

OLD WORLD HEMIONES AND NEW WORLD SLENDER SPECIES (MAMMALIA, EQUIDAE)

by

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RESUME

Description morphologique et biométrique de crânes, dents et os des membres d'hémionees actuels et fossiles de l'Ancien Monde (*E. hydruntinus* inclus) et d'espèces sveltes ("stilt-legged" et autres) du Nouveau Monde du Pliocène à l'Holocène. Un Appendice présente des techniques qui permettent d'évaluer des dimensions manquantes à partir de données accessibles.

Les fossiles discutés et/ou figurés proviennent d'Allemagne (Süssenborn), de Bolivie (Tarija), du Canada (Yukon), de Chine (Choukoutien, Gulongshan, Jiling, Loufangzi), de l'Equateur (Oil Fields), de l'Espagne (Venta Micena), de l'Ethiopie (Melka Kunturé), de France (Lunel-Viel), Grèce (Agios Georgios, Petralona), Hongrie (Dorog), Italie (Romanelli), du Mexique (Cedazo, San Josecito), de

Mongolie (Sjara-osso-gol), de l'ex Union Soviétique (Akhalkalaki, Binagady, Chokurcha, Chukochya, Kabazi, Kolyma, Krestovka, Kurtak, Staroselie, Tologoj), des USA (Alaska, Arkalon, Cedar Meadow, Channing, Conkling, Dry Mountains, Hay Springs, Leisey Shell Pit A, Lissie Formation, Natural Trap, Pool Branch, Powers Ranch, Rock Creek, San Diego, Santo Domingo, Seymour Formation, Shelter, Slaton, Trinity River). De nombreuses données numériques brutes ou élaborées statistiquement figurent dans les tableaux.

Il n'y a aucune preuve de l'existence d'hémiones de l'Ancien Monde dans le Nouveau ni de la présence d'équidés "stilt-legged" du Nouveau Monde dans l'Ancien. Ces derniers semblent apparaître au Blancan final (Santo Domingo, Nouveau Mexique) et sont probablement à l'origine d'*E. calobatus* (Arkalon, Rock Creek) et du plus petit *E. semiplicatus* (Channing, Rock Creek). Les espèces sveltes mais non "stilt-legged" trouvées à Natural Trap, Wyoming, il y a environ 12 ky appartiennent à *Amerhippus*. Toutes ces espèces présentent néanmoins des caractères particuliers sur les dents jugales inférieures observés aussi chez les Sussemiones (et certains hémiones) de l'Ancien Monde.

L'*Equus* sp. B svelte de Leisey Pit A, Floride, vieux d'environ 1.2 Ma, *Amerhippus francisci* et *E. tau* (probablement synonyme d'*E. quinni*) ont une même morphologie des dents jugales inférieures mais les crânes d'*A. francisci* et d'*E. tau*, sont très différents.

Les données paléontologiques suggèrent une origine commune pour les Sussemiones, *Amerhippus* et les équidés "stilt-legged" d'Amérique du Nord vers la fin du Blancan. Les hémiones de l'Ancien Monde apparaissent plus tard.

ABSTRACT

Morphological and biometrical description of skulls, teeth, and limb bones of extant and fossil Old World hemiones (including *E. hydruntinus*) and of New World 'stilt-legged' and other slender species from Blancan to Holocene. An Appendix presents ways in which the approximate size of some missing bones or dimensions may be deduced from available ones.

The discussed and/or illustrated fossils were found in Bolivia (Tarija), Canada (Yukon), China (Choukoutien, Gulongshan, Jiling, Loufangzi), Ecuador (Oil Fields), Ethiopia (Melka Kunturé), France (Lunel-Viel), Germany (Süssenborn), Greece (Agios Georgios, Petralona), Hungary (Dorog), Italy (Romanelli), Mexico (Cedazo, San Josecito), Mongolia (Sjara-osso-gol), Spain (Venta Micena), ex-Soviet Union (Akhalkalaki, Binagady, Chokurcha, Chukochya, Kabazi, Kolyma, Krestovka, Kurtak, Staroselie, Tologoj), USA (Alaska, Arkalon, Cedar Meadow, Channing, Conkling, Dry Mountains, Hay Springs, Leisey Shell Pit A, Lissie Formation, Natural Trap, Pool Branch, Powers Ranch, Rock Creek, San Diego, Santo Domingo, Seymour Formation, Shelter, Slaton, Trinity River). Numerous raw or statistically elaborated data are given in Tables.

There is no evidence for the existence of Old World hemiones in the New World nor of 'stilt-legged' equids in the Old World. The first 'stilt-legged' equid was found at Santo Domingo, New Mexico, and is believed to be Late Blancan. It was probably at the origin of *E. calobatus* (Arkalon, Rock Creek) and of the smaller *E. semiplicatus* (Channing, Rock Creek). Slender, but not 'stilt-legged', equids found at Natural Trap, Wyoming, ca. 12 ky ago belong to *Amerhippus*. All these species share with Old World Sussemiones (and some hemiones) peculiar patterns on the lower cheek teeth.

The slender *Equus* sp. B of Leisey Pit A, Florida, ca. 1.2 Ma, as well as *Amerhippus francisci* and *E. tau* (probably a senior synonym of *E. quinni*) share conventional lower cheek teeth patterns. The skulls of *A. francisci* and *E. tau*, however, are quite different.

Paleontological data suggest a common origin of *Amerhippus*, Sussemiones, and 'stilt-legged' equids during the late Blancan. Old World hemiones seem to have differentiated later.

INTRODUCTION

Paleontological and biomolecular data agree on a clear separation between caballines and the rest of extant *Equus*. According to molecular biology, this separation was quite old (about 2Ma ago); paleontology does not support such a date since the oldest known caballines are only about 0.7 My old (Eisenmann 2006b).

According to both paleontology and molecular biology, the extant hemiones of the Old World were the next group to branch off the common stem, possibly about 1Ma ago (Oakenfull et al. 2000; Eisenmann 2006b). Given the general history of equids, the emergence of hemiones may, at least as a working hypothesis, be sought in North America.

The purpose of this paper is to bring together the information now available to us on what were the Old and New World hemiones and hemione-like forms, and to what extent they may have been related. We give as many photographs and diagrams as possible in order to show, rather than describe, what we have observed. The quality of our photographs and reproductions of photographs is often poor but we trust that they provide enough information to atone for their defects.

We will begin by the Old World extant forms in order to give a good basis for the subsequent comparisons with fossils of the Old and New Worlds. Because of the too frequent lack of association between fossil skulls, teeth, and limb bones, a certain amount of guessing about what fits with what is necessary. To justify our guesses we have used scatter diagrams comparing various bone measurements in extant species of *Equus* for which associations are certain. They will be found in the Appendix.

Abbreviations for collections:

AC, MA: Laboratoire d'Anatomie Comparée, des Mammifères et Oiseaux du MNHN, Paris, France.

AMNH, FAM: American Museum of Natural History, New York, USA.

BEG: Bureau of Economic Geology, University of Texas.

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

FC: Fauna Cedazo, Mooser private collection, Mexico.

FM, PM: Field Museum, Chicago, USA.

IA: Geological Institute, Iakutsk, Russia.

IGM: Instituto Geologico, Mexico.

IVPP: Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China.

KU: Kansas University, USA.

LACM: County Museum, Los Angeles, USA.

MGU: Zoological Museum of the Moscow University, Moscow, Russia.

NMC: National Museums, Ottawa, Canada.

PA: Laboratoire de Paléontologie du Muséum national d'Histoire naturelle du MNHN, Paris, France.

PIN: Paleontological Institute, Moscow, Russia.

PMYU: Paleontological Museum of Yale University, USA.

RGU: University of Rostov Museum, Russia.

S: Süssenborn, Forschungsstation für Quartärpaläontologie, Weimar, Germany.

SI: Severtsov Institute, Moscow, Russia.

SMUMP: Southern Methodist University Museum of Paleontology, USA.

TAMU: Texas Agricultural and Mechanical University, USA.

TB: Tbilisi, Georgia.

TMM: Texas Memorial Museum, USA.

UCMP: University of California Paleontological Museum, Berkeley, USA.

UF: University of Florida, Gainesville, USA.

UMMP: University of Michigan, Paleontological Museum, Ann Arbor, USA.

UNSM: University of Nebraska State Museum, Lincoln, USA.

USNM: Smithsonian Institution, Washington, USA.

VM: Venta Micena, Institut "Miguel Crusafont", Sabadell, Spain.

ZIN: Zoological Institute, St Petersburg, Russia.

Abbreviations used in tables for data origin:

AA: Azzaroli 1998

AA & MV: Azzaroli & Voorhies 1993

AH: Arthur Harris, pers. comm.

BS et al.: Slaughter et al. 1962

CH: Hibbard 1953

CH 1955: Hibbard 1955

CH & DT: Hibbard & Taylor 1960

EL & MS: Lundelius & Stevens 1970

GM: Gabriella Mangano, pers. comm.

HO: Osborn 1929

JH: John Howe

JQ: Quinn 1957

MS: Skinner 1942

CH & DT: Hibbard & Taylor 1960
EL & MS: Lundelius & Stevens 1970
GM: Gabriella Mangano, pers. comm.
HO: Osborn 1929
JH: John Howe
JQ: Quinn 1957
MS: Skinner 1942
MW: Melissa Winans 1985
OH: Hay 1915
OM & WD: Mooser & Dalquest 1975
RH: Hulbert 1995
VE: V. Eisenmann
WD: Dalquest 1967
WD & JH: Dalquest & Hughes 1965
ZX et al.: Zhou et al. 1990

EXTANT AND RECENTLY EXTINCT HEMIONES

I. *EQUUS HEMIONUS*

The geographic distribution of the hemione specific group extends, or recently extended, from China to Syria (Denzau & Denzau 1999; Eisenmann & Mashkour 2000; Schreiber et al. 2000). The smallest subspecies was the hemippe, *E. hemionus hemippus* of Syria (HS for short); it disappeared in the second half of the 19th century. The largest subspecies or species is the kiang, inhabiting Tibet (K for short). The other subspecies are the dgzigtaj, *E. hemionus hemionus* of Mongolia (HM), the kulan, *E. hemionus kulan* of Turkmenistan (HT), the khur, *E. hemionus khur* of India (HI), and the onager, *E. hemionus onager* of Iran (HP). Detailed data on cheek teeth and limb bones were published by Eisenmann & Mashkour (2000). HO stands for specimens without certain geographical provenance.

In spite of size differences between the small hemippe and the other, quite larger hemiones, the resemblances between extant hemione skulls is evident (Fig. 1).

The limb bones and their proportions are also similar (Fig. 2 left).

But the variability of cheek teeth is very large. On the upper cheek teeth (Fig. 3), the protocone length and shape may be quite different, even inside the same subspecies: short or long (Figs. 3-1 and 2); lingually convex (Fig. 3-1) or concave (Fig. 3-3). The pli caballin is rare but may occur (P4/ on Fig. 3-4). The most constant character seems to be the depth of the post-protocone valley, but it may not be expressed (M1/ on Fig. 3-1, P3/ on Fig. 3-4).

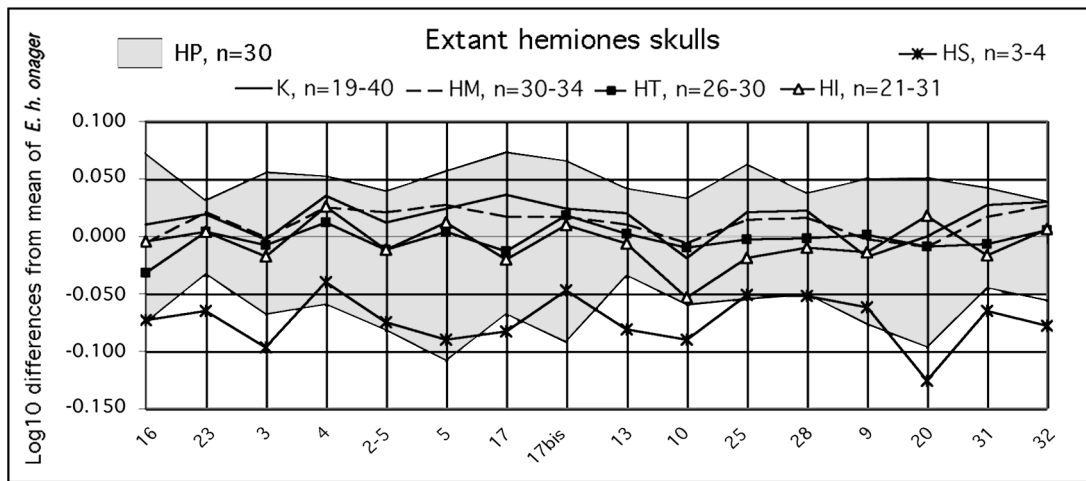


Figure 1.— Ratio diagrams of extant hemione skulls. Measurements (16-32) are described in Table 1. Subspecies abbreviations (HP-HS) are explained in the text.

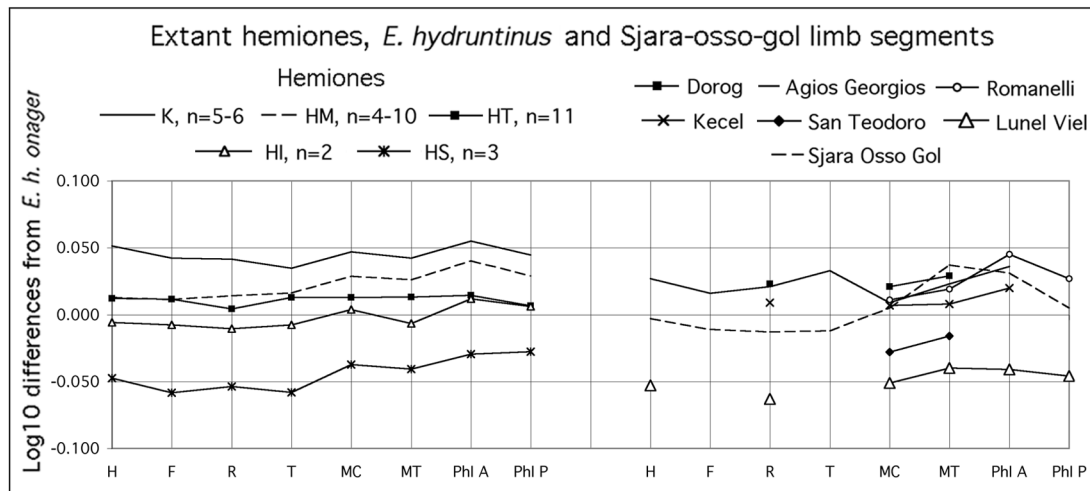


Figure 2.— Ratio diagrams of limb bones length: humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT), anterior first phalanx (Ph I A), posterior first phalanx (Ph I P). Measurements in Table 2. Subspecies abbreviations (HP-HS) explained in the text.

On the lower cheek teeth (Fig. 4), the vestibular groove can be pointed just like in an ass (Fig. 4-1), or caballoid (P/4 on Fig. 4-2); it may also exhibit the kind of "bridge" described in wild asses by Groves, 1966 (Fig. 4-3). The metastylid may be rounded (Fig. 4-1) or pointed (Figs. 4-5, 6). Usually the ectoflexid is shallow even in molars, but it may penetrate the isthmus of the double knot (M/1 on Fig. 4-2). A shallow linguaflexid (P/3 and P/4 of Figs. 4-4 and 5), although far from constant is the only character that is not frequently found in other extant *Equus*.

The lower incisors always have cups (Eisenmann 1979).

Limb bones are always slender but there are some differences not only in size but also in proportions (Fig. 5). The slenderest (3 relative to 1) MC III are those of the

hemippe (HS); kiangs (K) are distally wider at the supra-articular tuberosities (10).

The same features are observed on the MT III. Moreover, hemippes have flatter diaphyses (4). The samples are very poor, however, and we are still unable to give a good graph for khur metapodials.

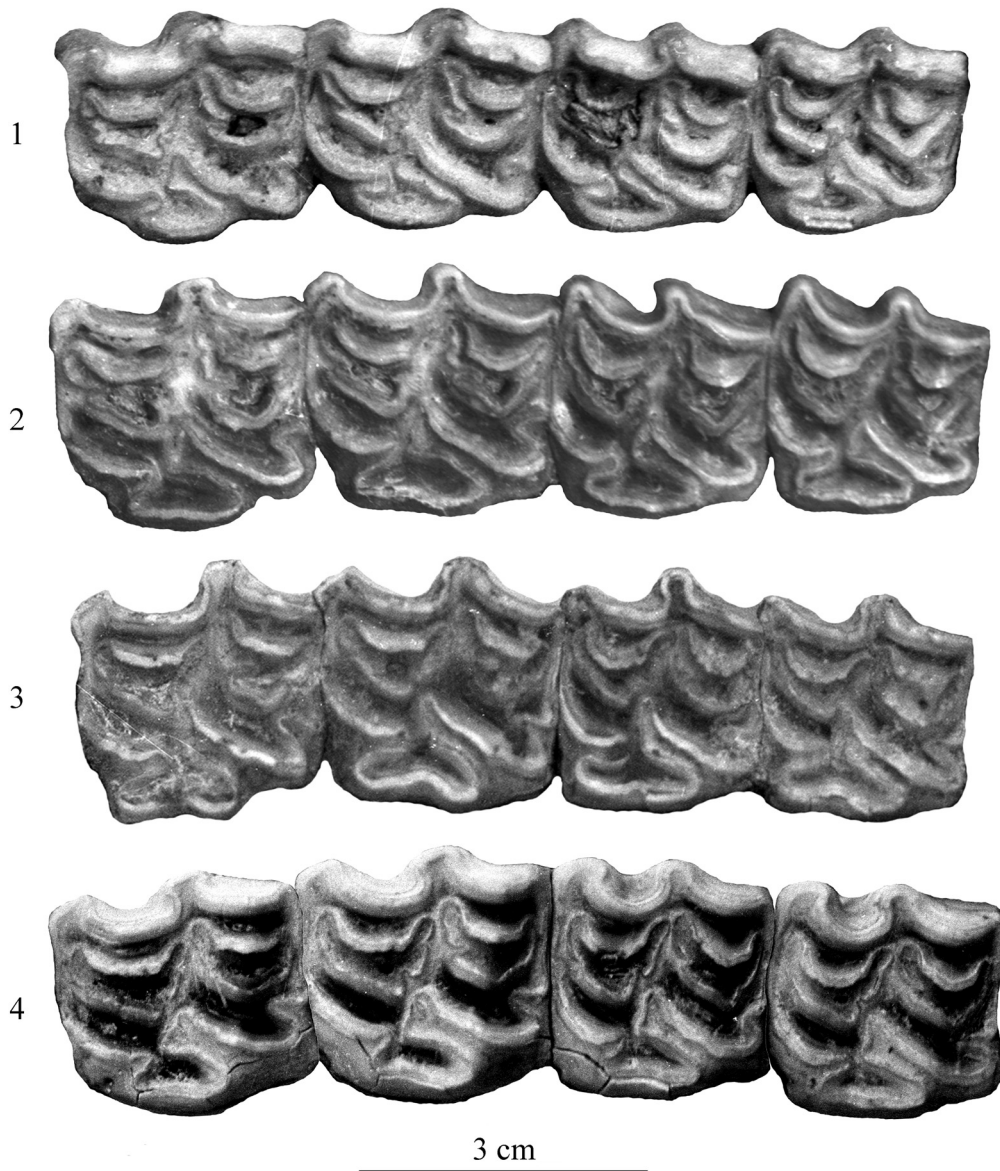


Figure 3.— Occlusal views of upper P3-M2 of some extant hemionids. 1: *E. h. khur*, BM 1940-358. 2: *E. h. khur*, BM 1946-594. 3: *E. h. kulan*, MGU 74787. 4: *E. kiang*, MGU 151314.

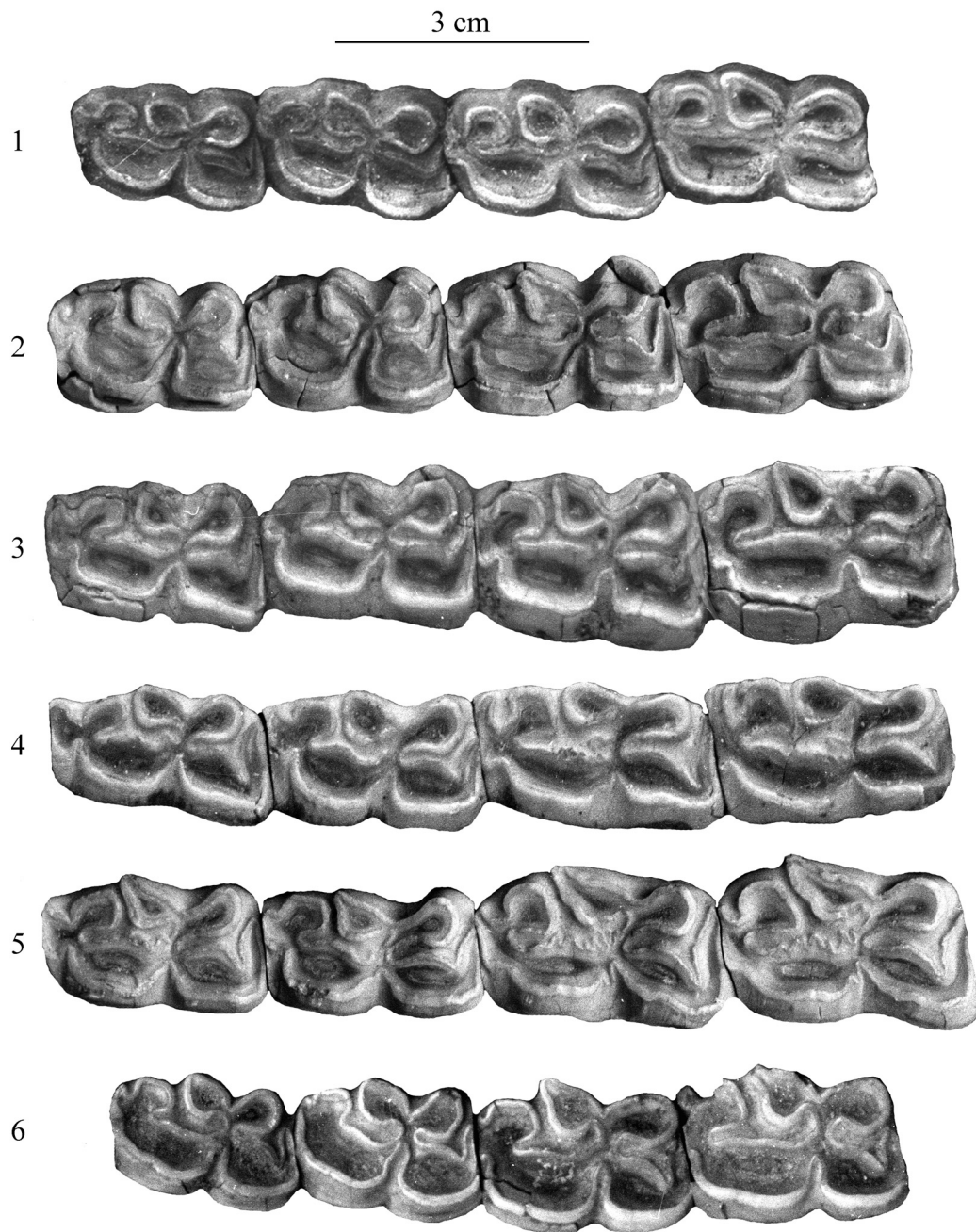


Figure 4.— Occlusal views of lower P3-M2 of some extant hemionos. 1: *E. h. khur*, BM 1940-358. 2: *E. h. hemionus*, AMNH 57201. 3: *E. h. hemionus*, MGU 43233. 4: *E. h. hemionus*, MGU 100535. 5: *E. h.* no origin, AMNH 60345. 6: *E. h. kulan*, MGU 74802.

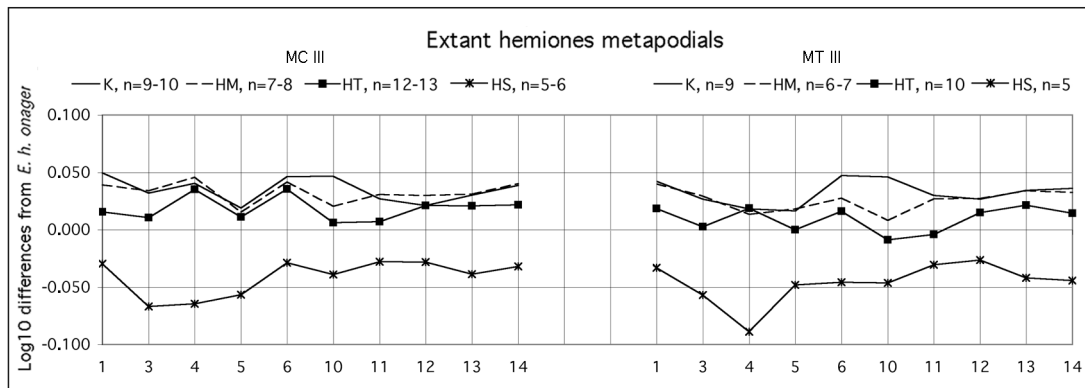


Figure 5.— Ratio diagrams of extant hemionid third metacarpals (MC III) and metatarsals (MT III). Measurements (1-14) explained in Tables 3-4. Data in Eisenmann & Mashkour (2000).

II. *EQUUS HYDRUNTINUS*

We know now that the recently extinct *E. hydruntinus* is closely related to extant hemionids (Orlando et al. 2006) but distinct (Burke et al. 2003), differing from them mostly by the skull and by the cheek teeth (Eisenmann & Mashkour 1999). The oldest *E. hydruntinus* was found at Lunel-Viel France (Bonifay 1991), and is believed to be ca 300 Ka. *E. hydruntinus* survived in the Holocene and may perhaps even been present at historical times in Portugal (Antunes 2006). The best preserved skull from the Late Pleistocene of Crimea (Fig. 6) is remarkable by its wide muzzle (17, 17bis) and by its very short naso-incisival notch (31).

Most characteristic of *E. hydruntinus* are the short protocones of the upper cheek teeth and the deep ectoflexids of the lower molars (Fig. 7).

Another characteristic is the microdonta (Fig. 8). Compared to the length of metapodials (Mc1 and Mt1), the dimensions of P3/-P4/ (Psize) and of M1/-M2/ (Msize) are small except in the oldest form of Lunel-Viel. The small size of the protocones (Pprot. and Mprot.) is also well illustrated on Fig. 8.

Samples are at all times very poor, so that the limb segments proportions are somewhat uncertain. It seems, however, that the MT III of *E. hydruntinus* are longer relative to the MC III than in extant hemionids as shown by the ratio diagram (Fig. 2 right) and the scatter diagram (Fig. 9). The Sjara-osso-gol material will be discussed later.

There were certainly several subspecies of *E. hydruntinus* (Fig. 10). The best represented are the smallest (and probably the oldest) *E. hydruntinus minor* of Lunel Viel (Bonifay 1991), one of the largest - *E. hydruntinus petralonensis* (Tsoukala 1991), and the type *E. hydruntinus hydruntinus* of Romanelli (Stehlin & Graziosi 1935).

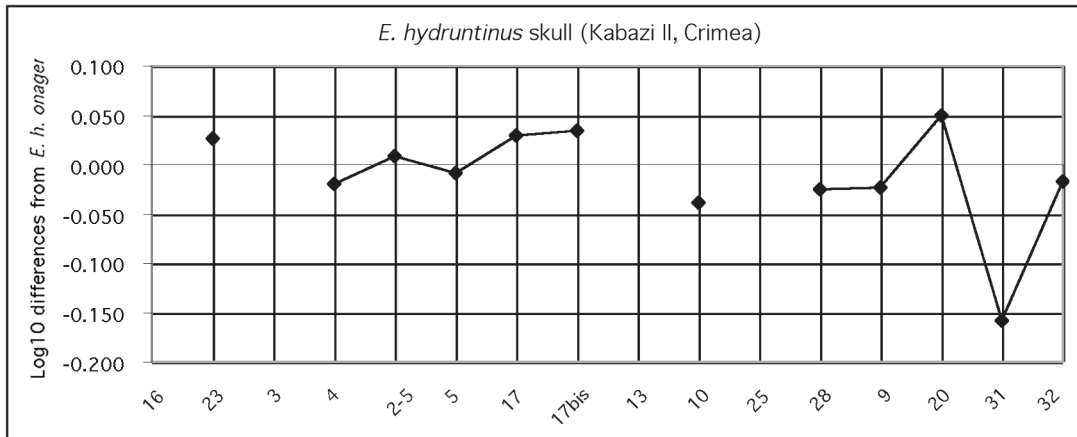


Figure 6.— Ratio diagrams of Kabazi *E. hydruntinus* skull. Measurements in Table 1.

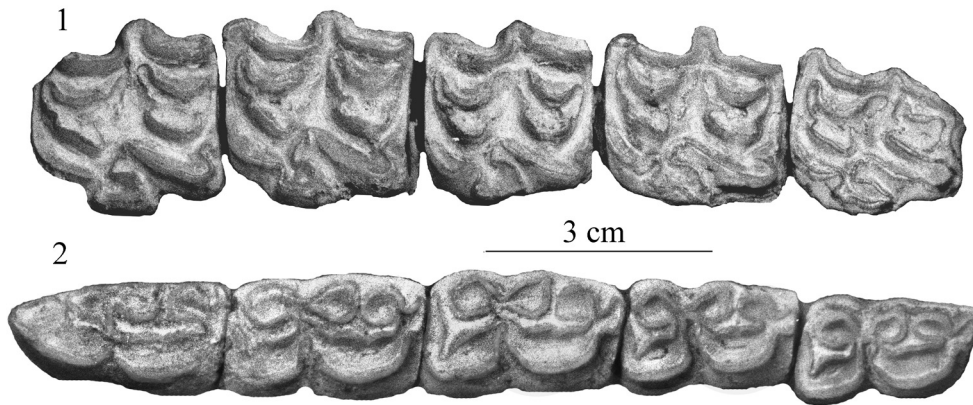


Figure 7.— Upper (1) and lower (2) cheek teeth of *E. hydruntinus* (Agios Georgios, SGK 76 and 574, University of Thessaloniki, Laboratory of Geology and Palaeontology).

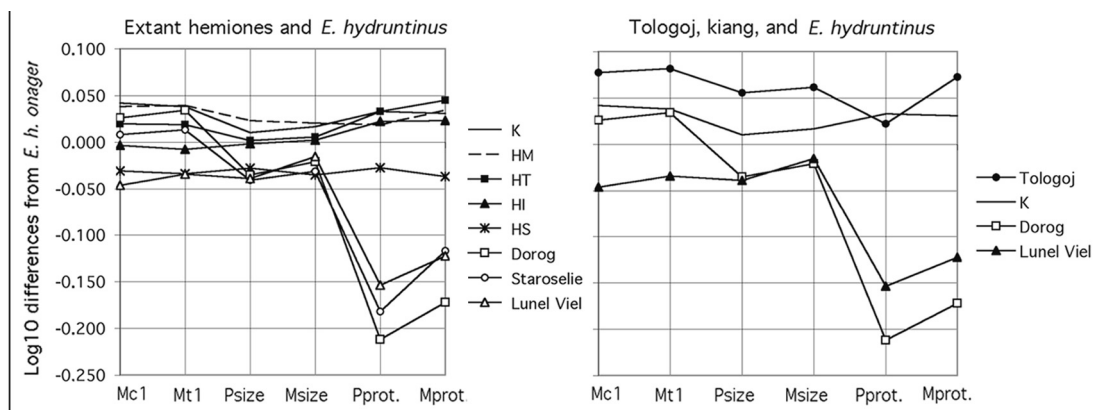


Figure 8.— Ratio diagrams comparing length of third metacarpals (Mc1) and metatarsals (Mt1), size of upper premolars (P) and molars (M), and protocone length of upper premolars (Pprot.) and molars (Mprot.) in extant hemionees (K, HM, HT, HI, HS; data in Eisenmann & Mashkour 2000), fossil hemione (Tologoj), and *E. hydruntinus* (Dorog, Staroselie, Lunel-Viel).

