Extant and fossil *Equus* (Mammalia, Perissodactyla) skulls: a morphometric definition of the subgenus *Equus*

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A sample of 225 skulls belonging to all extant species of Equus and of 33 fossil skulls of ages comprised between 3.4 Ma and 0.7 Ma was studied by multivariate analyses of size, shape, and form on four axial lengths. A simple bivariate discrimination using the overall palatal length and the cranial length allows an almost complete discrimination between modern (extant and young) equids (subgenus *Equus*) and old plesippine and stenonine forms. The modern pattern, possibly related to a bigger brain case, seems to appear less than 1.5 Ma ago in fossil species that can already be recognized as closely related to the extant Grevy's zebras, plains zebras, and horses. This does not support separate branchings of *Equus* species from a common plesippine stem.

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Introduction

Previous studies on the development and evolution of equid skulls have been concerned with scaling effects of ontogeny and phylogeny (Robb 1935) and with the reorganization of the skull to accomodate bigger cheek teeth (Reeve & Murray 1942). Working on fossils ranging over 55 My (from *Hyracotherium* to *Equus*), Radinsky (1984) showed how allometry and reorganization affect different skull and mandible variables, and in particular those related to the function of feeding. Incidentally Radinsky showed that in adult domestic horses, the slope for the facial length vs. the brain case length was smaller than the slope calculated for the whole fossil sample. Note that domestic horses were the only representatives of extant *Equus* in Radinsky's sample. We are more concerned with systematics and evolution than with functional analysis, and the span of time considered in the present paper is much shorter: about 3.5 Ma. We analysed several axial lengths (the widths are often unreliable in fossil skulls because of distortions) in 225 skulls of extant species and 33 fossil skulls. We wanted to explore the different patterns of proportions of axial lengths and to find out whether there is a way to distinguish skulls of extant *Equus* (Zebras, Asses, Hemiones, and Horses) from fossil monodactyl equids of different ages and geographical localizations. Although our primary interest was in discrimination, we tried also to interpret the interspecific differences in terms of form, size, and shape. This approach was particularly justified, since species of *Equus* exhibit major differences in size. The overall form was partitioned into two components, one of size, and one of shape, following the classical equation of Needham: form = size + shape (Needham 1950; Bookstein 1989). We used for that purpose the general framework of size and shape introduced by Mosimann (Mosimann 1970; Mosimann & James 1979; Reyment *et al.* 1984; Darroch & Mosimann 1985; Reyment 1985; Bookstein 1989; Rohlf 1990; Bookstein 1991), together with the more traditional bivariate and multivariate allometric approaches (Reyment *et al.* 1984; Marcus 1990; Klingenberg 1996).

Materials and Methods

Material examined

The extant species are represented by 51 Grevy's zebras, *E. grevyi* (mostly collected in the wild); 39 plains zebras, *E. burchelli boehmi* (all collected in the wild from the same locality: Kitengela, Kenya); 15 mountain zebras, *E. zebra zebra*; 41 donkeys, *E. asinus*; 21 kulans, *E. hemionus kulan* (all from the Badkhyz reserve, Turkmenistan); 11 wild horses, *E. przewalskii* (seven from old collections in the wild, two from Askania Nova, two from Russian zoos); 47 domestic horses of medium to large size, *E. caballus*. The smallest skull is that of a donkey whose basilar length is 323 mm, the largest skull is that of a gigantic draft horse whose basilar length is 662 mm.

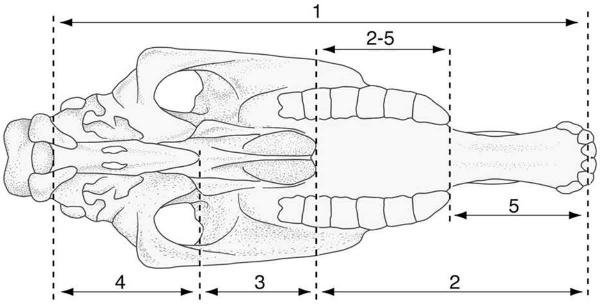

Fig. 1 Schematic ventral view of an *Equus* skull showing the measurements used in the present work. 1 = basilar length (from Prosthion to Basion); 2 = overall palatal length (from Prosthion to the posterior end of the palate; 3 = vomero-palatal length (from posterior end of the palate to the vomerine notch; 4 = cranial length (from the vomerine notch to Basion); 5 = muzzle length (from Prosthion to a line connecting the front of the second upper premolars); 2-5 = palatal length (from the line connecting the front of the second upper premolars to the posterior end of the palate).

The fossil sample comprises: 16 *Equus shoshonensis* (Hagerman Quarry, Idaho, USA); one *E. sanmeniensis* (Nihowan, China); seven *E. stenonis*: one from Kuruksai, Tadjikistan; one (composite) from La Puebla de Valverde, Spain; one from Saint-Vallier, France; four from Senèze, France; one *Equus* sp., Seymour Formation, Texas; one *Equus nalaikhaensis*, Nalaikha, Mongolia; one *E.* cf. *scotti*, Ulakhan-Sular, Siberia; two *E. mauritanicus*, Tighenif, Algeria. The largest fossil skull is that of *E.* cf. *scotti* from Siberia with a basilar length of 585 mm. These skulls are preserved in Museums and Institutes listed at the end of the paper.

Additional data on fossil horses were found in the litterature: one *E.* cf. *sanmeniensis*, Loc 32, China, M 1321 (Zdansky 1935); one *E. yunnanensis* V 42501, Madahai, China (Liu & Yu 1974); one (composite) *E. qingyangensis*, Bajiazui, China (Deng Tao 1999); one (composite) *E. stenonis mygdoniensis*, Gerakarou, Greece (Koufos 1992).

Geological ages of the fossils

The oldest species is the American 'plesippine' *E. shoshonensis*, about 3.4 Ma old (Repenning 1987).

The Chinese *E. sanmeniensis*, *E.* cf. *sanmeniensis*, *E. qingyangensis*, *E. yunnanensis*, and the Asian and European *E. stenonis* are about 2 Ma old or a little younger (Deng Tao 1999, and personal communication). The Chinese sites (Loc 32, Nihowan, Madahai, Bajiazui) are believed to be Villafranchian *sensu lato* (Forsten 1986). Kuruksai, Saint-Vallier, and La Puebla de Valverde are late Pliocene (Zhegallo 1988; Debard *et al.* 1994; Gautier & Heintz 1974). Gerakarou is early Pleistocene (Koufos 1992). This sample is referred to as 'stenonine'.

The other fossils are all younger than 1.5 Ma. *Equus* sp. belongs in the Gilliland fauna of the Seymour Formation, early Irvingtonian (Kurtén & Anderson 1980), about 1–1.5 Ma old (Lundelius *et al.* 1987: Table 7.3). *Equus* cf. *scotti* is probably of Akanyan age (= upper Olyorian), within the Brunhes magnetic period, i.e. younger than 0.8 Ma (A.V. Sher 1987, and pers. comm.). *Equus nalaikhaensis* is also believed to be younger than 0.8 Ma (Zhegallo *et al.* 1982). *Equus mauritanicus* of Tighenif (= Ternifine = Palikao) is about 0.7 Ma old (Geraads *et al.* 1986).

