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North American Caballines and Amerhippines of the Past 1 Million Years (Part 1)

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Abstract

Horses were widely distributed in North America during the Pleistocene epoch and their fossil remains are common in sedimentary deposits of this age. Despite their rich fossil record, the systematics and taxonomy of North American Pleistocene horses remain unresolved. We evaluated a large sample of cranial and postcranial horse fossils of Irvingtonian and Rancholabrean North American Land Mammal Age. In this study, we present Part 1 of our evaluation, which centers on caballine horses, *Equus* (*Equus*). We present data (measurements and photographs) and analyses (Simpson's ratio diagrams, scatter diagrams, and anatomical comparisons) that reveal morphological variation in North American caballine horses. These analyses serve as the basis for recognizing different morphospecies: *E. (E.) scotti*, *E. (E.) alaskae*, *E. (E.) lambei* (the latter two possibly representing "ecological variants" of a single species), *E. (E.) niobrarensis*, *E. (E.) pacificus*, and *E. (E.) complicatus*. How these morphospecies (or chronospecies or ecological variants) were phylogenetically related remains to be evaluated. *Equus (E.) hatcheri* may be considered as a morphological variant or chronological variant of *E. (E.) niobrarensis*. *Equus holmesi* is considered a junior synonym of *E. (E.) scotti*, while *E. bautistensis* may be regarded as a junior synonym of *E. (E.) pacificus*. *Equus laurentius* is a junior synonym of *E. (E.) caballus*, a synonymy proposed previously in other studies. We are uncertain about the nature of *E. midlandensis*. In addition, we identify morphometric and anatomical features that distinguish between *Equus* (*Equus*), North American *Equus* (*Amerhippus*), and *Equus* (*Hesperohippus*) *mexicanus*. This study aims to advance our understanding of the taxonomy of North American Pleistocene horses, providing a thoroughly documented catalogue as a basis for further studies.

Keywords: Pleistocene; equids; taxonomic review; *Equus*; *Amerhippus*; *Hesperohippus*; Canada; United States; Mexico



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1. Introduction

A number of studies have attempted to clarify the taxonomy of North American Pleistocene equids (e.g., [1–8]); despite these efforts, the taxonomy of this group remains unresolved. This is particularly problematic for Irvingtonian and Rancholabrean North American Land Mammal Age equids, as exemplified (Figure 1) in a recent literature survey of North American fossil horses [8]. The present work represents another attempt at

advancing our understanding of the systematics and taxonomy of North American Pleistocene equids, particularly caballine equids. At least, it provides a thoroughly documented catalogue as a basis for further studies.

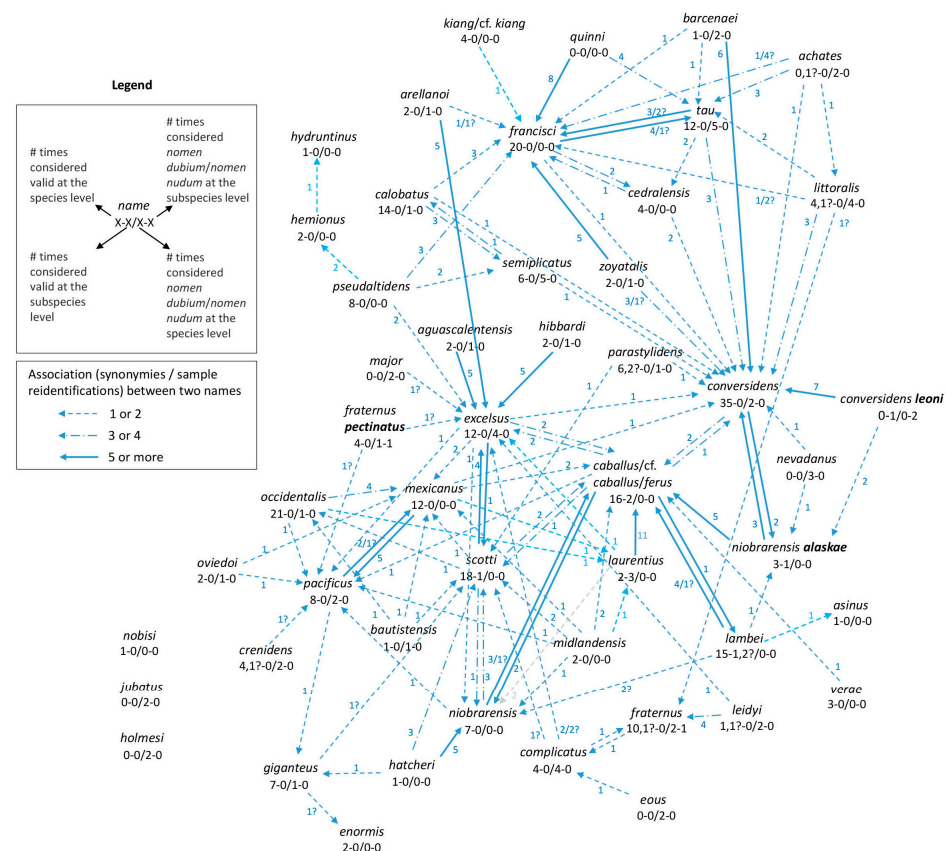


Figure 1. Taxa concept map of Irvingtonian and Rancholabrean equids based on a survey of 68 publications (modified from [8]). Numbers below names indicate the number of times a name was considered valid at the species or subspecies level and the number of times it was considered a nomen nudum or nomen dubium. Names in bold were originally described at the subspecies level, but were evaluated at the species level separately from the species names they were described under (e.g., *alaskae* was evaluated separately from *niobrarenensis*). The arrows denote the direction of synonymies and reidentifications of specimen samples. Numbers next to arrows indicate the number of times a name was synonymized with another and/or the number of times a sample was reidentified under another name. # = number; ? = uncertainty in the taxonomic conclusion as presented in the studies surveyed.

We analyzed cranial morphology (especially cranial proportions) to characterize North American caballine forms, but we also studied other skeletal elements including metapodials and dentition. We discuss anatomical features that allow discrimination between caballine, *Equus* (*Equus*), and amerhippine, *Equus* (*Amerhippus*), equids. We also discuss the peculiar case of *Equus* (*Hesperohippus*) *mexicanus*, which occupies an intermediate position between caballines and amerhippines. Our study is based on extensive comparisons of North American fossils with Old-World fossils, South American fossils, and extant species.

Previous morphological work recognized that extant species of *Equus* and several fossil forms possess a relatively large brain case [9]. This characteristic has been used to distinguish the genus *Equus* from two other phylogenetically close genera: *Plesippus* and *Allohippus* [9–11]. Some studies support the distinction between *Equus*, *Plesippus*, and *Allohippus* (e.g., [12]), but others do not (e.g., [13]). There is, however, agreement about the inclusion of caballines within *Equus* (e.g., [9–16]). Some recent studies also suggest that amerhippine equids belong within

the genus *Equus* (e.g., [12,14]). We provide further comments on the evolutionary relationship of caballine and amerhippine equids in Section 3.

In this article, we consider caballine and amerhippine equids as distinct subgenera: *Equus* (*Equus*) and *Equus* (*Amerhippus*). Morphological features that differ between caballines and amerhippines are discussed in Section 3. We are currently working on the second part of this study concerning amerhippines that will provide detailed descriptions, measurements, and an evaluation of the taxonomic status of *Haringtonhippus* and other slender-legged equids. Our study is divided in two parts to make it more manageable for ourselves and for the reader: one for North American caballines and *Equus* (*H.*) *mexicanus* and a second for North American amerhippines and *Equus* (*Sussemionus*) [17].

2. Preliminaries

2.1. Material

For our analyses and comparisons, we used data (including photographs and drawings) from the literature and data/photographs kindly provided by colleagues and museum curators (as indicated in the species accounts below and acknowledgements), in addition to data and photographs that we have personally collected. The data and figures in the main text and information and figures in the Supplementary Materials (Supplementary Files and Tables) present all relevant data used in our study. Other information (listings and complete data sets) may be found at <https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES> (accessed on 1 July 2024) and/or https://drive.google.com/drive/folders/1LXQTUaU54E9OaBzBIVkoOleUBgDrQqs6?usp=drive_link (accessed on 1 July 2024).

2.2. Methods of Description and Classification

The “corner stone” of our study is the cranial morphology (mandibular morphology is of a much lesser diagnostic value), but we also compare lower cheek teeth, upper cheek teeth, and limb bone proportions to distinguish groups of species. Recent studies have shown that the morphology of the cheek teeth (e.g., [16,18–20]) and metapodials (e.g., [19]) can be useful in the discrimination of extant and fossil equid species.

2.2.1. Cranial Morphology

We primarily used the relationships between various cranial measurements that may characterize specific groups. Supplementary File S1 is a schematic of an *Equus* cranium with all the measurements we may use; Figure 2 presents the fundamental basilar ones.

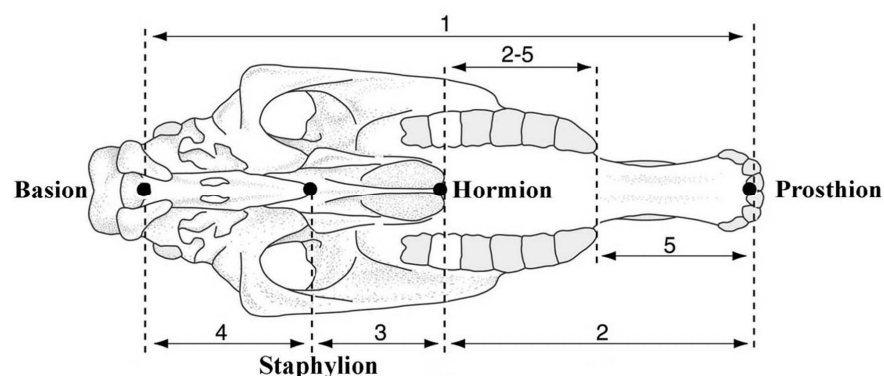


Figure 2. Schematic occlusal view of an *Equus* cranium. 1: Basilar length. 2: Overall palatal length. 2-5: Palatal length sensu stricto. 3: Vomerine length. 4: Post-vomerine length. 5: Muzzle length. Measurements defined at <https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/SYSTEME%20de%20MESURES-MEASUREMENTS%20SYSTEM> (accessed on 1 July 2024).

Comparisons were performed using scatter diagrams and Simpson's diagrams.

2.2.2. Lower Cheek Teeth Morphological Types (Figure 3)

We will refer to the morphology of lower cheek teeth as caballine (1); hemionine (2); zebrine (3); and asinine (4) (Figure 3). It must be stressed, however, that not all teeth belonging to true horses are caballine in morphology, nor are all teeth belonging to zebras zebrine. Actually, types 1, 2, 3, and 4 may be found in any species and even in the same tooth row. We use these terms as a short description of a morphological pattern.

The term “caballine” (1) stands for round metaconid + pointed metastylid + angular linguaflexid; the “1-2” type has a less angular linguaflexid than 1.

“Hemionine” (2) stands for round and elongated metaconid + pointed metastylid + shallow and flared (not angular) linguaflexid. A variant of the hemionine type 2 (2' in Figure 3) shows a slight “bridge” between metaconid and metastylid.

“Zebrine” (3) stands for round metaconid + pointed metastylid + deep and pointed linguaflexid. A variant of the zebrine type 3 (3' in Figure 3) has an elongated metaconid.

“Asinine” (4) stands for round metaconid + round metastylid + deep and pointed linguaflexid. A kind of “bridge” (4' in Figure 3) appears between metaconid and metastylid on some Wild African Asses (*E. (Asinus) africanus somaliensis*).

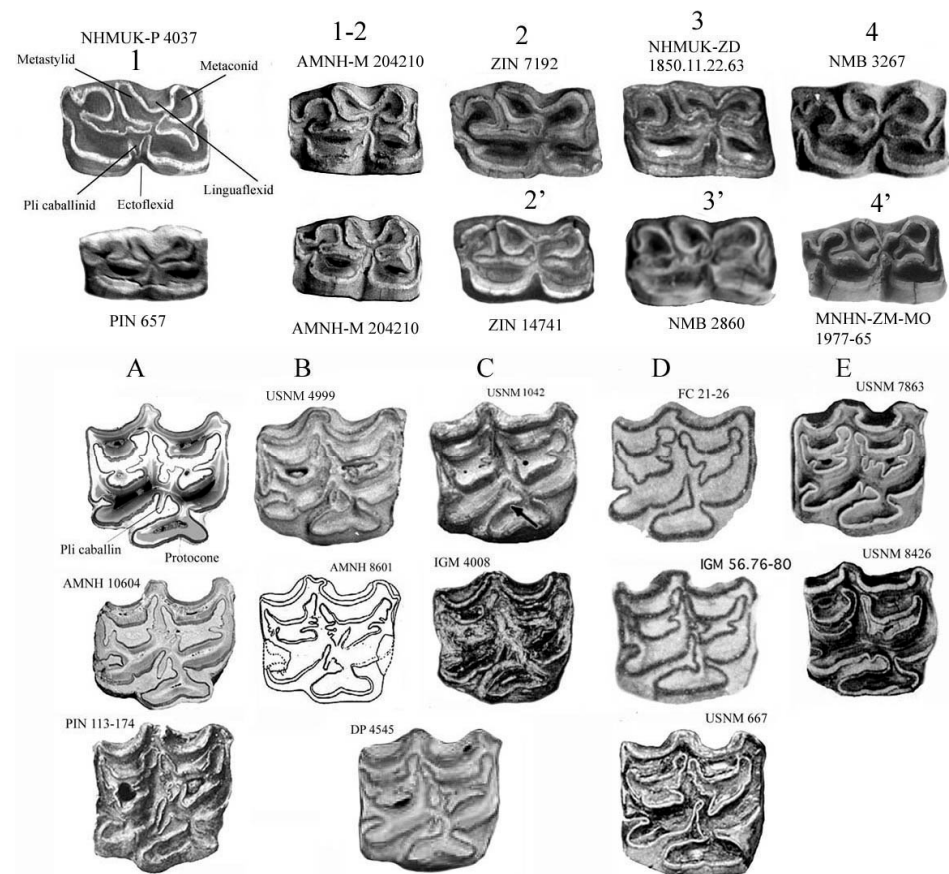


Figure 3. Lower and upper cheek teeth of extant and extinct equids (not to scale). The numbers and letters denote the morphological types discussed in the text (numbers for lower cheek teeth and letters for upper cheek teeth). Refer to Sections 2.2.2 and 2.2.3 for a description of morphological types. Lower cheek teeth are p3 except AMNH-M 204210 top and NMB 3267 which are p4, and PIN 657, AMNH-M 204210 bottom, and MNHN-ZM-MO 1977-65 which are m1. Upper cheek teeth are P4 except AMNH 8601 which is a P3.

2.2.3. Upper Cheek Teeth Morphological Types (Figure 3)

The morphology of *Equus* (we consider *Allohippus* and *Plesippus* as separate genera; see Introduction above) upper cheek teeth is extremely variable, even inside a tooth series. Overall, it seems that upper cheek teeth are not very reliable for species discrimination, unless teeth are compared at similar stages of wear (e.g., [16]).

For example, post-protoconal grooves are much deeper on little worn teeth. The fossettes of worn teeth lose enamel plications, the protocones lose any previous indentations or points become somewhat shapeless (USNM 8426).

Some features, however, may be of some value for describing and sometimes even characterizing New World species in teeth with different stages of wear (but still excluding teeth in early and late wear): the post-protoconal groove is very deep in FC 21-26, IGM 56.76-80, and USNM 667, although they are clearly not little worn.

Groups A and B (Figure 3) have in common well-developed plis caballin and grooved protocones, but they differ from each other in the relative length and shape of the protocones. In Group C, the protocones have a marked gibbosity (arrow on Figure 3C) and are less grooved. In Groups D and E, protocones are flat or very little grooved. In Group D, the post-protoconal valley is very deep.

2.2.4. Limb Bones

Comparisons use Simpson's diagrams, mostly of metapodial size and proportions but also of limb bones' relative lengths.

2.2.5. Morphological Characters and Species Determination

In extant species of *Equus*, characteristic cranial, dental, and skeletal features are usually linked and it is their very coexistence that characterizes a species (<https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/MORPHOLOGICAL%20CHARACTERS%20and%20SPECIES> (accessed on 1 July 2024)). We started our study by assuming that we would find the same for fossil species, but that assumption was often shaken. The question is how to choose the correct grouping when groupings based on cranial, teeth, and limb bone morphology do not coincide. In our paper's chapters and their subdivisions, we give preeminence to cranial characters followed by limb bone proportions, in particular when crania are lacking.

2.3. Techniques

2.3.1. Scatter Diagrams

We created scatter diagrams of different cranial proportions. Of particular relevance in this study are the Palatal, Franck's, Cheek, and Vertex indices (Figure 2; Supplementary File S1):

Palatal Index—Ratio of the palatal length sensu stricto (measurements 2-5) and the hornion–staphylion distance (measurement 3).

Franck's Index—Ratio of the distance between staphylion and basion (measurement 4) and the hornion–staphylion (measurement 3).

Cheek Index—Ratio of the cheek length (measurement 32) and the length of the naso-incisival notch (measurement 31).

Vertex Index—Ratio of the vertex length (measurement 18) and the basilar length (measurement 1).

2.3.2. Simpson's Diagrams

Simpson's ratio diagrams [21] provide rapid and easy comparisons, both of size and shape, for a single bone or a group of bones. A reference is used as the baseline for comparisons. The reference is provided by a single bone (or a group of bones), or means of a bone

sample, the dimensions of which are converted into decimal logarithms. By convention, logarithms of these dimensions are placed on the “0” line of the graph. In our study, we used an extant equid, *Equus (Hemionus) hemionus onager*, as reference. Dimensions of the material under study are also converted into decimal logarithms. Arithmetic differences between the reference logarithms and the logarithms of the studied dimensions are placed above the “0” line if they are positive (larger dimensions), or below if they are negative (smaller dimensions).

In such a logarithmic diagram, proportions remain unchanged whatever the absolute dimensions: diagrams of two bones differing by their size but identical by their proportions will appear one above the other but on parallel lines. The diagram interpretation is easier when pairs of dimensions describing main proportions are placed side by side. For instance, “gracile–robust” proportions appear immediately when “widths” are placed beside “lengths”. More information on Simpson’s diagrams can be found at <https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/OUTILS-TOOLS/DIAGRAMMES%20de%20SIMPSON> (accessed on 1 July 2024).

2.4. Abbreviations

dP/dp: Upper/lower deciduous premolars.

I/i: Upper/lower incisors.

M/m: Upper/lower molars.

MC: Third metacarpal.

MT: Third metatarsal.

P/p: Upper/lower premolars.

Ph1, Ph2, Ph3: First, second, third, phalanges.

Prot.: Protocone.

Lo: Anteroposterior length of tooth.

lo: Transversal length of tooth.

Institutional acronyms are found in the Supplementary Materials (Document S1).

2.5. Chronostratigraphic Framework

A chronostratigraphic chart of the last 1.5 million years for North America is found in the Supplementary Materials (Document S2).

3. Distinction Between Caballine and Amerhippine *Equus*

3.1. Conceptual Framework and Assumptions

3.1.1. Cranial Proportions and the Discrimination of Caballine Equids

There is general agreement in the taxonomic separation of caballine (true) horses from all other equids. It is based on anatomical characters (e.g., [10]) as well as on biomolecular results (e.g., [22]). However, there is no consensus on the taxonomy of caballine equids and different taxonomic schemes have been proposed (e.g., [2–7,16]).

A number of factors affect taxonomic interpretations of fossil equids, including caballine equids. Some of these factors are inherent to the fossil record and affect the nature of the samples available for study, such as organismic incompleteness (some skeletal elements are more likely to be preserved than others) and temporal and spatial incompleteness in the record. Other factors are biological in nature, such as convergence/parallelism, morphological constraints, and ecomorphological variation in time and space. And yet others are methodological in nature and relate to the manner in which we collect, analyze, and interpret morphological and molecular data, and in particular label (with formal specific or subspecific names) the fossils. The underlying assumptions are often not explicitly

stated. The result is that some factors can potentially lead to overestimating (taxonomic splitting) or underestimating (taxonomic lumping) equid diversity. Since the true diversity is not known, all taxonomic schemes represent hypotheses that may be testable only with additional study.

For the present study, the primary assumption is that various axial lengths of the cranium (e.g., muzzle, naso-incisival length, palate, distance from palate to vomer, and from vomer to basion) are taxonomically informative and can be used to characterize caballine equids; they seem to maintain reasonably stable reciprocal relationships and are not as susceptible to taphonomical distortions as other measurements. Our assumption is based on morphometric studies of a large sample of extant and fossil equid skulls ([9,10]). Indeed, crania of true horses (Palatal Index: Figure 4 and Supplementary File S2 [here Alaska and Yukon fossil caballines are included]), whether large (Draft) or small (Shetland ponies), have long palates (measurement 2-5) relative to the hormion–staphylion distance (measurement 3), while all other extant species have relatively shorter palates [10]. As is usual in any kind of biometrical comparison, there is some overlap between the measurements of true horses and other equids. Fortunately, it is not too pronounced.

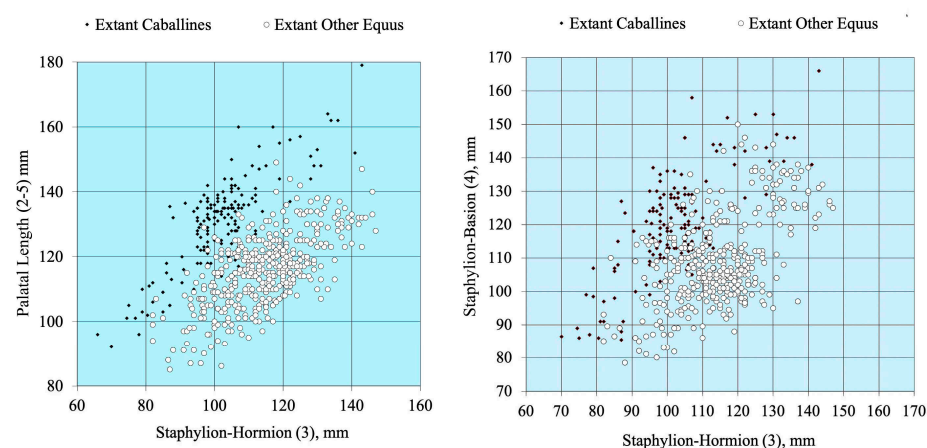


Figure 4. Palatal Index (left) and Franck's Index (right) in extant caballines and other extant *Equus*.

Accordingly, we assumed, as a starting point, that all fossil crania plotting together well inside the range of variation of modern true horses in a scatter diagram of the Palatal Index are caballine. They are as follows: several crania from northwestern North America (Yukon and Alaska) including the types of *E. (E.) lambei* and *E. (E.) alaskae* (Supplementary File S2); specimens UNSM 5980, UNSM 5981, and UNSM 1346 from Hay Springs, Nebraska, and SMNH 1515-8306 from Fort Qu'Appelle, Saskatchewan (Supplementary File S3); four crania from Rock Creek, Texas, referred to *E. (E.) scotti* and UMMNH 46899 from the Seymour Formation (Supplementary File S4); the cranium AMNH 95588 from Pool Branch, Florida (Supplementary File S5); the type of *E. (H.) mexicanus* (IGM 4009), but not UMPE-521 (Supplementary File S5) referred to *E. mexicanus* by Jiménez-Hidalgo et al. [23], both from Mexico. The specimen UCMP V-3605/32879 from Irvington, California, reported by Azzaroli [7] as a caballine, plots outside the range of variation of caballines (Supplementary File S5). Several other specimens may or may not be caballine and will be discussed later.

The Franck's Index is another way to discriminate caballine and non-caballine crania, at least in the Old World. In caballines, the distance between the staphylion and the basion (measurement 4) is relatively longer than the staphylion–hormion distance (measurement 3). Once again (Figure 4 and Supplementary File S6), there is an overlap between caballine and non-caballine equids. We will see later that the Palatal and Franck's indices sometimes give different results regarding the determination of a particular cranium.

3.1.2. Taxonomical Remarks

Equus (*E.*) *ferus* Boddaert, 1785 [24], is based on the recently extinct Russian Tarpan. Osteologically, it is represented by the skulls of two castrated males and the associated skeleton of one of them (ZIN 521). They were studied by Gromova [25] under the name of *E. caballus gmelini*. The Moscow MGU specimen S 94535 has extremely worn upper cheek teeth and lacks the mandible; when one of us (V.E.) saw it, it was falling to pieces—making it impossible to photograph. In consequence, the material is far from satisfactory. Both skulls mainly differ from *E. (E.) przewalskii* by more caballine Franck's and Palatal indices. On ZIN 521, the protocones are very short, like in *E. (E.) missi*. The skeleton has exceptionally short metapodials and short first posterior phalanges. The proportions and size are close to an Island pony. To our knowledge, no equivalent of this conformation was ever found in the Old-World Late Pleistocene (no associated bones at Missy). All of the common Late Pleistocene horses (such as *E. (E.) latipes*, *E. (E.) gallicus*, etc.) have completely different conformations and should not be referred to *E. (E.) ferus*.

The International Commission on Zoological Nomenclature has accepted the proposition of [26] to adopt the name of *E. ferus* for wild horses, while the name *E. caballus* is restricted to domestic forms; as both Tarpan have been castrated, their correct representation of a “wild” species is questionable. Azzaroli ([7], p. 2) probably had misgivings about this new nomenclature. For one thing, he wondered whether *E. przewalskii* was to be considered in that frame a subspecies of *E. ferus*. And while he assigned to *E. ferus* many remains of the Late Pleistocene or Holocene of Alaska, he did not refer to *E. lambei* or *E. niobrarensis* as subspecies of *E. ferus* but as distinct caballine species.

Nevertheless, the name of *E. ferus* has become commonly used, even reluctantly by two of us [11,12,16]. Here, however, we will not refer any North American caballine to *E. ferus* or to a subspecies of *E. ferus*.

Though we use specific names when mentioning caballine forms, we do not imply that these forms were true species under a biological species concept. After all, who can tell if the 40,000-year-old African *E. (E.) algericus* could produce fertile offspring with the 700,000-year-old North American *E. (E.) scotti*? Specialists already have trouble deciding whether *E. (E.) przewalskii* is specifically distinct from *E. (E.) caballus* (testicular anomalies were observed in 6 out of 12 hybrids studied by [27]). The fact remains that many fossils have in common characters we find in modern caballines and distinguish them as a subgenus of the genus *Equus*. Whether the morphological differences existing between caballine forms (for example, *E. (E.) lambei* and *E. (E.) scotti*) precluded them from having fertile offspring will remain undecided, but such differences may be described and it is convenient to use well-known specific names in doing so. Nonetheless, other questions remain: Are these “species” ecomorphs? Chronomorphs? Are resemblances an indication of parallel evolution? Or of close ancestral connections? This question is particularly pregnant when several caballines appear to be sympatric, as in the case of Hay Springs; although *E. (E.) niobrarensis* and *E. (E.) hatcheri* may have been simple morphs, we decided to use their names to describe and compare morphologies.

