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The evolutionary ecology of the endemic European Eocene *Plagiolophus* (Mammalia: Perissodactyla)

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ABSTRACT

The climatic cooling that began in the late middle Eocene and culminated in the Eocene-Oligocene transition meant major changes in Palaeotheriidae (Perissodactyla, Mammalia) biodiversity in Europe and could have caused the appearance of new dietary strategies. This work is the first to study the spatiotemporal response of one palaeotheriid genus (*Plagiolophus*) to the Eocene environmental and ecological changes using three dietary proxies: hypsodonty, mesowear and dental microwear texture analysis (DMTA). DMTA is applied for the first time to palaeotheriids. The high diversity and wide chrono-spatial distribution of *Plagiolophus* make it possible to evaluate spatiotemporal environmental variations, including palaeodiet. We study five *Plagiolophus* samples from late middle Eocene to early Oligocene from western Iberia to central Europe in order to (1) infer lifetime palaeodiet; (2) infer short-term palaeodiet; and (3) test temporal and spatial trends. All samples present an exclusion of abrasive foodstuff given low hypsodonty index; dominance of browsing given the low mesowear score; and browsing of tough foliage and exclusion of hard items in their diet given DMTA information. These factors point to *Plagiolophus* as a highly selective feeder that fed on plants with the same features irrespective of chronology or location: tough foliage (leaves from monocots or dicots) avoiding lignified or hard materials, without seasonal variations.

1. Introduction

During the Eocene (56–33.9 Ma), Europe was an archipelago formed by three main islands (Fig. 1A). This led to strong endemism caused by relative isolation with sporadic faunal exchanges, as well as to several adaptive radiations in different mammalian taxa. Among the clades that were highly diverse in western Europe were Euprimates, which included adapiforms and tarsiiforms (Godinot, 2015); Rodentia, which included theridomorphs (Vianey-Liaud and Marivaux, 2016); as well as Perissodactyla (Equoidea), which included palaeotheriids (Franzen, 2010). Those from western Iberia were endemic during most of the Eocene (Badiola et al., 2009; Perales-Gogenola et al., 2021). One of the most abundant and diverse genera among the palaeotheriids *sensu stricto* (or palaeotheres) (Franzen, 2010) was *Plagiolophus* Pomel, 1847 (Remy, 2004). This genus is documented almost solely in western Europe (including France, Germany, the United Kingdom, Spain, and Switzerland) from the middle Eocene (similar in age to the Land Mammal Paleogene level MP 12; ~48 Ma) to the early Oligocene (MP 25; ~27.6 Ma) (Remy, 2004; Speijer et al., 2020). As regards palaeodiversity, it comprises 17 species classified in three subgenera: *Paloplotherium* Owen, 1848 (ten species), *Fraasiolophus* Remy, 2004 (one species) and *Plagiolophus* Pomel, 1847 (six species) (Remy, 2004 and references therein) (Fig. S1).

Plagiolophus dentition is characterized by increasing heterodonty, little molarization of the premolars, and a reduction in the premolar series through time, together with enlargement of the molar series in some Oligocene species (Remy, 2004). The hypsodonty index (HI; the relative height of the molars) increases from the first brachyodont *Plagiolophus* to the last representative of the genus, which was nearly as hypsodont as the first grazing equid *Merychippus* Leidy, 1856 (Remy,

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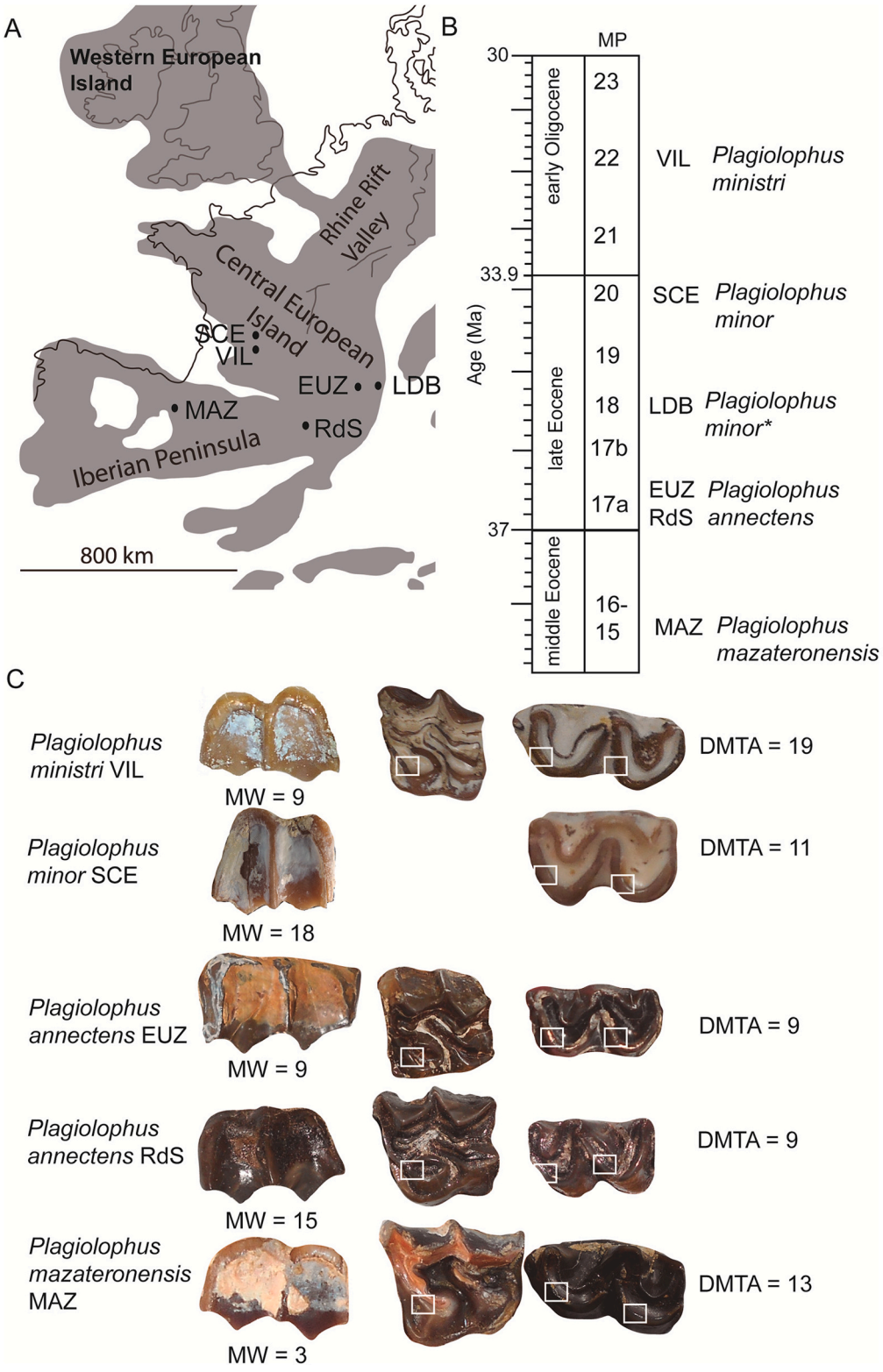

