D. Benor

STUDYING FOSSIL HORSES

EDITORS: MIKE WOODBURNE AND PAUL SONDAAR

Collected papers after the "New York International Hipparion Conference, 1981"

Volume I: Methodology

V. EISENMANN, M. T. ALBERDI, C. DE GIULI AND U. STAESCHE

E.J. BRILL

STUDYING FOSSIL HORSES

EDITORS: MIKE WOODBURNE AND PAUL SONDAAR

Collected papers after the "New York International Hipparion Conference, 1981"

Volume I: Methodology

V. EISENMANN, M. T. ALBERDI, C. DE GIULI AND U. STAESCHE

E.J. BRILL
LEIDEN • NEW YORK • KØBENHAVN • KÖLN
1988

Library of Congress Cataloging-in-Publication Data

New York International Hipparion Conference (1981:
American museum of Natural History)
Studying fossil horses.

Bibliography: p.
1. Horses, Fossil—Congresses. I. Woodburne,
Michael O. II. Sondaar, P. Y. III. Title.
QE882.U6N49 1981 569'.72 87-27741
ISBN 90-04-08616-1 (pbk.: v.1)

ISBN 90 04 08616 1

© *Copyright 1988 by E. J. Brill, Leiden, The Netherlands*

All rights reserved. No part of this book may be reproduced or translated in any form, by print, photoprint, microfilm, microfiche or any other means without written permission from the publisher

PRINTED IN THE NETHERLANDS BY E. J. BRILL

CONTENTS

Foreword VII
List of participants VIII

Introduction 1

General Remarks on Terminology, Definitions, and Equivalences of Measures 3

Skull and Mandible 5
- Skull: figures 1-3 6
- Mandible: figure 4 12

Teeth 17
- Upper Cheek teeth 17
  - How to distinguish isolated premolars and molars? 17
  - Characters that can be measured 18
  - Parameters that have to be calculated 18
  - Characters that have to be counted 19
  - Characters that have to be described 19
  - Upper cheek teeth of *Hipparion:* figure 5 20
  - Upper cheek teeth of *Equus*: figure 6 22
- Lower cheek teeth 24
  - How to distinguish isolated premolars and molars? 24
  - Characters that can be measured 24
  - Parameters that have to be calculated 25
  - Characters that have to be described 25
  - Lower cheek teeth of *Hipparion*: figure 7 26
  - Lower cheek teeth of *Equus*: figure 8 28
  - How to discriminate lower cheek teeth of *Equus* and *Hipparion*? 28
- Incisors 30
  - Lower incisors and cheek teeth of *Hipparion*: figure 9 30
  - Lower incisors of *Equus*: figure 10 32
  - Incisors in general 32

Limb Bones 35
- Scapula and Pelvis: figure 11 36
- Humerus: figure 12 38
- Radius: figure 13 40
- Ulna: figure 14 42
- Carpus: figures 15, 16, 17 44
- Third metacarpal: figure 18 48
- Femur: figure 19 50
- Tibia: figure 20 52
- Tarsus: figure 21 54
- Calcaneus: figure 22 55
- Talus: figure 23 56
- Other tarsals: figure 24 58

Third metatarsal: figure 25 60
Lateral metapodials of *Hipparion*: figure 26 62
First phalanges of *Equus* and *Hipparion*: figure 27 64
Second phalanges of *Equus* and *Hipparion*: figure 28 66
Third phalanges of *Equus* and *Hipparion*: figure 29 68

Bibliography 70

FOREWORD

Volume I of the "New York Hipparion Conference" is mostly dedicated to methodology; it proposes a standardized system to be used by all students in equids.

The usefulness of a standardized system, internationally applied, speaks for itself: when there is such an amount of material all around the world, no single person can collect data on the whole of it. At the same time, a geographically and chronologically broad knowledge is a prerequisite to understand phylogenetic relations and therefore also to propose reasonable correlations and biostratigraphies. The only way to acquire it is to compare one's own data with data published by other people. But the data must need be comparable, i.e. concern the same points observed in the same ways.

To construct such a system was the aim of a lot of more or less formal discussions among european "equid people" during the seventies. It culminated at the New York International Hipparion Conference sponsored by the National Science Foundation (Grant EAR 8110870), in November 1981, when 18 people from 8 countries accepted the invitations issued by R. H. Tedford, J. A. Van Couvering, M. O. Woodburne and P. Y. Sondaar and met at the American Museum to discuss and practise the system elaborated in Europe. At the end of the Conference, some modifications were proposed and it was also agreed that the ultimate system—as it is published here—was to be recommended for international use as a *minimum* set of measures and observations.

Everyone present at the Conference (see list on next page) participated to the discussions and the elaboration of the system here presented, and everyone agreed on the final version presented here. The persons entrusted with the redaction are however responsible for the texts and illustrations as well as for the personal comments they may introduce.

During the Conference, the system in course of elaboration was tested: the same material (one cranium, one mandible, one central metacarpal, one central metatarsal) were measured by every participant. In this way we hoped to check the consistency of the measures and, in consequence, their reliability. A quarry sample of Clarendonian horses was also observed, measured and discussed by all the participants. These data and their interpretations will be published in the next volume.

LIST OF PARTICIPANTS

ABERDI M. T., Instituto "Lucas Mallada", Consejo Superior de Investigaciones Cientificas, Museo Nacional de Ciencias Naturales, Jose Gutierrez Abascal 2, Madrid - 28006, Spain.

BERNOR R. L., College of Medicine, Department of Anatomy, Howard University, 520 W Street, Washington, D.C. - 20059, U.S.A.

DE GIULI C., Museo di Geologia e Paleontologia dell'Universita di Firenze, via La Pira 4, Firenze - 50121, Italy.

EISENMANN V., U.A. 12 du CNRS, Institut de Paléontologie, 8 rue Buffon, Paris - 75005, France.

EVANDER R. L., Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th, New York, N.Y. - 10024, U.S.A.

HOWE J.A., Bowling Green State University, Department of Geology, Bowling Green, Ohio - 43403, U.S.A.

HUSSAIN S. T., College of Medicine, Department of Anatomy, Howard University, 520 W Street, Washington, D.C. - 20059, U.S.A.

MACFADDEN B. J., Department of Natural Sciences, The Florida State Museum, University of Florida, Museum Road, Gainesville, Florida - 32611, U.S.A.

QIU Chansiang, Institute of Vertebrate Paleontology and Paleanthropology, Academie Sinica, P.O. Box 643, Beijing - 28, China.

SKINNER M. F., Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th, New York, N.Y. - 10024, U.S.A.

SOLOUNIAS N., Department of Cell Biology and Anatomy, School of Medicine, The John Hopkins University, 725 North Wolfe Street, Baltimore, Maryland - 21205, U.S.A.

SONDAAR P. Y., Instituut voor Aardwetenschappen, Rijksuniversiteit Utrecht, Budapestlaan 4, Postbus 80.021, Utrecht - 3508 TA, Netherlands.

STAESCHE U., Niedersächsisches Landesamt für Bodenforschung, Stilleweg 2, Postfach 51 01 53, 3000 - Hannover - 51, West Germany.

TEDFORD R. H., Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th, New York, N.Y. - 10024, U.S.A.

TOBIEN H., Institut für Geowissenschaften, FB 22, Johannes Gutenberg Universität, Saarstrasse 21, Postfach 3980, 6500 - Mainz - West Germany.

VAN COUVERING J. A., Micropaleontology Press, American Museum of Natural History, Central Park West at 79th, New York, N.Y. - 10024, U.S.A.

WINANS M., Vertebrate Paleontology Laboratory, Balcones Research Center, Building 6, 10100 Burnet Road, Austin, Texas - 78758, U.S.A.

WOODBURNE M. O., Department of Earth Sciences, University of California, Riverside, California - 92521, U.S.A.

INTRODUCTION

The present methodological system for the study of *Equus* and *Hipparion* bones and teeth is intended for people who need not be convinced of the usefulness of morphometry, and who agree that there is no real opposition nor mutual exclusion between "observing" and "measuring". These points were discussed at some length in a previous paper (Eisenmann 1986) and we will not come back to them.

Since at the basis of this new system lies an original "european" system that had been in use for more than 10 years, we should perhaps explain how, and what for, it was initially elaborated, and why it differs from another push at standardization, namely the "Guide to the measurements of animal bones" by A. von den Driesch (1976). The second point is easy: when the "Guide" was published, some of us had already been accumulating data for several years and could not switch to another system. Even so, a lot of measures are common to both systems and we noted them in tables of correspondence for each bone.

The other questions need a longer developement. In the foreword to A. von den Driesch "Guide", there is a sentence with which we deeply agree: "If they (the measurements) are useful, use them; if they are not, change them". But what is "useful"? In our opinion, a useful measurement is one which helps to express a visible difference between morphologies, compared at a particular time by a particular worker, for a particular purpose.

This definition implies that it is more important to try to quantify differences *one can see*, even if the measures are difficult to define and variable, than be content with precise but not diagnostic measurements. For example, when one looks at *Equus* first phalanges, one can see that anterior and posterior phalanges differ in the relative position of the supraarticular tuberosities. One of the best ways to discriminate anterior and posterior first phalanges of *Equus* (Eisenmann & De Giuli, 1974b; Dive & Eisenmann, in press) is to use this observation, although the relevant measures are *not* precise and have very high coefficients of variation. Our definition implies also that there is no "absolute" usefulness of a measurement. For example, the height of the zygomatic arc under the orbit is very useful to distinguish between skulls of Mountain and Plain Zebras (Eisenmann & De Giuli, 1974a); it is not very useful when comparing skulls of other species of *Equus* (Eisenmann, 1980). For this reason, the elaboration of a system is never really finished. For any particular worker, new materials bring new problems that need to be addressed by new observations and measures.

On the other hand, the particular worker is not alone. When he begins to work with (for example) equids, he is usually aware that other people have done so before. These people may have already found that some points were interesting; and they may have published data on them. If the new worker wants to use this experience and these data, he has naturally to take the same measurements other people take, or took. For this reason, any methodological system is usually composed of previously recommended measurements (or observations) and "new" ones, designed to answer some "new" specific questions. Since no one can accept as basis *all* the measurements that have ever been recommended, one usually takes as basis one particular system and modifies it according to his whims and his aims.

Concerning the postcranial skeleton, the "european system" emerged after discussions with P. Y. Sondaar who had worked on *Hipparion* limb bones (Sondaar, 1968), from the system of measurements published by Gromova (1963). After some minor additions during the next years, this system was applied first to *Equus*, then to *Hipparion*. At the moment, no one was aware that another system was

being elaborated in Archaeozoology (von den Driesch, 1976) and still another in North America (Willoughby, 1948, 1974). Our *Equus* system was integrally published in Eisenmann dissertation (1979a) and in the volume consecutive to the International symposium on equids held in 1982 at Tübingen (1986). Partial publications date from 1974b (Eisenmann & De Giuli) to "in press" (Dive & Eisenmann).

The cranial "system" emerged much in the same way, on the basis of the papers published by Osborn (1912), Motohashi (1930), Hooijer (1949) and (mostly) Gromova (1949), as well as on the basis of qualitative characters noted by Azzaroli (1966); again the system recommended by von den Driesch was not considered because it was not yet published. The first publication of our system dates to 1974a (Eisenmann & De Giuli); the last additions (Eisenmann, 1981b) were made after concertation with M. T. Alberdi, C. De Giuli, P. Sondaar and U. Staesche.

The teeth methodology was also the result of discussions using as basis Gromova observations and measurements (1949, 1952) and those of Alberdi (1972-1974), Cooke (1950), Forstén (1968), Gabunia (1959), Hooijer (1975), Petit (1939), Prat (1968), Sondaar (1961), Stirton (1941), Van Hoepen (1940), and probably others. The applications to *Equus* have been published by Eisenmann (1976, 1979b, 1980, 1981a). At that moment, we did not know the paper of Skinner & Hibbard (1972), in which are given observations very similar to those of Gromova, but with another terminology ("isthmus" for "stem" of the double knot in the lower cheek teeth, for example).

In short, the initial system was based mostly on the publications of Gromova, and it was reworked in the aim of comparing first Zebras, then other *Equus* species, then (much later) *Hipparion* species. It was empirically constructed with new measurements added "in disorder" to old ones whenever it seemed necessary. It has been "tested" by 10 years of practice on modern and fossil bones and teeth and submitted to multivariate analyses (Eisenmann & Turlot, 1978; Eisenmann & Karchoud, 1982; Dive & Eisenmann, in press). In doing so, not only something was found about the interspecific differences inside the genus *Equus*, but also about the relative "usefulness" of the measurements employed to express these differences. It was also made clear that, in many cases, a few measurements are not sufficient to correctly discriminate bones. For example, the gracility index usually employed to characterize metapodials is indeed important, but often it is not enough to achieve a specific determination.

The present system differs in several ways from the original one: 1) the order in which the measurements are proposed try to be practical and logical. For example, the first 15 skull measurements can all be taken on the ventral face of the skull; most of limb bones measurements are equivalent (numbers 1 and 2 deal with maximal and internal lengths, numbers 3 and 4 with diaphyseal breadth and depth, etc.). 2) The system has been modified to adapt not only to *Equus* but also to *Hipparion*: measures were added for the preorbital fossa of the skull (Woodburne & Bernor, 1980; Woodburne, MacFadden and Skinner, 1981), for the depth of the narial opening (Eisenmann, 1981b), as well as for lateral metapodials and phalanges (Sondaar, 1968). 3) The "usefulness" of some new measurements has not yet been tested. According to the wish of the majority of the participants, several "old" measurements were changed or even suppressed even though they seemed "good" to a minority. Some comments on the differences between the systems will be found in the next chapter ("General remarks on terminology, definitions, and equivalences of measurements").

GENERAL REMARKS ON TERMINOLOGY, DEFINITIONS, AND EQUIVALENCES OF MEASURES

Besides defining the measurements of equid bones and teeth as they were recommended by the New York Hipparion Conference, the aim of this paper is also to make these measurements easily recognizable and reproducible, even by little experienced people. Great emphasis is therefore laid on a clear presentation of the measurements by drawings. These figures and their captions constitute the main part of the paper. But some complementary explanations concerning the terminology used in describing bones and their orientations are also needed, although they cannot find room inside the captions, as well as some general comments on the definitions of measurements and their equivalences.

Terminology

There is a general agreement on the nomenclature of bones and their components (Barone, 1966; von den Driesch, 1976). When different names may be used, as for carpals and tarsals, we have tried to give the list of synonyms. Priority has been given to the names more usual in English.

Since we deal with equids alone (especially *Hipparion* and *Equus*), i.e. a selected and homogeneous group of Mammals, we need not consider the problems that may arise when dealing with various differently specialized animals. Even though, the terminology applied to the orientation of bones and definition of measurements is not quite uniform nor evident. Directions and orientations are in general named by reference to the living animal (or the mounted skeleton). Let us specify that *lateral* refers to the outer sides of an animal; *medial*, at the opposite, is near the plane of symmetry. By reference to the long axis of the body, are *anterior* the structures looking to the front and *posterior*, those looking to the rear. *Caudal* refers to a part closer to the tail, *cranial* to a part closer to the head; thus cranial may be a synomym for anterior and caudal for posterior. In the skull, structures looking upwards, and downwards, are named, respectively, *dorsal*, and *ventral*. In a limb or in any long limb bone, the *proximal* part is the one nearer the attachment to the trunk while the *distal* part is the one nearer the free end of the limb.

Definitions

For limb bones, measurements follow the three main spatial directions. The *length* is usually the greatest dimension and more or less proximo-distal. It is usually measured along the long axis of the bone. In some cases, a proximo-distal measurement may be called *height*. *Breadth*, width, and transverse diameter are synonyms; they qualify dimensions perpendicular to the length and medio-laterally orientated. *Depth* qualify dimensions perpendicular to length and breadth, and oriented in a antero-posterior direction; depth is naturally synonym of antero-posterior diameter. Length, breadth and depth were prefered because the same terms are used by von den Driesch "Guide" (1976) and in the book edited by R. H. Meadow and H. P. Uerpmann after an international symposium on equids (Eisenmann, 1986). For measurements which cannot fit any of the three main directions, the term *diameter* may be used, for example for the dimensions of some articular facets. It may happen also that breadths and widths are not exactly perpendicular to each other, nor to the length, or not exactly medio-laterally or antero-posteriorly oriented. Mention is made of such discrepancies when it seems necessary to avoid confusion. In most of these cases, one of the dimensions is defined between prominent points; such points are indicated on the figures by small black triangles.

Equivalences of the measurements

For most bones of *Hipparion* and *Equus*, measurements are identical. When necessary (skull, lateral metapodials and phalanges), additional figures and recommendations are given.

The equivalences to the most complete recent system (von den Driesch, 1976) and to the "old" system are given in short tables for most bones. In these tables, the proposals of this paper are referred to as "PP" (Present Paper), those of von den Driesch as "AVD", and those of Eisenmann as "VE".

Comments on the differences between the "new" and the "old" system will be made at the beginnings of the main chapters (Skull and Mandible, Teeth, Limb Bones).

For paired structures (limbs and teeth), it is the left ones that are always figured.

SKULL AND MANDIBLE

On the whole, the present methodology for the skull improves on the old one. The order of the measurements is easier to follow; some measures are defined in a more logical way (alveolar lengths instead of occlusal for the cheek teeth); several indifferent or redundant measures were suppressed; probably useful ones (palatal width, 2 occipital diameters, 8 measures for the preorbital area, etc.) were introduced. Some people may however regret the suppression of the measures for the diastema length, the cranial width, and 2 facial heights (numbers 6, 15, 26 and 27 in Eisenmann, 1986). For the mandible also, there is a general improvement, mostly by additions of new heights, but again the suppression of the diastema's length measure may be regretted.

SKULL

The Alveolar plane is the plane of reference.

Figure 1. - *Ventral view*

1. Muzzle length: from Prosthion (point situated between the bases of the I^1) to the middle of the line connecting the anterior borders of the P^2.
2. Palatal length: minimal length between the middle of the line connecting the anterior borders of the P^2 and the point P situated at the base of the Palatal spur.
3. Vomerine length: from the same point P to the middle of the Vomerine notch.
4. Post-vomerine length: from the middle of the Vomerine notch to Basion (point situated at the middle of the ventral border of the Foramen magnum).
5. Post-palatal length: from the point P to Basion (5 is roughly equal to 3 + 4).
6. Basilar length: from Prosthion to Basion.
7. Premolar length: alveolar and on the vestibular side, without the P^1, if present.
8. Molar length: alveolar and on the vestibular side.
9. Upper cheek teeth length: alveolar, without the P^1, if present.
10. Choanal length: in projection from point P to the point of meeting of the guttural and caudal parts of the Vomer (always approximative).
11. Minimal breadth of the Choanae.
12. Maximal breadth of the Choanae.
13. Palatal breadth: at the level of P^4-M^1.
14. Minimal Muzzle breadth: the points of the calliper on the Premaxillary ridges.
15. Muzzle breadth: between the posterior borders of the I^3.
16. Length of Fossa temporalis: maximal.
17. Length between Basion and the Foramen ethmoidalis.

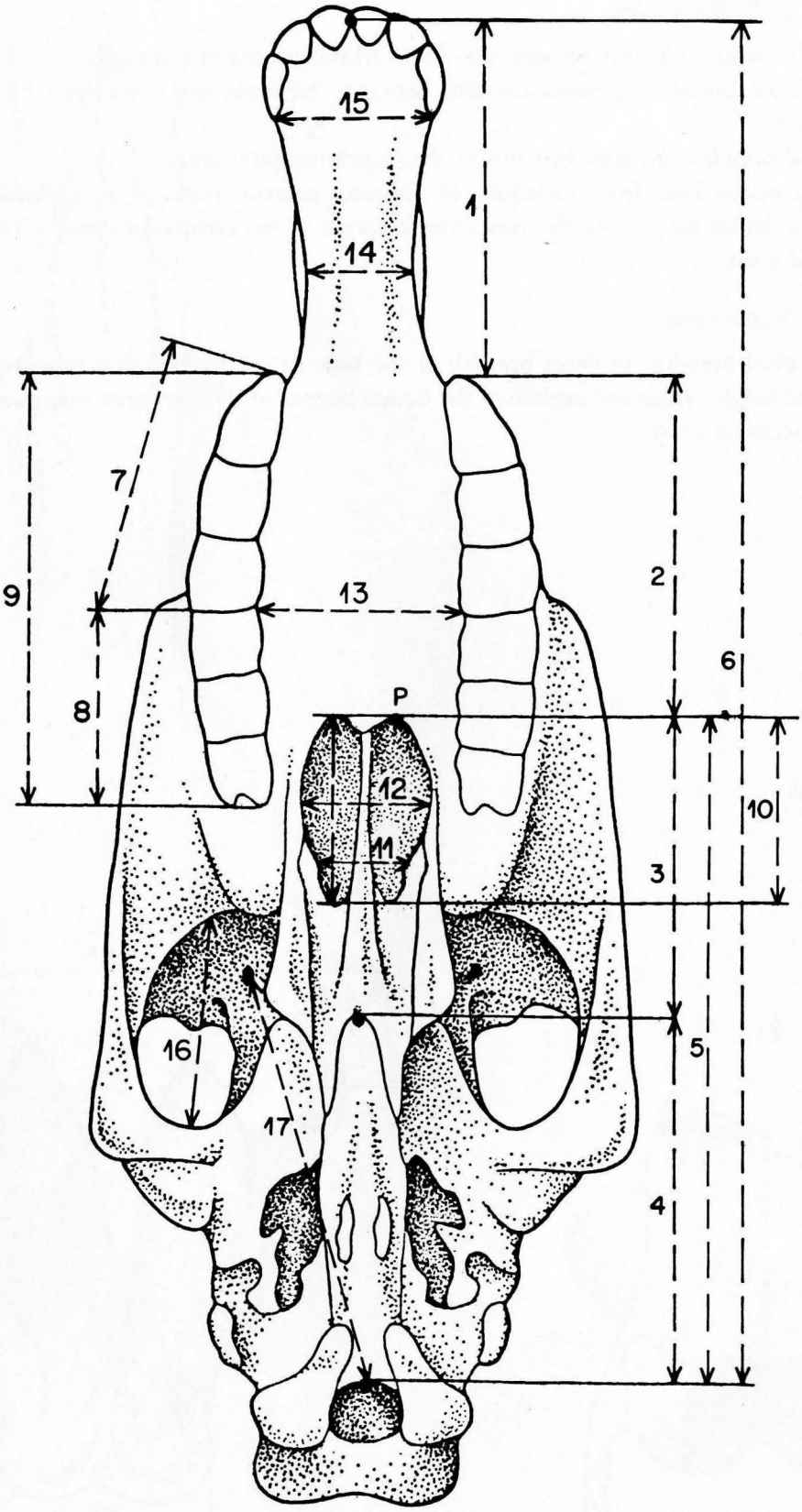

15
1
14
7
9
13
2
6
8
P
12
10
11
3
16
5
17
4

Figure 2.A - *Skull, Dorsal view*

18. Frontal breadth: greatest breadth between Orbital processes; compass.

19. Bizygomatic breadth: greatest breadth between the most exterior points of the Zygomatic arches; compass.

20. Occipital breadth: greatest breadth of the Supra-occipital crest.

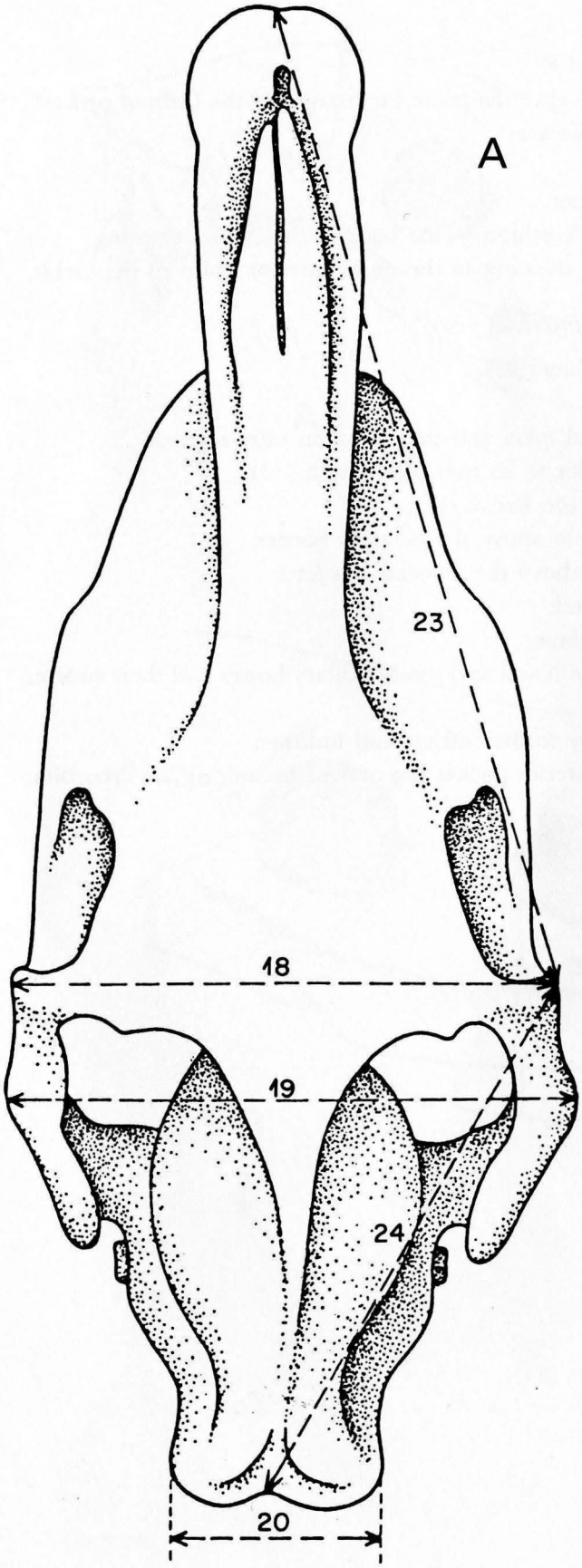
23. Anterior ocular line: from Prosthion to the most exterior point of the Orbital process.

