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ORIGINAL ARTICLE

# Information theoretical modeling of epigenetic dental character variation in hares (*Lepus europaeus*) from Türkiye: microphylogeographic or climatic effects?

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**Abstract**
The external phenotypic variation of brown hares (*Lepus europaeus*) from Türkiye could represent climate-related adaptation, despite low neutral population genetic differentiation. Here, we investigated whether minor occlusal character variation of brown hares, previously used in phylogenetic or phylogeographic contexts in hare species, exhibit phylogenetic or ecogenetic variation in Türkiye, i.e., whether it corresponds to neutral population differentiation or climate variation in Türkiye. We used multi-model inference, i.e., model ranking and model averaging for binary coded occlusal traits to distinguish possible phylogenetic (neutral population genetic) from ecogenetic (climatic) effects. Our logistic models revealed a few statistically important phylogenetic and ecogenetic signals, taking into account sex, age category, skull size, and geographic coordinates of sample location. All of the latter explanatory factors/variables also showed some effects on character variation, independent of population genetic and climate effects. This could be due to a developmental (ontogenetic) background of occlusal character variation. Our calculations of pairwise phenetic distances, i.e., C.A.B. Smith´s Mean Measures of Divergence (MMD) between populations were similarly low or non-significant as previously studied microsatellite-based genetic differentiation between populations. Notably, the MMD values were based on only three occlusal characters, the only ones that showed significant variation between at least two populations. Importantly, unlike the traditional MMD calculation, our character modeling was not limited by the lack of significant spatial variation in occlusal characters; moreover, it considered all explanatory factors that were of interest simultaneously, when testing phylogenetic or ecogenetic character causation.

**Keywords** Dental characters · *Lepus europaeus* · Ecogeographic variation · Information theory-based modeling · Phylogeographic variation · Türkiye

## Introduction

Inter- and intraspecific dental polymorphism in terrestrial mammals has been extensively studied in various contexts, such as paleontological and evolutionary analyses, systematics, ontogenetic development, ecological or functional adaptation, or phylogeography (e.g., Kurtén 1953, 1967; Sikorski 1982; Angermann 1984; Sikorski and Bernshtein 1984; Baryshnikov and Potapova 1990; Szuma 2007; Gomes Rodrigues et al. 2017; Korablev et al. 2017; Zuercher et al. 2021). In hares, jackrabbits, rabbits, and cottontails (Leporidae, Lagomorpha), specifically non-metrical occlusal characters, representing mainly presence or absence, shape, and configuration of diverse enamel folds, notches, and islands on the occlusal surface, have been addressed mainly in paleontological, phylogenetic, systematic and microphylogeographic studies (e.g., Forsyth Major 1898; Petter 1961; Hibbard 1963; Sych 1965; Angermann 1966; Sych and Sych 1977; Palacios and López 1980; Angermann and Feiler 1988; Thenius 1989; Fladerer and Reiner 1996; Ruedas 1998; Suchentrunk et al. 1994, 2000; Suchentrunk and Flux 1996; Suchentrunk 2004; Lopez-Martinez 2008; Romero-Palacios and Cervantes 2012), as well as to estimate levels

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of developmental homeostasis (Suchentrunk 1993, 2000; Alves et al. 2001).

Recently, the assumption of a polygenetic background of minor skeletal and dental traits (e.g., Berry 1963, 1990) was supported for some epigenetic occlusal characters by estimates of their narrow sense heritability in brown hares, *Lepus europaeus*, from a breeding station in Vienna, Austria (Schmidtberger 2015). In human's minor dental characters (e.g., Alt 1997) can be considered good proxies for the differentiation of the entire gene pool, as shown by a genomic study (Irish et al. 2020) based on SNPs (single nuclear polymorphisms).

Brown hares (*Lepus europaeus*) from Türkiye exhibit a variety of external phenotypes, possibly as an adaptation to the varying climate (Demirbaş et al. 2013), but exhibit comparatively low levels of population genetic differentiation both within the Anatolian Peninsula and between it and Turkish Thrace in the southeastern Balkans (Demirbaş et al. 2019). In this study, we used information theory-based modeling (e.g., Burnham and Anderson 2002) to test for microphylogeographic variation of epigenetic occlusal characters in hares from Türkiye. Specifically, we expected character variation parallel to microphylogenetic, i.e. neutral population genetic differentiation, as previously determined by a microsatellite study of the same individuals (Demirbaş et al. 2019), and possibly also to climatic variation in our study area. Given the overall low, but significant population genetic structuring of nuclear gene pools of brown hares both within the Anatolian Peninsula and between it and the population of Turkish Thrace as reported by Demirbaş et al. (2019), we expected overall low differentiation of epigenetic occlusal characters both within Anatolia and across the Dardanelles (Strait of Çanakkale), the Sea of Marmara, and the Bosphorus that form a migration barrier to hares since the disintegration of the land bridge in the Holocene. In contrast, if the climate has a strong effect on the formation of the occlusal characters, i.e., under ecogenetic character variation (e.g., Thorpe et al. 1991), the pattern of spatial differentiation in the studied occlusal characters should correspond to the differences in the local climatic conditions. Pronounced climate-related character variation and other factors, such as sex, age, and developmental causes (e.g., skull size) might blur or even disguise microphylogeographic signals when calculating C. A. B. Smith´s mean measure of divergence (MMD) according to Sjøvold (1977), as that statistical approach cannot account simultaneously for all possible factors of interest. Therefore, we have used logistic models to account simultaneously for diverse explanatory factors that possibly affected occlusal character variation in the hares from Türkiye. Our approach enabled us to statistically discriminate between phylogenetic and ecogenetic causation of character variation (e.g., Thorpe et al. 1991), and to identify possible additional affects by other biological and geographical background causes, independent from phylogenetic and/or climatic causation.

## Materials and methods

### Data collection

#### Hare specimens and dental characters

We screened a total of 7.470 teeth from both body sides in cleaned skulls of 304 georeferenced brown hares (*Lepus europaeus* Pallas, 1778) from 113 collection sites throughout Türkiye (Fig. 1) for minor non-metric occlusal variants (epigenetic characters) using a dissecting microscope (Olympus SZ61, 10X). Those variants concerned presence or absence of enamel folds, grooves, notches, islands, and the shape of the enamel fold lines in premolars and molars, as well as the occurrence of cement filling of the labial fold of the principal upper incisors, largely following Suchentrunk et al. (1994, 2000), Suchentrunk (2000), and Sert (2006). The definitions of the 25 selected occlusal characters, the binary codes of character states and overall frequencies are detailed in Table 1 and Fig. 2). We also calculated individual plication indices (IPI) based on all cheek teeth characters, except for characters 4 and 10 (state of plication not applicable) as percentage of plicated character states (1) of all scored characters per individual.

