

Original article

Ontogenetic changes and sexual dimorphism in the mandible of adult woolly mammoths (*Mammuthus primigenius*)[☆]

Changements ontogénétiques et dimorphisme sexuel de la mâchoire inférieure des mammoths laineux adultes (Mammuthus primigenius)

Diego J. Álvarez-Lao^{a,*}, Marcos Méndez^b

^a *Departamento de Geología, Universidad de Oviedo, C/Jesús Arias de Velasco s/n., 33005 Oviedo, Spain*

^b *Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, c/Tulipán s/n., 28933 Móstoles (Madrid), Spain*

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Abstract

Morphometric studies are a fundamental tool in paleontology to answer taxonomic, functional and evolutionary questions. In particular, appropriate functional interpretation often requires consideration of ontogenetic changes in the structures studied. The woolly mammoth (*Mammuthus primigenius*) is one of the most representative large mammal species of the Eurasian Pleistocene. Available ontogenetic studies on woolly mammoth mandible have focused on the first ontogenetic stages of the mandible development up to 4–5 years and have suggested that the symphyseal process is sexually dimorphic. In the present work, we studied ontogenetic changes and sexual dimorphism in 45 mandibles from subadult and adult stages (8–56 African Elephant Years). Our results show positive correlations among almost all the morphometric variables measured, as well as an increase of mandible size with age. This increase does not differ among the variables examined, although the highest values are related with the symphysis height and the opening of the horizontal branches, and the lower ones with the greatest length (dimension), which implies the increase in the relative mandible width and height throughout the individual life. Sexual dimorphism in the mandible is at best slight, and the symphyseal process is not diagnostic for sexing purposes. In addition, differences in age were an important confounding factor to assess sexual dimorphism and should be considered in future uses of sexual dimorphism assessment techniques.

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Keywords: *Mammuthus primigenius*; Mandible; Ontogenetic changes; Late Pleistocene; Sexual dimorphism

Résumé

Les études morphométriques sont un outil fondamental en paléontologie afin de répondre à des questions taxinomiques, fonctionnelles et évolutives. En particulier, une interprétation fonctionnelle appropriée exige souvent la prise en compte des variations ontogénétiques des structures étudiées. Le mammoth laineux (*Mammuthus primigenius*) est une des grandes espèces de mammifères du Pléistocène eurasiens les plus représentatives. Les études ontogénétiques disponibles sur la mâchoire inférieure de mammoth laineux se sont concentrées sur les premières étapes ontogénétiques du développement de la mâchoire inférieure jusqu'à 4-5 ans et ont suggéré que le processus de la symphyse soit sexuellement dimorphique. Dans le présent travail, nous avons étudié les changements ontogénétiques et le dimorphisme sexuel de 45 mâchoires inférieures de sub-adultes et d'adultes (8–56 Années d'Éléphants Africains). Nos résultats montrent des corrélations positives entre presque toutes les variables morphométriques mesurées, ainsi qu'une augmentation de taille de la mâchoire inférieure avec l'âge. Cette augmentation ne diffère pas parmi les variables examinées, bien que les valeurs les plus élevées soient liées à la hauteur de la symphyse et à l'ouverture des branches horizontales, et les plus faibles à la plus grande longueur, ce qui implique l'augmentation de la largeur et de la taille relatives de la mâchoire inférieure durant la vie de l'individu. Le dimorphisme sexuel dans la mâchoire inférieure, au mieux, léger, et le processus symphyseal n'est pas diagnostique pour la détermination du sexe. En outre, les différences d'âge sont un facteur important de confusion pour évaluer le dimorphisme sexuel et devraient être considérées dans de futures utilisations des techniques d'évaluation du dimorphisme sexuel.

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Mots clés : *Mammuthus primigenius* ; Mâchoire inférieure ; Changements ontogénétiques ; Pléistocène supérieur ; Dimorphisme sexuel

[☆] Corresponding editor: Gilles Escarguel.

* Corresponding author.

E-mail address: dalao@geol.uniovi.es (D.J. Álvarez-Lao).

1. Introduction

Morphometric studies are a fundamental tool in paleontology to answer taxonomic, functional and evolutionary questions (Oxnard, 1978; Bonnan, 2004; Hunt et al., 2008). In taxonomic studies, morphometry permits handling and interpreting variability of diagnostic elements and to remove the influences of confounding factors such as gender (sexual dimorphism; Plavcan, 1994) and age (ontogenetic change; Bastir et al., 2007) in such variability. In functional or evolutionary studies, sexual dimorphism or ontogenetic change often are the relevant factors, e.g., in inferences of sexual systems (Krishtalka et al., 1990) or in studies of phenotypic modularity or integration (Klingenberg, 2008). For example, phenotypic integration often requires the study of the ontogenetic changes in the relationships between morphological traits (Klingenberg, 2008).

The woolly mammoth (*Mammuthus primigenius*), the most representative species of the Holartic Pleistocene glaciations, has been a common subject of morphometric studies from several points of view. Evolutionary studies on molars (Aguirre, 1968, 1969a, 1969b; Maglio, 1972; Lister and Sher, 2001; Lister et al., 2005) have revealed an increase in hypsodonty, number of plates and lamellar frequency, and thinning of the enamel throughout the evolution of the mammoth lineage. Adaptive studies in mammoth populations have shown size reduction in insular populations from the northern Siberia island of Wrangel (Vartayán et al., 1993) and from the Channel Islands in California, USA (Agenbroad et al., 1999). Sexual dimorphism has been found for some skeletal elements, such as the pelvis (Lister, 1996), the skull, mandible and long bones (Haynes, 1991; Averianov, 1996). Ontogenetic changes in the skull, mandible and post-cranial skeleton have been studied by Maschenko (2002).

