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Mortality curves for horses from the Middle Palaeolithic site of Bau de l'Aubesier (Vaucluse, France): methodological, palaeo-ethnological, and palaeo-ecological approaches

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Abstract

A new methodology for estimating the age of death of horse, based on the degree of hypsondonty, has been established using the dental material of *Equus mosbachensis*, *Equus* cf. *taubachensis*, and *Equus* sp., which were hunted from the Mousterian levels of the Bau de l'Aubesier at Monieux (Vaucluse, France). Our model is based on a regression analysis of curvilinear type, and allows the precise determination of age classes intervals and the distribution of estimated ages, by systematically taking into account the standard deviation. These estimates were tested from all the paired teeth of horses belonging to the same individuals, from the sites of Bau de l'Aubesier and of Jaurens at Nespouls (Corrèze, France).

The age structures of the horses of Bau de l'Aubesier were compared in the different levels of the sequence with their frequencies, survival rates, and mortality rates corresponding to as many curves as often used in population ecology and demographics. The different age classes of a present-day natural African population (*Equus burchelli boehmi*), the individuals having died accidentally in the National Park of Akagera (Rwanda) following a bush fire, provide an interesting comparative catastrophic model with regard to the population dynamics, and permit us to evaluate the impact of Neandertals on the Equidae fossils of Bau de l'Aubesier. Our assemblage clearly indicates in the lower layers, a systematic selection of adult horses, as opposed to the upper sequence where juveniles and adults dominate. Ecological factors, such as seasonal migratory phenomena and herd gathering, which characterise many large size species are also tackled and could explain the high proportion of adults in French Middle Palaeolithic sites where horses were preferentially hunted.

Keywords: Horse teeth; Age determination; Mortality curves; Neandertal strategies

1. Introduction

One of the main tools to address animal exploitation by man is the interpretation of mortality curves. The precursory works of Kurtén [37] have paved the way with the recognition of different age classes based on the analysis of fossil dental material of carnivores and herbivores. These analyses precede the zooarchaeological approach, by evoking population dynamics, taphonomical conditions, and the effects of seasonality on the age structures of animal populations.

The methodological aspects developed by Kurtén, concerning crown height, the replacement of deciduous by permanent dentition, and the different degrees of tooth wear, together constitute the principal criteria currently employed to construct mortality curves at anthropics sites [6,15,16,35,45,46,47,51,74–76,78,79,84]. These criteria have been associated with the cementochronology, which is founded on the microscopic analysis of rings that form each year within the actual cementum structure [8,9,20,33,34,57,59,70,73].

As with many hypsodont herbivores, a significant correlation exists in horses between the height of the

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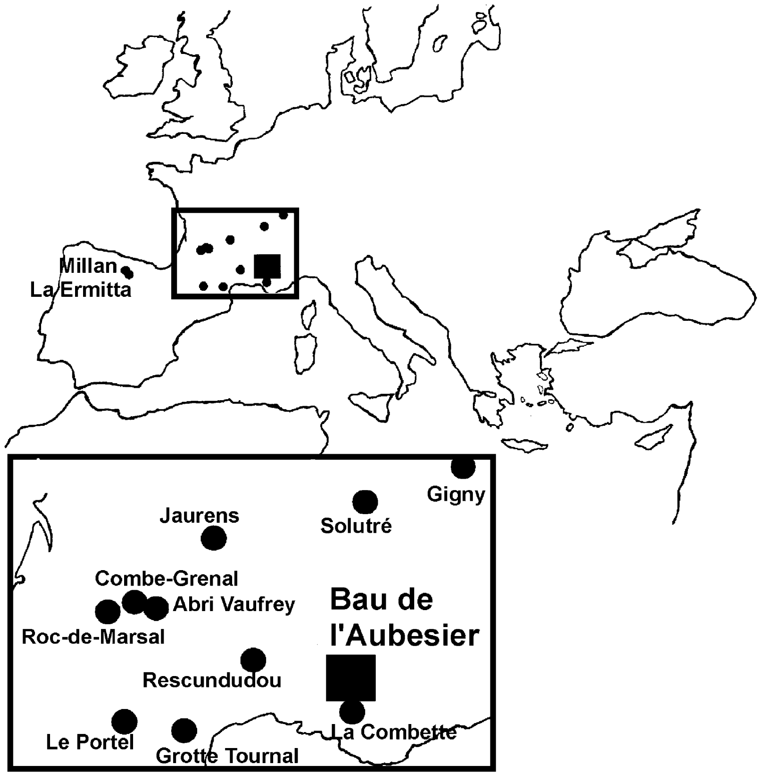

Fig. 1. Map of Europe indicating the location of the Bau de l'Aubesier and other Palaeolithic sites mentioned in the text.

crown and the age of the individual. The quadratic equations of Klein [28,29], discussed by Gifford-Gonzalez [19], which are often used in zooarchaeological studies to interpret the mortality curves of Cervidae, Equidae, and Bovinae [28–32], have not been retained here. In this study, we put forward a predictive model of age derived from the dental reference frame of Levine [45]. This model is then applied for *Equus mosbachensis* (levels I and J), *Equus* cf. *taubachensis* (level H), *Equus* sp. (Upper level) of Bau de l'Aubesier and the Wurmian form *Equus caballus* cf. *gallicus* of Jaurens. The Equidae age profiles of Bau are discussed throughout the stratigraphic sequence. The lower levels H, I, and J correspond to pre-Wurmian species and upper level (layers I–V) to a Wurmian horse. The mortality curves, of the lower levels in particular, have been compared with those of *Equus burchelli boehmi* from Akagera, the population structure here being typically catastrophic. This combined analysis puts into perspective the impact of Neandertals on these large ungulates, as well as their capacity to optimally exploit their environment during the Middle Palaeolithic. From this point of view, seasonal phenomena, age classes, hunting techniques, and topographical situation are considered, particularly from French patterns of Mousterian sites where horses dominate faunal spectrum [45].

2. General presentation of Bau de l'Aubesier

The rockshelter of Bau de l'Aubesier at Monieux (Vaucluse) is a vast cavity of more than 30 m wide and 15 m deep, which opens into a rocky hemicycle of the gorges of Nesque (Fig. 1). This site perched 60 m above the actual thalweg of the river was discovered in 1901 by F. Moulin and M. Bonnefoy [60]. The present excavations, undertaken since 1987 by a French–Canadian team, are under the responsibility of S. Lebel (University of Quebec, Montreal). The brecchia deposits amount to more than 12 m of thickness, with numerous angular rocks inclusions of different formats, sometimes contained within a yellowish sandy matrix (Fig. 2).

Since the discovery at Bau de l'Aubesier of a human tooth from the actual layer V [49,50], new teeth, certain of which were decayed, as well as a pathological Neandertal mandible have been uncovered with archaeological remains [41–43,80,81].

With the exception of levels L–M, which are sterile, the deposits consist of a high density of large and medium herbivores bones, teeth, and typical Mousterian lithic assemblages. Those archaeological remains are sometimes burnt to different degrees and associated, as in layers H and IV, with wood charcoal and ash

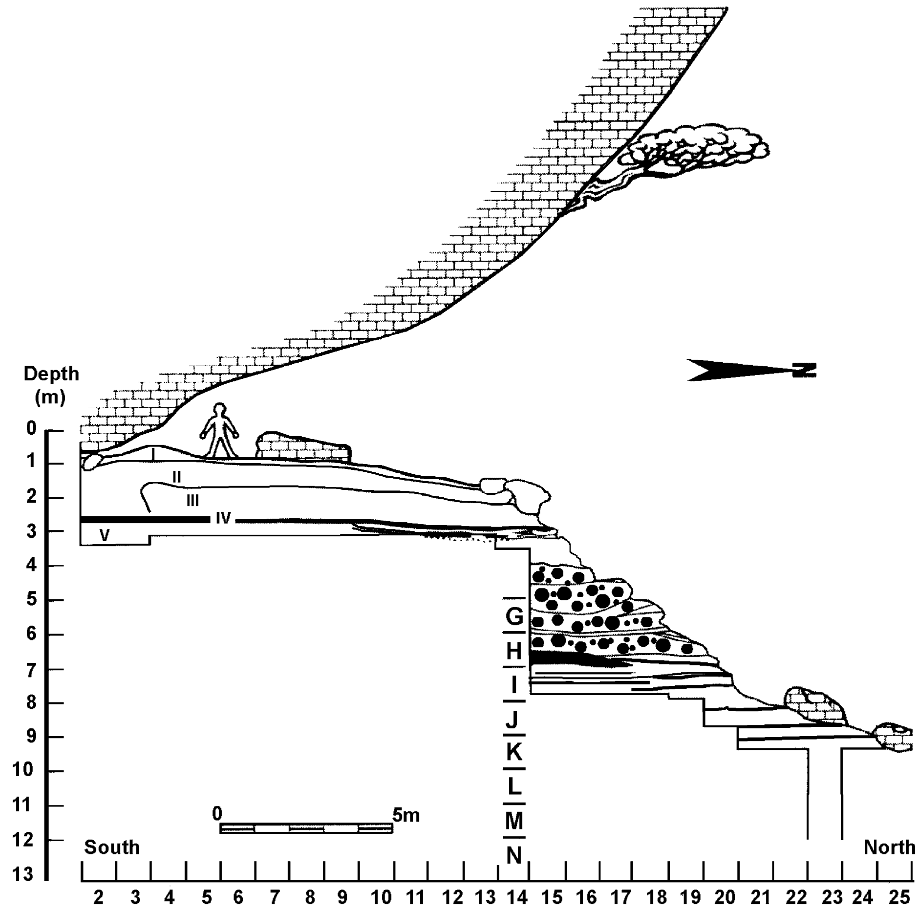

Fig. 2. Stratigraphic diagram of the Bau de l'Aubesier after Lebel et al. (Ref. [41], modified).

in highly organic sediment. The quasi-absence of carnivores in the whole sequence contrast with anthropic bone fracturation, cuts marks, and differential preservation of anatomical parts analysis, which indicate primary human accumulation in the cave and butchering activities [16]. The faunal list of de Lumley [48] has been modified following the works of Faure et al. [13,14]. As it stands today, the faunal assemblage throughout the sequence allows for the recognition of 19 taxas and particular species, such as *E. mosbachensis*, *E.* cf. *taubachensis*, and *Capra* cf. *caucasica*. These prove to be very good biostratigraphical markers and show that the Provence constitutes a particular biogeographical entity, as also testified by the presence of *Hemitragus cedrensis*. The upper level (layers I–V) corresponds to the beginning of the Upper Pleistocene (oxygen isotopic stage (OIS) 5d–a), levels G and H to the Eemian interglacial (OIS 5e), and levels I–N to the Middle Pleistocene (OIS 6–7) [16]. These results confirm the radiometric data in progress, in particular those from layer H1 dating to approximately 200,000 years [4,41].

