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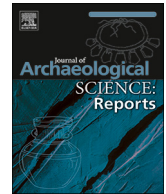
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Phenotypic diversity in Bronze Age pigs from the Alpine and Central Plateau regions of Switzerland

Miki Bopp-Ito^{a,*}, Thomas Cucchi^b, Allowen Evin^c, Barbara Stopp^a, Jörg Schibler^a

^a Integrative Prehistory and Archaeological Science, University of Basel, Spalenring 145, CH-4055, Basel, Switzerland

^b CNRS-Muséum National d'Histoire Naturelle, UMR 7209, Archéozoologie, Archéobotanique: Sociétés, Pratiques et Environnements, USM 303-Département Ecologie et Gestion de la Biodiversité, case postale 56 (bâtiment d'anatomie comparée), 55 rue Buffon, cedex 05 75231 Paris, France

^c Institut des Sciences de l'Evolution de Montpellier, UMR 5554 CNRS, Université de Montpellier, EPHE, IRD 226, Cirad 2 place Eugène Bataillon, CC065, cedex 5 34095 Montpellier, France

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ABSTRACT

Pig husbandry was one of the key components of Swiss Bronze Age communities. However, the extent of diversity within husbandry practices across these communities remains unclear, particularly for the Alpine and Swiss Central Plateau regions. Differences in tooth size and shape provide valuable proxies for exploring the history of pig populations and inferring changes to cultural and socio-economic behaviours. Thus, to explore geographical and chronological changes in pig husbandry in Bronze Age Switzerland, we tracked the phenotypic diversification of pig populations using the geometric morphometrics of the second and third lower molars as proxies. Our results confirmed the phenotypic homogeneity of Alpine pig populations during the Bronze Age, both in size and shape. Thus, strong homogeneity appeared to exist in the genetic make-up of pig herds in this area, which can probably be attributed to interactions among the local communities. Conversely, pig populations from the Swiss Central Plateau exhibited a greater diversification in shape between the eastern and western populations, indicating a lack of genetic interaction. In parallel, we observed a significant decline in the size of the east Central Plateau pig population during the Late Bronze Age, possibly due to shifts in husbandry practices induced by changes in forest management. Based on our findings, we hypothesise that geographical, topographical, environmental, and cultural factors influenced local pig husbandry practices and the phenotypic diversity of pig molars between regions in Bronze Age Switzerland. However, further investigations comparing Bronze Age pig populations over a broader scale are required, using genetic and isotopic markers to further test changes in husbandry practices and the genetic diversity.

1. Introduction

Pigs played an important role in the economy of the Swiss Bronze Age (Bopp-Ito, 2012; Plüss, 2011; Schibler, 2017; Schibler and Studer, 1998; Stopp, 2015). Based on the number of identified specimens, we know that pigs were the main domestic animals along with cattle, sheep, and goats. While the latter were exploited for meat, milk, and wool, or were used as working animals, most pigs were being slaughtered for meat at a young age (Hüster Plogmann and Schibler, 1997; Schibler, 2017); however, little is known about their husbandry practices. Furthermore, the phenotypic diversity of Swiss Bronze Age pigs over time and space, especially across the east and west parts of the Swiss Central Plateau (hereafter called Plateau) and Alpine regions, has

not previously been explored because osteometric data are limited due to heavy fragmentation and few adult individuals being available (Duval et al., 2015). Since the three regions previously mentioned are geographically, topographically, environmentally, and culturally divergent (Della Casa, 2013; Menotti, 2015a; Schibler, 2017; Reitmaier, 2012), they may also have required different husbandry practices (Schibler, 2017).

The earliest human presence in the Swiss Alpine region, up to over 2000 m above sea level (a.s.l.), was recorded during the Mesolithic (Cornelissen and Reitmaier, 2016; Hess et al., 2010). Human activity increased from the middle of the 4th millennium BC, the so called Copper Age (Late Neolithic), onwards (Della Casa, 2003). The number of settlements relevant to bronze production, copper mining activity,

Abbreviations: GMM, geometric morphometrics; CS, centroid size; GPA, Generalized Procrustes Approach; Plateau, Swiss Central Plateau; EBA, Early Bronze Age; MBA, Middle Bronze Age; LBA, Late Bronze Age; a.s.l., above sea level; RSFO, Rhine-Swiss-East France Urnfield culture (Rhin-Suisse-France orientale); IPAS, Integrative Prehistory and Archaeological Science

* Corresponding author.

E-mail addresses: miki.bopp@unibas.ch (M. Bopp-Ito), cucchi@mnhn.fr (T. Cucchi), allowen.evin@umontpellier.fr (A. Evin), barbara.stopp@unibas.ch (B. Stopp), joerg.schibler@unibas.ch (J. Schibler).

