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RESEARCH ARTICLE

Predictive use of modern reference osteological collections for disentangling the shape of Eurasian equid cheek teeth and metapodials in archaeological material

Azadeh F. Mohaseb[1,2] | Raphaël Cornette[3] | Michaela I. Zimmermann[4] | Hossein Davoudi[2] | Rémi Berthon[1] | Claude Guintard[5] | Thomas Cucchi[1] | Pauline Hanot[6] | Elmira Mohandesan[7,8] | Véra Eisenmann[9] | Joris Peters[4,10] | Marjan Mashkour[1,2]

[1]Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, AASPE UMR 7209, CNRS/Muséum national d'Histoire naturelle, Paris, France

[2]Bioarchaeology Laboratory, Central Laboratory, University of Tehran, Tehran, Iran

[3]Institut de Systematique, Evolution et Biodiversite, ISYEB, UMR 7205, CNRS/Muséum national d'Histoire naturelle, Paris, France

[4]Institute of Palaeoanatomy, Domestication Research and the History of Veterinary Medicine, LMU Munich, Munich, Germany

[5]Ecole Nationale Vétérinaire, de l'Agroalimentaire et de l'Alimentation, Nantes Atlantique, ONIRIS, Nantes, France

[6]Mécanismes Adaptatifs et Evolution, MECADEV UMR 7179, CNRS/Muséum national d'Histoire naturelle, Paris, France

[7]Department of Evolutionary Anthropology, University of Vienna, Vienna, Austria

[8]Human Evolution and Archaeological Sciences (HEAS), University of Vienna, Vienna, Austria

[9]Département des Sciences de la Terre, Laboratoire de Paléontologie, CNRS/Muséum national d'Histoire naturelle, Paris, France

[10]Bavarian State Collection of Palaeoanatomy, SNSB, Munich, Germany

Correspondence
Marjan Mashkour, Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, AASPE UMR 7209, CNRS/Muséum national d'Histoire naturelle, Paris, France.
Email: marjan.mashkour@mnhn.fr

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Abstract

Equids have shaped past Eurasian societies in many ways. This applies in particular to domestic horses, donkeys, and their hybrids. Key to documenting modes of exploitation and cultural trajectories in past societies is the correct taxonomic classification of tooth and bone specimens found in archaeological sites. However, close osteomorphological resemblance of wild and domestic equids and their economically valuable hybrids, that is, mules and hinnies, complicates the identification of intentionally fragmented or naturally damaged archaeological specimens. Here, we apply geometric morphometrics (GM) to mandibular teeth and metapodials, two skeletal elements commonly found in archaeological collections and known for their diagnostic properties using traditional morphometric methods. We registered a statistically representative set of 2D and 3D coordinates on mandibular teeth (P3, P4, M1, and M2) and metapodials of 92 domestic horses (*Equus caballus* Linnaeus, 1758), 70 domestic donkeys (*Equus asinus* Linnaeus, 1758), 30 hybrids, and 63 Asiatic wild asses (*Equus hemionus* Pallas, 1775). Taxonomic classification of these 255 specimens considered both *shape* and *form*, applying linear discriminant analysis, k-nearest neighbors algorithm, and artificial neural networks to seven combinations of taxa. We obtained correct classifications in over 87% and 80%, respectively, of the premolars and molars and in over 93% and 89%, respectively, of the metacarpals and metatarsals. This modern dataset was then used to classify equid specimens from three archaeological sites in the Middle East already analyzed morphologically. Taking into account the past zoogeography of wild equids and the historical distribution of their domesticated descendants and hybrids, the GM approach presented in this study offers the possibility to morphologically classify archaeological equids with far greater certainty than has been the case so far.

KEYWORDS
Azerbaijan, classification methods, donkey, geometric morphometrics, hemione, horse, Iran, mule

1 | INTRODUCTION

Extant equids include several species and subspecies that are widely distributed across Eurasia and Africa (Groves, 1986). First used as source of food and raw materials during Pleistocene and early Holocene times, two species became domesticated in the course of the mid-Holocene, namely, the wild horse, *Equus ferus* Boddaert, 1785, and the African wild ass, *Equus africanus* von Heuglin and Fitzinger, 1866 (Anthony, 1991; Anthony et al., 2006; Gaunitz et al., 2018; Grubb, 2005; Kimura et al., 2011; Librado et al., 2021; Rossel et al., 2008; Turner, 2005). As such, horses, *Equus caballus* Linnaeus, 1758, donkeys, *Equus asinus* Linnaeus, 1758, and their hybrids played and play multiple roles in ancient and modern cultures. They have been and still are exploited for traction, transport, cavalry, food, and leisure activities as well as in rituals and symbolism (e.g., Antikas, 2006; Dutto et al., 2004; Gazagnadou, 2001; Johnstone, 2006; Mallory, 1981; Olsen, 2006; Outram et al., 2009; Peters, 1998; Peters et al., 2017; Schwartz et al., 2006; Taylor et al., 2020; Uerpmann, 1991). In order to address properly the role and the status of equids in past societies, correct taxonomic classification of archaeological specimens is indispensable, which can however be quite problematic in regions where the distributions of wild equids overlap with one or more domestic forms and their hybrids. To achieve this goal, modern reference specimens housed in museums form the starting point, as only such individuals allow for reliable baselines to be established (e.g., Cucchi et al., 2017; Eisenmann, 1986; Eisenmann & Beckouche, 1986; Eisenmann & Mashkour, 2000; Hanot & Bochaton, 2018; Schreiber et al., 2000; Seetah et al., 2014).

Traditional osteomorphological and osteometrical approaches (Marcus, 1990) confirm that certain skeletal elements and in particular the skull, lower cheek teeth, metapodials, and first phalanges possess a high potential for inter-species distinction (e.g., Bökönyi, 1986; Dive & Eisenmann, 1991; Eisenmann, 1979, 1981, 1986, 1991, 1996; Eisenmann & Baylac, 2000; Eisenmann & Beckouche, 1986; Groves & Mazak, 1967; Payne, 1991; Peters, 1998). In the case of hybrids, however, identification is much more problematic and therefore often ambiguous (e.g., Bennett et al., 2017; Granado et al., 2020; Hanot et al., 2019).

One advantage of the skeletal elements mentioned above is that they are generally well preserved in Pleistocene and Holocene archaeofaunal assemblages. Previous geometric morphometric (GM) approaches already tested cranial and postcranial elements regarding their potential for disentangling fossil and recent equid taxa (Seetah et al., 2014; Hanot et al., 2017; Heck et al., 2018). Based on the study of four mandibular cheek teeth (P3, P4, M1, and M2) from 15 extant equid taxa, a strong taxonomic signature in the shape of the enamel folding, in particular, of the double knot (Eisenmann, 2017), could be demonstrated (Cucchi et al., 2017). Similarly, GM analysis on the distal part of the metapodials from wild horse populations (Bignon et al., 2005) has shown the potential of this approach for distinguishing ecomorphs in this taxon. More recently, the application of GM to the skull and post-cranial elements of horse, donkey, and their hybrids enabled to demonstrate that the skull, metapodials, and talus possessed reliable characters for discriminating between the respective populations as well (Hanot et al., 2017).

