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Comparative Osteology of Modern and Fossil Horses, Half-asses, and Asses

Contents

- | | |
|---|--|
| 1. Summary | 4. Teeth |
| 2. Introduction | 4.1. Upper cheekteeth |
| 3. Skulls | 4.2. Lower cheekteeth |
| 3.1. Horses | 4.3. Lower incisors |
| 3.2. Half-asses | 5. Post-cranial Skeleton |
| 3.3. Asses | 5.1. Metapodials |
| 3.4. Mules and hinnies | 5.2. General proportions |
| 3.5. Summary for ratio diagrams of skull material | 5.3. Relative lengths of the limb segments |
| 3.6. Number of supra-orbital foramina | 6. Conclusion |
| | 7. Acknowledgements |
| | 8. Literature |
| | 9. Appendix: Measurement System |

1. Summary

This paper is an illustrated summary of comparative osteology and odontology in recent *Equus* with particular stress on the discrimination of skulls, teeth, metapodials, and skeletal proportions for the subgenera *Equus*, *Hemionus*, *Asinus* and for some hybrids and fossils.

2. Introduction

Although a number of recent publications deal with the anatomy and systematics of Quaternary equids (e.g., AZZAROLI 1979, BENNETT 1980, CHURCHER/RICHARDSON 1978, EISENMANN 1976–1982, GROVES/WILLOUGHBY 1981), the Tübingen symposium (May 1982) made it quite clear that much more work is needed to improve our knowledge of their recent history and to answer such questions as: What species of *Equus* was (or were) domesticated? When? Where? Obviously, no progress in the understanding of the geographical and chronological distributions of domesticated and wild forms can be expected if we are not able to discriminate the osteological remains of the different species, varieties, and hybrids of *Equus*.

The purpose of the present paper is to summarize ten years of my own studies on the comparative osteology and odontology of modern equids with particular stress on the discrimination

of those species which are more likely to be found in the Middle East, namely horses, half-asses, and asses. Skulls, teeth, metapodials, and skeletal proportions will be discussed successively. Most of the data have already been published at length elsewhere. I hope, however, that a relatively short paper centered on this special problem may still be useful.

The present paper also gives me an opportunity to comment on methodology. Although more and more frequently applied in the natural sciences, morphometric methods are still looked upon with reluctance by some scholars who view them in opposition to more traditional approaches (e.g., AZZAROLI 1982: 75). In my opinion, there is no opposition nor mutual exclusion between different ways of dealing with material. Verbal descriptions, photographs, drawings, contingency tables, and measurements are equally useful as means to record information during study, to communicate the acquired experience to others, and to document the conclusions reached. Actually, the problem is not to choose, for some philosophical reason, between two opposite approaches but to strike a balance between all possible techniques according to which are more practical or convenient to use under a given set of circumstances.

Today, no one questions the fact that taxonomic distinctions or descriptions are more reliable when based on relatively large samples. In the case of equids, large samples cannot be brought together at the same time and in the same place; the information must be stored until it can be used. Notes, photographs, and sketches help to document observed morphologies, but, obviously, each specimen cannot be described in detail, photographed, and drawn. Each specimen can, however, be measured and the measurements stored in the same way as photographs or drawings.

The very term "morphometry" implies that measurements are expected to express morphology. If properly chosen, they do so indeed, and there is no contradiction between noting that a skull is deep and recording its height in millimeters. Naturally, there are characters which are more easily expressed by means other than measurement, e.g., presence or absence of a structure and occurrence of a particular pattern. Even these data, however, tolerate numerical treatment for, in addition to noting that a character is "occasionally" present, there is no harm in estimating the actual frequency of occurrence.

At the next stage of the study, when a large quantity of information has to be reviewed and summarized, numerical data are convenient because they can be easily analyzed by computer. The human mind cannot be expected to assimilate verbal descriptions or photographs of 350 skulls, whereas a computer is physically capable of synthesizing the information provided by 10,000 measurements. Multivariate analyses may simply confirm classical views, but they may also corroborate or make more specific mere impressions and bring to light unnoticed facts. They can help to eliminate useless variables and help to identify the more valuable ones. They can clearly express degrees of morphological closeness.

When the acquired experience must be communicated to other scholars, numerical data are also very practical. In particular, there is no other way to express ranges of variation. A numerical approach also permits us to provide simple guides to identification (e.g., ratio diagrams) allowing even inexperienced investigators to make correct determinations. When it comes to drawing conclusions, numerical data constitute a notably less plastic material than do pure observations of shapes, and they thus keep speculation within the bounds of a more rigid framework.

Let us consider the case of *Equus* metacarpals. Obviously, I could never have remembered the exact proportions of 400 modern and fossil bones observed on widely separated occasions over a span of ten years. Apart from some very striking characters, not much would have remained in my memory and certainly not enough to attempt interspecific determinations.

Such discriminations proved possible, however, when the measurements were subjected to multivariate analyses. Moreover, the published numerical data and ratio diagrams may help those with not so much experience with metapodials to compare and even identify his or her own collection of bones. Would this have been possible if the bones had merely been verbally described and just a few of them drawn?

There is no magic "truth" intrinsic to measurements, but they can and do help in practice.

3. Skulls

Five hundred skulls of modern *Equus* were observed and measured, but only 350 crania were complete enough to be subjected to various multivariate analyses under the direction of Professor BENZECRI (University of Paris VI). Mandibles proved to be less interesting and will not be discussed here. For each cranium, 10 qualitative characters were noted and 33 measurements taken. The system of measurements, inspired by GROMOVA (1959), is illustrated in Figures 1-5. Equivalences with the system of VON DEN DRIESCH (1976) are given in Table 1. Some of the qualitative characters are best illustrated in EISENMANN/DE GIULI (1974). All measure-

S K U L L								MANDIBLE	
V.E.	A.V.D.	V.E.	A.V.D.	V.E.	A.V.D.	V.E.	A.V.D.	V.E.	A.V.D.
1	3a	9	-	17	45*	25	-	1'	2
2	18a	10	-	17 bis	-	26	-	2'	-
3	-	10 bis	-	18	1	27	-	3'	15
4	5	11	43	19	-	28	-	4'	8a
5	-	12	4	20	-	29	36	4'bis	7a
6	21	13	41	21	31	30	34	5'	6a
7	24a	14	-	22	32	-	-	6'	-
7 bis	23a	15	38	23	15	-	-	7'	16*
8	22a	16	-	24	-	-	-	8'	20

Table 1 Equivalences between the skull and mandible measurements used here (V.E.) and those proposed by ANGELA VON DEN DRIESCH (A.V.D.). The numbers of the measurements refer to dimensions illustrated in Figures 1-5 for V.E. (this paper) and to pages 19-20 and 53-54 for A.V.D. (VON DEN DRIESCH 1976). Note that VON DEN DRIESCH measures the greatest breadth of the muzzle across the outer borders of the alveoli instead of across the posterior borders. As a result, her measurements will be 50 to 100 mm larger than mine. VON DEN DRIESCH also uses many other measurements (1976: 19-22, 53-54) which are not noted here.

ments and characters were submitted to various multivariate analyses (EISENMANN/TURLOT 1978, EISENMANN 1980), but only the principal results will be summarized here.

On the first plane of the correspondence analysis (Figure 6) appear six clusters corresponding to:

- Horses: *E.caballus* and *E.przewalskii*;
- Half-asses: *E.hemionus* and *E.kiang*;
- Asses: *E.asinus* and *E.africanus*;
- Mountain zebras: *E.zebra*;
- Grevy zebras: *E.grevyi*;
- Quaggas: *E.burchelli* and *E.quagga*.

Their discrimination is correct in more than 90 percent of the cases. When in later analyses, the number of variables was reduced to 10, the members of the six groups remained correctly discriminated in more than 85 percent of the cases (Figure 7). The 10 variables include: palatal length (measure L2), palate-basion distance (L3 + L4), frontal breadth (T13), supraoccipital breadth (T16), greatest and least muzzle breadths (T17 and T17 bis), height of the auditory meatus (O20), length of the anterior ocular line (L23), and facial and cranial heights (H25 and H28).

Different multivariate analyses demonstrated the outstanding diagnostic and descriptive value of 14 cranial measurements (not 7 as stated by AZZAROLI 1982: 75). These include: palatal length (measure L2—not tooth row as misunderstood by AZZAROLI 1982: 75), palate-hormion (L3) and hormion-basion (L4) distances, muzzle length (L5), choanal length (L9), choanal breadth (T10 bis), frontal breadth (T13), supra-occipital breadth (T16), greatest and least muzzle breadths (T17 and T17 bis), height of the auditory meatus (O20), length of the anterior ocular line (L23), facial height (H25) and cranial height (H28).

These 14 measurements are, therefore, used in the ratio diagrams (following SIMPSON 1941) which compare crania of modern and fossil *Equus*. In the present paper, the means of the measurements of 16 onagers were chosen as the standard, with the result that all forms discussed are described in relation to *E.hemionus onager*. The ratio diagrams were formed in the following fashion: values or averages of each measurement (e.g., palatal length, muzzle breadth, etc.) were converted to logarithms (base 10). Differences between the logs of the standard (*E.hemionus onager*—Table 2) and the logs of the other form were calculated and plotted on the diagram. The standard values (onager) correspond to the zero-line (i.e., differences equal to zero), and each larger value was plotted above and each smaller value was plotted below this zero-line.

Ratio diagrams are particularly useful because they can express differences in size and in proportions at the same time. For example, if two crania are similar in their proportions, their curves will be parallel, the distance between the curves depending upon the relative sizes of the crania. This property of ratio diagrams is particularly valuable because similarities in proportions can be difficult to assess if size is different. In addition, comparison is restricted to the more significant features. Finally, ratio diagrams can be used to compare incomplete specimens (particularly fossils) on which multivariate analysis cannot be carried out because of the absence of some measuring points.

Measures	n	\bar{x}	Log \bar{x}	min	max	s	v
16	15	57	1.755	47	66	4.70	8.25
23	16	344.8	2.537	325	365	14.73	4.27
3	16	118.6	2.074	107	133	8.50	7.16
4	16	102.3	2.010	94.5	114	5.85	5.71
2	16	217	2.336	195	237	12.51	5.76
5	16	105.2	2.022	92	120	8.70	8.27
17	15	55.6	1.745	48	66.5	5.10	9.17
17 bis	16	41	1.613	33	47.5	3.84	9.37
13	16	197.7	2.296	187	217	8.35	4.22
10 bis	16	39.3	1.595	32.5	45	3.38	8.60
25	16	101.5	2.006	93	118	6.31	6.21
28	15	87.9	1.944	80	98	4.95	5.62
9	16	63.1	1.800	58	70	3.38	5.36
20	16	14.1	1.151	13	16	0.86	6.11

Table 2 Cranial measurements of *E.hemionus onager*, the Persian half-ass, in mm. The numbers of the measurements refer to dimensions illustrated in Figures 1–5; n = number of specimens; \bar{x} = mean; log \bar{x} = logarithm (base 10) of the mean; min = minimum observed value; max = maximum observed value; s = standard deviation; v = $100s/\bar{x}$ = coefficient of variation.

3.1. Horses (Figures 8–11)

The first ratio diagram (Figure 8) compares the means of 25 *E.przewalskii* and 2 Arabian *E.caballus* crania to each other and to the standard *E.hemionus onager*. It is clear that the muzzle is longer (measure 5) and narrower (measures 17 and 17bis) in the Arabian than in the Przewalski horses. The supra-occipital crest is also narrower (measure 16) and the cranium higher (measure 28). Otherwise the two forms are similar.

The same figure shows how these horses differ from onagers. Horses are larger and have shorter distances between palate and vomer (measure 3), relatively narrow muzzles (measures 17 and 17 bis), and lower faces (measure 25).

On the next ratio diagram (Figure 9) are plotted one Canadian and one Siberian fossil crania and the means for 5 modern ponies. The fossil *E.lambeii* was described from the Yukon Territory by HAY (1917). SAVAGE (1951), GROVES (1974), and EISENMANN (1979, 1980) recognized the type cranium as belonging to a caballine form but QUINN (1957) followed by HARRINGTON/CLULOW (1973) (see also LAZAREV 1980) referred the same specimen to the genus *Onager* or to the subgenus *Asinus*. The ratio diagrams (Figures 8 and 9) show the following:

- the close similarities in size and proportions between the type specimen of *E.lambeii* and a cranium collected in Siberia (Kotelny Island) and described by PAVLOVA (1906);
- the close similarities in proportions between the Canadian and Siberian crania and those of modern ponies;
- the similarities between these three forms and the previously considered Przewalski and Arabian horses. Differences, however, do exist, particularly in length of muzzle (measure 5). (See also EISENMANN/CRÉGUT-BONNOURE/MOIGNE, in press.)

These facts lead us to treat the form *lambei* as a subspecies of *E.caballus* and to refer the Kotelny specimen also to this subspecies. The new cranium (LUM 1.222) published by HARRINGTON/CLULOW (1973) is larger but has the same proportions as the type specimen.

The ratio diagram for the modern heavy horse (mean of 7 specimens) is compared to that for *E.mosbachensis* in Figure 10. The fossil material is damaged and incomplete, but the known proportions are close to those of large modern *E.caballus*. Both forms have relative long (measure 5) and broad (measure 17 bis) muzzles. From the other horses (Figures 8 and 9) they both differ with respect to their narrow choanae (measure 10 bis) and their high faces (measure 25).

In Figure 11, modern ponies are compared to Würmian *E.caballus* cf. *germanicus* from Grenelle (PRAT 1968) and *E.caballus* cf. *gallicus* from Jaurens (MOURER-CHAUVIRÉ 1980) and Schussenried (VON REICHENAU 1915). Although the fossils are much larger, their proportions are not unlike those of the modern ponies, the main differences being in their narrower faces (measure 13) and choanae (measure 10 bis).

Thus, the comparative study of 4 modern and 6 fossil caballine forms shows five principal cranial morphologies defined by the shape of the muzzle and of the choanae. Wide choanae are associated with a short muzzle in modern ponies and *E.lambeii*, with an average muzzle in *E.przewalskii*, and with a long muzzle in Arabian horses. Narrow choanae are associated with a short muzzle in *E.caballus* cf. *germanicus* and cf. *gallicus* and with a long muzzle in modern heavy horses and *E.mosbachensis*.

Taking into consideration ALLEN's law, short muzzles may be an adaptation to cold conditions such as those found in the northern islands from whence came the ponies. Cold conditions may also have existed at the time when *E.lambeii* lived in Canada and Siberia and when *E.caballus* cf. *germanicus* and especially *E.caballus* cf. *gallicus* lived in Europe. On the other hand, the medium to long muzzles of Przewalski and Arabian horses would correspond to warmer climates. If this interpretation is correct, the long-muzzled *E.mosbachensis* lived under rather warm conditions. Concerning the significance of choanal width, no interpretation can presently be given.

3.2. Half-asses (Figures 12–13)

Figure 12 compares crania referred to *E.kiang* (24 specimens) and those of two forms of *E.hemionus*: the Persian (16 specimens) and the Mongolian (12 specimens). The zero-line represents the mean of measurements of the Persian *E.hemionus onager* and the vertical bars indicate the range of variation of this form. The kiangs and Mongolian hemiones seem to have very similar crania. Both are slightly larger than the onagers; their supra-occipital crests (measure 16) are relatively narrower, the distance from palate to vomer (measure 3) and the choanae (measure 9) are shorter, and their auditory meati (measure 20) are relatively smaller.

In Figure 13, *E.hemionus onager* is compared with the subspecies *hemippus*, *khur*, and *kulan*. Apart from their small size, short muzzle, and small auditory meatus, the extinct *E.hemionus hemippus* of Syria (3 specimens only!) did not differ very much from Turkmenian kulans and Indian khurs. Differences seem to be greater between onagers and other forms.

Thus, according to the cranial morphology of the studied samples, there are 3 groups of half-asses, namely: 1) kiangs and Mongolian hemiones which are usually considered as belonging to the different species *kiang* and *hemionus* (GROVES/MAZÁK 1967); 2) the extinct Syrian *E.hemionus hemippus*, Turkmenian *E.hemionus kulan*, and Indian *E.hemionus khur*; and 3) the Iranian *E.hemionus onager*. Caryotypes are still unknown for most of these forms, but it may be noted that they differ slightly between groups 2 and 3 with $2n = 56$ for *E.hemionus onager* (HSU/BENIRSCHKE 1971) and $2n = 55$ or 54 for *E.hemionus kulan* (RYDER 1978). More anatomical and cytogenetic studies are needed to understand the grouping of the half-asses.

3.3. Asses (Figure 14)

In most osteological collections, it is by no means clear which skulls belonged to wild, which to feral, and which to domestic asses. After excluding specimens of uncertain affinity, only 10 Nubian and 10 Somalian wild asses are left in my sample. Figure 14 shows that domestic forms seem slightly closer to the Nubian than to the Somalian form. Here again, better material would be useful, but it is still clear that asses form a more homogeneous group than do the horses and the half-asses.

3.4. Mules and hinnies (Figure 15)

Samples are small, particularly for hinnies. Moreover, some of the crania referred to mules may have come from hinnies and vice-versa. For both hybrids, the ratio diagrams are very similar except for the size which is larger in mules. It appears, also, that hinnies have relatively lower faces (measure 25) and shorter choanae (measure 9).

3.5. Summary for ratio diagrams of skull material

Horses are best characterized by the position of the hornion, the vomer being short. Other good characters are the shape of the muzzle (measure 17 being much larger than measure 17 bis) and the small size of the auditory meatus (measure 20).

Asses have broad supra-occipital crests (measure 16), orbits which are placed more anteriorly (measure 23), long vomers, large auditory meati (measure 20), and muzzles enlarged in the middle (measure 17bis).

Half-asses have high faces (measure 25) and long vomers, the longest being those of the onager.

Mules and hinnies look more like horses than like asses, but they have longer vomers and muzzles which are enlarged in the middle.

3.6. Number of supra-orbital foramina

Following MOTOHASHI (1930: 32), a number of authors have remarked that half-asses usually have several supra-orbital foramina while there is only one on each side in most horses and asses. Judging from what I have seen, these observations are correct, but the numbers of exceptions are greater than stated by BÖKÖNYI (1972: 14). In addition, the usual number of foramina is different in different half-asses (Table 3). The three specimens of *E.hemionus hemippus* which I have seen have a single foramen on each side just as in most asses and horses. In kiangs and Mongolian hemiones, both sides usually bear several foramina. In other hemiones, both patterns are equally frequent. Here again, the half-ass group appears less homogeneous than do the asses and horses.

	K	HM	H	HS	AS	AF	C	P
One foramen on both sides	4	-	13	3	19	11	19	7
One foramen on one side	4	5	4	-	-	2	1	2
Several foramens on both sides	14	6	12	-	-	-	2	2
Total	22	11	29	3	19	13	22	11

Table 3 Frequency of single or multiple supraorbital foramina. AF = *E.africanus*, AS = *E.asinus*, C = *E.caballus*, HM = Mongolian *E.hemionus*, HS = Syrian *E.hemionus hemippus*, H = other *E.hemionus*, K = *E.kiang*, P = *E.przewalskii*.

4. Teeth

4.1. Upper cheekteeth

I have tried to discriminate upper cheekteeth by using both measurements and qualitative observations. Measurements include occlusal length (OL) and breadth for each tooth and occlusal length of the protocone (PL). The protocone index ($PL \times 100/OL$) was also calculated for each tooth. Morphological observations include the numbers of folds in the fossettes, the frequency of isolated hypoglyphs and of open post-fossettes on the upper third molar, and the frequency of upper deciduous first premolars.