Ontogenetic studies in fossil organisms are not easy because they require a relatively high amount of well-preserved remains coming from a number of specimens at different developmental stages. In proboscideans, an additional problem is that ontogenetic changes occur almost during the whole life of these organisms, especially in male individuals (Haynes, 1991), so a representative sample requires a large number of specimens including all the developmental stages of the species. Although the fossil record of the woolly mammoth is relatively extensive and includes a wide range of death ages, findings of complete skeletons are very exceptional. Therefore, ontogenetic studies have to rely in particular elements. One of such elements is the mandible, for several reasons:

- it is a very robust bone that resists well the taphonomic processes; therefore it is frequently found in relatively complete conditions in fossil assemblages and provides a representative number of individuals to make statistical analyses;
- it allows to estimate the age of death of the specimen, based on tooth development;
- its size and shape change along the life of the specimens.

Early ontogenetic changes in mandibular shape have been studied by Maschenko (2002). During the first year of life, the

shape of the mandibular body is very shallow. The ascending ramus is very short and the coronoid process is sharply inclined backward; its angle with the mandibular body is greater than 115° . The symphyseal part is much longer than in adult phases. The main changes in the mandible during the first years of life, aside of an increase in size, are a progressive elevation of the ascending ramus, a shortening of the symphyseal part compared to the horizontal ramus, and an increase of the robustness (thickness) of the mandible. These changes are especially quick during the first four years of life. After this stage, the mandible acquires the proportions typical of adult individuals (Maschenko, 2002). According to Maschenko (2002), after these first years of life morphological changes in the mandible are less and slower.

Studies such as the one by Maschenko (2002) are useful steps forward but have limitations. First, analyses are completely narrative and no statistical analyses are provided. Second, sample size is low. Third, ontogenetic changes later in the life can occur but are not analysed. And fourth, the possibility of sexual dimorphism in the mandible remains unsettled. While Averianov (1996) states that the length of the symphysis is sexually dimorphic, other authors (Dick Mol, pers. com., 2005) have raised doubts about the reliability of this trait. Sexing elements of fossil species is easy when discrete, sex-specific traits are available or at least those traits show an obvious bimodal distribution (Plavcan, 1994). Otherwise it can be difficult because usually no sexed individuals are available as a reference (Rehg and Leigh, 1999). Here, we assess sexual dimorphism in the woolly mammoth mandible by applying techniques developed by paleoanthropologists (Plavcan, 1994; Josephson et al., 1996) which do not require comparison with sexed individuals.

The main objective of this study is to quantify ontogenetic changes and sexual dimorphism in woolly mammoth mandibles, using a large sample of individuals older than five years. Our specific questions are:

- Does ageing merely entail an increase in size of the mandible in the preadult and adult stages, or does it also involve a change in shape?
- Does the mandible simply increase in size as an integrated structure or can phenotypic modules be recognized in this ontogenetic change?
- Is there sexual dimorphism in the mammoth mandible and is symphysis length a useful indicator of it?

2. Material and methods

The woolly mammoth mandible sample studied here comes from the North Sea population, recovered between the British Isles and the European mainland, and stored in the National Natural History Museum (Naturalis) of Leiden and in the Natural History Museum at Rotterdam, both in The Netherlands. All the specimens ($n = 45$) were dredged from the locality named “Brown Bank” (close to the Dutch coast), whose radiocarbon dates place the mammoth occurrence between 44.1 and 28 ^{14}C ka BP, although most of the dates

range between 39 and 33 ^{14}C ka BP (Glimmerveen et al., 2004). Therefore, we consider this sample as geographically and chronologically homogeneous for our purposes.

We selected elements which allowed the measurement of a large number of morphometric variables. Our final sample consisted of 45 specimens and 11 variables (Fig. 1), although only 32 specimens provided data for GL (Greatest Length). The raw dataset is included in Appendix A. Variables studied follow Maschenko (2002) and Agenbrood (1994). We also included the width of the horizontal ramus (Whr), which apparently increases along the life of the specimens. We excluded very incomplete elements from the sample, as well as those variables that only can be measured in almost complete specimens (for instance, the greatest width or the greatest height).

The age of death of each specimen was estimated on the basis of molar development and wearing by analogy with living African elephants (*Loxodonta africana*), following the method of Laws (1966) modified by Jachmann (1988) and Craig (in Haynes, 1991). The age is provided in AEY (African Elephant Years) because we cannot assume with accuracy, up to date, that the life span of a woolly mammoth was exactly the same than the one of extant African elephants. The age of death of the sampled specimens ranges between 8 and 56 AEY ($m \pm SD = 35.3 \pm 13.9$; Figs. 2 and 3).

