

BEIHEFTE ZUM TÜBINGER ATLAS
DES VORDEREN ORIENTS

herausgegeben im Auftrag des Sonderforschungsbereichs 19
von Helmut Blume und Wolfgang Frey

Reihe A
(Naturwissenschaften)
19/1

Richard H. Meadow
and Hans-Peter Uerpmann (Eds.)

EQUIDS IN THE ANCIENT WORLD

1986

DR. LUDWIG REICHERT VERLAG · WIESBADEN

CIP-Kurztitelaufnahme der Deutschen Bibliothek

Equids in the ancient world / [diese Arbeit ist im Sonderforschungsbereich 19, Tübingen, entstanden], Richard H. Meadow and Hans-Peter Uerpmann (eds.). – Wiesbaden : Reichert, 1986.

(Beihefte zum Tübinger Atlas des Vorderen Orients : Reihe A, Naturwissenschaften ; 19,1)

ISBN 3-88226-282-6

NE: Meadow, Richard H. [Hrsg.]; Sonderforschungsbereich Orientalistik mit besonderer Berücksichtigung des Vorderen Orients (Tübingen); Tübinger Atlas des Vorderen Orients / Beihefte / A

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Diese Arbeit ist im Sonderforschungsbereich 19, Tübingen, entstanden und wurde auf seine Veranlassung unter Verwendung der ihm von der Deutschen Forschungsgemeinschaft zur Verfügung gestellten Mittel gedruckt.

Gesamtherstellung: Hubert & Co., Göttingen · Printed in Germany

Identification and Discrimination of Metapodials from Pleistocene and Modern *Equus*, Wild and Domestic

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1. Summary

Biometrical data and morphological comparisons using ratio diagrams are presented for anterior and posterior third metapodials of horses, hemiones, asses, hybrid equids, and *Equus hydruntinus*.

Each of these groups exhibits a characteristic morphology which is relatively independent of animal size, of geological age, and of state of domestication. The metacarpals (Mc III) tend to segregate better than the metatarsals (Mt III), there being some overlap between animal groups in the morphology of the latter. Slenderness is not the only discriminating feature. The existence of marked individual variation can make the discrimination of small samples rather hazardous while identification of isolated proximal and distal ends may prove impossible.

Generally speaking, third metacarpals are characterized by:

- a broad distal articulation (large DT: transverse diameter) in horses, hinnies, and the hybrid of *Equus hemionus* (male) x *E.caballus* (female);
- gracility in hemiones and especially in *E.hemionus hemippus*;
- greater development of the articular facet for the Os carpale III (magnum) in the asses and mules;

- deep proximal ends (large DAP: anterior-posterior diameter) in *E.hydruntinus*;
- a broad supra-articular diameter of the distal end (large DT) in the hybrid of *E.hemionus* x *E.asinus*.

The third metatarsals, while less distinctive, are:

- slender in hemiones (especially *E.hemionus hemippus*), asses, and hinnies;
- of reduced proximal breadth (DT) in *E.hydruntinus* and in the hybrid *E.hemionus* (male) x *E.caballus* (female);
- able to be differentiated only on the basis of distal proportions in asses and horses.

Domestication may affect distal articulations which appear broader and deeper in heavy horses, ponies, and some donkeys. The metapodials of *E.hemionus hemippus* do not at all resemble those of any of the hybrids studied. The metacarpals of *E.hydruntinus*, while similar to those of *E.tabeti*, are smaller and less gracile.

2. Acknowledgements

The metapodials of modern equids come from the museums and collections listed below. The name of each institution is preceded by the letter code which is used in the tables of measurements to be found in an appendix.

- 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
- 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
- HA : Zoologisches Institut und Zoologisches Museum, Hamburg, BRD
- KI : Institut für Haustierkunde, Kiel, BRD
- LD : Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands
- LY : Muséum d'Histoire Naturelle, Lyon, France
- MA : Laboratoire des Mammifères et Oiseaux du MNHN, Paris, France
- MU : Zoologische Sammlung des Bayerischen Staates, Munich, 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

The fossil remains of *E.mosbachensis* are to be found in the Naturhistorisches Museum, Mainz, BRD, and those of *E.hydruntinus* in the Istituto di Geologia e Paleontologia, Florence, Italy, where they were studied in collaboration with C. DE GIULI. The donkey metapodials

from Israel were measured in the Department of Zoology, Hebrew University, Jerusalem. We wish to sincerely thank the curators and technicians of all of these institutions for access to the collections and for their assistance.

This study, carried out under the auspices of L.A. 12 and L.A. 49 of the C.N.R.S., benefited in many ways from the assistance of R.C.P. 292 and 717 of the C.N.R.S. as well as of the Louis Leakey and Wenner Gren Foundations. The figures are the work of S. VRAIN and the typing of the tables and French text was carried out by E. MOLIN. E. HEINTZ provided valuable criticism on the manuscript. R. MEADOW translated the original French version into English.

3. Introduction

The domestication of equids is a domain of enquiry in which many points still remain obscure. The 1982 equid symposium in Tübingen, centered on Holocene equids of the Middle East, addressed two questions:

- at what point in time do equid remains from what are definitely domestic animals first appear in this area?
- to what species or hybrid forms do these remains belong?

Answers to these questions on the basis of osteological remains are not possible unless one can discriminate between all the different forms of equid that could have been present in the Middle East during the Holocene. These include wild and domestic horses, wild and domestic asses, hemiones, and hybrids. To these forms which still survive today can be added one fossil species, *Equus hydruntinus*, whose distribution in time and space still remains to be definitely determined.

In this paper, we propose to investigate to what degree the metapodials of these various forms are able to be differentiated.

Two articles by EISENMANN have already been devoted to the metapodials of equids (Mc III and Mt III). The first study (EISENMANN 1979) was concerned with modern wild equids and with the various fossil forms which were abundant in Europe and Africa. On the basis of biometrical data (14 measurements per metapodial), ratio diagrams were developed (following SIMPSON 1941). These diagrams represent the "average" morphologies of the metacarpals and metatarsals for each form studied. Together with tables of measurements (means, standard deviations, etc.), the ratio diagrams describe the metapodials of 11 species of *Equus*. In addition to this descriptive portion, the article includes consideration of the correlations between various dimensions of the third metapodials and attempts at functional, evolutionary, and phylogenetic interpretations.

The second article (EISENMANN/KARCHOUD 1982) is based on a much larger sample (400 modern and 400 fossil metapodials). The collection includes, in addition to the forms already studied, three North American fossil species and a few bones from modern hybrid forms. The same measurements as were used in the first study served as the basis for a multidimensional analysis which permitted the authors to determine resemblances among all of the forms and correlations between all of the measurements. This approach thereby offered a comprehensive view of the material studied. At the same time, ratio diagrams were used to characterize the average morphology of the metapodials of each species. These two approaches are complementary and by using both:

- discrimination between species or groups of species is often possible, particularly on the basis of the metacarpal, the principal distinguishing character being slenderness;
- it can be seen that the fossil metapodials have diaphyses which are relatively better developed than are the epiphyses;
- it is evident that fossil metatarsals have a facet for the Os tarsale IV (cuboid) which is better developed than in modern specimens.

These two reports provide both a set of data for reference and an attempt to discriminate between forms on the basis of metapodials. It is in the same spirit that the present work is conceived, the attempt being here to compare various domestic and wild forms.

4. Material and Methods

4.1. Material

Metapodials used come mostly from modern forms (horses, asses, hemiones, and hybrids) with various fossil forms presented for comparison. All specimens have epiphyses which are firmly fused to their diaphyses.

1. modern horses: *E.przewalskii*: 30 individuals
ponies: 4 individuals
draft horses: 5 individuals.

Instead of using an artificial average derived from horses of all kinds, we have chosen to study specimens from individuals at the two ends of the size range, sizes which, even though they may not correspond to pure races, nevertheless do at least have recognizable morphological characteristics. These domestic horses are contrasted to the wild horse as represented by *E.przewalskii* and to the fossil caballine form *E.mosbachensis*.

2. modern hemiones: *E.hemionus onager*: 16 individuals
E.hemionus hemippus: 2 individuals.

The Syrian hemione (*E.h.hemippus*) has been extinct for nearly a century and is very poorly known. (See Ducos, this volume, for a review.) The onager is much better represented in osteological collections and still lives in the wild in Iran.

3. modern asses: *E.africanus*: 7 individuals
E.asinus: 20 individuals.

The domestic material does not include representatives of large donkeys like those from Poutou, Malta, or Majorca and seems relatively homogeneous. The small numbers of wild asses available do not permit us to treat separately the sub-species from Nubia and Somalia.

4. modern hybrids: *E.asinus* (m) x *E.caballus* (f) (mules): 5 individuals
E.caballus (m) x *E.asinus* (f) (hinnies): 2 individuals
E.hemionus (m) x *E.caballus* (f): 1 individual
E.hemionus x *E.asinus*: 1 individual.

5. fossil specimens: *E.mosbachensis*: about 40 Mc III and Mt III.

The metapodials of this caballine species of Mindel-Riss date (FEJFAR/HEINRICH 1981) or of early Mindel date (BRÜNING 1978) have already been studied (EISENMANN 1979, EISENMANN/KARCHOUD 1982). They are used here as a supplement to the horse material.

E.hydruntinus: for both the Mc III and Mt III,

there are several whole bones and about 20 fragmentary specimens. This fossil form, defined by STEHLIN/GRAZIOSI (1935), was described as coming from an Upper Paleolithic context in Romanelli cave. The remains found in karstic fissures from the San Sidero region have also been attributed to this form (DE GIULI 1980). A detailed comparison of the metapodials from Romanelli and San Sidero has convinced us that they belong to the same species, and we have therefore grouped together the data from these two localities in the tables of measurements and ratio diagrams. The spatiotemporal distribution of *E.hydruntinus* is still poorly known as are also its phylogenetic affinities. Was it the ancestral form of the pony (ALIMEN 1946: 593), or an asinine equid (STEHLIN/GRAZIOSI 1935), or a stenonine equid (GROMOVA 1949A: 199; EISENMANN/PATOU 1980), or a zebrine equid (DAVIS 1980)?

E.asinus: c. 12 Mc III and 12 Mt III.

This material, still unpublished, comes from Ikrit (Israel) and dates to the Middle Bronze Age (DAVIS *in litt.*). (# 2000 BC - 1500 BC)

4.2. Methods

4.2.1. Measurement techniques.

Figures 1 through 5, which illustrate how the dimensions were taken, have been previously published (EISENMANN 1979). The measurements are the same for the Mc III and Mt III with the exception of some proximal dimensions and notably measurements 5 and 6 (articular breadth and depth for the metacarpal, greatest breadth and depth for the metatarsal). Three measurements have been abandoned; these are measure 2: lateral length, which is redundant when compared with measure 1: greatest length; and nos. 8' and 9: diameters of articular facets which are very variable. This leaves 12 measurements to be taken for each complete metapodial. The correspondences between the measurements of EISENMANN and those of VON DEN DRIESCH (1976) are summarized in Tables 1 and 2.

4.2.2. Elaboration and presentation of the data.

For each group of measurements, we have noted the range of variation and calculated the mean, the standard deviation, and the coefficient of variation. These data together with the number of observations are presented in Tables 3 to 13. The measurements of the metapodials of *E.mosbachensis*, elaborated in the same manner, have already been published (EISENMANN 1979). In addition, the dimensions of each metapodial, specimen by specimen, are listed in an appendix.

The ratio diagrams (Figures 6–19 following SIMPSON 1941) have the advantage over data lists of permitting us to make an immediate visual comparison of shapes and sizes. These figures are constructed by taking the logarithm (base 10) of each mean and comparing it with the log-

arithm of the mean of the comparable dimension in a reference taxon (line 0 on each diagram). Means larger than the reference are plotted above the 0-line with means smaller than the reference plotted below. This approach is identical to that utilized in the previous studies (see above) except that we have changed the reference taxon. In place of a mixture of various subspecies of *E.hemionus*, we have here used as a reference the subspecies *E.hemionus onager* alone. This change makes possible the comparison of the other subspecies of hemione with the onager.

The ratio diagrams are arranged to successively show:

1. the species grouped by sub-genera (i.e., horses, hemiones, asses) to permit within-group comparison of wild and domestic forms, large and small animals, and modern and fossil material;
2. the hybrids grouped with their respective parents (e.g., mules and hinnies with asses and horses) in order to see to what degree the parental morphology is reflected in the hybrids; and
3. the small equids (*E.hydruntinus*, *E.asinus*, *E.caballus*, and *E.hemionus hemippus*). These diagrams, which compare animals of different sub-genera but of similar size, are of interest because they juxtapose precisely those forms which one can expect to encounter in the Middle East during the Holocene.

We will now comment on the ratio diagrams, first those for the third metacarpal, then those for the third metatarsal.

5. Third metacarpals (Mc III)

5.1. Caballines (Fig. 6)

The ratio diagram for the caballines will be discussed measurement by measurement to serve as an example.

The line which connects measure 1 (greatest length) and measure 3 (breadth in the center of the shaft) indicates gracility or robustness. In comparison with a gracile form like *E.hemionus onager* which we use as the reference, we see that the metacarpals of *E.przewalskii*, while having a similar length, are characterized by a wider diaphysis, i.e., are more robust. This robustness is indicated on the ratio diagram by the length of the line segment which ascends from measure 1 to measure 3. Even longer ascending lines are evident in the cases of the other caballines whose metacarpal lengths and breadths are plotted on the graph. Multidimensional analyses show the great importance of this character in discriminating between species.

The next line segment, between measure 3 (mid-shaft breadth) and 4 (mid-shaft depth), indicates visually relative dimensions of the diaphysis in the middle of the bone. In *E.przewalskii*, mid-shaft depth is relatively less than in the reference species *E.hemionus onager*, this shown by the line descending between measures 3 and 4. Such a pattern seems to accompany greater robustness (EISENMANN, in press). We find it also in the other caballines.

Measures 5 and 6 reflect the size of the proximal end. Multidimensional analyses have shown that these dimensions are often more reduced in fossil forms when compared with the shaft measurements than they are in modern forms. This trend is evident for *E.mosbachensis* in Figure 6 where the point representing measure 5 is very low compared with measure 4.

Measures 10, 11, 12, 13, and 14 all refer to the distal end of the metacarpal: greatest supra-articular breadth (measure 10), breadth of the articular surface (measure 11), greatest depth of the sagittal ridge (DAP: measure 12), least depth of the medial condyle (measure 13), and greatest depth of the medial condyle (measure 14). Measures 10 and 11 are almost equal in *E.hemionus onager* (Table 6) and in *E.mosbachensis* (line segment parallel to the reference). In contrast, for all modern caballines, measure 11 is much greater than measure 10 and this is reflected in Figure 6 by the ascending line segment. The difference is clearer in domestic forms (ponies and heavy horses) than in the wild species *E.przewalskii*. The line between measures 13 and 14 reflects the degree of tapering of the medial condyle. It is evident from the ratio diagram that the greatest depth (measure 14) is relatively greater in the domestic forms.

Measures 7 and 8 reflect the sizes of the proximal articular facets. In all the caballines, the facet for the Os carpal IV (unciform, measure 8) tends to be relatively better developed than in *E.hemionus onager*. Measures 7 and 8, however, are among the most variable dimensions. This can be seen by examining the coefficients of variation in the tables and by observing the extreme values plotted for *E.przewalskii* in Figure 6.

In sum, the metacarpals of all the caballines, whether small or large, domestic or wild, fossil or modern, have a fairly similar morphology. Even so, *E.mosbachensis* can be distinguished from the modern taxa by the relatively reduced proximal and distal dimensions when compared with mid-shaft breadth (measure 3) and by the more or less equal distal breadths (measures 10 and 11). The domestic horses can be distinguished from their wild relatives by a relatively greater tapering of the medial condyle (measures 13 and 14) and by a relatively greater distal articular breadth (measure 11 compared with 10). Within the domestic horses, heavy draft animals can be separated from ponies not only by size but also by a relatively broader proximal end (measure 5 compared with 6).

5.2. Hemiones (Figure 7)

Equus hemionus hemippus is represented by only two specimens. As far as one can judge from these, their metacarpals are smaller than the smallest metacarpals of *E.hemionus onager* in almost all dimensions. This can be seen in Figure 7 where the line for *E.hemionus hemippus* is below the zero-line and outside the range of variation for the onager.