The diagram of mean occlusal length for wild horses, half-asses, and wild and domestic asses (Figure 16) shows that the wild species cannot be discriminated on the basis of tooth size, nearly all means falling within the range of variation for *E.kiang*. Protocone length (Figure 17) seems to be a better character with which to differentiate these species. The absolute length is greater in horses and less in asses. In the case of the average relative length of protocone in the fourth premolar and first molar, the protocone of the latter is relatively shorter in asses and half-asses than in horses. This same character is better expressed using the protocone index (Figure 18). The mean of this index is higher for the first molar than for the fourth premolar in horses and about equal or smaller in asses and half-asses. The variation is so great, however, that almost all mean protocone indices for wild species fall within the range of variation for *E.kiang*. Therefore, it should be stressed that, because of the amount of individual intraspecific variation, the reliability of any set of observations depends upon the sample. For example, the protocone index is not always smaller in the first molar of asses and larger in horses but only more frequently so (70% and 80% of the cases, respectively).

Most of the qualitative characters studied (Figure 19) may help to discriminate the upper cheekteeth of wild asses from those of half-asses and wild horses, but they are not always of value in separating the latter two groups. In *E.africanus*, the average number of folds in the third and fourth premolars is greater, while the frequency of isolated hypoglyphs in the third molar is higher and that of open post-fossettes is lower. There is no significant difference in the frequencies of wolf teeth among the adults of all the species reviewed.

4.2. Lower cheekteeth

Lower cheekteeth were also studied using measurements and qualitative observations. Measurements included occlusal length and breadth and postflexid length. The diagram of occlusal lengths (Figure 20) shows that nearly all of the mean values fall within the range of variation for *E.kiang*. Wild species, therefore, cannot very successfully be differentiated on the basis of tooth size alone. The length of the postflexid is partly dependent upon the depth of the ectoflexid (vestibular groove). Four morphological states can be observed: 1) the ectoflexid does not penetrate the stem of the double knot with the result that the postflexid is long (Figure 21); 2) the ectoflexid is deeper and reaches the end of the preflexid but remains distant from the end of the postflexid (Figure 22); 3) the ectoflexid penetrates the stem of the double knot (Figure 23) and it may even come 4) into contact with the linguaflexid causing it to become flattened (Figure 24) or pushing it lingually. The frequencies of short ectoflexids (state 1) on each tooth of the cheektooth row were calculated for each species of *Equus*. Ectoflexids are usually short in premolars while on molars they may be long as in *E.grevyi* or short as they

usually are in *E.asinus* (Figure 27). The other species are intermediate in their frequencies, but it is clearly possible in Figure 27 to discriminate wild horses from asses and half-asses, at least on the basis of the second and third molars.

Another important character for discrimination is the shape of the double knot. There are three basic morphologies which can be called “caballine”, “hemione”, and “asinine”. In the caballine type, the linguaflexid is “U”-shaped with angles where the sides of the “U” join the base (Figure 25). In the hemione type, the linguaflexid is shallow and smooth (Figure 26). In the asinine (or stenorine or zebnine) type, the linguaflexid is deep and pointed—“V”-shaped (Figure 21). When the ectoflexid is very deep, however, it may conceal the original asinine pattern by causing the linguaflexid to become flattened (Figure 24), but this result is quite different from the caballine “U” pattern (Figure 25) and must not be confused with it. Some American equids exhibit a hemione pattern with the metaconid having a constriction in its middle, but I have not seen enough material to be sure that this is really a fourth type of double knot morphology. Unfortunately for the use of these characters for the discrimination of different species of *Equus*, the shape of the double knot can be employed only on moderately worn third and fourth premolars and first and second molars. Furthermore, while only asses seem to always have the asinine pattern, horses may have caballine or hemione-like teeth and half-asses may have hemione or asinine-like patterns.

The protostylid frequently present on the deciduous and permanent second premolars of some zebras (principally Grevy zebras) is an interesting character but not very helpful when dealing with asses, half-asses, and horses in which it is rare or lacking.

4.3. Lower incisors

Cups are usually present on the lower incisors of modern equids. Their frequency depends on place in mandible (i. e., first, second, or third incisor), on their state of wear, and on what species is represented. The influence of these three factors is summarized in Figure 28. There one can see that hemiones (kiangs included) have the best developed cups with nearly 100 percent of cups being closed in slightly and moderately worn first and second incisors and 50 percent being closed in third incisors. Closed cups are more frequent in first and second incisors in asses than they are in horses but more frequent in third incisors in horses than in asses. In most cases, however, presence or absence of a closed cup on an incisor can not be used as a basis for discrimination between species.

5. Post-cranial Skeleton

5.1. Metapodials

The system of measurements used for metapodials is illustrated in EISENMANN/BECKOUCHE (this volume). Multivariate analyses have been carried out using 14 measurements from 400 modern and 400 fossil metapodials.

The first projection plane of the correspondence analysis for the metacarpal (Figure 29) shows that the main discriminating factor is slenderness. Long (MC 1) metacarpals of half-asses

(H + K) can be opposed to wide (MC 3) metacarpals of mountain zebras (Z). The metacarpals of asses (AD + A) and Grevy zebras (G), although differing in size, are similar in proportions. Metacarpals from Burchell zebras and quaggas (B + Q) are intermediate between horses (P + C) and mountain zebras (Z) and overlap with both. The metacarpals of horses, half-asses, and asses are well separated.

The situation for the metatarsals is not so clear (Figure 30). Asses and horses overlap. Slenderness remains the most important discriminating factor between half-asses and mountain zebras with the former having long (MT 1, MT 2) metatarsals and the latter wide distal ends (MT 10, MT 11).

Multivariate analyses here give an idea of the possibilities for discrimination between the different forms and a broad indication of similarities in shape. Slenderness, however, overshadows the other factors. As was also true for skulls, ratio diagrams are more convenient for the detailed study and comparison of individual specimens. Such ratio diagrams are presented and discussed in EISENMANN/BECKOUCHE (this volume).

To summarize, metacarpals are more diagnostic than metatarsals. Third metacarpals are characterized by:

- large distal articular breadths in horses, hinnies, and the hybrid of *E.hemionus* × *E.caballus*;
- slenderness in hemiones and particularly *E.hemionus hemippus*;
- the development of the facette for the Os carpale III (magnum) in asses and mules;
- large proximal depth (anterior-posterior diameter) in *E.hydruntinus*;
- large distal supra-articular breadth in the hybrid of *E.hemionus* × *E.asinus*.

Third metatarsals are characterized by:

- slenderness in hemiones (particularly *E.hemionus hemippus*), asses, and hinnies;
- small proximal dimensions in *E.hydruntinus* and the hybrid of *E.hemionus* × *E.caballus*;
- differing principally (sometimes only) in distal proportions in asses and horses.

5.2. General proportions

An average of 8 and a minimum of 6 measurements were taken on each limb bone excluding the scapula and pelvis. The system of measurements used is presented as an Appendix to this paper. Complete skeletons for only 135 individuals were found, so we also ran analyses on parts of skeletons. Three correspondence analyses were run: the first with astragali, calcanea, and phalanges from 149 individuals; the second with the other limb bones from 185 equids; and the third with all the limb bones from the 135 complete skeletons.

The first projection plane from the first analysis (Figure 31) shows relatively good discrimination occurring between modern species of *Equus*. Asses are characterized by their long first phalanges, half-asses by the length of the *trigonum phalangis* of the first phalanges, Przewalski horses by their huge third phalanges, Burchell zebras by wide first phalanges, and mountain zebras by their relatively large calcanea and astragali. Grevy zebras have nothing in particular to distinguish them from an "average" equid except perhaps the width of the second phalanx.

The first plane of the second analysis is shown in Figure 32. With the exception of Grevy and Burchell zebras, discrimination is good. Asses, half-asses, and Przewalski horses have long bones, Burchell zebras have wide bones. Przewalski horses have large distal ends of metapodi-

als, while mountain zebras have a long digital fossa on their tibiae (corresponding to the middle ligament of the patella) and large femora (especially the proximal end). The second plane of the same analysis (Figure 33) permits isolation of Grevy zebras because of their wide proximal humeri and large femoral diameters, these being opposed to Przewalski horses with wide and deep metapodials.

The final analysis using all the limb bones (although with a smaller sample) presents a general picture of skeletal proportions and of resemblances between species. Excepting Grevy zebra, the circular arrangement of the different species on the first plane (Figure 34) is not unlike the one proposed by BOURDELLE (1944: Figure 13) and is similar to the arrangement we found using skulls (Figure 6).

5.3 Relative lengths of the limb segments

Another correspondence analysis was performed using maximal lengths of the bones coming from 130 skeletons (KARCHOUD 1981). This analysis showed that very close relations exist between the anterior and posterior elements of homologous segments, i.e., humerus-femur, radius-tibia, etc. Further analyses of the corresponding ratios revealed specific patterns (Figure 35). Roughly, Burchell and mountain zebra are characterized by long femora, tibiae, and third metacarpals in opposition to asses, half-asses, Przewalski horses, and Grevy zebras with their long humeri, radii, and third metatarsals. Grevy zebras, horses, asses, and half-asses, however, do not separate out at that stage. A more detailed analysis focused on members of this last group (75 individuals) shows a dichotomy between, on the one side, asses and half-asses, and on the other side, Grevy zebras and Przewalski horses with half-asses being opposed to Grevy zebras and asses to Przewalski horses. Half-asses and asses are characterized by the lengths of the metapodials, first phalanges, tibiae, and radii; Grevy zebras by the lengths of the scapulae humeri, and femora; Przewalski horses by the lengths of the second and especially third phalanges. These rather global views provided by multivariate studies must all be broken down into more detail using, for example, ratio diagrams (EISENMANN 1984, EISENMANN/GUÉRIN 1984).

6. Conclusion

Here is not the place to discuss at length the taxonomy of the genus *Equus*, but I will, nevertheless, rapidly sketch it before concentrating on horses, half-asses, and asses. Based on my studies, I believe modern species can easily be classed into six subgenera: *Equus*, Linné; *Hemionus*, Stehlin & Graziosi; *Asinus*, Gray; *Hippotigris*, Hamilton Smith; *Quagga*, Shortridge; and *Dolichohippus*, Heller. This classification was first proposed by WILLOUGHBY (1974) although using somewhat different names. There is nearly general agreement on the first three subgenera (AZZAROLI 1979, GROVES/WILLOUGHBY 1981), precisely those we are dealing with presently, and there seems to be really no point in questioning that part of the taxonomy. There is, however, still room for different views at the specific or subspecific level, a situation to be expected given the complexity and scope of the problem.

The subgenus *Equus* includes two kinds of horses, the wild and the domestic. They are usually considered as being two distinct species (*E.przewalskii* and *E.caballus*) although their hybrids

are fertile and their karyotypes and proteins nearly identical. This problem of nomenclature leads to awkward questions. Should fossil wild horses which resemble modern races of domestic horses be considered as subspecies of *E. caballus* or as independent species? What if a modern race resembles *E. przewalskii*? There seems to be no satisfactory solution to this problem for the time being, and the present nomenclature will probably have to be reconsidered. In any case, skulls belonging to the subgenus *Equus* are all very similar, seeming to differ mostly in breadth of choanae and length of muzzle. With its short muzzle and broad choanae, the Canadian and Siberian fossil *E. caballus lambei* looks like a big modern European pony. At the opposite extreme, *E. mosbachensis* and the modern heavy horse have in common narrow choanae and long muzzles. Other combinations are found in the *germanicus-gallicus* group and in Przewalski and Arabian horses.

The morphology of teeth is much more variable than that of the skulls. Long protocones are not characteristic only of the subgenus *Equus* since they also are found in half-asses and in North American fossils of uncertain affinity. Lower cheekteeth may display deeper or less deep vestibular grooves and the shape of the double knot is not always as pictured in Figure 25. A caballine pattern, however, is never found in asses and thus I do not believe that the typical caballine lower teeth ascribed to *E. graziosii* (AZZAROLI 1979: Plates 3, 4, 5, 7) can belong to an ass.

Within the subgenus *Hemionus*, two species—*E. kiang* and *E. hemionus*—are usually distinguished. With the exception of the dwarf form *E. hemionus hemippus*, all subspecies of *E. hemionus* are very similar in size and shape. In addition, I am unable to discriminate the skulls supposed to belong to *E. kiang* and to the Mongolian half-ass *E. hemionus hemionus*. As a result, I would be tempted to consider the kiang as being a subspecies of *E. hemionus*. The subgenus clearly requires more study: all the different forms cannot easily be observed in the live state; protein and chromosome patterns are poorly known; and osteological samples are not very satisfactory, there being few skeletons of *E. hemionus hemippus* and kulans, frequent dental anomalies in onagers, and poor provenience information for Mongolian half-asses. A few dental characters are reliable separators, however: protocones are relatively long and vestibular grooves are usually shallow on lower molars (75–100% of second and third molars).

The asses seem to be a more homogeneous group than horses or half-asses. The skulls and skeletons of wild asses, however, are poorly represented in my sample, and separation of the two wild subspecies on the basis of comparative osteology is nearly impossible. Teeth are characterized by short protocones, always by asinine double knots (Figures 21, 23), and usually by shallow vestibular grooves on lower molars (Figure 21; 70–95% on second and third molars).

I have frequently been asked what material is “best” for the study of equids in general. The only good answer to this question is that the “best” material is a lot of all the different bones and teeth. If a hierarchy must be given, it will not always be the same but will depend on the problem at hand. Similarities between different subgenera are not equally reflected in each anatomical part. Skulls of asses and half-asses are relatively close to each other in shape but the upper cheekteeth are rather different. At the opposite extreme, the upper cheekteeth of horses and half-asses are not very different while the skulls are. Nor are the various subgenera equally “evolved” in each anatomical feature. If we agree that short protocones, deep vestibular grooves, and asinine double knots are primitive (plesiomorph) characters, the upper cheekteeth of horses and half-asses are more evolved than are the upper cheekteeth of asses. But, evolved (short) vestibular grooves are more frequent in asses and half-asses than in horses, and half-asses may exhibit primitive (asinine) patterns of the double knot as well as evolved (hemione or caballine) morphologies.

Thus it appears that the different anatomies of modern equids are the result of various combinations of a relatively small number of characters. All kinds of combinations, however, do not seem possible. Asses do not exhibit caballine double knots. Half-asses do not have robust metapodials. The difficult task is to specify which combinations do, and which do not, exist in the modern species and to discover new combinations in fossils. The first exercise helps to define the existing subgenera, the second to discover new ones.

7. Acknowledgements

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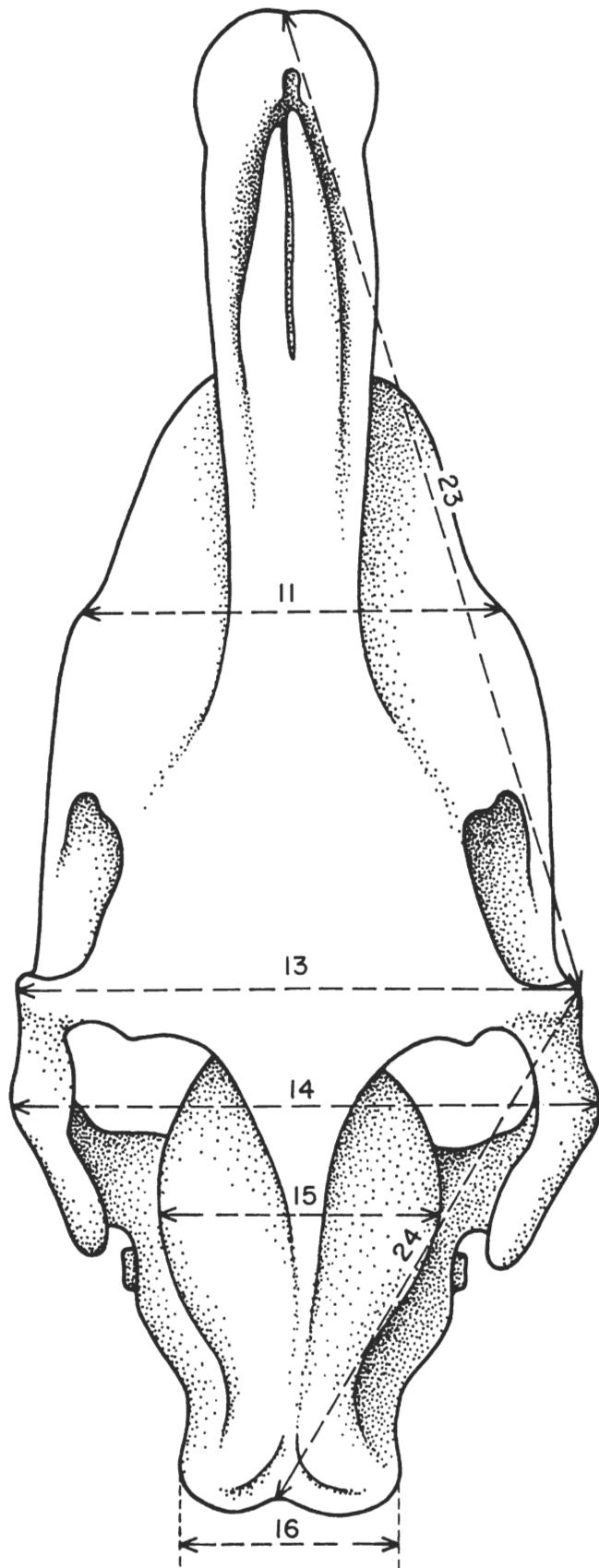


Fig. 1

Fig. 2:

Ventral view of an *Equus* skull. Measurements taken include:

- 1: basilar length;
- 2: palatal length;
- 3: distance from palate to hormion;
- 4: distance from hormion to basion;
- 5: muzzle length;
- 6: length of diastema;
- 7: occlusal length of the premolars excluding dP1;
- 7 bis: occlusal length of the molars;
- 8: occlusal length of the upper cheekteeth;
- 9: choanal length;
- 10: greatest choanal breadth;
- 10 bis: choanal breadth between the pterygoid processes;
- 12: distance between basion and anterior ends of P2;
- 17: muzzle breadth at the posterior borders of the I3;
- 17 bis: least muzzle breadth between the interalveolar borders;
- 29: breadth of the occipital condyles;
- 30: breadth of the foramen magnum.

Fig. 1:

Dorsal view of an *Equus* skull.

Measurements taken include:

- 11: breadth between the foremost points of the facial crests;
- 13: frontal breadth;
- 14: bizygomatic breadth;
- 15: greatest cranial breadth;
- 16: breadth of the supra-orbital crest;
- 23: anterior ocular line;
- 24: posterior ocular line.

