

Patterns of body size changes in fossil and living Equini (Perissodactyla)

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The importance of body mass prediction from several cranial, dental and appendicular variables in living Equini are studied. Relationships between the body mass changes and the ecogeographic picture of Equini evolution are also analysed. The metapodial and phalanx variables, particularly antero-posterior diameters, are better correlated with body mass than cranial variables in living Equini. Large sized species are correlated with cold climates, open habitats and/or soft soils; small ones are correlated with warm climates, more closed habitats and/or hard soils. Pleistocene horses from Europe and Africa follow an evolutionary trend opposite to their North American counterparts, from larger sized species to smaller ones. In South America the pattern of body size is different to those of the other continents. Species of *Hippidion* reaching large body mass, whereas some species of *Equus*, *E. andium*, follow a diminishing trend.

ADDITIONAL KEY WORDS: Allometric change Pliocene, Pleistocene – Europe – Africa – North and South America.

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INTRODUCTION

Body size in terms of body mass is one of the most important determinants of body architecture, physiology (Schmidt-Nielsen, 1975; Alexander, *et al.*, 1981;

McNab, 1990), ecology (Hutchinson & MacArthur, 1959; McNab, 1971; Damuth, 1981a, b; Janis 1986; Robinson & Redford, 1986) and social organization (Jarman, 1974; Clutton-Brock, Harvey & Rudder, 1977; Eisenberg, 1981; Janis, 1982).

Although the importance of body size as a major aspect of the adaptive strategy of animals was recognized over a century ago by palaeontologists (Cope, 1887; Depéret, 1909), interest was primarily focused on phyletic changes in body size through time and not on palaeoecological considerations (Fleagle, 1978, 1988). In addition, in the first scientific papers, the body mass estimations were made based on qualitative and subjective comparisons among extant species. In the last few years this practice is being abandoned and progressively replaced by predictions based on statistical considerations (Fleagle, 1978, 1988; Andrews, Lord & Nesbit Evans, 1979; Gingerich, Smith & Rosenberg, 1982; Scott, 1983; Legendre & Roth, 1988; Damuth & MacFadden, 1990; Gingerich, 1990). The first studies referring to statistical predictions of body mass of the Equidae were made by Hulbert (1984), MacFadden (1986), MacFadden & Hulbert (1990), Janis (1990) and Scott (1990) among others. The family Equidae Gray is very well identified as a monophyletic group that includes three subfamilies, Hyracotheriinae, Anchitheriinae and Equinae (MacFadden, 1992). The last of these represents the major adaptive radiation of hypsodont horses and includes Equini and Hippotheriini tribes (*sensu* Prothero & Schoch, 1989:532). The Equini tribe comprises eight genera, one widespread throughout the world (*Equus*), six endemic to North America: *Protohippus*, *Calippus*, *Pliohippus*, *Dinohippus*, '*Onohippidium*' and *Astrohippus* (Prothero & Schoch, 1989), and one endemic to South America: *Hippidion* (Alberdi, 1987; Alberdi & Prado, 1993).

According to Gingerich & Smith (1984:257), morphological features associated with each of those broadly defined aspects of structure, physiology, ecology and social organization of mammals "... can profitably be studied in relation with size, and none can be fully understood without considering size". There are at least three different ways in which the relationships of morphometric characteristics to body size are important: (1) functional inferences, (2) baseline comparisons, and (3) prediction of body mass in fossils (Gingerich & Smith, 1984). In this context, the purposes of our paper are: (a) to find the best estimates of body mass from bone and dental measurements in living Equini species; (b) to predict body mass of fossil Equini species, and (c) to analyse the patterns of body mass throughout time in different continents. Our fossil body size predictions are based on variables of the most frequently preserved and most taxonomically and ecologically informative skeletal elements of the tribe Equini.

MATERIAL AND METHODS

The total fossil samples came from different collections and material cited in the literature (Table 1).

Choice of variables

Before predicting body size of a fossil species from a length, area or volume measurement, the relationships between these variables and the body size in

TABLE 1. The predicted body mass (kg) for fossil species from different continents. n = number of samples. V = kind of measurement used to predict body mass. $\ln V$ = natural logarithm of measurement. AMNH = authors' data collected from the American Museum of Natural History

Species	n	V	$\ln V$	Predicted body mass (kg)
Europe				
<i>Equus stenonis livenzovensis</i> (Alberdi & Ruiz Bustos, 1989)	11	F5	3.706	562.84
<i>E. stenonis vireti</i> (Alberdi & Ruiz Bustos, 1989)	27	F5	3.652	466.37
<i>E. stenonis stenonis</i> (Alberdi & Ruiz Bustos, 1989)	6	F5	3.614	408.70
<i>E. stenonis guthi</i> (Boeuf, 1986)	7	F5	3.586	370.92
<i>E. stehlini</i> (Alberdi & Ruiz Bustos, 1989)	11	F5	3.544	320.53
<i>E. stenonis granatensis</i> (Alberdi & Ruiz Bustos, 1989)	1	F5	3.440	223.40
<i>E. sussenbornensis</i> (Alberdi et al. 1991)	3	F5	3.814	819.75
<i>E. altidens</i> (Alberdi et al. 1991)	6	F5	3.560	388.99
<i>E. mosbachensis</i> (Eisenmann, 1979)	25	MC13	3.541	671.15
<i>E. taubachensis</i> (Musil, 1977)	4	F5	3.751	580.56
<i>E. chosaricus</i> (Eisenmann, 1991)	26	MC11	3.998	530.59
<i>E. germanicus</i> (Eisenmann, 1991)	78	MC11	3.951	466.84
<i>E. hydruntinus</i> (De Giuli, 1982)	3	F5	3.423	210.39
<i>E. arcelini</i> (Eisenmann, 1991)	33	MC11	3.956	472.95
Africa				
<i>Equus numidicus</i> (Arambourg, 1969–1970)	5	MC1	5.485	473.90
<i>E. tabeti</i> (Eisenmann, 1979)	26	MC13	3.247	273.14
<i>E. mauritanicus</i> (Eisenmann, 1979)	63	MC13	3.343	366.50
North America				
<i>Pliohippus mirabilis</i> (AMNH)	1	MC13	2.955	111.94
<i>Pliohippus pernix</i> (AMNH)	1	MC13	3.114	181.99
<i>Dinohippus leidyanus</i> (AMNH)	14	MC13	3.030	140.75
<i>Astrohippus stocki</i> (Lance, 1950)	131	MC1	5.132	127.70
<i>'Onohippidion' galushai</i> (Alberdi & Prado, 1993)	31	F5	3.364	171.39
<i>Nannippus minor</i> (Lance, 1950)	1	MC1	5.036	89.38
<i>Dinohippus mexicanus</i> (Lance, 1950)	40	MC1	5.376	316.08
<i>Equus simplicidens</i> (AMNH)	6	F5	3.588	373.53
<i>E. conversidens</i> (Dalquest & Hughes, 1965)	5	MC13	3.285	306.13

TABLE 1. Continued.