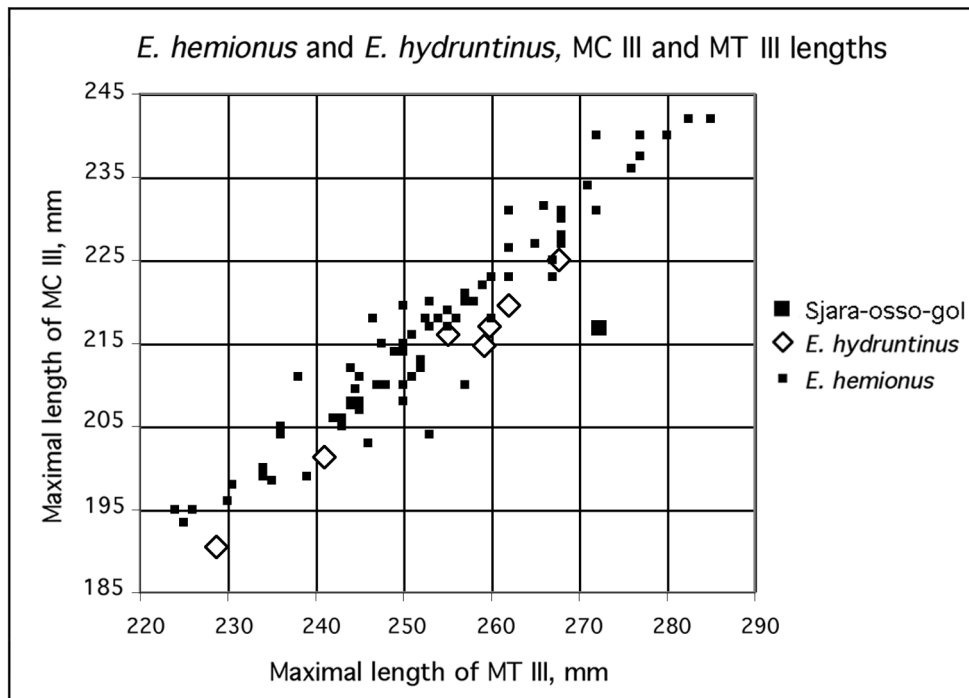


Figure 9.— Scatter diagram of third metatarsal (MT III) and metacarpals (MC III) lengths in extant hemionines and *E. hydruntinus*.

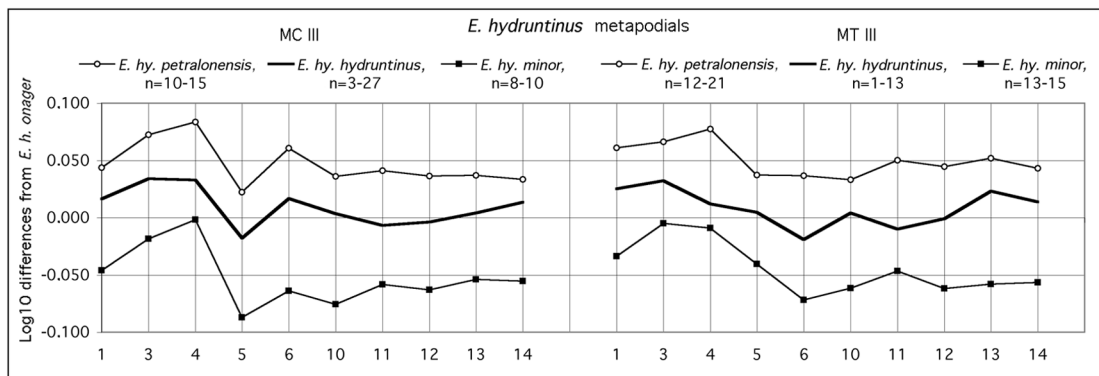


Figure 10.— Ratio diagrams of *E. hydruntinus* third metacarpals (MC III) and metatarsals (MT III). Measurements in Tables 3-4. n=number of specimens.

The size of MC and MT III is similar in *E. hydruntinus* and extant hemionines. But on the average, the MC III and MT III of *E. hydruntinus* (Fig. 11 left) are more robust 3 relative to 1) than in hemionines, and deeper in the diaphysis (4). Data in Eisenmann & Maskour 2000 and in Tables 3-4.

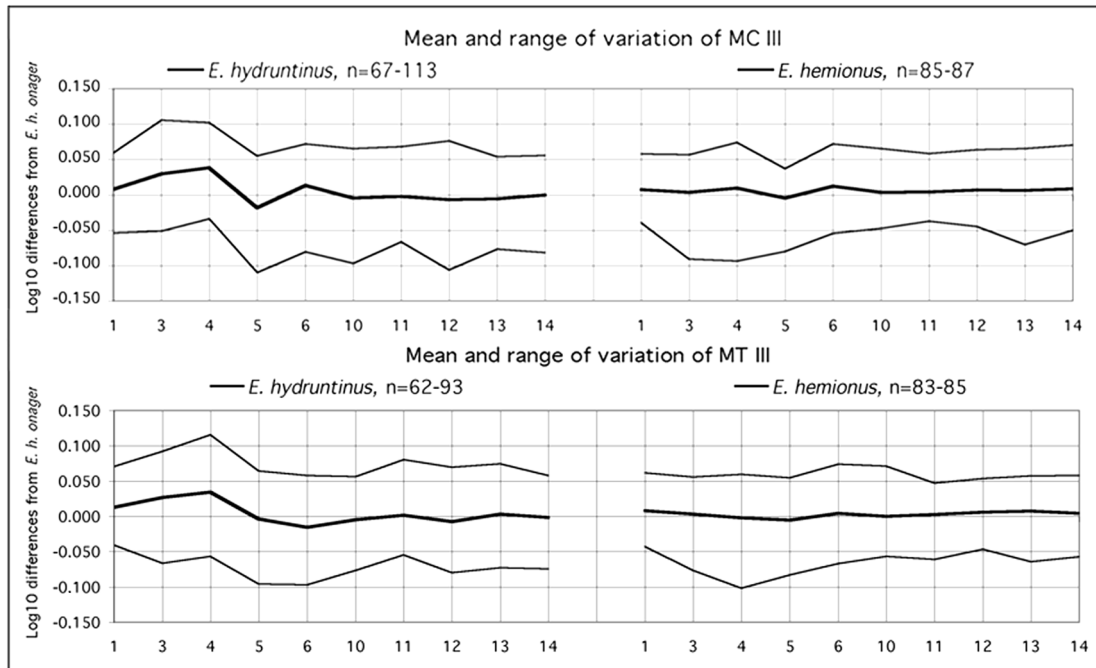


Figure 11.— Ratio diagrams comparing *E. hydruntinus* and *E. hemionus* third metacarpals (MC III) and metatarsals (MT III). Measurements in Tables 3-4. n=number of specimens.

III. OTHER OLD WORLD FOSSIL HEMIONES

According to the genetic studies of Oakenfull et al. (2000), the first hemiones of the Old World differentiated about 1 Ma. Some fossils, possibly slightly younger, were found in Transbaikalia (Vogt et al. 1995).

1. Tologoj, Transbaikalia

On the upper cheek teeth the protocones are rather small; the lower cheek teeth resemble extant hemiones: shallow linguaflexid on P/3, elongated metaconids (Fig. 12).

Although much larger, the third metapodials of Tologoj resemble more in their proportions *E. hydruntinus* than extant hemiones (Fig. 13).

But unlike recent *E. hydruntinus*, there is no microdontology and the protocones are not as small as in *E. hydruntinus* (Fig. 8).

Thus, the hemione of Tologoj seems somehow intermediate between *E. hydruntinus* and the extant hemiones.

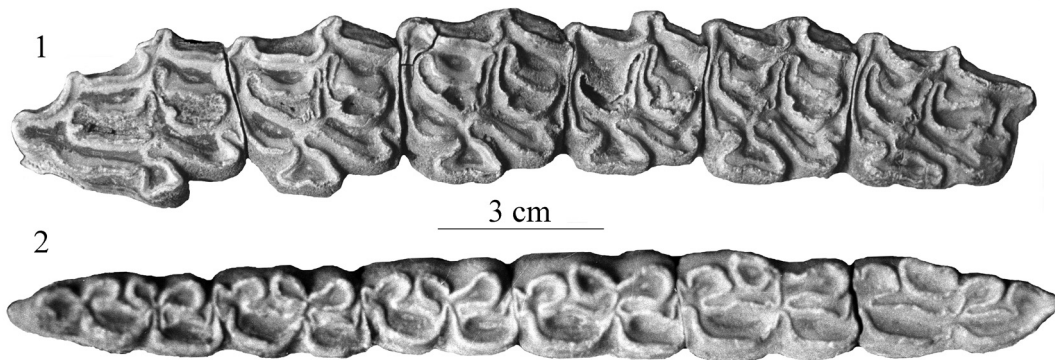


Figure 12. — Upper (PIN 729) and lower cheek teeth (PIN 2193) of Tologoj.

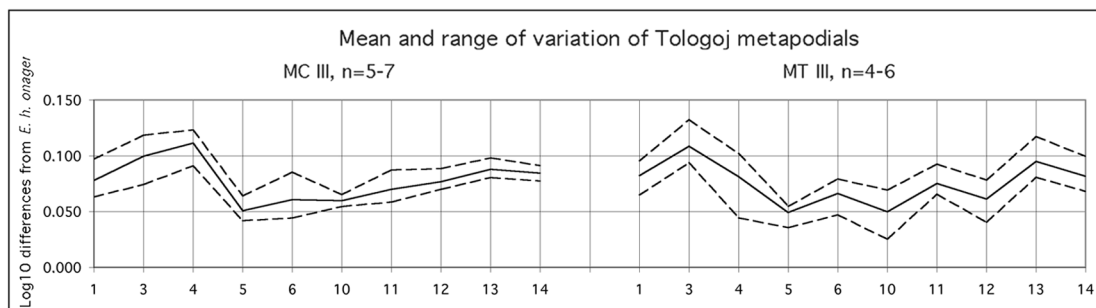


Figure 13. — Ratio diagrams of Tologoj third metacarpals (MC III) and metatarsals (MT III). Measurements in Tables 3-4. n = number of specimens.

2. Binagady, Azerbaidjan

A new subspecies of hemione, *Equus hemionus binagadensis*, was described by Eisenmann and Mashkour (1999) from the final Riss or the Riss-Würm of Binagady, near Baku. There are several well preserved fragments of adult skulls and mandibles and one juvenile (about one year old) skull. We have not seen the juvenile skull but Gadjev (1953) gave some dimensions which enable us to guess their probable adult size (following the technique described in Eisenmann and Geraads (2007).

The skull is small, the muzzle is very short, and the distance between Basion and posterior border of vomer is longer than usual in extant hemiones (Figs.14- 15). The skull is certainly different both from *E. hemionus* (Fig. 1) and *E. hydruntinus* (Fig. 6). Actually, it may even belong to a true species, rather than only a subspecies of hemione. The skull from Jiling will be discussed later.

The upper cheek teeth vary in size and protocone length but all have deep postprotoconal valleys and no pli caballin (Fig. 16). Most lower cheek teeth resemble those of asses: deep linguaflexids and shallow ectoflexids (Fig. 16-5).

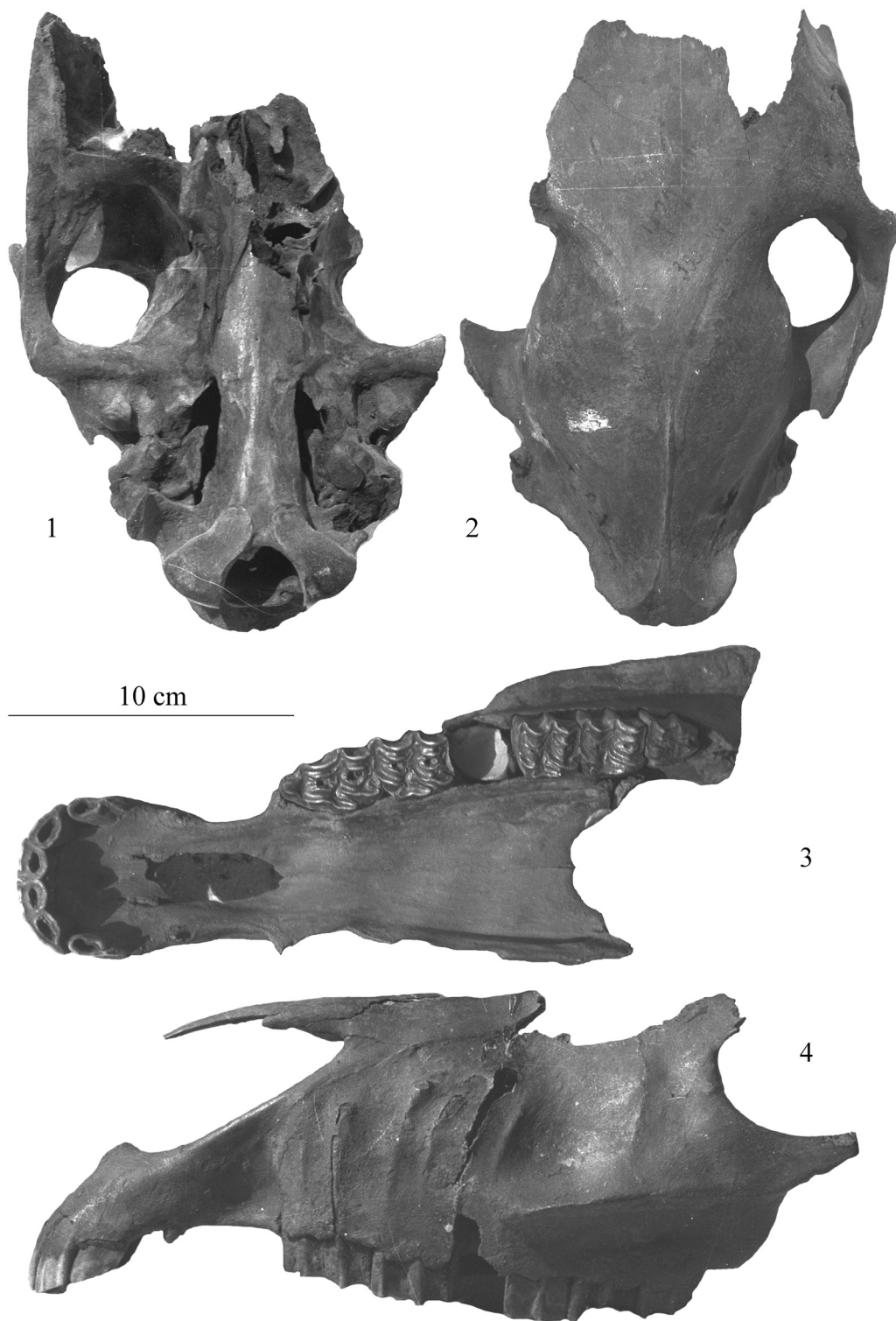


Figure 14.— *E. binagadensis* skulls. 1-2: PIN 395-446, ventral and dorsal views. 3-4: PIN 395-453 and 448, ventral view and profile.

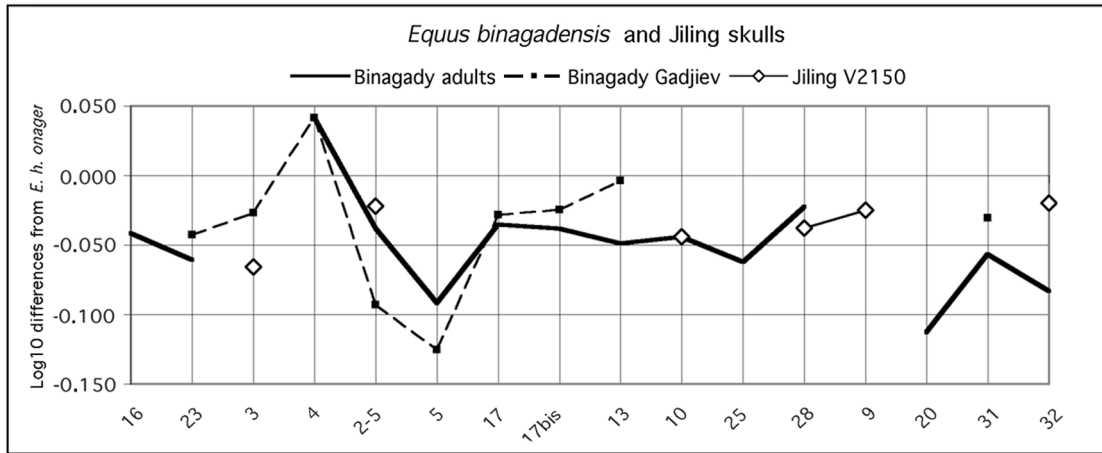


Figure 15.— Ratio diagrams of Binagady and Jiling skulls. Measurements in Table 1.

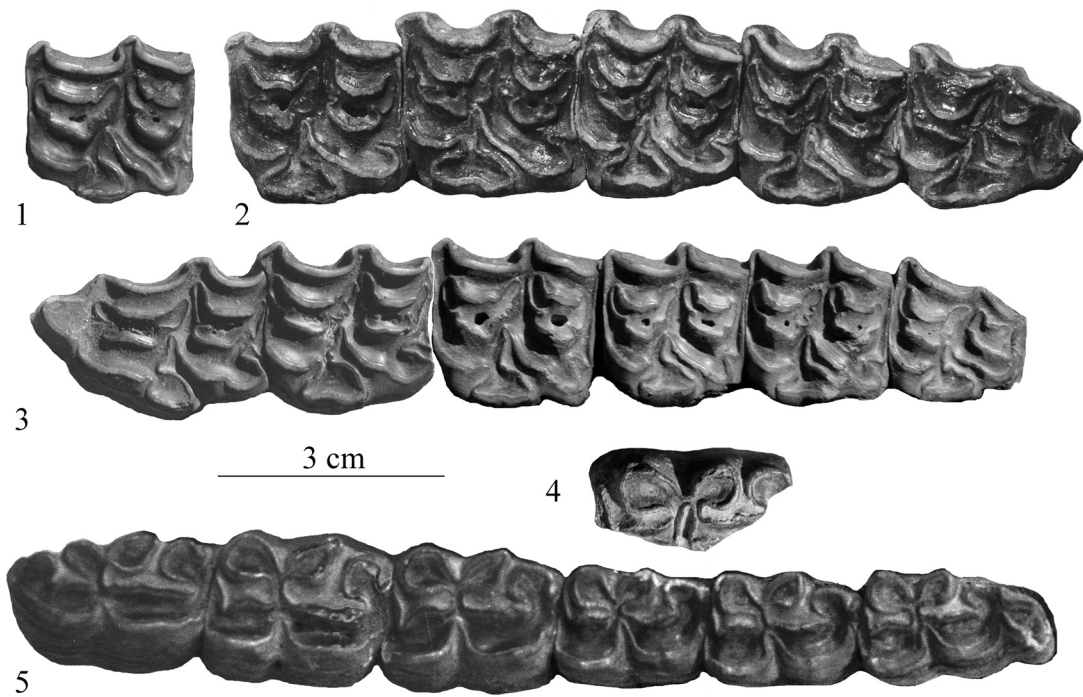


Figure 16.— *E. binagadensis* cheek teeth. 1: TB 222, upper P3 or P4. 2: TB 222', upper P3-M3. 3: PIN 395-454-2, upper P2-M3. 4: PIN 399-126, lower molar. 5: PIN 395-458, lower P2-M3.

One upper premolar (with a very short protocone (Fig. 16-1) and one lower molar with a deep ectoflexid (Fig. 16-4), as well as a few limb bones were tentatively referred to *E. hydruntinus*. It is, however, possible that they also belong to *E. binagadensis*.

The metapodials (Fig. 17) do not resemble extant hemiones (Fig. 5) or *E. hydruntinus* (Figs. 11-12).

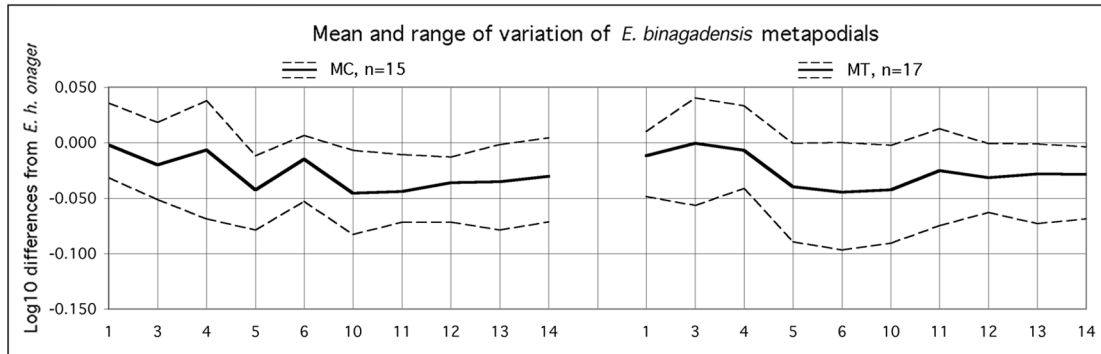


Figure 17.— Ratio diagrams of *E. binagadensis* third metacarpals (MC III) and metatarsals (MT III). Data in Tables 3-4 and Eisenmann & Mashkour (1999).

3. Kurtak, South-Central Siberia

Inside Late Pleistocene sediments of the North-Minusinsk Basin (Foronova 2006) were found hemione-like metapodials but no other bones or teeth. The MC III are very polymorphic. The MT III are extremely deep both in the diaphysis (4) and at the proximal end (Fig. 18).

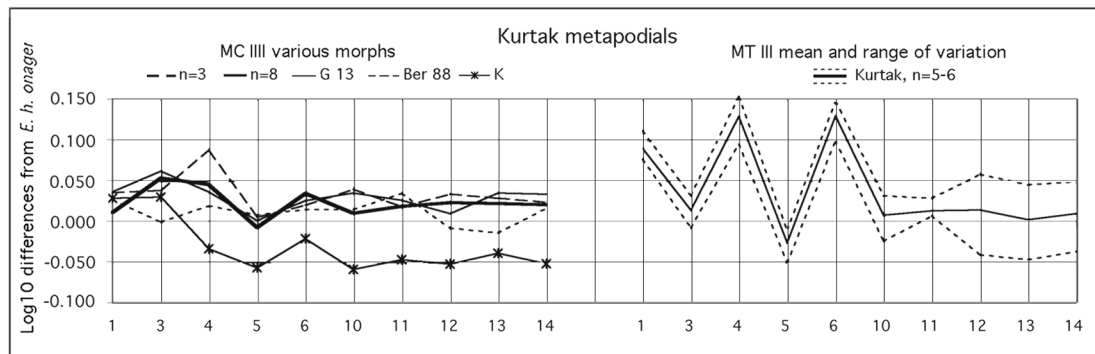


Figure 18.— Ratio diagrams of Kurtak third metacarpals (MC III) and metatarsals (MT III). Data in Tables 3-4.

4. Sjara-osso-gol, Ordos, Mongolia

Boule and Teilhard de Chardin (1928) described a subadult associated skeleton (mounted at the Museum of Paleontology in Paris), two other skulls, and some limb bones belonging to hemiones from the middle or late Paleolithic of Sjara-osso-gol. Unfortunately, the skulls are not well preserved and belong to juvenile or subadult

animals. The best skull (part of the mounted skeleton) is about the size of extant kiang and dziggetaj (Fig. 19).

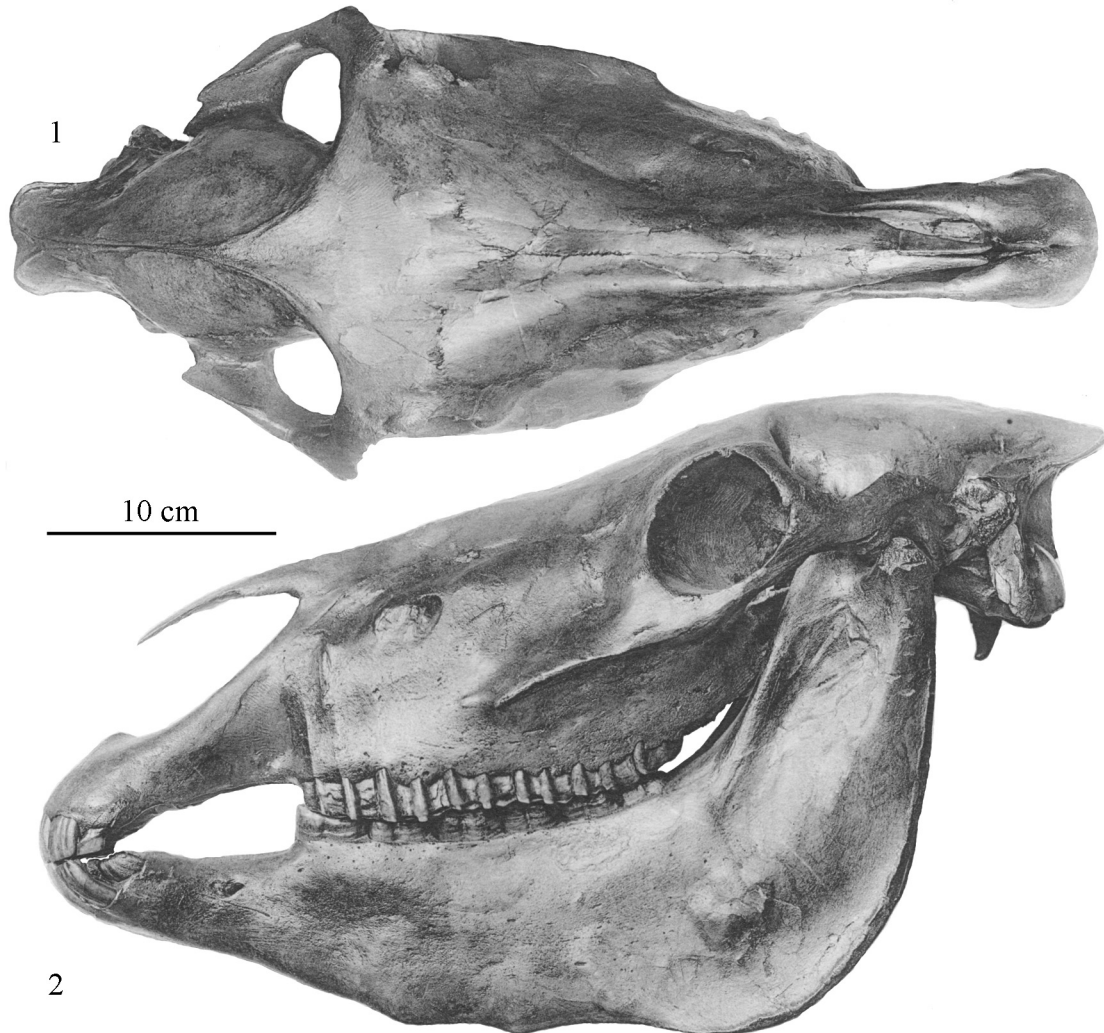


Figure 19.— Mounted skeleton skull from Sjara-osso-gol. Dorsal and profile views adapted from Boule & Teilhard 1928.

The upper and lower cheek teeth are typical of hemiones: pli caballin small or absent, deep post-protoconal valleys on the upper; elongated metaconids, very shallow linguaflexids and ectoflexids on the lower (Fig. 20).

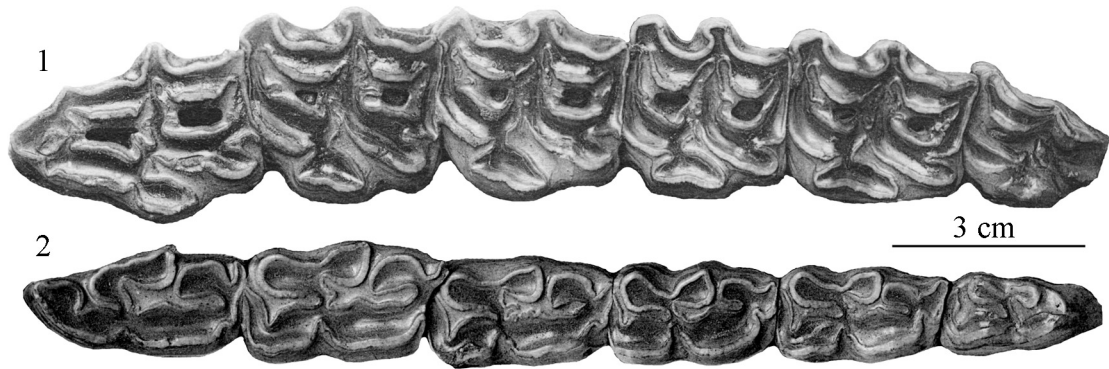


Figure 20.— Upper and lower cheek teeth from Sjava-osso-gol. Occlusal views adapted from Boule & Teilhard 1928.

There are some questions about the real association of the phalanges of the mounted skeleton. The major part of the material is unavailable for study. As much as may be guessed from the associated skeleton, the limb segment lengths (Figs. 9 and 10) present some resemblances with *E. hydruntinus*.

The MC III (Fig. 21) we were able to study are rather like those of *E. hydruntinus* (Fig. 11), but not the MT III which rather resemble those of Kurtak (Fig. 18).

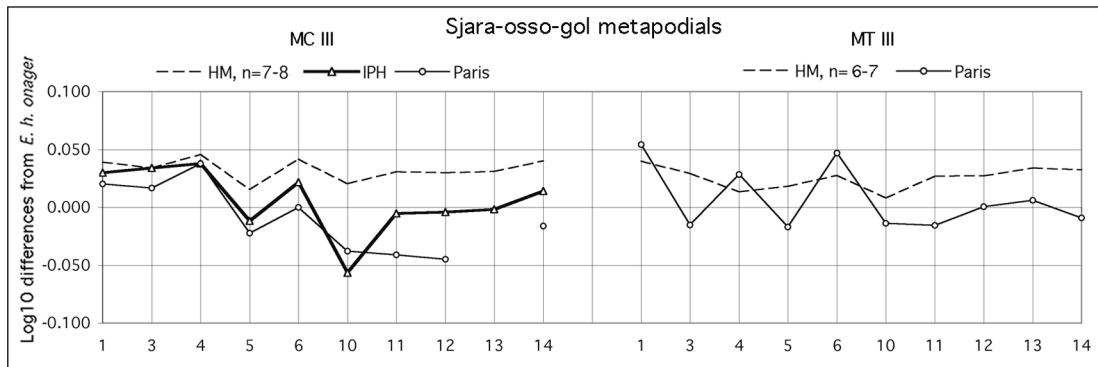


Figure 21.— Ratio diagrams of third metacarpals (MC III) and metatarsals (MT III) from Sjava-osso-gol compared to extant *E. h. hemionus* HM. Measurements in Tables 3-4. n=number of specimens.

5. Loufangzi, Huanxian, Gansu, China

Numerous teeth, mostly isolated, and a few limb bones (Deng & Xue 1999) are preserved in the Department of Geology of the Northwest University, Xi'An, Shaanxi, China. Even putting aside a few teeth of large size which may belong to a caballine, the variability is great. In some upper cheek teeth the post-protoconal valley is shallow (Fig. 22-2, 6), and a pli caballin may be present (Fig. 22-5). Protocones vary from very short (Fig. 22-7) to very long (Fig. 22-2, 10, 11). On the whole, the teeth illustrated in Fig. 22-2, 5, 6, 12 do not look hemione-like. One interpretation may be that the variability

does not only result from temporal heterogeneity but also from environmental stress: there are several teeth (as Fig. 22-1 and Fig. 23-4) showing hypoplasia on their crown.

