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Identification and Discrimination of First Phalanges from Pleistocene and Modern Equus, Wild and Domestic

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1. Summary

Three aspects of the first phalanges of fossil and modern *Equus* were studied including 1) anteroposterior dimorphism and discrimination, 2) interspecific differences and identification, 3) tentative morphofunctional interpretation.

The analyzed sample comprises more than 500 first phalanx specimens (measured by V.E.). Fossil species include one Villafranchian *E.stenonis* (Spain: La Puebla de Valverde) and four caballine forms ranging from the Middle to the Upper Pleistocene (France: La Caune de l'Arago, Lunel-Viel, Jaurens, and Solutré). The modern sample includes the three extant species of zebras, wild and domestic asses, various forms of half-asses, and the wild horse *E.prze-walskii*.

Biometrical data were elaborated by J.D., using various statistical methods (correspondence analysis, principal components analysis, ascending hierarchic classifications with the chisquare or the Euclidian metrics, and discriminant analysis).

In most cases, the discrimination between anterior and posterior phalanges is possible, both "at first glance" and by biometrical techniques. Anterior phalanges are more developed in their proximal part than are the posterior phalanges. This is expressed biometrically by the longer supra-tuberosital segments and the longer trigonum phalangis of the anterior phalanges. In a

few cases, evidence for a moderate amount of sexual dimorphism was found, large phalanges being more frequently male.

In *E.stenonis*, the anterior phalanges have a morphology rather similar to that of the posterior phalanges of modern *Equus*: long infra-tuberosital segments and short *trigonum phalangis*. The posterior phalanges of *E.stenonis* have the same characters but they are even more marked. The phalanges of modern *Equus* exhibit few interspecific differences other than in size and gracility. But using these characters, one can hope to achieve a correct specific identification provided that the sample is good enough.

In several cases, the characters distinguishing anterior and posterior phalanges were found to also distinguish taxonomic groups: fossil versus modern forms, wild versus domesticated animals, one subspecies versus another. An hypothesis is proposed relating these characters to the distribution of weight on the front and the hind limbs. The morphofunctional mechanism, however, is still unclear and the hypothesis has yet to be tested.

2. Introduction

In many fossil samples, first phalanges are well preserved and numerous. Even when samples are poor, a few first phalanges are usually present. Accordingly they deserve some attention in order to be used to best advantage.

Phalanges differ in size and in shape not only from one species to another but also from the front limb to the hind limb. In some cases, posterior phalanges belonging to one species can be mistaken for the anterior of another species. There are therefore two problems, often connected, these being to distinguish fore and hind phalanges of a given species and to distinguish fore and hind phalanges of different species.

From previous work devoted to the first of these problems has emerged a pragmatic way of sorting "at first glance" anterior from posterior first phalanges. Such techniques are the better for being tested, and that was our initial aim, this constituting the first part of this paper. In addition, whenever the material was suitable, we looked for the presence of sexual dimorphism. As the study progressed, we came to analyze more specimens from more species and began to look into the second problem. Thus, interspecific differences make up the second part of this paper. In carrying out our analyses there emerged some unexpected facts, possibly related to evolutionary trends. These, however, need more time and work to be completely elaborated and so presently they will only be introduced in a short third part of this paper.

Our sample includes material from all modern *Equus* species (although inequally represented) and a few fossil forms. The total amounts to more than 500 specimens. Owing to the fact that our methodology calls for 14 or 15 measurements for each bone, the very bulk of the data has required statistical treatment including not only calculation of means and standard deviations but also multivariate analyses (Benzécri et al. 1973). Comments by both archaeologists and biostatisticians have led us to try to explicate, at least a little, the more elaborate statistical methods we have used. We have thus devoted a few paragraphs to that in the "Methods" section. We, however, do not feel that it is necessary to again return to the matter of ratio diagrams (Simpson 1941) nor to the biometrical method (Fig. 1) explained in previously published papers (Eisenmann 1986, Eisenmann/De Giuli 1974). Individual measurements which may be useful for archaeozoologists and paleontologists can be found in the appendix.

Computations were carried out at the "Centre Informatique du Muséum National d'Histoire Naturelle" and at the "Centre Inter-Régional de Calcul Electronique" with funds from U.A. 184 (CNRS). Multivariate analyses have been performed with A.D.D.A.D. software (JAMBU/LEBEAUX 1983).

3. Methods

Multivariate analyses are convenient whenever it is necessary to synthesize data provided by a large number of specimens described by numerous measurements (variables). The data are treated so as to form a cloud of points in multidimensional space, there being as many points and as many dimensions as there are specimens and variables. The cloud is projected on appropriate planes that are defined by factorial axes. Factorial axes and planes are chosen to show as much as possible of the information ("variance" or "inertia") contained within the cloud. In practice, the first two or three factorial axes express most of the useful information. The interpretation takes into account apparent relations between specimens and variables. Roughly speaking, when specimens appear grouped on a plane, it means that they are similar; when variables are grouped, it means they are correlated; when some specimens are grouped with some variables, it means that these variables best "characterize" those specimens.

The appearance of the relations between specimens and variables depends upon the mathematical formulae ("metrics") by which distances between points are calculated within the multidimensional cloud. Two metrics are commonly used to calculate, respectively, the "Euclidian" and "chi-square" distances. If x_{ij} is the value for the j^{th} variable of the i^{th} specimen in a sample of "n" specimens:

the mean
$$m_j=1/n\sum_i x_{ij};$$
 the standard deviation $\sigma_j=\left(1/n\sum_i (m_j-x_{ij})^2\right)^{\frac{1}{2}};$ $x_i=\sum_i x_{ij};$ $x_j=\sum_i x_{ij};$ the Euclidian distance $d^2_{i,i'}=\sum_j \left((x_{ij}-x_{i'j})/\sigma_j\right)^2;$ the chi-square distance $d^2_{i,i'}=\sum_i 1/x_{,j}(x_{ij}/x_{i-}x_{i'j}/x_{i'})^2.$

Multivariate analyses can be based on either of these metrics but will give somewhat different results. Principal components analysis uses Euclidian distance and takes into account, first, the absolute size of the specimens. Correspondence analysis uses the chi-square distance and is concerned not with size but with relative proportions (shape); with this method factorial axes are the same for variables and specimens (R and Q method) which is of great interest for interpretation.

In addition to the general ways in which specimens are related to one another, it may be interesting to find out if separate groups appear. That defines the goal of "automatic" classifications. The first step is to calculate the distances between the members of each possible pair of

specimens. Afterward, the ascending hierarchic classifications (used in this study) proceed by aggregating the most similar specimens (where the distance is the smallest) into one class that is thereafter considered as a single specimen and then aggregated again with the next most similar specimen or class. Naturally, the distances between specimens can be calculated either by the Euclidian or the chi-square metrics. There are, moreover, different ways of calculating distances between a single specimen and a class composed of several specimens, as well as between one class and another. We used the criterion of the second order central moment of a partition (close to Ward's method, JAMBU/LEBEAUX 1983).

When factorial analyses show that differences exist between two groups of specimens (for instance, anterior and posterior phalanges), discriminant analysis helps to more precisely explain those differences. This type of analysis considers two "specimens": the average anterior phalanx and the average posterior phalanx and a double set of variables: means of the 14 variables measured on the anterior sample and means of the 14 variables measured on the posterior sample. Once again, distances between the specimens and the variables can be calculated in different ways; here we have used the chi-square metric. Naturally, the variables that discriminate best will be those that take the most different values in the two average specimens. A final point should be noted. Discriminant analysis makes use of the whole existing body of material, even incomplete specimens, because it employs means to represent theoretical "average" specimens. In the other factorial analyses, the specimens are real and therefore must be complete in order to be used.

4. Material

4.1. Primitive Equus

Equus stenonis cf. vireti: The site of La Puebla de Valverde, situated in northeastern Spain in the Teruel basin, has yielded a rich Middle Villafranchian fauna (Heintz 1978). A primitive Equus is represented by numerous skeletal and cranial remains (Eisenmann 1979, 1980, 1981). The phalanx sample, already studied by Eisenmann/De Giuli (1974), comprises 85 specimens, 41 of which were considered as anterior and 44 as posterior. Only half of them are well enough preserved to permit the complete set of measurements to be taken so that the factorial analyses were carried out on 19 supposed-anterior and 21 supposed-posterior phalanges.

4.2. Zebras

Equus grevyi: After discarding 4 juvenile, 2 abnormal, and 2 incomplete specimens, the sample comprises 26 anterior and 25 posterior phalanges from 26 skeletons, The origin of this material is Kenya (8), Ethiopia (2), zoological parks (12), and unknown (4). There are 11 males, 13 females, and 2 individuals of unknown sex.

Equus burchelli boehmi: This sample is basically the one studied by EISENMANN/DE GIULI (1974) but several young specimens were removed and a few others added. All are from Kenya. There are 19 anterior and 19 posterior phalanges belonging to 10 males, 8 females, and 1 individual of unknown sex.

Equus zebra: The whole sample comprises 50 phalanges but all measurements are available for only 21 anterior and 23 posterior specimens. The true mountain zebra, Equus zebra zebra, is probably represented by 7 skeletons while 16 probably belong to the subspecies E.zebra hartmannae. There are 13 females and 10 males.

4.3. Asses

These are quite a problem. Samples are small, identification and origin are sometimes uncertain and sex unknown. For example, one supposedly Nubian Wild Ass (Munich 1952-9) is very small. Another (BM 1904-6-12-1) looks very much like a large domestic donkey (the White Egyptian Ass, AC 1983-634). As it is, our samples are of four sorts:

- 1. subfossil domestic donkeys from Ikrit, Israel, dating to the Middle Bronze Age (Davis, in litt.): 15 phalanges sorted out as 10 anterior and 5 posterior. They are not perfectly preserved so that analyses were run, with 8 variables only, on 9 "anterior" and 4 "posterior" phalanges;
- 2. modern supposedly domestic donkeys: 13 skeletons (6 female, 4 male, 3 of unknown sex) with 13 anterior and 12 posterior phalanges;
- 3. supposed "Somali wild asses": 5 skeletons but only 4 anterior and 4 posterior phalanges are able to be analyzed;
- 4. supposed "Nubian wild asses": 3 anterior and 3 posterior phalanges.

4.4. Half-Asses

E.hemionus hemippus (Syria): 3 skeletons but only 2 anterior and 2 posterior phalanges with the complete set of measurements;

E.hemionus onager (Iran): 15 skeletons but only 14 anterior and 14 posterior phalanges with the complete set of measurements; 10 males, 3 females, and 1 individual of unknown sex;

E.hemionus kulan (Turkmenia): 6 skeletons but complete sets of measurements for only 3 anterior and 3 posterior phalanges;

E.hemionus khur (India): 3 skeletons with the complete sets of measurements;

E.hemionus hemionus or luteus (Mongolia): 6 skeletons but with complete sets of measurements for only 5 of them;

E.kiang (Tibet): 6 skeletons with complete sets of measurements;

E.hemionus or E.kiang (origin unknown): 8 skeletons with the complete sets of measurements.

4.5. Horses

4.5.1. Fossil material

La Caune de l'Arago: This is a cave situated near Tautavel (Pyrénées-Orientales, France). It has yielded pre-Neandertal human remains as well as a rich lithic industry and fauna (H. DE LUMLEY/M.-A. DE LUMLEY 1971, H. DE LUMLEY 1979, RENAULT-MISKOWSKY 1980). There was some controversy about whether it is Mindel (Crégut 1980 a, Guérin 1980) or Riss (Chaline 1971, 1981) in age, although now an age of 400–500 kya is generally accepted (BOUCHEZ et al. 1984).

In the upper levels were found numerous remains of a caballine horse (Moigne 1983), first referred to a subspecies of *E.mosbachensis* (Crégut 1980b) and later to a different, short-muzzled, horse resembling *E.chosaricus* (Eisenmann et al. 1985). The horse remains include 34 adult, more or less well-preserved, first phalanges that were sorted out as 13 anterior and 21 posterior. A very small number of phalanges (3 supposedly anterior and 9 supposedly posterior) were complete. We were therefore obliged to work with a restricted set of variables and in the end, analyses were run on a sample of 29 (11 supposedly anterior and 18 supposedly posterior) phalanges with 8 measurements only. Even so, 13 values (among the $29 \times 8 = 232$) were missing and had to be replaced by the corresponding means.

Lunel-Viel: These caves in Hérault, France, have yielded a rich and well-preserved fauna as well as lithic and bone industries. They are believed to have been filled during the Mindel-Riss Interglacial (M.-F. Bonifay/E. Bonifay 1965). The horse remains have been ascribed to a new subspecies of the Mindelian Mosbach species: E.mosbachensis palustris (M.-F. Bonifay 1980), but it has recently been pointed out (Eisenmann et al. 1985) that the skull does not have the long muzzle characteristic of E.mosbachensis and looks more like that of the medium-muzzled E.przewalskii. Among the horse fossils were 34 phalanges, 23 of which are complete enough to permit multivariate analyses; 10 were considered as anterior, 13 as posterior.

Jaurens: This site, situated south of Brive, Corrèze, France, contained a rich Upper Pleistocene vertebrate fauna dated to about 30,000 years B.P. The horse remains were studied by MOURER-CHAUVIRÉ (1980) who ascribed them to *E.caballus* cf. gallicus, a form intermediate between the older *E.caballus germanicus* and the somewhat younger *E.caballus gallicus* from Solutré (PRAT 1968). These remains included 63 first phalanges, 51 of which were suitable for multivariate analyses; 25 have been sorted out by us "at first glance" as anterior and 26 as posterior.

Solutré: The well known Upper Pleistocene site of Solutré, Saône-et-Loire, France (Combier 1955), has yielded a very rich collection of horse bones. All of it was supposed to come from the Gravetian breccia dated to about 25,000 years B.P. and was described as *E.caballus gallicus* by Prat (1968). Recent excavations have shown that older (about 30,000 years old) and younger (about 12,000 years old) horses were also present at Solutré (Combier/Thévenot 1976). The phalanges studied in the present paper belong to old collections stored in Lyon and form a quite homogeneous sample of 33 bones; they probably come from the Gravetian breccia (Combier, personal communication); 30 are complete and were sorted out at "first glance" as 17 anterior and 13 posterior.

4.5.2. E.przewalskii

Although relatively rich (23 skeletons, 14 of which are male and 9 female), the sample is far from satisfactory. Nearly all animals were reared in zoological gardens. Different breeding lines (VOLF 1960–1985) are represented, some of which are known not to be pure. As a result, this sample is one of the least homogeneous, and the heterogeneity is even present among those animals that are supposed to be "true" Przewalski horses.

