

Feeding strategies of circum-Mediterranean hipparionins during the late Miocene: Exploring dietary preferences related to size through dental microwear analysis

Guillem Orlandi-Oliveras, Meike Köhler, Julien Clavel, Robert S. Scott, Serdar Mayda, Tanju Kaya, and Gildas Merceron

ABSTRACT

The adaptive radiation of hipparionins after their Old World dispersal was linked with a trend towards smaller body sizes. The appearance of the small-sized forms has usually been associated to open environments and grazing diets. A recent approach, moreover, highlights the role of life history modifications related to habitat conditions as triggers of their size shifts. Here, we test the relationship between hipparionin size and diet analyzing the dental microwear textures of different-sized hipparionins from Vallesian and Turolian circum-Mediterranean localities. Our results show that hipparionins were mainly mixed-feeders and that there was no general link between body size and diet. However, we identified broader feeding spectra in western Mediterranean smaller forms and more specialized grazing diets in larger ones, a differentiation not found in the eastern Mediterranean hipparionins. At odds with the notion of more open habitats eastward, we detected a larger browsing component in eastern hipparionin diets. The consumption by extant equids of more woody browse during the dry season leads us to propose a greater seasonality as a possible cause. Considering the arguable role of external abrasives on the microwear, another interpretation might involve the presence of more grit in the eastern opener habitats. Interestingly, we found that sympatric hipparionins tend to have similar feeding habits, which points to the fact that their diets were influenced by the local environment. Our results, then, suggest that the small size of some hipparionins resulted from different selective pressures rather than to a general adaptation to increasing habitat opening.

Guillem Orlandi-Oliveras. Institut Català de Paleontologia Miquel Crusafont (ICP), Edifici Z, carrer de les Columnes s/n., Campus de la Universitat Autònoma de Barcelona, 08193 Bellaterra (Barcelona), Spain. guillem.orlandi@icp.cat

Meike Köhler. Institut Català de Paleontologia Miquel Crusafont (ICP), Edifici Z, carrer de les Columnes s/n., Campus de la Universitat Autònoma de Barcelona, 08193 Bellaterra (Barcelona), Spain and Institució Catalana de Recerca i Estudis Avançats (ICREA), passeig Lluís Companys 23, 08010 Barcelona, Spain. meike.kohler@icp.cat

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Julien Clavel. Univ Lyon, Université Claude Bernard Lyon 1, CNRS, ENTPE, UMR 5023 LEHNA, F-69622, Villeurbanne, France. julien.clavel@univ-lyon1.fr

Robert S. Scott. Department of Anthropology and Center for Human Evolutionary Studies, Rutgers, The State University of New Jersey, New Jersey 08901 New Brunswick, USA. robertsc@scarletmail.rutgers.edu

Serdar Mayda. Department of Biology, Faculty of Science, Ege University, Bornova 35100, Izmir, Turkey and Natural History Museum, Ege University, Bornova 35100, Izmir, Turkey. serdar.mayda@ege.edu.tr

Gildas Merceron. Laboratoire PALEVOPRIM, UMR 7262 CNRS and University of Poitiers, TSA 51106, 86073 Poitiers Cedex9, France. gildas.merceron@univ-poitiers.fr

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INTRODUCTION

The living Equidae are today represented by only a few species from the genus *Equus*, which chiefly graze and inhabit open habitats (Bauer et al., 1994; Moehلمان, 2002). However, in the past the Equidae exhibited much greater taxonomic richness (Woodburne and MacFadden, 1982; MacFadden, 1992, 2005) and a broader spectrum of dietary adaptations (MacFadden et al., 1999; Tütken et al., 2013; Semperebon et al., 2016) more comparable to modern African bovids (Gagnon and Chew, 2000). Similarly, extinct equids occupied more habitat types than their extant relatives (MacFadden, 1992; Semperebon et al., 2016) and showed a broader range of body sizes (MacFadden, 1992; Alberdi et al., 1995; Gould and MacFadden, 2004).

Hipparionins are an equid tribe that was especially diverse during the late Miocene, when its representatives were very abundant in many of the mammal assemblages from the Holarctic realm (Woodburne, 1989; Bernor et al., 1996). These three-toed horses radiated soon after their first dispersal from North America to the Old World (Woodburne, 1989, 2009; Bernor et al., 1996, 2003; Scott et al., 2003; Cantalapiedra et al., 2017). Consequently, sympatric and morphologically diverse species are found in western and eastern Mediterranean regions already during the beginning of the Vallesian (Forsten, 1997; Scott et al., 2003; Koufos, 2016) [European Land Mammal Age, 11.2–8.9 Ma (Hilgen et al., 2012)]. Although the hipparionins from circum-Mediterranean regions underwent an important taxonomic and morphological diversification (Forsten, 1968; Koufos, 1990; Bernor et al., 1990b, 1996), in central Europe the specific diversity was much lower (Forsten, 1978a; Bernor et al., 1990a). It is during the Turolian [European Land Mammal Age, 8.9–5.3 Ma (Hilgen et al., 2012)],

however, that the Old World hipparionin horses reached their highest taxonomic and ecological diversity (Bernor et al., 1990a, 1996; Scott and Maga, 2005; Merceron et al., 2016a). This diversification is marked by an increase in the range of body sizes, especially towards smaller sizes (Bernor et al., 1996; Ortiz-Jaureguizar and Alberdi, 2003). The “*Cremohipparion* clade” [sensu Bernor et al. (1996)], for instance, diversified along two opposite trajectories; leading to the appearance of a lineage characterized by large-sized horses (e.g., *Cremohipparion proboscideum*) and to the appearance of other forms that decreased in body size (e.g., *Cremohipparion matthewi*) (Bernor et al., 1996, 2016). Those hipparionins that decreased in body size may have evolved the small size independently (Woodburne and MacFadden, 1982; Bernor and Tobien, 1989). Hence, contrary to the commonly described phyletic size increase in Equidae, size decrease processes took place numerous times during their evolutionary history (MacFadden, 1992; Gould and MacFadden, 2004).

The shift towards smaller size in some hipparionins, together with their diversification, has been associated with increasing climate seasonality and its repercussions on floral communities (Bernor et al., 1990a, 1996; Saarinen, 2009). Accordingly, some authors have suggested that the small-sized hipparionins dwelt in more open habitats (Bernor et al., 1996, 2021; Saarinen, 2009) and were adapted to forage on less nutritious xerophytic forage (Forsten, 1968, 1978b). In the same way, small-sized *Equus* of the European Pleistocene have been suggested to inhabit open environments and to consume less browse than larger forms (Saarinen et al., 2021). On the other hand, some authors have argued that the smaller hipparionin forms were adapted to more closed and forested areas (Ortiz-Jaureguizar and Alberdi, 2003), like extant

“smaller zebras” (Alberdi et al., 1995, p. 363). The hipparionin size diminution trends, moreover, have been associated with shifts in adult mortality regimes in some cases, and resource availability in others (Orlandi-Oliveras et al., 2018). These two scenarios can also be indirectly linked to changes in habitat structure.

Animal body size is related to many physiological and ecological factors (Peters, 1983; Calder, 1984; Palkovacs, 2003). One of the central variables determining body size is growth rate, which in turn is strongly affected by the environmental effects on food availability and foraging risk (Dmitriew, 2011). Hence, the items consumed by an animal do not only depend on the availability and quality of the resources, but also on the competitive pressure and predation risk associated with the exploitation of these resources (Brown, 1988). In turn, these factors all depend on habitat type and structure. A general relationship can thus be described for body mass, diet, and habitat in extant African ungulates: large-sized species tend to inhabit open areas and graze on abundant low quality food, while smaller taxa generally browse on less abundant high quality items in closed habitats (Bell, 1971; Jarman, 1974; Case, 1979; Gagnon and Chew, 2000; Hopcraft et al., 2010).

It was long assumed that hipparionins were mostly open savanna grazers due to their high-crowned teeth (Matthew, 1926; Stirton, 1947; Stebbins, 1981; MacFadden and Hulbert, 1988). Because of that, their arrival to the Old World was tentatively linked to the spread of grasslands (Gabunia and Chochieva, 1982; MacFadden, 1992), a thesis no longer supported by posterior studies on hipparionin diets (Hayek et al., 1992; MacFadden et al., 1999; Kaiser, 2003; Tütken et al., 2013; Merceron et al., 2016a), by evidence of grassland presence predating their appearance (Strömberg, 2006; Strömberg et al., 2007), as well as a tree cover that may have been more dense as initially thought (Solounias, 1999). In this context, while some studies have not identified significant feeding differences between sympatric hipparionin species (Solounias et al., 2010; Clavel et al., 2012; Rey et al., 2013), others detected dietary niche-partitioning between taxa (MacFadden et al., 1999; Merceron et al., 2016a). Similarly, life history strategies have also been found to differ between hipparionins of different sizes (Orlandi-Oliveras et al., 2018, 2019). Although hipparionin dietary preferences have been extensively studied from a paleo-environmental point of view, the relationship between their size and diet has not yet been

explored. Due to 1) the long-time interval of hipparionin presence in the Old World, 2) their wide geographical distribution, and 3) their broad range of body sizes, hipparionins constitute a good model for exploring size related niche partitioning with respect to habitat and feeding preferences across closely-related ungulates.

In previous studies, the hipparionin size differences have been explored from a life history approach by means of bone and dental histology analysis (Orlandi-Oliveras et al., 2018, 2019). In this work, we first aim to evaluate the scaling relationship between ecological preferences (diet) and hipparionin body size. The present study, hence, might help to test the interpretations on hipparionin paleobiology obtained from previous life history inferences. Moreover, the obtained data will also shed light on the dietary preferences of the studied hipparionin groups as well as habitat differences between the Mediterranean areas through the late Miocene. We therefore applied Dental Microwear Texture Analysis (DMTA) on teeth of different-sized hipparionins from Vallesian and Turolian sites located on eastern and western Mediterranean basins, with special interest on sympatric taxa, to infer their diet. DMTA has proven to be a powerful tool for tracking fine grained differences in diet such as seasonal variations on extant species and has successfully been applied to fossil species (Merceron, et al., 2009, 2021; DeSantis, 2016; Berlioz et al., 2017; Martin et al., 2018; Hullot, et al., 2019). Our results will help to understand the dietary preferences of the hipparionins of diverse size classes, and to explore the changes they went through from Vallesian to Turolian in different areas of their distribution range. In this regard, we start from a series of hypothesis. First, if the hipparionin trend towards smaller body sizes represents adaptations to diet and habitat (cf. Forsten, 1978; Bernor et al., 1990a, 1996), we could expect shared dietary strategies among small hipparionins from their DMT. Second, the hipparionin dietary signal can help us to identify paleoecological differences between the western and eastern Mediterranean biomes, the latter is considered to have more open habitats (cf. Bonis et al., 1992), as we could also expect to identify changes on the floral associations from the Vallesian to the more dry and seasonal Turolian (cf. Fortelius et al., 1996). Finally, this data might help to shed more light on the dietary behavior of the different hipparionin groups analyzed, challenging the grazing specialization due to their hypsodont dentition.

MATERIAL AND METHODS

Sample and Study Area

The fossil specimens come from 20 late Miocene fossil sites of circum-Mediterranean basins (Figure 1). We have focused on localities that yielded large hipparionin assemblages and with those exhibiting a high hipparionin size diversity. We predominantly sampled the more diverse Turolian fossil sites. Far from being homogeneous, eastern Mediterranean faunas show some dissimilarities during most part of the Turolian (Kostopoulos, 2009; Koufos and Vlachou, 2016). We divided, hence, the eastern Mediterranean Turolian sample in the western Anatolian (Samos island and continental western Anatolia) and the Balkans bioprovinces (continental Greece and Bulgaria). Vallesian hipparionins come from western Mediterranean and from the Balkans, while Turolian forms come from the three bioprovinces studied (see Appendix 1 for detailed information).

Here we decided to use the broad sense of the genus *Hipparion* because of the lack of cranial material available for some of the analyzed taxa, which hinders their unequivocal determination

within the proposed supraspecific groupings (Bernor et al., 1996). We organized the eastern Mediterranean hipparionin taxa following the morphotypes defined by Vlachou (2013). We grouped the western Mediterranean hipparionins considering size morphotypes, which follow specific differences, due to the general lack of complete cranial material.

Microwear Data Acquisition

The sample studied comprises 372 teeth from a wide range of hipparionin populations (Table 1; Appendix 2). We discarded unworn and senile specimens with very worn molars, together with those that showed post-mortem alterations as observed on the microwear scans (see Calandra and Merceron, 2016). We preferably selected second upper or lower molars, although in some cases we also analyzed first/third molars and third/fourth premolars as variations in DMT along the tooth row are not significant (Ramdarshan et al., 2017). Following standard procedures, the occlusal surfaces of the teeth were cleaned using acetone-soaked cotton swabs to remove dust particles and glue. Afterwards, dental replicas were made using a



FIGURE 1. Geographic distribution of the localities from western Mediterranean (circles), Balkans (stars), and western Anatolian (squares) basins. Dashed contours depicting the areas with Vallesian localities sampled. 1. Vallès-Penedès Basin (Santiga, Can Llobateres, Can Poncic); 2. Teruel Basin (Concud, El Arquillo); 3. Cabriel Basin (Venta del Moro); 4. Axios Valley (Pentalophos, Ravin de la Pluie, Ravin des Zouaves-5 and Dytiko sites); 5. Thessaly (Perivolaki); 6. Mesta Valley (Hadjidimovo); 7. Chalkidiki Peninsula (Nikiti-1 and Nikiti-2); 8. Biga Peninsula (Gülpınar); 9. Muğla Yatağan Basin (Şerefköy-2); 10. Samos Island (Mytilinii-A, Mytilinii-B).

TABLE 1. Descriptive statistics of each DMT parameter for all the hipparionin populations included in the present study. Mean body mass (BM) and the mean values of the textural parameters are also shown for each hipparionin group. Asfc = complexity, ePLsar = anisotropy, HAsfc = heterogeneity of complexity calculated with a 64 cells mesh, Tfv = textural fill volume, N = sample size, sem = standard error of the mean.