Most skulls were from individuals hunted regularly in 2010 – 2020, a few were collected earlier. Each skull was assigned to one of the six genetic populations in Türkiye that have been determined earlier by a microsatellite study (Demirbaş et al. 2019; see also Fig. 1). The skulls are deposited at the Department of Biology, Faculty of Engineering and Natural Sciences at the University of Kırıkkale, Türkiye. Hares were sexed in many cases by inspection of (internal) reproductive organs, but numerous remained unsexed. They were classified as adults, i.e., fully grown and sexually mature, or not fully grown subadults, based on Stroh´s sign (presence of a distal lateral epiphyseal protrusion of the *Os ulnare*; Stroh, 1931), dry eye lens weights (Suchentrunk et al. 1994), the sutural ossification scheme of Cabón-Raczyńska (1964; but see Suchentrunk et al. 1994), and size and shape of the supraorbital processes that are usually smaller, more delicate, and with a more even edge in subadults. However, quite some skulls remained unclassified, due to missing eye lens weights and intermediate skull features. Skull size of fully grown brown hares may vary notably even within one homogenous population; the lower bound of condylobasal lengths (cbl) of fully grown adults may be reached already in subadults as early as five to six months of age in brown hares from a breeding station in Vienna, Austria (Suchentrunk and Davidovic 2004). Given the variable skull size of hares from Türkiye (Demirbaş

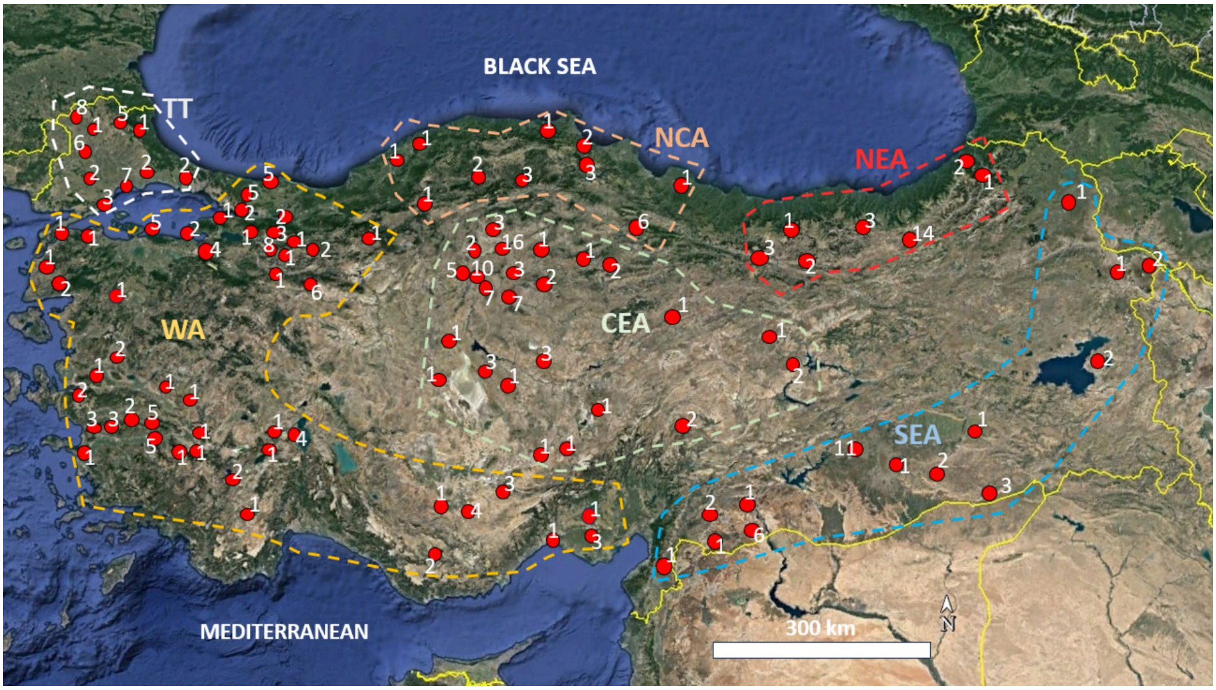


**Fig. 1** Sample distribution across Türkiye. Red dots are sample locations and associated white number are the sample sizes; the six populations are encircled by dashed lines and indicated by the following acronyms: TT– Turkish Thrace (*n* = 37), WA – West Anatolia (*n* = 108), CEA – Central/East Anatolia (*n* = 77), NCA – North/Central Anatolia (*n* = 21), NEA – North Eastern Anatolia (*n* = 26), SEA – South Eastern Anatolia (*n* = 35)

et al. 2013), we measured individual cbl to account for possible ontogenetic effects on the occlusal character formation (e.g., Sjøvold 1977).

### Bioclimtatic variables

We downloaded fifteen sample locality-specific climatic variables representing long-term means of ambient temperature (bio1, bio5-11) and precipitation (bio12-14, bio16-19) from the freely accessible WorldClim database (version 2, worldclim.org). Variables bio2-4 and bio15 were presently not considered, as they represented merely indices derived from the original variables. The standardised Box-Cox-transformed values were subjected to correlation matrix-based principal components analyses without additional rotation (PCA), separately for the temperature and the precipitation data, to obtain separate principal components ($PC_{temp}$, $PC_{precip}$), which allowed a straightforward interpretation of possible separate temperature and precipitation effects on the dental characters (see below for more details).

### Information theoretical models of occlusal character variation: model ranking and model averaging

We used a multi-model approach (e.g., Barton 2013; Burnham & Anderson 2002) to reveal possible statistically important population genetic and climatic effects on occlusal character expression by simultaneously controlling for potential additional biological effects such as sex, ontogenetic development (age class), body (skull) size, and spatial effects (geographical coordinates) independent from our population genetic assignments of individuals. We created a third category ("unknown") for missing data on sex or age class to keep all 304 individual data sets available for modeling. All our independent (explanatory) variables/factors in the models were checked for multicollinearity, which was absent (all VIF > 0.1, Tolerance < 10.0); hence, all explanatory variables could be used in the models. We used R (R Core Team 2021) to determine the respective best models by model ranking based on AICc values (i.e., Akaike information criterion for small sample sizes) and for model averaging to calculate values of "Relative Variable Importance" (RVI) for all explanatory variables in the models. The RVI values are equivalent to the probabilities of the respective explanatory variables to be present in the best model. We followed Burnham & Anderson (2002) and accepted an RVI value > 0.7 as indicative of a statistically meaningful effect of an independent (explanatory) variable (factor) on the dependent variable (i.e., occlusal character state).

