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A STUDY OF THE FOSSIL HORSE REMAINS FROM THE UPPER PLIOCENE OF IDAHO

By C. Lewis Gazin

Assistant Curator, Division of Vertebrate Paleontology, United States National Museum

INTRODUCTION

The record of fossil horses in North America is one of the most interesting and best known of the groups of mammals. The development of the horse through Tertiary time appears to have been most nearly continuous on this continent, stages of which are among the best represented of the mammals. Development of the horse has been relied on to a considerable extent as a guide to the various Cenozoic horizons in terrestrial deposits. In the study of this group much interest has been attached to the occasional discovery of intervening types bridging previous hiatuses in the sequence. *Plesippus* apparently bridges such a gap in the developmental sequence between earlier Pliocene horses and Quaternary *Equus*. *Plesippus shoshonensis*, the species encountered in the late Pliocene deposits near Hagerman, Idaho, appears to be an advanced stage in this genus, bordering on the equine types of recognized Pleistocene age.

Attention of the United States National Museum was first directed to the occurrence of fossil horse remains in the vicinity of Hagerman in 1928 by Dr. H. T. Stearns, of the United States Geological Survey, who was at the time engaged in a study of the geology and ground water of the region. To Elmer Cook, a resident of Hagerman and an amateur collector, belongs credit for discovering the fossils and bringing them to the attention of Dr. Stearns. A small but interesting collection of horse remains sent to the National Museum by Stearns resulted in the Smithsonian Institution sending the late Dr. J. W. Gidley to the locality in the following year and again in 1930. In 1931 the expedition was in charge of N. H. Boss, and the quarry opened by Gidley was further developed and additional material obtained. In 1934 I was permitted to continue the program in southern Idaho in order to obtain a better representation of the associated fauna from beds in the vicinity of the quarry and to make another collection of horses.

The principal quarry is located on the west slope of a hill or ridge projecting southward from the desert rim into a deeply dissected embayment (pl. 23, fig. 1). The hill is in T. 7 S., R. 13 E., Twin Falls County, on the west side of the Snake River, opposite the town of Hagerman. In addition to the main quarry several smaller quarries and prospect holes were opened on the south and southwest slopes of the hill and at about the same horizon, which is 55 to 60 feet or more below the desert surface and a few hundred feet above the river.

I am indebted to Dr. Alexander Wetmore and C. W. Gilmore, of the National Museum, for encouragement in making this investigation and to the staff of preparators in the division of vertebrate paleontology for the excellent preparation and handling of the material. Acknowledgment also is made of the courtesy extended by the staff of the division of mammals of the National Museum in permitting access to the collections of recent horses. Dr. Walter Granger, Dr. Barnum Brown, and Dr. E. H. Colbert, at the American Museum of Natural History, graciously aided in allowing me to examine and measure mounted skeletons of *Plesippus simplicidens* and *Equus scotti*, and Dr. C. L. Camp and R. A. Stirton, of the University of California, kindly loaned me type material from the Pacific coast region. The drawings were made by Sydney Prentice.

PREVIOUS STUDIES IN SOUTHERN IDAHO

Paleontological investigations of Neocene and Quaternary deposits in the Snake River Basin have resulted in recognition of several horizons of vertebrate life. The earliest of these terrestrial series is the Payette formation, which apparently includes at least two faunal horizons, the older being middle or upper Miocene[1] and the later lower Pliocene.[2] The Idaho formation, with which we are here more concerned, is widely distributed over the western portion of the Snake River Basin and is not easily separated from the underlying Payette in areas where the two are in contact. The Idaho beds were

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[1] Chaney, R. W., Amer. Journ. Sci., ser. 5, vol. 9, pp. 214–222, 1922; and Gazin, C. L., Carnegie Inst. Washington Publ. 418, pp. 37–86, 1932.

[2] Buwalda, J. P., Science, new ser., vol. 60, pp. 572–573, 1924.

named by Cope [3] on the basis of fish remains collected by Clarence King and others from exposures in the vicinity of Catherine and Castle Creeks and were believed to be Pliocene in age. The earliest reports on these fishes were made by Leidy [4] and Cope [5] in 1870. Deposits in the region generally referred to the Idaho formation probably comprise more than one horizon and apparently may be included within the limits of upper Pliocene and lower Pleistocene.

A collection of mammalian remains obtained by Clarence King from Idaho beds exposed along Sinker Creek, a short distance to the west of Castle Creek, included material identified by Leidy [6] as representing *Equus excelsus* and *Mastodon mirificus.* Collections made by N. F. Drake and others for Lindgren [7] were obtained at various localities, some of which may have come from deposits other than the Idaho formation. Among these materials F. A. Lucas identified *Mastodon, Castor, Equus, Rhinoceros, Procamelus, Cervus,* and an antelope. An equid type in the collection was believed by Marsh to represent *Protohippus.* A collection made by Russell [8] included a camel, an edentate, and fish remains, which Lucas considered to be of Pliocene age.

Later, in 1917, Merriam [9] discussed the relationship of the Idaho vertebrate fauna to other Pliocene assemblages, and in 1918 [10] he described three new species from these beds, *Ischyrosmilus idahoensis, Neotragoceras lindgreni,* and *Equus idahoensis.* In 1927, O. P. Hay [11] cited all the forms then known to occur in the Idaho formation and possibly older beds together with those that came from later river gravels, and the whole was considered of Pleistocene age, primarily on the basis of materials coming exclusively from the stream gravels of undoubted Quaternary age.

OCCURRENCE AND PRESERVATION OF MATERIAL

The great bulk of quarry material occurred in a lens of reddish, bog-iron stained sand. Isolated bones and articulated skeletal portions were found scattered through the lens but were most concentrated near the bottom, lying near or on a more indurated limy layer, which in places varies to a thin gravel zone. The lens is irregular in outline but decidedly concave upward in the north-south profile, resembling a channel fill. The bog-iron staining suggests boggy conditions during accumulation of the bones, but this may have been produced subsequently by migrating waters, as even at present this channel above

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[3] Cope, E. D., Proc. Acad. Nat. Sci. Philadelphia, vol. 35, pp. 134-166, 1883.

[4] Leidy, Joseph, Proc. Acad. Nat. Sci. Philadelphia, vol. 22, pp. 70-71, 1870.

[5] Cope, E. D., Proc. Amer. Philos. Soc., vol. 11, pp. 538-547, 1870.

[6] Leidy, Joseph, Proc. Acad. Nat. Sci. Philadelphia, vol. 22, p. 67, 1870.

[7] Lindgren, Waldemar, 20th Ann. Rept. U. S. Geol. Surv., pt. 3, p. 99, 1900.

[8] Russell, I. C., U. S. Geol. Surv. Bull. 199, p. 56, 1902.

[9] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 10, pp. 431-434, 1917.

[10] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 10, pp. 523-530, 1918.

[11] Hay, O. P., Carnegie Inst. Washington Publ. 322B, pp. 261-269, 1927.

the more impervious clays collects and yields water during the moist seasons. It appears unlikely that the animals were transported by water any distance after death but accumulated naturally around a water hole, aided possibly by bog trapping. There is no certain evidence of trapping, as in many places the depth of the fossiliferous lens between the underlying clay and the stratified, undisturbed overlying sand is hardly sufficient. Erosion, however, may have removed a portion of the zone, although this is not evident. At the periphery of the lens the bones extend into the unstained or less colored sand but in a more restricted zone, and in places on the south slope of the hill occur in a concretionary layer with a considerable portion of the material firmly cemented in large blocks of gray to white limy sand.

The bone material occurring in the more pervious red sand has to a large extent been affected by plastic distortion in which the bones, particularly in many of the skulls, have been warped and bent. Material, however, obtained in the hard concretionary patches is less distorted but prepared only with considerable time and labor.

The material collected in and about the principal quarry during the four seasons of work includes over 130 skulls and a large quantity of other skeletal material, some of which was discovered in a position of articulation. About a quarter to a third of the skulls include lower jaws, and 8 or 10 specimens are comprised of the greater part of the skeleton.

ASSOCIATED FAUNA AND ENVIRONMENT

Contemporary with *Plesippus shoshonensis* in the Hagerman lake beds was a large fauna including fishes, amphibians, reptiles, and a variety of birds and mammals. Remains of these animals were found at various localities within a distance of about 9 miles to the south of the quarry, a number being also represented in the quarry intermingled with the horse bones. The following is a list of the vertebrate forms known to occur in the Hagerman lake beds:

FOSSIL VERTEBRATES FOUND AT HAGERMAN, IDAHO

- Pisces:
  - Various forms, principally cyprinid.
- Amphibia:
  - Remains of frogs.
- Reptilia:
  - Testudinata:
    - *Pseudemys idahoensis* Gilmore.
  - Serpentes:
    - *Thamnophis* sp.
- Aves:
  - Colymbiformes:
    - *Colymbus* sp.
    - Colymbid sp.
  - Pelecaniformes:
    - *Pelecanus halieus* Wetmore.
    - *Phalacrocorax idahensis* (Marsh).
    - *Phalacrocorax auritus* (Lesson).
    - *Phalacrocorax* sp.
  - Anseriformes:
    - *Cygnus* sp. a.
    - *Cygnus* sp. b.
    - *Chen pressa* Wetmore.
    - *Querquedula* sp.
    - Anatid sp.
  - Gruiformes:
    - Gruid sp.
    - *Gallinula chloropus* (Linnaeus).
    - Rallid sp.
- Mammalia:
  - Edentata:
    - *Megalonyx leptonyx*? (Marsh).
  - Insectivora:
    - *Blarina gidleyi* Gazin.
  - Carnivora:
    - Canid sp.
    - *Hyaenognathus* or *Borophagus* sp.
    - *Lutravus*? *idahoensis* Gazin.
    - *Lutravus*? *cookii* Gazin.
    - *Lutra* (*Satherium*) *piscinaria* Leidy.
    - *Felis lacustris* Gazin.
    - *Machairodus*? *hesperus* Gazin.
  - Proboscidea:
    - Mastodont sp.
  - Perissodactyla:
    - *Plesippus shoshonensis* Gidley.
  - Artiodactyla:
    - *Platygonus*, n. sp.
    - Camelid, possibly *Camelops arenarum* Hay.
    - Camelid, possibly *Procamelus* or *Tanupolama*.
    - Cervid sp.
    - *Ceratomeryx prenticei* Gazin.
  - Lagomorpha:
    - *Hypolagus* near *vetus* (L. Kellogg).
    - *Hypolagus limnetus* Gazin.
    - *Alilepus*? *vagus* Gazin.
  - Rodentia:
    - Citellid sp.
    - Marmot sp.
    - *Thomomys gidleyi* Wilson.
    - *Castor accessor*? Hay.
    - *Ondatra idahoensis minor* Wilson.
    - *Mimomys primus* (Wilson).

Perhaps the most noticeable feature of the foregoing list is the number of aquatic types represented. This character of the fauna is even more evident in the frequency in which bones of these types are encountered compared to those representing forms having a less aquatic habit. The fish and frog remains are of common occurrence. The birds, though rare, are all of aquatic habit, according to Dr. Wetmore. Except horse, which is abundantly represented only at the quarry, and possibly peccary, by far the most numerous mammalian remains are of water-loving types, as beaver, muskrat, otter, and otter-like mustelids. Such an assemblage suggests a well-watered area with lakes or streams and possibly swampy sections. Carbonaceous zones are not uncommon in the sedimentary series as exposed, but considerable portions of the formation are noticeably gypsiferous, indicating periods of desiccation.

EVIDENCE AS TO AGE OF BEDS

The Idaho formation was early believed by Cope to be Pliocene on the basis of the fish remains that he described from these beds, and subsequent small collections of land vertebrates from various localities for the most part probably within the Idaho formation were considered as Pliocene by Leidy, Lucas, and Marsh. Merriam,[12] in 1917, reviewed the vertebrate evidence for the Pliocene age of various deposits in the Pacific coast and Great Basin regions and concluded for the Idaho beds that they were late Pliocene verging on Pleistocene. More recently Hay[13] expressed the opinion that the Idaho beds were Nebraskan in age. His reasons for considering them Pleistocene were unfortunately based primarily on materials coming from the river gravels in the eastern portion of the Snake River Basin, which are apparently no part of the Idaho formation.

The Hagerman lake beds, which may be considered a part of the Idaho formation, have produced a fauna that is probably an associated assemblage. Whether these forms were contemporaneous with those described from localities farther west believed to be within the Idaho formation there may be some doubt. It is my opinion that if these faunas are of different age the Hagerman assemblage may be slightly older than those at Bruneau River, Castle Butte near Grand View, Sinker Creek, and scattered occurrences in the Nampa-Caldwell region not coming from the Payette or Ironsides horizons. This opinion is based on the difference between certain of the Mammalia occurring at Hagerman and similar forms found elsewhere in the formation. Moreover, the fish assemblage seems not to include several of the large types abundantly represented in the more typical Idaho beds.

The Mammalia found at Hagerman appear to be in an advanced Pliocene stage both in development of several of the forms represented and in the composition of the fauna. Most noticeable is the absence of forms typically Pleistocene in age, as mylodont sloths, mammoths, *Mastodon americanus*, true *Equus*, bison, musk-ox, *Ursus*, *Castoroides*, and *Lepus*. Most of these are recognized in early or lower Pleistocene, possibly Aftonian, as indicated by Calvin's[14] work, or Yarmouth

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[12] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 10, no. 22, pp. 421–443, 1917.

[13] Hay, O. P., Carnegie Inst. Washington Publ. no. 322B, p. 269, 1927.

[14] Calvin, Samuel, Bull. Geol. Soc. Amer., vol. 20, pp. 341–356, pls. 16–27, 1909; vol. 22, pp. 207–216, pls. 18–24, 1911.

according to Lugn and Schultz.[15] Moreover, several of the forms present as *Hyaenognathus* or *Borophagus*, *Lutravus*?, *Plesippus*, mastodont, *Mimomys*, and the rabbits show Pliocene affinities, many of the remaining genera as recognized being less restricted in time. The presence of a true cervid is not necessarily indicative of Quaternary age, as fragmentary remains have also been reported from the upper Etchegoin and Eden beds in California. *Megalonyx*, though well known in the Pleistocene, has been found in several Pliocene deposits.

On the basis of the vertebrate remains the Hagerman horizon appears not far removed from the Blanco stage in Texas. The differences between the faunas from two localities may be only of geographic significance. The Blanco shows a greater wealth of Proboscidea but fewer members of the microfauna. A comparative list of the known Mammalia in the two faunas is given on the next page.

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[15] Lugn, A. L., and Schultz, C. B., Nebraska State Mus. Bull. 41, vol. 1, pp. 319–393, 1934.