Age	Bioprovince	hipparionin group	Size class	Locality	mean BM (kg)	N	mean Asfc	sem Asfc	mean ePLsar	sem ePLsar
Vallesian	Western Mediterranean	<i>?primigenium</i>	Small	Santiga	154 ^d	13	2.00	0.34	3.28	0.51
		<i>primigenium</i>	Large	Can Llobateres	194 ^d	47	2.22	0.12	3.43	0.31
				Can Poncic	205 ^d	11	1.50	0.22	3.69	0.54
				All	200	58	2.09	0.11	3.48	0.27
	Balkans	<i>macedonicum</i>	Small	Axios Vallesian	103 ^e	4	2.96	0.56	3.30	0.49
				Nikiti-1	81 ^e	2	1.86	0.16	3.13	0.49
				All	92	6	2.59	0.43	3.25	0.34
		<i>primigenium</i>	Large	Axios Vallesian	167 ^e	12	2.78	0.46	3.88	0.60
				Nikiti-1	214 ^e	2	2.12	0.43	2.64	1.51
				All	191	14	2.68	0.40	3.70	0.55
Turolian	Western Mediterranean	<i>periafricanum</i>	Small	El Arquillo	31 ^d	17	2.30	0.45	2.89	0.31
		<i>gromovae</i>	Small	El Arquillo	84 ^f	34	1.80	0.16	3.56	0.28
		<i>cf. matthewi</i>	Large	Venta del Moro	124 ^g	20	1.17	0.13	4.81	0.42
		<i>concudense</i>	Large	Concud	178 ^g	24	1.16	0.09	5.39	0.38
		<i>primigenium</i>	Large	El Arquillo	192 ^f	5	1.78	0.54	4.35	1.05
	Balkans	<i>macedonicum</i>	Small	Nikiti-2	76 ^e	17	1.95	0.15	5.35	0.44
				Ravin des Zouaves-5	71 ^e	11	2.75	0.20	4.10	0.68
				Perivolaki	73 ^e	11	2.72	0.45	2.69	0.44
				Dytiko sites ^b	62 ^e	6	2.38	0.46	2.65	0.67
				All	71	45	2.39	0.15	4.03	0.32
		<i>dietrichi</i>	Large	Nikiti-2	113 ^e	4	1.74	0.22	5.40	1.03
				Perivolaki	127 ^e	6	3.37	0.77	2.53	0.41
				Dytiko sites ^b	144 ^e	21	1.99	0.18	3.91	0.42
				All	128	31	2.22	0.21	3.84	0.35
		<i>proboscideum</i>	Large	Ravin des Zouaves-5	202 ^e	1	2.00	-	5.44	-
				Hadjidimovo	183 ^d	18	2.29	0.19	4.21	0.48
				Perivolaki	165 ^e	1	2.11	-	3.27	-
				All	183	20	2.27	0.17	4.23	0.43

polyvinyl siloxane silicone of medium consistency (ISO 4823, President Regular Body, Coltène-Whaledent). These molds were scanned with the “TRIDENT” Leica DCM8 white-light confocal profilometer (PALEVOPRIM lab CNRS University of Poitiers, France) with a 100× lens (numerical aperture = 0.90; working distance = 0.9 mm). We scanned preferentially the lingual facets of paracone and buccal facets of protoconid, but

metacone and hypoconid were selected when the former showed alterations. The lateral resolution (x,y) of the scans was set to 0.129 µm, and the vertical spacing to less than 0.002 µm. Once scanned, the surfaces were saved as .plp files by LeicaScan software (Leica Microsystems) and imported for processing to LeicaMap following procedures shown in Merceron et al. (2016a). A 200 × 200 µm area was extracted and saved as a .sur file. All the

TABLE 1 (continued).

Age	Bioprovince	hipparionin group	Size class	Locality	mean BM (kg)	N	mean Asfc	sem Asfc	mean eplsar	sem eplsar
Turolian	Western Anatolia	<i>primigenium</i>	Large	Hadjidimovo	256 ^d	17	2.08	0.18	4.28	0.51
				Gülpınar	81 ^d	7	2.39	0.84	4.25	0.82
				Şerefköy-2	83 ^d	17	2.16	0.19	3.90	0.39
		<i>macedonicum</i>	Small	Samos new Collection ^c	108 ^e	3	1.95	0.81	3.29	0.62
				All	91	27	2.20	0.25	3.92	0.32
				Gülpınar	161 ^d	10	1.86	0.27	4.04	0.43
		<i>dietrichi</i>	Large	Samos new Collection ^c	201 ^e	3	1.79	0.31	2.73	0.50
				All	181	13	1.85	0.22	3.74	0.37
				Şerefköy-2	201 ^d	19	2.01	0.16	3.88	0.44
		<i>proboscideum</i>	Large	Samos new Collection ^c	238 ^e	9	1.41	0.12	4.08	0.86
				All	220	28	1.82	0.12	3.95	0.40

Note: Fossil sites of Pentalophos and Ravin de la Pluie (a); Dytiko-1, Dytiko-2 and Dytiko-3 (b); Mytilinii A and Mytilinii B (c). Mean body mass estimations were based on metapodial measures and were calculated in this study (d) or obtained from: Vlachou (2013) (e), Orlandi-Oliveras et al. (2018) (f) and Pesquero and Alberdi (2012) (g).

specimens were scanned and processed at PALEVOPRIM (CNRS and University of Poitiers, France). Photo-simulations of the surfaces analyzed are available in Appendix 3.

Dental Microwear Texture Variables and Statistical Analyses

The scans obtained from DMTA can be quantified repeatably, limiting the risks for intra- and inter-observer errors compared to other microwear techniques (Ungar et al., 2003; Scott et al., 2005, 2006; DeSantis et al., 2013). The surfaces were processed using Toothfrax and Sfrax software (Surfract, <http://www.surfract.com>) applying Scale Sensitive Fractal Analysis (SSFA) and following the standard procedures detailed in Scott et al. (2006). SSFA generates a set of Dental Microwear Texture (DMT) parameters that quantify the enamel surface. These are described in Scott et al. (2005, 2006). In the present study, we focused on the ones that better reflect surface textural attributes correlated to diet: complexity (area scale fractal complexity, Asfc), anisotropy (exact proportion of length scale anisotropy of relief at the resolution of 1.8 μm , eplsar), heterogeneity of complexity with an 8 \times 8 mesh (heterogeneity of area scale fractal complexity, HAsfc), and textural fill volume with square edge set at 2 μm (Tfv) (Scott et al., 2006).

Here we consider the heterogeneity of complexity over 64 cells per scan, because this setting contributed the most to the variance in our sample (tested via Principal Component Analysis, Appendix 4). Finally, a linear combination of all four dental microwear texture parameters was performed by means of a Principal Component Analysis. The most explicative principal component (PC1) has been used as a proxy of the overall microwear texture, gathering the major variance from the four DMT variables. Unfortunately, because extant equids are mostly grazers, there is no extensive dataset to which to compare the DMT of extinct equids with that of extant forms with different diets. However, we considered a sample of wild Burchell's zebras and semi-wild asses from Iran as comparative baseline (see Figure 2). Also, we relied on the framework provided by Scott (2012) in which the DMT has been explored in relation to diet in another group of ungulates with much diverse dietary adaptations.

The DMTs of extant mammals have shown to be correlated to the mechanical properties of the food processed in their diet (hardness and toughness). This has proven to be true despite the amount of exogenous abrasives present (Merceron et al., 2016b; Schulz-Kornas, et al., 2020; Ackermans, et al., 2020b; Hua, et al., 2020). The con-

TABLE 1 (continued).

Age	Bioprovince	hipparionin group	Size class	Locality	mean BM (kg)	N	mean HAsfc	sem HAsfc	mean Trfv (µm²)	sem Trfv (µm²)
Vallesian	Western Mediterranean	<i>?primigenium</i>	Small	Santiga	154 ^d	13	0.605	0.052	48995	2309
		<i>primigenium</i>	Large	Can Llobateres	194 ^d	47	0.432	0.017	42658	1430
				Can Poncic	205 ^d	11	0.485	0.028	43019	1683
				All	200	58	0.442	0.015	42726	1196
	Balkans	<i>macedonicum</i>	Small	Axios Vallesian	103 ^e	4	0.426	0.082	46358	5055
				Nikiti-1	81 ^e	2	0.388	0.061	51683	444
				All	92	6	0.414	0.055	48133	3390
		<i>primigenium</i>	Large	Axios Vallesian	167 ^e	12	0.388	0.022	43898	2136
				Nikiti-1	214 ^e	2	0.510	0.008	42243	8015
				All	191	14	0.405	0.022	43662	2010
Turolian	Western Mediterranean	<i>periafricanum</i>	Small	El Arquillo	31 ^d	17	0.579	0.080	43353	1868
		<i>gromovae</i>	Small	El Arquillo	84 ^f	34	0.488	0.029	42824	1545
		<i>cf. matthewi</i>	Large	Venta del Moro	124 ^g	20	0.434	0.024	46778	2079
		<i>conculdense</i>	Large	Concul	178 ^g	24	0.431	0.026	43961	2193
		<i>primigenium</i>	Large	El Arquillo	192 ^f	5	0.361	0.037	43050	4220
	Balkans	<i>macedonicum</i>	Small	Nikiti-2	76 ^e	17	0.412	0.020	42982	1855
				Ravin des Zouaves-5	71 ^e	11	0.475	0.047	41073	2247
				Perivolaki	73 ^e	11	0.467	0.063	43848	2025
				Dytiko sites ^b	62 ^e	6	0.480	0.049	50561	2518
				All	71	45	0.450	0.021	43738	1124
		<i>dietrichi</i>	Large	Nikiti-2	113 ^e	4	0.454	0.048	40964	3888
				Perivolaki	127 ^e	6	0.472	0.042	44124	2455
				Dytiko sites ^b	144 ^e	21	0.503	0.037	41592	2649
				All	128	31	0.491	0.027	42001	1896
<i>proboscideum</i>				Large	Ravin des Zouaves-5	202 ^e	1	0.356	-	27397
	Hadjidimovo	183 ^d	18		0.585	0.038	38219	2153		
	Perivolaki	165 ^e	1		0.454	-	55049	-		
	All	183	20		0.567	0.036	38519	2187		

sumption of tough food—such as mature grasses—tends to produce high anisotropic textures, whereas the processing of harder and more brittle items—such as woody browse—results in textures of lower anisotropy indices and high complexities. Generalists and mixed-feeders consume diverse types of resources with varying mechanical properties, which it appears to increase the heterogeneity of the texture complexity (see review in

Calandra and Merceron, 2016). Therefore, the dietary ecology of extinct taxa can be revealed by means of their dental microwear textures.

Correlation between body size and diet. Body mass estimates have been used as a measure of body size (Damuth and MacFadden, 1990). We compiled from the literature body mass estimations based on metapodial measures (Pesquero and Alberdi, 2012; Vlachou, 2013; Orlandi-Oliveras et

TABLE 1 (continued).

Age	Bioprovince	hipparionin group	Size class	Locality	mean BM (kg)	N	mean HAsfc	sem HAsfc	mean Tfv (μm^2)	sem Tfv (μm^2)
Turolian	Western Anatolia	<i>primigenium</i>	Large	Hadjidimovo	256 ^d	17	0.620	0.056	42308	1859
				Gülpınar	81 ^d	7	0.629	0.044	47139	3881
		<i>macedonicum</i>	Small	Şerefköy-2	83 ^d	17	0.379	0.031	41791	2002
				Samos new Collection ^c	108 ^e	3	0.546	0.058	34852	7100
				All	91	27	0.462	0.031	42407	1833
		<i>dietrichi</i>	Large	Gülpınar	161 ^d	10	0.584	0.056	44344	1751
				Samos new Collection ^c	201 ^e	3	0.452	0.043	38931	2359
				All	181	13	0.553	0.046	43095	1554
		<i>proboscideum</i>	Large	Şerefköy-2	201 ^d	19	0.432	0.018	42361	2169
				Samos new Collection ^c	238 ^e	9	0.409	0.017	34554	3009
				All	220	28	0.425	0.013	39852	1866

al., 2018), and calculated our own estimations using published data (Forsten and Kaya, 1995; Clavel et al., 2012) and own measures (Appendix 5). Calculations were performed using equations from Scott (1990) and Eisenmann and Sondaar (1998). We tested the link between the hipparionin size and their dietary preferences using linear least squares regressions: mean body mass estimates per population were correlated to our obtained dietary proxies [i.e., each DMT variable and the calculated principal component (PC1)].

Dietary differences between hipparionin populations. While considering the size differences, we have further explored the dietary diversity shown among hipparionins through time and space. In this regard, eastern and western Mediterranean hipparionins were differentiated, divided depending on the age of the fossil association (Vallesian/Turolian), and separated by their size category. Our smallest “work unit” was hipparionin population, which we defined as each group present in a specific fossil locality. The mean body masses estimates of the sampled populations range from 31 kg (*periafricanum* group from El Arquillo) to more than 250 kg (*primigenium* group from Hadjidimovo) (Table 1). We used a 100 kg threshold to establish two body size categories, dividing the large- to medium-sized hipparionins (> 100 kg), and the small-sized ones (< 100 kg), which separates quite well the forms considered by previous authors as

small-sized hipparionins (Alberdi, 1989; Bernor, et al., 1996). However, despite surpassing the 100 kg threshold, we included into the small group the medium- to small-sized *Hipparion* sp. from the western Mediterranean early Vallesian (Forsten, 1997) (154 kg), the *Hipparion macedonicum* from the Axios Valley Vallesian (103 kg), and the *H. cf. matthewi* from Samos (108 kg), by considering the larger body masses of their sympatric taxa (Table 1), and that these groups represent the smallest forms present in their associations (Appendix 1). Thus, the body mass of the large members from the eastern Mediterranean ranges from 113 kg to 281 kg, while in the small taxa range from 62 kg to 108 kg. In the western Mediterranean, the body mass of the large hipparionins goes from 124 kg to 205 kg, and from 31 kg to 154 kg (84 kg, excluding the early Vallesian form) in the small members.

To explore the variation on the dental microwear texture related to regional, chronological, and body size factors, a first set of analyses based on three-way ANOVAs were performed for each DMT parameter. Post-hoc pairwise comparisons tests, the Tukey's Honest Significant Differences test (HSD) and the less conservative Fisher's Least Significant Differences test (LSD), were then used in tandem to identify the source of variation. These parametric procedures were applied to rank-transformed variables for approximating distribution free (e.g., non-parametric) tests

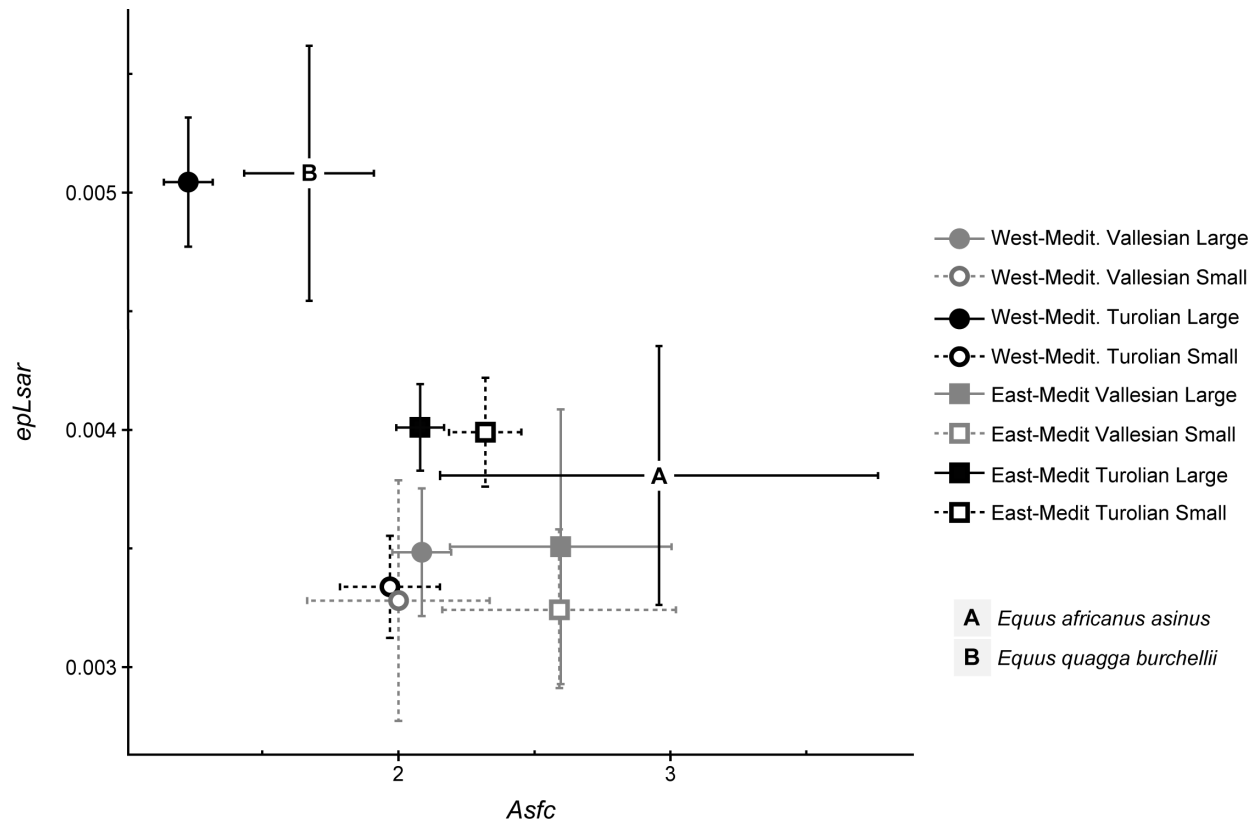


FIGURE 2. Bivariate plot showing the mean and the standard error of the mean for the complexity (Asfc) and anisotropy (epLsar) variables. The symbol type (circle/square) represents the region, the filling of the symbol differentiates between hipparionin size types, and the color if they are from Vallesian (grey) or Turolian (black) assemblages. Extant wild *Equus africanus asinus* (A) and *Equus quagga burchellii* (B) are included for comparison.