Specifically, we modeled only the following occlusal characters that had reasonable frequencies of alternative character states (0/1): ch-3, ch-4, ch-5, ch-6, ch-9, ch-18,

**Table 1** The examined occlusal characters, the respective binary character states (see also Fig. 2) and the associated frequency for character state (1), as used for linear models and MMD calculations (for frequency calculations see Material and methods)

| Occlusal Characters | Tooth | Character Description and Binary Codes |
|---|---|---|
| ch-1 | $P_3$ | Mesial re-entrant fold (filled with cement): absent (0)/present (1), 95.1% |
| ch-2 | $P_3$ | Additional mesial re-entrant fold (with cement): absent (0)/present (1), 2.0% |
| ch-3 | $P_3$ | Anterior lingual re-entrant fold (with cement): absent (0)/present (1), 13.5% |
| ch-4 | $P_3$ | Posterior external re-entrant fold breaking through the lingual enamel wall and separating trigonid and talonid completely: no (0)/yes (1), 30.9% |
| ch-5 | $P_3$ | Margins of posterior external re-entrant fold forming one extra fold in its most lingual section; additional fold extending mesially: no (0)/ yes (1), 19.7% |
| ch-6 | $P_3$ | Mesial margin of posterior external re-entrant fold plicate (plication either strong or slight): no (0/) yes (1), 14.8% |
| ch-7 | $P_3$ | Distal margin of posterior external re-entrant fold plicate: no (0)/yes (1),7.6% |
| ch-8 | $P_3$ | Distal margin of posterior external re-entrant fold forming one extra fold in its lateral part: no (0)/ yes (1), 7.9% |
| ch-9 | $P_3$ | Trigonid with at least one enamel lake: no (0)/yes (1), 11.5% |
| ch-10 | $P_3$ | Cement layer of mesial re-entrant fold stretching lingually and covering also anterior lingual re-entrant fold (if present): no (0)/yes (1), 0.3% |
| ch-11 | $P_3$ | Margin of anterior external re-entrant angle shows strong plication (three or more fairly distinctly developed plicae): no (0)/ yes (1), 8.2% |
| ch-12 | $P_4$ | Distal margin of lateral re-entrant fold with one extra fold in its lateral section (occassionaly a double fold): no (0) yes (1), 6.9% |
| ch-13 | $P_4$ | Mesio-lateral enamel wall of trigonid with one-fold (filled with cement): no (0)/yes (1), 0.0% |
| ch-14 | $M_1$ | as ch-13, no (0)/yes (1), 0.7% |
| ch-15 | $M_2$ | Distal margin of lateral re-entrant fold (slightly or distinctly) plicated: no (0)/yes (1), 1.0% |
| ch-16 | $M_3$ | Trigonid and talonid connected by a dentine bridge coated with an enamel layer: no (0)/yes (1), 1.6% |
| ch-17 | $P^3$ | Distal margin of lingual re-entrant fold (hypostria) with a distinct fold in lingual section (axis of fold in linguo-buccal direction or slightly inclined): no (0)/yes (1), 11.5% |
| ch-18 | $P^3$ | Distal margin of hypostria plicated or undulating: no (0)/yes (1), 46.7% |
| ch-19 | $P^4$ | as ch-17: no (0)/yes (1), 2.0% |
| ch-20 | $M^1$ | as ch-17: no (0)/yes (1), 0.3% |
| ch-21 | $M^2$ | as ch-17: no (0)/yes (1), 0% |
| ch-22 | $P^2$ | Margin of central mesial fold plicated (or undulating): no (0)/yes (1), 3.0% |
| ch-23 | $P^2$ | Mesial fold lingually of central mesial fold: absent (0)/present (1), 95.7% |
| ch-24 | $P^2$ | Mesial fold buccally of central mesial fold: present (1)/absent (0), 68.1% |
| ch-25 | $I^1$ | Labial fold (notch) filled with cement: absent (0)/present (1), 5.3% |

ch-24. In addition, we also run models for the IPI values to test for potential population genetic and climatic effects of plication intensity of individual occlusal surfaces.

The syntax of our initial logistic General Additive Models (GAM) for those occlusal characters was:

$$\begin{aligned} & \mathrm{m = gam(char} \sim \mathrm{sex + age + population + s(cbl) + s(latitute,\ longitude)} \\ & \quad \mathrm{+ s(PC_{temp}1) + s(PC_{temp}2) + s(PC_{precip}1) + s(PC_{precip}2),\ data = dat,} \\ & \quad \mathrm{family = binomial)} \end{aligned}$$

were “char” was the binary coded occlusal character, “sex” and “age” were coded as three categories (see above), respectively, “population” was coded as assignment to one of the six genetic populations (see above), “cbl” was used as measured on the individual skulls, “latitude” and “longitude” were used as for the locality-specific geographic coordinates, and the four climate factors ($PC_{temp}1$, $PC_{temp}2$, $PC_{precip}1$, $PC_{precip}2$) represented the individual scores of the respective principal components as obtained from our PCAs of the original locality-specific climate data. For the continuous variables in our models, we used splines (s), i.e., non-linear function estimates, to allow for potential non-linear variation of the variables. However, we re-run the models without splines for all variables that were found to have linear variation.

For the individual plication indices (IPI), we used Box-Cox-transformed values and the below starting syntax of general additive models based on Gaussian distribution:

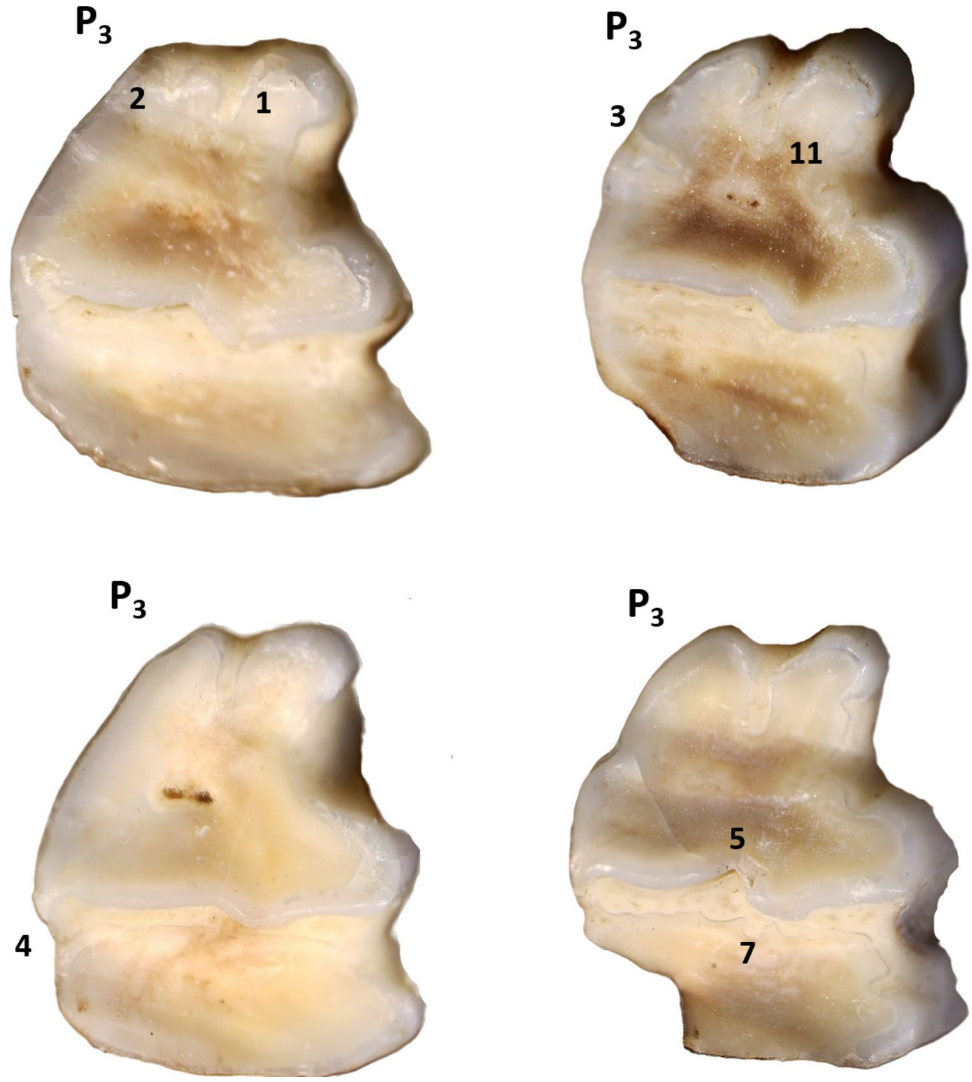


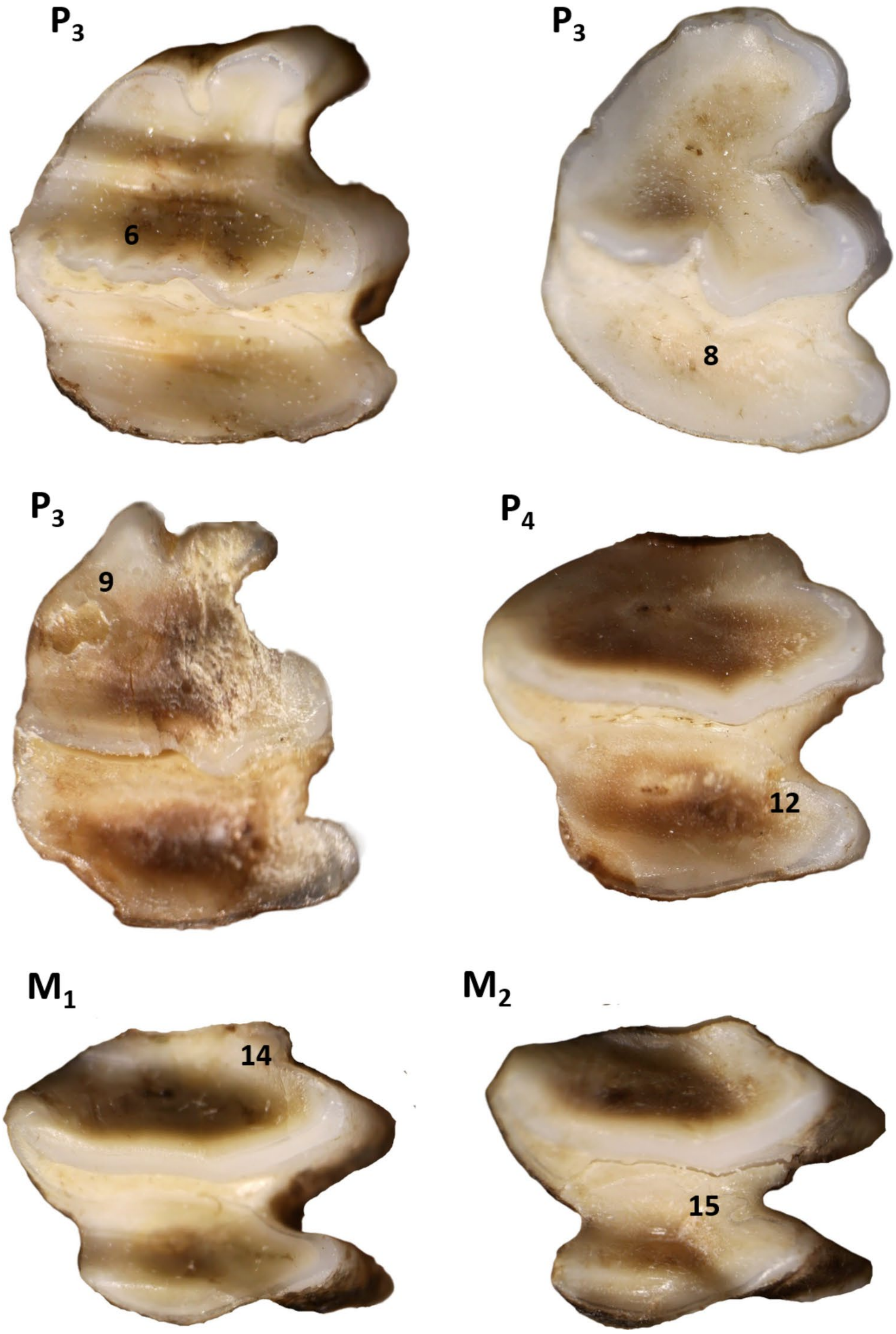
**Fig. 2** Occlusal characters used in Turkish hares

$$m = \mathrm{gam}(\mathrm{trIPI} \sim \mathrm{sex} + \mathrm{age} + \mathrm{population} + s(\mathrm{cbl}) + s(\mathrm{latitute},\ \mathrm{longitute}) + s(PC_{temp}1) + s(PC_{temp}2) + s(PC_{precip}1) + s(PC_{precip}2))$$

## Phenetic differentiation – Smith´s Mean Measure of Divergence (MMD)

We calculated frequencies of character state (1) of each occlusal character for teeth from right body sides only, as our matched-pairs signed rank-tests revealed that all presently asymmetric character states in individuals represented fluctuating asymmetry (FA, i.e., undirected deviations from perfect bilateral symmetry) that is indicative of developmental homeostasis (e.g., Van Valen 1962; Zakharov 1981; Palmer and Strobeck 1986; see also Suchentrunk 1993; Shadrina and Pertodi 2024). Under FA, characters scored on one body side represent already the statistically meaningful information for epigenetic differentiation. However, we used left body side character state information, whenever right body side information was not available. Moreover, in rare cases of missing characters on both body sides, we estimated character states from the respective character-specific information by all other samples. Specifically, we used the R platform (R Core Team 2021) and the Package "AntropMMD" 3.1.0 of 12 Oct. 2022 (Santos 2018), based our calculations on Anscombe´s transformations of frequency states, and considered pairwise MMD values significantly higher than zero when above the double standard deviation (Sjøvold 1977; Harris and Sjøvold 2004). To visualize the spatial divergence pattern as obtained by the MMD calculations, we used the multidimensional scaling option of the package.