2.1. Ontogenetic changes

Correlation between morphometric variables was studied in three ways. Firstly, Pearson correlation was used to calculate the correlation matrix among the morphometric traits. No Bonferroni correction was applied to the resulting matrix (Gotelli and Ellison, 2004). Secondly, we removed the effect of age on the correlation among the morphometric traits by means of a GLM (General Linear Model) in which the 11 morphometric traits were the dependent variables and the estimated age was the independent variable. This analysis tests for a general effect of estimated age on the morphometric traits and provides a partial correlation matrix among the morphometric traits, in which the effect of estimated age has been removed. Thirdly, a Principal Component Analysis (PCA) was performed. Significance of the loadings of the original variables on each extracted factor was assessed by means of the broken-stick criterion (Peres-Neto et al., 2003). PCA excluding ($n = 45$) or including ($n = 32$) GL yielded similar results, so only those with GL are presented.

The relation between morphometric variables and age was studied in two ways. First, each morphometric variable was related to the estimated age using type II regression, after \log_{10} transformation of both morphometric variables and age, as recommended for morphometric and scaling studies (LaBarbera, 1989). Type II regression is suitable when both independent and dependent variables are measured with error (Gotelli and Ellison, 2004). Differences among morphometric variables in their increase with age were studied by testing differences in the slope of their relationship with the estimated age, by means of a t -test following Zar (1999). Second, the sample score on each factor in the PCA was correlated with the estimated age using Pearson correlation.

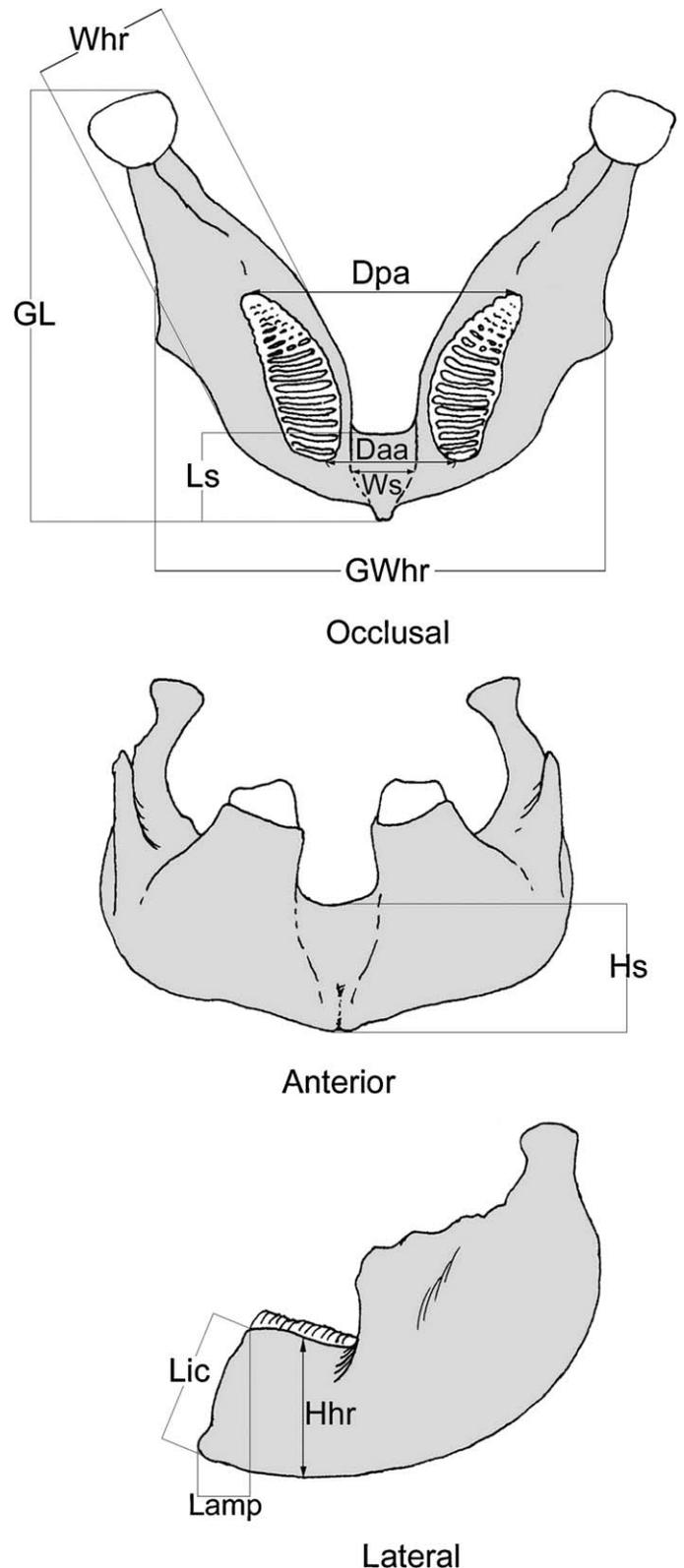


Fig. 1. Metrical variables measured in woolly mammoth mandibles. GL, Greatest Length; GWhr, Greatest Width between the horizontal ramus; Hhr, Height of the horizontal ramus; Whr, Width of the horizontal ramus; Lamp, Length between the anterior edge of mental process and the anterior edges of alveoli; Lic, Length of the interalveolar crest; Hs, Height of the symphysis; Ls, Length of the symphysis; Ws, Width of the symphysis; Daa, Distance between the horizontal branches at the level of anterior edge of alveoli; Dpa, Distance between the horizontal branches at the level of posterior edge of alveoli.