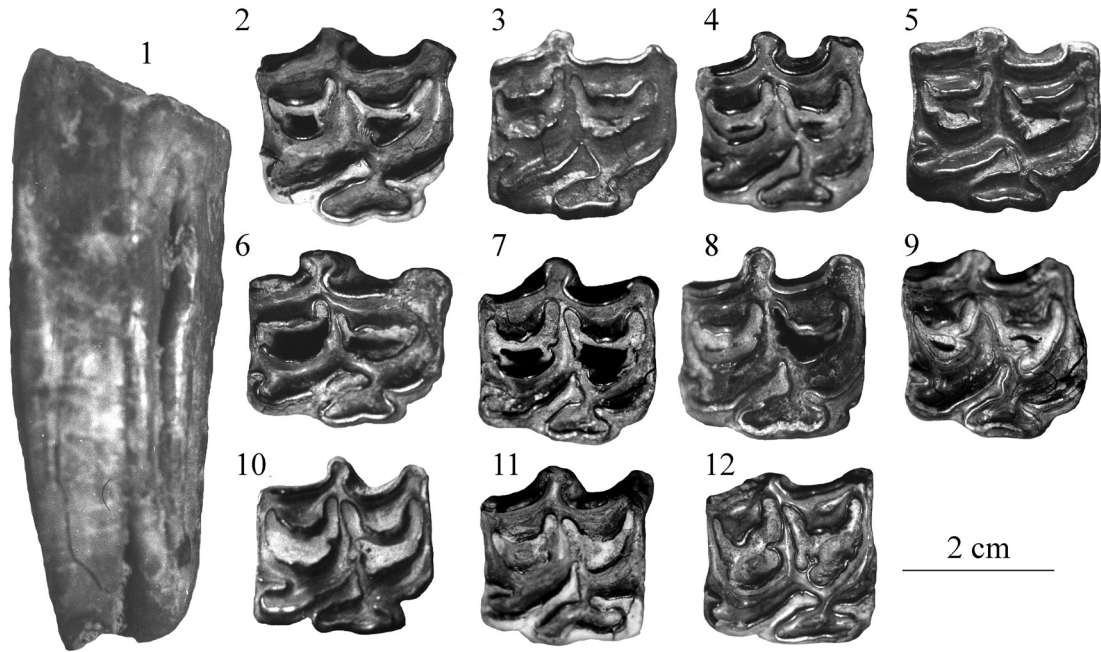


Figure 22.— Upper cheek teeth from Loufangzi. 1: P3 or P4, 840. 2:-P3 or P4, -87. 3: P3 or P4, 867. 4: P3 or P4, 824. 5: P3 or P4, 964. 6: P3 or P4, 804. 7: M1 or M2, 817. 8: M1 or M2, 816. 9: M1 or M2, 801. 10: M1 or M2, 819. 11: M1 or M2, M 63111. 12: M1 or M2, 818.

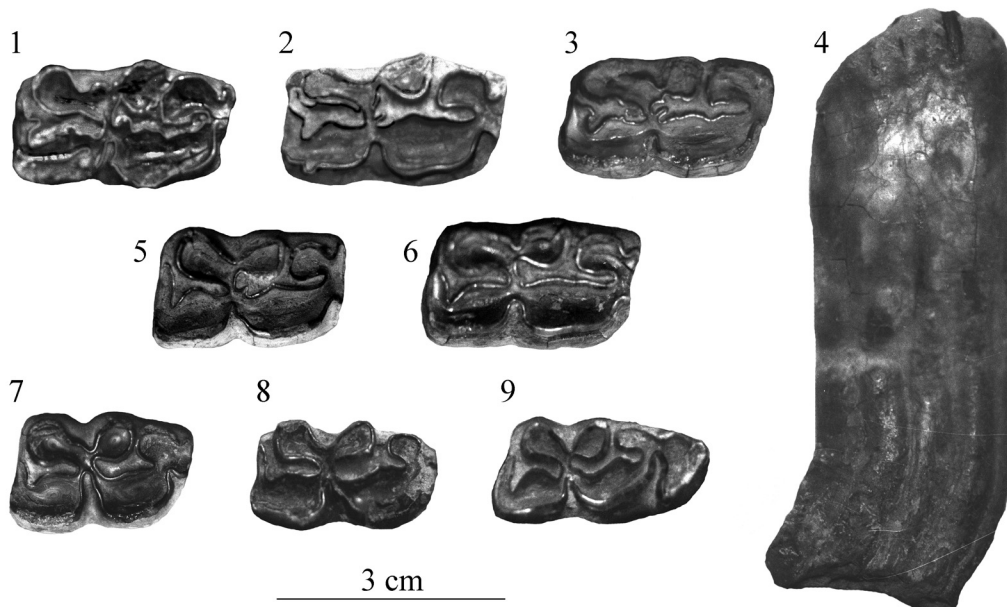


Figure 23.— Lower cheek teeth from Loufangzi. 1: P3 or P4, 9106. 2: P3 or P4, 9141. 3: P3 or P4, 9181. 4: M3, no number. 5: P3 or P4, 9145. 6: P3 or P4, 9147. 7: M1 or M2, 975. 8: M1 or M2, 8119. 9: M2, 8128.

The lower cheek teeth also vary in size (compare Fig. 23-1, 2, 3, 6 to 7) and in the shape of the double knot: shallow linguaflexid on Fig. 23-2, bridge on 1 and 3, pointed linguaflexid on 6 and 9.

Variation in size and shape appears also on the metapodials (Fig. 24).

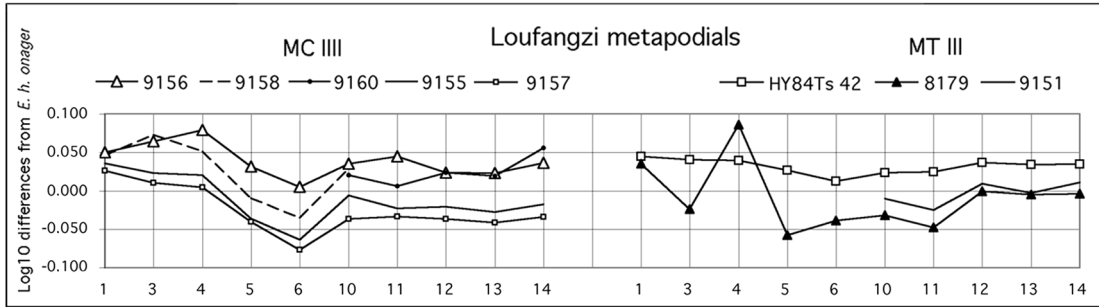


Figure 24.— Ratio diagrams of Loufangzi third metacarpals (MC III) and metatarsals (MT III). Data from Deng & Xue 1999.

6. Yushu, Jiling, China

A few hemione fossils, preserved at the Institute of Vertebrate Paleontology, Beijing, China, including a fragment of skull, V 2150 (Fig. 15 and 25). The skull and the dentition are small, quite smaller than those of *Sjara-osso-gol*. The profile is ram-nosed, unlike at *Sjara-osso-gol*. The muzzle was probably short and very wide.

The right and left upper premolars are quite different from each other (Fig. 26).

The single MT III (V 2179) is very large (Fig. 29 right) and cannot belong to the same form.

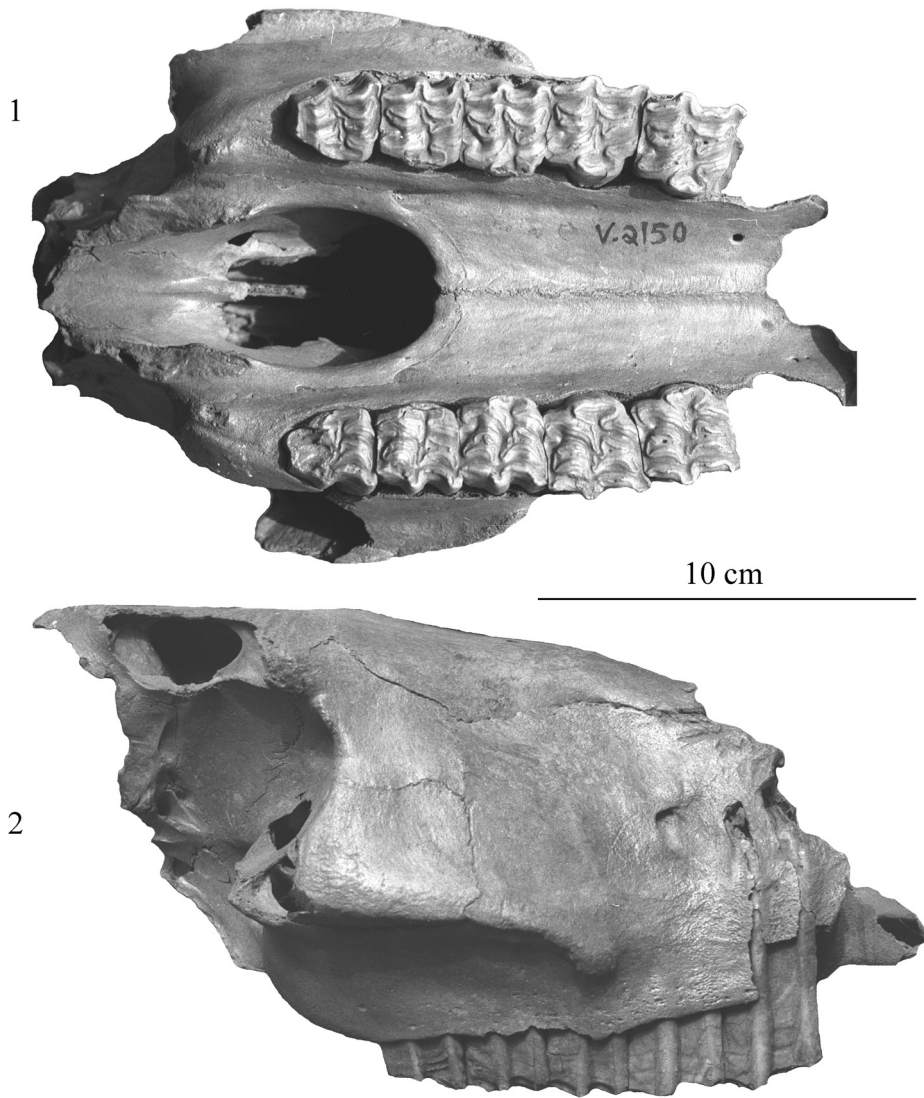


Figure 25.— Skull fragment V 2150 from Jiling. Occlusal (1) and profile (2) views. Data in Table 1.

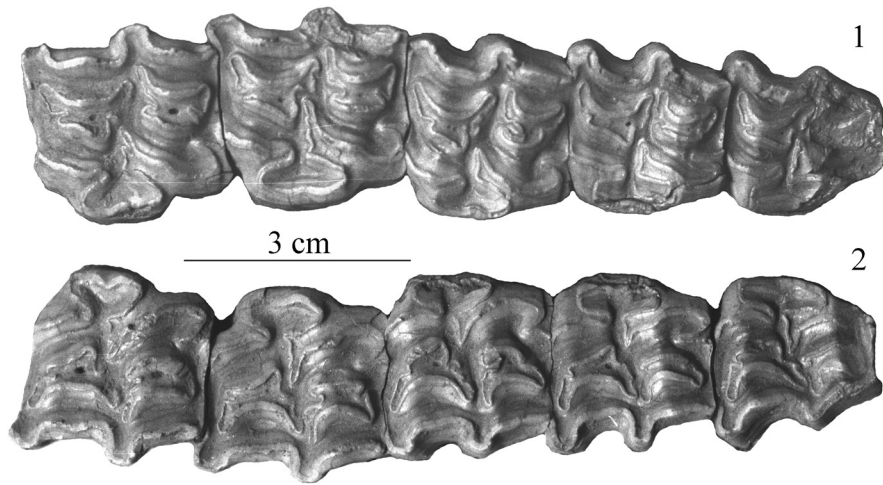


Figure 26.— Upper cheek teeth of V 2150, Jiling. 1: left. 2: right.

7. Gulongshan Cave, Dalian, China

From the Late Pleistocene of this cave, Zhou et al. (1990) published a discriminant analysis of the numerous metacarpals belonging to caballines and hemiones. Unfortunately they provided no data on the MT III.

The metacarpals are smaller than at Tologoj. They are rather similar to *E. hydruntinus* but larger (Fig. 27).

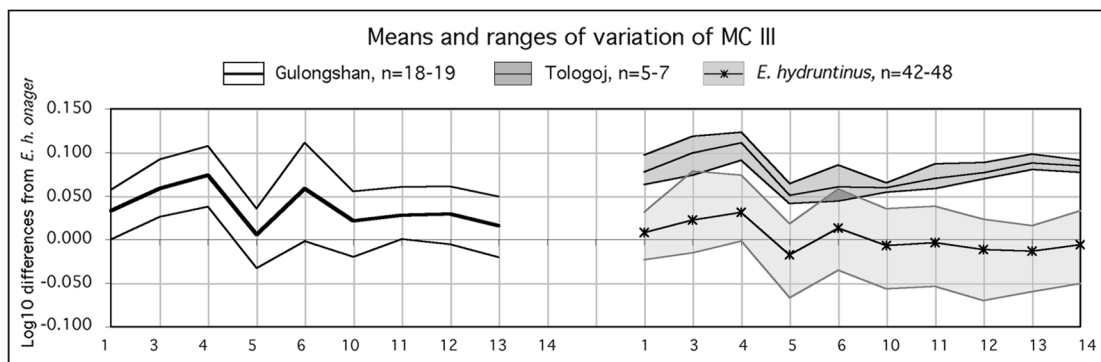


Figure 27.— Ratio diagrams of third metacarpals (MC III) of Gulongshan, Tologoj, and *E. hydruntinus*. Data Xuexin et al., and Tables 3-4.

8. Conclusion

Thus, to our present state of knowledge, the Old World group of hemiones comprises the extant species *E. hemionus* with various subspecies, the recently extinct *E. hydruntinus*, and the pre-Würmian *E. binagadensis*. *E. hydruntinus* differs from other hemiones by its microdonta and its small protocones. The skull of *E. hydruntinus* (Fig. 28) is characterized by its very short naso-incisival notch (31), and possibly by its

rather caballine Basion-vomer-palate proportions (3, 4). *E. binagadensis* seems also to have the same kind of proportions and a specially short and wide muzzle (5, 17, 17bis). The Sjara-osso-gol *Equus* belongs to *E. hemionus*. The status of Jiling skull is unclear, probably a local extinct small subspecies of *E. hemionus*.

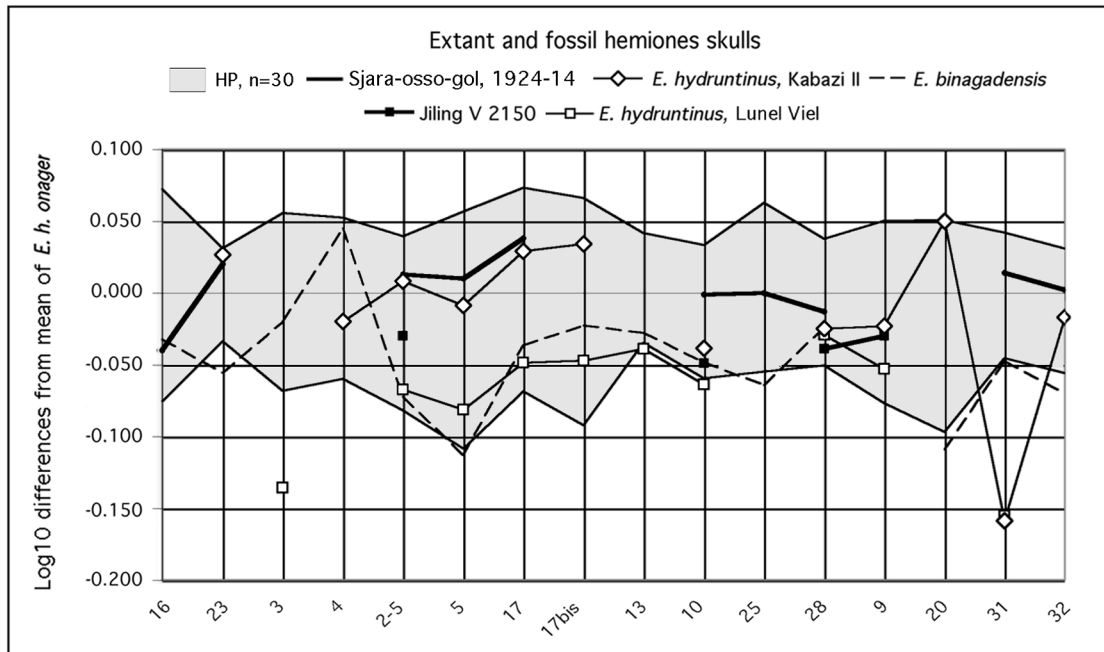


Figure 28.— Ratio diagrams of extant and fossil hemione skulls. Data in Table 1.

Almost all studied metapodials enter inside the range of variation of extant *E. hemionus* (Fig. 29). The most atypic are found in China (Jiling) and South Central Siberia (Kurtak).

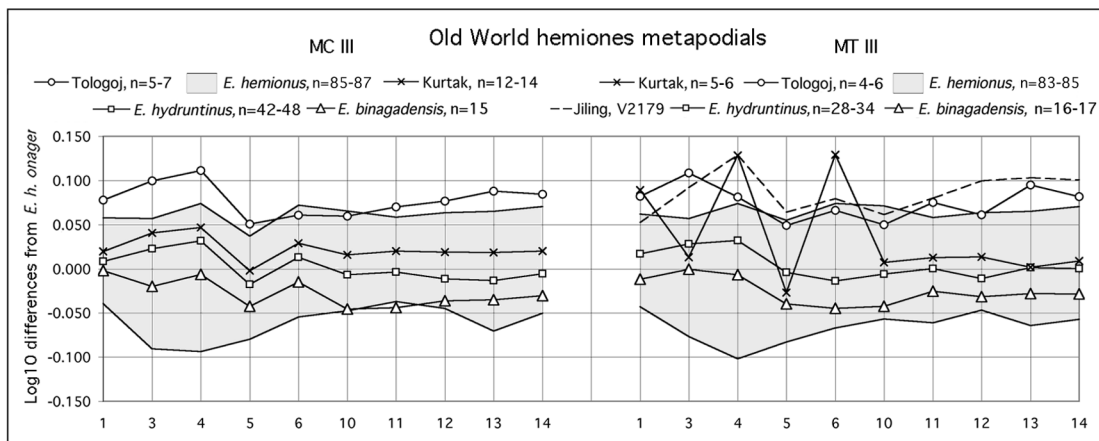


Figure 29.— Ratio diagrams of Old World hemione third metacarpals (MC III) and metatarsals (MT III). Measurements in Tables 3-4. n=number of specimens.

Altogether, the variability of Old World extant and fossil hemiones is not very large except in the cheek teeth patterns.

SUSSEMIONES

From around 1.5 to 0.5 Ma, a group of *Equus*, informally named "Sussemiones" (Eisenmann 2006b) is quite well represented in the Old World. It comprises robust as well as slender species. The slenderest (*E. granatensis* of Venta Micena, *E. hipparionoides* of Akhalkalaki) have small protocones like *E. hydruntinus*, but as the hemione of Tologoj they are not very microdont. Anyway, Sussemiones differ from other *Equus*, in particular hemiones and *E. hydruntinus*, by quite original cheek teeth enamel patterns.

On the lower cheek teeth the frequency of stylids, sometimes isolated, is remarkable. Plis protostylids occur on P/2 (Fig. 30-1) and may be very developed on P/3-M/2 (Fig. 30-2). True ectostylids may be present (Fig. 30-3) as well as very developed or even isolated hypostylids (Fig. 30-5). The shape of the double knot of many lower premolars resembles some extant hemiones, but in an extreme way (Fig. 30-4): the metaconid is elongated, sometimes bilobated, the lingual valley is at times nearly absent. Unlike extant hemiones, another particularity is the frequency of very deep vestibular valleys, on molars (Fig. 30-4) and even on some premolars.

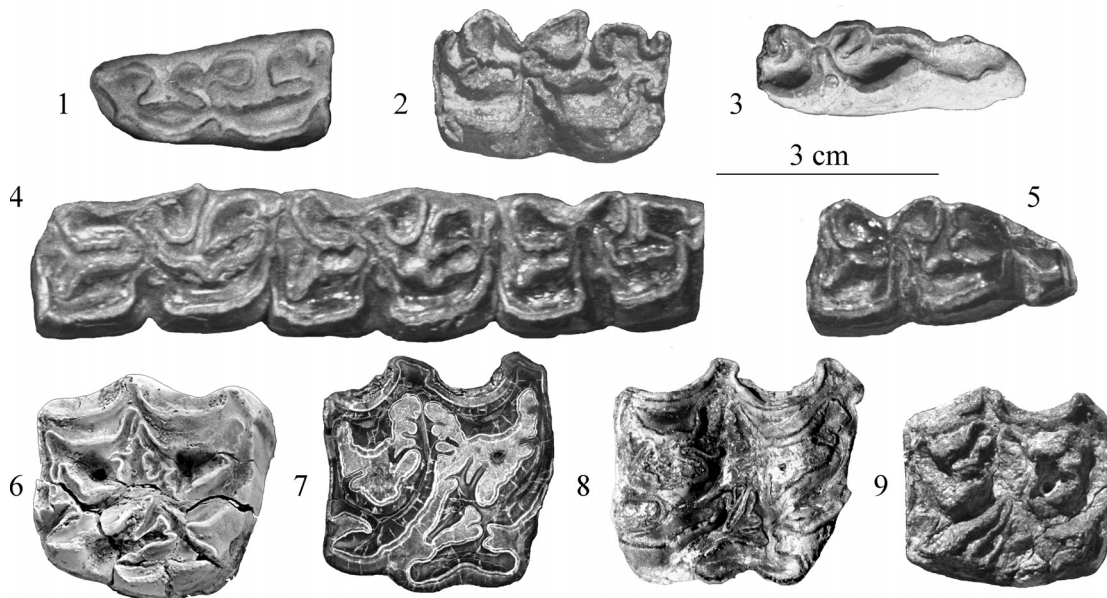


Figure 30.— Sussemiones cheek teeth. 1: *E. granatensis*, Venta Micena, lower P2, VM 3572. 2: *E. cf. suessenbornensis*, Akhalkalaki, lower P4, TB 99. 3: *E. granatensis*, Venta Micena, lower M3, VM 84-C3-J9-16. 4: *Equus* sp., Krestovka, lower P3-M1, SI 851-74/8. 5: *E. verae*, Chukochya Loc 21, lower M3, SI 835-123. 6: *Equus* sp., Melka Kunture, Garba IV, upper P3 or P4, MK 74-7150. 7: *E. cf. verae*, Loc 26, upper P3 or P4, SI 2998-243. 8: *E. suessenbornensis*, upper P3 or P4, S 17-5226. 9: *E. hipparionoides*, Akhalkalaki, upper P4, TB 100.

But the depth of the vestibular valley is very variable: associated teeth may have very deep and very shallow valleys. Both features are uncommon in extant species.

On the upper cheek teeth, the most strange are the plis caballin. They often have a very large base (Fig. 30-6,7), may be multiple (Fig. 30-8), club-shaped (Fig. 30-9). Such morphologies are unknown in extant species. They are frequent in Alaska, Chukochya, and at Süssenborn, but they occur even in Ethiopia, at Melka Kunturé (Fig. 30-6). The enamel is often very plicated and the postprotoconal valley may be very deep (Fig. 30-7).

The skull of *E. coliemensis* IA 1741 (Early Middle Pleistocene of North-Eastern Siberia, Lazarev 1980) belongs to this group (Eisenmann and Kuznetsova 2004, Eisenmann 2006b). It resembles extant hemiones (Fig. 31).

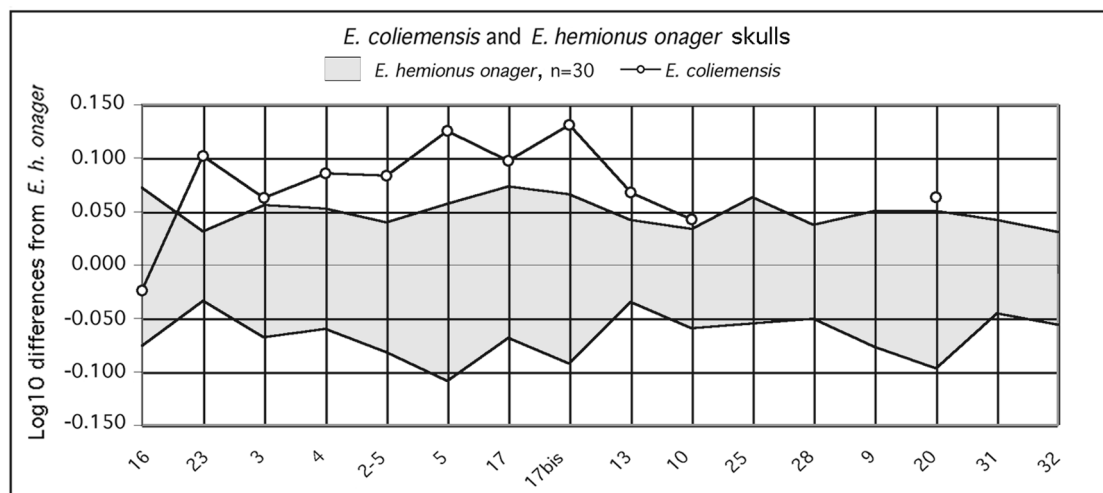


Figure 31.— Ratio diagram of *E. coliemensis* skull compared to extant *E. hemionus onager*. Data in Table 1.

The occurrence in Sussemiones of Old World hemione characters, such as slenderness, elongated metaconids, relative microdonta and small protocones, in association with clearly apomorphic enamel patterns (shared by robust species of Sussemiones) seems to indicate that the 'slender, hemione-hydruntinus model' was quite widespread in time and geography.

STILT-LEGGED AND HEMIONE-LIKE EQUIDS OF NORTH AMERICA

Since hemiones are characterized by slender limb bones that separate them easily from other extant Old World *Equus*, they should be easily identifiable in North America. It is however very difficult, because in North America, contrary to the Old World, possible hemiones were not the only slender species to be found during the Quaternary. Since Troxell (1915) described *E. calobatus* as 'he who walks on stilts', the locution, 'stilt-legged' is applied to them. Regardless of their relationships, to true

hemiones or to stilt-legged equids, slender boned species ranged at least from the Late Blancan to the Rancholabrean, from Mexico to Alaska, and varied in size from gigantic to very small.

The recognition of the hypothetical first hemione in North America is therefore linked to a better description and understanding of the 'stilt-legged' group.

Unfortunately, most of these fossils are not directly associated and many are fragmentary. As often in paleontology, some informative specimens, were 'referred' to species the types of which are less diagnostic. After giving a definition of the 'stilt-legged' group, we will consider the types, the really associated, and the obviously referable fossils before discussing the rest of the material.

I. FIRST STILT-LEGGED *EQUUS*

Stilt-legged equids should be defined by the characteristic proportions of their limb bone segments rather by the slenderness of each individual bone or by teeth characters that may be found in other groups, in particular true hemiones. In stilt-legged equids, the length of the distal bones (metapodials and first phalanges, and to a lesser extent - radius) relative to the proximal ones (humerus, femur, and tibia), is exceptional. The nearest proportions we have been able to find are those of the camel (data from Osborn 1929), but the camel humerus is quite longer and its metatarsal quite shorter. Typical stilt proportions are only found found at Santo Domingo, in *E. calobatus*, and *E. semiplicatus* (Fig. 32).

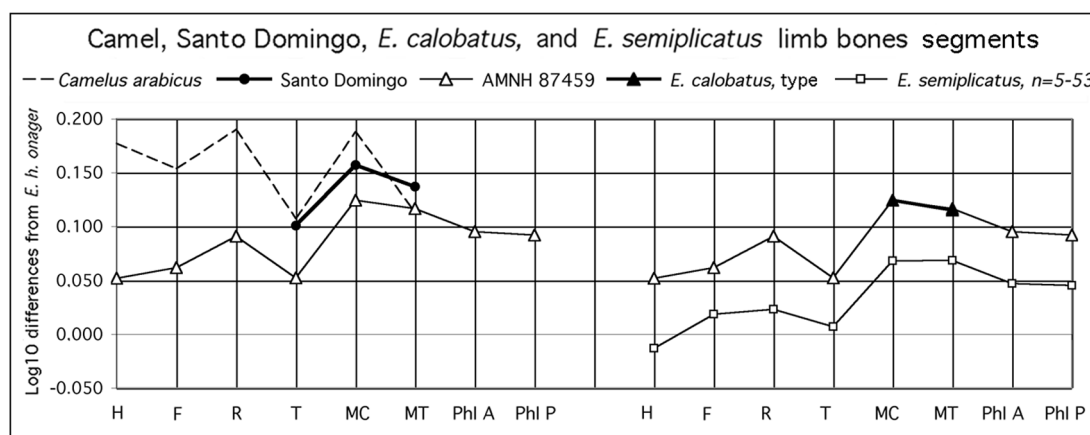


Figure 32.— Ratio diagrams of limb bones segments in stilt-legged equids. Data in Table 2.

The first stilt-legged *Equus* appears to be Late Blancan (around 2 My?). Actually there is no proof that it is not a *Plesippus*, since we do not know its skull. But we know that it was as large or larger than *E. calobatus*, and probably slightly smaller than the first *Equus* from Anza Borrego (Eisenmann 2006b). The associated bones (AMNH 11654) were found in New Mexico, in the Santo Domingo Basin (Azzaroli & Voorhies 1993).

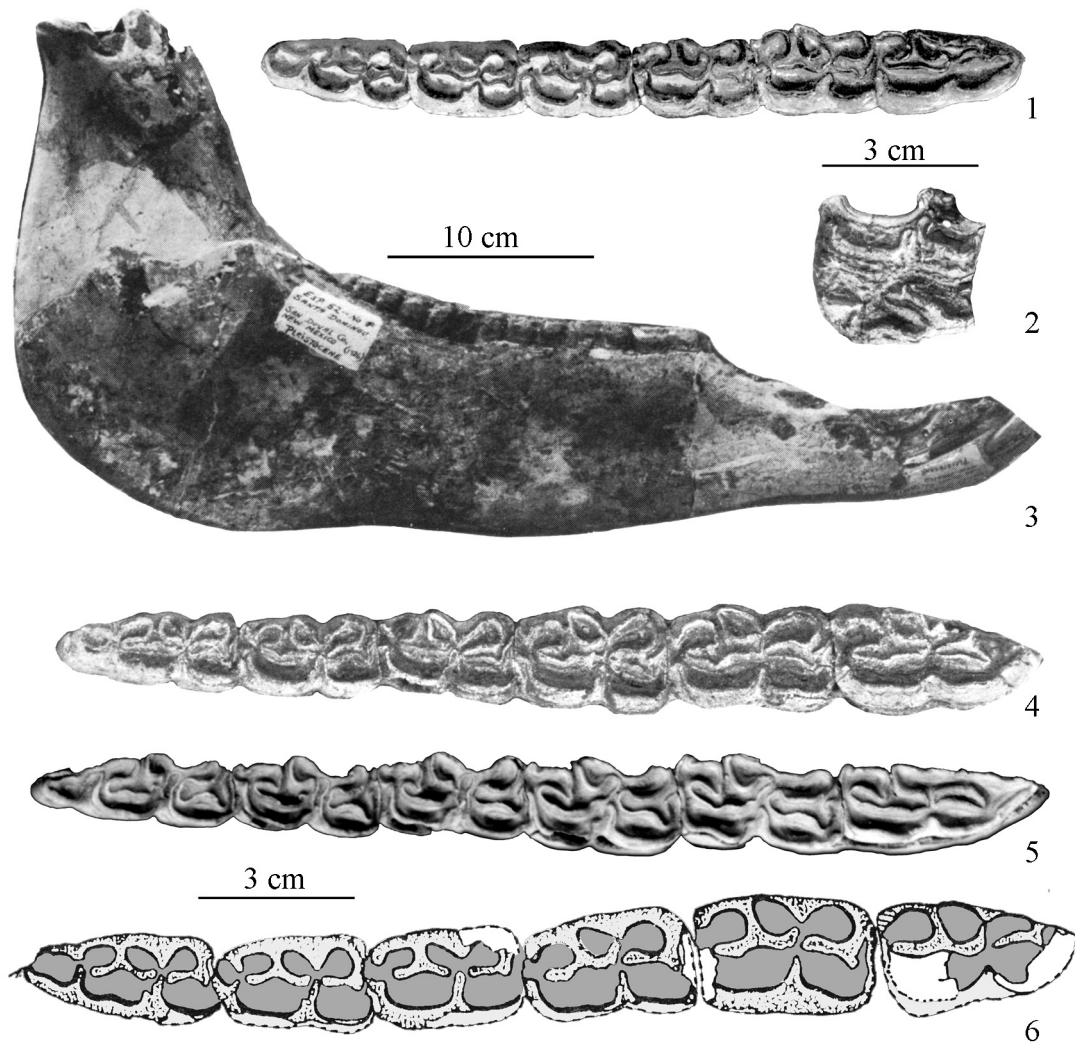


Figure 33.— 1: Dry Mountains, AMNH 116502, lower P2-M3. 2: Santo Domingo, AMNH 116153, upper P3 or P4. 3: Santo Somingo, AMNH 116153, mandible. 4: Santo Domingo, AMNH 116153, lower P2-M3. 1-4 adapted from Azzaroli & Voorhies (1993). 5: Lost Chicken, lower P2-M3, courtesy A. Sher. 6: Anza Borrego, lower P2-M3, LACM-IVCM 2673, adapted from Downs & Miller (1994).

