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Insights into archaeological and modern neotropical biomes: Examining diet and shape variation through white-tailed deer lower third molar

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ABSTRACT

The white-tailed deer (*Odocoileus virginianus* Zimmermann 1780) holds significant ecological importance across the Americas, both historically and in modern times. This species ranges from southern Canada to Brazil and exhibits polytypic characteristics, adapting well to diverse habitats including temperate, subtropical, semi-arid, rainforest, and savanna environments. In paleontology and archaeology, the comparison of dental characteristics between extant mammal species with known diets is commonly employed to infer the feeding behaviors of their ancient counterparts. This method assumes that extant and fossil species share similar dietary preferences, aiding in the identification of past environmental contexts. Consequently, we employed a multiproxy approach, combining the study of dental wear and 2D geometric morphometrics, to investigate potential relationships between molar shape, diet, and biomes among extant white-tailed deer populations across the Americas. Our analysis included a comparison with archaeological data from Panama. We sampled 274 extant lower second molar specimens for micro- and mesowear analysis, along with 105 lower third molar specimens from natural science museums for 2D geometric morphometric analysis. These were compared with a sample of 65 archaeological specimens from Panama. Our findings revealed distinct variations in the shape of lower m3 molars among extant white-tailed deer populations across different biomes, with notable differences observed in the archaeological samples as well. Micro- and mesowear analyses also indicated biome-related differences, suggesting a general browsing diet for white-tailed deer with nuanced variations across biomes. Mesowear analysis further suggested a dietary spectrum ranging from pure browsers to browser-mixed feeders. These findings offer valuable insights for the interpretation of fossil deer specimens recovered from archaeological sites.

1. Introduction

1.1. Neotropical biomes

In biogeography, the Neotropic ecozone is one of the terrestrial realms encompassing South America (including temperate southern regions), Central America, the Caribbean islands, and southern parts of North America (southern Florida and coastal central Florida). The Neotropic region features distinct flora and fauna compared to the Nearctic realm (Central and northern North America), owing to the long-standing separation between these continents. The formation of the Isthmus of Panama connected the two continents, facilitating the Great American Interchange and leading to some similarities in the flora and fauna of the region (Morrone, 2014).

The Neotropics encompass a variety of biomes, including moist and dry broadleaf forests, coniferous forests, temperate broadleaf forests, grasslands, savannas, shrublands, Mediterranean forests, woodlands, scrublands, deserts, xeric shrublands, and mangroves (Morrone, 2014). A biome is a large-scale ecosystem that occupies extensive areas at the (sub)continental scale or as a complex of smaller, isolated patches across these large areas. Each of the biomes consists of intricate fine-scale biotic communities, characterized by distinctive flora, fauna, vegetation types, and animal communities. Biome patterns are influenced by large-scale (macroclimate) and medium-scale (soil, water, disturbance) factors,

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with biome structures providing feedback to the environment. Typically, a biome is identified by a characteristic physiognomy (a combination of plant and animal life forms), though ecological feedback processes and disturbances can result in multiple stable states coexisting within the same geographic area. Biomes assemble (and disassemble) over both ecological and evolutionary timescales, shaping their functionality by selecting organisms with traits best suited to environmental challenges (Mucina, 2019). According to Mucina (2019), biomes are a valuable ecological and evolutionary concept for categorizing the biosphere into spatial and functional units that can be modeled and predicted with varying levels of accuracy and precision. For this reason, we have chosen to use this unit in our study. Specifically, we will focus on the biomes inhabited by white-tailed deer: Dry Broadleaf Forest (DBF), Moist Broadleaf Forest (MBF), Grasslands, Savannas, and Scrublands (GSS), Tropical Coniferous Forest (TCF), and Paramo (PAR) (Fig. 1).

1.2. White-tailed deer (Odocoileus virginianus Zimmermann 1780)

The white-tailed deer has been a significant species across the Americas both in Pre-Columbian times [e.g., Canada (Berg and Bursey, 2000), the United States (Byrd, 2011), Mexico (Blasco Martín et al., 2019), Guatemala (Emery, 2008), Belize (Boileau and Stanchly, 2020), the West Indies (Giovas, 2018), Panama (Cooke, 2004; Martínez-Polanco et al., 2021), Colombia (Correal, 1990), and Ecuador (Stahl and Athens, 2002)] and in modern times [e.g., the United States (Campbell et al., 2005), Mexico (Barrera-Bassols and Toledo, 2005; Weber, 2014), and Colombia (Martínez Salas et al., 2016)]. The white-tailed deer was important to pre-Columbian communities in the ancient anthropogenic savannas of central Panama, not only as a food resource, but also as symbols of standard cosmological spaces (Cooke, 2005). Deer antlers and bones were commonly employed for making artefacts and ornaments (Cooke, 2004; Martínez-Polanco et al., 2021). Male deer with branched antlers are frequently represented on polychrome ceramics and occasionally on cast-gold pendants after about 2300 cal yr BP (Cooke, 2004; Cooke and Jiménez-Acosta, 2010).

This species ranges from southern Canada to Brazil (Eisenberg, 1989; Smith, 1991; Gallina et al., 2019) and is highly adaptable, thriving in diverse habitats from temperate and subtropical regions to semi-arid environments, rainforests, and savannas (Eisenberg, 1989; Emmons, 1999). The white-tailed deer's habitat use depends on the quality, quantity, and diversity of available forage (Danields, 1991; Sánchez-Rojas et al., 1997; Gallina et al., 2010; Ramírez Lozano, 2012). Thirty-eight subspecies have been described, of which 24 live in Latin America. In the particular case of Panama, three subspecies inhabits the country today (*O. v. chiriquensis*, *O. v. truei*, and *O. v. rothschildi*) (Smith, 1991; Gallina et al., 2019).

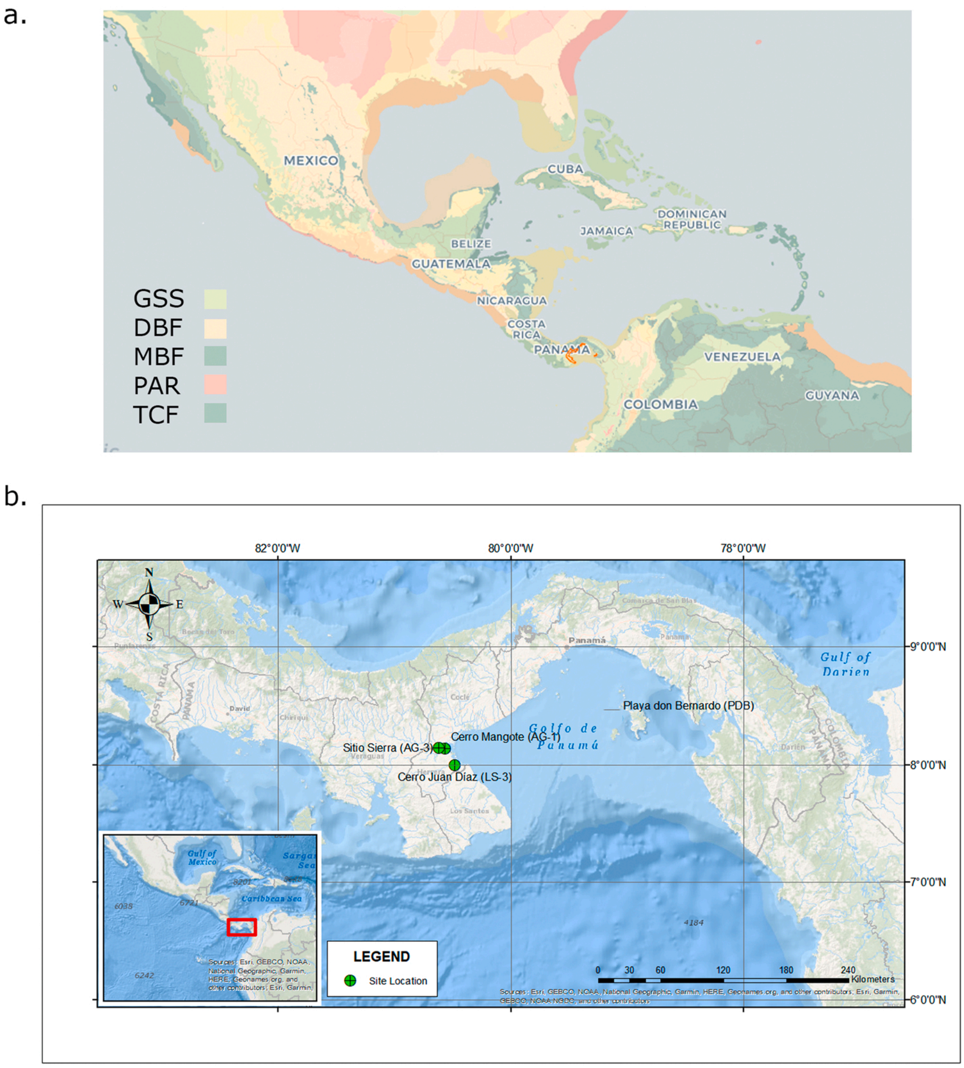

Fig. 1. . a. Biomes in which extant population of white-tailed deer (*Odocoileus virginianus*) inhabits. Based on DOPA (European Commission, 2024) Abbreviations: DBF: Dry broadleaf forests; GSS: Grasslands, savannas, and shrublands; MBF: Moist broadleaf forests; PAR: Paramo; TCF: Tropical Coniferous Forest. b. Geographical location of the archaeological sites located at Parita Bay, Panama.