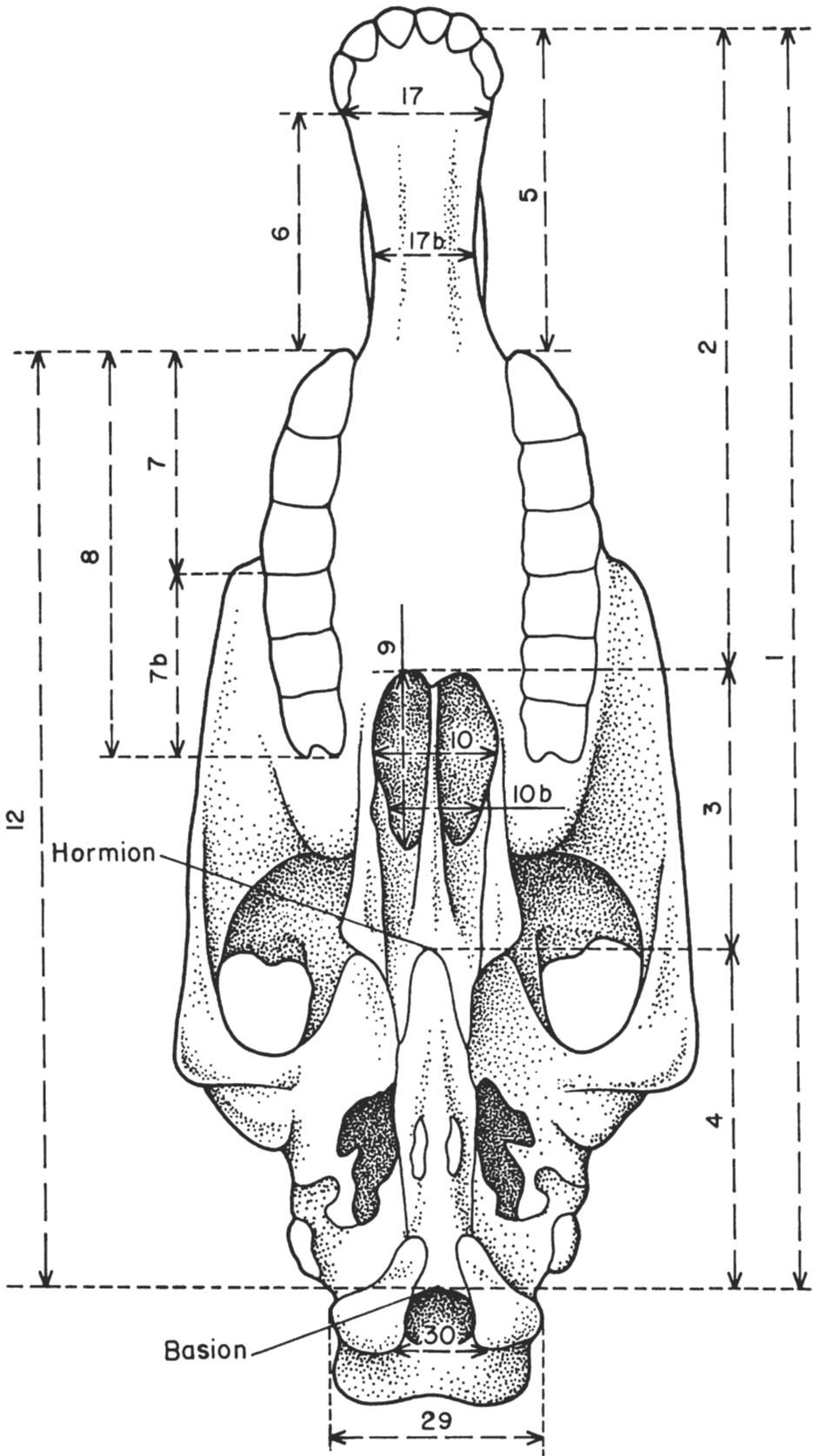


Fig. 2

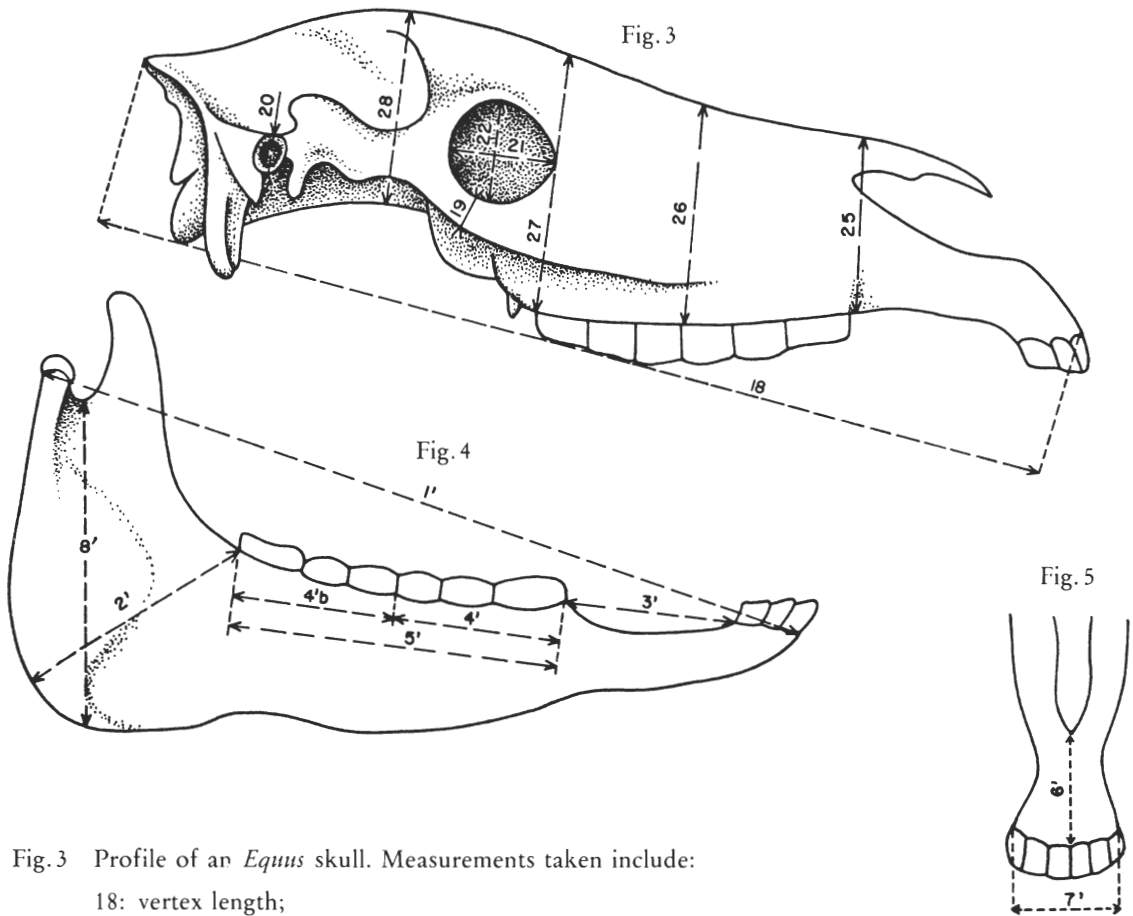


Fig. 3 Profile of an *Equus* skull. Measurements taken include:

- 18: vertex length;
- 19: infra-orbital height
- 20: height of the external auditory meatus;
- 21: anterior-posterior diameter of the orbit;
- 22: dorso-ventral diameter of the orbit;
- 25: facial height in front of P2;
- 26: facial height between P4 and M1;
- 27: facial height behind M3;
- 28: cranial height behind the orbits.

Fig. 4 Profile of an *Equus* mandible. Measurements taken include:

- 1': greatest length;
- 2': greatest length of the angular part;
- 3': length of the diastema;
- 4': occlusal length of the premolars excluding the dP1;
- 4' bis: occlusal length of the molars;
- 5': occlusal length of the lower cheekteeth;
- 8': height of the vertical ramus.

Fig. 5 Ventral view of an *Equus* mandible. Measurements taken include:

- 6': length of the symphysis;
- 7': breadth of the mandible at the posterior borders of I3.

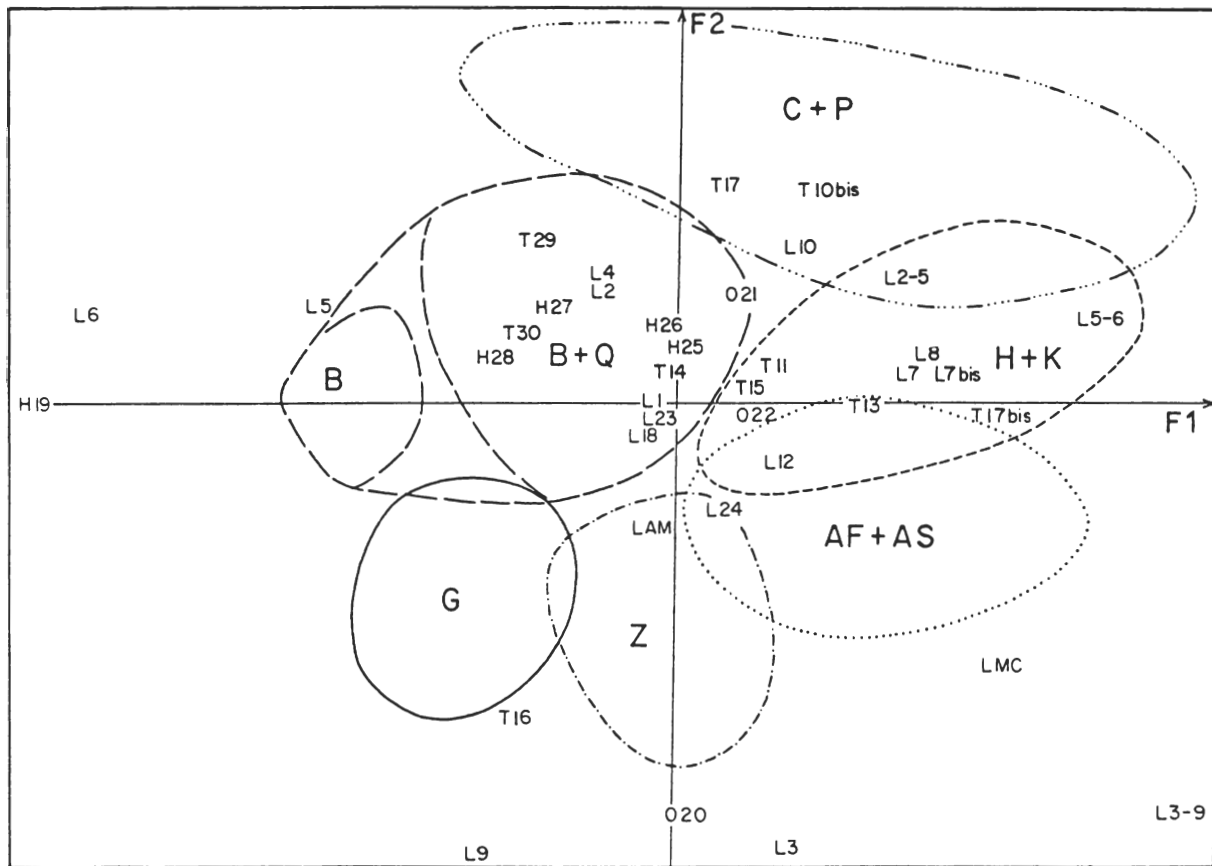


Fig. 6 First plane of projection of a correspondence analysis of modern *Equus* skulls (30 measurements x 349 specimens); F1 = 24.6%, F2 = 15.1% of explained variance.

The analyzed taxa are:

AF = *E.africanus*, AS = *E.asinus*, B = *E.burchelli*,
 C = *E.caballus*, G = *E.grevyi*, H = *E.hemionus*, K = *E.kiang*,
 P = *E.przewalskii*, Q = *E.quagga*, Z = *E.zebra*.

The measurements taken are illustrated in Figures 1-3

(H = heights, L = lengths, O = orificial diameters, T = breadths);

LAM = L12 - L8; LMC = L3 + L4 - LAM.

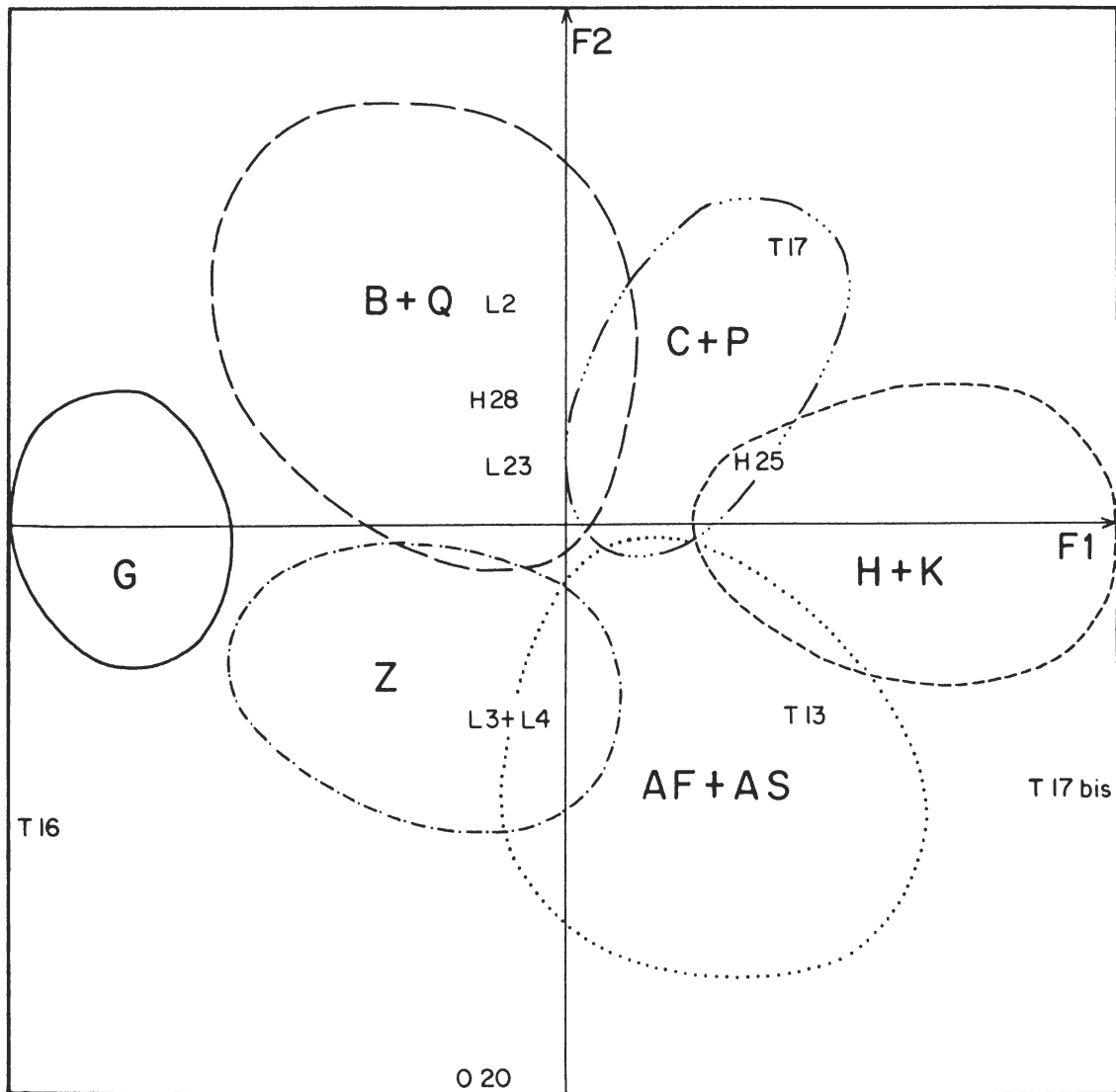


Fig.7 First plane of projection of a correspondence analysis of modern *Equus* skulls (10 measurements x 349 specimens); F1 = 29%, F2 = 22.2% of explained variance. Same abbreviations as in Figure 6.

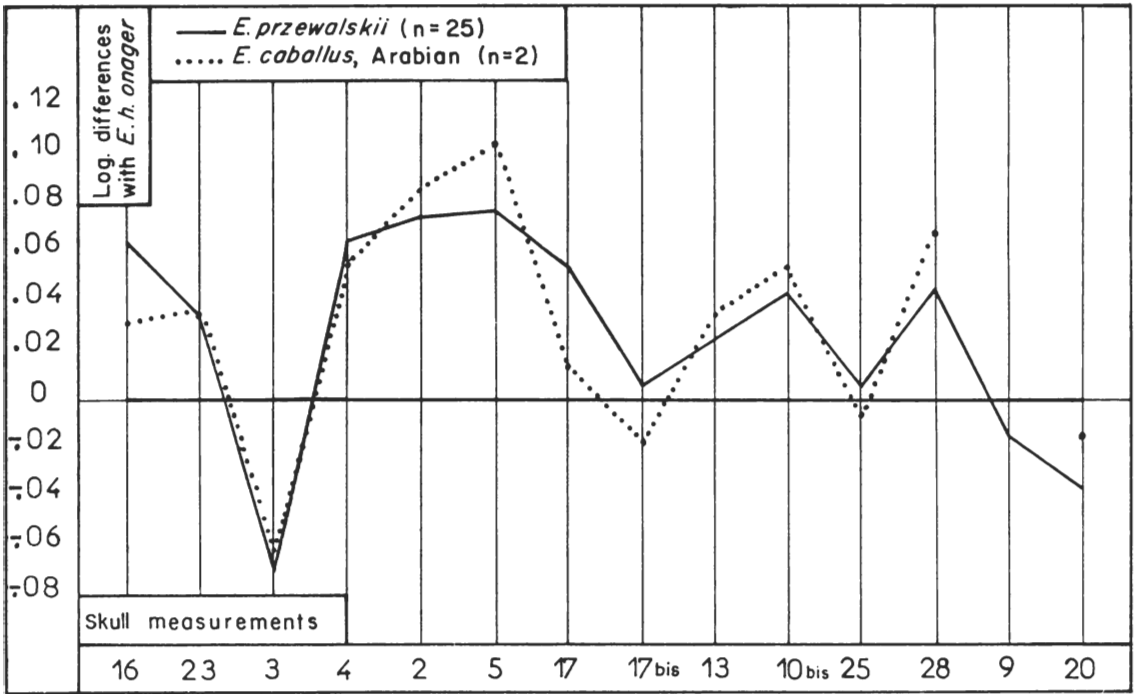


Fig. 8 Ratio diagrams of the cranial measurements (means) of Arabian and Przewalski horses compared to *E. hemionus onager* (reference line). For description of the measurements see Figures 1-3; n = number of specimens.

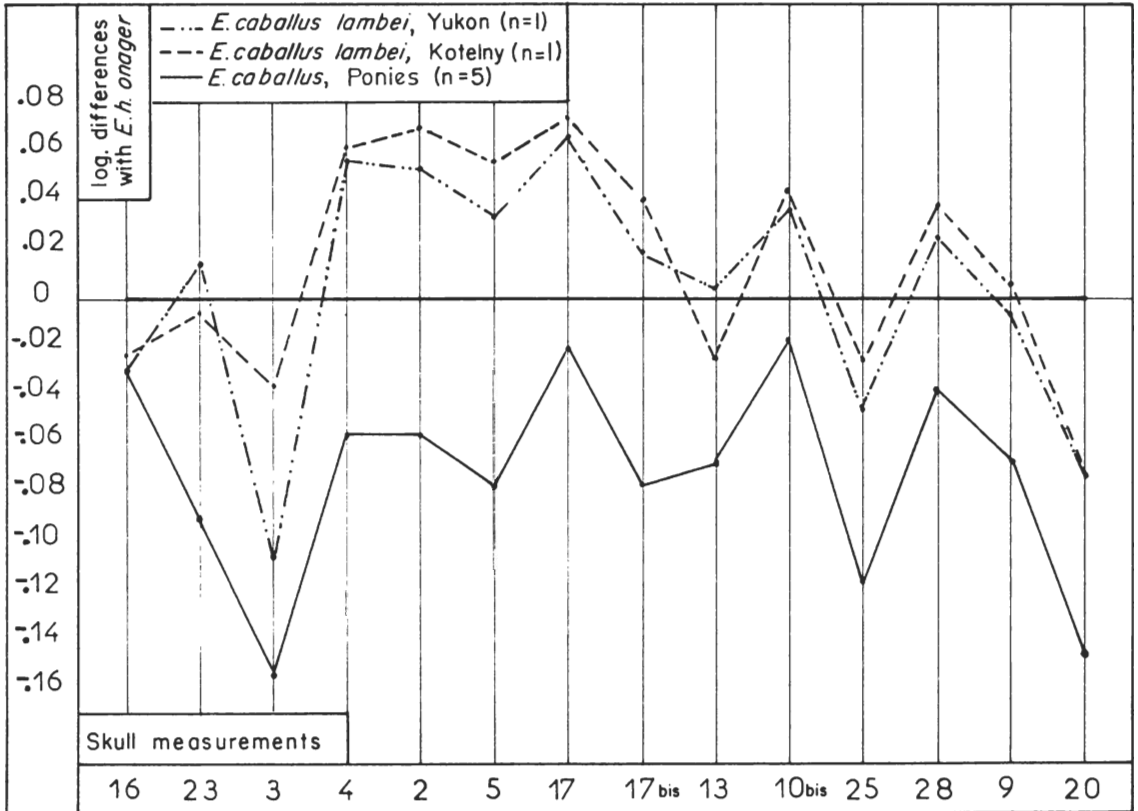


Fig. 9 Ratio diagrams of the cranial measurements of modern ponies and fossil Canadian and Siberian horses.