Measurements

A system of skull measurements was proposed by one of us (Eisenmann 1980, 1986). Here we use only four measurements (Fig. 1) the sum of which broadly adds up to the basicranial length (measurement 1): length of the muzzle (measurement 5) from Prosthion to a line uniting the front of the second upper premolars (P2); length of the palate *sensu stricto* from the line connecting the front of the P2 to the posterior end of the palate (measurement 2–5); distance between the posterior border of the palate and the vomerine notch (measurement 3); distance between the vomerine notch and the Basion (measurement 4). The lengths of the muzzle and of the palate *sensu stricto* may be added to give an overall palatal length (measurement 2) which very roughly corresponds to the estimation of the facial length used by Radinsky (TRL of Radinsky 1984). The distance between the vomerine notch and the Basion (measurement 4) is a rough estimation of the braincase length (BRCL of Radinsky 1984).

For sake of brevity, we will now write simply: muzzle length for measurement 5, palatal length for 2–5, overall palatal length for 2, vomero-palatal length for 3, and cranial length for 4.

For multivariate analyses, we did not use the overall palatal length, but its two components: muzzle length and palatal length separately. In *Equus* sp. of the Seymour Formation, the vomero-palatal length could not be measured; for that reason the skull was only studied in bivariate analyses.

Morphometric analyses

Shape parameters were calculated following Mosimann general procedure (Mosimann & James 1979): given a size measure (G), a vector of shape parameters, the Log-shape ratios, may be constructed by Log(Xi/G), where Xi stands for the set (or vector) of raw measurements, gathered onto the ith individual. Size was calculated as the mean of all variates for each individual, after Log transformation. It is proportional to the geometric mean (Bookstein 1989). Since all measurements may be added to recover almost exactly the length of the skull, this size parameter is proportional to the basicranial length. It is an isometric size reference (Bookstein 1989), since it weights equally each variate. Log-shape ratios are based on geometric similarity considerations. They are not therefore free from allometry (Darroch & Mosimann 1985), contrarily to residuals calculated by regression from a multivariate allometric size measurement such as the first axis of a within-group PCA (Jolicoeur 1963; Darroch & Mosimann 1985; Klingenberg 1996). Since most regression slopes in the present study (as well as in Radinsky 1984) are close to 1.0, an isometric size reference appeared particularly well suited. Allometry was tested by the multiple correlation of size onto the Log-shape ratios (Mosimann 1970; Mosimann & James 1979).

Size and shape patterns were analysed through a PCA of the Log-shape ratios, and plots of the PCA axes were contrasted to the size reference. Form discriminations were calculated using Fisher's discriminant functions or canonical variate analyses of Log transformed data. Mahalanobis D2 were corrected for the numbers of measurements and individuals (Marcus 1990). They were transformed into $\Delta 2 = (N\text{-}g\text{-}p\text{-}1)/(N\text{-}g)^*D2 - (ni + nj)^*p/ni^*nj$, where N is the total number of specimens of the g groups, ni and nj are the size of groups i and j, and p is the number of measurements. Standard error, confidence intervals for misclassification percentages, together with the statistical significance of Mahalanobis D2 were estimated by bootstraps using 10000 samples. Statistical analyses were performed using SAS for Windows (v. 6.10) and especially devised MATLAB (v. 5.0) functions.

Results

Size and shape differentiations

The ANOVA of isometric size differences calculated excluding single specimens was highly significant: $F = 190.27$, $df1 = 9$, $df2 = 256$, $P < 0.0001$). Duncan multiple tests define 5 groups of size: 1. donkeys, 2. kulans and plains zebras, 3. mountain zebras, 4. wild horses, and 5. all fossils together with domestic horses and Grevy's zebras. Bonferoni and Scheffé multiple tests are more conservative and recognize only three groups, lumping together the previous groups 2, 3, and 4.

The first 3 PCA axes calculated using the Log-shape ratios explain, respectively, 56.41, 25.86 and 17.73% (total = 100%) of the variability. Figure 2A-C contrast these PCA axes against the isometric size variability.

The first axis opposes mainly vomero-palatal length and cranial length (Fig. 2A) without much allometric influence (only 6.14% of the axis variability are explained by size). It opposes most of the plains zebras, *E. mauritanicus*, *E.* cf. *scotti*, and wild and domestic horses to most of the donkeys, kulans, stenonine forms and all the plesippine *E. shoshonensis*. Mountain zebras and Grevy's zebras are intermediate. In the case of plains zebras and kulans, the opposition is clearly independent of size. The opposition between domestic horses and the fossil stenonine and plesippine species is also independent of size.

The second axis (Fig. 2B) corresponds to the opposition between the muzzle length and the palatal length. Only 2.5% of this axis variability are explained by size. Plains and Grevy's zebras have long muzzles, kulans and horses, especially wild, have short muzzles. Azzaroli (1966) had also noted that 'in Przewalski's horses, the bony palate is longer than in *E. caballus*'.

Axis 3 (Fig. 2C) opposes the overall palatal length to the cranial length. It appears to be more correlated with size (17% of this axis variability are due to allometry. This is especially the case for the gradation between donkeys, mountain zebras, and wild and domestic horses. The rest of the differences are not allometric: kulans are still opposed to plains zebras, but plesippine and stenonine forms are opposed to Grevy's zebras, while domestic horses lie in between. The Mongolian *E. nalaikhaensis* plots near Grevy's zebras and *E.* cf. *scotti* plots near horses.

Form and shape discriminations

The canonical variate analysis of Log measurements is highly significant (Wilk's lambda = 0.01866, $F = 48.19$, $df1 = 36$, $df2 = 916.11$, $P < 0.0001$). The first three axes explain, respectively, 70.84, 15.04 and 9.26% of the variability (total = 95.14%).

The first axis (Fig. 3A,B) clearly corresponds to a between-group size factor: the correlation between the projections onto this canonical axis and isometric sizes reaches 0.945 ($P < 0.0001$). The whole sample is split into small-medium sized skulls (donkeys, kulans, plains zebras and mountain zebras), and medium-large sized skulls (wild and domestic horses, Grevy's zebras, and all fossil skulls).

The second axis (Fig. 3A) is mostly defined by the opposition between the central region (vomero-palatal length and, to a lesser degree, palatal length) and the cranial length. It opposes old fossil to young fossil and extant species. Old fossils have comparatively large central regions and short cranial lengths. Only 4.8% of the variability of this axis are explained by isometric size.