The line segment between measures 1 and 3 descends, this indicating gracility more marked than in the onager. The breadth of the distal articular surface (measure 11) is greater than the supra-articular breadth (measure 10) and both are relatively greater than mid-shaft breadth (measure 3), a fact which makes the metacarpal seem quite "wasted". The greatest depth of the medial condyle (measure 14) and the facet for the Os carpal IV (unciform, measure 8) are relatively well developed.

In sum, the metacarpals of *E.hemionus hemippus* and *E.h.onager* are more different in form from each other than are the metacarpals of the various caballines.

5.3. Asses (Figure 8)

One immediately obvious feature about the asses is the very similar form and size of the metacarpals of modern domestic donkeys and those of the Middle Bronze Age. The archaeological specimens, however, are a bit shorter and more robust. In contrast, the metacarpals of the wild

asses are larger and have a relatively greater mid-shaft depth (measure 4). They are also more “waisted” than those of the domestic donkeys.

For all the asses, the distal breadth measurements (measures 10 and 11) are about equal and the greatest depth of the medial condyle (measure 14) is relatively well developed. Above all, the articular facet for the Os carpale III (magnum, measure 7) is much better developed than that for the Os carpale IV (unciform, measure 8). On the whole, the asses form a very homogeneous group where only size and the proportions of the diaphysis separate wild and domestic forms.

5.4. Mules and hinnies (Figure 9)

There is a marked difference in size between mules and hinnies, the former being larger. One reason for this seems to be the intentional use of large mares with very large jacks as, for instance, in France with “mule mares” and Poitou jacks (AUDIOT 1978).

According to our small sample, the morphology of the two hybrids is not identical. The metacarpal of the hinnie seems more gracile, the breadth of its distal articulation (measure 11) is greater than that of the supra-articular area (measure 10), the facets for the Os carpale III (magnum, measure 7) and the Os carpale IV (unciform, measure 8) are smaller than in the mule.

We do not know anything about the morphology of the metacarpals of the actual parents of these hybrids, and therefore it must be with care that we discuss resemblances with horses and donkeys. It seems that the metacarpal of the mule resembles that of the donkey, distinguished principally from it by a better developed sagittal ridge (measure 12). We have not found the marked resemblance between mule and horse which has been suggested by WILLOUGHBY (1974: 393). The metacarpal of the hinnie resembles more that of the domestic horse (Figure 6) from which it differs principally in its gracility and in the weak development of the facet for the Os carpale IV (unciform, measure 8).

On the whole, the metacarpals of the two hybrids seem most similar in form to those of their respective fathers.

5.5. *E.hemionus* (male) x *E.caballus* (female) (Figure 10)

The single specimen of this cross (AC 1906–59, MNHN, Paris) resembles the metacarpals of the caballines although it stands apart in its gracility and in the relatively greater dimension of the least depth of the medial condyle (measure 13). In contrast to the previously discussed hybrids, it is the similarity to the mother which is most marked.

5.6. *E.hemionus* x *E.asinus* (Figure 11)

Which species provided the father and which the mother for this single specimen (AC 1870–251, MNHN, Paris) is unknown. The metacarpal is characterized by a very deep shaft (measure 4), a feature markedly different from both the hemione and the ass. The dimensions of the proximal facets (measures 7 and 8) are similar to those of the hemione, but, all in all, there is no marked resemblance with either parental species.

5.7. *E.hydruntinus* (Figure 12)

Both the absolute dimensions of the metacarpals and their proportions are not very different from those of *E.hemionus onager* although the shaft is more robust (measures 3 and 4). The configuration of the curve recalls particularly that of *E.tabeti* (EISENMANN 1979, Figure 17) an animal which is only a little larger and more gracile. The two species both have distal metacarpal breadths (measures 10 and 11) which are reduced in relation to proximal depth (measure 6) and facets for the Os carpale IV (unciforme, measure 8) which are relatively large. We should note that *E.tabeti* is a Villafranchian species from North Africa (ARAMBOURG 1970: 107).

5.8. Metacarpals of small size (Figure 12)

The comparison of graphs for the smaller sized animals reveals various features:

The metacarpals of *E.hydruntinus* from Romanelli and San Sidero have dimensions which are greater than those of the other "small" forms and they are characterized by distal breadths which are relatively reduced.

Metacarpals of *E.hydruntinus* and *E.asinus* are similar in their degree of gracility while those of the ponies are much more robust and those of *E.hemionus hemippus* much more gracile. In *E.asinus*, the facet for the Os carpale IV (unciform, measure 8) is relatively less well developed.

5.9. Summary for the metacarpals

The ranges of variation presented in the figures and in the tables show the amount of variation present within a single species and even within a variety. Such individual variation can lead to uncertainties in the identification and comparison of single or small numbers of metacarpals. In spite of this fact, however, there certainly exists a general resemblance between the metacarpals of various races, varieties, or sub-species belonging to the same species or to closely related species. Thus, one can easily define "caballine" (Figure 6) or "asinine" (Figure 8) configurations. The hemione group seems less homogeneous (perhaps because of quantitative or qualitative shortcomings of the samples), at least that part which concerns *E.hemionus onager* and *E.hemionus hemippus*.

MILNE-EDWARDS (1869) suggested that *E.hemionus hemippus* might have been a hybrid of hemione and horse or of hemione and ass. The morphology of the metacarpal (Figures 7, 10-11) does not lend support to this hypothesis.

The various hybrids have, unfortunately, been studied only from a very few specimens. It seems that the metacarpals of hinnies and of the cross between a male hemione and female horse resemble more those of horses while the metacarpals of mules resemble more those of asses.

The metacarpals of *E.hydruntinus* resemble those of *E.tabeti*. They separate clearly from those of the other species and hybrids studied.

The distinction between metacarpals of animals of small size (ponies, domestic donkeys, *E.hemionus hemippus*) rests principally in the relative size, breadth, and depth of the diaphysis (measures 1, 3, 4). It is practically impossible to distinguish between isolated proximal ends of metacarpals of ponies and *E.hemionus hemippus* or between isolated distal ends of donkeys and *E.hemionus hemippus*.

6. Third metatarsals (Mt III)

6.1. Caballines (Figure 13)

Onto a general morphological resemblance of the group are superimposed certain evident differences. *E.mosbachensis* is distinguished from modern horses by relatively small dimensions for the proximal breadth (measure 5) and for the facet of the Os tarsale IV (cuboid, measure 8). The domestic horses have very well developed distal articular ends (measure 11). The large caballines (*E.mosbachensis* and draft horses) have more robust metatarsals (measures 1–3). The draft horses have facets for the Os tarsale III (large cuneiform, measure 7) which are relatively poorly developed and greatest distal depths (measure 14) which are relatively great.

6.2. Hemiones (Figure 14)

The metatarsals are characterized by their gracility. Those of *E.hemionus hemippus* differ from those of the onager by their generally more reduced dimensions. The shaft diameters (measures 3 and 4) and the least depth of the medial condyle (measure 13) are especially reduced in *E.hemionus hemippus* when compared with the onager.

6.3. Asses (Figure 15)

The metatarsals of asses are almost identical in form with the exception of the remarkable gracility evident in modern domestic donkeys. Apart from a greater overall robustness, the metatarsals of Bronze Age donkeys differ from those of the modern donkeys in having a broader distal articulation (measure 11) and a smaller articulation for the Os tarsale III (large cuneiform, measure 7). The wild asses have metatarsals which are larger but whose distal depths (measures 12, 13, 14) are relatively reduced.

A comparison between Figures 13 and 15 shows that the metatarsal proportions of *E.przewalskii* are very close to those of *E.africanus*. To a lesser degree there is a resemblance between the metatarsals of all the asses and horses. The only character which works well to distinguish the two groups is the relative proportions of the distal articular surface: the least depth of the medial condyle (measure 13) is relatively smaller than the depth of the sagittal ridge (measure 12) in the horses than it is in the asses.

6.4. Mules and Hinnies (Figure 16)

The metatarsals of hinnies are smaller and more gracile than those of mules, although, in the former, the following are relatively larger: breadth of distal articular surface (measure 11), least depth of medial condyle (measure 13), and facet for the Os tarsale IV (cuboid, measure 8). Because of the similarity between metatarsals of horses and asses, research into which parent a hybrid resembles more is particularly fruitless. Note also that the measurements of hinny metatarsals all fall within the range of variation for the onager.

6.5. *E.hemionus* (male) x *E.caballus* (female) (Figure 17)

The single metatarsal resembles those of caballines except for its greater gracility (measures 1–3), reduced proximal breadth (measure 5), and smaller facet for the Os tarsale III (large cuneiform, measure 7).

6.6. *E.hemionus* x *E.asinus* (Figure 18)

The proportions of this metatarsal are close to those of the asses except that the diaphysis is thicker (measure 4) and the supra-articular distal breadth (measure 10) is relatively greater. In addition, the proximal dimensions (measures 5, 6, 7) are relatively reduced.

6.7. *E.hydruntinus* (Figure 19)

The metatarsals are similar to those of *E.hemionus onager* except that they are most robust (measures 1–3) with a proximal depth (measure 6) relatively reduced and the least depth of the medial condyle (measure 13) relatively greater.

6.8. Metatarsals of small size (Figure 19)

On the whole, the metatarsals of *E.hydruntinus* are larger than those of the other “small” forms and their gracility is intermediate between that of the domestic donkeys and that of the ponies.

The most gracile metatarsals belong to *E.hemionus hemippus*.

The ponies are characterized by distal breadths (especially articular breadths) which are relatively great.

6.9. Summary for the Metatarsals

Metatarsals belonging to individuals of one species or to a group of related species have similar morphologies but one can also find major likenesses between the metatarsals of groups as different as the horses and the asses.

The morphology of the metatarsal of *E.hemionus hemippus* does not much resemble that of any of the hybrids studied.

The metatarsal of *E.hydruntinus* separates out well from those of the other species and hybrids studied, except perhaps for *E.hemionus onager*.

Finally, for small-sized metatarsals, one of the best ways to distinguish the different forms is by gracility. It is practically impossible to differentiate between isolated proximal ends of asses and ponies and between isolated distal ends of asses and *E. hemionus hemippus*.

7. Conclusions

At the beginning of this essay we emphasized the need to establish the degree to which the metapodials of *Equus* forms known from the Holocene in the Middle East could be differentiated and identified and the degree to which domestication affected their morphology. Various responses can be made to these questions.

Each of the three major equid groups studied here (caballines, asses, and hemiones) has metapodials whose morphology is relatively homogeneous and specific to that group and which permits them to be differentiated from the others. On the whole, homogeneity is greater in the ass group than in the caballine group and much greater than in the hemione group. As far as the various hybrids are concerned, the material available to us is not sufficient to make definitive statements. It does suggest, however, that the metapodials of mules and hinnies differ principally in size, and there seems to be a certain predominance of characters with a morphology similar to those of the paternal side. This predominance is not, however, found in the case of the hemione-horse cross. It would be unreasonable for us to elaborate upon the morphology of hybrids based on single examples of hemione-ass and hemione-horse crosses but at least we can say that nothing substantiates the hypothesis that *E.hemionus hemippus* of Syria was an hybrid. As for *E.hydruntinus*, the metapodials of that species apparently do not fall in with those of any group of modern equids, although their metapodials do resemble those of another fossil species, *E.tabeti*. It is curious that in the morphology of its metapodials as well as in the morphology of its teeth (EISENMANN/PATOU 1980), *E.hydruntinus* resembles Villafranchian species in spite of its recent age. In general, identification of single metapodials or discrimination on the basis of very small collections is hazardous because of the complicating factor of individual variation. The identification of isolated proximal and distal ends is especially problematical. On the whole, however, metacarpals are easier to distinguish than are metatarsals.

Domestication perhaps manifests itself by developments in the distal articulation. We have noted a broadening of the articulation on the metacarpals and metatarsals of ponies and draft horses and on the metatarsals of the Bronze Age domestic donkeys from Ikrit. Moreover, the same articulation is also relatively thicker in the metacarpals of ponies and in the metatarsals of both ponies and draft horses.

On several occasions we have pointed out that the data obtained for the metacarpals and metatarsals do not present the same picture. This is surprising if one considers that there ought to be a close relationship between the anterior and posterior metapodials of the same animal. Analysis of these relationships and their limits could allow us to see to what degree one can predict the characteristics of one metapodial from those of the corresponding one. Overall, metacarpals seem to provide more information than do metatarsals. This situation seems to indicate that, in the case of equids, the functional role of front limbs is, or was, more differentiated than that of rear limbs.

Until just recently, the elements of the post-cranial skeleton have rarely been made the subject of detailed studies. It is now clear, however, that studies such as that made here on the metapodials are very important both from a theoretical point of view and for the practical aid they provide in permitting identification of commonly found elements. These results ought to provide encouragement for studies on other bones of the post-cranial skeleton.

8. Literature

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Note added in proof

While this paper was in press, it was found that another North African equid beside *E. tabeti* had metacarpals similar to those of *E. hydruntinus*. It has recently been described under the name of *Equus melkiensis* and dates to the Upper Pleistocene. BAGTACHE, B./HADJOUIS, D./EISENMANN, V., 1984, Présence d'un *Equus* caballine (*E. algericus* n. sp.) et d'une autre espèce nouvelle d'*Equus* (*E. melkiensis* n. sp.) dans l'Atérien d'Allobroges, Algérie. Comptes-Rendus de l'Académie des Sciences, Paris 298 (Série II), 609–612.

VÉRA EISENMANN, L. A. 12 du CNRS, Institut de Paléontologie, 8 rue Buffon, 75005 Paris, France.
SOPHIE BECKOUCHE, L. A. 49 du CNRS et Laboratoire d'Anatomie Comparée, 55 rue Buffon, 75005 Paris, France.

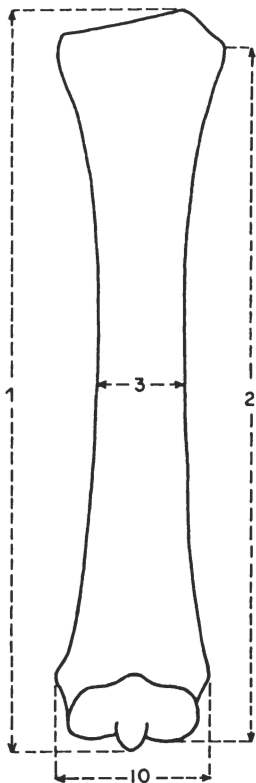


Fig. 1

Fig. 1 Dorsal (anterior) view of a left *Equus* metacarpal (Mc III). 1) Greatest length; 2) lateral (external) length; 3) breadth in the middle of the shaft (diaphysis); 10) distal supra-articular breadth (transverse diameter: DT).

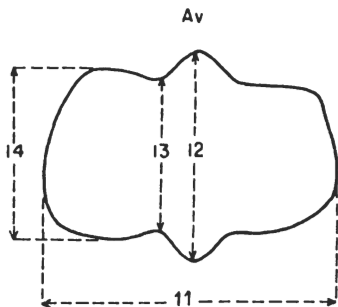


Fig. 2

Fig. 2 Distal (inferior) view of the distal end of a left *Equus* metacarpal (Mc III) or metatarsal (Mt III); "Av" = dorsal. 11) Breadth (DT) of the distal articulation; 12) depth (DAP) of the sagittal crest; 13) least depth (DAP) of the medial (internal) condyle; 14) greatest depth (DAP) of the medial (internal) condyle.

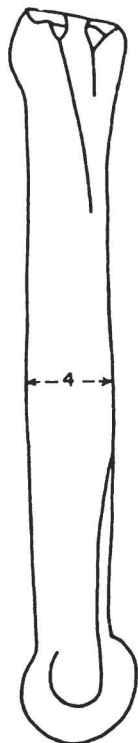


Fig. 3 Lateral (external) view of a left *Equus* metacarpal (MC III). 4) Mid-shaft depth (anterior-posterior diameter: DAP).

