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THE OSTEOLOGY OF THE MANUS
OF FOSSIL AND RECENT EQUIDAE
with special reference to phylogeny and function

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I. INTRODUCTION

In the study of fossil horses often less attention is paid to the post cranial parts, though there are many interesting facts and features to be seen which can improve our insight into the taxonomy and evolution of the horse. Many genera and species of horses are known only by teeth and skull characteristics, though there exists an abundant material of post cranial bones.

The original aim of this study was to see whether the extensive material of fossil horses of Chihuahua (Mexico) stored in the Los Angeles County Museum would enable us to differentiate the previously described 4 horse species, on the morphological characteristics of the manus bones. The horses, *Neohipparion floresi*, *Nannippus* c.f. *minor*, *Pliohippus* *Pliohippus mexicanus* and *Pliohippus Astrohippus stocki* have so far mainly been known by their skull and teeth characteristics (LANCE, 1950, STIRTON, 1955). In the Hemphillian material from Chihuahua the bones are present in big quantities and are well preserved.

In order to understand whether the morphological differences found in the manus were primitive or progressive, it was necessary to go into the phylogeny and function of the manus and to study the changes from the Oligocene *Mesohippus* to the present *Equus*. It turned out that, though much has been written about horse locomotion and evolution, some important changes have never been evaluated sufficiently well or have been interpreted wrongly.

Once concerned with this it became the main subject of this study. The Chihuahua horses were taken as example of what kind of different locomotion in horses we can encounter in Hemphillian North American horses.

The major changes in post cranial skeleton during the horse evolution so far described can be summarized as follows:

- a. increase in the size.
- b. development of a locomotion mechanism which was more efficient in running for a bigger animal. The better performance of the running mechanism of a bigger animal which left the forest and became a grazing animal in the open grassland involves the more pendulum action of the limbs and loss of lateral flexibility (seen in the fusian between radius — ulna and tibia — fibula, ulna and fibula tend to become vestigial). The development of pulley-like joints, the loss of padded feet, reduction of the side toes and in consequence the increase in weight falling on the enlarged third digit. The development of a ligamental springing mechanism in monodactyl horses.

The relative lengthening of the phalanges and in consequence the lift

of the foot from the ground, thereby losing its pad, however has never been evaluated sufficiently well. This relative lengthening of the phalanges resulted in proportional increase in the pressure in the fetlock joint. The phylogenetical changes found by CAMP and SMITH (1942) in the digital ligaments must be explained by or are associated with this. Also a change in size and shape of the sesamoid bones can be noted. The sesamoid bones are interposed in the course of the ligaments and tendons and enable them to act in a mechanical advantage. Also these bones that are functionally so important have never been studied adequately in fossil horses.

In this study an attempt will be made to explain functionally the phylogenetical changes in the manus.

Original material from *Meshippus*, *Parahippus*, *Merychippus*, *Anchitherium*, *Nannippus*, *Hipparion*, *Pliohippus* and *Equus* was investigated.

The fundamental and penetrative study of the digital ligaments of CAMP and SMITH (1942) was a constant source of data and guide to the functional anatomy of the horse foot.

The following abbreviations are used:

C.M. =Carnegie Museum, Pittsburgh

G.I.U. =Geological Institute, Utrecht

L.C.M. =Los Angeles County Museum

U.F. =University of Florida

The following names for the carpal bones are used (between brackets synonyms):

- A. Proximal row, Navicular (scaphoid radiale), Lunatum (semilunare, intermedium), Triquetrum (ulnare, pyramidale), Pisiform (accessory).
- B. Distal row, Trapezium (carpale 1), Trapezoideum (carpale 2), Magnum (carpale 3), Hamatum (unciform, carpale 4.5).

All measurements are given in millimeters.

SUMMARY

The phylogeny of the horse manus is described and an attempt is made to explain its function. For this reason original horse fossils from North America and Eur-Asia were studied. The phylogeny of the manus bones is first considered separately and next in relation. When the manus was studied as a whole it turned out that the general procedure to put the manus of fossil horses in the same position as *Equus*, when its phylogeny was described, is wrong and therefore it gives misleading results. When we compare in this way, for example, *Mesohippus* with *Equus* in rest position, the fetlock joint of *Mesohippus* will be in maximum dorsal flexion and the manus rests on the tip of its third digit; this position probably never occurred during locomotion. And thus the impression is created that the laterals are farther from the ground.

The morphological differences between *Anchitherium* and *Mesohippus* are explained allometrically.

In the *Parahippus*-*Equus* lineage we find a lengthening of the median phalanges, greater flexibility of the fetlock joint and a change in position of the manus which finally results in that of *Equus*.

The phylogeny of the digital ligaments given by CAMP and SMITH (1942) is considered as accompanying:

1. lengthening of the central phalanges, because of it the foot lost its pad, more weight was brought down the third digit,
2. the fetlock joint became more flexible and about 40° more dorsal flexion was possible in *Equus* when compared with *Mesohippus*,
3. the lengthening of phalanges had great mechanical consequences because a heavier strain was thereby put on the fetlock joint and ligaments,
4. a same lateral movement in the fetlock joint results in a direct proportional (to the lengthening) movement on the ground.

The degeneration of the muscle interosseous into a tendon took place relatively late in the phylogeny of the horse. Only in monodactyl horses is the tendification complete. This could be learned from the shape of the third metacarpal.

Three types of feet are distinguished:

1. the padded foot in the *Mesohippus*-*Anchitherium* lineage. The lateral digits are also in contact with the surface in rest position. The lateral metapodials were still able to spread from the distal part of the central metacarpal.

2. the tridactyl tip toe foot, for example, *Parahippus*, *Merychippus*, *Hipparion*. This foot is still tridactyl but in rest position the laterals do no longer touch the ground. This was due to the lengthening of the central phalanges. The lateral metapodials are tightly bound to the central. The position of the fetlock joint can be regulated to a certain extent by the musculus interosseous which results in quite an "all-round" foot type.
3. the monodactyl "springing" foot type for example, *Pliohippus*, *Plesippus*, *Equus*. The central phalanx lengthening is maximal. The musculus interosseous is changed into a tendon which together with the digital ligaments forms the so-called "automatic springing mechanism".

Some other properties of skull and limbs we have related to the phylogeny and function of the manus.

Finally it is tried to reconstruct the paleoecology of the fossil horses and specially that of the Chihuahua horses.

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II. PHYLOGENY

A. CARPUS

Studied material. In describing the phylogenetic changes in the carpus from *Mesohippus* to *Equus* the following material was studied:

a right manus from *Mesohippus* C M 996 (Oligocene, Wyoming).

Parahippus material from Thomas farm (Chilchrist county Florida) stored in the Museum of Comparative Zoology and the University of Florida (Miocene).

Neohipparion, *Nannippus*, *Pliohippus* material from loc. 275 Yepmora (Chihuahua Mexico) stored in the Los Angeles County Museum (Hemphillian).

Hipparion material from several Spanish and European localities.

Anchitherium from Steinheim (Germany) stored in the Geological Institute Utrecht.

specimen of *Merychippus* and other horses were studied from different provenance, while several data were taken from the literature which will be indicated in the text.

1. *Os navicular* (fig. 1)

The os navicular is the largest of the proximal row and imparts the weight of the body to the os magnum and the trapezoid. The proximal part is convex in front and concave behind and articulates with the medial facet on the distal end of the radius. In general the intensity of the concavity and convexity is most pronounced in the geological younger horses (fig. 1A).

In *Mesohippus* the anterior part of the bone is narrower than the posterior part, while in *Parahippus* this is changing and the anterior part is broader than the posterior. This is also found in *Merychippus* and *Hipparion*, but in *Equus* and *Pliohippus* we can observe a broader posterior part which is sometimes in contact with the lunatum. In the tridactyl horses the lunatum and os navicular are in contact only on the anterior side (fig. 1C d, e). The extra contact with the lunatum in *Equus* shows a more restricted movement between these bones in *Equus* as in the primitive horses (less lateral movement in the carpal joint, as GROMOVA (1952) explains it in describing the differences between *Equus* and *Hipparion*). In *Mesohippus*, though the posterior part of the navicular is broader than the anterior, no contact existed between the posterior side of this bone and the lunatum, because the tuberosity on this part (typical for later horses) had not yet developed. The broader posterior part can be explained by the fact that a bigger part of the weight was shifted to the

trapezoideum. This is also clearly seen when we study the distal side of the navicular (fig. 1B).

In *Mesohippus* the surface of the articulation facet for the trapezoideum exceeds in size that of the magnum. In later horses the facet for the trapezoideum decreases in relation to that of the much broader magnum.

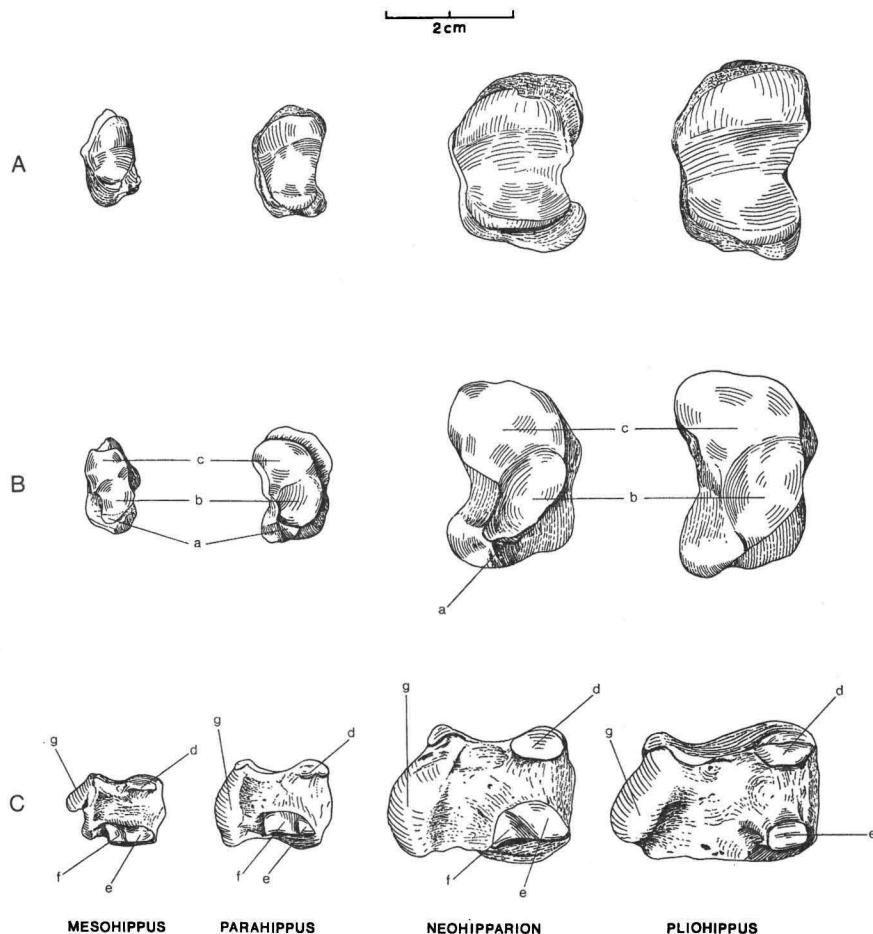


Fig. 1. Os navicular (right).

<i>Mesohippus</i> sp.	coll. no. 996 C.M.
<i>Parahippus leonensis</i>	coll. no. 4088 U.F.
<i>Neohipparion floresi</i>	coll. L.C.M.
<i>Pliohippus mexicanus</i>	coll. L.C.M.

A. proximal view B. distal view C. lateral view

- a. facet for articulation with trapezium
- b. facet for articulation with trapezoideum
- c. facet for articulation with magnum
- d. proximal facet for articulation with lunatum
- e. distal facet for articulation with lunatum
- f. lateral facet for articulation with magnum
- g. volar tuberosity

Only in *Equus* can we notice a proportional increase in the facet for articulation with the trapezoideum. This seems to be in contradiction with the general evolutionary trend. The trapezoideum imparts the weight to the second metacarpal which is reduced the most in *Equus*. We can explain this perhaps as follows: in *Equus* we note that the distal articulation surface of the trapezoideum possesses also a facet of articulation with the Mc III, lacking in earlier horses, so part of the weight is shifted to the Mc III (fig. 6C b). On the distal volar side of the navicular we notice in primitive horses a clear facet of articulation with the trapezium which is greatly reduced or lacking in *Equus* (fig. 1C a). This facet is variable in size and it makes an angle with the facet for trapezoideum. It seems that in *Mesohippus* the angle is less pronounced than it is in the later horses and some of the weight was still imparted to the trapezium. In *Parahippus* and later horses the trapezium was more attached to the carpal and did not bear weight and might have had some function as an accessory bone interposed in a tendon. The lateral surface of the navicular bears an upper and a lower facet on its anterior part for articulation with the lunatum. These facets are the most pronounced in *Pliohippus* and *Equus* (fig. 1C d, e).

In tridactyl horses we notice another important facet, posterior to the distal facet for the lunatum (fig. 1C f). This facet is in articulation with the os magnum when the carpal joint is flexed. The height of the bone in the back exceeds in the tridactyl horses the same measurement in the front. Perhaps this can be correlated with the changed stand of the manus.

2. *lunatum* (fig. 2)

The proximal part of the bone is saddle-shaped and articulates with the middle facet on the distal part of the radius. On the distal surface there are two articulation facets on its anterior side, one for the magnum and one for the hamatum. In *Mesohippus* these facets make a sharp angle; in the later horses this angle is less sharp and is in *Equus* nearly 180° (fig. 2A a, b). In primitive horses the facet for articulation with the hamatum is relatively big and shows that more weight is shifted via the hamatum to the fourth metacarpal (fig. 2B b). The facet of articulation with the magnum is convex on the anterior side and concave on the posterior side. This concavity is more pronounced in tridactyl horses and is more bowl-shaped in *Equus* (fig. 2B d) which suggests that in the more primitive horses more lateral movement was possible. In this way we can explain also the more concave facet for the hamatum in *Mesohippus* and *Parahippus*.

3. *triquetrum* (fig. 3)

GROMOVA (1952) notes as differences between *Hipparion* and *Equus* in the triquetrum the following:

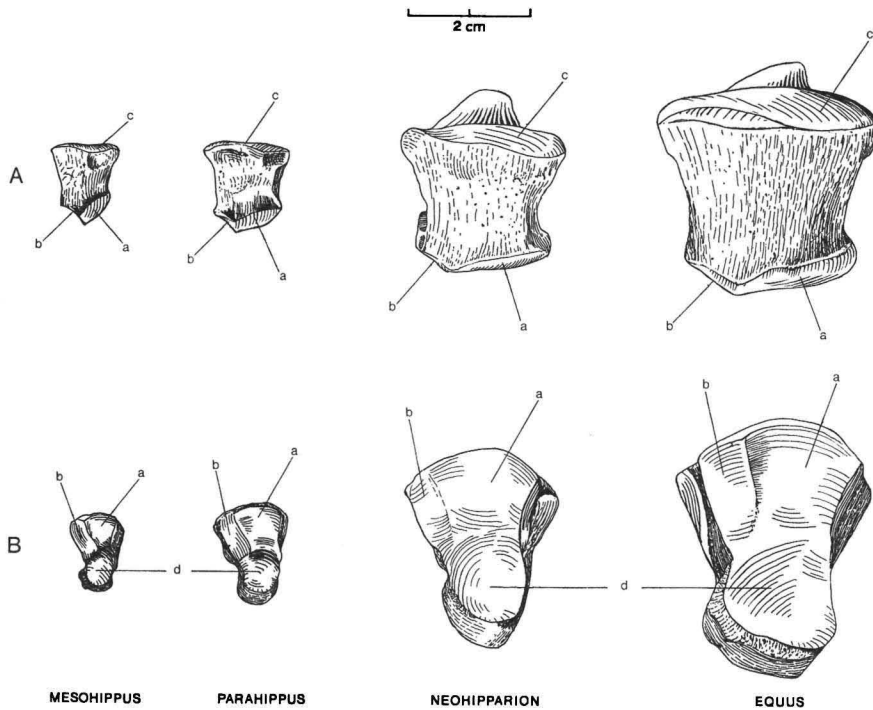


Fig. 2. Right lunatum.

<i>Meshippus</i> sp.	coll. no. 996 C.M.
<i>Parahippus leonensis</i>	coll. no. 4091 U.F.
<i>Neohipparion floresii</i>	coll. L.C.M.
<i>Equus caballus</i>	coll. G.I.U.

A. dorsal view B. distal view

- a, d. facets for articulation with magnum
 b. facet for articulation with hamatum
 c. facet for articulation with radius

- a. the bone is relatively higher in *Hipparion*.
- b. the distal articulation surface is more curved in *Equus*.
- c. the distance between the facets proximal articulating with ulna and pisiform (fig. 3A a, b) is in *Hipparion* greater than in *Equus*. In the latter they are often connected.

The same differences can be noted between *Neohipparion* and *Equus*. In *Meshippus* and *Parahippus* the facets for ulna and pisiform are also in most cases connected. KOVALEVSKY (1873) notes the same in *Paleotherium magnum*. The angle between the facets is less pronounced in the older horses as *Meshippus* and *Parahippus* and the triquetrum in these horses is not relatively higher than in *Equus* and even relatively lower. In the youngest horses the facets for the lunatum are the most pronounced (fig. 3B c, d) and shows that here these carpal bones were more tightly together and less lateral movement was possible.

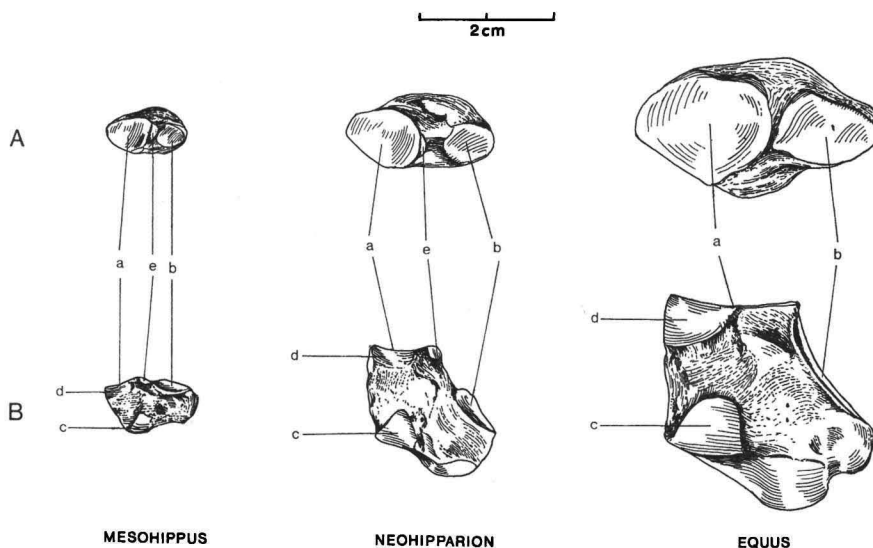


Fig. 3. Triquetrum (right).

<i>Mesohippus</i> sp.	coll. no. 996 C.M.
<i>Neohipparion floresii</i>	coll. L.C.M.
<i>Equus caballus</i>	coll. G.I.U.

- A. proximal view B. medial view
 a. facet for articulation with ulna
 b, e. facets for articulation with pisiform
 d, c. facets for articulation with lunatum

4. *pisiform* (fig. 4)

This bone is situated behind the former bone and does not directly bear weight. It is interposed in the course of the tendons of the middle and lateral flexors of the carpus. Also the posterior border furnishes attachment to the transverse carpal ligament.

GROMOVA (1952) describes important differences between the pisiform of *Hipparion* and *Equus*, namely that in *Equus* the pisiform is higher and also that the groove for the long tendon of ulnaris lateralis is more pronounced in *Hipparion*. This might be considered as a general trend from *Mesohippus* to *Equus*. The pisiform is in *Mesohippus*, *Parahippus* etc. even lower than in *Hipparion*.

The facets for articulation of the os triquetrum and ulna are closer to each other in *Mesohippus*, *Parahippus* and *Equus* than in *Hipparion*. The angle between the facets in the tridactyl horses is sharper than in *Equus* (fig. 4 a, b) (see also triquetrium). The higher pisiform can be explained because it enables the muscles in the later horses to act at a mechanical advantage.

5. *trapezium* (fig. 5)

This bone is irregular in shape and is present in all primitive horses.

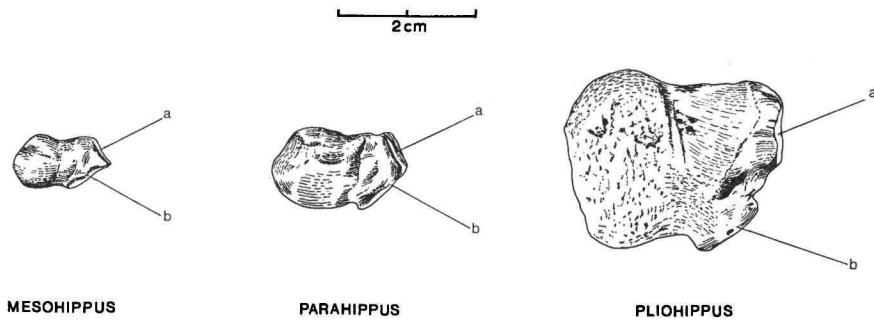


Fig. 4. Pisiform (right).

<i>Mesohippus</i> sp.	coll. no. 1027 C.M.
<i>Parahippus leonensis</i>	coll. no. 4084 U.F.
<i>Pliohippus mexicanus</i>	coll. L.C.M.

- a. facet for articulation with ulna
b. facet for articulation with triquetrum

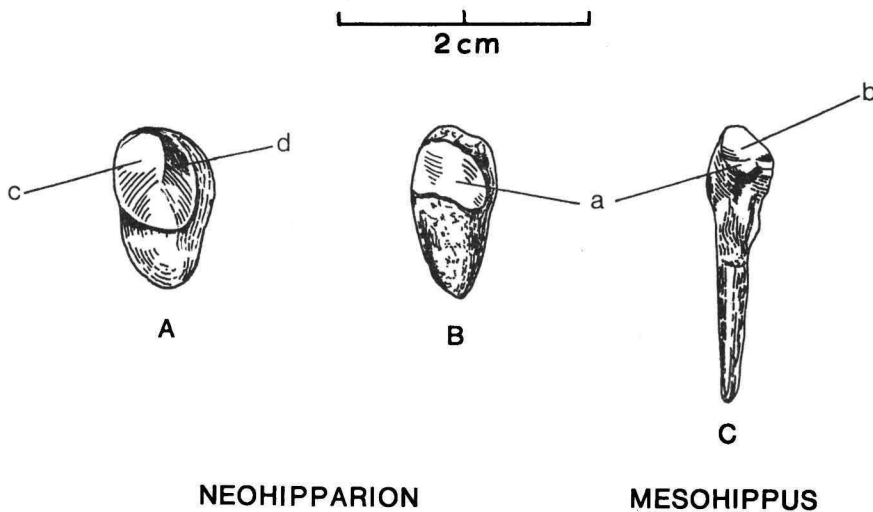


Fig. 5. A. trapezium? B. C. fifth metacarpal.

A. <i>Neohipparion floresi</i> ?	coll L.C.M.
B. <i>Neohipparion floresi</i>	coll. L.C.M.
C. <i>Mesohippus</i> sp.	coll. no. 996 C.M.

- c. facet for articulation with trapezoid?
d. facet for articulation with Mc II
a. articulation facet with the Mc IV
b. articulation facet with the hamatum

It possesses mostly two articulation facets; on the navicular, trapezoideum and Mc II corresponding facets are found (fig. 5A c, d).

CHUBB (1912) found in 57 % of the *Equus* manus dissected by him a rudimentary trapezium, but the articulation facets were here for the

greater part lost. Sisson and Grossman (1964) note that in a good many specimens it is present only on one side. In *Plesippus* GAZIN (1936) the trapezium is present with clear articulation facets. In *Nannippus* the trapezium is not found and this absence is considered as a generic character, MATTHEW (1926).

In general we may say that in the phylogeny of the horse the trapezium gradually reduces in size. In *Meshippus* the bone is still interposed between the navicular and the second metacarpal, while in later horses it is more closely attached to the carpus.

6. *trapezoideum* (fig. 6)

The trapezoideum shifts the weight from the navicular to the second

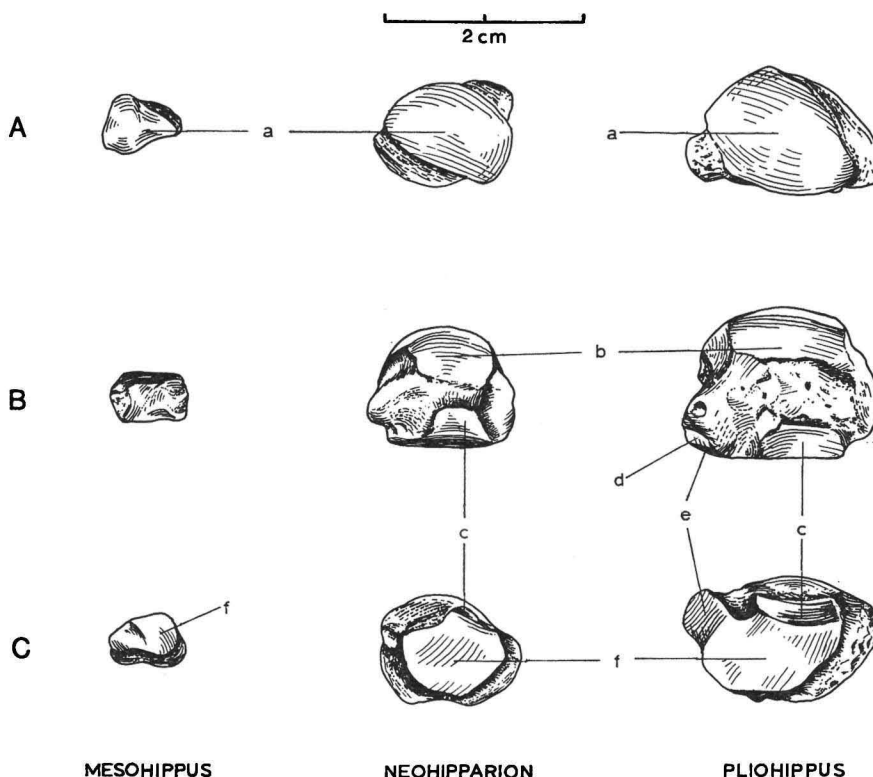


Fig. 6. Trapezoideum (right).