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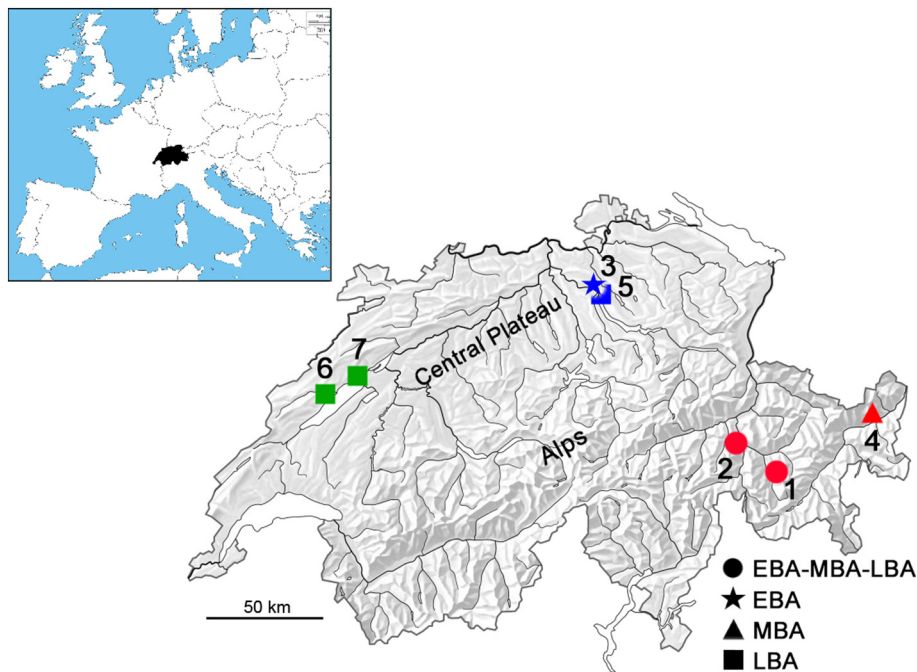


Fig. 1. Location of studied sites: numbers refer to the archaeological sites listed in Table 1. Red symbols (Nos. 1, 2, and 4) indicate Alpine sites, blue symbols (Nos. 3 and 5) indicate sites from the east Plateau, and green symbols (Nos. 6 and 7) indicate sites from the west Plateau. EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Archaeological samples used in the present study.

Region	Period	Map No.	Settlement	Sample size		Archaeozoological References
				M2	M3	
Alpine	LBA	1	Savognin-Padnal, Horizont B	7	16	Bopp-Ito, unpubl.
	LBA	2	Cresta-Cazis, Planum 14	1	2	Plüss, 2007
	MBA	1	Savognin-Padnal, Horizont C	3	7	Bopp-Ito, unpubl.
	MBA	1	Savognin-Padnal, Horizont D	15	21	Bopp-Ito, unpubl.
	MBA	2	Cresta-Cazis, Planum 10–12	9	15	Plüss, 2007
	MBA	4	Scuol-Avant Muglins	12	26	Rehazek, unpubl.
	EBA	1	Savognin-Padnal, Horizont E	1	3	Bopp-Ito, unpubl.
	EBA	2	Cresta-Cazis, Planum 1–5, 8	14	11	Plüss, 2007
			Total	62	101	
	West Plateau	LBA	6	Cortailod-Est	4	8
LBA		7	Hauterive-Champréveyres C 3	8	3	Studer, 1991
			Total	12	11	
East Plateau	LBA	5	Zürich-Alpenquai	9	10	Wettstein, 1924
	EBA	3	Zürich-Mozartstrasse, 1u & 1o	26	17	Hüster Plogmann and Schibler, 1997
			Total	35	27	
		Total	109	139		

“Map no.” corresponds to locations in Fig. 1. unpubl. = unpublished reference, Plateau = Central Plateau, EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age.

farming, and pasturing were expanded during the Early Bronze Age (EBA) due to the influx of immigrants from the north and south (Della Casa et al., 2016; Dietre et al., 2016; Jecker, 2015; Murbach-Wende, 2016; Rageth, 1986; Reitmaier, 2010, 2012; Schaer, 2003), immigrants who might have brought livestock with them (Bopp-Ito et al., 2018). This, so called, Inner Alpine Bronze Age culture continued until the Middle Bronze Age (MBA) (Rychner et al., 1998). The increase in human activity above the tree line induced the expansion of grasslands (Nicolussi, 2012) and the culture changed to the Rhine-Swiss-East France Urnfield (Rhin-Suisse-France orientale) (RSFO), Main-Schwaben, and Laugen-Melaun cultures during the Late Bronze Age (LBA) (Jennings, 2016; Rychner et al., 1998). The Alpine economy was developed by the intensification of supra-regional trading and traffic, bronze production, and dairy based pastoralism using vertical transhumance (Della Casa, 2007; Jecker, 2015; Jennings, 2015a; Rageth, 1986; Reitmaier, 2010, 2012; Reitmaier et al., 2013, 2017). Vertical transhumance played an especially important role in the economic