3.1.3. Evolutionary Relationship Between Caballine and Amerhippine *Equus*

Orlando et al. [14] found similarities between short mitochondrial DNA sequences of South American equids from Argentina referred to *Equus* (*Amerhippus*) *neogeus* and those of *Equus caballus*. Furthermore, they found that the *Equus* (*Amerhippus*) haplotype appears among typical *Equus* (*Equus*)—i.e., caballine horse—haplotypes in median-spanning network analyses [14]. In consequence, there may be some doubt about the validity of the subgenus *Amerhippus*. In their conclusions, Orlando et al. [14] state that, according to currently available ancient DNA data, at least two equid lineages were present in North

America during the Late Pleistocene, namely, caballine horses (*sensu stricto*) and “stilt legged horses” *sensu lato*—a group of slender-limbed horses named by [28].

The study by Orlando et al. [14] provided a first attempt at evaluating the evolutionary relationships of *Equus* (*Amerhippus*) *neogeus* and the validity of the subgenus *Amerhippus* using molecular data. Here, we addressed the issue from the anatomical point of view by comparing extant caballine specimens, amerhippine fossils, and other American fossils which either by cranial, dental, or skeletal characters cannot be included into *Equus* (*Equus*) based on the characters discussed below.

3.2. Observations

3.2.1. Cranial Proportions of Caballine and Amerhippine *Equus* and the Particular Case of *Equus* (*H.*) *mexicanus*

Caballines can be well enough discriminated from Old-World non-caballine *Equus* by the Palatal and Franck’s indices (Figure 4). The discrimination is more difficult in the New World as shown by the scatter diagrams of the Palatal, Franck’s, Cheek, and Vertex indices (Supplementary Files S7–10, Figures 5–8). The best separation between caballines and other crania is afforded by the Cheek Index—comparing the relative lengths of the narial notch and cheek (Figure 5, Supplementary File S7); in this plot, *E. (H.) mexicanus* falls within the caballines. On the scatter diagram corresponding to the Franck’s Index, only *E. (H.) mexicanus*, *E. (A.) occidentalis* (including the cranium UMPE-521 from Oaxaca), UNSM 5978 from Hay Springs, and FAM 42811 from Papago Springs plot apart from the rest (Figure 6, Supplementary File S8).

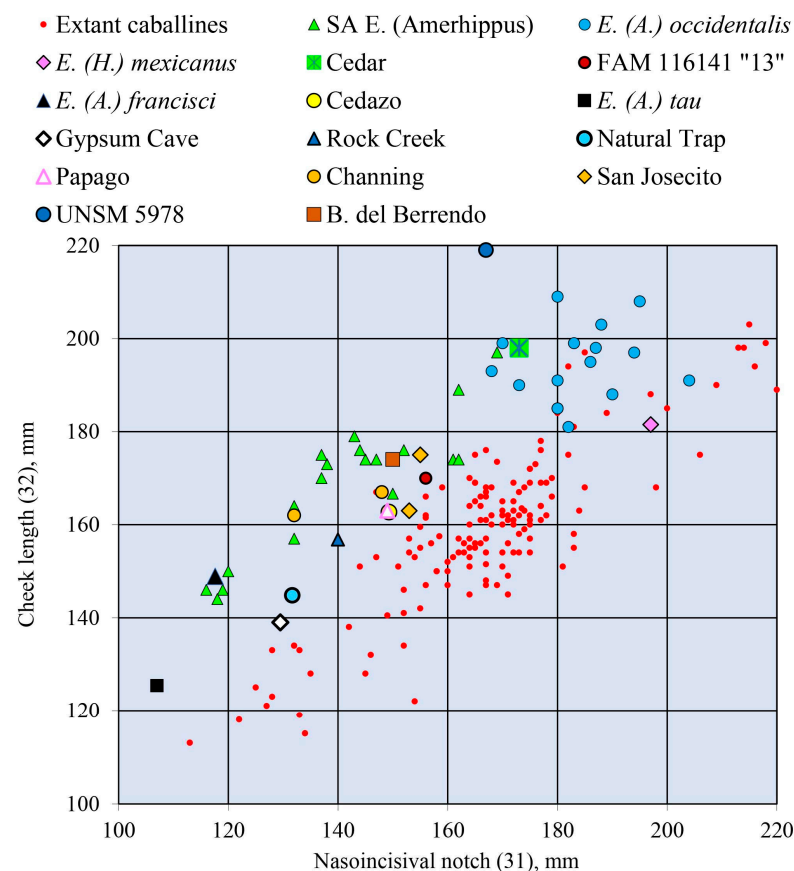


Figure 5. Cheek Index in extant caballines, South American amerhippines (SA *E. (Amerhippus)*), and various North American fossil crania.

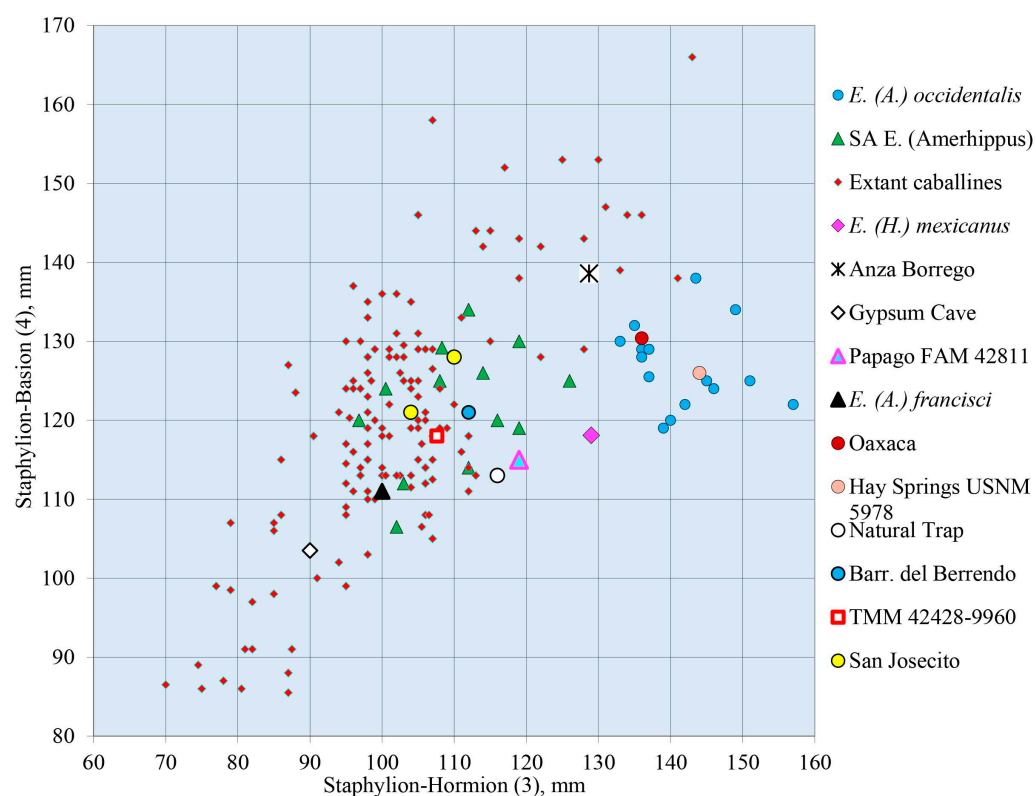


Figure 6. Franck's Index in extant caballines, South American amerhippines (SA *E. (Amerhippus)*), and various North American fossil crania.

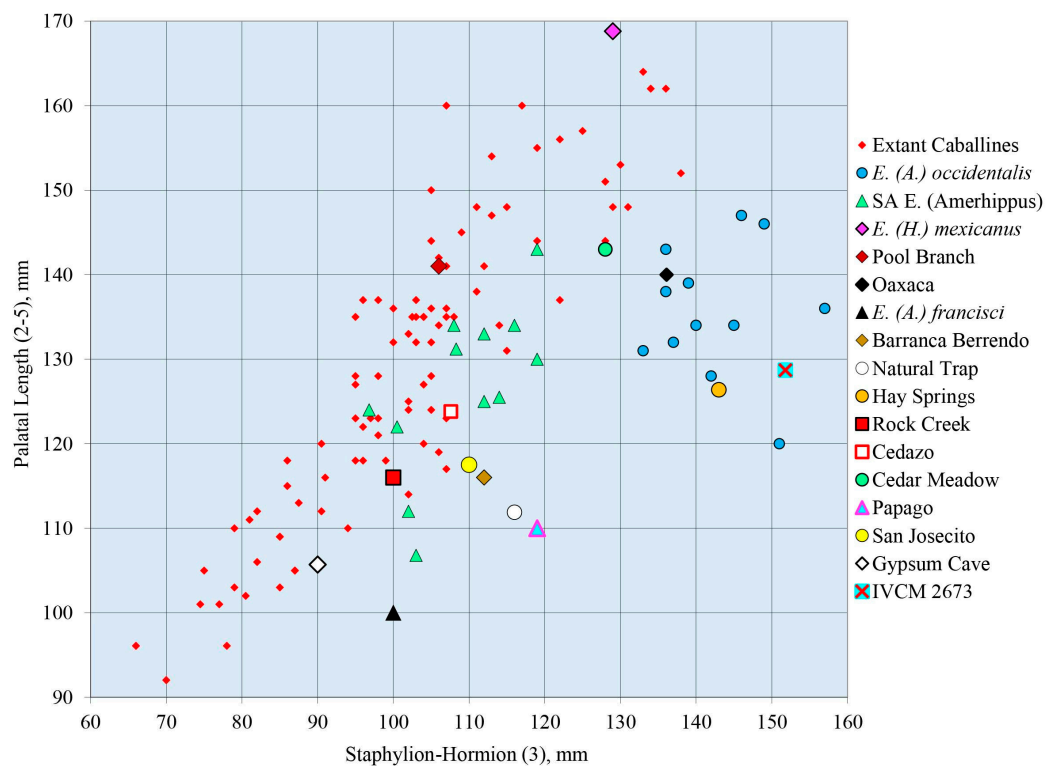


Figure 7. Palatal Index in extant caballines, South American amerhippines (SA *E. (Amerhippus)*), and various North American fossil crania.

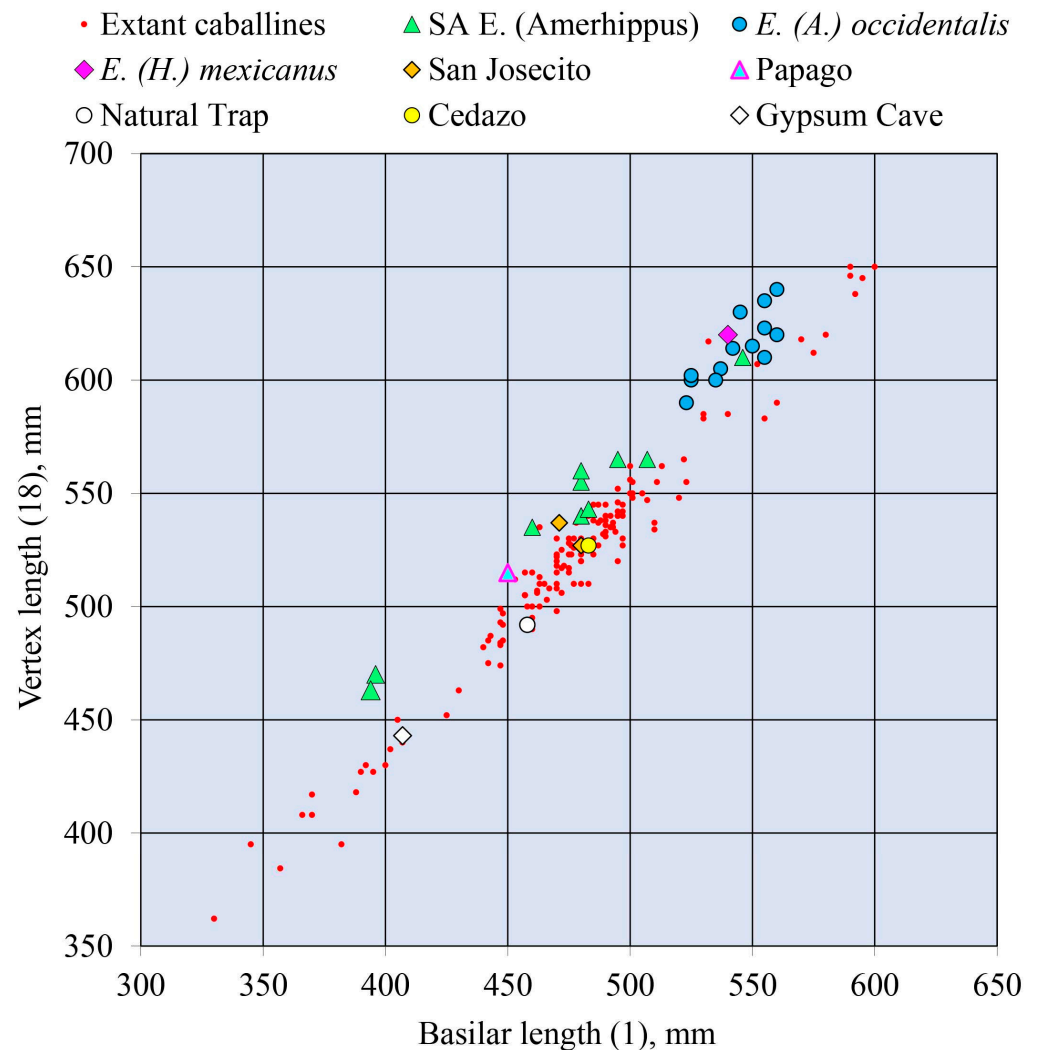


Figure 8. Vertex Index in extant caballines, South American amerhippines (SA *E. (Amerhippus)*), and various North American fossil crania.

Supplementary File S11 summarizes our observations. It must be stressed that *E. (A.) occidentalis* almost never overlaps with other species on all of these scatter diagrams and that it is the only species to do so. We have already remarked on the particular case of *E. mexicanus*: caballine according to the Palatal and Cheek indices, but not caballine by the Franck's and Vertex indices. This may well grant it the subgeneric rank of *Hesperohippus* bestowed by Hibbard [29].

3.2.2. Upper and Lower Cheek Teeth

South American amerhippines have variable cheek teeth patterns (Figure 9), some of which may be found in North American caballines (Group E in upper teeth, Figure 3) and amerhippines (Groups 3 and 4 in lower teeth, Figure 3).

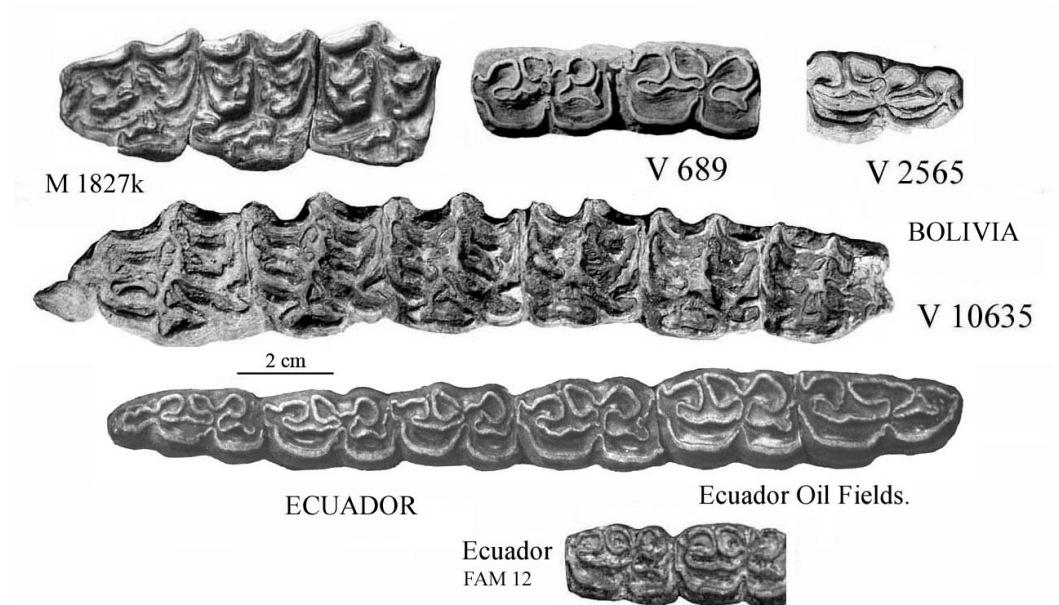


Figure 9. Upper and lower cheek teeth of South American amerhippines illustrating different morphologies. V 689, V 2565, M 1827k, and V10635 are from Tarija, Bolivia. Ecuador Oil Fields and FAM 12 are from Ecuador.

North American upper teeth belonging to caballines fall into Groups A and B; protocones with gibbosities (Group C) are exceptional. The association of deep post-protoconal valleys with blunt, roundish, mesial and distal ends of protocones (Group D) never occurs in caballines. Protocones with blunt, roundish mesial and distal ends (Group E) occur in the very worn teeth of the type of *E. (E.) lambei* (Figure 10) and the type of *E. (E.) hatcheri* (Figure 11).

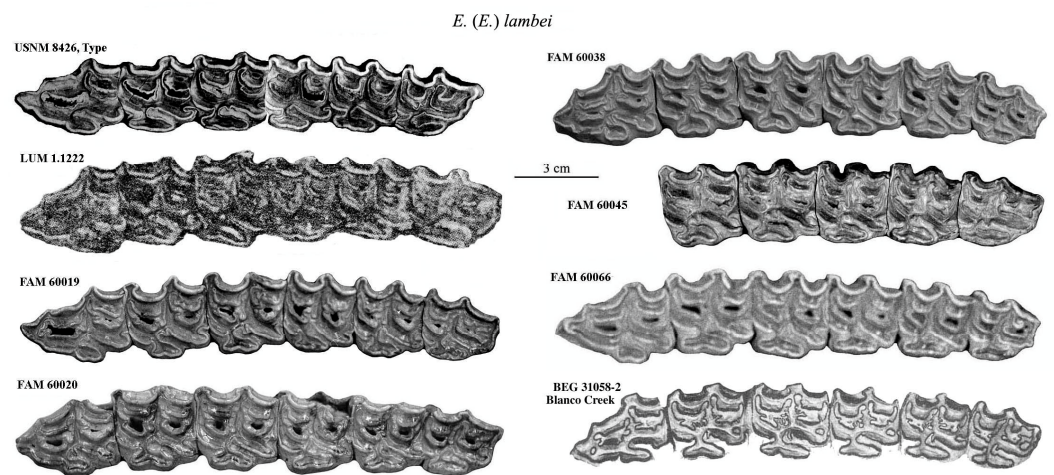
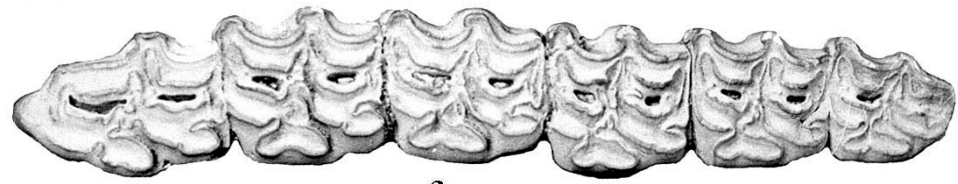


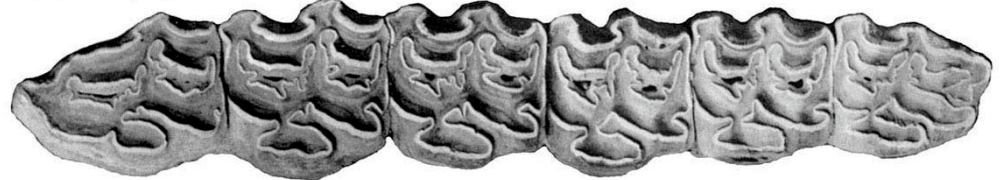
Figure 10. Upper P2-M3 of seven specimens referred to *E. (E.) lambei* (USNM 8426, type specimen; LUM 1.1222; FAM 60019, 60020, 60038, 60045, and 60066 from different localities in Alaska and Yukon) and the specimen BEG 31058-2 from Blanco Creek, Texas. Occlusal view. BEG 31058-2 modified from [3].

E. (E.) niobrarensis, USNM 4999



3 cm

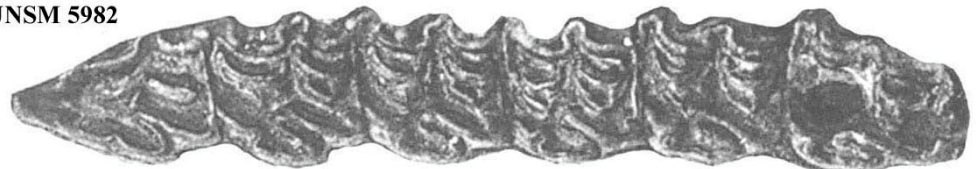
E. (E.) hatcheri, USNM 7868



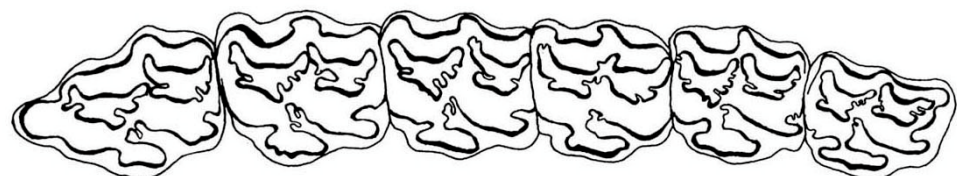
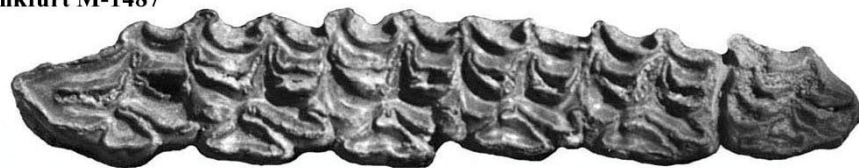
UNSM 5980



UNSM 5982



Frankfurt M-1487



Slaton, TMM 6643

Figure 11. Upper P2-M3 of USNM 4999 (type of *E. (E.) niobrarensis*), USNM 7868 (type of *E. (E.) hatcheri*), UNSM 5980, UNSM 5982, Frankfurt M-1487, and TMM 6643. Occlusal view. Photos of UNSM 5980 and UNSM 5982 modified from [7]. TMM 6643 modified from [30].

Most lower teeth belonging to caballines fall into Groups 1 and 1-2. Group 3 is sometimes observed in some teeth, but Group 4 is never present in caballines. Plis protostylid in American lower teeth south of Alaska and Yukon are a sure indication of amerhippine affinity; protostylids are very rare in caballines [31], common in South American amerhippines [31], and are known in Beringian sussemiones [11,17]. Lower m1 molars appear to be the most reliable for discrimination between caballine and amerhippines.

3.2.3. Lower Incisors

Caballine lower incisors have infundibula (“cups”) at least on i1 and i2 (we have observed only one exception!). Part of the definition of amerhippines is the lack of these

infundibula [32], but exceptions do exist (Figure 12): there is an infundibulum on the i1 of AMNH 1753 and on the i1 and i2 of Ecuador # 8, both from Punin, Ecuador.

3 E12-11.5

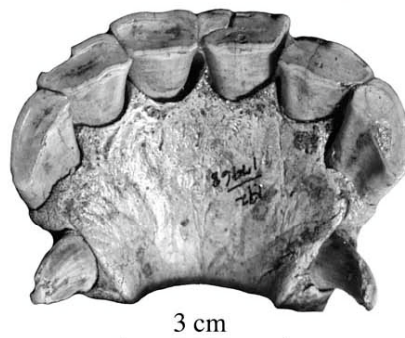
Rancho La Brea



5 cm

LACM 192-17968

San Josecito



Ecuador # 8, Punin



LACM 3500-6

Rancho La Brea



AMNH 1753, Punin



Figure 12. Lower incisors of amerhippines. 3 E12-11.5 and LACM 3500-6 from Rancho La Brea, California; LACM 192-17968 from San Josecito Cave, Mexico; Ecuador #8 and AMNH 1753 from Punin, Ecuador. Occlusal view.

3.2.4. Metapodials

In MC and MT of extant and most fossil Old-World caballines, the distal articular breadths are larger than the supra-articular ones; in MC, the keel depth may be relatively larger than the distal articular breadth. However, the distal articular breadths may be larger than the supra-articular ones in some non-caballine fossil MT, as well as in caballines.

3.3. Comments

Our analyses identified morphological similarities between caballines and amerhippines. For example, the two groups overlap in the scatter plot of the Franck's Index and, to a lesser degree, in the scatter plot of the Palatal Index. They may also have similar tooth morphologies (e.g., Group E in upper teeth and Group 3 in lower teeth) and limb bones in some individuals as will be discussed later. The similarities between caballines and amerhippines is one of the reasons for the existence of problematic forms, which will be addressed in Part 2 of our study.

However, there are some differences and morphological tendencies that can be used to discriminate between caballines and amerhippines. For example, the Cheek Index and, to some degree, the Vertex Index may be used to separate caballine and amerhippine crania. In the upper teeth, Group D teeth do not occur in caballines, and Group C teeth are rarely found in caballines; both of these morphologies are often seen in amerhippines. In the lower teeth, Group 4 teeth are not found in caballines, whereas this morphology is present in amerhippines; in addition, it is not uncommon for amerhippine lower cheek teeth to possess a pli protostylid [31]. Cups in the i1 and i2 are almost always absent in amerhippines but present in caballines [33].

Our observations point to a great diversity among amerhippines, strongly suggesting the presence of more than one lineage or form. *Equus* (A.) *occidentalis* is certainly one of them. We are currently progressing on Part 2 of our study which will provide more detailed descriptions and measurements of North American amerhippines.

The singular position of the Tequixquiac cranium, holotype of *Equus* (H.) *mexicanus*, leads us to support that it belongs not just to another lineage, but rather to the subgenus *Equus* (*Hesperohippus*) erected by [29]. This will be discussed further in Section 6.

4. North American Caballines

4.1. Well-Represented North American Caballines

Equus (E.) *scotti* Gidley, 1900, from the middle Irvingtonian of Rock Creek, Texas, is the first well-represented caballine in North America and one of the best represented Middle Pleistocene caballine horses in the world. The late Irvingtonian crania from Hay Springs, including the types of *E.* (E.) *niobrarensis* Hay, 1913a, and *E.* (E.) *hatcheri* Hay, 1915, are all badly preserved and/or very old or juvenile. The other relatively well represented North American caballine forms—*E.* (E.) *alaskae* Hay, 1913b, and *E.* (E.) *lambei* Hay, 1917—are of Rancholabrean age and primarily inhabited Alaska and Yukon.

4.1.1. *Equus* (E.) *scotti* Gidley, 1900 [34]

The Rock Creek fauna, Texas, is supposed to be of an early Irvingtonian age, but the *E.* (E.) *scotti* fossils come from another quarry ([35], p. 35). According to [36], it is situated only 4.5 m below the Lava Creek B Ash dated at 0.61 Ma. Repenning ([37], Figure 8.1) places it in the Irvingtonian II.