Their diet changes with the seasons due to fluctuations in food availability, cover, and water (Sánchez-Rojas et al., 1997). During periods of high rainfall, abundant food resources are available, though dietary diversity may decrease as deer selectively feed on young leaves of trees, shrubs, and vines (Sánchez-Rojas et al., 1997; Bello et al., 2001; Arceo et al., 2005). In dry seasons, deer focus their foraging on the most nutritious fruits and leaves of trees, shrubs, and herbs available (Sánchez-Rojas et al., 1997; Bello et al., 2001). In some North American populations, females have been found to have different diet quality than males (McCullough, 1985; Beier, 1987); however, it is not well known if this variation occurs in neotropical populations.

Although it is true that the white-tailed deer is perhaps the most studied species of mammal in America, a gap remains in our understanding of the dietary ecology of current deer populations, potentially biasing comparisons with archaeological assemblages. Therefore, this paper aims to study the feeding habits of present-day white-tailed deer across various biomes in the Americas through dental wear analysis. Additionally, the molar shapes will be examined to identify biome-related differences using a 2D geometric morphometrics approach. These data from extant deer species will be compared with archaeological deer specimens from Parita Bay (Pacific, Panama) to determine whether the archaeological samples are similar to or different from extant populations both in terms of shape and feeding habits. This study is anticipated to serve as a reference for interpreting data from paleontological or archaeological contexts in comparable regions.

2. Materials and methods

2.1. Materials

For the 2 Dimension Geometric Morphometric analysis, we chose the third lower molar (m3) because it is the last tooth on the tooth row and, hence, posteriorly less constrained in comparison with teeth at intra-row positions. Additionally, the m3 is considered a significant phenotypic marker of adaptation to natural or anthropogenic environments (Cucchi et al., 2019; Jeanjean et al., 2022). Another advantage of m3 is its easily distinguishable shape compared to other teeth. This feature proves particularly advantageous in archaeological contexts where isolated pieces are prevalent, providing a reliable identification of the materials (Cucchi et al., 2019; Jeanjean et al., 2022; 2023; Pelletier et al., 2023). In total, 105 individuals were studied, 81 extant individuals (48 males and 33 females); and 24 archaeological specimens (Table 1, SP.1).

For mesowear and microwear analysis, second lower molars (m2) with intermediate dental wear that were intact and undamaged were selected. A total of 274 individuals were examined for mesowear, including 150 extant individuals (85 males and 64 females) and 124 archaeological specimens (Table 1, SP.1). For microwear, 207 individuals were studied, consisting of 142 extant individuals (76 males and 66 females) and 65 archaeological specimens (Table 1, SP.1).

Considering the age of the individuals, we selected adult animals between 2 and 4.5 years old, following Severinghaus's (1949) descriptions. At two years of age, white-tailed deer are considered to have adult teeth; the third molar is fully erupted, lingual ridges of the first and second lower molars are sharp and lower premolars have little wear, dentin is not visible on all three molars or is not as wide as the enamel, and moderate wear is present on the premolars. At 4 years and 6 months of age the lingual ridge of the first molar is quite worn, its secondary ridges can be observed, the dentin of the first and second molar is as wide as the surrounding enamel, moderate and moderate to high wear is present in the second and third premolars respectively, and the third molar is still sharp (Severinghaus, 1949).

The extant specimens are housed at the American Museum of Natural History, New York, USA (AMNH), Smithsonian National Museum of Natural History, Washington D.C., USA (NMNH), Naturhistorisches Museum Wien, Wien, Austria (NMW) and Museum für Naturkunde, Berlin, Germany (ZMBM). The archaeological specimens are housed at the Smithsonian Tropical Research Institute, Panama City, Panama (STRI) (Table 1; SP.1). We utilized museum catalogue data to categorize the deer according to their respective biomes. By leveraging their geographical locations, we accessed information through the Digital Observatory for Protected Areas (DOPA) Explorer portal (European Commission, 2024). The following biome categories were employed: Dry Broadleaf Forest (DBF), Moist Broadleaf Forest (MBF), Grasslands, Savannas, and Scrublands (GSS), Tropical Coniferous Forest (TCF), and Paramo (PAR). Table 1 provides the specific count of individuals categorized by biome. For the GMM analysis we only studied those groups with more individuals (DBF, MBF and GSS) (Fig. 1a).

Moist Broadleaf Forests (MBF): are typically found in large, discontinuous patches around the equatorial belt and between the Tropics of Cancer and Capricorn. These tropical and subtropical moist forests are characterized by minimal annual temperature variation and high rainfall, exceeding 200 centimeters annually. Dominated by semi-evergreen and evergreen deciduous tree species, MBF is prevalent on the Caribbean side of Central America. It also covers extensive areas in parts of South America, including the Venezuelan Amazon and northern Guianas, accounting for the Amazonian forest. Some of the rainiest and wettest forests in the world are located along a strip of northwestern Colombia, where the lower elevation of the Andes and a seasonal weakening of the Pacific high pressure system allow rain-bearing winds to reach the coast and northern Ecuador (Piperno and Pearsall, 1998).

Dry Broadleaf Forest (DBF): These forests occur in warm climates year-round and can receive several hundred centimeters of rain annually but experience long dry seasons lasting several months, varying by location. Seasonally dry tropical forests have annual rainfall less than 1600 mm, with at least 5–6 months receiving less than 100 mm. The vegetation is mostly deciduous during the dry season, with deciduousness increasing as rainfall decreases. In the driest forests, there is a notable increase in evergreen and succulent species. Tropical dry forests are primarily tree-dominated ecosystems with a more or less continuous canopy, where grasses are a minor element (Pennington et al., 2000; 2018; Dexter et al., 2018). The largest areas of seasonally dry tropical forests in South America are in northeastern Brazil (the 'caatingas', extending south to eastern Minas Gerais), and in the Caribbean regions of Colombia and Venezuela. Smaller and more isolated areas of these forests are found in dry valleys in the Andes of Bolivia, Peru, Ecuador, and Colombia, in coastal Ecuador and northern Peru, in the 'Mato

Table 1
Sample description discriminated by biomes and sex.

	2D-GMM			Mesowear			Microwear		
	Male	Female	Total	Male	Female	Total	Male	Female	Total
Dry broadleaf forests	15	7	**22**	10	6	**16**	10	6	**16**
Moist broadleaf forests	26	18	**44**	44	36	**81**	37	38	**75**
Paramo	0	0	**0**	6	3	**9**	5	3	**8**
Grasslands, savannas, and shrublands	7	8	**15**	19	17	**36**	19	17	**36**
Tropical coniferous forest	0	0	**0**	6	2	**8**	5	2	**7**
Archaeological	0	0	**24**	0	0	**124**	0	0	**65**
Total	**48**	**33**	**105**	**85**	**64**	**274**	**76**	**66**	**207**

Grosso de Goiás′ in Central Brazil, and scattered throughout the Brazilian cerrado biome on fertile soils. In Central America, seasonally dry forests are concentrated along the Pacific coast from Guanacaste in northern Costa Rica to just north of the Tropic of Cancer in the Mexican state of Sonora. There is also a patch of DBF in Parita Bay, Panama (Pennington et al., 2000; 2018; Dexter et al., 2018).

Tropical Coniferous Forest (TCF): As a former component of Gondwanaland, South American forests have floristic affinities that differ substantially from those of North America. The genus *Pinus*, which is significant in the temperate forests of North America, also dominates or co-dominates the montane forests of Mexico and northern Central America, reaching its southern limit in Nicaragua at around 12°N latitude. South of this latitude, extensive conifer-dominated forests are not found again until the subtropical latitudes of southeastern Brazil and the temperate latitudes of the southern Andes. However, the floristic affinities of these southern South American coniferous forests are very different from those in northern Central America (Veblen et al., 2005). This study will focus on the Central American TCF, where extant populations of white-tailed deer are found.

Grasslands, Savannas, and Shrublands (GSS): This biome, also known as the Llanos and Cerrados, is found in South America. The Llanos include the Colombian-Venezuelan Llanos, the Magdalena River Valley Llanos in Colombia, and the Llanos de Mojos in Bolivia. The Cerrados encompass the Campos Cerrado and Campos do Humaitá in Brazil. Characterized by annual rainfall levels between 90 and 150 centimeters, the Llanos are found on highly leached soils, with dominant trees being sclerophyllous evergreens. The tree-to-grass ratio in this biome varies with water availability. Fire-tolerant grass layer is an important component of savannas (Antagana et al., 2014; Pennington et al., 2018).

Páramos (PAR): The Andean páramo is a biogeographical province consisting of high-elevation ecosystems located above the montane treeline in the mountains of northern Peru, Ecuador, Colombia, and Venezuela (Luteyn et al., 1999). This region spans nearly 20° latitude around the equator and ranges from 3000 to 5000 m in elevation. The páramo climate is characterized by high humidity, cold temperatures, strong winds, and intense solar radiation. Temperatures decrease with elevation, ranging from 9°C to 3°C. Temperature and precipitation are key factors shaping the plant diversity in the páramo, which hosts a rich biodiversity of over 1300 non-vascular plant species and 3400 vascular plant species (Luteyn et al., 1999).