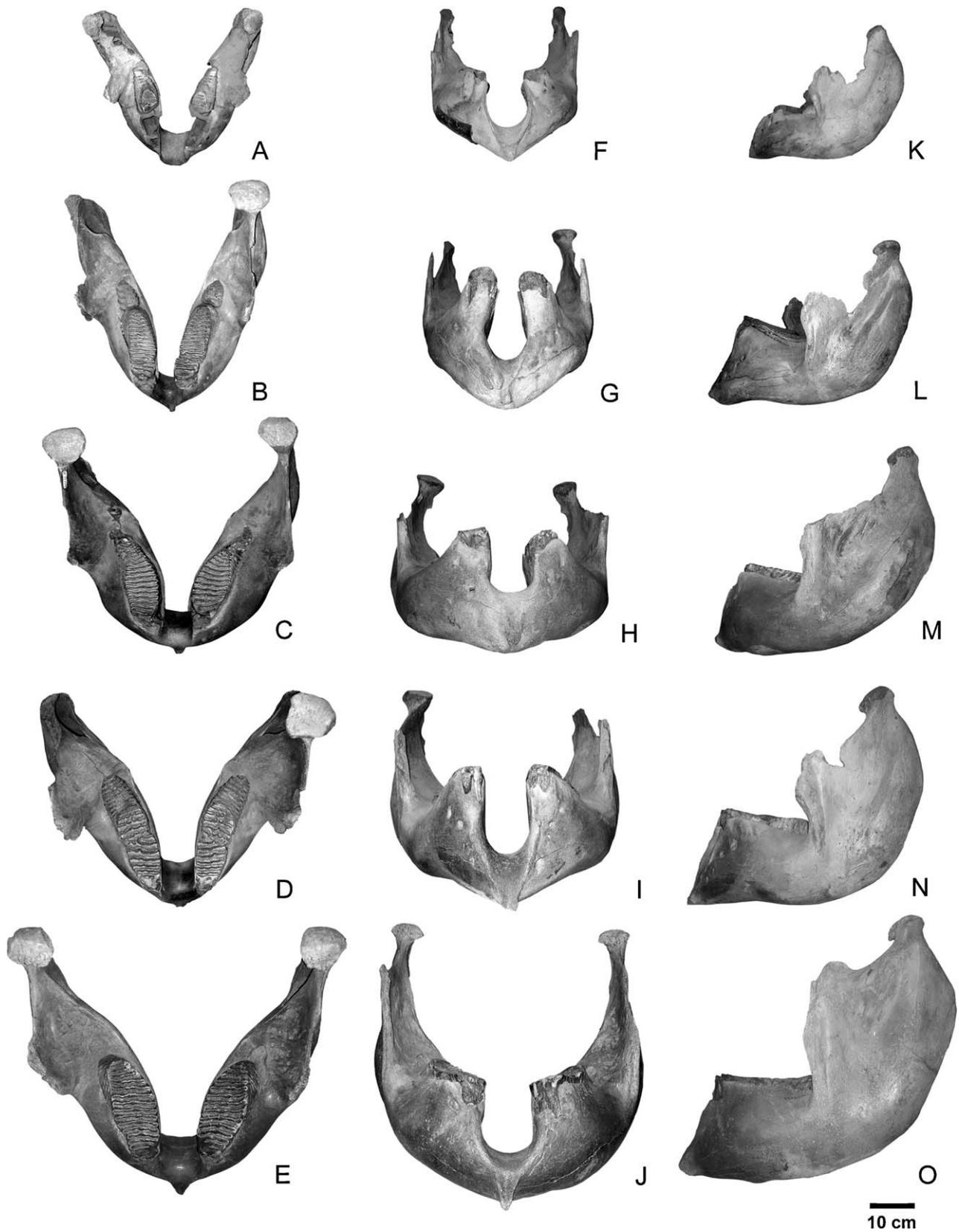


Fig. 2. Five examples of different ontogenetic growth stages in *Mammuthus primigenius* mandibles (all them coming from the North Sea). A, F, K, 8 AEY; B, G, L, 13 AEY; C, H, M, 26-28 AEY; D, I, N, 32-34 AEY; E, J, O, 49-53 AEY. A–E: occlusal views; F–J, anterior views; K–O, lateral views.

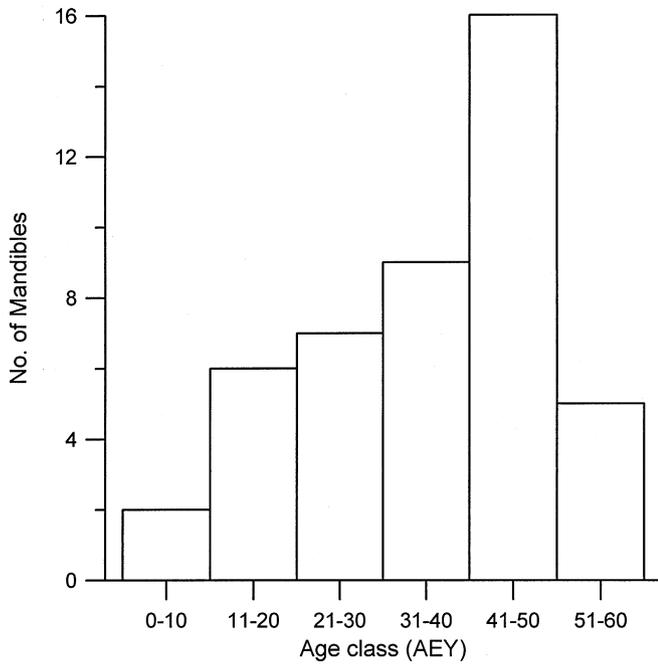


Fig. 3. Frequency histogram of the ages (in African Elephant Years, AEY) represented in the woolly mammoth mandibles studied in this work.