24. Posterior ocular line: from the most exterior point of the Orbital process to the middle of the Supra-occipital crest.

Figure 2.B - *Occipital view*

21. Basioccipital breadth: greatest breadth at the base of the Paroccipital processes.

22. Occipital height: from the middle of the dorsal border of the Foramen magnum to the middle of the Supra-occipital crest.


A
23
18
19
24
20

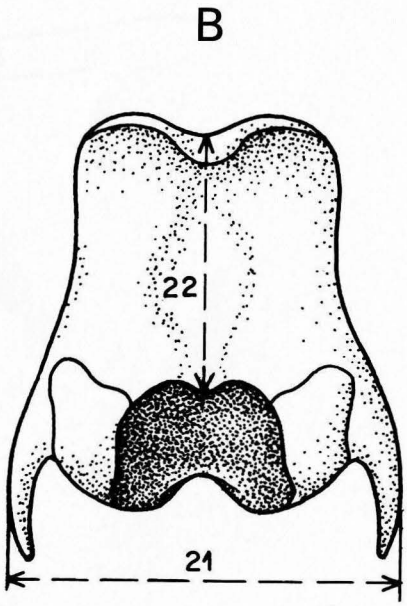

B
22
21

Figure 3.A - *Skull, profile*

25. Facial height: with the compass, in front of P^2.
26. Cranial height: with the compass, at the level of the posterior margin of the Orbital process.
27. Exterior height of the Meatus auditivus externus.
28. Antero-posterior Orbital diameter.
29. Orbital diameter perpendicular to the former.
30. Length of the Naso-incisival notch: from Prosthion to the back of the Narial opening.
31. Cheek length: from the back of the Narial opening to the most anterior point of the Orbit.

Figure 3.B. - *Skull, profile (In case of presence of a Preorbital fossa)*

32. Distance between the Orbit and the Preorbital fossa.
33. Length of the Preorbital fossa: maximal.
34. Distance between the back of the Preorbital fossa and the Foramen infra-orbitale.
35. Height of the Preorbital fossa: perpendicular to its maximal length (33).
36. Distance between the Preorbital fossa and the Facial crest.
37. Height of back of the Foramen infra-orbitale above the alveolar border.
38. Height of the back of the Preorbital fossa above the alveolar border.

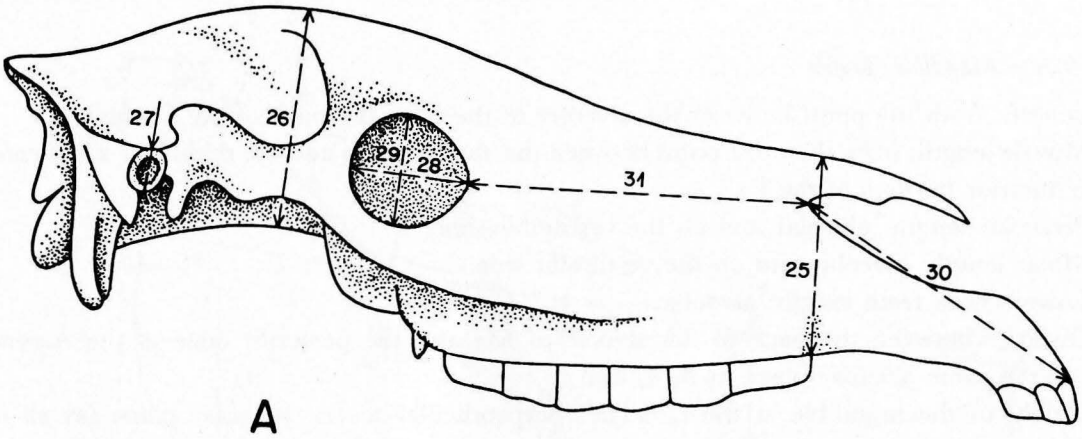
Some qualitative characters should also be noted:

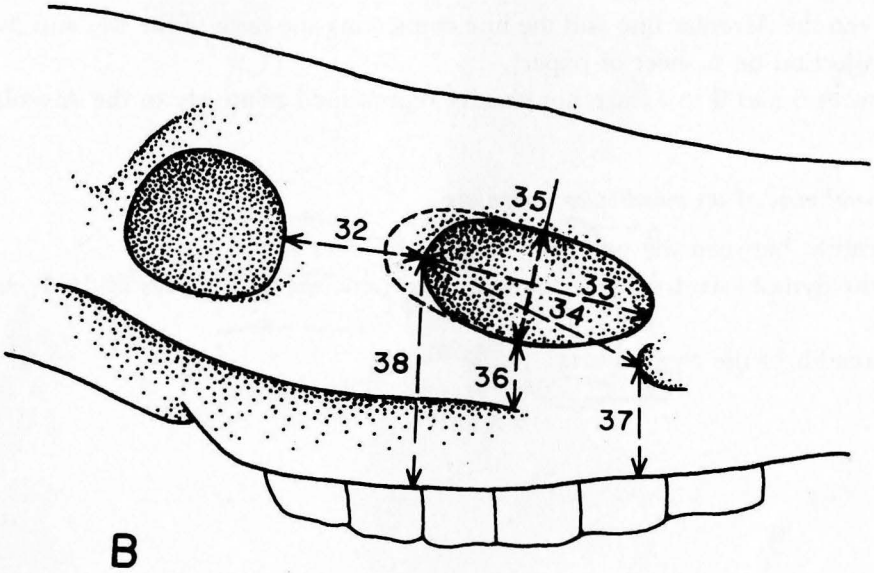
—axis of the Fossa relatively to the Alveolar plane;

—position of the Orbit and of the Lacrymal, the Nasal and the Maxillary bones and their sutures relatively to the Fossa;

—projection of the limits of the Fossa relatively to the Infraorbital foramen;

—presence and degree of development of the posterior pocket and of the rim limiting the Preorbital fossa (Woodburne & Bernor, 1980).


27
26
29
28
31
25
30
A


32
35
33
34
38
36
37
B

MANDIBLE

Figure 4.A - *Mandible, profile*

1. Length: from the point between the alveoles of the I_1 to the back of the Condyle.

2. Muzzle length: from the same point between the alveoles of I_1 and the middle of a line connecting the anterior borders of the P_2.

3. Premolar length: alveolar and on the vestibular side.

4. Molar length: alveolar and on the vestibular side.

5. Lower cheek teeth length: alveolar.

6. Distance between the back of the alveole of M_3 and the posterior edge of the Ascending ramus: in the same alveolar plane as 3, 4, and 5.

8. Height of the mandible at the Condyle: perpendicular to the Alveolar plane (as all other heigths), from the top of the Condyle to the plane tangent to the Horizontal ramus of the mandible.

9. Height of the Ascending ramus: from the bottom of the depression between Condyle and Coronoid process to the same plane.

10. Height of the jaw posterior to M_3 (always perpendicular to the Alveolar plane).

11. Height of the jaw between P_4 and M_1.

12. Height of the jaw in front of P_2.

15. Angle between the Alveolar line and the line connecting the back of the M_3 and the top of the Condyle (after projection on a sheet of paper).

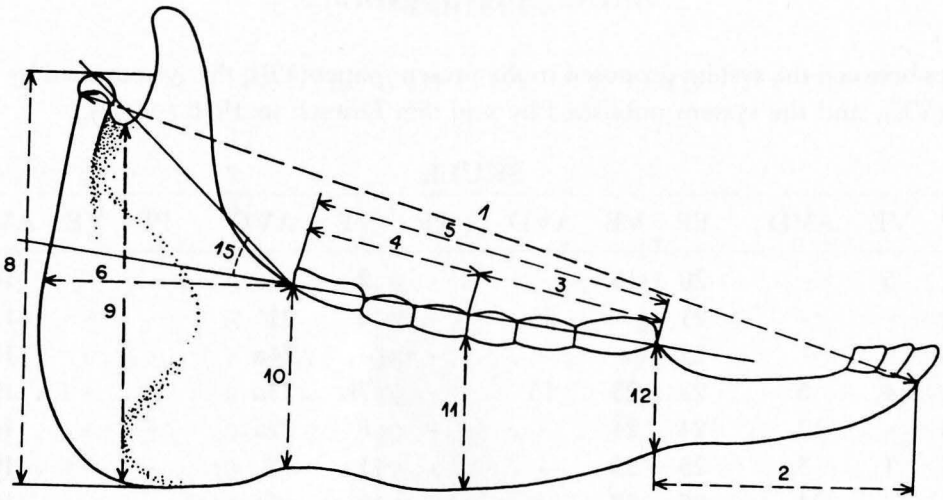
Note that measures 6 and 8 to 12 are not exactly represented relatively to the Alveolar plane on fig. 4.A.

Figure 4.B. - *Ventral view of the mandibular symphysis*

7. Muzzle breadth: between the posterior alveolar borders of the I_3.

13. Length of the Symphysis: from the point situated between the alveoles of the I_1 and the back of the Symphysis.

14. Minimal breadth of the Symphysis.



A

B

SKULL AND MANDIBLE

Equivalences between the system proposed in the present paper (PP), the system used by Eisenmann since 1974 (VE), and the system published by von den Driesch in 1976 (AVD).

SKULL

PP	VE	AVD	PP	VE	AVD	PP	VE	AVD	PP	VE	AVD
1	5	-	20	16	-	-	2	18a	-	-	10
2	-	-	21	-	35	-	6	21	-	-	11
3	3	-	22	-	-	-	7	24a	-	-	12
4	4	5	23	23	15	-	7b	23a	-	-	13
5	-	17	24	24	-	-	8	22a	-	-	14
6	1	3a	25	25	-	-	11	43	-	-	16
7	-	24	26	28	-	-	12	4	-	-	19
8	-	23	27	20	-	-	15	38	-	-	20
9	-	22	28	21	31	-	18	1	-	-	33
10	9	-	29	22	32	-	19	-	-	-	37
11	10b	-	30	31	-	-	26	-	-	-	39
12	10	-	31	32	-	-	27	-	-	-	40
13	-	-	32	-	-	-	29	36	-	-	42
14	17b	-	33	-	-	-	30	34	-	-	44
15	17	45*	34	-	-	-	-	2	-	-	46
16	-	-	5	-	-	-	-	6	-	-	47
17	-	-	36	-	-	-	-	7	-	-	48
18	13	41	37	-	-	-	-	8	-	-	49
19	14	-	38	-	-	-	-	9	-	-	50

* AVD measures the greatest breadth of the muzzle across the outer borders of the alveoli instead of the posterior borders; her measurements would be in consequence 5 to 10 mm bigger.

AVD uses also many other measurements (Von den Driesch, 1976, p. 19-22). Her measure 13 is roughly equal to PP (30 + 31) and VE (31 + 32).

MANDIBLE

PP	VE	AVD	PP	VE	AVD
1	1′	2	-	-	1
2	-	-	-	-	4
3	-	8	-	-	5
4	-	7	-	-	17
5	-	6	-	-	21
6	-	3	-	-	23
7	7′	16*	-	-	24
8	-	19	-	-	25
9	8′	20	-	-	-
10	-	22a	-	-	-
11	-	22b	-	-	-
12	-	22c	-	-	-
13	6′	-	-	-	-
14	-	18	-	-	-
15	-	-	-	-	-
-	2′	-	-	-	-
-	3′	15	-	-	-
-	4′	8a	-	-	-
-	4′-b				
		7a	-	-	-
-	5′	6a	-	-	-

* AVD takes this measurement across the outer borders of the alveoli instead of the posterior borders; accordingly her values would be 5 to 10 mm bigger.

AVD uses also 8 other measurements (Von den Driesch, 1976, p. 52-54).

TEETH

The many features significant in equid teeth require a special treatment to make the best use of their discriminating value. Some of them can be and should be measured, others will be counted, described, or their presence or absence merely stated. A detailed nomenclature has already been developed for the various characters of different kind of teeth. In the present paper, an effort has been made to standardize the nomenclature, to define and illustrate several patterns of protocones, double knots, and incisor morphologies in *Equus* and in *Hipparion*, and to explain how teeth should be measured, plications counted, and stages of wear taken in account.

In this paper we will consider only the permanent teeth because milk teeth are usually rarer, more difficult to observe, and less reliable for interspecific discrimination. The observations and measurements recommended for permanent teeth can however be used for milk teeth also.

When dealing with isolated teeth, the first step is to try to distinguish the different categories. No difficulties arise in separating P2 and M3 (both upper and lower). But the distinction between P3 and P4, or M1 and M2, or even between premolars (P3 and P4) and molars (M1 and M2) may prove very difficult. Not a single character of the many proposed by various authors (especially Cooke, 1950 and Gromova, 1952) is absolutely reliable when used alone, but when several of them are combined, in most cases a distinction is possible; if distinction between P3 and P4, and between M1 and M2 seem too uncertain, it should at least be tried to separate the sample in four categories: P2, P3 and P4, M1 and M2, M3. Special paragraphs deal with this question.

Since Gidley (1901) it is well known that the shape and size of equid teeth vary greaty with wear. Wear related variations have been studied in great detail by Petit (1939) and Howe (1970) in *Equus*, and by Sondaar (1961) in *Hipparion*. In order to neutralize these variations, different ways of measuring equid teeth have been proposed. Some authors recommend to distinguish several classes of wear and to submit the data on each class to a separate study; Gromova recommended to distinguish four stages of wear in *Hipparion* teeth; she was followed by Alberdi (1972, 1974). Musil (1969) proposed to distinguish three stages in *Equus*. In any case, the number of teeth in each wear-stage sample is smaller than the total number. To avoid such a reduction of the sample, other authors proposed to measure every tooth at the same height (i.e. at the same distance from the roots); Sondaar (1961) measured the teeth at 1 cm from the roots, Forstén (1968) exactly at the base of the crown, Prat (1968) and Hooijer (1975) at 2 cm from the roots. Eisenmann (1980) objected that the measurements taken too close to the roots are not really reliable because they include the cement (which is by itself very variable in thickness) and because the tooth is no longer in "normal" function; she pointed also that it is quite impossible to measure in this way teeth that are *not* isolated which is a pity since they are the only ones for which the place inside the row is absolutely certain. For *Hipparion* the New York Conference decided to recommend both occlusal (without the cement) and "1 cm from the roots" measurements on isolated teeth; occlusal measurements should be studied by stages of wear (four stages must be recognized). For *Equus*, are recommended occlusal measurements (without the cement) on not too worn or not too unworn teeth, and a set of measurements at the supposed mid-height of the crown, when possible.

Points specific to upper or lower cheeck teeth will be discussed in the corresponding chapters.

UPPER CHEEK TEETH

How to distinguish isolated premolars and molars?

Leaving aside the P^2 and the M^3, this is by no means an easy task, either in *Equus* or in *Hipparion*. A lot of characters have been proposed in the litterature. None is absolutely reliable. The best way seems to use several characters at the same time.

In the same series (and usually in the same species) molars are smaller than premolars. In the same series, molars (specially the M^1) are always more worn than premolars; in result, their occlusal shape is already quadrate when that of the premolars is still rectangular (length larger than width); later on, the occlusal shape of worn molars becomes rectangular in the other direction (width larger than length), while premolars are still quadrate. In molars, specially in M^2, the posterior width is smaller than the anterior width. Usually, the entire upper cheek row is mesio-distally convex. In result, premolars, specially P^3, have their occlusal surface tilted in the front direction; molars, specially M^2, have their occlusal surfaces tilted backwards. In premolars, the vestibulo-anterior horn of the postfossette tends to be more developed in the vestibular direction than the vestibulo-posterior horn of the prefossette; in molars, both horns reach roughly the same level.

By using the sum of these characters, one may hope to arrange at least part of a good sample of isolated teeth according to their exact position in the row and to study separately the 6 kinds of upper cheek teeth. For the rest of the sample, it may happen that only a distinction in 4 categories (P^2, P^3 or P^4, M^1 or M^2, M^3) is possible or even that the distinction between P^4 and M^1 is difficult. These problems usually arise for very worn teeth which are not very useful anyway; or for very unworn teeth in which case the best solution is to have them cut at mid-height, if it is possible.

Characters that can be measured

—Tooth height. The measurement is to be taken from the uppermost margin of the anterior root to the anterostyle in P^2 (fig. 5A), and to the parastyle in other upper cheek teeth (fig. 6B).

When possible, the maximum height of each kind of tooth (P^2, P^3, P^4, etc.) is estimated. The maximum is divided by 4 in order to distinguish 4 stages of wear for each kind of tooth. For example, if the maximum height for P^4 is 60 mm, all the P^4 the height of which is comprised between 60 and 45 mm belong to the first stage of wear, those measuring 30 to 45 mm belong to the second stage, those measuring 15 to 30 mm to the third, and those between 0 and 15 mm to the fourth. When measuring a complete tooth row, the determination of the stage of wear will usually be approximative.

—Length and breadth of the tooth, protocone length (and protocone breadth in *Hipparion*). These measurements are taken on the occlusal surface, excluding the cement (fig. 6C) and collected separately for teeth belonging to different stages of wear.

When dealing with isolated cheeck teeth of *Hipparion*, additional measures are taken at 1 cm from the roots (they usually have to include the cement, and the measure of breadth of the protocone is naturally impossible). For *Equus*, this set of measures is replaced by one taken at the supposed mid-height. In the case of *Equus* M^3, the measurements at mid-height seem much less variable then the occlusal ones. It is recommended not to include very worn or very unworn cheek teeth in the statistics (which amounts more or less to use only the teeth belonging to the two intermediate stages of wear).

Parameters that have to be calculated

—Hypsodonty indices (HI). Very important to estimate the degree of adaptation to a rough diet, the hypsodonty index should only be calculated for unworn or very little worn teeth, i.e. using the maximal height of the crown. It must be calculated separately for each kind of tooth (P^2, P^3, P^4, etc.).

In *Hipparion*, the HI = tooth length at 1 cm above the roots × 100 / maximal height. In *Equus*, the HI = tooth length at mid-height × 100 / maximal height. So that, the more hypsodont the tooth, the smaller the HI.

—Protocone indices (PI). Important for interspecific discriminations, these indices should also be calculated separately for each kind of tooth and only for teeth normally worn. PI = occlusal length of the protocone × 100 / occlusal length of the tooth. In unworn teeth, if the cement is not too thick,

it may be possible to use the mid-height lengths for *Equus*, and the "1 cm above the roots" lengths in *Hipparion*.

Characters that have to be counted

—Enamel plications. Are counted as plications the ones situated on the anterior and posterior walls of the pre- and postfossette, and the pli(s) caballin(s); other grooves or constrictions as in the hypoconal area or on the para- and mesostyle are not counted but have to be observed (see below).

The counting may be difficult for two reasons. First, one may not know if one has to count the invaginations *inside* or *outside* the fossette (on fig. 5B, there would be 2 plis protoloph in the first case, and only one in the second). Secondly, it may be difficult to decide if one is seeing a "true plication" or just a mere "wrinkle" of the enamel. It has been decided:

1. that the plications are to be considered as invaginations *inside* the fossette and evaginations in the direction of the protocone (on the figure 5B, there are 2 plis protoloph but only one pli caballin). Note that the pli protoconule was previously defined as an evagination, i.e. in a direction opposite to that of the other plications;

2. that in a "true" plication, the length is superior to the enamel thickness (suggestion of Dr Staesche). If not, the "wrinkling" of the enamel should be merely noted.

When a plication is very broad and seems to result from the fusion of two plis, it may be counted for two (for example, the first invagination posterior to the pli protoconule in fig. 5B). When a plication is bifurcated, each branch is counted as one plication. For the tooth illustrated in fig. 5B, the plication number may be conveniently noted in the following way: plis fossette / pli(s) caballin(s) = 2-8-4-1 / 1, which means that there are 2 plis on the anterior wall of the prefossette, 8 on its posterior wall, 4 on the anterior wall of the postfossette, 1 on its posterior wall, and 1 pli caballin.