Hagerman	*Blanco**
EDENTATA:	
Megalonyx leptonyx? (Marsh).	*Megalonyx leptostomus* Cope.
	Mylodon sp. (probably *Megalonyx*).
	Glyptotherium texanum Osborn.
CARNIVORA:	
Canid sp.	
Hyaenognathus or *Borophagus* sp.	*Borophagus diversidens* Cope.
	Amphicyon sp. (probably *Borophagus*).
Lutravus? *idahoensis* Gazin.	*Canimartes cumminsii* Cope.
Lutravus? *cookii* Gazin.	
Lutra (*Satherium*) *piscinaria* Leidy.	
Felis lacustris Gazin.	*Felis hillanus* Cope.
Machairodus? *hesperus* Gazin.	
PROBOSCIDEA:	
Mastodont.	*Serridentinus praecursor* (Cope).
	Rhynchotherium falconeri Osborn.
	Cordillerion tropicus (Cope).
	Stegomastodon successor (Cope).
PERISSODACTYLA.	
Plesippus shoshonensis Gidley.	*Plesippus simplicidens* (Cope).
	?*Plesippus cumminsii* (Cope).
	Nannippus phlegon (Hay).
	Neohipparion sp. (probably *Nannippus*).
ARTIODACTYLA:	
Platygonus, n. sp.	*Platygonus bicalcaratus* Cope.
	Platygonus texanus Gidley.
Camelid, possibly *Camelops arenarum* Hay.	*Pliauchenia spatula* Cope.
Camelid, possibly *Procamelus* or *Tanupolama*.	
Cervid sp.	
Ceratomeryx prenticei Gazin.	
LAGOMORPHA:	
Hypolagus near *vetus* (L. Kellogg).	
Hypolagus limnetus Gazin.	
Alilepus? *vagus* Gazin.	
RODENTIA:	
Citellid sp.	
Marmot sp.	
Thomomys gidleyi Wilson.	
Castor accessor? Hay.	
Ondatra idahoensis minor Wilson.	
Mimomys primus (Wilson).	

* The Blanco faunal list is essentially as given by Gidley in 1903, with the notations by me, and the mastodont assemblage is as listed in a page proof of Professor Osborn's forthcoming monograph on the Proboscidea.

REVIEW OF LITERATURE ON PLESIPPUS

The genus *Plesippus* was proposed by Matthew[16] to include the species *Pliohippus simplicidens* (Cope)[17] from the Blanco formation

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[16] Matthew, W. D., Amer. Mus. Nov., no. 131, pp. 1-2, 1924. See also Quart. Rev. Biol., vol. 1, no. 2, pp. 162-164, 1926.

[17] Cope, E. D., Proc. Amer. Philos. Soc., vol. 30, pp. 124-125, 1892.

of Texas and *Pliohippus proversus* Merriam [18] from the upper Etchegoin in the Coalinga region of California. *P. simplicidens* was originally described as a species of *Equus* but later referred by Gidley [19] to *Pliohippus.* The intermediate character of the teeth in these forms between *Pliohippus* and *Equus* as noted by Merriam and additional characters exhibited in the skeletons collected by Matthew and Simpson in the Blanco beds formed the basis for the genus *Plesippus.* A third species, *Equus cumminsii* Cope,[20] also from the Blanco, was later included by Matthew and Stirton [21] in *Plesippus.* This species was early referred to *Protohippus* by Gidley [22] and then to *Pliohippus* by Merriam [23] and by Osborn.[24] In 1930, Gidley [25] described the equid material from Hagerman to which he gave the name *Plesippus shoshonensis.* Subsequent finds of equid material that have been referred to *Plesippus* include teeth identified by Vander Hoof [26] as *Plesippus proversus* from the Tehama beds in California.

Mammalian material described by Frick [27] in 1921 from the San Timoteo Hills near the San Jacinto Mountains in southern California included equid specimens referred to *Pliohippus,* which may well represent *Plesippus.* Material designated as *Pliohippus francescana* and perhaps that named *Pliohippus osborni* appear from the illustrations to represent a stage of development comparable to that in material elsewhere referred to *Plesippus.*

CHARACTERS OF THE GENUS PLESIPPUS

The characters outlined by Matthew as defining the genus *Plesippus* are for the most part intermediate between those of *Pliohippus* and of *Equus.* With the accumulation of additional evidence showing the continuity from one genus to another, recognition of the limits of these genera necessarily becomes more arbitrary and perhaps questionable. The following diagnosis of *Plesippus* is taken from Matthew's [28] description of the Blanco material that he referred to *Plesippus simplicidens:*

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[18] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 9, no. 18, pp. 525–534, 1916.

[19] Gidley, J. W., Bull. Amer. Mus. Nat. Hist., vol. 14, art. 9, pp. 123–125, 1901.

[20] Cope, E. D., 4th Ann. Rept., Geol. Surv. Texas, 1892, p. 67, 1893.

[21] Matthew, W. D., and Stirton, R. A., Univ. California Publ. Bull. Dept. Geol. Sci., vol. 19, no. 17, pp. 359, 367 (tables), 1930.

[22] Gidley, J. W., Bull. Amer. Mus. Nat. Hist., vol. 14, art. 9, pp. 126–127, 1901.

[23] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 9, no. 18, pp. 526–527, 1916.

[24] Osborn, H. F., Mem. Amer. Mus. Nat. Hist., new ser., vol. 2, pt. 1, pp. 168–169, 1918.

[25] Gidley, J. W., Journ. Mamm., vol. 11, no. 3, pp. 300–303, 1930.

[26] Russell, R. D., and Vander Hoof, V. L., Univ. California Publ. Bull. Dept. Geol. Sci., vol. 20, no. 2, pp. 17–21, figs. 4–6, 1931.

[27] Frick, Childs, Univ. California Publ. Bull. Dept. Geol., vol. 12, no. 5, pp. 277–424, 1921.

[28] Matthew, W. D., Amer. Mus. Nov., no. 131, p. 2, 1924.

This form is of the size and limb-proportions of the average Pleistocene species of *Equus*, much larger and more robust than true *Pliohippus*. The teeth are most like *Pliohippus*, but longer crowned and less curved, with heavier mesostyle and larger more nearly isolated protocone. The cement lakes of the upper molars are narrower, and their enamel borders have a few simple inflections. The skull has the elongate proportions of *Equus*, in contrast to the shorter skull of typical *Pliohippus* and earlier equids. It retains in the forefoot tiny vestigial nodules representing the trapezium and fifth digit, progressively reduced in the earlier stages of Equidae, normally absent in modern *Equus*. The splints are from two-thirds to three-quarters of the length of the cannon bone, nearly or quite as much reduced as in *Equus*, while in true *Pliohippus* the splints are almost as long as the cannon bone, and it is not certain that the lateral phalanges had entirely disappeared.

After further study of the Blanco material Matthew[29] observed that "the animal compares in size and most proportions with the Arab horse, but the hoofs are much smaller, the back shorter, and the barrel less rounded and convex." He also noted that the lateral digits or splints end "in a thin flattened and expanded sliver instead of the little knob of *Equus*", and that "the fibula is reduced to a splint which in *Plesippus* is distinctly shorter than in any species of *Equus*." Moreover, the skull was observed to have shallow facial pockets or fossae, more reduced than in *Pliohippus*.

A number of outstanding characters are noted in the Hagerman material, many of which were observed by Gidley in the more limited collection he had at his disposal, and most of these are probably of generic significance. The cranium is short and markedly deflected from the distinctly elongate facial portion. The preorbital fossa anterior to the lachrymal bone is conspicuously developed along the line of the suture between the nasal and maxilla. The rostrum is deep anteriorly and narrow across the nasals. The first premolar above is well developed and almost always present. The first premolar below is simple and commonly present in young individuals. The cheek teeth approach in appearance those in *Equus*, somewhat more so in the earlier stages of wear. The feet are comparatively small, and the splint bones are reduced but with their average length relatively greater than in *Equus*. A few trapezia were found, but very nearly all the trapezoids show well-marked facets as evidence for articulation with a trapezium. A single fifth metacarpal was discovered. These apparently left little or no impression on the fourth metacarpal or outer splint as evidence of their possibly more general occurrence.

PLESIPPUS SHOSHONENSIS Gidley

Specific characters.—The characters of the species, though not clearly separated from those defining the genus, may be briefly outlined as follows: The skull is large and the relatively short cranium exhibits a narrow, sharply overhanging occipital crest. The teeth

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[29] Matthew, W. D., Quart. Rev. Biol., vol. 1, no. 2, pp. 162–164, 1926.

are large with a moderately simple pattern. The robust incisors are noticeably erect and P^1 is well developed. The dorsal and lumbar vertebrae are relatively elongate with narrow centra. The zygapophyses are comparatively close together, and the metapophyses usually project forward noticeably. The limb bones are moderately slender and the feet distinctly small and narrow. Greater detail will be found in the comparative study of the skeleton. Many of the characters there observed may be of specific importance, but comparisons were somewhat handicapped by the limited quantity of recent skeletal material available, other than skulls and jaws.

Comparisons with other species.—Of the comparisons which may be made with various species of fossil horses perhaps the most pertinent concerns *Equus idahoensis.* The species was described by Dr. J. C. Merriam[30] from a few teeth obtained by the University of California in beds believed to belong to the Idaho formation. The type, a much-worn isolated premolar, was found at a locality near Fromans Ferry, about 8 miles southwest of Caldwell, Idaho. Referred to this species were also an isolated lower premolar from Fromans Ferry and a little worn upper tooth, presumably M^1, from a locality about 4½ miles southeast of Payette, Idaho. Comparisons with this species were made by Dr. Gidley and accompanied his description of *P. shoshonensis,* but it seems desirable here to recapitulate and add further observations apparent upon examination of a large number of Hagerman dentitions.

The anteroposterior length of the type tooth of *Equus idahoensis* is equaled or exceeded in only two Hagerman specimens, and the area of the occlusal surface is greater than in any tooth, including those of the largest individuals in an early adult stage. When comparison is made with teeth in a comparable stage of wear the difference in size is more noticeable. The development of the protocone anterior to the isthmus is more progressive than in our form at this stage of wear, and the constriction of the isthmus as well as the transverse development of the protocone is noticeably greater. In the Hagerman specimens the reentrant forming the anterior wall of the protocone becomes much reduced in advanced wear, resulting in a broad union between protocone and protoconule.

The anteroposterior length of the lower premolar from Fromans Ferry is equaled or exceeded in three of our specimens, but the width and crown area are greater than in any of the Hagerman material. However, the enamel pattern of this tooth is not so *Equus*-like as in lower teeth of *Equus pacificus* from the Fossil Lake region of central Oregon.

The upper tooth from near Payette, referred to *E. idahoensis,* appears less curved and is more hypsodont than in our material where

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[30] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 10, pp. 527-530, 1918.

these characters can be observed. In Hagerman specimens of equal vertical length the pattern shows them to be less worn, as the enamel lakes are not then isolated as they are in the Payette tooth. Moreover, the lakes in the latter specimen are more constricted with the margins somewhat more elaborately crenulated than is usual in *P. shoshonensis.*

The foregoing observations would appear unimportant were it not for the large number of dentitions available for comparisons, which give reasonable definition to the variability of *P. shoshonensis.* The greater size of *Equus idahoensis* occurring at more western localities in the Idaho beds is further suggested by foot material obtained in 1934 from deposits exposed along Sinker Creek. However, a last upper molar (U.S.N.M. .no. 687), collected by Clarence King on Sinker Creek and considered by Leidy to represent *Equus excelsus,* can be closely matched in the Hagerman collection.

The genotype, *Plesippus simplicidens* (Cope), is based on a single upper cheek tooth and referred lower teeth from the Blanco beds of Texas but more adequately represented by skeletal material in the American Museum of Natural History collected by Matthew and Simpson. This material formed the basis of Matthew's [31] description of *Plesippus.*

The skull of *Plesippus simplicidens* (Amer. Mus. no. 20077) is within the size range exhibited by skulls of *P. shoshonensis.* The cranium is relatively a little longer and the facial length appears relatively less, even though the premaxillae are restored with a greater diastema between I^3 and P^2. The lachrymal fossa is noticeably developed, as in Idaho specimens where this character is not obscured by crushing; moreover, a very shallow malar fossa is present. The nasals are slightly concave longitudinally and narrow transversely over the lachrymal fossae and are also infolded along the median line. The supraoccipital is narrow and somewhat overhanging though not so conspicuously so as in the Idaho form. The basicranial line is deflected from the basifacial line to a marked degree as in *P. shoshonensis,* but the angulation is not so acute at the contact of the basisphenoid and vomer, the longitudinal profile of the ventral margin of the basioccipital and basisphenoid being more concave. The ventral surface of the basioccipital and basisphenoid is rounded transversely and is slightly rough but not keeled as observed in some *Equus caballus* skulls from individuals of equally advanced age. The external audital tube, as in *P. shoshonensis,* is directed upward and backward to a marked degree. Also, as in the Idaho skulls, the distance from the palate to the posterior margin of the vomer is distinctly greater than the distance from the vomer to the foramen magnum.

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[31] Matthew, W. D., Amer. Mus. Nov., no. 131, p. 2, 1924.

The cheek teeth in the skull of *Plesippus simplicidens* are badly checked and in an advanced stage of wear, with the fossettes in M^1 nearly obliterated. In all the cheek teeth the fossettes through wear are much constricted and the protocone broadly united with the protoconule. The occurrence of P^1 is indicated by a small alveolus.

The dorsal and lumbar vertebrae appear slightly shorter and perhaps less slender than in *P. shoshonensis.* Measurements given for the articulated series of vertebrae of *P. simplicidens* in table 3 are relatively great on account of spacing of the vertebrae in the mounted skeleton. The bones of the fore limb relative to those of the hind limb are larger than in articulated skeletons of *Plesippus shoshonensis.* The proportions of the hind limb of *P. simplicidens* compare favorably with those of the hind limb of an average-sized individual of *P. shoshonensis,* although the third metatarsal appears short and relatively less slender than in the Idaho material. The scapula of the Texas form shows a broad area with a double ridge between the glenoid surface and the tuber scapulae, as in the Idaho form, and a similarly proportioned glenoid surface. Also, as in *P. shoshonensis,* the ridge between the bicipital grooves on the proximal end of the humerus is less outstanding than the inner and outer ridges.

The essential differences between *Plesippus shoshonensis* and *P. simplicidens* lie in the somewhat longer facial and shorter cranial portions in the skull of *P. shoshonensis,* with a sharper angle between the vomer and basisphenoid, and in a more elongate back and smaller fore limbs. The two occur at localities widely separated geographically; however, there is little to suggest any significant interval of time between the two forms.

Plesippus proversus (Merriam) [32] from the upper Etchegoin in the Coalinga region of California was originally described as a species of *Pliohippus,* but recognized by Dr. Merriam as an intermediate stage between *Pliohippus* and *Equus.* The type (Univ. Calif. no. 21330) is an isolated upper cheek tooth, presumably M^2, and referred specimens from the same locality include portions of several upper and lower cheek teeth, and incomplete foot remains.

The material representing this species does not justify extensive comparisons, although a few characters appear significant in recognizing the position of this species and in distinguishing between it and *P. shoshonensis.* The teeth are of good size and show moderate curvature. The pattern is essentially simple, perhaps more so than is common in *P. shoshonensis.* The protocone is elongate in the type with very little of it projecting anterior to the isthmus leading to the protoconule. The outline of the protocone is more nearly a smooth oval than is common in the Idaho teeth. In the foot material the

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[32] Merriam, J. C., Univ. California Publ. Bull. Dept. Geol., vol. 9, no. 18, pp. 525–534, 1916.

distal end of a metapodial is relatively narrow and deep as compared with the Idaho material, and a first and second phalanx in the collection are distinctly small, even for a hind foot. The first phalanx is incomplete, but enough of it remains to show that it was much shorter than in *P. shoshonensis*.