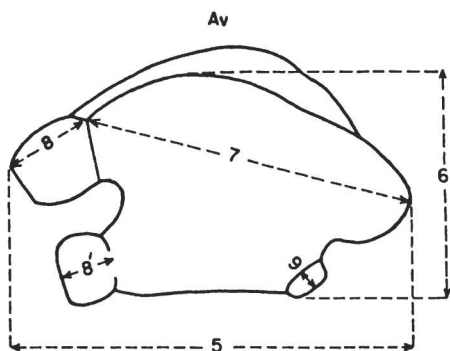


Fig. 4 Proximal (superior) view of the proximal end of a left *Equus* metacarpal (Mc III); "Av" = dorsal. 5) Breadth (DT) of the proximal articular surface; 6) depth (DAP) of the proximal articular surface; 7) diameter of the articular facet for the Os carpale III (magnum); 8, 8') diameters of the articular facets for the Os carpale IV (unciform); 9) diameter of the articular facet for the Os carpale II (trapezoid).

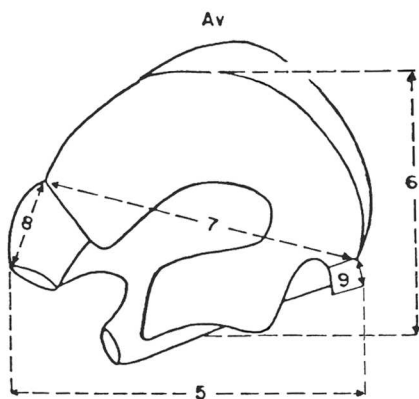


Fig. 5 Proximal (superior) view of the proximal end of a left *Equus* metatarsal (Mt III); "Av" = dorsal. 5) Greatest proximal breadth (DT); 6) greatest proximal depth (DAP); 7) diameter of the articular facet for the Os tarsale III (large cuneiform); 8) diameter of the articular facet for the Os tarsale IV (cuboid); 9) diameter of the articular facet for the Os tarsale II (small cuneiform).

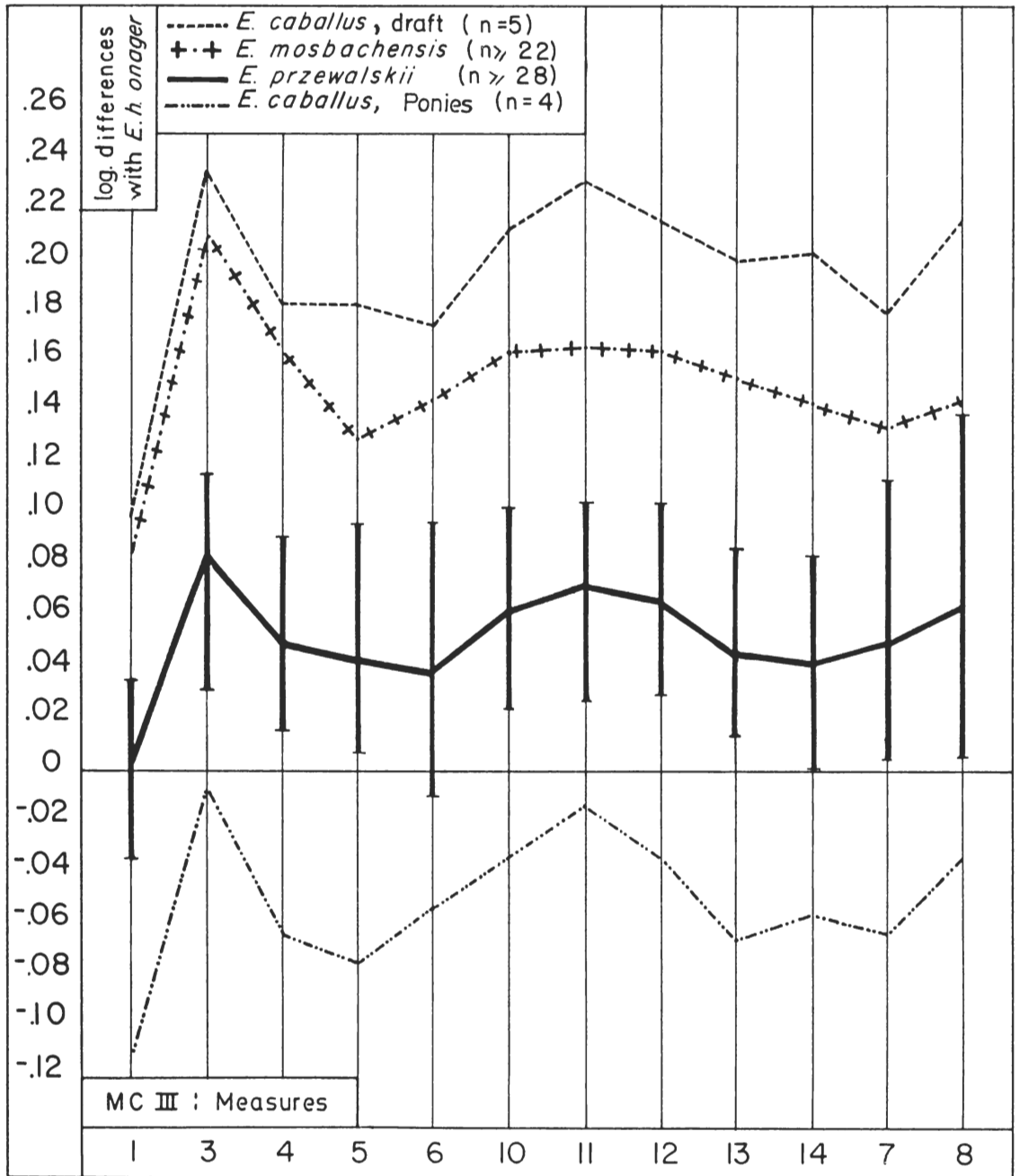


Fig. 6 Ratio diagrams of mean dimensions of metacarpals of various caballines, modern and fossil. The range of variation (minimum and maximum observed values) is plotted for *Equus przewalskii*. See Figures 1–4 for explication of the measurements.

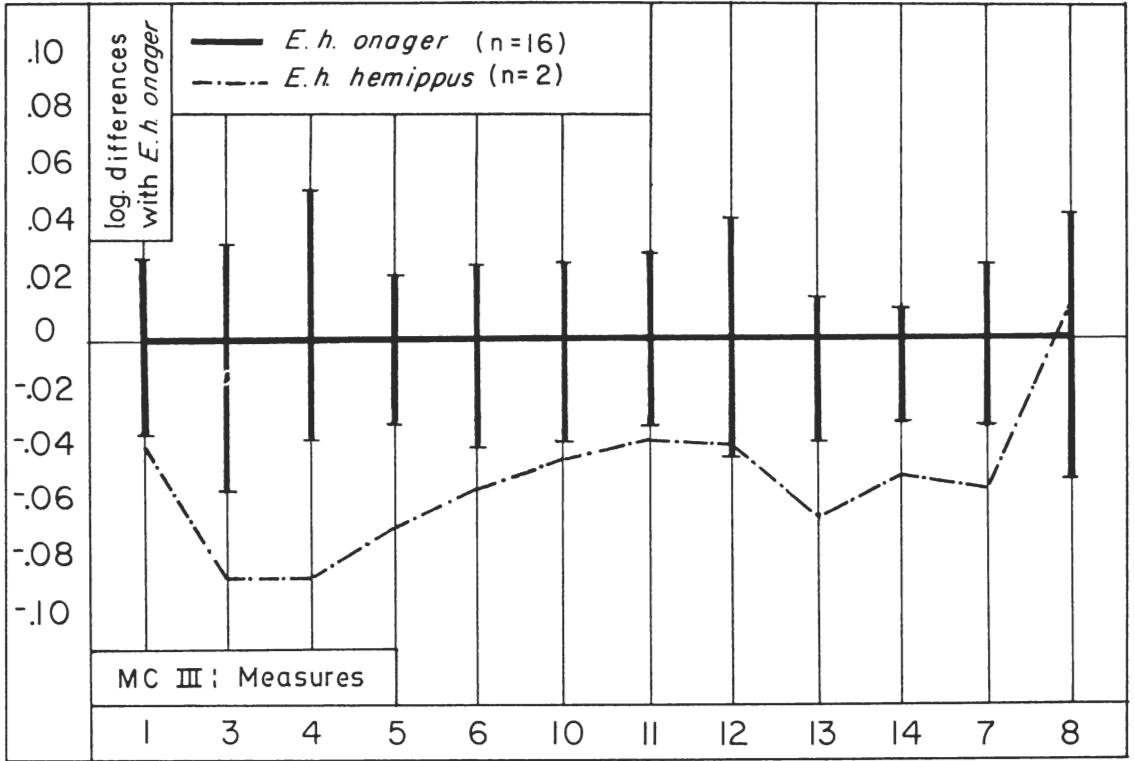


Fig. 7 Ratio diagrams of mean dimensions of metacarpals of various hemionus. The range of variation is plotted for *Equus hemionus onager*. See Figures 1-4 for explication of the measurements.

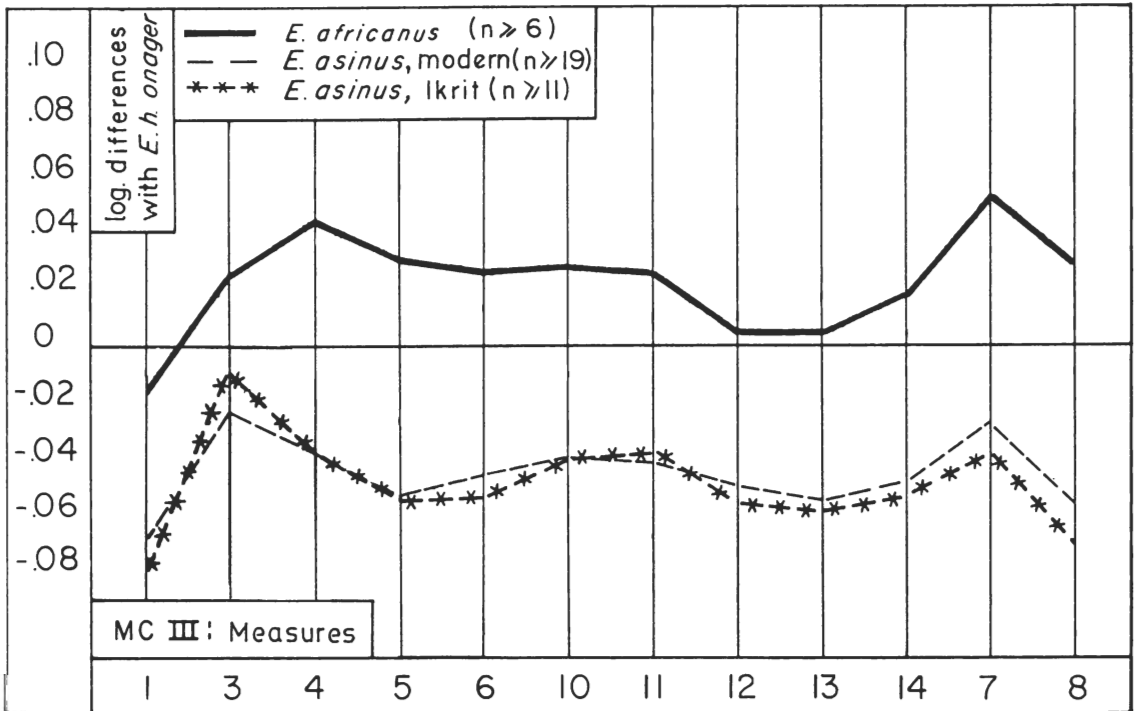


Fig. 8 Ratio diagrams of mean dimensions of metacarpals of various asses, modern and fossil. See Figures 1-4 for explication of the measurements.

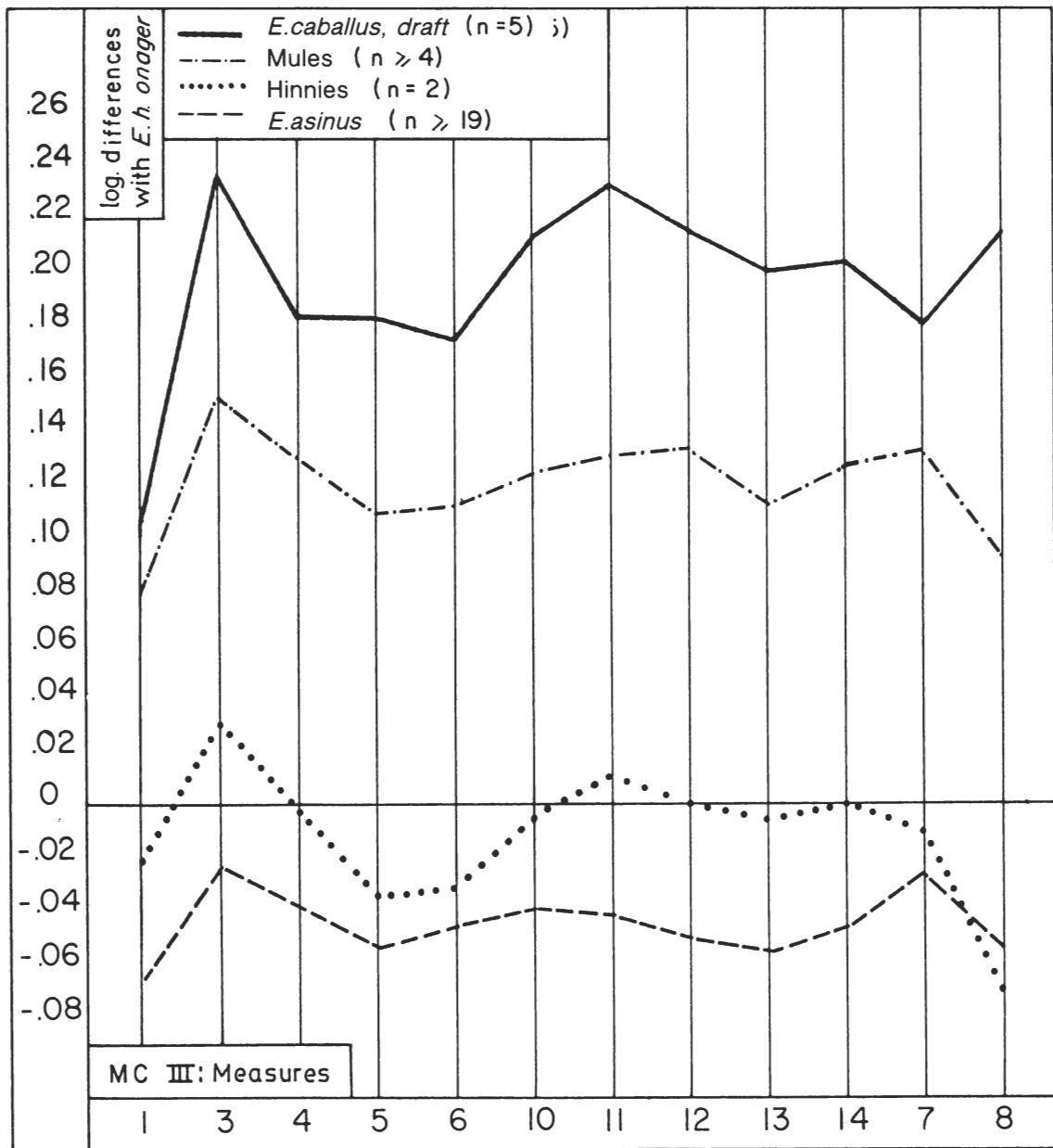


Fig. 9 Ratio diagrams of mean dimensions of metacarpals of mules, hinnies, and their parent species. See Figures 1-4 for explication of the measurements.