When using the terms of plis prefossette or plis postfossette, one should precise if one is speaking "sensu stricto" or including in the former the plis protoloph and protoconule, and in the latter, the plis hypostyle. When giving the total number of plications by tooth, one should precise if the plis caballins are or not included.

Characters that have to be described

—Shape of the protocone (see below and fig. 5C for *Hipparion*, 6A for *Equus*).

—Characters of the fossettes. If the fossettes communicate one with the other, of if they are opened at one or other wall, these characters may be included in the plication formula:

• if the pre- and postfossettes were united in the tooth figured in 5A, these features could be noted by inserting an "equal sign" (=) between the numbers of plications on the posterior wall of the prefossette and that on the anterior wall of the postfossette; the formula would appear as follows: 2-8 = 4-1/1;

• if, moreover, the posterior wall of the postfossette were open, a "o" could be added after the plication number for the posterior wall of the postfossette: 2-8 = 4-1o/1.

—Hypoconal area. The presence of a constriction (as in P^4 of fig. 5A) or an islet (as in M^3 of fig. 5A) should be noted.

—Development of para- and mesostyles. Their widths and the presence or absence of grooves on them should be noted.

—The occurrence of wolf teeth (dP^1) should also be noted.

This list of observations is not limitative; any observations believed to be of some interest should naturally be added.

FIGURE 5: UPPER CHEEK TEETH OF HIPPARION

A: Occlusal view of a left tooth row;

B: Occlusal view of an upper left tooth;

C: Occlusal views of selected shapes of protocones to be used as references in the descriptions.

Figures 5A and 5B illustrate the nomenclature of the different features appearing on the occlusal surfaces. The nomenclature is the same for *Hipparion* and for *Equus*.

In *Hipparion*, protocones may be described by reference to several main shapes (fig. 5C). The protocone may be more or less round (1, 2, 3 and 4), and its lingual border may be convex (1, 2, 3 and 4), flat (5), or concave (6). In addition, the protocone (whatever its shape) may be united to the protoconule (7) and/or bear a "spur" (8). Shapes vary with the degree of wear.

The enamel plications should be counted separately:

—on the anterior wall of the prefossette (they are sometimes named "plis protoloph";

—on the posterior wall of the prefossette (it may be possible to distinguish the "pli protoconule" from the plis "prefossette");

—on the anterior wall of the postfossette (sometimes named "plis postfossette");

—on the posterior wall of the postfossette (sometimes named "plis hypostyle");

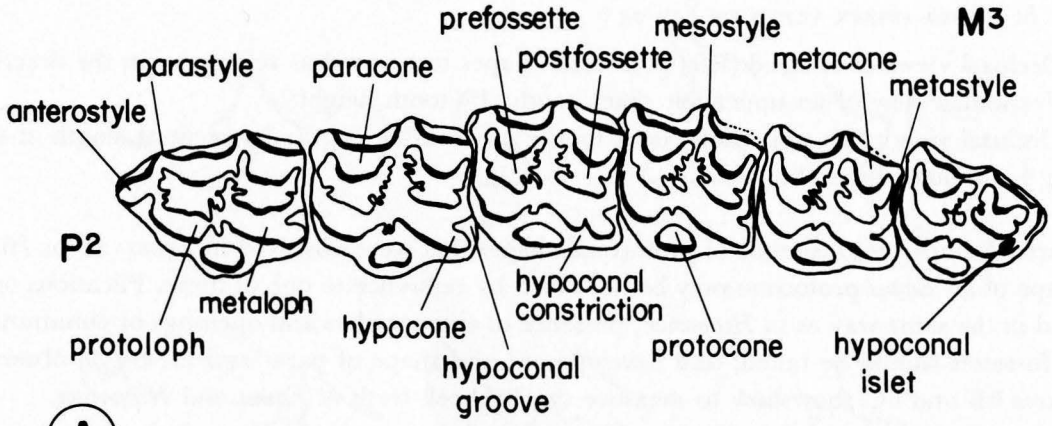
—in the lingual groove, in front of the protocone: "plis caballins".

For the way of counting plications and writing the plication formula, see above.

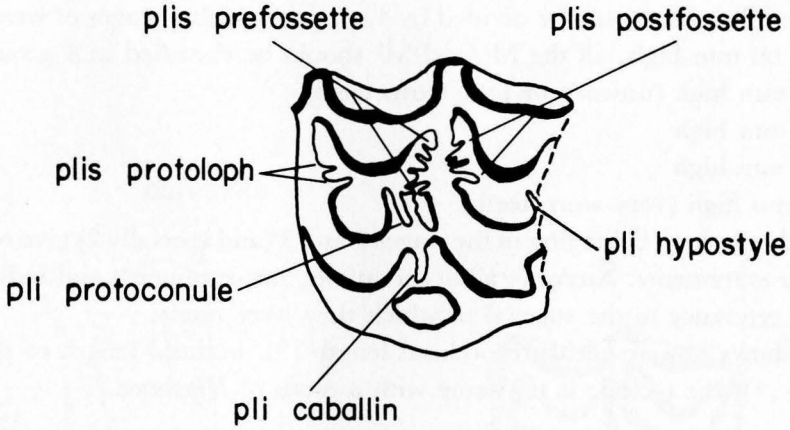
In the hypoconal area, the presence of a constriction (P^4 of fig. 5A) or of an islet (M^3 of fig. 5A) should be noted.

Other features to be noted are the development of the para- and mesostyle (width, presence of a groove) and the occurrence of a wolf tooth (dP^1).

Specific determinations based on lacteal teeth should be avoided because their morphology is usually similar in different species (baring size differences parallel to the size differences of the permanent teeth).


prefossette
mesostyle
M3
parastyle
paracone
postfossette
metacone
metastyle
anterostyle
P2
metaloph
hypoconal
constriction
hypocone
protoloph
hypoconal
groove
protocone
hypoconal
islet

A


plis prefossette
plis postfossette
plis protoloph
pli hypostyle
pli protoconule
pli caballin

B

C

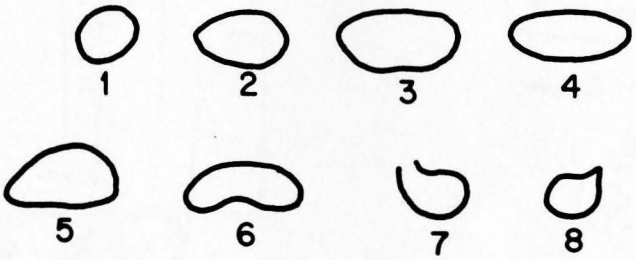

1
2
3
4
5
6
7
8

FIGURE 6: UPPER CHEEK TEETH OF EQUUS

A: Occlusal views of selected (left) protocone shapes to be used as references in the descriptions;
B: Vestibular view of an upper left cheek tooth; 1 = tooth height;
C: Occlusal view of an upper left cheek tooth; 2 = occlusal length; 3 = occlusal length of the protocone; 4 = occlusal breadth.

Figure 6A illustrates a sample of protoconal shapes that were observed in *Equus*; as for *Hipparion*, the shape of an *Equus* protocone may be described by reference to one of these. Plications are to be counted in the same way as in *Hipparion*; presence of enamel islets and openings or communications of the fossettes should be noted; and development and shape of para- and mesostyle observed.

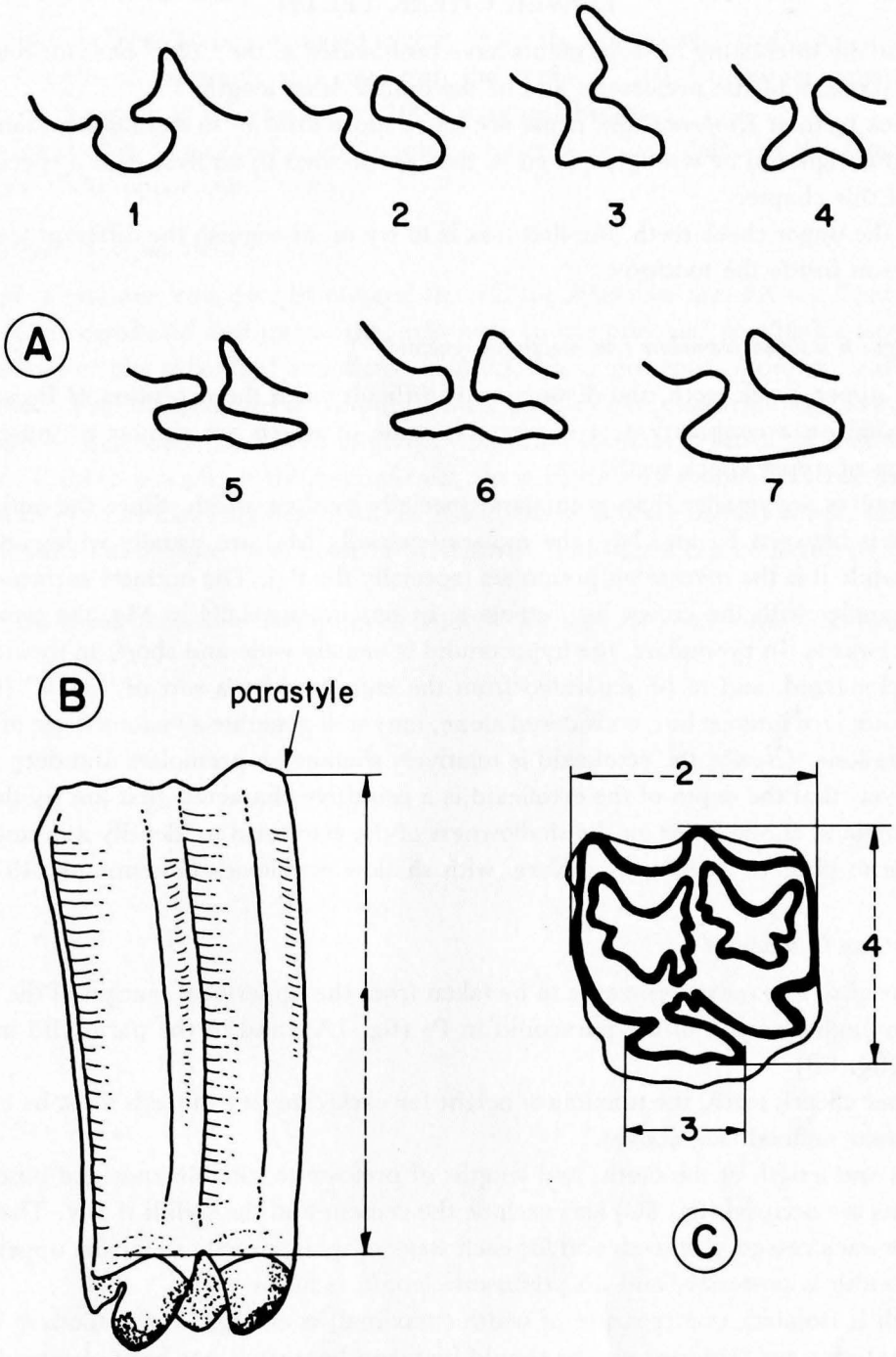
Figures 6B and 6C show how to measure upper cheek teeth of *Equus* and *Hipparion*.

Let us repeat that most of qualitative characters and dimensions of the teeth depend on their state of wear. When dealing with a sample of equid cheek teeth, one should measure the height of several unworn P^3 or P^4, and M^1 or M^2, and M^3 at the parastyle (fig. 6B, measure 1), or at the anterostyle for the P^2. These heights should be divided by 4, to distinguish 4 stages of wear. For example, if an unworn M^1 is 60 mm high, all the M^1 and M^2 should be classified in 4 groups:

1. 60 to 45 mm high (unworn or little worn teeth)
2. 45 to 30 mm high
3. 30 to 15 mm high
4. 15 to 0 mm high (very worn teeth).

In practice, only the teeth belonging in the stages 2 and 3 (and specially 2) give reliable occlusal observations and measurements. Anyway, all observations, measurements and indices should be accompanied by the reference to the stage(s) in which they were made.

Figure 6C shows how to measure occlusal length (2), occlusal length of the protocone (3) and occlusal width (4); the technic is the same with a tooth of *Hipparion*.


1
2
3
4
A
5
6
7
B
parastyle
2
4
3
C

LOWER CHEEK TEETH

Two potentially interesting measurements have been added to the "old" ones for the lower cheek teeth: measurements of the prefossette and of the double knot lengths.

Lower cheek teeth of *Hipparion* and *Equus* are much more difficult to distinguish than upper. This problem is often ignored or wrongly solved so that we decided to address it in a special paragraph at the end of this chapter.

But as for the upper cheek teeth, the first task is to try to distinguish the different teeth according to their position inside the toothrow.

How to distinguish isolated premolars and molars in general?

As for the upper cheek teeth, the distinction is difficult (with the exception of P_2 and M_3), and should be based on a conjunction of characters, some of which are similar to those used in the discrimination of upper cheek teeth.

Usually, molars are smaller than premolars, specially by their width. Since the entire cheek row is at his widest between P_4 and M_1, the molars (specially M_2) are usually wider anteriorly than posteriorly, while it is the reverse on premolars (specially the P_3). The occlusal surfaces are more or less at right angles with the crown in premolars; in molars, specially in M_2, the crown is distally incurved backwards. In premolars, the hypoconulid is usually wide and short; in molars, it tends to be thinner, elongated, and to be separated from the entoconid by a sort of "neck" (fig. 7B).

Another point is of interest but, considered alone, may well generate a vicious circle of observations and interpretations. *Usually*, the ectoflexid is relatively shallow on premolars and deep in molars. It seems, however, that the depth of the ectoflexid is a primitive character, first lost by the premolars, then by the molars. If one relies on the shallowness of the ectoflexid to identify a premolar, one will never be able to observe "evolved" molars, with shallow ectoflexids (Eisenmann, 1977).

Characters that can be measured

—Tooth height. The measurement is to be taken from the uppermost margin of the anterior root to the antero-lingual corner of the paraconid in P_2 (fig. 7A), and to the parastylid in other lower cheek teeth (fig. 8B).

As for upper cheeck teeth, the maximum height for each category of teeth must be estimated and 4 stages of wear defined (see above).

—Breadth and length of the tooth, and lengths of prefossette, double knot and postfossette. The measurements are occlusal (fig. 8C) and exclude the cement and the stylids if any. They are studied separately for each category of teeth and for each stage of wear, exactly as for the upper cheek teeth. On P_2, the width is posterior, and no prefossette length is taken.

If the tooth is isolated, one measure of width (maximal) is enough. If the tooth is included in a cheek row, anterior *and* posterior widths should be taken because it has been observed (Pr Tobien) that their relative size may change during evolution: in North-American tridactyl equids, the maximal width seems always anterior, not only in molars as usual, but also in premolars (with the exception of P_2).

For isolated cheek teeth, additional total length and breadth are taken at 1 cm above the roots in *Hipparion*, and at supposed mid-height in *Equus*.

Parameters that have to be calculated

—Hypsodonty indices. To be calculated exactly as for the upper cheek teeth (see above). For *Hipparion*, HI = Length of the tooth at 1 cm from the roots × 100 / maximal height. For *Equus*, HI = Length of the tooth at mid-height × 100 / maximal height.

—Indices for preflexid, postflexid, and double knot may be calculated in the same way as protocone indices of the upper cheek teeth.

Characters that have to be described

—Shape of the double knot (see below and fig. 7C for *Hipparion* and 8A for *Equus*).

—Depth of the ectoflexid and its position relatively to the pre- and postflexids (see below).

—Occurrences of plis caballinid and antecaballinid. Their presence, number, and development should be noted. The other enamel plications (usually on the flexids) are rare and more or less constant in number so that there is no need to give a "plication formula"; but if the enamel is wrinkled (fig. 7C:1) or if there is a pli on the linguaflexid, these characters should be recorded.

—The stylids must be carefully described. In *Equus*, the stylids are usually simple plications of the enamel; their isolation is quite exceptional. In *Hipparion*, both states can be found (fig. 7A and 7B).

Lower lacteal cheek teeth are hardly more suitable for specific determinations than upper.

FIGURE 7: LOWER CHEEK TEETH OF HIPPARION

A: Occlusal view of a left lower tooth row;
B: Occlusal view of a left lower cheek tooth;
C: Selected lower cheek teeth showing different double knots.

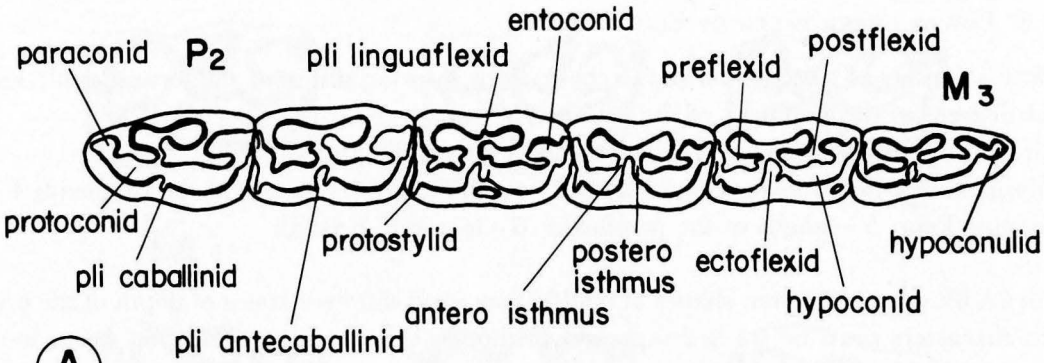
Figures 7A and 7B illustrate part of the nomenclature. Other names exist to describe different features of equid lower cheek teeth. For example, the "protolophid" is the part situated in front of the ectoflexid, while the "hypolophid" is situated behind. The linguaflexid is also named "lingual groove", and the ectoflexid is the "vestibular groove". The isthmus may also be described as the "stem" of the double knot. The pli caballinid is sometimes named "ptychostylid". When protostylids and hypostylids are not isolated as in 7B, but appear as a simple plication (protostylid on fig. 7A), some authors assimilate them, respectively, to the parastylid and the hypoconulid.

As for the upper cheek teeth, all characters depend of the stage of wear which is to be similarly defined (see fig. 8B and corresponding text).

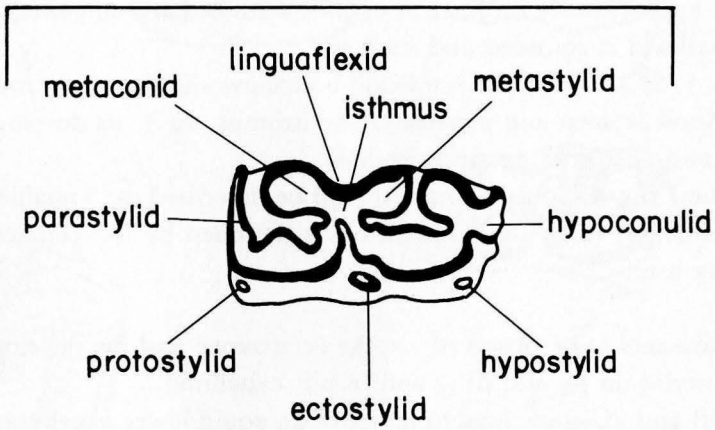
The double knot must be carefully observed. The depth of the linguaflexid and the shape of the metaconid and metastylid must be noted. Some of the most representative shapes are illustrated on fig. 7C (1-4) and fig. 9D and E on middle-worn teeth (stage 2 of wear). One of the peculiar shapes is the "caballine" in which metaconid and metastylid are angular instead of rounded (fig. 7C:4 and fig. 9E). Caballine double knots are evolved features in *Hipparion* found in the last species of the genus in Eurasia and Africa.

The depth of the ectoflexid and its position relatively to the isthmus, the preflexid, and the postflexid are other very important characters. They are illustrated on *Equus* teeth in figure 8A. The ectoflexid may be shallow and not penetrate the isthmus (1, 2, 3); it may be deeper and reach the level of the preflexid but remain on the vestibular side of the postflexid (4); it may penetrate the isthmus (5) and even come in contact with the linguaflexid (6). The depth of the ectoflexid may help to distinguish between premolars and molars but it is also a character modified by evolution in *Hipparion* and *Equus*.

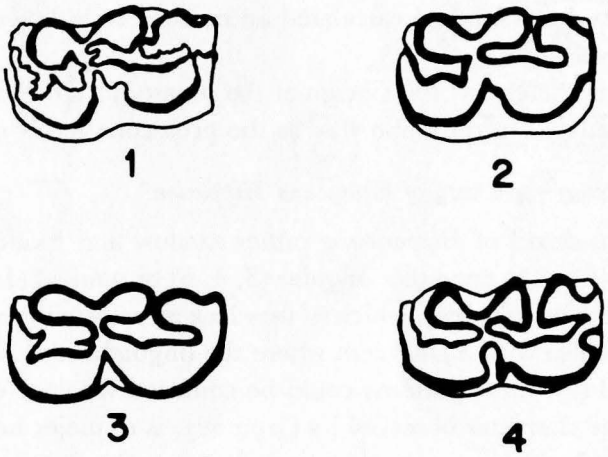
The occurrence, shape, size, number, and height of stylids must be carefully noted. When the ectostylids are very well developed (as in some African *Hipparion*), their maximal occlusal diameter should be measured as well as their heigth from the base of the crown (do they reach the occlusal surface? What is their maximum height, absolutely and relatively to the maximal height of the tooth?). Let us remind that although ectostylids are frequently present and well developed in Plio-Pleistocene African *Hipparion* with caballine double knots, the two characters are independent. In Eurasia (and even in Africa) caballine teeth of *Hipparion* without ectostylids do occur. This means that the lack of ectostylid should never to be considered as enough to discriminate *Hipparion* and *Equus* lower cheek teeth, in spite of what has too often been believed.


paraconid
P2
pli linguaflexid
entoconid
preflexid
postflexid
M3
protoconid
pli caballinid
protostylid
pli antecaballinid
antero isthmus
postero isthmus
ectoflexid
hypoconid
hypoconulid

A


DOUBLE KNOT
linguaflexid
metaconid
isthmus
metastylid
parastylid
hypoconulid
protostylid
hypostylid
ectostylid

B


1
2
3
4

C

FIGURE 8: LOWER CHEEK TEETH OF EQUUS

A: Occlusal views of selected left lower cheek teeth showing different shapes of double knots and different degrees of development of the ectoflexid;

B: Lingual view of a right lower cheek tooth; 1 = tooth height;

C: Occlusal view of left lower cheek tooth; 2 = tooth length; 3 = length of the preflexid; 4 = length of the double knot; 5 = length of the postflexid; 6 = maximal breadth.

Figure 8A illustrates different shapes of double knots and different states of depth of the ectoflexid. The two characters must be studied separately although the interpretation of an *Equus* tooth must consider the combination of both.

Figures 1 and 2 show double knots with clearly pointed, "V-shaped", linguaflexids. In 5, the linguaflexid appears more blunted; it is quite flattened and angular, "U-shaped', in 3, 4 and 6. In 7, the linguaflexid is rounded and shallow.