<i>Meshippus</i> sp.	coll. no. 996 C.M.
<i>Neohipparion floresi</i>	coll. L.C.M.
<i>Pliohippus mexicanus</i>	coll. L.C.M.

A. proximal view B. lateral view C. distal view

- a. proximal articulation surface
- b, c. facets for articulation with the magnum
- d. posterior facet for articulation with the magnum
- e. facet for articulation with the Mc III
- f. distal articulation surface with Mc II

metacarpal bone. As the metacarpal is more highly situated in primitive horses and the articulation surface is relatively bigger (Mc II is more developed in these horses) the bone is relatively low. The proximal articulation surface is saddle-shaped in *Mesohippus* and convex in more advanced horses as *Parahippus*, *Merychippus* (fig. 6A a). The convexity is continued in the volar surface. Below this we can observe a clear facet for the trapezium in *Mesohippus* and *Parahippus*.

On the lateral surface two distinct facets are visible for articulation with the magnum. In the most advanced monodactyl horses we find also a third facet on the posterior distal side (fig. 6 d). On the distal articulation we find one facet corresponding with the Mc II. Only in the advanced monodactyl horses we do find a second facet on the posterior side articulating with the Mc III (fig. 6 e). This facet and the facet on the posterior-lateral side for the magnum informs us that more of the weight from the trapezoideum is transferred to the central metapodial in the monodactyl horses.

In some *Parahippus* specimens from Thomas farm the trapezoideum had grown together with the magnum.

7. *magnum* (fig. 7)

The magnum is the largest bone of the distal row. Many changes can be noted in the shape and the function of this bone from *Mesohippus* to *Equus*.

The width of the bone in relation to the anterior-posterior diameter increases gradually. The medial part expands most from *Mesohippus* to *Equus* (fig. 7A a). The magnum is transferring the weight to the third metacarpal. As this bone became more important during the evolution of the horse, whereas the other metacarpals were reduced it is understandable that the magnum became bigger in relation to the other bones.

The proximal surface consists of two facets separated by an anterior-posterior ridge. The medial facet (corresponding to the navicular, fig. 7 a) is concave. The lateral facet is concave in front (fig. 7 c) and convex behind, where it encroaches on the volar surface (fig. 7 d). On the medial side of the posterior part of the magnum we can observe a clear articulation facet with the navicular. This facet is clear in tridactyl horses (fig. 7 b) but vague or mostly absent in monodactyl horses. The facet on the anterior proximal side of the magnum for articulation with the navicular (fig. 7 a) in *Mesohippus* is relatively narrow and broader in the *Parahippus*-*Merychippus*-*Equus* line.

On the medial surface we note three facets on the anterior side. The facet for the metacarpal II is very prominent in *Mesohippus* (fig. 7 f) because the second metacarpal reaches far above the third metacarpal. In later horses this facet is less pronounced and in *Equus* sometimes lacking. The angle between this facet and the distal articulation facet of

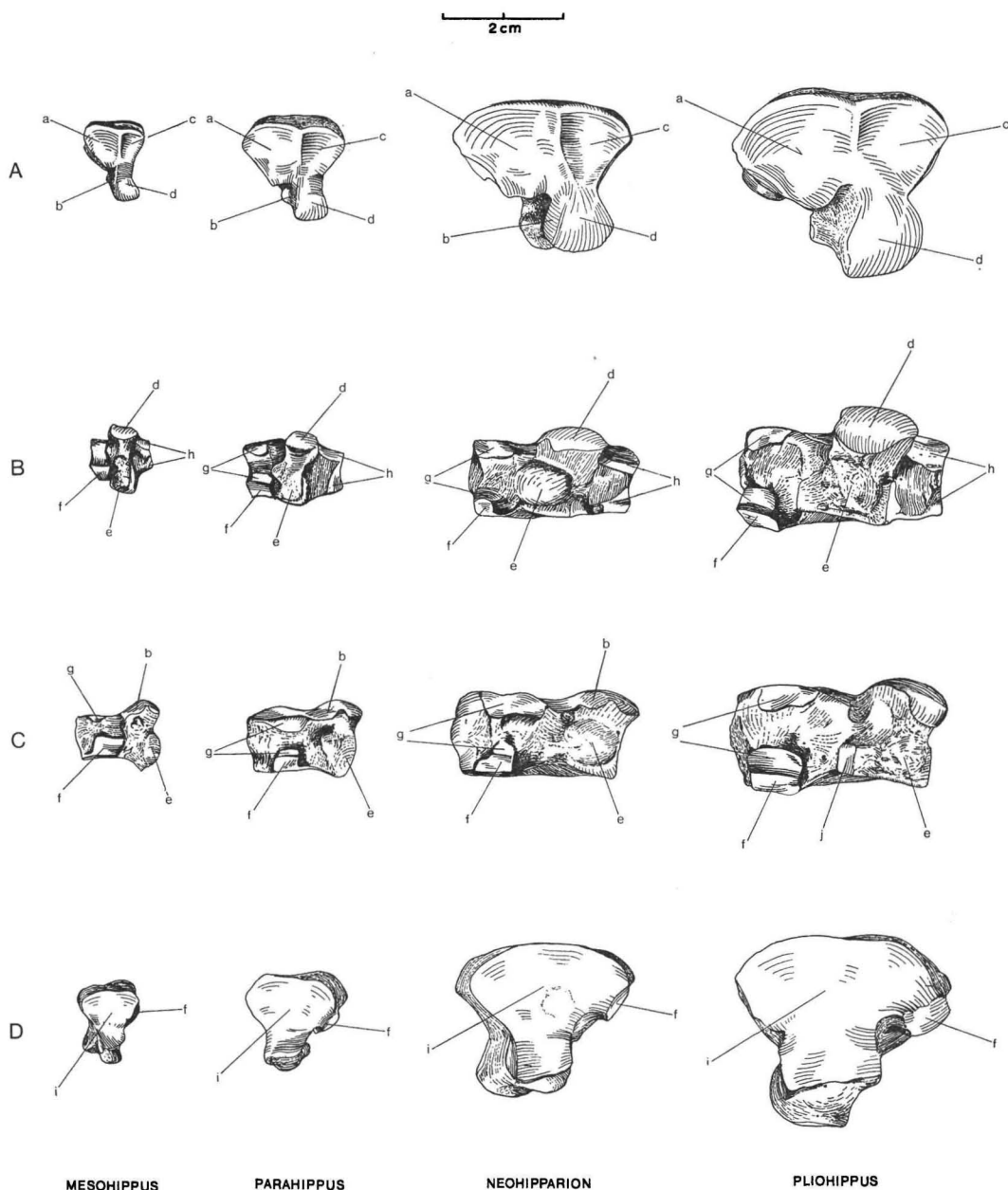


Fig. 7. Magnum (right).

Meshippus sp. coll. no. 996 C.M. *Neohipparion floresi* coll. L.C.M.
Parahippus leonensis coll. no. 4090 U.F. *Pliohippus mexicanus* coll. L.C.M.

A. proximal view B. volar view C. medial view D. distal view

- a. facet for articulation with the navicular
- b. posterior facet for articulation with the navicular
- c, d. facets for articulation with the lunatum
- e. scar for attachment of the musculus interosseus
- f. facet for articulation with the Mc II
- g. facets for articulation with the trapezoideum
- h. facets for articulation with the hamatum
- i. distal articulation surface with Mc III
- j. posterior articulation facet with the trapezoideum

the magnum in *Mesohippus* is bigger than in later horses. The two facets on the medial side proximal to the former are in articulation with the trapezoid. In some advanced monodactyl horses we find a fourth facet also for articulation with the trapezoid on the distal posterior side (fig. 7C j). Further we note a tendency that the anterior facets for articulation with the trapezoid (fig. 7 g) become more pronounced in later horses. Together with the posterior facet in advanced monodactyl horses we may conclude that in the later horses the magnum and trapezoid are more tightly together and less movement between these bones was possible.

On the lateral side of the magnum three facets are found for the hamatum. In general these facets are more pronounced in more advanced horses, but mostly irregular in shape.

The distal articulation surface of the magnum in *Mesohippus* occurs on its posterior end, concave in antero-posterior direction. This is also seen, but less pronounced, in later horses like *Parahippus* (fig. 7 c), *Merychippus* and *Hipparion*. In monodactyl horses this is more flat. The curve in antero-posterior direction, in *Mesohippus* even saddle-shaped, distal surface of the magnum may learn that between this bone and the third metacarpal a movement was possible in antero-posterior direction. In recent horses no movement between these bones is possible.

On the volar distal side in tridactyl horses there is a rough, round tuberosity for attachment of the tendon for the musc. interossei; in *Equus* this is more ridge-shaped (fig. 7 e).

8. *hamatum* (fig. 8)

The os hamatum is relatively higher in primitive horses. It imparts the weight from the lunatum and triquetrum to the third and fourth metacarpal.

The proximal surface is convex and curves outward and downward encroaching on the lateral and volar surface (fig. 8B e). Below this articulation facet we find in primitive horses a clear facet for the Mc V (fig. 8B f). This facet is absent in *Equus*.

On the medial surface we find an anterior facet and posterior facet for articulation with the magnum (fig. 8A d, a). These facets are the most pronounced in the later horses and show that here the bones were more tightly together.

The facet for articulation with the third metacarpal (fig. 8 c, b) makes an angle with the distal articulation surface of the hamatum which approaches 90°. From *Mesohippus* to *Equus* the angle decreases gradually and in consequence more weight is shifted from the hamatum to the third metacarpal.

9. *the carpus as a whole*

Practically all the movement occurs at the radio-carpal joint and

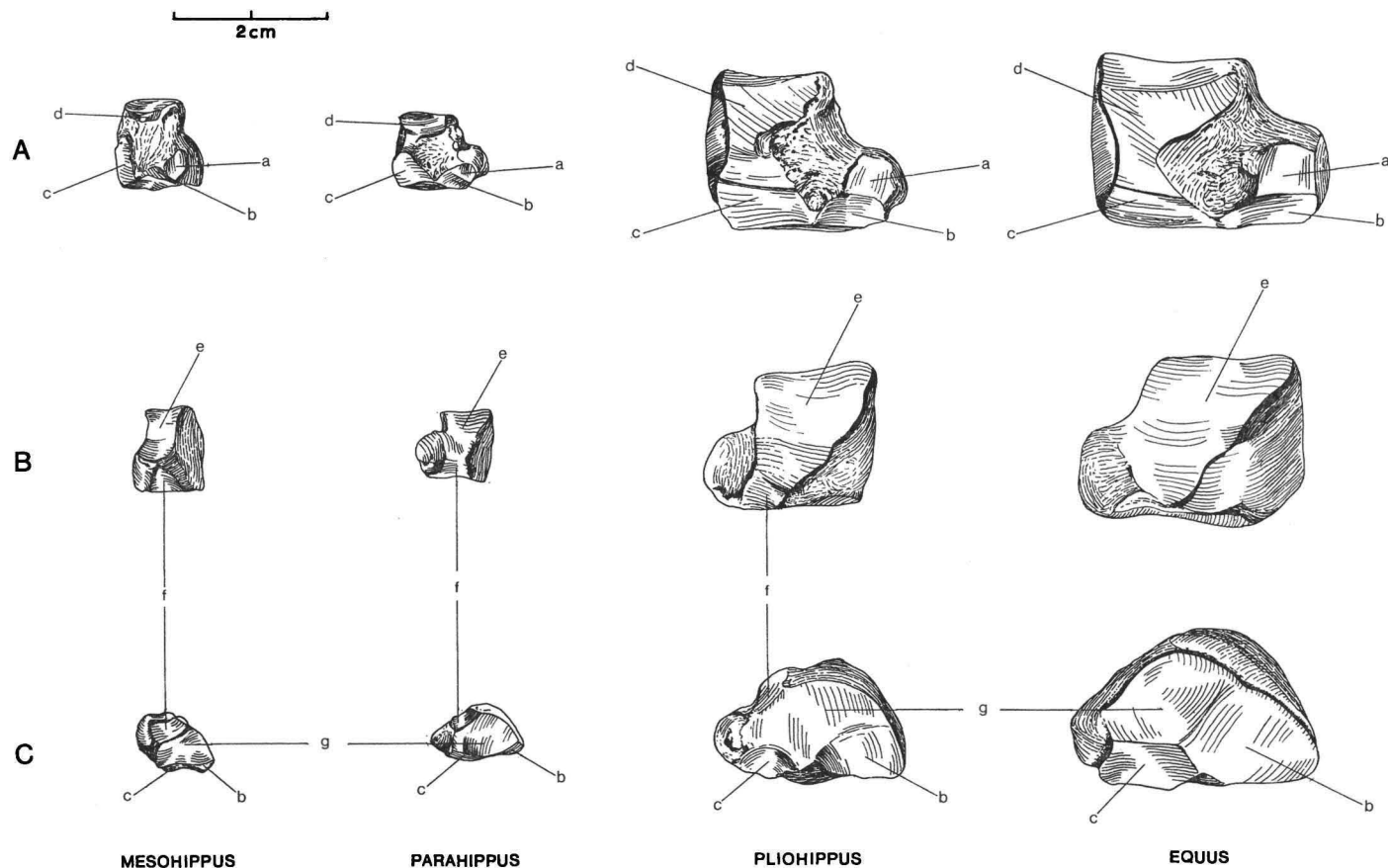


Fig. 8. Hamatum (right).

Mesohippus sp. coll. no. 996 C.M.*Pliohippus mexicanus*

coll. L.C.M.

Parahippus blackbergi coll. no. 4098 U.F.*Equus caballus*

coll. G.I.U.

A. medial view B. lateral view C. distal view

a-g. facets for articulation; a, d. for magnum; c, b. for Mc III; e. for triquetrum; f. for Mc V; g. for Mc IV

intercarpal joints. The distal row remains in contact with the metacarpus in *Equus*. In tridactyl horses some movement between the distal row and metacarpus must have been possible.

In primitive horses the carpus is relatively higher. From *Mesohippus* to *Equus* we note a relative size increase in facets which shift direct or indirect the weight to the third metacarpal.

The trapezium becomes rudimentary or is lacking in *Equus*. In *Mesohippus* the trapezium must have imparted some weight to the second metacarpal depending on the shape of the bone and its corresponding facets on the Mc II and the navicular.

Between trapezoideum-magnum-hamatum we observe in the geologically younger horses clearer articulation facets which show that the distal row of the carpus was more tightly together and acted more as one bone. This is also seen by the shape and direction of the facets.

B. METACARPUS

1. *metacarpal III* (fig. 9, 10, 11, 12)

The third metacarpal shows a number of important changes in the shape of the bone, facets and area of attachment for ligaments and tendons which can be explained by the change in the locomotion apparatus. In *Mesohippus* the bone is already the biggest of the metacarpals and the second and fourth are further reduced compared with *Hyracotherium*.

Proportional length

In the literature often we find that in the phylogeny of the horse there should be a relative lengthening of the central metapodial in relation to the other bones (femur-tibia, radius-humerus). This is, however, in its generality not true. In Table I we find data for some fossil and recent horses. There is some variation in proportional length of the third metacarpal, and it appears from this table that in the *Hipparion* group the metacarpal is somewhat longer in *H. elegans* and *Neohipparion whitneyi*. These two mentioned species are, however, very slenderly built (GIDLEY 1903 and GROMOVA 1952). Anyway there are no striking differences between *Mesohippus bardii*, *Anchitherium aurelianense*, *Hipparion* sp. from Pikermi (Greece) and recent *Equus* species.

The data given in Table I are far from complete, but as the difference in one group ((*Neo*) *Hipparion*) is bigger than that between *Mesohippus* and *Equus*, we may expect that the proportional length of the third metacarpal may have a significance for the species level, though it does not tell us anything about the place of the horse in the phylogeny.

Proximal articulation surface (fig. 9 and 11)

In the more primitive horses generally, the anterior-posterior diameter is proportionally bigger in older horses (Table II). This is very clear when

TABLE I. Comparative proportions between humerus—radius and third metacarpal in some horses, all measurements in mm.

	I length humerus	II length radius	III length Mc III	IV total length humerus + radius + Mc III	Index		
					I/IV × 100	II/IV × 100	III/IV × 100
<i>Meshippus</i> <i>bardii</i> after GIDLEY 1903	1 ex. 115	1 ex. 122	1 ex. 80	317	36	38	26
<i>Merychippus</i> <i>calamarius</i> after HENSHAW 1942	1 ex. 223	1 ex. 227	1 ex. 163	613	36	37	27
<i>Anchitherium</i> <i>aurelianense</i> after WEHRLI 1938	1 ex. 230	1 ex. 250	3 ex. 207	687	34	36	30
<i>Neohipparion</i> <i>withneyi</i> after GIDLEY 1903	1 ex. 190	1 ex. 245	1 ex. 215	650	29	38	33
<i>Hipparion</i> <i>elegans</i> after GROMOVA 1952	1 ex. 212	5 ex. 242	35 ex. 198	652	33	37	30
<i>Hipparion</i> sp. pikermi after FORSTEN 1968	3 ex. 263	277	30 ex. 212	752	35	37	28
<i>Equus</i> <i>caballus</i> after GIDLEY 1903	1 ex. 350	1 ex. 375	1 ex. 263	988	35	38	27
<i>Equus</i> <i>preswalski</i> after GROMOVA 1949	8 ex. 266	8 ex. 319	8 ex. 225	810	33	39	28

we compare for example *Meshippus* with *Astrohippus*. In general we may assume that the width at the proximal part of the Mc III tends to increase in relation to the diameter during the evolution of the horse.

In *Parahippus blackbergi* and *Neohipparion floresii* we find a very pronounced volar tubercle for the attachment of the tendon for the muscle interossei (fig. 10, 1h and fig. 11, 2h) which exaggerates the diameter in these horses. In general we may say that in the tridactyl horses in lineages *Parahippus*–*Merychippus*–*Hipparion* this is a tuberosity, whereas in monodactyl horses it is more ridge-shaped.

TABLE II. (Mc II and Mc III).

	<i>Meshippus</i> sp. C.M. 996		<i>Anchitherium</i> <i>aurelianense</i> after WEHRLI 1938		<i>Parahippus</i> <i>leonensis</i>		<i>Merychippus</i> <i>calamarius</i> after HENSHAW 1942		<i>Hipparion</i> <i>concudense</i>	
	Mc II	Mc III	Mc II	Mc III	Mc II	Mc III	Mc II	Mc III	Mc II	Mc III
1. ant.-post. diam. proximal part	8,7	10,8	15,0	23,0	10,1	15,5	12,0	19,0	16,6	28,2
2. width of the proximal part	7,1	11,0	11,5	29,0	8,8	19,1	9,0	26,0	12,2	36,8
3. ant.-post. diam. of the shaft	7,2	6,0	16,0	15,2	6,4	11,0	7,0	14,0	12,5	20,5
4. width of the shaft	3,7	10,2	7,0	22,5	2,8	15,0	6,0	18,0	17,0	27,8
5. distal diam.	9,0	9,0	21,5	22,0	18,2	—	15,0	20,0	16,5	27,3
6. distal width	7,0	11,0	13,5	32,0	7,2	—	8,0	25,5	8,5	33,4
7. index Mc II/Mc III \times 100 measurement 1.	74		65		65		63			
8. index of the same m. 2	64		39		46		34			
9. index of the same m. 3	120		105		58		50		60	
10. index of the same m. 4	36		31		18		33		25	
11. index of the same m. 5	100		95		—		75		60	
12. index of the same m. 6	64		42		—		31		25	

The facet for articulation with the magnum on the posterior part is slightly convex in anterior-posterior direction in *Meshippus*, which is in the monodactyl horses straight. From *Meshippus* to *Equus* we note that the angle between the facet articulating with the hamatum (fig. 10 and fig. 11 a) and that for the magnum become less pronounced. In *Meshippus* this angle is close to 100° , in *Parahippus* $\pm 120^\circ$ and in *Equus* $\pm 160^\circ$. Together with the decrease in the angle between the facets for articulation with the magnum and hamatum the latter becomes more significant in geologically younger horses especially at its posterior side (fig. 10 and fig. 11 a).

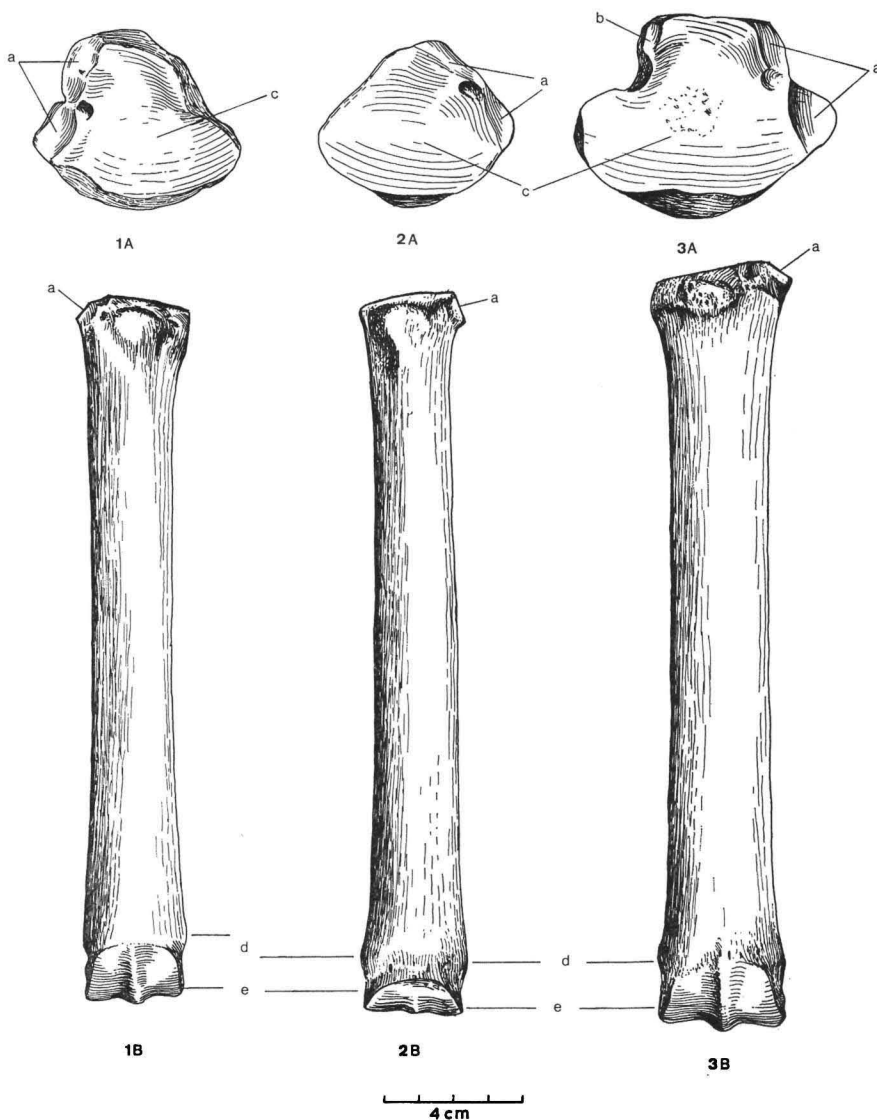


Fig. 9. Third metacarpal.