P. proversus appears to be a somewhat earlier stage of *Plesippus* than found at Hagerman although this cannot be certainly demonstrated without far more adequate material from the upper Etchegoin. The material from the Tehama beds, referred by Vander Hoof[33] with proper conservatism to *P. proversus*, exhibits a slightly more complex pattern, but here again the Coalinga material does not justify detailed comparisons.

COMPARATIVE STUDY OF THE SKELETON OF PLESIPPUS SHOSHONENSIS

In the study and description of the skeletal structure of *Plesippus shoshonensis* comparison is made primarily with the large zebra *Equus* (*Dolichohippus*) *grevyi*. A large series of skulls of this species are available in the National Museum collections, and being of a wild species they do not show the effects of domestication and selective breeding so apparent in a series of *Equus caballus* skulls. Moreover, the fossil species compares favorably in size of skull and limb proportions with *E. grevyi*. The general skeletal material of *E. grevyi* in the collection is, however, much more limited, and for this reason detailed comparisons of vertebrae and limbs between fossil horse and the recent zebra are not entirely satisfactory. The *E. caballus* vertebrae and limb material are also scant.

Skull.—The skull of *Plesippus shoshonensis* is elongate, with the cranium relatively shorter than in *E. grevyi*. Perhaps the most distinctive character of the fossil skulls is the greater angle between the basicranial and basifacial axes than in modern species (pl. 24, fig. 2; pl. 25, fig. 1; pl. 26, fig. 2). The degree of cytocephaly or bending of the face on the cranium combined with the relative shortness of the latter has given the basicranial area a noticeably different appearance. The vomerine index is greater or the distance from the palate to the posterior notch in the vomer is relatively much greater with respect to the distance between the vomer and foramen magnum (pl. 25, figs. 2, 3) than in either *E. caballus* or *E. grevyi*.

The point of greatest deflection appears to be at the junction of the vomer and the fused basisphenoid and presphenoid bones, with the notch formed by the vomer and pterygoids more obtuse in the fossils. The basioccipital and basisphenoid are broad and generally rounded ventrally. In some old individuals of *E. caballus* the basioccipital is

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[33] Russell, R. D., and Vander Hoof, V. L., Univ. California Publ. Bull. Dept. Geol. Sci., vol. 20, no. 2, pp. 17–21, figs. 4–6, 1931.

noticeably narrow and sharply constricted along the median line. The distance between the postglenoid and paroccipital processes is shorter, accompanied by a more posterior and upward direction of the external auditory tube, which passes through a higher and more acute notch in the squamosal (see pl. 25, fig. 1). Moreover, the periotic appears more crowded between the squamosal and exoccipital, and the opening of the postglenoid or temporal canal is more obscured than in *E. grevyi.* The bending of the cranium has also given the line of the occiput a greater backward tilt, and the occipital crest is much narrower and more sharply overhanging.

In the facial region the skull is characterized by a prominent fossa along the line of the naso-maxillary suture just anterior to the lachrymal bone. In some specimens, as in the type, there is also indication of a slight fossa near the anterior margin of the jugal. In longitudinal profile the skulls show a distinct dorsal concavity as in *E. grevyi,* which in the fossils is immediately above the prominent facial fossae. The width across the nasals at this point is less, but the depth of the rostrum anterior to the dorsal concavity appears greater than in *E. grevyi* and the width between the orbits appears greater. The nasofrontal suture deviates considerably from a straight line, somewhat as in *E. caballus,* much more than in *E. grevyi,* which exhibits an only slightly inflected nasofrontal suture. The premaxillo-maxillary portion anterior to the cheek teeth is elongate and relatively heavy as in *E. grevyi,* and the anterior extremity is deep with the incisors recurved as in that species, less procumbent than in individuals of *E. caballus* of comparable age. The palate is noticeably broad in specimens where this portion is not distorted by crushing, and in many of the skulls the palatal surface of the rostrum appears more sharply constricted immediately anterior to the cheek teeth (pl. 25, figs. 2, 3), although the body portion of the premaxillae is as heavy and wide or perhaps slightly wider than in Grevy's zebra. The nasal process of the premaxilla is deep posteriorly, more so than is common in *E. caballus.* The cheek teeth occupy a longer portion of the maxilla than in *E. grevyi,* and the posterior extent of the cheek teeth in some of the specimens is somewhat greater with respect to the orbit and glenoid fossa than in *E. grevyi* skulls in comparable stages. The distance between the incisors and cheek teeth varies appreciably but averages somewhat less than in *E. grevyi.* Also the surface of occlusion on the incisors appears on the average to be more nearly in line with the occlusion of the cheek teeth. In *Equus* the position of the occlusion of the incisors is generally somewhat lower.

Indices or ratios of various measurements of the skulls, while apparently significant in a series of recent skulls where accurate measurements can be made, can not be determined satisfactorily or even approximately in the Hagerman collection where based on measurements taken in different directions. This is due to the warped condition of most specimens and to a certain degree of crushing in at least one direction. Simple measurements, while they may be satisfactory in one direction, are in most cases approximate or only estimated in a direction right angles to this.

Superior dentition.—The incisor teeth are large and broad with deep cups that persist with wear nearly as long as the enamel pattern on the cheek teeth. The enamel on labial surface of the incisors usually shows shallow grooves, and in the third incisor the enamel on the lingual surface is generally interrupted in unworn or slightly worn teeth in one or two places, about midsection and near the posterior margin of the cup. At the midpoint the enamel is sometimes infolded forming a ridge or spur extending down the inner wall of the cup. Occasionally this spur is seen in the second incisor, as in no. 12543. I^3 is further characterized by a prominent style along the posterior margin of the column.

The canine is present in nearly all adult individuals although much reduced in the females. In the males the tooth is large with the crown portion transversely compressed along the anterior and posterior margins. The compressed portions are curved inward so that the external surface of the tooth is evenly rounded and the lingual surface shows two marginal valleys.

The first premolar or "wolf tooth" is large and present in nearly every specimen, including some of the most aged individuals, as in no. 12530. This tooth perhaps should be considered as belonging to the deciduous series, as its eruption takes place with them although it is not replaced, and in the case of the fossil material persists along with the permanent teeth. In the unworn condition the tooth generally consists of a prominent central portion or cusp with a narrow ridge extending anteriorly toward a subdued cusp or style and posteriorly along the buccal side of the tooth to a conspicuous enlargement or cusp. In the larger of the teeth there is also generally a small cuspule postero-internal to the central cusp and antero-internal to the posterior cusp, and in wear apparently unites first with the posterior cusp forming a deep reentrant extending postero-externally from the lingual surface (fig. 21, no. 12543). The pattern in many cases is complicated by other small reentrants and grooves around the posterior cusp and lingually between the anterior style and central cusp.

The principal cheek teeth are well cemented and of large size with the greatest width generally through the third premolar, occasionally the fourth premolar is equally wide. The external styles are outstanding but simple and in general noticeably compressed anteroposteriorly, especially in the molar series. This is particularly true of the mesostyles in most dentitions, except in P^3 where this style may show one or two antero-external grooves (fig. 21, no. 12541). In specimens where the styles are somewhat constricted inwardly the flattened lateral surface of the style is faced sharply forward. The concavity between the styles in many specimens is more acute in the first two molars than in the premolars as in no. 12546 (fig. 21).

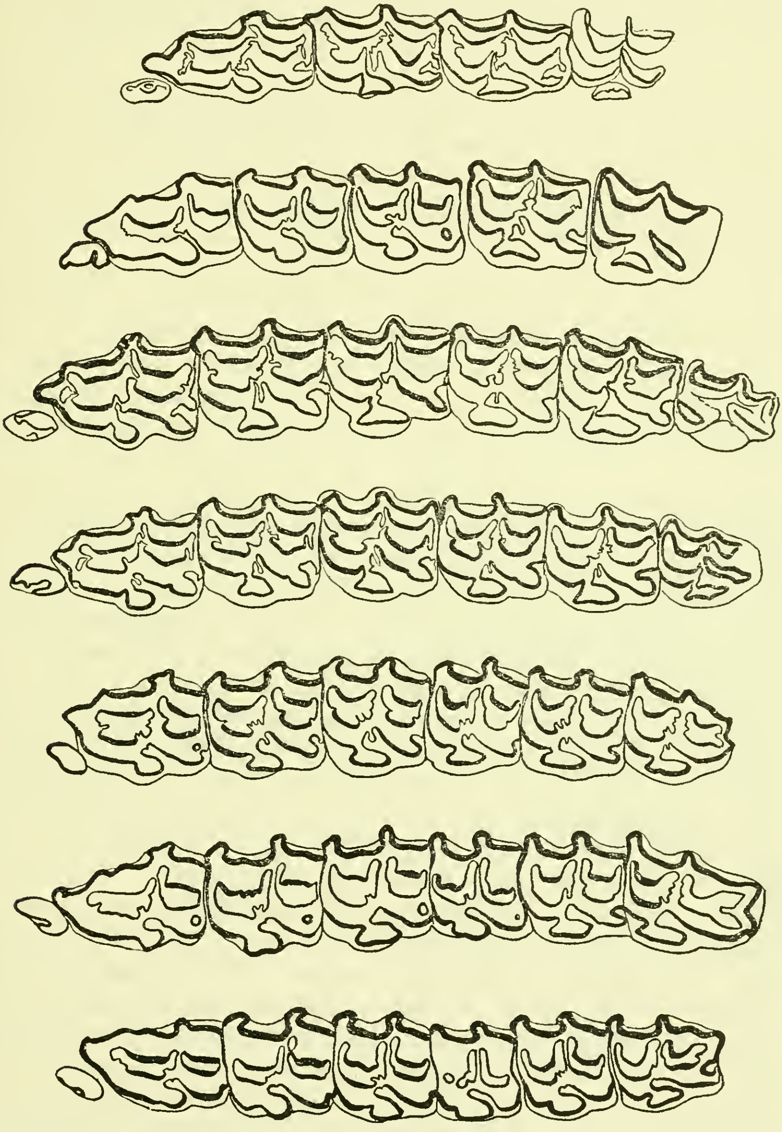

FIGURE 21.—*Plesippus shoshonensis* Gidley. Enamel patterns of left upper cheek teeth in seven selected individuals arranged according to age. In the first two dentitions the premolars belong to the deciduous set. U.S.N.M. nos. (from top to bottom) 12494, 12520, 12541, 12543, 12576, 12546, and 12548. One-half natural size. Hagerman lake beds, upper Pliocene, Idaho.

The fossettes are relatively large and usually simple. The plications on the metaloph between the fossettes are commonly small and numerous in very early stages of wear, but markedly reduced or obliterated in moderate wear. A slight pli prefossette may persist in some specimens in advanced wear. Moreover, a single or double pli prefossette may persist longer in P^3 than in other teeth. The posterior fossette plications on the metaloph in some instances are fewer and somewhat larger. A single or double pli postfossette may persist longer than the pli prefossette, though usually an early reduction takes place as on the anterior wall of the metaloph. The pli protoloph and pli protoconule in the anterior fossette are noticeably developed in early wear. The pli protoloph is early reduced in the molars but in the premolars is very persistent and may be double or triple as in no. 11989. In P^2 the protoloph unites with the anterior style of this tooth in two places isolating a small lake (fig. 21, no. 12543), which may persist until the tooth is moderately well worn. The pli protoconule though not heavy is apparently the most persistent plication in the anterior fossettes and can be seen in teeth of advanced wear. It is difficult to determine whether this plication arises from the crochet or protoconule, certainly very near the junction of the two. It may be single or double, and in a few teeth it is found to be triple (fig. 21, no. 12576). The pli hypostyle is not well developed in most of the specimens and like the pli protoloph is much reduced in the molars except in some specimens in early wear where the premolars are in the stage of eruption. In M^3 a prominent plication may arise from the posterior wall of the postfossette (fig. 21, no. 12576 and no. 12546), but this region of M^3 is very irregular and occasionally the posterior fossette is open in advanced stages. The pli caballin extending into the postprotoconal valley is best developed in P^3 and P^4 and may be long and slender in early stages of wear but reduced to a greater extent than the pli protoconule with moderate wear. In many dentitions the pli caballin is only feebly developed in the molars and perhaps early obliterated or reduced to a very slight plication, which may persist to advanced wear.

The appearance of the protocone varies considerably with wear and between teeth in the same dentition. In early wear the pattern is sharply triangular, uniting with the protoconule after the initial truncation of the column. The sides of the triangle are nearly straight at first, although in some teeth the lingual wall of the column shows a shallow groove nearly as in *Equus*, though generally more subdued. Unlike *Equus* this wall in many cases may be noticeably convex, as in specimen no. 12573. With moderate wear the postero-external wall exhibits a simple convexity. The antero-external wall in early stages of wear is generally straight and generally remains more nearly so in the premolars. In M^1 and M^2 the anterior extremity approaches in moderate wear the "heel" seen in *Equus*. With progressive wear the angles of the protocone in all teeth become more rounded, the sides more convex or sinuous, and the isthmus of attachment widens with the shortening of the antero-external wall. In advanced wear (fig. 21, no. 12548) the protocone column generally becomes smaller and more rounded, and the enamel reentrant defining the anterior portion of the column is much reduced. At this stage the fossettes are simple and U-shaped, and the teeth more strongly resemble those in *Pliohippus*.

The anteroposterior length and transverse width of the protocone vary considerably between the teeth in the same dentition. The width is noticeably greater in P^3 and P^4 than in the molars, usually being relatively narrow in M^3. The length is shortest in P^2 where the column is simple with little or no portion projecting anterior to the isthmus. The protocone increases in length posteriorly, although P^4 in many dentitions shows a larger and more angular column than in M^1, on account of the disparity in stage of wear between the two teeth. In M^3 the protocone reaches a length nearly half that of the occlusal surface of the crown, and the postero-external wall is usually more sinuous than in other teeth. The antero-external wall of this column in M^3 is commonly short and straight throughout wear and projecting but very little anterior to the isthmus.

The hypocone is simple and tapers to nearly a point postero-internally in early wear but becomes blunt with moderate attrition. It is separated from the metaconule by a slight constriction and does not project lingually so far as does the protocone. In the premolars there is generally a spur projecting inward from the hypostyle forming a section of the posterior wall of the tooth. In well-advanced wear this spur may unite with the distal portion of the hypocone, thereby isolating a small enamel lake (fig. 21, no. 12546). This spur from the hypostyle is absent in the first two molars of nearly every dentition, and only rarely in very advanced wear was the hypocone observed to unite distally with the hypostyle, except through obliteration of the enamel reentrant between them. In M^3, however, the hypostyle commonly unites with the distal end of the hypocone rather than with the metaconule, except where the postfossette remains open. Union is frequently made later, in more advanced wear, with the metaconule also, leaving a lake as in some of the premolars. Occasionally in M^3 the hypostyle unites first with the metaconule (fig. 21, no. 12548), in which case a closer resemblance is seen to other cheek teeth in the series.