2.1.1. *The archaeological setting*

The archaeological specimens were sourced from Cerro Mangote (AG-1), Sitio Sierra (AG-3), and Cerro Juan Díaz (LS-3), all of which are located in Parita Bay. This volcanic, active Pacific coast region is the northwestern extension of the larger Panama Bay. Politically, Parita Bay is part of the Herrera and Coclé provinces, and geographically, it lies in the northeastern corner of the Azuero Peninsula (Fig. 1b). Known as the "dry crescent" (Arco Seco), this area experiences strong north-south trade winds that intensify desiccation during the typical 4–5-month dry season (Cooke et al., 2008). Throughout the isthmus, wet season precipitation is significantly influenced by orography. Around Parita Bay, convectional uplift and electric storms are less frequent compared to other parts of the country. During the wet season (May-December), the landscape is lush and green, with seasonal swamps forming in low-lying areas, and rivers from the central mountain range (Cordillera Central) or the hilly spine of the Azuero Peninsula provide fresh water. In the sunny dry season (strongest from January to April), the water table drops sharply, and evapotranspiration is rapid. Smaller streams may dry out, and vegetation cut for field clearing burns quickly (Cooke et al., 2008). By April, the landscape turns brown and parched (Cooke et al., 2008).

Vegetation history indicates an early Holocene onset of fire-induced forest removal in the central Pacific lowlands and foothills. However, gallery forests with tall trees such as barrigón (*Bombax barrigon*) and higuerón (*Ficus* spp.) remain lush and tall along stretches of major rivers like the Santa María, Parita, and La Villa, where the three archaeological sites are located (Piperno, 2011b). Surviving wooded patches contain many fire-tolerant taxa with xeromorphic characteristics (e.g., microphyllous leaves, thorns, thick bark) and drought-adapted species such as chumico (*Curatella americana*) and nance (*Byrsonima crassifolia*), which often occur in large stands (Linares, 1977).

Cerro Mangote (AG-1): is the oldest site sampled in this study, dating primarily to Panama's Late Preceramic period, which marks the early stages of agriculture and its transition to more extensive practices. Located in the Aguadulce District of Coclé Province, Panama, Cerro Mangote lies at the edge of Parita Bay, just inland from a geomorphologically unstable zone of high tidal flats and marine channels (Clary et al., 1984; Cooke and Ranere, 1999) (Fig. 1). During its Late Preceramic occupation, circa 5900–3020 cal BCE, the site's distance from the active shoreline varied between approximately 2–5 km (Cooke, 1984; Cooke and Ranere, 1999). Phytolith encrustation on edge-ground cobbles indicates maize consumption during this period (Piperno, 2011a) (Fig. 1b).

Sitio Sierra (AG-3): dates to a period of established agricultural village life. It is currently located 4 km southeast of La Loma village (Aguadulce District, Coclé Province, Panama), on the north bank of the River Santa María, and 12.5 km from its current marine outlet (Fig. 1b). The village was established by the end of the first millennium CE and was continuously occupied until the first Spanish contact (1515–1519 CE). The archaeological record shows no evidence of a hierarchical settlement structure (Cooke, 1979; 2011) (Fig. 1b).

Cerro Juan Díaz (LS-3): belongs to the period of village agriculture and social differentiation. Located on the coastal plain bordering Parita Bay, it spans both banks of the tidal valley of the Parita River and is dominated by a 42 m hill in Los Santos Province (Fig. 1b). Although currently 4.3 km inland from the active marine shore, it would have been 0.25–1 km closer to the coast during its period of occupation (Cooke, 1998). Cerro Juan Díaz served as both a residential and mortuary site from 200 BCE to 1600 CE, with dwelling floors, kitchen debris, and refuse pits interspersed with numerous complex burials, some containing multiple individuals (Díaz, 1999; Cooke et al., 2000) (Fig. 1b).

For this study, we grouped all the teeth into a single sample, considering that biome is a broad analysis category and all the teeth are from the same geographical area, Parita Bay. Today Parita Bay is classified as Dry Broadleaf Forest (European Commission, 2024) and in the Holocene was drier and more open than what exists today (Piperno and Pearsall, 1998).

2.2. *Methods*

2.2.1. *2D-Geometric morphometrics (2D-GMM)*

GMM analysis is the statistical study of shape and size and their covariations with other variables. In zooarchaeology, GMM has largely been used to explore domestication and population variation (Cucchi et al., 2011; 2017; 2019; Owen et al., 2014; Drake et al., 2015; Duval et al., 2015; Bopp-Ito et al., 2018). In recent years, there has been a notable interest among researchers in investigating the variation in the shape of the molars using 2D geometric morphometric models. Geometric morphometrics methods applied to selenodont teeth of diverse Artiodactyla have proven to be a powerful tool set to discriminate among taxa (Cucchi et al., 2019; Jeanjean et al., 2022; 2023; Uzunidis et al., 2022; Pelletier et al., 2023).

With a Canon T3i camera coupled to a Canon macro lens EF-S 60 mm, occlusal surface of m3s were photographed perpendicular to the lens with the tooth roots equally visible on both sides. For all the specimens the lone left m3 were selected.

Following the dental morphology nomenclature proposed by Bärmann and Rössner (2011), landmarks were digitized from images with TPSdig2 v. 2.17 (Rohlf, 2005). All the landmarks were acquired by a single operator (MFMP). 14 landmarks and 76 semilandmarks were placed along m3's enamel inner edges (Fig. 2). Type 1 landmarks were positioned on the point of maximum curvature of the enamel fold on the occlusal surface. As for the semi-landmarks, the protoconid was our starting point and from it we moved counterclockwise, following the shape of the molar. We positioned 12 landmarks between the antero-protoconid and the lingual part of the protoconid (respectively landmarks 1 and 2 in Fig. 2), along with nine landmarks between the lingual part of the protoconid and the postero-protoconid (respectively landmarks 2 and 3 in Fig. 2). For the antero-hypoconid to the lingual part of the hypoconid, we placed nine landmarks (respectively landmarks 4 and 5 in Fig. 2), and another nine landmarks were placed between the lingual part of the hypoconid and the postero-hypoconid (respectively landmarks 5 and 6 in Fig. 2). Surrounding the hypoconulid, we positioned nine landmarks (between landmarks 7 and 8 in Fig. 2). At the entoconulid we placed six landmarks (between landmarks 9 and 10 in Fig. 2). Between the postero-entoconid (entostylid) and antero-entoconid, 18 landmarks were placed (between landmarks 11 and 12 in Fig. 2). Lastly, 18 landmarks were located between the postero-metaconid (metastylid) and the antero-metaconid (mesostylid) (respectively landmarks 13 and 14 in Fig. 2).

Subsequently, the resulting landmark configuration was rotated, translated, and scaled using Generalized Procrustes Analysis (GPA) (Rohlf and Slice, 1990; Bookstein, 1991). This procedure removes the effects of position and orientation and minimizes the influence of size (Bookstein, 1996; Dryden and Mardia, 1998), producing Procrustes shape coordinates for further analysis. Then, statistical analyses were firstly carried out on reference material. Groups were considered according to biome (DBF, MBF and GSS) and sex (male-female). After that, the archaeological material was included in another category in the biome group (ARC) to explore its size and shape in relation to known groups. Size was analyzed by using the Analysis of Variance (ANOVA) and t-test (threshold set at $p < 0.05$), in order to compare the log-centroid size among the different groups (and their interaction) and evaluate if the observed differences were statistically significant. A Principal Component Analysis (PCA) was carried out to reduce the dimensionality of shape data and to identify the main directions of variation in the Procrustes coordinates by visualizing shape differences in the morphospace.

A Multivariate Analysis of Variance (MANOVA) was performed on Procrustes coordinates to evaluate shape differences among different groups. We aimed at determining if there were significant shape differences between the groups according to sex and biome. When MANOVA yielded significant differences among groups, we performed pairwise comparisons to identify which specific groups differed from each other. P values were corrected using the "Benjamini-Hochberg" method to decrease the false discovery rate (Benjamini and Hochberg, 1995). Finally, a Multivariate regression of Procrustes coordinates on log-transformed centroid sizes was used to analyze allometry, in order to understand how size affects shape and to identify patterns of variation related to size. All these analyses were carried out on RStudio 2021.09.0 (RStudio Team, 2022) using the packages "geomorph" (Adams and Otárola-Castillo, 2013) and "Morpho" (Schlager, 2017).

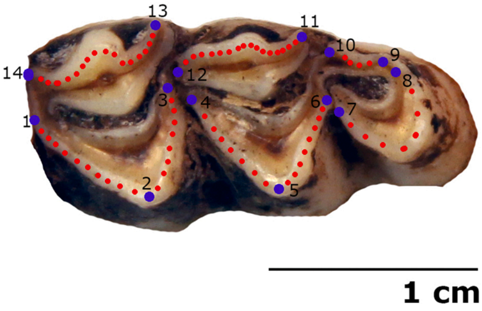

Fig. 2. Landmark on the m3 configuration employed for this study.

2.2.2. *Tooth mesowear*

Fortelius and Solounias (2000) proposed a method known as mesowear in order to characterize the diet of a particular species from a particular location in space and time. They used the three main dietary categories of herbivores, such as browser, grazer, and mixed feeder, as defined by Hofmann and Stewart (1972). Mesowear is the result of attrition and abrasion over a long period, and it reflects the average annual diet of an animal (Fortelius and Solounias, 2000; Ackermans et al., 2020). The relative contribution of attrition and abrasion to the total wear should be considered to understand this method, in which sharp cusps mean that attrition (tooth on tooth) predominates strongly and blunt cusps are the product of abrasion (food on tooth). Leaf-browsing herbivores have an attritional wear pattern (producing sharp molar cusps), and grazing animals, with high abrasive diets, have blunt molar cusps (Fortelius and Solounias, 2000).

