2002).

The Tighennif remains represent the oldest direct evidence of human fossils in northern Africa. However, the earliest evidence of hominins in the Maghreb is much older. It is found in the intramontane basin of Beni Fouda (Guelta Zerga, Algeria) in an area known as Oued Boucherit, with a sequence containing different archaeological and paleontological levels spanning from 3.9 to 1.6 Ma (Duval et al., 2021). In this sequence, at the Ain Boucherit site, Oldowan lithic tools were recovered, along with the oldest cut

marks in northern Africa (2.4 – 1.9 Ma; Sahnouni et al., 2018). In the same region (**Fig. 1**), the occurrence of Acheulean stone tools in Member U of the Ain Hanech Formation is estimated to be 1.67 Ma (Duval et al., 2021), and the Oldowan technology is reported in three archaeological levels dated to ~1.8 Ma at both Ain Hanech and El Kherba (Sahnouni and De Heinzelin, 1998; Sahnouni et al., 2002, 2012; Parés et al., 2014, 2023; Duval et al., 2021). In the Constantine Basin (Algeria), which is biochronologically close to Ain Hanech, the relatively unknown site of Mansourah is located, with abundant faunal remains and bifacial artifacts associated with the Oldowan industry (Thomas, 1884, 1886; Chaid-Saoudi et al., 2006; Sahnouni and Van der Made, 2009). In the same basin, the palaeontological site of Aïn Jourdel (~2.5 Ma) is also present (Thomas, 1884, 1886; Duval et al., 2021).

In western Morocco (**Fig. 1**), near Casablanca, the oldest archaeological sites date back to the Early and Middle Pleistocene (Raynal et al., 2001, 2002, 2017; Mohib et al., 2019; Gallotti et al., 2021). So far, the oldest site with evidence of *Homo* presence corresponds to Unit L of Thomas I Quarry and its abundant Acheulean lithic tools (~1.3 Ma) (Raynal and Texier, 1989; Gallotti et al., 2020, 2021, 2023; Raynal et al., 2023a). In Thomas I Quarry, above the L level, is the Grotte à Hominidés (~0.77 Ma), where the oldest *Homo* remains on the Atlantic coast were discovered (Ennouchi, 1975; Geraads, 1980a; Geraads et al., 1980, 2022a; Raynal et al., 2023b, 2010; Daujeard et al., 2016, 2020; Gallotti et al., 2021; Raynal, 2021; Perini et al., 2023).

A few kilometres from Thomas I Quarry, in the Oulad Hamida Quarry 1 (originally Thomas III), is the Grotte des Rhinocéros site (~0.7 and ~0.5 Ma). In this site, in addition to abundant faunal remains, especially of Rhinocerotidae, a *Homo* tooth associated with lithic industry has been recovered (Ennouchi, 1975; Geraads, 1980a; Raynal et al., 1993, 2023b; Rhodes et al., 2006; Raynal and Mohib, 2016; Daujeard et al., 2020; Geraads et al., 2022a). On the outskirts of Casablanca is the Ahl al Oughlam site, dated to ~2.5 Ma, one of the richest Neogene sites in terms of mammal taxonomic diversity in northern Africa (Raynal et al., 1990; Geraads, 2002, 2006; Geraads et al., 2010, 2022b).

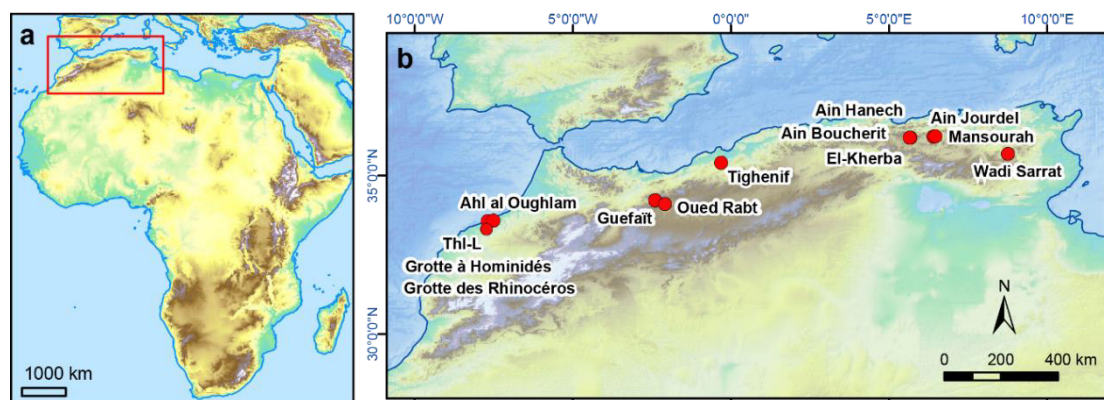


Figure 1. Location of some of the most important archaeological and palaeontological sites in northern Africa from the Plio-Pleistocene transition to the early Middle Pleistocene.

In eastern Morocco, near the border with Algeria in the geographical area of Aïn Beni Mathar-Guefaït (Jerada province), several sites have been discovered and excavated since 2006. These include the Early Pleistocene sites of Aïn Tabouda, Gara Soultana, and Charchara 1 with Mode 1 lithic tools and the Middle Pleistocene site of Oued Rabt with Mode 2 lithic tools (Sala-Ramos et al., 2022). The oldest site, although palaeontological, is Guefaït. Biochronologically, it is positioned at the Plio-Pleistocene transition (~2.5 Ma; Parés et al., 2023), contemporaneous with Ahl al Oughlam, and it contains a diverse array of taxa in its fossiliferous levels (Sala-Ramos et al., 2017, 2022; Aouraghe et al., 2019a; Piñero et al., 2020; Alba et al., 2021; Madurell-Malapeira et al., 2021).

As of today, in other regions of northern Africa, such as Tunisia, Egypt, and Libya, there are no sites with evidence of hominins during the Early Pleistocene, and the oldest evidence dates back to the Middle Pleistocene.

In the Le Kef province of Tunisia, in the Wadi Sarrat basin (~0.7 Ma), fauna remains associated with Acheulean tools have been discovered (Martínez-Navarro et al., 2014). About 200 to 300 km South of Le Kef are the palaeontological sites of Lac Ichkeul and Ain Brimba, attributed to the Late Pliocene (~3 Ma) based on fauna analysis (Arambourg and Arnould, 1949; Arambourg and Coque, 1959; Geraads, 2008; Duval et al., 2021).

In Egypt, two notable sites are located in the Dakhleh and Kharga oases in the central-northern part of the Egyptian Western Desert. Radiometric dating and lithic industry evidence indicate occupations in this territory between 0.4 and 0.2 Ma (Churcher et al., 1999, 2008; Kleindienst, 2019, 2023). Palaeontologically, the Late Miocene sequence of Wadi El-Natron (Qaret El-Muluk formation), about 100 km west of Cairo, is significant. The macrofauna assemblage includes a wide variety of fossil taxa such as *Hippopotamus*, *Sivatherium*, *Hipparion*, or *Crocodylus* (Andrews, 1902; El-Shahat et al., 1997), and the oldest presence of *Macaca* in Africa (Stromer, 1913; Geraads, 1987).

In Libya, the Jebel Akhdar area in Cyrenaica, northeastern Libya, is rich in Upper Pleistocene sites (Garcea, 2023). The oldest presence of *Homo* is found in the Haua Fteah cave, which contains one of the most complete diachronic sequences in northern Africa, spanning from 150 to 10 ka (Jacobs et al., 2017). It includes fossil remains of early *Homo sapiens* from a Levallois-Mousterian layer dated to 73 - 65 ka (Douka et al., 2014). In this region, the palaeontological sites of the Sahabi formation, located 130 km South of the current coastal city of Agedabia, stand out. Biochronologically dated between the Late Miocene and Early Pliocene (~6 Ma), it is one of the most diverse faunal sites in northern Africa for this period, with many taxa linked to aquatic environments (Petrocchi, 1943; Boaz et al., 1979; Bernor and Pavlakis, 1987).

2.3. State of the art of paleoenvironmental studies in northern Africa

Despite the numerous archaeological and palaeontological sites identified in the Maghreb from the Plio-Pleistocene transition to the early Middle Pleistocene, very little is known

about the ecological and climatic conditions that allowed mammals, including hominins, to disperse and occupy these territories.

The scarcity of information on the palaeoenvironment in northern Africa contrasts with the extensive studies conducted in other African regions, particularly in the eastern and southern, where significant archaeological work has been carried out (Dart, 1925; Leakey, 1928; Broom, 1938). In eastern Africa, reconstructions of the Pleistocene landscape have been conducted at various open-air sites such as Aramis, Hadar, Ledi-Geraru, Gona, Konso-Gardula, Dikika, and Shungura (Ethiopia), as well as Oldupai, Laetoli, and Peninj (Tanzania), and Kanjera, Nachukui, Koobi Fora, Kanapoi, and Tugen Hills (Kenya), and Chiwondo (Malawi) (Lee-Thorp et al., 1989; Feibel et al., 1991; Bonnefille et al., 2004; Ségalen et al., 2007; Kingston and Harrison, 2007; Levin et al., 2008; Bonnefille, 2010; Kingston, 2011; Bedaso et al., 2013; Van Der Merwe, 2013; Cerling et al., 2015; Robinson et al., 2017, 2021; Lüdecke et al., 2018; Patalano, 2019; Mercader et al., 2021; Bobe and Reynolds, 2022).

While fewer in number than in eastern Africa, southern Africa has also seen many studies on the ecological context of the Early Pleistocene. The rich palaeoanthropological record in cave sites such as Wonderwerk, Makapansgat, Malapa, Swartkrans, Cooper's, Sterkfontein, Kromdraai, and Drimolen has allowed the reconstruction of the ecological context of various hominin species (Grine, 1987; Reed, 1997; Luyt and Lee-Thorp, 2003; Lee-Thorp and Sponheimer, 2005; Ségalen et al., 2007; Lee-Thorp et al., 2007, 2010; Williams and Patterson, 2010; Holt et al., 2016; Lehmann et al., 2016; Ecker et al., 2018; Peterson et al., 2018; Grine et al., 2020; Bobe and Reynolds, 2022).

In Central Africa (Chad), studies of palaeoenvironments have been conducted at late Pliocene sites dating from 7 to 3 Ma, where two hominin species, Toros-Menalla, Kossom Bougoudi, Kollé, and Koro-Toro, have been found (Zazzo et al., 2000; Ségalen et al., 2007; Schuster et al., 2009; Lee-Thorp et al., 2012; Bobe and Reynolds, 2022).

Beyond these African regions having a greater tradition in terms of fieldwork, they also possess specific geological characteristics and sedimentary contexts that favour the excellent preservation of fossil remains, such as the eastern African Rift Valley, the intracratonic basin of Lake Chad, and the fossil-rich cave deposits in southern Africa (Kullmer, 2015). In contrast, the fossil record of mammals is very scarce in areas covered by dense tropical rainforests (Central Africa), where diagenetic processes do not contribute to the preservation of remains, and fieldwork becomes more challenging (Rosas et al., 2022). These humid forests are the habitat of current large African primates and could have been crucial areas in the evolution of Hominidae. However, no primate fossils from the last 10 Ma have been discovered in these environments (Almécija et al., 2021; Foley and Lahr, 2023).

In the case of northern Africa, very few palaeoecological studies have been conducted. Inferences about the type of environment have been made based on the presence or absence of different faunal taxa, as seen in late Middle Pleistocene deposits in the Dakhleh Oasis (Egypt; Churcher et al., 1999, 2008). Similar inferences have been drawn from

Early Pleistocene sites such as Tighennif (Algeria; Geraads et al., 1986), Aïn Boucherit, Aïn Hanech, and El-Kherba (Algeria; Sahnouni et al., 2011), the Unit L of the Thomas I Quarry (Morocco; Gallotti et al., 2021), or the Late Miocene in the Sahabi Formation (Libya; Boaz et al., 1979; Griffin, 2006). Despite covering different regions and geological times, they share common indicators such as Hippopotamidae or Crocodylidae, suggesting the presence of rivers and lakes in currently arid or desert areas.

However, the initial study providing direct information about the landscape type was published in 1996, analysing stable carbon and oxygen isotopes of fauna from the Tighennif site. This study compared isotopic values from Early Pleistocene sites in eastern Africa to those in the North, concluding that unlike the East, where the predominance of C₄ plant consumption by herbivores was evident, the pattern in the North was markedly different, with a consumption of C₃ plants and a total absence of C₄ plants (Bocherens et al., 1996). Recently, a study focusing on reconstructing the diet of fossil *Theropithecus* in northern Africa analysed multiple herbivore species from Tighennif and some from the Ahl al Oughlam site. The results also indicated a prevalence of C₃ plant consumption for all species from both sites. In the case of *Theropithecus*, C₃ grasses were consumed (Fannin et al., 2021). *Theropithecus* is a Pleistocene African species known for its predominant consumption of C₄ grasses in eastern and southern Africa (Souron, 2018). The fact that this species in the North predominantly consumes C₃ plants indicates the limited presence of C₄ vegetation in the northern part of the continent. Another example is found in the El-Kherba site in Algeria, where stable carbon isotope analyses of pedogenic carbonates also indicated a predominance of C₃ vegetation (Sahnouni et al., 2011). A single study of dental wear was conducted at three Moroccan sites: Taforalt (Oujda region), El Khenzira (El Jadida), and Bizmoune (Essaouira). The study spanned the end of the Middle Pleistocene to the beginning of the Holocene. The results indicated diverse feeding behaviours potentially linked to climate changes, competitive relationships, and specific adaptive strategies for certain taxa (Uzunidis et al., 2023).

The significance of the presence of C₃ vs. C₄ plants is situated within the debate on the expansion of C₄ ecosystems characterised by open grassland habitats and arid climates. This C₄ expansion has been linked to a series of both local and global events such as decreasing atmospheric CO₂, higher temperatures, increasing water stress, the emergence of bipedalism, aridity, seasonality, or potential changes in the diet of ungulates and their association with hypsodonty (Bouchenak-Khelladi et al., 2009; Edwards et al., 2010; Polissar et al., 2019; Crocker et al., 2022; Peppe et al., 2023). These factors could significantly influence the evolution of mammals, including hominins.

It is crucial to consider that the global C₄ ecosystem expansion around 10 - 8 million years ago marked a significant shift in the landscape, leading to the replacement of C₃ grasses by C₄ grasses in existing open and dry environments in low-to mid-latitude and altitude regions (Ehleringer et al., 1991; Cerling, 1992; Cerling et al., 1997; Edwards et al., 2010; Polissar et al., 2019). However, the distribution of C₃ or C₄ plants is not uniform across Africa, varying geographically and chronologically. During the Plio-Pleistocene, eastern, southern, and central Africa were predominantly characterised by C₄ grassland (Zazzo et

al., 2000; Ségalen et al., 2007; Strömberg, 2011), relegating C₃ grasses to altitudes above 2000 m and in the forest understory (Tieszen et al., 1979; Young and Young, 1983; Balasse and Ambrose, 2005). The ecological context of these areas, marked by the high abundance of C₄ grasses, especially in eastern Africa, has facilitated the application of the C₄-grazers and C₃-browsers classification, widely used in studies analysing mammalian diets based on tooth enamel $\delta^{13}\text{C}$ values (Vogel, 1978; Zazzo et al., 2000; Sponheimer and Lee-Thorp, 2003; Lee-Thorp and Sponheimer, 2005; Levin et al., 2008; Bedaso et al., 2013; Cerling et al., 2015; Uno et al., 2018).

This clear distinction between C₄-grazers and C₃-browsers is not applicable at high latitudes in Africa, where the contribution of C₄ plants is non-existent or marginal. This pattern has been observed in multiple studies conducted during the Pliocene and Early to Middle Pleistocene in Europe (García García et al., 2009; Edwards et al., 2010; Domingo et al., 2013; Szabó et al., 2022). The same observation applies to studies conducted in northern Africa on Pliocene and Early Pleistocene archaeological and palaeontological sites mentioned above (Bocherens et al., 1996; Sahnouni et al., 2011; Fannin et al., 2021). All these studies, based on carbon isotope evidence in pedogenic carbonates and faunal remains, reveal vegetation consisting of C₃ plants, encompassing all available resources such as trees, woody shrubs, bushes, and grasses.

This complexity makes distinguishing different diets and habitats for mammals challenging, making it difficult to establish a consistent ecological reconstruction with a single method.

· Chapter 3: Study region and analysed materials ·

3.1. Eastern Morocco

3.1.1. *Plio-Pleistocene transition site of Guefaït-4*

3.1.1.1. Site description

The palaeontological site of Guefaït-4 (GFT-4; 34° 13' 3.4" N, 2° 24' 13.2" W) is located near the Guefaït village in eastern Morocco. Since 2006, a Moroccan-Spanish interdisciplinary project has carried out several field surveys in the Aïn Beni Mathar/Guefaït region (Jerada Province, eastern Morocco) to map archaeological and palaeontological sites, establishing their geochronological context and the evolution of human peopling in the area (Aouraghe et al., 2016). GFT-4 was discovered in 2015 by the team from Mohamed I University of Oujda led by Dr Hassan Aouraghe during geological surveys in the Aïn Beni Mathar - Guefaït Basin (High Plateaus Region of Oriental Province, Morocco; **Fig. 2**) and is included in the ongoing Spanish-Moroccan research project (Sala-Ramos et al., 2022). The site was identified by the exposure of a gray-marly fossiliferous level rich in vertebrate fauna, now recognised as part of Unit 2 within the Plio-Pleistocene stratigraphic section of Dhar Iroumyane (Parés et al., 2023). This sedimentary layer extends over a considerable distance and includes specific geolocated sites referred to as Guefaït-4.1 (GFT-4.1), 4.2 (GFT-4.2), and 4.3 (GFT-4.3); these trenches are located close to one another.

During the 2017-2019 seasons, more than 3325 fossil remains of large vertebrates were recovered in a 2 m thick trench covering 28 m² at the locality GFT-4.2. The eastern section of the trench (GFT-4.2) presented a litho-stratigraphic section divided into 15 sedimentological units (**Fig. 3**) that were grouped into three field levels during the excavation (Level 0, Level 1 and Level 2). Level 0 includes units 5, 6, 7 and 8 and has a thickness of 60 cm. It is a level of reddish loams altered by humidity changes probably related to slope erosion. This level 0 presents many fossil remains (*ca.* 14.5% of the total 3D coordinate remains). Level 1 includes units 9 to 14 and has a thickness of 60 cm. These are greenish and grey reducing clays and loams with abundant calcareous nodules in units 11 and 12. This level contains a higher density of palaeontological remains (*ca.* 85.5%). Unit 15, composed of light grey nodular limestones and equivalent to field level 2, does not present palaeontological remains, nor does the top of the sequence formed by units 1, 2, 3 and 4, which comprise limestone and organic soils. GFT-4.2 locality is located in a palustrine unit where mudstones, marls, palustrine limestones and conglomerate channels suggest a wetland environment characterised by water bodies and stream inputs. Sampling in GFT stratigraphic section 4.2 was conducted on a sequence of mudstones, including carbonates interbedded between palustrine limestone layers (**Fig. 3**).

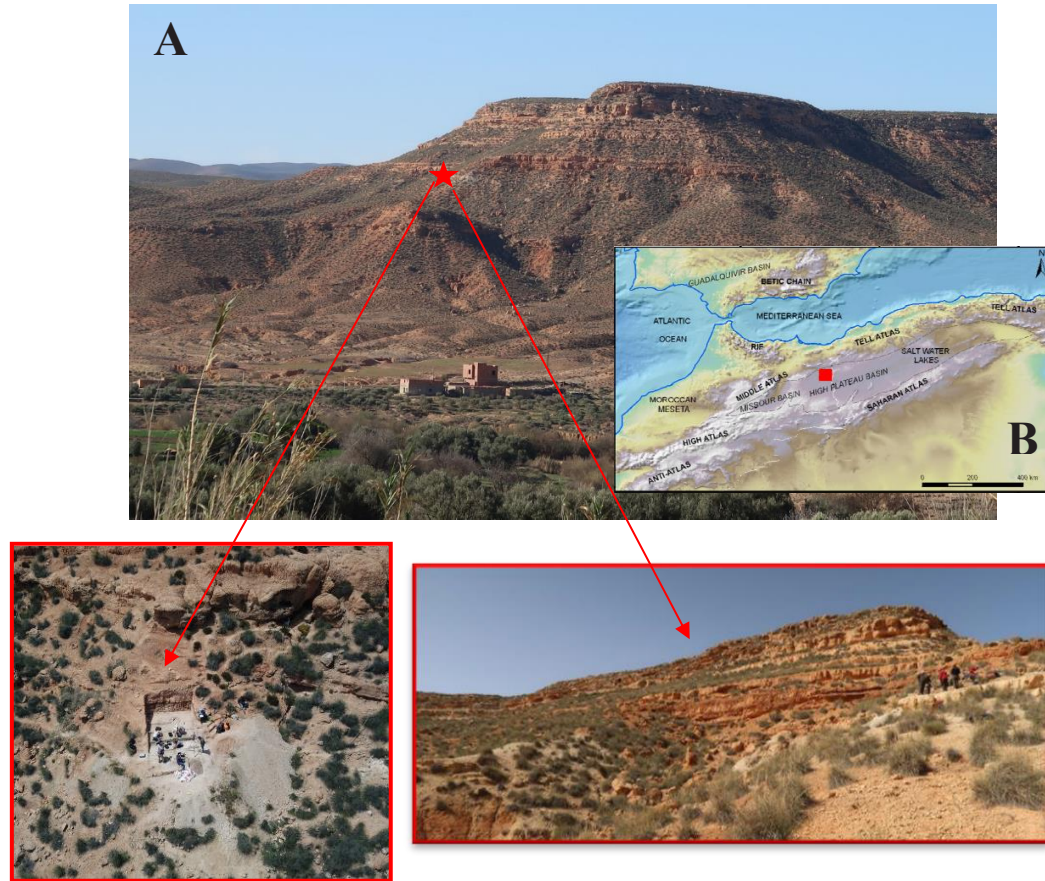


Figure 2. A, Different perspectives from the Guefaït-4 site and -4.2 locality taken during the 2019 fieldwork (pictures by Alfonso Benito-Calvo and Antonio Rodríguez-Hidalgo). B, Context of the study area in northern Africa.

Mudstones are indicative of mainly low-energy fine-grained clastic sedimentation by decantation in a pond of relatively carbonated water, where the greenish-to-brown colour gradation suggests an evolution from reduction conditions to more oxidised conditions towards the top, including a dark-coloured mudstone layer at the top suggesting a possible increase in organic matter. The preliminary taphonomic study of the macrovertebrate faunal remains indicates that GFT-4.2 is a natural accumulation site. The site formation likely involved the death and rapid burial of corpses/skeletons in a periodically flooded bed, with contributions from bones transported by small, low-energy watercourses. This is evidenced by anatomical associations, semi-connections, anatomical connections, and small dispersions (a few metres) of anatomical elements from single individuals. The rapid burial is further supported by the low incidence of weathering on the cortical surfaces: 95.5% of the remains are unaffected, 0.2% are affected at Stage 1, and 0.1% are affected at Stage 2 according to the criteria of Behrensmeyer (1978). Despite the inherent difficulties in establishing sedimentary rates in palustrine environments, namely wetlands and marshes with complex sedimentation processes resulting from the interplay of biological, chemical, and physical factors, the short sequence in GFT-4.2, covering only 28 m² and 120 cm thick, suggests a geologically brief period. As supported by taphonomic

data, the rapid burial of remains would have resulted in a thicker stratigraphic column if the accumulation had occurred over a more extended period.

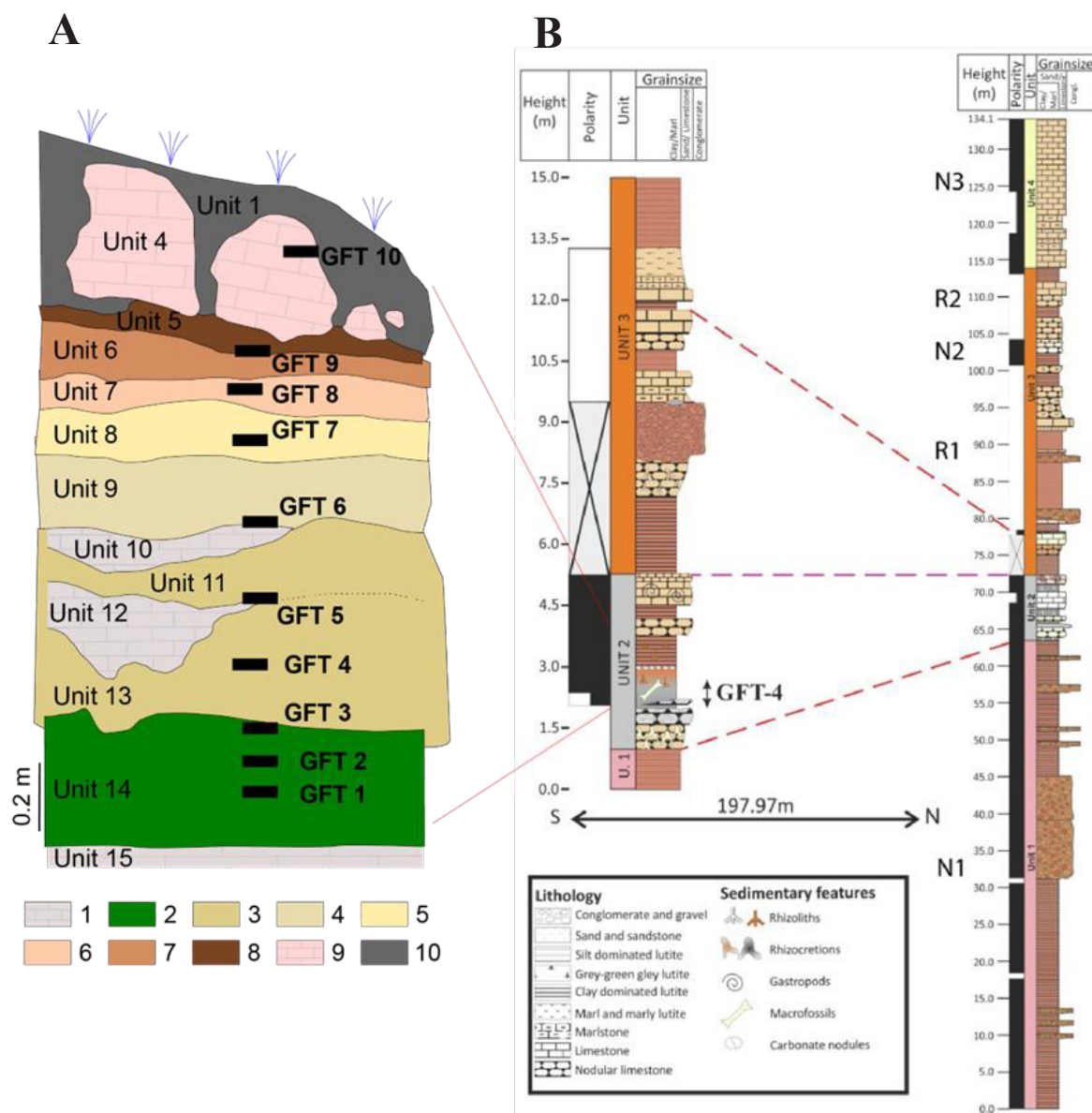


Figure 3. Stratigraphic section of GFT-4.2 locality. **A**, Legend of the stratigraphic section GFT-4.2: 1, Greenish massive marl; 2, Greenish grey crumby marl; 3, White limestone; 4, Grey crumby marl; 5, Mudstone with carbonate nodules; 6, Light brown mudstone; 7, Brown mudstone; 8, Dark brown mudstone; 9, Brecciated limestone. The black rectangles represent the locations where sediment samples for different analyses were collected: plant waxes (GFT 1 to 10), pollen (GFT 1, 2, 4, 6, 8, and 10), and micro-crustaceans and algae remains (GFT 1, 3, and 5). **B**, General sequence provided by Parés et al. (2023).

The approximate age of GFT-4.2 is based on a combination of proxies. Paleomagnetic analyses indicate a correlation with the last part of the Gauss chron, with the fossiliferous levels being slightly older than the Gauss-Matuyama transition (Parés et al., 2023). The

data derived from large and small vertebrates suggest, along with palaeomagnetism, that this locality is dated to the Late Pliocene near the Plio-Pleistocene transition. The absence of *Equus*, with the oldest African *Equus* record dating to 2.44 Ma at Ain Boucherit (Sahnouni et al., 2018; Duval et al., 2021), indicates that GFT-4.2 is older than this date.

Considering the known temporal distribution of other large vertebrates, GFT-4.2 could be correlated to the top of the Gauss chron, extending the temporal range of several taxa in northern Africa to that period. Additionally, the rodent assemblage found at GFT-4.2 provides supporting evidence for an age close to the Plio-Pleistocene transition. The presence of the Muridae *Paraethomys pusillus*, *Paraethomys chikeri*, *Golunda aouraghei*, and *Praomys* cf. *skouri*, along with other rodent species, suggests an age that aligns with this transitional period. This is further reinforced by the presence of *Praomys* cf. *skouri*, which is considered a marker of the beginning of the Pleistocene in the continental record of northern Africa.

Overall, the combined evidence from vertebrate fossils indicates a Late Pliocene age close to the Plio-Pleistocene transition for GFT-4.2 (Hajji, 2010; Agustí et al., 2017; Sala-Ramos et al., 2017, 2022; Aouraghe et al., 2019b, 2019a; Piñero et al., 2020; Alba et al., 2021; Madurell-Malapeira et al., 2021; Parés et al., 2023).

3.1.1.2. Materials

Two types of materials were used for the ecological reconstruction of GFT-4.2.

Firstly, sediment samples ($n = 10$) were collected from the stratigraphic section of the site to analyse plant wax biomarkers (**Fig. 3 and 4**). Secondly, large mammal teeth were examined for mesowear ($n = 60$), microwear ($n = 105$), and stable isotopes ($n = 194$). A total of 11 different taxa were analysed.

The fossils of various mammal species were found in GFT-4.2, including *Gazella* sp., Tragelaphini, Canidae, *Macaca* cf. *sylvanus*, *Hexaprotodon* sp., Suinae, *Stephanorhinus africanus*, *Anancus* sp., *Hipparion* s.l., *Dinofelis* sp. and Hyaenidae (**Fig. 5**).

All samples were primarily obtained from the 28 m² trench and its corresponding sections within the GFT-4.2 locality, corresponding to field levels 0 and 1 and the same chronology. These fossils are housed in the Faculty of Science at Mohammed I University in Oujda, Morocco.

The raw data containing information on the analysed samples can be found in the **appendices (plant waxes biomarkers on pp. 249; dental mesowear and microwear on pp. 244 to 248, and carbon and oxygen stable isotopes on pp. 233 to 242).**

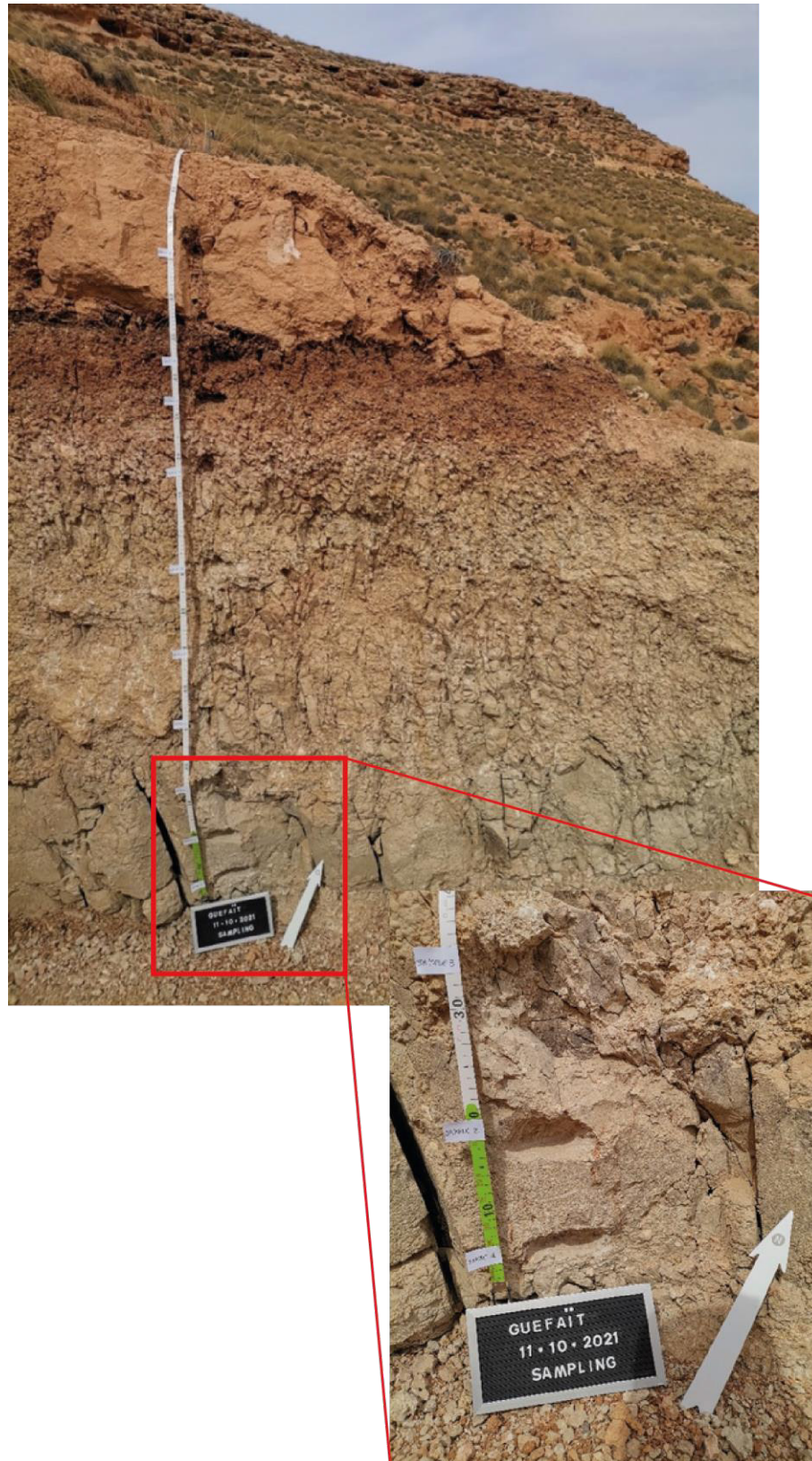


Figure 4. The sampled stratigraphic section at GFT-4.2. The box indicates the greenish-grey crumbly marl, one of the units (unit 13 and 14) with the highest fossil accumulation (see Fig. 3). The exact location of the samples analysed are depicted in Fig. 3.

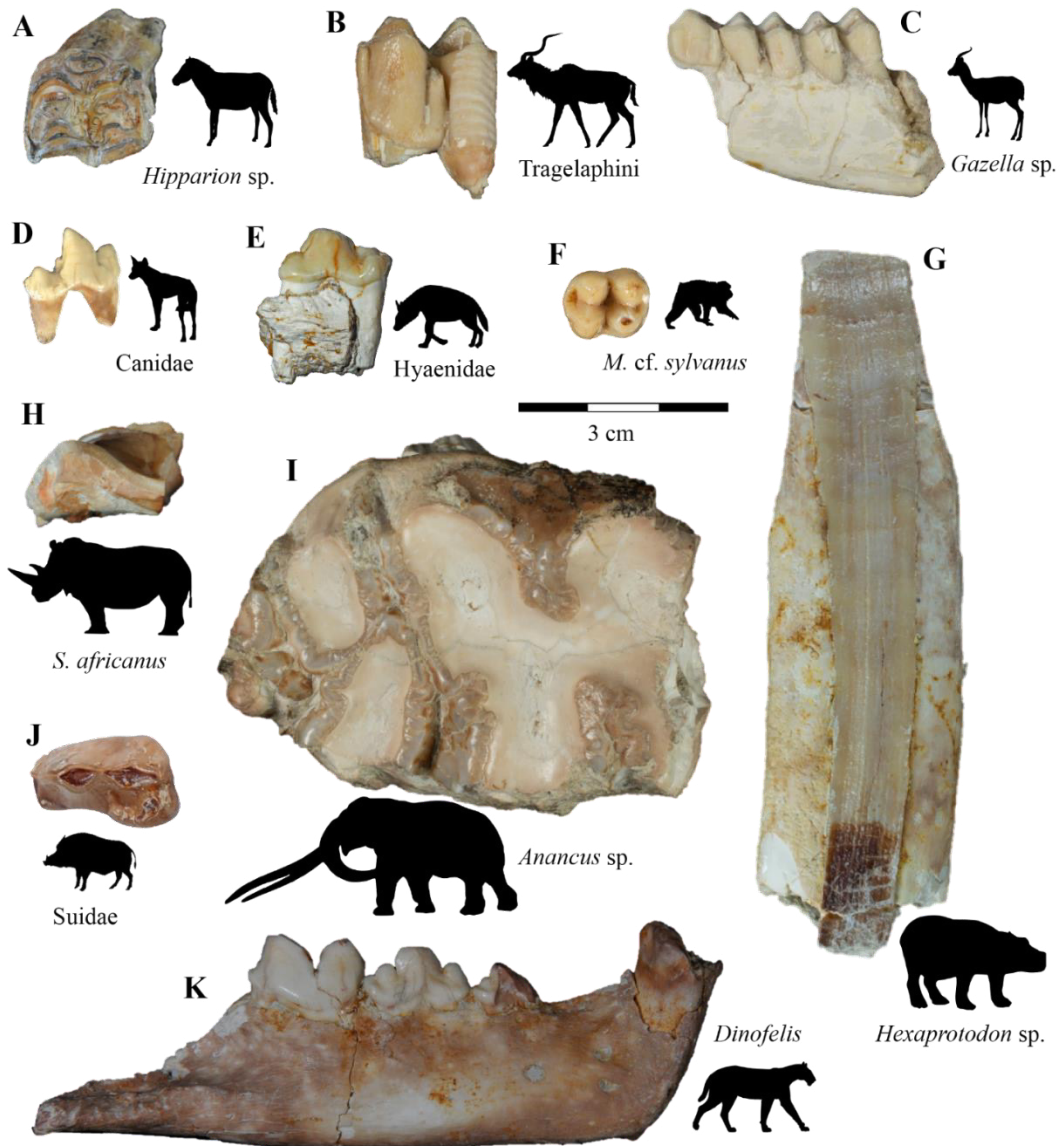


Figure 5. Teeth of some of the 11 large mammal taxa analysed in GFT-4.2. **A**, *Hipparion* s.l. (GFT4.2-19-Q12/23; occlusal view). **B**, *Tragelaphini* (GFT4.2-18-S14/29; buccal view). **C**, *Gazella* sp. (GFT4.2-19-T15/3; mandible buccal view). **D**, *Canidae* (GFT4.2-19-R14/54; buccal view). **E**, *Hyenidae* (GFT4.2-19-T13/1; buccal view). **F**, *M. cf. sylvanus* (GFT4.2-18-Q14/13; occlusal view). **G**, *Hexaprotodon* sp. (GFT4.2-19-Q15/224; canine). **H**, *S. africanus* (GFT4.2-19-Q13/47; occlusal view). **I**, *Anancus* sp. (GFT4.2-19-S15/91; occlusal view). **J**, *Suinae* (GFT4.2-19-R13/9; occlusal view) and **K**, *Dinofelis* (GFT4.2-19-Q15/237; mandible buccal view).

3.1.2. Middle Pleistocene site of Oued Rabt

3.1.2.1. Site description

The Oued Rabt (OR) archaeological site is an open-air site discovered during fieldwork in 2006 and extensively surveyed in 2009. Situated on the right bank of the Oued Rabt tributary of Oued Charef, it lies upstream in the Oued Charef – el Haï – Za valley within

the Aïn Beni Mathar – Guefaït basin (ABM-GFT) (**Fig. 6**). This basin represents the westernmost area of the Haut Plateaux and Salt Lake region of Maghreb, a physiographic unit located between the Mediterranean and Saharan domains. Isolated from the Atlantic coast, the Middle-Tell Atlas encloses it to the North and the High-Saharan Atlas to the South and West. ABM-GFT is traversed by the Charef-Haï-Za river system, a tributary of the Moulouya, the primary catchment in eastern Morocco.

The archaeological assemblage at OR comprises Mode 2 lithic tools (180 tools covering all categories of the chaîne opératoire) (Sala-Ramos et al., 2022). Most of these tools were recovered from the top of the sequence within three conglomerate levels capped by three cemented layers. The area covered by these levels varies, ranging from 50 m² for level 3 to 120 m² for level 1. No bone material has been preserved at OR.

Preliminary dating places the site chronologically in the early Middle Pleistocene (Personal communication – Robert Sala-Ramos).

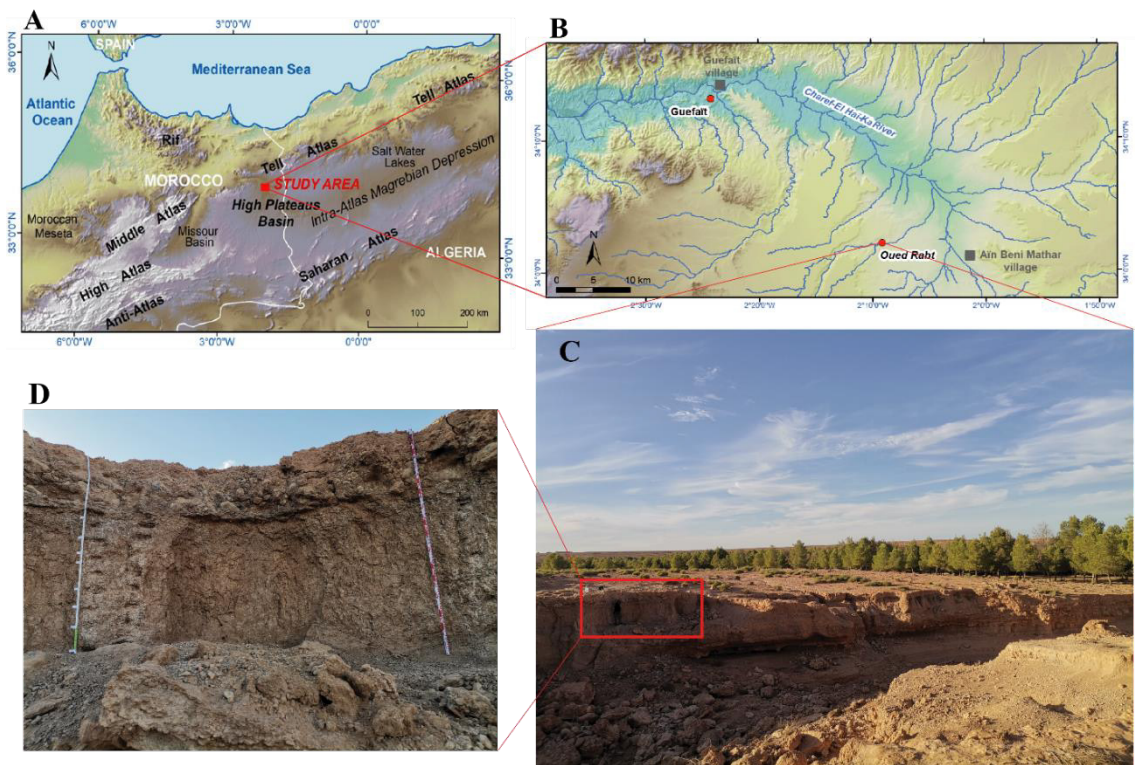


Figure 6. A, Context of the study area in northern Africa. B, Local context of Oued Rabt site, in relation to the other analysed site GFT-4.2. C and D, Different perspectives from the OR site taken during the 2021 sampling fieldwork.

3.1.2.2. Material

For the environmental reconstruction of the Oued Rabt site, 10 sediment samples from the stratigraphic profile have been used to analyse plant wax biomarkers (**Fig. 7**). The detailed information of the selected samples can be found in **results pp. 101 to 103**.



Figure 7. The sampled stratigraphic section at OR.

3.2. Western Morocco

3.2.1. Plio-Pleistocene transition site of Ahl al Oughlam

3.2.1.1. Site description

The fossiliferous locality of Ahl al Oughlam ($33^{\circ}34'11''\text{N}$, $07^{\circ}30'44''\text{W}$) is an abandoned sandstone quarry located at the Southeast transition of the city of Casablanca (Morocco), 6.5 km from the present-day Atlantic shore (**Fig. 8**; Raynal et al., 1990; Geraads et al., 2022b).

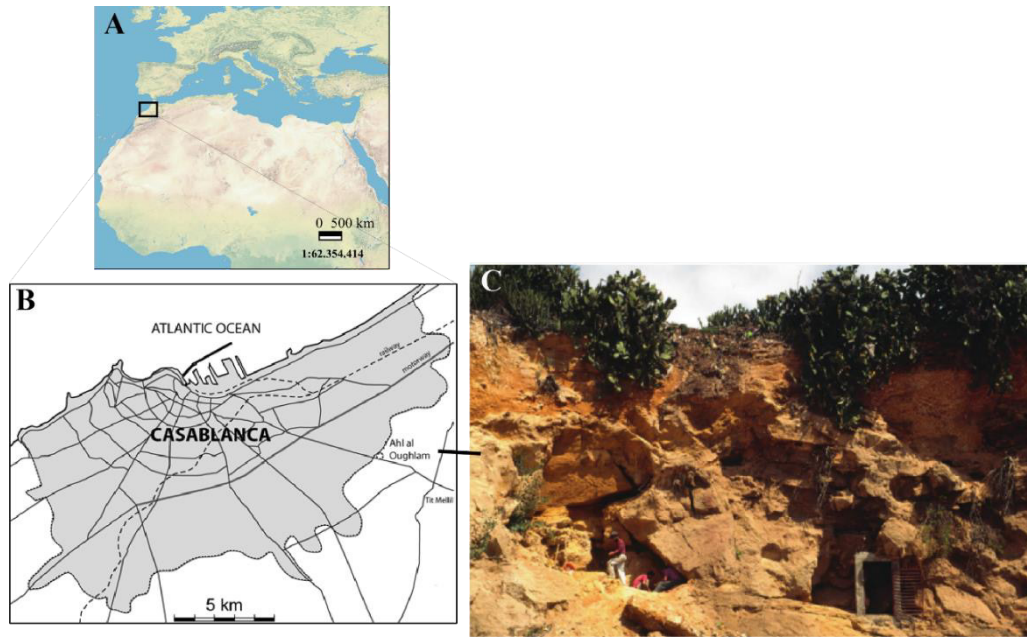


Figure 8. A, Context of the study area in Africa. B, Location of the site on the outskirts of the present city of Casablanca. C, Excavation of Ahl al Oughlam from the 1990s (Geraads et al., 2022b).

Stratigraphically, the quarry cuts through calcarenite intertidal, supratidal and aeolian deposits correlative to sea-level high stands associated with a platform developed about 105 m a.s.l. which belongs to the Ahl al Oughlam Morphostratigraphic Unit (Lefèvre and Raynal, 2002; Lefèvre et al., 2021; Geraads et al., 2022b), formerly included in the Messaoudian stage of Biberson’s Moroccan Quaternary Chronostratigraphy (Biberson, 1961a; Stearns, 1978).

The site was investigated in 1953 by Biberson (Biberson, 1961a, 1961b), under the name of Carrière Déprez, who reported the occurrence of some broken pebbles that he considered as representing reworked artifacts of the “archaic pebble culture” representing an initial stage of northern African technological evolution. Raynal and Texier (1989) demonstrated that they are actually “geofacts” of natural origin found in marine deposits. In 1985, J.-P. Raynal and J.-P. Texier discovered abundant fossil faunal remains in karst formations, specifically in a network of fissures and interconnected galleries between calcarenite blocks at the foot of what was once a palaeoshoreline.

A biostratigraphic analysis of the mammal assemblage dates this locality to the Plio-Pleistocene transition, indicating an approximate age of 2.5 Ma (Geraads, 1997; Geraads et al., 2022b). The genus *Equus* is absent, suggesting the site is older than 2.3 Ma (Geraads, 2006).

The mammalian fauna includes at least fifty-five species of both small and large mammals. A new species of *Hipparion*, *H. pomeli*, has been described subsequently from the site (Eisenmann and Geraads, 2007). The vertebrate fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards and snakes) and fishes. The most

unexpected element of the mammalian fauna is a walrus, a pinniped marine mammal. No living or fossil walrus was previously known in the eastern Atlantic, South of Belgium (Geraads, 2006).

The site was formed along the oceanic seashore, which explains why both marine and terrestrial forms are found among birds. A list of the identified faunal taxa is given in several publications (Raynal et al., 1990; Geraads, 1993, 1995, 1996, 1997, 2002, 2004, 2006; Alemseged and Geraads, 1998; Geraads and Amani, 1998; Geraads and Metz-Muller, 1999; Eisenmann and Geraads, 2007; Mourer-Chauviré and Geraads, 2008, 2010; Geraads et al., 2010; Gunnell et al., 2011; Sen and Geraads, 2023).

3.2.1.2. Materials

To perform the ecological reconstruction of Ahl al Oughlam, teeth from 6 taxa of large mammals were used, yielding results for a total of 46 samples for dental mesowear, 60 for microwear, and 82 for stable isotope analysis. The species included in this research are the following: *Sivatherium maurusium*, *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., Alcelaphini, and *Anancus osiris* (Fig. 9).

Raw data in **appendices (mesowear pp. 284 to 286; microwear pp. 284 to 286, and stable isotopes pp. 281 to 283).**

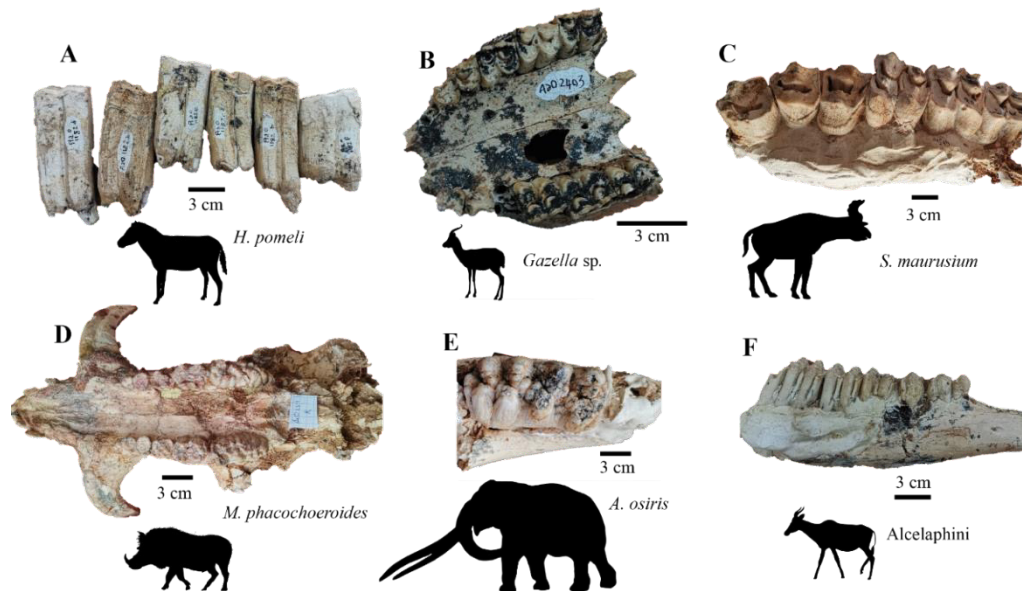


Figure 9. Teeth of some of the 6 large mammal taxa analysed in AaO. **A.** *H. pomeli* (AaO 1182; lower molars and premolars). **B.** *Gazella* sp. (AaO 2403; maxilla). **C.** *S. maurusium* (AaO 274; maxilla). **D.** *M. phacochoeroides* (AaO 239; maxilla). **E.** *A. osiris* (AaO 3935; mandible). **F.** Alcelaphini (AaO 2101; mandible).

3.2.2. Middle Pleistocene sites of Grotte à Hominidés and Grotte des Rhinocéros

3.2.2.1. Sites description

3.2.2.1.1. Grotte à Hominidés

Grotte à Hominidés (GH) is an archaeological site situated at Thomas I Quarry (33.568° N, -7.696° W) on the western outskirts of Casablanca, Morocco (**Fig. 10**). The first fossils and lithic industry were recovered from the quarry by Philippe Beriro and Pierre Biberson in the 1950s and 1960s (Biberson, 1961a). However, the site was not internationally recognised until the discovery of a hominin fossil in 1969 (Ennouchi, 1969). All these archaeological remains were subsequently studied in the 1980s (Geraads, 1980a; Geraads et al., 1980). In 1988, excavations in Thomas I Quarry were conducted under the Franco-Moroccan cooperative research project '*Préhistoire de Casablanca*' (Raynal et al., 2001, 2023a; Mohib et al., 2019; Geraads et al., 2022a). Between 1994 and 2011, several excavations took place at ThI-GH, retrieving new fauna remains and lithic industry (Geraads et al., 2010; Raynal et al., 2010), as well as additional *Homo* sp. remains (Raynal et al., 2011).

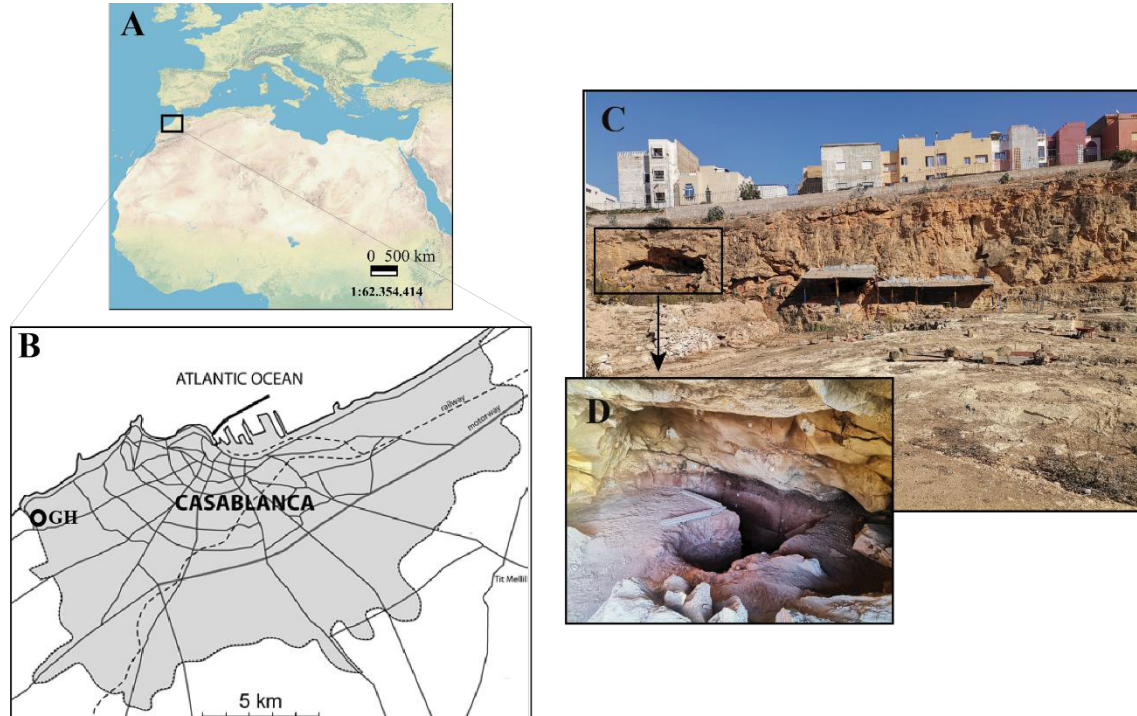
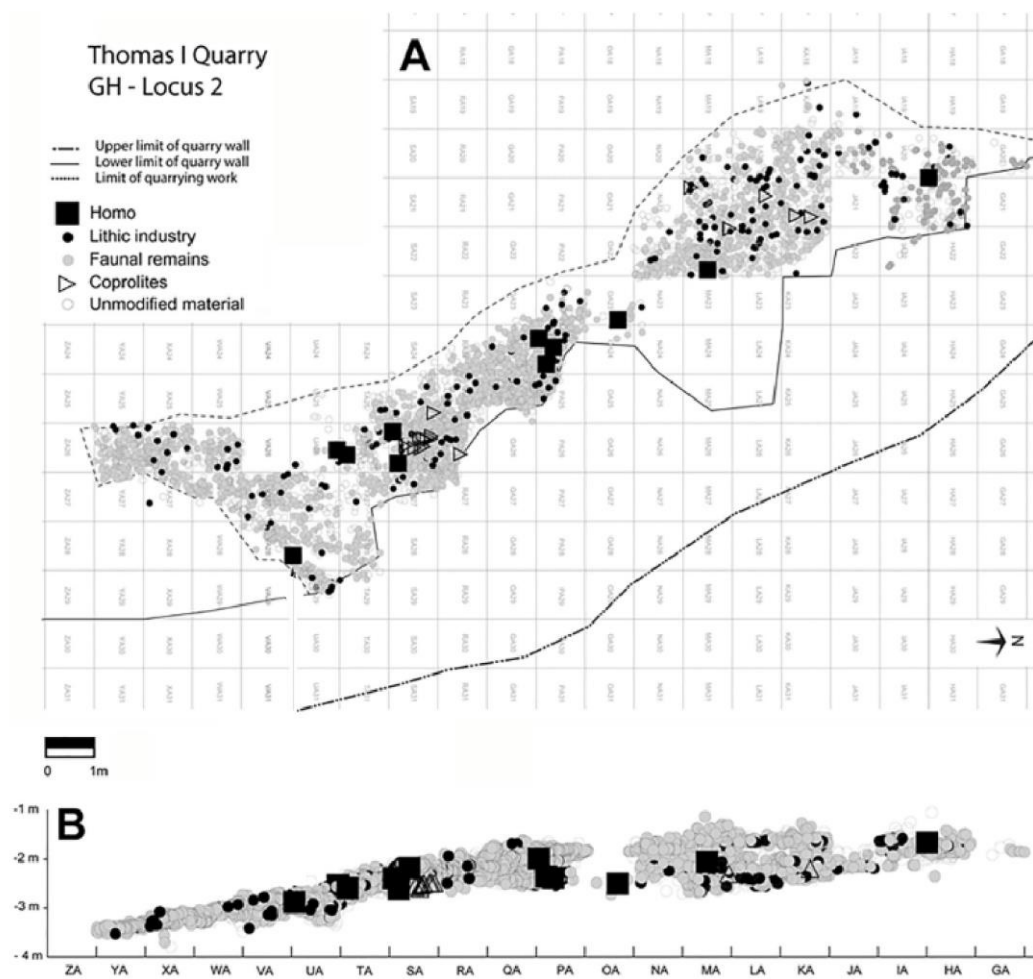


Figure 10. A, Context of the study area in northern Africa. B, Location of the site in the present city of Casablanca. C, GH site in Thomas I Quarry, Locus 2 (**Fig. 11**). D, Views of part of the ThI-GH cave are still preserved today.

The stratigraphic sequence of the cave comprises five units, ranging from the Upper Pleistocene to the Middle Pleistocene. Unit 1 displays massive bedded rubefied sands containing abundant microfauna. Beneath this, there's a multilayered dripstone floor interbedded with loose red sands (stratigraphic units 2-3). Stratigraphic unit 4 comprises bioclastic and quartzose well-sorted sands primarily derived from reworked loose littoral deposits. This unit rests on plurimetric collapsed blocks of older calcarenites embedded in coarse sands and calcirudite with a coarse coquinoïd matrix forming stratigraphic unit 5. This lowermost intertidal unit fossilises a notch in the polyphase paleoshoreline, featuring cliffs and deep cavities cut into older formations (Lefèvre and Raynal, 2002).



Taphonomic studies suggest that carnivores played a significant role in bone modification and accumulation within this stratum (Daujeard et al., 2012, 2016).

Previous OSL dating obtained on Unit 4 provided an age ranging from 391 ± 32 ka to 420 ± 34 ka, and a human tooth provided a laser ICP-MS age of $501 + 89/-66$ ka (Raynal et al., 2010, 2011). However, the magnetostratigraphic framework developed on all the deposits of the Thomas Quarry I has highlighted the presence of the Matuyama-Brunhes transition (~ 0.77 Ma) occurring within the fossiliferous units 4 and 5 deposits of ThI-GH (Gallotti et al., 2021; Perini et al., 2023; Raynal et al., 2023a).

3.2.2.1.2. *Grotte des Rhinocéros*

The Grotte des Rhinocéros (GDR; 33.567° N, -7.701° W) was discovered in 1991 as part of the France-Morocco cooperative program in Casablanca (Raynal et al., 1993, 2023b), situated at Oulad Hamida 1 Quarry, formerly known as Ben Sida 1. This quarry, an extension of the former Carrière Thomas III, lies approximately 1 km from the current Atlantic coast (**Fig. 12**). When initially uncovered, the quarry had already encroached upon the rear section of the cave, leaving only the lower portion of its stratigraphy visible.

Its name derives from the abundance of fossilised Rhinocerotidae remains within its confines. Systematic excavations were conducted in 1996 and continued intermittently from 2005 to 2009, spanning five archaeological campaigns. These efforts recovered a large amount of Acheulean lithic artifacts alongside a diverse fauna, all within a meticulously documented stratigraphic context (Daujeard et al., 2020).

Notably, it marked the first Moroccan Acheulean site to be dated using Electron Spin Resonance (ESR) dating techniques (Rhodes et al., 1994, 2006) and was subsequently designated as the type-locality for the Second Regional Acheulean (SRA).

The cave is situated within an early Middle Pleistocene shoreline of the Oulad Hamida Formation. Its chronological placement within the Pleistocene palaeoshoreline succession in Casablanca suggests an age predating MIS 15 (Lefèvre and Raynal, 2002; Raynal and Mohib, 2016).

Although the total length of the cave remains unknown, its dimensions at the bottom, as revealed by the quarry's excavation, measure approximately 7 meters in height and 12 meters in width. The cavity was filled with a 7-meter-thick stratified accumulation of calcareous sandy materials, organised into two primary lithostratigraphic units: the upper set (units 1 to 4) and the lower set (units 5 to 6). Sediment deposition, primarily facilitated by low-energy processes such as aeolian transport and runoff, has played a pivotal role in preserving the integrity of the archaeological assemblages comprising bone fragments and lithic artifacts. The facies and architectural characteristics of the deposits effectively negate the possibility of a pitfall accumulation.

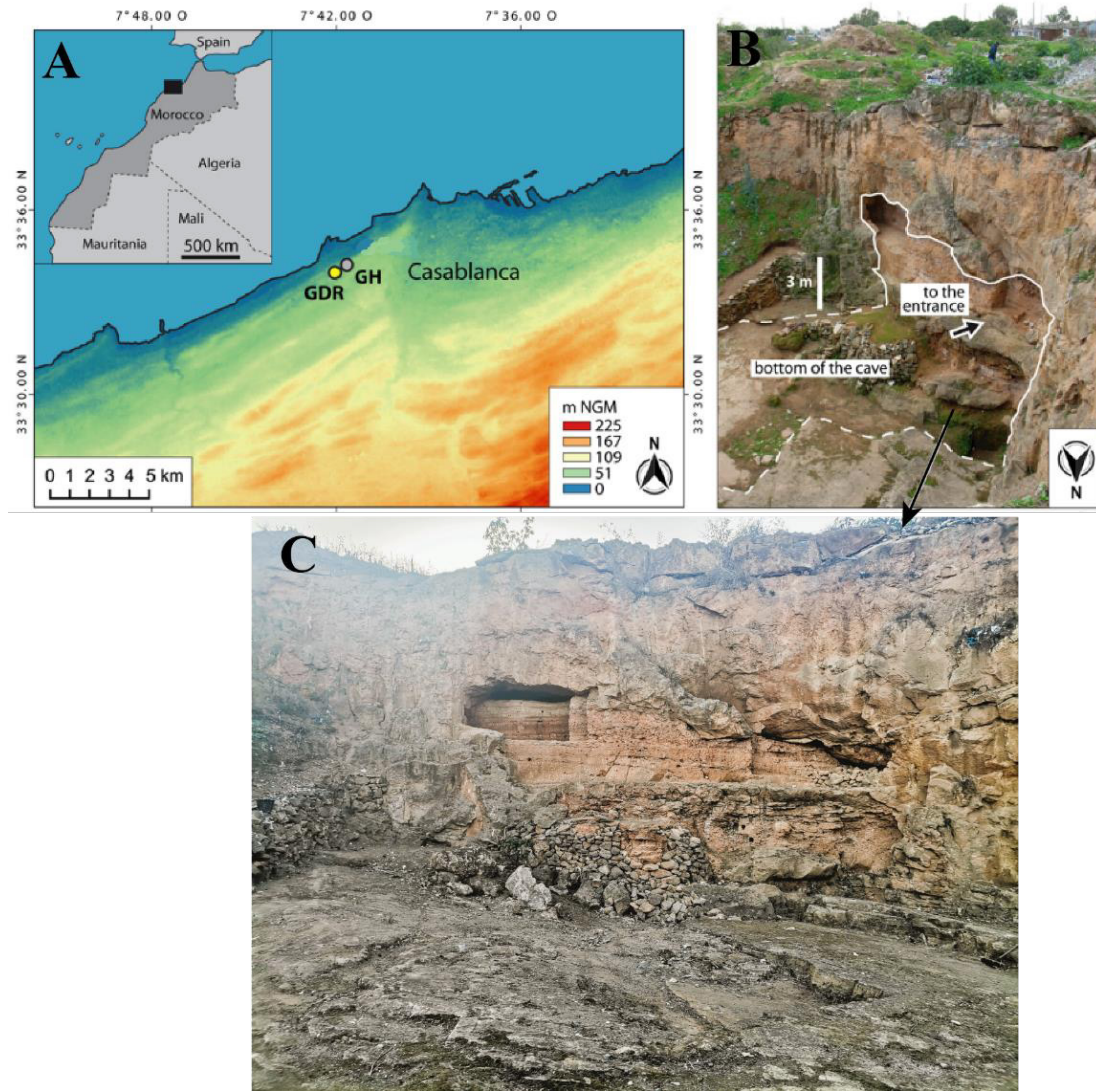


Figure 12. Extracted from the publication of Daujeard et al. (2020). **A.** Context of the study area in Africa and location of the sites ThI-GH and OHQ1-GDR in the present city of Casablanca. **B.** Oblique view of the site and limits of the present-day cave (picture by Mathieu Ru  ). **C.** Frontal view of the site.

Combined ESR with U-series dating of seven Bovidae and Rhinocerotidae teeth from lower and upper sets provide ages of 720-690 ka and 548-522 ka, respectively. The homogeneity of the external rose date allowed the calculation of an isochron age of 696 ka, consistent with the oldest ages from Unit 5 (**Fig. 13**).

The faunal assemblage lacks *Homotherium* and *Metridiochoerus* and appears younger than that of Tighennif in Algeria, a site dating to about 1 Ma. However, OHQ1-GDR rodents exhibit closer affinities to those of Tighennif than those of Jebel Irhoud (Morocco), recently dated to ~0.3 Ma. Moreover, numerous extinct forms and similarities to early Pleistocene taxa suggest an early stage in the evolution of Middle Pleistocene assemblages, likely exceeding 0.5 Ma, consistent with the combined US-ESR dating.

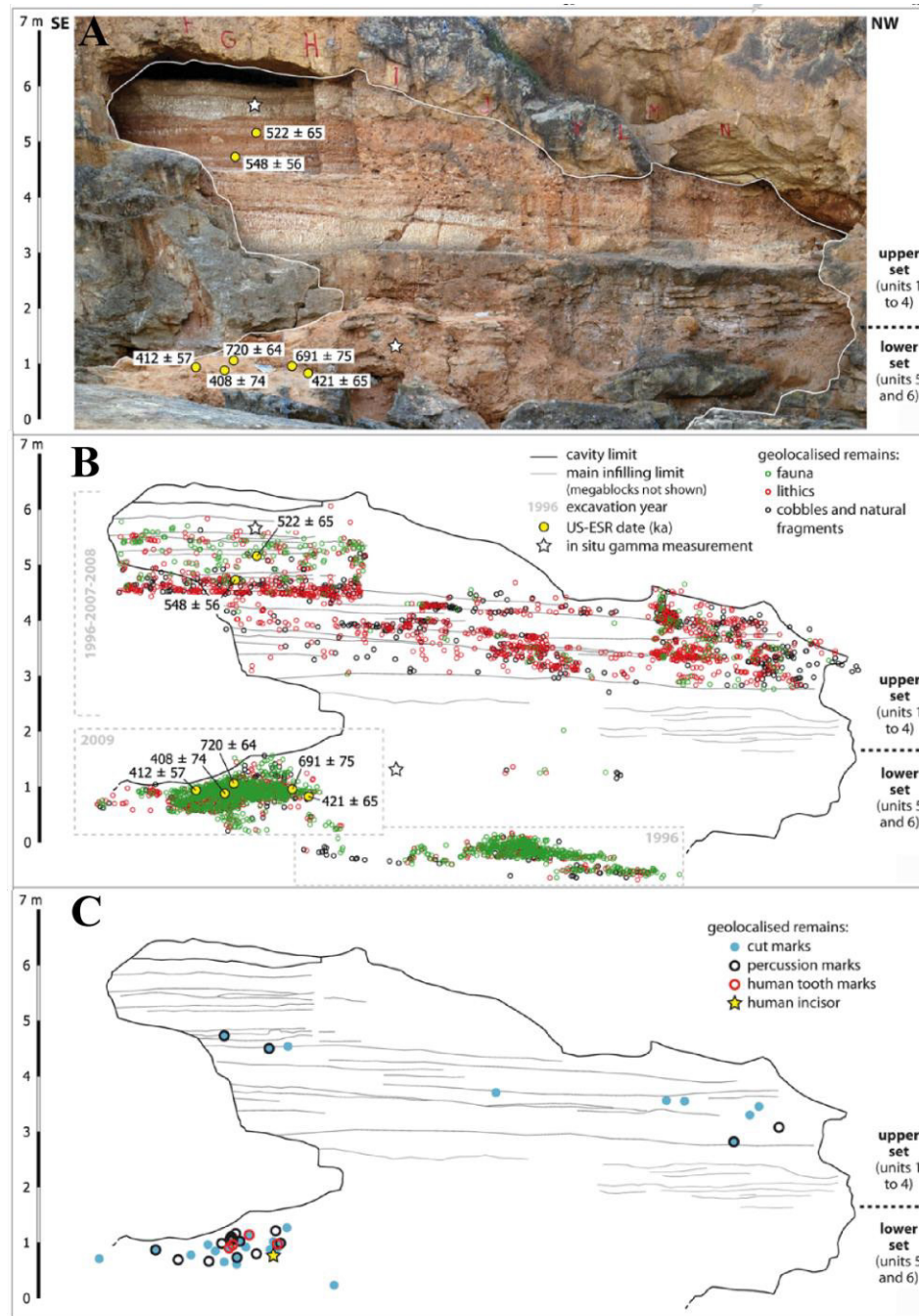


Figure 13. Extracted from the publication by Daujeard et al., 2020. **A**, Projection of the US-ESR dates (ka) on an orthophoto of the infilling (picture by D. Lefèvre). **B**, Projection of the US-ESR dates and all the coordinated remains (drawings by M. Rué). **C**, Projection of the human-modified remains presented in this article (only those with XYZ coordinates) and of the hominin incisor (drawings by M. Rué).

The limited differential bone preservation and well-preserved bone surfaces indicate a high degree of assemblage preservation (Raynal et al., 1993; Daujeard et al., 2012, 2020). Surface illegibility percentages are low (6 - 12%), though variations exist between levels, with more poorly preserved surfaces being more common in the upper set. Low bone destruction values further support good bone preservation, with most articular portions of long bones remaining intact. The high epiphysis/diaphysis ratio for both series indicates

good preservation of the spongy parts of long bones. Taphonomic modifications include carnivore tooth marks, abrasion striations, root markings, long bone fragmentation, and evidence of human-made marks on several bones. A total of 37 cut-marked specimens were observed at OHQ1-GDR: 28 in the lower set and 9 in the upper set, constituting approximately 1% of the total readable bone elements for the two series and 3.8 and 5.5% of the identified bone remains. In addition to the ungulates analysed in this thesis, the site is abundant in carnivores (Hyaenidae, Ursidae, Felidae, and Canidae), birds, and rodents (Daujeard et al., 2020; Raynal et al., 2023b). Furthermore, a single *Homo* tooth was found in situ during the excavation of the Lower units (GDR-2009-8448). It is a well-preserved left second incisor without pathological conditions (Daujeard et al., 2020).

3.2.2.2. Materials

3.2.2.2.1. Grotte à Hominidés

To perform the ecological reconstruction of ThI-GH, teeth from 6 taxa of large mammals were used, yielding results for a total of 41 samples for dental mesowear, 49 for microwear, and 56 for stable isotope analysis. The species included in this research are the following: *Ceratotherium mauritanicum*, *Theropithecus oswaldi*, *Camelus thomasi*, *Gazella cf. atlantica*, Alcelaphini, and *Equus cf. mauritanicus* (Fig. 14).

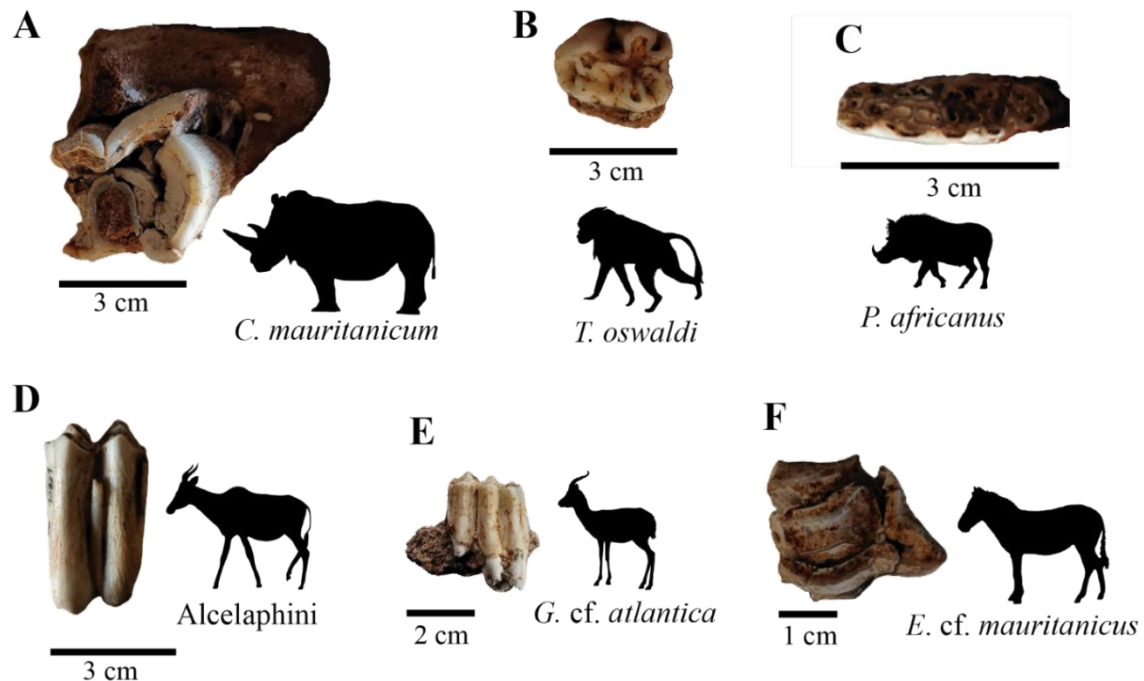


Figure 14. Some teeth from 6 large mammal taxa were analysed in ThI-GH. **A**, *C. mauritanicum* (GH 10218; maxilla). **B**, *T. oswaldi* (GH 90; molar occlusal view). **C**, *P. africanus* (GH 206; molar occlusal view). **D**, Alcelaphini (GH 10731; lower molar buccal view). **E**, *G. cf. atlantica* (GH 9; molar buccal view). **F**, *E. cf. mauritanicus* (GH 1; upper molar occlusal view).

Raw data containing all information of the analysed samples are provided in appendices (dental mesowear and microwear pp. 298 to 299, and stable isotopes pp. 290 to 291).

3.2.2.2.1. Grotte des Rhinocéros

To perform the ecological reconstruction of OHQ1-GDR, teeth from 6 taxa of large mammals were used, yielding results for a total of 54 samples for dental mesowear, 74 for microwear, and 83 for stable isotope analysis. The species included in this research are the following: *Ceratotherium mauritanicum*, *Theropithecus oswaldi*, *Phacochoerus africanus*, *Gazella cf. atlantica*, Alcelaphini, and *Equus cf. mauritanicus* (Fig. 15).

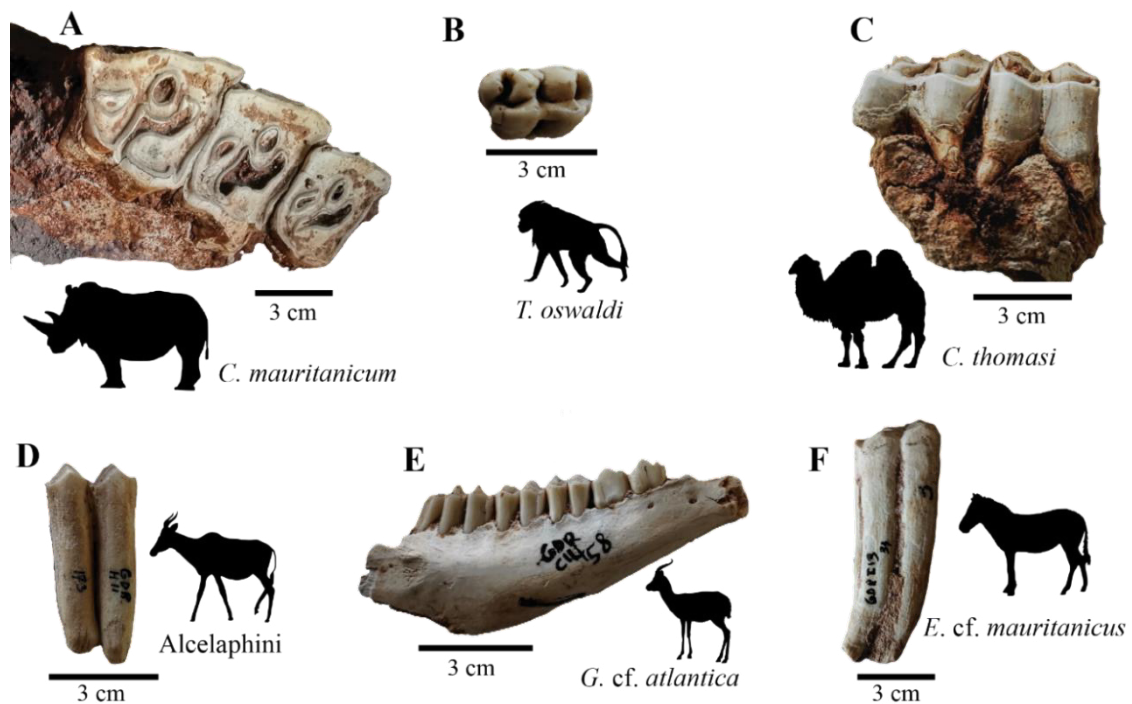


Figure 15. Some teeth from 6 large mammal taxa were analysed in OHQ1-GDR. **A**, *C. mauritanicum* (GDR 8355; maxilla). **B**, *T. oswaldi* (GDR 91; molar occlusal view). **C**, *C. thomasi* (GDR 87; maxilla). **D**, Alcelaphini (GDR 173; lower molar buccal view). **E**, *G. cf. atlantica* (GDR 58; mandible). **F**, *E. cf. mauritanicus* (GDR 33; lower molar buccal view).

Raw data containing all information of the teeth analysed samples are provided in appendices (dental mesowear pp. 300 to 302; dental microwear pp. 300 to 302, and carbon and oxygen stable isotopes pp. 292 to 293).

3.3. Reference collection of extant cercopithecines

In order to compare the fossil remains of *M. cf. sylvanus* and *Theropithecus oswaldi* included in this thesis, a reference collection of dental microwear has been developed for extant cercopithecids. The extant Cercopithecoidea comparative sample for the buccal microtexture and occlusal microwear analyses correspond to 56 well-preserved left second lower molars. We excluded 11 samples from occlusal microwear analysis and 12 from buccal microtexture due to bad preservation or other defects on the analysed surface. The selected species have well-defined habitat and dietary preferences and include six extant species (*Theropithecus gelada*, *Mandrillus sphinx*, *Lophocebus albigena*, *Cercocebus atys*, *Papio hamadryas* and *Macaca mulatta*) (**Fig. 16**). Whenever possible, we chose specimens of the same taxa from close localities to minimise the variability of their dietary regime. We selected the extant species based on the criteria of phylogenetic affinity (Perelman et al., 2011) and the dental morphology that characterises all cercopithecines, namely bilophodont molars (Kay and Hylander, 1978; Monson and Hlusko, 2014). The data regarding the selection of samples, such as their specific origin, sex, laterality, or tooth type, can be found in **appendices pp. 274 to 276 and 278**. This comparative sample established a broad spectrum of ecological and dietary diversity.

1. *Theropithecus gelada* (gelada baboon) specimens from Ethiopia have a plant-based dietary regime (Dunbar and Bose, 1991), with more than 80% consisting of blades (Mau et al., 2009). However, those *T. gelada* living on the Guassa Plateau also incorporate large quantities of forbs into their diet (Fashing et al., 2014) and are often selective of rare tender forbs on the plateau (Souron, 2018).

2. *Mandrillus sphinx* (mandrill) is a frugivore primate that usually lives in gallery forest. Fruits, supplemented with various plant parts like leaves and flowers, constitute the *Mandrillus* diet. However, when fruit is scarce due to seasonality, *M. sphinx* fallback on mechanically challenging items like seeds and hard-shell fruits from the forest floor (Hoshino, 1985; Lahm, 1986; Tutin et al., 1997; Powell et al., 2017).

3. *Cercocebus atys* (sooty mangabey) forages on the forest's floor and shrub layers, relying on hard-shelled nuts like *Sacoglottis gabonensis* year-round. Yet, due to seasonal fluctuations, the total contribution of *S. gabonensis* can range from 19 to 80% of the monthly diet (Daegling et al., 2011; McGraw et al., 2014).

4. *Lophocebus albigena* (grey-cheeked mangabey) is classified as a hard object feeder (Lambert et al., 2004; McGraw et al., 2011) that consumes a significant portion of hard seeds and nuts (Lambert et al., 2004). In actuality, due to seasonal fluctuations, *L. albigena* is a generalist that consumes a high (40%) percentage of soft ripe fruit (Lambert et al., 2004) in addition to seeds, flowers and young leaves (Poulsen et al., 2001). During seasons with low fruit availability, *L. albigena* will eat bark that, although hard, is rich in protein and soluble sugars (Rogers et al., 1994; Olupot, 1998). This fall-back feeding strategy has also been described for Barbary macaques (*Macaca sylvanus*; Ménard and Mohamed, 1999).

5. *Macaca mulatta* (rhesus macaque) has the most extensive geographical distribution, with its ranges spanning from Afghanistan to India, Pakistan, China, Thailand and Vietnam, among others (Sengupta et al., 2014). Its wide distribution reflects a highly opportunistic feeding strategy, even though fruits may constitute as much as 70% of their diet in some regions (Fooden, 2007), yet less than 9% in other ecosystems, such as Pakistan (Goldstein and Richard, 1989). They are semi-terrestrial primates that can feed on species in different forest strata (Albert et al., 2013).

6. *Papio hamadryas* (hamadryas baboon) inhabit the savanna lowlands ecosystems of eastern Africa. They are considered generalist omnivores, relying mainly on fruits, flowers, seeds, and leaves. Some studies have suggested that fruits and flowers are seasonal preferred foods (Dunbar and Bose, 1991; Swedell et al., 2008), being the most critical component of the baboon's diet (Dunbar and Dunbar, 1974). However, *P. hamadryas* from the Ethiopian highlands exploit high nutritional quality leaves and blades of graminoid plants (21.2%) throughout the year, while fruits and flowers were the least abundant, following a seasonal pattern according to rainfall (Ibrahim et al., 2023). The highland *P. hamadryas*, however, did not exhibit a significant dietary change between seasons, showing an adaptative pattern for this species between ecosystems.

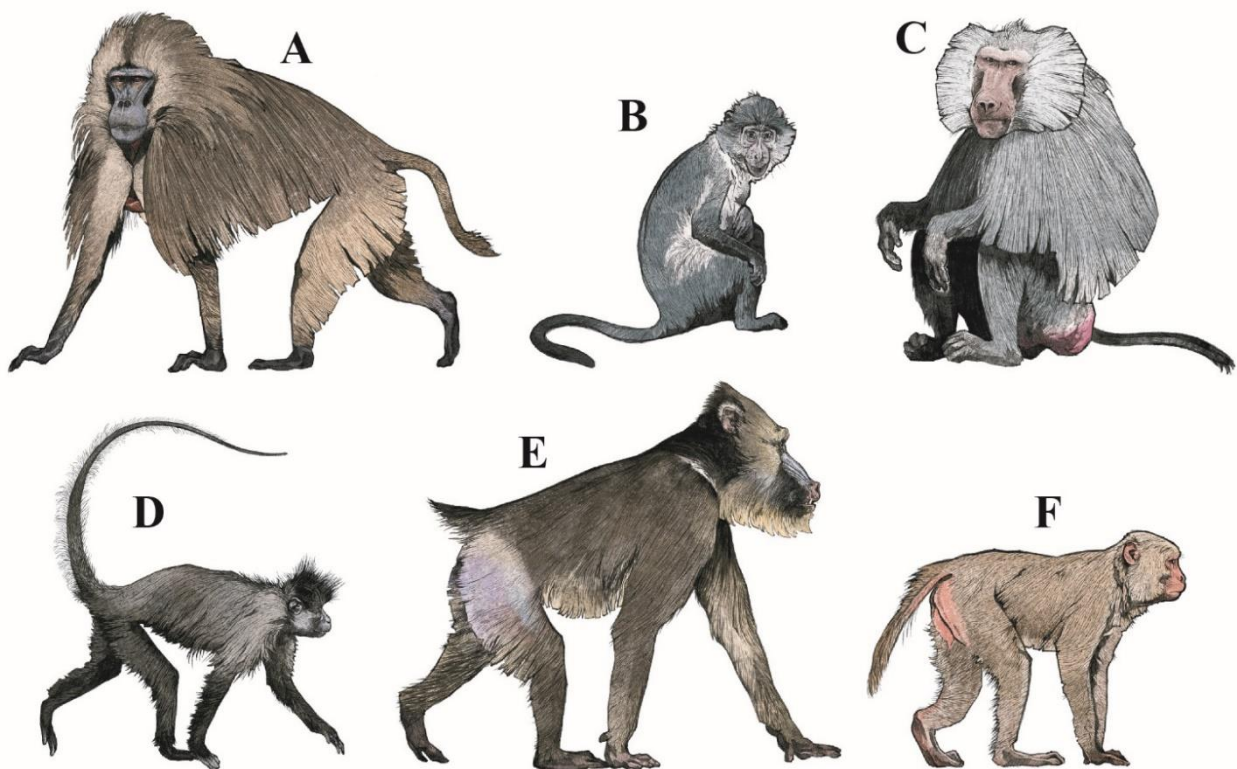


Figure 16. A, *Theropithecus gelada*. B, *Cercocebus atys*. C, *Papio hamadryas*. D, *Lophocebus albigena*. E, *Mandrillus sphinx*. F, *Macaca mulatta* (illustrations by Diego Rodríguez-Robredo).

· Chapter 4: Methods ·

4.1. Complementarity of selected methods

Given the diverse temporal resolutions employed in this thesis, it is crucial to highlight the complementarity of the selected methods to achieve the greatest possible insight into the ecological context in alignment with the outlined objectives (**Fig. 17**).

For studies related to large mammal teeth, we combine five high-resolution approaches that cover different stages in the animal's life: bulk analysis of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of tooth enamel bioapatite reflects the first years of life related to crown formation times (Lee-Thorp et al., 1989; Passey and Cerling, 2002); sequential analysis of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of the dental crown provides higher resolution than bulk (Passey and Cerling, 2002; Zazzo et al., 2005), obtaining values at different seasons/moments of the animal's life; tooth mesowear reflects the last months/years before death (Kaiser and Schulz, 2006; Rivals et al., 2007; Solounias et al., 2014; Ackermans et al., 2021); tooth occlusal microwear reflects the last days/weeks before death (Grine, 1986; Teaford and Oyen, 1989); and finally, analysis of microtextures of the buccal surface provides information on the last weeks/months of life (Romero et al., 2012), in the case of primates. This gives us four approaches with a "long-term" resolution that likely spans over a month or more. On the other hand, we have occlusal microwear and sequential carbon and oxygen, which would be "short-term" and allow us to obtain seasonal data (Rivals and Tornero, 2020). Altogether, this provides information about a significant portion of the animals' lives.

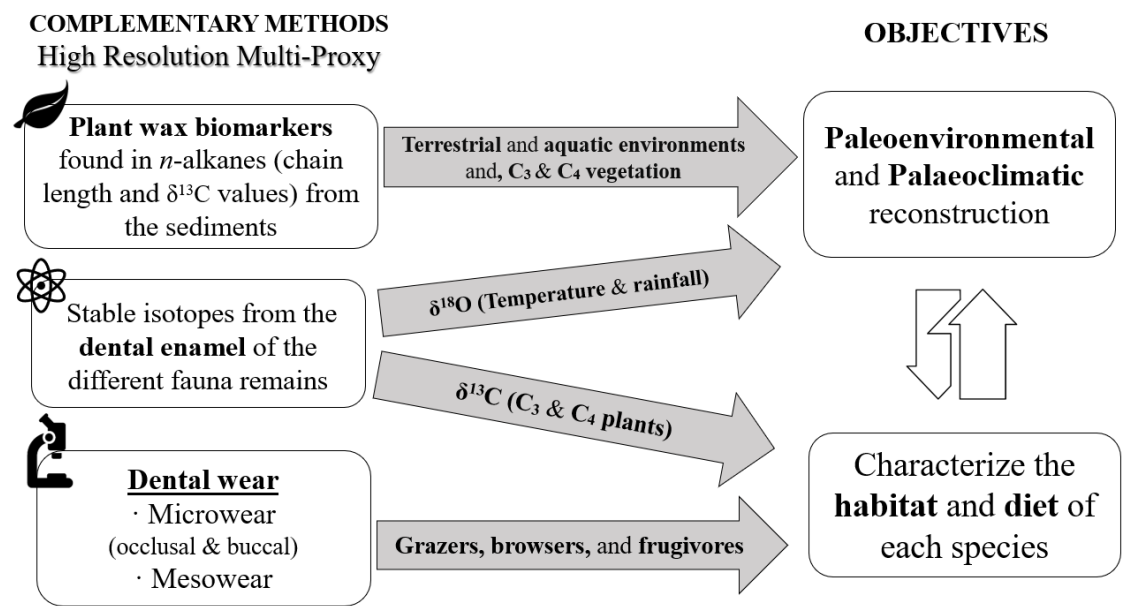


Figure 17. Linkage between the complementarity of the selected methods and the main objectives of the thesis

Regarding sediment analysis, we can obtain a landscape reconstruction that is complementary to that obtained from the animals. The combination of carbon isotopes in fauna and *n*-alkane chains allows for comparing the proportions of C₃-C₄ plants in the area from different sources. Plant waxes provide a more localised reconstruction, while fauna give a more regional one, as they may depend on mobility patterns or dietary preferences.

Combining all these approaches, this work aims to provide a robust ecological reconstruction of the study area.

4.2. Enamel carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope analysis

In terrestrial ecosystems, plants utilise three different photosynthetic pathways known as C₃ (Calvin cycle), C₄ (Hatch-Slack cycle), and crassulacean acid metabolism (CAM). These groups possess distinct carbon isotopic compositions due to the differential carbon discrimination between C₃ and C₄ plants during photosynthesis (Farquhar et al., 1989). Modern C₃ plants (including most trees, woody shrubs, bushes, herbs and temperate grasses) employing the C₃ photosynthetic pathway exhibit an average isotopic $\delta^{13}\text{C}$ value of -28.5‰ (global range -37 to -20‰), with typical C₃ plants having a maximum value of -23‰ and a threshold of -31.5‰ for closed-canopy forests (Kohn, 2010).

For this study, we employed an average $\delta^{13}\text{C}$ value of -27‰ for modern C₃ plants, excluding samples from the understory of closed-canopy forests below -31.5‰ (Kohn, 2010). Meanwhile, modern C₄ plants (primarily tropical grasses and sedges) utilising the C₄ photosynthetic pathway have an average isotopic composition of -12‰ (global range -14 to -10‰) (Cerling et al., 1997; Cerling and Harris, 1999; Kohn and Cerling, 2002). Crassulacean Acid Metabolism (CAM) plants may exhibit $\delta^{13}\text{C}$ values resembling C₃ and C₄ plants. The identification of CAM plant contributions in diets is complex. However, these plant types are typically not predominant in mammalian herbivore diets in Africa and often possess chemical defences that discourage consumption by mammals (Cerling et al., 2015). Moreover, CAM plants constitute only 5% of terrestrial plant biomass (Ehleringer et al., 1991), and these plants do not seem to be consumed by the different taxa in the study areas.

The abundance of atmospheric CO₂ has varied over time (Tippie et al., 2010), influencing the carbon values of plants during photosynthetic fixation (Farquhar et al., 1989). Corrections for these effects are crucial to compare current plant carbon isotope values and those consumed by animals in the past. In our study, we corrected the $\delta^{13}\text{C}$ values of modern plants by +1.5‰ due to the difference between the pre-industrial $\delta^{13}\text{C}_{\text{CO}_2}$ value of approximately -6.5‰ during the Early and Middle Pleistocene (Tippie et al., 2010), and the $\delta^{13}\text{C}_{\text{CO}_2}$ value of about -8‰ when the reference collection of modern plants was gathered (Kohn, 2010).

Dental enamel is one of the most commonly used materials for isotopic analysis and for reconstructing the paleoecology and paleodiet of extinct vertebrates due to its excellent

preservation, lower susceptibility to recrystallisation processes, and ability to preserve the original isotopic signal (Lee-Thorp and van der Merwe, 1987; Koch et al., 1994). Dental enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results in fossils have demonstrated reliability in samples dating back millions of years (Lee-Thorp et al., 1989).

Carbon from plants ingested by herbivores is metabolised and assimilated as carbonate into the biogenic apatite. This process induces isotopic fractionation, resulting in a $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment (Krueger and Sullivan, 1984; Koch, 1998). However, this enrichment can vary depending on the animal. In large mammals, it ranges from approximately +12–15‰ (Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005; Tejada-Lara et al., 2018; Malone et al., 2021). Cerling and Harris (1999) established an average $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment factor of $14.1 \pm 0.5\text{‰}$ for extant African large herbivorous ungulates. Passey et al. (2005) found different enrichment factors of $+13.3 \pm 0.3\text{‰}$ for non-ruminant pigs and $+14.6 \pm 0.3\text{‰}$ for ruminant cows in a controlled feeding study. For chimpanzees (*Pan troglodytes*) at Ngogo in Kibale National Park in Uganda, the calculated enrichment factor was $+11.8 \pm 0.3\text{‰}$ (Malone et al., 2021). Tejada-Lara et al. (2018) determined a positive correlation between body mass and enamel-diet enrichment fractionation (expressed as $\epsilon^*_{\text{enamel-diet}}$). Thus, animals with a lower weight, such as a *Gazella* weighing approximately ~30 kg, would have a $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment factor of about +12‰, while heavier animals like *Anancus*, around ~5000 kg, would exhibit an enrichment of around +15‰.

For the AaO site, where there was a better understanding of the possible body mass of the analysed species, we used formula (1) from Tejada et al. (2018) to calculate the $\epsilon^*_{\text{enamel-diet}}$ based on the estimated body mass.

$$(1) \quad \epsilon^* = 2.4 + 0.034 (\text{Body Mass})$$

We calculated an average enrichment based on the proposed methods for the other fauna sites (GFT-4.2, ThI-GH and OHQ1-GDR). We used an average enrichment between the lower +12‰ and the higher +15‰, i.e., +13.5‰, to interpret tooth enamel $\delta^{13}\text{C}$ values and estimate the potential consumption of C_3 or C_4 plants. Consequently, mammalian diets from GFT-4.2, displaying tooth enamel $\delta^{13}\text{C}$ values of $< -16\text{‰}$, indicate diets from closed canopy vegetation; values below ca. $< -12\text{‰}$ suggest pure C_3 plant consumption; values from -8 to 0‰ indicate a mixed C_3 - C_4 diet, and values above ca. > 0 or 1‰ are indicative of a predominant of pure C_4 vegetation diet. Any differences introduced by potential taxon-specific enrichment factors would not change this overall perspective, given the size of the observed variation.

We estimated (4) the fraction of C_4 vegetation consumed by AaO herbivores using $\delta^{13}\text{C}$ modern plant values, a cut-off value of -24‰ for C_3 vegetation ecosystems (Kohn, 2010) and -12‰ for C_4 vegetation (Cerling et al., 1997). The fossil $\delta^{13}\text{C}_{\text{enamel}}$ values have been corrected for $\delta^{13}\text{C}$ of Plio-Pleistocene atmospheric CO_2 and $\epsilon^*_{\text{enamel-diet}}$ to obtain the $\delta^{13}\text{C}_{\text{diet-meq}}$.

$$(4) \quad \% \text{C}_4 = 100 \times (\delta^{13}\text{C}_{\text{diet-meq}} - \delta^{13}\text{C}_{\text{C}_3}) / (\delta^{13}\text{C}_{\text{C}_4} - \delta^{13}\text{C}_{\text{C}_3})$$

The $\delta^{13}\text{C}$ values in plants and animals have also been proposed to estimate mean annual precipitation (MAP) in the fossil record. We use the formulae (2 and 3) developed by Kohn (2010) and Kohn et al. (2015) to estimate the MAP, which applies corrections for altitude, latitude, and $\delta^{13}\text{C}$ of atmospheric CO_2 from the average modern equivalent of diet composition ($\delta^{13}\text{C}_{\text{diet-meq}} = \delta^{13}\text{C}_{\text{enamel}} - \epsilon^*_{\text{enamel-diet}} - \text{Plio-Pleistocene atmospheric } \text{CO}_2$):

$$(2) \quad \text{MAP} = 10^{\wedge} [\Delta^{13}\text{C} - 2.01 + 0.000198 \times \text{elev} - 0.0129 \times |\text{lat}| / 5.88] - 300$$

Where *elev* is elevation in meters, *lat* is latitude in degrees, and

$$(3) \quad \Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{diet-meq}}) / (1 + \delta^{13}\text{C}_{\text{diet-meq}} / 1000)$$

This formula has been applied to sites where species consume a total or almost total C_3 plants, such as AaO, ThI-GH, and OHQ1-GDR. Following Kohn's (2010) requirements for applying the formula, environments with C_4 plants, such as GFT-4.2, cannot be interpreted because high $\delta^{13}\text{C}$ values may reflect C_4 consumption rather than aridity.