In figures 1, 2, 3, and 7, the ectoflexid is shallow and does not enter inside the isthmus. In 5 and 6, the ectoflexid is deep and penetrates the isthmus. In 4, its developement and position relatively to the pre- and postflexid are intermediate.

Among the 7 figures, only 3 and 4 should be described as "caballine", because of the angulation of the linguaflexid. In 6, the linguaflexid is flattened by the contact with the ectoflexid; it is not angulated by itself.

Other characters to be observed are the occurrence and the development of the wolf tooth (dP_1), of the protostylid on P_2 and dP_2, and of plis caballinid.

Figures 8B and 8C show how to measure an equid lower cheek tooth. The height is measured at the antero-lingual corner of the paraconid on P_2 and at the parastylid on all other teeth. The stages of wear are to be defined as for upper cheek teeth (see text corresponding to fig. 6).

Figure 8C shows how to measure the occlusal length (2), the lengths of the preflexid and postflexid (3 and 5), the length of the double knot (4) and the maximal width, which is here anterior (6).

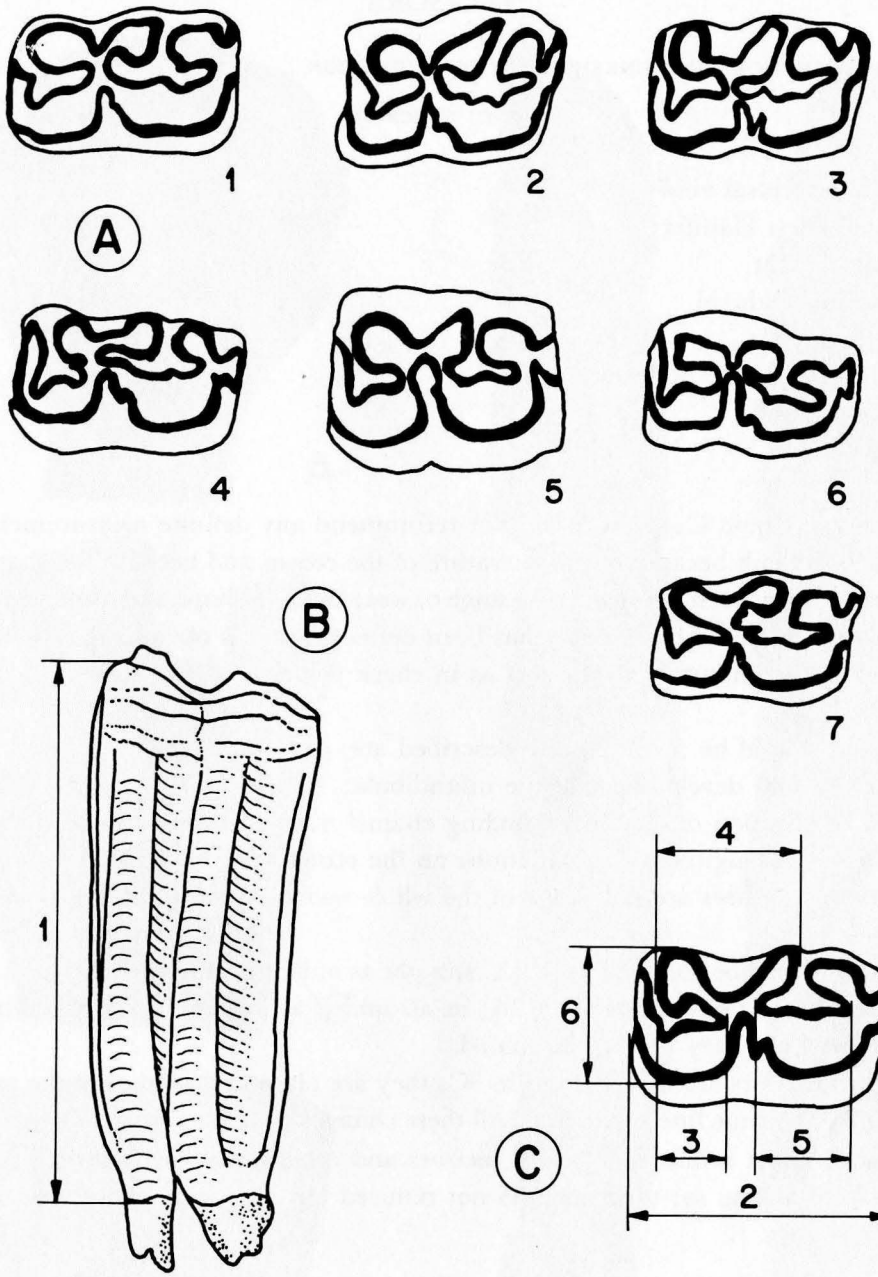
The hypsodonty index should be calculated on unworn or little worn P_3-P_4 and M_1-M_2, exactly as for the upper cheek teeth:

HI = Length at mid-height × 100 / heigh at the parastylid. Postflexid, preflexid and double knot indices may be calculated in the same way as the protocone index of the upper cheek teeth.

How to discriminate lower cheek teeth of Equus and Hipparion?

Usually, the linguaflexid of *Hipparion* is rather shallow and rounded (fig. 7B and 9D). Most of *Equus* linguaflexids (fig. 8A) are either angular (3, 4, 6) or pointed (1, 2). So that the problem arises with "caballine" teeth of *Hipparion*, which (if they lack an ectostylid) could be confused with caballine teeth of *Equus*. And also with *Equus* teeth where the linguaflexid is shallow and rounded (7) or not very clearly pointed (5); these patterns could be confused with the usual pattern of *Hipparion*.

In these cases, one character observed by Gromova, is of major help. In most *Hipparion* (fig. 7B, 9D, and 9E) the preflexid bears two symmetrical "horns" pointing in the vestibular direction. In most *Equus* (fig. 8A); the preflexid is asymmetric and only the anterior horn is well developed.


1
2
3
A
4
5
6
B
7
1
4
6
3
5
C
2

INCISORS

FIGURE 9: LOWER INCISORS AND CHEEK TEETH OF HIPPARION

(Not to scale)

Lower incisors, occlusal views
A: Vallesian, Bou Hanifia
B: Pliocene, Hadar
C: Pleistocene, Olduvai

Lower cheek teeth series, occlusal views
D: Turolian, Samos
E: Pliocene, Omo

The International Equid Conference did not recommend any definite measurement for incisors. These are indeed difficult because of the curvature of the crown and because the shape and dimensions of the incisors vary even more with the stage of wear than do shape and dimensions of the cheek teeth. Naturally, no index of hypsodonty has been defined but it is obvious that the observation of the crown height is as important in incisors as in cheek teeth.

Characters that should be observed and described are:
—the occurrence and development of the infundibula;
—the degree of plication of the corresponding enamel marks on the occlusal surfaces;
—the occurrence of longitudinal crenulations on the crown (fig. 9B and C).

Other interesting features are the shape of the whole incisival series and the possible involution of the third incisors.

The incisival row may be rounded as in 9A, straight as in 9C, or intermediate as in 9B. The third incisors may be perfectly developed as in 9A, or atrophied as in 9C. In 9B, the third incisors are not entirely erupted but they are not atrophied.

When the third incisors are atrophied as in 9C, they are placed at the rear of the second incisors, the latter being on the same line as the first. All these changes contribute to give a quadrate aspect to the incisival row so that reduction of third incisors and quadrate shape appear linked. Figure 9B shows that it is not always so: third incisors not reduced but placed posteriorly to the second.

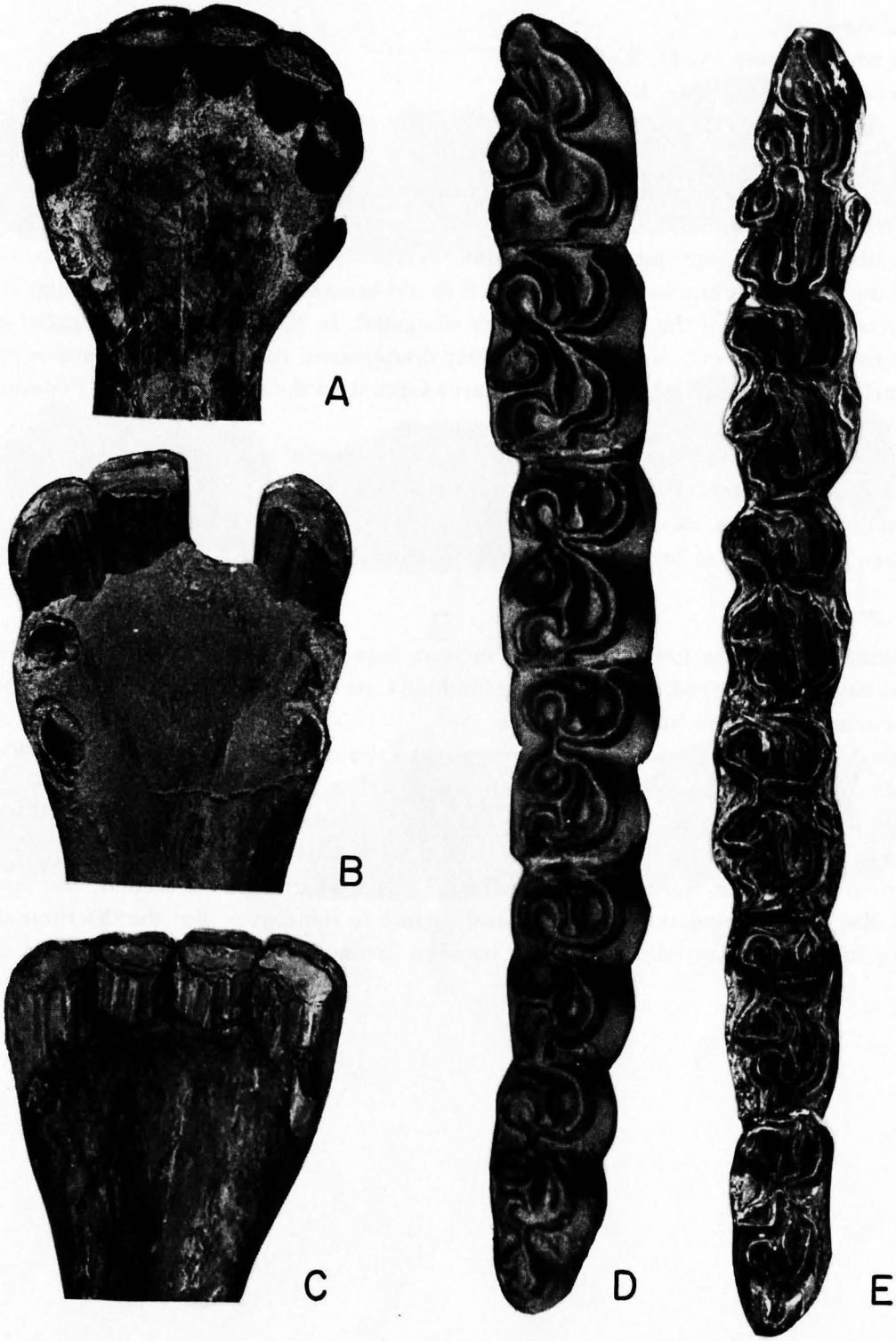

A
B
C
D
E

FIGURE 10: LOWER INCISORS OF EQUUS

Occlusal views of:
Little worn incisors: A, D, E, F and G
Moderately worn incisors: B and H
Very worn incisors: C and I.

The main characters to be studied are the frequency and degree of development of the infundibula on the lower incisors (infundibula are constant on upper incisors).

Figures 10A, B and C show the usual conditions in *Equus*, where infundibula are present and well developed on all incisors but wear completely off in old animals. In A, the marks (rings of enamel formed by cross sections of the infundibula) are elongated. In B, they are less elongated in I_2 and tend to be round in I_1. In C, they have completely disappeared: the sort of circles appearing on the occlusal surfaces are *not* enamel marks but patterns formed by the secondary ivory deposited in the pulpar cavity.

In some *Equus*, infundibula are totally lacking in every stage of wear. Compare the similar stages of wear of A-G, B-H, and C-I.

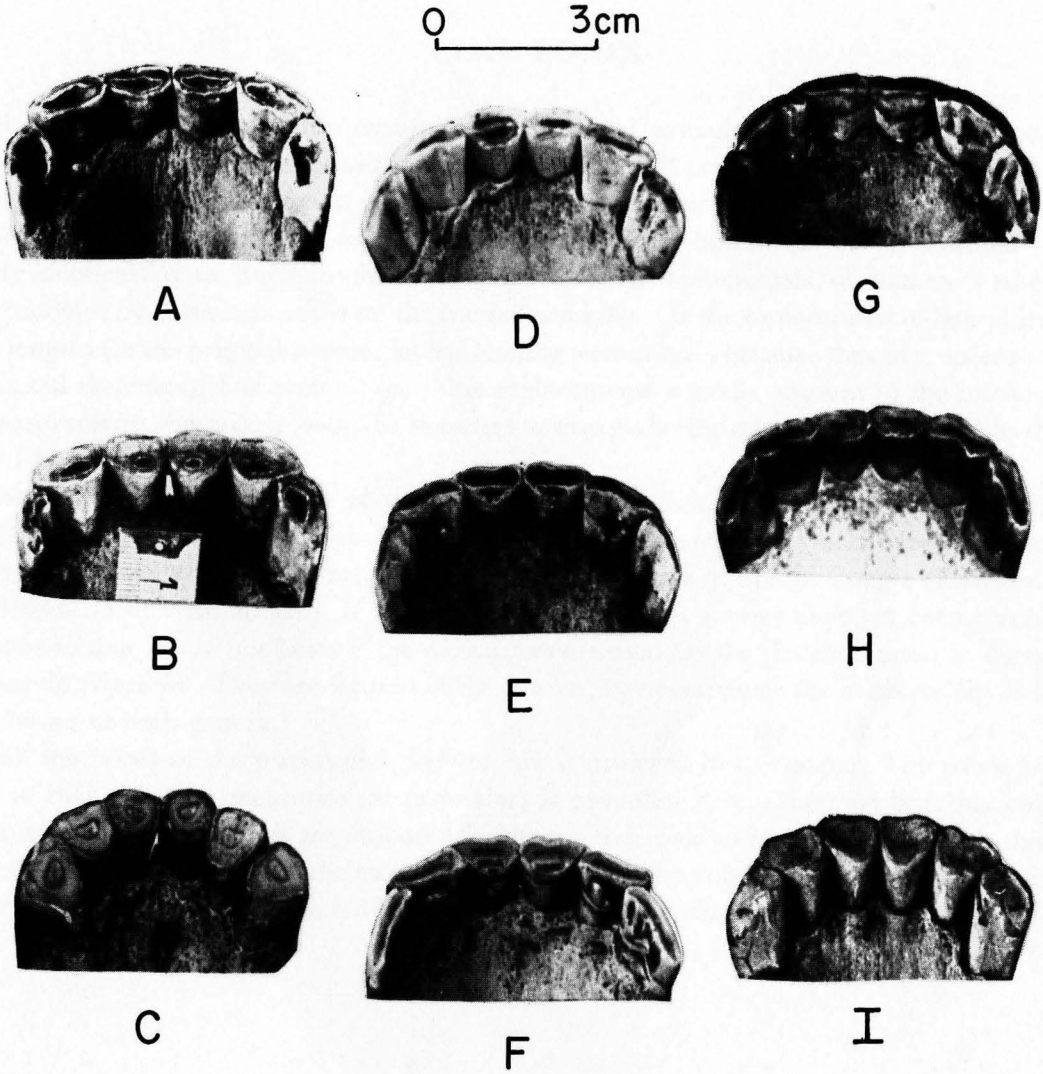
Between these extremes, all kind of intermediate conditions exist: infundibulum on a single I_1 (D); rudimentary infundibula in both I_1 and enamel outgrowths on I_2 (E), or in I_2 and I_3 (F).

Incisors in general

The distinction between lower and upper incisors may be difficult. Upper incisors are usually larger and have more curved crowns. The infundibula are always present; they are more central, while they tend to be more lingual in lowers.

Hipparion incisors have usually shorter crowns than those of *Equus*. In evolved, Pio-Pleistocene forms, the crowns may be as high as in *Equus*, but they may nearly always be distinguished by the occurrence of crenulations on the crowns and of plications inside the marks.

The distinction between isolated first, second and third incisors may be helped by the fact that, at the same stage of wear, third incisors have larger occlusal surfaces than second, and second than first, and also by the angulation of the occlusal surface to the crown. But the discrimination may prove very difficult and, at times, impossible between first and second or between second and third.


0 3cm
A
D
G
B
E
H
C
F
I

LIMB BONES

Some new measurements (for example several distal articular diameters introduced for the humerus) will no doubt prove interesting. Many readers will probably also find useful the illustrations of carpal and tarsal bones and of their mutual relations, as well as lists of their different names.

Some changes would be completely neutral if they did not hinder the use of "similar" but not "exactly identical" data. Such are the replacements, for the metapodials, of diameters taken on the lateral condyles by diameters taken on the medial condyles. Or the replacement of lateral lengths by medial lengths (in the original system, lateral lengths were chosen because they are easier to measure on mounted skeletons). For some of us, these replacements actually amount to the introduction of new measurements, because it would be senseless to stop gathering data in the same way as they were collected for years and years.

A special problem arises for the phalanges of the central digit. Obviously, anterior and posterior phalanges should be measured separately. In *Equus*, the discrimination between fore and hind phalanges can usually be done (Prat, 1957), at least in the case of first phalanges (Eisenmann & De Giuli, 1974b; Dive & Eisenmann, in press). But no equivalent studies have yet been conducted on hipparions so that we do not know if the measurements used for the discrimination in *Equus* will be of any use in *Hipparion*. They are figured in the system, however, since the methodology is intended for the bones of both genera.

Not all the bones of the postcranial skeleton are considered in this paper. The pelvis is usually broken so that only one measurement (articular) is proposed here. The vertebrae are completely omitted, and no measurements are proposed for the small carpals and tarsals. We suggest that people who need study these bones take the measurements proposed by von den Driesch (1976) for the pelvis and the vertebrae, and by Gromova (1952) for the small carpals and tarsals.

FIGURE 11: SCAPULA AND PELVIS

A. Scapula: Lateral view
B. Scapula: Cross section at the highest point of the spina
C. Scapula: Distal view
D. Peluis: Lateral view

SCAPULA

PRESENT PAPER	VE	AVD
1. Maximal length: measured parallel to the spina	5	DHA
2. Minimal breadth at the neck	4	SLC
3. Maximal breadth of the articular process	3	GLP
4. Articular maximal breadth	1	LG
5. Articular maximal depth (this measurement is usually not at right angle with the latter)	2	BG
6. Maximal depth of the spina: to be taken with a compass because of the concavity of the scapula; alternatively, a calliper may be used if an object of known thickness, (about 2 cm) is put between the measured point on the concave face of the scapula and the end of the calliper.	-	-

See also von den Driesch, 1976, p. 75.

PELVIS

PRESENT PAPER	VE	AVD
1. Diameter of acetabulum	1	LAR

See also van den Driesch, 1976, p. 83.

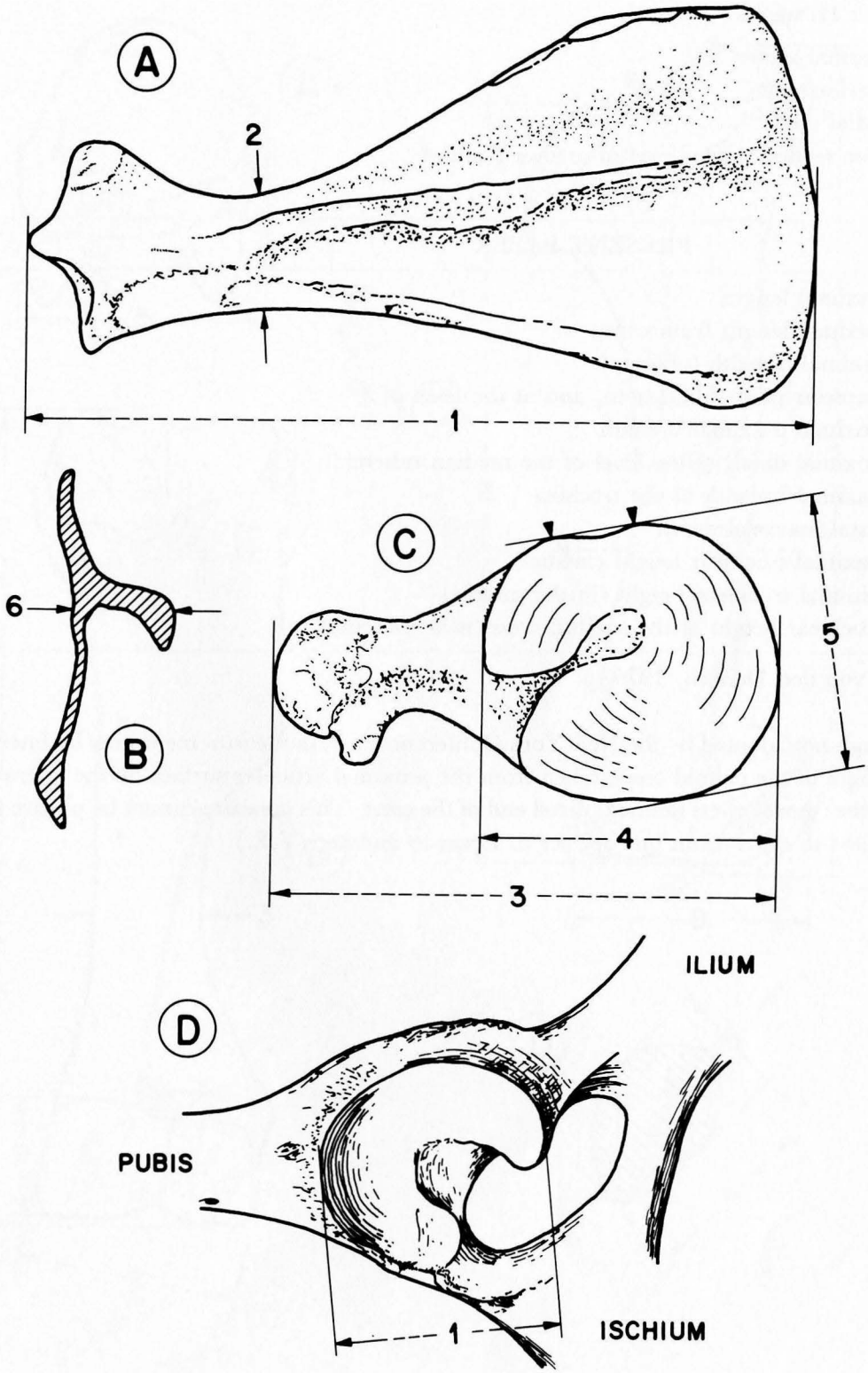

A
2
1
6
B
C
5
4
3
ILIUM
D
PUBIS
1
ISCHIUM

FIGURE 12: HUMERUS

A: Proximal view
B: Anterior view
C: Medial view
D: Cross section at the level of arrows 3 and 4

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Maximal length from caput	2	GLC
3. Minimal breadth (oblique)	3	SD
4. Diameter perpendicular to, and at the level of 3	-	-
5. Proximal maximal breadth	4	Bp
6. Proximal depth at the level of the median tubercule	5	-
7. Maximal breadth of the trochlea	6	BT
8. Distal maximal depth	7	-
9. Maximal trochlear height (medial)	-	-
10. Minimal trochlear height (in the middle)	8	-
11. Trochlear height at the sagittal crest (near the condyle)	-	-

See also von den Driesch, 1976, p. 77.