Species	<i>n</i>	V	<i>Ln V</i>	Predicted body mass (kg)
<i>E. scotti</i> (Winans, 1989)	138	MC13	3.477	555.01
<i>E. alaskae</i> (Winans, 1989)	46	MC13	3.348	372.03
<i>E. francisci</i> (Winans, 1989)	53	MC13	3.344	367.60
<i>E. occidentalis</i> (AMNH)	2	MC13	3.490	574.21
<i>E. laurentius</i> (Winans, 1989)	107	MC13	3.530	648.71
South America				
<i>Hippidion devillei</i> (Alberdi & Prado, 1993)	13	F5	3.479	255.69
<i>H. principale</i> (Alberdi & Prado, 1993)	17	F5	3.648	460.35
<i>H. saldiasi</i> (Alberdi & Prado, 1993)	4	F5	3.490	265.60
<i>Equus insulatus</i> (Prado & Alberdi, 1994)	24	F5	3.570	350.72
<i>E. andium</i> (Prado & Alberdi, 1994)	56	F5	3.436	220.30
<i>E. neogeus</i> (Prado & Alberdi, 1994)	9	F5	3.592	378.79
<i>E. santaelenae</i> (Prado & Alberdi, 1994)	9	F5	3.570	350.72

TABLE 2. The mean body mass in extant Equini species from Walker (1983) and Macdonald (1984) quoted in Janis (1986, 1990). *From Gambaryan (1974). **Authors' data collected from the Anatomie Comparée collections (MNHN, Paris)

	<i>n</i>	Body mass (Kg)	Body mass (Ln)
<i>Equus asinus</i>	4	220	5.394
<i>E. burchelli</i>	29	235	5.460
<i>E. greyi</i>	10	400	5.991
<i>E. hemionus</i>	6	250	5.521
<i>E. kiang</i>	6	300	5.704
<i>E. przewalskii</i>	4	350	5.858
<i>E. zebra</i>	19	260	5.561
<i>E. quagga</i> *	2	400	5.991
<i>E. caballus</i> (ponies)**	4	180	5.193
<i>E. caballus</i> (heavy horses)**	2	800	6.697

the living species of the same group need to be established. We have used body mass as a measurement of body size, according to Gingerich *et al.* (1982:82), because its use "... facilitates comparison among animals of different head-and-body shape".

Body mass of the nine extant Equini species (including *Equus quagga*, extinct c. 1880; see Churcher & Richardson, 1978) has been taken from the literature specified in Table 2. To predict body mass in fossil Equini, we have investigated

the relationship between body mass and several measurements of skulls, mandibles, dentition (occlusal areas of upper and lower teeth), third metapodials, and first phalanx in extant *Equus*.

The skeletal variables come from Alberdi & Ruiz-Bustos (1989), Alberdi, Caloi & Palombo (1988), Bocuf (1986), Eisenmann (1979, 1980, 1981), Eisenmann & Beckouche (1986) and Dive & Eisenmann (1991). The nomenclature variables are after Eisenmann *et al.* (1988), summarized as C = cranial dimensions; MD = mandible dimensions; P/p = upper and lower premolars, M/m upper and lower molars; MC = metacarpal, MT = metatarsal and F for the phalanx dimensions (Fig. 1).

Sexual dimorphism has not been considered in this analysis. Winans (1989) showed that differences in size and proportions between the sexes are lost within the general intraspecific variation in *Equus*. Eisenmann (1979) analysed the morphometric variation of the metapodials of living horses and stated that the coefficient of variation shows some low values for all variables.

Body mass and all measurements correspond to the arithmetic mean for all adult specimens that make up the samples for each species.

Figures 2 and 3 show the correlation between body mass of Equini species and the major climatic environmental changes in Europe and North America. In those cases where recent taxonomic revisions have not been carried out, or where controversy exists on the validity of a certain species, we have considered only the most representative species.

Statistical analysis

We used length, area and mass as body size measurements. These different dimensions are related in complex geometric ways. Any modification in size led to a modification in shape (allometric change), unless all lengths were modified by equal proportions. Only here (isometric change), does shape remain constant, although surface and volume change disproportionately (Gingerich & Smith, 1984). The general power function equation, used both in studies of isometry and allometry (Gould, 1972, 1974), is customarily written as

$$Y = aX^b \quad (1)$$

or, in logarithmic terms

$$L_n Y = L_n a + b L_n X \quad (2)$$

where Y is body mass, X is a measurement of length or area, b is the exponent or allometric scaling coefficient, and a is a constant.

We have used Pearson's correlation coefficient, r , (Simpson, Roe & Lewontin, 1960) with the aim of deciding which of the variables is more related to body mass. Those variables that show the highest r values, have been used to predict body mass in fossil species. Since r is often a poor indicator of the predictive power of the independent variable (Smith, 1981, 1984), two additional parameters were calculated. These are the percent coefficient of determination ($\%R$) and percent standard error of the estimate ($\%SEE$). $\%R$ shows what percentage of the observed variation in the dependent variable can be explained by variation