Superior deciduous dentition.—The upper milk teeth are exhibited in 35 or more of the skulls in the collections. Stages are represented from that in which the teeth are erupting to the period where they are replaced by the permanent series. A large proportion of these skulls, however, are at a stage in which the first true molar is just erupting. In the course of replacement Dp^2 is lost at about the time M^2 is in early wear and M^3 is just erupting. The central incisors are replaced apparently a little earlier, at about the time M^2 is commencing to wear. Dp^3 and Dp^4 are replaced in order, with P^4 beginning to wear at about the same time or slightly ahead of M^3. The lateral milk incisors are somewhat slower to be replaced, with I^2 erupting at about the time P^4 and M^3 begin to wear, at an age probably between 4 and 5 years, and I^3 is the last to appear. The permanent canine comes in at about the time of I^2 or I^3 in the males, perhaps earlier in the females where this tooth is much smaller.

The deciduous incisors are a little larger than in *Equus grevyi*, particularly in their labio-lingual width. The crowns are brachydont, with shallow, occasionally cement-coated cups. The first incisors are generally the heaviest and the third the shortest crowned and weakest. The third incisor is also usually somewhat constricted transversely near the posterior end.

The milk canine was not observed in any of the specimens, although most of the immature skulls show either an alveolus or a roughened area at this point. In a few instances the size of the alveolus suggests a tooth larger than in the modern horses observed.

The three deciduous premolars (fig. 21, no. 12494 and no. 12520) are of comparatively large size and with the anteroposterior length relatively great. The teeth are moderately hypsodont but much less so than the permanent cheek teeth. Accompanying the greater relative length of the occlusal surface the fossettes are elongate and the protoloph is noticeably wide anterior to the prefossette. The teeth are generally well cemented except in the fossettes where cementation is usually not complete, and in one instance (no. 13842) the dentine was not completely developed in the cusp area. The mesostyles on the outer walls of Dp^3 and Dp^4 are compressed as in the permanent teeth, but the area between the styles is more flattened and the parastyles are relatively heavy though apparently not heavier than in *E. grevyi*. The fossettes are generally simple and show a plicate border highly variable as in the permanent teeth, with the pli protoconule usually the best developed. The fossettes also show a tendency to remain open. The anterior fossette in many dentitions remains open with appreciable wear through the postprotoconal valley, especially in Dp^2, with the pli protoconule projecting from the protoloph and a highly variable pli caballin extending into the postprotoconal valley from the crochet. The posterior fossette in Dp^4 is commonly open posteriorly external to the hypostyle (fig. 21, no. 12494), and in a few instances, as in no. 12484, the postfossette in Dp^2 is open through the posthypoconal valley.

The protocone on Dp^2 and Dp^3 though large is usually simple and rounded, resembling this cusp in P^2. In Dp^4 this cusp or column appears more advanced showing a more angular antero-internal extremity, a greater anteroposterior extent, and a flatter inner wall. With wear the protocone in each case becomes more nearly oval and broadly connected to the protoloph.

The hypocone is small in comparison with that in the permanent teeth, and the valley defining it posteriorly is somewhat irregular but reduced with wear much earlier than that posterior to the protocone. The hypostyle generally extends a strong plication lingually, and in one or two instances the valley or reentrant posterior to the hypocone is closed posteriorly, leaving, as in some of the permanent premolars, an isolated lake. More commonly such an isolated lake is formed in early wear near the anterior end of Dp^2 similar to that in P^2.

Mandible.—The mandibles (pls. 27, 28) vary appreciably in size and shape, although certain features are observed that are distinctive or that show an average difference from mandibles of modern types. The portion of the jaw below the dentition is relatively deep and heavy in young adults, and the line of the occlusal surface of the cheek teeth is more convergent anteriorly with the general direction of the inferior margin of the ramus. The ventral margin shows a pronounced vascular impression anterior to the angle, which is perhaps not so sharply deflected at this point as in *E. grevyi* but anterior to this point, and centered approximately below P_4 is a very marked ventral convexity, which in most cases is distinctly more prominent than in *E. grevyi* and much more so than in *E. caballus.* In young individuals the inferior margin of the ramus is more nearly straight (pl. 27, fig. 1, no. 12560). From the ventral convexity forward in adults the lower margin of the jaw rises more rapidly than in *E. grevyi* to the symphysial portion, which with the incisors is broader and generally higher with respect to the line of the cheek teeth. The distance between the incisors and the cheek teeth is great though averaging somewhat less than in *E. grevyi.* The portion of the fused mandibles between the incisors and premolars is constricted dorsally to about the extent in *E. grevyi,* but perhaps more abruptly so immediately behind the canines (pl. 28).

The ascending ramus is directed backward about as in *E. grevyi* with the posterior margin below the condyle nearly vertical (pl. 27, fig. 2, no. 12553) with respect to the ventral plane or table surface when resting normally. In *E. caballus* the anterior margin tends to be more nearly vertical, and the posterior margin rises upward and generally forward to the condyle. The anterior surface of the ascending ramus appears wider in the fossil jaws than in *E. grevyi* and the fossa on the upper portion of the outer surface of the ascending ramus appears better defined than in the recent zebra and horse.

Inferior dentition.—The lower incisors are large and broad, with the enamel on the labial surface thicker than that on the lingual surface and generally grooved or slightly irregular. The cup in the first two incisors is well toward the lingual surface and is less deeply impressed than in the upper incisors, as it is more rapidly reduced or obliterated, particularly in I_1. In unworn I_1 and I_2 the inner wall of the tooth is appreciably lower than the outer and generally uneven or cuspate. I_3 is broadly open on the lingual side and in most cases does not exhibit a lingual stylar cusp, nor does the enamel form a cup, although in a few instances a small cup is present.

The lower canine, lying a short distance posterior to the third incisor, is very similar in the males to that in the upper jaw, though perhaps a little smaller. In the females the tooth is small, occasionally absent, but generally more erect than in *E. grevyi.*

P_1 is usually present in young specimens; associated with the milk dentition, to which series it may well belong. It is a small simple conical cusp, not unlike that seen in young specimens of *E. grevyi.* Unlike P^1 this tooth is apparently lost with the eruption of the permanent premolars.

The lower cheek teeth (fig. 22) are large, robust, and heavily cemented, with little or no lateral curvature. The greatest width is generally across the third premolar or second tooth in the series. The pattern of the teeth though variable is rather simple and with few or no plications on the major reentrants on the lingual side of the teeth, except in early stages of wear. The two internal enamel reentrants of the premolars in early wear may show an irregular plicate condition, more noticeable in the posterior fold in which a slight plication opposite the ectostylid persists in some dentitions to advanced wear. These lingual loops are as extensive as in recent *Equus* dentitions but are generally less compressed transversely.

The parastylid is simple and of variable length and commonly shows a single flexure about midway along the posterior wall, except in P_2 where the development characteristic of this tooth is seen. In a few instances in P_3, in dentitions where the parastylid is shortest, a slight style is seen extending outward from the antero-external angle of the tooth. In one case, no. 12533, this portion of the tooth appears as if the parastylid were reversed and directed externally.

The metaconid-metastylid columns are usually simple and rounded, with the metastylid possibly somewhat less angular than is usual in the *Equus* material observed. The groove between the columns is generally acute but on the average much shallower or less deeply impressed than in *E. grevyi* or *E. caballus.* In *E. caballus* this groove is usually more widely open.

The entoconid and adjoining hypoconulid are simple and rounded in moderate wear, with no significant features to distinguish them in the fossil form.

On the outer surface the external walls of the protoconid and hypoconid appear more convex in many of the specimens than in *E. grevyi* or *E. caballus*, although in some dentitions flattening is noticeable. The reentrant between the columns is shallow and acute in the premolars though deeper and more open in the molars. The

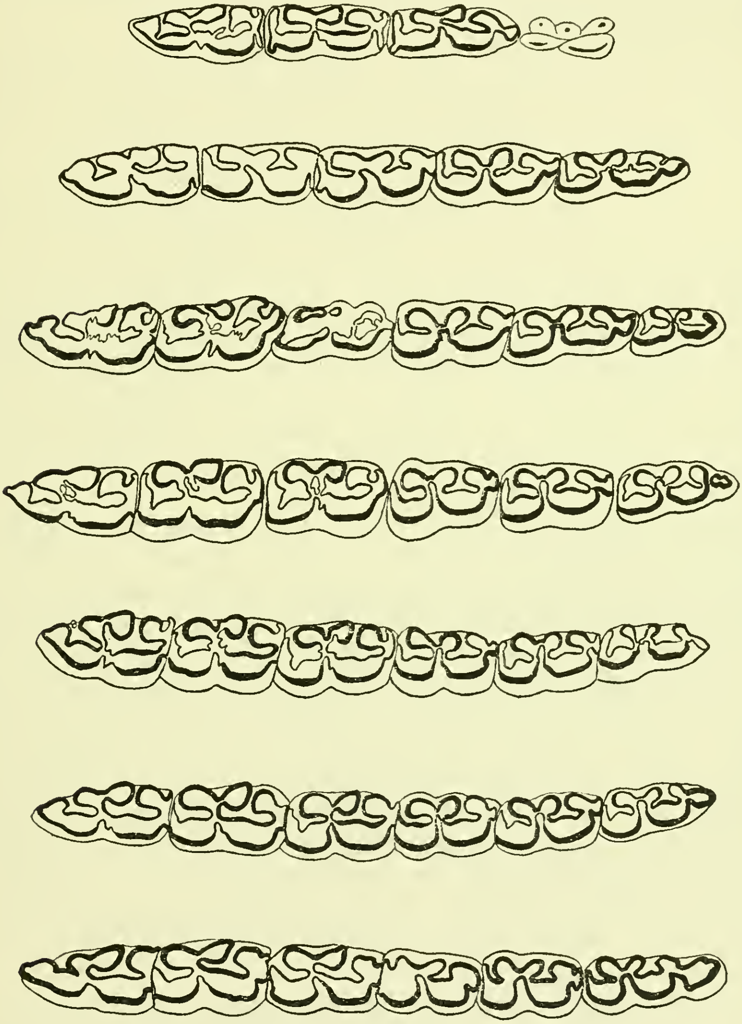

FIGURE 22.—*Plesippus shoshonensis* Gidley. Enamel patterns of left lower cheek teeth in seven selected individuals arranged according to age. In the first two dentitions the premolars are deciduous. U.S.N.M. nos. (from top to bottom) 12560, 12785, 12776, 12790, 12553, 12504, and 12546. One-half natural size. Hagerman lake beds, upper Pliocene, Idaho.

ectostylid is only slightly developed in the premolars except in early wear and in the molars is generally feeble or absent.

With advanced wear (fig. 22, no. 12504 and no. 12546) the walls of the outer columns become more convex, and the lingual reentrants are reduced in extent and are more compressed. The lingual walls of the inner columns are well rounded except for the metastylid, which may become more acute posteriorly. The anterior lingual fold shows the most marked reduction with the outer median fold most persistent. The anterior branch of the posterior lingual fold is also retained relatively late.

The differences between molars and premolars of the lower dentition are very noticeable, and in addition to the greater size of the premolars the two principal enamel loops from the inner wall are more deeply impressed and less transversely compressed than in the molars. In the posterior reentrant the anterior wing extends almost to the anterior loop and lingually nearly to the groove between the metaconid and metastylid, noticeably constricting the union between these columns. In the molars the reentrant from the outer surface between the protoconid and hypoconid extends nearly to the groove between the metaconid and metastylid, widely separating the contiguous portions of the anterior and posterior lingual folds. The hypoconulid is more shortened anteroposteriorly in the premolars. In the molars this cusp reaches its maximum development in M_3 and is moderately well developed in slightly worn M_1 and M_2.

Inferior deciduous dentition.—As is true of the young skulls, a relatively large number of the immature mandibles are in a stage of development in which the milk premolars are in moderately early wear with M_1 just erupting, probably a little less than a year old, meeting death perhaps early in spring. The replacement of the lower milk teeth is in the same order as in the upper jaw. Di_1 is first to go, followed by the milk premolars in order, and Di_2 as M_3 erupts. Di_3 is replaced about the time P_4 and M_3 commence wear.

The lower milk incisors are simple, low crowned, and shallow cupped. The cup in Di_3 is usually imperfectly formed or nearly absent, and in a few specimens there is a small cusp or a style in the middle or anterior portion of the embayment. In no specimen was a milk canine observed. A small opening at about the position of the canine might well be a foramen such as is seen in recent immature mandibles.

The well-cemented lower deciduous premolars (fig. 22, no. 12560 and no. 12785) though hypsodont are relatively short crowned compared to the permanent cheek teeth. The milk teeth are narrow and relatively elongate anteroposteriorly. The columns are transversely compressed and generally show simple or little-plicated enamel walls. The reentrant between the outer columns is shortest in Dp_2 and deepest in Dp_4, with an ectostylid usually best developed in Dp_2. In each dentition the metaconid increases in length anteroposteriorly in succeeding teeth and the metastylid decreases. The groove between these columns in most dentitions is shallow though somewhat acute. The two lingual reentrants are transversely compressed though of considerable anteroposterior extent. A marked feature of the milk premolars, more noticeable in the fossil material than in recent jaws, is the development of slender styles transversely along the anterior and posterior walls of the teeth (fig. 22, no. 12560), except in relatively little worn dentitions. The parastylid and an antero-external style usually extend the width of the tooth in the fossil Dp_3 and Dp_4, and the hypoconulid combined with a hypostylid extends an enamel surface across the posterior wall of Dp_2 and Dp_3. The parastylid of Dp_2 and the hypoconulid of Dp_4 are normally extended fore and aft.

Hyoid.—Parts of the hyoid have been found associated with the skull in several cases, and in a few the assembly is well preserved and nearly complete (pl. 29). The stylohyal is about the length of that in *E. grevyi*, as represented in two specimens, but is deeper and more robust, particularly through the middle section. This element is similar to that in *E. caballus* but less variable in size, and the muscular or posteroventral angle is well rounded though less attenuated than in the few recent specimens observed. Also the process that connects with the tympanohyal is less drawn out.

The epihyals were not found in any of the specimens, and the ceratohyals are not very well preserved, but these appear proportioned about as in the Arabian horse, not so heavy as in some of the larger domestic forms. The basihyal is moderately robust with a prominent lingual or glossohyal process which shows a more marked concavity or groove along each side than in any recent material examined. A single basihyal of *E. grevyi* shows a much shortened lingual process. The thyrohyal is variable in length and shows a prominent groove along the ventromedial surface extending from the basihyal well toward the posterior extremity. This portion of the thyrohyal examined in *Equus caballus* is conspicuously flattened ventrally.

Vertebrae.—The cervical series (pl. 31, fig. 1) is about as long as in the Arabian horse, but in most cases somewhat slenderer. Compared with the large zebra the neck is a little longer and relatively perhaps a little slenderer. Except for less width across the posterior articular surfaces, the atlas shows no significant characters distinguishing it from that of the recent horse. The neural spine of the axis is distinctly less outstanding and less convex in the fossil form than in either *E. caballus* or *E. grevyi*, and the width of the anterior articular surface for the atlas is less than in *E. caballus*. In the remaining portion of the series the centra are about the length of those in the Arabian horse; however, the length measured dorsally over the anterior and posterior zygapophyses is relatively less, particularly in the third, fourth, and fifth cervicals, on account of the smaller size of the articular facets and less overlap of the zygapophyses between these vertebrae than in either *E. caballus* or *E. grevyi.* The width across the transverse processes and across the prezygapophyses and postzygapophyses is variable but generally less than in the Arabian horse at hand.