- | | |
|--|--------------|
| 1. <i>Neohipparion floresi</i> right | coll. L.C.M. |
| 2. <i>Anchitherium aurelianense</i> left | coll. G.I.U. |
| 3. <i>Pliohippus mexicanus</i> left | coll. L.C.M. |

A. proximal view B. dorsal view

- a. facet for articulation with the hamatum
- b. facet for articulation with the trapezoideum
- c. facet for articulation with the magnum
- d. attachment scar for the superficial layer of the collateral ligament
- e. articulation surface with the first phalanx

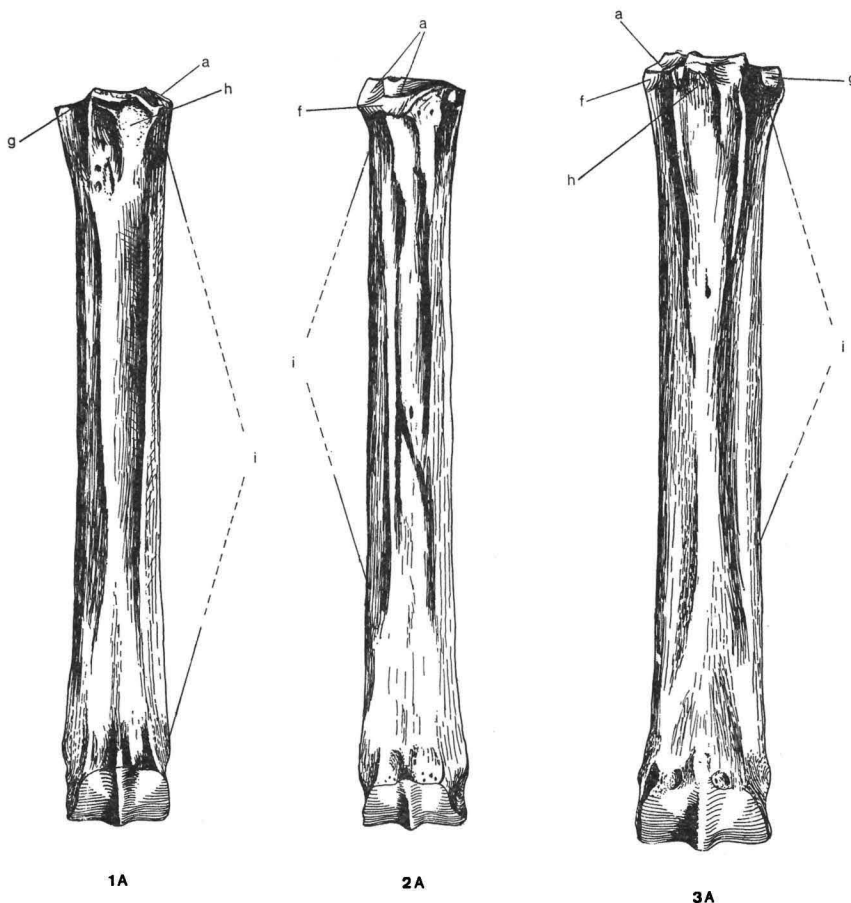


Fig. 10A. Third metacarpal, volar view

- | | |
|--|--------------|
| 1. <i>Neohipparion floresi</i> right | coll. L.C.M. |
| 2. <i>Anchitherium aurelianense</i> left | coll. G.I.U. |
| 3. <i>Pliohippus mexicanus</i> left | coll. L.C.M. |

- a. facet of articulation with the hamatum
- d. attachment scar for the superficial layer of the collateral ligament
- f. facet of articulation with the Mc IV
- g. facet of articulation with the Mc II
- h. attachment scar (tuberosity) for tendon (musculus) interosseus
- i. scar for attachment of the interosseous metacarpal ligaments

In *Equus* often a facet is found on the posterior medial side for articulation with the trapezoideum (fig. 9, 3A b). This facet is lacking in all tridactyl horses and occurs only in the more advanced monodactyl horses (more weight is borne by the third digit).

The shaft

The shaft of the metacarpal is roughened on both sides for the attachment area of ligaments for the lateral metapodials (the interosseous metacarpal ligament) (fig. 10 and fig. 11 i).

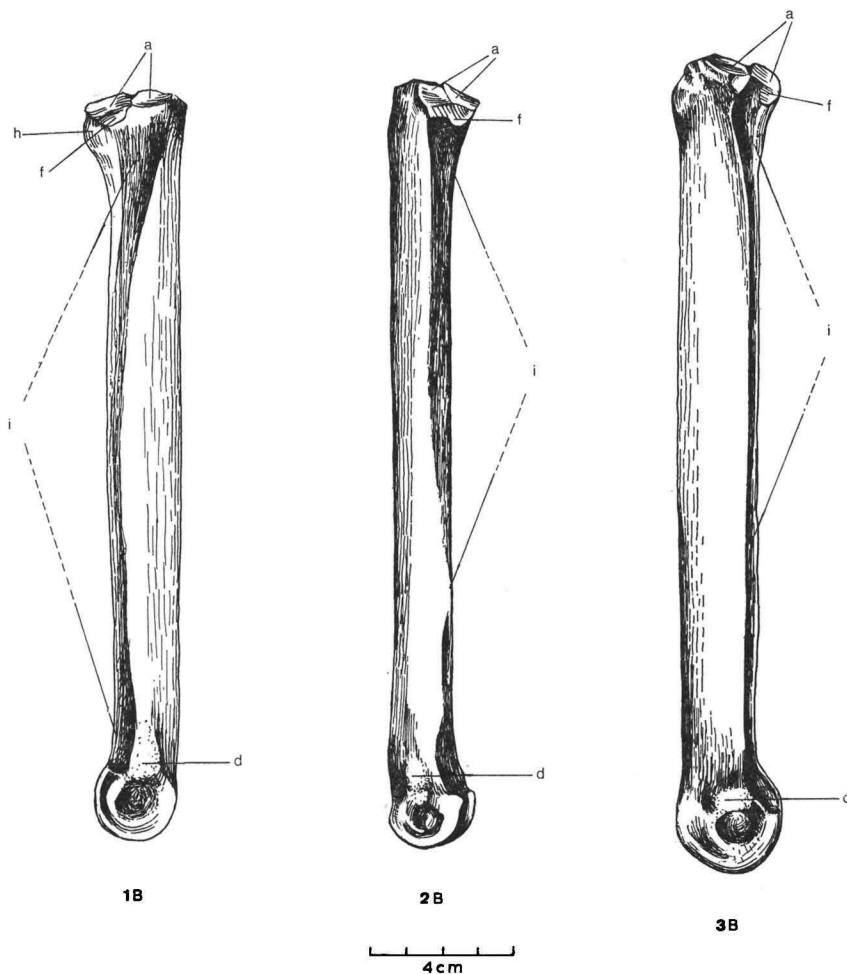
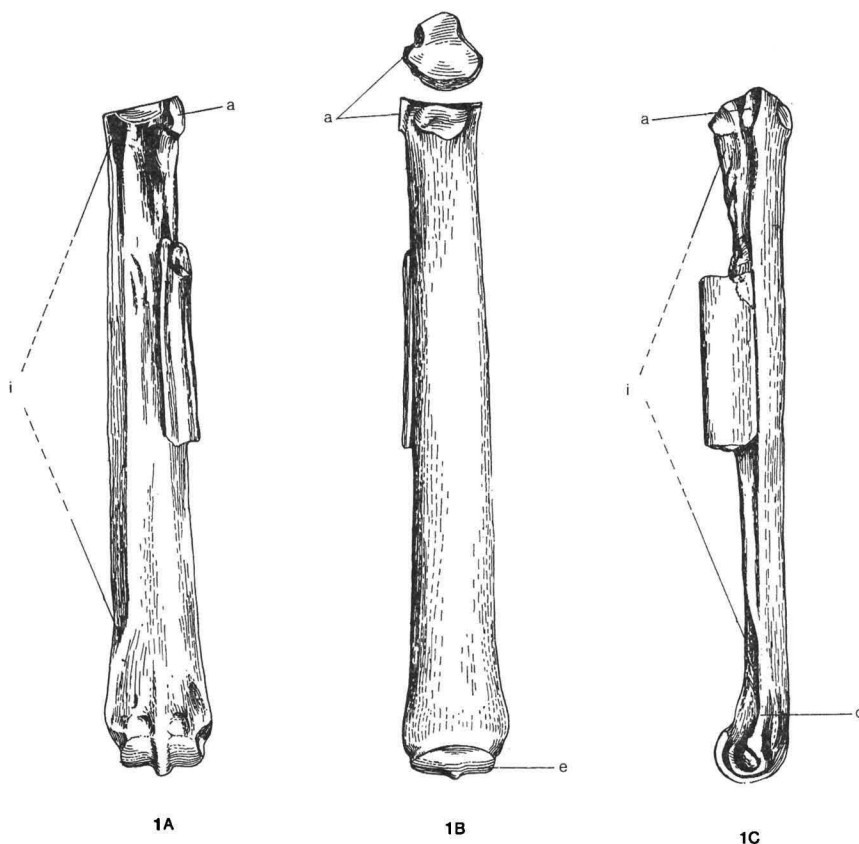


Fig. 10B. Third metacarpal, lateral view

In the tridactyl horses *Parahippus*, *Merychippus* and *Hipparion* we can follow this up to the distal articulation surface of the bone (fig. 10, 1B i; fig. 11, 2C i) where it ends in a cavity. In *Mesohippus* and *Anchitherium* the scar reaches not so far (fig. 10, 2B i and fig. 11 1A i) and also the concavity found in the former horses is not found above the distal articulation surface. In monodactyl horses the rough area reaches only up to $2/3$ of the metacarpal (fig. 10, 3B i). This is in some respect more similar to *Mesohippus* and *Anchitherium* only the area in the monodactyl horses lies more on the volar side, whereas in the former it is on the lateral and medial side of the metacarpal.

The diameter of the metacarpal in *Mesohippus* is a flattened ellipse, in *Equus* more semi-cylindrical and flattened on the volar side. *Anchitherium* is more like *Mesohippus* while in *Parahippus*, *Merychippus* and *Hipparion* it is more like *Equus*, only in these tridactyl horses do we find a more or



Third metacarpal.

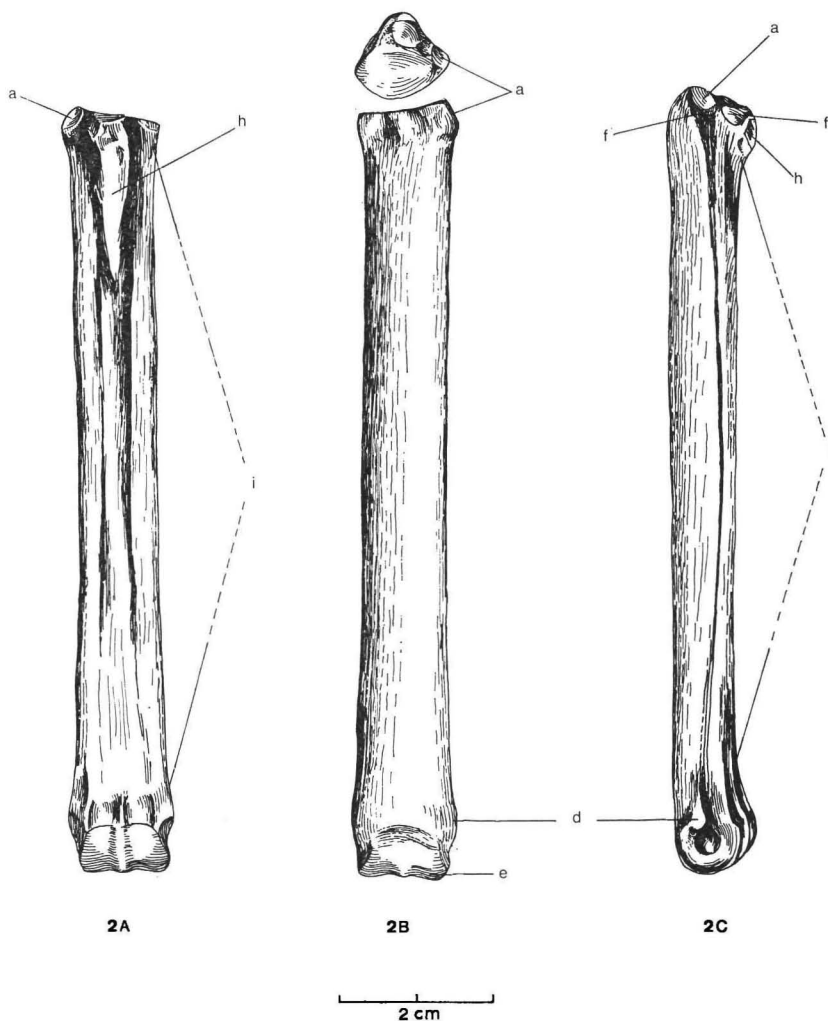
Fig. 11.1. *Mesohippus* sp. right coll. no. 996 C.M.

A. ventral view B. proximal and dorsal view C. lateral view

- a. facet for articulation with the hamatum
- d. attachment scar for superficial layer of the collateral ligament
- e. articulation surface with the first phalange
- f. facets for articulation with Mc IV
- h. attachment tuberosity for the musculus interosseous
- i. scar for attachment of the interosseous metacarpal ligaments

less pronounced gully on the volar side. In monodactyl horses this is flat or even a little convex (*Equus*).

On the lateral and medial side of the third metacarpal above the distal articulation surface we find a scar for the attachment of the superficial layer at the collateral ligaments (fig. 9 d, 10 d, 11 d, 12). In *Equus*, *Anchitherium* and *Mesohippus* this scar is found in the middle of the bone and is more oval-shaped; in *Parahippus*, *Merychippus* and *Hipparion* it is seen more in the front and the tuberosities are more pronounced. Posteriorly of this tuberosity we find two concavities in these horses (the end of the interosseous metacarpal scar) in which the distal part of



Third metacarpal.

Fig. 11.2. *Parahippus blackbergi* left coll. G.I.U.

the lateral metapodial fits. This was still firmly bound to the central by the interosseous metacarpal ligaments. From the placement of the scars for attachment of the superficial collateral ligaments in *Anchitherium* and *Meshippus* and also the absence of the concavity as described in *Parahippus* etc. we may conclude that the distal parts of the laterals in *Meshippus* and *Anchitherium* were free from the central. Similarly CAMP and SMITH (1942) explained that in *Eohippus* the laterals were not firmly bound to the central and the foot was able to spread.

Distal articulation surface

The distal articulation surface for the first phalanx and the proximal sesamoid bones is composed of two condyles. In *Meshippus*, *Parahippus*,

Merychippus and *Anchitherium* these condyles are separated by a sagittal crest on the posterior side. In *Hipparion*, *Pliohippus* and *Equus* this crest is also clearly developed on the anterior side of the metacarpal. In *Equus* this crest is the most pronounced. The development of the sagittal crest runs parallel in the first place to the lengthening of the central phalanges and secondly the reduction of the laterals in the phylogeny of the horse and prevents the fetlock joint from too much lateral dislocation (GROMOVA, 1952). STEININGER (1963) notes also the sagittal crest on the anterior side of an *Anchitherium* from the Pannon in Austria. The mentioned third metacarpal belongs however not to *Anchitherium*, but to *Hipparion*, and is somewhat damaged.

The rounding of the pulley-like articulation joint in the phylogeny from *Parahippus*, *Merychippus* to *Pliohippus* and *Hipparion* is the most pronounced in the latest horses. In *Parahippus* it is about half a circle, in *Equus* it exceeds it and the distal articulation joint of the metacarpus covers $\pm 220^\circ$. In *Parahippus* it is about 180 degrees. In *Mesohippus* and *Anchitherium* it is clearly less than 180° which can be seen in fig. 9, 2B; fig. 11, 1B e and fig. 12) where the articulation in these horses encroaches only little on the anterior surface of the metacarpal compared with *Parahippus*, *Hipparion* and *Pliohippus* (fig. 9, 1B e, 3B e and fig. 11 2B e and fig. 12). The shape of the distal articulation surface tells us about the movement possible in the fetlock joint. In tridactyl horses the distal articulation surface is somewhat curved dorsally, this is shown in fig. 12. Above the joint we find a clear fossa in the *Parahippus*-*Merychippus* lineage (fig. 12 d) which gives the proximal phalanx more freedom when

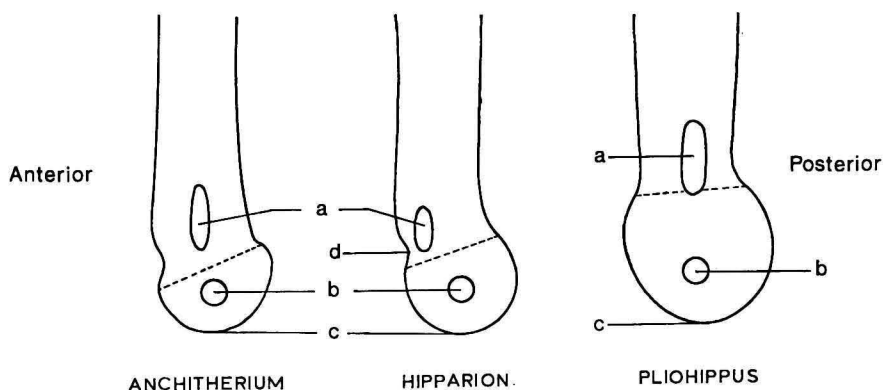


Fig. 12. Distal part of the third metacarpus in outline, lateral view, showing attachment prominences for the fetlock collateral ligaments a. superficial layer b. deep layer.

In *Anchitherium* and *Pliohippus* the attachment prominence for the superficial layer is situated in the axis of the bone, while in *Hipparion* it is a tuberosity on the anterior side.

The distal articulation joint (c) is bent backward in *Hipparion* and *Anchitherium*. There is a clear increase in articulation surface and rounding from the left to the right.

the fetlock joint is flexed. In monodactyl horses the articulation surface is more pulley-like around the shaft (*Pliohippus*, fig. 12 c) which gives the proximal phalanx the maximum flexibility in dorsal direction. The concavity found in tridactyl horses is here also absent (it would have had no function). In *Mesohippus* and also in *Anchitherium* the curvature of the distal articulation encroaches only little on the anterior side of the bone. Here no concavity is found proximal to the joint. The flexion of the fetlock joint could not have been so big. It is known that the angle between the anterior side of the metacarpal and the same side of the first phalange approaches 90° in maximum flexion of the *Equus* fetlock. In *Mesohippus* and *Anchitherium* it is near to 140°. In *Parahippus*, *Merychippus* and *Hipparion* the angle of maximum flexion of the fetlock joint must have been close to that of *Equus*. In the phylogeny of metacarpus there is a clear difference in the bones from *Mesohippus* and *Anchitherium* on the one side and *Parahippus*, *Merychippus*, *Pliohippus*, *Hipparion* and *Equus* on the other in relation to the distal articulation surface.

If we measure the width of the distal articulation surface and that just above this articulation surface at the tubercles than in tridactyl horses the second measurement will exceed the first, while in monodactyl horses this is just the opposite.

2. lateral metacarpals (fig. 13, 14 and 15)

Proximal articulation surface

The Mc II articulates proximally with the trapezoideum; on its lateral side we find a facet of articulation with the magnum and Mc III. The posterior facet for articulation with the Mc III is lacking in tridactyl horses whereas in most of the fossil horses (monodactyl and tridactyl) a facet for articulation with the trapezium is found. The same can be said of the articulation facet for the Mc V on the Mc IV. On the volar side of the Mc IV in *Mesohippus* we find that $\frac{1}{4}$ is roughened for attachment ligaments of the Mc V.

The shaft

The shafts of the lateral metacarpals are three-sided. The anterior-posterior diameter is in the *Mesohippus*–*Anchitherium* lineage fairly constant while in the *Parahippus*–*Merychippus*–*Hipparion* group this diameter is much less in the middle of the shaft than on its proximal part.

When we compare measurements (Table II) of the lateral with the central we note several differences. *Anchitherium* and *Mesohippus* show similarities and the bone is quite massive, while in *Parahippus*, *Merychippus* and *Hipparion* the bone is relatively more slender especially in the middle of the shaft. We see a decrease in the width and diameter of the distal articulation joint of the lateral metacarpal in relation to the central in *Hipparion* if compared with *Merychippus*.

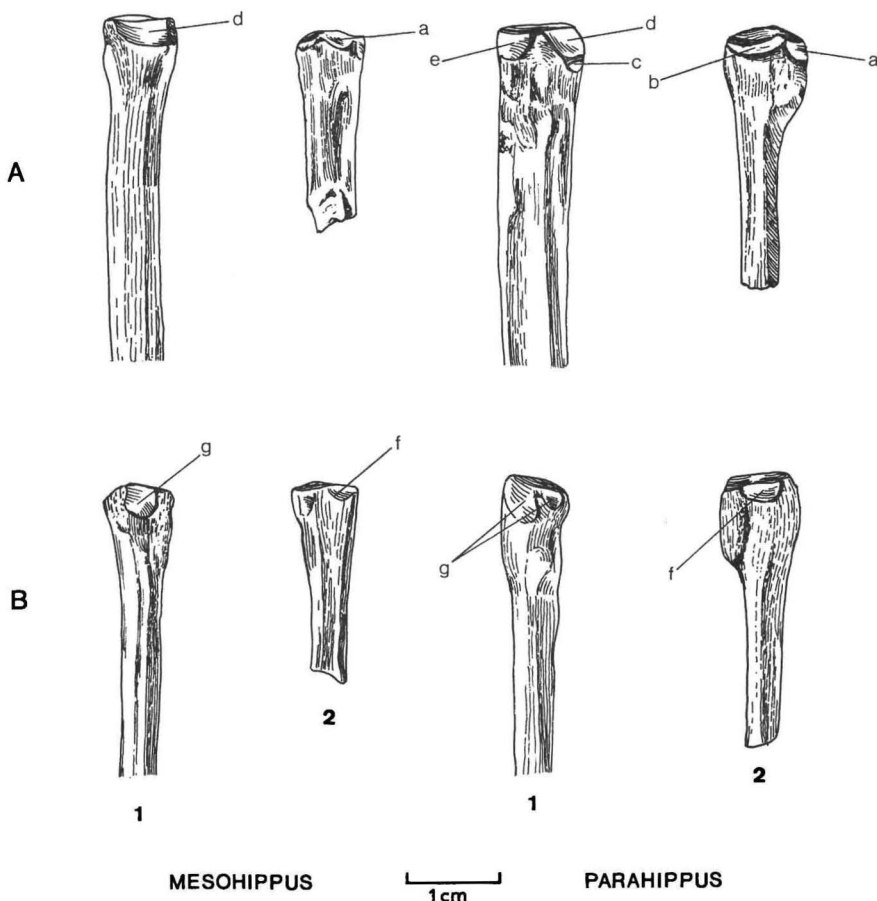


Fig. 13. Lateral metacarpals (right) 1. Mc II 2. Mc IV.

Meshippus sp. coll. no. 996 C.M.

Parahippus sp. coll. no. 4086 U.F.

A. Mc II lateral view
Mc IV medial view

B. volar view

- a. facet for articulation with Mc III
- b. facet for articulation with Mc III
- c. facet for articulation with Mc III
- d, e. facet for articulation with magnum
- f. facet for articulation with Mc V
- g. facet for articulation with trapezium

Distal articulation surface

The distal articulation surface with the proximal lateral phalanx in *Meshippus*–*Anchitherium* and also in *Parahippus*–*Merychippus* has still on the volar side a sagittal crest; in *Hipparion* this is very faint or even absent (fig. 14, 2B).

Mc V (fig. 5)

The *Mc V* is in *Mesohippus* still a good recognizable bone with a clear facet for the hamatum and a smaller facet for articulation with the *Mc IV*. In more advanced horses the facet of articulation for the hamatum becomes less important and is often not even present in, for example, *Hipparion*. In *Hipparion* the *Mc V* articulates mostly only with the *Mc IV*. In *Plesippus* and *Pliohippus* this bone is situated higher and its main articulation

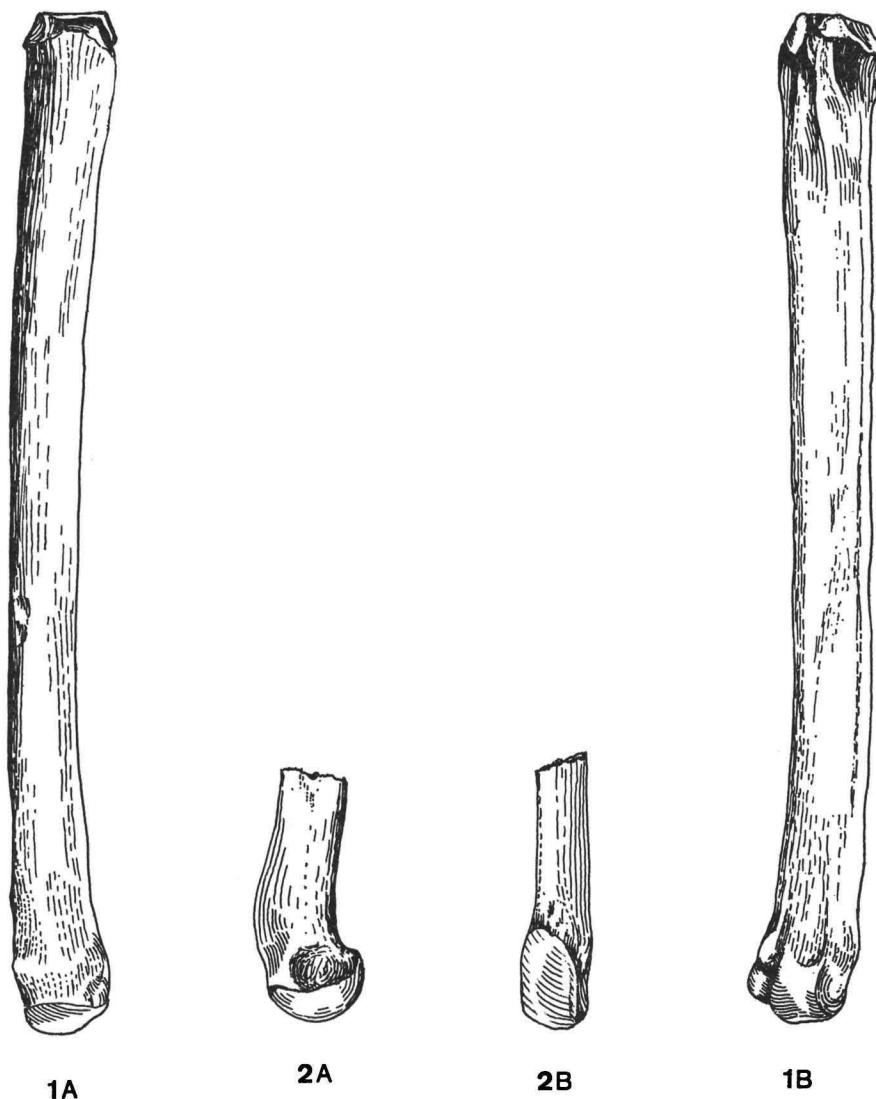


Fig. 14. Lateral metacarpal (*Mc II*) drawn to the same length.