The $\delta^{18}\text{O}$ values within enamel bioapatite are closely linked to various water sources, including drinking water such as springs, rivers, lakes, and water holes, as well as plant-based or food-derived water found in leaves, grass, and fruits (Longinelli, 1984; Luz and Kolodny, 1985). Moreover, metabolic processes involving carbohydrates also contribute to these values (Bryant and Froelich, 1995). As a result, factors such as precipitation, altitude, humidity, aridity, and local temperatures significantly influence the isotopic composition of available water and food sources (Pederzani and Britton, 2019). Oxygen values can also vary within the same habitat, especially in tropical forest environments, depending on where the species forages. Species feeding in the upper part of the canopy tend to have higher $\delta^{18}\text{O}$ values as opposed to species feeding in the understory, which tend to have lower $\delta^{18}\text{O}$ values (Krigbaum et al., 2013; Crowley, 2014; Fannin and McGraw, 2020).

In arid environments, evaporation causes the enrichment of ^{18}O isotopes and depletion of ^{16}O isotopes in both open-water reservoirs and plant tissues (Gonfiantini et al., 1965). However, this process significantly impacts plants more, given their larger surface area for transpiration. Consequently, it is expected that animals reliant on plant-based water intake (non-obligate drinkers) would exhibit elevated $\delta^{18}\text{O}_{\text{enamel}}$ values in comparison to obligate drinkers, who directly access surface water sources (Bocherens et al., 1996; Kohn, 1996). The divergence in $\delta^{18}\text{O}$ values between these groups indicates increased aridity levels, with a more considerable disparity suggesting more arid conditions (Lehmann et al., 2016; Roberts et al., 2018; Lüdecke et al., 2022). In this work, we rely on the fundamental principle of obligate and non-obligate drinkers (Nicholson, 1985; Kohn, 1996; Levin et al., 2006; Blumenthal et al., 2017), which has been successfully

applied in other articles to establish the degree of relative aridity (Lehmann et al., 2016; Domingo et al., 2017; Roberts et al., 2018; Lüdecke et al., 2022).

For this thesis, we used the sampling and sample pre-treatment protocol established by Koch et al. (1997) and later modified by Tornero et al. (2013) (**Fig. 18**). Tooth surfaces were systematically cleaned with a tungsten abrasive drill bit to remove any extraneous material. Enamel powder for bulk analysis was extracted using a diamond-tipped drill along the entire buccal surface to ensure the most representative measurement for the whole period of enamel formation (**Fig. 18A**). For sequential samples, each sample was a groove that measured 1-2 mm in width and was perpendicular to the tooth growth axis, extending through the thickness of the enamel layer. The distance from the base of each sample groove to the enamel-root junction of the farthest sample margin was recorded. *Hipparion* s.l. was selected for the sequential analysis because of its pronounced hypsodonty and the detailed knowledge of its dental development (Orlandi-Oliveras et al., 2019).



Figure 18. Different steps of the stable isotopes protocol for sampling and pre-treatment at Biomarkers laboratory (IPHES-CERCA; Tarragona, Spain).

Powdered enamel samples weighing between 3.5 to 9.5 mg (**Fig. 18B**) were chemically treated at the Biomarkers Laboratory of the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), wherein samples were treated with 0.1 M acetic acid CH_3COOH (0.1 ml solution/0.1 mg of sample) for four hours (**Fig. 18C**), neutralised with distilled water (5 rinsings) (**Fig. 18D and E**), and dried (**Fig. 18F**) (Koch et al., 1997; Tornero et al., 2013).

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of carbonates were determined using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252) at the Environmental Isotope Laboratory, University of Arizona, USA (**Fig. 18G**). Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C . The isotope ratio measurement is normalised using a two-point method based on repeated measurements of the calcium carbonate international standards of NBS-19 ($\delta^{18}\text{O} = -2.20\text{‰}_{\text{VPDB}}$, $\delta^{13}\text{C} = +1.95\text{‰}_{\text{VPDB}}$) and NBS-18 ($\delta^{18}\text{O} = -23.2 \pm 0.1\text{‰}_{\text{VPDB}}$, $\delta^{13}\text{C} = -5.014 \pm 0.035\text{‰}_{\text{VPDB}}$) with a precision of $\pm 0.11\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 sigma). Samples are typically run in sessions of 46 measurements, with precision and normalisation determined for each session. Standards make up 13% of all measurements. Carbon and oxygen isotope composition was reported in δ notation, where $\delta^{13}\text{C}$ or $\delta^{18}\text{O} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, and δ is expressed in per mil, ‰. Carbon and oxygen values were reported relative to the Vienna Pee Dee Belemnite (VPDB) standard.

4.3. Tooth wear analysis

4.3.1. Tooth mesowear analysis

Dental mesowear is one of the two methods used in this thesis to reconstruct the diet and habitat of herbivores. This dental wear technique is widely used today (Ackermans, 2020) and involves scoring the height and sharpness of molar tooth cusps with the naked eye. Mesowear patterns were described in terms of facet development by Butler (1952) and Janis (1990). However, macroscopic observation of dental wear has not been a pioneering field of study within the scientific community. Primarily due to the reluctance of palaeontologists to consider food ingestion as a significant factor in wear (Every, 1970), this is reflected in dental wear publications (Calandra and Merceron, 2016). The first studies directly linked diet and wear employed microscopic techniques (Rensberger, 1978; Walker et al., 1978).

One of the debates surrounding mesowear concerns its temporal resolution. Although the exact period that it can cover during an animal's life is still unknown (Ackermans, 2020), there is a consensus that it reflects the animal's diet over the months or years before its death (long-term) and that mesowear does not change over short periods such as seasonal changes (Kaiser and Schulz, 2006; Rivals and Solounias, 2007; Solounias et al., 2014; Ackermans et al., 2021). There are few experimental studies on this technique, mainly

due to the difficulty of conducting long-term research. However, studies conducted on goats (Solounias et al., 2014; Ackermans et al., 2018; Stauffer et al., 2019) and sheep (Ackermans et al., 2020, 2021) confirm this proxy as representing a general lifetime signal.

The first standardised method for qualitatively measuring occlusal relief (low or high) and cusp shape (sharp, rounded or blunt), which are related to attritive and abrasive wear on dental enamel, was not published until 2000 (Fortelius and Solounias, 2000). The authors primarily analysed the paracone of upper molars from a database of 64 extant species of ungulates. The methodological principle used in this article has been maintained in the main methodological articles on mesowear published subsequently, including this thesis (see Ackermans, 2020, for a review of the history of mesowear). Although the method was initially applied to the upper M2, it was later extended from the upper P3 to M3 (Kaiser and Solounias, 2003). In this study, the extended Kaiser and Solounias 2003 method was used to analyse the buccal side of molars and premolars, as well as the lingual part of the lower molars for Bovidae (Fraser et al., 2014; Dumouchel and Bobe, 2020). The lower molars of Equidae were excluded based on Kaiser and Solounias (2003) suggestion that mandibular molars reflect a more grazing signal than upper molars.

In this thesis, we have excluded teeth for two main reasons: 1) because the cusps were broken and damaged, and it was not possible to analyse the mesowear. 2) when the specimen was unworn or excessively worn due to ontogenic age. The effect of ontogenic age on cusp sharpness has been documented for young individuals who do not yet have wear facets and old individuals. In contrast, mesowear exhibits a weaker correlation with age in intermediate age groups but a stronger association with dietary factors (Rivals et al., 2007). We applied the method introduced by Mithlbaehler et al. (2011) for Equidae (**Fig. 19**), which utilises seven cusp categories ranging from high and sharp (stage 0) to completely blunt with no relief (stage 6). A low-abrasion diet such as browsing, which induces high attrition, preserves sharpened apices on buccal cusps as teeth wear down, while a high-abrasion diet results in more rounded and blunted buccal cusp apices. The average value of the individual mesowear data from a single sample corresponds to the mesowear score (MWS). For Bovidae, the method of Mithlbaehler et al. (2011) has been employed, but with a slightly adapted mesowear scale (**Fig. 20**) to the morphology of this family (Rivals et al., 2013).



Figure 19. Mesowear score scale for Equidae (upper molars) extracted from Mithlbaehler et al. (2011).

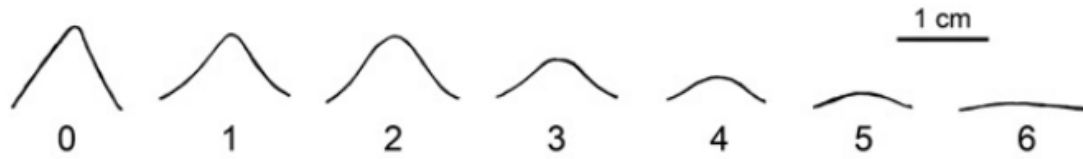


Figure 20. Mesowear score scale adapted for Bovidae and Cervidae (upper and lower molars) extracted from Rivals et al. (2013).

To compare the data collected on extinct herbivores from the sites analysed, we used a reference collection of dental mesowear in extant ungulates consisting of 95 species and 4444 samples (Fortelius and Solounias, 2000; Rivals et al., 2010, 2013, 2015a; Rivals and Semprebon, 2017).

The list of extant species that can be used for comparison is as follows: *Aepyceros melampus*, *Alcelaphus buselaphus*, *Alces alces*, *Alces alces* (Europe), *Alces alces* (North America), *Ammodorcas clarkei*, *Ammotragus lervia*, *Antidorcas marsupialis*, *Antilocapra americana*, *Axis axis*, *Axis porcinus*, *Bison bison athabasca*, *Bison bison bison*, *Bison bonasus*, *Boselaphus tragocamelus*, *Bubalus mindorensis*, *Budorcas taxicolor*, *Camelus bactrianus*, *Camelus dromedarius*, *Capra caucasica*, *Capra ibex*, *Capra pyrenaica*, *Capreolus capreolus*, *Capricornis sumatraensis*, *Cephalophus dorsalis*, *Cephalophus natalensis*, *Cephalophus niger*, *Cephalophus nigrifrons*, *Cephalophus silvicultor*, *Ceratotherium simum*, *Rucervus duvaucelii*, *Cervus elaphus* (Europe), *Cervus elaphus* (N. America), *Cervus nippon*, *Rusa unicolor* (= *Cervus unicolor*), *Connochaetes taurinus*, *Dama dama*, *Dama dama mesopotamica*, *Damaliscus lunatus*, *Dendrohyrax arboreus*, *Dendrohyrax dorsalis*, *Dicerorhinus sumatrensis*, *Diceros bicornis*, *Equus quagga*, *Equus grevyi*, *Gazella gazella*, *Gazella dorcas*, *Nager granti* (= *Gazella granti*), *Eudorcas thomsonii* (= *Gazella thomsoni*), *Giraffa camelopardalis*, *Hemitragus hylocrius*, *Hemitragus jemlahicus*, *Heterohyrax brucei*, *Hippotragus equinus*, *Hippotragus niger*, *Hyemoschus aquaticus cottoni*, *Kobus ellipsiprymnus*, *Lama glama*, *Lama guanicoe*, *Lama guanicoe* (Lago Cardiel, Argentina), *Vicugna vicugna*, *Litocranius walleri*, *Moschiola meminna* (= *Tragulus memmina*), *Muntiacus muntjak*, *Muntiacus reevesi*, *Odocoileus hemionus*, *Odocoileus virginianus*, *Okapia johnstoni*, *Oreamnos americanus*, *Ourebia ourebi*, *Ovibos moschatus*, *Ovis ammon darwini*, *Ovis ammon polii*, *Ovis canadensis*, *Pantholops hodgsoni*, *Procapra gutturosa*, *Procavia capensis capensis*, *Rangifer tarandus* (Qamanirjuaq), *Rangifer tarandus* (Banks Island), *Redunca fulvorufula*, *Redunca redunca*, *Rhinoceros sondaicus*, *Rhinoceros unicornis*, *Rupicapra pyrenaica*, *Rupicapra rupicapra*, *Saiga tatarica*, *Sigmoceros lichtensteinii*, *Syncerus caffer aequinoctialis*, *Taurotragus oryx*, *Tetracerus quadricornis*, *Tragelaphus angasi*, *Tragelaphus eurycerus* (= *Boocercus eurycerus*), *Tragelaphus imberbis*, *Tragelaphus scriptus*, *Tragelaphus strepsiceros*, *Tragulus javanicus* and *Tragulus napu*.

The statistical analysis was performed using Past 4.02 software (Hammer et al., 2001). Bivariate graphs and ANOVA statistical tests with Tukey's pairwise comparison were conducted for the mesowear results.

4.3.2. Tooth microwear analysis

4.3.2.1 Occlusal low magnification microwear analysis

The investigation of dental microwear has a rich history in elucidating the dietary preferences and ecological niches of extinct and extant species. For a comprehensive review of the different techniques of dental microwear, see Teaford et al. (2013) and Ungar (2015). The first dental microwear study was conducted on human dental remains using an optical microscope (Dahlberg and Kinzey, 1962). In the mid-1970s, scanning electron microscopy (SEM) at high magnifications (~ 100 - 500x) became widespread in dental microwear studies. The first study focused on comparing the differences between the diets of Paleo-Indians and contemporary Americans (Shkurkin et al., 1975). Studies were also conducted on the microwear of *Homo erectus* from Tautavel (Puech, 1977). Additionally, the first works that differentiated different types of diets in extant small mammals and classified them as grazers or browsers based on the microwear pattern were carried out (Rensberger, 1978; Walker et al., 1978). The work of Walker et al. (1978) published in *Science* was particularly influential. They qualitatively examined the pits and scratches of two wild hyraxes, *Heterohyrax brucei* and *Procavia capensis johnstoni*. They were the first to relate microwear traits such as pits with a browsing diet and scratches with a more abrasive grazing diet. Several SEM studies, both quantitative and qualitative, followed in the 1980s. These works aimed to standardise the method and adjust variables that could influence the results, such as the type of teeth, facets, scanning electron microscope settings, metric rules, and magnification.

The majority of studies aimed to distinguish the microwear pattern of the occlusal surface of fossil hominins and extant primates as a reference collection (Puech et al., 1980, 1983; Grine, 1981, 1986; Gordon, 1982, 1988; Teaford and Walker, 1984; Kay, 1986). In the late 1990s and early 2000s, two new microscopic techniques were introduced for studying dental microwear. On the one hand, the Dental Microwear Texture Analysis (DMTA) uses three-dimensional surface measurements obtained through white-light confocal microscopy and scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2006). On the other hand, the dental microwear pattern analysis was also conducted using low-magnification light microscopy (MacFadden et al., 1999; Solounias and Semprebon, 2002; Godfrey et al., 2004; Semprebon et al., 2004).

One of the debates surrounding the dental microwear method is its temporal resolution. As with dental mesowear, the exact time frame the signal covers is still under investigation (Ackermans et al., 2021). However, the signal reflects a short-term dietary effect that likely covers the last few days or weeks before death (Teaford and Oyen, 1989).

This signal has been defined as the 'last supper' effect (Grine, 1986). Therefore, the dental microwear pattern can reveal the diet of the animal based on the local and seasonal environmental resources available shortly before its death.

The low magnification microwear technique was developed as an alternative to SEM, which, despite its effectiveness in reconstructing species ecology (Covert and Kay, 1981; Grine, 1986, 1987; Solounias et al., 1988), remains an expensive and time-consuming tool. This makes it challenging to create an extensive reference collection of extant animals. Furthermore, pits and scratches may occasionally be observed under SEM magnification based solely on arbitrary metric rules (Semperebon et al., 2004). Semperebon et al. (2004) demonstrated that this method is economical, fast, and manual and can distinguish between different types of diets without the need for high magnification.

For this thesis, we have employed the low-magnification method published by Solounias and Semperebon in 2002 (**Fig. 21**). We chose a low-magnification microwear approach because an extensive dental microwear reference collection of extant species, particularly those of African origin, is available (Solounias and Semperebon, 2002).



Figure 21. Different steps of the dental microwear protocol for cleaning, moulding, and casting at Biomarkers Laboratory (IPHES-CERCA; Tarragona, Spain). See the video by Martínez-Polanco et al. (2021) for more details.

Before starting the sampling process, one aspect to consider is the tooth selection and the specific area to be analysed. Solounias and Semprebon (2002) and Semprebon et al. (2004) analysed the mesio Buccal cusp of the second upper molars (usually the paracone of M²). Subsequent studies have demonstrated the robustness and similarity of the results by expanding the selection of upper and lower teeth from P4 to M3. For this study, we have used this criterion established by Xafis et al. (2017).

The protocols for cleaning, moulding, casting, and examining, as well as the criteria for feature classification used (**Fig. 21**), are consistent with those established by Solounias and Semprebon (2002) and Semprebon et al. (2004).

Firstly, the original tooth surface is cleaned to ensure the resulting cast is suitable for observation. We use a swab to clean the tooth surface with acetone (~99%; **Fig. 21A**) and then with ethanol (~96% **Fig. 21B**) to remove any residual acetone. Although the drying and evaporation of acetone and ethanol are pretty rapid, it is essential to wait a few minutes (~5 - 10) because if we apply the silicone when it is still wet, it will not be possible to analyse the mould under the binocular microscope. Once it is completely dry, we proceed to apply the high-resolution silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set) with the dispensing gun (**Fig. 21C**). The cartridges contain two tubes that mix the silicone and the catalyst. The mould usually takes between 5 and 10 minutes to set, depending on the ambient temperature and humidity conditions. After the high-resolution silicone has been set, a new layer of low-resolution silicone (Heraeus Putty Regular Set) is added to provide support to the mould and allow it to be filled with epoxy (**Fig. 21D**). The transparent casts were made using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). The epoxy and catalyst must be mixed in precise proportions, as specified by the manufacturer. For EPO 150, the components are measured by weight, with the catalyst accounting for 25% of the total epoxy used (e.g. 100 g of epoxy requires 25 g of catalyst) (**Fig. 21E and F**). When pouring the epoxy into the moulds, it is important to be careful as bubbles can form and interfere with microwear analysis under the microscope. To prevent this, the mould base can be filled slowly with a pipette, and the rest can be poured directly. Once the resin has solidified (~48 h), the transparent positive can be removed from the mould (**Fig. 21G**) and analysed using the Zeiss Stemi 2000C stereomicroscope at the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA, Tarragona).

The stereomicroscope enables magnification up to 50x, although microfeature counting is performed at 35x. It is crucial to adjust the transmitted light during observation, manipulating its intensity and the projection angle. The right ocular has a reticle with an area of 0.16 mm², which was used for counting. Whenever possible, we have conducted two counts to address sample variability. A specialist researcher (IRP) performs microwear analysis to reduce inter-observer error.

The casts were screened under the stereomicroscope, and we discarded the specimens showing poor preservation or taphonomic defects. These correspond to non-dietary microfeatures that may be generated during the diagenetic process or fresh microfeatures that may be produced during the excavation and recovery of the remains or their

subsequent storage (King et al., 1999; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2023, 2024).

The variables used in this study (**Fig. 22**) are small and large pits (round scars), coarse, fine and hypercoarse scratches (elongated scars with parallel sides), gouges (irregular edges and much larger and deeper than the large pits), puncture pits (deepest in their centres, symmetrical, crater-like features with regular edges), and cross scratches (oriented perpendicular to the majority of scratches). The Scratch Width Score (SWS) is determined by the ratio of fine to coarse scratches on each tooth surface. A score of '0' indicates predominantly fine scratches, '1' indicates a mixture of fine and coarse scratches, and '2' shows predominantly coarse scratches. To achieve a more precise categorisation of grazers, browsers, and mixed feeders, we used the percentage of individuals possessing scratch numbers that fall between 0 and 17 in the 0.16 mm² area (0-17%) (Semperebon and Rivals, 2007).

We captured microphotographs using a Blackfly S digital camera and the Kiviy Mic Capture Z software. We merged images from various focal planes and produced a single image with a greater depth of field using the Helicon Focus 7 software. Finally, we added scale bars using ImageJ.

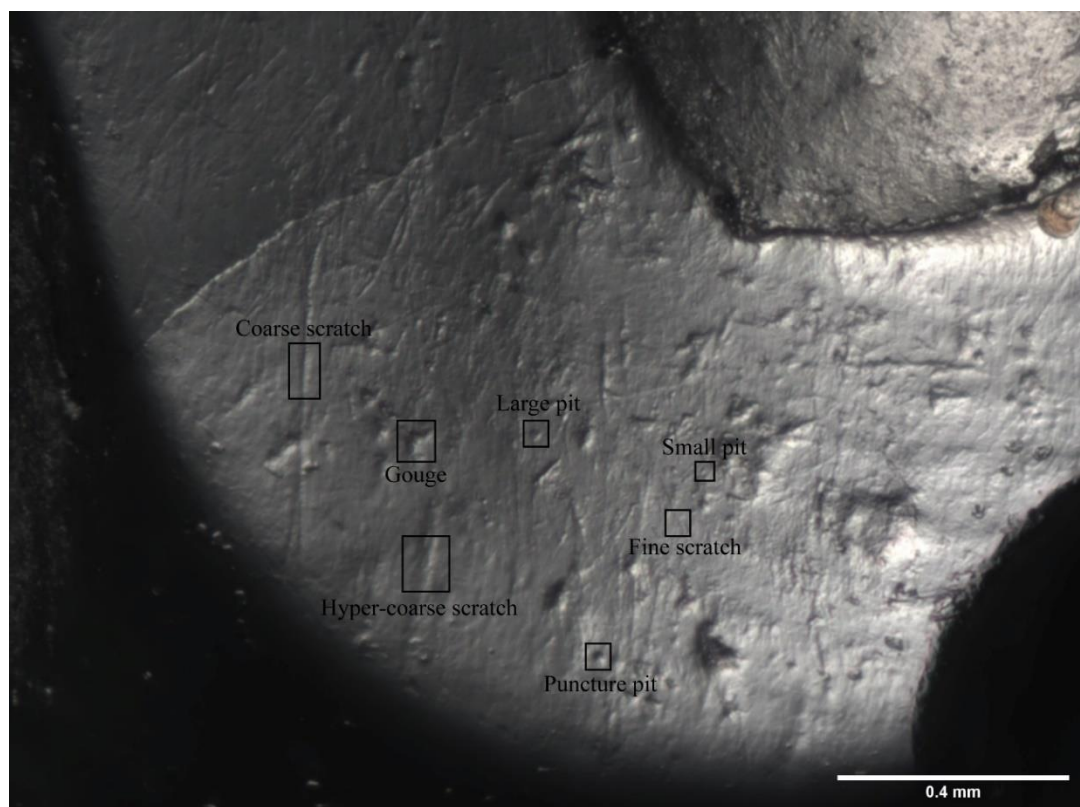


Figure 22. Microphotographs at 35x magnifications indicating the occlusal microwear variables analysed (Hypercoarse, coarse and fine scratches, small and large pits, puncture pits and gouges). Sample: *C. atys* (PAP1992); Scale bar = 0.1 mm.

In order to compare with extinct herbivores from the sites analysed. We used a reference collection of dental microwear in extant ungulates consisting of 88 species and 2988 specimens (Solounias and Semprebon, 2002; Rivals and Solounias, 2007; Rivals et al., 2007, 2015b; Rivals and Semprebon, 2011; Rivals, 2012; Semprebon et al., 2016). In general, fossil species with a higher number of pits and a lower number of scratches are classified as extant browsers, while species with a higher number of scratches and a lower number of pits are classified as extant grazers. Mixed feeders fall between these two groups. The following R script generated the microwear bivariate graphs (Rivals, 2019).

The list of extant species that can be used for comparison is as follows: *Alcelaphus buselaphus*, *Alces alces*, *Alces alces* (Europe), *Alces alces* (North America), *Ammotragus lervia*, *Antilocapra americana*, *Axis axis*, *Bison bison athabasca*, *Bison bison bison*, *Bison bonasus*, *Boselaphus tragocamelus*, *Bubalus mindorensis*, *Budorcas taxicolor*, *Camelus bactrianus*, *Camelus dromedarius*, *Capra caucasica*, *Capra ibex*, *Capra pyrenaica*, *Capreolus capreolus*, *Capricornis sumatraensis*, *Cephalophus dorsalis*, *Cephalophus natalensis*, *Cephalophus niger*, *Cephalophus silvicultor*, *Ceratotherium simum*, *Rucervus duvaucelii*, *Cervus elaphus* (Europe), *Cervus elaphus* (N. America), *Cervus nippon*, *Rusa unicolor* (= *Cervus unicolor*), *Connochaetes taurinus*, *Dama dama*, *Dama dama mesopotamica*, *Diceros bicornis*, *Elephas maximus*, *Equus quagga*, *Equus grevyi*, *Gazella gazella*, *Gazella dorcas*, *Nager granti* (= *Gazella granti*), *Eudorcas thomsonii* (= *Gazella thomsoni*), *Giraffa camelopardalis*, *Hemitragus hylocrius*, *Hemitragus jemlahicus*, *Hippopotamus amphibius*, *Hippotragus niger*, *Hyemoschus aquaticus cottoni*, *Hylochoerus meinertzhageni*, *Kobus ellipsiprymnus*, *Lama glama*, *Lama guanicoe*, *Lama guanicoe* (Lago Cardiel, Argentina), *Loxodonta Africana*, *Loxodonta cyclotis*, *Vicugna vicugna*, *Litocranius walleri*, *Mazama americana*, *Moschus moschiferus*, *Muntiacus muntjak*, *Muntiacus reevesi*, *Odocoileus hemionus*, *Okapia johnstoni*, *Oreamnos americanus*, *Ovibos moschatus*, *Ovis ammon darwini*, *Ovis ammon polii*, *Ovis canadensis*, *Pantholops hodgsoni*, *Phascolarctos cinereus*, *Procapra gutturosa*, *Potamochoerus porcus*, *Rangifer tarandus* (Qamanirjuaq), *Rangifer tarandus* (Banks Island), *Rupicapra pirenaica*, *Rupicapra rupicapra*, *Saiga tatarica*, *Sus scrofa*, *Tapirus bairdii*, *Tapirus terrestris*, *Taurotragus oryx*, *Tetracerus quadricornis*, *Tragelaphus eurycerus* (= *Boocercus eurycerus*), *Tragelaphus imberbis*, *Tragelaphus scriptus*, *Tragelaphus strepsiceros* and *Tragulus javanicus*.

For extant cercopithecids, we created a new dental microwear reference collection that can be compared with fossils. For more information on the species used, refer to **appendices pp. 274 to 276**.

4.3.2.3 Buccal microtexture analysis

This technique analyses the 3D microtexture of dental surfaces. It was developed in the early 2000s (Ungar et al., 2003, 2007; Scott et al., 2005, 2006) to propose a more objective and reproducible method for reconstructing the diet and habitat of fossil species than previous methods. According to Ungar et al. (2003), scanning electron microscopy (SEM) does not accurately represent surfaces in three dimensions, and the identification and

measurement of individual features using SEM is laborious and subjective. Concerning the low magnification dental microwear, they argued that the method is susceptible to significant interobserver variability. These initial studies focused on analysing the microtexture of the occlusal surface of extant primates (Ungar et al., 2003; Scott et al., 2006), fossil hominins (Scott et al., 2005), and extant and extinct African bovids (Ungar et al., 2003, 2007). They used Scale-Sensitive Fractal Analysis (SSFA) with Toothfrax and Sfrax software and complexity and anisotropy parameters. Anisotropy has been linked to food toughness. High anisotropy is found for surfaces dominated by parallel scratches. Complexity has been associated with food hardness. More complex surfaces exhibit pits and scratches of different sizes (Scott et al., 2006). Scott et al. (2006) introduced additional parameters, such as heterogeneity, scale of maximal complexity, and textural fill volume. Kaiser and Brinkmann (2006) later developed another approach based on 2D standard parameters (International Organization for Standardization (ISO) 4287). This method was further extended with 3D roughness ISO/FDIS parameters (ISO 25178; Schulz et al., 2010; Calandra et al., 2012). The initial studies used the occlusal surface of the tooth to analyse microtextures with a confocal microscope. Although the usefulness of the buccal surface in discriminating diets with SEM had already been demonstrated (Ungar and Teaford, 1996; Galbany and Pérez-Pérez, 2004; Galbany et al., 2009; Martínez et al., 2016), there are few microtexture studies based on buccal surfaces (Aliaga-Martínez et al., 2017; Hernando et al., 2022; Martínez et al., 2022).

For this thesis, we analysed the buccal surface of both extant and fossil Cercopithecidae molars. To achieve this, we used the same individuals and teeth in both analyses. We have primarily used M2, which is the most commonly used tooth for both occlusal (Scott et al., 2012; Merceron et al., 2021) and buccal (Ungar and Teaford, 1996; Galbany et al., 2009; Martínez et al., 2020) dental microwear studies among non-human primates.

The exact time it takes for buccal microwear marks to form is unknown, as are all the factors that influence their formation. However, *in vivo* experimental studies have shown that buccal microwear patterns provide 'long-term' dietary signals and have slower turnover rates than dental occlusal microwear analysis (Romero et al., 2012).

In this protocol, the original specimens (**appendices pp. 274 to 276**) were cleaned using acetone and alcohol-soaked cotton swabs. Vinyl impressions were then taken using high-resolution silicon President's Jet Regular Body (Coltène-Whaledent). Positive casts were made using Ferropur (FeroCa®) polyurethane (Martínez et al., 2022). Buccal areas were imaged using a Sensofar Plu Neox laser scanning confocal microscope. The microscope had a 20× (0.45NA) objective, a spatial sampling of 0.83 µm, an optical resolution of 0.31 µm, a vertical resolution of 20 nm, and a z-step interval of 1 µm (Ibáñez et al., 2020; Martínez et al., 2022). The buccal surfaces were positioned horizontally with the objective perpendicular to them. An image of the microscope's field of view (500 × 600 µm) was captured. 3D photosimulations can be found in **appendices pp. 265 to 270**. Four subsamples of 138 × 102 µm (a standard area in DMTA studies) were then cropped from this image using Digital Surf's Mountain 7® software.

The S-filter was tested before obtaining the 38 parameters, following the methodology of Winkler et al. (2022). The workflow involved levelling the surface to remove plane inclination, eliminating curvature using a 2nd-degree polynomial, removing anomalous points by applying upper and lower 0.5% thresholds (a total of 1% of threshold values) using the threshold operator included in the same software, and applying a spatial filter (Gaussian 3×3). The Gaussian filter was applied because it is widely used for technical surfaces. It was applied after the trimming because it is sensitive to outliers (Schulz et al., 2013). Surface roughness was later quantified according to 38 ISO 25178/ISO 12781 parameters (Martínez et al., 2022).

To standardise the measured area on the buccal surface at a statistical level, we calculated the median of the parameters derived from one to four measurements of a single buccal surface (Scott et al., 2006; Calandra et al., 2012; Martínez et al., 2022). The median per specimen was used for analysis. Texture data was log-transformed for analysis due to non-normal distributions of some texture parameters (Shapiro-Wilk, $p < 0.05$). To avoid excluding any parameters, including those with negative values such as *Ssk*, we applied a log transformation to the data using the formula $\log [1 + \text{parameter}]$. Outliers were identified for both the original and log-transformed variables based on their Standardised residual values (absolute value > 3) and were subsequently removed from the final dataset (Schulz et al., 2013; Martínez et al., 2022). To test the null hypothesis that microwear textures do not differ between teeth from different species, we conducted an analysis of variance (ANOVA) with pairwise testing (Tukey's honest significant difference [HSD]) for each texture parameter of each species. In cases where the homogeneity of variance test (Levene's test) indicated unequal variances, we used Welch's ANOVA. We selected the parameters that exhibited significant differences between species and applied a linear discriminant analysis (LDA). Addinsoft™ XLSTAT-3.02 statistical packages were used to perform descriptive statistics, tests, and graphs.

4.4. Plant wax biomarkers analysis

Plant wax biomarkers are a relatively new method to reconstruct past environments, including vegetation composition, rainfall intensity, temperature, and other climatic and environmental dynamics. Traditionally used in the field of earth sciences and applied to large sedimentary records in oceans and lakes (Eglinton and Eglinton, 2008; Castañeda et al., 2009), and more recently applied to archaeological and human evolution contexts (Magill et al., 2013; Patalano et al., 2021b). This method is based on the molecular and isotopic characterisation of *n*-alkanes, *n*-alkanoic acids, and *n*-alkanols from the lipid waxes of plants recovered from sediments. The protocol used in this work was established by Patalano et al. (2020).

The first step is to collect sediment samples (**Fig. 23A**). It is necessary to measure the exact location where each sample was collected. In this case, as we are dealing with archaeological and palaeontological sites, we have sampled the same stratigraphic

sequence. Sterilised tools are used to collect sediment samples (approximately 100 g) every 5 cm, starting from the bottom of the vertical column. All collected samples are stored in individual paper bags to absorb any possible moisture.

Once the sample arrives at the laboratory, it is oven-dried for at least 48 hours before extraction. After drying, it is homogenised using a mortar and pestle (**Fig. 23B and 23C**). The extraction and isolation of plant wax then begins. The sediments are introduced into the pressurised solvent extraction (Büchi Speed Extractor E-916) in three 10-minute cycles using a 9:1 (v:v) DCM:MeOH mixture at 100°C and 103 bar/1500 psi (**Fig. 23D**). Solvent containing the total lipid extract (TLE) was concentrated to ~1 mL using a Büchi Syncore-Plus evaporator and then evaporated to dryness using a steady stream of N₂ in separate (**Fig. 23E**), 4 mL glass vials. The TLE was separated into neutral, acid, and polar fractions by Aminopropyl column chromatography using 4 mL each of 2:1 dichloromethane:isopropanol, 4% acetic acid in diethyl ether, and methanol, respectively (**Fig. 23F**). Normal (*n*-) alkanes were isolated from the neutral fraction using silver nitrate-infused silica gel column chromatography with 4 mL hexane. The resulting solvent in the 4 mL vials is evaporated using nitrogen gas (**Fig 23H**).



Figure 23. Protocol for plant wax biomarkers analysis at Max Planck Institute of Geoanthropology (Jena, Germany). **A**, Sampling of the GFT-4.2 sequence. **B**, Homogenisation of sediments using a mortar. **C**, Weighing of samples for analysis. **D**, Introduction of samples into the Büchi Speed Extractor E-916. **E**,

Introduction of samples into the Büchi SyncorePlus evaporator. **F**, Isolation of *n*-alkanes using silver nitrate-infused silica gel column chromatography. **G**, Final result after performing chromatography columns. **H**, Evaporation of the solvent from the vials with nitrogen gas to prepare the samples for analysis in the GC.

The *n*-alkanes were characterised molecularly using an Agilent 7890B Gas Chromatograph (GC) System equipped with an Agilent HP-5 capillary column (**Fig. 23I**) (30 m length, 0.25 mm i.d. and 0.25 µm film), and coupled to a 5977A Series Mass Selective Detector (MSD) at the Max Planck Institute for the Science of Human History (now Geoanthropology), Jena, Germany. Samples were injected in pulsed split mode at 290 °C, and the GC oven was programmed from 60°C (1 min hold) to 150°C at 10 °C/min, then to 320 °C at 6 °C/min (10 min hold). Helium was the carrier gas with a constant flow of 1.1 mL/min. The MS source was operated at 230°C with 70 eV ionisation energy in the electron ionisation (EI) mode and a full scan rate of *m/z* 50-650. Plant wax *n*-alkanes were identified by comparing mass spectra and retention times with an external C₂₁-C₄₀ standard mixture.

The average chain length, or the weight-averaged number of carbon homologues of the C₂₁-C₃₃ *n*-alkanes, was calculated as follows:

$$ACL = \frac{21(C_{21}) + 22(C_{22}) + \dots + 32(C_{32}) + 33(C_{33})}{C_{21} + C_{22} + \dots + C_{32} + C_{33}}$$

Where C_{*x*} is the abundance of the chain length with *x* carbons.

Generally, short-chain homologues (C₁₇-C₂₁ *n*-alkanes) characterise aquatic algae (Cranwell et al., 1987), mid-chain homologues (C₂₁-C₂₅ *n*-alkanes) characterise submerged and floating aquatic macrophytes (Barnes and Barnes, 1978; Cranwell, 1984; Ficken et al., 2000), and long-chain homologues (C₂₇-C₃₅ *n*-alkanes) characterise terrestrial vegetation (Eglinton and Hamilton, 1967). Average chain length, or the weight-averaged number of carbon homologues of the C₂₁-C₃₃ *n*-alkane, is higher in C₄ grasses (Rommerskirchen et al., 2006), but also correlates with higher growing season temperature and aridity (Dodd and Poveda, 2003; Castañeda et al., 2009; Duan and He, 2011; Carr et al., 2014; Bush and McInerney, 2015).

The carbon preference index (CPI), which examines the odd-over-even carbon number predominance and serves as an indicator for hydrocarbon maturity and degradation (Duan and Xu, 2012), was calculated using the abundances of odd and even chain lengths from C₂₁ to C₃₃ and the following formula:

$$CPI = \frac{(C_{21} + C_{23} + C_{25} + C_{27} + C_{29} + C_{31}) + (C_{23} + C_{25} + C_{27} + C_{29} + C_{31} + C_{33})}{2 \times (C_{22} + C_{24} + C_{26} + C_{28} + C_{30} + C_{32})}$$

The CPI of *n*-alkanes is used to examine the odd-over-even carbon number predominance but also to distinguish sedimentary organic matter deriving from terrestrial plants and that from bacterial or petroleum sources (Bray and Evans, 1961; Castañeda and Schouten, 2011; Diefendorf et al., 2011; Jaeschke et al., 2018), and as an indicator for hydrocarbon maturity or degradation (Duan and Xu, 2012). Alkanes deriving from land plants display carbon chains typically with CPI >5.0, while petrogenic and marine inputs or mature samples are characterised by considerably lower CPI values of ≤1.0. There is a wide range of CPI observed in modern African plants ranging from <1 to 99, with 96.0% of all CPI values being greater than or equal to 1, 81.2% greater than or equal to 2, and 60.7% greater than or equal to 5 (Bush and McInerney, 2013).

The submerged/terrestrial ratio (STR), which differentiates alkanes produced by either submerged or terrigenous plants, with terrestrial plants generally having values <0.25 (Liu and Liu, 2017), was calculated as follows:

$$STR = \frac{C_{25}}{C_{21} + C_{23} + \dots + C_{31} + C_{31}}$$

The aquatic plant ratio (P_{aq}), which differentiates fatty acids produced by either algae or terrigenous plants, with terrestrial plants generally having values <0.1 (e.g., Ficken et al., 2000), was calculated as follows:

$$Paq = \frac{C_{23} + C_{25}}{C_{23} + C_{25} + C_{29} + C_{31}}$$

Compound-specific carbon isotope ratios ($\delta^{13}C$) of *n*-alkane homologues C_{25} - C_{31} were measured using an Agilent 7890A GC System equipped with an Agilent DB-1MS-UI capillary column (60 m length, 0.25 mm i.d. and 0.25 μ m film), coupled to a Thermo Fisher Scientific Delta V Plus Isotope Ratio Mass Spectrometer at the Max Planck Institute for Biogeochemistry, Jena, Germany. 1.0 μ L samples were injected in splitless mode at 320 °C, and the GC oven was maintained for 1 min at an initial temperature of 110 °C before the temperature was increased to 320°C at 5 °C/min (7 min hold). All the samples were measured in triplicates. Helium was the carrier gas with a constant flow maintained at 1.8 mL/min. We report on the C_{29} - C_{33} *n*-alkanes as they were the most abundant in all samples.

The accuracy of the $\delta^{13}C$ was evaluated against an international standard laboratory mixture (Indiana A7, Arndt Schimmelmann, University of Indiana) injected after every three sample injections.

The standard deviation of the C_{16} - C_{30} *n*-alkane working standard was ≤0.5‰ for $\delta^{13}C$. Drift corrections were determined by the standards run after every sample. Isotopic ratios are expressed as $\delta^{13}C$ values in per mil (‰) relative to the Vienna Pee Dee Belemnite (VPDB) standard with the following equation:

$$^{13}\text{C} = \left(\left(\frac{^{13}\text{C}}{^{12}\text{C}} \text{Sample} \div \frac{^{13}\text{C}}{^{12}\text{C}} \text{Standard} \right) - 1 \right) \times 1000$$

All $\delta^{13}\text{C}$ mean values are reported with their standard deviation.

Compound-specific isotope analysis is necessary to make inferences on plant community composition and the main sources of plant waxes to depositional environments. The *n*-alkane $\delta^{13}\text{C}$ values provide information on plant type and photosynthetic pathway (O’Leary, 1981), the intensity and duration of sunlight (Yang et al., 2009), canopy structure and wax production (Suh and Diefendorf, 2018), plant taxonomy (Chikaraishi and Naraoka, 2003), and the total concentration of atmospheric CO_2 (Schubert and Hope Jahren, 2015). In terrestrial contexts, variations in $\delta^{13}\text{C}$ are influenced by biological differences in photosynthetic pathways and the degree to which different plant types discriminate against ^{13}C during carbon fixation, which leads to distinct and, for the most part, non-overlapping values between C_3 and C_4 plants (O’Leary, 1981; Ehleringer, 1989; Farquhar et al., 1989). C_3 plants typically have bulk leaf $\delta^{13}\text{C}$ ranging between -35 to -20‰. C_4 plants, which do not discriminate against the heavier ^{13}C to such a large degree, have values that span from -15 to -7‰.

Plant wax *n*-alkanes are further depleted from their bulk values by about -7 to -5‰ for C_3 vegetation and -10 to -8‰ for C_4 vegetation (**Fig. 24**). Therefore, depending on plant ecological lifeform, water availability, canopy structure, and other factors, C_3 terrestrial plant *n*-alkane values can range from -42 to -25‰ (average -35‰), while C_4 plants range from about -26 to -14‰ (average -21 ‰) (O’Leary, 1981; Collister et al., 1994; Bi et al., 2005; Rommerskirchen et al., 2006; Vogts et al., 2009).

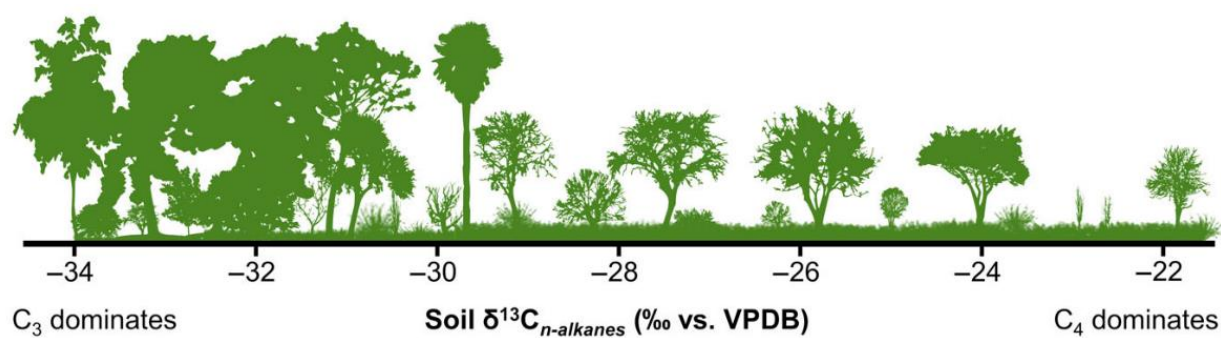


Figure 24. $\delta^{13}\text{C}$ values of *n*-alkanes in soil (C_3 to C_4 plants transition) are presented according to the predominant habitat, as extracted from Patalano et al. (2021).

· Chapter 5: Results ·

5.1. Eastern Morocco

5.1.1. Paper I: Ramírez-Pedraza et al. (2024). Arid, mosaic environments during the Plio-Pleistocene transition and early hominin dispersals in northern Africa. Nature Communications (Accepted).

Arid, mosaic environments during the Plio-Pleistocene transition and early hominin dispersals in northern Africa

Iván Ramírez-Pedraza^{1,2,3*}, Carlos Tornero^{4,1}, Hassan Aouraghe⁵, Florent Rivals^{1,2,6}, Robert Patalano^{7,3}, Hamid Haddoumi⁵, Isabel Expósito^{1,2}, Antonio Rodríguez-Hidalgo^{8,1}, Steffen Mischke⁹, Jan van der Made¹⁰, Pedro Piñero^{1,2}, Hugues-Alexandre Blain^{1,2}, Patrick Roberts^{3,11,12}, Deepak Kumar Jha¹¹, Jordi Agustí^{1,2,6}, Christian Sánchez-Bandera^{1,2}, Abdelkhalek Lemjidi¹³, Alfonso Benito-Calvo¹⁴, Elena Moreno-Ribas^{1,2}, Aïcha Oujaa¹³, Hicham Mhamdi⁵, Mohamed Souhir⁵, Al Mahdi Aissa⁵, M. Gema Chacón^{1,2,15}, Robert Sala-Ramos^{1,2}.

¹Institut Català de Paleoeologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain.

²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain.

³isoTROPIC Research Group, Max Planck Institute of Geoanthropology, Jena, Germany.

⁴Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain.

⁵Faculté des Sciences, Département de Géologie, Université Mohammed Premier, Oujda, Morocco.

⁶Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain.

⁷Department of Biological and Biomedical Sciences, School of Health and Behavioral Sciences, Bryant University, Smithfield, USA.

⁸Consejo Superior de Investigaciones Científicas, Instituto de Arqueología (CSIC-Junta de Extremadura), Mérida, Spain.

⁹Institute of Earth Sciences, University of Iceland, Reykjavík, Iceland.

¹⁰Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, Madrid, Spain.

¹¹Department of Archaeology, Max Planck Institute of Geoanthropology, Jena Germany

¹²School of Archaeology, University of Philippines, Diliman, Quezon City, Philippines.

¹³Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

¹⁴Centro Nacional de Investigación Sobre la Evolución Humana (CENIEH), Burgos, Spain.

¹⁵UMR 7194 - Histoire Naturelle de l'Homme Préhistorique (MNHN/CNRS/UPVD), Paris, France.

Corresponding author e-mail: ramirezpedrazaivan@gmail.com

The earliest archaeological evidence from northern Africa dates to *ca.* 2.44 Ma. Nevertheless, the palaeoenvironmental setting of hominins living in this part of the continent at the Plio-Pleistocene transition remains poorly documented, particularly in comparison to eastern and southern Africa. The Guefaït-4 fossil site in eastern Morocco sheds light on our knowledge of palaeoenvironments in northern Africa. Our study reveals the oldest known presence of C₄ plants in the northern part of the continent in a mosaic landscape that includes open grasslands, forested areas, wetlands, and seasonal aridity. This diverse landscape and resource availability likely facilitated the occupation of the region by mammals, including potentially hominins. Our regional-scale study provides a complementary perspective to global-scale studies and highlights the importance of considering the diversity of microhabitats within a given region when studying species-dispersal dynamics.

Introduction

Reconstructing past environments is critical to understanding the ecological dynamics of mammalian, including early hominin, occupation of regions within and beyond Africa. While the landscape of the Plio-Pleistocene transition has been extensively studied in eastern^{1–8}, central^{9,10}, and southern Africa^{2,11–14}, there is a notable knowledge gap for the northern African region. The presence of sites with hominin-associated artifacts in Algeria^{15,16} and Morocco^{17,18} during the Early Pleistocene, dating to as early as 2.44 Ma, has put a spotlight on northern Africa for investigating hominin evolution and dispersals. Nevertheless, detailed insights into the palaeoenvironment of this region at that time remain sorely lacking.

The area presently occupied by the Sahara Desert has experienced, for over 8 Myr, short-lived (~8–14 kyr) periods of greening¹⁹, known as Green Sahara Periods (GSPs), that have facilitated the dispersal of diverse animal species^{19,20}. Large-scale global studies have established the picture of a gradual shift towards a drier climate and greater environmental variability in the transition from the Pliocene to the Pleistocene, influenced by the Northern Hemisphere Glaciation^{21–24}. However, the impact of these global-scale climate shifts on regional ecosystems and biodiversity is unclear²⁵. Regional-scale studies provide critical, complementary perspectives to global models, where opposing local trends and a diversity of microhabitats in the same region can be explored²⁶.

We present palaeoecological proxy information from the Guefaït-4.2 (GFT-4.2; 34° 13' 3.4" N, 2° 24' 13.2" W) fossil locality in eastern Morocco, dated close to the Plio-Pleistocene transition²⁷ (Fig. 1; Supplementary Note 1 and Supplementary Fig. 1 to 3). GFT-4.2 was excavated with a trench of 28 m², revealing a 180 cm sequence formed by a palustrine event, in which more than 3000 large vertebrate remains were buried. Taphonomic study indicates a time-averaged fossil assemblage formed relatively quickly (in geological terms), consistent with the palaeomagnetic, stratigraphic, and biochronological data (Supplementary Note 1). We utilised bulk and sequential enamel stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analysis, stable carbon isotope analysis from plant wax *n*-alkanes, dental microwear and mesowear analyses, and analyses of small vertebrates, pollen, micro-crustaceans and algae to provide on-site ecological evidence. Our approach aims to offer a holistic landscape reconstruction using the distinct palaeoenvironmental perspectives and varying temporal and spatial resolutions each proxy provides (Supplementary Note 2 and Supplementary Tables 1 and 2). We produce insights into the environmental conditions prevailing in northwestern Africa at the time of the documented presence of early hominins in the region.

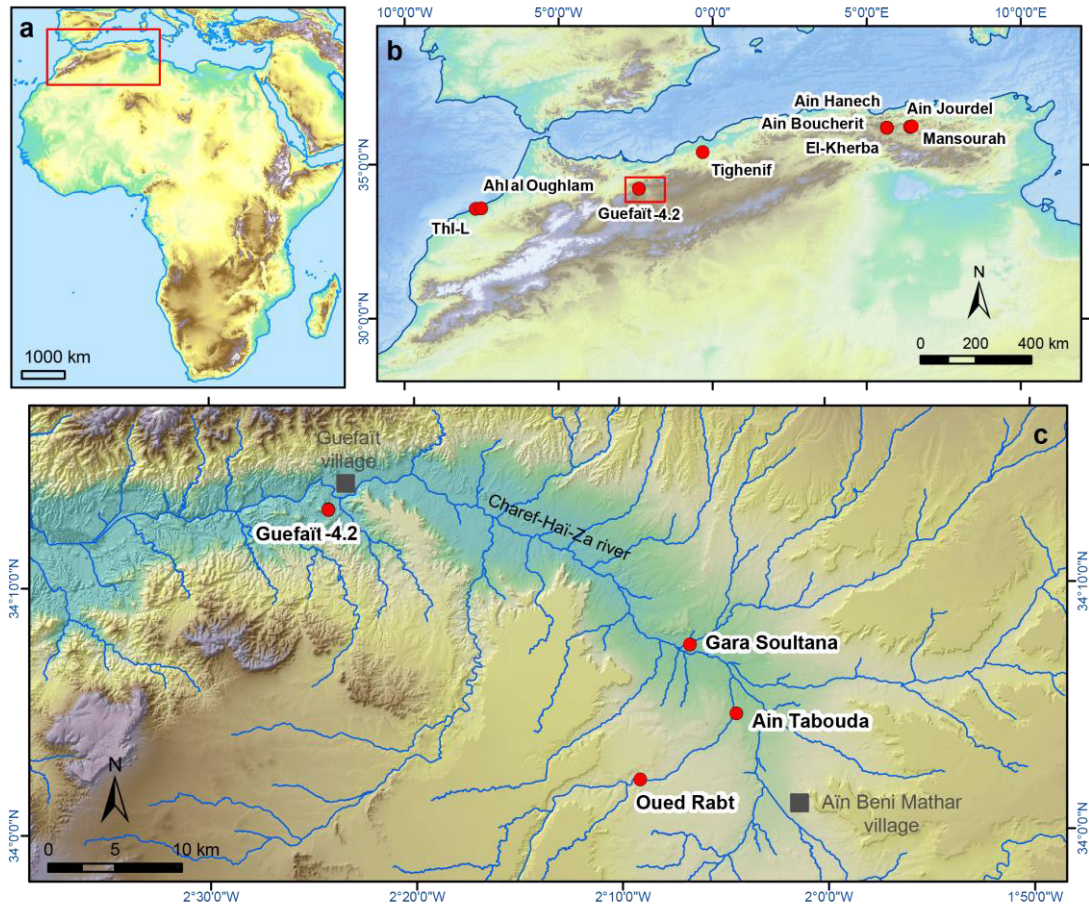


Fig. 1. Archaeological and palaeontological sites. **a**, Context of the study area in Africa. **b**, Early Pleistocene (Thomas Quarry I - Unit L (Thi-L), Tighennif, El-Kherba, Ain Hanech, Mansourah and Ain Boucherit) and Plio-Pleistocene transition (Ahl al Oughlam, Ain Jourdel and Guefaït-4.2) sites of Morocco and Algeria. **c**, Position of Guefaït-4.2 and other study area sites attributed to Early Pleistocene (Gara Soultana and Aïn Tabouda) and Middle Pleistocene (Oued Rabt).

Results

Stable isotope analysis of large vertebrate tooth enamel

$\delta^{13}\text{C}$ values indicate a dominance of C_3 plant consumption (trees, woody shrubs, bushes, herbs and temperate grasses) by mammals ($\delta^{13}\text{C}$ range = -13.3‰ to -1.4‰; median = -9‰; $n = 172$; Fig. 2 and 3). However, abundant consumption of C_4 plants (likely tropical grasses, shrubs and sedges) is reported in some sampled taxa. *Hipparion sensu lato* ($n = 61$; range = -11.3 to -1.4‰; median = -7.3‰) and *Tragelaphini* ($n = 42$; range = -11.6 to -3.9‰; median = -9.2‰) display the greatest variability in $\delta^{13}\text{C}$ values, including the highest values within the assemblage. *Gazella* sp. ($n = 19$; range = -12.2 to -7.1‰; median = -10.4‰) and *Anancus* sp. ($n = 12$; range = -8.4 to -5.2‰; median = -6.9‰) exhibit mixed C_3 and C_4 values, with focus towards a C_3 plant-based diet. *Stephanorhinus africanus* ($n = 9$; range = -10.8 to -9.1‰; median = -9.6‰), *Suinae* ($n = 4$; range = -11.8 to -9.8‰; median = -10.8‰), *Hexaprotodon* sp. ($n = 13$; range = -13.3 to -8.6‰; median = -9.6‰), and *Macaca cf. sylvanus* ($n = 4$; range = -12.5 to -11.8‰; median = -12.3‰²⁸) exhibit exclusive C_3 plant consumption, with the latter two species presenting the lowest

values of the assemblage. The $\delta^{13}\text{C}$ values observed in carnivorans reflect those of their prey^{29–31}. In the case of GFT-4.2, all carnivorans including the Canidae ($n = 6$; range = -11.2 to -9.1‰; median = -9.8‰), *Dinofelis* sp. ($n = 1$; -11‰), and Hyaenidae ($n = 1$; -8.9‰) were consuming animals with a C_3 plant-based diets.

The $\delta^{18}\text{O}$ values of all animal samples ($n = 172$; Fig. 2) measured from GFT-4.2 range from -6.5‰ to 8.8‰ with a median of -1.5‰. *Gazella* sp. ($n = 19$; range = -2.5 to 8.8‰; median = -0.8‰) exhibits the highest $\delta^{18}\text{O}$ values in the assemblage, followed by Tragelaphini ($n = 42$; range = -2.3 to 3.8‰; median = 0.2 ‰), Canidae ($n = 6$; range = -1.1 to 4.5‰; median = -0.6‰), and *M. cf. sylvanus* ($n = 4$; range = 0.6 to 1.8‰; median = 1‰²⁸), which also have values towards the higher end of the spectrum. *Hexaprotodon* sp. ($n = 13$; range = -6.5 to -4‰; median = -5.1‰) shows the lowest $\delta^{18}\text{O}$ values of any taxon, followed, in this order, by Suinae ($n = 4$; range = -5.1 to -3.3‰; median = -3.6‰), *S. africanus* ($n = 9$; range = -3.4 to -1.5‰; median = -3‰), *Anancus* sp. ($n = 12$; range = -3.3 to -0.9‰; median = -2.8‰), and *Hipparion* s. l. ($n = 61$; range = -5 to 1.1‰; median = -2‰). Unlike Canidae, the other two carnivores, *Dinofelis* sp. ($n = 1$; -1.4‰) and Hyaenidae ($n = 1$; -3.4‰), have $\delta^{18}\text{O}$ values towards the lower end of the overall range. The complete dataset of bulk $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of mammalian teeth ($n = 170$) is presented in Fig. 2 and described in Supplementary Table 3.

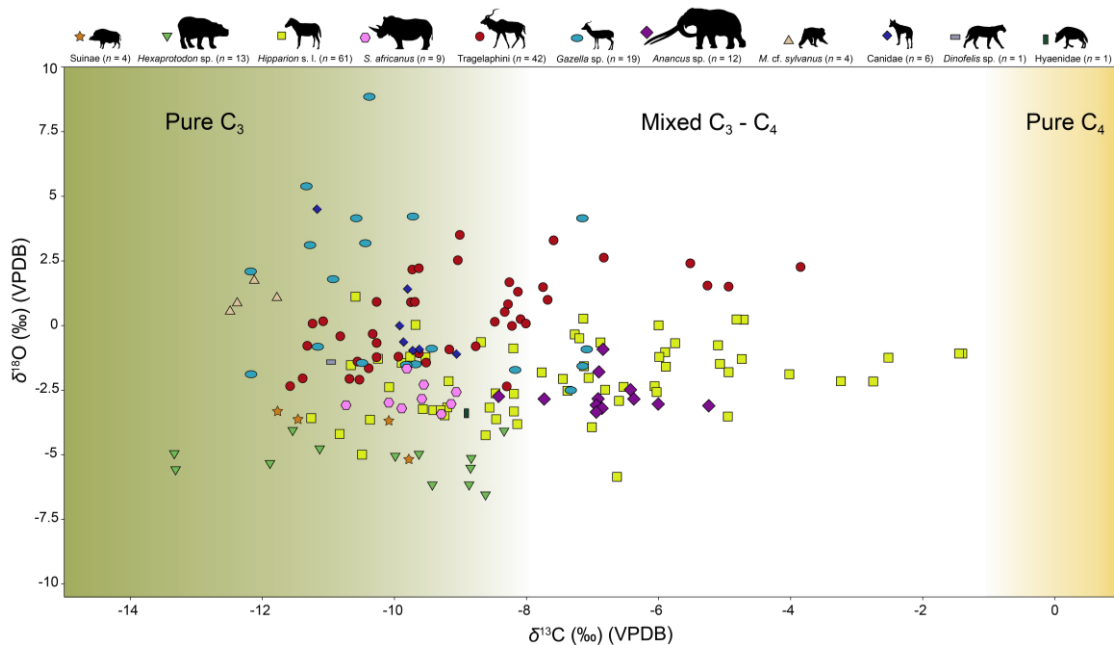


Fig. 2. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the tooth enamel of fossil fauna from GFT-4.2. The isotopic data for *M. cf. sylvanus* have been previously published in²⁸. Each point corresponds to a tooth enamel sample with a total of 168. Silhouettes from <http://phylopic.org> under public domain licence. Source data are provided as a Source Data file.

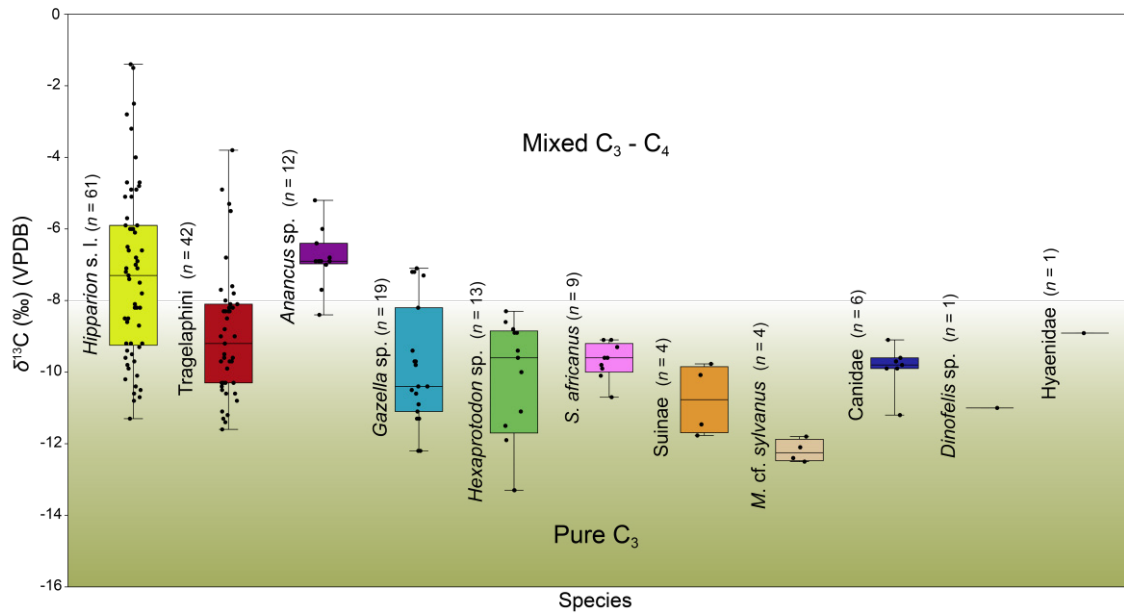


Fig. 3. Jitter boxplots of $\delta^{13}\text{C}$ values of fossil fauna from GFT-4.2. Boxes represent the interquartile range (IQR), defined by the 25th (Q1) and 75th (Q3) percentiles, with the median value indicated by a line within the box. Whiskers extend from the box to the minimum and maximum values within 1.5 times the IQR from the quartiles, while data points outside this range are considered outliers. Error bars show the standard deviation (SD). Each point corresponds to a tooth enamel sample. Source data are provided as a Source Data file.

The difference in $\delta^{18}\text{O}$ values between non-obligate and obligate drinkers is a proxy for estimated paleoaridity^{32–37}. This difference in GFT-4.2 is 3‰ (obligate drinker mean: -2.5‰, non-obligate drinker mean: 0.5 ‰; Fig. 4 and Supplementary Note 3). The results have been compared to the difference between non-obligate and obligate drinkers in Laikipia (1.7‰) and Tsavo (2.2‰) in Kenya, defined as semi-arid savannas^{5,38}. We also compare our data to results from fossil fauna remains from the Ahl al Oughlam site (1.9‰; Supplementary Note 3), penecontemporaneous to GFT-4.2, located in western Morocco, and defined as a dry environment³⁹. Our findings show a greater difference between non-obligate and obligate drinkers GFT-4.2 compared to both the current savannas of Laikipia and Tsavo and the fossil site of Ahl al Oughlam, indicating a more arid environment.

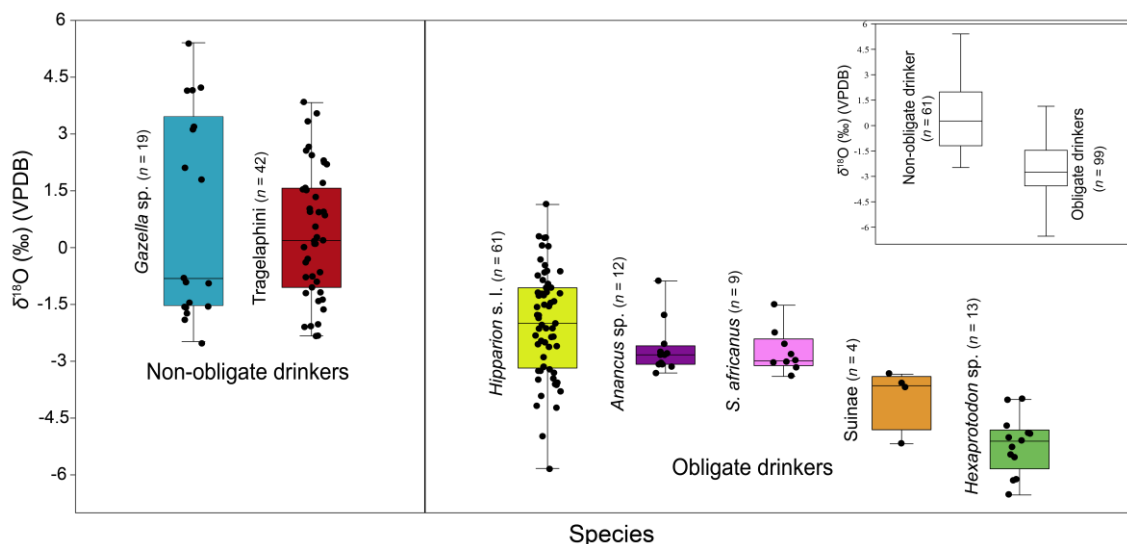


Fig. 4. Jitter boxplots of $\delta^{18}\text{O}$ values for non-obligate and obligate drinking taxa from GFT-4.2. Boxes represent the interquartile range (IQR), defined by the 25th (Q1) and 75th (Q3) percentiles, with the median value indicated by a line within the box. Whiskers extend from the box to the minimum and maximum values within 1.5 times the IQR from the quartiles, while data points outside this range are considered outliers. Error bars show the standard deviation (SD). Each point corresponds to a tooth enamel sample. The boxplots in the upper right corner correspond to all $\delta^{18}\text{O}$ values of taxa grouped as non-obligate drinkers (*Gazella* sp. and *Tragelaphini*) and obligate drinkers (*Hexaprotodon* sp., *Suinae*, *S. africanus*, *Anancus* sp., and *Hipparion* s. l.). Source data are provided as a Source Data file.

For the intra-tooth sequences of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values, we analysed eight teeth of *Hipparion* s. l., comprising 180 intra-tooth enamel samples (Fig. 5 and Supplementary Table 4). Lower $\delta^{18}\text{O}$ values are associated with the cold/wet season, while higher values correspond to the warm/dry season. For $\delta^{13}\text{C}$, values above -8‰ would indicate the consumption of C_4 plants. We observed two distinct trends in the sampled teeth of this taxon. In the first (samples in Fig. 5a, b, c, d and e), the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values exhibit the same seasonal oscillation, with a higher consumption of C_4 plants during the warmer/drier season. In the case of one sample in Fig. 5a, the dominant consumption of C_3 plants extended throughout the entire year, while in one sample in Fig. 5b, this pattern occurred with the consumption of C_4 plants. However, in the second trend (samples in Fig. 5g and h), an inverse relationship between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ maximum and minimum values was observed, indicating a greater consumption of C_4 plants during the colder season. This inverse relationship between $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ may be associated with the altitudinal mobility of *Hipparion* s. l., indicating a higher consumption of C_3 plants in the highlands during the warm/dry season and a higher consumption of C_4 plants in the lowlands during the cold/wet season. This aligns with the fact that GFT-4.2 is in a mountainous region with altitudes ranging from 600 to 1700 meters. The sample in Fig. 5f shows a progressive increase in the consumption of C_4 plants without a clear correlation with $\delta^{18}\text{O}$ values.

The cross-correlations analysis showed a significant relationship between intra-tooth $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ in seven of the eight samples (Supplementary Table 3 and Supplementary Fig.

4). The sample without correlation is GFT4.2-2019-R15/115 (Fig. 5f). Among the seven specimens with significant correlation, two (Fig. 5g and h) are negatively correlated, while five display positive cross-correlation coefficients (Fig. 5a, b, c, d and e).

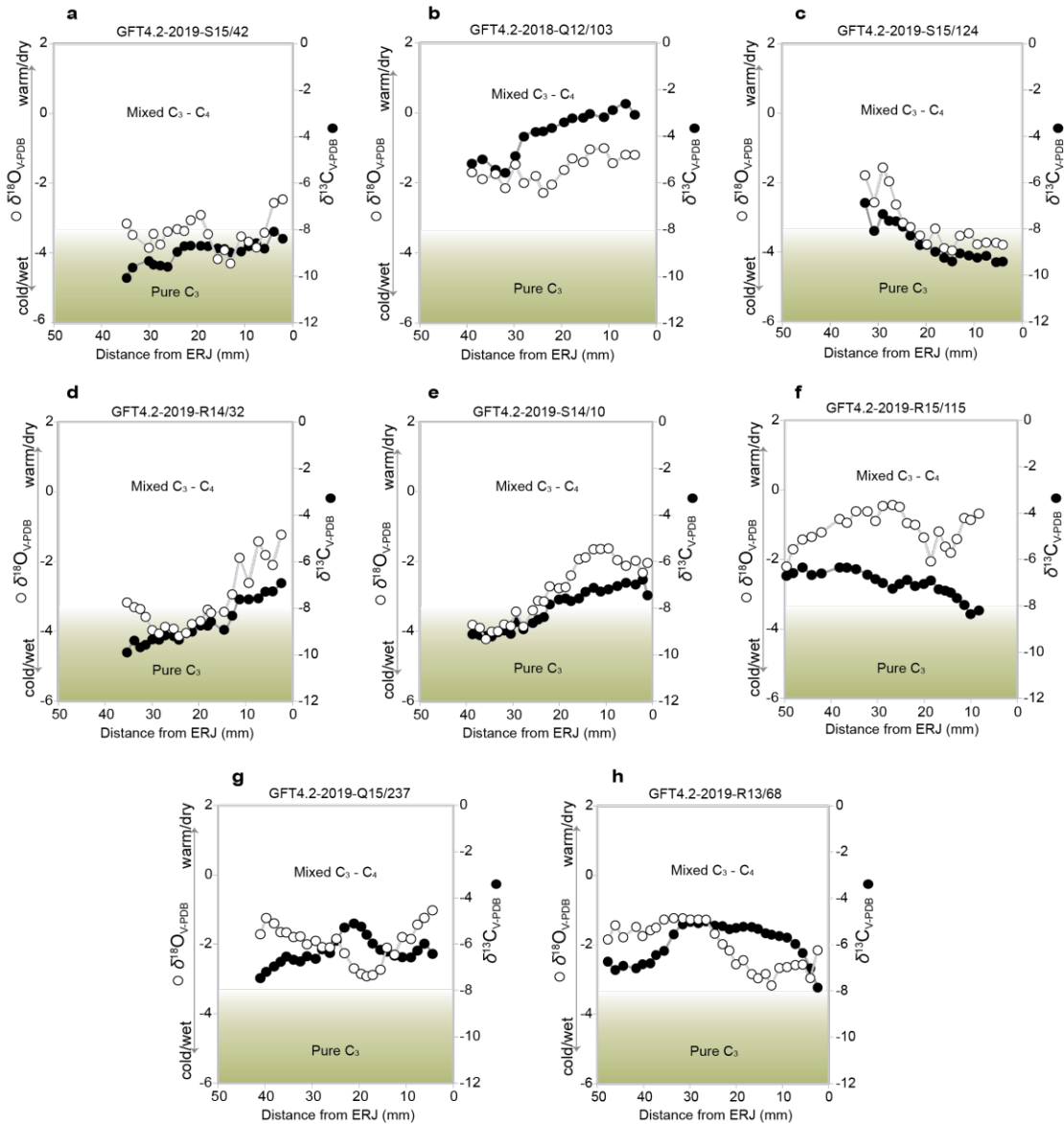


Fig. 5. Sequential analysis of carbon and oxygen values of bioapatite enamel from *Hipparion* s. l. of GFT-4.2. ERJ = enamel-root junction. Source data are provided as a Source Data file.

Dental wear.

The mesowear analysis measures the relief and sharpness of worn cusp apices on occlusal surfaces, ranging from sharp cusps and high relief (indicative of low abrasion and high attrition) to low relief with rounded cusps (indicative of high abrasion and low attrition). The mesowear scores (MWS) of the three analysed taxa from GFT-4.2 show a narrow range of MWS median values, from 1.4 to 3.1 (Fig. 6 and Supplementary Table 6). These

MWS indicate low levels of abrasion for *Gazella* sp. (MWS = 1.4) and Tragelaphini (MWS = 1.9), suggesting a mixed feeding dietary trait dominated by leaf and fruit browsing. In *Hipparion* s. l., despite the MWS being 3.1, there is a high degree of variability among samples, indicating a wide range of dietary abrasiveness, ranging from browse-dominated mixed feeders to pure grazers.

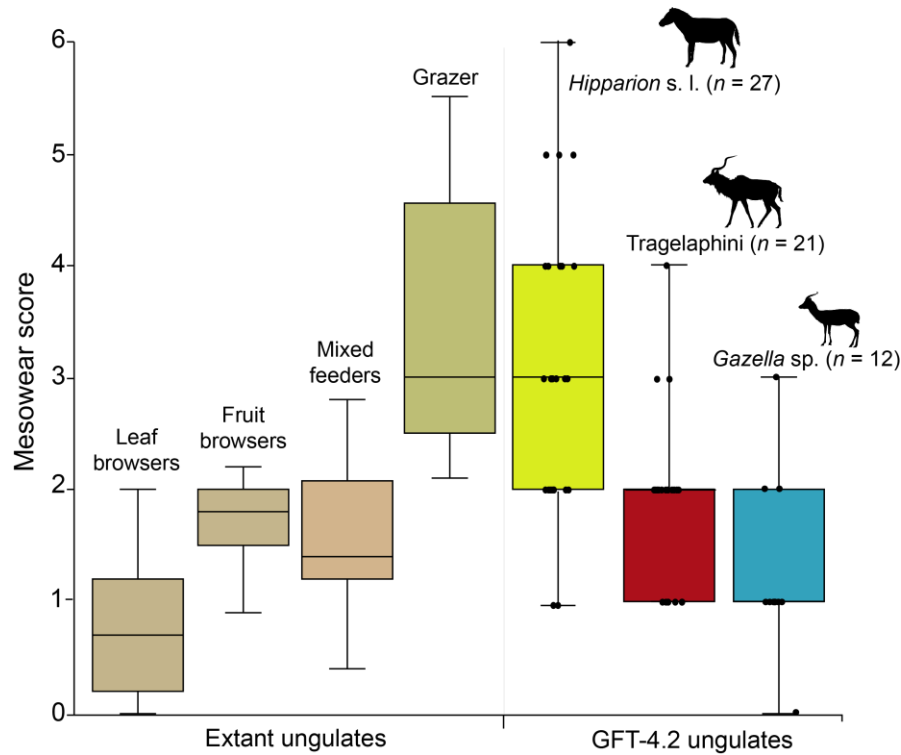


Fig. 6. Boxplot with mesowear scores (MWS) of the ungulates from GFT-4.2. Boxes represent the interquartile range (IQR), defined by the 25th (Q1) and 75th (Q3) percentiles, with the median value indicated by a line within the box. Whiskers extend from the box to the minimum and maximum values within 1.5 times the IQR from the quartiles, while data points outside this range are considered outliers. Error bars show the standard deviation (SD). Each point corresponds to a tooth enamel sample. Extant ungulates database⁴⁰. Silhouettes from <http://phylopic.org> under public domain licence. Source data are provided as a Source Data file.

The microwear analysis classifies the extinct taxa along a continuum of dietary abrasiveness, ranging from pure browsers to pure grazers, including mixed feeders, based on the average number of pits and scratches (Fig. 7 and Supplementary Table 6). The *Hipparion* s. l. and the two Bovidae exhibit browse-dominated dietary traits, whereas *Hexaprotodon* sp., *S. africanus*, and Suinae show grass-dominated traits, with *Anancus* sp. exhibiting a pure grass-feeding pattern (Fig. 7). As with mesowear, microwear results reveal a wide range of diets, ranging from browse-dominated mixed feeders to pure grazers. Species in the browsing feeding space (*Hipparion* s. l. and the two Bovidae) have a higher number of pits and a lower number of scratches. By contrast, species in the grazer feeding space (*Hexaprotodon* sp., *S. africanus* and Suinae) have a lower number of pits

and a higher number of scratches. *Anancus* sp. is placed among the extant pure grazers because it has the lowest number of pits (11.5). All taxa, except Suinae, exhibit puncture pits.

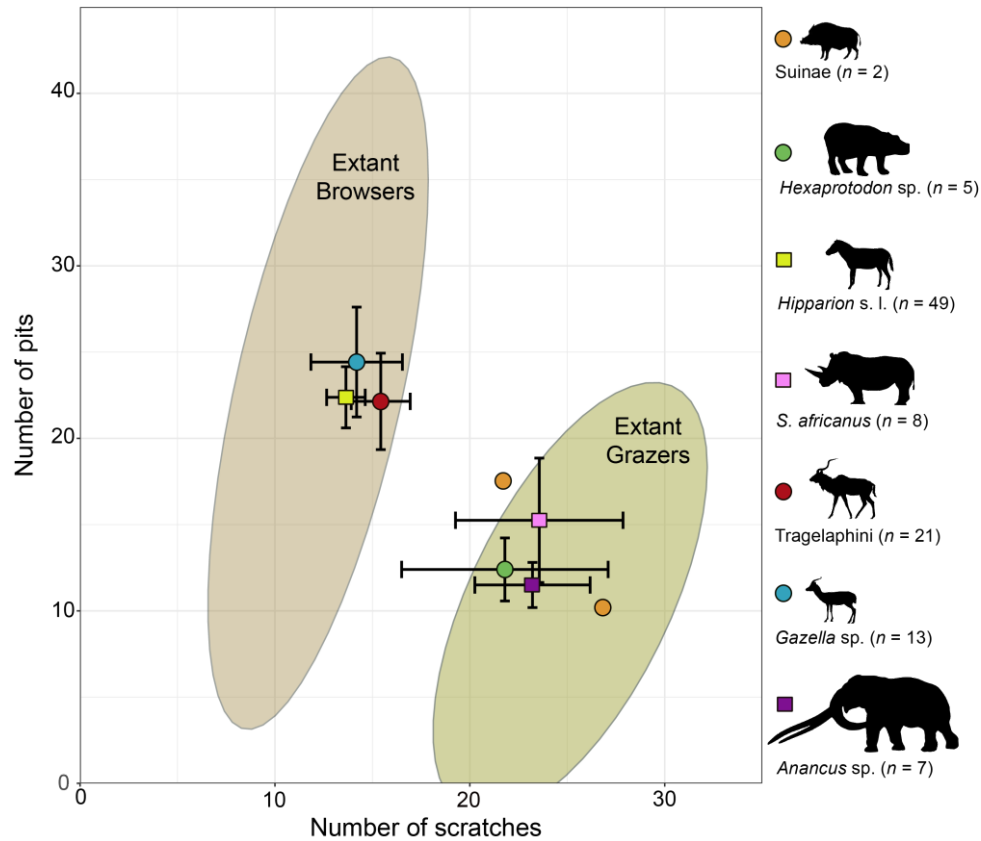


Fig. 7. Bivariate plot of the average numbers of pits and scratches for the species from GFT-4.2. Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$). Extant ungulates based on the database⁴¹. Silhouettes from <http://phylopic.org> under public domain licence. Source data are provided as a Source Data file.

Plant Wax Biomarkers

Odd-numbered, long-chain (i.e., C_{27} - C_{31}) lengths dominate the n -alkane biomarker distributions in plants and sediments. Of the ten samples analysed, all but one have C_{31} as the dominant n -alkane, with the C_{29} and C_{27} alkanes being the second and third most abundant compounds, respectively (Supplementary Note 4 and Supplementary Table 7). The relative abundances of the C_{25} and C_{27} n -alkanes are highly correlated (Spearman's correlation, $r_s = 0.89$, $p = 0.007$), as are the relative abundances of C_{29} and C_{31} (Spearman's correlation, $r_s = 0.98$, $p < 0.001$), indicating that C_{25} , C_{27} , C_{29} and C_{31} were synthesised by multiple plant-life forms^{42,43}. Furthermore, C_{25} and C_{27} co-vary in opposite directions to that of C_{29} and C_{31} throughout the sequence (Fig. 8), suggesting that both submerged or emergent and terrestrial plants contributed biomarkers to the investigated sediments. The average chain length (ACL₂₁₋₃₃) ranges from 26.8 to 29.7 (28.2 ± 0.3 , $n =$

10), consistent with previous measurements of modern ACL from African terrestrial plants^{44–48}. The carbon preference index (CPI) of the C₂₁-C₃₃ *n*-alkanes ranges between 2.3 and 10 (5.6 ± 0.9 , $n = 8$). These values are typical of plant-derived CPI values^{49–52} and indicate no significant plant wax degradation occurred^{53,54}. The aquatic plant ratio (P_{aq})⁵⁵ ranges between 0.0 and 0.6, while the submerged/terrestrial ratio (STR)⁵⁶ ranges between 0.0 and 0.31, trending with the P_{aq} values (Fig. 8).

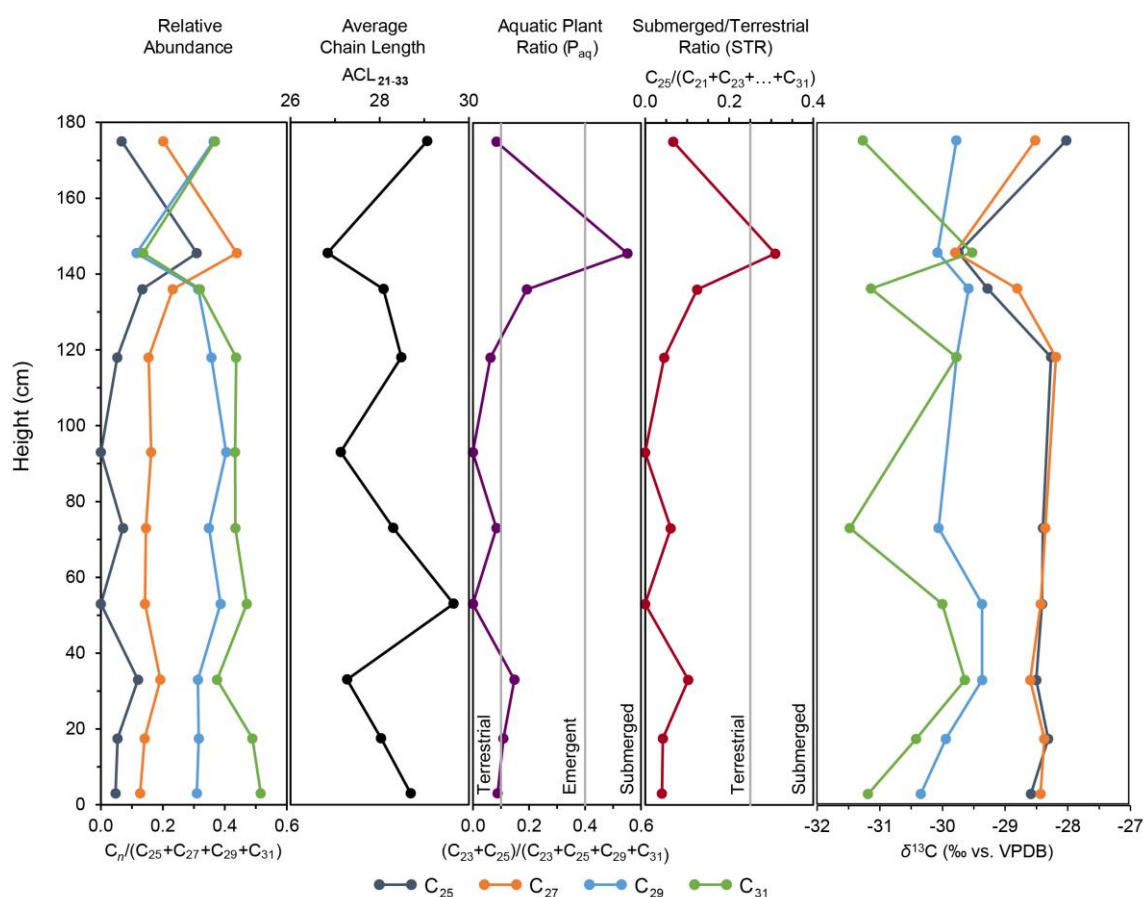


Fig. 8. Isotopic and biomarker signatures of GFT-4.2 plant wax *n*-alkanes. See Methods for ACL calculation. Submerged or floating aquatic plants tend to have STR values greater than 0.25, whereas for the Aquatic Plant Ratio (P_{aq}), aquatic plants tend to have values greater than 0.7, and values ranging between 0.1 and 0.7 typically represent a mixed input of terrestrial, emergent and submerged aquatic plants. The percentages of compound abundances are relative to the dominant *n*-alkanes (C₂₅ + C₂₇ + C₂₉ + C₃₁). Higher values reflect relatively increased inputs of the respective compounds. Source data are provided as a Source Data file.

The $\delta^{13}\text{C}$ data from the C₂₅-C₃₁ *n*-alkanes further show that there are differences between the C₂₅ and C₂₇ *n*-alkanes and C₂₉ and C₃₁ (Student t-test two-tailed (t-test) $p < 0.0001$; Mann-Whitney *U* test (MWU) $p < 0.0001$; Fig. 8). $\delta^{13}\text{C}$ values range between -31.5‰ and -28.0‰ ($-29.4 \pm 1.0\text{‰}$, $n = 36$) and, when separated by *n*-alkane homologue, between -29.7‰ and -28.0‰ (C₂₅, $-28.6 \pm 0.5\text{‰}$, $n = 9$), -29.8‰, and -28.2‰ (C₂₇, $-28.6 \pm 0.5\text{‰}$, $n = 9$), -30.3‰ and -29.4‰ (C₂₉, $-29.8 \pm 0.3\text{‰}$, $n = 9$), and -31.5‰ and -29.5‰ (C₃₁, $-30.5 \pm 0.8\text{‰}$, $n = 9$). These $\delta^{13}\text{C}$ data suggest a C₃-dominated environment. There is a roughly

2.0‰ mean difference between C₃₁ and both C₂₅ (t-test, $p = <0.0001$; MWU, $p = <0.0001$) and C₂₇ (t-test, $p = <0.0001$; MWU, $p = 0.0001$), with the largest variation of 3.2‰ (GFT 10) between C₃₁ and C₂₅ and of 3.1‰ (GFT 5) between C₃₁ and C₂₇. Additionally, the mean difference between C₂₉ and both C₂₅ (t-test, $p = 0.0001$; MWU, $p = 0.001$) and C₂₇ (t-test, $p = <0.0001$; MWU, $p = 0.001$) is 1.2‰, with the largest variation between C₂₉ and C₂₅ being 1.8‰ (GFT 1 and 10) and between C₂₉ and C₂₇ being 1.9‰ (GFT 1). On the other hand, C₂₉ and C₃₁ differ on average by only 0.8‰ (t-test, $p = 0.03$; MWU, $p = 0.1$), and C₂₅ and C₂₇ differ on average by only 0.2‰ (t-test, $p = 1$; MWU, $p = 0.719$). This suggests that the plant-wax input into GFT-4.2 sediments is characterised by two groups; one source contributing predominantly C₂₅ and C₂₇ *n*-alkanes, and the other contributing C₂₉ and C₃₁ *n*-alkanes.

Pollen analysis

Concentrations of pollen, spores and other palynomorphs are low throughout the sequence (22.1-286.8 palynomorphs per gram of dry sediment). Tree cover is suggested in four samples by the presence of pine (*Pinus* sp.) and evergreen oak (*Quercus ilex-coccifera* type) and the occasional presence of alder (*Alnus*). Shrub vegetation is not represented, due to the scarce pollen dispersion of these taxa. Herbaceous vegetation is represented by wild grasses (Poaceae), Asteraceae (Tubuliflorae and Liguliflorae types), Amaranthaceae, Apiaceae and Fabaceae (Supplementary Fig. 5 and Supplementary Table 8).

Non-pollen palynomorphs (NPP) include mainly fungal spores such as *Polyporisorites*, *Polyadosporites*, *Glomus* sp., *Exesisporites* and hyphae. Trilete spores from mosses or ferns have also been identified. Other palynomorphs identified (HdV 303 or “protists”) have an undetermined ecological origin or are linked to chitin remains of insects and mites (HdV 52⁵⁷). Additionally, microcharcoal concentrations are low, ranging from 18.4 to 157.9 particles per gram (Supplementary Fig. 5).

Small vertebrates

The rodent assemblage is composed of four murine species (*Paraethomys pusillus*, *Paraethomys chikeri*, *Golunda aouraghei*, and *Praomys* cf. *skouri*), two gerbils (Gerbillidae indet. 1, Gerbillidae indet. 2), a ctenodactyline (*Irhoudia* sp.), a sciurid (*Atlantoxerus* sp.), and a glirid (*Eliomys* sp.) (Supplementary Note 5 and Supplementary Fig. 6). The herpetofaunal assemblage includes an anuran (Anura indet., an alytid or ranid frog), a lizard (Lacertidae indet.), an anguid lizard (*Ophisaurus sensu lato*), and two snakes (Natricidae/Elapidae indet. and Colubridae/Lamprophiidae indet.) (Supplementary Note 4 and Supplementary Fig. 7).

Micro-crustaceans and algae remains

The sediment samples from the GFT-4.2 section yielded ostracod valves and algae remains (Supplementary Fig. 8 and Supplementary Note 6). The recorded ostracod taxa comprise *Ilyocypris* sp., *Cypridopsis vidua*, *Neglecandona neglecta*, *Cyprideis torosa*,

Potamocypris sp., *Heterocypris salina*, *Herpetocypris* sp., *Cypris pubera*, and *Psychrodromus* sp. (ordered by decreasing abundance). Additionally, green macroalgae represented by gyrogonites from three distinct charophyte species occur in two samples, with one sample including as many as 217 gyrogonites per 100 g.

Discussion

Our transdisciplinary, multiproxy approach demonstrates a high degree of habitat variability and environmental heterogeneity at Guefaït-4.2 at the time of the Plio-Pleistocene transition. Wetlands are evidenced by the presence of emergent and submerged plants, as suggested by plant wax biomarkers, non-pollen palynomorphs, and taxa such as ranid or alytid frog indicate a permanent water source. Micro-crustaceans and green algae taxa indicate the presence of a shallow, mostly fresh to slightly brackish water body with a dense aquatic plant cover on the floor. Living hippopotami need to submerge in water, and *Hexaprotodon* sp. suggests a water depth that was never less than 1.5 m. The geological and stratigraphical context of GFT-4.2, characterised by clays, marls and palustrine limestones, including local conglomerates and sandstones^{58,59}, also supports the presence of water bodies. Meanwhile, tree pollen, dental microwear of species with a leaf-browsing diet, and species like *M. cf. sylvanus*, *P. cf. skouri*, and *Ophisaurus* s. l.⁶⁰ indicate the presence of woodlands and humid environments. Additionally, previous studies on the GFT-4.2 macaques link their ecology to the presence of trees²⁸. The presence of puncture pits in most large vertebrates suggests the consumption of hard objects, such as fruits or seeds^{61,62}. Open grasslands are identified through wild grass pollen and mammalian taxa with a grazing diet (C₃ and C₄ grasses). Some small-vertebrate taxa in the assemblage are also characteristic of open grassy ecosystems, such as *G. aouraghei*⁶³, and indeed most of the heliophilic reptiles, and *Irhoudia* sp. and *Eliomys* sp. exhibit a preference for rocky habitats^{64,65}.

This environmental mosaic is further highlighted by the isotopic data. The $\delta^{13}\text{C}$ values in plant waxes and large vertebrates indicate a predominance of C₃ plants in the region. However, *Hipparion* s. l., Tragelaphini, *Anancus* sp., and *Gazella* sp. also consumed C₄ plants (grasses, sedges or woody shrubs), which may be due to their ability to move over greater distances and select their food. Aridity and warm temperatures are evidenced by the presence of C₄ plants⁶⁶. The significant differences in $\delta^{18}\text{O}$ values between obligate and non-obligate drinkers corroborates the hypothesis of lower rainfall totals. Additionally, the sequential isotopic analysis performed on *Hipparion* s. l. shows some individuals with marked seasonal aridity, with higher consumption of C₄ plants during the warm/dry season, while others exhibit a diet associated with seasonal altitudinal mobility. Some species are associated with arid conditions, such as gundis (*Irhoudia* sp.⁶⁷), ground squirrels (*Atlantoxerus* sp.^{68,69}), *G. aouraghei* and the giant tortoise (*Centrochelys*). Also, changes in the abundance of microcharcoals in the sediments suggest the proliferation of natural forest fires during arid periods⁷⁰. This combination of proxies reveals the important role of temperature and precipitation seasonality in the region.

Together our proxy data demonstrate that the overall environmental context in GFT-4.2 and its surroundings was highly ecotonal. A permanent water body was likely fed by streams or rivers draining the neighbouring highlands, and these were probably surrounded by either forests with overlapping canopies or woodlands with canopies that did not overlap extensively. The riparian woodland would have then transitioned into a wooded grassland that contained stretches of grasses and other herbs and only scattered woody plants. There was likely another structural change toward an open grassland with woody species only occurring in specialised microhabitats that were dependent on water availability. Finally, these lowland dry grasslands would have transformed into montane forests at higher elevations. Climatically, the region was probably generally warm with very arid summers and potentially even semi-desertic conditions, with the vegetation structure dictated by periodic fluctuations in water availability due to seasonal droughts.

It is important to note the varying temporal and spatial scales of our proxies when considering the reconstructed landscape diversity (Supplementary Table 1 and Supplementary Note 2). Pollen and plant waxes can be transported over long distances by various factors, providing reconstructions of the wider region. For example, evidence of forest reconstructed by these proxies at GFT-4.2 could be a riparian forest or woodland in the immediate vicinity of the site or a more distant (e.g. high-altitude) representation. It is also important to note that the production of pollen and waxy compounds varies with plant type and species^{50,71}, meaning that certain habitats will be over- or under-represented. Meanwhile, our dental wear and stable isotope results are heavily influenced by the dietary preferences of the sampled large vertebrate taxa, with grazers, for example, finding patches of forage in landscapes even where grassland areas are limited⁷. This complicates predicting the extent of these grasslands, something further exacerbated by the fact that these taxa can range widely. However, having several taxa of small and large vertebrates in GFT-4.2 and applying multiple proxy approaches in the same sequence (Supplementary Fig. 2) makes the ecological reconstruction more robust. Indeed, the various scales of these proxies are also a strength, further highlighting the environmental diversity experienced on local and regional scales.

The diet of some taxa in GFT-4.2 provides the oldest known evidence of significant consumption of C₄ plants by large herbivores in northern Africa, especially by *Hipparion* s. l. C₄ plants are virtually absent during the Late Pliocene and Early Pleistocene in Europe^{72,73} and northern Africa^{39,74,75}, and their presence in GFT-4.2 opens up the possibility of an ecosystem not previously considered in these latitudes, contributing to the regional habitat heterogeneity at a time that coincides with the earliest hominin occupations in northern Africa. To date, the oldest hominin occupation is found in Algeria at the Aïn Boucherit site (2.44 Ma⁷⁶; Fig. 1b), which has a chronology slightly younger than GFT-4.2, and is also located in the Intra-Atlas Maghrebian Depression⁷⁷. In addition, the Aïn Beni Mathar – Guefaït Basin (Fig. 1c) is rich in archaeological sites like the Early Pleistocene sites of Aïn Tabouda and Gara Soultana with Mode 1 lithic tools, or the Middle Pleistocene site of Oued Rabt with Mode 2 lithic tools¹⁸. This reinforces the likely continuous presence of hominins in the region in which our site is located.

C₄ plants constituted a significant component of the diet and habitat of several early hominins during the Late Pliocene and Early Pleistocene in eastern and southern Africa^{8,78–80}. Even in Central Africa, 3,000 km from the Rift Valley, the diet of

Australopithecus bahrelghazali from Koro Toro in Chad (3.5 Ma⁸¹) was dominated by the consumption of C₄ plants⁹. Nevertheless, the C₄ open dry grasslands and shrublands were only one component of these hominin-occupied landscapes. The presence of C₄ plants was part of a mosaic ecosystem comprising a great diversity of resources, including wetlands and savannas^{9,82,83}, as is also the case of GFT-4.2. In contrast to some classical theories linking hominins to specific habitats^{84–86}, recent studies in eastern Africa provide evidence for the important role of climate and habitat variability in hominin evolution^{26,87–89}. Additionally, increased ecological resource variability is considered a major factor in species' adaptive versatility^{83,90–92}.

The aridity observed in GFT-4.2 is consistent with the global trend towards progressive aridification during the Plio-Pleistocene transition^{22,24}. The period from ~2.7 to 2.55 Ma coincides with the presence of East African Rift System paleolake periods^{19,93} and seven Green Sahara Periods¹⁹, which could have created significant green corridors connecting eastern and northern Africa. However, the regional landscape complexity presented in GFT-4.2 can only be fully understood through terrestrial context studies, preferably on-site, complementing those conducted at a global scale in marine records. The Aïn Beni Mathar - Guefaït Basin likely contributed to the formation of spatially variable, ecologically diverse, and environmentally complex habitats, ranging from open dry grasslands to riparian humid forests. This broad spectrum of habitats created numerous resource-rich microhabitats, providing opportunities for niche diversification and specialisation among mammals, including hominins. The regional mosaic environment, combined with several Green Sahara Periods in the Plio-Pleistocene transition, may have facilitated the dispersal of mammal communities (including hominins) from central or eastern Africa to northern Africa, occupying ecosystems with resource availability similar to their original habitats.