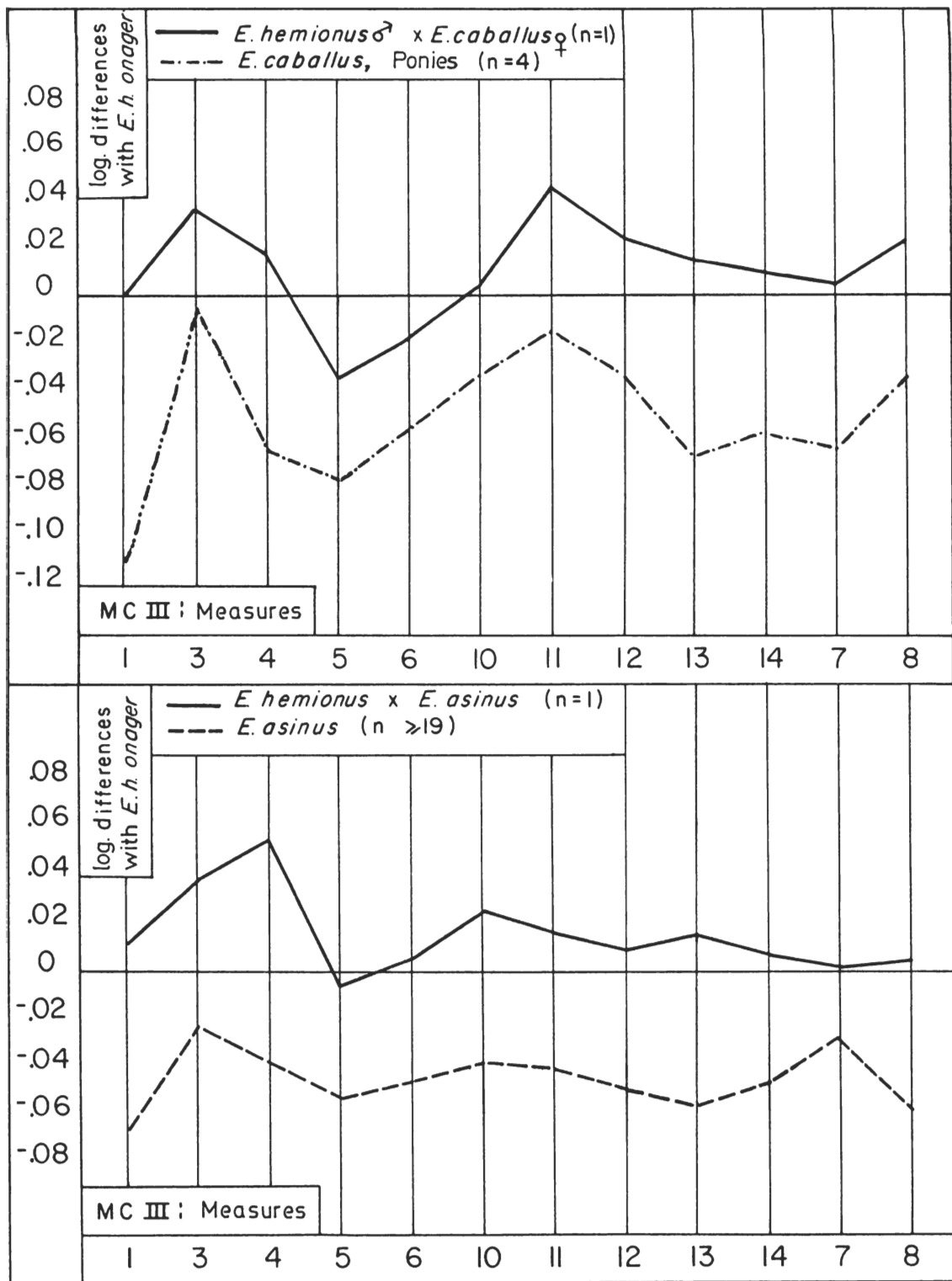


Fig. 10-11 Ratio diagrams of mean dimensions of metacarpals of hybrids of hemione and horse or ass and their parent species. See Figures 1-4 for explanation of the measurements.

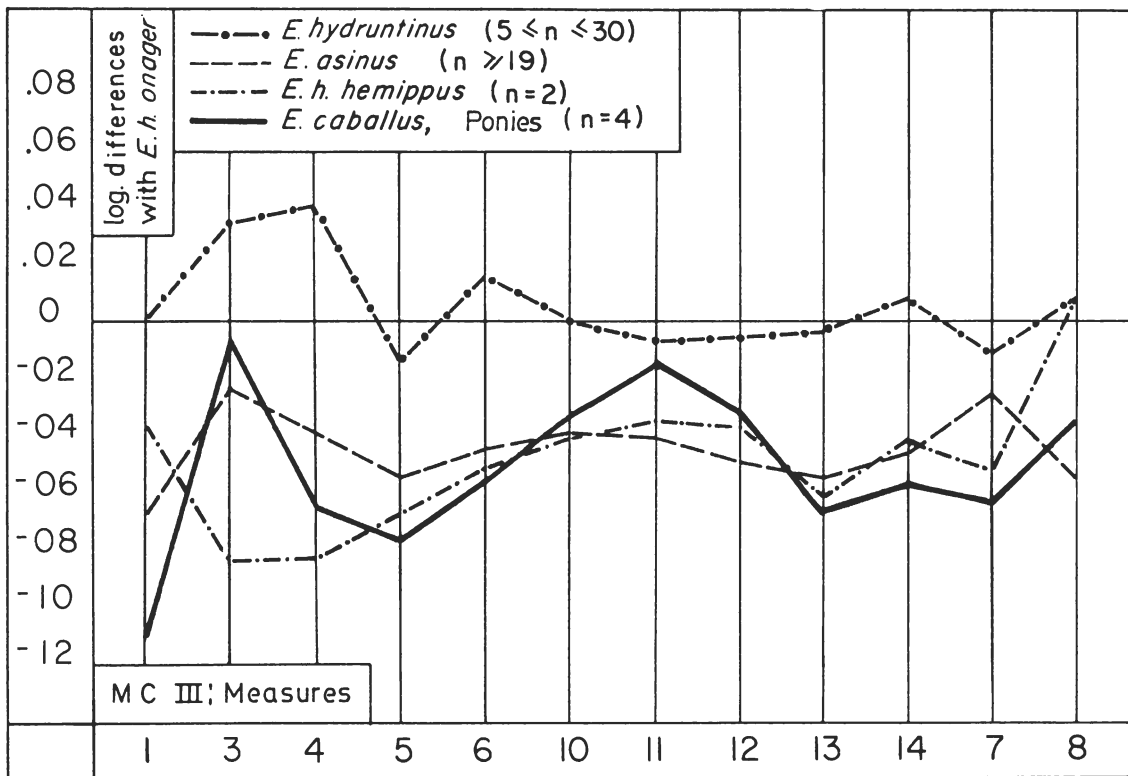


Fig. 12 Ratio diagrams of mean dimensions of metacarpals of small sized caballines, hemiones, and asses and *Equus hydruntinus*. See Figures 1-4 for explication of the measurements.

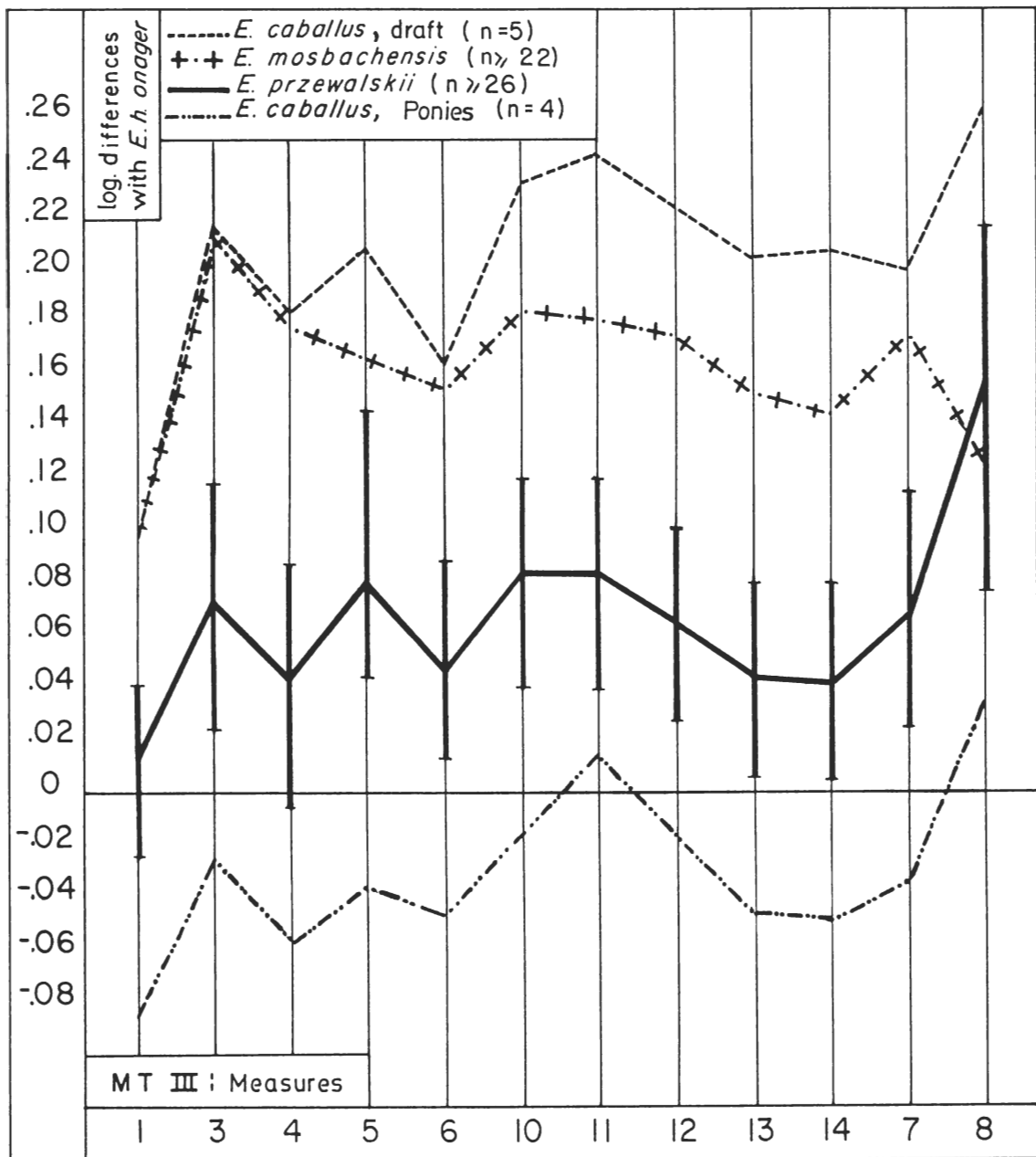


Fig. 13 Ratio diagrams of mean dimensions of metatarsals of various caballines, modern and fossil. The range of variation (minimum and maximum observed values) is plotted for *Equus przewalskii*. See Figures 1-3, 5 for explanation of the measurements.

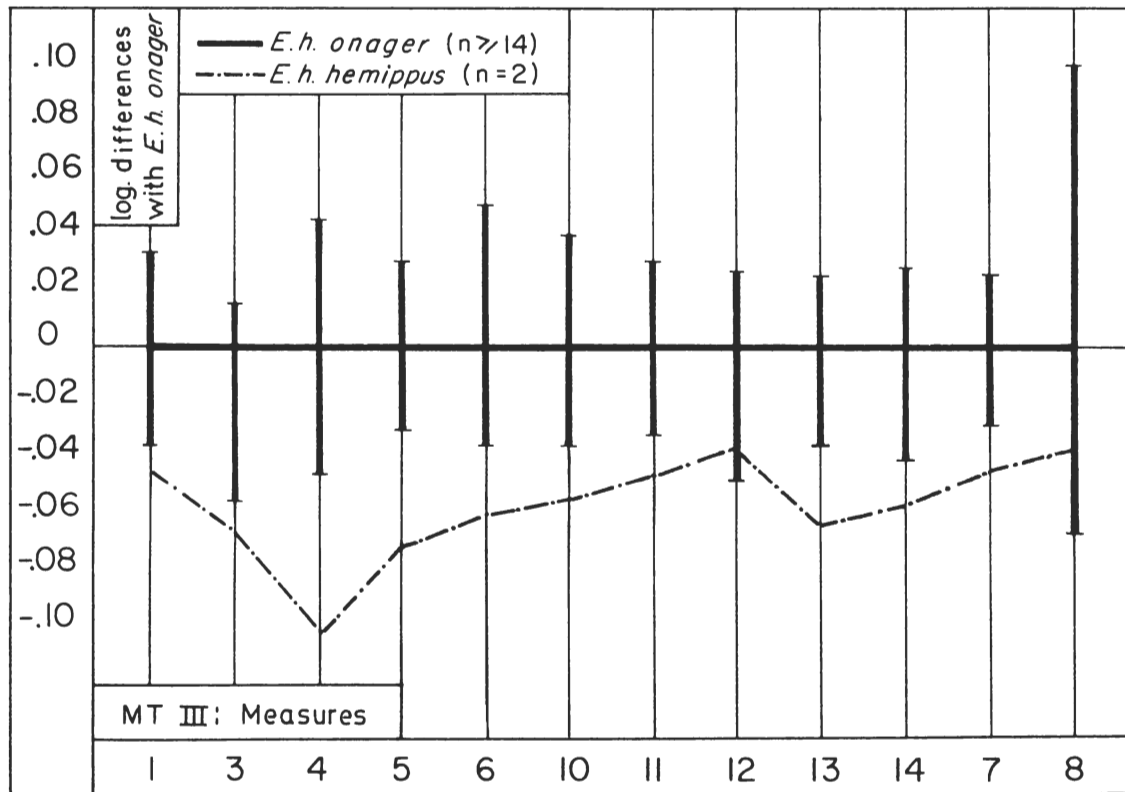


Fig. 14 Ratio diagrams of mean dimensions of metatarsals of various hemionus. The range of variation is plotted for *Equus hemionus onager*. See Figures 1–3, 5 for explanation of the measurements.

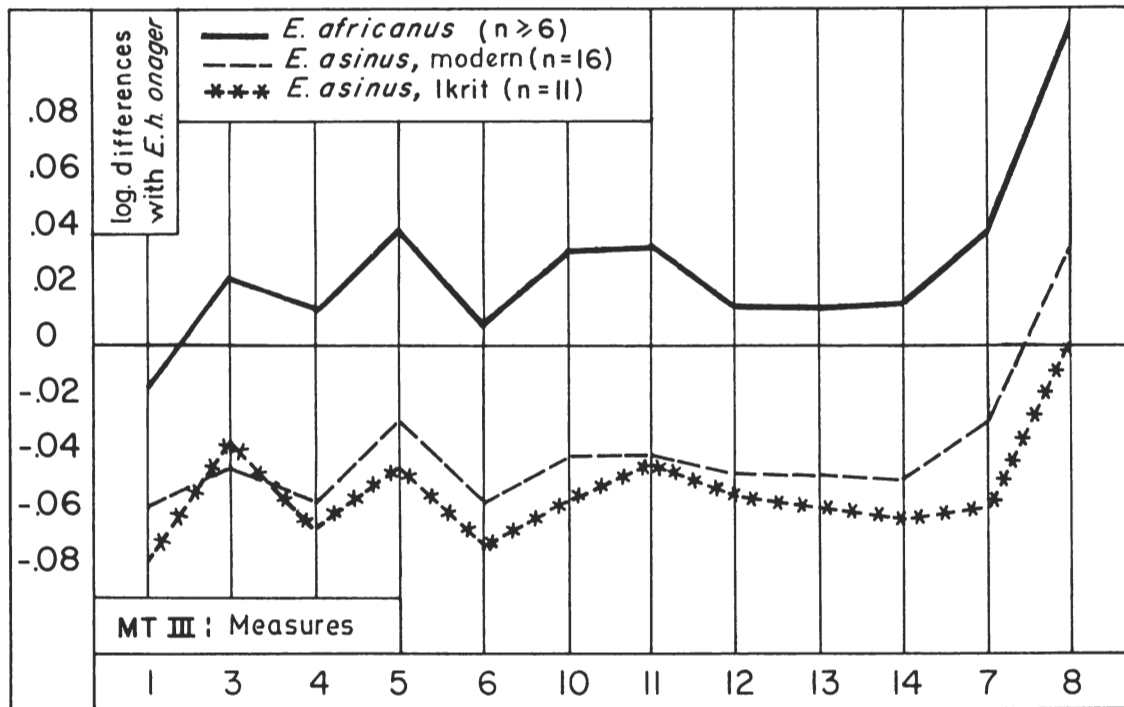


Fig. 15 Ratio diagrams of mean dimensions of metatarsals of various asses, modern and fossil. See Figures 1-3, 5 for explication of the measurements.