1. *Mesohippus* sp. coll. no. 996 C.M.
2. *Hipparion concudense* coll. G.I.U.

A. medial view B. volar view

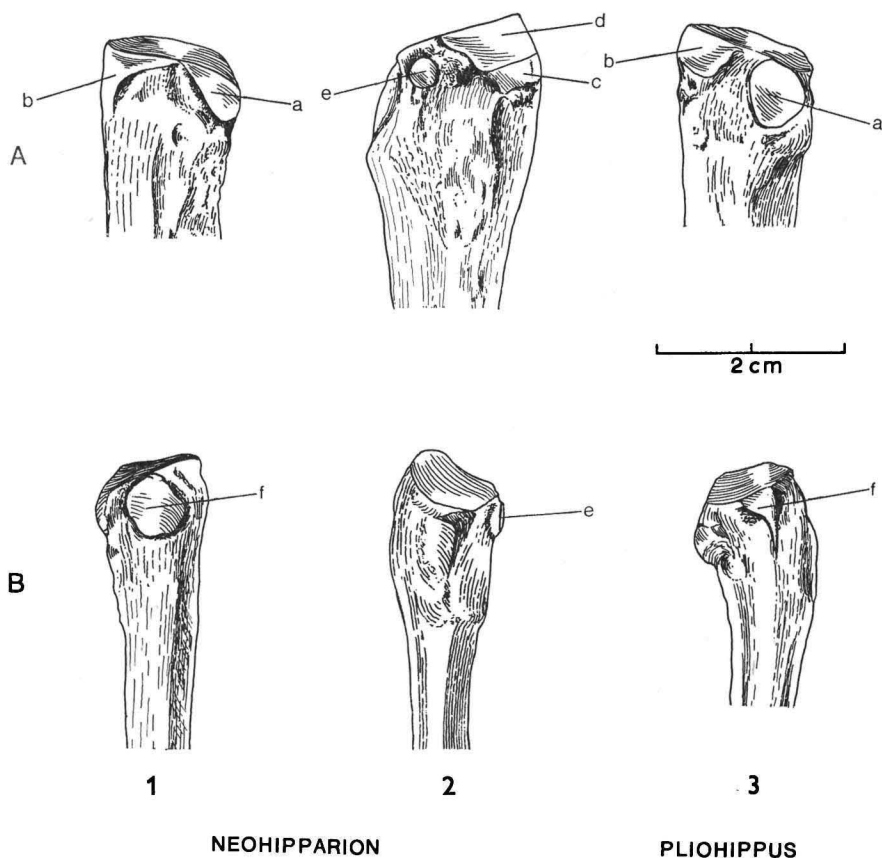


Fig. 15. Right proximal part of lateral metacarpals.

1. *Neohipparion floresi* coll. L.C.M.

2, 3. *Pliohippus mexicanus* coll. L.C.M.

1 and 3 Mc IV 2 Mc II

a, b, c, e. facets for articulation with Mc III

f. facet for articulation with Mc V

is with hamatum (fig. 8B f) which is also seen in MATTHEW (1926, fig. 21, p. 163).

3. Proximal sesamoid bones (fig. 16)

Very little is known about the change in shape of these bones from *Mesohippus* to *Equus* though these bones had an important function in the locomotion of the animal as it enables the tendons to act at a mechanical advantage. GROMOVA (1952) has noted already important differences between *Hipparion* and *Equus* in these bones. In *Hipparion* the bones are relatively more narrow in lateral—medial direction and also the diameter is less pronounced in *Hipparion*.

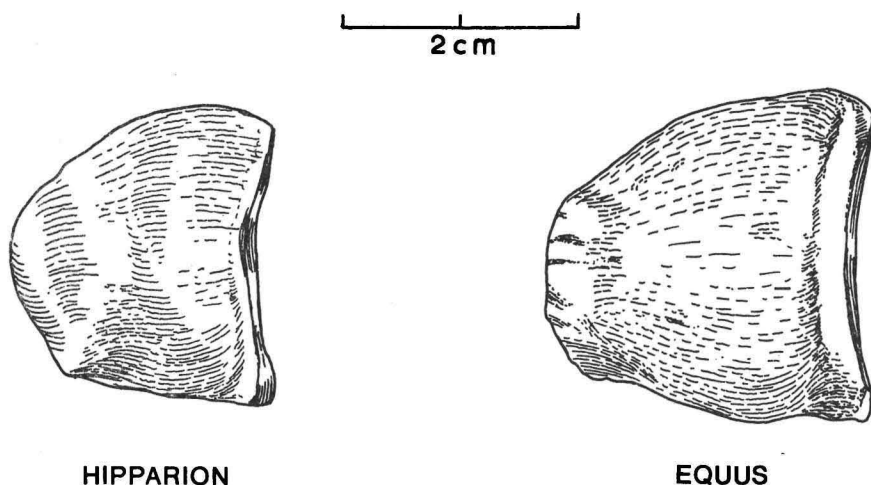


Fig. 16. Proximal sesamoid bone.

Hipparion concudense coll. G.I.U.*Equus caballus* coll. G.I.U.

TOBIEN (1959), in describing a complete articulated skeletal material from *Hipparion*, notes the presence of a pair of sesamoid bones at the laterals.

C. PHALANGES

1. *first phalanx of the median digit* (fig. 17)

One of the major changes in the phylogeny of the horse is the relative lengthening of the first phalanx.

In Table III the length relation between the third metacarpal and first central phalanx is given. The phalanx of *Meshippus* is very short about $\frac{1}{6}$ of the third metacarpal whereas in *Equus* it is mostly less than $\frac{1}{3}$, so the phalanx in *Equus* is relatively about twice as long. The *Anchitherium* phalanges are closer to *Meshippus* than to *Equus*, while *Hipparion* is closer to *Equus*. We may expect from *Meshippus* a gradual lengthening of the phalanx via *Parahippus*–*Merychippus* towards *Equus* while a non-significant lengthening took place in the *Meshippus*–*Anchitherium* lineage. In the first group the phalanx is more slender in the middle, while in the *Meshippus*–*Anchitherium* lineage it is more robust and has a straight shaft.

This relative lengthening of the first phalanx has never sufficiently well been evaluated. MATTHEW (1926) has noted longer phalanges in *Merychippus* but he does not go further into this matter. CAMP and SMITH (1942, p. 81) write: "The Lower Miocene (Arikareean) phalanges assignable to *Parahippus* and *Merychippus* begin to show a narrowing and lengthening of the digit" but on p. 86 "The ancestral form of the

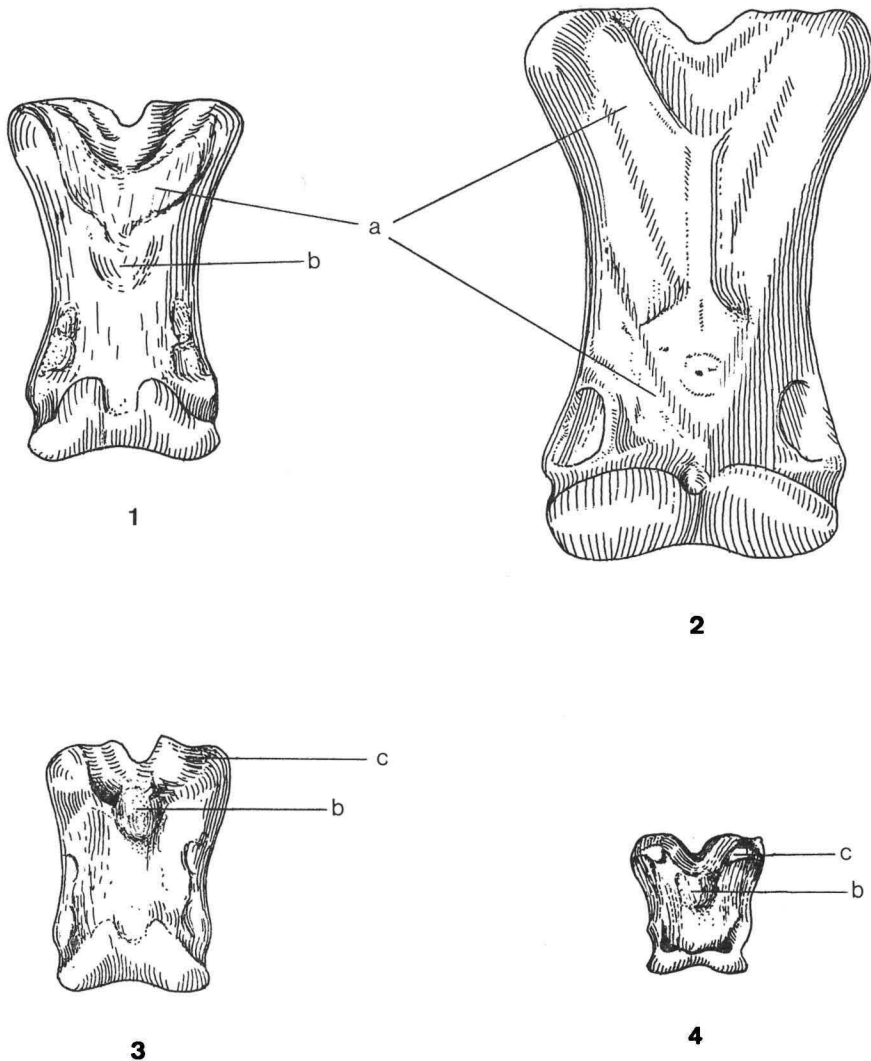


Fig. 17. First central phalanx.

volar view.

1. *Hipparion concudense*
2. *Equus caballus*
3. *Anchitherium aurelianense*
4. *Meshippus* sp.

- a. V scar
- b. central scar
- c. cruciate scars

first and second phalanges in the *Equidae* has undergone relatively little change in course of time". The first statement which is more relevant is in contradiction with the last. There is a distinct change in the ancestral form of the phalanx which from *Meshippus* to *Equus* becomes relatively twice as long whereas the relative length of other limb bones do not change essentially.

The study of CAMP and SMITH (1942) has provided us with magnificent data about the phylogeny of the digital ligaments of the horse of which I

TABLE III. Length relation Mc III—first central phalange.

	<i>Meshippus</i> sp. C.M. 996	<i>Anchitherium</i> sp. Spain G.I.U.	<i>Anchitherium</i> <i>aurelianense</i> after WEHRLI 1938	<i>Merychippus</i> <i>caramaius</i> after HENSHAW 1942
I. Length Mc III	91,5	181,0	3 ex. 210,0	163,0
II. Length first central phalange	14,5	32,0	3 ex. 43,0	42,0
Index I/II $\times 100$	630	570	490	390
	<i>Hipparion</i> <i>elegans</i> after GROMOVA 1952	<i>Hipparion</i> <i>conculdense</i> after SONDAAR 1962	<i>Equus</i> <i>preswalski</i> after GROMOVA 1949	
I. Length Mc III	35 ex. 198,3	5 ex. 207,5	8 ex. 225,1	
II. Length first central phalange	14 ex. 58,2	18 ex. 60,6	8 ex. 74,0	
Index I/II $\times 100$	340	340	300	

want to mention the gradual development of the V scar, the attachment area for the superficial oblique ligament, in the lineage *Parahippus*–*Merychippus*–*Hipparion* and *Merychippus*–*Equus* (fig. 17; 1, 2 a –) (Table XVIII). In the more primitive of these horses a clear central scar is still visible for the central ligament. In *Meshippus* no oblique scar is found and the central scar is distinct. In *Anchitherium* and *Hypohippus* the central becomes greatly enlarged (fig. 17; 3, 4 b), but no trace of a scar for the oblique sesamoid ligament is found.

The groove on the proximal articulation surface, corresponding to the sagittal crest on the central metacarpal is fading at its anterior part in *Meshippus* and *Anchitherium*; shallow or vague in *Parahippus*–*Merychippus*; shallow in *Hipparion*; deep on the whole surface in *Equus*. GROMOVA (1952) in explaining the differences between *Hipparion* and *Equus* has noted that the crest on the metapodial and in consequence the groove on the phalange prevents lateral dislocation in the fetlock joint and that the lateral phalanges had still a function in this way. Perhaps we may account for the difference between *Parahippus* and *Hipparion* in the same way. The laterals in *Parahippus* were still more functional and closer to the ground-plane and could prevent lateral dislocation of the fetlock.

2. second phalanx of the third digit

The differences in the second phalanx in the geologically older and younger horses are not so striking as in the first and third.

The proximal articulation surface is less convex in anterior-posterior direction in *Meshippus* and *Anchitherium* than in *Hipparion* and *Equus*. The angle, proximal articulation surface with the axis of the bones, is more oblique in *Meshippus*.

3. third phalanx of the central digit (fig. 18)

The angle of inclination between the ground-plane and anterior slope of the phalanx is smaller in primitive horses. GROMOVA (1952) has noted an angle of 36–56° in *Equus*; in our specimen of *Meshippus* this is $\pm 20^\circ$.

More striking still is the angle between the articulation surface and the ground-plane in *Meshippus*, close to 90°, while in *Equus* it is more parallel to the ground-plane. This angle fixes the direction of the second phalanx which consequently will be less oblique to the ground-plane in *Equus* than in *Meshippus*, which is typical for plantigrade foot type like the rhino and the tapir.

In fig. 18 arrows are drawn perpendicular to the articulation surface so as to indicate the second phalanx in rest-position. In *Meshippus* and *Anchitherium* the directions are close to each other and oblique, whereas in *Hipparion* this angle of the second phalanx with the ground-plane is much larger.

The ground-plane of the phalanx is somewhat curved in *Meshippus* in anterior-posterior direction while in *Parahippus*–*Merychippus*–*Hipparion*–*Equus* it is flat. If we compare the length of the three central phalanges there is a relative lengthening of the first phalanx in relation to the third in the *Meshippus*–*Equus* lineage. (Table IV).

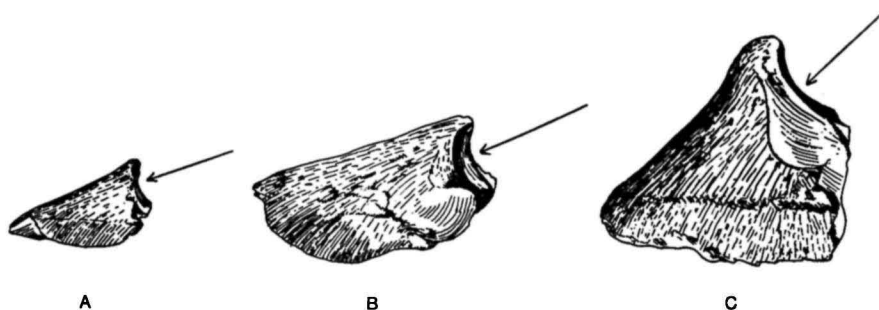


Fig. 18. Third phalanx of the central digit.

- | | |
|-------------------------------------|--------------------|
| A. <i>Meshippus</i> sp. | coll. no. 996 C.M. |
| B. <i>Anchitherium aurelianense</i> | coll. G.I.U. |
| C. <i>Hipparion concudense</i> | coll. G.I.U. |

Arrows are (drawn) perpendicular to the articulation surface to indicate the second phalanx in rest position.

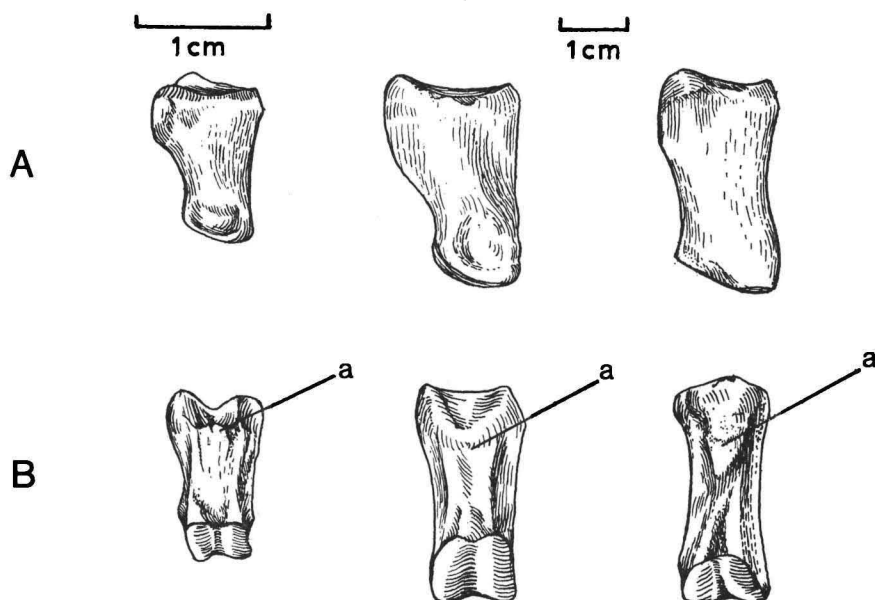
Meshippus in relation to *Anchitherium* and *Hipparion* twice enlarged

4. *lateral phalanges* (fig. 19)

In the lateral phalanges there are important changes to be noted in the phylogeny of the horse. In general the lateral phalanges are more slender in geologically younger horses, see Table IV.

If we compare the width of the lateral with the same measurement of the central phalanx (Table IV index 1 and 2) we may conclude that the laterals are reduced in later horses. If we compare the length of the third with the first lateral phalanx we note the same as in the central phalanges, namely that the length of the first is becoming relatively longer in relation to the third. However, the total length of the three lateral phalanges in relation to that of the central is reducing, as has been stated before. In *Anchitherium* the length relations and also the general shape are more similar to *Mesohippus* (fig. 19) so here the relative reduction is not so striking as in the *Merychippus*–*Hipparion* lineage.

As is seen in the lateral metapodials the distal articulation surface had a sagittal crest on the dorsal part in *Mesohippus*, *Anchitherium*, *Parahippus* and *Merychippus*, so in these horses we find on the proximal articulation surface a groove on the posterior side of the first lateral phalanx which is



MESOHIPPUS ANCHITHERIUM HIPPARION

Fig. 19. First lateral phalanx.

A. lateral view B. volar view

Mesohippus sp.

coll. no. 996 C.M.

Anchitherium sp. (Spain)

coll. G.I.U.

Hipparion concudense

coll. G.I.U.

TABLE IV. Measurements of phalanges.

	Meshippus						Anchitherium aurelianense after WEHRLI 1938					
	Ph. I median	Ph. I lateral	Ph. II median	Ph. II lateral	Ph. III median	Ph. III lateral	Ph. I median	Ph. I lateral	Ph. II median	Ph. II lateral	Ph. III median	Ph. III lateral
maximum length	14,0	12,0	11,0	10,0	18,0	17,0	3 ex. 43,0	3 ex. 33,0	3 ex. 26,2	3 ex. 17,7	1 ex. 45,0	1 ex. 39,0
proximal width	11,8	7,7	11,2	6,5	15,2	6,0	31,0	14,0	27,5	15,0	44,0	
proximal diam.	9,2	8,3	7,3	8,1	9,0	9,5	22,0	20,5	17,0	20,0		
distal width	8,8	5,2	9,7	5,5			27,0	13,0	24,8	13,0		
distal diam.	5,8	5,5	5,8	5,4								
index length relation lateral/median phalanx x 100	86		91		94		77		68		86	
index width relation lateral/median phalanx x 100	65		58		39		45		54		00	

	Hipparion elegans after GROMOVA 1952						Equus preswalski after GROMOVA 1949		
	Ph. I median	Ph. I lateral	Ph. II median	Ph. II lateral	Ph. III median	Ph. III lateral	Ph. I median	Ph. II median	Ph. III median
maximum length	12 ex. 58,2	21 ex. 32,5	20 ex. 33,7	25 ex. 15,3	3 ex. 45,8	25 ex. 30,3	74,5	45,0	51,0
proximal width	30,6	10,0	30,2	10,9	46,3	9,9	52,7	49,5	7,5
proximal diam.	24,1	15,5	21,5	15,3	28,3	13,6	34,0	30,0	40,0
distal width	25,9	9,6	29,4	9,2			44,7	50,0	
distal diam.	15,5	12,1	16,3	12,0			24,3	25,5	
index length relation lateral/median phalanx x 100	56		45		66				
index width relation lateral/median phalanx x 100	33		36		21				

fading on its anterior side. In *Hipparion* this groove is lacking and the articulation surface is bowl-shaped.

TOBIEN (1953) in describing the function of the lateral toes gives some data about the attachment scars of the tendons and ligaments in the laterals which are also found in, for example, *Mesohippus*. In general the scars are more pronounced in the more primitive horses. The scar for the tendon sublimus and the second lateral phalanx is very pronounced and developed as a spine in *Parahippus* and *Merychippus*.

D. THE MANUS AS A WHOLE

The phylogeny of the horse manus includes several changes in which we can distinguish three lineages (Table V):

- I. *Mesohippus*–*Anchitherium* lineage.
The general shape of the manus remains the same, but there is a clear size increase. Differences in morphology of the bones may be explained allometrically.
- II. *Mesohippus*–*Parahippus*–*Merychippus*–*Pliohippus*–*Equus* lineage.
Here we find a relative lengthening of the first central phalanx and reduction of the lateral phalanges which finally will lead to the monodactyl *Equus*.
- III. *Mesohippus*–*Parahippus*–*Merychippus*–*Hipparion* lineage.
Also a relative lengthening of the first central phalanx and reduction in size of the laterals can be noted, but here the end form will be still tridactyl.

Before going into the differences in these phylogenetical lineages it is necessary to review first some of the existing ideas which are sometimes contradictory. Much has been written about the question if the laterals did touch the ground and were functional or not.

TABLE V. Relative proportions lateral-central digit.

	<i>Mesohippus</i> sp.	<i>Hipparion</i> sp.
I. Total length Mc III + phalanges	124	330
II. Length Mc III	89	205
III. Total length Mc II + phalanges	115	255
IV. Total length central phalanges	35	125
V. Total length lateral phalanges	30	68
VI. Index II/III $\times 100$	77	80
VII. Index I/III $\times 100$	107	129
VIII. Index IV/V $\times 10$	116	188

ROBB (1936) has stated that the lateral toes in polydactyl horses were as well developed in geologically younger as in older forms, and he believes in two modes of evolution in the history of the foot of the horse, continuous and discontinuous. P. 273 "Continuous variation is in accord with the principles governing the relative growth of parts, whereby any augmentation of total size favours unequally its component parts. Given that digits II and IV are initially shorter than digit III in the primitive *Eohippus*, and granted that the apex of the longest digit will support the body weight, it is obvious that progressive elongation of the limb observed in *Meshippus* and *Merychippus* tends to elevate the paramedian toes and eventually deprives them of an opportunity for weight-bearing.

Discontinuous variation is observed in the abrupt transformation from a three-toed to a one-toed foot". Robb based this on data of the length relation lateral metapodial + phalanges and central metapodial, while in the conclusion he mentions the length relation between the whole digit III and lateral digit.

If we are to draw conclusions on the length relation between the digits it will be necessary to compare homologous elements. If the length relation is taken between lateral digit and central digit the relations will be totally different (Table V).*) Robb's conclusions therefore are misleading and wrong. The more so as he starts with the wrong supposition that the apex of the third digit will support the body weight in polydactyl horses; functional and allometrical changes are not considered either.

FORSTEN (1968) follows Robb, but measures the length of the lateral metacarpals in relation to the central of geological older and younger *Hipparion*. Against this method we make the following objections:

1. It is unnecessarily laborious because from the volar side of the third metacarpal we can learn the length of the lateral as it is attached with its whole length to the third metacarpal in *Hipparion*, leaving a clear scar. In consequence the relation between the two will remain the same.
2. Measuring the length of the lateral and taking its relation to the central is less exact because we have the problem of comparing bones of different individuals or even different species.

Since the preceding pages have shown that one of the main changes in horse evolution is the relative lengthening of the central phalanges, it is obvious that the statement of FORSTEN (1968) that the metapodial is quite sufficient when investigating the development stage of the foot, is wrong. The well documented method followed by GROMOVA (1952) gives

* A manus of *Meshippus* and *Hipparion* is taken as example. Index VI shows the relation used by Robb and only a slight difference exists in this between the two horses (77-80). Index VIII (relation lateral-central digit) is more relevant for the development stage of the foot and shows clear differences (116-186).

some interesting results and shows that in the genus *Hipparion* there are also differences in the development of the lateral digits. Gromova takes the relation between length, width-diameter of the lateral phalanges with the same measurements of the third digit; also the articulation surfaces of the lateral and central metapodials are compared. This author finds, for example, that the laterals in *H. longipes* are relatively less developed in relation to *H. moldavicum*. Some other features show also that *H. longipes* was more advanced, like the relatively big facets for entocuneiform and cuboid on the third metatarsal. This may explain that more weight was borne by the central metapodial and fits in with the observation of relatively reduced and slender lateral digits.

In the phylogeny of the horse the more generally accepted idea is a reduction in the lateral toes which were still functional (MATTHEW, 1926; SIMPSON, 1951). TOBIEN (1953) adds to this that from *Mesohippus* there is a relative lengthening of the central digit and by it the elevation of the digit from the ground while the foot lost its pad. SIMPSON (1955) states that there was a sequence from one adaptive type of foot mechanism to another with the fluctuations in the various lines.

In Table V some measurements of *Mesohippus* and *Hipparion* are given. If we compare the total length of the lateral phalanges with the same length of the central we do not see many differences between these two measurements in *Mesohippus* (30 mm and 33 mm) while in *Hipparion* the lateral toe is relatively much shorter (68 mm and 125 mm). This relative shortening of the lateral or rather the relative lengthening of the central phalanges is quite clear in the lineage from *Mesohippus* towards *Equus*.