(Conover and Iman, 1981). Facing unbalanced factorial designs, here we used Type II sums of squares (SS) because it has been proved to be more powerful than Type III SS and does not depend on the arbitrary order of the model terms (Langsrud, 2003). Because marginality principle applies to multifactorial ANOVA designs (Nelder, 1977; Langsrud, 2003), the significance of the main effects was only interpreted when the interaction term was insignificant.

Moreover, a second set of analyses consisting in three-way nested ANOVAs were performed to explore in more detail the hipparionin dietary regimes during the Turolian, when this clade achieved its higher taxonomic and size diversity. Here, we tested for differences on the dental microwear textures between the three bioprovinces surveyed (western Mediterranean, Balkans and western Anatolia) and the hipparionin groups present within these areas (Appendix 1), while also considering the localities in which these groups are present. Differences were tested on the four DMT variables and on our calculated PC1. Again, HSD

and LSD were used as post-hoc tests, and all the variables were rank-transformed prior to the analyses. A significance level of $\alpha = 0.05$ has been used for all tests.

RESULTS

Relationship between Hipparionin Diet and Size

The first principal component (PC1) built with the four DMT variables, and considered as a more direct dietary proxy, gathered 34.6% of the total variance (Table 2). The variance of this PC1 is chiefly explained by complexity (Asfc, 45.2%), anisotropy (epLsar; 28.5%), and heterogeneity of complexity (HAsfc; 26.3%), whereas textural filled volume (Tfv) accounts for less than the 0.1% of it. Anisotropy is positively correlated with this principal component, while Asfc, HAsfc, and Tfv are negatively correlated. Hence, higher PC1 values are linked to less complex enamel surfaces, which in turn are more anisotropic and homogeneous, and have smaller microwear features; traits which are typically shown by tough leaf browsing species,

TABLE 2. Results of the Principal Component Analysis performed with the four DMT variables. Percentage of variance explained by the principal component and contribution of each variable to the principal components are shown. *r*: correlation coefficient between the DMT variables and the principal components; *r*²: proportion of variance of the principal component explained by each variable.

Component	% of variance	cumulative % of variance	Asfc		epLsar		HAsfc		Tfv	
			<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²	<i>r</i>	<i>r</i> ²
PC1	34.58	34.58	-0.672	0.452	0.534	0.285	-0.513	0.263	-0.023	0.001
PC2	25.16	59.73	0.083	0.007	0.138	0.019	-0.010	0.000	0.987	0.974
PC3	23.26	83.00	-0.023	0.001	0.673	0.453	0.735	0.540	-0.084	0.007
PC4	17.00	100	-0.735	0.540	-0.493	0.243	0.444	0.197	0.135	0.018

and most especially, grazing species (Hedberg and DeSantis, 2017; Merceron et al., 2021). The regressions of this PC1 and the four microwear textural parameters with the hipparionin body mass show no significant correlation (Table 3, Appendix 6). Thus, there seems to be no general relationship between the microwear signal and the hipparionin body mass when all the complete sample is considered. However, some significant correlations are detected when separating the three bioprovinces. Heterogeneity of complexity (HAsfc) is negatively correlated with hipparionin body mass in western Mediterranean ($p < 0.01$), while it is positively correlated in the Balkans sample ($p < 0.01$) (Table 3). Moreover, the PC1 is positively correlated with the hipparionin body mass in the western Mediterranean area ($p = 0.03$). In all cases, there is a high dispersion of the data—with R^2 always below 0.05 (Table 3)—because the dependent variables (DMT parameters) show high variability as individual data are considered, whereas the independent variable (mass) is represented by mean values per each population. The low R^2 values may hinder interpretations, but from these results we can elucidate a trend that can be further explored through the subsequent analyses.

Spatial and Temporal Dietary Variations Related to Hipparionin Size

In our first model we test whether three factors—geological age, geographic region, and body size—contribute to the variance of the dental microwear texture and might have influenced the hipparionin diet. Our results confirm that these three factors explain the variations in dental microwear textures, being in many cases involved in significant interactions (Table 4). Hence, changes in the dental microwear textures due to one of these factors follow different directions depending on a second factor. We detect a significant decrease on the complexity parameter (Asfc)

from the Vallesian to the Turolian in the large hipparionins, but not for smaller ones (Table 5), which maintain high levels of complexity during the Turolian (Figure 2). Moreover, complexity is generally higher in the eastern hipparionins compared to the western groups (Figure 2). Anisotropy (epLsar), on the other hand, increases from Vallesian to Turolian in both regions (Table 4; Figure 2). In the western Mediterranean, the small-sized hipparionins show significantly lower anisotropy (epLsar) values than the larger forms, while in the east the means between both size groups are similar (Table 6; Figure 2). The western Mediterranean small hipparionins have also higher values of heterogeneity of complexity (HAsfc) than the large-sized forms from the same region. In the eastern Mediterranean, we detect the opposite trend, since large-sized species show higher HAsfc than the smaller ones (Table 6; Figure 3C). Heterogeneity of complexity also tends to increase from the Vallesian to the Turolian in hipparionins from eastern basins, while it does not vary in the western area (Table 7; Figure 3C). Finally, the textural fill volume (Tfv) of the small Vallesian forms is higher than that of the larger Vallesian ones, a trend that is not followed during the Turolian (Table 5; Figure 3D).

Hipparionin Diets during the Turolian

Nested ANOVAs on the more diverse Turolian sample show that the microwear patterns differ between hipparionin groups within the same bioprovince, and between the hipparionin populations within the same group (Table 8). Moreover, differences on the Asfc and HAsfc between the three bioprovinces are detected. In this regard, complexity (Asfc) values are generally higher in the Balkans than in western Anatolia, while western Mediterranean hipparionins show the lowest complexities (Appendix 7.1). Differences in heterogeneity of complexity (HAsfc) are only significant between the Balkan sample and the less heterogeneous

TABLE 3. Summary of the linear regressions of the DMT parameters and the calculated principal component (PC1) against body mass. Graphs available at Appendix 6.

Summary Linear Regressions	Asfc		epLsar		HAsfc		Tfv		PC1	
	p-value	R ²	p-value	R ²	p-value	R ²	p-value	R ²	p-value	R ²
All Data	0.084	0.008	0.185	0.005	0.901	<0.001	0.087	0.008	0.116	0.007
Western Mediterranean	0.601	0.002	0.125	0.014	0.006	0.044	0.889	<0.001	0.028	0.028
Balkans	0.328	0.007	0.591	0.002	<0.001	0.010	0.121	0.018	0.449	0.004
Western Anatolia	0.121	0.036	0.990	<0.001	0.526	0.006	0.169	0.029	0.204	0.024

TABLE 4. ANOVA results for rank-transformed textural variables. Significant differences highlighted in bold.

Source of Variance	Asfc				epLsar			
	df	SS	F	p-value	df	SS	F	p-value
Age	1	295805	30.229	< 0.001	1	151118	13.777	< 0.001
Region	1	506330	51.743	< 0.001	1	8926	0.814	0.368
Size	1	92512	9.454	0.002	1	78955	7.198	0.008
Age x Region	1	22074	2.256	0.134	1	17151	1.564	0.212
Age x Size	1	80214	8.197	0.004	1	29078	2.651	0.104
Region x Size	1	32516	3.323	0.069	1	110058	10.034	0.002
Error	365	3571703			365	4003657		

Source of Variance	HAsfc				Tfv			
	df	SS	F	p-value	df	SS	F	p-value
Age	1	2	0.000	0.990	1	2482	0.220	0.639
Region	1	2396	0.221	0.639	1	31786	2.820	0.094
Size	1	306	0.028	0.867	1	32824	2.912	0.089
Age x Region	1	113296	10.432	0.001	1	16282	1.444	0.230
Age x Size	1	27647	2.546	0.111	1	75853	6.729	0.010
Region x Size	1	160919	14.818	< 0.001	1	29595	2.625	0.106
Error	365	3963924			365	4114613		

Note: df: degree of freedom; SS: Sum of Square; F: F-statistic

microwear signatures of the western Mediterranean hipparionins (Appendix 7.2).

Turolian hipparionin groups significantly differ in all parameters but Tfv (Table 8). The most notable differences are found between two large-sized groups from the western Mediterranean (*concondense* and cf. *matthewi*) and the rest (Figures 3, 4; Appendix 7.3). Their dental microwear textures are less complex (low Asfc) and tend to be more anisotropic (high epLsar) and homogeneous (low HAsfc) than in other hipparionins (Table 1; Figure 3; Appendix 7.3), showing, hence, higher PC1 scores (Figure 4). The general higher complexity values of

the Balkans hipparionins are also detected in the inter-group comparisons, since some groups (e.g., *macedonicum* and *proboscideum*) show minor Asfc differences compared to other forms from western Anatolia and the western Mediterranean (Figure 3A; Appendix 7.3). Other significant differences are found between the large-sized *proboscideum* and *primigenium* groups from the Balkans compared to other hipparionins that have lower heterogeneity values (HAsfc) (Figure 3C; Appendix 7.3). These inter-group dissimilarities apart, the locality from which the samples came from is also an important factor affecting the variance of our

TABLE 5. Summary of post-hoc results on Region-Size interaction. DMT parameters rank-transformed before analysis. The name of the parameter is shown if the difference were significant. When both LSD and HSD detect significant differences, the name of the parameter is shown in bold.

Age x Size Interaction		Vallesian		Turolian	
		Small	Large	Small	Large
Vallesian	Small				
	Large	Tfv			
Turolian	Small	Tfv			
	Large	Tfv	Asfc	Asfc	

TABLE 6. Summary of post-hoc results on Region-Size interaction. DMT parameters rank-transformed before analysis. The name of the parameter is shown if the difference were significant. When both LSD and HSD detect significant differences, the name of the parameter is shown in bold.

Region x Size Interaction		Western Mediterranean		Eastern Mediterranean	
		Small	Large	Small	Large
Western Mediterranean	Small				
	Large	epLsar, HAsfc			
Eastern Mediterranean	Small	HAsfc			
	Large	epLsar	HAsfc	HAsfc	

sample (Table 8). Focusing on the groups present in more than one locality, pairwise comparisons between fossil sites show that there are minor differences in DMT parameters between populations (Appendices 7.4–7.7). Most of these dissimilarities are caused by the high epLsar values of *Nikiti-2 macedonicum* and *dietrichi* morphotypes in comparison with other populations from the same groups; together with the higher HAsfc values from Gülpınar and Hadjidimovo hipparionins (Table 1; Appendices 7.4–7.7). On the other hand, when considering the localities with sympatric taxa, no significant differences are found among forms coexisting on the same fossil site (Appendices 7.8–7.15). Only some minor variations are detected inside El Arquillo locality, with higher heterogeneity (HAsfc) values in the small-sized *periafricanum* and *gromovae* hipparionins compared to that of the larger *primigenium* group (Figure 3C; Appendix 7.15).

DISCUSSION

Paleoecology of Hipparionins in Relation to Their Size

The linkage between body size and dietary strategy is a matter still debated in extant ungulates (Codron et al., 2007; De longh et al., 2011). Contrary to previous interpretations (Bell, 1971; Jarman, 1974; Gagnon and Chew, 2000), more recent studies failed to detect a correlation

between body mass and diet type in extant African herbivores (Codron et al., 2007), and even between their body mass and the quality of the forage they ingest (De longh et al., 2011). A lack of association between size and diet has also been found in Pleistocene ungulates (Saarinen et al., 2016) and in Eocene brontotheres (Mihlbachler and Solounias, 2002). Similarly, our results show that there is no evidence to support a general link between hipparionin size and their dietary preferences at a global scale. However, at a regional scale we still detect 1) an effect of size on the dental microwear texture and 2) a slight coupling between the hipparionin body size and the heterogeneity of complexity of their dental microwear textures. This later tendency, however, follows opposite directions: in the Balkans the small hipparionins' diets were less generalized than those of the larger species, while western Mediterranean small forms fed on wider spectra of preferred items. Moreover, the small hipparionins from the western Mediterranean consumed fewer tough items than the larger taxa, a trend not found in the eastern groups. Accordingly, there is a significant decrease in the grazing behavior related to the size decrease in western Mediterranean, but not in the other bioprovinces. These biogeographical differences within size groups strengthen the idea of no general correlation between diet and hipparionin size.