In earlier GM studies dealing with equids, Asiatic wild asses, referred to frequently as onagers or hemiones, were largely ignored despite populating vast areas of Holocene arid Asia, as reflected by their numerous osseous remains in archaeological sites stretching from Turkey to Mongolia. However, in order to detail the mode of exploitation of equids by ancient societies in this wide geographic region, unequivocal distinction of hemiones from similar sized equids including donkeys, domestic horses, and mules is essential (Mashkour, 2002). Except for the Syrian onager *Equus hemionus hemippus* Saint Hilaire, 1855, a subspecies of hemione that went extinct in the late 1920s, current taxonomy recognizes four subspecies, that is, the Persian onager *Equus hemionus onager* Boddaert, 1785, the Indian wild ass *Equus hemionus khur* Lesson, 1827, the Turkmenian kulan *Equus hemionus kulan* Groves and Mazák, 1967, and the Mongolian wild ass *Equus hemionus hemionus* Pallas, 1775. The choice of hemiones for our GM study includes the onager and the kulan as the most common subspecies curated in European natural history collections.

In this study, we present the use of GM techniques as a useful tool for identifying different equid species based on their morphological characters (Bookstein, 1991; Rohlf & Marcus, 1993), which have been proven to be more powerful than traditional morphometrics. We then combined GM techniques with three classification methods, more precisely linear discriminant analysis (LDA) (Baylac & Frieß, 2005), k-nearest neighbors (k-NN) algorithm (Guo et al., 2003; Venables & Ripley, 2002), and artificial neural networks (ANN) (Dastres & Soori, 2021; Dobigny et al., 2002; Ripley, 1996) in order to optimize specific identification of modern equids.

The focus of our study will be the comparison of shape, size, and form between modern domestic horses, domestic donkeys, mules (*E. asinus* ♂ × *E. caballus* ♀), hinnies (*E. caballus* ♂ × *E. asinus* ♀), and hemiones.

When applying GM together with classification methods to a representative number of individuals for each (sub)group, several assumptions can be tested. First, all equid taxa considered here can be distinguished using GM, but classification results per element vary according to the reference collection available for comparison. Second, between skeletal elements, the rate of success of correct classification varies. Third, size is a valid criterion for separating domestic donkeys from the other equid taxa. This study concludes by testing the results obtained with modern equids to a Central Asian archaeofaunal assemblage.

2 | MATERIALS AND METHODS

2.1 | Modern reference collection

The combination of GM and classification methods used in this study is applied to the most discriminant cranial and skeletal elements, as described above, of four equid taxa that are the four mandibular cheek teeth—the third and fourth premolars (P3 and P4) and the first and second molars (M1 and M2)—and the metacarpal (MC) and the metatarsal (MT). The collection studied totals 255 modern adult individuals; it is composed of 92 domestic horses, 70 domestic donkeys, 30 hybrids (21 mules and 9 hinnies), and 63 hemiones (44 *E. hemionus kulan*, 13 *E. hemionus onager*, and 6 *E. hemionus*). The skeletons are housed in several Natural History Museums and Institutions (Table S1). All individuals are adults with fully erupted teeth and fused epiphyses. As GM is sensitive to the preservation quality of the bones, certain skeletal elements had to be removed, more precisely damaged bone or tooth, individuals showing very advanced tooth wear, or very young equids precluding exact positioning of landmarks. The modern assemblage studied thus comprises 672 skeletal elements, that is, 443 mandibular teeth (126 P3s, 98 P4s, 94 M1s, and 125 M2s) and 229 metapodials (115 MCs and 114 MTs) (Table S1). We systematically selected left elements for analysis, but in case of absence, right elements were analyzed and mirrored to the left.

2.2 | Archaeological material

To test the reliability of the GM methods and protocols developed in this study for the distinction of equid taxa, we selected 11 skeletal elements (7 teeth and 4 metapodials) from three archaeological sites in the Middle East: The Neolithic settlement (5th millennium BCE) of Alikemek Tepesi in the south of the Republic of Azerbaijan near the Iranian border (1P3 and 1M1) (Berthon, 2014; Narimanov, 1977, 1987), the Iron Age level (2nd millennium BCE) of Tepe Hasanlu in North-western Iran (2P3s, 1P4, 1M1, and 1M2) (Davoudi & Mashkour, 2019; Hejebri Nobari et al., 2016), and the medieval site of Shahre Qumis (1MC and 3MTs) (Hansman & Stronach, 1974; Mashkour et al., 2021) in North-eastern Iran.

2.3 | GM techniques, statistical approaches, and classification methods

The mandibular cheek teeth have been analyzed applying 2D GM on two sets of analogous and digital photographs detailing the occlusal surface of the teeth following our previously developed protocol (Cucchi et al., 2017). For digitizing landmarks on teeth, we used TpsDig2 version 2.17 (Rohlf, 2010, 2015). For the metapodials, we followed a 3D GM template published by Hanot et al. (2017), using a Microscribe 3D digitizer. Missing landmarks were estimated using a thin plate spline (Gunz et al., 2009). Superimposition of landmarks of different specimens was performed by generalized Procrustes analysis (GPA) (Adams et al., 2004; Bookstein, 1991; Gower, 1975; Rohlf & Slice, 1990; Zelditch et al., 2004). To reduce the dimensionality of our multivariate dataset while preserving as much variability as possible (Baylac & Frieß, 2005), we performed a between-group principal component analysis (PCA) on Procrustes coordinates, which is often used in case sample size of each group is smaller than the number of variables (Boulesteix, 2005; Cardini et al., 2019; Mitteroecker & Bookstein, 2011). We projected the shape visualization using the shape coordinates of the PCA and their position along the first and second PC axes (Monteiro, 1999). Boxplots based upon log-transformed centroid size (the square root of the sum of the squared distances of all landmarks from their centroid) were used to illustrate *size* differences between equid taxa.

Centroid size differences and significance among different species were measured through a one-way analysis of variance (ANOVA), followed by a post hoc Tukey honest significant difference test (TukeyHSD) (Tukey, 1984), which calculates the differences between the means as well as the confidence interval and the *p*-value for each pair of taxa. A pairwise permutation multivariate analysis of variance (MANOVA) was performed for comparisons between group levels, with FDR correction for multiple testing to assess differences in *shape* and their significance. A Procrustes ANOVA with permutation procedure was applied to investigate the effects of allometry (relationship between size and shape) as potential impact factors on the discrimination of equid species. Test results with *p*-values <0.05 are considered significant.

The mandibular cheek teeth and metapodials have been analyzed using both *shape* and *form* analyses. In *shape* analysis, we used only the Procrustes coordinates, and we analyzed the shape of the skeletal elements independently from the size. In *form* analysis, both Procrustes coordinates and centroid size were taken into consideration, in order to investigate the effect of size on the classification process (Mitteroecker et al., 2013).

The classification of equid taxa is based on three complementary methods, that is, LDA, k-NN, and ANN. These classification methods served to obtain the most information possible from the *shape* and *form* differences between the four equid taxa.

In order to properly compare the results of the three classification methods, first, the reference dataset has been split into 80% randomly selected as training and 20% as test data set in a way that all species contributed proportionately to both datasets. For the classification of modern equids, a leave-one-out cross validation was performed (Kuhn & Johnson, 2013).