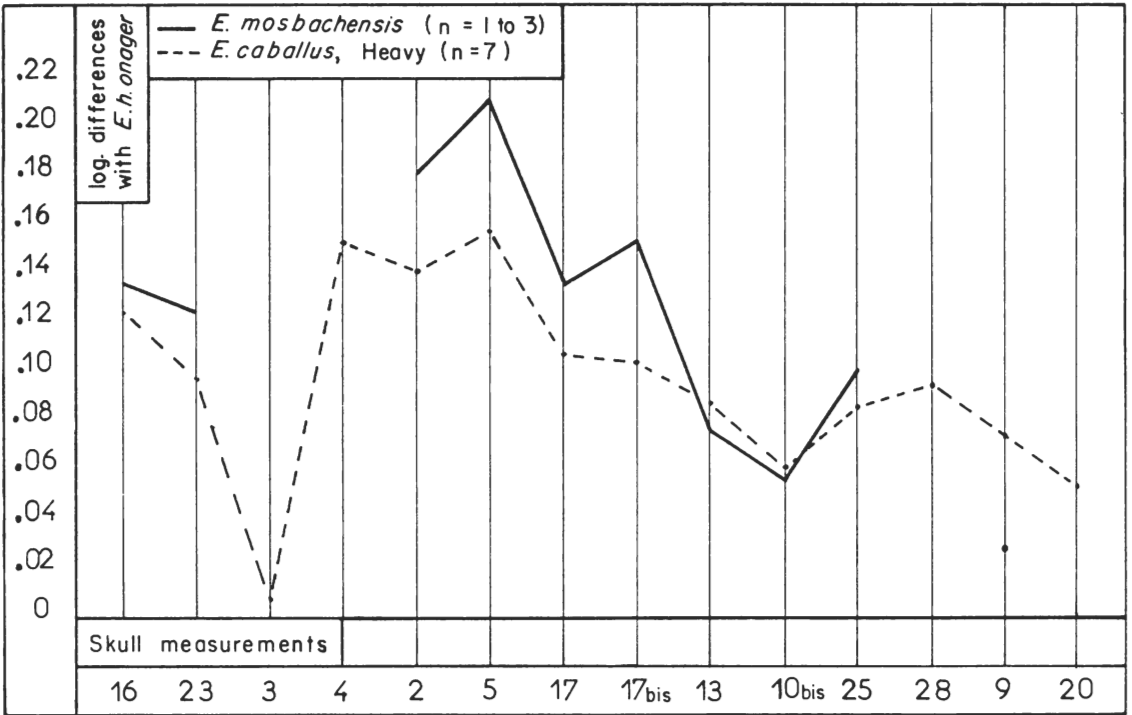


Fig. 10 Ratio diagrams of the cranial measurements of modern heavy horses and the fossil *E. mosbachensis*.

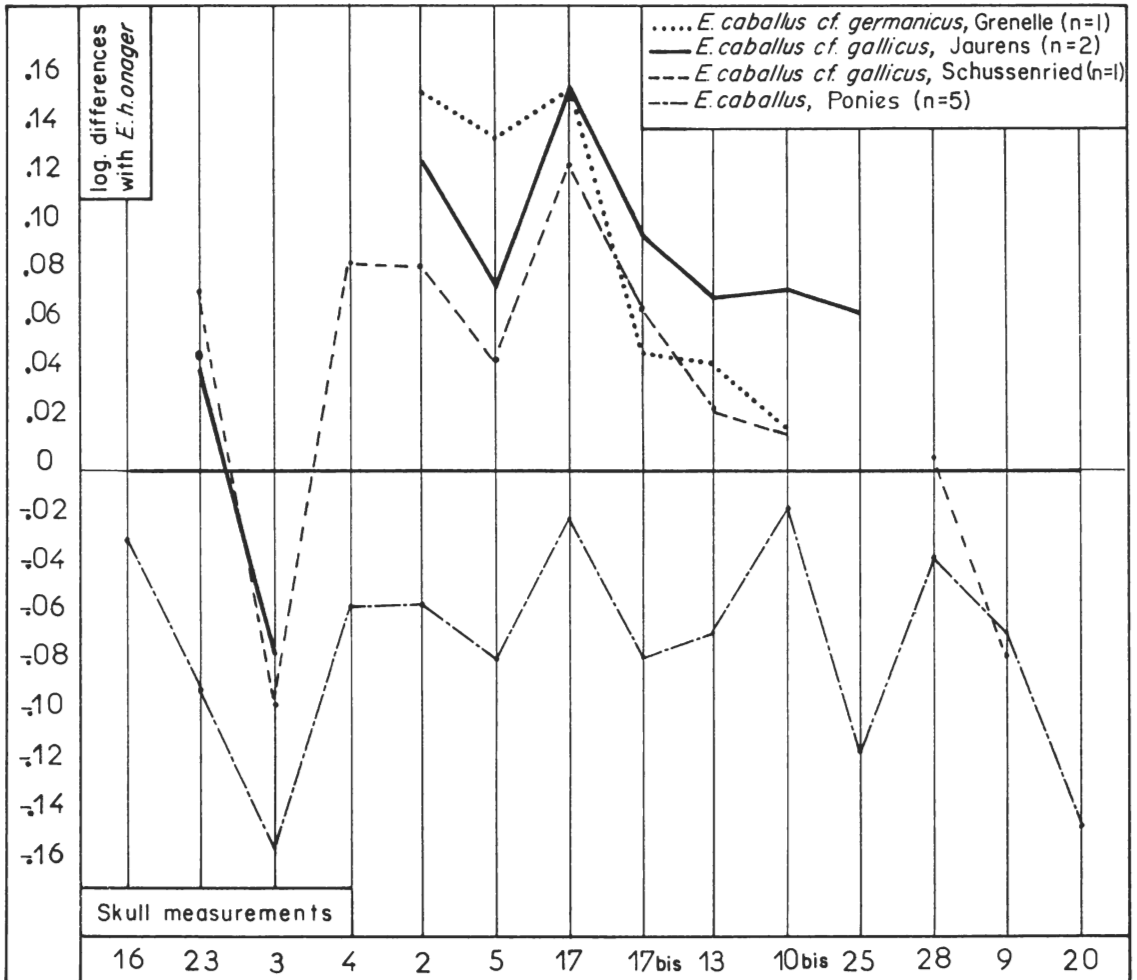


Fig. 11 Ratio diagrams of the cranial measurements of modern ponies and fossil horses from France and Germany.

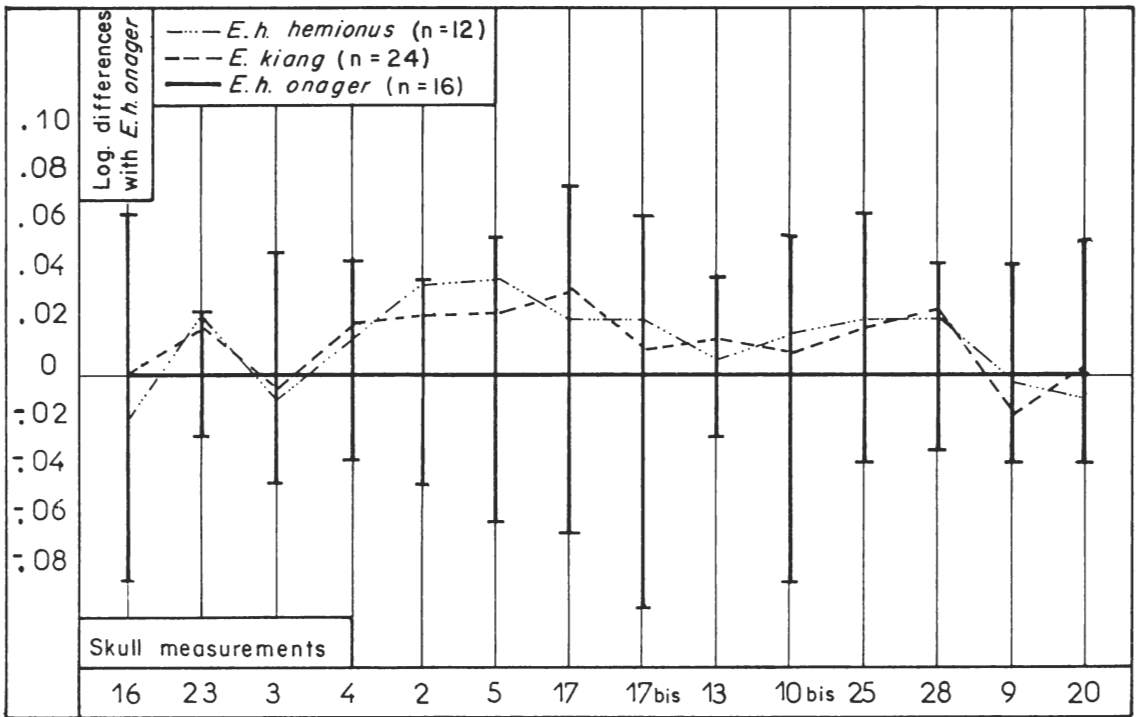


Fig. 12 Ratio diagrams of the cranial measurements of kiangs and Mongolian hemiones. The range of variation for *E. hemionus onager*, the reference species, is also indicated.

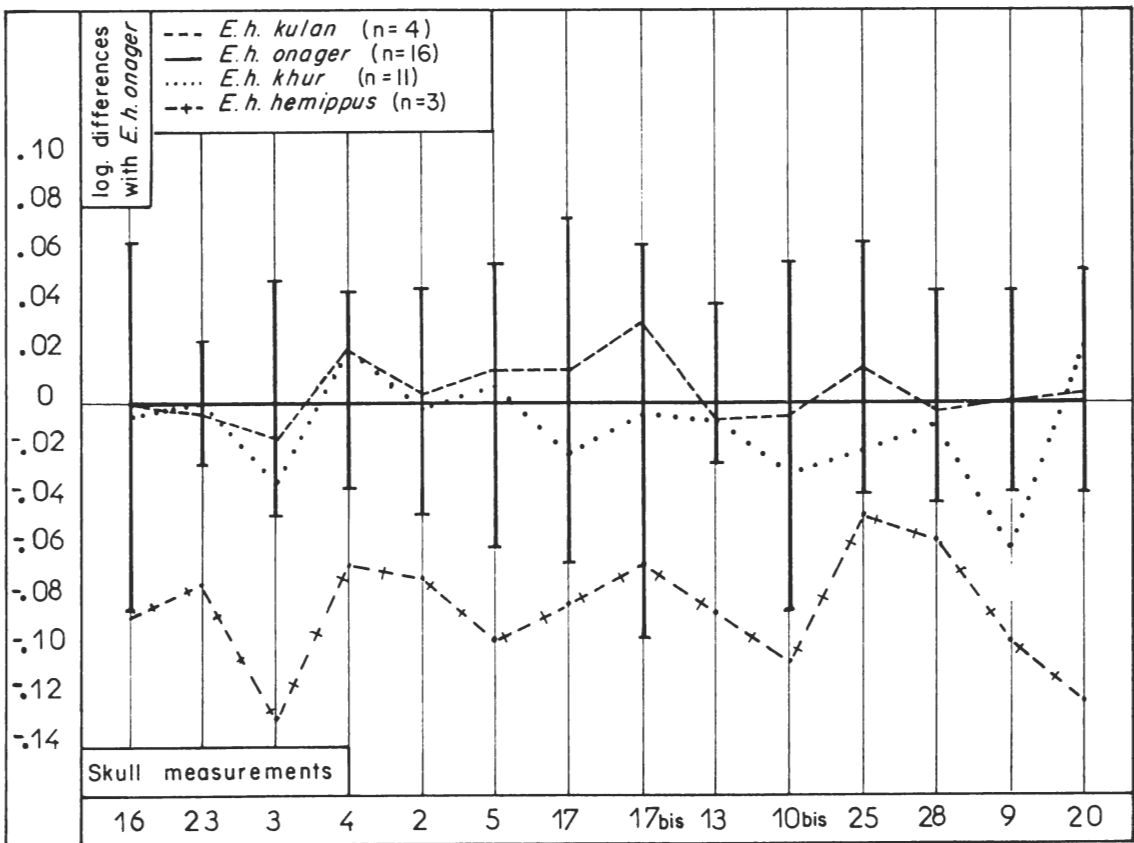


Fig. 13 Ratio diagrams of the cranial measurements of Turkmenian, Indian, and Syrian hemiones compared to the Persian onager: *E. hemionus onager*. The range of variation for the latter is also indicated.

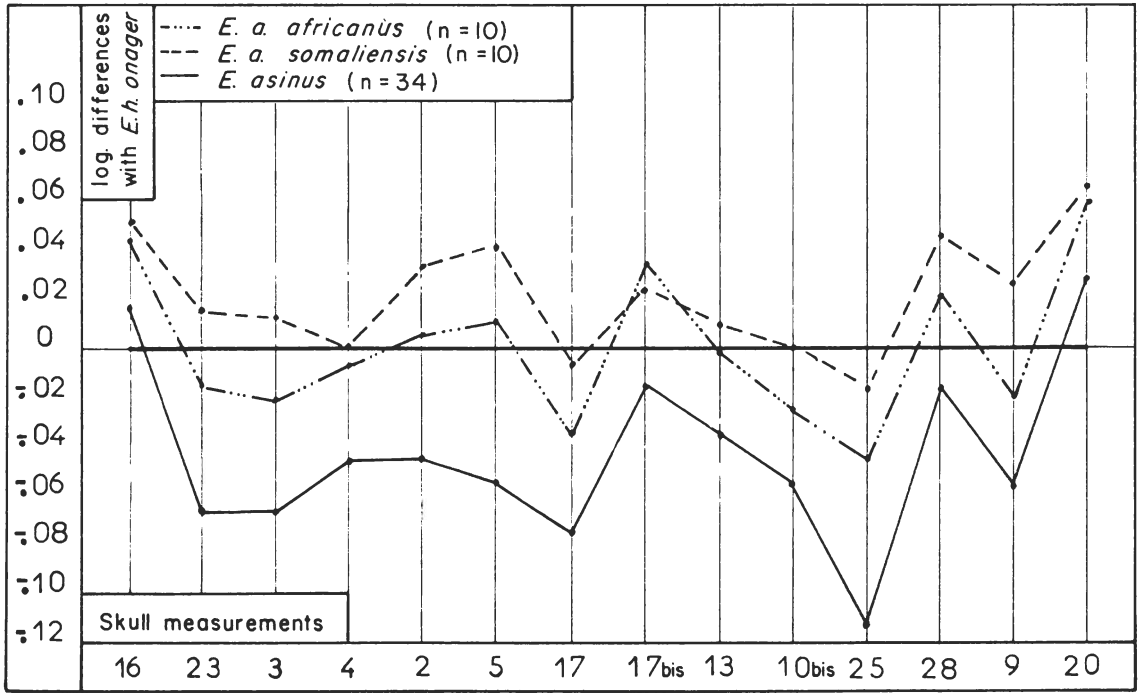


Fig. 14 Ratio diagrams of the cranial measurements of domestic and wild asses.

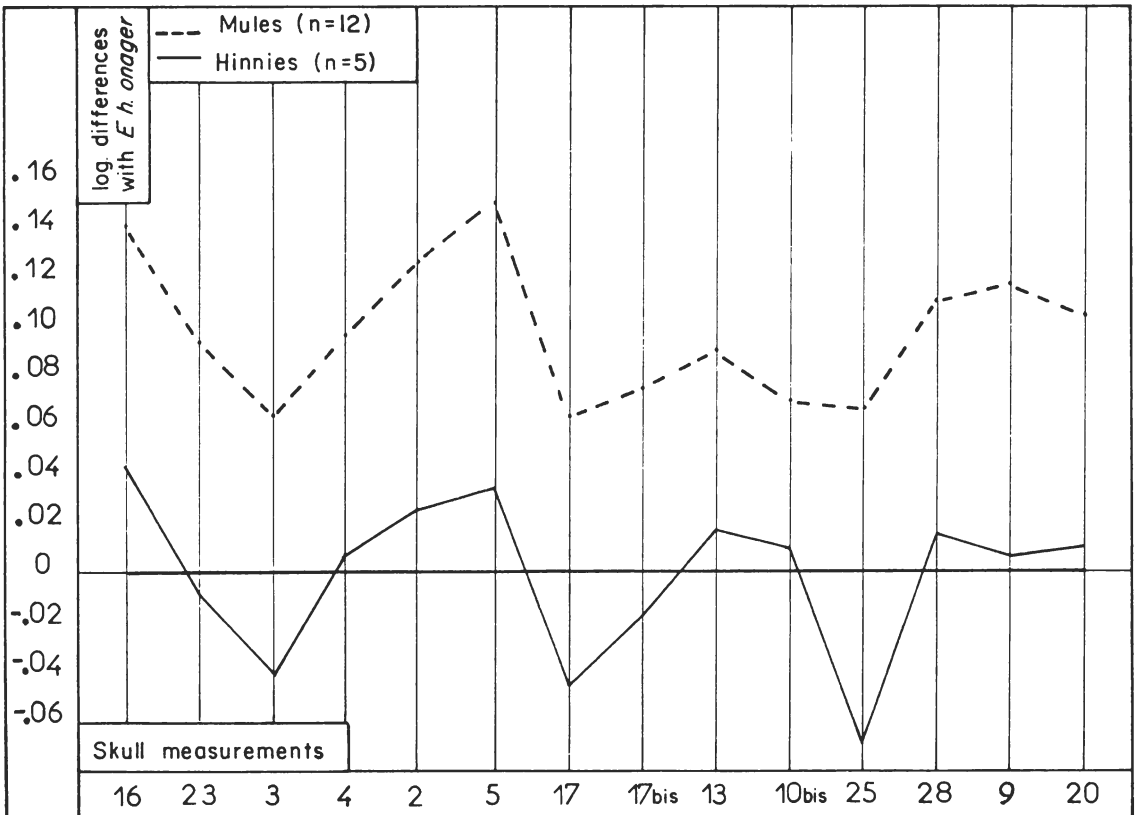


Fig. 15 Ratio diagrams of the cranial measurements of mules and hinnies.

