



**Università
degli Studi
di Ferrara**

International Erasmus Mundus Master in

QUATERNARY AND PREHISTORY



**Erasmus
Mundus**

**Decoding Diets: Microwear and Mesowear insights
into red deer teeth from the Late Epigravettian at
Riparo Tagliente (Italy)**

Sandhra Saravanan

Supervisor: Florent Rivals

Co-supervisor: Federica Fontana

Academic year 2023/2024



Acknowledgements

This has been an incredible journey. I owe this to everyone who stood beside me through both highs and lows. I would like to express my deepest gratitude to a few without whom this accomplishment would not have been possible.

First and foremost, I would like to extend my heartfelt thanks to my supervisor, Florent Rivals. Your guidance, dedication, and continuous support have played a pivotal role in shaping this research. To my co-supervisor, Federica Fontana, your kindness and understanding have been constant throughout this journey. I sincerely thank you for your unwavering support and for allowing me access to study the materials from the site. Another name that must be mentioned is Marta Arzarello, the director of the IMQP, for her invaluable support both academically and administratively.

A special mention goes to Sharada Channarayapatna, a mentor and tutor I will never forget. Your guidance has been instrumental in helping me navigate the field of archaeology, and I cannot express enough gratitude for your help in shaping my path.

I am eternally grateful to my Amma and Achan for believing in me, especially as I made life-changing decisions like moving to Europe to study Archaeology. Your unwavering support and encouragement have meant the world to me. To Adwaith, thanks for being the pillar of strength at times when I couldn't find my own. And to my grandmother who takes immense pride in seeing her grandchildren grow into independent individuals—your wisdom and inspiration have always pushed me to aim higher.

To Saal, my best friend, for being your genuine self and encouraging me to reach for amazing things. And to JP, for always being the kindest and wisest presence whenever I hit a roadblock. Your optimistic perspective has consistently helped me see things from a better angle, and I will always cherish the bond we share. I can't thank you both enough for being my constant support system throughout this journey.

Finally, to my friends, Ankita, Prasanna, Sai, Dalila, Sandra, Nagisa, Deyvis, and Divyendu—your friendship and emotional support have been a source of strength throughout this journey, and I am incredibly thankful for each of you.

Abstract

Riparo Tagliente, situated in northeastern Italy, contains one of the primary archaeological sequences of the Upper Pleistocene in southwestern Europe, dating approximately from 45,000 to 10,000 years BP. The aim is to elucidate the dietary variations and seasonal preferences of the species *Cervus elaphus* from the Late Epigravettian of the site to understand its occupation history, from stratigraphic layers 1 to 13. This study employs microwear and mesowear analyses on dental remains of red deer to infer dietary traits and seasonal variations. This species was chosen for its consistent presence throughout all stratigraphic layers, rendering it an optimal candidate for determining long-standing dietary patterns within the site. The initial objective is to ascertain the possible seasonal variations in the dietary habits of the species and to reconstruct their paleoecology by comparing the dental microwear patterns with those of extant populations of closely related species from various geographical areas. Secondly, to study the mesowear data to understand the effects of long-term dietary habits such as general dietary preferences and adaptations of an animal over its lifetime. Findings unveil significant insights into the ecological dynamics and human-animal interactions within the Riparo Tagliente site. By correlating microwear and mesowear patterns with environmental proxies, dietary preferences among the species is found out to be mixed feeding with a slight inclination towards browse. This has identified the past vegetation with the help of corroborating archaeozoological, palynological and malacofaunal evidence to be a site with open forest covers. Seasonal adaptations of *Cervus elaphus* over time is observed as occupying the site for more than one season which is an indicative of responses to climatic fluctuations and alterations in resource availability. These ecological dynamics not only shape the foraging behaviours of red deer but also leave valuable imprints on the archaeological record, reflecting the adaptive strategies of human groups inhabiting the site.

Ultimately, this study contributes to a comprehensive understanding of past ecosystems and human-animal relationships that provide valuable insights into the subsistence strategies of ancient communities and the broader ecological context in the Riparo Tagliente region where they sustained.

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Chapter 1. Introduction

1.1 Study background

The Epigravettian (approximately 23,000 and 12,000 cal BP) is one of the major cultural periods of the Late Palaeolithic in Europe and can be characterized by its unique climatic conditions and adaptations. It is distinct for its environmental shift including the Last Glacial Maximum and the following warming phases. Apart from the environmental factors, the Epigravettian phase is also notable for its complex social structures, advancements in technological innovations and specific techno-typological signatures, cultural developments, and symbolic thinking (Bortolini et al., 2021; Oxilia et al., 2021; Peresani, 2023).

The Italian peninsula holds a significant place in the study of Late Pleistocene time especially during the Late Epigravettian and Late Palaeolithic periods. The period 126,000 to 11,000 years ago, has a huge role in shaping the lives of Homo sapiens in the Upper Palaeolithic. These regions' climate shifts and environmental conditions have forced humans to adapt to innovative subsistence strategies and large-scale migrations. These adaptations not only fostered demographic and behavioural changes but also led to the development of distinct archaeological cultures across Europe, particularly in the Italian peninsula (Peresani, 2023). Major environmental transformations happened during the deglaciation of the Alpine regions, resulting in different vegetation and distinctiveness in faunal species (Bertola et al., 2007). These constant changes are also pointed out as a reason for the subsequent re-occupation of the Alpine areas. Riparo Tagliente is one such site which is the first to have found evidence of reusing settlements (Fontana et al., 2018) and provides important information on subsistence strategies, paleoecology, cultural dynamics, and faunal exploitation etc.

1.2 Objectives

This study focuses on the Late Epigravettian period of the site Riparo Tagliente, and studies the red deer (*Cervus elaphus*) dental specimens. It is steered by two main objectives that aim to expand our understanding of both the paleoenvironment and human-animal interactions during this period.

1. The first objective is to analyse the dietary preferences of *C. elaphus* during the Late Epigravettian at Riparo Tagliente with the goal of reconstructing the paleoenvironment based on these dietary patterns.
2. The second objective is to investigate the variation in seasonality and the duration of occupation at the site during the Late Epigravettian, which will provide insights into paleoclimate and the site's adaptation to it.

1.3 Hypothesis

The study hypothesizes that both modern and fossil species of *Cervus elaphus* exhibit dietary flexibility where some individuals graze, others primarily browse, and many adapt to a mixed feeding strategy that includes both grazing and browsing. This hypothesis is based on evidence from existing literature and previous research, which suggests that *C. elaphus* has consistently demonstrated this adaptive feeding behaviour across different environments and time periods.

1.4 Why Riparo Tagliente?

Riparo Tagliente is a significant archaeological site with an abundance of fossil remains from various chronological periods, making it a valuable resource for understanding past environments and species. The site's rich repertoire of archaeological evidence offers pivotal insights into the relationships between environmental changes and the resilience and adaptability of Late

Palaeolithic societies. Cervids are among the top three important ungulates that help in determining a site's paleoecology along with equids and bovids. Red deer fossil remains comprised of almost 50-70% (Bartolomei. G. et al., 1982; Bertola et al., 2007) of the faunal remains in all the layers of the Epigravettian sequence making it a reliable species to study to understand the dietary trends and through that the variation in seasonality.

The site of Riparo Tagliente was chosen as the study area for this research due to its well-preserved stratigraphic sequences provide invaluable data on the technological, subsistence, and settlement strategies employed by Late Palaeolithic societies in response to shifting climatic condition. Located in the Mount Lessini area, Riparo Tagliente is one of the most significant sites in the region, making it a key location for studying these aspects. Additionally, the site presents a unique opportunity for dental wear analysis, an underexplored method in palaeolithic sites in the region. This is particularly relevant considering recent investigations at the nearby site of Vajo Salsone (Thun Hohenstein et al., 2024), where dental wear on red deer teeth provided insights into the species' dietary and seasonal transition from the Middle to Upper Palaeolithic periods. By focusing on Riparo Tagliente, this study aims to contribute to a broader understanding of the Epigravettian period in the Italian Alps, shedding light on the resilience and adaptability of humans and animals in the face of climatic and environmental challenges.

1.5 Methodology utilised

Microwear and mesowear analysis has been proven to be a good proxy in understanding the dietary preferences of an individual and their seasonal variations. Microwear analysis reveals short-term dietary shifts and the specific abrasive nature of consumed foods, while mesowear analysis offers insights into long-term feeding strategies and general dietary trends (Fortelius & Solounias, 2000; Solounias & Semprebon, 2002).

Microwear and mesowear are non-destructive methods which directly reflect the physical properties of the diet, unlike isotopic analysis, which can be influenced by environmental factors and may provide average dietary inputs over extended periods. This direct approach offers more precise reconstructions of diet and is essential in archaeological contexts where specimen preservation is critical. For isotopic analysis, in most cases where stable environmental baselines for the comparative analysis might be absent or is poorly understood, microwear and mesowear can yield detailed dietary information with fewer limitations.

Dental wear analyses are non-destructive, making them suitable for preserving specimens for future research. They also complement other methods, such as isotopic analysis, dental calculus studies, and geometric morphometrics, providing a multi-dimensional understanding of past ecosystems and ungulate behaviour. This research is part of a broader project that integrates isotopic analysis (carbon and oxygen) with microwear and mesowear to offer a comprehensive view of the dietary habits and environmental interactions of the species during this period.

1.6 Research significance

This research is the first to examine dental wear in *Cervus elaphus* (red deer) from the Late Epigravettian layers of Riparo Tagliente. By focusing on this specific period, the study not only provides insights into the palaeodiet and environmental conditions of the time but also lays the groundwork for future investigations into other layers of the site. A comparative analysis across these layers could significantly enhance our understanding of the site's paleoenvironment, dietary shifts, and seasonal variations over time.

Prior to this study, there was limited evidence regarding the specific dietary habits of red deer during the Late Epigravettian period at Riparo Tagliente. Through the methodologies equipped

here, this research provides a detailed understanding of their diet and offers more precise insights into their feeding strategies than before.

This study addresses gaps in knowledge on how these animals interacted with their environment, particularly concerning the vegetation they consumed, and contributes to a clearer picture of the paleoenvironment during this period. Also, the findings offer valuable information on the subsistence strategies of Late Epigravettian humans at Riparo Tagliente, suggesting how they might have exploited red deer as a resource and how their activities could have influenced or been influenced by the availability of this major game species. The study's results facilitate more precise comparisons with other research on ungulate ecology and evolution, enhancing our understanding of how large herbivores like red deer fit into broader ecological models and past environments.

Chapter 2. Late Epigravettian and Late Palaeolithic European sites

The Italian peninsula is rich in cultural and biological fossil records, particularly from the Pleistocene period. During the Late Pleistocene glacial cycle (ca 126 cal ka BP – 11 cal ka BP), Upper Palaeolithic *Homo sapiens* underwent significant biological changes. They responded by increasing their resilience and migrating on a large scale, connecting different regions of Europe. This led to demographic and behavioural changes, fostering the synchronous and diachronic development of various archaeological cultures across various locations and periods (Peresani, 2023). Consequently, the timing and patterns of numerous scalar shifts from the Last Glacial Maximum (ca 26 cal ka BP - 18 cal ka BP) to the beginning of the Last Glacial Interstadial (14.7 cal ka BP) are key chronological events in Italy. Research continues to explore how Upper Palaeolithic groups adapted biologically, culturally, and socially to the climate changes of the Late Pleistocene (Peresani, 2023).

