

REVIEW

Historical distribution, habitat requirements and feeding ecology of the genus *Equus* (Perissodactyla)

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ABSTRACT

1. Dietary traits of nine extant *Equus* species (*E. africanus*, *E. ferus*, *E. grevyi*, *E. hartmannae*, *E. hemionus*, *E. khur*, *E. kiang*, *E. quagga* and *E. zebra*) were reconstructed and ranked in a continuum reflecting the relative proportions of abrasion and attrition.

2. In order to match them automatically with climatic data, localities were referenced within a 2° worldwide grid system using geographical information system software. The mesowear score was used as a proxy variable to test the covariance of diet with mean annual precipitation, evapotranspiration, mean annual climatic water balance and mean annual temperature.

3. Seven of the nine equid species presented mesowear signatures, indicating a grass-dominated diet, and we found interspecific as well as intraspecific variability. Non-gramineous food components shifted the equilibrium towards the attrition-dominated end in *E. africanus* and *E. khur*, indicating an intermediate diet. Especially in *E. zebra*, additional sources of exogenous abrasives (grit and soil) might increase dietary abrasiveness. In *E. quagga*, dietary flexibility and the capability to cope with increased abrasiveness are considered keystone factors allowing its large geographical range.

4. The broad, species-specific range of climate parameters associated with the habitats was used to define the thresholds of the species' feeding niches. Our data suggest that climate as represented by the variables we used does not, in the first instance, relate to the tooth wear signature of equids.

5. We thus conclude that the tooth wear signature is more specific to the feeding strategy and should be regarded a dietary trait rather than an immediate imprint of climate. However, tooth wear can be used to infer local dietary traits and might therefore become an important tool in conservation management.

Keywords: abiotic habitat variables, dietary adaptation, horse, resource partitioning, wild ass

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INTRODUCTION

Following the classification of Groves (2002), nine extant species are recognized within the genus *Equus*: the African taxa *Equus africanus* (African wild ass), *E. grevyi* (Grevy's zebra), *E. quagga* (plains zebra), *E. hartmannae* (Hartmann's mountain zebra) and *E. zebra* (cape mountain zebra); and the Asian taxa *E. ferus* (wild horse), *E. hemionus* (Asiatic wild ass, dschiggetai), *E. kiang* (kiang) and *E. khur* (Indian wild Ass, khur).

The geographical ranges of all of these species have declined significantly during the past 200 years and are increasingly fragmented compared with the ranges at the beginning of the 19th century (Heptner et al. 1966, Duncan 1992, Bauer et al. 1994, Neumann-Denzau & Denzau 1999, Moehlman 2002). Bauer et al. (1994) consider competitive exclusion and specific adaptation to be the major determinants of the extant distribution patterns. Contact areas of distributions between extant equid species currently occur in southern and western Africa (*E. zebra* and *E. quagga*), in eastern Africa (*E. quagga*, *E. grevyi* and *E. africanus*) and in central Asia (*E. ferus* and *E. hemionus*).

Equids are hind-gut fermenters and occur in steppe, semi-desert and desert environments. They are well adapted to low-quality food (Janis 1976, Neumann-Denzau & Denzau 1999), mainly digesting large quantities of grass (Nowak 1991). Despite these similarities among species, each taxon has a specific spectrum of dietary sources. A total of 295 gramineous, herbaceous and shrub-like plant taxa have been described as food plants for *Equus* species (Bannikov 1948, 1958, 1981, Ali 1949, Vesey-Fitzgerald 1965, Heptner et al. 1966, Casebeer & Koss 1970, Solomatin 1973, Kuper 1978, Grobler 1983, Shah 1993, Prasad et al. 1994, Harris & Miller 1995, Aganga & Tsopito 1998, Pereladova et al. 1999, Singh 1999, Roeder 2000, Lengger et al. 2007, Yin et al. 2007). *E. hartmannae*, *E. africanus* and *E. ferus* feed on large quantities of dicotyledonous herbs and shrubs (Kingdon 1979, Pereladova et al. 1999, Roeder 2000), while mostly monocotyledons are consumed by the other species in this genus.

Tooth wear in herbivorous ungulates is related to the two major factors: abrasion (tooth-food contact) and attrition (tooth-tooth contact). Animals with abrasion-dominated tooth wear have blunter cusps with lower relief, and animals with attrition-dominated tooth wear develop sharper cusps with higher reliefs. Phytolith-rich plants, such as monocotyledons, are proposed to be highly abrasive, while most dicotyledonous plants, such as shrubs and herbs, are less so (Kaufman et al. 1985, Carnelli et al. 2001). Additionally, exogenous grit results in an abrasive wear pattern, but the contribution of endogenous and exogenous abrasives to total abrasion is controversial (Merceron et al. 2007, Sanson et al. 2007, Kaiser et al. 2009, Hummel et al. 2011). The mesowear method (Fortelius & Solounias 2000) thus measures the relative abrasiveness of a diet, irrespective of its origin, induced by both inherent abrasives of food items and the content of abrasive exogenous grit (Kaiser & Rössner 2007).

Local climatic conditions should result in specific feeding behaviours of individuals. Within a local population, these behaviours and the climatic conditions should be reflected as a heuristic indicator in the measured mesowear signal (Kaiser & Schulz 2006). It should, thus, be possible to track environmental conditions using mesowear signatures as an environmental proxy (Kaiser 2003, 2009, Kaiser & Rössner 2007, Schulz et al. 2007). The mesowear signature has been used as a species-specific characteristic, mainly to assign species to a feeding-type category. In this practice, the

probability that the mesowear signal also reflects characteristics of the habitat such as aridity or dustiness, which may also be species specific, is disregarded. In addition, both living in certain habitats and eating certain foods may be characteristics that vary between individuals or subpopulations of a species. In this respect, the mesowear signal can be used – as can many other morphological or physiological proxies – as a measure of the phenotypic flexibility of a species. Only a few approaches take into account the influence of both local conditions (Rivals et al. 2010) and intraspecific variability in feeding behaviour (Rivals et al. 2009).

Mesowear signatures in extinct horses suggest that their diets were influenced by the Cenozoic climate and its impact on vegetation and habitat structure (Mihlbachler et al. 2011). Of extant equids, mesowear signatures have thus far only been evaluated in *E. grevyi*, *E. quagga* (Fortelius & Solounias 2000, Kaiser & Solounias 2003, Kaiser & Schulz 2006) and *E. hemionus* (Schulz et al. 2007). Fortelius and Solounias (2000) employed *E. grevyi* and *E. quagga* as comparative species in their initial mesowear analysis of 64 extant ungulates and recognized a typical grazing trait in both species.