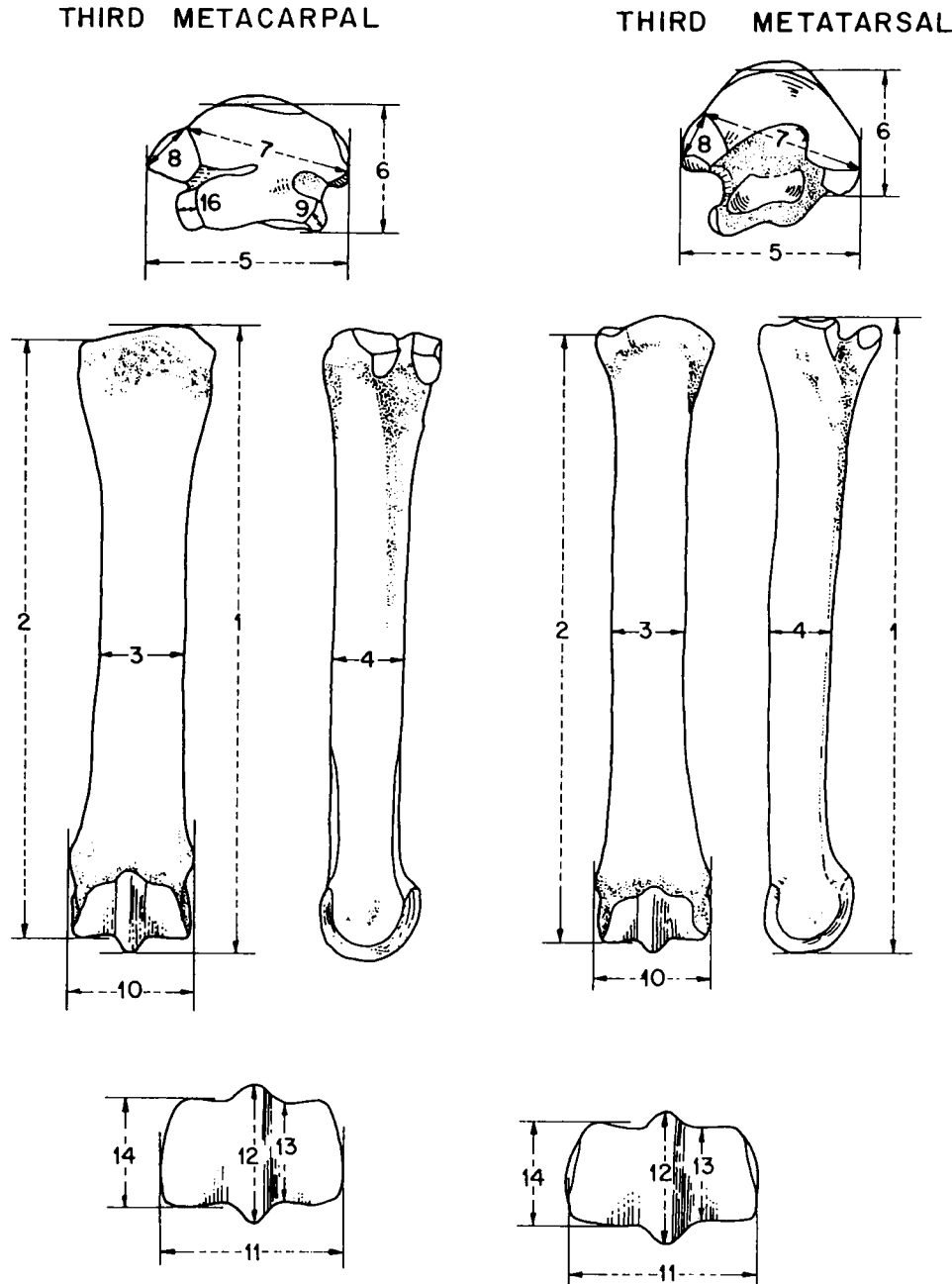


Figure 1. The variables of the cranial, mandible, metacarpal, metatarsal and first phalanx of the third digit (according to Eisenmann *et al.*, 1988).

in the independent variable, and vice versa. R was calculated as:

$$R = r^2 \tag{3}$$

The %SEE reflects the general ability of the independent variable to predict accuracy among regressions (Smith, 1981, 1984). The computational work was

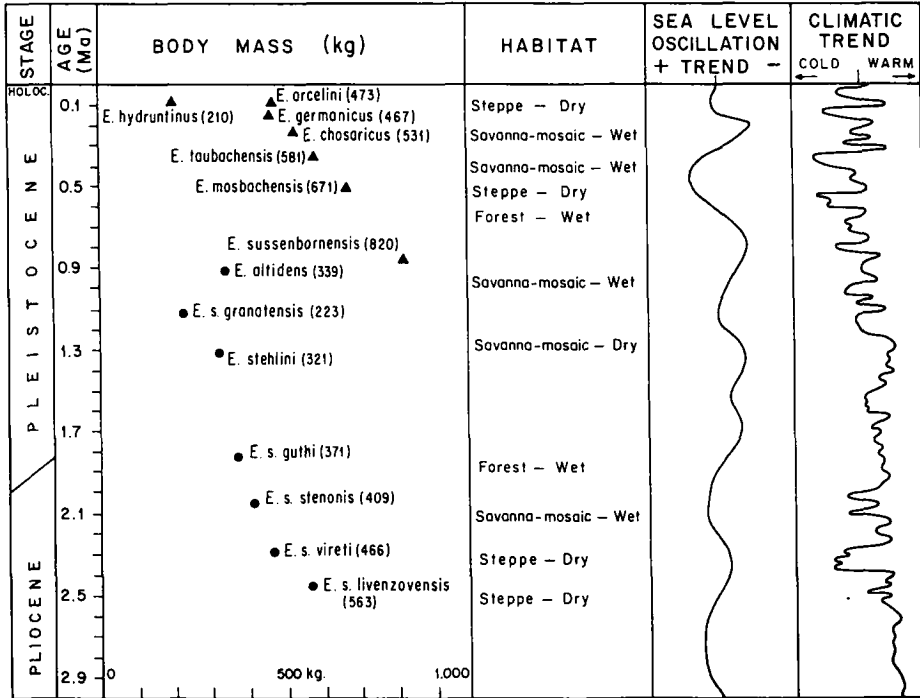


Figure 2. The Equini fossils, from Europe, and the correlation between body mass and the major climatic environmental changes. The body mass, in kilograms, is included in brackets under each species name. Climate trend redrawn from Shackleton (1984) and Shackleton & Hall (1984). Sea level oscillation adapted from Vail, Mitchum & Thompson (1977) and Summerhayes (1986).

done using the STATGRAPHICS package, version 5.0 (1991). Further details on statistical methods can be found in Sokal & Rohlf (1980) and Van Valkenburgh (1990).

RESULTS

Correlation coefficient (r), percent determination coefficient ($\%R$), slopes, intercepts and percent standard errors of the estimate ($\%SEE$) are provided for each regression in Tables 3 and 4. The variables F5 ($r = 0.991$, $\%R = 98.25$) and MC13 ($r = 0.982$, $\%R = 96.61$) are the most highly correlated with body mass. Both variables show a lowest value of $\%SEE$, of the order of 6% and 9%, respectively.

Areas are proportional to the square of lengths, and volumes of the cube of lengths, only in geometrically similar objects (Derome, 1978). In our case, if body mass increased as the cube of a linear dimension, the slope of the regression line would be 3, and the relationship between the two dimensions would be isometric. The slope of the line in F5, 3.476 (Table 4), is not much higher than 3 ($P < 0.01$), suggesting that body mass is positively allometric with respect to proximal depth (Fig. 1). In MC13, the body mass increases at nearly the same rate as the cube of distal minimal depth of the lateral condyle (slope = 3.056; $P < 0.01$).

In general, the correlation coefficients of the cranial and dental variables and

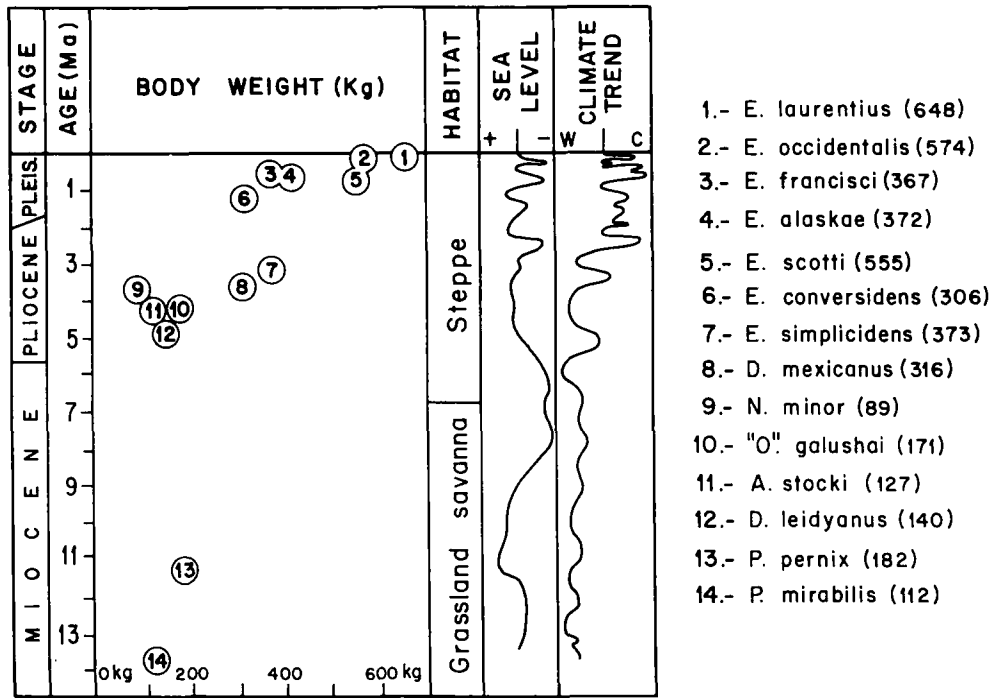


Figure 3. The Equini fossils, from North America, and the correlation between body mass and the major climatic environmental changes. The body mass, in kilograms, is included in brackets after each species name. Climate trend and sea level oscillation adapted from the same authors as in Fig. 2.