**Fig. 2** (continued)



## Results

### Occlusal characters

We based all our calculations (except for MMD calculations, see below) on 25 dichotomised occlusal characters (Table 1) all of which showed FA when tested by Wilcoxon matched pairs signed-rank tests (see specifically Suchentrunk 1993 for non-metric occlusal character variation in hares). There was no significant association of character states between characters (Fisher´s exact tests and strict Bonferroni corrections for multiple tests (Rice 1989). Hence, all characters could be treated as independent characters in our statistical tests.

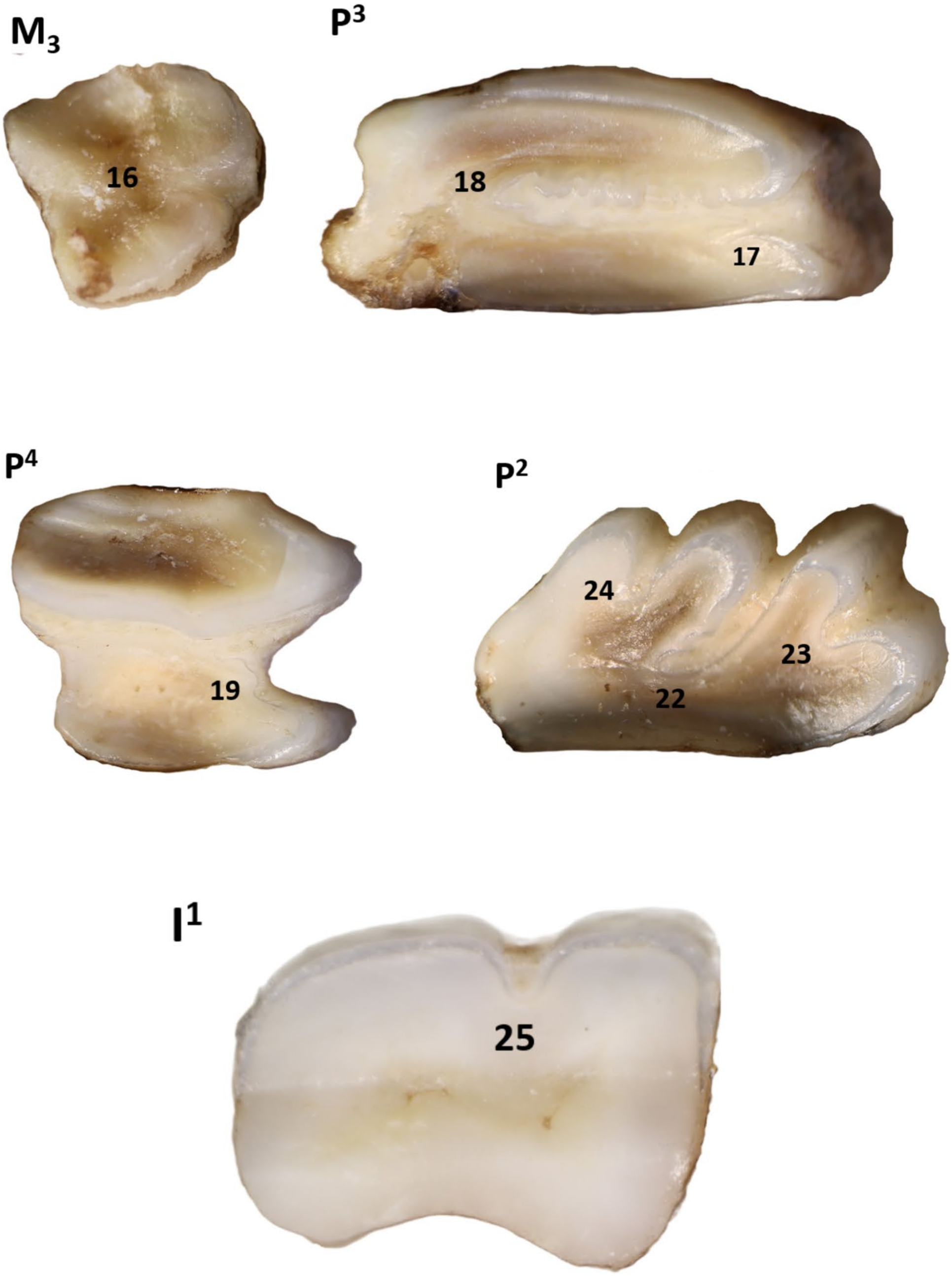


**Fig. 2** (continued)

## Bioclimatic variables

The PCA of the individual transformed locality-specific values of ambient temperature means yielded two PCs, the first one, $PC_{temp}1$, representing 70.9% of the initial character variability and the second one, $PC_{temp}2$, reflecting 14, 53% of the initial character variability. According to the loadings of the initial temperature values (Table 2), $PC_{temp}1$ was interpreted as reflecting general ambient temperature except for the wettest quarter of the year, while $PC_{temp}2$ was interpreted as reflecting ambient temperature of the wettest quarter of the year. Our PCA of the individual transformed precipitation values also resulted in two PCs, with the first one, $PC_{precip}1$, representing 56.26% of the initial character variability and the second one, $PC_{precip}2$, representing 40.9% of the initial character variability. According to the loadings of the initial precipitation values (Table 3), $PC_{precip}1$ was interpreted as a general precipitation factor with less emphasis on the driest and warmest quarter of the year, while $PC_{precip}2$ was interpreted as reflecting particularly precipitation during the driest and warmest quarter of the year.

**Table 2** Loadings of initial temperature values into $PC_{temp}1$ and $PC_{temp}2$; bio1-11tr are standardised Box-Cox-transformed individual values of bio1 = mean annual temperature, bio5 = maximum temperature of warmest month, bio6 = temperature of coldest month, bio8 = mean temp. of wettest quarter, bio9 = mean temp. of driest quarter, bio10 = mean temp. of warmest quarter, bio11 = mean temp. of coldest quarter

| Temperature variables | $PC_{temp}1$ | $PC_{temp}2$ |
|---|---|---|
| bio1_tr | .993 | -.014 |
| bio5_tr | .823 | .271 |
| bio6_tr | .849 | -.229 |
| bio8_tr | -.094 | .906 |
| bio9_tr | .921 | .127 |
| bio10_tr | .965 | .128 |
| bio11_tr | .888 | -.192 |

**Table 3** Loadings of initial precipitation values in $PC_{precip}1$ and $PC_{precip}2$; bio12-19tr are standardised Box-Cox-transformed individual values of bio12 = mean annual precipitation, bio13 = precipitation of wettest month, bio14 = precip. of driest month, bio16 = precip. of wettest quarter, bio17 = precip. of driest quarter, bio18 = precip. of warmest quarter, bio19 = precip. of coldest quarter

| Precipitation variables | $PC_{precip}1$ | $PC_{precip}2$ |
|---|---|---|
| bio12_tr | .984 | -.107 |
| bio13_tr | .882 | -.433 |
| bio14_tr | .559 | .824 |
| bio16_tr | .879 | -.450 |
| bio17_tr | .575 | .814 |
| bio18_tr | .441 | .889 |
| bio19_tr | .764 | -.573 |

### Information theoretical model results

Our first step of modeling of the dichotomised occlusal character variation checked for the presence of splines. Based on these results, we constructed our final starting models with or without splines for the independent variables, as listed in Table 4. All possible models that could be derived from these initial models were then run for the respective dependent variable. The RVI values of the exploratory (independent) variables/factors resulting from model averaging are listed in Table 4, along with the respective initial model and the deviance explained (DE).