The late Upper Pleistocene period is marked by several climatic oscillations corresponding to Marine Isotopic Stage 2 (MIS 2) (Berto et al., 2018). After the Last Glacial Maximum (LGM), the final phase of MIS 2 included three significant climatic events. First, Heinrich Event 1 (approximately 16,500 to 14,600 years ago) which is an arid phase leading to significant glacial collapses and periglacial rearrangements across the Alpine region, marking the beginning of the Late Glacial according to some authors (Berto et al., 2018). Secondly, temperate (Bølling-Allerød) interstadial signifies a period of rapid temperature increases and forest development, marking a warm phase with minor oscillations, especially noted in the northern Alps (Berto et al., 2018). And finally, Younger Dryas, a cold oscillation equivalent to Greenland Stadial 1 (Berto et al., 2018).

2.1 Environmental shifts and human settlement patterns

During the Late Glacial period, the eastern Italian Alpine region experienced significant environmental transformations that directly influenced human settlement patterns. As the glaciers retreated, the deglaciation process began to reshape the landscape. Radiocarbon dating of larches in the Revine basin marks this shift, highlighting the gradual emergence of environments previously covered by peripheral branches of Alpine glaciers during the Last Glacial Maximum (Bertola et al., 2007). These changing environments set the stage for the first significant Epigravettian settlements along the pre-Alpine margins. Among these, Riparo Tagliente stands out as the earliest documented site in the southeastern Alpine region to exhibit evidence of human occupation following the Last Glacial Maximum (Fontana et al., 2018). The site's Late Epigravettian layers, particularly layers 14-5, reveal pollen records indicating a temperate climate characterized by grasslands, conifers, and deciduous trees (Fontana et al., 2019).

Before the end of the Upper Pleistocene, faunal assemblages in the Italian Peninsula exhibited strong regionalism. Differences between northern and southern faunal assemblages were notable, especially during the Late Glacial. These regional variabilities were influenced by geographic features like the Alpine chain, the Apennines, and the Mediterranean Sea (Berto et al., 2018).

2.2 Expansion of Forests and Human Adaptation

The Bølling-Allerød interstadial period brought about further environmental changes, most notably the expansion of forests and the stabilization of mountain slopes. These developments facilitated the anthropogenic colonization of the pre-Alps and the southern Dolomites. During this time, human groups established seasonal camps at medium-low altitudes, such as the Grotta del

Clusantin, Pradis or valley floors like Riparo Villabruna in the beginning phase, developing full occupation of the territory during the Allerød period (Bertola et al., 2007).

The late glacial settlement network was organized around the logistical occupation of the Alpine ecotone, a transitional zone between coniferous forests and open environments. This system defined a network of seasonal sites, some of which served as locations for complementary activities, reflecting a strategic approach to exploiting the diverse resources offered by this dynamic landscape (Bertola et al., 2007).

2.3 Seasonal Occupation and Mobility

Understanding the lifestyle of Epigravettian hunters during the Late Glacial period requires focus on the seasonality of their settlement patterns. Four key sites - Riparo Tagliente, Riparo Soman, Riparo Dalmeri, and Riparo La Cogola offer insights into the seasonal nature of human occupation.

The seasonal use of upland sites like Riparo Dalmeri, and Riparo La Cogola has been determined based on the presence of young ungulate teeth, whose eruption periods are well-documented. These sites were typically occupied between summer and autumn (Bertola et al., 2007). Riparo Dalmeri offers a clear example of seasonal use. Analysis of ibex teeth from the site revealed that most hunting occurred at the end of summer and the beginning of autumn, coinciding with the ibex mating season (Bertola et al., 2007). The presence of painted stones, some depicting ibex and deer, suggests a symbolic or ritualistic aspect to the site, possibly linked to hunting practices. The overwhelming presence of ibex remains which is over 90% of the ungulate bones indicates that Dalmeri was primarily a high-altitude hunting camp, used specifically for ibex during these seasons (Bertola et al., 2007).

In contrast, valley bottom sites like Riparo Soman and Riparo Tagliente (See Chapter 3) were occupied from spring to autumn, supporting the idea that winter camps were likely located further south, in the pre-Alpine valleys or plains (Bertola et al., 2007).

This seasonal migration between valley bottoms and upland sites reflects a sophisticated understanding of the environment, allowing Late Glacial hunters to maximize resource use across different altitudes and seasons (Bertola et al., 2007). These findings illustrate the adaptability and mobility of Late Epigravettian societies, whose survival strategies were closely tied to the seasonal availability of resources in the challenging Alpine environment

2.4 Subsistence strategies and faunal exploitation in the Late Glacial Alps

In the late 1990s, the primary evidence regarding hunted animals and hunting strategies in the mountainous environment of northeastern Italy was based on the study of faunal bone remains from several valley floor sites like Riparo Tagliente, Riparo Soman, and Riparo Villabruna, which were repeatedly occupied during the Late Glacial period (Bertola et al., 2007). The discovery of rich faunal remains at two mid-to-high altitude sites of Riparo Dalmeri and Riparo La Cogola and the archaeozoological study of all mammals remains from the Epigravettian sequence at Riparo Tagliente have expanded the knowledge on subsistence strategies and land use in the alpine and pre-alpine regions by hunters (Bertola et al., 2007).

Among the ungulates, the ibex, red deer, and chamois were the most hunted and are present in all sites, while the elk, bovines, roe deer, and wild boar are less frequent (Bertola et al., 2007). During colder periods that dominated in the first part of the Late Glacial, alpine meadow species like the ibex and chamois have a strong presence even at lower altitudes (Bertola et al., 2007). Climatically and environmentally significant are the rare occurrences of elk, an indicator of cold climate and

wetland environments, and wild boar which is an indicator of temperate and forested environments. Some carnivores, such as the fox, wolf, and bears are also present, while the lynx and wildcat are rare. There always was a constant presence of hares, marmots, and beavers in the site (Bertola et al., 2007). During the warmer phase of the temperate interstadial specifically the Bølling-Allerød period led to the expansion of forests around 12,400-12,300 14c cal BC (Bertola et al., 2007) and the retreat of glaciers which in turn influenced the distribution of different species like red deer became abundant, wild boar, and elks.

Variations among species, while representing the result of hunting or fishing activities, also reflect climatic changes. Human groups' subsistence strategies focus on adult ungulates capable of providing the maximum resource input like skin, meat, etc. (Bertola et al., 2007). Within some shelters, such as Tagliente, Dalmeri, and La Cogola, the differential distribution of faunal remains has allowed the identification of specific areas designated for carcass exploitation (Bertola et al., 2007). Post-depositional processes have altered most anthropic evidence over time, significantly reducing the faunal remains and often limiting the documentation to lithic industries alone (Bertola et al., 2007).

2.5 Cultural and environmental dynamics of the Epigravettian period in northern Italy

The Epigravettian techno-complex is one of the major European Upper Palaeolithic cultural periods and its origins can be traced back to the Late Glacial Maximum when it brought a cultural separation between the Western Atlantic and the Mediterranean-Balkan area of the continent according to Palma di Censola & Bietti (1983). Across the wide territory extending from southeastern France to Russia to southwest Anatolia, the characteristic features of Epigravettian

time have been noted (Bertola et al., 2007; Palma di Censola & Bietti, 1983). Even when the data across these geographic areas are discontinuous, there is a cultural homogeneity that can be traced by the lithic industries and the faunal assemblages and artistic expressions that present several similarities (Fasser et al., 2022; Fontana et al., 2020).

Particularly, the Balkans and Italy have similarities in the distribution of artefact types around this period, which points to a hypothesis of long-distance mobility for the Epigravettian hunter-gatherers (Bortolini et al., 2021; Fasser et al., 2022; Peresani et al., 2021). According to Oxilia et al. (2021), the Eastern Alpine region of Italy is one of the best-suited geographic locations to study the environmental and cultural influence on the subsistence and dietary preferences of the hunter-gatherer groups of the last glaciation. This is predominantly due to the region's geographic diversity, which includes a wide range of landscapes of high mountains, plateaus, river valleys and alpine lakes. This diversified array of environments presents different ecological conditions that shaped the environmental and cultural experiences of the hunter-gatherers (Bortolini et al., 2021; Oxilia et al., 2021).

For the pre-history of Northern Italy, the end of the Pleistocene was a significant point which witnessed the first human reoccupation of the Alps triggered by environmental conditions after the Last Glacial Maximum due to the retreat of the Würm glaciers (Bortolini et al., 2016). The Southern Alps valleys were occupied by the Late Epigravettian groups, as it is testified in Riparo Tagliente (Bortolini et al., 2016; Fontana et al., 2002). The site's Late Glacial sequence is crucial in understanding the technological and subsistence strategies of Late Epigravettian hunter-gatherers in the Southern Alps (Berto et al., 2018).

Chapter 3. Riparo Tagliente

3.1 Geographic location

Located on the foothills of Monte Tregnago in Stallavena di Grezzana, Verona, Italy, Riparo Tagliente is an archaeological site discovered in 1958 by Francesco Tagliente (Fontana et al., 2019). The site is located at an altitude of 250 meters above sea level in the Monti Lessini. The shelter is made of oolitic limestone and lies on the left slope of Valpantena, one of the main valley bottoms (Fontana et al., 2009). In the northeastern part of Italy, specifically in Lessini, Riparo Tagliente represents the shift from cold and arid conditions to temperate ones. The site is located amongst rich mosaics of landscapes and topographic situations such as the plain, valley-bottom,



Figure 1. Riparo Tagliente location map (Credits: Google Earth)

rocky slopes, and the top of the massif (Fontana et al., 2009) . The abundant lithic and mineral resources locally available were exhaustively exploited by the Palaeolithic groups that occupied the shelter.

3.2 History of excavations



Figure 2. Riparo Tagliente panoramic view (Fontana et al., 2019)

The site was discovered in 1958 during a surface survey in the locality of Stallavena by Dr. Francesco Tagliente (1918 - 2008) (Fontana et al., 2009; Bartolomei et al., 1982). At the base of Mount Tregnago, several prehistoric materials were found.

A team of researchers from the Museo Civico di Storia Naturale di Verona, composed of F. Zorzi, A. Pasa and F. Mezzena started the excavation in 1962 and continued till 1964 (Bartolomei. G. et al., 1982). Only in 1967 did the University of Ferrara begin to manage the direction of excavations which are still in progress. From then, it was Prof. P. Leonardi and after him, Prof. A. Broglio and

Prof. A. Guerreschi who headed the research (Bartolomei et al., 1982). To date, the research is headed by Prof. F. Fontana. After a decade of inactivity, the site has reopened in 2023 for excavations. The excavations are conducted with the permission of the Italian Ministry of Cultural Heritage and Archaeological Superintendency of Veneto, Italy.

Until the mid-1970s, the focus of the excavations was on a long trench running transversely to the shelter and a smaller trench in the innermost area. Since the late 1970s, the excavation efforts in the Late Epigravettian deposit have expanded to the northern part of the site. This expansion aims to understand the resource exploitation patterns and the organization of living spaces across various phases of occupation (Fontana et al., 2009). Riparo Tagliente site has helped reconstruct the lifestyle of Epigravettian hunters during the Late Glacial period by considering seasonality, exploitation of faunal resources, lithic technology, and symbolic practices. Other sites like Riparo Soman, Riparo Dalmeri, and Riparo La Cogola have also contributed significantly to decoding the Epigravettian period (Bertola et al., 2007).