body mass are low. However, there are some dental variables with high values of r ($C8 = 0.906$, $C7 = 0.888$), but these do not appear to predict body mass as well as do metapodial variables (%SEE ranges from 14 to 44). The results for mandible variables generally follow those for cranial and dental ones. When the variables for lower and upper teeth are considered, only P_4 shows a high correlation coefficient ($r = 0.944$). Metacarpal and metatarsal variables both have similar patterns. The antero-posterior diameters show higher correlation coefficients than lengths and breadths (Table 4). The correlation coefficient of phalanx variables and body mass is the highest (0.934 to 0.991). Among the phalanx variables the %SEE are about 6 to 17.

Results of the regression of body mass on the most significant skeletal variables in extant species are summarized in Figure 4. Body masses are estimated using first phalanx ($F5 = r\ 0.991$), but in those cases where we did not have these bones we chose metacarpals ($MC13 = r\ 0.982$, $MC11 = r\ 0.960$, $MC1 = r\ 0.940$). Given one of these variables (in \ln), it is possible to predict the body mass substituting this value ($\ln X$) into equation (2) and replacing the slope and y-intercept by the corresponding values shown in Tables 3 and 4. Table 1 presents the body mass predictions for fossil species. Figure 5 displays the stratigraphic distribution of body mass in living and fossil Equini species in (a) Europe, (b) Africa, (c) North America and (d) South America. We can see a different pattern of chronological body mass changes for each continent. There is a diminishing tendency in body mass in Europe and Africa, while in

TABLE 3. Variables of skulls, mandibles and teeth. Numbers after Eisenmann *et al.* (1988). C = cranial; MD = mandible; P/M = upper premolars and molars; p/m = lower premolars and molars. r = correlation coefficient. % R = per cent coefficient of determination. In the teeth R are calculated from the occlusal area. %SEE = per cent standard error of the estimate. *Non-significant correlation ($P > 0.05$). The skull, maxillar, mandibular and upper cheek teeth data are obtained from Eisenmann (1980): tables 25 and 38 for *E. grevyi*; t.29 and 39 for *E. burchelli*; t.30 and 40 for *E. quagga*; t.31 and 41 for *E. zebra*; t.36 and 46 for *E. przewalskii*; t.33 and 43 for *E. asinus*; t.34 and 44 for *E. hemionus*; and t.35 and 45 for *E. kiang*. The lower cheek teeth data from Eisenmann (1981): t.9 for *E. grevyi*; t.10 for *E. burchelli*; t.11 for *E. quagga*; t.12 for *E. zebra*; t.17 for *E. przewalskii*; t.14 for *E. asinus*; t.15 for *E. hemionus*; and t.16 for *E. kiang*

Variables	r	% R	Slope	Intercept	%SEE
C1	0.776	60.24	2.104	-4.246*	28.50
C3	0.358	12.86	1.214*	0.027*	42.19
C4	0.894	80.02	3.505	-10.869	20.20
C6	0.853	72.91	3.590	-16.278	23.52
C7	0.888	78.98	5.223	-17.569	20.72
C8	0.906	82.15	4.679	-14.316	14.09
C9	0.892	79.58	5.033	-19.757	20.42
C10	0.429	18.46	1.449*	-0.375*	40.81
C11	0.623	38.84	4.023*	-9.055*	35.34
C12	0.813	66.20	4.570	-11.872	26.27
C14	0.659	43.51	2.847	-4.832*	33.97
C15	0.848	71.95	4.095	-11.006	23.93
C18	0.739	54.69	3.998*	-15.431*	30.42
C19	0.798	63.70	4.535	-18.124	27.23
C20	0.506	25.67	1.536*	-0.674*	38.96
C23	0.830	68.79	3.464	-14.671	25.17
C24	0.714	51.08	3.318	-11.700*	31.61
C25	0.737	54.46	2.767	-6.955*	30.50
C26	0.747	55.93	3.938	-12.250*	30.00
C27	0.176	3.12	0.572*	4.195*	44.48
C28	0.801	64.27	6.076	-19.081	27.01
C29	0.644	41.53	4.884	-13.873*	34.56
MD1	0.861	74.28	3.682	-16.380	22.92
MD2	0.803	64.56	2.080	-3.483*	26.90
MD3	0.899	80.93	5.336	-17.803	19.73
MD4	0.877	76.92	4.320	-13.050	21.71
MD5	0.900	81.16	4.910	-19.172	19.62
MD7	0.728	53.01	2.712	-5.061*	30.98
MD9	0.784	61.51	2.625	-8.165*	28.04
MD13	0.642	41.22	2.741	-6.258*	34.65
P2	0.808	65.41	2.416	-10.583	26.58
P3	0.872	76.17	2.824	-12.750	22.06
P4	0.831	69.17	2.223	-8.723	25.09
M1	0.805	64.94	2.856	-12.463	26.76
M2	0.803	64.58	2.606	-10.816	26.89
M3	0.910	82.82	1.640	-4.569	18.73
p2	0.854	73.07	1.505	-3.378*	23.46
p3	0.915	83.87	1.874	-5.609	18.15
p4	0.944	89.18	2.001	-6.319	14.86
m1	0.865	74.90	1.916	-5.482	22.64
m2	0.889	79.16	1.774	-4.592	20.63
m3	0.881	77.67	1.461	-2.938*	21.35

TABLE 4. Variables of third metacarpals, third metatarsals and first phalanges. Numbers after Eisenmann *et al.* (1988). MC = metacarpal; MT = metatarsal; F = phalanx. r and % R as in Table 3. %SEE = per cent standard error of the estimate. *Non-significant correlation ($P > 0.05$). MCIII and MTIII data are taken from Eisenmann (1979): t.2 for *E. greyi*; t.3 for *E. burchelli*; t.4 for *E. zebra*; t.6 for *E. przewalskii*; t.1 for *E. hemionus*; and *E. asinus* from Eisenmann & Beckouche (1986: t.9). FIII from Dive & Eisenmann (1991): t.3 for *E. greyi*; t.4 for *E. asinus*; t.5 for *E. kiang*; Appendix for *E. burchelli*, *E. zebra*, *E. przewalskii*, and *E. hemionus*.