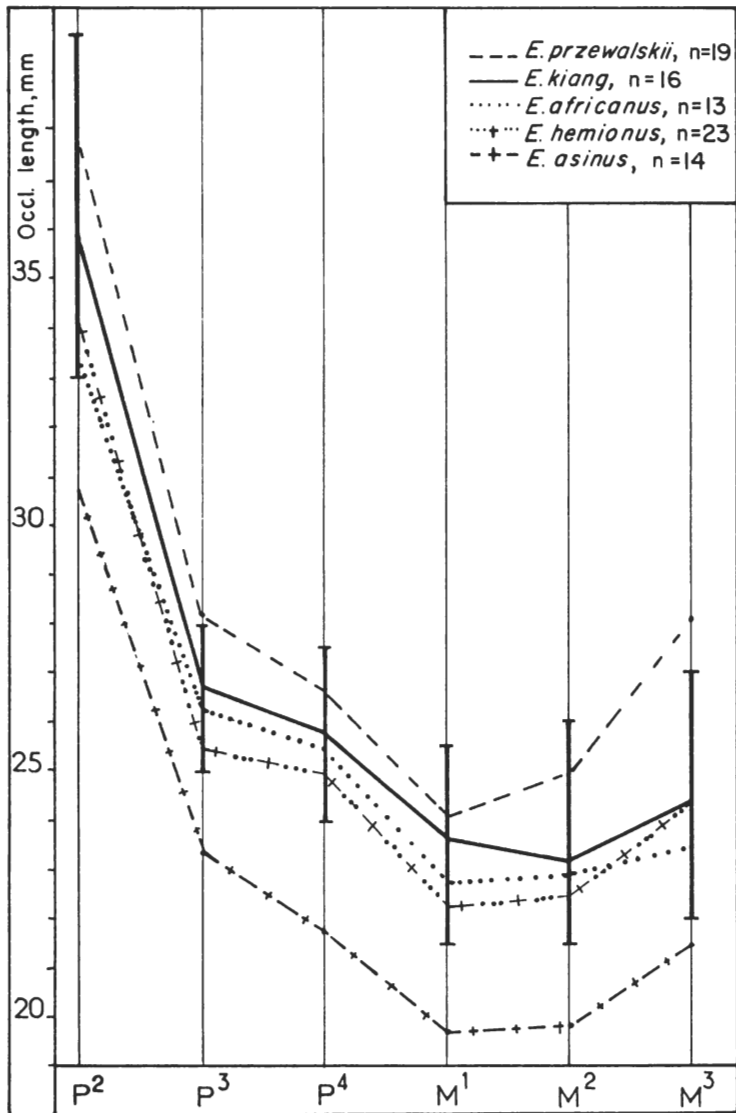


Fig. 16 Mean occlusal lengths in mm of the upper cheekteeth of asses, half-asses, and wild horses. The range of variation is indicated for *E. kiang*; n = number of specimens.

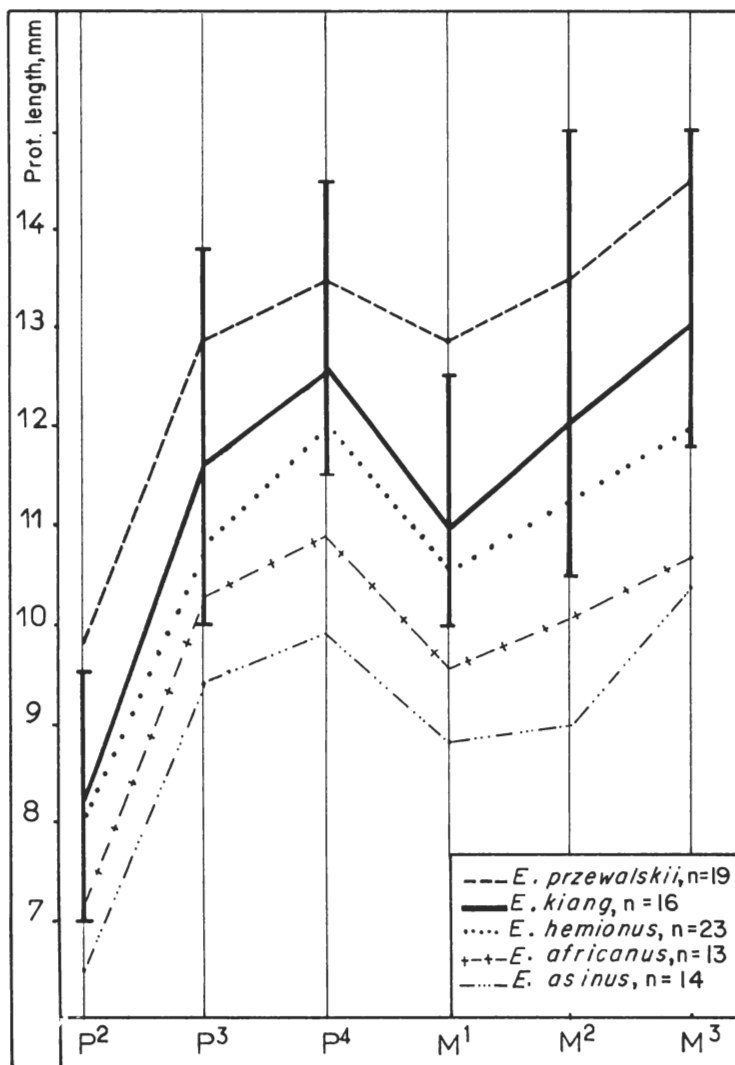


Fig. 17 Mean protocone lengths of the upper cheekteeth of asses, half-asses, and wild horses. The range of variation is indicated for *E. kiang*; n = number of specimens.

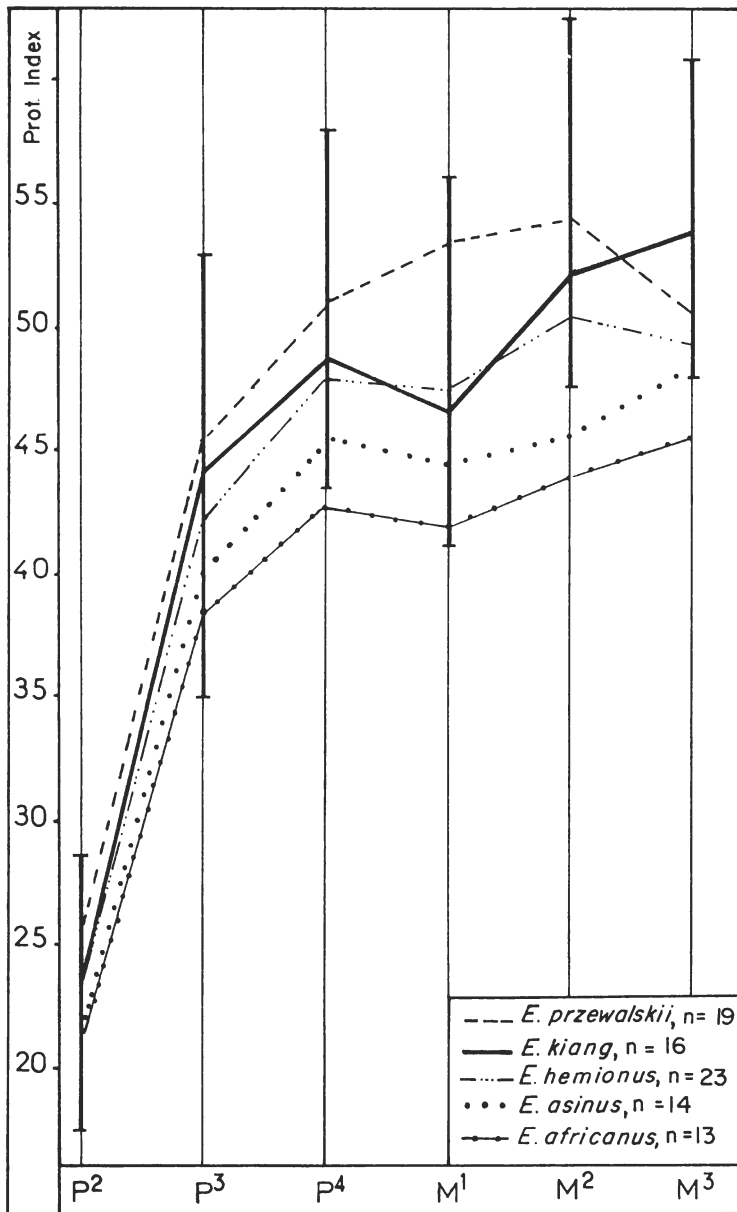


Fig. 18 Mean protocone indices for the upper cheekteeth of asses, half-asses, and wild horses. The range of variation is indicated for *E. kiang*; n = number of specimens.

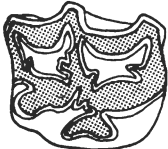

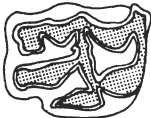

	P3 P4 	M3 	M3 	dP1 
<i>E. africanus</i>	<u>7-8</u>	<u>64%</u>	<u>0</u>	31%
<i>E. hemionus</i>	4-5	29%	39%	30%
<i>E. kiang</i>	3-4	47%	27%	30%
<i>E. przewalskii</i>	4-5	47%	27%	25%

Fig. 19 Qualitative characters of the upper cheekteeth of wild asses, half-asses, and wild horses: average number of folds on P3 and P4; frequency of isolated hypoglyphs on M3; frequency of open post-fossettes on M3; frequency of dP1 in adult specimens.

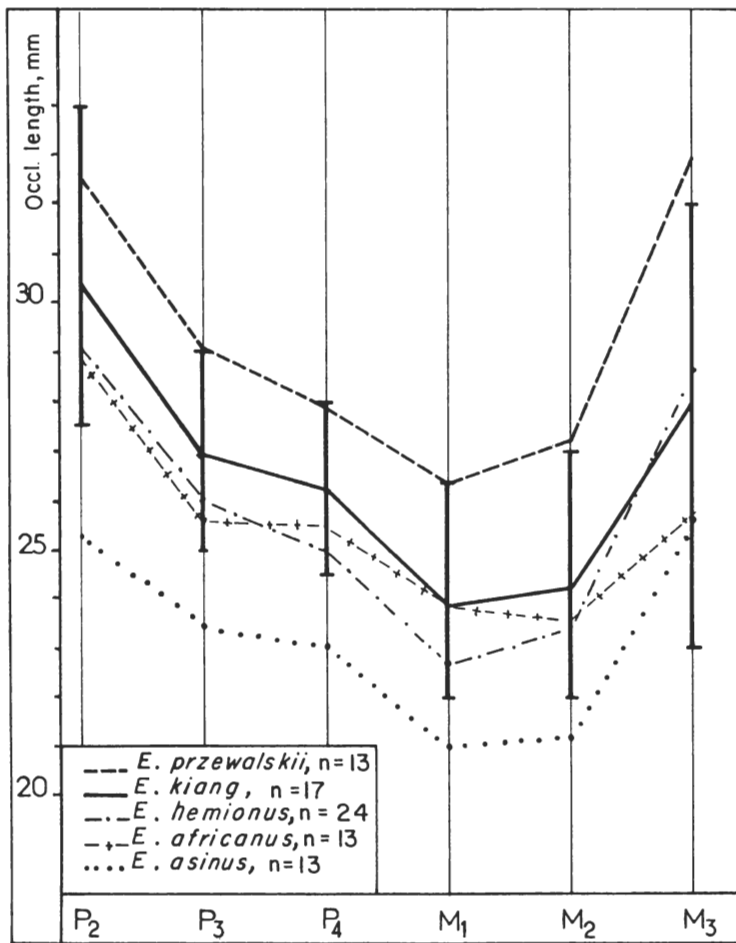


Fig.20 Mean occlusal lengths in mm of the lower cheekteeth of asses, half-asses, and wild horses. The range of variation is indicated for *Equus kiang*; n = number of specimens.

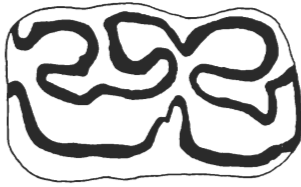


Fig. 21 Right mandibular P3 or P4 showing an asinine double knot and a shallow ectoflexid and long post flexid.

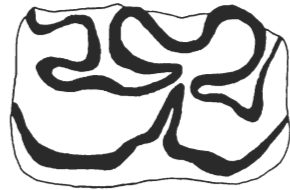


Fig. 22 Right mandibular P3 or P4 with a moderately developed ectoflexid.

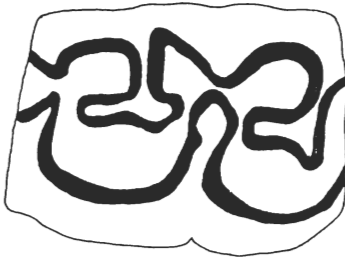


Fig. 23 Right mandibular M1 or M2 with a deep ectoflexid and a small postflexid.

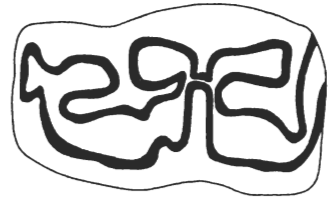


Fig. 24 Right mandibular M1 or M2 with a flattening contact between ectoflexid and linguaflexid.

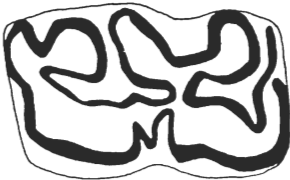


Fig. 25 Right mandibular P3 or P4 with a typical caballine double knot.

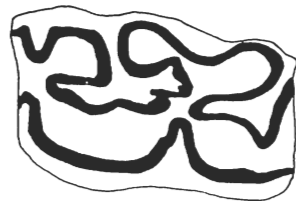


Fig. 26 Right mandibular P3 or P4 with a hemione double knot.

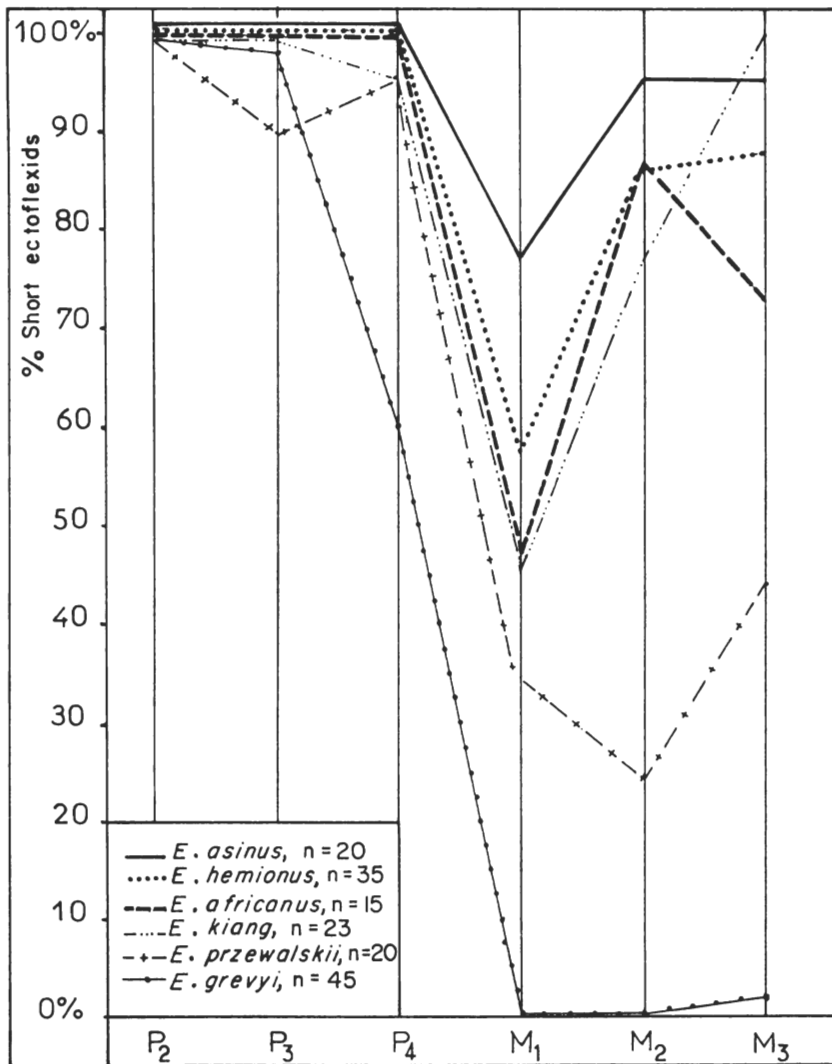


Fig. 27 Frequency of short ectoflexids (as in Figures 21, 25–26) on the lower cheekteeth of asses, half-asses, wild horses, and Grevy zebras.

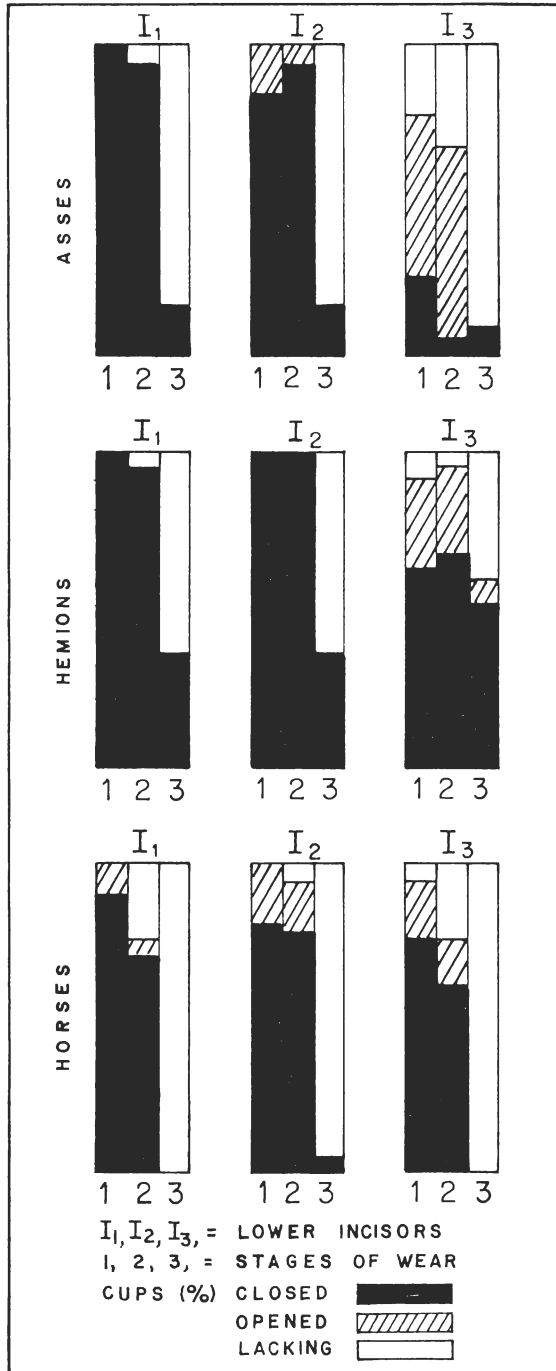


Fig. 28 Frequency of perfectly closed cups on the lower incisors of asses, hemions (kiangs included), and horses.