3.3 Stratigraphy of the site

The stratigraphic sequence can be divided into two deposits where the lower one can be classified as early and middle Würm and contains Mousterian and Aurignacian assemblages while the upper



Figure 3. External area of excavation (Image credits: <https://old.stum.unife.it/ricerca/quaternario-e-preistoria/scavi/riparo-tagliente/il-sito>)

one is referred to as the Late Glacial and related to the Late Epigravettian (Fontana et al., 2018). The Late Epigravettian series exhibits variable thickness, being thinner and more compact under the shelter's overhang and thicker externally. A river erosive surface occurred during the first part of the Late Glacial, creating a slope then covered by deeply human-influenced layers. Radiocarbon dating of the Late Epigravettian stratigraphic sequence points to a chronological span between 17,219 and 15,940 years cal BP and locates these occupations in the first part of the Late Glacial and the beginning of the Late Glacial Interstadial (GS-2.1a) (Fontana et al., 2018). Layers 10-8 (12,040±170 BP), 10a (12,650±160 BP), 10c (13,070±170 BP), 10e (13,270±170 BP), 14 (12,000±400 BP), and 15-16 (13,430±180 BP) from the northern sector of the Epigravettian series were previously radiocarbon dated. More recently, stratigraphic units 13 trincea and 13a in the same sector of the Epigravettian series were radiocarbon dated to 13,250±80 BP and 13,450±70 BP, respectively (Bartolomei et al., 1982; Fontana et al., 2009, 2018).

In the lower part of the deposit (layers 17-14), the faunal assemblage is dominated by ibex and marmot. From layer 13 to layer 5, there is an increase in temperate species, with red deer becoming dominant from layers 12 to 10. Similar trends are observed in the malacofaunal and microfaunal assemblages (Bartolomei. G. et al., 1982; Berto et al., 2018). In the inner area, only the bottom portion of the sequence is preserved, corresponding to layers 13 to 15/18 in the outer zone, with a more precise correlation currently being developed (Fontana et al., 2009, 2018). There are two parts of the shelter – internal and external which are divided by shelter drip-line. There is an objective difficulty in stratigraphic correlation between these two areas. (Bartolomei. G. et al., 1982).

Two main combustion structures were found in the 1980s and 90s dating to an earlier phase of Late Epigravettian occupation and were excavated within the Mousterian deposit (US 250) and the Epigravettian area (US 13a) below the overhang of the shelter (Bertola et al., 2007). The first one

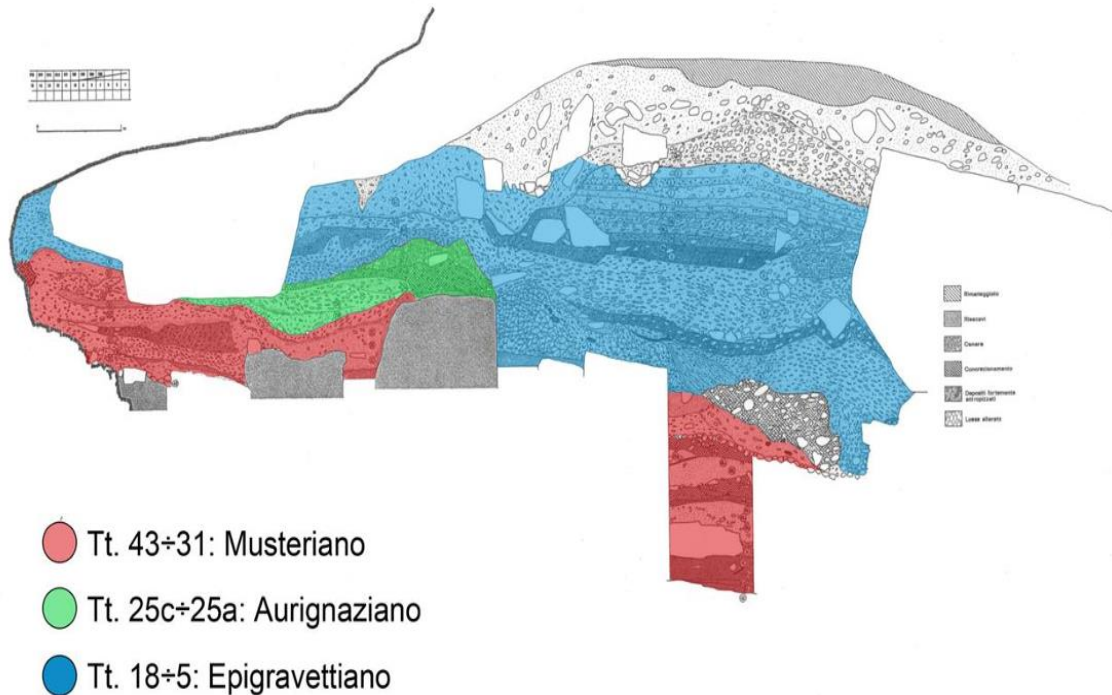


Figure 4. Stratigraphic deposition depicting Mousterian, Aurignacian and Epigravettian sequences of the site (Fontana et al., 2019)

was an irregular pit resulting from successive digging and emptying phases. It was filled with silt, small bone fragments, and burnt lithic debris. The second had a subcircular shape with a fill of ashes, bones, burnt flints, and thermally altered pebbles (Bertola et al., 2007).

Towards the exterior, the Late Glacial deposit stratigraphy thickens to about 2 meters, contrasting with the internal stratigraphy that develops only for a few tens of centimetres, even considering that the upper part of the series was removed by historical interventions. The layers thicken near a scarp formed by fluvial erosion before the Epigravettian occupations, which separates the older series (Mousterian and Aurignacian deposits) from the more recent one (Epigravettian deposits), and thin towards the exterior, following the slope. The thickness increase is due to anthropogenic accumulations of various materials: ashes, gravel, lithic debris, etc. distributed differently across



Figure 5. The external part of the site where the stratigraphic units are labelled and the internal area is also visible.

zones. These accumulations alternate and combine, especially in the lower part of the series, with blocks and clasts from rock wall collapse and degradation (Bertola et al., 2007; Fontana et al., 2002, 2018).

The transition zone between the inside and outside of the shelter features layers rich in combustion residues and anthropically deposited river gravel, resulting from the emptying of combustion

structures and cleaning of internal areas. These mix with significant concentrations of lithic debris outside the rock overhang, particularly where large limestone blocks attest to a substantial collapse event in the early phase of the Epigravettian occupation (Bertola et al., 2007). These concentrations are primarily lithic knapping debris and other finds. Analysis of these and other similar concentrations in the underlying layers suggests that the external area between the collapsed boulders was used for discarding various materials. The continuous accumulation of sediments and remains complicates the reading of the stratigraphic sequence but in some cases, it was possible to isolate the accumulation of materials, attributable to single short-term episodes, as confirmed by analytical studies (Bertola et al., 2007).

3.4 Seasonal occupation and hunting practices at Riparo Tagliente during the Epigravettian

At Riparo Tagliente, ibex prevails during the cold phase of the Dryas I, while deer becomes predominant during the temperate Bølling phase. The sequence ends with the beginning of the Allerød (Bertola et al., 2007). The age of death of ungulates shows that hunting was primarily directed towards young adults and adults, indicating the exploitation of animals in the age group that provides the highest quantity and best quality of meat.

Riparo Tagliente is considered a long-term settlement, frequented for most of the year (Fontana et al., 2002; 2009; 2018). The presence of foetal or newborn bones, as well as the degree of dental wear, suggests that the shelter was occupied during late spring and summer. Most ungulates give birth in late May or early June, and the discovery of full-term newborn bones indicates that hunting occurred from March to November (Bertola et al., 2007). This suggests a nearly year-round occupation, with the only gap possibly during the coldest winter months (Bertola et al., 2007).

Although there is no direct evidence for winter occupation in the three winter months (December, January and February), it cannot be ruled out.

Differences between ungulate species do not seem solely due to human activities like hunting strategies, butchering, and carcass transport but are influenced by climatic changes and the environment surrounding the sites.

3.5 Archaeological material distribution at the site

Bone tools, colouring material, artworks and burial were found at the site. The working of bone and antler is evidenced by objects of well-defined typology, created using specific techniques. The



Figure 7. Plaque engraving of a lion



Figure 6. A deer metapodial tool

hard animal materials used for making tools and weapons come exclusively from ungulates: red deer, roe deer, and marginally ibex at Riparo Tagliente (Bertola et al., 2007). Along with the finished artifacts, blanks were prepared for making tools or weapons, pieces abandoned during production, and residues, which attest to onsite manufacturing (Bertola et al., 2007). Some bone artifacts, such as awls, were always made from diaphyseal splinters produced by breaking long bones (Bertola et al., 2007).



Figure 8. Perforated shell ornament

Many tools, such as awls, spatulas, smoothers, and small perforators, were used in the processing and treatment of hides and more generally of other soft materials (for example, wood); others were used in hunting, attached to wooden shafts. Thirty artefacts were made from animal hard matter from Riparo Tagliente and fall into the category of ornamental objects. These are pendants made from perforated mammal teeth and bone fragments and malacofaunal elements (Bartolomei. G. et al., 1982; Bertola et al., 2007).

In particular, the site of Riparo Tagliente has a rich repertoire of cervid dental remains and this research explores the diet and seasonality of the red deer or *Cervus elaphus* species that are present at the site. *Cervus elaphus* species was chosen as it is present in abundance in almost all layers of the Late Epigravettian and it could give detailed insight into the paleoenvironment and climate through dental wear analysis. The aim is to elucidate the species' dietary variations and seasonal preferences throughout the occupation history of the site, from stratigraphic layers 1 to 13. This

study employs microwear and mesowear analyses on dental remains of red deer (*Cervus elaphus*) to infer dietary traits.

Chapter 4. Materials and Methods

4.1 Materials

The materials utilized in this study come from the site of Riparo Tagliente in Verona, Italy and the study specimens are ancient dental remains of red deer (*Cervus elaphus*) which were found in the Late Epigravettian levels. The samples are from the excavations carried out between 1960s and 1970s (Bartolomei. G. et al., 1982) and belong to the Late Epigravettian stratigraphic layers 1, 4, 5, 6, 7, 8, 9, 10 and 13. Some of the layers have internal subdivisions – 5 scarpata, 6a, 7b, 10a, 10b, 10c, 10d, 10e, 10f. Layer 10 f might have been excavated between the 70s and the 80s (Bartolomei. G. et al., 1982). The species *Cervus elaphus* was of interest as it was present abundantly in all the stratigraphic layers of the site and was well-suited for microwear and mesowear analysis. Data was collected on 72 maxillary and mandibular fragments with intact teeth present. It was also necessary that the occlusal surfaces of the teeth presented wear facets for both microwear and mesowear.

The samples were selected for analysis based on their preservation condition. Completely fragmented samples, samples with taphonomic alterations, and decidual or unworn teeth belonging to young individuals cannot be analyzed as they do not show any wear. They were thus discarded. This does not mean that all samples in a bad condition of preservation were discarded. Under the microscope, a minimal work area is required for quantifying the scratches and pits and if the tooth has an occlusal surface with a slightly better side, it is considered as an eligible sample for analysis. Also, it is not always the case where the sample is in good condition and has optimal occlusal surfaces for analysis. Anatomical identification of the teeth to determine if they are premolar, molar and their positions (1,2,3 and if they belong to upper, lower, right or left) was also noted.

4.2 Sample preparation

The sample preparation stage consists of cleaning the samples, creating negative casts of the samples and making positive resin moulds. This process is done to obtain a replica of the original archaeological material to analyze non-destructively at a macroscopic and microscopic scale. Also, this is a feasible and accessible option as one does not require the original anymore once the cast is made. This is a useful method to study materials from different sites in different geographic locations.

For mesowear, no cleaning is necessary as the cusp shape and relief of teeth are observed but concerning microwear, debris, preservatives and other residues can compromise the result and thus cleaning of the sample is mandatory (Green & Croft, 2018).

Cleaning of the samples for preparation is necessary for obtaining clear results. Three main stages of cleaning are -

1. Acetone – this can be applied by a cotton swab over the occlusal surface and outer surfaces.
2. Ethanol – after applying acetone, 96% ethanol is applied over the occlusal surface to remove any acetone remaining on the teeth.
3. Drying – the teeth are left to dry thoroughly at room temperature (Martínez-Polanco et al., 2021).