Several points are remarkable: (1) the extreme positions on the positive side are occupied by specimens of the plesippine *E. shoshonensis*, i.e. the oldest species; (2) most of Grevy's zebras plot closer to domestic horses, than to stenonine or plesippine forms. Although Azzaroli & Voorhies (1993) referred various stenonine and plesippine

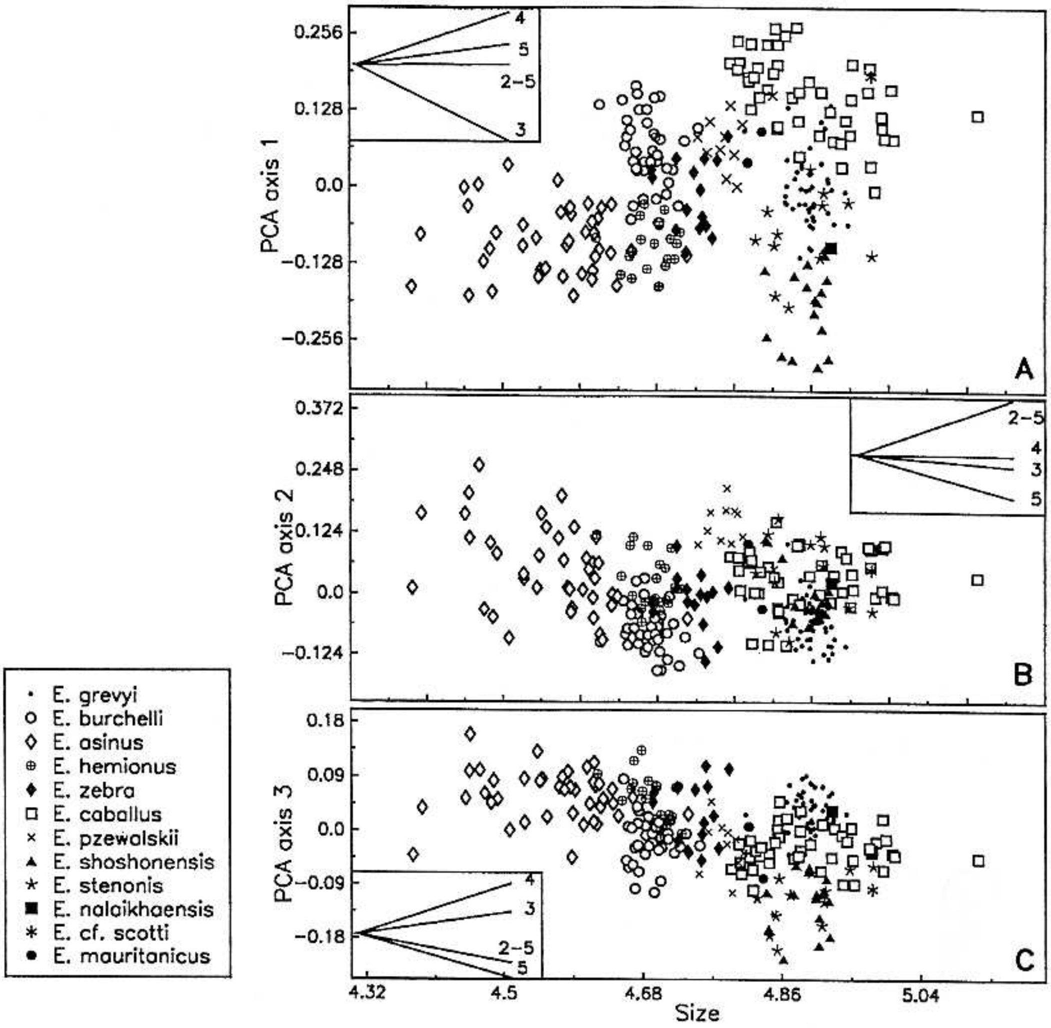

Fig. 2 Principal components analysis of shape: plots of the first (A), second (B), and third (C) shape components onto the isometric size measure. Enclosed figures illustrate the weights of shape variates onto the PCA axes. Weights for the size measure are those of an isometric vector whose elements are equal to $1/v\sqrt{p} = 0.5$, where p is the number of variates.

species to the subgenus *Dolichohippus*, Azzaroli (1965) had noticed that *E. grevyi* has a much longer brain case than *E. stenonis*; (3) *E. mauritanicus* and *E.* cf. *scotti* are close to the extant species.

The third axis (Fig. 3B) highlights the importance of vomero-palatal, cranial, and muzzle lengths, while the palatal length has a very small negative contribution. On this axis, the main segregation is that of Grevy's zebras and the Mongolian *E. nalaikhaensis* (which plots near the centroid of *E. grevyi*).

Since the first canonical axis may be considered as a size axis, differences between wild and domestic horses involve both size and shape as can be deduced from the oblique position of the respective groups in Fig. 3A,B. This observation is reinforced by results of discriminant functions. Differences in either form or shape (Table 1) oppose palatal length to the cranial and muzzle lengths: wild horses have relatively short cranial and muzzle lengths and long palates. The misclassification percentage is higher when size is excluded, but almost 90% of the individuals are still correctly classified into wild or domestic when shape is used alone.

The influence of allometry in these discriminations was assessed by a comparison between the directions of discriminant vectors and the multivariate allometric size direction for domestic horses (Table 2). It is not possible to have a correct estimation of the allometry within wild horses because the sample is too small. In our sample of domestic horses, the palatal length is almost isometric, the vomero-palatal length shows a positive allometry, cranial