The dorsal vertebrae (pl. 30) show marked variation in size, in length and robustness of the spines, and in the development of the processes but nevertheless exhibit in the articulated series a few characters that appear to be significant. The length of the dorsal series is distinctly longer in mature individuals than in either the Arabian horse or the zebra material used to compare with. The individual vertebrae appear to be about the size of those in the Arabian horse, but the centra are relatively longer, distinctly longer than in the *E. grevyi* column. The spines on the average are slightly shorter and in several instances appear more backward directed in the anterior portion of the series than in *E. caballus,* and after about the sixth or seventh vertebrae the vertebrarterial canal is usually closed posteriorly. After the first or second dorsal the width across the zygapophyses is noticeably less in the fossil material, in which respect the vertebrae are like those in *E. grevyi.* Also, the metapophyses though variable in size and shape project forward more noticeably than in the *E. caballus* material at hand, and in the posterior part of the series are slender and elongate as in *E. grevyi.* The posterior portion of the dorsal series though maintaining relatively long centra are generally not so enlarged as in the *E. caballus* column.

The relatively long centrum characterizing the dorsal vertebrae is carried back in the lumbars and in most cases is noticeably slenderer than in the *E. caballus* and *E. grevyi* material. The spines and transverse processes are highly variable in length and robustness, with the spines commonly elongate and moderately slender. The metapophyses though apparently more distinct from the prezygapophyses than in the *E. caballus* material are reduced posteriorly more noticeably than in *E. grevyi.* Although the individual vertebrae are normally separate in the posterior portion of the series the last two may be fused together (pl. 31, fig. 2), as in some recent individuals, and in a few cases fused to the sacrum.

As in the dorsal and lumbar vertebrae the segments of the sacrum appear relatively elongate anteroposteriorly. The width is variable but across the anterior portion is a little less than in the *E. caballus* material. The distance across the lateral surfaces for articulation with the transverse processes of the sixth lumbar is about equal to that in the *E. grevyi* skeleton, distinctly less than in the *E. caballus* material.

The caudals show little of interest; however, in comparison with recent material the neural arch is apparently completed in a greater number of the proximal elements. In several individuals the first one or two caudal vertebrae are fused with the sacrum (pl. 31, fig. 2).

Sternum and ribs.—The segments of the sternum are preserved in only a few individuals, and these are badly crushed and distorted but apparently are not otherwise distinguishable from modern material. A certain quantity of fragmentary material representing sternal ribs is included in the collection, but these elements, being essentially cartilaginous in the animal during life, are very spongy and without significant shape.

The size of the ribs in these animals appears to have varied considerably between individuals. Some correspond favorably in length and curvature with those in the *E. grevyi* skeleton; in other specimens the ribs are larger than in the Arabian horse. Generally, however, they appear relatively broader than in either form and perhaps more deeply grooved on the inner side and externally, although these cavities may have been emphasized largely by crushing. The first few ribs in most cases are shorter and heavier than in the Arabian skeleton.

Scapula.—The scapulae vary appreciably in size but perhaps average shorter than in *E. caballus*. Few differences were observed in the fossil material to distinguish it from modern forms. The glenoid surface for articulation with the humerus appears relatively long anteroposteriorly, in part because of the forward extension of the anteromedian portion of this surface. In *E. grevyi* and *E. caballus* the glenoid surface appears transversely wider, with the inner portion short anteroposteriorly and the portion external to the glenoid notch projecting more forward of that inward from the notch. Moreover, in the fossils a heavier ridge extends from the inner half of the glenoid surface to the coracoid process, approaching in strength the ridge between the outer portion of the glenoid surface and the large tuber scapulae, giving this region a wider anteroventral aspect. A depression of varying markedness extends from the glenoid notch to the coracoid dividing the tuberosity into two processes. An approach is seen in the development of the inner ridge between the glenoid surface and coracoid process in *E. grevyi*. It is least developed in the *E. caballus* scapulae observed.

Humerus.—The humerus (pl. 32, figs. 3, 4; pl. 33, figs. 3, 4) corresponds closely in size to that in *E. grevyi* and is more uniform than in *E. caballus*, which commonly possesses a much larger humerus.

The fossil humeri are distinctly *Equus*-like but show a few differences from the modern form. The ridge between the bicipital grooves on the anterior surface of the proximal end is distinctly less outstanding (pl. 33, figs. 3, 4) and somewhat shorter longitudinally than in *Equus*. The greater or lateral tuberosity projects anteriorly to a noticeable extent although relatively not so much as in earlier horses. The ridge external to the bicipital grooves continues distally a short distance on the anterior surface somewhat more prominent on the average than in *Equus grevyi*, and the anterior face of this portion of the humerus may be somewhat narrower. The deltoid tuberosity is prominent but generally not so rugged, and the rugose portion is not developed longitudinally to the extent seen in mature *E. grevyi* humeri. On the distal portion of the humerus the epicondyles appear in most specimens to close proximally over the olecranon or supratrochlear fossa somewhat more acutely than in the few humeri of *E. grevyi* observed.

Radius and ulna.—The fused radius and ulna (pl. 32, figs. 7, 8; pl. 33, figs. 7, 8) are about the size of those in *E. grevyi*, somewhat shorter than in most *E. caballus*, and show little to distinguish them from the corresponding parts of the modern forms. The olecranon is relatively deeper fore and aft and perhaps somewhat shorter in length on the average, and the inner surface shows a broad excavation, which is much more conspicuous than in modern ulnae observed. The shaft of the ulna is much reduced, the degree of reduction as in the living horses varying from a continuous sliver to complete absence from most of the distal half of the radius. The distal extremity of the ulna is fused with the radius and articulates with the cuneiform and pisiform. The width across the articulating surfaces on the distal end of the radius in most of the fossil specimens is less than in the few modern radii available.

Carpus.—The proximal or radial surface of the scaphoid is strongly flexed with the posterior portion wide and turned upward posteriorly. The notch on the lunar side of the radial surface of the scaphoid is deep and placed about as in specimens of *E. grevyi*. In *E. caballus* the notch appears shallow and nearer the posterior margin. On the external side the distal facet for the lunar appears larger in the fossil material than in *Equus*. On the distal surface the confluent facets for the trapezoid and magnum are generally somewhat constricted anteroposteriorly at the line of contact. The inner or medial surface usually shows a strong tubercle anteroproximally as in *E. grevyi* but more prominent than in the *E. caballus* scaphoids observed.

The posterior concavity on the proximal surface of the lunar is strong as in the scaphoid and shows less tendency to be convex transversely than in *E. caballus* and forms a sharper angle with the portion of the radial facet on the scaphoid side of the lunar. The posterior extremity of the radial facet projects upward sharply.

The cuneiform varies appreciably in proportions and in size and shape of the facets. As in other carpal elements there is very little to distinguish it from the cuneiform in *E. grevyi* and *E. caballus*. The facet for the pisiform in most specimens is not so elongate as in the few cuneiforms of *E. caballus* at hand.

The pisiform corresponds closely to that in *E. grevyi* and *E. caballus* and in the highly variable facets shows no differences from these forms. The posterior portion is relatively thick transversely and is generally less expanded dorsoventrally than in the recent material.

The trapezium, as indicated by the faceting on the trapezoid, was originally present in nearly every case. However, in the collections the trapezium is present only in the fore feet that were disarticulated in the laboratory. Their scarcity is due no doubt to their small size, hence being overlooked in the field. The bone is either nodular or flattened and from the trapezoid is directed backward and toward the outer side of the foot, presenting a convex posteromedian surface and a longitudinally concave surface facing outward and toward the body of the carpus. Matthew [34] has inadvertently shown the trapezium in articulation primarily with the scaphoid in the Blanco skeleton. The known Hagerman specimens vary from 11 to 18 mm in length, with articular facets 8 to 13 mm long. None of these show facets for articulation with the second metacarpal, although such articulation probably occurred in many individuals. In *E. caballus* the trapezium is considered to be present in about half the cases, and in most of these no articulation occurs with the trapezoid.

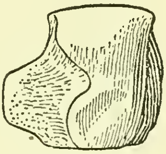

FIGURE 23.—*Plesippus shoshonensis* Gidley. Left trapezoid, U. S. N. M. no. 13827, posterior view showing facet for trapezium. Natural size. Hagerman lake beds, upper Pliocene, Idaho.

The trapezoids vary appreciably in size, particularly in the length of the projection carrying the posterior facet for the magnum. The facet for the trapezium is nearly always large and clearly indicated (fig. 23). It is continuous with the large facet for the cuneiform, although in many cases it is set off by a marked transverse constriction of the surface. In only 3 cases out of 72 is the facet for the trapezium absent. In these instances the smooth surface does not extend entirely or nearly to the distal facet for the inner splint bone; however, it is not unlikely that a trapezium existed but perhaps did not make contact with the trapezoid. In the limited *Equus* material at hand only one pair of *E. caballus* trapezoids showed distinct facets for trapezia, and two of the three pairs of *E. grevyi* trapezoids.

The magnum is close in size to that in the large zebra or in the Arabian horse. The surface for articulation with the lunar is more

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[34] Matthew, W. D., Quart. Rev. Biol., vol. 1, fig. 21, p. 163, 1926.

constricted between the anterior and posterior portions than in the modern material observed. On the distal surface the posterior portion of the facet for the third metacarpal averages distinctly narrower than in the *Equus* material.

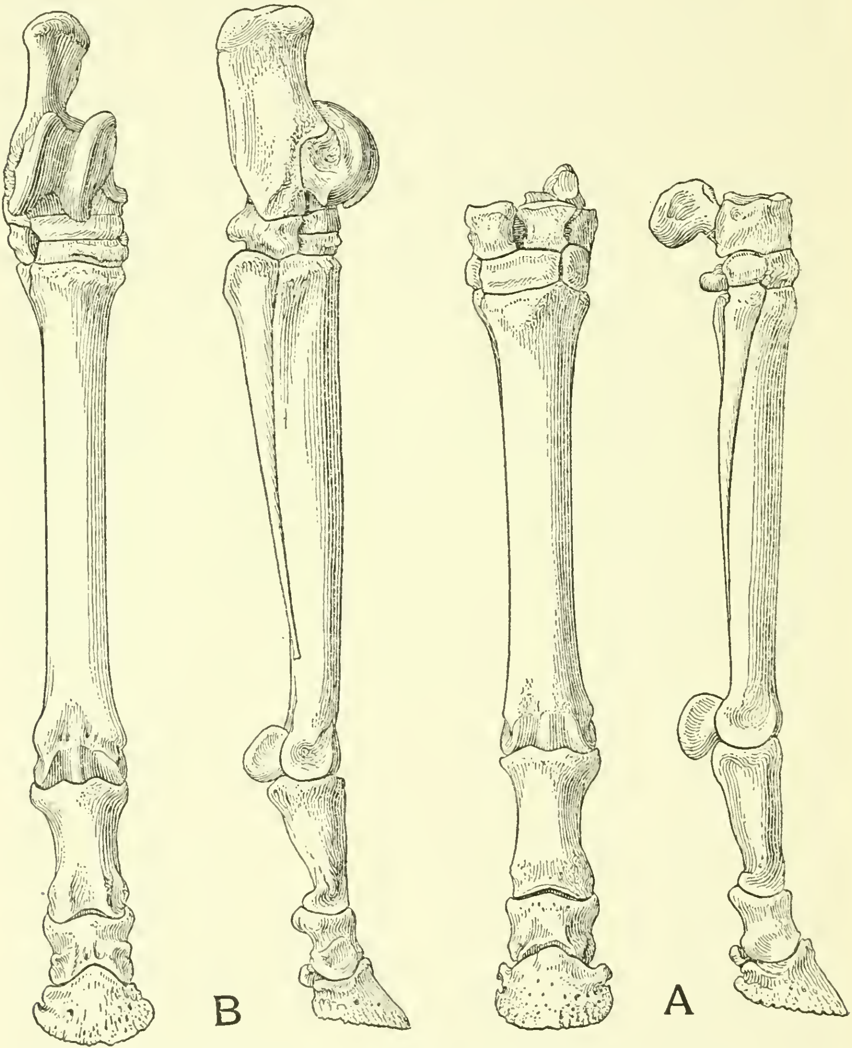

FIGURE 24.—*Plesippus shoshonensis* Gidley: A, Articulated left fore foot, U.S.N.M. no. 13794, anterior and medial views; B, articulated right hind foot, U.S.N.M. no. 13792, anterior and lateral views. One-fourth natural size. Hagerman lake beds, upper Pliocene, Idaho.

The unciform shows marked variation in the relative size and shape of the articular facets and in the length of the process projecting postero-internally. The facet for articulation with the cuneiform in many specimens is relatively narrow and slightly more concave transversely than in *E. caballus* or *E. grevyi*, although in other specimens the difference is not apparent. The proportion of the distal surface resting on the external splint varies appreciably but in a number of specimens appears somewhat smaller than in the few unciforms of *Equus* at hand.

Metacarpus.—The third metacarpals (fig. 24, A) are remarkably uniform in size over a large number of specimens, the extremes differing about 23 mm in length. The bone is near in size to that of *E. grevyi*, but with the extremities slightly narrower in most of the specimens. The third metacarpal in *E. caballus* shows a far greater range in size between individuals and the distal portion is relatively much wider and thicker than in the fossils. Also the distal articulating surface extends farther up the posterior surface than in the fossil.

The second and fourth metacarpals or splint bones appear relatively heavy and average somewhat greater in length than in *E. grevyi* and *E. caballus*. The distal extremity in many is flattened and expanded but perhaps not enlarged to the extent seen in some recent horses.

A fifth metacarpal has been observed in only one specimen, and in this case it was smaller than the trapezium that was also present. The bone is nodular in shape and about 11.5 mm long, with a small facet on one side. The proximal end of the fourth metacarpal in this individual is relatively short anteroposteriorly, with the faceted proximal surface carried a very short distance down the posterior surface, presumably for the fifth metacarpal. The vestigial fifth metacarpal if originally present in a larger number of individuals, left no certain indication on either the fourth metacarpal or unciform of its more general occurrence. It is rarely found in *Equus*.

The proximal sesamoids articulating with the posterior portion of the distal articulating surface are variable in size but relatively narrower than in *E. caballus* and possibly than in *E. grevyi*.

Anterior phalanges.—The first two phalanges (fig. 24, A) of the fore foot, though not so much shorter than in *E. caballus*, are very much narrower. The terminal phalanx or hoof is considerably smaller than in an average horse, and the anterior surface is more steeply inclined. The phalanges compare favorably with those in the zebra, although the proximal end of the first phalanx is somewhat deeper anteroposteriorly.

Innominate bone.—The pelvic girdle shows considerable variation in size and proportions between individuals due in part to age differences and in a large measure to sex dimorphism. Other than perhaps a smaller average size no significant differences were detected to distinguish the pelvis from that in modern horses.