Mesowear signatures are sensitive to changes in habitat conditions and are used to track environmental and dietary changes, as well as habitat fragmentation in Holocene environments (Schulz & Kaiser 2007). Habitat fragmentation is often the cause of species becoming threatened or endangered, since the existence of a viable habitat is critical to the survival of any species (Rosenzweig 1995). The conservation status (Anonymous 2009) of the equid species is as follows: critically endangered (*E. africanus*), endangered (*E. ferus*, *E. grevyi* and *E. hemionus/khur*), vulnerable (*E. zebra*) and least concern (*E. kiang* and *E. quagga*), so identifying contemporary environmental and dietary changes is of great interest for conservation.

We aimed to evaluate variability and flexibility in the mesowear signatures of the extant Equidae. We examined the relationship between mesowear signatures and habitat variables, and explored how this relationship might suggest climate-related differences in the feeding ecology of extant equids. As a prerequisite for hypothesis testing, we established a specific signature of climate-driven habitat parameters [mean annual precipitation (MAP), mean annual evapotranspiration (ETP), mean annual climatic water balance (KW) and mean annual temperature (T)] associated with the geographical range of each equid species. We tested the hypothesis that the mesowear signature of each species reflects abiotic parameters, such as climatic variables, which impact the abrasiveness of the diet. Therefore, we established the thresholds of the abiotic parameters as well as of the mesowear signature at the species and subspecies levels. In addition, wear signatures tracking feeding history were applied to short time-frame analyses of endangered species in order to track changes in food choice. This method could be a helpful tool in conservation management.

METHODS

Linking geographical data with tooth wear data

Geographical information system software (ArcView GIS 3.2; ESRI Inc., Redlands, California, USA) was used to link the geographical data of sampling localities with climatic data. This required specimens with distinct locality data from museum catalogues; we transferred these data to decimal degree coordinates using printed resources (Andree 1899, Castiglioni 1987) and digital resources (<http://www>.

fallingrain.com, <http://earth-info.nga.mil/gns/html/>). To meet modelling requirements, geographical data generally must be in a grid format or refer to a specified area or region or to a linear feature (e.g. a river) or reference point (a named locality or landmark). Locality information from museum catalogues proved to be very heterogeneous in this respect, so data quality had to be evaluated thoroughly, and only localities with <math><100\text{km}^2</math> accuracy were included. Therefore, we developed a new method to match localities with climatic data automatically by referencing localities within a 2° worldwide grid system using ArcView (2° grid method). We are aware of the risk of overweighting data from areas with only a few localities and therefore excluded all grid cells with fewer than five localities. Area-weighted means of climatic variables were calculated for 2° grid cells with five or more localities. Species summary data (mean, median, standard deviation and minimum and maximum values of climatic variables) were generated for all grid cells where a species was recorded to occur.

Climatic data at a resolution of 30 angular seconds were obtained from the Shuttle Radar Topography Mission (<http://srtm.usgs.gov>). MAP (in millimetres) and T (in °C) were retrieved from the United Nations International Institute for Applied Systems Analysis (Leemans & Cramer 1991) program. Data were only available between the years 1961 and 1990. We consider this to be an adequate core period of the sampling interval of the material, which was collected during the 159 years between 1846 and 2005. Predicted evapotranspiration (ETP, in millimetres, after the Penman–Montheith method) came from the International Institute of Applied System Analysis and the Food and Agriculture Organization of the United Nations (<http://www.iiasa.ac.at/> and <http://www.fao.org/geonetwork/srv/en/main.search>). The KW (in millimetres) was calculated as the difference between MAP and ETP (according to DIN 4049-3, Anonymous 1994) and is an indicator of aridity, as described by Hupfer and Kuttler (2005).

Sample structure and mesowear scoring

Fortelius and Solounias (2000) devised the mesowear method to evaluate the dental wear equilibrium, as established by prolonged cumulative dental wear that represents a comparatively long period of the dietary history of an individual animal. Refinements of this method were reported by Kaiser and Fortelius (2003), Kaiser et al. (2009) and Merceron et al. (2007). Only adult specimens in which the last molar is in occlusion and the first molar (M1) retains an occlusal shape similar to the second molar (M2) are examined.

Fortelius and Solounias (2000) restricted their study by using only the upper M2. Here, we include the upper fourth premolar, the M1, the M2 and the third upper molar, as suggested by Kaiser and Solounias (2003). The method reduces ungulate tooth wear to two variables: occlusal relief and cusp shape. Occlusal relief is classified as high or low, depending on how high the cusps rise above the valley between them. The second mesowear variable, cusp shape, includes three attributes: sharp, round and blunt, according to the degree of facet development.

Two approaches of mesowear analysis were applied: (i) the percentages of mesowear variable frequencies (%high, %sharp and %blunt) in samples from each species were calculated and cluster analyses performed (Euclidean distance, complete linkage and furthest neighbours), as described by Fortelius and Solounias (2000) and (ii) following similar methods to Mihlbachler and Solounias (2006), Rivals and Semprebon (2006), Rivals et al. (2007), Croft and Weinstein (2008) and Kaiser

et al. (2009), a mesowear score value was computed for each sample. Following Kaiser et al. (2009), individual molar cusp shape and relief scores were converted to single mesowear scores as follows: a combination of high relief and sharp cusps was assigned a score of 0; a combination of high relief and rounded cusps was assigned a score of 1; a combination of low relief and rounded cusps was assigned a score of 3; a combination of low relief and sharp cusps was assigned a score of 2; and a combination of low relief and blunt cusps was assigned a score of 4. Mesowear scores for each individual within a sample were then averaged. Teeth from young and old adult individuals were discarded from the sample because mesowear is sensitive to the age of individuals (Fortelius & Solounias 2000, Schulz et al. 2007). To produce a comparative data set related to the mesowear signature classification of both approaches, we followed Fortelius and Solounias (2000) and Kaiser and Solounias (2003) and used a set of 2007 wild-shot adult ungulate specimens representing 48 extant species classified in the conservative classification of species into dietary categories such as grazers, browsers or intermediate feeders. The dietary classification scheme of Fortelius and Solounias (2000) is applied using the data set indicated by the variable classes 'typical of its dietary class' and 'no particular class'.