LDA is used as a tool for classification, trying to find a linear combination of features that separates two or more groups. It produces robust and interpretable results even without a normality assumption. LDA is sensitive to the number of shape predictors (Evin et al., 2013; Kovarovic et al., 2011), so we reduced the number of variables by using the PC scores instead of the primary data and considered nine and five PC axes, respectively, for teeth and metapodials in order to reach 75%–85% of the total variability enabling us to use a smaller number of variables than the sample size of the smallest group (Mitteroecker & Bookstein, 2011). In addition, since in LDA the sample size heterogeneity has been reported to cause a bias in favor of the larger groups contributing to the dataset (Evin et al., 2013), sample size of horses and hemiones has been reduced randomly to achieve a more balanced sample ratio with donkeys and hybrids.

Compared to LDA, the k-NN algorithm is a non-parametric approach. It is less sensitive to the number of specimens and therefore still useful if sample size is low (Baylac & Frieß, 2005; Cornette et al., 2015; Guillaud et al., 2015). Conversely, it does not tell us which predictors are important. In order to obtain the best possible rate of correct reclassification using k-NN, the number of nearest neighbors (k) varied from $k = 1$–10 (Ripley, 1996; Venables & Ripley, 2002). We thus selected the highest global rate (average of rates for each species) as the best rate of classification. In some cases, the best global rate does not guarantee the best rate for each species. The individual rates per species can be consulted in the supporting information (Tables S12–S18).

ANN is a subset of the machine learning approach inspired by the human brain and is composed of input, hidden layers, and output layers. It captures the complex characteristics of a dataset and has a high potential for discrimination and classification of patterns. Moreover, there is a low risk of noise and outliers using this method (Dastres & Soori, 2021; Haykin, 2008). In comparison to the LDA and k-NN algorithms, it is more powerful and provides better classification rates (Ripley, 1996, 1998). However, ANN does not provide information about variates contrary to the two other methods.

For ANN, we selected two hidden layers with, respectively, five and three nodes.

All analyses were computed with the "R" language (R Core Team, 2022) (Table 1).

We propose a predictive classification system by the preselection of the modern reference collection according to various possible scenarios for the co-existence of equids during the Late Glacial and Holocene in the fossil record in Eurasia. The seven targeted taxonomic combinations allow for a more powerful statistical analysis and taxonomic distinction: Group1: horse, donkey, hybrids, hemiones; Group2: horse, donkey, hybrids; Group3: horse, donkey, hemiones; Group4: horse, hemiones; Group5: horse, hybrids; Group6: donkey, hybrids; and Group7: donkey, hemiones (Table 2). We used heat maps for the visualization of correct classification rates, where the lowest rates are shown in red and the highest rates in green.

Taking the close morphological resemblance between the horse–donkey hybrids as well as the two subspecies of hemiones, we thus considered it meaningful to examine first the differences in *size* and *shape* within each group in order to know whether mules and hinnies on the one hand and onagers and kulans on the other can be merged; this would enable us to enhance sample size and to obtain a more balanced sample ratio. Furthermore, since a pronounced sexual dimorphism in our equid sample would lead to additional subgroups, the effects of sex on the *size* and *shape* of the studied elements in the different taxonomic units were assessed prior to further analyses.

TABLE 1 List of functions and libraries used to perform GM statistical and classification analyses in R programming language.

Analysis	R function	R library	Reference
Thin plate spline	estimate.missing	Geomorph	Adams and Otárola-Castillo (2013)
Generalized Procrustes analysis	gpagen	Geomorph	Adams and Otárola-Castillo (2013)
Between-group principal component analysis	groupPCA	Morpho	Schlager (2017)
One-way analysis of variance	aov	stats	R Core Team (2022)
Post hoc Tukey honest significant difference test	TukeyHSD	stats	R Core Team (2022)
Pairwise permutation MANOVA	pairwise.perm.manova	RVAideMemoire	Hervé (2022)
Procrustes ANOVA for allometry	procD.lm	Geomorph	Adams and Otárola-Castillo (2013)
Linear discriminant analysis (LDA)	lda	MASS	Venables and Ripley (2002)
K-nearest neighbors algorithm (k-NN)	knn & knn.cv	Class	Venables and Ripley (2002)
Artificial neural networks (ANN)	neuralnet	neuralnet	Fritsch and Günther (2019)

3 | RESULTS

3.1 | Hybrids: mule and hinny

The results of ANOVA show no significant size difference between mules and hinnies for the mandibular cheek teeth. While the difference in size is significant for the metacarpal ($p < 0.01$), it is hardly significant for the metatarsal ($p = 0.04$).

The results of MANOVA show no significant shape difference between mules and hinnies for any skeletal elements (Table S2). These results allow us to pool mules and hinnies altogether into a single "hybrids" group to reduce the effects of a small sample size for hybrids that are comparably rare in museum collections.

However, due to the significant difference in the centroid size of metacarpals between mules and hinnies, the range of centroid sizes could extend and overlap with the parental species. To avoid this problem and the probable misclassification between horses, donkeys, and their hybrids, the *form* analysis of metacarpals is not recommended for equid combinations including hybrids, even if the rate of correct classification is higher than *shape* analysis.

TABLE 2 The combination of four equid taxa.

Equid combinations	Horse	Donkey	Hybrids	Hemiones
Group1	✓	✓	✓	✓
Group2	✓	✓	✓	
Group3	✓	✓		✓
Group4	✓			✓
Group5	✓		✓	
Group6		✓	✓	
Group7		✓		✓

3.2 | Hemiones: kulan and onager

Applying the same procedure, the difference in size between kulans and onagers was not significant for the mandibular cheek teeth and the metacarpal, but significant for the metatarsal ($p < 0.01$). MANOVA showed no significant difference in shape between the two subspecies for mandibular cheek teeth, while the differences for metacarpal ($p = 0.02$) and metatarsal ($p < 0.01$) turned out significant (Table S2). That said, because the shape overlaps between hemiones and other equid taxa in PCA are minor for the metacarpal and non-existent for the metatarsal, the differences noted in shape between kulans and onagers would not be relevant for the further analyses of the four equid taxa. For subsequent analysis, we thus decided to pool kulans and onagers into a single "hemiones" group.

3.3 | Sexual dimorphism

We tested sexual dimorphism on the individuals for which this information was available. Hybrids could not be tested on either teeth or metapodials, and donkeys were not analyzed on the mandibular cheek teeth. In the case of horses and hemiones (teeth and metapodials) as well as donkeys (metapodials), the results of ANOVA for size and MANOVA for shape confirm the absence of significant morphometric differences between males and females (Table S3).