Equus (E.) *scotti* is represented by several skulls (Supplementary Table S1), more or less fragmentary crania, and limb bones [34]. The type AMNH 10606, illustrated by ([1], Pl. XX), is a mounted skeleton, the cranium of which is impossible to study in detail (Supplementary File S12); however, ([38], Table 1) gave several measurements of the cranium and ([1], Figure 25) provided a drawing of the left M1. AMNH 10612 illustrated by ([34], Figure 3) is not the type skull.

Both Gidley ([1], plate XVIII A and table in p. 136) and Hay ([39], Figures 68 and 69 and table in p. 182) provided illustrations and some measurements of another specimen (AMNH 10628) recovered from the type locality; however, we note that there are slight differences in the enamel pattern of the upper cheek teeth illustrated by these authors

(Supplementary File S13). There are also some differences (Supplementary Table S1) between the measurements reported by [39] and the measurements that can be calculated using the figure published by ([1], plate XVIII A). Because of these discrepancies, we omit AMNH 10628 (and another specimen measured by [39]) from the calculations of mean values of crania of *E. (E.) scotti* (Supplementary File S14).

Johnston [40] provided photographs and measurements of a cranium and associated mandible (Supplementary File S15) recovered in 1936 from the type locality. Both the latter and AMNH 10612 (Figure 13) may be laterally compressed which would account for their very narrow choanae. CMN 2381 (Figure 14) seems to be the best-preserved cranium of this species known to date.

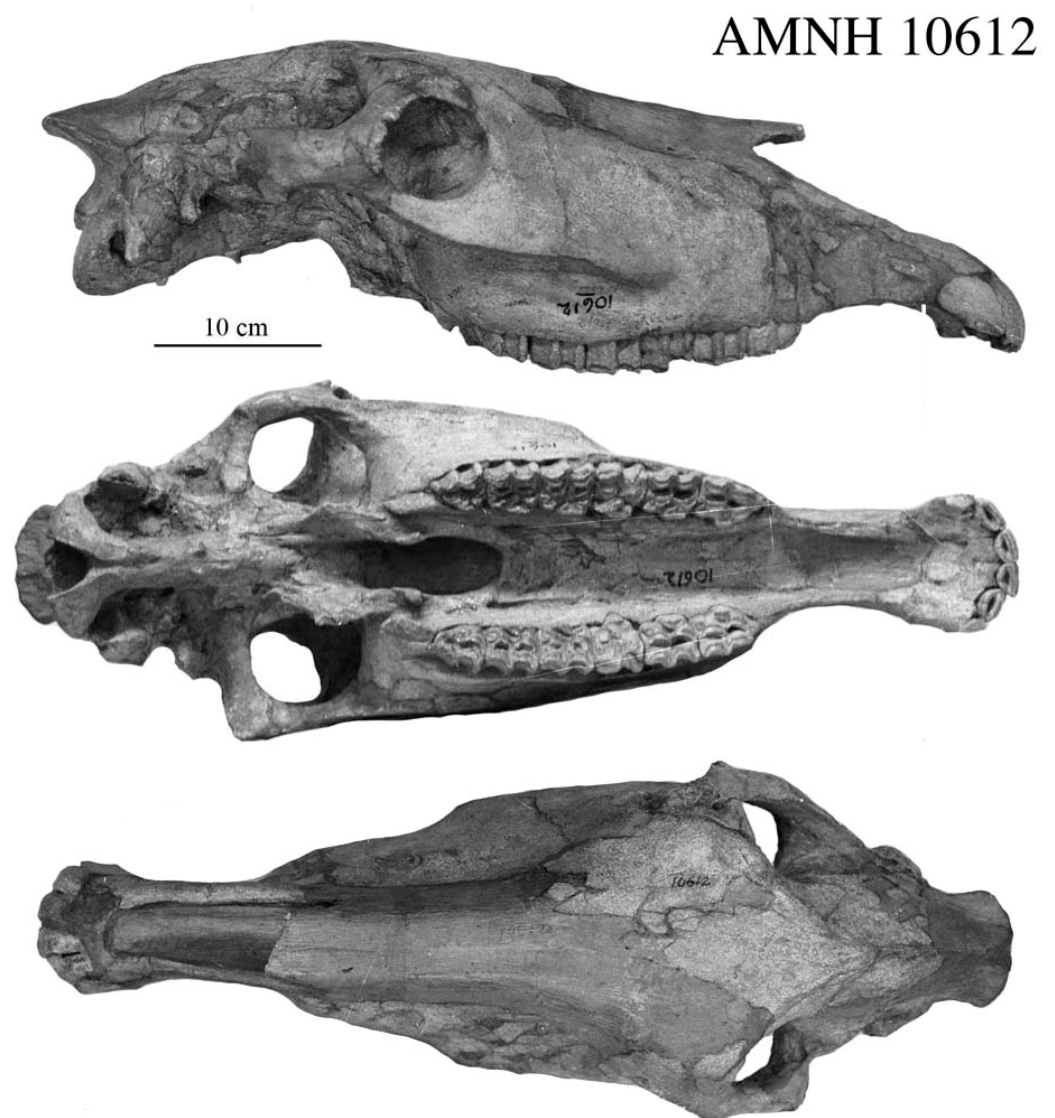


Figure 13. *Equus (E.) scotti* cranium (AMNH 10612) from Rock Creek, Texas. Lateral, ventral, and dorsal views.

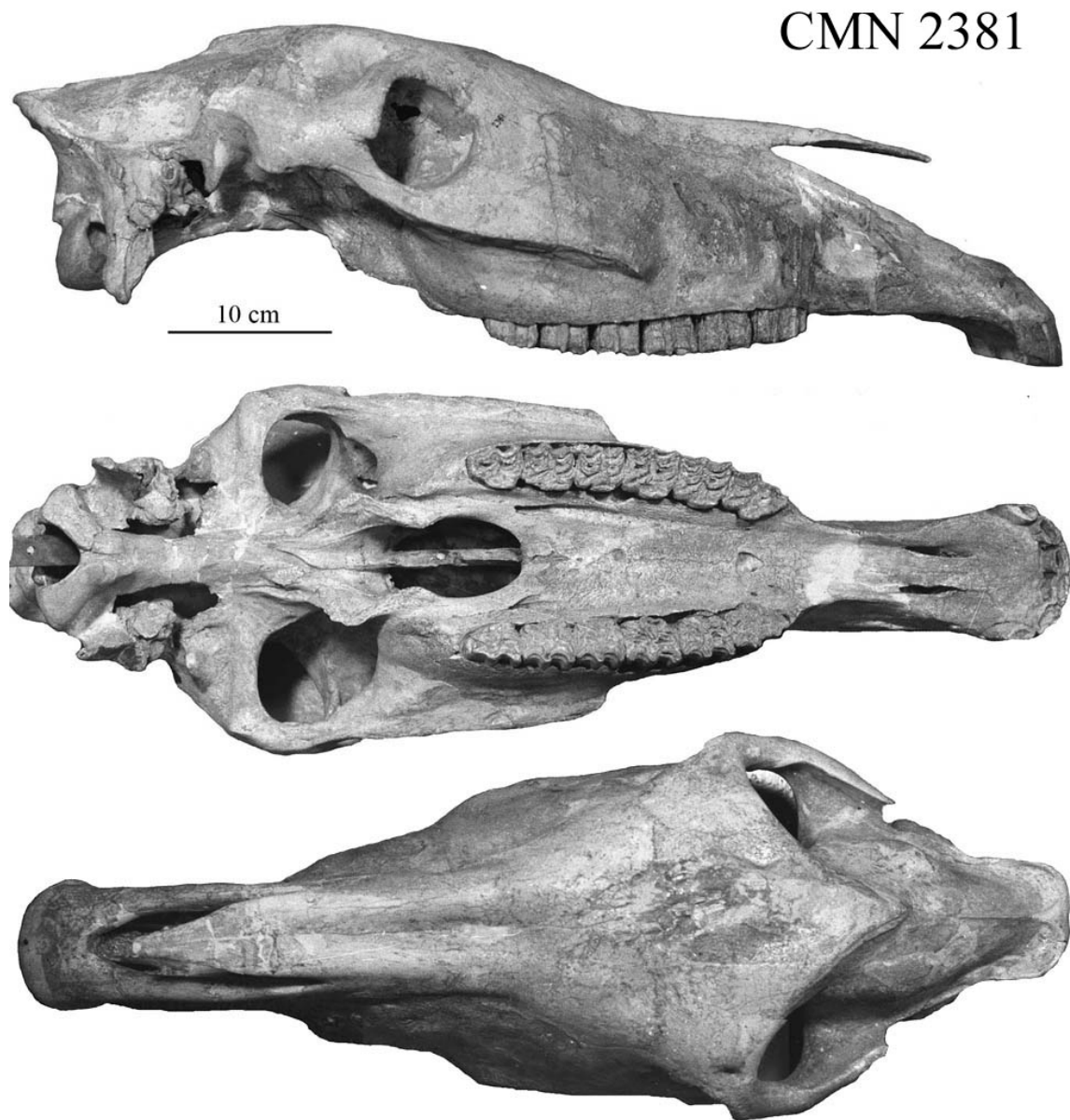


Figure 14. *Equus (E.) scotti* cranium (CMN 2381) from Rock Creek, Texas. Lateral, ventral, and dorsal views.

The Simpson's diagram (Supplementary File S14) shows that the cranium of *E. (E.) scotti* has a moderately long muzzle and rather small choanae.

The enamel of the upper cheek teeth is plicated (Figure 15); the protocones are moderately long and symmetrically grooved. Post-protoconal valleys are deep. Pli caballins are very developed except on the worn teeth of the specimen reported by [40]. We refer them to Group A.

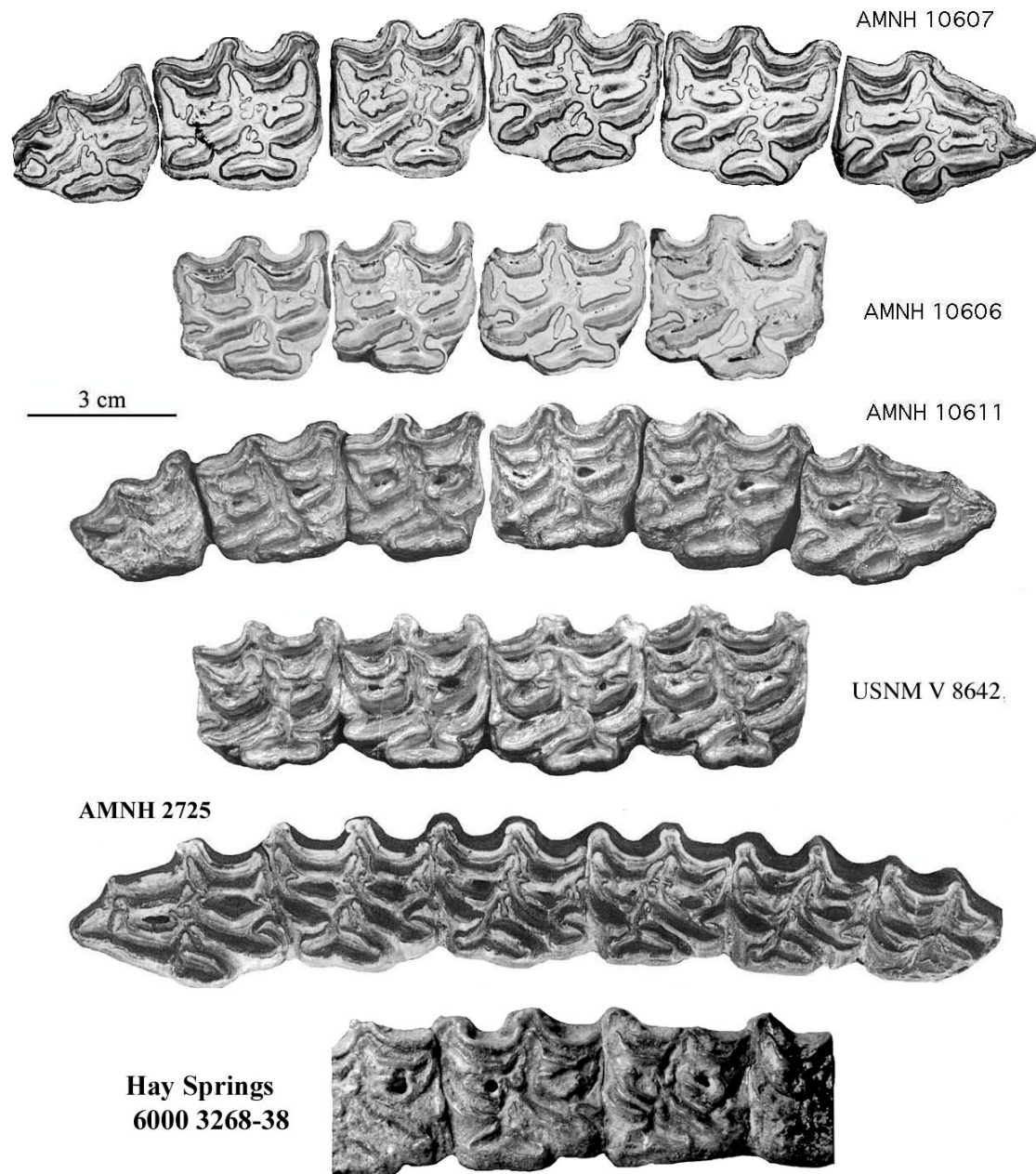


Figure 15. Upper P2-M3 of *E. (E.) scotti* (AMNH 10606, 10607, 10611), specimens with ‘*E. (E.) scotti*-like’ morphology from Hay Springs, Nebraska (AMNH 2725 and Hay Springs 6000 3268-38), and the holotype of *E. holmesi* (USNM V 8642). Occlusal view.

On the lower molars (Figure 16), the double knots are clearly caballine on m1 and m2, less so on other teeth; ectoflexids are shallow. Molars belong to our Group 1; some lower premolars belong to Groups 2 and 3.

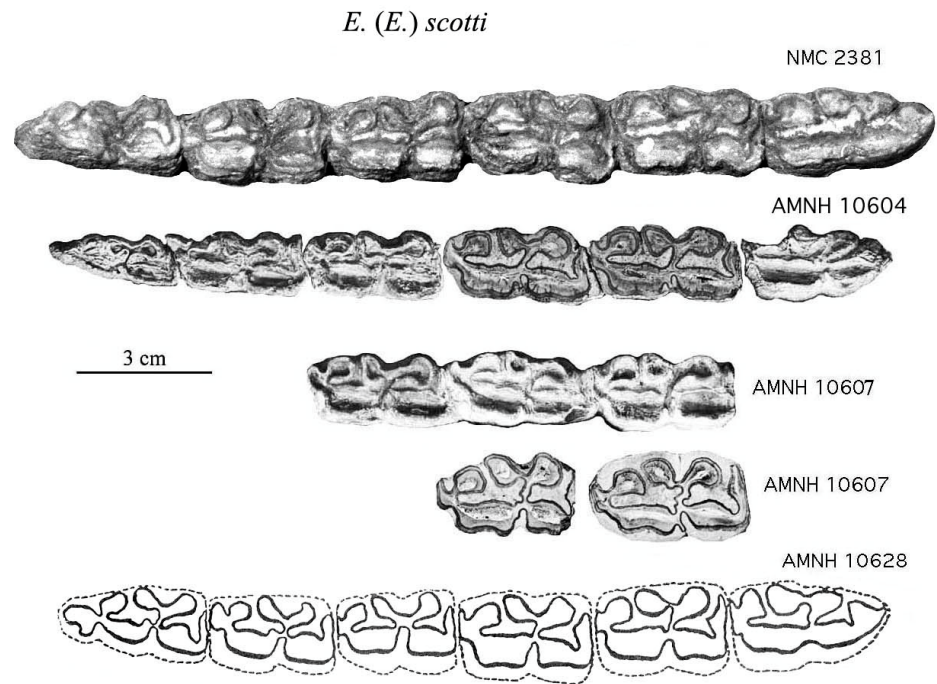


Figure 16. Lower p2-m3 of specimens referred to *E. (E.) scotti* (NMC 2381, AMNH 10604, 10607, and 10628). Occlusal view. Drawing of AMNH 10628 modified from [39].

Cups are well developed at least on i1 and i2.

The limb bones are robust. Rock Creek metapodials are very variable in proportions (Supplementary File S16) while the samples of anterior and posterior first phalanges are quite homogeneous (Supplementary File S17).

Two other crania (Supplementary File S14) may be clearly referred to, or related to, *E. (E.) scotti*:

- A large skull broken in two fragments (UMMNH 46899a and b; Supplementary Table S1) from the Seymour Formation, Texas, referred to *E. (E.) scotti* by [41]. The Franck's Index cannot be evaluated, but the Palatal Index is caballine. The upper dentition of another specimen (UMMNH 46898) illustrated by these authors can also be easily referred to *E. (E.) scotti*.
- Eisenmann ([11,42], Figure 60 in [11]) referred to *E. (E.) scotti* a very well-preserved skull (Supplementary Table S1) collected at Ulakhan Bet Sular, along the Adycha River (affluent of the Iana, northern Siberia). It is preserved at the Severtsov Institute of Moscow as N° 160-455 (ex "Bet 55"). Size, proportions, and location of the posterior palatine foramen are very close to *E. (E.) scotti*, but the frontal region is flat instead of bulging. Both Franck's and Palatal indices are caballine. The upper cheek teeth also resemble those of *E. (E.) scotti*; the lowers are not known. According to Sher (personal communication), it comes from magneto-positive deposits probably inside the lower Brunhes. Many large metapodials collected by Sher at Chukochya and Adycha may also be referred to *E. (E.) scotti*.

Many Pleistocene large caballines may possibly be related or referred to *E. (E.) scotti*, in particular the large horses from Old Crow (Yukon), and the slightly smaller MT YG 148-2 from Thistle Creek (Yukon), dated to around 700,000 years ago and which produced a full genome sequence [15]. Other large fossils from Cedral, Mexico, described as *E. mexicanus* by [43] and as *E. ferus* by [16], have morphologies similar to *E. (E.) scotti*. This issue will be discussed below in the chapter devoted to *E. (H.) mexicanus*. *Equus midlandensis* also has a morphology similar to *E. (E.) scotti*; it will be discussed below in Section 5.

Equus (E.) scotti was considered by [7] as a synonym of *E. excelsus* Leidy, 1858 (Niobrara River Valley, Nebraska), an opinion that has been adopted by some researchers (e.g., [44]). Azzaroli [7] argued that the two equids were about the same size and both had pointed protocones and plicated enamel. One of us (V.E.) provided evidence rejecting this synonymy [10]. The enamel pattern of the holotype of *E. excelsus* (USNM 667) ([10], Figure 11) is quite different from *E. (E.) scotti* ([10], Figure 9). In *E. excelsus*, the P4, M1, and M2 are not very plicated, have no pli caballin, and the protocones are not pointed. On the P4, the post-protoconal valley is very deep. By all these characters, USNM 667 much more closely resembles *E. (A.) occidentalis* of Rancho La Brea than any *E. (E.) scotti*.

4.1.2. *Equus (E.) alaskae* and *Equus (E.) lambei* (Supplementary File S2, Supplementary Table S2)

The caballines *E. (E.) alaskae* and *E. (E.) lambei* are also well represented. They are Rancholabrean in age and are known primarily from Alaska and Yukon.

- *Equus (E.) alaskae* Hay, 1913b, type: cranium of a young male, USNM 7700 (Figure 17), from Sullivan's Creek, Tofty, Central Alaska, described as *E. niobrarensis alaskae* [45]. The muzzle is rather long relative to the palate (Supplementary File S18).

E. (E.) alaskae, USNM 7700

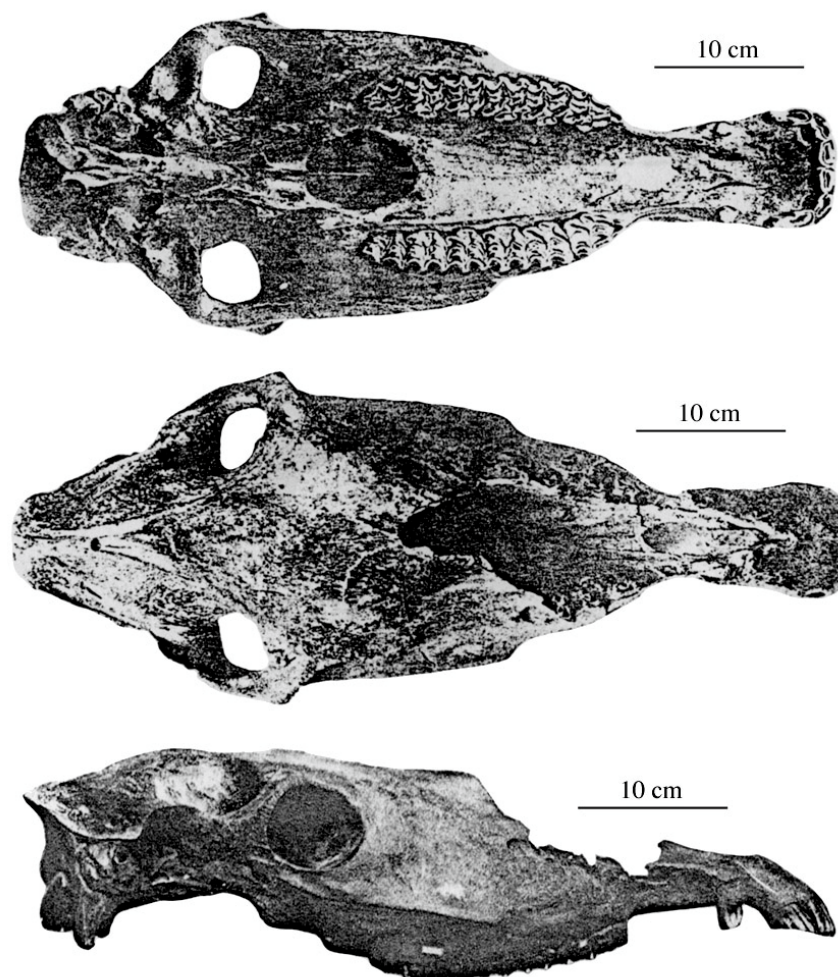


Figure 17. *Equus (E.) alaskae* cranium (USNM 7700, type specimen) from Sullivan's Creek, Alaska. Ventral, dorsal, and lateral views. Modified from [45].

The Simpson's diagram of cranial dimensions (Supplementary File S18) shows that in addition to the type USNM 7700, other specimens that may be referred to *E. (E.) alaskae* are as follows: FAM 60001, 60010, 60011, and 60071 (Figure 18) from Alaska; CMN (formerly NMC) 17254 and 17905 from Yukon; and IA 5059, PIN 301-5 (Figure 19), and PIN 301-533 from North Eastern Siberia. Basilar lengths are 475–495 mm long.

FAM 60071

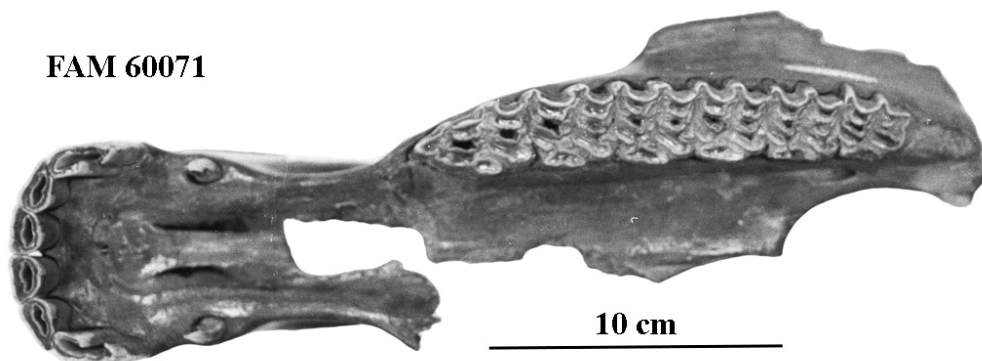


Figure 18. Partial cranium (FAM 60071) from Alaska referred to *E. (E.) alaskae*. Ventral view.

PIN 301-5

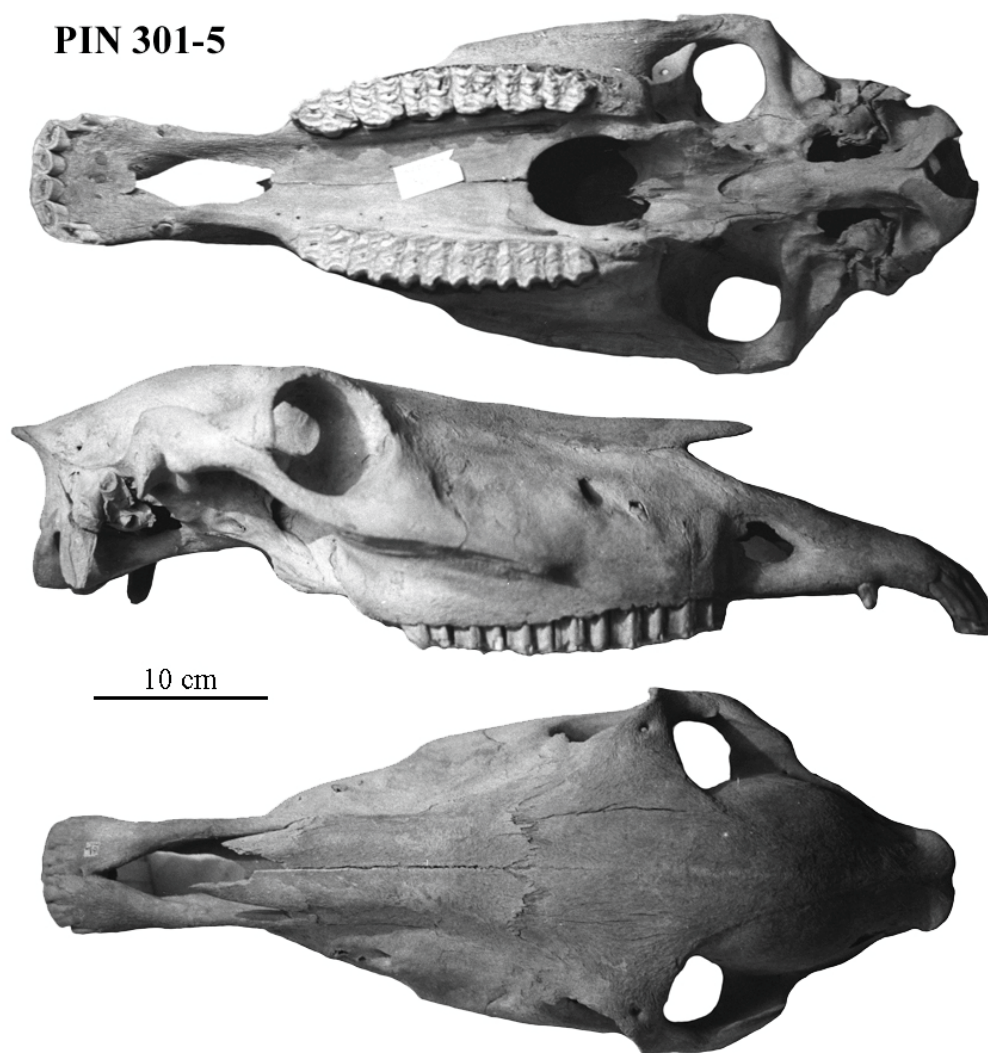


Figure 19. Cranium (PIN 301-5) from North Eastern Siberia referred to *E. (E.) alaskae*. Ventral, lateral, and dorsal views.