Variables	r	% R	Slope	Intercept	%SEE
MC1	0.940	88.46	3.713	-14.209	17.33
MC2	0.914	83.61	3.269	-11.700	20.66
MC3	0.938	88.08	2.612	-3.223*	17.61
MC4	0.897	80.47	2.597	-2.498*	22.55
MC5	0.934	87.35	2.817	-5.204	18.14
MC6	0.960	92.31	3.356	-5.685	14.15
MC7	0.917	84.19	2.952	-5.903	20.29
MC8	0.940	88.39	2.632	-1.299*	17.39
MC9	0.724	52.58	0.803	4.687	35.14
MC10	0.944	89.27	2.818	-4.963	16.71
MC11	0.960	92.16	2.738	-4.672	14.28
MC12	0.972	94.62	2.916	-4.490	11.83
MC13	0.982	96.61	3.056	-4.313	9.39
MC14	0.975	95.20	3.103	-4.695	11.18
MC16	0.794	63.15	1.240	3.094	30.97
MT1	0.932	86.87	3.521	-13.688	18.49
MT2	0.908	82.51	3.489	-13.409	21.34
MT3	0.923	85.33	2.420	-2.471*	19.54
MT4	0.929	86.31	2.579	-2.885*	18.88
MT5	0.935	87.48	2.617	-4.336	18.05
MT6	0.937	87.93	2.712	-4.226	17.72
MT7	0.948	89.99	2.793	-4.686	16.14
MT8	0.891	79.44	2.172	0.429*	23.13
MT10	0.955	91.28	2.485	-3.702	15.06
MT11	0.951	90.48	2.468	-3.626	15.74
MT12	0.973	94.84	2.768	-4.061	11.58
MT13	0.959	92.07	2.830	-3.521	14.37
MT14	0.964	93.01	2.804	-3.721	13.49
F4	0.934	87.30	2.491	-3.936	16.83
F5	0.991	98.25	3.476	-6.548	6.24
F6	0.943	89.05	2.693	-4.285	15.63

North America the general trend is the opposite, with body mass increasing over time. The decrease in size of the caballoid horses in the middle late Pleistocene has been also recently discussed by Forsten (1993). Finally, there are two different lineages that show both tendencies as being evident in South America.

DISCUSSION

Equini predictions

Two general remarks can be made: (1) metapodial elements are better predictors of body mass than cranial elements, and (2) antero-posterior diameters of metapodial and first phalanx are better estimators of body mass than lengths

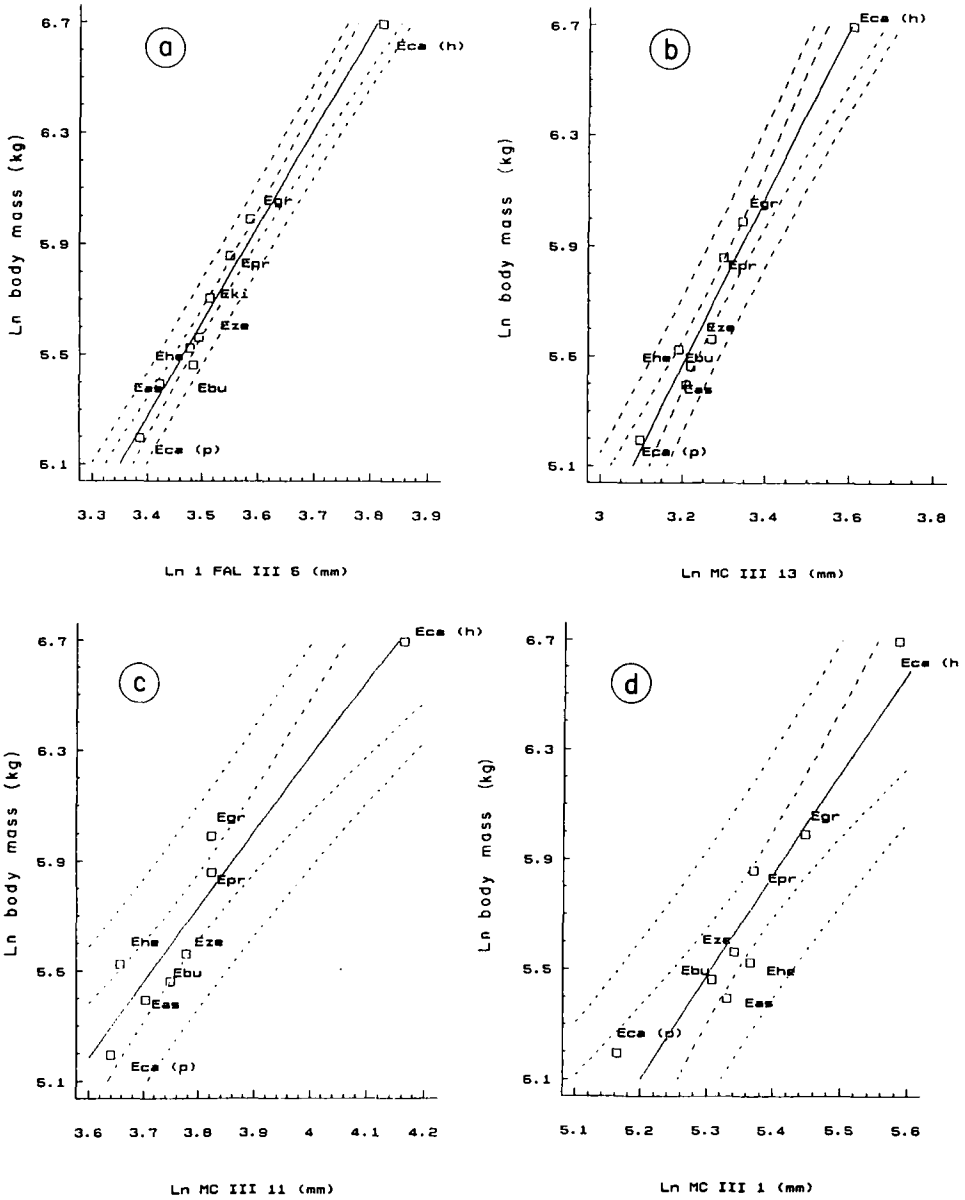


Figure 4. Graphic representation of the regression of body mass from the measurements in extant species, from (a) F5 measurement, (b) MC13 measurement, (c) MC11 measurement, (d) MC1 measurement. See Table 1. Abbreviations: Ehe = *E. hemionus*; Epr = *E. przewalskii*; Eki = *E. kiang*; Eca(p) = *E. caballus* (ponies); Eca(h) = *E. caballus* (heavy horses), others as in Fig. 5b. Ln = natural logarithm.

and breadths. We might expect *a priori* that some skeletal dimensions would have a close relationship to body mass as a logical consequence of the fact that body mass is normally transmitted through limbs to the substrate (Hylander, 1985; Jungers, 1987, 1988). Also, the higher prediction values of maximal depths, as opposed to lengths and breadths, of metacarpal and phalanx could