Fig. 1. A, palaeogeography (sea in white and land in grey) of Europe during the middle Eocene (Lutetian), which includes the location of the Palaeogene sites studied here. The present-day geography is partially outlined in black. Modified from Franzen (2003). EUZ = Euzet-les-Bains; LDB = La Débruge; MAZ = Mazaterón; RdS = Roc de Santa I; SCE = St. Capraise d'Eymet; VIL = Villebramar. B, chronological column of the Palaeogene sites where the studied samples were recovered and sample number for the following analyses of each population of *Plagiolophus* (Perissodactyla, Mammalia). C, specimens and the samples of the different *Plagiolophus* species used in this study. *P. ministri* VIL (upper lingual VIL-VF-12444; upper occlusal VIL-VF-12250; lower occlusal VIL-VF-10290). *P. minor* SCE (upper lingual SCE-VF-10126; lower occlusal SCE-VF-10183). *P. annectens* EUZ (upper labial and occlusal StH 2598; lower occlusal StH 420). *P. annectens* RdS (upper labial and occlusal IPS-244; lower occlusal IPS-28). *P. mazateronensis* MAZ (upper labial and occlusal STUS 2634; lower occlusal 9224). Squares represent the facets used in DMTA.

2004; Bravo-Cuevas and Ferrusquía-Villafranca, 2006).

These variations in dentition, in combination with changes in the masticatory musculature and the distribution of the masticatory forces, strongly suggest that the different *Plagiolophus* species may have had diverse dietary preferences through their long evolutionary history, being browsers first, then mixed-feeders, and finally grazers (Remy, 2004). As grasslands were not widespread during the Eocene or early Oligocene (Crepet and Feldman, 1991), we can rule out that they were obligate grazing mammals. However, grasses and other herbaceous monocots may have played a secondary role in their diet. Indeed, the increase in the HI value during the Eocene, together with the two other studied proxies (mesowear and DMTA microwear values), could indicate the presence of a more abrasive diet in the latest Eocene or early Oligocene palaeotheriids. In fact, it has been hypothesized that these dietary changes were the results of the slow degradation of environmental conditions during the Eocene in western Europe, with the spread of more open landscapes, increased aridity, and more marked seasonality (Remy, 2004). During the early and middle Eocene, the climate was humid and intertropical, with more arid periods in the late middle Eocene that resulted in the proliferation of more abrasive vegetation (Blondel, 2001; Franzen, 2003). During the late Eocene, important changes in the European mammals and flora occurred due to rapid climate cooling, which could have led to the appearance of dietary strategies based on different vegetation types adapted to seasonal changes (Blondel, 2001; Franzen, 2003; Remy, 2004). During the middle Eocene, palaeotheres characterized by a more hypsodont and lophodont dentition were favoured and gradually replaced the brachyodont equoids (Blondel, 2001; Franzen, 2003), the subfamily Pachynolophinae Pavlow, 1888 or the European "equids" [*sensu* Franzen, 2010]. In the light of the dental morphology (e.g., the precocious development of coronal cementum and the high hyposodonty index) of the endemic palaeotheriids (Badiola and Cuesta, 2008; Badiola et al., 2009a; Perales-Gogenola et al., 2021), the environmental changes could have started earlier in western Iberia. However, none of these ecological and evolutionary dietary hypotheses has been tested.

The few early studies based on tooth wear suggested that Eocene *Plagiolophus* was a browser that also consumed a small number of fruits and ate tougher, but less abrasive food than *Palaeotherium medium* (Joomun et al., 2008), and that the latest representative, *Plagiolophus minor*, fed on more abrasive diets (Joomun et al., 2010). The aim of this work is to test the hypothesis of dietary changes as the main drivers of the evolutionary history of the genus *Plagiolophus* through time and space. To this end, we apply a combination of dental morphology (e.g., hypsodonty) and independent dental dietary proxies (e.g., dental mesowear, dental microwear texture analyses or DMTA) in conjunction with body mass assessment to five different *Plagiolophus* samples from the middle Eocene to early Oligocene of the Iberian Peninsula and western Europe (Fig. 1). This is the very first time that the combination of these three dental dietary proxies, which provide complementary ecological information as they cover different time windows, has been applied to palaeotheriids. Whereas dental microwear textures reflect the physical, mechanical food properties and their inner composition over the last few days to weeks before death (Teaford and Oyen, 1989a; Teaford et al., 2017), molar hypsodonty is the result of phenotypic natural selection acting over hundreds to thousands of generations (Davis and Pineda-Munoz, 2016). Recent experimentation on living sheep and goats attests to the fact that dental mesowear reflects feeding habits over an extended period, ranging from years to the whole lifespan of the specimen (Ackermans et al., 2018, 2020).