To make the moulds, polyvinylsiloxane silicone (Provil Novo Light CD2 regular; Martínez-Polanco et al., 2021), a high-precision material used in human dentistry is used (Semprebon et al., 2004). This material has great temporal stability, exceptional elastic recovery, perfect resolution, and high accuracy detailing up to 1 micron (Galbany et al., 2011). This can be done using a dispenser gun and a silicone cartridge. It has a quick setting time of 10 to 15 minutes, which is

ideal for making more samples in a short period. The silicone is applied directly to the surface to be replicated. Some points to keep note of while doing so are to avoid air bubbles to retain the quality of the replica made.

Once the silicone is dry, it is removed, and a wall made of a mixture of silicone putty (Turboflex Putty Soft) is built around the mould to hold the casting compound (Green & Croft, 2018). The height of the wall should not be more than 0.75 mm (Martínez-Polanco et al., 2021). The casts are made with high-quality two-part high-precision transparent epoxy resin (Epoxy EPO-1060/1585 - Martínez-Polanco et al., 2021) to create a positive replica of the tooth (Green & Croft, 2018; Solounias & Semprebon, 2002). In the mixing ratio, the hardener should be 25% of the total mixture. The resin mixture is precisely poured into the silicone mould and left to dry (Martínez-Polanco et al., 2021). Using compressed air, the resin is spread evenly in the mould. Surface bubbles from the poured mixture are removed using a toothpick and the mixture is smoothed out for better results (Green & Croft, 2018). Masks and gloves are advisable during the process as the substances used are toxic.

After 48 hours, once the resin is solidified, the positive moulds obtained were observed with a standard stereomicroscope at 35x magnification to identify and quantify types of marks on the enamel of the occlusal relief in an area of 0.16 mm² ocular reticule (Semprebon et al., 2004; Solounias & Semprebon, 2002) .



Figure 9. The silicone mould (left) and resin replica (right) of the specimen RT6417

4.3 Methodology

The methodologies used in analysis to reconstruct diet and identify seasonality are microwear and mesowear.

4.3.1. Mesowear

The term mesowear was coined by Fortelius & Solounias (2000) and it refers to the macroscopic wear on teeth that is visible to the naked eye (Green & Croft, 2018). This develops over an animal's lifetime and provides insight into the average diet of a species in a specific location over time. Mesowear cannot detect seasonal changes in diet due to its cumulative nature. Two types of wear must be considered when one studies the wear facets in the teeth of herbivorous mammals. Browsers, that consume leaves of dicotyledonous plants, twigs, fruits, or browse, have teeth working against one another making the type of wear where the enamel is eroded to create sharp-edged enamel surfaces with well-developed facets and this type of wear is attrition (Green & Croft, 2018). On the other hand, grazing herbivores which consume grasses and other low-growing vegetation have substantial amounts of internal opaline silicates that wear the tooth enamel which



Figure 10. Specimens from the site labelled and digitized for future reference (Image credits: Dr Drucker)

results in abrasion type of wear (Ackermans, 2020; Green & Croft, 2018). According to Ackermans (2020) grazing animals feed close to the ground in open habits and could also ingest dust and grit. Whether the major factors causing tooth wear are phytoliths or external abrasives is still debated. Mesowear develops over an animal's lifetime, so it is impossible to detect seasonal changes in diet (Green & Croft, 2018; Rivals et al., 2013). Fortelius & Solounias, (2000) in the original literature summarize it as “the average diet of a particular species from a particular location in space and time”.

4.3.2. Microwear

Microwear is the term used to describe the microscopic damage to enamel that happens during mastication (Green & Croft, 2018). Unlike mesowear, microwear is not a long-term signal as the ingestion of new particles will lead to the elimination of previous microwear traces and the creation

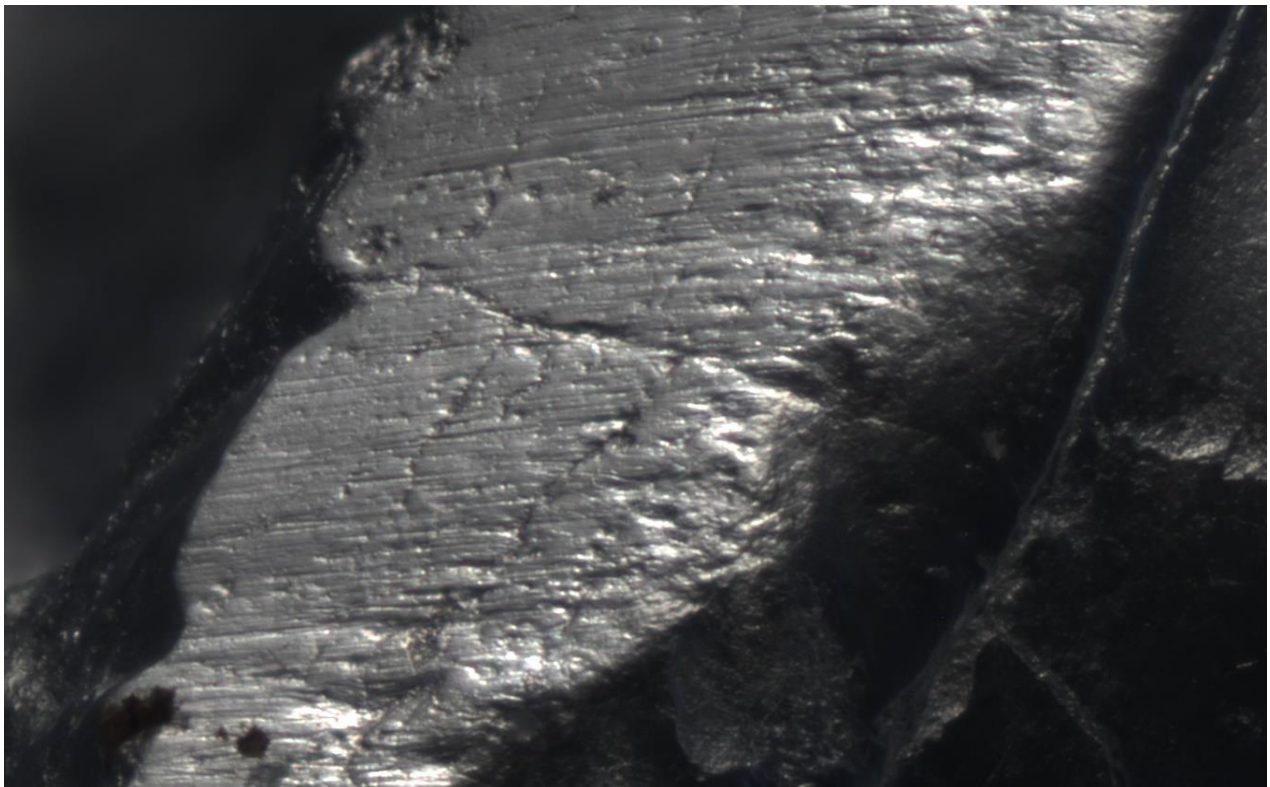


Figure 11. Microscopic image of the occlusal surface of the specimen RT5978 taken with a stereo microscope.

of new wear marks, hence providing information within a short temporal scale – days to weeks. (Green & Croft, 2018). This brief time scale reflects the feeding habits of the animal at the time of its death, which in turn is indicative of the prevalent ecological conditions at that time.

Dental enamel undergoes the action of abrasive particles, resulting in a series of microwear features on the surface and among them 'pits' and 'scratches' are more significant. Microwear features exhibit significant variability in their density depending on the animal's feeding habit, allowing clear distinctions between different feeding ecologies. This helps determine whether an animal has a diet typical to browsers or grazers, the ecological conditions in which their activities developed, and the duration of human occupations at a specific site.

The samples are analysed using a stereo microscope (Zeiss Stemi 2000-C) under 35x magnification and are quantified within the 0.16 mm² ocular grid for both scratches and pits on the occlusal

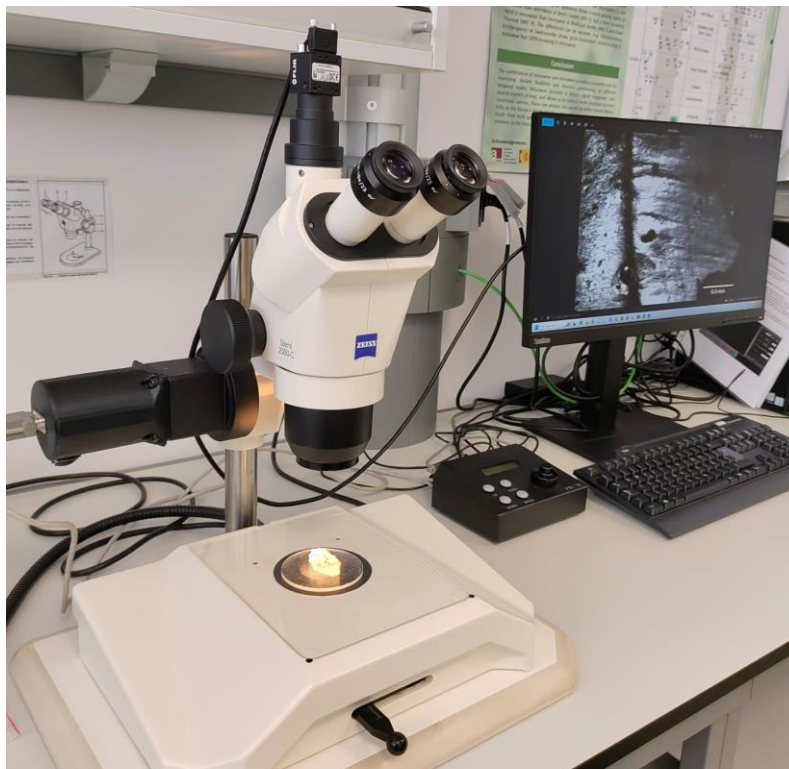


Figure 12. Zeiss Stemi 2000-C stereomicroscope used for the analysis.

surface of the teeth. Quantification and identification of both scratches and pits are performed on two separate locations on the tooth to obtain an average score for both from a sample.

Microwear was quantified in the mesial area (paracone or protocone) of the upper teeth and the meso lingual area (protoconid) of the lower teeth as established by Semprebon et al., (2004) and Solounias & Semprebon, (2002). The mould was illuminated with an adjustable light source to observe the various microwear marks, which have different depths and reflect light differently, creating lights and shadows to help in identification (Solounias & Semprebon, 2002). In the 0.16 mm² area, microscopic marks identified as pits and scratches were categorized into several types (Semprebon et al., 2004).

4.4 Sample Analysis

4.4.1. Mesowear analysis

Regarding the mesowear study, the standardized method was used (Mihlbachler et al., 2011). This method is based on a cusp wear scale with seven categories (0 to 6), ranging from high and sharp cusps to category 0, to flattened cusps in category 6. The mesowear was analysed from the buccal view of the upper teeth and the lingual part of the lower teeth. The degree of mesowear is noted and for each taxon, an average mesowear score (MWS) is obtained.