system of the Alpine region (Della Casa, 2013; Reitmaier et al., 2017) and deforestation for pastoralism was intensified (Dietre et al., 2016). Due to this, cattle became an even more important source of meat and the demand for cattle as working animals and for milk production increased (Bopp-Ito, 2012; Bopp-Ito et al., 2018; Plüss, 2011; Stopp, 2015); however, dairy activity has not been confirmed by lipid analysis (Carrer et al., 2016) at the Alpine sites discussed in this paper. Recent studies have provided new insights into cattle husbandry practices in the Alpine region (Bopp-Ito et al., 2018; Harmath et al., 2017; Reitmaier et al., 2017), although knowledge remains limited about pig husbandry practices.

In comparison, the lake shore settlements in the east and west Plateau regions were inhabited from approximately 4300 BC onwards, and the exploitation of cattle for dairy production, or for use as working power, began from the Middle Neolithic onwards (Ebersbach et al., 2012; Schibler, 2017). Some sites continued to be inhabited until the Bronze Age, even though major climatic crises arose (Arbogast et al.,

Table 2
Grouping of settlements and cultural background.

Map	Settlement	Dating	Dating	Group	Altitude	Culture	
No.		BC	References		(ca. m)		
1	Padnal H-B	1350/1300–900/800	C14	Rageth, 1986 & pers. com.	Alpine LBA	1223	RSFO, Main-Schwaben, Laugen-Melaun
2	Cazis P14	1350–1100/800	C14	Wyss, 2002	Alpine LBA	765	RSFO, Main-Schwaben, Laugen-Melaun
2	Cazis P14	1300–400	Typo.	Murbach-Wende, 2016	Alpine LBA		RSFO, Main-Schwaben, Laugen-Melaun
1	Padnal H-C	1450–1350/1300	C14	Rageth, 1986 & pers. com.	Alpine MBA		Inneralpine
1	Padnal H-D	1550–1450	C14	Rageth, 1986 & pers. com.	Alpine MBA		Inneralpine
2	Cazis P10–12	1800–1550	C14	Wyss, 2002	Alpine MBA		Inneralpine
2	Cazis P10–12	1750–1300	C14	Murbach-Wende, 2016	Alpine MBA		Inneralpine
4	Scuol	1400	C14	Seifert, M., pers. com.	Alpine MBA	1200	Inneralpine
1	Padnal H-E	1950/1900–1550	C14	Rageth, 1986 & pers. com.	Alpine EBA		Inneralpine
2	Cazis P1–5, 8	2400–1800	C14	Wyss, 2002	Alpine EBA		Inneralpine
2	Cazis P8	1850–1700	C14	Murbach-Wende, 2016	Alpine EBA		Inneralpine
2	Cazis P1–5	2000–1850	C14	Murbach-Wende, 2016	Alpine EBA		Inneralpine
6	Cortaillod	1010–955	Den.	Hochuli et al., 1998	W. P. LBA	400	RSFO (West Swiss group)
7	Champ	1054–1037	Den.	Hochuli et al., 1998	W. P. LBA	400	RSFO (West Swiss group)
5	Alpenquai	LBA	Typo.	Hochuli et al., 1998	E. P. LBA	400	RSFO (Central and East Swiss group)
3	Mozart	EBA	Typo.	Bleicher, 2011	E. P. EBA	404	Arbon

EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age, Typo. = Typology, Den. = Dendrochronology, pers. com. = personal communication, RSFO = Rhine-Swiss-East France Urnfield culture (Rhin-Suisse-France orientale), E. P. = East Plateau, W. P. = West Plateau, Cazis P = Planum, Padnal H = Horizont, Mozart = Zürich-Mozartstrasse, Alpenquai = Zürich Alpenquai, Champ. = Hauterive-Champréveyres, Cortaillod = Cortaillod-Est, Cazis = Cresta-Cazis, Padnal = Savognin-Padnal, Scuol = Scuol-Avant Muglins.

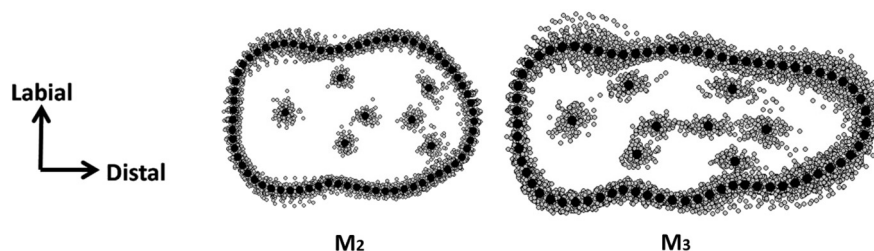


Fig. 2. Visualisation of the second (left image; M_2) and third (right image; M_3) lower molar coordinates of all specimens after superimposition.