Using this triplet of dietary proxies, the objectives of this study are: (1) to infer the palaeodiet of five *Plagiolophus* samples through comparisons with various datasets of modern species with known differences in diet; (2) to ascertain whether a temporal trend existed; and (3) to assess whether the most widespread species, *P. annectens*, adapted its feeding habits to local conditions (Figs. 1A-B).

2. Geological and geographical context

The site of Mazaterón is situated near the village of Mazaterón (Castile and León, Spain) in the Almazán Basin, in the eastern sector of the Duero Basin (Fig. 1A). The depositional setting is a shallow lacustrine/palustrine system, which was subject to constant flooding and drying processes (e.g., Alonso-Gavilán et al., 2004; Huerta and Armenteros, 2006). In terms of the European Land Mammal Ages, it is Robiacian in age (42.7–37.2 Ma; Fig. 1B) (Cuesta, 1999; Antunes et al., 1997).

The Roc de Santa I site is situated near the contemporaneous fossil site of Sossís (Conca de Dalt, Lleida, Spain) (Casanovas-Cladellas, 1975) in the Graus-Tremp Basin (Southern Pyrenean Basin, Spain) (Figs. 1A-B). Sossís is interpreted as a wetland made up of low vegetation comprising mosses, reeds, and aquatic plants as well as trees (Casanovas et al., 1998).

The Euzet-les-Bains site, which is early late Eocene in age like the Roc de Santa site, is in southeastern France (Figs. 1A-B), approximately 400 km southeast of the sites of Villebramar and St. Capraise d'Eymet. Among the recovered fossils are aquatic plants and fish (Depéret, 1917; Aguilar et al., 1997), which suggests a nearby water source.

According to several palaeontological studies, the site of St. Capraise d'Eymet (Dordogne, France) is assigned to level MP 20, but as the fossil assemblage of this site is quite poor in micromammal fossils, it is not a particularly good landmark (Aguilar et al., 1997; Gagnaison and Leroux, 2013). Villebramar would have been dry open woodland associated with marshy forests and an open, dry environment, probably a scrub woodland type, according to the *Ronzotherium-Anthracotherium* association (Uhlig, 1999; Emery et al., 2007; Becker et al., 2009). For information on the La Débruge site (Headonian, MP 18, Figs. 1A-B), see Joomun et al. (2008) and references therein.

The biochronological scale used in this paper is the Mammal Palaeogene (MP) reference levels (Schmidt-Kittler, 1987; Aguilar et al., 1997). We use the traditionally accepted ages for the chronostratigraphy of the MP levels of Europe (more details in Badiola et al., 2009).

3. Material and methods

Five samples belonging to four *Plagiolophus* species were studied (Figs. 1A-B; Table 1). The *Plagiolophus mazateronensis* specimens are housed at the Sala de las Tortugas de la Universidad de Salamanca (Spain); the *P. annectens* specimens from Roc de Santa I are housed at the Institut Catalá de Paleontologia (Spain); the *P. annectens* specimens from Euzet-les-Bains are housed at the Naturhistorisches Museum Basel (Switzerland); and the *P. minor* and *P. ministri* specimens are housed at the Université de Poitiers (France). See supplementary information (Tables S1–S4) for a complete list of the material studied. As comparative data, various modern ungulate datasets for HI, molar mesowear and DMTA are used.

Table 1
Body mass (mean value in kg) and hypsodonty index (HI) of five populations of *Plagiolophus*.

Taxon	N	Site	Body Mass (kg)	Number	HIm3
Plagiolophus mazateronensis	3	Mazaterón	118.71	STUS 9236	1.3
Plagiolophus annectens	7	Euzet	34.80	StH 2586	0.97
Plagiolophus annectens	35	Roc de Santa I	40.60	IPS-243	1.25
Plagiolophus minor	7	St Capraise d'Eymet	26.56	SCE-VF-10180	1.27
Plagiolophus ministri	16	Villebramar	53.61	VIL-VF-10320	1.49

3.1. Hypsodonty and body mass

For the lower molars, the relative crown height, or hypsodonty index (HI), was measured as m3 height/m3 width following Janis (1988). A lower tooth is classified as brachyodont when HI is less than 1.5, mesodont when it is between 1.5 and 3, and hypsodont when it is greater than 3 (Janis, 1990) (Table S2). The results are compared with the information on HI in Fortelius and Solounias (2000). Body mass was calculated applying the formula of Legendre (1986) when at least one first lower molar (m1) was available (Table 1; Table S3).

3.2. Mesowear analysis

Dental mesowear was preferentially scored on upper second molars (M2) (Table 2). However, first and third upper molars, M1 and M3, were also included to increment the sample size, as many molars were either unworn or excessively worn (Fortelius and Solounias, 2000) (Table S1, Fig. S2). The mesowear score (MS), calculated following Kaiser et al. (2009), was compared with the scores of 5491 individuals belonging to 75 extant ungulate species (Kaiser et al., 2013:Table 1).

3.3. Dental microwear texture analysis (DMTA)

DMTA was performed following the standard procedures (Merceron et al., 2016). Replicas of dental facets were produced with a silicone (medium consistency), polyvinyl siloxane (Coltène Whaledent, President Regular Body, ISO 4823). Preferentially, second upper or lower molars of adult specimens were used. However, third or first molars were considered when the second molars were weathered, excessively worn or too recently erupted (Table S4). Scans (320 × 280 μm) were produced on replicas using TRIDENT, a Leica DCM8 confocal surface profilometer with a 100× lens (Leica Microsystems; Numerical Aperture = 0.90; working distance = 0.9 mm; see details in Merceron et al., 2016) at the PALEVOPRIM Lab of the University of Poitiers, France. One surface (200 × 200 μm; 1088 × 776 pixels) was cropped from the original scans and saved as .sur files (Supporting Information).