Maxillary teeth of 704 individuals representing nine extant equid species were investigated (Table 1). To exclude any human influences on the habitat selection of each equid species, only wild animals were included in the analyses. In case of *E. ferus*, we follow the recommendation of the International Commission of Zoological Nomenclature (Anonymous 2003) and refer explicitly to the wild taxon *E. ferus przewalskii*. Each specimen is represented by one upper tooth row (either the right or the left side, depending on which was better preserved). Specimens derived from 558 geo-referenced sampling localities (N-lo in Table 1) and are represented by the following individual numbers (N-in in Table 1): for the African species, *E. africanus* N-in = 8, *E. grevyi* N-in = 54, *E. hartmannae* N-in = 117, *E. quagga* N-in = 288 and *E. zebra* N-in = 31 and for the Asian species, *E. ferus* N-in = 15, *E. hemionus* N-in = 152, *E. kiang* N-in = 32 and *E. khur* N-in = 5. For collection localities, see Fig. 1. The material analyzed is housed at the following collections: Museum für Naturkunde Berlin, Naturmuseum Senckenberg Frankfurt am Main, Zoologisches Museum Hamburg, Museum für Haustierkunde Halle/Saale, Zoologisches Museum Hamburg, Natural History Museum London, Bayerische Staatssammlung München, American Museum of Natural History New York, Smithsonian Museum Washington, Naturalis Leiden, Muséum national de l'Histoire naturelle Paris, Naturhistorisches Museum Bern, Zoological Museum Moscow, Russian Academy of Science St. Petersburg, Naturhistorisches Museum Wien, National Museum Windhoek, Etosha National Park Okaukuejo, Transvaal Museum Pretoria and the Private Collection of Katharina Hecker in Pretoria. Additionally, three skulls of carcasses from a reintroduced *E. ferus przewalskii* population in Hustai Nuruu, Mongolia, were scored in the field and included. To avoid intra-observer error, scoring was only performed by the first author. Taxa with fewer than 25 individuals per sample were excluded.

E. quagga is the only extinct equid species which was sympatric with other equids (*E. grevyi*, *E. hartmannae* and *E. zebra*). In order to test for interspecific niche separation, the nonparametric multiple comparison *H*-test (after Kruskal & Wallis 1952) was used to carry out multiple variance analyses of the values of the grid pattern-weighted climatic variables (MAP, ETP, KW and T). The aim was to identify climatic variables limiting the geographical range.

Table 1. Mesowear and climate data of the *Equus* taxa

Taxon	%H	%S	%B	SCORE	SD	N-lo	N-te	N-in	MAP	SD	ETP	SD	KW	SD	T	SD
<i>Equus africanus</i>	66.7	29.3	12.5	1.5	1.38	8	30	8	145	189.30	741	65.42	-588	235.35	27.5	2.81
<i>E. a. somaliensis</i>	100	25	0	0.8	0.50	2	7	3	102	0	823	0	-721	0	27.7	0
<i>E. a. africanus</i>	50	16.7	25	2.1	1.44	3	12	3	487	172.63	699	32.33	-213	139.72	27.5	0.17
<i>Equus ferus przewalskii</i>	58.1	9.3	11.6	1.9	1.25	12	50	15	221	72.75	286	35.15	-68	100.03	-1.3	2.26
<i>E. f. przewalskii</i> (reintroduced)	62.5	0	12.5	1.9	1.25	1	10	3	222	NA	286	NA	-64	NA	-1.4	NA
<i>E. f. przewalskii</i> (extinct)	63.6	4.5	0	1.7	0.95	7	26	8	119	83.14	319	42.80	-185	116.84	1.5	2.58
<i>E. f. gmelin</i>	100	60	0	0.4	0.55	2	6	2	605	0	220	0	385	0	7.2	0
<i>Equus grevyi</i>	52.7	6.6	8.6	2.0	1.14	47	210	54	608	225.50	636	67.89	-28	272.55	21.8	3.14
<i>Equus hartmannae</i>	48.8	2.6	16.5	2.2	1.23	112	449	117	319	129.68	546	32.03	-227	148.40	18.0	1.09
<i>Equus hemionus</i>	56.5	8.3	8.3	1.9	1.19	125	474	152	116	67.91	375	65.66	-259	80.05	4.6	5.03
<i>E. h. onager</i>	50	0	12.5	2.1	1.25	3	11	3	100	51.96	470	19.63	-370	32.33	17.1	0.69
<i>E. h. kulan</i>	69.1	18.2	14.5	1.6	1.26	18	66	23	238	13.91	517	5.89	-279	20.03	15.9	0.73
<i>E. h. hemionus</i>	53.1	6.9	5.6	1.9	1.15	89	348	90	116	83.58	375	25.50	-259	88.30	4.6	1.96
<i>E. h. blanfordi</i>	75	25	25	1.5	1.73	1	4	1	181	NA	565	NA	-385	NA	23.8	NA
<i>Equus khur</i>	65	30	5	1.5	1.10	5	20	5	427	97.87	657	8.62	-230	106.49	27.7	0.20
<i>Equus kiang</i>	55.7	7.9	6.8	1.9	1.16	28	100	32	308	336.41	288	38.98	15	335.74	-2.1	4.47
<i>Equus quagga</i>	49.1	7.2	13.3	2.1	1.23	194	1116	288	775	310.34	535	60.65	213	338.10	20.6	2.34
<i>E. q. antiquorum</i>	45.1	1.8	11	2.2	1.15	34	130	16	361	75.81	547	10.01	-185	83.11	17.3	2.35
<i>E. q. zambesiensis</i>	76.5	20	0	1.3	0.98	5	8	6	900	0	498	0	402	0	20.6	0
<i>E. q. crawshayi</i>	61.3	12.9	16.1	1.8	1.33	16	32	7	819	115.73	546	30.50	280	144.75	22.0	0.90
<i>E. q. boehmi</i>	57.7	7.7	9.7	1.9	1.21	82	6	93	1013	289.63	554	60.91	465	336.61	20.6	2.21
<i>E. q. quagga</i>	100	50	0	0.5	0.58	1	8	2	357	NA	514	NA	-157	NA	14.9	NA
<i>Equus zebra</i>	31.4	12.9	30.6	2.6	1.26	27	105	31	464	212.84	507	17.10	-29	226.07	16.5	3.64

%H, percentage of high occlusal relief; %S, percentage of sharp cusps; %B, percentage of blunt cusps; SCORE, mesowear score value; N-te, number of dental specimens (fourth premolar, first, second and third upper molar); N-in, number of individuals; N-lo, number of localities representing the taxon; MAP, mean annual precipitation; ETP, mean annual evaporation; KW, mean annual climatic water balance; T, mean annual temperature; SD, standard deviation; NA, data not available.