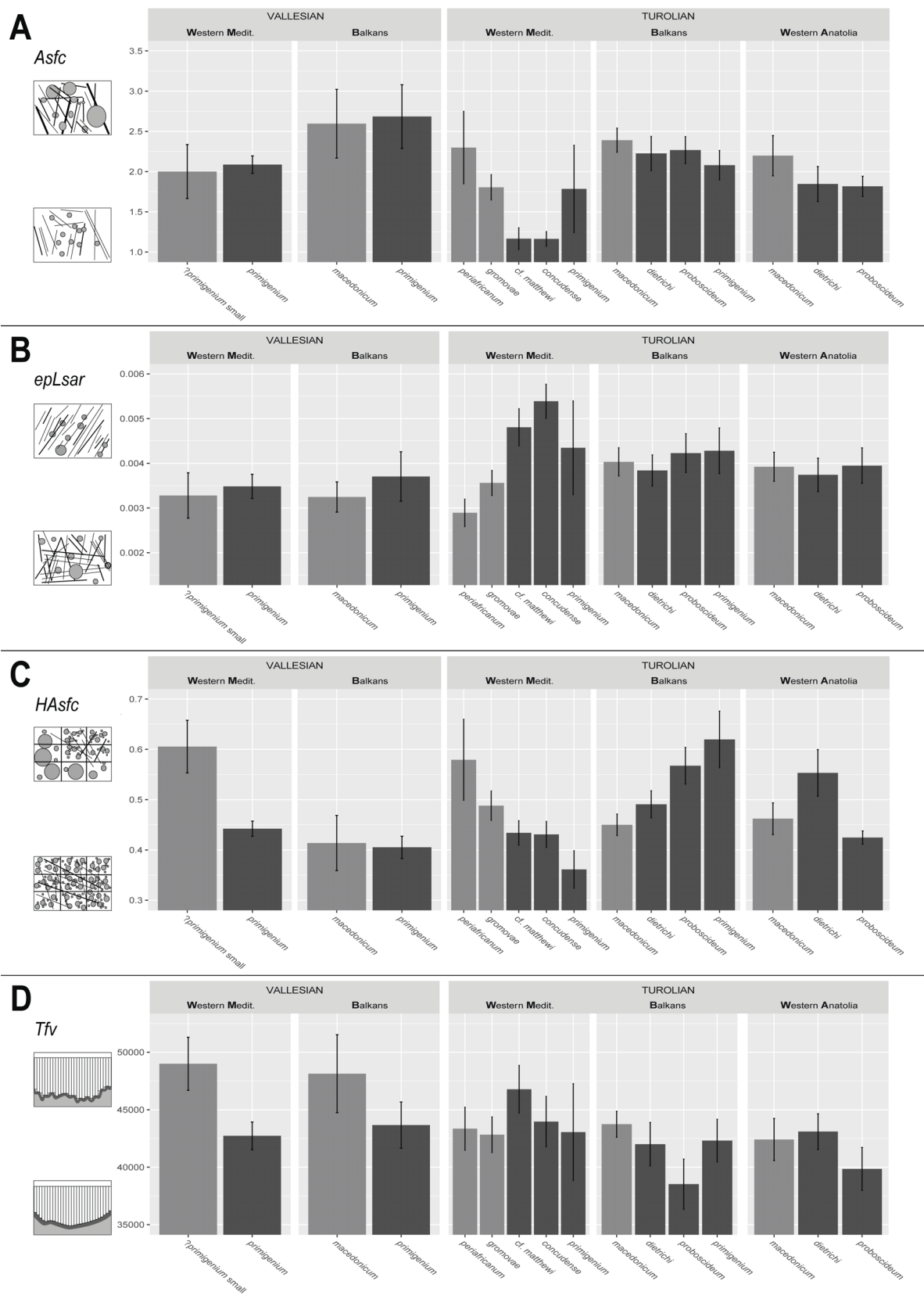


FIGURE 3. Bar charts with the mean and the standard error of the mean of the four DMT parameters for each hipparion group. Small-sized forms shown in light grey, larger ones in dark grey. **A:** *Asfc*. **B:** *epLsar*. **C:** *HAsfc*. **D:** *Tfv*

TABLE 7. Summary of post-hoc results on Age-Region interaction. DMT parameters rank-transformed before analysis. The name of the parameter is shown if the difference were significant. When both LSD and HSD detect significant differences, the name of the parameter is shown in bold.

Age x Region Interaction		Western Mediterranean		Eastern Mediterranean	
		Vallesian	Turolian	Vallesian	Turolian
Western Mediterranean	Vallesian				
	Turolian				
Eastern Mediterranean	Vallesian				
	Turolian			HAsfc	

TABLE 8. Nested ANOVA results for rank-transformed textural variables and PC1 of Turolian taxa. Significant differences highlighted in bold.

Source of Variance	Asfc				epLsar				HAsfc			
	df	SS	F	p-value	df	SS	F	p-value	df	SS	F	p-value
Bioprovince	2	297866	29.200	< 0.001	2	5116	0.435	0.648	2	35666	3.132	0.045
Group (Bioprovince)	9	137469	2.995	0.002	9	162174	3.065	0.002	9	185064	3.611	< 0.001
Locality (Group)	11	97747	1.742	0.065	11	164959	2.551	0.004	11	159116	2.540	0.005
Error	258	1315898			258	1516729			258	1469134		

Source of Variance	Tfv				PC1			
	df	SS	F	p-value	df	SS	F	p-value
Bioprovince	2	27124	2.129	0.121	2	125488	11.502	< 0.001
Group (Bioprovince)	9	50479	0.881	0.543	9	199755	4.069	< 0.001
Locality (Group)	11	128135	1.829	0.050	11	116326	1.939	0.035
Error	258	1643242			258	1407411		

Note: df: degree of freedom; SS: Sum of Square; F: F-statistic

Paleoenvironmental inferences should preferably be based on the dietary habits of a broad range of ungulates rather than from the diets of a reduced group of them. Nevertheless, the opportunistic feeding habits of at least some hipparionins (Tütken et al., 2013), and the fact that their dietary strategies are related to the available vegetation and, thus, to the habitat properties (Kaiser, 2003), allows us to get a broad idea of the environment in which these hipparionins might have dwelt. Considering the absence of a global relationship between size and diet, we suggest that there could be no general correspondence between hipparionin size and their habitat preferences. However, further habitat proxies might be necessary to make finer interpretations on the habitats of the different-sized hipparionin forms, especially considering the

finding that many hipparionin taxa were mixed-feeders, so they could have dwelled both in more forested or open bushy habitats. As the small-sized forms analyzed seem to not strictly have similar dietary regimes (thus, probably occupying different types of landscapes) our results seem to indicate that the vegetation composition might have not directly affected their body size. Other physiological, ecological, and life history factors may have had a significant influence on the size decrease trends undergone by some hipparionins (Orlandi-Oliveras et al., 2018) and other equids (Saarinen et al., 2016, 2021). At a regional scale, however, western Mediterranean small taxa seem to be related to wider dietary spectra and, during the Turolian, to more browsing diets compared to that of their larger counterparts. Therefore, we infer that

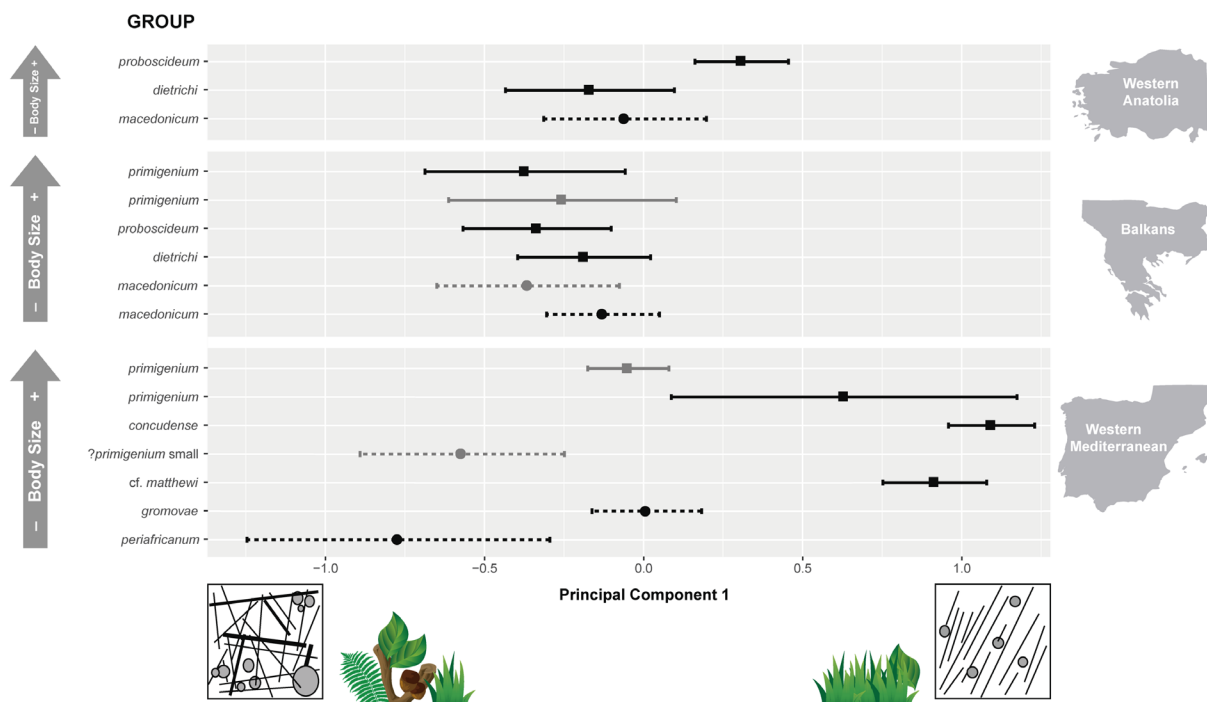


FIGURE 4. Mean values and confidence intervals (2x standard error of the mean) of the microwear Principal Component 1 for each hipparionin group. Dashed lines used for small-sized groups and continuous for large-sized. Grey color represents Vallesian hipparionins and black color the Turolian hipparionins.

these smaller hipparionins probably preferred more heterogeneous and somewhat denser habitats. Small eastern Mediterranean hipparionins, on the other hand, have similar microwear textures to those of the larger species, suggesting that they might have occupied comparable niches.

Temporal and Biogeographical Differences in Hipparionin Diets

The study of the dietary strategies of the circum-Mediterranean hipparionins further allows us to compare their feeding preferences and potential habitats through time and space. In this regard, the eastern Mediterranean habitats are supposed to be more open than those from the western side (Bonis et al., 1992; Koufos, 2006), while a general trend of increasing seasonality and habitat opening has been suggested in all the Mediterranean area from Vallesian to Turolian (Fortelius et al., 1996), a pattern which is corroborated with ectotherms vertebrates (Böhme et al. 2008, 2011). These latter temporal changes have been linked to an increase of xerophytic vegetation and the development of open landscapes with a rich herbaceous layer that includes grasses (Agustí et al., 2003; Jiménez-Moreno et al., 2007). The xerophytic foliage with thicker epidermis and grasses at least available

seasonally may have contributed to the observed higher anisotropy in the Turolian forms. In the eastern Mediterranean, besides, hipparionins generally differed from Vallesian to Turolian by the broadening of their diets, which were already based on mixed-feeding strategies. This dietary niche expansion suggests the prevalence of mosaic habitats that allow the exploitation of food resources with diverse physical properties. Recent isotopic studies did not detect a major climate nor habitat change during the Vallesian-Turolian transition in this area (Merceron et al., 2013; Rey et al., 2013), but only a slight decrease in the precipitation regime (Rey et al., 2013). However, Böhme et al. (2008, 2011) have shown more severe variations in environmental conditions through Europe during the late Vallesian and at the Vallesian/Turolian transition. Wider seasonal variations and more perturbations during the Turolian, could then have enhanced the presence of heterogeneous landscapes with grasses, bushes, and shrubs (Merceron et al., 2005a, 2016a; but see Solounias et al. 1999), that would have provided a high variety of resources, including both browse and graze. This diversity might have favored the coexistence of diverse hipparionin taxa, which do not strongly dif-

fer in dietary strategies (Solounias et al., 2010) as our results suggest.

Broadly, the main differences between regions lie in the different patterns observed through the hipparionin size range (see previous section), and the more complex dental microwear textures of eastern hipparionins compared to western forms. Therefore, compared to western Mediterranean hipparionins, the Balkans groups have dental microwear textures suggesting broader diets that include items of harder nature, a dietary regime compatible with a more mixed-feeding strategy. As stated, the eastern Mediterranean is typically supposed to be more arid and less wooded than the western realm during the late Miocene, based on the comparison of the fossil mammal assemblages (Bonis et al., 1992; Koufos, 2006) and to other proxies that point to the open character of the eastern habitats (Merceron et al., 2005a, 2010, 2016a; Ioannidis and Koufos, 2009; Koufos et al., 2009; Strömberg et al., 2007; Rey et al., 2013). Hence, the eastern Mediterranean biotope has mainly been characterized by an open dry savanna with a rich layer of grasses and with some bushes and shrubs (Merceron et al., 2005a, 2016a; Koufos et al., 2009), although other proxies suggest the existence of more densely wooded areas (Solounias et al., 1999, 2010; Denk, 2016; Denk et al., 2018). In this context, we might have expected more grazing feeding strategies in the eastern Mediterranean taxa compared to western ones.

On the contrary, the large hipparionins from the Turolian western Mediterranean are the species that grazed more, while eastern hipparionins have microwear textures consistent with the consumption of harder items (higher complexities) of diverse physical properties. We might interpret this pattern as a consequence of seasonal dry conditions given the open character of the eastern Mediterranean habitats, and that the late Miocene environments were arguably subject to significant precipitation shifts (Merceron et al., 2005b, 2013). Indeed, during the dry seasons, extant African ungulates widen their dietary niches thus following less strict grazing diets (De longh et al., 2011). Accordingly, extant equids tend to include higher quantity of harder woody browse in their diets during periods of low food availability due to drought (Estes, 1991; Moehlman, 2002). The lower selective behavior and higher intake rates of the hindgut fermenters (Janis, 2008) can facilitate the broadening of their diets and compensate for the resource fluctuations. Moreover, studies on fossil mammals coping with instable or limited resource

supplies also point towards an expansion of the dietary regimes and the inclusion of more browse material (Winkler et al., 2013; Smith and DeSantis, 2018). It is during the drought periods in seasonal climates with harsh dry seasons that the herbaceous layer and notably monocots are deeply impoverished, as their radicular net does not go deep enough to access water resources. Therefore, the increase in the browsing behavior of hipparionins during these periods may be related to the seasonal depletion of herbaceous monocotyledons due to their lower water competitive capacity compared to bushes, shrubs, and herbaceous dicots whose roots go deeper in soil (Hipondoka et al., 2003; Wang et al., 2010; Donzelli et al., 2013; February et al., 2013). Once rains are back, then, herbaceous are more reactive to gain water (Hipondoka et al., 2003; Scheiter and Higgins, 2007). Keeping in mind how monocots and dicots access to water resources, the absence of strictly grazing hipparionins in the eastern Mediterranean is not surprising. Besides, finding the most grazing hipparionins in the western Mediterranean makes sense as well, since water shortages might be less severe and thus monocots might have remained more abundant all around the year, especially at places where flooding or megaherbivores stop the growth of a bushy/tree layer. The more humid conditions near lakes and floodplains can, moreover, support a richer layer of herbaceous vegetation (Rodgers, 1982), which is more present in the diets of our large western Mediterranean hipparionins. Indeed, the populations that show a stronger grazing signal (*Hipparion concudense* from Concud, and *Hipparion* cf. *matthewi* from Venta del Moro) come from fossil associations developed on lacustrine environments (Montoya et al., 2006; Pesquero et al., 2013). Hipparionin obligate grazers, hence, were rather rare and probably inhabited somewhat humid environments and/or faced seasonal migrations. Similarly, the extant zebra species that graze more (*Equus quagga* and *Equus zebra*) are in turn those which undergo larger migrations and are more water-dependent (Bell, 1971; Estes, 1991; Moehlman, 2002).