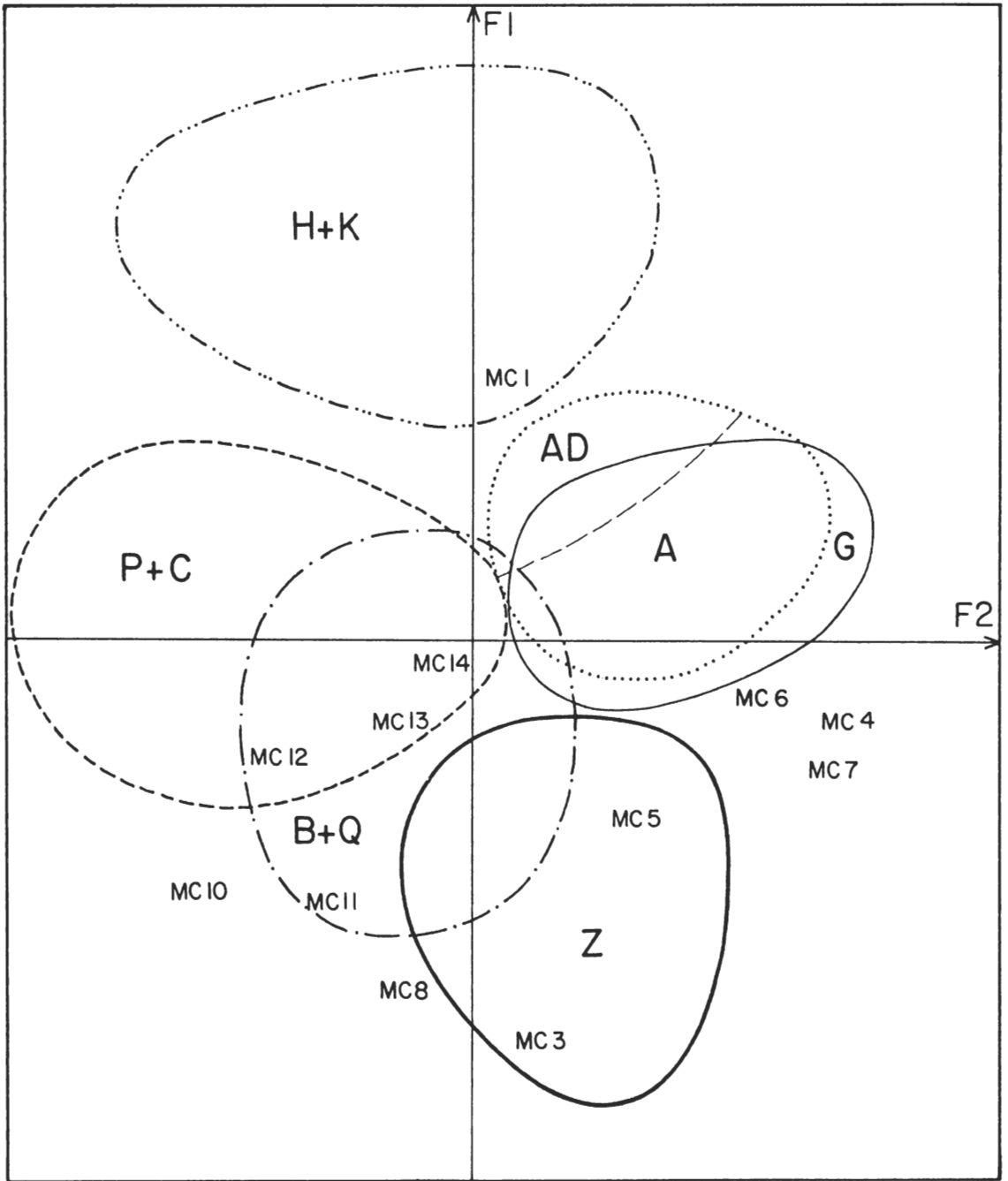


Fig. 29 First plane of projection of a correspondence analysis of *Equus* metacarpals (12 measurements x 200 specimens); F1 = 58.9%, F2 = 10.1% of explained variance. The analyzed taxa are: A = *E.africanus*, AD = *E.asinus*, B = *E.burchelli*, C = *E.caballus*, G = *E.grevyi*, H = *E.hemionus*, K = *E.kiang*, P = *E.przewalskii*, Q = *E.quagga*, Z = *E.zebra*. The measurements are: 1) greatest length; 3) breadth (DT) in the middle of the shaft (diaphysis); 4) mid-shaft depth (anterior-posterior diameter: DAP); 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 carpal III (magnum); 10) distal supra-articular breadth (transverse diameter: DT); 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.

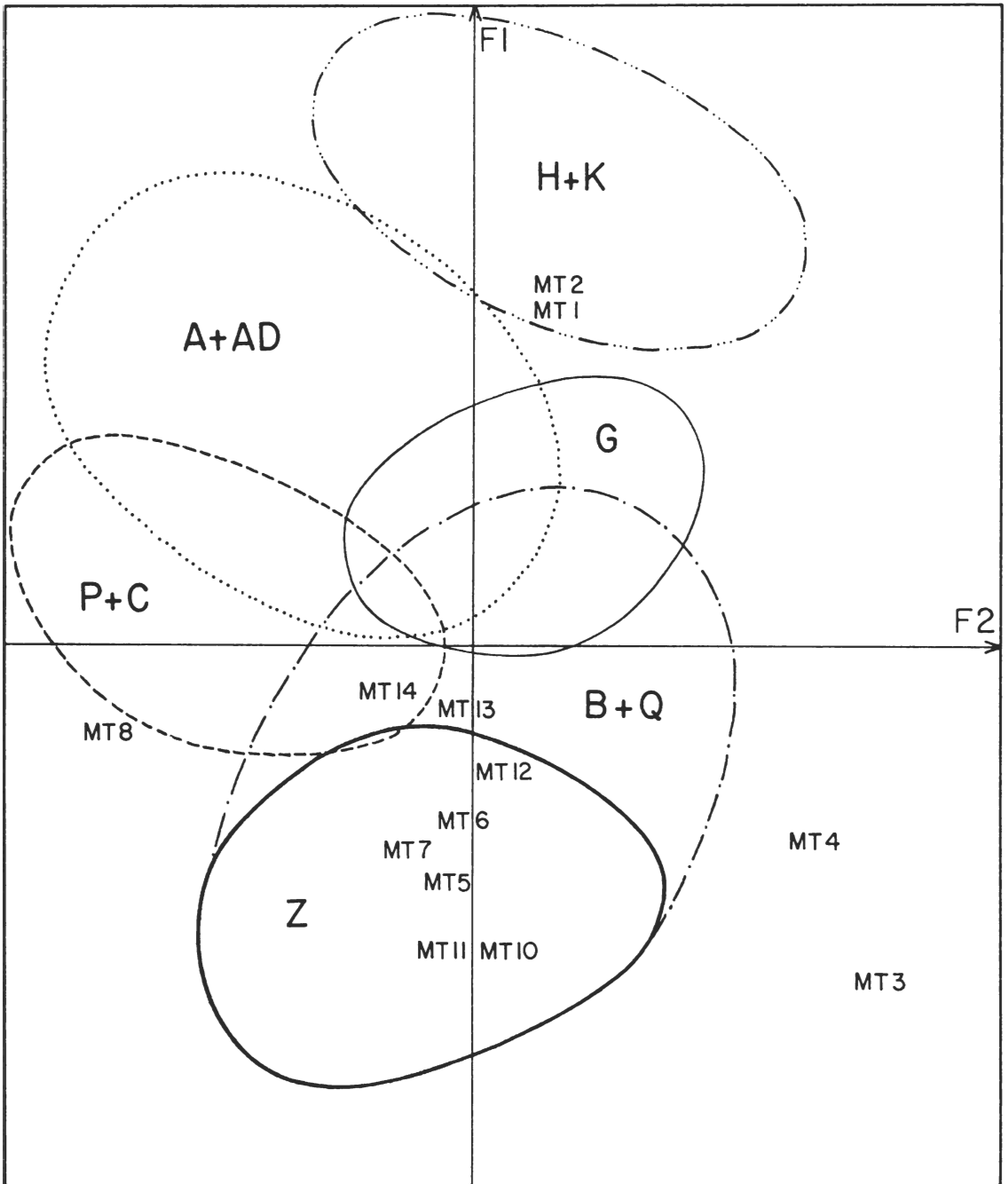


Fig. 30 First plane of projection of a correspondence analysis of *Equus* metatarsals (12 measurements x 200 specimens); F1 = 59.5%, F2 = 13.5% of explained variance. Same abbreviations as in Figure 29 except: 2) lateral (external) length; 5) and 6) are greatest breadth and depth instead of articular breadth and depth; 7) and 8) are diameters of the articular facets for the Os tarsale III (large cuneiform) and Os tarsale IV (cuboid).

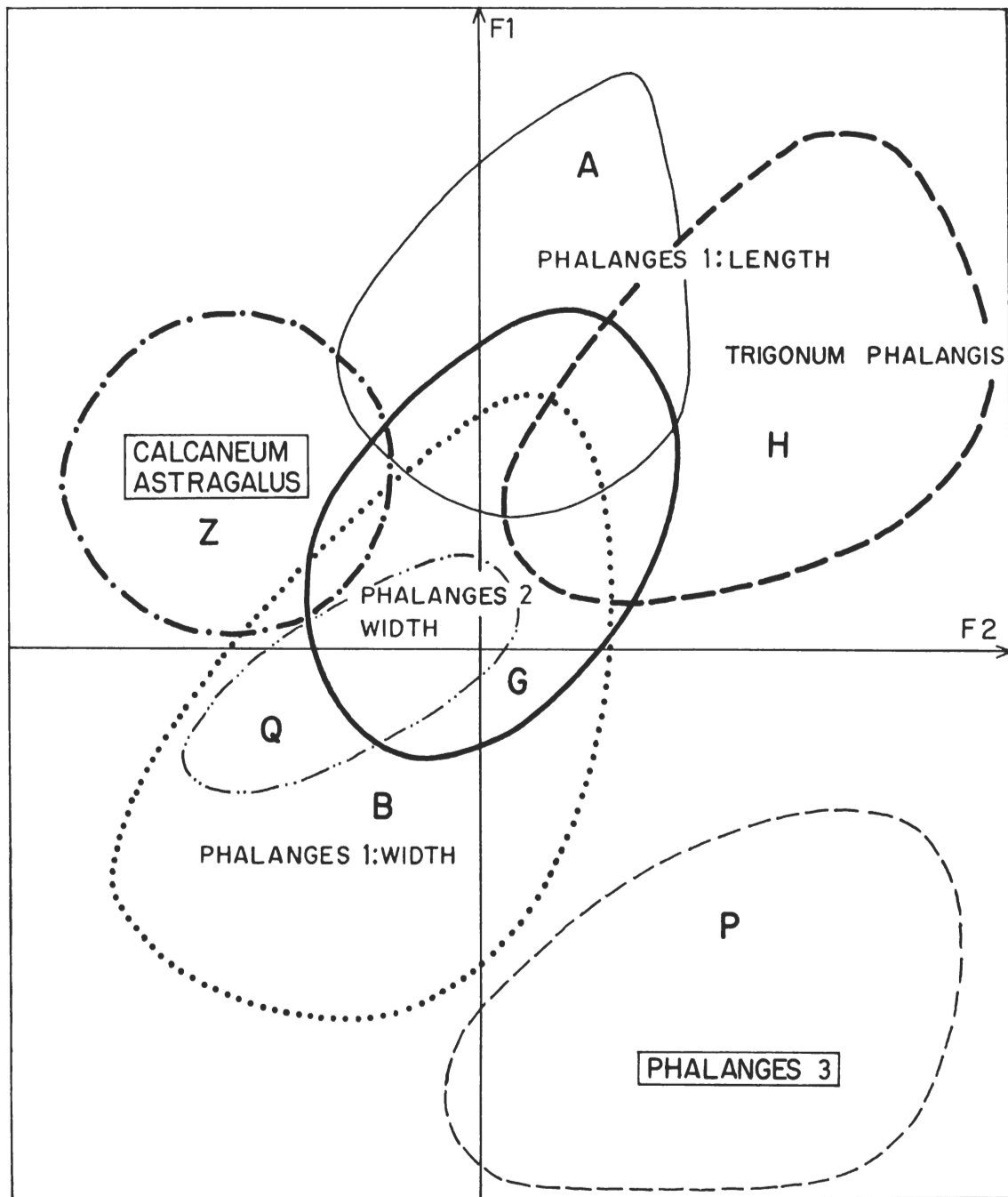


Fig. 31 First plane of projection of a correspondence analysis of modern *Equus* astragali, calcanea, phalanges (68 measurements x 149 individuals); F1 = 29%, F2 = 15% of explained variance. The analyzed taxa are: A = Asses, B = *E. burchelli*, G = *E. grevyi*, H = Half-asses, P = *E. przewalskii*, Q = *E. quagga*, Z = *E. zebra*.

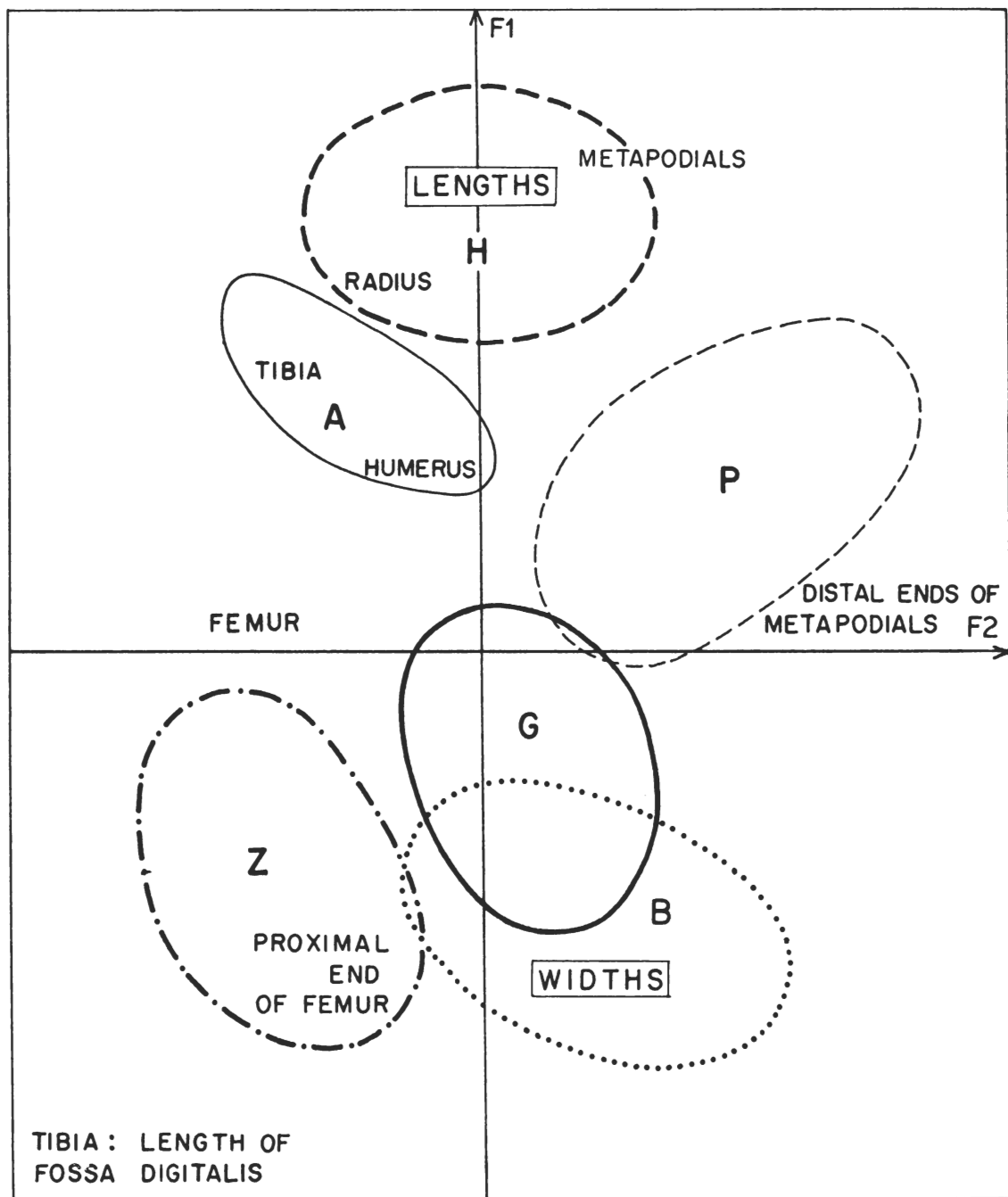


Fig. 32 First plane of projection of a correspondence analysis of modern *Equus* humeri, radii, femora, tibiae, and third metapodials (62 measurements x 185 individuals); F1 = 42.4%, F2 = 8.6% of explained variance. Same abbreviations as in Figure 31.

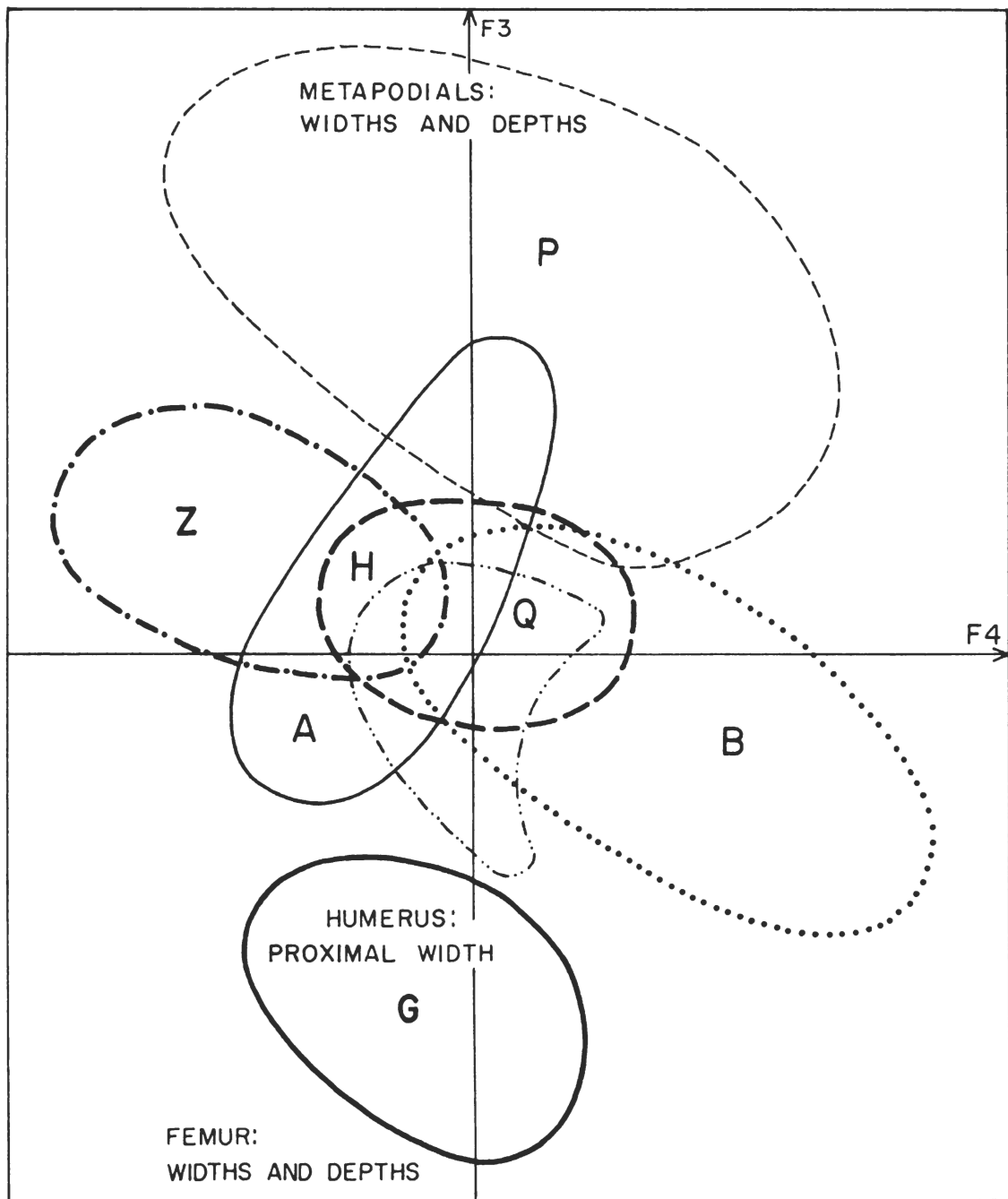


Fig. 33 Second plane of projection of a correspondence analysis of modern *Equus* humeri, radii, femora, tibiae, and third metapodials (62 measurements x 185 individuals); F3 = 6.5%, F4 = 4.4% of explained variance. Same abbreviations as in Figure 31.