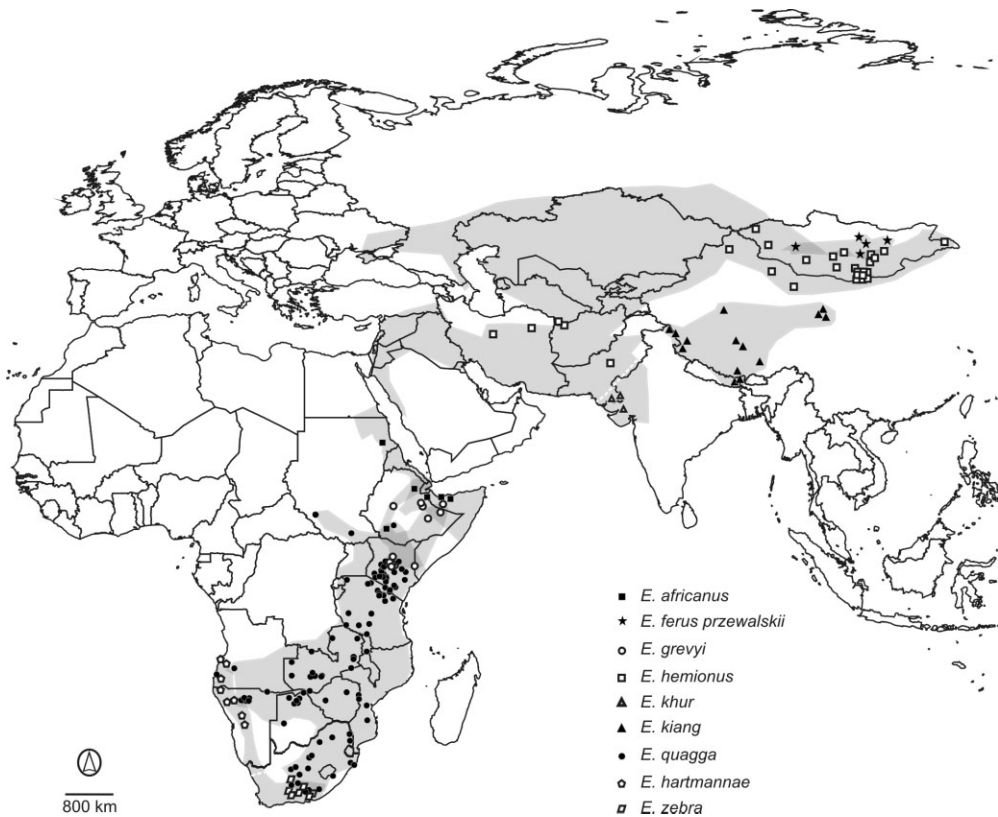


Fig. 1. Sampling localities and historic geographical ranges of *Equus*. The *Equus* sampling localities are indicated by symbols. The historic geographical ranges of the equid taxa are grey-shaded areas (after Heptner et al. 1966, Moehlman 2002, Neumann-Denzau & Denzau 1999).

Linear regressions with ordinary least squares were used to explore the effects of the climate factors on the mesowear variables (occlusal relief and cusp shape) in *Equus* taxa. Statistical analyses were conducted using Systat 12.0 (SYSTAT Software Inc., Richmond, California, USA).

RESULTS

Habitat settings

The sampling localities represent three of the six floristic kingdoms (Good 1947): the Holarctic, the Palaeotropical and the Cape floristic kingdom, and thus reflect the known distribution of the genus *Equus* (Fig. 1). The climate classification scheme of W. P. Koeppen and R. Geiger after Kottek et al. (2006) is used to classify climate conditions in the areas of species overlap or in contact areas of distributions. The following contact areas (Fig. 1) and climate classifications (Kottek et al. 2006) are evident in Africa: *E. africanus* and *E. grevyi* are in contact in Ethiopia, and the climate at the contact zone is characterized as arid steppe; *E. grevyi* and *E. quagga* are in contact in Kenya; the climate is equatorial steppe; *E. quagga* and *E. hartmannae* are in contact in the arid steppe climate of Namibia; and *E. quagga* and *E. zebra* have contact areas in the arid steppe climate of South Africa. In Asia, a contact zone or overlap of distribution is detected only for *E. ferus* and *E. hemionus* in the arid steppe environment of Mongolia.

Climate data, related to the localities and calculated according to the 2° grid method to evaluate the range of habitat settings of each species (Table 1), indicate the following species-specific habitat preferences: *E. africanus* occurs in areas with extremely hot and very dry climatic conditions ($T = 27.5\text{ }^{\circ}\text{C}$, $\text{MAP} = 145\text{mm}$, $\text{KW} = -588\text{mm}$), whereas all of the remaining taxa are associated with more temperate climates with higher MAP and lower T values (*E. hartmannae* $T = 18\text{ }^{\circ}\text{C}$, $\text{MAP} = 319\text{mm}$, $\text{KW} = -227\text{mm}$; *E. zebra* $T = 16.5\text{ }^{\circ}\text{C}$, $\text{MAP} = 464\text{mm}$, $\text{KW} = -29\text{mm}$; *E. grevyi* $T = 21.8\text{ }^{\circ}\text{C}$, $\text{MAP} = 608\text{mm}$, $\text{KW} = -28\text{mm}$). The highest MAP and KW values are observed in the habitats of *E. quagga* ($T = 20.6\text{ }^{\circ}\text{C}$, $\text{MAP} = 775\text{mm}$, $\text{KW} = 213\text{mm}$), indicating that this species experiences the most humid habitat conditions within the genus. The ranges of MAP in the habitats of the Asian species ($\text{MAP}_{\text{eqkhu}} - \text{MAP}_{\text{eqhem}} = 310\text{mm}$) are smaller than in the African species ($\text{MAP}_{\text{eqqua}} - \text{MAP}_{\text{eqafr}} = 630\text{mm}$), but the temperature range is broader ($T_{\text{difference African species}} = 11\text{ }^{\circ}\text{C} > T_{\text{difference Asian species}} = 29.8\text{ }^{\circ}\text{C}$; Fig. 2). *E. khur* is found in the hottest