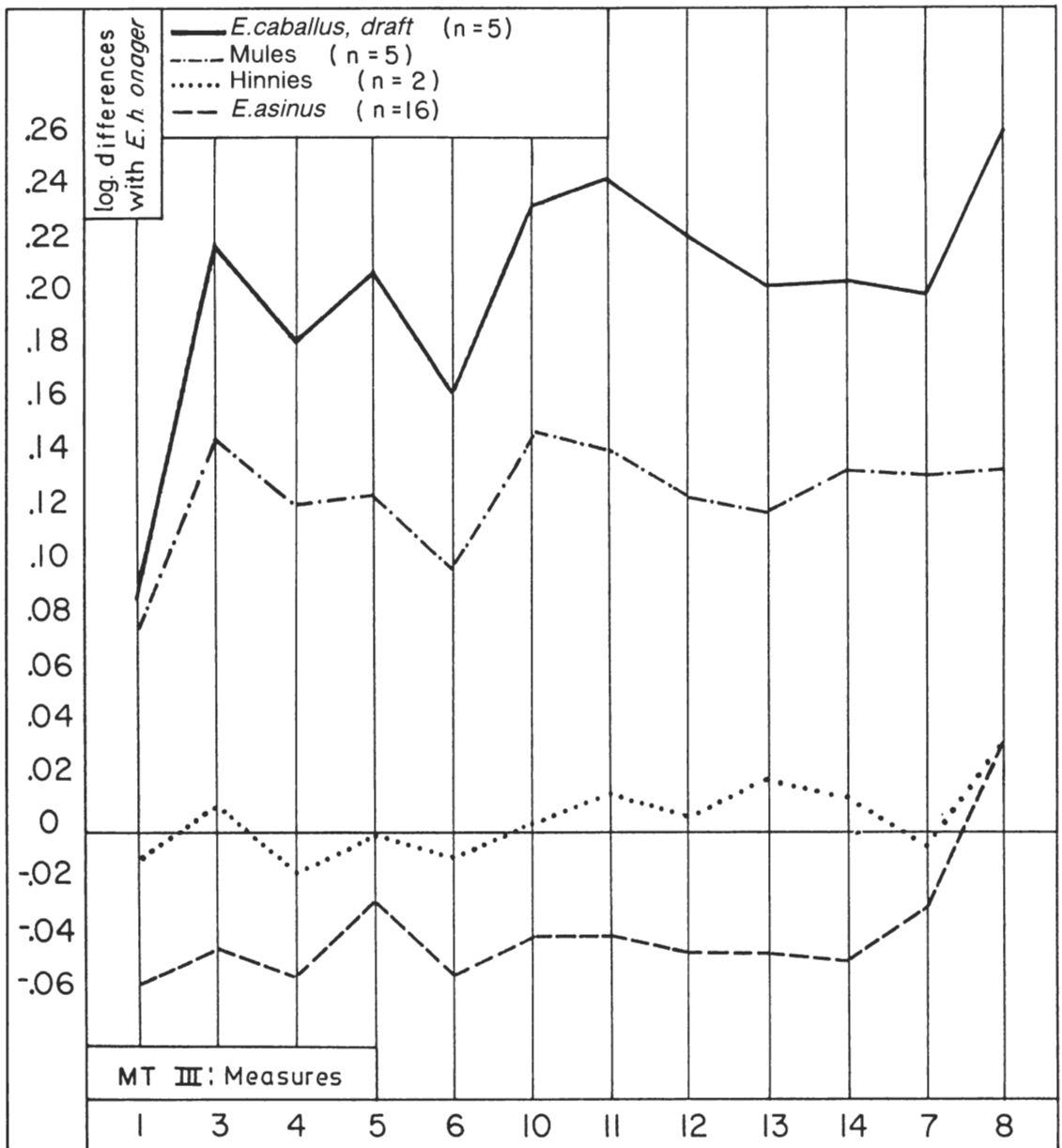


Fig. 16 Ratio diagrams of mean dimensions of metatarsals of mules, hinnies, and their parent species. See Figures 1-3, 5 for explication of the measurements.

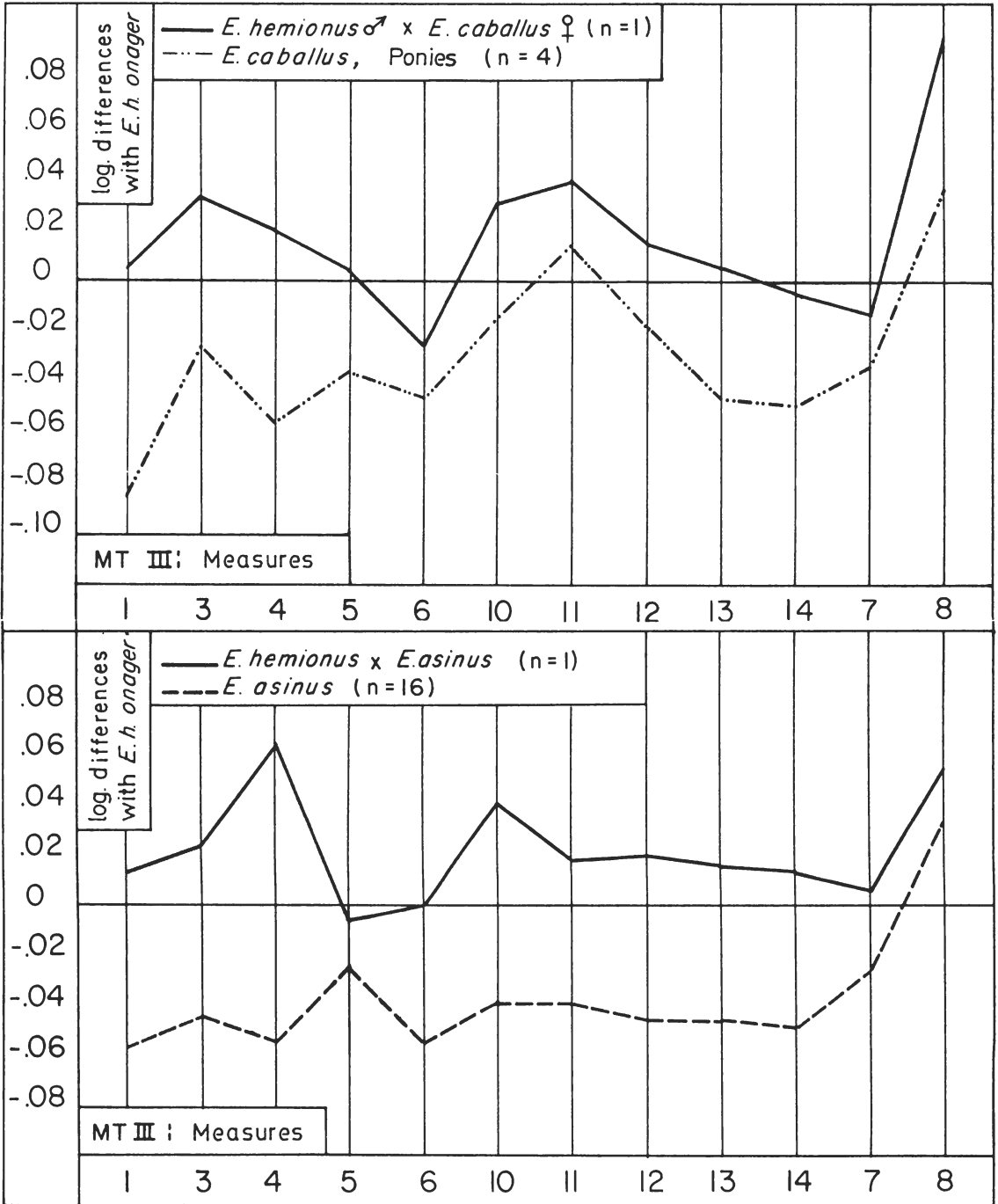


Fig. 17-18 Ratio diagrams of mean dimensions of metatarsals of hybrids of hemione and horse or ass and their parent species. See Figures 1-3, 5 for explication of the measurements.

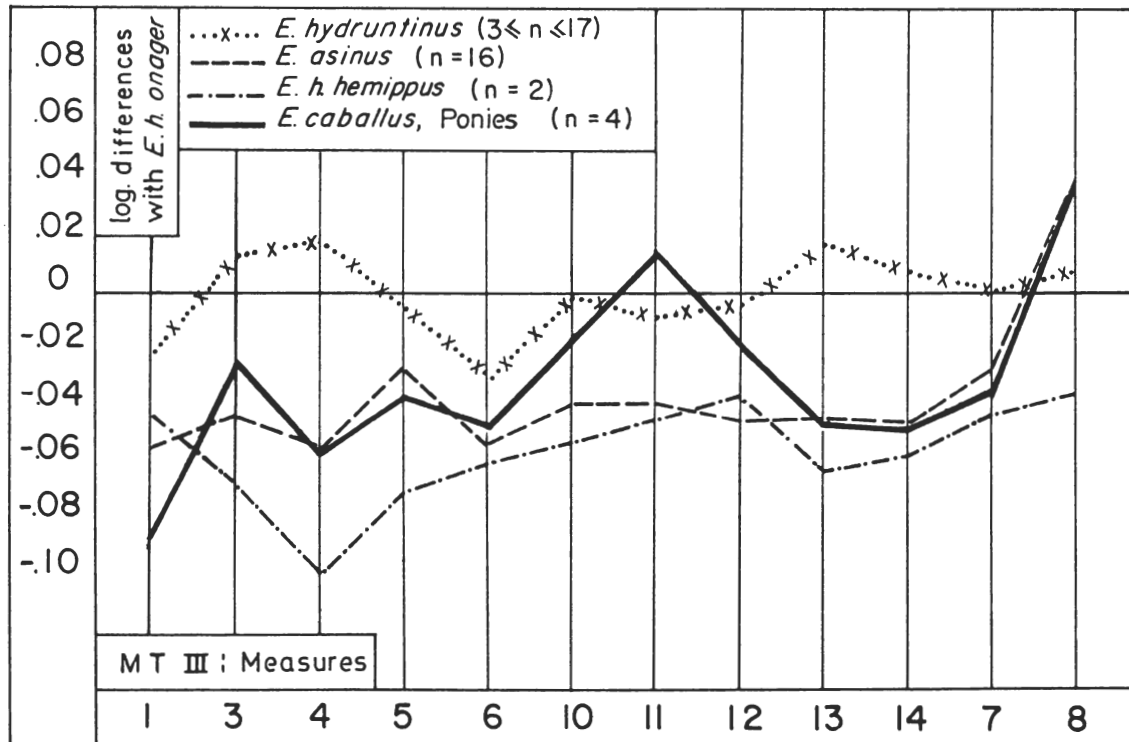


Fig. 19 Ratio diagrams of mean dimensions of metatarsals of small sized caballines, hemiones, and asses and *Equus hydruntinus*. See Figures 1–3, 5 for explication of the measurements.

MC III					
V.E.	A.V.D.	V.E.	A.V.D.	V.E.	A.V.D.
1	<i>GL</i>	6	-	10	<i>Bd</i>
2	<i>Ll</i>	7	-	11	
3	\approx <i>SD</i>	8	-	12	<i>Dd</i>
4	-	8'	-	13	-
5	<i>Bp</i>	9	-	14	-

Table 1 Equivalences between the system of measurements used here for the third metacarpal and that to be found in VON DEN DRIESCH (1976).

MT III					
V.E.	A.V.D.	V.E.	A.V.D.	V.E.	A.V.D.
1	<i>GL</i>	6	<i>Dp</i>	10	<i>Bd</i>
2	<i>Ll</i>	7	-	11	
3	\approx <i>SD</i>	8	-	12	<i>Dd</i>
4	-	9	-	13	-
5	<i>Bp</i>	-	-	14	-

Table 2 Equivalences between the system of measurements used here for the third metatarsal and that to be found in VON DEN DRIESCH (1976).

Tables 3–13 Measurements in millimeters (mm) for third metacarpals and third metatarsals.

Mes. = dimension (measure); the numbers 1 to 14 refer to the system of measurement defined in Figures 1–5;

n = number of specimens studied;

\bar{x} = mean;

min. = minimum value observed;

max. = maximum value observed;

s = standard deviation;

v = coefficient of variation.

Note: commas should be read as decimal points.

<i>Equus przewalskii</i>								
	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	29	214,6	197	231	6,39	2,98	
	3	29	31,3	28	34	1,63	5,18	
	4	29	23,6	22	26	1,23	5,20	
	5	29	47,8	44	54	2,35	4,91	
	6	28	29,7	26,5	34	1,71	5,74	
	7	28	38,6	34,5	44,5	2,39	6,19	
	8	28	14,3	12,5	17	1,12	7,85	
	10	29	44,9	41	49	1,77	3,94	
	11	29	45,5	41	49	2,05	4,50	
	12	29	34,4	31,5	37,5	1,56	4,53	
	13	29	26,9	25	29,5	1,26	4,69	
	14	29	28,7	26	31,5	1,39	4,86	
	MT III	1	30	255,8	234	272	7,45	2,91
		3	30	29,7	26,5	33	1,45	4,88
4		30	28	25	31	1,38	4,93	
5		29	48,8	45	57	2,40	4,92	
6		29	39,2	36	43	1,91	4,87	
7		26	42,1	38	47	2,29	5,44	
8		26	12,6	10,5	14,5	1,05	8,34	
10		30	46,2	42	50,5	2,27	4,91	
11		29	45,2	41	48,1	1,90	4,22	
12		29	34,9	32	38	1,59	4,58	
13		29	26,1	24	28,5	1,35	5,20	
14		29	28,8	26,5	31,5	1,41	4,90	

Table 3

<i>Equus caballus</i> (heavy)								
	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	5	268,2	253	288	15,58	5,81	
	3	5	44,8	41	51	4,15	9,26	
	4	5	32,1	28,5	37	3,54	11,04	
	5	5	65,7	59	71	5,02	7,64	
	6	5	40,6	37	46	3,36	8,28	
	7	5	51,9	46	57	4,64	8,94	
	8	5	20,3	18	22	1,56	7,71	
	10	5	63,2	59	68	4,44	7,02	
	11	5	65,6	61	70	3,78	5,76	
	12	5	48,5	44	53,1	3,39	6,99	
	13	5	38,3	35	43	3,11	8,13	
	14	5	41,4	38	45,5	3,03	7,32	
	MT III	1	5	307,2	289	324	15,67	5,10
		3	5	41,5	32	48	6,22	14,99
4		5	38,6	36	42	2,61	6,75	
5		5	65,7	62	71	4,84	7,37	
6		5	51,2	49	54	2,28	4,45	
7		5	57,2	54	60	2,68	4,69	
8		5	16,1	13,5	19,5	2,72	16,92	
10		5	65,6	61	71	4,77	7,28	
11		5	66	63	70	3,67	5,57	
12		5	50,3	47	55	3,23	6,43	
13		5	38,0	35,5	42	2,76	7,26	
14		5	42,4	40	46	2,61	6,15	

Table 4

Equus caballus (ponies)

	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	4	164,5	131	187	25,09	15,25	
	3	4	25,5	22	30	3,32	13,01	
	4	4	18,3	15	22	3,30	18,10	
	5	4	36,1	31,5	41	3,97	10,98	
	6	4	24	21	26	2,16	9,00	
	7	4	29,8	24	33	4,27	14,36	
	8	4	11,4	10,2	14	1,75	15,30	
	10	4	36	32	41	4,24	11,78	
	11	4	37,3	32	43	4,57	12,28	
	12	4	27,3	24	29,2	2,41	8,84	
	13	4	20,7	18	22,5	2,13	10,28	
	14	4	22,8	20	25	2,22	9,75	
	MT III	1	4	203	161	230	30,69	15,12
		3	4	23,6	21	28	3,04	12,86
4		4	22,2	19	26,1	3,11	14,03	
5		4	37,3	31,5	43,5	5,54	14,83	
6		4	31,4	28	33	2,29	7,29	
7		4	33,4	29	39	4,38	13,14	
8		4	9,6	9	10,3	0,67	7,05	
10		4	36,9	32	42	4,48	12,15	
11		4	38,5	32,7	44	4,73	12,27	
12		4	28,8	25	31	2,68	9,30	
13		4	21,3	18	23	2,36	11,12	
14		4	23,5	20	25,8	2,58	11,02	