2006; Schibler and Jacomet, 2010). Animal husbandry in the east and west Plateau regions was influenced by the different cultures and climatic conditions throughout the Neolithic and Bronze Age (Schibler, 2017; Stopp, 2015). The culture in the east and west Plateau regions changed to the RSFO culture during the LBA; however, the RSFO culture was still separated into the east and west Swiss groups (Jennings, 2016; Rychner et al., 1998), influencing the trade and exchange of both portable objects and immovable features (Jennings, 2015a). Environmental change occurred in the east Plateau region because of greater deforestation from the Late Neolithic onwards (Doppler et al., 2017), with deforestation intensifying during the LBA (Bleicher et al., 2013). Unfortunately, knowledge about deforestation in the west Plateau region is lacking due to an absence of studies. In parallel, agricultural technology improved with the production of new cereals such as spelt (Jacomet, 1998) and, as a consequence, the hunting of wild animals declined in comparison to the Neolithic period (Schibler, 2017).

Recent studies in the Alpine region have provided us with a large amount of zooarchaeological data from two sites with stratigraphic sequences from the EBA to the LBA: Cresta-Cazis (hereafter called Cazis) (Plüss, 2007, 2011), and Savognin-Padnal (hereafter called Padnal) (Bopp-Ito, 2012; Bopp-Ito et al., 2018), and a MBA site, Scuol-Avant Muglins (hereafter called Scuol) (Rehazek, unpublished). Thus, data from the Plateau sites could be supplemented with data from the Alpine sites, facilitating in-depth investigations of the chronological and regional diversification in pig phenotypes.

To investigate diversity in Swiss Bronze Age pigs, we used dental morphological diversity quantified with geometric morphometrics (GMM) (Bookstein, 1991, 1997; Gunz et al., 2005; Rohlf, 2000; Strauss and Bookstein, 1982; Zelditch et al., 2004). This approach has proven to be effective at differentiating pig populations (Cucchi et al., 2009,

2011, 2016; Duval et al., 2015; Evin et al., 2013, 2014, 2015a, 2015b, 2017; Ottoni et al., 2013). Although, it can be difficult to distinguish wild boars, the size of which was influenced by environmental factors (Albarella et al., 2009; Davis, 1981; Payne and Bull, 1989; Rowley-Conwy et al., 2012), from free-range domestic pigs because they regularly mated when moving freely through the forests (Frantz et al., 2015; Larson et al., 2007). However, these previous GMM studies on pigs revealed the phenotypic diversity within and between domestic, wild (including subspecies), captive wild, hybrid, and insular *Suidae*. Furthermore, teeth preserve well (e.g. Hüster Plogmann and Schibler, 1997) and are less affected by environmental variables than other body parts (Kassai et al., 2005; Laurikkala et al., 2003; Thesleff, 2006). Indeed, the cheek teeth of horses have recently been proven to carry a phylogenetic signal (Cucchi et al., 2017). The size and shape of pig teeth were influenced by the idiosyncratic cultural choices of local husbandry practices (Cucchi et al., 2016; Duval et al., 2015; Duval et al., unpublished). This study, therefore, aimed to assess the chronological and regional phenotypic differentiation in pig populations from Alpine and Plateau sites during the Bronze Age. The results were then applied to detect changes and differences in human–pig relationships relative to husbandry practices, and to analyse the economic and cultural interactions among human communities.

2. Materials and methods

The Bronze Age covers three successive chronological periods: EBA (2200–1600 BC), MBA (1600–1300 BC), and LBA (1300–800 BC) (Rychner, 1998). We divided the pig populations into three geographic regions; (1) the Alpine population, (2) the east Plateau population, and (3) the west Plateau population in what is now Switzerland (Fig. 1,