3. Materials and methodology for the establishment of age classes from the dental material of horse

Age estimates for horses have been the subject of many Veterinary Science works from the second half of the 19th century, owing to the economic role played by the horse in Europe [11,58,77]. More recent studies of population structure of the wild African species *E. burchelli boehmi* confirm the validity of these estimates (H. Klingel and U. Klingel cited in Ref. [46]). For Levine [45], the use of eruption stages and dental wear tables derived from domestic horses constitute a truly justified methodological basis for comparing the population structures of different wild Equidae.

The height of lower and upper cheek teeth is taken along the vestibular face, and measured between the departure of the roots and the crown (Fig. 3, measures 1 and 2). We did not take into consideration incisors, which are too few in comparison with the cheek teeth. It is noteworthy, however, that recent works show that they are very good markers of age, not only in horses, but also in donkeys [55,56,63,67].

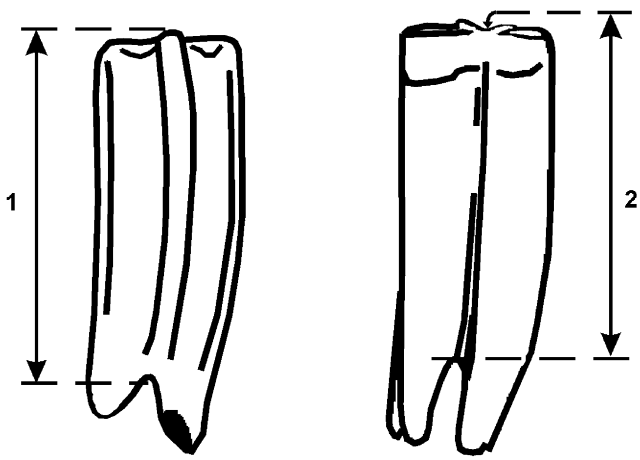

Fig. 3. Illustrations of tooth measurements of *Equus*. 1, left superior cheek tooth height; 2, left lower cheek tooth height.

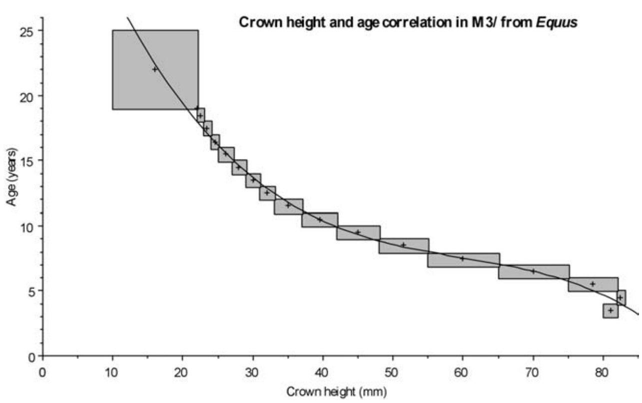

Fig. 4. Distribution of the crown height and age intervals for M3/ of *Equus* and fitting curve (polynomial order 3) associated with median points. The grey squares represent the 95% confidence intervals.

To estimate the age of the fossil horses and establish their mortality profiles, we propose here a model based on a polynomial regression on the order of 3, correlating crown height of upper and lower cheek teeth with age. This model highlights the variations of dental wear between the teeth, which are hardly affected, and the ones, which are the most worn (Fig. 4). The equation, which ties age with the height of the crown, is as follows:

$$\text{age} = \sum_{k=0}^{3} a_k \cdot (\text{crown height})^k$$

with a_k being the regression coefficients, crown height is measured in millimetres, and age in years.

This curvilinear regression model is a particular case of the general linear regression model [64]. Regression coefficients have been calculated using least square linear regression analysis (for details on least square regression techniques, see, for example, Refs. [64,69]).

Data used for calculations are those provided as reference for age estimates by Levine [45, Appendix VI, pp. 348–349]. For the dates of eruption and replacement of deciduous by permanent teeth, we have used the works of Montané et al. [58]. This reference frame being presented in the form of age and dental height intervals (Tables 1–3), we used the technique of randomisation by recalculating 1000 times the regression parameters from values taken randomly in these intervals (for randomisation techniques, see, for example, Ref. [54]). Thus, for each tooth according to its position (e.g. P/2, P3/...), height and age values were taken randomly in the respective intervals for each age groups. The parameters of the polynomial regression were then calculated. Tables 4 and 5 summarise the results of these calculations and provide the median value and the limits corresponding to the first and the last quartile (i.e. 25 and 75%) of the determination coefficient (R^2), the average standard deviation of prediction, as well as the regression coefficients (i.e. intercept and slopes). The distribution of determination coefficients and prediction error for the 1000 runs are illustrated in Figs. 5 and 6, respectively, for upper third molar.

The ages of various teeth of Bau de l'Aubesier were then estimated, along with the associated prediction errors. Thus, 1000 predictions, with their error, were obtained, and median value was used in the analyses, which are presented in the following discussion. The more detailed results for the M3/ number 576 of Bau de l'Aubesier are given in Table 6 and they are illustrated in Figs. 7 and 8.

4. Test and validity of the model from the cheek teeth of the horses of Bau de l'Aubesier and Jaurens and age groups

To validate our model, all associated teeth on maxillae or mandibles from Bau de l'Aubesier and Jaurens were used. The dental material of the first site corresponds to the large pre-Wurmian horses *E. mosbachensis* and *E.* cf. *taubachensis* associated, respectively, with lowers layers J, I, and H. Similarly, we used all the connected teeth of the palaeontological site of Jaurens where a Wurmian form of smaller size *E. caballus* cf. *gallicus* was recognised [23,24,62]. In total, for these two sites, 52 cheek teeth corresponding to 19 fragments of mandible or maxilla are available for analysis (Appendix A). The principle of the test is simple and the hypothesis is as follows: the paired teeth of one same specimen must give a concordant age due to the independent equations established for each of them. If we compare the confidence interval defined at 2 prediction errors around the median value (i.e. at $p<0.05$), results are concordant for 51 teeth and 18 specimens, only one P/3 on mandible FSL 303.480 from Jaurens gives an age significantly older than the three molars

Table 1
Reference values for age interval and crown height used for calculation (after Levine [45])

Age (years)	P2/ (mm)	P3/ (mm)	P4/ (mm)	M1/ (mm)	M2/ (mm)	M3/ (mm)
1–2						
2–3	65–70			92–89	88–89	
3–4	68–70	81–80	85–83	89–80	89–86	80–82
4–5	70–68	80–76	85–81	80–73	86–80	82–83
5–6	65–60	76–70	81–74	73–66	80–74	82–75
6–7	60–54	70–63	74–65	66–59	74–67	75–65
7–8	54–48	63–57	65–58	59–53	67–60	65–55
8–9	48–42	57–50	58–51	53–48	60–53	55–48
9–10	42–37	50–45	51–45	48–43	53–48	48–42
10–11	37–32	45–40	45–41	43–40	48–42	42–37
11–12	32–28	40–36	41–37	40–36	42–39	37–33
12–13	28–24	36–33	37–35	36–33	39–35	33–31
13–14	24–20	33–30	35–32	33–30	35–33	31–29
14–15	20–18	30–27	32–30	30–27	33–31	29–27
15–16	18–16	27–25	30–28	27–25	31–29	27–25
16–17	16–14	25–22	28–27	25–24	29–28	25–24
17–18	14–13	22–20	27–26	24–23	28–27	24–23
18–19	13–11	20–19	26–25	23–22	27–27	23–22
19–25	11–5	19–10	25–10	22–10	27–10	22–10
Age (years)	P/2 (mm)	P/3 (mm)	P/4 (mm)	M/1 (mm)	M/2 (mm)	M/3 (mm)
1–2				91–83		
2–3				91–89	86–83	
3–4	60–59	81–82		89–81	86–82	77–70
4–5	59–55	82–78	80–79	81–72	82–76	77–78
5–6	55–49	78–69	79–73	72–64	76–70	78–71
6–7	49–43	69–60	73–65	64–56	70–63	71–64
7–8	43–38	60–52	65–56	56–49	63–57	64–58
8–9	38–33	52–45	56–48	49–44	57–50	58–51
9–10	33–28	45–39	48–42	44–38	50–44	51–46
10–11	28–24	39–34	42–37	38–33	44–39	46–42
11–12	24–20	34–30	37–33	33–29	39–35	42–37
12–13	20–17	30–28	33–31	29–26	35–32	37–33
13–14	17–15	28–25	31–30	26–24	32–29	33–29
14–15	15–12	25–23	30–28	24–22	29–27	29–26
15–16	12–10	23–22	28–27	22–21	27–24	26–24
16–17	10–8	22–20	28–27	21–20	24–23	24–23
17–18	8–6	20–19	28–27	21–20	23–22	23–22
18–19	6–5	20–19	28–27	20–19	22–21	22–21
19–25	5–4	19–10	27–10	19–10	21–10	21–10

Table 2
Reference values for crown height of undetermined P3–P4 and M1–M2 and age intervals used for calculation (after Levine [45])

Crown height (mm)	P3–4/ (years)	M1–2/ (years)
90–100	3–5	1–3.5
80–90	3–5	2.5–5
70–80	3–6.5	4–6.5
60–70	3–7.75	5.5–8
50–60	7.5–9.75	7–9.5
40–50	9–11.25	8.5–11.5
30–40	11–15	11–15.5
20–30	14–18	14–25
0–20	15–25	14–25
Crown height (mm)	P/3–4 (years)	M/1–2 (years)
90–100		1–3
80–90	3–4.5	2–4.5
70–80	4.5–6.5	4–6
60–70	6–7.5	5.25–7.5
50–60	7–8.75	6.5–9
40–50	8.25–10.25	8–11
30–40	10–14	9.75–14
20–30	12–17	11.75–20
0–20	14–25	18–25

Table 3
Reference values for age (in month) of replacement for deciduous and of eruption for permanent teeth used for calculation (after Montané et al. [58])

Upper tooth	Replacement (month)	Lower tooth	Replacement (month)
D2/	<28	D/2	<26
D3/	<38	D/3	<30
D4/	<45	D/4	<40
Upper tooth	Eruption (month)	Lower tooth	Eruption (month)
P2/	28–34	P/2	26–32
P3/	38–42	P/3	30–34
P4/	45–50	P/4	40–44
M1/	10–12	M/1	10–12
M2/	20–26	M/2	20–26
M3/	40–50	M/3	40–50

(Appendix A). If we choose a confidence interval at 1 prediction error (i.e. at $p<0.33$), seven results on 52 teeth and five on 19 specimens fail to overlap the estimated ages. The test carried out from the dental material of the fossils species of Bau de l'Aubesier and Jaurens suggests a relative similarity in the respective wear of various teeth of the same row. Thus, later in our study, we use this empirical test to decide on the use of confidence intervals at ± 2 prediction errors.