In studies about horse phylogeny the feet of the fossil horses are compared with the modern horse in rest-position. The third metacarpal is then perpendicular to the ground and so the foot of *Mesohippus* etc. is figured in the same way, but it has never been checked whether this was the case or not. If not, the figures will present the wrong picture and are therefore misleading. In describing the phylogeny of the manus bones we have shown that there exist considerable differences in the fetlock, pastern and coffin joint. We see differences in size, shape and directions of the articulation surfaces. If we figure now the manus of *Mesohippus* in a rest-position and use *Equus* as example then the animal is standing on the top of the third phalanx and the fetlock joint is in maximum dorsal flexion. How the animal walked in this way is not explainable and to consider this as rest-position of the *Mesohippus* is most probably incorrect. If we compare the manus of *Mesohippus* now with that of a tapir we get a more functional position. This is also the position the preparators reconstructed—the articulated manus (fig. 20). Now the sole of the third phalanx will be parallel to the ground-plane while the fetlock joint is not in maximum flexion. Starting with this we get in the phylogeny of the horse also a change in the position of the hand, which will to a great extent affect the function of the laterals.

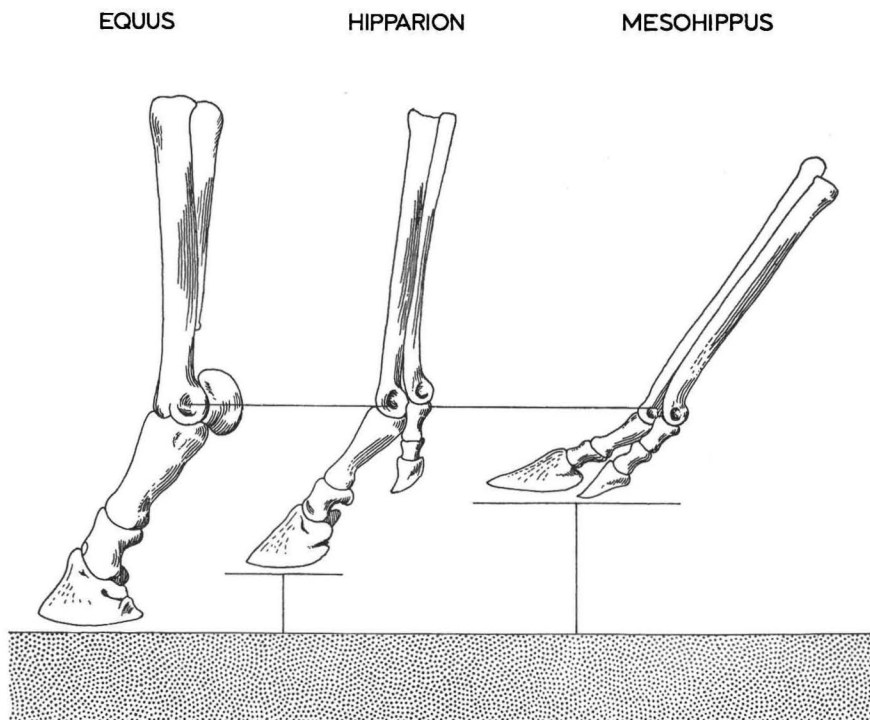


Fig. 20. Figured to same size the manus of *Equus*, *Hipparion* and *Mesohippus* in rest position. A line is drawn through the fetlock joint. By lengthening of the first central phalanx and change of the manus position in the phylogeny, the fetlock joint becomes higher from the ground plane.

The main changes in the phylogeny of the horse manus can be summarized as follows:

Mesohippus–*Anchitherium* lineage

In structure the manus of *Mesohippus* towards *Anchitherium* remains the same. We find, however, an increase in size and the central is expanding with this a little more than the lateral metapodials, which may be explained as a allometrical change.

The central metacarpal became less inclined to the ground-plane. Lateral digits did touch the ground also in rest-position in *Mesohippus* as in *Anchitherium*. The central phalanges make a sharp angle with the ground-plane and the fetlock joint is close to the ground. The first phalanx is short and massive.

The movement of the fetlock joint in dorsal–ventral direction is restricted while in some lateral movement was possible. In maximal flexion the angle between metacarpal and first phalanx was about 140°.

Lateral phalanges are well developed. The lateral metapodials were not firmly bound along the whole shaft of the central metacarpal and could spread on their distal parts from the central. The lateral metapodials

are well developed, the width and diameter of the shaft are constant, which gave the bone strength so it could act still independantly.

The carpal bones still shifted much weight to the lateral metapodials and were not firmly bound to each other as they are in the *Equus* lineage.

Mesohippus-Parahippus-Merychippus-Hipparion lineage

Here we find that the fetlock joint is higher from the ground (fig. 20):

1. by the lengthening of the central phalanges.
2. the inclination between ground-plane and the central phalanges is becoming less oblique; the metacarpal approaches the *Equus* position when the foot is in rest.

The lateral phalanges will also come higher from the ground because no relative lengthening is found in the lateral phalanges.

The fetlock joint becomes more flexible in dorsal-ventral direction and the lateral movement becomes restricted.

On the volar side of the first phalanx there is a development of the V scar, while the central scar becomes less pronounced.

The lateral metapodials are bound firmly by the intercarpal ligament along the whole surface to the central metacarpal and did act with it as one bone. The shaft of the lateral is reduced in the middle while the proximal and distal articulation joints are still well developed in geologically older horses. In *Parahippus* and *Merychippus* we still find a sagittal crest on the distal articulation surface which is fading in *Hipparion*.

The carpals become more firmly bound to each other and less lateral movement was possible. More weight of the body is shifted to the central metacarpal. From *Parahippus* we find on the volar side of the Mc III a developed tuberosity for attachment of the muscle interosseous which may be explained that the muscle interosseous has to support more strength by the lengthening of the central phalanx and was more powerful (see chapter IV).

Mesohippus-Parahippus-Merychippus-Pliohippus-Equus lineage

We note the same as in the former, but in *Pliohippus* the horse became monodactyl and it lost the lateral digits. It is here that we find the most developed oblique scar on the first central phalanx; the central scar is no longer found in *Equus*.

The fetlock joint has a maximal flexibility by a pulley-like distal joint of the metacarpal and is elevated high from the ground.

III. THE MANUS OF THE CHIHUAHUA HORSES

1. GENERAL REMARKS ON THE MATERIAL

The horses from Chihuahua have previously been studied by LANCE (1950) and STIRTON (1955). The material came from an area west of Chihuahua. LANCE (1950) gives some data about the geology of the region where the fossils were collected in several localities. In all the localities the fauna was quite similar. For the present study only material was chosen from locality 275, to make certain that we had horses of which we may expect that they were living contemporaneously; moreover locality 275 was also the quarry which yielded the greatest number of horse fossils. The specimens were well preserved, so all articulation facets could be studied, measured and compared.

LANCE (1950) places the fauna from the Chihuahua in the Late Hemphillian because he found similarities between Chihuahua and the fossils from Hemphill, and he states that the horse fossils are related but more advanced than those from Hemphill.

It was possible to differentiate between the four horses on size and morphology of the bones. In locality 275 *Astrohippus* showed to be the most common. For the classification and taxonomy of the horses we follow LANCE (1950) and STIRTON (1955).

For a general description of the bones one is referred to the first chapter of this paper and only the most distinctive characters and its meaning are described. The measurements are given in Table VI till XV. Some characteristic measurements which show the differences between the *Pliohippus*, *Astrohippus*, *Neohipparion* and *Nannippus* are plotted in scatter diagrams.

2. DESCRIPTION OF THE BONES

Navicular (Plate I, Table VI)

The navicular of the four horses could be distinguished by their size. In *Nannippus* no facet of articulation was found for the trapezium in the four studied specimens. According to MATTHEW (1926) the lack of trapezium is a generic character of *Nannippus*. In *Neohipparion* the facet of articulation with the trapezium was found in two of the six bones. In *Pliohippus* a small facet occurred in three of the seven bones, and in *Astrohippus* in seventeen of the twenty-seven bones. The presence of this facet in *Astrohippus* may be considered as primitive.

On the lateral side we find behind the anterior facet for articulation with the lunatum, another facet for articulation with the magnum is seen in *Neohipparion* and *Nannippus*. This facet is not present in *Equus*, but is seen in *Mesohippus*, *Merychippus* and the European *Hipparion*, and

TABLE VI. *Navicular*

	<i>Nannippus</i>			<i>Neohipparion</i>			<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.	min.	mean	max.	min.	mean	max.
	4 ex.			6 ex.			26 ex.			7 ex.		
1. diam. ant.-post.	19,7	20,1	20,3	29,0	30,6	31,5	24,0	26,9	28,1	32,8	33,4	34,3
2. width anterior	12,8	13,2	13,4	18,0	19,6	21,2	15,5	17,5	20,5	21,1	23,7	24,5
3. width posterior	10,8	11,6	12,4	17,2	19,8	21,2	13,6	16,6	19,4	19,8	21,2	23,0
4. height anterior	14,1	14,4	14,8	19,3	20,8	21,7	17,5	18,4	19,6	23,0	24,0	26,0
5. height posterior	13,3	13,8	14,3	19,4	21,0	21,8	15,8	17,1	18,4	20,8	22,4	24,8
6. facet for trapezium present in	0 ex.			2 ex.			17 ex.			3 ex.		

seems to be restricted to tridactyl horses where mostly the posterior part of the magnum is somewhat higher. In *Pliohippus*, *Astrohippus* and *Nannippus* the anterior height of the navicular is larger than the same measurement at its posterior part. In *Neohipparion* the two measurements are about the same and the tendency is that on the other hand, the posterior part is higher (Table VI). In *Hipparion* (GROMOVA, 1952) the height of the posterior part is always greater than the same measurement at the front, caused by the facet of articulation for the trapezium. This, however, can not be the case because we should have found the same in *Astrohippus* where this facet is a more stable characteristic than it is in *Neohipparion*.

If we study the distal surface of the navicular we will notice that the posterior part which articulates with the trapezoideum is relatively the largest in *Pliohippus* and the smallest in *Neohipparion*. This seems to be contradictory because more weight is shifted via the trapezoideum to the second metacarpal; in reality this is not true because in *Pliohippus* and also in *Astrohippus* to a less degree a facet of articulation is developed with the third metacarpal on the posterior distal part of the trapezoideum, so a part of the weight is now shifted to the third metacarpal.

Lunatum (Plate IID, Table VII)

No lunatum of *Nannippus* was present. The most striking differences were found at the distal articulation surface of the bone. If we take the relation between the width of the facet for articulation with the magnum and that of the facet for hamatum we shall notice in *Neohipparion* a relatively much larger facet for hamatum than in *Pliohippus* and *Astrohippus*. The facet of articulation for the distal part of the magnum in *Neohipparion* is more concave than it is in *Pliohippus* and *Astrohippus*. This articulation facet is here more flat and elongated in anterior-posterior direction. The relatively small facet for hamatum (less weight to the fourth metacarpal) and the more flattened articulation surface for magnum

TABLE VII. *Lunatum*

	<i>Neohipparion</i>			<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.	min.	mean	max.
	3 ex.								
1. diameter ant.-post.	25,0	25,7	26,2	22,5	23,5	25,5	31,1	31,9	33,0
2. maximal width	21,0	21,9	22,6	15,5	17,5	19,5	23,0	24,1	26,5
3. maximal height	19,3	20,2	21,5	16,0	17,8	19,5	21,3	22,0	22,8
4. width facet for hamatum	6,6	7,3	8,3	3,5	4,8	6,1	5,5	6,4	7,9
5. width facet for magnum	11,4	12,3	12,9	10,0	11,4	12,8	15,3	15,8	16,5

(less lateral movement) are progressive characters in *Astrohippus* and *Pliohippus*. On the whole the lunatum in *Neohipparion* is broader than it is in *Pliohippus* and *Astrohippus* if we consider the index anterior-posterior diameter and width.

Triquetrum (Plate ID, Table VIII)

It is difficult to say to which group of horses the triquetrum, which is the most irregular bone of the proximal carpals, belonged. Mainly the division was done by its size and then we noticed that in *Astrohippus* only in 4 out of the 16 bones the facet for articulation with the ulna and pisiform were united. In *Pliohippus* this connection was much more common, and so in this characteristic *Pliohippus* was somewhat more progressive.

Pisiform (Table IX)

GROMOVA (1952) attaches much value to the relative height of the pisiform; a high pisiform is progressive. If we consider the index height/length we will see that *Pliohippus* and *Astrohippus* have the highest pisiform. That of *Nannippus* is also relatively high.

Trapezium (Plate II C 1)

This bone is also found in the Chihuahua collection of the Los Angeles County Museum. The shape is irregular and it was not possible to refer

TABLE VIII. *Triquetrum*

	<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.
	4 ex.			3 ex.		
1. oblique height	16,3	18,0	19,8	21,1	21,8	23,0
2. the same in projection	13,3	13,7	14,2	16,0	17,0	18,0
3. maximum width	10,0	10,4	11,5	13,7	14,5	15,5
4. diameter maximal	18,3	19,2	20,1	23,5	24,9	26,2
5. distance between facet for hamatum and pisiform	3,5	4,5	5,0	4,5	5,6	6,5

TABLE IX. *Pisiform*

	<i>Nannippus</i> min. mean max. 3 ex.			<i>Neohipparion</i> 1 ex.	<i>Astrohippus</i> min. mean max. 12 ex.			<i>Pliohippus</i> min. max. 2 ex.	
1. height	13,2	14,5	15,3	23,2	20,0	22,2	24,0	28,0	28,5
2 length	19,6		22,3	32,5	25,5	26,9	29,0	34,0	35,0

them to a group. This is understandable because the facets for articulation with this bone are very inconstant in shape and size on the navicular, trapezoideum and second metacarpal of *Pliohippus*, *Astrohippus* and *Neohipparion*. The trapezium found mostly have two facets for articulation; confusing this bone with the Mc V is not impossible.

Trapezoideum (Plate II B 2, 3, 4; Table X)

In the trapezoideum we can make a clear division between the groups because the second metacarpal is situated somewhat higher in *Neohipparion* than in *Pliohippus* and *Astrohippus*; the trapezoideum in *Neohipparion* is lower. In *Neohipparion* also the facets for articulation with the magnum are less developed, especially the distal one.

No posterior facet for articulation with the magnum is found in *Neohipparion*. In *Astrohippus* we found in six out of eighteen bones this facet mostly somewhat undeveloped and it was seen on the small tuberosity on the posterior lateral side of the bone. In *Pliohippus* this facet was found to be in all six bones well developed. In four out of six bones of *Pliohippus* there was a distinct facet for articulation with the third metacarpal. *Pliohippus* is in this aspect the most advanced horse and more weight is shifted from the trapezoideum to the central metapodial. The clear facets of articulation with the magnum in *Astrohippus* and *Pliohippus* show that in these horses the trapezoideum and magnum were more tightly together than in *Neohipparion* and less lateral movement was possible.

The proximal articulation encroaches on the volar side up to the distal

TABLE X. *Trapezoideum*

	<i>Neohipparion</i> min. mean max. 5 ex.			<i>Astrohippus</i> min. mean max. 18 ex.			<i>Pliohippus</i> min. mean max. 6 ex.		
1. diameter ant.-post.	15,8	16,8	17,9	12,8	14,1	16,2	19,2	20,4	21,7
2. width	11,2	11,8	12,8	8,4	10,0	11,5	13,2	13,8	15,2
3. height	13,0	13,6	15,1	10,0	11,6	13,2	15,3	16,5	17,3
4. distal facet for magnum present in	0 ex.			5 ex. (little developed)			6 ex.		

articulation surface in *Pliohippus* and *Astrohippus*. In *Neohipparion* there is mostly a small gap between the two facets.

Magnum (Plate III, Table XI)

The magnums of locality 275 were easy to distinguish on morphological differences and size.

a. proximal articulation surface

The posterior articulation surface for lunatum encroached in *Pliohippus* also on the volar side. In the magnum of *Neohipparion* we can notice a facet on the posterior part articulating with the navicular.

b. medial surface

The two facets for articulation with the trapezoideum on the anterior side were less pronounced in *Hipparion* and *Nannippus*. In *Neohipparion* the lower facet (above that of the articulation facet of Mc II) was even lacking in three out of seven bones. In *Neohipparion* and *Nannippus* on the posterior part we did not find a facet of articulation with the trapezoideum. In *Astrohippus* this facet is present in eleven out of the thirty-seven magnums, but little developed. In *Pliohippus* five out of the six bones had the facet for trapezoideum on the posterior side and the facet was well developed. This is consistent with the finds in the trapezoideum and we may draw the same conclusions. The *Pliohippus* is the most progressive as the articulation facets for the trapezoideum are the most developed and so these two bones are more tight together.

c. lateral side

The articulation surfaces for the hamatum were more clear and more developed in *Pliohippus* and *Astrohippus* than they were in *Neohipparion* and *Nannippus*.

TABLE XI. *Os magnum*

	<i>Nannippus</i>			<i>Neohipparion</i>			<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.	min.	mean	max.	min.	mean	max.
	4 ex.			6 ex.								
1. diameter ant.-post.	17,8	18,4	19,2	25,2	25,7	26,3	22,2	24,5	26,0	30,1	31,7	34,0
2. width (max.)	19,3	19,8	20,3	30,4	31,1	32,3	24,5	27,3	28,8	35,0	36,8	38,5
3. height (anterior)	9,5	9,7	10,3	13,0	13,9	14,3	10,3	11,5	12,9	15,2	16,2	17,0
4. width of the distal posterior part	8,5	8,9	9,2	10,8	12,2	12,7	9,8	11,5	13,8	13,8	15,0	16,5
5. height (posterior)	11,4	11,8	12,4	14,5	15,1	16,0	12,3	13,2	14,7	16,4	17,7	19,5
6. width of facet for Mc II	2,5	2,7	3,0	3,6	4,2	5,0	1,6	3,0	4,2	2,7	4,8	5,5
7. width of facet for Mc III	17,0	18,0	18,9	27,2	27,6	28,2	22,5	25,5	27,6	32,0	33,9	35,2
8. angle between 6 and 7	114°	124°	130°	105°	111°	120°	112°	127°	143°	124°	137°	143°

TABLE XII. *Hamatum*

	<i>Nannippus</i> 1 ex.	<i>Neohipparion</i> 5 ex. min. mean max.			<i>Astrohippus</i> 20 ex. min. mean max.			<i>Pliohippus</i> 16 ex. min. mean max.		
1. diam. (ant.-post.) oblique	13,7	19,8	20,8	22,0	16,6	19,1	20,6	24,0	25,7	28,5
2. width perpendicular diam.	7,8	13,3	13,6	14,2	11,1	12,5	15,4	15,2	17,1	19,5
3. maximal height	11,0	16,1	16,6	17,3	12,5	13,8	15,9	17,2	19,0	21,2
4. number of specimen with facet for Mc V	0	3 ex.			20 ex.			16 ex. well developed		

d. distal side

The angle between the articulation facets in *Neohipparion* and *Nannippus* between Mc III and Mc II was more sharp than in *Pliohippus* and *Astrohippus*. In the last two horses the contact between the facets was crest-like.

Hamatum (Plate II A, Table XII)

a. medial side

The facets of articulation with the magnum were better developed in *Astrohippus* and *Pliohippus* than in *Neohipparion* and *Nannippus*.

The facets for Mc III were relatively larger in *Nannippus*, *Pliohippus* and *Astrohippus* than in *Neohipparion*.

b. lateral side

Below the facet of articulation with the triquetrum a clear facet was found in ten out of sixteen hamatums of *Pliohippus*; such a facet was less developed or lacking in *Astrohippus*, *Nannippus* and *Neohipparion*; similar facets were found in *Merychippus*, *Mesohippus* etc. and articulates with the Mc V. The facet in *Pliohippus* was even more developed than in *Merychippus*. On the Mc IV of *Pliohippus* we found also small facets on the lateral side which may indicate the presence of a Mc V. This bone must have articulated more with the hamatum according to the facet found on this bone. The facet was always in contact with the articulation surface for the os triquetrum. The angle between this facet for Mc V and Mc IV varied in *Pliohippus* between 100° and 115°; in *Merychippus* this was 142°. It seems as if the Mc V has moved along the hamatum. In *Neohipparion* where also a Mc V was present this bone articulated only with the Mc IV. The reason why the facet for articulation with the Mc V suddenly developed in this way in the hamatum of *Pliohippus* is not clear because in all other manus characteristics this horse is the most progressive of the four. Perhaps it had still a small function, similar to that of a sesamoid bone. From the studies of MATTHEW (1926) and GAZIN (1936) we learned that in *Plesippus* the Mc V was also well developed and situated similar.

Lateral metapodials (Plate IV C, D; Tables XIII and XIV).

Mc II proximal articulation surface

In *Pliohippus* there was in four out of the fourteen bones a small articulation facet with the trapezium. In *Astrohippus* in ten out of the nineteen and in *Neohipparion* in five out of the six. In this character *Pliohippus* is progressive and the reduction of the trapezium already took place.

The posterior facet (on the lateral side) for articulation with the Mc III is lacking in *Neohipparion*, but present and developed in *Pliohippus* and *Astrohippus*. As in all carpal bones we see that they are pressed together in monodactyl horses, and in consequence the facets between these bones are better developed.

Mc IV proximal articulation surface

In *Pliohippus* three out of the seventeen bones show a facet for

TABLE XIII. Mc II proximal part

	<i>Neohipparion</i>			<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.	min.	mean	max.
	6 ex.			19 ex.			14 ex.		
1. diameter ant.-post.	12,8	13,8	14,5	11,9	13,4	15,7	15,0	17,1	20,0
2. width	9,9	10,2	10,7	8,5	9,5	10,6	11,5	12,2	13,0
3. a height ant. facet for Mc III	3,2	4,3	5,0	3,5	4,4	5,5	3,5	4,7	6,0
b height post. facet for Mc III	not present			3,5	5,1	6,2	3,7	5,5	8,5
4. presence of facet for trapezium	in 5 ex.			in 10 ex.			in 4 ex.		

TABLE XIV. Mc IV proximal part

	<i>Neohipparion</i>			<i>Astrohippus</i>			<i>Pliohippus</i>		
	min.	mean	max.	min.	mean	max.	min.	mean	max.
	7 ex.			14 ex.			17 ex.		
1. diameter ant.-post.	13,8	14,8	17,0	11,4	12,2	13,0	15,0	16,0	18,2
2. width	8,5	9,6	10,8	8,7	9,8	10,5	11,0	11,9	12,5
3. angle between the two facets for Mc III	140°	152°	167°	122°	131°	143°	130°	135°	142°
4. a height ant. facet for Mc III	3,0	3,8	4,2	3,0	3,8	5,1	3,0	4,3	5,8
b height post. facet for Mc III	4,0	5,0	6,5	2,5	3,9	4,7	4,0	5,8	7,8
5. facet for Mc V							in 3 ex. facet present		
a height	2,6	5,0	6,3	no facet present			2,0	3,3	5,2
b width	3,2	5,5	7,2				3,2	6,1	6,0

Mc V; in *Astrohippus* no facet for Mc V was found (one dubious case out of thirteen bones); in *Neohipparion* the facet was present in all of the seven bones. If we compare the facet for Mc V in *Neohipparion* and *Pliohippus* the one of *Neohipparion* is bigger and the angle this facet makes with the facet for hamatum is sharper (80°), in *Pliohippus* this is 135° . In *Pliohippus* the facet is connected with the facet of hamatum, in *Neohipparion* this was not the case. The Mc V articulated in *Pliohippus* mainly with the hamatum (see hamatum) and in *Neohipparion* mainly with the Mc IV.

Third metacarpal (Plates IV A, B and V; Table XV)

The main differences between tridactyl and monodactyl horses as is discussed in chapter II B 1 were found between *Neohipparion* and *Astrohippus*-*Pliohippus*. *Nannippus* did not have all the typical characters of a tridactyl horse, for example, the width at the distal articulation exceeded the same measurement just above the distal articulation surface at the tubercles. This was also found in *Pliohippus* and *Astrohippus* and other monodactyl horses, but in tridactyl horses like our *Neohipparion* the width at the tubercles is the largest.