Besides the physical properties of the food and its phytolith content, the dental wear of ungulate teeth has been related to the action of exogenous particles of grit and dust (Sanson et al., 2007; Lucas et al., 2014; Madden, 2014). The role of these particles on the microwear signal is an issue still debated, mostly because they are diverse in nature, hardness, dimension, shape, density, and periodicity (Merceron et al., 2016b; Schulz-Kornas

et al., 2020). On one hand, some studies have highlighted the fact that their presence does not significantly alter the dietary signal of the DMT (Burgman et al., 2016; Merceron et al., 2016b; Adams et al., 2020). On the other hand, other experiments have demonstrated that grit particles of different size can have an influence on the DMTA parameters (Ackermans et al., 2020b; Schulz-Kornas et al., 2020). Actually, the inclusion of dust (simulating natural abundance with diameter below 100 μm) has shown to not increase the complexity of the microwear texture most likely because those particles actually mimic phytoliths of biosilica (Merceron et al., 2016b). However, larger sand particles of millimetric grit could have an impact on microwear through the generation of large pits (Solounias and Semperebon, 2002), so arguably increasing complexity (Hedberg and DeSantis, 2017). Indeed, recent studies have shown that the size of the grit particles have a stronger effect than their concentration (Ackermans et al., 2020b; Schulz-Kornas et al., 2020), and that the processing of large grit particles can result in higher DMT complexities (Ackermans et al., 2020b). Nevertheless, at least among ruminants, rumen acts as a washing mechanism, which allow rumination free of large grit particles as they decant by gravity at the bottom of the dietary bolus. Hipparionins, however, did not have this washing mechanism. For this reason, it could be possible to relate the higher complexity of the DMTs of the eastern Mediterranean hipparionins to the higher presence of grit in their drier opener environments compared to those of the western Mediterranean.

The dietary reconstructions proposed here potentially reflect the last weekly to monthly preferences, due to the nature of the dental microwear studies (Teaford and Oyen, 1989; Teaford et al., 2017). On the other hand, long-term feeding strategies can be reached from mesowear and isotopic analyses when serial sampling is privileged, which can provide other comparative proxies for diet and overcome possible caveats. The short-term nature of microwear studies could represent a limitation, so future paleoenvironmental studies comparing both regions might require the study of diverse ungulate groups, together with the inclusion of isotopic and/or mesowear data that complements the information obtained from the microwear texture.

Diets of Hipparionin Groups and Populations

Previous studies have suggested a mixed-feeding and opportunistic dietary strategy in the *primigenium* hipparionins from the central Euro-

pean Vallesian (Kaiser, 2003; Tütken et al., 2013). Accordingly, we show that the Vallesian forms analyzed here were intermediate feeders. Within each region, the coexisting different-sized Vallesian hipparionins did not strongly differ in dental microwear textures, supporting quite similar feeding habits, except for the broader dietary spectra of the smaller western Mediterranean forms. In this case, they followed a more generalist diet than the larger hipparionins of the same area, including a wider range of preferred items in a weekly basis, suggesting different habits between these groups. On the other hand, the *primigenium* and the *macedonicum* hipparionins from the eastern Mediterranean Vallesian show similar dietary preferences, consistent with their comparable enamel carbon isotopes (Rey et al., 2013). We may then suggest that these groups had similar preferences of feeding habits and possibly habitats preferences. Compared between regions, the dental microwear textures of large-sized *primigenium* hipparionins are more complex in the eastern than in the western Mediterranean Vallesian, consistent with the general pattern observed comparing both areas (see previous section). However, this contrasts with a previous mesowear study that suggests a more browsing diet in the western Mediterranean *primigenium* forms compared to those of the east (Scott et al., 2013). This disagreement can be related to the distinct time scales addressed with the meso- and the microwear studies (Davis and Pineda-Munoz, 2016). On one hand, the mesowear signal might illustrate the long-term feeding preferences (Ackermans et al., 2020a) of the hipparionins due to closer habitats in the west and opener habitats in the east (Koufos, 2006; Scott et al., 2013). On the other hand, our shorter term dental microwear results might reveal the seasonal addition of woodier browse due to a stronger seasonal depletion of monocot resources in the eastern Mediterranean or the higher presence of large grit particles in the more open environment eastwards. Another provocative alternative would be to consider molar mesowear relief and cusp shape are not only dependent from the proportion of silica bearing plants in diet but also from the proportion of fibrous component (lignin, cellulose) in the dietary bolus. Besides, the grit presence could also have contributed.

When we focus on the diverse Turolian hipparionin assemblages, the greatest differences are found when comparing the large-sized western hipparionins with the others. As mentioned before, western Mediterranean *H. concudense* and *H. cf.*

matthewi most likely fed on grasses, while the other hipparionins were probably mixed-feeders including then more browse in their diets. The Turolian *primigenium* group from the western Mediterranean could also have followed a somewhat grazing strategy. However, the small sample hinders a more reliable interpretation. Further comparisons are not possible since no other dental wear studies on Turolian western Mediterranean hipparionins have hitherto been done. The smaller hipparionins from this region, on the other hand, were generalist mixed-feeders that fed on a higher percentage of browse than other western hipparionins. In the eastern Mediterranean, and especially in the Balkans bioprovince, the hipparionins show again more complex microwear textures, which we have mainly related to the higher consumption of browse during seasonal dry phases when the herbaceous layer is poor (see previous section). In this regard, the Balkans' *macedonicum* group included in their diet—besides grasses—more quantity of hard browse material in comparison to other western Mediterranean and western Anatolian hipparionins. This group, however, fed likely on a narrow range of items on a daily basis (as suggested by the low HAsfc values), thus pointing to a seasonal mixed-feeding strategy rather than a “meal-by-meal” one (Solounias and Semperebon, 2002).

Previous dietary reconstructions of eastern Mediterranean Turolian hipparionins have mainly inferred grazing diets (Hayek et al., 1992; Koufos et al., 2009; Solounias et al., 2010). Our results rather point to more intermediate feeding preferences both in a daily or seasonal basis. Similar mixed-feeding diets have also been suggested within the *proboscideum* group (Hayek et al., 1992; Solounias et al., 2010), while other authors indicated a more grazing tendency for this group (Koufos et al., 2009; Clavel et al., 2012). In our sample, although being mixed-feeders, the *proboscideum* hipparionins from the western Anatolia represent the forms that grazed more of the eastern Mediterranean. On the contrary, the Balkan *proboscideum* group depicts a “meal-by-meal” generalist feeding behavior (sensu Solounias and Semperebon, 2002) as shown by their higher HAsfc values. The *dietrichi* and *macedonicum* hipparionins, on the other hand, do not differ in diet between the two eastern bioprovinces. In the case of the *dietrichi* group, our inferred mixed-feeding strategy agrees with previous interpretations based on material from Samos (Koufos et al., 2009), but contrasts with those that suggest a clear grazing diet (Hayek et al., 1992; Solounias et al., 2010). Our results also point to

intermediate feeding preferences in the *macedonicum* hipparionins, in contrast to previously reported grazing diets (Hayek et al., 1992; Koufos et al., 2006; Solounias et al., 2010). Merceron et al. (2016a) also detected lower grass consumption preferences compared to obligate grazers (variable grazing) and even mixed-feeding within the *dietrichi* and *macedonicum* groups; a pattern that they related to the inclusion of more browse during dry seasons. This last interpretation can be supported by our results pointing to intermediate feeding preferences but with narrow daily/weekly dietary spectra.

Local populations within each hipparionin group also show some differences in their microwear textures. For example, the *macedonicum* and *dietrichi* hipparionins from Nikiti-2 grazed more than their analogues from Perivolaki. To a lesser extent, the *macedonicum* hipparionins from Nikiti-2 consumed higher proportion of grasses than those from the localities of Ravin des Zouaves-5 and Dytiko. Additionally, broader dietary preferences have been detected in the *macedonicum* group from Gülpınar, and in the *proboscideum* and *primigenium* hipparionins from Hadjidimovo in comparison to their counterparts from other sites. Comparable dietary variations within the same hipparionin group present in different localities have already been identified (Kaiser, 2003). These differences illustrate the influence of the local environments; like the possible presence of a richer herbaceous layer including monocots in Nikiti-2, as well as a more diverse habitat structure or higher intra- or inter-specific competition levels in Gülpınar and Hadjidimovo sites.

In agreement with this pattern, we find a quite homogeneous dental microwear texture within each fossil site, with no significant differences between hipparionin groups coexisting on the same locality. We therefore suggest that the taxa present in one area exploited similar resources. This does not mean there was no niche partitioning between species, but other factors than strictly diet may have contributed. The same low degree of dietary differentiation has also been found in previous studies on hipparionin diets (Koufos et al., 2006; Solounias et al., 2010; Clavel et al., 2012), in other extinct perissodactyls (Mihlbachler and Solounias, 2002), and even in extant ungulate assemblages (De longh et al., 2011). The presence of various hipparionin groups with no clear trophic niche differentiation can therefore be explained by: 1) the wide mixed-feeding strategies that allow them to consume a large variety of

resources (diminishing the trophic competition), 2) the body size differences that might favor the exploitation of different herbaceous strata (Koufos et al., 2006) in a diverse and rich environment (Solounias et al., 2010), or 3) by differences on social and migratory behaviour. The coexistence in Hadjidimovo of two large hipparionins, *Hipparion mediterraneum* and *Hipparion brachypus* (Hristova, 2009) that show some of the broadest dietary spectra of our sample (higher HAsfc), may support the hypothesis of an expansion of the dietary preferences due to competition rather than a niche differentiation strategy. In our sample, however, we have also detected some minor differences that may suggest a case of niche differentiation within El Arquillo fossil site from the western Mediterranean area. Here, the smallest hipparionins follow a more browse dominated generalist diet compared to the larger *primigenium* group.

Hypsodonty and Hipparionin Diets

Surprisingly, the larger and more grazing taxon from El Arquillo has lower-crowned teeth, while the smaller and more mixed-feeders *periafricanum* and *gromovae* hipparionins show the highest hypsodonty index of the western Mediterranean Turolian (Pesquero, 2003). Despite their hypsodont teeth, most of the hipparionin groups analyzed here have shown to be intermediate feeders. The same lack of correspondence between the hipparionin high-crowned teeth and a strict grazing diet have been discussed in various studies dealing with dental wear and isotopes (Hayek et al., 1992; MacFadden et al., 1999; Solounias et al., 2010; Tütken et al., 2013). Similarly, extant ungulates show discrepancies between diet and their dental morphology, as shown by the red deer ingesting large quantity of monocots (Azorit et al., 2012; Berlioz et al., 2017) despite their mesodont teeth, or the hypsodont teeth of the mouflon considering their mixed feeding preferences (Marchand et al., 2013; Merceron et al., 2021).

When testing the general correspondence between grazing diets and hypsodonty within Equidae representatives, both Strömberg (2006) and Muhlbachler et al. (2011) identified large periods of time when the selective pressures leading to higher crowned teeth (e.g., dietary abrasives) were weak. However, the same authors found that during specific intervals there were strong selective pressures leading to a rapid change on equids' dentition (Strömberg, 2006; Muhlbachler et al., 2011). In the case of hipparionin horses, MacFadden et al. (1999) initially proposed that the

increased tooth height appeared once within the clade as an adaptation to more abrasive diets, and that this condition was retained despite the following shifts in the dietary strategies. This interpretation, however, fails to explain the observed hypsodonty increase through time in many hipparionin groups (Alberdi, 1989). Alternatively, other authors emphasized that hipparionin hypsodont teeth could represent an adaptation to flexible dietary habits (Kaiser, 2003; Tütken et al., 2013). In agreement with this interpretation, our results show that most of the hypsodont hipparionins had mixed-feeding strategies either in a daily or a seasonal basis. This feeding flexibility might have represented an advantageous trait during the climatic shifts occurred during the late Miocene (Tütken et al., 2013), since herbivores dealing with instable resource supplies tend to expand their dietary breaths (Winkler et al., 2013). Nonetheless, hypsodonty has also been related to increasing environment aridity, as indicated by the inverse correlation of the hypsodonty with the rainfall and humidity (Fortelius et al., 2002). In this sense, airborne grit has been hypothesized to favor higher crowned teeth [see Strömberg (2006)] due to its contribution to dental wear (Sanson et al., 2007; Madden, 2014). Interestingly, however, recent studies have demonstrated that despite different grit loads in the grass consumed by African buffaloes, their dental wear rate does not significantly differ (Sanson et al., 2017).

Whether by means of phytolith or grit wear, higher-crowned teeth might also contribute to the achievement of a longer life span (Carranza et al., 2004; Veiberg et al., 2007; Jordana et al., 2012), which is linked to a generally slower life history (Stearns, 1992). Indeed, as well as by the diet quality, the wear degree has shown to be influenced by the optimal timing of tooth use in relation to the schedule of growth and reproduction through life (Pérez-Barbería et al., 2015). More hypsodont teeth, then, can be related to a higher resource assignation to the soma maintenance rather than to current reproductive performance, a life history strategy which is in turn coupled to longer reproductive lifespans (Veiberg et al., 2007; Carranza et al., 2008). Enamel folding complexity on the occlusal surface, moreover, might have also played an important role in the efficiency of the hipparionin tooth durability (Famoso and Davis, 2016); while in the *Equus* genus dental functionality is chiefly maintained by means of increased crown heights due to the extension of the crown formation time (Nacarino-Meneses et al., 2017; Orlandi-Oliveras

et al., 2019). The relationship between life history and dental development (Smith, 1991, 2000), together with the inferred slow molar formation and relatively late eruption of hipparionins' molars (Orlandi-Oliveras et al., 2019), make us interpret the lack of linkage between hypsodonty and diet in hipparionins as possible evidence of the role of life history in the evolution of tooth hypsodonty within this group.

Size Decrease Trends

The decrease in hipparionin size has mainly been related to an adaptation to open landscapes (Bernor et al., 1996; Forsten, 1997; Saarinen, 2009) and to feeding on plants of increasing xerophytism (Forsten, 1968, 1978b). Accordingly, Saarinen et al. (2021) demonstrated that this relationship holds true in the Pleistocene *Equus* of Europe, as large-sized forms were more associated to forested habitats while the smaller *Equus* to opener ones. In the case of hipparionins, on the other hand, Ortiz-Jaureguizar and Alberdi (2003) suggested more closed-habitat affinities for the small forms, while in a recent review Bernor et al. (2021) related the smaller taxa to grazing open habitat dwellers.

If the hipparionin small size (that is, the trend towards smaller size) was the consequence of direct adaptation to specific diets or habitats (i.e., the spread of opener habitats and/or xerophytic flora), we would expect shared dietary regimes and habitat preferences among small-sized forms. Here, however, we do not find a common dietary pattern shared between the small-sized hipparionins of Vallesian and Turolian assemblages from the circum-Mediterranean regions. In consequence, we interpret that the size differences were not directly promoted by a common dietary or habitat shift but might instead represent independent adaptations that otherwise led to similar size decrease tendencies.

Indeed, the small- and large-sized groups from the eastern Mediterranean did not follow contrasting dietary regimes during the Vallesian and the Turolian. This suggests that the cause or causes triggering the small-sized hipparionin appearance were not directly related to dietary differences. Otherwise, it lends support to the idea that shifts in other factors probably underlay these changes [e.g., mortality regimes shift (Orlandi-Oliveras et al., 2018)]. During the Vallesian, the main dietary difference detected in the western Mediterranean hipparionins resides in the more generalist diets followed by the smaller hipparionins. The

smaller form, hence, probably dwelt in more heterogeneous habitats as already proposed by Forsten (1997). The sharpest dietary dissimilarities between size groups, however, are found in the western Mediterranean Turolian. Nowadays, the large size of extant grazing plain zebras allows them to go through the seasonal migrations following the grasses fluxes (Moehlman, 2002). In the western Mediterranean, likewise, larger-sized hipparionins were the taxa with the stronger grazing tendencies, and they might arguably undergo seasonal migrations when the resources in monocotyledonous were depleted. The smaller and more hypsodont species, on the other hand, followed browse-dominated mixed-feeding strategies; probably exploiting the available resources in somewhat closer habitats, and broadening the spectrum of ingested items during seasons of lower resource availability. Accordingly, bone and dental paleohistological studies have pointed towards relative slower-life histories in these more hypsodont small-sized forms in comparison to larger hipparionins from the western Mediterranean Turolian (Orlandi-Oliveras et al., 2018, 2019). Similarly, extant roe deer populations of less productive environments are smaller, more hypsodont, and more longer-lived than larger-sized roe deer populations inhabiting highly productive environments (Veiberg et al., 2007).