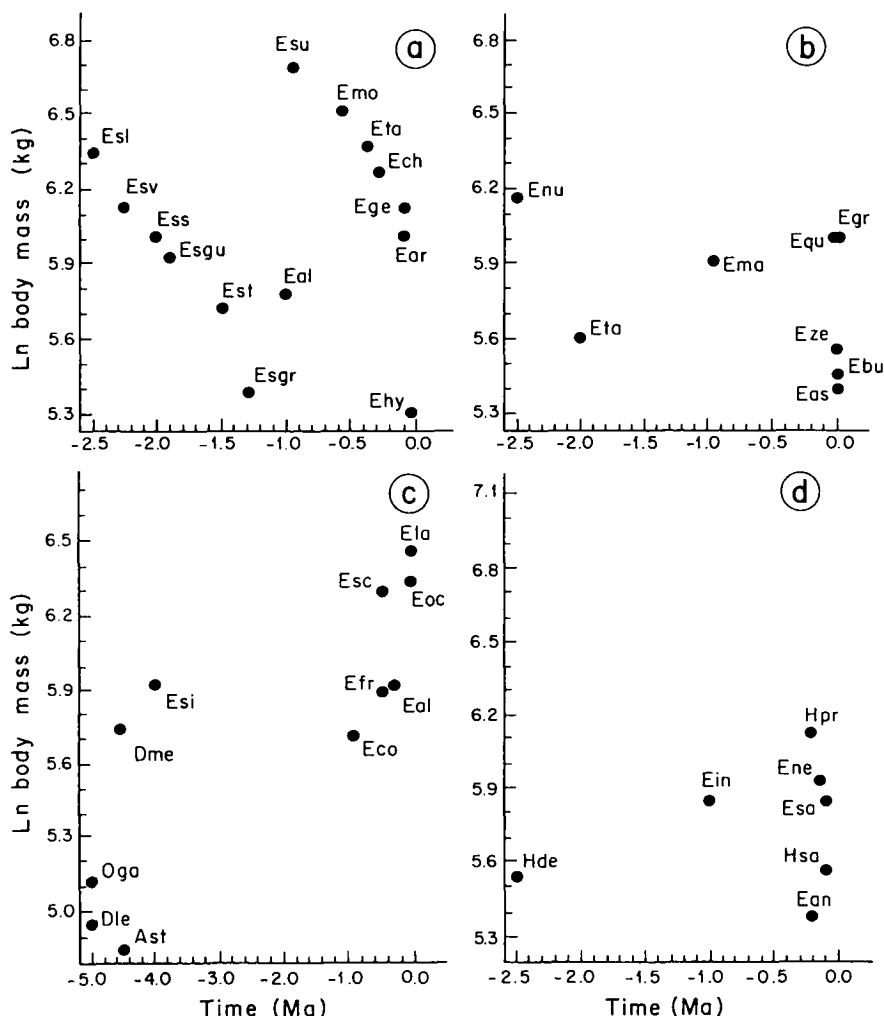


Figure 5. Distribution of body mass in fossil Equini species with respect to geological time, from (a) Europe, (b) Africa, (c) North America; (d) South America. Abbreviations: (a) Esl = *Equus stenonis livenzovensis*; Esv = *E. s. vireti*; Ess = *E. s. stenonis*; Esqu = *E. s. guthi*; Est = *E. stehlini*; Esgr = *E. s. granatensis*; Ealt = *E. altidens*; Esu = *E. sussenbornensis*; Emo = *E. mosbachensis*; Eta = *E. taubachensis*; Ech = *E. chosaricus*; Ege = *E. germanicus*; Ear = *E. arcelini*; Ehy = *E. hydruntinus*; (b) Enu = *E. numidicus*; Eta = *E. tabeti*; Ema = *E. mauritanicus*; Egr = *E. grevyi*; Equ = *E. quagga*; Eze = *E. zebra*; Ebu = *E. burchelli*; Eas = *E. asinus*; (c) Ast = *Astrohippus stocki*; Dle = *Dinohippus leidyanus*; Oga = "*Onohippidion galushai*"; Dme = *D. mexicanus*; Esi = *E. simplicidens*; Eco = *E. conversidens*; Eal = *E. alaskae*; Esc = *E. scottii*; Ela = *E. laurentius*; Efr = *E. francisci*; Eoc = *E. occidentalis*; (d) Ein = *E. insulatus*; Ean = *E. andium*; Esa = *E. santaelenae*; Ene = *E. neogaeus*; Hde = *Hippidion devillei*; Hsa = *H. saldiasi*; Hpr = *H. principale*. Ln = natural logarithm.

be expected, since while the depths change in direct proportion with body mass, the lengths and breadths present some independent variation. The last variables are related to kind of substrate (Eisenmann, 1984; Alberdi & Prado, 1993; Prado & Alberdi, 1994).

There is some difficulty in comparing our results with those of other authors because they use either different perissodactyl groups (Janis, 1990; Scott, 1990) or different size ranges for extant *Equus* (MacFadden, 1986). For example,

whereas we have only used Equini perissodactyls, Janis has used Equidae, Rhinocerotidae and Tapiridae perissodactyls, and Procaviidae hyracoids. Without entering into a discussion of the phylogenetic reasons why Janis lumped together perissodactyls and hyracoids (different opinions can be found in Simpson, 1945; Fischer, 1986; Benton, 1988; Novacek, 1989, 1990; Prothero, Manning & Fischer, 1988; Wyss, Novacek & McKenna, 1987), her generalized regressions were different. Her work is probably better for more generalized perissodactyls such as some hyracoid forms.

Pattern of body mass changes

Europe

There are two monophyletic groups of *Equus* species in Europe (Bonadonna & Alberdi, 1987; Alberdi & Bonadonna, 1988; Forsten, 1988; see Figure 5a): the 'stenonian' group (*Equus stenonis livenzovensis*, *E. s. vireti*, *E. s. stenonis*, *E. s. guthi*, *E. s. granatensis*, *E. stehlini* and *E. altidens*), and the 'caballine' group (*Equus sussenbornensis*, *E. mosbachensis*, *E. tabeti*, *E. chosaricus*, *E. germanicus* and *E. arcelini*). *E. hydruntinus* is not included because its phylogenetic relationships with both groups are not clear. This species has some dental similarities with stenonian horses, and other osteologic resemblances with asses (Stehlin & Graziosi, 1935; Azzaroli, 1979; Forsten, 1990). The 'stenonian' group may have been a result of the anagenetic process while the 'caballine' group may have been cladogenetic. In fact, there are many varying opinions on this point (Nobis, 1971; Alberdi & Ruiz Bustos, 1985; Boeuf, 1986; Bonadonna & Alberdi, 1987; Forsten, 1988; Azzaroli, 1990) and also on the relationship of these two lineages to modern zebras (Azzaroli, 1979, 1990; Forsten, 1992; Eisenmann, 1992). Indeed, both lineages show the same pattern of reducing body mass at two different times (Fig. 5a).

Therefore, in this pattern two cases of synchronism can be observed. The first, which is more reliable, is between *E. altidens* (stenonian group) and *E. sussenbornensis* (caballine group), and the second is between two caballines *E. arcelini* and *E. hydruntinus*. In the first case, both species are sympatric (Alberdi, Caloi & Palombo, 1988, 1991; Alberdi & Ruiz Bustos, 1989), but their large differences in body mass (Table 1) suggest that maybe these species occupied different niches. In this way Forsten (1988:30–31) suggests that "stenonid and caballoid horses of the genus *Equus* differ ecologically. The stenonids evidently have narrower niches. Ecological flexibility in the caballoids is not reflected in heightened morphological variation, however, but in behavioral versatility". She then goes on to explain this in more detail: "If the frequency with which different forms of the genus *Equus* are found sympatrically is a measure of stenotopy versus eurytopy, the fossil stenonids and their relatives, the zebras, are the most stenotopic. They are able to partition the horse niche without competition, both with one another and with equids of other subgroups (asinines, caballoids). Caballoids horses are eurytopic with little ability to share their niche with other caballoids" (1990:76). In the second case, both species could be not sympatric (De Giuli, 1982; Eisenmann, 1991), but the origin of *E. hydruntinus* is not so clear. Forsten (1986) thinks it possible that it is a derived species from *E. altidens*. In Eurasia only a few fossil caballine sites are shown to occur in sympatry. In this way, Forsten (1993:74) shows ... "Character displacement in competing species does not seem a valid explanation for size decrease in

the ecological generalized caballoids. Possibly the wide ecological niche of these horses, which presumably required non-overlapping specific ranges, was the reason for the rarity of caballoids sympatry".