Although not adopted by the New York Conference, a 12th measurement may be interesting: that of the length of the deltoid crest, taken from the proximal articular surface on the lateral side of the bone, to the (more or less defined) distal end of the crest. This measure cannot be precise but it seems nevertheless to differ from one species of *Equus* to another (V.E.).

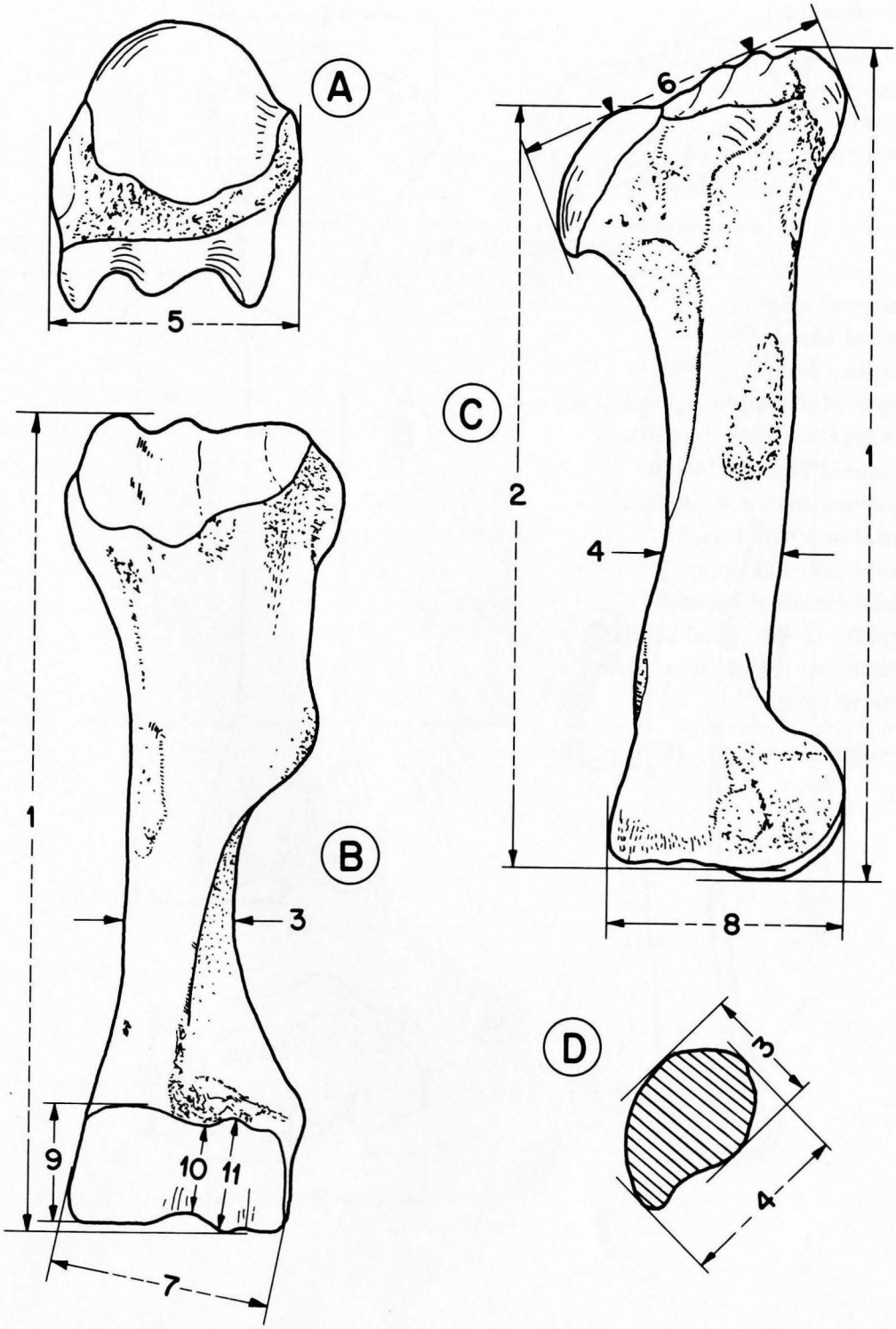

A
5
B
1
3
9
10
11
7
C
6
2
1
4
8
D
3
4

FIGURE 13: RADIUS

A: Proximal view
B: Anterior view
C: Lateral view
D: Distal view

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Medial length	*	*
3. Minimal breadth	3	SD
4. Depth of diaphysis at level of 3	-	-
5. Proximal articular breadth	5	BFp
6. Proximal articular depth	6	-
7. Proximal maximal breadth	4	Bp
8. Distal articular breadth	8	BFd
9. Distal articular depth	9	-
10. Distal maximal breadth	7	Bd
11. Breadth of the radial condyle	10	-
12. Breadth of the ulnar condyle	11	-
*. Lateral length	2	Ll

See also von den Driesch, 1976, p. 79.

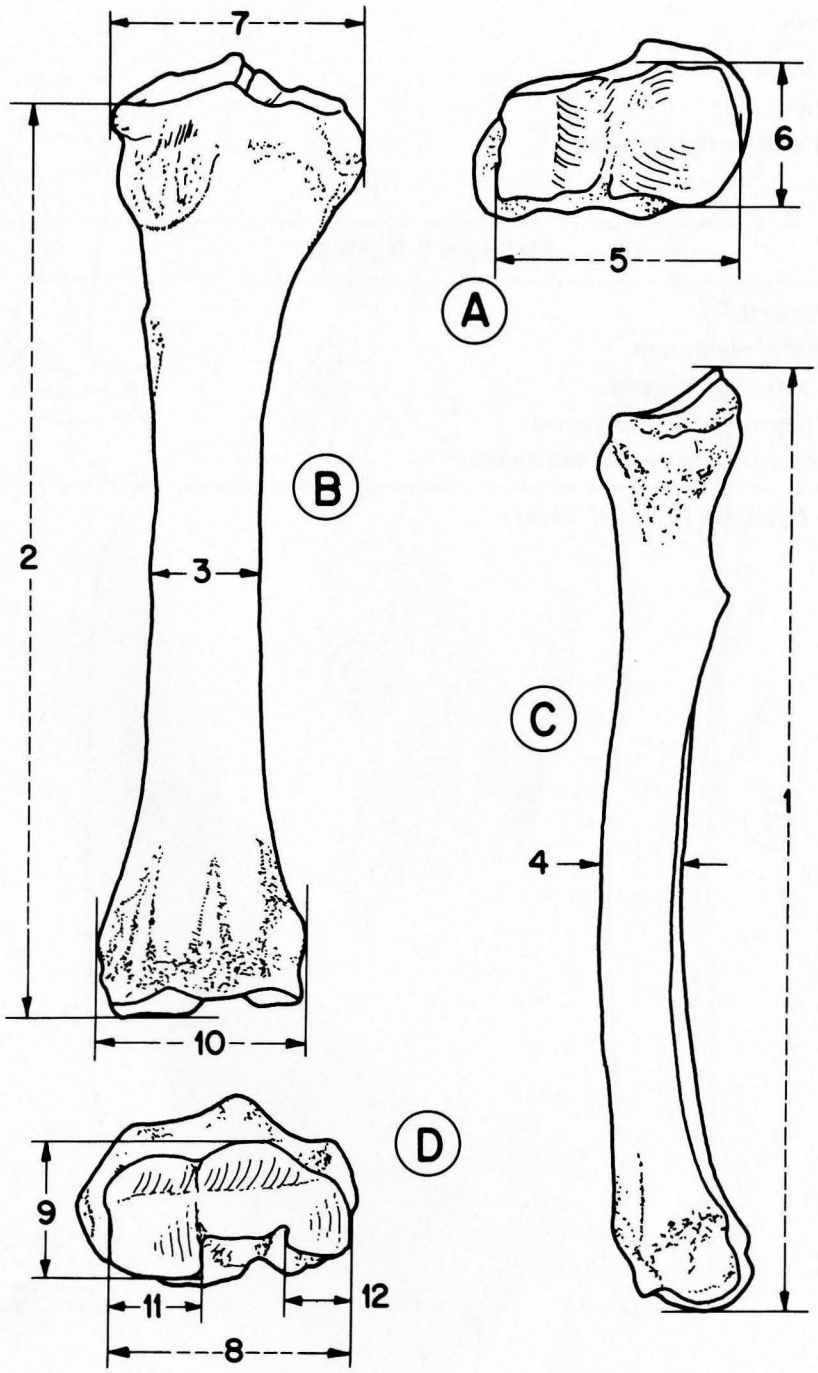
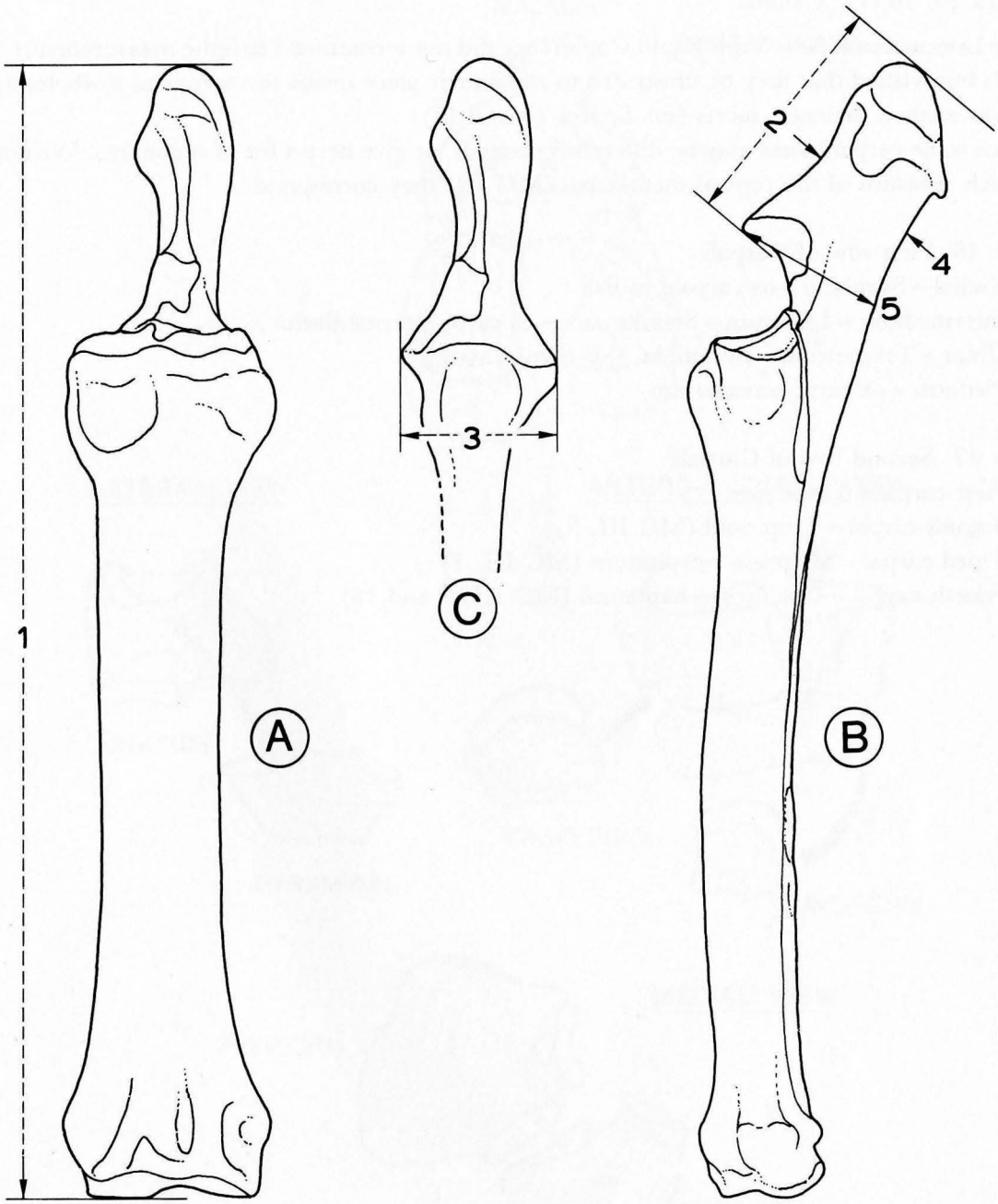

7
6
5
A
B
2
3
C
1
4
10
D
9
11
12
8

FIGURE 14: ULNA

A. Anterior view
B. Lateral view
C. Proximal end, anterior view

PRESENT PAPER	AVD
1. Maximal length	GL
2. Length of the olecranon	LO
3. Maximal articular breadth	BPC
4. Minimal depth of the olecranon	SDO
5. Depth across the Processus anconaeus	DPA

After von den Driesch (1976, p. 79-81).


1
A
3
C
2
4
5
B

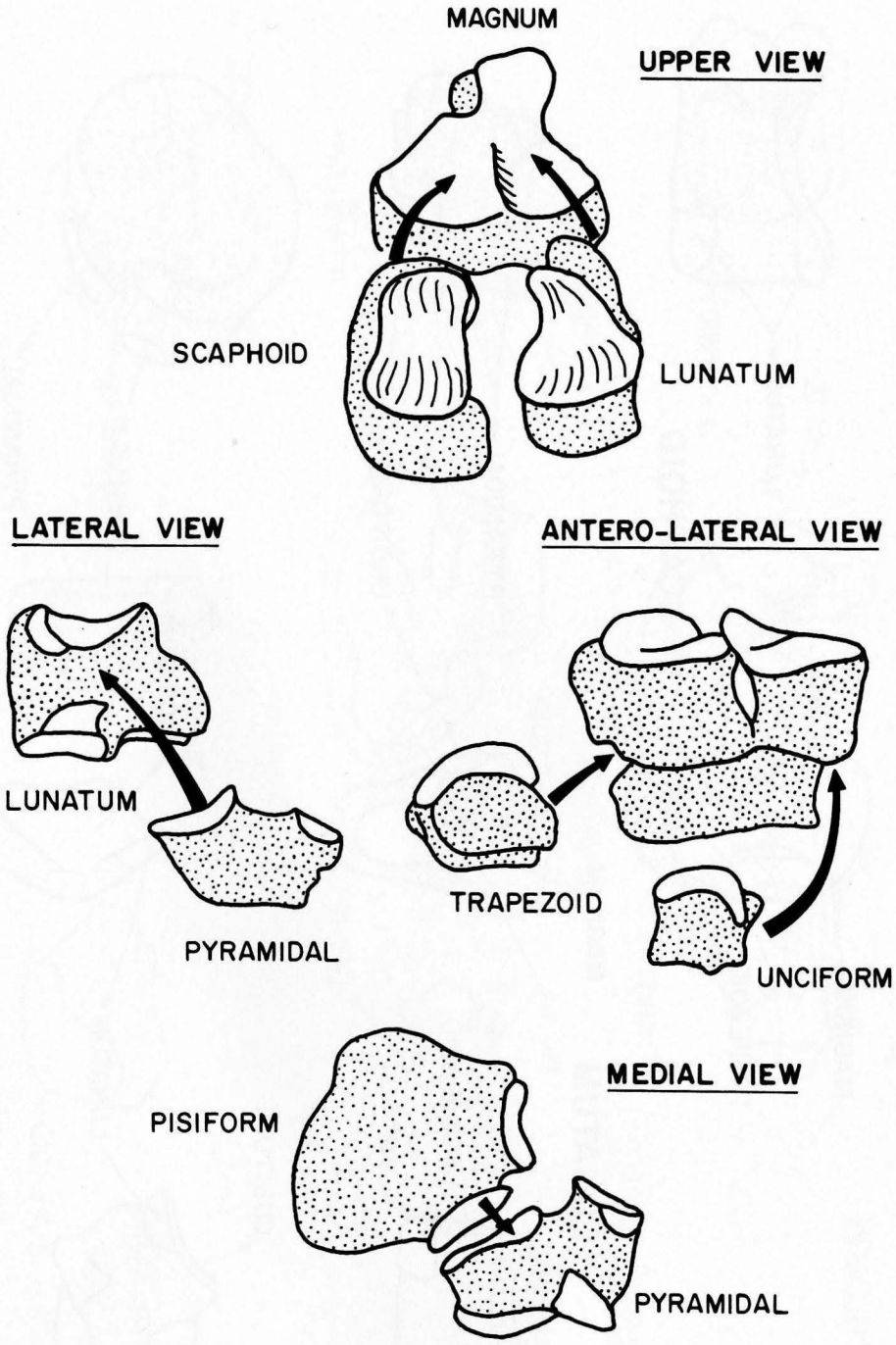
FIGURES 15, 16, 17: CARPUS

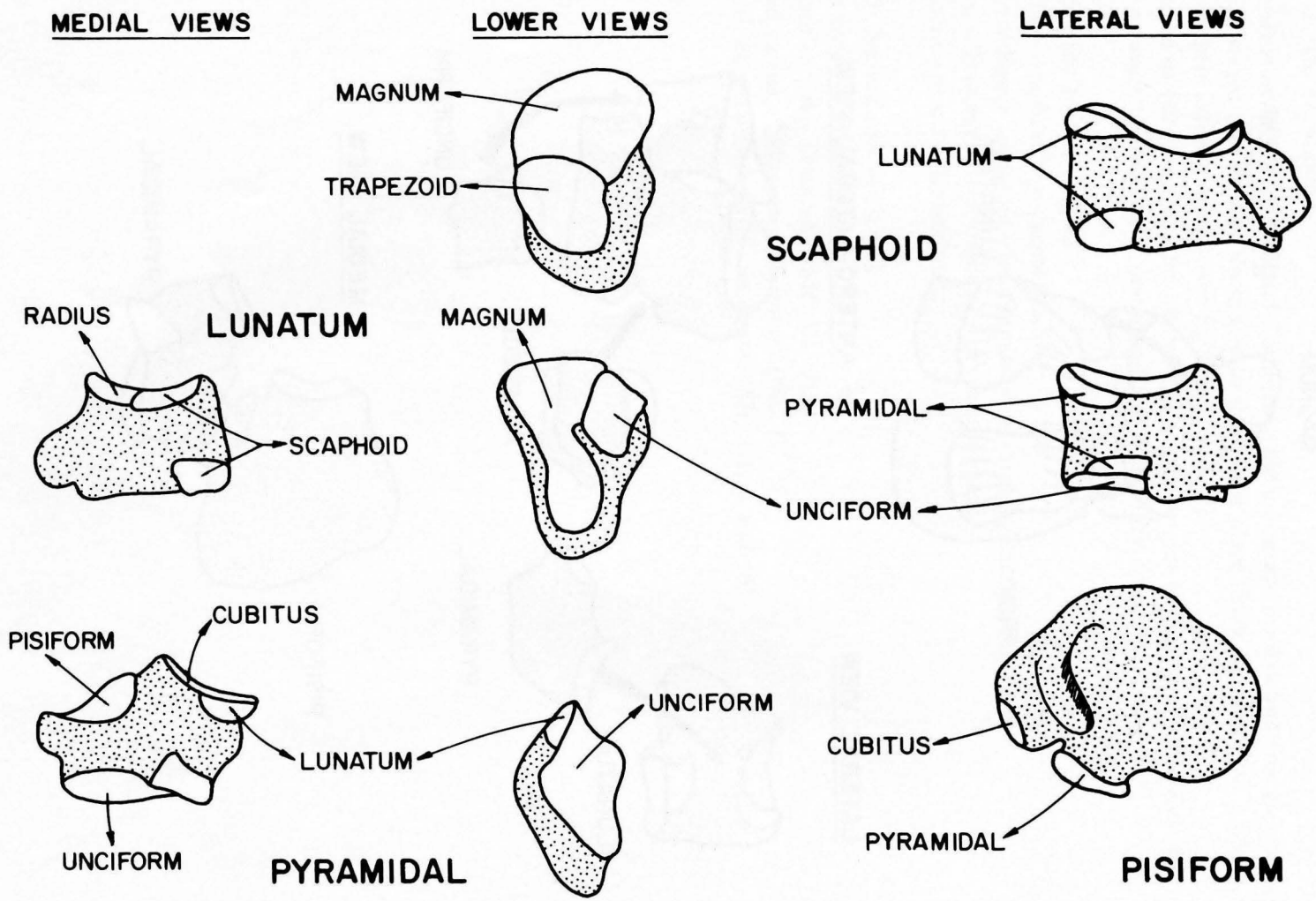
The International New York Equid Conference did not recommend definite measurements for the carpals but wished that they be illustrated to show their place inside the carpus as a whole, and the function of their articular facets (see figures 16 and 17).

Since some carpal bones may be differently named, we give here a list of synonyms. We note also to which measure of the central metacarpal (MC III) they correspond.