Beside a tibia and two metapodials, there are one mandible, with a long symphysis (Fig. 33-3), and an upper premolar. According to the size of the mandible (Appendix 1, 3), the basilar length of the skull was about 600mm long. The enamel pattern (Fig. 33-2) of the upper premolar AMNH 116153 (Azzaroli & Voorhies 1993, Plate 4-4) is rather caballoid: long assymetrical protocone, pli caballin. The lower cheek teeth AMNH 116153 figured by Azzaroli & Voorhies (1993 Plate 4-3a) are more hemione-like (Fig. 33-4) than those of Anza Borrego (Fig. 33-6), but much less so than those of Dry Mountains, Arizona, AMNH 116502 (Fig. 33-1) or the 'hyper-hemione' cheek teeth of Lost Chicken (Fig. 33-5) both believed to be about the same age. The pattern is

similar to *E. calobatus* from Arkalon (Fig. 37-1) and Seymour Formation (Fig. 37-2).

There is no information on the limb bones of the Blancan Lost Chicken. The MT III found at Dry Mountains (Azzaroli and Voorhies 1993, Plate 6-3, AMNH 116501), is not slender indicating that an hemione-like pattern on lower cheek teeth is not necessarily linked with a stilt legged body. We have already noted the same for the Sussemiones of the Old World.

The metacarpal of Santo Domingo is similar to *E. calobatus* (Fig. 34). The metatarsal is deeper in the diaphysis and has a more developed distal end.

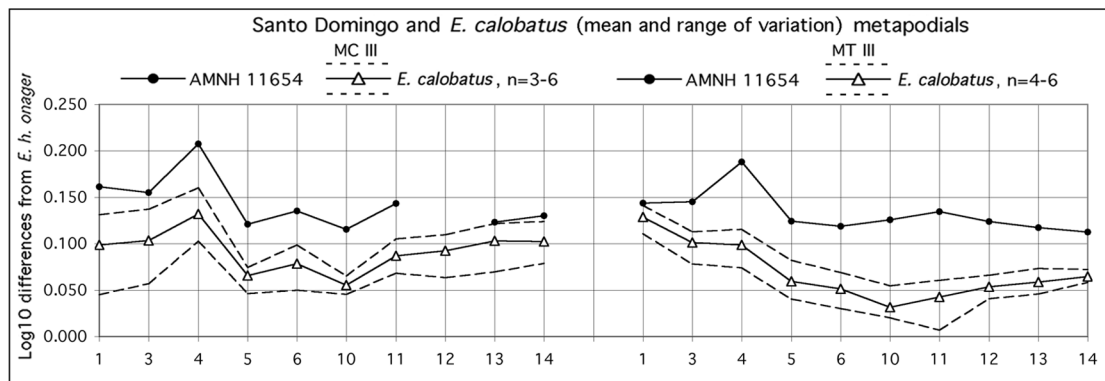


Figure 34.— Ratio diagrams of third metacarpals (MC III) and metatarsals (MT III) of Santo Domingo and *E. calobatus*. n=number of specimens. Data in Tables 3-4.

II. LARGE AND MIDDLE SIZED STILT-LEGGED *EQUUS*

1. Localities and Chronology

The ages of *E. calobatus* and *E. semiplicatus* are not precise. It seems that the oldest finds are those of *E. calobatus*, inside the upper levels of Arkalon Gravel Pit, Meade Fm., Seward Co., Kansas, which could be early Pleistocene (Fig. 35). *E. semiplicatus* appears later, at Channing, Dalhart, probably at the beginning of the middle Pleistocene. Both species seem to coexist at Rock Creek. *E. cf. calobatus* is present at Arkalon Terrace (possibly contemporary with Rock Creek) and at Hay Springs in the upper middle Pleistocene.

Rock Creek, Briscoe Co., Texas

Rock Creek is a name used to refer to several localities, more or less close to each other. The exact provenance and ages are not quite clear, probably early middle Pleistocene. Three equid species were described: *E. scotti* (several complete skeletons), *E. calobatus* (possibly associated metatarsal (MT) and metacarpal (MC)), and *E. semiplicatus* (one tooth). In his description of *E. scotti*, Gidley (1900) says that

the skeletons were found 'in a bed of compact sand at the head of Rock Creek, about the middle of the *Equus*, or Sheridan, beds, which are about 100 feet in thickness at this place'. Kurten and Anderson (1980) note that the main fauna comes from another quarry. Troxell (1915) states that the bones of *E. calobatus* were found at the Mylodon Camel Quarry. The type upper molar of *E. semiplicatus* comes from Tule Canyon (Rock Creek) and the referred upper series from Rock Creek beds (Quinn 1957). But the paratype of *E. semiplicatus*, a damaged upper molar, is from San Diego, Texas, far south of Rock Creek, as are the skull and metatarsal mentioned by Azzaroli (1998). While assignment of limb bones to *E. scotti* and *E. calobatus* is easy, the sorting out of the rest of the material is not, and the tentatives are subject to discussion.

		<i>E. hem-E.hydr</i> Kabazi	TRUE STILT-LEGGED EQUIDS							
10 Ky									Natural Trap	Two Creeks
20 Ky			Cueva Quebrada							Wisconsin II
25 Ky										
30 Ky								Conkling, Shelter	<i>E. francisci</i> Gold Run	Plum Point
35 Ky				<i>E. tau</i> (= <i>E. quinni</i>) Trinity River				Alaska, Yukon		
50 Ky			Ingleside Pit							
										Wisconsin I
100 Ky			Fossil Lake							Sangamon
0.2 My		Binagady		Cedazo						
0.3 My		Lunel Viel								
0.4 My					<i>E. calobatus</i> Hay Springs	<i>E. cf calobatus</i> Hay Springs	<i>E. semiplicatus</i> Hay Springs	<i>E. pseudaltidens</i> Powers Ranch Coleman	Hay Springs Cragin	Illinoian
0.5 My	"SUSSEMIONES"									
	<i>E. collimensis</i>	<i>E. granatensis</i>		Slaton			Slaton		Lissie Fm.	Yarmouth
	Süssenborn Gomboré II	Süssenborn								
	Cueva Victoria Akhalkalaki	Cueva Victoria Akhalkalaki		Rock Creek	Arkalon Terrace		Channing			Kansan
1 My	Chukochoya		Tologoj							
					Holloman Seymour Arkalon G.P.	Calosahatchee Fm.				
				<i>Equus sp. B</i> Leisey Pit A				Pool Branch		
	Garba IV									
1.5 My		Venta Micena								
2 My	Alaska, Arizona									Santo Domingo

Figure 35.— Schematic chronology of Old and New World hemione-like equids.

2. *E. calobatus*

Mylodon Camel Quarry. Given the lack of certainty about the association of the MC (Table 3) and MT (Table 4), Hibbard (1953) proposed for type the MT III, PMYU

13470. It is very long and the diaphysis is very narrow resulting in a slenderness similar to extant hemionines. But the most striking character is the relative narrowness of the proximal and distal ends, reminiscent not of hemionines but of the smaller and extinct Old World *E. hydruntinus*. Azzaroli 1998 gave some dimensions of two other MT from Rock Creek (AMNH 116510 and TMM 41286-1).

The cotype third metacarpal (MC) of *E. calobatus* is very long and slender, as is the MT (Fig. 36).

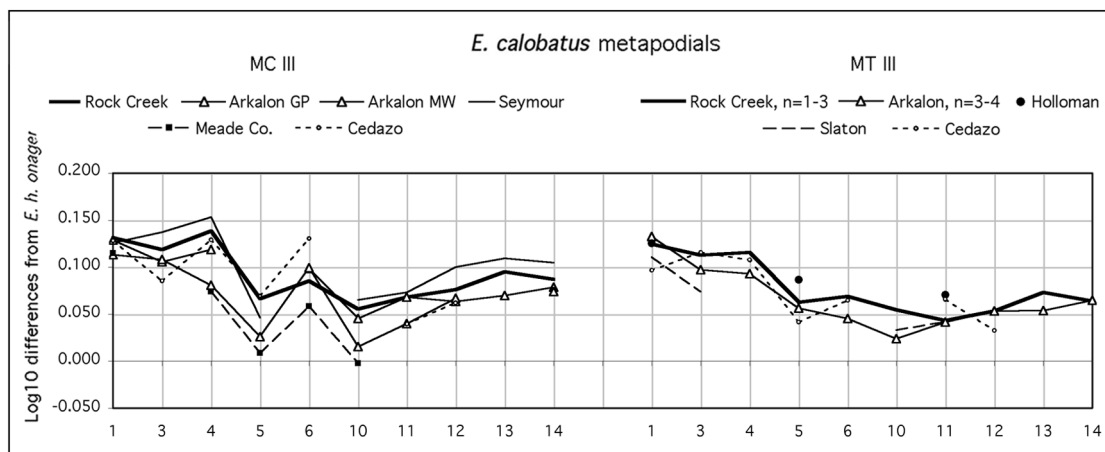


Figure 36.— Ratio diagrams of *E. calobatus* third metacarpals (MC III) and metatarsals (MT III). Data in Table3 -4.

Obviously referable to *E. calobatus* because of size and slenderness are several first phalanges (Table 5), anterior and posterior, from Rock Creek, belonging also to Yale Peabody Museum collections. The anterior (PHI A) are numbered 19, 78, 142, and 3196-97. The posterior (PHI P) are numbered 3196-144 and -349.

Referred Material

Absolutely similar to the type and cotype are one MT (TMM 934-6) from **Holloman**, Gravel Pit, Frederick, Oklahoma, (Fig. 36 right) described by Quinn (1957), and one MC (Fig. 36 left) from the **Seymour Formation**, Texas (UMMP 46555). Hibbard & Dalquest (1966) figured a sectioned lower series, UMMP 39382, from the Seymour Formation, which may belong to this species (Fig. 37-2). A first posterior phalanx (UMMP 46509) belongs to the same form.

From Arkalon 1 Gravel Pit, Meade Fm., Seward Co., Kansas, associated limb bones of a subadult (FAM 87459) provide an excellent information on the general body proportions of this stilt legged *Equus* (Table 2). The relations between limb segments lengths are surprising (Azzaroli 1998, Eisenmann 2003) and unknown in extant *Equus* (Fig. 32). This partial skeleton was found at the top of the section, in the clay, silty, ash layer. The associated lower cheek series (Fig. 37-1) was sectioned and figured by Skinner (1972). It is 180mm long and quite similar to UMMP 39382 of Seymour

Formation (Fig. 37-2) figured by Hibbard & Dalquest (1966).

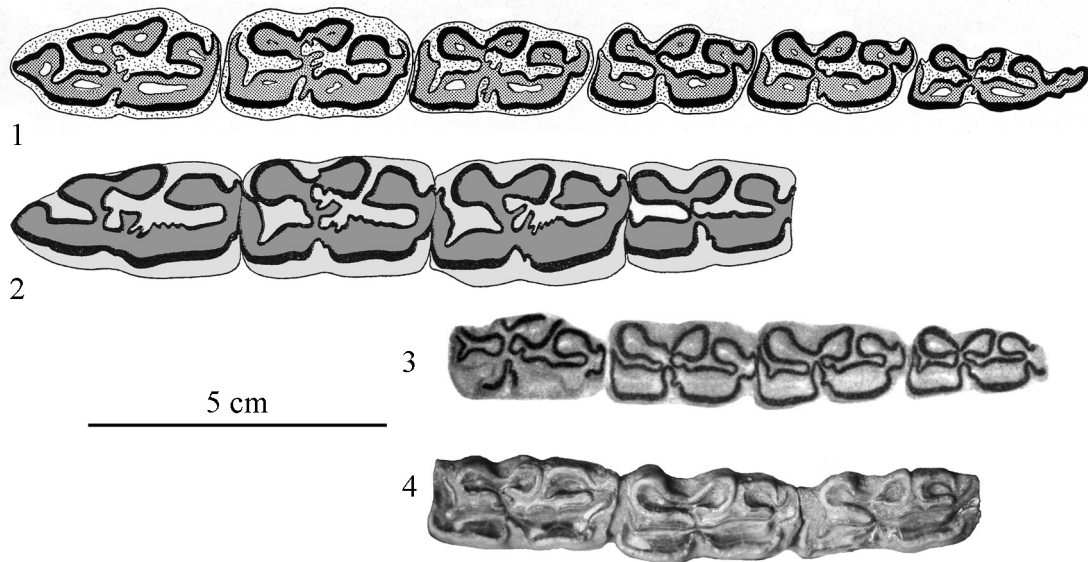


Figure 37.— 1: Arkalon Gravel Pit, FAM 87459, lower P2-M3, adapted from Skinner (1972). 2: Seymour Formation, UMMP 39382, lower P2-M1, adapted from Hibbard & Dalquest (1966). 3: Cedazo, FC 58.16-18, lower P4-M3, adapted from Mooser (1959). 4: Hay Springs, UNSM 31.7.4.38, lower P4-M2.

An adult MC (Winans 1985) is slightly shorter than the juvenile FAM 87459. From a silty ash, near Arkalon, Hibbard (1953) mentioned a MT (UMMP 6842) 330mm long. Another MT (UMPP 29071) was also found in the upper levels of Arkalon.

From Meade County, Kansas, there is a juvenile MC preserved at Ann Arbor (UMMP 27023).

From Slaton, Texas. Slightly smaller but otherwise similar metatarsal and anterior first phalanx (TMM 882-337 and 285) were described by Dalquest (1967).

Some additional information comes from Mexico. **From Cedazo,** Mooser & Dalquest (1975) described a very long and slender MC (FC 705) and one MT (FC 703). The lower cheek teeth FC 56.16-18 from Cedazo (Fig. 37-3) may also belong to *E. calobatus*.

So may the lower UNSM 31.7.4.38 from **Hay Springs** (Fig. 37-4).

To summarize, we know that the USA *E. calobatus* was a tall horse, with very slender limb bones and strange limb proportions. There are no associated skull or

dentitions to the type. However on the basis of the cheek lengths and of the metapodial distal widths, the skull was about 500mm long (Appendix 3, 4). The cheek teeth were about 180mm long. The double knot tended to be 'hemione-like' and the ectoflexid was shallow on the molars (Fig. 37). The upper cheek teeth are unknown.

3. *E. cf. calobatus*

From Hay Springs, the little worn lower P4-M2 illustrated above show hemione-like features. The fragmentary MC (UNSM 6586) is less gracile but deeper in the diaphysis (Fig. 38, Table 3), than in *E. calobatus*. Also from Hay Springs, a few MT or or fragments of MT are more robust and with more developed distal ends than in *E. calobatus* (Fig.38, Table 4).

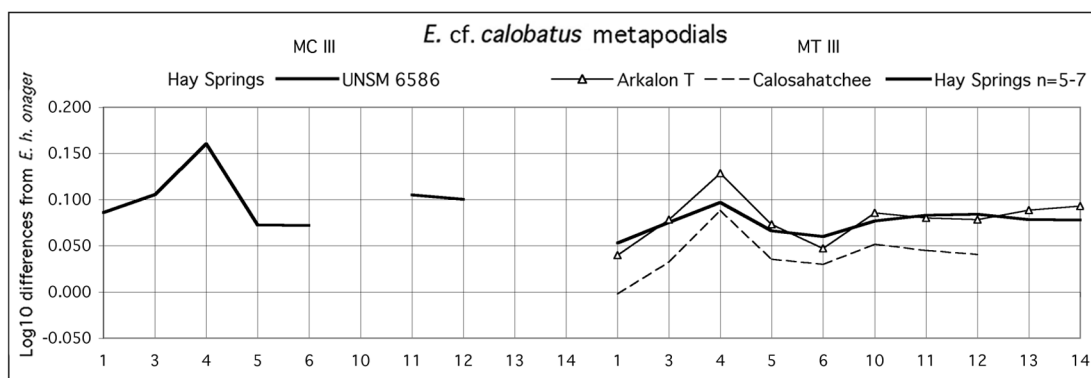


Figure 38.— Ratio diagrams of *E. cf. calobatus* third metacarpals (MC III) and metatarsals (MT III). Data in Tables 3-4. Arkalon T=Arkalon Terrace.

At **Arkalon 2** (Terrace 1-2) was found a MT III (UMMP 33358) shorter and not as narrow at the diaphysis and epiphyses as in *E. calobatus* (Fig. 38, Table 2). A similar morphology is shown by a specimen from Calosahatchee, Florida (Field Museum of Chicago 14323).

Altogether, these bones are closer to hemiones than to stilt-legged forms because of their well developed distal epiphyses.

4. *E. semiplicatus*

a. Rock Creek and San Diego, Texas

The type (Tule Canyon, Rock Creek) is an upper molar with simple enamel and a tiny pli caballin. Judging from figure 2 in Plate XXIII of Cope (1893), it could be a right M2, about 26mm long and wide, with a protocone 15mm long (Fig. 39-1).

Quinn (1957, Plate II-5) referred to *E. semiplicatus* an upper right series (TMM 276-2, Fig. 39-3) from Rock Creek beds (166mm long) and Azzaroli (1998) a nearly complete skull (AMNH 8600) from San Diego. The cheek teeth series of the skull (Fig.

9-4) is 162mm long and the basilar length may be estimated at ca. 450mm (Appendix 3). The paratype fragmentary upper molar of *E. semiplicatus* (Cope 1893) comes also from San Diego Fig. 39-2). It is slightly smaller (25mm) than the type.

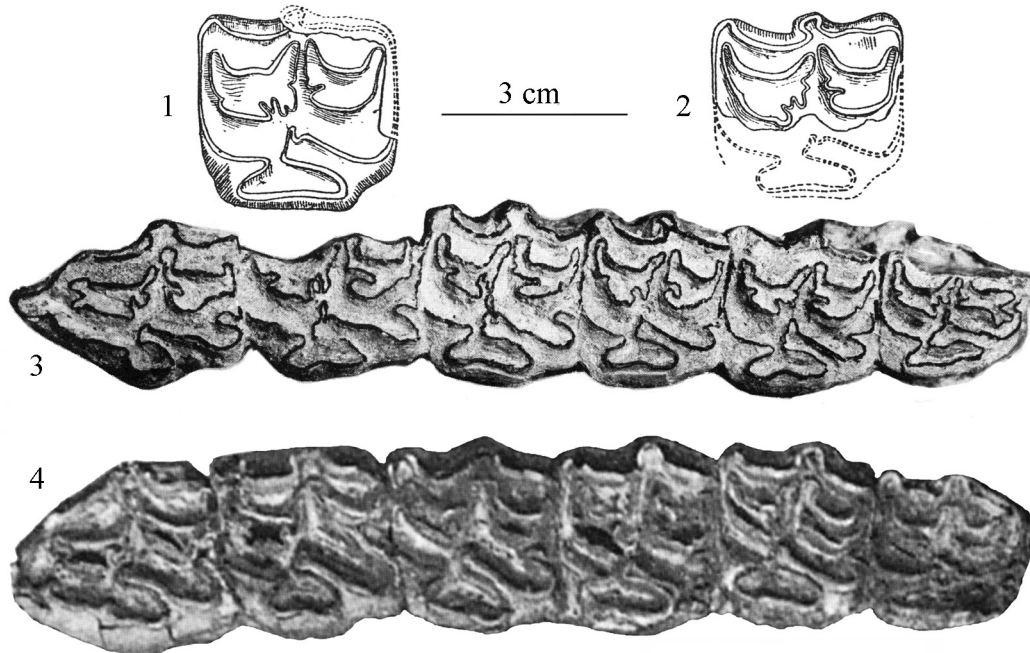


Figure 39.— Upper cheek teeth of *E. semiplicatus*. 1: Tule Canyon, upper M1 or M2, adapted from Cope 1893. 2: San Diego, upper M1 or M2, adapted from Cope 1893. 3: Rock Creek, P2-M3, TMM 276-2, adapted from Quinn 1957. 4. San Diego, P2-M3, AMNH 8600, adapted from Azzaroli 1998.

Skull morphology will be discussed later, in comparison with specimens from Channing. Tooth morphology and size of TMM 276-2 and AMNH 8600 are compatible with the perhaps schematic illustration of the type upper molar of *E. semiplicatus*.

b. Hay Springs, Nebraska

One skull (UNSM 1349, Sheridan 2, U8) possibly belongs to *E. semiplicatus* (see below). The upper cheek teeth length is 163.3mm. Some specimens from Hay Springs are part of the collections of the Senckenberg Museum at Frankfurt. One is an upper cheek teeth series (M-1487). It is 161mm long; the enamel is not very plicated but the teeth are rather worn (Fig. 40). This is the size of the teeth of the skull AMNH 8600 cited above. There are eight MC and five MT (Tables 1, 2) and seven anterior and five posterior first phalanges (Table 5) referable to *E. semiplicatus* (Howe 1979). There are also at Hay Springs enigmatic hemione-like metapodials that we referred to *E. cf. calobatus*.

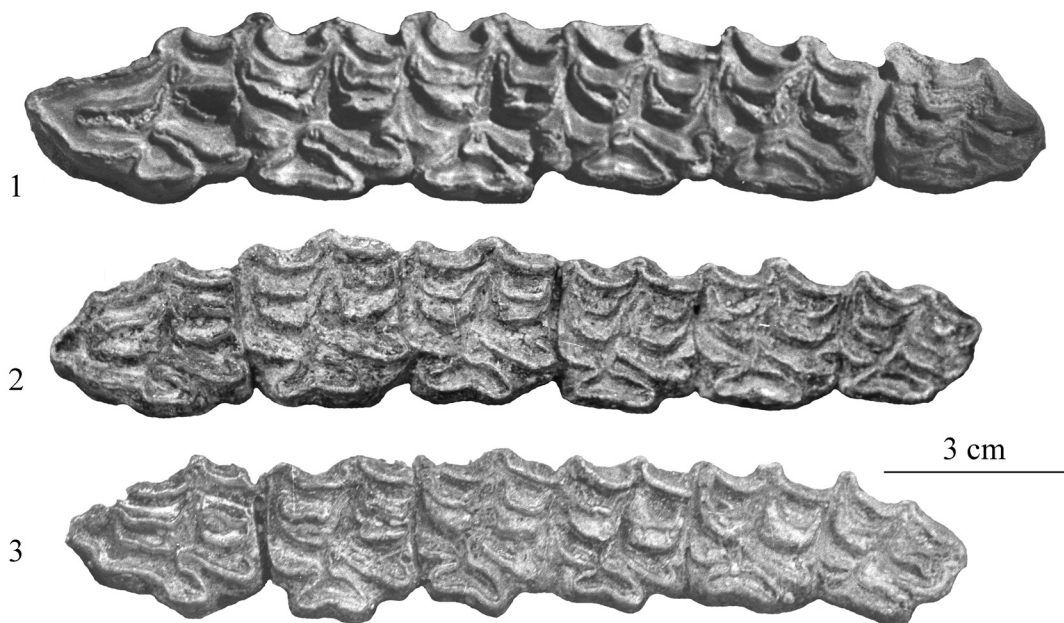


Figure 40.— Upper cheek teeth of *E. semiplicatus*. 1: Hay Springs, M 1487. 2: Channing, FAM 11656. 3: Channing, AMNH 54-1074-1.

c. Channing (Dalhart), Texas

The best documented stilt legged *Equus* is yet incompletely described, although Azzaroli (1998) published beautiful photographs of skulls and teeth. The limb bones are very numerous (Table 6) and there are in the Frick collection at the AMNH three more or less fragmentary skulls, all of aged individuals (FAM 116156, 116158, and 54-1074-1), a fragment of cranium (16-391), and two mandibles: one subadult (FAM 22-570 and 564), one young adult AMNH 116506).

- Skulls

The skulls are not well preserved so that many dimensions are imprecise (Table 7). Nevertheless, the general characters are clear enough. Basilar lengths range from ca. 422 to ca 440mm, about the size of the extant *E. hemionus onager*. But the palate is shorter, the muzzle longer and wider, and the face probably not so high. Judging from the dimension of the post-orbital line of FAM 54-1074-1 (166mm), the Basion-vomer distance was about 90-100mm (Appendix 2); this estimation is in good accordance with the 96mm measured on the fragment 16-391. The distance between Basion and posterior border of palate of FAM 11656 is 208mm; thus the length between palate and vomer was about 108-118mm and the Franck and Palatal indices were not caballine (Eisenmann 2006a).

According to the illustrations of Azzaroli (1998), the skull AMNH 8600 is slightly larger, with a longer and wider muzzle. The skull of Hay Springs UNSM 1349 is also larger, but more like Channing. In comparison with Old World hemiones (Figs.1, 28, 41) *E. semiplicatus* skulls have longer muzzles (5) and shallower faces (25).

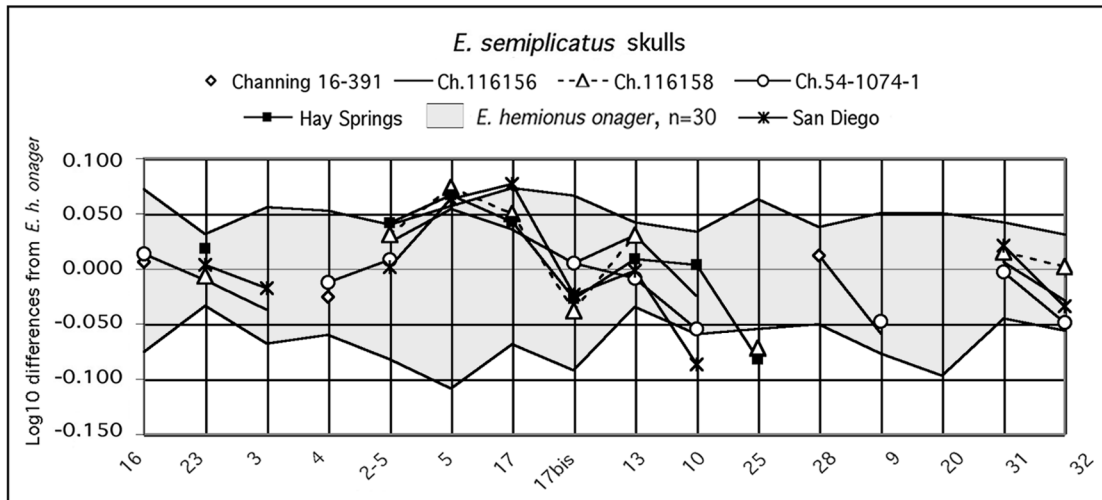


Figure 41.— Ratio diagrams of *E. simplicatus* skulls. Ch.= Channing. Data in Table 7.

- Upper cheek teeth (Fig. 40)

The cheek teeth series are ca. 150mm long. The mesio-distal lengths of P2 seem rather short. The middle upper cheek teeth (P3/-M2/) are not very large (22.5-25.5mm). The protocones of the middle teeth, all rather worn, are relatively long:11.5 (P3/) to14.2mm. The enamel is simple, the plis caballin are lacking or very small, the postprotocone valley is occasionally deep.

- Lower cheek teeth (Fig. 42)

The lower cheek teeth have shallow ectoflexids both on premolars and molars. On the middle teeth, metaconids tend to be elongated.

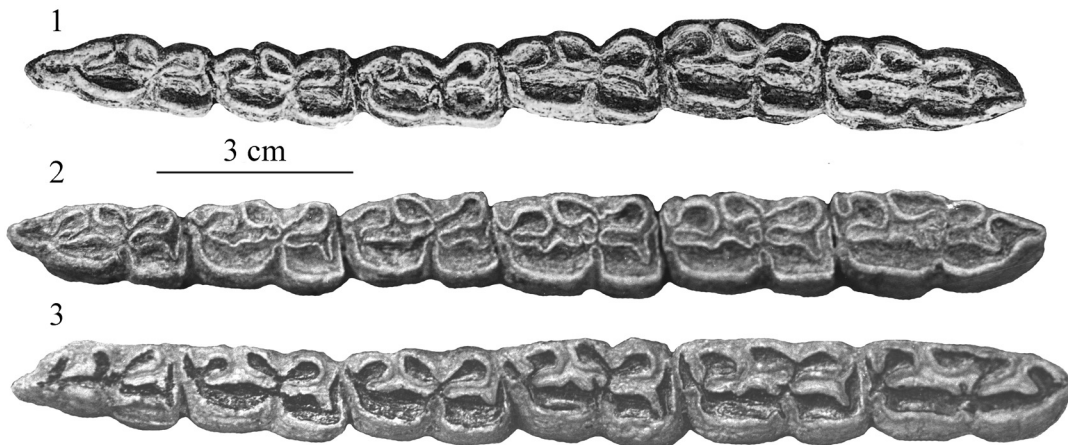


Figure 42.— Lower cheek teeth of *E. simplicatus* from Channing. 1: FAM 116156. 2: FAM 116159.

- Lower incisors

Perfect cups are present on all incisors (Azzaroli 1998, pl. 9-2b). The squarish arcade is that of a grazer (Eisenmann 1998).

- Metapodials

The well preserved and numerous MC III and MT III of Channing (Table 6) are similar to those of Hay Springs. If the teeth of *E. semiplicatus* present some resemblances with extant hemiones, the metapodials are different. Metacarpals and metatarsals are relatively narrow at their epiphyses (Fig. 43), more like in *E. hydruntinus*, which has, however, shallower distal keels.

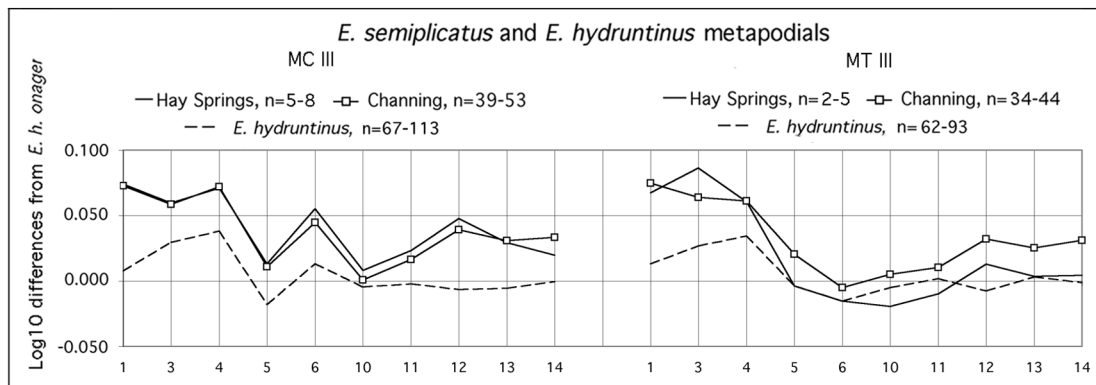


Figure 43.— Ratio diagrams of *E. semiplicatus* third metacarpals (MC III) and metatarsals (MT III) compared to *E. hydruntinus*. n=number of specimens. Data in Tables 3, 4, 6.

- Limb segments lengths

Like in *E. calobatus*, and unlike in extant hemiones and *E. hydruntinus*, metapodials are extremely long relative to humeri, femora, and tibiae (Fig. 32 right).

d. Slaton, Texas

Dalquest & Hughes (1965) and Dalquest (1967) gave some dimensions of four anterior phalanges that we refer to *E. semiplicatus* (Table 5).

e. Cedazo, Mexico

From Cedazo, Mooser & Dalquest (1975) referred to *E. tau* a MT (FC 712) which seems close to *E. semiplicatus*.

5. Conclusions

To summarize, *E. semiplicatus* clearly differed from all Old World hemiones by skull and limb bones segments proportions. It resembled *E. calobatus* but was quite smaller (Fig. 32). *E. calobatus* is considered by Azzaroli (1998) as a junior synonym of *E. semiplicatus*. Indeed, some metacarpal (Fig. 44) dimensions overlap. The overlap is even bigger in MT.