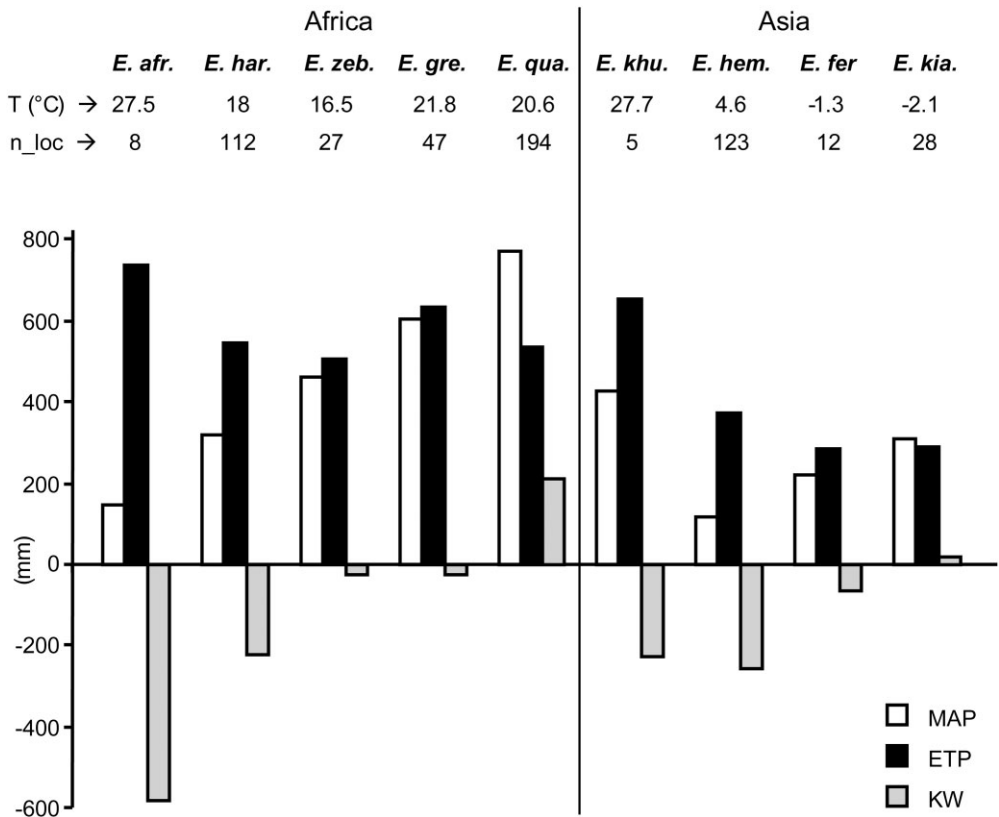


Fig. 2. Climatic variables for the sampling localities of the *Equus* taxa. Comparison of the main climatic variables for the African and Eurasian localities for *Equus* taxa (*E. afr.* = *E. africanus*, *E. har.* = *E. hartmannae*, *E. zeb.* = *E. zebra*, *E. gre.* = *E. grevyi*, *E. qua.* = *E. quagga*, *E. khu.* = *E. khur*, *E. hem.* = *E. hemionus*, *E. fer.* = *E. ferus przewalskii*, *E. kia.* = *E. kiang*) based on the 2° grid method. Median values of the climate variables as indicated in Table 1 are given. MAP, mean annual precipitation (millimetres); ETP, mean annual potential evaporation (millimetres); KW, mean annual climatic water balance (millimetres); T, mean annual temperature (°C); n_loc, number of localities sampled.

Table 2. Differences between climatic variables and tooth wear variables (Kruskal-Wallis tests, P-values indicating significant differences in bold) for each of *E. grevyi*, *E. hartmannae* and *E. zebra*, compared to *E. quagga*

Climatic variables	<i>E. grevyi</i>	<i>E. hartmannae</i>	<i>E. zebra</i>
MAP	1.000	<0.0001	<0.0001
ETP	<0.0001	0.680	0.321
KW	0.419	<0.0001	<0.0001
T	<0.0001	<0.0001	1.000
Score	0.068	0.024	0.333
Occlusal relief	0.273	0.005	0.837
S	0.036	0.085	0.236
R	0.203	<0.0001	0.236
B	0.307	<0.0001	0.007

MAP, mean annual precipitation; ETP, mean annual evapotranspiration; KW, mean annual climatic water balance (millimetres); T, mean annual temperature (°C); Score, mesowear score value; occlusal relief (H, high or L, low); cusp shape (S, sharp; R, round; B, blunt).

but not the driest environments inhabited by equids (T = 27.7 °C, MAP = 427mm, KW = -230mm), while the central Asiatic populations of *E. kiang* (T = -2.1 °C, MAP = 308mm, KW = 15mm) and *E. ferus* (T = -1.3 °C, MAP = 221mm, KW = -68mm) inhabit the coldest areas.

The grid pattern-weighted MAP, ETP, KW and T from the sympatric species localities indicate that the habitat of *E. quagga* is characterized by significantly higher evaporation and temperature than the habitat of *E. grevyi* ($P < 0.0001$, Table 2). This is indicative of *E. quagga* inhabiting more humid environments than *E. grevyi*. The habitats of *E. quagga* differ in their MAP, KW and T ($P < 0.0001$) from those of *E. hartmannae*. The habitats of *E. hartmannae* are characterized by higher aridity (Fig. 2, Table 2). Comparison of the ranges of *E. zebra* and *E. quagga* reveals a significantly higher water supply in the habitat of *E. quagga* ($P < 0.0001$), as indicated by precipitation and climatic water balance data (Fig. 2, Table 2).

E. grevyi has less sharp cusps ($P = 0.036$, Table 2), and *E. zebra* has more blunt cups ($P = 0.007$, Table 2) than *E. quagga*. *E. hartmannae* has a lower occlusal relief ($P = 0.005$, Table 2) as well as more blunt cusps ($P \geq 0.0001$, Table 2) than *E. quagga*.

Species average mesowear signature

The seven equid species *E. grevyi*, *E. quagga*, *E. hartmannae*, *E. zebra*, *E. ferus*, *E. kiang* and *E. hemionus* are classified within the dietary spectrum of grazers (cluster tree, Fig. 3). *E. grevyi*, *E. quagga*, *E. hartmannae*, *E. ferus*, *E. kiang* and *E. hemionus* are very similar to the variable grazers *Alcelaphus buselaphus* (hartebeest) and *Connochaetes taurinus* (blue wildebeest) in showing seasonal and geographical variability in their diet (Gagnon & Chew 2000). *E. zebra* clusters with the obligate grazers without seasonal or geographical variability in their diet. However, surprisingly, two equid species (*E. africanus* and *E. khur*) are classified within the group of grazers, browse-graze intermediate feeders (alongside *Aepyceros melampus*, *Litocranius walleri* and *Ammodorcas clarkei*) and generalists (alongside *Tragelaphus angasi* and *Oreotragus oreotragus*; Fig. 3). The mesowear scores observed (Table 1) range from 2.56 (*E. zebra*) to 1.45 (*E. khur*). The mesowear score plot identifies *E. grevyi*, *E. quagga*, *E. hartmannae*, *E. ferus*, *E. kiang* and *E. hemionus* as falling