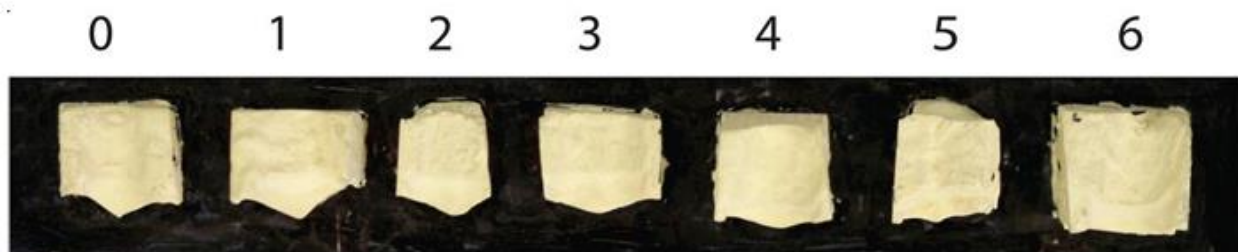


Figure 13. Mesowear scale used to score MSW according to (Mihlbachler et al., 2011) scale

For scoring mesowear, two variables are taken into consideration – Occlusal relief and Cusp shape. Occlusal relief is the cusp height which can be scored metrically in preference to subjectively analysing from digital photographs and this accounts to high or low. The cusp shape is scored as sharp, rounded, or blunt (Green & Croft, 2018). Mesowear gives the average result of several years of feeding. It reproduces the overall wear of an individual over its whole lifetime (Fortelius & Solounias, 2000; (Solounias & Semprebon, 2002).



Figure 14. Specimens RT 8469 and RT 8550 (Image credits Dr. Drucker)

4.4.2. Microwear analysis

Scratches

Scratches are elongated narrow micro stripes with parallel sides, and can be classified as "fine scratches," "coarse scratches," or "hyper coarse scratches." Their appearance and light reflectivity distinguished their categories. Fine scratches were narrow, shallow and less refractive, while coarse scratches were wider, deeper and highly refractive. Both types reflect light and appear as shiny, whitish lines, though fine scratches are dimmer due to their narrowness. Hyper coarse scratches are very deep and wide, and appeared as dark fissures due to low reflectivity. They

sometimes have a puncture point at the end, indicating the element that created the point was dragged across the enamel (Semprebón et al., 2004). For scratches, the following observations were made in this study:

Scratch Number (NS)

The number of scratches in the selected grid of 0.16 mm² is counted. While placing the square grid, it is kept such that the scratch direction is parallel to one of the parallel sides of the square. This helps in getting fully long scratches across the square grid and makes the counting easier.

Scratch Width Score (SWS)

As mentioned above, scratches are classified according to their width: fine (superficial and low refractivity), coarse (deep and higher refractivity), and hyper-coarse (deeper, wider, and much darker). Each of the different width combinations is assigned a number but to be counted as one, each type should be present more than four times in the analysed area.

- Only fine scratches → 0
- Fine scratches along with coarse scratches → 1
- Only Coarse scratches → 2
- Coarse scratches along with hyper coarse scratches → 3
- Only hyper-coarse scratches → 4

After obtaining the number of scratches, calculate the average for all dental samples. The result will indicate the average scratch width ranging from 0 to 4.

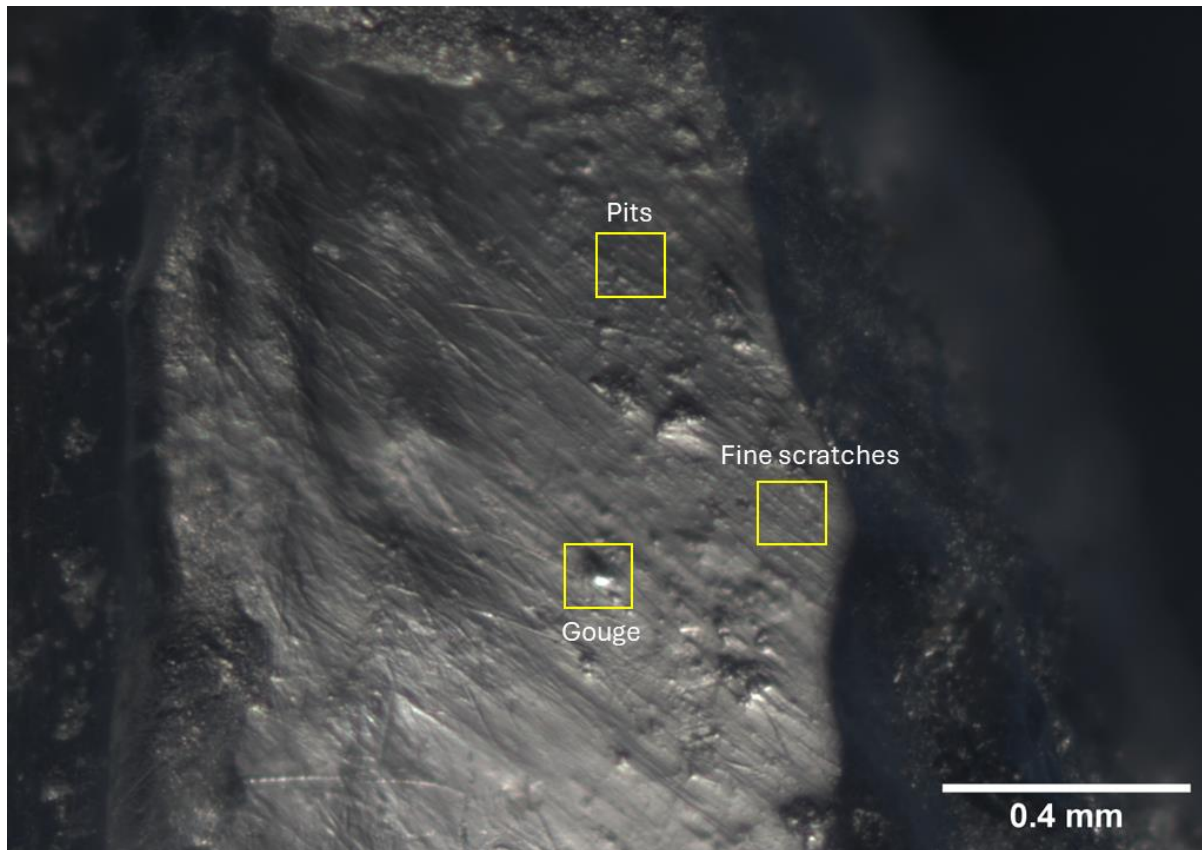


Figure 15. Specimen RT 6417's occlusal surface (x 35) showing the microwear scoring parameters.

Cross-scratches (XS)

These are scratches oriented perpendicular to the other scratches on the analysed surface of the tooth, which can indicate an alteration in the chewing cycle. They are also noted only if they are present more than four times in the analysed area of each tooth. Numbers are assigned to them as follows:

- All micro-scratches in the same direction (fewer than four crosses) → 0
- Two or more orientations (more than four crosses) → 1

Pits

The points that have a circular or semicircular shape are classified as large pits or small pits. Differential refraction of light (Semprebon et al., 2004) was used to classify pits based on their sizes. Small pits are shallow, reflecting light easily and appearing bright and white, while large pits are wider, deeper, and less reflective, never appearing bright. Among the large pits, "puncture pits" are very deep and symmetrical, resembling craters with regular margins, appearing dark due to their low light reflectivity. These varied in size, with large puncture pits have a diameter of 0.1 mm or more, small puncture pits 0.03 mm or less, and medium puncture pits falling between these extremes. Gouges (G) are crater-shaped with irregular, asymmetrical margins (Solounias & Semprebon, 2002; Semprebon et al., 2004).

Number of Pits (NP)

Pits in the area to be analysed are counted.

Large Pits (LP)

These are deep, symmetrical pits with regular margins and low refractivity. Mostly appears in frugivores and other species with diets that include seeds, fruits, and leaves. More than 4 large pits indicate presence.

- Absence → 0
- Presence → 1

Concisely, this study uses the following variables:

1) Total number of pits (NP) and total number of scratches (NS), averaged from two counts per tooth in separate places on the occlusal surface.

- 2) Presence of > 4 large pits (LP) and gouges (G).
- 3) Average width of the scratches (SWS) classified from 0 (fine scratches) to 4 (hyper-coarse scratches).
- 4) Presence of > 4 cross scratches (XS) and hyper-coarse scratches (HC).
- 5) Mesowear score (MWS)

4.5 Analysing seasonal death events

The standard deviation (SD) and coefficient of variation (CV) of scratches are calculated to analyse death events over different time scales. SD alone struggles to distinguish between deaths occurring in warm seasons versus longer periods, while CV alone has difficulty separating short, cold-season events from more prolonged ones. By combining both measures in a 2D mapping approach, it becomes possible to classify three scenarios: (A) one season (or shorter), (B) a period longer than one season, and (C) two separate events that occurred in different non-contiguous seasons (Rivals et al., 2015). This method is validated through a classification methodology based on the naïve Bayes classifier and helps in categorizing new samples accurately (Rivals et al., 2015).

The 2D approach visually represents these scenarios on an SD-CV plane as a heat map (Fig 16) where samples fall into distinct regions corresponding to different types of death events. The classification tool not only categorizes samples but also highlights cases where classifications may be uncertain, especially when events do not fit neatly into one category. This uncertainty is visually represented by coloured bands along the boundaries of the regions on the SD-CV plane, indicating the probability of a sample belonging to an adjacent category. Coupling SD and CV in this way provides a more accurate and refined understanding of seasonal death patterns and helps researchers categorize and interpret their data more effectively (Rivals et al., 2015).

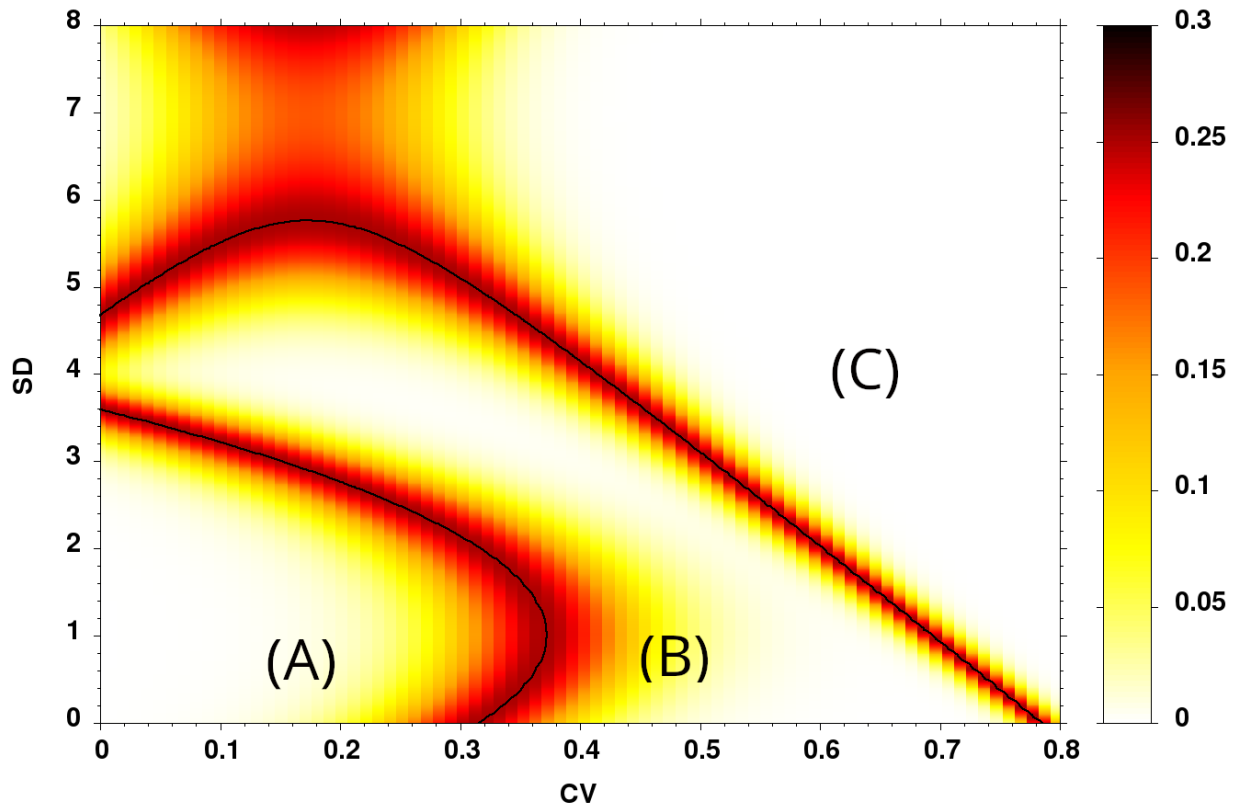


Figure 16. Bivariate graph in which the coefficient of variation (CV) is the X axis and the standard deviation (SD) is the Y axis. A) Seasonal death (equal to or less than one season), B) death throughout the year (more than one season). C) death at different times of the year (more than six months apart).