CONCLUSIONS

The dental microwear textures of the northern circum-Mediterranean hipparionins mainly point towards mixed-feeding strategies. Some exceptions are present, since large-sized forms of the Turolian western Mediterranean grazed more than the rest. When considering all the hipparionins analyzed, we do not find a common relationship between their dietary preferences and their size. However, despite this lack of general correlation, the western Mediterranean large-sized forms tended to have narrower dietary breadths further associated to a higher percentage of grassy consumption in comparison to smaller hipparionins. On the other hand, the different-sized hipparionins from the eastern bioprovinces followed similar intermediate feeding strategies, including both browse and grasses in their diets (in some cases in a more seasonal basis and others in a more daily-weekly basis). Although we did not reconstruct the paleoenvironmental conditions from the sole diet of hipparionins, their opportunistic feeding adaptations give us clues about the habitats in which they might have dwelt. Therefore, due to the differential

dietary regimes among the small-sized forms analyzed, our results question the idea that hipparionin size decrease was a direct adaptation to habitat openness.

The broad comparison between Vallesian and Turolian hipparionin assemblages from different areas also allowed us to detect some general spatiotemporal differences regarding the hipparionin feeding strategies. The inclusion of tough items in their diets tended to increase from Vallesian to Turolian; in the eastern Mediterranean, a further widening of the dietary strategies is also detected. This could reflect a general increase in plant xerophytism, and the presence of more heterogeneous environments in the eastern Mediterranean late Miocene. More solid paleoenvironmental inferences, however, should be based on dietary reconstructions of more diverse ungulate assemblages (adding other dietary proxies as isotopes and mesowear) and the study of macrobotanical and palynological remains. When comparing the eastern and western Mediterranean regions, we find significant higher complexity values in the eastern forms, specifically on the Balkans. One possible interpretation to this observation is the presence of higher levels of millimetric grit eastwards (probably linked to a more arid environment). However, considering previous studies comparing both areas (Bonis et al., 1992; Koufos, 2006), we also relate this to the presence of more dry seasonal episodes (Merceron et al., 2005a, 2016a) inducing the consumption of harder woody browse by eastern hipparionins. Similarly, extant equids (Estes, 1991; Moehلمان, 2002) and other ungulates (De longh et al., 2011) include higher proportion of browse during the dry seasons in savanna and more arid environments.

In some cases, the diet of the hipparionin groups differs between the fossil sites surveyed, probably reflecting the season at which most of the specimens died and the influence of local conditions. Accordingly, coexisting hipparionins show no differences on the dental microwear patterns, thus suggesting no strong dietary niche partitioning over the traditional grazing-browsing couple. Alternatively, the segregation might have existed among the frame of mixed-feeders and browsers (exploiting different resources but with similar mechanical properties). The general mixed-feeding strategy inferred in most of the hypsodont hipparionin groups shows no support to the assumption of grazing diets due to high hypsodonty indices. This supports, hence, that hypsodonty within the group

might have been influenced by its role on dietary flexibility (Tütken et al., 2013) and life history (Veiberg et al., 2007), although the presence of grit due to habitat openness can also be involved. Finally, the different ecologies shown by the small-sized hipparionins make us conclude that the size decrease trends were probably achieved independently rather than related to a common habitat shift.

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APPENDICES

APPENDIX 1. INFORMATION ON THE HIPPARIONIN SAMPLE.

APPENDIX 1.1. Western Mediterranean

The Vallesian hipparionins from the western Mediterranean area come from the fossil sites of Can Llobateres, Can Poncic and Santiga. All three localities are situated on the Vallès-Penedès Basin (northeastern Iberian Peninsula) (Figure 1, main text) and are placed on medial to distal facies of alluvial origin (Casanovas-Vilar et al., 2014). The classical fossil site of Can Llobateres registers the early/late Vallesian (MN9/MN10) transition and has been divided into two different levels with estimated ages of 9.72 Ma and 9.65 Ma, respectively (Casanovas-Vilar et al., 2011). Both Can Poncic and Santiga were dated on the early Vallesian with an estimated age of 10.4 to 9.9 Ma (Casanovas-Vilar et al., 2011). Based on a Vallesian hipparionin cranium of the Vallès-Penedès, Pirlot (1956) established the species *Hipparion catalaunicum*. Thereafter, Vallesian hipparionins from this basin have been generally assigned to this taxon. The similarities between this form with the central European *Hipparion primigenium* [= *Hippotherium primigenium* sensu Bernor et al. (1996)] (Forsten, 1968; Woodburne and Bernor, 1980) have led some authors to include it within the *H. primigenium* species (Forsten, 1968; Alberdi, 1974; Tomàs et al., 2010), and differentiate it at subspecific level (Alberdi, 1974; Tomàs et al., 2010). The presence of one single large species have been proposed in Can Poncic and Can Llobateres (Scott et al., 2013). We consider both populations to pertain to the *H. primigenium catalaunicum* subspecies following Tomàs et al. (2010). In Santiga, however, it is evident that at least two species are present, an abundant medium-sized to small hipparionin and a much rarer large one (Forsten, 1997). Although unnamed, the small/medium-sized hipparionin from Santiga represent a different taxon compared to larger Vallesian forms, although it might also be related to the *primigenium* group. Here we refer to this form as *Hipparion* sp. (?*primigenium* small). Due to the lack of dentognathic material of the large species from Santiga, we only analyze the microwear texture of the small hipparionin from this site.

The Turolian material from this area come from the localities of Concud, El Arquillo and Venta del Moro. The classical fossil sites from Concud and El Arquillo are located in the Teruel Basin (central eastern Iberian Peninsula), and Venta del Moro in the Cabriel Basin (central eastern Iberian Peninsula) (Figure 1, main text). Both Concud and Venta del Moro sites were formed in marginal lacustrine environments with abundant vegetation (Montoya et al., 2006; Pesquero et al., 2013). The locality of Concud (MN12) has an estimated age of 7.2–7.1 Ma, while El Arquillo and Venta del Moro are dated on the MN13 with estimated ages of 6.2 Ma (van Dam et al., 2001) and 5.8–5.5 Ma (Opdyke et al., 1997), respectively. Recently, however, a magnetostratigraphic study by Gibert et al. 2013 dated Venta del Moro at 6.23 Ma. Still, El Arquillo site is deemed to be older because of the absence of *Paraethomys miocaenicus*, similarly to Las Casiones, which was dated at 6.33 Ma (van Dam, 1997; van Dam et al., 2006). During the middle Turolian (MN12) the most common species was *Hipparion concudense*, a medium to large sized hipparionin [178 kg (Pesquero and Alberdi, 2012)] that is very abundant in Concud (Pesquero and Alberdi, 2012). On the other hand, at least three different sized hipparionins inhabited the Teruel Basin during the late Turolian (MN13). The three sympatric taxa identified in El Arquillo have been referred to *Hipparion periafricanum*, *Hipparion gromovae*, and *H. primigenium truyolsi* (Alberdi, 1974). The two dwarf hipparionins of this site, *H. periafricanum* and *H. gromovae*, are the smallest members of this clade in the Iberian Peninsula (Ortiz-Jaureguizar and Alberdi, 2003; Pesquero, 2003). *H. primigenium truyolsi*, on the other hand, was much larger (Ortiz-Jaureguizar and Alberdi, 2003). An association of three sympatric forms has also been reported in the Venta del Moro. Morphometric comparisons of the most common hipparionin from this site has allowed its assignment to the species *Hipparion matthewi* (Pesquero et al., 2007), which is also present in eastern Mediterranean basins. This identification, however, has recently been questioned (Koufos, 2016b; Koufos and Vlachou, 2016), so here we decided to refer this medium-sized hipparionin as *H. cf. matthewi* and to differentiate it from the eastern Mediterranean forms. Pesquero et al. (2007), based on the material from Venta del Moro, also proposed the synonymy of *H. gromovae* and *H. matthewi*. Because we are interested in testing dietary differences related to size, the body mass differences between *H. gromovae* from El Arquillo (84 kg) and *H. cf. matthewi* from Venta del Moro (123 kg) (Table 1, main text), together with the lack of cranial traits to compare, make us

consider both populations two different sets of data. Besides *H. cf. matthewi*, there are two other hipparionins present in Venta del Moro: a much rarer large form determined as *H. primigenium*, and a probable smaller subspecies of *H. cf. matthewi* (Pesquero et al., 2007). Due to the scarcity of remains assigned to these two last forms, here we only analyze the microwear texture of the medium-sized *H. cf. matthewi* from Venta del Moro. All the hipparionin teeth and mandibles from western Mediterranean sites are stored at the collections of the Institut Català de Paleontologia Miquel Crusafont (ICP), Barcelona, and of the Museo Nacional de Ciencias Naturales (MNCN), Madrid.

APPENDIX 1.2. Balkans

The Vallesian hipparionins pertain to the localities of Ravin de la Pluie and Pentalophos from the Axios Valley (southeastern Balkan Peninsula), and to Nikiti-1, which is located in the Chalkidiki Peninsula (southeastern Balkan Peninsula) (Figure 1, main text). Ravin de la Pluie was dated to the lower part of the late Vallesian (MN10) with an estimated age of ~9.3 Ma based on a combination of biochronological and paleomagnetostratigraphical data (Sen et al., 2000; Koufos, 2006a). Nikiti-1 is correlated based on its mammalian assemblage to the upper part of the late Vallesian with an estimated age ranging from 9.3 to 8.7 Ma (Koufos, 2006b, 2016a). Pentalophos' chronology is not clear, although its faunal association indicates that it could be slightly older than Ravin de la Pluie (Koufos, 2006a, 2006b, 2013). Following Vlachou (2013), two hipparionin morphotypes were present in Macedonia during the Vallesian: the small *macedonicum* and the large *primigenium* morphotype. The material of the small *macedonicum* morphotype has been assigned to the *Hipparion macedonicum* species, while the larger hipparionins of the *primigenium* morphotype have been referred to *Hipparion* aff. *giganteum* in Nikiti-1, and to *Hipparion* cf. *sebastopolitanum* in Pentalophos and Ravin de la Pluie (Koufos et al., 2016; Vlachou, 2013).

Numerous Turolian localities have yielded rich hipparionin assemblages in the Balkan region. The Turolian sample analyzed here comes from the localities of Nikiti-2, Ravin des Zouaves-5, Hadjidimovo, Perivolaki and Dytiko. The oldest fossil site is Nikiti-2 (Chalkidiki Peninsula) (Figure 1, main text), dated to the early Turolian (MN11) with an age comprised between 8.7–8.2 Ma (Koufos, 2016a). Four different hipparionins are recognized here: two small taxa of the *macedonicum* morphotype (*Hipparion sithonis* and *H. macedonicum*), a larger form that pertains to the *dietrichi* morphotype (*Hipparion philippus*), and a rare and large hipparionin of the *proboscideum* group identified as *Hipparion* cf. *proboscideum* (Vlachou, 2013; Koufos and Vlachou, 2016). Ravin des Zouaves-5 (Axios Valley) is also an early Turolian site (MN11) dated at ~8.2 Ma (Koufos, 2006b). In this locality, Koufos and Vlachou (2019) reported five different taxa: *H. macedonicum* and *H. sithonis* of the *macedonicum* morphotype, *H. proboscideum* and *H. cf. mediterraneum* of the *proboscideum* morphotype, and *H. philippus* of the *dietrichi* morphotype. From this site, here we analyzed mainly specimens of *H. macedonicum* due to their availability. Hadjidimovo locality (Mesta Valley, central Balkan Peninsula) (Figure 1, main text) was dated between the early-middle Turolian (MN11–MN12) with an estimated age of ~7.5 Ma (Spassov, 2002). Three species have been identified, although the major bulk of the material corresponds to the two large species *Hipparion mediterraneum* [*proboscideum* morphotype sensu Vlachou (2013)] and *Hipparion brachypus* [*primigenium* morphotype sensu Vlachou (2013)] (Hristova, 2009), which are the species herein analyzed. We also sampled the hipparionins from Perivolaki (Thessaly, southeastern Balkan Peninsula) (Figure 1, main text), a site dated on the upper middle Turolian (MN12) with an estimated age of 7.3–7.1 Ma (Koufos, 2006a, 2006b). In Perivolaki, three different species are found: *H. macedonicum*, *H. philippus* and *H. proboscideum*; forming a similar association than other early and middle Turolian sites from the Axios Valley. Finally, the youngest locality is represented by the three Dytiko sites (DKO, DTK, DIT; Axios Valley) (Figure 1, main text), which were dated to the late Turolian (MN13) (Koufos, 2006b). Three hipparionin taxa are identified in the Dytiko faunal assemblage: the large *Hipparion* aff. *platygenys* [*dietrichi* morphotype sensu Vlachou (2013)], the small *Hipparion* cf. *macedonicum*, and a medium-sized rare form resembling to *Hipparion moldavicum* and tentatively assigned to the *proboscideum* morphotype (Vlachou, 2013). Because of the scarcity of some of the material from the species mentioned, we did not consider for analysis the *proboscideum* group from Nikiti-2 nor from the Dytiko sites, and only include one specimen from Ravin des Zouaves-5. The fossil material analyzed here from Hadjidimovo is stored at the Asenovgrad Museum (a division of the National Museum of Natural History of Sofia, Bulgaria) and the specimens from the Greek localities come from the Laboratory of Geology and Paleontology, Aristotle University of Thessaloniki, Greece.