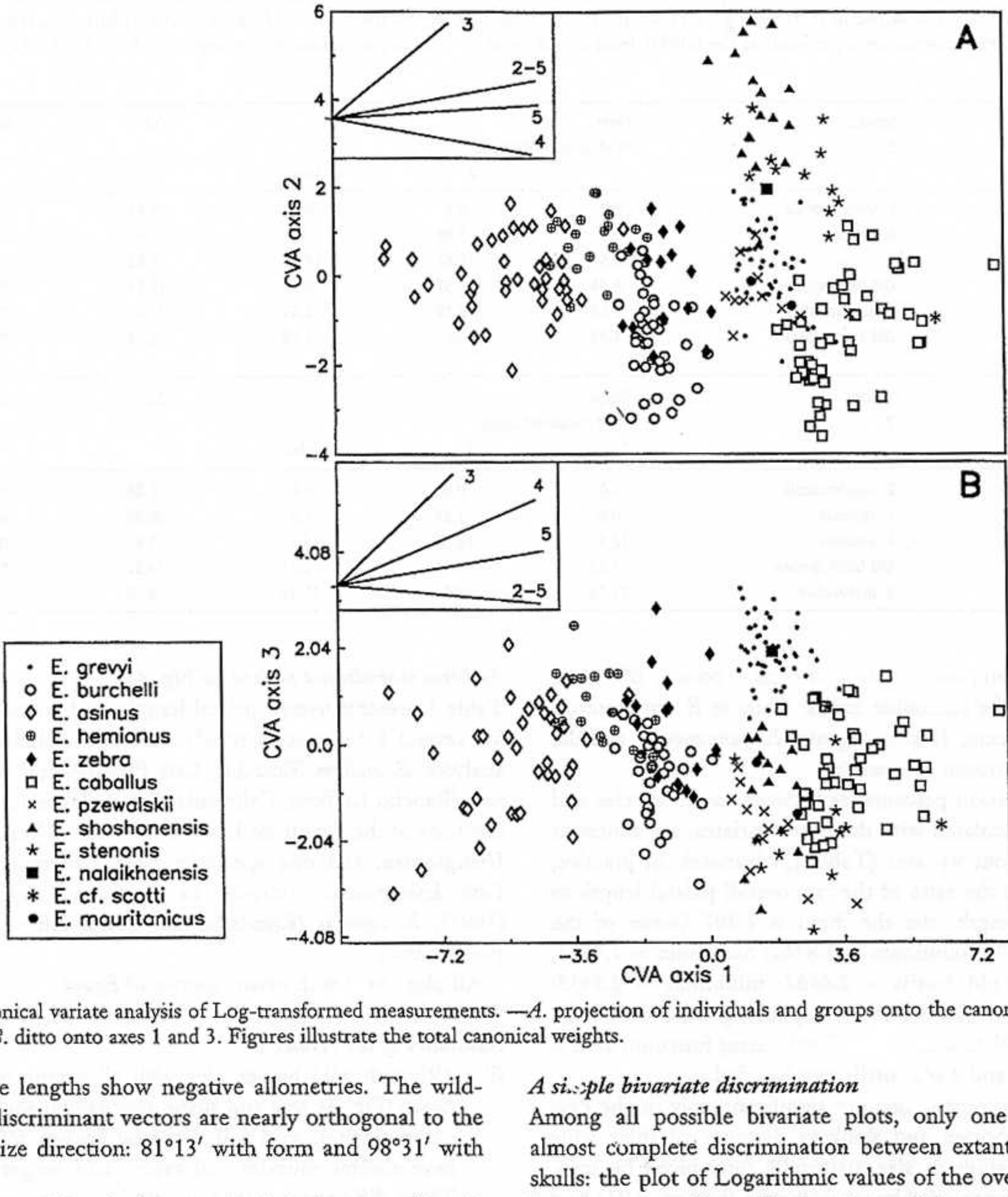

Fig. 3 Canonical variate analysis of Log-transformed measurements. —*A*. projection of individuals and groups onto the canonical variates 1 and 2. —*B*. ditto onto axes 1 and 3. Figures illustrate the total canonical weights.

and muzzle lengths show negative allometries. The wild-domestic discriminant vectors are nearly orthogonal to the domestic size direction: 81°13′ with form and 98°31′ with shape.

Differences either in form or in shape between Grevy's zebras, stenonine and plesippine forms were investigated by discriminant functions (Table 1). Using either form or shape alone, there is no overlap between Grevy's zebras and the plesippine *E. shoshonensis*. In the case of Grevy's zebra and stenonine forms, only one Grevy's specimen is classified with stenonine forms. The misclassification is higher between stenonine forms and the plesippine *E. shoshonensis*, and reaches 14.3% either with form or with shape.

Discriminant functions between extant specimens and old fossils lead to misclassification percentages lower than 3% (Table 1).

A simple bivariate discrimination

Among all possible bivariate plots, only one allows an almost complete discrimination between extant and fossil skulls: the plot of Logarithmic values of the overall palatal lengths against Logarithmic values of the cranial lengths. As can be seen on Fig. 4, all extant skulls domestic or wild, whatever the species, and whatever the size, are roughly aligned. The slope of the major axis calculated with the group centroids of each extant species is 0.986 ($P = 0.0008$). Among fossils, five specimens are close to the extant, while the 28 other plot apart, because of relatively shorter cranial lengths. There is almost no overlap with this dataset. The specimens plotting among extant species come from very different places (Algeria, Mongolia, North-eastern Siberia, and Texas) but they are all younger than 1.5 Ma. The other group (with relatively short cranial lengths) is composed of older species: about 3.4 Ma for the

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Table 1 Results of discriminant functions using form (upper part of the table) or shape (lower part of the table): misclassification percentages, corrected Mahalanobis distances (~~2~~), and significances of the Box M-test for heteroscedaticity of the within covariance matrices. All discriminations are significant at the 0.0003 level as indicated by bootstraps resampling, or higher. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species 1	Species 2	Form % of misidentifications 1	 2	 Total	Δ2	Box M
E. grevyi	E. shoshonensis	0.0	0.0	0.0	19.43	NS
E. grevyi	E. stenonis	0.0	1.96	1.6	21.66	*
E. shoshonensis	E. stenonis	12.5	16.67	14.3	3.53	*
Modern species	Old fossil species	0.44	3.57	0.79	16.71	***
E. caballus	E. przewalskii	2.13	9.10	3.45	10.46	**
Modern species	Old fossils (bivariate)	1.78	0.0	1.58	16.38	***

Species 1	Species 2	Shape % of misidentifications 1	 2	 Total	Δ2	Box M
E. grevyi	E. shoshonensis	0.0	0.0	0.0	19.85	NS
E. grevyi	E. stenonis	0.0	1.96	1.6	20.80	NS
E. shoshonensis	E. stenonis	12.5	16.67	14.3	3.82	NS
Modern species	Old fossil species	2.22	7.14	2.77	14.92	***
E. caballus	E. przewalskii	12.76	0.0	10.35	4.09	*

American plesippine E. shoshonensis, about 2 Ma or a little less for the stenonine forms: Chinese *E. sanmeniensis*, *E.* cf. *sanmeniensis*, *E. qingyangensis*, *E. yunnanensis*, and the Asian and European *E. stenonis*.

Misclassification percentages between extant species and old fossils, calculated with these two variates, are almost as low as with four variates (Table 1, bivariate). In practice, one could use the ratio of the raw overall palatal length to the cranial length: the threshold is 2.387 (mean of the extant = 2.1177; minimum = 1.8362; maximum = 2.4412; mean of the old fossils = 2.6562; minimum = 2.3438: maximum = 3.1522). The corresponding misclassification is almost equal to that of the discriminant function: 1.98% with 3 extant and 2 old fossils misclassified.

Intraspecific regressions are significant only in the case of domestic horses and donkeys, because of their wide range of variation in size artificially introduced by man. Major axes slopes are almost isometric (horses: 0.923 and donkeys: 1.146).

Table 2 Allometric weights in domestic horses and discriminant functions weights between domestic and wild horses on form and shape.

Measurements	Allometry	Discrimination Form	Discrimination Shape
Palatal length (2–5)	0.519	−0.397	−0.805
Vomero-palatal length (3)	0.697	−0.101	−0.027
Cranial length (4)	0.327	0.787	0.462
Muzzle length (5)	0.372	0.461	0.370

Additional skulls not plotted on Fig. 4

Table 3 presents overall palatal lengths and cranial lengths for several fossil species which were not included in the analyses: *E. andium* (Ecuador, Late Pleistocene); *E. occidentalis* (Rancho La Brea, California, Rancholabrean); *E. francisci* (cast of the type from Lissie Formation, Texas, Middle Irvingtonian, and one specimen from Channing, Texas, Late Irvingtonian, referred to *E. francisci* by Winans (1985); *E. capensis* (Elandsfontein, South Africa, Middle Pleistocene).

All plot along with extant species of *Equus*.

Summary of the results

(i) Although wild horses plot with all extant species of *Equus* (Fig. 4), size and shape analyses do show differences between wild and domestic horses: wild horses have shorter muzzles and crania and longer palates. These differences with domestic horses are nearly free from allometry.