3.4 | Age

Due to the insufficient number of equid specimens with a known age class, we were unable to examine the effect of age on the shape

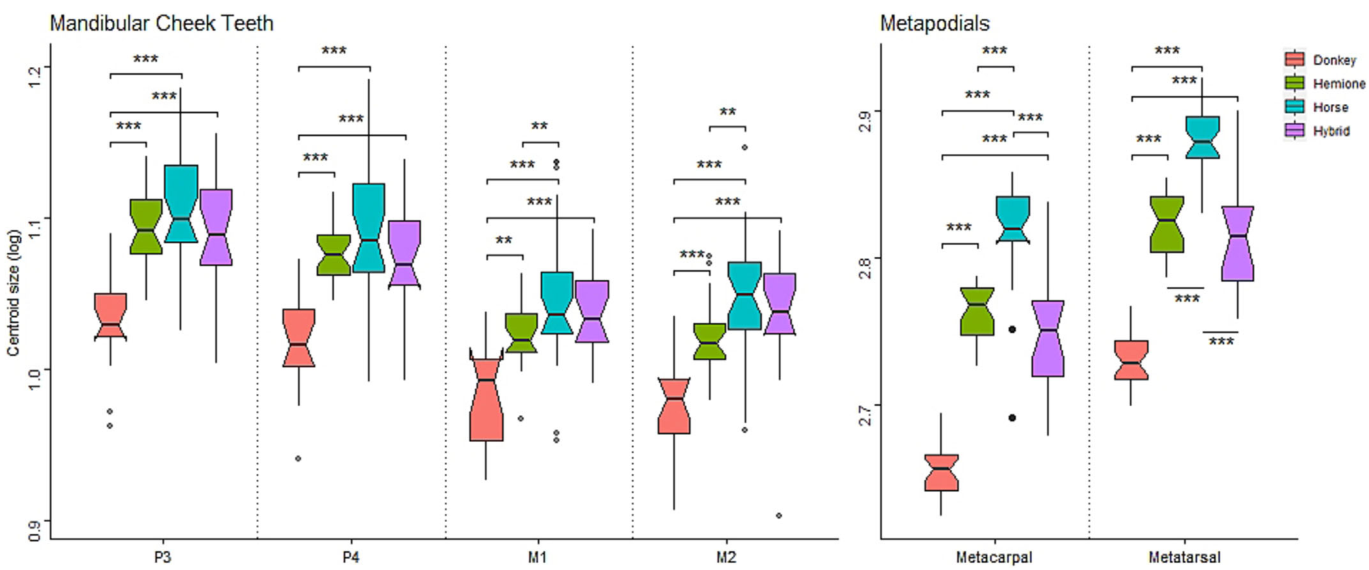


FIGURE 1 Boxplots showing the difference in log-transformed centroid size for mandibular teeth and metapodials. Significant pairwise differences are shown by either two or three stars indicating respectively significant ($p < 0.05$) and highly significant ($p < 0.01$) levels. [Colour figure can be viewed at wileyonlinelibrary.com]

variation of the occlusal enamel pattern of the teeth and the shape of metapodials.

3.5 | Size, shape, and allometry

3.5.1 | Mandibular cheek teeth

The results of ANOVA indicate that donkeys exhibit significantly smaller centroid size than horses, hybrids, and hemiones in all teeth. For M1 and M2, hemiones are significantly smaller than horses well visible in the boxplots of the centroid size (Figure 1 and Table S4).

The pairwise permutation MANOVA also shows a significant difference in shape between four taxa for four teeth (Table S4). As such, allometry was not significant for any of the mandibular teeth.

The results of PCA on the occlusal shape of all mandibular teeth show a separation between four taxa on the first two principal components (PC1 and PC2) (Figure 2). For P3 (PC1 + PC2 = 92% of the total variance), the main divergence to the horse from donkey, hemiones, and, to a lesser extent, hybrids could be observed along PC1. However, the divergence between donkey, hybrids, and hemiones is along PC2. For P4 (94%), the shape changes along PC1 are between horse, donkey, and hybrids. The divergence from donkey and hybrids to hemiones is seen along PC2. For M1 and M2 (96%), PC1 illustrates

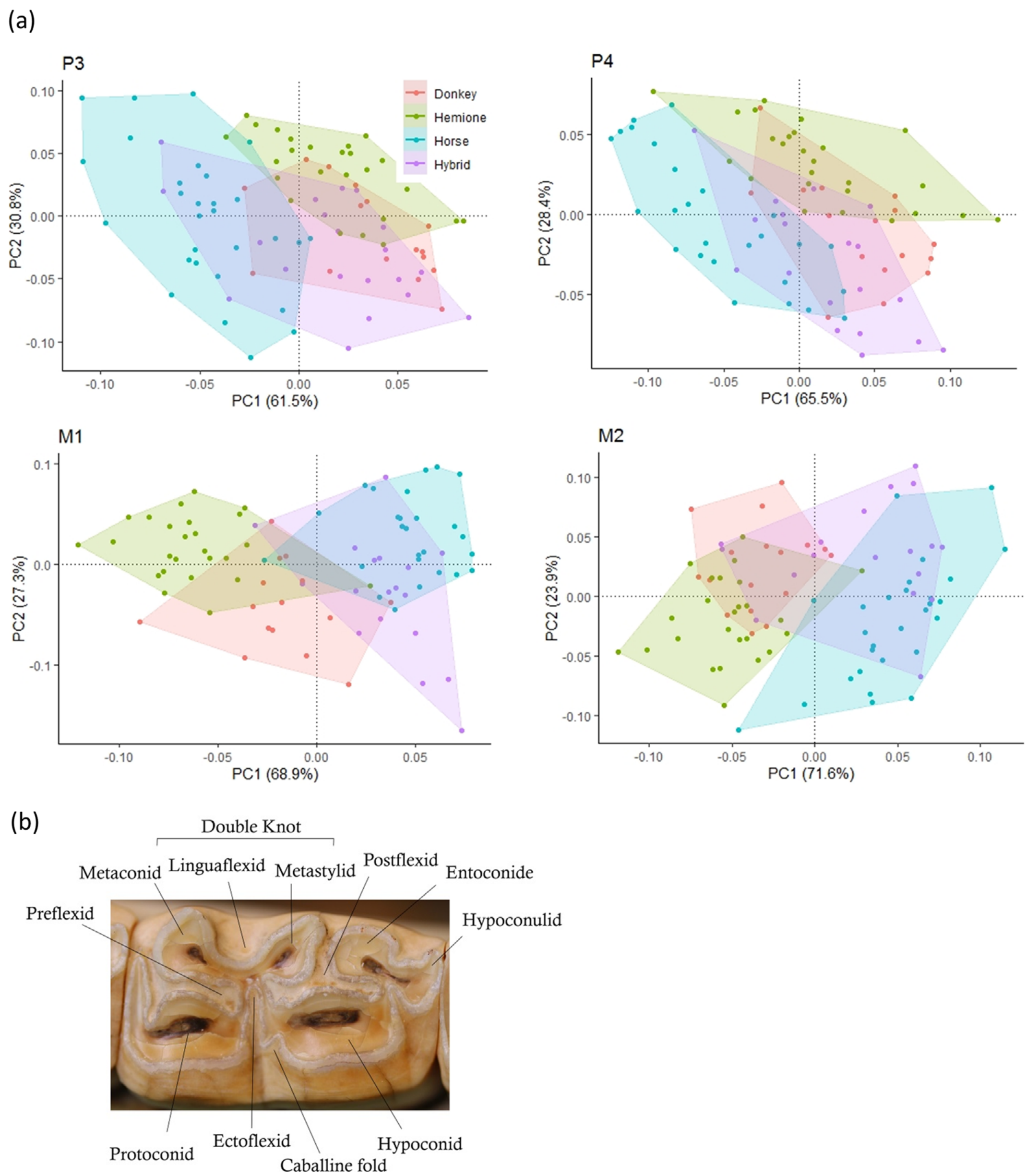


FIGURE 2 (a) Scatterplot of PC1 and PC2 (principal component analysis) for the shape of the occlusal surface of the mandibular cheek teeth (P3, P4, M1, and M2). (b) Occlusal view of an M2 (*Equus caballus*, specimen E342, NHM, Vienna). [Colour figure can be viewed at wileyonlinelibrary.com]

the separation of donkey and hemiones from horse and hybrids, while PC2 demonstrates the separation of donkey and hybrids from horse and hemiones. We also obtained the morphometric criteria on the occlusal shape of the teeth based on the average GMM shape of each equid taxon (Table 3).