Methods

Permissions, outreach, and engagement

All permits and authorisations for the excavation, sampling and study of the materials involved in this work were granted by the Direction du Patrimoine Culturel, Département de la Culture, Ministère de la Culture et de la Communication du Royaume du Maroc: 2016 - 2017 Ref. 734/15-06-2016 (Director: Abdellah ALAOUI), 2018 Ref. 1121/n°17/901/21-07-2017 (Director: Abdellah ALAOUI), 2019 Ref. 042/n°1157/01-08-2018 (Director: Youssef KHIARA). This Moroccan-Spanish project has carried out several different social and local engagement activities (students and local population) through different activities at the Musée Universitaire d'Archéologie et du Patrimoine (Université Mohammed Premier, BV Mohammed VI B.P. 524 Oujda 60000 Maroc - <https://www.ump.ma/fr/musee-universitaire-darcheologie-et-du-patrimoine>). Activities include guided visits and open days for (1) secondary school students and their teachers from Oujda and the Oriental region, (2) foreign researchers from various countries and institutions, (3) teachers of subjects related to archaeology and geology. We have also organised visits to excavations for secondary school students from Jerada, Aïn Béni Mathar and Guefaït, and introductory seminars and training in archaeology for university students from various faculties of the Mohammed Premier University.

Stable isotope analysis

Stable carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope analysis was performed on 11 large vertebrate taxa obtained from GFT-4.2 (Supplementary Fig. 3). Additionally, eight *Hipparion* s. l. teeth were selected for sequential analysis, resulting in the collection of 348 enamel bands for stable oxygen and carbon isotope analyses, 168 for bulk and 180 for sequential analysis (Supplementary Table 3 and 4). Buccal or lingual surfaces were systematically cleaned with a tungsten abrasive drill bit to remove any extraneous material. In *Hipparion* s. l. molars and premolars, the cementum was removed when necessary to access the enamel. Enamel powder for bulk analysis was extracted using a diamond-tipped drill along the entire buccal or lingual surface, following a line from apical to cervical extremities, to ensure the most representative measurement for the whole period of enamel formation. Due to the unknown exact mineralisation period for all the teeth and taxa analysed, we do not rule out the possibility that in this bulk average, we might be capturing part of the signal (some months) associated with the lactation period in some teeth. However, this signal (^{13}C depletion or ^{18}O enrichment) does not seem to be reflected in our results, showing consistent results among all samples analysed from the same taxa.

For sequential samples, we sampled from the crown apex to the enamel-root junction (close to the cervix of the crown). Each sample was a groove measuring 1-2 mm in width, perpendicular to the tooth growth axis, and extending through the thickness of the enamel layer. *Hipparion* s. l. was selected for the sequential analysis due to its pronounced hypsodonty and the well-documented dental development⁹⁴. The permanent cheek teeth mineralisation and eruption sequence for *Hipparionini* is M_1 , M_2 , (P_2 , P_3), P_4 and M_3 ^{94,95}. Since the M_1 is the first to mineralise and record the signal from maternal milk during the initial months of mineralisation, we avoided sampling this tooth for the sequential analysis. The teeth sampled for GFT-4.2 were: $\text{P}_{3/4}$ right, M_3 left, M_2 right, M_3 right, $\text{P}_{3/4}$ right, P_3 left, P_4 left, and M_2 left (Supplementary Table 4). The enamel mineralisation period for extant *Equus* is approximately ~30 months for M_2 , ~22 months for P_3 , ~32 months for P_4 , and ~34 months for M_3 ⁹⁶. However, some studies on *Hipparionini* based on intra-tooth isotopic analysis suggest a shorter mineralisation period for this genus (~12 months for M_2 ; ~18 months for P_3 ; ~24 months for P_4 and M_3)^{97,98}. Our intra-tooth analyses support this shorter mineralisation for GFT-4.2 *Hipparion* s. l. teeth, showing sequences likely to span approximately 12-24 months.

Powdered enamel samples weighing between 3.5 to 9.5 mg were chemically treated at the Biomolecular Laboratory of the Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA) using protocols modified from Koch et al.⁹⁹ and Tornero et al.¹⁰⁰, wherein samples were treated with 0.1 M acetic acid CH_3COOH (0.1 ml solution/0.1 mg of sample) for four hours, neutralised with distilled water (5 rinsings), and freeze-dried. The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of carbonates were determined using an automated carbonate preparation device (KIEL-III) coupled to a gas-ratio mass spectrometer (Finnigan MAT 252) at the Environmental Isotope Laboratory, University of Arizona, USA. Powdered samples were reacted with dehydrated phosphoric acid under vacuum at 70°C. The isotope ratio measurement is normalised using a two-point method based on repeated measurements of the calcium carbonate international standards of NBS-19 ($\delta^{18}\text{O} = -2.20\text{‰}_{\text{VPDB}}$, $\delta^{13}\text{C} = +1.95\text{‰}_{\text{VPDB}}$) and NBS-18 ($\delta^{18}\text{O} = -23.2 \pm$

0.1‰VPDB, $\delta^{13}\text{C} = -5.014 \pm 0.035\text{‰VPDB}$) with a precision of $\pm 0.11\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 sigma). Samples are typically run in sessions of 46 measurements with precision and normalisation determined for each session. Standards make up 13% of all measurements. Carbon and oxygen isotope composition was reported in δ notation, where $\delta^{13}\text{C}$ or $\delta^{18}\text{O} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{18}\text{O}/{}^{16}\text{O}$, and δ is expressed in per mil, ‰. Carbon and oxygen values were reported relative to the Vienna Pee Dee Belemnite (VPDB) standard.

The cross-correlation analysis was generated using the “ccf” function in R (version 4.4.0) to assess the cross-correlation pattern between the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ intra-tooth analysis and identify different forms of seasonal dietary responses (Supplementary Table 3 and Supplementary Fig. 4). The original R script is available in the following publication¹⁰¹. To establish if there were significant differences between the $\delta^{18}\text{O}$ values between OD and non-OD taxa from different localities, we conducted a Welch's ANOVA using PAST 4.02¹⁰² after confirming that the samples did not have a normal distribution (normality test) and also lacked homogeneity in variance (Levene's test). The vertebrate faunal list of GFT-4.2 is in Supplementary Table 4.

Dental wear analysis

Dental specimens of ungulates were studied through mesowear and microwear analyses to assess dietary traits. This approach reflects the animal's diet over the months or years before its death (long-term), as mesowear score does not change over short periods such as seasonal variations^{103–106}. For the macroscopical mesowear analysis, 60 molars were analysed (Supplementary Table 6). Unworn teeth, highly worn teeth, and those with broken or damaged cusp apices, were omitted from mesowear analysis. Cusp sharpness is sensitive to ontogenetic age among young and dentally senescent individuals. However, for intermediate age groups, mesowear is found to be less sensitive to age and more strongly related to diet¹⁰⁷. Mesowear analysis is a method used to evaluate the relief and sharpness of worn cusp apices in ways that are correlated with the relative amounts of attritional and abrasive wear that they cause on the dental enamel. Mesowear was scored macroscopically from the buccal side of upper molars and the lingual side of lower molars, preferably the sharpest cusp¹⁰⁸. Additionally, we have utilised teeth ranging from P3 to M3, as proposed by Kaiser and Solounias¹⁰⁹. A diet with low levels of abrasion, such as browse (high attrition), maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion results in more rounded and blunted buccal cusp apices. In this study, the standardised method introduced by Mihlbachler et al.¹⁰⁸ was employed. The method is based on seven cusp categories (0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the individual mesowear data from a single sample corresponds to the mesowear score (MWS). The Fig. 6 was run using PAST 4.02¹⁰².

For the dental microwear analysis, a total of 191 molars and premolars were selected and moulded (Supplementary Table 6). The microwear signal reflects a short-term dietary effect, likely covering the last few days or weeks before death¹¹⁰. This signal has been defined as the 'last supper' effect¹¹¹. Therefore, the dental microwear pattern can reveal the animal's diet based on the local and seasonal environmental resources available shortly before death. All moulded specimens were carefully screened under the

stereomicroscope, and 86 were discarded from the microwear study due to bad preservation or other taphonomical defects^{112–114}. Before moulding, the occlusal surface of each specimen was cleaned using acetone and then 96% ethanol. The surface was moulded using high-resolution and light viscosity silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set), and transparent casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). Enamel microwear features were observed via standard light microscopy using a Zeiss Stemi 2000C stereomicroscope at 35× magnification on high-resolution epoxy casts of teeth, following the cleaning, moulding, casting, examination protocol and classification of features defined by Solounias and Semprebon⁴¹ and Semprebon et al.⁶¹. We used both upper and lower teeth from P4 to M3 according to Xafis et al.¹¹⁵. A standard 0.16 mm² ocular reticle was employed to quantify the number of small and large pits (round scars), scratches (elongated scars with parallel sides), gouges (irregular edges and much larger and deeper than large pits) and puncture pits (deepest at their centres, symmetrical, crater-like features with regular margins). A quantitative count of total pits and scratches was conducted for the variables mentioned. However, for the remaining variables, a qualitative assessment of presence or absence was performed (1 = presence; 0 = absence). The scratch width score (SWS) is obtained by giving a score of ‘0’ to teeth with predominantly fine scratches per tooth surface, ‘1’ to those with a mixture of fine and coarse types of textures, and ‘2’ to those with predominantly coarse scratches. In order to achieve a more precise categorisation of grazers, browsers, and mixed feeders, we used the percentage of individuals possessing scratch numbers that fall between 0 and 17 in the 0.16 mm² area (0–17%)¹¹⁶. The results were compared with a database constructed from extant ungulate taxa⁴¹. The microwear bivariate graphs (Fig. 7) were generated using the following R script¹¹⁷.

Plant Wax Biomarkers

Plant Biomarker Extraction and Isolation. A set of ten samples (GFT 1 to GFT 10) from GFT-4.2 depositional sequence was analysed (see sampling location in Supplementary Fig. 2). Dry, homogenised sediment was subject to pressurised solvent extraction (Büchi Speed Extractor E-916) in three 10 min-cycles in 9:1 (v:v) DCM:MeOH at 100°C and 103 bar/1500 psi. The solvent containing the total lipid extract (TLE) was concentrated to ~1 mL using a Büchi Syncore-Plus evaporator and then evaporated to dryness using a steady stream of N₂ in separate, 4 mL glass vials. The TLE was separated into Neutral, Acid, and Polar fractions by Aminopropyl column chromatography using 4 mL each of 2:1 Dichloromethane:Isopropanol, 4% Acetic Acid in Diethyl Ether, and Methanol, respectively. Normal (*n*-) alkanes were isolated from the Neutral fraction using silver nitrate infused silica gel column chromatography with 4 mL Hexane.

Molecular Characterization. The *n*-alkanes were analysed with an Agilent 7890B Gas Chromatograph (GC) System equipped with an Agilent HP-5 capillary column (30 m length, 0.25 mm i.d. and 0.25 µm film) and coupled to a 5977A Series Mass Selective Detector (MSD) at the Max Planck Institute of Geoanthropology, Jena, Germany. Samples were injected in pulsed split mode at 290°C, and the GC oven was programmed from 60°C (1 min hold) to 150°C at 10°C/min, then to 320°C at 6°C/min (10 min hold).

Helium was the carrier gas with a constant flow of 1.1 mL/min. The MS source was operated at 230°C with 70 eV ionisation energy in the electron ionisation (EI) mode and a full scan rate of m/z 50-650. Plant wax n -alkanes were identified by comparing mass spectra and retention times with an external C₂₁-C₄₀ standard mixture.

Average chain length (ACL), or the weight-averaged number of carbon homologues of the C₂₁-C₃₃ n -alkanes, was calculated as follows (Eq. 1):

$$ACL = \frac{21(C_{21})+22(C_{22})+\dots+32(C_{32})+33(C_{33})}{C_{21}+C_{22}+\dots+C_{32}+C_{33}} \quad (1)$$

Where C_{*x*} is the abundance of the chain length with *x* carbons.

The carbon preference index (CPI), which examines the odd-over-even carbon number predominance and serves as an indicator for hydrocarbon maturity and degradation⁵³, was calculated using the abundances of odd and even chain lengths from C₂₁ to C₃₃ and the following formula (Eq. 2):

$$CPI = \frac{(C_{21}+C_{23}+C_{25}+C_{27}+C_{29}+C_{31})+(C_{23}+C_{25}+C_{27}+C_{29}+C_{31}+C_{33})}{2 \times (C_{22}+C_{24}+C_{26}+C_{28}+C_{30}+C_{32})} \quad (2)$$

The submerged/terrestrial ratio (STR), which differentiates alkanes produced by either submerged or terrigenous plants, with terrestrial plants generally having values < 0.25⁵⁶, was calculated as follows (Eq. 3):

$$STR = \frac{C_{25}}{C_{21}+C_{23}+\dots+C_{31}+C_{31}} \quad (3)$$

The aquatic plant ratio (P_{aq}), which differentiates n -alkyl compounds produced by either algae or terrigenous plants, with terrestrial plants generally having values < 0.1⁵⁵, was calculated as follows (Eq. 4):

$$P_{aq} = \frac{C_{23}+C_{25}}{C_{23}+C_{25}+C_{29}+C_{31}} \quad (4)$$

Compound-Specific Carbon Isotope Analysis. $\delta^{13}C$ values of n -alkane homologues C₂₅-C₃₁ were measured using an Agilent 7890A GC System equipped with an Agilent DB-1MS-UI capillary column (60 m length, 0.25 mm i.d. and 0.25 μ m film), coupled to a Thermo Fisher Scientific Delta V Plus Isotope Ratio Mass Spectrometer at the Max Planck Institute for Biogeochemistry, Jena, Germany. Samples of 1.0 μ L were injected in splitless mode at 320°C, and the GC oven was maintained for 1 min at an initial temperature of 110°C, before the temperature was increased to 320°C at 5°C/min (7 min hold). All the samples were measured in triplicates. Helium was the carrier gas with a constant flow maintained at 1.8 mL/min. We report $\delta^{13}C$ values of C₂₅-C₃₁ n -alkanes as they were the most abundant in all samples.

The accuracy of the $\delta^{13}\text{C}$ values was evaluated against an international standard laboratory mixture (Indiana A7, Arndt Schimmelmann, University of Indiana) injected after every three sample injections. The standard deviation of the $\text{C}_{16}\text{-C}_{30}$ *n*-alkane working standard was $\leq 0.5\text{‰}$ for $\delta^{13}\text{C}$. Drift corrections were determined by the standards run after every sample. Carbon isotope composition was reported in δ notation, where $\delta^{13}\text{C} = [(R_{\text{sample}}/R_{\text{standard}}) - 1]$, $R = {}^{13}\text{C}/{}^{12}\text{C}$, and δ is expressed in per mil, ‰. Carbon values were reported relative to the Vienna Pee Dee Belemnite (VPDB) standard. All mean $\delta^{13}\text{C}$ values are reported with their standard deviation.

Finally, linear regression and Spearman's rank test were used to correlate the molecular characterisations of ACL, CPI, and the $\delta^{13}\text{C}$ values of the individual $\text{C}_{25}\text{-C}_{31}$ *n*-alkanes, while Student *t*-tests and Mann–Whitney *U*-tests were used to test the significance of differences between the $\text{C}_{25}\text{-C}_{31}$ $\delta^{13}\text{C}$ values. These tests were performed after confirming the normal distribution (normality test) and the homogeneity in variance (Levene's test) of our data. All tests were run using PAST 4.03¹⁰² and an Alpha (α) of 0.05.

Pollen analysis

A set of six samples (GFT 1, 2, 4, 6, 8 and 10) from GFT-4.2 depositional sequence was analysed (see sampling location in Supplementary Fig. 2a). Samples were treated with HCl, KOH, concentration with heavy liquid, and a final step with $\text{HF}^{118,119}$. Counting was performed with an Olympus Cx41 microscope at 600 magnifications. Fossil pollen and Non Pollen Palynomorphs (NPP) were identified using published keys^{120–127}. Pollen, NPP and microcharcoal concentrations were calculated using the volumetric method (particles/g of dry sediment) described in^{119,128}.

Small vertebrates

The small vertebrate material referred to here was recovered from sediment collected at the GFT-4 site, including GFT-4.2 locality (Supplementary Fig. 2a), during the excavation campaigns of 2017 and 2018. All sediment was water-screened using superimposed 4-, 1- and 0.5-mm mesh sieves. The collection from GFT-4 includes 330 rodent teeth corresponding to nine different taxa and 47 disarticulated cranial and postcranial bones of amphibians and squamates comprising at least five taxa. The vertebrate faunal list of GFT-4.2 is in Supplementary Table 4.

Micro-crustaceans and algae remains

Three sediment samples (GFT 1, 3 and 5 (GFT 5 is a sterile sample); see sampling location in Supplementary Fig. 2a) of 70–120 g from the GFT-4.2 section were disaggregated by treatment with 3% H_2O_2 for 48 hours. The material was washed through 100- μm , 250- μm and 1000- μm sieves, dried, and calcareous remains picked from sieve residues under a low power binocular Olympus SZ60 microscope. A Hitachi TM3000 scanning electron microscope was used for ostracod-valve documentation and to support identification, which was mostly based on the key for the modern Algerian fauna¹²⁹, and western and central European fauna¹³⁰.

Digital mapping

Digital terrain model source was carried out using ArcGIS 10.8 software (ETOPO2 (NGDC)), available at the Digital Mapping and 3D Analysis Laboratory (CENIEH, Spain) and TanDEM-X (DLR).

Data availability

All data generated or analysed during this study are included in this published article (and its supplementary information files). Original fossils are housed at the Musée Universitaire d'Archéologie et du Patrimoine at the Université Mohammed Premier (Oujda, Morocco). The source data for Figures 2, 3, 4, 5, 6, 7, 8 and Supplementary Figures 4 and 5 are provided as a Source Data file. Source data are provided in this paper.

Code availability

No code has been created for this study. The R scripts used are based on previously published data, which are available in the references.

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Author contributions

I.R.-P. conceived and designed this research. A.A., A.R.-H., J.v.d.M., H.A., A.O., L.A., J.A., P.P., H.H., C.S.-B., I.R.-P., A.B.-C., H.M., E.M.-R., M.S., R.S.-R. and M.G.CH. participated in the fieldwork and provided materials and background for the research. A.R.-H., H.A., and J.v.d.M. identified the macrofaunal remains. A.R.-H. supervised the excavation. I.R.-P. and C.T. conducted the stable isotope analysis in faunal remains. I.E. conducted the pollen analysis. I.R.-P. and F.R. performed the dental wear analysis. S.M. conducted the micro-crustaceans and algae analysis. P.P. and J.A. carried out the analysis of the rodent remains. H.A.B., and C.S.-B. carried out the analysis of the herpetofauna remains. R.P., P. R., D.K.J, and I.R.-P. performed the plant wax biomarkers analysis. A.B.-C., conducted the mapping and the stratigraphic section. M.G.CH., R.S.-R., and H.A. are the principal investigators of the project and are responsible for project research objectives, administration and funding acquisition. I.R.-P. wrote the paper with input from all authors.

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Brooke Crowley,
University of Cincinnati,
United States

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Bay Path University,
United States
Mugino O. Kubo,
The University of Tokyo, Japan

*CORRESPONDENCE

Iván Ramírez-Pedraza
✉ ramirezpedrazaivan@gmail.com
Laura M. Martínez
✉ lmartinez@ub.edu

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Multiproxy approach to reconstruct fossil primate feeding behavior: Case study for macaque from the Plio-Pleistocene site Guefaït-4.2 (eastern Morocco)

Iván Ramírez-Pedraza^{1,2*}, Laura M. Martínez^{3,4*}, Hassan Aouraghe⁵,
Florent Rivals^{1,2,6}, Carlos Tornero^{1,7}, Hamid Haddoumi⁵,
Ferran Esteban-Sánchez^{4,8}, Antonio Rodríguez-Hidalgo^{1,2,9},
Jan van der Made¹⁰, Aïcha Oujaa¹¹, Juan José Ibáñez⁸,
Hicham Mhamdi⁵, Mohamed Souhir⁵, Al Mahdi Aissa⁵,
M. Gema Chacón^{1,2,12} and Robert Sala-Ramos^{1,2}

¹Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain, ²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain, ³Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Secció de Zoologia i Antropologia Biològica, Universitat de Barcelona, Barcelona, Spain, ⁴Institut d'Arqueologia de la Universitat de Barcelona, Barcelona, Spain, ⁵Faculté des Sciences, Département de Géologie, Université Mohamed Premier, Oujda, Morocco, ⁶Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain, ⁷Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain, ⁸Archaeology of Social Dynamics (ASD), Institución Milá y Fontanals (IMF), Spanish National Research Council (CSIC), Barcelona, Spain, ⁹Instituto de Evolución en África (IDEA, Madrid), Madrid, Spain, ¹⁰Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, Madrid, Spain, ¹¹Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco, ¹²UMR 7194 - Histoire Naturelle de l'Homme Préhistorique (CNRS/MNHN/UPVD), Paris, France

The genus *Macaca* belongs to Cercopithecidae (Old World monkeys), Cercopithecinae, Papionini. The presence of *Macaca* in North Africa is well known from the Late Miocene to the Late Pleistocene. However, the diet of fossil *Macaca* has been poorly described in the literature. In this study, we investigated the feeding habits of *Macaca* cf. *sylvanus* ($n=4$) from the Plio-Pleistocene site Guefaït-4.2 in eastern Morocco through multiproxy analysis combining analyses of stable carbon and oxygen isotopes from tooth enamel, buccal microtexture, and low-magnification occlusal dental microwear. For both microwear analyses, we compared the macaques with a new reference collection of extant members of Cercopithecoidea. Our occlusal microwear results show for the fossil macaque a pattern similar to the extant *Cercocebus atys* and *Lophocebus albigena*, African forest-dwelling species that are characterized by a durophagous diet based mainly on hard fruit and seed intake. Buccal microtexture results also suggest the consumption of some grasses and the exploitation of more open habitats, similar to that observed in *Theropithecus gelada*. The $\delta^{13}\text{C}$ of *M. cf. sylvanus* indicates a C_3 based-diet without the presence of C_4 plants typical of the savanna grassland in eastern Africa during this period. The high $\delta^{18}\text{O}$ values of *M. cf. sylvanus*, compared with the contemporary ungulates recovered from Guefaït-4.2, could be associated with the consumption of a different resource by the primate such as leaves or fresh fruits from the upper part of trees. The complementarity of these methods allows for a dietary reconstruction covering a large part of the individual's life.

KEYWORDS

habitat, paleodiet, Africa, buccal microtexture, occlusal microwear, stable isotopes

Introduction

Modern Cercopithecoidea primates inhabit a wide range of habitats, including tropical forests, high-altitude woodlands, and savanna grasslands (Jablonski et al., 2000). This adaptability across a range of environments began with a radiation within and beyond Africa, probably due to the increasingly open and fragmented environments of the Late Miocene and the Plio-Pleistocene (Elton, 2007; Hughes et al., 2008; Roos et al., 2019). For example, the closing of the Tethys Ocean and subsequent aridification of northern Africa (Zhang et al., 2014), and fluctuations in Milankovitch cycles (DeMenocal, 1995), formed intermittent biogeographical barriers. It is hypothesized that these ecological barriers diversified Cercopithecoidea, specifically the Papionini tribe, into different genera. *Theropithecus* adapted to wet lowlands, *Papio*, *Cercocebus*, *Lophocebus*, and *Mandrillus* filled niches within more forested environments, while *Macaca* became more-generalized and settled a wide variety of habitats within higher latitudes (Delson, 1980). Paleontological and molecular evidence indicates that the macaque lineage originated during the Miocene in Africa and diverged from other African Papionini around 7–5.5 Ma (Delson, 1980; Tosi et al., 2005; Roos et al., 2019). According to the fossil record, macaques dispersed throughout Eurasia during the Late Miocene, inhabiting primarily the Mediterranean region 6–5 Ma (Alba et al., 2014; Piñero et al., 2017) and then in the Late Pliocene, eastern Asia (~4 Ma; Szalay and Delson, 1979; Elton, 2007; Meloro and Elton, 2012). In this radiation, macaques experienced a rapid diversification into several species (Elton and O'Regan, 2014; Roos et al., 2019). The genus *Macaca* consists of approximately 23 extant species and occupies more diverse ecological environments and geographical ranges (from 10° south to over 40° north latitude) than any other genus of nonhuman primates. In fact, the expansion of this genus in Africa and Eurasia is one of the most successful among primates (Jablonski, 2002; Jablonski and Frost, 2010; Fleagle, 2013; Roos et al., 2019), and its ecological distribution and adaptative capacity reflect great dietary diversity and interspecific behavioral responses to seasonality (Kato et al., 2014).

The oldest macaque fossils in Africa have been found in the Miocene paleontological sites of Menacer (Algeria, *Macaca* sp.; Arambourg, 1959) and Wadi Natrum (Egypt, *Macaca lybica*; Stromer, 1913, 1920). Other *Macaca* fossil remains have been recorded in the Pliocene Tunisian sites of Garaet Ichkeul (Szalay and Delson, 1979; Delson, 1993; Alemseged and Geraads, 1998) and Ain Brimba (Arambourg and Coque, 1959; Arambourg, 1979; Szalay and Delson, 1979). Contemporaneous to the remains of *Macaca* cf. *sylvanus* from the Guefait-4.2 (GFT-4.2) site in eastern Morocco analyzed in this work, fossil remains of *Macaca* sp. have been found in the Plio-Pleistocene site of Ahl al Oughlam in western Morocco (Geraads, 2006). *Macaca sylvanus* has also been described from the Late Pleistocene sites of Chrafate and Ez Zarka in Morocco (Ouahbi et al., 2001; Fooden, 2007), and in the Middle and Late Pleistocene sites of Traras, Monts des Nedroma, Afalou bou Rhummel, and Tamar Hat in Algeria (Pomel, 1892; Joleaud, 1926; Delson, 1974; Szalay and Delson, 1979; Geraads, 1987; Fooden, 2007).

At present, there is only one species of the genus *Macaca* in Africa, *M. sylvanus* (Barbary macaques) from Algeria (Chiffa, Tigounatine, Icetcifère, Akfadou, and Kherrata) and Morocco (High Atlas, Middle Atlas, and Rif; Fooden, 2007). Field observations have defined feeding

habits as varied and to include an important seasonal component, with diet consisting of more than 100 species of plants, fungi, lichens, mosses, and animal prey (Deag, 1983; Ménard, 1985; Ménard and Vallet, 1986). Studies that have taken into account the annual composition of the diet indicate that seeds, leaves, and herbs are the main foods of Barbary macaques in Akfadou and Tigounatine (Algeria; Ménard, 1985; Ménard and Vallet, 1986, 1996). However, in the Rif mountains of northern Morocco, more than 50% of their diet is based on seeds (Mehlman, 1988), and some studies of the populations that inhabit the Middle Atlas suggest that fruits could constitute a significant part of their diet (Deag, 1983; Drucker, 1984; Ménard and Mohamed, 1999), demonstrating high intra-species local variation at the population level. Nevertheless, the diet of fossil *M. cf. sylvanus* is virtually unknown, with the exception of a study on dental microwear of *Macaca* sp. from the Pliocene of northwestern China, which suggests a hard-object feeder or extractive forager, without grass consumption (Williams and Holmes, 2011).

Previous work on the feeding habits of African Plio-Pleistocene Cercopithecidae, through analysis of stable isotopes and dental microwear, have mainly focused on Eastern Africa (Teaford, 1993; Ungar and Teaford, 1996; Cerling et al., 2011, 2013a,b; Sponheimer et al., 2013; Levin et al., 2015; Shapiro et al., 2016; Robinson et al., 2017; Ungar et al., 2017; Martin et al., 2018; Souron, 2018; Manthi et al., 2020; Merceron et al., 2021) and Southern Africa (Lee-Thorp et al., 1989, 2010; Daegling and Grine, 1999; Codron et al., 2005; El-Zaatari et al., 2005; Scott et al., 2005; Fourie et al., 2008; Williams and Patterson, 2010; Williams and Holmes, 2011; Sponheimer et al., 2013; Grine et al., 2020). In these studies, the most represented genera are *Theropithecus*, *Parapapio*, and *Papio*, among which there is a consensus on the predominance of a graminivore diet with a high component of C₄-based resources for *Theropithecus* (Lee-Thorp et al., 1989; Cerling et al., 2013a; Levin et al., 2015; Souron, 2018) and more diverse food intake with a proportion of C₃ plants in the diet of *Parapapio* and *Papio* (Lee-Thorp et al., 1989; Codron et al., 2005; Fourie et al., 2008; Williams and Patterson, 2010; Levin et al., 2015). In Northern Africa, analysis of the feeding behavior of *Theropithecus oswaldi leakeyi* (Jolly, 1972; Delson, 1993) from Tighennif (ca. 1 Ma) and *Theropithecus atlanticus* (Alemseged and Geraads, 1998) from Ahl al Oughlam (ca. 2.5 Ma) suggest a different pattern in carbon values, with a clear domination of C₃ plants, although other authors suggest bulk-feeding graminivory (Fannin et al., 2021).

Many cercopithecoid fossils have been recovered from the same sites where Hominin fossils have been found (Delson, 1980). The genus *Homo* experienced a similar out-of-Africa dispersion during the Pleistocene and inhabited the same ecosystems as members of Papionini. Therefore, both lineages had to confront the same climatic constrictions and habitat partitioning. Understanding the ecology of the fossil Cercopithecoidea primates is of interest for interpreting the paleoecology and niche partitioning of both groups. Consequently, we aimed to analyze the feeding strategies of *M. cf. sylvanus* from GFT-4.2 on different timescales using, for the first time, a multi-proxy approach. On the one hand, the isotopic signal ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) of tooth enamel bioapatite provides dietary information during the first years of the animal's life following the tooth mineralization times proposed by Sirianni and Swindler (1985) for the extant *Macaca nemestrina*. On the other hand, dental microwear analysis, combining buccal (microtexture analysis) and occlusal (low magnification) surfaces, provides dietary information over the long term (weeks to

months; Romero et al., 2012; Hernando et al., 2021) and short term (last days; Sempere et al., 2004), respectively, but always toward the end of the animal's life. Occlusal microwear studies in primates have suggested that mechanical properties of food items are the primary cause of different microwear pattern among primates. For instance, primates that incorporate hard objects, such as seeds and nuts, have more pitted surfaces than folivores primates that exhibit heavily scratched areas (Ungar, 1996; Scott et al., 2006). Occlusal microwear has a short-term turnover therefore, occlusal microwear patterns provide information on the nature of food intake during the last days prior to death (Teaford and Oyen, 1989). On the other hand, buccal surfaces should only interact with the food items consumed while they are being processed in the oral cavity (Ungar and Teaford, 1996; Romero et al., 2012), and experimental studies have shown that the buccal pattern is more stable through time, at least in the absence of significant dietary shift (Romero et al., 2012).

We hypothesize that combining occlusal and buccal microwear analyses will strengthen the dietary discrimination among these species. Based on the dietary information of extant *M. sylvanus* from Morocco and Algeria, we expect, for the GFT-4.2 specimens, a buccal and occlusal pattern similar to folivore-frugivore primates with the incorporation of seeds during the dry season. In the case of stable carbon and oxygen isotopes, we expect values similar to those of the *Theropithecus* from Ahl al Oughlam (Morocco). That is, a predominance of C₃ plants in the diet and high oxygen values in relation to ungulates. To compare the dental microwear of *M. cf. sylvanus* from GFT-4.2, we present a new reference collection of wild modern cercopithecines including the same individuals for both microwear methods. The integration of the data obtained from these three high-resolution techniques has allowed us to obtain a more precise and robust picture of the feeding habits of *M. cf. sylvanus* from GFT-4.2.

Site: GUEFAÏT-4.2

An interdisciplinary Spanish–Moroccan project started in 2006 as an international cooperation between the Université Mohamed Premier Oujda (UMP, Eastern Morocco) and the Catalan Institute for Human Palaeoecology and Social Evolution from Tarragona (IPHES-CERCA, Catalonia, Spain). The aim of this cooperation is to establish the geochronological and archeo-paleontological context of the Ain Beni Mathar/Guefaït fluvio-lacustrine basin, in the northern part of the High Plateaus (Jerada Province, Eastern Morocco; Aouraghe et al., 2016; Chacón et al., 2016; Sala-Ramos et al., 2022). One of the systematic surveys in the region revealed the fossiliferous level of Guefaït-4. This horizon yielded a rich and diverse faunal assemblage of vertebrates, which was systematically excavated at the GFT-4.2 site (reptiles, amphibians, and both small and large mammals), including the macaque fossil remains analyzed in this work (Alba et al., 2021). The fossil remains were concentrated in a palustrine level constituted of clay and marls, at the base of Unit 2, within the Dhar Iroumyane stratigraphic section (Aouraghe et al., 2019b). The fieldwork carried out between 2017 and 2019 recovered more than 3,000 fossil remains in an excavated area of 28 m². Biostratigraphic correlations with other sites in Northern Africa, such as the lower levels of the Ain Boucherit site in Algeria (Sahnouni et al., 2018) and Ahl al Oughlam in Morocco (Geraads, 2006), suggest an age close to the Plio-Pleistocene boundary (2.58 Ma). The absence of the genus *Equus* (despite the abundance of

Hipparion equid remains; Aouraghe et al., 2019a,b) indicates an age older than ~2.4 Ma (Sahnouni et al., 2018). This chronological limit is supported by the study of the murid assemblage (Agustí et al., 2017; Piñero et al., 2019), the carnivore assemblage (Madurell-Malapeira et al., 2021), and preliminary paleomagnetism studies (Parés et al., 2020).

Materials

A total of six teeth of *M. cf. sylvanus* were recovered from GFT-4.2 during the fieldwork in 2018 and 2019 (Alba et al., 2021). The materials are housed in the Faculty of Science, Mohammed I University in Oujda, Morocco. We discarded two of them for the final analysis because they correspond to dental germ fragments (GFT4.2018-1-P13-191, right M2 or M3, and GFT4.2019-1-R15-45, right M2).

The studied teeth ($n = 4$) correspond to a left upper central incisor (I¹, GFT4.2018-1-Q14-70), a right lower first molar (M₁, the lingual crown fragment of GFT4.2018-1-Q14-13), a right second lower molar (M₂, GFT4.2019-1-S15-65), and a left lower third molar (M₃, GFT4.2019-1-R13-63). All four available fossil teeth (M₁, M₂, M₃, and I¹) were sampled for stable isotope analysis, three (M₁—GFT140, M₂—GFT138, and M₃—GFT137) were sampled for buccal dental microtexture analysis, and two (M₁—GFT140 and M₂—GFT138) were samples for occlusal dental microwear analysis. M₃ was discarded for the occlusal dental microwear analysis due to the absence of wear facets on this surface. Metrical comparisons suggests that the incisor would belong to a different individual than the lower molars. However, it cannot be ruled out that the lower molars were from the same individual (Alba et al., 2021).

The extant Cercopithecoidea comparative sample for the buccal microtexture and occlusal microwear analyses correspond to a total of 41 well-preserved left second lower molars (M₂; Supplementary Table 1). We excluded 10 samples from occlusal microwear analysis and 12 samples from buccal microtexture due to bad preservation or other taphonomic defects on the analyzed surface. The selected species have well-defined habitat and dietary preferences and include five extant species (*Theropithecus gelada*, *Mandrillus sphinx*, *Lophocebus albigena*, *Cercocebus atys*, and *Macaca mulatta*). Whenever possible, we chose specimens of the same taxa from close localities to minimize the variability of their dietary regime. We selected the extant species based on the criteria of phylogenetic affinity (Perelman et al., 2011) and the dental morphology that characterizes all cercopithecines, namely bilophodont molars (Kay and Hylander, 1978; Monson and Hlusko, 2014). This comparative sample served to establish a broad spectrum of ecological and dietary diversity.

1. *Theropithecus gelada* specimens from Ethiopia have a plant-based dietary regime (Dunbar and Bose, 1991), with more than 80% consisting of blades (Mau et al., 2009). However, those *T. gelada* living on the Guassa Plateau also incorporate large quantities of forbs into their diet (Fashing et al., 2014), and are often selective of tender forbs that are rare on the plateau (Souron, 2018).
2. *Mandrillus sphinx* is a frugivore primate that usually lives in gallery forest. Fruits, supplemented with various plant parts like leaves and flowers, constitute the *Mandrillus* diet. However, when fruit is scarce due to seasonality, *M. sphinx* fallback on

mechanically challenging items like seeds and hard-shell fruits from the forest floor (Hoshino, 1985; Lahm, 1986; Tutin et al., 1997; Powell et al., 2017).

3. *Cercocebus atys* forages on the forest's floor and shrub layers, relying on hard-shelled nuts like *Sacoglottis gabonensis* year-round. Yet, due to seasonal fluctuations, the total contribution of *S. gabonensis* can range anywhere from 19% to 80% of the monthly diet (Daegling et al., 2011; McGraw et al., 2014).
4. *Lophocebus albigena* is classified as a hard object feeder (Lambert et al., 2004; McGraw et al., 2011) that consumes a significant portion of hard seeds and nuts (Lambert et al., 2004). In actuality, due to seasonal fluctuations, *L. albigena* is a generalist that consumes a high (40%) percentage of soft ripe fruit (Lambert et al., 2004) in addition to seeds, flowers and young leaves (Poulsen et al., 2001). During seasons with low fruit availability, *L. albigena* will eat bark that, although hard, is rich in protein and soluble sugars (Rogers et al., 1994; Olupot, 1998). This fall-back feeding strategy has also been described for Barbary macaques (*Macaca sylvanus*; Ménard and Mohamed, 1999).
5. *Macaca mulatta* has the largest geographical distribution with its ranges spanning from Afghanistan to India, Pakistan, China, Thailand and Vietnam, among others (Sengupta et al., 2014). Its wide distribution reflects highly opportunistic feeding strategy, even though fruits may constitute as much as 70% of their diet in some regions (Fooden, 2007), yet less than 9% in other ecosystems, such as Pakistan (Goldstein and Richard, 1989). They are semi-terrestrial primates that can also feed up with species that are in different strata of the forest (Albert et al., 2013).

We have not included extant *M. sylvanus* specimens because they have a narrow distribution, and some populations are fed by humans like those of Gibraltar (Spain). Therefore, the baseline samples included in the present study consist of wild specimens with well-defined diet and habitat. To contextualize the oxygen and carbon values of *M. cf. sylvanus*, we have also included contemporaneous herbivore samples from GFT-4.2 corresponding to the same paleontological level 1. These samples include the remains of Tragelaphini ($n = 4$), *Gazella* sp. ($n = 4$), and *Hipparion* sp. ($n = 4$). The list of specimens sampled and analyzed and the raw data for stable isotope analysis are provided in Supplementary Table 2.

Methods

Stable isotope analysis

Tooth surfaces were cleaned with a tungsten abrasive drill bit to remove any adhering external material. Enamel powder for bulk isotope analysis was then obtained using a diamond-tipped drill, passed along the full length of the buccal surface to ensure a representative measurement for the entire period of enamel formation.

Powdered enamel samples (2–6 mg) were chemically treated at the Biomolecular Laboratory of IPHES. Chemical treatment of samples was based on protocols originally proposed by Koch et al. (1997) and later modified by Tornero et al. (2013). The samples were treated for 4 h in 0.1 M acetic acid [CH_3COOH] (0.1 mL solution/0.1 mg of sample), neutralized with distilled water, and freeze-dried.

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of tooth enamel bioapatite were measured using an automated carbonate preparation device (KIEL-III) coupled to a

gas-ratio mass spectrometer (Finnigan MAT 252) at the Environmental Isotope Laboratory, University of Arizona, United States. Samples were reacted with dehydrated phosphoric acid under a vacuum at 70°C. The accuracy and precision of the measurements were checked and calibrated using the calcium carbonate international standards (NBS-19 and NBS-18). Replicate measurements of the standards during analysis had errors of $\pm 0.1\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 sigma). Carbon isotope composition is reported in δ notation, where $\delta^{13}\text{C} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1]$, $\text{R} = ^{13}\text{C}/^{12}\text{C}$, and δ is expressed as per mil notation (‰). Carbon and oxygen values are reported relative to PDB (Vienna Pee Dee Belemnite).

In terrestrial ecosystems there is a marked isotopic distinction between the two photosynthetic pathways in plants, C_3 (Calvin cycle) and C_4 (Hatch-Slack cycle), which differ mainly in their discrimination against ^{13}C during the fixation of CO_2 (Farquhar et al., 1989). Modern plants that use the C_3 photosynthetic pathway (including most trees, woody shrubs, bushes, herbs and temperate grasses) have an average isotopic composition of -28.5‰ (global range -20 to -37‰), with -23‰ as the maximum value recommended for typical C_3 plants and a cutoff of -31.5‰ for closed-canopy forests (Kohn, 2010). Due to the fact that we discarded the presence of that environment in GFT-4.2. For this study, we use the average $\delta^{13}\text{C}$ value of -27‰ for modern C_3 plants, excluding analyses from the understory of closed-canopy forests below -31.5‰ (Kohn, 2010). Modern plants that use the C_4 photosynthetic pathway (primarily tropical grasses and sedges) have an average isotopic composition of -12‰ (global range -10 to -14‰ ; Cerling and Harris, 1999; Kohn and Cerling, 2002). Crassulacean Acid Metabolism (CAM) plants can have $\delta^{13}\text{C}$ values corresponding to both C_3 and C_4 plants. However, such plants do not seem to be consumed by primates (Cerling et al., 2013a). The $\delta^{13}\text{C}$ values of atmospheric CO_2 have fluctuated over time and this impacts $\delta^{13}\text{C}$ values in plants (Fiedli et al., 1986; Keeling et al., 2017). We have corrected by $\sim +1.5$ the $\delta^{13}\text{C}$ values of modern plants, due to the difference between the pre-Industrial $\delta^{13}\text{C}_{\text{CO}_2}$ value of $\sim -6.5\text{‰}$ established for the Plio-Pleistocene (Tippie et al., 2010) and the $\delta^{13}\text{C}_{\text{CO}_2}$ value of $\sim -8\text{‰}$ corresponding to the time at which the plants were collected (Kohn, 2010). In this paper, we have used the enamel-diet enrichment factor of $+11.8 \pm 0.3\text{‰}$ calculated for chimpanzees (*Pan troglodytes*) at Ngogo in Kibale National Park in Uganda for macaques (Malone et al., 2021) and the enamel-diet enrichment factor of $+14.1 \pm 0.5\text{‰}$ for ungulates (Cerling and Harris, 1999; Passey et al., 2005) to interpret tooth enamel $\delta^{13}\text{C}$ values and estimate potential consumption of C_3 - or C_4 -plant. These isotopic enrichment factor values for C_3 and C_4 plants are assumed to provide tooth enamel values of $< -18.2\text{‰}$ for closed canopy diets, $< -13.7\text{‰}$ for pure C_3 diets, $< -9.7\text{‰}$ for C_3 -dominated diets, from -9.7 to -0.7‰ for C_3 - C_4 mixed feeders, $> -0.7\text{‰}$ for C_4 -dominated diets and $> +1.3\text{‰}$ for pure C_4 diets in primates and tooth enamel values of $< -15.9\text{‰}$ for closed canopy diets, $< -11.4\text{‰}$ for pure C_3 diets, $< -7.4\text{‰}$ for C_3 -dominated diets, from -7.4 to $+1.6\text{‰}$ for C_3 - C_4 mixed feeders, $> +1.6\text{‰}$ for C_4 -dominated diets and $> +3.6\text{‰}$ for pure C_4 diets in ungulates.

The $\delta^{18}\text{O}$ values in enamel bioapatite is directly related to the drinking water (i.e., springs, rivers, lakes, water holes), plant/food water (i.e., leaves, grass, fruit) and metabolic water by reaction with carbohydrates. Consequently, the precipitation, altitude, humidity/aridity and local temperatures will have an effect on the $\delta^{18}\text{O}$ of locally available water and food (Longinelli, 1984; Luz and Kolodny, 1985; Bryant and Froelich, 1995; Pederzani and Britton, 2019). Oxygen values can also vary within the same habitat, especially in tropical forest

environments, depending on where the species forages. Species feeding in the upper part of the canopy tend to have higher $\delta^{18}\text{O}$ values as opposed to species feeding in the understory which tend to have lower $\delta^{18}\text{O}$ values (Krigbaum et al., 2013; Crowley, 2014; Fannin and McGraw, 2020).

The approximate initial and final mineralization estimated for the extant *Macaca nemestrina* (Sirianni and Swindler, 1985), in relation to the teeth analyzed in fossil *M. cf. sylvanus*, is *ca.* birth to 1 year for M_1 , I^1 *ca.* 1 to 2 years for I^1 , *ca.* 1 to 2.5 years for M_2 and *ca.* 3 to 4 years for M_3 . Related to dental development, the only permanent tooth to begin development prenatally in the non-human primates is the first molar, which may have one to three cusps mineralized at birth and a complete development of the crown for about 1 year (Sirianni and Swindler, 1985). Relatively recent studies in *Macaca mulatta* suggest that the longest weaning periods are *ca.* 10 months and the shortest weaning period, between 2 and 5 months (Reitsema et al., 2015). Considering the data on nursing and mineralization timing in extant *Macaca*, we assume that the I^1 , M_2 and M_3 enamel apatite should reflect a post-weaning signal and the M_1 enamel apatite could therefore reflect a pre-weaning signal for the *M. cf. sylvanus* from GFT-4.2. This allows us to reconstruct the diet from birth to approximately 4 years of age.

The bivariate graphs were made with the Past 4.02 software (Hammer et al., 2001).

Occlusal microwear analysis (low magnification)

Enamel microwear features were observed *via* standard light microscopy using a Zeiss Stemi 2000C stereomicroscope at 35× magnification on high-resolution epoxy casts of teeth, following the cleaning, molding, casting, and examination protocol developed by Solounias and Sempredon (2002) and Sempredon et al. (2004). We used the wear facets of the mesiobuccal cusp of M_2 (normally the paracone of M_2). Before molding, the occlusal surface of each specimen was cleaned using acetone and then 96% ethanol. The surface was molded using high-resolution silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set), and transparent casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). A standard 0.16 mm² ocular reticle was employed to quantify the number of small pits (round scars—relatively shallow, refract light easily and consequently appear bright and shiny) and large pits (round scars—deeper, wider, and consequently less refractive), coarse scratches (elongated scars with parallel sides—narrow, and barely etched into the enamel surfaces) and fine scratches (elongated scars with parallel sides—wider and more obviously etched into the enamel surface), gouges (features with irregular edges and much larger and deeper than large pits), puncture pits (craterlike features with regular margins), and cross scratches (oriented perpendicularly to the majority of scratches; Supplementary Figure 1). The scratch width score (SWS) was obtained by giving a score of “0” to teeth with predominantly fine scratches per tooth surface, “1” to those with a mixture of fine and coarse types of textures, and “2” to those with predominantly coarse scratches. We took microphotographs using a Blackfly S digital camera and the Kivv Mic Capture Z software. We used the Helicon Focus 7 software to merge images from various focal planes and to produce a single image with a greater depth of field. We added scale bars using ImageJ. We compared the quantitative results with the reference dataset of the extant

Cercopithecidae species. A single observer (IRP) analyzed all specimens to avoid inter-observer errors. We used the Addinsoft™ XLSTAT-3.02 statistical packages to generate the linear discriminant analysis (LDA) and the correspondence analysis (CA).

Buccal microtexture analysis

The original specimens (Supplementary Table 1) were cleaned with acetone and alcohol-soaked cotton swabs, and vinyl impressions were made using President's Jet Regular Body (Coltène-Whaledent). Positive casts were made with Ferropur (Feroce®) polyurethane (Martínez et al., 2022). Buccal areas were obtained using a Sensofar Plu Neox laser scanning confocal microscope, with a 20× (0.45NA) objective, a spatial sampling of 0.83 μm, an optical resolution of 0.31 μm, a vertical resolution of 20 nm, and a z-step interval of 1 μm (Ibáñez et al., 2020; Martínez et al., 2022). Buccal surfaces were placed perpendicular to the objective in a horizontal position and an image of the field of view of the microscope (600 μm × 500 μm) was obtained (see 3D photosimulations in Supplementary Figure 3). From this image, four subsamples of 138 μm × 102 μm (a standard area in DMTA studies) were cropped using the Mountain 7® software from Digital Surf.¹ We have tested the S-filter prior to the obtention of the 38 parameters, following (Winkler et al., 2022). The workflow included leveling the surface to remove plane inclination, eliminating the curvature applying a 2nd degree polynomial, removing the anomalous points by applying upper and lower 0.5% (a total of 1% of threshold values), following the threshold operator included in the same software and applying a Spatial filter (Gaussian 3 × 3). The Gaussian filter was applied because is widely used for technical surfaces and was applied after the trimming because it is sensitive to outliers (Schulz et al., 2013). Surface roughness was later quantified according to 38 ISO 25178/ISO 12781 parameters (Martínez et al., 2022; Supplementary Table 5).

To standardize the measured area on the buccal surface, we calculated the median of the parameters derived from the several (one to four) measurements of a single buccal surface (Scott et al., 2006; Calandra et al., 2012; Martínez et al., 2022), and used the median per specimen for analysis. We used log-transformed texture data for analyses because some texture parameters have non-normal distributions (Shapiro–Wilk, $p < 0.05$). To ensure we did not exclude any parameter (e.g., S_{sk} has negative values), we log transformed the data as $\log [1 + \text{parameter}]$ (Supplementary Table 6). We identified the outliers for both original and log-transformed variables according to their Studentized residual values (absolute value > 3) and removed them from the final data set (Schulz et al., 2013; Martínez et al., 2022). To test the null hypothesis that microwear textures do not differ between teeth from different species, we applied analysis of variance (ANOVA) with pairwise testing (Tukey's honest significant difference [HSD]) to each texture parameter for each species. Where homogeneity of variance test (Levene's test) revealed evidence of unequal variances, we used Welch's ANOVA. We selected the parameters that showed significant differences between species and applied a linear discriminant analysis (LDA). Descriptive statistics, tests and graphs were performed using Addinsoft™ XLSTAT-3.02 statistical packages.

¹ www.digitalsurf.com

Results

Stable isotope analysis

The $\delta^{13}\text{C}$ values of all samples measured in GFT-4.2 range from -12.5 to -8.1‰ ($n = 16$; [Supplementary Table 2](#)). *Macaca cf. sylvanus* carbon values range from -12.5 to -11.8‰ ($n = 4$), with a mean of $-12.3 \pm 0.3\text{‰}$. The values for the herbivore samples from GFT-4.2 are: *Hipparion* sp. ($n = 4$; range = -10.4 to -9.2‰ ; mean = $-9.5 \pm 1\text{‰}$), *Tragelaphini* ($n = 4$; range = -11.3 to -8.1‰ ; mean = $-10 \pm 1.5\text{‰}$), and *Gazella* sp. ($n = 4$; range = -12.2 to -9.4‰ ; mean = $-10.9 \pm 1.1\text{‰}$). The $\delta^{13}\text{C}$ values of the *M. cf. sylvanus* and ungulates from GFT-4.2 range from -12.5 to -8.1‰ , these values correspond to a C_3 -dominated diets for macaques and ungulates.

The $\delta^{18}\text{O}$ values range from -3.5 to 1.8‰ ($n = 16$; [Supplementary Table 2](#)). *Macaca cf. sylvanus* oxygen values range from 0.6 to 1.8‰ , with a mean of $1 \pm 0.5\text{‰}$. The values for the herbivore samples from GFT-4.2 are: *Hipparion* sp. ($n = 4$; range = -3.6 to -0.3‰ ; mean = $-1.8 \pm 0.7\text{‰}$), *Tragelaphini* ($n = 4$; range = -1.4 to 0.3‰ ; mean = $-0.5 \pm 0.4\text{‰}$), and *Gazella* sp. ($n = 4$; range = -1.7 to 1.8‰ ; mean = $-0.4 \pm 0.8\text{‰}$).

The mineralization of M_1 in non-human primates starting from birth of the individual may reflect the nursing signal and thus affecting carbon and oxygen isotope values. However, our results do not indicate a ^{13}C depletion or ^{18}O enrichment in relation to the other *M. cf. sylvanus* teeth analyzed with a post-weaning isotopic signal ([Supplementary Table 2](#)).

Occlusal microwear analysis (low magnification)

The *M. cf. sylvanus* dental microwear pattern is characterized by a high number of pits ($\text{NP} = 28.5$) and a medium number of scratches ($\text{NS} = 16$). The extant cercopithecids show a similar pattern, namely a higher number of pits than scratches ([Table 1](#)). *Lophocebus albigena*

has the highest number of pits ($\text{NP} = 40.6$; raw data in [Supplementary Table 3](#)). The exception is *T. gelada* with a microwear pattern dominated by scratches. Considering the SWS, all species show a high proportion of coarse scratches, and gouges are present in all species except *T. gelada*. *L. albigena* ($\text{G} = 4.3$), *M. sphinx* ($\text{G} = 3.8$), and the fossil macaque ($\text{G} = 4$) have a high abundance of gouges. *L. albigena* ($\text{PP} = 5.4$), *M. mulatta* ($\text{PP} = 4.3$), and the fossil macaque ($\text{PP} = 4.5$) have the highest number of puncture pits; this trait is absent in *T. gelada* and *M. sphinx*. All extant and fossil primates analyzed have a few hyper-coarse scratches and lack cross scratches ([Table 1](#)).

We performed correspondence analysis to compare four microwear variables (pits, scratches, puncture pits, and gouges) of the extant species and macaque from GFT-4.2 ([Figure 1](#)). We plot the results for discriminant functions 1 and 2 (DF1 and DF2, respectively) because they explain a higher percentage of the variance than the other axes ([Supplementary Table 4](#)). Three groups are well defined in the graph. The first group is located on the left and comprises *T. gelada*. The second group, located in the middle, includes *M. sphinx*. The third group, on the right, includes *L. albigena*, *C. atys*, and *M. mulatta*. *T. gelada* falls far from the other species because it has the highest number of scratches ($\text{NS} = 25.9$), the smallest number of pits ($\text{NP} = 10.1$), and the absence of puncture pits and gouges. *M. sphinx* has intermediate microwear values relative to the other two groups. This species has more pits than *T. gelada*, but also more scratches than the components of the third group. *M. sphinx* does not have puncture pits. The last group (*L. albigena*, *C. atys*, and *M. mulatta*) is characterized by a high number of pits ($\text{NP} > 30$) and a small number of scratches ($\text{NS} < 12$). The two specimens of the fossil macaque are located near the third group.

We performed LDA including the four microwear variables (pits, scratches, puncture pits, and gouges) to predict group membership of the fossil *M. cf. sylvanus* specimens from GFT-4.2. The LDA showed significant between-species differences (Wilks' $\lambda = 0.05$; $F = 20.826$; $p < 0.0001$) and correctly classified 90.48% of the species. The two first discriminant functions explained 96.68% of the total variance. DF1 (85.88%) was positively correlated with scratches and negatively correlated with the presence of puncture pits and pits. DF2 (10.80%) was

TABLE 1 Summary of tooth microwear data of the extant and fossil Cercopithecidae analyzed.

Species	Occlusal microwear analysis (low magnifications)								
		N	NS	NP	SWS	PP	HC	G	XS
Extant— <i>Theropithecus gelada</i>	M	7	25.9	10.1	1.6	0	0.4	0	0
	SD		0.8	3.3		0		0	
Extant— <i>Lophocebus albigena</i>	M	5	11.6	40.6	2	5.4	0	4.3	0
	SD		1.5	4.4		1.8		2.2	
Extant— <i>Cercocebus atys</i>	M	7	10.8	31.9	2	3.7	0	3	0
	SD		2.2	2.7		1.3		0.6	
Extant— <i>Macaca mulatta</i>	M	5	11.7	38.5	2	4.3	0	1.9	0
	SD		1	2.6		0.8		1.1	
Extant— <i>Mandrillus sphinx</i>	M	5	15.4	20	2	0	0	3.8	0
	SD		0.7	1.3		0		0.9	
Fossil <i>Macaca cf. sylvanus</i>	M	2	16	28.5	1.5	4.5	0	4	0
	SD		4.2	3.5		0		0	

N, number of specimens; SD, standard deviation; M, mean; NS, average number of scratches; NP, average number of pits; SWS, scratch width score; PP, average number of puncture pits; HC, average number of hypercoarse scratches; G, average number of gouges; XS, average number of cross scratches; (Raw microwear data in [Supplementary Table 3](#)).

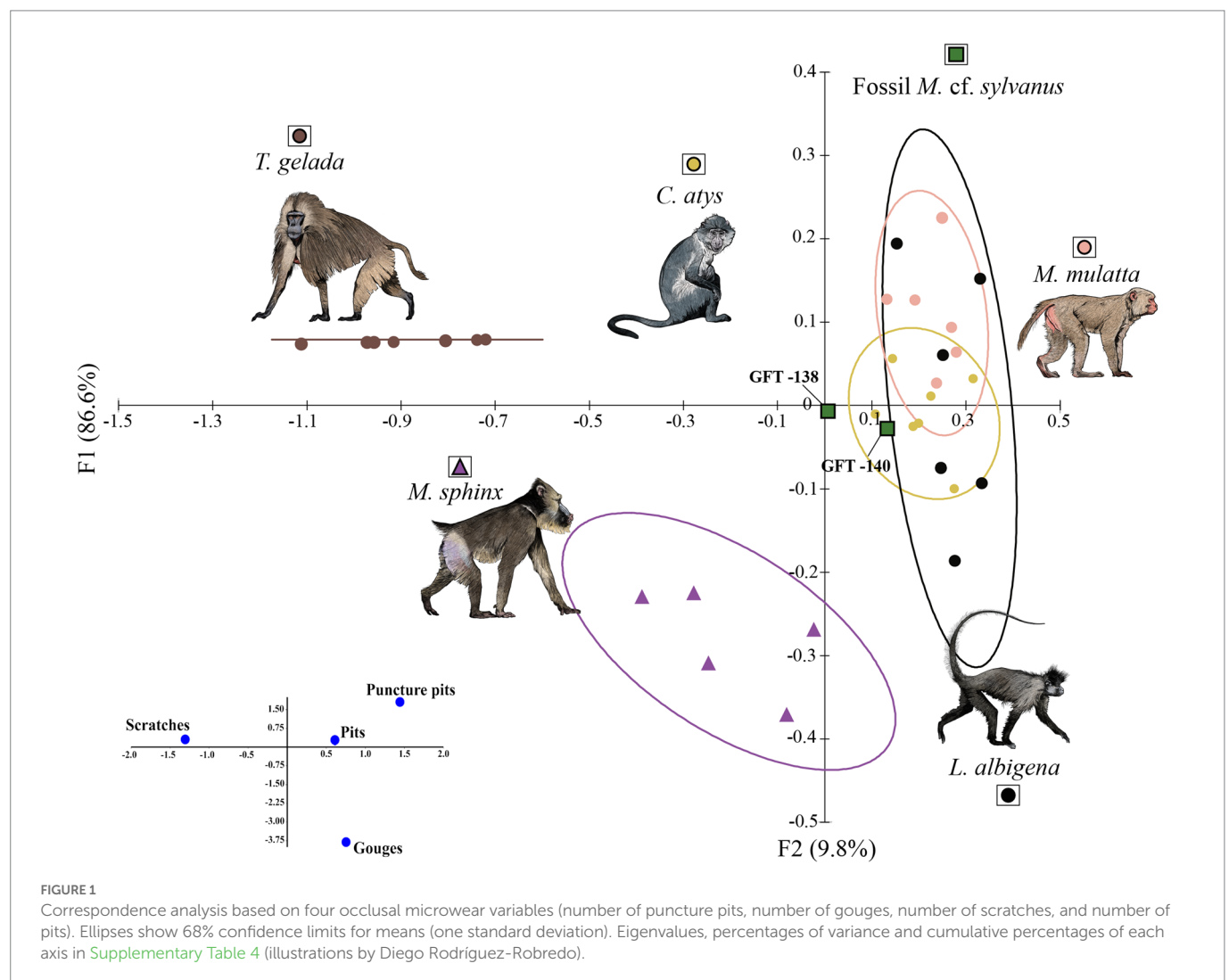
negatively correlated with the presence of gouges. GFT140 was classified as *C. atys* (99% of predicted classification probability) and GFT138 was classified as *L. albigena* (83% of predicted probability).

Buccal microtexture analysis

A total of 15 buccal enamel microtexture parameters out of the 38 (39.47%) showed significant differences (ANOVA and Tukey's HSD *post hoc* procedure $p < 0.05$ and Welch correction, see [Supplementary Table 7](#)) among the Cercopithecoidea species. The main significant differences are between the folivore-frugivore *M. mulatta* and the graminivorous *T. gelada* and the hard fruit eater *C. atys* and the folivore-frugivore *M. sphinx*. *T. gelada* mainly differentiate from *M. mulatta* in volume parameters, functional and flatness (V_v , V_{mc} , V_{vc} , S_{xp} , S_{mc} , $FLTp$, $FLTv$, and $FLTq$ $p < 0.05$) while the hard fruit eater differentiates from *M. sphinx* in spatial, feature and flatness parameters (Sal , Shv , $FLTp$, $FLTt$, $FLTv$, and $FLTq$; [Supplementary Figure 4](#)). No significant differences are found between hard fruit eaters taxa, the arboreal *L. albigena* and terrestrial *C. atys* and, only one difference was found between the hard fruit eaters and the graminivorous *T. gelada* (the feature parameter *Spc* between *L. albigena* and *T. gelada* $p < 0.05$).

The LDA includes the 15 parameters to classify the extinct GFT-4.2 samples. DF1 and DF2 account for the 82.51% of the total original variance (Wilks' $\lambda = 0.014$; $F = 1.371$; p -value = 0.143). DF1 (57.15%) is positively correlated with flatness and volume parameters and negatively with *Shv* (mean hill volume) DF2 (25.36%) was positively correlated with all the parameters except for *Spc* ([Figure 2](#); see [Supplementary Table 8](#) for the r values and significance). Overall, 86.21% of the teeth were correctly classified in their taxonomic category. Mixed feeders that incorporate more seeds and leaves compared to the other of species, such as *M. sphinx* and *M. mulatta*, have the highest loadings for DF2. Their buccal surfaces show the greatest texture relief, with sharp features and different slopes and heights compared to hard fruit eaters and *T. gelada*. *M. sphinx* and *M. mulatta* incorporate more seeds and leaves in their diets compared to the rest of species and their buccal surfaces show coarse features (high *Sal*) that is significantly flatter than *T. gelada* and *C. atys*. Moreover, *T. gelada* has the lowest loading for DF1, differing from *L. albigena*, because these features are rounded (lower *Spc*).

The extant LDA model have been used to predict group membership of the fossil specimens from GFT-4.2. GFT-137 is classified as *T. gelada* (74.9% of probability as *T. gelada* and 25.1% as



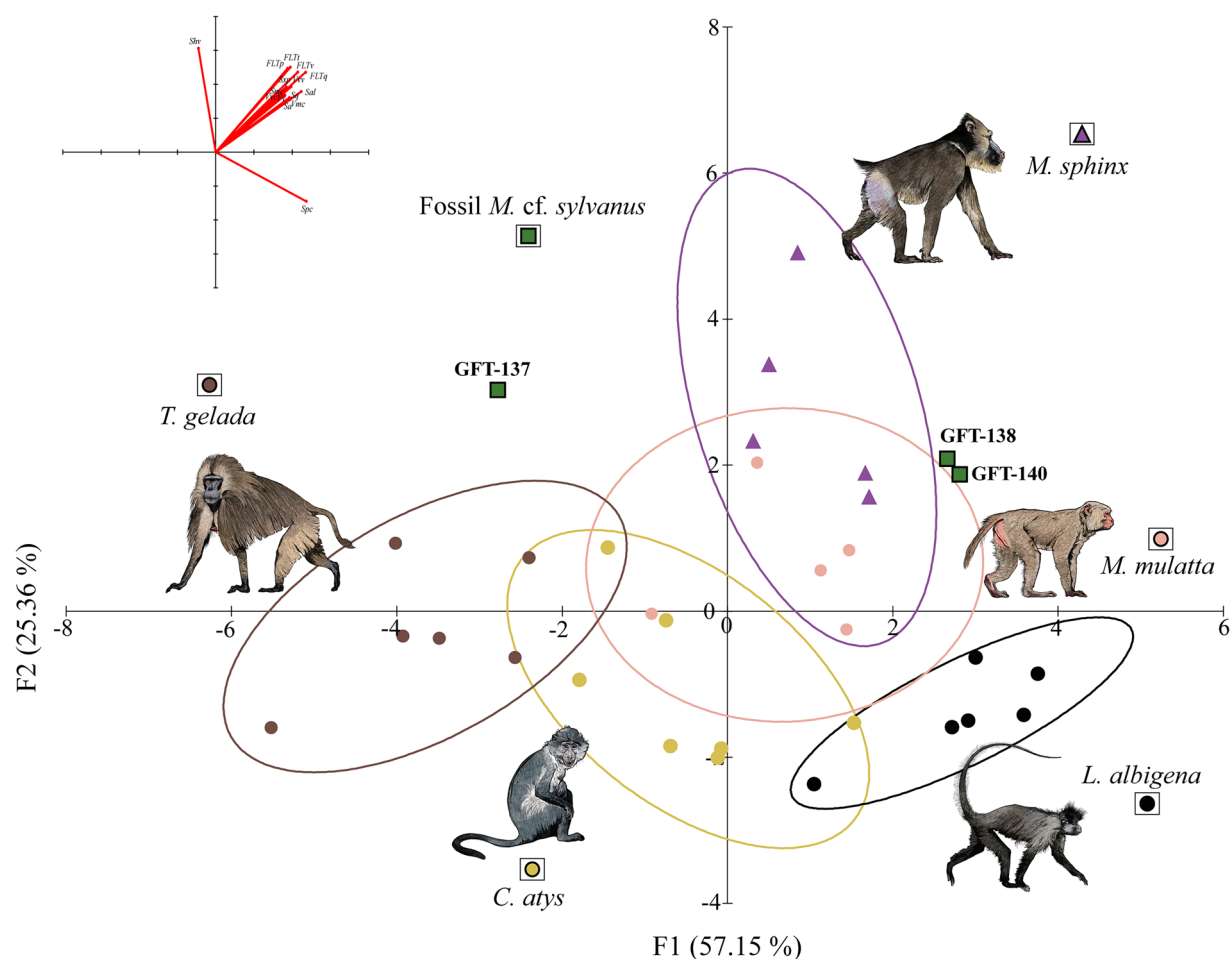


FIGURE 2

Plot of the two first discriminant functions (DF1-2) of buccal-dental microtextural parameters. Ellipses show 68% confidence limits for means (one standard deviation). On the top left are the loadings of the ISO texture parameters onto DFs. Raw data in [Supplementary Table 8](#) (illustrations by Diego Rodríguez-Robredo).

M. sphinx), GFT-138 (Figure 3) as *M. mulatta* (97.5% of probability) and GFT140 as *M. sphinx* (69.8% of probability as *M. sphinx* and 26.7% as *L. albigena*). The mean height, volume and flatness parameters of the three specimens from GFT-4.2 differ significantly ($p < 0.05$) from both *C. atys* and *T. gelada*, and were similar to folivores and seed eaters. Two GFT-4.2 specimens, therefore, resemble to primates that exploit seasonally leaves, fruits and seeds in major proportion, on the ground of mixed forest. GFT137, however, is classified as *T. gelada* a graminivorous primate that exploit also forbs in open ecosystems, due to similarities on buccal microtexture feature parameters.

Discussion

Our multiproxy analysis suggests a different short-term (occlusal) and long-term (buccal) feeding habits of *M. cf. sylvanus* from GFT-4.2, but with an overall dominance of abrasive, tough and brittle food items in an environment dominated by C_3 plants. The most commonly consumed foods would be fruit, seeds and leaves but also some grasses (Table 2). This dietary variety reflects the ability and flexibility of fossil macaques to consume different foods. As well as the richness of

resources, and probably microhabitats, present in the GFT-4.2 area during the Plio-Pleistocene.

Based on short-term resolution, the occlusal microwear analysis classifies the *M. cf. sylvanus* specimens (GFT138 and GFT140) as *L. albigena* and *C. atys*, which have a diet rich in hard fruit and seeds (Poulsen et al., 2001; Shah, 2003; Lambert et al., 2004; Daegling et al., 2011; McGraw et al., 2011, 2012, 2014). The extant *L. albigena* and *C. atys* species and the fossil *M. cf. sylvanus* have puncture pits and gouges, which is a distinctive microwear feature of hard-object feeders (Godfrey et al., 2004; Semperebon et al., 2004; Williams and Geissler, 2014). Both *Cercocebus* and *Lophocebus* have thicker enamel compared to other primate groups, which allows both genera to rely on hard foods throughout the year (McGraw et al., 2012). *Macaca cf. sylvanus* occlusal surfaces differs significantly from the extant *T. gelada*, which is characterized by an almost exclusively graminivorous diet with seasonal incorporation of forbs (Fashing et al., 2014; Jarvey et al., 2018). The occlusal microwear pattern of *T. gelada* is dominated by a high number of scratches and the absence of puncture pits and gouges. This surface is characteristic of animals with grass-dominated feeding habits (Godfrey et al., 2004; Semperebon et al., 2004). Even if it was not the dominant food item in their diet, we cannot exclude that *M. cf. sylvanus* consumed

some grasses due to the large number of scratches found in specimen GFT138.

Occlusal microwear and buccal microtexture analysis group fossil *M. cf. sylvanus* with different extant species, an outcome that is explained by differences in the temporal resolution and turnover of the analyzed tooth surfaces. Buccal microtexture analysis provides medium long-term, compared to occlusal microwear, from weeks to months (Romero et al., 2012) temporal resolution classifying two of the three *M. cf. sylvanus* specimens (GFT 138, and GFT 140) from GFT-4.2 as *M. sphinx* and *M. mulatta*. These species primarily consume fruits, leaves, and seeds in closed and riparian forests during the wet season, and seeds foraged from the ground year-round. The sample included in the present analysis comes from the population that inhabit Pakistan where *M. mulatta* rely primarily on leaves and fruits depending on their availability (Goldstein and Richard, 1989; Sengupta and Radhakrishna,

2016). Both taxa, therefore, consume abrasive items from the ground in mixed forest. *Mandrillus sphinx* and *M. mulatta* diet also includes herbs such as piths and blades and occasionally woody tissue during seasons of heightened fruit scarcity (Sengupta and Radhakrishna, 2016; Hongo et al., 2017). Based on observations of *M. sphinx* from Gabon, more seeds are consumed during the dry season than in the peak fruit season. Moreover, finely crushed seeds in fecal samples indicate that *M. sphinx* uses the occlusal surface to fracture seeds (Hongo et al., 2017), and this mechanical action correlates with gouges on these surfaces (Figure 3; Supplementary Figure 2). *M. sphinx* consumes large nuts, like *S. gabonensis*, during seasons of heightened fruit scarcity (Hongo et al., 2017). Hard items are consumed habitually by *L. albigena* and *C. atys* year-round (McGraw et al., 2012). The microtexture buccal pattern of *M. sphinx*, characterized by higher relief, with peaks and dales and coarse features compared with the rest of analyzed species, may correlate with the presence of more abrasive fractured seeds or phytoliths from the leaves that are processed in the oral cavity while being fractured along occlusal surfaces. The similarity in the microtexture pattern of the two GFT-4.2 specimens with *M. sphinx* and *M. mulatta* suggests that *M. cf. sylvanus* regularly consumed abrasives food items. The LDA of the buccal microtexture plot two specimens (GFT138 and GFT140) close to each other and to the hard fruit eaters (Figures 1,2). All these species rely on hard-shelled fruits and seeds with seasonal fluctuations. Specially, *M. mulatta* diet resembles *M. sphinx* (Sengupta and Radhakrishna, 2016) with more soft fruit ingestion in the former. Both *M. mulatta* and *M. sphinx* incorporate hard and brittle dietary resources but, this is dependent on fruit availability during the year (Sengupta and Radhakrishna, 2016). When fruit is scarce, *M. mulatta* relies heavily on seeds. However, the buccal microtexture pattern of the GFT137 is also similar to *T. gelada* (Figure 2). *Theropithecus gelada* is a graminivorous primate that inhabit the open highlands of Ethiopia and consume grasses and forbs (Jarvey et al., 2018; Souron, 2018).

Three out of four extant species in which the microwear classifies the macaque of GFT-4.2 are species whose diet is related to the presence of trees. In this sense, oxygen values could also reinforce this link. The four *M. cf. sylvanus* specimens (GFT137, GFT138, GFT139, and GFT140) from GFT-4.2 show high $\delta^{18}\text{O}$ values compared with the contemporary ungulates recovered from the same site. The same pattern occurs with other fossil cercopithecines (*T. atlanticus* and *T. oswaldi*) from North Africa (Figure 4). Extant *M. sylvanus* are highly adaptable and have an eclectic diet which adds to the variables that can affect their oxygen isotope values. A significant amount of their water ingestion comes from leaf, fruit and vegetable consumption, especially during the rainy season. Meanwhile, during the dry season, they drink more water from open water sources (Fooden, 2007). In the case of *M. cf. sylvanus*

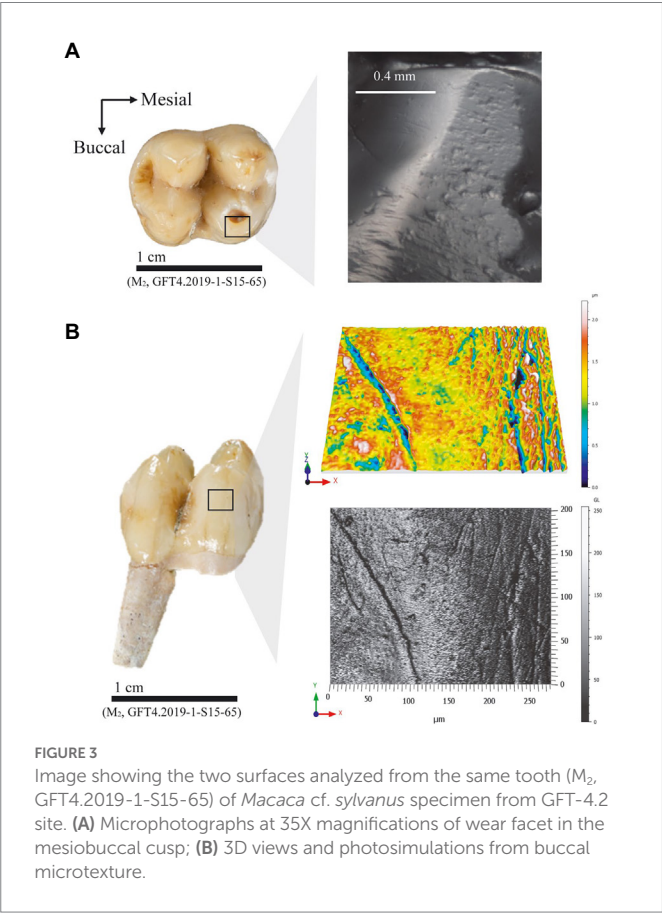


FIGURE 3
Image showing the two surfaces analyzed from the same tooth (M₂, GFT4.2019-1-S15-65) of *Macaca cf. sylvanus* specimen from GFT-4.2 site. (A) Microphotographs at 35X magnifications of wear facet in the mesiobuccal cusp; (B) 3D views and photosimulations from buccal microtexture.

TABLE 2 Summary of the results provided by the three methods used to reconstruct the diet and habitat of *Macaca cf. sylvanus* from GFT-4.2.

Methods	Diet and habitat reconstruction	Timescales
$\delta^{13}\text{C}$ values	C ₃ resource-based diet. Woodland ecosystem.	The first ~4 years of life. Possible nursing signal: M ₁ Post-weaning: I ¹ , M ₂ , M ₃
$\delta^{18}\text{O}$ values	Folivore-frugivore foraging in the canopy (Woodland).	The first ~4 years of life. Possible nursing signal: M ₁ Post-weaning: I ¹ , M ₂ , M ₃
Buccal microtexture	Folivore-frugivore with hard item consumption and some grass intake (Similar to extant <i>Mandrillus sphinx</i> , <i>Macaca mulatta</i> , and <i>Theropithecus gelada</i>).	Toward the end of the animal's life (Long-term/weeks to months)
Occlusal microwear	Hard-fruit eater with leaf and seed intake (Similar to extant <i>Lophocebus albigena</i> and <i>Cercocebus atys</i>).	Toward the end of the animal's life (short-term/last days)

The timescale represented by the enamel isotopic signature has been defined following the work of dental development in the species *Macaca nemestina* (Siriani and Swindler, 1985) and the weaning period defined for *M. mulatta* (Reitsema et al., 2015).

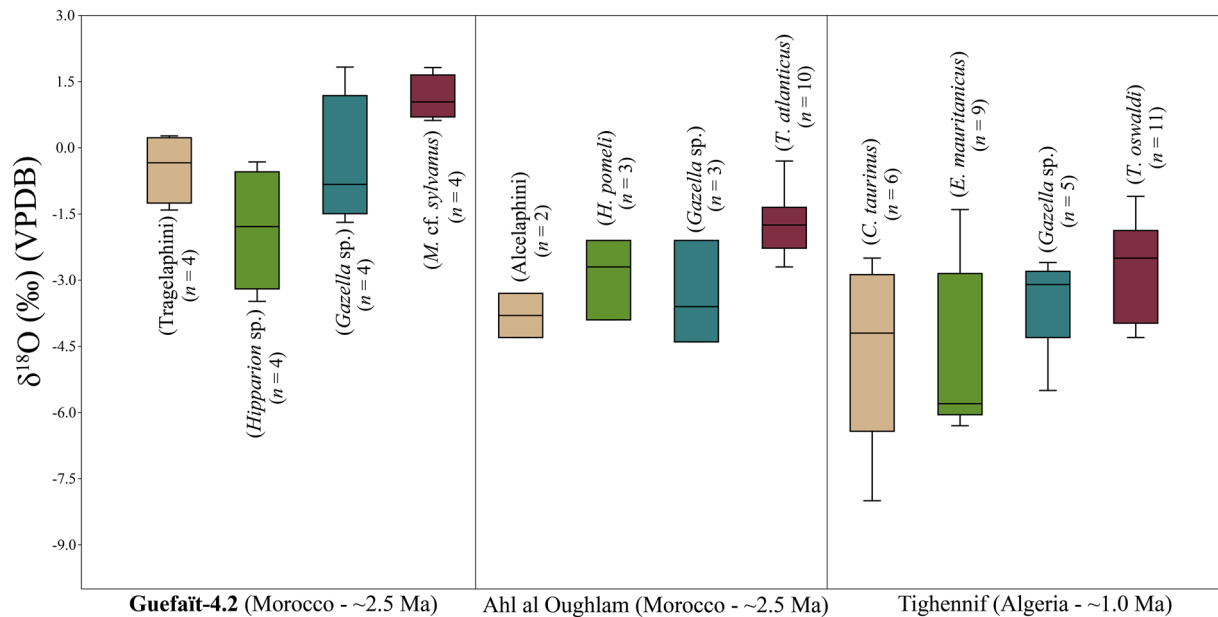


FIGURE 4

Box plots for $\delta^{18}\text{O}$ values of *Macaca cf. sylvanus*, *Hipparion* sp., *Gazella* sp. and *Tragelaphini* from GFT-4.2 in comparison with extinct *Theropithecus* and ungulates from the Plio-Pleistocene sites of Ahl al Oughlam and Tighennif in North Africa published in Fannin et al. (2021). The boxes show the median and the lower (25%) and upper (75%) quartiles.

from GFT-4.2, the differences in oxygen values in relation to contemporary ungulates could be associated with differential access to and consumption of certain food resources by the primates, such as fresh fruits and leaves from trees. Sun-exposed leaves, especially in arid conditions, are particularly sensitive to evaporative fractionation that could lead to ^{18}O enrichment (Gonfiantini et al., 1965; Barbour, 2007; Crowley et al., 2015; Carter and Bradbury, 2016; Fannin and McGraw, 2020). Other authors argue that this enrichment by evapotranspiration also occurs in other parts of the plant like fruits (Yakir, 1997; McCarroll and Loader, 2004). Paleoenvironmental data of GFT-4.2 based on the study of paleoherpetological and small mammal records, suggest dry conditions in an open woodland habitat with a permanent water body nearby (Agustí et al., 2017; Piñero et al., 2019; Alba et al., 2021).

Considering that aridity affects all GFT-4.2 taxa, we suggest that the oxygen enrichment of *M. cf. sylvanus* may be due to the ingestion of some different foods. An example in extant primates is the one exposed by Moritz et al. (2012) that measured the $\delta^{18}\text{O}_{\text{hair}}$ from two baboon species (*Papio anubis* and *Papio hamadryas*) which inhabit the arid hybrid zone of Awash National Park (Ethiopia). The diets of the two species in this area are similar and both obtain their meteoric water from the same source (Awash River). However, the oxygen values of *P. hamadryas* are relatively enriched due to the ingestion of a greater proportion of ^{18}O -enriched leaf water in the arid thornbush. Krigbaum et al. (2013) show how $\delta^{18}\text{O}_{\text{ap}}$ values of different cercopithecids covary depending on foraging position in the closed tropical canopy forest (Taï forest, Côte d'Ivoire). Higher humidity on the forest floor is associated with low $\delta^{18}\text{O}_{\text{ap}}$ values, with enrichment of ^{18}O observed along a vertical gradient. The *C. atys* exhibits low $\delta^{18}\text{O}_{\text{ap}}$ values relative to guenons and colobines, which reflects the *C. atys* terrestrial foraging habits. Although we do not have a tropical canopy forest in GFT-4.2, these differences in $\delta^{18}\text{O}$ values between feeding on the ground and in the upper parts of the tree could explain the ^{18}O enrichment of macaques compared to ungulates.

The ^{18}O enrichment points to a diet based on tree foraging in a forest ecosystem. These findings are consistent with the microtexture and low magnification signals and support the carbon isotope results of *M. cf. sylvanus* from GFT-4.2. The $\delta^{13}\text{C}$ values indicate consumption of C_3 plants (i.e., trees, shrubs, fruit/seeds, and C_3 -grass adapted to a mild growth season). *M. cf. sylvanus*, *Hipparion* sp., *Gazella* sp. and *Tragelaphini* from GFT-4.2 have been compared with the fossil *T. atlanticus* from Ahl al Oughlam, Morocco (ca. 2.5 Ma) and *T. oswaldi* from Tighennif, Algeria (ca. 1 Ma) and other ungulates from the same sites (Fannin et al., 2021; Figure 5; Supplementary Table 2). The *M. cf. sylvanus* ($n = 4$) mean is $-12.3 \pm 0.3\text{‰}$, the *T. atlanticus* ($n = 10$) mean is $-12.4 \pm 0.8\text{‰}$, and the *T. oswaldi* ($n = 11$) mean is $-11.3 \pm 1.9\text{‰}$ (Figure 5). These three fossil species show similar median carbon values and no consumption of C_4 plants. Except for one individual of *T. oswaldi* from Tighennif with a $\delta^{13}\text{C}$ value of -5.9‰ that includes some C_4 plant consumption.

Our data differ from the mean $\delta^{13}\text{C}$ values of $1.9 \pm 1.8\text{‰}$ ($n = 49$) from Plio-Pleistocene fossils of *Theropithecus* from Eastern Africa, 3.5 to 1.5 Ma. In Southern Africa, *Theropithecus* living 2.8 and 1.6 Ma have mean value of $-2.4 \pm 1.4\text{‰}$ ($n = 13$). In both areas, these species indicate a strongly C_4 -based diet composed mostly of grasses (Cerling et al., 2011; Souron, 2018), especially after the 2 Ma (Figure 6). The carbon values of *M. cf. sylvanus* from GFT-4.2 are similar to the $\delta^{13}\text{C}$ values of C_3 consumers *Papio* (2.1 to 1.6 Ma; $-9.8 \pm 2.3\text{‰}$; $n = 26$), *Parapapio* (2.8 to 1.7 Ma; $-8.4 \pm 2\text{‰}$; $n = 38$), and *Cercopithecoides* (2.8 to 1.7 Ma; $-9.8 \pm 3.6\text{‰}$; $n = 12$) from the Plio-Pleistocene of Southern Africa (Figure 6; Lee-Thorp et al., 1989; Codron et al., 2005). The largest proportion of Southern African cercopithecids fall into the C_3 – C_4 mixed feeders' area, suggesting a consumption of some C_4 plants (Figure 6). Cercopithecids with carbon values resembling those of GFT-4.2 macaques are the *Cercopithecoides haasgati* (2.1 Ma; $-12.3 \pm 1.4\text{‰}$; $n = 2$) from Haasgat HGD, *Papio robinsoni* (1.85 Ma; $-11.2 \pm 0.9\text{‰}$; $n = 5$) and *Parapapio jonesi* (1.85 Ma; $-11.2 \pm 2.3\text{‰}$; $n = 2$) from Swartkrans (Figure 6). The $\delta^{13}\text{C}$ values of *C. haasgati* could

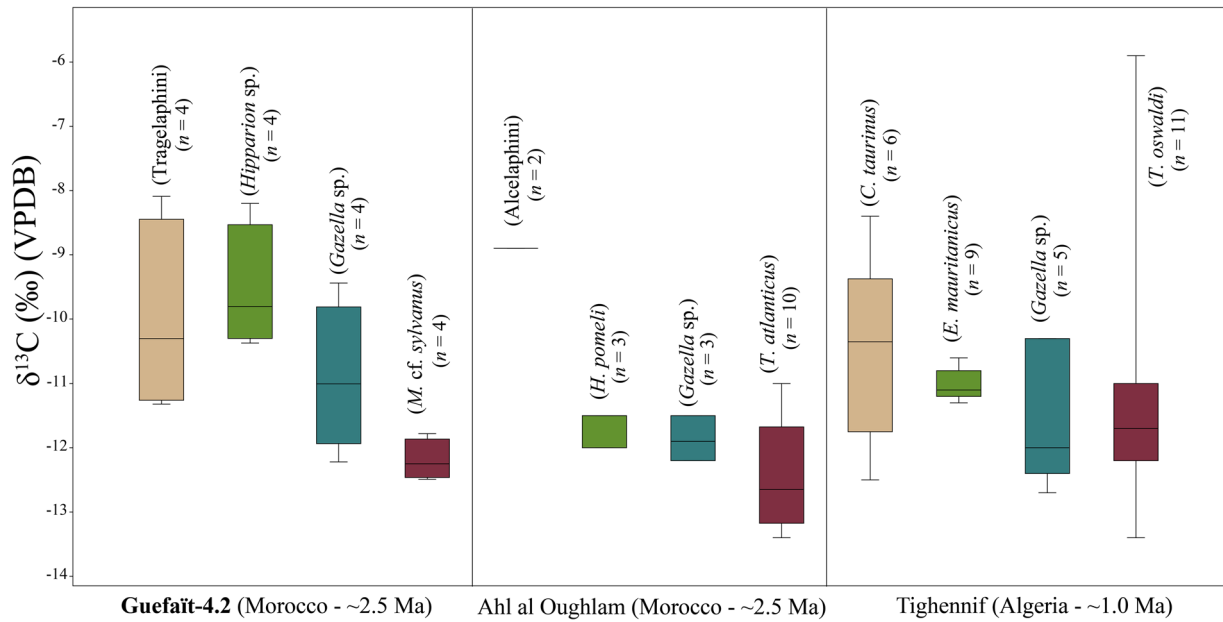


FIGURE 5
 Box plots for $\delta^{13}\text{C}$ values of *Macaca cf. sylvanus*, *Hipparion* sp., *Gazella* sp. and *Tragelaphini* from GFT-4.2 in comparison with extinct *Theropithecus* and ungulates from the Plio-Pleistocene sites of Ahl al Oughlam and Tighennif in North Africa published in Fannin et al. (2021). The boxes show the median and the lower (25%) and upper (75%) quartiles.

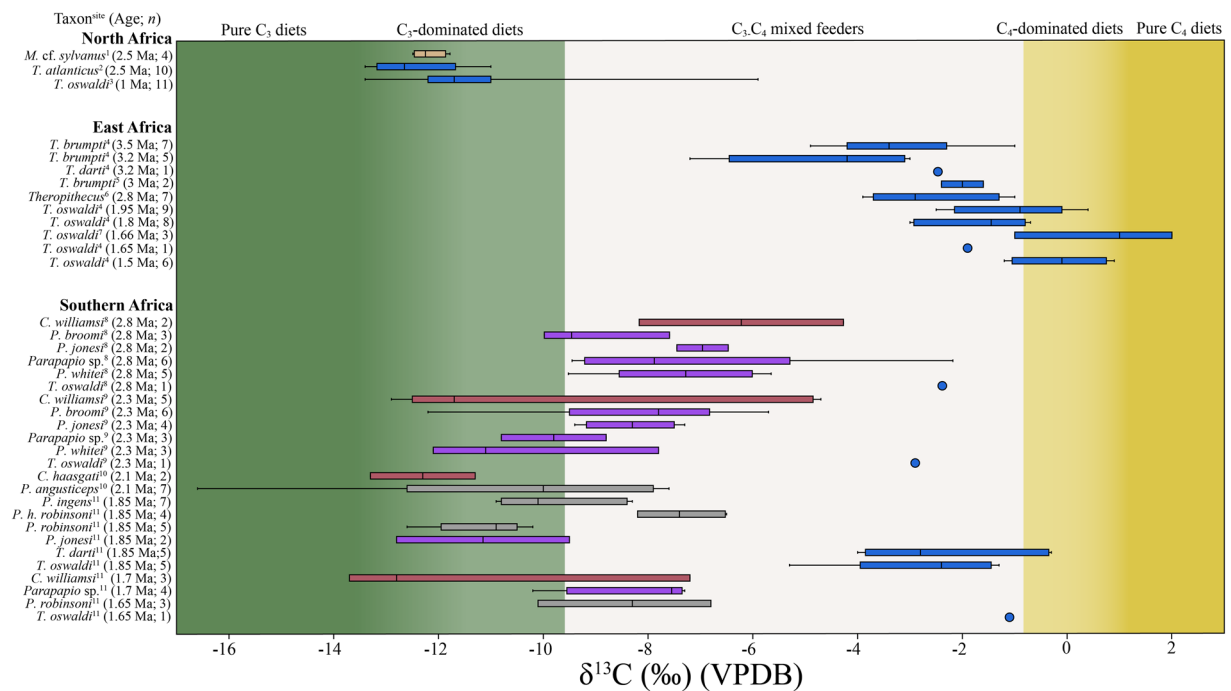


FIGURE 6
 Box plots comparing the $\delta^{13}\text{C}$ values of Plio-Pleistocene fossil cercopithecids (3.5 to 1 Ma) from North Africa (data from this study and Fannin et al., 2021). Sites: 1=Guefai 4.2; 2=Ahl al Oughlam; 3=Tighennif, East Africa [data from Levin et al. (2015), Robinson et al. (2017), and Uno et al. (2018)]. Sites: 4=Koobi Fora, East Turkana; 5=Nachuki, West Turkana; 6=Ledi-Geraru, Gurumaha; 7=Bed II, Olduvai and Southern Africa [data from Levin et al. (2015)]. Sites: 8=Makapansgat, 3 and 4; 9=Sterkfontein; 10=Haasgat HGD; 11=Swartkrans. The boxes show the median and the lower (25%) and upper (75%) quartiles. The colors of the box plots represent the different genus (beige for *Macaca*, blue for *Theropithecus*, red for *Cercopithecoides*, purple for *Parapapio*, and gray for *Papio*).

indicate a preference toward food sources associated with closed woodland environments (Adams et al., 2013). This interpretation is consistent with the carbon values of all of them, including the fossil macaque. Feeding habits of *P. robinsoni* and *P. jonesi* from Swartkrans have been reconstructed as a frugivore-folivore on the basis of cusp form (Benefit, 2000). We also propose this using the occlusal and buccal microwear for *M. cf. sylvanus* from GFT-4.2, although the exploitation of grasses and forbs in a more open habitats cannot rule out due to the buccal microtexture pattern of GFT137 and the high number of scratches on the occlusal surface of GFT138. Carbon isotopic signal of the *Macaca* from GFT-4.2 would indicate that these consumed grasses would be C_3 . Consumption of C_3 grasses has also been identified in the diet of *T. oswaldi* from the Plio-Pleistocene site of Ahl al Oughlam (Morocco), as well as in extant *T. gelada* at Guassa Plateau (Ethiopia; Fannin et al., 2021).

The microwear analysis shows that the diet of the fossil macaque is close, among others, to that of extant *M. sphinx*, *L. albigena*, and *C. atys*, species that live in dense tropical forests. Isotopic studies on extant *M. sphinx* and *C. atys* have shown carbon values strongly affected by canopy effect. According to Oelze et al. (2020), the $\delta^{13}C$ values of *M. sphinx* hair sections from Gabon are within the range ($-25.1\text{‰} \pm 0.3\text{‰}$) of those obtained from the hair of chimpanzees and gorillas in Loango National Park. Like these species, mandrills live in dense forest habitats. Another study by Krigbaum et al. (2013) on bone apatite from seven sympatric cercopithecine species, including *C. atys*, in the Taï forest (Côte d'Ivoire) obtained carbon values range between -19.9‰ and -17.9‰ for all species. In contrast, the carbon values of *M. cf. sylvanus* from GFT-4.2 ($-12.3 \pm 0.3\text{‰}$) do not correspond to those of a species foraging in a closed canopy forest. Considering the enamel-diet enrichment factor for primates ($+11.8 \pm 0.3\text{‰}$; Malone et al., 2021) and the cutoff of -30‰ ($\delta^{13}C_{CO_2}$ corrected by $\sim +1.5$) for closed-canopy forests (Kohn, 2010), the $\delta^{13}C$ values of tooth enamel for a diet in a closed-canopy forest should be lower than $\sim -18\text{‰}$ for fossil *Macaca*. The carbon values of the taxa analyzed are compatible with an open woodland. This is in line with the paleoherpetological and small mammal work in which taxa characteristic of open woodland have been defined (Agustí et al., 2017; Piñero et al., 2019).

The use of these three methods has allowed us to produce a paleodietary reconstruction at different times in the life of the individuals, although we cannot discard that the analyzed molars belong to the same specimen. The isotopic signal, corresponding to approximately the first 4 years of life, is in agreement with the data of the two dental microwear proxies in the diet-tree relationship for *M. cf. sylvanus*, and the absence of C_4 typical of open grassland. Buccal and occlusal microwear turnover is a dynamic process; however, the buccal signal is more stable in the long term and may indicate the diet consumed year-round (Romero et al., 2012). Whereas the low magnification occlusal microwear results may indicate the consumption of hard fruit and seeds similar to mangabeys the last days or weeks prior to death (Semperebon et al., 2004), perhaps representing the diet of a single season. The buccal microtexture analysis suggest that the abrasiveness of their diet was similar to primates (*M. sphinx* and *M. mulatta*) that consumes hard, tough, and brittle food items year round with the incorporation of leaves, and the consumption of grasses as *T. gelada* does. The complementarity of these proxies helps to differentiate between seasonal, short-term durophagous species from those that exploit tough and brittle items actively in a long term, broadening the dietary range of consumed resources throughout the year.

Conclusion

Our research represents the first report related to the feeding ecology of fossil *Macaca* during the Plio-Pleistocene in Africa. Our results highlight a tight correlation between the fossil *M. cf. sylvanus* specimens from GFT-4.2 and extant primates with a predominant abrasive, tough and brittle food items. Evidence from the multiproxy analysis suggests that the macaques foraged for food in a wooded habitat, but also foraging in more open environments. The versatility of macaques to occupy wide habitat ranges makes them a useful candidate for analogies with hominins and for understanding how they adapted to different environments. Evidence of early hominins in North Africa is dated close to the Plio-Pleistocene boundary (ca. 2.4 Ma) at the Ain Boucherit site in Algeria. The ecological context of this first human population is a key question to understand the dispersions of humans and other mammals in these territories. Considering the proximity of GFT to Ain Boucherit, understanding the feeding ecology of *M. cf. sylvanus* from GFT may provide clues about some of the ecological resources that these early humans may have had. This initial investigation is only one step toward understanding the feeding habits of *M. cf. sylvanus*. More data are needed from additional individuals to be able to confidently interpret foraging ecology of this species.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding authors. The surface data are available from the corresponding author upon reasonable request.

Author contributions

IR-P, LM, FR, CT, and FE-S conceived and designed this research. IR-P and LM performed the laboratory analyses and collected and analyzed the data. JI provided access to the laser scanning confocal microscope. AA, AR-H, JM, HA, AO, HH, IR-P, HM, MS, RS-R and MC participated in the fieldwork and provided materials and background for the research. MC, RS-R, and HA are in charge of the project administration and the funding acquisition. AR-H supervised the excavation. AR-H, HA, and JM identified the faunal remains. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1011208/full#supplementary-material>

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5.1.3. *Oued Rabt*

5.1.3.1. Plant wax biomarkers analysis

Plant wax biomarker distributions are dominated by odd-numbered, higher chain lengths, indicating a terrestrial plant wax source in most samples (i.e., C₃₁, C₂₉). Most samples, however, also contain odd-numbered, mid-chain length *n*-alkanes (i.e., C₂₁), indicative of emergent plants (**Fig. 25**).

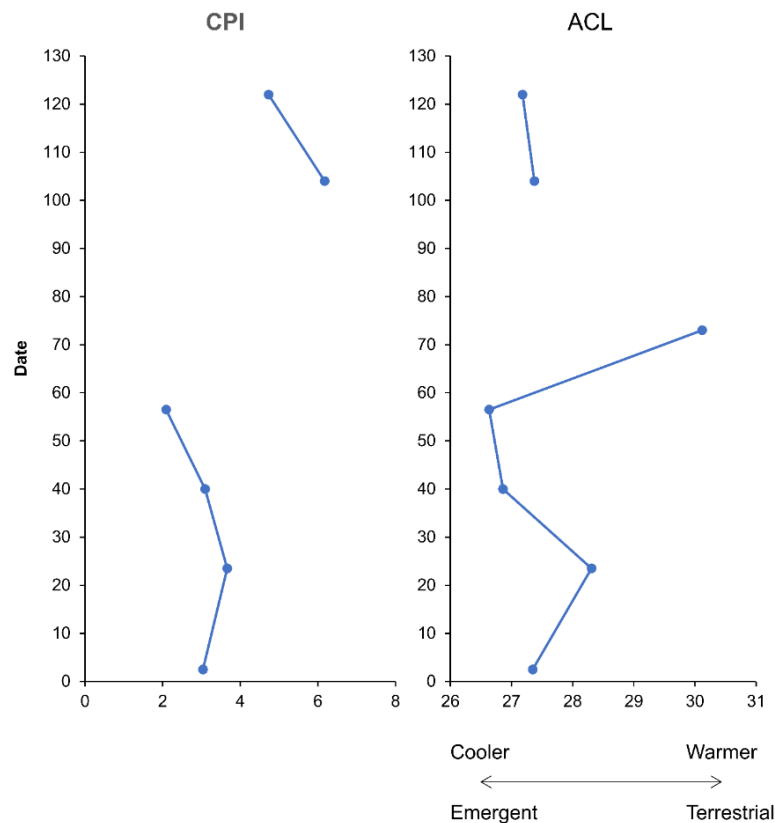


Figure 25. Carbon preference index (CPI) for OR 01, OR 02, OR 03, OR 04, OR 07 and OR 08 samples, and average chain length (ACL) for OR 01, OR 02, OR 03, OR 04, OR 05, OR 07 and OR 08 samples.