Fig. 16: First row of Carpals
Radial = Scaphoid = os carpale radiale
Intermedium = Lunatum = Semilunaire = os carpi intermedium
Ulnar = Triquetrum = Pyramidal = os carpi ulnare
Pisiform = os carpi accessorium

Fig. 17: Second row of Carpals
First carpal = Trapezium
Second carpal = Trapezoid (MC III, 9)
Third carpal = Magnum = capitatum (MC III, 7)
Fourth carpal = Unciform = hamatum (MC III, 8 and 16)


MAGNUM
UPPER VIEW
SCAPHOID
LUNATUM
LATERAL VIEW
ANTERO-LATERAL VIEW
LUNATUM
PYRAMIDAL
TRAPEZOID
UNCIFORM
MEDIAL VIEW
PISIFORM
PYRAMIDAL


MEDIAL VIEWS
LOWER VIEWS
LATERAL VIEWS
MAGNUM
TRAPEZOID
LUNATUM
SCAPHOID
RADIUS
LUNATUM
SCAPHOID
MAGNUM
PYRAMIDAL
UNCIFORM
PISIFORM
CUBITUS
LUNATUM
UNCIFORM
PYRAMIDAL
UNCIFORM
CUBITUS
PYRAMIDAL
PISIFORM

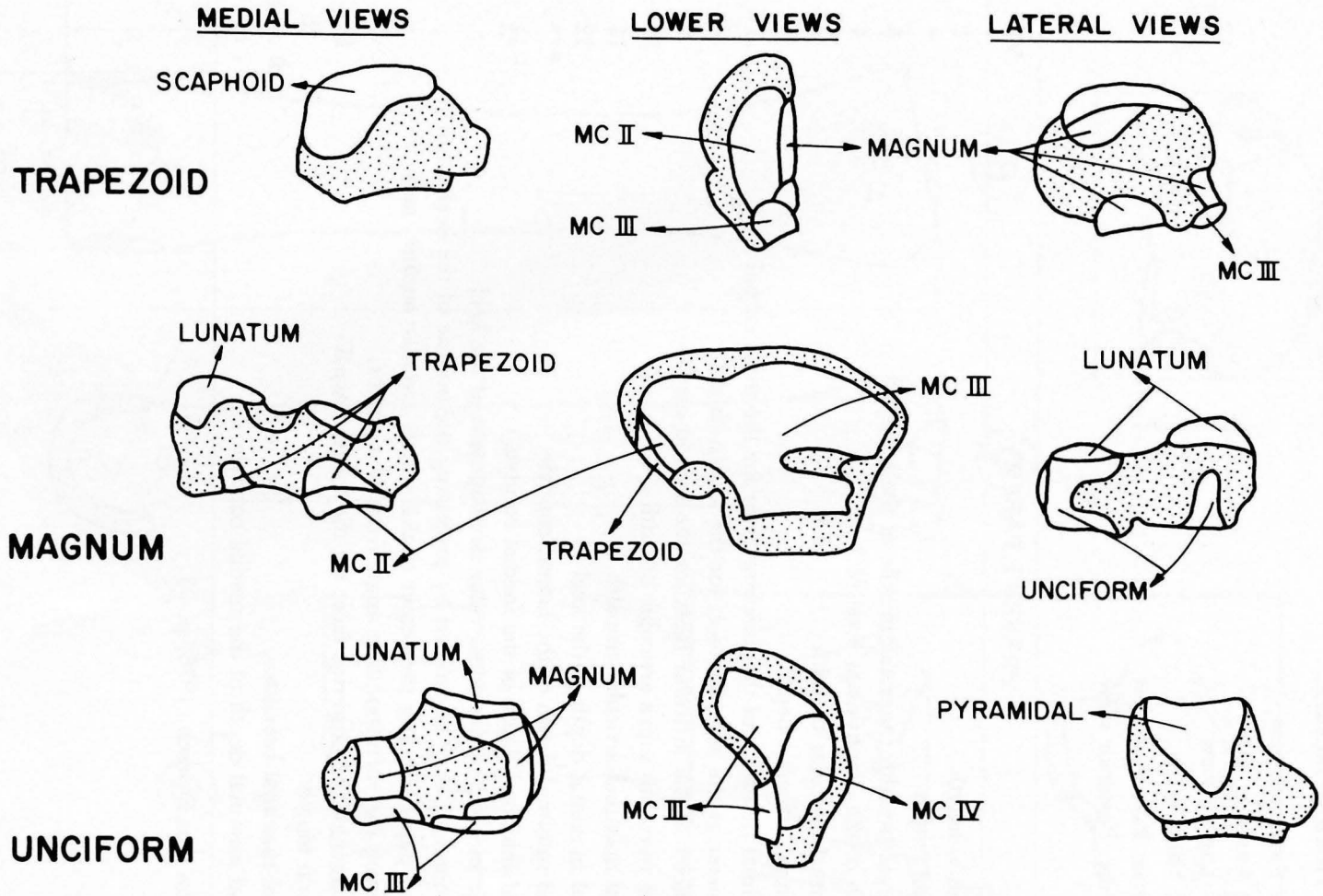

MEDIAL VIEWS
LOWER VIEWS
LATERAL VIEWS
TRAPEZOID
SCAPHOID
MC II
MC III
MAGNUM
MC III
MAGNUM
LUNATUM
TRAPEZOID
MC II
TRAPEZOID
MC III
LUNATUM
UNCIFORM
UNCIFORM
LUNATUM
MAGNUM
MC III
MC III
MC IV
PYRAMIDAL

FIGURE 18: THIRD METACARPAL

A. *Equus*: Proximal view
B. *Equus*: Anterior view
C. *Equus*: Lateral view
D. *Equus*: Distal view
E. *Hipparion*: Proximal view
F. *Hipparion*: Posterior view

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Medial length	*	*
3. Minimal breadth (near the middle of the bone)	3	SD
4. Depth of the diaphysis at level of 3	4	-
5. Proximal articular breadth	5	Bp
6. Proximal articular depth	6	-
7. Maximal diameter of the articular facet for the third carpal	7	-
8. Diameter of the anterior facet for the fourth carpal	8	-
9. Diameter of the articular facet for the second carpal	9	-
10. Distal maximal supra-articular breadth	10	**
11. Distal maximal articular breadth	11	**
12. Distal maximal depth of the keel	12	Dd
13. Distal minimal depth of the lateral condyle	***	-
14. Distal maximal depth of the medial condyle	14	-
15. Angle measuring the dorso-volar development of the keel (this character may be studied by projecting the outline of the keel on a sheet of paper, finding the center of this nearly circular outline, and measuring the corresponding angle from that center)	-	-
16. Diameter of the posterior facet for the fourth carpal	8′	-
*. Lateral length	2	Ll
**. Distal maximal breadth	10 or 11	
***. Distal minimal depth of the medial condyle	13	-

See also von den Driesch, 1976, p. 93.

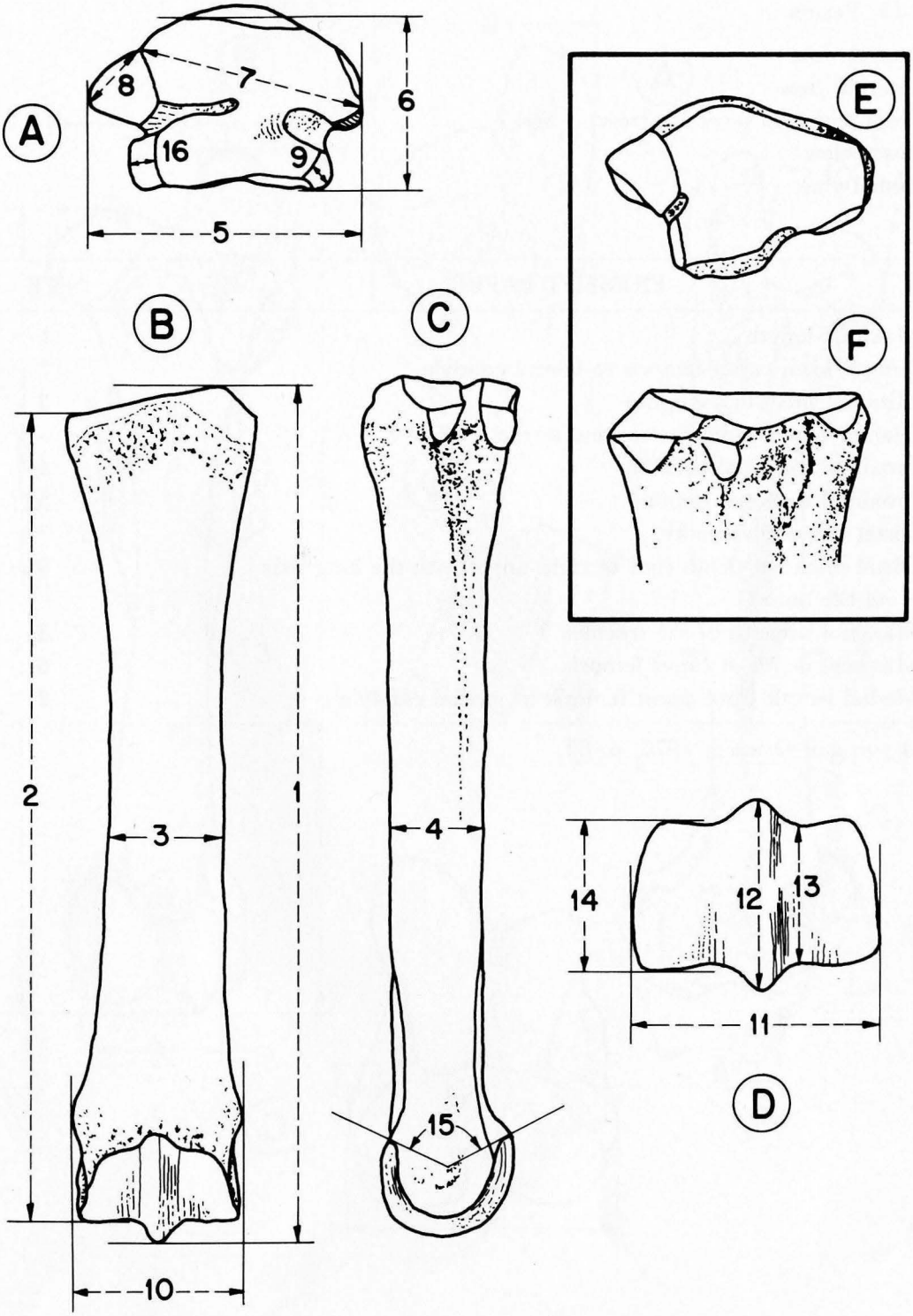

A
8
7
6
16
9
5
B
C
E
F
2
1
3
4
14
12
13
11
D
15
10

FIGURE 19: FEMUR

A. Lateral view
B. Anterior view
C. Cross secton at level of arrows 3 and 4
D. Distal view
E. Medial view

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Length from caput femoris to lateral condyle	*	*
3. Minimal breadth (oblique)	3	SD
4. Diameter perpendicular to, and at the level of 3	-	-
5. Proximal maximal breadth	4	Bp
6. Proximal maximal depth	5	-
7. Distal maximal breadth	7	Bd
8. Distal maximal depth (not at right angle with the long axis of the bone)	9	-
9. Maximal breadth of the trochlea	8	-
10. Maximal depth of caput femoris	6	DC
*. Medial length from caput femoris to medial condyle	2	GLC

See also von den Driesch, 1976, p. 85.

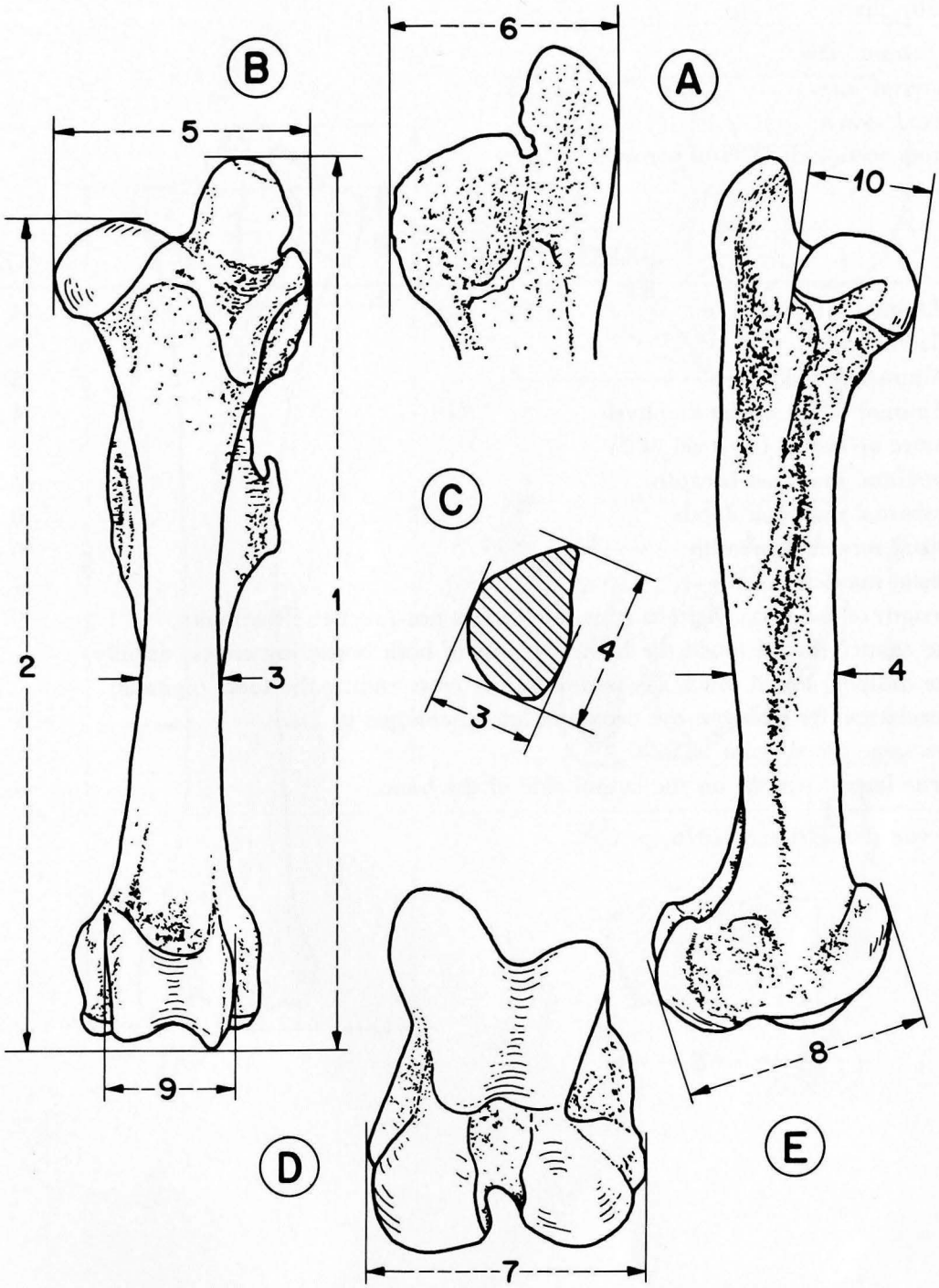
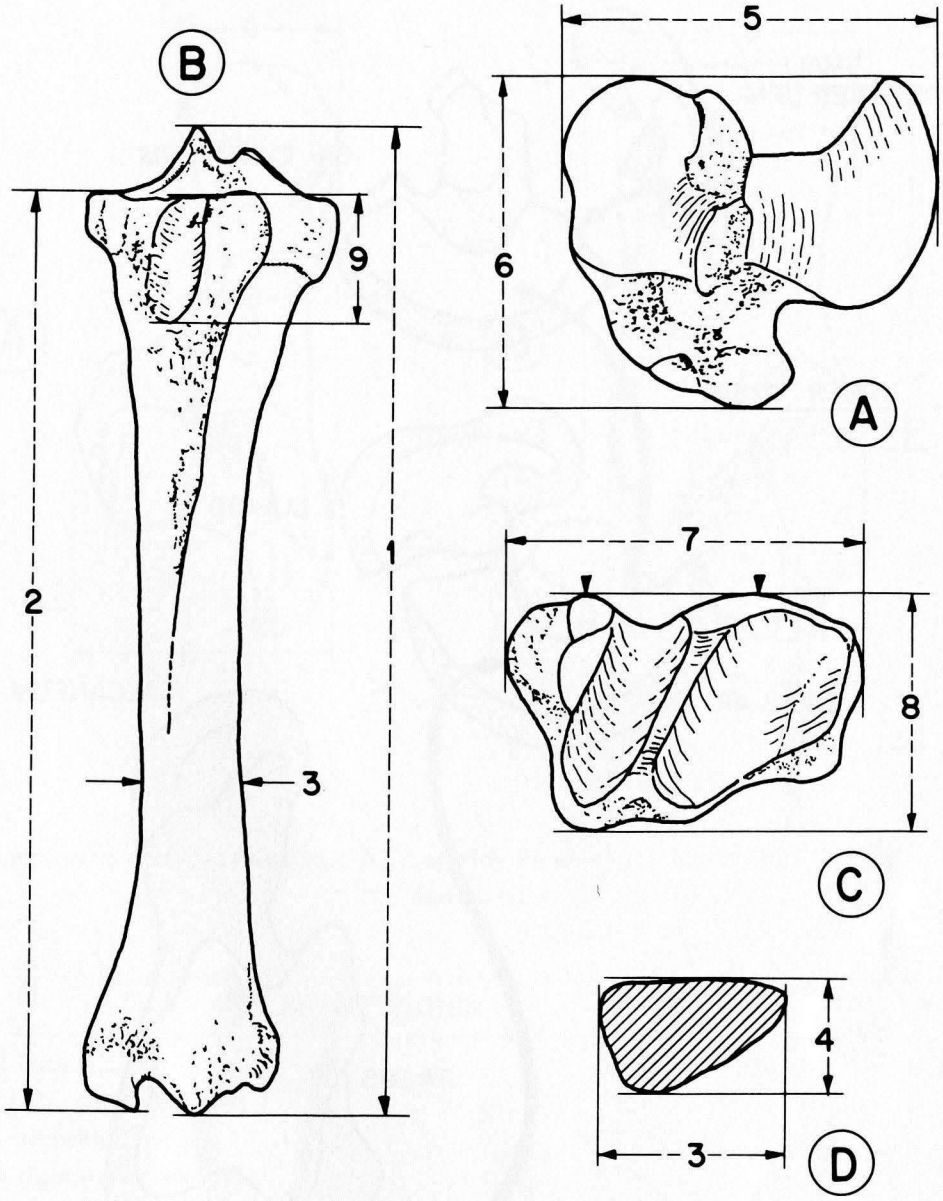

B
5
1
2
3
9
D
6
A
C
4
3
7
10
4
8
E

FIGURE 20: TIBIA

A. Proximal view
B. Anterior view
C. Distal view
D. Cross section at level of arrow 3

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Medial length	*	**
3. Minimal breadth	3	SD
4. Minimal depth of the diaphysis (more or less at the level of 3)	4	-
5. Proximal maximal breadth	5	Bp
6. Proximal maximal depth	6	-
7. Distal maximal breadth	8	Bd
8. Distal maximal depth	7	Dd
9. Length of the fossa digitalis (this measure is not precise. Proximally, the caliper should touch the highest points of both bordering crests; distally, the calliper should touch the middle of the crest ending the fossa digitalis)	9	-
*. Paralateral length from the proximal lateral condyle to the same distal point as in 1	2	3
**. True lateral length, on the lateral side of the bone	-	Ll

See also von den Driesch (1976, p. 85).


B
1
2
3
9
5
6
A
7
8
C
4
3
D

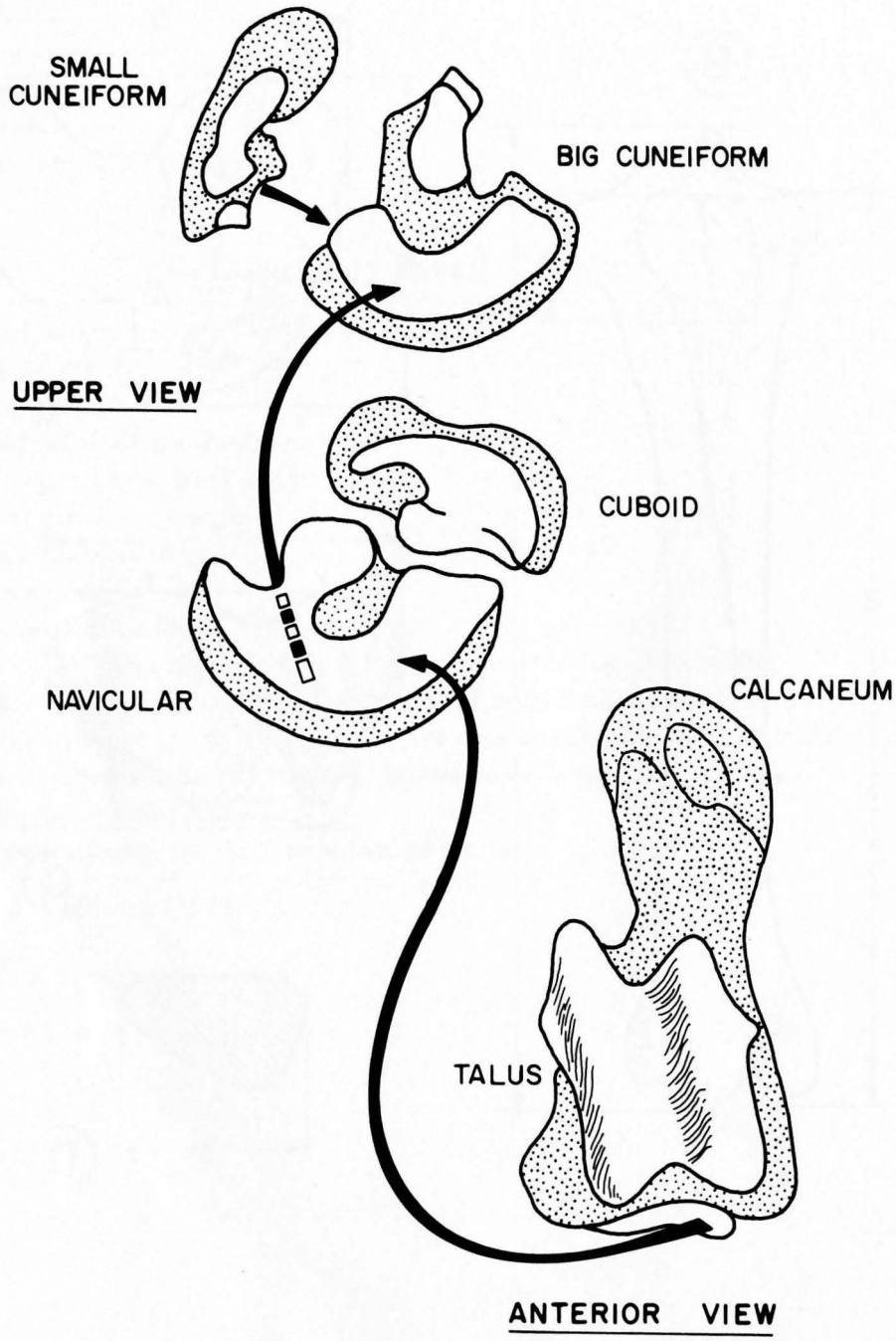


FIGURE 21: TARSUS

General structure.

See next pages for calcaneus (fig. 22), talus (fig. 23) and other tarsal bones (fig. 24).