According to Table 4, the average standard deviation of prediction for the well-identified dental categories varies between 0.25 and 0.65, except for P/4, which presents a higher value, 1.34, and to a lesser degree, M/1 with 0.83. To take into account this error of prediction in the definition of age interval groups, we took one 3 years duration, which corresponds at least to the average intervals confidence with 95% for the various dental categories except P/4.

Taking into account the age estimation error associated with each tooth and the age groups fixed at 3 years, we divided the individuals proportionally into these intervals. Thus, for example, for the individual corresponding to the M3/ number 576 of Bau de l'Aubesier, the estimated age is 12.995 ± 0.7798 years (Table 6). So, the confidence interval of its age, for $p<0.05$, ranges between 11.435 and 14.555. This interval overlaps the age category 9–12 years and 12–15 years. Consequently,

Table 4
Median values and 1st and 3rd quartiles for determination coefficient (R^2) and mean prediction error for each tooth category obtained after 1000 random runs (see details in text for calculation and also Figs. 5 and 6)

Tooth	Determination coefficient	Mean prediction error
P2/	0.986 (0.981–0.989)	0.544 (0.404–0.729)
P3/	0.993 (0.988–0.995)	0.257 (0.182–0.409)
P4/	0.986 (0.978–0.991)	0.494 (0.315–0.765)
P3–4/	0.971 (0.955–0.982)	1.566 (0.968–2.440)
M1/	0.990 (0.984–0.993)	0.389 (0.267–0.598)
M2/	0.986 (0.978–0.991)	0.534 (0.345–0.828)
M3/	0.985 (0.976–0.989)	0.532 (0.379–0.817)
M1–2/	0.980 (0.965–0.989)	1.119 (0.596–1.905)
P/2	0.982 (0.968–0.991)	0.636 (0.278–1.218)
P/3	0.988 (0.980–0.992)	0.414 (0.290–0.692)
P/4	0.959 (0.944–0.970)	1.343 (0.977–1.756)
P/3–4	0.975 (0.957–0.989)	1.123 (0.570–2.002)
M/1	0.980 (0.973–0.984)	0.827 (0.639–1.145)
M/2	0.990 (0.985–0.993)	0.366 (0.271–0.566)
M/3	0.981 (0.975–0.986)	0.652 (0.500–0.871)
M/1–2	0.974 (0.956–0.985)	1.691 (1.000–2.834)

18.1% of age interval is placed in category 9–12 and 81.9% in the category 12–15. It is, thus, the sum of these proportions, which is calculated in the age classes intervals, and which makes it possible to establish the age profiles of the principal levels of Bau de l'Aubesier.

5. Impact of Neandertals on the age structures of the horses from Bau de l'Aubesier

The eco-ethological data for current animal populations are more and more often integrated in zooarchaeological studies, which relate to mammal mortality. Our analysis falls under this approach, which now constitutes a major methodological basis. Indeed, the contribution of modern species' population dynamics, according to their age group, their sex, their seasonal behavioural characteristic, and their vital catchment area allows us to understand the human exploitation of fossil taxa in a better way.

In the levels H, I, J, and in the upper level, the dental material of Bau de l'Aubesier corresponds to a MNI frequency of at least 49 individuals (NISP=353) (Appendix B). These counts are, without doubt, largely underestimated by the regrouping of the P3–P4 and M1–M2, which individually are very difficult to separate. In addition, when one takes into account all the broken teeth as well as the whole of the incisors, the MNI frequency in these levels is 61 individuals with a NISP equivalent to 776. Thus, there is no proportional correlation between this two indices [21,52]. In the following discussion, without rejecting the significance of the MNI [82], we choose to present our results by taking into account only the NISP for calculation of frequencies.

The differential conservation of the dental material can constitute a significant bias in the underestimation of certain age groups. However, we find that the percentages of dental preservation between the right and left teeth clearly indicate that the original deposits in each level were little modified by natural, human, or animal agents, and that they can be compared with one another (Table 7). These percentages were calculated according to the method of Brain [5]. Taking level H as an example, where one counts 62 right teeth for 64 left teeth, and if it is considered that there are in an individual as many right teeth as left teeth, we should observe on the whole 128 teeth. According to our count, in this level, there are only 126 teeth, which demonstrates an excellent preservation between the right and left cheek teeth, at 98.4%.

Throughout the stratigraphic sequence of Bau de l'Aubesier, the age structures of the horses were analysed based on living animal statistics, which are mainly employed in population ecology of wildgame management [10,12,68,72]. They have also been discussed and applied in palaeontology [37–40] and in rare zooarchaeological studies [36]. It is on the basis of these works that we present life table indices in Table 8, which make it possible to understand the mortality of the fossil horses in a better way, namely

(f_x) mortality, corresponding to the frequencies of dead animals in each age group x ($f_x=l_x-l_{x+1}$),
(l_x) survival, corresponding to the frequencies of the individuals who survive in successive age groups. By convention, the value of the first age group is very often set at 1000 in order to proportionally increase the values that follow ($l_{x+1}=l_x-f_x$),
(q_x) mortality rates associated with each age group, which is calculated by the ratio of f_x and l_x. In our study, this is represented as $q_2=f_x(l_x)\times 1000$.

It should be noted that the age structure of a stable population, in phase of non-colonisation is always the same in terms of survival, mortality, and fertility rates [1]. No argument suggests a rejection of this hypothesis with regard to the wild horses hunted at Bau de l'Aubesier; this is why it was understood that the same age structures of live populations remained identical through time and that the distortions observed between the profiles of the various levels resulted primarily from the human impact.

As shown in Fig. 9, the age structures of the horses of Bau de l'Aubesier significantly differ between, on the one hand, the upper level, and on the other hand, the lower levels H, I, and J, where it is the adults between 6 and 15 years who are best represented in terms of frequency (f_x). In this interval, in the upper level, the slope of the survival curve (l_x) is much more curved. In the remainder of the sequence, one clearly observes that the death

Table 5
Median and 1st and 3rd quartiles for regression coefficients values (intercept and slopes) for each tooth category (for R^2 and mean prediction error, see Table 4)

Tooth	a_0	a_1	a_2	a_3
P2/	28.290625 (26.353363 to 30.171387)	−1.028377 (−1.190930 to −0.844264)	0.019429 (0.014805 to 0.023475)	−0.000141 (−0.000173 to −0.000106)
P3/	33.658749 (30.289289 to 37.008980)	−1.041913 (−1.264793 to −0.810369)	0.015383 (0.010605 to 0.019831)	−0.000087 (−0.000116 to −0.000058)
P4/	40.593780 (32.289368 to 50.619394)	−1.318328 (−1.943015 to −0.793651)	0.018488 (0.008426 to 0.030175)	−0.000096 (−0.000164 to −0.000035)
P3–4/	25.617811 (20.196373 to 31.821285)	−0.406405 (−0.773996 to −0.106842)	0.001078 (−0.004027 to 0.007621)	0.000009 (−0.000027 to 0.000037)
M1/	35.572249 (31.609917 to 39.523341)	−1.064404 (−1.295958 to −0.816891)	0.013784 (0.009216 to 0.017850)	−0.000066 (−0.000089 to −0.000041)
M2/	41.143669 (32.914821 to 51.746716)	−1.312885 (−1.926719 to −0.821504)	0.018273 (0.009355 to 0.029140)	−0.000095 (−0.000154 to −0.000044)
M3/	40.634788 (33.676067 to 47.836483)	−1.482155 (−1.952857 to −1.007424)	0.023170 (0.013527 to 0.032427)	−0.000128 (−0.000186 to −0.000069)
M1–2/	32.599580 (23.238694 to 45.880592)	−0.870571 (−1.526330 to −0.385963)	0.010151 (0.002157 to 0.020601)	−0.000046 (−0.000100 to −0.000005)
P/2	23.931106 (22.937546 to 24.988043)	−0.940985 (−1.056517 to −0.827191)	0.020425 (0.016747 to 0.023877)	−0.000174 (−0.000207 to −0.000141)
P/3	37.758397 (34.266402 to 41.217578)	−1.447331 (−1.685125 to −1.202156)	0.024167 (0.018887 to 0.028979)	−0.000141 (−0.000172 to −0.000107)
P/4	46.789425 (33.787452 to 65.583474)	−1.766535 (−2.963280 to −0.922818)	0.027637 (0.010829 to 0.051201)	−0.000153 (−0.000295 to −0.000048)
P/3–4	29.285176 (22.397935 to 36.761642)	−0.835852 (−1.293294 to −0.405435)	0.011519 (0.003648 to 0.019858)	−0.000061 (−0.000112 to −0.000013)
M/1	36.176726 (33.582843 to 38.780519)	−1.309214 (−1.475466 to −1.135188)	0.020176 (0.016652 to 0.023249)	−0.000110 (−0.000128 to −0.000090)
M/2	36.936030 (32.407243 to 41.135158)	−1.236690 (−1.507833 to −0.941424)	0.018852 (0.012830 to 0.023980)	−0.000105 (−0.000135 to −0.000070)
M/3	36.102387 (31.230599 to 40.974192)	−1.203143 (−1.535885 to −0.848178)	0.018695 (0.011244 to 0.025858)	−0.000110 (−0.000157 to −0.000062)
M/1–2	32.587336 (27.885828 to 37.248828)	−0.927905 (−1.224870 to −0.651256)	0.011631 (0.006785 to 0.017051)	−0.000056 (−0.000085 to −0.000029)

Given a crown height (=H, in mm), the equation for age (in year) is: Age=$a_0+a_1H+a_2H^2+a_3H^3$.