5. Discrimination between anterior and posterior phalanges

5.1. Introduction

PRAT (1957) was probably the first author to devote an entire paper to the practical problem of discriminating between anterior and posterior phalanges of Equus. Although the material used is not clearly specified, Prat was dealing with the domestic horse (E.caballus). He stated that first anterior phalanges are not always longer than posterior ones but that the latter are less broad in the middle and relatively deeper proximally. Prat also pointed to some qualitative differences in the shape of the proximal end, it being more asymmetric in first posterior phalanges, and moreover suggested differences in the second and third phalanges. Nearly 20 years later, Eisenmann/de Giuli (1974) approached the same problem using other species (E.burchelli boehmi, a plains zebra and E.stenonis cf. vireti, a Villafranchian form) and restricting themselves to the first phalanges for which they introduced a system of 13 measurements per bone. They found that, on anterior phalanges, the trigonum phalangis (CAMP/SMITH 1942) is longer and the supra-articular tuberosities are situated closer to the disal end. They confirmed the relatively greater proximal depth noted by Prat for the posterior phalanges.

In 1981, a Canadian student, Genia Kedney, applied the Eisenmann/de Giuli biometrical system to a sample of 15 Equus caballus and used discriminant function analyses (probably with a Euclidian metric) to distinguish the 30 anterior and 30 posterior phalanges. Judging from the unpublished manuscript, her results are in agreement with what had been pointed by Prat (1957) and Eisenmann/de Giuli (1974) with two differences. In her caballine sample, the supra-articular tuberosities of the anterior phalanges are not situated closer to the distal end but farther away from the proximal end and the supra-articular breadth is wider on anterior phalanges. We think it useful to return to the same question, using the same system of measurements (with an additional 14th measurement: the distal supra-articular breadth and, in some cases, a 15th: the distal articular depth), a richer and more varied body of material, and more sophisticated methods: multifactorial correspondence and principal components analyses.

We will begin by comparing a "first glance" sorting of fossil phalanges (La Caune de l'Arago) with the results of multivariate analyses on the same sample. We then use the same methods on a modern sample of *E. grevyi* for which the position of the phalanges are known for sure.

5.2. La Caune de l'Arago

5.2.1. Introduction

Some 34 adult, more or less well-preserved first phalanges were sorted out as 13 anterior and 21 posterior. The main criterion for the sorting was the more "waisted" aspect of the posterior phalanges. In the modern Burchell's zebra studied by EISENMANN/DE GIULI (1974) and many other equids, posterior phalanges seem narrower at the "waist" (smaller breadth) in contrast to the proximal and distal breadths (the latter, at the supra-articular tuberosities). Part of the impression may be caused by the relative shortness of the bone. Moreover, on these posterior phalanges, the supra-articular tuberosities are not only more developed but also situated more proximally, enhancing the contrast between these "hips" and the "waist". After confronting

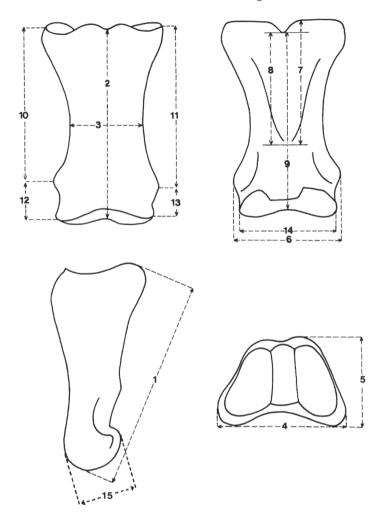


Fig. 1 System of measurements for the first phalanges (Ph 1):

- 1. Greatest length
- 2. Anterior length
- 3. Smallest breadth
- 4. Proximal breadth
- 5. Proximal depth
- 6. Distal supra-articular breadth
- 7. Greatest length of trigonum phalangis
- 8. Smallest length of trigonum phalangis
- 9. Posterior length
- 10. Medial supra-tuberosital length
- 11. Lateral supra-tuberosital length
- 12. Medial infra-tuberosital length
- 13. Lateral infra-tuberosital length
- 14. Distal articular breadth
- 15. Distal articular depth. This measurement has been added at the suggestion of an international symposium in New York, 1981. We have not yet enough data to evaluate its significance.

this anthropomorphic description with the system of measurements of Figure 1, one could expect posterior phalanges to be: 1) shorter than the anterior phalanges (Measures 1,2, and 9); 2) proximally and distally broader (Measures 4 and 6); 3) possibly narrower in the middle (Measure 3); and 4) to posses smaller values for Measures 10 and 11 and/or larger values for Measures 12 and 13.

After measuring the phalanges, histograms were drawn for the whole sample (pooling supposed anterior and posterior phalanges). The only histograms that seem clearly unimodal are those for Measures 6, 13, and 14. Most seem bimodal (2, 3, 4, 5, 9, 10, 12) or unclear. Coefficients of variation (v = 100 × standard deviation/mean) are usually less than 4 although they are notably larger for the proximal depth (Measure 5) and for the measures related to supraarticular tuberosities (10, 11, 12, and 13). After sorting the collection into anterior and posterior elements, samples were, of course, reduced and histograms as well as coefficients of variation are more difficult to interpret. It is noteworthy, however, that the coefficients of variation drop markedly for precisely those measures for which they were anormally high: 5, 10, 11, 12, and 13. This should mean that the dimorphism between anterior and posterior phalanges is expressed by these measurements.

5.2.2. The analyses

The next step was to see if the "first glance" sorting would be confirmed by multivariate analyses and for what characters. Let us already note that, in general, it was confirmed and that most characters were the same as the ones used in our "first glance" identification. Due to imperfect preservation, several measurements were missing for several phalanges. Accordingly, the analyses were run for 8 measures (2, 3, 4, 5, 7, 10, 12, 14) of 29 phalanges.

Correspondence analyses (Figure 2): The first axis, F(actor) 1, accounts for 67 percent of the total inertia (variance) and opposes variables 5 and 12 to variable 10. On the side of variables 5 (proximal depth) and 12 (internal infra-tuberosital length) are placed phalanges that have been identified as posterior. On the side of variable 10 (internal supratuberosital length) are the phalanges identified as anterior. It can be said that (supposed) anterior phalanges are more

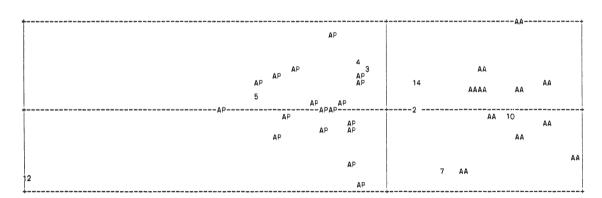


Fig. 2 Correspondence analysis for 8 measures on 29 first phalanges belonging to the fossil horse from La Caune de l'Arago. First axis horizontal, second axis vertical. AA = supposed anterior phalanges; AP = supposed posterior phalanges. The measurements 2, 3, 4, etc. are illustrated on Fig. 1.

developed proximal to their tuberosities whereas the (supposed) posterior are more developed distal to their tuberosities as well as being proximally deeper. The second axis (F2) accounts for 11 percent of the inertia and opposes lengths to breadths, namely the length of the *trigonum phalangis* (7) and the infratuberosital length (12) to the least (3) and proximal (4) breadths. Thus (supposed) anterior phalanges are rather long and (supposed) posterior are rather wide.

Principal components analysis: F1 is a size-axis largely defined by lengths (because in the set of measurements used there are 5 lengths and only 3 breadths). F2 and F3 suggest pretty much the same things as F1 and F2 of the correspondence analysis.

Ascending hierarchic classification (using chi-square metric): Nearly 58 percent of the total inertia is explained by the (supposed) anteroposterior dimorphism. The whole sample is separated into two discrete groups: one of (supposed) anterior and one of (supposed) posterior phalanges.

Discriminant analysis: The distinction between the average (supposed) anterior and average (supposed) posterior phalanges is naturally based on the already discussed characters and variables. Infra-tuberosital lengths (12 and 13) and proximal depth (5) characterize the "posterior" phalanges while "anterior" phalanges are characterized by supra-tuberosital lengths (10 and 11).

5.2.3. Conclusion

Among a sample of a Middle Pleistocene horse phalanges, a clear dichotomy can be made using "first-glance" criteria. Multivariate analyses confirm this dichotomy and identify which measurements actually discriminate. Most of these are related to the anthropomorphic model of contrasting "waist" and "hips". The proximal depth, not used during the first-glance sorting but noted by Prat (1957) appears equally valid. Supra-articular breadth, noted by Kedney, does not appear to discriminate.

Considering that the characters involved in dichotomizing the fossil sample are more or less the same as those found useful in distinguishing anterior and posterior phalanges of modern horses (Prat, Kedney) and Burchell's zebras (Eisenmann/de Giuli), we have grounds to believe that the dichotomy in the fossil material is the result of body position and not something related to sex, age, or some other factor. It seemed desirable, however, to test this assumption on other samples of *Equus* to see if the same characters were always involved. We tried first *Equus przewalskii* but the sample appeared to be not homogeneous at all, probably because it included different breeding lines (Volf 1960–1985) and more or less pathological specimens resulting from a long life in captivity. Although *E.przewalskii* will be discussed later, it is the best sample of a modern wild *Equus* we have, namely that of *E.grevyi*, that will be used as the principal example and discussed in some detail next.

5.3. Equus grevyi

5.3.1. First set of analyses

The first set of analyses was run with all of the 14 variables for 26 anterior and 25 posterior phalanges.

Correspondence analysis (Figure 3): F1 accounts for 62 percent of the total inertia and opposes infra-tuberosital lengths (12 and 13) characterizing posterior phalanges to the length

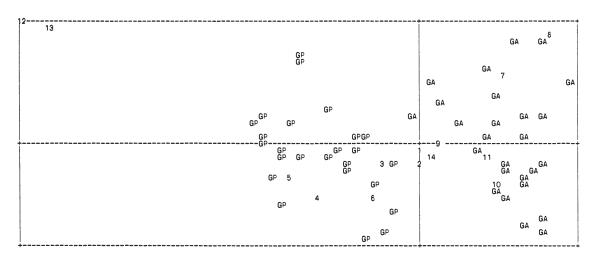


Fig. 3 Correspondence analysis for 14 measures on 51 first phalanges belonging to the modern *Equus grevyi*. First axis horizontal, second axis vertical. GA = anterior phalanges; GP = posterior phalanges. See Fig. 1 for the system of measurements.

of the *trigonum phalangis* (8) characterizing anterior phalanges. F2 (19 percent of the inertia) roughly opposes lengths (7, 8, 12, 13) and breadth (4). No sexual dimorphism appears on any of the axes.

Principal components analysis (Figure 4): On the plane defined by the first two axes (57 percent and 20 percent of inertia), anterior and posterior phalanges are clearly separated by a diagonal. Anterior are longer (1, 2, 9) and have longer supra-tuberosital segments (10, 11). Distal articular breadth (14) is strongly correlated with the lengths so that variable appears also on the side of the anterior phalanges. Posterior phalanges have longer infra-tuberosital segments (12, 13) and are proximally broader (4) and deeper (5). A probable element of sexual dimorphism appears on this plane; in each group of anterior and posterior phalanges, most of the larger specimens belong to male and most of the smaller to females.

Hierarchic ascending classification: Both Euclidian and chi-square based classifications clearly separate anterior and posterior phalanges. Moreover, using the Euclidian metric, males and females tend to cluster in different sub-classes: for posterior phalanges, one is composed of 9 females and 1 male whereas the other includes 4 females and 10 males; for anterior phalanges, one sub-class comprises 8 females and 1 male, the other 6 females and 10 males. No sexual dimorphism appears in the chi-square based classification.

Discriminant analysis: In accordance with the previous observations, posterior phalanges are characterized by long infra-tuberosital segments (12, 13) and large proximal ends (4, 5). Anterior phalanges are characterized by the length of the *trigonum phalangis* (8).

5.3.2. Second set of analyses

Another set of analyses was run with only 8 variables, namely those that had to be used for the fossil Arago sample: measures 2, 3, 4, 5, 7, 10, 12, and 14.

Correspondence analysis: F1 (67 percent of the inertia) correctly discriminates anterior and posterior phalanges. We find again that posterior phalanges are proximally more voluminous

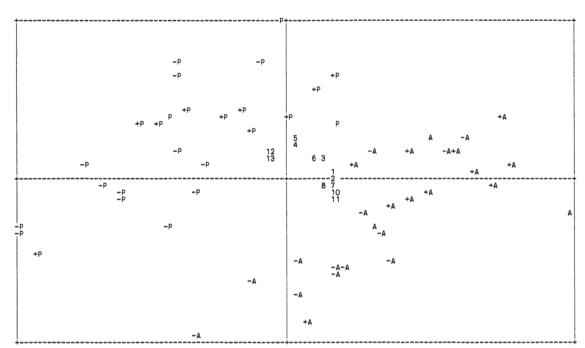


Fig. 4 Principal components analysis for 14 measures on 51 first phalanges belonging to the modern Equus grevyi. First axis horizontal, second axis vertical. A = anterior phalanges; P = posterior phalanges; + = males; - = females. Measures 9 and 14 were not printed by the computer because they are too close to other measures. Measure 9 is very close to measures 1 and 2; measure 14 is very close to measures 3 and 6.

(4, 5) and have a longer infra-tuberosital segment (12) while anterior phalanges have a long trigonum phalangis (7) and supra-tuberosital segment (10). F2 (10% of the inertia) opposes lengths (7, 12) and breadth (4).

Principal components analysis: The first plane shows the same pattern as in the analysis with 14 variables, namely good separation between anterior and posterior phalanges, the latter having longer infratuberosital segments and more developed proximal ends. Sexual dimorphism is also expressed in the same way.

Ascending hierarchic classifications: Both classifications (based on the chi-square and the Euclidian metrics) perfectly separate anterior and posterior phalanges but no clear separation by sex appears.

5.3.3. Conclusion

Anterior and posterior *E.grevyi* first phalanges can be perfectly separated by multivariate analyses based on chi-square or Euclidian metrics. Among the discriminating characters appear the same ones that provided the dichotomy in the fossil sample previously discussed: supra-and infra-tuberosital lengths, length of the *trigonum phalangis* and proximal depth. In some analyses, greater proximal breadth is an additional character for the posterior phalanx. Male pha-

langes are not always larger than female but this sexual dimorphism does show up in some of the analyses. Analyses run with a reduced set of variables (8 instead of 14) provide the same results as those run with the complete set.