TABLE XV. Mc III

	<i>Nannippus</i> 1 ex.	<i>Astrohippus</i> min. mean max. 27 ex.			<i>Neohipparion</i> min. mean max. 6 ex.			<i>Pliohippus</i> min. mean max. 16 ex.		
1. length	154,5	171,5	179,7	187,8	199,3	205,2	209,0	212,5	218,9	224,5
3. width of the proximal articulation surface	22,8	29,0	30,6	33,7	31,7	32,2	33,0	36,0	39,0	42,0
4. ant.-post. diameter of the proximal part	17,4	20,3	20,6	23,6	26,1	27,5	28,2	26,3	27,9	30,5
5. ant.-post. diameter of the proximal articulation surface	16,5	19,3	20,7	22,0	23,0	24,1	25,0	25,0	26,2	28,1
6. width of the posterior part of the articulation surface	11,5	11,6	13,4	14,7	14,0	14,4	15,3	15,0	17,1	19,9
7. width of the articulation surface for the hamatum	07,0	6,5	7,7	9,5	7,1	7,7	8,5	8,7	9,9	12,2
8. width of the articulation surface for the magnum	19,3	24,5	26,0	29,2	26,3	27,5	29,2	32,0	33,5	36,0
9. width of the distal part of the bone at the tubercles	18,0	24,3	25,9	27,2	29,0	29,8	30,3	33,7	35,2	37,2
10. width of the distal articulation surface	19,5	25,8	27,4	29,4	28,4	29,6	30,6	34,6	36,2	40,0
11. ant.-post. diameter of the distal articulation surface	18,0	20,2	21,2	23,0	23,2	24,0	25,0	26,5	29,3	31,1
12. ant.-post. diameter in the middle	13,0	15,7	16,6	17,5	18,2	18,9	19,8	20,8	22,0	24,3
13. width at the middle	13,5	19,2	20,4	22,0	20,8	22,6	23,0	24,5	27,2	29,5
14. angle between facet for magnum and hamatum	147°	134°	140°	149°	134°	138°	152°	138°	143°	153°

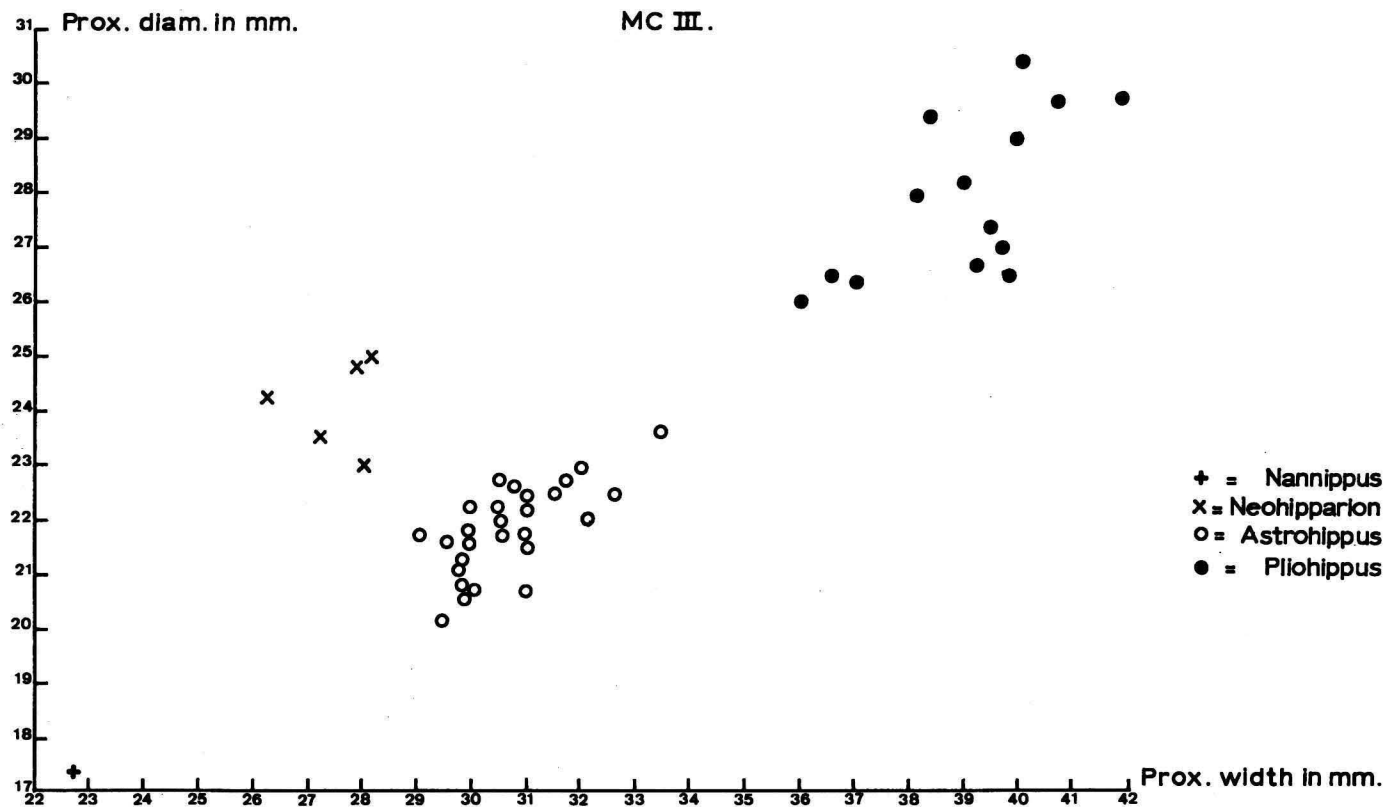


Fig. 21. Scatter diagram of relation between the proximal width and diameter of the third metacarpal in the Chihuahua horses, showing the relatively narrow metacarpal of *Neohipparion floresi*. The relations in *Nannippus* c.f. *minor* are more like *Pliohippus mexicanus* and *Astrohippus stocki*.

At the proximal articulation surface we found in *Pliohippus* often a still distinct facet of articulation with the trapezoideum (absent in *Astrohippus*). Below the proximal articulation surface on the volar side of the metacarpal we found in *Neohipparion* a tuberosity for attachment of the tendon for the muscle interosseous. In *Pliohippus* and *Astrohippus* this was more like a ridge and the interosseous ligament had here perhaps developed already.

Also on the volar side of the shaft we noticed in *Neohipparion* on either side roughened areas for attachment ligaments of the lateral metapodials. In *Pliohippus* and *Astrohippus* it reached only up to $\frac{2}{3}$ of the bone. We find in *Neohipparion* a gulley in which the muscle interosseous was lodged. In *Astrohippus* and *Pliohippus* the volar side is more flat.

If we take the proximal width and diameter of the metacarpal than we notice a distinct difference: In *Neohipparion* the diameter is larger in relation to *Pliohippus* and *Astrohippus*. *Nannippus* is closer to the last two horses (fig. 21).

3. CONCLUSIONS ON THE CARPUS OF THE CHIHUAHUA HORSES

Neohipparion floresi had all the characters as described in the first chapter for a functional tridactyl locomotion. *Pliohippus mexicanus* and *Astrohippus stocki* are monodactyl and some primitive characters are found in these horses like fifth metacarpal and trapezium, in *Equus caballus* these are mostly absent or more reduced. *Nannippus* does not fit in this general picture and shows characters of tridactyl and monodactyl horses in its carpus. The magnum and navicular are more like *Neohipparion* but in *Nannippus* c.f. *minor* from Chihuahua no fifth metacarpal and trapezium was found; in this respect this horse is more advanced than *Pliohippus mexicanus* and *Astrohippus stocki*. The lacking of Mc V and trapezium was described as a generic character for *Nannippus* by MATTHEW (1926).

Another striking difference with tridactyl horses is that the width of the distal articulation surface of the metacarpal exceeds in *Nannippus* the width just above this articulation surface at the tubercles. This is a constant feature found in monodactyl horses (GROMOVA, 1952).

Between *Pliohippus mexicanus* and *Astrohippus stocki* there are also morphological differences besides the size. On the whole *Pliohippus mexicanus* is more progressive in its carpal bones and articulation joints.

In the trapezoideum we found a clear facet on the posterior part for articulation with the magnum and third metacarpal. This is absent or faint in *Astrohippus stocki*. In *Astrohippus* the percentage of facets for articulation with the trapezium on the navicular is higher. In one aspect (a distinct facet for the Mc V was found on the hamatum) *Pliohippus mexicanus* was primitive.

IV. BIODYNAMICA AND FUNCTION OF THE MANUS

A. JOINTS

Carpal

The movement of the carpal joint is mainly that of flexion and extension. In *Equus* the movement is practically restricted to the radio-carpal and inter carpal joints. It is seen from the foregoing chapters that the carpal bones were not bound so tightly together in the tridactyl horses, especially so in the *Mesohippus*–*Anchitherium* lineage, and this shows that in these horses more lateral movement and rotation could be produced. A greater flexibility can be noted in dorsal–volar direction. Flexion between the distal row of the carpus and metacarpus was possible, while in *Equus* they remained in contact during movement. In maximum flexion we may expect that the position of the metacarpus to the ground-plane is about the same as in *Equus*, while in extension this is more oblique in *Mesohippus* and *Anchitherium* (the rest-position of the manus is in principle different in *Mesohippus*–*Anchitherium* as has been stated in chapter II D). The horses of the *Mesohippus*–*Merychippus*–*Equus* lineage are closer to *Equus* in the function and position of the carpal joint. The movements in the carpal bones are quite complex and it is difficult to trace its functional changes during the phylogeny of the horse.

Fetlock, pastern and coffin

Thanks to the magnificent study on the phylogeny and functions of the digital ligaments of the horse by Camp and Smith we now know far more about phylogenetical changes in the attachment scars for the digital ligaments, and from this the functional changes of the digital ligaments are explained. No attention was, however, paid to the relative lengthening of the median phalanges.

CAMP and SMITH (1942) p. 87 consider the development of the complex ligamentary system to be accompanied with

1. the increased weight falling on the enlarged third digit.
2. the reduction of the foot pads.
3. the achievement of axial symmetry in the phalanges.
4. the loss of lateral flexibility associated with the development of the pulley-like joint and the pendulum action of the limbs.
5. the loss of intrinsic foot musculature.
6. especially the development of elastic springiness.

We, however, are of the opinion that the complexity of the ligamentary system is accompanied by:

1. lengthening of the central phalanges, the foot lost by this its pad, more weight was brought upon the third digit (in principle point 1, 2 and 5 of Camp and Smith).
2. the fetlock joint became more flexible and about 40° more dorsal flexion was possible in *Equus* if compared with *Mesohippus* (chapter II B 1).
3. the lengthening of phalanges had great mechanical consequences because by this more pressure was brought upon the fetlock joint.
4. a same lateral movement in the fetlock joint will result in direct proportional (to the lengthening) movement on the ground.

It is seen from the foregoing points that the function of fetlock joint is affected most by the lengthening of the phalanges and must be better fortified against too much lateral and dorsal flexion. From chapter II B 1 we have seen that the sagittal crest on the metacarpal is developing, which may be explained to avoid lateral movements as GROMOVA (1952) did.

During jumping and running enormous pressure is brought upon the hoof, the fetlock will be bent and the ligaments are then in extension. If we take *Equus* the phalanges and metacarpal will make an angle of about 150° at the fetlock joint in rest position; at that moment the metacarpal will be about perpendicular to the ground. In maximal flexion the joint may be bent up to 100° or less (CAMP and SMITH (1942)). The fetlock is supported by a number of ligaments of which the interosseous tendon and the oblique sesamoid ligament have an important function in the present horse (automatic springing mechanism). The proximal sesamoid bones are interposed to the ligaments just mentioned. The tendon interosseous lies on the volar side of the metacarpal and it arises from the distal row of carpal bones and the proximal part of the metacarpus; it extends downwards to the distal fourth of the metacarpal where it divides into two separate branches and inserts into the proximal sesamoid bones. The ligamentum obliquus is triangular and attached to the same sesamoid bones. On the first phalanx a triangular rough area is found (V scar). According to CAMP and SMITH (1942) the V scar is developing during the evolution of the horse and in *Merychippus* the oblique ligament is something new and is developed out of the cruciate ligament. In figure 22 an outline is given of the fetlock joint and its biostatics. For simplification the three phalanges are taken as a whole (Movements of the coffin and pastern joint are of lesser importance).

We can apply now the following formula to this system:

$$Sa - K l \cos \beta = 0 \quad \text{or} \quad S = K(1/a) \cos \beta$$

In other words:

The tension in the ligaments is directly proportional to the length of the phalanges and inversely proportional to the diameter of the sesamoid. In consequence, when the phalanges became relatively twice as long, which is the case from *Mesohippus* to *Equus*, the tension in the digital

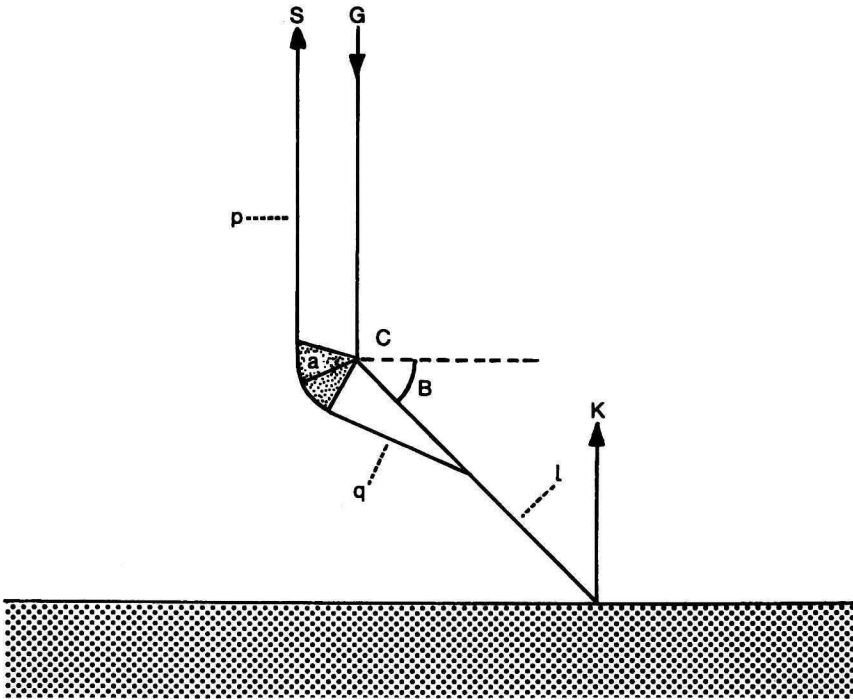


Fig. 22. Outline of the simplified biostatics in the fetlock joint (c).

C = fetlock joint

K = pressure on the hoof

G = vertical weight of the animal

l = length of phalanges

B = angle of metapodial and phalanges $-90^\circ = \beta$

a = diameter of sesamoid bone which is considered as a circle sector and can rotate around point C.

p = oblique sesamoid ligament

q = interosseous ligament (muscle)

S = tension in the ligaments

To get balance, the total system of the moments has to be zero in C. The tension S in p and q is the same because the points of attachments are in both cases at the same distance (a) of C.

ligament which supports the fetlock joint will be twice as great. The increase in size of the sesamoid will reduce this tension, however. It is now clear that the size of the sesamoid bones is of importance for the whole biodynamics of the foot.

The angle β is minimal when the fetlock joint is in maximal dorsal flexion. $\cos \beta$ will have then the maximal value and in consequence also the tension in the ligament (S). The minimal angle of β is not the same in all horses as is stated before and will change during the phylogeny. In *Mesohippus* it is $\pm 50^\circ$ while in *Equus* less than 10° . It is clear that the tension (S) will increase directly proportional to $\cos \beta$.

We can assume that the oblique scar is developing together with the phalanx lengthening and the greater flexibility of the fetlock joint from *Parahippus* onward. The function might be explained now as follows:

1. to prevent lateral displacement of the sesamoid bones (which is also the function of the cruciate ligament from which it was derived).
2. to prevent lateral dislocation of the fetlock joint together with the better developed sagittal crest on the distal articulation joint of the third metacarpal. The oblique scar is more expanding and the central scar is disappearing. The oblique course of the ligamentum obliquum is better adapted to prevent lateral dislocation.
3. better support of the fetlock joint to prevent too much dorsal flexion.
4. finally in *Equus* it will be part of the automatic springing mechanism. It is here that the oblique ligament has to endure the most strength. The V scar is the most pronounced and its attachment surface reaches up to $\frac{2}{3}$ of the phalanx length (Table XVIII). This shows that the ligament was longer and so more elastic (springing mechanism); also that its attachment to the phalanx was stronger (greater area of attachment and the angle of its attachment with the first phalange was sharper and in consequence the force perpendicular to the bone became reduced).

This supposition finds also support in the fact that we do not find an oblique ligamentary scar in the *Mesohippus*-*Anchitherium* lineage. Here the central scar remains prominent. In this phylogenetic line we do not find the phalanx lengthening or an important increase in fetlock joint flexibility.

CAMP and SMITH (1942) compare the action of the fetlock joint and "springing ligaments" with a boy jumping on a pogo stick. The harder the impact the higher the bounce up to the capacity of the apparatus. According to them the development of this springing mechanism (interosseous tendon and the oblique ligament) would have had influence on the complexity of the digital ligaments, and the degeneration of the muscle interosseous into a tendon would already have been a fact in *Merychippus*.

Studying the volar side of the metacarpal III (chapter II B 1) we find morphological characters which can perhaps be explained by the fact that still in most tridactyl horses the "tendofication" of the muscle interosseous was not yet complete and only in monodactyl horses this was the case; our conclusion is based on the fact that the volar surface of the third metacarpal is concave and gulley-like (for lodging a muscle), while on the proximal part a clear tuberosity is found for the attachment of a tendon. In *Equus* we do not find such a pronounced gulley as in the just mentioned tridactyl horses and the attachment area is more ridge-shaped which is more suitable for the attachment of the band-shaped interosseous tendon.

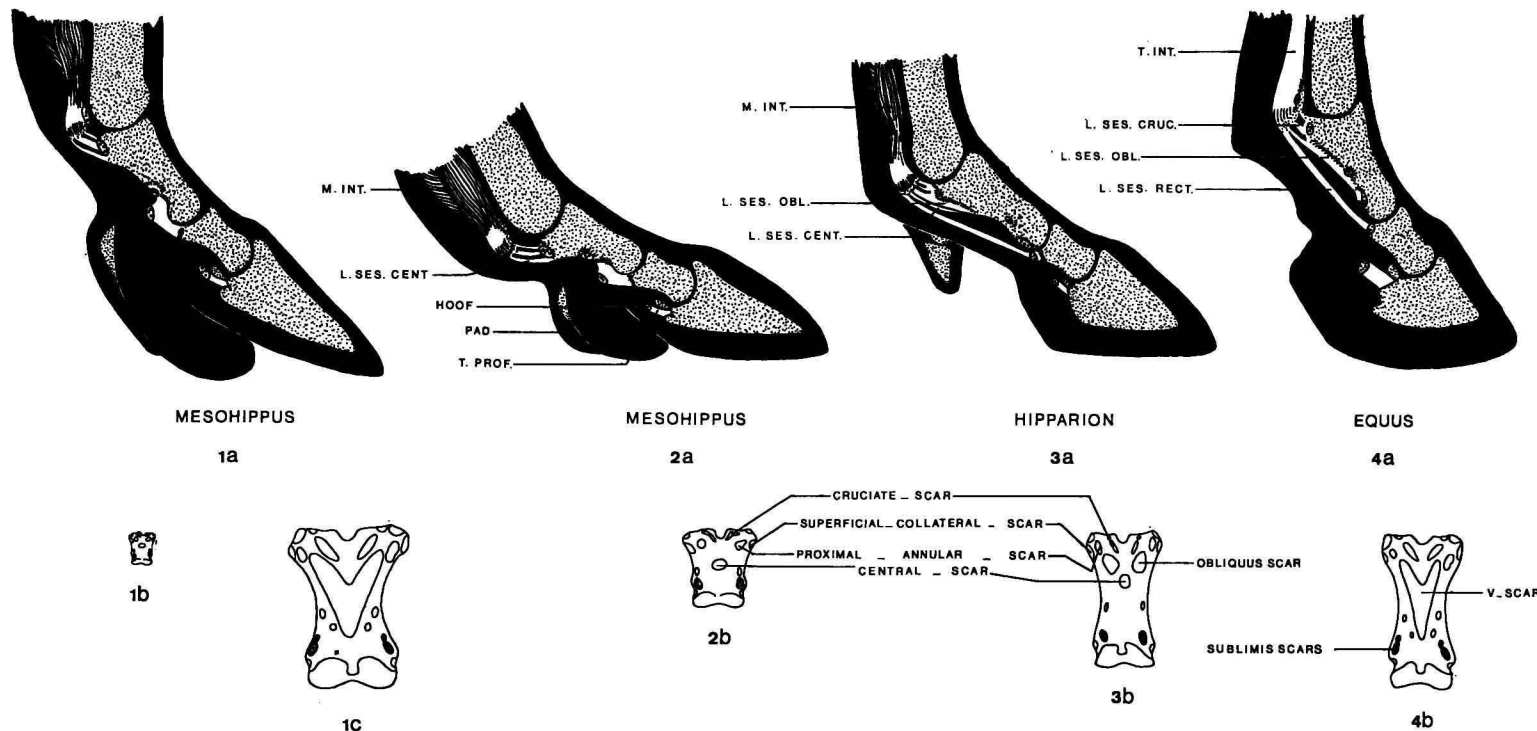


Fig. 23. Restorations of the feet and sesamoidean ligaments in *Mesohippus*, *Hipparion* and *Equus* adapted from Camp and Smith 1942. Drawn on the same length.

M. int. = musculus interosseus

T. int. = tendon interosseus

L. ses. cent. = ligamentum sesamoideum centrale

T. prof. = tendon of musculus flexor digitorum profundus

L. ses. obl. = ligamentum sesamoideum obliquum

L. ses. rect. = ligamentum sesamoideum rectum

L. ses. crus. = ligamentum sesamoideum cruciatum

1a. After CAMP and SMITH (1942). In this position the fetlock joint is close to maximal dorsal flexion. The third phalanx is placed oblique to the ground plane, so the fetlock joint comes higher, and the footpad looks quite unnatural.

2a. The rest position of *Mesohippus* as is proposed in this paper. It is more like that of a tapir. The foot had a pad between the three digits and so situated below the phalanges that it could support the first and the second. The position of the Mc III is oblique to the ground

3a. Foot of *Hipparion* in restposition. The foot lost its pad by the relative lengthening of the median phalanges and fetlock came from the ground. The position of the metacarpal III was more like *Equus*. There was still a musculus interosseus and the animal could regulate the position of the foot actively. There was probably, as CAMP and SMITH (1942) suggested in *Merychippus*, an enlarged digital cushion and frog.

4a. The foot of *Equus*.

Below, volar views of first phalanx of the third digit.

1b, 1c. *Mesohippus* and *Equus* after CAMP and SMITH (1942) showing the digital ligamental scars.

2b, 3b, 4b. The phalanges are drawn on the following scale: the proximal width is taken constant while the length is taken in relation to the third metacarpal.

The advantage of the interosseous muscle in tridactyl horses might have been that it could regulate to a certain extent actively the position of the fetlock joint which became impossible in the automatic springing mechanism. So the degeneration of the muscle interosseous into a tendon is something which occurs fairly late in the horse evolution, and it is not possible to associate this with the complexity of digital ligaments starting from *Merychippus*.

B. TYPE OF FOOT

In figure 23 outlines are given of three foot types which probably occurred during the phylogeny of the horse. Restoration of the manus in Plate 8 given by Camp and Smith is taken as a starting point from which our figure is adapted.

The manus are all drawn to the same length. In 2a, 3a and 3b the total length of the phalanges is taken constant. In 2b, 3b and 4b the width is taken constant while the length is given in relation to the length of the metacarpus. In 1a after Camp and Smith the *Mesohippus* manus is put in *Equus* position while the length of the first phalanx is similar to *Equus* (4a). Because of this the foot pad looks quite unnatural. In 2a the foot of *Mesohippus* is placed in the position as proposed in this paper. The foot is placed in rest position (according the articulation surfaces of the several joints) and more like a tapir.

On the first phalanx, which is relatively short, a clear central scar was found. The lateral digits touch the ground also in rest position. The laterals could still spread independently from the central. The musculus interosseous is well developed. This kind of "padded tridactyl foot" we find in the *Mesohippus*-*Anchitherium* lineage. In 3a *Hipparion* foot is figured. This type of foot "tridactyl tip toe" can be found also in *Parahippus*-*Merychippus*. The horse lost its pad and started to walk on the top of the lengthened third digit. The laterals were only in function under special circumstances as running, when sinking into soft ground, with the start and as SHOTWELL (1961) explained in dodging manoeuvres. The lateral metacarpals were firmly bound to the central and could not act independently. The position of the foot is more *Equus*-like. The interosseous muscle had not yet changed into a tendon and the horses could, to a certain extent, regulate the foot position. The phalanx has a distinct V scar while the central scar is relatively less important. Perhaps here the ligamentum sesamoideum rectum was developed.

In 4 the foot of *Equus*, which is similar to that of *Pliohippus*, *Pleshippus*, "the monodactyl springing foot type". The laterals were lost. The interosseous muscle is degenerated to a tendon and the so-called springing ligaments are well developed. The fetlock is far from the ground-plane and the animal possesses relatively long phalanges with an distinct V scar for the oblique ligament. The central scar is lost. The long size of the V scar must have had two advantages:

1. better attachment to the first phalanx.
2. it shows that the oblique ligament was relatively long and thus more elastic, which promoted the spring effect.

Together with the long phalanges the possibility of a big dorsal flexion in this foot type must be very favorable for the "pogo stick" effect. This foot was highly specialized for running efficiently and fast over greater distances and was in this aspect more adapted than its tridactyl forerunner. The tridactyl could start perhaps quicker but did not have the endurance of the monodactyl.

V. THE MANUS PHYLOGENY IN CONNECTION WITH OTHER CHARACTERISTICS

A. MESOHIPPIUS

In the *Meshippius* manus lateral flexibility was observed, this is found also in the pes where we find a similar foot pad as in the manus. In *Meshippius* there is still a distinct ulna which is not so tightly fused with the radius as in later horses. Also the fibula was still present along the whole shaft of the tibia.

Skull: the premaxilla does not protrude much in comparison with later horses. The free parts of the nasals are short; the orbita is not closed totally by a bone and is open behind; the teeth are chitmalodont¹⁾ and clearly lophodont. The premolars (except the P¹) are molariform and the whole aspect of the dentition was that of a browser.

B. ANCHITHERIUM

The previously described characteristics for *Meshippius* are also applicable to *Anchitherium* and the larger size is the only clear notable difference. Though so far there is no complete skull described of *Anchitherium*, we may expect that this will be similar to that of *Hypshippius*, a very closely related genus. Here the orbita is not closed, in addition the teeth of the group are also difficult to distinguish from *Meshippius* on the morphology of the ridges, though we have of course again a clear difference in size. *Anchitherium* had a similar foot pad on the pes as it had on the manus. The differences in morphology of *Anchitherium* with *Meshippius* can be explained allometrically. The animal remains a typical browser with padded feet.