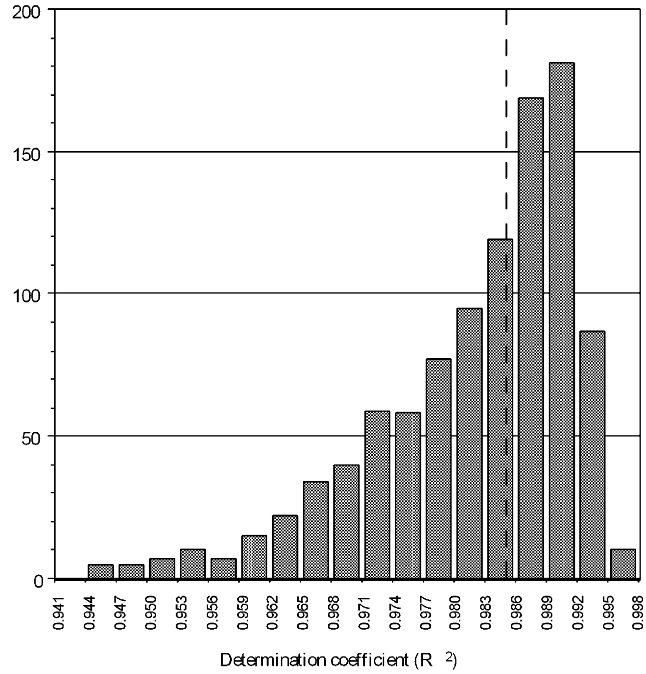

Fig. 5. Frequency distribution of the determination coefficient (R^2) for M3/ of *Equus* obtained from 1000 runs (for explanation, see text). Dashed line, median value.

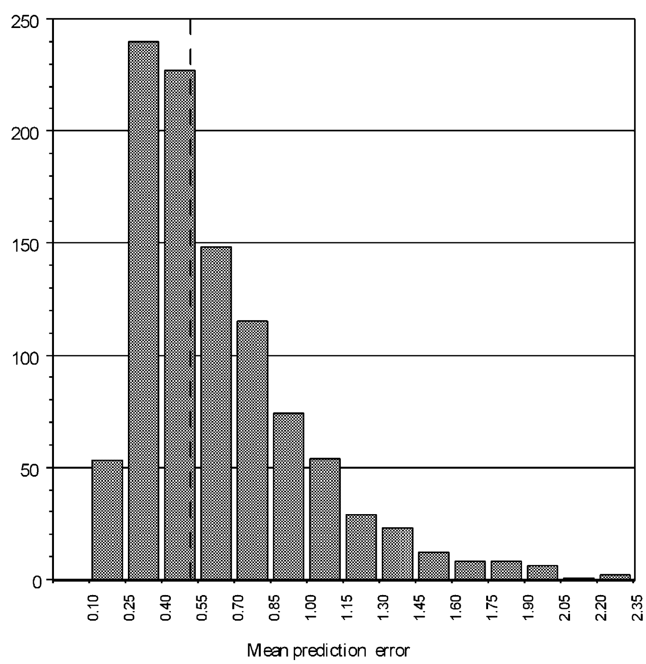

Fig. 6. Frequency distribution of the mean prediction error for M3/ of *Equus* obtained from 1000 runs (for explanation, see text). Dashed line, median value.

rates (q_x) of the horses of more than 9 years are much higher. We note, however, that the adults of more than 18 years are not represented, respectively, in H and J levels, whereas they are represented in the upper and I levels of the deposit. These indications suggest that the higher sequences represent a hunting directed at the younger and older animals, in contrast with the continuous killing of prime-aged individuals in the lower levels. Systematic scavenging is difficult to envisage because mortality profiles in the various layers are completely different from those generated by large carnivores or from animals that died naturally. This is valid not only for horses, but also for other taxa at Bau. It is, of course, impossible to completely exclude random scavenging from the profiles [16].

Table 6
Predicted ages and prediction errors calculated for M3/ (number 576) from Bau de l'Aubesier with equations resulting from 1000 runs (also see Figs. 7 and 8)

	Estimated age	Prediction error
Median value	12.995	0.7798
1st quartile	12.799	0.6556
3rd quartile	13.209	0.9633

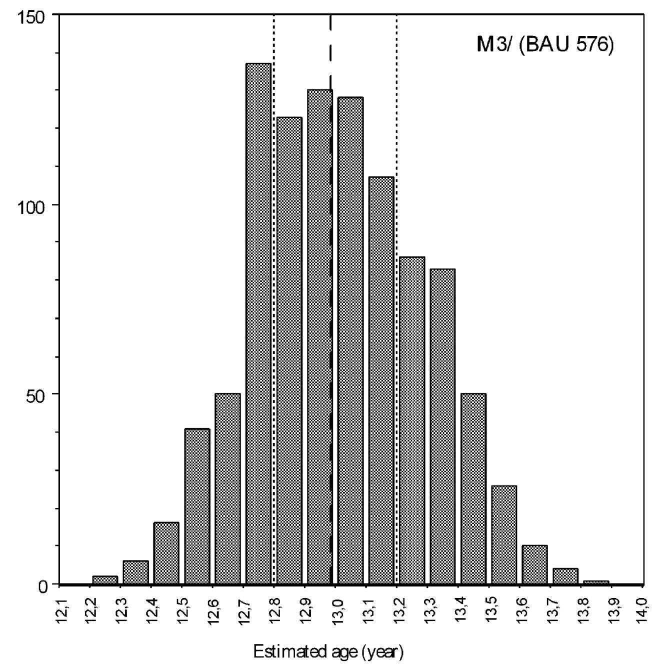

Fig. 7. Frequency distribution of the ages calculated for M3/ (number 576) from Bau de l'Aubesier with equations resulting from 1000 runs (for explanation, see text). Dashed line, median value; dotted lines, 1st and 3rd quartiles.

If one accepts a behavioural analogy between the social groups of living and fossil Equidae, then one may suppose that Neandertals lived along side two principal types of social units: the family groups, very variable in number, but always including one lone stallion, at least one female and a young of the year; the bachelor groups,

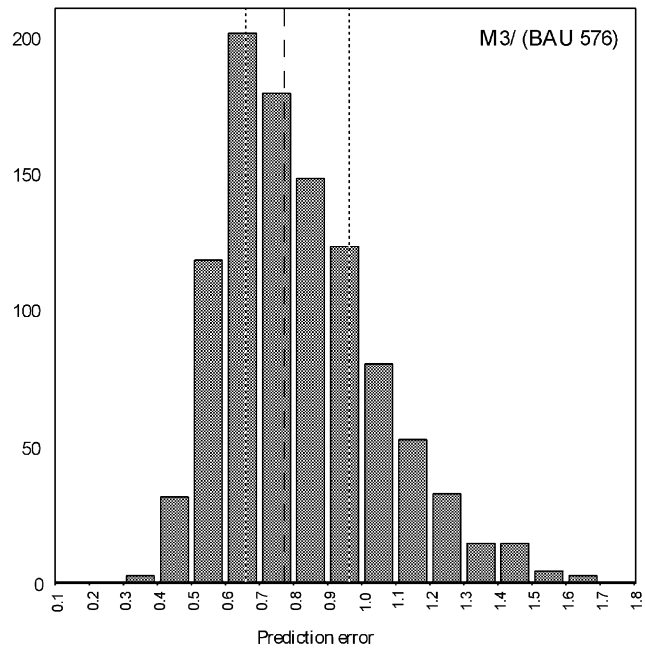

Fig. 8. Frequency distribution of the prediction error calculated for M3/ (number 576) from Bau de l'Aubesier with equations resulting from 1000 runs (for explanation, see text). Dashed line, median value; dotted lines, 1st and 3rd quartiles.

made up primarily of male sub-adults and adults of more than 3 years, sometimes associated with very old stallions.

Ultimately in Fig. 9, the recurrence of the same age structures in the lower levels testifies to a selective hunting directed at adults rather than very young or very old individuals. The exclusive hunting of bachelors groups is not possible owing to the significant proportion of juveniles. On the other hand, the age structure from the upper level stands out from those of the subjacent deposits. It reflects a selective choice by Neandertals of juveniles, sub-adults (0–6 years) and older horses, particularly of more than 12 years, as indicated by the frequency (f_x), and the other associated curves (l_x) and (q_x).

In present-day wild Equidae, the births take place between April and June, with a majority in May, while being largely lower during the remainder of the year [27,44]. By analogy with these modern observations, we have admitted a birthing period in May with ± 1 month. The data concerning the first stages of eruption were borrowed from Montané et al. [58] and correspond, for some of them, to those of Guadelli [22]. The permanent teeth least affected by tooth wear were used in order to estimate the months during which certain horses were killed in the whole sequence. The results are limited by the number of teeth available (n=25). Nevertheless, they very often indicate a regular hunting during a relatively short lapse of time, during the summer until the beginning of the autumn, i.e.

upper level (n=2)—July to September (± 1 month);
level H (n=14)—July to September (± 1 month);
level H (n=1)—November (± 1 month);
level I (n=6)—July to September (± 1 month);
remains (n=2)—July (± 1 month).

It is noteworthy that even if one considers a delayed birthing period, one still observes a regular mortality in juveniles for each levels, which is well circumscribed within a time span, which must correspond to seasonal hunts.

A possible migration of the horses may have determined this type of strategy in human groups. The current data on wild horse populations indicate that it is because the stallion defends its particular harem more than a strictly limited territory, that various social units can gather in herds and move in a seasonal way depending on abundance of food [27]. We are well familiar with the great herd gatherings of African zebras, which migrate during the rainy and dry seasons according to the food availability [53]. In addition, it is noted that in temperate, sub-Arctic, and mountainous zones, the majority of ungulates also gather in herds according to the season [18]. It is, thus, possible that seasonal factors generated more or less significant groups of horses in the Middle Palaeolithic and that they were hunted during these periods of gathering.