Mesowear analysis involves the observation of cusp morphology and proceeds by describing the sharpness and the relief of molar tooth cusps (Fortelius and Solounias, 2000). These attributes are scaled from 0 (sharp cusps and high relief) to 6 (blunt surfaces); mesowear is scored on each specimen then averaged for each sample (MWS) (Mihlbachler et al., 2011; Rivals et al., 2013; Rivals et al., 2018; Rivals et al., 2017). We compared the mesowear scores between males and females using a t-test. To evaluate differences between biomes, we employed a Kruskal-Wallis test for equal medians, followed by Mann-Whitney pairwise comparisons to identify specific group differences if significant. These analyses were conducted using PAST software (Hammer et al., 2001).

2.2.3. *Tooth microwear*

Abrasion of food particles over the tooth enamel produces microscopic scars on the surface of the enamel, called the microwear pattern. This pattern is quickly produced and continuously overwritten as the teeth wear down and thus indicates the diet of the last days or weeks before death (Grine, 1986). Taking into account that there is a high variability in the hardness and abrasiveness of plants and also in the parts and age of the plant, all of these characteristics produce different patterns on the tooth enamel (Solounias and Semprebon, 2002). These patterns respond to animal food preferences and their dietary ecology and bring insights about the paleoenvironmental conditions weeks or even days before the animal's death (Solounias and Semprebon, 2002; Davis and Pineda Munoz, 2016; DeSantis, 2016; Xafis et al., 2017). Microwear has been used to differentiate among browsers, grazers, and mixed feeders in extant ungulates and in the fossil record by studying the microscopic features visible on the tooth enamel (Solounias and Semprebon, 2002). Based on the quantification of microscopic pits and scratches, Solounias and Semprebon (2002) established a classification of the diets in extant ungulates. The microwear texture analysis, resource distribution, and seasonal variations in the diet of extant deer species is used to study differential feeding behavior between species and sexes under restricted conditions (Berlioz et al., 2017).

We followed the method proposed by Solounias and Semprebon (2002) and Semprebon et al. (2004). Microwear analysis was comprised of several steps: 1) selecting teeth, 2) making a mold of the occlusal surface using a material appropriate for high-resolution dental impressions, such as light body polyvinylsiloxane, and 3) making a cast using transparent epoxy. In order to observe the epoxy casts under transmitted light, we used a Zeiss Stemi 2000 C stereomicroscope at 35× magnification. The microwear features (pits and scratches) were quantified on the enamel bands and on the mesiobuccal cusp of the second molar within a standard (0.4 ×0.4 mm) area using an ocular reticle. The quantification of scratches allows us to distinguish three dietary categories: browsers (numbers of scratches in the range of 0–17), grazers (numbers of scratches in the range of 17.5–29.5), and mixed feeders, which present some overlapping values (Solounias and Semprebon, 2002). In this article, the R code proposed by Rivals (2019) was used to create the bivariate plots. This code used the packages “readxl”, “ggrepel”, “plyr”, “lattice”, “Rmisc”, and “ggplot2” for drawing plots (RStudio Team, 2022). We compared the mesowear scores, scratches and pits between males and females using a t-test or a F test if the data did not meet the assumptions to carry out this test. To evaluate differences between biomes, we employed a Kruskal-Wallis test for equal medians, followed by Mann-Whitney pairwise comparisons to identify specific

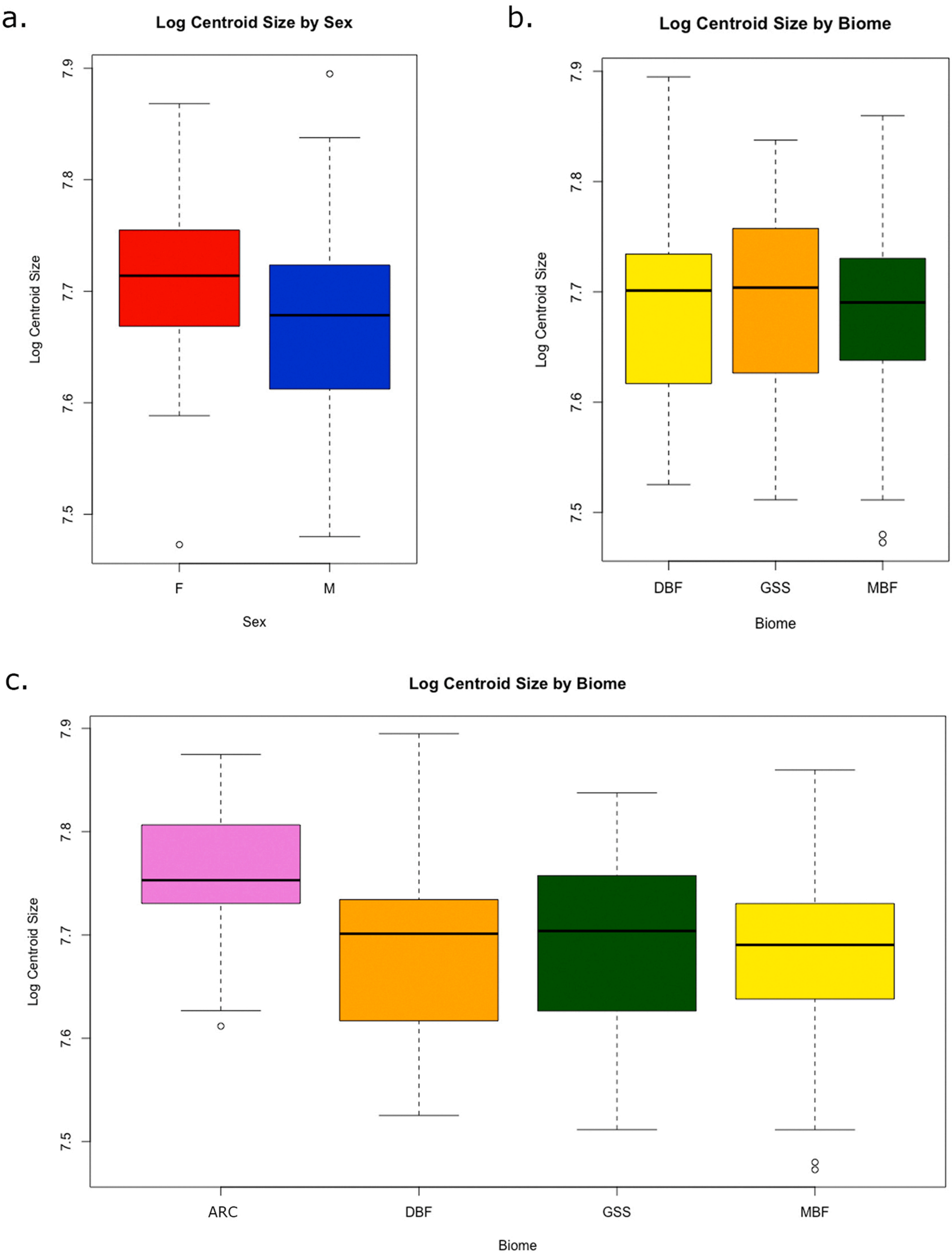

Fig. 3. Box plot of the Log. Centroid Size of lower third molar of white-tailed deer (*Odocoileus virginianus*) discriminated by: a. Extant Biomes; b. Sex and c. Extant biomes and archaeological sample.

group differences if significant. These analyses were conducted using PAST software (Hammer et al., 2001).

There are other features that could be identified on the enamel bands, including: 1. cross scratches, which are oriented with different directions than the majority of the scratches, 2. large pits (LP), which are double-sized pits, and 3. gouges, which are similar to large pits but with irregular edges and are 2 or 3 times larger and deeper. The scratch textures are ranked using the scratch width score (SWS): 0 (fine scratches), 1 (mixture of fine and coarse scratches), and 2 (coarse scratches). The SWS is obtained by averaging the individual values for each sample (Rivals et al., 2007).

3. Results

3.1. 2D-GMM

Size variation: The ANOVA of the log-transformed centroid size by biome did not show significant differences (F=0.384, df=2, p=0.682) (Fig. 3a). A t-test comparing the log-transformed centroid size by sex yielded significant differences (t=2.26, p=0.026) (Fig. 3b). However, the interaction between sex and biome on the log-transformed centroid size was not significant (F=1.434, df=5, p=0.222). When the archaeological sample was included in the ANOVA analysis, we obtained significant differences (F=5.405, df=3, p=0.00172) according to biome. Pairwise comparisons indicated significant differences between Dry Broadleaf Forest and Archaeological samples (p=0.0341), and between Moist Broadleaf Forest and Archaeological samples (p=0.00080) (Fig. 3c).