### MMD values – phenetic differentiation

When calculating Sjøvold´s (1977) pairwise "mean measure of divergence" (MMD) between the six genetic populations in Türkiye (Demirbaş et al. 2019), we only used the three characters (ch-8, ch-22, ch-23), which showed significant variation in at least one pairwise comparison (Sjøvold 1977). Their character state frequencies were independent from sex or age class and cbl, and there was no significant association between them according to our Fisher´s exact tests. Only five out of all fifteen pairwise MMD values between the six genetic populations were significantly higher than zero (Table 5). The scatter plot resulting from Multidimensional Scaling of the MMD values is shown in Fig. 3. It indicated rather similar epigenetic differentiation levels in all pairwise comparisons. But the hares from Turkish Thrace (TT) showed on avarage a somewhat elevated epigenetic separation from all Anatolian hares, except for hares from Northeastern (NEA) and Southeastern Anatolia (SEA). Noteably, the MMD values for TT and those latter two populations were statistically not significant (Table 5).

## Discussion

The foremost aim of our study was to test the dichotomised epigenetic occlusal traits found presently in the brown hares from different parts of Türkiye for microphylogeographic or climatic variation, i.e., for microphylogenetic or ecogenetic causation. Basically, all the presently found occlusal characters have been found and analysed already earlier in other brown hare populations in population genetic, phylogenetic, and ecological studies (Suchentrunk 1993, 2000; Suchentrunk et al. 1994, 2000; Sert 2006). For the first lower premolar ($P_3$) all variants were in accordance with the typical "*Lepus* pattern" (Angermann 1966; see also Petter 1961) that occurs with diverse variation in other *Lepus* species as well (e.g., Palacios and López 1980; Suchentrunk and Flux 1996; Suchentrunk et al. 2000; Alves et al. 2001; Angermann and Feiler 1988; Suchentrunk 2004; Lopez-Martinez et al. 2008; Romero-Palacios and Cervantes 2012). Consistent with these latter studies, all presently described occlusal characters showed fluctuating asymmetry (FA), i.e., a stochastic component of phenotypic variation that indicates largely developmental instability (e.g., Graham et al. 2010), which is affected by both environmental and genetic (especially epistatic) stress (e.g., Palmer and Strobeck 1986; Leamy and Klingenberg 2005; Graham et al. 2010; Graham and Özemer 2016). Therefore, contrary to suggestions of scoring character states of nonmetrical traits in analyses of epigenetic divergence (e.g., Ossenberg 1981), we avoided confounding possible spatially different levels of developmental homeostasis and interindividual spatial variation in character states by using individual character state scores from the right side of the body only (see also e.g., Suchentrunk and Flux 1996; Suchentrunk et al. 2000). However, whenever teeth were missing on the right body side or when characters of right teeth could not be scored, we scored the characters of the left teeth. That procedure was consistent with the principle of using one side of the body for character assessment, because under FA, probabilities of character states are statistically equal for both sides of the body. Thus, our data set covered all relevant information on inter-individual variation for spatial analyses.

**Table 4** Modeling results of occlusal characters. Given are the respective final models, the deviance explained (DE), and the RVI values for the explanatory factors/variables in decreasing order. Statistically important RVI values are in bold

**ch-3** ~ sex + age + population + cbl + latitute*longitude + PC$_{temp}$1 + s(PC$_{temp}$2) + PC$_{precip}$1 + PC$_{precip}$2; **DE** = 11.4%

**RVI**: **sex = 0.93**, **cbl = 0.92**, s(PC$_{temp}$2) = 0.38, PC$_{temp}$1 = 0.33, latitude = 0.33, age = 0.32, PC$_{precip}$1 = 0.31, longitude = 0.30, PC$_{precip}$2 = 0.28, population = 0.05, latitude*longitude = 0.04

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**ch-4** ~ sex + age + population + s(cbl) + s(latitute*longitute) + PC$_{temp}$1 + PC$_{temp}$2 + s(PC$_{precip}$1) + s(PC$_{precip}$2); **DE** = 16.8%

**RVI: s(latitude*longitude) = 0.99**, **s(cbl) = 0.90**, **s(PC$_{precip}$1) = 0.79**, s(PC$_{precip}$2) = 0.63, PCt$_{emp}$1 = 0.32, PC$_{temp}$2 = 0.31, population = 0.29, age = 28, sex = 0.13

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**ch-5** ~ sex + age + population + s(cbl) + s(latitute*longitute) + PC$_{temp}$1 + PC$_{temp}$2 + s(PC$_{precip}$1) + s(PC$_{precip}$2), **DE** = 13.8%

**RVI**: **s(cbl) = 0.93**, **sex = 0.85**, s(PC$_{precip}$1) =0.68, s(PC$_{precip}$2) =0.63, PC$_{temp}$2= 0.41, s(latitute*longitute) = 0.40, P$_{Ctemp}$1 = 0.34, age = 0.12, population = 0.08

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**ch-6** ~ sex + age + population + age + s(cbl) + s(latitute*longitute) + PC$_{temp}$1 + s(PC$_{temp}$2) + s(PC$_{precip}$1) + s(PC$_{precip}$2), **DE** = 21.5%

**RVI**: **s(latitude*longitute) = 0.74**, s(cbl) = 0.66, s(PC$_{precip}$1) = 0.46, s(PC$_{precip}$2) =0.42, age = 0.32, PC$_{temp}$1 = 0.31, s(PC$_{temp}$2) = 0.31, sex = 0.31, population = 0.20

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**ch-9** ~ sex +age + population + cbl + s(latitute*longitute) + s(PC$_{temp}$1) + s(PC$_{temp}$2) + PC$_{precip}$1 + s(PC$_{precip}$2), **DE** = 71.2%

**RVI**: **s(latitude*longitute) = 0.99**, **cbl = 0.97**, **s(PC$_{precip}$2) = 0.96**, **s(PC$_{tempfac}$2) = 0.96**, **s(PC$_{tempfac}$1) = 0.96**, **population = 0.94**, **age = 0.80, sex = 0.78**, PC$_{precip}$1 = 0.15