Table 3 Additional data on natural logarithms of overall palatal lengths (v2) and cranial lengths (distance between Vomer and Basion = v4) in fossil *Equus*.

		log (v2)	log (v4)
E. andium	AMNH, *n*°14	5.438	4.668
E. occidentalis	Mean of $n = 12–19$	5.614	4.845
E. francisci type	Cast of TAMU 2518	5.371	4.710
Channing	AMNH 18–392	5.460	4.700
E. capensis	Cape Town, E 21025	5.697	4.956

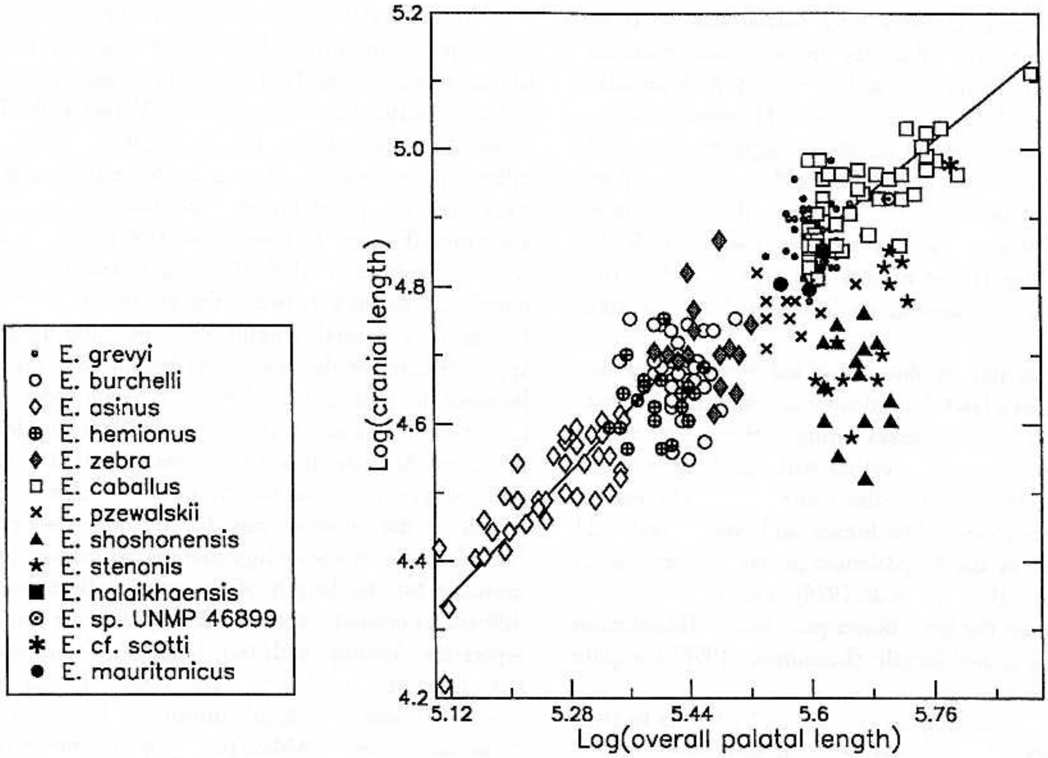

Fig. 4 Bivariate allometry of cranial length vs. overall palatal length. Projection of individuals and groups. Lines correspond to the only two significant major axes (for domestic horses and donkeys).

(ii) Skulls of *Equus* grevyi, the dolichohippine zebra, plot quite far from the stenonine and plesippine species Figs 3A, 3B, 4). Discriminant functions perfectly discriminate Grevy's zebras from the plesippine *E. shoshonensis*; only one Grevy's zebra skull is misclassified inside the group of stenonine equids.

(iii) All extant species of *Equus*, including *E. grevyi*, have similar proportions between the length of the cranium and the overall palatal length. The same proportions are found in the fossil species of *Equus* younger than 1.5 Ma: the Ecuadorian *E. andium*, the Californian *E. occidentalis*, the Texan *Equus* sp. and *E. francisci*, the Siberian *E.* cf. *scotti*, the Mongolian *E. nalaikhaensis*, the North African *E. mauritanicus* and the South African *E. capensis*.

(iv) The older species that we studied, whether in the New World (plesippines forms) or in the Old World (stenonines forms) have relatively shorter crania.

Discussion

On the validity of the commonly recognized taxa

1. The systematics and nomenclature of caballine horses is a matter of controversy (Eisenmann 1991a; Forsten 1993; Groves 1994; Eisenmann 1998). Although Przewalski's wild horses are clearly horses, their relation to fossil and domestic horses are far from clear, even on genetic grounds (Ryder 1994). Part of the surprisingly large variation appearing when the skulls of Zoo individuals are studied may be related to more or less documented hybridizations with domestic horses. For this reason, we have tried to restrict our study to the specimens collected in the wild (before the time when Przewalski's horses became extensively collected and imported in Western Europe) and to Russian collections; our sample is small but as reliable as may be.

When plotting muzzle length vs. palatal length, Forsten (1987: Fig. 2) found that wild horses overlap almost completely whith domestic horses; she concluded that there is no clear difference in the relative muzzle length of all caballoid horses, whether fossil or extant, and rejected the hypothesis that short muzzles may be some adaptation to cold. When our observations are plotted on the same diagram, the range of variation of the wild horse is very much less, as is the overlap with domestic horses. The differences in our observations are certainly due to the use of different samples: as noted above, we took care to use mostly specimens collected in the wild.

According to our data set, the skulls of wild horses of Przewalski are distinguishable by their short cranial and muzzle lengths and relatively long palatal length. If we assume the same size allometry in wild and domestic horses, the shorter muzzles and crania of *E. przewalskii* could be explained by size differences. However, such an explanation would not hold for their longer palate, which should be almost isometric. The difference in palatal length may well indicate that occidental domestic horses were not bred from Przewalski's horses. George & Ryder (1986) and Ryder (1994) discuss some genetic data that may, if they are confirmed, be interpreted in the same way.

Short muzzles may be observed in animals living in cold conditions (Allen's law); indeed they are common in Shetland ponies and in fossil horses dating to the last glaciation (Eisenmann *et al.* 1985). Together with the long hair and the erected mane, short muzzles contribute to the resemblance between Przewalski's horses and some fossil wild horses depicted by the Magdalenian people, for example at Les Combarelles (Capitan *et al.* 1924). This resemblance is however, limited: the limb bones proportions (Eisenmann 1991b) and the cranial lengths (Eisenmann 1998) are quite different.

2. The genus *Dolichohippus* was coined by Heller in 1912 for the Grevy's zebra because of the overall elongation of its skull. *Dolichohippus* is still commonly used at a subgeneric level (Groves & Willoughby 1981). Skinner (1972), struck by the overall elongation of the Pliocene North American skulls referred to *Plesippus*, considered *Plesippus* as a junior synonym of *Dolichohippus*. He was followed by several authors (Kurten & Anderson 1980; Azzaroli & Voorhies 1993).

Samson (1975), however, remarked that the Vomer index of Franck was quite different in Grevy's zebras and *Plesippus* (the Vomer index is the ratio between our vomero-palatal length [distance between the posterior border of the palate and the vomerine notch] and our cranial length [distance between the vomerine notch and the Basion]). Samson's observations were confirmed by Forsten & Eisenmann (1995) on larger samples: when compared to the cranial length, the vomero-palatal length is much longer in the plesippine *E. shoshonensis* than in Grevy's zebra.

The present study confirms Samson (1975) and Forsten & Eisenmann (1995) previous conclusions: there is no reason to apply the generic or subgeneric name of 'Dolichohippus' either to stenonine or plesippine equids.