Shape variation: To explore shape variation, we analyzed the Procrustes coordinates by using MANOVA, which revealed significant differences between biomes (F=3.14, df=2, p=0.0034). Pairwise comparisons showed statistical differences between Dry Broadleaf Forest and Moist Broadleaf Forest (p=0.0007), as well as between Dry Broadleaf Forest and Grasslands, Savannas, and Scrublands (p=0.0193) (Table 2a). When examining differences between sexes, no significant differences were found (F=0.961, df=1, p=0.379). However, the interaction between biomes and sex showed significant differences (F=1.9854, df=5, p=0.0124). Specifically, there are differences between males and females from Dry Broadleaf Forest, females from Dry Broadleaf Forest and Grasslands, Savannas, and Scrublands, and females from Dry Broadleaf Forest and males from Grasslands, Savannas, and Scrublands (Table 2b). Including the archaeological samples in the MANOVA indicated significant shape differences (F=2.663, df=3, p=0.0016). Pairwise comparisons demonstrated that the archaeological sample differs from other groups: Dry Broadleaf Forest vs. Archaeological (p=0.0020), Grasslands, Savannas, and Scrublands vs. Archaeological (p=0.0180), and Moist Broadleaf Forest vs. Archaeological (p=0.0020) (Table 2c).

The first principal component (PC1) accounts for 46.76 % of the variation, while the second principal component (PC2) explains 7.7 %. In Fig. 4a, it is observed that along the positive values of PC1, the shape of the m3 tends to be elongated, whereas on the negative side, it tends to be compressed. For PC2, the shape of the hypoconulid varies: in the positive values, it tends to be oval and projected, while in the negative values, it tends to be round and straight. Additionally, there are differences between the postero-metaconid (metastylid) and the antero-metaconid (mesostylid); on the positive side, they tend to be concave, and on the negative side, they tend to be convex (Fig. 4a). When the archaeological individuals are included, they generally cluster along the X-axis between −0.1 and 0.1, and along the Y-axis between −0.05 and 0.05. However, no clear pattern emerges (Fig. 4b).

Allometry: The regression allometry (Procrustes coordinates on log-transformed centroid sizes) is not significant when analyzing the extant groups by biome (p=0.1346), accounting for only 1.89 % of the variation. The plot of log centroid size against the regression score by biome does not reveal any clear pattern (Fig. 5a). However, when including the archaeological samples, the regression becomes significant (p=0.0120), explaining 3.22 % of the shape variation. Fig. 5b shows that the archaeological individuals tend to be larger than the modern specimens.

Table 2
Shape pairwise comparisons: a. White-tailed deer extant individuals by biomes; b. White-tailed deer extant individuals by biomes and sex; c. White-tailed deer extant individuals and archaeological individuals by biomes. Abbreviations: DBF: Dry broadleaf forests; GSS: Grasslands, savannas, and scrublands; MBF: Moist broadleaf forests; ARC: Archaeological; M: Male; F: Female.

a.				
Pairwise Comparison	**Mean Distance**	**Standard Error (SE)**	**t-value**	**p-value**
DBF vs. MBF	0.05553917	0.03731799	2.7319.439	**0.0007**
DBF vs. GSS	0.05612226	0.04891857	2.0380.204	**0.0193**
MBF vs. GSS	0.02201132	0.04346061	−0.5988285	0.7228
b.				
Pairwise Comparison	**Mean Distance**	**Standard Error (SE)**	**t-value**	**p-value**
DBF-F vs DBF-M	0.06754295	0.06690693	1.7229.360	**0.0473**
DBF-F vs GSS-F	0.09459672	0.07495666	2.2884.827	**0.0071**
DBF-F vs GSS-M	0.10038416	0.07942482	2.2699.547	**0.0087**
DBF-F vs MBF-F	0.09224533	0.06495894	2.5990.542	**0.0020**
DBF-F vs MBF-M	0.10127750	0.06127957	2.9182.682	**0.0003**
DBF-M vs GSS-F	0.04387645	0.06406475	0.5537721	0.2962
DBF-M vs GSS-M	0.04847359	0.06593599	0.7498604	0.2339
DBF-M vs MBF-F	0.03501479	0.05123705	0.5198277	0.2995
DBF-M vs MBF-M	0.04345167	0.04599840	1.5086136	0.0733
GSS-F vs GSS-M	0.03602956	0.07490000	−0.8118811	0.7901
GSS-F vs MBF-F	0.02854000	0.06255396	−1.0034.762	0.8452
GSS-F vs MBF-M	0.02632494	0.05829184	−1.0587.941	0.8522
GSS-M vs MBF-F	0.03329278	0.06511319	−0.5493233	0.7054
GSS-M vs MBF-M	0.03239173	0.06177114	−0.4368155	0.6590
MBF-F vs MBF-M	0.01919616	0.04531156	−1.3162.448	0.9089
c.				
Pairwise Comparison	**Mean Distance**	**Standard Error (SE)**	**t-value**	**p-value**
DBF vs. MBF	0.05553332	0.03762866	2.6159924	**0.0020**
DBF vs. GSS	0.05610877	0.04872635	2.0503295	**0.0180**
MBF vs. GSS	0.02200938	0.04383675	−0.5626234	0.7036
DBF vs. ARC	0.06359278	0.04301111	2.625716	**0.0020**
MBF vs. ARC	0.03062984	0.03697365	1.1596239	0.1333
GSS vs. ARC	0.02982801	0.04853223	0.2323736	0.3933

3.2. Tooth mesowear

The mesowear scores of white-tailed deer are generally low. The lowest score is from the Tropical Coniferous Forest (MSW = 0.00), followed by the Paramo (MSW = 0.11), Moist Broadleaf Forest (MSW = 0.71), Dry Broadleaf Forest (MSW = 0.93), and Grasslands, Savannas, and Scrublands (MSW = 1.97) (Table 4, Fig. 6). These results indicate that deer from the Tropical Coniferous Forest and Paramo are exclusive browsers. In contrast, deer from the Moist Broadleaf Forest and Dry Broadleaf Forest are primarily browsers but include plants such as herbs in their diet. The deer from Grasslands, Savannas, and Scrublands have a high intake of herbs in their diets. Considering the archaeological individuals from Panama, the MSW score (1.09) suggests that these animals were browsers with a tendency towards mixed diets, similar to those from the Dry Broadleaf Forest. The Kruskal-Wallis test for equal medians (H = 21.92; p = $p < 0.001$) indicates a significant difference between the sample medians. The results of the Mann-Whitney pairwise comparison test are presented in Table 4. The analysis shows that the median MSW of Grasslands, Savannas, and Scrublands is similar to that of Dry Broadleaf Forest but different from other biomes. The median MSW of the Paramo is similar to that of Moist Broadleaf Forest but different from other biomes. For Dry Broadleaf Forest, the median MSW is similar to that of Grasslands, Savannas, and Scrublands, Moist Broadleaf Forest, and the archaeological sample. The median MSW of Moist Broadleaf Forest is similar to that of Paramo and Dry Broadleaf

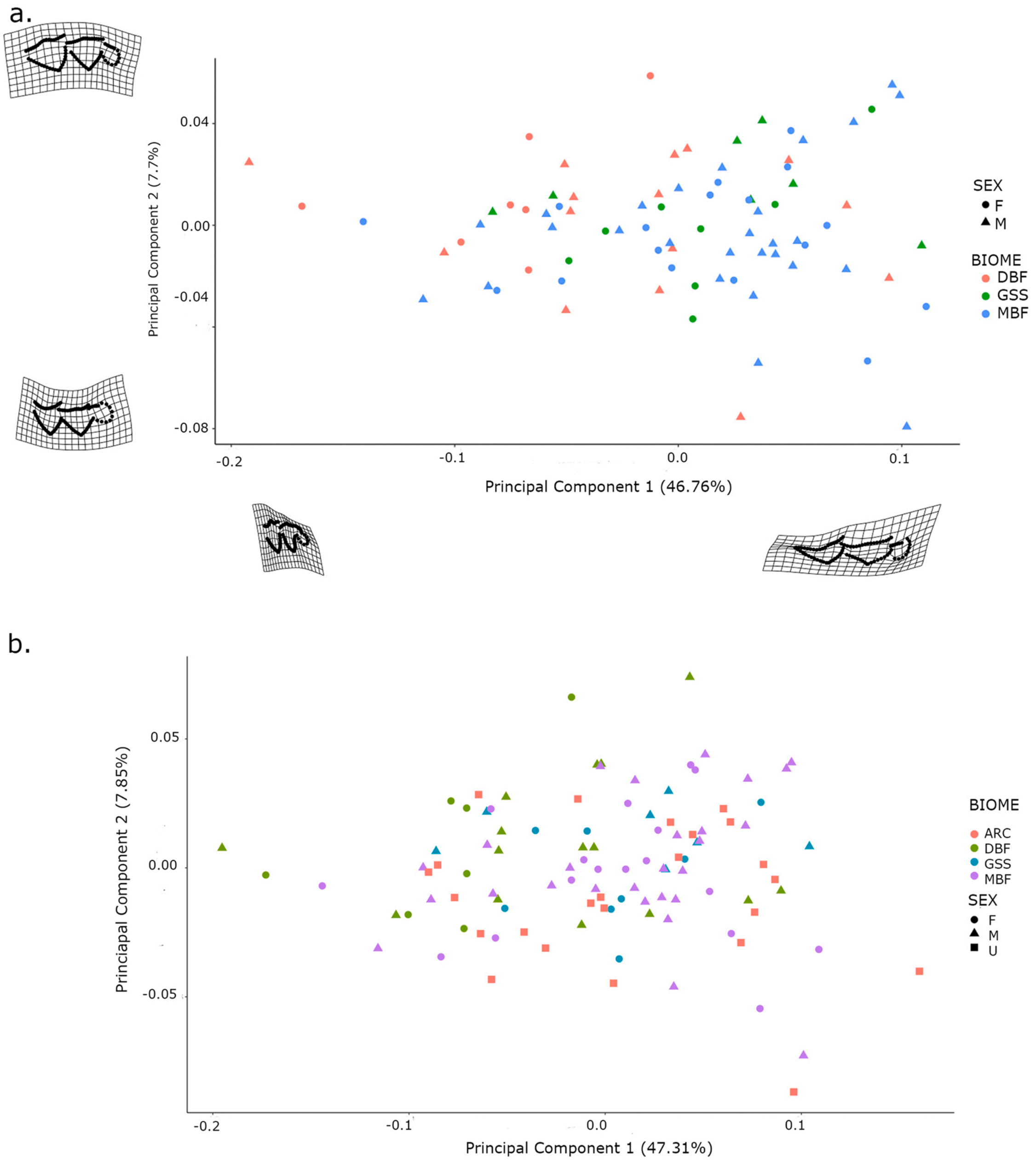

Fig. 4. Principal component analyses (PCA) of lower third molar of white-tailed deer (*Odocoileus virginianus*) discriminated by: a. Extant Biomes and their corresponding shapes; b. Extant biomes, archaeological sample and sex.