5.4. Other Samples

5.4.1. General pattern

The same multivariate analyses as for *E.grevyi* were applied to 9 other populations of zebras, asses, half-asses, horses, and *E.stenonis* (i.e., correspondence and principal components analyses, ascending hierarchic classifications using both the chi-square and the Euclidian metrics). All were run both with the complete set of measures (14 or 15) and with the restricted set (the 8 measures used in the study of La Caune de l'Arago). The results are roughly identical. In correspondence analysis, the first axis (60-84 percent of the total inertia) opposes infratuberosital lengths (12, 13) and sometimes proximal breadth and depth (4, 5) to supra-tuberosital lengths (10, 11) and/or lengths of the *trigonum phalangis* (7, 8) – that are also "supra-tuberosital." The second axis (6.5-19 percent of the inertia) opposes lengths to breadths and depths.

In principal components analysis appear the same trends with the difference that total lengths (1, 2, 9) are added to supra-tuberosital in their opposition to infra-tuberosital lengths and proximal breadth and depth.

In both kinds of analyses, the first axis usually separates quite well anterior and posterior phalanges. Principal components analyses may also show a sexual dimorphism, phalanges belonging to males being in general larger than phalanges belonging to females.

In the ascending hierarchic classifications, the separation between anterior and posterior phalanges is usually good with the chi-square metric, poor with the Euclidian metric; the latter may show some sexual dimorphism.

In the discriminant analyses, the measures characteristic of posterior phalanges are 12, 13, and sometimes 4 and 5. Anterior phalanges are characterized by measures 8, 10, and sometimes 7 and 11.

To summarize, sexual dimorphism, when present, is size related. The differences between anterior and posterior phalanges are not so much related to the size as to shape. They lie principally in the relative development of the supra- and infra-tuberosital segments. Proximal breadth and depth and minimal breadth are more rarely involved. The ratio diagrams of Figure 5 illustrate the anteroposterior dimorphism in *E.hemionus onager*. The average anterior phalanx is used as reference (as in the other ratio diagrams of this paper). The average posterior phalanx differs from the anterior by its shorter *trigonum phalangis* (7) and supra-tuberosital length (10). There is nearly no overlap of the two ranges of variation for these measores.

5.4.2. Particular points

E.stenonis cf. *vireti*: The first glance sorting is confirmed by most analyses. Out of the 40 phalanges, one supposedly anterior is placed with the posterior, but only in analyses using the Euclidian metric with the reduced set of variables. In the ascending hierarchic classification with the chi-square metric, most of the partition (72-74 percent) is explained by the (supposed) anterior-posterior dimorphism.

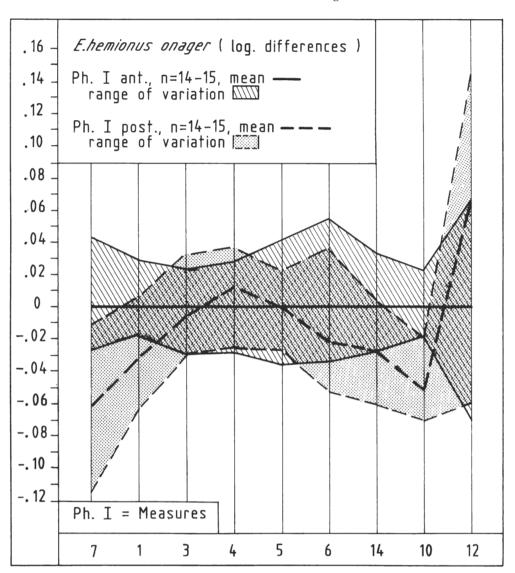


Fig. 5 Ratio diagrams of the means and ranges of variation (between the minimal and maximal observed values) for the anterior and posterior first phalanges of *Equus hemionus onager*. See Fig. 1 for the system of measurements, and Table 1 for the measurements.

E.burchelli boehmi: One of the 38 phalanges is constantly misplaced. This certainly anterior phalanx has a "posterior" morphology because of its well-developed infra-tuberosital lengths. The posterior of the same individual exhibits the same peculiarity which makes it appear as "superposterior" on the analyses. Slight sexual dimorphism appears in the hierarchic classification with the Euclidian metric on 14 variables. One class contains 14 males and 4 females, the other 6 males and 12 females.

E.zebra: Out of 44 phalanges, 3 posterior and 2 anterior are occasionally misplaced. The principal components analysis on 8 variables shows an interesting point. The first axis opposes the

TABLE 1

	Equus hemionus onager								
	mes.	n	x	min.	max.	s	v	log.	
	1	15	76.5	73.3	82	2.27	2.96	1.884	
	2	15	69.8	66	76	2.57	3.68	1.844	
	3	15	24.6	23	26	1.02	4.17	1.390	
	4	15	41.1	38.5	44	1.68	4.07	1.614	
	5	15	30.8	28.5	34	1.53	4.97	1.489	
	6	15	36.7	34	41.8	1.98	5.40	1.564	
Ph. I Ant	7	14	48.1	45	53	2.54	5.29	1.682	
	8	15	42.8	39	47	2.50	5.83	1.632	
	9	14	69.1	66	75	2.21	3.20	1.840	
	10	14	58.5	56	62	2.06	3.52	1.767	
	11	14	58.4	55	63	2.34	4.00	1.767	
	12	14	10.3	8.8	12	0.94	9.09	1.014	
	13	14	10.2	8.9	11	0.65	6.42	1.007	
	14	15	35.6	33.3	38.5	1.53	4.29	1.551	
	1	15	71.2	66.5	78	2.58	3.62	1.853	
	2	15	64.9	60.7	69	2.06	3.18	1.812	
	3	15	24.3	23	26.5	1.01	4.15	1.386	
	4	15	42.4	39	45	1.85	4.36	1.627	
	5	15	30.9	29	32.5	1.19	3.84	1.490	
	6	15	35	32.6	40	2.05	5.85	1.544	
Ph. I Post	7	14	41.8	37	47	2.48	5.92	1.621	
	8	15	36.5	32	41	2.42	6.62	1.562	
	9	14	63.5	59.8	69	2.10	3.31	1.803	
	10	14	52.2	50	56	1.90	3.64	1.717	
	11	14	52.6	50	57	2.01	3.82	1.721	
	12	14	12	9	14.5	1.44	12.00	1.080	
	13	13	11.2	8	13	1.46	13.10	1.049	
	14	14	33.3	31	36	1.53	4.60	1.523	

Tables 1-5 Measurements in millimeters for anterior and posterior first phalanges.

mes. = dimension (measure); the numbers 1 to 15 refer to the system of measurements defined in Figure 1;

n = number of specimens studied;

x = mean;

min. = minimum value observed;

max. = maximum value observed;

s = standard deviation;

v = coefficient of variation;

log. = decimal logarithm.

phalanges with well-developed supra-tuberosital segments (mostly anterior) to phalanges with well-developed distal ends (mostly posterior). In both sub-classes, *E.zebra zebra* individuals have more distally developed phalanges ("more posterior") than do *E.zebra hartmannae*. The second axis opposes robust to less robust bones. Phalanges belonging to males are robust with the exception of one. The skull of this individual was not available so that the male sex marked on the label could not be confirmed by the presence of canines. Phalanges belonging to females may be robust or not. The sub-specific dimorphism superimposed on the anteroposterior dimorphism is probably responsible for the relatively high number of misplaced phalanges.

Asses: In the analyses run with the 14 variables on the wild and domestic modern asses, the sample appears as a continuum between the anterior and posterior "poles". In consequence, the hierarchic ascending classifications fail to discriminate properly between anterior and posterior phalanges. Other analyses were run with the reduced set of variables in order to include the subfossil Ikrit sample. The results are even worse because Ikrit phalanges are shifted in the posterior direction. Thus, several anterior Ikrit phalanges are placed on the posterior side of the axis. In accordance, in the hierarchic classification with the chi-square metric, one group is purely anterior while the other contains posterior phalanges as well as several anterior (mostly from Ikrit).

E.hemionus onager: Out of 27 or 28 phalanges, 2 are occasionally misplaced in the analyses using the chi-square metric. The anteroposterior dimorphism seems weaker than in the previously studied species. In the hierarchic ascending classifications the two groups fuse into one much earlier than in other species (at 40-50 percent instead of 60-80 percent of the total inertia). The great number of males renders the sample improper for research on sexual dimorphism.

The horse from Lunel-Viel: One supposedly anterior phalanx (LVI-10-16589), and one supposedly posterior (LVI-9-2921) phalanx (out of 23) are "misplaced."

The horse from Jaurens: The first glance sorting was relatively difficult: 10 phalanges were only doubtfully identified as anterior or posterior. Thus we were not surprised to find 6 of the phalanges "misplaced" (or should we say that their identifications were corrected?) by the analyses. If these analyses are correct, FSL 302-212 and 255 should be posterior, FSL 302-205, 211, 216, and 332 should be anterior, and our sample contains 27 fore and 24 hind phalanges instead of 25 fore and 26 hind.

The horse from Solutré: The Solutré sample like the one from Jaurens contains several (4) phalanges doubtfully identified as anterior or posterior. Two of them and a third one are "misplaced" by the analyses. If these are correct, SOL"2" and 144 should be anterior, SOL 141 should be posterior, and our sample should contain 18 anterior and 12 posterior phalanges instead of 17 and 13.

E.przewalskii: The sample (46 phalanges) looks quite heterogeneous with 6 phalanges being usually "misplaced". In some cases (LD 359, AMNH 32686, 32696, AC 1929–35) the phalanges seem shifted in the posterior direction (anterior are classed with posterior whereas some posterior tend to occupy an extreme "hyperposterior" position on the cloud). In other cases, posterior phalanges look like anterior (e.g., MA 1964–107, BA 10877).

Following the suggestion of O.RYDER (personal communication) we looked for possible differences between what are believed to be "pure" *E.przewalskii* and animals belonging to mixed or doubtful breeds. Toward that end, various analyses were run separately on anterior and posterior phalanges. In the correspondence analysis for the anterior phalanges, the first axis

opposes, as usual, infra-tuberosital to supra-tuberosital lengths, i.e., "posterior" to "anterior" morphologies. On the "posterior" side, we find 5 "pure" *E.przewalskii* and 4 doubtful whereas on the "anterior" side are 4 pure and 10 doubtful. The analysis for the posterior phalanges is more striking. *All* supposed pure *E.przewalskii* are on the "posterior" side of F1 together with 3 doubtfully pure Przewalski horses. Two of these latter (AC 1935–486 and 1941–322) were also placed on the "posterior" side in the correspondence analysis for the anterior phalanges. Thus it seems that the heterogeneity of our sample is explained by the fact that pure Przewalski horses usually have more developed infra-tuberosital segments both on anterior and on posterior phalanges than do horses belonging to mixed breeding lines.

5.5. Conclusions

In most cases, first phalanges of all species of Equus can be discriminated at first glance by looking at the relative position of the supra-articular tuberosities (located more distally in anterior first phalanges). Additional criteria, less reliable, are the length of the trigonum phalangis and the greatest length (both larger in anterior phalanges) and, occasionally, the distal articular breadth (larger in anterior phalanges) and the proximal depth (larger in posterior phalanges). In some taxa, the anteroposterior dimorphism is more obvious than in others. For example, zebra phalanges usually contrast more than do those of horses, the latter being at times more difficult to differentiate. Discrimination is easier within homogeneous samples. In most cases, first glance identification is confirmed by multivariate analyses. Contradictions appear usually only when first glance identification was questionable. The discriminant characters are the same as those used in first glance identifications. When populations are homogeneous, discrimination can be nearly perfect. This is true both for modern (Grévy's and Burchell's zebras) and for fossil samples (La Puebla de Valverde, Arago). When populations are heterogeneous, discrimination is not so good, e.g., 13 percent misplaced phalanges among 46 specimens of E.przewalskii. The reason for this is that the shape differences that express anteroposetrior dimorphism within an homogeneous sample may also express other features. For example, E.zebra zebra individuals generally have a more "posterior" morphology than do E.zebra hartmannae specimens. The same seems to be true for "pure" E.przewalskii in relation to mixed breeding lines.

The best statistical discriminations are achieved by correspondence analysis and ascending hierarchic classification based on the chi-square metric. In the principal components analysis appear, at the same time, shape-related anteroposterior dimorphism and size differences that may or may not be related to it. Size and shape are also intricately bound in classifications based on the Euclidian metric. The agreement between analyses using the complete set of measures (14) and the restricted set (8) validates the results obtained when only the latter could be used.

In practice, if an homogeneous sample of 15–20 phalanges has to be sorted as anterior and posterior, one can use either the first glance and/or the biometrical techniques. If the measures recommended in this paper are used, multivariate analyses will differentiate anterior and posterior phalanges with an error of about 1–3 percent. If, however, one isolated phalanx has to be identified as anterior or posterior, one can analyse its measures together with those of a sample including anterior and posterior phalanges belonging to the same (supposed) taxon as the isolated phalanx. A severe mistake in choosing the comparative taxon would become evi-

dent through the analyses. Within the same species, without problems due to pathology or domestication, the risk of error can be evaluated as being 4-6 percent. In bad cases, it can increase up to 15 percent, but there, the method indicates its own limits: overlappings of anterior and posterior clouds and low percentage of inertia explained by anteroposterior dimorphism. For one problematical isolated phalanx, one can also compare the corresponding ratio diagram with those published in this paper.

Naturally, anteroposterior discrimination is closely bound to taxonomic identification that has been (artificially) isolated for discussion in the next part of this study.

6. Interspecific differences

6.1. Introduction

The more extensive studies of equid first phalanges of which we are aware are those of CAMP/SMITH (1942), GROMOVA (1949), and SONDAAR (1968). These authors, however, were more interested in functional evolution (from the primitive tridactyl forms to the modern monodactyl Equus) than in specific differences within the genus Equus.

We have approached the question of interspecific differences using two kinds of methods. The first includes multivariate analyses that permit us to obtain a general view of the entire genus *Equus* or of its subgroups. The second involves the use of ratio diagrams in order to make more detailed comparisons and to better illustrate some points. Since we were no longer interested in anteroposterior dimorphism, we were able, at times, to use analyses run only on one kind of phalanges (anterior or posterior). Posterior phalanges were frequently chosen because they often reveal greatest differences from one species to another.

6.2. General view of the genus Equus

When all phalanges are pooled together in correspondence analyses, the first axis expresses slenderness by opposing measure 3 (and, to a lesser degree, measures 4 and 5) to measures 1, 2, 9, 10, and 11. Slender species are half-asses, asses and Grevy's zebras. Robust species include most of the horses and *E.stenonis* cf. vireti. The second axis opposes infra-tuberosital lengths (12 and 13) to lengths of the trigonum phalangis (7 and 8). Posterior phalanges are on the first side, anterior on the other. Both anterior and posterior phalanges of *E.stenonis* cf. vireti are entirely on the "posterior" side of F2. Figure 6 shows the same analysis run using average dimensions for posterior phalanges of the best represented populations. (If all bones were represented there would be too much overlapping for clarity in the figure. These overlappings do exist, however, even if they are not apparent on Fig. 6.) Average anterior phalanges are entered as supplementary elements which means that they are placed on the figure but do not affect the relative position of posterior phalanges. On Figure 6, the points representing average anterior phalanges are united by straight (interrupted) lines to the points representing the average posterior phalanges of the same species. These lines are roughly parallel, which means that the same differences separate anterior and posterior phalanges of all the studied species.