After treating the surfaces (see details in Merceron et al., 2016), the DMTA was performed using scale-sensitive fractal analysis (SSFA) with Leica Map v. 8.0 (Leica Microsystems) following Scott et al. (2006). Three variables were extracted from the surface: complexity (Asfc), anisotropy (epLsar) and heterogeneity of complexity (HAsfc calculated with an 81-cell mesh; see Scott et al., 2006 for further details; Table 3). The dispersion of the values follows the Levine equations (Plavcan and Cope, 2001; Merceron et al., 2021). The dental microwear textures of the fossil samples were compared with those of 202 wild-shot specimens belonging to seven extant species of ruminants with known differences in feeding preferences, including browsers (*Alces alces* $n = 48$, *Capreolus capreolus*, $n = 18$), mixed-feeders (*Bison bonasus* $n = 25$, *Cervus elaphus* $n = 22$, *Ovis ammon* $n = 23$, *Rupicapra rupicapra* n = 22) and a semi-wild cattle population representing the grazing pole (*Bos taurus* $n = 44$) (Merceron et al., 2021).

Differences between the samples were statistically tested using parametric analyses. Data were either Box-Cox- or rank-transformed to meet the assumptions for a parametric test; then one-way analyses of variance (ANOVAs) and pairwise comparisons (Fisher's LSD and

Table 3
Descriptive statistics (mean, standard error of the mean (S.e.m.), and dispersion) for SSFA parameters (Asfc, $HAsfc_{81\text{-cells}}$ and epLsar) for *Plagiolophus mazateronensis*, two samples of *P. annectens*, *P. minor* and *P. ministri*, including the mean value and the standard error of the mean value.

Species		Asfc	$HAsfc_{81\text{-cells}}$	epLsar*
P. mazateronensis (Mazaterón, $n = 13$)	*n*	13	13	13
	Mean	1.22	0.61	5.983
	S.e.m.	0.31	0.05	0.567
	Dispersion	0.68	0.18	0.31
P. annectens (Roc de Santa, $n = 9$)	*n*	9	9	9
	Mean	1.55	0.54	6.250
	S.e.m.	0.26	0.06	0.940
	Dispersion	0.35	0.23	0.31
P. annectens (Euzet, $n = 9$)	*n*	9	9	9
	Mean	0.83	0.65	6.886
	S.e.m.	0.12	0.10	1.219
	Dispersion	0.39	0.40	0.53
P. minor (St. Capraise d'Eymet, $n = 11$)	*n*	11	11	11
	Mean	1.23	0.61	5.725
	S.e.m.	0.19	0.07	0.579
	Dispersion	0.42	0.20	0.30
P. ministri (Villebramar, $n = 19$)	*n*	19	19	19
	Mean	1.46	0.56	6.550
	S.e.m.	0.17	0.03	0.668
	Dispersion	0.38	0.18	0.33
Alces alces ($n = 48$)	*n*	48	48	48
	Mean	4.10	1.57	2.230
	S.e.m.	0.47	0.15	0.222
	Dispersion	0.54	0.43	0.63
Bison bonasus (n = 25)	*n*	25	25	25
	Mean	2.31	0.97	3.283
	S.e.m.	0.31	0.10	0.38
	Dispersion	0.47	0.37	0.55
Bos taurus ($n = 44$)	*n*	44	44	44
	Mean	1.57	0.78	5.172
	S.e.m.	0.14	0.06	0.32
	Dispersion	0.35	0.38	0.40
Capreolus capreolus ($n = 18$)	*n*	18	18	18
	Mean	2.61	0.69	6.053
	S.e.m.	0.59	0.05	0.55
	Dispersion	0.67	0.24	0.38
Cervus elaphus ($n = 22$)	*n*	22	22	22
	Mean	1.34	0.89	6.050
	S.e.m.	0.12	0.12	0.55
	Dispersion	0.32	0.27	0.41
Ovis ammon ($n = 23$)	*n*	23	23	23
	Mean	1.99	0.67	3.701
	S.e.m.	0.18	0.04	0.524
	Dispersion	0.38	0.20	0.53
Rupicapra rupicapra ($n = 22$)	*n*	22	22	22
	Mean	1.80	0.89	4.209
	S.e.m.	0.20	0.12	0.375
	Dispersion	0.36	0.34	0.39

* $\times 10^3$.

Table 2
Traditional mesowear parameters, mesowear score and hypsodonty index (HI) of five populations of *Plagiolophus*. MS, mesowear score; MAZ, Mazaterón; EUZ, Euzet-les-Bains; RdS, Roc de Santa I; SCE, St. Capraise d'Eymet; VILL, Villebramar.

Species	*Plagiolophus mazateronensis*	*Plagiolophus annectens*	*Plagiolophus annectens*	*Plagiolophus minor*	*Plagiolophus ministri*
Site	MAZ	EUZ	RdS	SCE	VILL
Sample	3	9	15	18	9
MS	3 (0.33)	9 (0.11)	15 (0.27)	18 (1.05)	9 (0.89)
High (%)	3 (100)	9 (100)	15 (100)	14 (77.78)	9 (100)
Low (%)	0 (0)	0 (0)	0 (0)	4 (22.22)	0 (0)
Sharp (%)	2 (66.67)	8 (88.89)	11 (73.33)	7 (38.89)	8 (88.89)
Round (%)	1 (33.33)	1 (11.11)	4 (26.67)	11 (61.11)	1 (11.11)
Blunt (%)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
HI_{m3}	1.3	0.97	1.25	1.50	1.50

Tukey's HSD) were performed for each texture and dispersion parameter (Tables S5–8). The software used was SPSS 26 (SPSS Inc., Chicago, IL, USA) and Past 3.0 (Hammer and Harper, Oslo, Norway) (Hammer et al., 2001).