3.5.2 | Metapodials

The results of ANOVA indicate that donkeys have significantly smaller centroid size than the other taxa. Moreover, hybrids and hemiones are significantly smaller than horses (Figure 1 and Table S4).

The MANOVA presents significant differences in shape between four taxa for both metapodials (Table S4). The first two PCs obtained from the shape of metapodials (98%) illustrate a clear separation between four taxa. For metacarpal (Figure 3a), there is a divergence between horse and the other taxa along PC1 with hybrids situated in between. The PC2 shows a divergence between hemiones and donkey/hybrids. For the metatarsal (Figure 3b), horse is separated from donkey/hemiones along PC1. The hybrids are plotted in between with more similarities to horse. The PC2 represents differences in shape between donkey and hemiones. The differences in shape between all taxa on the proximal, distal dorsal, and distal palmar parts of metapodials are presented in Figure 3a,b.

Allometric adjustments in shape variation are significant in metacarpal (86%) and metatarsal (89%) ($p < 0.05$). However, the allometric slopes do not run parallel in the different equid taxa. Consequently, due to the absence of homogeneity of slopes, calculation of common allometric directions by multivariate regression was not possible (Klingenberg, 1996).

3.6 | Taxonomic classification: group combinations using LDA, k-NN, and ANN

We computed this evaluation system inspired by former studies of, for example, Clutton-Brock et al. (1990), Zeder and Pilaar (2010), and Zeder and Lapham (2010). Our analytic procedure is described with one example based on the *form* analysis of P4 in Group1, where the rates of correct and wrong classifications as well as the projected misidentified specimens for each equid species are presented separately for LDA, k-NN, and ANN (Tables 4 and S5). The classification rates of hybrids through LDA will be explained to show the method of calculation.

For hybrids, 75% of P4s is correctly classified as hybrids, and 25% is misclassified as hemiones. The values in the row "%Wrong" correspond to the proportion of misclassified specimens ($0 + 0 + 25 = 25$). The values in the row "projected %misidentified" are another way of representing the misidentified specimens. These values correspond to the proportion of specimens assigned to a taxon, while should have been correctly classified to another taxon. In the same example, 89% of the specimens was in total assigned to hybrids. This number is calculated by adding the percentage of correctly identified hybrids (75%) plus the percentage of specimens from other taxa incorrectly identified as hybrids (horses = 14%). So, the rate of other taxa misidentified as hybrids would be 15.7% (14/89).

The rates of correct classification (Figure 4) and the comparative rates of correct and wrong classifications as well as projected misidentified between classification methods using *shape* and *form* analyses for the seven defined combinations are shown in Tables S5–S10.

3.6.1 | Group1: horse, donkey, hybrids, and hemiones

As a general comment, we can observe that the best classifications are provided by the *form* analysis. The best classified teeth are, respectively, P4 using LDA (91%), P3 using LDA (89%), M1 using LDA, and M2 using k-NN/ANN (80%). As for the metacarpals (see results in Section 3.1), the shape analysis is a better choice. Both metapodials are classified with similar rates of 89%, using LDA and k-NN and shape analysis for the former and using LDA and both analyses for the latter (Figure 4 and Table S5).

Summary results: In Group1, for teeth, the premolars, LDA, and *form* analysis are recommended. For metapodials, both metacarpal and metatarsal are good choices using LDA and k-NN in *shape* for the former and LDA in *shape* and *form* for the latter.

3.6.2 | Group2: horse, donkey, and hybrids

In this group, P3 is the most accurately classified tooth using k-NN and ANN in *shape* (90%) followed by P4 using LDA regardless of the analysis and ANN in *form* (88%). Although M2 (80%) is better classified than M1 (73%), both molars represent the elements with less classification power.

For metacarpal, *shape* analysis is recommended using k-NN and ANN (95%). Metatarsal is best classified using ANN and *form* analysis (90%) where donkey and hybrids are classified with a rate of 100% (Figure 4 and Table S6).

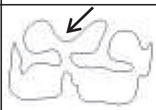
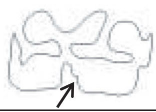
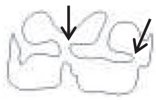
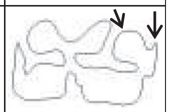
Summary results: In order to achieve the highest classification rates for all taxa, it is best to analyze both P3 and P4 if present, because, in the former, horse and hybrids and, in the latter, donkey provide the classification rates of 100%. For metapodials, the metacarpal is a better choice than metatarsal.

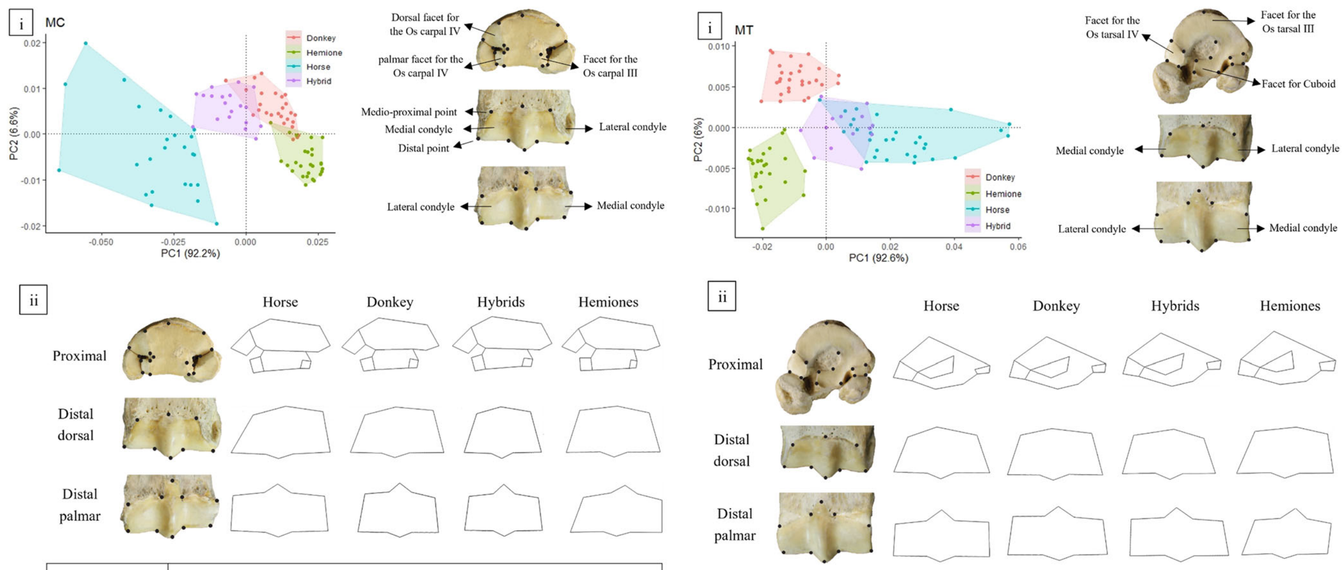
3.6.3 | Group3: horse, donkey, and hemiones

For Group3, the best classifications (100% accuracy) are provided by P3 and M2 using LDA in *form* and LDA in both *shape* and *form*, respectively. The other two cheek teeth, M1 and P4, also provide high classification rates between 94% and 89%.