The upper cheek teeth of the holotype and referred specimens are polymorph: the North American USNM 7700 (holotype) and FAM 60071 fall into Groups B and E, whereas the Siberian PIN 301-5 and IA 5059 fall into Groups A and E, respectively (Figure 20).

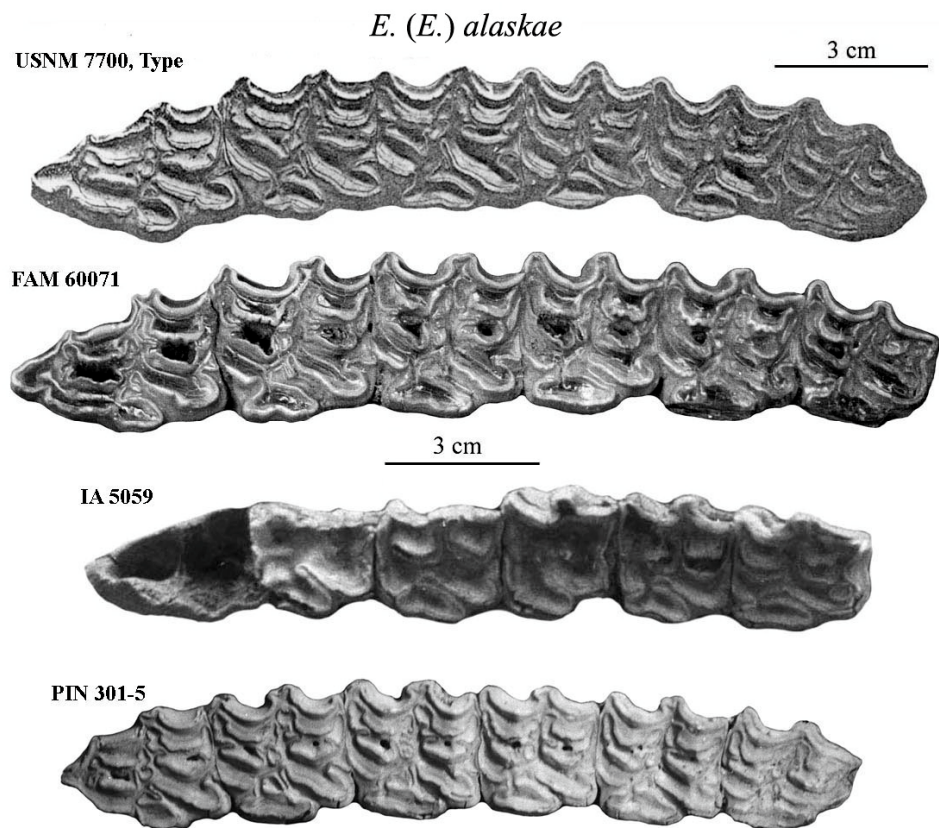


Figure 20. Upper P2-M3 of specimens referred to *E. (E.) alaska* (USNM 7700, type specimen; FAM 60071; IA 5059; PIN 301-5). Occlusal view.

The lower cheek teeth fall into Group 1. Cups are present on lower incisors.

- *Equus (E.) lambei* Hay, 1917 [46], type: skull of an old mare, USNM 8426, from Gold Run Creek (=Dawson 32), Yukon, ca. 15,000 years old (Figure 21). The skull L 1-1222 probably comes from the same locality [47]. Although referred to *Onager* by Quinn [3], *E. (E.) lambei* is a caballine [10,48].

The type cranium of *E. (E.) lambei* is smaller than other crania assigned to *E. (E.) lambei* and *E. (E.) alaska*. Relative to the palate, the muzzle is shorter than in *E. (E.) alaska* (Supplementary File S19). The Simpson's diagram (Supplementary File S19) shows crania with similar proportions. They are as follows: L 1-1222; CMN (formerly NMC) 9924, 33992, 17262, and 34803a; FAM 60012, 60013, 60019, 60020, 60023, 60038, 60045, 60048, and 60066. They were found in different localities in Alaska and Yukon (Supplementary File S19; see photographs at "Localities → Alaska–Yukon": https://drive.google.com/drive/folders/1lXhM3clTcZXn3XroVh6PNph58BYMw1CS?usp=share_link (accessed on 1 July 2024)).

E. (E.) lambei, USNM 8426

Figure 21. Type specimen of *E. (E.) lambei* (USNM 8426) collected from Gold Run Creek, Yukon. Cranium in ventral, dorsal, and lateral views. Mandible in lateral view.

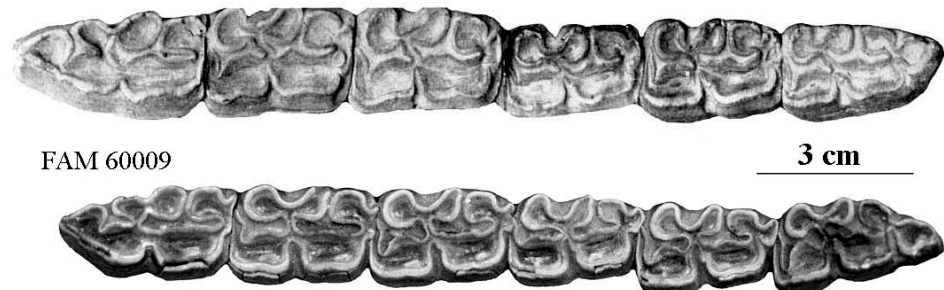
Relatively similar skulls were also found in NE Siberia (*E. (E.) lenensis* IA 33) and in France (Jaurens; *E. (E.) gallicus* LY 302-486/7) (Supplementary File S19).

Crania assigned to *E. (E.) lambei* are small and the type skull is the smallest. A larger specimen, heavily restored (BEG 31058-2) and found at Blanco Creek, Texas, was referred to *Onager lambei* by [3]. The cranial preservation is so bad that it is hard to compare it to other North American fossil crania. The cheek teeth of BEG 31058-2 show some similarities to caballine teeth such as the morphology of the protocones (Figure 10); this specimen will be discussed in a section on problematic forms in Part 2 of our study.

The very worn upper cheek of the type fall into Group E. The others fall mostly into Groups A and B (Figure 10).

The lower cheek teeth fall into Groups 1 and 1-2; the ectoflexid (vestibular valley) is shallow even on the molars as in *E. (E.) alaskae* (Figure 22). Cups are present on lower incisors.

E. (E.) lambei, USNM 8426, Type



E. (E.) alaskae, FAM 60071



Figure 22. Lower p2-m3 of specimens referred to *E. (E.) lambei* (USNM 8426, type specimen; FAM 60009) and *E. (E.) alaskae* (FAM 60071). Occlusal view.

There are a few metapodials that by their small size may have belonged with the type cranium (Supplementary File S20). But since all other crania are much larger, these small specimens cannot be considered as typical.

According to the correlations between basilar lengths and metapodial distal breadths in extant *Equus* (<https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/OUTILS-TOOLS/CORRELATIONS%20between%20Basilar%20Length%20and%20distal%20widths%20of%20Metapodials> (accessed on 1 July 2024)), the latter should measure 42 to 47 mm in both *E. (E.) lambei* and *E. (E.) alaskae*. Among the dozens of metapodials from Yukon and Alaska of that size and their many different proportions, we were unable to differentiate *E. (E.) lambei* from *E. (E.) alaskae* metapodials, but it may be assumed that, in both, the MC lengths ranged from 198 to 228 mm with an average of 211 mm (Supplementary File S21) and the MT lengths ranged from 237 to 262 mm with an average of 250 mm (Supplementary File S22). Recently, Landry et al. [49] identified overlap in the MT dimensions of a large sample of Pleistocene horse specimens from the Yukon. The continuous variation in MT size and degree of slenderness led these authors [49] to question the reliability of metapodials as taxonomic indicators for Beringian horses when analyzed in isolation from other skeletal elements.

Most of the caballine metapodials from Dry Cave [50] could belong to some *E. (E.) alaskae*–*E. (E.) lambei* kind of horse (Supplementary Files S21 and S22).

Equus (E.) lambei from Natural Trap Cave, Wyoming

Natural Trap Cave has produced a large collection of horse fossils, but only a small portion of the horse assemblage is caballine [16,20]. John A. Howe kindly communicated to one of us (V.E.) his data on horse fossils from Natural Trap Cave (dated to ca. 20,000 years ago). Several fossils from this site may be referred to *E. (E.) lambei*: two fragmentary mandibles UNSM 47238 and KUVF 51079 (the latter associated with a palate) (Figure 23, Supplementary File S23), two MC, six anterior Ph1, five anterior Ph2, two femora, two tibiae, three tali, five posterior Ph1 and seven posterior Ph2, and possibly two Ph3 (Supplementary File S24).

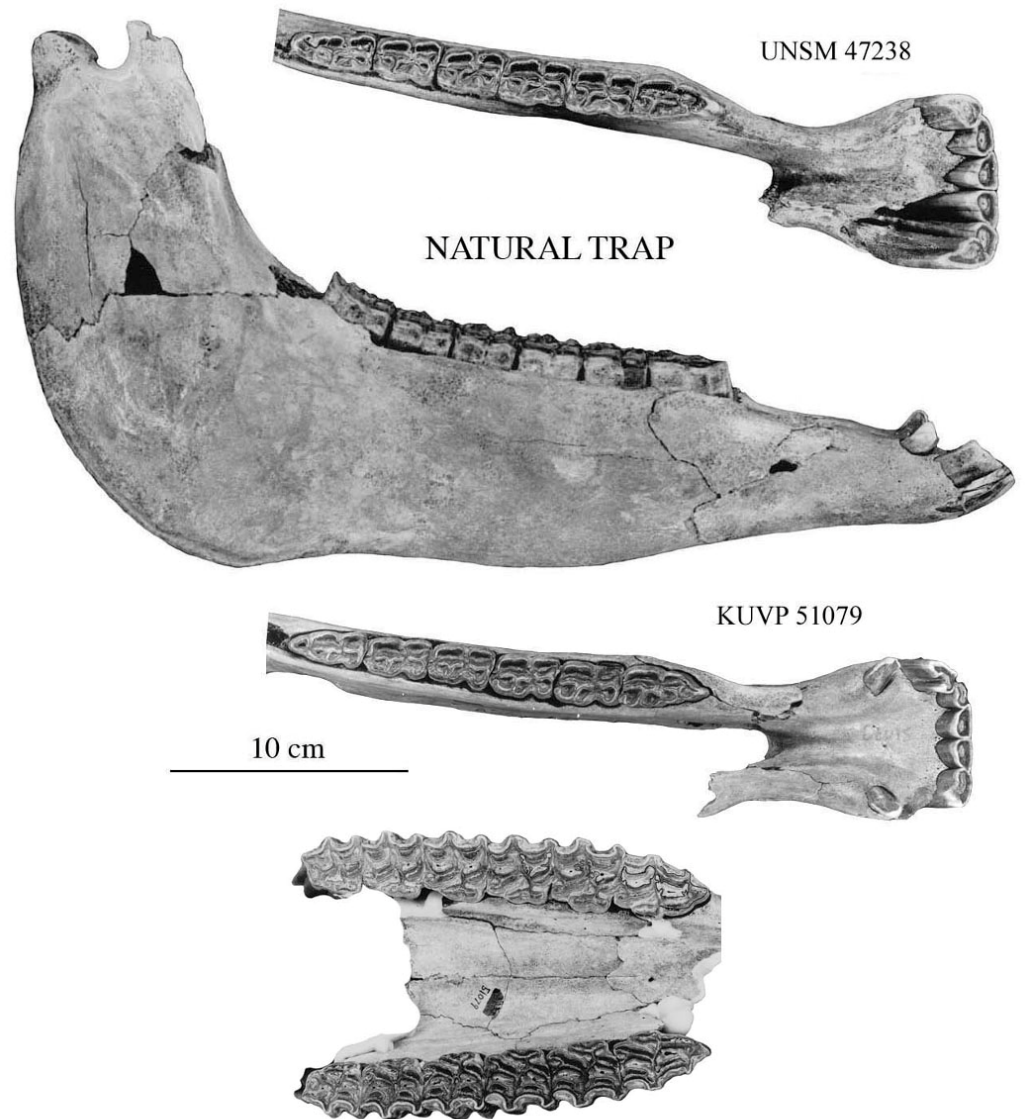


Figure 23. Partial mandibles (UNSM 47283 and KUPV 51079) and palate (KUPV 51079) from Natural Trap Cave referred to *E. (E.) lambei*. Lateral and occlusal views.

According to the correlations existing between mandibles and crania dimensions (<https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/OUTILS-TOOLS/CORRELATIONS%20between%20CRANIA%20and%20MANDIBLES> (accessed on 1 July 2024)), the muzzle width of KUPV 51079 was ca. 71 mm and the muzzle length ca. 118 mm (Supplementary File S23); the basilar length was around 500 mm, just as in *E. (E.) lambei*.

The lower cheek teeth have the usual caballine pattern. In UNSM 47238, infundibula are well developed on all lower incisors but only on i1 and i2 in KUPV 51079. Protocones are long and grooved (Figure 24).

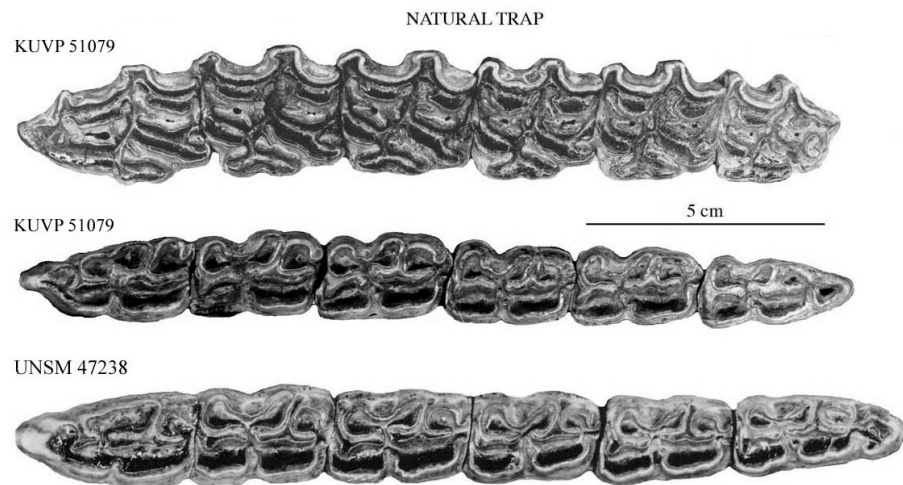


Figure 24. Cheek teeth of *E. (E.) lambei* (KUVVP 51079 and UNSM 47238) from Natural Trap Cave. Occlusal view.

4.1.3. Comments on *E. (E.) scotti*, *E. (E.) alaskae*, and *E. (E.) lambei*

To sum up, *E. (E.) alaskae* and *E. (E.) lambei* were much smaller than *E. (E.) scotti*, and their cranial proportions are completely different (Supplementary File S25). Figure 25 and Supplementary File S23 compare the main anatomical features of *E. (E.) alaskae* and *E. (E.) lambei*. Particularly, they illustrate the very large relative protocone lengths of *E. (E.) lambei* and *E. (E.) alaskae*, particularly in *E. (E.) lambei*. We propose that *E. (E.) alaskae* and *E. (E.) lambei* are “ecological variants” of a single species. It appears that *E. (E.) alaskae* and *E. (E.) lambei* differ mainly by muzzle proportions. Since usually muzzles tend to shorten in cold conditions (Allen’s rule), it may be supposed that *E. (E.) lambei* lived during very cold times and *E. (E.) alaskae* during milder times. This is a hypothesis that may be tested through radiometric dating, stratigraphic work, stable isotope analysis, and population level genetic analysis.

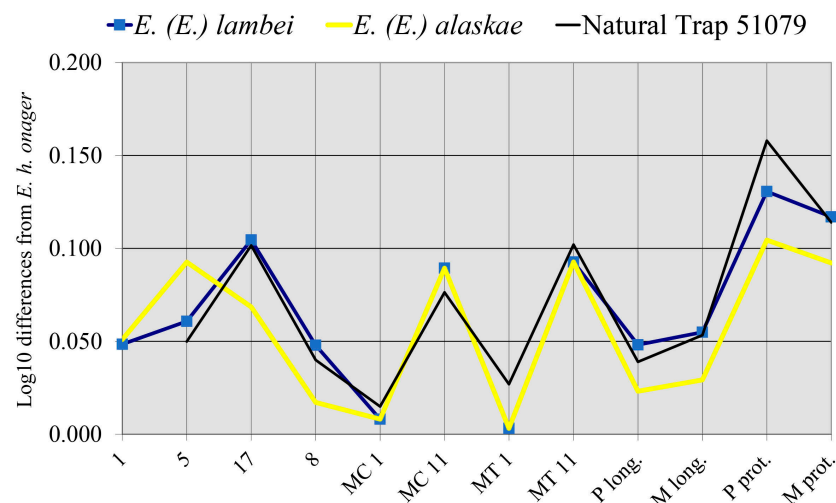


Figure 25. Simpson’s ratio diagrams of *E. (E.) lambei* ($n = 5–16$), *E. (E.) alaskae* ($n = 5–16$), and *E. (E.) lambei* from Natural Trap (KUVVP 51079) cranial, metapodial, and tooth measurements. 1: Basilar length. 5: Muzzle length, 17: Muzzle breadth at the posterior borders of I3. 8: Length of cheek teeth P2–M3. MC 1: Maximal length of third metacarpal. MC 11: Distal articular breadth of third metacarpal. MT 1: Maximal length of third metatarsal. MT 11: Distal articular breadth of third metatarsal. P long.: P3–P4 size calculated as $(Lo + lo)/2$ of P3–P4. M long.: M1–M2 size calculated as $(Lo + lo)/2$ of M1–M2. P prot.: P3–P4 protocone length. M prot.: M1–M2 protocone length.

4.2. Hay Springs Sheridan Equus Beds Caballines

The late Irvingtonian crania from Hay Springs, Nebraska, including the types of *E. (E.) niobrarensis* and *E. (E.) hatcheri*, are all badly preserved and/or very old or juvenile.

Almost all data were communicated to one of us (V.E.) by John Howe. Almost all measurements of limb bones (hundreds of them) were taken by John Howe and two of his students. Many field and accession numbers are the same for several bones, and many bones seem to have been measured several times by the same person or by different persons; in that case, means of different dimensions (labelled x) were computed. Photographs of dentitions are without scale and often bear field numbers while in the table of measurement specimens are mostly referred to by accession numbers. It is not always clear whether the number is “field” or “accession”. Data and photographs communicated by John Howe are available in HOWE HAY SPRINGS: <https://drive.google.com/drive/folders/1yeU9HtK2iG4Cv8HVWHbCMgTH7KyKKhl5?usp=sharing> (accessed on 1 July 2024).

The fossils of Sheridan Beds come from several localities—Sh 1 to Sh 6 *Equus* beds—but the bulk were found in Sh 5 Gordon Quarry 5. There is no information about the provenance of quite a number of fossils (“Sh 0”). According to [51], most of the fossils from Sheridan County Fossil Quarries can be attributed to the late Kansan and Yarmouth (Pre-Illinoian).

4.2.1. Crania (Supplementary Files S3 and S26, Supplementary Table S3)

There are at least 12 more or less preserved crania from Hay Springs and 2 fragmentary mandibles. Nine show caballine characters although some were referred to the subgenus *Asinus* by [52]. Specimens from *Equus* Sheridan Beds (excluding Sh 5 Gordon Quarry 5) are as follows:

- USNM 4999, skull, type of *Equus (E.) niobrarensis*.
- USNM 7868, skull, type of *E. (E.) hatcheri*; referred to *E. niobrarensis* by [7].

Azzaroli [7] remarked that “the type skulls of *E. niobrarensis* and *E. hatcheri* are of restricted interest because of the extensive restorations they underwent” and it is true indeed. Moreover, their very different enamel patterns may be, at least in part, the consequence of wear. We consider, however, that these patterns may be used to classify other fossils and will employ them for further morphological descriptions.

- UNSM 1346, fragmentary juvenile skull; referred to *E. niobrarensis* by [7].
- AMNH 2725, fragmentary skull; referred to *E. complicatus* by [1] and to *E. excelsus* (our *E. (E.) scotti*) by [7].
- AMNH 11642, fragmentary mandible; referred to *E. excelsus* (our *E. (E.) scotti*) by [7].

Specimens from the locality Sh 5 Gordon Quarry 5 include the following: UNSM 5980, UNSM 5981, and UNSM 5982 crania; UNSM 9417, a fragmentary mandible referred to *E. niobrarensis* by [7]; and UNSM 5989, a fragmentary cranium possibly also from the locality of Gordon.

We have used modified photos from [7] of UNSM 5980, 5982, 1346, and 9417 and AMNH 2725 and AMNH 11642; we have no photographs for UNSM 5981 nor 5989 crania, and only Howe’s measurements for the latter.

Due, at least in part, to bad preservation, reconstructions, and juvenile or very old age, the cranial dimensions and proportions are rather variable (Supplementary Files S26 and S27). The type cranium and mandible of *E. (E.) niobrarensis* belong to a young adult mare; the type cranium and mandible of *E. (E.) hatcheri* belong to an old stallion. Possibly the differences between muzzle lengths and breadths may thus be explained. The long muzzle of the old stallion UNSM 5981 may also be due to its age. Two specimens, however, stand apart: UNSM 1346 and UNSM 5989.

UNSM 1346 is the cranium of a 2-year-old colt. It is laterally compressed, but otherwise sufficiently well-preserved. Its large size is remarkable. Its basilar length (560 mm) would be about 580 mm as an adult (<https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/OUTILS-TOOLS/CRANIAL%20GROWTH%20Extrapolations%20in%20Equus> (accessed on 1 July 2024)). This would correspond to metapodial distal breadths of around 54 mm (Supplementary File S28). Another remarkable character is the uncommonly large basion–staphylion length (measurement 4). The fragmentary UNSM 5989 appears to have been even larger.

4.2.2. Dentition

The upper cheek teeth of AMNH 2725 resemble those of *E. (E.) scotti* (Figure 15). Those of UNSM 4999 have shorter protocones and lesser plicated enamel; similar patterns are found at Dry Cave [50], Rancho La Brea, and on the teeth from the Fossil Lake area referred to *E. pacificus* by [1] as will be illustrated later. They fall into Groups A, B, and E.

There is nothing particular about the lower cheek teeth from Hay Springs except for the slightly larger size of *E. (E.) hatcheri* and AMNH 11642 (Figure 26). Ectoflexids are often shallow even on molars. Most fall into Groups 1 and 1-2.

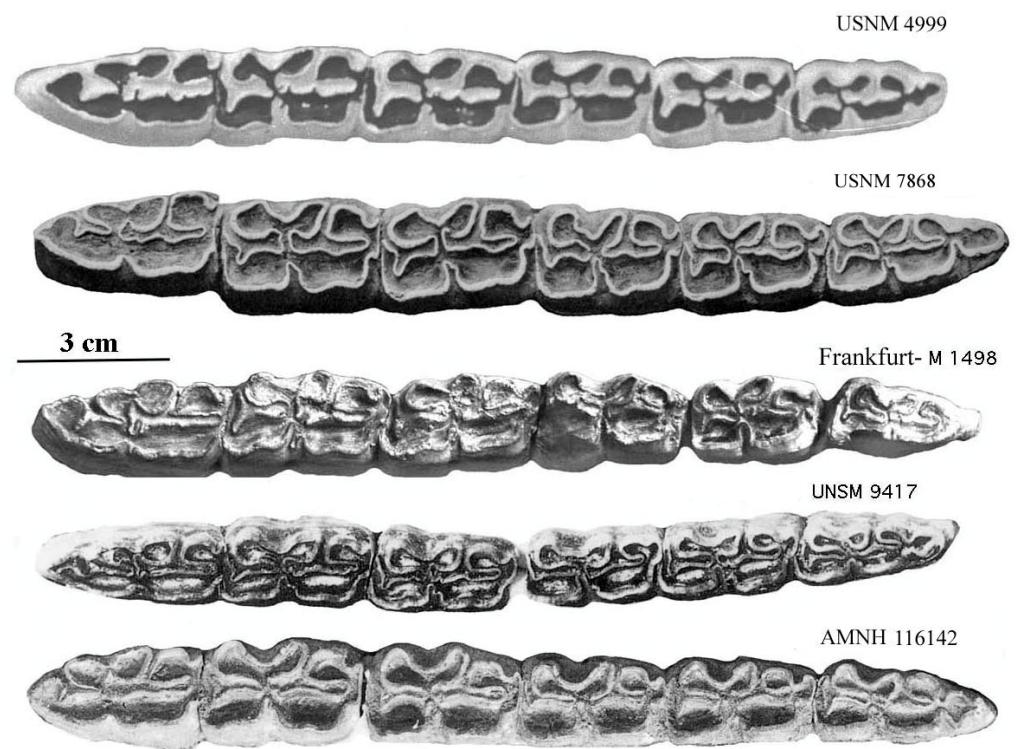


Figure 26. Lower p2-m3 from Hay Springs: UNSM 4999, *E. (E.) niobrarensis* type, cast; UNSM 7868, *E. (E.) hatcheri* type, cast; Frankfurt M-1498; UNSM 9417; and AMNH 116142 (ex. FM 2725). Occlusal view.

Cups are present on i1 and i2; not perfectly developed on i3 of UNSM 4999.

Upper cheek teeth of UNSM 5980, UNSM 5982, UNSM 7868, and Frankfurt M-1487 belonged to old animals (Figure 11). The shorter and/or flatter protocones of *E. (E.) hatcheri* type (UNSM 7868) and UNSM 5982 and 5980 may thus be accounted for; but the differences between the '*E. (E.) scotti*-like' AMNH 2725 and the type of *E. (E.) niobrarensis* (UNSM 4999) cannot be ascribed to wear. If they were sympatric–contemporaneous, they must be considered as representing different species, as suggested by Azzaroli ([7], Plate 18, p. 10). If they were *not* contemporaneous, it may be supposed that the '*scotti*-like' morph evolved into a '*niobrarensis*-like' morph and that they are both chronospecies of a caballine lineage.