C. PARAHIPPUS-MERYCHIPPUS

These two genera show a number of changes which are a trend to the same specialisation. *Merychippus* is geologically the youngest of the two and derived from the first. As SIMPSON (1961) wrote: "The group of *Merychippus* was actually a complete splitting up into different lineages that eventually evolved in a number of different genera of grazing horses".

Some of the trends in the *Parahippus-Merychippus* lineage which goes parallel with the phylogeny of the manus are:

¹⁾ As the term brachiodont has been used before in human dental morphology in another sense, KORENHOF (1960) introduced therefore for low-crowned teeth the term chitmalodont as opposed to hypsodont (high-crowned teeth).

The hind foot lost its pad by lengthening of the central phalanges. The position of the hind foot changes as the front leg did. The ulna reduced further and the shaft was tightly bound to the radius. The fibula is reduced and the shaft becomes vestigial.

The premaxilla tends to protrude further, while the orbita closes by the development of a supraorbital process of the frontal bone. This configuration is something new in the horses that changed clearly their habitat from browsing to grazing. SIMPSON (1951) explains the function of the circled bone around the eye-socket to support the strength of the skull. We can understand this as the chewing mechanism became more powerful and so the skull must be adapted to support more stress and strain. The teeth become gradual more hypsodont and coated with cement.

The change of the locomotion apparatus can be explained by the change of habitat, seen also in the chewing mechanism. This has already been stated in many previous studies.

In some cases there is doubt about the place of a genus in the phylogeny. I want to mention here *Archaeohippus* of which the generally accepted idea is that this tiny horse tends to parallel *Anchitherium* (SIMPSON, 1932; STIRTON, 1940), *Archaeohippus* was proposed by Gidley in 1906 on material from the Mascall beds and originally described as *Anchitherium ultimum* Cope. SIMPSON (1932) describes a new species *A. nanus* from Thomas farm, which was made synonymous with *Parahippus blackbergi* by WHITE (1942) and BADER (1956). DOWNS (1956), however, in describing the Mascall fauna maintains the generic name of *Archaeohippus* in the species *blackbergi* and discusses several characters of the genus *Archaeohippus* which shows advanced characters. *A. blackbergi* is in relation to *A. ultimus* even more primitive; the first has 4 features in the teeth which may be considered as primitive while 2 are advanced, in the second it is 3-3.

The study of the post cranial parts of *A. blackbergi* from Thomas farm shows us from the preceding chapters that this horse had a locomotion similar to that of *Parahippus* and *Merychippus* and well distinguishable from horses of the *Mesohippus*-*Anchitherium* lineage. There was a relative median phalanx lengthening. The laterals were tightly bound to the central and could not spread any more. The foot lost its pad. In comparison to the teeth the foot structure was further evolved, and the animal had probably changed already his habitat. In evolution it is often seen that teeth will preserve more conservative characters while the locomotion is evolving quicker and is losing its primitive features when it is without function.

To consider *Archaeohippus* as a separate genus is a matter of taste. According to Stirton, Downs and others in tooth characters it is distinct from *Parahippus* while in foot structure it is more similar to *Parahippus*. Any way the animal must have been in habitat closer to *Parahippus* as

to *Anchitherium* and in the phylogeny it is closer to the first.¹⁾ This observation may give support to WHITE's idea (1942) who puts *Archaeohippus blackbergi* in the following phyletic series: *P. blackbergi*—*P. barbouri*—*P. leonensis*—*Merychippus gunturi*.

D. HIPPARION

The *Hipparion* manus was still tridactyl and in function similar to that of *Merychippus*, though a number of differences have been stated in the preceding chapters.

In the radius there is further reduction of the ulna. The teeth are hypsodont. In the Palearctic *Hipparion* there is a big variation which FORSTEN (1968) considers adaptive and the evolution was that of speciation. The Euro-Asiatic *Hipparion* are better known by the painstaking and penetrive study of GROMOVA (1952) who established very clearly its morphological and functional characteristics. The systematics of the *Hipparion* are quite complex and many species are described.

In a recent study FORSTEN (1968) has given a revision of the *Hipparion* and considers many of those species non valid and gives a phylogeny of Palearctic *Hipparion*. Though we agree with Forsten that the number of species is high, we do not adhere to the method followed by this author. FORSTEN (1968) starts from the opinion that *Hipparion* should be discussed in the same terms as recent animals. Further she considers specimens from different quarries (in geography and time) without sufficient evidence as local populations of the same species. The species concept is a very complicated one, but generally it is accepted that we can not use one single definition for it, and that it is difficult to apply the species concept of recent animals to that of fossils (CAIN (1953) and SIMPSON (1951 b) since it takes no account of the passage of time. We do not know anything of fossils about genetics, besides a thannatocenose is not identical to a biocenose. If we have material from two localities of which we do not know that they are absolutely synchronous and from a same biotope, we have to consider them seperately. SIMPSON (1951 b) defines this as follows: "To consider the two (or more) lots of associated specimen as samples of different local populations and derive from their estimates of morphological variation in those populations".

FORSTEN (1968) considers the relative massivity of the metapodials as an important feature for separating species of *Hipparion*. She distinguishes, for example, in the localities of Maragha, Pikermi and Samos the species of *H. primigenium* and *H. mediterraneum*; the first is the more massive one, while the other is of more slender build. They are in these localities, according to Forsten local populations of the same species.

¹⁾ This confirms also the statements of MATTHEW 1932. *Archaeohippus* belongs without question in the protohippine group and not in the anchitheriine group.

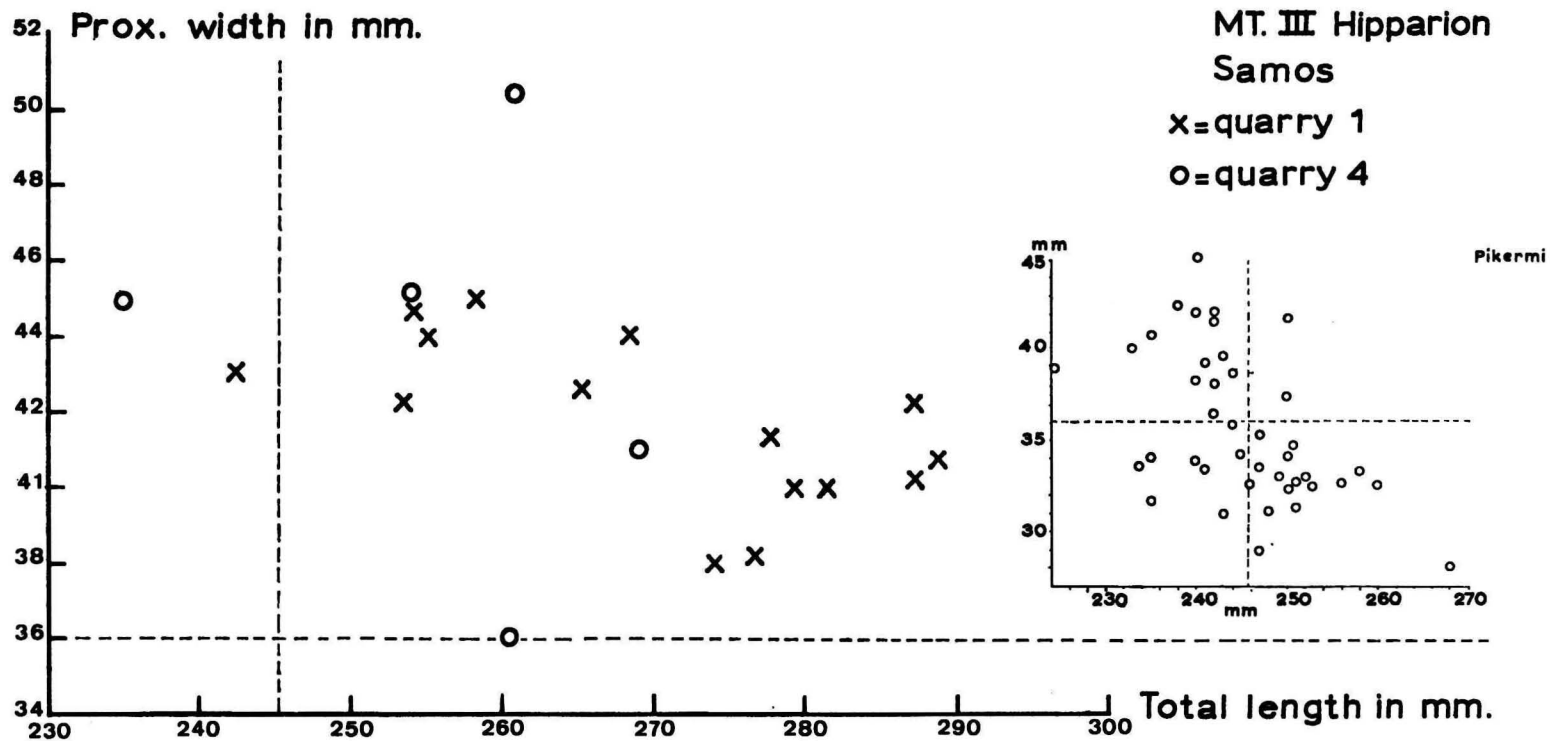


Fig. 24. Scatter diagrams of the length proximal width relation in the third metatarsals from *Hipparion* found in Samos (A. M. N. H. BROWN expedition 1924) and inset from PIKERMİ after PIRLOT (1956).

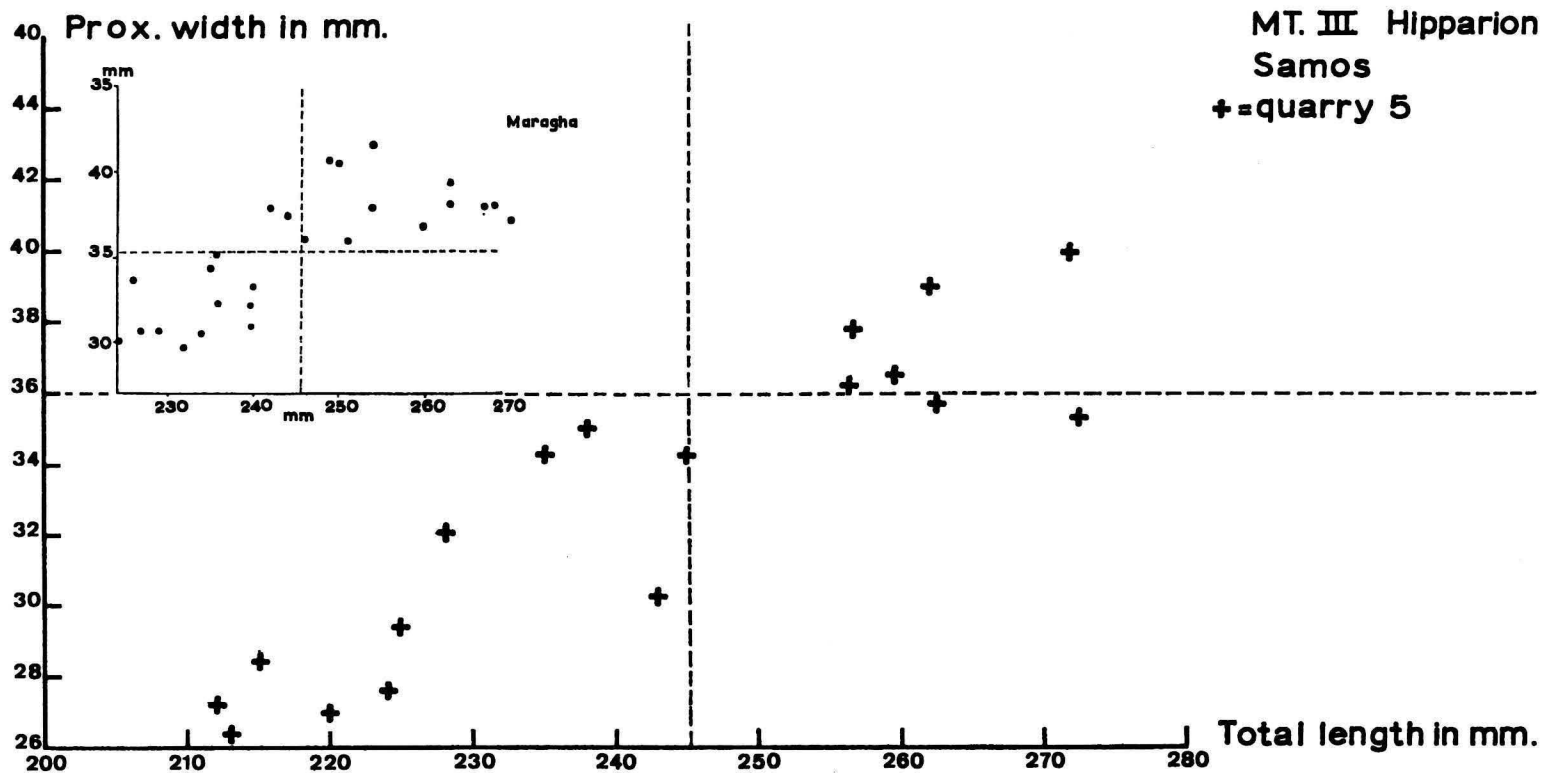


Fig. 25. Scatter diagrams of the length proximal width relation in the third metatarsals from *Hipparion* found in Samos (A. M. N. H. BROWN expedition 1924) and inset from MARAGHA after PIRLOT (1956).

Her scatter diagram of the length/width relation in the Mt III shows it to be very amorphous and it is not clear on which supposition the 95 % equi-probability axis are drawn from the two species. In other words which criterion was applied to separate a metapodial of *primigenium* or *mediterraneum* as there are no clear groupings in her scatter.

If we take the scatters of PIRLOT (1956) fig. 24 and 25 we get a totally different picture of the localities Pikermi and Maragha. In the first we have long and relatively slender bones and short more massive ones, while in Maragha the last group is lacking and with the increase in length the metatarsal width is increasing proportionally. The two scatters are clearly different. To consider the bones of these localities as belonging to local populations looks somewhat unnatural. The more so if we take into account:

1. that we do not know what is the time difference between the two localities.
2. the geographical distance is considerable.
3. the fauna is different in the two localities. In Pikermi we do not find, for example, *Chilotherium*, *Urmiatherium*, *Iranotherium* and *Parataxidea* which genera are restricted to Asia (Samos excluded).

Even when we discuss the fossils as recent animals it is not realistic to consider the fossils from Maragha and Pikermi as local populations of the same species.

From the Mt III length-proximal width scatter of Samos from Pirlot we learned that there was no clear grouping as there is in Pikermi and Maragha; this is probably the result of mixing material from different localities in old collections. Fig. 24 and 25 present scatters for different quarries in Samos excavated by Dr. Barnum Brown and stored in the A.M.N.H. In quarry 5 we see a grouping similar to that of Maragha, while in quarry 1 and 4 it is more like Pikermi. During a survey in Samos to relocate the quarries of Dr. Brown it was found that there was also a time stratigraphic difference between the quarries, though the relative age could not be traced owing to the fact of tectonical disturbance, and our ignorance of Browns quarry numbering. In Samos which is close to the Turkish coast we may perhaps assume that Samos during the Pliocene was a part of Turkey while in another period it was connected to Europe (Greece) and we have had here two waves of migrations one with animals from Europe and the other from Asia.

The paleogeography of Europe during the Neogene is very complicated and difficult to trace back, because of tectonical disturbances during this period. We have also had isolated regions, as Crusafont showed several times in Spain, endemismes. Neither must we exclude the possibility of parallelism in the speciation of *Hipparion*; so the phylogeny of *Hipparion* in the old world is very complicated and can only be solved if we get

to know more of the paleogeography, stratigraphy and paleoecology of the several *Hipparion* localities and if the *Hipparion* from those localities are studied as being from different local populations. So far we can say that there is a considerable variation in *Hipparion*. For some of the differences GROMOVA (1952) has given plausible reasons, but there is still a lot to study before we can speak about a clear phylogenetic tree of *Hipparion* in the old world.

E. NANNIPPUS

It was seen that the manus of *Nannippus* did not fit completely in the outline given for *Hipparion*. The genus *Nannippus* is not well understood. Most authors refer all the smaller *Hipparion*-like creatures to *Nannippus*. STIRTON (1940) traces back the genus *Nannippus* throughout the whole Pliocene and speaks of primitive species where the distal keel is rather faint on the anterior face of the facet, but in which there are well-developed lateral digits (page 186). However, in all Pliocene species of horses we see an anteriorly developed keel on the distal part of the central metapodials except in the *Anchitherium*-like horses (for example *Hypohippus*).

After considering the material from Blanco on which the genus was based (stored in the American Museum), it becomes clear that this genus is so specialized that we must restrict the generic name *Nannippus* to a much smaller group. There are small *Hipparion*-like animals which do not belong to the genus *Nannippus*, for example the species *lenticulare*, which do not have the generic characters.

MATTHEW (1926) had already noticed most important characteristics in describing the subgenus *Nannippus*. These features include: the extreme high-crowned teeth; the absence of the fifth metacarpal and trapezium, which bones are always present in *Hipparion* and are also found in *Pliohippus* and *Plesippus*.

In the *Nannippus* material from Blanco we can also observe other characters in which it differs from other Pliocene horses in that it shows a high specialization always from the typical primitive condition. In this specialization it sometimes exceeds *Equus caballus*. Among such advanced features are:

1. the angle between the facet for the hamatum and magnum at the Mc III is relatively flat. The facet for the unciform is large.
2. the facet for the cuboid and ento-cuneiform at the Mt III is greatly developed in comparison with *Hipparion* (see Table XVI) and more weight was borne by the third metatarsal. In most of the American species of *Hipparion* the facet of the ento-cuneiform is even absent. These two characters are very *Equus*-like. Perhaps the lateral metapodials did not retain any function in *Nannippus*?

TABLE XVI. Ratio between the facets for cuneiform III and cuboid of Mt III

Index	$\frac{\text{width fac. cuboid}}{\text{width fac. cuneiform III}} \times 100$	$\frac{\text{width fac. cuneiform II}}{\text{width fac. cuneiform III}} \times 100$
<i>Nannippus phlegon</i>	35-39 (3 ex.)	19-20
<i>Hipparion moldavicum</i> (after GROMOVA 1952)	21-31,6 (50 ex.)	0-17,4

TABLE XVII. The width of the distal part of the Mc III of the joint and tubercles

	<i>Equus caballus</i>	<i>Nannippus phlegon</i>	<i>H. moldavicum</i> (after GROMOVA 1952)	<i>Nannippus</i> sp. nov. Chihuahua
Width distal part Mc III at the joint	54,0	3 ex. 20,6, 22,2, 23,0	11 ex. 29,0-32,5	19,5
Width at the tubercles of the Mc III	51,5	20,0, 20,4, 22,2	32,0-35,0	18,0

TABLE XVIII. Index length V scar on length of the phalange

<i>Merychippus</i>	V/P varies between 1/4 and 1/3
<i>Hipparion</i>	V/P varies between 1/3 and 1/2
<i>Astrohippus ansae</i>	V/P equals slightly less than 1/2
<i>Nannippus phlegon</i> , <i>Plesippus</i>	V/P equals 1/2 or slightly more
<i>Equus</i>	V/P equals 2/3 more or less

V = length of V scar

after CAMP and SMITH 1942

P = length of phalange

3. if we consider the distal part of the third metacarpals of *Nannippus* we can observe that the width at the joint exceeds the width at the tubercles above the latter; this too is an *Equus*-like characteristic. In *Hipparion* we see just the opposite. (Table XVII).
4. CAMP and SMITH (1942) give some important data for the ligaments of *Nannippus* (p. 82). *Nannippus* has a flat, straight-edge V scar (with but little differentiation of the central ligamentary scar), small proximal prominences, small lateral volar areas, and extensive central volar areas of a kind not observed in other genera! Also the length of the oblique ligamentary scar in relation to the length of the phalange is in *Nannippus* nearly equal to that of *Equus* species. The greater length of the V scar is a progressive characteristic in the evolution of the horse (Table XVIII).
5. the milk dentition is extremely high-crowned, and typically in the

lowers the ectostylid is missing or very little developed (a feature characteristic for *Hipparion*).

6. in the lower permanent dentition no protostylid is present. Nearly always a protostylid occurs in *Hipparion*.
7. the antero-posterior length of P2 is relatively small and very often even shorter than the same measurement in P3. In consequence the premolar series (P2-P4) is sometimes shorter than the molar series (M1-M3); a rare characteristic among equids. The generic characteristics of *Nannippus* are consequently easily distinguishable. It is a very distinct and specialized group of Late Pliocene horses which are known from fossils of the Blanco formation (MATTHEW, 1926); Chihuahua, Mexico (LANCE, 1950); Meade formation, Kansas (HIBBARD, 1956) and BREWSTER, Polk county, Florida.

Nannippus is a very distinct group of Late Pliocene horses and is usually found associated with a monodactyl horse (*Plesihippus*, *Astrohippus* etc.). The lateral metapodials were reduced and their function was probably already lost.

The limbs and dentition of *Nannippus* show in some respects greater specialization than in *Equus*.

Nannippus is an end-form of the *Hipparion* lineage which in some respect exceeds in specialization *Equus*.

F. EQUUS

The morphology of the recent horse is well known and we shall not go into details here.

There are at the moment still six living species (SIMPSON, 1951):

Equus caballus caballus

Equus caballus prjeswalskii

Equus hemionus

Equus asinus

Equus quagga burchelli

Equus zebra

Equus grevyi

Equus hemionus is a typical steppe-dwelling animal while *Equus zebra* is living in a mountaneous biotope. Often different generic names are used such as *Hippotigris*, *Asinus*, *Hemionus*.

One of the most striking differences in separating the living Equidae is the colour of the fur. GROMOVA (1949) states that it is extremely difficult to separate African donkey from the zebra because they have a big

analogy in the teeth, though it is a distinct natural species. As it is already difficult to separate the living species of *Equus* when we have only bones and teeth, we can understand the nomenclatural problems in *Hipparion*. The more so as *Hipparion* inhabited the palearctic regions for about 10 million years, whereas *Equus* did so for less than two million years.

VI. PALEOECOLOGY OF HORSES IN GENERAL AND OF THE CHIHUAHUA HORSES IN SPECIAL

We learned from the recent *Equus* that it is difficult to trace their habitat if we find only their limbs and teeth. Therefore we have to be very careful if we want to say something definitive about ecology of the fossil species. The differences between the genera are bigger and we may make some speculations about them.

It is clear that *Meshippus* and *Anchitherium* were browsers with their padded feet and chitamelodont teeth. They were never found in big quantities like the grazing horses, and if found as a fossil they are usually only a small percentage of the total quantity of fossil animals. In the Oligocene they are outnumbered by the oreodonts. In the Miocene *Anchitherium* is outnumbered in America by the grazing horses and in Europe by artiodactyls like deers and antelopes. The occurrence of *Hypohippus* with grazing horses shows that they were not in direct competition. The radiation of horses in the Miocene of North America may be explained by the relative lack of artiodactyls, and once they entered the more grass country biotype they encountered relatively little competition. In the same period in Euro-Asia we see a radiation in the artiodactyls. The arrival of *Anchitherium* did not greatly disturb this situation. With *Hipparion*, however, this was different, the whole fauna changed and they outnumbered the artiodactyls and were prominent till the end of the Pliocene when the bovids start to become more important. With the arrival of *Hipparion* *Anchitherium* became gradually extinct though it was shown that they were not in direct competition in North America; perhaps we can explain this as follows: by the arrival of *Hipparion* we get a shifting in the fauna and some artiodactyls had to look for exile in the forest which finally caused the extinction of *Anchitherium*.

The tridactyl *Hipparion* had an all-round foot and a dentition for grass-eating. Though it is difficult to trace their ecology it is in general accepted (more hypsodont teeth) that later *Hipparion* were living in the open country (steppe-like). In this area the all-round foot of *Hipparion* was of not much use and with the arrival of *Equus* it was clear that this animal with the springing mechanism was in advantage in the open country to the *Hipparion* which had not such an endurance, and so became extinct.

Perhaps we can explain the occurrence of the four Chihuahua horses as follows:

Astrohippus stocki was the most common of the four horses and was found about twice as much as *Pliohippus mexicanus*. *Neohipparion floresi* and *Nannippus* c.f. *minor* were in the minority. From the small *Nannippus*

only a few bones were present. The four horses had the hypsodont teeth in common which do suggest that they all had a grazing habit. The presence of four or more different horses in the Pliocene fauna of North America is quite common. In the old world, however, only one or two species of *Hipparion* are found. Here we find a great many artiodactyls like antelopes and cervidae who outnumbered the genera of perissodactyls. The antelopes are lacking in the American fauna and the antilocapridae could not cover the whole ecological niche which was covered in the old world by the antelopes. Perhaps the horses replaced them in North America. The comparison SIMPSON (1951) made: that the general form of *Nannippus* probably suggested a small gazelle rather than an ordinary horse, will fit in with this supposition when we accept that the convergency in the skeleton is also found in the mode of life. *Nannippus* survives even in the Pleistocene and shows also in the dentition an extreme specialisation.

Neohipparion had a functional tridactyl locomotion. That this tridactyl horse could survive between the better adapted walkers and springers as *Pliohippus mexicanus* and *Astrohippus stockii* must have had a reason, and suggests that they were having probably different grazing habitats.