For metapodials, metacarpal is better classified than metatarsal. For metacarpal, the correct classification rate reaches 100% using all

TABLE 3 Diagnostic criteria characterizing the mandibular cheek teeth (P3, P4, M1, and M2) allowing to separate horse, donkey, hybrids, and hemiones.

	Criteria		Linguaflexid	Caballine fold	Postflexid	Ectoconid & Hypoconulid
	Mean Shape	Taxa				
P3		Horse	U-Shape	Prominent, more expressed	Symmetric	Not observed
		Donkey	V-shape, more acute	Slight or absent	Asymmetric, fold more expressed	Not observed
		Hybrids	V-Shape	Prominent	Asymmetric	Not observed
		Hemiones	V-Shape	Slight or absent	Asymmetric, left side curved, expressed upwards	Not observed
P4		Horse	U-Shape	Prominent	Symmetric	Not observed
		Donkey	V-Shape	Slight or absent	Asymmetric, fold prominent, more expressed, left side curved	Not observed
		Hybrids	V-Shape	Slight or absent	Asymmetric	Not observed
		Hemiones	V-Shape, more obtuse	Slight or absent	Asymmetric, fold prominent, left side curved, expressed upwards	Not observed
M1		Horse	U-Shape	Slight	Symmetric	U-Shape
		Donkey	V-Shape	Absent	Asymmetric, Left site curved, expressed downwards	V-Shape
		Hybrids	V-Shape	Slight or absent	Asymmetric	V-Shape
		Hemiones	V-shape, more obtuse	Slight or absent	Asymmetric, Left site curved, expressed upwards	U-Shape
M2		Horse	U-Shape	Prominent, more expressed	Symmetric, with fold	U-Shape
		Donkey	V-Shape	Slight	Asymmetric	V-Shape
		Hybrids	V-Shape	Prominent	Symmetric	V-Shape
		Hemiones	V-Shape, more obtuse	Slight	Asymmetric, Left site curved, expressed upwards	V-Shape



Proximal	The palmar facet for the Os carpal IV has a rectangular shape in horses and horse x donkey hybrids, whereas in donkeys and hemiones it exhibits a more square shape. The gap between the dorsal and palmar facets for the Os carpal IV is narrower in horses and horse x donkey hybrids compared to donkeys and hemiones. In hemiones, the facet for the Os carpal III is smaller in comparison to the three other taxa.
Distal dorsal	The ratio of height and width of the medial and lateral condyles in horse x donkey hybrids is larger in comparison to their homologues in horses, donkeys, and hemiones. In horses and donkeys, the shape of medial and lateral condyles is asymmetric.
Distal palmar	The ratio of height and width of the medial and lateral condyles in donkeys and horse x donkey hybrids is larger in comparison to their homologues in horses and hemiones. In hemiones, the shape of the medial and lateral condyles is asymmetric.

(a)

Proximal	In horses, the facet for the Os tarsal IV is rectangular in comparison to the three other taxa which exhibit a more square shape. In hemiones, the shape between the facets of Os tarsal III and cuboid represents a triangular shape, whereas in horses, donkeys, and their hybrids, it has a trapezoid shape.
Distal dorsal	The proximal margin of the medial condyle is wider than its homologue in the lateral condyle in horse x donkey hybrids and hemiones. In horses and donkeys, the opposite can be observed. In hemiones, the medial margin of the medial condyle is more oblique compared to its homologue in the three other taxa.
Distal palmar	In horses, the ratio of height and width of the medial and lateral condyles is smaller than that in the three other taxa. In hemiones, the medial and lateral margins of the condyles run parallel and more oblique compared to their homologues in the three other taxa.

(b)

FIGURE 3 (a) (i) Scatterplot of PC1 and PC2 (Principal Component Analysis) for the shape of metacarpal (MC). (ii) Differences in the shape of proximal, distal dorsal, and distal palmar articular surfaces of the metacarpal of horses, donkeys, their hybrids, and hemiones (Peters, 1987; metacarpal photos after Hanot et al., 2017). (b) (i) Scatterplot of PC1 and PC2 (Principal Component Analysis) for the shape of metatarsal (MT). (ii) Differences in the shape of proximal, distal dorsal, and distal palmar of the metatarsal between horses, donkeys, their hybrids, and hemiones (Peters, 1987; Metatarsal photos after Hanot et al., 2017). [Colour figure can be viewed at wileyonlinelibrary.com]

methods and *form* analysis. Metatarsal is also classified with high rates using k-NN regardless of the analysis and ANN in *shape* (92%) (Figure 4 and Table S7).

Summary results: In this group, P3, M2, and metacarpals are the best choices for classification.

3.6.4 | Group4: horse and hemiones

For Group4, the rates are highly correct. The P3 (LDA in *form*), M1 (LDA and ANN, both analyses), and M2 (k-NN, both analyses) are correctly classified with a rate of 100%. Although P4 shows lower rates, its results are still satisfying (92%, ANN, both analyses).

Metapodials are also highly correctly classified. For metacarpal, the rate of correct classification is 100% regardless of the method and analysis. For metatarsal, a rate of 94% is obtained using k-NN in *shape* and ANN in both analyses (Figure 4 and Table S8).

Summary results: In this group, P3, M1, M2, and metacarpals are the best choices for classification.

3.6.5 | Group5: horse and hybrids

In Group5, the P3 and M2 are the most accurately classified teeth that reach a rate of 100% using k-NN in *shape* and *form* for the former and ANN in *shape* for the latter. The rate for P4 using ANN in *shape* is 91%, and the M1 represents the lowest rates.

The metacarpal is better classified than metatarsal. For metacarpal, a rate of 100% is obtained regardless of the method or analysis except for k-NN in *form*. For metatarsal, the k-NN in *form* results in a rate of 92% correct classification (Figure 4 and Table S9).

TABLE 4 Group1—*Form* analysis on P4.

P4	LDA					k-NN						ANN				
	Horse	Donkey	Hybrid	Hemione	Overall	No. of Ks	Horse	Donkey	Hybrid	Hemione	Overall	Horse	Donkey	Hybrid	Hemione	Overall
Horse	86	0	0	0	90.9	k = 10	86	0	0	0	86.4	86	0	0	0	86.4
Donkey	0	100	0	0			14	100	25	0		14	80	0	17	
Hybrids	14	0	75	0			0	0	50	0		0	20	100	0	
Hemiones	0	0	25	100			0	0	25	100		0	0	0	83	
% wrong	14	0	25	0			14	0	50	0		14	20	0	17	
Projected % misidentified	0	0	15.7	20			0	28.1	0	20		0	27.9	16.7	0	

Note: Rates of correct and wrong classification and projected misidentified, using LDA, k-NN, and ANN.