Chapter 5. Results

The dental remains of *Cervus elaphus* recovered during the 1960s-1970s excavation of Riparo Tagliente consisted of specimens of different preservation states. Of all the 72 specimens received for the study, a few were discarded as they did not fit the criteria for the study.

Table 1. Summary of Mesowear and Microwear Dental Analysis from Riparo Tagliente

US	Mesowear		Microwear							
	No. of samples	MWS	No. of samples	N. pit	N. scr	LP%	G%	SWS	XS%	HC%
1	1	2	1	28	16.5	100	100	2	0	0
4	5	1.8	2	34.2	14.7	50	50	2	0	0
5	7	1.5	4	21	19.3	75	25	1.5	0	0
6	7	2	7	26.5	18.5	57	42	1.1	0	0
7	8	1.7	9	26.7	18	66	66	1.3	0	0
8	7	1.7	2	23	16.5	50	100	2	0	0
9	9	1.8	6	30.5	21.7	0	0	1.6	0	0
10a	7	2	5	28.3	16.9	60	20	1.2	0	0
10b	2	2	1	23.5	21	0	0	2	0	0
10c	4	2	4	26.8	21.3	75	50	1.5	25	0

10d	4	1.7	4	25.5	21.7	25	0	1.2	25	0
10e	1	1	1	31	16	0	0	1	0	0
10f	1	2	-	-	-	-	-	-	-	-
13	2	2	3	27.1	19.3	66	0	1.3	0	0

N = Number of specimens; MWS = Mesowear score; Npit = Average number of pits; Nscr = Average number of scratches; LP% = Percentage of individuals with large pits; G% = Percentage of individuals with gouges; SWS = Scratch width score; XS% = Percentage of individuals with cross scratches; HC% = Percentage of individuals with hyper-coarse scratches.

5.1 Mesowear Analysis

A total of 65 samples were analysed for mesowear out of the initial 72. Eight dental pieces were excluded due to the poor condition of their cusps, which had either been altered by taphonomic processes or were not sufficiently developed to form wear facets due to ontogenetic reasons (Rivals et al., 2007). All the teeth that were analysed and deemed suitable had sharp, high cusps, with mesowear scores (MWS) ranging between 1 and 3 on the mesowear score scale by Muhlbachler et al., (2011).

The samples used for mesowear analysis came from US 1, 4, 5, 6, 7, 8, 9, 10, 13, and their sub-layers. The number of specimens analysed from US 1, 4, 5, 6, 7, 8, 9, and 13 range from 1 to 9 specimens (Table 1). Samples from US 10 and its sub-layers were grouped separately due to their sizable numbers. The sub-layers 10a, 10b, 10c, 10d, 10e, and 10f had 7, 2, 4, 4, 1, and 1 sample each, respectively. Other US samples and their sub-layers were combined because they contained too few individuals to calculate an average MWS.

Samples from US 1, 6, 10a, 10b, 10c, 10f, and 13 exhibited a high average mesowear score of 2. The lowest average mesowear score was 1, observed in the sample from US 10e, which might indicate an individual with very sharp cusps. The overall average mesowear score for all 65 individuals analysed from the site is 1.8, indicating a low-abrasion diet.

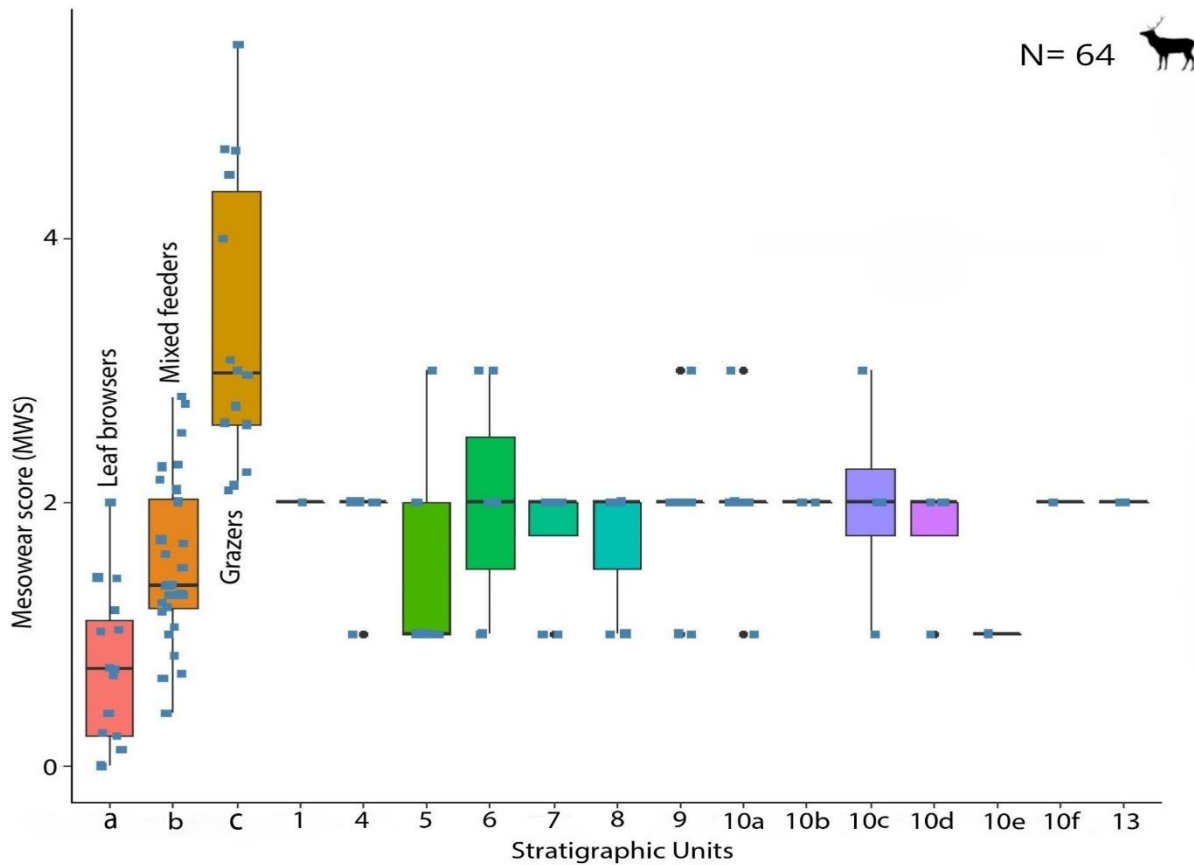


Figure 17. Box plot with the mesowear values of extant species compared with the samples from the site of Riparo Tagliente. The first three box plots in the diagram are that of the extant species dietary regime and the rest of the box plots are of the samples from Riparo Tagliente.

To understand the diet of the individuals from Riparo Tagliente, they are compared with that of the diet of the extant ungulates (Figure 17). Each US with a sizeable number of individuals (y-axis) is plotted against their mesowear score (MWS) (x-axis). The first three box plots from the left are the diet regime of the extant species and the rest of the box plot is that of the samples from Riparo Tagliente.

5.2 Microwear Analysis

A total of 49 dental samples were analysed for microwear. Twenty-three samples were discarded due to poor preservation (taphonomic damages) or ontogenetic factors (too young or too old individuals). The number of pits observed ranged from 12 to 43, with two counts recorded per sample. The average number of pits across all analysed material was 27. Large pits were observed in 48% of the individuals, while gouges were present in 34.8%.

Regarding scratches, the number ranged from 12 to 30.5. The average number of scratches, calculated after observing two counts per individual, was 18.5 scratches per counting unit. The average scratch width score (SWS) was 1.5, with an equal distribution of fine and coarse scratches. Hyper-coarse scratches were rarely observed. Cross-scratches were noted in only two samples.

5.3 Dietary inference based on Microwear analysis

The number of pits and scratches observed in the samples allows researchers to identify the dietary preferences of the individuals. To represent this graphically, a bivariate graph was plotted with the number of scratches on the x-axis and the number of pits on the y-axis. Two Gaussian confidence ellipses were included in the graph, representing the diets of extant ungulates (browsers and grazers) based on data from Solounias & Semprebon (2002). Depending on where the species from the studied archaeological site falls within this graph, its dietary tendencies at the time of death can be inferred.

In the bivariate graph (Fig. 18), five layers US 1, 4, 8, 10a and 10e fall within the browsing diet area. Eight stratigraphic units (US 5, 6, 7, 9, 10b, 10c, 10d and 13) are between the values of browsers and grazers, indicating a mixed diet. No considerable number of individuals fall exclusively in the grazer category. Some individuals from different substratum from the site were

classified together, except for those from US 10, where each substratum was plotted individually due to the significantly high number of individuals in each sub-layer (Fig. 18).

The analysis of pits and scratches, combined with the plotted graphs, suggests that this group of individuals had a slight preference for browsing, with a dominant number of individuals displaying mixed feeding behaviour. This data reflects their diet in the days or weeks before death, as it is based on microwear analysis.