This likely suggests a growing environment near shore or along stream channels. The average chain length (ACL₂₁₋₃₃) ranges from 26.63 to 30.12 (27.69 ± 0.5 , $n = 7$), consistent with previous reports of modern ACL from African terrestrial plants (Dodd and Poveda, 2003; Carr et al., 2014; Bush and McInerney, 2015). The carbon preference index (CPI) of the C₂₁-C₃₃ *n*-alkanes ranges between 2.09 and 6.17 (3.80 ± 0.6 , $n = 6$) (**Fig. 25**). These values are typical of plant-derived CPI values (Bray and Evans, 1961; Castañeda and Schouten, 2011; Diefendorf et al., 2011; Jaeschke et al., 2018) and indicate that no significant plant wax degradation occurred (Duan and Xu, 2012; Jha et al., 2024). The aquatic plant (P_{aq}) value ranges between 0.00 and 0.2, while the submerged/terrestrial

ratio (STR) ranges between 0.0 and 0.07, trending with the P_{aq} values (**Fig. 26**). Both these metrics likely suggest an overlap in terrestrial and emergent plant wax sources (**Fig. 27**) and may reflect variability in inputs from both terrestrial (C_{29} , C_{31}) and emergent plants (C_{21} - C_{25}) (Ficken et al., 2000; Liu and Liu, 2017). Average chain length (ACL) is another metric used as a vegetation proxy because it has been shown to be higher in C_4 grasses (Rommerskirchen et al., 2006) but also correlates with higher growing season temperature and aridity (Dodd and Poveda, 2003; Castañeda et al., 2009; Duan and He, 2011; Bush and McInerney, 2015). ACL due to the relative increase in C_{21} and C_{22} in OR 01, OR 03 and OR 04 samples, could indicate greater water availability, promoting the growth of emergent plants. This is supported by the STR and P_{aq} , which also suggest inputs from emergent and terrestrial plants.

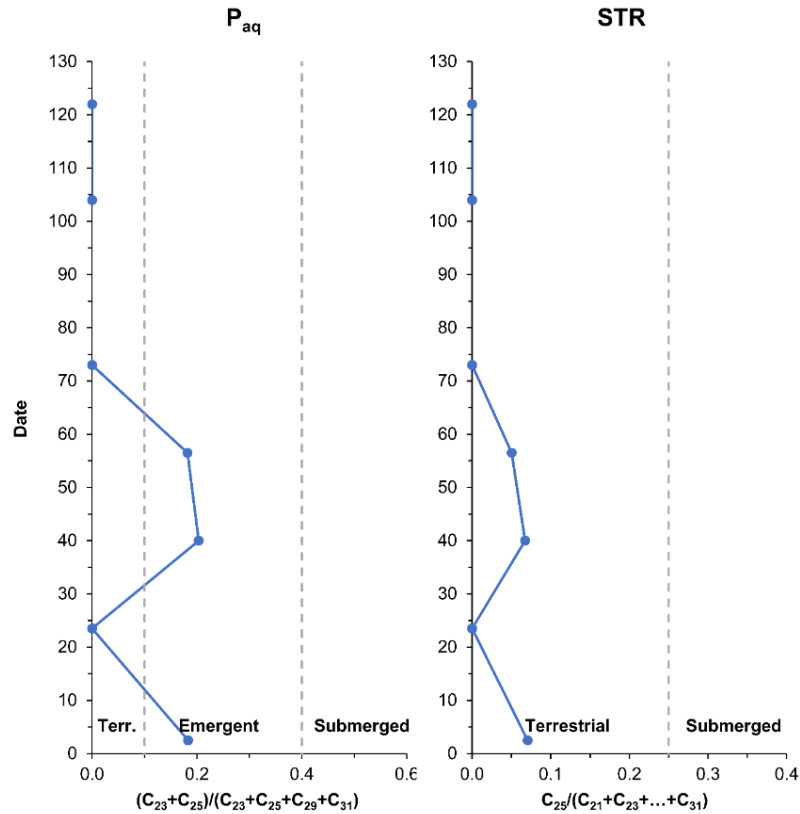


Figure 26. Submerged/terrestrial ratio (STR) and Aquatic Plant Ratio (P_{aq}) of OR samples (OR 01 to OR 05 samples).

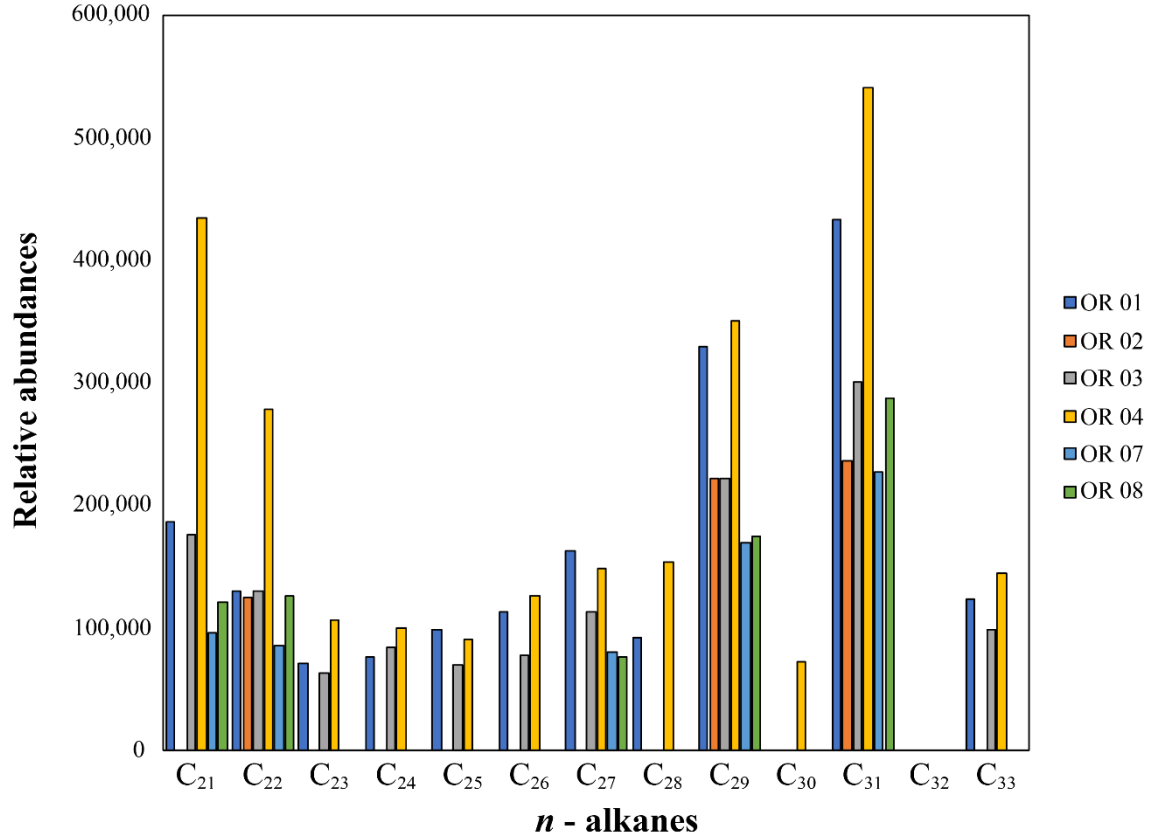


Figure 27. Relative abundances of *n*-alkanes in OR samples.

5.2. Western Morocco

5.2.1. Paper III: Ramírez-Pedraza et al. (2023). Palaeoecological reconstruction of Plio-Pleistocene herbivores from the Ahl al Oughlam site (Casablanca, Morocco): Insights from dental wear and stable isotopes. Quaternary Science Reviews (Published).



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Palaeoecological reconstruction of Plio-Pleistocene herbivores from the Ahl al Oughlam site (Casablanca, Morocco): Insights from dental wear and stable isotopes

Iván Ramírez-Pedraza^{a,b,c,*}, Florent Rivals^{a,b,d}, Carlos Tornero^{e,a}, Denis Geraads^f, Jean Paul Raynal^{g,h}, David Lefèvreⁱ, Abderrahim Mohib^{h,j}

^a Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain

^b Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain

^c IsoTROPIC Research Group, Max Planck Institute of Geanthropology, Jena, Germany

^d Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain

^e Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain

^f CR2P-UMR 7207, CNRS, MNHN, Sorbonne Université, Paris, France

^g Université de Bordeaux, CNRS, UMR 5199 PACEA, Pessac Cedex, France

^h Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco

ⁱ Université Paul Valéry Montpellier 3, CNRS, LabEx ARCHIMEDE and UMR 5140 Archéologie des Sociétés Méditerranéennes, Campus Saint Charles, Montpellier, France

^j Direction Provinciale de la Culture, Avenue Mohammed V, Quartier Administratif, Kénitra, Morocco

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ABSTRACT

In this article, we use a multiproxy approach based on stable isotope analyses ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$), mesowear, and microwear dental analysis to reconstruct the climate, diet, and habitat of Plio-Pleistocene herbivores at the site of Ahl al Oughlam in western Morocco. This study has been conducted on teeth from several taxa (*Sivatherium maurusium*, *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., *Alcelaphini* and *Anancus osiris*), enabling a robust ecological reconstruction. Our isotopic results suggest a predominance of C_3 plant consumption for all analyzed species, while dental wear indicates a varied diet, with evidence for both browsing and grazing behavior being present. The combination of proxies indicates a landscape dominated by open C_3 grasslands in an arid climate, as supported by the Mean Annual Precipitation (MAP) results. These findings contribute to the ongoing debate on the ecological context that facilitated the Plio-Pleistocene dispersal, occupation, and evolution of mammals and hominins in northern Africa, for which limited information is available.

1. Introduction

1.1. The archaeopaleontological context during the Plio-Pleistocene in North Africa

The richness and diversity of mammalian fossil remains in the Maghreb during the Late Pliocene and Early Pleistocene (Geraads, 2002; Raynal et al., 2002; Sahnouni and Van der Made, 2009; Sahnouni et al., 2011; Van der Made et al., 2021) provides evidence that the Sahara Desert was not always a natural barrier for mammals in the past. The region experienced multiple green and humid phases, known as Green Sahara periods (GSPs), over millions of years, including the

Plio-Pleistocene. During these events, the present desert area consisted of river basins and extensive lakes (Van Zinderen Bakker, 1962; Larrasoana et al., 2003, 2013; Castañeda et al., 2009; Grant et al., 2017, 2022; Larrasoana, 2021). These environmental conditions would have facilitated episodes of mammalian dispersal from sub-Saharan locations to the north of Africa (Geraads, 2010; Zouhri et al., 2017; Van der Made et al., 2021).

To date, the oldest artifacts and stone tool-cut marked bones in North Africa associated with the presence of hominins have been found at the site of Aïn Boucherit (~1.9 and ~2.4 Ma) in the Beni Fouda intramontane basin in northeast Algeria (Sahnouni et al., 2018; Duval et al., 2021). In the same area, Acheulean technology has been described at the

* Corresponding author. Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain.

E-mail address: ramirezpedrazaivan@gmail.com (I. Ramírez-Pedraza).

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sites of Aïn Hanech and El Kherba (~1.8 Ma) (Sahnouni et al., 2002, 2012, 2017; Parés et al., 2014; Duval et al., 2021, 2023; Van der Made et al., 2021). In the Constantine Basin (Algeria), biochronologically close to Aïn Hanech, is the little-known site of Mansourah, with abundant faunal remains and bifacial artifacts associated with the Oldowan industry (Thomas, 1884, 1886; Chaid-Saoudi et al., 2006; Sahnouni and Van der Made, 2009) and the palaeontological site of Aïn Jourdel (~2.5 Ma) (Thomas, 1884, 1886; Duval et al., 2021). The oldest human remains have been found in western Algeria at Tighennif, also called Ternifine, ~1 Ma (Arambourg and Hoffstetter, 1963; Geraads et al., 1986; Bocherens et al., 1996; Geraads, 2016; Van der Made et al., 2021). In western Morocco, near Casablanca, the earliest archaeological sites date back to the Early and Middle Pleistocene (Raynal et al., 2001, 2002, 2017; Mohib et al., 2019; Gallotti et al., 2022). Up to now, the oldest site with human presence corresponds to unit L of Thomas Quarry I and its abundant ancient Acheulean lithic tools (~1.3 Ma) (Raynal and Texier, 1989; Gallotti et al., 2020, 2021, 2023). The former Thomas III Quarry, in which *Homo* remains were found (Ennouchi, 1975; Geraads et al., 1980, 2022a and b; Raynal, 2021) was renamed Oulad Hamida 1 Quarry when the *Grotte des Rhinocéros* (~0.7 Ma) was discovered and yielded a single *Homo* remain associated with stone tools and fauna (Raynal et al., 1993, 2023b; Rhodes et al., 2006; Daujeard et al., 2012, 2020; Raynal and Mohib, 2016; Gallotti et al., 2022). In Thomas Quarry I, above level L, is located the Hominid Cave (~0.5/0.7 Ma), where early *Homo* remains on the Atlantic shore were discovered (Ennouchi, 1975; Geraads et al., 1980, 2022a; Raynal et al., 2010, 2023a; Daujeard et al., 2016, 2020; Raynal, 2021). On the outskirts of Casablanca sits the site of Ahl al Oughlam (AaO), the richest Neogene faunal site in North Africa dated to ~2.5 Ma (Raynal et al., 1990; Geraads, 2006; Geraads et al., 2010, 2022b) and whose ecological context is investigated in this work.

In eastern Morocco, close to the Algerian border in the Aïn Beni Mathar–Guefaït area (Jerada province), several sites have been discovered and excavated since 2006: the Early Pleistocene sites of Aïn Tabouda, Gara Soultana and Charchara 1 with Mode 1 lithic tools, and the Middle Pleistocene site of Oued Rabt with Mode 2 lithic tools (Sala-Ramos et al., 2022). The oldest site, although palaeontological, is Guefaït. This one is biochronologically located at the Plio-Pleistocene boundary (~3–2.5 Ma; Parés et al., 2023), contemporaneous with Ahl al Oughlam, and contains a large diversity of taxa in its fossiliferous levels (Sala-Ramos et al., 2017, 2022; Aouraghe et al., 2019; Piñero et al., 2019; Alba et al., 2021; Madurell-Malapeira et al., 2021; Ramírez-Pedraza et al., 2023).

Work based on palaeoecological reconstructions are underrepresented in North Africa, despite the abundance of archaeopalaeontological sites found from the Late Pliocene to the Early Pleistocene in this territory. In Morocco, the studies published to date are focused on the palaeoecology of the Plio-Pleistocene primates of Ahl al Oughlam (*Theropithecus*; Fannin et al., 2021) and Guefaït-4.2 (*Macaca*; Ramírez-Pedraza et al., 2023). In Algeria, there are more extensive studies available, such as the analysis of carbon and oxygen stable isotopes in herbivores from Tighennif (~1 Ma) (Bocherens et al., 1996; Fannin et al., 2021), and the research based on stable isotopes of pedogenic carbonates from El Kherba (~1.8 Ma) (Sahnouni et al., 2011). However, there still remains a knowledge gap in this area regarding the reconstruction of habitats at the Plio-Pleistocene boundary. This contrasts with the numerous and comprehensive studies carried out in eastern (Kingston and Harrison, 2007; Ségalen et al., 2007; Levin et al., 2008; Bedaso et al., 2013; Cerling et al., 2015; Robinson et al., 2017, 2021; Lüdecke et al., 2018; Mercader et al., 2021), southern (Lee-Thorp and Sponheimer, 2005; Lee-Thorp et al., 2007, 2010; Ségalen et al., 2007; Lehmann et al., 2016) and central Africa (Zazzo et al., 2000; Ségalen et al., 2007; Lee-Thorp et al., 2012) focused on the ecological contexts of Plio-Pleistocene hominins and large herbivores.

1.2. The distribution of C₃–C₄ plants in North Africa

One of the commonly used methods for reconstructing past environments has been the analysis of stable carbon isotope ratios (¹³C/¹²C) in dental enamel bioapatite. This biogenic material is particularly useful due to its resistance to diagenetic processes, preserving the original isotopic signal (Wang and Cerling, 1994). The carbon isotope ratios are primarily influenced by the differential fractionation between the two photosynthetic pathways (C₃ and C₄) used by plants consumed by animals, and it is associated with specific types of landscapes or environmental conditions. The proportion of C₃ or C₄ plants is not distributed homogeneously throughout Africa, varying both geographically and chronologically. Global C₄ ecosystem expansion around 8–10 million years ago, due to the decrease of atmospheric CO₂, higher temperatures and increasing water-stress represents a significant change in the landscape that led to the replacement of C₃ grasses by C₄ grasses in existing open and dry environments in low-to mid-latitude and altitude regions (Ehleringer et al., 1991; Cerling, 1992; Cerling et al., 1997; Edwards et al., 2010; Polissar et al., 2019). During the Plio-Pleistocene, eastern, southern and central Africa were dominated by C₄ grassland (Zazzo et al., 2000; Ségalen et al., 2007; Strömberg, 2011), relegating C₃ grasses to altitudes above 2000 m and in the forest understory (Tieszen et al., 1979; Young and Young, 1983; Balasse and Ambrose, 2005). The ecological context of these areas, characterized by the high abundance of C₄ grasses, especially in Eastern Africa, has allowed the application of the C₄-grazers and C₃-browsers classification, which is widely used in studies analyzing the diet of mammals based on the analysis of tooth enamel δ¹³C values (Vogel, 1978; Zazzo et al., 2000; Sponheimer and Lee-Thorp, 2003; Lee-Thorp and Sponheimer, 2005; Levin et al., 2008; Bedaso et al., 2013; Cerling et al., 2015; Uno et al., 2018).

This clear distinction between C₄-grazers and C₃-browsers is not valid at high latitudes, as the contribution of C₄ plants is non-existent or marginal. This pattern has been observed in multiple studies conducted during the Pliocene and Early Pleistocene in Europe (Edwards et al., 2010; Domingo et al., 2013; Szabó et al., 2022). The same observation applies to studies conducted in North Africa on Pleistocene and Pliocene archaeological and palaeontological sites mentioned above (Bocherens et al., 1996; Sahnouni et al., 2011; Fannin et al., 2021). All of them, based on carbon isotope evidence, reveal a vegetation consisting of C₃ plants including all available resources such as trees, woody shrubs, bushes and grasses. This makes it challenging to discern different diets and habitats for mammals and therefore to draw a consistent ecological reconstruction with this single method.

To address this challenge, we combine three high-resolution approaches that cover different moments in the animal's life: the δ¹⁸O and δ¹³C values of tooth enamel bioapatite (which reflect the first years of life related to the crown formation times), tooth mesowear (which reflects the last months/years before death) and tooth occlusal microwear (which reflects the last days/weeks before death). By combining these approaches, this work aims at providing a robust ecological reconstruction of the Ahl al Oughlam (AaO) mammal communities, which will shed light on their diets, habitats, and seasonality.

Up to the present, there is no evidence of hominins at AaO. The earliest known occupation on the Atlantic coast, in western Morocco, corresponds to level TH-L at 1.3 Ma (Gallotti et al., 2023). However, 2.5 Ma ago, hominins were widespread in East and South Africa (Hammond and Mongle, 2023), in Chad, at the Koro Toro site (3.5 Ma; Brunet et al., 1995), and in Northern Africa with the oldest occupation at Aïn Boucherit at 2.4 Ma (Sahnouni et al., 2018). The absence of hominins in AaO does not necessarily imply their absence during the Plio-Pleistocene in the area, as it is possible that they have simply not been discovered in the fossil record. Another possibility could be that the environmental conditions did not facilitate the occupation of this area. In this study, we have also compared the ecology of the taxa from AaO with the same taxa from other sites in North, South, East, and Central Africa.

Understanding the role of this territory is crucial in contributing to

the debate about the first hominin dispersions and occupations, as well as highlighting the importance of North Africa in the adaptation and development of mammal behavior during the Late Pliocene and Early Pleistocene.

2. Site: Ahl al Oughlam

The fossiliferous locality of Ahl al Oughlam (33°34'11"N, 07°30'44"W) is an abandoned sandstone quarry located at the southeast boundary of the city of Casablanca (Morocco), 6.5 km from the present-day Atlantic shore (Fig. 1; Raynal et al., 1990; Geraads et al., 2022b). Stratigraphically, the quarry cuts through calcarenitic intertidal, supratidal and aeolian deposits correlative to sea-level highstands associated with a platform developed about 105 m a.s.l. which belong to the Ahl al Oughlam morphostratigraphic unit (Lefèvre and Raynal, 2002; Lefèvre et al., 2021; Geraads et al., 2022b), formerly included in the *Messaoudian* stage of Biberson's Moroccan Quaternary Chronostratigraphy (Biberson, 1961a; Stearns, 1978). The site was investigated in 1953 by Biberson (Biberson, 1961a, 1961b), under the name of *Carrière Déprez*, who reported the occurrence of some broken pebbles that he considered as representing reworked artifacts of the "archaic pebble culture" representing an initial stage of North African technological evolution. Raynal and Texier, 1989 demonstrated that they are actually "geofacts" of natural origin found in marine deposits. In 1985, J.-P. Raynal and J.-P. Texier discovered abundant fossil faunal remains in karst formations and in a network of fissures and interconnected galleries between calcarenite blocks, at the foot of what was once a palaeoshoreline.

The fillings lack stratification. Given that the populations of the diverse rodent species within the interconnected fissures exhibit no

significant distinctions in tooth measurements, they can be regarded as synchronous on a geological scale. Since absolute dating and paleomagnetic analysis are unattainable, the age of the fossiliferous fillings hinges on the identification and evolutionary stages of various taxa (Geraads, 2002, 2010). A biostratigraphic analysis of the mammal assemblage dates this locality to the Plio-Pleistocene boundary, indicating an approximate age of 2.5 Ma (Geraads, 1997; Geraads et al., 2022b). The genus *Equus* is absent, suggesting that the site is older than 2.3 Ma (Geraads, 2006). The mammalian fauna includes at least fifty-five species of both small and large mammals. A new species of *Hipparion*, *H. pomeli*, has been described subsequently from the site (Eisenmann and Geraads, 2007). The vertebrate fauna also includes amphibians, reptiles (tortoises, crocodiles, amphisbaenids, lizards and snakes) and fishes. The most unexpected element of the mammalian fauna is a walrus, a pinniped marine mammal. No living or fossil walrus was previously known in the Eastern Atlantic, south of Belgium (Geraads, 2006). The site was formed along the oceanic seashore which explains why both marine and terrestrial forms are found among birds. A list of the identified faunal taxa is given in several publications (Raynal et al., 1990; Geraads, 1993, 1995, 1996, 1997, 2002, 2004, 2006; Alemseged and Geraads, 1998; Geraads and Amani, 1998; Geraads and Metz-Muller, 1999; Eisenmann and Geraads, 2007; Mourer-Chauviré and Geraads, 2008; Geraads et al., 2010; Mourer-Chauviré and Geraads, 2010; Gunnell et al., 2011; Sen and Geraads, 2023).

3. Material & methods

The material sampled and analyzed is currently stored at the *Institut national des Sciences de l'Archéologie et du Patrimoine* (INSAP) in Rabat (Morocco). The species included in this research are the following:

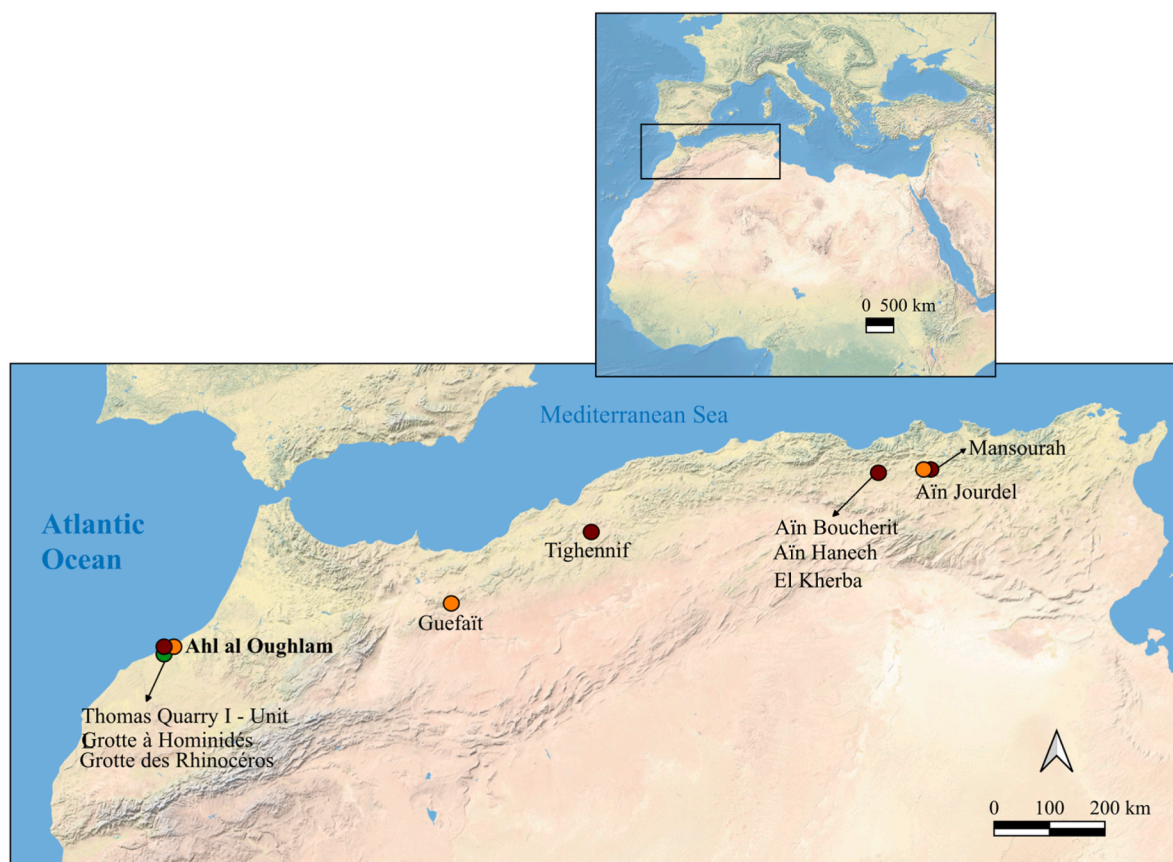


Fig. 1. Location map of North African sites mentioned in the text. Plio-Pleistocene boundary sites = orange circle (Ahl al Oughlam (this study), Guefaït and Aïn Jourdel); Early Pleistocene sites = brown circle (Thomas Quarry I-Unit L, Tighennif, Aïn Boucherit, Aïn Hanech, El Kherba and Mansourah); Middle Pleistocene sites = green circle (Grotte des Rhinocéros and Grotte à Hominidés).

Sivatherium maurusium, *Hipparion pomeli*, *Metridiochoerus phacochoeroides*, *Gazella* sp., *Alcelaphini* and *Anancus osiris*.

3.1. Stable isotopes (^{13}C and ^{18}O)

In this study, we performed stable carbon (^{13}C) and oxygen (^{18}O) isotope analysis of 82 fossil fauna specimens recovered from AaO (Supplementary Table 1). Sampling has been conducted on the buccal surface of molars and premolars from adult individuals. The tooth surfaces were cleaned with a tungsten abrasive drill bit to remove any adhering external material. Enamel powder for bulk analysis was obtained using gentle abrasion with a diamond-tipped drill.

Powdered enamel samples were chemically treated at the biomolecular laboratory at the *Institut Català de Paleoeologia Humana i Evolució Social* (IPHES - CERCA). Samples weighed from 3.5 to 9.5 mg. Chemical treatment of samples was based on protocols originally proposed by Koch et al. (1997) and later modified in Tornero et al. (2013). Samples were treated for 4 h in 0.1 M acetic acid [CH_3COOH] (0.1 ml solution/0.1 mg of sample), neutralized with distilled water and freeze-dried.

The ^{18}O and ^{13}C of carbonates were measured using an automated carbonate preparation device (KIEL-III) coupled with a gas-ratio mass spectrometer (Finnigan MAT 252) at the environmental isotope laboratory at the University of Arizona, US. Powdered samples were allowed to react with dehydrated phosphoric acid under a vacuum at 70 °C. Accuracy and precision of the measurements were checked and calibrated using calcium carbonate international standards (NBS-19 and NBS-18). Replicate measurements of the standards during analysis had errors of $\pm 0.1\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 sigma). Carbon isotope composition is reported in δ notation, where $\delta^{13}\text{C} = [(\text{R}_{\text{sample}}/\text{R}_{\text{standard}}) - 1]$, $\text{R} = ^{13}\text{C}/^{12}\text{C}$ and δ is expressed in per mil, ‰. Carbon and oxygen values are reported relative to PDB (Vienna Pee Dee Belemnite).

The modern plants using a C_3 photosynthetic pathway (including most trees, woody shrubs, bushes, herbs and grasses) have an average isotopic $\delta^{13}\text{C}$ value of -28.5‰ (global range -20 to -37‰), with -23‰ as the maximum value for typical C_3 plants and a cut-off of -31.5‰ for closed-canopy forests (Kohn, 2010). In this work, we use the average $\delta^{13}\text{C}$ value of -27‰ for modern C_3 plants, excluding analyses from the understory of closed-canopy forests below -31.5‰ (Kohn, 2010). Modern plants that employ the C_4 photosynthetic pathway (primarily tropical grasses and sedges) have an average isotopic composition of -12‰ (global range -10 to -14‰) (Cerling et al., 1997; Cerling and Harris, 1999; Kohn and Cerling, 2002). The bivariate graphs were made with the Past 4.02 software (Hammer et al., 2001). All mean values in the text are followed by their standard deviation.

3.1.1. Estimation of enrichment factor, $\%C_4$, $\delta^{13}\text{C}_{\text{diet-meq}}$ and MAP

Abundance of atmospheric CO_2 has been changing over time (Tippel et al., 2010) with a consequent influence on the carbon values of plants during its fixation in the photosynthesis process (Farquhar et al., 1989). To make a comparison between the carbon values of present-day plants with those consumed by animals in the past, it is crucial to perform corrections. In our work, we have corrected the $\delta^{13}\text{C}$ values of modern plants by $+1.5\text{‰}$, due to the difference between the pre-Industrial $\delta^{13}\text{C}_{\text{CO}_2}$ value of $\sim -6.5\text{‰}$ established for the Plio-Pleistocene (Tippel et al., 2010), and the $\delta^{13}\text{C}_{\text{CO}_2}$ value of $\sim -8\text{‰}$ at the time the reference collection of modern plants was collected (Kohn, 2010). When plants are consumed, a fixation occurs in the tooth enamel of the animals, a process of isotopic fractionation (Krueger and Sullivan, 1984; Koch, 1998; Cerling and Harris, 1999; Passey et al., 2005). In this study, we use formula (1) in Tejada-Lara et al. (2018) which determines that there is a positive correlation between body mass and enamel-diet enrichment fractionation (expressed as $\epsilon^*_{\text{enamel-diet}}$). The $\epsilon^*_{\text{enamel-diet}}$ has been calculated from the estimation of the body mass of the species analyzed: *S. maurusium* (Basu et al., 2016), *H. pomeli* (Bernor et al., 2021), *Gazella*

sp. and *Alcelaphini* (Bibi and Kiessling, 2015), *M. phacochoeroides* (Rannikko, 2019) and *A. osiris* (Larramendi, 2016).

$$\epsilon^* = 2.4 + 0.034 (\text{Body Mass}) \quad (1)$$

The $\delta^{13}\text{C}$ values in plants and animals have also been proposed to estimate mean annual precipitation (MAP) in the fossil record. We use formulae (2 and 3) developed in Kohn (2010) and Kohn et al. (2015) to estimate the MAP, which applies corrections for altitude, latitude, and $\delta^{13}\text{C}$ of atmospheric CO_2 from the average modern equivalent of diet composition ($\delta^{13}\text{C}_{\text{diet-meq}} = \delta^{13}\text{C}_{\text{enamel}} - \epsilon^*_{\text{enamel-diet}} - \text{Plio-Pleistocene atmospheric } \text{CO}_2$):

$$\text{MAP} = 10^{\Delta^{13}\text{C} - 2.01 + 0.000198 \times \text{elev} - 0.0129 \times |\text{lat}| / 5.88} - 300 \quad (2)$$

where *elev* is elevation in meters, *lat* is latitude in degrees, and

$$\Delta^{13}\text{C} = (\delta^{13}\text{C}_{\text{atm}} - \delta^{13}\text{C}_{\text{diet-meq}}) / (1 + \delta^{13}\text{C}_{\text{diet-meq}} / 1000) \quad (3)$$

where $\delta^{13}\text{C}_{\text{atm}}$ is the carbon isotope of atmospheric CO_2 (-6.5‰ in the Plio-Pleistocene; Tiple et al., 2010) and $\delta^{13}\text{C}_{\text{diet-meq}}$ is the modern equivalent of diet composition ($\delta^{13}\text{C}_{\text{diet-meq}}$) estimated from $\delta^{13}\text{C}_{\text{enamel}}$ after $\epsilon^*_{\text{enamel-diet}}$ correction (see formula (1)).

We estimated (4) the fraction of C_4 vegetation consumed by AaO herbivores using $\delta^{13}\text{C}$ modern plant values, -24‰ for C_3 vegetation ecosystems (Kohn, 2010) and -12‰ for C_4 vegetation (Cerling et al., 1997). The fossil $\delta^{13}\text{C}_{\text{enamel}}$ values have been corrected for $\delta^{13}\text{C}$ of Plio-Pleistocene atmospheric CO_2 and $\epsilon^*_{\text{enamel-diet}}$ to obtain the $\delta^{13}\text{C}_{\text{diet-meq}}$.

$$\%C_4 = 100 \times (\delta^{13}\text{C}_{\text{diet-meq}} - \delta^{13}\text{C}_{\text{C}_3}) / (\delta^{13}\text{C}_{\text{C}_4} - \delta^{13}\text{C}_{\text{C}_3}) \quad (4)$$

3.1.2. Obligate drinkers vs. non-obligate drinkers taxa

To calculate relative aridity in AaO, we relied on the fundamental principle of different drinking behaviors exhibited by mammals (Nicholson, 1985; Kohn, 1996; Levin et al., 2006; Blumenthal et al., 2017). In arid environments, both open water sources and plant water and tissues experience evaporation of ^{16}O and enrichment of ^{18}O (Gonfiantini et al., 1965). However, this evaporative effect is more pronounced in plants. As a result, it is anticipated that animals primarily obtaining water through plant consumption (non-obligate drinkers) will display higher $\delta^{18}\text{O}_{\text{enamel}}$ values compared to obligate drinkers relying on direct access to surface water (Bocherens et al., 1996; Kohn, 1996). The greater the difference in $\delta^{18}\text{O}$ values between these two groups, the higher the aridity (Lehmann et al., 2016; Roberts et al., 2018; Lüdecke et al., 2022). For this comparison, we selected the most reliable species from AaO to classify the mentioned categories. Specifically, we chose *S. maurusium* and *Gazella* sp. as non-obligate drinkers, and *H. pomeli* and *A. osiris* as obligate drinkers. Generally, grazers among ungulates have a higher dependence on surface water than browsers (Western, 1975; Faith, 2018). This pattern is supported by the dental wear results from AaO, which classified *S. maurusium* and *Gazella* sp. as browsers and *H. pomeli* and *A. osiris* as grazers.

3.2. Dental wear analysis

3.2.1. Dental mesowear analysis

A total of 74 molars were studied using mesowear analysis, excluding 28 teeth that were unworn, extremely worn, or had broken or damaged cusp apices (Supplementary Table 2). The sensitivity of cusp sharpness to ontogenetic age has been documented for both young and old individuals. Conversely, mesowear displays a weaker correlation with age in intermediate age groups, and demonstrates a stronger relationship with dietary factors (Rivals et al., 2007). The mesowear analysis method assesses the relief and sharpness of worn cusp apices, which are related to attritive and abrasive wear on dental enamel. These analyses were performed on the buccal side of upper molars and the lingual side of

lower molars, with a preference for the paracone of the upper M2. To evaluate wear on teeth from P3 to M3, we used the extended mesowear method proposed by Kaiser and Solounias (2003). In this study, we applied the method introduced by Mühlebacher et al. (2011), which uses seven cusp categories ranging from high and sharp (stage 0) to completely blunt with no relief (stage 6). A low-abrasion diet such as browsing, which induces high attrition, preserves sharpened apices on buccal cusps as teeth wear down, while a high-abrasion diet results in more rounded and blunted buccal cusp apices. The bivariate graph was performed with the Past 4.02 software (Hammer et al., 2001).

3.2.2. Dental microwear analysis

The investigation of dental microwear has a rich history in elucidating the dietary preferences and ecological niches of fossil species. Starting with early studies in the late 1970s, which employed scanning electron microscopy (SEM) at high magnifications (~100–500x) (Rensberger, 1978; Walker et al., 1978), to subsequent research employing low-magnification light microscopy (MacFadden et al., 1999; Solounias and Semperebon, 2002), and more recently, dental microwear texture analysis (DMTA) utilizing three-dimensional surface measurements acquired through white-light confocal microscopy and scale-sensitive fractal analysis (Ungar et al., 2003; Scott et al., 2006). Despite all methods being valid and complementary, for this study, we opted for a low-magnification microwear approach due to the accessibility of an extensive microwear reference collection of extant species, particularly those of African origin (Solounias and Semperebon, 2002).

In this work, a total of 109 molars and premolars were selected and molded. After examination of the molds under a stereomicroscope, 49 specimens were discarded due to poor preservation or taphonomic defects (Supplementary Table 2) (El-Zaatar, 2010; King et al., 1999). Examination of enamel microwear features was conducted through standard light microscopy, using a Zeiss Stemi 2000C stereomicroscope at a magnification of 35× on high-resolution epoxy casts of the teeth. The cleaning, molding, casting, and examination protocols, as well as feature classification criteria, were consistent with those established by Solounias and Semperebon (2002) and Semperebon et al. (2004). Upper and lower teeth, spanning from P4 to M3, were included in the analysis following Xafis et al. (2017). The occlusal surface of each specimen was first cleaned with acetone and 96% ethanol before being molded with high-resolution silicone (Heraeus Kulzer, PROVIL novo

Vinylpolysiloxane, Light C.D. 2 regular set) and transparent casts were created using clear epoxy resin (C.T.S. Spain, EPO 150 + K151). Scoring of microwear features, including small and large pits (round scars), scratches (elongated scars with parallel sides), gouges (irregular edges and much larger and deeper than the large pits), puncture pits (deepest at their centers, symmetrical, craterlike features with regular margins), and cross scratches (oriented perpendicularly to the majority of scratches), was performed using a standard 0.16 mm² ocular reticle. In order to achieve a more precise categorization of grazers, browsers, and mixed feeders, we used the percentage of individuals in a sample possessing scratch numbers that fall between 0 and 17 (Semperebon and Rivals, 2007). The scratch width score (SWS) was calculated based on the ratio of fine to coarse scratches ("0" predominantly fine scratches per tooth surface, "1" to those with a mixture of fine and coarse scratches, and "2" to those with predominantly coarse scratches). The results were compared with a database constructed from extant ungulate taxa (Solounias and Semperebon, 2002; Rivals and Semperebon, 2011). To reduce inter-observer error, dental microwear analysis was conducted by a single experienced researcher (IRP).

4. Results

4.1. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$)

The $\delta^{13}\text{C}$ values of all taxa measured in AaO ranged from −14.1 to −8‰ with a mean and standard deviation of $-11.4 \pm 1.2\text{‰}$ ($n = 82$) (Fig. 2). The data for each species are described below: *H. pomeli* ($n = 16$; range = −13.5 to −10.6‰; mean = $-11.7 \pm 0.9\text{‰}$), Alcelaphini ($n = 18$; range = −13 to −8‰; mean = $-10.3 \pm 1.3\text{‰}$), *Gazella* sp. ($n = 18$; range = −12.8 to −10.6‰; mean = $-11.6 \pm 0.6\text{‰}$), *S. maurusium* ($n = 6$; range = −14.1 to −10.8‰; mean = $-12.4 \pm 1.4\text{‰}$), *M. phacochoeroides* ($n = 23$; range = −13.2 to −8.4‰; mean = $-11.7 \pm 1.2\text{‰}$) and *A. osiris* ($n = 1$; −13.3‰). The two taxa with the highest variability and the most positive values are Alcelaphini and *M. phacochoeroides*. *Gazella* sp. and *H. pomeli* are the species with the lowest variability and *S. maurusium* is the species with the most negative values.

The $\delta^{18}\text{O}$ values ranged from −3 to 2.9‰ with a mean and standard deviation of $-0.6 \pm 1.2\text{‰}$ ($n = 82$) (Fig. 3). The data for each species are described below: *H. pomeli* ($n = 16$; range = −3 to 0.2‰; mean = −1.8

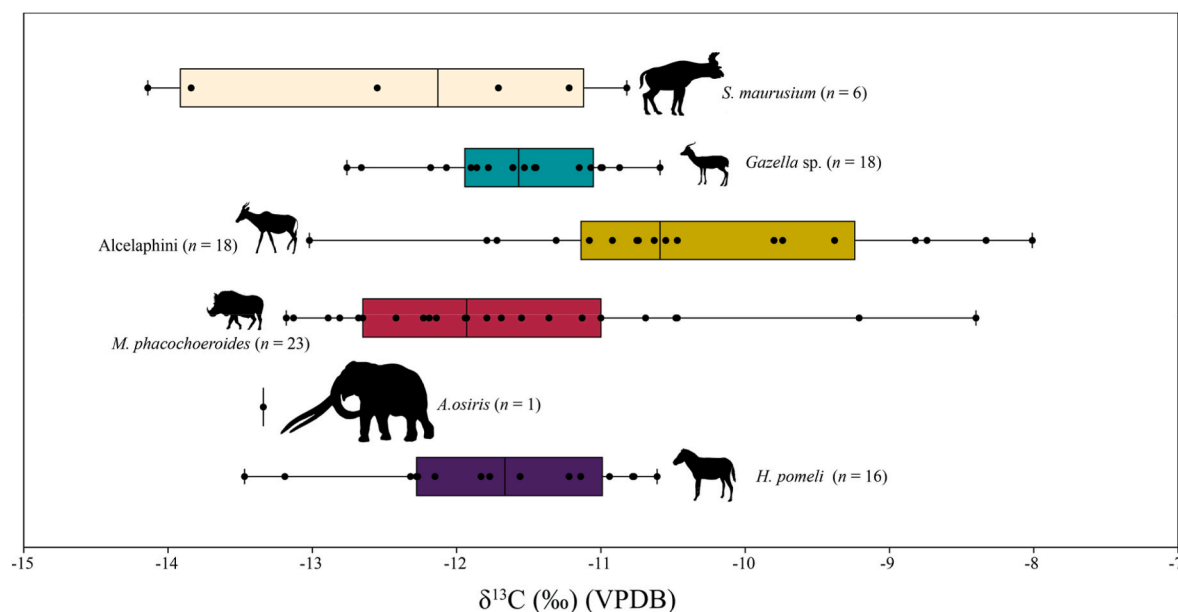


Fig. 2. Jitter boxplots for $\delta^{13}\text{C}$ values of the ungulates from the Plio-Pleistocene site of AaO. Boxes = first and third quartile for each taxon, whiskers = full range for each taxon and hashes within boxes = median value.

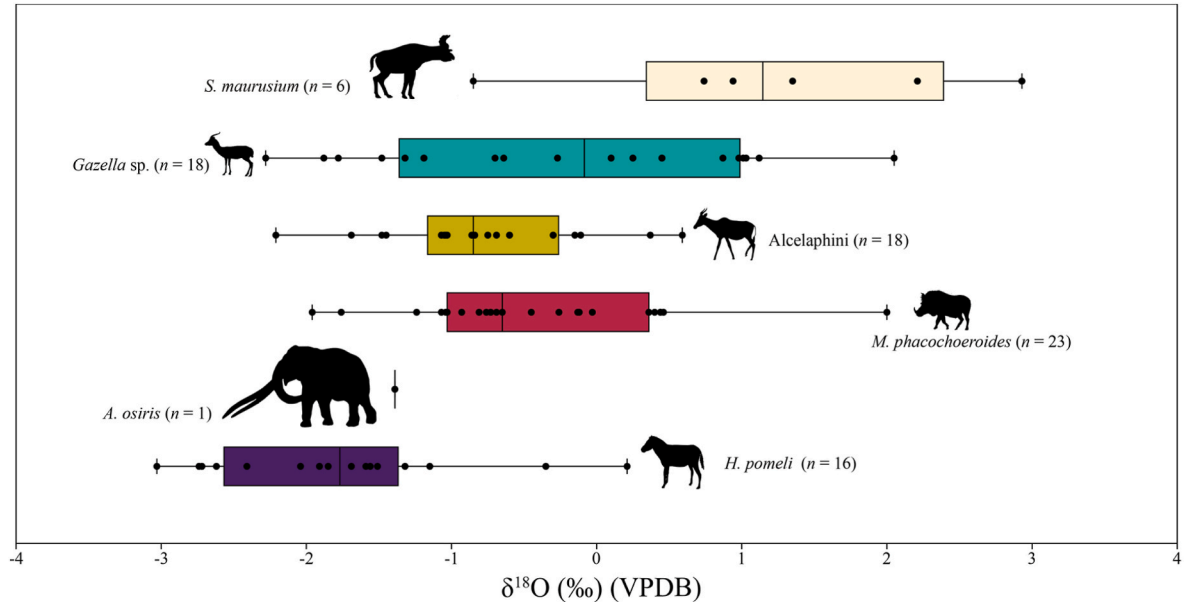


Fig. 3. Jitter boxplots for $\delta^{18}\text{O}$ values of the ungulates from the Plio-Pleistocene site of AaO. Boxes = first and third quartile for each taxon, whiskers = full range for each taxon and hashes within boxes = median value.

$\pm 0.9\text{‰}$), Alcelaphini ($n = 18$; range = -2.2 to 0.6‰ ; mean = $-0.8 \pm 0.7\text{‰}$), *Gazella* sp. ($n = 18$; range = -2.3 to 2.1‰ ; mean = $-0.2 \pm 1.3\text{‰}$), *S. maurusium* ($n = 6$; range = -0.9 to 2.9‰ ; mean = $1.2 \pm 1.3\text{‰}$), *M. phacochoeroides* ($n = 23$; range = -1.8 to 2‰ ; mean = $-0.4 \pm 0.9\text{‰}$) and *A. osiris* ($n = 1$; -1.4‰). The whole isotopic dataset is provided in [Supplementary Table 1](#).

4.1.1. Estimation of enrichment factor, $\%C_4$, $\delta^{13}C_{\text{diet-meq}}$ and MAP

The $\epsilon^*_{\text{enamel-diet}}$ of the AaO species ranges from 12.4 to 14.7‰, depending on the body mass. C_4 plants are virtually absent in the diet of AaO species. They are only present, in low percentages, in four individuals of Alcelaphini ($\%C_4 = 4, 5, 8$ and 11%) and in one individual of *M. phacochoeroides* ($\%C_4 = 6\%$) ([Supplementary Table 1](#)). The MAP results are estimated in [Table 1](#). In order to calculate it, the five individuals with C_4 presence have been excluded based on the criteria established by [Kohn \(2010\)](#). The average $\delta^{13}C_{\text{diet-meq}}$ value (-26.1‰) and MAP (385 mm/yr) suggest a relatively arid environment for AaO, defined by [Kohn \(2010\)](#) as ecosystems with a MAP $\leq 500 \text{ mm/yr}$ and $\delta^{13}C_{\text{diet-meq}}$ values between -26 and -24‰ ([Table 1](#); [Supplementary Table 1](#)).

4.1.2. Obligate drinkers vs. non-obligate drinkers taxa

The ANOVA statistical test and Tukey’s pairwise comparison show significant differences in the $\delta^{18}O_{\text{enamel}}$ values among the obligate drinkers ($n = 17$; *A. osiris* and *H. pomeli*) and non-obligate drinkers ($n = 24$; *S. maurusium* and *Gazella* sp.) with a p -value of 1.819. The non-obligate drinkers mean is 0.15‰ and the obligate drinker mean is 1.77‰ , implying a difference between the two groups of 1.9‰ .

4.2. Dental wear analysis

4.2.1. Dental mesowear analysis

Some authors have observed differences in the mesowear score between the upper and lower molars of the same individuals ([Kaiser and Fortelius, 2003](#)). Since the *Gazella* sp. and Alcelaphini teeth analyzed include both upper and lower molars, we conducted an ANOVA statistical test and Tukey’s pairwise comparison to enhance the analysis conducted. The statistical results did not reveal significant differences in the mesowear score values between lower molars ($n = 5$) and upper molars ($n = 12$) of *Gazella* sp., with a p -value of 0.9694, nor between lower molars ($n = 13$) and upper molars ($n = 9$) of Alcelaphini, with a p -value of 0.9826.

The mesowear pattern of AaO specimens is characterized by occlusal surfaces ranging from sharp cusps and high relief (low abrasion) to low relief with rounded cusps (high abrasion). It corresponds to mesowear scores with values from 0 to 5 ([Table 2](#); [Fig. 4](#)). All three Bovidae have sharp cusps, which means that attrition predominates strongly over abrasion. The *S. maurusium* has the lowest level of abrasion with a MWS of 1, falling in the MWS average of extant leaf browsers. The *Gazella* sp. has also a low average MWS (1.2), being in the range of MWS of extant mixed feeders but with a tendency towards a browsing diet. The Alcelaphini, with variability in abrasion levels, has an average MWS of 2.2 and is categorized as a grass-dominated mixed feeder. In the case of the Equidae *H. pomeli*, the MWS indicates high levels of abrasion, with a MWS average of 4.3. This pattern places *H. pomeli* among extant grazers.

4.2.2. Dental microwear analysis

At AaO, all herbivores display browsing or mixed feeding dietary

Table 1
Summary of $\delta^{13}C$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}C_{\text{diet-meq}}$ (‰), $\%C_4$ and Mean Annual Precipitation (MAP - mm/yr).

Species	n	$\delta^{13}C$ (‰)	Body Mass (Kg)	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}C_{\text{diet-meq}}$ (‰)	$\%C_4$	MAP (mm/yr)
<i>S. maurusium</i>	6	-12.4 ± 1.4	1236	+14	-27.9 ± 1.4	0	1041 ± 760
Alcelaphini	18	-10.3 ± 1.3	200	+13.2	-23.9 ± 1.3	1.5 ± 3.2	177 ± 210
<i>Gazella</i> sp.	18	-11.6 ± 0.6	30	+12.4	-24.1 ± 0.6	0	139 ± 112
<i>H. pomeli</i>	16	-11.7 ± 0.9	250	+13.3	-26.5 ± 0.9	0	400 ± 269
<i>M. phacochoeroides</i>	23	-11.7 ± 1.2	297	+13.4	-26.5 ± 1.2	0.3 ± 1.3	455 ± 274
<i>A. osiris</i>	1	-13.3	5000	+14.7	-29.6	0	1996
All species	82	-11.4 ± 1.2	-	+13.2	-26.1 ± 1.4	0.4 ± 1.7	385 ± 419

Table 2
Summary of mesowear and microwear data of the fossil assemblages from AaO. Abbreviations: *n*, number of specimens; MWS, mesowear score; NS, average number of scratches; NP, average number of pits; SD, standard deviation; SWS, scratch width score; %PP, percentage of specimens with puncture pits; %HC, percentage of specimens with hyper-coarse scratches; %LP, percentage of specimens with large pits; %G, percentage of specimens with gouges; %XS, percentage of specimens with cross scratches; %0–17, percentage of specimens with number of scratches ranging between 0 and 17.

Species	Mesowear		Microwear											
	<i>n</i>	MWS	<i>n</i>	NS	SD	NP	SD	SWS	%PP	%HC	%LP	%G	%XS	%0–17
<i>S. maurusium</i>	4	1	4	12.8	1.9	24.75	2.7	1	0	0	50	100	25	100
Alcelaphini	22	2.2	17	20.0	2.6	20.1	3.4	1.1	11.8	0	82.4	29.4	11.8	17.6
<i>Gazella</i> sp.	17	1.2	8	9.5	1.6	23.4	4.6	1	0.0	0	100	50	12.5	100
<i>H. pomeli</i>	6	4.3	13	20.6	3	19.1	4	1	15.4	0	84.6	7.7	0	0
<i>M. phacochoeroides</i>	–	–	18	19.7	4.6	23	3.6	0.9	5.6	0	83.3	22	100	33.3
<i>A. osiris</i>	–	–	1	26	–	25.5	–	1	0	100	100	0	100	0

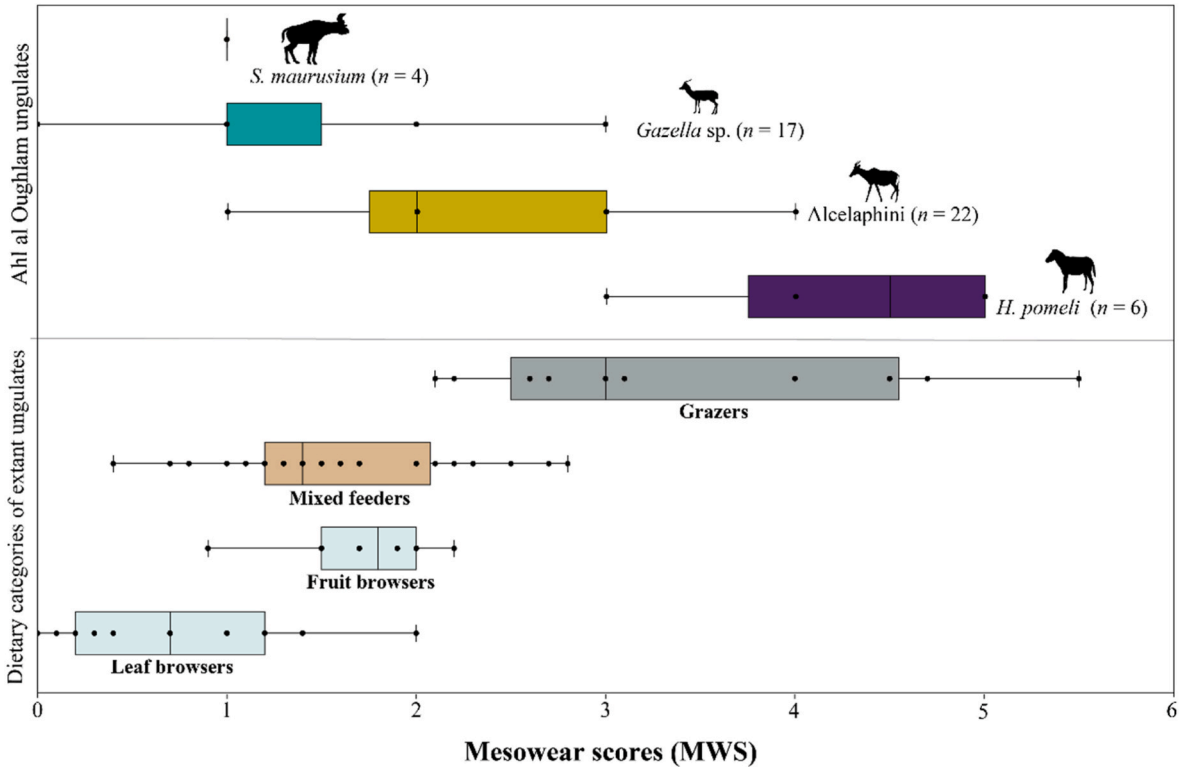


Fig. 4. Jitter boxplot with mesowear scores (MWS) of the ungulates from AaO. Boxes = first and third quartile for each taxon; whiskers = full range for each taxon and hashes within boxes = median value. Extant ungulates database (Fortelius and Solounias, 2000).

traits (Fig. 5). The species analyzed are classified into two groups. The first group includes the *S. maurusium* and *Gazella* sp. and plot among extant browser ungulates. The second group, which includes Alcelaphini, *H. pomeli*, *M. phacochoeroides* and *A. osiris*, plot among extant mixed feeders. The first group has microwear patterns characterized by a high number of pits (NP = 24.1) and a small number of scratches (NS = 11.2) and the second group has a microwear pattern defined by a similar number of pits (NP = 21.9) and scratches (NS = 21.6). *Gazella* sp. (NS = 9.5) and *S. maurusium* (NS = 12.8) are the species with a lower number of scratches, and *H. pomeli* (NS = 20.6) and *A. osiris* (NS = 26) have a higher number of scratches. All species have a similar and a relatively high number of pits. The *A. osiris* (NP = 25.5) and *S. maurisium* (NP = 9.5) have the highest abundance of pits. Although the Alcelaphini, *H. pomeli*, *M. phacochoeroides* and *A. osiris* in Fig. 5 are classified among extant mixed feeders, the high number of scratches (see Table 2, NS and 0–17%) indicates a high proportion of grasses in their diet.

The SWS, being between 0.9 and 1.1, indicates a mixture of both fine and coarse scratches for all species. Hyper-coarse scratches have been found only in *A. osiris*. Cross scratches are absent in *H. pomeli* and present

in a low percentage in Alcelaphini, *Gazella* sp. and *S. maurusium*. *A. osiris* and *M. phacochoeroides* have them in 100% of the individuals. This trait is characteristic of animals with a bunodont dental morphology as in the case of the latter two species. Gouges have been observed in all species except in *A. osiris* and their presence is remarkable in the four individuals of *S. maurusium*. Puncture pits are present in a low percentage in Alcelaphini, *H. pomeli* and *M. phacochoeroides*, and large pits are present in all species in proportions varying from 50% to 100% of the individuals.

5. Discussion

5.1. Palaeodiet

The combination of the three approaches allows us to characterize the dietary preferences of the different taxa, as well as to reconstruct the general ecological context (Table 3). In AaO, all species have a predominantly plant-based C₃ diet with values ranging from –14 to –8‰, with a small consumption of C₄ plants in Alcelaphini and

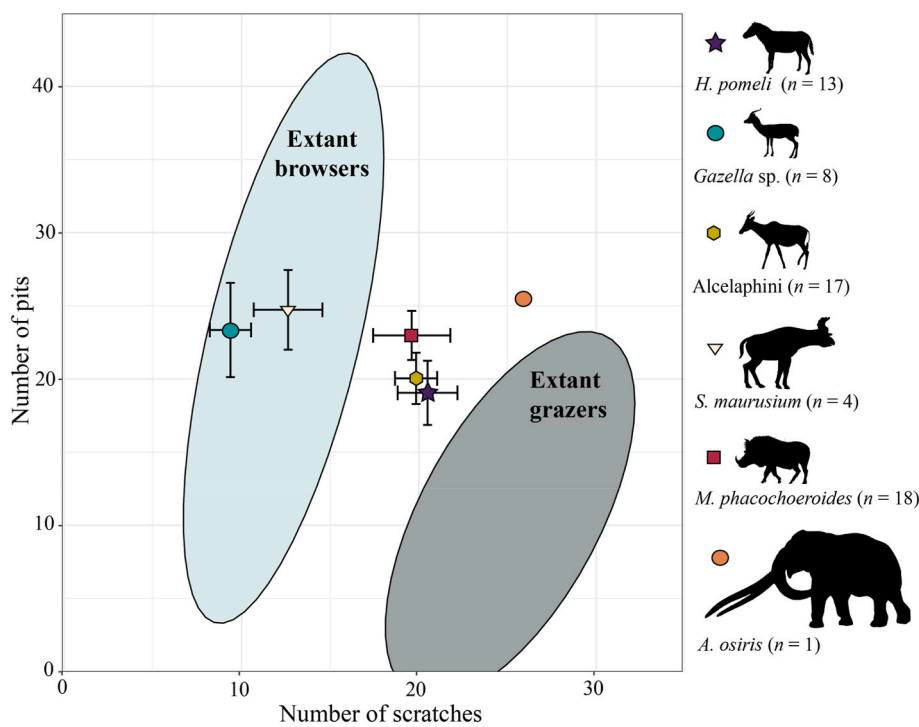


Fig. 5. Bivariate plot of the average numbers of pits and scratches for the species from AaO. Error bars correspond to standard deviation (± 1 SD) for the fossil samples. Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant browsers and grazers based on the database from Solounias and Semprebon (2002).

Table 3
Summary of dietary interpretations based on tooth wear and stable carbon isotope data. Abbreviations: B = browser, MF-B = browsing-dominated mixed feeder, MF = mixed feeder, MF-G = grass-dominated mixed feeder, and G = grazer. The parentheses indicate the consumption of C₄ plants (in very low percentage) in some species.

Species	Stable isotopes	Mesowear	Microwear
<i>S. maurusium</i>	C ₃	B	B
Alcelaphini	C ₃ (C ₄)	MF-G	MF-G
<i>Gazella</i> sp.	C ₃	MF-B	B
<i>H. pomeli</i>	C ₃	G	MF-G
<i>M. phacochoeroides</i>	C ₃ (C ₄)	–	MF-G
<i>A. osiris</i>	C ₃	–	MF-G

M. phacochoeroides (Table 1). In some contexts, interpreting the carbon isotopic signal can be complex, especially when there are no extreme values that can indicate high consumption of C₄ plants linked to grass consumption (ca. $\delta^{13}\text{C} > 0\text{‰}$; Cerling and Harris, 1999) or the presence of C₃ closed canopy forests (ca. $\delta^{13}\text{C} < -16\text{‰}$; Kohn, 2010), types of environments in which the signal is obvious. In AaO, there is both inter- and intra-species variability in carbon values. Recent isotopic studies on extant species in sub-Saharan Africa have shown a weak relationship between intra-taxon variation in $\delta^{13}\text{C}_{\text{enamel}}$ (C₃ and C₄) and corresponding changes in herbivore diet and vegetation structure (woody cover). Therefore, adopting a community-level approach when making inferences about vegetation using isotopic data, focusing on the relationships between different taxa is recommended. This approach allows for a more accurate understanding of the vegetation dynamics and ecological context (Robinson et al., 2021). In AaO, the interspecific difference between Alcelaphini and *S. maurusium* is striking and could represent different ecological niches and diets (Fig. 2). Dental wear analysis (micro- and mesowear) shows variable feeding traits that range from browser to mixed-feeder to grazer behavior, including Alcelaphini with a grass-dominated, mixed-feeding diet or *S. maurusium* as the most browsing taxon (Table 3). Oxygen isotope data are consistent with the

dental wear feeding pattern, with browser species having more positive values (*S. maurusium* and *Gazella* sp.) than the rest, and grass-dominated mixed feeders having more negative values. The correlation in oxygen is higher between the most grazing species, according to dental wear pattern, such as *H. pomeli*, and the most browsing ones such as *S. maurusium*, showing very distant values between them. This could suggest the consumption of different resources, such as the preference for grasses by the former and leaves by the latter.

5.1.1. Comparison of AaO with other African sites

The *Sivatherium maurusium* from AaO has the most negative C₃ carbon values ($\delta^{13}\text{C}$ mean = $-12.4 \pm 1.4\text{‰}$) and the most positive oxygen values (Figs. 2 and 3) compared to other AaO species. These oxygen and carbon values could be attributed to the preferential consumption of leaves from the upper parts of trees or shrubs which is consistent with dental wear patterns suggesting a browsing diet for AaO *S. maurusium*. The same isotopic pattern in $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values has also been observed in *Sivatherium* from Hadar and Aramis (Ethiopia; ~4–3 Ma) (Wynn et al., 2016) and Makapansgat (South Africa; ~3 Ma (Lee-Thorp et al., 2010). Although this species is known from various North African sites such as Ain Boucherit, Ain Hanech and El-Kherba (Early Pleistocene; Algeria), Ain Jourdel (Late Pliocene; Algeria), and Ichkeul and Ain Brimba (Late Pliocene; Tunisia), this is the first time that data on its diet has been obtained from this area.

In East Africa, the Giraffidae were represented by two genera: *Giraffa* and *Sivatherium*, from the early Pliocene onwards. *Sivatherium* became extinct during the Middle Pleistocene. Overall, its diet underwent changes in the Turkana Basin (Kenya), being a browser (C₃ plants) at ~4 Ma and switching to grazing (C₄ plants) between ~2.5 and 1 Ma (Cerling et al., 2015). In the Chiwondo beds (Malawi; ~2.5 Ma), *Sivatherium* exhibited less negative $\delta^{13}\text{C}$ values ($n = 1$; $\delta^{13}\text{C} = -7.9\text{‰}$) than the purely browsing fossil *Giraffa* ($n = 2$; $\delta^{13}\text{C}$ mean = $-12.1 \pm 1.1\text{‰}$), indicating that it incorporated some C₄ grass in its diet (Bocherens et al., 2011). In Olduvai (Tanzania; ~1.8 Ma), a multiproxy approach suggested a mixed diet for *S. maurusium*, C₄-dominated or mixed diets, a

mesowear characteristic of grazers, but with microwear indicating a browsing-dominated mixed diet, likely due to seasonal changes in its diet (Uno et al., 2018).

In South Africa, *Sivatherium* maintained its preference for C₃ plants from ~5 to 3 Ma. In the Langebaanweg site (~5 Ma), the $\delta^{13}\text{C}$ mean value ($n = 26$) is $-11.5 \pm 1.1\text{‰}$ (Franz-Odenaal et al., 2002). However, hypsodonty indices, dental mesowear, and dental microwear suggested mixed feeding dietary traits with a browsing tendency for this species (Franz-Odenaal and Solounias, 2004). In the Makapansgat Limeworks Member 3 (~3 Ma), *Sivatherium* exhibited carbon values ($n = 2$; $\delta^{13}\text{C}$ mean = $-11.4 \pm 0.1\text{‰}$) similar to those of *Giraffa* ($n = 8$; $\delta^{13}\text{C}$ mean = $-11 \pm 0.9\text{‰}$) at the same site (Sponheimer and Lee-Thorp, 2009). The diet of AaO *Sivatherium* follows the same C₃-browser pattern as that of the rest of Africa during the ~3 to 2.5 Ma period, but further multiproxy studies are needed in more recent North African sites such as Ain Hanech or El-Kherba (~1.8 Ma) to determine whether this dietary pattern remains the same or changes, as in the case of East Africa.

The Alcelaphini from AaO is the taxon with the least negative carbon values, with a predominance of C₃ plant consumption values (mean $\delta^{13}\text{C} = -10.3 \pm 1.3\text{‰}$), indicating even some C₄ consumption (Table 2). The results of micro- and mesowear tooth analysis indicate a mixed diet, but with a high content of grasses in its feeding ecology. In general, this taxon is indicative of open dry environments, both during the African Pliocene and Pleistocene and in extant populations. Regardless of the consumption of C₃ or C₄ plants, their feeding behavior is predominantly grazing (Vrba, 1984; Sponheimer et al., 1999, 2003; Bobe and Behrensmeyer, 2004; Cerling et al., 2015).

Different species of Alcelaphini were present in North Africa from the Late Pliocene (Arambourg, 1979; Geraads and Amani, 1998) until they were declared extinct in this area in 1994 (Mallon and Kingswood, 2001), but the only fossil record of their diet has been carried out at the site of Tighennif (1 Ma; Algeria). At this site, the Alcelaphini tribe is represented by the species *Connochaetes taurinus prognus*. The pattern of $\delta^{13}\text{C}$ values ($n = 6$; mean $\delta^{13}\text{C} = -10.5 \pm 1.4\text{‰}$) is similar to that observed in the Alcelaphini from AaO (Bocherens et al., 1996; Fannin et al., 2021). Compared to the carbon values of different ungulates analyzed in Tighennif, this species has the most positive carbon values, indicating, as in the case of AaO, a small consumption of C₄ plants in some individuals.

In central Africa, 2500 km west of the Rift Valley, at the Koro Toro site (Chad; ~3.5–3 Ma), Alcelaphini have a grazing diet based on C₄ plants with an average $\delta^{13}\text{C}$ value ($n = 6$) of $1.4 \pm 0.8\text{‰}$ (Zazzo et al., 2000).

In eastern Africa (Turkana Basin), the remarkable predominance and similarity in the C₄ isotopic signature of Alcelaphini from approximately ~4.4 Ma to present-day specimens is particularly notable (White et al., 2009; Cerling et al., 2015). In Olduvai (Tanzania; ~1.8 Ma), the carbon isotope data indicate C₄-dominated diets, while dental wear classifies this species as a grass-dominated mixed feeder (Uno et al., 2018).

In southern Africa, Wonderwerk Cave has a longer temporally stratified sequence from the Early Pleistocene to the Holocene, with the presence of Alcelaphini in all layers. They show a progressive increase in C₄ consumption from 50% in the Early Pleistocene to 100% in the Holocene (Ecker et al., 2018). In the Makapansgat Limeworks Member 3 (~3 Ma), Alcelaphini (*Parmularius*, *Damaliscus* and *Connochaetes*) have C₄ values, in contrast to the Tragelaphini from the same level, which have a clear C₃ values. Ecomorphological and microwear data confirm a grazing diet for the former and a browsing for the latter (Sponheimer et al., 1999; Schubert et al., 2006). In Haasgat cave (~2.6–1.9 Ma), as in Makapansgat, Alcelaphini have a C₄ consumption while Tragelaphini have C₃ plant consumption values (Adams et al., 2013). In Swartkrans cave (~1.9–1.8 Ma), the Alcelaphini *Connochaetes* sp. also has a C₄-based diet (Lee-Thorp et al., 1989). However, in other South African sites, the Alcelaphini carbon values are clearly C₃, although attributed to grass consumption. This is the case of Hoedjiespunt (~0.35–0.25 Ma) with a mean $\delta^{13}\text{C}$ ($n = 16$) of $-9.8 \pm 1.3\text{‰}$, Elandsfontein (~1.0–0.6

Ma) with a mean $\delta^{13}\text{C}$ ($n = 19$) of $-10.3 \pm 1.2\text{‰}$, and Langebaanweg (~5 Ma) with a mean $\delta^{13}\text{C}$ ($n = 7$) of $-10.8 \pm 1\text{‰}$ (Lehmann et al., 2016).

The *Hipparion pomeli* from AaO has a diet based on C₃ plants ($\delta^{13}\text{C}$ mean = $-11.7 \pm 0.9\text{‰}$). It is the species with the highest mesowear score, indicative of a grazing diet. Microwear classifies it as a mixed feeder, but the high number of scratches is related to a high consumption of grasses. The presence of *Hipparion* between ~3.5 and 1.7 Ma is well documented in North Africa in sites such as Ain Brimba and Lake Ichkeul in Tunisia, Ain el Bey, Ain el Hadj Baba, Ain Jourdel, Mansourah, Ain Boucherit, Ain Hanech, Puits Caroubi, Carrière Brunie, Carrières Quartier St-Pierre in Algeria, and Fouarat, Oued Akrech, and Guefaït in Morocco. The dating of the youngest North African hipparion record occurs at Ain Hanech (~1.7 Ma) (Van der Made et al., 2022). Regarding studies on the feeding habits of this species in North Africa, there are only preliminary results for the *Hipparion* sp. from the Guefaït site (~3–2.5 Ma; Morocco), which show a predominance of C₃ plant consumption ($n = 4$; $\delta^{13}\text{C}$ mean = $-9.5 \pm 1\text{‰}$), although with less negative carbon values than those of the *H. pomeli* from AaO (Ramírez-Pedraza et al., 2023).

In Central Africa, diachronic (~6–3 Ma) isotopic studies carried out on the species *Hipparion* cf. *hasumense* in Chad show a clear predominance of C₄ plant consumption. In Kossom Bougoudi (~6–5 Ma), the average $\delta^{13}\text{C}$ ($n = 6$) is $-1.3 \pm 0.8\text{‰}$, and in the Koro Toro site (~3.5–3 Ma) the average $\delta^{13}\text{C}$ value ($n = 2$) is $0.9 \pm 1.1\text{‰}$ (Zazzo et al., 2000).

In East Africa, as was the case with the Alcelaphini, the hipparion equid *Eurygnathohippus* has continuity in C₄-grazer plant consumption from ~4 to 1.5 Ma (Bocherens et al., 2011; Cerling et al., 2015; Manthi et al., 2020). Other methods such as microwear and mesowear also indicate a grazing diet for the *Eurygnathohippus* from Olduvai (Tanzania; ~1.8 Ma) (Uno et al., 2018).

In southern Africa, the *Hipparion* from Langebaanweg (~5 Ma) has a $\delta^{13}\text{C}$ mean value ($n = 6$) of $-11.3 \pm 0.9\text{‰}$, implying a consumption of C₃ plants (Franz-Odenaal et al., 2002). Other lines of evidence, such as mesowear analysis, in this species are consistent with grazing behavior (Franz-Odenaal et al., 2003). Therefore, it would have a diet based on C₃ grasses, like the *H. pomeli* from AaO. In contrast, at the Makapansgat site (~3 Ma), the *Hipparion* indicates C₄ plant consumption (Sponheimer and Lee-Thorp, 2009; Lee-Thorp et al., 2010). In general, during the African Plio-Pleistocene, *Hipparion* had a diet mainly based on the consumption of C₄ grasses. Grass consumption has also been observed in AaO, although with the intake of C₃ plants. Despite the low presence of C₄ plants in North Africa during the study period, some species in AaO show a consumption of C₄ plants, but this is not the case for *H. pomeli*, which may indicate slightly different dietary preferences compared to its relatives in other parts of Africa.

The *Metridiochoerus phacochoeroides* from AaO shows a predominance of C₃ plant carbon values (mean $\delta^{13}\text{C} = -11.7 \pm 1.2\text{‰}$), but with significant variability, including a small percentage of C₄ consumption in one individual as observed in Alcelaphini. Microwear analysis shows a mixed diet, although with significant consumption of grasses, like other species classified as mixed feeders. The combination of both proxies indicates a preferential diet based on C₃ grass consumption.

The genus *Metridiochoerus* first appeared in Africa ~3.5 Ma. *Metridiochoerus phacochoeroides* is endemic to northern Africa and is distinct from the east and South African representatives of the genus. Besides AaO, *Metridiochoerus* is rare in North Africa, but is also known from its type-locality Ain Jourdel (Thomas, 1884).

In East Africa, *Metridiochoerus* between ~4 and 1 Ma were predominantly grazers with high C₄-grazer proportions (Harris and Cerling, 2002; Cerling et al., 2015; Souron, 2017; Uno et al., 2018). Dental microwear analysis conducted on *Metridiochoerus* from Olduvai (~1.8 Ma, Tanzania) points to mixed feeding and grazing behavior (Uno et al., 2018). In the Chiwondo Beds in Malawi (~2.5–1.5 Ma), *M. andrewsi* and *M. compactus* exhibit a predominant consumption of C₃ plants (Lüdecke et al., 2016).

Little is known about the diet of *Metridiochoerus* in South Africa. Some populations of *M. andrewsi* from Elandsfontein (~1.0–0.6 Ma) were consuming mostly C₃ plants (Luyt et al., 2000), but due to the overall predominance of C₃ plants in this area, as in the Chiwondo Beds in the Malawi Rift, could have been including grasses in their diet as well.

The *Gazella* sp. from AaO has carbon values that correspond to a C₃ plant-based diet (mean $\delta^{13}\text{C} = -11.6 \pm 0.6\text{‰}$). Microwear analysis shows a browser pattern; however, mesowear analysis indicates a mixed diet with a browsing tendency. This could imply a more purely browsing diet over a relatively brief period and a more varied consumption of plants, including grasses in their diet, for most of the year. As with Alcelaphini, *Gazella* has been present in North Africa since the Pliocene (Sahnouni et al., 2011; Van der Made et al., 2021) until the present day in Morocco, Algeria, and Tunisia (Schmid et al., 2005).

In North Africa, isotopic studies have been carried out on this genus in both Tighennif (~1 Ma; Algeria) with a mean $\delta^{13}\text{C}$ value ($n = 5$) of $-11.9 \pm 0.9\text{‰}$ and Guefât (~3–2.5 Ma; Morocco) with a mean $\delta^{13}\text{C}$ value ($n = 4$) of $-10.9 \pm 1.1\text{‰}$. At both sites, there is a clear predominance of C₃ plant consumption by *Gazella* (Fannin et al., 2021; Ramírez-Pedraza et al., 2023).

In East Africa, *Gazella janenschi* from the Laetolil Beds (~4.3–3.5 Ma) has carbon values ranging from -1.9 to -9.8‰ , implying a variable diet from C₄-grazing to C₃-browsing (Kingston and Harrison, 2007). This dietary flexibility has also been observed in different Antilopini analyzed in the Turkana Basin (Kenya), with extracted proportions of the isotopic signal of 17% C₄-grazing, 75% mixed C₃–C₄, and 8% C₃-browsing for the period of ~4.3 to 2.3 Ma, and 54% C₄-grazing, 46% mixed C₃–C₄, and 0% C₃-browsing for the period ~2.3 to 1.0 Ma (Cerling et al., 2015). The multiproxy study (isotopes, microwear, and mesowear) of Antilopini from Olduvai (1.8 Ma) also indicates a mixed feeder diet (Uno et al., 2018). The *Gazella* sp. from AaO, as well as those from the Pleistocene and Pliocene in Africa in general, seem to have the plasticity to consume distinct types of plants, adapting to seasonal availability. Even in East Africa before ~2.3 Ma, with a predominance of C₄ grassland in the area, they maintain a percentage of contribution from C₃ plant consumption.

In South Africa, *Gazella vanhoepeni* from Makapansgat (~3 Ma) is considered either a browser or a mixed-feeder preferring browsing based on isotopic, ecomorphological, microwear, and mesowear dental studies (Schubert et al., 2006). The diachronic and multiproxy study (isotopes, dental microwear texture, and mesowear analysis) of Antilopini (*Antidorcas*) from Sterkfontein Member 4 (~2.8–2 Ma) and Swartkrans Members (~2–0.8 Ma) also indicates a mixed diet with a certain browsing tendency for this genus (Sewell et al., 2019).

5.2. Palaeohabitat and palaeoclimate

The results of the combination of proxies suggest for AaO a landscape with a predominance of open and dry habitat, composed of C₃ woody plants and grasses and a low presence of C₄ plants. The closed canopy forest is absent in the surroundings of AaO, since no species has $\delta^{13}\text{C}_{\text{diet-meq}}$ values below -31.5‰ , which is established as a limit for this habitat.

5.2.1. Dry environment and seasonality

The Mean Annual Precipitation (MAP) in AaO measured 385 mm/year, indicating a dry climate. The aridity of the region is supported by the fact that environments dominated by C₃ plants with a MAP of 500 mm/year or less are typically associated with arid conditions. This aridity pattern is also evident in the Tighennif site (1 Ma; Algeria), recording a MAP of 297 mm/year (Supplementary Table 3). This reinforces the enduring prevalence of dry climates even with established hominin presence in North Africa. Kohn (2010) argues that the indicator's reliability depends on the mean MAP of all analyzed taxa. Thus, the average MAP remains the critical factor for assessing the robustness of this indicator. However, the variability in $\delta^{13}\text{C}_{\text{enamel}}$, MAP,

and $\delta^{13}\text{C}_{\text{diet-meq}}$ values, both inter- and intra-species (Table 1), suggests the presence of microhabitats (Patalano et al., 2021). In arid regions like those surrounding AaO and Tighennif, there can be localized areas of higher humidity, particularly in close proximity to water sources. Vegetation in these zones may exhibit lower $\delta^{13}\text{C}$ values than expected for the surrounding dry environment, especially in a particularly wet year or season (Kohn, 2010). This variability in the values could also be explained by the dynamics of the assemblage accumulation. Although the formation data of the site suggest a rapid accumulation over time (Geraads et al., 2022b), we cannot precisely determine how long it took to form, potentially encompassing many years with diverse climates and resources for consumption.

In dry environments, C₄ plants exhibit greater efficiency than C₃ plants under conditions of low atmospheric CO₂ concentration, high temperatures, and moisture stress (Ehleringer et al., 1991; Cerling et al., 1993). Therefore, the presence of C₄ plants in the diet of Alcelaphini and *M. phacochoeroides*, even in small proportions, aligns with arid environments. The variability in $\delta^{13}\text{C}_{\text{enamel}}$ values within species, especially in the aforementioned species, may suggest the existence of pronounced seasonal fluctuations.

Relative to aridity, the difference observed in the $\delta^{18}\text{O}$ values of obligate and non-obligate drinkers in AaO (1.9‰) is slightly higher than the difference found in herbivores from the Tsavo (1.7‰) region (Kenya), which has been defined as a dry savannah with vegetation characterized by semi-desert bushland with riparian woodland and a MAP of 500 mm/yr (Cerling et al., 2003, 2015). The species *S. maurusium* exhibits the highest $\delta^{18}\text{O}$ values, even in comparison to *Gazella* sp. Given that dental wear patterns indicate a browsing diet for both species, the elevated $\delta^{18}\text{O}$ values in *S. maurusium* may be attributed to its consumption of leaves from tall plants that it has access to due to its large size. Sun-exposed leaves, particularly in arid conditions, are highly sensitive to evaporative fractionation, resulting in an enrichment of ^{18}O (Gonfiantini et al., 1965; Barbour, 2007).

In this line, the combination of tooth microwear (short-term) and tooth mesowear (long-term) proxies has been used as a tool to identify seasonality (Sánchez-Hernández et al., 2016). Considering that microwear reflects the signal of a short-term diet, such as a single season, while mesowear reflects a longer period including probably all seasons, discrepancies in the results between both proxies would be indicative of dietary changes due to seasonal availability of resources. In AaO, *S. maurusium* exhibits a browsing pattern with the two proxies, indicating that its diet does not change throughout the year. For *Gazella* sp., tooth mesowear indicates browse-dominated mixed feeding, while microwear suggests browsing. This species is likely to have a more diverse diet, characterized by a higher consumption of grasses throughout the year, along with a significant increase in browsing during a particular season. In the case of Alcelaphini and *H. pomeli*, tooth mesowear indicates grass-dominated mixed feeding and grazing, respectively, while microwear suggests mixed feeding. It indicates a predominant consumption of grasses throughout the year with the introduction of other food items during specific periods of the year.

5.2.2. C₃ grassland and open habitat

In all species from AaO, the most discriminant microwear feature is the number of scratches, which is different in browsers and mixed feeders (Fig. 5). The high number of scratches in mixed feeders indicates significant consumption of grasses (see %0–17 in Table 2). However, the number of pits is very similar between browsers and mixed feeders with grazing tendencies. The relatively high number of pits and the presence of large pits in all species could be caused by incidental ingestion of abrasive grit resulting from feeding close to the ground in open and arid habitats (Semperebon and Rivals, 2007; Hoffman et al., 2015). This enables us to emphasize two environmental aspects: (1) The prevalence of taxa with a C₃ plant-based diet, many of which consume a significant amount of grasses, indicating the significant presence of C₃ grasslands in the study area. This assertion is corroborated by previous research on

the feeding habits of *Theropithecus atlanticus* in AaO. In that study, they employed time- and graminivore-calibrated carbon stable isotope values to illustrate a progressive transition towards an increased dependence on high-throughput bulk-feeding graminivory and proposed a consumption of grasses exhibiting a distinct C_3 isotopic signature (Fannin et al., 2021). (2) The presence of C_3 grassland, feeding close to the ground, and the presence of *T. atlanticus* (Alemseged and Geraads, 1998; Fannin et al., 2021) are indicators of open habitats. It is noteworthy that no other cercopithecine species have been discovered at the AaO site in Morocco. Additionally, while no fossil remains of *Theropithecus* have been found at the contemporaneous site of Guefaït in Morocco, the presence of *M. cf. sylvanus* has been noted (Alba et al., 2021). Previous ecological studies suggest that this macaque inhabited a woodland ecosystem, where it had a folivorous-frugivorous diet with hard item consumption which was primarily based on C_3 plants (Ramírez-Pedraza et al., 2023). This indicates a low wood cover in the landscape of western Morocco during the Plio-Pleistocene boundary. In the same line, the relative frequency of two species of bovids found in Guefaït and AaO may provide insight into the predominant environmental conditions. Specifically, Tragelaphini are associated with wooded and humid habitats, while Alcelaphini are linked to more open environments (Bobe et al., 2007). Notably, the abundance of Alcelaphini and the scarcity of Tragelaphini in AaO is significant (Geraads and Amani, 1998; Geraads et al., 2022a), while the opposite trend is observed in Guefaït (Sala-Ramos et al., 2022; Ramírez-Pedraza et al., 2023). Previous works on AaO have used a method for predicting palaeohabitats using measurements (height/width proportions) of bovid astragali (DeGusta and Vrba, 2003). The proportions of this bone in the bovids from AaO confirm the absence of heavy wood cover and the predominance of open habitat (Geraads et al., 2022a).

6. Conclusion

This research highlights the importance of integrating different proxies for palaeoecological reconstructions, being particularly useful in areas where there is a predominance of C_3 plants such as in North Africa, where it is more challenging to define the diet and habitat of mammals from stable isotope analysis alone. In this work, the complementarity of dental wear analysis has allowed us to determine diets that range from grazing to browsing behavior. Our multiproxy analysis indicates that during the Plio-Pleistocene boundary in the western coastal region of Morocco, open C_3 grasslands and shrubland predominated in an arid climate.

The most notable distinction between taxa from East, South, and Central Africa in comparison to those from the North is their extensive reliance on C_4 plants, which are associated with tropical grasses from open arid habitats. In the AaO area, although there was a predominance of C_3 plants, the environment was similarly arid and characterized by open grasslands. This aridity was also evident in Tighenif, even with the presence of hominins in the region. Therefore, the dry environment should not have been a limitation to hominins occupation in North Africa. Despite AaO being one of the most abundant fossil fauna sites in North Africa during the Plio-Pleistocene, taxon diversity remains relatively low compared to contemporary sites in the East and South. This could be attributed to the limited diversity of habitats in AaO, such as the absence of woody vegetation or, for instance, the possible lack of permanent water sources, as indicated by the absence of taxa like Hippopotamidae, crocodiles, or freshwater birds (Geraads et al., 2022a).

However, further research in different archaeological and palaeontological sites from the Early Pleistocene and Late Pliocene in the Maghreb is necessary to gain a holistic understanding of the ecological and climatic dynamics that contributed to the dispersal, occupation, and evolution of mammals and early hominins.

Credit author statement

Iván Ramírez-Pedraza: Conceptualization, Formal analysis, Visualization, Investigation and Writing - Original Draft; Florent Rivals: Supervision and Writing - Review & Editing; Carlos Tornero: Supervision and Writing - Review & Editing; Denis Geraads: Writing - Review & Editing; Jean Paul Raynal: Writing - Review & Editing; David Lefèvre: Project administration and Writing - Review & Editing; Abderrahim Mohib: Project administration, Resources and Writing - Review & Editing.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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5.2.2. Palaeoecological reconstruction of herbivores from Grotte à Hominidés (ThI-GH) and Grotte des Rhinocéros (OHQ1-GDR)

5.2.2.1. Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{18}\text{O}$) at ThI-GH and OHQ1-GDR

The $\delta^{13}\text{C}$ values of all taxa measured in ThI-GH ranged from -14.5 to -8.1‰ with a mean and standard deviation of $-11.2 \pm 1.4\text{‰}$ ($n = 56$) (**Fig. 28**). The data for each species are described below: *Ceratotherium mauritanicum* ($n = 12$; range = -13.3 to -10‰; mean = $-11.8 \pm 1\text{‰}$), Alcelaphini ($n = 12$; range = -11.9 to -8.1‰; mean = $-10.1 \pm 1.2\text{‰}$), *Gazella* cf. *atlantica* ($n = 15$; range = -14.5 to -8.9‰; mean = $-11.6 \pm 1.5\text{‰}$), *Phacochoerus africanus* ($n = 2$; 11.9 and 12.2‰), *Equus* cf. *mauritanicus* ($n = 5$; range = -12.8 to -10.3‰; mean = $-11.5 \pm 0.9\text{‰}$) and *Theropithecus oswaldi* ($n = 10$; range = -12.9 to -8.2‰; mean = $-11 \pm 1.4\text{‰}$). The two taxa with the highest variability and the most positive values are *T. oswaldi* and *G. cf. atlantica*. *C. mauritanicum* is the species with the lowest variability and *G. cf. atlantica* has the most negative values.

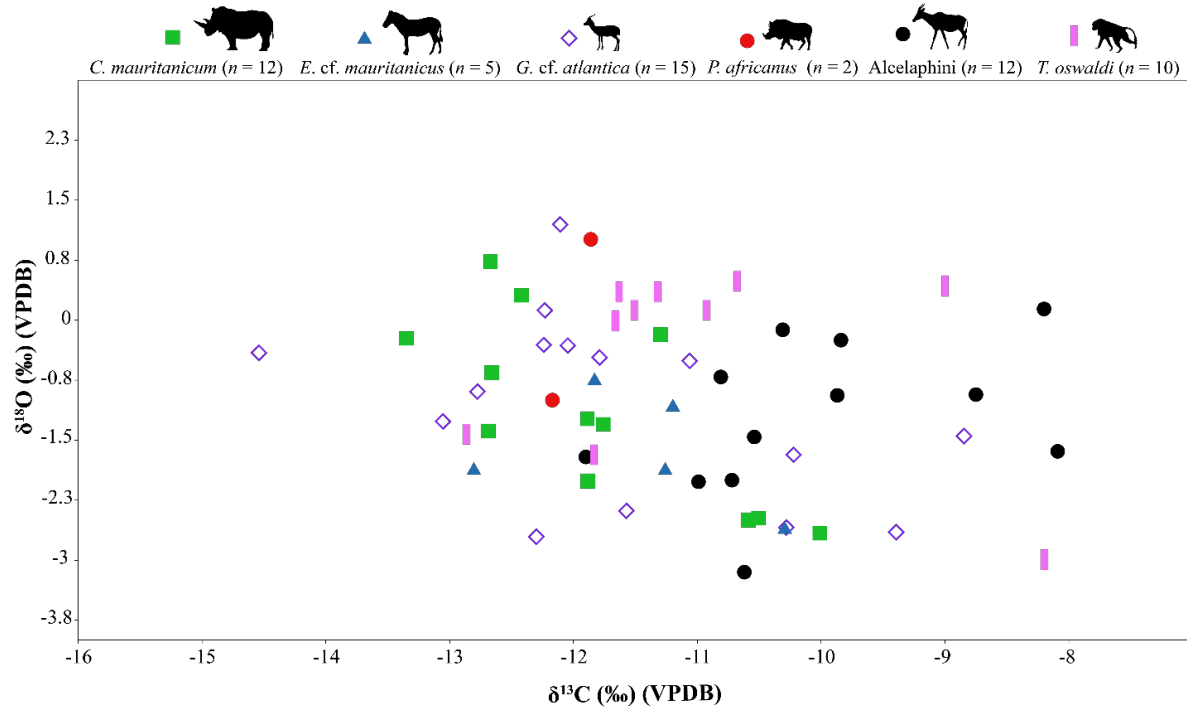


Figure 28. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the tooth enamel of fossil fauna from ThI-GH.

The $\delta^{18}\text{O}$ values ranged from -3.2 to 1.2‰ with a mean and standard deviation of $-1 \pm 1.1\text{‰}$ ($n = 56$) (**Fig. 28**). The data for each species are described below: *C. mauritanicum* ($n = 12$; range = -2.6 to 0.7‰; mean = $-1.1 \pm 1.1\text{‰}$), Alcelaphini ($n = 12$; range = -3.2 to 0.1‰; mean = $-1.2 \pm 0.9\text{‰}$), *G. cf. atlantica* ($n = 15$; range = -2.7 to 1.2‰; mean = $-1.1 \pm 1.1\text{‰}$), *P. africanus* ($n = 2$; -1 and 1 ‰), *E. cf. mauritanicus* ($n = 5$; range = -2.6 to -0.7

‰; mean = -1.6 ± 0.7 ‰) and *T. oswaldi* ($n = 10$; range = -3 to 0.5 ‰; mean = -0.4 ± 1.2 ‰). The species with the highest variability and positive values is *G. cf. atlantica*. *E. cf. mauritanicus* is the species with the lowest variability and, Alcelaphini and *T. oswaldi* are the species with the most negative values (raw data for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of ThI-GH in appendices pp. 290 to 291).

The $\delta^{13}\text{C}$ values of all taxa measured in OHQ1-GDR ranged from -14.5 to -5.1 ‰ with a mean and standard deviation of -11.1 ± 1.4 ‰ ($n = 83$) (Fig. 29). The data for each species are described below: *C. mauritanicum* from the Upper set (UP) ($n = 5$; range = -12 to -9.4 ‰; mean = -10.5 ± 1.1 ‰), *C. mauritanicum* from the Lower set ($n = 30$; range = -12.3 to -9.7 ‰; mean = -11 ± 0.7 ‰), Alcelaphini from the LW ($n = 16$; range = -12.7 to -9.1 ‰; mean = -10.9 ± 1.4 ‰), *G. cf. atlantica* from the UP ($n = 9$; range = -14.5 to -10 ‰; mean = -12 ± 1.4 ‰), *G. cf. atlantica* from the LW ($n = 15$; range = -14 to -10.7 ‰; mean = -12 ± 1 ‰), *Camelus thomasi* from the LW ($n = 4$; range = -9.9 to -5.1 ‰; mean = -7.7 ± 2.4 ‰), *E. cf. mauritanicus* from the LW ($n = 8$; range = -12.3 to -10.3 ‰; mean = -10.8 ± 0.6 ‰) and *T. oswaldi* from the LW ($n = 1$; range = -12.2 ‰). The two taxa with the highest $\delta^{13}\text{C}$ values variability are *G. cf. atlantica* and *C. thomasi*. Also, *C. thomasi* is the species with the most positive values. *E. cf. mauritanicus* is the species with the lowest variability, and *G. cf. atlantica* is the species with the most negative values.

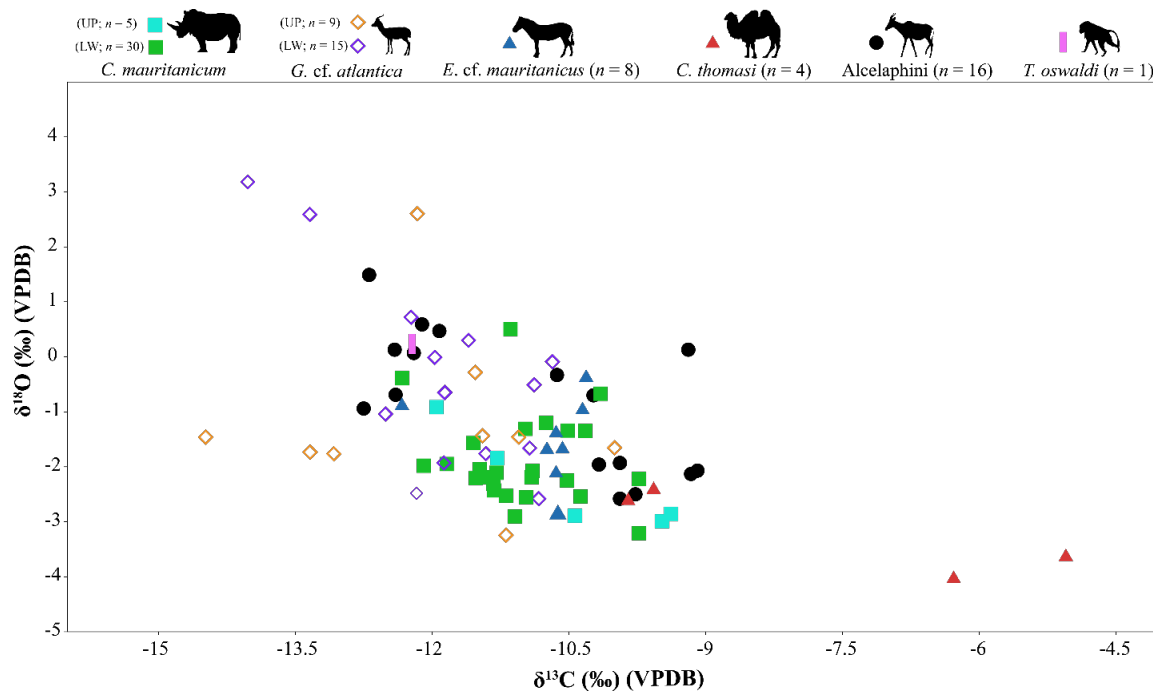


Figure 29. The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values from the tooth enamel of fossil fauna from OHQ1-GDR.

The $\delta^{18}\text{O}$ values ranged from -4 to 3.2 ‰ with a mean and standard deviation of -1 ± 1.4 ‰ ($n = 83$) (Fig. 29). The data for each species are described below: *C. mauritanicum* from the UP set ($n = 5$; range = -3 to -0.9 ‰; mean = -2.3 ± 0.9 ‰), *C. mauritanicum* from the

LW set ($n = 30$; range = -3.2 to 0.5‰ ; mean = $-1.9 \pm 0.8\text{‰}$), Alcelaphini from the LW ($n = 16$; range = -2.6 to 1.5‰ ; mean = $-0.8 \pm 1.3\text{‰}$), *G. cf. atlantica* from the UP ($n = 9$; range = -3.2 to 2.6‰ ; mean = $-1.2 \pm 1.6\text{‰}$), *G. cf. atlantica* from the LW ($n = 15$; range = -2.6 to 3.2‰ ; mean = $-0.5 \pm 1.7\text{‰}$), *Camelus thomasi* from the LW ($n = 4$; range = -4 to -2.4‰ ; mean = $-3.1 \pm 0.8\text{‰}$), *E. cf. mauritanicus* from the LW ($n = 8$; range = -2.8 to -0.3‰ ; mean = $-1.5 \pm 0.8\text{‰}$) and *T. oswaldi* from the LW ($n = 1$; range = 0.2‰). In this case, the species with the highest variability and the most positive values is *G. cf. atlantica*. *C. mauritanicus* is the species with the lowest variability, and *C. thomasi* is the species with the most negative values (**raw data for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of OHQ1-GDR in appendices pp. 292 to 293**).