The evolutionary history of European Equidae is closely related with major climatic changes (Alberdi & Bonadonna, 1988, 1990; Alberdi, 1989; Forsten, 1993). In the last 13 Mya, two main migratory events have been recorded (Berggren, Kent & Van Couvering, 1985): (1) 'Hipparion Datum', approximately 12.5 Mya, according to the last authors; (2) 'Equus Datum', around 2.6 Mya ago. The latter event has had two phases, the "stenonian event" (= 'Equus datum') and the 'Caballine event', about 1-0.8 Mya (Alberdi & Bonadonna, 1988). The first migratory event according to Woodburne (1989) and other American authors took place in at least two different periods, around 12 Mya and 9.5 Mya respectively. The last two *Equus* migratory events can be correlated with sea-level falls, dropping of marine temperatures and spread of tundra and steppe habitats (Zagwijn, 1986; Alberdi & Bonadonna, 1988). The record shows that the first immigrant species, in all cases, had the largest known body mass within each lineage. This has not happened by chance, since a large-sized animal will be selectively favoured in those habitats because it has more physiological and ecological advantages than the smaller ones. In general, large mammals have higher heat retention per unit volume than smaller ones, and large-bodied mammals have more elevated metabolic rates. Consequently, they need to compensate for this higher energetic cost with a higher food intake (McNab, 1990). Naturally, whatever their trophic specialization, they also need larger areas (Eisenberg, 1990). Large-bodied mammals have the capacity to use larger areas of space more efficiently than smaller ones, because the per-gram cost of fast locomotion is higher for smaller than for larger forms (Taylor, Heglund & Maloiy, 1982). In terrestrial environments, the cost of the locomotion varies in a regular manner with body size (Taylor, 1977; Taylor *et al.*, 1982). Also, maximum speed covaries positively with body size, though step frequency covaries negatively with body size (Eisenberg, 1990; it is possible to see a different view in Alexander, Langman & Jayes, 1977, and Garland, 1983). The higher speed of a large terrestrial mammal is due to the stride length (Calder, 1984). Finally, large body size is correlated with increased brain size, social organization, high speed, and better stamina, which are, in a herbivorous mammal, very important abilities to ward off predators (see Valverde, 1964, 1967; Jerison, 1973; Stanley, 1973; Eisenberg, 1981, and references therein).

Within the stenonian group, body mass decrease has been observed in *E. stenonis* and shows a chronocline variation that involves five subspecies (Fig. 2). This trend follows the inverse direction of Cope's rule, going from large to small body size (Stanley, 1973). This reduction in size is correlated with a decrease in the extension of grasslands and steppes, and with a parallel increase of woodlands, particularly those composed of deciduous trees (Zagwijn, 1986) (Fig. 2). Caballines replace stenonians in the Middle Pleistocene (Forsten, 1988; Alberdi & Bonadonna, 1988), and present a similar trend but within a wider cladogenetic process. However, there are some differences between both patterns. Caballines exhibited body mass changes faster than stenonians (Fig. 2). Though vegetation transformations were more or less similar to those that accompanied stenonian body mass changes, temperatures were different (Fig. 2). During the decrease of body mass in caballines, strong and frequent temperature changes

occurred (Shackleton, 1984; Shackleton & Hall, 1984). Additionally, during the greater part of this interval, sea levels were lower than those recorded during the stenorhine evolution (Vail, Mitchum & Thompson, 1977; Summerhayes, 1986). Consequently, coevolution of plant communities and caballines took place predominantly under cold-temperate and wet climatic conditions.

Africa

In Africa the same two principal monophyletic groups of horses are recognized as in Europe (Churcher & Richardson, 1978): stenorhines (*E. numidicus* and *E. tabeti*) and caballines (*E. mauritanicus*, *E. grevyi*, *E. quagga*, *E. zebra*, and *E. burchelli*). *E. asinus* is not included in these groups because phylogenetic relationships of asses (and hemionines) with horses are still under debate (Azzaroli, 1979; Eisenmann, 1979; Bennett, 1980; Forsten, 1988).

The African stenorhine group appears simultaneously as the European forms (2.5 Mya), but with a shorter temporal record (Fig. 5b). African stenorhines show the same pattern of body mass decrease as European ones, and thus we may interpret that this pattern is driven by similar global climatic changes. This group is also replaced by caballines, which are recorded for the first time in the Middle Pleistocene. Diachronic records of both groups have been found in Africa. Body mass pattern of African caballines is only slightly different than European ones. Body mass showed a very slight increase from *E. mauritanicus* to *E. grevyi*, and, probably even to *E. quagga* (we are cautious in this latter case because quaggas have also been related to *E. caballus* [Bennett, 1980]). On the other hand, body mass suffered a strong decrease from *E. mauritanicus* to *E. zebra*, *E. burchelli* and *E. asinus*. (Fig. 5b).

In general, large-sized extant zebras live in open habitats dominated by herbaceous vegetation (e.g. savanna) evolved upon soft soils. By contrast, smaller zebras have preferred woodland habitats, developed over harder grounds (Duerst, 1926; Gromova, 1949; Eisenmann, 1984; Eisenmann & Karchoud, 1982; Eisenmann & Guérin, 1984). It can be appreciated that body mass, in general, bears a strong relationship to these environmental components and, consequently, that it can be used to predict some ecological preferences of fossil species. Thus, we may infer that: (1) *E. numidicus* and *E. mauritanicus* lived in open habitats, with a savanna or steppe-like vegetation on soft grounds; and (2) *E. tabeti* lived in a more enclosed habitat (woodland-savanna?) over a hard substrate. This picture partially agrees with Eisenmann's (1984) ecological inferences from her studies of limb-bone lengths and proportions. The only difference between both results relates to the ecological requirements of *E. mauritanicus*, since Eisenmann points out that this species would have lived in an enclosed habitat with soft ground. However, she observes that her inference is not supported by other important eco-indicators such as the bovids and giraffids (Eisenmann, 1984:192). In fact, Geraads (1981) maintained that bovids lived in an open and dry environment in northern Africa during the middle Pleistocene. These inferences are concordant with those derived from our analysis.