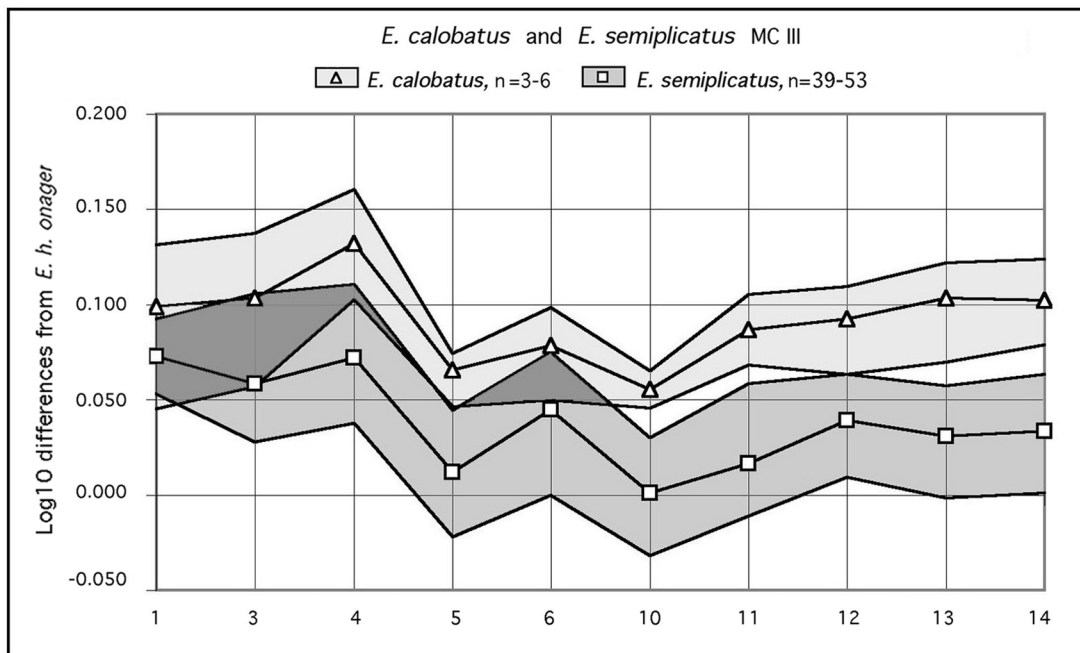


Figure 44.— Ratio diagrams of *E. calobatus* and *E. semiplicatus* (Channing) ranges of variation of third metacarpals (MC III). n=number of specimens.

There is no doubt that both share enough original characters to be considered as closely related, but because of their size differences, and their possible coexistence at Rock Creek, we prefer to retain both their names. It seems likely that the Santo Domingo form was related to *E. calobatus* and *E. semiplicatus* and that this probable group was present in North America from the Late Blancan (Santo Domingo) to the Early Rancholabrean (Hay Springs). Neither can be included inside the Old World hemione group.

III. SMALL SLENDER *EQUUS*

1. *Amerhippus francisci*, Lissie Formation, Texas, type: TAMU 2518

A. francisci is a small species known by a skull and associated radius, a MT, and a posterior PHI.

- According to Hay (1915) the skull basilar length is 414mm. A cast of the skull studied at the American Museum of Natural History (Table 7), probably slightly larger than the original, enables us to propose additional measurements to those published by Hay. Besides its smaller size, *A. francisci* skull differs from those referred to *E. semiplicatus* (Fig. 45) by its shallow narial notch (31), by a narrower forehead (13) as noted already by Azzaroli (1998), and also by the quite longer distance between vomer and Basion (4). If the measures we have taken on the cast are to be trusted, the basicranial proportions are those of a horse, not of an ass or hemione. The skull of *A.*

francisci, however, does not resemble any Old World *Equus*; the less dissimilar skulls are those of *E. fraternus* of Cedar Meadow, Florida (FAM 116143 and FLA 2363776) and a yet undescribed skull of Peruvian *Amerhippus*.

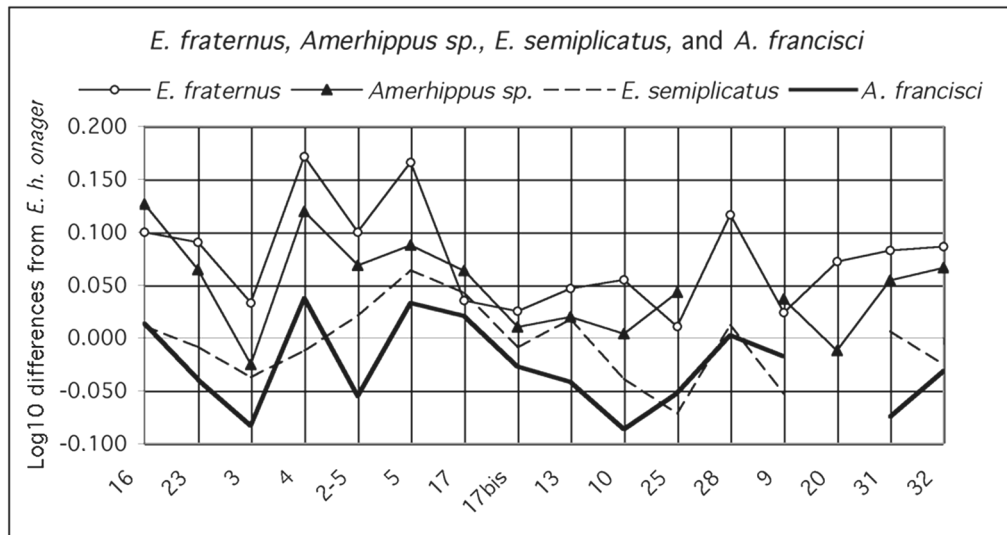


Figure 45.— Ratio diagrams of *E. fraternus*, *Amerhippus sp.*, *E. semiplicatus*, and *A. francisci* skulls. Data in Table 7.

- The occlusal dimensions of the middle teeth (P3/-M2/) are 20.5 to 23mm, the protocones are 9 (P3/) to 12mm long (Fig. 46). The enamel is simple, there are no plis caballin, the postprotoconal valley is moderately deep.

The lower cheek teeth have "V" linguaflexids, rounded metaconids, slightly pointed metastylids (Fig. 46). This morphology is extremely common and may be found from the Pliocene (*Plesippus*, *Allohippus*) to the present days (asses, zebras). However during the Pliocene and in extant zebras, ectoflexids are rarely shallow both on premolars and molars. By this character *A. francisci* is more like an ass than like a zebra.

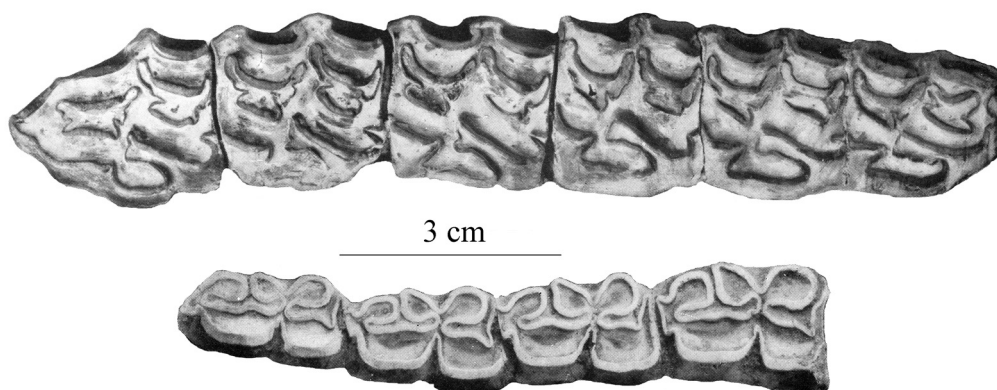


Figure 46.— Upper and lower cheek teeth of *A. francisci*, TAMU 2518, adapted from Hay (1915).

- But unlike asses and like *E. fraternus* (Azzaroli 1995) and *Amerhippus*, *A. francisci* is said to lack cups on the lower incisors (we have not seen the type material).

- As in other stilt legged forms, the metatarsal is slender and narrow at the proximal and distal ends. Its dimensions are close to the minimal observed at Channing (Fig. 47, right), but the keel is less developed. Azzaroli (1998) already noted the poor development of the volar ridge above the keel.

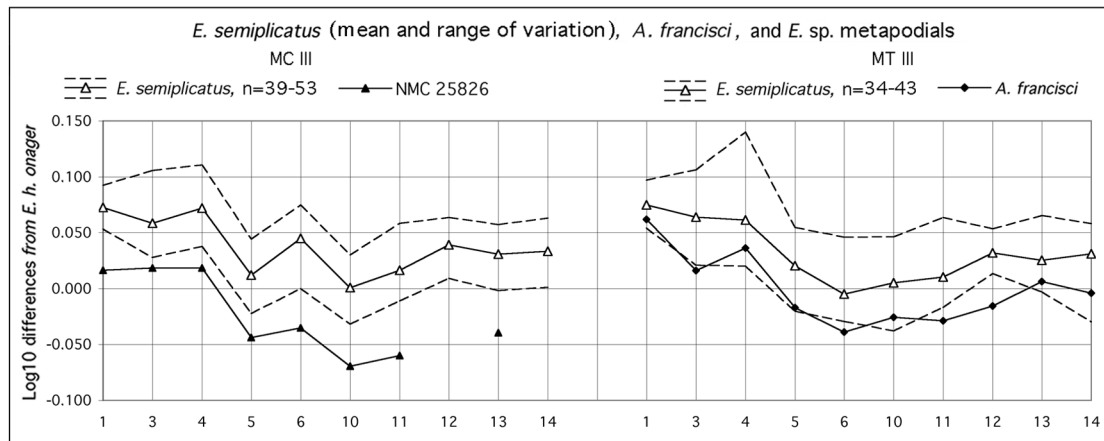


Figure 47.— Ratio diagrams of *E. semiplicatus*, Channing, *Amerhippus?* from Lost Chicken, and *A. francisci* third metacarpals (MC III) and metatarsals (MT III). Data in Tables 3, 4, 6.

- As much as can be guessed from the existing limb bones, their relative length is similar to *E. calobatus* and *E. semiplicatus*. At all events, the radius is very short relative to the MT III (Fig. 57 right).

Other fossils possibly belonging to *A. francisci* are one anterior phalanx from Hay Springs (33-38-1-9), two phalanges (KU 7473 and 7478) of Cragin Quarry, Kansas (Hibbard & Taylor 1960), and one anterior phalanx of Papago Springs, Texas. Skinner (1942) gave some measurements of the Papago Springs phalanx and noted that it could not belong to the other, less slender and larger species. The first phalanges tentatively referred to *A. francisci* seem even slenderer (Fig. 49) than those of *E. calobatus* and *E. semiplicatus*; the material is however very poor.

It would seem logical to consider *A. francisci* as the next step in decreasing size from the giant of Santo Domingo, after *E. calobatus* and *E. semiplicatus*. The lack of cups is not a solid argument against this hypothesis since cups may be present or lacking inside the same extant species of Plains zebra, *E. burchelli*: the cups are present in the southern forms and absent in the northern (Eisenmann 1979). But the skulls and teeth of northern *E. burchelli* do not differ from the southern, while the skulls and lower cheek teeth of *E. semiplicatus* and *A. francisci* do differ. The skull characters, added to the lack of cups, is a good argument to consider this small slender species as an *Amerhippus*.

2. *Amerhippus francisci* in Alaska ?

A palate from Cripple Creek, Alaska (FAM 60033) has about the same size as *A.*

francisci, but the protocones of the molars are quite longer (Fig. 48).

Curiously enough, the size and proportions of a MC from Lost Chicken, Alaska (NMC 25826) fit with what could be expected for a small *A. francisci* (Fig. 46, left).



Figure 48. — Upper P3-M3 FAM 60033 from Cripple Creek, Alaska.

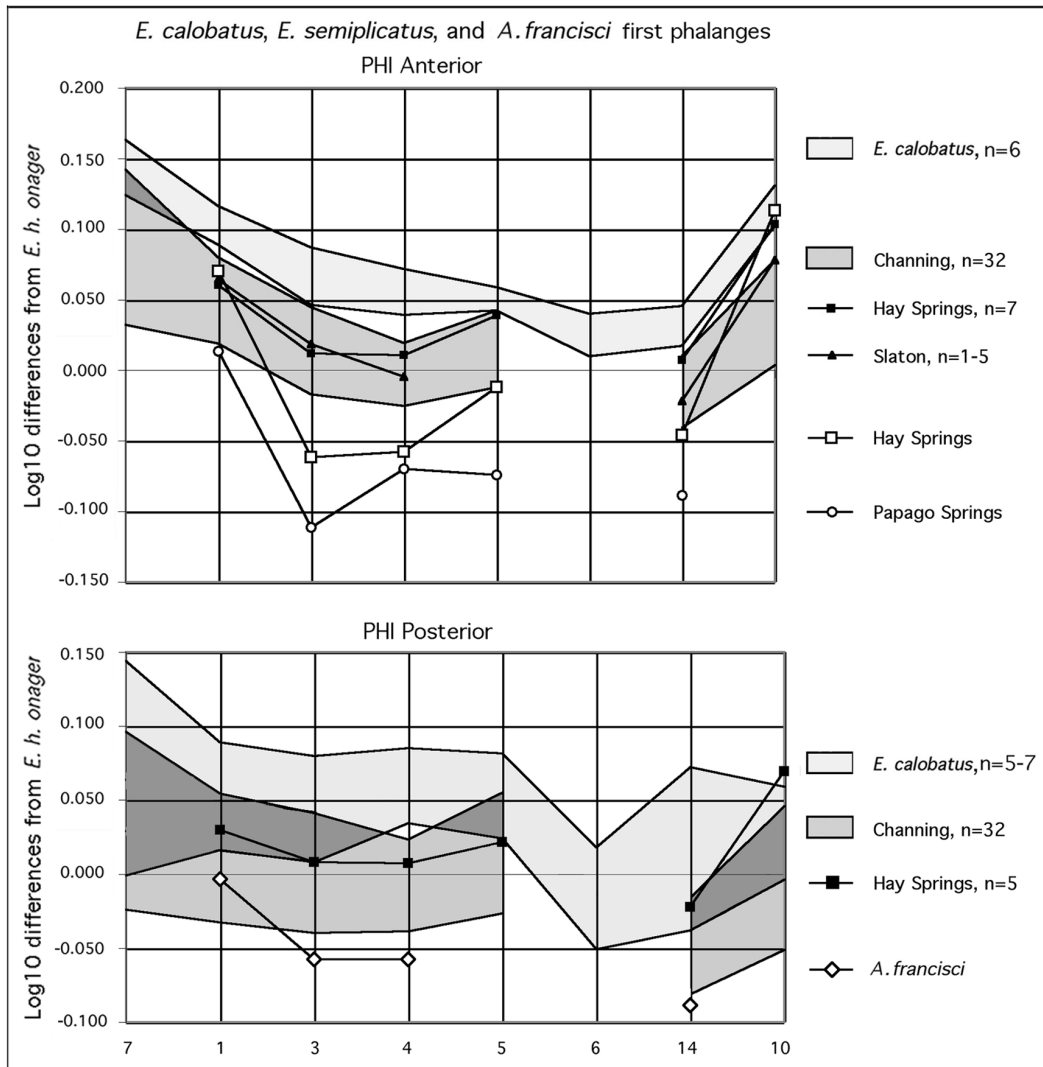


Figure 49. — Ratio diagrams of first phalanges of *E. calobatus*, *E. semiplicatus*, and *A. francisci*. Data in Tables 5-6.

3. *E. tau*

Mooser & Dalquest (1975) discussed the problems linked to the description of *E. tau*: the holotype was poorly figured by Owen (Hibbard 1955); moreover, it is lost.

It seems however that the upper cheek length of the type was 122mm, about the same length as the very worn series of the skull FC 673 (118.4mm). Since there is only one equid in Cedazo small enough to fit this size, Mooser & Dalquest referred several specimens to *E. tau*. The fragmentary skull (FC 673) was referred by Azzaroli (1995) to *A. francisci*. Although the skull is senile and laterally crushed (Fig. 50), the axial lengths seem reliable enough. We evaluated several dimensions (Table 7) using the data provided by Mooser & Dalquest and the photographs published by Azzaroli (1995, Text-Fig. 6).

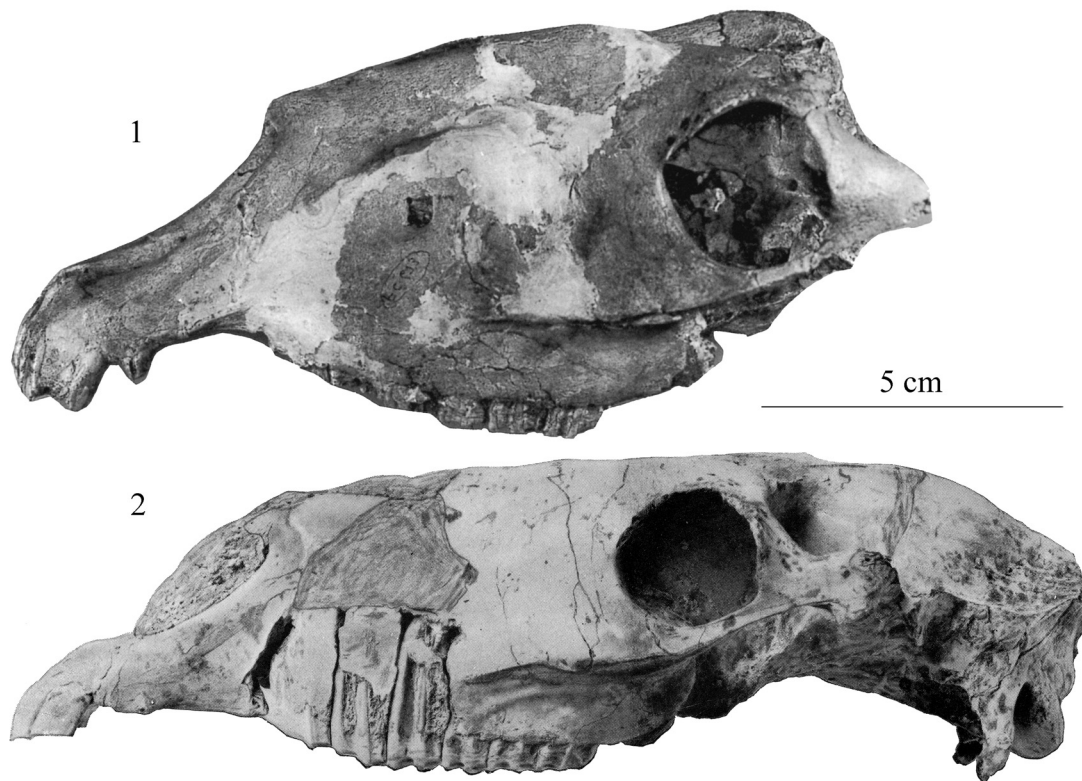


Figure 50.— Profiles of skulls of 1: *E. tau*, FC 673, adapted from Azzaroli (1998) and 2. *A. francisci*, TAMU 2518, adapted from Hay (1915). Data in Table 7.

- Though similar in size, the skull of *E. tau* differs from *A. francisci* by a quite shorter muzzle. Very surprisingly, it has quite a '*hydruntinus*-like' aspect (Fig. 51).

- The upper cheek teeth of the skull are too worn to be informative but the teeth IGM 56.76-80 referred by Mooser (1969, Fig. 4) to *Onager littoralis* are also 'hemione-like': no pli caballin, deep post-protocone valley (Fig. 52). On the lower cheek

teeth of FC 672, the metaconid tends to be elongated, which is again a hemione character.

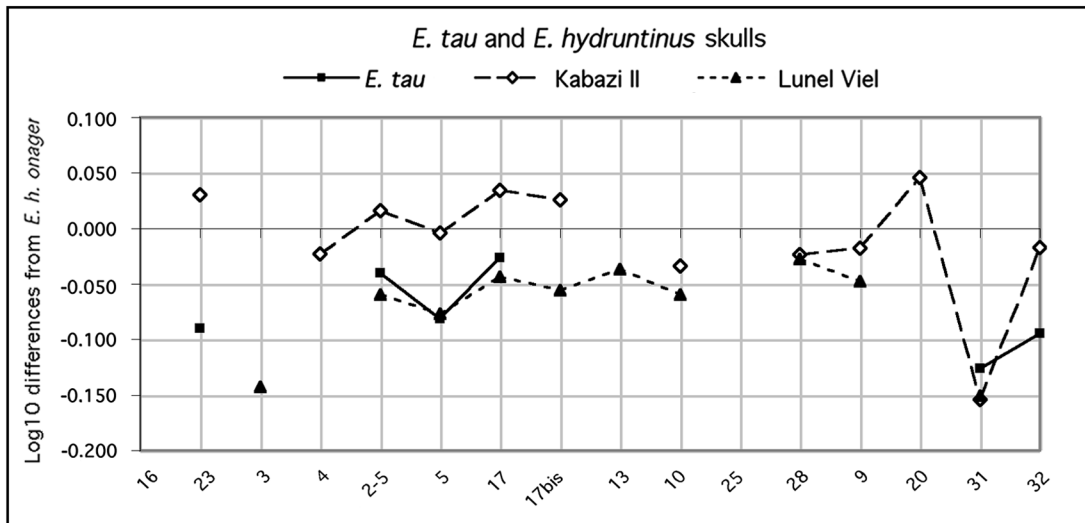


Figure 51.— Ratio diagrams of *E. tau* and *E. hydruntinus* skulls. Data in Tables 1, 7.

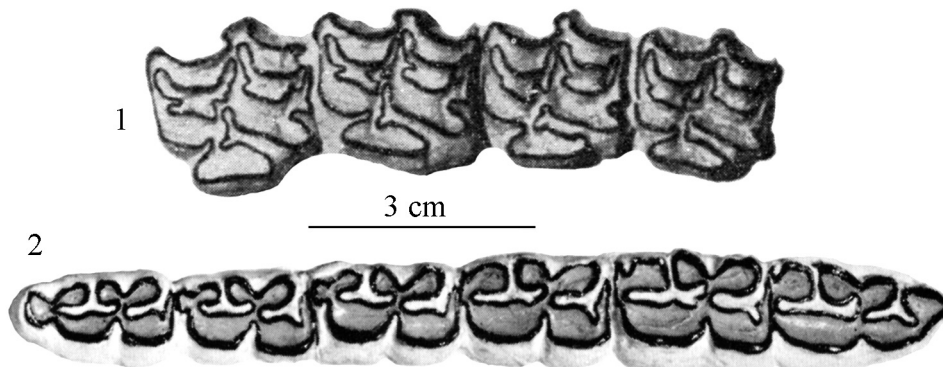


Figure 52.— *E. tau* cheek teeth from Cedazo. 1: IGM 56 76-80, upper P3-M2. 2: FC 672, lower P2-M3. Adapted from Mooser (1969).

- The upper cheek teeth we refer to *E. tau* differ from *A. francisci* by their smaller size and the depth of the post-protocone valley. The lower cheek teeth of *E. tau* have more elongated metaconids. But the main difference seems to be in the muzzle proportions.

- A MT (FC 708) is slenderer in the diaphysis than *A. francisci* (Fig. 53) but with a relatively larger distal end.

Thus it seems that *E. tau* and *A. francisci* shared small size and slenderness but were distinct species. Therefore we propose as neotype for *E. tau* the skull FC 673 and refer to the same species the upper cheek teeth IGM 56.76-80 and the MT FC 708.

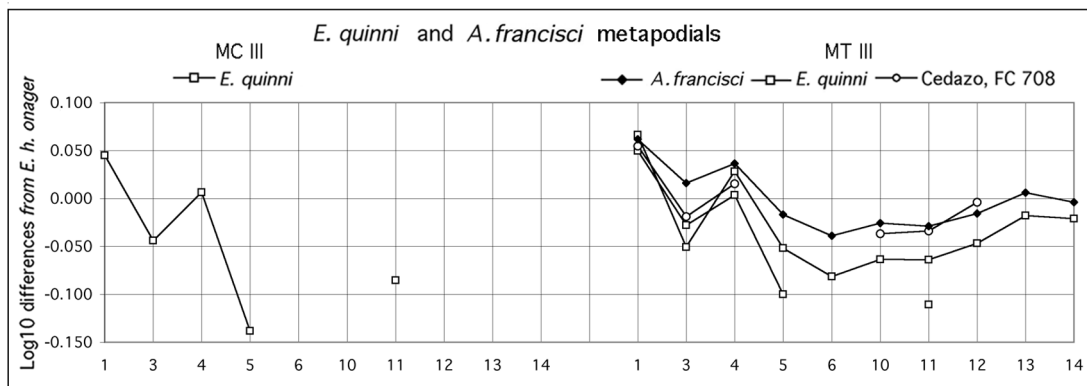


Figure 53.— Ratio diagrams of *E. quinni* and *A. francisci* third metacarpals (MC III) and metatarsals (MT III). Data in Tables 3-4.

4. *E. quinni*, Trinity River, Dallas Co., Texas

The type of *E. quinni* is a MT, SMUMP 60228 (Slaughter et al. 1962). There are also another MT (SMUMP 60174), one MC, and two upper molars. The teeth are smaller than in *A. francisci* (18 and 19mm), the protocones are 11mm long.

The MC paratype of *E. quinni* is very slender; the metatarsals are about the same length as in *A. francisci* and *E. tau* but much slenderer at mid-diaphysis (Fig. 53).

Given the resemblances between the MT, it seems possible that *E. quinni* is a junior synonym of *E. tau*.

5. Conclusions

The small stilt legged Equids are not related to each other as the large ones are. By its skull, *A. francisci* belongs to a group completely different both from Old World hemiones and other stilt legged species. It may be related to *E. fraternus* of Cedar Meadow, Florida and both belong very probably inside *Amerhippus*.

E. tau, probably a senior synonym of *E. quinni*, is the only stilt legged *Equus* the skull of which resembles Old World hemiones, in particular *E. hydruntinus*.

There is moreover an enigmatic *Equus* in Alaska, possibly related to *A. francisci*.

IV. SLENDER AMERHIPPIUS

1. *Amerhippus pseudaltidens*, Powers Ranch, Texas, *Onager altidens* Quinn 1957, type: BEG 31186-36. Renamed *E. pseudaltidens* by Hulbert (1995).

This species is known by subadult upper and lower teeth to which Quinn referred several adult limb bones.

- The muzzle is long. The teeth were sectioned quite near the top of the crown and may thus exhibit characters linked to an early stage of wear (Fig. 55). The occlusal dimensions of the middle teeth are rather large: 26 to 29mm. The P2-P4 length is about 90mm.

- Unlike in *E. calobatus* and *E. semiplicatus*, the P2/ appears normally long, and its protocone is oblique. Rather similar upper cheek teeth are found in *E. fraternus* of Cedar Meadow.

- A pli protostylid is present on the P/2 and a pli caballinid on the P/3 and P/4. The occurrence of a pli protostylid on P/2 is rare in extant *Equus* species, except in *E. grevyi* where it may be considered as a good diagnostic character. Such a pli is frequently present in South American equids (Fig. 54-5) and in Sussemiones (Fig. 30-1).

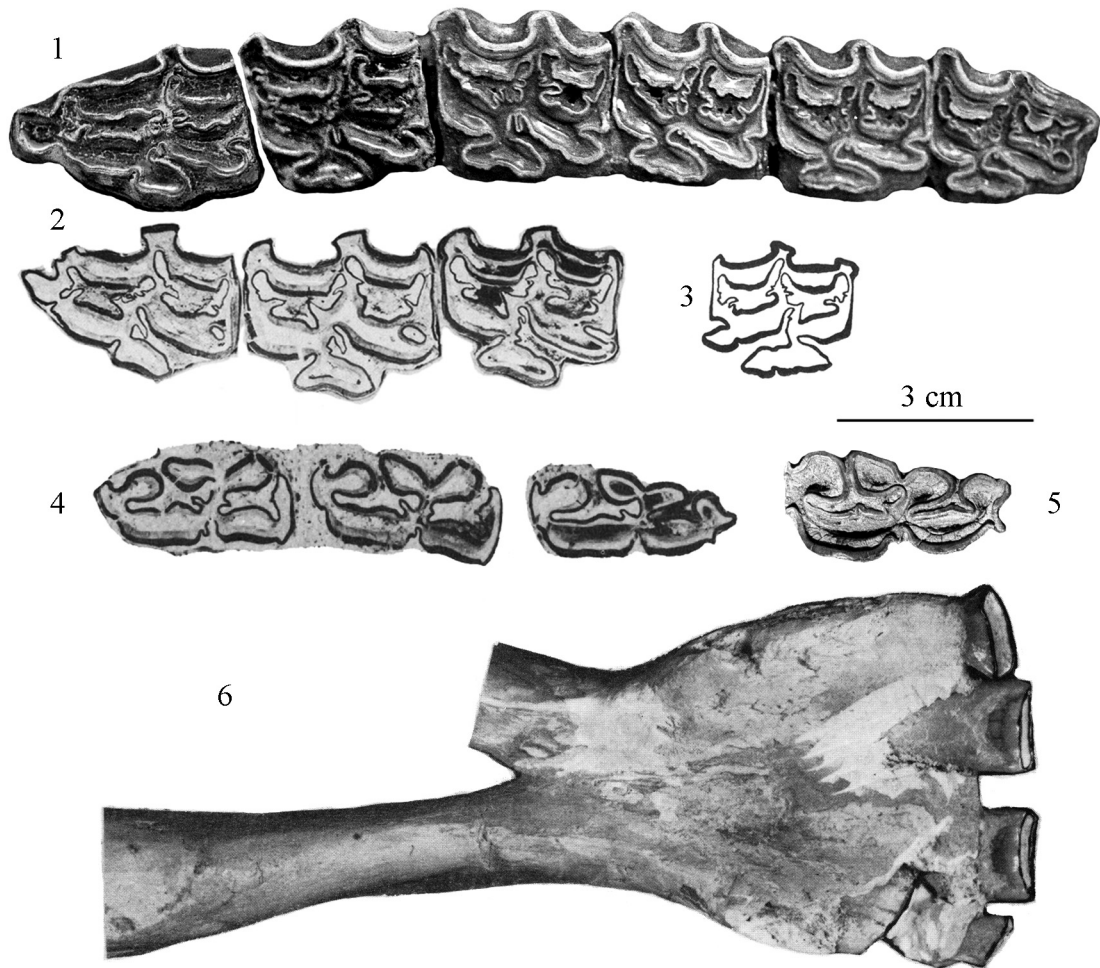


Figure 54.— *E. fraternus*, *A. pseudaltidens*, and *E. littoralis* cheek teeth. 1: *E. fraternus*, Cedar Meadow, FAM 116143. 2: *A. pseudaltidens*, Powers Ranch, BEG 31186-36, upper P2-P4. 3: *E. littoralis*, Powers Ranch, BEG 31186-13, upper P3 or P4. 4: *A. pseudaltidens*, Powers Ranch, BEG 31186-35. 5: lower P2, *Amerhippus* of Tarija, V 2565. 6: *A. pseudaltidens*, Powers Ranch, BEG 31186-35. Figures 2, 3, 4, and 6 adapted from Quinn (1957).

- The lower I1 and I2 have no cups.

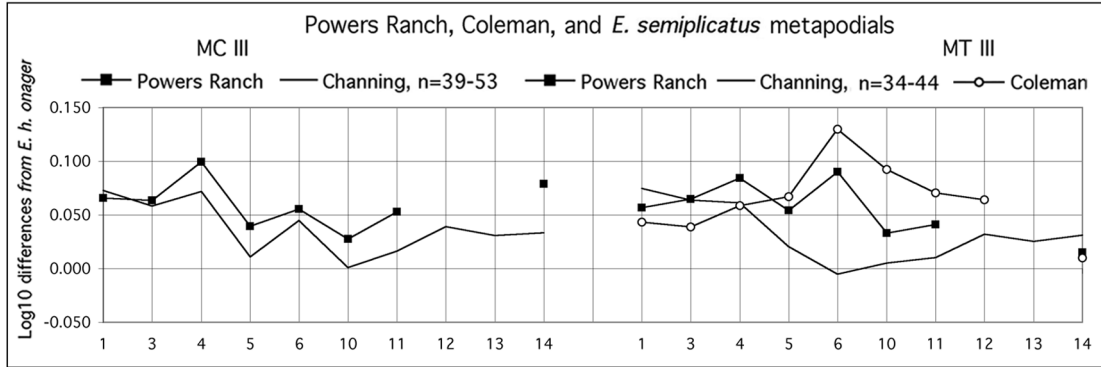


Figure 55.— Ratio diagrams of *A. pseudaltidens* (Powers Ranch, Coleman) and *E. semiplicatus* (Channing) third metapodials. n=number of specimens. Data in Tables 3, 4, 6.