2.2. Sexual dimorphism

We assessed bimodality in the 11 morphometric traits by using the formula

$$b = \frac{M_3^2 + 1}{M_4 + \frac{3(n-1)^2}{(n-2)(n-3)}}$$

where M_3 is skewness, M_4 is kurtosis and n is sample size (Der and Everitt, 2002). Values of b greater than 0.55 indicates significant bimodality. No bimodality was detected (see Results). Sexing specimens of fossil species is easy when discrete, sex-specific traits are available or at least those traits show an obvious bimodal distribution (Plavcan, 1994). Otherwise it can be difficult because usually no sexed individuals are available as a reference (Rehg and Leigh, 1999). We did not make any a priori sex scoring and instead tested whether any of the measured traits showed indication of sexual dimorphism using three different methods: the “mean technique” (Plavcan, 1994), the “method of moments (MoM) technique” (Josephson et al., 1996), and “mixture analysis” (Dong, 1997). All these methods are common among primatologists and assess the degree of sexual dimorphism in traits for which no bimodal distribution is evident, i.e., when the distribution of the trait values for male and female individuals greatly overlap, producing a unimodal distribution in the pooled sample. The two first methods perform optimally when the sex ratio in the sample is balanced but are relatively robust to biases in sex ratio and intraspecific sex variability (Plavcan, 1994; Josephson et al., 1996; Regh and Leigh, 1999). They overestimate dimorphism when actual dimorphism is less than 1.5 (Rehg and Leigh,

1999). Mixture analysis does not perform as well as the mean technique when dimorphism is minimal and the sex ratio is balanced (Plavcan, 1994).

The mean technique estimates sexual dimorphism by dividing the pooled sample into two halves, above and below the sample mean, and calculating a new mean value for each half (Plavcan, 1994). Sexual dimorphism is then estimated as M/F , where M and F are the mean values of the trait for the subsamples above and below the pooled sample mean, respectively (Plavcan, 1994). The MoM technique also starts with a pooled sample of mean μ . The mean value for males is estimated as $\mu + \delta$, where δ is the difference between the pooled sample mean and the male subsample mean value of the trait (Josephson et al., 1996). δ is estimated from the moments of the pooled sample using the formula:

$$\delta = \left(-m_1^4 + \frac{3}{2}m_2^2 - \frac{1}{2}m_4 \right)^{1/4}$$

where m_i is the i^{th} moment about the origin (Josephson et al., 1996). The estimate of sexual dimorphism is $e^{2\delta}$. In the MoM technique, negative values of δ are set to zero (Josephson et al., 1996). Mixture analysis assesses the maximum separation of male and female values which could be contained within a pooled distribution. The best model, i.e. a single or two overlapped distributions, can be chosen by selecting the model with the lowest Akaike Information Criterion (AIC) value. Differences in AIC values around two or lower indicate similar performance of models; differences in AIC values of 4–7 indicate different performance of models.

Statistical analyses were performed with SPSS 15.0, excepting mixture analysis, which was carried out with the freeware PAST 1.93 (Hammer et al., 2001), and the GLM, which was carried out with Statistica 9.1 (StatSoft, Inc., Tulsa, OK, USA).

3. Results

3.1. Correlations between morphometric traits

All morphometric traits shown significantly positive relations with each other, excepting for Lamp (Length between the anterior edge of mental process and the anterior edges of alveoli) and Daa (Distance between the horizontal branches at the level of anterior edge of alveoli), which had no significant correlation between them or with most of the remaining traits, and the correlation between Lic (Length of the interalveolar crest) and Ws (Width of the symphysis) (Table 1). Nevertheless, correlation coefficients were not strong in general (only 5 from 41 statistically significant correlations $r > 0.71$).

The GLM analysis revealed a significant effect of estimated age on the morphometric traits (Wilks lambda_{10, 34} = 0.522, $P = 0.006$). After removing the influence of estimated age, the structure of correlations among morphometric traits did not qualitatively change (Table 1). In general, partial correlation coefficients were slightly lower than the univariate (uncorrected) correlation coefficients, excepting in the case of Lamp,

Table 1

Correlation matrix among the 11 morphometric traits measured on mammoth mandibles. Pearson correlation coefficients and significance of the correlation are shown above the diagonal. Partial correlation coefficients after removing correlation with age are shown below the diagonal; values smaller than their corresponding values in the upper matrix are indicated in bold.