4.2.3. Limb Bones

Except for a few large specimens possibly belonging to the large *Equus*, the bulk of well-preserved caballine MC from Hay Springs ($n = 46$) is relatively homogenous, the main differences being the larger depth of the keel in 13 of them (Supplementary File S29). The matter is different for the MT. First, there are more of them, and secondly, two groups may be distinguished: 40 are slightly smaller and deeper in the diaphysis than the other 50; we do not know how much significance these differences may have. The distal articular breadths of the MC and MT would be consistent with basilar lengths of 500 to 540 mm for the corresponding crania (<https://veraeisenmann.com/index.php?ref=/public/WEB/EQUIDES%20MONODACTYLES/OUTILS-TOOLS/CORRELATIONS%20between%20Basilar%20Length%20and%20distal%20widths%20of%20Metapodials> (accessed on 1 July 2024)); these are the dimensions of all Hay Springs crania, except the juvenile UNSM 1346 whose basilar length is ca. 580 mm. A large MT (HS 6515) may have belonged to this latter form.

4.2.4. Comments of Hay Springs Sheridan *Equus* Beds Caballines

We refer UNSM 1346 and 5989 to *Equus* (*E.*) sp. and AMNH 2725 and Hay Springs 6006 3268-38 to *E. (E.) scotti* or *E. aff. E. (E.) scotti* (Figure 15); several other upper cheek teeth have the same enamel pattern but, unfortunately, the available photographs have no scale.

We refer to *E. (E.) niobrarensis* UNSM 5980, UNSM 5982, and M-1487 of the collections in Frankfurt. *Equus (E.) hatcheri* may be considered as a morphological variant or chronological variant of *E. (E.) niobrarensis*.

Crania of *E. (E.) niobrarensis* are smaller than those of *E. (E.) scotti*. They differ mainly by their wider choanae (Supplementary File S30, measurement 10).

4.3. Hay Springs-like Fossils

Slaton, Lubbock County, Texas

Among the Early Illinoian equid fossils found at Slaton, the TMM 6643 upper and TMM 4800 lower series were referred to *E. niobrarensis* by Dalquest (Figure 2 in [30]), although he noted the greater resemblance of the upper series with the type of *E. hatcheri*. Other caballine remains are several series or associated teeth and several associated limb bones. The metatarsal TMM 5249 could belong to *E. (E.) scotti* (Supplementary File S16) but, unlike for *E. (E.) scotti* skeletons, it is longer relative to the associated tibia (see comparison of limb proportions in Section 6.2). This is a very rare occurrence; as far as we know, such proportions happen only in *E. (E.) przewalskii*—22 out of 35 skeletons.

Dry Cave, Eddy County, New Mexico

In addition to the published data, we are indebted to A.H. Harris for sharing detailed measurements (Supplementary Files S21 and S22).

Although most of the Late Pleistocene caballine metapodials from Dry Cave [50] could belong to some *E. (E.) alaskae*–*E. (E.) lambei* kind of horse, there are some MC that fall inside the range of variation of Hay Springs caballines and some which are larger. The size of MC UTEP 31-57 and 22-692 and of MT 31-64 would be consistent with the size of UNSM 1346 from Hay Springs.

Ingleside, Texas

Among the Late Pleistocene equid material from Ingleside, the mandible TMM 30967-410, probably associated with the large, badly preserved cranium TMM 30967-401 (Figure 27), was referred to *E. complicatus* by ([53], Figures 54 and 56, Table 45, p. 64). Both cranium and mandible resemble the type of *E. (E.) hatcheri*. Lundelius [53] did not illustrate the teeth of the cranium but gave their occlusal length and width dimensions in his Table 46 together with other specimens he also referred to *E. complicatus*. Unfortunately, he did

not give any dimension for the upper P2-M3 series TMM 30967-379 he illustrated in his Figure 55 (Figure 28), but they seem rather similar to the type of *E. (E.) hatcheri*.

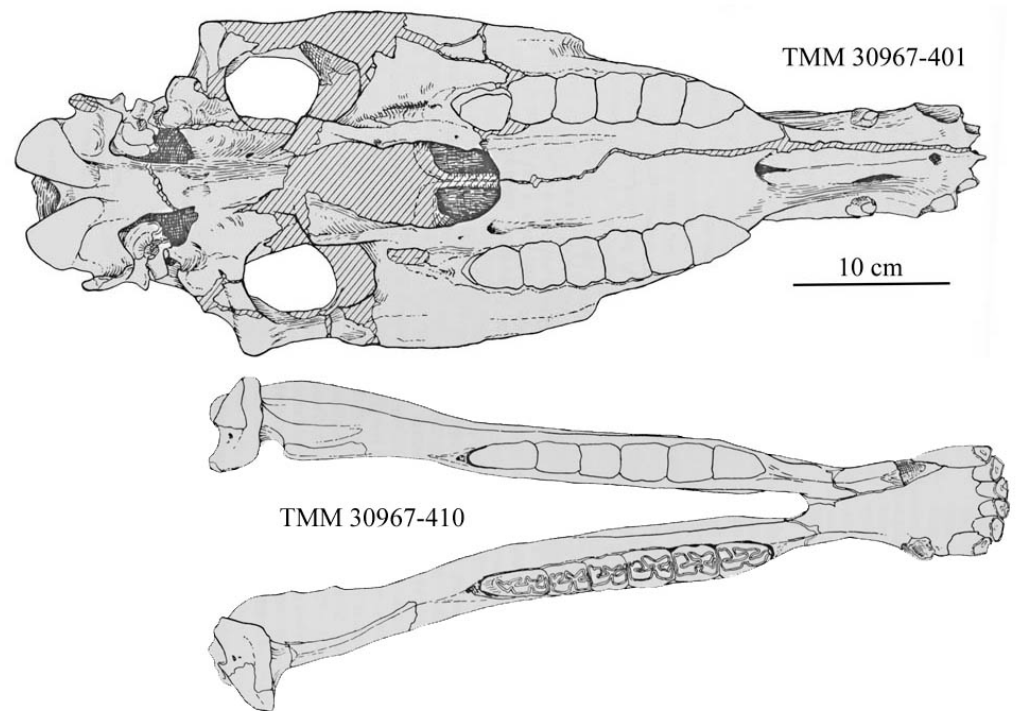


Figure 27. Cranium and associated mandible TMM 30967-401 and TMM 30967-410 from Ingleside, Texas. Ventral and dorsal views, respectively. Modified from [53].

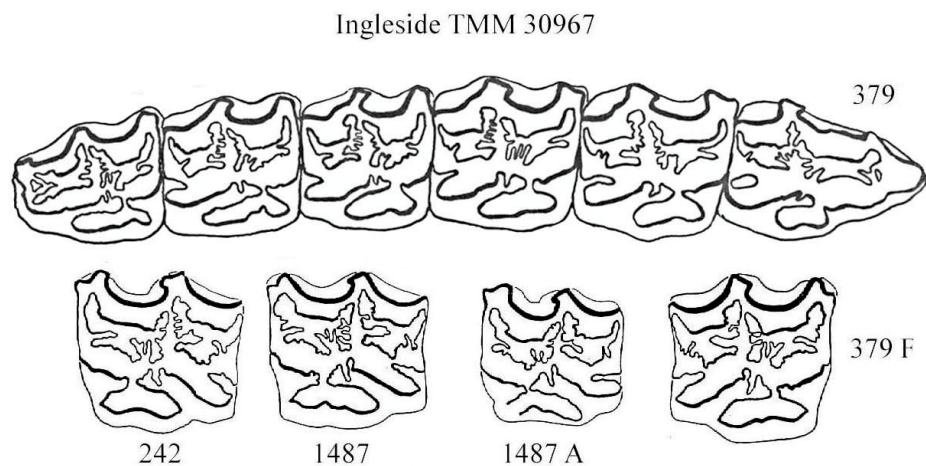


Figure 28. Upper cheek teeth from Ingleside, Texas. Occlusal view. Modified from [53].

Also from Ingleside, Lundelius ([53], Figure 58) referred to *E. pacificus* four upper premolars (TMM 30967-242, 1487, 1487A, and 379F) that resemble AMNH 2725—another specimen from Hay Springs—and three first anterior phalanges.

The enamel of all Ingleside upper cheek teeth is very plicated as at Hay Springs and in *E. (E.) scotti* to which it was probably related.

4.4. Caballine *Equus* from Fort Qu'Appelle (Supplementary File S3, Supplementary Table S4)

Khan [54] referred to *E. scotti*—which he considered a senior synonym to *E. niobraren-sis*—a cranium, several dentitions, and limb bones from the Echo Lake gravel beds near Fort

Qu'Appelle, Saskatchewan. He believed them to belong in the Sangamon Interglacial or, at the latest, to a Wisconsin interstadial. Azzaroli [7] referred these fossils to *E. niobrarensis*.

The cranium SMNH 1515-8306 (Figure 29) belonged to an old mare. It has a long muzzle, remarkably short choanae, and a remarkably long distance between the basion and staphylion. The cranium is smaller than both *E. (E.) scotti* and *E. (E.) niobrarensis* (Supplementary File S30), and has a much longer basion–staphylion distance, and is narrower at the middle of the diastema (measurement 17bis).

SMNH 1515-8306
Fort Qu'Appelle

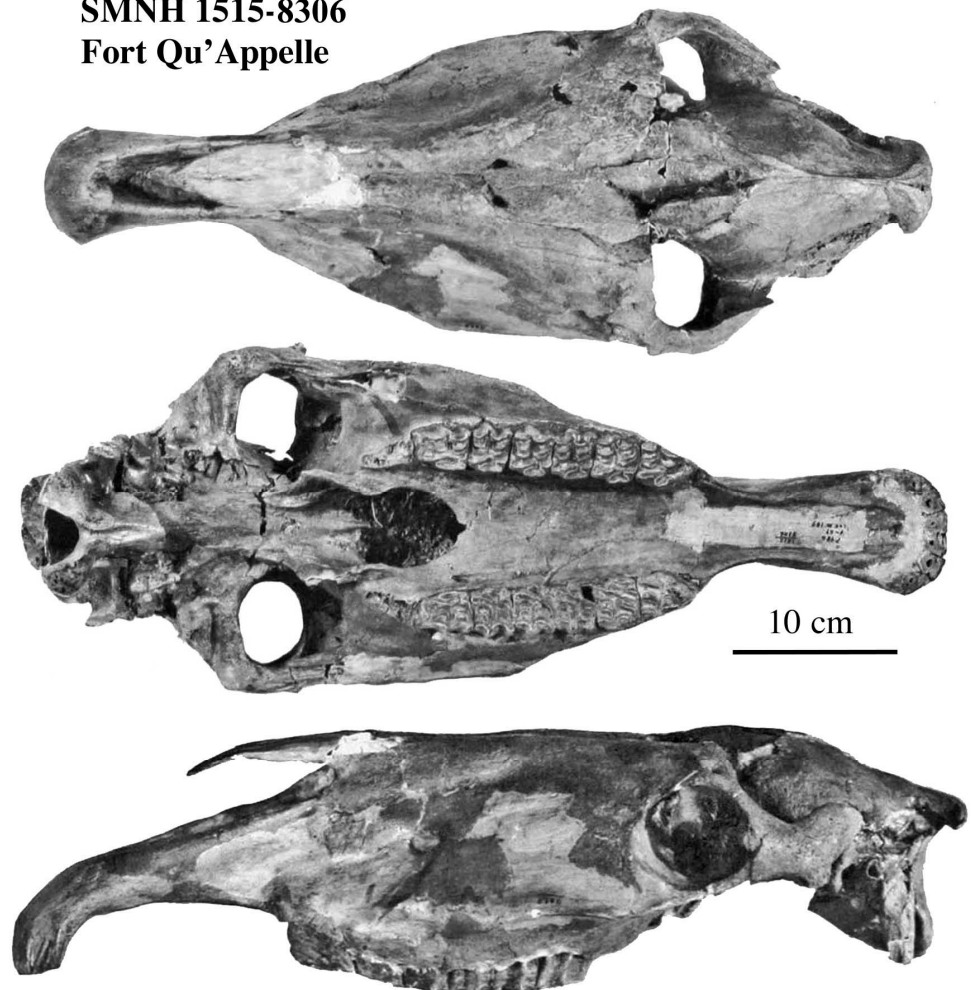


Figure 29. Cranium (SMNH 1515-8306) of caballine *Equus* from Fort Qu'Appelle. Dorsal, ventral, and lateral views. Modified from [54].

On the upper very worn cheek teeth, the protocones are slightly or not grooved unlike the type of *E. (E.) niobrarensis*; the lower cheek teeth have the usual Group 1 caballine pattern (Figure 30).

Unfortunately, the samples of limb bones from Fort Qu'Appelle are highly heterogeneous (Supplementary File S31): one MC (SMNH 8004-1410) could be referred to an *Equus* as large as *E. (E.) scotti*, while SMNH 7737-1042 must certainly belong to *E. (E.) alaskae* or *E. (E.) lambei*; all MT can be referred to some large *E. (E.) alaskae* or *E. (E.) lambei* form.

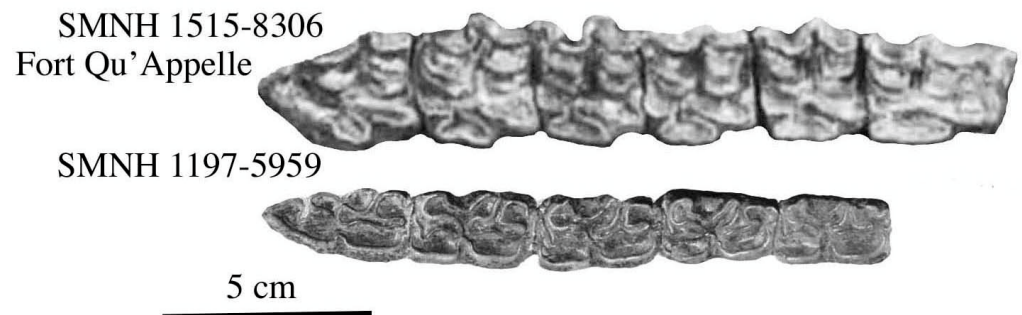


Figure 30. Upper (SMNH 1515-8306) and lower (SMNH 1197-5959) P2-M3 of caballine *Equus* from Fort Qu'Appelle. Occlusal view. Modified from [54].

4.5. *Equus* (*E.*) *pacificus* Leidy, 1868 (Figure 31)

Leidy [55] created *E. pacificus* based on one upper P3 from Martinez, Contra Costa, California; it was not illustrated but the measurements are those of a large *Equus*: 35 mm and 32 mm of occlusal length and width. According to these dimensions, *E. (E.) pacificus* would be one of the largest *Equus* in the world [56]. Gidley [1] referred to this species (based on size and Leidy's [55] description of the holotype) several specimens from the Fossil Lake area, Oregon, including three upper cheek teeth that are illustrated in his Figure 11 (Figure 31, top row). The teeth illustrated by Gidley [1] resemble the holotype of *E. (E.) niobrarensis* (Group B) but are much larger. Some authors consider *E. pacificus* a valid name (e.g., [3,53]) and refer to Gidley's [1] description and illustration when discussing this species, but others consider it a nomen vanum or nomen dubium (e.g., [2,8]); resolving this nomenclatural issue is beyond the scope of our study. We recognize a very large form of *Equus* (*Equus*) known primarily from the western USA that we tentatively refer to as *E. (E.) pacificus*, pending further consideration of the nomenclatural status of this species name.

Also, from the Fossil Lake area, Oregon, Cope [57] illustrated and referred to *E. occidentalis* three clearly caballine lower cheek teeth (Figure 31, bottom row). These teeth are similar in size to the teeth of *E. (E.) pacificus* described by Gidley [1], and we refer them to that taxon. Data on large limb bones from Fossil Lake, referred to *E. (E.) pacificus*, are in Supplementary File S32. Other *Equus* from Fossil Lake will be discussed in a further study.

In addition to the numerous fossils of *E. (A.) occidentalis*, the Rancho La Brea collections include associated upper and lower dentitions UCMP 9G 14-10.5, dated at 12,000 or 35,000 years ago, that we refer to *E. (E.) pacificus* based on tooth morphology, although they are smaller than most specimens referred to this taxon (Figure 31). We also refer to *E. (E.) pacificus* the P3-M3 series UTEP 22-1608 from Dry Cave, New Mexico (Figure 31). This series was identified as *E. niobrarensis* by [50] and as *E. ferus* by [16].

The holotype of *E. bautistensis* Frick, 1921 [58] (three upper cheek teeth catalogued as UCMP 23238) is similar in size and morphology to teeth of *E. (E.) pacificus* (Figure 31). *Equus bautistensis* may be regarded as a junior synonym of *E. (E.) pacificus*, pending further consideration of the nomenclatural status of the species name of the latter.

The upper teeth of specimens we refer to *E. (E.) pacificus* fall into Group B, and the lower teeth fall into Groups 1 and 1-2.

From Ingleside, Texas, Lundelius [53] referred to *E. pacificus* four upper cheek teeth, mentioned above (TMM 30967-242, 1487, 1487A, and 379F) (Figure 28); we already noted their resemblances with the '*E. (E.) scotti*-like' AMNH 2725 from Hay Springs.

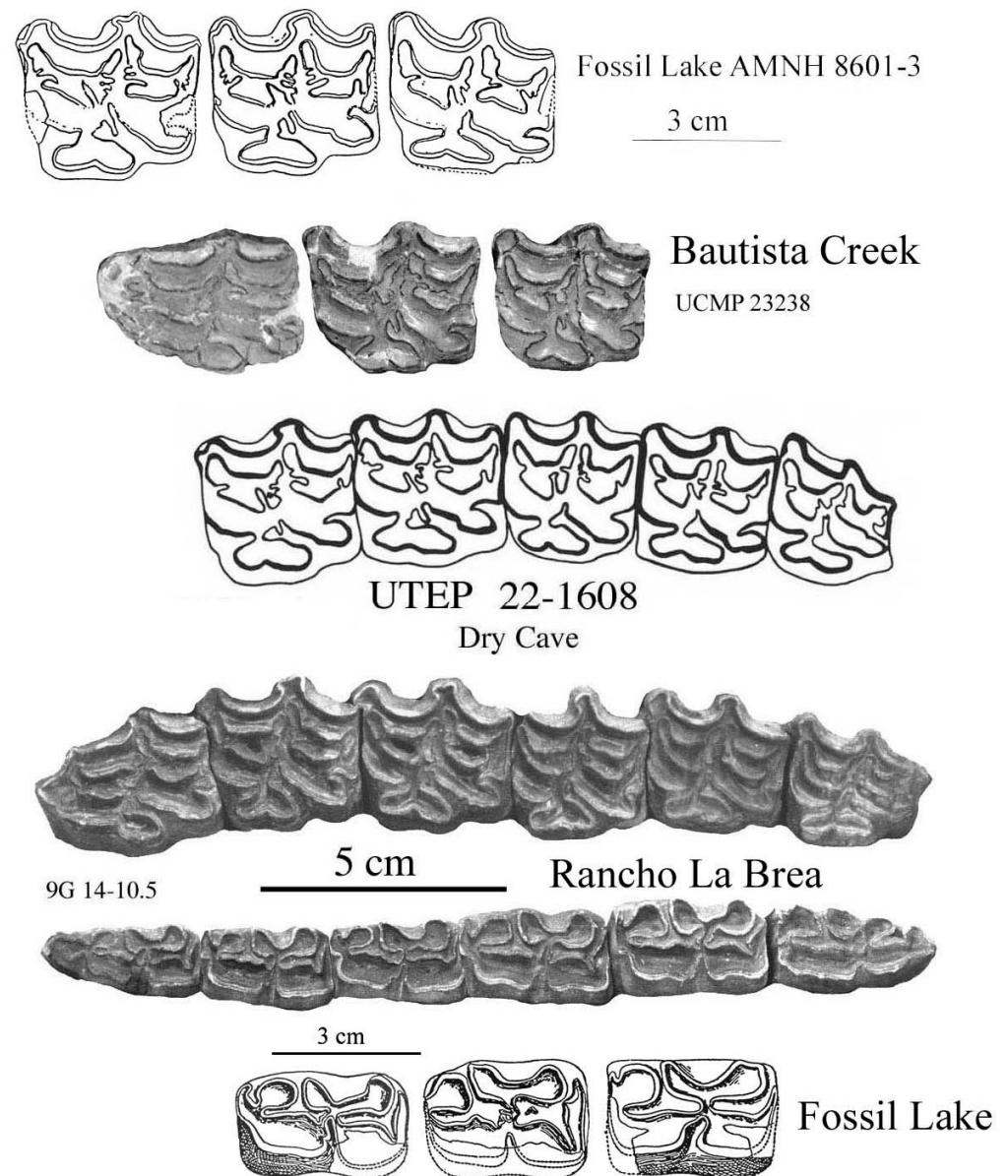


Figure 31. Upper and lower cheek teeth referred to *E. (E.) pacificus*: AMNH 8601-1, 2, and 3, and unnumbered teeth from the Fossil Lake area; UCMP 23238 from Bautista Creek; UTEP 22-1608 from Dry Cave; and UCMP 9G 14-10.5 from Rancho La Brea. Occlusal view. AMNH 8601-3 modified from [1]. Unnumbered lower teeth from the Fossil Lake area modified from [57]. UTEP 22-1608 modified from [50].

4.6. *Equus (E.) complicatus* Leidy, 1858 [59], (Figure 32)

Equus (E.) complicatus (initially named *E. americanus* Leidy, 1847) was the first named *Equus* in the USA. As for many other old names, its history is exceedingly complicated [60]. Although Savage [2] considered it a nomen vanum and Azzaroli [7] a nomen dubium, we will follow Gidley's [1] observations based on the fossils described and illustrated by Leidy ([61], Plate 8, p. 265). A historical account of the processes leading Leidy to describe *E. complicatus* and the reasons for distinguishing it, or not, from *E. fraternus* and *E. leydii* will be provided in a separate paper on North American amerhippines (Part 2 of our study).

The lectotype chosen by Gidley [1] is an M2 from the vicinity of Natchez, Mississippi, now bearing the accession number ANSP 11424 in the Academy of Natural Sciences of Drexel University, Philadelphia; the three other specimens illustrated by Leidy [61] certainly belong to the same species although both M3 were referred to *E. fraternus* (Figure 32, top

row). On the upper molars, the enamel is plicated and protocones have pointed mesial and distal ends (Group A); the lower premolar has an angular caballine double knot with a pointed metaconid and metastylid (Group 1).

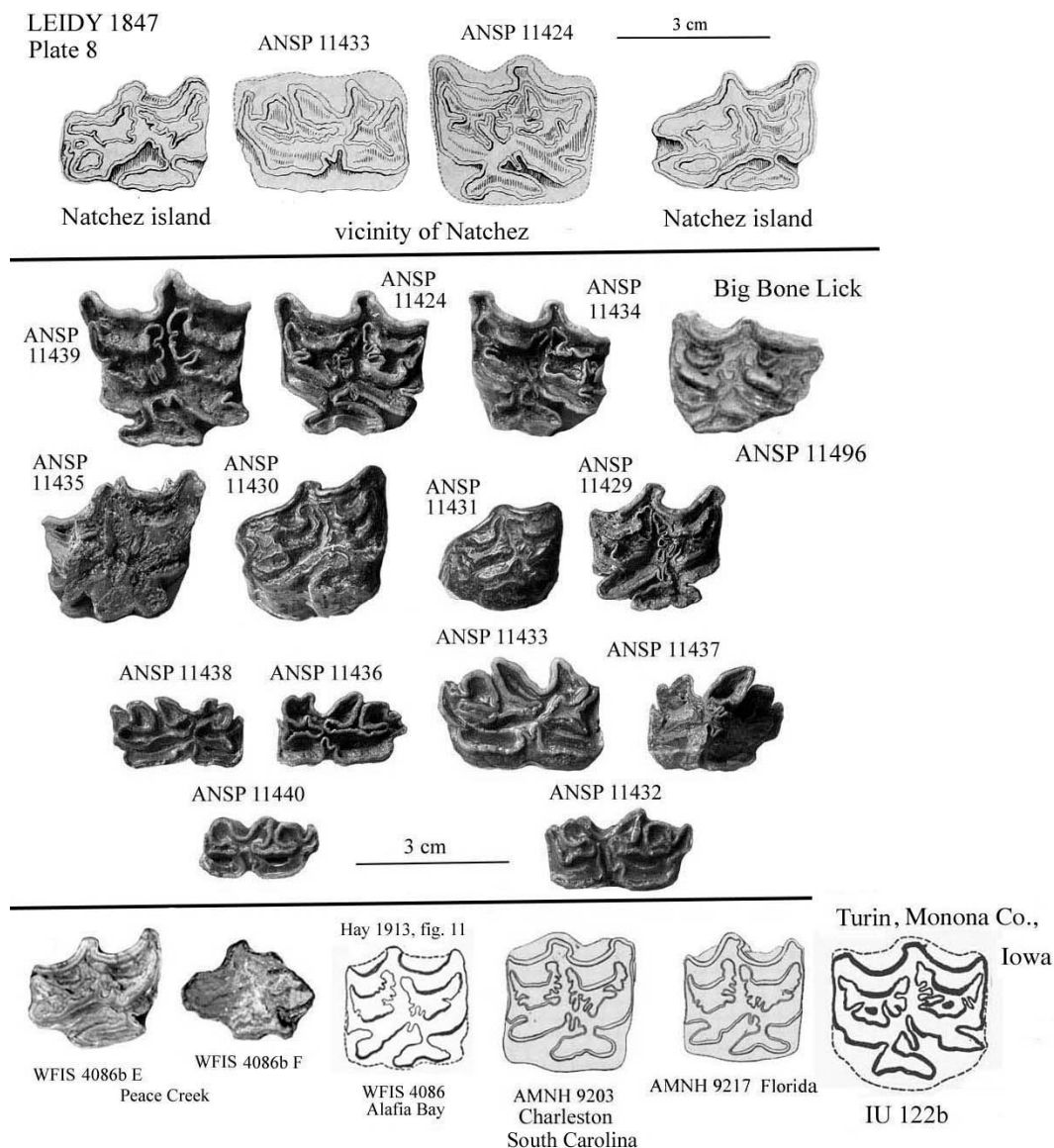


Figure 32. Lectotype of *E. (E.) complicatus* (ANSP 11424) and other teeth referred to this morphospecies. The top row reproduces original illustrations published by [61]: ANSP 11424 (lectotype [1]), ANSP 11433, and two M3 from Natchez Island originally referred by Leidy to *E. fraternus*. The next four rows show photographs of teeth from the same sample studied by Leidy [61] including the lectotype specimen, and one upper M3 from Big Bone Lick (ANSP 11496); we refer these teeth to *E. (E.) complicatus* except ANSP 11440 which we refer to *E. littoralis*. The last row shows upper teeth from Florida, South Carolina, and Iowa referred to *E. (E.) complicatus*. All teeth in occlusal view. Teeth in top row modified from [61]. Photos of teeth in middle section kindly provided by Dr. Daeschler with the exception of ANSP 11496, which was modified from [60]. Photos of WFIS 4086b E and WFIS 4086b F kindly provided by Ms. Dorwaldt. Drawing of WFIS 4086 modified from ([62], Figure 11). AMNH 9203 and AMNH 9217 modified from [1]. IU 122b modified from [39].