6. Comparison of age structures of the horses from Bau de l'Aubesier with those of a natural population of zebras (*E. burchelli boehmi*) from the National Park of Akagera (Rwanda)

The number of dental material of the lower levels allowed us to compare the mortality of the horses of the Bau with that of a natural African population of zebras (*E. burchelli boehmi*) from the National Park of Akagera in Rwanda, where the individuals died in an accidental way following a bush fire. In Akagera, the ages were obtained from the height of M1/ and the examination of the incisors [71]. This natural population, estimated in 1968 at approximately 1500 individuals by Spinage [72], provides a catastrophic age structure and a reliable comparative model to evaluate the impact of Neandertals in the whole of the levels H, I, and J of Bau de l'Aubesier. From a methodological point of view, it is very difficult, even impossible, to characterise the precise image of a live population at the time of collection of carcasses, because the frequency of juveniles, in particular of newborns, is often underestimated compared with that of adults [10]. Other than the fluctuation of numbers inherent in the seasonal phenomena, which modifies the age groups, the principal bias is especially related to the differential preservation (mainly animal impact and physico-chemical phenomena), which tends to minimise the representation of younger ones. It should be noted,

Table 7
Differential preservation between the right and left teeth of horses from Bau de l'Aubesier

	Left teeth	Right teeth	Total expected	% Differential preservation
Upper level	23	18	46	89.13
Level H	64	62	128	98.44
Level I	79	66	158	91.77
Level J	20	21	42	97.62
All levels	186	167	372	94.89

Table 8
Life table and mortality indices of horses from Bau de l'Aubesier (see details in text for calculation)

Age classes (years)	% Age classes	f_x	l_x	q_x
Upper level (NISP=41)				
0–3	38.24	382.35	1000.00	382.35
3–6	21.96	219.57	617.65	355.50
6–9	13.94	139.44	398.07	350.29
9–12	12.86	128.59	258.63	497.21
12–15	5.68	56.76	130.04	436.47
15–18	3.69	36.89	73.28	503.44
18–21	2.11	21.14	36.39	580.97
21–25	1.52	15.25	15.25	1000.00
Level H (NISP=126)				
0–3	27.88	278.78	1000.00	278.78
3–6	18.46	184.63	721.22	255.99
6–9	27.15	271.54	536.60	506.04
9–12	18.56	185.62	265.06	700.31
12–15	6.27	62.73	79.43	789.73
15–18	1.67	16.70	16.70	1000.00
Level I (NISP=145)				
0–3	16.97	169.71	1000.00	169.71
3–6	16.73	167.29	830.29	201.48
6–9	31.91	319.11	663.00	481.32
9–12	21.73	217.31	343.88	631.94
12–15	8.87	88.66	126.57	700.49
15–18	3.25	32.53	37.91	858.20
18–21	0.46	4.63	5.38	861.67
21–25	0.07	0.74	0.74	1000.00
Level J (NISP=41)				
0–3	26.51	265.07	1000.00	265.07
3–6	11.88	118.82	734.93	161.68
6–9	29.64	296.42	616.11	481.12
9–12	24.05	240.51	319.69	752.32
12–15	7.91	79.12	79.18	999.30
15–18	0.01	0.06	0.06	1000.00

however, that in Akagera, the excellent preservation of juvenile craniums compared with adults ones, together collected just after the bush fire, does not justify the calculation of a corrective factor to set against the differential preservation of these same juveniles [72].

The mortality based on life tables of the entire horse population of the Bau de l'Aubesier (levels H, I, and J) is totally different from that of the zebras of Akagera (Table 9). As shown in Fig. 10, in terms of frequency (f_x), the first two age groups are less well represented, on the other hand, the proportion of adults from 6 to 15 years is significantly higher than that of Akagera, whose numbers are greater in the following age groups. The distortion observed between the death rates (q_x) of these two populations is distinctively marked in the 6–18 years interval, and suggests at Bau de l'Aubesier, a more important hunting of horses corresponding to this interval. This distortion is all the more significant for the following reason: "because it is least affected by bias, the mortality rate curve (q_x) is the most efficient life table series for comparing the pattern of mortality with age in different populations" [10, p. 906]. Indeed, the method of calculation detailed previously shows that if there is a bias in the estimate of the first age group, the error associated with each value (l_x) will be iterative in the successive age groups. This is not the case for the mortality rate (q_x), which deals only with the number of individuals having survived in the age group considered.

In addition, the survival rate of fossil assemblages gives us the approximate image of the population if all the individuals had survived. It corresponds to the survival curve of the natural population of Akagera, typical of those that are usually described with a regular decrease of the successive age classes [72] (as shown in Fig. 10, with l_x). Comparing with the population of Bau de l'Aubesier, we clearly observe the distortion for the individuals of more than 9 years, thus confirming the human impact on the fossil assemblage.

7. Age structures of horses and hunting strategies in the French Middle Palaeolithic

The selective hunting of adults according to the seasonal phenomena was also considered in the Middle Palaeolithic layers, where this ungulate of large size dominates the faunal spectrum. We shall mention the dental material of horses from layer 14 of Combe-Grenal, which constitutes, according to Levine [45] and Guadelli (personal communication), one of the richest archaeological assemblages for this period (NISP=435). In this level, it is the prime-aged adult individuals who were preferentially hunted. Moreover, the hunting technique consisted in leading groups of horses towards a snowdrift, a river bed, or towards an enclosure undoubtedly located close to the site [45,

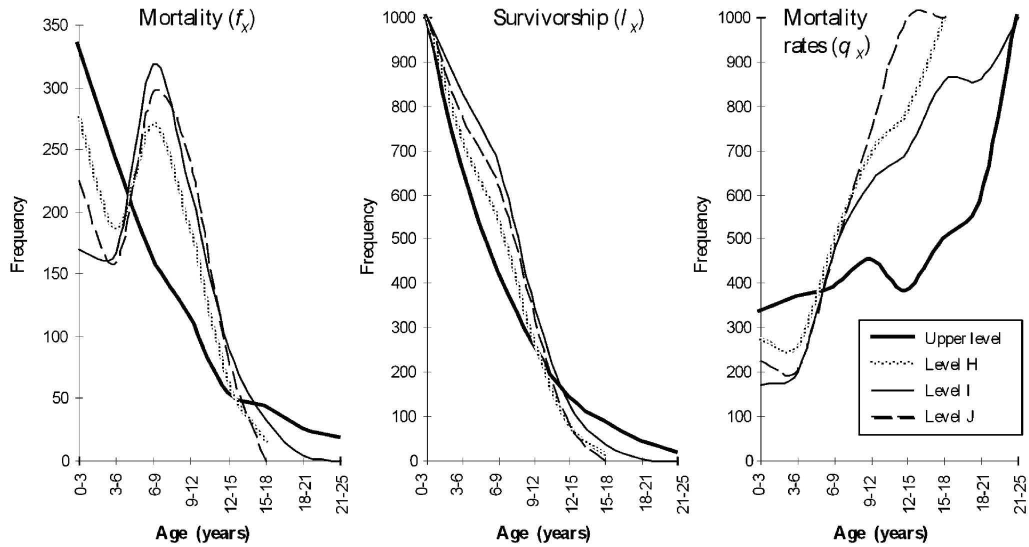

Fig. 9. Mortality and survivorship curves of horses from Bau de l'Aubesier.

Table 9
Life tables of zebras from the natural population of Akagera in Rwanda (data from Spinage [72]) and of horses from Bau de l'Aubesier (levels H+I+J)

Age classes (years)	% Age classes	f_x	l_x	q_x
Akagera (n=128)				
0–3	29.69	296.88	1000.00	296.88
3–6	14.84	148.44	703.13	211.11
6–9	7.81	78.13	554.69	140.85
9–12	15.63	156.25	476.56	327.87
12–15	14.84	148.44	320.31	463.41
15–18	12.50	125.00	171.88	727.27
18–21	3.91	39.06	46.88	833.33
21–25	0.78	7.81	7.81	1000.00
Bau de l'Aubesier—levels H+I+J (NISP=312)				
0–3	22.63	226.29	1000.00	226.29
3–6	16.79	167.92	773.71	217.03
6–9	29.69	296.92	605.79	490.14
9–12	20.76	207.56	308.87	672.01
12–15	7.69	76.94	101.31	759.44
15–18	2.19	21.87	24.37	897.49
18–21	0.22	2.15	2.50	861.67
21–25	0.03	0.35	0.35	1000.00

p. 126]. Levine also mentions other Mousterian sites like Roc-de-Marsal (Gironde) and La Baume de Gigny (Jura) where horses were butchered, respectively, in proximity of a cliff dominating the valley of the Vézère, and at the foot of a rocky face. In both cases, the sample size does not allow an interpretation of the possible horse social units. Let us state, however, that at both of these sites, sub-adults, and adults especially, dominate most often in age profiles [45, Figs. 80–89 and 94–97].

Other sites highlight relatively short occupations as La Combette (Vaucluse), where the remains of some horses were consumed. Here, it seems that it is during a very short halt of Neandertals that sub-adults were stalked [7]. On the contrary, at the cave-site of Le Portel (Ariège), the established profiles of two Mousterian levels does not indicate a deliberate selection of any particular age group [17]. At the cave-site of Rescoundudou (Aveyron), horse was hunted along with deer in a regular way by Neandertals, near a water source [25,26]. At the Tournal Cave (Aude), horse often dominates the assemblage depending on the level of occupations. The latter was preferentially hunted by Neandertals despite the fact that Bovinae and ibexes abounded around the site. This choice was perhaps related to seasonal occupations in winter and in summer, but in all cases, it seems to have been small social units, which were preferred without ruling out the possibility that some individuals may have been scavenged [65,66]. Finally, let us mention the Upper Palaeolithic site of Solutré (Saône-et-Loire), which is certainly the best example where seasonal migration was established for horses. This animal would have been hunted at the foot of the Roche, during moving between the plains of the Saône in winter, and the high plateaus in summer [83].