	GWhr	Hhr	Whr	Lamp	Lic	Hs	Ls	Ws	Daa	Dpa	GL
GWhr	–	0.740***	0.666***	–0.069	0.469***	0.642***	0.444	0.470***	0.214	0.512***	0.660***
Hhr	0.668	–	0.787***	0.189	0.637***	0.851***	0.583***	0.337*	0.358*	0.684***	0.657***
Whr	0.544	0.722	–	0.010	0.470***	0.867***	0.520***	0.306*	0.362*	0.612***	0.512**
Lamp	0.012	0.299	0.128	–	0.323*	0.162	0.281	0.011	0.025	–0.033	0.040
Lic	0.397	0.595	0.393	0.390	–	0.545***	0.712***	0.122	0.056	0.312*	0.413*
Hs	0.538	0.811	0.826	0.275	0.488	–	0.547***	0.321*	0.336*	0.639***	0.566***
Ls	0.363	0.530	0.452	0.348	0.686	0.486	–	0.137	0.140	0.364*	0.449**
Ws	0.386	0.233	0.167	0.066	0.039	0.209	0.053	–	0.639***	0.518***	0.501***
Daa	–0.004	0.194	0.141	0.113	–0.084	0.157	0.010	0.589	–	0.603***	0.427*
Dpa	0.365	0.597	0.467	0.054	0.209	0.533	0.267	0.442	0.493	–	0.654***
GL	0.620	0.616	0.436	0.084	0.359	0.505	0.409	0.429	0.321	0.610	–

***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$

N = 45 individuals, except for correlations with GL (N = 32)

in which the partial correlation coefficients slightly increased with respect to the univariate correlation coefficients (Table 1).

The PCA analysis extracted three main factors with eigenvalues of 5.64, 1.34 and 1.22, respectively. These factors explain 51.3, 12.2 and 11.1% of the variance in the data, respectively. The positive side of the first factor was related to increasing values of GL, GWhr (Greatest Width between the horizontal ramus), Hhr (Height of the horizontal ramus), Whr (Width of the horizontal ramus) and Hs (Height of the symphysis), suggesting a strong correlation between this factor and general size of the mandible (Table 2). The positive side of the second factor was related to high values of Daa, and the positive side of the third factor was related to high values of Lamp, i.e., prominence of the mental process.

3.2. Ontogenetic changes

All morphometric traits show mild ($0.3 < R^2 < 0.7$) statistically significant positive correlations with the estimated age, excepting GL and Lamp (Table 3; Fig. 4). The slope of the relationship with the estimated age ranges from 0.286 in GWhr to 0.461 in Dpa (Distance between the horizontal branches at the

Table 2

Loading of the original morphometric traits on each of the three first principal components extracted by PCA analysis. Values in bold indicate significant loadings according to the broken-stick criterion (Peres-Neto et al., 2003).

Variable	Factor 1	Factor 2	Factor 3
GWhr	0.877	–0.094	–0.184
Hhr	0.910	–0.227	0.041
Whr	0.805	–0.183	–0.341
Lamp	–0.048	–0.158	0.877
Lic	0.635	–0.493	0.208
Hs	0.834	–0.108	–0.240
Ls	0.636	–0.377	0.279
Ws	0.601	0.523	0.282
Daa	0.572	0.614	0.169
Dpa	0.765	0.403	–0.041
GL	0.787	0.124	0.123

level of posterior edge of alveoli). However, no significant differences were found between slopes (all $P > 0.05$). Estimated age was significantly positively related to the sample scores on the first axis of the PCA ($R^2 = 0.603$, $P < 0.001$; Fig. 5), but not to the sample score on the second and third axes ($R^2 = 0.258$, $P = 0.155$ and $R^2 = -0.100$, $P = 0.585$, respectively).

3.3. Sexual dimorphism

No bimodality was found in any of the morphometric traits (Table 4). The mean technique indicated a sexual dimorphism ranging from 1.196 in GL to 1.618 in Lamp; the upper and lower halves of the pooled sample differed in age for seven of the 11 morphometric traits studied (Table 4).

The MoM technique showed sexual dimorphism in all but four variables: GWhr, Lamp, Ws and GL (Table 4). Estimates of sexual dimorphism using MoM were lower than those estimated using the mean technique and ranged from 1.036 in Lic to 1.168 in Dpa.

Table 3

Relationship between the 11 morphometric traits measured on mammoth mandibles and estimated age (\log_{10} -transformed data for analysis). The coefficient of determination (R^2), the F-value and significance (P) of the regression, and the value of the type II regression slope are shown. Variables are arranged by increasing slope.

Variable	R^2	$F_{1,50}$	P	Type II slope
log GL	0.298	0.089	0.098	0.000
log Lamp	0.209	0.044	0.169	0.000
log GWhr	0.511	0.261	0.000	0.286
log Whr	0.631	0.399	0.000	0.288
log Ws	0.326	0.106	0.029	0.304
log Lic	0.303	0.092	0.043	0.307
log Hhr	0.511	0.261	0.000	0.339
log Ls	0.315	0.099	0.035	0.378
log Daa	0.487	0.237	0.001	0.394
log Hs	0.552	0.304	0.000	0.406
log Dpa	0.557	0.310	0.000	0.461