Forest. Finally, the median MSW of the archaeological sample differs from that of Grasslands, Savannas, and Scrublands, Paramo, and Moist Broadleaf Forest (Table 4).

We also examined whether there are differences between females and males, but found no significant differences (F = 1.44; p = 0.12) when considering all groups together. When males and females are separated within the Grasslands, Savannas, and Scrublands biome, there are no significant differences observed (F=1.43, p=0.46). Similarly, in the case of the Moist Broadleaf Forest biome, the same trend is observed (F=1.15, p=0.67). However, the sample sizes for the Dry Broadleaf Forest, Paramo, and Tropical Coniferous Forest biomes are too small for comparison.

3.3. Tooth microwear

The t-test shows no significant differences between males and females in the number of scratches (t=1.24, p=0.36) and pits (t=1.17, p=0.50) when considering all groups together. When the sample is divided by biomes, we found insignificant differences in the number of scratches (t=2.67, p=2.03) and pits (F=1.16, p=0.76) in the Grasslands, Savannas, and Scrublands biome. In the Moist Broadleaf Forest biome, there are insignificant differences in the number of pits (F=1.29, p=0.45) but significant differences in the number of scratches (F=1.19, p=0.04). The sample size for the Dry Broadleaf Forest, Paramo and Tropical Coniferous Forest biomes are too small for comparison.

Microwear analysis indicates that the deer were typical browsers at the time of death, with a gradation among biomes. The number of scratches and the median number of pits (Table 3) place their values in the medium and lower part of the 95 % confidence ellipse compared to reference browsers (Fig. 7). We observed a low number of scratches, ranging from 10 to 12, and a variable number of pits, ranging from 6 to 15 (Table 3). For pits, we found significant differences between the sample means (H=70.24, p<0.001). The median number of pits in Grasslands, Savannas, and Scrublands differs from all other biomes,

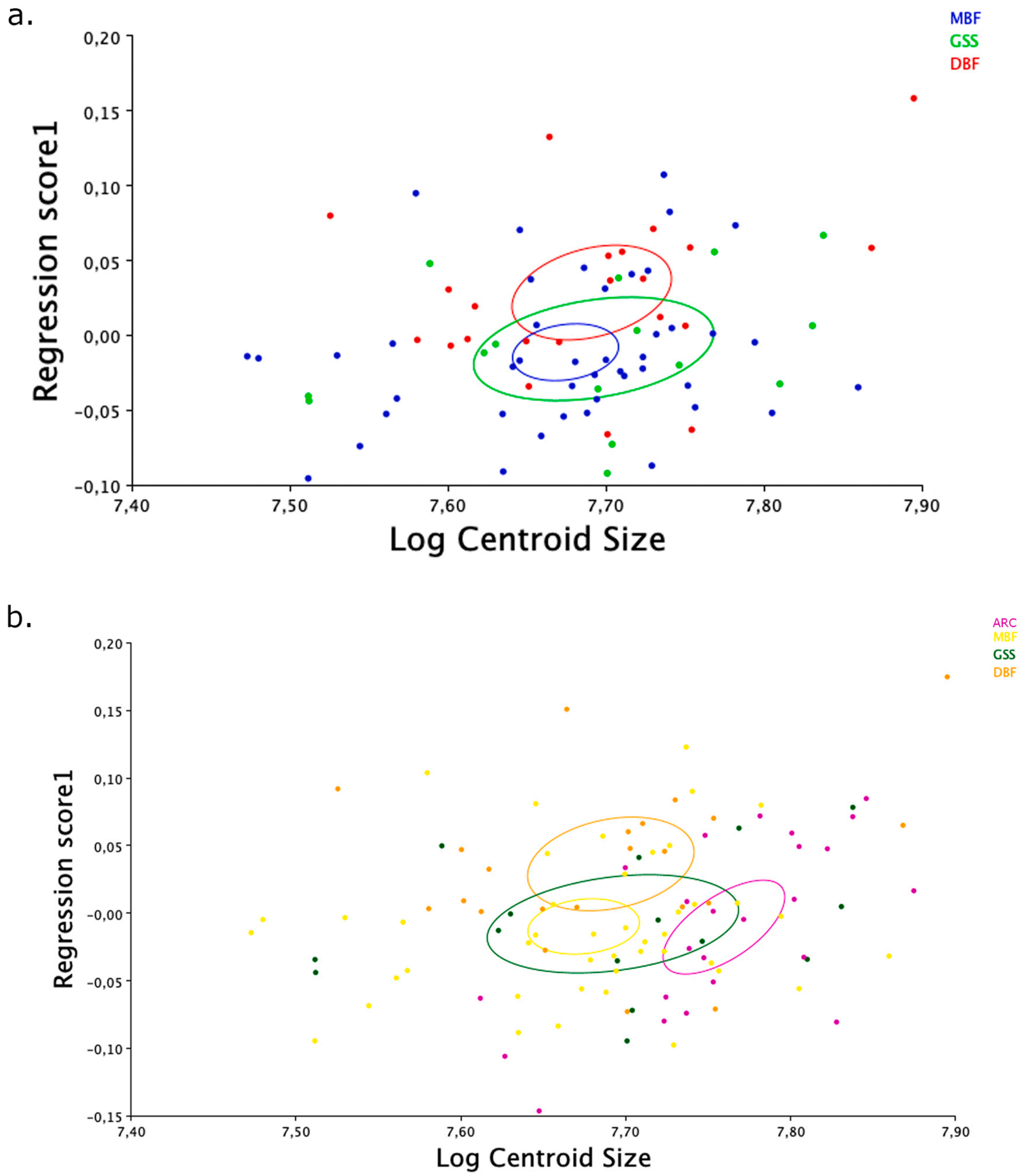

Fig. 5. Plot of the log Centroid Size and Regression Score for the third lower molar of white-tailed deer (*Odocoileus virginianus*) arranged by: a. extant biomes and b. extant biomes and the archaeological sample.

showing the same trend as in the archaeological samples. In the Dry Broadleaf Forest, the medians are similar to those in the Paramo, Tropical Coniferous Forest, and Moist Broadleaf Forest Table 4. The median number of pits in the Tropical Coniferous Forest is also similar to that in the Paramo and Moist Broadleaf Forest (Table 5). Regarding the medians of scratches, there are no significant differences (H=8.51, p=0.12).

Considering microwear features, the scratch width score (SWS) was variable, ranging from 0.01 to 0.87. Cross scratches were more evident in the Paramo (77.78 % of the individuals) and absent in the Tropical Coniferous Forest. Gouges were infrequent, found only in the Dry Broadleaf Forest and Moist Broadleaf Forest. In contrast, large pits were more frequently observed in the Paramo, followed by Grasslands, Savannas, and Shrublands, Tropical Coniferous Forest, Moist Broadleaf Forest, and Dry Broadleaf Forest. Large pits were absent in the archaeological sample (Table 3).