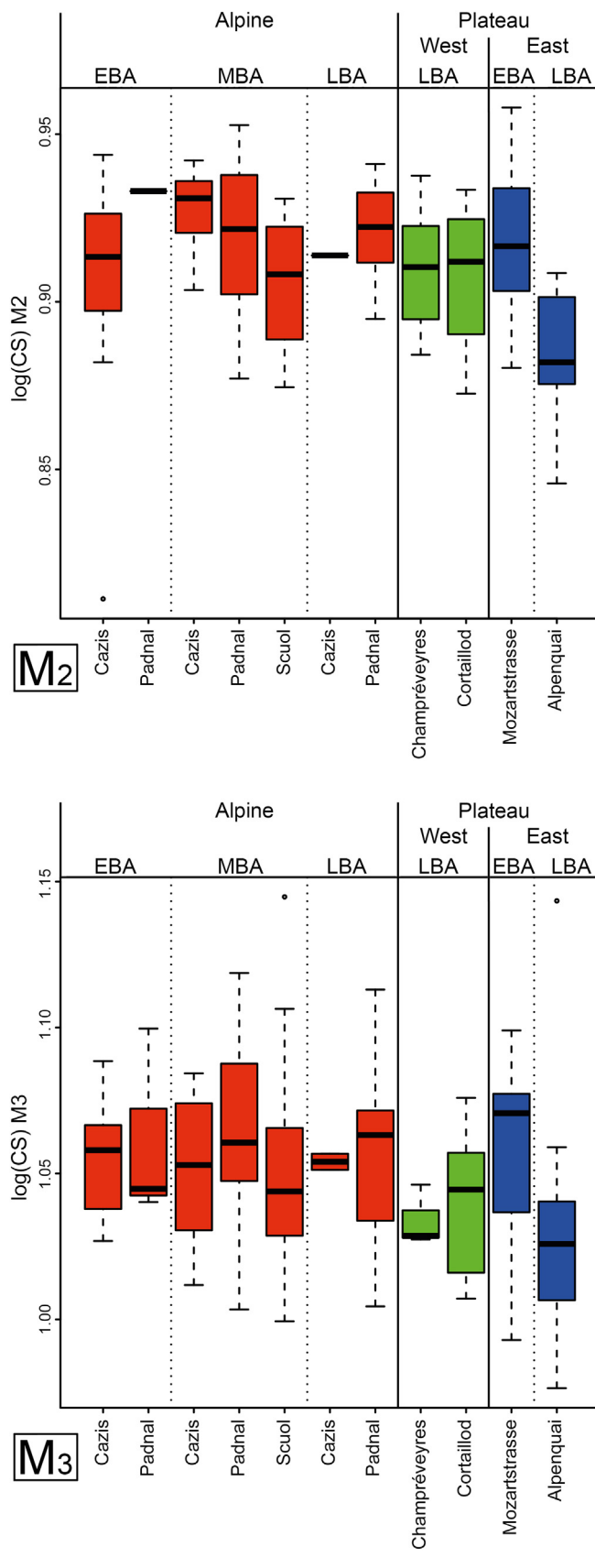


Fig. 3. Boxplots of the second (upper slide; M_2) and third (lower slide; M_3) lower molar centroid size variation. Plateau = Central Plateau, EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age, Cazis = Cresta-Cazis, Padnal = Savognin-Padnal, Scuol = Scuol-Avant Muglins, Champréveyres = Hauterive-Champréveyres, Cortailod = Cortailod-Est, Mozartstrasse = Zürich-Mozartstrasse, Alpenquai = Zürich-Alpenquai.

Table 1). The Alpine sites are located in the Alpine valleys approximately 750–1200 m a.s.l. (Table 2). Cazis and Padnal were inhabited during the Bronze Age and Scuol was inhabited during the MBA (Murbach-Wende, 2016; Rageth, 1986; Wyss, 2002; Seifert, Personal communication). The climatic influence on the Alpine samples used in this study is not known due to the lack of dendrochronology (Schibler, 2017).

The Plateau sites in this study were lake dwellings located at approximately 400 m a.s.l. (Table 2). Zürich-Mozartstrasse (hereafter called Mozartstrasse) at Lake Zurich in the east Plateau region was inhabited from the Early Neolithic to the EBA (Bleicher, 2011; Hüster Plogmann and Schibler, 1997). However, there is no dendrochronological dating for the EBA samples from Mozartstrasse used in this study (Hüster Plogmann and Schibler, 1997). Zürich-Alpenquai (hereafter called Alpenquai) (Wettstein, 1924) was one of the central trading sites in the east Plateau region during the LBA (Jennings, 2015a). Alpenquai was occupied throughout the Hallstatt B period (from ca. 1050 to 800 BC) and several layers were dated based on dendrochronology (Jennings, 2015b; Künzler Wagner, 2005; Mäder, 2001a, 2001b; Wiemann et al., 2012). However, since our samples came from a very early excavation by dredger (Jennings, 2015b) only typological dating was available. Cortailod-Est (Chaix, 1986), and especially Hauterive-Champréveyres (hereafter called Champréveyres) (Studer, 1991) at Lake Neuchâtel, were one of the largest trading sites in the west Plateau region (Jennings, 2015a). From both the east and west Plateau sites, only EBA and LBA data were available because the lake shores were abandoned due to climatic deterioration during the MBA (Della Casa, 2013; Menotti, 2015a, 2015b).

The permanent second (M_2) and third (M_3) lower molar teeth were used as phenotypic markers. Archaeological specimens were identified as domestic pigs using traditional biometry data (Albarella et al., 2009; Boessneck et al., 1963; Rowley-Conwy and Dobney, 2007; Rowley-Conwy et al., 2012) and the reference collection of the Institute of Integrative Prehistory and Archaeological Science (IPAS), University of Basel, Switzerland. However, a few specimens were difficult to identify as either domestic pigs or wild boars (or hybrids) because of an overlap in size (Evin et al., 2013, 2014); therefore, we could not completely exclude the possibility that our samples include a few wild boar (or hybrid) specimens. Only specimens from animals older than one year, based on teeth eruption and wear patterns (Habermehl, 1975; Horard-Herbin, 1997), were analysed in the present study. Detailed information about the samples is provided in Supplementary Table 1.