If we compare the distribution of carbon and oxygen values for all species of ThI-GH and OHQ1-GDR from UP and LW set, we observe that they are very similar. In the case of carbon (**Fig. 30**), the most positive values stand out for *C. thomasi* from OHQ1-GDR, indicating a significant percentage of C_4 plant consumption. Regarding oxygen values (**Fig. 31**), the distributions of values are again very similar, with somewhat more positive values for *G. cf. atlantica* from OHQ1-GDR. In the individual species comparison (**Fig. 32**), almost identical $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are also noticeable.

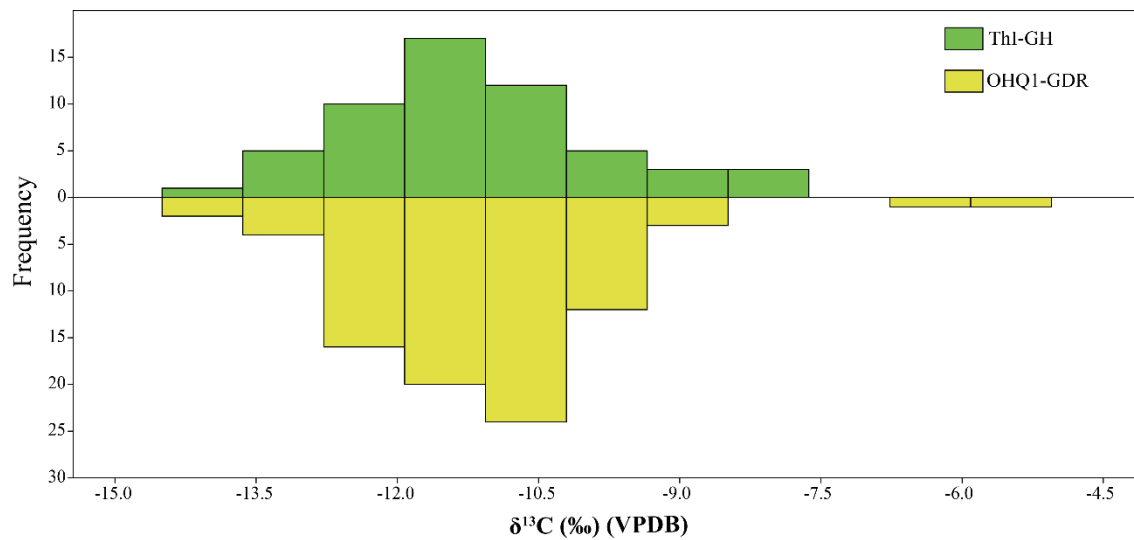


Figure 30. Frequency histogram of $\delta^{13}\text{C}$ values from ThI-GH and OHQ1-GDR.

The average $\delta^{13}\text{C}$ modern equivalent of diet composition (diet-meq) value (-25.8‰) and Mean Annual Precipitation (MAP) of 361 mm/yr for ThI-GH, and the average $\delta^{13}\text{C}_{\text{diet-meq}}$ value (-25.9‰) and MAP of 301 mm/yr for OHQ1-GDR, suggest a relatively arid environment for both sites (samples with $\delta^{13}\text{C}$ values with a diet-meq higher than -24‰ have been discarded due to possible C_4 consumption, as stated by Kohn (2010). This aridity is defined by Kohn (2010) as ecosystems with a $\text{MAP} \leq 500$ mm/yr and $\delta^{13}\text{C}_{\text{diet-meq}}$

values between -26 and -24‰ (raw data for MAP calculation in appendices pp. 294 to 295 and 296 to 297).

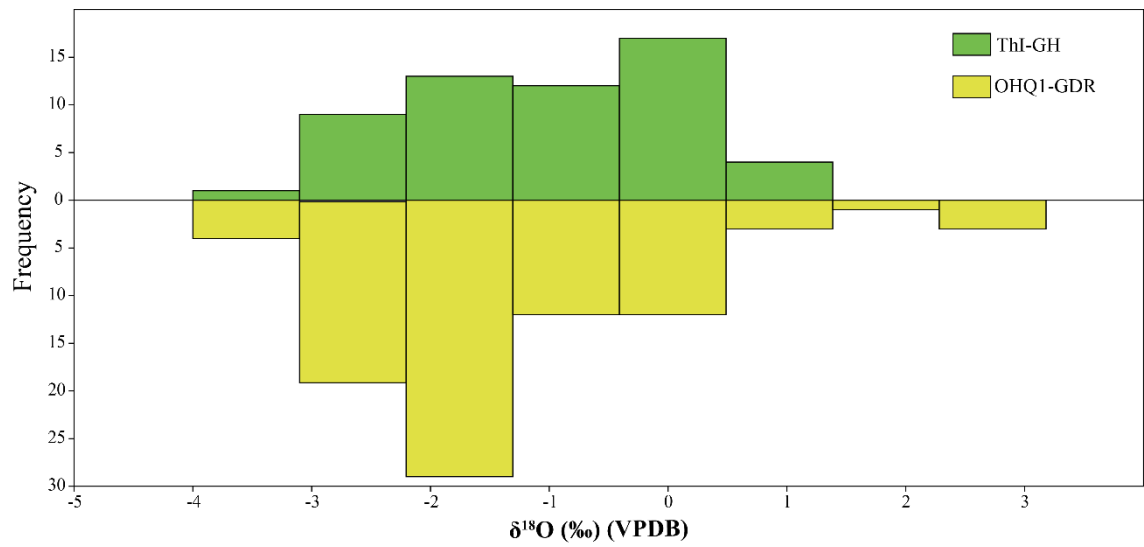


Figure 31. Frequency histogram of $\delta^{18}\text{O}$ values from ThI-GH and OHQ1-GDR.

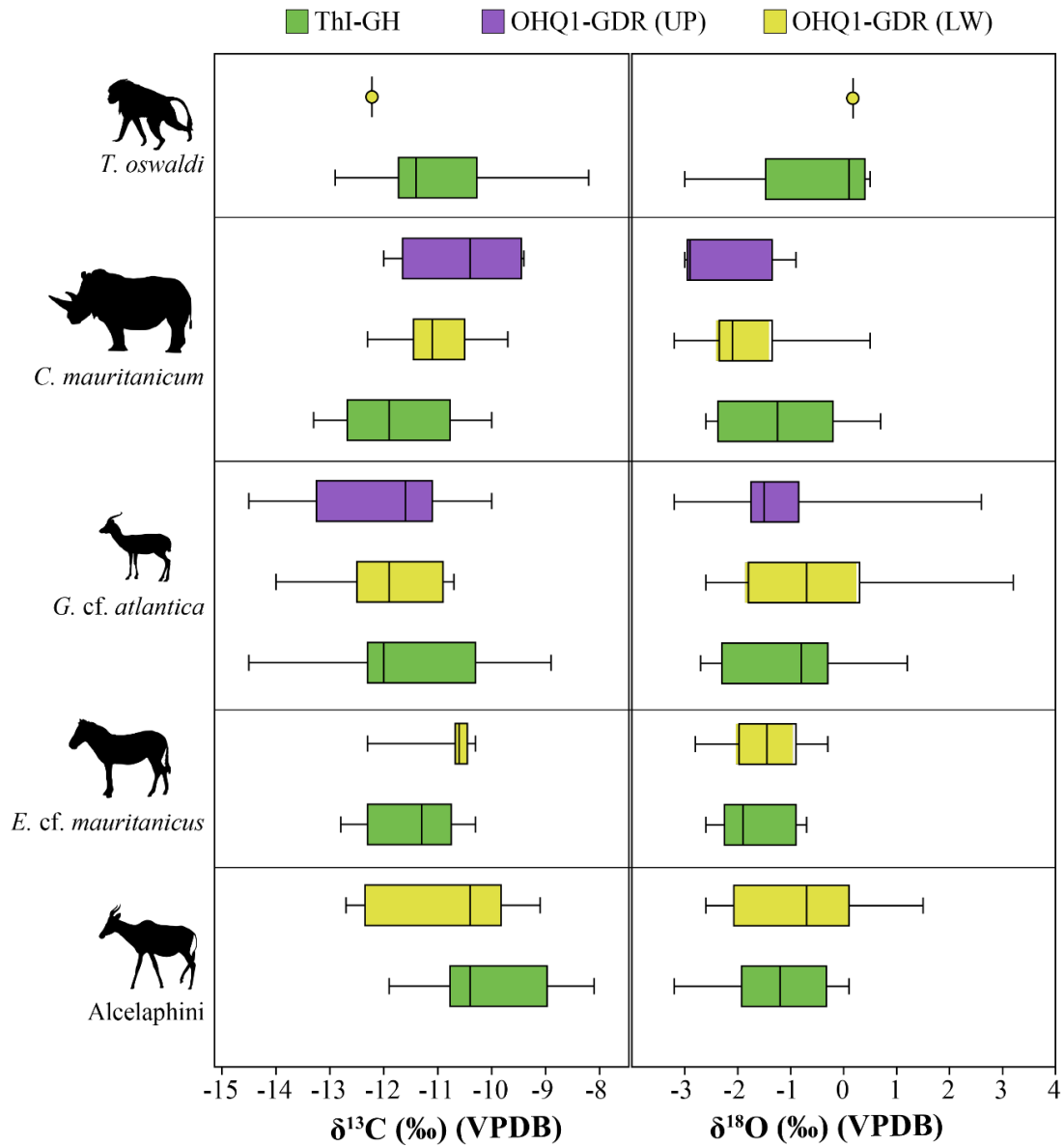


Figure 32. Boxplots for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of the ungulates from ThI-GH and OHQ1-GDR (UP and LW set). Boxes = first and third quartile for each taxon, whiskers = full range for each taxon and hashes within boxes = median value.

5.2.2.2. Dental mesowear analysis at ThI-GH and OHQ1-GDR

The mesowear pattern of ThI-GH specimens ($n = 41$) is characterised by occlusal surfaces ranging from sharp cusps and high relief (low abrasion) to low relief with rounded cusps (high abrasion). It corresponds to mesowear scores with values from 1 to 6 (**Fig. 33**). The *G. cf. atlantica* has the lowest level of abrasion with a MWS of 1.3, falling in the MWS average of extant mixed feeders and fruit browsers with browser tendency. The Alcelaphini, with variability in abrasion levels, has an average MWS of 2 and is categorised as a mixed feeder. In the case of *E. cf. mauritanicus*, the MWS indicates high

levels of abrasion, with a MWS average of 5. This pattern places this species among extant grazers (**raw data in appendices pp. 298 to 299**).

As in ThI-GH, the mesowear pattern of OHQ1-GDR specimens ($n = 54$) is characterised by occlusal surfaces ranging from sharp cusps and high relief (low abrasion) to low relief with rounded cusps (high abrasion). It corresponds to mesowear scores with values from 0 to 6 (**Fig. 33**). The *G. cf. atlantica* from UP has the lowest level of abrasion with a MWS of 1, falling in the MWS average of extant leaf and fruit browsers. The *G. cf. atlantica* and Alcelaphini from LW have also a low average MWS (1.4), being in the range of MWS of extant mixed feeders but with a tendency towards a browsing diet. In the case of *E. cf. mauritanicus*, *C. thomasi* and *C. mauritanicum*, the MWS indicates high levels of abrasion, with a MWS average of 3, 4 and 4.4, respectively, falling among extant grazers.

The pattern is nearly identical for the same species in both sites, *G. cf. atlantica* and Alcelaphini. *E. cf. mauritanicus* exhibits a grazing diet in both sites; however, it has a slightly higher mesowear score in ThI-GH than OHQ1-GDR.

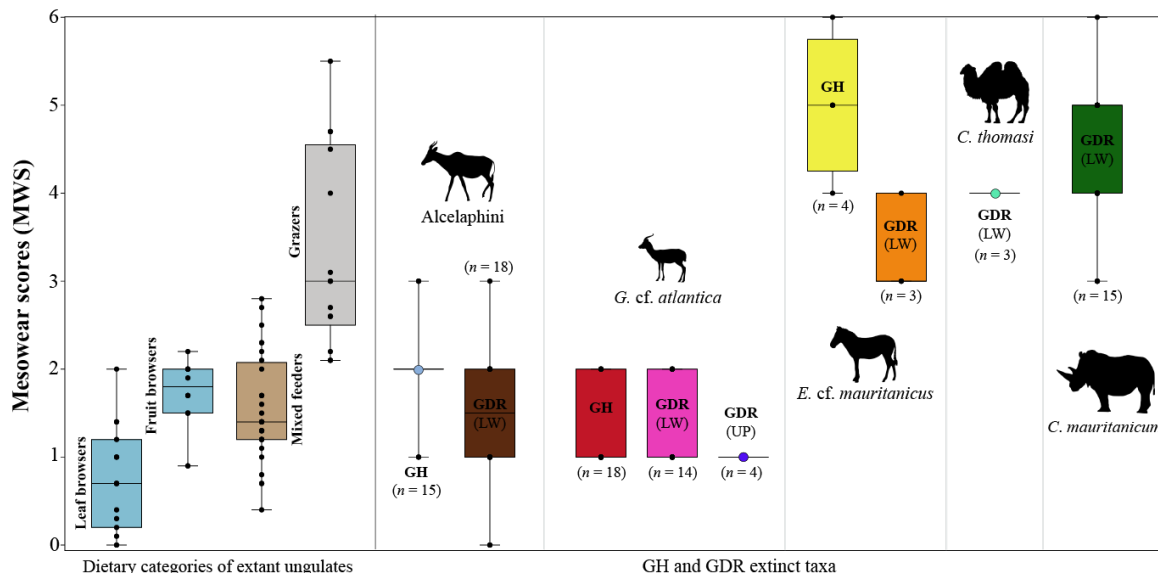


Figure 33. Jitter boxplot with mesowear scores (MWS) of the ungulates from ThI-GH and OHQ1-GDR. Boxes = first and third quartile for each taxon; whiskers = full range, and hashes within boxes = median value. Extant ungulates database (Fortelius and Solounias, 2000).

5.2.2.3. Dental microwear analysis at ThI-GH and OHQ1-GDR

At ThI-GH, all herbivores ($n = 49$) show browsing or mixed feeding traits (**Fig. 34**) and are classified into two groups (**raw data in appendices pp. 298 to 299**). The first group includes the *G. cf. atlantica* and plot among extant browser ungulates. The second group comprises Alcelaphini, *P. africanus*, *E. cf. mauritanicus* and *C. mauritanicum* plots among extant mixed feeders. On the one hand, *G. cf. atlantica* has a dental microwear pattern characterised by a high number of pits (NP = 35.1) and a small number of scratches

(NS = 9.3). On the other hand, the species of the second group have a microwear pattern defined by a similar number of pits (NP = 24.8) and scratches (NS = 20). *G. cf. atlantica* (NS = 9.3) is the species with a lower number of scratches, and *E. cf. mauritanicus* (NS = 25.5) and Alcelaphini (NS = 25.5) have a higher number of scratches. The *G. cf. atlantica* (NP = 35.1) has the highest abundance of pits, and *C. mauritanicum* (NP = 23.1) has the lowest number of pits. Despite the differences with *G. cf. atlantica*, all species generally have a high number of pits. Although the Alcelaphini, *C. mauritanicum*, *P. africanus* and *E. cf. mauritanicus* in **Fig. 34** are classified among extant mixed feeders, the high number of scratches indicates a high proportion of grasses in their diet.

The SWS, between 1 and 1.4, indicates a mixture of fine and coarse scratches for all species. Hyper-coarse scratches have been found only in one *G. cf. atlantica* specimen. Cross scratches are absent in *E. cf. mauritanicus*, Alcelaphini and *G. cf. atlantica*, but in 100% of individuals in *C. mauritanicum* and *P. africanus*. The presence of large pits, gouges, and puncture pits in all individuals of all species was remarkable. The identified pattern is typical of the consumption of hard objects like fruits or seeds (Sempredon et al., 2004; Godfrey et al., 2004). In this scenario, as it appears in both browsers and grazers, it is likely a result of unintentional ingestion of abrasive grit during feeding close to the ground. This pattern indicates open habitats and arid environments (Sempredon and Rivals, 2007).

The same pattern of ThI-GH is observed in OHQ1-GDR. All herbivores ($n = 74$) display browsing or mixed feeding dietary traits (**Fig. 34**). The species analysed are classified into two groups. The first group includes the *C. thomasi* and *G. cf. atlantica* from UP and LW set plot among extant browser ungulates. The second group includes Alcelaphini, *E. cf. mauritanicus* and *C. mauritanicum* from UP and LW plots among extant mixed feeders. The first group has microwear patterns characterised by a high number of pits (NP = 36.5) and a small number of scratches (NS = 10.6), and the second group has a microwear pattern defined by a similar number of pits (NP = 27.6) and scratches (NS = 23). *G. cf. atlantica* from LW (NS = 9.5) is the species with a lower number of scratches, and *E. cf. mauritanicus* (NS = 24.9) and *C. mauritanicum* from LW (NS = 24.8) have a higher number of scratches. All species have a relatively high number of pits. The *G. cf. atlantica* from LW (NS = 37.1) and UP (NS = 36.8) have the highest abundance of pits. As in ThI-GH, although the Alcelaphini, *E. cf. mauritanicus* and *C. mauritanicum* from UP and LW are classified among extant mixed feeders, the high number of scratches indicates a high proportion of grasses in their diet.

The SWS, between 0.9 and 1.2, indicates a mixture of fine and coarse scratches for all species. Hypercoarse scratches have been found only in one individual of *C. mauritanicum* from the LW set and in two *G. cf. atlantica* from the UP set. In the case of large pits, gouges and puncture pits, the pattern observed in ThI-GH is repeated. These dietary traits appear in 100% of the individuals analysed and in all species.

The ungulates from both sites occupy the same ecological niche. However, all species from OHQ1-GDR have a slightly higher number of both pits and scratches.

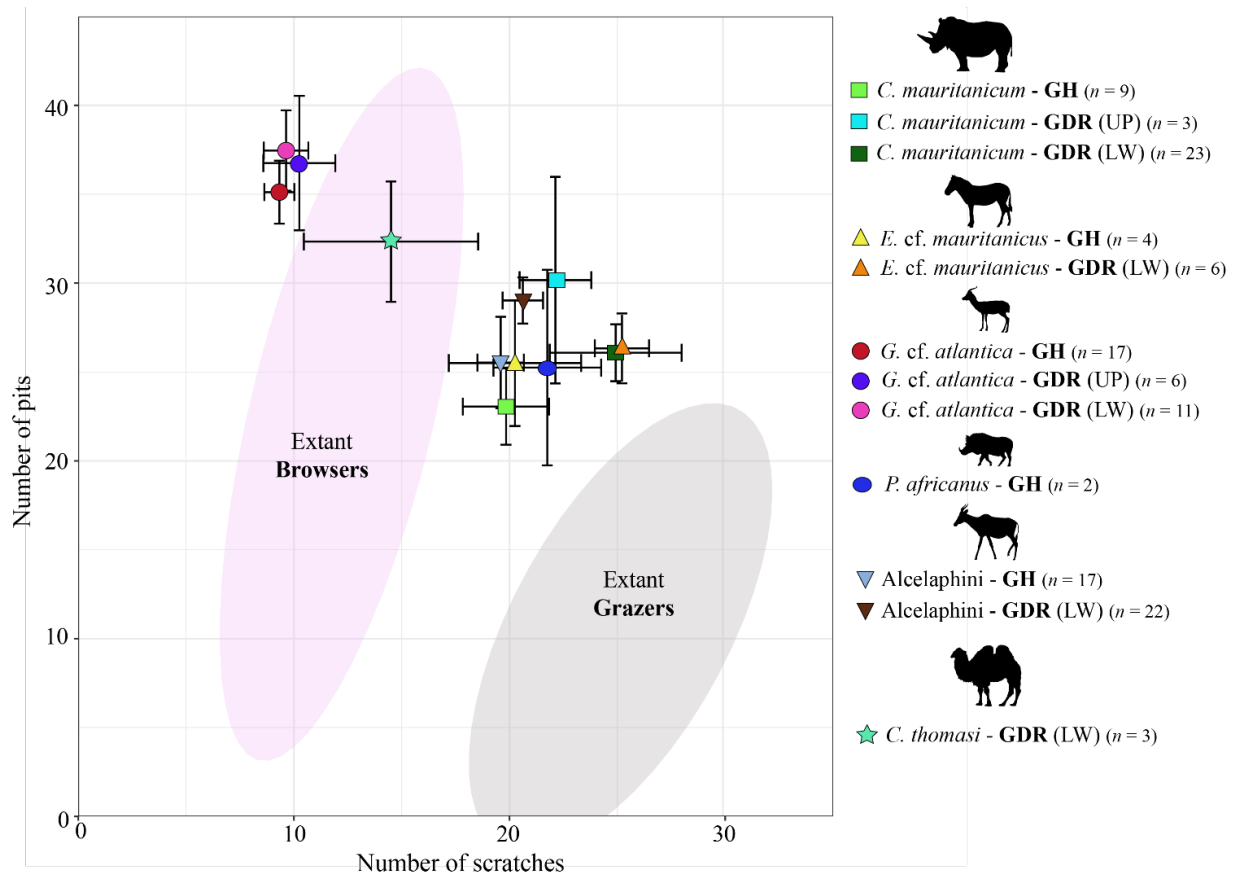


Figure 34. Bivariate plot of the average numbers of pits and scratches for the species from ThI-GH and OHQ1-GDR. Error bars correspond to the fossil samples' standard deviation (± 1 SD). Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant browsers and grazers based on the database from Solounias and Semperebon (2002).

Both sites are located in the same area at a short distance from each other; however, they correspond to different temporal periods: ThI-GH (~ 0.77 Ma), GDR-UP (~ 0.5 Ma), and GDR-LW (~ 0.7 Ma). The results from the three proxies do not indicate changes in diet or landscape over that ~ 0.3 Ma difference. The two faunal assemblages exhibited similar ecological conditions at the time of their respective formation.

5.2.3. Paper IV: Martínez et al. (2024). Ecological context of Theropithecus oswaldi from the early Middle Pleistocene site of Grotte à Hominidés at Thomas Quarry I through dental microwear analysis (Casablanca, Morocco) (Under review).

Ecological context of *Theropithecus oswaldi* from the early Middle Pleistocene site of Grotte à Hominidés at Thomas Quarry I (Casablanca, Morocco) through dental microwear analysis

Laura M. Martínez ^{a, b *}, Iván Ramírez-Pedraza ^{c, d *}, Ferran Estebaranz-Sánchez ^b, Florent Rivals ^{c, d, e}, Carlos Tornero ^{f, c}, Luis Hidalgo-Trujillo ^{a, b}, Juan José Ibáñez ^g, Camille Daujeard ^h, Denis Geraads ⁱ, Rosalia Gallotti ^{j, k}, Jean Paul Raynal ^{k, l}, David Lefèvre ^j, Abderrahim Mohib ^{l, m}

**Corresponding authors*

^a Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Secció de Zoologia i Antropologia Biològica, Universitat de Barcelona, Barcelona, Spain,

^b Institut d'Arqueologia de la Universitat de Barcelona, Barcelona, Spain

^c Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.

^d Universitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain

^e ICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

^f Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain.

^g Archaeology of Social Dynamics (ASD), Institución Milá i Fontanals de Investigación en Humanidades (IMF), Spanish National Research Council (CSIC), Barcelona, Spain

^h Histoire Naturelle de l'Homme Préhistorique, (HNHP, UMR 7194), MNHN, CNRS, UPVD, Paris, France

ⁱ CR2P-UMR 7207, CNRS, MNHN, Sorbonne Université, Paris, France.

^j LabEx ARCHIMEDE, et UMR 5140 Archéologie des sociétés méditerranéennes, Université de Montpellier Paul Valéry – CNRS, Campus Saint Charles, 34199 Montpellier, France.

^k Université Bordeaux, CNRS, UMR 5199 PACEA-PPP, Bâtiment B18 Allée Geoffroy Saint-Hilaire CS 50023, 33615 Pessac Cedex, France.

^l Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

^m Direction provinciale de la Culture, Avenue Mohammed V, quartier administratif, Kénitra, Morocco.

** Corresponding authors*

E-mail address: lmartinez@ub.edu (L. M. Martínez) and ramirez.pedraza.ivan@gmail.com (I. Ramírez-Pedraza).

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Abstract

Theropithecus is a genus of primates widely distributed across Africa during the Early and Middle Pleistocene. However, nowadays, only *Theropithecus gelada* exists in the highlands of Ethiopia. This taxon is characterised by a diet primarily consisting of C₄ grasses with seasonal dietary shifts to leaves and forbs. The evidence of extinct *Theropithecus* in eastern Africa suggests an increase of C₄ resources along the lineage, reaching nearly 100% C₄ plant consumption by 1 Ma. However, there is limited data on the feeding ecology of *Theropithecus* in northern Africa after 1 Ma. In this study, we analyse the ecology of *Theropithecus oswaldi* from the early Middle Pleistocene site of Grotte à Hominidés (western Morocco) through a combined analysis of occlusal microwear (low magnification) and buccal microwear texture analysis. For both approaches, we compared the microwear pattern of *T. oswaldi* with a reference collection of extant members of Cercopithecoidea. Our occlusal microwear results show that *T. oswaldi* exhibits a pattern similar to extant *Mandrillus sphinx* and, to a lesser extent, to *T. gelada*. The buccal analysis reveals a pattern similar to open savanna dweller *Papio hamadryas* suggesting a broader dietary spectrum compared to that described in extant *T. gelada*. Although our results indicate the ingestion of grasses (i.e., a high number of scratches), *T. oswaldi* likely had a more varied diet that included other food items such as fruits, seeds, or leaves. The complementarity of these methods allows for dietary reconstruction on different temporal ranges, suggesting that *Theropithecus* from northern Africa did not have a diet as heavily based on the consumption of grasses as their early Middle Pleistocene counterparts from eastern Africa.

1. Introduction

1.1. *The fossil record of Theropithecus from the Plio-Pleistocene boundary to the Middle Pleistocene.*

The evolutionary history of primates is a series of adaptation and diversification events (Roos et al., 2019). *Theropithecus* is a medium to large-sized papionine genus with robust dentition and a distinctive cranial morphology that first emerged in the fossil record of eastern Africa during the Pliocene, approximately 4 million years ago (Ma) (Cerling et al., 2013; Frost et al., 2014). It constituted a prominent presence in the fossil primate assemblage across southern, eastern, and northern Africa during the Plio-Pleistocene (Jolly, 1972; Dechow and Singer, 1984; Delson and Hoffstetter, 1993; Alemseged and Geraads, 1998; Jablonski and Frost, 2010; Frost et al., 2020; Getahun et al., 2023). Currently, only one surviving species, *Theropithecus gelada*, persists, with most of the population residing in select regions of Ethiopia's northern and southern highlands (Girmay and Dati, 2020).

This genus occupied most of the African continent and dispersed beyond Africa, primarily during the Early Pleistocene (Hughes et al., 2008). To date, fossil evidence of *Theropithecus* outside of Africa has been found at three sites: Mirzapur in India, dating between 1 and 0.6 Ma (Gupta and Sahni, 1981; Azzaroli and Napoleone, 1982; Nanda, 2002; Patnaik et al., 2014), Cueva Victoria in Spain, dating to approximately 0.9 Ma (Gibert et al., 1995, 2016; Ferràndez-Cañadell et al., 2014; Martínez et al., 2020), and perhaps Ubeidiya in Israel, dating to approximately 1.4 Ma (Belmaker, 2010; Geraads and de Bonis, 2020).

The oldest fossil evidence of *Theropithecus* in northern Africa is found in two Plio-Pleistocene boundary sites (~2.5 Ma). On the one hand, the Ahl al Oughlam site on the Atlantic coast of Morocco, and the other hand, the Aïn Jourdel site located East of Algeria (Thomas, 1884; Geraads, 1987, 2002, 2006; Raynal et al., 1990; Delson, 1993; Alemseged and Geraads, 1998). The Aïn Jourdel *Theropithecus* remains consist of an isolated single lower probably first molar (Thomas, 1884; Delson, 1993; Alemseged and Geraads, 1998) most similar to early *Theropithecus darti* (Delson, 1993). Ahl al Oughlam *Theropithecus* remains are contemporaneous or slightly earlier than those from Aïn Jourdel according to Alemseged and Geraads (1998). The published remains include a

frontal bone (AaO-15), a partial left mandible (AaO-288), a canine (AaO-303), and multiple postcanine teeth (3 premolars, 1 M¹, 2 M² and 10 M³) (Alemseged and Geraads, 1998). These Plio-Pleistocene *Theropithecus* remains were initially attributed to *Theropithecus atlanticus* (Thomas, 1884) (Delson, 1993; Alemseged and Geraads, 1998). Later studies found morphological similarities between *T. atlanticus* and *T. darti*, indicating a probable evolutionary link (Alemseged and Geraads, 1998; Delson, 1993).

During the Early and Middle Pleistocene, the sites of Tighennif (~1 Ma) in Algeria (Geraads, 1987, 2016; Duval et al., 2021), Oulad Hamida 1 Quarry - Grotte des Rhinocéros (OHQ1-GDR; ~0.7 Ma) (Daujeard et al., 2020; Raynal et al., 2023b) and Thomas Quarry I - Grotte à Hominidés (ThI-GH; ~0.77 Ma) (Raynal et al., 2010, 2023a; Gallotti et al., 2021; Perini et al., 2023, 2024) yielded fossil remains of *T. oswaldi*. The fossil remains from ThI-GH represent one of the latest evidences of this cercopithecine in northern Africa.

1.2. Palaeoecology of Theropithecus from the Plio-Pleistocene boundary to the Middle Pleistocene.

Extinct *Theropithecus* were assumed to be graminivorous based on dental morphology (Jolly, 1972). The high crowned bilophodont molars with high cusp reliefs and curved infoldings of enamel suggest a graminivore diet (Jablonski, 1993). However, several works have provided abundant stable isotope (Cerling et al., 2013; Levin et al., 2015; Wynn et al., 2016) and dental microwear (Shapiro et al., 2016; Merceron et al., 2021) evidence discussing the palaeodietary evolution of the genus. Before 3 Ma, *T. oswaldi* consumed a non-negligible amount of C₃ plants in addition to the C₄ resources (Souron, 2018). However, after 2 Ma, the feeding ecology of *T. oswaldi* was dominated by C₄ plants, and by 1.0 Ma, *T. oswaldi* from Kenya had a nearly 100% C₄-based diet (Cerling et al., 2013). In contrast, evidence from the Ledi Geraru site from Ethiopia suggests that ~2.8 Ma *Theropithecus* had already shifted to diets more strongly dominated by C₄ graminoids. Moreover, the microwear results of *Theropithecus* from the Shungura Formation display significant variations on occlusal dental microtextures, suggesting several dietary shifts over time in relation to changes in seasonality (Martin et al., 2018). While evidence suggests that in eastern Africa, the paleo landscape was characterized by C₄ open grasslands, the isotopic evidence from Ahl al Oughlam (~2.5 Ma) and Tighennif

(~1 Ma) situated both in northern Africa suggests a dominance of C₃ grasses for *Theropithecus*, with low C₄ consumption (Fannin et al., 2021; Ramírez-Pedraza et al., 2023). However, by 2 Ma, *T. oswaldi* would change to bulk-feeding graminivory that increased through time (Fannin et al., 2021). Therefore, although there was a trend to increase the proportion of C₄ in *Theropithecus* diets, the complex northern and eastern African ecosystems during the Plio-Pleistocene may have led to different ¹³C/¹²C ratios in relation to the landscape heterogeneity.

Out of Africa, the dental microwear analysis of *T. oswaldi* from Cueva Victoria (~0.9 Ma; Cartagena, Spain), situated in the southeastern Iberian Peninsula, suggests an abrasive diet for these specimens, different from that observed in extant *T. gelada*. The results of Cueva Victoria, with a similar age to Tighennif in Algeria, suggest a variable diet for the genus that inhabited Mediterranean ecosystems combined with C₃ grasslands (Martínez et al., 2020).

1.3 Palaeoecology of the ThI-GH site

The faunal assemblage of ThI-GH is dominated by gazelles (*Gazella* cf. *atlantica*) and Alcelaphini. Along with the presence of Hippotragini (*Oryx* sp.), zebra *Equus* cf. *mauritanicus*, and rhino *Ceratotherium mauritanicum*, these ungulates suggest an open environment (Daujeard et al., 2016; Geraads et al., 2022). Furthermore, the presence of only one species of non-human primate in the fossil assemblage, *T. oswaldi*, is another indicator of generally poor tree cover (Geraads, 2010; Raynal et al., 2010; Geraads et al., 2022).

Preliminary studies of dental wear in the herbivores of ThI-GH also point to a similar trend, indicating a predominance of arid climate with open landscapes dominated by grasslands and shrublands (Ramírez-Pedraza et al., 2024). Many of the analyzed taxa (Alcelaphini, *C. mauritanicum*, *Phacochoerus* cf. *africanus*, and *E.* cf. *mauritanicus*) exhibit a high number of scratches, suggesting a significant consumption of grasses. Additionally, all species, both browsers and mixed feeders, show a high number of pits. This elevated number, combined with the presence of large pits and gouges in all species, is likely due to incidental ingestion of abrasive grit resulting from feeding close to the ground, a characteristic feature of open habitats and dry environments (Semprebon and Rivals, 2007).

The paper aims to reconstruct the palaeodietary signal of *T. oswaldi* from ThI-GH. The palaeoecological reconstruction of these specimens will help to understand how *Theropithecus* confronts the climatic variabilities of northern Africa and addresses the issue of exploitation of grasslands as primary resources.

2. Site description and archaeological context

Thomas Quarry I - Grotte à Hominidés (ThI-GH) is an archaeological site situated (33.568° N, 7.696° W) to the South-west of Casablanca, Morocco (**Fig. 1**). The first mammalian fossils were recovered from the quarry by Pierre Biberson in the 1950s and 1960s (Biberson, 1961). However, the site was not internationally recognized until the discovery of a hominin fossil in 1969 (Ennouchi, 1969). Fossils and archaeological artifacts collected by Philippe Beriro during the quarry work in the 1960s and 1970s were studied by Denis Geraads (Geraads, 1980; Geraads et al., 1980). In 1988, excavations in Thomas Quarry I were conducted under the Moroccan-French cooperative research project 'Préhistoire de Casablanca' (Raynal et al., 2001, 2023a; Mohib et al., 2019; Geraads et al., 2022). Between 1994 and 2012, several excavations took place at ThI-GH, retrieving new fauna remains and lithic industry (Raynal et al., 2010), as well as additional *Homo* sp. remains (Raynal et al., 2011).

The stratigraphic sequence of the cave comprises six units, ranging from the Upper Pleistocene to the early Middle Pleistocene (Lefèvre et al., 2021; Raynal et al., 2023a). Unit 1 displays massive bedded rubefied sands containing abundant microfauna. Beneath this, there's a multilayered dripstone floor interbedded with loose red sands (stratigraphic units 2-3). Stratigraphic units (SU) 4 and 5 are composed of bioclastic and quartzose well-sorted sands primarily derived from reworked loose littoral deposits. These units rest on plurimetric collapsed blocks of older calcarenites embedded in coarse sands and calcirudite with a coarse coquinoïd matrix forming stratigraphic unit 6. This lowermost unit fossilizes a notch in the paleoshoreline, featuring cliffs and deep cavities cut into older formations.

The archaeological remains (*Homo* fossils, lithic industries, and fauna) are concentrated in SU 4 and 5 (Raynal et al., 2010, 2023a; Lefèvre et al., 2021; Geraads et al., 2022), including the teeth of *T. oswaldi* analysed in this study. Taphonomic studies suggest that

carnivores played a significant role in bone modification and accumulation within this stratum (Daujeard et al., 2012, 2016). Previous OSL dating obtained on SU 4 provided an age ranging from 391 ± 32 thousand years ago (ka) to 420 ± 34 ka, and a human tooth provided a laser ICP-MS age of $501 +89/-66$ ka (Raynal et al., 2010, 2011). However, the magnetostratigraphic framework developed on all the deposits of the Thomas quarry has highlighted the presence of the Matuyama-Brunhes transition (0.773 Ma) occurring within the fossiliferous SU 4 and 5 deposits of ThI-GH (Gallotti et al., 2021; Perini et al., 2023, 2024; Raynal et al., 2023a).

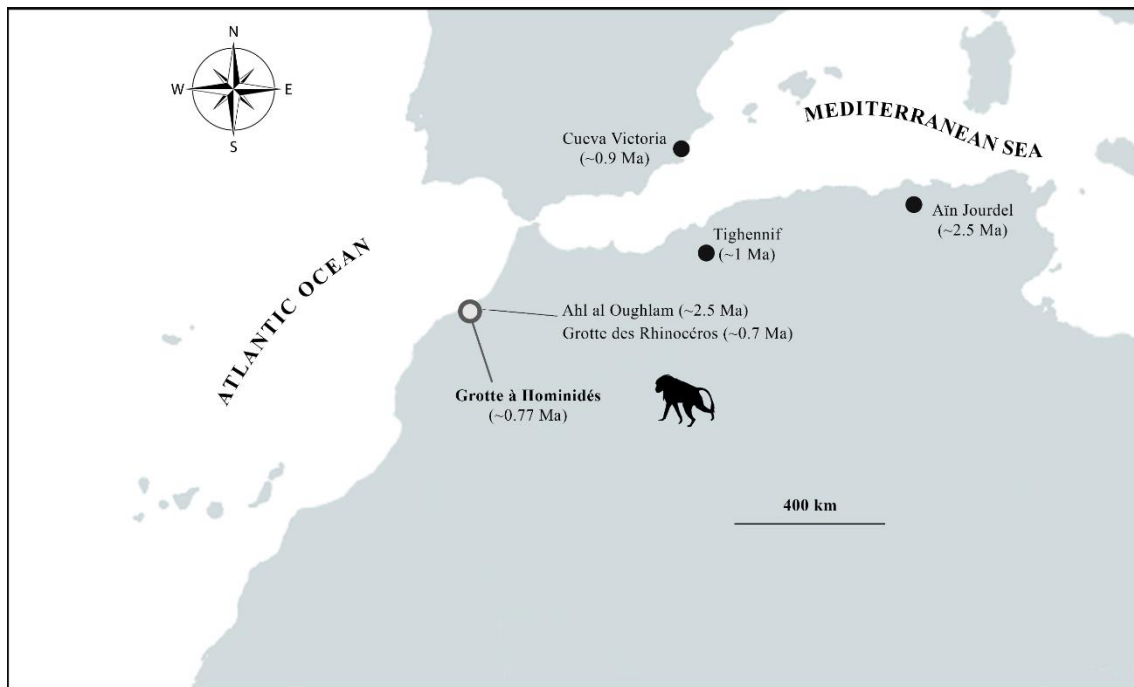


Figure 1. Locations of sites in northern Africa and the Iberian Peninsula with fossils of *Theropithecus* from the Plio-Pleistocene boundary to the early Middle Pleistocene, including the *T. oswaldi* from ThI-GH analysed in this work.

3. Materials

3.1. *T. oswaldi* fossils from ThI-GH

For this study, we analysed eight teeth of *T. oswaldi* from ThI-GH recovered during the 1994, 1995, and 2006 excavations. The teeth are as follows: a right second upper molar (M^2 , ThI-GH - MA22 - 48; Sample ID: T48), a right third upper molar (M^3 , ThI-GH - XA26 - 139; Sample ID: T139), a left third upper molar (M^3 , ThI-GH - WA26 - 90; Sample ID: T90), a right second lower molar (M_2 , ThI-GH - MA22 - 50; Sample ID:

T50), and four premolars (P₄, ThI-GH - P24 - 91; Sample ID: T91; P, ThI-GH - HA21 - 28; Sample ID: T28; P, ThI-GH - TA28; Sample ID: T211; P, ThI-GH - XA26; Sample ID: T210). After examination under the stereomicroscope and confocal microscope, three teeth were excluded from occlusal microwear analysis and buccal analysis due to poor preservation or other taphonomic defects on the analysed surface (Martínez and Pérez-Pérez, 2004; El-Zaatari, 2010; Uzunidis et al., 2021; Micó et al., 2023).

3.2. Reference collection of extant Cercopithecoidea

The extant Cercopithecoidea comparative sample corresponds to 56 well-preserved lower second molars (M₂) of six extant Papionini species (*Theropithecus gelada*, *Mandrillus sphinx*, *Lophocebus albigena*, *Cercocebus atys*, *Papio hamadryas* and *Macaca mulatta*). We excluded 11 samples from occlusal microwear analysis and 12 from buccal microtexture due to poor preservation.

The selected species cover a wide range of feeding ecologies, from hard fruit forest dwellers to grass-eating and opportunistic savanna habits. Whenever feasible, specimens of the same taxon were sourced from proximate localities to minimise the variability of their dietary regime. The species were selected based on the criteria of phylogenetic affinity (Perelman et al., 2011). This baseline sample established a broad spectrum of ecological and dietary diversity. The ecological data for *T. gelada*, *M. sphinx*, *L. albigena*, *C. atys* and *M. mulatta* has been described in Ramírez-Pedraza et al. (2023). For this article, we have added the dental microwear data of *P. hamadryas* (**raw data in Supplementary Online Material [SOM] Table S1 and Table S3**) from the Muséum National d'Histoire Naturelle, Paris. These specimens were collected in the late nineteen-sixties and early nineteen-seventies during several field and sampling missions headed by the museum (see the original country of the samples in Ramírez-Pedraza et al. (2023)).

Papio hamadryas mainly inhabits the savanna lowlands ecosystems of eastern Africa and some highlands ecosystems of Ethiopia. These primates are considered generalist omnivores, relying primarily on fruits, flowers, seeds, and leaves. Hamadryas baboons usually reside in arid and semi-desert areas of lower altitudes with high year-round temperatures (Dunbar and Dunbar, 1974; Swedell et al., 2008; Ibrahim et al., 2023), although they also exploit moist lowlands, including woodlands (Zinner et al., 2001). In

these dry and lower altitude ecosystems, the resources are scarce and widely dispersed, consuming a narrow array of plant species (Swedell et al., 2008). In the lowlands habitats of Ethiopia, *P. hamadryas* exploit fruits and flowers as preferred foods (Dunbar and Bose, 1991; Swedell et al., 2008). However, *P. hamadryas* from the Ethiopian highlands exploit high nutritional quality leaves and blades of graminoid plants (21.2%) throughout the year, while fruits and flowers were the least abundant, following a seasonal pattern according to rainfall (Ibrahim et al., 2023). The highland *P. hamadryas*, however, does not exhibit a significant dietary change between seasons, showing an adaptative pattern for this species between ecosystems.

4. Methods

This study followed the cleaning, moulding, casting, and examination protocol outlined by Solounias and Semprebon (2002) and Semprebon et al. (2004). Before moulding, each original specimen's occlusal surface underwent cleaning with acetone followed by 96% ethanol. Post-cleaning, high-resolution silicone (Heraeus Kulzer, PROVIL novo Vinylpolysiloxane, Light C.D. 2 regular set) was used for moulding the surface, and transparent casts were generated using clear epoxy resin (C.T.S. Spain, EPO 150 + K151).

4.1. Occlusal Microwear Analysis (Low Magnification)

Occlusal enamel microwear features were examined through standard light microscopy employing a Zeiss Stemi 2000C stereomicroscope at 35× magnification, utilising a standard ocular reticle of 0.16 mm². We analyzed wear facets of the mesiobuccal cusp of M2 (Godfrey et al., 2004; Semprebon et al., 2004). The quantified variables include small pits (round scars, relatively shallow, refractive), large pits (round scars, deeper, wider, less refractive), hypercoarse scratches (deep, trenchlike, and wider than coarse or fine scratches), coarse scratches (elongated scars with narrow, parallel sides, barely etched), fine scratches (elongated scars with wider, more etched appearance), gouges (irregular edges, larger and deeper than large pits), puncture pits (craterlike with regular margins), and cross scratches (oriented perpendicularly to the majority of scratches). The scratch width score (SWS) categorises teeth based on predominant scratch types: '0' for predominantly fine scratches, '1' for a mixture of fine and coarse textures, and '2' for predominantly coarse scratches. Microphotographs were captured using a Blackfly S

digital camera and Kivy Mic Capture Z software. Images were merged and enhanced for depth of field using Helicon Focus 7 software. Scale bars were added using ImageJ. Our results were compared with the extant Cercopithecidae species dental microwear reference dataset from Ramírez-Pedraza et al., 2023, including extant *Papio hamadryas* presented here. A single observer (IRP) analysed all specimens to minimise inter-observer errors at the Biomarkers lab in IPHES-CERCA (Tarragona, Spain). The Addinsoft™ XLSTAT-3.02 statistical packages were employed for conducting linear discriminant analysis (LDA).

4.2. Buccal Microwear Texture Analysis

The original extant specimens were cleaned with acetone and alcohol-soaked cotton swabs, and vinyl impressions were made using President's Jet Regular Body (Coltène-Whaledent). Positive casts were made with Ferropur (FeroCa®) polyurethane (Martínez et al., 2022; Ramírez-Pedraza et al., 2023). Buccal areas were obtained using a Sensofar Plu Neox laser scanning confocal microscope, with a 20× (0.45NA) objective, a spatial sampling of 0.83 µm, an optical resolution of 0.31 µm, a vertical resolution of 20 nm, and a z-step interval of 1 µm (Ibáñez et al., 2020; Martínez et al., 2022). Buccal surfaces were placed perpendicular to the objective in a horizontal position, and an image of the field of view of the microscope (600 x 500 µm) was obtained. From this image, four subsamples of 138 × 102 µm (a standard area in DMTA studies) were cropped using the Mountain 8® software from Digital Surf (www.digitalsurf.com) and 38 ISO parameters were obtained using Mountains 7® software, following prior procedures (Martínez et al., 2022; Winkler et al., 2022; Ramírez-Pedraza et al., 2023) (**see SOM Table S2 for the description of the parameters**). The workflow included levelling the surface to remove plane inclination, eliminating the curvature by applying a 2nd degree polynomial, removing the anomalous points by applying upper and lower 5% of threshold values, following the threshold operator included in the same software and applying a Spatial filter (Gaussian 3x3). The Gaussian filter was applied because it is widely used for technical surfaces and was applied after the trimming because it is sensitive to outliers (Schulz et al., 2013). Surface roughness was later quantified according to 38 ISO (International Organization for Standardisation) 25178/ISO 12781 parameters (Martínez et al., 2022). A single observer (LMM) analysed all specimens to minimise inter-observer errors.

To standardise the measured area on the buccal surface, we calculated the median of the parameters derived from four measurements of a single buccal surface (Scott et al., 2006; Calandra et al., 2012; Martínez et al., 2022) and used the median per specimen for analysis. We used log-transformed texture data for analyses because some texture parameters have non-normal distributions (Shapiro–Wilk, $p < 0.05$). To ensure we did not exclude any parameter (e.g., *Ssk* has negative values), we transformed the data as $\log [1 + \text{parameter}]$. We identified the outliers for both original and log-transformed variables according to their Studentised residual values (absolute value > 3) and removed them from the final data set (Schulz et al., 2010; Martínez et al., 2022). To test the null hypothesis that microwear textures do not differ between teeth from different species, we applied analysis of variance (ANOVA) with pair-wise testing (Tukey’s honest significant difference [HSD]) to each texture parameter for each species. Where the homogeneity of variance test (Levene’s test) revealed evidence of unequal variances, we used Welch’s ANOVA. We selected the parameters that showed significant differences between species and applied a stepwise linear discriminant analysis (LDA). Descriptive statistics, tests and graphs were performed using Addinsoft™ XLSTAT-3.02 and SPSS v. 25 statistical packages.

5. Results

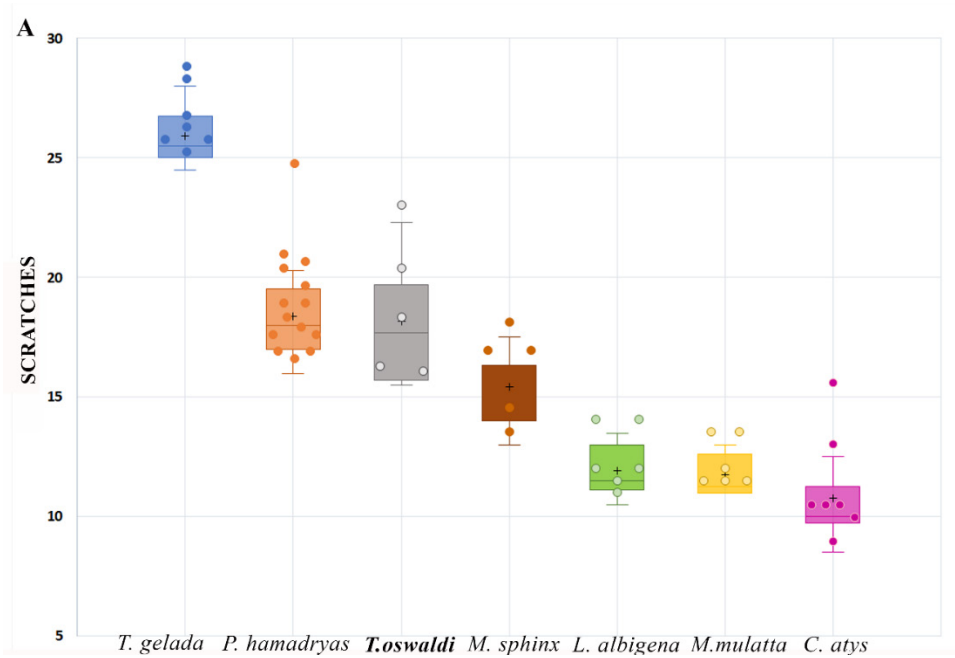
5.1. Occlusal Microwear Analysis (Low Magnification)

The occlusal dental microwear pattern of fossil *T. oswaldi* is characterised by a higher average number of scratches ($S = 18.2$) than pits ($P = 14.9$). When compared to extant cercopithecids, only *T. gelada* exhibits a higher number of scratches than pits, although *P. hamadryas* also displays a substantial count of scratches ($S = 18.5$) (**Table 1; Fig. 2**). Both extinct and extant *Theropithecus* species share the presence of hypercoarse scratches, but in a residual manner. However, *T. oswaldi*, unlike *T. gelada*, has puncture pits ($PP = 0.8$) and gouges ($G = 1.4$) (**Fig. 3**).

Table 1. Summary of occlusal microwear data from analysed samples of extant *P. hamadryas* and fossil *T. oswaldi* compared with the extant Cercopithecidae database from Ramírez-Pedraza et al. (2023). Abbreviations: *n*, number of specimens; SD, standard deviation; M, mean; NS, average number of scratches; NP, average number of pits; SWS, scratch width score; PP, average number of puncture pits;

HC, average number of hypercoarse scratches; G, average number of gouges; XS, average number of cross scratches; (raw microwear data in SOM Table S1 and Figure S1).

Species	Occlusal Microwear Analysis (Low Magnifications)													
	<i>n</i>	NS	SD	NP	SD	SWS	PP	SD	HC	SD	G	SD	XC	SD
<i>T. gelada</i>	7	25.9	0.8	10.1	3.3	1.6	0	0	0.4	0.5	0	0	0	0
<i>L. albigena</i>	5	11.6	1.5	40.6	4.4	2	5.4	1.8	0	0	4.3	2.2	0	0
<i>C. atys</i>	7	10.8	2.2	31.9	2.7	2	3.7	1.3	0	0	3	0.6	0	0
<i>M. mulatta</i>	5	11.7	1	38.5	2.6	2	4.3	0.8	0	0	1.9	1.1	0	0
<i>M. sphinx</i>	5	15.4	0.7	20	1.3	2	0	0	0	0	3.8	0.9	0	0
<i>P. hamadryas</i>	14	18.5	2.1	36.9	7	0.6	2	0.7	0	0	3.2	0.8	0.3	0.5
<i>T. oswaldi</i> (T48)	1	17.7	-	16	-	2	1	-	0.0	-	2	-	2.3	-
<i>T. oswaldi</i> (T139)	1	19.7	-	12	-	2	1.3	-	0.3	-	1.3	-	3	-
<i>T. oswaldi</i> (T90)	1	15.7	-	11	-	1	0.5	-	0.3	-	0.3	-	0	-
<i>T. oswaldi</i> (T50)	1	22.3	-	14.7	-	2	0	-	0.0	-	0.5	-	0	-
<i>T. oswaldi</i> (T211)	1	15.5	-	21	-	2	1	-	0.3	-	3	-	4	-



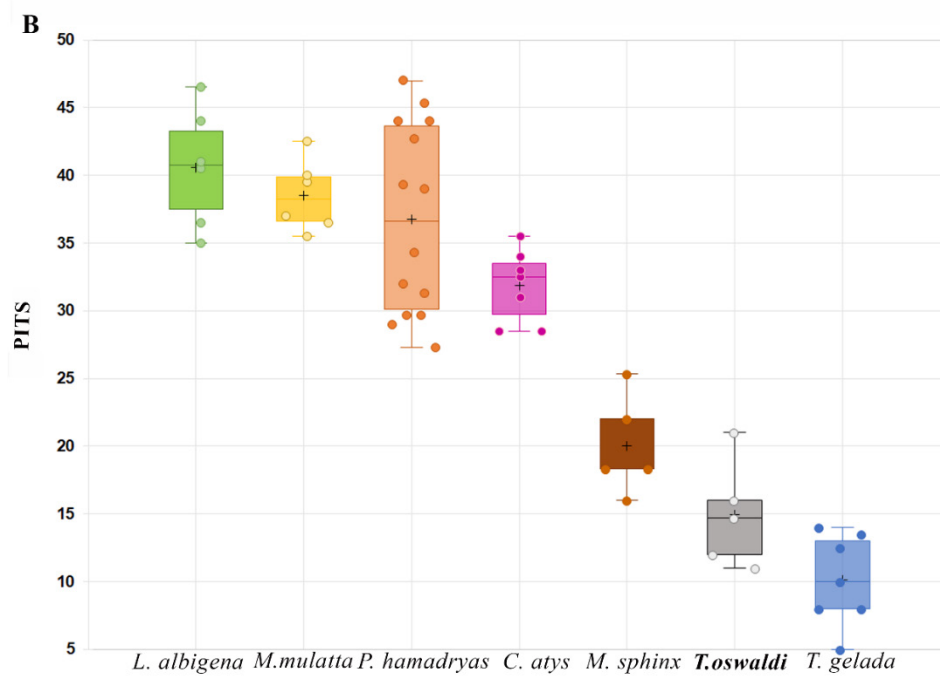


Figure 2. Dispersigram and boxplot comparing the average number of scratches (A) and pits (B) among fossil *T. oswaldi* from ThI-GH and extant Cercopithecidae. Boxes represent the first and third quartiles for each taxon, whiskers indicate the full range for each taxon, and hashes within the boxes denote the median value.

The LDA performed across the six extant species and *T. oswaldi*, encompassing four dental microwear variables (pits, scratches, puncture pits, and gouges), distinguishes four groups (**Fig. 3**). The first group, positioned on the left, comprises *T. gelada* due to its highest number of scratches ($S = 25.9$), the smallest count of pits ($P = 10.1$), and the absence of puncture pits and gouges. The second and third groups consist of *M. sphinx* and *P. hamadryas*, respectively. Both species display more pits than *T. gelada* but also more scratches than the components of the fourth group. *Papio hamadryas* is positioned in the upper middle because it has more pits ($P = 36.9$) than *M. sphinx* ($P = 20$). The lower number of pits and absence of PP in *M. sphinx* position it in the lower middle of the graph. The fourth group (*L. albigena*, *C. atys*, and *M. mulatta*) is characterised by a high number of pits ($P > 30$), a low count of scratches ($S < 12$), and the highest numbers of PP and G. The fossil *T. oswaldi* samples are situated near extant *T. gelada* and *M. sphinx* (**Fig. 3**).

We have also used the LDA to predict the group membership of the fossil *T. oswaldi* specimens from ThI-GH. The LDA revealed significant between-species differences (Wilks' $\lambda = 22.410$; $F = 0.05$; $p < 0.0001$) and accurately classified 86.7% of the species.

The first two discriminant functions explained 89.5% of the total variance. DF1 (75.2%) showed a positive correlation with scratches and a negative correlation with the presence of puncture pits and pits. DF2 (14.4%) displayed a negative correlation with the presence of gouges. T50 was classified as *T. gelada* (99% predicted classification probability), T28 was classified as *M. sphinx* (99% predicted probability), T139 was classified as *M. sphinx* (70% predicted probability) and *T. gelada* (30% predicted probability), T90 was classified as *M. sphinx* (99% predicted probability), and T211 was classified as *M. sphinx* (99% predicted probability).

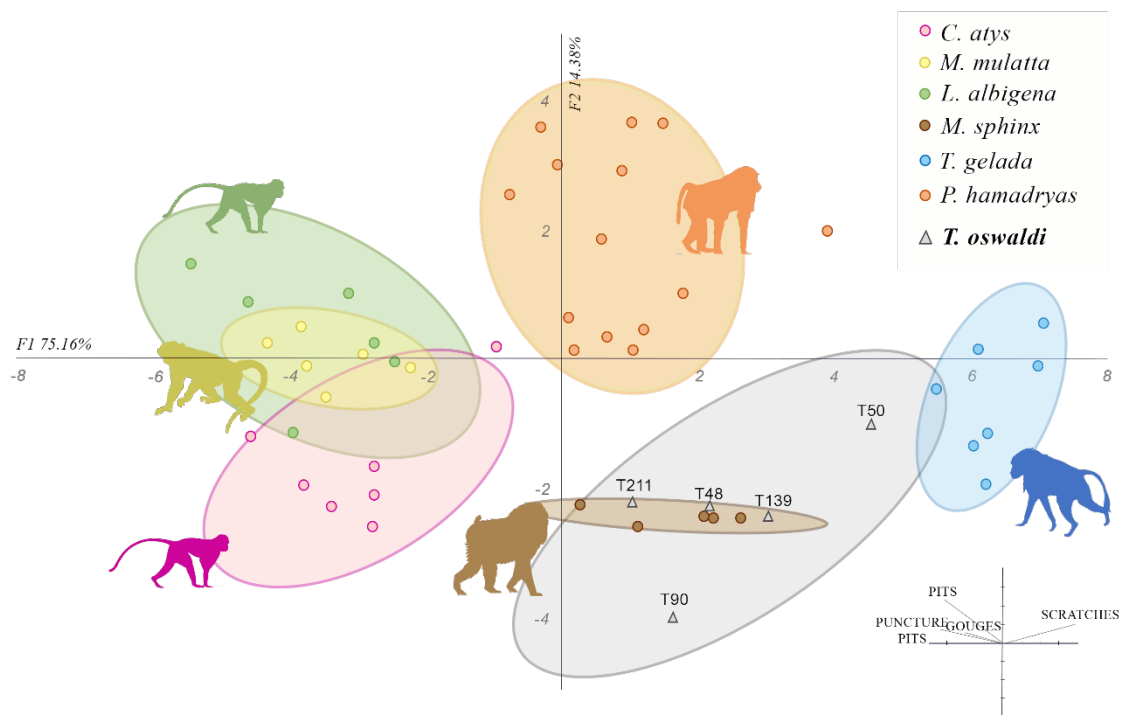


Figure 3. Linear discriminant analysis (LDA) based on four occlusal microwear variables (means of the number of puncture pits, gouges, scratches, and pits). Ellipses show 68% confidence limits for means (one standard deviation).

5.2. Buccal Microwear Texture Analysis

A total of 23 buccal enamel microtexture parameters out of 38 (60.52%) showed significant differences (ANOVA with Welch correction and Tukey's HSD *post hoc* procedure $p < 0.05$) among the Cercopithecoidea extant species (**raw data in SOM Table S3**). The main significant differences were between the savanna dweller *P. hamadryas* and the folivore-frugivore *M. mulatta*, and the arboreal hard fruit eater *L. albigena*. *P. hamadryas* mainly differentiates from *M. mulatta* in volume and feature parameters (V_{vc} ,

Vv, *Vmc*, *Smc*, *Sal*) and from *L. albigena* feature and functional parameters (*Smr1*, *Sdv*, *Shv*, *Sal*, *Spc*, *Sha*). *Papio hamadryas* also differs from these two species in all flatness parameters. On the other hand, *C. atys* also displays several differences with *M. sphinx*, mainly in flatness and feature parameters (*FLTt*, *FLTv*, *FLTq*, *Sda*, *Sha*, *Shv* and *Sal*). No significant differences were found between the hard fruit eaters' taxa, the arboreal *L. albigena* and the terrestrial *C. atys*, nor were any significant differences observed between *T. gelada*, *C. atys*, and *M. mulatta* with *L. albigena* and *M. sphinx* (**Table 2**).

Table 2. Summary of *post hoc* test on texture parameters obtained from buccal surfaces of extant Papionini primates. Variables written under the diagonal are significant with HSD. Blank cells under the diagonal show no significant differences among taxa.

Species	<i>T. gelada</i>	<i>P. hamadryas</i>	<i>M. mulatta</i>	<i>C. atys</i>	<i>L. albigena</i>	<i>M. sphinx</i>
<i>P. hamadryas</i>	<i>Shv</i> , <i>Smr1</i>					
<i>M. mulatta</i>	<i>Sa</i> , <i>Smc</i> , <i>Vv</i> , <i>Vmc</i> , <i>Vvc</i> , <i>FLTp</i> , <i>FLTq</i>	<i>Sq</i> , <i>Sku</i> , <i>Sa</i> , <i>Smc</i> , <i>Sal</i> , <i>Vv</i> , <i>Vmc</i> , <i>Vvc</i> , <i>FLTt</i> , <i>FLTp</i> , <i>FLTv</i> , <i>FLTq</i>				
<i>C. atys</i>		<i>Sal</i> , <i>Sda</i> , <i>Shv</i> , <i>Smr1</i>	<i>FLTq</i>			
<i>L. albigena</i>	<i>Spc</i> , <i>FLTq</i>	<i>Sku</i> , <i>Sal</i> , <i>Spc</i> , <i>Sha</i> , <i>Sdv</i> , <i>Shv</i> , <i>Smr1</i> , <i>FLTp</i> , <i>FLTv</i> , <i>FLTq</i>				
<i>M. sphinx</i>	<i>Sal</i> , <i>FLTt</i> , <i>FLTp</i> , <i>FLTv</i> , <i>FLTq</i>	<i>Sal</i> , <i>Smr2</i> , <i>FLTt</i> , <i>FLTp</i> , <i>FLTv</i> , <i>FLTq</i>		<i>Sal</i> , <i>Sda</i> , <i>Sha</i> , <i>FLTt</i> , <i>FLTv</i> , <i>FLTq</i>	<i>Spc</i> , <i>Sda</i> , <i>Sha</i>	

The LDA included the 23 parameters to classify the extinct *T. oswaldi* specimens (**Fig. 4 and Table 2**). DF1 and (83.59%) and DF2 account for 97.54% of the total variance (Wilks' $\lambda < 0.045$; $F = 1.784$; $p\text{-value} = 0.0001$). DF1 (83.59%) positively correlated with feature parameters and negatively with volume and flatness parameters. DF2 (13.95%) negatively correlated with *Spc* and *Spd*, indicating that the surface had numerous sharp peaks. The stepwise LDA selected three parameters to better discriminate between surfaces (*Shv*, *Spc* and *FLTq*). In the stepwise LDA, 79.49% of the teeth were correctly classified in their taxonomic category. *P. hamadryas* and *T. gelada* are positioned in the

positive part of the LDA scatterplot, notably due to differences in height distribution (*Sku*) and to have surfaces with low volume and flatness parameters and high feature parameters.

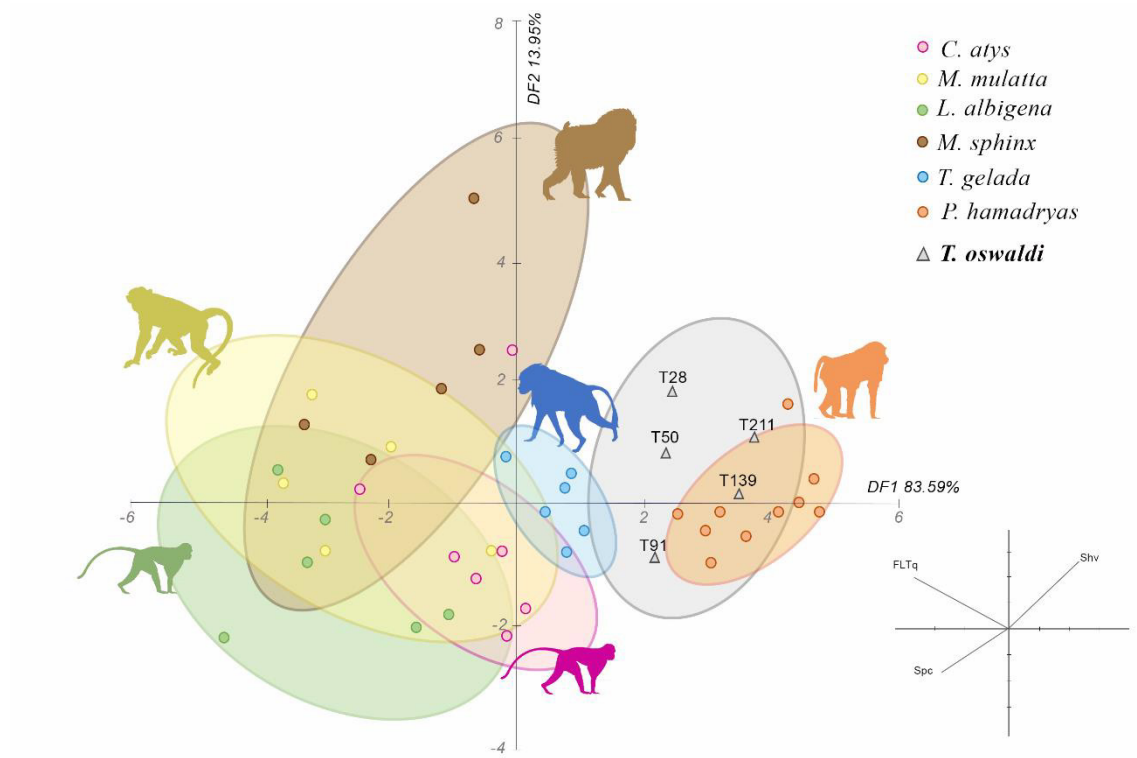


Figure 4. Linear Discriminant Analysis (LDA) shows the two first discriminant functions (DF1-2) of buccal-dental microtextural parameters. Ellipses show 68% confidence limits for means (one standard deviation). The ISO (International Organization for Standardisation) texture parameters loadings onto DFs are on the bottom right.

Their surfaces are characterised by rough peaks and non-deep dales with some deep striations. On the other hand, *L. albigena* was positioned in the negative values of the DF2, with high values of *Spc* and *Spd* indicating that those surfaces are characterized by a high density of sharp peaks and high values of anisotropy-based parameters (*Sal*). *M. sphinx* is situated in the positive part of the DF2 and the negative part of the DF1, correlating with high volume and flatness parameters, indicating that their surfaces exhibit deep dales and coarse features with the highest *Sal* values. The extinct *T. oswaldi* specimen T91 was the only specimen classified as *T. gelada* (52% of predicted probability, followed by a 42.4% of predicted probability of *P. hamadryas*). However, the *T. oswaldi* fossils (T91, T50, T139, T28 and T211) were classified as *P. hamadryas* with

a range of predicted probability from 0.537 to 0.995%. All extinct fossils were classified as *P. hamadryas* or *T. oswaldi* as the first or second predicted group. None of them showed a buccal surface similar to mangabeys, *Macaca* or *Mandrillus*, suggesting a buccal area with rough peaks and low dale volumes. Although *T. gelada* surfaces were characterised by fine peaks, *P. hamadryas* had deeper striations than the other buccal surfaces observed.

6. Discussion

Our results from occlusal and buccal microwear and microtexture analysis of the early Middle Pleistocene *T. oswaldi* from ThI-GH in western Morocco suggest a different dietary reconstruction compared to extant *T. gelada* from the Ethiopian Highlands increasing the dietary spectrum of the extinct *Theropithecus*.

Occlusal and buccal microwear methodology are indicative of dietary habits of extant and extinct primate species but differ in the temporal resolution and turnover rates of the analyzed tooth surface (Teaford and Walker, 1984; Godfrey et al., 2004; Estebaranz et al., 2009; Williams and Patterson, 2010). Dietary reconstruction studies suggest that while occlusal signal reflects the diet of the last days or week before the specimen death, offering a short-term resolution (Grine, 1986; Teaford and Oyen, 1989), buccal microwear is indicative of a medium long-term signal, from weeks to months (Romero et al., 2012). Therefore, combining both techniques could offer paleodietary reconstruction at different timespans, allowing a broad reconstruction of the taxa (Ramírez-Pedraza et al., 2023).

Occlusal microwear surface patterns from *T. oswaldi* show similarities with extant *M. sphinx* and *T. gelada*. The high number of striations in *T. oswaldi* suggests significant grass consumption, similar to *T. gelada*. However, it differs from *T. gelada* in having a higher presence of pits, as well as puncture pits and gouges (absent in *T. gelada*), which are characteristic of diets that include hard items such as fruits or seeds (Godfrey et al., 2004; Semprebon et al., 2004). This pattern indicates a more diverse diet, resembling the frugivore species *M. sphinx*, rather than a diet predominantly based on grasses like the extant *T. gelada*.

The buccal surfaces of extinct *T. oswaldi* are characterised by a low density of sharp peaks with deep striations, similar to those observed in *P. hamadryas*. This open habitat dweller consumes a high variability of resources, including tough and hard items such as underground storage organs (USOs), fruits and seeds throughout the year (Dunbar and

Bose, 1991; Swedell et al., 2008). However, extant baboon populations differ in their dietary compositions, with fruit intakes varying across seasons and localities.

The wide dietary spectrum of *Papio* is expected to produce different dental microwear textures between samples (Merceron et al., 2021). This ecological variability differs from that of the *T. gelada* grass-eating specialist, although some studies agree with the higher variability of the geladas diet too (Fashing et al., 2014; Souron, 2018). Long-term studies have shown seasonal dietary shifts in the *T. gelada* diet, with differences in the proportion of leaves and forbs ingested throughout the year (Fashing et al., 2014; Abu et al., 2017). In Guassa Plateau, an almost intact tall-grass ecosystem, geladas consume a high proportion of graminoids, representing 56.8% of their yearly diet, followed by 37.8% of forbs that the geladas seek opportunistically due to being less tough and having more nutritional leaves than the graminoids ones (Fashing et al., 2014). The study also reported seasonal dietary variations with herbaceous monocotyledon blades and inflorescences being especially consumed during the wet season, whereas the consumption of USOs is higher during the dry season (Fashing et al., 2014). The authors considered mechanically challenging USOs as fallback foods that never exceed 28% of the diet. Although underground items normally are covered in grit that potentially could produce microwear on dental enamel (Teaford et al., 2017), geladas have been seen to clean USOs before their ingestion (Fashing et al., 2014). The wide dietary spectrum of *P. hamadryas* would draw fewer ecological differences between this species and *T. gelada*. However, the extant model discriminated between both groups, differentiating *P. hamadryas* occlusal surfaces with the presence of gouges and puncture pits that were not observed on *T. gelada* surfaces and the higher number of pits for *P. hamadryas*. *T. oswaldi* occlusal surfaces were also characterised by a few pits similar to *M. sphinx* but higher than *T. gelada*.

In contrast, buccal microtexture suggest surfaces with low anisotropy, as *P. hamadryas* and *T. gelada* show, with high differences in height distribution, with high areas of valleys (*Sda*) and hills (*Sha*). These surfaces are characteristic of small particles that produce low texture relief (Calandra et al., 2012), potentially including phytoliths and dust from monocot leaves, creating a more plastic deformation (Lucas et al., 2014). These surfaces have also been described for *P. cynocephalus* in occlusal areas (Calandra et al., 2012).

Strontium stable isotope studies from northern Africa Plio-Pleistocene sites (Tighennif and Ahl al Oughlam) on extinct *Theropithecus* suggested that juveniles of *Theropithecus* exploited a wide home range in open C₃ habitats to support their graminivory feeding

ecology (Fannin et al., 2021). Exploiting a wider habitat is an opportunity to find different resources, increasing the variability of abrasiveness items similar to *Papio* in the long buccal term compared to the occlusal microwear results. Moreover, hand adaptations of *T. oswaldi* suggest behavioural habits similar to *Papio*, which can occasionally exploit arboreal strata (Elton, 2002). However, the dental microwear and microtexture analysis of the present study differentiates the *T. oswaldi* reconstruction from arboreal species such as *L. albigena*.

Although the *Theropithecus* lineage shows the same morphological dental adaptations with high crowned molars with enamel infoldings (Jablonski, 1993), the presence of *T. oswaldi* in different African areas and its expansion beyond this continent suggests that *T. oswaldi* probably was an opportunistic species, with plasticity in the dietary regime. Differences in the palaeoecological reconstruction based on dental microwear and enamel carbon isotopes between eastern (Cerling et al., 2013; Shapiro et al., 2016; Souron, 2018; Uno et al., 2018; Merceron et al., 2021), southern (El-Zaatari et al., 2005; Williams and Geissler, 2014), northern Africa (Fannin et al., 2021), and also Cueva Victoria site in Spain (Martínez et al., 2020) support the hypothesis of different types of resources exploited in a variable range of habitats and latitudes from C₃/C₄ grasslands to Mediterranean ecosystems. Moreover, some studies have corroborated a change in the isotopic signal through time in the lineage, suggesting that *T. oswaldi* was adapted to ecological changes in seasonal and long-term climatic effects in African ecosystems (Cerling et al., 2013; Negash et al., 2020).

7. Conclusions

The present study contributes to interpreting the feeding ecology of *T. oswaldi* from ThI-GH from the late Early to early Middle Pleistocene transition. Our results suggested a different dietary microwear signal from extant *T. gelada*, that consumes basically grasses combined with USOs and forbs seasonally. The *T. oswaldi* palaeoecological reconstruction suggests an abrasive diet, with the presence of more puncture pits and gouges on the occlusal surfaces and deep striations with rough peaks, similar to more omnivore species that consume leaves and blades of graminoid plants as well as flowers, fruits and seeds according to rainfall in open ecosystems or semi-open ecosystems. Differences in dental microwear and microtexture signal from northern Africa compared

to other African and Spanish sites suggest a wide dietary econiche for *T. oswaldi*, probably as a response to different climatic conditions and resource availability. Future research on the ecology of *Homo* sp. from ThI-GH will shed light on whether there was niche partitioning with *T. oswaldi*, and on the relationship between Hominini and Papionini in the early Middle Pleistocene of the Moroccan Atlantic coast.

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· Chapter 6: Discussion ·

6.1. Enamel carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) stable isotope analysis in northern Africa

In general, and considering the sites analysed to date in northern Africa from the Plio-Pleistocene transition to the early Middle Pleistocene, C_3 plant consumption was predominant by mammals (**Fig. 35**). Except for GFT-4.2, there are no significant differences in the distribution of carbon values across the other four sites, despite spanning different chronologies and considerable geographical distances between the sites on the Atlantic coast (Grotte à Hominidés, Grotte des Rhinocéros, and Ahl al Oughlam) and Tighennif. The average $\delta^{13}\text{C}$ values for all species are nearly identical: ThI-GH ($-11.2 \pm 1.4\text{‰}$), OHQ1-GDR ($-11.1 \pm 1.4\text{‰}$), AaO ($-11.4 \pm 1.2\text{‰}$), and Tighennif ($-11.1 \pm 1.2\text{‰}$). This similarity is remarkable when considering the values for the same taxa, such as Alcelaphini or *Gazella* in ThI-GH, OHQ1-GDR, and AaO, implying minimal changes in diet and likely in the landscape over time along the Atlantic coast.

Despite the predominance of C_3 plants, the values are not negative enough (approximately below -16‰) to indicate a closed canopy forest landscape in any of the five sites. However, the wide range of C_3 values, ranging from -14.5 to -8‰ , suggests different landscape types with a predominance of open C_3 grassland, both xeric and mesic (Domingo et al., 2013), and sparse tree coverages. Among the Plio-Pleistocene sites (~ 2.5 Ma), GFT-4.2 and AaO appear to differ in the abundance of tree cover, with AaO showing less abundance. This scarcity of cover seems to extend over time and be present near ThI-GH and OHQ1-GDR.

The carbon isotope value pattern of GFT-4.2 is distinct, particularly compared to the contemporaneous AaO site. In GFT-4.2, the mean $\delta^{13}\text{C}$ value is more positive than in the other sites ($-8.5 \pm 2.2\text{‰}$). This pattern is observed across all species within the same family compared to the other sites (**Fig. 35**). For the first time, there is evidence of significant consumption of C_4 plants and probably the presence of C_4 grassland in the northern African region. This consumption of C_4 plants is also present in an individual of *T. oswaldi* from Tighennif (Fannin et al., 2021) and in two *C. thomasi* from OHQ1-GDR. The significant presence of C_4 plants in GFT-4.2 is itself linked to aridity. C_4 plants exhibit greater efficiency in arid environments than C_3 plants under conditions of low atmospheric CO_2 concentration, high temperatures, and moisture stress (Ehleringer et al., 1991; Cerling and Quade, 1993). Aridity is a widespread pattern across all sites, not only due to the presence of C_4 plants in some of them but also through their Mean Annual Precipitation (MAP). The MAP in AaO was 385 mm/yr, in Tighennif 297 mm, in ThI-GH 361 mm/yr and OHQ1-GDR 301 mm/yr. The region's aridity is supported by environments dominated by C_3 plants with a MAP of 500 mm/year or less, typically associated with arid conditions.

Evidence of this trend can be found in Morocco's Late Pleistocene Atlantic coast sites (El Harhoura 2 and Taforalt) (Jeffrey, 2016). The $\delta^{13}\text{C}$ values in the enamel of small mammals indicate predominantly open C_3 vegetation in this area. However, the Gerbillinae from Taforalt have a small C_4 plant contribution to their diet at specific periods during MIS 2, MIS 3 and MIS 5 (Jeffrey, 2016).

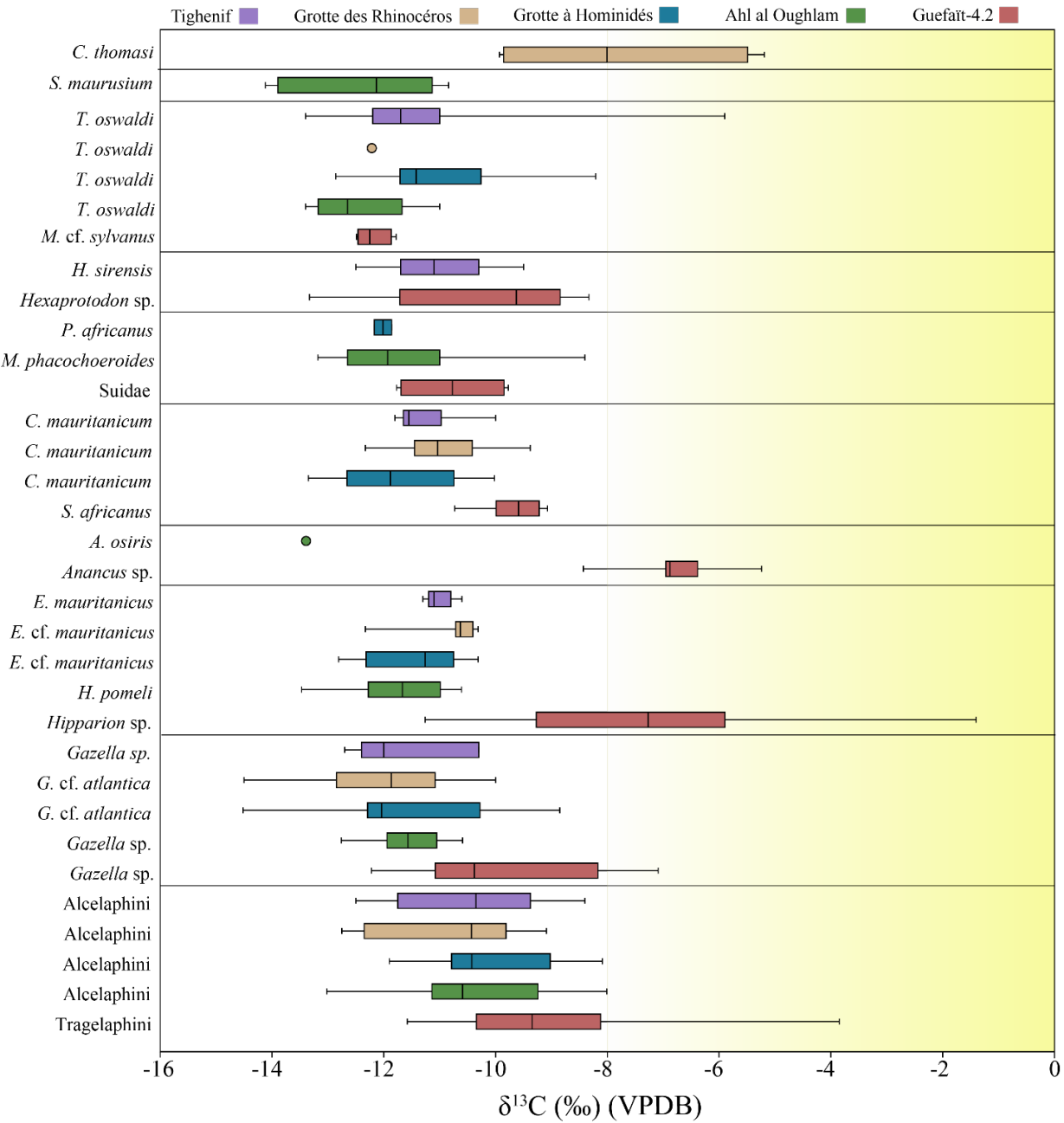


Figure 35. $\delta^{13}\text{C}$ values of the different taxa analysed in this work for the AaO, GFT-4.2, ThI-GH and OHQ1-GDR sites, and also the published $\delta^{13}\text{C}$ values for Tighennif (Bocherens et al., 1996; Fannin et al., 2021), and *T. oswaldi* from AaO (Fannin et al., 2021).

The $\delta^{18}\text{O}$ values within enamel bioapatite are closely linked to various water sources. In arid environments such as those presented in these sites, evaporation causes the enrichment of ^{18}O and depletion of ^{16}O isotopes. As with the $\delta^{13}\text{C}$ values, GFT-4.2 exhibits the most remarkable differences in oxygen values, indicating both interspecific and intraspecific variability. The most negative and positive values are observed compared to the other sites along the Atlantic coast (**Fig. 36**). This variability, considering the differences between non-obligate and obligate, indicates the presence of an arid environment. However, this aridity was present in all the sites.

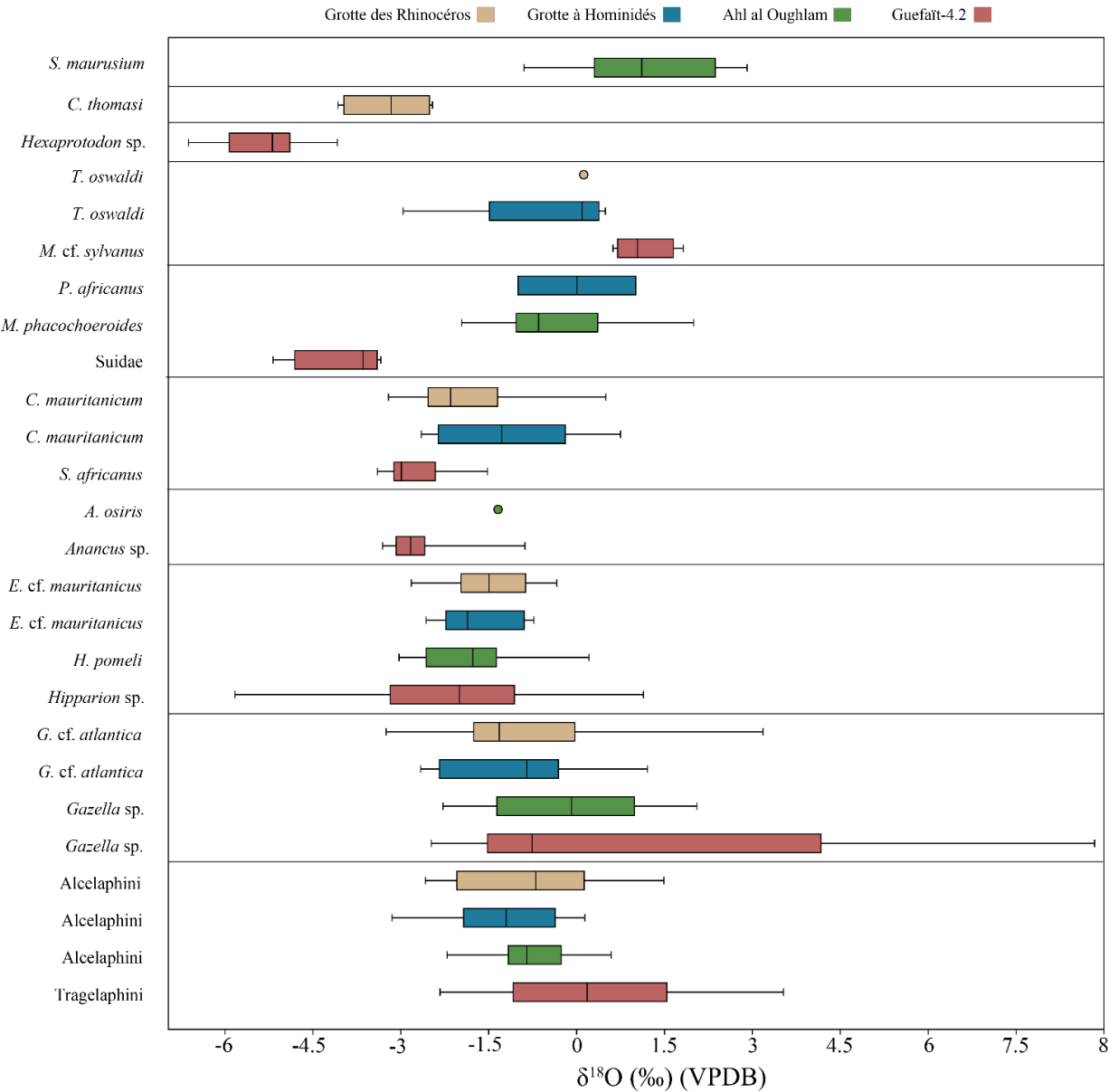


Figure 36. $\delta^{18}\text{O}$ values of the different taxa analysed in this work for the AaO, GFT-4.2, ThI-GH and OHQ1-GDR sites

What distinguishes the pattern of the large mammals from GFT-4.2 from the other sites?

In line with the $\delta^{13}\text{C}$ values, there is significant evidence of C_4 plant consumption, which, based on the sequential analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of *Hipparion*, occurred to a greater extent during the warm season (see discussion in Paper I pp. 61). The *Hipparion*, along with *Gazella* sp. and Tragelaphini, are the taxa from GFT-4.2 that exhibit the most significant variability in $\delta^{13}\text{C}$ values. These same taxa also show the highest variability in $\delta^{18}\text{O}$ values. In the case of $\delta^{18}\text{O}$ values, the differences between taxa, particularly between non-obligate and obligate drinkers, are quite pronounced in GFT-4.2 (see Paper I, pp. 60 to 61). In the case of AaO, ThI-GH, and OHQ1-GDR, although differences exist between non-obligate and obligate drinkers, these differences are less pronounced. For instance, there is minimal variability in the $\delta^{18}\text{O}$ values between *Ceratotherium* (obligate drinker) and *Gazella* (non-obligate) in ThI-GH and OHQ1-GDR. When comparing the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values of Equidae, *Gazella*, or Alcelaphini from AaO, ThI-GH, and OHQ1-GDR, there are no significant changes observed among the same taxa (Fig. 32).

Furthermore, variability is considerably lower than that observed in GFT-4.2 (Fig. 36). For instance, the differences in variability in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are significant when analysing the same genus (*Hipparion*) between the contemporaneous sites GFT-4.2 and AaO. The *Hipparion* from GFT-4.2 experiences greater seasonal changes than those from AaO, but this variability is not only evident through the sequential analysis of the *Hipparion* from GFT-4.2 but also by comparing the variability in the bulk analysis between both species from the two sites (Fig. 35). This suggests that, despite the pervasive aridity, the climate would be more stable throughout the year in the sites along the Atlantic coast. Conversely, in the area of GFT-4.2, located further inland and in a mountainous region, aridity was likely more pronounced, and the climate more extreme, with the presence of harsher warm months.

6.2. Tooth mesowear analysis in northern Africa

The dental mesowear analysis, like isotopic analysis, provides a "long-term" resolution, in this case, covering the last months/years before the death of the animals (Solounias et al., 2014; Ackermans et al., 2021). This makes them methods that encompass dietary patterns over several seasons. The general pattern of mesowear in the four northern African sites exhibits a similar level of abrasiveness among the same taxa, irrespective of the site and its corresponding location or chronology (Fig. 37). This general similarity in browser-grazer trends among the same taxa indicates a continuity over time in dietary preferences and diet abrasiveness.

The classification of the species would be primarily based on three groups. In the first category, the *Gazella* species exhibits the lowest mesowear score. This is comparable to the MWS of extant mixed feeders but with a tendency towards a browsing diet. In the

second group, the Bovidae (Tragelaphini and Alcelaphini) exhibit a general mixed feeder pattern, with the Alcelaphini of AaO representing a more abrasive dietary niche, including individuals with a grazer MWS. The Alcelaphini of OHQ1-GDR exhibits the lowest MWS, similar to the *Gazella*. In the third category, the Equidae exhibit a mixed feeder grazer diet, representing the most abrasive dietary profile. Even though the *Hipparion* of GFT-4.2 has an average grazing diet, there are also individuals with a mixed feeder and browser diet.

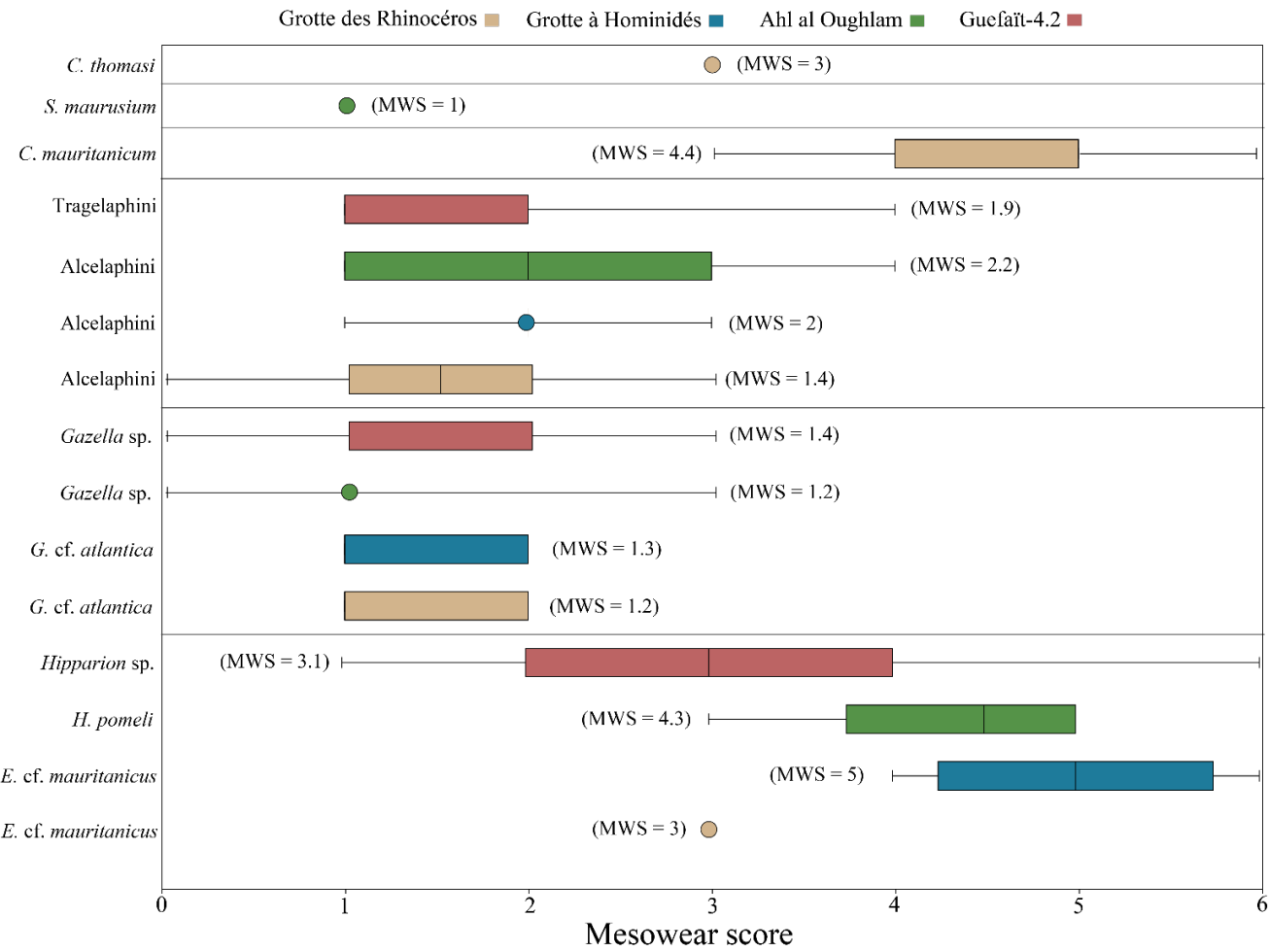


Figure 37. Boxplot with mesowear scores (MWS) of the ungulates from AaO, GFT-4.2, ThI-GH and OHQ1-GDR sites.

When the MWS is combined with the results of stable isotopes, the variability observed in *Hipparion* is also evident in the $\delta^{13}\text{C}$ values, with individuals exhibiting a pure C_3 diet and others exhibiting a near-pure C_4 diet. By examining the grazing pattern of all Equidae from different sites concerning the carbon signal, it is possible to infer the presence of grassland landscapes, predominantly C_3 in AaO, ThI-GH and OHQ1-GDR, and mixed C_3 and C_4 in GFT-4.2. The MWS of *C. thomasi* from OHQ1-GDR also indicates a grazing diet that includes grasses of both C_3 and C_4 types. However, the MWS of the *Ceratotherium* from OHQ1-GDR is highly abrasive, with a clear preference for C_3

grasses, which suggests the presence of C₃ grassland. The *Sivatherium* of AaO is the species with the lowest MWS, and this diet is notably less abrasive than other species. This is consistent with the observation that it has the most negative $\delta^{13}\text{C}$ values and the highest $\delta^{18}\text{O}$ values. This could be attributed to its consumption of leaves from tall plants, which it has access to due to its large size.

At the Upper Pleistocene site of El Khenzira, also located on the Atlantic coast of Morocco and very close to ThI-GH, OHQ1-GDR, and AaO, *Equus* exhibits the highest MWS values falling within the range of extant grazers (MWS = 4.3; Uzunidis et al., 2023), as observed in ThI-GH, OHQ1-GDR, AaO, or GFT-4.2. Gazelles, on the other hand, display a varied diet, with some showing a browsing tendency (*Gazella* sp., MWS = 2.7; *Gazella atlantica*, MWS = 2.3) and others being predominantly browsers (*Gazella dorcas*, MWS = 1.5). The *Gazella atlantica* from El Khenzira would have a slightly more abrasive diet than those from ThI-GH and OHQ1-GDR (Uzunidis et al., 2023).

6.3. Tooth microwear analysis in northern Africa

In contrast to the methods of mesowear and the stable isotopes of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, dental microwear offers a "short-term" resolution that provides insights into the dietary habits of animals in the days and weeks preceding their death (Grine, 1986; Teaford and Oyen, 1989). Consequently, the information obtained is likely to be seasonal and to reflect the animal's diet at the site, given the rapid turnover of the occlusal surface.

Dental microwear exhibits two different patterns, analogous to those observed in the values of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$. This suggests that considering the different temporal resolutions of the methods (short-term vs. long-term), the overall differences in the dietary patterns of the large vertebrates from ThI-GH, OHQ1-GDR, and AaO, compared to the patterns of the taxa from GFT-4.2, would be identifiable both on an "annual" scale as well as on a seasonal level. In ThI-GH, OHQ1-GDR, and AaO, dental microwear data indicate that the taxa are classified as browsers and others as mixed feeders. In contrast, GFT-4.2 indicates that the taxa are classified as browsers and others as grazers (**Fig. 38**). In GFT-4.2, there appear to be two distinct dietary patterns that likely imply different ecological niches, consistent with the variability observed in the carbon and oxygen values of the taxa from GFT-4.2. However, the pattern is strikingly similar in ThI-GH, OHQ1-GDR, and AaO. Regardless of whether the taxa are browsers or mixed feeders, they exhibit a very high number of pits in all three sites. Furthermore, all mixed feeders exhibit a high number of scratches, which would otherwise place them alongside extant grazers if not for the high number of pits. The relatively high number of pits and the presence of large pits in all taxa may be attributed to the ingestion of abrasive grit resulting from feeding near the ground in open and arid habitats (Semprebon and Rivals, 2007; Hoffman et al., 2015). Furthermore, the same taxa are observed in the same locations at all three sites (ThI-GH, OHQ1-GDR, and AaO): the *Gazella* being browsers and the Alcelaphini and Equidae mixed feeders (**Fig. 38**). This similar pattern aligns with the data from $\delta^{13}\text{C}$ and

$\delta^{18}\text{O}$ and mesowear, reinforcing the argument that there were indeed few changes in the diet of different taxa and thus in the type of landscape between the Plio-Pleistocene and early Middle Pleistocene in the Atlantic Coast sites. Nevertheless, there are some differences between ThI-GH, OHQ1-GDR, and AaO. In the first two sites, the overall number of pits and the presence of puncture pits and gouges in the taxa is higher than in AaO. This may be attributed to greater aridity, correlating with the Mean Annual Precipitation (MAP) calculated for each site. OHQ1-GDR exhibits the lowest annual precipitation (301 mm/yr), followed by ThI-GH (361 mm/yr), and finally AaO (385 mm/yr).