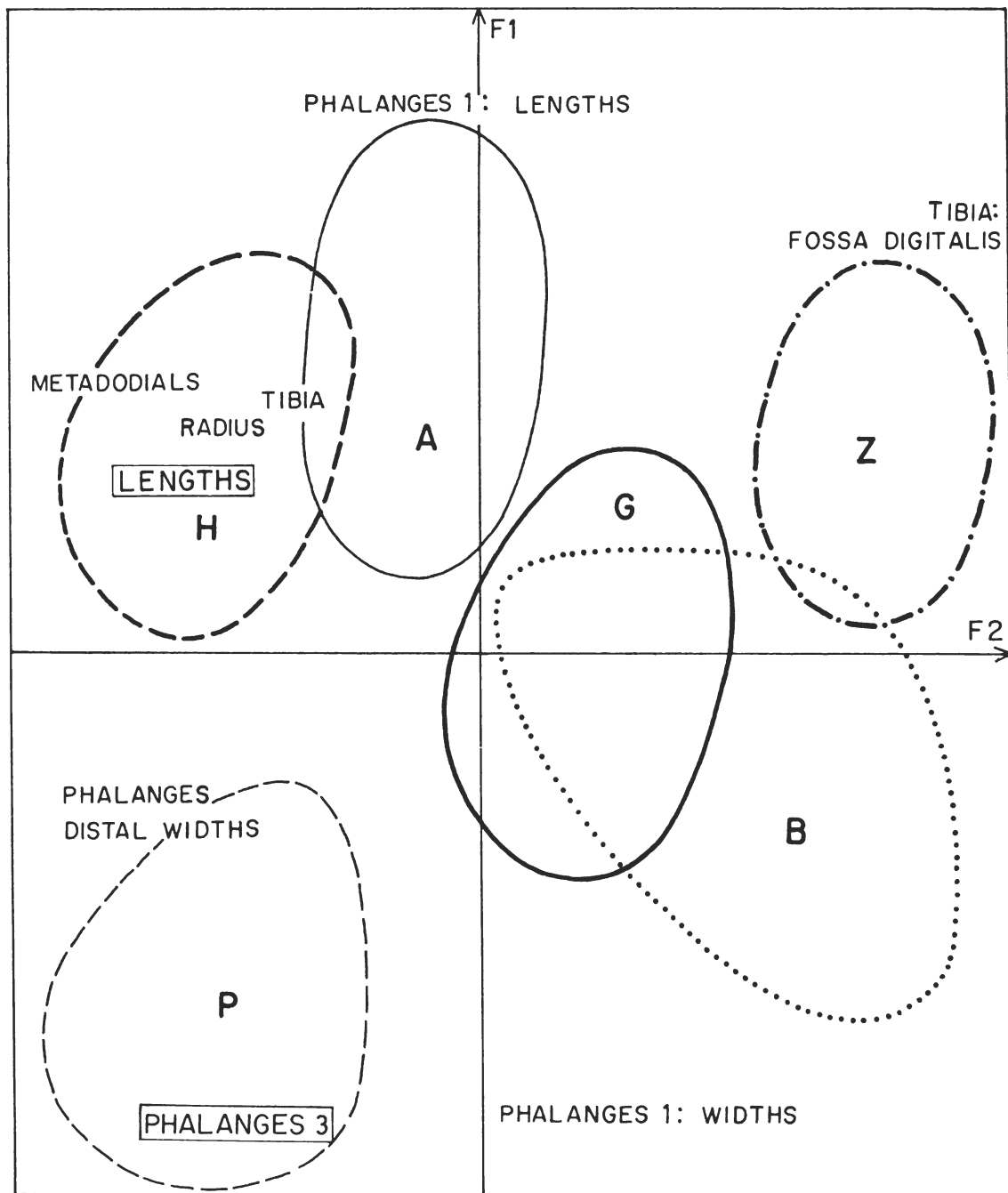


Fig. 34 First plane of projection of a correspondence analysis of modern *Equus* limb bones (130 measurements x 135 skeletons). Same abbreviations as in Figure 31.

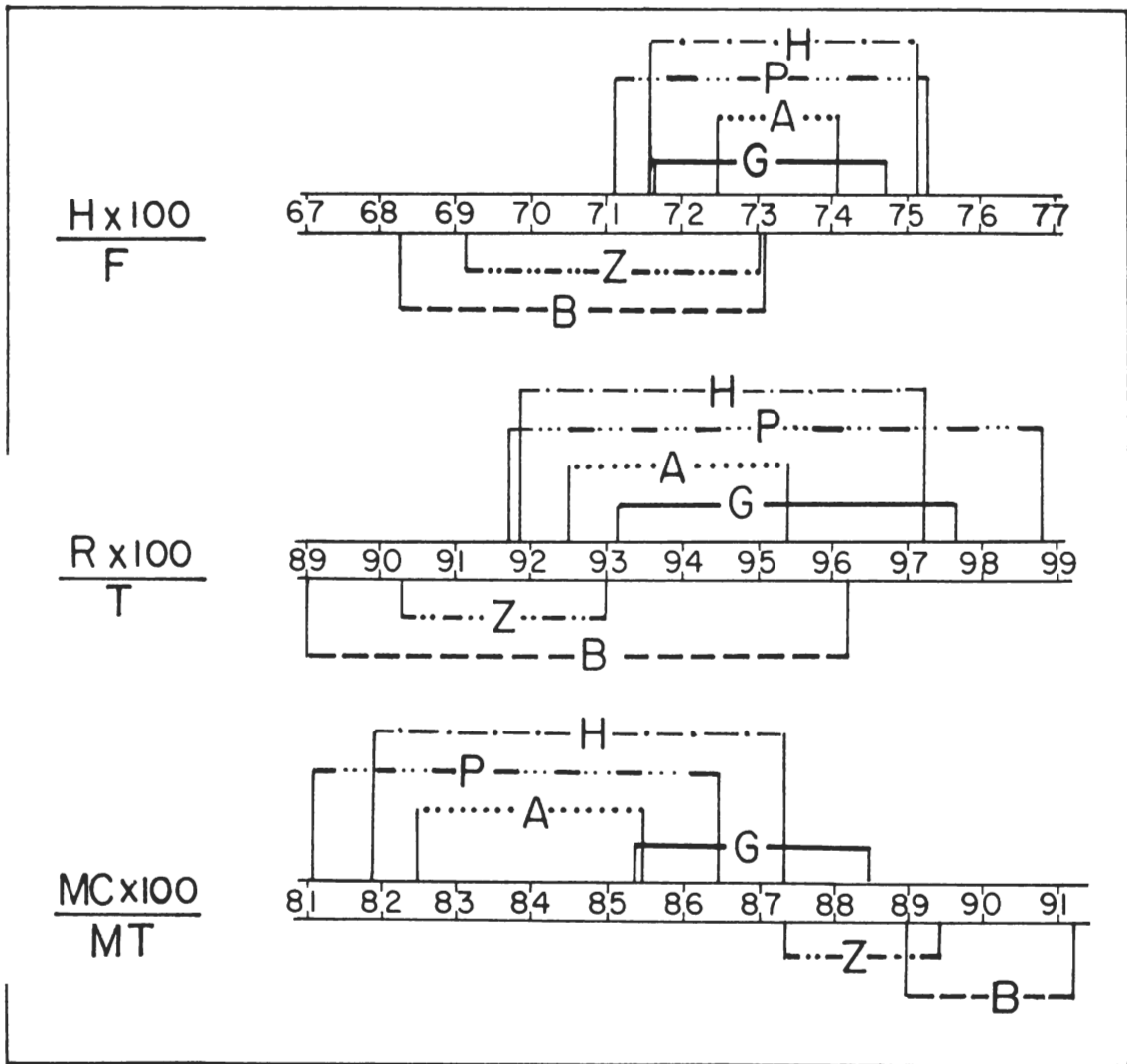


Fig. 35 Relative lengths of the limb segments (Humerus/Femur, Radius/Tibia, MC III/MT III) in modern *Equus*; A = Asses, B = *E. burchelli*, G = *E. grevyi*, H = Half-asses, P = *E. przewalskii*, Z = *E. zebra*.

9. Appendix: Measurement System

System of post-cranial skeletal measurements used by VÉRA EISENMANN (EISENMANN 1976, 1979, 1983, 1984, this volume, in press A, in press B; EISENMANN/BECKOUCHE, this volume; EISENMANN/DE GIULI 1974; EISENMANN/KARCHOUD 1982; EISENMANN/PATOU 1980; KARCHOUD 1980, 1981) with correspondences to dimensions defined by ANGELA VON DEN DRIESCH (1976). Note that VON DEN DRIESCH dimensions in () indicate approximate but not exact correspondence to EISENMANN dimensions.

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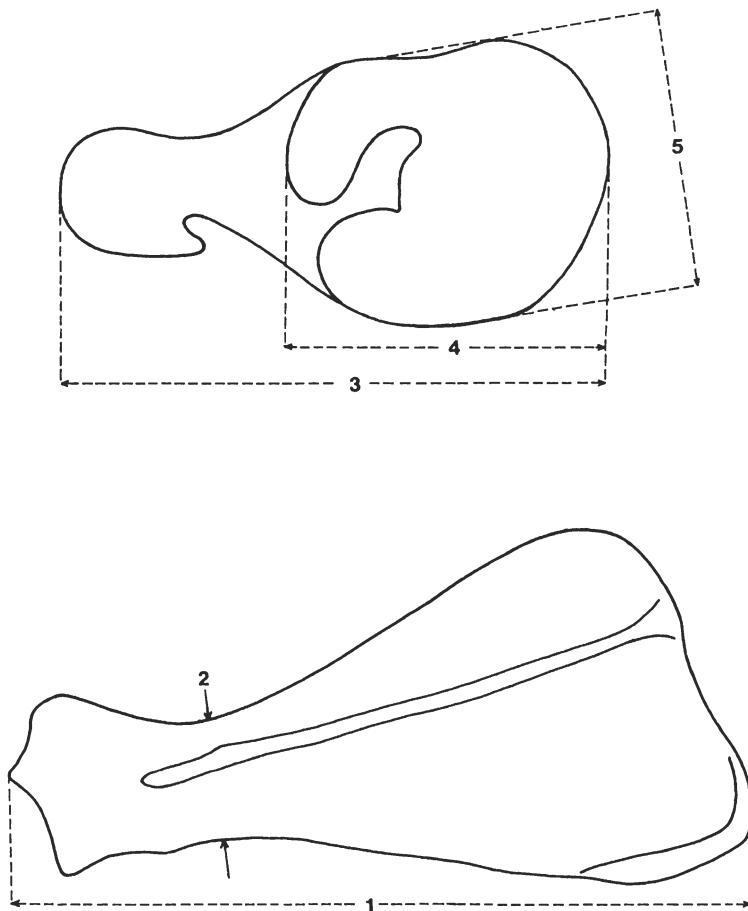


Fig. 36 Scapula:

1. Greatest length (height)
2. Smallest anteroposterior diameter (length of neck)
3. Greatest anteroposterior diameter (length of glenoid process)
4. Anteroposterior glenoid diameter (length of glenoid cavity)
5. Transverse glenoid diameter (breadth of glenoid cavity)

DHA
SLC
GLP
LG
BG

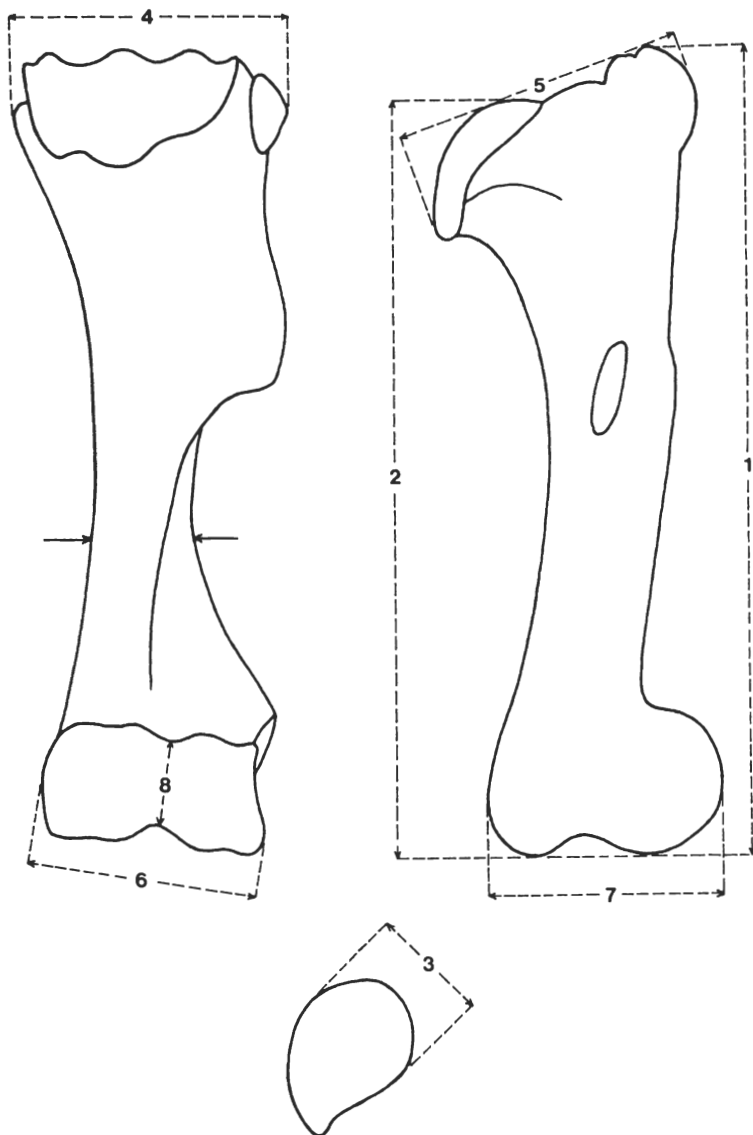


Fig. 37 Humerus:

- | | |
|---------------------------------|------|
| 1. Greatest length | GL |
| 2. Posterior length (from head) | GLC |
| 3. Smallest breadth (of shaft) | SD |
| 4. Proximal breadth | Bp |
| 5. Proximal depth | (Dp) |
| 6. Distal articular breadth | BT |
| 7. Distal medial depth | - |
| 8. Smallest height of trochlea | - |

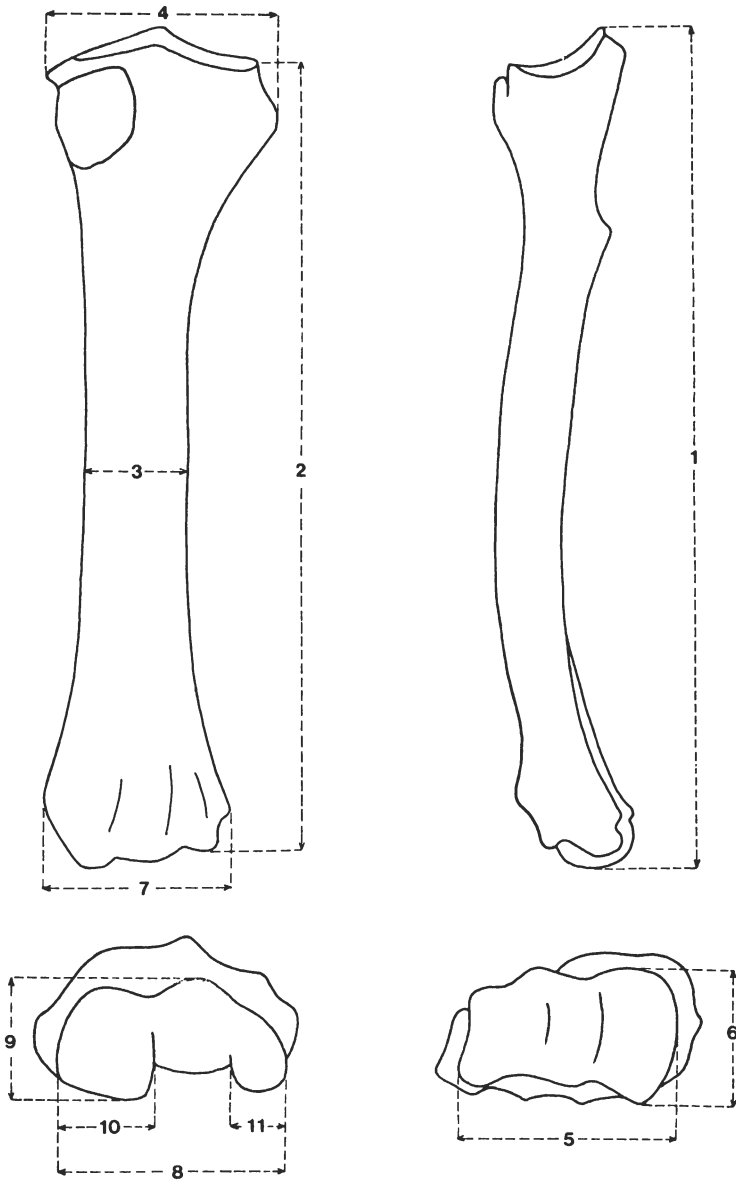


Fig. 38 Radius:

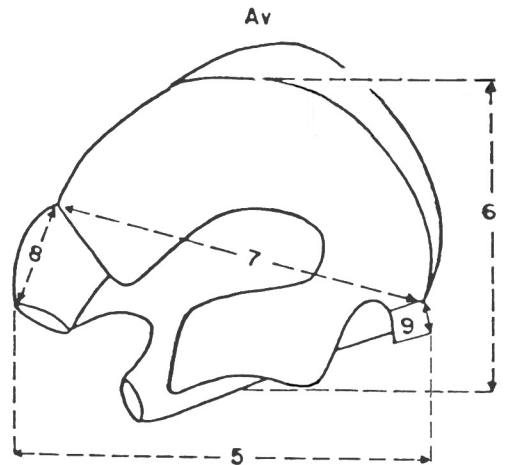
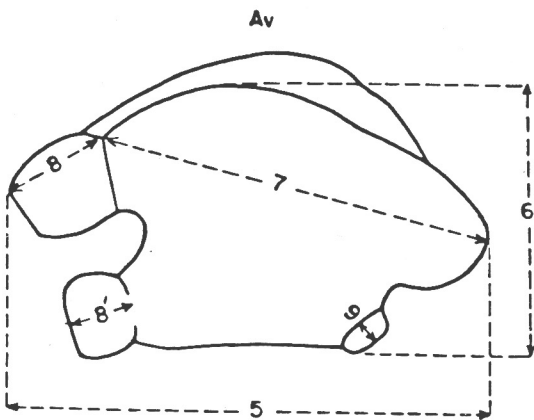
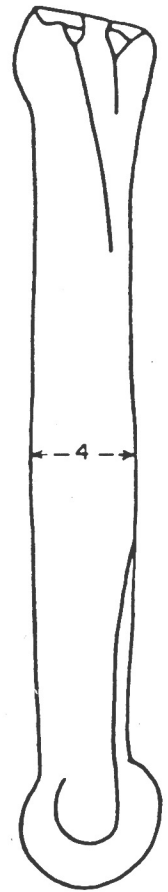
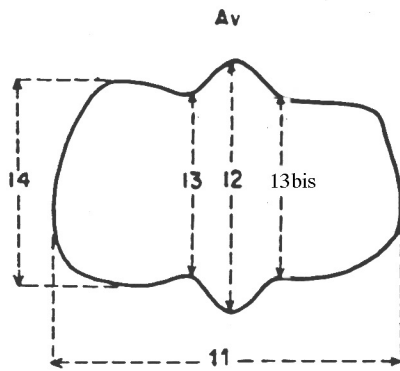
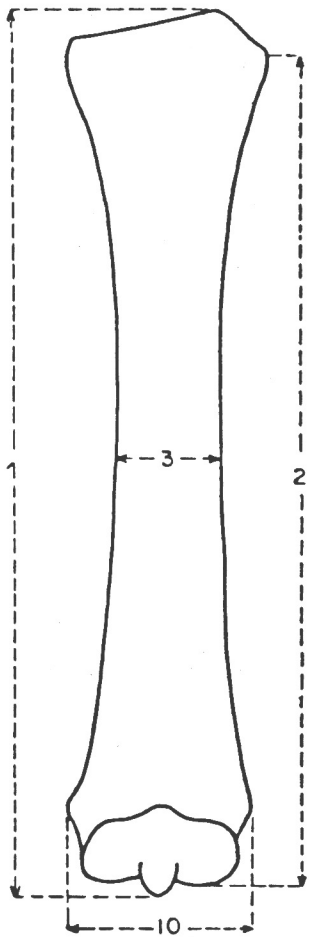
- | | |
|------------------------------------|-----|
| 1. Greatest length | GL |
| 2. Lateral length | Ll |
| 3. Smallest breadth | SD |
| 4. Proximal breadth | Bp |
| 5. Proximal articular breadth | BFp |
| 6. Proximal articular depth | - |
| 7. Distal breadth | Bd |
| 8. Distal articular breadth | BFd |
| 9. Greatest distal articular depth | - |
| 10. Breadth of radial condyle | - |
| 11. Breadth of ulnar condyle | - |