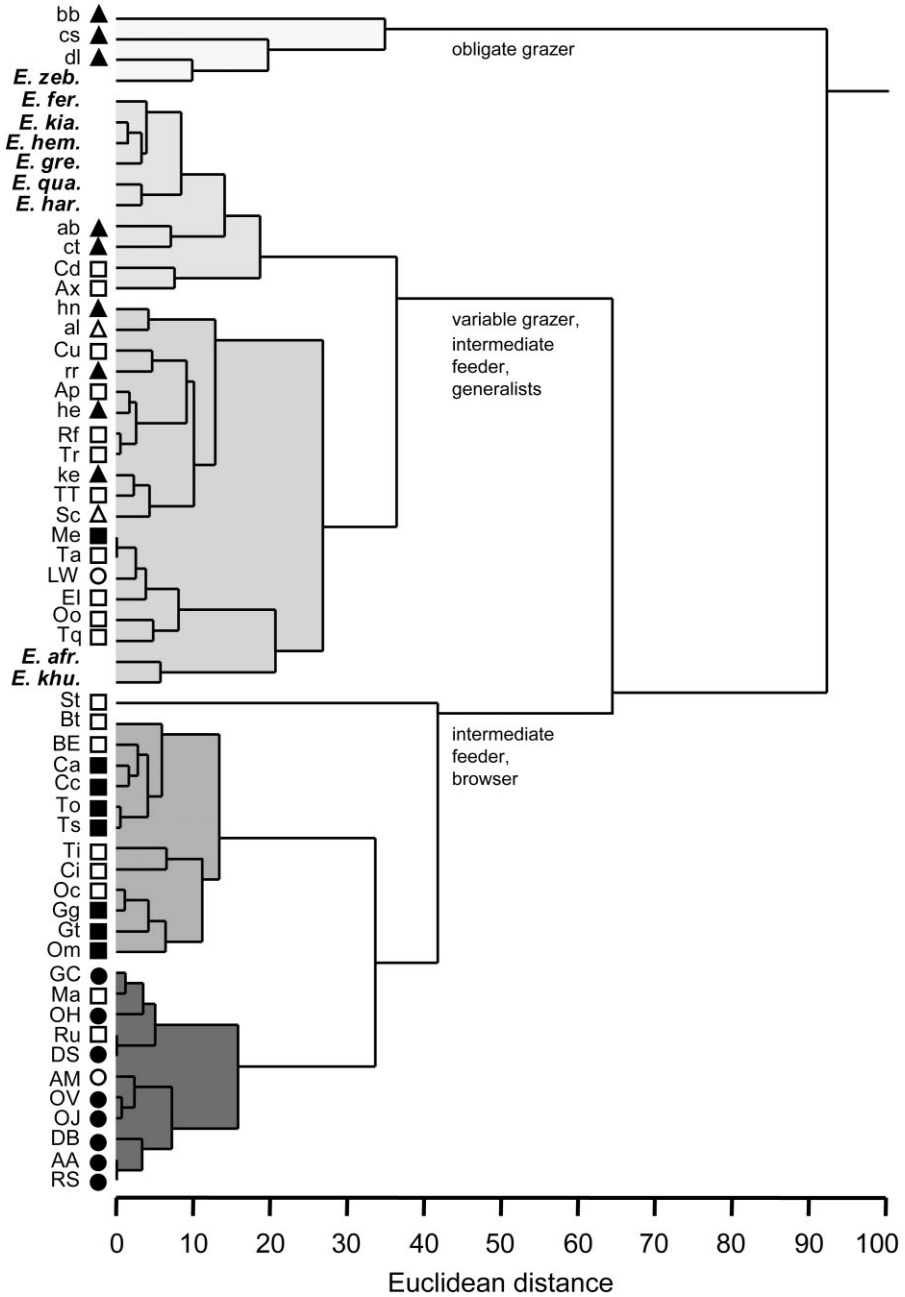


Fig. 3. Hierarchical cluster diagram plotting the mesowear data sets of equids within the reference species, according the conservative classification of Fortelius and Solounias (2000), divided into the dietary categories browser (circles), intermediate feeder (squares) and grazer (triangles). Abbreviations and symbols as for Fig. 4.