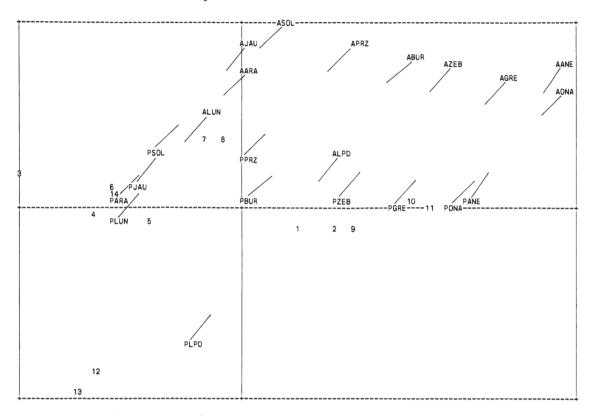


Fig. 6 Correspondence analysis for 14 measures on average posterior (P) phalanges belonging to 11 populations of modern and fossil Equus. Average anterior phalanges (A) are introduced as supplementary data. First axis horizontal, second axis vertical.

ANE = domestic ass; ARA = fossil horse from La Caune de l'Arago; BUR = Kenyan Burchell's zebra; GRE = Grevy's zebra; JAU = fossil horse from Jaurens; LPD = E.stenonis cf. vireti from La Puebla de Valverde; LUN = fossil horse from Lunel-Viel; ONA = E.hemionus onager; PRZ = E.przewalskii; SOL = fossil horse from Solutré; ZEB = E.zebra.

Figures 7 and 8 compare the ratio diagrams of a horse, an *Estenonis*, and the Kenyan Burchell's zebra. The horse and Burchell's zebra have very similar phalanges, especially anterior ones. The phalanges of *Estenonis* differ by having a shorter *trigonum phalangis* (measure 7) and a longer infra-tuberosital segment (measure 12). Species with slenderer phalanges are compared in Figures 9 and 10. Anterior and posterior phalanges of domestic asses are very similar to the ones of *Eshemionus onager* (Fig. 9; Figs. 5 and 10). *Equus grevyi* phalanges are clearly more robust. Kiang phalanges are characterized by their relatively narrow distal ends (measure 14) and long supra-tuberosital segments (measures 10). The three species differ from *Estenonis* by measures 7 and 12.

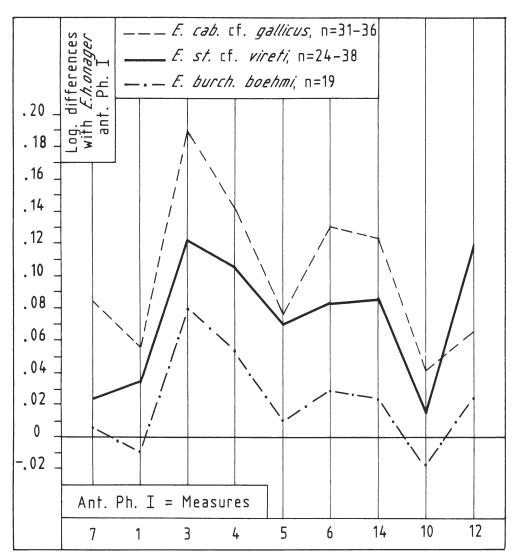


Fig. 7 Ratio diagrams for the average values of robust anterior first phalanges belonging to *E.caballus* cf. gallicus from Jaurens, *E.stenonis* cf. vireti from La Puebla de Valverde, and *E.burchelli boehmi* from Kenya. n = number of specimens. See Fig. 1 for the system of measurements and Table 2 for the measurements (EISENMANN/DE GIULI 1974: Tables III and IV).

TABLE 2

	Equus caballus cf. gallicus (Jaurens)									
	mes.	n	x	min.	max.	s	v	log.		
	1	27	85.7	82	92	2.24	2.61	1.932		
	2	27	76.2	73	84	2.67	3.51	1.882		
	3	27	37.5	35	42.5	1.89	5.04	1.574		
	4	27	57.6	54	65	2.61	4.54	1.760		
	5	27	37.8	35	43	1.84	4.86	1.577		
	6	27	49.3	46.5	54.3	1.79	3.64	1.692		
	7	27	58.4	54	64	2.40	4.12	1.766		
Ph. I Ant	8	27	50.1	45	55	2.53	5.05	1.699		
	9	27	74.8	71	81	2.57	3.44	1.873		
	10	27	62.6	59	67	2.07	3.30	1.796		
	11	27	62.3	57	68	2.32	3.72	1.794		
	12	27	12.7	11	15.5	1.20	9.45	1.103		
	13	27	12.5	10	15	1.29	10.32	1.097		
	14	27	47	45	50	1.52	3.23	1.672		
	15	27	25.7	24	29	1.16	4.52	1.410		
	1	24	83.2	80	89	2.28	2.74	1.920		
	2	24	74.4	72	80	2.03	2.73	1.871		
	3	24	36.7	34	41	1.66	4.52	1.564		
	4	24	58.8	55	65	2.32	3.95	1.769		
	5	24	40.8	38	45	1.51	3.70	1.610		
	6	24	47.7	45.2	53	2.08	4.35	1.678		
	7	24	53.6	50	58	1.91	3.56	1.729		
Ph. I Post	8	24	45.8	42	51	2.29	5.00	1.660		
	9	24	71.6	68	76	2.10	2.93	1.855		
	10	24	56	52	61	2.28	4.08	1.748		
	11	24	56.6	53	60	1.83	3.23	1.752		
	12	24	16.7	15	20	1.32	7.94	1.222		
	13	24	15	13	18	1.02	6.82	1.176		
	14	24	45.7	43	49	1.48	3.25	1.660		
	15	24	26	24	28.2	1.04	4.00	1.415		

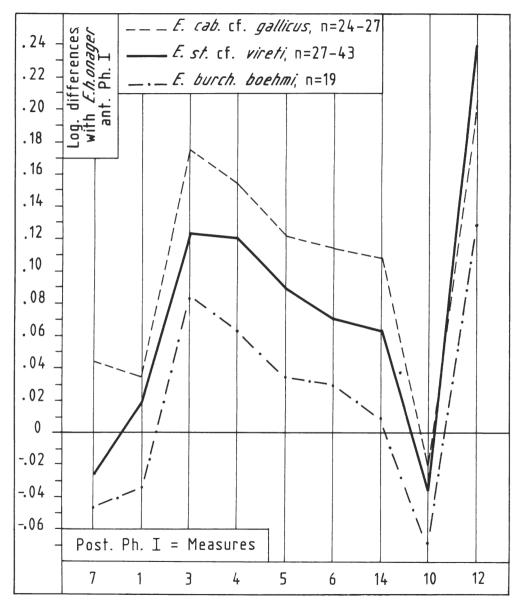


Fig. 8 Ratio diagrams for the average values of robust posterior first phalanges. Same species and abbreviations as in Fig. 7.

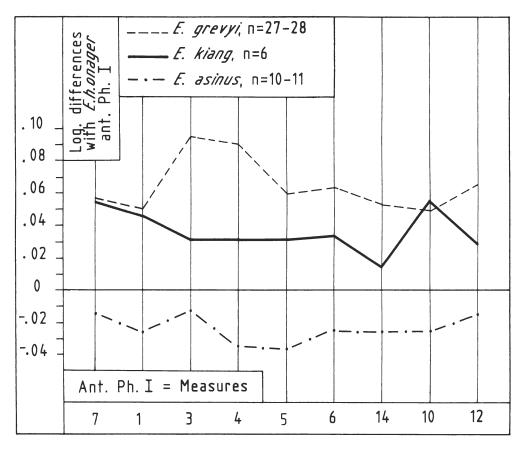


Fig. 9 Ratio diagrams for the average values of slender anterior first phalanges. Same abbreviations as in Fig. 7. See also Tables 3, 4, and 5.

TABLE 3

	Equus grevyi								
	mes.	n	x	min.	max.	s	v	log.	
	1	28	86.2	80	91	2.69	3.12	1.935	
	2	28	79.6	74	85.5	2.69	3.38	1.900	
	3	28	30.7	28.5	33	1.28	4.16	1.488	
	4	28	50.7	48	54	1.81	3.56	1.705	
	5	28	35.4	33	37	1.26	3.56	1.550	
	6	28	42.4	40	45	1.26	3.33	1.627	
Ph. I Ant	7	28	54.9	50	61	3.01	5.47	1.740	
	8	28	49.1	41	56	3.37	6.86	1.691	
	9	28	77.5	70	82	2.80	3.61	1.889	
	10	28	65.6	62	72	2.36	3.60	1.817	
	11	28	66.7	63	73	2.17	3.26	1.824	
	12	28	12.1	9.7	15	1.52	12.63	1.081	
	13	28	11.3	9	14	1.34	11.94	1.052	
	14	27	40.2	37.5	43	1.25	3.11	1.604	
	1	27	81.1	75	87	2.93	3.61	1.909	
	2	27	74.8	69	81	2.75	3.68	1.874	
	3	27	29.6	27.5	31.5	1.13	3.84	1.471	
	4	27	51.7	48.5	55	1.96	3.78	1.714	
	5	27	36.7	34.5	39	1.25	3.40	1.564	
	6	27	41.7	39	44.5	1.57	3.76	1.620	
Ph. I Post	7	27	49.1	44	55	2.51	5.11	1.691	
	8	27	42.3	36	48	2.49	5.89	1.626	
	9	27	71.9	65	78	2.99	4.16	1.857	
	10	27	59.3	55	65.5	3.02	5.09	1.773	
	11	27	60.6	54.5	66.5	2.91	4.81	1.783	
	12	27	14.5	12	17	1.29	8.85	1.162	
	13	27	13.1	10.5	15.5	1.47	11.21	1.118	
	14	26	37.6	34.5	40	1.31	3.48	1.575	

TABLE 4

	Equus asinus									
	mes.	n	x	min.	max.	s	v	log.		
	1	11	72.2	64	82	5.45	7.55	1.859		
	2	11	65.5	57	76	5.23	7.98	1.816		
	3	11	23.9	22	26	1.36	5.68	1.378		
	4	11	38	35	41.1	1.77	4.66	1.580		
	5	11	28.3	26.1	32.5	1.66	5.87	1.452		
	6	11	34.5	31	38.6	1.93	5.59	1.538		
Ph. I Ant	7	11	46.5	41	52	3.39	7.28	1.668		
	8	10	41.6	37	47.4	3.51	8.43	1.619		
	9	10	64.2	57	74.5	5.37	8.36	1.808		
	10	11	55.2	47	65	5.05	9.14	1.742		
	11	11	56.1	50	64.8	4.46	7.94	1.749		
	12	11	9.9	9	12	0.91	9.11	0.998		
	13	11	9.2	8	11	0.94	10.27	0.963		
	14	11	33.6	31	36.2	1.62	4.83	1.526		
	1	10	67.5	61	76	4.82	7.14	1.829		
	2	10	61.7	56	70	4.55	7.38	1.790		
	3	10	23.2	22	25.6	1.28	5.53	1.366		
	4	10	40	35	43.2	2.28	5.85	1.591		
	5	10	28.4	27	32.3	1.65	5.81	1.453		
	6	10	32.9	29	38.2	2.27	6.90	1.517		
Ph. I Post	7	10	40.8	34	46	3.84	9.41	1.611		
	8	10	35.9	29	41.5	3.93	10.94	1.555		
	9	10	60.5	53.5	70.1	5.05	8.35	1.782		
	10	10	49.9	44	56	4.64	9.31	1.698		
	11	10	50.3	45	58	4.26	8.48	1.701		
	12	10	12	11	14	0.85	7.08	1.079		
	13	10	10.7	10	13	1.03	9.65	1.029		
	14	10	31.2	29	35	1.75	5.63	1.494		

TABLE 5

	Equus kiang								
	mes.	n	x	min.	max.	S	v	log.	
	1	6	85.5	83	87.5	1.48	1.73	1.932	
	2	6	78.8	78	81	1.17	1.49	1.897	
	3	6	29.3	25.5	27	0.59	2.23	1.421	
	4	6	44.2	42	46.1	1.50	3.39	1.645	
	5	6	33.1	32.2	34	0.60	1.81	1.520	
	6	6	39.6	37.5	41	1.22	3.07	1.598	
Ph. I Ant	7	6	54.8	52	58	1.94	3.54	1.739	
	8	6	50.1	48	53	1.62	3.24	1.700	
	9	6	78.2	77	81	1.51	1.93	1.893	
	10	6	66.2	64	70	2.14	3.23	1.821	
	11	6	66.8	66	69	1.17	1.75	1.825	
	12	6	11	10	12	0.91	8.24	1.043	
	13	6	9.9	9	11	1.02	10.29	0.996	
	14	6	36.9	36	38	0.90	2.43	1.567	
	1	6	78.6	77	82	2.03	2.59	1.895	
	2	6	72.8	71	76.5	2.66	3.65	1.862	
	3	6	25.9	25.5	26.5	0.39	1.52	1.414	
	4	6	45.1	41.5	47.4	2.25	4.98	1.654	
	5	6	34	33.5	34.7	0.50	1.46	1.532	
	6	6	37.6	35.5	39.5	1.44	3.82	1.575	
Ph. I Post	7	6	48.8	47	51	1.33	2.72	1.689	
	8	6	42.8	41	46	1.72	4.02	1.632	
	9	6	70.6	68.5	74	2.06	2.92	1.849	
	10	6	57.7	54	61	2.68	4.64	1.761	
	11	6	58.3	54	62	2.75	4.72	1.766	
	12	6	13.3	10.3	16	2.14	16.12	1.124	
	13	6	12.7	10.5	16	2.32	18.29	1.103	
	14	6	34.6	33.5	35.2	0.64	1.85	1.539	

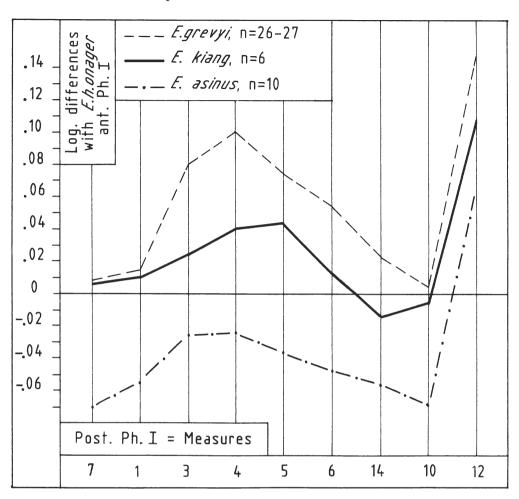


Fig. 10 Ratio diagrams for the average values of slender posterior first phalanges. Same species and abbreviations as in Figure 7.