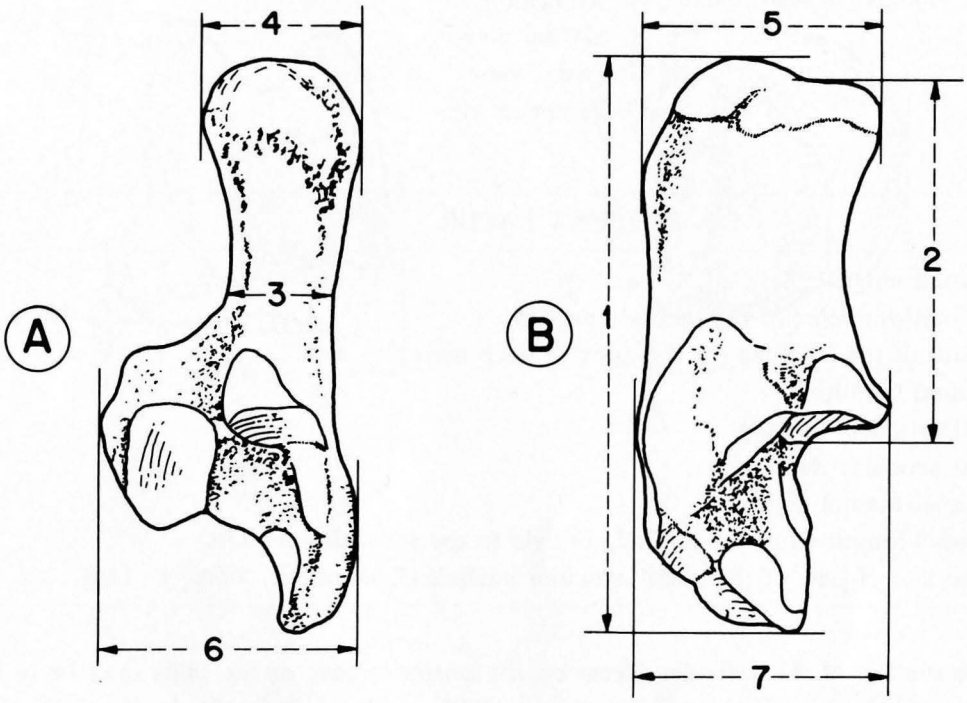


FIGURE 22: CALCANEUS (OR CALCANEUM), A: Anterior view
B: Medial view

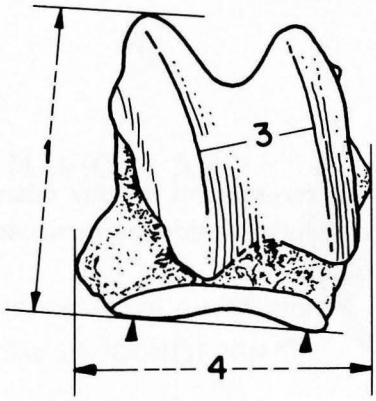
PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Length of the proximal part	2	-
3. Minimal breadth	4	-
4. Proximal maximal breadth	5	-
5. Proximal maximal depth	6	-
6. Distal maximal breadth	3	GB
7. Distal maximal depth	7	-

V.E. suggests that the measure of the maximal length of the articular facet on the sustentaculum tali may be of interest.

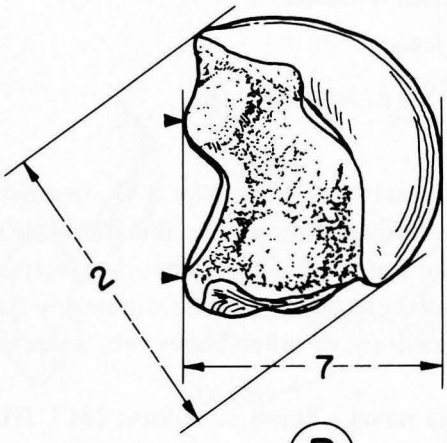
FIGURE 23: TALUS (or Astragalus), A: Anterior view
B: Medial view
C: Distal view
D: Posterior view

PRESENT PAPER	VE	AVD
1. Maximal length	*	GH
2. Maximal diameter of the medial condyle	2	LmT
3. Breadth of the trochlea (at the apex of each condyle)	4	-
4. Maximal breadth	3	GB
5. Distal articular breadth	5	BFd
6. Distal articular depth	6	-
7. Maximal medial depth	7	-
*. Maximal length from the medial condyle to the most distal point on the lateral part of the distal articular surface (Eisenmann, 1986, p. 116)	1	-

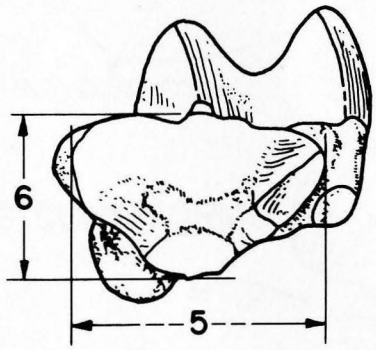
The observation of the articular facets on the posterior face of the talus may be of interest for discriminating *Equus* and *Hipparion* (Eisenmann, 1985, p. 32, pl. 3, fig. 3). In *Hipparion*, the posterior edge of the lateral condyle for the tibia (a) is thin and sharp; the underlying facet articulating with the calcaneum (b) is bordered by this edge but the two articular surfaces are in continuity. In most species of *Equus*, the edge is blunt and some non-articular bone comes in between a and b (exceptions may be found in Asses and Hemiones). Other differences may also be found between species of *Equus*: for example, in *Equus zebra*, the distal end of the articular surface for the calcaneum (c) is very often separated from the articular surface for the MT III; in most other *Equus*, the two surfaces are in continuity (V.E.).



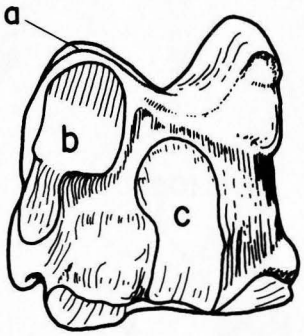
A



B



C



D

FIGURE 24: OTHER TARSALS

A. Medial views
B. Distal views
C. Lateral views

The International New York Equid Conference did not recommend definite measurements for these bones but wished that they be illustrated to show their place inside the tarsus as a whole (see fig. 21), and the function of their articular facets (this figure).

Since most of these bones may be differently named, we give here a list of synonyms. We note also to which measure of other bones they correspond.

First + second tarsal = Small cuneiform (MT III, 9)
Third tarsal = Large cuneiform (MT III, 7)
Fourth tarsal = Cuboid (MT III, 8)
Navicular = Scaphoid = os tarsi centrale (Talus, 5)

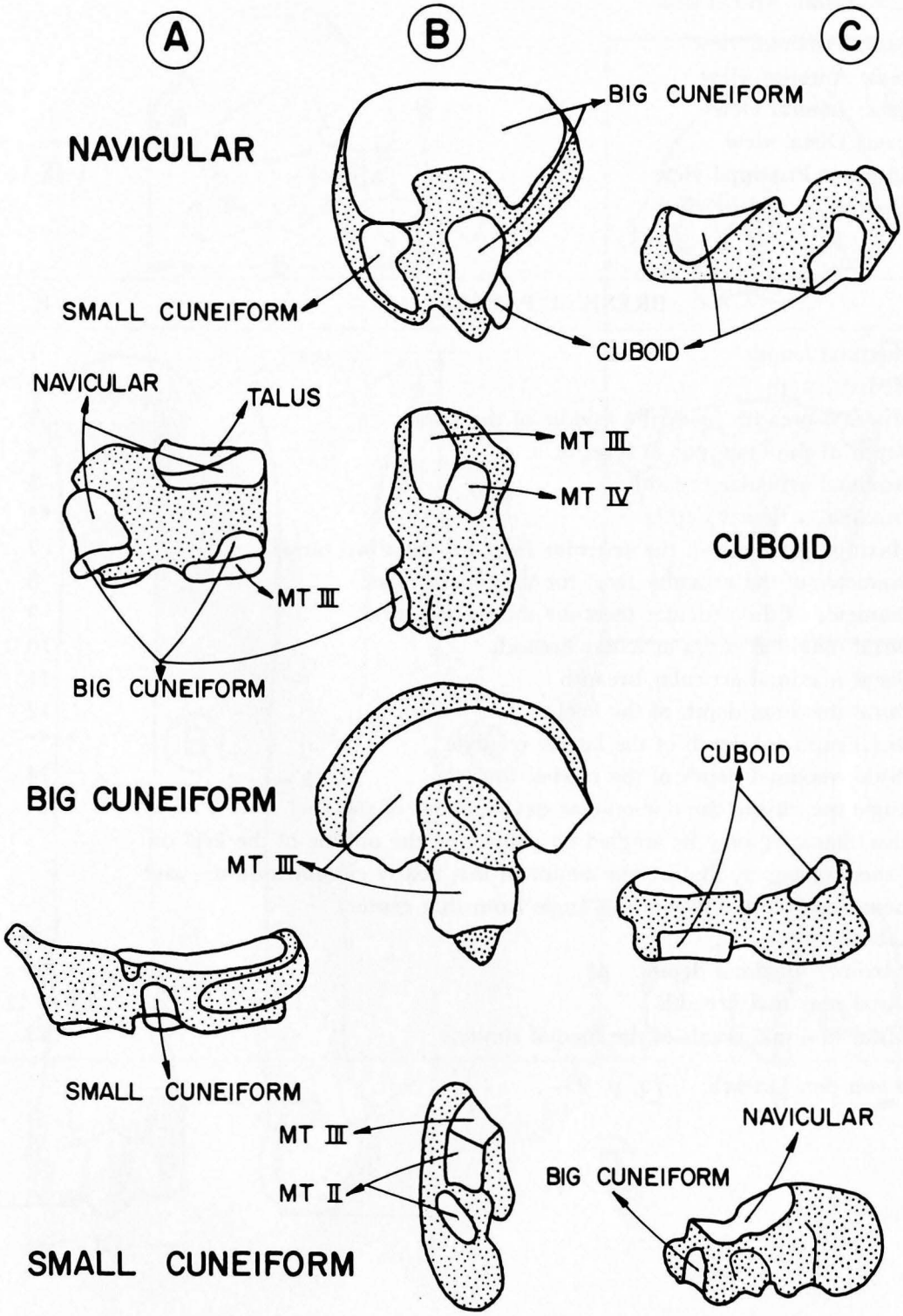

A
B
C
NAVICULAR
BIG CUNEIFORM
SMALL CUNEIFORM
CUBOID
NAVICULAR
TALUS
MT III
MT IV
CUBOID
MT III
BIG CUNEIFORM
BIG CUNEIFORM
CUBOID
MT III
SMALL CUNEIFORM
MT III
MT II
NAVICULAR
BIG CUNEIFORM
SMALL CUNEIFORM

FIGURE 25: THIRD METATARSAL

A. *Equus*: Proximal view
B. *Equus*: Anterior view
C. *Equus*: Lateral view
D. *Equus*: Distal view
E. *Hipparion*: Proximal view
F. *Hipparion*: Posterior view

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Medial length	*	*
3. Minimal breadth (near the middle of the bone)	3	SD
4. Depth of the diaphysis at level of 3	4	-
5. Proximal articular breadth	5	Bp
6. Proximal articular depth	**	**
7. Maximal diameter of the articular facet for the third tarsal	7	-
8. Diameter of the articular facet for the fourth tarsal	8	-
9. Diameter of the articular facet for the second tarsal	9	-
10. Distal maximal supra-articular breadth	10	***
11. Distal maximal articular breadth	11	***
12. Distal maximal depth of the keel	12	Dd
13. Distal minimal depth of the lateral condyle	****	-
14. Distal maximal depth of the medial condyle	14	-
15. Angle measuring the dorso-volar development of the keel (this character may be studied by projecting the outline of the keel on a sheet of paper, finding the center of this nearly circular outline, and measuring the corresponding angle from that center)	-	
*. Lateral length	2	Ll
**. Proximal maximal depth	6	Dp
***. Distal maximal breadth	10 or 11	
****. Distal minimal depth of the medial condyle	13	-

See also von den Driesch, 1976, p. 93.

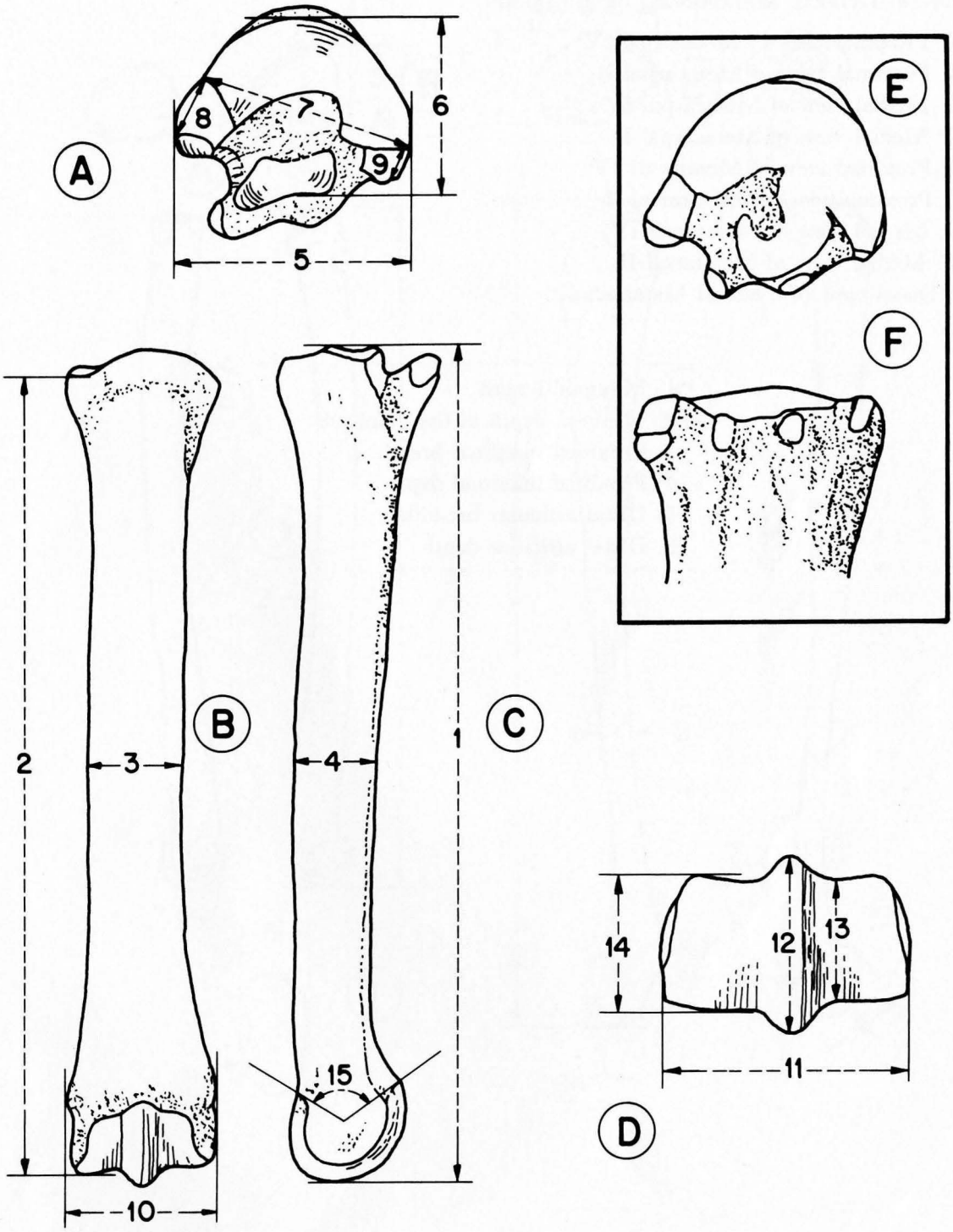

A
8
7
6
9
5
E
F
B
C
2
3
4
1
15
10
14
12
13
11
D

Figure 26: Lateral Metapodials of Hipparion

A: Proximal view of Metacarpal IV
B: Proximal view of Metacarpal II
C: Medial view of Metacarpal IV
D: Medial view of Metacarpal II
E: Proximal view of Metatarsal IV
F: Proximal view of Metatarsal II
G: Medial view of Metatarsal IV
H: Medial view of Metatarsal II
I: Distal view of a lateral Metapodial

1. Maximal length
2. Minimal depth of the diaphysis
3. Proximal maximal breadth
4. Proximal maximal depth
5. Distal articular breadth
6. Distal articular depth

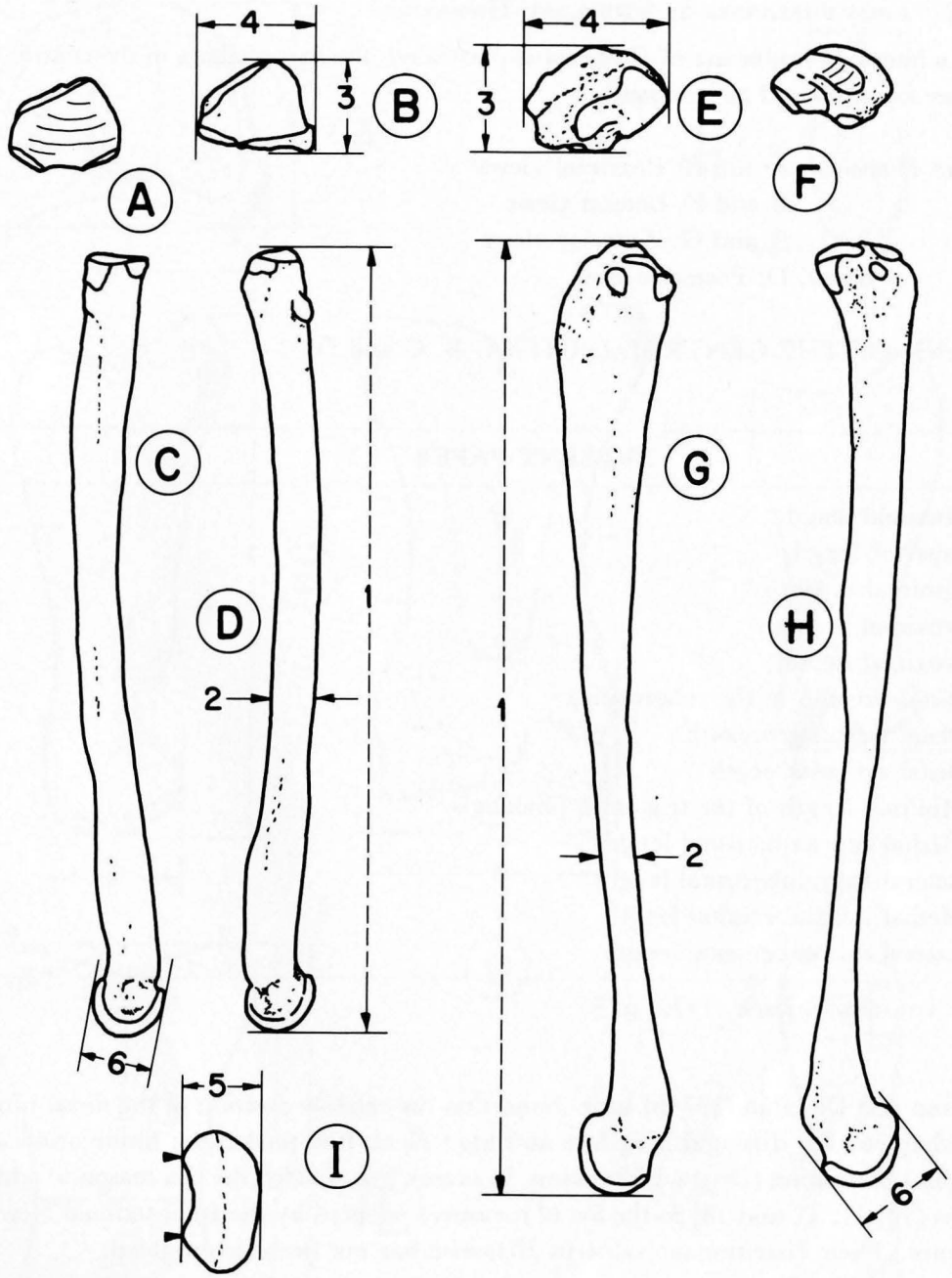

4
3
B
4
3
E
A
F
C
D
1
2
G
1
2
H
6
5
I
6

FIGURE 27: FIRST PHALANGES OF EQUUS AND HIPPARION

(Only a lateral first phalanx of *Hipparion* is illustrated; the first phalanx of the central digit of *Hipparion* may be measured as in *Equus*).

Equus and *Hipparion*, A and E: Proximal views
B and F: Lateral views
C and G: Anterior views
Equus, D: Posterior view

PHALANX OF THE CENTRAL DIGIT (A, B, C and D)

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Anterior length	2	-
3. Minimal breadth	3	SD
4. Proximal breadth	4	Bp
5. Proximal depth	5	Dp
6. Distal breadth at the tuberosities	6	Bd
7. Distal articular breadth	14	BFd
8. Distal articular depth	15	-
9. Minimal length of the trigonum phalangis	8	-
10. Medial supratuberosital length	10	-
11. Lateral supratuberosital length	11	-
12. Medial infratuberosital length	12	-
13. Lateral infratuberosital length	13	-

See also von den Driesch, 1976, p. 97.

Eisenmann and De Giuli (1974b) have found that the relative position of the distal tuberosities was a good character for distinguishing fore and hind *Equus* first phalanges; multivariate analysis confirmed this observation (Dive & Eisenmann, in press). We decided for this reason to add the relevant measures (10, 11, 12 and 13) to the list of measures adopted by the International New York Equid Conference. Their discriminant value in *Hipparion* has not been investigated.