Summary results: In this group, P3 using k-NN, both shape and form, M2 using ANN in *form*, and metacarpals using all methods and *shape* analysis are the best choices for classification.

3.6.6 | Group6: donkey and hybrids

In Group6, the P4 (k-NN in *form*), M1 (LDA and k-NN in *form* and ANN in both analyses), and M2 (LDA in *shape*) are the best classified teeth with a rate of 100%. For P3, we used k-NN and ANN in both analyses to reach a rate of 87%.

In this group, both metapodials show highly correct results (100%). For metacarpal, a rate of 100% is obtained regardless of the method and analysis except for ANN and *shape* (93%). For metatarsal, this rate is obtained regardless of the method and analysis (Figure 4 and Table S9).

Summary results: In this group, all bones and teeth except P3 are suitable choices for classification. For metacarpals, *shape* analysis is the best choice.

3.6.7 | Group7: donkey and hemiones

In Group7, the M1 (k-NN in both analyses and ANN in *form*) and M2 (LDA in *form* and k-NN in both analyses) are the best classified teeth with a rate of 100%. For P3, we used k-NN in *form* to reach a rate of 92%.

In this group, both metapodials show highly correct results (100%) regardless of the method and analysis, except for ANN in *shape* for the metacarpal (Figure 4 and Table S11).

Summary results: In this group, the molars and metapodials are suitable choices for classification.

3.7 | Archaeological application

We applied this method to a set of archaeological samples from the Caucasus and the Iranian Plateau and selected those samples with very typical morphological and metric characteristics (Figure 5). We assumed the possible presence of equid taxa in each site, from geographical, chronological, and cultural perspectives.

In Alikemek Tepesi, only horses and hemiones are expected to be present in that period, and therefore, Group4 was targeted. In Tepe Hasanlu and Shahr-e Qumis, we also expect donkeys and hybrids, besides horse and hemiones. We, therefore, used Group1 for the GM classification for these two sites (Table 5).

For the specific assignment of archaeological teeth and metapodials, we used the classification method and the analysis that provided the highest classification rates. In Alikemek Tepesi, both P3 and M1 match with horses using LDA in *form* for the former and LDA and ANN in *shape/form* for the latter. In Tepe Hasanlu, the teeth of the (T521) match with hemiones using LDA in *form* for P3, P4, and M1 and ANN in *form* for M2. The isolated P3 (T517) is attributed to the

FIGURE 4 Heat map showing the rates of correct classification of mandibular cheek teeth and metapodials using *shape* and *form* analyses in LDA, k-NN, and ANN for all groups (G1–G7). The rates are shown from lowest (red) to highest (green). [Colour figure can be viewed at wileyonlinelibrary.com]

horse using LDA in *form* analysis. In Shahr-e Qumis, a very small metacarpal (MM5) is attributed to the donkey using ANN in *form* analysis. Three metatarsals are, respectively, attributed to donkey (MM94), hybrid (MM135), and horse (MM140) using LDA in *shape*/*form* analysis.

4 | DISCUSSION

In this methodological study, we examined the diagnostic properties of modern reference collections for the correct morphological classification of four widespread equid taxa, that is, the horse, the donkey,

FIGURE 5 Map showing the location of three archaeological sites from Azerbaijan and Iran: Alikemek Tepesi, Tepe Hasanlu, and Shahr-e Qumis. [Colour figure can be viewed at wileyonlinelibrary.com]

their hybrids, and hemiones. We estimated the impact of three statistical methods, LDA, k-NN, and ANN, on seven taxonomic combinations through *shape* and *form* analyses. We demonstrated that due to the absence of a significant difference in *shape* between mules and hinnies and a minor difference in *shape* between two subspecies of *Equus hemionus* most common in natural history collections and included in this study, that is, onager and kulan, there is the possibility of pooling each of the two pairs to enhance sample size. We also tested the effect of sexual dimorphism, on *size* and *shape* of teeth and metapodials, which proved to be not significant, thus confirming the results presented in previous studies (Eisenmann & Kuznetsova, 2004; von den Driesch & Boessneck, 1974). Most conspicuous is the difference in *size* between the donkey and the other taxa, which can be observed in all skeletal elements.

Although LDA and ANN have some methodological limitations (Evin et al., 2013), the two methods are clearly the best choices, provided sample size of each taxon can be increased and variability reduced. In case we are dealing with small sample size, k-NN is a better alternative because of its lower sensitivity to lower numbers of comparative specimens.

4.1 | Mandibular cheek teeth

As a result, the combinations including horse, donkey, and hybrids (G1 and G2) show the lowest rates of correct classification (∼90%) probably because of the presence of hybrids and their morphological similarities to both parental species. In other combinations, however, there are at least two teeth that reach classification rates of 100%. Regarding the two analyses, except for Group1 wherein *form* analysis works better than *shape* for all teeth, there is no specific model for choosing between *shape* or *form* analyses. Concerning the choice of classification method, LDA and ANN generally offer better results than k-NN, which moreover depends on the tooth selected for classification.

The GM approach applied to the equid mandibular cheek teeth in this study has been initially accomplished in our previous study on 15 equid taxa (Cucchi et al., 2017). The taxonomic accuracy for all teeth was satisfactory while the P3 turned out to be the best classified tooth. Based on our detailed analyses, however, it is now obvious that the choice of the most promising element(s) depends on the combination used to separate taxonomically modern reference specimens. We thus claim that the most suitable teeth for G1 are both premolars, for G2 the P3, for G3 the P3 and M2, for G4 both premolars and M1, for G5 the P3 and M1, for G6 the P4 and both molars, and for G7 both molars.

4.2 | Metapodials

For metapodials, k-NN and ANN generally provide higher rates than LDA, which depends on the combination used for identifying the archaeological material. In combinations G1 to G5, metacarpals can be classified correctly with higher accuracy than metatarsals. In the case of metacarpals, the rates of correct classification surpass 93%, whereby Group1 shows the lowest rates of success compared to the

TABLE 5 The specific assignment of the archaeological remains from Alikemek Tepesi, Tepe Hasanlu, and Shahr-e Qumis.

			Shape			Form		
Site	**Skeletal element**	**Code**	**LDA**	**k-NN**	**ANN**	**LDA**	**k-NN**	**ANN**
Alikemek Tepesi Azerbaijan Chalcolithic	P3	AKT040				Horse		
	M1	AKT016	Horse		Horse	Horse		Horse
Tepe Hasanlu North-west Iran Iron Age	P3	T521				Hemione		
	P4					Hemione		
	M1					Hemione		
	M2							Hemione
	P3	T517				Horse		
Shahr-e Qumis North-east Iran Medieval	Metacarpal	MM5						Donkey
	Metatarsal	MM94	Donkey			Donkey		
	Metatarsal	MM134	Hybrid			Hybrid		
	Metatarsal	MM140	Horse			Horse		

other groups exhibiting a 100% rate. For metatarsals, the rates are satisfactory as well, Group1 showing the lowest (89%) and Group6 and Group7 the highest rate of correctly classified specimens (100%).