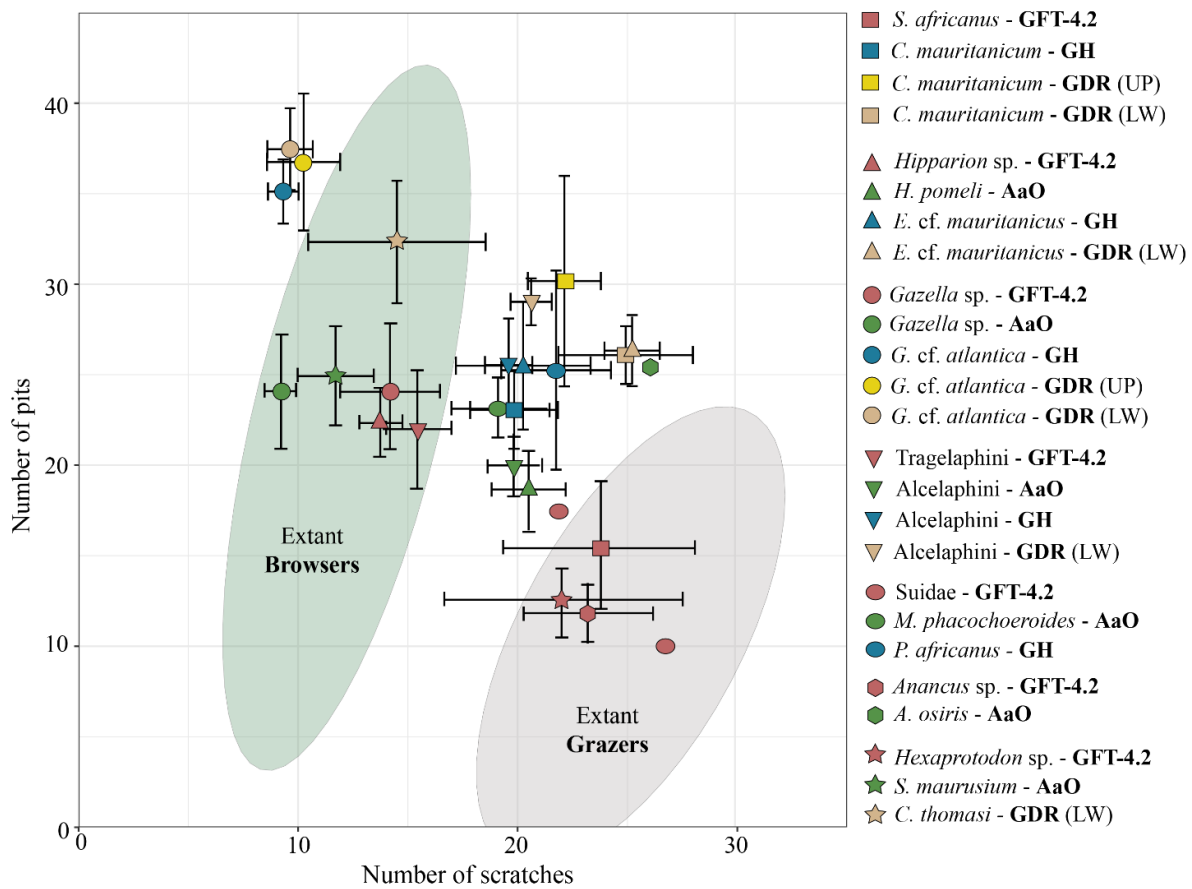


Figure 38. Bivariate plot of the average numbers of pits and scratches for the taxa from AaO, GFT-4.2, ThI-GH, and OHQ1-GDR sites. Error bars correspond to the fossil samples' standard deviation (± 1 SD). Plain ellipses correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the extant browsers and grazers based on the database from Solounias and Semperebon (2002).

At the Upper Pleistocene site of El Khenzira, *Equus* exhibits a mixed feeder microwear pattern, characterised by a high number of scratches, which indicate a significant consumption of grass (Uzunidis et al., 2023). This pattern is similar to that observed in *Equus* from ThI-GH and OHQ1-GDR, as with mesowear. This indicates consistency in *Equus*'s dental wear pattern and diet across a temporal span from the early Middle

Pleistocene to the Upper Pleistocene on the Atlantic coast. In contrast, gazelles display a browsing diet with a high number of pits, as observed in ThI-GH, OHQ1-GDR, AaO, and GFT-4.2 (Uzunidis et al., 2023). The *Equus* from Taforalt, an Upper Pleistocene site situated close to GFT-4.2, displays a microwear pattern indicative of a grazing diet, in contrast to the browsing *Hipparion* from GFT-4.2. In this instance, the specimen exhibits a number of scratches that are strikingly similar to those observed in the *Equus* from OHQ1-GDR.

Another factor that provides information about the habitat type is the simple presence or absence of specific taxa. In this instance, two families are particularly useful for diagnostic purposes: Bovidae and Cercopithecidae. Concerning the Bovidae, the presence of Tragelaphini in GFT-4.2 is noteworthy, as this taxon is typically associated with wooded and humid habitats (Bobe et al., 2007; Blondel et al., 2018). Conversely, in AaO, ThI-GH, and OHQ1-GDR, there are no Tragelaphini recorded in the fossil record, but abundant fossil remains of Alcelaphini, a taxon linked to more open environments (Bobe et al., 2007). A similar pattern is observed in the case of Cercopithecidae. In GFT-4.2, the fossil record includes remains of *M. cf. sylvanus*, a species typically associated with more wooded environments (Fooden, 2007; Elton and O'Regan, 2014). In contrast, in ThI-GH, OHQ1-GDR, and AaO, the fossil record comprises *Theropithecus* remains linked to more open landscapes and grass consumption (Elton, 2002; Souron, 2018).

This allows us to infer two aspects: 1) The GFT-4.2 site exhibits greater tree cover and habitat diversity than all other Atlantic coast sites. 2) As demonstrated by the multiproxy analysis presented in this thesis, there is no evidence to suggest significant changes in landscape on the Atlantic coast from the Plio-Pleistocene transition to the early Middle Pleistocene.

Similarly, the analysis of occlusal microwear of *M. cf. sylvanus* from GFT-4.2 and *T. oswaldi* from ThI-GH further supports these arguments (**Fig. 39**). The macaque exhibits a microwear pattern characterised by numerous pits, puncture pits, and gouges, in addition to a relatively low number of scratches. This pattern is consistent with a diet characterised by the consumption of hard fruits, along with some leaf and seed intake. Conversely, *T. oswaldi* exhibits a pattern characterised by a higher number of scratches than pits, suggesting a diet with significant grass consumption associated with open grassland landscapes. However, the dental microwear pattern of *T. oswaldi* from ThI-GH indicates that they also consumed other food such as fruits, seeds, or leaves. The predominance of grass consumption by *Theropithecus* has also been identified in *Theropithecus* fossils from the AaO (~2.5 Ma) and Tighennif (~1 Ma) sites in northern Africa (Fannin et al., 2021), suggesting that despite chronological differences, the species exhibits a similar abrasive diet.

When comparing the results of occlusal microwear with the buccal microwear texture analysis of *M. cf. sylvanus* from GFT-4.2 and *T. oswaldi* from ThI-GH, certain discrepancies are observed. On the occlusal surface, the fossil macaque shows a dietary

pattern similar to that of extant *L. albigena* and *C. atys*. In contrast, on the buccal surface, it is more similar to extant *T. gelada*, *M. sphinx*, and *M. mulatta* (see **Paper II**, pp. 93). In the case of *T. oswaldi*, the occlusal pattern indicates similarity with the diet of extant *M. sphinx* and *T. gelada*. At the same time, the buccal surface is more similar to the diet of extant *P. hamadryas* and *T. gelada*. These discrepancies may be primarily due to the different temporal resolutions of the methods. On the one hand, occlusal microwear has a short-term resolution, meaning the dietary signal is markedly seasonal. On the other hand, buccal microwear has a long-term resolution, capturing an average dietary signal across all seasons. This could explain, for example, why the diets of the macaques from GFT-4.2 and *T. oswaldi* from ThI-GH show similarities to a greater number of extant cercopithecoid species with a more varied diet.

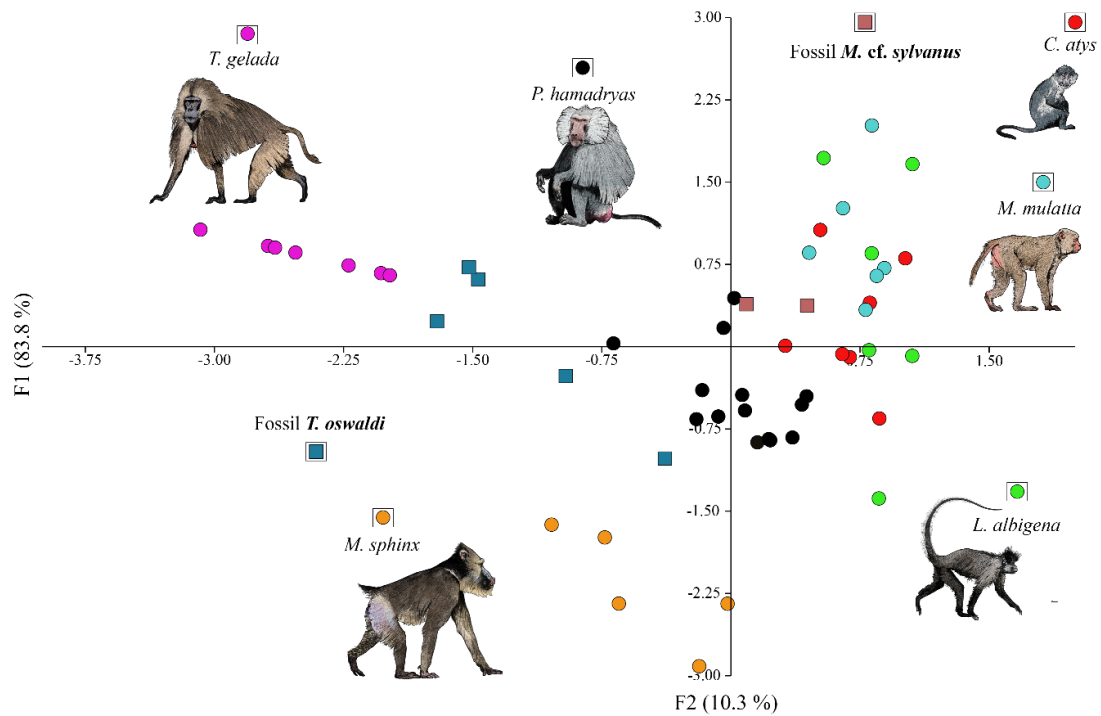


Figure 39. Correspondence analysis based on four occlusal microwear variables: average number of puncture pits, number of gouges, number of scratches, and number of pits. A comparison was made between the microwear patterns of extant cercopithecoids and the fossil remains of *M. cf. sylvanus* from GFT-4.2 and *T. oswaldi* from ThI-GH.

The $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values also corroborate these findings (**Fig. 36**). The *T. oswaldi* from ThI-GH exhibits more positive carbon values than *M. cf. sylvanus* from GFT-4.2, with some individuals even indicating a percentage of C_4 plant consumption. A comparison of the faunal assemblages from the two sites reveals that these differences are evident. In a context like GFT-4.2, where C_4 plants are present, the *M. cf. sylvanus* species exhibits the most negative $\delta^{13}\text{C}$ values, indicating a diet composed exclusively of C_3 plants.

Conversely, *T. oswaldi* are among the species in ThI-GH with the most positive $\delta^{13}\text{C}$ values. If we apply the enamel-diet enrichment factor of $+11.8 \pm 0.3\text{‰}$ calculated for chimpanzees (*Pan troglodytes*) at Ngogo in Kibale National Park, Uganda (Malone et al., 2021), two specimens of *T. oswaldi* from ThI-GH (see **appendices pp. 291**) with values ranging from -9.7 to -0.7‰ would suggest a C_3 – C_4 mixed feeder diet. This could imply some consumption of C_4 plants, likely grasses, by these two *T. oswaldi* individuals. About $\delta^{18}\text{O}$ values, the values of *M. cf. sylvanus* are more positive than those of *T. oswaldi*, which could be attributed to the consumption of tree leaves.

6.4. Plant wax biomarkers analysis in northern Africa

Plant wax biomarker distributions in GFT-4.2 (~2.5 Ma) and Oued Rabt (~0.5 Ma) from western Morocco are dominated by odd-numbered, higher chain lengths, indicating a terrestrial plant wax source in most samples, with C_{31} as the dominant *n*-alkane in all samples for both sites (**Fig. 27 and appendices pp. 249**). However, some samples also contain odd-numbered, mid-chain length *n*-alkanes (i.e., C_{21}), indicative of emergent plants. In the case of GFT-4.2, one sample suggests a submerged plant wax source supported by Submerged/terrestrial ratio (STR) and Aquatic Plant Ratio (Paq) (see **Paper I results pp. 64 to 65**). The average chain length (ACL_{21-33}) for both sites is the same, ranging from 27 to 30. These data indicate that throughout the stratigraphic sequence, there is a presence in GFT-4.2 and OR of a predominance of terrestrial plants with inputs from emergent plants. This would imply water resources with greater and lesser water abundance periods throughout the sequence.

Unfortunately, the low preservation of organic matter in OR has prevented the extraction of compound specific isotope data at this site, making it impossible to conduct a robust ecological comparison between the two. GFT-4.2 is at least 2 million years older than OR, so one would expect better organic matter preservation in the latter. However, the hydrological dynamics of both sites may have played an important role in preserving organic matter, GFT-4.2, in a palustrine environment, and OR is a river system (Sala-Ramos et al., 2022). The higher water speed in OR would have generated greater erosion. This pattern has also been observed in the palynological analysis between the two sites, with poorer results obtained in the case of OR (Personal communication – Isabel Expósito).

In GFT-4.2, $\delta^{13}\text{C}$ values in *n*-alkanes indicate a C_3 -dominated environment. This fits with $\delta^{13}\text{C}$ values in the enamel of large vertebrates, which also indicate a predominance of C_3 plant consumption. However, *Hipparion* s. l., Tragelaphini, *Anancus* sp., and *Gazella* sp. also consumed C_4 plants, which were not detected in the *n*-alkanes of the plant waxes. This would imply that there was no presence of C_4 plants directly at the GFT-4.2 site, but they were present at varying distances from the site. In this sense, the animals could move over greater distances and select their food.

Previous work on stable carbon and oxygen isotopes of pedogenic carbonates from El-Kherba (~1.8 Ma) in Algeria also indicates a predominance of C₃ in the landscape (Sahnouni et al., 2011), as in the case of GFT-4.2, Tighennif, ThI-GH, and OHQ1-GDR. The evidence also shows a strong positive trend toward more positive $\delta^{13}\text{C}$ (including the possibility of some C₄ presence) and $\delta^{18}\text{O}$ of pedogenic carbonates over time, suggesting increased aridity (Sahnouni et al., 2011). This aridity is also present in GFT-4.2, AaO, Tighennif, ThI-GH, and OHQ1-GDR.

6.5. General comparison with ecological data from the similar chronologies in Africa and Europe

The Maghreb is limited by two significant geographical barriers: the Mediterranean Sea to the North, separating it from the Iberian Peninsula, and the Sahara Desert to the South, separating it from Sub-Saharan Africa. However, the Sahara was not always a desert and experienced multiple green events lasting thousands of years that could have facilitated the exchange of mammals between northern Africa and the rest of Africa and Eurasia. During the Plio-Pleistocene transition (Guefaït-4.2 and Ahl al Oughlam), there were at least seven episodes of Sahara greening, specifically between 2.7 and 2.55 Ma. Moreover, this period coincided with one of the East African Rift System lake periods (Larrasoaña et al., 2013). During the early Middle Pleistocene, approximately seven episodes of Sahara greening also occurred (Larrasoaña et al., 2013).

Previous studies show a similarity between the fauna of eastern Africa, and to a lesser extent, southern Africa, and the fauna of northern Africa during the Plio-Pleistocene transition (Geraads, 2010). Despite the latitudinal difference, the taxonomic similarities with eastern Africa are much more significant than with European sites. What about the similarities in ecological context during the Plio-Pleistocene transition?

There are very few European sites from 3 to 2.5 Ma. At 2.6 Ma is the Huelago site (Guadix-Baza basin, Iberian Peninsula), where samples of Bovidae and Cervidae were analysed, showing a pure consumption of C₃ plants (Domingo et al., 2013). In general, the pattern of sites from the Late Pliocene to the Early Pleistocene in Europe is one of predominance of C₃ ecosystems with landscapes ranging from woodland to woodland-mesic grassland. The carbon isotopic values demonstrate that the spatial distribution of vegetation was broadly similar to that of the present day, with the most "closed" vegetation in Central and northern Italy, while open mesic grassland vegetation covers can be reconstructed for the Iberian Peninsula, Central France, and the Carpathian Basin (Szabó et al., 2022).

In Africa, sites dating from 3 to 2.5 Ma are also scarce. However, unlike Europe, which had more "humid" environments, the Plio-Pleistocene transition in Africa is characterised by more open landscapes with arid climates. In central Africa, at the Koro Toro site (3.5 Ma) in Chad, the paleoenvironmental data indicate a landscape with extensive C₄ dry grasslands and sparse trees bordering an expanded lake and associated stream channels

(Zazzo et al., 2000; Lee-Thorp et al., 2012). In eastern Africa, in the Turkana Basin, there is a mixed C₃/C₄ landscape from 4 to 2.4 Ma, and from 2.4 to 1 Ma, C₄ grasslands predominate (Cerling et al., 2015). However, in the Chiwondo beds in the Malawi Rift between 4.3 and 0.6 Ma, the majority of herbivores had a mixed C₃/C₄ diet with a large consumption of C₃ plants, suggesting a regionally heterogeneous environment (Lüdecke et al., 2016). These ecosystem patterns in Malawi differ from most reconstructed environments further North in the eastern Rift, where open grassland savannas have dominated since approximately 2.5 Ma.

Without the predominant presence of C₄ plants, the landscape during the Plio-Pleistocene transition in northern Africa would resemble more closely that observed in eastern Africa, with a mosaic landscape dominated by open and arid habitats.

In the early Middle Pleistocene, the similarity between the fauna of eastern and northern Africa reaches its peak (Geraads, 2010). In Europe, similarities between species in northern Africa are recorded, such as evidence of lynx immigration (Geraads, 1980b).

The number of archaeological sites from this chronology (~0.8-0.5 Ma) in Europe is also very scarce, and the pattern in the carbon isotopic signal is the same as that observed for Plio-Pleistocene sites. There is a predominance of C₃ ecosystems in Central and southern Italy (Isernia La Pineta, Guado San Nicola, Grotta Romanelli, Notarchico, Cava Campani, Sessano, Vallo di Diano, and Fontana Ranuccio) with landscapes of closed forests, woodland and grasslands with temperate and humid climates (Zanazzi et al., 2022; Briatico and Bocherens, 2023). This landscape has also been observed at early Middle Pleistocene sites in the Iberian Peninsula, such as Punta Lucero and Atapuerca (Gran Dolina) (García García et al., 2009; Domingo et al., 2017) and the Mauer site in Germany (Wagner et al., 2011).

Few archaeological sites have been discovered in Africa during this chronology. In the eastern, notable sites include Melka Kunture (0.6 Ma) and Asbole (0.8-0.64 Ma) in the Awash Valley, Ethiopia. The environment is highly diverse in both locations, with a mixed presence of C₃/C₄ plants. This diversity encompasses mosaic landscapes with arid C₄-dominated open-vegetated regions, riparian and mountain forests, and areas with patches of bushes and thickets (Bedaso et al., 2010; Briatico et al., 2024).

In southern Africa, Wonderwerk Cave (strata 9-6; 0.9-0.4 Ma) shows an expansion of arid environments dominated by C₄ grasses (Ecker et al., 2018). This coincides with global evidence of increasing aridity based on marine- and terrestrial-based proxy records (Lehmann et al., 2016). However, at the Elandsfontein site (1.0-0.6 Ma), there is a predominance of C₃ ecosystems in a context where ancient spring deposits indicate available surface water, suggesting an oasis for mammalian fauna within a relatively drier landscape in the early Middle Pleistocene (Braun et al., 2013; Lehmann et al., 2016).

The ecological context of the early Middle Pleistocene in Europe and Africa generally follows the same pattern observed during the Plio-Pleistocene. In Europe, environments are characterised by C₃ ecosystems in more forested areas with temperate, humid, and colder climates. In contrast, the landscapes are arid and open in eastern and southern

Africa, generally with C₄ plants. These open and arid landscapes are part of diverse ecosystems, including freshwater sources and riparian forests.

· Chapter 7: Conclusions ·

The earliest evidence of hominins in northern Africa dates to at least 2.44 Ma, as reported by Sahnouni et al. (2018). Their presence is documented in the Maghreb from the Early Pleistocene to the early Middle Pleistocene (1.8, 1.7, 1.3, 0.77, 0.7, 0.5, and 0.4 Ma). Furthermore, one of the oldest known fossil remains of *Homo sapiens*, dating to approximately 0.3 Ma, were discovered in Morocco (Hublin et al., 2017). In addition to the Maghreb, other hominin fossils have been found in Central Africa (Chad) as early as ~3.5 Ma (Brunet et al., 1995). This evidence suggests that hominins inhabited a range of locations across Africa during the Pliocene and Pleistocene periods, extending the concept of the cradle of humanity to encompass the entire continent.

On a larger scale, the current Sahara Desert has experienced green episodes since 8 Ma, which may have facilitated the dispersal of various species, including hominins, northward across the continent (Larrasoña et al., 2013). However, there is a lack of knowledge regarding the regional and local ecological context of archaeological and paleontological sites in this territory.

This thesis reconstructs the environment during different periods of the Plio-Pleistocene transition and early Middle Pleistocene in Morocco, spanning various areas such as the Atlantic coast and the mountainous region of Ain Beni Mathar-Guefaït. The periods in question are ~2.5 Ma (Guefaït-4.2 (GFT-4.2) and Ahl al Oughlam (AaO), ~0.7 and ~0.5 Ma (Grotte des Rhinocéros (OHQ1-GDR)), ~0.77 Ma (Grotte à Hominidés (ThI-GH)) and ~0.5 Ma (Oued Rabt (OR)).

Regardless of the location and chronology of the sites, there is a clear dominance of C₃ plants and arid open landscapes, characterised by grasslands and shrublands, from the Plio-Pleistocene transition to the early Middle Pleistocene in Morocco. These similarities are evident in the AaO, OHQ1-GDR, and ThI-GH sites on the Atlantic coast, where no significant changes in the diet of the analysed mammals and, consequently, in the habitat have been observed over the past 2 Ma. A clear pattern of arid open C₃ grasslands persists, and the faunal taxa found at the three sites are very similar, supporting a diachronic similarity. This has implications for human evolution, as the AaO has no evidence of hominin presence to date, while the ThI-GH and OHQ1-GDR do. This indicates that the *Homo* sp. from ThI-GH and OHQ1-GDR were adapted to arid climates and open spaces, in line with the findings of Zeller et al. (2023) and Foister et al. (2023), which suggest that early African hominins predominantly inhabited open environments such as grasslands and dry shrublands. However, the environmental context at AaO during the Plio-Pleistocene transition was strikingly similar to that of ThI-GH and OHQ1-GDR, suggesting that it may have been a potentially suitable environment for hominins.

There is no evidence of an anthropic presence at the Plio-Pleistocene transition on the Atlantic coast to date. This may be because hominins had not yet reached this specific territory, or they have not yet been found in the fossil record. The oldest known presence in this area is dated to approximately ~1.3 Ma in Unit L of the Thomas I Quarry. In this

site, Gerbillinae dominates the rodent assemblage, which also indicates an arid environment (Raynal et al., 2023a). This aridity is also evident at the archaeological site of Tighennif (~1 Ma) in Algeria, with a similar Mean Annual Precipitation (MAP) to ThI-GH and OHQ1-GDR, suggesting that this climate was a common feature of northern Africa over time. There are some discrepancies regarding the presence of taxa, such as Hippopotamidae in Tighennif and Unit L, which indicate the presence of permanent water, in contrast to ThI-GH, OHQ1-GDR, and AaO, where this is absent. Notably, the genus *Theropithecus* is the only non-human primate present in ThI-GH, OHQ1-GDR, AaO, and Tighennif, and this primate is mainly associated with open habitats.

A comparison of the ecological context of AaO with that of the contemporary site GFT-4.2 (~2.5 Ma) has revealed certain differences. In GFT-4.2, the oldest known presence of abundant C₄ plants in the northern part of the continent in a mosaic landscape has been detected. While aridity was present in this area as in ThI-GH, OHQ1-GDR, AaO, or Tighennif, in GFT-4.2, there was a predominance of open grassland habitat with C₃ and C₄ plants. The evidence from the ecological data also indicates that the landscape and resources in this case were diverse, including forested areas and wetlands. The presence of *Macaca* and the absence of *Theropithecus* suggest greater vegetation cover, which is supported by the different diets of the two genera. Another aspect to consider is the observed more extreme climate depending on the season, with increased aridity and consumption of C₄ plants, especially during the warm season. The different locations of the sites could also explain this. ThI-GH, OHQ1-GDR, and AaO are close to the Atlantic coast, which may explain the relatively mild seasonal change observed at these sites. However, GFT-4.2 is the most inland site analysed and is situated in a mountainous area, which could contribute to the more pronounced climatic changes observed at this site.

Despite the absence of an anthropic presence in GFT-4.2 to date, the site is geographically proximate to the Ain Boucherit site (~2.44 Ma) in Algeria, which is also situated within the Intra-Atlas Maghrebien Depression. This leads us to hypothesise that the heterogeneity and variability in the available resources in the landscape likely facilitated the occupation of the region by early hominins and other mammals.

The scientific consensus is that the Northern Hemisphere Glaciation was a gradual process occurring between ~3.5 and 2.5 Ma, resulting in progressive African aridity (Trauth et al., 2021). This aridity on a global scale has been identified in all sites analysed in this thesis from the Plio-Pleistocene transition to the early Middle Pleistocene. However, as previously stated, the ecological context of GFT-4.2 is quite distinct from that of AaO. This work remarks the significance of conducting local palaeoecological studies directly at archaeological and palaeontological sites, contrasting these large-scale global studies. Understanding these local dynamics may be a pivotal factor in comprehending the variety of landscapes occupied by these early hominins. The presence of microhabitats may explain why some dispersals occurred, and the complexity of these dynamics can only be understood through high-resolution local palaeoecological studies.

Finally, it is important to note that despite increasing research in northern Africa, it remains a relatively underexplored region compared to other parts of Africa. Further

research is required in different archaeological and palaeontological sites from the Plio-Pleistocene transition to the Middle Pleistocene in the Maghreb. This is necessary to understand the ecological and climatic dynamics that contributed to the dispersal, occupation, and evolution of mammals and early hominins.

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· Appendices ·

Supplementary information:

Arid, mosaic environments during the Plio-Pleistocene transition and early hominin dispersals in northern Africa

Iván Ramírez-Pedraza^{1,2,3*}, Carlos Tornero^{4,1}, Hassan Aouraghe⁵, Florent Rivals^{1,2,6}, Robert Patalano^{7,3}, Hamid Haddoumi⁵, Isabel Expósito^{1,2}, Antonio Rodríguez-Hidalgo^{8,1}, Steffen Mischke⁹, Jan van der Made¹⁰, Pedro Piñero^{1,2}, Hugues-Alexandre Blain^{1,2}, Patrick Roberts^{3,11,12}, Deepak Kumar Jha¹¹, Jordi Agustí^{1,2,6}, Christian Sánchez-Bandera^{1,2}, Abdelkhalek Lemjidi¹³, Alfonso Benito-Calvo¹⁴, Elena Moreno-Ribas^{1,2}, Aïcha Oujaa¹³, Hicham Mhamdi⁵, Mohamed Souhir⁵, Al Mahdi Aissa⁵, M. Gema Chacón^{1,2,15}, Robert Sala-Ramos^{1,2}.

¹Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain.

²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain.

³isoTROPIC Research Group, Max Planck Institute of Geoanthropology, Jena, Germany.

⁴Department of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain.

⁵Faculté des Sciences, Département de Géologie, Université Mohammed Premier, Oujda, Morocco.

⁶Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain.

⁷Department of Biological and Biomedical Sciences, School of Health and Behavioral Sciences, Bryant University, Smithfield, USA.

⁸Consejo Superior de Investigaciones Científicas, Instituto de Arqueología (CSIC-Junta de Extremadura), Mérida, Spain.

⁹Institute of Earth Sciences, University of Iceland, Reykjavík, Iceland.

¹⁰Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, Madrid, Spain.

¹¹Department of Archaeology, Max Planck Institute of Geoanthropology, Jena Germany

¹²School of Archaeology, University of Philippines, Diliman, Quezon City, Philippines.

¹³Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

¹⁴Centro Nacional de Investigación Sobre la Evolución Humana (CENIEH), Burgos, Spain.

¹⁵UMR 7194 - Histoire Naturelle de l'Homme Préhistorique (MNHN/CNRS/UPVD), Paris, France.

This PDF file includes:

Supplementary Note 1: Site background (Guefaït-4 site and -4.2 locality)

Supplementary Note 2: Different temporal resolutions of proxies (macrofauna)

Supplementary Note 3: Stable carbon and oxygen isotope analysis (macrofauna)

Supplementary Note 4: Plant wax biomarkers

Supplementary Note 5: Small vertebrate analysis

Supplementary Note 6: Micro-crustaceans and algae remains

Supplementary Figures 1 to 8

Supplementary Tables 1 to 9

References

Supplementary Note 1: Site background (Guefaït-4 site and -4.2 locality)

Guefaït-4 palaeontological site (GFT-4) was discovered in 2015 by the team from Mohamed I University of Oujda during geological surveys in the Aïn Beni Mathar - Guefaït Basin (High Plateaus Region of Oriental Province, Morocco) and is included in the ongoing Spanish-Moroccan research project¹. The site was identified by the exposure of a gray-marly fossiliferous level rich in vertebrate fauna, now recognised as part of Unit 2 within the Plio-Pleistocene stratigraphic section of Dhar Iroumyane². This sedimentary layer extends over a considerable distance and includes specific geolocated sites referred to as Guefaït-4.1 (GFT-4.1), 4.2 (GFT-4.2), and 4.3 (GFT-4.3). During the 2017-2019 seasons, more than 3325 fossil remains of macro-vertebrates were recovered in a ~2-m thick trench covering 28 m² at the locality GFT-4.2. The eastern section of the trench (GFT-4.2) presented a litho-stratigraphic section divided into 15 sedimentological units that were grouped into three field levels during the excavation (Level 0, Level 1 and Level 2). Level 0 includes units 5, 6, 7 and 8 and has a thickness of 60 cm. It is a level of reddish loams altered by humidity changes probably related to slope erosion. This level 0 presents a considerable amount of fossil remains (*ca.* 14.5% of the total 3D coordinate remains). Level 1 includes units 9 to 14 and has a thickness of 60 cm. These are greenish and grey reducing clays and loams with abundant calcareous nodules in units 11 and 12. This level contains a higher density of paleontological remains (*ca.* 85.5%). The Unit 15 composed of light gray nodular limestones and equivalent to field level 2, does not present paleontological remains, nor does the top of the sequence is formed by units 1, 2, 3 and 4, which comprise limestone and organic soils (**Supplementary Figure 1 and 2**).

GFT-4.2 locality is located in a palustrine unit where mudstones, marls, palustrine limestones and conglomerate channels suggest a wetland environment characterised by water bodies and stream inputs (**Supplementary Figure 2a and 2b**). Sampling in GFT stratigraphic section 4.2 (**Supplementary Figure 2a**) was conducted on a sequence of mudstones, including carbonates, which are interbedded between palustrine limestone layers. Mudstones are indicative of mainly low energy fine-grained clastic sedimentation by decantation in a pond of relatively carbonated water, where the greenish-to-brown colour gradation suggests an evolution from reduction conditions to more oxidised conditions towards the top, including a dark coloured mudstone layer at the top suggesting a possible increase in organic matter.

The research conducted at GFT-4.2 involved collecting 3D spatially referenced macrofaunal remains (all determinable remains and indeterminable remains larger than 2 cm in maximum length), small vertebrate remains, and 3D spatially referenced sediment samples for palaeomagnetism, stable carbon isotope analysis, including plant wax *n*-alkanes, and analysis of pollen, micro-crustaceans, and algae. All samples were obtained from the 28 m² trench and its corresponding sections within the GFT-4.2 locality. Additionally, some sampling to obtain small vertebrate was carried out outside the trench, a few meters away in the same fossiliferous stratum corresponding to field levels 0 and 1.

The fossil accumulation at GFT-4.2 spans a period longer than a single catastrophic event. While we cannot determine the exact duration of the accumulation, we have multiple lines of evidence indicating that the time-averaged fossil assemblage of GFT-4.2 represents a short duration. These evidences are:

1) Chronology and sedimentary context: all samples to constrain the age of the GFT-4.2 sequence were collected on-site, which allowed us to establish a precise approximation that, while not providing an absolute date, places us in a homogeneous chronological context². Additionally, the overall context suggests a restricted geological timeframe, with no observed abrupt paleomagnetic, biostratigraphic, or sedimentary changes. Sedimentologically, although 15 stratigraphic units were defined within the 180 cm sequence (**Supplementary Figure 2a**), all are part of a palustrine event characterised by a quite homogeneous litho-stratigraphic section composed mainly of mudstones and nodular limestones.

2) Taphonomic evidence: the taphonomic study of the macrovertebrate faunal remains indicates that GFT-4.2 is a natural accumulation site. The site formation likely involved the death and rapid burial of corpses/skeletons in a periodically flooded bed, with contributions from bones transported by small, low-energy watercourses. This is evidenced by anatomical associations, semi-connections, anatomical connections, and small dispersions (a few metres) of anatomical elements from single individuals. The rapid burial is further supported by the low incidence of weathering on the cortical surfaces: 95.5% of the remains are unaffected, 0.2% are affected at Stage 1, and 0.1% are affected at Stage 2 according to the criteria of Behrensmeyer (1978)³. Despite the inherent difficulties in establishing sedimentary rates in palustrine environments, namely wetlands and marshes with complex sedimentation processes resulting from the interplay of biological, chemical, and physical factors, the short sequence in GFT-4.2, covering only 28 m² and 120 cm thick, suggests a geologically short period. As supported by taphonomic data, the rapid burial of remains would have resulted in a thicker stratigraphic column if the accumulation had occurred over a longer period and all the recovered fossils were concentrated within 120 cm.

3) Taxonomic homogeneity: in the 180 cm sequence of GFT-4.2, the remains of large mammals are concentrated within 120 cm, with 85% located in the first 60 cm (from the bottom to the top of the sequence) in field level 1, and the remaining 14.5% found in approximately the next 60 cm (field level 0). The representation of taxa in both levels or units is consistent (despite the differences in accumulation percentages), indicating taxonomic homogeneity within these 120 cm. If we were representing different landscapes or significantly different time periods between levels 0 and 1, we would expect to see different taxa. However, we observe the same taxa across both levels.

4) Homogeneity in diet and habitat across the sequence: the same large vertebrate taxa show the same dietary patterns with dental microwear and mesowear, as well as stable isotopes, regardless of whether they belong to level 0 or level 1 (**Supplementary Table**

3 and 5). The presence of pollen taxa is also homogeneous in the sequence (180 cm). Although concentrations are low, we see the same tree and herbaceous taxa in the same sediment samples throughout the sequence (**Supplementary Figure 5 and Supplementary Table 8**). Our results do not reflect changes in the type of landscape throughout the entire sequence.

The approximate age of GFT-4.2 is based on a combination of proxies. Paleomagnetic analyses indicate a correlation with the last part of the Gauss chron, with the fossiliferous levels being slightly older than the Gauss-Matuyama boundary². The data derived from macrovertebrates and microvertebrates suggest, along with palaeomagnetism, that this locality is dated to the Late Pliocene, near the Plio-Pleistocene transition. The absence of *Equus*, with the oldest African *Equus* record dating to 2.44 million years ago (Ma) at Ain Boucherit⁴, indicates that GFT-4.2 is older than this date. Considering the known temporal distribution of other large vertebrates, GFT-4.2 could be correlated to the top of the Gauss chron, extending the temporal range of several taxa in North Africa to that period. Additionally, the rodent assemblage found at GFT-4.2 provides supporting evidence for an age close to the Plio-Pleistocene transition. The presence of *Paraethomys pusillus*, *Paraethomys chikeri*, *Golunda aouraghei*, and *Praomys* cf. *skouri*, along with other rodent species, suggests an age that aligns with this transitional period. This is further reinforced by the persistence of late Pliocene murids in GFT-4 and the presence of *P.* cf. *skouri*, which is considered a marker of the beginning of the Pleistocene in the continental record of North Africa. Overall, the combined evidence from vertebrate fossils indicates a Late Pliocene age close to the Plio-Pleistocene transition for GFT-4.2^{1,2,5-12}.

Supplementary Note 2: Different temporal resolutions of proxies (macrofauna)

For the ecological reconstruction based on large mammal teeth, we combine three high-resolution approaches that cover different moments in the animal's life: the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values of tooth enamel bioapatite (long term; which reflect an average of the diet related to the period of enamel mineralization¹³), tooth mesowear (long term; which reflects the last months/years before death¹⁴⁻¹⁷), and tooth occlusal microwear (short term; which reflects the last days/weeks before death^{18,19}). A summary of the results provided by the three methods is presented in **Supplementary Table 2**. Here, we present a detailed description of each species.

***Hipparion* s. l.:** The long-term results show great variability in diet with consumption of both C₃ and C₄ plants, oscillating from browser to grazer. Despite this oscillation, the mesowear places a large part of the samples alongside extant grazers (**Fig. 6**), leading us to deduce that a significant portion of their diet could be based on the consumption of grasses, in this case both C₃ and C₄ grasses. However, C₄ species comprise 79% of monocots and include grasses (Poaceae) and sedges (Cyperaceae), as well as 21% of dicots such as Amaranthaceae, and Euphorbiaceae^{20,21}. In GFT-4.2, Amaranthaceae is present. The Amaranthaceae family consists of herbaceous or slightly suffrutescent plants (with a woody stem only at the base), and approximately 28% of the species in the Amaranthaceae family use the C₄ pathway²². Therefore, we cannot rule out the

consumption of C₄ dicots, which would be linked to a more browser-like signal according to the microwear and mesowear.

The sequential analysis shows that this C₄ consumption would fluctuate throughout the year, increasing during the warmer periods (Fig. 5). However, the short-term (microwear) results show a generalised consumption of browse, except for the samples GFT 8, 9, 43, 17, 131, and 159 (see Supplementary Table 6). These specimens have several scratches exceeding 17 (10.2%), implying significant grass consumption²³. Considering that microwear represents a more local, seasonal signal and is closer to the site, this would mean that the *Hipparion* s. l. had a generally low-abrasive diet near GFT-4.2 towards the end of their life, likely based on the leaves of shrubs or trees.

The presence of *Hipparion* is well documented in Early Pleistocene sites such as Ain Boucherit, Ain Hanech, Mansourah, Ain Jourdel, and Ahl al Oughlam. At Ahl al Oughlam, *Hipparion pomeli* shows a diet consisting entirely of C₃ plants and dental wear indicative of a grazer behavior²⁴.

Tragelaphini: This taxon is the second highest consumer of C₄ plants in GFT-4.2, although there is a clear overall predominance of the C₃ signal. As with *Hipparion* s. l., we cannot rule out the consumption of C₄ plants, including C₄ dicots. This type of feeding behaviour linked to the consumption of C₄ dicots has been suggested for Tragelaphini from the Shungura Formation in Ethiopia^{25,26}. The mesowear (long-term) suggests a mixed feeding dietary trait with a predominant consumption of leaf and fruit browsing, but also including grass consumption as a mixed feeder. Three specimens exhibit a clear grazer pattern (GFT 148, 28A, and 144). However, similar to *Hipparion* s. l., Tragelaphini shows a browser signal in the short term, suggesting a low-abrasion diet likely based on the leaves of shrubs or trees in GFT-4.2 and its surroundings. Nevertheless, in Tragelaphini, 33.3% of the specimens have a scratch number exceeding 17, implying that one-third of them are consuming a considerable amount of grass.

Tragelaphini appears in the fossil record of several sites, such as Tighennif, Mansourah, Ain Hanech, El-Kherba, and Ain Jourdel²⁷, and in low percentages at Ahl al Oughlam²⁸.

Gazella sp.: This taxon has a general pattern similar to Tragelaphini but with a lower consumption of grasses. Only four specimens (GFT 211, 126, 190, and 249) show consumption of C₄ plants (including C₄ dicots) and with slightly positive values (around -7‰). Additionally, it has the mesowear score closest to leaf browsers, although still within the range of mixed feeders (Fig. 6). For microwear (short term), only 3 out of 13 samples (23%) have a scratch number exceeding 17. Therefore, it is the taxon with the most dominant browser consumption in GFT-4.2.

Gazella has been present in North Africa since the Pliocene^{27,29} and continues to exist today in Morocco, Algeria, and Tunisia³⁰. The *Gazella* sp. from Ahl al Oughlam (~2.5 Ma) and Tighennif (~1 Ma) has carbon values that correspond to a C₃ plant-based diet^{24,31,32}. Similar to GFT-4.2, the microwear of the *Gazella* from Ahl al Oughlam shows

a browser pattern; however, mesowear analysis indicates a mixed diet with a browsing tendency.

***Hexaprotodon* sp., Suinae and *S. africanus*:** The dietary patterns of these three taxa are very similar. All have a signal indicating the consumption of C₃ plants, and the microwear suggests a grazer diet. This would imply a predominant consumption of C₃ grasses for these taxa. Only one specimen of *Hexaprotodon* sp. (GFT 173) shows a microwear pattern close to that of extant browsers. Additionally, *Hexaprotodon* sp. is the taxon with the most depleted $\delta^{18}\text{O}$ values. This fits with the fact that water in aquatic plants is not as ^{18}O -enriched as water in land plants³³, suggesting an aquatic lifestyle for *Hexaprotodon* sp. A similar pattern has been observed for the Hippopotamidae of Tighennif (~1 Ma) in Algeria^{31,32}. The Hippopotamidae is also present in Ain, Boucherit, Ain Hanech and El-Kherba²⁷ in Algeria and Thomas Quarry I - Unit L (~1.3 Ma)³⁴ in Morocco.

***Anancus* sp.:** *Anancus* sp. predominantly consumes C₃ plants but also includes C₄ plants in its diet. The microwear analysis indicates a grazer pattern for all specimens, suggesting that this taxon could be consuming both C₃ and C₄ grasses. Although the data suggest a grazer pattern based on the microwear analysis, we cannot rule out that the percentage of C₄ consumption might be linked to the ingestion of C₄ dicot plants. This consideration is particularly relevant when taking into account the different temporal resolutions of the proxies (long term vs. short term). *Anancus* is present in Ain Hanech, Ain Boucherit, and Ahl al Oughlam sites²⁷. The *Anancus osiris* from Ahl al Oughlam has a diet of C₃ plants and microwear that indicates a mixed-feeder behavior with a tendency towards grazing²⁴.

Supplementary Note 3: Stable carbon and oxygen isotope analysis (macrofauna)

In terrestrial ecosystems, plants utilise three different photosynthetic pathways known as C₃ (Calvin cycle), C₄ (Hatch-Slack cycle), and crassulacean acid metabolism (CAM). These groups possess distinct carbon isotopic compositions due to the differential carbon discrimination between C₃ and C₄ plants during photosynthesis³⁵. Modern C₃ plants employing the C₃ photosynthetic pathway exhibit an average isotopic $\delta^{13}\text{C}$ value of -28.5‰ (global range -37 to -20‰), with typical C₃ plants having a maximum value of -23‰ and a threshold of -31.5‰ for closed-canopy forests³⁶. For this study, we employed an average $\delta^{13}\text{C}$ value of -27‰ for modern C₃ plants, excluding samples from the understory of closed-canopy forests below -31.5‰³⁶. Meanwhile, modern C₄ plants utilising the C₄ photosynthetic pathway have an average isotopic composition of -12‰ (global range -14 to -10‰)^{37–39}. Crassulacean Acid Metabolism (CAM) plants may exhibit $\delta^{13}\text{C}$ values resembling C₃ and C₄ plants. The identification of CAM plant contributions in diets is complex. However, these plant types are typically not predominant in mammalian herbivore diets in Africa and often possess chemical defences that discourage consumption by mammals⁴⁰. Moreover, CAM plants constitute only 5% of terrestrial plant biomass⁴¹, and according to our pollen study, they do not appear to be present in the study area.

The abundance of atmospheric CO₂ has varied over time⁴², influencing the carbon values of plants during photosynthetic fixation³⁵. Corrections for these effects are crucial to

facilitate a comparison between current plant carbon isotope values and those consumed by animals in the past. In our study, we corrected the $\delta^{13}\text{C}$ values of modern plants by +1.5‰ due to the difference between the pre-industrial $\delta^{13}\text{C}_{\text{CO}_2}$ value of approximately -6.5‰ during the Plio-Pleistocene⁴², and the $\delta^{13}\text{C}_{\text{CO}_2}$ value of about -8‰ when the reference collection of modern plants was gathered³⁶.

Dental enamel is one of the most commonly used materials for isotopic analysis and for reconstructing the paleoecology and paleodiet of extinct vertebrates due to its excellent preservation, lower susceptibility to recrystallisation processes, and ability to preserve the original isotopic signal^{43,44}. Dental enamel $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ results in fossils have demonstrated reliability in samples dating back millions of years⁴⁵. Carbon from plants ingested by herbivores is metabolised and assimilated as carbonate into the biogenic apatite. This process induces isotopic fractionation, resulting in a $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment^{46,47}. However, this enrichment can vary depending on the animal. In large mammals, it ranges from approximately +12–15‰^{38,47–50}. Cerling and Harris³⁸ established an average $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment factor of $14.1 \pm 0.5\%$ for extant African large herbivorous ungulates. Passey et al.⁴⁸ found different enrichment factors of $13.3 \pm 0.3\%$ for non-ruminant pigs and $14.6 \pm 0.3\%$ for ruminant cows in a controlled feeding study. For chimpanzees (*Pan troglodytes*) at Ngogo in Kibale National Park in Uganda, the calculated enrichment factor was $+11.8 \pm 0.3\%$ ⁵⁰. Tejada-Lara et al.⁴⁹ determined a positive correlation between body mass and enamel-diet enrichment fractionation. Thus, animals with a lower weight, such as a *Gazella* weighing approximately 30kg, would have a $\delta^{13}\text{C}_{\text{enamel-diet}}$ enrichment factor of about +12‰, while heavier animals like *Anancus*, around 5000kg, would exhibit an enrichment of around +15‰.

Taking all these factors into account, for this study, we used an average enrichment between the lower +12‰ and the higher +15‰, i.e., +13.5‰, to interpret tooth enamel $\delta^{13}\text{C}$ values and estimate potential consumption of C_3 or C_4 plants. Consequently, mammalian diets from GFT-4.2, displaying tooth enamel $\delta^{13}\text{C}$ values of $< -16.5\%$, indicate diets from closed canopy vegetation; values below *ca.* $< -12\%$ suggest pure C_3 plant consumption; values from -8 to 0‰ indicate a mixed C_3 - C_4 diet, and values above *ca.* > 0 or 1‰ are indicative of a predominant C_4 vegetation diet. Any differences introduced by potential taxon-specific enrichment factors would not change this overall perspective, given the size of the observed variation.

The $\delta^{18}\text{O}$ values within enamel bioapatite are closely linked to various water sources, including drinking water such as springs, rivers, lakes, and water holes and plant-based or food-derived water found in leaves, grass, and fruits^{51,52}. Moreover, metabolic processes involving carbohydrates also contribute to these values⁵³. As a result, factors such as precipitation, altitude, humidity, aridity, and local temperatures significantly influence the isotopic composition of available water and food sources⁵⁴. In arid environments, evaporation causes the enrichment of ^{18}O and depletion of ^{16}O isotopes in both open water reservoirs and plant tissues⁵⁵. However, this process significantly impacts plants to a greater extent, given their larger surface area for transpiration. Consequently, it is expected that animals reliant on plant-based water intake (non-obligate drinkers)

would exhibit elevated $\delta^{18}\text{O}_{\text{enamel}}$ values in comparison to obligate drinkers, which directly access surface water sources^{31,56}. The divergence in $\delta^{18}\text{O}$ values between these groups indicates increased aridity levels, with a larger disparity suggesting more arid conditions^{57–59}.

In this work, we rely on the fundamental principle of obligate (OD) and non-obligate drinkers (non-OD)^{56,60–62}, successfully applied in other articles to establish the degree of relative aridity^{57–59,63}. For this comparison, we chose the most reliable taxa from GFT-4.2 to categorize the mentioned groups based on the extant classifications of modern taxa as OD and non-OD^{61,62,64}. Specifically, Tragelaphini and *Gazella* sp. were selected as non-OD, while *Hexaprotodon* sp., Suinae, *S. africanus*, *Anancus* sp., and *Hipparion* sensu lato were designated as OD (**Fig. 4**). We also based our classification on dental wear data, considering that, generally, grazers among ungulates have a higher dependence on surface water than browsers^{56,64–66}. In this case, the patterns of the various species perfectly match the $\delta^{18}\text{O}$ values. The more browser taxa according to mesowear and microwear, such as *Gazella* sp. and Tragelaphini, have higher $\delta^{18}\text{O}$ values and have been classified as non-OD. Those with lower $\delta^{18}\text{O}$ values, such as *Hexaprotodon* sp., Suinae, *S. africanus*, or *Anancus* sp., show a grazer pattern according to microwear and have been classified as OD. *Hipparion* s. l. has also been classified as OD because, despite the microwear showing a browser pattern, the mesowear indicates a clear grazer dominance, and its signal has a significant weight as a long-term indicator. The Welch's ANOVA revealed significant differences in the $\delta^{18}\text{O}_{\text{enamel}}$ values between the OD ($n = 95$) and non-OD ($n = 61$) from GFT-4.2, with a p -value of $6.004\text{e-}17$. Data from the OD and non-OD in GFT-4.2 were compared to those of present-day mammals classified as non-OD and OD in the savannas of Laikipia and Tsavo in Kenya^{40,67}. Specifically, the non-OD in Laikipia ($n = 31$) comprised *Gazella granti* and Tragelaphini, while the OD ($n = 44$) included *Equus burchelli*, *Ceratotherium simum*, *Diceros bicornis*, *Loxodonta africana*, *Hippopotamus amphibius*, and *Phacochoerus africanus*. A Welch's ANOVA demonstrated significant differences in the $\delta^{18}\text{O}$ enamel values among the OD and non-OD from Laikipia, with a p -value of 0.000234 . In Tsavo, the OD ($n = 20$) encompassed Tragelaphini, *Gazella granti*, and *Kobus ellipsiprymnus*, while the non-OD ($n = 92$) consisted of *Equus burchelli*, *Diceros bicornis*, *Loxodonta africana*, *Hippopotamus amphibius*, and *Phacochoerus africanus*. The Welch's ANOVA showed significant differences in the $\delta^{18}\text{O}$ enamel values among the OD and non-OD from Tsavo, with a p -value of $7.993\text{e-}10$. The Welch's ANOVA between the OD and non-OD from GFT-4.2 and the OD and non-OD from Ahl al Oughlam showed significant differences (p -value of $1.02\text{e-}13$). These differences are significant between the OD of GFT-4.2 and the non-OD of Ahl al Oughlam (p -value of $6.112\text{e-}07$), and between the OD of Ahl al Oughlam and the non-OD of GFT-4.2 (p -value of $9.097\text{e-}06$).

These present reference locations were selected due to the large number of species analysed and their similarity to GFT-4.2 concerning the taxon studied. This facilitated a more accurate comparison.

Supplementary Note 4: Plant wax biomarkers

Generally, short-chain homologues (C₁₇-C₂₁ *n*-alkanes) characterise aquatic algae⁶⁸, mid-chain homologues (C₂₁-C₂₅ *n*-alkanes) characterise submerged and floating aquatic macrophytes^{69–71}, and long-chain homologues (C₂₇-C₃₅ *n*-alkanes) characterise terrestrial vegetation⁷².

The CPI of *n*-alkanes is used to examine the odd-over-even carbon number predominance, but also to distinguish sedimentary organic matter derived from terrestrial plants and that from bacterial or petroleum sources^{73–76}, and as an indicator for hydrocarbon maturity or degradation⁷⁷. Alkanes derived from land plants display carbon chains typically with CPI >5.0, while petrogenic and marine inputs or mature samples are characterised by considerably lower CPI values of ≤1.0. There is a wide range of CPI observed in modern African plants ranging from <1 to 99, with 96.0% of all CPI values being greater than or equal to 1, 81.2% greater than or equal to 2, and 60.7% greater than or equal to 5⁷⁸.

Average chain length, or the weight-averaged number of carbon homologues of the C₂₁-C₃₃ *n*-alkane, has been shown to be higher in C₄ grasses⁷⁹, but also correlates with higher growing season temperature and aridity^{80–84}.

Compound-specific isotope analysis is necessary to make inferences on plant community composition and the main sources of plant waxes to depositional environments. The *n*-alkane δ¹³C values provide information on plant type and photosynthetic pathway⁸⁵, the intensity and duration of sunlight⁸⁶, canopy structure and wax production⁸⁷, plant taxonomy⁸⁸, and the total concentration of atmospheric CO₂⁸⁹. In terrestrial contexts, variations in δ¹³C are influenced by biological differences in photosynthetic pathways and the degree to which different plant types discriminate against ¹³C during carbon fixation, which leads to distinct and, for the most part, non-overlapping values between C₃ and C₄ plants^{35,85,90}. C₃ plants typically have bulk leaf δ¹³C ranging between -35 to -20‰. C₄ plants, which do not discriminate against the heavier ¹³C to such a large degree, have values that span from -15 to -7‰. Plant wax *n*-alkanes are further depleted from their bulk values by about -7 to -5‰ for C₃ vegetation and -10 to -8‰ for C₄ types. Therefore, depending on plant ecological lifeform, water availability, canopy structure, and other factors, C₃ terrestrial plant *n*-alkane values can range from -42 to -25‰ (average -35‰), while C₄ plants range from about -26 to -14 ‰ (average -21‰)^{79,85,91–93}.

Supplementary Note 5: Small vertebrate data

Small vertebrates have been widely used as palaeoclimatic and palaeoecological indicators^{1–4}. The main criterion used to ascertain the habitat(s) of a living taxon is based on actualism, where interpretations of the habitat of an extinct species is based on its phylogenetic relationships with extant species, and on its association with taxa whose ecological requirements are known^{97,98}. Dental patterns can also be used for rodents^{99,100}. Some of the rodents from GFT-4.2 are illustrated in **Supplementary Fig. 6**, while some amphibians and squamate reptiles are represented in **Supplementary Fig. 7**.

Paraethomys pusillus and *Paraethomys chikeri* are the most abundant rodents at GFT-4 (132 and 78 molars, respectively), together making up 64% of the whole rodent assemblage. The genus was a widely distributed murine rodent both in northern Africa

and southwestern Europe since the Late Miocene. The North African *Paraethomys* lineage is the most diversified and longest-lived, the genus becoming extinct during the late Middle Pleistocene¹⁰¹.

Golunda aouraghei represents the last surviving species of the genus *Golunda* in Africa⁹. It is the third most numerous rodent in the assemblage, with 16% of the total rodent abundance (52 specimens). Hitherto, this extinct species has only been identified at GFT-4. The Indian bush rat (*G. ellioti*) is the only extant member of the genus, its geographic range restricted to Asia. The living species can be found in varied habitat conditions, including subtropical or tropical dry forests, shrublands and grasslands¹⁰². Changes affecting the molar morphology are usually interpreted as ecological adaptations¹⁰³. Observing the molar morphology of *G. aouraghei* can provide some clues about the environment in which it evolved. Presumably, *G. aouraghei* originated from the North African *G. jaegeri* during the Plio-Pleistocene transition after acquiring a slightly larger chewing surface and stephanodonty. Piñero et al.⁹ interpreted this as a molar adaption in response to increasing demands for wear tolerance in progressively more open and arid environments. *G. aouraghei* would then be the result of an adaptation to fibrous diet due to the expansion of open grassy habitats around the Plio-Pleistocene transition in Africa^{9,104}.

Praomys cf. *skouri* is scarcely represented in the rich sample from GFT-4, with only two specimens. This species is an extinct Early Pleistocene murid endemic from North Africa^{105–107}. The genus *Praomys* is probably of African origin, its species diversification occurred at around 6.5–5 Ma¹⁰⁸. The genus *Praomys* disappeared from North Africa in the Late Pleistocene^{107,109}. Currently, the genus is endemic to Sub-Saharan Africa. Most of the living species inhabit lowland or montane moist forests, although two of them (*Praomys daltoni* and *Praomys derooi*) preferably occupy open savanna woodlands^{110,111}.

Two gerbillines of different size have been identified at the studied site. The large-sized gerbil accounts for 3% (10 teeth), whereas the small-sized one represents the least abundant rodent at GFT-4, with only one identified specimen.

The subfamily Ctenodactylinae (gundis) is represented at GFT-4 by *Irhoudia* sp., accounting for 5% of the rodent association (18 specimens). The genus *Irhoudia* has been recognised in Late Miocene to Early Pleistocene sites from Morocco^{112–114}. Gundis are known from the Early Miocene up to the present, and today this group comprises five species. The extant gundis are inhabitants of rocky habitats, sheltering in rock fissures, in desert, or semi-desert areas across the northern parts of Africa¹¹⁵.

The ground squirrel *Atlantoxerus* sp. is relatively well-represented at GFT-4, with a prevalence of 11% among rodents (35 specimens). Nowadays, the genus *Atlantoxerus* is represented by the single species *A. getulus* from North Africa. It lives under arid or semiarid conditions, preferring sparsely vegetated areas of the Atlas Mountains^{116,117}.

The dormouse *Eliomys* sp. is only represented by two teeth. The living *Eliomys* species in northern Africa, i.e. *E. munbyanus* and *E. melanurus*, occur in a wide range of habitats, from humid forest to semi-desert. They have a preference for rocky habitats^{118,119}.

As far as amphibians and squamate reptiles are concerned, GFT-4 documents an anuran (Anura indet., alytid or ranid), a lizard (Lacertidae indet.), an anguid lizard (*Ophisaurus* sensu lato), and two snakes (Natricidae/Elapidae indet. and Colubridae/Lamprophiidae indet.). In its composition, the GFT-4 assemblage is quite uncommon for an open-air site, with a higher representation of the squamates over the anurans. In GFT-1, for example, even if the faunal composition is quite similar to the one observed for GFT-4, this ratio is inverse and anuran elements are quite abundant¹²⁰.

Anurans are represented by four very fragmented elements (an angulosplenic, a toothed maxilla, a tibiofibula, and a distal phalanx). The phalanx presents a similar morphology to the distal phalanx described in the site of GFT-1 and attributed to an indetermined alytid frog¹²⁰, with a large, shallow ventral concavity followed distally by a small bulge in its proximal part. However, this last comparison has to be taken cautiously, as it is not a diagnostic character, and the anurans remains from GFT-4 may thus correspond with an alytid or a ranid frog, based on the toothed maxilla.

Lacertid lizards are represented by both cranial (seven fragments of dentaries or maxillae) and post-cranial elements (a hemipelvis, a sacral vertebra, a caudal vertebra, and four fragments of vertebrae). Their pertaining to the family Lacertidae is mainly based on the teeth morphology and their pleurodont insertion on the bone. The teeth are isodont, cylindrical and mono-, or bicuspid and on the dentaries the Meckelian canal is wide open.

The most represented taxa (57% of the herpetofaunal assemblage) are the anguid lizards referred to the genus *Ophisaurus* sensu lato (i.e, including Eurasian, North American, and the North African species *Hyalosaurus koellikeri*), with a total of 27 elements, mainly osteoderms and a few vertebrae. In absence of tooth-bearing elements, it is not possible to go further into the taxonomical attribution of the taxa represented at GFT-4. In North Africa, besides the mention of undetermined anguid lizards (Anguidae indet.) in the middle Miocene of Beni Mellal (Morocco)¹²¹ and the late Miocene (Vallesian) of Asif Assermo (Morocco)¹²², *Ophisaurus* s.l has been reported in the early late Miocene (Vallesian) of Oued Zra (Morocco)¹²², whereas *Ophisaurus* sensu stricto (i.e., including only Eurasian and North African taxa) is first recorded from the latest Miocene of GFT-1¹²⁰. *Ophisaurus* sp. has been reported from the Pliocene of Oued Athmenia (Algeria), and *Ophisaurus* sp. from the Early Pleistocene of Irhoud Ocre (Morocco). Finally, the extant Moroccan species *H. koellikeri* has been described since the earliest Pleistocene at Ahl al Oughlam (Morocco)¹²³. Even if a more precise taxonomic attribution is not possible at GFT-4, the anguid lizard may certainly pertain to the North African clade, represented since the latest Miocene. The only extant representative of the North African clade, *H. koellikeri*, is found in central-western Morocco^{124,125}. According to Escoriza and Comas¹²⁴, the proportion of tree crown cover is the variable that best explains the *H. koellikeri* occurrence, and to a lesser extent other abiotic factors, including substrate, topography, and climatic conditions^{124,126}. *H. koellikeri* inhabits forests and/or woodlands (68% average tree crown cover per 0.0625 km²), mainly composed of evergreen oaks (*Quercus ilex* and *Q. suber*, 68.43%)¹²⁴. The evergreen broadleaf tree cover values of the

H. koellikeri current distribution areas range from 13.1 to 28.3% (percentage coverage per km²). This range contemplates 68% of the extant distribution of *H. koellikeri*¹²⁷.

Finally, two snake taxa are represented in GFT-4 (Natricidae/Elapidae indet. and Colubridae/Lamprophiidae indet.). The attribution to Natricidae/Elapidae indet. is based on a relatively small trunk vertebra bearing an hypapophysis, while a trunk vertebra (without hypapophysis) and an elongated caudal vertebra have been attributed to Colubridae/Lamprophiidae indet. The remaining material (a fragment of pterygoid, a caudal vertebra, three fragments of vertebrae, and a rib), with no diagnostic characters, has been attributed to Serpentes indet. Although poorly studied, Colubridae s. l. is not rare in the fossil Neogene localities of North Africa. Some colubrid snakes (*Psammophis*, *Coluber*, and *Elaphe*) have been mentioned in the middle Miocene of Beni Mellal¹²¹. Indeterminate colubrids/lamprophiids have been reported from the middle Miocene of Pataniak 6 (Morocco) and the late Miocene of Oued Zra¹²². Finally, in the Pleistocene of North Africa, the following taxa have been mentioned: *Hemorrhois hippocrepis*, *Malpolon monspessulanus*, cf. *Macroprotodon*, *Dasypeltis*, *Natrix maura*, *Coronella girondica*, and *Spalerosophis*^{122,123}. Concerning Natricidae, *Natrix maura* has been mentioned in the Middle Pleistocene of Wadi Sarrat¹²⁸ (Tunisia), and in the Holocene from El Harhoura 2¹²³ and Guenfouda¹²⁹ (Morocco). Concerning Elapidae, only the fossil species *Naja antiqua* has been reported from the middle Miocene of Beni Mellal^{121,130}, and also possibly from the late Miocene from GFT-1¹²⁰.

Supplementary Note 6: Micro-crustaceans and algae remains

One sample, GFT 1, included some gyrogonites, one valve and one carapace of *Potamocypris* sp., and one large fragment of a valve of *Psychrodromus* sp. The sediment material is a dense, hard limestone and some gypsum crystals precipitated from the washed sieve residues. Gyrogonites show that there was relatively clean water body in which charophytes were growing and *Potamogeton* and *Psychrodromus* often occur in small water bodies in wetlands including springs, ponds or slowly flowing streams. Some *Potamocypris* species tolerate more brackish conditions. The few ostracod specimens found in the sample are possibly due to the poor disaggregation of the dense limestone and resulting poor recovery, or the locally low abundance in wetland deposits representing large habitat differences on a local scale (spring, stream, pond and terrestrial deposits close to each other).

Sample GFT 3 included relatively many ostracod species and specimens, and also many gyrogonites. *Ilyocypris* sp. was very abundant and species of this taxon include dwellers of stagnant water bodies or those occurring more often in slowly flowing waters. The similarly abundant *Cypridopsis vidua* and accompanying taxa such as *Heterocypris salina*, *Herpetocypris* sp. and *Cypris pubera* are typical wetland taxa which tolerate slightly saline conditions¹³¹. *Cypridopsis vidua* represents a phytophylic taxon, indicating the presence of macrophytes or macroalgae and, thus, sufficient light penetration in the water body. Both the smooth and the noded forms of *Cyprideis torosa* were recorded with more or less similar abundances in the sample, indicating slightly brackish conditions

with a salinity of probably less than 5‰¹³¹. A shallow, slightly brackish water body with a dense charophyte cover on the floor is inferred.

Ilyocypris sp.: The members of the genus are widely distributed in stagnant and flowing waters, in lakes, ponds, swamps, springs, slowly flowing streams and rivers. Some of the species are also abundant in slightly saline waters. Several species typically occur in lakes whilst others are rather restricted to flowing waters¹³¹.

Cypridopsis vidua: The species is commonly found in densely vegetated (aquatic plants) flowing and also stagnant water bodies such as ponds and streams. It is also found in temporary ponds, and in springs, and it requires well oxygenated waters^{131–133}.

Neglecandona neglecta: Widely distributed in springs, ponds, lakes and streams. The species prefers relatively cold waters. It occurs in fresh and slightly saline waters, and tolerates temporary hypoxic conditions¹³¹.

Cyprideis torosa: The species tolerates a large salinity range, from oligohaline to hyperhaline conditions. Often dominating in coastal brackish waters such as coastal ponds, lagoons and estuaries. Valves with tubercles (nodes, *C. torosa* f. *torosa*) are more abundant in oligohaline waters whilst those without tubercles (*C. torosa* f. *littoralis*) dominate in more brackish conditions¹³¹.

Potamocypris sp.: The species of the genus typically occur in springs, ponds and slowly flowing streams. Some species occur in freshwater and in slightly brackish conditions too¹³¹.

Heterocypris salina: Typically inhabiting slightly brackish, small water bodies such as ponds, springs, and slowly flowing streams. Often occurring in small seasonal water bodies^{131–133}.

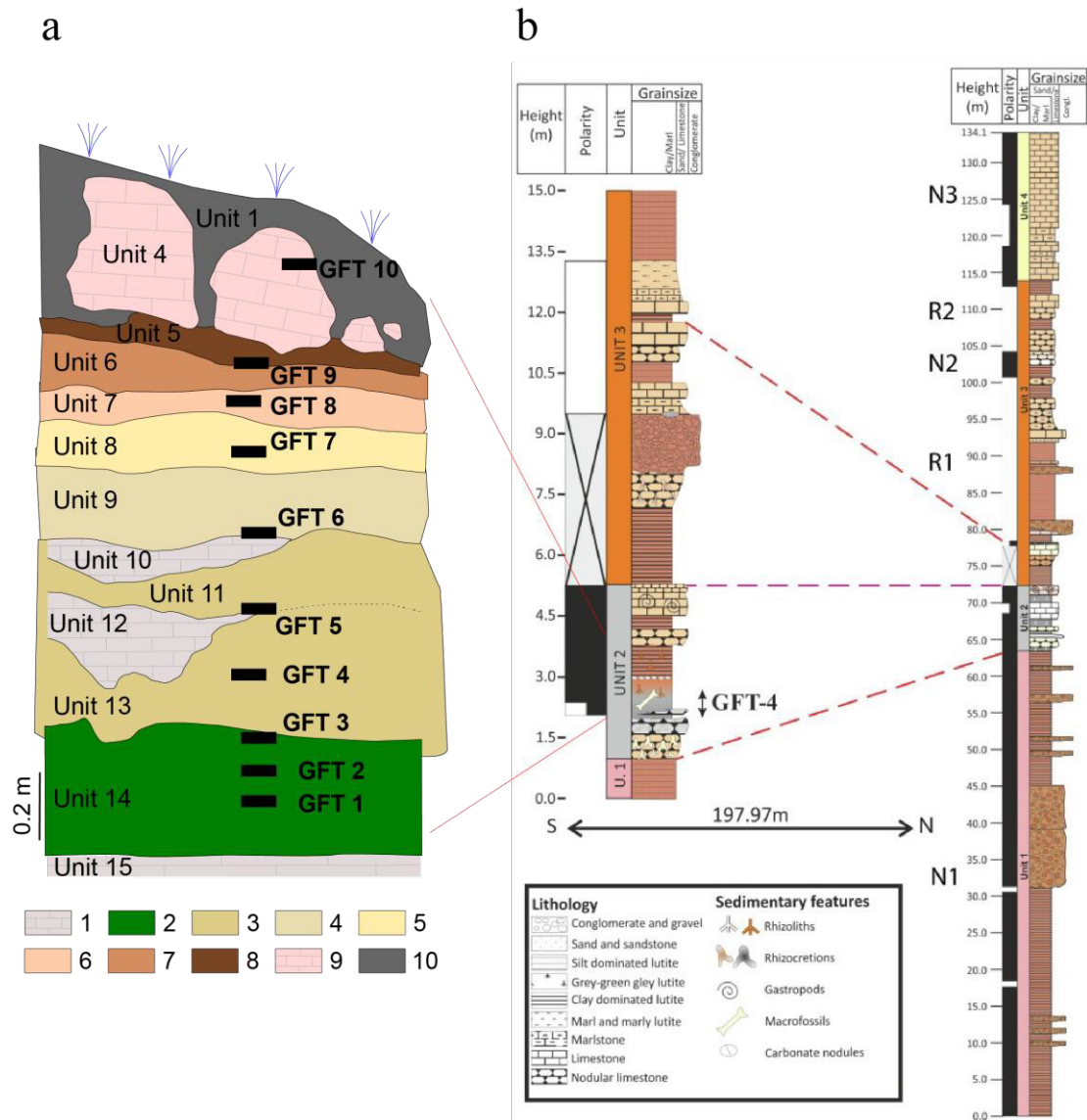
Herpetocypris sp.: Most species of the genus are commonly found in small, stagnant and densely vegetated waters bodies such as ponds and swamps, or slowly flowing streams, and in springs¹³¹.

Psychrodromus sp.: The species of the genus typically occur in springs and streams flowing from springs¹³¹.

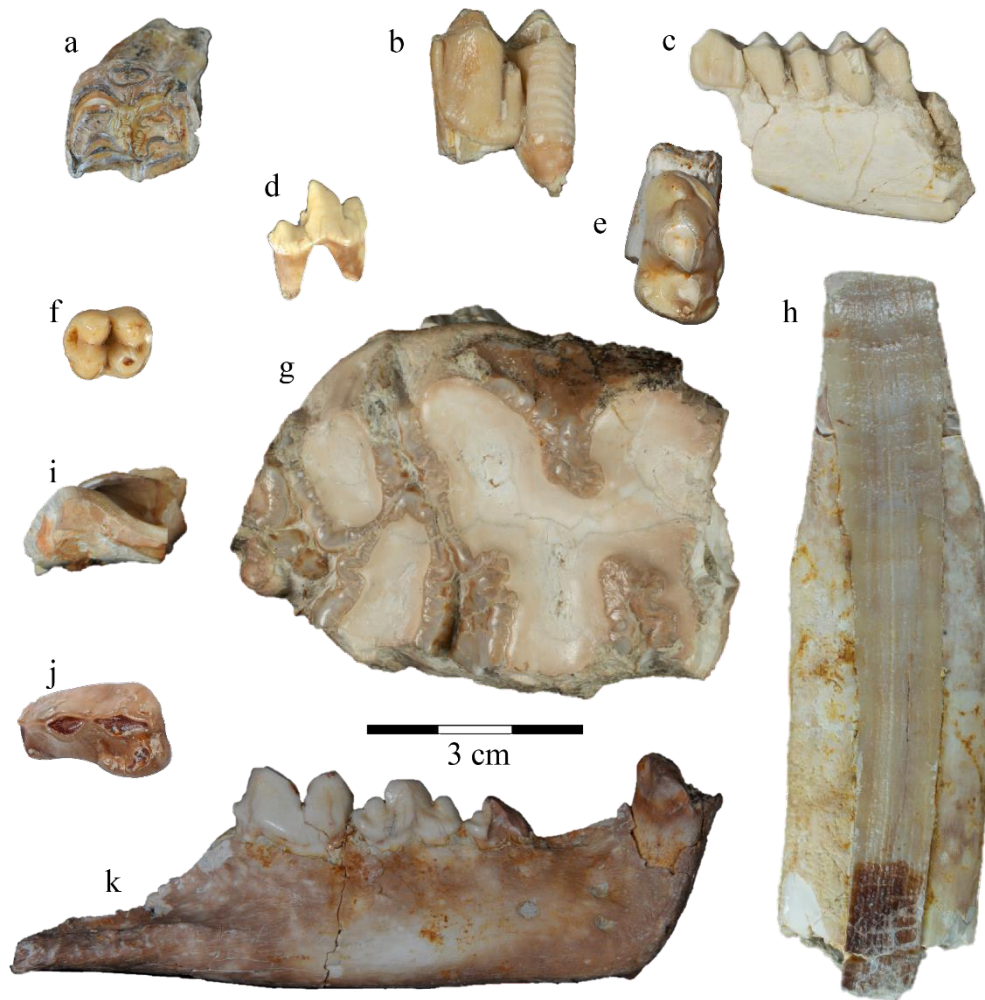
Charophyte gyrogonites: Charophytes occur in stagnant and slowly flowing, fresh to brackish waters. The algae require light and the occupied depth range in a specific water body, thus, depends on the turbidity of the water and the light penetration.



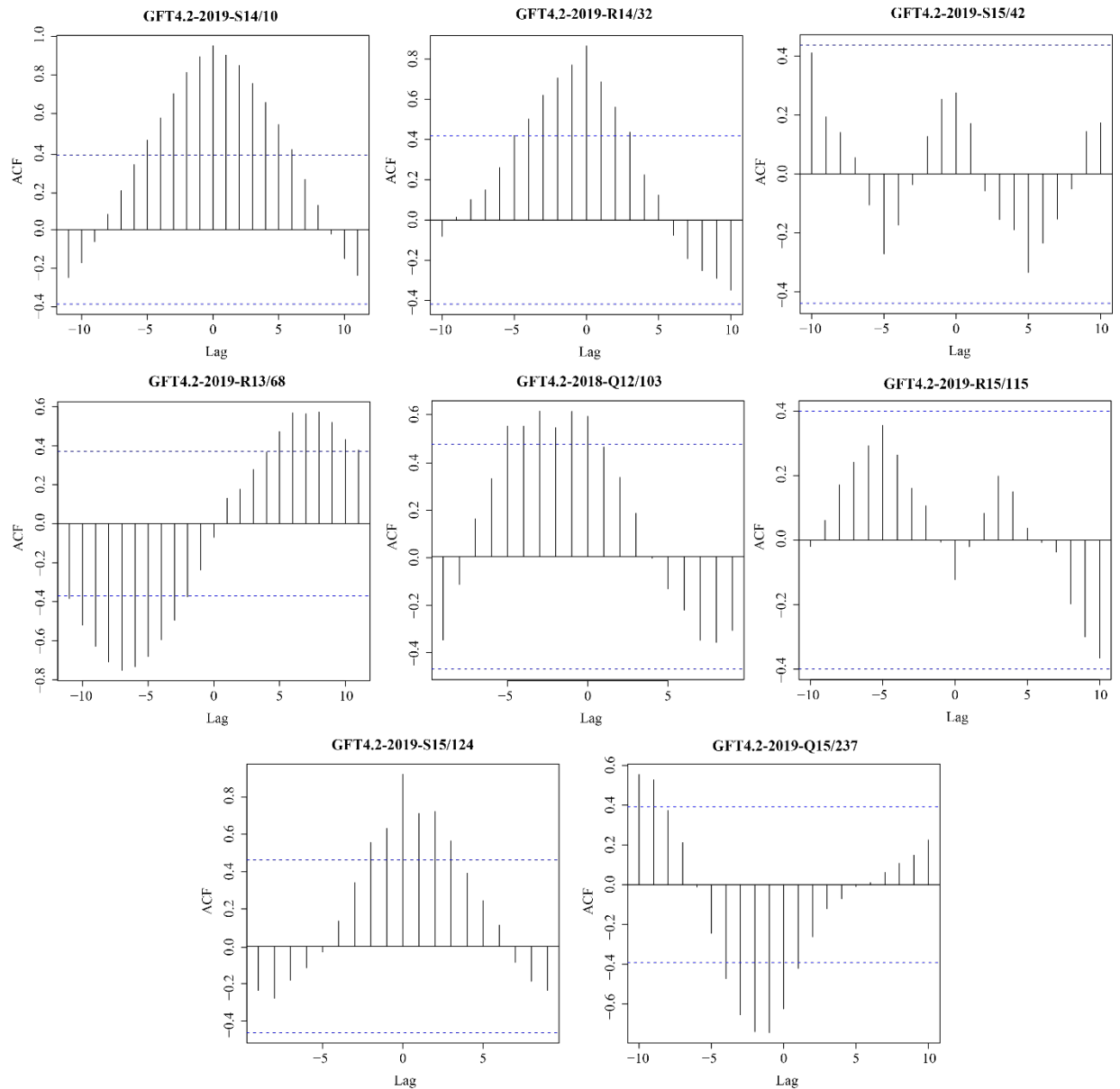
Supplementary Figure 1. Different perspectives from the Guefaït-4 site and -4.2 locality taken during the 2019 fieldwork (pictures by Alfonso Benito-Calvo and Antonio Rodríguez-Hidalgo).



Supplementary Figure 2. Stratigraphic section of GFT-4.2 locality. **a**, Legend of the stratigraphic section GFT-4.2: 1, Greenish massive marl; 2, Greenish grey crumby marl; 3, White limestone; 4, Grey crumby marl; 5, Mudstone with carbonate nodules; 6, Light brown mudstone; 7, Brown mudstone; 8, Dark brown mudstone; 9, Brecciated limestone. The black rectangles represent the locations where sediment samples for different analyses were collected: plant waxes (GFT 1 to 10), pollen (GFT 1, 2, 4, 6, 8, and 10), and micro-crustaceans and algae remains (GFT 1, 3, and 5). **b**, General sequence provided by Parés et al.².

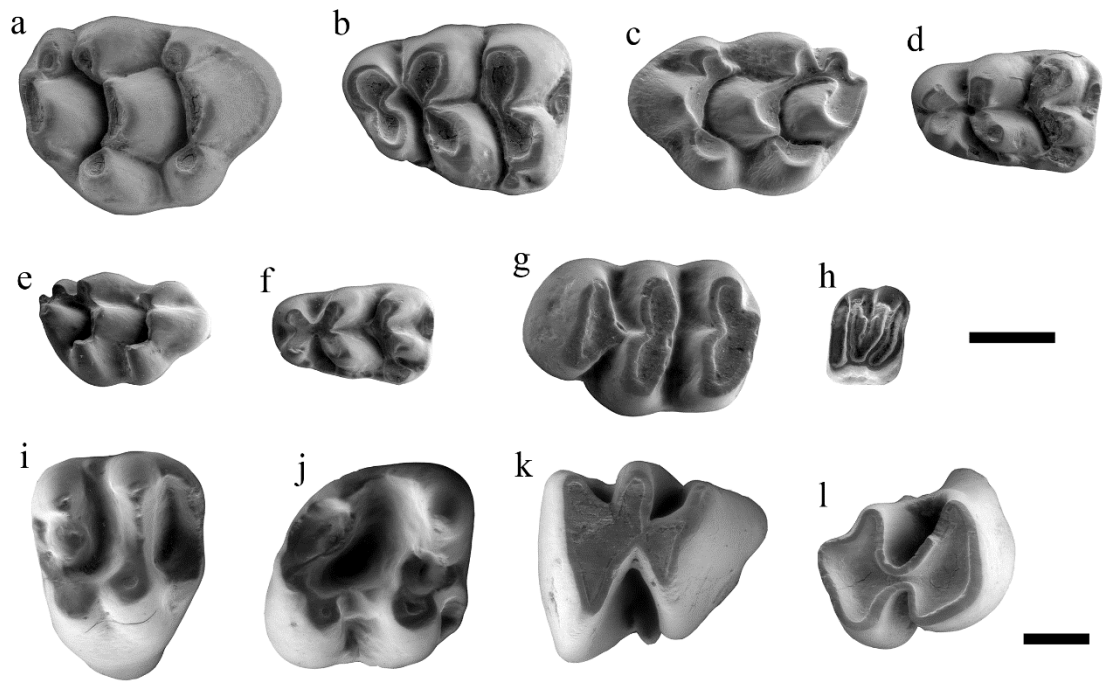


Supplementary Figure 3. Teeth of some of the macrofauna taxa analysed in GFT-4.2. **a**, *Hipparion* s. l. (GFT4.2-19-Q12/23; M² right; occlusal view). **b**, *Tragelaphini* (GFT4.2-18-S14/29; M_{1/2} left; buccal view). **c**, *Gazella* sp. (GFT4.2-19-T15/3; mandible buccal view). **d**, *Canidae* (GFT4.2-19-R14/54; M₁ right; buccal view). **e**, *Hyaenidae* (GFT4.2-19-T13/1 ; Pm₄ right; buccal view). **f**, *M. cf. sylvanus* (GFT4.2-18-Q14/13; M₂ left; occlusal view). **g**, *Anancus* sp. (GFT4.2-19-S15/91; M_{1/2}/DP₄; occlusal view). **h**, *Hexaprotodon* sp. (GFT4.2-19-Q15/224; upper incisor). **i**, *S. africanus* (GFT4.2-19-Q13/47; M/Pm; occlusal view). **j**, *Suinae* (GFT4.2-19-R13/9; D² left; occlusal view) and **k**, *Dinofelis* sp. (GFT4.2-19-Q15/237; mandible buccal view).

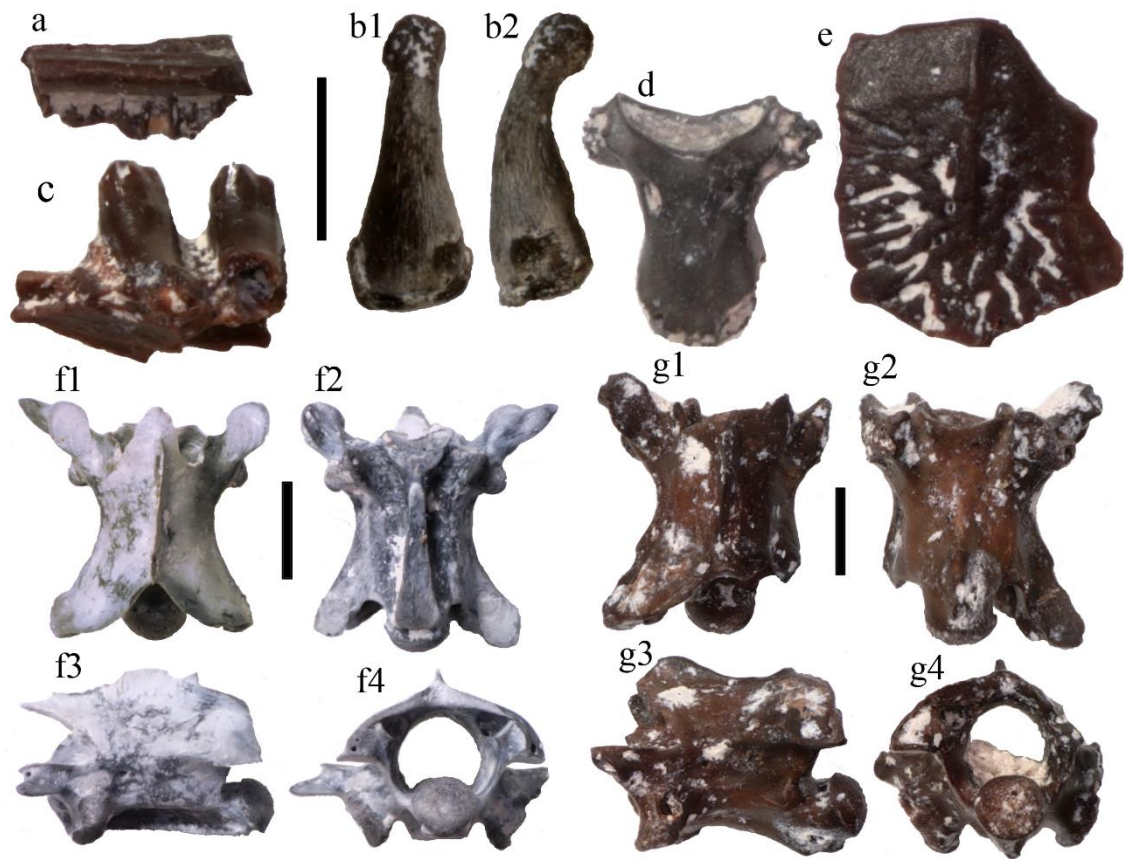


Supplementary Figure 4. Results of cross-correlation analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ of intra-tooth sequential analysis of *Hipparion* s. l. from GFT-4.2. Horizontal dashed lines = confidence interval of the correlation coefficients (95%).

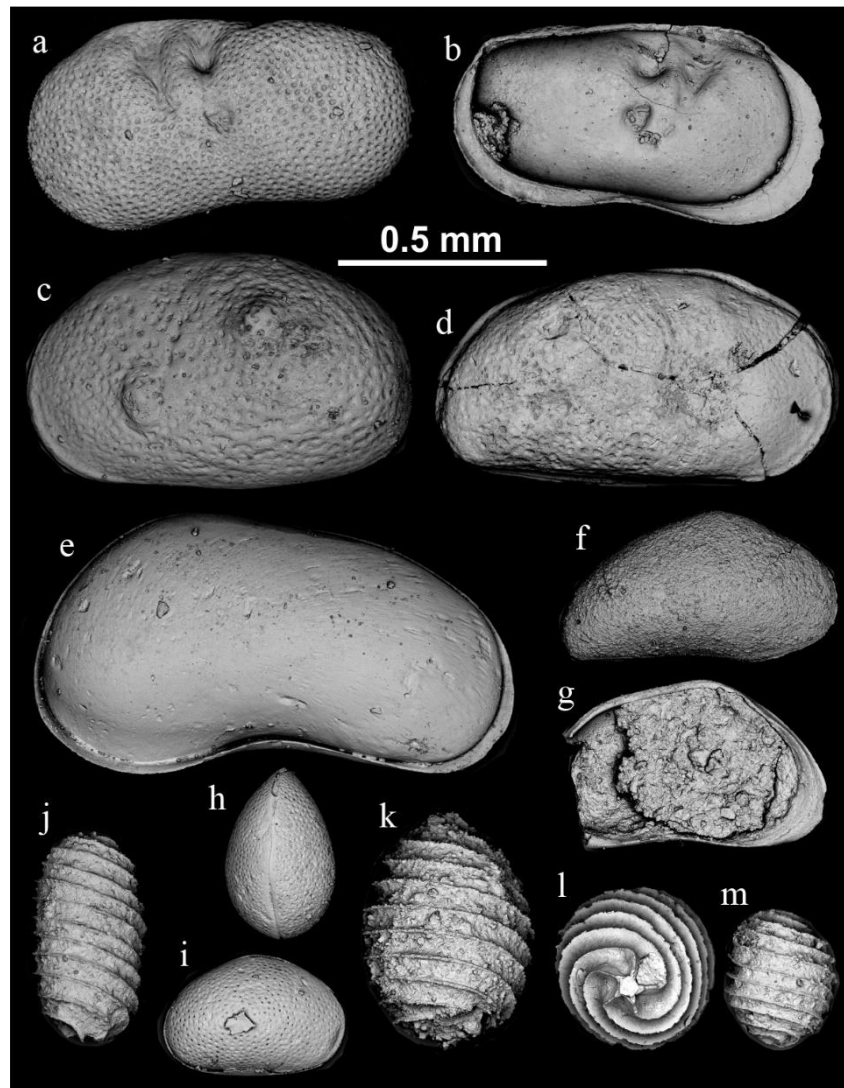




Supplementary Figure 6. ESEM photographs of rodents from GFT-4.2. **a**, M¹ of the murine *Golunda aouraghei*. **b**, M₁ of the murine *Golunda aouraghei*. **c**, M¹ of the murine *Paraethomys chikeri*. **d**, M₁ of the murine *Paraethomys chikeri*. **e**, M¹ of the murine *Paraethomys pusillus*. **f**, M₁ of the murine *Paraethomys pusillus*. **g**, M¹ of the gerbil Gerbillidae indet. **h**, M¹ of the glirid *Eliomys* sp. **i**, M¹ of the sciurid *Atlantoxerus* sp. **j**, M₂₋₃ of the sciurid *Atlantoxerus* sp. **k**, M₃ of the ctenodactyline *Irhoudia* sp. **l**, DP⁴ of the ctenodactyline *Irhoudia* sp. Scale bars equal 1 mm. The upper scale goes with A–H, whereas the lower scale goes with I–L.



Supplementary Figure 7. Photographs of amphibians and squamate reptiles from GFT-4.2. **a**, maxilla of *Anura* indet. (Alytid or Ranid), in medial view. **b**, terminal phalanx of *Anura* indet., in dorsal (b1) and right lateral (b2) views. **c**, fragment of maxilla or dentary of *Lacertidae* indet., in medial view. **d**, trunk vertebra of *Ophisaurus* s. l., in ventral view. **e**, osteoderm of *Ophisaurus* s. l., in dorsal view. **f**, trunk vertebra of *Colubridae/Lamprophiidae* indet., in dorsal (f1), ventral (f2), left lateral (f3), and posterior (f4) views. **g**, trunk vertebra of *Natricidae/Elapidae* indet., in dorsal (g1), ventral (g2), left lateral (g3), and posterior (g4) views. Scale bars equal 1 mm. The upper scale goes with A–E.



Supplementary Figure 8. Ostracods and charophyte remains from GFT-4.2: **a-b**, *Ilyocypris* sp. **a**, left valve (LV) external view (ev). **b**, LV internal view (iv). **c-d**, *Cyprideis torosa* f. *torosa*. **c**, ♀ LV ev. **d**, ♂ carapace (CPX) right valve (RV) visible. **e**, *Neglecandona neglecta* CPX RV visible. **f-g**, *Potamocypris* sp. **f**, RV ev, **g** LV iv. **h-i**, *Cypridopsis vidua*. **h**, CPX dorsal view. **i**, CPX RV visible. **j-k**, gyrogonites. **j**, type 1 lateral view (lv). **k**, type 2 lv. **l**, type 2 basal view. **m**, type 3 lv.

Supplementary Table 1. Potential information and area described, dispersion constraints and limitations of all methods used.

Evidence	Potential information	Potential area described	Dispersion constraints	Limitations
Bulk analysis ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$)	Reflect an average of the diet related to the period of enamel mineralization ¹³ . Long-term diet and habitat information.	From local to extra-regional. Depends on the migratory behaviour of each species.	-	Lack of precision in diet-enamel fractionation and enamel mineralization. Subject to the dietary preferences of each taxon.
Intra-tooth analysis ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$)	Reflect seasonal changes in diet related to the period of enamel mineralization ¹³ . Long-term diet and habitat information.	From local to extra-regional. Depends on the migratory behaviour of each species.	-	Lack of precision in diet-enamel fractionation and enamel mineralization. Subject to the dietary preferences of each taxon.
Dental microwear	Reflects the diet of the last days/weeks before death ¹⁴⁻¹⁷ . Short-term diet and habitat information.	From local environmental conditions	-	Taphonomic processes can affect the occlusal surface and microwear features ^{134,135} . Subject to the dietary preferences of each taxon.
Dental mesowear	Reflects the diet of the last months/years before death ^{18,19} . Long-term diet and habitat information.	From local to extra-regional. Depends on the migratory behaviour of each species.	-	Ease of cusp breakage in fossil assemblages, especially the sharpness. Subject to the dietary preferences of each taxon.
Pollen	Vegetation and climate reconstruction, environmental changes. Highest taxonomic resolution ¹³⁶⁻¹³⁸ .	From local to extra-regional ¹³⁶⁻¹³⁸	Type of pollen transportation (anemophilous, zoophilous, water), pollen production rate, and characteristics of the depositional context ¹³⁶⁻¹³⁸	Partial loss of pollen due to the alternation of wet and dry conditions and other post-depositional processes ¹³⁶⁻¹³⁸
NPPs	Local environmental conditions ¹³⁶⁻¹³⁸ .	From local environmental conditions ¹³⁶⁻¹³⁸	Favorable conditions for sporulation ¹³⁶⁻¹³⁸	Partial loss of spores due to the alternation of wet and dry conditions and other post-depositional processes ¹³⁶⁻¹³⁸
Small vertebrates	Vegetation cover and climate reconstruction, environmental changes ^{139,140}	From on-site (pond) and local to regional environmental conditions ^{139,140}	Taphonomical bias due to raptors or small-carnivores. Overrepresentation of local habitats in some cases ^{139,140}	Ecological plasticity may affect a precise ecological reconstruction. Loss of information for higher taxonomical categories ^{139,140}
Plant waxes	Plant landscape ecology, photosynthetic pathway, and changes in temperature and hydroclimate ^{35,85}	Local, on-site and regional, subcontinental scale environmental and climate 11	Production varies by taxonomic group due to differences in growth strategies and plant physiology ¹⁴¹	Preservation dependent on initial burial dynamics and resistance to biological decay ¹⁴²
Micro-crustaceans	Inferences of water salinity, temperature, permanence, flow, and presence of macrophytes ^{131,143}	Assemblages may represent lakes, or more local conditions in a wetland or stream ^{131,143}	Ostracod remains are typically dispersed in lakes very locally (metre scale), but transported in flowing waters ^{131,143}	Good preservation in sediments of carbonate-saturated water bodies or in dried sediments ^{131,143} .
Green algae	Inferences of shallow and rather clean water ^{131,143} .	Gyrogonites may represent slowly flowing waters, ponds, or the littoral zones of lakes ^{131,143} .	Gyrogonites might be transported in flowing waters whilst they represent the local environment in stagnant water bodies.	Good preservation in sediments of carbonate-saturated water bodies or in dried sediments.

Supplementary Table 2. Summary of the results of the three methods used in large mammal teeth from GFT-4.2. Abbreviations: B = browser, MF = mixed feeder, and G = grazer; OD = obligate drinker, non-OD = non-obligate drinker.

Taxa	Methods			
	Stable isotope analysis		Dental wear	
	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$	Mesowear	Microwear
<i>Hipparion</i> s. l.	C ₃ - C ₄	OD	B - MF - G	B
<i>Gazella</i> sp.	C ₃ - C ₄	non-OD	B - MF	B
Tragelaphini	C ₃ - C ₄	non-OD	B - MF	B
<i>S. africanus</i>	C ₃	OD	-	G
Suinae	C ₃	OD	-	G
<i>Hexaprotodon</i> sp.	C ₃	OD	-	G
<i>Anancus</i> sp.	C ₃ - C ₄	OD	-	G
Canidae	C ₃	-	-	-
Hyaenidae	C ₃	-	-	-
<i>Dinofelis</i> sp.	C ₃	-	-	-

Supplementary Table 3. Stable carbon and oxygen isotope values relating to all fossil taxa from GFT-4.2 analysed in this study. All samples were recovered from Level 1, except for GFT 141, 80, 58, 124, 85, 211, 82, 192, 227 and 53, which belong to Level 0.