Femur.—The length of the femur corresponds to that in *E. grevyi* or moderate-sized individuals of *E. caballus*, but the extremities appear somewhat slenderer on the average (pl. 32, figs. 1, 2; pl. 33, figs. 1, 2). The width of the proximal end across the head and anterior portion of the greater trochanter is generally less, and the neck below the head may be more constricted anteroposteriorly. Between the lesser trochanter and the third trochanter the anterior face of the shaft is commonly narrower or less flattened anteriorly, although not in every case. On the distal end of the femur the distance between the epicondyles averages less and the articular surfaces of the condyles are slightly narrower. The distance from the anterior surface of the trochlea to the posterior surfaces of the condyles is also somewhat less in most specimens than in *E. grevyi* or *E. caballus*. It is possible that most of these differences and many of those in other parts of the skeleton would disappear were a larger series of modern skeletons available; however, it is likely that in many cases an average difference would be maintained.

The patellae do not exhibit any characters of special interest and apparently do not differ in any important respect from those in *Equus*.

Tibia and fibula.—The tibia (pl. 32, figs. 5, 6; pl. 33, figs. 5, 6) is of moderate size, and, as observed in the femur, the proximal and distal portions are slightly less in diameter than in a large zebra or an Arabian horse. The articular facets average smaller than in the available modern tibiae of about the same length. The cnemial crest appears prominent and rugged as in modern forms.

In the few fibulae (see figs. 5 and 6 of pls. 32 and 33) preserved it appears, as observed by Matthew in the Blanco material, that reduction has progressed to a greater extent than in modern *Equus*. The fibula tapers abruptly and where complete is found to terminate at 7 or 8 cm, or a small fraction of the length of the tibia, whereas in the *Equus* skeletons observed the fibula extends about halfway down the tibia, or somewhat farther.

Tarsus.—The astragalus is surprisingly conservative in form although it shows a range in size variation. Astragali in *E. grevyi* and *E. caballus* correspond closely in detail to those in the fossil form and show no important differences other than perhaps a somewhat greater backward extent of the proximal portions of the trochlear ridges, and a greater size range in the *E. caballus* material.

The calcaneum is about as large as in *E. grevyi* or an Arabian horse and shows little to distinguish it from *Equus*. The sustentaculum is less prominent than in the Arabian horse, and the long axis of the sustentacular facet is more nearly parallel to the vertical axial plane. In the specimen of an Arabian horse the sustentacular facet in both the astragalus and calcaneum is directed downward and more inward than in the fossil material. In other *Equus* specimens the inward projection of this facet is not so pronounced.

The posterior margin of the navicular in many cases is more deeply notched than in the *E. grevyi* material, noticeably in the outline of the facet for the astragalus as this surface extends well out onto the postero-internal prominence. On the distal surface the smaller facets are irregular in size and shape and may or may not be confluent with the larger facet for the external cuneiform.

The fused internal and middle cuneiforms present an irregular shape and vary in size among individuals. The anterior and posterior portions of the proximal facet for the navicular may be broadly confluent or nearly separate. On the distal surface the facets for the second metatarsal may be distinct or meet at a sharp angle. The size of the facet for the third metatarsal is variable though generally small. No persistent differences were observed in comparison with modern material. In one of the fossil skeletons the internal and middle cuneiforms were found separated, as was also observed in one of the recent individuals of *E. caballus.*

On the external cuneiforms the proximal facets for the navicular are commonly separated but those on the distal surface for the third metatarsal are generally continuous between the anterior and posterior portions. In nearly every specimen the external cuneiform shows a facet postero-internally for articulation with the second metatarsal. In *Equus caballus* articulation between these bones is much less common, and none of the material at hand shows evidence of it, although two of the three observed pairs of ectocuneiform bones belonging to *E. grevyi* show facets for the inner splint.

On the proximal surface of the cuboid the width anteriorly across the facets for the astragalus and calcaneum appears narrower in much of the material, and the surface is perhaps more convex transversely than in the *E. caballus* material at hand. Also, the posterior portion of the facet for the calcaneum is not directed inward so noticeably in most of the fossils. On the distal surface the facet for the fourth metacarpal though varying appreciably in size is almost always undivided. The few *E. caballus* cuboids observed show the facet for fourth metacarpal divided and with the posterior segment distinctly small. The cuboids in the *E. grevyi* material more closely correspond to those in the fossil form.

Metatarsus.—The third metatarsals (fig. 24, B), as in the case of the third metacarpals, show a certain uniformity and correspond nearly in size to that in *E. grevyi.* The extremes of length differ by about 20 mm. The size range is far less than in *E. caballus,* and the distal articular surface is relatively much narrower transversely and does not extend so far up the posterior surface as in the specimens of that species examined. The distal portion, however, appears relatively deep anteroposteriorly as compared with *E. grevyi*. The distal portion is deep relative to its width in comparison with *E. caballus*, although the keel is less outstanding.

The splint bones are robust proximally, particularly the outer, and the length where complete is variable but apparently averaging somewhat longer than in recent material. They taper or flatten distally and may be slightly expanded at the end but the enlargement is not so pronounced as in some recent horses. The second metatarsal usually shows a facet of variable size for articulation with the external cuneiform.

The proximal sesamoids articulating with the distal surface of the third metatarsal are smaller than in the front foot, and as in the latter are relatively narrower than in *E. caballus*.

Posterior phalanges.—The phalanges of the hind foot (fig. 24, B), as in the fore foot, are much narrower than in *E. caballus* and more closely approach the proportions seen in *E. grevyi*. There is little difficulty in distinguishing between phalanges of the fore and hind foot of one individual but with isolated toe bones identification is often uncertain. The first phalanx of the hind foot is a little shorter, the proximal end a little heavier, and the distal end narrower. The second phalanx is narrower and perhaps a little longer. The hoof is somewhat narrower, and the anterior margin though not pointed is less rounded than in the fore foot. The right and left sides may be distinguished by the slight asymmetry of the elements, very readily in the first phalanx but not so easily in the distal element.

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TABLE 1.—*Measurements (in millimeters) of skull and superior dentition**

Measurement	*Plesippus shoshonensis*							*P. simplicidens*	*Equus scotti*
	U.S.N.M. no. 12494, immature	U.S.N.M. no. 12541, ♀	U.S.N.M. no. 12542, ♂	U.S.N.M. no. 12573, ♂	U.S.N.M. no. 12543, ♀	U.S.N.M. no. 11986 (type), ♂	U.S.N.M. no. 12535, ♀	Amer. Mus. no. 20077, ♀	Amer. Mus. no. 10606 (type), ♀?
Vertex length, from median incisive border to middle of occipital crest	521	593	612	[a] 612	620	637	[a] 588	[e] 596	[e] 600
Basilar length, from median incisive border to anterior edge of foramen magnum	493	529	527	535	542	561	[a] 509	[e] 530	[a] 535
Facial length, from median incisive border to line between posterior borders of orbits	[a] 327	421	432	430	[a] 434	456	[a] 416	[e] 411	[e] 419
Cranial length, from line between posterior borders of orbits to middle of occipital crest	[a] 160	179	[a] 187	[a] 191	[a] 187	184	[a] 183	[e] 188	[e] 185
Frontal width at posterior borders of orbits	[a] 200	[a] 210	228	[a] 228	[a] 240	[a] 225	[a] 230	[e] 190	[a] 220
Width across outer margins of glenoid fossae	193	[a] 211	218		[a] 224		[a] 212	[e] 203	[a] 198
Vertical diameter of orbital cavity	48.7	[a] 52				55		58.4	[e] 56
Horizontal diameter of orbital cavity	58	63.5	[a] 65			61.3	[a] 62	[e] 61	72.5
Convexity of nasofrontal suture, distance from anterior extent of suture to line between posterior extremities of suture	23	31	32.5						[e] 25
Distance from posterior border of palate to middle of posterior edge of vomer	131	133	140	154	149		140	137	[e] 138
Distance from middle of posterior edge of vomer to anterior edge of foramen magnum	94	108	109	98	[a] 110		[e] 95	104	[e] 118
Craniopalatal angle (between basifacial and basicranial lines)	22°	27°	20°	23°	25°		[a] 27°	[a] 22°	[a] 15°
Diastema between I^3 and P^2	94	109	90.2	103	115	125	[a] 105	[e] 125	95
Muzzle width at posterior alveolar borders of I^3	61.2	72.3	[a] 72	[a] 75	71.5	71.5	73.7	[e] 76	[a] 80
Width of palate between P^2	52.3	[a] 49.5	51.1	45.2	55.7		[a] 47		[a] 51
Length, P^2–M^3 at wearing surface		202	198	190	193	188	181	185	[a] 194
Length, P^2–P^4 at wearing surface	[d] 118	114	108	106	108	104	97	100	[a] 104
Length, M^1–M^3 at wearing surface		92	94	85.5	88	86.9	84.2	87.4	[a] 92
P^1, anteroposterior diameter	13.4	14	19.8	9.2	15.9	15	18.2		
P^3, anteroposterior diameter	[d] 35	36.5	34.5	32.9	33	31.2	30.9	32.2	[a] 33
P^3, greatest transverse diameter excluding cement	[d] 25	31.5	30.3	30.7	29	32.4	29.1	[e] 32.5	[a] 29
M^2, anteroposterior diameter		32.9	32.3	30	30.5	28.1	26.5	29.3	30.8
M^2, greatest transverse diameter excluding cement		27.5	26.4	29	27.7	29.7	28.4	[e] 30	26
Approximate age (in years)	1	4.5	4.5	5	5	15	25–30	25–30	3.5

* Craniometry in large part follows Osborn.

[a] Approximate.

[e] Estimated.

[d] Deciduous teeth.

TABLE 2.—*Measurements (in millimeters) of mandible and inferior dentition*

Measurement	*Plesippus shoshonensis*								*Equus scotti*
	U.S.N.M. no. 12560, immature	U.S.N.M. no. 12541, ♀	U.S.N.M. no. 12553, ♂	U.S.N.M. no. 12573, ♂	U.S.N.M. no. 12504, ♀	U.S.N.M. no. 11986 (type), ♂	U.S.N.M. no. 12522, ♂	U.S.N.M. no. 12538, ♂	Amer. Mus. no. 10606 (type), ♀?
Length of mandible from base of central incisor to posterior margin of condyle	400	482	471	493	470	507	472	[a] 471	467
Height of mandible from condyle to base	204	258	223	222	255	257	214	241	249
Width of symphysis	54	70	60	[a] 63	61.6	59.2	60.4	[a] 60	[a] 73
Depth of jaw at posterior border of M_3	----------	141	120	120	135	122	117	108	135
Depth of jaw between P_4 and M_1	80	100	90	88.8	92.4	[a] 92	90	80.8	97
Depth of jaw between P_2 and P_3	63.7	83.7	74.5	78	79.5	[a] 81	81.2	73.1	[a] 83
Diastema between I_3 and P_2	86.3	102	98.3	97	95.4	127	95.5	[a] 111	[a] 110
Length, P_2–M_3, along alveoli	----------	206	189	195	192	185	188	173	[•] 190
Length, P_2–M_3, along wearing surface	----------	200	184	190	187	185	181	168	[•] 180
Length, P_2–P_4, along wearing surface	[d] 107	107	98	105	100	93	91	89	93
Length, M_1–M_3, along wearing surface	----------	94.1	86	89	88.1	92	86.7	80.4	----------
P_3, anteroposterior diameter	[d] 33.5	35.2	31.2	33	32.4	[a] 29	30.2	28.5	[*] 29
P_3, transverse diameter excluding cement	[d] 12.7	18.5	17.1	17.8	17.2	----------	16.7	14.6	[*] 14
M_2, anteroposterior diameter	----------	33.5	29.1	30.7	29	[a] 28	27.5	25	[*] 34
M_2, transverse diameter excluding cement	----------	14.5	13.8	14.2	14.7	----------	14.2	13.5	[*] 14
Approximate age (in years)	1	4.5	5	5	5	15	15–20	25–30	3.5

[a] Approximate.

[d] Deciduous.

[*] Teeth only slightly worn.

[•] Estimated.

TABLE 3.—*Measurements (in millimeters) of vertebrae*

Measurement	*Plesippus shoshonensis*					*P. simplicidens*	*Equus scotti*
	U.S.N.M. no. 13792	U.S.N.M. no. 13794	U.S.N.M. no. 12155	U.S.N.M. no. 12573	U.S.N.M. no. 12578	Amer. Mus. no. 20076	Amer. Mus. no.10606-7-9
Length of articulated cervical series	----------	----------	592	[a] 558	----------	[b] 660	[b] 580
Length of articulated dorsal series	[a] 910	[a] 785	[a] 810	----------	----------	[b] 760	[a] 900
Width across anterior articular surface on centrum of fourth dorsal	32	35	----------	[a] 34	----------	[a] 37	[a] 38
Length of articulated lumbar series	[a] 305	[a] 290	----------	----------	[a] 310	[a] 305	[a] 330
Width across anterior articular surface on centrum of third lumbar	38. 3	36	39	----------	41	37	45
Length of sacrum measured along centra	[a] 207	[a] 206	[a] 207	----------	----------	----------	210

[a] Approximate.

[b] Estimated.

TABLE 4.—*Measurements (in millimeters) of fore limb*

Measurement	*Plesippus shoshonensis*						*P. simplicidens*	*Equus scotti*
	U.S.N.M. no. 13795	U.S.N.M. no. 13791	U.S.N.M. no. 13794	U.S.N.M. no. 12576	U.S.N.M. no. 12573	U.S.N.M. no. 12577	Amer. Mus. no. 20076	Amer. Mus. no. 10606–8
Greatest length of scapula	[a] 338	[a] 357	396	320	[a] 362	354	373	350
Greatest width of scapula		[a] 180		196	[a] 184	176	[a] 195	[a] 173
Length of humerus from head to inner condyle	281	[a] 272	[a] 280	267	[a] 278	[a] 280	287	295
Width of proximal end of humerus	105			99	[a] 92	[a] 88	107	101
Width of distal articular surface of humerus	81.5	78	76	78	[a] 84.5	76	[a] 80	89
Distance across inner surface of condyle and epicondyle of humerus	85.5	83	88.4	85.7	[a] 90	83	[a] 84	98.5
Greatest length of fused radius and ulna	436	402	[a] 426		424	415	429	428
Length of radius between articular surfaces measured along inner side	336	316	334		324	321	[a] 334	334
Length of olecranon from sigmoid notch	81.3	77		74	81.5	77	[a] 80	[a] 78
Width of proximal articular surface of radius	79.9	77.3	[a] 75	76	82	74.5	82	87.5
Width of distal articular surface of radius and ulna	63.8	62	62.8		66	60	[a] 64	72.7
Greatest length of third metacarpal	250	246	254	242	242	240	[a] 252	[a] 238
Width of proximal articular surface of third metacarpal	50.9	50	49	46.5	53	48.5	51.2	56
Depth of proximal articular surface of third metacarpal	33.5	31.7	32.5	30	33.3	31.5	[a] 34	37
Width across distal articular surface of third metacarpal	46.6	44.2	47.2	43.5	47.8	43.3	46	56.8
Depth of inner portion of distal articular surface of third metacarpal	33.1	30.8	32.7	30.9	32.7	30.3	33.2	36.5
Depth across keel of distal articular surface of third metacarpal	35.8	34.7	36.9	34.6	36.6	32.3	34	42.3
Length of inner splint bone		[a] 185	193	[a] 185	183	[a] 177		160
Length of outer splint bone			180		177	179	179	170
Greatest length of first phalanx	87.3	82.5	86.2	85	86.2	86	[a] 86	[a] 92
Width of proximal end of first phalanx	50.2	48.5	51	47.9	50.5	46	53.2	60.5
Depth of proximal portion of first phalanx	36.5	36	36	34.2	38.5	35	37	41
Width of distal articular surface of first phalanx	43	39.9	41.7	40	41.6	39.5	43.5	50
Greatest length of second phalanx	49.9	43.6	47.9	47	48	46.6	[a] 48	[a] 48
Width of proximal end of second phalanx	51	47.6	48	48.7	50.7	47	50.5	57.9
Depth of proximal portion of second phalanx	32.1	30	31	30.8	31.3	30.5	32.2	33
Width of distal articular surface of second phalanx	46.3	44.4	45.2	41.5	45	42	47.4	51
Distance from extensor process to anterior extremity of hoof		48.2	47.3	50	45.2		46	50.3
Distance from anterior extremity of hoof to line between posterior extremities	[a] 60	60	59.5	64.3	56.5		59.3	65
Greatest width of hoof	68.7	62.5	59.5	60	59.3		64.3	81.5

[a] Approximate.