Although there are some resemblances between *E. (E.) complicatus* and *E. (E.) scotti*, as noted by Gidley [1] and Azzaroli [7], we follow Gidley [1] and consider *E. (E.) complicatus* as a different species in particular because of differences in the double knot patterns, including the presence of an indentation on the lingual side of the metaconid.

Photos of teeth belonging to the same sample in the collections of the Academy of Natural Sciences of Drexel University (ANSP) were kindly communicated to us by Dr. Daeschler (Figure 32). The difference in size inside this sample is very large and there are morphological differences too.

We tentatively distinguish the smaller upper ANSP 11429, 11431, and WFSI 4086b E and F, and the smaller lower ANSP 11432, 11436, and 11438 as a small form of *E. (E.) complicatus* and refer ANSP 11440 to *E. littoralis* Hay, 1913a [62], which will be discussed in Part 2 of our study. We also refer to the small form of *E. (E.) complicatus* AMNH 9217 from near Charleston (South Carolina), AMNH 9203 from some locality in Florida, and an upper molar from Alafia Bay (Florida). The M3 ANSP 11496 and the very large MC and MT from the late Wisconsin of Big Bone Lick (Kentucky) may belong to *E. (E.) complicatus* [60]. The upper premolar IU 122b from the Aftonian (Pre-Illinoian) of Turin (Iowa) may belong to an early *E. (E.) complicatus*.

Apart from what has been published by [60], we have found no information on the limb bones of *E. (E.) complicatus*.

Numerous fossils from various locations in North America were referred to *E. complicatus* by different authors [1,3,39,53,63–66]. We consider some of them as amerhippines and we will discuss them in Part 2 of our study.

4.7. *Equus holmesii* Hay, 1920 [65]

This species was described by [65]. The type is a series of upper cheek teeth (P3-M2), numbered USNM V 8642 from Afton, Oklahoma.

Equus holmesii has rarely been discussed in the recent literature of North American fossil horses ([8], Supplementary Text and Supplementary Table S6). Our study suggests that the holotype of *E. holmesii* possesses morphological traits that identify it as a caballine (e.g., upper cheek teeth with Group A and B morphologies), but it is not remarkable enough to grant a specific name; overall, it resembles teeth of *E. (E.) scottii* (Figure 15). We regard *E. holmesii* as a junior synonym of *E. (E.) scottii*.

4.8. *Equus laurentius* Hay, 1913a [62] (Supplementary Table S4)

The holotype of *E. laurentius* is a cranium and mandible, KUMNH 347, recovered from what were thought to be Upper Pleistocene deposits near Lawrence, Kansas. Additional data were published in [67]. In 1957, Quinn [3] discussed the question of the fossilization of the holotype and gave arguments in favor of an age of more than 1200 years. Discussions about that topic lasted for years until Scott et al. [68] settled the problem by proving that the cranium and mandible belonged to two separate individuals of the modern domestic horse (*Equus (E.) caballus*). Taylor et al. [69] contend that the cranium and the mandible belong to the same individual. Regardless of whether they belong to the same individual or not, both the cranium and mandible show pathologies that are indicative of bridling and riding, supporting the interpretation that they belong to a domestic horse [69]. *Equus laurentius* is a junior synonym of *E. (E.) caballus* [68].

The cranium belongs to a middle-aged stallion (Figure 33; composite from [62]) of moderate size. The upper cheek teeth have protocones that are rather short and are not grooved; on the lower cheek teeth, double knots are caballine (Group 1) and ectoflexids are deep on the molars (Figure 34; composite from [62]).

E. laurentius
KUMNH 347

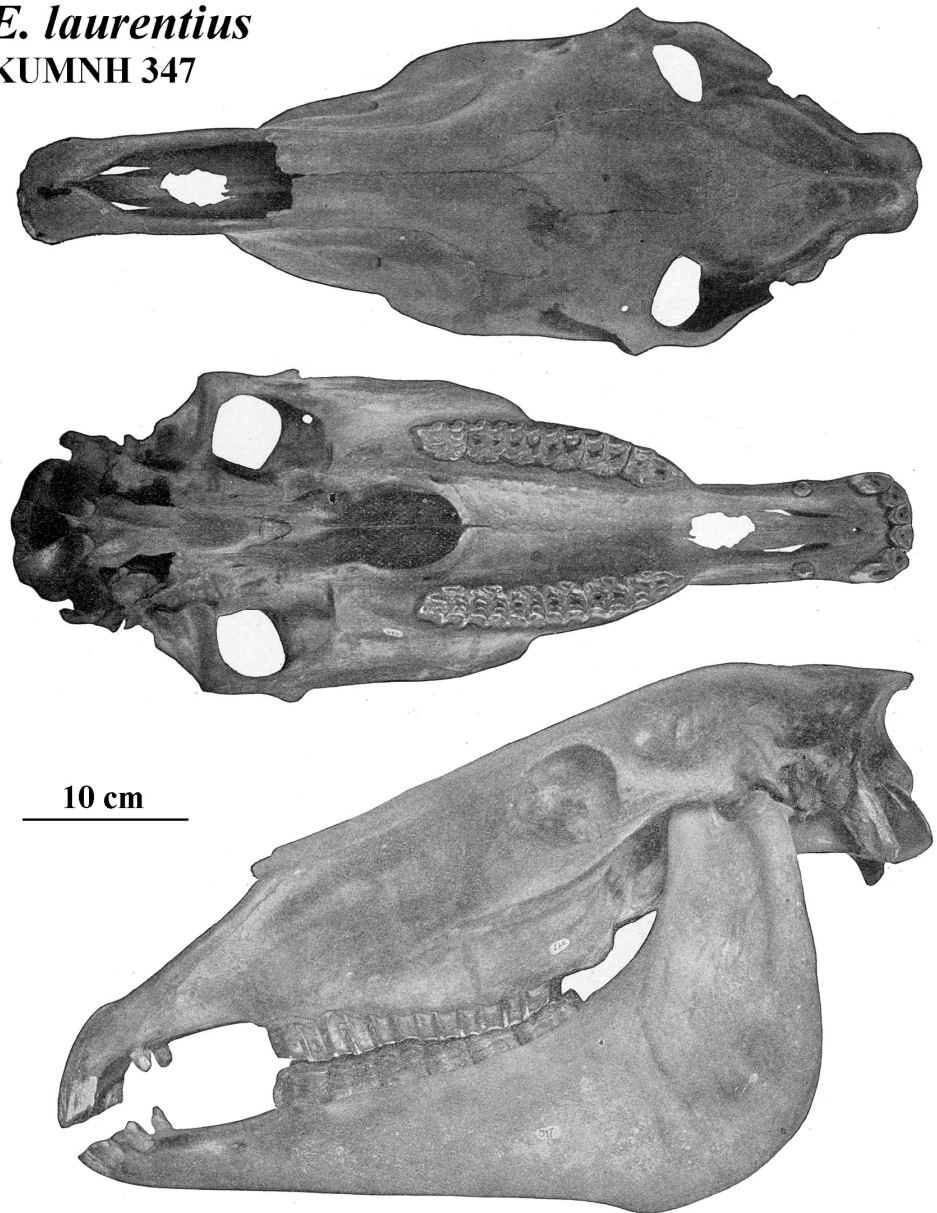


Figure 33. Holotype of *E. laurentius* (KUMNH 347), collected from the Kaw River near Lawrence, Kansas. Cranium in dorsal, ventral, and lateral views. Mandible in lateral view. Modified from [62].

***E. laurentius*, KUMNH 347**

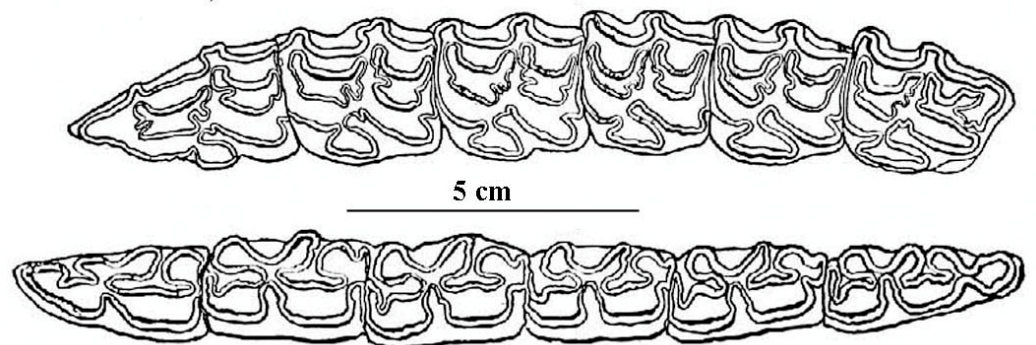


Figure 34. Upper and lower P2-M3 of *E. laurentius* (KUMNH 347, holotype). Occlusal view. Modified from [62].

Hay [39] also referred to *E. laurentius* a partial palate ([39], Plate XIII); the protocones are longer on this series than on the cranium KUMNH 347. The teeth are too worn to compare them in more detail to other teeth of North American fossil caballines.

Quinn [3] referred to *E. caballus laurentius* two cheek teeth (TMM 937-191 upper and TMM 937-252 lower molar) from Blackwater Draw, Portales, New Mexico (Figure 35). The protocone of the upper molar is much longer than in the corresponding tooth of KUMNH 347. The ectoflexid of the lower molar is shallow. These teeth were identified as *E. niobrarensis* by [70] and as *E. ferus* by [16].

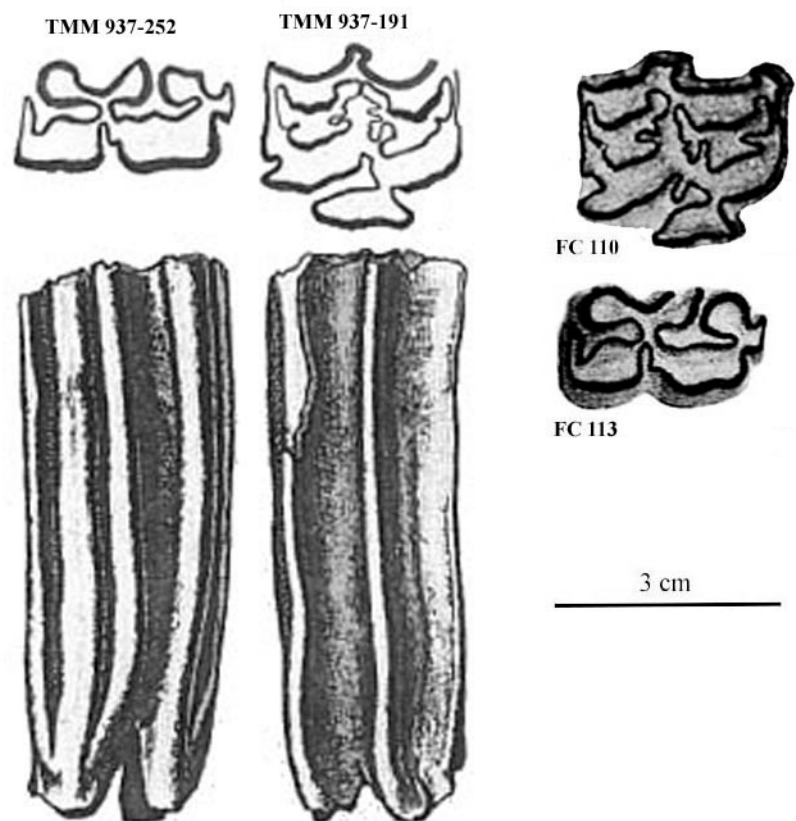


Figure 35. Lower (TMM 937-252) and upper (TMM 937-191) molars from Portales, New Mexico, referred by [3] to *E. caballus laurentius*. Lower molar in occlusal and lingual views. Upper molar in occlusal and buccal views. Upper (FC 110) and lower (FC 113) premolars from Cedazo, Mexico, referred by [68] to *E. caballus laurentius*. Occlusal view. TMM 937-252 and 937-191 modified from [3]. FC 110 and 113 modified from [71].

Mooser [71] also referred to *E. caballus laurentius* one upper premolar FC 110 and one lower premolar FC 113 from the Fauna Cedazo, Aguascalientes, Mexico (Figure 35). Both teeth differ from the corresponding teeth of KUMNH 347. The protocone of FC 110 is longer and pointed; the double knot of the lower tooth corresponds to Group 1-2.

4.9. Summary

We summarize below our observations and suggest some interpretations.

- The best documented and most ancient North American caballine species, *Equus* (*E.*) *scotti*, was about the size of an Arabian horse but had heavier bones, wider third phalanges, and less cursorial limb bone proportions (see comparison of limb proportions in Section 6.2.). Its weight may be estimated at 500–600 kg [56]. The maximal observed metapodial distal breadth is 59 mm, and the longest MC and MT are 246 and 291 mm long, respectively. The basilar skull length is 530 to 600 mm.

- The later *E. (E.) niobrarensis* was slightly smaller but probably had the same limb proportions; it differs, however, by cranial and dental features. The horse from Fort Qu'Appelle may be referred to *E. (E.) niobrarensis*, and the western *E. (E.) pacificus* may be related to *E. (E.) niobrarensis*, but this needs to be evaluated further.
- The juvenile cranium UNSM 1346 from Hay Springs belongs to a caballine, but it is unique compared to other North American caballine crania we studied by its large size and the long distance between basion and staphylion; we refer to it as *Equus (E.)* sp. We also refer to *Equus (E.)* sp. the large cranium UNSM 5989 also recovered from Hay Springs.
- Both *E. (E.) alaskae* and *E. (E.) lambei* primarily inhabited Yukon, Alaska, and NE Siberia during the Late Pleistocene. They both were about the size of *E. (E.) przewalskii* but with heavier bones. The associated limb bones FAM 71467 from Fox 33 and (not certainly associated) from Natural Trap Cave have the same relative lengths as *E. (E.) scotti*. Basilar lengths of fossil skulls of *E. (E.) alaskae* and *E. (E.) lambei* are similar (averages of 489 mm and 483 mm). Metapodial distal breadths measured 42 to 47 mm in both *E. (E.) lambei* and *E. (E.) alaskae*. The cranial proportions (Figure 25) differ only by the muzzle length and breadth: *E. (E.) lambei* crania have shorter and broader muzzles probably adapted to cold conditions according to Allen's rule; it is remarkable that there are no intermediate morphologies. We hypothesize that *E. (E.) alaskae* and *E. (E.) lambei* are "ecological variants" of a single species.
- *Equus (E.) complicatus* was a large form, probably restricted to southeastern North America. Unfortunately, only its upper and lower cheek teeth are well documented.

Thus, several discrete entities we treat as morphospecies existed in North America during the last 700,000 years: *E. (E.) alaskae*–*E. (E.) lambei* in the North, *E. (E.) complicatus* in the East, and *E. (E.) pacificus* in the West. *Equus (E.) scotti* and *E. (E.) niobrarensis* are morphologically different enough to qualify as distinct morphospecies if they were sympatric at Hay Springs, or as chronospecies if they were not contemporaneous. Whatever the case, and whatever their polymorphism, all these forms were undoubtedly caballine.

Our identification of *E. (E.) scotti*, *E. (E.) lambei*, and *E. (E.) alaskae* as caballine equids is consistent with recent morphological and molecular studies [8,15,16,72], even if the specific nomenclature used in those studies is different from the one presented here. Likewise, *E. (E.) niobrarensis* has been recognized as caballine in recent studies, but its taxonomic validity has been questioned [16], ([8], Supplementary Text and Supplementary Table S6).

Regarding *E. laurentius*, recent radiocarbon dating and osteological analyses have conclusively shown that its holotype belongs to a domestic horse [68,69]. Thus, *E. laurentius* is a junior synonym of *E. (E.) caballus*. Similarly, the holotype of *E. holmesii* has morphological traits that identify it as a caballine; however, our evaluation suggests that the holotype resembles teeth of *E. (E.) scotti*. *Equus holmesii* is considered a junior synonym of *E. (E.) scotti*. The holotype of *E. bautistensis* is similar in size and morphology to teeth of *E. (E.) pacificus*. *Equus bautistensis* may be regarded as a junior synonym of *E. (E.) pacificus*.

Now, however, we have to face a challenging problem, that of the identity of *E. midlandensis* and *E. mexicanus*.

5. *Equus midlandensis*

Quinn [3] described *E. midlandensis* Quinn, 1957, from Scharbauer Ranch, Midland County, Texas, and referred to this species teeth and bones from Baggett ranch, Odessa, Texas, and from Clovis site, 7 miles north of Portales, New Mexico.

Some other teeth and bones found in New Mexico and Texas (Blackwater Draw and Lubbock) were referred by [3] to *E. caballus caballus*, by [70] to *E. scotti*, and by [16] to *E.*

ferus. Other relevant specimens from Late Pleistocene localities in Texas and Mexico are also discussed below.

5.1. *Equus midlandensis* Holotype

The type material includes a fragment of a very young adult male mandible, associated upper cheek teeth, and several limb bones, all believed to belong to one individual (TMM 998, various elements) [3]. The material dates to the Late Pleistocene, post Sangamon [3].

The type mandible TMM 998-1 (Figure 36) has a height of 101.5 mm at the middle of p4. The overall size is large, close to that of the mandibles AMNH 10612 and CMN 2381 of *E. (E.) scotti* from the Irvingtonian of Rock Creek, Texas, but the diastema and muzzle lengths are much shorter (which may be because of the subadult age of the Texan specimen). Infundibula are present on i1 and i2, open on the unerupted i3.

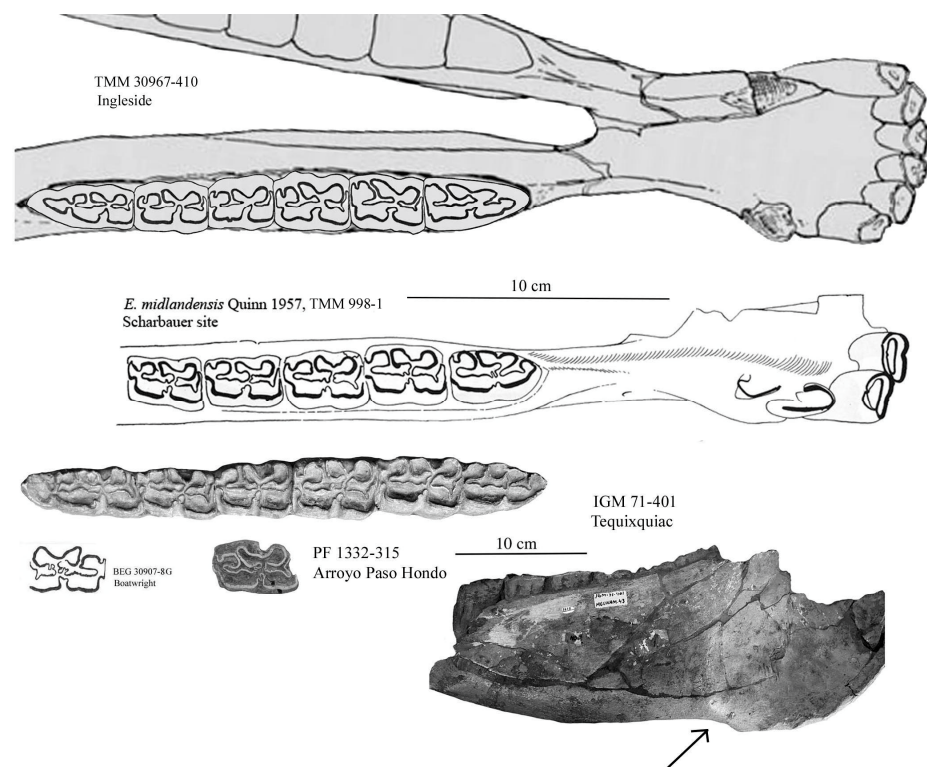


Figure 36. Mandible of *E. midlandensis* (TMM 998-1, holotype), Scharbauer Ranch, Texas. Also shown are mandibles TMM 30967-410 from Ingleside and IGM 71-401 from Tequiquiac (black arrow points to the pronounced concavity between ascending and horizontal ramus) and lower premolars BEG 30907-8G from Boatwright and PF 1332-315 from Arroyo Paso Hondo. All specimens in occlusal view. IGM 71-401 also shown in lateral view. TMM 998-1 and BEG 30907-8G modified from [3]. TMM 30967-410 modified from [53].

A right ramus from Tequiquiac (IGM 71-401) was tentatively referred to *E. mexicanus* by ([29], p. 73). It has the same height beneath the middle of p4 as in the type of *E. midlandensis* and the pronounced concavity between the ascending and horizontal ramus usually found in true horses. The pattern of the teeth is typically caballine, especially on the molars: angular lingual valley, rounded metaconid, pointed metastylid (Group 1). The isthmus of the double knot is very high, like in *E. (E.) scotti* (Figure 16), and the ectoflexid is shallow on all teeth (Figure 36). The lower p3 from Arroyo Paso Hondo, Fauna Cedazo, certainly belongs to a caballine but maybe not to *E. midlandensis*.

The associated upper cheek teeth of *E. midlandensis* resemble *E. (E.) scotti* (Figure 15) more than *E. (H.) mexicanus* (Figure 37).

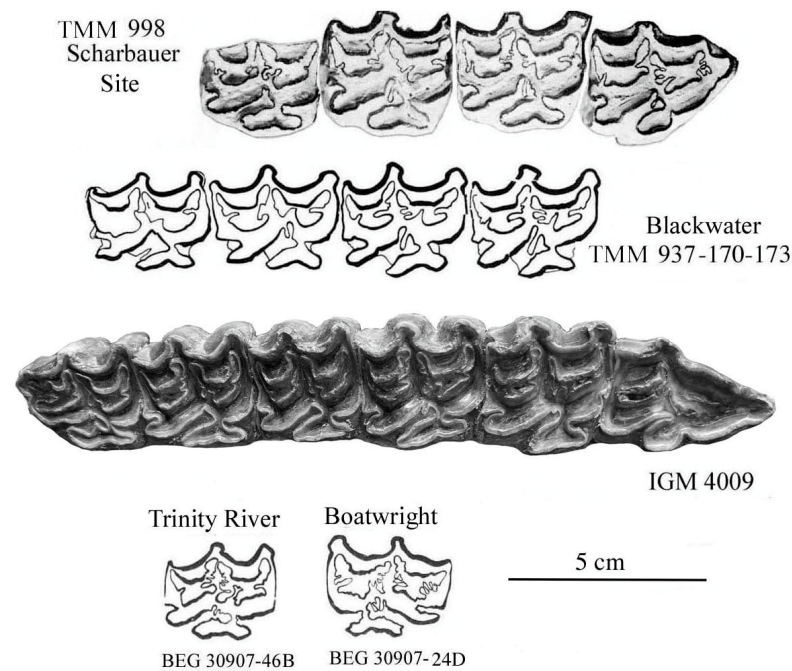


Figure 37. Upper cheek teeth of *E. midlandensis* from Scharbauer Site (TMM 998, type specimen), *E. (H.) mexicanus* (IGM 4009, type specimen), and other teeth from different localities in New Mexico and Texas (TMM 937-170-173, Blackwater Draw; BEG 30907-46B, Trinity River; and BEG 30907-24D, Boatwright). Occlusal view. TMM 998, TMM 937-170-173, BEG 30907-46B, and BEG 30907-24D modified from [3].

The metatarsal TMM 998-3 is robust. It has about the same size and proportions as *E. (E.) scotti* and the MT DP 4118 from Cedral referred to *E. mexicanus* by [43] (Figure 38 and Supplementary File S33).

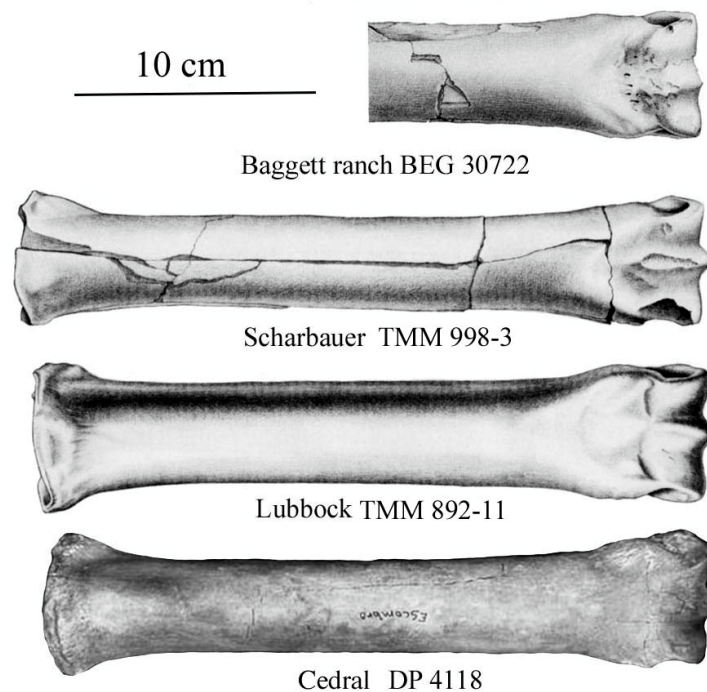


Figure 38. Third metatarsals from Baggett Ranch (BEG 30722), Scharbauer (TMM 998-3, type of *E. midlandensis*), Lubbock (TMM 892-11), and Cedral (DP 4118). Anterior view. BEG 30722, TMM 998-3, and TMM 892-11 modified from [3].

5.2. Referred Specimens

- Baggett Ranch, Odessa, Texas, and Clovis site, 7 miles north of Portales, New Mexico

There are no measurements nor drawings of the cheek teeth from Baggett Ranch (BEG 30422) and Clovis site lower cheek teeth (TMM 937) mentioned by [3]. Although supposed to belong to a single individual [3], it is doubtful that the caballine limb bones from Baggett Ranch (Figure 39) may even belong to the same species based on their proportions (Supplementary File S33).