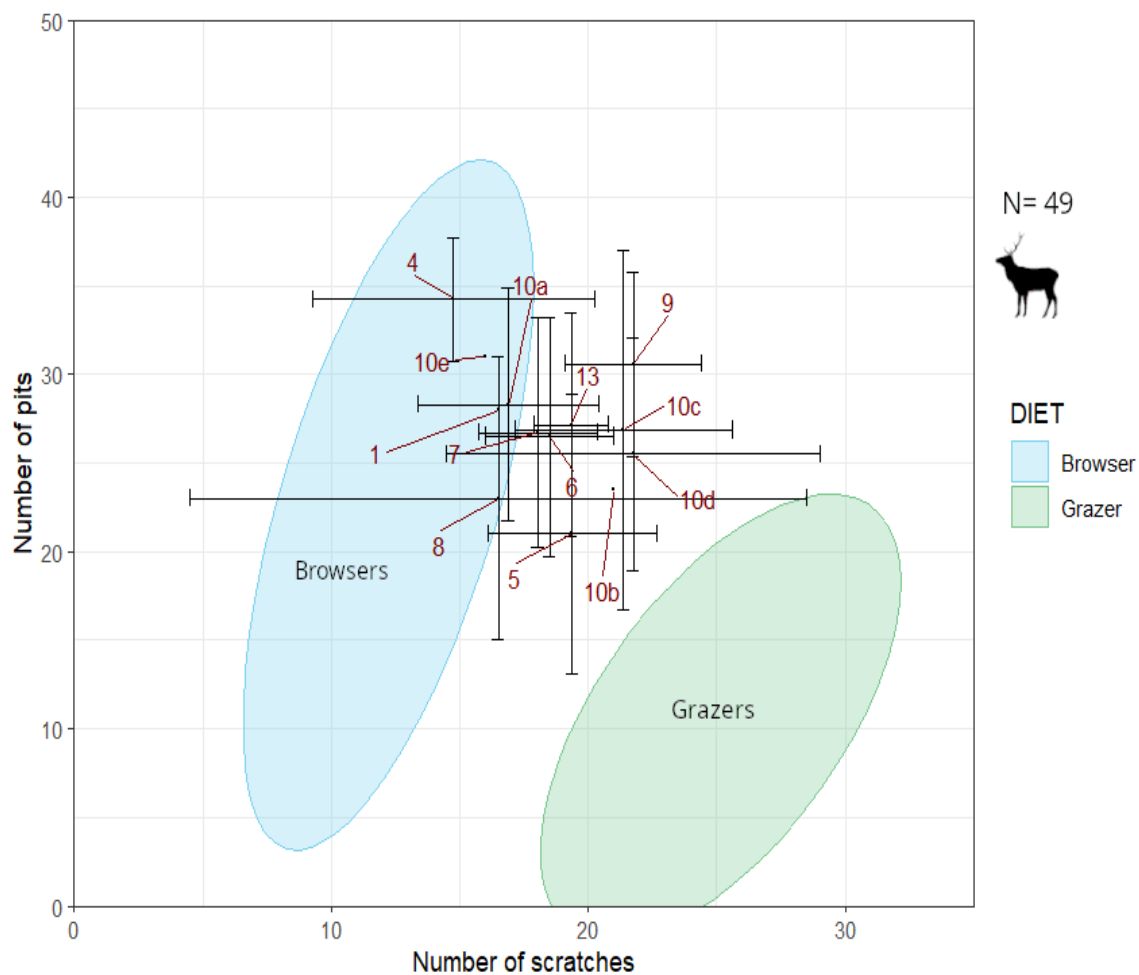


Figure 18. Bivariate plot where the X-axis represents the average number of scratches from each US, and the Y-axis represents pits. The error bars correspond to the standard deviation (SD) for the individuals from each layer. The ellipses correspond to Gaussian confidence ellipses ($p= 0.95$) and are in the areas where current species with browsing and grazing diets are found by *m Solounias and Semprebon (2002)* and *Rivals et al. (2010)*.

5.4 Variability in Seasonality

A heatmap is plotted to understand the duration of mortality events. The standard deviation (SD) of scratches and coefficient of variation (CV) of scratches are plotted on the y-axis and x-axis, respectively. The boundary line heat map is plotted such that there are three areas with the error probability – A, B, and C. Region A refers to seasonal or shorter events. Region B represents occupation longer than one season and region C refers to separate events that occurred at various non-consecutive seasons (Rivals et al., 2015).

Table 2. Variability of the microwear signal based on the SD and CV values of scratches

Unit	N	Mean Scratches	SD	CV	Zone	Duration
1	1	-	-	-	-	-
4	2	-	-	-	-	-
5	4	-	-	-	-	-
6	7	18.5	3.304	0.1785945946	B	longer than 1 season
7	9	18.0555	3.45	0.191077511	B	longer than 1 season
8	2	-	-	-	-	-
9	6	21.75	3.2365	0.1488045977	B	longer than 1 season
10	15	19.8571	5.0469	0.2541609802	B	longer than 1 season
13	3	-	-	-	-	-

To assess seasonality, only units with a sample size of five or more individuals were considered, as a smaller number of individuals would not yield statistically reliable data. Therefore, in this

analysis, only layers 6, 7, 9, 10, and their respective sub-strata were utilized to generate the heatmap (Figure 19). All individuals analysed in this study fall within region B, suggesting that the site was occupied for extended periods, likely spanning multiple seasons, and that mortality events occurred throughout the year.

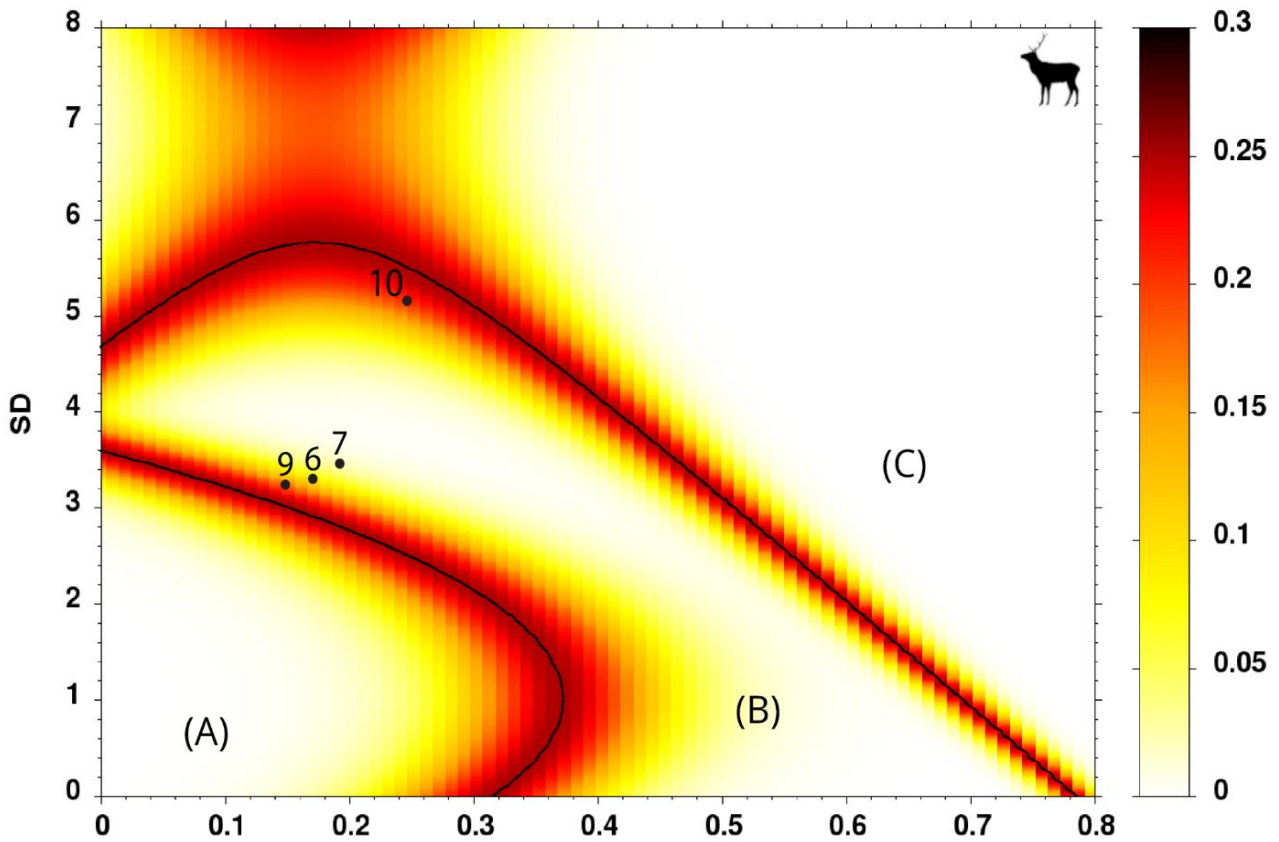


Figure 19. Bivariate plot - coefficient of variation (CV) and standard deviation (SD) calculated based on the number of scratches and plotted on the x-axis and y-axis, respectively

Chapter 6. Discussion

The 72 specimens subjected to analysis from the Late Epigravettian at the site of Riparo Tagliente yielded significant results that could aid in understanding the dietary habits and seasonal behaviour of *C. elaphus* from the site. For understanding the paleoecology and subsistence strategies of the population, the findings from both the microwear and mesowear analysis are interpreted as follows.

6.1 Mesowear analysis

The mesowear analysis on 64 red deer dental remains from Riparo Tagliente reveals dominance of a low-abrasion diet among the group of individuals, as indicated by the average mesowear score of 1.8. This suggests that the individuals primarily consumed soft vegetation, but this data also leans towards mixed feeding practices among the individuals. The presence of sharp, high cusps in the analysed teeth further supports this conclusion, as such dental characteristics are typically associated with species that feed on leaves and other soft plant materials, rather than the more abrasive grasses consumed by grazers.

There are some interesting observations in the mesowear scores throughout various stratigraphic units. The specimens from the stratigraphic units 1, 6, 10a, 10c, 10f and 13 exhibited an average mesowear score of 2 which is higher than the others. Moreover, 1 specimen from the stratigraphic units 5 scarpata, 2 from US6 and 1 each from US 9, 10c and 10a exhibited a mesowear score of 3 which indicated high abrasion. Although the individuals from the US 5 scarpata, 9, 10c and 10a have a higher mesowear score (3), they cannot be relied fully for analysing the dietary preferences of all the population from the respective stratigraphic layers as these specimens present a result at the individual level (Loffredo & DeSantis, 2014). Such single specimens from the stratigraphic

layers need to be analysed geochemically to get clearer dietary determinations. However, all the specimens which scored higher mesowear scores according to the (Mihlbachler et al., 2011) scale, could indicate that they all lived in a timeframe where a slightly more abrasive diet was prevalent. This indicates a higher preference for the consumption of grass by individuals who had the availability of open grasslands or vegetation with more abrasion. Additionally, the average mesowear score of the sample from US 10e suggests a young individual with minimal wear and this could also indicate that diet varied across individuals of different age groups.

The remaining specimens exhibited an average mesowear score ranging between 1.5 and 1.8, encompassing individuals from stratigraphic layers 4, 5, 7, 8, and 10d. These scores are insufficient to indicate a grazing diet but align more closely with a browsing diet. The lower mesowear score suggests these individuals primarily consumed softer diets with fewer abrasives. This pattern may reflect the presence of more forested environments, where available vegetation consisted predominantly of woody and non-woody dicotyledonous plants suitable for browsing (Fortelius & Solounias, 2000).

6.2 Dietary traits and paleoecology of red deer

This variation in mesowear scores across units and among individuals suggests that dietary habits were not uniform and might have been influenced by both environmental factors and the age of the animals. It is also linked to the specific types of plants available and selectively consumed by the red deer. These findings emphasize the need to analyse additional ungulates and their dietary preferences at the site to draw more comprehensive conclusions on the dietary landscape and the factors influencing it.

The range and distribution of red deer during the Late Pleistocene were significantly influenced by climatic fluctuations, particularly during and after the Last Glacial Maximum (LGM). According to previous studies, the pattern of red deer prevalence is observed to be contracted during colder periods and expanded during warmer intervals (Meiri et al., 2013; Niedziałkowska et al., 2021). Following the LGM, as deglaciation progressed, red deer began to recolonize the European continent, moving northward as the climate warmed. In a study conducted, the biome analysis of red deer remains from the Late Pleistocene reveals a strong preference for forested environments. Approximately 57% of the dated deer records were in several types of forests, including coniferous, mixed, and deciduous forests (Sykut et al., 2023). This preference for forested habitats is consistent with what is known about red deer ecology, as forests provide both shelter and a diverse range of forage. Interestingly, woodlands, particularly in southern and western Europe, represented the second most common biome occupied by red deer, accounting for 29% of the samples (Sykut et al., 2023). This indicates that red deer were also adapted to open, dry woodlands.

The absence of individuals falling exclusively within the grazer category highlights the limited role of grasses in their diet, reinforcing the idea that the population was primarily adapted to forested environments with abundant leafy vegetation. The stratigraphic variation in dietary patterns further suggests that environmental conditions and food availability may have fluctuated over time influenced by seasonal variations, influencing the feeding behaviour of the populations.

The results suggest that *Cervus elaphus* species from the Riparo Tagliente site exhibited mixed feeding behaviours in the past, underscoring the species' high ecological flexibility. When plotted on a bivariate graph, with mesowear scores against groups of individuals from each stratigraphic unit, the data revealed a mixed feeding pattern, with a slight tendency among certain individuals

towards browsing diets. These findings align with the general hypothesis of red deer as ecologically plastic "intermediate feeders," supporting their classification as neither purely browsing nor grazing ruminants (Di Stefano et al., 2015). A study conducted by Gebert & Verheyden-Tixier (2001) analysing the stomach contents of extant red deer species to understand variations in diet also corroborates that red deer species are among the category of intermediate feeders with a mixed diet composed of graze and browse.