LATERAL FIRST PHALANX OF HIPPARION (E, F and G)

1. Maximal length
2. Proximal maximal breadth
3. Proximal maximal depth
4. Distal maximal breadth
5. Minimal breadth of the diaphysis

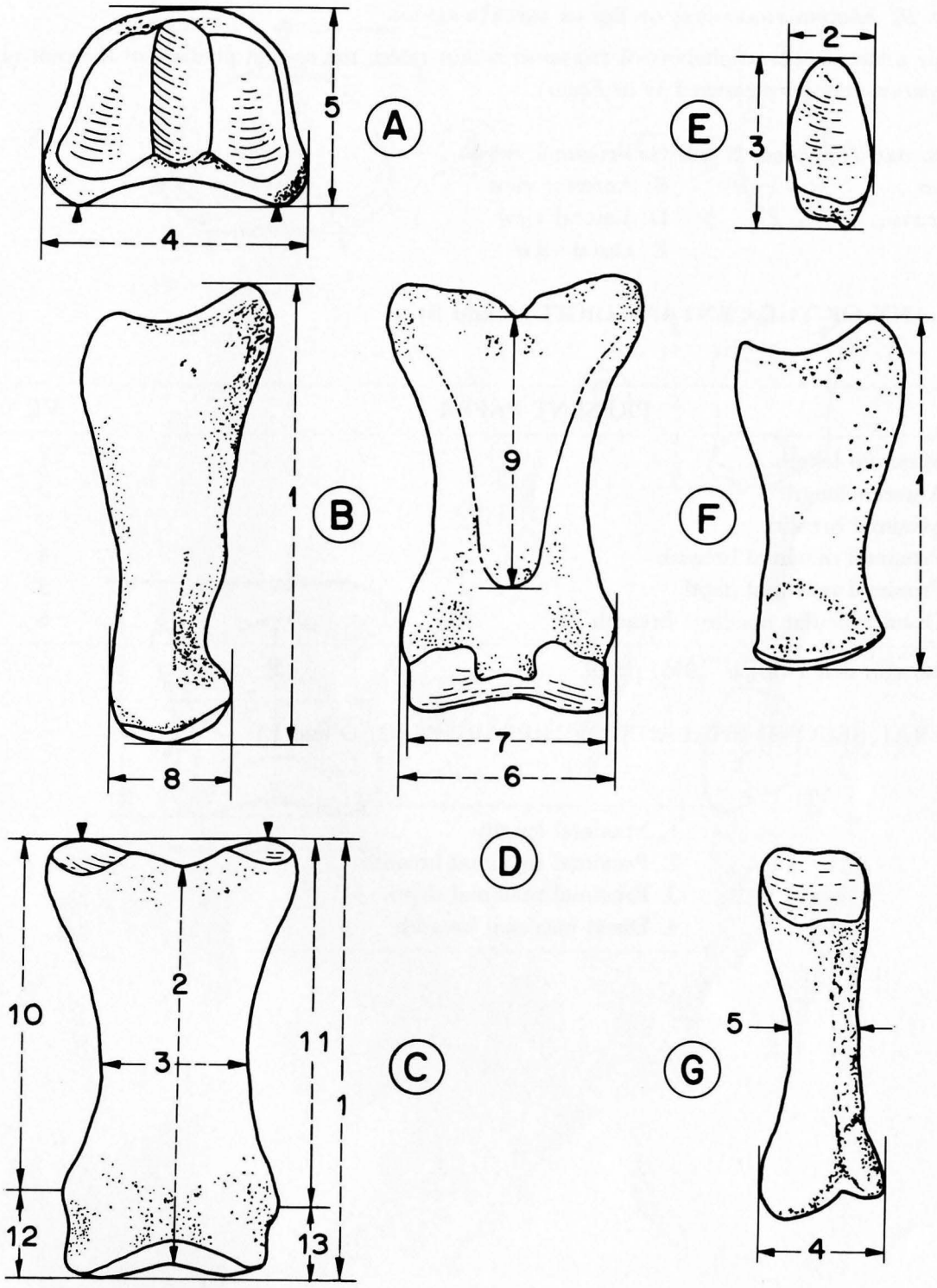

A
5
4
E
2
3
B
1
8
D
9
7
6
F
1
C
10
2
3
11
1
12
13
G
5
4

FIGURE 28: SECOND PHALANGES OF EQUUS AND HIPPARION

(Only a lateral second phalanx of *Hipparion* is illustrated; the second phalanx of the central digit of *Hipparion* may be measured as in *Equus*).

Equus and *Hipparion*, A and C: Proximal views
Equus, B: Anterior view
Hipparion, D: Lateral view
E: Distal view

PHALANX OF THE CENTRAL DIGIT (A and B)

PRESENT PAPER	VE	AVD
1. Maximal length	1	GL
2. Anterior length	2	-
3. Minimal breadth	3	SD
4. Proximal maximal breadth	4	Bp
5. Proximal maximal depth	5	Dp
6. Distal articular maximal breadth	6	Bd

See also von den Driesch, 1976, p. 99.

LATERAL SECOND PHALANX OF HIPPARION (C, D and E)

1. Maximal length
2. Proximal maximal breadth
3. Proximal maximal depth
4. Distal maximal breadth

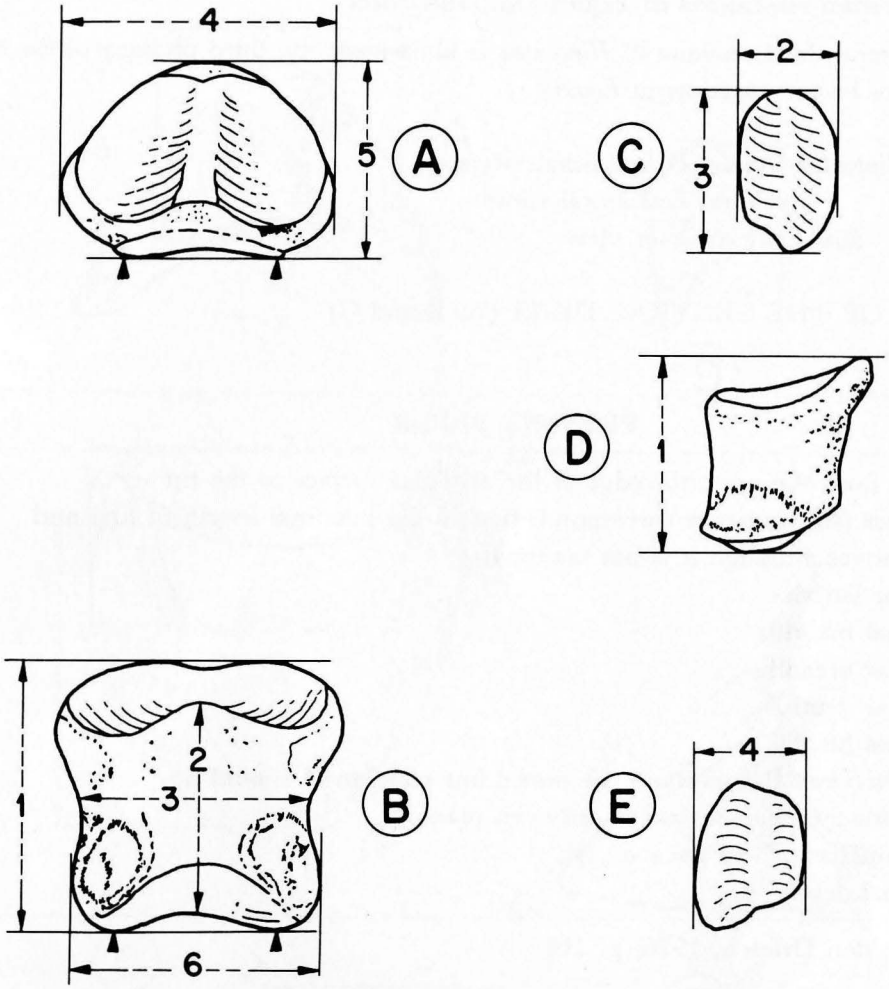

4
5
A
2
C
3
D
1
2
3
1
B
6
4
E

FIGURE 29: THIRD PHALANGES OF EQUUS AND HIPPARION

(Only a lateral third phalanx of *Hipparion* is illustrated; the third phalanx of the central digit of *Hipparion* may be measured as in *Equus*).

Equus and *Hipparion*, A and D: proximal views
C and E: Lateral views
Equus, B: Anterior view

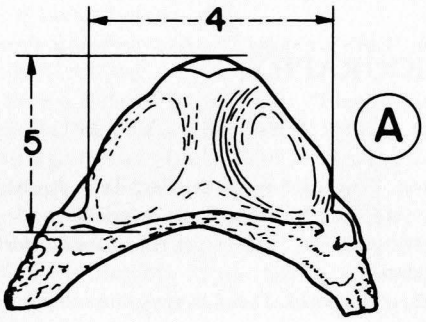
PHALANX OF THE CENTRAL DIGIT (A, B and C)

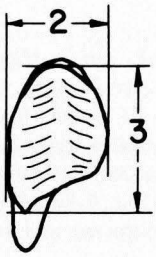
PRESENT PAPER	VE	AVD
1. Length from the posterior edge of the articular surface to the tip of the phalanx (this measure corresponds best to the maximal length of first and second phalanges although it is not maximal).	-	-
2. Anterior length	1	Ld
3. Maximal breadth	4	GB
4. Articular breadth	6	BF
5. Articular depth	5	LF
6. Maximal height	3	HP
7. Angle between the sole and the dorsal line (this angle should be measured with the phalanx laid on an even plane)	-	
8. "Circumference" of the sole	7	-
*. Maximal depth	2	GL

See also von den Driesch, 1976, p. 101.

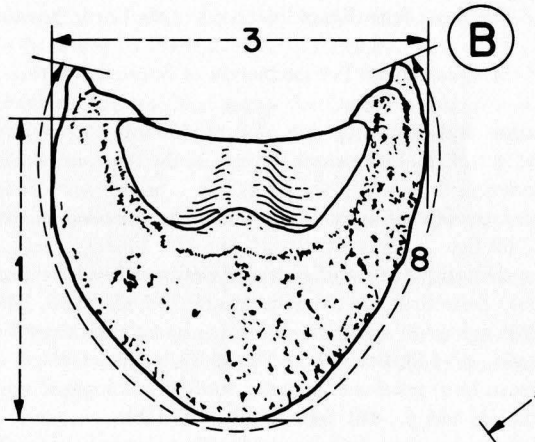
LATERAL THIRD PHALANX OF HIPPARION (D and E)

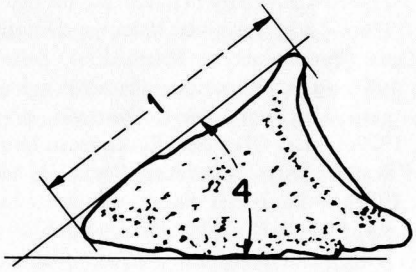
1. Anterior length
2. Proximal articular breadth
3. Proximal articular depth
4. Angle between the sole and the dorsal line (may be measured after projecting the profile of the phalanx on a sheet of paper)



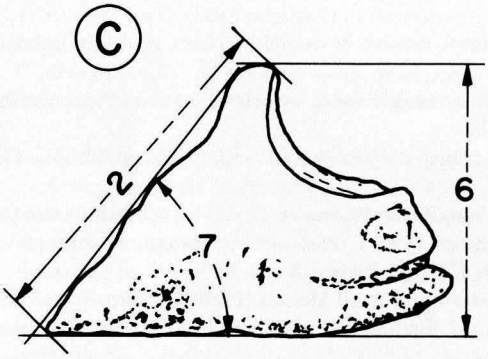


D





E



BIBLIOGRAPHY

ALBERDI, M.-T., 1972.—El genero *Hipparion* en Espana. Vol. 1: Texto, 368 p.; Vol. 2: Tablas y figuras, 235 tabl., 79 fig., 47 pl. Madrid.

ALBERDI, M.-T., 1974.—El genero *Hipparion* en Espana. Nuevas formas de Castilla y Andalucia, revision e historia evolutiva. Trabajos sobre Neogeno-Cuaternario, 1, 146 p., 56 tabl., 7 pl., Madrid.

ALBERDI, M.-T., ANTUNES, M. T., SONDAAR, P. Y., ZBYSZEWSKI, G., 1978.—Les *Hipparion* du Portugal. Ciencias da Terra (UNL), 4, p. 129-156, 10 fig., 2 pl., 11 tabl., Lisboa.

AZZAROLI, A., 1966.—Pleistocene and living Horses of the old World. Palaeontographia italica, 61 (n.s. 31): 1-15, 46 pl., Pisa.

BARONE, R., 1966.—Anatomie comparée des Mammifères domestiques. Tome 1: Ostéologie. Lyon, Ecole Nationale Vétérinaire, Laboratoire d'Anatomie, 811 p.

CAMP, C. L. & SMITH, N., 1942.—Phylogeny and function of the digital ligaments of the horse. Memoirs, Univ. of California, 13 (2): 69-124, 41 fig., 4 pl.

COOKE, H. B. S., 1950.—A critical revision of the Quaternary Perissodactyla of Southern Africa. Annals of the South African Museum, 31 (4): 393-479, 31 fig.

DIVE, J. & V. EISENMANN, in press.—Identification and discrimination of first phalanges from Pleistocene and modern *Equus*, wild and domestic. *In*: R. H. MEADOW & H. P. UERPMANN, Equids in the Ancient World. Beihefte zum Tübinger Atlas des Vorderen Orients, Wiesbaden.

DRIESCH, A. VON DEN, 1976.—A guide to the measurement of animal bones from Archaeological sites. Peabody Museum Bulletins, Harvard University (1), 137 p., 62 fig.

EISENMANN, V., 1976.—Le protostylide: valeur systématique et signification phylétique chez les espèces actuelles et fossiles du genre *Equus* (Perissodactyla, Mammalia). Zeitschrift für Säugetierkunde, Bd 41, H. 6, 349-365, 10 fig., 4 tabl.

EISENMANN, V., 1977.—Les Hipparions africains: valeur et signification de quelques caractères des jugales inférieures. Bull. Mus. natn. Hist. nat., Paris, 3ème sér., n° 438, Sci. Terre 60, 69-87, 4 fig., 1 pl., 4 tabl.

EISENMANN, V., 1979a.—Les Chevaux (*Equus* sensu lato) fossiles et actuels: étude craniologique et odontologique. Thèse Doctorat d'Etat, Sciences Naturelles, Paris VI, 444 p., 121 fig., 28 pl., 106 tabl.

EISENMANN, V., 1979b.—Etude des cornets des dents incisives inférieures des *Equus* actuels et fossiles. Palaeontographia italica, 71 (n.s. 41), 55-75, 3 fig., 2 pl., 3 tabl.

EISENMANN, V., 1979c.—Les métapodes d'*Equus* sensu lato (Mammalia, Perissodactyla). Géobios, vol. 12, fasc. 6, 863-886, 19 fig., 11 tabl.

EISENMANN, V., 1980.—Les Chevaux (*Equus* sensu lato) fossiles et actuels: crânes et dents jugales supérieures. Cah. Paléont., 186 p., 67 fig., 22 pl., 72 tabl.

EISENMANN, V., 1981a.—Etude des dents jugales inférieures des *Equus* actuels et fossiles. Palaeovertebrata, Montpellier, vol. 10, fasc. 3-4, 127-226, 19 fig., 4 pl., 32 tabl.

EISENMANN, V., 1981b.—Les caractères évolutifs des crânes d'*Hipparion* s.l. et leur interprétation. C.R.Ac.Sc., Paris, t. 293, série II, 735-738, 2 fig.

EISENMANN, V., 1985.—Les Equidés des gisements de la vallée de l'Omo en Ethiopie (collections françaises). *In*: les Faunes plio-pléistocènes de la basse vallée de l'Omo (Ethiopie), T. 1: Périssodactyles-Artiodactyles (Bovidae). Cah. Paléontol., Travaux de Paléontologie est-africaine, Eds CNRS, Paris: 13-55, 14 fig., 5 pl., 21 tabl.

EISENMANN, V., 1986.—Comparative osteology of modern and fossil Horses, Halfasses and Asses. *In*: MEADOW, R. H. & H. P. UERPMANN, eds, Equids in the ancient world. Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A, Wiesbaden. 15 p., 36 fig., 2 tabl.

EISENMANN, V. & C. DE GIULI, 1974a.—Caractères distinctifs entre vrais Zèbres (*Equus zebra*) et Zèbres de Chapman (*Equus burchelli antiquorum*) d'après l'étude de 60 têtes osseuses. Mammalia, t., 38, n° 3, 509-543, 7 fig., 18 tabl.

EISENMANN, V. & C. DE GIULI, 1974b.—Caractères distinctifs des premières phalanges antérieures et postérieures chez certains Equidés actuels et fossiles. Bull. Soc. géol. Fr., (7), XVI, n° 4, 352-361, 8 fig., 4 tabl.

EISENMANN, V., & TURLOT, J.-C., 1978.—Sur la taxinomie du gentre *Equus* (Equidés). Les Cahiers de l'Analyse des Données, vol. III, (2): 179-201, 12 fig., 6 tabl.

EISENMANN, V. & A. KARCHOUD, 1982.—Analyses multidimensionnelles des métapodes d'*Equus*. Bull. Mus. natn. Hist. nat., Paris, 4ème série, t. 4 (1-2), Section C, 75-103, 12 fig., 5 tabl.

EISENMANN, V. & S. BECKOUCHE, 1986.—Identification and discrimination of metapodials of modern and Pleistocene *Equus*, wild and domestic. *In*: R. H. MEADOW & H. P. UERPMANN, Equids in the Ancient World. Beihefte zum Tübinger Atlas des Vorderen Orients, Reihe A, Wiesbaden. 13 p., 19 fig., 13 tabl.

FORSTEN, A. M., 1986.—Revision of the Palearctic *Hipparion*. Acta Zoologica Fennica, 119, 134 p., 42 fig., 4 pl., 27 tabl.

FORSTEN, A., 1983.—The preorbital fossa as a taxonomic character in some old world *Hipparion*. J. of Paleontology, 57 (4), p. 686-704, 6 fig.

GABUNIA, L. K., 1959.—K Istorii Gipparionov (po materialam Neogena SSSR). Izdatel'stvo Akademii Nauk SSSR, 570 p., 69 fig., 23 pl., 109 tabl., 3 cartes.

GIDLEY, J. W., 1901.—Tooth characters and revision of the North American species of the genus *Equus*. Bullet. Am. Mus. Nat. Hist., 14 (9): 91-141, 27 fig.

GROMOVA, V. I., 1949.—Istorija loshadej (roda *Equus*) v Starom Svete. Chast' 1. Obzor i opisanie form. Trudy paleont. Inst., Akad. Nauk SSSR, Moskva, 17 (1): 373 p., 53 fig., 8 pl., 20 tabl.

GROMOVA, V. I., 1949.—Istorija loshadej (roda *Equus*) v. Starom Svete. Chast' 2. Evoljutsija i klassifikatsija roda. Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 17 (2), 162 p.

GROMOVA, V. I., 1952.—Gippariony (rod *Hipparion*) po materialam Taraklii, Pavlodara i drugim. Trudy Paleontologicheskogo Instituta Akademii Nauk SSSR, 36, 475 p., 54 fig., 13 pl., 136 tabl. 17 tabl. h.t.

GROMOVA, V. I., 1959.—O skelete tarpana (*Equus caballus gmelini* Ant.) i drugikh sovremennykh dikikh loshadej. (Chast' 1). Byulleten' Moskovskova obshchestva ispytatelej prirody, otdel Biologii, 64 (4): 99-124, 8 fig., 12 tabl.

GROMOVA, V. I., 1963.—O skelete tarpana (*Equus caballus gmelini* Ant.) i drugih sovremmenykh dikikh loshadej. (Chast' 2). Trudy Moskovskova obshchestva ispytatelej prirody, 10: 10-61, 21 fig., 28 tabl.

HOOIJER, D. A., 1949.—Observations on a calvarium of *Equus sivalensis* Falconer & Cautley from the Siwaliks of the Punjab, with craniometrical notes on recent Equidae. Archs neerl. Zool., 8: 243-266, 2 tabl., 1 pl., Leiden.

HOOIJER, D. A., 1975.—Miocene to Pleistocene Hipparions of Kenya, Tanzania and Ethiopia. Zoologische Verhandelingen, 142: 75 p.

HOWE, J. A., 1966.—Observations on Changes in the Conformation and Enamel Pattern of Horse Teeth Due to Wear. The Compass of Sigma Gamma Epsilon, 44 (1): 10-18, 3 pl., 1 tabl.

HOWE, J. A., 1970.—The range of variation in *Equus* (*Plesippus*) *simplicidens* Cope from the Broadwater quarries of Nebraska. Journal of Paleontology, 44 (5): 958-968, 3 fig., 5 tabl.

HUSSAIN, S. T., 1975.—Evolutionary and functional anatomy of the pelvic limb in fossil and recent Equidae (Perissodactyla, Mammalia). Anat., Histol., Embryol., 4: 179-222.

MOTOHASHI, H., 1930.—Craniometrical studies on skulls of wild asses from West Mongolia. Nem. Tottori agric. Coll., 1: 62 p., 5 pl., 6 fig., Tottori.

MUSIL, R., 1969.—Die Pferde der Pekarna-Höhle. Zeitschr. Tierzücht. Züchtungsbiol., 86 (2): 147-193, 2 fig., 5 tabl.

OSBORN, H. F., 1912.—Craniometry of the Equidae. Mem. American Museum of Natural History, n.s., 1 (3): 57-100, 17 fig., 1 tabl., New York.

PETIT, M., 1939.—Anatomie des molaires des Equidés, Cheval et Ane. Imprimerie Toulousaine, 328 p., 206 fig., 110 tabl., Toulouse.

PRAT, F., 1957.—Sur la discrimination des phalanges antérieures et postérieures d'Equidés. Procès-Verbaux de la Société Linnéenne de Bordeaux, *97*, 22-25.

PRAT, F., 1968.—Recherches sur les Equidés pléistocènes de France. Thèse de Sci. nat., Bordeaux: Fac. sci., 4 vol., 662 p., 149 fig., 126 tabl.

SEN, S., SONDAAR, P. Y., STAESCHE, U., 1978.—The biostratigraphical applications of the genus *Hipparion* with special reference to the Turkish representatives. Kon. Ned. Akad. Wetensch., Proceedings, series B, 81 (3), p. 370-385, 4 tabl.

SKINNER, M. F., HIBBARD, C. W. et al., 1972.—Early Pleistocene preglacial and glacial rocks and faunas of North-Central Nebraska. Bulletin of the American Museum of Natural History, 148 p., 60 fig., 21 tabl., New York.

SKINNER, M. F. & MACFADDEN, B. J., 1977.—*Cormohipparion* n.gen. (Mammalia, Equidae) from the North American Miocene (Barstovian-Clarendonian). J. of Paleont., 51(5), p. 912-926, 7 fig., Lawrence.

SONDAAR, P. Y., 1961.—Les *Hipparion* de l'Aragon méridional. Estudios geologicos, Inst. Invest. "Lucas Mallada", 17 (3-4), 209-305, 57 fig., 10 pl., 27 tabl.

SONDAAR, P. Y., 1968.—The osteology of the manus of fossil and recent Equidae with special reference to phylogeny and function. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, Natuurkunde, 25 (1), 76 p.

STAESCHE, U. & P. Y. SONDAAR, 1979.—*Hipparion* aus dem Vallesium und Turolium (Jungertiär) der Türkei. Geologisches Jahrbuch, B 33: 35-79, 26 fig., 5 tabl., Hannover.

STIRTON, R. A., 1941.—Development of characters in horse teeth and the dental nomenclature. Journal of Mammalogy, 22 (4): 434-446, 10 fig., Baltimore.

VAN HOEPEN, E. C. N., 1940.—Oor die Tande van die Equinae. I. Die Snytande van die Onderkaak. Tydskr. vir Wetenskap en Kuns, 1 (1): 101-114, 15 fig.

WILLOUGHBY, D. P., 1948.—A statistical study of the metapodials of *Equus occidentalis*. Bulletin of the Southern California Academy of Sciences, 47 (3): 84-94, 4 fig., 2 tabl.

WILLOUGHBY, D. P., 1974.—The Empire of *Equus*. Barnes Ed., 475 p., 251 fig., 31 tabl., New York.

WOODBURNE, M. O. & BERNOR, R. L., 1980.—On superspecific groups of some Old World Hipparionine Horses. J. of Paleont., 54 (6), p. 1319-1348, 7 fig., 4 tabl.

WOODBURNE, M. O., MACFADDEN, B. J. and SKINNER, M. F., 1981.—The North American *"Hipparion"* datum and implications for the Neogene of the Old World. Géobios, n° 14, fasc. 4: 493-524, 10 fig., 2 tabl.

ZHEGALLO, V. I., 1978.—Gippariony Tsentral'noj Azii. Sovmestnaya Sovetsko-Mongol'skaya paleontologicheskaya Ehkspeditsiya, Trudy, 7: 152 p., 80 fig.