6.3. Particular Subgroups

6.3.1. Zebras and Equus stenonis

Ratio diagrams as well as multivariate analyses show that the three species of zebras have similar first phalanges. They differ mostly by size as is shown by the principal components analysis (Figure 11) where posterior specimens are classed from small (Burchell's zebra) to large (Grevy's zebras) along the first axis (62 percent of inertia).

When the posterior phalanges of the three zebras are studied together with *E.stenonis* cf. vireti in a correspondence analysis (Figure 12), the four species are arrayed in a crescent-like scatter on the plane defined by the first two axes (57 percent and 16 percent of inertia). *E.stenonis*, characterized by long infra-tuberosital segments, is at one end of the crescent. In the middle

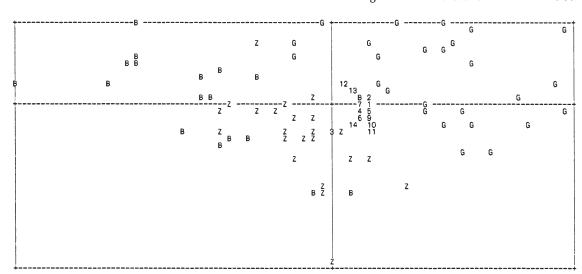


Fig. 11 Principal components analysis for 14 measures on 68 posterior first phalanges belonging to modern zebras. First axis horizontal, second axis vertical. B = Kenyan *E.burchelli*; G = *E.grevyi*; Z = *E.zebra*.

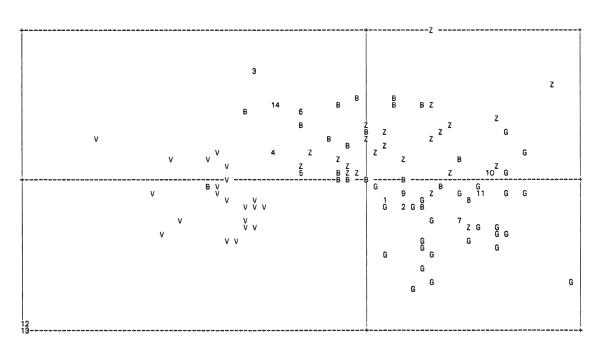


Fig. 12 Correspondence analysis for 14 measures on 89 posterior first phalanges belonging to modern and fossil Equus. First axis horizontal, second axis vertical. B = Kenyan E.burchelli; G = E.grevyi; V = E.stenonis cf. vireti, Z = E.zebra.

part of the crescent are placed the overlapping Burchell and mountain zebras. They differ from *E.grevyi* (at the other end of the crescent) by their robustness and the relative shortness of the *trigonum phalangis*. In short, the zebra most remote from *E.stenonis* cf. *vireti* is *E.grevyi*. It is also the most distinctly separate of the other zebras.

6.3.2. Domestic and wild asses

The correspondence analysis run with the 14 variables for modern ass anterior phalanges (more numerous than the posterior) shows a rather homogeneous scatter (Figure 13) where the two first axes bear 46 percent and 22 percent of the total inertia. Wild asses, however, appear usually to have more robust bones and more developed infra-tuberosital segments than do domestic asses. An interesting point concerns the differences between supposed Nubian and supposed Somali wild asses. The "Nubian" specimens (NA 10 = MU 1952-9 and NA 11 = MU 1963-133) appear very close to "Somali" specimens (SA 3 = BA 3597, SA 4 = BA 10858, and SA 9 = BL 30353). But another "Nubian" ass (NA 3 = BM 1904-6-12-1) comes very close to one domestic "White Egyptian ass" (DA 52 = AC 1893-634). Moreover, one

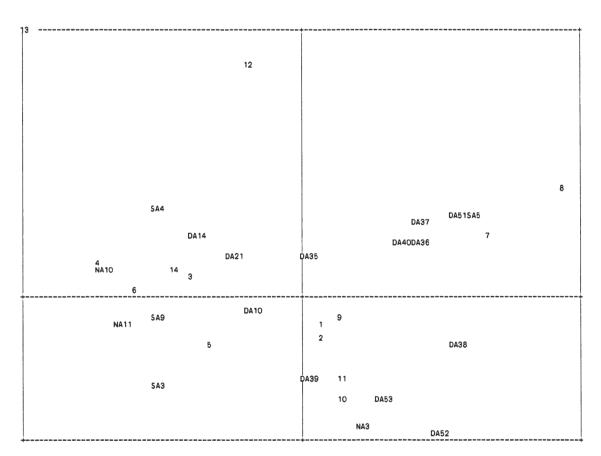


Fig. 13 Correspondence analysis for 14 measures on 19 anterior first phalanges belonging to modern wild and domestic asses. First axis horizontal, second axis vertical. DA = domestic asses; NA = Nubian wild asses; SA = Somali wild asses.

"Somali" specimen (SA $5 = BE\ 216$) is placed close to the other "White ass" of our sample (DA $51 = AC\ 1875-28$). It will certainly be interesting to compare these forms more thoroughly.

The principal components analysis of the same data distinguishes small and large specimens. Most of the domestic specimens are small and most of wild are large. There are, however, one small wild (MU 1952-29) and four large domestic (the two "White Egyptian," AMNH 15675, and 135017) specimens.

Another set of analyses was run with a restricted number of variables (8) which allowed us to add the fossil phalanges from Ikrit. In the correspondence analysis, the first axis expresses slenderness. Most of Ikrit phalanges, although domestic, are placed close to the wild (robust) bones. Because of their small size, however, they appear together with the domestic forms in the principal components analysis.

6.3.3. Half-asses

The correspondence analysis run with 14 variables on 52 posterior phalanges also shows a rather homogeneous cloud. The first axis (52 percent of the inertia) opposes breadths and depths to lengths, especially lengths of the *trigonum phalangis*. Mongolian hemiones and Syrian hemippes are on the "slender side" while most of the Iranian onagers are on the "broad side". Kiangs and kulans, however, fall very near the middle or on both sides. In any event, the samples are very poor: 2 hemippes, 3 kulans, and 3 khurs only. The second axis (20 percent of inertia) opposes supra- and infra-tuberosital lengths but these have no taxonomic relevance. The same facts appear using the hierarchic classification based on the chi-square metric. Hemiones and hemippes are grouped together; onagers, khurs, and kulans are in another group; kiangs are found in both groups.

6.3.4. Half-asses and domestic asses

One of the practical problems encountered by archaeozoologists working on the Middle East is distinguishing between the bones of asses and half-asses. Even as we were working on this paper, P.-Y. Gagnier asked one of us to identify a small sub-adult phalanx found in Syria at Ras-al-Bassit (30 K north of Lattaquié) in levels he believed at the time to be about 2500 years old (we learned later that they belong actually to the late Bronze age (1600–1200 B. C.: Gagnier 1986)). At "first glance" the phalanx seemed to be anterior but we were not very optimistic that we could determine if it had belonged to a domestic ass or to the extinct hemippe. Nevertheless, we drew the ratio diagrams and ran a correspondence analysis using this specimen and phalanges from half-asses and domestic asses. The ratio diagrams confirmed our supposition that the phalanx was an anterior one and showed that it bears remarkable similarities to hemippe phalanges, especially to that from the Museum of Comparative Zoology, Harvard (Figure 14). A comparison with Figure 9 shows that in hemippe, anterior phalanges are slenderer than in asses and have a longer supra-tuberosital segment. The same characters are also to be found in kiangs (Fig. 9).

In the correspondence analysis (Figure 15) done with the restricted set of variables because we lack one measure for the Ras-al-Bassit specimen, domestic asses are scattered all over the first plane. Most specimens, however, lie on the "robust side" of F1, together with most of the onagers and khurs. On the "slender side" of F1 are placed most of the kiangs, Mongolian

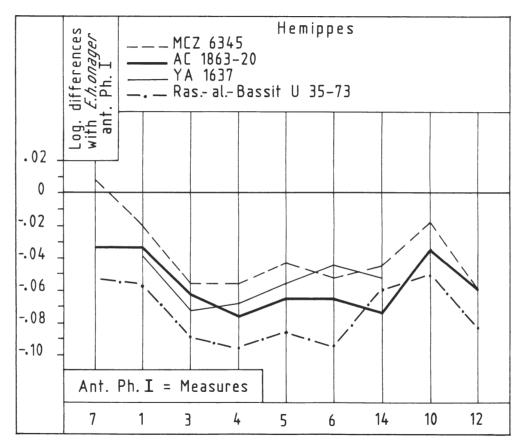


Fig. 14 Ratio diagrams of individual measurements for the anterior first phalanges of modern adult *E.hemionus hemippus* and one subadult specimen dated to 1200 to 1600 B.C.

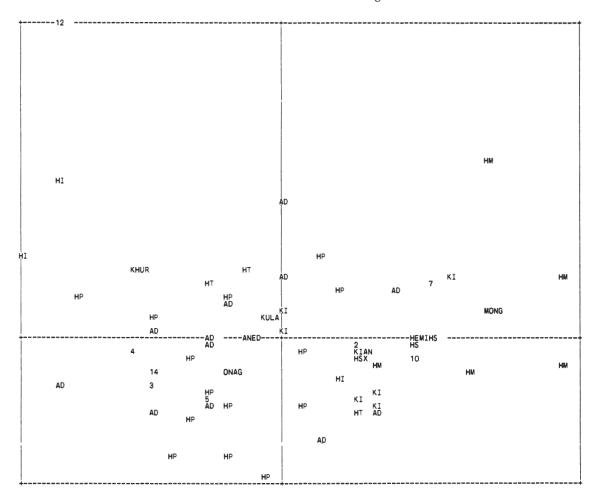


Fig. 15 Correspondence analysis for 14 measures on 43 anterior first phalanges belonging to half-asses and domestic asses. First axis horizontal, second axis vertical. DA = domestic asses; HI = E.hemionus khur; HM = E.hemionus hemionus; HP = E.hemionus onager, HS: E.hemionus hemippus; HT = E.hemionus kulan; KI = E.kiang; HSX = possible E.hemionus hemippus from Ras-al-Bassit.

hemiones, and the hemippes. The Ras-al-Bassit phalanx lies in the vicinity of the hemippe phalanges. We believe, therefore, that it did belong to an hemippe although the possibility that it was a donkey cannot be eliminated by this analysis. Thus, it seems possible to distinguish Mongolian hemiones and Syrian hemippes from other taxa because of their slenderness, but all other specimens have very similar proportions. In most of the cases, only size enables one to discriminate half-ass from domestic ass phalanges. We must stress, however, that our samples are not good; it could be that better samples would bring better results.

6.3.5. Horses

On Figure 16 (first plane of a correspondence analysis with the 14 variables) appear the individual posterior specimens (represented by dashes, slashes, crosses, etc.) as well as the "aver-

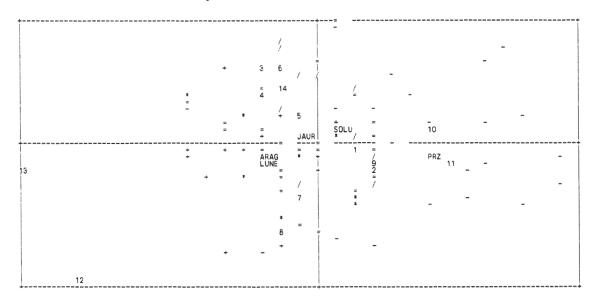


Fig. 16 Correspondence analysis for 14 measures on 81 posterior first phalanges belonging to modern and fossil horses. First axis horizontal, second axis vertical.

* = Arago; + = Lunel-Viel; = = Jaurens; / = Solutré; - = E.przewalskii.

age" posterior phalanges for the horses from Arago, Lunel-Viel, Jaurens, and Solutré and for *E.przewalskii*. It is remarkable that the average points lie on a parabolic line and in chronlogical order from the oldest Arago and Lunel-Viel (Mindel to Riss?) specimens to the youngest (modern) *E.przewalskii* through the Jaurens and Solutré horses (Würm). We are well aware that there is significant overlap of all these populations (conspicuous in Fig. 16), but we do not think that the chronological sequence of the "average" phalanges is purely a matter of chance. This kind of configuration, called Guttman's effect (Benzécri 1973: vol. 2: 484, 599) is characteristic of continuous modifications from any cause (climatic, spatial, temporal, etc.) within a sample. In the present case, they may well reflect horse evolution.

The clearest differences between the oldest and the youngest samples are (again!) related to those characters that express anteroposterior dimorphism. The phalanges of *E.przewalskii* are more "anterior-like" (they have longer supra-tuberosital segments) than are the phalanges coming from Arago and Lunel-Viel. If we accept the sequence of Figure 16 as being significant, there may be an evolutionary trend within the horse group with a progressive change of more "posterior-like" phalanges to more "anterior-like" ones. In this regard, it is well to note that the oldest *Equus* phalanges analyzed in this study, those of *E.stenonis*, are also the most "posterior-like" (Fig. 6). Could the same evolutionary trend exist not only within the horse group but also within the genus *Equus*?

6.4. Conclusion

The phalanges of the fossil *E.stenonis* (circa 2 mya) are clearly distinct from those of all modern species due to their overall more "posterior" morphology and their shorter *trigonum phalangis*.

The same sort of distinction, although less marked, exists when considering the phalanges of the fossil horses and those of modern *E.przewalskii*.

The modern species differ one from another mostly in degree of gracility and in size.

Two facts already noted during the study of the skulls (EISENMANN 1980) and of the metapodials (EISENMANN 1979) are confirmed with the phalanges: 1) the zebra morphologically the most similar to *E. stenonis* is not *E. grevyi* but *E. burchelli* and 2) the modern species most similar to horses is also *E. burchelli*.

7. Tentative functional interpretation and conclusion

The anteroposterior dimorphism in *Equus* first phalanges is a well established fact, but the characters involved in this dimorphism (longer supra-tuberosital segment and longer *trigonum* phalangis in the anterior phalanges) appear, at times, to be related to other factors. Indeed, we have found a more or less pronounced "posteriorization" of the phalanges in the following cases:

E.stenonis versus all other modern Equus species (Fig. 6);

E.burchelli versus E.grevyi and E.zebra (Fig. 7, 9, 12, and unpublished ratio diagrams);

E.zebra zebra versus E.zebra hartmannae;

wild asses versus modern donkeys (Fig. 13);

fossil donkeys versus modern donkeys;

fossil horses versus E.przewalskii (Fig. 16).