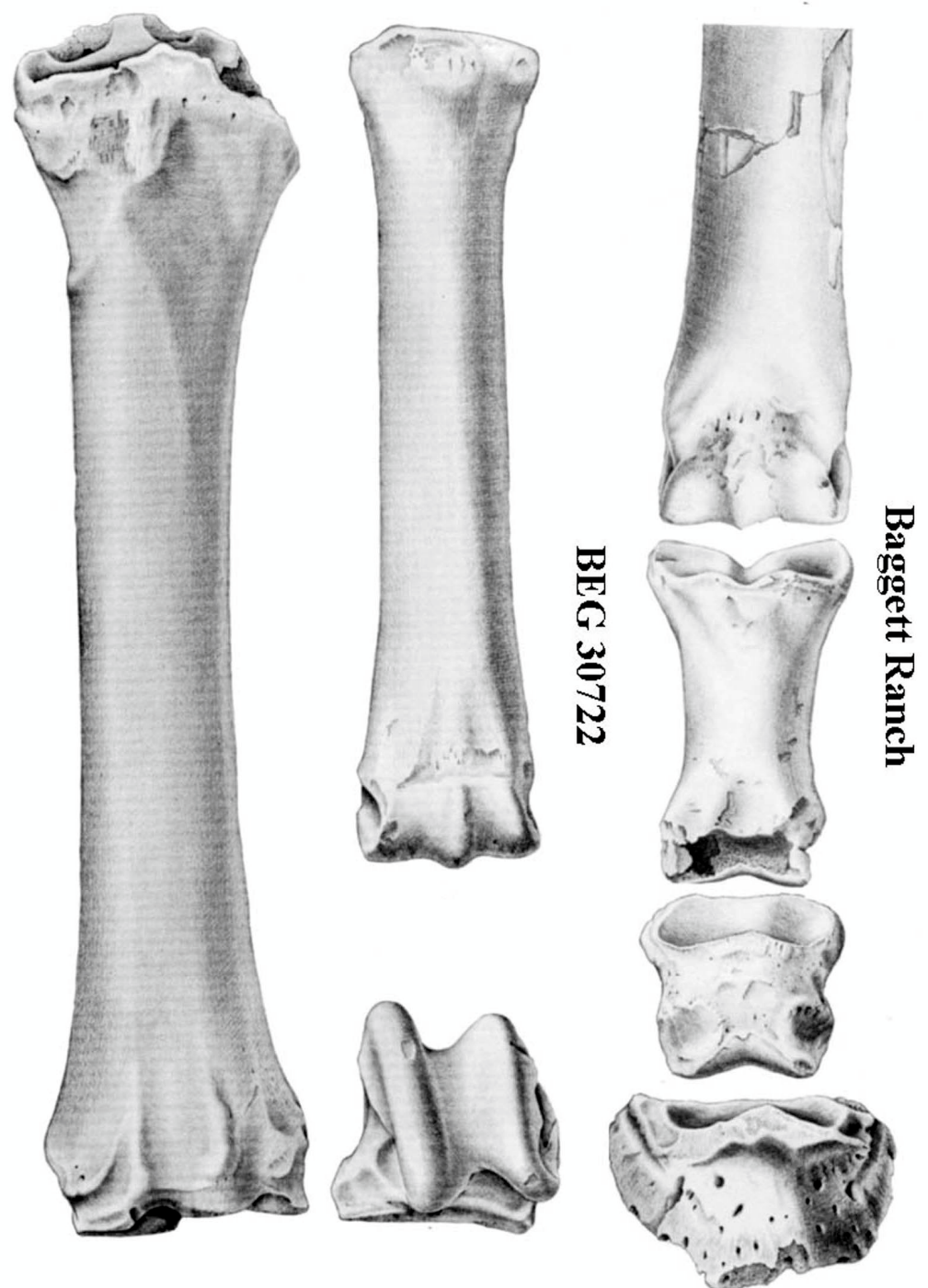


Figure 39. Limb bones from Baggett Ranch, Odessa, Texas (BEG 30722) referred by [3] to *E. midlandensis*. Modified from [3].

5.3. Other Relevant Specimens

- Blackwater Draw, Roosevelt County, New Mexico and Lubbock, Texas

The fossils from the Wisconsin of Blackwater Draw referred by [3] to *E. caballus caballus* were referred by [70] to *E. scotti* and by [16] to *E. ferus*.

The upper cheek teeth (TMM 937-170, Figure 37) are very similar to the holotype of *E. (H.) mexicanus*: the protocones are long, symmetrically grooved, and pointed like in sectioned premolars of *E. (E.) scotti*. Post-protoconal valleys are deep. Pli caballins are very developed. Like in *E. (E.) scotti*, the lower cheek teeth have caballine double knots with high isthmus and shallow ectoflexids even on the molars. Lundelius [70] referred TMM 937-170 and other specimens from Blackwater Draw to *E. scotti*; furthermore, he considered *E. midlandensis* as a junior synonym of *E. scotti*.

In addition to a damaged radius (TMM 937-240), there is an astragalus from Blackwater Draw and an MT (TMM 892-11) from Lubbock. The latter (Figure 38) more closely resembles the one from Baggett Ranch by its large distal supra-articular width.

- Boatwright and Trinity River, Texas

We are uncertain about the taxonomic assignment of the upper and lower teeth BEG 30907-24D and 30907-8G from Boatwright, Texas, and the upper BEG 30907-46B from Trinity River referred by [3], respectively, to *E. complicatus* and *E. fraternus* (Figures 36 and 37).

Slaughter [73] referred to *E. midlandensis* two upper cheek teeth from Hill-Lower Schuler, Trinity River, Texas, and noted resemblances with *E. scotti*. As in *E. (E.) scotti* and *E. midlandensis*, the enamel is plicated but the wide and grooved styles are very different. Moreover, the referred MC, SMUMP 60079, is smaller and more gracile (Supplementary File S33).

- Ingleside, Texas

We tentatively refer to *E. midlandensis* three first anterior phalanges from Ingleside, Texas (originally referred by [53] to *E. pacificus*), based on their smaller size and proportions compared to specimens we refer to *E. (E.) pacificus* (Supplementary Files S32 and S33).

5.4. Comments

To sum up, we see caballine characters in most fossils from Texas and New Mexico referred to *E. midlandensis*. The type mandible, however, has a striking resemblance to a mandible found in Tequixquiac—type locality of *E. (H.) mexicanus*. Is *E. midlandensis* a junior synonym of *E. (H.) mexicanus*? Or were they two large *Equus* species, one of them caballine (*E. midlandensis*), sympatric in Texas, New Mexico, and Mexico?

6. *Equus (Hesperohippus) Mexicanus*

As mentioned in Section 3, the cranial proportions of the holotype of *Equus mexicanus* are unique. This leads us to support that it belongs to the subgenus *Equus (Hesperohippus)* erected by [29].

6.1. *Equus (Hesperohippus) mexicanus* Holotype

Hibbard [29] described as *Equus (Hesperohippus) mexicanus* a cranium (Supplementary Table S5; Supplementary File S5) from Tajo de Tequixquiac, No. 48 (HV-3), now catalogued as IGM 4009 [74] (Figure 40). There are no associated fossils. Hibbard did not mention any lower incisors. No limb bones are known. Hibbard considered its age as Late Pleistocene.

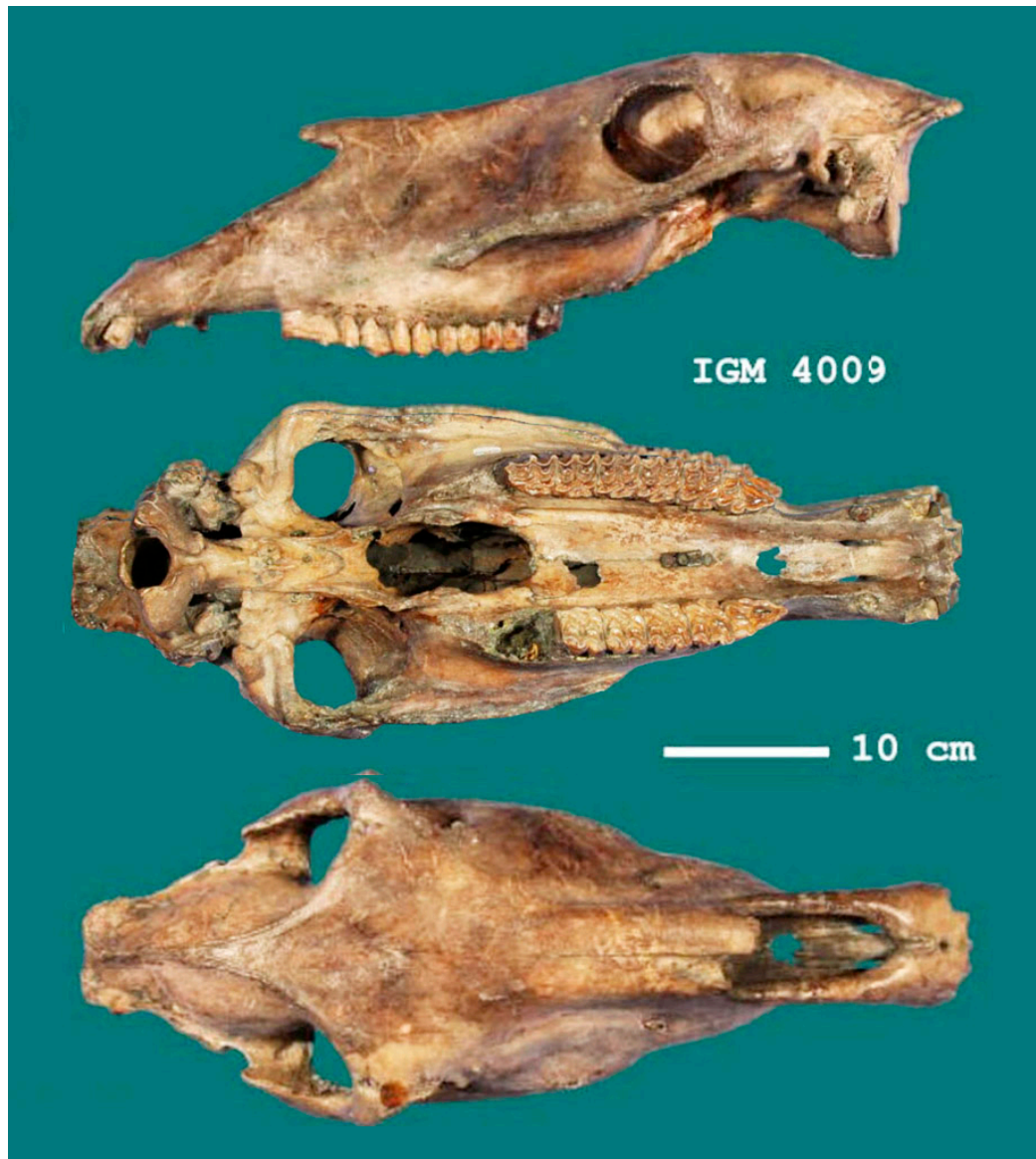


Figure 40. Holotype of *Equus (Hesperohippus) mexicanus* (IGM 4009) from Tequixquiac, Mexico. Lateral, ventral, and dorsal views. Image from UNIPALEO (www.unipaleo.unam.mx (accessed on 15 November 2024)).

This cranium was first referred to *E. excelsus* by [75] and to *E. occidentalis* by [76]. Because of its size, *E. (H.) mexicanus* has been considered a junior synonym of any of the large North American species, in particular *E. (E.) scotti* and *E. (A.) occidentalis* whose crania are well documented (see detailed discussion in [43,44]). Winans [6] included *E. mexicanus* in her *E. laurentius* group. *Equus laurentius* is a typical caballine and so is *E. (E.) scotti*, whereas *E. (H.) mexicanus* is not. Other authors (e.g., [43,53]) have considered *E. mexicanus* and *E. pacificus* as synonyms.

The cranial morphologies of *E. (E.) scotti*, *E. (A.) occidentalis*, and *E. (H.) mexicanus* are distinct from one another (Figure 41 and Supplementary File S34). A recent phylogenetic analysis of derived Equini also identified *E. mexicanus* as distinct from *E. occidentalis* and caballine equids [12]. Other recent studies also recognize *E. scotti*, *E. occidentalis*, and *E. mexicanus* as distinct taxa [8].

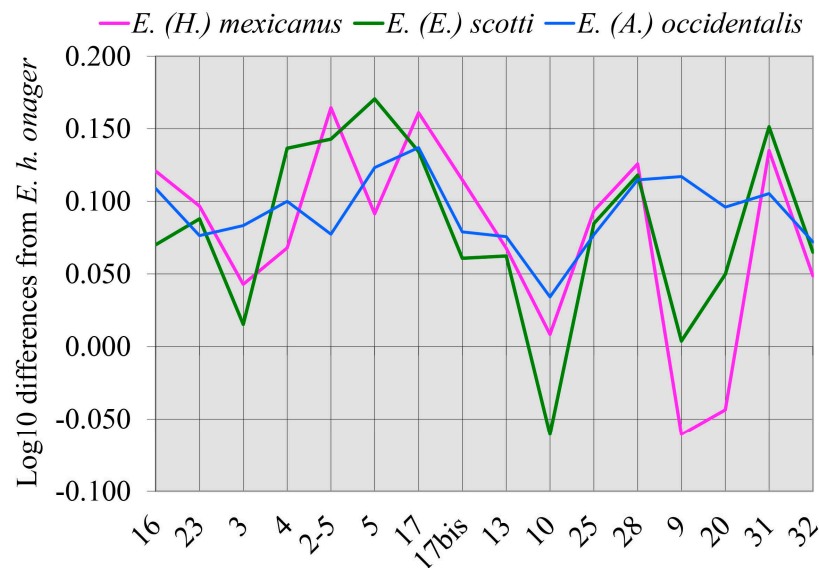


Figure 41. Simpson's ratio diagrams of *E. (H.) mexicanus* ($n = 1$), *E. (E.) scotti* ($n = 3-6$), and *E. (A.) occidentalis* ($n = 12-20$) cranial proportions. 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length.

Thorough observations and comparisons led Hibbard ([29], p. 73) to state that “the skull does not show any close relationship to the true horses or to zebrine forms, a fact noted by Cope”. Hibbard [29] rightly stressed this point, which seems to have escaped proper notice. *Equus (H.) mexicanus* plots with caballines according to the Palatal Index and Cheek Index (Supplementary Files S5 and S7) but not according to the Franck's Index, where it is rather aligned with *E. (A.) occidentalis* (Supplementary File S8). Hibbard ([29], p. 73) stated also that “the majority of the skull characters resemble those of the asses and are, in some respects, nearer to the Asiatic (*Hemionus*) than to the African (*Asinus*).” Indeed, the Franck's Index is close to that of hemiones (Supplementary File S35), and the Vertex Index (greatest length/basilar length proportions) is close to that of *E. (Amerhippus) occidentalis* (Supplementary File S10). There is another remarkable point: of all the monodactyl equid crania that we have ever seen, *E. (H.) mexicanus* is the only one where the palatine foramina are situated at the level of the posterior end of M3.

The upper cheek teeth are rather worn (Figure 42); the enamel is plicated, the protocones are long and pointed, and the styles are grooved, like in our Group A.

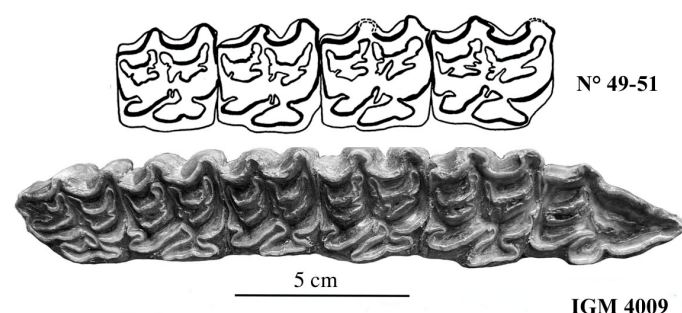


Figure 42. Upper P3-M2 (N° 49-51) questionably referred by [29] to *E. (H.) mexicanus* and upper P2-M3 of *E. (H.) mexicanus* (IGM 4009, holotype). Both specimens are from Tequiquiac, Mexico. Occlusal view. N° 49-51 modified from [29].

6.2. Referred Specimens

- Tequixquiac, Estado de México

We have already mentioned the right ramus, IGM 71-401, tentatively referred to *E. (H.) mexicanus* by [29]. The enamel pattern of the teeth is typically caballine, especially on the molars: angular lingual valley, rounded metaconid, pointed metastylid (Group 1). The isthmus of the double knot is very high, and the ectoflexid is shallow on all teeth (Figure 36).

Hibbard [29] also questionably referred to *E. (H.) mexicanus* four associated P3-M2, N° 49-51 (Figure 42), and one m1 (N° 49-57). The protocones of the specimen N° 49-51 are very different from the holotype, being shorter and not pointed ([29], Figure 4c), and the measurements given by Hibbard ([29], Table VIII) do not agree with the drawing.

- Barranca del Muerto, Estado de México

The mandible (Figure 43; Supplementary Table S5) LACM 308-123901 [7] fits well with the holotype cranium in size and proportions. The concavity between the ascending and horizontal ramus is less marked than in IGM 71-401 (Figure 36, black arrow). Infundibula are present on i1 and i2 and absent on i3.

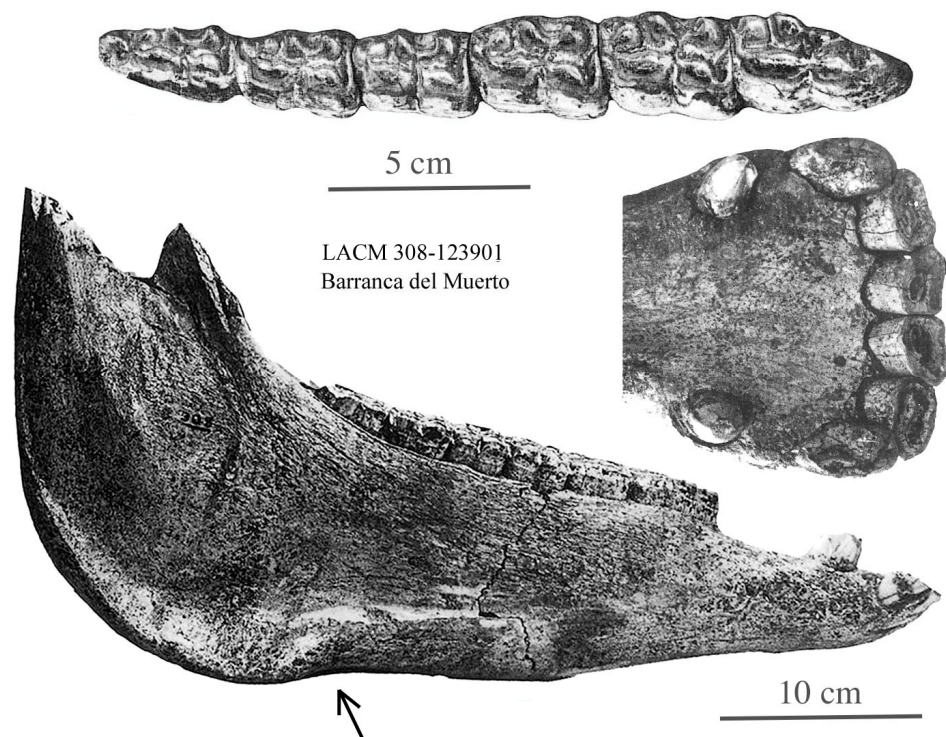


Figure 43. Mandible (LACM 308-123901) referred by [7] to *Equus mexicanus* collected from Barranca del Muerto, Municipio de Tequixquiac, Distrito Zumpango, Mexico. Mandible in lateral view; close up of incisors and cheek teeth in occlusal view. The black arrow points to the shallow concavity between ascending and horizontal ramus. Modified from [7].

- Cedazo, Aguascalientes

Cranial and mandibular fragments FC 678 and FC 679 (Supplementary Table S5) may also belong to *E. (H.) mexicanus* as suggested by [77].

- Cedral, San Luis Potosí

From the Late Pleistocene of Central Mexico, Alberdi et al. [43] described three species of equids. The largest, referred to as *E. mexicanus*, is represented by upper and lower

cheek teeth and limb bones. The enamel patterns of both uppers and lowers are extremely polymorphic. A few upper cheek teeth like DP 2576 and DP 2574 resemble the holotype of *E. (H.) mexicanus* from Tequixquiac, although the protocones are less pointed, but some others have very small protocones like DP 2595 (Figure 44) that do not seem compatible with the teeth of the holotype of *E. (H.) mexicanus*. Differences between the lower cheek teeth are even more marked (Figure 45). DP 2322, 4605, and 4610 resemble the *E. mexicanus* from Barranca del Muerto, the others less so, or not at all. A morphometric analysis of upper and lower cheek teeth of Cedral specimens referred to *E. mexicanus* indicated a caballine affinity for this morph [16]. Unfortunately, there is no cranial material from Cedral referred to *E. mexicanus* that can be compared to the holotype of *E. (H.) mexicanus*.

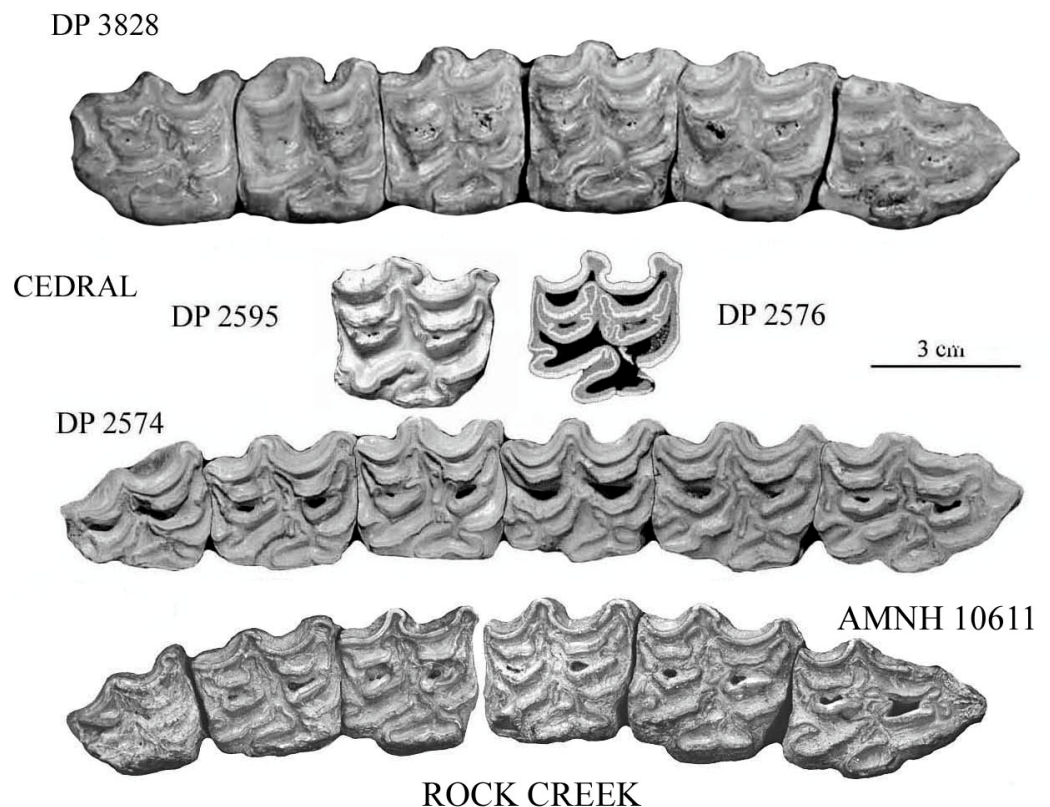


Figure 44. Upper cheek teeth referred by [43] to *Equus mexicanus* from Cedral (DP 3828, 2595, 2576, and 2574) and *Equus (E.) scotti* from Rock Creek (AMNH 10611). Occlusal view.

Comparisons of the large metapodials and first phalanges from Cedral (Supplementary File S36) with those of *E. (E.) scotti* from Rock Creek and *E. (A.) occidentalis* from Rancho La Brea show that the Cedral specimens are very similar to *E. (E.) scotti* in overall size and proportions, and less so to *E. (A.) occidentalis* (Supplementary Files S37–S40). *Equus (A.) occidentalis* stands completely apart by the proportions of its limb segments (Supplementary File S41).

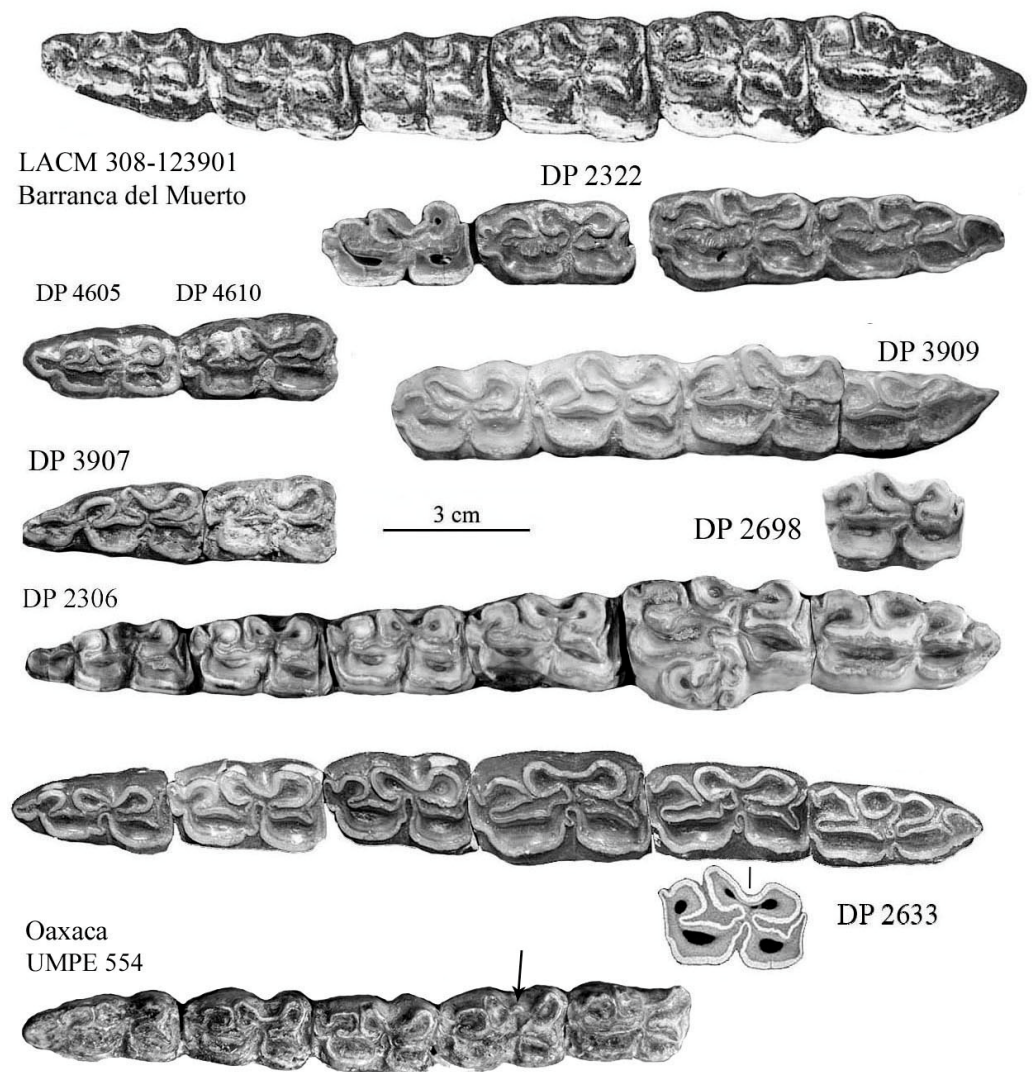


Figure 45. Lower cheek teeth referred by [23,43] to *Equus mexicanus* from Cedral and Oaxaca, and LACM 308-123901 from Barranca del Muerto. Occlusal view. Black arrow points to “bridge” between metaconid and metastylid in the p4 of UMPE 554. LACM 308-123901 modified from [7]. UMPE 554 modified from [23].