4. Results

4.1. Hypsodonty index, body mass, and mesowear score

All the studied *Plagiolophus* species have brachyodont molars like those of modern browsers (Janis, 1990) (Fig. 2A), and even lower molar crowns than the species of *Plagiolophus* mentioned by earlier works (Fig. 2A) (Joomun et al., 2008, 2010). However, we find a slight increase in hypsodonty over time from 0.97 to 1.49 except in *P. mazateronensis* (1.3), which is consistent with previous works (Table 1) (Remy, 2004; Joomun et al., 2010). Regarding body size in our taxonomical sampling, *P. mazateronensis* Cuesta, 1994 is the largest species (118.71 kg), and *P. minor* (Cuvier, 1804) Pomel, 1847 the smallest (26.56 kg) (Table 1, S3). The body mass does not seem to influence or bias the mesowear and microwear results. MS and DMTA (Tables 2–3), as shown by the statistical analyses of DMTA (Tables S7–S8), do not appear to be major factors driving the size differences among populations. All the species but *P. minor* from Saint Capraise d'Eymet (with 77.78%) and from La Débruge (88.2%) (Joomun et al., 2020) have 100% high occlusal relief on their cheek teeth. The cusp shapes vary between species, however (Fig. 2B; Table 1). Joomun et al. (2010) observed that most specimens from Frohnstetten, Soumailles and Ronzon have rounded cusps, and even those from La Débruge have some rounded cusps. By contrast, most specimens in this study have sharp, not rounded cusps (Table 2). This could be due to different environmental conditions in the above-mentioned sites from those studied here, as observed in the high occlusal relief values (Joomun et al., 2010). Joomun et al. (2010) focused their study on central European sites from the late Eocene to early Oligocene, whereas in this study we include other southern European sites, including ones in western Iberia, from the late middle Eocene to the Late Eocene.

For the populations studied here, the mesowear score ranges between 0.11 and 1.05 (Table 2). We observe a tendency towards a higher percentage of sharp cusps and less round cusps from *P. mazateronensis* from Mazaterón to *P. annectens* (Owen, 1848) Stehlin, 1904 from Euzet-les-Bains (Table 2). *Plagiolophus ministri* Brunet and Jehenne, 1989 from Villebramar shows the same mesowear as the latter, whereas *P. minor* from St. Capraise d'Eymet shows a higher percentage of rounded than sharp cusps (Table 2).

The mesowear score and hypsodonty index (Kaiser et al., 2009) situate *Plagiolophus* in the browser range, close to the mixed-feeder range (Fig. 2B). They plot next to browsing ruminants occupying quite different habitats (e.g., arid drylands, tropical rainforest, etc.), such as *Giraffa camelopardalis*, *Odocoileus virginianus*, *A. alces*, *C. capreolus*, *Hyemoschus aquaticus* and *Litocranius walleri* (Figs. 2B and S4). These species inhabit a variety of different landscapes both near and far away from water sources, such as arid drylands, savannahs, or tropical rainforest, and they feed on a great variety of vegetation (e.g., *H. aquaticus* feeds on the leaves, fruits, and buds of trees) (Robin, 1990; Nowak, 1999; Franzmann, 2000; Renecker and Schwartz, 2007).

4.2. Dental microwear textures

All the *Plagiolophus* samples show significant differences with respect to some of the comparative extant species, most notably with respect to the browsing cervid *A. alces* and the three mixed-feeding bovids (*B. bonasus, R. rupicapra,* and *O. ammon*). They differ from these extant species mainly in combining low complexity (Asfc<2.0; cf. Scott, 2012), high anisotropy (epLsar>5.0 × 10^{-3}; cf. Scott, 2012) and to a lesser extent a low heterogeneity of complexity (Table S6). The differences are smaller with respect to the browsing *C. capreolus,* the mixed-feeding *C. elaphus*, and the grazing *B. taurus*. The only significant variation among the fossil samples concerns the texture complexity. *Plagiolophus ministri* differs from *P. annectens* from Euzet-les-Bains and *P. mazateronensis* in having higher values, whereas the late middle Eocene species *P. mazateronensis* from western Iberia also differs from the late Eocene *P. annectens* from Roc de Santa I (northeastern Iberia) in having higher values. It is noteworthy that the two samples of *P. annectens* differ from each other.

Raw variables apart, the distribution of the dental microwear texture parameters also differs between species. The fossil species of *Plagiolophus* differ most notably from the browser *A. alces*, the mixed-feeder *B. bonasus* and the grazer *B. taurus* in having higher/lower dispersion of either anisotropy or heterogeneity of complexity, or both (Table S8). Only the dispersion of the heterogeneity of complexity significantly varies among the fossil species. The sample of *P. annectens* from Euzet-les-Bains differs from all other species of *Plagiolophus*. There is no difference between the two samples of *P. annectens*.

Although non-significant, the western Iberian late middle Eocene species *P. mazateronensis* shows both the highest mean and widest dispersion in complexity among the samples of *Plagiolophus* (Table S4). There is a spatiotemporal trend in complexity towards higher values from the late Eocene species *P. annectens* of Euzet-les-Bains to the Oligocene species *P. ministri* of Villebramar (Table 3). The highest and lowest complexity values correspond to *P. annectens* from Roc de Santa I and *P. annectens* from Euzet-les-Bains, respectively (Table S5). There is no apparent trend in time for anisotropy and heterogeneity of complexity (Table S5, Fig. S5).

5. Discussion

5.1. Three dietary proxies targeting feeding ecology at three temporal scales

Hypsodonty is understood to be an adaptation to counterbalance the loss of dental tissue due to the ingestion of abrasive endogenous or exogenous material while eating. It occurred in many clades among mammals during the Cenozoic (Mendoza and Palmqvist, 2008; Damuth and Janis, 2011; Witzel et al., 2018). This dietary proxy sheds light on feeding adaptation on a timescale of at least hundreds of generations (Davis and Pineda-Munoz, 2016). One of the most commonly cited examples among Perissodactyla is equids. The increase in molar hypsodonty in the evolutionary history of equids is seen as reflecting the opening of the landscape and the spread of grassland during the Neogene (Strömberg, 2006; Mihlbachler et al., 2011). Although equids are adapted to grazing, several extant species have a wider feeding spectrum (Moehlman et al., 1998; Pereladova et al., 1999; Smith and Pearson, 2005; Schulz and Kaiser, 2013). Many extinct species also tended to widen their food resources (MacFadden et al., 1999; Kaiser, 2003; Scott et al., 2006; Tütken et al., 2013). At no time in the Eocene and Oligocene do any of the species of the palaeotheriid *Plagiolophus* show the high hypsodonty index seen among extant grazing equids, which clearly rules out the predominance of abrasive foodstuffs that would have promoted the natural selection of such a dental phenotype. However, there is one exception among the palaeotheriids, and this is the new endemic late Eocene species *Leptolophus* described in western Iberia, which shows a hypsodonty index similar to that of some Neogene equids (Perales-Gogenola et al., 2021). This early hypsodonty in an Eocene palaeotheriid could indicate a different dietary strategy from the one adopted by *Plagiolophus*.