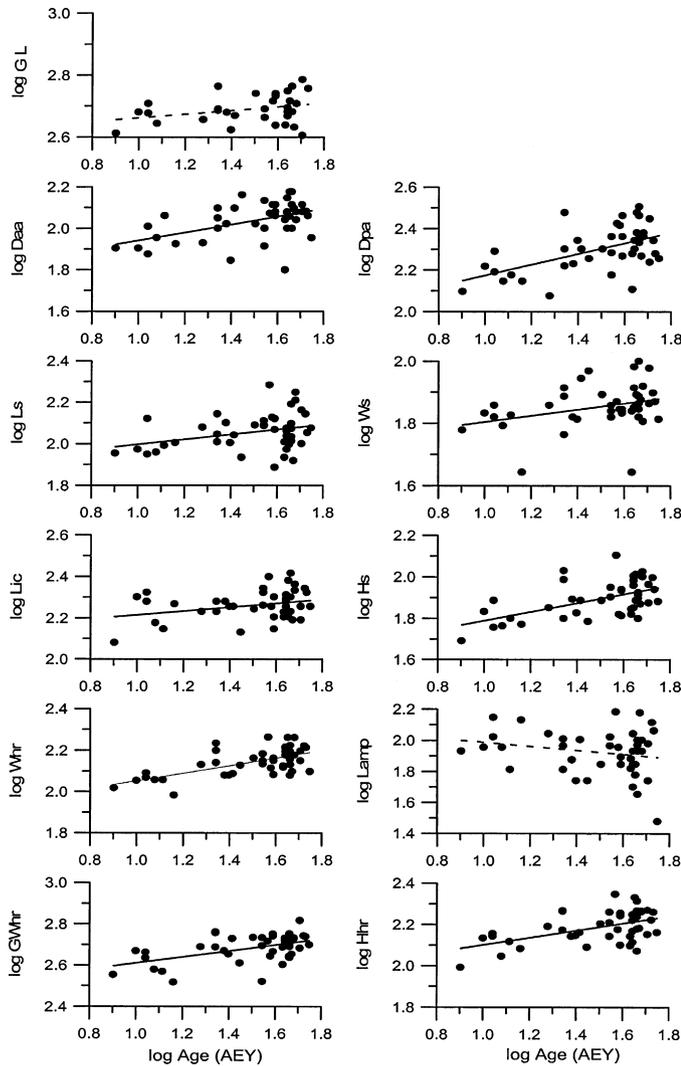


Fig. 4. Relationship between estimated age and the 11 morphometric variables measured on woolly mammoth mandibles (data \log_{10} -transformed). Non significant relationships are indicated by dashed lines (see Table 3). $N = 45$ individuals, excepting for GL ($N = 32$).

In general, mixture analysis indicated a low sexual dimorphism. Models considering a single normal distribution had clearly lower AIC values than models considering two overlapped distributions for Hhr, Whr, Lic, Hs, Daa and GL (Table 4). For GWhr, Lamp, Ls (Length of the symphysis) and Dpa, both models performed equally well. A model with two overlapped distributions performed better than a single normal distribution for Ws (Table 4). However, a look to the predicted mean values for these two distributions indicated rather similar mean values and a large difference in variance ($m \pm SD = 69.98 \pm 4.13$ and 74.81 ± 15.09 , respectively).

4. Discussion

4.1. Ontogenetic changes

Almost all morphometric traits increased in size with increasing individual age. This is in agreement with the fact that

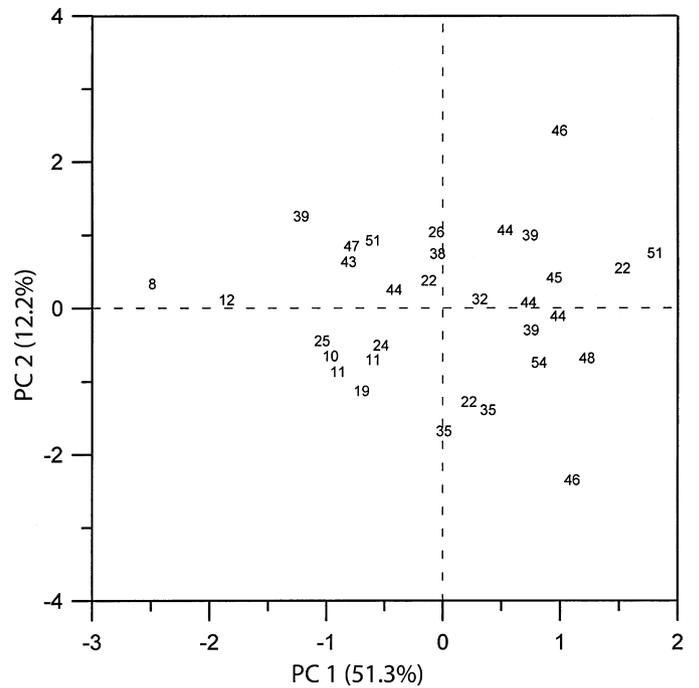


Fig. 5. Biplot of the two first principal components extracted by PCA, showing the mandibles coded by age (AEY).

in the woolly mammoths, like in the modern elephants, growth occurs along almost all the life of the individuals. This trend is especially evident in long bones, whose growth continues until advanced ontogenetic stages, when the epiphysis fuses (Haynes, 1991; Lister, 1999).

Individuals in early ontogenetic stages have a long symphysis, which decreases markedly in relative length and increases in height along the first five years of life (Maschenko, 2002). The anterior edge of the mental process (interalveolar crest) becomes more upright during these first stages (Maschenko, 2002). In adult stages, one of the traits more related with the age was Hs. Thus the relative height and

Table 4

Values of bimodality (b) and sexual dimorphism estimated for the 11 morphometric variables measured on woolly mammoth mandibles. For the Mean technique, values in bold indicate that the upper and lower halves of the pooled distribution significantly differed in age (Mann-Whitney U-test). For the mixture analysis, the AIC-values under a single (AIC_1) and two overlapped distributions (AIC_2) are given.