SHOTWELL (1961) explains the occurrence of *Hipparion* and *Pliohippus* in the same region of the Hemphillian also by their different grassland habitats, open grassland and savanna respectively. The movement of *Pliohippus* into the Northern Great Basin, according to Shotwell, seems to coincide with the appearance of extensive grass lands of prairie and plains type in the region. In older layers only *Hipparion* was found. In flora and fauna there were more aquatic-loving elements. During time here the relative proportions of aquatic and woodland-forest habitats would decrease. SHOTWELL (1961) supposes that the dispersal of *Hipparion* was more confined to the savanna and that the foot of *Hipparion* was functional in an area where obstructions were present; the lateral toes supplied added traction in dodging manoeuvres. This might be true to a certain extent and in special cases. We may add to this, and perhaps this was more important in our Chihuahua horses, that the tridactyl locomotion profited by soft, sandy or muddy soil in which this type of foot did not sink down so far (CAMP and SMITH, 1942). Even more important is that the animal could draw out its foot more easily as it could contract the three toes. The tridactyl *Neohipparion floresi* from Chihuahua show characteristics which suggest a well-developed muscle interosseous, and so it could regulate actively the position of the foot which was more flexed in the fetlock joint when the animal was grazing on soft ground. This foot type had here the advantage, an automatic springing mechanism would have been of no use. *Astrohippus stockii* and *Pliohippus mexicanus* had both the springing mechanism and covered the open grass country. They had a slightly different habitat because of their different size. The locomotion does not show essential differences between the two animals.

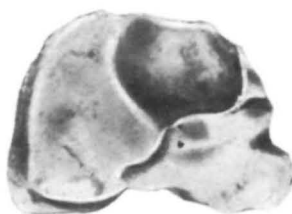
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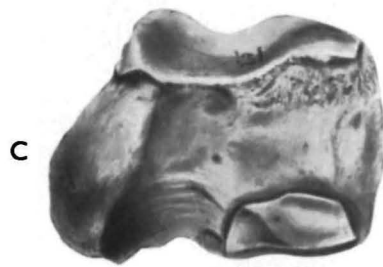
PLATES I-V

PLATE I

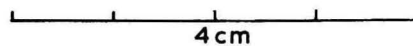


A

B



1



3

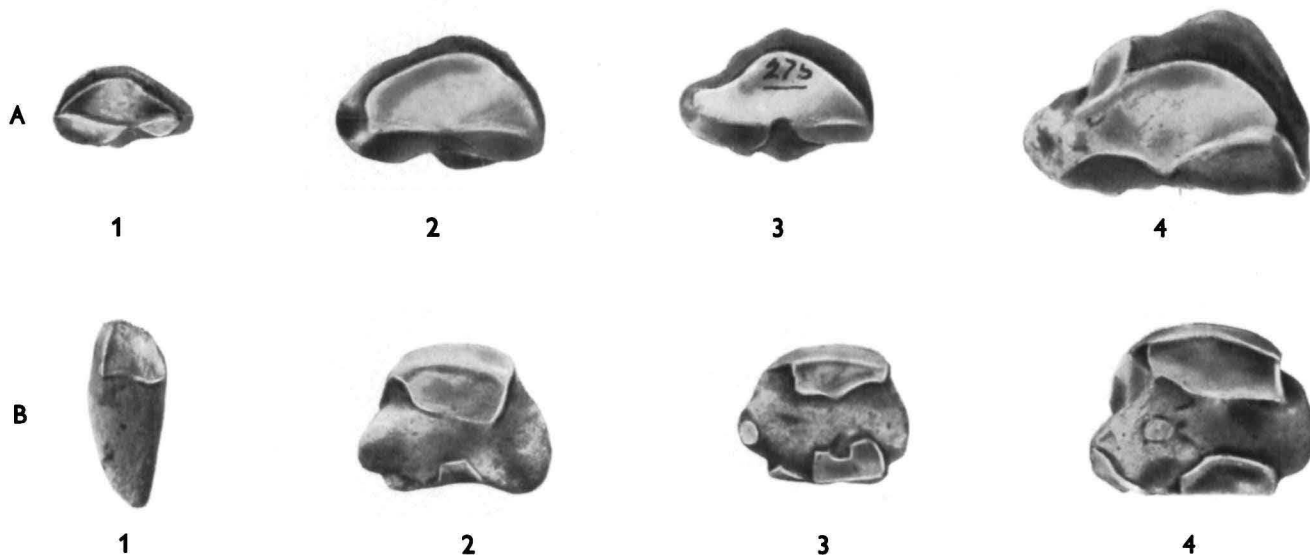
4

Navicular

- A. proximal view
- B. distal view
- C. lateral view
- triquetrum*
- D. medial view

- 1. *Neohipparion floresi*
- 2. *Nannippus* c.f. *minor*
- 3. *Astrohippus stocki*
- 4. *Pliohippus mexicanus*

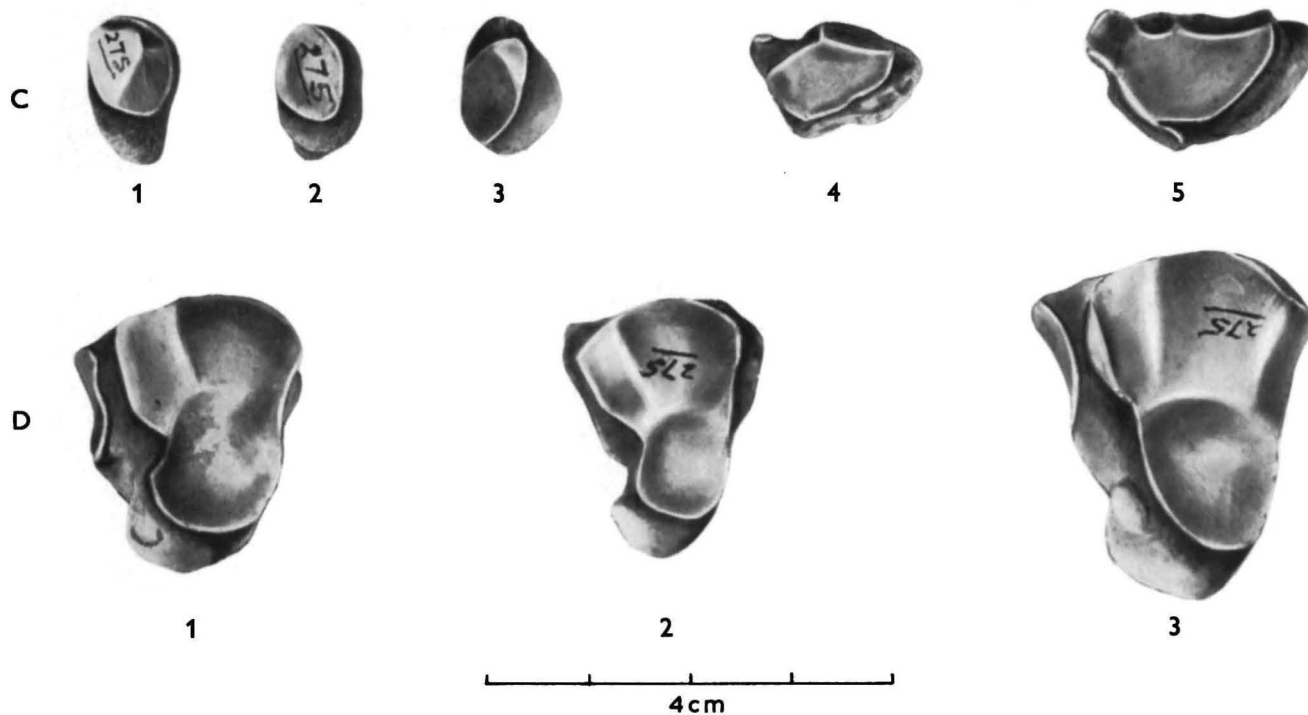
PLATE II



A. *Hamatum*
distal view

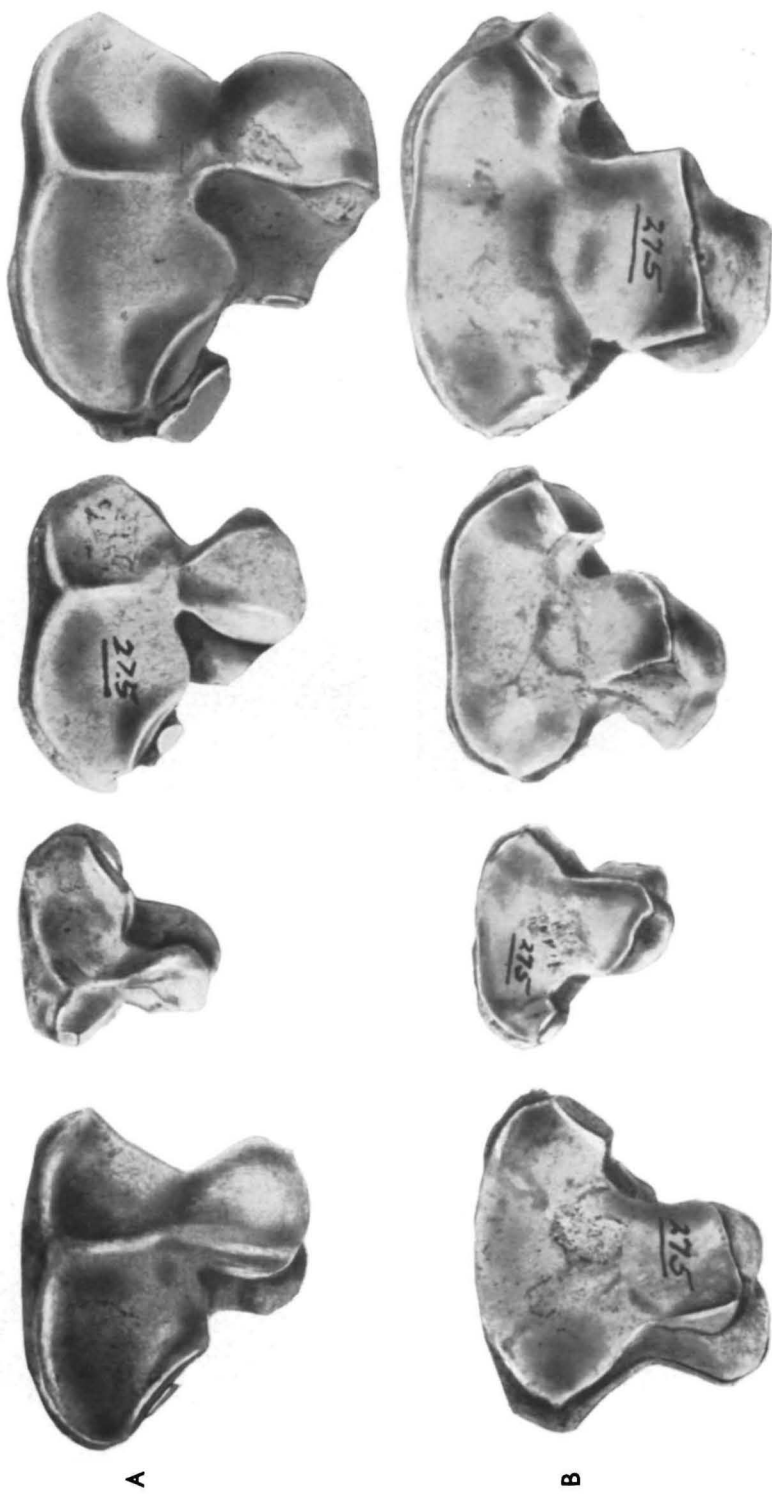
B. *Mc V*
B. *Trapezoideum*
lateral view

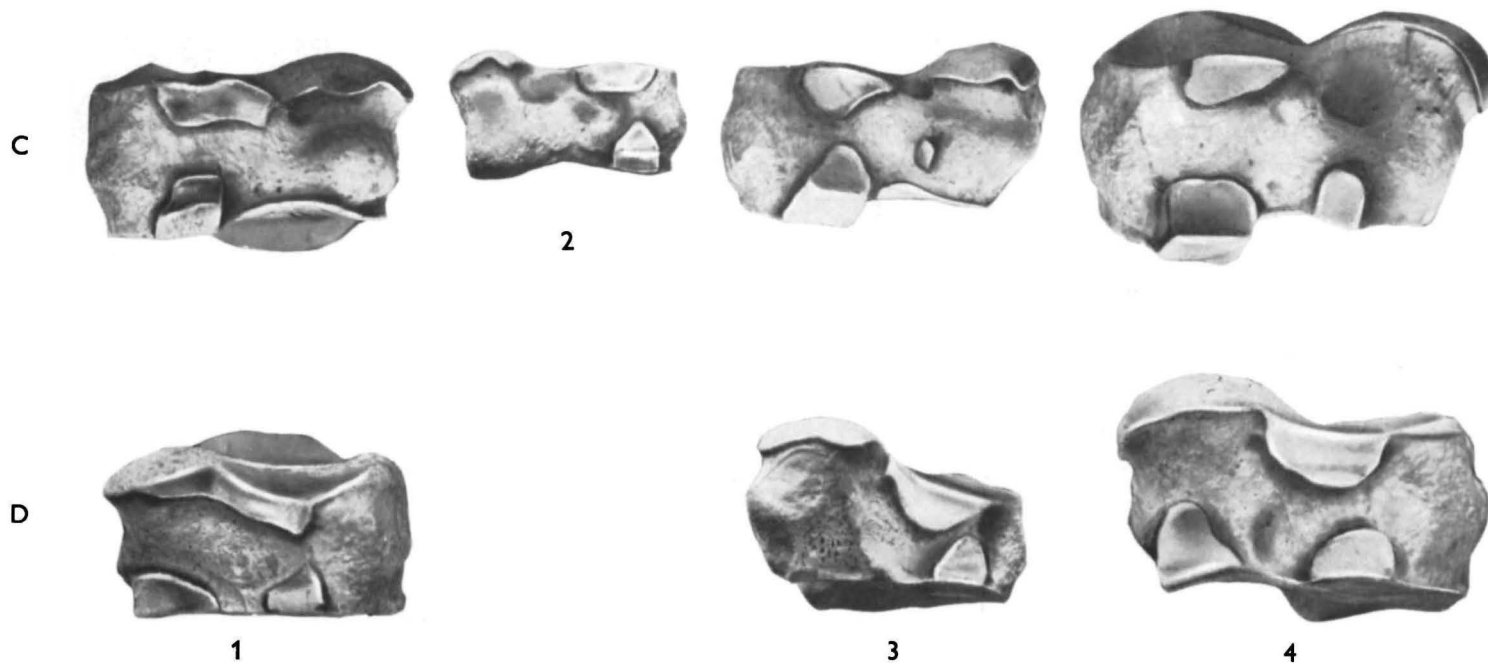
1. *Nannippus* c.f. *minor*
 2. *Neohipparion floresi*
 3. *Astrohippus stockii*
 4. *Pliohippus mexicanus*
1. *Neohipparion floresi*
 2. *Neohipparion floresi*
 3. *Astrohippus stockii*
 4. *Pliohippus mexicanus*



- | | |
|------------------------------------|--------------------------------------|
| C. <i>Trapezoideum</i> | 4. <i>Astrohippus stockii</i> |
| distal view | 5. <i>Pliohippus mexicanus</i> |
| C. <i>Trapezium</i> or <i>Mc V</i> | 1, 2, 3. <i>Pliohippus mexicanus</i> |
| D. <i>Lunatum</i> | 1. <i>Neohipparion floresi</i> |
| distal view | 2. <i>Astrohippus stockii</i> |
| | 3. <i>Pliohippus mexicanus</i> |

PLATE III





Magnum

- A. proximal view
- B. distal view
- C. medial view
- D. lateral view

- 1. *Neohipparion floresi*
- 2. *Nannippus* c.f. *minor*
- 3. *Astrohippus stockii*
- 4. *Pliohippus mexicanus*

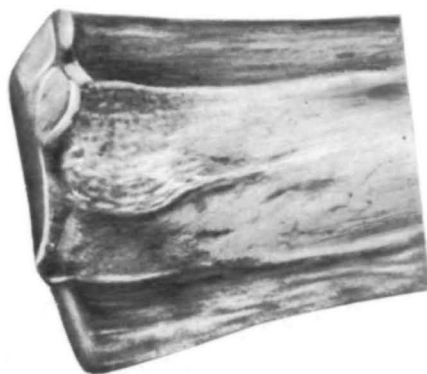
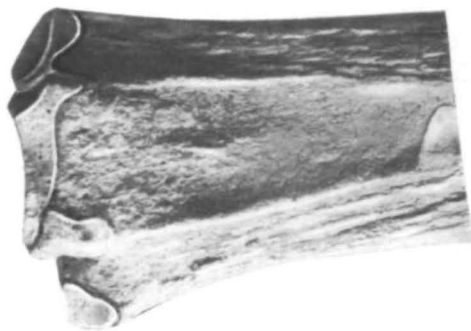
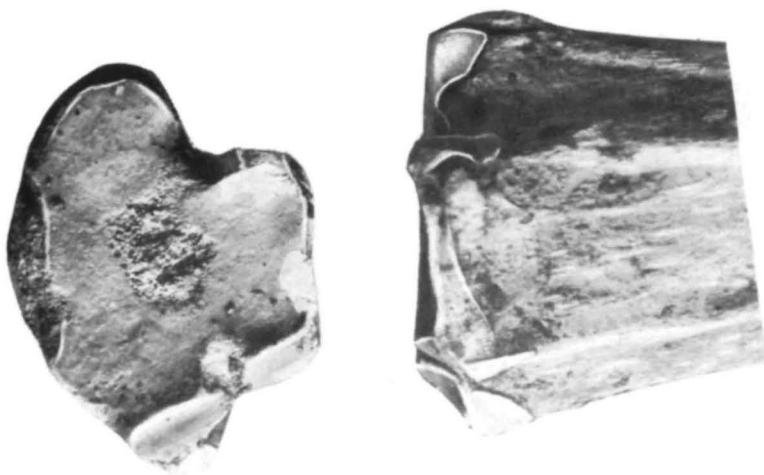
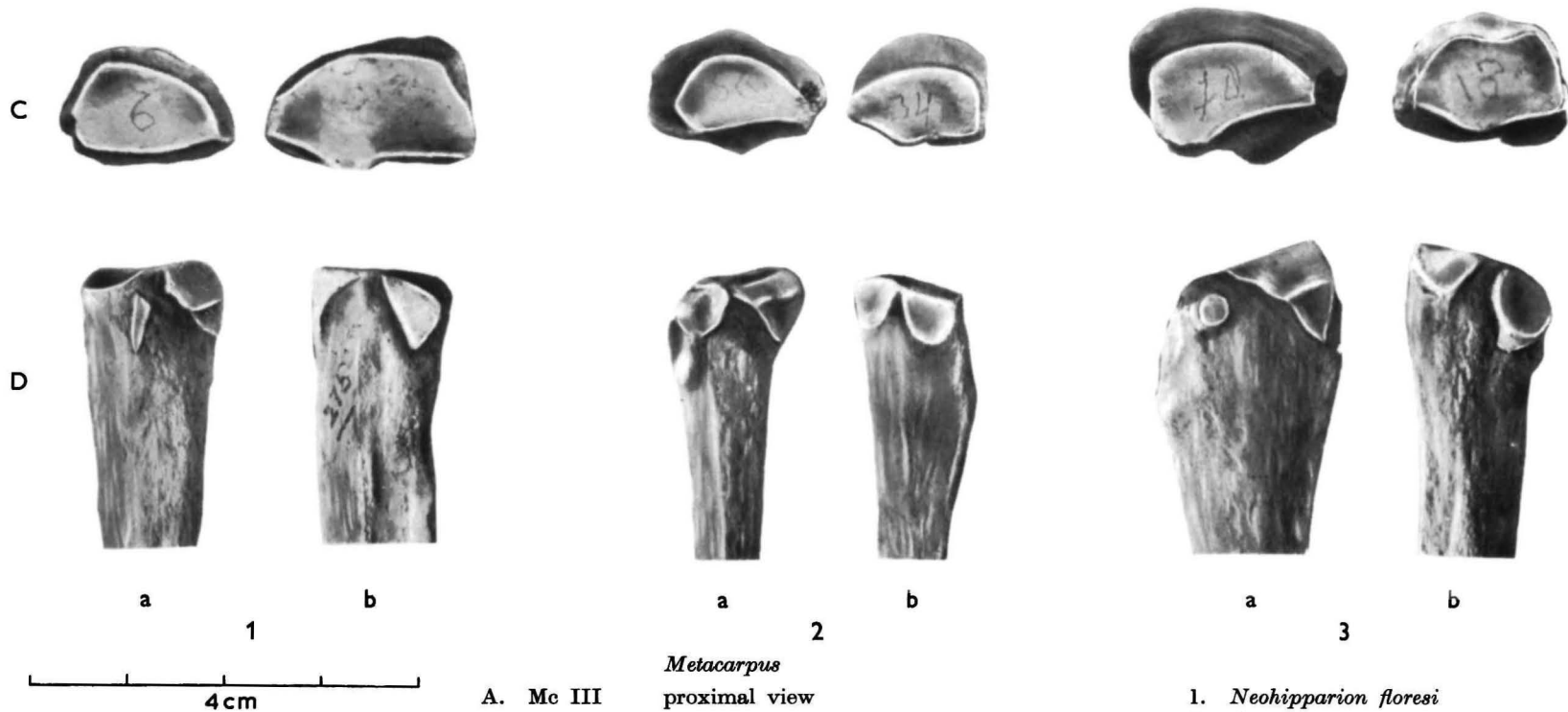


PLATE IV

A

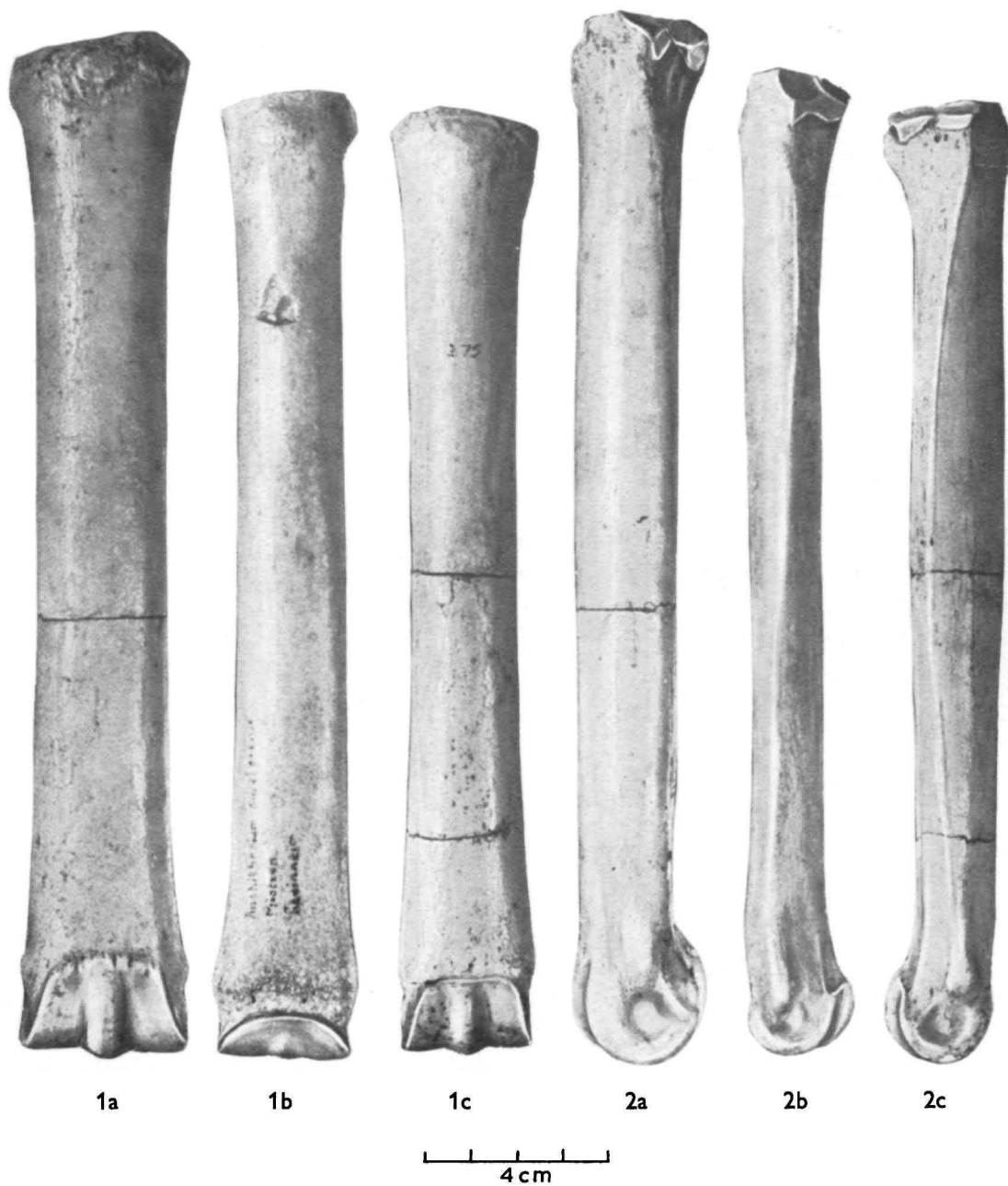
B



- Metacarpus*
- | | | |
|----|----------|---|
| A. | Mc III | proximal view |
| B. | Mc III | volar view |
| C. | a. Mc II | proximal view |
| | b. Mc IV | |
| D. | a. Mc II | showing articulation facets with Mc III |
| | b. Mc IV | |

1. *Neohipparion floresi*
2. *Astrohippus stockii*
3. *Pliohippus mexicanus*

PLATE V



Third metacarpal
 1. dorsal view
 2. lateral view

a. *Pliohippus mexicanus*
 b. *Anchitherium aurelianense*
 c. *Neohipparion floresi*