The predominance of browsing is confirmed by the lifetime signal (Ackermans et al., 2018, 2020) provided by dental mesowear. The fact that none of the species of *Plagiolophus* shows a high mesowear score is new evidence that their diet excluded silica-bearing and dust-laden food. However, being browsers does not mean that these species occupied exclusively dense woody forest, as present-day browsers may be present in both dense forest and more open bushland. The absence of blunt cusps

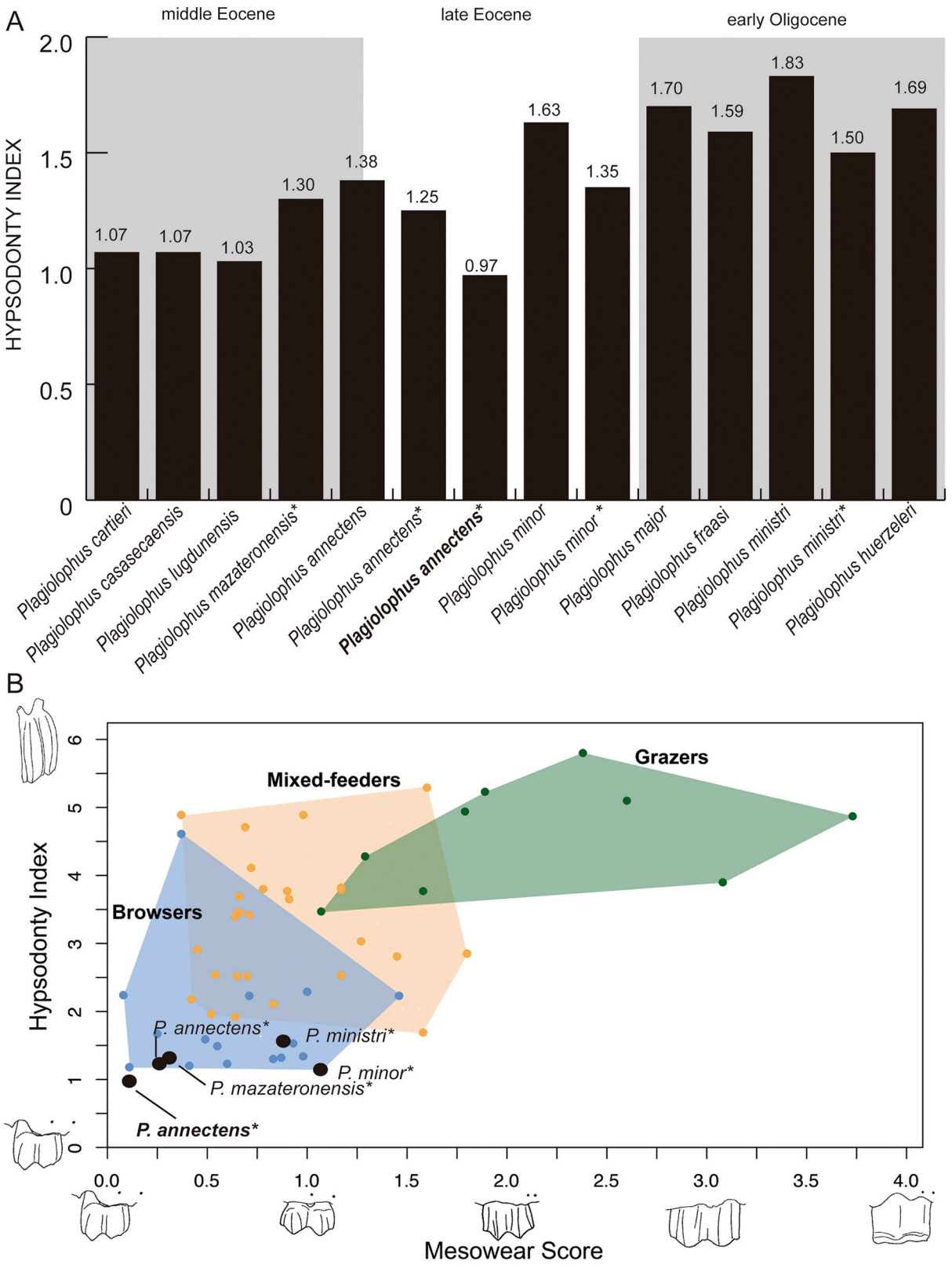

Fig. 2. A, Hypsodonty index measured following Janis (1990). B, molar mesowear score of different *Plagiolophus* species in comparison to a modern ungulate dataset (Kaiser et al., 2013). * = samples studied in this work (*P. mazateronensis* from Mazaterón; *P. annectens* from Roc de Santa I; bold *P. annectens* from Euzet-les-Bains; *P. minor* from St. Capraise d'Eymet; and *P. ministri* from Villebramar); the rest correspond to mean values calculated by Kaiser et al. (2009).

in any of the studied species, also observed in Joomun et al. (2008, 2010), indicates that their diet did not contain a high proportion of abrasive material such as silica-bearing grasses, which is consistent with the absence of grasslands during the Eocene in Europe (Winkler et al., 2020), or a high proportion of the dust-laden food abundant in open landscapes. This is consistent with the results obtained using the hypsodonty index.