4. Discussion

4.1. *Differences between males and females*

The white-tailed deer is a dimorphic species, with males being larger and possessing antlers (Smith, 1991). Interestingly, our study of lower third molar size found that females tend to have larger molars compared to males, though the shape of the lower m3 does not differ between sexes. This trend is also observed in red deer. Carranza et al. (2004) examined 2141 males and 739 females aged 2–18 years, harvested in natural populations of Iberian red deer (*Cervus elaphus hispanicus*) in southwestern Spain. They discovered that the molariform teeth of male red deer are smaller than expected for their body mass and are less

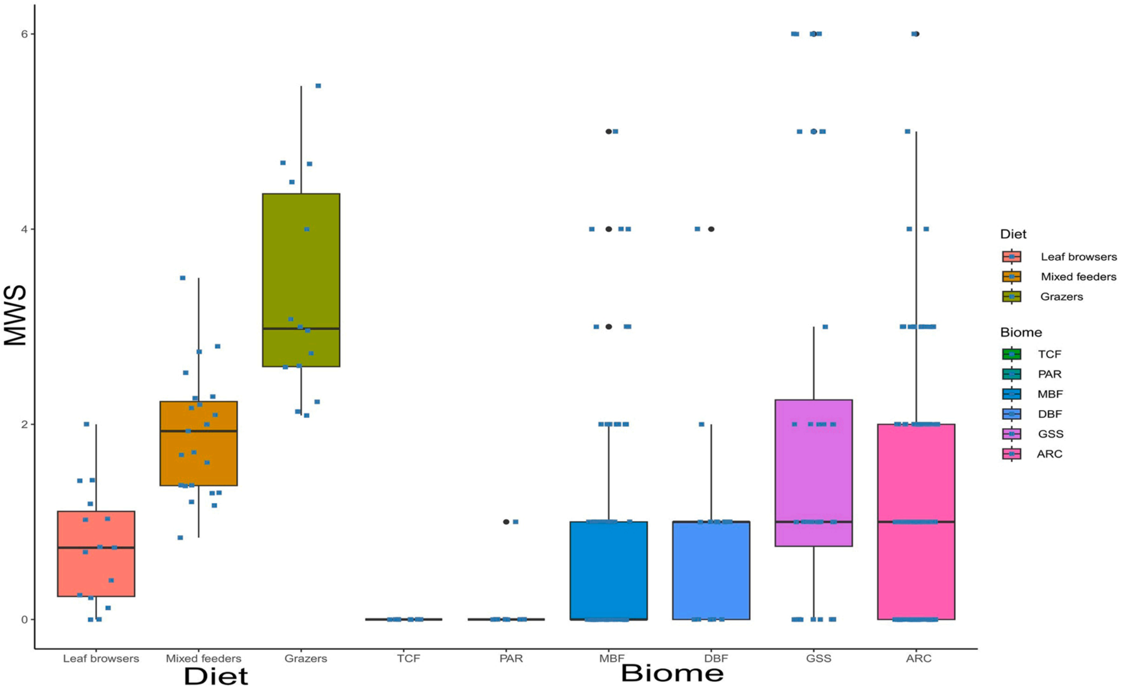

Fig. 6. Mesowear results for the white-tailed deer (*Odocoileus virginianus*) discriminated by biomes in comparison with data on ungulates with known diet: Data from Fortelius and Solounias (2000), Rivals et al., 2013; Rivals et al., 2011; Rivals et al., 2014. Error bar correspond to standard error of the mean (±1 SEM).

Table 3
Summary of mesowear and microwear data for the white-tailed deer (*Odocoileus virginianus*) by biomes. Abbreviations: n: sample size; MWS: Mesowear score; NS: Number of scratches; NP: Number of pits; %LP: percentage of specimens with large pits; % XS: percentage of specimens with cross scratches; SWS: scratches width score (from 0: fine scratches only to 2: coarse scratches only).

		Mesowear		Microwear						
		n	MWS	n	Scratches	Pits	%LP	%G	%XS	SWS
Dry broadleaf forests	M	16	0.94	16	10.03	15.00	18.75	6.25	0.00	0.12
	SD		1.00		1.89	8.95				
	CV		1.06		0.19	0.60				
Moist broadleaf forests	M	81	0.72	75	12.86	10.95	36.00	2.70	8.00	0.41
	SD		1.16		6.15	2.82				
	CV		1.61		0.48	0.26				
Paramo	M	9	0.11	8	11.12	12.94	88.89	0.00	77.78	0.87
	SD		0.33		5.17	2.11				
	CV		3.00		0.46	0.16				
Grasslands. savannas. and shrublands	M	36	1.97	36	12.08	8.50	81.08	0.00	8.01	0.86
	SD		2.06		2.00	3.56				
	CV		1.05		0.17	0.42				
Tropical coniferous forest	M	8	0.00	7	11.28	13.42	50.00	0.00	0.00	0.50
	SD		0.00		1.40	5.19				
	CV		0.00		0.12	0.39				
Archaeological	M		1.1		11.17	6.96	0.00	0.00	1.53	0.01
	SD	124	1.18	65	2.50	3.17				
	CV		1.07		0.22	0.46				

durable compared to those of females. This finding correlates with the differences in reproductive lifespan between the sexes (Carranza et al., 2004).

Regarding feeding habits, mesowear analysis revealed no significant differences, indicating that both males and females are primarily browsers in their later years. Microwear analysis also showed no significant differences, except in the Moist Broadleaf Forest, where a minimal significant difference in the number of pits was observed. Previous studies of mesowear and microwear of white-tailed deer populations in the Grasslands, Savannas, and Shrublands of Colombia also found no dietary differences between males and females (Martínez-Polanco et al., 2023).

A classic study (1967–1974) on the botanical composition of white-tailed deer diets at E.S. George Reserve, Michigan, reported no significant differences in food habits between sexes and age classes. There was substantial year-to-year variation in forage classes consumed due to differences in food availability (McCullough, 1985). A subsequent study in the same reserve examined the rumen contents of 8 male and 20 female deer collected between January and February 1981. The study found that while both sexes primarily browsed during the winter, females consumed more grass and less browse compared to males. Adult female deer on the George Reserve consistently selected a higher quality diet than adult males during the study period (Beier, 1987).

Another study analyzing the rumen contents of white-tailed deer at Hatchie National Wildlife Refuge in Tennessee from 1983 to 1986 revealed significant differences in diet composition between the sexes in

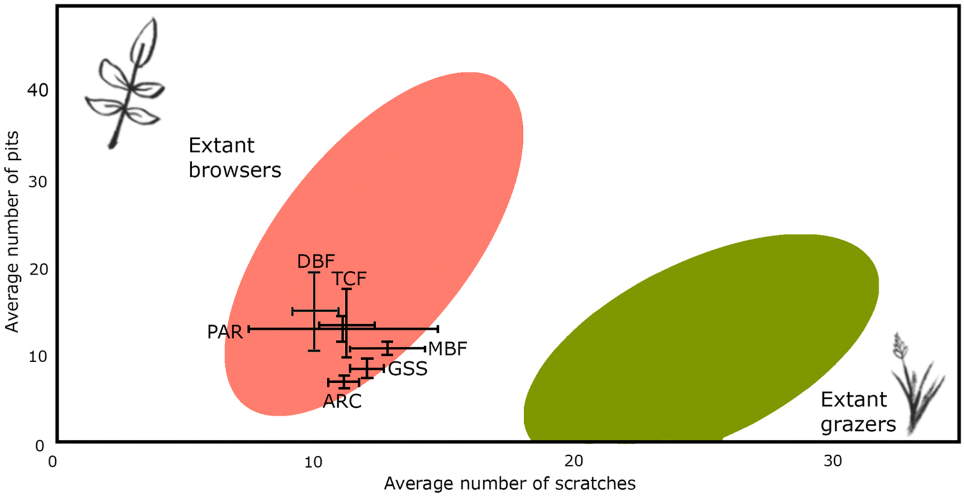

Fig. 7. Bivariate plot of the average numbers of pits and scratches of the white-tailed deer (*Odocoileus virginianus*) discriminated by biomes. Error bars correspond to standard error of the mean (±1 SEM). Ellipses correspond to the Gaussian confidence ellipses (p = 0.95) on the centroid for the extant leaf browsers and grazers from Solounias and Semprebon (2002).

Table 4
Mesowear pairwise comparison by biome. Abbreviations: DBF: Dry broadleaf forests; GSS: Grasslands, savannas, and shrublands; MBF: Moist broadleaf forests; ARC: Archaeological; PAR: Paramo; TCF: Tropical Coniferous Forest.

	GSS	PAR	DBF	MBF	ARC
GSS		**0.00107**	0.1053	**0.000107**	**0.04513**
PAR	**0.00107**		**0.007717**	0.1042	**0.004178**
DBF	0.1053	**0.007717**		0.1039	0.7197
MBF	**0.000107**	0.1042	0.1039		**0.002418**
ARC	**0.04513**	**0.004178**	0.7197	**0.002418**	

October, but not in January. For this reason, the authors rejected the hypothesis that females consumed a higher quality diet than males, as the intersexual differences in diets were inconsistent (Weckerly and Nelson, 1990). In the Neotropics, Buenrostro-Silva (2005) investigated sexual segregation and diet quality in a tropical dry forest in the Sierra de Huautla, Morelos, Mexico, finding that females consumed a higher quality diet (indicated by higher fecal nitrogen values) compared to males (cited by Gallina et al., 2010; Mandujano et al., 2014; Weber, 2014). This topic warrants further attention in future research.

4.2. *White-tailed deer feeding diets across biomes*

This study reveals differences in the shape, but not the size, of the lower m3, particularly between the Dry Broadleaf Forest and the Moist Broadleaf Forest, as well as between the Dry Broadleaf Forest and the Grasslands, Savannas, and Scrublands. While these shape differences could be related to feeding habits, our mesowear and microwear data do not support this hypothesis. We found no significant differences in mesowear scores or micro-scratches between these groups, except for a difference in the number of pits between the Dry Broadleaf Forest and the Grasslands, Savannas, and Scrublands (Table 5).

A study on the diet of white-tailed deer through microhistological analysis at the Chamela Biological Station in a Mexican tropical dry forest revealed seasonal variations in their dietary habits. The deer consumed fewer species during the rainy season and increased their diet diversity in the dry season. However, only 12 species from six families were predominant in their diet. In the rainy season, young leaves, which have higher nutritional quality and fewer secondary compounds than mature leaves, were a key resource. During the dry season, fruits became an important dietary component (Arceo et al., 2005).