This study used GMM methods and statistical analyses following a standardized protocol described by Cucchi et al. (2011, 2016), Evin et al. (2013, 2015b), and references therein. Images were obtained with a 2D digital camera (Nikon D90 and D300S with a 60 mm Micro lens; Nikon Corporation, Tokyo, Japan). We acquired seven and eight landmarks on the occlusal surfaces of 109 M_2 and 139 M_3 respectively, and 70 semi-landmarks (both M_2 and M_3) according to Cucchi et al. (2011) and Evin et al. (2013) using tpsDig2 version 2.16 (Rohlf, 2010a) and tpsUtil version 1.53 (Rohlf, 2012). Generalized Procrustes analysis (GPA) was performed using the Procrustes distances approach to slide the semi-landmarks (Fig. 2) using tpsRelw version 1.49 (Rohlf, 2010b). The centroid size (CS) and shape variables (Procrustes coordinates) were obtained after the GPA.

We tested the heterogeneity of log-transformed CS between pig populations with a Kruskal-Wallis rank sum test and visualized the variation in size using boxplots. Pairwise comparisons of the populations were performed using multiple Wilcoxon rank tests by pooling the specimens by region and chronological phase.

Differences in shape were tested using multivariate analyses of variance (MANOVA), quantified by leave-one-out cross validation of discriminant analyses (canonical variate analysis), and were visualized by neighbour-joining networks based on Mahalanobis distances. Before multivariate analyses, the dimensionality of the shape data was reduced following Baylac and Friess (2005) by selecting the N first components

Table 3

Multi-test comparisons (p values) of the second (upper table; M_2) and third (lower table; M_3) lower molar centroid size between pig populations (pairwise Wilcoxon rank tests after Benjamini and Hochberg correction).

M_2	Alpine	Alpine	Alpine	East P	East P	West P
	EBA	MBA	LBA	EBA	LBA	LBA
Alpine EBA		0.479	0.428	0.289	< 0.01	0.719
Alpine MBA			0.792	0.847	< 0.001	0.230
Alpine LBA				0.984	< 0.01	0.305
East P EBA					< 0.001	0.155
East P LBA						< 0.05
West P LBA						

M_3	Alpine	Alpine	Alpine	East P	East P	West P
	EBA	MBA	LBA	EBA	LBA	LBA
Alpine EBA		0.831	1.000	0.681	< 0.05	< 0.05
Alpine MBA			0.912	0.573	< 0.05	< 0.05
Alpine LBA				0.503	< 0.05	0.092
East P EBA					0.059	0.066
East P LBA						0.387
West P LBA						

Significant p values are bold and highlighted. $\alpha = 0.05$.

P = Central Plateau, EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age, α = significant level.

of a principal component analysis that maximizes variability between the groups. Cross-validation percentages corresponded to the maximum value of the 95% confidence interval obtained for a balanced sample size between groups (100 iterations), as per Evin et al. (2013).

Differences were considered significant if $p < 0.05$ (significance level $\alpha = 0.05$), where the significance of the p values was examined after adjustment for multi-test comparisons following the methods described by Benjamini and Hochberg (1995).

Statistical analyses were performed using R v 2.13.1 (R Development Core Team, 2011), with the packages ‘ape’ (Paradis et al., 2004), ‘geomorph’ (Adams and Otárola-Castillo, 2013), and ‘Rmorph’ (Baylac, 2012).

3. Results

3.1. Diversity in the molar size of pig populations

When the specimens were analysed by site and period (Fig. 3), only the M_2 size differed between populations (for M_2 : $X^2 = 24.2$, $p = 0.007$, for M_3 : $X^2 = 15.9$, $p = 0.1$). However, when specimens were divided into six populations by region and period, both the M_2 ($X^2 = 16.5$, $p = 0.006$) and M_3 ($X^2 = 11.2$, $p = 0.048$) showed significant differences. Pairwise comparisons (Table 3) revealed that the M_2 size of the east Plateau LBA population was significantly smaller than that of all other populations (Fig. 3). These findings also show that the molar size of the Alpine populations did not change throughout the Bronze Age, but that molar size in the east Plateau populations declined from the EBA to the LBA.

3.2. Diversity in the molar shape of pig populations

Regional and chronological populations (specimens divided by region and period) differed with respect to both their M_2 ($F [60, 480] = 2.62$, $p = 7e-9$) and M_3 ($F [70, 620] = 2.1$, $p = 9e-07$) shapes. Discriminant analyses a posteriori classified only 45.8% of the M_2 and 41.75% of the M_3 to the correct group. These low percentages are the result of a notable overlap of all Alpine and east Plateau LBA populations.