APPENDIX 1.3. Western Anatolia

The Turolian hipparionins from the western Anatolian bioprovince come from the localities of Şerefköy-2, Gülpınar and the Samos new collections. The specimens from Samos pertain to the MTLA/B sites found in the Adrianos ravine during the recent excavations (Mytilinii Basin, Samos Island) (Figure 1, main text), which were dated on the late middle Turolian (~7.1 Ma) (Koufos et al., 2009; Vlachou and Koufos, 2009). At least five hipparionin taxa pertaining to four different morphotypes are present there: *H. cf. matthewi* (*macedonicum* morphotype), *Hipparion* aff. *forstenae* (*proboscideum* morphotype), *H. cf. proboscideum* (*proboscideum* morphotype), *H. dietrichi* (*dietrichi* morphotype) and *H. brachypus* (*primigenium* morphotype) (Vlachou and Koufos, 2009; Vlachou, 2013). In the Anatolian Peninsula, the locality of Şerefköy-2 (Muğla Yatağan Basin, western Anatolia) (Figure 1, main text) has been referred to the middle Turolian (MN12) based on its fossil mammal assemblage (Kaya et al., 2012). Four to five different hipparionin forms might be present in this site, a rare and large species similar to *H. brachypus*, two medium hipparionins broadly referred as *Hipparion*, and two small forms only identified as belonging to the *Cremohipparion* group [sensu Bernor et al. (1996)] (Kaya et al., 2012). The medium-sized hipparionins show similarities to *H. mediterraneum* specimens (Kaya et al., 2012). In consequence, we included here the medium sized forms to the *proboscideum* group. We further relate the small hipparionins of Şerefköy-2 to the species *H. matthewi*, as it has been done with the majority of the small-sized forms from eastern Mediterranean basins (Koufos, 2016b), thus including them to the *macedonicum* group defined by Vlachou (2013). Finally, Gülpınar fossil site is located on the Biga Peninsula (northwestern Anatolia) (Figure 1, main text) and corresponds to a sedimentary sequence of fluvial origin dated on early-middle Turolian (MN11–MN12) (Forsten and Kaya, 1995; Koufos et al., 2018). Three different forms have been distinguished in Gülpınar. The smallest hipparionin has been identified as *H. cf. matthewi* (*macedonicum* morphotype) and the medium-sized form show affinities to *H. dietrichi* from the classic Samos quarries (Forsten and Kaya, 1995). Due to these similarities, here we include this form to the *dietrichi* group defined by Vlachou (2013). The larger hipparionin remains from Gülpınar have not been determined. We did not analyze the dental microwear textures of the largest taxon—usually related to *H. brachypus* (Vlachou and Koufos, 2009; Kaya et al., 2012)—from the western Anatolian fossil sites due to its scarcity. The material from Samos is stored at the Paleontological Museum of Mytilinii, Samos, Greece, and the material from continental Anatolian sites at the Natural History Museum of Ege University of Izmir, Turkey.

APPENDIX 1.4. References

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APPENDIX 2. RAW DATA OF ALL THE HIPPARIONIN SAMPLE ANALYZED.

Orlandi-Oliveras, Guillem (2022), "Appendices for: Feeding strategies of circum-Mediterranean hipparionins during the late Miocene: exploring dietary preferences related to size through Dental Microwear Analysis", Mendeley Data, V1. <https://data.mendeley.com/datasets/np65bh8tgw/2>

APPENDIX 3. PHOTOSIMULATIONS OF THE MICROWEAR SURFACES.

Orlandi-Oliveras, Guillem (2022), "Appendices for: Feeding strategies of circum-Mediterranean hipparionins during the late Miocene: exploring dietary preferences related to size through Dental Microwear Analysis", Mendeley Data, V1. <https://data.mendeley.com/datasets/np65bh8tgw/2>

APPENDIX 4.

Results of the Principal Component Analysis performed with the ten settings used to calculate HAsfc (4, 9, 16, 25, 36, 49, 64, 81, 100, and 121 cells). Percentage of variance explained by the principal component and the contribution of each setting to the principal components are shown.

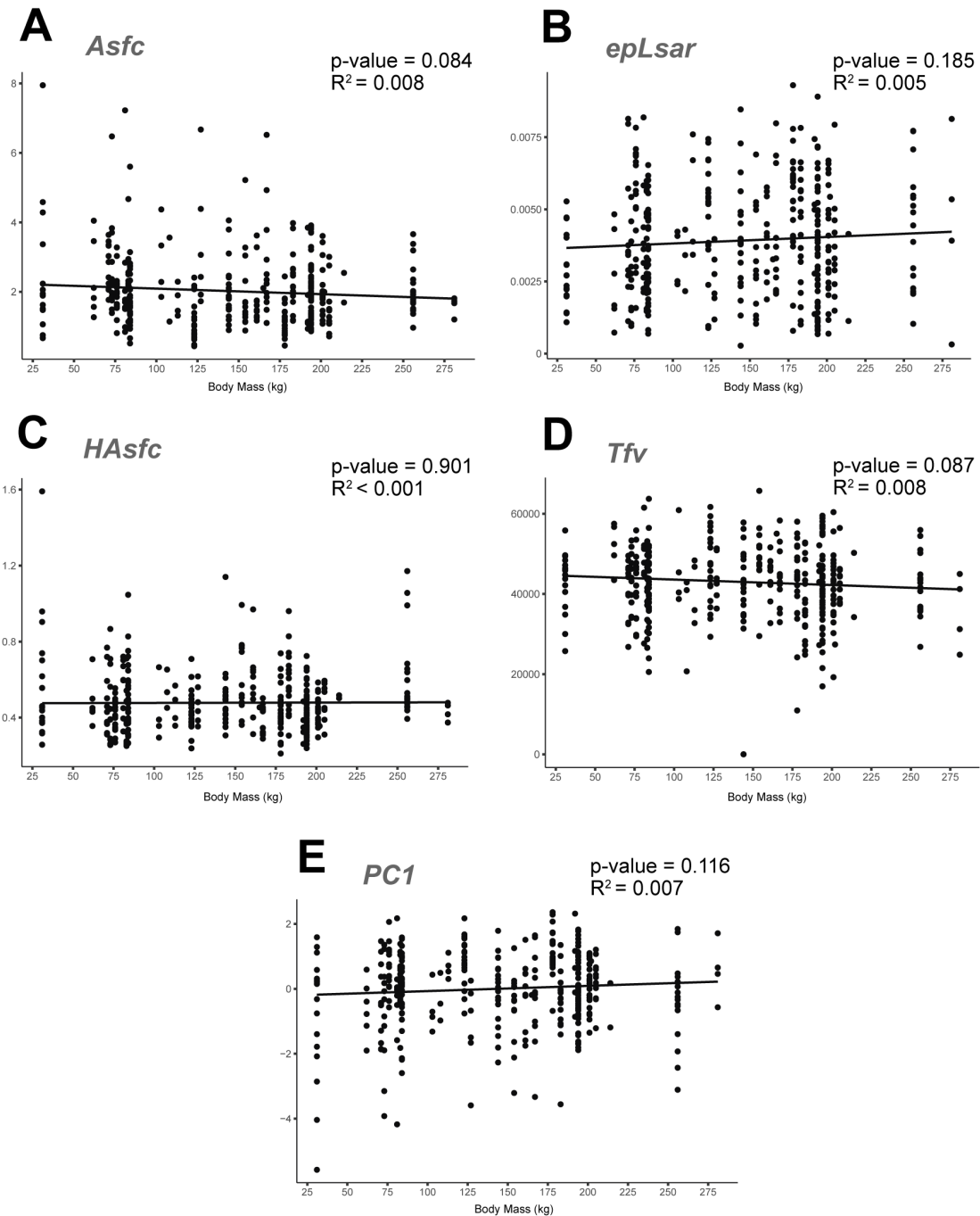
Component	% of variance	H4	H9	H16	H25	H36	H49	H64	H81	H100	H121
PC1	84.31	5.11	8.26	9.87	10.69	11.06	11.09	11.15	10.99	10.89	10.89
PC2	7.88	60.94	15.86	3.57	0.02	0.62	2.46	2.68	4.66	5.18	4.03

APPENDIX 5. METAPODIAL MEASURES AND BODY MASS ESTIMATIONS.

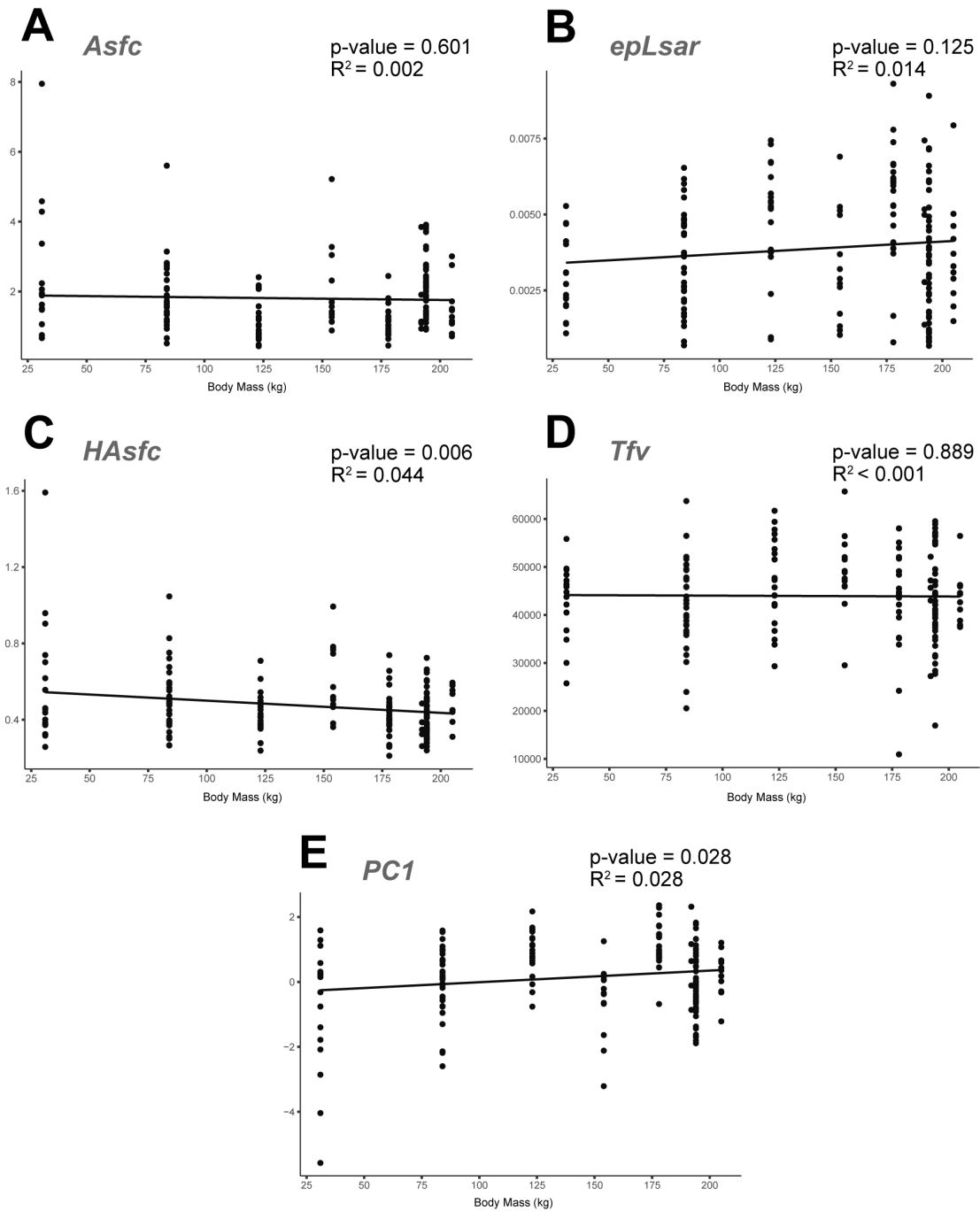
Orlandi-Oliveras, Guillem (2022), "Appendices for: Feeding strategies of circum-Mediterranean hipparionins during the late Miocene: exploring dietary preferences related to size through Dental Microwear Analysis", Mendeley Data, V1. <https://data.mendeley.com/datasets/np65bh8tgw/2>

APPENDIX 6. LINEAR REGRESSIONS ON DMT PARAMETERS VERSUS BODY MASS.

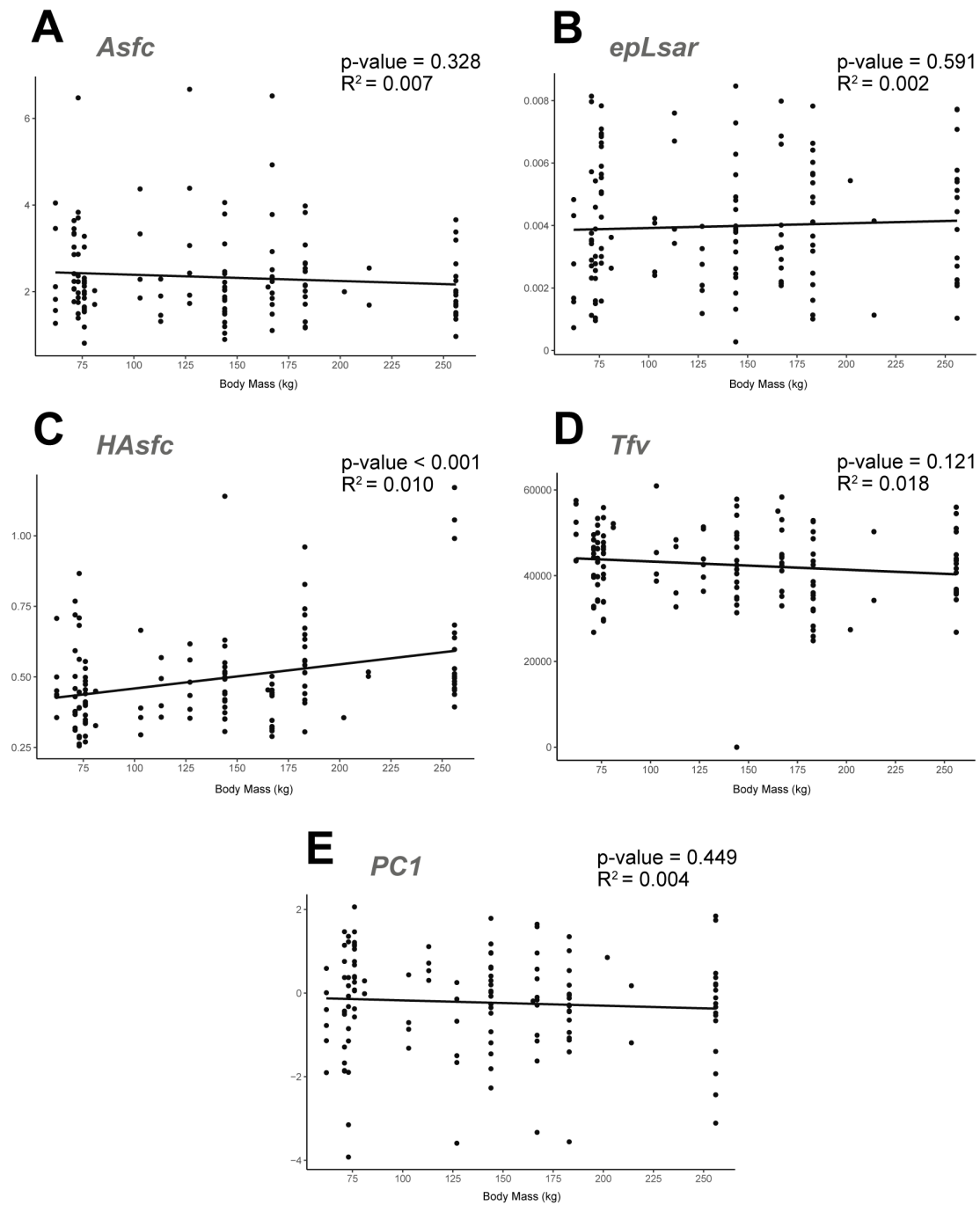
APPENDIX 6.1. Linear regressions of microwear textural parameters and the calculated principal component against body mass for all hipparionins. Correlation statistics included in each graph. **A:** Regression of the *Asfc* values. **B:** *epLsar*. **C:** *HAsfc*. **D:** *Tfv*. **E:** *PC1*.