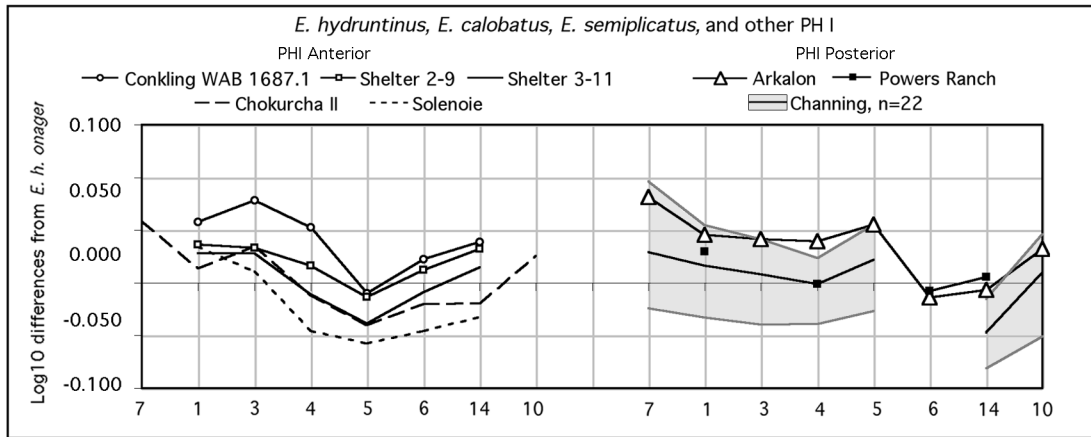


Figure 56.— Ratio diagrams of first phalanges of *E. hydruntinus* (Chokurcha II, Solenoie), *Equus* sp. (Conkling, Shelter), *E. calobatus* (Arkalon), *A. pseudaltidens* (Powers Ranch), and *E. semiplicatus* (Channing). Data in Tables 5-6.

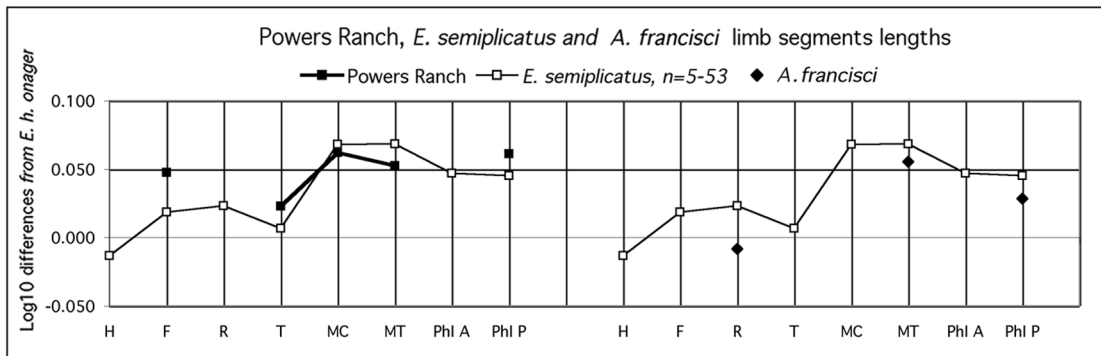


Figure 57.— Ratio diagrams of *A. pseudaltidens* (Powers Ranch), *E. semiplicatus* (Channing), and *A. francisci* limb bones lengths. Data in Table 2.

- The referred metapodials (BEG 31186-3 and 7) are long and slender but their proximal and distal ends are not so small (Fig. 55). Winans (1985) gave the dimensions of a MT from Coleman, Florida (Irvingtonian) that seems close to the Powers Ranch MT dimensions.

- The posterior first phalanx also has a more developed distal end than either *E. calobatus* or *E. semiplicatus* (Fig. 56 right).

- Metapodials are long relative to the femur and tibia, but not as much as at Channing (Fig. 57 left).

Altogether, these limb bones seem intermediate between those of typical stilt legged forms and extant hemiones. Their referral to the type teeth could be questioned because another upper premolar (BEG 31186-13), referred to *E. littoralis*, was found at the same locality. Its enamel pattern (Fig. 54-3) is more consistent with what can be expected from the proportions of the limb bones but the size is too small (21.6mm). In conclusion, the association of cheek teeth absolutely not hemione-like with slender limb bones is unusual in *Equus*. The occurrence of a pli protostylid on P/2 and the lack of cups point to an affinity with *Amerhippus*. If so, we have another slender *Amerhippus*, beside *A. francisci*.

2. *Amerhippus* sp. of Natural Trap, Wyoming, ca 12 Ky.

There is evidence for the presence of four species at Natural Trap:

- a caballine represented by the upper and lower series UNSM 51079 and by a fragment of mandible UNSM 47238 with cups on the incisors;

- a large *Amerhippus*;

- an *E. cf. conversidens*;

- a small *Amerhippus*, to which belong most specimens.

a. Large *Amerhippus*

- A badly preserved skull (UNSM 51330) is very large (basilar length: 552mm) but rather narrow. The auditory meatus seems very small (not figured on Fig. 58). The muzzle is long and uncommonly wide. The skull, such as it appears, resembles a specimen of *Amerhippus* of Tarija, Bolivia (Chicago Field Museum PM 142-14). The corresponding distal articular widths of metapodials should be more than 45mm (Appendix 4).

- Cheek teeth

The associated series UNSM 56806 VY are not quite adult. The teeth are large (176mm for the lower series). The metaconids of M/1 and M/2 are elongated (and bilobated on M/1), as in some specimens from Loufangzi and from *Amerhippus* (Figs. 23a-b, 59).

- This large species was very probably slender as shown by five humeri, one radius, three tibiae, and three third phalanges (UNSM 31447 - probably anterior; 50818 and 52567 - probably posterior; Fig. 65). According to correlations in extant slender

species the distal articular width of third metapodials would have been: MC11 around 45-45.5; MT11 around 44-44.5. One slender MC (UNSM 50987) probably belongs to this species (Fig. 62). The large and slender equid of Natural Trap is too poorly represented for a discussion of its proportions (Fig. 66).

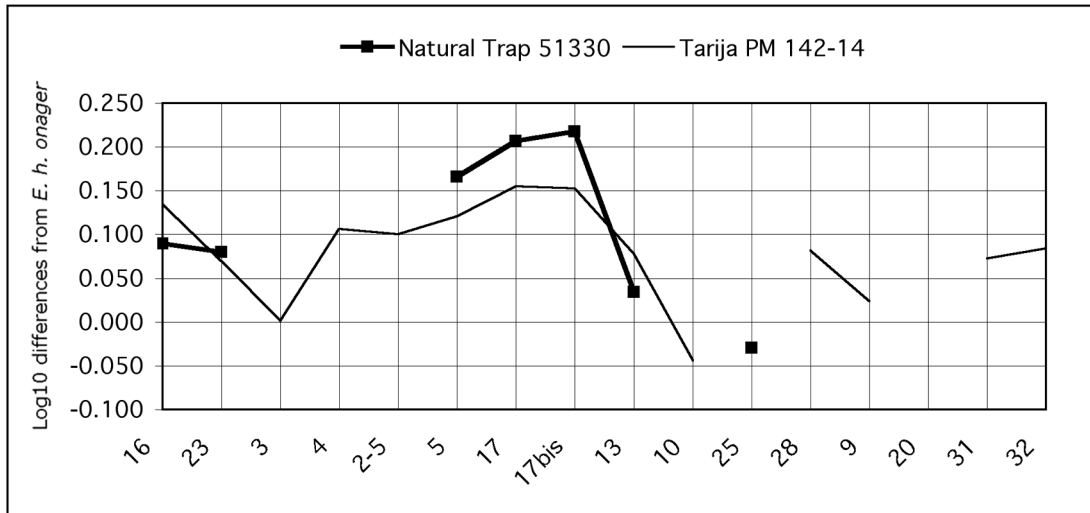


Figure 58.— Ratio diagrams of Natural Trap and Tarija skulls. Data in Table 7.

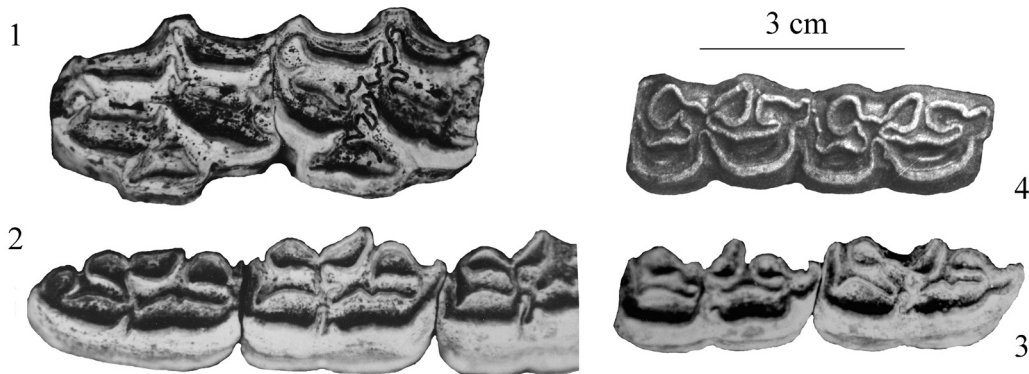


Figure 59.— Associated upper and lower cheek teeth UNSM 56806 (1-3) and lower M1-M2 (4) of *Amerhippus* (FAM, Ecuador, Oil Fields).

b. Small *Amerhippus*

It is well represented by a mandible, without cups on the incisors (Fig. 60).

On the basis of the mandible dimensions, the skull basilar length was about 437mm (Appendix 1, 3). Probably belong to the same species the lower P2-P4 UNSM 42589.

Average dimensions of twelve MC were given by Winans (1985) but we have now the data on 49-57 MC and 58-64 MT from Natural Trap measured by one of us (JH). There are also data on other limb bones. We will consider only the gracile

specimens. Their variation is very large. We have tried to sort them as well as we could.

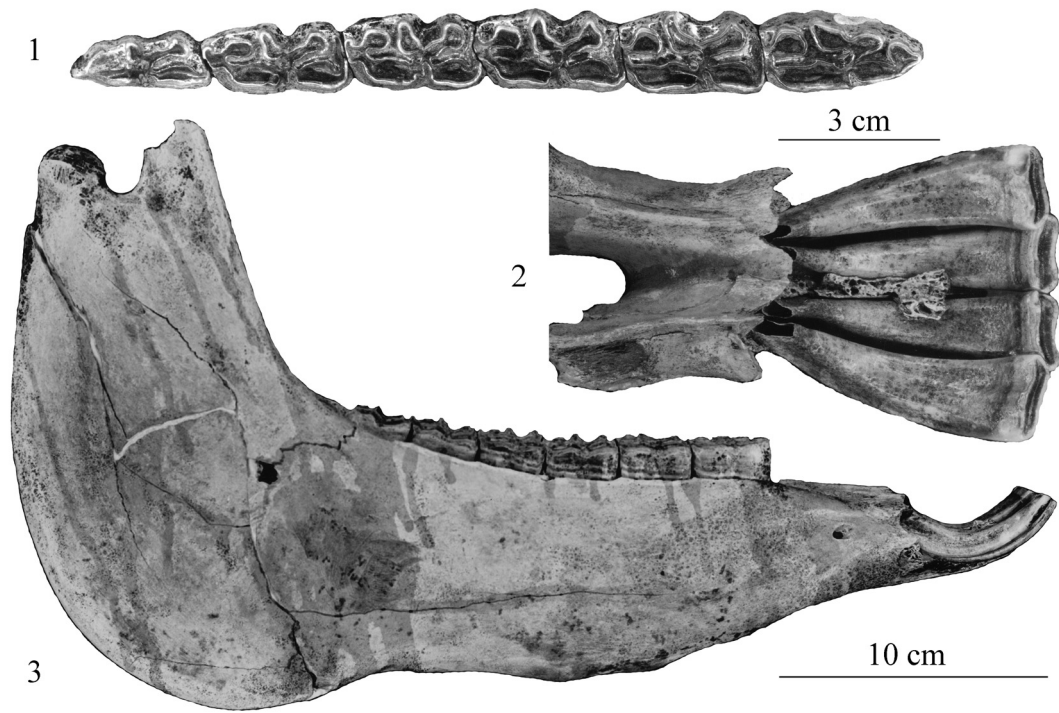


Fig. 60.— Small *Amerhippus* from Natural Trap, NT 500NW515. 1: Lower cheek teeth. 2: Symphysis. 3: Mandible.

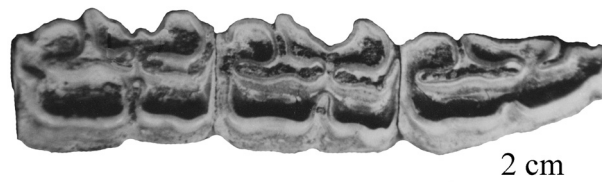


Figure 61.— Small *Amerhippus* from Natural Trap, UNSM 42589, lower P2-P4.

- Five metacarpals have abnormally small widths. Possibly they were pathological or not quite mature; they were ignored. One individual (represented by right and left metacarpals) has strange proportions (UNSM 57642); it was not included in the statistics. Another (also represented by right and left metacarpals) has deeper distal ends than the rest (UNSM 50987) and was referred to the large *Amerhippus*. The rest of gracile metacarpals (n = 46-52) may be considered as a homogeneous sample (Fig. 62). The bulk of slender MC are close in size and proportions (Figure 64 left) to extant Mongolian hemiones, *E. hemionus hemionus*, to slender equids from Yukon and Alaska (Dawson 37: NMC 35468, 35497, 35397, Dawson unknown locality: NMC 36155); (Gold Run: NMC 13472-32), and, surprisingly enough, from Pool Branch, Florida (Winans 1985).

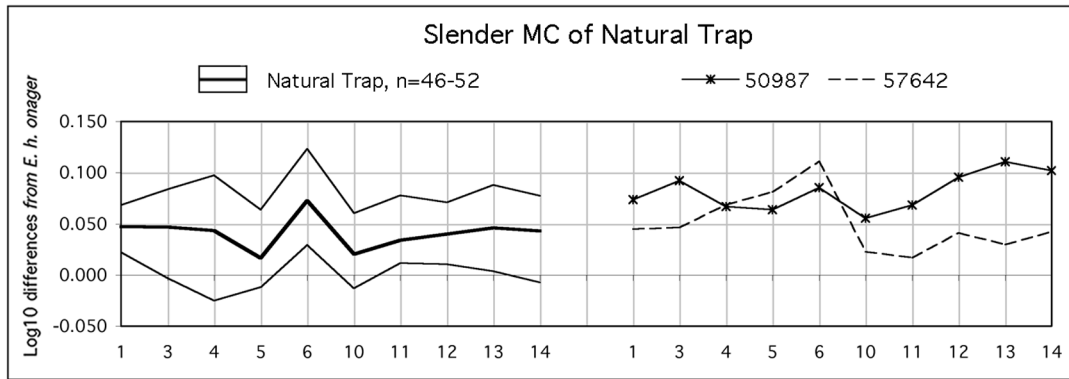


Figure 62.— Ratio diagram of Natural Trap slender MC III mean and range of variation (n=number of specimens) and of two other MC III. Data in Table 8.

- Three metatarsals (UNSM 50817 and 52203, very probably of the same individual, and UNSM 32818) have deeper distal ends than the rest. Another (UNSM 52327) is smaller and more robust (Fig. 63). Many are abnormally flat. They were not included in the statistics. The rest of gracile metatarsals (n=34) may be considered as a homogeneous sample.

The bulk of slender MT of Natural Trap are also similar to extant hemionos (Fig. 64 right) but with deeper proximal epiphyses and diaphyses. So are the MT of Dawson: NMC 25178-16 (associated to a posterior first phalanx NMC 24177), 25188-13, 34775-?, 35498-37, 37835-39, 35626-40) described by Harington & Clulow (1973).

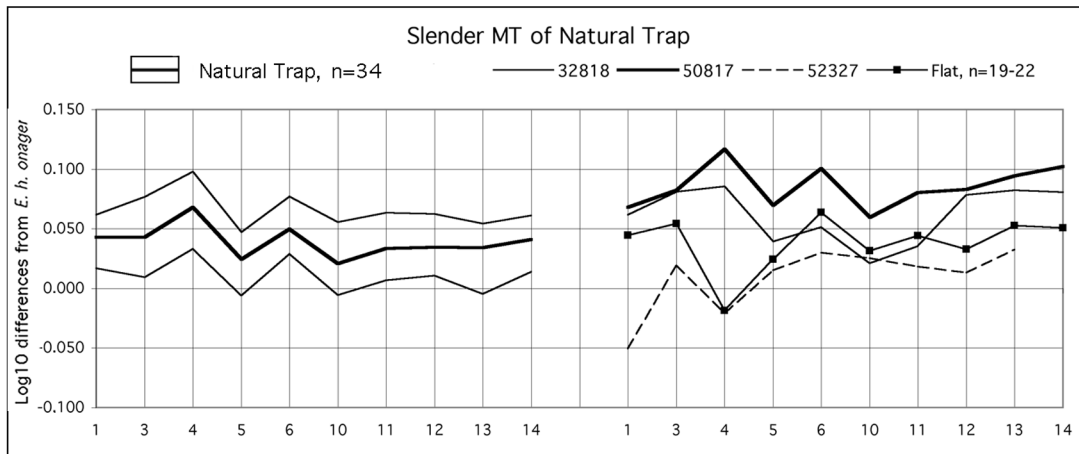


Figure 63.— Ratio diagram of Natural Trap slender MT III mean and range of variation (n=number of specimens) and other MT III. Data in Table 8.

- First Phalanges (PH1)

Again several gracile specimens (UNSM 31447 - probably anterior; 50818 and 52567 - probably posterior) differ from the bulk and were referred to the large

Amerhippus. For the rest, means of anterior phalanges of Natural Trap and extant *E. hemionus hemionus* are close; those of posterior phalanges are more different (Fig. 65).

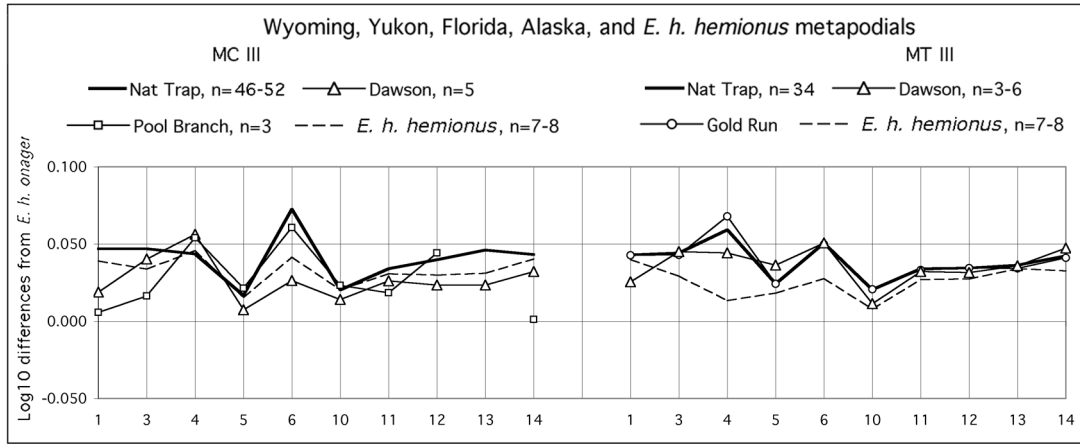


Figure 64.— Ratio diagrams of *Equus* and/or *Amerhippus* sp. (Natural Trap, Dawson, Gold Run, Pool Branch) and *E. h. hemionus* third metapodials. Data in Tables 3, 4, 8.

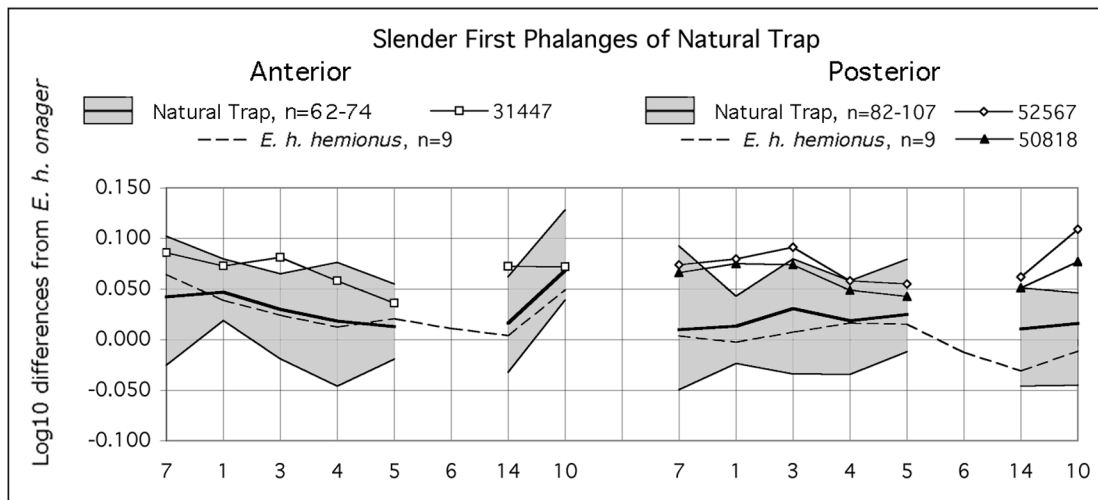


Figure 65.— Ratio diagram of Natural Trap slender PH1 mean and range of variation (n=number of specimens) and other slender PH1. Data in Table 8.

- The limb bones proportions (Fig. 66) of the best represented equid of Natural Trap are not those of a stilt-legged equid: metapodials and first phalanges are not elongated relatively to proximal bones as they are in *A. pseudaltidens* of Powers Ranch. The slender equid of Natural Trap had hemione-like proportions.

c. Interpretation

- Because of several lower cheek teeth characters and of the lack of cups, we refer to *Amerhippus* sp. the bulk of equid remains from Natural Trap. If so, that is the third

known slender *Amerhippus*. It was not a stilt-legged equid, its limb bones proportions being more hemione-like.

- We refer also to *Amerhippus* the large and slender form, much less documented but whose fragmentary skull resembles a specimen from Tarija (Bolivia).

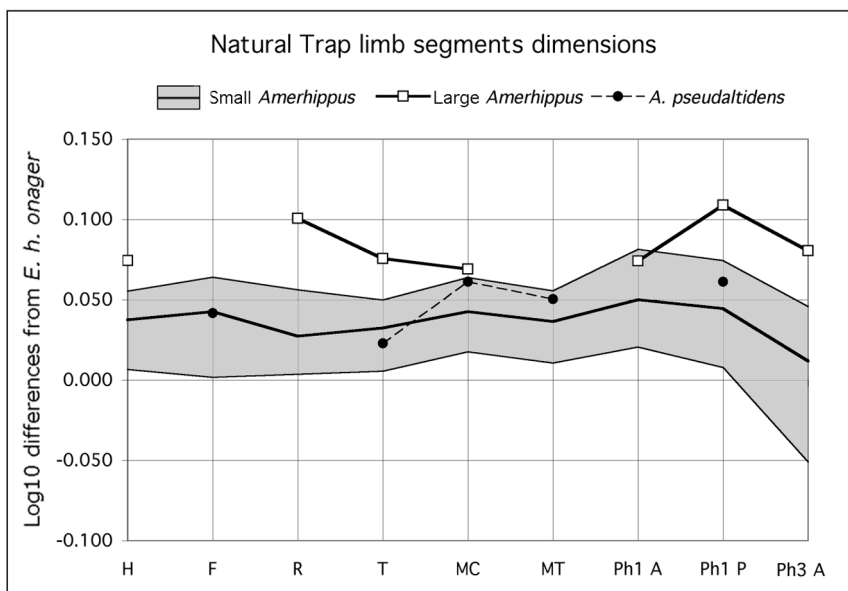


Figure 66. — Ratio diagram of limb bones lengths and third anterior phalanx width. H: humerus, F: femur, R: radius, T: tibia, MC: third metacarpal, MT: third metatarsal, Ph1 A: first anterior phalanx, Ph1 P: first posterior phalanx, Ph3 A: third anterior phalanx. Data in Table 2.

V. UNCERTAE SEDIS AND HEMIONE-LIKE *EQUUS*

As we have seen, stilt-legged forms are characterized by the relative lengths of their limb bones. When no information exists on the lengths of humerus, radius, femur, or tibia, it is difficult to decide whether some slender equid belonged to the stilt legged group or to hemione-like one.

1. *Equus* sp. B of Leisey Shell Pit A, Florida

Hulbert (1995) described as *Equus* sp. B teeth and metapodials from this Irvingtonian locality (around 1.2 Ma).

- The muzzle was probably about 120mm long and very wide. All lower incisors have well developed cups (Fig. 67).

- The upper cheek teeth have long protocones and no pli caballin; the lower cheek teeth have shallow ectoflexids and rather zebra-like double knots. Upper and lower P2 are rather short like in *E. semiplicatus* (Fig. 68). On the basis of cheek teeth length, the

skull basilar length was 400-450mm.

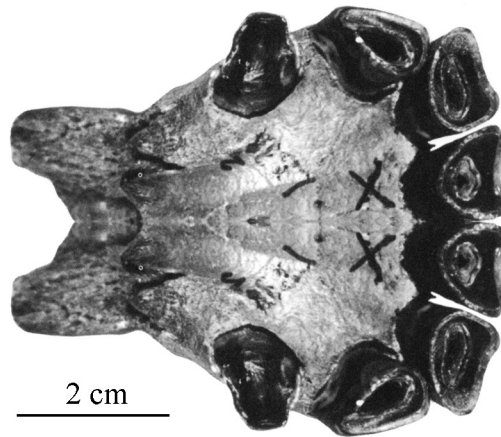


Figure 67.— Mandibular symphysis of *Equus* sp. B from Leisey Shell Pit A, UF 85785, adapted from Hulbert (1995).

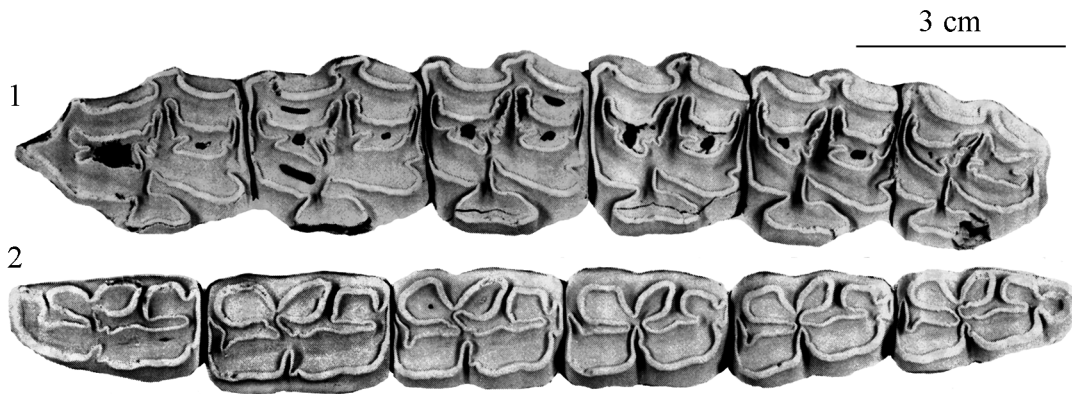


Figure 68.— Upper and lower cheek teeth of *Equus* sp. B. 1: UF 80850. 2: UF 83309. Adpoted from Hulbert (1995).

- As noted by Hulbert, metapodials resemble hemiones, and also *E. hydruntinus* (Fig. 69).

A MT from Fossil Lake, Oregon, (UCMP 2437) and another from Ingleside Pit, Texas (BEG 30907-6) published by Quinn (1957) may belong to the same form. There again, there is some likeness with *E. hydruntinus* but the distal epiphyses are larger. Pending information on the other limb bones, it is impossible to say whether *Equus* sp. B belonged to the stilt legged group.

2. *Equus* sp. of Conkling and Shelter, New Mexico, Plum Point Interstadial?

Data (Table 5) were kindly provided by A. Harris. Three first phalanges, if they are anterior, compare well with two specimens belonging to *E. hydruntinus* (Fig. 56 left).

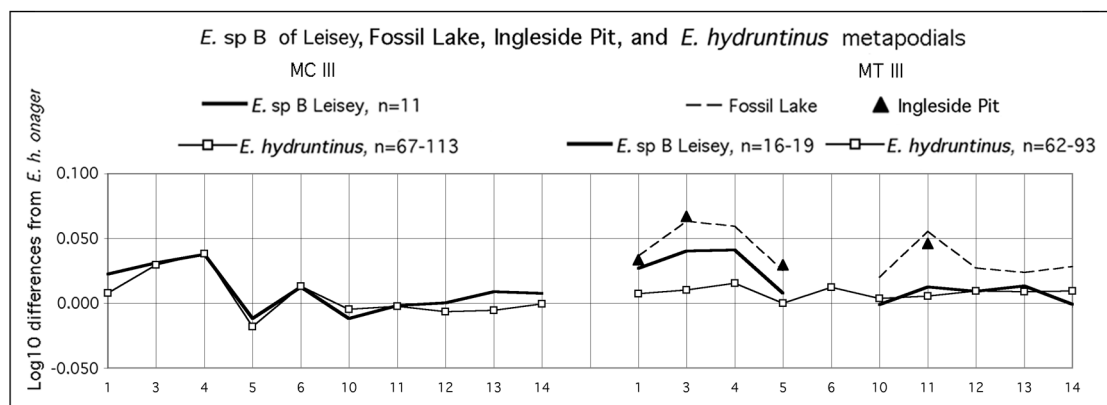


Figure 69.— Ratio diagrams of *Equus* sp. B, *E. hydruntinus*, and other (Fossil Lake, Ingleside Pit) third metapodials. Data in Table 3-4.

DISCUSSION AND CONCLUSIONS

1. Summary of characters

- Skull and teeth

The following table (Fig. 70) summarizes the main characters we used in comparing Old World Hemiones to slender New World equids.

	Lower incisors	Muzzle		Postprotoc. valley	Pli caballin	Metaconid
	Cups	Short	Wide	Deep		Elongated
Hemiones	+	+	+	+	no	+
Santo Domingo		no		no	+	+
<i>E. calobatus</i>						+
<i>E. semiplicatus</i>	+	no	no	no		+
<i>E. sp. B Leisey</i>	+	+	+	+	no	no
<i>E. tau</i>		+	+	+	no	no
<i>A. francisci</i>	no	no	no	no	no	no
<i>A. pseudaltidens</i>	no	no		+	+	
A. Nat Trap large			+	+	+	+
A. Nat Trap small	no	+	+			+

Figure 70.— Comparison of main skull and teeth characters in hemiones and New World slender equids.

It shows that there is no New World equid presenting all Hemiones characters, the closest being *E. tau* and the most unlike Hemiones - *A. francisci*.

- Third metapodials (Fig. 71)

Stilt metapodials differ from Old World extant hemiones by deep diaphyses (4) at least on MC III, relatively more narrow proximal epiphyses (5) and often by relatively larger distal articular breadths (11). By these features they resemble more *E. hydruntinus*. In the not-stilt-legged *Amerhippus* of Natural Trap (Fig. 64) proximal depths are especially developed.

- Limb segments proportions

The extreme elongation of metapodials relative to proximal bones (Figs. 32, 57) has never been found yet elsewhere than in the New World. It exists since the Late Blancan and is present in *A. francisci* which, however, differs by its skull from other stilt-legged equids.