In order to try to explain this circumstance, we have looked for possible functional significance in the osteological characters involved and noted especially what sort of ligaments and/or tendons are inserted in the region of the supra-articular tuberosities and of the *trigonum phalangis*.

On the "V-scar" of the *trigonum phalangis* are inserted the oblique sesamoidean ligaments (CAMP/SMITH 1942: 74 and fig. 12) that belong to the group of distal sesamoido-phalangeal ligaments (BARONE 1968: 197).

In the region of the supra-articular tuberosities, there are various structures "inserted in or in close association with" the scutum medium (a fibro-cartilaginous plate situated below and behind the head of the second phalanx): the tendo flexor digitorum sublimis, the ligamentum sesamoideum rectum, and two pairs of volar ligaments (CAMP/SMITH 1942: 75). Most of these, however, are inserted on the volar surface of the bone, behind the supra-articular tuberosities. Following BARONE (1968: 196–198), the tuberosities themselves provide points of insertion only for the lower part of the lateral volar ligament and for the collateral ligament of the pastern associated with the suspensory ligament of the navicular sesamoid.

DENOIX (1984: 13) stresses the functional importance of the collateral ligament and of the volar ligaments related to the *scutum medium* as well as of the oblique sesamoidean ligaments. All of these structures are clearly important in limiting lateral movement and in sustaining the foot during the "automatic spring effect" described by CAMP/SMITH (1942: 95). The significance of the anteroposterior dimorphism of their points of insertion, however, is not clear.

Another approach to this problem is to look in a more general way for differences in the functions of the fore and hind limbs.

Classically, the anterior limb bears and receives the weight of the body whereas the posterior limb provides propulsion (Barone 1966: 41, 489, 625). Horses and their relatives belong to that large group of animals with their center of gravity nearer the forefeet (Gray 1959: 65). In the horse, about 55 percent of the body weight is supported by the front limbs and 45 percent by the hind limbs (Denoix, personal communication). We thus propose that the differences that exist between anterior and posterior phalanges are in some way related to differential division of weight between the fore and hind limbs. Anterior phalanges presenting a relatively "posterior" morphology might indicate that the center of gravity lay farther to the rear (i.e., the cranial part of the animal was relatively less heavily loaded and the caudal part was relatively more heavily loaded). Such a circumstance would help to explain why characters related to anteroposterior dimorphism seem also, at times, to be related to very different factors (e.g., subspecific differences, differentiation between wild and domestic, modern and fossil).

One way of testing our hypothesis would be to determine the relative anterior to posterior load of the above mentioned taxa by weighing the front and hind parts of the living animal (making it step on scales successively with its front and hind feet). Naturally, this could be done (easily or not!) only with the modern species. At the moment, however, we have no data of this kind and all we can do is to suggest some indirect arguments. Thus, *E.burchelli* has a relatively small head when compared to *E.zebra* and especially when compared to *E.grevyi*. Could it be that the reduced weight of the head contributes to a relatively heavier hind part of the animal?

Domesticated asses are used to carrying additional weight (people or goods). Could the absence of such "extra-loading" account for the more "posterior" morphology of phalanges in wild asses? The equally "posterior" morphology of the fossil donkeys from Ikrit could indicate that these freshly domesticated animals were not yet fully adapted to their new weight-bearing requirements. Finally, the difference between "pure" *E.przewalskii* and animals coming from mixed breeding lines could be explained in the same way, namely that pure wild horses have never carried extra loads while in the case of mixed lines, some ancestors were domesticated and thus had done so.

In conclusion, it is probable that more than one factor is responsible for our observations and that the load-factor, if real, is not the only factor at work. It is, however, the only one that we are able to suggest at the moment.

8. Acknowledgements

The phalanges of modern *Equus* come from the museums and collections listed below. The name of each institution is preceded by the letter code that is used in the tables of measurements in the appendix to this volume.

AA: Museum of Zoology, University of Michigan, Ann Arbor, Michigan, USA

AC: Laboratoire d'Anatomie Comparée du Muséum National d'Histoire Naturelle (MNHN), Paris, France

AD: Natural History Museum, Addis Adeba, Ethiopia AM: Zoologisch Museum, Amsterdam, The Netherlands

BA: Naturhistorisches Museum, Basel, Switzerland

BE: Naturhistorisches Museum, Bern, Switzerland

BL: Zoologisches Museum der Humboldt Universität, Berlin, DDR

BM: British Museum (Natural History), London, Great Britain

CH: Field Museum of Natural History, Chicago, Illinois, USA

EV: Ecole nationale Vétérinaire, Maisons-Alfort, France

FR: Naturmuseum und Forschungsinstitut Senckenberg, Frankfurt, BRD

GE: Muséum d'Histoire Naturelle, Genève, Switzerland

HA: Zoologisches Institut und Zoologisches Museum, Hamburg, BRD

HV: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.

KI: Institut für Haustierkunde, Kiel, BRD

LD: Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands

LG: Zoological Institute of the USSR Academy of Sciences, Leningrad, USSR

LY: Muséum d'Histoire Naturelle, Lyon, France

MA: Laboratoire des Mammifères et Oiseaux du MNHN, Paris, France MU: Zoologische Sammlung des Bayerischen Staates, München, BRD

NA: National Museums of Kenya, Nairobi, Kenya

NY: American Museum of Natural History, New York, USA

PA: Institut de Paléontologie du MNHN, Paris, France

YA: Peabody Museum, Yale University, New Haven, Connecticut, USA

ZU: Zoologisches Museum der Universität, Zürich, Switzerland.

The phalanges of *E.stenonis* from La Puebla de Valverde belong to the collections of the Institut de Paléontologie of the MNHN, Paris. Those of the caballine forms from La Caune de l'Arago, Lunel-Viel, Jaurens, and Solutré belong to the collections of the Laboratoire d'Anthropologie of the Faculté de Médecine, Secteur Nord, Marseille; the Laboratoire de Géologie du Quaternaire of the Faculté des Sciences de Luminy, Marseille; and to the Département des Sciences de la Terre of the Université Claude Bernard, Lyon. Those of the fossil donkey from Ikrit were studied in the Department of Zoology, Hebrew University, Jerusalem.

We are deeply thankful to all curators, colleagues and friends who have given us access to their collections and who, in different ways, have helped us to study them. For the fossil collections, we thank in particular M.-F. Bonifay, C. Mourer-Chauviré, E. Crégut, S. Davis, C. de Giuli, P. Y. Gagnier, C. Guérin, E. Heintz, H. de Lumley, R. Meadow, and A.-M. Moigne. We also thank J. Combier, J.-M. Denoix, and O. A. Ryder for interesting comments and suggestions.

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APPENDIX

Equus przewalskii

14	40.7	39.0	43.7	44.0	40.0	38.7	45.5	41.5	41.5	40.0	40.0	43.0	38.1	45.5	43.0	41.0	42.1	39.1	41.0	38.5	37.0	40.0	45.9	39.0	40.0	41.0
13	9.7	11.9	8.1	10.5	13.0	12.0	10.0	10.5	15.0	9.5	10.0	12.0	9.0	13.0	14.0	10.0	11.5	11.8	11.0	10.0	8.5	10.0	9.5	10.0	10.0	10.0
12	10.1	10.2	10.5	0.6	12.0	12.0	11.0	11.5	15.0	10.0	10.0	12.0	0.6	14.0	15.0	10.0	11.3	10.9	11.0	11.5	0.6	11.0	11.0	10.0	9.5	10.0
11	56.5																									
10	56.0	55.2	60.1	64.0	55.0	57.0	62.0	61.5	53.0	0.09	0.09	63.0	58.0	58.0	58.0	58.0	57.0	57.3	62.0	58.0	57.0	0.09	0.09	58.0	63.0	63.0
6	67.0	64.7	70.9	73.0	61.2	70.0	72.0	74.0	0.79	68.5	70.0	0.97	0.99	72.0	74.0	0.79	67.4	67.1	72.0	0.89	65.0	0.89	0.89	0.89	73.0	71.0
œ	46.0	43.0	46.0	52.0	45.0	45.5	47.0	48.0	47.0	45.0	45.0	49.0	45.0	47.0	46.0	43.0	45.0	45.0	45.0	44.0	40.0	46.0	44.0	43.0	49.0	43.0
7	53.0	48.0	52.0	59.0	20.0	53.0	54.0	54.0	52.0	49.0	51.0	54.0	49.0	55.0	53.0	54.0	47.0	52.0	50.0	49.0	46.0	53.0	1		54.0	
9	42.4	44.2	44.5	46.5	43.5	43.2	45.5	45.0	43.0	45.0	42.0	45.0	42.0	46.2	47.0	43.0	47.1	43.6	45.0	41.0	40.5	44.0	44.0	41.0	45.0	44.0
5	32.3	32.9	35.5	35.5	31.5	33.5	34.5	36.0	34.0	35.0	33.0	37.0	32.0	35.5	36.0	34.0	35.0	32.7	33.5	33.0	32.0	34.0	33.0	33.0	34.0	34.0
4	51.2	49.6	50.1	52.5	49.0	50.0	52.5	50.0	48.0	52.0	47.0	50.5	47.5	51.0	50.0	48.0	55.0	49.9	48.5	48.0	46.0	50.0	50.0	47.0	48.0	50.0
က	32.2	31.3	33,1	33.5	33.5	32.0	33.0	33.0	34.0	34.5	31.0	33.0	32.0	36.5	37.0	32.0	33.0	32.1	32.0	31.0	29.0	33.0	33.2	31.0	30.0	33.0
8	68.7	65.6	71.5	74.5	0.89	72.0	73.5	0.97	0.89	71.0	70.0	78.0	0.69	74.0	75.0	0.69	70.5	68.4	74.0	70.0	0.79	71.0	72.0	70.0	75.0	75.0
nt: 1	76.0		79.9	82.0	74.0	79.0	81.0	82.5	0.97	78.0	78.0	84.0	75.0	81.0	81.0	77.0	75.1	75.9	80.0	0.97					82.0	•
Measurement:	1 2 2	ဇ	4	7	6	1 10				19	20	22	39	41	42	43	44	45	47	48	49	52	53	54	22	28
Coll.no. /	AC 1932.46 AC 1935.486	, ,	AC 1962.228	MA 1964.107	AC 1973.109			BM 1963.1.25.1	LD 359	BL 60363	•	MU 1953.147	_	NY 32686				AC 1929.37	NY 204071	NY 80062	NY 90198	BA 10881	BA 10877	HV 51058	BE 93-75	BE 76-80 (2a)

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14	38.5	39.0	37.1	42.0	42.0	37.5	37.5	40.0	40.0	39.0	39.0	39.0	41.0	37.0	41.0	41.0	38.5	39.0	37.0	39.5	37.0	36.0	38.0	41.0	37.0	39.0	39.0
13	9.6	14.6	13.0	10.9	11.0	11.0	14.0	12.5	12.0	16.0	11.0	10.0	14.5	12.0	14.0	12.0	11.0	12.4	11.0	12.0	11.5	11.0	15.0	10.5	13.0	12.0	13.0
12	•	•	•	•	•		16.0	•			•																
11							51.0																				
10	51.0	50.9	50.1	55.3	58.5	52.0	50.0	52.0	55.0	47.0	54.0	54.0	56.0	53.0	51.0	52.0	50.0	51.0	51.0	55.0	48.0	50.0	53.0	56.0	51.0	56.0	54.0
0	62.0	61.0	60.7	8.99	0.69	63.0	65.0	0.79	70.0	(28)	64.0	64.0	72.0	63.5	65.0	0.79	62.0	64.0	61.3	65.0	61.0	0.09	64.0	65.0	64.0	0.89	0.39
∞	39.0	34.0	37.0	39.0	48.0	43.0	41.0	40.0	43.0	36.0	38.0	40.0	45.0	40.0	46.0	41.0	36.0	38.0	38.0	39.0	37.0	38.0	40.0	40.0	40.0	41.0	38.0
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က	30.6	31.0	30.9	32.9	32.0	31.0	30.5	32.0	33.0	32.0	34.0	31.0	32.0	31.5	33.0	36.0	30.0	32.9	30.6	32.0	30.0	27.5	31.5	33.0	30.0	29.0	32.0
2	0.99	62.7	63.6	0.69	72.0	65.0	70.0	0.69	72.0	63.0	68.0	0.79	75.0	0.79	70.0	71.0	64.0	66.5	65.0	0.69	64.0	63.0	0.89	0.69	67.0	0.69	70.0
nt: 1	70.2	72.1	71.0	76.3	79.5	71.0	73.5	75.0	78.0	70.0	74.0	74.0	81.5	72.0	75.0	0.97	70.0	72.4	71.2	75.0	70.0	0.89	74.0	0.97	73.0	0.97	0.97
Measurement:	1	2	က	4	7	6	10	11	13	14	19	20	22	33	41	42	43	44	45	47	48	49	55	53	54	22	28
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Equus kiang Phalanx 1 anterior

14	36.1	38.0 38.0 36.5	37.0		14	35.0	35.2	35.0	34.2	34.5
13	0.6	11.0 10.5 11.0	0.6		13	12.0	12.0	16.0	15.0	10.5
12	10.2	12.0 11.5 12.0	10.0		12	10.3	14.0	15.0	16.0	13.0
11	67.0	66.0 66.0 69.0	0.99		11	57.5	58.0	54.0	62.0	58.0
10	67.0	65.0 64.0 70.0	65.0		10	59.0	56.0	54.0	0.09	56.5
6	78.0	77.0 77.5 81.0	77.0		6	68.5	0.69	70.0	74.0	70.0
∞	49.5	50.0 50.0 53.0	50.0		∞	42.0	42.0	43.0	46.0	43.0
7	55.0	54.0 55.0 58.0	55.0	sterior	7	49.0	47.0	49.0	51.0	49.0
9	39.0	40.0 41.0 40.0	40.2	Phalanx 1 posterior	9	38.8	37.0	38.0	37.0	39.5
ည	34.0	33.0 33.0 33.0	32.2	halan	c)	34.7	34.0	34.5	33.5	34.0
4	46.1	45.0 45.0 44.0	43.0	-	4	47.4	47.0	46.0	45.3	43.5
က	25.5	26:2 27.0 26.0	27.0		က	26.0	26.2	26.0	25.5	26.5
7	79.1	78.0 78.0 81.0	78.0		01	71.5	71.0	71.0	0.97	71.0
nt: 1		85.0 85.5 87.5			nt: 1	77.3				
reme	- LC !	17 32 39			reme	⊢ 1	17	32	39	
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Equus hemionus hemionus