Moreover, the fossil skulls that look most like Grevy's zebras are both quite younger than *E. shoshonensis* or *E. stenonis* (this study and unpublished data). One belongs to *Equus* sp. of the Seymour Formation, USA, early Irvingtonian, the other is the type of *E. nalaikhaensis*, Mongolia, probably younger than 0.8 Ma.

3. Gromova (1949) seems to be the first author to note that in plesippine forms the vomer reaches far back, more so than in extant equids. The usual expression of the more or less posterior development of the Vomer is the Franck's Vomer index (see above). However, the Vomer index itself differs also among extant equids: domestic horses are far away from plesippine forms, while hemiones and donkeys are closer (Forsten & Eisenmann 1995). The meaning of the Vomer index is difficult to understand. As we have noted, the distance between the vomerine notch and the Basion (our cranial length) may be interpreted as an approximation of the brain case length. But the distance between the posterior border of the palate and the vomerine notch (our vomero-palatal length) has no clear interpretation. Actually, it has two components: the length of the choanae plus the length of the vomer. While the length of the choanae may be in some way related to breathing and/or vocalizing, there is no evident functional meaning for the length of the vomer. Both lengths are difficult to estimate, and that is why they are not analysed separately. Anyway, with our data, the Vomer index does not satisfactorily discriminate extant (mean = 98.6; s = 13.25) and old fossil (mean = 129.55; s = 17.22) monodactyl equids. Although highly significant ($t = 9.18$, d.f. = 251, $P < 0.0001$) the difference leads to relatively high misclassification percentages of 15.11% for the extant, 21.43% for the old fossil, and 15.81% for the total.

The present study shows, however, that another combination of skull measurements — overall palatal length and cranial length — enables to group all extant species of *Equus* together and to discriminate them from Pliocene monodactyl plesippine and stenonine horses: the extant species and the fossils less than 1.5 Ma old have relatively longer brain cases (Fig. 4). Our results are in accordance and extend Radinsky's remark that domestic horses (his only extant specimens) have bigger cranial lengths relative to facial lengths when compared to all the fossils he has studied (Radinsky 1984). It is tempting to interpret this difference as an increase of the brain case.

4. There have been various taxonomical interpretations of the monodactyl equids, and in particular, of the position of the Pliocene North American so called 'plesippine' horses (i.e. akin or belonging to the genus *Plesippus*), the European and Asian so called 'stenonine' horses (i.e. akin or belonging to the species *Equus stenonis*), in relation to the extant 'dolichohippine' horses (i.e. akin to the extant Grevy's zebras), and to other extant equids. Various generic names have been proposed (*Plesippus* Matthew 1924; *Allohippus* Kretzoi, 1938; *Dolichohippus* Heller, 1912). These names were used at different levels and in various combinations: for example, Samson (1975) considered *Plesippus* to represent a genus comprising the subgenus

Allohippus to which he referred *E. stenonis*, while Gromova (1949) and Azzaroli (1982) use both *Allohippus* and *Plesippus* only at a subgeneric level. Some authors chose to refer all the corresponding species simply to the genus *Equus* (Stirton 1940; Eisenmann 1980; MacFadden 1994).

Most of the skull characters proposed to justify these generic or subgeneric distinctions are difficult to quantify and do not show a clear cut between old and extant monodactyl forms. According to Matthew (1924, 1926), Gidley (1930), followed by Gazin (1936), the distinctive skull features of plesippine forms are the presence of shallow facial pits, the greater (than in extant equids) angulation of the basioccipital region, and the elongation of the muzzle and face relative to cranium. The taxonomical value of the first character is very doubtful: in contrast to the well defined facial fossae of some Hipparions, the diffuse and shallow facial (malar) pits seen in some skulls of *Plesippus* and even of some extant *Equus*, seem to be mechanically related to the height of the upper cheek teeth and to the thickness of the bones. The second character is difficult to estimate (especially in fossil skulls) and is quite variable: 10 to 31° in domestic horses according to Osborn (1912). Thus, among the three characters proposed by Gidley and Gazin, only the relative cranial shortness vs. the muzzle and face elongations appear as reliable for distinguishing *Plesippus* from *Equus*. This character, however, has not been explored or quantified until now.

General taxonomical and phylogenetic implications

1. One of us (Eisenmann 1979) proposed two cladograms of the extant species of *Equus*, and a third in which are included three fossil forms. The latter, tentatively suggested a common ancestor for the Quagga group (including *E. burchelli*, *E. quagga*, and *E. mauritanicus*) and *E. stenonis*. This cladogramm is not supported by the present study because it would entail a parallel evolution of the cranial proportions in the Quagga line and in the other branch of extant species of *Equus*.

2. Bennett (1980) proposed another cladogramm and a zoogeographical phylogram for the genus *Equus*, including extant and fossil species. According to her, the genus *Equus* is diphyletic with an *E. asinus*-like branch and a *E. zebra*-like branch. The *E. asinus*-like branch includes Asses, Hemiones, and *E. scotti* (which for us is a relative of *E. caballus*). The *E. zebra*-like branch includes the African *E. burchelli* (as a sister group to the Californian *E. occidentalis*), *E. caballus* (as a sister group of the South African *E. quagga*), *E. zebra* (as a sister group to the North American *E. hatcheri*, a probable synonym of *E. scotti* in our opinion), and *E. stenonis* as the sister group or ancestor of *E. grevyi*. Apart of the surprising positions of *E. scotti*, *E. hatcheri*, *E. quagga*, and *E. occidentalis*, the overall interpretation of Bennett implies that an elongated cranium is a symplesiomorphy, and its shortening — a synapomorphy of stenonine and plesippine forms with a reversal in *E. grevyi*. More knowledge about the various *Dinohippus* species is necessary to discuss that point.

3. Azzaroli (1992, 1995) proposed another evolutionary tree of the genus *Equus*. According to Azzaroli: — all the *Equus* species derive by branchings off a common plesippine ancestor. If true, it would mean that the relative elongation of the cranium observed by us in all extant and young *Equus* was acquired separately by parallel evolution. Our observations rather support the existence of a common *Equus* ancestor distinct from, and possibly younger than, the plesippine species; — the Kenyan *E. koobiforensis* is considered by Azzaroli as the ancestor of *E. grevyi* and possibly of the other extant zebras. Although the skull of *E. koobiforensis* could not be included in our analyses because of an imperfect preservation, its relatively short cranium (Eisenmann 1980; plate XII) does not support such an ancestry (unless in case of parallel evolution).

4. The most recent biomolecular studies on phylogenetic relationships within the genus *Equus* (Oakenfull & Clegg 1998) suggest that a horse lineage (*E. przewalskii* and *E. caballus*) diverged from a zebra-ass lineage (*E. zebra*, *E. burchelli*, *E. grevyi*, *E. hemionus*, and *E. asinus*) about 1.2 Ma ago, and that the zebra group separated from the donkey-hemione group about 0.4 Ma ago. While the first point is compatible with palaeontological data (*E. scotti*, the first horse-like fossil in our opinion, is Irvingtonian), the second date is not supported by our data: *E. mauritanicus* (about 0.7 Ma old) is definitely a plain zebra, without any ass character. In our opinion *E. nalaikhaensis* and *Equus* sp. of the Seymour Formation, both probably about 1 Ma old, resemble *E.grevyi* more than any other extant species; we cannot, however, be as absolutely sure as for *E.mauritanicus* that they were not in any way related to asses.