TABLE 5.—*Measurements (in millimeters) of hind limb*

Measurement	*Plesippus shoshonensis*					*Plesippus simplicidens*		*Equus scotti*
	U.S.N.M. no. 13795	U.S.N.M. no. 13792	U.S.N.M. no. 12576	U.S.N.M. no. 12155	U.S.N.M. no. 13826	Amer. Mus. no. 20077	Amer. Mus. no. 20076	Amer. Mus. no. 10606–7–9
Length of femur from head to inner condyle	374	[a] 361	347		370	360	[a] 366	[a] 382
Width of femur across head and anterior portion of greater trochanter	126		106	[a] 120	[a] 110	119	125	140
Width of distal end of femur across condyles	96.6	94.7	86	[a] 99	94	[a] 99	99	108
Depth of distal extremity of femur across inner portion	124	121	124		121	[a] 127	[a] 119	134
Greatest length of tibia	385	370	361	[a] 370	370	362	360	358
Width of proximal end of tibia	105	98	97	97	98.5	98.9	101	107
Greatest width of distal extremity of tibia	78.2	78	73.5	[a] 75	72	75.5	73.7	82
Width across distal articular surface of tibia	54	54	51	[a] 55	54	55	[a] 55	[a] 61
Length of calcaneum	118	116	104	[a] 118	119	120	114	127
Length of astragalus on inner side	60.5	[a] 58	59	[a] 61	63	60.5	[a] 60	[a] 66
Width of astragalus across tuberosities	63	62.2	59.5		61.5	[a] 64	63.5	68.8
Length of third metatarsal	279	281	276	[a] 280	282	270	[a] 272	[a] 266
Width of proximal articular surface of third metatarsal	51	48	48.5	[a] 50	49	[a] 45	47	54
Depth of proximal articular surface of third metatarsal	39	35.5	35	[a] 38	[a] 38	[a] 42		47
Width of distal articular surface of third metatarsal	47.5	44.8	42.9	46	46.1	[a] 47	46	55.2
Depth of inner portion of distal articular surface of third metatarsal	33.1	30.5	30	31.3	31.1	[a] 34	33	33.8
Depth across keel of distal articular surface of third metatarsal	37	35.5	34.2	35.8	36.7	[a] 37	[a] 36	41
Length of inner splint bone	210	219			218	215	171	184
Length of outer splint bone	219	[a] 221			219	212	[a] 216	200
Length of first phalanx	83	80.2	78.3	79.7	79.6	78	[a] 78	[a] 87.7
Width of proximal end of first phalanx	51.6	49	47	50.2	49.5	52.8	52.4	61.6
Depth of proximal end of first phalanx	38.5	37.8	35.4	37.5	38.7	[a] 38	37.2	42
Width across distal articular surface of first phalanx	40.3	39	38	40.4	38	[a] 42	40.7	44.8
Length of second phalanx	49.5	47.5	47.2		47.8	50.2	[a] 49	[a] 49.5
Width of proximal end of second phalanx	49.5	47.7	46.7		45.8	[a] 48	48.7	54.2
Depth of proximal end of second phalanx	31.4	31	31		31	[a] 32	31.5	35.6
Width of distal articular surface of second phalanx	42.5	40.5	39.8		38.8	[a] 40	41	48.5
Distance from extensor process to anterior extremity of hoof	49	46.5	50.6		48.5	51	47	61
Distance from anterior extremity of hoof to line between posterior extremities	54.6	51.7	54.6		60	60.2	[a] 57	[a] 71
Greatest width of hoof	65	62	58.9		[a] 54	58.5	60.5	75.2

[a] Approximate.

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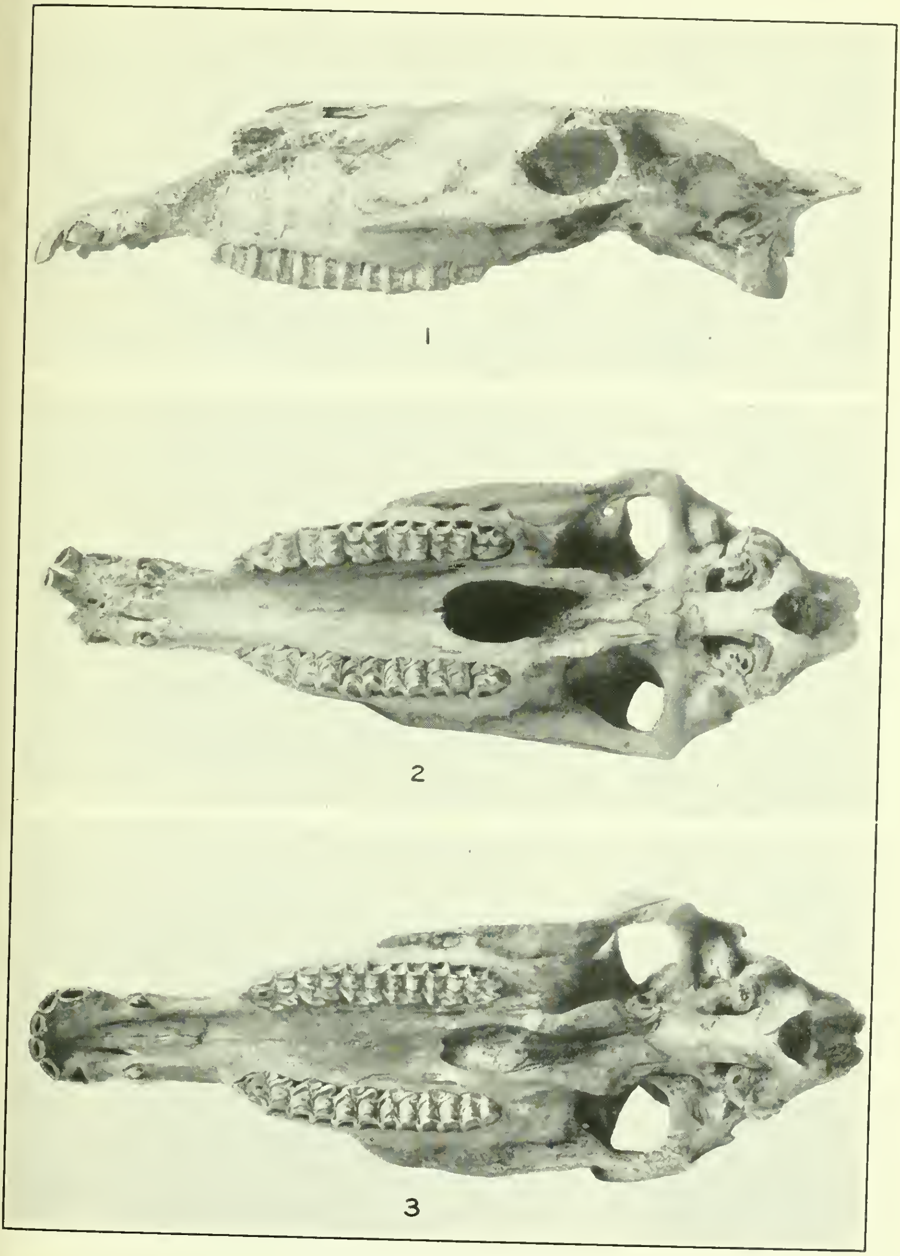
1. View of *Plesippus* quarry and fossil-bearing beds to the south as seen from the desert rim near Hagerman, Idaho.

2. View of the quarry during removal of plaster-encased blocks of *Plesippus* bones. Material can be seen in place in right foreground.

PLESIPPUS SHOSHONENSIS.

Skull and mandible, type specimen, U.S.N.M. no. 11986: 1, Dorsal view; 2, lateral view. About two-elevenths natural size. Hagerman lake beds, upper Pliocene, Idaho.



PLESIPPUS SHOSHONENSIS.

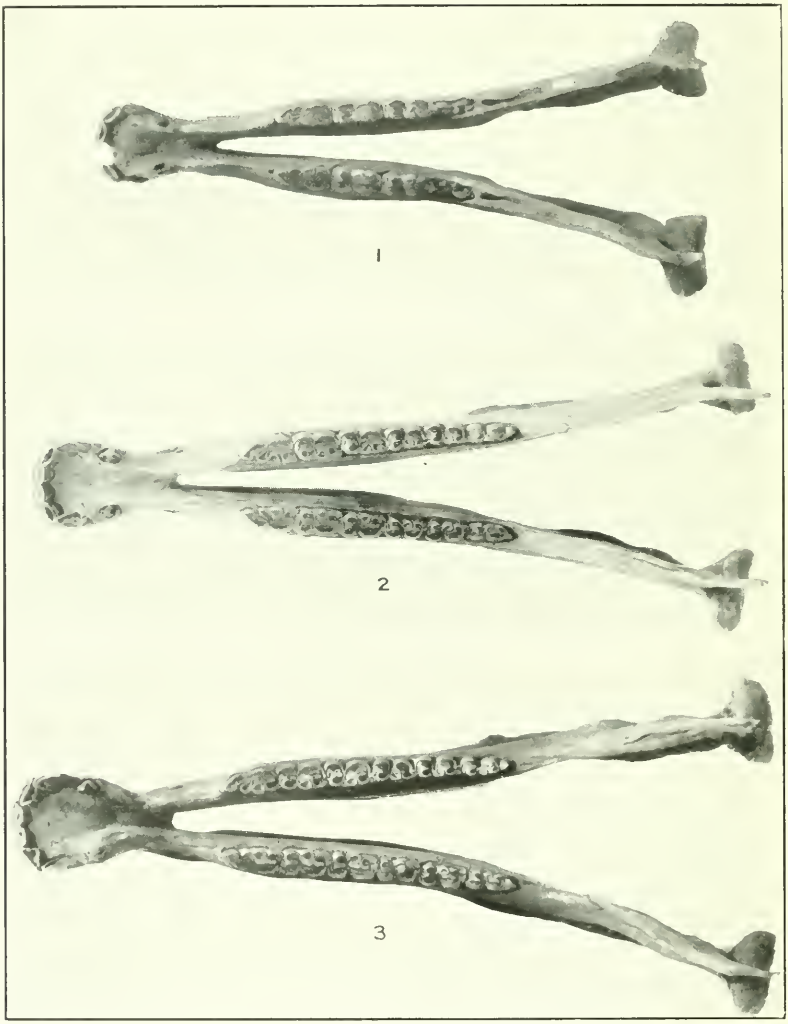
Skulls: 1, U.S.N.M. no. 12542, lateral view; 2, U.S.N.M. no. 12542, palatal view; 3, U.S.N.M. no. 12573, palatal view. About two-elevenths natural size. Hagerman lake beds, upper Pliocene, Idaho.

PLESIPPUS SHOSHONENSIS.

Skull (immature), U.S.N.M. no. 12494: 1, Dorsal view; 2, lateral view; 3, palatal view. About one-fifth natural size. Hagerman lake beds, upper Pliocene, Idaho.

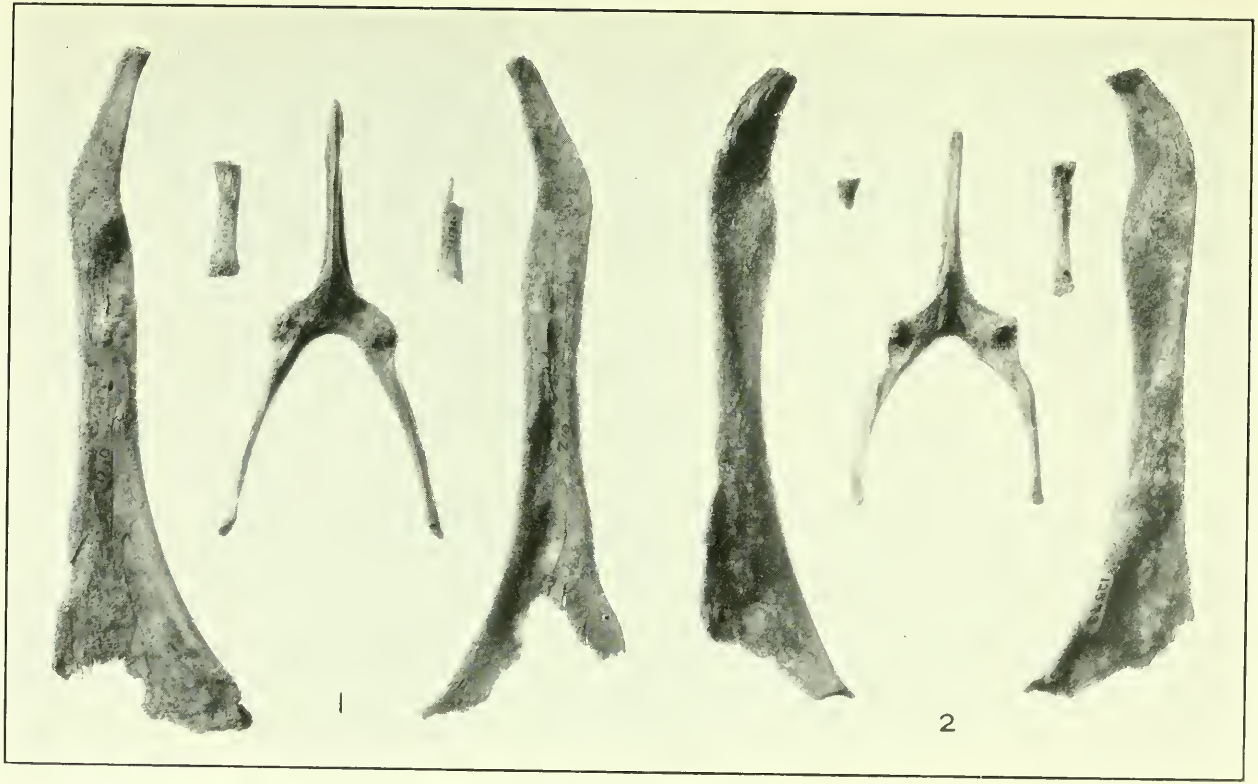
PLESIPPUS SHOSHONENSIS.