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**ch-18** ~ sex + age + population + s(cbl) + s(latitute*longitute) + PC$_{temp}$1 + PC$_{temp}$2 + s(PC$_{precip}$1) + PC$_{precip}$2, **DE** = 15.8%

**RVI**: **s(cbl) = 0.99**, **s(latitute*longitute) = 0.84**, s(PC$_{precip}$1) = 0.58, PC$_{precip}$2 = 0.38, PC$_{temp}$2 = 0.36, PC$_{temp}$1 = 0.36, age = 0.29, sex = 0.14, population = 0.14

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**ch-24** ~ sex + age + population + s(cbl) + s(latitute*longitute) + PC$_{temp}$1 + s(PC$_{temp}$2) + s(PC$_{precip}$1) + s(PC$_{precip}$2), **DE** = 19%

**RVI**: s**(cbl) = 0.96**, **s(PC$_{precip}$2) = 0.80**, s(PC$_{temp}$2) = 0.48, age = 0.44, s(PC$_{precip}$1) = 0.42, s(latitute*longitute) = 0.39, PC$_{temp}$1 = 0.30, population = 0.24, sex = 0.10

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**trIPI** ~ sex + age + population + s(cbl) + s(latitute*longitute) + s(PC$_{temp}$1) + s(PC$_{temp}$2) + s(PC$_{precip}$1) + s(PC$_{precip}$2), **DE** = 12,2%

**RVI: s(latitute*longitute) = 0.80**, **s(cbl) = 0.70**, PC$_{precip}$2 = 0.50, sex = 0.47, s(PC$_{temp}$1) = 0.44, PC$_{precip}$1 = 0.39, age =0.37, s(PC$_{temp}$2) = 0.36, population = 0.13

**Table 5** Pairwise MMD values between the six genetic populations in Türkiye. Pairwise MMD values are above the diagonal and associated double standard deviations are below the diagonal. MMD values significantly above zero are indicated by an asterisk

| | CEA | NCA | NEA | SEA | TT | WA |
|---|---|---|---|---|---|---|
| CEA | - | 0.072854 | 0.080282 | 0 | 0.089079* | 0.137336* |
| NCA | 0.042989 | - | 0.035663 | 0.065826 | 0.11268* | 0 |
| NEA | 0.047639 | 0.071303 | - | 0.060266 | 0.044947 | 0.035697 |
| SEA | 0.032032 | 0.055696 | 0.060346 | - | 0.039172 | 0.130967* |
| TT | 0.032663 | 0.056326 | 0.060976 | 0.04537 | - | 0.158164* |
| WA | 0.017476 | 0.04114 | 0.04579 | 0.030183 | 0.030813 | - |

As in earlier studies (Suchentrunk et al. 1994, 2000), we did not find any significant association of character states in pairwise comparisons of characters. This suggested on the one hand absence of (functionally) favoured morphotypes; on the other hand, we could consider all characters as statistically independent, particularly for the calculation of epigenetic divergence, i.e., pairwise MMD values between the genetic populations determined earlier by a microsatellite study (Demirbaş et al. 2019).

Typically, various biological factors that could potentially influence and obscure spatial (or, for example, historic) patterns, such as sex, age, and body size, have been tested separately and independently from tests of differences between spatial samples (e.g., Sjøvold 1977). Such separate tests to select traits for MMD calculations were also conducted when investigating non-metric occlusal characters in hares from Israel, where no clear association with temperature and precipitation data was found for the dental traits along a steep ecological gradient (Suchentrunk et al. 2000). However, from a statistical perspective inclusion of all factors of interest or variables with potential effects on occlusal character states should be included in one statistical model. The traditional tests to select characters for calculations of epigenetic divergences often lead to a reduction of characters. This could affect the final MMD results. Our multi-modeling approach included all independent (explanatory) variables/factors of interest in the respective starting models. It allowed us to detect potentially separate signals of spatial and climatic effects of single explanatory variables/factors on character variation by accounting at the same time for the other variables/factors of interest. Moreover, by including geographical coordinates in addition to individual population genetic and climate-related data in the models we were able to separate possible microphylogenetic effects, as indicated by overall population genetic differentiation, from other possible (unknown) geographical effects. This was possible because of the absence of serious multicollinearity in the input data.

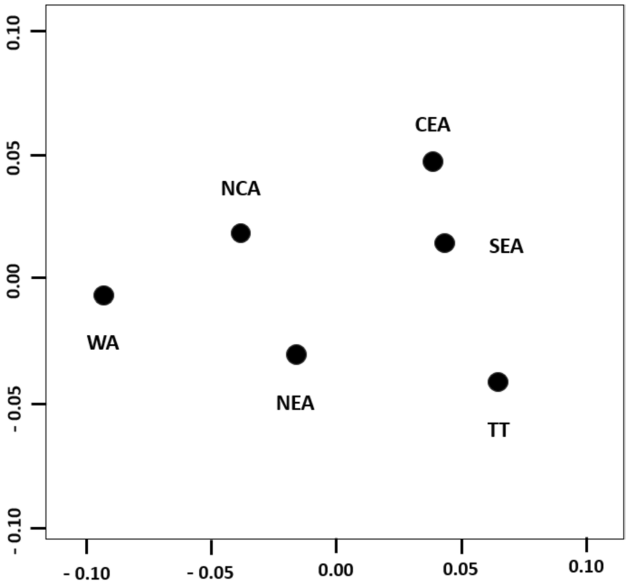

**Fig. 3** Scatterplot of population-specific dimension coordinates as obtained from 2-dimensional multidimensional scaling of MMD values. Population acronyms as in Fig. 1

Following the concept of phylogenetic and ecogenetic variation of phenotypic characters (Thorpe et al. 1991), i.e., largely parallel patterns of spatial character variation for different character systems under (micro-) phylogeographic causation compared to different patterns under ecogeographic (functional) causation, and according to the previous data of occlusal character variation in hares from different environments (Suchentrunk et al. 1994, 2000; Suchentrunk 2000), we expected ecogenetic signals in the occlusal traits, i.e., some variation of character states in parallel to the pronounced spatial pattern of climate variation across Türkiye (e.g., Gönençgil and Acar 2021). However, given the overall shallow but significant population genetic differentiation of hares across Türkiye on the one hand (Demirbaş et al. 2019) and the relatively pronounced climate differences on the other, we did not necessarily expect a good matching of the pattern of epigenetic differentiation with the pattern of population differentiation. This was specifically not expected for the hares from northwestern Anatolia and Turkish Thrace, given their relatively close geographical sampling locations and the similar climate in that area. Moreover, the region of Turkish Thrace in the southeastern Balkans was repeatedly connected with northwestern Anatolia during late Pleistocene and early Holocene periods (e.g., Gökaşan et al. 1997;