Conclusions

Apart from probably endemic forms as *E. andium*, *E. occidentalis* and *E. francisci*, the fossil specimens plotting close to the extant species of *Equus* have marked similarities with one or other of these: *E. mauritanicus* and *E. capensis* resemble plains zebras and quaggas (Eisenmann 1980, 2000 (in press); *E.* cf. *scotti* resembles *E. caballus* (Eisenmann 1992); and *E. nalaikhaensis* as well as *Equus* sp. of the Seymour Formation have many points in common with *E. grevyi*. The similarities appear in skull characters (some not analysed here), as well as in teeth characters, and limb bones proportions. That is not to say that all the characters themselves are 'modern'. Actually, species of *Equus* are original combinations of characters which frequently may be traced far back in time. That is why a species of *Equus* cannot be safely recognized if only one or a few characters are known. In most cases, the characters themselves are not diagnostic; what is diagnostic is their association. Tattersall (1993) commented on a similar case with species of Lemur.

The main point of the present study is that one cranial character seems common to all extant species of *Equus*: all these species have relatively long cranial lengths (Fig. 4) roughly aligned along isometric directions. According to the geological, unfortunately not very precise, information, this *Equus* pattern appears around 1 Ma, and seems already diversified into specific patterns where the extant forms can be approximately recognized. The pattern is clearly different from the plesippine and stenonine patterns and does not support separate branching of *Equus* species from a common plesippine stem.

Accordingly, the name of *Equus* may be used at a subgeneric level to regroup all extant species together with at least *E. occidentalis*, *E. francisci*, *Equus* sp. of the Seymour formation, *E. nalaikhaensis*, *E.* cf. *scotti*, *E. mauritanicus*, and E. capensis.

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References

Azzaroli, A. (1965). The two Villafranchian Horses of the Upper Valdarno. *Palaeontographia italica*, *59*(n. s. 29), 1–12.

Azzaroli, A. (1966). Pleistocene and living Horses of the old World. *Palaeontographia italica*, *61*(n. s. 31), 1–15.

Azzaroli, A. (1982). On Villafranchian Palaearctic Equids and their allies. *Palaeontographia italica*, *72*(n. s. 42), 74–97.

Azzaroli, A. (1992). Ascent and decline of monodactyl equids: a case for prehistoric overkill. *Annales Zòologicae Fennici*, *28*, 151–163.

Azzaroli, A. (1995). A synopsis of the Quaternary species of Equus in North America. *Bolletino Della Societa Paleontologica Italiana*, *34 (2)*, 205–221.

Azzaroli, A. & Voorhies, M. (1993). The Genus Equus in North America. The Blancan species. *Palaeontographia Italica*, *80*, 175–198.

Bennett, D. K. (1980). Stripes do not a zebra make. *Systematical Zoology*, *29 (3)*, 272–287.

Bookstein, F. L. (1989). Size and shape: a comment on semantics. *Systematical Zoology*, *38 (2)*, 173–180.

Bookstein, F. L. (1991). *Morphometric Tools for Landmark Data Geometry and Biology*. Cambridge University Press.

Capitan, L., Breuil, H. & Peyrony, D. (1924). *Les Combarelles aux Eyzies (Dordogne). Publications de l'Institut de Paléontologie Humaine*.

Darroch, J. N. & Mosimann, J. E. (1985). Canonical and principal components of shape. *Biometrika*, *72*, 241–252.

Debard, E., Faure, M. & Guérin, C. (1994). Stratigraphie du gisement villafranchien moyen de Saint-Vallier (Drôme). *Comptes Rendus de l'Académie Des Sciences*, *318*, 1283–1286.

Deng Tao (1999). Equus qingyangensis sp. nov. (Perissodactyla, Equidae) from the Early Pleistocene of Qingyang, Gansu, China. *Vertebrata Palasiatica, 37 (1)*, 62–74.

Eisenmann, V. (1979). Caractères évolutifs et phylogénie du genre Equus (Mammalia, Perissodactyla). *Comptes Rendus de l'Académie des Sciences*, Paris, sér. *D, 288*, 497–500.

Eisenmann, V. (1980). *Les Chevaux (Equus sensu lato) fossiles et actuels: crânes et dents jugales supérieures.* Cahiers de Paléontologie du CNRS, Paris.

Eisenmann, V. (1986). Comparative osteology of modern and fossil Horses, Halfasses, and Asses. In R. H. Meadow & H. P. Uerpmann (Eds) *Equids in the Ancient World* (pp. 67–116). *Beihefte zum Tbinger Atlas des Vorderen Orients*, Reihe A, Wiesbaden.

Eisenmann, V. (1991a). Les Chevaux quaternaires européens (Mammalia, Perissodactyla). Taille, typologie, biostratigraphie et taxonomie. *Géobios, 24 (6)*, 747–759.

Eisenmann, V. (1991b). Proportions squelettiques de Chevaux quaternaires et actuels. *Géobios, Mémoire Spécial, 13*, 25–32.

Eisenmann, V. (1992). Origins, dispersals, and migrations of Equus (Mammalia, Perissodactyla). *Courier der Forschung-Institut Senckenberg, 153*, 161–170.

Eisenmann, V. (1998). Quaternary Horses: _ possible candidates to domestication. Proceedings of the XIII International Congress of Prehistoric and Protohistoric Sciences, Forli, Italia, 8–14 September 1996, 6, Tome 1, 27–36. Workshop 3. The Horse: its domestication, diffusion and role in past communities. ABACO Edizioni.

Eisenmann, V. (2000). *Equus capensis* (Mammalia Perissodactyla) from Elandsfontein. *Palaeontologia africana*, 36, in press.

Eisenmann, V., E. Crégut & A.-M. Moigne (1985). *Equus mosbachensis* et les grands Chevaux de la Caune de l'Arago et de Lunel-Viel: crâniologie comparée. *Bulletin du Muséum National d'Histoire Naturelle, 4ème série, Section C, 7 (2)*, 157–173.

Forsten, A. (1986). Chinese fossil horses of the genus Equus. *Acta Zoologica Fennica, 181*, 1–40.

Forsten, A. (1987). A comment on equid craniolgy. *Mammalia, 51 (3)*, 455–460.

Forsten, A. (1993). Size decrease in Late Pleistocene-Holocene caballoid horses (Genus Equus), Intra- or Interspecific evolution? A discussion of alternatives. *Quaternary International, 19*, 71–75.

Forsten, A. & Eisenmann, V. (1995). Equus (Equus) simplicidens (Cope), not Dolichohippus. *Mammalia, 59 (1)*, 85–89.

Gautier, F. & Heintz, E. (1974). Le gisement villafranchien de La Puebla de Valverde (Province de Teruel, Espagne). *Bulletin du Muséum National d'Histoire Naturelle, Sciences de la Terre, 36 (228)*, 113–136.

Gazin, C. L. (1936). A study of the fossil horse remains from the upper Pliocene of Idaho. *Proceedings of the United States National Museum, 83 (2985)*, 281–320.

George, M. Jr & Ryder, O. A. (1986). Mitochondrial DNA Evolution in the Genus Equus. *Molecular Biology and Evolution, 3 (6)*, 535–546.