8. Conclusions

At Bau de l'Aubesier, horse constituted a game of choice for Neandertals. Its dental frequency (NISP=776) places this site among the richest European archaeological deposits where Equidae dominate. The new methodological approach, derived from the use of Levine's [45] referential dental collection, allowed for an inter-specific comparison between *E. mosbachensis*, *E.* cf. *taubachensis*, *E.* sp., and *E. caballus* cf. *gallicus*. From

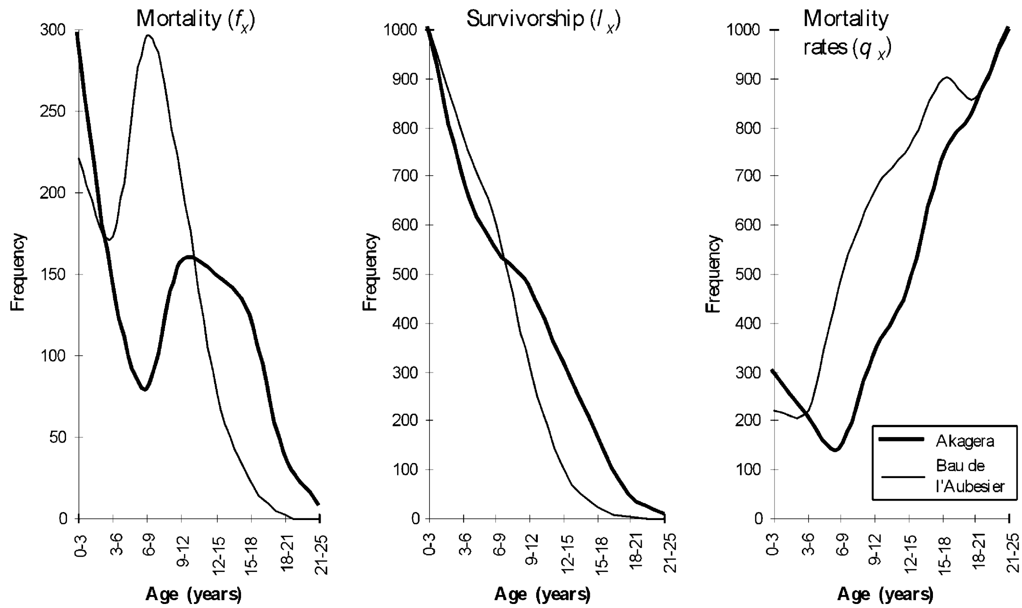

Fig. 10. Mortality and survivorship curves of horses from Bau de l'Aubesier (levels H, I, and J) compared with those of the natural population of zebras from Akagera (Rwanda).

a methodological point of view, the testing of the age estimates obtained from the paired teeth and the precise evaluation of the age groups intervals indicate that our predictive equations are reliable for the construction of mortality curves. The combined analysis of frequency, survival, and mortality rates highlights the impact of Neandertals on the adult age classes of horses in the lower archaeological levels from Bau de l'Aubesier. The distortion observed between the catastrophic age structure of the entire natural population of zebras of Akagera and that of the fossil horses confirms an hunting pressure directed principally at adults in levels H, I, and J. Moreover, the eruption stages and dental replacement indicate, for the Bau de l'Aubesier, specific periods of frequentation by Neandertals, during summer months until the beginning of autumn.

The age structures indicate that hunting strategies of successive human populations in the various levels of occupation cannot be reduced to the exclusive scavenging of carcasses, as has been suggested by Binford [2] for Klasies River Mouth in South Africa or for the Abri Vaufrey in Dordogne [3].

Undoubtedly, the hunters of Bau de l'Aubesier regularly frequented various hunting territories, which correspond to the living areas of the main species of the site. These territories are a broken and abrupt landscape of limestone crests dominating the river of Nesque, and an immense plateau more or less open according to periods of occupation. We observe a similar situation in Spain, such as the middle valley of Arlanza at Burgos in the Millán and Ermita Caves, from which Neandertals could control various biotopes characterised by a fluvial environment, which today constitute one of the main roads of natural communication employed by different ungulates [61].

Finally, at Bau de l'Aubesier, the migratory phenomena and herd gatherings at certain periods of the year were undoubtedly characterised by large size species such as the horse. In fact, a more systematic hunting would have been used by Neandertals during their hunting campaigns. This would explain why in the majority of Middle Palaeolithic sites, Equidae age profiles are often characterised by identical population structures with a high frequency of adult individuals, often interpreted as the result of a massive butchery.

Acknowledgements

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Appendix A.

Estimated age for associated teeth from Bau de l'Aubesier and Jaurens with confidence interval of prediction at $\pm 2\sigma$ (p<0.05) and $\pm 1\sigma$ (p<0.33) (s., left; d., right)

Number: teeth	Crown height	Estimated age	p<0.05	p<0.33
Bau de l'Aubesier				
59: P4/–M1 s.				
P4/	59.2	7.73	6.14–9.31	6.94–8.52
M1/	54.4	7.64	6.30–8.98	6.97–8.31
14: M2/–M3/ d.				
M2/	53.0	8.92	7.34–10.50	8.13–9.71
M3/	53.4	8.13	6.49–9.77	7.31–8.95
966: M2/–M3/ d.				
M2/	71.4	6.42	4.78–8.06	5.60–7.24
M3/	70.2	6.46	4.77–8.16	5.62–7.31
576: M2/–M3/ d.				
M2/	34.7	13.73	12.18–15.28	12.96–14.51
M3/	31.7	13.00	11.44–14.55	12.22–13.78
896: P4/–M3/ d.				
P4/	60.0	7.63	6.04–9.22	6.83–8.42
M1/	58.9	6.95	5.59–8.31	6.27–7.63
M2/	63.9	7.38	5.75–9.01	6.56–8.19
M3/	58.4	7.65	5.96–9.33	6.80–8.49
144: M1/–M2/s.				
M1/	47.4	8.94	7.61–10.27	8.27–9.60
M2/	62.6	7.53	5.91–9.16	6.72–8.35
732: P/4–M/1 s.				
P/4	41.0	10.26	7.74–12.78	9.00–11.52
M/1	48.7	7.56	5.59–9.52	6.58–8.54
Jaurens				
FSL 303.443: P/4–M/1 s.				
P/4	55.0	7.87	5.23–10.51	6.55–9.19
M/1	47.7	7.68	5.72–9.64	6.70–8.66
FSL 303.446: M/1–M/3 d.				
M/1	31.6	11.46	9.51–13.41	10.49–12.44
M/2	32.4	12.97	11.67–14.26	12.32–13.61
M/3	37.7	11.61	9.87–13.35	10.74–12.48
FSL 303.461: P/2–P/3 d.				
P/2	17.3	12.86	11.12–14.59	11.99–13.72
P/3	24.5	14.71	13.36–16.07	14.04–15.39
FSL 303.461: P/3–M/3 s.				
P/3	33.8	10.95	9.56–12.34	10.25–11.65
P/4	41.5	10.13	7.61–12.66	8.87–11.39
M/1	30.1	12.04	10.10–13.98	11.07–13.01
M/2	34.8	12.16	10.85–13.46	11.51–12.81
M/3	33.0	13.00	11.26–14.74	12.13–13.87
FSL 303.463: P/2–P/3 d.				
P/2	23.5	10.82	9.09–12.55	9.96–11.69
P/3	31.1	11.85	10.46–13.23	11.15–12.54
FSL 303.466: P/2–P/3 s.				
P/2	14.8	13.91	12.19–15.62	13.05–14.77
P/3	22.4	15.84	14.48–17.20	15.16–16.52
FSL 303.447: P/2–M/3 d.				
P/2	34.5	8.58	6.83–10.33	7.71–9.45
P/3	49.2	8.13	6.71–9.55	7.42–8.84

Number: teeth	Crown height	Estimated age	p<0.05	p<0.33
P/4	58.2	7.59	4.90–10.27	6.24–8.93
M/1	51.2	7.27	5.30–9.24	6.29–8.25
M/3	53.4	8.60	6.82–10.39	7.71–9.50
FSL 303.447: P/3–P/4 s.				
P/3	50.5	8.00	6.58–9.42	7.29–8.71
P/4	58.8	7.54	4.85–10.23	6.19–8.88
FSL 303.471: M/1–M/2 d.				
M/1	30.6	11.84	9.90–13.79	10.87–12.82
M/2	35.4	11.97	10.67–13.27	11.32–12.62
FSL 303.473; M/1–M/3 d.				
M/1	62	6.34	4.31–8.38	5.32–7.36
M/2	60.3	7.45	6.11–8.80	6.78–8.13
M/3	61	7.47	5.64–9.29	6.56–8.38
FSL 303.478: P/4–M/3 s.				
P/4	72.4	6.06	3.44–8.69	4.75–7.38
M/1	62.7	6.29	4.25–8.33	5.27–7.31
M/2	62.3	7.21	5.86–8.57	6.54–7.89
M/3	62	7.31	5.49–9.13	6.40–8.22
FSL 303.480: P/3–M/3 s.				
P/3	19.9	17.38	16.01–18.76	16.70–18.07
M/1	25.5	14.07	12.15–15.98	13.11–15.03
M/2	34.6	12.22	10.92–13.52	11.57–12.87
M/3	35.5	12.22	10.48–13.97	11.35–13.09

Appendix B.

List of *Equus* teeth from Bau de l'Aubesier (s., left; d., right)

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
X	D2/ s.	Upper	Deciduous	1.208	0.5625
271	D2/ d.	J	Deciduous	1.208	0.5625
359	D2/ s.	J	Deciduous	1.208	0.5625
359	D2/ s.	J	Deciduous	1.208	0.5625
85	D2/ s.	I	Deciduous	1.208	0.5625
611	D2/ s.	I	Deciduous	1.208	0.5625
1365	D2/ d.	I	Deciduous	1.208	0.5625
460	D2/ d.	H	Deciduous	1.208	0.5625
931	D2/ d.	H	Deciduous	1.208	0.5625
318	D3/ d.	Upper	Deciduous	1.625	0.7708
271	D3/ d.	J	Deciduous	1.625	0.7708
359	D3/ s.	J	Deciduous	1.625	0.7708
359	D3/ s.	J	Deciduous	1.625	0.7708
611	D3/ s.	I	Deciduous	1.625	0.7708
48	D3/ s.	H	Deciduous	1.625	0.7708
143	D3/ s.	H	Deciduous	1.625	0.7708
143	D3/ s.	H	Deciduous	1.625	0.7708
276	D3/ d.	H	Deciduous	1.625	0.7708
320	D3/ d.	H	Deciduous	1.625	0.7708
320	D3/ d.	H	Deciduous	1.625	0.7708
439	D3/ s.	H	Deciduous	1.625	0.7708
867	D3/ d.	H	Deciduous	1.625	0.7708
265	D4/ s.	J	Deciduous	1.917	0.9167
271	D4/ d.	J	Deciduous	1.917	0.9167
359	D4/ s.	J	Deciduous	1.917	0.9167