The third dietary proxy, the dental microwear texture, reflects the physical properties and the inner composition of the food. Several experiments (Teaford and Oyen, 1989a; Teaford et al., 2017; Winkler et al., 2020) and analyses of captured wild mammals (Walker et al., 1978; Teaford and Robinson, 1989b; Teaford and Glander, 1991; Merceron et al., 2010; Berlioz et al., 2017; Percer et al., 2018) have proven that dental microwear textures vary on a daily to weekly basis, making it possible to record seasonal variations in the diet. All the samples of *Plagiolophus* have low complexity and relatively high anisotropy. The low complexity rules out the consumption of hard items such as nuts or roots, and the high anisotropy points to the consumption of tough foliage.

5.2. Dietary composition of Plagiolophus

Both molar mesowear and the hypsodonty index support browsing adaptations and habits in all the *Plagiolophus* samples. However, browsing habits encompass wide food resources ranging from herbaceous dicots, tree, bush and scrub leaves, shoots, stems and barks, to fruits, nuts and even buds. All these organs have different shapes, different inner compositions, and mechanical properties requiring different processing while eating (Ramdarshan et al., 2016). Leaves need a shearing motion between occluding facets, most specifically when they are mature, poor in water content and tough (Teaford and Robinson, 1986; Ramdarshan et al., 2016). Seeds and nuts require crushing actions to extract the maximum amount of energy. Barks also require a long chewing cycle before being ingested. All these organs and the ways in which they are consumed generate a variety of microwear textures (Teaford and Oyen, 1989b; Ramdarshan et al., 2016).

Compared with the extant ruminant species for which ecological data are known (Merceron et al., 2021), *Plagiolophus* shows differences in terms of microwear with respect to most mixed-feeders and the browsing *A. alces*. This supports the idea that the *Plagiolophus* species avoided hard or challenging items such as fruits, barks, seeds, and nuts. *Plagiolophus* shares similar textures with the grazing *B. taurus*, the mixed-feeder *C. elaphus* and the browsing *C. capreolus* in avoiding hard food and instead focusing on leafy material. These three comparative samples of extant species share high anisotropy and low to moderate complexity on their shearing molar facets. Based on these comparisons, we conclude that *Plagiolophus* fed on leafy material, avoiding lignified tissues such as bark or hard items such as nuts and seeds. One potential extant equivalent could be the roe deer *C. capreolus*, a highly selective, inflexible feeder in all seasons, which avoids eating many abundant plant species and focuses mainly on one to three plant species in each season, specifically the most energetic ones (Tixier and Duncan, 1996; Tixier et al., 1997, 1998).

5.3. Interspecific dietary variations among Plagiolophus

When anisotropy is plotted against complexity (Fig. 3A), although all the samples appear in the same dispersion space, the variation in *P. mazateronensis* from Mazaterón is the greatest (Fig. 3A). This could indicate that some individuals in this population fed on softer materials than others. By contrast, *P. annectens* from Euzet-les-Bains shows the smallest variation in complexity (Asfc) and the largest variation in anisotropy (epLsar), indicating a more selective/specialized diet than the other samples, including the *P. annectens* population from Roc de Santa I.

P. mazateronensis shows the largest dispersion of complexity (Disp-Asfc, Fig. 3B), whereas its heterogeneity of complexity ($HAsfc_{81\text{-cells}}$) is wide but similar to other samples. The largest range of heterogeneity of complexity is found in *P. annectens* from Euzet-les-Bains, which could indicate access to a wide spectrum of food at the individual scale. This condition is most likely true for most individuals in the population, as the dispersion of complexity is low compared with *P. mazateronensis*. The ANOVAs show significant differences among the *Plagiolophus* samples in complexity, heterogeneity and anisotropy (Table S6). Fisher's LSD test is less conservative than Tukey's HSD test. Although no differences are seen in Tukey's HSD between fossil samples, we can thus see a few in Fisher's LSD. Fisher's LSD test shows marginal differences for complexity (Asfc) between the two samples of *P. annectens* and between *P. mazateronensis* and *P. annectens* from Roc de Santa I. Significant differences in Fisher's LSD test are also found between *P. ministri* and *P. mazateronensis* and *P. annectens* from Euzet-les-Bains (Table S7). There are also differences in the dispersion of heterogeneity of complexity