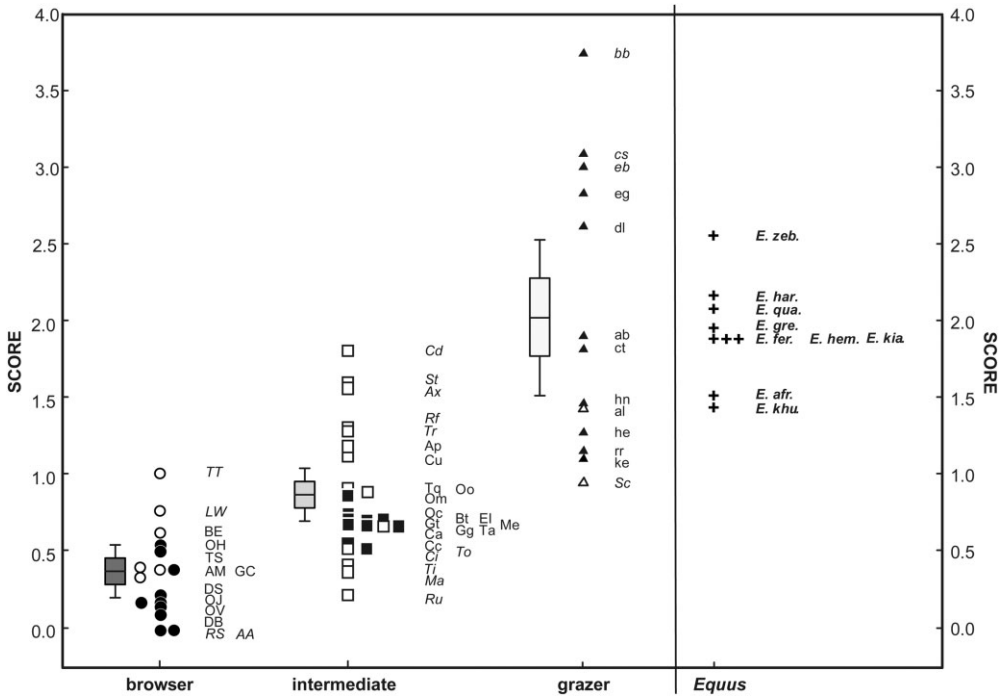


Fig. 4. Mean mesowear score values (SCORE) plotted by species. Boxes indicate the mean and the standard error of the mesowear score values; whiskers indicate the double standard error for the dietary category. The reference species are added according the conservative classification of Fortelius and Solounias (2000), divided into the dietary categories browser (circles), intermediate feeder (squares) and grazer (triangles). Species classified as ‘typical’ for their dietary category are shown by filled symbols, while species classified to ‘no particular class’ are indicated by open symbols; key to lettering: AA = *Alces alces*, ab = *Alcelaphus buselaphus*, al = *Alcelaphus lichtensteini*, AM = *Antilocapra americana*, Ap = *Axis porcinus*, Ax = *Axis axis*, bb = *Bison bison*, BE = *Tragelaphus eurycerus*, Bt = *Budorcas taxicolor*, Ca = *Capricornis sumatraensis*, Cc = *Cervus canadensis*, Cd = *Cervus duvauceli*, Ci = *Capra ibex*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, Cu = *Cervus unicolor*, DB = *Diceros bicornis*, dl = *Damaliscus lunatus*, DS = *Dicerorhinus sumatrensis*, El = *Ammodorcas clarkei*, GC = *Giraffa camelopardalis*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, LW = *Litocranius walleri*, Ma = *Antidorcas marsupialis*, Me = *Aepyceros melampus*, Oc = *Ovis canadensis*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, Om = *Ovibos moschatus*, Oo = *Ourebia ourebi*, OV = *Odocoileus virginianus*, Rf = *Redunca fulvorufula*, rr = *Redunca redunca*, RS = *Rhinoceros sondaicus*, Ru = *Rhinoceros unicornis*, sc = *Syncerus caffer*, St = *Saiga tatarica*, Ta = *Tragelaphus angasi*, Ti = *Tragelaphus imberbis*, To = *Taurotragus oryx*, Tq = *Tetracerus quadricornis*, Tr = *Boselaphus tragocamelus*, TS = *Tragelaphus scriptus*, TT = *Tragelaphus strepsiceros*, *Equus* taxa printed in bold italics: *E. afr.* = *E. africanus*, *E. har.* = *E. hartmannae*, *E. zeb.* = *E. zebra*, *E. gre.* = *E. grevyi*, *E. qua.* = *E. quagga*, *E. khu.* = *E. khur*, *E. hem.* = *E. hemionus*, *E. fer.* = *E. ferus przewalskii*, *E. kia.* = *E. kiang*. Additionally, reference species classified as extreme values or as outliers are represented in italics.

within the lower and upper quartiles of the grazers (Fig. 4). *E. africanus*, *E. khur* and *E. zebra* are plotted as outliers but remain within the double standard error range of grazers. The African species have mostly higher scores (*E. hartmannae* = 2.21, *E. quagga* = 2.06, *E. grevyi* = 1.95 and *E. africanus* = 1.5) than the Asian species (*E. kiang* = 1.88, *E. hemionus* = 1.87 and *E. ferus* = 1.86). We thus find a broad, species-specific range of mesowear signatures among *Equus* species (Table 1). This is

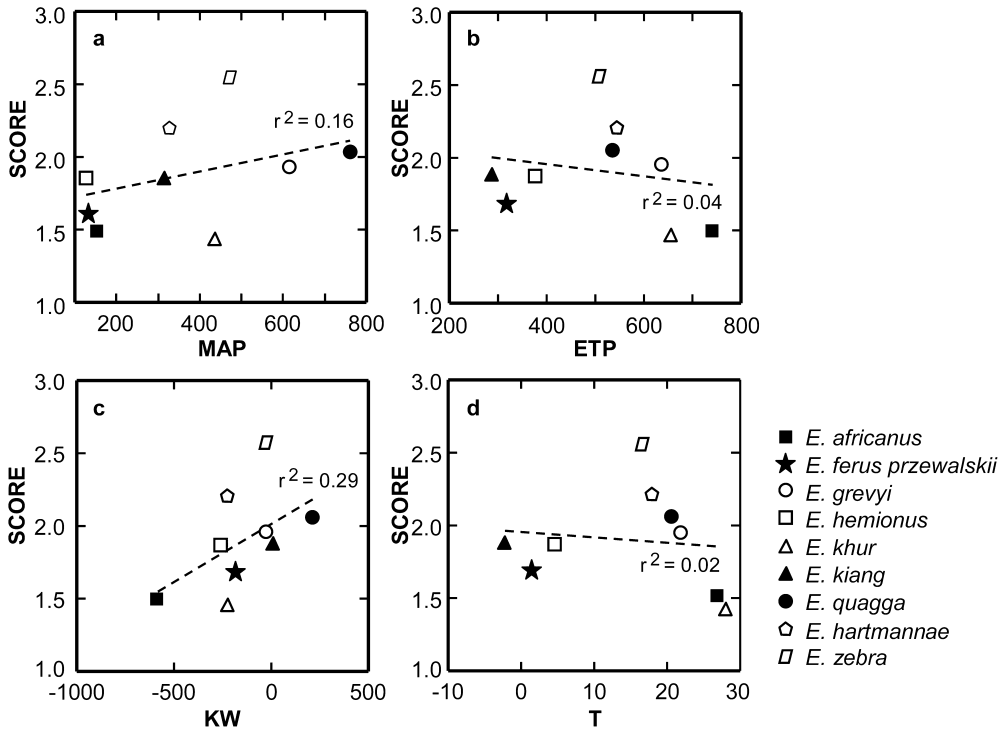


Fig. 5. Scatter plots of climate variables and mean mesowear score values (SCORE) indicating the ordinary least squares regressions between the climate variables (a) MAP, mean annual precipitation (millimetres), (b) ETP, mean annual evaporation (millimetres), (c) KW, mean annual climatic water balance (millimetres), and (d) T, mean annual temperature ($^{\circ}$ C), plotted by equid species.

consistent with the grazing spectrum classification but indicates a more differentiated diet and abrasiveness spectrum than has been thought.

High ratios of sharp cusps (>28%) and high reliefs (>64%) occur in the species living in the most arid habitats (*E. africanus* and *E. khur*), while higher ratios of round cusps are more frequent in the more humid environments of all other equid species (Fig. 5a–c, Table 1). Round cusps are frequent in *E. quagga* (% r = 80) and *E. kiang* (% r = 85), which are found in non-arid environments, as indicated by positive KW values (KW = MAP–ETP). *E. quagga* is clearly associated with the widest range of MAP, ETP and score values of the equid species (Table 1).

Subspecies average mesowear signature

The subspecies scores of *E. quagga* range from 1.33 (*E. q. zambesiensis*) to 2.17 (*E. q. antiquorum*, Table 1). This wide range indicates a high degree of dietary flexibility in *E. quagga*. In *E. hemionus* (N-in = 152), the scores range from 1.58 in *E. h. kulan* to 2.13 in *E. h. onager*, a smaller range than in *E. quagga*. We find a very homogenous mesowear signature in *E. ferus* (N-in = 15) samples: the extinct *E. ferus przewalskii* (score = 1.68) differs only slightly from the sample of the reintroduced subspecies *E. f. przewalskii* (score = 1.88).

Linking mesowear and climate variables

Mesowear variables and climate variables were tested in order to identify the climate variables controlling the dental wear equilibrium in a given habitat. In our data set, there was no linear correlation between the habitat parameters and mesowear scores (ordinary least squares, $r^2_{\text{MAP}} = 0.16$, $P_{\text{MAP}} = 0.29$, $r^2_{\text{ETP}} = 0.04$, $P_{\text{ETP}} = 0.61$, $r^2_{\text{KW}} = 0.29$, $P_{\text{KW}} = 0.14$, $r^2_{\text{T}} = 0.02$, $P_{\text{T}} = 0.75$; Fig. 5).