Sample ID	Element	Taxa	$\delta^{13}\text{C}$ (‰) (VPDB)	S.D.	$\delta^{18}\text{O}$ (‰) (VPDB)	S.D.
GFT 116	Molar lower	<i>Anancus</i> sp.	-5.24	0.004	-3.08	0.052
GFT 177	Molar	<i>Anancus</i> sp.	-6.91	0.008	-2.83	0.016
GFT 178	Molar	<i>Anancus</i> sp.	-7.74	0.023	-2.79	0.049
GFT 97	Molar	<i>Anancus</i> sp.	-6.01	0.004	-3.04	0.011
GFT 185	M _{1/2} /DP ₄	<i>Anancus</i> sp.	-6.42	0.027	-2.54	0.035
GFT 191	M/P	<i>Anancus</i> sp.	-6.84	0.002	-0.88	0.030
GFT 212	Molar	<i>Anancus</i> sp.	-6.85	0.039	-3.14	0.017
GFT 214	Molar	<i>Anancus</i> sp.	-6.91	0.021	-1.78	0.035
GFT 226	Molar	<i>Anancus</i> sp.	-6.37	0.013	-2.83	0.013
GFT 228	M/P	<i>Anancus</i> sp.	-6.96	0.027	-3.08	0.017
GFT 229	M _{1/2}	<i>Anancus</i> sp.	-8.43	0.043	-2.75	0.070
GFT 90	Molar	<i>Anancus</i> sp.	-6.94	0.039	-3.31	0.028
GFT 186	M ₃ left	Tragelaphini	-7.68	0.007	1.02	0.030
GFT 157	Premolar upper	Tragelaphini	-10.53	0.023	-2.07	0.042
GFT 192	M ₃ right	Tragelaphini	-7.59	0.014	3.32	0.048
GFT 193	M ₃ right	Tragelaphini	-9.01	0.017	3.53	0.019
GFT 227	M ₃ left	Tragelaphini	-8.28	0.022	0.85	0.017
GFT 159	I ₁ left	Tragelaphini	-10.39	0.016	-1.63	0.029
GFT 53	Molar upper	Tragelaphini	-9.73	0.015	2.19	0.026
GFT 138	Molar upper left	Tragelaphini	-8.33	0.031	0.55	0.022
GFT 184	M ^{1/2} left	Tragelaphini	-10.27	0.044	-1.20	0.036
GFT 103	Molar lower left	Tragelaphini	-9.04	0.024	2.55	0.015
GFT 119	P ⁴ left	Tragelaphini	-8.30	0.008	-2.33	0.043
GFT 215	P ₂ right	Tragelaphini	-10.33	0.013	-0.30	0.024
GFT 124	Premolar	Tragelaphini	-9.75	0.025	0.93	0.039
GFT 73	M/P	Tragelaphini	-7.75	0.020	1.51	0.012
GFT 71	M ² left	Tragelaphini	-11.16	0.022	0.23	0.041
GFT 98	Dp ³ left	Tragelaphini	-10.82	0.005	-0.39	0.017
GFT 163	P ³ left	Tragelaphini	-9.17	0.030	-0.90	0.046

GFT 172	M _{1/2} right	Tragelaphini	-4.94	0.016	1.53	0.023
GFT 203	M _{1/2} right	Tragelaphini	-8.26	0.005	1.70	0.034
GFT 206	M ^{1/2} left	Tragelaphini	-5.26	0.018	1.57	0.079
GFT 151	I ₁ left	Tragelaphini	-10.61	0.017	-2.09	0.035
GFT 58	P ³ right	Tragelaphini	-5.52	0.013	2.43	0.020
GFT 80	Molar upper right	Tragelaphini	-9.63	0.006	2.24	0.012
GFT 75	M/P	Tragelaphini	-8.13	0.005	0.34	0.011
GFT 141	P ₄ left	Tragelaphini	-8.77	0.019	-0.78	0.010
GFT 149	M ^{1/2} right	Tragelaphini	-6.83	0.031	2.65	0.010
GFT 165	M/P	Tragelaphini	-8.01	0.024	0.10	0.055
GFT 169	M _{1/2} left	Tragelaphini	-9.63	0.011	-1.05	0.021
GFT 170	I ₂ left	Tragelaphini	-11.39	0.031	-2.02	0.054
GFT 183	Premolar upper	Tragelaphini	-11.24	0.016	0.10	0.040
GFT 4	M ₃ right	Tragelaphini	-9.48	0.051	-1.27	0.044
GFT 51	M/P	Tragelaphini	-11.51	0.014	-0.91	0.010
GFT 217	M/P	Tragelaphini	-10.27	0.010	-0.65	0.084
GFT 218	M _{1/2} right	Tragelaphini	-3.85	0.020	2.29	0.033
GFT 223	Molar	Tragelaphini	-10.27	0.027	0.94	0.041
GFT 224	M _{1/2} right	Tragelaphini	-10.56	0.031	-1.37	0.008
GFT 225	M ₃ left	Tragelaphini	-8.22	0.007	0.01	0.055
GFT 92	M _{1/2} right	Tragelaphini	-8.13	0.048	1.33	0.019
GFT 93	P ₃ left	Tragelaphini	-8.48	0.032	0.17	0.014
GFT 146	Molar lower	Tragelaphini	-11.58	0.020	-2.32	0.006
GFT 150	I ₂ right	Tragelaphini	-9.69	0.005	0.94	0.035
GFT 188	M ^{1/2} right	Tragelaphini	-9.94	0.013	-1.18	0.067
GFT 82	M _{1/2} right	Tragelaphini	-8.24	0.006	3.83	0.044
GFT 232	M ₁ left	Canidae	-9.80	0.017	1.44	0.079
GFT 233	P _{3/4} left	Canidae	-9.05	0.030	-1.13	0.080
GFT 234	M ₁ right	Canidae	-11.17	0.025	4.53	0.048
GFT 235	M ₁ left	Canidae	-9.72	0.001	-0.94	0.011
GFT 236	M ₁ right	Canidae	-9.86	0.011	-0.61	0.008
GFT 253	M ₂ left	Canidae	-9.62	0.025	-0.89	0.012
GFT 231	P ⁴ left	Canidae	-9.92	0.032	0.02	0.035

GFT 96	M ² left	<i>Gazella</i> sp.	-8.17	0.029	-1.69	0.015
GFT 126	M _{1/2} right	<i>Gazella</i> sp.	-7.09	0.035	-0.90	0.031
GFT 138	Molar upper left	<i>Gazella</i> sp.	-10.99	0.010	-0.65	0.040
GFT 182	Molar upper	<i>Gazella</i> sp.	-10.49	0.036	-1.41	0.056
GFT 211	P ₃ left	<i>Gazella</i> sp.	-7.15	0.022	4.17	0.053
GFT 213	Molar	<i>Gazella</i> sp.	-11.31	0.013	3.15	0.044
GFT 219	M ₃ left	<i>Gazella</i> sp.	-10.38	0.013	8.84	0.004
GFT 222	M _{1/2} right	<i>Gazella</i> sp.	-11.33	0.013	5.41	0.027
GFT 115	M _{1/2} right	<i>Gazella</i> sp.	-10.93	0.035	1.83	0.031
GFT 122	M _{1/2} left	<i>Gazella</i> sp.	-12.18	0.035	2.14	0.056
GFT 131	M ³ left	<i>Gazella</i> sp.	-10.58	0.009	4.18	0.050
GFT 123	M ₁ left	<i>Gazella</i> sp.	-12.29	0.012	-1.66	0.053
GFT 190	M/P	<i>Gazella</i> sp.	-7.16	0.025	-1.54	0.070
GFT 249	Molar upper	<i>Gazella</i> sp.	-7.32	0.023	-2.48	0.018
GFT 248	Premolar	<i>Gazella</i> sp.	-10.44	0.007	3.22	0.029
GFT 113	P ² right	<i>Gazella</i> sp.	-9.72	0.019	4.25	0.056
GFT 118	P ₄ left	<i>Gazella</i> sp.	-9.68	0.008	-1.51	0.020
GFT 91	M _{1/2} left	<i>Gazella</i> sp.	-9.82	0.035	-1.52	0.058
GFT 105	M _{1/2} right	<i>Gazella</i> sp.	-9.64	0.015	-0.49	0.019
GFT 238	M/P	<i>Hipparion</i> s. l.	-4.74	0.039	-1.27	0.044
GFT 55	M/P upper right	<i>Hipparion</i> s. l.	-9.24	0.053	-3.45	0.192
GFT 59	P ² right	<i>Hipparion</i> s. l.	-8.47	0.011	-2.60	0.006
GFT 60	P ^{3/4} left	<i>Hipparion</i> s. l.	-6.63	0.023	-5.83	0.021
GFT 61	Premolar lower right	<i>Hipparion</i> s. l.	-9.41	0.022	-3.25	0.057
GFT 62	M ³ right	<i>Hipparion</i> s. l.	-4.94	0.042	-1.78	0.008
GFT 67	I ₂ right	<i>Hipparion</i> s. l.	-7.01	0.011	-3.91	0.034
GFT 81	Incisive	<i>Hipparion</i> s. l.	-8.46	0.031	-3.60	0.068
GFT 104	P _{3/4} right	<i>Hipparion</i> s. l.	-5.89	0.030	-1.57	0.016
GFT 107	P ⁴ right	<i>Hipparion</i> s. l.	-5.90	0.030	-0.96	0.054
GFT 153	Premolar lower left	<i>Hipparion</i> s. l.	-9.20	0.034	-3.14	0.048
GFT 154	I ₁ right	<i>Hipparion</i> s. l.	-9.57	0.019	-3.21	0.018
GFT 160	M ³ right	<i>Hipparion</i> s. l.	-7.06	0.021	-2.00	0.008
GFT 162	M ² right	<i>Hipparion</i> s. l.	-7.14	0.015	0.29	0.037
GFT 56	M/P	<i>Hipparion</i> s. l.	-9.50	0.019	-1.26	0.031
GFT 57	P ^{3/4}	<i>Hipparion</i> s. l.	-8.40	0.011	-0.93	0.007

GFT 167	M ₂ right	<i>Hipparion</i> s. l.	-7.77	0.035	-1.79	0.053
GFT 168	M ^{1/2} right	<i>Hipparion</i> s. l.	-10.25	0.030	-1.26	0.044
GFT 87	P ₂ left	<i>Hipparion</i> s. l.	-7.13	0.031	-1.55	0.052
GFT 88	Premolar lower left	<i>Hipparion</i> s. l.	-11.26	0.020	-3.56	0.066
GFT 89	P _{3/4} right	<i>Hipparion</i> s. l.	-1.40	0.009	-1.06	0.059
GFT 99	P _{3/4} right	<i>Hipparion</i> s. l.	-9.89	0.038	-1.42	0.061
GFT 101	M/P	<i>Hipparion</i> s. l.	-8.14	0.013	-3.79	0.064
GFT 106	M/P lower	<i>Hipparion</i> s. l.	-10.49	0.003	-4.97	0.016
GFT 135	M ₃ left	<i>Hipparion</i> s. l.	-4.71	0.020	0.25	0.039
GFT 136	P ³ right	<i>Hipparion</i> s. l.	-6.60	0.022	-2.89	0.034
GFT 137	M ² right	<i>Hipparion</i> s. l.	-2.52	0.038	-1.22	0.011
GFT 202	M ² right	<i>Hipparion</i> s. l.	-8.56	0.017	-3.15	0.031
GFT 209	P _{3/4} left	<i>Hipparion</i> s. l.	-9.76	0.015	-1.18	0.092
GFT 210	M _{1/2} right	<i>Hipparion</i> s. l.	-9.68	0.043	0.05	0.043
GFT 84	P ^{3/4} left	<i>Hipparion</i> s. l.	-7.27	0.039	-0.32	0.023
GFT 86	P ² right	<i>Hipparion</i> s. l.	-4.90	0.015	-3.48	0.012
GFT 95	P ₂ left	<i>Hipparion</i> s. l.	-6.53	0.022	-2.35	0.036
GFT 102	P ^{3/4} right	<i>Hipparion</i> s. l.	-9.30	0.026	-3.25	0.019
GFT 110	M/P	<i>Hipparion</i> s. l.	-5.75	0.036	-0.66	0.029
GFT 112	M ₃ left	<i>Hipparion</i> s. l.	-8.19	0.010	-2.62	0.073
GFT 120	P ² right	<i>Hipparion</i> s. l.	-5.07	0.024	-1.46	0.015
GFT 121	M ₂ right	<i>Hipparion</i> s. l.	-4.82	0.029	0.26	0.008
GFT 123	M/P	<i>Hipparion</i> s. l.	-2.75	0.003	-2.14	0.013
GFT 125	Dp _{3/4} right	<i>Hipparion</i> s. l.	-9.18	0.026	-2.13	0.065
GFT 127	P ² right	<i>Hipparion</i> s. l.	-3.24	0.034	-2.13	0.007
GFT 128	M ₃ right	<i>Hipparion</i> s. l.	-8.19	0.025	-3.30	0.077
GFT 129	M ₂ right	<i>Hipparion</i> s. l.	-6.06	0.023	-2.32	0.060
GFT 132	M/P upper	<i>Hipparion</i> s. l.	-8.62	0.021	-4.22	0.059
GFT 133	P ⁴ right	<i>Hipparion</i> s. l.	-7.38	0.042	-2.50	0.044
GFT 134	P _{3/4} right	<i>Hipparion</i> s. l.	-1.45	0.038	-1.06	0.065
GFT 140	P ² left	<i>Hipparion</i> s. l.	-5.10	0.006	-0.74	0.013
GFT 69	Incisive	<i>Hipparion</i> s. l.	-10.27	0.012	-3.39	0.049
GFT 147	Premolar lower	<i>Hipparion</i> s. l.	-10.83	0.029	-4.17	0.048
GFT 148	Premolar upper left	<i>Hipparion</i> s. l.	-6.81	0.024	-2.46	0.059
GFT 161	M/P	<i>Hipparion</i> s. l.	-6.03	0.014	-2.55	0.044
GFT 108	M _{1/2} right	<i>Hipparion</i> s. l.	-10.16	0.011	-2.19	0.068
GFT 64	P ⁴ left	<i>Hipparion</i> s. l.	-7.41	0.019	-2.06	0.037
GFT 187	P _{3/4} left	<i>Hipparion</i> s. l.	-10.66	0.007	-1.51	0.009
GFT 195	M ¹ left	<i>Hipparion</i> s. l.	-8.69	0.039	-0.62	0.018
GFT 199	P ^{3/4} left	<i>Hipparion</i> s. l.	-7.20	0.029	-0.47	0.030
GFT 204	M ^{1/2} right	<i>Hipparion</i> s. l.	-10.59	0.026	1.14	0.018

GFT 207	P ⁴ /M ¹ right	<i>Hipparion</i> s. l.	-5.99	0.042	-1.19	0.034
GFT 180	M ^{1/2} left	<i>Hipparion</i> s. l.	-4.02	0.032	-1.86	0.014
GFT 189	P ^{3/4} right	<i>Hipparion</i> s. l.	-6.00	0.008	0.03	0.048
GFT 205	M ² right	<i>Hipparion</i> s. l.	-6.88	0.038	-0.63	0.021
GFT 94	P ₂ left	<i>Hexaprotodon</i>	-11.13	0.019	-4.72	0.008
GFT 174	P _{3/4} left	<i>Hexaprotodon</i>	-9.42	0.028	-6.13	0.022
GFT 175	Canine/incisive	<i>Hexaprotodon</i>	-8.85	0.013	-5.48	0.051
GFT 176	Incisive	<i>Hexaprotodon</i>	-8.84	0.013	-5.11	0.028
GFT 198	Canine lower left	<i>Hexaprotodon</i>	-9.99	0.032	-5.03	0.021
GFT 200	Premolar	<i>Hexaprotodon</i>	-11.89	0.042	-5.28	0.041
GFT 220	Incisive lower	<i>Hexaprotodon</i>	-9.63	0.016	-4.93	0.026
GFT 245	M/P lower	<i>Hexaprotodon</i>	-11.54	0.057	-4.01	0.059
GFT 109	Premolar	<i>Hexaprotodon</i>	-8.33	0.041	-4.04	0.065
GFT 113	Incisive	<i>Hexaprotodon</i>	-8.87	0.014	-6.16	0.039
GFT 216	Dp	<i>Hexaprotodon</i>	-13.33	0.014	-4.91	0.072
GFT 221	M/P	<i>Hexaprotodon</i>	-8.62	0.016	-6.53	0.082
GFT 110	Premolar	<i>Hexaprotodon</i>	-13.32	0.030	-5.55	0.023
GFT 85	Molar upper	<i>S. africanus</i>	-10.08	0.031	-2.99	0.036
GFT 111	M/P lower right	<i>S. africanus</i>	-9.59	0.022	-2.83	0.058
GFT 117	Molar lower	<i>S. africanus</i>	-9.15	0.009	-3.03	0.033
GFT 142	M/P	<i>S. africanus</i>	-9.07	0.028	-2.56	0.023
GFT 194	Molar	<i>S. africanus</i>	-9.90	0.014	-3.18	0.042
GFT 230	M/P	<i>S. africanus</i>	-9.55	0.019	-2.26	0.044
GFT 237	P ₃ right	<i>S. africanus</i>	-9.29	0.008	-3.40	0.025
GFT 125	Molar lower	<i>S. africanus</i>	-10.73	0.016	-3.05	0.037
GFT 244	M/P lower	<i>S. africanus</i>	-9.80	0.014	-1.52	0.020
GFT 171	P ₂ right	Suinae	-10.08	0.035	-3.70	0.042
GFT 173	M/P	Suinae	-9.77	0.008	-5.18	0.066
GFT 239	M/P	Suinae	-11.77	0.012	-3.34	0.050
GFT 250	D ² left	Suinae	-11.46	0.011	-3.59	0.024
GFT 247	P ₄ right	Hyaenidae	-8.91	0.026	-3.37	0.060
GFT 246	M ₂ right	<i>Dinofelis</i> sp.	-10.96	0.026	-1.39	0.014

Supplementary Table 4. Sequential $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ measurements from fossil *Hipparion* s. l. from GFT-4.2 analysed in this study. All samples were recovered from Level 1.

Sample ID	Dist. from ERJ (mm)	$\delta^{13}\text{C}$ (‰) (VPDB)	Standard deviation	$\delta^{18}\text{O}$ (‰) (VPDB)	Standard deviation
GFT4.2-2018-Q12/103 P _{3/4} right	38.97	-5.18	0.025	-1.70	0.054
	36.72	-4.99	0.014	-1.89	0.035
	33.96	-5.43	0.037	-1.75	0.059
	31.89	-5.56	0.030	-2.15	0.063
	29.76	-4.85	0.056	-1.47	0.073
	27.97	-4.02	0.060	-2.00	0.083
	25.47	-3.82	0.029	-1.80	0.013
	23.89	-3.79	0.028	-2.28	0.065
	22.08	-3.65	0.027	-2.04	0.085
	19.47	-3.40	0.046	-1.63	0.062
	17.71	-3.23	0.009	-1.30	0.019
	15.4	-3.21	0.014	-1.41	0.016
	14.01	-3.04	0.006	-1.04	0.018
	11.02	-3.19	0.014	-1.00	0.034
	9.19	-2.88	0.011	-1.44	0.016
	6.45	-2.61	0.010	-1.19	0.071
	4.52	-3.09	0.011	-1.20	0.065
GFT4.2-2019-Q15/237 M ₃ left	41.00	-7.46	0.026	-1.71	0.067
	39.72	-7.19	0.024	-1.24	0.029
	38.06	-6.96	0.011	-1.40	0.020
	36.69	-6.75	0.039	-1.65	0.036
	35.45	-6.53	0.004	-1.66	0.038
	33.92	-6.66	0.036	-1.79	0.022
	32.50	-6.74	0.023	-1.77	0.051
	31.09	-6.52	0.028	-2.00	0.004
	29.22	-6.62	0.030	-1.90	0.009
	27.85	-6.22	0.026	-2.08	0.055
	26.22	-6.37	0.013	-2.09	0.034
	24.81	-5.84	0.031	-1.84	0.015
	23.12	-5.28	0.029	-2.26	0.044
	21.11	-5.10	0.010	-2.69	0.051
	19.57	-5.24	0.028	-2.85	0.029
	18.39	-5.59	0.027	-2.92	0.044
	17.14	-5.96	0.029	-2.89	0.008
	15.47	-6.24	0.006	-2.73	0.015
	14.11	-6.32	0.008	-2.10	0.024

		12.49	-6.49	0.086	-2.30	0.023
		10.84	-6.56	0.046	-1.79	0.023
		9.00	-6.56	0.036	-1.84	0.017
		7.59	-6.27	0.038	-1.43	0.035
		6.13	-5.97	0.039	-1.24	0.070
		4.40	-6.41	0.026	-1.02	0.084
GFT4.2-2019-R15/115 M _{1/2} right		49.59	-6.703	0.014	-2.203	0.032
		48.17	-6.59	0.018	-1.71	0.044
		46.15	-6.34	0.038	-1.42	0.040
		44.19	-6.67	0.014	-1.35	0.083
		42.06	-6.60	0.034	-1.22	0.014
		38.17	-6.34	0.021	-0.83	0.060
		36.62	-6.35	0.008	-0.94	0.074
		34.65	-6.42	0.046	-0.61	0.055
		32.2	-6.66	0.042	-0.62	0.045
		30.48	-6.84	0.042	-0.89	0.056
		28.91	-7.01	0.027	-0.46	0.036
		26.78	-7.26	0.008	-0.43	0.068
		25.29	-7.05	0.027	-0.48	0.058
		23.68	-6.88	0.015	-0.95	0.049
		21.95	-7.14	0.014	-1.00	0.091
		20.1	-7.05	0.038	-1.36	0.030
		18.58	-6.91	0.027	-2.05	0.051
		16.88	-7.29	0.032	-1.19	0.017
		15.46	-7.35	0.048	-1.63	0.038
		14.31	-7.43	0.043	-1.81	0.055
		12.98	-7.67	0.013	-1.41	0.011
		11.37	-7.96	0.037	-0.81	0.012
		10.02	-8.36	0.013	-0.86	0.036
		8.26	-8.20	0.060	-0.68	0.042
GFT4.2-2019-R13/68 M ₃ right		47.74	-6.72	0.011	-1.85	0.051
		46.11	-7.09	0.013	-1.44	0.044
		44.41	-6.90	0.008	-1.78	0.015
		41.61	-7.01	0.008	-1.48	0.048
		40.22	-6.84	0.031	-1.75	0.023
		38.54	-6.79	0.005	-1.58	0.036
		37.31	-6.44	0.029	-1.50	0.041
		35.56	-6.26	0.006	-1.27	0.040
		33.48	-5.54	0.023	-1.23	0.016
		31.53	-5.12	0.017	-1.24	0.065
		29.89	-5.01	0.063	-1.27	0.010
		28.17	-5.06	0.004	-1.27	0.048
		26.49	-4.99	0.006	-1.27	0.085

		24.62	-5.17	0.006	-1.68	0.032
		22.91	-5.19	0.026	-1.98	0.025
		21.45	-5.32	0.015	-2.16	0.007
		20.03	-5.27	0.027	-2.56	0.007
		18.41	-5.22	0.007	-2.44	0.006
		16.62	-5.23	0.056	-2.84	0.021
		15.24	-5.31	0.010	-2.96	0.053
		13.6	-5.50	0.016	-2.84	0.039
		12.33	-5.56	0.042	-3.17	0.053
		10.64	-5.62	0.007	-2.66	0.033
		8.95	-5.68	0.012	-2.64	0.042
		7.17	-5.96	0.022	-2.58	0.014
		5.6	-6.35	0.029	-2.57	0.024
		3.94	-7.01	0.006	-2.96	0.041
		2.35	-7.85	0.010	-2.15	0.023
GFT4.2-2019-S15/124 P ^{3/4} right		32.71	-6.87	0.017	-1.79	0.032
		30.81	-8.08	0.024	-2.57	0.045
		29.01	-7.36	0.023	-1.56	0.066
		27.74	-7.65	0.008	-1.96	0.021
		26.25	-7.66	0.019	-2.63	0.046
		24.85	-7.90	0.051	-3.15	0.025
		23.3	-8.28	0.015	-3.28	0.089
		21.29	-8.69	0.055	-3.52	0.081
		19.86	-8.69	0.035	-3.77	0.043
		18.12	-8.98	0.039	-3.32	0.040
		16.26	-9.24	0.015	-3.89	0.036
		14.61	-9.40	0.031	-3.95	0.067
		12.98	-9.05	0.004	-3.53	0.039
		11.13	-9.15	0.008	-3.46	0.050
		9.37	-9.24	0.013	-3.77	0.031
		7.53	-9.16	0.035	-3.72	0.063
GFT4.2-2019-R14/32 P ³ left		5.44	-9.44	0.011	-3.73	0.039
		4.09	-9.41	0.027	-3.79	0.058
		35.32	-9.90	0.009	-3.17	0.025
		33.76	-9.39	0.003	-3.30	0.055
		32.49	-9.68	0.035	-3.36	0.032
		31.33	-9.57	0.003	-3.58	0.023
		29.92	-9.34	0.045	-3.96	0.050
		28.47	-9.35	0.009	-4.06	0.094
		27.19	-9.17	0.005	-3.87	0.021
		25.34	-9.20	0.039	-3.92	0.019
		24.22	-9.36	0.021	-4.13	0.064
		22.66	-9.07	0.048	-4.04	0.058

		21.44	-9.01	0.010	-3.79	0.062
		19.63	-8.75	0.008	-3.70	0.022
		18.12	-8.75	0.010	-3.38	0.025
		17.39	-8.58	0.033	-3.47	0.026
		14.59	-8.93	0.017	-3.44	0.043
		12.86	-8.32	0.029	-2.93	0.052
		11.31	-7.62	0.021	-1.89	0.031
		9.32	-7.62	0.047	-2.61	0.024
		7.28	-7.58	0.005	-1.42	0.062
		5.77	-7.29	0.017	-1.81	0.035
		4.23	-7.27	0.038	-2.10	0.011
		2.40	-6.92	0.028	-1.23	0.030
	GFT4.2-2019-S14/10	38.72	-9.13	0.007	-3.81	0.036
	P ⁴ left	37.12	-9.17	0.012	-3.90	0.024
		35.82	-9.20	0.011	-4.22	0.008
		34.6	-9.22	0.078	-4.01	0.040
		33.22	-9.04	0.005	-4.00	0.056
		31.88	-8.96	0.044	-3.80	0.029
		30.46	-9.10	0.011	-3.85	0.048
		29.33	-8.60	0.020	-3.43	0.005
		27.77	-8.91	0.008	-3.86	0.035
		25.75	-8.64	0.005	-3.40	0.036
		24.6	-8.50	0.025	-3.12	0.074
		23.34	-8.39	0.047	-3.14	0.041
		22.11	-7.84	0.024	-2.71	0.026
		20.13	-7.63	0.016	-2.76	0.034
		18.72	-7.58	0.039	-2.73	0.013
		17.54	-7.70	0.033	-2.40	0.023
		15.81	-7.59	0.013	-1.93	0.053
		14.43	-7.30	0.026	-1.88	0.034
		12.67	-7.12	0.039	-1.65	0.029
		11.15	-7.29	0.011	-1.64	0.040
		9.47	-7.19	0.008	-1.63	0.029
		7.57	-7.05	0.018	-1.96	0.061
		5.7	-6.91	0.033	-2.12	0.068
		3.63	-6.99	0.016	-1.98	0.057
		2.09	-6.78	0.027	-2.32	0.058
		1.08	-7.45	0.030	-2.04	0.022
	GFT4.2-2019-S15/42	34.76	-10.08	0.009	-3.16	0.018
	M ^{1/2} left	33.5	-9.63	0.024	-3.48	0.045
		30.09	-9.35	0.023	-3.85	0.055
		29.15	-9.50	0.030	-3.45	0.042
		27.7	-9.54	0.023	-3.76	0.051

	26.17	-9.60	0.011	-3.39	0.078
	24.17	-8.95	0.034	-3.32	0.010
	22.69	-8.71	0.022	-3.37	0.012
	21.35	-8.69	0.030	-3.06	0.066
	19.25	-8.69	0.030	-2.91	0.038
	17.72	-8.71	0.023	-3.46	0.064
	15.73	-8.80	0.034	-4.18	0.072
	14.28	-8.82	0.013	-3.92	0.011
	13.04	-8.97	0.037	-4.30	0.048
	10.8	-8.94	0.020	-3.53	0.037
	9.26	-8.71	0.036	-3.68	0.071
	7.62	-8.57	0.022	-3.85	0.043
	5.93	-8.81	0.036	-3.42	0.061
	3.95	-8.08	0.044	-2.57	0.006
	2.1	-8.39	0.016	-2.46	0.283

Supplementary Table 5. Results of cross-correlation analysis of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ intra-tooth sequential analysis of *Hipparion* s. l. from GFT-4.2.

Sample ID	Dominant lag position	Cross-correlation coefficient	Statistical significance
GFT4.2-2019-S15/42	-10	0.411	S
GFT4.2-2019-S14/10	0	0.951	S
GFT4.2-2019-R14/32	0	0.865	S
GFT4.2-2019-S15/124	0	0.920	S
GFT4.2-2019-R13/68	-7	-0.751	S
GFT4.2-2019-R15/115	10	-0.366	NS
GFT4.2-2019-Q15/237	-1	-0.744	S
GFT4.2-2018-Q12/103	-3	0.614	S

Supplementary Table 6. Raw dental microwear and mesowear data from all taxa analysed from GFT-4.2. Abbreviations: NTS = number of total scratches, NTP = number of total pits, SWS = scratch width score, PP = presence of puncture pits, HC = presence of hypercoarse scratches, LP = presence of large pits and G = presence of gouges. All samples were recovered from Level 1, except for GFT 82, 41, 28A, 27A, 192, 133, 53, 39 and 40, which belong to Level 0.

Sample ID	Element	Taxa	Microwear							Mesowear
			NTS	NTP	SWS	PP (0/1)	HC (0/1)	LP (0/1)	G (0/1)	
GFT 80	M lower	<i>Anancus</i> sp.	21	10	1	0	0	1	0	-
GFT 89	M	<i>Anancus</i> sp.	22	13	1	1	0	1	0	-
GFT189	M _{1/2} /DP ₄	<i>Anancus</i> sp.	21	9.5	1	1	0	1	0	-
GFT 190	M	<i>Anancus</i> sp.	32	12.5	1	1	0	0	0	-
GFT 191	M	<i>Anancus</i> sp.	22	10	1	1	0	0	0	-
GFT 193	M _{1/2}	<i>Anancus</i> sp.	22.5	11.5	1	1	0	0	0	-
GFT 203	M/P	<i>Anancus</i> sp.	22	14	1	0	0	1	0	-
GFT 105	Molar lower left	Tragelaphini	13	10	0	1	0	1	0	-
GFT 129	P ⁴ left	Tragelaphini	18	31	1	1	0	1	0	-
GFT 48	M/P	Tragelaphini	13	21	1	0	0	0	0	2
GFT 57	P ³ left	Tragelaphini	19	17	1	1	0	1	0	-
GFT 161	M _{1/2} right	Tragelaphini	13	20	1	0	0	1	0	-
GFT 164	M ^{1/2} left	Tragelaphini	17.5	13	1	1	0	1	0	2
GFT 39	M/P	Tragelaphini	20	30	1	1	0	1	0	-
GFT 53	M _{1/2} right	Tragelaphini	20	17.5	1	0	0	1	0	2
GFT 64	M _{1/2} right	Tragelaphini	17	26	1	1	0	1	0	2
GFT 95	M _{1/2} right	Tragelaphini	20	26.5	1	1	0	1	0	-
GFT 133	P ₄ left	Tragelaphini	16	25	1	0	0	0	0	-
GFT 134	P ₃ left	Tragelaphini	14	21	1	1	0	1	0	-
GFT 145	Premolar upper	Tragelaphini	10	24	1	0	0	1	0	-
GFT 148	M ^{1/2} right	Tragelaphini	13	23	1	0	0	0	0	3
GFT 156	M ^{1/2} left	Tragelaphini	12	14	2	0	0	0	0	2
GFT 177	M/P	Tragelaphini	13.5	18	1	0	0	1	0	1
GFT 192	M ₃ left	Tragelaphini	13	23	1	0	0	0	0	-
GFT27A	P ³ right	Tragelaphini	22	38	1	0	0	1	0	2
GFT28A	Premolar upper left	Tragelaphini	10	22	1	0	0	1	0	3
GFT 144	M ^{1/2} left	Tragelaphini	14	20	1	0	0	1	0	4
GFT 13	Molar	Tragelaphini	16	25	1	0	0	1	0	-
GFT143	M ₃ right	Tragelaphini	-	-	-	-	-	-	-	1
GFT 38	M _{1/2} left	Tragelaphini	-	-	-	-	-	-	-	2
GFT 50	M/P	Tragelaphini	-	-	-	-	-	-	-	2

GFT 60	M ₃ left	Tragelaphini	-	-	-	-	-	-	-	2
GFT 62	M ^{1/2} left	Tragelaphini	-	-	-	-	-	-	-	2
GFT 85	M/P	Tragelaphini	-	-	-	-	-	-	-	2
GFT 106	M _{1/2} left	Tragelaphini	-	-	-	-	-	-	-	1
GFT 146	M ₃ left	Tragelaphini	-	-	-	-	-	-	-	1
GFT 152	M ₃ right	Tragelaphini	-	-	-	-	-	-	-	1
GFT 155	M ^{1/2} right	Tragelaphini	-	-	-	-	-	-	-	2
GFT 178	M _{1/2} right	Tragelaphini	-	-	-	-	-	-	-	1
GFT 87	M ₃ left	<i>Gazella</i> sp.	15	27	2	0	0	1	0	1
GFT 41	P ₃ right	<i>Gazella</i> sp.	22	40	1	0	0	1	0	-
GFT 70	M _{1/2} left	<i>Gazella</i> sp.	13	22	1	0	0	1	0	3
GFT 92	M ^{1/2} left	<i>Gazella</i> sp.	13	24	1	1	0	0	0	2
GFT 104	M ³ left	<i>Gazella</i> sp.	17	22	2	0	0	1	0	1
GFT 107	M _{1/2} right	<i>Gazella</i> sp.	11	23	2	0	0	1	0	2
GFT 124	M _{1/2} right	<i>Gazella</i> sp.	9	24	2	0	0	1	0	1
GFT 125	P ² right	<i>Gazella</i> sp.	14	28	2	0	0	1	0	-
GFT 132	M _{1/2} right	<i>Gazella</i> sp.	12	26	2	1	0	1	0	1
GFT 141	M/P	<i>Gazella</i> sp.	13.5	17.5	1	0	0	1	0	1
GFT 176	Molar	<i>Gazella</i> sp.	23	21	1	0	0	1	0	1
GFT 179	M ₃ left	<i>Gazella</i> sp.	10	17	2	0	0	1	0	3
GFT 52	Molar upper right	<i>Gazella</i> sp.	12	26	1	1	0	0	0	-
GFT 121	M _{1/2} left	<i>Gazella</i> sp.	-	-	-	-	-	-	-	0
GFT 182	M _{1/2} right	<i>Gazella</i> sp.	-	-	-	-	-	-	-	1
GFT 8	M/P left	<i>Hipparion</i> s. l.	17	45	1	0	0	1	0	-
GFT 9	P ₃ right	<i>Hipparion</i> s. l.	21	44	1	0	0	1	0	-
GFT 16	Molar	<i>Hipparion</i> s. l.	19	21	1	1	0	1	0	-
GFT 17	M _{1/2} right	<i>Hipparion</i> s. l.	21	36	1	1	0	1	0	2
GFT 20	Premolar	<i>Hipparion</i> s. l.	12	15	1	0	0	1	0	-
GFT 27	M/P	<i>Hipparion</i> s. l.	8	15.5	2	0	1	1	0	-
GFT 29	M/P	<i>Hipparion</i> s. l.	16.5	29	2	1	0	1	0	-
GFT 34	P ² right	<i>Hipparion</i> s. l.	9	17	1	0	0	1	0	3
GFT 43	M/P upper right	<i>Hipparion</i> s. l.	20	14	1	1	0	1	0	-
GFT 44	M/P	<i>Hipparion</i> s. l.	15	22	1	1	0	1	0	-
GFT 45	M ³ right	<i>Hipparion</i> s. l.	13	18.5	1	1	0	1	0	1

GFT 46	P _{3/4} right	<i>Hipparion</i> s. l.	16	21	1	0	0	1	0	-
GFT 54	M/P upper	<i>Hipparion</i> s. l.	13	15	1	0	0	1	0	-
GFT 58	M ₃ left	<i>Hipparion</i> s. l.	15	22.5	1	1	0	1	0	-
GFT 61	M/P lower	<i>Hipparion</i> s. l.	12	20	1	0	0	1	0	-
GFT 63	M ^{1/2} right	<i>Hipparion</i> s. l.	15	26	1	0	0	1	0	4
GFT 67	P _{3/4} right	<i>Hipparion</i> s. l.	10	24	2	0	0	1	0	3
GFT 69	P _{3/4} right	<i>Hipparion</i> s. l.	7	26	2	0	0	1	0	-
GFT 72	P ^{3/4} right	<i>Hipparion</i> s. l.	8	18	2	1	1	1	0	5
GFT 74	Premolar lower left	<i>Hipparion</i> s. l.	16	20	1	0	0	1	0	-
GFT 77	P ² left	<i>Hipparion</i> s. l.	11	25	1	0	0	1	0	5
GFT 79	P _{3/4} right	<i>Hipparion</i> s. l.	9	16.5	1	0	0	1	0	-
GFT 83	P _{3/4} right	<i>Hipparion</i> s. l.	14	23	1	0	0	1	0	-
GFT 86	M ^{1/2} right	<i>Hipparion</i> s. l.	14	17.5	2	0	0	1	0	3
GFT 88	P ² right	<i>Hipparion</i> s. l.	15	18	1	0	0	1	0	5
GFT 90	M ₃ right	<i>Hipparion</i> s. l.	15	18.5	1	0	0	1	0	-
GFT 91	P ₂ left	<i>Hipparion</i> s. l.	13	26.5	1	1	0	1	0	-
GFT 98	P ^{3/4} left	<i>Hipparion</i> s. l.	11	9	2	1	0	1	0	6
GFT 99	P ² right	<i>Hipparion</i> s. l.	16	12.5	1	0	0	1	0	4
GFT 100	M _{1/2} right	<i>Hipparion</i> s. l.	15	27	1	0	0	1	0	-
GFT 101	M/P upper	<i>Hipparion</i> s. l.	14	19	1	0	0	1	0	-
GFT 113	P ^{3/4} right	<i>Hipparion</i> s. l.	13	21.5	1	0	0	1	0	3
GFT 114	M/P	<i>Hipparion</i> s. l.	12	27.5	1	0	0	1	0	-
GFT 117	M/P	<i>Hipparion</i> s. l.	14	26	1	0	0	1	0	-
GFT 120	P ² right	<i>Hipparion</i> s. l.	11	18	1	0	0	1	0	-

GFT 128	M ^{1/2} right	<i>Hipparion</i> s. l.	16	22	1	0	0	1	0	1
GFT 130	M _{1/2} right	<i>Hipparion</i> s. l.	13	25	1	0	0	1	0	-
GFT 131	M/P	<i>Hipparion</i> s. l.	21	30.5	1	0	0	1	0	-
GFT 142	P ⁴ left	<i>Hipparion</i> s. l.	9	18	2	0	0	1	0	2
GFT 159	M ^{1/2} left	<i>Hipparion</i> s. l.	18.5	24.5	1	0	0	1	0	2
GFT 162	M ^{1/2} right	<i>Hipparion</i> s. l.	12	20.5	2	0	0	1	0	2
GFT 166	P ^{3/4} right	<i>Hipparion</i> s. l.	9	25	2	0	1	1	0	2
GFT 167	P _{3/4} left	<i>Hipparion</i> s. l.	12.5	30	2	0	1	1	0	-
GFT 168	M _{1/2} right	<i>Hipparion</i> s. l.	14.5	24	2	0	0	1	0	-
GFT 201	M/P	<i>Hipparion</i> s. l.	13	30	2	0	0	1	0	-
GFT 150	P ^{3/4} right	<i>Hipparion</i> s. l.	13	22	1	0	0	1	0	-
GFT 151	M ^{1/2} left	<i>Hipparion</i> s. l.	13	23	1	1	0	1	0	4
GFT 163	M ^{1/2} right	<i>Hipparion</i> s. l.	14.5	19	1	1	0	1	0	3
GFT 165	P ⁴ /M ¹ right	<i>Hipparion</i> s. l.	9	19	2	0	0	1	0	4
GFT 55	P ³ left	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	2
GFT 68	P ³ right	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	5
GFT 73	P ^{3/4} right	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	3
GFT 102	M/P upper	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	2
GFT 109	Premolar upper left	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	4
GFT 154	M ¹ left	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	2
GFT 160	M ^{1/2} right	<i>Hipparion</i> s. l.	-	-	-	-	-	-	-	3
GFT 12	Premolar	<i>Hexaprotodon</i>	25	14	1	0	0	1	0	-
GFT 97	P ₂ left	<i>Hexaprotodon</i>	30	10.5	1	0	0	0	0	-
GFT 158	Premolar	<i>Hexaprotodon</i>	19	12	1	0	0	1	0	-
GFT 173	P _{3/4} left	<i>Hexaprotodon</i>	14.5	10.5	1	1	0	1	0	-
GFT 186	M/P	<i>Hexaprotodon</i>	20.5	15	2	0	0	1	0	-
GFT 82	Molar upper	<i>S. africanus</i>	20	13	2	0	1	1	0	-

GFT 84	Molar lower	<i>S. africanus</i>	17	13	1	0	0	1	0	-
GFT 94	M/P lower right	<i>S. africanus</i>	30	22	1	0	0	1	0	-
GFT 123	M/P	<i>S. africanus</i>	17	8	1	0	0	1	0	-
GFT 153	Molar	<i>S. africanus</i>	32.5	13.5	1	0	0	1	0	-
GFT 194	M/P	<i>S. africanus</i>	26	23	1	0	0	1	0	-
GFT 199	P ₃ right	<i>S. africanus</i>	19	12.5	1	1	0	0	0	-
GFT29A	M/P lower	<i>S. africanus</i>	27	17	1	0	0	1	0	-
GFT200	M/P	Suinae	22	17	1	0	0	1	0	-
GFT204	M/P	Suinae	27	10	1	0	0	1	0	-

Supplementary Table 7. Biomarker metrics, relative abundances and $\delta^{13}\text{C}$ values of GFT-4.2 plant wax *n*-alkanes.

Sample	Biomarker metrics					Relative abundances				$\delta^{13}\text{C}$ (VPDB)							
	CPI ₂₁₋₃₃	ACL _{Odd}	ACL _{All}	P _{Aq}	STR	C ₂₅	C ₂₇	C ₂₉	C ₃₁	C ₂₅	S.D.	C ₂₇	S.D.	C ₂₉	S.D.	C ₃₁	S.D.
10	-	29.1	29.1	0.08	0.07	0.07	0.20	0.36	0.37	-28.0	0.3	-28.5	0.1	-29.8	0.2	-31.3	0.3
9	2.3	27.2	26.8	0.55	0.31	0.31	0.44	0.12	0.14	-29.7	0.1	-29.8	0.0	-30.1	0.0	-29.5	0.0
8	4.0	28.5	28.1	0.19	0.12	0.13	0.23	0.31	0.32	-29.3	0.1	-28.8	0.1	-29.6	0.1	-31.1	0.2
7	6.3	28.8	28.5	0.06	0.05	0.05	0.15	0.36	0.44	-28.3	0.1	-28.2	0.1	-29.8	0.1	-29.8	0.1
6	5.6	28.0	27.1	0.00	0.00	0.00	0.16	0.40	0.43	-	-	-	-	-	-	-	-
5	8.4	28.8	28.3	0.08	0.06	0.07	0.15	0.35	0.43	-28.4	0.1	-28.4	0.1	-30.1	0.1	-31.5	0.1
4	-	29.7	29.7	0.00	0.00	0.00	0.14	0.39	0.47	-28.4	0.2	-28.4	0.2	-29.4	0.1	-30.0	0.2
3	10.0	27.8	27.3	0.15	0.10	0.12	0.19	0.31	0.37	-28.5	0.1	-28.6	0.1	-29.4	0.1	-29.6	0.1
2	3.5	28.7	28.0	0.11	0.04	0.05	0.14	0.32	0.49	-28.3	0.1	-28.4	0.4	-29.9	0.6	-30.4	0.6
1	5.0	29.2	28.7	0.09	0.04	0.05	0.13	0.31	0.52	-28.6	0.4	-28.4	0.2	-30.3	0.2	-31.2	0.1

Supplementary Table 8. Concentration values of the taxa identified in GFT-4.2 (grains, palynomorphs or particles per gram of dry sediment).

	Samples					
Taxon	GFT 10	GFT 8	GFT 6	GFT 4	GFT 2	GFT 1
<i>Pinus</i> sp.	2.0	0	0.9	2.7	0	0
Evergreen <i>Quercus</i>	4.0	0	0.9	4.0	2.1	0
<i>Alnus</i>	0	0	0	1.3	0	0
Poaceae	4.0	0	0	0	0	0
Asteraceae tubuliflorae	2.0	0	0	0	2.1	0
Asteraceae liguliflorae	2.0	1.2	0	1.3	1.1	0
Chenop. / Amarant.	0	0	0	1.3	0	0
Apiaceae	6.1	0	0	1.3	0	0
Fabaceae	0	0	0.9	0	0	0
Pollen indet.	8.1	3.7	3.5	8.1	4.2	0
Trilete spores	2.0	0	0	0	0	0
HdV 303	8.1	0	0	1.3	1.1	0
Protists	12.1	7.4	7.9	13.5	10.6	26.2
HdV 1073	0	0	0.9	1.3	1.1	0
<i>Gloeotrichia</i>	2.0	1.2	0	2.7	1.1	1.9
<i>Botryococcus</i>	0	0	0.9	0	0	0
Algae (varia)	2.0	0	0	0	0	0
Hyphae	86.9	0	0.9	1.3	1.1	0
<i>Polyadosporites</i>	18.2	0	0	0	0	0
<i>Polyporisporites</i>	18.2	2.5	0.9	1.3	0	0
<i>Glomus</i> sp.	60.6	0	1.7	0	1.1	0
<i>Pluricellaesporites</i>	6.1	1.2	0.9	0	0	0
Pucciniaceae	4.0	1.2	0.9	1.3	0	0
<i>Exesisporites</i>	14.1	0	0	1.3	0	0
HdV 52	14.1	4.9	2.6	4.0	2.1	0
HdV 36	4.0	0	0	0	0	0
HdV 36c	0	0	0.9	0	0	0
Zoo (varia)	4.0	0	0.9	1.3	0	0
Scolecodonte	2.0	0	0.9	0	0	0
Microcharcoal	121.2	18.4	26.2	157.9	22.2	129.2
PC total	286.8	22.1	33.2	49.9	27.5	28.1
Number of taxa	22	7	15	16	10	2

Supplementary Table 9. Vertebrate faunal list of the site of Guefaït-4.2.

Order	Family	Species
Anura	Alytidae/Ranidae	Alytidae vel Ranidae indet.
Squamata	Lacertidae	Lacertidae indet.
	Anguidae	<i>Ophisaurus</i> sensu lato
	Natricidae/Elapidae	Natricidae vel Elapidae indet.
	Colubridae/Lamprophiidae	Colubridae vel Lamprophiidae indet.
Rodentia	Sciuridae	<i>Atlantoxerus</i> sp.
	Gliridae	<i>Eliomys</i> sp.
	Muridae	<i>Paraethomys pusillus</i>
		<i>Paraethomys chikeri</i>
		<i>Golunda aouraghei</i>
		<i>Praomys</i> cf. <i>skouri</i>
		Gerbillidae indet. 1
		Gerbillidae indet. 2
	Ctenodactylidae	<i>Irhoudia</i> sp.
Testudines	Testudinidae	cf. <i>Centrochelys</i> ? <i>punica</i>
Proboscidea	Anancidae	<i>Anancus</i> sp.
Primates	Cercopithecidae	<i>Macaca</i> cf. <i>sylvanus</i>
Carnivora	Canidae	Canidae
	Hyaenidae	Hyaenidae
	Felidae	<i>Felis</i> cf. <i>sylvestris</i>
		<i>Dinofelis</i> sp.
Perissodactyla	Equidae	<i>Hipparion</i> sensu lato
	Rhinocerotidae	<i>Stephanorhinus africanus</i>
Artiodactyla	Suidae	Suinae
	Hippopotamidae	<i>Hexaprotodon</i> sp.
	Giraffidae	cf. <i>Sivatherium</i>
	Bovidae	<i>Gazella</i> sp.
		Tragelaphini

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Supplementary information

**Multiproxy approach to reconstruct fossil primate feeding behavior:
Case study for macaque from the Plio-Pleistocene site Guefaït-4.2
(eastern Morocco)**

Iván Ramírez-Pedraza^{1,2*}, Laura M. Martínez^{3,4*}, Hassan Aouraghe⁵, Florent Rivals^{1,2,6}, Carlos Tórner^{1,7}, Hamid Haddoumi⁵, Ferrán Estebanz⁸, Antonio Rodríguez-Hidalgo^{1,2,9}, Jan van der Made¹⁰, Aïcha Oujaa¹¹, Juan José Ibáñez⁸, Hicham Mhamdi⁵, Mohamed Souhir⁵, Al Mahdi Aïssa⁵, M. Gema Chacón^{1,2,12}, Robert Sala-Ramos^{1,2}

¹Institut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain

²Departament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain

³Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Secció de Zoologia i Antropologia Biològica, Universitat de Barcelona, Spain

⁴Institut d'Arqueologia de la Universitat de Barcelona. Barcelona, Spain.

⁵Faculté des Sciences, Département de Géologie, Université Mohamed Premier, Oujda, Morocco

⁶Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain

⁷Department of Prehistory, Autonomous University of Barcelona (UAB), 08193 Bellaterra, Spain.

⁸Archaeology of Social Dynamics (ASD), Institución Milá y Fontanals (IMF), Spanish National Research Council (CSIC), Barcelona, Spain

⁹Instituto de Evolución en África (IDEA, Madrid), Madrid, Spain

¹⁰Consejo Superior de Investigaciones Científicas (CSIC), Museo Nacional de Ciencias Naturales, Departamento de Paleobiología, Madrid, Spain

¹¹Institut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco

¹²UMR 7194 - Histoire Naturelle de l'Homme Préhistorique (CNRS/MNHN/UPVD), Paris, France.

***Corresponding authors.**

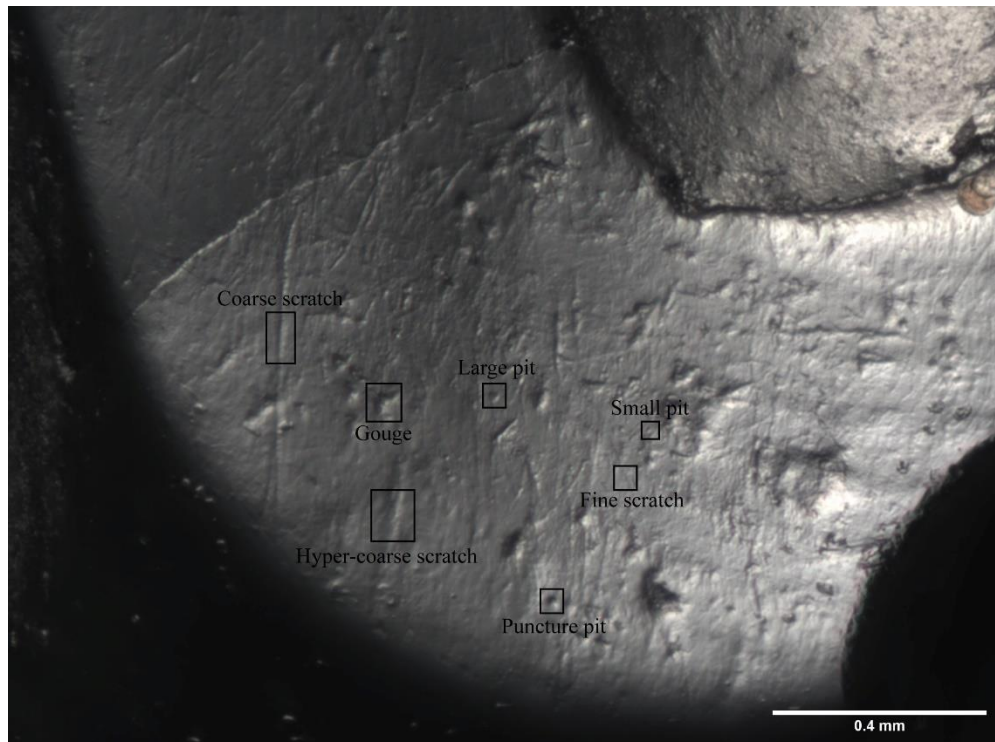


Fig. S1. Microphotographs at 35X magnifications indicating the occlusal microwear variables analyzed (Hyper-coarse, coarse and fine scratches, small and large pits, puncture pits and gouges). Sample: *C. atys* (PAP1992); Scale bar = 0.1 mm.

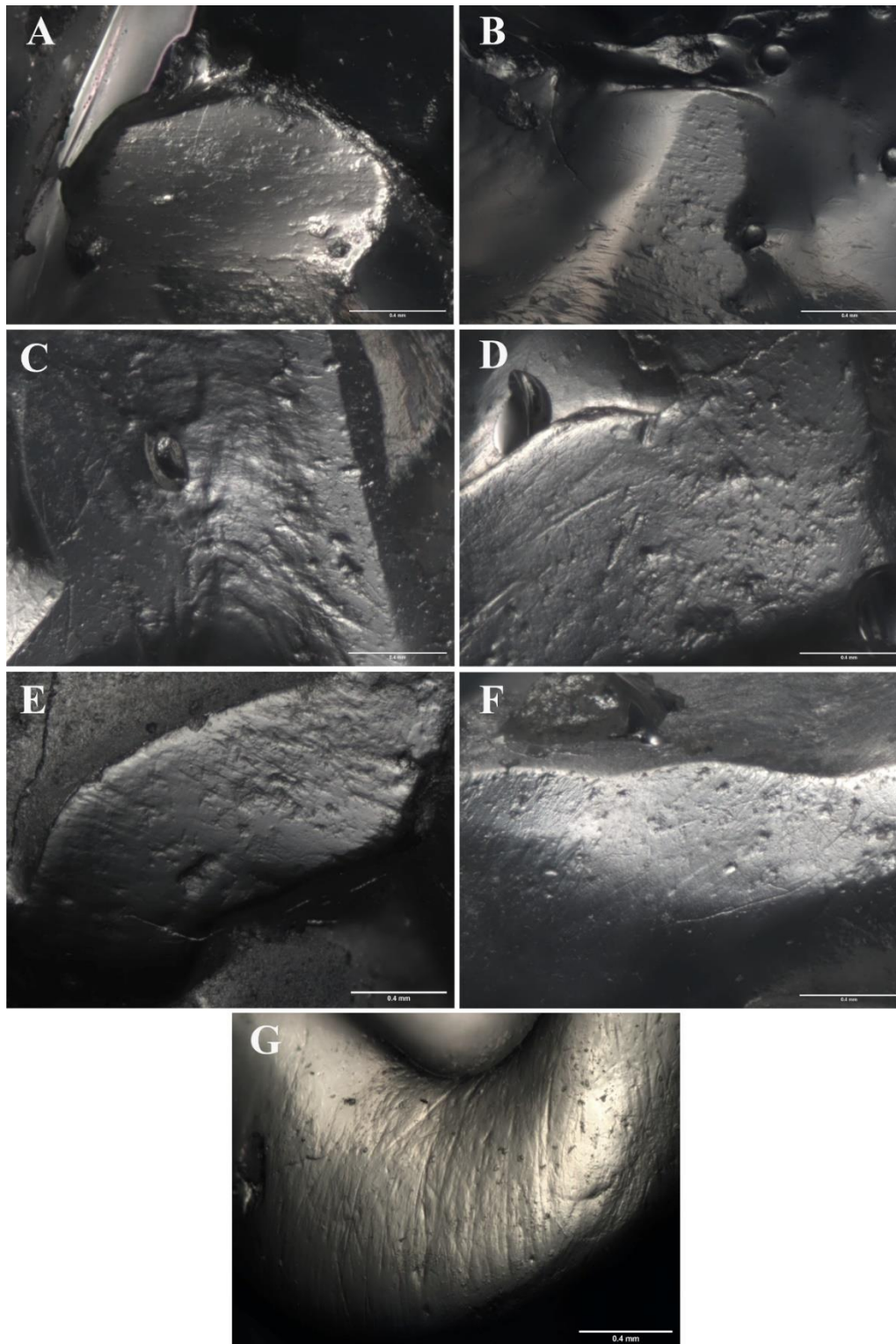
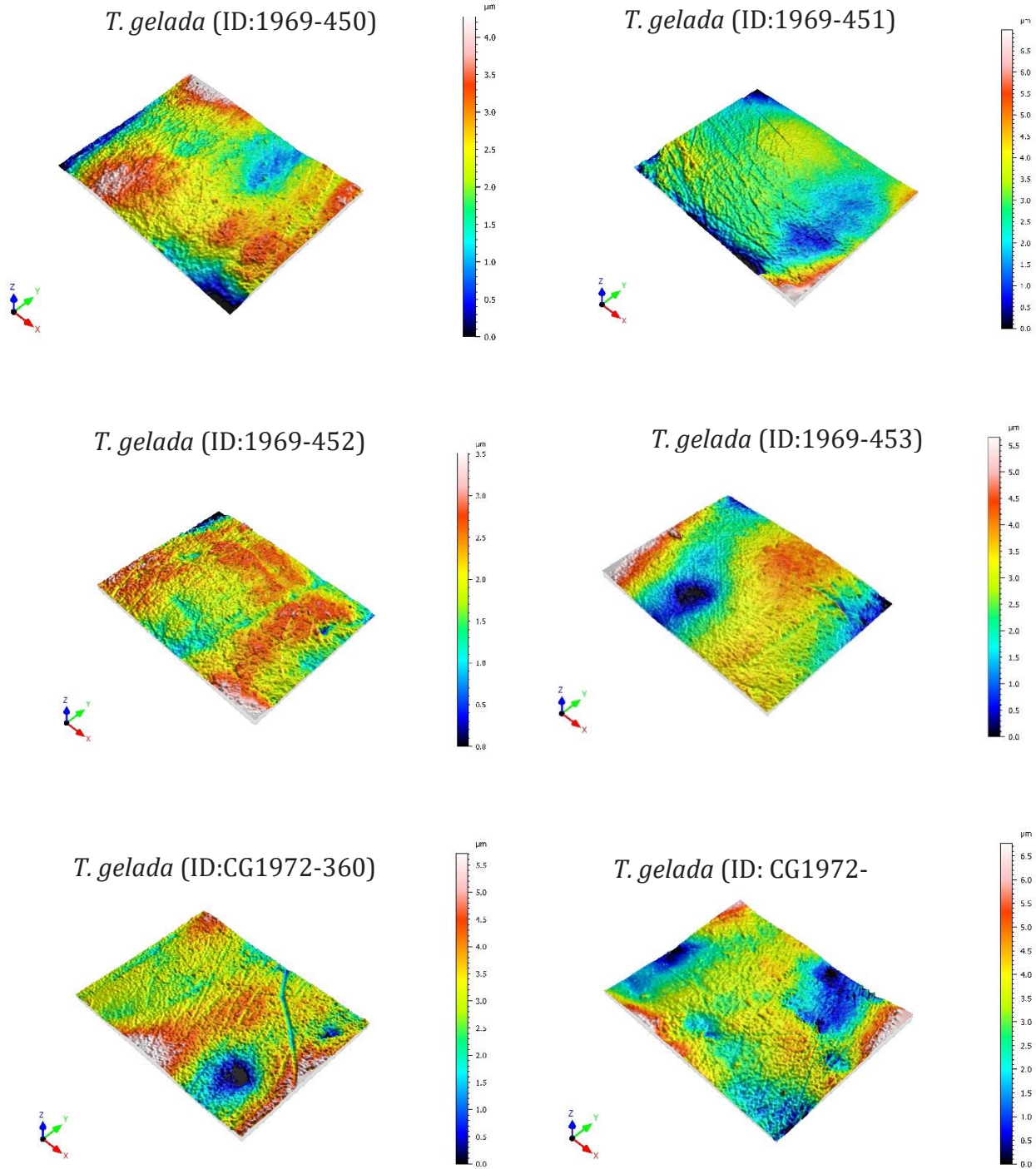
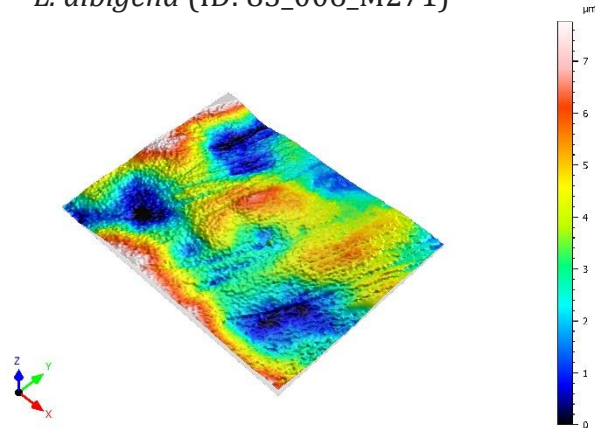


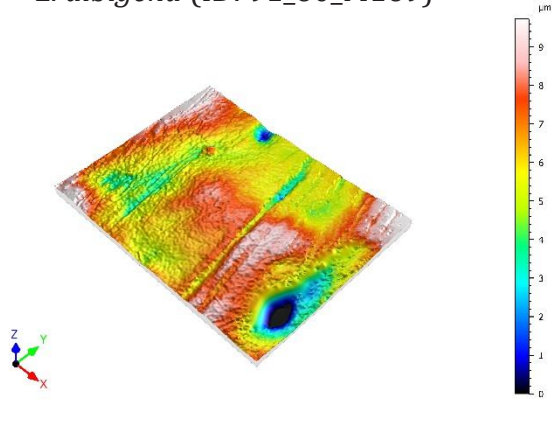
Fig. S2. Microphotographs at 35X magnifications. Samples (A) *M. cf. sylvanus* – GFT 140; (B) *M. cf. sylvanus* – GFT 138; (C) *L. albigena* (PAP1762); (D) *C. atys* (PAP1972); (E) *M. sphinx* (PAP1865); (F) *M. mulatta* (B107); (G) *T. gelada* (CG1972-361). Scale bar = 0.1 mm.



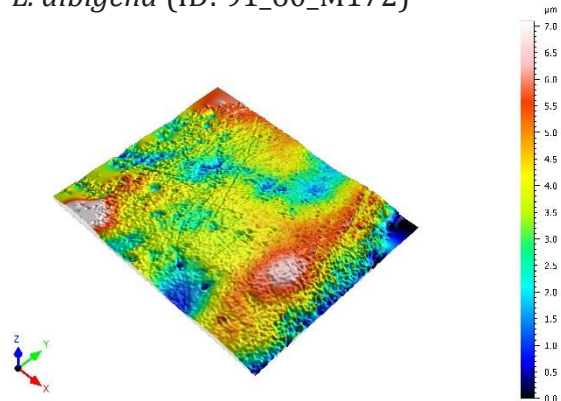
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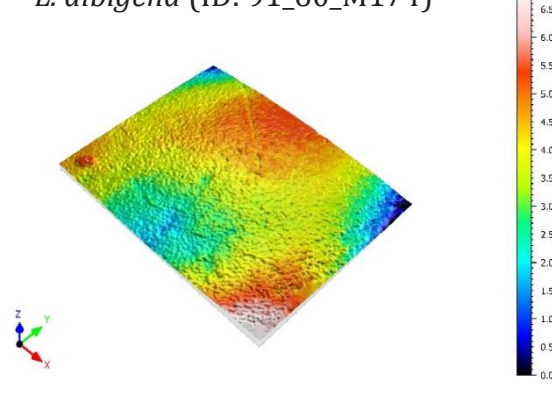
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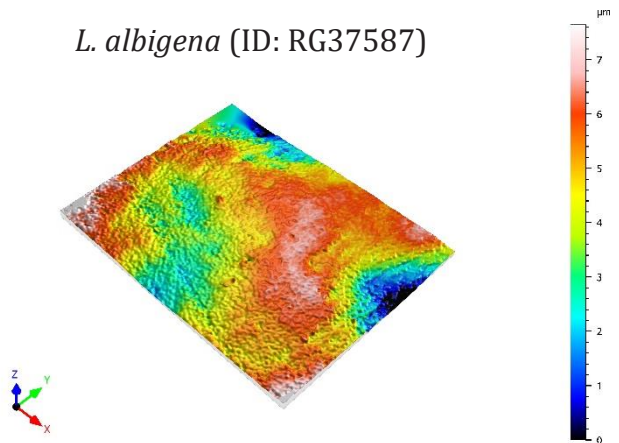
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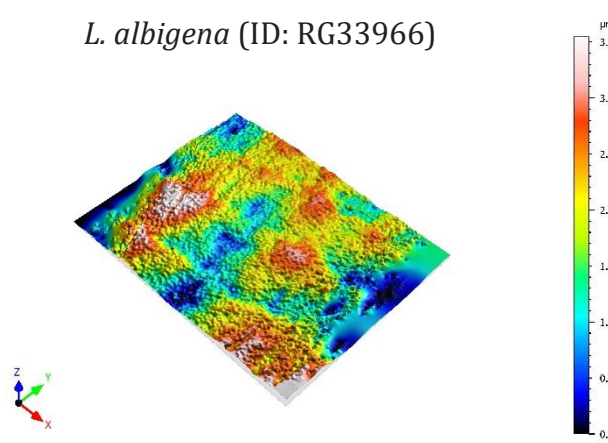
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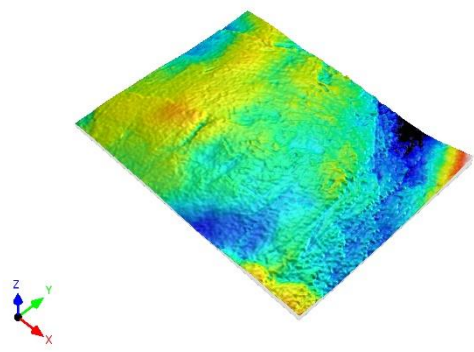
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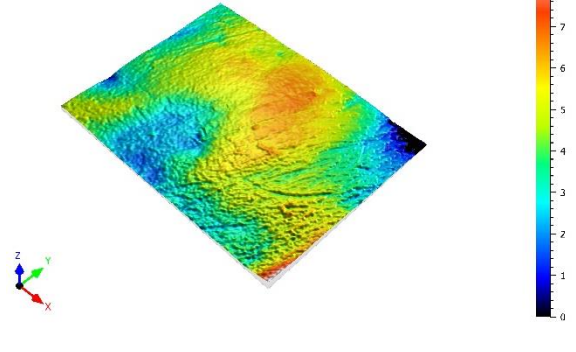
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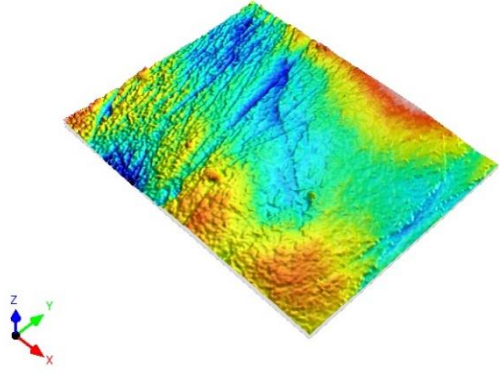
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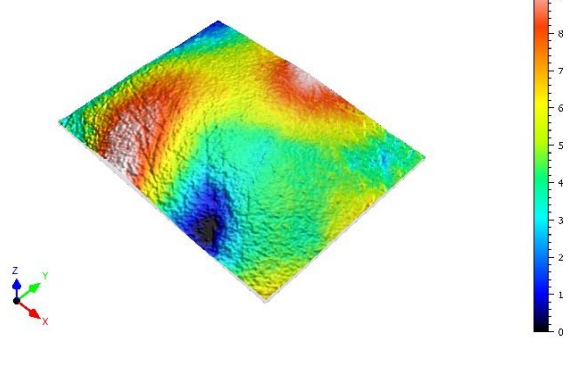
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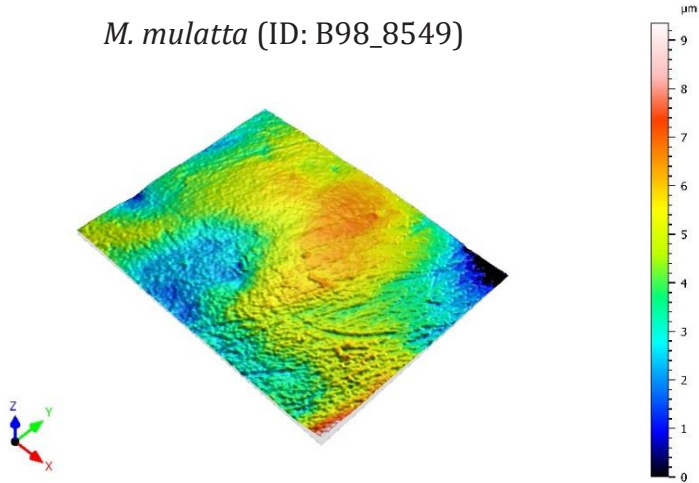
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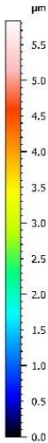
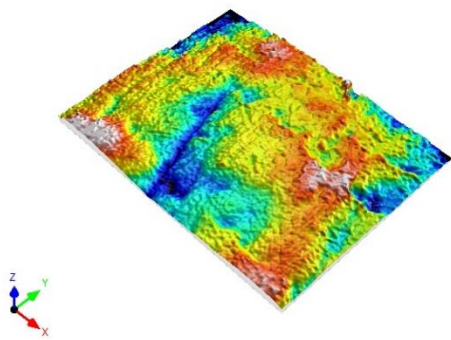
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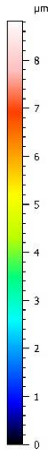
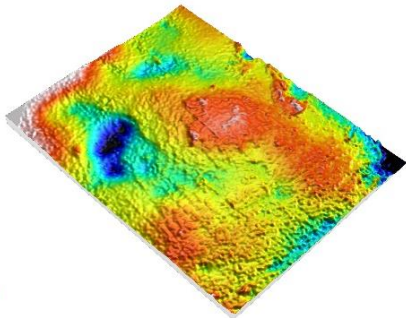
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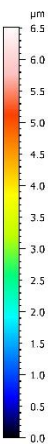
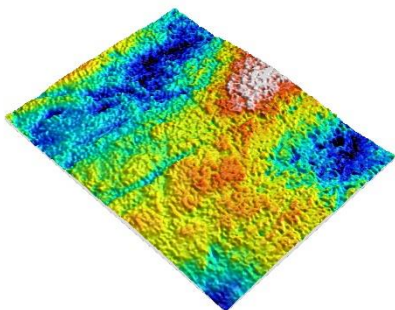
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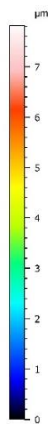
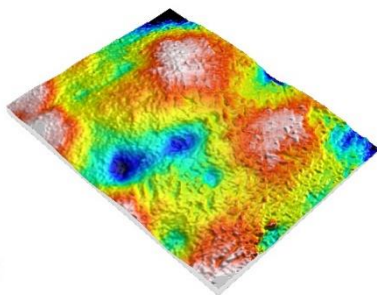
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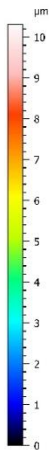
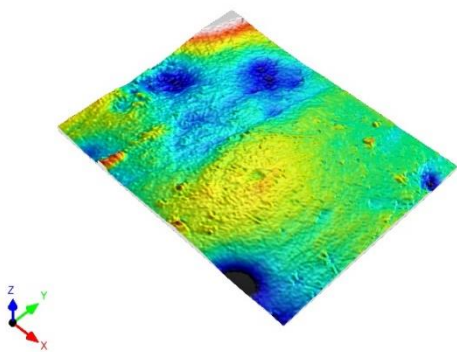
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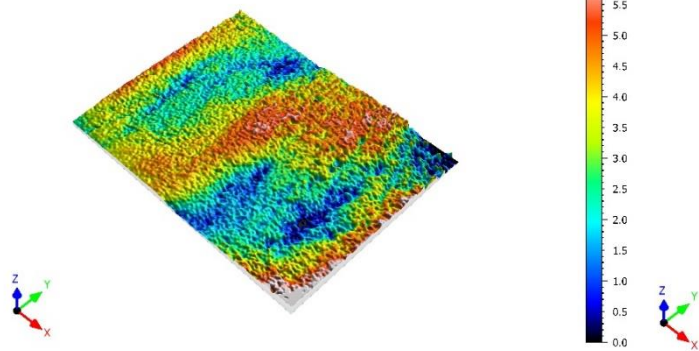
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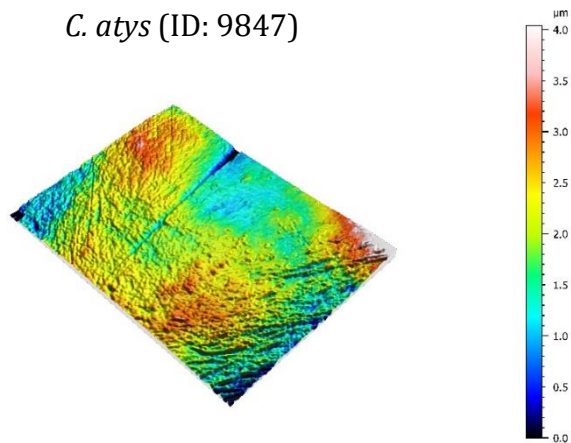
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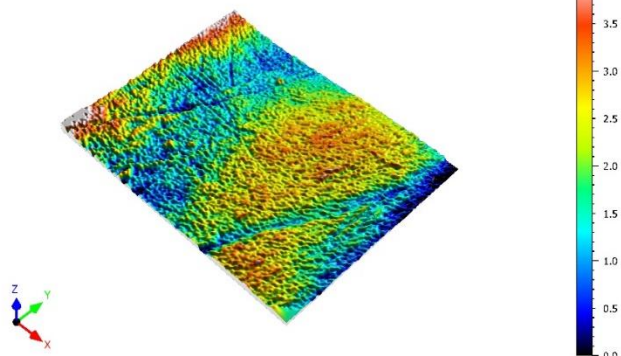
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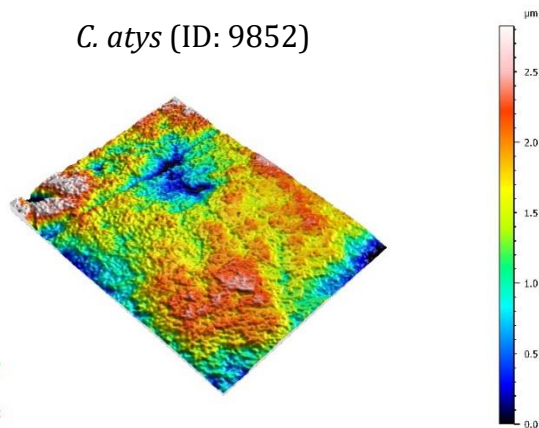
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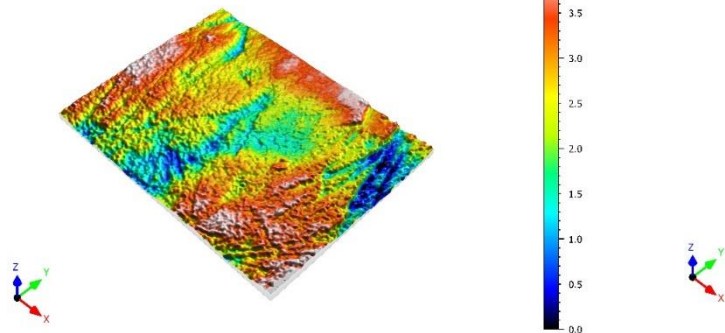
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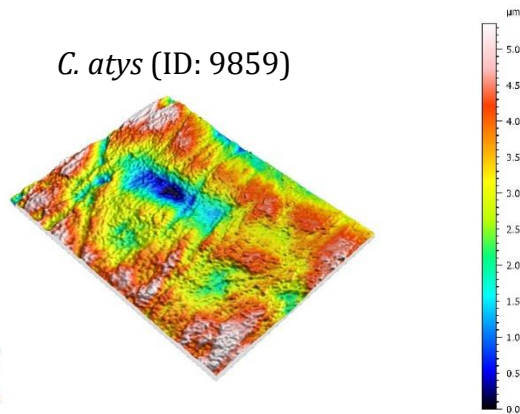
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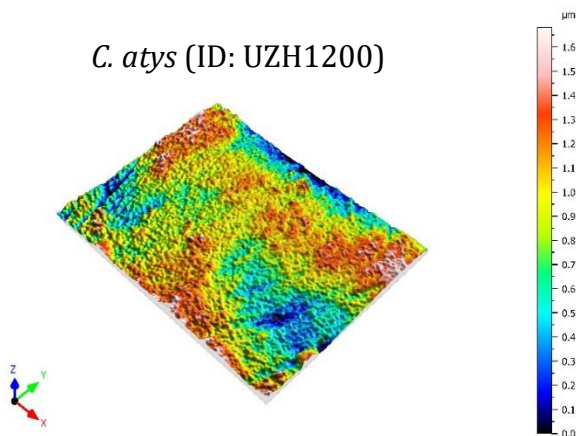
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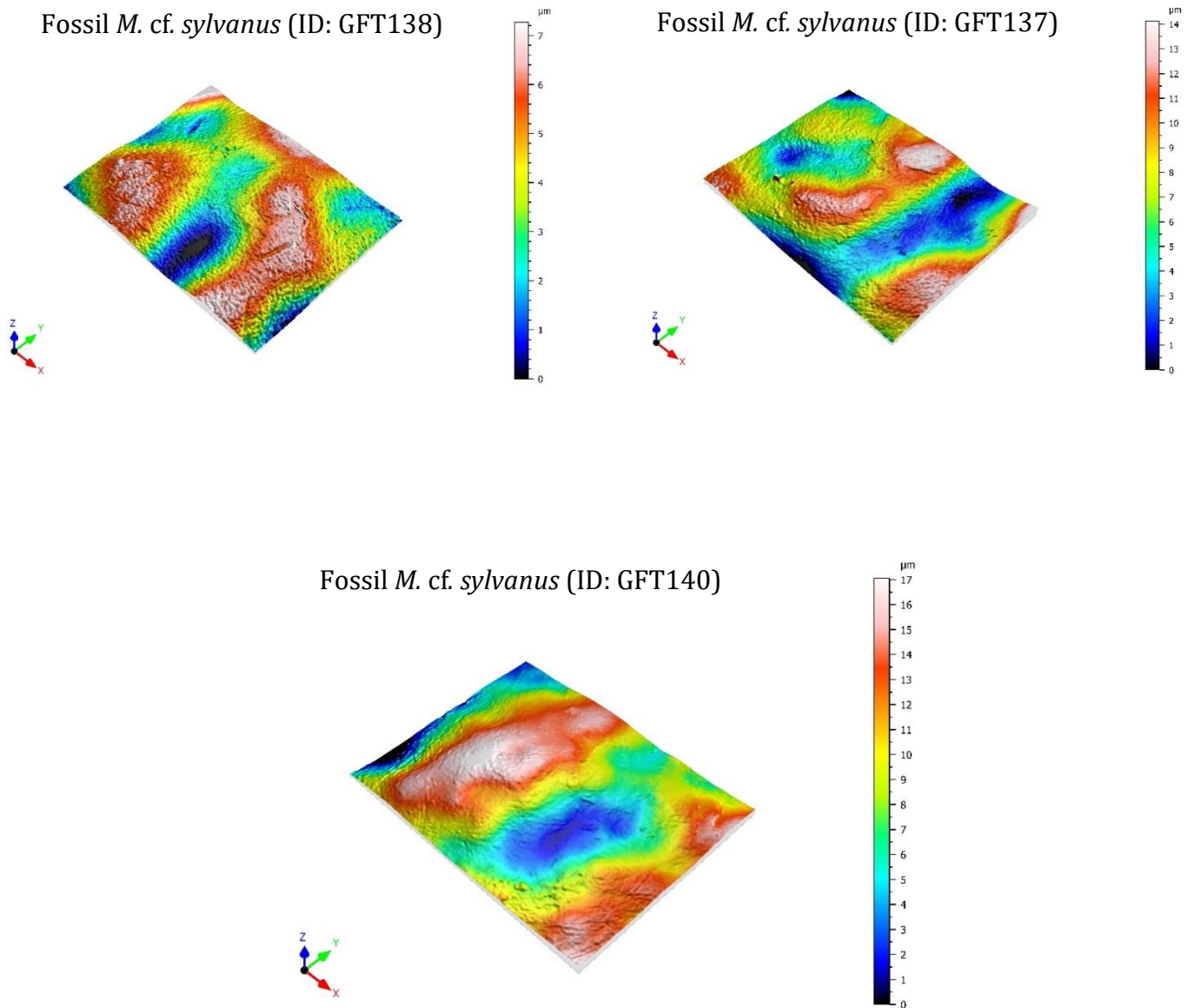
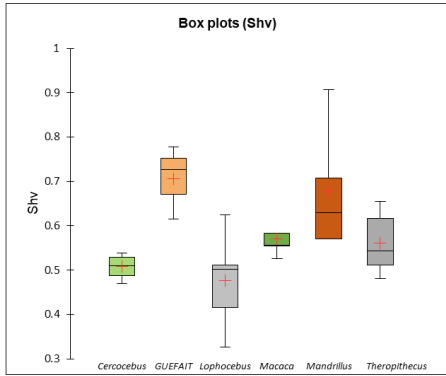
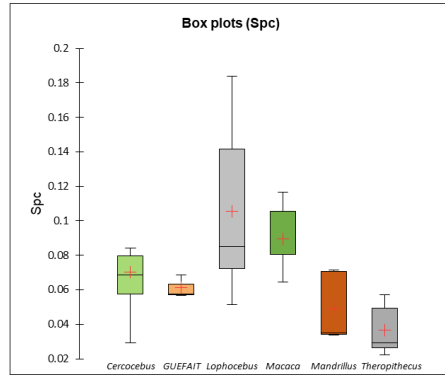
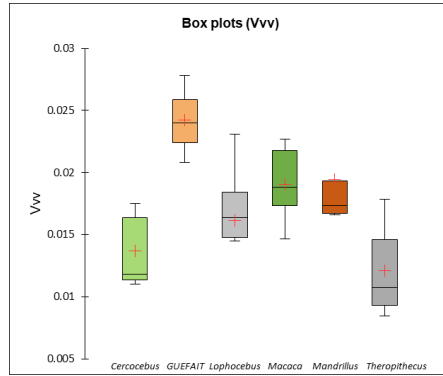
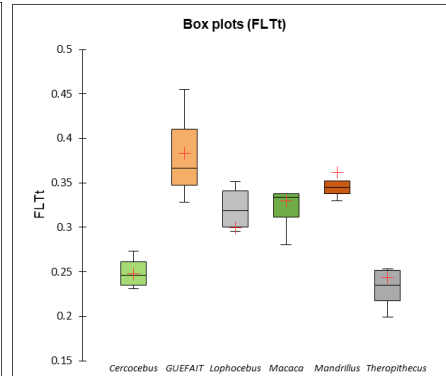
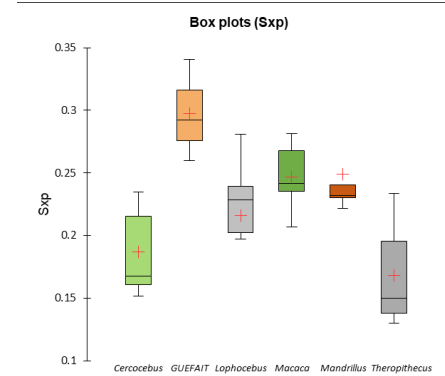
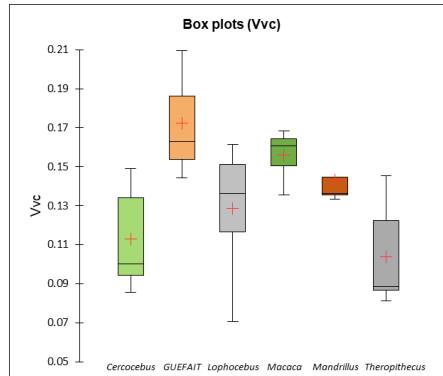
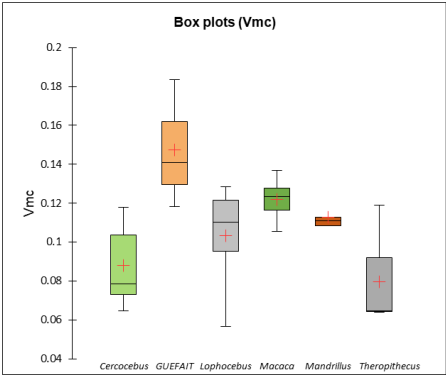
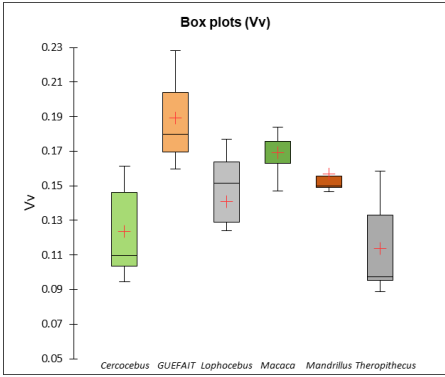
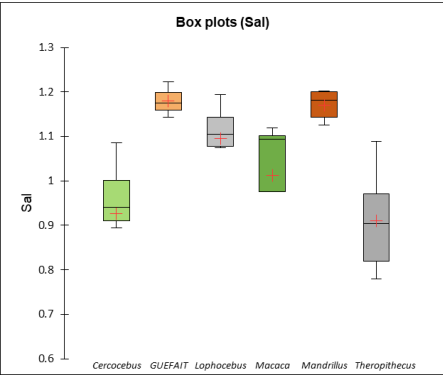
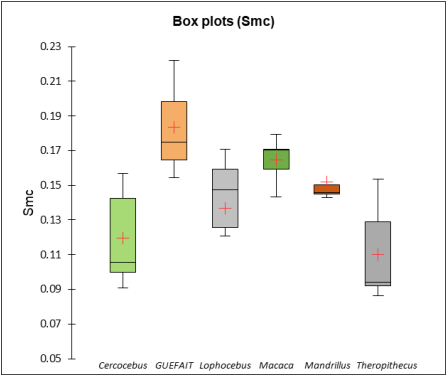
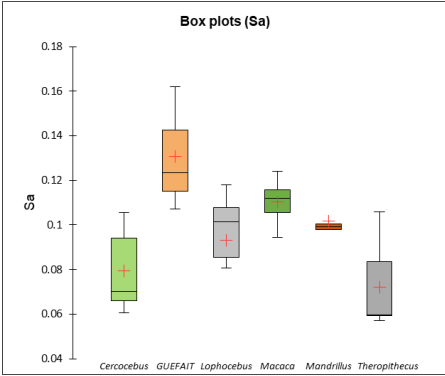
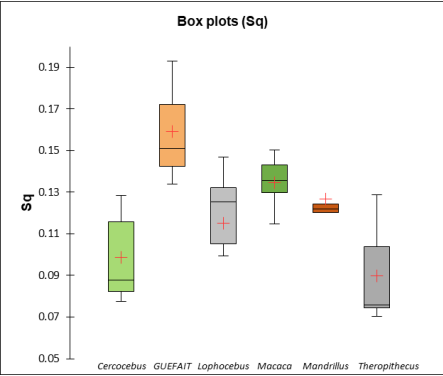
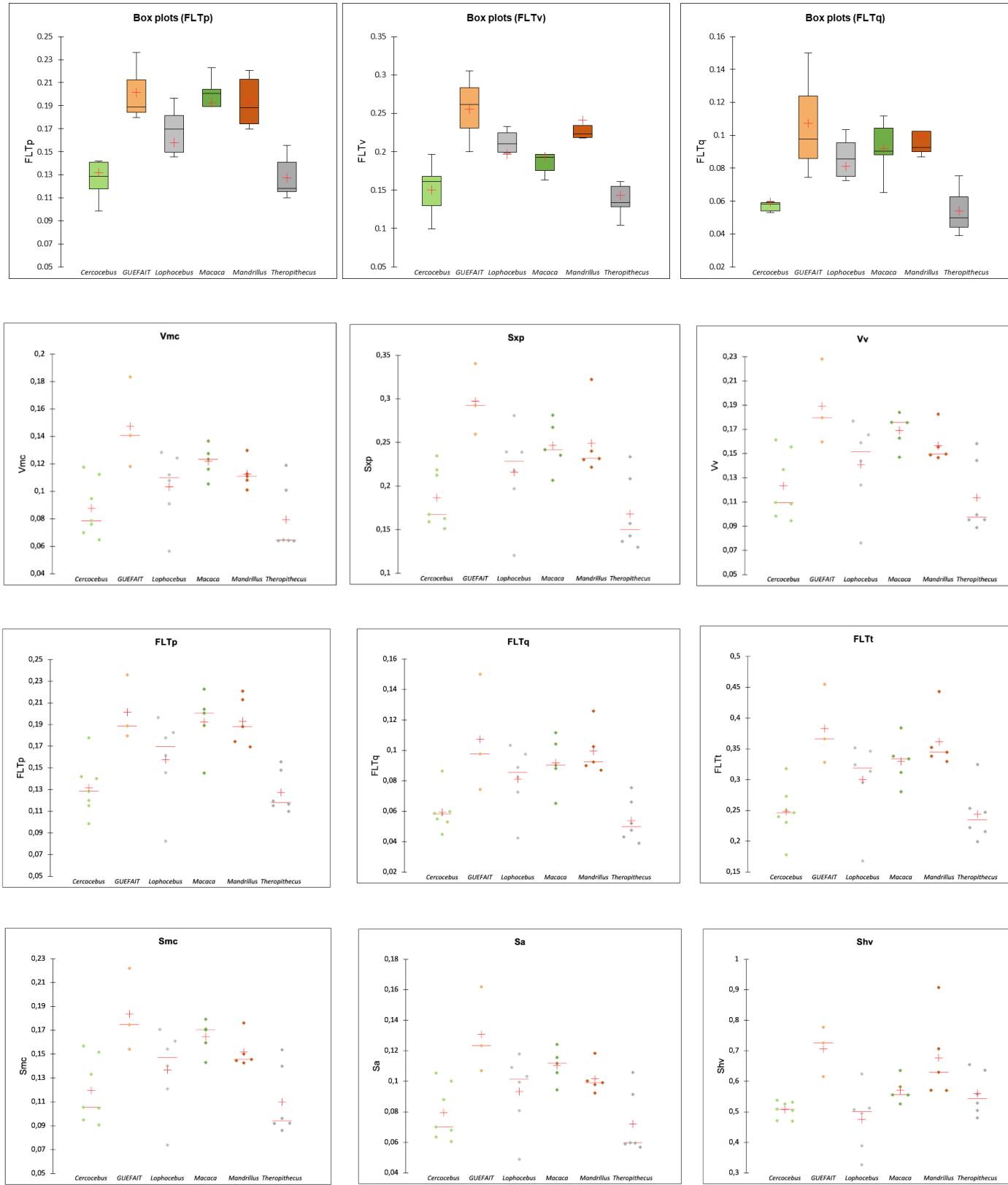


Fig. S3. 3D photosimulations (400x500 μm) of representative enamel surface scans of different individuals of extant (*T. gelada*, *L. albigena*, *M. mulatta*, *M. sphinx* and *C. atys*) and extinct (*M. cf. sylvanus*) primate for buccal microwear texture analysis.





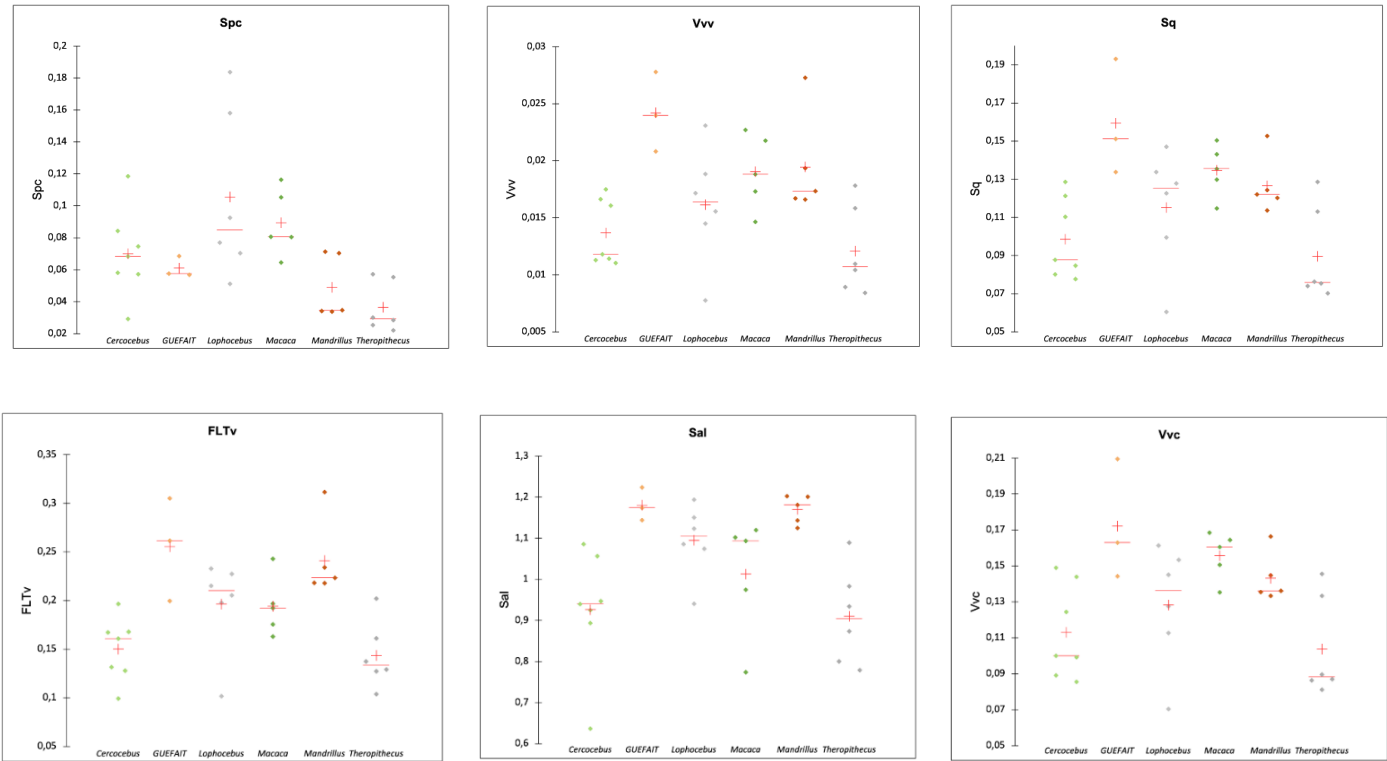


Fig. S4. Box plots comparing buccal microtexture parameters between extant and extinct primate species. The red cross is the mean values of each parameter by group and the red line is the median (inferior chart) texture analysis.

Table S1. Information on selected samples of extant cercopithecines for both microwear methods (Abbreviations: OMA = Occlusal Microwear Analysis; BMTA = Buccal Microwear Texture Analysis). In red: samples discarded due to bad preservation or other taphonomic defects on the analyzed surface. All analyzed teeth correspond to lower left second molars (M₂).

Method	Specimen ID	Museum reference	Species	Museum	Specimen Origin
OMA	B100	15168	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
OMA	B115	34571	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
OMA	B107	7904	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
OMA	B98	8549	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
OMA	B103	8583	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
OMA	B96	35270	<i>M. mulatta</i>	RMCA	Karachi (Pakistan)
OMA	PAP1733	91.060-M172	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1742	83.006-M271	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1750	91.060-M169	<i>L. albigena</i>	RMCA	Kisangani (Democratic Republic of the Congo)
OMA	PAP1754	RG37587	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1760	91.060-M174	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1762	RG33966	<i>L. albigena</i>	RMCA	Ikozi (Democratic Republic of the Congo)
OMA	PAP1995	91.060.m164	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1774	91.060. M164	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
OMA	PAP1859	PAL108	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1861	5199	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1866	UZH12481	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1526	1999_077	<i>M. sphinx</i>	RMCA	Cameroon
OMA	PAP1868	UZH8829	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1865	12481	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1867	8829	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1870	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1857	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1874	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
OMA	PAP1972	9849	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1924	9847	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1978	9852	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1984	9854	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1986_2	9859	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP3076	73.018.M359	<i>C. atys</i>	RMCA	Cameroon

OMA	PAP1992	UZH1200	<i>C. atys</i>	IMAZ	Democratic Republic of the Congo
OMA	PAP1914	-	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1932	-	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1946	-	<i>C. atys</i>	IMAZ	Liberia
OMA	PAP1175	1969-450	<i>T. gelada</i>	MNHN	Ethiopia
OMA	PAP774	1969-451	<i>T. gelada</i>	MNHN	Ethiopia
OMA	PAP757	1969-452	<i>T. gelada</i>	MNHN	Ethiopia
OMA	PAP778	1969-453	<i>T. gelada</i>	MNHN	Ethiopia
OMA	PAP1165	CG1972-360	<i>T. gelada</i>	MNHN	Ethiopia
OMA	PAP1181	CG1972-361	<i>T. gelada</i>	MNHN	Ethiopia
OMA	-	1934-251	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	B100	15168	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
BMTA	B115	34571	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
BMTA	B107	7904	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
BMTA	B98	8549	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
BMTA	B103	8583	<i>M. mulatta</i>	RBINS	Karachi (Pakistan)
BMTA	B96	35270	<i>M. mulatta</i>	RMCA	Karachi (Pakistan)
BMTA	PAP1733	91.060-M172	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1742	83.006-M271	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1750	91.060-M169	<i>L. albigena</i>	RMCA	Kisangani (Democratic Republic of the Congo)
BMTA	PAP1995	91.060.m164	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1760	91.060-M174	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1762	RG33966	<i>L. albigena</i>	RMCA	Ikozi (Democratic Republic of the Congo)
BMTA	PAP1774	91.060. M164	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1754	RG37587	<i>L. albigena</i>	RMCA	Tshopo (Democratic Republic of the Congo)
BMTA	PAP1870	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1857	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1866	UZH12481	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1526	1999_077	<i>M. sphinx</i>	RMCA	Cameroon
BMTA	PAP1868	UZH8829	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1865	12481	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1867	8829	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1859	PAL108	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1861	5199	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1874	-	<i>M. sphinx</i>	IMAZ	Port-Gentil, Gabon
BMTA	PAP1972	9849	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1924	9847	<i>C. atys</i>	IMAZ	Liberia

BMTA	PAP1978	9852	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1984	9854	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1986_2	9859	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP3076	73.018.M359	<i>C. atys</i>	RMCA	Cameroon
BMTA	PAP1992	UZH1200	<i>C. atys</i>	IMAZ	Democratic Republic of the Congo
BMTA	PAP1914	-	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1932	-	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1946	-	<i>C. atys</i>	IMAZ	Liberia
BMTA	PAP1175	1969-450	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	PAP774	1969-451	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	PAP757	1969-452	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	PAP778	1969-453	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	PAP1165	CG1972-360	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	PAP1181	CG1972-361	<i>T. gelada</i>	MNHN	Ethiopia
BMTA	-	1934-251	<i>T. gelada</i>	MNHN	Ethiopia

Table S2. Raw carbon and oxygen stable isotope data for *M. cf. sylvanus* and ungulates from GFT- 4.2.