- Río Sabinal, Oaxaca

1. A partial cranium from Oaxaca State, Mexico, referred to *E. mexicanus* (UMPE 521) by ([23], Figure 4-A) has basicranial proportions that are different from the holotype of *E. (H.) mexicanus* (Supplementary Files S8 and S9). In fact, UMPE 521 (Figure 46) is similar to specimens of *E. (A.) occidentalis* (Supplementary File S42) and its cheek teeth also show the morphology observed in this species (Figure 46); UMPE 521 may be referred to *E. (A.) occidentalis*.
2. The enamel pattern of the partial mandible UMPE 554 from Oaxaca ([23], Figure 4-B and C) is very perplexing. In addition to caballine patterns on other teeth, a *non-caballine* bridge affects the p4 (Figure 45). We have already commented on this kind of “bridge” (Figure 3); let us just stress that we have never seen one so pronounced in association with caballine double knots.

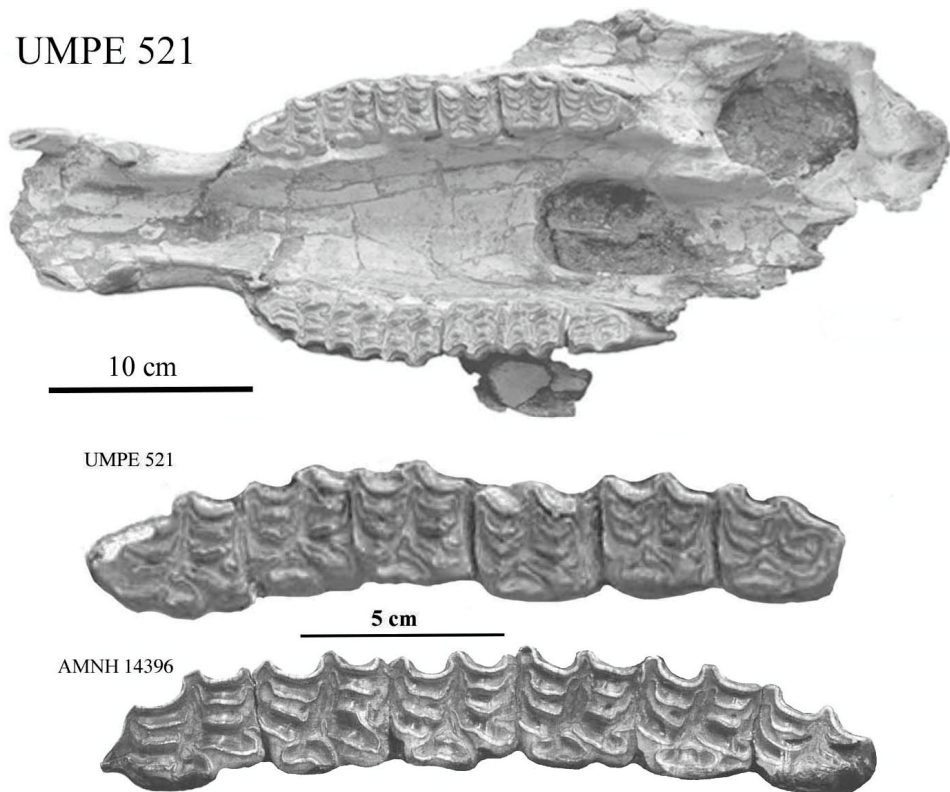


Figure 46. Partial cranium (UMPE 521) from Oax-17 Río Sabinal, Oaxaca state, Mexico; ventral view. Upper P2-M3 of specimen UMPE 521 and *E. (A.) occidentalis* (AMNH 14396) from Rancho La Brea; occlusal view. UMPE 521 modified from [23].

- Other referrals

Priego-Vargas [44] referred to *E. mexicanus* an upper cheek tooth series (LACM-9063 A 82797.64) from San Marcos, Jalisco, Mexico. Miller et al. [78] referred to *E. mexicanus* the juvenile P3-M3 USPLA 012 and the very worn p2-m3 USPLA 039 from Rancho Carabanchel, near Cedral, Mexico.

6.3. Taxonomic Remarks

We are certain that the holotype cranium of *E. (H.) mexicanus* shows a unique blend of amerhippine and caballine characters. The upper cheek teeth of the holotype are caballine in overall morphology.

Several mandibles and lower cheek teeth referred to *E. mexicanus* may, or may not, belong to this species. Molars of IGM 71-401 from Tequixquiac, LACM 308-123901 from Barranca del Muerto, and UMPE 554 from Oaxaca have caballine double knots; others from Cedral are variable. The overall polymorphism is astonishing (Figure 47).

Large metapodials and first phalanges from Cedral are caballine, but more robust than *E. (E.) scotti*, and so is the MT UMPE 489 from Oaxaca (Supplementary Files S36 and S38).

We are thus confronted with an entirely original, large cranium, with caballine teeth, not associated but found with more or less caballine lower teeth and limb bones. If not for the cranial proportions, most of these fossils could be considered caballine and indeed comparative studies of tooth morphology found them to be so. Cranial proportions, however, should not be ignored and we agree with [29] that the cranium IGM 4009 deserves the name of *E. (Hesperohippus) mexicanus*. Analysis of DNA of the holotype of *E. (H.) mexicanus* will be helpful to clarify its relationship to other North American equids.

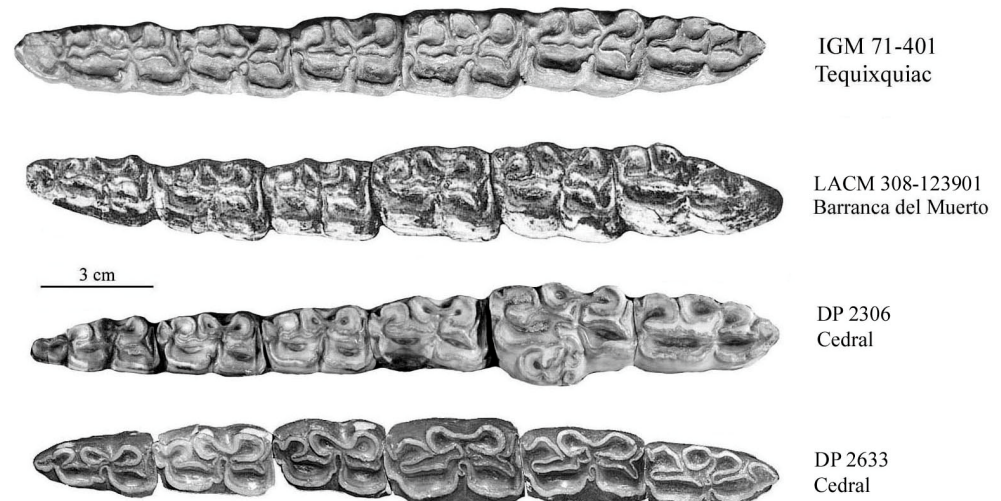


Figure 47. Lower p2-m3 from Tequixquiac (IGM 71-401), Barranca del Muerto (LACM 308-123901), and Cedral (DP 2306 and 2633; the p3 of DP 2306 shows malformation of the enamel on the buccal side of the tooth). LACM 308-123901 modified from [7].

In the meantime, we consider with caution all fossils lacking crania assigned to this taxon (e.g., some material from Tequixquiac, Cedral, Oaxaca), and suggest referring to them as *E. "mexicanus"*.

7. General Conclusions

We studied cranial, dental, and postcranial remains of North American fossil equids of Irvingtonian and Rancholabrean age to characterize caballine forms and *Equus (H.) mexicanus*.

Our analyses suggest that in the Old World, caballines, *Equus (Equus)*, can be discriminated from other equids using basicranial proportions, specifically the Palatal Index and Franck's Index. In the Americas, these two indices do not completely discriminate caballines from other equids as some amerhippines, *Equus (Amerhippus)*, overlap with caballines. However, other cranial proportions (i.e., Cheek Index and Vertex Index) allow better discrimination between caballines and amerhippines. We also documented some differences between these groups in metapodial dimensions and dental morphology.

We found morphological differences within North American caballines. These differences allow us to identify different forms. Though we use specific names when mentioning caballine forms, we do not imply that these forms were true species under a biological species concept. Our intent is to bring attention to the fact that there are morphological differences within North American caballines. Such differences may be described, and it is convenient to use well-known specific names in doing so. Nonetheless, other questions remain: Are these "species" ecomorphs? Chronomorphs? Are resemblances indication of parallel evolution? Or of close ancestral connections? In our study, we also remarked on problems associated with the use of the name *Equus (E.) ferus* for fossil caballine horses. Thus, we did not refer any North American caballine to *E. (E.) ferus* or to a subspecies of *E. (E.) ferus*.

The best represented caballines in North America are *E. (E.) scotti* of Irvingtonian age and *E. (E.) alaskae* and *E. (E.) lambei* of Rancholabrean age. These forms are represented by well-preserved cranial and postcranial remains. We hypothesize that *E. (E.) alaskae* and *E. (E.) lambei* are "ecological variants" of a single species. *Equus (E.) niobrarensis* cranium and upper cheek teeth are intermediate by size and morphology between the Irvingtonian *E. (E.) scotti* and the Rancholabrean *E. (E.) alaskae* and *E. (E.) lambei*; cranium proportions are similar to *E. (E.) scotti* and *E. (E.) alaskae*, while cheek teeth characters are similar to *E.*

(*E.*) *lambei* and *E.* (*E.*) *alaskae* (Supplementary File S43). Other North American caballine forms that we recognize are *E.* (*E.*) *pacificus* and *E.* (*E.*) *complicatus*. A caballine cranium from Fort Qu'Appelle (SMNH 1515-8306) may be referred to *E.* (*E.*) *niobrarensis*. Two large caballine crania from Hay Springs (UNSM 1346 and UNSM 5989) show unique features that prompted us to identify them as *Equus* (*E.*) sp. *Equus laurentius* is a junior synonym of *E.* (*E.*) *caballus*. *Equus holmesii* is considered a junior synonym of *E.* (*E.*) *scotti*, while *E. bautistensis* may be regarded as a junior synonym of *E.* (*E.*) *pacificus*. We are uncertain about the nature of *E. midlandensis*.

On the whole, although there are more localities in North America, the species are less documented than in the Old World. Another distinction is the apparent lack of difference in the limb bone length proportions between *E.* (*E.*) *scotti* and the only documented specimen of *E.* (*E.*) *alaskae*–*E.* (*E.*) *lambei* (FAM 71467) with associated limb bones (Supplementary File S41).

The cranial proportions of the holotype of *E.* (*H.*) *mexicanus* show a unique blend of amerhippine and caballine characters. This led us to support that it belongs not just to another lineage, but rather to the subgenus *Equus* (*Hesperohippus*) erected by [29]. Metapodials that can be confidently referred to *E.* (*H.*) *mexicanus* are not known. In the absence of cranial remains, we considered with caution fossils assigned to this taxon and suggest referring to them as *E.* “*mexicanus*”. The partial cranium UMPE 521 from Oaxaca, Mexico, described as *E. mexicanus* by [23] may be referred to *E.* (*A.*) *occidentalis*.

We hope that the data, analyses, and interpretations provided in this study will stimulate further research into the taxonomy and systematics of Pleistocene horses and will motivate DNA studies of the holotype of *E.* (*H.*) *mexicanus* and other North American fossil horses.

Supplementary Materials: The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/quat8040068/s1>, Document S1. Institutional acronyms; Document S2. North American chronostratigraphic chart of the last 1.5 million years; Supplementary Table S1. Measurements of *E. scotti* crania (NMC 2381, FM 12895, AMNH 10612, 10606, 10608, 10628) and crania referred to (or related to) *E. scotti* (UMMNH 46899, SI 160-455). Also shown are measurements of the cranium TMM 30967-401, identified as *E. complicatus* by Lundelius [53]. Refer to Supplementary File S1 for a diagram and description of the measurements; Supplementary Table S2. Measurements of the type specimen of *E. alaskae* (USNM 7700), crania referred to *E. alaskae* (FAM 60001, 60010, 60011, 60071; CMN 17905; IA 5059; PIN 301-5 and 301-533), type specimen of *E. lambei* (USNM 8426), and crania referred to *E. lambei* (L 1-1222; CMN 9924, 33992, 17262, 34803a; FAM 60012, 60013, 60019, 60020, 60023, 60038, 60045, 60048, 60066). Also shown are measurements of crania of *E. lenensis* (IA 33) and *E. gallicus* (302-486/7). Refer to Supplementary File S1 for a diagram and description of the measurements; Supplementary Table S3. Measurements of caballine crania from Hay Springs, Nebraska, including the type specimens of *E. niobrarensis* (USNM 4999) and *E. hatcheri* (USNM 7868). Refer to Supplementary File S1 for a diagram and description of the measurements; Supplementary Table S4. Measurements of caballine cranium (SMNH 1515-8306) from Fort Qu'Appelle, Saskatchewan, and the type specimen of *E. laurentius* (KU 347). Refer to Supplementary File S1 for a diagram and description of the measurements; Supplementary Table S5. Measurements of the type specimen of *E. mexicanus* (IGM 4009), and cranial and mandibular specimens referred to *E. mexicanus* (FC 678, 679; LACM 308-123901). Refer to Supplementary File S1 for a diagram and description of the cranial measurements. Description of the mandibular measurements is shown in the table; Supplementary File S1. Schematic of an *Equus* cranium showing the measurements that we used to study fossil and extant specimens; Supplementary File S2. Palatal Index (graph and data) in extant caballines, other extant *Equus*, and Alaska–Yukon caballines; Supplementary File S3. Palatal Index (graph and data) in extant caballines, other extant *Equus*, and caballines from Hay Springs, Nebraska (UNSM 5980, UNSM 5981, UNSM 1346) and Fort Qu'Appelle, Saskatchewan (SMNH 1515-8306); Supplementary File S4. Palatal Index (graph and data) in extant caballines, other extant *Equus*, and *E. scotti* from Rock Creek (AMNH 10606, 10612, no n°; CMN 2381) and the Seymour Formation (UMMNH 46899a and b); Supplementary File S5. Palatal Index (graph and data) in extant caballines, other

extant *Equus*, the type specimen of *E. mexicanus* (IGM 4009) from Tequiquiac, Mexico, and crania from Irvington, California (UCMP V-3605/32879), Pool Branch, Florida (AMNH 95588), and Oaxaca, Mexico (UMPE-521); Supplementary File S6. Franck's Index (graph and data) in extant caballines and other extant *Equus*; Supplementary File S7. Cheek Index (graph and data) in extant caballines, South American and North American amerhippines, and *E. (Hesperohippus) mexicanus*; Supplementary File S8. Franck's Index (graph and data) in extant caballines, South American and North American amerhippines, *E. (Hesperohippus) mexicanus*, and other North American equids; Supplementary File S9. Palatal Index (graph and data) in extant caballines, South American and North American amerhippines, *E. (Hesperohippus) mexicanus*, and other North American equids; Supplementary File S10. Vertex Index (graph and data) in extant caballines, South American and North American amerhippines, and *E. (Hesperohippus) mexicanus*; Supplementary File S11. Summary of Cheek, Franck's, Palatal, and Vertex indices in extant caballines, South American and North American amerhippines, *E. (Hesperohippus) mexicanus*, and other North American equids; Supplementary File S12. Cranium and mandible of type specimen (AMNH 10606) of *Equus scotti* in lateral view. Modified from Gidley ([1], Pl. XX); Supplementary File S13. Illustrations of palate and cheek teeth of specimen AMNH 10628 of *Equus scotti* in ventral/occlusal view. Modified from Gidley ([1], Plate XVIII A) and Hay ([39], Figure 69); Supplementary File S14. Simpson's ratio diagrams and data of *E. scotti* crania (NMC 2381, FM 12895, AMNH 10612, 10606, 10608, 10628) and crania referred to *E. scotti* (UMMNH 46899, SI 160-455). 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 8: Length of cheek teeth (P2-M3); Supplementary File S15. Ventral, dorsal, and lateral views of a cranium and mandible (in lateral view) of *Equus scotti* from the type locality, Rock Creek, Texas. Modified from Johnston [40]; Supplementary File S16. Simpson's ratio diagrams and data of *E. scotti* third metacarpals (MC) and third metatarsals (MT). 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT); Supplementary File S17. Simpson's ratio diagrams and data of *E. scotti* anterior and posterior first phalanges (Ph1). 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 7: Greatest length of *trigonum phalangis*. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth; Supplementary File S18. Simpson's ratio diagrams and data of the type specimen of *E. alaskae* (USNM 7700) and crania referred to *E. alaskae* (FAM 60001, 60010, 60011, and 60071; CMN 17905 and 17254; IA 5059; PIN 301-5 and 301-533). 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 2: Overall palatal length. 8: Length of cheek teeth (P2-M3); Supplementary File S19. Simpson's ratio diagrams and data of the type specimen of *E. lambei* (USNM 8426) and crania referred to *E. lambei* (L 1-1222, CMN 9924, 33992, 17262, 34803a, FAM 60012, 60013, 60019, 60020, 60023, 60038, 60045, 60048, 60066). Also shown are crania of *E. lenensis* (IA 33) and *E. gallicus* (302-486/7). 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 8: Length of cheek

teeth (P2-M3); Supplementary File S20. Simpson's ratio diagrams and data of third metacarpals (MC) and third metatarsals (MT) that are comparable in size to the type of *E. lambei*. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT); Supplementary File S21. Simpson's ratio diagrams and data of third metacarpals (MC) of *E. lambei-E. alaskae* from Alaska and Yukon, and equids from Dry Cave, Burnet Cave, and Carter's Cave. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum. 8: Diameter of the anterior facet for the unciform (MC); Supplementary File S22. Simpson's ratio diagrams and data of third metatarsals (MT) of *E. lambei-E. alaskae* from Alaska and Yukon, and equids from Dry Cave. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the big cuneiform. 8: Diameter of the anterior facet for the cuboid; Supplementary File S23. Simpson's ratio diagrams and data of *E. lambei* ($n = 5-16$), *E. alaskae* ($n = 5-15$), and *E. (E.) lambei* from Natural Trap (KUVF 51079) cranial, metapodial, and tooth measurements. 1: Basilar length. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 8: Length of upper P2-M3. MC 1: Maximal length of third metacarpal. MC 11: Distal articular breadth of third metacarpal. MT 1: Maximal length of third metatarsal. MT 11: Distal articular breadth of third metatarsal. P long.: Upper P3-P4 size calculated as $(Lo + lo)/2$ of P3-P4. M long.: Upper M1-M2 size calculated as $(Lo + lo)/2$ of M1-M2. P prot.: Upper P3-P4 protocone length. M prot.: Upper M1-M2 protocone length; Supplementary File S24. Simpson's ratio diagrams and data of limb bones from Natural Trap Cave identified as *Equus (E.) lambei*. Third metacarpals (MC) 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. Femora 1: Greatest length. 2: Medial length. 3: Minimum width. 5: Proximal maximum width. 8: Distal maximum width. 10: Distal maximum depth medial side. Tali 2: Proximal length. 5: Proximal depth. 6: Distal depth. Anterior and posterior first phalanges (Ph1) 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 7: Greatest length of *trigonum phalangeis*. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth. Anterior and posterior second phalanges (Ph2) 1: Maximal length. 3: Minimal breadth. 4: Maximal proximal breadth. 5: Proximal depth. 6: Maximal distal breadth. Anterior and posterior third phalanges (Ph3) 1: Anterior length. 3: Height. 4: Plantar breadth. 5: Articular breadth. 6: Articular depth; Supplementary File S25. Simpson's ratio diagrams and data of crania of *E. scotti*, *E. alaskae*, and *E. lambei*. 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditory meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 8: Length of cheek teeth (P2-M3); Supplementary File S26. Caballine crania from Hay Springs, Nebraska (photos), including the holotypes of *E. niobrarensis* (USNM 4999) and *E. hatcheri* (USNM 7868). Ventral, lateral, and dorsal views. Photos of UNSM 5980, 5982, 1346, and AMNH 2725 are modified from Azzaroli ([7], Plates 3, 4, 5, 6, and 18). Drawing of USNM 4999 from Hay [66]; Supplementary File S27. Simpson's ratio diagrams and data of caballine crania from Hay Springs, Nebraska, including the holotypes of *E. niobrarensis* (USNM 4999) and *E. hatcheri* (USNM 7868). 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length

sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 8: Length of cheek teeth (P2-M3); Supplementary File S28 Scatter plot and data of cranial basilar length and third metacarpals (MC) and third metatarsals (MT) distal articular breadths in extant species of *Equus*; Supplementary File S29. Simpson's ratio diagrams and data of caballine third metacarpals (MC) and third metatarsals (MT) from Hay Springs, Nebraska, and third metatarsal (TMM 5249) from Slaton, Texas. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT); Supplementary File S30. Simpson's ratio diagrams and data of crania of *E. scotti* ($n = 3-6$), *E. niobrarensis* ($n = 2-6$), and caballine cranium from Fort Qu'Appelle (SMNH 1515-8306), Saskatchewan. 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length; Supplementary File S31. Simpson's ratio diagrams and data of third metacarpals (MC) and third metatarsals (MT) from *E. scotti*, *E. alaskae-lambeii*, and Fort Qu'Appelle, Saskatchewan. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT); Supplementary File S32. Simpson's ratio diagrams and data of caballine limb bones from Fossil Lake, Oregon, and Ingleside, Texas. Third metacarpals (MC) and third metatarsals (MT) 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT). Anterior and posterior first phalanges (Ph1) 7: Greatest length of *trigonum phalangis*. 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth; Supplementary File S33. Simpson's ratio diagrams and data of limb bones of *E. midlandensis* (type), *E. scotti*, and other specimens from Texas and Mexico. Third metacarpals (MC) and third metatarsals (MT) 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT). Anterior and posterior first phalanges (Ph1) 7: Greatest length of *trigonum phalangis*. 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth. Radius (R) 1: Maximal length. 3: Minimal breadth of the diaphysis. 4': Minimal depth of the diaphysis. 4: Maximal proximal breadth. 5: Articular proximal breadth. 6: Articular proximal depth. 7: Maximal distal breadth. 8: Articular distal breadth. 9: Articular distal depth; Supplementary File S34. Simpson's ratio diagrams and data of crania of *E. mexicanus* (IGM 4009, type), *E. scotti* ($n = 3-6$), and *E. occidentalis* ($n = 14-21$). 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine

length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length; Supplementary File S35. Franck's Index (graph and data) in extant caballines, extant hemiones, and *E. mexicanus* (IGM 4009, type); Supplementary File S36. Simpson's ratio diagrams and data of limb bones from Cedral, Cedazo, and Oaxaca, Mexico, referred to *E. mexicanus* by Alberdi et al. [43], Mooser and Dalquest [77], and Jiménez-Hidalgo et al. [23]. Third metacarpals (MC) and third metatarsals (MT) 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 13bis: Least depth of the lateral condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum (MC) or for the big cuneiform (MT). 8: Diameter of the anterior facet for the unciform (MC) or for the cuboid (MT). Anterior and posterior first phalanges (Ph1) 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 14: Distal articular breadth. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 8: Minimal length of *trigonium phalangeis*; Supplementary File S37. Simpson's ratio diagrams and data of third metacarpals (MC) of specimens referred to *E. mexicanus* (Alberdi et al. [43]), *E. scotti*, and *E. occidentalis*. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the magnum. 8: Diameter of the anterior facet for the unciform; Supplementary File S38. Simpson's ratio diagrams and data of third metatarsals (MT) of specimens referred to *E. mexicanus* (Alberdi et al. [43]; Jiménez-Hidalgo et al. [23]), *E. scotti*, *E. occidentalis*, and Hay Springs caballines. 1: Maximal length. 3: Breadth at the middle of the diaphysis. 4: Depth of the diaphysis at the same level. 5: Proximal breadth. 6: Proximal depth. 10: Distal supra-articular breadth. 11: Distal articular breadth. 12: Depth of the sagittal crest. 13: Least depth of the medial condyle. 13bis: Least depth of the lateral condyle. 14: Greatest depth of the medial condyle. 7: Diameter of the facet for the big cuneiform. 8: Diameter of the anterior facet for the cuboid; Supplementary File S39. Simpson's ratio diagrams and data of anterior first phalanges (Ph1) of specimens referred to *E. mexicanus* (Alberdi et al. [43]), *E. scotti*, and *E. occidentalis*. 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 7: Maximal length of *trigonum phalangeis*. 8: Minimal length of *trigonum phalangeis*. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth; Supplementary File S40. Simpson's ratio diagrams and data of posterior first phalanges (Ph1) of specimens referred to *E. mexicanus* (Alberdi et al. [43]), *E. scotti*, and *E. occidentalis*. 1: Maximal length. 3: Minimal breadth. 4: Proximal breadth. 5: Proximal depth. 6: Distal supra-articular breadth. 7: Maximal length of *trigonum phalangeis*. 8: Minimal length of *trigonum phalangeis*. 10: Medial supra-tuberosital length. 12: Medial infra-tuberosital length. 14: Distal articular breadth; Supplementary File S41. Simpson's ratio diagram and data of maximal limb bone length (H: humerus. F: Femur. R: Radius. T: tibia. MC: third metacarpal. MT: third metatarsal. PhIA: anterior first phalanx. PhIP: posterior first phalanx) and plantar breadth of anterior third phalanx [PhIIIA (4)] in specimens referred to *E. mexicanus* from Cedral (Alberdi et al. [43]), *E. scotti*, *E. occidentalis*, *E. lambei*–*E. alaskae*, *E. cf. scotti*, *E. cf. midlandensis*, caballine from Slaton, extant *E. caballus* (Arabian horse), and extant *E. zebra*; Supplementary File S42. Simpson's ratio diagrams and data of the cranium of *E. mexicanus* (IGM 4009, type) from Tequixquiatic, cranium from Oaxaca (UMPE 521), and *E. occidentalis* ($n = 13$ – 21) from Rancho La Brea. 16: Breadth of the supra-occipital (lambdoidal) crest. 23: Anterior ocular line. 3: Vomerine length. 4: Post-vomerine length. 2-5: Palatal length sensu stricto. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 17bis: Least muzzle breadth (between the crests). 13: Frontal breadth. 10: Greatest choanal breadth. 25: Facial height in front of P2. 28: Cranial height. 9: Length of choanae. 20: Height of the external auditive meatus. 31: Length of the naso-incisival notch; 32: Cheek length. 1: Basilar length. 8: Length of cheek teeth (P2-M3); Supplementary File S43. Simpson's ratio diagrams and data of *E. scotti* ($n = 3$ – 14), *E.*

lambei ($n = 5\text{--}16$), *E. alaskae* ($n = 5\text{--}15$), and *E. niobrarensis* (holotype) cranial, metapodial, and tooth measurements. 1: Basilar length. 5: Muzzle length. 17: Muzzle breadth at the posterior borders of I3. 8: Length of upper P2-M3. MC 1: Maximal length of third metacarpal. MC 11: Distal articular breadth of third metacarpal. MT 1: Maximal length of third metatarsal. MT 11: Distal articular breadth of third metatarsal. P long.: Upper P3-P4 size calculated as $(Lo + lo)/2$ of P3-P4. M long.: Upper M1-M2 size calculated as $(Lo + lo)/2$ of M1-M2. P prot.: Upper P3-P4 protocone length. M prot.: Upper M1-M2 protocone length.

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