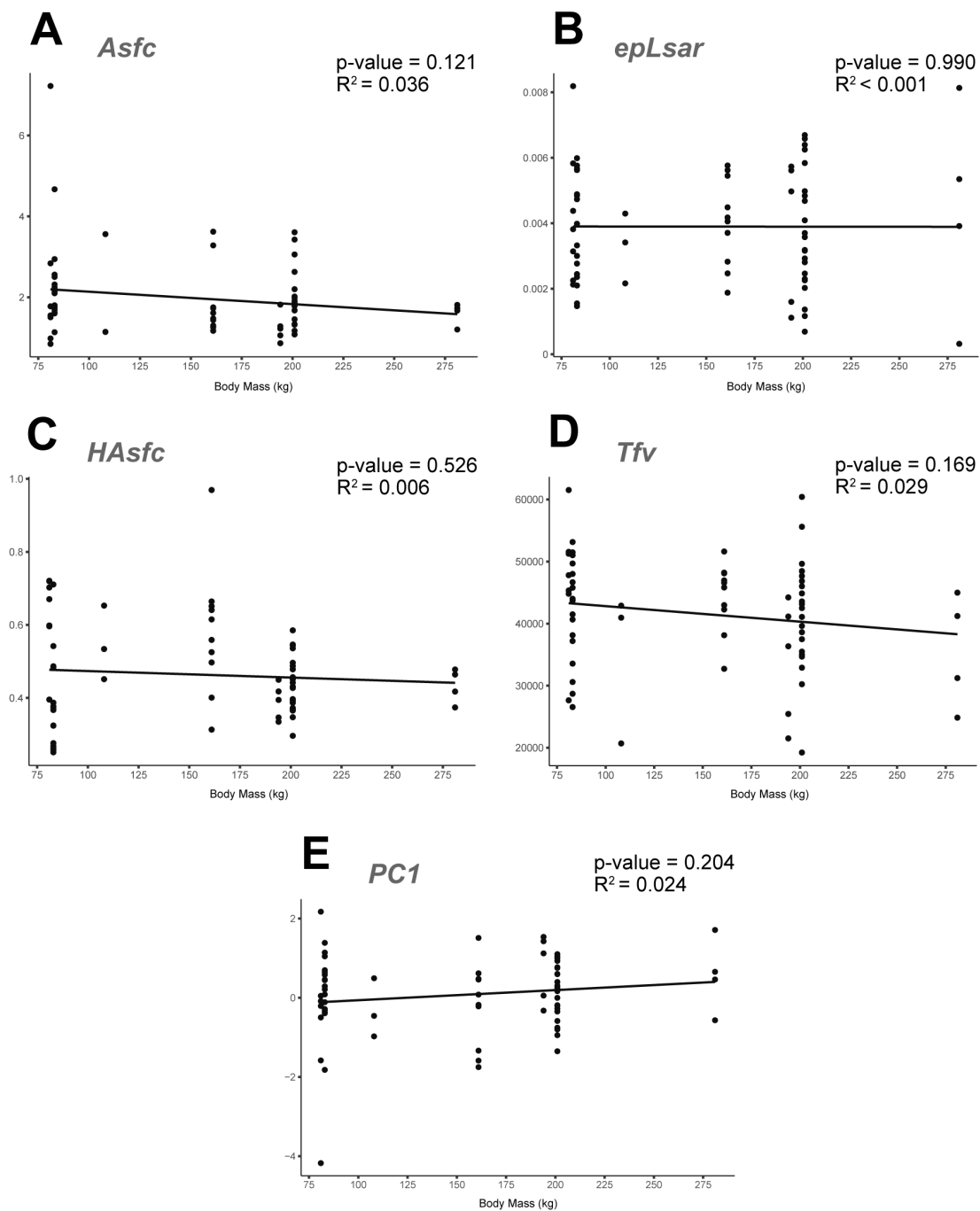
APPENDIX 6.2. Linear regressions of microwear textural parameters and the calculated principal component against body mass for western Mediterranean hipparionins. Correlation statistics included in each graph. **A:** Regression of the *Asfc* values. **B:** *epLsar*. **C:** *HAsfc*. **D:** *Tfv*. **E:** *PC1*.



APPENDIX 6.3. Linear regressions of microwear textural parameters and the calculated principal component against body mass for hipparionins from the Balkans. Correlation statistics included in each graph. **A:** Regression of the *Asfc* values. **B:** *epLsar*. **C:** *HAsfc*. **D:** *Tfv*. **E:** *PC1*.



APPENDIX 6.4. Linear regressions of microwear textural parameters and the calculated principal component against body mass for western Anatolian hipparionins. Correlation statistics included in each graph. **A:** Regression of the *Asfc* values. **B:** *epLsar*. **C:** *HAsfc*. **D:** *Tfv*. **E:** *PC1*.



APPENDIX 7. POST-HOC PAIRWISE COMPARISONS WITH TUROLIAN HIPPARIONIN DATA.

APPENDIX 7.1. Post-hoc tests on ranked complexity (Asfc). P-values from HSD test are depicted above the grey diagonal and those from LSD are under it. Significant p-values represented in bold.

BIOPROVINCE	Western Mediterranean	Balkans	Western Anatolia
Western Mediterranean		< 0.001	0.001
Balkans	< 0.001		0.011
Western Anatolia	< 0.001	0.004	

APPENDIX 7.2. Post-hoc tests on ranked heterogeneity of complexity (HAsfc). P-values from HSD test are depicted above the grey diagonal and those from LSD are under it. Significant p-values represented in bold.

BIOPROVINCE	Western Mediterranean	Balkans	Western Anatolia
Western Mediterranean		0.049	0.935
Balkans	0.019		0.189
Western Anatolia	0.727	0.081	

APPENDIX 7.3. Summary of post-hoc tests on ranked parameters showing significant differences between the Turolian hipparionin groups. Significant differences between groups obtained from HSD test are depicted above the grey diagonal and those from LSD are under it.

Bioprovince		West Mediterranean					Balkans				Western Anatolia		
Turolian hipparionin groups		<i>periafricanum</i>	<i>gromovae</i>	<i>cf. matthewi</i>	<i>conculdense</i>	<i>primigenium</i>	<i>macedonicum</i>	<i>dietrichi</i>	<i>proboscideum</i>	<i>primigenium</i>	<i>macedonicum</i>	<i>dietrichi</i>	<i>proboscideum</i>
Western Mediterranean	<i>periafricanum</i>			epLsar	Asfc, epLsar, PC1								
	<i>gromovae</i>				Asfc, epLsar, PC1		Asfc						
	<i>cf. matthewi</i>	Asfc, epLsar, PC1	Asfc, epLsar, PC1				Asfc	Asfc	Asfc, PC1	Asfc, PC1	Asfc, PC1		Asfc
	<i>conculdense</i>	Asfc, epLsar, PC1	Asfc, epLsar, PC1				Asfc, PC1	Asfc, PC1	Asfc, PC1	Asfc, HAsfc, PC1	Asfc, PC1	PC1	Asfc, PC1
	<i>primigenium</i>	HAsfc	HAsfc							HAsfc			
Balkans	<i>macedonicum</i>	Asfc, epLsar	Asfc,	Asfc, PC1	Asfc, epLsar, PC1	Asfc,				HAsfc			
	<i>dietrichi</i>		Asfc,	Asfc, epLsar, PC1	Asfc, epLsar, PC1	HAsfc,							
	<i>proboscideum</i>	epLsar, PC1	Asfc, HAsfc, PC1	Asfc, HAsfc, PC1	Asfc, epLsar, HAsfc, PC1	Asfc, HAsfc, PC1	HAsfc, PC1	PC1					HAsfc
	<i>primigenium</i>	epLsar	HAsfc	Asfc, HAsfc, PC1	Asfc, epLsar, HAsfc, PC1	HAsfc	HAsfc	HAsfc					HAsfc
Western Anatolia	<i>macedonicum</i>			Asfc, PC1	Asfc, epLsar, PC1				HAsfc	HAsfc			
	<i>dietrichi</i>			Asfc, HAsfc, PC1	Asfc, epLsar, HAsfc, PC1	HAsfc	Asfc, HAsfc		Asfc		HAsfc		
	<i>proboscideum</i>	epLsar		Asfc, PC1	Asfc, epLsar, PC1		Asfc		Asfc, HAsfc, PC1	HAsfc		HAsfc	

APPENDIX 7.4. Summary of post-hoc tests on parameters showing significant differences between localities. Here represented the results from pairwise comparisons between localities with hipparionins of the *macedonicum* group. Significant differences obtained from the HSD test are above the grey diagonal and those from LSD are under it.

<i>macedonicum</i> group		Balkans				Western Anatolia		
	Locality	NIK	RZO	PER	DTK	GLP	MYSE	MTLA/B
Balkans	Nikiti-2 (NIK)			epLsar				
	Ravin des Zouaves-5 (RZO)	epLsar						
	Perivolaki (PER)	epLsar, PC1						
	Dytiko (DTK)	epLsar, PC1	Tfv					
Western Anatolia	Gülpınar (GLP)	HAsfc, PC1	HAsfc	HAsfc			HAsfc	
	Şerefköy-2 (MYSE)	epLsar			Tfv	HAsfc		
	Samos (MTLA/B)				Tfv		HAsfc	

APPENDIX 7.5. Summary of post-hoc tests on parameters showing significant differences between localities. Here represented the results from pairwise comparisons between localities with hipparionins of the *dietrichi* group. Significant differences obtained from the HSD test are above the grey diagonal and those from LSD are under it.

<i>dietrichi</i> group		Balkans			Western Anatolia	
	Locality	NIK	PER	DTK	GLP	MTLA/B
Balkans	Nikiti-2 (NIK)					
	Perivolaki (PER)	epLsar, PC1				
	Dytiko (DTK)					
Western Anatolia	Gülpınar (GLP)					
	Samos (MTLA/B)	epLsar				

APPENDIX 7.6. Summary of post-hoc tests on parameters showing significant differences between localities. Here represented the results from pairwise comparisons between localities with hipparionins of the *proboscideum* group. Significant differences obtained from the HSD test are above the grey diagonal and those from LSD are under it.

<i>proboscideum</i> group		Balkans			Western Anatolia	
	Locality	RZO	PER	HD	MYSE	MTLA/B
Balkans	Ravin des Zouaves-5 (RZO)					
	Perivolaki (PER)	Tfv				
	Hadjidimovo (HD)					
Western Anatolia	Şerefköy-2 (MYSE)			HAsfc		
	Samos (MTLA/B)		Tfv, PC1	HAsfc, PC1	Tfv	

APPENDIX 7.7. Summary of post-hoc tests on parameters showing significant differences between localities. Here represented the results from pairwise comparisons between localities with hipparionins of the *primigenium* group. Significant differences obtained from the HSD test are above the grey diagonal and those from LSD are under it.

<i>primigenium</i> group		Western Mediterranean	Balkans
	Locality	ARQ	HD
Western Mediterranean	El Arquillo (ARQ)	HSD test →	
Balkans	Hadjidimovo (HD)	HAsfc	← LSD test

APPENDIX 7.8. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Nikiti-2 locality.

Nikiti-2 (NIK)	<i>macedonicum</i>	<i>dietrichi</i>
<i>macedonicum</i>	HSD test →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>dietrichi</i>	Asfc: - epLSar: 0.968 HAsfc: 0.480 Tfv: 0.667 PC1: 0.811	← LSD test

APPENDIX 7.9. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Perivolaki locality.

Perivolaki (PER)	<i>macedonicum</i>	<i>dietrichi</i>	<i>proboscideum</i>
<i>macedonicum</i>	HSD test →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>dietrichi</i>	Asfc: - epLSar: 0.813 HAsfc: 0.569 Tfv: 0.997 PC1: 0.389		Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>proboscideum</i>	Asfc: - epLSar: 0.744 HAsfc: 0.779 Tfv: 0.184 PC1: 0.203	Asfc: - epLSar: 0.669 HAsfc: 0.997 Tfv: 0.198 PC1: 0.408	← LSD test

APPENDIX 7.10. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Hadjidimovo locality.

Hadjidimovo (HD)	<i>proboscideum</i>	<i>primigenium</i>
<i>proboscideum</i>	HSD test →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>primigenium</i>	Asfc: - epLSar: 0.970 HAsfc: 0.990 Tfv: 0.257 PC1: 0.187	← LSD test

APPENDIX 7.11. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Dytiko locality. Significant p-values represented in bold.

Dytiko (DTK)	<i>macedonicum</i>	<i>dietrichi</i>
<i>macedonicum</i>	HSD test →	Asfc: - epLSar: 0.998 HAsfc: 1.000 Tfv: 0.913 PC1: 1.000
<i>dietrichi</i>	Asfc: - epLSar: 0.144 HAsfc: 0.806 Tfv: 0.040 PC1: 0.323	← LSD test

APPENDIX 7.12. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Gülpınar locality.

Gülpınar (GLP)	<i>macedonicum</i>	<i>dietrichi</i>
<i>macedonicum</i>	HSD test →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>dietrichi</i>	Asfc: - epLSar: 0.991 HAsfc: 0.448 Tfv: 0.444 PC1: 0.516	← LSD test

APPENDIX 7.13. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Samos new collections.

Samos (MTLA/B)	<i>macedonicum</i>	<i>dietrichi</i>	<i>proboscideum</i>
<i>macedonicum</i>	HSD →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000	Asfc: - epLSar: 1.000 HAsfc: 0.971 Tfv: 1.000 PC1: 0.995
<i>dietrichi</i>	Asfc: - epLSar: 0.663 HAsfc: 0.353 Tfv: 0.850 PC1: 0.691		Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000
<i>proboscideum</i>	Asfc: - epLSar: 0.475 HAsfc: 0.066 Tfv: 0.902 PC1: 0.111	Asfc: - epLSar: 0.213 HAsfc: 0.479 Tfv: 0.723 PC1: 0.267	← LSD

APPENDIX 7.14. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from Şerefköy-2 locality.

Şerefköy-2 (MYSE)	<i>macedonicum</i>	<i>proboscideum</i>
<i>macedonicum</i>	HSD test →	Asfc: - epLSar: 1.000 HAsfc: 0.997 Tfv: 1.000 PC1: 1.000
<i>proboscideum</i>	Asfc: - epLSar: 0.972 HAsfc: 0.124 Tfv: 0.881 PC1: 0.659	← LSD test

APPENDIX 7.15. Results of the post-hoc tests from pairwise comparisons between hipparionin groups from El Arquillo locality. Significant p-values represented in bold.

El Arquillo (ARQ)	<i>periafricanum</i>	<i>gromovae</i>	<i>primigenium</i>
<i>periafricanum</i>	HSD →	Asfc: - epLSar: 1.000 HAsfc: 1.000 Tfv: 1.000 PC1: 1.000	Asfc: - epLSar: 0.995 HAsfc: 0.840 Tfv: 1.000 PC1: 1.000
<i>gromovae</i>	Asfc: - epLSar: 0.175 HAsfc: 0.645 Tfv: 0.779 PC1: 0.743		Asfc: - epLSar: 1.000 HAsfc: 0.909 Tfv: 0.985 PC1: 1.000
<i>primigenium</i>	Asfc: - epLSar: 0.112 HAsfc: 0.027 Tfv: 0.970 PC1: 0.604	Asfc: - epLSar: 0.397 HAsfc: 0.039 Tfv: 0.830 PC1: 0.450	← LSD