Yaltirak et al. 2000). The land bridges have provided chances for gene flow across the today´s water bodies of the Bosphorus, the Sea of Marmara, and the Strait of Çanakkale (Dardanelles), as indicated by various mtDNA-based phylogeographic studies that have demonstrated the distribution of Anatolian-typical haplotypes particularly in the southeastern (and southern) Balkans (Kasapidis et al. 2005; Sert et al. 2005; Sert 2006; Stamatis et al. 2009; Djan et al. 2017; Stefanović et al. 2019; 2020). Allozyme- and microsatellite-based studies have, however, indicated an only low level of population genetic differentiation between the hares from the Anatolian Peninsula and Turkish Thrace (Sert et al. 2005; Demirbaş et al. 2019). The latter studies have also shown low but significant spatial differentiation among Anatolian hares. A similarly low level of morphological differentiation of hares across whole Türkiye has also been demonstrated in a recent multivariate and geometric morphometric study of skulls (Demirbaş et al. 2023). Nevertheless, skull size and shape were significantly related to the population genetic assignment and only marginally affected by climatic variation. Consequently, we considered skull size and shape of hares from Türkiye as showing microphylogenetic variation.

Correspondingly, we also found geographical variation in the occlusal characters in the Turkish hares, altogether at a very low level, as evidenced by the MMD values between the genetic populations. Only three (12% of all examined) occlusal characters showed significant variation in pairwise comparisons of the six genetic populations and were therefore used for MMD calculations. Nevertheless, one third of all MMD values indicated significant epigenetic differentiation, including the hares from Turkish Thrace in three out of five pairwise comparisons. The mean (MMD = 0.12) of all three statistically significant MMD values involving hares from Turkish Thrace and a population from the Anatolian Peninsula, respectively, was numerically even smaller than that for the two pairwise comparisons between Anatolian populations (0.134); that finding corresponded to the population genetic interpretation of an only small overall nuclear gene pool divergence between brown hares from Turkish Thrace and the Anatolian Peninsula supposedly because of gene flow in evolutionarily relatively recent times (Demirbaş et al. 2019). Moreover, the fact that most of the MMD values for pairwise comparisons of populations from the Anatolian Peninsula were not significantly above zero was in line with the little genetic differentiation of Anatolian brown hares as concluded in the latter study. However, epigenetically closest to the hares from Turkish Thrace were the hares from northeastern and southeastern Anatolia; actually, they did not show significant MMD values in the comparisons with the hares from Turkish Thrace, possibly resulting from too small sample sizes.

Remarkably, only one occlusal character (ch-9) used for modeling did show variation among the six genetic populations as identified by Demirbaş et al. (2019), which corresponded to microphylogenetic causation of character variation. All other signals of spatial variation of character states (for ch-4, ch-6, ch-9, ch-18) showed nonlinear combined effects of geographical latitude and longitude of sampling locations, independent from climatic parameters, age class, sex, and body (skull) size, as well as from the population genetic assignment. Interestingly, variation of character ch-9 with a high explanatory value (according to the DE for the models) was both affected by the population genetic assignment and independently by geographical coordinates. All the signals of spatial variation of characters apart from that in parallel to population genetic differentiation may indicate variation due to selective forces that were not reflected by the currently considered climatic variables, such as specific variation in the vegetation or soil composition (soil chemistry), which may influence growing enamel layer formation. However, given the shallow gene pool differentiation in the presently studied hares the sample size both of our dental character system and of individuals studied could have been too small for obtaining more population genetic signals in our models. A finer-grained population genetic differentiation analyses (such as by SNPs, i.e., single nucleotide polymorphisms) might provide a better spatial genetic resolution and possibly a better phylogenetic matching of occlusal characters.

Nevertheless, obviously, sample sizes in terms of individuals and occlusal characters studied presently were not too small for proving ecogenetic (climatic) effects on three characters (ch-4, ch-9, ch-24) independent from neutral population genetic differentiation and other geographical variation. In fact, we found few but still somewhat more significant signals of climate effects on the occlusal character variation than of microphylogeographic variation parallel to population genetic differentiation as assessed by microsatellite variation (Demirbaş et al. 2019). While variation of character ch-4 was affected by overall precipitation, independent from geographical location or population genetic assignment, variation of ch-9 was affected by both ambient temperature and overall precipitation, and ch-24 again by precipitation. In the face of the limited climate variation that has been captured in the present study, a more pronounced climatic effect on occlusal character variation in hares may occur, independent from microphylogenetic causation, when studied in larger geographic contexts.

As both sex, age class, and body size (skull size) had also independently statistically important effects on character state expressions of several characters, a developmental (Angelone et al. 2014) and sex-related background might be expected along with environmental conditions to modify the epigenetic occlusal characters. Somewhat surprisingly, the overall individual index of folding and plication (IFI) of the occlusal surface in the dentition of the hares from

Türkiye did neither vary spatially nor was it obviously affected by population genetic or developmental factors currently introduced in our models. That supports our above hypothesis that all currently analysed occlusal characters do not functionally combine in one or more favored morphotypes during the ontogeny of the individuals apart from the general pattern as described earlier for several species of the genus *Lepus* (e.g., Angermann 1966). Noteably, the IFI (individual folding index) was not affected by any climatic parameters studied currently, although frequencies of single occlusal variants were affected by ambient temperature or precipitation. This corresponds to the initially found independence of single variants of individual teeth and may suggest the largely absence of morphogenetic fields, i.e., the absence of certain genes that regulate folding or plication of whole teeth. Nevertheless, general folding or plication and crenulation of enamel lines on the occlusal survace obviously differs clearly between Leporid taxa (e.g., Hibbard 1963) and *Lepus* species (e.g., Suchentrunk 2004; Romero-Palacios and Cervantes 2012), which may hint toward such major gene effects on the higher taxonomic level.

In conclusion, our multi-model inference enabled us to discriminate between phylogenetic, ecogenetic, and supposedly also developmental effects on occlusal character variation in hares from Türkiye, by maintaining all individual samples in the analyses and by testing simultaneously. Contrary, traditional calculations of pairwise phenotypic divergence (i.e., MMD values) of non-metrical dental or skeletal characters have traditionally used sample sets that have been statistically homogenous for various non-spatial factors, such as sex or age, and body size, and have thereby often lead to sample sizes reductions (Sjøvold 1977). Our modeling results indicated spatial differentiation in the hares only partly paralleling the earlier found population genetic pattern of hares from Türkiye and additional spatial effects, independent from climatic effect. In addition, climate effects on epigenetic variation of some few occlusal characters could also been shown in our present study. Hence, both (micro-) phylogenetic and ecogenetic variation could be proved for the occlusal characters of hares from Türkiye, apart from likely developmental causation of variation in some characters.

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## Declarations

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

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