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
359	D4/ s.	J	Deciduous	1.917	0.9167
369	D4/ s.	J	Deciduous	1.917	0.9167
397	D4/ d.	I	Deciduous	1.917	0.9167
611	D4/ s.	I	Deciduous	1.917	0.9167
276	D4/ d.	H	Deciduous	1.917	0.9167
431	D4/ d.	H	Deciduous	1.917	0.9167
867	D4/ d.	H	Deciduous	1.917	0.9167
1078	D4/ s.	H	Deciduous	1.917	0.9167
235	D3–4/ d.	Upper	Deciduous	1.917	0.9167
10	D3–4/ s.	H	Deciduous	1.917	0.9167
439	D3–4/ s.	H	Deciduous	1.917	0.9167
297	P2/ s.	Upper	Unworn	2.583	0.1250
338	P2/ d.	Upper	35.0	10.088	0.7942
572	P2/ s.	Upper	Unworn	2.583	0.1250
737	P2/ s.	Upper	46.3	8.333	0.8163
X	P2/ d.	Upper	35.0	10.088	0.7942
188	P2/ d.	J	33.0	10.485	0.7937
198	P2/ d.	J	36.0	9.903	0.7943
255	P2/ d.	J	42.7	8.843	0.8046
364	P2/ s.	J	22.6	13.417	0.7951
474	P2/ s.	J	29.7	11.236	0.7956
199	P2/ s.	I	38.2	9.530	0.7964
447	P2/ s.	I	46.0	8.376	0.8154
663	P2/ s.	I	47.3	8.196	0.8200
691	P2/ d.	I	45.4	8.460	0.8135
841	P2/ d.	I	23.4	13.130	0.7965
919	P2/ d.	I	49.5	7.872	0.8268
974	P2/ d.	I	63.6	5.111	0.8005
1209	P2/ s.	I	27.3	11.881	0.7973
X	P2/ d.	I	33.0	10.485	0.7937
6	P2/ d.	H	39.6	9.307	0.7978
34	P2/ d.	H	37.6	9.624	0.7958
42	P2/ s.	H	Unworn	2.583	0.1250
95	P2/ s.	H	26.6	12.088	0.7976
286	P2/ d.	H	Unworn	2.583	0.1250
536	P2/ d.	H	Unworn	2.583	0.1250
680	P2/ d.	H	51.3	7.609	0.8312
710	P2/ d.	H	41.0	9.091	0.8004
806	P2/ s.	H	45.5	8.445	0.8138
931	P2/ d.	H	Unworn	2.583	0.1250
276	P3/ d.	J	51.7	8.779	0.5537
59	P4/ s.	I	59.2	7.729	0.7926
896	P4/ d.	I	60.0	7.627	0.7952
379	P3–4/ d.	Upper	65.0	6.012	1.4412
X	P3–4/ s.	Upper	Unworn	3.667	0.2500
15	P3–4/ s.	J	49.0	9.257	1.4202
63	P3–4/ d.	J	55.0	7.895	1.4057
209	P3–4/ d.	J	40.6	11.418	1.4582
383	P3–4/ d.	J	51.2	8.729	1.4115
405	P3–4/ s.	J	50.7	8.848	1.4132
519	P3–4/ s.	J	45.6	10.092	1.4363
341	P3–4/ s.	I	56.3	7.598	1.4077
400	P3–4/ s.	I	50.9	8.799	1.4125
573	P3–4/ s.	I	68.0	5.568	1.4559
581	P3–4/ s.	I	81.2	4.252	1.4567
716	P3–4/ d.	I	34.4	13.238	1.4735

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
826	P3–4/ d.	I	71.0	5.203	1.4678
967	P3–4/ s.	I	69.5	5.382	1.4618
967	P3–4/ s.	I	34.2	13.295	1.4733
1228	P3–4/ s.	I	63.0	6.338	1.4304
21	P3–4/ d.	H	54.0	8.101	1.4034
102	P3–4/ d.	H	33.2	13.603	1.4695
135	P3–4/ s.	H	51.4	8.680	1.4108
159	P3–4/ d.	H	78.2	4.468	1.4692
271	P3–4/ s.	H	53.3	8.259	1.4041
367	P3–4/ s.	H	33.4	13.550	1.4707
507	P3–4/ d.	H	46.7	9.812	1.4306
566	P3–4/ d.	H	Unworn	3.667	0.2500
568	P3–4/ d.	H	54.5	8.000	1.4036
583	P3–4/ s.	H	74.4	4.829	1.4690
599	P3–4/ s.	H	58.0	7.263	1.4093
604	P3–4/ d.	H	57.8	7.300	1.4085
606	P3–4/ d.	H	68.5	5.507	1.4581
620	P3–4/ s.	H	72.6	5.010	1.4702
629	P3–4/ s.	H	52.0	8.535	1.4082
647	P3–4/ s.	H	65.7	5.911	1.4449
662	P3–4/ s.	H	31.4	14.168	1.4604
711	P3–4/ d.	H	51.6	8.631	1.4099
1092	P3–4/ s.	H	66.6	5.778	1.4491
59	M1/ s.	I	54.4	7.638	0.6713
896	M1/ d.	I	58.9	6.950	0.6813
144	M1/ s.	H	47.4	8.937	0.6650
896	M2/ d.	I	63.9	7.379	0.8150
966	M2/ d.	I	71.4	6.417	0.8208
14	M2/ d.	H	53.0	8.920	0.7892
144	M2/ s.	H	62.6	7.535	0.8115
576	M2/ d.	H	34.7	13.733	0.7757
34	M1–2/ d.	Upper	86.0	3.759	1.2412
65	M1–2/ d.	Upper	72.2	5.653	1.2499
65	M1–2/ d.	Upper	38.7	11.912	1.2703
341	M1–2/ d.	Upper	76.4	5.124	1.2571
1046	M1–2/ d.	Upper	Unworn	1.500	0.3333
62	M1–2/ s.	J	47.3	9.612	1.2348
162	M1–2/ d.	J	38.7	11.912	1.2703
162	M1–2/ d.	J	55.6	8.004	1.1953
229	M1–2/ d.	J	71.3	5.763	1.2466
252	M1–2/ d.	J	61.0	7.122	1.1999
254	M1–2/ s.	J	62.2	6.936	1.2036
313	M1–2/ d.	J	64.0	6.691	1.2101
332	M1–2/ d.	J	46.3	9.847	1.2406
63	M1–2/ s.	I	58.8	7.460	1.1942
129	M1–2/ d.	I	71.0	5.794	1.2451
234	M1–2/ s.	I	42.6	10.799	1.2594
276	M1–2/ s.	I	Unworn	1.500	0.3333
289	M1–2/ d.	I	50.9	8.844	1.2154
324	M1–2/ d.	I	76.5	5.110	1.2569
373	M1–2/ d.	I	Unworn	1.500	0.3333
387	M1–2/ s.	I	76.0	5.184	1.2563
398	M1–2/ s.	I	51.9	8.640	1.2094
432	M1–2/ s.	I	68.2	6.150	1.2329
473	M1–2/ d.	I	92.0	2.785	1.3149
483	M1–2/ s.	I	30.0	14.842	1.2916

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
488	M1–2/ s.	I	21.0	18.691	1.4719
490	M1–2/ s.	I	43.0	10.684	1.2570
500	M1–2/ s.	I	40.0	11.517	1.2684
505	M1–2/ s.	I	38.7	11.912	1.2703
515	M1–2/ d.	I	45.1	10.133	1.2477
524	M1–2/ d.	I	Unworn	1.500	0.3333
589	M1–2/ d.	I	72.2	5.653	1.2499
598	M1–2/ d.	I	28.6	15.356	1.3014
603	M1–2/ d.	I	46.0	9.918	1.2423
617	M1–2/ s.	I	81.0	4.507	1.2462
626	M1–2/ d.	I	54.6	8.168	1.1984
649	M1–2/ d.	I	61.6	7.034	1.2013
657	M1–2/ s.	I	61.3	7.080	1.2009
715	M1–2/ d.	I	39.5	11.681	1.2693
728	M1–2/ s.	I	84.3	4.011	1.2408
768	M1–2/ d.	I	51.0	8.823	1.2148
775	M1–2/ s.	I	63.4	6.767	1.2077
863	M1–2/ d.	I	Unworn	1.500	0.3333
898	M1–2/ d.	I	67.0	6.297	1.2271
932	M1–2/ d.	I	69.0	6.037	1.2359
960	M1–2/ d.	I	39.0	11.821	1.2701
979	M1–2/ d.	I	82.5	4.286	1.2433
1027	M1–2/ d.	I	78.0	4.908	1.2549
1096	M1–2/ s.	I	33.8	13.534	1.2729
1125	M1–2/ s.	I	44.5	10.292	1.2503
1204	M1–2/ s.	I	27.7	15.695	1.3108
1340	M1–2/ d.	I	72.6	5.605	1.2517
1465	M1–2/ s.	I	82.7	4.257	1.2431
X	M1–2/ s.	I	83.0	4.212	1.2430
12	M1–2/ s.	H	47.9	9.479	1.2310
20	M1–2/ d.	H	42.6	10.799	1.2594
20	M1–2/ s.	H	Unworn	1.500	0.3333
38	M1–2/ s.	H	43.2	10.637	1.2558
47	M1–2/ d.	H	Unworn	1.500	0.3333
49	M1–2/ s.	H	41.7	11.044	1.2646
51	M1–2/ s.	H	53.7	8.319	1.2014
60	M1–2/ d.	H	Unworn	1.500	0.3333
80	M12/ s.	H	Unworn	1.500	0.3333
136	M12/ s.	H	Unworn	1.500	0.3333
184	M1–2/ s.	H	63.4	6.767	1.2077
201	M1–2/ d.	H	43.2	10.637	1.2558
210	M1–2/ d.	H	67.3	6.258	1.2285
345	M1–2/ d.	H	52.9	8.462	1.2043
346	M1–2/ s.	H	81.8	4.387	1.2444
571	M1–2/ s.	H	Unworn	1.500	0.3333
575	M1–2/ s.	H	60.8	7.150	1.1993
620	M1–2/ s.	H	48.0	9.454	1.2305
644	M1–2/ d.	H	59.8	7.298	1.1965
651	M1–2/ d.	H	79.0	4.778	1.2531
700	M1–2/ s.	H	67.8	6.196	1.2309
709	M1–2/ d.	H	50.6	8.906	1.2171
717	M1–2/ d.	H	54.2	8.233	1.1994
914	M1–2/ d.	H	75.2	5.279	1.2558
1168	M1–2/ d.	H	37.5	12.309	1.2734
651	M3/ s.	Upper	17.2	21.455	0.9081
803	M3/ s.	Upper	Unworn	3.750	0.2083