	14	35.0 36.8 37.8 36.8		14	33.0 33.0 34.0 33.2 32.0
	13	13.0 10.0 10.0 9.5		13	12.0 11.5 11.5 10.0
	12	13.0 10.0 10.5 10.5		12	14.0 12.5 15.0 12.0
	11	68.0 70.0 67.0 69.0		111	62.0 63.0 58.0 58.0 61.0
	10	68.0 71.0 65.0 67.0		10	59.5 62.0 55.0 57.0
	6	75.0 82.0 75.0 77.0		6	67.0 75.0 69.0 68.0 72.0
	∞	52.0 54.0 52.0 52.0 58.0		∞	39.0 52.0 45.0 48.0 50.0
ioriani	7	58.0 59.0 60.0 57.0 57.0	Phalanx 1 posterior	7	44.0 50.0 57.0 51.0 53.0
rnalana i anterior	9	34.8 38.5 37.5 38.0 39.0	к 1 ро	9	33.0 37.0 36.5 36.5 34.0
rnalan	သ	31.2 32.5 33.5 33.0 31.3	Phalan	2	31.0 33.0 32.0 34.0
	4	41.0 43.0 43.5 41.0		4	42.1 44.0 41.0 42.0
	က	24.0 25.8 26.5 27.0 26.0 26.0		က	24.5 25.1 26.2 26.0 25.5 23.0
	2	76.5 82.0 78.0 77.0		2	69.0 75.0 70.0 68.0
	nt: 1	82.0 88.7 90.0 85.0 86.0		nt: 1	74.8 80.2 82.0 77.0 77.0
	Measurement: 1	1 5 13 14 16 17		/ Measurement: 1	1 5 13 14 16 16
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Equus hemionus kulan

14	35.0	35.0	14	32.5
13	10.0	10.0	13	13.0 32.5 11.5 33.0
12	9.0	12.0	12	13.0
11	61.0	61.0	11	54.0
10	61.0	0.09	10	54.0
6	70.0	74.0	6	65.0
∞	48.0	46.0	∞	40.0
7	53.0 51.0 53.0 48.0	30.5 38.5 48.0 Phalanx 1 posterior	7	46.0 45.0 39.0 45.0
9	38.5 38.5 37.4 35.5	38.5 x 1 po	9	36.0 36.2 35.9 33.8
2	31.0 33.0 32.6 31.0	30.5 Phalan	2	32.0 33.2 32.5 32.5
4	42.0 42.5 42.2	42.0	4	43.0 42.2 43.0 42.7
3	25.0 25.0 25.3 25.7	25.0	က	24.0 23.5 23.9 25.5 23.4
2	70.5 74.0 74.8 71.2	73.0	0	66.0 65.5 68.4 65.2
ement: 1	2 78.5 4 81.0 6 80.5 7 79.5		ement: 1	2 73.0 4 72.5 6 74.6 7 73.2 8 73.7 9 74.0
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Equus hemionus khur

14	34.0 36.0 37.0		14	33.0 33.5 34.5
13	11.5 11.0 13.0		13	9.5 12.0 15.0
12	9.5 12.5 14.0		12	10.0 15.0 15.0
11	59.5 55.0 59.0		11	55.5 50.0 52.0
10	59.5 55.0 57.0		10	54.5 49.0 52.0
6	73.2 69.0 69.0		6	67.0 63.5 63.0
∞	45.5 42.0 44.0		∞	40.0 36.5 35.0
7	50.0 46.0 51.0	Phalanx 1 posterior	7	45.0 41.5 42.0
9	36.2 39.0 37.5	х 1 ро	9	34.6 37.5 36.0
5	29.6 30.1 32.0	Phalan	2	30.2 31.0 31.0
4	42.0 43.5 44.0		4	42.5 43.5 44.0
က	23.7 25.0 27.0		က	23.2 23.5 26.0
87	71.5 67.0 72.0		73	66.0 64.0 66.0
nent: 1	1 78.8 10 75.0 11 78.0		ent: 1	1 72.4 10 70.5 11 72.0
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Phalanx 1 posterior

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32.0 33.5 34.5 34.5 34.5 33.0 33.0 33.0 33.0 33.0 33.0

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552.7 552.0 552.0 552.0 552.0 553.0 550.5 550.0 550.0 550.0 550.0

51.8 550.0 551.0 551.0 550.0 550.0 551.0 551.0

62.5 63.5 63.0 63.0 64.0 63.0 63.0 63.0 63.0 63.0

41.0 47.0 42.0 39.0 41.0 45.0 37.0

411.2 441.2 39.0 442.3 442.0 445.0 445.0 445.0

23.0 23.5 25.0 23.2 26.0 28.0 28.5

65.5 69.0 65.5 63.0 65.0 64.0

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58.0 56.0 57.5 57.5 58.0 63.0 63.0 59.5 55.0 55.0 55.0 55.0

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67.9 67.0 70.1 67.5 75.0 70.0 66.0 67.5 71.0

447.5 445.0 550.0 550.0 553.0 552.5 572.0 447.0 447.0 448.0

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42.1 39.6 441.3 38.5 38.5 441.0 441.0 443.0 443.0 443.0 441.6 44.0

23.0 25.5 24.5 26.0 24.0 26.0 26.0

76.0 70.5 66.0 72.0 67.0 68.0

73.3 76.5 775.0 82.0 775.0 775.0 777.0 777.0 777.0 777.0

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Equus hemionus hemippus

	14	30.0 31.6 32.0	31.0		14	27.0 29.0 28.5
	13	9.0	7.5		13	9.0
	12	9.0	8.5		12	11.0
	11	55.0	1		11	51.0
	10	54.0 56.0			10	49.0 5
	6	66.0	0.09		6	37.0 61.5 4 35.0 39.0 63.0 E
	∞	42.0 42.0 43.0	38.0	,	∞	37.0 35.0 39.0
Phalanx 1 anterior	7	26.5 31.5 44.5 4 27.0 33.0 4 28.0 32.5 49.0 4	42.5	Phalanx 1 posterior	7	40.5
x 1 ar	9	31.5 33.0 32.5	29.5	к 1 ро	9	29.1 30.2 30.0
Phalan	ಬ	26.5 27.0 28.0	25.0	halan	ည	26.5 2 26.9 3 27.0 3
	4	34.4 35.0 36.0	33.0	_	4	35.1 36.3 36.5
	က	21.3 20.8 21.5	20.0		က	21.1 20.3 21.5
	0	65.5 64.0 66.0	0.09		0	62.4 60.0 64.0
	nt: 1	70.8 70.0 73.0	67.0		nt: 1	66.7 65.2 68.5
	Measurement:	01 00 100	<u>_</u>		Measurement:	232
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	Coll.no.	AC 65 YA 1637 HV 6345	Ras al		Coll.no.	AC 65 YA 1637 HV 6345

Equus africanus africanus

	14	9.5 37.0 11.0 32.0 10.5 39.0		14	34.0 30.0 35.0
	13	9.5 11.0 10.5		13	10.5 11.0 13.5
	12	10.0 9.0 11.0		12	12.0 12.0 15.0
	11	65.0 50.0 59.0		11	57.5 45.0 54.0
	10	64.0 50.0 59.0		10	58.0 44.0 53.0
	6	45.0 74.0 6 34.0 58.0 5 40.0 69.0 5		6	71.0 53.0 66.0
	∞	45.0 34.0 40.0		∞	40.0 32.0 38.0
Phalanx 1 anterior	7	1.0	Phalanx 1 posterior	7	45.0 38.0 43.0
	9	32.5 37.0 5 26.5 33.5 4 32.0 40.1 4	х 1 ро	9	32.5 37.0 4 28.0 34.0 3 32.5 38.0 4
Phalan	2	32.5 26.5 32.0	Phalan	5	32.5 28.0 32.5
	4	12.0 37.0		₹	43.0 38.0 45.0
	က	75.5 26.5 4 59.5 22.5 3 72.0 26.0 4		က	27.0 43.0 23.5 38.0 26.0 45.0
	73	75.5 59.5 72.0		2	71.0 54.0 67.0
	nt: 1	82.2 67.5 78.0		nt: 1	77.5 62.0 75.0
	ureme	3 10 11		Measurement: 1	3 10 11
	Coll.no. / Measurement:	BM 1904.6.12.1 MU 1952.9 MU 1963.133		Coll.no. / Meas	BM 1904.6.12.1 MU 1952.9 MU 1963.133

Equus africanus somaliensis

						,	Phalan	rnalanx I anterior	terior							
Coll.no.	_	Measurement:	Ξ.	2	က	4	2	9	7	∞	6	10	11	12	13	14
BA 3597 BA 10858 BE 216 BL 30253 CH 1428		3 7 4 4 7 7 8 8 5 8 15 8 8 8	75.3 74.0 80.0 78.0 80.0	68.6 68.0 73.0 72.0	26.5 26.0 26.0 26.0 26.5	43.1 42.0 40.5 44.0 43.2	30.7 30.0 31.0 30.5 30.5	30.7 37.0 45.0 30.0 37.0 45.0 31.0 37.0 54.0 30.5 38.0 46.0 30.5 37.7	45.0 45.0 54.0 46.0 	40.0 41.0 51.0 41.0 51.0	68.5 68.0 73.0 71.0	63.5 54.0 62.0 59.0	64.5 56.0 62.0 60.0	11.5 12.0 12.0 11.0	11.0	37.0 35.5 36.5 37.5 36.0
Coll.no.	_	Measurement: 1		2	က	4	2	9	7	∞	6	10	11	12	13	14
BA 3597 BA 10858 BE 216 BL 30253 CH 1428		3 7 4 7 7 5 7 9 7 15 7 15 7 7	70.1 70.0 74.5 75.0	64.9 65.0 68.5 69.0 70.0	26.5 25.5 25.5 26.5 25.5	43.5 44.0 42.0 47.0	31.9 31.5 30.5 32.0 32.5	36.0 36.5 35.0 37.0	40.3 41.5 45.0 43.0	35.0 37.5 41.0 37.0 44.0	63.0 63.0 68.0 68.0	56.0 49.0 54.0 52.0	58.5 49.0 55.0 54.0	14.0 15.0 14.0 14.0	12.0 13.0 13.0	35.0 35.0 36.0 35.0

Equus asinus Phalanx 1 anterior

		Jerome Dive and vera Lise	nmann
	14	32.0 33.5 32.0 34.0 35.0 35.0 34.5 32.0 34.5 36.8 36.2	30.0 30.5 30.5 29.0 31.7 32.0 31.5 32.0 31.0 29.0 36.0 35.0
	13	8.5 9.0 10.0 10.0 11.0 9.0 8.0 8.5 7.0	13 10.0 12.0 10.5 13.0 10.0 11.0 11.0 10.0 10.0
	12	9.0 10.0 10.0 11.0 11.0 11.0 10.0 9.5 9.0 11.0	12.0 12.0 12.5 111.5 111.0 112.0 112.0 113.0 12.0 12.0
	11	52.0 59.0 59.0 54.0 59.0 57.0 57.0 60.0	46.0 53.0 45.5 47.5 52.0 52.0 54.0 50.0 45.0
	10	51.0 58.5 58.5 53.0 55.0 58.0 58.0 58.0 65.0	10 44.5 53.0 44.0 47.0 52.0 53.0 55.0 56.0 44.0
	6	61.0 57.0 63.0 64.0 68.0 69.0 64.0 65.0 57.0 71.5 74.5	9 63.5 53.5 53.0 60.0 65.0 65.0 65.1 70.1
	∞	38.0 37.0 39.0 42.0 46.0 45.0 40.0 40.0 40.0 41.4 33.0	8 29.0 37.5 30.5 35.0 36.5 41.5 38.0 36.5 34.0 40.0
1 ancertor	7	0 43.0 0 46.0 5 41.0 0 45.0 7 47.0 0 50.0 0 44.0 0 52.0 6 52.0 3 37.0 posterior	7 34.0 43.0 35.0 40.0 41.0 44.5 35.0
י ד	9	34. 335. 335. 335. 1	6 322.5 322.0 333.0 332.0 332.0 332.0 332.0 332.0 332.0 332.0
ı malalık	2	28.2 29.0 27.0 27.5 28.0 28.0 28.0 28.0 27.2 29.0 26.1 29.0 32.5 23.0	5 27.3 28.0 27.0 27.0 27.0 30.0 29.0 29.0 28.0 28.0 27.0 30.8 30.8
	4	37.5 38.0 37.0 39.0 39.0 39.0 39.0 39.0 39.0 42.0 41.1	4 39.0 39.0 39.0 39.3 40.0 40.0 40.0 39.5 31.0
	က	24.1 22.0 23.0 23.0 23.0 25.0 25.0 26.0 26.0 26.0 18.0	3 23.2 23.2 22.0 222.0 224.0 225.0 255.0 255.0 255.0 255.0
	8	62.5 68.0 63.0 66.0 68.0 70.0 65.0 70.5 70.5	2 64.5 56.0 59.0 63.0 64.0 66.0 66.0 66.0 57.0
	nt: 1	66.4 75.5 64.0 70.0 72.5 76.0 76.0 74.0 73.0 65.0 77.0	62.1 70.0 61.0 66.0 68.0 70.0 72.0 68.0 62.0 73.5 76.0
	Measurement:	110 111 121 335 336 337 339 521 53	Measurement: 10 65 11 76 11 76 13 68 35 68 36 77 37 72 39 68 40 65 51 77 55 76
	Coll.no. /	NA 3952 LY 834 BE 5.11.1952 AC 1933.397 PA 1979 NY 15675 NY 135017 NY 204141 NY 100280 YA 1622 AC 1875.28 AC 1875.28 AC 1893.634 GE 797.52	Coll.no. / NA 3952 LY 834 BE 5.11.1952 AC 1933.397 PA 1979 NY 15675 NY 135017 NY 100280 YA 1622 AC 1893.634 GE 797.52