Another important conclusion derived from the body mass prediction is that the presence or absence of competition between sympatric species can be inferred. It is well known that different species of equids can live together in Africa. The pairs of sympatric species are *E. grevyi*-*E. asinus* and *E. grevyi*-*E. burchelli* in East Africa, and *E. zebra*-*E. burchelli* in southwestern African (Forsten,

1988). Each of these species pairs present high mass differences, which imply different ecological preferences (Fig. 5b). The only exception to this pattern is the displacement of *E. burchelli* by *E. asinus*. Both species were sympatric in North Africa during the latest Pleistocene, but Burchell's zebra was displaced by the African asses due to human presence (Churcher & Richardson, 1978). With respect to *E. burchelli* and *E. quagga* (species with the same average body mass), competition was avoided by their allopatric distribution (Churcher & Richardson, 1978; Eisenmann, 1980), and their different habitat requirements, i.e. savannas for *E. burchelli* and semiarid areas for *E. quagga* (Churcher & Richardson, 1978).

North America

In this continent two groups are recognized (Fig. 5c). The first one is formed by species of the genera '*Onohippoidon*', *Dinohippus*, *Astrohippus* and *Equus simplicidens*; the second group includes the rest of the *Equus* species.

According to MacFadden's (1986) evolutionary picture, the body mass of fossil horses increased during the last 10 Mya. Our results for the Plio/Pleistocene horses agree with this picture. The pattern of body mass increase is in accordance with the climatic and floristic changes recorded for this time in North America. Thus, this trend is correlated with a general expansion of open habitats on the continent, with steppes as the predominant bioma in midcontinental North America, and with a general trend to more cold climates (Fig. 3). In a parallel development, deserts became established over a great expanse of Mexico and the southwestern United States, and a steppe-tundra biota spread across all of Beringia (Webb, 1977, 1989; Forsten, 1989). As in Europe, large-bodied horses lived in cold and open habitats.

South America

In South America also, two groups can be recognized (Alberdi, 1987). The first includes the *Hippidion* species, all endemic to South America, and the second includes the *Equus* species. *Hippidion* is phylogenetically related to *Pliohippus* from the Pliocene of North America, and became dispersed throughout South America during the Great American Biotic Interchange (*sensu* Webb, 1985) that occurred about 2.5 Mya because of the dry-land connection formed by the isthmus of Panamá. On the other hand, *Equus* dispersed throughout South America during the middle Pleistocene.

Within the *Hippidion* group, the middle sized *H. devillei* produced two species with differing body mass: (1) *H. saldiasi*, which has a similar body mass, and (2) *H. principale*, which reaches a greater size. In the *Equus* group, the large-sized *E. insulatus*, produced two different sized groups: (1) *E. santaeelenae* and *E. neogeus*, which both maintain or increase their body mass, and (2) the small *E. andium* (Table 1 and Fig. 5d). According to the Old World pattern, large-sized animals were better adapted to live in open habitats, under dry and cold climates, and on soft substrate. On the other hand, smaller ones lived in relatively closed biomas (e.g. woodland-savannas) with warm climates and a hard substrate. These inferences are in accord with the conclusions of Alberdi & Prado (1992, 1993), who suggest that: (1) *H. devillei* lived in open habitats under a warm and dry climate; (2) *H. saldiasi* lived in southwestern Patagonia, Argentina, and southeastern Chile, in a more wooded habitat with cold and

wet climatic conditions; (3) *H. principale* lived in Tarija (Bolivia), Buenos Aires province (Argentina) and Uruguay, in open habitats under a cold and wet climate; (4) *E. insulatus* from Tarija (Bolivia) and Río Chiche (Ecuador), *E. neogeus* from the Buenos Aires province (Argentina) and Brazil, and *E. santaeleenae* from the Santa Elena peninsula (Ecuador) have lived in open habitats; and (5) *E. andium* from Ecuador has lived in a mountainous habitat.

The pattern and evolution of body size change of the South American horses is different from those of the other continents. In *Hippidion*, *H. saldiasi* has retained the body mass, but with a decrease in the distal parts of the legs, while *H. principale* has increased its body mass (Fig. 5d). Elsewhere, in *Equus* species, *E. neogeus* and *E. santaeleenae* developed a slightly higher body mass than *E. insulatus*, while *E. andium* remained small. We believe that the differences between *Equus* and *Hippidion* species are a consequence of the migration time of both genera to South America, and of its different habitat distribution during the Pleistocene. *Hippidion* is recorded for the first times in South America in the Early Pleistocene ('Uquian' Land Mammal Age, Alberdi & Prado, 1993). At this time, steppes had been replaced by grasslands as the predominant open habitat in the continent (Ortiz Jaureguizar, 1989; Pascual & Ortiz Jaureguizar, 1990), in accordance with the fluctuating global climate changes for the late Pliocene-Pleistocene (Frakes, 1979). Consequently, there was the opportunity for reaching larger body mass, like *H. principale*. By contrast, the first appearance of *Equus* occurs in the Middle Pleistocene (Ensenadan Land Mammal Age, Prado & Alberdi, 1994) when several rapid environmental changes related to glaciation took place. As a general trend, open habitats were predominant in the southern part of the continent and more so in the areas closest to the eastern edge of the Andean chain in the central and septentrional regions. In the rest of the continent these habitats were occasionally interrupted by 'islands' of wooded habitats of varying extent. *E. andium*, the smaller South American *Equus* species lived, as did the rest of the species, in open habitats, but it was the only South American horse that inhabits a mountain region, on a hard substrate. *E. santaeleenae* and *E. neogeus*, two species of similar body size, lived in open habitats but they were not sympatric. On the other hand, *H. principale* and *E. neogeus*, species of both genera with larger body size, were sympatric, but with their differing body mass (460 kg and 378 kg respectively) and substrate requirements (wetter for *H. principale* and drier for *E. neogeus*, Prado & Alberdi, 1994), avoided competition.

CONCLUSIONS

(1) Metapodial and phalanx variables are better correlated with body mass than cranial variables in living Equini. Also, antero-posterior diameters of the metapodial and phalanx have higher correlation with body mass than length and breadth (F5 for the first phalanx and MC13 for the metacarpal third, Fig. 1).

(2) Maximal depths have higher body mass prediction values due to depths change in direct proportion with body mass, as a consequence that body mass is normally transmitted through limbs, specially through phalanges.

(3) In all continents evolutionary history of Equini was strongly influenced by environmental conditions and kind of substrates. Small body sized species

are basically correlated with warm climates and biomas with an important wooded component (e.g. woodland-savannas) and hard substrates. By contrast, large sized species are correlated with cold climates and open biomas (e.g. steppes and grasslands) and soft substrates. Taking into account only climates, Equini body size follows a clinal variation according to Bergman's rule.

(4) In Europe and Africa, Pleistocene horses follow an evolutionary trend from large sized species to small ones. By contrast, North American horses follow an evolutionary trend from small sized genera and species to large ones. Both trends are apparently driven by environmental conditions, which changes from warm and wooded habitats to cold and open ones in eastern land masses, and from warm, humid, and open habitats to colder and drier ones in North America (Figs 2, 3).

(5) The pattern of body size change of the South American horses is different to those of the other continents. The differences between *Equus* and *Hippidion* species trends are a consequence of the migration time of both genera to South America, and its different habitat distribution during the Pleistocene.

(6) *Hippidion* is recorded for the first time in South America when the steppes had replaced grasslands and there was an opportunity for reaching larger body mass. *Equus*, in contrast, appears later, when several short-time environmental changes related to glaciation took place, and open habitats were predominant in the southern part of the continent. Consequently, only the smaller *E. andium* colonized the high mountains and the rest of the species lived in the open habitats.

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