Taxa	Sample	Tooth	Fieldwork reference	$\delta^{13}\text{C}$ (‰) (VPDB)	$\delta^{18}\text{O}$ (‰) (VPDB)
<i>M. cf. sylvanus</i>	GFT241	I ¹	GFT4.2018-1-Q14-70	-11.78	1.14
<i>M. cf. sylvanus</i>	GFT242	M ₁	GFT4.2018-1-Q14-13	-12.49	0.62
<i>M. cf. sylvanus</i>	GFT240	M ₂	GFT4.2019-1-S15-65	-12.12	1.82
<i>M. cf. sylvanus</i>	GFT243	M ₃	GFT4.2019-1-R13-63	-12.38	0.94
Tragelaphini	GFT139	P ₂	GFT4.2019-1-S14-53	-8.09	0.27
Tragelaphini	GFT197	M ^{1/2}	GFT4.2019-1-R15-08	-11.32	-0.76
Tragelaphini	GFT108	M ^{1/2}	GFT4.2019-1-S14-49	-11.08	0.19
Tragelaphini	GFT196	M ^{1/2}	GFT4.2019-1-S15-17	-9.52	-1.41
<i>Gazella</i> sp.	GFT152	M	GFT4.2019-1-R15-28	-9.44	-0.87
<i>Gazella</i> sp.	GFT155	P ₄	GFT4.2019-1-S14-69	-11.08	-0.76
<i>Gazella</i> sp.	GFT115	M _{1/2}	GFT4.2019-1-S14-47	-10.93	1.83
<i>Gazella</i> sp.	GFT156	M ₃	GFT4.2019-1-S15-38	-12.22	-1.86
<i>Hipparion</i> sp.	GFT166	P ^{3/4}	GFT4.2019-1-R14-42	-8.20	-0.86
<i>Hipparion</i> sp.	GFT143	P ^{3/4}	GFT4.2019-1-Q15-276	-10.37	-3.62
<i>Hipparion</i> sp.	GFT179	M _{1/2}	GFT4.2019-1-S12-80	-10.08	-2.36
<i>Hipparion</i> sp.	GFT164	P ^{3/4}	GFT4.2019-1-Q15-156	-9.53	-1.21

Table S3. Occlusal Microwear Analysis (Low Magnification) raw data of *M. cf. sylvanus* from GFT-4.2 and extant cercopithecines. All analyzed teeth of extant cercopithecines correspond to lower left second molars (M₂).

Species	Specimen ID	U/L	Sex	Side	Average PITS	Average SCRATCHES	Average GOUGES	Average PUNCTURE PITS
<i>C. atys</i>	PAP3076	L	F	L	33	8.5	3.5	2.5
<i>C. atys</i>	PAP1992	L	M	L	34	15	3	3
<i>C. atys</i>	PAP1978	L	F	L	28.5	10	3	3
<i>C. atys</i>	PAP1924	L	-	L	32.5	9.5	2.5	4
<i>C. atys</i>	PAP1986	L	-	L	28.5	12.5	2.5	5
<i>C. atys</i>	PAP1984	L	F	L	31	10	2.5	2.5
<i>C. atys</i>	PAP1972	L	F	L	35.5	10	4	6
<i>L. albigena</i>	91.060.m164	L	F	L	40.5	11	6	2.5
<i>L. albigena</i>	91.060M172	L	M	L	44	11.5	6.5	7
<i>L. albigena</i>	83.006.M271	L	M	L	35	10.5	3	5
<i>L. albigena</i>	91.060.M174	L	M	L	36.5	13.5	1	4.5
<i>L. albigena</i>	91.060.M169	L	F	L	46.5	11.5	3	7.5
<i>L. albigena</i>	1762	L	-	L	41	13.5	6	6
<i>M. mulatta</i>	B115 34571	L	M	L	36.5	13	1.5	4.5
<i>M. mulatta</i>	B103 8583	L	M	L	40	11.5	1	5.5
<i>M. mulatta</i>	B98 8549	L	M	L	35.5	13	0.5	3
<i>M. mulatta</i>	B96 35270	L	indet.	L	39.5	11	3	4.5
<i>M. mulatta</i>	B100 15168	L	F	L	42.5	11	2	4
<i>M. mulatta</i>	B107 7904	L	-	L	37	11	3.3	4.3
<i>M. sphinx</i>	12481	L	M	L	22.0	14.0	5.3	0
<i>M. sphinx</i>	8829	L	F	L	25.3	13.0	3.7	0
<i>M. sphinx</i>	1999-077-M001	L	F	L	18.3	16.3	4.3	0
<i>M. sphinx</i>	PAP1870	L	M	L	16.0	17.5	2.5	0
<i>M. sphinx</i>	PAP1857	L	F	L	18.3	16.3	3.3	0
<i>T. gelada</i>	1969-450	L	M	L	5	25	0	0
<i>T. gelada</i>	1969-451	L	F	L	10	27.5	0	0
<i>T. gelada</i>	1969-452	L	F	L	12.5	28	0	0
<i>T. gelada</i>	1969-453	L	F	L	8	25.5	0	0
<i>T. gelada</i>	1934-251	L	F	L	14	26	0	0
<i>T. gelada</i>	CG1972-360	L	M	L	13.5	24.5	0	0
<i>T. gelada</i>	CG1972-361	L	F	L	8	25	0	0
Fossil <i>M. cf. sylvanus</i>	GFT140	L	-	R	26	13	4	4.5
Fossil <i>M. cf. sylvanus</i>	GFT138	L	-	R	31	19	4	4.5

The following supplementary tables (S4, S5, S6, S7 and S8) can be downloaded from the provided link and contain information related to the statistical analyses conducted for the buccal microtexture:

<https://www.frontiersin.org/articles/10.3389/fevo.2023.1011208/full#supplementary-material>

Table S4. Eigenvalues and variance percentages of each axis of the correspondence analysis of Figure 1.

Table S5. Description of the 3D areal surface texture parameters used in the present study (ISO 25178 and ISO 12781).

Table S6. Values of the Log [(parameters)+1] used in the buccal microwear texture analysis by taxa.

Table S7. Analysis of the Variance (ANOVA), Welch correction and HSD Tukey's *post hoc* multiple comparison between groups for buccal microwear texture analysis.

Table S8. Raw data of the linear discriminant analysis (LDA) for buccal microwear texture analysis.

Supplementary information

Palaeoecological reconstruction of Plio-Pleistocene herbivores from the Ahl al Oughlam site (Casablanca, Morocco): Insights from dental wear and stable isotopes

Iván Ramírez-Pedraza^{a,b,c,*}, Florent Rivals^{a,b,d}, Carlos Tornero^{e, a}, Denis Geraads^f, Jean Paul
Raynal^{g,h}, David Lefèvreⁱ, Abderrahim Mohib^{h,j}

^aInstitut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Tarragona, Spain.

^bDepartament d'Història i Història de l'Art, Universitat Rovira i Virgili (URV), Tarragona, Spain.

^cisoTROPIC Research Group, Max Planck Institute of Geoanthropology, Jena, Germany.

^dInstitució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain.

^eDepartment of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain.

^fCR2P-UMR 7207, CNRS, MNHN, Sorbonne Université, Paris, France.

^gUniversité de Bordeaux, CNRS, UMR 5199 PACEA, Pessac cedex, France.

^hInstitut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

ⁱUniversité Paul Valéry Montpellier 3, CNRS, LabEx ARCHIMEDE and UMR 5140 Archéologie des
sociétés méditerranéennes, Campus Saint Charles, Montpellier, France.

^jDirection provinciale de la Culture, Avenue Mohammed V, quartier administratif, Kénitra, Morocco.

***Corresponding author.** Institut Català de Paleoecologia Humana i Evolució Social (IPHES-
CERCA), Tarragona, Spain.

E-mail address: ramirezpedrazaivan@gmail.com (I. Ramírez-Pedraza)

Table S1. Raw data of $\delta^{13}\text{C}$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}\text{C}_{\text{diet-meq}}$ (‰) and Mean Annual Precipitation (MAP - mm/yr) from AaO.

Site	Sample	Species	$\delta^{18}\text{O}$ (‰) (VPDB)	$\delta^{13}\text{C}$ (‰) (VPDB)	Body Mass	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}\text{C}_{\text{diet-meq}}$ (‰)	MAP (mm/yr)
AaO	AaO_79	<i>S. maurusium</i>	2.21	-10.82	1246	14.0	-26.36	317
AaO	AaO_80	<i>S. maurusium</i>	2.93	-13.84	1246	14.0	-29.39	1839
AaO	AaO_81	<i>S. maurusium</i>	1.35	-14.14	1246	14.0	-29.69	2117
AaO	AaO_82	<i>S. maurusium</i>	-0.85	-11.71	1246	14.0	-27.25	590
AaO	AaO_83	<i>S. maurusium</i>	0.94	-12.55	1246	14.0	-28.10	956
AaO	AaO_84	<i>S. maurusium</i>	0.74	-11.22	1246	14.0	-26.76	428
AaO	AaO_177	<i>H. pomeli</i>	-2.72	-11.22	250	13.3	-26.02	237
AaO	AaO_178	<i>H. pomeli</i>	-1.69	-10.78	250	13.3	-25.58	149
AaO	AaO_179	<i>H. pomeli</i>	-1.56	-10.61	250	13.3	-25.41	118
AaO	AaO_180	<i>H. pomeli</i>	-1.51	-12.28	250	13.3	-27.08	528
AaO	AaO_181	<i>H. pomeli</i>	-2.04	-12.32	250	13.3	-27.12	540
AaO	AaO_182	<i>H. pomeli</i>	-0.35	-11.77	250	13.3	-26.57	373
AaO	AaO_183	<i>H. pomeli</i>	-1.91	-10.94	250	13.3	-25.74	179
AaO	AaO_184	<i>H. pomeli</i>	-3.03	-12.27	250	13.3	-27.07	523
AaO	AaO_185	<i>H. pomeli</i>	-1.32	-11.14	250	13.3	-25.94	220
AaO	AaO_186	<i>H. pomeli</i>	-2.74	-13.19	250	13.3	-27.99	905
AaO	AaO_187	<i>H. pomeli</i>	-1.15	-11.83	250	13.3	-26.63	389
AaO	AaO_188	<i>H. pomeli</i>	-2.41	-13.47	250	13.3	-28.27	1050
AaO	AaO_189	<i>H. pomeli</i>	-1.85	-11.22	250	13.3	-26.02	237
AaO	AaO_190	<i>H. pomeli</i>	-2.62	-12.15	250	13.3	-26.95	485
AaO	AaO_191	<i>H. pomeli</i>	0.21	-10.77	250	13.3	-25.57	146
AaO	AaO_192	<i>H. pomeli</i>	-1.59	-11.56	250	13.3	-26.36	316
AaO	AaO_193	<i>M. phacochoeroides</i>	-0.26	-11.94	297	13.4	-26.82	444
AaO	AaO_194	<i>M. phacochoeroides</i>	-0.65	-12.89	297	13.4	-27.77	797
AaO	AaO_195	<i>M. phacochoeroides</i>	0.44	-12.65	297	13.4	-27.53	695
AaO	AaO_196	<i>M. phacochoeroides</i>	-0.13	-12.19	297	13.4	-27.07	525
AaO	AaO_197	<i>M. phacochoeroides</i>	0.36	-11.36	297	13.4	-26.23	286
AaO	AaO_198	<i>M. phacochoeroides</i>	-0.03	-12.14	297	13.4	-27.02	508
AaO	AaO_199	<i>M. phacochoeroides</i>	-1.07	-8.40	297	13.4	-23.28	-124
AaO	AaO_200	<i>M. phacochoeroides</i>	-0.12	-11.55	297	13.4	-26.43	334

AaO	AaO_201	<i>M. phacochoeroides</i>	-0.76	-13.13	297	13.4	-28.01	912
AaO	AaO_202	<i>M. phacochoeroides</i>	-0.69	-12.23	297	13.4	-27.11	537
AaO	AaO_203	<i>M. phacochoeroides</i>	0.46	-11.93	297	13.4	-26.80	440
AaO	AaO_204	<i>M. phacochoeroides</i>	-0.73	-13.18	297	13.4	-28.06	938
AaO	AaO_205	<i>M. phacochoeroides</i>	-1.24	-12.81	297	13.4	-27.69	763
AaO	AaO_206	<i>M. phacochoeroides</i>	-0.45	-12.68	297	13.4	-27.56	708
AaO	AaO_207	<i>M. phacochoeroides</i>	-0.93	-11.69	297	13.4	-26.57	373
AaO	AaO_208	<i>M. phacochoeroides</i>	-1.96	-10.48	297	13.4	-25.36	110
AaO	AaO_209	<i>M. phacochoeroides</i>	0.40	-11.79	297	13.4	-26.67	399
AaO	AaO_242	<i>M. phacochoeroides</i>	2.00	-11.13	297	13.4	-26.00	233
AaO	AaO_243	<i>M. phacochoeroides</i>	0.44	-12.42	297	13.4	-27.30	607
AaO	AaO_244	<i>M. phacochoeroides</i>	-0.81	-11.00	297	13.4	-25.88	207
AaO	AaO_249	<i>M. phacochoeroides</i>	-1.76	-10.69	297	13.4	-25.57	146
AaO	AaO_250	<i>M. phacochoeroides</i>	-1.03	-10.47	297	13.4	-25.35	107
AaO	AaO_251	<i>M. phacochoeroides</i>	-1.04	-9.21	297	13.4	-24.09	-56
AaO	AaO_210	<i>Gazella</i> sp.	0.25	-12.76	30	12.4	-26.63	389
AaO	AaO_211	<i>Gazella</i> sp.	0.10	-11.07	30	12.4	-24.94	46
AaO	AaO_212	<i>Gazella</i> sp.	1.03	-11.00	30	12.4	-24.87	36
AaO	AaO_213	<i>Gazella</i> sp.	2.05	-10.59	30	12.4	-24.47	-15
AaO	AaO_214	<i>Gazella</i> sp.	0.98	-11.61	30	12.4	-25.49	131
AaO	AaO_215	<i>Gazella</i> sp.	0.87	-10.87	30	12.4	-24.74	19
AaO	AaO_216	<i>Gazella</i> sp.	1.12	-12.66	30	12.4	-26.54	364
AaO	AaO_217	<i>Gazella</i> sp.	1.01	-11.61	30	12.4	-25.49	132
AaO	AaO_218	<i>Gazella</i> sp.	-1.19	-12.18	30	12.4	-26.05	244
AaO	AaO_219	<i>Gazella</i> sp.	-0.27	-10.99	30	12.4	-24.87	35
AaO	AaO_220	<i>Gazella</i> sp.	-0.64	-11.45	30	12.4	-25.33	104
AaO	AaO_221	<i>Gazella</i> sp.	-1.78	-11.90	30	12.4	-25.77	185
AaO	AaO_222	<i>Gazella</i> sp.	-1.88	-11.78	30	12.4	-25.66	163
AaO	AaO_223	<i>Gazella</i> sp.	-2.28	-11.53	30	12.4	-25.41	118
AaO	AaO_224	<i>Gazella</i> sp.	-1.48	-11.46	30	12.4	-25.34	106
AaO	AaO_225	<i>Gazella</i> sp.	0.45	-11.86	30	12.4	-25.73	177
AaO	AaO_251	<i>Gazella</i> sp.	-0.70	-11.15	30	12.4	-25.02	57
AaO	AaO_252	<i>Gazella</i> sp.	-1.32	-12.07	30	12.4	-25.95	221

AaO	AaO_226	Alcelaphini	-1.07	-11.31	200	13.2	-26.01	234
AaO	AaO_227	Alcelaphini	-0.11	-11.72	200	13.2	-26.42	333
AaO	AaO_228	Alcelaphini	-1.48	-10.75	200	13.2	-25.45	125
AaO	AaO_229	Alcelaphini	-1.45	-8.33	200	13.2	-23.03	-141
AaO	AaO_230	Alcelaphini	-0.75	-11.79	200	13.2	-26.49	351
AaO	AaO_231	Alcelaphini	-0.15	-13.02	200	13.2	-27.72	775
AaO	AaO_232	Alcelaphini	-1.04	-8.82	200	13.2	-23.52	-107
AaO	AaO_233	Alcelaphini	-0.84	-11.08	200	13.2	-25.78	187
AaO	AaO_234	Alcelaphini	-0.30	-10.92	200	13.2	-25.61	155
AaO	AaO_235	Alcelaphini	-0.86	-9.80	200	13.2	-24.50	-11
AaO	AaO_236	Alcelaphini	0.59	-10.63	200	13.2	-25.33	105
AaO	AaO_237	Alcelaphini	-1.03	-8.74	200	13.2	-23.44	-113
AaO	AaO_238	Alcelaphini	-1.05	-9.38	200	13.2	-24.08	-57
AaO	AaO_239	Alcelaphini	-1.69	-10.55	200	13.2	-25.25	92
AaO	AaO_240	Alcelaphini	-2.21	-9.74	200	13.2	-24.44	-19
AaO	AaO_241	Alcelaphini	0.37	-8.01	200	13.2	-22.71	-161
AaO	AaO_254	Alcelaphini	-0.69	-10.74	200	13.2	-25.44	124
AaO	AaO_255	Alcelaphini	-0.60	-10.47	200	13.2	-25.17	79
AaO	AaO_245	<i>A. osiris</i>	-1.39	-13.34	5000	14.7	-29.56	1996

Table S2. Raw dental microwear and mesowear data from all taxa analysed from AaO. Abbreviations: NTS = number of total scratches, NTP = number of total pits, SWS = scratch width score, PP = presence of puncture pits, HC = presence of hypercoarse scratches, LP = presence of large pits and G = presence of gouges.

Site	Sample	Species	Dental Microwear								Mesowear
			NTS	NTP	SWS	PP	HC	LP	G	XC	
AaO	274	<i>S. maurusium</i>	10	25.5	1	0	0	1	1	0	-
AaO	274a	<i>S. maurusium</i>	-	-	-	-	-	-	-	-	1
AaO	2621	<i>S. maurusium</i>	-	-	-	-	-	-	-	-	1
AaO	143	<i>S. maurusium</i>	13.5	24	1	0	0	0	1	0	-
AaO	3844	<i>S. maurusium</i>	-	-	-	-	-	-	-	-	-
AaO	3729?	<i>S. maurusium</i>	13	28	1	0	0	1	1	1	1
AaO	3013	<i>S. maurusium</i>	14.5	21.5	1	0	0	0	1	0	1
AaO	4742	<i>H. pomeli</i>	23.5	22	1	0	0	1	0	0	5
AaO	190	<i>H. pomeli</i>	-	-	-	-	-	-	-	-	-
AaO	70	<i>H. pomeli</i>	-	-	-	-	-	-	-	-	-
AaO	1182	<i>H. pomeli</i>	19	16	1	0	0	1	0	0	5
AaO	2259	<i>H. pomeli</i>	-	-	-	-	-	-	-	-	-
AaO	2048	<i>H. pomeli</i>	17.5	24	1	0	0	1	0	0	5
AaO	2263	<i>H. pomeli</i>	21.5	19	1	0	0	1	0	0	3
AaO	1180	<i>H. pomeli</i>	17.5	18.5	1	1	0	1	0	0	-
AaO	2257	<i>H. pomeli</i>	20.5	17	1	1	0	0	0	0	-
AaO	41	<i>H. pomeli</i>	17.5	18	1	0	0	1	0	0	-
AaO	2250	<i>H. pomeli</i>	19.5	20	1	0	0	1	0	0	-
AaO	1181	<i>H. pomeli</i>	20.5	19.5	1	0	0	1	0	0	-
AaO	1179	<i>H. pomeli</i>	28	22	1	0	0	1	1	0	4
AaO	37	<i>H. pomeli</i>	19	26	1	0	0	1	0	0	4
AaO	1020	<i>H. pomeli</i>	20	15	1	0	0	1	0	0	-
AaO	1229	<i>H. pomeli</i>	24	11	1	0	0	0	0	0	-
AaO	2258	<i>H. pomeli</i>	-	-	-	-	-	-	-	-	-
AaO	16	<i>M. phacochoeroides</i>	16.5	19	1	0	0	1	0	1	-
AaO	1388	<i>M. phacochoeroides</i>	23	26	1	0	0	1	1	1	-
AaO	3583	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	3483a	<i>M. phacochoeroides</i>	29	23.5	0	0	0	1	0	1	-
AaO	1478	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2586	<i>M. phacochoeroides</i>	15.5	26.5	1	0	0	1	0	1	-
AaO	900	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2585	<i>M. phacochoeroides</i>	17	18.5	1	0	0	1	1	1	-
AaO	2591	<i>M. phacochoeroides</i>	21	26	1	0	0	1	0	1	-
AaO	4402	<i>M. phacochoeroides</i>	28.5	26	1	0	0	0	0	1	-
AaO	807 o 007	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2075	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-

AaO	917	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	4404	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	4405	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	4410	<i>M. phacochoeroides</i>	15	25	1	0	0	1	0	1	-
AaO	XXX2	<i>M. phacochoeroides</i>	20	20.5	0	0	0	1	0	1	-
AaO	2082	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2086	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	914	<i>M. phacochoeroides</i>	18.5	18.5	1	0	0	1	0	1	-
AaO	3586	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	6	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	4400	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2587	<i>M. phacochoeroides</i>	15	20	1	0	0	1	0	1	-
AaO	2590	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	3568	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	2081	<i>M. phacochoeroides</i>	13	18.5	1	0	0	0	1	1	-
AaO	2022 o 32	<i>M. phacochoeroides</i>	21	24.5	1	0	0	1	0	1	-
AaO	1489	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	275	<i>M. phacochoeroides</i>	18.5	24	1	0	0	1	0	1	-
AaO	926	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	3478	<i>M. phacochoeroides</i>	17.5	31.5	1	1	0	1	1	1	-
AaO	5	<i>M. phacochoeroides</i>	26.5	21.5	1	0	0	0	0	1	-
AaO	239	<i>M. phacochoeroides</i>	-	-	-	-	-	-	-	-	-
AaO	3b	<i>M. phacochoeroides</i>	18	23	1	0	0	1	0	1	-
AaO	141	<i>M. phacochoeroides</i>	21.5	21.5	1	0	0	1	0	1	-
AaO	1885	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	1412	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	0
AaO	285	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	3949	<i>Gazella</i> sp.	8.5	21.5	1	0	0	1	1	0	1
AaO	1148	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	2404	<i>Gazella</i> sp.	9.5	23.5	1	0	0	1	1	0	1
AaO	563	<i>Gazella</i> sp.	9.5	19.5	1	0	0	1	0	0	1
AaO	2475	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	-
AaO	238	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	XXX3	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	0
AaO	3681	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	-
AaO	1144	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	-
AaO	4235	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	1225	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	3
AaO	2406	<i>Gazella</i> sp.	11	24.5	1	0	0	1	1	0	-
AaO	1883	<i>Gazella</i> sp.	6.5	17.5	1	0	0	1	0	0	-
AaO	XXX4	<i>Gazella</i> sp.	12	27	1	0	0	1	0	0	-
AaO	3010	<i>Gazella</i> sp.	9	32	1	0	0	1	0	0	-

AaO	1033	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	-
AaO	2403	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	2
AaO	287	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	3
AaO	1202	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	3986	<i>Gazella</i> sp.	10	21.5	1	0	0	1	1	1	1
AaO	3975	<i>Gazella</i> sp.	-	-	-	-	-	-	-	-	1
AaO	232	Alcelaphini	20.5	22.5	1	0	0	1	0	0	2
AaO	83	Alcelaphini	-	-	-	-	-	-	-	-	2
AaO	1093	Alcelaphini	20	21	1	0	0	1	1	0	4
AaO	76	Alcelaphini	21	27	1	0	0	1	1	0	
AaO	212	Alcelaphini	18.5	24	2	0	0	1	0	0	2
AaO	2317	Alcelaphini	21.5	19.5	1	0	0	0	0	0	2
AaO	2066	Alcelaphini	-	-	-	-	-	-	-	-	1
AaO	2316	Alcelaphini	20.5	23	1	0	0	1	0	0	3
AaO	2101	Alcelaphini	-	-	-	-	-	-	-	-	2
AaO	224	Alcelaphini	-	-	-	-	-	-	-	-	3
AaO	3917	Alcelaphini	19	15.5	1	0	0	1	0	0	2
AaO	272	Alcelaphini	21	15.5	1	0	0	1	0	0	1
AaO	2067	Alcelaphini	20.5	18	1	0	0	1	1	1	2
AaO	495	Alcelaphini	25	16	2	0	0	0	0	0	3
AaO	1142	Alcelaphini	-	-	-	-	-	-	-	-	2
AaO	2308	Alcelaphini	17	15.5	1	0	0	0	0	0	4
AaO	3920	Alcelaphini	-	-	-	-	-	-	-	-	2
AaO	276	Alcelaphini	15	20	1	0	0	1	0	0	3
AaO	2241	Alcelaphini	14.5	18	1	0	0	1	0	0	-
AaO	4104	Alcelaphini	18.5	19.5	1	0	0	1	1	0	-
AaO	3032	Alcelaphini	23	23.5	1	0	0	1	0	0	-
AaO	4295	Alcelaphini	-	-	-	-	-	-	-	-	1
AaO	XXX5	Alcelaphini	20	22.5	1	1	0	1	0	0	3
AaO	133	Alcelaphini	19	20	1	1	0	1	1	1	2
AaO	3964	Alcelaphini	-	-	-	-	-	-	-	-	1
AaO	3968	Alcelaphini	-	-	-	-	-	-	-	-	2
AaO	3935	<i>A. osiris</i>	26	25.5	1	0	1	1	0	1	-

Table S3. Raw data of $\delta^{13}\text{C}$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}\text{C}_{\text{diet-meq}}$ (‰) and Mean Annual Precipitation (MAP - mm/yr) from Tighennif (Data extracted from Fannin et al., 2021).

Site	Species	$\delta^{13}\text{C}$ (‰) (VPDB)	Body Mass	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}\text{C}_{\text{diet-meq}}$ (‰)	MAP (mm/yr)
Tighennif	<i>Connochaetes</i>	-9.70	200	13.2	-24.40	-16
Tighennif	<i>Connochaetes</i>	-10.50	200	13.2	-25.20	95
Tighennif	<i>Connochaetes</i>	-10.20	200	13.2	-24.90	49
Tighennif	<i>Connochaetes</i>	-11.50	200	13.2	-26.20	295
Tighennif	<i>Connochaetes</i>	-8.40	200	13.2	-23.10	-133
Tighennif	<i>Connochaetes</i>	-12.50	200	13.2	-27.20	597
Tighennif	<i>Equus</i>	-11.30	280	13.4	-26.15	283
Tighennif	<i>Equus</i>	-10.90	280	13.4	-25.75	195
Tighennif	<i>Equus</i>	-10.70	280	13.4	-25.55	156
Tighennif	<i>Equus</i>	-10.90	280	13.4	-25.75	195
Tighennif	<i>Equus</i>	-11.10	280	13.4	-25.95	237
Tighennif	<i>Equus</i>	-11.20	280	13.4	-26.05	260
Tighennif	<i>Equus</i>	-11.10	280	13.4	-25.95	237
Tighennif	<i>Equus</i>	-10.60	280	13.4	-25.45	138
Tighennif	<i>Equus</i>	-11.20	210	13.2	-25.92	231
Tighennif	<i>Gazella</i>	-12.20	30	12.4	-26.07	265
Tighennif	<i>Gazella</i>	-12.30	30	12.4	-26.17	289
Tighennif	<i>Gazella</i>	-10.30	30	12.4	-24.17	-41
Tighennif	<i>Gazella</i>	-12.70	30	12.4	-26.57	394
Tighennif	<i>Gazella</i>	-11.80	30	12.4	-25.67	180
Tighennif	<i>Ceratotherium</i>	-11.80	2000	14.3	-27.57	746
Tighennif	<i>Ceratotherium</i>	-11.50	2000	14.3	-27.27	625
Tighennif	<i>Ceratotherium</i>	-10.00	2000	14.3	-25.77	200
Tighennif	<i>Ceratotherium</i>	-11.60	2000	14.3	-27.37	664
Tighennif	<i>Ceratotherium</i>	-11.60	2000	14.3	-27.37	664
Tighennif	<i>Ceratotherium</i>	-11.30	2000	14.3	-27.07	552
Tighennif	<i>Hippopotamus</i>	-12.50	1500	14.1	-28.13	1017
Tighennif	<i>Hippopotamus</i>	-12.00	1500	14.1	-27.63	773
Tighennif	<i>Hippopotamus</i>	-10.60	1500	14.1	-26.23	304
Tighennif	<i>Hippopotamus</i>	-10.00	1500	14.1	-25.63	172
Tighennif	<i>Hippopotamus</i>	-9.50	1500	14.1	-25.13	84
Tighennif	<i>Hippopotamus</i>	-11.40	1500	14.1	-27.03	538
Tighennif	<i>Hippopotamus</i>	-11.30	1500	14.1	-26.93	505
Tighennif	<i>Hippopotamus</i>	-11.10	1500	14.1	-26.73	441
Tighennif	<i>Hippopotamus</i>	-10.90	1500	14.1	-26.53	383
Tighennif	<i>Theropithecus</i>	-12.00	20	12.2	-25.71	186

Tighennif	<i>Theropithecus</i>	-11.70	20	12.2	-25.41	130
Tighennif	<i>Theropithecus</i>	-12.40	20	12.2	-26.11	272
Tighennif	<i>Theropithecus</i>	-11.70	20	12.2	-25.41	130
Tighennif	<i>Theropithecus</i>	-13.40	20	12.2	-27.11	563
Tighennif	<i>Theropithecus</i>	-11.00	20	12.2	-24.71	22
Tighennif	<i>Theropithecus</i>	-12.20	20	12.2	-25.91	227
Tighennif	<i>Theropithecus</i>	-11.00	20	12.2	-24.71	22
Tighennif	<i>Theropithecus</i>	-11.00	20	12.2	-24.71	22
Tighennif	<i>Theropithecus</i>	-12.10	20	12.2	-25.81	206

Supplementary information

Results 5.2.2.

Palaeoecological reconstruction of herbivores from Grotte à Hominidés (ThI-GH) and Grotte des Rhinocéros (OHQ1-GDR)

Table S1. Raw data of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope values with the standard deviation (S.D.) from ThI-GH tooth mammal samples.

Site	Sample ID	Taxa	$\delta^{13}\text{C}$ (‰) (VPDB)	S.D.	$\delta^{18}\text{O}$ (‰) (VPDB)	S.D.
ThI-GH	10051	Alcelaphini	-9.9	0.042	-0.9	0.015
ThI-GH	219	Alcelaphini	-10.7	0.055	-2.0	0.058
ThI-GH	10222	Alcelaphini	-8.1	0.010	-1.6	0.004
ThI-GH	11385	Alcelaphini	-8.2	0.020	0.1	0.056
ThI-GH	10325	Alcelaphini	-10.6	0.006	-3.2	0.049
ThI-GH	224	Alcelaphini	-10.8	0.012	-0.7	0.016
ThI-GH	224B	Alcelaphini	-10.3	0.007	-0.1	0.060
ThI-GH	223	Alcelaphini	-11.9	0.020	-1.7	0.068
ThI-GH	10364	Alcelaphini	-8.7	0.048	-0.9	0.059
ThI-GH	10350	Alcelaphini	-10.5	0.008	-1.5	0.034
ThI-GH	222B	Alcelaphini	-11.0	0.026	-2.0	0.040
ThI-GH	12139	Alcelaphini	-9.8	0.016	-0.2	0.072
ThI-GH	205	<i>E. cf. mauritanicus</i>	-11.8	0.011	-0.7	0.094
ThI-GH	20	<i>E. cf. mauritanicus</i>	-11.2	0.010	-1.1	0.077
ThI-GH	48	<i>E. cf. mauritanicus</i>	-11.3	0.024	-1.9	0.081
ThI-GH	1	<i>E. cf. mauritanicus</i>	-12.8	0.068	-1.9	0.077
ThI-GH	10324	<i>E. cf. mauritanicus</i>	-10.3	0.015	-2.6	0.067
ThI-GH	221	<i>G. cf. atlantica</i>	-12.0	0.014	-0.3	0.051
ThI-GH	221B	<i>G. cf. atlantica</i>	-12.1	0.073	1.2	0.079
ThI-GH	9	<i>G. cf. atlantica</i>	-8.9	0.016	-1.4	0.088
ThI-GH	220	<i>G. cf. atlantica</i>	-12.2	0.030	-0.3	0.053
ThI-GH	220B	<i>G. cf. atlantica</i>	-12.2	0.006	0.1	0.041
ThI-GH	66	<i>G. cf. atlantica</i>	-12.3	0.005	-2.7	0.039
ThI-GH	11175	<i>G. cf. atlantica</i>	-10.3	0.013	-2.6	0.098
ThI-GH	1203	<i>G. cf. atlantica</i>	-11.1	0.021	-0.5	0.044
ThI-GH	1325	<i>G. cf. atlantica</i>	-12.8	0.042	-0.8	0.067
ThI-GH	30	<i>G. cf. atlantica</i>	-13.0	0.049	-1.2	0.094
ThI-GH	12311	<i>G. cf. atlantica</i>	-9.4	0.006	-2.6	0.039
ThI-GH	226	<i>G. cf. atlantica</i>	-14.5	0.022	-0.4	0.006
ThI-GH	10599	<i>G. cf. atlantica</i>	-10.2	0.005	-1.7	0.047
ThI-GH	11078	<i>G. cf. atlantica</i>	-11.8	0.007	-0.4	0.025
ThI-GH	4	<i>G. cf. atlantica</i>	-11.6	0.033	-2.3	0.034
ThI-GH	204	<i>C. mauritanicum</i>	-11.9	0.053	-2.0	0.023
ThI-GH	201	<i>C. mauritanicum</i>	-12.6	0.058	-0.6	0.046
ThI-GH	6	<i>C. mauritanicum</i>	-12.4	0.035	0.3	0.020
ThI-GH	11	<i>C. mauritanicum</i>	-12.7	0.013	0.7	0.034
ThI-GH	200	<i>C. mauritanicum</i>	-12.7	0.046	-1.4	0.052
ThI-GH	203	<i>C. mauritanicum</i>	-11.7	0.027	-1.3	0.011
ThI-GH	202	<i>C. mauritanicum</i>	-13.3	0.009	-0.2	0.061

ThI-GH	20	<i>C. mauritanicum</i>	-10.6	0.061	-2.5	0.067
ThI-GH	12174	<i>C. mauritanicum</i>	-11.9	0.007	-1.2	0.048
ThI-GH	15-10276	<i>C. mauritanicum</i>	-10.0	0.072	-2.6	0.092
ThI-GH	12082	<i>C. mauritanicum</i>	-10.5	0.057	-2.5	0.036
ThI-GH	10218	<i>C. mauritanicum</i>	-11.3	0.003	-0.2	0.054
ThI-GH	206	Suidae	-11.9	0.003	1.0	0.035
ThI-GH	10576	Suidae	-12.2	0.006	-1.0	0.067
ThI-GH	209	<i>T. oswaldi</i>	-11.7	0.014	0.0	0.053
ThI-GH	1517	<i>T. oswaldi</i>	-11.3	0.019	0.3	0.011
ThI-GH	1628	<i>T. oswaldi</i>	-10.7	0.051	0.5	0.061
ThI-GH	1790	<i>T. oswaldi</i>	-10.9	0.005	0.1	0.025
ThI-GH	1848	<i>T. oswaldi</i>	-11.5	0.027	0.1	0.087
ThI-GH	19135	<i>T. oswaldi</i>	-9.0	0.023	0.4	0.053
ThI-GH	2050	<i>T. oswaldi</i>	-12.9	0.007	-1.4	0.031
ThI-GH	21208	<i>T. oswaldi</i>	-8.2	0.024	-3.0	0.056
ThI-GH	2291	<i>T. oswaldi</i>	-11.8	0.059	-1.7	0.159
ThI-GH	23211	<i>T. oswaldi</i>	-11.6	0.021	0.4	0.022

Table S2. Raw data of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ isotope values with the standard deviation (S.D.) from OHQ1-GDR tooth mammal samples.

Site	Sample ID	Level	Taxa	$\delta^{13}\text{C}$ (‰) (VPDB)	S.D.	$\delta^{18}\text{O}$ (‰) (VPDB)	S.D.
OHQ1-GDR	39	Lower set	Alcelaphini	-10.63	0.012	-0.33	0.055
OHQ1-GDR	173	Lower set	Alcelaphini	-9.94	0.015	-2.58	0.040
OHQ1-GDR	36	Lower set	Alcelaphini	-12.40	0.032	-0.69	0.082
OHQ1-GDR	114	Lower set	Alcelaphini	-9.16	0.025	-2.13	0.046
OHQ1-GDR	37	Lower set	Alcelaphini	-12.75	0.022	-0.94	0.043
OHQ1-GDR	254	Lower set	Alcelaphini	-10.23	0.012	-0.70	0.032
OHQ1-GDR	97	Lower set	Alcelaphini	-9.09	0.031	-2.07	0.030
OHQ1-GDR	280	Lower set	Alcelaphini	-11.92	0.041	0.47	0.037
OHQ1-GDR	204	Lower set	Alcelaphini	-9.19	0.023	0.13	0.043
OHQ1-GDR	7308	Lower set	Alcelaphini	-9.77	0.044	-2.50	0.077
OHQ1-GDR	7595	Lower set	Alcelaphini	-12.11	0.011	0.59	0.045
OHQ1-GDR	X13	Lower set	Alcelaphini	-9.94	0.011	-1.93	0.034
OHQ1-GDR	7101	Lower set	Alcelaphini	-12.69	0.028	1.49	0.041
OHQ1-GDR	8311	Lower set	Alcelaphini	-12.41	0.009	0.13	0.032
OHQ1-GDR	7099	Lower set	Alcelaphini	-12.20	0.011	0.07	0.077
OHQ1-GDR	7660	Lower set	Alcelaphini	-10.17	0.016	-1.96	0.018
OHQ1-GDR	7568	Lower set	Camelidae	-5.05	0.024	-3.60	0.015
OHQ1-GDR	26	Lower set	Camelidae	-9.57	0.014	-2.38	0.043
OHQ1-GDR	87B	Lower set	Camelidae	-9.85	0.008	-2.58	0.011
OHQ1-GDR	87A	Lower set	Camelidae	-6.28	0.004	-4.00	0.020
OHQ1-GDR	91	Lower set	<i>E. cf. mauritanicus</i>	-10.62	0.031	-2.82	0.030
OHQ1-GDR	5557	Lower set	<i>E. cf. mauritanicus</i>	-10.74	0.040	-1.65	0.076
OHQ1-GDR	33	Lower set	<i>E. cf. mauritanicus</i>	-10.57	0.006	-1.64	0.033
OHQ1-GDR	22	Lower set	<i>E. cf. mauritanicus</i>	-10.64	0.010	-2.08	0.057
OHQ1-GDR	105	Lower set	<i>E. cf. mauritanicus</i>	-10.64	0.035	-1.35	0.098
OHQ1-GDR	62	Lower set	<i>E. cf. mauritanicus</i>	-10.35	0.034	-0.93	0.066
OHQ1-GDR	68	Lower set	<i>E. cf. mauritanicus</i>	-10.31	0.037	-0.34	0.050
OHQ1-GDR	171	Lower set	<i>E. cf. mauritanicus</i>	-12.33	0.032	-0.85	0.063
OHQ1-GDR	122	Upper set	<i>G. cf. atlantica</i>	-12.18	0.013	2.61	0.024
OHQ1-GDR	155	Upper set	<i>G. cf. atlantica</i>	-14.50	0.060	-1.46	0.088
OHQ1-GDR	228	Upper set	<i>G. cf. atlantica</i>	-13.37	0.032	-1.74	0.022
OHQ1-GDR	5425	Upper set	<i>G. cf. atlantica</i>	-10.00	0.008	-1.64	0.040
OHQ1-GDR	5234	Upper set	<i>G. cf. atlantica</i>	-11.45	0.013	-1.43	0.029
OHQ1-GDR	5971	Upper set	<i>G. cf. atlantica</i>	-11.18	0.026	-3.25	0.012
OHQ1-GDR	X11	Upper set	<i>G. cf. atlantica</i>	-13.08	0.035	-1.79	0.051
OHQ1-GDR	6322	Upper set	<i>G. cf. atlantica</i>	-11.05	0.055	-1.45	0.042
OHQ1-GDR	6208	Upper set	<i>G. cf. atlantica</i>	-11.55	0.026	-0.27	0.091
OHQ1-GDR	8	Lower set	<i>G. cf. atlantica</i>	-12.96	0.037	-1.21	0.034
OHQ1-GDR	50	Lower set	<i>G. cf. atlantica</i>	-12.17	0.008	-2.48	0.022
OHQ1-GDR	59	Lower set	<i>G. cf. atlantica</i>	-11.60	0.052	0.30	0.084

OHQ1-GDR	19	Lower set	<i>G. cf. atlantica</i>	-10.68	0.019	-0.09	0.060
OHQ1-GDR	56	Lower set	<i>G. cf. atlantica</i>	-11.87	0.003	-1.93	0.053
OHQ1-GDR	137	Lower set	<i>G. cf. atlantica</i>	-13.34	0.016	2.59	0.054
OHQ1-GDR	57	Lower set	<i>G. cf. atlantica</i>	-12.51	0.015	-1.04	0.028
OHQ1-GDR	58	Lower set	<i>G. cf. atlantica</i>	-10.93	0.040	-1.66	0.087
OHQ1-GDR	17	Lower set	<i>G. cf. atlantica</i>	-10.83	0.020	-2.58	0.054
OHQ1-GDR	6809	Lower set	<i>G. cf. atlantica</i>	-11.86	0.019	-0.65	0.022
OHQ1-GDR	6810	Lower set	<i>G. cf. atlantica</i>	-11.41	0.015	-1.76	0.040
OHQ1-GDR	8386	Lower set	<i>G. cf. atlantica</i>	-11.97	0.006	-0.01	0.062
OHQ1-GDR	7140	Lower set	<i>G. cf. atlantica</i>	-10.88	0.006	-0.51	0.036
OHQ1-GDR	7584	Lower set	<i>G. cf. atlantica</i>	-12.23	0.010	0.72	0.083
OHQ1-GDR	8264	Lower set	<i>G. cf. atlantica</i>	-14.02	0.026	3.18	0.026
OHQ1-GDR	34	Upper set	<i>C. mauritanicum</i>	-9.38	0.004	-2.85	0.069
OHQ1-GDR	5355	Upper set	<i>C. mauritanicum</i>	-11.95	0.029	-0.91	0.031
OHQ1-GDR	5428	Upper set	<i>C. mauritanicum</i>	-11.29	0.006	-1.84	0.027
OHQ1-GDR	X10	Upper set	<i>C. mauritanicum</i>	-10.43	0.026	-2.89	0.043
OHQ1-GDR	5237	Upper set	<i>C. mauritanicum</i>	-9.48	0.017	-2.98	0.016
OHQ1-GDR	17	Lower set	<i>C. mauritanicum</i>	-10.91	0.016	-2.19	0.056
OHQ1-GDR	150	Lower set	<i>C. mauritanicum</i>	-11.14	0.031	0.50	0.093
OHQ1-GDR	X12	Lower set	<i>C. mauritanicum</i>	-10.37	0.017	-2.54	0.043
OHQ1-GDR	66	Lower set	<i>C. mauritanicum</i>	-12.09	0.026	-1.98	0.028
OHQ1-GDR	167	Lower set	<i>C. mauritanicum</i>	-11.32	0.011	-2.43	0.046
OHQ1-GDR	6908	Lower set	<i>C. mauritanicum</i>	-10.32	0.034	-1.35	0.038
OHQ1-GDR	8106	Lower set	<i>C. mauritanicum</i>	-9.73	0.028	-3.21	0.093
OHQ1-GDR	7042	Lower set	<i>C. mauritanicum</i>	-11.84	0.030	-1.95	0.033
OHQ1-GDR	7448	Lower set	<i>C. mauritanicum</i>	-10.51	0.024	-1.34	0.030
OHQ1-GDR	7425	Lower set	<i>C. mauritanicum</i>	-10.75	0.022	-1.20	0.045
OHQ1-GDR	7039	Lower set	<i>C. mauritanicum</i>	-11.52	0.022	-2.21	0.075
OHQ1-GDR	7180	Lower set	<i>C. mauritanicum</i>	-11.19	0.014	-2.53	0.044
OHQ1-GDR	7675	Lower set	<i>C. mauritanicum</i>	-9.73	0.040	-2.22	0.045
OHQ1-GDR	7569	Lower set	<i>C. mauritanicum</i>	-11.29	0.012	-2.11	0.065
OHQ1-GDR	8063	Lower set	<i>C. mauritanicum</i>	-10.97	0.025	-2.55	0.053
OHQ1-GDR	6	Lower set	<i>C. mauritanicum</i>	-11.48	0.026	-2.04	0.101
OHQ1-GDR	21	Lower set	<i>C. mauritanicum</i>	-10.98	0.010	-1.31	0.071
OHQ1-GDR	6	Lower set	<i>C. mauritanicum</i>	-10.52	0.010	-2.25	0.078
OHQ1-GDR	16	Lower set	<i>C. mauritanicum</i>	-12.33	0.013	-0.39	0.082
OHQ1-GDR	8355A	Lower set	<i>C. mauritanicum</i>	-10.90	0.042	-2.07	0.065
OHQ1-GDR	31	Lower set	<i>C. mauritanicum</i>	-11.55	0.030	-1.57	0.039
OHQ1-GDR	?9	Lower set	<i>C. mauritanicum</i>	-11.33	0.007	-2.31	0.078
OHQ1-GDR	6	Lower set	<i>C. mauritanicum</i>	-10.15	0.024	-0.67	0.014
OHQ1-GDR	101	Lower set	<i>C. mauritanicum</i>	-11.44	0.024	-2.19	0.032
OHQ1-GDR	17	Lower set	<i>C. mauritanicum</i>	-11.09	0.031	-2.90	0.044
OHQ1-GDR	157	Lower set	<i>T. oswaldi</i>	-12.22	0.028	0.18	0.055

Table S3. Raw data of $\delta^{13}\text{C}$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}\text{C}_{\text{diet-meq}}$ (‰) and Mean Annual Precipitation (MAP - mm/yr) from ThI-GH.

Site	Sample ID	Species	$\delta^{13}\text{C}$ (‰) (VPDB)	Body Mass	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}\text{C}_{\text{diet-meq}}$ (‰)	MAP (mm/yr)
ThI-GH	10051	Alcelaphini	-9.87	200	13.2	-24.57	-3
ThI-GH	219	Alcelaphini	-10.72	200	13.2	-25.42	121
ThI-GH	10222	Alcelaphini	-8.09	200	13.2	-22.79	-157
ThI-GH	11385	Alcelaphini	-8.20	200	13.2	-22.90	-150
ThI-GH	10325	Alcelaphini	-10.62	200	13.2	-25.32	104
ThI-GH	224	Alcelaphini	-10.81	200	13.2	-25.51	137
ThI-GH	224B	Alcelaphini	-10.31	200	13.2	-25.01	56
ThI-GH	223	Alcelaphini	-11.90	200	13.2	-26.60	383
ThI-GH	10364	Alcelaphini	-8.75	200	13.2	-23.45	-113
ThI-GH	10350	Alcelaphini	-10.54	200	13.2	-25.24	90
ThI-GH	222B	Alcelaphini	-10.99	200	13.2	-25.69	169
ThI-GH	12139	Alcelaphini	-9.84	200	13.2	-24.54	-7
ThI-GH	205	<i>E. cf. mauritanicus</i>	-11.82	250	13.3	-26.62	387
ThI-GH	20	<i>E. cf. mauritanicus</i>	-11.19	250	13.3	-25.99	231
ThI-GH	48	<i>E. cf. mauritanicus</i>	-11.26	250	13.3	-26.06	248
ThI-GH	1	<i>E. cf. mauritanicus</i>	-12.81	250	13.3	-27.61	733
ThI-GH	10324	<i>E. cf. mauritanicus</i>	-10.31	250	13.3	-25.11	71
ThI-GH	221	<i>G. cf. atlantica</i>	-12.04	30	12.4	-25.91	215
ThI-GH	221B	<i>G. cf. atlantica</i>	-12.10	30	12.4	-25.97	228
ThI-GH	9	<i>G. cf. atlantica</i>	-8.85	30	12.4	-22.73	-161
ThI-GH	220	<i>G. cf. atlantica</i>	-12.23	30	12.4	-26.10	257
ThI-GH	220B	<i>G. cf. atlantica</i>	-12.23	30	12.4	-26.10	257
ThI-GH	66	<i>G. cf. atlantica</i>	-12.29	30	12.4	-26.17	271
ThI-GH	11175	<i>G. cf. atlantica</i>	-10.28	30	12.4	-24.15	-50
ThI-GH	1203	<i>G. cf. atlantica</i>	-11.06	30	12.4	-24.94	45
ThI-GH	1325	<i>G. cf. atlantica</i>	-12.79	30	12.4	-26.66	401
ThI-GH	30	<i>G. cf. atlantica</i>	-13.02	30	12.4	-26.89	469
ThI-GH	12311	<i>G. cf. atlantica</i>	-9.40	30	12.4	-23.28	-125
ThI-GH	226	<i>G. cf. atlantica</i>	-14.52	30	12.4	-28.40	1129
ThI-GH	10599	<i>G. cf. atlantica</i>	-10.23	30	12.4	-24.11	-55
ThI-GH	11078	<i>G. cf. atlantica</i>	-11.79	30	12.4	-25.66	165
ThI-GH	4	<i>G. cf. atlantica</i>	-11.57	30	12.4	-25.45	125
ThI-GH	204	<i>C. mauritanicum</i>	-11.87	1800	14.2	-27.60	728
ThI-GH	201	<i>C. mauritanicum</i>	-12.65	1800	14.2	-28.37	1112
ThI-GH	6	<i>C. mauritanicum</i>	-12.42	1800	14.2	-28.14	985
ThI-GH	11	<i>C. mauritanicum</i>	-12.66	1800	14.2	-28.38	1117
ThI-GH	200	<i>C. mauritanicum</i>	-12.69	1800	14.2	-28.42	1139
ThI-GH	203	<i>C. mauritanicum</i>	-11.75	1800	14.2	-27.47	675

ThI-GH	202	<i>C. mauritanicum</i>	-13.35	1800	14.2	-29.07	1582
ThI-GH	20	<i>C. mauritanicum</i>	-10.56	1800	14.2	-26.29	300
ThI-GH	12174	<i>C. mauritanicum</i>	-11.89	1800	14.2	-27.61	736
ThI-GH	15- 10276	<i>C. mauritanicum</i>	-10.02	1800	14.2	-25.74	180
ThI-GH	12082	<i>C. mauritanicum</i>	-10.51	1800	14.2	-26.24	288
ThI-GH	10218	<i>C. mauritanicum</i>	-11.29	1800	14.2	-27.01	510
ThI-GH	206	<i>P. africanus</i>	-11.86	90	12.8	-26.21	281
ThI-GH	10576	<i>P. africanus</i>	-12.17	90	12.8	-26.51	359
ThI-GH	209	<i>T. oswaldi</i>	-11.66	60	12.7	-25.83	197
ThI-GH	1517	<i>T. oswaldi</i>	-11.32	60	12.7	-25.49	132
ThI-GH	1628	<i>T. oswaldi</i>	-10.68	60	12.7	-24.85	33
ThI-GH	1790	<i>T. oswaldi</i>	-10.92	60	12.7	-25.09	67
ThI-GH	1848	<i>T. oswaldi</i>	-11.52	60	12.7	-25.69	170
ThI-GH	19135	<i>T. oswaldi</i>	-9.00	60	12.7	-23.17	-133
ThI-GH	2050	<i>T. oswaldi</i>	-12.86	60	12.7	-27.03	516
ThI-GH	21208	<i>T. oswaldi</i>	-8.21	60	12.7	-22.38	-179
ThI-GH	2291	<i>T. oswaldi</i>	-11.85	60	12.7	-26.02	238
ThI-GH	23211	<i>T. oswaldi</i>	-11.62	60	12.7	-25.79	190

Table S4. Raw data of $\delta^{13}\text{C}$ (‰), Body Mass (Kg), $\epsilon^*_{\text{enamel-diet}}$ (‰), $\delta^{13}\text{C}_{\text{diet-meq}}$ (‰) and Mean Annual Precipitation (MAP - mm/yr) from OHQ1-GDR.

Site	Sample ID	Species	$\delta^{13}\text{C}$ (‰) (VPDB)	Body Mass	$\epsilon^*_{\text{enamel-diet}}$ (‰)	$\delta^{13}\text{C}_{\text{diet-meq}}$ (‰)	MAP (mm/yr)
OHQ1-GDR	39	Alcelaphini	-10.63	200	13.2	-25.33	106
OHQ1-GDR	173	Alcelaphini	-9.94	200	13.2	-24.64	5
OHQ1-GDR	36	Alcelaphini	-12.40	200	13.2	-27.10	539
OHQ1-GDR	114	Alcelaphini	-9.16	200	13.2	-23.86	-78
OHQ1-GDR	37	Alcelaphini	-12.75	200	13.2	-27.45	667
OHQ1-GDR	254	Alcelaphini	-10.23	200	13.2	-24.93	44
OHQ1-GDR	97	Alcelaphini	-9.09	200	13.2	-23.79	-85
OHQ1-GDR	280	Alcelaphini	-11.92	200	13.2	-26.62	388
OHQ1-GDR	204	Alcelaphini	-9.19	200	13.2	-23.89	-76
OHQ1-GDR	7308	Alcelaphini	-9.77	200	13.2	-24.46	-16
OHQ1-GDR	7595	Alcelaphini	-12.11	200	13.2	-26.81	445
OHQ1-GDR	X13	Alcelaphini	-9.94	200	13.2	-24.64	5
OHQ1-GDR	7101	Alcelaphini	-12.69	200	13.2	-27.39	644
OHQ1-GDR	8311	Alcelaphini	-12.41	200	13.2	-27.11	541
OHQ1-GDR	7099	Alcelaphini	-12.20	200	13.2	-26.90	473
OHQ1-GDR	7660	Alcelaphini	-10.17	200	13.2	-24.87	35
OHQ1-GDR	7568	Camelidae	-5.05	800	13.8	-20.39	-247
OHQ1-GDR	26	Camelidae	-9.57	800	13.8	-24.90	40
OHQ1-GDR	87B	Camelidae	-9.85	800	13.8	-25.19	83
OHQ1-GDR	87A	Camelidae	-6.28	800	13.8	-21.61	-212
OHQ1-GDR	91	<i>E. cf. mauritanicus</i>	-10.62	250	13.3	-25.41	120
OHQ1-GDR	5557	<i>E. cf. mauritanicus</i>	-10.74	250	13.3	-25.54	142
OHQ1-GDR	33	<i>E. cf. mauritanicus</i>	-10.57	250	13.3	-25.37	112
OHQ1-GDR	22	<i>E. cf. mauritanicus</i>	-10.64	250	13.3	-25.44	123
OHQ1-GDR	105	<i>E. cf. mauritanicus</i>	-10.64	250	13.3	-25.44	124
OHQ1-GDR	62	<i>E. cf. mauritanicus</i>	-10.35	250	13.3	-25.15	77
OHQ1-GDR	68	<i>E. cf. mauritanicus</i>	-10.31	250	13.3	-25.11	70
OHQ1-GDR	171	<i>E. cf. mauritanicus</i>	-12.33	250	13.3	-27.13	548
OHQ1-GDR	8	<i>G. cf. atlantica</i>	-12.96	30	12.4	-26.83	451
OHQ1-GDR	50	<i>G. cf. atlantica</i>	-12.17	30	12.4	-26.05	244
OHQ1-GDR	59	<i>G. cf. atlantica</i>	-11.60	30	12.4	-25.47	130
OHQ1-GDR	19	<i>G. cf. atlantica</i>	-10.68	30	12.4	-24.55	-5
OHQ1-GDR	56	<i>G. cf. atlantica</i>	-11.87	30	12.4	-25.75	181
OHQ1-GDR	137	<i>G. cf. atlantica</i>	-13.34	30	12.4	-27.21	578
OHQ1-GDR	57	<i>G. cf. atlantica</i>	-12.51	30	12.4	-26.39	326
OHQ1-GDR	58	<i>G. cf. atlantica</i>	-10.93	30	12.4	-24.80	26
OHQ1-GDR	17	<i>G. cf. atlantica</i>	-10.83	30	12.4	-24.70	13
OHQ1-GDR	6809	<i>G. cf. atlantica</i>	-11.86	30	12.4	-25.73	178
OHQ1-GDR	6810	<i>G. cf. atlantica</i>	-11.41	30	12.4	-25.28	97

OHQ1-GDR	8386	<i>G. cf. atlantica</i>	-11.97	30	12.4	-25.85	201
OHQ1-GDR	7140	<i>G. cf. atlantica</i>	-10.88	30	12.4	-24.76	21
OHQ1-GDR	7584	<i>G. cf. atlantica</i>	-12.23	30	12.4	-26.10	257
OHQ1-GDR	8264	<i>G. cf. atlantica</i>	-14.02	30	12.4	-27.90	862
OHQ1-GDR	17	<i>C. mauritanicum</i>	-10.91	1800	14.2	-26.63	392
OHQ1-GDR	150	<i>C. mauritanicum</i>	-11.14	1800	14.2	-26.86	459
OHQ1-GDR	X12	<i>C. mauritanicum</i>	-10.37	1800	14.2	-26.09	254
OHQ1-GDR	66	<i>C. mauritanicum</i>	-12.09	1800	14.2	-27.81	823
OHQ1-GDR	167	<i>C. mauritanicum</i>	-11.32	1800	14.2	-27.04	519
OHQ1-GDR	6908	<i>C. mauritanicum</i>	-10.32	1800	14.2	-26.05	244
OHQ1-GDR	8106	<i>C. mauritanicum</i>	-9.73	1800	14.2	-25.45	127
OHQ1-GDR	7042	<i>C. mauritanicum</i>	-11.84	1800	14.2	-27.56	712
OHQ1-GDR	7448	<i>C. mauritanicum</i>	-10.51	1800	14.2	-26.23	286
OHQ1-GDR	7425	<i>C. mauritanicum</i>	-10.75	1800	14.2	-26.48	349
OHQ1-GDR	7039	<i>C. mauritanicum</i>	-11.52	1800	14.2	-27.24	589
OHQ1-GDR	7180	<i>C. mauritanicum</i>	-11.19	1800	14.2	-26.91	476
OHQ1-GDR	7675	<i>C. mauritanicum</i>	-9.73	1800	14.2	-25.46	127
OHQ1-GDR	7569	<i>C. mauritanicum</i>	-11.29	1800	14.2	-27.01	508
OHQ1-GDR	8063	<i>C. mauritanicum</i>	-10.97	1800	14.2	-26.70	410
OHQ1-GDR	6	<i>C. mauritanicum</i>	-11.48	1800	14.2	-27.20	573
OHQ1-GDR	21	<i>C. mauritanicum</i>	-10.98	1800	14.2	-26.70	413
OHQ1-GDR	6	<i>C. mauritanicum</i>	-10.52	1800	14.2	-26.24	289
OHQ1-GDR	16	<i>C. mauritanicum</i>	-12.33	1800	14.2	-28.05	937
OHQ1-GDR	8355A	<i>C. mauritanicum</i>	-10.90	1800	14.2	-26.62	388
OHQ1-GDR	31	<i>C. mauritanicum</i>	-11.55	1800	14.2	-27.27	599
OHQ1-GDR	?9	<i>C. mauritanicum</i>	-11.33	1800	14.2	-27.06	523
OHQ1-GDR	6	<i>C. mauritanicum</i>	-10.15	1800	14.2	-25.87	206
OHQ1-GDR	101	<i>C. mauritanicum</i>	-11.44	1800	14.2	-27.16	559
OHQ1-GDR	17	<i>C. mauritanicum</i>	-11.09	1800	14.2	-26.81	445
OHQ1-GDR	157	<i>T. oswaldi</i>	-12.22	60	12.7	-26.39	326

Table S5. Raw dental microwear and mesowear data from all taxa analysed from ThI-GH. Abbreviations: NTS = number of total scratches, NTP = number of total pits, SWS = scratch width score, PP = presence of puncture pits, HC = presence of hypercoarse scratches, LP = presence of large pits and G = presence of gouges.

Site	Sample	Species	Dental Microwear								Mesowear
			NTS	NTP	SWS	PP	HC	LP	G	XC	
ThI-GH	219	Alcelaphini	18.5	26	1	1	0	1	1	0	2
ThI-GH	10325	Alcelaphini	-	-	-	-	-	-	-	-	2
ThI-GH	10350	Alcelaphini	21	29.5	1	0	0	1	1	0	-
ThI-GH	10222	Alcelaphini	18.5	29.5	1	1	0	1	1	0	-
ThI-GH	10051	Alcelaphini	19	28.5	1	1	0	1	1	0	-
ThI-GH	10364	Alcelaphini	17.5	30.5	1	1	0	1	1	0	3
ThI-GH	11254	Alcelaphini	19	20	2	1	0	1	1	0	2
ThI-GH	11385	Alcelaphini	18	26.5	1	1	0	1	1	0	2
ThI-GH	10337	Alcelaphini	21	24	1	1	0	0	0	0	-
ThI-GH	223	Alcelaphini	18	20	2	0	0	1	1	0	2
ThI-GH	224	Alcelaphini	-	-	-	-	-	-	-	-	2
ThI-GH	224B	Alcelaphini	-	-	-	-	-	-	-	-	1
ThI-GH	11	Alcelaphini	23.5	21	1	1	0	1	1	0	2
ThI-GH	222	Alcelaphini	21	22.5	1	1	0	1	1	0	-
ThI-GH	79	Alcelaphini	22	18	1	0	0	1	1	0	-
ThI-GH	10453	Alcelaphini	24.5	38.5	1	1	0	1	1	0	-
ThI-GH	11174	Alcelaphini	-	-	-	-	-	-	-	-	2
ThI-GH	12	Alcelaphini	-	-	-	-	-	-	-	-	2
ThI-GH	10643	Alcelaphini	19	31	1	1	0	1	1	0	3
ThI-GH	10082	Alcelaphini	17	25	1	1	0	1	1	1	2
ThI-GH	78	Alcelaphini	17	20	1	1	0	1	1	0	2
ThI-GH	11264	Alcelaphini	18.5	23.5	1	1	0	1	1	0	1
ThI-GH	48	<i>E. cf. mauritanicus</i>	18	25.5	1	1	0	1	1	0	-
ThI-GH	21	<i>E. cf. mauritanicus</i>	-	-	-	-	-	-	-	-	5
ThI-GH	1	<i>E. cf. mauritanicus</i>	20.5	28	1	1	0	1	1	0	5
ThI-GH	10324	<i>E. cf. mauritanicus</i>	18	28	1	1	0	1	1	0	4
ThI-GH	20	<i>E. cf. mauritanicus</i>	24.5	20.5	0	1	0	1	0	1	6
ThI-GH	206	Suidae	21	26	1	0	0	0	-	1	-
ThI-GH	10576	Suidae	20.5	22.5	1	1	0	1	-	1	-
ThI-GH	225	<i>G. cf. atlantica</i>	11	32.5	1	0	0	1	1	0	1
ThI-GH	221	<i>G. cf. atlantica</i>	10	40	1	1	1	1	1	0	1
ThI-GH	221B	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
ThI-GH	10325	<i>G. cf. atlantica</i>	8	38	2	1	0	1	1	0	1
ThI-GH	11345	<i>G. cf. atlantica</i>	8	30	2	1	0	1	1	0	-
ThI-GH	226	<i>G. cf. atlantica</i>	8	34	2	1	0	1	1	0	2
ThI-GH	66	<i>G. cf. atlantica</i>	9	37	1	1	0	1	1	0	1
ThI-GH	11078	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1

ThI-GH	10790	<i>G. cf. atlantica</i>	12.5	36	1	1	0	1	1	0	2
ThI-GH	10258	<i>G. cf. atlantica</i>	10	34	1	1	0	1	1	0	2
ThI-GH	4	<i>G. cf. atlantica</i>	8	38	2	1	0	1	1	0	1
ThI-GH	12311	<i>G. cf. atlantica</i>	9	33	1	1	0	1	1	0	1
ThI-GH	11175	<i>G. cf. atlantica</i>	9	34.5	2	1	0	1	1	0	2
ThI-GH	10215	<i>G. cf. atlantica</i>	10.5	31	1	1	0	1	1	0	2
ThI-GH	10898	<i>G. cf. atlantica</i>	11.5	34	1	1	0	1	1	1	1
ThI-GH	436	<i>G. cf. atlantica</i>	9	34	1	1	0	1	1	1	-
ThI-GH	30	<i>G. cf. atlantica</i>	9	34	1	1	0	1	1	0	1
ThI-GH	11027	<i>G. cf. atlantica</i>	7	45	1	1	0	1	1	0	1
ThI-GH	12503	<i>G. cf. atlantica</i>	9	32	2	1	0	1	1	0	1
ThI-GH	9	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
ThI-GH	11	<i>C. mauritanicum</i>	16.5	22.5	1	1	0	0	-	1	-
ThI-GH	204	<i>C. mauritanicum</i>	22	17	1	1	0	1	-	1	-
ThI-GH	20	<i>C. mauritanicum</i>	21	19.5	1	1	0	1	-	1	-
ThI-GH	202	<i>C. mauritanicum</i>	22.5	24.5	1	1	0	1	-	1	-
ThI-GH	6	<i>C. mauritanicum</i>	17.5	25.5	1	1	0	1	-	1	-
ThI-GH	201	<i>C. mauritanicum</i>	16.5	27.5	1	1	0	1	-	1	-
ThI-GH	10218	<i>C. mauritanicum</i>	24.5	25	1	1	0	1	-	1	-
ThI-GH	12082	<i>C. mauritanicum</i>	17	22	1	0	0	1	-	1	-
ThI-GH	10276	<i>C. mauritanicum</i>	21	24	1	1	0	0	-	1	-

Table S6. Raw dental microwear and mesowear data from all taxa analysed from OHQ1-GDR. Abbreviations: NTS = number of total scratches, NTP = number of total pits, SWS = scratch width score, PP = presence of puncture pits, HC = presence of hypercoarse scratches, LP = presence of large pits and G = presence of gouges. * = samples from the Upper set.

Site	Sample	Species	Dental Microwear								Mesowear
			NTS	NTP	SWS	PP	HC	LP	G	XC	
OHQ1-GDR	5812	Alcelaphini	17.5	27.5	1	1	0	1	1	0	0
OHQ1-GDR	280	Alcelaphini	22	26	1	1	0	1	1	1	0
OHQ1-GDR	39	Alcelaphini	22	29	1	1	0	1	1	0	2
OHQ1-GDR	97	Alcelaphini	19.5	28	1	1	0	1	1	0	-
OHQ1-GDR	173	Alcelaphini	-	-	-	-	-	-	-	-	2
OHQ1-GDR	37	Alcelaphini	21	26	1	1	0	1	1	0	1
OHQ1-GDR	204	Alcelaphini	19.5	34	1	0	0	1	0	0	3
OHQ1-GDR	114	Alcelaphini	20	26.5	1	1	0	1	1	0	1
OHQ1-GDR	254	Alcelaphini	17	27	1	1	0	1	1	0	2
OHQ1-GDR	36	Alcelaphini	-	-	-	-	-	-	-	-	2
OHQ1-GDR	6208	Alcelaphini	22	31	1	1	0	0	1	1	-
OHQ1-GDR	6983	Alcelaphini	-	-	-	-	-	-	-	-	2
OHQ1-GDR	8311	Alcelaphini	20	23	1	1	0	1	1	0	0
OHQ1-GDR	6903	Alcelaphini	24	26.5	1	1	0	1	1	0	-
OHQ1-GDR	7660	Alcelaphini	21.5	28.5	0	1	0	1	1	1	2
OHQ1-GDR	7680	Alcelaphini	19.5	30.5	0	1	0	1	1	0	-
OHQ1-GDR	6842	Alcelaphini	20.5	34.5	1	1	0	1	1	0	-
OHQ1-GDR	7099	Alcelaphini	20.5	31.5	1	1	0	1	1	1	1
OHQ1-GDR	7595	Alcelaphini	26	28	1	1	0	1	1	1	2
OHQ1-GDR	X13	Alcelaphini	20.5	31	1	1	0	1	1	0	2
OHQ1-GDR	7101	Alcelaphini	17	28.5	1	1	0	1	1	1	1
OHQ1-GDR	8368	Alcelaphini	22	32.5	1	1	0	1	1	0	-
OHQ1-GDR	7679	Alcelaphini	20.5	31.5	1	0	0	1	1	0	1
OHQ1-GDR	7308	Alcelaphini	23	32.5	1	1	0	1	1	0	1
OHQ1-GDR	13	Alcelaphini	18	25	1	1	0	1	1	0	-
OHQ1-GDR	7568	Camelidae	13	34.5	1	1	0	1	1	1	-
OHQ1-GDR	26	Camelidae	18.5	33.5	1	1	0	1	1	0	4
OHQ1-GDR	87a	Camelidae	-	-	-	-	-	-	-	-	4
OHQ1-GDR	87b	Camelidae	12	29	2	1	0	1	1	0	4
OHQ1-GDR	91	<i>E. cf. mauritanicus</i>	22	24	1	1	0	0	0	1	-
OHQ1-GDR	22	<i>E. cf. mauritanicus</i>	-	-	-	-	-	-	-	-	3
OHQ1-GDR	5557	<i>E. cf. mauritanicus</i>	22	26	1	1	0	0	0	1	-
OHQ1-GDR	62	<i>E. cf. mauritanicus</i>	31	25	1	1	0	0	1	1	3
OHQ1-GDR	171	<i>E. cf. mauritanicus</i>	22.5	27	1	1	0	1	1	1	-
OHQ1-GDR	105	<i>E. cf. mauritanicus</i>	28	29.5	1	1	0	1	1	0	-
OHQ1-GDR	68	<i>E. cf. mauritanicus</i>	24	25	1	0	0	1	1	0	3

OHQ1-GDR	155	<i>G. cf. atlantica</i> *	-	-	-	-	-	-	-	-	1
OHQ1-GDR	5234	<i>G. cf. atlantica</i> *	10	43	1	1	1	1	-	0	1
OHQ1-GDR	5425	<i>G. cf. atlantica</i> *	10	33	1	1	1	1	-	0	1
OHQ1-GDR	X11	<i>G. cf. atlantica</i> *	8	30.5	1	0	0	1	-	1	-
OHQ1-GDR	6322	<i>G. cf. atlantica</i> *	9	37.5	1	1	0	1	-	0	1
OHQ1-GDR	6208	<i>G. cf. atlantica</i> *	10.5	40.5	0	1	0	1	-	0	-
OHQ1-GDR	5971	<i>G. cf. atlantica</i> *	14	36	2	0	0	1	-	0	-
OHQ1-GDR	59	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
OHQ1-GDR	50	<i>G. cf. atlantica</i>	9	33	1	1	0	1	1	0	2
OHQ1-GDR	57	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
OHQ1-GDR	19	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
OHQ1-GDR	8	<i>G. cf. atlantica</i>	7	35	1	1	0	1	1	0	2
OHQ1-GDR	71	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	2
OHQ1-GDR	56	<i>G. cf. atlantica</i>	-	-	-	-	-	-	-	-	1
OHQ1-GDR	137	<i>G. cf. atlantica</i>	9.5	36.5	1	1	0	1	1	1	1
OHQ1-GDR	8386	<i>G. cf. atlantica</i>	9.5	30.5	1	1	0	1	1	0	2
OHQ1-GDR	6810	<i>G. cf. atlantica</i>	8	36	2	1	0	1	1	0	1
OHQ1-GDR	7140	<i>G. cf. atlantica</i>	9	39	1	1	0	1	1	0	-
OHQ1-GDR	6809	<i>G. cf. atlantica</i>	11	37	1	1	0	1	1	0	1
OHQ1-GDR	8264	<i>G. cf. atlantica</i>	8	42	1	1	0	1	1	0	-
OHQ1-GDR	7584	<i>G. cf. atlantica</i>	10.5	42	2	1	0	1	1	1	2
OHQ1-GDR	58	<i>G. cf. atlantica</i>	12	40	1	1	0	1	1	1	1
OHQ1-GDR	17	<i>G. cf. atlantica</i>	12.5	41	1	1	0	1	1	0	1
OHQ1-GDR	34	<i>C. mauritanicum</i> *	23.5	25.5	1	1	0	1	1	1	-
OHQ1-GDR	5355	<i>C. mauritanicum</i> *	21	29.5	1	0	0	1	1	1	-
OHQ1-GDR	X10	<i>C. mauritanicum</i> *	21	35.5	1	1	0	1	1	1	-
OHQ1-GDR	X12	<i>C. mauritanicum</i>	28.5	16.5	1	1	0	0	1	1	4
OHQ1-GDR	66	<i>C. mauritanicum</i>	21	25.5	1	1	0	1	1	1	-
OHQ1-GDR	17	<i>C. mauritanicum</i>	21.5	28.5	1	1	0	1	1	1	-
OHQ1-GDR	7425	<i>C. mauritanicum</i>	20.5	27	1	1	0	1	1	1	-
OHQ1-GDR	7180	<i>C. mauritanicum</i>	23.5	26	1	1	0	1	1	1	5
OHQ1-GDR	7675	<i>C. mauritanicum</i>	27.5	28.5	1	1	1	1	1	1	-
OHQ1-GDR	8106	<i>C. mauritanicum</i>	26	28.5	1	1	1	1	1	1	4
OHQ1-GDR	7448	<i>C. mauritanicum</i>	24.5	25.5	1	1	0	1	1	1	-
OHQ1-GDR	6908	<i>C. mauritanicum</i>	27.5	25	1	1	0	1	1	1	-
OHQ1-GDR	8063	<i>C. mauritanicum</i>	22	26	1	0	0	1	0	1	-
OHQ1-GDR	7042	<i>C. mauritanicum</i>	27	27	1	1	1	1	1	1	-
OHQ1-GDR	7569	<i>C. mauritanicum</i>	28	27	1	1	0	1	1	1	5
OHQ1-GDR	7039	<i>C. mauritanicum</i>	23	29	0	1	0	1	1	1	
OHQ1-GDR	21	<i>C. mauritanicum</i>	27	25	1	1	1	1	1	1	4
OHQ1-GDR	6	<i>C. mauritanicum</i>	28.5	19	1	1	0	1	1	1	4
OHQ1-GDR	6	<i>C. mauritanicum</i>	24.5	25.5	1	1	0	1	1	1	5
OHQ1-GDR	31	<i>C. mauritanicum</i>	22.5	31.5	1	1	0	0	1	1	5

OHQ1-GDR	6	<i>C. mauritanicum</i>	29	22.5	1	1	0	0	1	1	5
OHQ1-GDR	?9	<i>C. mauritanicum</i>	21	36.5	1	1	0	1	0	1	3
OHQ1-GDR	17	<i>C. mauritanicum</i>	24	34.5	1	1	0	1	1	0	3
OHQ1-GDR	16	<i>C. mauritanicum</i>	-	-	-	-	-	-	-	-	3
OHQ1-GDR	1 o 101	<i>C. mauritanicum</i>	29	26.5	1	1	0	0	1	1	-
OHQ1-GDR	8355A	<i>C. mauritanicum</i>	25.5	22.5	1	1	0	0	1	0	6
OHQ1-GDR	8355B	<i>C. mauritanicum</i>	-	-	-	-	-	-	-	-	5
OHQ1-GDR	8355C	<i>C. mauritanicum</i>	-	-	-	-	-	-	-	-	5
OHQ1-GDR	XXX	<i>C. mauritanicum</i>	20	20	1	1	0	1	1	1	-

Supplementary information

Ecological context of *Theropithecus oswaldi* from the early Middle Pleistocene site of Grotte à Hominidés at Thomas Quarry I through dental microwear analysis (Casablanca, Morocco)

Laura M. Martínez^{a, b *}, Iván Ramírez-Pedraza^{c, d *}, Ferran Estebarez-Sánchez^b, Florent Rivals^{c, d, e}, Carlos Tornero^{f, c}, Luis Hidalgo-Trujillo^{a, b}, Juan José Ibáñez^g, Camille Daujeard^h, Denis Geraadsⁱ, Rosalia Gallotti^{j, k}, Jean Paul Raynal^{k, l}, David Lefèvre^j, Abderrahim Mohib^{l, m}

^aDepartament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Secció de Zoologia i Antropologia Biològica, Universitat de Barcelona, Barcelona, Spain,

^bInstitut d'Arqueologia de la Universitat de Barcelona, Barcelona, Spain

^cInstitut Català de Paleoecologia Humana i Evolució Social (IPHES-CERCA), Zona Educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.

^dUniversitat Rovira i Virgili, Departament d'Història i Història de l'Art, Avinguda de Catalunya 35, 43002 Tarragona, Spain

^eICREA, Pg. Lluís Companys 23, 08010 Barcelona, Spain

^fDepartment of Prehistory, Autonomous University of Barcelona (UAB), Bellaterra, Spain.

^gArchaeology of Social Dynamics (ASD), Institución Milá i Fontanals de Investigación en Humanidades (IMF), Spanish National Research Council (CSIC), Barcelona, Spain

^hHistoire Naturelle de l'Homme Préhistorique, (HNHP, UMR 7194), MNHN, CNRS, UPVD, Paris, France

ⁱCR2P-UMR 7207, CNRS, MNHN, Sorbonne Université, Paris, France.

^jLabEx ARCHIMEDE, et UMR 5140 Archéologie des sociétés méditerranéennes, Université de Montpellier Paul Valéry – CNRS, Campus Saint Charles, 34199 Montpellier, France.

^kUniversité Bordeaux, CNRS, UMR 5199 PACEA-PPP, Bâtiment B18 Allée Geoffroy Saint-Hilaire CS 50023, 33615 Pessac Cedex, France.

^lInstitut National des Sciences de l'Archéologie et du Patrimoine (INSAP), Rabat, Morocco.

^mDirection provinciale de la Culture, Avenue Mohammed V, quartier administratif, Kénitra, Morocco.

***Corresponding authors.**

Figure S1. Microphotographs at 35x magnifications of wear facet in the mesiobuccal cusp in the occlusal surface of *Theropithecus oswaldi* from ThI-GH.

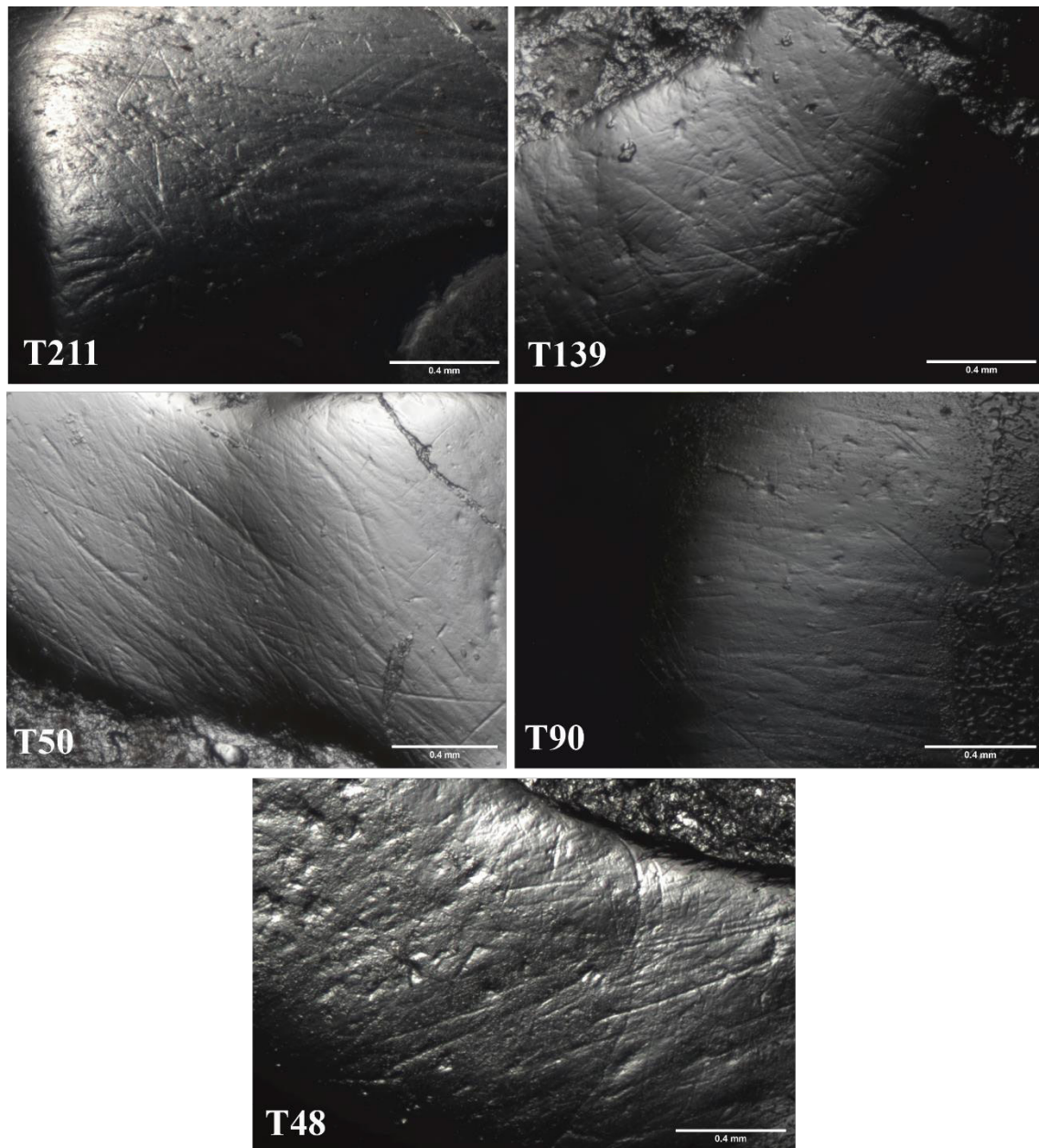


Table S1. Occlusal microwear analysis (low magnification) raw data of *Theropithecus oswaldi* from ThI-GH and extant *Papio hamadryas*. All analyzed teeth of extant cercopithecines correspond to lower second molars (M2).

Species	Specimen ID	U/L	Side	Average PITS	Average SCRATCHES	Average GOUGES	Average PUNCTURE PITS
<i>P.hamadryas</i>	PAP3792	L	Left	39.3	17.0	3.0	1.0
<i>P.hamadryas</i>	PAP3788	L	Left	42.7	20.3	3.3	1.7
<i>P.hamadryas</i>	PAP3769	L	Right	31.3	19.0	3.0	1.3
<i>P.hamadryas</i>	PAP3796	L	Left	44.0	19.7	4.7	2.3
<i>P.hamadryas</i>	PAP3813	L	Left	29.0	18.3	3.3	3.3
<i>P.hamadryas</i>	PAP3812	L	Left	29.7	18.3	4.0	2.3
<i>P.hamadryas</i>	PAP3808	L	Left	44.0	16.3	3.7	2.7
<i>P.hamadryas</i>	PAP3825	L	Left	29.7	17.3	2.3	1.3
<i>P.hamadryas</i>	PAP3786	L	Left	27.3	24.0	2.3	1.7
<i>P.hamadryas</i>	PAP3817	L	Left	32.0	16.0	2.7	1.7
<i>P.hamadryas</i>	PAP3767	L	Left	47.0	17.7	4.0	2.7
<i>P.hamadryas</i>	PAP3822	L	Left	39.0	20.0	1.7	2.7
<i>P.hamadryas</i>	PAP3802	L	Left	45.3	17.0	3.7	1.7
<i>P.hamadryas</i>	PAP3772	L	Left	34.3	16.3	4.3	2.3
Fossil <i>T. oswaldi</i>	T48	U	Right	16.0	17.7	2.0	1.0
Fossil <i>T. oswaldi</i>	T139	U	Right	12.0	19.7	1.3	1.3
Fossil <i>T. oswaldi</i>	T90	U	Left	11.0	15.7	0.3	0.5
Fossil <i>T. oswaldi</i>	T50	L	Right	14.7	22.3	0.5	0.0
Fossil <i>T. oswaldi</i>	T211	-	-	21.0	15.5	3.0	1.0

Table S2. Description of the 3D area surface texture parameters used in the present study (ISO 25178 and ISO 12781).

Category	Parameter	Description (condition)	Standard	Unit
Area	<i>Sda</i>	Mean dale area	ISO 25178	μm^2
Area	<i>Sha</i>	Mean hill area	ISO 25178	μm^2
Density	<i>Sal</i>	Autocorrelation length ($s = 0.2$)	ISO 25178	mm
Density	<i>Spd</i>	Density of peaks	ISO 25178	$1/\mu\text{m}^2$
Spatial	<i>Str</i>	Texture aspect ratio ($s = 0.2$)	ISO 25178	n/a
Spatial	<i>Std</i>	Texture direction	ISO 25178	n/a
Height	<i>Sl0z</i>	Ten-point height	ISO 25178	μm
Height	<i>S5p</i>	Five-point peak height	ISO 25178	μm
Height	<i>S5v</i>	Five-point pit height	ISO 25178	μm
Height	<i>Sa</i>	Arithmetic mean height or mean surface roughness	ISO 25178	μm
Height	<i>Sku</i>	Kurtosis of height distribution of surface	ISO 25178	n/a
Height	<i>Sp</i>	Maximum peak height, height between the highest peak and the mean plane	ISO 25178	μm
Height	<i>Sq</i>	Root-mean-square height, Standard deviation of the height distribution	ISO 25178	μm
Height	<i>Ssk</i>	Skewness of height distribution of surface	ISO 25178	n/a
Height	<i>Sv</i>	Maximum pit height, depth between the mean plane and the deepest valley.	ISO 25178	μm
Height	<i>Sxp</i>	Extreme peak height, difference in height between the q and p material ratio ($p = 50\%$, $q = 97.5\%$)	ISO 25178	μm
Height	<i>Sz</i>	Maximum height, height between the highest peak and the deepest valley	ISO 25178	μm
Height	<i>FLTt</i>	Peak to valley flatness deviation of the surface (Gaussian Filter, 0.025 mm)	ISO 12781	μm
Height	<i>FLTp</i>	Peak to reference flatness deviation (Gaussian Filter, 0.025 mm)	ISO 12781	μm
Height	<i>FLTv</i>	Reference to valley flatness deviation (Gaussian Filter, 0.025 mm)	ISO 12781	μm
Height	<i>FLTq</i>	Root mean square flatness deviation (Gaussian Filter, 0.025 mm)	ISO 12781	μm
Hybrid	<i>Sdq</i>	Root mean square gradient of the surface	ISO 25178	n/a
Hybrid	<i>Sdr</i>	Developed interfacial area ratio	ISO 25178	%
Peak sharpness	<i>SpC</i>	Arithmetic mean peak curvature	ISO 25178	$1/\mu\text{m}$
Plateau size	<i>SmC</i>	Inverse areal material ratio ($p = 10\%$)	ISO 25178	μm
Material ratio	<i>Sk</i>	Core roughness depth. Height of the core material	ISO 25178	μm
Material ratio	<i>Spk</i>	Reduced peak height, Mean height of the peaks above the core material	ISO 25178	μm
Material ratio	<i>Svk</i>	Reduced pit depth, Mean depth of the valleys below the core material	ISO 25178	μm

Material ratio	<i>Smr1</i>	Surface bearing area ratio (the proportion of the surface which consists of peaks above the core material)	ISO 25178	%
Material ratio	<i>Smr2</i>	Surface bearing area ratio (the proportion of the surface which would carry the load)	ISO 25178	%
Volume	<i>Sdv</i>	Mean dale volume	ISO 25178	μm^3
Volume	<i>Shv</i>	Mean hill volume	ISO 25178	μm^3
Volume	<i>Vm</i>	Material volume at a given material ratio ($p = 10\%$)	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
Volume	<i>Vmc</i>	Material volume of the core at a given material ratio ($p = 10\%, q = 80\%$)	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
Volume	<i>Vmp</i>	Material volume of the peaks of the surface	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
Volume	<i>Vv</i>	Void volume at a given material ratio ($p = 10\%$)	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
Volume	<i>Vvc</i>	Void volume of the core ($p = 10\%, q = 80\%$)	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
Volume	<i>Vvv</i>	Void volume of the pit at a given material ratio ($p = 80\%$)	ISO 25178	$\mu\text{m}^3/\mu\text{m}^2$
n/a = no unit				

Table S3. Values of the Log [(parameters)+1] used in the LDA buccal microwear texture analysis by taxa.

Species	Sq	Sku	Sa	Smc	Sxp	Sal	V _r	V _{mp}	V _{mc}	V _{vc}	V _{vv}	Spd	Spc	Sda	Sha	Sdv	Snr1	Snr2	FLTp	FLTv	FLTq
<i>C. atys</i>	0.078	0.655	0.061	0.091	0.151	0.894	0.095	0.005	0.065	0.086	0.011	0.002	0.068	2.097	2.162	0.423	1.058	1.952	0.178	0.098	0.045
<i>C. atys</i>	0.129	0.590	0.105	0.157	0.235	0.637	0.161	0.007	0.118	0.149	0.017	0.005	0.119	1.901	1.902	0.610	1.026	1.957	0.231	0.142	0.059
<i>C. atys</i>	0.088	0.624	0.070	0.106	0.168	1.086	0.110	0.005	0.079	0.100	0.012	0.003	0.058	2.173	2.152	0.483	1.069	1.959	0.246	0.120	0.058
<i>C. atys</i>	0.080	0.650	0.064	0.095	0.159	1.057	0.099	0.004	0.070	0.089	0.011	0.003	0.057	2.085	2.136	0.462	1.051	1.947	0.250	0.115	0.055
<i>C. atys</i>	0.121	0.595	0.100	0.152	0.219	0.940	0.156	0.005	0.112	0.144	0.016	0.003	0.075	2.090	2.088	0.568	1.031	1.957	0.318	0.178	0.086
<i>C. atys</i>	0.085	0.627	0.068	0.105	0.163	0.925	0.109	0.004	0.076	0.099	0.011	0.002	0.029	2.227	2.205	0.551	1.046	1.958	0.240	0.128	0.053
<i>C. atys</i>	0.110	0.676	0.088	0.133	0.213	0.947	0.137	0.005	0.095	0.124	0.017	0.004	0.084	1.948	1.958	0.598	1.050	1.952	0.273	0.140	0.060
<i>L. albigena</i>	0.147	0.667	0.118	0.171	0.281	1.086	0.177	0.009	0.128	0.161	0.023	0.004	0.158	1.957	1.953	0.629	1.097	1.947	0.313	0.162	0.082
<i>L. albigena</i>	0.134	0.584	0.109	0.161	0.239	1.194	0.166	0.006	0.124	0.153	0.017	0.002	0.184	2.274	2.207	0.539	1.059	1.954	0.352	0.196	0.103
<i>L. albigena</i>	0.123	0.577	0.099	0.140	0.218	1.151	0.144	0.005	0.108	0.127	0.016	0.002	0.077	2.197	2.193	0.496	1.025	1.956	0.346	0.183	0.097
<i>L. albigena</i>	0.128	0.645	0.103	0.154	0.239	1.074	0.159	0.007	0.112	0.145	0.019	0.004	0.093	2.007	2.024	0.547	1.038	1.953	0.324	0.178	0.089
<i>L. albigena</i>	0.060	0.619	0.049	0.074	0.121	0.940	0.076	0.003	0.057	0.070	0.008	0.004	0.051	1.999	1.982	0.329	1.050	1.957	0.168	0.082	0.043
<i>L. albigena</i>	0.100	0.598	0.081	0.121	0.197	1.123	0.124	0.004	0.091	0.113	0.014	0.003	0.071	2.067	2.072	0.473	1.050	1.957	0.296	0.146	0.073
<i>M. mulatta</i>	0.150	0.593	0.124	0.179	0.281	1.120	0.184	0.007	0.137	0.168	0.023	0.002	0.081	2.224	2.260	0.600	1.046	1.950	0.384	0.223	0.112
<i>M. mulatta</i>	0.143	0.615	0.116	0.170	0.267	0.774	0.176	0.008	0.128	0.161	0.022	0.003	0.116	2.063	2.054	0.585	1.082	1.949	0.334	0.204	0.090
<i>M. mulatta</i>	0.115	0.595	0.095	0.143	0.207	0.975	0.147	0.006	0.105	0.135	0.015	0.003	0.081	2.072	2.058	0.558	1.045	1.960	0.280	0.145	0.065
<i>M. mulatta</i>	0.136	0.589	0.112	0.171	0.242	1.094	0.176	0.007	0.123	0.164	0.019	0.003	0.105	2.134	2.133	0.597	1.074	1.956	0.338	0.201	0.104
<i>M. mulatta</i>	0.130	0.602	0.106	0.159	0.235	1.102	0.163	0.005	0.116	0.151	0.017	0.002	0.065	2.161	2.204	0.502	1.091	1.956	0.312	0.189	0.088
<i>M. sphinx</i>	0.124	0.622	0.100	0.150	0.230	1.125	0.156	0.007	0.113	0.145	0.017	0.001	0.034	2.429	2.415	0.719	1.068	1.958	0.345	0.213	0.092
<i>M. sphinx</i>	0.120	0.602	0.098	0.145	0.232	1.144	0.149	0.006	0.111	0.136	0.017	0.003	0.071	2.128	2.149	0.622	1.047	1.963	0.338	0.174	0.090
<i>M. sphinx</i>	0.122	0.617	0.099	0.146	0.240	1.201	0.150	0.006	0.108	0.135	0.019	0.003	0.071	2.149	2.164	0.493	1.083	1.957	0.352	0.170	0.103
<i>M. sphinx</i>	0.114	0.619	0.092	0.143	0.222	1.181	0.147	0.005	0.101	0.133	0.017	0.002	0.035	2.295	2.281	0.540	1.064	1.957	0.330	0.188	0.087

<i>M. sphinx</i>	0.153	0.653	0.118	0.176	0.322	1.202	0.183	0.009	0.130	0.166	0.027	0.001	0.034	2.462	2.576	0.788	0.907	1.103	1.961	0.443	0.221	0.312	0.126
<i>P. hamadryas</i>	0.045	0.648	0.036	0.057	0.085	0.764	0.059	0.003	0.039	0.055	0.005	0.002	0.019	2.288	2.306	0.489	0.547	1.116	1.960	0.116	0.065	0.060	0.022
<i>P. hamadryas</i>	0.122	0.649	0.092	0.135	0.240	0.657	0.140	0.007	0.097	0.123	0.019	0.003	0.059	2.136	2.187	0.669	0.716	1.054	1.947	0.217	0.125	0.119	0.048
<i>P. hamadryas</i>	0.100	0.669	0.078	0.122	0.187	0.843	0.127	0.007	0.083	0.116	0.014	0.002	0.032	2.452	2.373	0.858	0.847	1.136	1.954	0.259	0.163	0.133	0.057
<i>P. hamadryas</i>	0.125	0.667	0.098	0.142	0.250	0.603	0.147	0.007	0.107	0.132	0.020	0.002	0.065	2.189	2.253	0.733	0.801	1.050	1.945	0.226	0.123	0.139	0.046
<i>P. hamadryas</i>	0.150	0.679	0.120	0.174	0.285	0.572	0.180	0.008	0.128	0.163	0.025	0.004	0.092	2.042	2.000	0.788	0.786	1.089	1.947	0.260	0.133	0.171	0.053
<i>P. hamadryas</i>	0.086	0.648	0.067	0.101	0.181	0.722	0.104	0.005	0.073	0.094	0.014	0.002	0.039	2.184	2.239	0.642	0.636	1.075	1.941	0.182	0.100	0.101	0.038
<i>P. hamadryas</i>	0.080	0.714	0.064	0.098	0.159	0.725	0.101	0.005	0.071	0.091	0.011	0.002	0.034	2.309	2.314	0.648	0.727	1.127	1.946	0.168	0.105	0.101	0.031
<i>P. hamadryas</i>	0.073	0.649	0.058	0.087	0.147	0.737	0.091	0.004	0.061	0.082	0.010	0.002	0.026	2.269	2.292	0.591	0.605	1.082	1.951	0.177	0.085	0.092	0.037
<i>P. hamadryas</i>	0.076	0.644	0.061	0.094	0.143	0.769	0.097	0.004	0.066	0.089	0.010	0.002	0.027	2.355	2.357	0.683	0.755	1.146	1.956	0.178	0.096	0.101	0.036
<i>P. hamadryas</i>	0.059	0.628	0.047	0.076	0.107	0.734	0.079	0.003	0.052	0.071	0.007	0.002	0.025	2.232	2.255	0.539	0.681	1.115	1.953	0.149	0.091	0.077	0.031
<i>T. gelada</i>	0.129	0.611	0.106	0.154	0.234	0.934	0.158	0.007	0.119	0.146	0.018	0.003	0.057	2.076	2.082	0.635	0.636	1.034	1.956	0.325	0.156	0.202	0.076
<i>T. gelada</i>	0.070	0.596	0.057	0.086	0.136	1.089	0.089	0.004	0.064	0.081	0.009	0.002	0.022	2.241	2.272	0.464	0.505	1.045	1.960	0.216	0.115	0.128	0.048
<i>T. gelada</i>	0.113	0.617	0.092	0.140	0.209	0.800	0.144	0.006	0.101	0.133	0.016	0.004	0.056	2.078	2.053	0.619	0.655	1.039	1.955	0.254	0.148	0.138	0.066
<i>T. gelada</i>	0.076	0.660	0.060	0.092	0.157	0.983	0.095	0.004	0.064	0.086	0.011	0.002	0.025	2.229	2.239	0.541	0.558	1.110	1.955	0.247	0.119	0.161	0.052
<i>T. gelada</i>	0.074	0.619	0.060	0.096	0.130	0.779	0.100	0.004	0.065	0.090	0.008	0.003	0.029	2.137	2.144	0.478	0.481	1.058	1.957	0.199	0.117	0.104	0.039
<i>T. gelada</i>	0.075	0.631	0.059	0.092	0.143	0.874	0.095	0.004	0.064	0.087	0.010	0.003	0.030	2.104	2.103	0.511	0.529	1.056	1.953	0.222	0.110	0.129	0.043
T211	0.102	0.207	0.083	0.127	0.189	0.679	0.132	0.003	0.092	0.122	0.014	0.001	0.024	0.488	0.489	0.214	0.732	0.308	0.471	0.214	0.120	0.114	0.044
T28	0.138	0.203	0.111	0.171	0.243	0.677	0.176	0.002	0.123	0.162	0.019	0.001	0.010	0.511	0.515	0.166	0.733	0.311	0.471	0.263	0.150	0.147	0.060
T50	0.103	0.209	0.083	0.123	0.194	0.693	0.127	0.003	0.091	0.117	0.014	0.002	0.023	0.488	0.485	0.209	0.646	0.309	0.471	0.220	0.108	0.136	0.048
T91	0.071	0.220	0.057	0.088	0.132	0.723	0.091	0.002	0.063	0.084	0.009	0.001	0.011	0.509	0.510	0.188	0.545	0.324	0.471	0.158	0.084	0.080	0.032
T139	0.092	0.209	0.073	0.107	0.179	0.701	0.110	0.002	0.076	0.098	0.013	0.001	0.012	0.497	0.498	0.170	0.699	0.313	0.471	0.206	0.101	0.123	0.042