Equus zebra zebra

nterior
x 1 a
Phalan

ication	and	ט	150	-111	1111	iau	OH	OI	11130	Гпа	ianges) 11	OII.	ı ı	ieis	100	Le I	ie	
14	1 ;	41.0	39.2	38.0	40.5	40.0	38.1	39.5			14	ļ	38.0	38.0	37.0	38.5	38.1	36.5	36.2
13	1 8	0.0	11.5	9.0	11.0	11.0	10.0	10.0			13	ı	13.0	14.0	11.0	13.0	11.5	12.0	12.0
12	!	1	11.5	10.5	13.0	11.5	11.0	11.5			12	!	15.5	13.5	12.0	15.0	12.5	14.0	11.5
11	1 8	0.09	56.0	57.0	59.0	60.09	61.0	59.0			11	1	53.0	51.0	54.0	53.0	54.0	56.0	54.0
10	!	1	55.0	57.0	59.0	0.09	61.0	59.0			10	ļ	50.0	51.0	53.0	52.0	55.0	55.0	53.0
O	1 6	69.0	68.5	0.99	70.0	70.0	70.0	70.0			6	ŀ	64.0	66.0	64.0	66.0	66.0	68.0	0.99
∞	1 :	44.0	42.0	42.0	43.0	44.0	50.0	41.0			∞	1	38.0	40.5	39.0	41.0	40.0	39.0	36.0
7	51.0	49.0	46.0	47.0	51.0	49.0	56.0	48.0		Phalanx 1 posterior	7	40.0	44.0	44.0	43.0	48.0	45.0	46.0	41.0
9	37.4	(42)	40.0	38.1	42.0	40.0	37.0	39.0		к 1 ро	9	37.8	42.0	39.0	38.5	41.0	39.0	36.0	38.5
ĸ	30.0	34.0	32.0	30.5	34.0	33.0	30.5	33.0		Phalan	S	32.0	35.0	34.0	33.0	34.0	35.0	33.0	34.0
4	44.1	47.5	47.0	45.0	48.0	47.0	42.5	46.0			4	44.6	49.0	48.0	47.0	49.0	49.0	45.0	46.0
က	27.1	29.5	30.0	29.0	30.0	30.0	27.0	29.5			ಣ	27.8	30.0	30.5	30.0	31.0	30.0	28.5	29.0
23	68.8	0.69	67.5	68.0	71.0	71.0	71.0	72.0			2	65.3	66.0	65.0	66.0	67.0	67.0	69.0	67.0
nt: 1	75.8	77.0	76.5	75.0	80.0	78.0	78.0	78.5			nt: 1	71.2	74.0	72.5	72.0	74.0	74.0	75.0	73.0
Measurement:	<u>ი</u> ;	24	48	49	63	65	99	89			Measurement:	6	24	48	49	63	65	99	89
Coll.no. / Mea	111	46.3.23.10	329	13415	83602	99700	42753	90199			Coll.no. / Mea	111	46.3.23.10	329	13415	83602	99700	42753	90199
Col	LG	BM	BL	BL	Ŋ	ΝŽ	NY	Ň			Col	LG	BM	BL	BL	Σ	NY	N	N

Equus zebra hartmannae

40.0 52.0	30.5 40.0 52.0	48.6 32.5 41.3 48.5 47.0 30.5 40.0 52.0	0 75 0 07 5 0 75 0 75	
42.0 52.0 42.0 51.0	33.5 42.0 51.0 4	51.0 30.5 40.0 52.0 51.0 33.5 42.0 51.0	29.0 47.0 30.5 40.0 52.0 31.0 51.0 33.5 42.0 51.0	28 80.0 72.0 31.0 51.0 33.5 42.0 51.0
41.2 54.0 41.8 49.5	34.0 41.2 54.0 4 32.2 41.8 49.5	49.0 34.0 41.2 54.0 47.9 32.2 41.8 49.5	32.5 49.0 34.0 41.2 54.0 429.5 47.9 32.2 41.8 49.5	30 84.5 75.5 32.5 49.0 34.0 41.2 54.0 4 31 79.0 73.0 29.5 47.9 32.2 41.8 49.5
41.0 51.0	32.0 41.0 51.0	48.0 32.0 41.0 51.0 49.0 49.0	30.0 48.0 32.0 41.0 51.0 43.0 49.0 4	33 79.5 70.0 30.0 48.0 32.0 41.0 51.0 42 32.0 49.0 34.1 49.0 4
38.5	34.1 49.0 45.0 33.0 38.5 50.0 43.0	49.0 34.1 49.0 45.0 47.0 33.0 38.5 50.0 43.0	32.0 49.0 34.1 49.0 45.0 30.2 47.0 33.0 38.5 50.0 43.0	32.0 49.0 34.1 49.0 45.0 83.0 73.5 30.2 47.0 33.0 38.5 50.0 43.0
38.5 50.0 41.0 54.0	33.0 38.5 50.0 32.5 41.0 54.0	47.0 33.0 38.5 50.0 6 50.0 32.5 41.0 54.0 6	30.2 47.0 33.0 38.5 50.0 33.0 50.0 32.5 41.0 54.0	83.0 73.5 30.2 47.0 33.0 38.5 50.0 480.0 70.0 33.0 50.0 32.5 41.0 54.0
38.5	34.1 33.0 38.5 32.5 41.0	49.0 34.1 47.0 33.0 38.5 50.0 32.5 41.0	32.0 49.0 34.1 30.2 47.0 33.0 38.5 33.0 50.0 32.5 41.0	42 32.0 49.0 34.1 47 83.0 73.5 30.2 47.0 33.0 38.5 5 55 80.0 70.0 33.0 50.0 32.5 41.0
32.2 32.0 34.1 33.0 32.5		447.0 48.0 49.0 50.0	29.5 47.9 30.0 48.0 32.0 49.0 30.2 47.0 33.0 50.0	31 79.0 73.0 29.5 47.9 33 79.5 70.0 30.0 48.0 42 32.0 49.0 47 83.0 73.5 30.2 47.0 55 80.0 70.0 33.0 50.0
	47.0 51.0 47.0 47.9 47.9 48.0 49.0 47.0	31.2 48.6 29.0 47.0 31.0 51.0 51.0 29.5 47.9 30.0 48.0 32.0 49.0 32.0 49.0 33.0 50.0 33.0 50.0		75.5 32.5 73.0 29.5 70.0 30.0 32.0 73.5 30.2 70.0 33.0
		80.0 84.5 79.0 79.5 83.0		

Phalanx 1 posterior

14	40.0 388.0 399.5 399.5 388.0 388.0 390.0 390.0 390.0
13	12.5 11.3 9.1 10.7 10.7 113.5 114.0 113.0 113.0 113.0 114.0 114.0
12	13.5 12.5 10.8 10.8 111.1 113.0 113.0 113.0 113.0 113.0
11	55 50 50 50 50 50 50 50 50 50 50 50 50 5
10	54.6 60.0 57.7 56.0 56.2 56.0 57.0 57.0 57.0 57.0 57.0 57.0 57.0 57
6	69.2 69.2 67.0 67.0 67.0 70.0 68.7 66.5 66.5 67.0 64.0
œ	39.6 41.0 42.8 38.5 40.0 37.0 41.0 40.0 38.0 34.0 38.0
7	43.9 46.0 46.0 43.5 43.5 44.0 44.0 44.0 44.0 44.0 44.0 44.0 44
9	41.0 41.8 39.6 43.9 40.0 40.0 40.3 38.0 38.5 40.0 38.5
S,	36.2 35.7 35.7 35.7 35.0 34.0 34.0 34.5 33.0 33.0 33.0 33.0
4	51.5 499.7 488.2 50.2 51.0 50.0 50.0 50.0 649.5 649.5 749.5 77.5
က	30.7 31.9 32.1 34.1 30.0 30.0 31.9 30.0 30.0 30.0 30.0 30.5
2	69.6 73.0 70.0 68.5 70.0 68.0 71.0 71.0 66.0 66.5 66.5 70.0
nt: 1	75.9 75.9 75.0 76.0 74.0 74.0 74.0 74.0 77.0 77.0 77.0 77
Measureme	1 2 3 3 11 30 31 31 32 44 47 55 69
Coll.no. / Measurement: 1	AC 1932.364 AC 1933.562 AC 1936.325 AC 1948.54 AM 7691 BM 28.9.11.416 BM 63.6.13.1 AC 1919.59 BE 1961.25 BL 53065 BL 53065 BL 55246 MU 1954.179 MU 1960.237 BA 10918 NY 90240

Equus burchelli Phalanx 1 anterior

	14	37.0	39.0	36.0	37.2	40.0	38.2	36.0	37.0	38.0	38.0	39.0	40.0	39.1	36.0	35.0	38.0	37.0	37.5	37.5
	13	12.0	8.0	9.5	10.0	9.0	9.0	7.0	11.5	11.0	9.0	9.0	10.0	11.5	9.0	9.5	10.0	10.5	10.0	0.6
	12	13.5	9.0	10.0	10.5	10.0	10.0	10.0	11.0	12.0	13.0	11.0	12.0	11.0	10.5	10.0	11.0	11.0	9.5	12.0
	11	51.0	57.0	54.0	57.0	59.5	55.0	57.0	54.5	56.0	58.0	61.0	59.0	58.5	52.0	53.0	55.5	55.5	51.5	63.0
	10	50.5	57.0	54.0	57.0	0.09	54.0	56.0	54.5	55.0	55.0	0.09	58.5	0.09	51.0	52.5	55.0	56.0	58.0	63.0
	O	64.0	0.99	65.0	68.0	70.0	65.0	65.5	67.0	67.0	0.69	0.69	71.0	71.0	62.0	64.5	0.89	0.99	68.0	76.0
	∞	38.0	45.0	43.0	43.0	44.0	45.0	46.0	43.0	44.0	46.0	45.0	46.0	45.0	40.0	38.0	47.0	48.0	43.0	49.0
	7						47.0													
1	9						38.5													
	Ω	31.5	30.5	31.0	32.0	33.0	30.0	31.0	31.5	31.0	31.5	30.5	34.5	35.0	30.0	29.2	32.0	30.5	33.5	33.0
	4	46.5	49.5	42.0	47.5	47.5	47.0	44.5	44.5	45.5	46.0	46.0	49.5	49.5	44.0	46.5	47.5	47.0	48.0	50.0
	က	30.0	29.0	27.0	29.5	31.0	30.0	28.5	29.2	29.0	30.0	30.0	30.0	31.0	29.0	29.0	29.0	29.0	30.0	30.5
	0	64.0	68.0	0.99	0.69	72.0	66.5	67.0	0.69	68.0	0.69	72.0	73.5	72.5	61.0	64.5	0.69	67.0	0.69	75.0
	nt: 1	72.0	75.0	71.5	75.0	78.5	72.0	74.0	73.0	74.5	77.0	78.0	79.0	78.5	70.0	69.5	75.0	73.5	77.0	82.5
	Measurement:	2	9	7	∞	6	10	11	12	13	14	15	16	17		46	47	48	20	51
	\														1/2					
	Coll.no.	MU 1954-7	NA 3932				NA 3938													NA 3955

Phalanx 1 posterior

14	36.0	35.2	35.5	39.1	36.0	35.0	34.5	37.0	37.0	37.0	39.0	40.0	34.0	34.0	36.2	35.2	36.0	36.2
13	14.0	11.0	12.0	12.5	13.0	10.5	11.0	12.0	12.0	10.5	12.0	12.0	11.0	11.5	12.0	12.0	11.5	12.0
12	16.0	12.0	14.0	12.5	13.0	14.0	15.0	15.0	15.0	13.0	15.0	14.5	14.0	12.0	15.0	14.0	12.5	15.0
11	47.0 51.0	50.0	51.0	54.5	48.0	51.0	49.0	51.0	51.0	55.3	54.0	54.5	44.0	49.0	51.5	51.5	53.0	56.5
10	47.0	51.0	49.5	54.0	48.5	49.0	46.0	48.0	48.5	53.0	52.0	53.5	41.5	48.0	50.0	50.5	53.0	56.5
6	60.0	62.0	62.5	66.0	60.09	63.0	60.09	62.5	63.0	64.0	68.0	67.0	56.0	60.09	66.0	63.0	63.0	0.69
∞	34.0	39.0	36.0	39.0	37.0	38.0	38.0	39.0	38.0	37.0	39.0	39.0	34.0	35.0	42.0	41.0	37.0	44.0
7	41.0	43.0	41.0	45.0	42.0	43.0	43.0	45.0	45.0	41.0	43.0	44.0	39.0	41.0	45.0	46.0	43.0	48.0
9	38.5	36.0	41.5	42.0	38.0	33.0	38.0	38.0	38.5	40.5	41.0	43.0	36.5	37.5	39.0	38.5	43.0	42.5
lЮ	32.0																	
4	47.5	43.0	48.0	48.5	49.0	46.0	45.5	47.0	45.5	48.0	50.5	51.5	44.0	47.0	49.5	47.0	48.0	50.5
က	29.0	28.0	29.0	32.5	31.5	27.5	29.0	30.5	29.5	30.0	30.5	32.5	29.5	28.3	30.0	29.5	30.0	31.0
2	60.0	62.0	65.0	68.0	65.5	63.5	62,5	65.0	64.0	66.0	68.0	69.5	56.0	60.09	66.5	65.0	64.0	68.5
nt: 1	68.0	68.5	70.0	74.0	69.0	70.5	67.0	70.5	71.0	72.5	75.0	75.5	63.5	66.5	72.0	70.0	73.0	77.5
Measurement:	0.0	7	∞	6	10	11	12	13	14	15	16	17		46	47	48	50	51
\	h-												2 1/2					
coll.no.	1954-7 3932	3934	3936	3937	3938	3941	3942	3944	3945	3948	3950	3958	3949 2	3946	3956	3957	3943	3955
Col	MO																	

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14	34.5 34.5 34.5 34.5 35.0 36.0 37.0 37.0 38.0 38.0 38.0 38.0 38.0 38.0 38.0 38	
13	13.50 14.10 15.50 17.00	•
12	14.5 14.5 15.5 16.0 16.0 17.5 17.5 17.5 17.5 17.5 17.5 17.5 17.5	
11	665.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0 667.0	•
10	63.0 63.5 63.5 63.5 63.5 63.5 63.5 63.0 64.0 64.0 64.0 64.0	•
6	777.0 746.5 746.5 746.5 746.5 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0 747.0	•
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7	56.0 57.0 57.0 57.0 57.0 67.0	49.0
9	422.0 442.5 442.0 440.0 441.5 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0 441.0	41.5
2	38.5 34.5 34.5 34.5 34.5 34.5 37.0 38.0 38.0 38.0 38.0 38.0 38.0 38.0 38	
4	522.0 524.0 524.0 525.0 526.0 527.0 52	49.0
က	31.0 29.5 27.5 27.5 28.5 29.0 31.5 31.0 30.0 29.0 31.0 30.0 29.0 31.0 30.0 29.0 31.0 30.0 29.0 30.0 29.0	•
7	81.0 777.0 778.5 773.5 773.0 773.0 778.0 778.0 778.0 775.0 775.0 775.0 775.0 775.0 776.0 776.0	
ıt: 1	883.0 833.5 833.0 776.5 779.0 779.0 882.0 882.0 882.0 882.0 882.0 780.0 882.0 780.0 882.0	80.0
Measurement:	11 14 16 16 17 17 18 18 18 18 19 10 10 10 10 10 10 10 10 10 10 10 10 10	92
Meası	4	
\	.58 .75 .75 .8.17 .96 .96 .113 .113	
Coll.no.	1913.58 1931.392 1939.75 885 3965 3967 3968 5145 10876 10873 1923.177 10918 6879 7111 1953.96 1965.113 3966 3970 5.2.14 82038 204065 70086 90345	9899
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