Unrooted neighbour-joining networks based on Mahalanobis distances showed a structuration of the variation in molar shape for both M_2 and M_3 (Fig. 4). The east Plateau and Alpine populations exhibited an important phenotypic distance for M_2 during the EBA. However, the

distance between these populations decreased during the LBA. Compared to the significant distance between the east Plateau EBA and the east Plateau LBA populations, no significant difference was observed between the Alpine populations. M_3 , on the other hand, displays a strong geographic signal, which clearly separates the three regional pig populations.

4. Discussion

Our analyses revealed an overall size homogeneity of the teeth of Bronze Age pigs from Switzerland. However, we did observe one pig population with smaller molars in the east Plateau region during the LBA at the site of Alpenquai, for which there are several possible explanations.

Natural factors influence the size of wild boars (Albarella et al., 2009; Rowley-Conwy et al., 2012), including climate (Davis, 1981; Payne and Bull, 1989). Therefore, domestic Alpenquai pigs would also have been influenced by these environmental factors if they were kept in the forest. Major climate deterioration around lake settlements in both the east and west Plateau regions occurred during the final stage of the LBA (Menotti, 2015a, 2015b). Since the west Plateau settlements were occupied before the final stage of the LBA (cf. Table 2), the molar size of the pig populations at those sites was probably not yet influenced by the climate deterioration. However, it is not known if the Alpenquai samples used in this study (Wettstein, 1924) belong to the older or younger Hallstatt B period during the LBA (e.g. Mäder, 2001a, 2001b), due to the lack of dendrochronological dating when they were excavated in the early 20th century. Consequently, we cannot completely exclude the possibility of climatic effects on the Alpenquai samples. However, the climate during the LBA in the east and west Plateau regions might have been favourable for the duration of the lake side settlements (Menotti, 2015b). Therefore, the smaller molar size of the Alpenquai pigs may be due to other factors.

Changes in husbandry practices, such as the reduction of nutrient supply (Tonge and McCance, 1965) or confinement during an animal's growth, could act as environmental perturbations that affect the developmental process, causing a decline in the size of animals (Cucchi et al., 2016). Such changes in husbandry practices could have been induced by the decline of the forest cover close to the Lake Zurich settlements. The intensification of food management during the LBA (Bleicher et al., 2013) might have forced pig herders from Alpenquai to

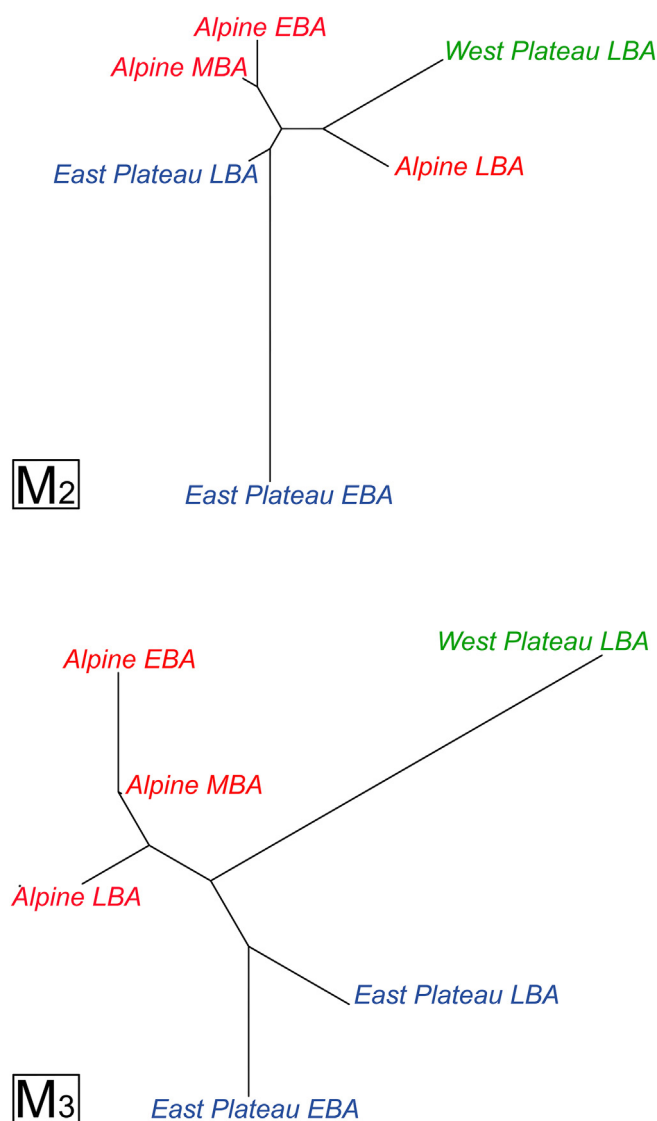


Fig. 4. Unrooted neighbour-joining networks based on Mahalanobis distances of the second (upper slide; M₂) and third (lower slide; M₃) lower molar divided by region and period. Plateau = Central Plateau, EBA = Early Bronze Age, MBA = Middle Bronze Age, LBA = Late Bronze Age.