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
1475	M3/ s.	Upper	45.3	9.236	0.7958
60	M3/ s.	J	65.0	7.056	0.8589
229	M3/ d.	J	68.2	6.715	0.8550
382	M3/ s.	J	60.0	7.513	0.8484
70	M3/ s.	I	62.4	7.305	0.8553
94	M3/ d.	I	67.3	6.817	0.8580
195	M3/ s.	I	41.8	9.930	0.7889
207	M3/ s.	I	32.5	12.678	0.7818
208	M3/ d.	I	68.3	6.703	0.8546
446	M3/ s.	I	67.5	6.795	0.8574
513	M3/ s.	I	69.2	6.594	0.8515
563	M3/ s.	I	54.3	8.033	0.8249
634	M3/ d.	I	24.0	16.762	0.7770
712	M3/ d.	I	64.4	7.112	0.8585
713	M3/ d.	I	27.0	15.135	0.7706
720	M3/ d.	I	37.5	11.013	0.7862
767	M3/ d.	I	52.0	8.283	0.8143
816	M3/ d.	I	77.5	5.264	0.8111
819	M3/ d.	I	70.8	6.383	0.8441
896	M3/ d.	I	58.4	7.648	0.8434
966	M3/ d.	I	70.2	6.465	0.8475
1123	M3/ d.	I	63.0	7.249	0.8567
1404	M3/ d.	I	53.7	8.099	0.8221
14	M3/ d.	H	53.4	8.130	0.8207
33	M3/ s.	H	38.4	10.758	0.7866
82	M3/ d.	H	35.9	11.492	0.7849
89	M3/ d.	H	58.7	7.626	0.8445
133	M3/ s.	H	58.7	7.626	0.8445
133	M3/ s.	H	47.1	8.939	0.7986
229	M3/ d.	H	64.0	7.151	0.8580
246	M3/ d.	H	Unworn	3.750	0.2083
251	M3/ d.	H	Unworn	3.750	0.2083
255	M3/ d.	H	37.0	11.160	0.7858
264	M3/ d.	H	55.6	7.901	0.8311
279	M3/ s.	H	52.9	8.180	0.8184
291	M3/ d.	H	25.4	15.979	0.7715
292	M3/ s.	H	49.5	8.596	0.8048
318	M3/ s.	H	38.7	10.678	0.7868
452	M3/ s.	H	Unworn	3.750	0.2083
576	M3/ d.	H	31.7	12.995	0.7798
611	M3/ s.	H	61.4	7.393	0.8528
779	M3/ s.	H	Unworn	3.750	0.2083
785	M3/ d.	H	64.7	7.085	0.8588
X	M3/ s.	H	Unworn	3.750	0.2083
208 ou 308	D/2 s.	Upper	deciduous	1.125	0.5208
822	D/2 s.	I	Deciduous	1.125	0.5208
X	D/2 d.	I	Deciduous	1.125	0.5208
280	D/2 s.	H	Deciduous	1.125	0.5208
822	D/3 s.	I	Deciduous	1.292	0.6042
X	D/3 d.	I	Deciduous	1.292	0.6042
785	D/4 d.	Upper	Deciduous	1.708	0.8125
822	D/4 s.	I	Deciduous	1.708	0.8125
913	D/4 s.	H	Deciduous	1.708	0.8125
94	D/3–4 s.	Upper	Deciduous	1.708	0.8125
792	D/3–4 d.	Upper	Deciduous	1.708	0.8125
1076	D/3–4 s.	Upper	Deciduous	1.708	0.8125

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
X	D/3–4 s.	Upper	Deciduous	1.708	0.8125
367	D/3–4 d.	I	Deciduous	1.708	0.8125
383	D/3–4 s.	H	Deciduous	1.708	0.8125
454	D/3–4 s.	H	Deciduous	1.708	0.8125
656	D/3–4 d.	H	Deciduous	1.708	0.8125
90	P/2 s.	Upper	21.6	11.369	0.8683
590	P/2 s.	Upper	Unworn	2.417	0.1250
785	P/2 d.	Upper	Unworn	2.417	0.1250
788	P/2 s.	Upper	52.2	5.621	0.8870
1041	P/2 s.	Upper	43.1	7.310	0.9092
X	P/2 s.	Upper	Unworn	2.417	0.1250
X	P/2 s.	Upper	Unworn	2.417	0.1250
213	P/2 d.	J	Unworn	2.417	0.1250
265	P/2 s.	I	32.0	8.987	0.8647
267	P/2 s.	I	30.0	9.345	0.8607
299	P/2 s.	I	27.7	9.803	0.8592
361	P/2 s.	I	28.6	9.618	0.8593
419	P/2 d.	I	Unworn	2.417	0.1250
459	P/2 s.	I	Unworn	2.417	0.1250
482	P/2 s.	I	21.3	11.458	0.8685
557	P/2 s.	I	Unworn	2.417	0.1250
665	P/2 s.	I	53.0	5.431	0.8862
700	P/2 s.	I	Unworn	2.417	0.1250
753	P/2 d.	I	26.5	10.073	0.8603
846	P/2 d.	I	37.8	8.083	0.8893
231	P/2 s.	H	Unworn	2.417	0.1250
275	P/2 s.	H	Unworn	2.417	0.1250
337	P/2 d.	H	52.4	5.573	0.8871
338	P/2 d.	H	32.5	8.901	0.8661
422	P/2 s.	H	58.2	3.952	0.9603
774	P/2 d.	H	38.7	7.957	0.8931
994	P/2 s.	H	44.6	7.074	0.9105
1034	P/2 s.	H	Unworn	2.417	0.1250
1128	P/2 s.	H	52.4	5.573	0.8871
1232	P/2 s.	H	26.5	10.073	0.8603
1017	P/3 s.	H	Unworn	2.667	0.0833
732	P/4 s.	I	41.0	10.258	1.2612
281	P/3–4 d.	J	56.0	7.819	1.2266
364	P/3–4 d.	J	69.7	6.205	1.2692
60	P/3–4 d.	I	48.0	8.910	1.2092
433	P/3–4 s.	I	53.9	8.083	1.2162
460	P/3–4 s.	I	41.4	10.112	1.2437
462	P/3–4 d.	I	49.8	8.644	1.2051
543	P/3–4 s.	I	43.5	9.693	1.2295
586	P/3–4 d.	I	41.8	10.018	1.2414
750	P/3–4 s.	I	43.3	9.731	1.2310
890	P/3–4 d.	I	46.4	9.169	1.2141
960	P/3–4 s.	I	54.0	8.068	1.2170
1374	P/3–4 s.	I	40.6	10.278	1.2481
1439	P/3–4 d.	I	32.0	12.411	1.2749
26	P/3–4 d.	H	36.9	11.110	1.2661
135	P/3–4 s.	H	26.7	14.105	1.2605
177	P/3–4 d.	H	74.2	5.582	1.2545
419	P/3–4 d.	H	51.0	8.469	1.2067
721	P/3–4 s.	H	83.3	4.136	1.4223
732	P/3–4 d.	H	63.5	6.948	1.2685

Number	Tooth	Level	Crown height (mm)	Estimated Age (years)	Prediction error
790	P/3–4 d.	H	57.0	7.698	1.2324
891	P/3–4 s.	H	42.6	9.865	1.2367
727	M/1 s.	I	61.5	6.379	1.0160
732	M/1 s.	I	48.7	7.557	0.9815
85	M/1–2 d.	Upper	23.0	16.806	1.5187
161	M/1–2 s.	Upper	47.2	8.919	1.4747
567	M/1–2 d.	Upper	24.5	16.118	1.5104
689	M/1–2 s.	Upper	27.3	14.878	1.5133
785	M/1–2 s.	Upper	46.0	9.161	1.4787
801	M/1–2 d.	Upper	68.0	5.864	1.5003
X	M/1–2 d.	Upper	34.5	12.213	1.5222
148	M/1–2 s.	J	37.0	11.442	1.5224
200	M/1–2 s.	J	36.0	11.748	1.5215
217	M/1–2 s.	J	58.8	7.025	1.4598
X	M/1–2 d.	J	69.5	5.692	1.5059
324	M/1–2 s.	I	46.1	9.142	1.4783
347	M/1–2 s.	I	45.2	9.330	1.4828
363	M/1–2 d.	I	Unworn	1.500	0.3333
411	M/1–2 d.	I	45.5	9.267	1.4811
419	M/1–2 d.	I	Unworn	1.500	0.3333
637	M/1–2 d.	I	44.0	9.584	1.4905
715	M/1–2 s.	I	67.0	5.981	1.4943
960	M/1–2 s.	I	36.2	11.679	1.5212
1185	M/1–2 s.	I	75.0	5.055	1.5178
1390	M/1–2 s.	I	34.9	12.093	1.5229
1444	M/1–2 s.	I	62.5	6.518	1.4737
109	M/1–2 s.	H	35.6	11.879	1.5225
127	M/1–2 d.	H	54.5	7.650	1.4580
327	M/1–2 d.	H	79.0	4.532	1.5128
714	M/1–2 d.	H	81.2	4.232	1.5060
643	M/3 d.	Upper	Unworn	3.750	0.2083
776	M/3 s.	Upper	72.9	5.246	0.8891
X	M/3 s.	Upper	Unworn	3.750	0.2083
294	M/3 d.	I	Unworn	3.750	0.2083
391	M/3 s.	I	Unworn	3.750	0.2083
448	M/3 s.	I	37.2	11.743	0.8721
604	M/3 s.	I	64.7	6.864	0.9048
666	M/3 d.	I	35.6	12.191	0.8728
677	M/3 s.	I	81.0	2.966	1.1827
723	M/3 s.	I	Unworn	3.750	0.2083
1363	M/3 s.	I	51.5	8.890	0.8868
1458	M/3 s.	I	41.2	10.765	0.8697
1903	M/3 d.	I	26.5	15.469	0.8605
X	M/3 s.	I	37.4	11.687	0.8720
X	M/3 d.	I	68.4	6.200	0.8920
107	M/3 s.	H	Unworn	3.750	0.2083
208	M/3 s.	H	Unworn	3.750	0.2083
1239	M/3 s.	H	49.2	9.255	0.8794

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