Previous classical metric analyses and GM approaches have evidenced that metapodials are among the most discriminant postcranial elements (Eisenmann & Beckouche, 1986; Hanot et al., 2017). The LSR (log size ratio) diagrams on metapodials show better discrimination for metacarpals (Eisenmann & Beckouche, 1986), while the application of GM analyses to horse, donkey, and hybrid metapodials led to the conclusion, that metatarsals were more suitable for correct classification (Hanot et al., 2017). In the latter study, wherein the taxonomic combination (horse, donkey, and hybrids) is equivalent to Group2 of our study, only k-NN is used as the classification method, in which *shape* provides higher rates of success than in *form* analysis. When comparing the success rates of k-NN obtained from Group2 with those published by Hanot et al. (2017), the most important contradiction is that in our study, the metacarpal generally provides higher rates of correct classification than metatarsal, regardless of the kind of analysis performed. Also, metacarpal provides better results in *form* (100%) than in *shape*. Regarding the best approach for assigning taxonomically metapodials, k-NN appears most suitable for classifying metacarpals, while for metatarsals, ANN provides the highest correct rates in case of *form* analysis (90%).

4.3 | Archaeological assignments

The assignment of the two teeth from Alikemek Tepesi to horse, analyzed within Group4, highlights the specificity of this site, which at present is the only one in the South Caucasus witnessing such a significant proportion of equid remains for the Neolithic period (∼7% of the number of identified specimens). The fact that only horses could be identified in a region where hemiones potentially occurred as well, likely points to specialized hunting behavior. The importance of this observation should not be underestimated in view of recent palaeogenomic analyses (Librado et al., 2021) confirming the lower Volga-Don area to the north of the Caspian Sea as the potential region of origin of horse domestication postulated earlier by zooarchaeological work (Anthony, 2007; Kelekna, 2009).

In Iron Age II layers (1050–800 BC) of Tepe Hasanlu, the allocation of one mandible to a hemione using the Group1 combination questions the past biodiversity and dispersal of these steppe-adapted animals on the Iranian Plateau. The species' identification south of Lake Urmia region dated back to some 2–3000 years ago (1st millennium BCE). This is surprising because currently, the northwestern part of Iran benefits from semi-arid climatic conditions with an average annual rainfall of 300 mm. In this respect, a recent reconstruction of paleo-rain over the Lake Urmia basin is of particular interest (Sharifi et al., 2019), since revealing a period of abrupt decline in precipitation precisely during the Iron Age II (3000–2750 BP) that may have favored the presence of hemiones in the plains surrounding Tepe Hasanlu. A line of supporting evidences are coming from Neor Lake and Lake Almalou, 280 km and 85 km east of Lake Urmia, respectively. High-resolution multi-proxy peat record from Neor Lake indicated multiple dry periods centered at 3000 and 2750 years BP (Sharifi et al., 2015). Pollen record from Almalou Lake revealed decline in aquatic/subaquatic plants as well as in cultivated trees and anthropogenic herbs suggesting prevalence of dry conditions during the Iron Age II (3000–2750 BP) (Djamali et al., 2009).

From the metapodials of Shahr-e Qumis, analyzed using the Group1 combination, two donkeys, one horse, and one hybrid could be identified. These results highlight the significance of a medieval city located on the trade itineraries of the Silk Road, where pack animals were essential for the (trans)regional transfer of goods (Hansman & Stronach, 1974).

5 | CONCLUSIONS

The results presented in this study clearly show that the statistical methods of LDA, k-NN, and ANN applied here can be further improved by increasing the sample size of all four equid taxa. This can be performed by using securely identified specimens housed in Museum and Scientific Institution collections or by cross-referencing with additional methodologies, particularly ancient DNA, the results of which are beginning to become more widely available (Lepetz et al., 2021; Sharif et al., 2022). The statistical analyses presented in this study are performed with the open-access R programming language, including a large number of packages and codes that facilitate the manipulation of the data. The three classification methods of LDA, k-NN, and ANN are based on simple codes and algorithms that are user-friendly and not time-consuming. For the classification of equid mandibular cheek teeth and metapodials, we thus recommend this combination of methods.

This study demonstrates the validity of 2D and 3D GMM for identifying wild and domestic equids as well as the hybrids of the latter occurring in Holocene Eurasia and the importance of these methods for classifying taxonomically (pre)historic specimens found in archaeological sites. Selected because of their high survival rate in archaeological contexts, analysis of modern mandibular cheek teeth and metapodials demonstrated the existence of highly significant *shape* criteria allowing us to classify correctly the different equid taxa examined in this study. Our study shows that the accuracy of the specific attribution of the archaeological remains depends directly on the sample size and variability of the modern reference collection used as a baseline for comparison. This can be illustrated by increasing the sample size for donkeys and horse × donkey hybrids, for which identification has always been problematic. Addressing the importance of horses, donkeys, and mules in the economy of past societies necessitates correct specific identification with the least erroneous assignment between closely related taxa. The successful distinction of hemiones from domestic forms of equids is another important outcome of this study, which at the same time helps to reconstruct hunting activities through time.

AUTHOR CONTRIBUTIONS

Marjan Mashkour, Azadeh F. Mohaseb, Véra Eisenmann, and Joris Peters conceived and designed the research. Véra Eisenmann, Azadeh F. Mohaseb, Marjan Mashkour, Joris Peters, Michaela I. Zimmermann, Claude Guintard, and Elmira Mohandesan collected field data. Azadeh F. Mohaseb performed data analysis. Raphaël Cornette conducted the statistical analysis with Azadeh F. Mohaseb. Pauline Hanot commented the GMM statistical aspects. Thomas Cucchi commented on the visualization of GMM data. Azadeh F. Mohaseb, Hossein Davoudi, Rémi Berthon, and Marjan Mashkour provided archaeological samples and context. Azadeh F. Mohaseb, Marjan Mashkour, and Joris Peters drafted the manuscript. Marjan Mashkour and Joris Peters supervised the research and writing. Marjan Mashkour, Joris Peters, and Elmira Mohandesan funded the research. All authors provided drafts on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in InDoRES at https://doi.org/10.48579/PRO/A8AXWC.

ORCID

Azadeh F. Mohaseb https://orcid.org/0000-0003-3130-6603
Raphaël Cornette https://orcid.org/0000-0003-4182-4201
Michaela I. Zimmermann https://orcid.org/0000-0002-7888-6855
Hossein Davoudi https://orcid.org/0000-0002-5236-1444
Rémi Berthon https://orcid.org/0000-0003-1215-0965
Claude Guintard https://orcid.org/0000-0003-0195-8766
Thomas Cucchi https://orcid.org/0000-0001-6021-5001
Pauline Hanot https://orcid.org/0000-0001-9420-3949
Elmira Mohandesan https://orcid.org/0000-0002-4563-9276
Véra Eisenmann https://orcid.org/0000-0002-5010-3468
Joris Peters https://orcid.org/0000-0003-0894-2628
Marjan Mashkour https://orcid.org/0000-0003-3630-9459

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