Geraads, D., Hublin, J.-J., Jaeger, J.-J., Tong, H., Sen, S. & Toureau, P. (1986). The Pleistocene hominid site of Ternifine, Algeria: new results on the environment, age, and human industries. *Quaternary Research, 25*, 380–386.

Gidley, J. W. (1930). A new Pliocene horse from Idaho. *Journal of Mammalogy, 11 (3)*, 300–303.

Gromova, V. I. (1949). Istorija loshadej (roda Equus) v Starom Svete. Chast' 2. Evoljutsija i klassifikatsija roda. *Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 17 (2)*.

Groves, C. P. (1994). Morphology, Habitat, and Taxonomy. In L. Boyd & K. A. Houpt (Eds) *Przewalski's horse, the history and biology of an endangered species* (pp. 39–59). State University of New York Press.

Groves, C. P. & Willoughby, D. P. (1981). Studies on the taxonomy and phylogeny of the genus Equus. *Mammalia, 45 (3)*, 321–354.

Jolicoeur, P. (1963). The multivariate generalisation of the allometric equation. *Biometrics, 19*, 497–499.

Klingenberg, C. P. (1996). Multivariate allometry. In L. F. Marcus, M. Corti, A. Loy, G. J. P. Naylor & D. E. Slice (Eds) *Advances in Morphometrics* (pp. 23–49). New York: Plenum Press.

Koufos, G. (1992). Early Pleistocene equids from Mygdonia basin (Macedonia, Greece). *Palaeontographia Italica, 79*, 167–199.

Kurtén, B. & Anderson, E. (1980). *Pleistocene Mammals of North America.*Columbia University of Press, New York.

Liu Houyi & Yu Yuzhu (1974). New materials of E. yunnanensis in Yanmou, Yunnan. On diagnosis of E. yunnanensis and phylogeny of Equus in Asia. *Vertebrata Palasiatica, 12 (2)*, 26–134.

Lundelius, E. L. Jr, Churcher, C. R., Downs, T., Harington, C. R., Lindsay, E. H., Schultz, G. E., Semken, H. A., Webb, S. D. & Zakrzewski, R. J. (1987). The North American Quaternary sequence. In M. O. Woodburne (Ed) *Cenozoic Mammals of North America, Geochronology and Biostratigraphy* (pp. 211–235). University of California Press.

MacFadden, B. J. (1994). *Fossil Horses. Systematics, Paleobiology, and Evolution of the Family Equidae.* Cambridge University Press.

Marcus, L. (1990). Traditional morphometrics. In F. J. Rohlf & F. L. Bookstein (Eds) *Proceedings of the Michigan Morphometric Workshop 2* (pp. 77–122). Ann Arbor, Michigan: The University of Michigan Museum of Zoology.

Matthew, W. D. (1924). A new link in the ancestry of the horse. *American Museum Novitates, 131*, 130–131.

Matthew, W. D. (1926). The evolution of the horse. A record and its interpretation. *Quarterly Review of Biology, 1 (2)*, 139–185.

Mosimann, J. E. (1970). Size allometry: Size and shape variables with characterizations of the lognormal and generalized gamma distribution. *Journal of the American Statisticians Association, 65*, 930–945.

Mosimann, J. E. & James, F. C. (1979). New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution, 33*, 444–459.

Needham, A. E. (1950). The form transformation of the abdomen of the female pea-crab. *Pinnotheres Pisum Leach. Proceedings of the Royal Society B, 137*, 115–136.

Oakenfull, E. A. & Clegg, J. B. (1998). Phylogenetic relationships within the genus Equus and the evolution of alpha and theta genes. *Journal of Molecular Evolution, 47*, 772–783.

Osborn, H. F. (1912). Craniometry of the Equidae. *Memoirs of the American Museum of natural History*, n. *S., 1 (3)*, 57–100.

Radinsky, L. (1984). Ontogeny and phylogeny in horse skull evolution. *Evolution, 38 (1)*, 1–15.

Reeve, E. C. R. & Murray, E. D. F. (1942). Evolution of the horse skull. *Nature, 150*, 402–403.

Repenning, C. A. (1987). Biochronology of the Microtine Rodents of the United States, In M. O. Woodburne (Ed) *Cenozoic Mammals of North America, Geochronology and Biostratigraphy* (pp. 236–268). University of California Press.

Reyment, R. A. (1985). Multivariate morphometrics and analysis of shape. *Mathematical Geology, 17 (6)*, 591–609.

Reyment, R. A., Blackith, R. E. & Campbell, N. A. (1984). *Multivariate Morphometrics*. Academic Press, London.

Robb, R. C. (1935). A study of mutations in evolution. Part I: Evolution of the Equine skull. Part II: Ontogeny of the Equine skull. *Journal of Genetics, 31*, 39–52.

Rohlf, F. J. (1990). Morphometrics. *Annual Review of Ecology and Systematics, 21*, 299–316.

Ryder, O. A. (1994). Genetic Studies of Przewalski's horses and their Impact on Conservation. In: L. Boyd & K. A. Houpt (Eds) *Przewalski's Horse, The history and biology of an endangered species* (pp. 75–92). State University of New York Press.

Samson, P. (1975). Les Equidés fossiles de Roumanie. *Geologica Romana, 14*, 165–352.

Sher, A. V. (1987). Olyorian land mammal age of Northeastern Siberia. *Palaeontographia Italica, 74*, 97–112.

Skinner, M. F. (1972). Order Perissodactyla, In M. F. Skinner & C. W. Hibbard (Eds) *Early Pleistocene Preglacial and Glacial Rocks and Faunas of North-Central Nebraska* (pp. 117–125). *Bulletin of the American Museum of Natural History* 148 (1).

Stirton, R. A. (1940). Phylogeny of North American Equidae. University of California Publications. *Bulletin of the Department of Geological Sciences, 25 (4)*, 165–198.

Tattersall, I. (1993). Speciation and morphological differentiation in the genus Lemur. In W. H. Kimbel & L. B. Martin (Eds) *Species, Species Concepts, and Primate evolution* (pp. 163–176). New York: Plenum Press.

Winans, M. C. (1985). Revision of North American fossil species of the genus Equus (Mammalia: Perissodactyla: Equidae). Dissertation, University of of Texas, Austin.

Zdansky, O. (1935). Equus und andere Perissodactyla. *Palaeontologia Sinica, Series C, 6 (5)*, 1–54.

Zhegallo, V. I., Zazhygin, V. S., Kolosova, G. N., Malaeva, E. M., Mutzaeva, V. E., Sotnikova, M. V., Vislobokova, I. A., Dmitrieva, E. D. & Dubrovo, I. A. (1982). Nalaikha – oporny' razrez nijnego pleistotsena Mongolii. *Stratigrafia i Paleogeografia Antropogeǹa, INQUA, Kommissia po ijucheniu chetvertichnogo perioda*, 124–142.

Zhegallo, V. I. (1988). Semeistvo Equidae. In K. V. Nikiforova & E. A. Vangengeim (Eds) *Biostratigrafia Pozdnego Pliotsena-Rannego Pleistotsena Tadjikistana* (pp. 52–65). Kommissia po izucheniu chetvertichnogo perioda, Nauka.