Table 5

Equus hemionus onager

	Mes.	n	\bar{x}	min.	max.	s	v
MC III	1	16	212	196	227	8,94	4,22
	3	16	25,9	23	28	1,36	5,28
	4	16	21,1	19,5	24	1,34	6,38
	5	16	43,2	40,5	46	1,72	3,98
	6	16	27,1	25	29	1,23	4,54
	7	16	34,2	32	36,5	1,51	4,42
	8	16	12,3	11	14	0,96	7,78
	10	16	38,7	36	41,3	1,58	4,08
	11	16	38,5	37	41,5	1,30	3,39
	12	16	29,4	26,5	30,5	1,00	3,42
	13	16	24,1	22,2	25	0,98	4,06
14	16	25,9	24,3	26,5	0,72	2,78	
MT III	1	16	247,5	230	268	10	4,04
	3	16	25,1	22,2	26,1	1,16	4,63
	4	16	25,3	23	28	1,38	5,46
	5	16	40,5	38	43	1,69	4,17
	6	15	35	32,5	39	1,93	5,51
	7	14	36	34	38	1,22	3,40
	8	14	8,7	7,5	11	1,45	16,51
	10	16	38,2	35,5	41,3	1,84	4,83
	11	16	37,4	35	40	1,54	4,13
	12	16	30,1	27	32	1,23	4,11
	13	16	23,7	22	25	1,02	4,32
14	16	26,2	24	28	1,07	4,09	

Table 6

Equus hemionus hemippus

	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	2	194,2	193,4	195	1,13	0,58	
	3	2	21,3	21	21,7	0,49	1,33	
	4	2	17,5	17	18	0,71	4,04	
	5	2	37	35,9	38	1,48	4,02	
	6	2	24	23,9	24,1	0,14	0,59	
	7	2	30,5	29,8	31,2	0,99	3,24	
	8	2	12,6	12,5	12,7	0,14	1,12	
	10	2	35,1	34,7	35,5	0,56	1,61	
	11	2	35,5	35,3	35,6	0,21	0,60	
	12	2	27,1	26,5	27,7	0,85	3,13	
	13	2	20,9	20,5	21,3	0,56	2,71	
	14	2	23,4	23,1	23,6	0,35	1,51	
	MT III	1	2	224,5	224	225	0,71	0,31
		3	2	21,5	21	22	0,71	3,29
4		2	20	20	20	0	0	
5		2	34,5	33,5	35,5	1,41	4,10	
6		2	30,5	30	31	0,71	2,32	
7		2	32,8	30,5	35	3,18	9,71	
8		2	8,1	8	8,1	0,07	0,88	
10		2	33,8	33,5	34	0,35	1,05	
11		2	33,9	32,5	35,2	1,91	5,64	
12		2	27,8	27,5	28	0,35	1,27	
13		2	20,6	20,4	20,7	0,21	1,03	
14		2	23,1	23	23,1	0,07	0,31	

Table 7

<i>Equus africanus</i>							
	Mes.	n	\bar{x}	min.	max.	s	v
MC III	1	7	204,3	198,5	212,5	5,02	2,45
	3	7	27,5	26	29,5	1,34	4,87
	4	6	23,5	22	27	1,87	7,96
	5	7	46,3	44,3	48	1,36	2,94
	6	7	28,8	27,5	30	0,87	3,02
	7	7	38,5	38	40	0,78	2,04
	8	7	12,8	11	15	1,32	10,24
	10	7	41,4	39,1	45	2,21	5,34
	11	7	40,6	38,9	43	1,27	3,12
	12	7	29,6	29	31,5	0,92	3,11
	13	7	24,2	23,5	25,5	0,72	2,96
	14	7	26,6	25,1	28,5	1,12	4,20
MT III	1	7	240,2	232	248	5,91	2,46
	3	7	26,5	24,5	29	1,58	5,96
	4	6	26,1	24,5	27,5	1,17	4,46
	5	7	44,5	43,5	47	1,24	2,78
	6	7	35,7	32,5	37	1,60	4,48
	7	7	39,4	36	40	2,05	5,20
	8	7	11,4	8,7	14	1,99	17,47
	10	7	41,3	39	44	2,03	4,93
	11	7	40,5	39	42	1,22	3,01
	12	7	31	30,2	32	0,72	2,33
	13	7	24,3	24	25	0,46	1,90
	14	7	27,1	25,5	28,9	1,19	4,38

Table 8

<i>Equus asinus</i>								
	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	20	181,9	160,5	203	12,78	7,03	
	3	20	24,6	18,5	28,2	2,38	9,69	
	4	20	19,3	15,5	21,5	1,73	8,95	
	5	20	38,3	31	42	3,21	8,37	
	6	20	24,4	20	27	2,10	8,61	
	7	20	32,1	25	36	2,86	8,91	
	8	20	10,9	7,5	13	1,40	12,91	
	10	19	35,4	30	39	2,49	7,03	
	11	20	35,1	29	38,5	2,66	7,60	
	12	20	26,2	21	29	2,29	8,75	
	13	20	21,3	18	24	1,69	7,93	
	14	20	23,2	19	28	2,12	9,11	
	MT III	1	16	217,7	190	239	13,62	6,25
		3	16	22,8	19	26	1,67	7,34
4		16	22,4	17,3	25	2,12	9,46	
5		16	38,1	32	42	2,96	7,76	
6		16	31	26	35	2,51	8,08	
7		16	33,8	29	37	2,60	7,70	
8		16	9,5	7	11,5	1,15	12,09	
10		16	35	29	38	2,63	7,52	
11		16	34,2	29,5	37	2,05	6,01	
12		16	27,1	23	30	1,94	7,17	
13		16	21,4	17	24	1,77	8,30	
14		16	23,5	20	26	1,75	7,43	

Table 9

<i>Equus asinus</i> : Ikrit								
	Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	12	176,4	169	186,5	7,09	4,02	
	3	13	25,3	23	26,5	0,91	3,58	
	4	13	19,3	18,5	20	0,66	3,43	
	5	13	38,2	36	41	1,58	4,13	
	6	13	24	22	25,5	1,08	4,52	
	7	13	31,5	29	34	1,77	5,62	
	8	13	10,5	9	12	0,88	8,38	
	10	12	35,4	34	36,1	0,62	1,75	
	11	11	35,3	33	37	1,10	3,12	
	12	12	25,8	24	28,5	1,42	5,48	
	13	12	21,1	20	22	0,70	3,32	
	14	12	23	22	24,1	0,83	3,64	
	MT III	1	11	208,7	199	221,5	8,40	4,02
		3	11	23,2	21,5	25	1,10	4,75
4		11	21,8	21	24	0,91	4,15	
5		11	36,8	34	39	1,66	4,51	
6		11	29,8	28	32	1,50	5,02	
7		11	33	30	36	2,08	6,32	
8		11	8,9	7	11	1,32	14,81	
10		11	33,7	32,5	35,5	1,04	3,09	
11		11	34	32,5	35	0,98	2,89	
12		11	26,6	24,5	28,5	1,36	5,11	
13		11	20,7	19	22,2	1,01	4,87	
14		11	22,8	21,5	24	0,84	3,70	

Table 10

<i>Equus caballus</i> ♀ x <i>Equus asinus</i> ♂							
Mes.	n	\bar{x}	min.	max.	s	v	
MC III	1	5	255,6	235	270	12,89	5,04
	3	5	36,9	33	40,5	3,01	8,15
	4	5	28,6	26,5	32	2,22	7,76
	5	5	55,8	53,5	60,5	2,72	4,89
	6	5	35,3	33	39	2,28	6,46
	7	5	46,6	45	49	1,51	3,25
	8	5	15,4	12,5	18	2,04	13,27
	10	4	51,8	49	55,2	2,83	5,47
	11	5	52,1	49	55,4	2,67	5,12
	12	5	40,1	37	46	3,50	8,74
	13	5	31,5	29	36	2,69	8,54
	14	5	34,6	31,5	40	3,26	9,44
MT III	1	5	296,3	275	311	13,22	4,46
	3	5	35,3	31,5	39	2,77	7,86
	4	5	33,6	30	38	2,98	8,89
	5	5	54,4	51	59	3,20	5,89
	6	5	44,1	40	48,5	3,24	7,36
	7	5	49,3	47	53	2,94	5,98
	8	5	12,1	11	14,5	1,47	12,18
	10	5	54,0	49	59	3,74	6,92
	11	5	52,0	49	56,5	2,92	5,62
	12	5	40,4	38	45	2,88	7,13
	13	5	31,2	28,2	35,5	2,69	8,62
	14	5	36,1	32,6	36,8	3,21	8,88

Table 11

Equus caballus ♂ x *Equus asinus* ♀

	Mes.	n	\bar{x}	min.	max.	s	v
MC III	1	2	202,3	192,5	212	13,79	6,82
	3	2	27,8	27	28,5	1,06	3,82
	4	2	21	20	22	1,41	6,73
	5	2	40	38	42	2,83	7,07
	6	2	25,3	24,5	26	1,06	4,20
	7	2	33,5	33	34	0,71	2,11
	8	2	10,5	10	11	0,71	6,73
	10	2	38,3	36,5	40	2,47	6,47
	11	2	39,5	37	42	3,53	8,95
	12	2	29,5	28,5	30,5	1,41	4,79
	13	2	23,8	23	24,5	1,06	4,46
	14	2	26	25	27	1,41	5,44
	MT III	1	2	242,5	230	255	17,68
3		2	25,8	25,5	26	0,35	1,37
4		2	24,5	23	26	2,12	8,66
5		2	40,5	40	41	0,71	1,74
6		2	34,3	33	35,5	1,77	5,16
7		2	35,5	35	36	0,71	1,99
8		2	9,5	9	10	0,71	7,44
10		2	38,5	36	41	3,53	9,18
11		2	38,8	37,5	40	1,77	4,56
12		2	30,5	29	32	2,12	6,95
13		2	24,8	24,5	25	0,35	1,43
14		2	27	27	27	0	0

Table 12

<i>Equus hydruntinus</i>								
Mes.	n	\bar{x}	min.	max.	s	v		
MC III	1	5	212,8	207,5	219	4,40	2,06	
	3	12	28	27	30	0,95	3,39	
	4	11	23,2	22	27,5	1,49	6,42	
	5	5	42	41,5	43	1,24	2,97	
	6	5	28,2	27,5	29,5	0,78	2,76	
	7	5	33,4	32	34,5	0,94	2,82	
	8	5	12,7	11,5	13,7	0,95	7,50	
	10	24	38,9	35,5	41	1,41	3,63	
	11	26	37,9	35,5	40	1,10	2,90	
	12	27	29,1	28	31	0,83	2,86	
	13	30	24	22	26	0,91	3,79	
	14	26	26,4	25	28,3	0,95	3,61	
	MT III	1	3	235,6	220	247,8	14,21	6,03
		3	5	25,8	20	28	3,28	12,70
4		4	26,4	22	29	3,09	11,72	
5		4	40,1	36	42	2,78	6,93	
6		4	32,6	30	34	1,89	5,78	
7		4	36	35	37	0,82	2,28	
8		4	8,9	5,5	10,5	2,32	25,91	
10		13	38,1	35	41	1,67	4,38	
11		17	36,7	34	42	1,72	4,69	
12		15	29,9	28	33	1,21	4,06	
13		17	24,6	23	26	0,93	3,77	
14		14	26,8	25	28	0,95	3,56	

Table 13

Appendix

Individual measurements of equid metapodials. For measurement definitions see fig. 1–5; for museum abbreviations see ‘Acknowledgements.’

Ponies – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
AC 1937.59	131	125	22.0	15.0	31.5	21.0	24.0	10.5	5.0	0	32.0	32.0	24.0	18.0	20.0
AC 1873.385	160	154	25.0	16.0	35.0	24.0	29.0	11.0	6.0	4.5	33.0	36.0	27.0	20.0	22.0
NY 204044	180	173	25.0	20.0	37.0	26.0	33.0	10.2	4.5	0	38.0	38.0	29.2	22.3	24.0
CH 46019	187	181	30.0	22.0	41.0	25.0	33.0	14.0	8.0	0	41.0	43.0	29.0	22.5	25.0

Ponies – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
AC 1937.59	161	156	21.0	19.0	31.5	28.0	29.0	9.0	3.5	32.0	32.7	25.0	18.0	20.0
AC 1873.385	200	195	22.5	20.5	34.0	32.0	31.0	10.0	5.0	35.0	37.5	29.0	21.0	23.0
NY 204 044	221	214	23.0	23.0	40.5	33.0	34.5	9.0	5.0	38.0	40.0	31.0	23.0	25.0
CH 46 019	230	222	28.0	26.1	43.5	32.5	39.0	10.3	5.0	42.5	44.0	30.3	23.0	25.8

Heavy Horses – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
NY 98	253	244	41.0	28.5	67.5	40.0	51.5	21.5	12.5	9.0	60.0	64.0	48.2	39.0	41.5
AC 1884.2253	253	245	42.0	29.0	59.0	37.0	46.0	18.0	9.0	0	59.0	61.0	44.0	35.0	38.0
AC 1926.301	268	257	43.0	32.0	62.0	39.0	49.0	20.0	9.0	5.0	61.0	64.0	47.0	36.0	39.0
AC 1891.107	279	268	47.0	34.0	69.0	41.0	56.0	22.0	10.5	7.0	68.0	70.0	50.0	38.5	43.0
NY 183	288	278	51.0	37.0	71.0	46.0	57.0	20.0	13.5	0	68.0	69.0	53.1	43.0	45.5

Heavy Horses – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
NY 98	289	281	32.0	36.0	62.5	51.0	56.0	13.5	7.0	61.0	64.0	49.5	38.1	42.0
AC 1884.2253	295	287	40.0	36.0	62.0	49.0	54.0	14.0	3.5	61.0	63.0	47.0	36.0	40.0
AC 1926.301	306	300	41.5	39.0	62.0	49.0	56.0	15.0	0.1	65.0	63.0	48.0	35.5	40.0
AC 1891.107	322	312	46.0	40.0	71.0	53.0	60.0	18.5	7.0	70.0	70.0	52.0	38.0	44.0
NY 183	324	317	48.0	42.0	71.0	54.0	60.0	19.5	8.3	71.0	70.0	55.0	42.5	46.0

Equus przewalskii – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
AC 1973.109	197	189	32.5	22.0	45.5	27.0	35.0	14.0	5.0	5.0	44.0	44.5	31.5	25.0	26.0
NY 90198	206	198	28.0	22.0	44.0	27.0	34.5	14.0	8.0	0	43.0	41.0	32.0	25.5	27.0
MU 1951.173	208	201	28.0	22.0	44.5	26.5	34.5	14.0	5.0	0.1	41.0	41.0	32.5	25.5	26.5
LD 359	208	199	33.0	25.0	49.0	32.0	40.0	14.0	0	0	44.0	46.0	35.0	27.0	29.0
BL 60363	209	201	32.0	24.0	48.5	29.0	38.0	14.5	7.5	0.1	47.5	45.5	34.0	26.0	27.0
BM 1960.2.1.	209	0	29.2	23.3	45.4	30.0	37.0	12.8	0	0	41.6	43.8	33.9	27.5	28.2
AM 11.913	211	203	33.0	23.0	48.0	30.0	37.0	14.0	5.0	4.0	46.0	45.0	34.0	27.0	28.5
AC 1975.124	211	204	32.3	23.0	45.0	29.0	39.0	13.0	5.5	5.5	45.0	45.0	32.5	25.0	28.0
AM 11595	211	203	29.0	22.0	47.0	29.0	35.0	14.5	6.5	0.1	44.0	42.5	33.0	26.0	27.0
BL 60606	211	204	32.0	23.0	46.0	28.0	36.5	14.5	6.0	0.1	44.3	43.0	34.0	25.5	28.0
NY 32696	212	204	33.0	25.5	50.0	32.0	40.0	17.0	8.0	0.1	47.0	49.0	36.5	29.0	31.0
BM 1907.5.15	213	206	31.0	24.0	47.0	29.0	39.0	13.5	7.5	6.0	43.5	43.5	34.0	27.5	29.0
AC 1941.322	214	0	30.0	24.0	47.0	0	0	0	0	0	43.0	44.0	34.0	27.0	30.0
BM 1963.1.25	214	207	33.0	25.5	49.0	30.0	40.0	14.5	9.0	7.5	46.5	47.0	35.5	28.5	29.5
AC 1929.35	215	206	31.5	24.0	51.0	30.0	40.0	14.0	7.0	2.0	45.0	47.0	35.0	27.0	29.5
AC 1935.486	215	207	31.0	23.0	50.0	29.0	39.0	14.5	8.0	0.1	45.0	46.0	33.0	26.5	28.0
BM 1945.6.11	215	208	30.0	23.0	50.0	31.0	41.5	12.5	7.5	7.0	44.5	47.0	35.5	28.0	29.5
AC 1975.125	216	210	33.0	22.0	47.0	29.0	39.0	15.0	6.0	4.0	48.0	47.0	34.2	26.8	29.0
BM 1902.9.25	216	207	29.5	23.0	46.0	30.0	38.0	14.0	7.0	7.5	44.5	46.5	33.0	26.5	29.0
NY 35854	216	208	30.0	22.0	46.0	29.5	37.0	14.0	7.5	4.0	44.0	45.0	35.0	26.3	29.0
FR 35389	217	208	30.0	23.0	49.0	30.0	40.0	15.0	7.0	7.0	43.0	45.0	34.5	26.0	28.0
NY 80062	218	209	30.0	23.0	45.0	28.0	37.0	13.0	7.5	0.1	44.0	44.0	34.2	26.3	28.1
AC 1932.56	218	210	30.5	24.0	46.0	30.0	36.0	13.5	6.0	6.0	44.0	46.0	33.0	26.0	27.0
AC 1929.37	218	210	31.0	25.0	46.0	29.0	40.0	14.0	6.0	6.0	42.5	44.0	33.0	26.5	28.0
BM 1961.5.10	220	0	30.7	24.0	49.0	32.0	38.8	16.0	0	0	46.2	43.8	36.1	27.9	29.0
NY 32686	220	210	33.0	25.0	49.0	32.0	40.0	17.0	8.0	4.0	45.0	47.5	36.4	28.5	30.0
NY 204071	221	215	31.0	23.0	48.5	32.5	42.0	14.0	8.0	9.0	45.0	46.5	35.0	27.2	28.0
MU 1953.647	222	211	33.0	25.0	51.5	30.5	40.5	15.0	9.5	0	46.0	47.0	37.0	29.5	30.5
MA 1964.107	222	215	32.0	24.0	47.0	29.0	38.0	13.0	5.0	4.0	49.0	47.0	35.0	27.5	29.0
AC 1962.228	224	215	33.0	26.0	50.0	31.0	40.0	14.0	7.0	6.5	47.0	47.5	35.0	27.5	29.0
AM 981	231	220	34.0	25.0	54.0	34.0	44.5	17.0	8.5	6.0	46.0	46.0	37.5	29.0	31.0