DISCUSSION

Abiotic habitat variables and mesowear signature

Bauer et al. (1994) were the first to provide abiotic habitat variables for the three species: *E. grevyi*, *E. quagga* and *E. africanus*. Bauer et al. (1994) explain the largely allopatric character of the historic geographical ranges of *E. africanus* and *E. grevyi*, as well as *E. grevyi* and *E. quagga*, as the result of two simultaneously active factors: (i) competitive exclusion and (ii) different habitat requirements of the two species in each of these pairs. Our data set extends the spectrum (Fig. 2) to all nine extant equid species and in general confirms the findings of Bauer et al. (1994).

Seven (*E. ferus*, *E. grevyi*, *E. hartmannae*, *E. hemionus*, *E. kiang*, *E. quagga* and *E. zebra*) of the nine equids exhibit a mesowear signature indicating a grass-dominated diet. This typical grazing trait has long been agreed to represent the general dietary strategy for this main food component of the extant Equidae (Nowak 1991). We therefore cannot accept our hypothesis (that the mesowear signature of each species reflects abiotic parameters, such as climatic variables, impacting the abrasiveness of the diet), and we conclude that there is no evident relationship between mesowear score and climate. This result implies that the overall abrasiveness as measured with mesowear is independent of climate variables. Kaiser et al. (2013) correlated the MAP with dental parameters of 75 ungulate species. Correlations with MAP were stronger for the index of hypsodonty than for mesowear. Therefore, climate variables related to MAP are probably poor predictors of mesowear variables. Our data on MAP support the conclusions found by Kaiser et al. (2013).

We find a large spectrum of distinct dietary traits within the genus *Equus*. The range of the mesowear signatures in extinct horses has been demonstrated (e.g. Fortelius & Solounias 2000, Solounias & Semprebon 2002, Kaiser 2003, Kaiser et al. 2003, Kaiser & Franz-Odenaal 2004, Bernor et al. 2004, 2010, Kaiser & Bernor 2006, Mihlbachler et al. 2011). It has been concluded that Neogene equids represented a broad spectrum of dietary traits, ranging from browsing (Kaiser & Franz-Odenaal 2004) to grazing (Fortelius & Solounias 2000, Solounias & Semprebon 2002), which corresponds to that of the extant bovidae. In the modern Equidae, the spectrum of dietary traits was traditionally considered narrow. Grazing is considered a general dietary adaptation of the genus (Nowak 1991). Our results show that the range of diet traits represented in modern *Equus* is more diverse than previously acknowledged.

Within that range, the signature of the two wild asses (*E. africanus* and *E. khur*) is remarkable in that it is highly attrition dominated, which is indicative of a browsing strategy. This is consistent with feeding observations by various authors (Bannikov 1948, 1958, 1981, Ali 1949, Heptner et al. 1966, Solomatin 1973, Shah 1993, Prasad et al. 1994, Singh 1999, Lengger et al. 2007, Yin et al. 2007) reporting a substantial non-gramineous component, consisting of dicotyledonous shrubs and herbs, in the diet. Those foods mostly contain fewer endogenous abrasives than grass (Kaufman et al. 1985, Carnelli et al. 2001, Merceron et al. 2007). We thus conclude that the wild

asses (*E. africanus* and *E. khur*) inhabiting the most arid areas of Africa and Asia cannot be considered the most dedicated grazers, neither within the Equidae nor within their biomes.

E. zebra and *E. quagga* both feed on nearly 100% grasses (Penzhorn 1982a, Grobler 1983, Nowak 1991). Therefore, we expected them to present similar score values. In fact, of these well-established grazers, *E. zebra* has the highest score value. It is the only equid clustering with the obligate grazers of the comparative ungulate data set. The most parsimonious explanation for this observation is that high score values are related to the obligate grazing trait and to an additional source of exogenous abrasives in the diet of this species. One possible source of additional abrasives could be soil or grit eaten incidentally, as reported by Penzhorn (1982b). The fact that soil eating is not observed in other equid species may not be taken as evidencing the absence of such behaviour. Future field studies of equids should therefore include investigation of the contribution of grit to the mesowear signature.

For *E. grevyi* and *E. quagga*, the mesowear signatures are much more similar, which indicates more similar diets. This result also agrees well with the results of field studies by Klingel (1967, 1974a, b, 1977). Our data therefore give another indication that the two taxa in fact have similar dietary niches or even share the same feeding niche. Rowen and Ginsberg (1992) and Churcher (1993) observed that in years of high precipitation, the geographical range of *E. quagga* is shifted more towards the north. Our climate data support this observation, as *E. quagga* habitats have higher humidity than those occupied by *E. grevyi* (Fig. 2). In combination with the high dietary flexibility of *E. quagga*, this might represent a keystone for the large geographical range of *E. quagga* in central, southern and eastern Africa.

Intraspecific variability of the mesowear signature

The variability observed at the subspecies level within the African *E. quagga* (0.84) and the Asian *E. hemionus* (0.55) groups confirms observations made in Pleistocene ungulates (Rivals 2008). In the sample of locally extinct *E. ferus przewalskii* analyzed, we find a homogeneous mesowear signature which suggests that the reintroduced animals have the same dietary range as the wild Przewalski horses. Both of these ranges indicate a particularly narrow dietary niche. This in turn indicates that the reintroduced population has a diet similar in abrasiveness to the extinct population. We thus conclude that reintroduction was successful in respect of the dietary needs of the species. Our data provide rarely obtained insight into the availability and utilization of resources of an endangered species. The dental mesowear signature thus seems to be a suitable tool to test for reintroduction success. Furthermore, data sampled from museum specimens are the only resource available for reconstructing the past dietary flexibility of *E. ferus przewalskii* populations. Monitoring the mesowear signature as a proxy for the dietary resources exploited can be considered an important tool in evaluating the success of introductions and other conservation measures.

CONCLUSION

For the first time, climatic habitat variables (MAP, ETP, KW and T) of all extant equid species are provided. The data indicate the range of habitat requirements represented in the genus. Our data further suggest that aridity as represented by climate variables MAP, ETP, KW and T does not, in the first instance, relate to the dental wear

signature of equids. Within our set of species, the wild asses illustrate this phenomenon. Both species (*E. africanus* and *E. khur*) inhabit the most arid habitat but have the most attrition-dominated mesowear signatures. If climate impacted mesowear by a simple increase of abrasiveness in dry habitats, this would not be the case. We found no evidence for a strict relationship between climate and the overall abrasiveness of a species' diet (our hypothesis was rejected). We thus conclude that mesowear, which is indicative of a specific feeding strategy, should be regarded as a dietary proxy rather than a climate proxy. There is little potential for modelling climate variables and climate change from tooth wear proxies. However, tooth wear proxies can be used to infer local dietary traits of populations and track them through space and time. This may be a valuable tool in conservation management.

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