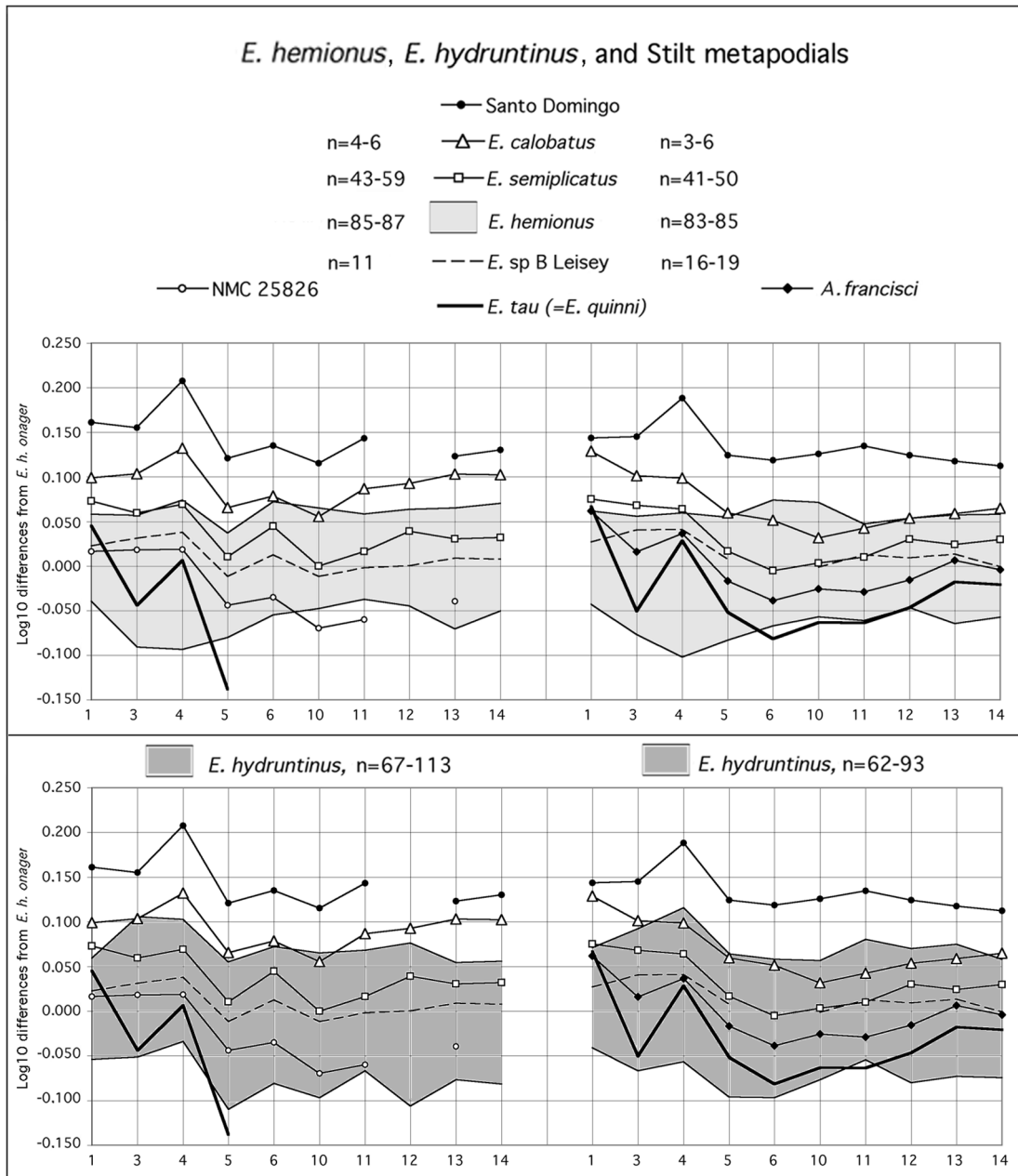


Figure 71.— Ratio diagrams of various New World slender *Equus* compared to Old World *E. hemionus* and *E. hydruntinus* third metapodials. Data in Tables 3, 4, 6, 8.

2. Discussion

A recent molecular study (Weinstock et al. 2005) brings evidence supporting the endemism of all North American stilt-legged and hemione-like equids (NWSL for short). Three calibration points based on paleontological data are used for divergence date estimations:

- 55 Ma for most recent common ancestor (MRCA) of rhinoceroses and equids,
- 3 or 4 Ma for MRCA of hippidion and NWSL,
- 1.3 Ma for the base of the caballine clade.

Old World zebras, asses, and hemiones form a basal polytomy, anterior to the node uniting hippidions, NWSL, and caballines, i.e. before 3 to 4 Ma.

From a zoological point of view, it is difficult to admit that caballines are closer to hippidions than to Old World hemiones, asses, and zebras; and even more that they interbreed with the latter after a separation of more than 3 Ma. This proximity is as astonishing as that previously found between hippidions and Old World hemiones (Orlando et al. 2003). Let us note that in that paper the studied hippidion bones were eventually (and reluctantly) assigned to *Amerhippus* by one of the authors (VE), precisely because of the surprise caused by the molecular results. It is also difficult to accept that there is nothing more than a convergence between NWSL and Old World hemiones. Admittedly, cursorial adaptations may develop in parallel. But the quite peculiar occlusal pattern of the lower cheek teeth, appearing now and again in New World (Fig. 72-1,3,4), and Old World equids (Fig. 72-2,5,6), looks more like a common genetic character than a parallelism.

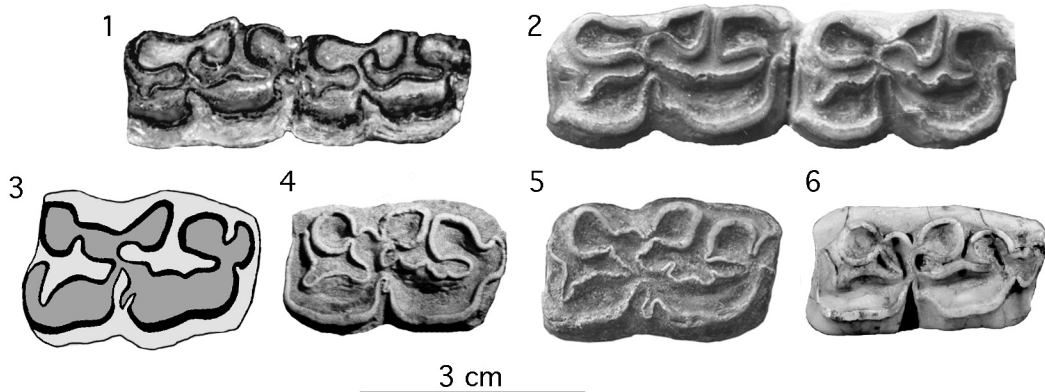


Figure 72.— New and Old World lower cheek teeth. 1: Dry Mountains, AMNH 116502, P3-P4, adapted from Azzaroli & Voorhies 1993. 2: Venta Micena, VM 84 C3 B9 12, P3-P4. 3: Arkalon Gravel Pit, UMMP 29069, M1, adapted from Hibbard 1953. 4: Tarija, V 689, P4. 5: Choukoutien, IVPP-CKT 1930-5, P3 or P4. 6: *E. kiang*, FMNH 182, M1.

3. Conclusion

We propose that Old World hemiones, Sussemiones, *Amerhippus*, and NWSL have a common origin in the Late Blancan of North America (Fig. 73).

- *Amerhippus* have originated in North America, possibly from forms like AMNH 116502 of Dry Mountains, Arizona (Fig. 33-1). Some of them became slender, like the Powers Ranch *A. pseudaltidens*, *A. francisci*, and the Natural Trap *Amerhippus*.

- Sussemiones possibly differentiated in Beringia as suggested by the lower cheek series found at Lost Chicken, Alaska (Fig. 33-5). They were extremely successful and dispersed into all Eurasia and Africa (Eisenmann 2006b). Only part of them (*E. granatensis* group) adapted to dry environments, acquiring slenderness, cursorial proportions, and relatively simple enamel pattern on the upper cheek teeth. Other (*E. coliemensis* group) exhibit large size and extremely complicated enamel patterns possibly related to humid conditions.

- In North America, true stilt-legged Equus (*E. calobatus*, *E. cf. calobatus*, *E. semiplicatus*) originated also during the Late Blancan, as shown by the *Equus* of Santo Domingo.

- *Equus* sp. B of Leisey does not look like a true stilt-legged equid. It may be at the origin of *E. tau*.

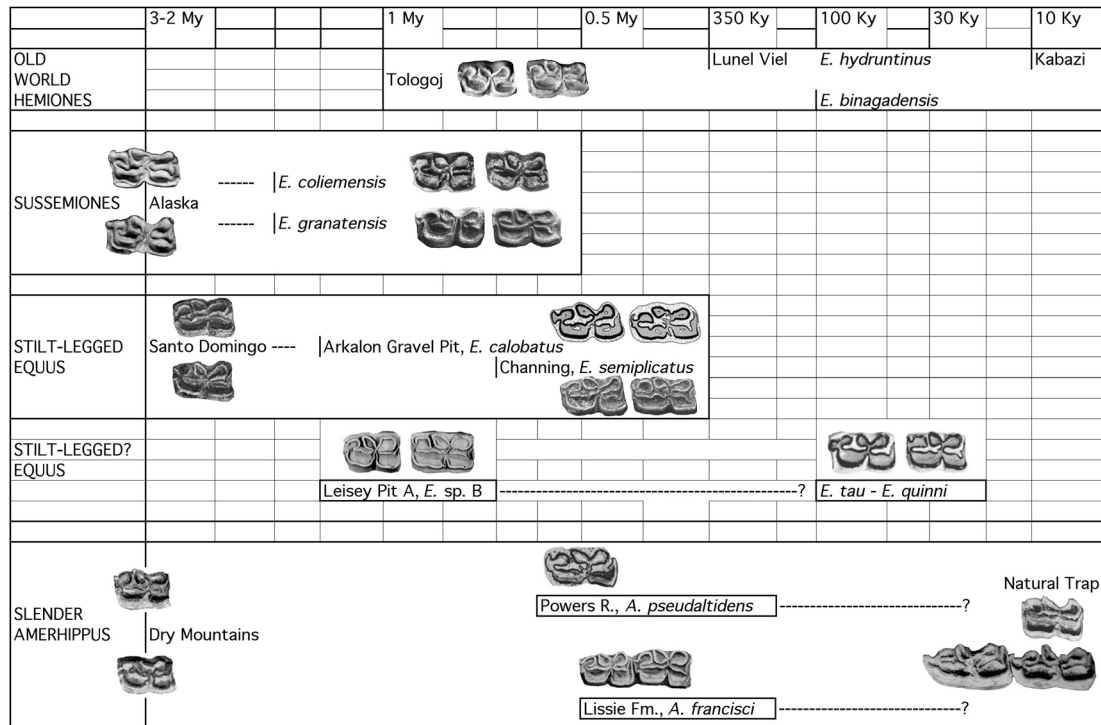


Figure 73.— Possible relationships between New and Old World equids.

- Old World hemiones differentiated later, either from a yet unknown Beringian ancestor (not necessarily slender!), or from a North American migrant that could have resembled *Equus* sp. B of Leisey. The Old World hemiones may be defined, in addition to slenderness and cursorial proportions, by the shortness of the muzzle, the development of deep post-protoconal valleys and loss of pli caballins on the upper

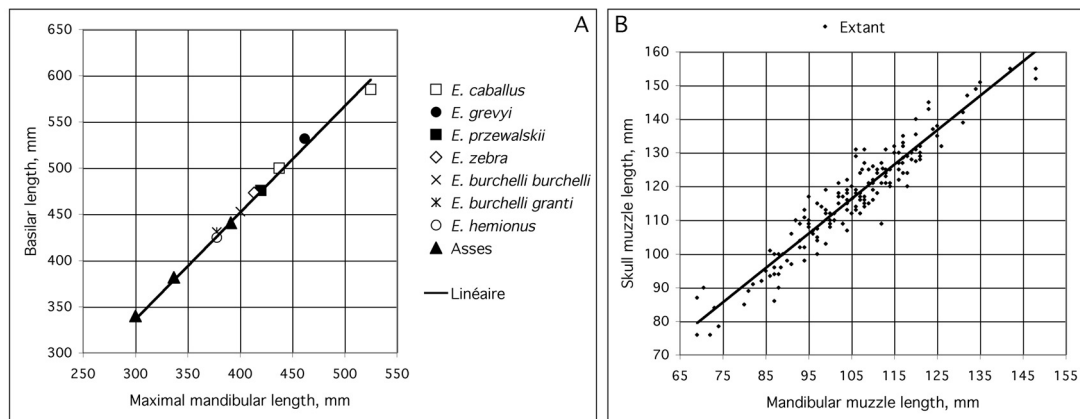
cheek teeth. *E. hydruntinus* is apomorphic by microdnty, short protocones, and shallow ectoflexids on molars.

APPENDIX

When one has to deal with fossil samples where some bones or informations are missing, it may be convenient to 'guess' the missing dimensions. Although correlations between size of bones, skulls, or dentitions are not precise, they do exist and render possible some estimations.

The following scatter diagrams illustrate these correlations. They are based on extant *Equus* associated material.

1. Relations between basilar length of the skull and maximal length of the mandible (A) and between the skull muzzle length and the mandibular muzzle length (B).

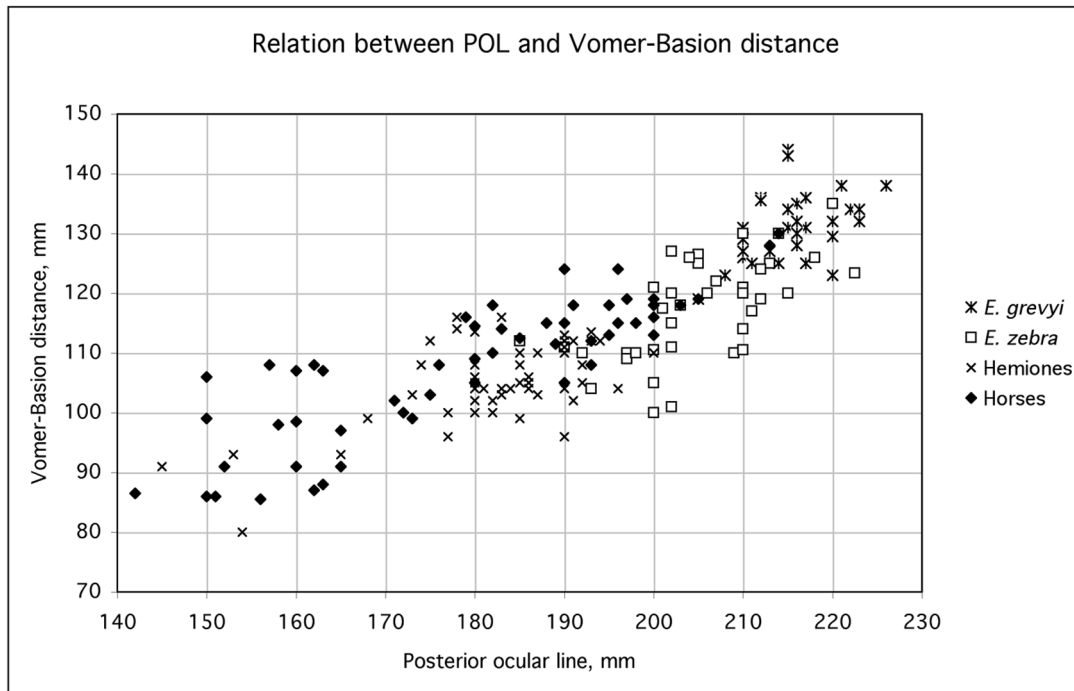


Appendix Fig. 1.— (A) is based on average dimensions observed in 61 *E. caballus*, 55 *E. grevyi*, 37 *E. przewalskii*, 59 *E. zebra*, 27 *E. africanus*, 31 *E. burchelli granti*, 31 *E. burchelli burchelli*, 28 *E. hemionus kulan*, and 52 *E. asinus*. We have added a minimum value (*E. asinus*) and a maximum value (*E. caballus*). (B) is based on 38 *E. caballus*, 9 *E. grevyi*, 35 *E. przewalskii*, 9 *E. zebra*, 9 *E. africanus*, 19 *E. burchelli burchelli*, 24 *E. hemionus kulan*, and 19 *E. asinus*.

Being based on average values, the (A) correlation is especially good: $R^2 = 0.9836$. The basilar length (y) = maximal mandibular length (x) * 1.525 - 9.5315.

The (B) correlation is good enough: $R^2 = 0.893$. The skull muzzle length (y) = mandibular muzzle length (x) * 1.0277 + 8.3459.

2. Relation between Basion-Vomer distance and Postorbital line length.



Appendix Fig. 2.— Scatter diagram (in mm) of Basion-vomer distance versus Postorbital line length based on 32 *E. grevyi*, 41 *E. zebra*, 51 hemionos (*E. hemionus* and *E. kiang*), and 55 Horses (12 *E. przewalskii* and 43 *E. caballus*).

The correlations is not so good: $R^2 = 0.744$. A rough estimation of the Basion-vomer distance is however possible. The Basion-vomer distance (y) = Postorbital line length (x) * 0.5732 + 3.236.

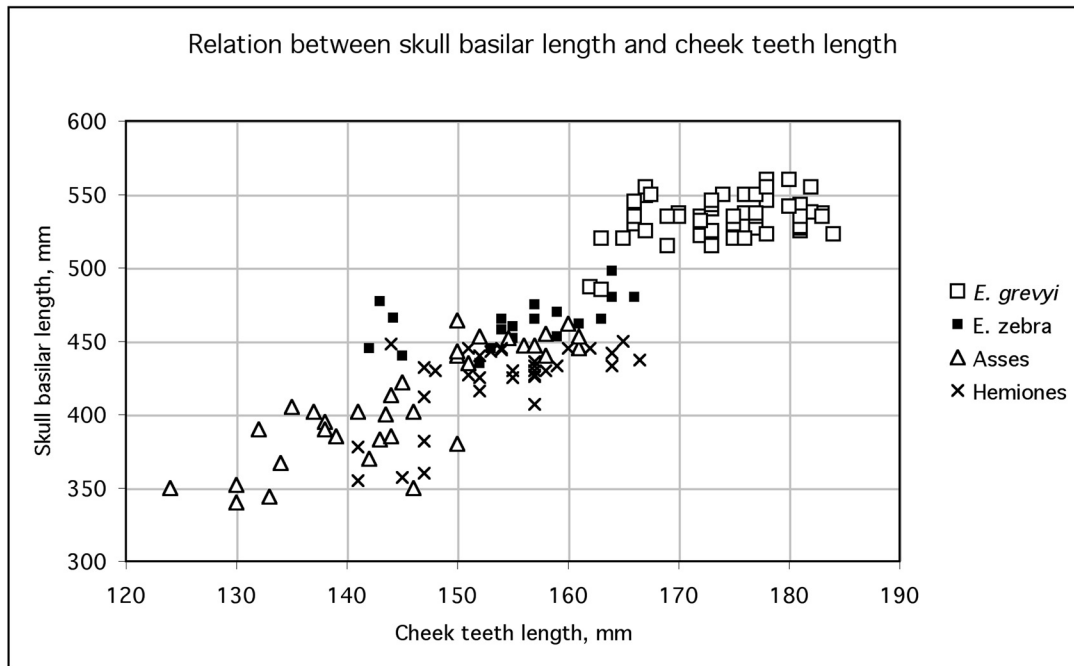
3. Relations between cheek teeth length and skull basilar length

The correlation is $R^2 = 0.8161$. The basilar length (y) = cheek teeth length (x) * 3.8974 - 154.53. The cheek teeth length (y) = basilar length (x) * 0.2094 + 61.78.

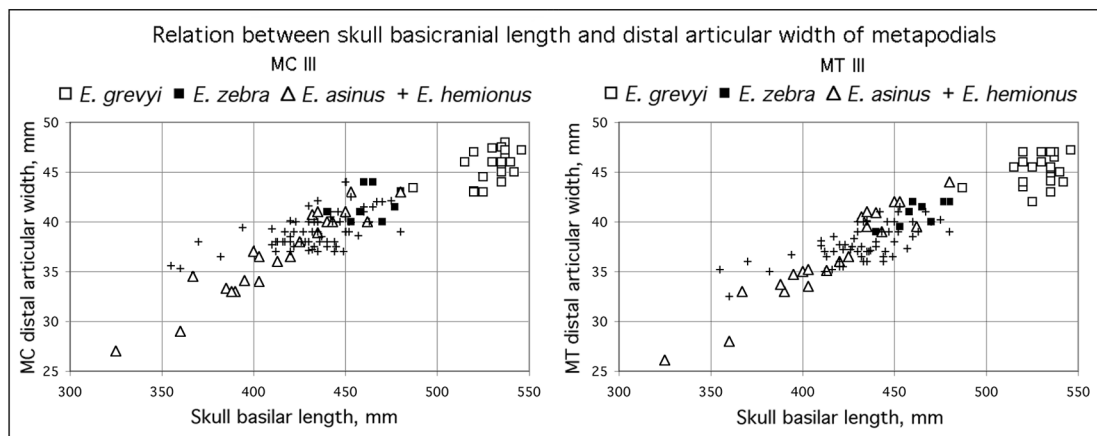
4. Relations between metapodial distal articular width and skull basilar length.

The correlation for MC is $R^2 = 0.8153$. The distal articular width of MC (y) = basilar length (x) * 0.0726 + 7.4217. The basilar length (y) = distal articular width of MC (x) * 11.227 - 0.1552.

The correlation for MT is $R^2 = 0.8511$. The distal articular width of MT (y) = basilar length (x) * 0.0782 + 4.0611. The basilar length (y) = distal articular width of MC (x) * 10.885 + 22.901.



Appendix Fig. 3.— Scatter diagram (in mm) of skull basilar length versus cheek teeth length based on 58 *E. grevyi*, 19 *E. zebra*, 34 Asses (14 *E. asinus* and 20 *E. africanus*), and 33 hemiones (*E. hemionus* and *E. kiang*).



Appendix Fig. 4.— Scatter diagram (in mm) of distal articular width of MC III versus skull basilar length (left) based on 24 *E. grevyi*, 8 *E. zebra*, 22 *E. asinus*, and 65 *E. hemionus*. Scatter diagram (in mm) of distal articular width of MT III (right) versus skull basilar length based 24 *E. grevyi*, 8 *E. zebra*, 21 *E. asinus*, and 63 *E. hemionus*.

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A simple look at the 'abbreviations for collections' at the beginning of the paper will show to how many colleagues and/or curators we are indebted for in this work. Other studied collections are referred to in the text without appearing in the list. We wish in particular to thank Dr. Deng Tao of the Institute of

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ANNEXE
(Tables)

		n=21-31	IV 13580	IV 18698	Kabazi 91	Kabazi 92	PIN 453-448	PIN 446	PIN 447	Gadjiev juv	[Gadjiev ad.]	Sjara-osso-gol	Jiling, V 2150	IA 1741
		<i>E. h. onager</i>	<i>E. hydruntinus minor</i>		<i>E. hydruntinus</i>							<i>E. hemionus</i>	<i>E. hemionus</i>	<i>E. coliemensis</i>
Basilar length	1	435			358.3							433		538
Overall palatal length	2	222	197		[220]	190						233		282
Palatal length, s.s.	2-5	115.9	[99]		117.8	104				72	[91.7]	119	108	140
Vomerine length	3	116.9		85.5						90	[111.6]		[102]	[133]
Postvomerine length	4	101			85.9 or 96.5		>112	>77		100	[112]	198		[123]
Muzzle length	5	105.2	87		102.8	84				69	[77.8]	107.5		[140]
Diastema	6	74	58		82.8	51						[82]		112
Length of P2-P4	7	86.7	81.5	78	78.4	81						94	[78]	[101]
Length of M1-M2	7bis	70.7	62.5	63	65.4	66.1	69					76		82
Upper cheek teeth length	8	156.9	145	141	143.9	149.3	148					169	[147]	[180]
Choanal length	9	63.2		56		60								59
Maximal choanal breadth	10	48.2		41.5		44	[43]					[48]		43
Minimal choanal breadth	10bis	39.6		32								54	33.5	42
Breadth between anterior borders of facial crests	11	147.1		136		101.4	[132]					151	127	164
Distance between Basion and P2	12	330.9				255.3						325		[398]
Frontal breadth	13	197.1		[180]		157.3		175		158	[194.3]			230
Bizygomatic breadth	14	181.5						162				174		210
Cranial breadth	15	99.7		[95]		65.9		94	98			103		105
Breadth of the supra-occipital crest	16	55.9						50	54			51		53
Muzzle breadth at posterior borders of I3	17	56.2	[50]			58		51		42	[51.8]	[61]		70
Muzzle breadth between interalveolar borders	17bis	40.8	36.5			44		38		34	[39.2]	[27]		55
Vertex length	18	489.8				367.5						490		590
Infra-orbital height	19	11.3		11.2		18			8					11
Height of external auditory meatus	20	14.2			16			10.2	12					16.5
Antero-posterior diameter of the orbit	21	57.9				52.2	[56]	54						62
Dorso-ventral diameter of the orbit	22	54.7		53		44.4	[56]	50						58.5
Anterior ocular line	23	348.8				370	[300]			272	[312.8]	365		440
Posterior ocular line	24	186.7			119.2	116.3		162				[180]		225
Facial height in front of P2	25	102.1				65.1	88					102		
Facial height between P4 and M1	26	122.9		110		80.7						130	109	
Facial height behind M3	27	124.3		113		71.1						128	112	
Cranial height behind the orbits	28	89.9		84		76.6		[80]	91			87	82	
Breadth at the occipital condyles	29	67.6			93			64	74			63		90
Breadth of the foramen magnum	30	31.4			29.8			28	32			34		34
Length of narial opening	31	144.2	101			100.2		125.5		111	[133.3]	149		
Cheek length	32	162.1				156		134				163	[155]	

Table 1.— Skull measurements in mm of some Old World skulls. n=number of specimens, juv: raw data of a juvenile skull, ad.: estimated corresponding dimensions of the same skull, if adult. Approximative dimensions between brackets.

				H	F	R	T	MC	MT	Ph I A	Ph I P	Ph III A (4)
VE	n=8-10	Extant	<i>E. h. onager</i>	241.3	329.7	293.5	313	214.1	250.8	76.3	71.2	54
VE	n=5-6	Extant	<i>E. kiang</i>	271.7	363.5	323	339	238.6	276.5	86.6	78.9	62.4
VE	n=4-10	Extant	<i>E. h. hemionus</i>	248.6	338.5	303.2	324.9	228.8	266.4	83.7	76.1	54.9
VE	n=11	Extant	<i>E. h. kulan</i>	248.1	338.7	296.4	322.4	220.6	258.5	78.9	72.3	58.6
VE	n=2	Extant	<i>E. h. khur</i>	238.0	324	286.5	307.5	216	247	78.4	72.2	56
VE	n=3	Extant	<i>E. h. hemippus</i>	216.3	288.3	259.3	273.8	196.5	228.3	71.3	66.8	45.8
VE	n=1	Sjara-ossogol	<i>E. h. hemionus</i>	240	321	285	305	217	273	82	72	
VE, GM	n=1-17	Romanelli	<i>E. hy. hydruntinus</i>					220	262	84.7	75.6	55.1
VE	n=1-3	Dorog	<i>E. hy. danubiensis</i>			310		225	267.7			
VE	n=1	Kecel	<i>E. hy. danubiensis</i>			300		218	255	80		60
VE	n=1-6	Agios Georgios	<i>E. hydruntinus</i>	257	342	308	338	219.5	259.2	84.4		57.5
VE	n=1	San Teodoro	<i>E. hydruntinus</i>					201	241.5			
VE	n=1-14	Lunel Viel	<i>E. hy. minor</i>	214		254		190.5	228.7	69.5	63.9	
HO	n=1	Extant	<i>Camelus arabicus</i>	363	470	455	400	330	325			
VE	n=1	AMNH 116154	Santo Domingo				395	307	344			
VE	n=1	PMYU 13470	<i>E. calobatus</i> type					285	327			
VE	n=1	FAM 87459	<i>E. calobatus</i>	272	380	362	353	285	328	95	88	
CH, VE	n=1	UMMP 29071	<i>E. calobatus</i>						338		89	
WD	n=1	TMM 882	<i>E. calobatus</i>						319	93.8		
JH	n=5-53	Channing	<i>E. semiplicatus</i>	234.1	344.2	309.6	318	250.4	293.6	85	79	
OH, EL & MS	n=1	TAMU 2518	<i>A. francisci</i>			288			285		[76]	
JQ	n=1	Powers Ranch	<i>A. pseudaltidens</i>			368		330	247	283	82	
JH	n=21-106	Natural Trap	<i>Amerhippus</i> sp. x	263	363.7	312.5	337.2	236.1	272.8	85.6	78.9	55.5
JH		Natural Trap	<i>Amerhippus</i> sp. min.	245	331	296	317	223	257	80	72.5	48
JH		Natural Trap	<i>Amerhippus</i> sp. max.	274	382	334	351	248	285	92	84.5	60
JH	n=1-5	Natural Trap	<i>Amerhippus</i> sp. large	286.4		370	372.5	251		90.5	91.5	65

Table 2.— Maximal lengths in mm of humerus (H), femur (F), radius (R), tibia (T), third metacarpal (MC), third metatarsal (MT), anterior first phalanx (Ph I A), posterior first phalanx (Ph I P) and maximal breadth of third anterior phalanx (Ph III A (4)). n=number of specimens, x= mean, min.=minimum, max.=maximum. Data origin in first column.

		<i>E. calobatus</i>	<i>E. calobatus</i>	<i>E. calobatus</i>	<i>E. calobatus</i>	<i>E. calobatus</i>	<i>E. calobatus</i>
	VE	VE	VE	MW	VE	VE	OM & WD
	Santo Domingo	Rock Creek	Arkalon	Arkalon	Seymour	Meade Co., juv	Cedazo
	AMNH 116154	PMYU 13470	FAM 87459		UMMP 46555	UMMP 27023	FC 705
Maximal length	1	307	286.5	285	275	283	284.4
Minimal breadth	3	37	34	33	33.2	35.5	31.5
Depth at level of 3	4	34	29	27.7	25.4	[27.5]	28.4
Proximal articular breadth	5	57	50.3		45.8	[48]	50.6
Proximal articular depth	6	37	33	34	34.1		36.6
Max. diameter of 3rd carpal facet	7	50	43				
Max. diameter of 4th carpal facet	8	18	15	15			
Distal max. supra-articular breadth	10	50.5	44	43	40.1	45	38.5
Distal max. articular breadth	11	53.5	45	45	42.2	45.5	42.1
Distal max. depth of keel	12		35	34	34.3	37	33.9
Distal min. depth of medial condyle	13	32	30	28.3		31	
Distal max. depth of medial condyle	14	35	31.7	31.1	30.8	33	
		<i>E. cf calobatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>
	JH		JH	JH	JH	JH	JH
	Hay Springs		Hay Springs Sh2	Hay Springs Sh5	Hay Springs Sh1	Hay Springs	Hay Springs
	UNSM 65(7 ?)86		UNSM 6242, juv ?	UNSM 6245-2	UNSM 6377	UNSM 6779-1	UNSM 6782
Maximal length	1	258.5		246.5	245	[251]	254.3
Minimal breadth	3	33			27.3	28.5	31.5
Depth at level of 3	4	30.5		21.3	27.8	25	24.7
Proximal articular breadth	5	51		41	45	47.6	43.5
Proximal articular depth	6	32			[32.6]	31.8	30.1
Max. diameter of 3rd carpal facet	7				39.3	39.9	45
Max. diameter of 4th carpal facet	8				12.8	15.6	13
Distal max. supra-articular breadth	10			36.7	43.1	42.8	37.5
Distal max. articular breadth	11				43.6	42.9	37.6
Distal max. depth of keel	12	49		29.9	[37.7]	34.9	32.4
Distal min. depth of medial condyle	13	37		24.7	25	27.7	25.4
Distal max. depth of medial condyle	14			26.4	27	28.3	25.5
		<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>E. semiplicatus</i>	<i>A. cf. francisci ?</i>
	JH	JH	VE	MW	MW	MW	VE
	Hay Springs	Hay Springs	Hay Springs Sh 6	Cueva Quebrada	Quarry G	Quarry G	Lost Chicken
	UNSM 6790	UNSM 6795	88-28-7-37, juv	n=1-2	min	G*3"	NMC 25826
Maximal length	1	250	253.0	248	230	245	220
Minimal breadth	3	32	30.0	[25]	28.3	26.3	27
Depth at level of 3	4		28.5	22	23.9	21.7	22
Proximal articular breadth	5	47.5	45.5	41	44.4	41.5	39
Proximal articular depth	6		29.5	29	29.3	28.5	25
Max. diameter of 3rd carpal facet	7		37.8	34			33.5
Max. diameter of 4th carpal facet	8		12.3	11			10
Distal max. supra-articular breadth	10		39.6	37	39.1	35.7	33
Distal max. articular breadth	11	42	40.0	37	39.7	37.4	33.5
Distal max. depth of keel	12	32	33.0	30	30.4	30.1	
Distal min. depth of medial condyle	13		26.8	25			
Distal max. depth of medial condyle	14		28.6	27	27.5	27	[22]

Table 3a.— Measurements in mm of third metacarpals. n=number of specimens, min.=minimum, max.=maximum, *hy.*: *hydruntinus*. Approximative dimensions between brackets.