Variable	b	Sexual dimorphism			
		Mean technique	MoM technique	AIC_1	AIC_2
GWhr	0.34	1.257	1.000	514.7	513.6
Hhr	0.37	1.345	1.115	432.3	437.4
Whr	0.39	1.280	1.104	408.2	412.5
Lamp	0.35	1.1618	1.	430.2	432.4
Lic	0.33	1.285	1.036	438.6	443.4
Hs	0.39	1.395	1.136	385.0	389.3
Ls	0.44	1.371	1.078	420.2	419.9
Ws	0.22	1.248	1.	350.6	346.8
Daa	0.38	1.387	1.111	410.6	415.5
Dpa	0.39	1.467	1.168	485.0	486.8
GL	0.41	1.196	1.	351.7	356.6

robustness of the symphysis also increased progressively during the adult life. Another trait highly related with age was *Whr*. The increase of this trait with age was expected, since it is directly related with molar replacement. The horizontal ramus became progressively wider in order to accommodate each new molar which, in every case, is broader than the previous one. In the mental process, an irregular development during the adult stages was observed. In some individuals it became shorter with the interalveolar crest almost in vertical position, whereas others developed a long and narrow symphyseal process. Intermediate cases were also observed. This variability in the development of the mental process explains that the variables *Lamp* and *Lic* did not show a regular growth pattern along the individual age.

The greatest length of the mandible (*GL*) is considered a key variable because it influences the changes in relative width and height of the jaw, both of which increase markedly during the first years of life in woolly mammoths (Maschenko, 2002). *GL* was not related to age (Table 2; Fig. 3). Therefore, the continuous growth of mandible width and height shown here implied that the increase in the relative mandible width and height with increasing age continues during the adult stages of life in woolly mammoth. This increase of the mandible relative height throughout the individual development was also observed for extant elephants (Eales, 1931). The skull of the extant elephants also shows a parallel increase in relative height or shortening along the ontogeny (Gregory, 1903). Apparently, these trends occur at a lesser rate in adult ages than in the first stages of development, but it cannot be shown statistically here because we have not enough detailed data from the younger stages.

Increases in relative width and height of the skull and mandible occur also along the proboscideans phylogeny (Eales, 1931; Maglio, 1973; Prothero and Schoch, 2002). The long and low skull of primitive proboscideans (gomphotheres, mastodonts) became shortened and more vertical in mammoths, shifting the center of gravity and putting different stresses on the occipital condyle at the back of the skull, and the nuchal muscles that hold the head up. These transformations have been interpreted as a mechanical adaptation linked to very large tusk size (Eales, 1931; Prothero and Schoch, 2002; Lister et al., 2005). A similar interpretation seems reasonable for the ontogenetic change in mandible relative width and height found here because the size of the tusks increases along the life of the individual (Fisher and Beld, 2003).

4.2. Sexual dimorphism

The most reliable element to assess the sexual dimorphism is the pelvis (Lister, 1996), whose shape is very different in both sexes. Long bones provide also outstanding information because bimodality is often observed (Haynes, 1991). Averianov (1996) suggested that mandibles with presence of a long and narrow symphyseal process, possibly belong to male individuals. Nevertheless, this feature is not in agreement with our results. Among the North Sea collection, there are very robust specimens (males, almost without doubt) in which this

feature is not present. Dick Mol (pers. com., 2005) considers that this feature is not diagnostic to estimate the sexual dimorphism and our quantitative results provide support for this opinion.

In fact, we found at best slight indications of sexual dimorphism in subadult and adult mammoth mandibles. Both the mean and the MoM techniques indicated a slight sexual dimorphism in the mandible. However, dimorphism was in general less than 1.5 and under these conditions both methods show a trend to overestimate dimorphism (Rehg and Leigh, 1999). In addition, an exploration of the mean technique revealed that differences in age can also be a confounding factor. This can be particularly relevant for species, such as the woolly mammoth, where growth continues during the adult stage. Mixture analyses did not suggest sexual dimorphism for most variables. The only apparently sexually dimorphic trait, *Ws*, has shown a divergence in variance, not so much in the average value. For extant elephants, sexual differences in the mandible are not very pronounced, apart from overall size and robustness (Todd, 2010).

Assessment of sexual dimorphism in fossil species remains challenging (Plavcan, 1994; Rehg and Leigh, 1999). In the woolly mammoth, a few complete skeletons of known sex are available but scattered in different research institutions from different countries. Although it would have been desirable to test our sample against the mandibles of such sexed skeletons, this was beyond our logistic possibilities. Publication of the relevant morphometric information of those sexed skeletons is necessary in order to make further progress in the study of sexual dimorphism in woolly mammoth.

We can conclude that in the adult stages of the woolly mammoth life, a progressive linear growth occurs in the mandible along the same morphometrical trends of that in the early stages of development. These changes can be related with the continuous growth of the tusks and with the molar replacement along the individual ontogeny. Sexual dimorphism in the mandible is at best slight and traits such as the symphyseal process follow a quantitative, unimodal variation and are not diagnostic for sexing purposes. In addition, attempts to assess sexual dimorphism in this and other animals should be aware of the potential confounding factor introduced by age differences.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.geobios.2010.10.007](https://doi.org/10.1016/j.geobios.2010.10.007).

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