Equus przewalskii – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
AC 1973.109	234	228	31.5	27.0	46.5	36.0	38.0	12.5	7.0	45.2	44.2	32.0	25.0	26.5
NY 90198	246	242	28.0	25.0	45.0	38.0	38.0	13.0	5.0	44.5	41.0	33.0	25.0	27.5
BM 1902.9.25	248	241	27.5	26.5	46.5	37.0	40.0	10.5	5.0	42.5	45.5	33.2	26.0	29.0
MU 1951.173	249	243	29.0	28.5	46.5	37.5	41.0	11.5	6.0	42.0	42.5	33.2	24.5	27.0
LD 359	249	0	30.0	26.0	49.0	40.0	0	0	0	44.0	46.5	34.5	26.0	29.0
BM 1960.2.1.	250	0	28.5	26.3	46.8	36.7	41.1	12.6	0	43.8	43.3	34.0	26.0	28.0
BM 1907.5.15	250	240	30.0	27.0	46.5	40.0	40.0	12.0	4.0	15.0	43.5	35.0	26.5	29.0
AC 1929.37	252	246	29.0	27.5	47.0	40.0	40.0	11.0	5.0	44.5	43.5	34.0	25.0	28.0
BM 1963.1.25	252	246	31.0	29.5	51.0	41.0	43.0	12.0	2.5	48.0	46.5	36.0	27.5	30.5
AC 1935.486	253	249	30.0	27.5	49.0	38.5	43.0	13.5	5.0	43.0	44.0	33.5	25.0	28.0
BM 1945.6.11	253	246	26.5	27.5	52.5	42.0	45.5	14.5	5.0	46.5	47.5	36.8	28.0	30.5
AM 11595	253	242	29.0	29.0	47.0	39.0	0	0	0	46.0	42.0	34.0	25.0	27.0
BL 60606	254	249	31.0	28.0	47.0	38.0	40.5	14.0	4.5	49.0	44.0	34.0	25.0	28.0
AC 1975.124	255	248	30.0	28.0	48.0	38.0	42.0	13.0	5.0	47.0	45.3	33.0	24.0	28.0
MU 1932.22	255	248	29.0	27.5	50.0	40.0	43.0	12.0	4.0	49.0	45.0	34.0	25.5	28.0
AM 11913	255	244	31.0	29.5	48.0	39.0	0	0	0	47.5	44.0	33.5	25.0	28.0
NY 32696	255	248	31.0	29.0	57.0	39.0	41.0	13.0	6.0	47.0	48.0	37.0	28.0	31.0
FR 35389	257	246	30.0	29.5	47.5	37.5	42.0	12.0	5.0	44.2	44.0	35.0	26.0	28.0
AC 1929.35	257	247	29.0	27.0	50.0	40.0	42.0	11.5	5.0	47.0	46.0	34.5	26.0	28.5
BL 60363	257	245	30.0	27.0	49.0	40.0	42.5	14.5	5.0	49.0	45.0	34.0	25.0	28.0
AC 1941.322	257	0	28.0	29.0	0	0	0	0	0	47.0	0	0	0	0
NY 35854	257	251	28.0	26.5	48.0	37.0	41.0	13.0	5.5	43.2	43.2	35.0	25.0	28.0
AC 1932.46	260	251	29.0	27.0	48.0	39.0	42.5	12.0	0.1	44.5	45.0	34.0	25.0	28.0
NY 32686	260	253	31.0	30.0	50.0	42.0	44.0	13.0	5.0	45.0	46.5	37.0	27.5	30.5
AC 1975.125	261	255	33.0	29.0	50.0	36.0	43.0	14.0	4.5	50.5	47.0	35.0	25.0	28.5
AC 1962.228	262	255	31.0	30.0	48.0	41.0	43.0	13.0	5.0	50.0	47.5	37.5	28.5	31.5
MU 1953.147	262	256	31.5	29.0	52.0	42.0	47.0	12.5	4.0	48.0	47.5	38.0	28.5	31.5
NY 80062	264	256	28.0	27.0	47.0	37.0	39.0	13.0	5.5	46.0	44.0	35.0	26.0	29.0
BM 1961.5.10	264	0	28.5	28.0	50.0	40.5	44.3	13.0	0	47.0	43.7	36.7	27.8	29.5
MA 1964.107	268	258	31.0	31.0	49.0	41.0	45.0	11.0	7.5	48.5	47.5	37.0	28.0	31.0
NY 204071	269	263	29.0	27.0	50.0	37.0	45.0	13.2	5.0	45.0	47.0	36.0	27.0	28.5
AM 981	272	264	31.0	29.0	51.0	43.0	45.0	12.0	5.0	48.0	48.1	37.2	28.0	30.5

Domestic Donkeys – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
BE 5.11.1952	161	155	24.0	17.0	37.5	21.5	30.0	10.5	5.0	3.0	36.0	34.5	24.0	21.0	22.5
HOFFSTETTER	161	156	18.5	15.5	31.0	20.0	25.0	7.5	5.5	4.0	30.5	29.0	22.0	18.0	19.0
AC 550	163	157	28.2	18.3	38.0	25.0	33.0	11.0	6.0	0.1	39.0	38.0	29.0	24.0	28.0
AC 1930.86	167	162	21.7	17.0	34.0	22.0	28.0	9.5	7.0	2.0	32.0	33.0	24.2	19.0	22.0
FAC.D'ARCHED	171	165	20.0	16.0	33.0	20.0	28.5	11.0	5.5	0	30.0	29.0	21.0	18.0	19.0
AC 551	178	172	24.0	19.0	36.0	24.0	31.0	10.0	6.0	3.5	34.5	35.0	26.0	21.5	22.0
YA 1622	179	174	24.0	19.0	37.5	25.0	32.5	11.0	5.0	0	35.0	33.0	25.0	20.5	22.1
NA 3952	179	173	24.3	19.8	37.1	23.5	32.0	8.6	4.7	0.1	35.1	34.1	26.1	21.0	22.3
AC 1933.397	180	175	26.0	20.0	40.0	26.5	34.0	12.0	6.0	4.0	36.5	36.5	26.5	22.0	24.0
MU 1952.9	181	176	24.0	21.0	40.0	24.5	33.0	11.0	4.0	4.0	35.5	34.0	25.0	20.0	22.0
NY 204141	183	178	25.0	20.0	36.0	23.0	30.0	10.5	6.0	5.0	33.3	33.3	25.0	20.0	22.0
EV 3	183	176	28.0	19.0	41.0	25.0	34.5	12.5	5.0	0.1	35.0	38.5	29.0	22.0	24.5
EV 301	185	177	25.0	20.0	42.0	27.0	35.0	13.0	0	6.0	37.0	37.0	29.0	23.0	25.0
EV 1	188	182	25.5	20.0	42.0	27.0	36.0	11.5	7.5	5.0	38.0	37.0	29.0	23.0	25.0
EV 2	188	183	24.0	21.0	37.0	25.0	30.0	11.5	6.0	0.1	37.0	35.5	25.7	20.5	23.0
PA 1979	194	189	26.0	20.0	41.0	26.0	34.5	12.5	6.0	4.5	36.5	36.5	27.5	22.0	25.0
NY 100280	194	189	27.0	21.0	42.0	25.5	34.1	12.0	6.0	0.1	37.5	36.0	28.0	23.0	24.2
NY 135017	200	195	25.0	20.0	42.0	26.0	36.0	9.0	5.0	2.0	37.0	36.5	28.0	23.0	25.2
NY 15675	201	194	26.0	21.0	40.0	25.5	33.0	12.0	7.5	5.0	38.0	38.0	27.5	22.5	24.2
LY 384	203	198	26.0	21.5	40.0	26.0	33.0	11.0	5.0	0	0	37.0	27.0	22.0	24.0
AC 1893.634	212	205	29.0	22.5	48.0	29.0	38.0	14.0	7.0	5.0	41.0	40.0	31.5	25.5	28.0
AC 1875.28	215	209	29.5	24.0	46.0	27.5	37.0	13.0	6.5	4.0	41.5	43.0	31.5	27.0	29.0
BM 87.12.9.1	223	222	32.7	25.0	50.5	34.0	0	0	0	0	47.0	47.2	35.0	0	30.7
BM 81.1338	230	0	35.0	26.3	52.2	32.8	42.1	15.9	0	0	50.0	48.2	36.7	31.8	34.0

Equus africanus – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
<i>africanus</i>															
MU 1963.133	199	191	28.0	23.0	45.5	29.0	38.0	13.0	8.5	0.1	40.0	41.0	29.2	23.5	26.0
BM 4.6.12.1	202	198	29.5	24.0	48.0	30.0	38.0	15.0	9.5	0.1	41.0	40.7	31.5	25.5	28.5
<i>somaliensis</i>															
BA 10858	201	196	27.0	22.0	46.5	27.5	40.0	11.0	8.0	5.0	39.1	38.9	29.0	24.0	26.5
BA 3597	203	197	26.6	0	44.3	29.2	38.0	13.2	0	3.3	40.2	40.0	29.0	23.7	25.1
CH 1428	205	192	29.0	27.0	45.5	29.5	39.0	13.0	8.0	4.0	45.0	43.0	30.0	24.3	27.5
BE 216	210	204	26.5	22.0	46.5	28.0	39.0	11.5	8.5	6.5	40.5	40.0	30.0	25.0	27.0
BL 30253	213	207	26.0	23.0	48.0	28.5	38.0	13.5	7.0	5.5	44.0	41.0	29.0	24.0	26.0

Domestic Donkey – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
AC 1903.335	0	0	0	0	34.0	30.0	30.0	8.5	5.0	0	0	0	0	0
BE 5.11.1952	190	187	21.0	21.0	36.5	31.0	30.0	9.0	2.0	35.0	33.0	25.0	21.0	23.0
FAC. D'ARCHE	204	200	19.0	17.3	32.0	27.5	29.0	7.0	5.5	29.0	29.5	23.0	17.0	20.0
AC 1930.86	207	203	20.0	18.5	32.5	26.0	30.0	10.0	0.5	30.0	31.1	25.0	20.0	21.0
AC 551	207	204	23.0	22.0	38.0	27.5	34.0	8.0	5.0	33.0	35.0	28.0	22.0	26.0
AC 1903.326	207	204	22.0	24.0	35.0	29.0	32.0	9.0	6.0	33.5	32.0	26.0	20.5	22.5
MU 1952.9	213	208	24.0	23.0	40.0	30.0	34.0	10.0	4.0	36.0	33.5	25.5	20.0	23.0
AC 1933.397	214	208	24.0	22.5	39.5	33.0	34.0	10.0	5.0	35.0	35.2	27.5	22.0	24.0
NA 3952	215	211	23.1	21.5	39.5	32.0	34.5	8.0	6.2	34.5	34.7	27.1	20.3	22.3
YA 1622	216	211	23.0	23.0	36.0	30.0	32.0	10.0	5.0	35.0	33.0	26.0	20.0	23.0
EV 302	220	218	23.5	22.0	42.0	35.0	37.0	11.0	4.0	37.0	37.0	30.0	23.0	25.0
EV 1	223	222	23.0	25.0	39.0	33.0	34.0	9.0	4.5	38.0	35.0	27.0	21.0	23.0
NY 100280	228	223	26.0	24.2	41.5	33.2	37.0	9.5	4.0	38.0	35.1	28.0	23.0	24.0
PA 1979	232	229	22.5	23.0	40.0	31.0	37.0	10.3	5.0	35.0	36.0	29.0	23.5	26.0
NY 15675	233	230	24.0	24.0	40.0	33.0	35.0	10.0	8.0	37.0	36.5	29.0	23.0	25.0
LY 384	238	235	23.5	25.0	38.5	32.0	34.0	11.5	2.0	35.5	35.0	27.5	21.5	23.0
NY 135017	239	236	23.0	23.0	40.0	33.0	37.0	10.0	6.0	38.0	36.0	30.0	24.0	26.0
AC 1893.634	246	243	27.0	26.5	45.0	38.0	40.0	10.0	3.0	40.0	39.5	32.0	26.5	28.0
AC 1875.28	255	250	28.0	29.0	44.0	37.0	39.0	9.0	6.0	42.0	44.0	33.0	27.0	30.0
BM 81.1338	265	0	31.8	29.0	48.9	39.5	45.0	15.0	0	50.0	48.7	38.2	31.0	35.0
BM 87.12.9.1	265	261	30.0	26.0	51.5	40.0	45.0	12.0	0	45.3	45.5	35.6	0	31.2

Equus africanus – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
<i>africanus</i>														
MU 1963.133	232	227	27.0	25.5	43.5	37.0	39.0	10.0	5.0	41.0	39.5	30.5	24.0	26.5
BM 4.6.12.1	235	227	29.0	27.5	45.0	36.0	39.5	9.5	5.7	41.5	40.5	32.0	25.0	28.5
<i>somaliensis</i>														
BA 10858	239	233	24.5	24.5	44.0	36.5	39.0	12.0	6.0	40.0	39.5	30.5	24.0	26.5
CH 1428	240	230	28.0	27.0	43.5	36.5	40.0	12.5	5.5	44.0	42.0	32.0	24.5	28.9
BA 3597	241	238	25.5	0	45.0	32.5	39.5	8.7	6.7	39.5	40.9	30.9	24.1	25.5
BE 216	248	243	25.5	25.5	44.0	35.0	36.0	14.0	5.0	39.0	39.0	31.0	25.0	27.0
BL 30253	248	248	26.0	27.0	47.0	37.0	43.0	13.0	7.0	44.0	42.0	30.2	24.0	27.0