	<i>E. quinni</i>	<i>A. pseudaltidens</i>	<i>Equus</i> sp.					<i>Amerhippus</i> ?
	BS et al.	JQ & MW	MW					VE
	Moore Pit	Powers Ranch	Vero					Dawson
	SMJMP 60578	BEG 31186-3	Vero min					n=5
Maximal length	1	235	246.5	248				221.2
Minimal breadth	3	23.4	30	27.7				28.4
Depth at level of 3	4	21.4	26.5	25.2				24
Proximal articular breadth	5	31.4	47.3	47.1				43.9
Proximal articular depth	6		30.8	35.5				28.8
Max. diameter of 3rd carpal facet	7							36.5
Max. diameter of 4th carpal facet	8							12
Distal max. supra-articular breadth	10		41.3	46				40
Distal max. articular breadth	11	31.6	43.5	45.5				40.8
Distal max. depth of keel	12			35.2				31
Distal min. depth of medial condyle	13							25.4
Distal max. depth of medial condyle	14		31.1	31.4				27.9
	<i>E. hemionus</i>	<i>E. h. onager</i>	<i>E. hemionus</i>	<i>E. hemionus</i>	<i>E. hemionus</i>	<i>Equus</i> sp. B		<i>Amerhippus</i> ?
	VE	VE	VE	ZX et al.	VE	RH		MW
	All	Iran	Sjara-osso-gol	Gulongshan	Tologoj	Leisey 1A		Pool Branch
	n=85-87	n=16	n=2	n=18-19	n=5-7	n = 11		n=3
Maximal length	1	215.6	212	224.5	228.5	253.4	223,1	214.7
Minimal breadth	3	26.1	25.9	27.5	29.6	32.5	27.8	26.9
Depth at level of 3	4	21.6	21.1	23	25	27.2	23	23.9
Proximal articular breadth	5	42.7	43.2	41.5	43.7	48.5	42	45.3
Proximal articular depth	6	27.9	27.1	27.8	31	31.2	27.9	31.2
Max. diameter of 3rd carpal facet	7	34.6	34.2	32.8		39.6	34.7	
Max. diameter of 4th carpal facet	8	12.6	12.3	12.8		14.5	13.6	
Distal max. supra-articular breadth	10	39.1	38.7	34.8	40.7	35	37.7	40.9
Distal max. articular breadth	11	38.8	38.5	36.5	41	29.5	38.3	40.1
Distal max. depth of keel	12	29.8	29.4	27.8	31.4	31.5	29.4	32.5
Distal min. depth of medial condyle	13	24.5	24.1	24	25	44.4	24.6	
Distal max. depth of medial condyle	14	26.4	25.9	25.9		45.2	26.4	26
	<i>E. hydruntinus</i>	<i>E. hy. hydruntinus</i>	<i>E. hy. petralonensis</i>	<i>E. hy. danubiensis</i>				
	VE	VE & GM	VE	VE				
	All	Romanelli	Petralona	Dorog				
	n=67-113	n=3-27	n=10-16	n=2				
Maximal length	1	215.6	220	234.4	225			
Minimal breadth	3	27.7	28	30.6	29.5			
Depth at level of 3	4	23	22.8	25.6	24.3			
Proximal articular breadth	5	41.4	41.4	45.5	43.5			
Proximal articular depth	6	27.9	28.2	31.2	29.5			
Max. diameter of 3rd carpal facet	7	33.7	33.6	36.7	36.3			
Max. diameter of 4th carpal facet	8	12	11.2	14	11			
Distal max. supra-articular breadth	10	38.3	39	42	41			
Distal max. articular breadth	11	38.3	38	42.3	40.3			
Distal max. depth of keel	12	28.9	29.1	32	29.1			
Distal min. depth of medial condyle	13	23.8	24.3	26.2	23.8			
Distal max. depth of medial condyle	14	25.9	26.8	28	26			

Table 3b.— Measurements in mm of third metacarpals. n=number of specimens, min.=minimum, max.=maximum, *hy.*: *hydruntinus*. Approximative dimensions between brackets.

	VE	<i>E. calobatus</i> VE	<i>E. calobatus</i> AA	<i>E. calobatus</i> AA	<i>E. calobatus</i> CH, VE	<i>E. calobatus</i> VE	<i>E. calobatus</i> VE	<i>E. calobatus</i> CH	
	Santo Domingo AMNH 116154	Rock Creek PMYU 13470	San Diego ? AMNH 116510	Rock Creek TMM 41286-1	Arkalon UMMP 29071	Arkalon UMMP 26963	Arkalon GP FAM 87459	near Arkalon UMMP 6842	
Maximal length	1	344	327	319	342	338	340	328	330
Minimal breadth	3	35	32.5			32	30	32	
Depth at level of 3	4	39	33			32	30	32	
Proximal articular breadth	5	54	46.5	45	49	44.5	45	49	
Proximal depth	6	46	41			37.5	38	41	
Max. diameter of 3rd tarsal facet	7	50	43			42	42	44	
Diameter of 4th tarsal facet	8	14	11.5			10	10	12	
Distal max. supra-articular breadth	10	51	43.3			41	40	40	
Distal max. articular breadth	11	51	43	38	43	40.3	41	42.2	
Distal max. depth of keel	12	40	34			34	35	33	
Distal min. depth of medial condyle	13	31	28			26.3	27	27	
Distal max. depth of medial condyle	14	34	30.4			30	30.4	31	
		<i>E. calobatus</i> JQ	<i>E. calobatus</i> WD	<i>E. calobatus</i> OM & WD	<i>E. cf calobatus</i> VE	<i>E. cf calobatus</i> VE	<i>E. cf calobatus</i> MW	<i>E. cf calobatus</i> RH	<i>E. cf calobatus</i> VE
		Holloman TMM 934-6	Slaton TMM 882 K337	Cedazo FC 703	Arkalon UMMP 33358	Calosahatchee FM 14323	Pool Branch min.	Pool Branch min.	Fossil Lake UCMP 2437
Maximal length	1	330	319	308.9	271	246	253	258	269
Minimal breadth	3		29.7	32.7	30	27	29.15	28.5	29
Depth at level of 3	4			32.4	34	31	30.5	30.5	29
Proximal articular breadth	5	49.5	46.2	44.6	48	44	43.7	43	43
Proximal depth	6			40.6	39	37.5	40.9	35.2	35.5
Max. diameter of 3rd tarsal facet	7				43	40		40	39
Diameter of 4th tarsal facet	8				9.5	11		9	11
Distal max. supra-articular breadth	10		41.2		46.5	43	42.5	45	40
Distal max. articular breadth	11	44	41.2	43.5	45	41.5	41.7	42.4	42.5
Distal max. depth of keel	12			32.4	36	33	30.3	33.5	32
Distal min. depth of medial condyle	13				29	[23.2]		25.5	25
Distal max. depth of medial condyle	14				32.5	27.5	25.1	29.1	28
		<i>E. cf calobatus</i> JQ	<i>E. semiplicatus</i> OM & WD	<i>E. cf calobatus</i> JH	<i>E. semiplicatus</i> VE	<i>E. semiplicatus</i> JH	<i>E. semiplicatus</i> JH	<i>E. semiplicatus</i> JH	<i>E. semiplicatus</i> JH
		Ingleside Pt ? BEG 30907-6	Cedazo FC 712	Hay Springs n=5-7	Hay S, Sh 3 UNSM 273-38	Hay S, Sh 3 UNSM 1527	Hay S, Sh 3 UNSM 1597	Hay Springs UNSM 6497	Hay Springs UNSM 6792
Maximal length	1	267	297	279.3	290	289	287.5	288	288
Minimal breadth	3	29.3	28	29.8	30.2	30.2	30.9	31	30.5
Depth at level of 3	4		28	31.6	29.5	28.7	29.1	29	29
Proximal articular breadth	5	43.4	35.4	47.2	40	40	40.5	41	39.5
Proximal depth	6			40.2	35	33.1	36.3	32.5	32
Max. diameter of 3rd tarsal facet	7			45.1	38.5	38.7	37.4		
Diameter of 4th tarsal facet	8			11.6	10	7.5	8.4		
Distal max. supra-articular breadth	10		[39.5]	45.6	37	36.7	35.8		
Distal max. articular breadth	11	41.6	38	45.3	37	36.2			36.5
Distal max. depth of keel	12		32	36.5	31	31	30.8	31	31
Distal min. depth of medial condyle	13			28.3	23.5	24.2			
Distal max. depth of medial condyle	14			31.4	27	26			

Table 4a.— Measurements in mm of third metatarsals. n=number of specimens, min.=minimum, max.=maximum, *hy.*: *hydruntinus*. Approximative dimensions between brackets.

	<i>A. francisci</i>	<i>E. quinni</i>	<i>E. quinni</i>	<i>E. tau</i>	<i>A. pseudaltidens</i>	<i>A. pseudaltidens</i>	<i>A. pseudaltidens</i>	<i>Amerhippus ?</i>	
	VE	VE	BS et al	OM & WD	JQ	MW	MW	MW	
	Trinity River	Moore Pit	Moore Pit	Cedazo	Powers Ranch	Powers Ranch	Powers Ranch	Coleman	
	TAMU 2518	SMLMP 60228	SMLMP 60174	FC 708	BEG 31186-7	BEG 31186-7	BEG 31186-7		
Maximal length	1	285	288	277	280.2	283	280	282	273
Minimal breadth	3	26	22.3	23.5	24	[29.8]	28.7	28.8	27.4
Depth at level of 3	4	27.5	27	25.5	26.2		30	31.4	29
Proximal articular breadth	5	39	36	32.2		45.5	46	46.4	47.3
Proximal depth	6	32	29				43	43.1	47.2
Max. diameter of 3rd tarsal facet	7	36.5	32						
Diameter of 4th tarsal facet	8	10	8						
Distal max. supra-articular breadth	10	36	33		[35.1]	[41.7]	40.7	41.25	47.3
Distal max. articular breadth	11	35	32.3	29	34.6	[42]	[40.3]		44
Distal max. depth of keel	12	29	27		29.8		30.55	32.1	34.9
Distal min. depth of medial condyle	13	24	22.7						
Distal max. depth of medial condyle	14	26	25				26.7	27.7	26.9
					<i>Amerhippus ?</i>	<i>Amerhippus ?</i>	<i>Equus sp. B</i>	<i>E. hemionus</i>	
					VE	VE	RH	VE	
					Dawson	Lost Chicken	Leisey 1A	Tologoj	
					n=3-6	NMC 25820	n=16-19	n=4-6	
Maximal length	1				262.2	267	263	263	287
Minimal breadth	3				27.8	28	27.5	27.5	31.1
Depth at level of 3	4				28.0	28.1	27.8	27.8	28
Proximal articular breadth	5				44.1	42	41.3	41.3	44
Proximal depth	6				39.3	36	32.5	32.5	39
Max. diameter of 3rd tarsal facet	7				40.3	40	38.2	38.2	41.5
Diameter of 4th tarsal facet	8				8.5	9	8.8	8.8	9
Distal max. supra-articular breadth	10				39.2	41.5	38.1	38.1	40.5
Distal max. articular breadth	11				40.3	40.5	38.5	38.5	43.5
Distal max. depth of keel	12				32.3	33	30.7	30.7	33
Distal min. depth of medial condyle	13				25.7	26.2	24.4	24.4	28.5
Distal max. depth of medial condyle	14				29.3	30	26.2	26.2	30.7
		<i>E. hemionus</i>	<i>E. h. onager</i>	<i>E. hemionus</i>	<i>E. hemionus</i>	<i>E. hydruntinus</i>	<i>E. hy. hydruntinus</i>	<i>E. hy. petralonensis</i>	<i>E. hy. danubiensis</i>
		VE	VE	VE	VE	VE	VE & GM	VE	VE
		All	Iran	Sjara-osso-gol	Jiling	All	Romanelli	Petralona	Dorog
		n=80-85	n=16	n=1	V 2169	n=46-93	n=1-14	n=6-21	n=1-7
Maximal length	1	251.8	247.5	280	268	254.7	262	284.4	267.7
Minimal breadth	3	25.2	25.1	24.2	28.9	26.7	27	29.2	27.3
Depth at level of 3	4	25.2	25.3	27	30.5	27.4	26	30.2	28.9
Proximal articular breadth	5	40	40.5	39	40	40.2	41	44.2	42.5
Proximal depth	6	35.3	35	39	38	33.8	33.5	38.1	36.5
Max. diameter of 3rd tarsal facet	7	36.2	36	37	40	36.4	35.5	41.4	39.3
Diameter of 4th tarsal facet	8	9.2	8.7	10		9.3	10	10.7	9.9
Distal max. supra-articular breadth	10	38.2	38.2	37	40.7	37.8	38.5	41.2	39.7
Distal max. articular breadth	11	37.6	37.4	36.1	41	37.6	36.6	42	39.3
Distal max. depth of keel	12	30.5	30.1	30.1	30.7	29.5	30	33.3	29.5
Distal min. depth of medial condyle	13	24.1	23.7	24	25.6	23.8	25	26.7	24.5
Distal max. depth of medial condyle	14	26.5	26.2	25.7	28.3	26.2	27.1	29	27

Table 4b.— Measurements in mm of third metatarsals. n=number of specimens, min.=minimum, max.=maximum, *hy.*: *hydruntinus*. Approximative dimensions between brackets.

<i>E. calobatus; E. hydruntinus</i>	VE	VE	VE	VE	VE	WD	JH	VE	VE
	Arkalon	Rock Creek	Rock Creek	Rock Creek	Rock Creek	Slaton	Hay Springs	Chokurcha II	Solenioe
PHI Anterior	FAM 87459a	PMYU 19	PMYU 78	PMYU 142, juv	PMYU 3196-97	TMM 882-285	UNSM 16355	2	no number
Maximal length	1	95	95.5	100	100.1	99	93.8	94	79
Minimal breadth	3	28.5	29	28.2	30	28	26	27.3	26.6
Proximal breadth	4	45.1	46.5	47	48.5	46	43.6	45	40
Proximal depth	5	34.1	35.3	35	35	35		34	28.1
Distal breadth at tub.	6	37.5	40	39	40.2	39.5			35
Trigunum phalangis L.	7	65	64	70	70	67			55
Supra-tub. medial L.	10	75	74	77	77	79		78	62
Infra-tub. medial L.	12	13	12	13	13	12			11.1
Distal articular breadth	14	38	37.5	38.1	39.5	37.2	36.9	37	34
	VE	VE	VE	VE	VE	VE	JH		
	Arkalon	Arkalon	Rock Creek	Rock Creek	Fossil Lake	Seymour	Hay Springs		
PHI Posterior	FAM 87459b	FAM 87459c	PMYU 3196.144	PMYU 3196.349	BK 2437	UMMP 46509	UNSM 15541		
Maximal length	1	85	88	87		79.5	82	94	
Minimal breadth	3	27	25	26.5	29.5	26	26	29.2	
Proximal breadth	4	45	45	46	49.5	45	[44.5]	50	
Proximal depth	5	35	35	34	37.2	32.6		37	
Distal breadth at tub.	6	35.5	35	38.2		32.6		36	
Trigunum phalangis L.	7	58	53	57	67	51		48	
Supra-tub. medial L.	10	63	67	64		58		59	
Infra-tub. medial L.	12	14.5	13	15		13		14	
Distal articular breadth	14	35	33.2	36		32.6		34.7	42
	JH	JH	JH	JH	JH	JH	JH		
<i>E. semiplicatus</i>	Hay Springs	Hay Springs	Hay Springs	Hay Springs	Hay Springs	Hay Springs	Hay Springs		
PHI Anterior	UNSM 15568	UNSM 15912	UNSM 8050	UNSM 8187	UNSM 18-11-7	UNSM 22-19-7			
Maximal length	1	82	90	92	90	89	85		
Minimal breadth	3	23.3	25.7	26.4	25.6	26.7	24.5		
Proximal breadth	4	41	43	44	41	45	41		
Proximal depth	5	32	35	35	33	35	34		
Supra-tub. medial L.	10	68.5	76.4	79.1	76.9	75.9	68.5		
Distal articular breadth	14	33	42	38	36	36	34		
	JH	WD & JH	WD & JH	WD & JH	WD	AH	AH	AH	
	Hay Springs	Slaton	Slaton	Slaton	Slaton	Conkling	Shelter 1010/	S-2-9	S-3-11
PHI Anterior	UNSM 8216	4666	4667	5120 or 5126	6583	WAB 1687.1	83.2	83.2	81.7
Maximal length	1	88	88.2	85.7	89	87.3	{87.5}	83.2	81.7
Minimal breadth	3	24.4	24.9	[28.2]	23.8	25.2	29.4	26.5	26.2
Proximal breadth	4	40	38.8	41.7		38.7	46.4	42.7	40.1
Proximal depth	5	32					>30.1	29.9	28.2
Distal breadth at tub.	6		36	34			38.6	37.7	35.9
Supra-tub. medial L.	10	73.9	70		31.3	33			
Distal articular breadth	14	34	33.9	34			38.9	38.3	36.8
	Hay Springs	Hay Springs	Hay Springs	Hay Springs	Hay Springs				
	JH	JH	JH	JH	JH				
PHI Posterior	UNSM 7-7	UNSM 10520	UNSM 15923	UNSM 3-20-7	UNSM 15775				
Maximal length	1	78	84	82	82	84			
Minimal breadth	3	24.9	25.5	24.4	24.7	25.5			
Proximal breadth	4	43	41	41	44	40			
Proximal depth	5	33	32	31	34	32			
Supra-tub. medial L.	10	64.3	71.1	67.8	68.3	71.6			
Distal articular breadth	14	34	35	33	33	34			
	JH	CH & DT	MS						
<i>E. francisci</i> and cf.	Hay Springs	Cragin Quarry	Papago Springs						
PHI Anterior	UNSM 38-1-9	KU 7478							
Maximal length	1	90	77.4	79					
Minimal breadth	3	21.3	20.3	19					
Proximal breadth	4	36	35.5	[35]					
Proximal depth	5	30		26					
Supra-tub. medial L.	10	75.9							
Distal articular breadth	14	32	28	29					
	OH	CH & DT							
	Trinity River	Cragin Quarry							
PHI Posterior	TAMU 2518	KU 7473							
Maximal length	1	[76]	79.6						
Minimal breadth	3	21.5	22.4						
Proximal breadth	4	36	36.4						
Distal articular breadth	14	29	30.4						

Table 5.— Measurements in mm of first phalanges (PHI). tub.: distal tuberosities, L.: length, n=number of specimens. Approximative dimensions between brackets.

Channing, MC							
	n	x	min	max	s	v	
Maximal length	1	53	250.4	239.4	262.1	5.43	2.17
Minimal breadth	3	41	29.6	27.6	33	1.37	4.63
Depth at level of 3	4	39	24.9	23	27.2	1.12	4.49
Proximal articular breadth	5	49	44.4	41	47.8	1.64	3.70
Proximal articular depth	6	44	30,0	27.1	32.2	1.18	3.94
Max. diameter of 3rd carpal facet	7	47	38.3	34.5	42	1.76	4.59
Max. diameter of 4th carpal facet	8	45	13.6	11.5	16.5	1.06	7.81
Distal max. supra-articular breadth	10	47	38.8	36	41.5	1.30	3.35
Distal max. articular breadth	11	53	39.9	37.5	44	1.35	3.38
Distal max. depth of keel	12	50	32.1	30	34	0.96	2.97
Distal min. depth of medial condyle	13	48	25.9	24	27.5	0.77	2.96
Distal max. depth of medial condyle	14	47	28,0	26	30	0.94	3.36
Channing, MT							
	n	x	min	max	s	v	
Maximal length	1	43	293.6	280	309	6.57	2.24
Minimal breadth	3	34	29	26.3	32	1.38	4.76
Depth at level of 3	4	37	29.1	26.5	34.9	1.56	5.37
Proximal articular breadth	5	40	42.5	38.7	46	1.66	3.90
Proximal depth	6	35	34.6	32.7	38.9	1.32	3.83
Max. diameter of 3rd tarsal facet	7	35	40.6	36.5	45	1.93	4.74
Diameter of 4th tarsal facet	8	35	10.3	8	13	1.02	9.88
Distal max. supra-articular breadth	10	37	38.6	35	42.5	1.33	3.44
Distal max. articular breadth	11	44	38.3	36	43.3	1.38	3.61
Distal max. depth of keel	12	42	32.4	31	34	0.76	2.35
Distal min. depth of medial condyle	13	41	25.1	23.5	27.5	0.86	3.42
Distal max. depth of medial condyle	14	39	28.2	24.5	30	1.14	4.04
Channing, PHI Anterior							
	n	x	min	max	s	v	
Maximal length	1	32	85.1	80	92,0	2.89	3.39
Minimal breadth	3	32	25.6	23.6	27.2	1.05	4.08
Proximal breadth	4	32	41	38.8	43,0	1.13	2.76
Proximal depth	5	32	32.1	30	34,0	0.94	2.93
Trigunum phalangis length	7	32	57.2	51.8	66.7	3.60	6.3
Supra-tub. medial length	10	32	64.8	59	70	2.64	4.08
Infra-tub. medial length	12	32	12.9	10	15	1.39	10.76
Distal articular breadth	14	32	34.2	32.4	36.4	1.07	3.13
Channing, PHI Posterior							
	n	x	min	max	s	v	
Maximal length	1	22	79.4	71	86.8	3.66	4.61
Minimal breadth	3	22	25	22.4	27	1.38	5.52
Proximal breadth	4	22	41	37.6	43.4	1.52	3.71
Proximal depth	5	22	32.4	29	35	1.42	4.37
Trigunum phalangis length	7	22	51.4	45.5	60	3.78	7.35
Supra-tub. medial length	10	22	59.8	52	65	3.66	6.13
Infra-tub. medial length	12	22	13.3	10	19	1.86	14.03
Distal articular breadth	14	22	31.9	29.5	34.3	1.44	4.50
<i>E. h. onager</i> , PHI Anterior							
	n	x	min	max	s	v	
Maximal length	1	15	76.5	73.3	82	2.27	2.96
Minimal breadth	3	15	24.6	23	26	1.02	4.17
Proximal breadth	4	15	41.1	38.5	44	1.68	4.07
Proximal depth	5	15	30.8	28.5	34	1.53	4.97
Distal supra-articular breadth	6	15	36.7	34	41.8	1.98	5.40
Trigunum phalangis length	7	14	48.1	45	53	2.54	5.29
Supra-tub. medial length	10	14	58.5	56	62	2.06	3.52
Infra-tub. medial length	12	14	10.3	8.8	12	0.94	9.09
Distal articular breadth	14	15	35.6	33.3	38.5	1.53	4.29

Table 6.— Measurements in mm of third metacarpals (MC), third metatarsals (MT), and first phalanges (PHI) of *E. semiplicatus* from Channing and of first anterior phalanges of *E. h. onager*. tub.: distal tuberosities, n=number of specimens, x= mean, min.=minimum, max.=maximum, s=standard deviation, v=coefficient of variation (100*s/x).

	AA	VE	VE	VE	VE	VE	VE	OM & WD, AA	VE	CH 1955	OM & WD	JH	VE	
	San Diego		<i>E. semiplicatus</i>				Hay Springs	<i>A. francisci</i>	<i>E. tau</i>	<i>E. fraternus</i>	<i>E. mexicanus</i>	' <i>E. calobatus</i> '	<i>Amerhippus</i> sp.	<i>Amerhippus</i>
	AMNH 8600	16-391	FAM 116156	FAM 116158	54-1074-1	UNSM 1349	Lissie Fm.	Cedazo	Cedar Meadow	Tequiquiac	Cedazo	FC 686	Natural Trap	Tarija
							Cast	FC 673	two skulls	MNHN 48	FC 678	FC 686	UNSM 51330	PM 142 14
Basilar length	1		446		>434	471	420		[535]	527			552	515
Overall palatal length	2	[234]	244	244		246	212	[192.2]	295	292				280
Palatal length, s.s.	2-5	[114]	120	122	115.8	125	100	[103.6]	143	[161.1]				143
Vomerine length	3	[114]				>103	98		128	125				119
Postvomerine length	4		96				111			115				130
Postpalatal length	3+4		208		202	223	209							242
Muzzle length	5	[120]	117.6	123		121	112	[86]	152	[130.9]	[144.3]			137
Diastema	6	[90]	87	92			75	[68]	120	89.7	114		152	
Length of P2-P4	7		82	79	79	87	73	[58]	96	103	101.1	99.6	111	94
Length of M1M2	7bis		69		69	79	62	[58]	78	88			95	82
Upper cheek teeth length	8	[159]	151		149	163.3	137	118.4	172	198		181	80	177
Choanal length	9		54.6		56	70	60		[66]				174.5	66
Maximal choanal breadth	10	[45]	45		42	48	39		54	[47.7]				43
Minimal choanal breadth	10bis		35		33	41	32		43					37
Breadth between anterior borders of facial crests	11			148					160					
Distance between Basion and P2	12		334.6		332		312						[180]	
Frontal breadth	13	[195]	210	210	[192]	[200]	178		218	236	[220]		403	[234]
Bizygomatic breadth	14			[182]	174.2	202	169		230		216		212	208
Cranial breadth	15		102				96		114		105			
Breadth of the supra-occipital crest	16		58	59		59	[59]		[72]	85	>58.1			78
Muzzle breadth at posterior borders of I3	17	[66]	60	62		61	58	51	60	90	[90]		70.3	79
Muzzle breadth between interalveolar borders	17bis	[39.3]	42	38	42	39	39		44	[53.1]			89	59
Vertex length	18				[495]								68.5	
Infra-orbital height	19			9	[10]		8		16		613			
Height of external auditory meatus	20												10.9	
Antero-posterior diameter of the orbit	21		[61]	59		61	62	52	63	72			8.6	63
Dorso-ventral diameter of the orbit	22			58		56	54	52	57	63.5			52.5	52
Anterior ocular line	23	[348]	320 or 337	340		360	315	[280.4]	425	[406.7]			55.8	405
Posterior ocular line	24	[150]			162 or 166	[175]							415	223
Facial height in front of P2	25		[64]	86		84	[90]		104	[114.9]			210	
Facial height between P4 and M1	26		112	110					132				94.8	
Facial height behind M3	27								158				139	
Cranial height behind the orbits	28		92	92		[70]	[90]		[117]				140	[108]
Breadth at the occipital condyles	29		73	78		75	67							
Breadth of the foramen magnum	30		36	33.5		29	34						82	
Length of narial opening	31	[150]	145	[148]	[142]	[138]	[120.5]	[107]	173	[187.5]			38	169
Cheek length	32	[150]	[151]	[163]	145	[176]	150.5	[130.6]	198	[166.2]				197

Table 7.— Skull measurements (in mm) of some New World skulls. Approximative dimensions between brackets.

Natural Trap, MC								UNSM 50987	UNSM 57642	
	n	x	min	max	s	v				
Maximal length	1	48	236.1	223	248	6.25	2.65	251	235	
Minimal breadth	3	51	28.8	25.7	31.4	1.23	4.26	32	28.8	
Depth at level of 3	4	52	23.3	19.9	26.4	1.76	7.54	24.6	24.7	
Proximal articular breadth	5	51	44.8	42	50	1.58	3.52	50	52	
Proximal articular depth	6	51	32	29	36	1.67	5.23	33	35	
Max. diameter of 3rd carpal facet	7	51	37.3	34.5	42	1.70	4.57	41.3	36	
Max. diameter of 4th carpal facet	8	49	13.4	11	16.3	1.25	9.30	14.3	14.8	
Distal max. supra-articular breadth	10	51	40.6	37.6	44.5	1.45	3.57	44	40.8	
Distal max. articular breadth	11	46	41.6	39.5	46	1.54	3.71	45	40	
Distal max. depth of keel	12	49	32.2	30.1	34.6	1.13	3.50	36.6	32.3	
Distal min. depth of medial condyle	13	50	26.8	24.3	29.5	1.06	3.97	31.1	25.8	
Distal max. depth of medial condyle	14	48	28.7	25.5	31	1.13	3.94	32.8	28.6	
Natural Trap, MT								UNSM 32818	UNSM 50817	UNSM 52327
	n	x	min	max	s	v				
Maximal length	1	34	272.8	257	285	6.74	2.47	285	289	220
Minimal breadth	3	34	27.7	25.6	29.9	1.30	4.71	30.2	30.3	26.2
Depth at level of 3	4	34	29.6	27.3	31.7	1.11	3.75	30.8	33.1	24.1
Proximal articular breadth	5	34	42.9	40	45.2	1.32	3.09	44.4	47.6	42
Proximal depth	6	34	39.3	37.7	41.8	1.32	3.36	39.4	44.1	37.5
Max. diameter of 3rd tarsal facet	7	34	40.1	35.1	40.5	1.08	2.85	38.7	43.7	41
Diameter of 4th tarsal facet	8	34	8.9	6.8	11.6	1.06	11.90	6.8	10.8	8.5
Distal max. supra-articular breadth	10	34	40.1	37.7	43.4	1.48	3.70	40.1	43.8	40.5
Distal max. articular breadth	11	34	40.4	38	43.3	1.36	3.37	40.6	45	39
Distal max. depth of keel	12	34	32.5	30.8	34.7	1.00	3.07	36	36.4	31
Distal min. depth of medial condyle	13	34	25.6	23.4	26.8	0.77	2.99	28.6	29.4	25.5
Distal max. depth of medial condyle	14	34	28.8	27.1	30.2	0.74	2.57	31.6	33.2	
Natural Trap, PHI Anterior								UNSM 31447		
	n	x	min	max	s	v				
Maximal length	1	74	85.6	80	92	2.73	3.20	90.5		
Minimal breadth	3	74	26.3	23.5	28.5	0.92	3.51	29.6		
Proximal breadth	4	70	42.8	37	49	1.88	4.39	47		
Proximal depth	5	70	31.7	29.5	35	1.18	3.71	33.5		
Trigunum phalangeis length	7	62	53.3	45.4	60.8	3.88	7.28	58.6		
Supra-tub. medial length	10	66	68.6	64	78.5	2.91	4.25	69		
Infra-tub. medial length	12	66	11.1	7	16	2.27	20.46	12		
Distal articular breadth	14	72	36.9	33	41	1.46	3.96	42		
Natural Trap, PHI Posterior								UNSM 50818	UNSM 52567	
	n	x	min	max	s	v				
Maximal length	1	106	78.9	72.5	84.5	2.55	3.23	91	92	
Minimal breadth	3	107	26.3	22.7	29.5	1.08	4.08	29.1	30.3	
Proximal breadth	4	98	42.9	38	47	1.64	3.81	46	47	
Proximal depth	5	102	32.6	30	37	1.23	3.78	34	35	
Trigunum phalangeis length	7	82	49.2	42.9	59.5	3.55	7.22	56	57	
Supra-tub. medial length	10	89	60.7	52.7	65	2.86	4.72	69.8	75.2	
Infra-tub. medial length	12	88	11.4	8	17	1.79	15.78	14.2	14.3	
Distal articular breadth	14	105	36.4	32	40	1.34	3.67	40	41	

Table 8.— Measurements in mm of third metacarpals (MC), third metatarsals (MT), and first phalanges (PHI) of *Amerhippus* sp. from Natural Trap tub.: distal tuberosities, n=number of specimens, x= mean, min.=minimum, max.=maximum, s=standard deviation, v=coefficient of variation (100*s/x).