The isotopic analysis conducted as part of this research indicates that the red deer species' diet consisted of C3 plants, suggesting that the vegetation was primarily composed of open forest cover. Additionally, the climatic conditions corresponding to each stratigraphic unit are further clarified. Warmer conditions are observed in Unit 9, while Units 10, 5, and 6 exhibit much colder climatic phases. These colder periods are marked by a notable decline in temperature, as evidenced by the abundance of large mammals associated with cold environments found within these layers (Ammanova, 2024).

6.3 Microwear analysis

The dietary patterns of 49 specimens were examined through microwear analysis. The observed range in the number of pits (12 to 43) and scratches (12 to 30.5) suggests a diet that included a variety of food types, from softer, leaf-based diets to more abrasive materials. However, the average number of pits are 27 and the scratches are 18.5 and this aligns with the mixed feeding behaviour observed in other ungulate species that consume both browsing and grazing vegetation (Rivals & Lister, 2016).

The presence of large pits in 48% of the individuals and gouges in 34.8% indicates that some individuals likely consumed harder or more fibrous plant material, possibly due to seasonal

availability or individual dietary preferences. The average scratch width score (SWS) of 1.5, with an equal distribution of fine and coarse scratches, suggests a balanced diet with a mix of different food textures. The rarity of hyper-coarse scratches and cross-scratches further supports the interpretation of a primarily browsing diet with occasional ingestion of harder materials.

The bivariate graph plotting pits against scratches provides a clear visualization of the dietary tendencies of the Riparo Tagliente *Cervus elaphus* species. The placement of samples from US 1, 4, 8, 10a, and 10e within the browsing diet area confirms that these individuals predominantly consumed browse, i.e. low abrasive vegetation. However, most samples, particularly from US 5, 6, 7, 9, 10b, 10c, 10d, and 13, fall between the values of browsers and grazers, indicating a mixed diet. This distribution suggests that while browsing was prevalent, these individuals also consumed grasses or other abrasive materials, possibly as a seasonal adaptation or in response to food scarcity.

6.4 Dietary inference and ecological implications

The microwear analysis of red deer (*Cervus elaphus*) teeth from Riparo Tagliente indicates a mixed-feeding dietary strategy, reflective of their adaptability to seasonal resource availability. Both scratches and pits on dental surfaces suggest that these animals consumed browse (shrubs and leaves) and graze (grasses), showing flexible feeding behaviour. Isotopic analysis further supports this by revealing a diet predominantly composed of C3 plants, which are characteristic of open forest environments, including shrubs, herbs, and grasses.

To place the dietary patterns of Riparo Tagliente's red deer in a broader ecological context, it is valuable to compare findings from other Late Epigravettian sites. A recent study by Drucker et al, (2024) on large ungulates from the northeastern Iberian Peninsula during the Upper Palaeolithic

found that *Cervus elaphus* exhibited mesowear patterns consistent with extant leaf browsers and mixed feeders, while microwear analysis revealed similar feeding strategies. This aligns with the findings at Riparo Tagliente, highlighting the adaptability of red deer across different regions.

In contrast, research by Thun Hohenstein et al. (2024) on ungulates from the Middle Palaeolithic site of Vajo Salsone suggests a different dietary pattern. Here, microwear data indicate a predominance of high-abrasive diets, suggesting a group of animals that primarily engaged in grazing, unlike the more varied feeding strategies observed at Riparo Tagliente.

However, there is currently no published dental wear data from other Late Epigravettian sites in close proximity to Riparo Tagliente to allow for a more direct comparative analysis of ungulate dietary habits and vegetation. This gap in data limits a comprehensive regional understanding of the dietary strategies employed by herbivores during this period. Nonetheless, the mixed-feeding strategy of the red deer at Riparo Tagliente reflects their ability to adapt to dynamic environmental conditions, a pattern that appears consistent with findings from other regions of Europe during the Late Epigravettian.

6.5 Variability of the microwear signal and the seasonality of occupation of the site

The variability in microwear patterns, reflecting short-term dietary changes, serves as a valuable tool for inferring the timing of site occupation relative to seasonal resource availability (Uzunidis & Rivals, 2023). The microwear data of an individual is highly sensitive to the short-term diet regime of the individual and it fluctuates depending on the season reflecting the availability of certain plant types seasonally. The specimens analysed from Riparo Tagliente's late Epigravettian sequences exhibited an average number of scratches as 18.5 and this is not aligned to the very

abrasive wear pattern scale but to a moderately abrasive diet (Rivals et al., 2013) which in turn gives the result of mixed feeding. Mixed feeding suggests that the animals were consuming a combination of grasses and browse, reflecting a diet that varied either seasonally or in response to fluctuating resource availability within a particular season.

When microwear patterns from multiple individuals within a single stratigraphic layer shows consistent wear types, it suggests a homogenous diet and hence a specific season of occupation. But, when there is a high degree of variability within the same unit, it may indicate that the site was occupied repeatedly across different seasons with the diet shifting accordingly. This calculation can be effectively conducted on the stratigraphic sequence when a minimum of five individuals are present, as this threshold is necessary to serve as a reliable marker of dietary habits. Among the 49 individuals analysed across layers 13 to 1, only layers 6, 7, 9, and 10 contain more than five individuals each. The specimens from layer 6 exhibit a mean scratch value of 18.5, while those from layer 7 have a mean value of 18. layer 9 shows a mean value of 21.75, indicating a diet associated with more abrasive materials. Finally, the mean scratch value of all specimens from layer 10, when combining all its substrata, is 19.8 (Table 2).

The heatmap analysis of seasonality is based on the standard deviation (SD) and coefficient of variation (CV) of scratches (see Materials and Methods chapter), provides additional context for understanding the timing of mortality events. By focusing on stratigraphic units with sufficient sample sizes (US 6, 7, 9, and 10), the heatmap reveals distinct patterns that correlate with different occupation periods. When plotted the standard deviation (SD) of scratches against their coefficient of variation (CV) all the specimens belonged to region B (Figure 19), representing longer occupations, indicating that the site was inhabited for extended periods, possibly through multiple seasons.

As the microwear data shows mixed feeding it suggests that the site may have been occupied year-round with animals adapting to the seasonal availability of diverse diets. This result could also imply that the individuals lived during a period of seasonal transition, such as spring or autumn, when both grasses and browse were accessible. Another interpretation could be that the individuals occupied the site during a time of environmental variability where both open grasslands and forested areas were accessible letting the animals graze and browse as necessary.

The palynological study conducted on the layers from 14-5 comes to back this hypothesis stating the period can be characterized by the appearance of common trees and plants which grows in cool-humid and temperate climates such as *Betula*, *Corylus* sp., *Quercus Robur*, *Ulmus* and some herbaceous species. The climatic conditions are characterized as hot-humid in layers 10 and 9, with the prevalence of thermophilic species like *Fraxinus*, *Cotinus*, and *Ostrya* (Bartolomei. G. et al., 1982; Fontana et al., 2009).

This pattern of seasonal occupation is further supported by the presence of faunal remains that are indicative of hunting practices adapted to the seasonal availability of different game species. The studied faunal associations of the Epigravettian deposits show the same alternation of species found in the older layers, with an increasing percentage in dominance of deer.

In layers 15 through 13, the majorly dominated species are that belong to the periglacial climate like marmot, ibex and wolverine. In contrast, the layers from 13 to 4 are characterised by species associated with the temperate climate like the deer, roe deer, and wild boar. This data can be corroborated with that of the palynological results confirming the climate to be temperate. The presence of deer with varying degrees of tooth wear and eruption stages across different layers suggests that these animals were hunted at different times of the year, further supporting the seasonality inferred from the microwear data. There is a recurrence of the ibex in layers 5 and 6

which could indicate a harsher climatic condition (Bartolomei. G. et al., 1982; Bertola et al., 2007; Fontana et al., 2009).

Additionally, from the faunal analysis on some specimens for determining age it was found that the peak occupation of the site took place during the months of May to June (Fontana et.al, 2009) which is a transitional season between Spring and Summer. In accordance with the temperate phase, studies also shows that the site had to be occupied for at least 10-11 months or in some cases, or possibly year-round, corroborating the microwear analysis showing seasonal variation in the dental remains of red deer from Riparo Tagliente. Layers 13 through 5 show a phase corresponding to the Bølling and Allerød interstage with a strong influence of anthropogenic alterations. The malacofaunal analysis of the Epigravettian layers (Girod, 2011) at the site notes the disappearance of *Pupilla muscorum*, likely assumed to be because of the increase in xerophilous species and temperate elements. In layers 12 through 6, the xerophilous species *Chondrina megacheilos* is well represented but shows a decline in layers 5 and 4 (Girod, 2011).

Overall, the microwear and mesowear data indicating mixed feeding behaviour in *Cervus elaphus* from Riparo Tagliente suggests a flexible, opportunistic feeding strategy in response to dynamic environmental conditions. Mesowear and microwear are good proxies for understanding the dietary ecology and seasonal variations of the *C. elaphus* species at the site of Riparo Tagliente. The sample size used for both these methodologies is good enough to give a modest result. Pairing it up with isotopic analysis, the samples yield good results. There could be errors in microwear analysis in the identification and measurements of scratches and pits through lenses or images and there could be variations among different users analysing the same samples (Green & Croft, 2018).

Chapter 7. Conclusion

The relevance of this research lies in its contribution to the understanding of Late Epigravettian paleoecology. Combined mesowear and microwear analyses provide a detailed understanding of the dietary habits and seasonal behaviours of the *Cervus elaphus* population at Riparo Tagliente. The findings indicate a mixed-feeding strategy with diet variations likely influenced by seasonal changes in vegetation and individual differences in age and preferences. The seasonality analysis suggests that the site was occupied for extended periods, potentially across multiple seasons.

By combining microwear analysis, isotopic data, and stratigraphic information, this study has reconstructed the dietary behaviour of red deer, offering a window into the vegetation structure and climate of the region. The predominance of C3 plants in the diet suggests the presence of open forest environments, while the fluctuations in climatic conditions across different stratigraphic units, ranging from warm phases in US 9 to colder conditions in US 10, indicate that red deer adapted their feeding habits to these changes. However, since the study focuses exclusively on specimens from the Late Epigravettian layers, the findings are chronologically specific and should be cautiously compared with other studies at this multi-period site. A broader comparative analysis with other ungulate species from Riparo Tagliente could provide further insights.

Future research could expand on these findings by examining the impact of climatic fluctuations on diet and migration patterns. Potential areas include cementum analysis for age estimation and determining the time of death, strontium and sulphur isotope analysis for reconstructing diet and migratory behaviours, dental calculus analysis to identify dietary phytoliths, and geometric morphometrics to assess feeding behaviours, wear patterns, and intraspecific variation in occlusal morphology. Moreover, incorporating a zooarchaeological perspective would offer valuable

insights into human-animal interactions, taphonomic processes in site formation, and post-depositional wear, further enriching our understanding of the *Cervus elaphus* population at Riparo Tagliente.

While the tooth wear analyses of red deer teeth from Riparo Tagliente provide valuable insights, there are several research gaps that could be addressed in future studies. These include the need for comparative studies with other species and sites, integration with other analytical methods, detailed seasonal and dietary analysis, consideration of taphonomic effects, exploration of human influence on red deer, etc. Addressing these gaps could lead to a more comprehensive understanding of the ecological adaptations and interactions of red deer during the Late Epigravettian period. These findings help reconstruct not only the paleoecology of red deer in this period but also the broader subsistence practices of the human populations that relied on them.

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