Equus hemionus – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
hemippus															
YA 1637	193	185	21.0	17.0	38.0	24.1	31.2	12.5	7.0	1.0	34.7	35.6	27.7	20.5	23.1
AC 65	195	190	21.7	18.0	35.9	23.9	29.8	12.7	0	0.1	35.5	35.3	26.5	21.3	23.6
onager															
KI 1576	196	191	26.5	20.5	43.0	25.5	32.5	12.0	6.5	2.5	38.5	38.0	30.0	25.0	26.5
LD 12507	198	191	23.5	20.0	43.0	27.5	35.0	12.0	9.0	2.5	36.5	38.0	30.0	24.0	25.0
HA 7045	199	193	25.5	22.0	41.0	27.0	32.0	12.5	7.0	0.1	36.0	37.0	30.5	25.0	26.0
YA 5098	205	196	27.0	21.0	40.5	25.5	32.5	12.5	6.1	0	37.5	37.7	29.0	22.2	24.3
AC 1901.9	208	203	23.0	19.5	41.0	25.0	32.0	13.0	7.0	4.5	37.5	37.0	26.5	23.0	25.0
AC 1978.50	210	205	26.5	20.5	42.5	28.0	35.5	11.5	6.0	0.1	40.5	41.5	29.0	23.0	27.0
KI 1662	211	205	26.5	21.5	44.5	29.0	33.0	13.0	8.0	3.0	39.0	38.0	29.0	24.5	26.5
AM 11827	211	206	25.0	19.5	44.0	26.5	34.5	11.0	6.0	3.0	38.5	37.0	29.0	23.0	25.5
NY 35670	216	210	26.0	22.0	44.0	28.0	36.0	13.0	8.0	0.1	37.5	39.0	30.1	25.0	26.5
HA 5881	217	213	27.5	24.0	45.5	29.0	35.0	13.0	0	0	41.3	40.0	30.0	25.0	26.5
HA 7158	218	210	27.5	24.0	45.0	28.5	35.5	14.0	7.0	0.1	41.0	40.0	30.5	25.0	26.0
LY 383	218	214	26.0	20.5	43.0	29.0	35.0	11.0	7.0	2.0	38.0	37.5	29.5	24.0	25.5
AC 1902.487	219	213	26.0	21.0	41.5	28.0	33.0	11.0	6.0	3.0	38.0	38.0	28.5	24.5	26.0
CH 97880	220	210	28.0	21.0	42.0	26.0	35.0	12.0	6.8	0.1	40.0	39.0	29.0	23.0	26.0
AM 17667	220	215	25.3	21.0	46.0	27.0	35.5	12.0	6.0	0.1	40.2	40.0	30.5	25.0	26.5
AC 1893.509	227	221	25.0	20.0	45.0	27.0	36.5	14.0	7.0	5.0	39.5	38.5	29.5	25.0	26.5
khur															
BM 57.7.18.1	199	194	26.0	21.0	43.0	27.5	33.5	13.1	8.0	4.0	37.5	40.0	28.0	23.0	25.6
AC 549	215	209	25.9	21.9	44.1	27.7	34.1	14.0	0	4.6	38.9	39.4	28.3	23.8	26.7
MU 1965.207	217	212	28.0	22.0	45.0	26.5	35.5	13.0	7.0	4.0	39.5	40.0	30.0	25.0	27.0
kulan															
KI 3480	214	209	26.0	21.0	44.0	28.1	34.5	12.0	7.0	3.0	37.5	38.0	29.5	24.5	27.0
BM 1971.2210	215	209	26.0	22.5	46.0	30.0	37.0	12.5	7.0	4.0	39.0	40.0	30.0	25.0	27.3
TBILISSI	220	214	26.2	0	43.0	31.1	0	0	0	0	39.5	41.3	30.0	24.6	0
TBILISSI	226	217	26.8	0	46.8	33.6	0	0	0	0	41.6	39.4	32.4	26.2	0
MU 1962.203	227	221	26.0	23.0	45.0	29.0	38.0	13.0	6.5	2.0	41.0	39.0	33.0	27.0	28.0
LG 19046	229	0	26.4	21.9	0	0	0	0	0	0	0	0	0	0	0
hemionus															
BA 3529	222	216	24.2	0	44.8	28.6	36.4	11.6	0	0.1	39.5	40.1	31.0	25.3	27.5
NY 57209	231	226	29.0	22.5	44.0	31.0	37.5	11.5	7.0	3.0	41.3	42.1	32.3	27.0	29.5
NY 57212	232	225	28.0	25.0	46.0	30.0	39.0	11.0	9.0	3.0	41.0	40.0	32.0	26.0	28.5
NY 57214	234	227	28.0	23.0	45.0	30.0	36.0	14.0	7.0	0.1	41.0	44.0	32.0	26.2	28.2
NY 57201	236	227	28.0	24.0	44.0	30.0	37.0	14.0	8.0	0.1	40.0	40.0	30.0	24.0	27.0
NY 57208	240	234	27.0	24.5	46.0	30.0	38.2	13.5	7.0	3.0	42.0	41.0	33.5	28.0	30.5
kiang															
BL 32172	238	230	28.0	23.5	47.0	30.0	37.5	14.0	7.0	2.0	44.5	42.0	31.0	25.0	27.5
AC 1963.363	240	234	27.0	23.0	47.0	30.0	37.5	14.0	6.0	2.0	42.5	40.5	30.0	26.0	29.0
MU 572	242	235	28.0	24.0	46.0	30.5	38.5	13.0	10.0	0.1	43.0	41.5	31.5	25.5	28.5
AM 985	248	237	28.0	23.0	45.0	30.0	36.0	14.0	8.0	3.5	43.0	41.0	31.0	26.5	29.0
subsp. ?															
AC 1928.2	206	200	25.0	19.0	42.0	25.5	31.0	14.0	5.0	2.0	40.0	37.0	27.0	23.0	24.0
AC 1912.332	207	201	23.0	19.0	40.0	24.0	31.5	13.0	7.0	3.0	38.5	38.0	27.5	24.0	25.5
AC 1905.259	208	201	23.0	20.0	40.0	26.0	32.0	13.0	6.0	3.0	36.5	37.5	27.5	22.5	25.0
AC 1880.1103	209	202	28.0	22.0	44.0	27.0	35.0	13.0	7.0	4.0	40.5	42.0	29.0	24.0	26.5
AC 1909.208	214	208	25.0	21.0	40.0	26.0	32.0	13.0	6.0	4.0	39.0	37.0	28.0	23.0	25.0
AC 548	221	214	25.5	21.0	42.5	26.5	34.0	12.5	7.0	4.0	38.0	39.0	29.0	23.5	26.5
BA 1398	223	217	29.1	0	46.0	27.8	36.0	14.2	0	4.6	43.0	44.2	31.4	26.4	30.1
NY 60345	231	226	27.0	22.3	41.0	28.0	34.0	12.0	7.5	2.5	37.5	37.3	29.5	25.0	27.5

Equus hemionus – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
hemippus														
AC 65	224	222	22.0	20.0	33.5	31.0	30.5	8.1	0	33.5	32.5	27.5	20.7	23.1
YA 1637	225	217	21.0	20.0	35.5	30.0	35.0	8.0	4.5	34.0	35.2	28.0	20.4	23.0
onager														
KI 1576	230	226	24.5	24.0	39.5	34.0	34.0	5.0	5.0	37.5	37.0	30.0	24.0	27.0
LD 12507	231	227	22.2	23.6	39.0	35.0	35.5	8.0	7.5	36.0	36.0	30.0	24.0	25.0
AM 11827	238	235	24.0	23.0	41.0	38.0	0	7.5	0	36.0	36.0	29.0	22.0	24.0
HA 7045	239	233	26.0	25.0	40.5	34.0	35.0	9.5	7.0	35.5	35.5	30.5	23.5	25.5
YA 5098	243	237	26.1	25.2	38.0	32.5	35.0	8.0	6.8	38.3	37.6	30.0	22.6	25.3
KI 1662	245	241	26.0	25.0	38.0	34.0	35.0	0	5.0	38.0	37.0	30.0	24.0	26.0
AC 1978.50	245	242	25.0	27.5	43.0	33.0	36.0	11.0	8.0	40.0	38.5	29.0	23.0	27.0
AM 17667	250	244	25.0	27.0	40.5	40.0	0	0	0	41.0	39.0	31.5	24.0	27.0
AC 1901.9	250	245	23.0	24.0	39.0	35.0	35.0	10.0	7.0	37.0	35.0	27.0	22.0	25.0
NY 35670	251	246	26.0	25.5	41.0	37.0	37.0	9.0	3.0	39.0	39.0	32.0	25.0	28.0
HA 7158	253	249	26.0	26.0	43.0	37.0	37.0	9.0	7.5	41.0	40.0	32.0	25.0	27.0
HA 5881	253	243	26.0	28.0	41.5	39.0	37.5	8.0	4.0	41.3	40.0	31.2	25.0	27.0
LY 383	254	250	25.5	26.0	42.0	34.5	37.0	9.5	7.0	37.0	37.5	29.5	23.0	25.5
AC 1902.487	255	252	25.5	24.5	41.0	34.0	35.0	9.0	8.0	38.0	37.0	30.0	25.0	27.0
CH 97880	258	245	25.9	25.8	39.0	33.0	37.0	9.5	5.7	38.5	38.0	30.0	23.0	27.0
ac 1893.509	268	257	25.0	25.0	43.0	36.0	38.0	10.0	5.0	37.0	36.0	30.0	24.0	26.5
khur														
BM 57.7.18.1	235	230	25.0	24.0	41.5	35.0	37.0	10.0	6.0	37.0	37.7	29.0	23.0	26.0
MU 1965.207	247	242	27.0	26.0	40.0	36.0	36.2	7.0	6.5	39.0	39.0	30.0	24.0	26.5
AC 549	248	244	25.0	24.8	41.2	33.1	38.0	8.9	8.0	38.0	36.7	30.1	23.8	26.2
kulan														
KI 3480	249	244	24.5	25.0	42.0	36.0	36.0	8.0	7.5	38.0	36.5	30.0	25.0	28.0
BM 1971.2210	250	245	24.5	26.0	42.0	39.0	36.0	10.0	7.5	38.5	39.0	31.0	26.0	28.5
TBILISSI	257	251	26.1	0	41.1	34.1	0	0	0	39.6	40.5	30.1	24.2	0
TBILISSI	260	253	25.8	0	40.0	38.5	0	0	0	38.0	38.3	32.2	25.9	0
MU 1962.203	262	257	25.0	26.0	42.0	36.5	36.0	8.5	5.2	38.0	37.0	33.0	26.0	29.0
LG 19046	265	0	25.6	26.0	0	0	0	0	0	38.2	37.4	0	0	0
hemionus														
BA 3529	259	257	22.9	0	41.0	36.3	39.0	8.8	5.7	38.0	36.0	31.0	25.0	27.1
NY 57212	266	260	27.3	26.0	42.0	37.0	38.0	11.0	6.0	39.0	39.0	33.0	26.0	28.5
NY 57209	268	263	28.0	28.0	42.5	37.0	38.0	10.0	5.0	39.0	40.2	32.1	25.5	28.7
NY 57214	271	265	26.0	25.0	42.0	37.2	39.0	10.0	6.0	38.0	40.0	31.0	25.0	28.0
LG 14741	272	0	26.9	25.1	0	0	0	0	0	39.4	41.5	0	0	0
NY 57201	276	269	26.5	26.0	40.0	36.5	36.5	9.0	7.0	37.0	39.0	30.0	24.0	26.5
NY 57208	277	271	27.0	26.5	45.0	37.0	40.0	11.0	6.0	40.0	40.0	34.0	27.0	30.0
kiang														
AC 1963.363	272	267	26.5	28.0	43.5	41.0	39.0	10.0	3.0	42.0	40.0	32.0	26.5	28.5
BL 32172	277	272	27.0	27.0	43.0	39.0	39.0	11.0	4.5	44.0	41.0	32.0	25.5	28.5
MU 572	283	276	26.5	27.0	46.0	40.0	40.5	11.0	7.5	42.0	41.0	33.0	26.0	29.0
AM 985	285	283	26.5	27.0	44.0	41.5	40.0	10.0	7.5	42.0	40.0	32.5	26.5	29.5
subsp. ?														
AC 1928.2	242	237	24.0	26.0	37.0	35.5	34.0	9.0	6.0	39.0	36.0	29.0	23.0	24.5
AC1880.1103	243	237	27.0	27.0	43.0	36.0	39.0	9.0	6.0	40.0	40.0	30.0	24.0	26.5
AC 1905.259	244	241	24.0	25.0	37.0	33.0	33.0	8.0	6.5	35.5	35.5	28.5	22.5	25.0
AC 1912.332	245	241	24.0	25.0	36.0	34.0	34.0	10.0	7.0	37.0	36.5	29.5	24.0	26.5
AC 1909.208	250	243	25.5	27.0	39.0	35.0	35.0	9.5	7.0	39.0	36.0	28.5	23.0	26.0
BA 1398	257	255	29.0	28.0	43.5	37.5	37.0	11.0	3.9	43.5	40.5	32.2	26.3	29.1
AC 548	257	251	26.0	25.0	41.0	35.0	36.5	10.5	6.0	36.5	37.5	30.2	23.5	26.5
NY 60345	272	265	27.0	25.5	40.5	36.0	36.0	8.0	7.0	37.5	38.0	31.5	25.0	27.5

Hybrids – MC

museum-no.	1	2	3	4	5	6	7	8	8'	9	10	11	12	13	14
mules															
MU 1970.5	216	211	30.9	22.5	48.1	30.0	39.5	15.1	9.5	4.5	43.0	44.2	33.0	26.8	29.2
NY 14116	235	227	35.0	27.0	55.0	33.0	46.0	15.0	9.0	7.0	49.0	49.0	38.0	30.0	33.0
AC 543	254	245	39.0	28.0	54.5	35.5	45.0	16.5	8.5	6.0	53.0	54.0	40.0	31.0	35.5
NY 204211	259	251	37.0	29.5	55.5	34.0	47.0	15.0	9.0	7.0	56.0	52.0	39.5	31.5	35.0
AA 98766	260	251	33.0	26.5	53.5	35.0	46.0	12.5	7.0	6.0	50.0	50.0	37.0	29.0	31.5
AA 1534	270	262	40.5	32.0	60.5	39.0	49.0	18.0	10.0	7.0	55.2	55.4	46.0	36.0	40.0
hinnies															
NY 204139	193	187	27.0	20.0	38.0	24.5	33.0	11.0	7.0	0.1	36.5	37.0	28.5	23.0	25.0
NY 75334	212	206	28.5	22.0	42.0	26.0	34.0	10.0	7.0	4.0	40.0	42.0	30.5	24.5	27.0
others															
AC 1906.59	212	206	28.2	22.0	40.0	26.0	33.9	13.0	7.0	5.8	39.1	42.6	31.0	25.0	26.5
AC 1870.251	218	210	28.3	24.0	42.5	27.5	34.5	12.5	6.5	5.0	41.0	40.0	30.0	25.0	26.4

AC 1906.59 : horse x hemione

AC 1870.251 : donkey x hemione

Hybrids – MT

museum-no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14
mules														
MU 1970.5	262	256	26.5	27.0	45.0	38.0	43.0	15.0	8.3	44.3	44.2	33.4	26.0	29.5
NY 14116	275	267	34.0	30.0	51.0	40.0	47.0	11.0	7.0	49.0	49.0	38.0	30.0	34.0
NY 204211	299	294	36.0	33.5	56.0	46.0	52.0	12.5	7.0	55.0	51.8	40.0	31.5	36.8
AC 543	300	289	36.0	34.5	54.0	43.0	47.5	11.5	6.0	55.0	53.0	41.0	31.0	36.5
AA 98766	301	294	31.5	32.0	52.0	43.0	47.0	11.0	5.1	52.0	50.0	38.0	28.2	32.6
AA 1534	311	304	39.0	38.0	59.0	48.5	53.0	14.5	7.0	59.0	56.5	45.0	35.5	41.0
hinnies														
NY 204139	230	226	25.5	23.0	40.0	33.0	35.0	9.0	6.5	36.0	37.5	29.0	24.5	27.0
NY 75334	255	249	26.0	26.0	41.0	35.5	36.0	10.0	6.0	41.0	40.0	32.0	25.0	27.0
others														
AC 1906.59	250	245	27.0	26.5	41.0	33.0	35.0	11.0	7.7	41.0	41.0	31.0	24.0	26.0
AC 1870.251	255	251	26.5	29.5	40.0	35.0	36.5	10.0	6.0	42.0	39.0	31.5	24.5	27.0

AC 1906.59 : horse x hemione

AC 1870.251 : donkey x hemione