Fig. 39 Third Metacarpal (Mc III):

1. Greatest length	GL
2. Lateral length	LI
3. Breadth in middle of shaft	(SD)
4. Depth in middle of shaft	–
5. Breadth of proximal articular surface	Bp
6. Depth of proximal articular surface	–
7. Diameter of articular facet for Os carpale III	–
8. Diameter of anterior articular facet for Os carpale IV	–
8'. Diameter of posterior articular facet for Os carpale IV	–
9. Diameter of articular facet for Os carpale II	–
10. Distal supra-articular breadth	(Bd)
11. Distal articular breadth	(Bd)
12. Depth of sagittal crest	Dd
13. Smallest depth of the medial condyle	–
14. Greatest depth of the medial condyle	–

Third Metatarsal (Mt III):

1. Greatest length	GL
2. Lateral length	LI
3. Breadth in middle of shaft	(SD)
4. Depth in middle of shaft	–
5. Proximal breadth	Bp
6. Proximal depth	Dp
7. Diameter of articular facet for Os tarsale III	–
8. Diameter of articular facet for Os tarsale IV	–
9. Diameter of articular facet for Os tarsale II	–
10. Distal supra-articular breadth	(Bd)
11. Distal articular breadth	(Bd)
12. Depth of sagittal crest	Dd
13. Smallest depth of medial condyle	–
14. Greatest depth of medial condyle	–



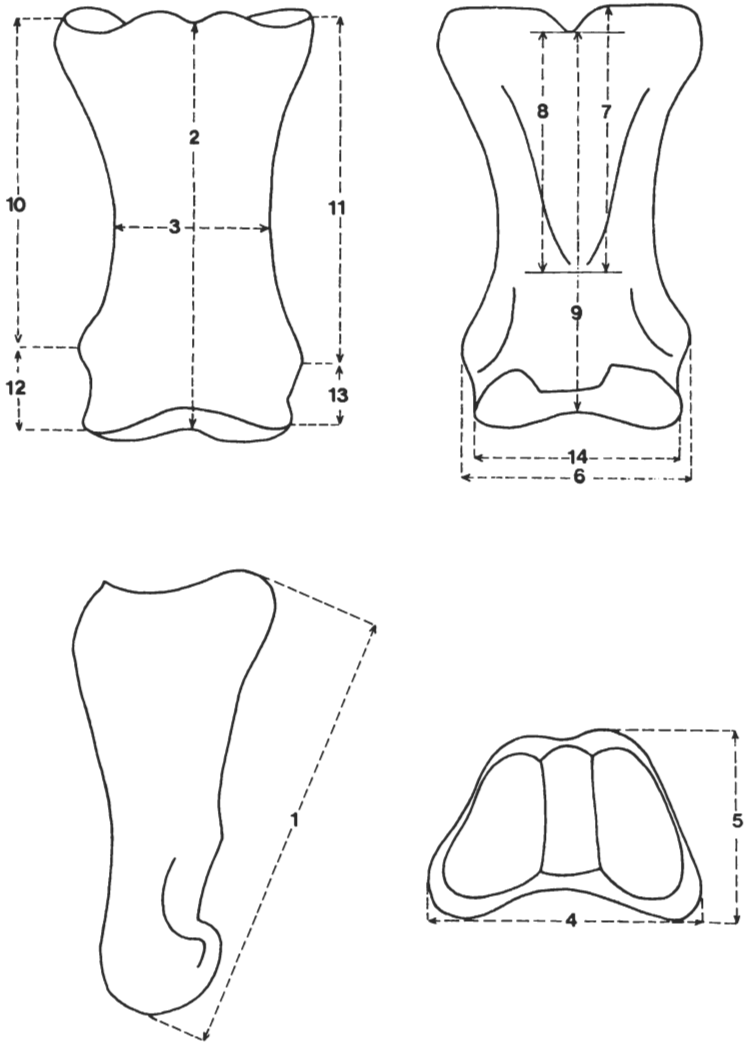


Fig. 40 First Phalanges (Ph. 1):

1. Greatest length	GL
2. Anterior length	—
3. Smallest breadth	SD
4. Proximal breadth	Bp
5. Proximal depth	Dp
6. Distal supra-articular breadth	Bd
7. Greatest length of trigonum phalangis	—
8. Smallest length of trigonum phalangis	—
9. Posterior length	—
10. Medial supratuberosital length	—
11. Lateral supratuberosital length	—
12. Medial infratuberosital length	—
13. Lateral infratuberosital length	—
14. Distal articular breadth	BFd

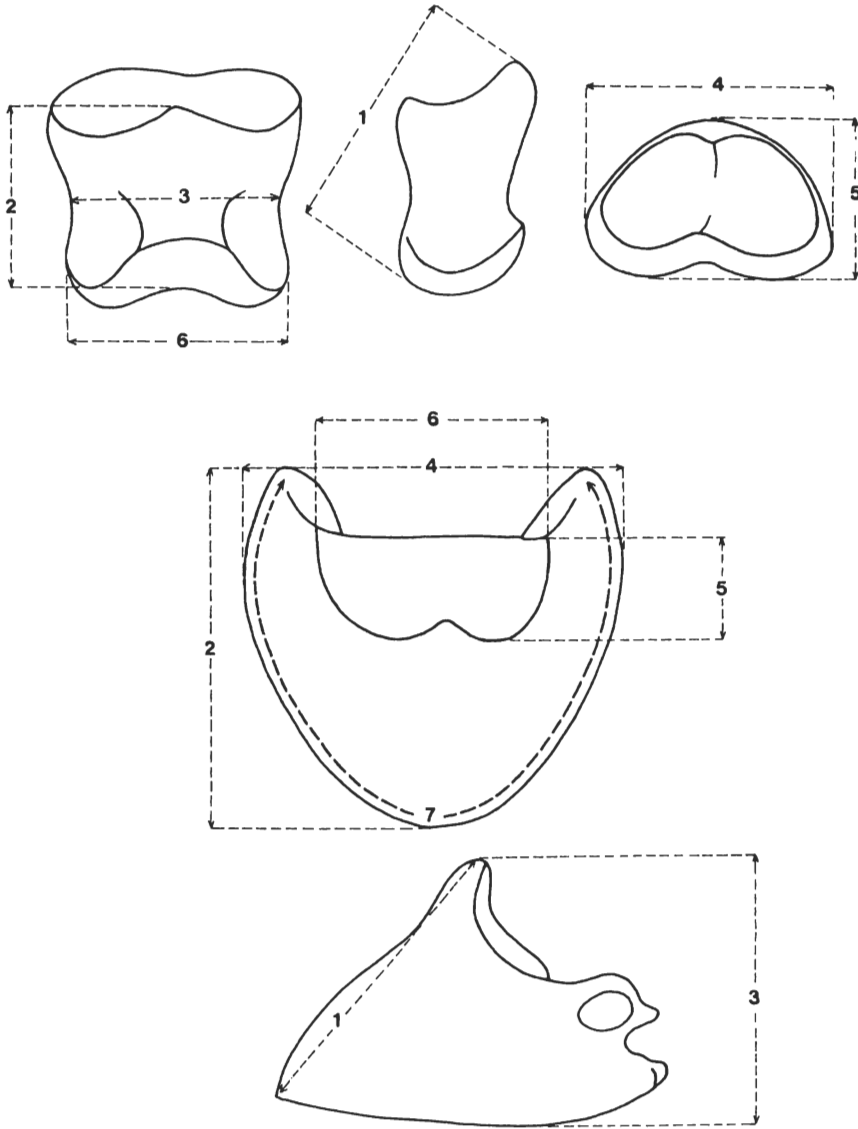


Fig. 41 Second Phalanges (Ph. 2):

- | | |
|-----------------------------|----|
| 1. Greatest length | GL |
| 2. Anterior length | - |
| 3. Smallest breadth | SD |
| 4. Proximal breadth | Bp |
| 5. Proximal depth | Dp |
| 6. Distal articular breadth | Bd |

Third Phalanges (Ph. 3):

- | | |
|---------------------------------------|----|
| 1. Anterior length | Ld |
| 2. Greatest anteroposterior diameter | GL |
| 3. Height | HP |
| 4. Greatest breadth | GB |
| 5. Articular anteroposterior diameter | LF |
| 6. Articular breadth | BF |
| 7. Distal "circumference" | - |

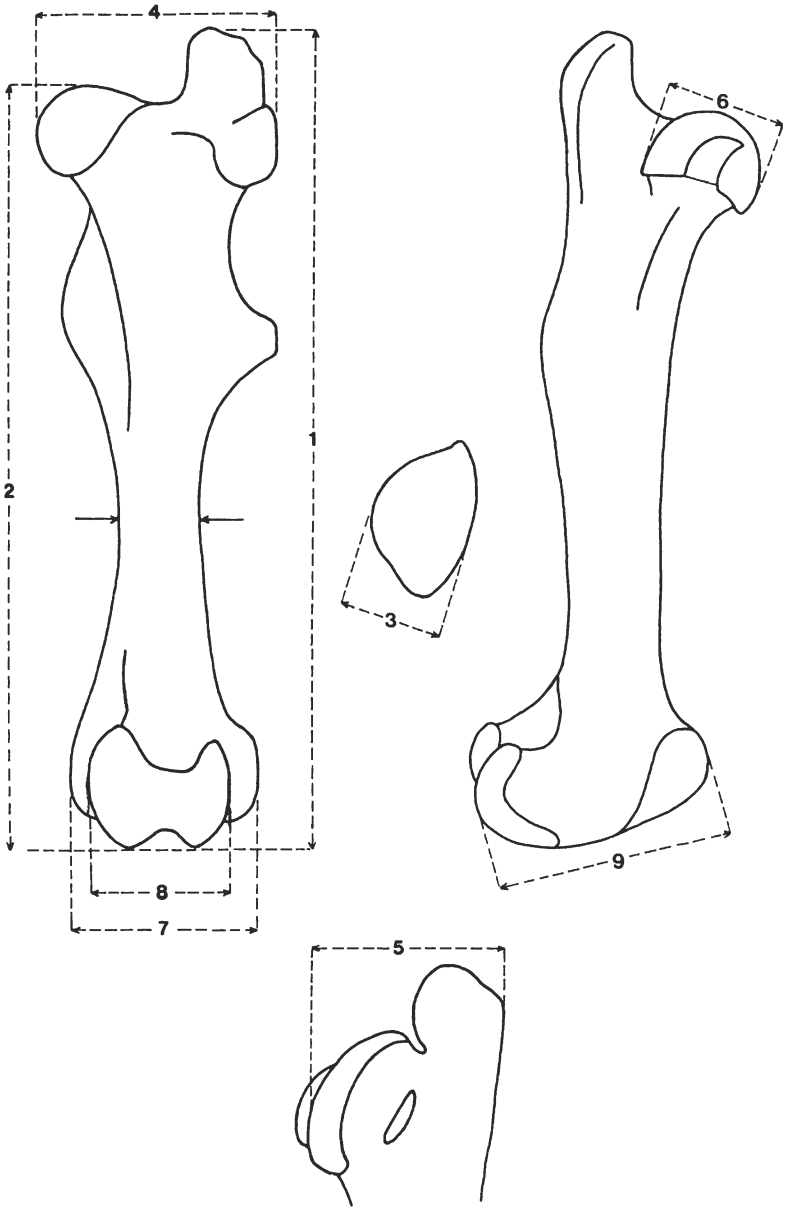


Fig. 42 Femur:

1. Greatest length	GL
2. Medial length	GLC
3. Smallest breadth	SD
4. Proximal breadth	Bp
5. Proximal depth	-
6. Depth of caput femoris	DC
7. Distal breadth	Bd
8. Distal articular breadth	-
9. Distal medial breadth	-

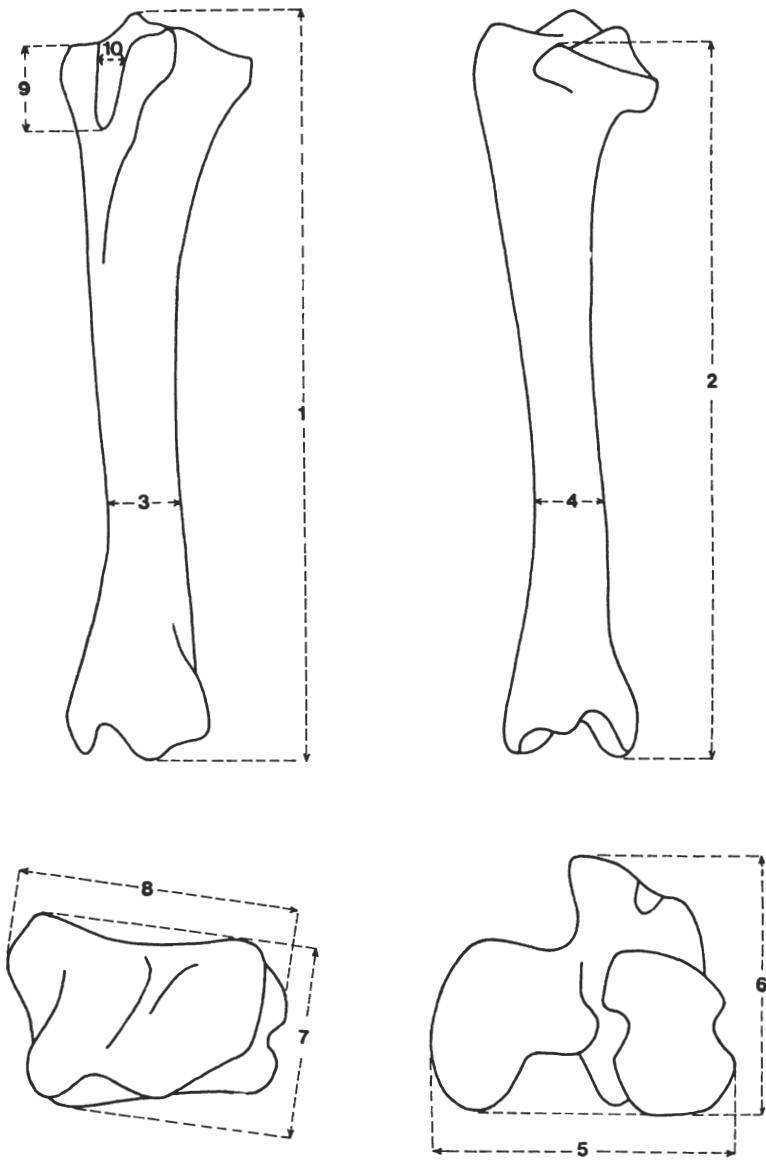


Fig. 43 Tibia:

- | | |
|--|-----|
| 1. Greatest length | GL |
| 2. Lateral length (use same distal point as for greatest length) | (L) |
| 3. Smallest breadth | SD |
| 4. Smallest depth | - |
| 5. Proximal breadth | Bp |
| 6. Proximal depth | - |
| 7. Distal depth | Dd |
| 8. Distal breadth | Bd |
| 9. Length of fossa digitalis | - |
| 10. Breadth of fossa digitalis | - |

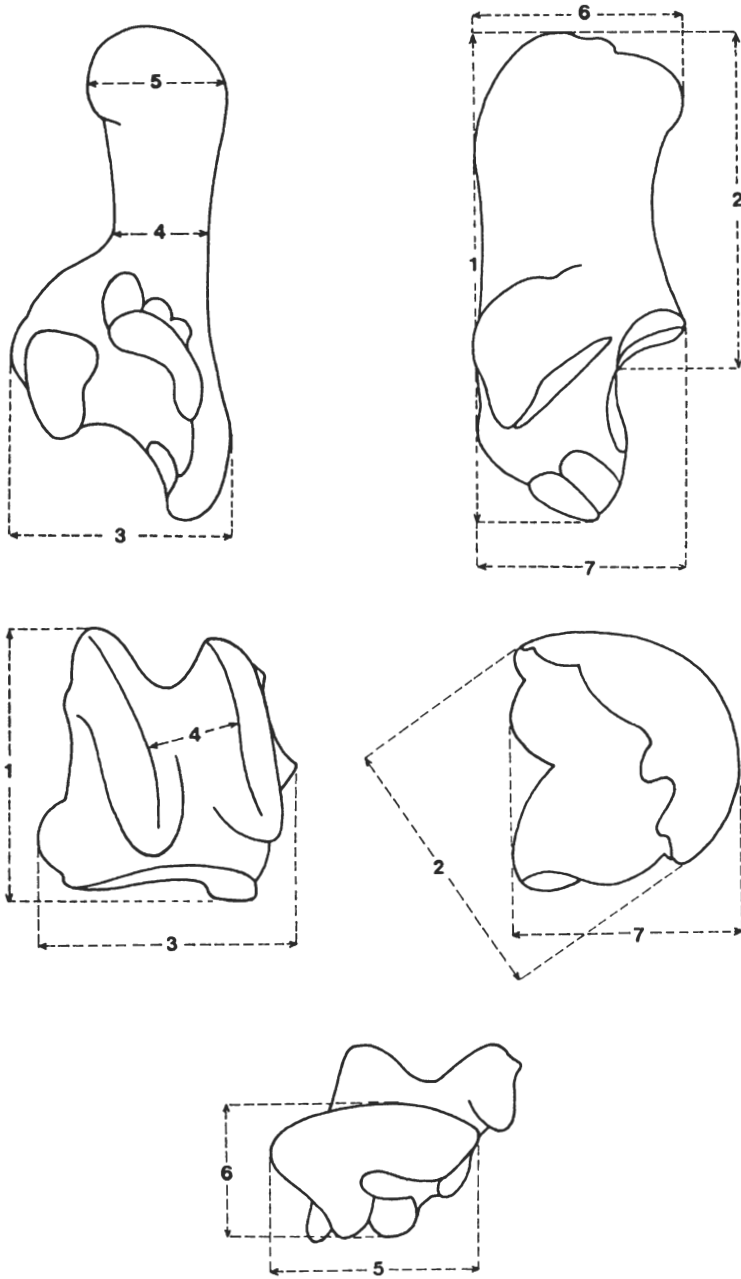


Fig. 44 Talus:

- | | |
|------------------------------|------|
| 1. Greatest length | (GH) |
| 2. Medial length of trochlea | LmT |
| 3. Greatest breadth | GB |
| 4. Trochlear breadth | - |
| 5. Distal articular breadth | BFd |
| 6. Distal articular depth | - |
| 7. Medial depth | - |

Calcaneum:

- | | |
|----------------------------|----|
| 1. Greatest length | GL |
| 2. Length of proximal part | - |
| 3. Greatest breadth | GB |
| 4. Smallest breadth | - |
| 5. Proximal breadth | - |
| 6. Proximal depth | - |
| 7. Distal depth | - |