change from forest to farmyard husbandry. In fact, small ruminants at Alpenquai are postulated to have been kept indoors at times (Kühn and Heitz-Weniger, 2015). The lack of size reduction in LBA Alpenquai cattle (Bopp-Ito et al., 2018) showed that Alpenquai people did not change their husbandry practices or the environment for cattle, but they might have changed pig husbandry practices, and perhaps sheep and goat husbandry practices, in order to keep them on the settlement as farmyard animals. However, further studies exploring pig diet are necessary. In addition, the use of biochemical indicators, such as isotopic analyses (Doppler et al., 2017; Balasse et al., 2016; Cucchi et al., 2016; Frémondeau et al., 2012; Reitmaier et al., 2017) would be helpful to refine our hypothesis.

The M₂ results revealed no significant changes in shape over time among the Alpine populations. However, the M₂ results indicated a divergence in shape between the EBA and LBA for the east Plateau pig populations. The history of the west Plateau population is not known, due to the lack of zooarchaeological material from the EBA. Considering that variation in M₂ shape reflects changes in the history of pig populations (Cucchi et al., 2011, 2016), several plausible explanations for the change in shape of M₂ between the east Plateau EBA and

LBA populations are available. Different choices, such as free-ranging forest or farmyard husbandry could have influenced molar size and shape (Cucchi et al., 2016). Alternatively, pigs from the east Plateau EBA might have been genetically different from all other populations. However, our hypotheses are again based on limited information from the east Plateau region, and further evidence from genetic (Evin et al., 2015a; Meiri et al., 2013; Ottoni et al., 2013) approaches are necessary to support this hypothesis.

Contrary to the results observed for M₂, M₃ shows a clear geographic signal clustering the pig populations into three regions. In particular, the lack of change in molar size and shape of Alpine pigs indicates that the Alpine community relied on stable populations of pigs, suggesting the retention of the same breeding strategy through time. Two plausible explanations exist for the unchanged phenotype of Alpine pig teeth. One explanation is that continuous immigrants into the Alpine region (Jecker, 2015; Reitmaier et al., 2017) brought the same phenotypic pig populations with them. Alternatively, the MBA and LBA immigrants continued to use EBA pigs as the original prototype for breeding, as, unlike the EBA immigrants, they brought little or no animals with them. This autonomy in pig husbandry at the Alpine sites was also documented for cattle husbandry, which showed no size reduction of the animals (Bopp-Ito et al., 2018). Furthermore, the decline of mitochondrial DNA haplotypes of cattle at the Alpine site of Padnal (Harmath et al., 2017) suggests that breeding occurred within the limited cattle population of the Alpine region. The same might have happened to the pig population. However, further studies are required to confirm this hypothesis.

The phenotype in the west Plateau LBA pig population is noticeably different to that of the east Plateau and the Alpine populations. A lack of genetic interaction among these three regional pig populations might have occurred due to the topographical, geographical, and environmental divergence, and different cultural traditions between the Alpine and Plateau regions, as well as between east and west Plateau regions (e.g. Della Casa, 2013; Jennings, 2015a; Menotti, 2015a, 2015b; Reitmaier, 2012). These regional differences influenced to animal husbandry practices (e.g. Bopp-Ito et al., 2018; Cucchi et al., 2016; Duval et al., 2015; Plüss, 2011; Schibler, 2017; Schibler and Studer, 1998; Stopp, 2015). We hypothesise that geographical, topographical, environmental, and cultural factors probably influenced local pig husbandry practices and the phenotypic diversity of pig molars between regions (Cucchi et al., 2016; Duval et al., 2015).

5. Conclusions

Analysis of the phenotypic diversification of molar size and shape proxies revealed changes in pig husbandry in Bronze Age Switzerland, demonstrating that husbandry choices were influenced by different geographical, topographical, environmental, and cultural situations between three regions. Chronological continuity within the Alpine region suggests the stability of pig husbandry practices and the close interrelationship of human communities in this region. Conversely, the Plateau region showed the greater phenotypic diversity over time and space, possibly due to the more open topographical situation than the Alpine region and different cultural traditions between east and west Plateau human communities. The small molars of LBA east Plateau pig population might be due to the strong impact of deforestation on pig husbandry practices. However, a broader study using comparative materials, primarily from eastern and western Switzerland is required, alongside genetic and isotopic information, in order to explore these trends further.

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