The microwear characteristics of fruit browsers include: 1. A variable average scratch count, 2. A moderate to high average pit count, 3. A high occurrence of large pits, 4. A variable raw scratch distribution, 5. Presence of puncture pits, 6. Mixed scratch texture, with hypercoarse scratches observed in bark consumers (e.g., black rhinoceros) or consumers of hard fruits and seeds, and 7. Variable gouging, generally higher or coarser in species encountering grit in their food (Semprebon et al., 2011). In our study, we identified only large pits and gouges, which are present in the Dry Broadleaf Forest and may be related to the consumption of fruits.

Rotti et al. (2018) investigated the feeding habits of *Morenelaphus*, an extinct cervid from South America. Their microwear analysis revealed a mixed-feeder diet, indicated by high pit values and a significant frequency of individuals with a low number of fine scratches, suggesting grass consumption, possibly including grit. The authors proposed that these individuals inhabited open, dry, and grass-dominated areas during the Pleistocene-Holocene transition, which might have triggered a nutritional crisis leading to the extinction of *Morenelaphus*. Given that deer typically avoid grasses due to their low nutritional content, *Morenelaphus*'s need to include them in their diet is notable (Rotti et al., 2018). The average number of pits and scratches in *Morenelaphus* is higher than those found in the present study, suggesting that the extant

Table 5
Pits pairwise comparison by biome. Abbreviations: DBF: Dry broadleaf forests; GSS: Grasslands, savannas, and shrublands; MBF: Moist broadleaf forests; ARC: Archaeological; PAR: Paramo; TCF: Tropical Coniferous Forest.

	DBF	GSS	PAR	MBF	TCF	ARC
DBF		**0,007507**	0,4997	0863	9,73E−01	**3,67E−05**
GSS	**0,007507**		**0,001229**	**1,45E−05**	**0,01012**	**9,18E−03**
PAR	0,4997	**0,001229**		**0,04421**	0,8618	**8,40E−05**
MBF	0863	**1,45E−05**	**0,04421**		0,2828	**1,50E−12**
TCF	9,73E−01	**0,01012**	0,8618	0,2828		**0,0008718**
ARC	**3,67E−05**	**9,18E−03**	**8,40E−05**	**1,50E−12**	**0,0008718**	

populations and the archaeological specimens from Parita Bay did not experience the same severe climatic conditions as *Morenelaphus* did.

A recent study on the dental wear of a population of white-tailed deer in the Grasslands, Savannas, and Scrublands of Los Llanos, Colombia, revealed that their diet consisted of shrubs and herbs from both forests and savannas, with seasonal variations. Tooth mesowear indicated a grass-dominated diet in their later years, while microwear analysis showed a browser diet at the time of death (Martínez-Polanco et al., 2023). The absence of gouges and puncture pits in the microwear traits of PNN-El Tuparro deer suggests they did not consume fruits and seeds at the time of death. However, stomach content analysis of white-tailed deer in Venezuela indicated that fruit intake was significant during the dry season in the Bajo Llano and the wet season in the Alto Llano, with particular consumption of palm fruits and certain Leguminosae trees (Brokx and Andressen, 1970). Martínez-Polanco et al. (2023) suggested that fruit consumption might not leave marks on the teeth. However, this paper shows that traits such as large pits and gouges are present in deer from the Dry Broadleaf Forest. A possible explanation could be that the fruits in the Dry Broadleaf Forest are harder, while those in the Grasslands, Savannas, and Scrublands are softer, which might explain the absence of these traits in the latter.

The diet of white-tailed deer in a Tropical Coniferous Forest was studied through microhistological analysis of their pellets, observations of feeding habits, and examination of stomach contents from a population in the Sierra Madre de Oaxaca (Oaxaca, Mexico). The study found that the deer's annual diet consisted of 42 species from 23 botanical families, with arboreal and bush families being the most common. According to the similarity index, 56 % of the species consumed during the rainy season were also eaten in the dry season, likely due to their consistent availability year-round. The preference index showed that some species important in the dry season were not as significant in the wet season. Only one grass species was frequently and preferentially consumed during the dry season (González and Briones-salas, 2012). Another study in this biome was conducted at Sierra de El Laurel in Tlachihila, Zacatecas (Navarro-Cardona et al., 2018). The researchers analyzed the botanical composition of the deer's diet using a microhistological examination of their pellets. They also assessed the carrying capacity in two habitats, one fragmented and one conserved, and determined the population density of the deer in both dry and wet seasons. The study revealed that the deer consumed 25 species from 17 families. The diet was similar in both areas, primarily consisting of herbaceous plants, followed by shrubs, with trees and grasses being the least consumed. Additionally, deer density was not affected by habitat fragmentation (Navarro-Cardona et al., 2018). Our findings on the diet of deer in the Tropical Coniferous Forest, specifically regarding mesowear, show an absence of grass consumption. This observation aligns with the results of both González and Briones-salas (2012) and Navarro-Cardona et al. (2018).

A study was conducted in the Moist Broadleaf Forest within the experimental unit of Colegio de Postgraduados in Campeche, Mexico, from October 2010 to May 2012. The diet of white-tailed deer was analyzed through microhistological examination of feces using reference material. In this region, the deer's diet comprised 40 species from 15 families. The highest species richness was observed during the rainy season with 29 species. Deer showed a preference for shrubs throughout all seasons and herbaceous species particularly during the rainy season. Shrubs accounted for 48 % of their diet, herbaceous species for 27.2 %, grasses for 4.2 %, and tree species for 3.2 %. The greatest dietary diversity occurred in the rainy season, coinciding with an increased consumption of herbaceous plants due to their availability and higher nutritional value at that time (Granados et al., 2014). Mesowear analysis indicated that deer in the Moist Broadleaf Forest are primarily browsers with a tendency towards mixed feeding, incorporating various plant types into their diet. This dietary diversity was also reflected in the range of scratches observed in the microwear study.

An interesting finding of this research is that the archaeological sample from Parita Bay in Panama differs in both the size and shape of the lower m3 from the extant individuals in the Dry Broadleaf Forest biome. It was expected that the archaeological deer would be similar to those from this biome since this area is currently classified as Dry Broadleaf Forest (European Commission, 2024), and in the past, the environment surrounding Parita Bay was drier and more open than it is today (Piperno and Pearsall, 1998). The mesowear scores indicate that both groups were mixed feeders with a browsing tendency. A higher mesowear score may suggest the consumption of coarser browse or the presence of more grit, rather than simply an increase in grass intake. In Parita Bay, seasonal winds that deposit dust and grit on vegetation (Cooke et al., 2008) could explain the high mesowear scores. The microwear analysis shows no significant variation in the number of scratches, though differences in the number of pits are evident (see Table 5).

In a previous paper, we analyzed the archaeological data by site (Martínez-Polanco et al., 2020). The samples from Cerro Mangote and Cerro Juan Díaz exhibited low scratch and pit variation, suggesting that white-tailed deer were more likely hunted at these locations during the rainy season (May to December) when the deer had a more selective diet. Conversely, the samples from Sitio Sierra displayed a higher frequency of pits and pit variation, indicating that deer were likely hunted primarily during the dry season. During the dry months, a wide diversity of available plant species and plant parts (such as fruits, seeds, leaves, and woody forage) from various shrubs and trees contribute to a more variable diet for white-tailed deer (Martínez-Polanco et al., 2020). It is possible that the variations in pits are linked to the season in which the animals were hunted, as demonstrated in the case of Sitio Sierra. This suggests that further investigation is needed into the variation in the number of pits, the presence of large pits, puncture pits, and gouges in Neotropical cervids.

5. Conclusions

This study marks the first instance of examining the feeding habits of white-tailed deer by using a multiproxy approach, which includes tooth wear analyses and geometric morphometrics (GMM), and incorporates samples from several biomes across the Americas. Our results indicate that the shape of the lower third molar varies significantly across biomes, particularly between Dry Broadleaf Forest and Moist Broadleaf Forest, as well as between Dry Broadleaf Forest and Grasslands, Savannas, and Scrublands. Mesowear analysis shows that all white-tailed deer were primarily browsers, though some exhibited mixed feeding habits and included more abrasive plants, especially those inhabiting Grasslands, Savannas, and Scrublands. Microwear analysis further confirms that all white-tailed deer were browsers at the time of their death, with subtle differences in their browsing behavior. Notably, the presence or absence of pits and their variability, observed in this study, is an intriguing aspect that warrants further investigation. The findings will serve as a reference for archaeological and paleontological research.

The archaeological sample from Parita Bay differs in size and shape from current populations of white-tailed deer. Additionally, contrasting dietary patterns are evident in the mesowear and microwear characteristics of the archaeological deer from Panama when compared to their modern counterparts. While it is possible to make direct comparisons of the diet and molar shape of white-tailed deer between extant contemporary animals and those found in archaeological contexts, caution is necessary. As demonstrated in this case, the shape, size, and diet of the animals are distinct. Nevertheless, these data can serve as valuable reference in both archaeological and paleontological studies.

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CRediT authorship contribution statement

Florent Rivals: Writing – review & editing, Validation, Methodology, Formal analysis, Conceptualization. **María Fernanda Martínez-Polanco:** Writing – original draft, Visualization, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ana Belén Galán López:** Writing – review & editing, Visualization, Methodology, Formal analysis.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Martinez-Polanco, M.F. reports financial support was provided by SYNTHESYS. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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