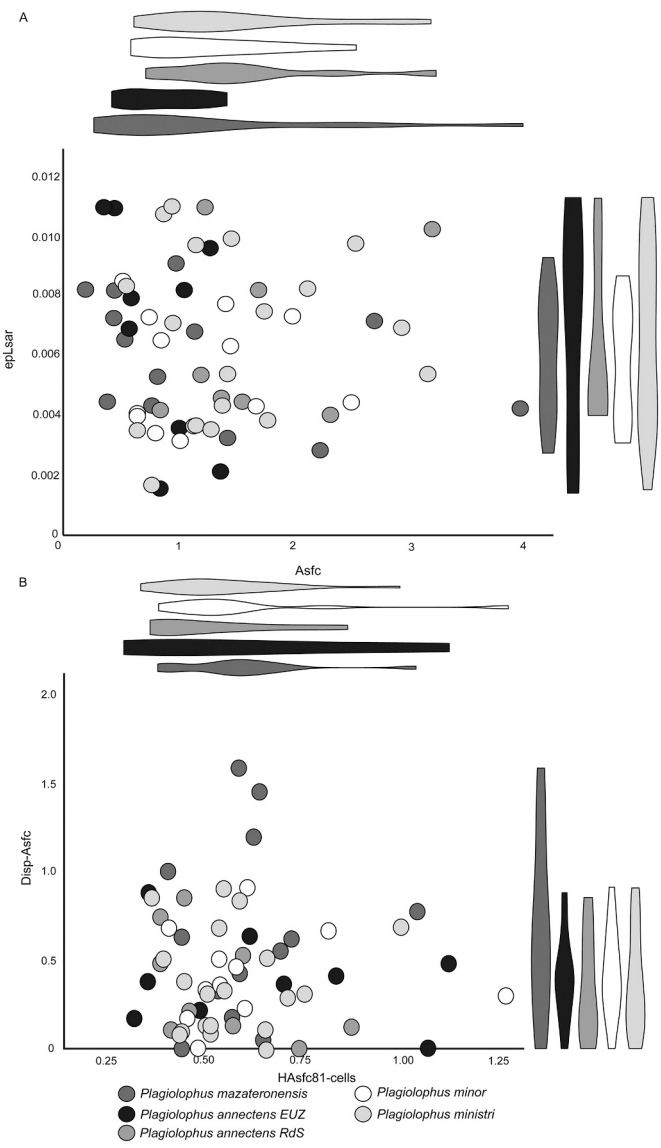

Fig. 3. Bivariate plots and violin diagrams for the five samples of *Plagiolophus*. A, dispersion plot of anisotropy (epLsar) versus complexity (Asfc) between the five *Plagiolophus* samples. Right, violin plot for anisotropy. Above, violin plot for complexity. B, dispersion plot of dispersion of complexity (Disp-Asfc) versus heterogeneity of complexity ($HAsfc_{81\text{-cells}}$) between the five *Plagiolophus* samples. Right, violin plot for dispersion of complexity Disp-Asfc. Above, violin plot for heterogeneity of complexity ($HAsfc_{81\text{-cells}}$).

between *P. annectens* from Euzet-les-Bains and *P. mazateronensis*, *P. minor* and *P. ministri* (Table S8).

We compared the main DMTA parameters to a dataset for modern ungulates from Europe that comprises browsers, mixed-feeders and a grazer (Moehlman et al., 1998). When our data are plotted together (Fig. S6), few inferences can be drawn. All the *Plagiolophus* samples seem to plot together, within the ranges of mixed-feeders. There is, however, a trend towards a higher mesowear score and hypsodonty index for *P. ministri* from Villebramar (Oligocene, MP 22), whereas the mesowear score is lower for the samples that lived before the *Grande Coupure* (Eocene-Oligocene transition). The exception is *P. minor* from La Débruge (MP 18), which is closer to *P. ministri* from Villebramar than to the other pre-*Grande-Coupure* samples. Joomun et al. (2010) made similar observations for *P. minor* samples, which tends towards a more abrasive diet after the *Grande Coupure* (MP 20/21). Statistical analyses performed on the modern ungulate dataset and *Plagiolophus* show significant differences for all the parameters except for the dispersion of complexity (Disp-Asfc) and dispersion of anisotropy (Disp-epLsar) (Table S6). Post-hoc results are summarised in Tables S7–8.

High anisotropy has been associated with grass-eating habits (Scott, 2012; Merceron et al., 2016), although other studies show that it is not specifically related to grass-eating habits but to tough leaf-eating (Merceron et al., 2010, 2021; Hedberg and DeSantis, 2017; Hullot et al., 2019). This means that anisotropy might be better regarded not as positively correlated with the proportion of herbaceous monocots but as negatively correlated with the frequency of lignified tissues or hard and brittle items. Here, the combination of medium to high anisotropy (epLsar) and low to intermediate complexity (Asfc) (Fig. 3A) for all the *Plagiolophus* samples seems to point to a predominance of leafy material in the diet, without the presence of lignified materials, fruits or seeds. The leafy material could be herbaceous monocot or dicot foliage, requiring slicing rather than crushing movements. No strong seasonal variations are observed in any population. The small range of heterogeneity of complexity ($HAsfc_{81\text{-cells}}$) points to a selective diet focused on few food items sharing the same characteristics.

The wide chrono-spatial distribution of *Plagiolophus* could have made this genus potentially useful in assessing environmental variations through time and space (Fig. S1). The mainly homogenous values seen in all the *Plagiolophus* samples suggest highly selective and invariable feeding behaviour, on plants with the same features, in all the samples. The small differences seen in the raw values do not result in statistically significant differences (Table S6). This seems to contradict the hypothesis that there might have been differences between *Plagiolophus* populations from different regions and chronologies that are reflected in their palaeodiet. However, a highly selective and invariable palaeotheriid feeder such as *Plagiolophus* is probably not the best palaeoecological indicator to test the hypothesis that is addressed here: that dietary changes were mainly driven by the slow degradation of environmental conditions during the Eocene in western Europe, with the spread of more open landscapes, increasing aridity, and a more marked seasonality (Blondel, 2001; Remy, 2004). In fact, *Plagiolophus* is the only palaeotheriid genus that passed the Eocene-Oligocene boundary.

6. Conclusions

Despite the wide chrono-spatial distribution of the palaeotheriid perissodactyl *Plagiolophus*, the information obtained from three different dietary proxies (hypsodonty, mesowear and microwear) has not revealed any significant changes in diet through time and space. In all the studied samples from the middle Eocene to the early Oligocene, the low hypsodonty index suggests the absence of abrasive foodstuffs; the low mesowear score, ruling out silica-bearing and dust-laden food, suggests the dominance of browsing activity; and the microwear information suggests the browsing of tough foliage as opposed to hard items.

There are no significant differences in diet among the studied samples. *Plagiolophus* would have eaten tough leaves from monocots or dicots, requiring a slicing motion, and would have avoided lignified or hard materials that required crushing actions. No marked seasonal variations in its diet are apparent. *Plagiolophus* was a highly selective and invariable feeder that fed on few plants with the same features irrespective of chronology or location. Such a selective feeder like Plagiolophus might not be a good palaeoecological indicator, so it would be interesting to ascertain the hypothesis addressed here in other palaeotheriid perissodactyls as well.

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Data availability

Datasets related to this article can be found at https://figshare.com/s/84d28b97dbe7db68fa3e

[Temporary link until manuscript acceptance], hosted at Figshare (Perales-Gogenola et al., 2022)].

Declaration of Competing Interest

We declare no conflict of interest.

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Appendix A. Supplementary data

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