Mandibles: 1, U.S.N.M. no. 12560 (immature); 2, U.S.N.M. no. 12553; 3. U.S.N.M. no. 12573. Lateral views. About one-fifth natural size. Hagerman lake beds, upper Pliocene, Idaho.



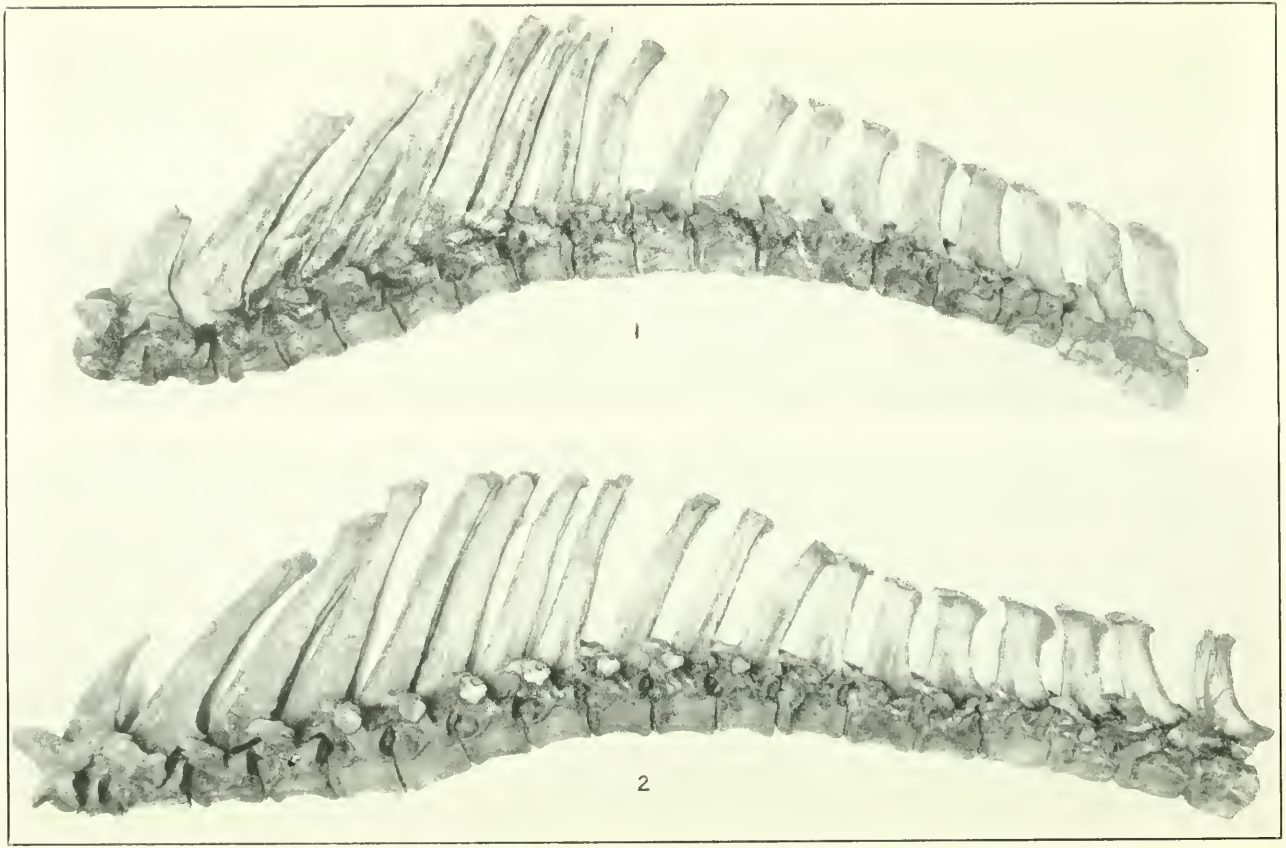
PLESIPPUS SHOSHONENSIS.

Mandibles: 1, U.S.N.M. no. 12560 (immature); 2, U.S.N.M. no. 12553; 3, U.S.N.M. no. 12573. Occlusal views. About one-fifth natural size. Hagerman lake beds, upper Pliocene, Idaho.



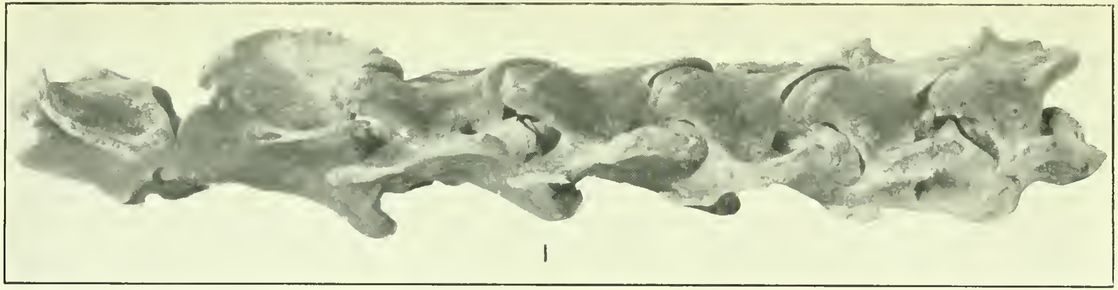
PLESIPPUS SHOSHONENSIS.

Hyoid bones: 1, U.S N.M. no. 13792; 2, U.S.N.M. no. 12573. Lateral views of stylohyals and ceratohyals and dorsal views of fused basihyal and thyrohyals. About one-half natural size. Hagerman lake beds, upper Pliocene, Idaho.



PLESIPPUS SHOSHONENSIS.

Dorsal vertebrae: 1, U.S.N.M. no. 13794; 2, U.S.N.M. no. 13792. Lateral views. About three-sixteenths natural size. Hagerman lake beds, upper Pliocene, Idaho.



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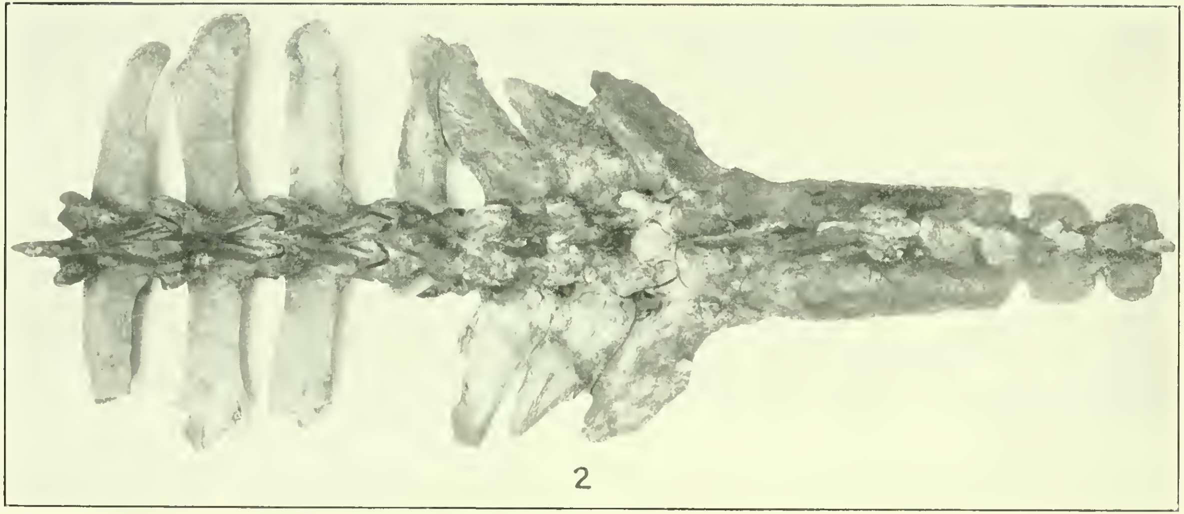

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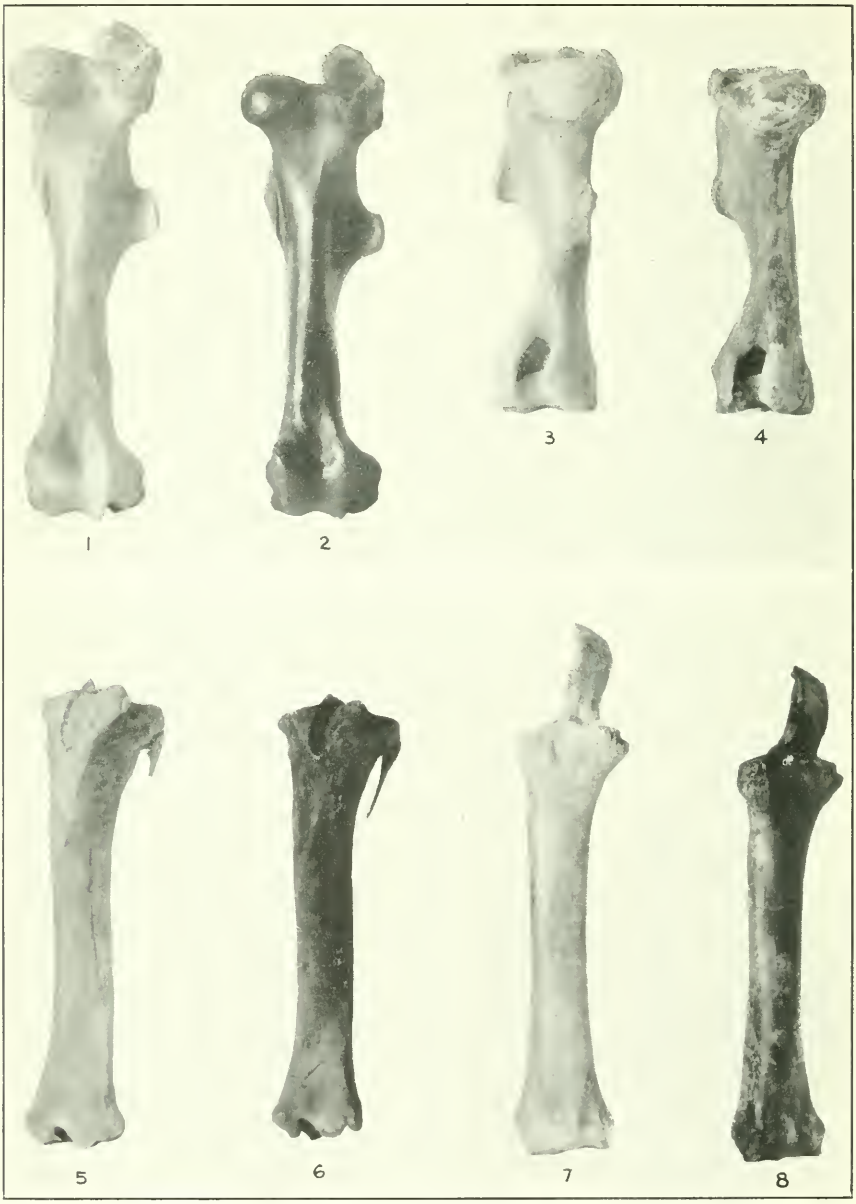
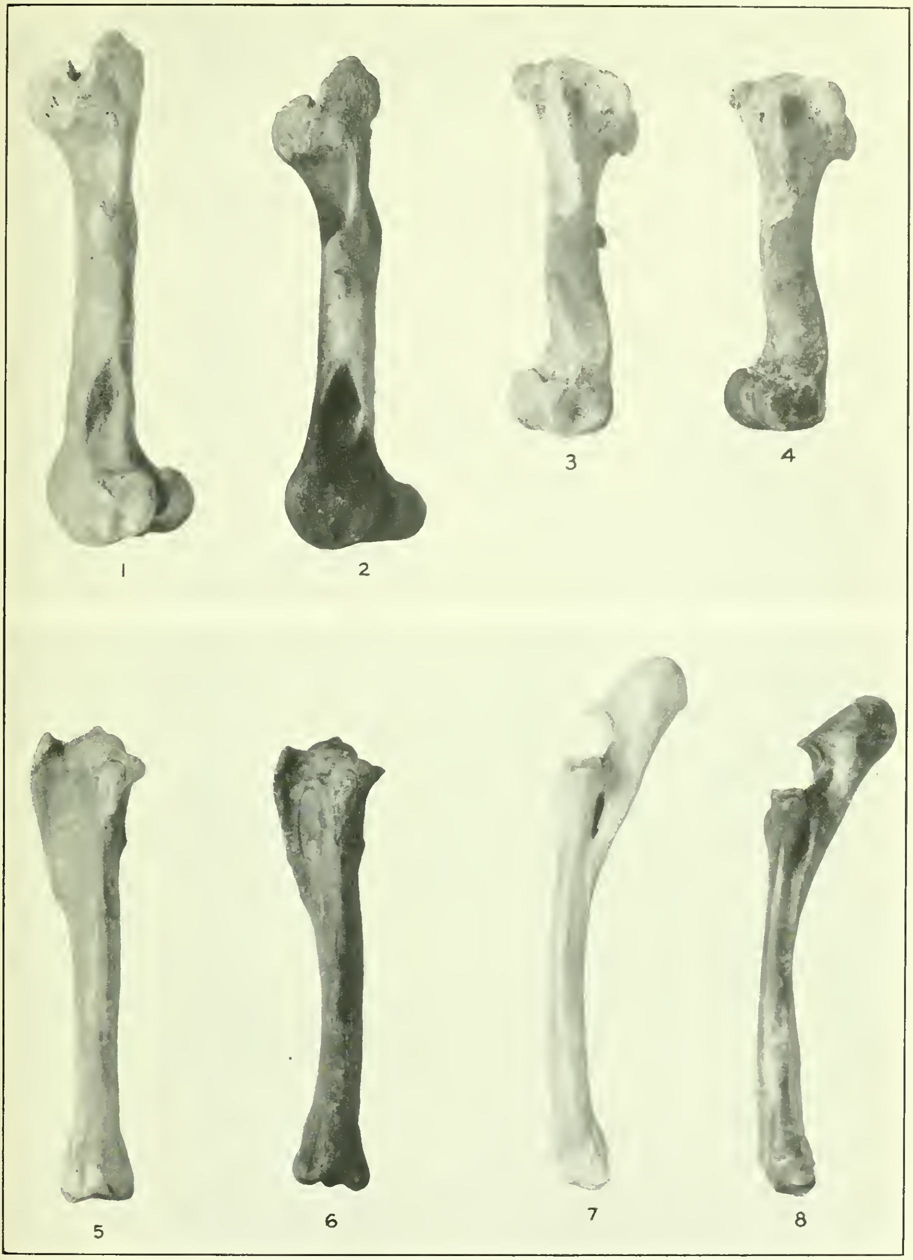
PLESIPPUS SHOSHONENSIS.

1, Cervical vertebrae, U.S.N.M. no. 12573, lateral view; 2, lumbar and sacral vertebrae, U.S.N.M no. 13792, dorsal view. About one-fourth natural size. Hagerman lake beds, upper Pliocene, Idaho.



PLESIPPUS SHOSHONENSIS.

Limb bones: 1, Femur, U.S.N.M. no. 13795; 2, femur, U.S.N.M. no. 13815; 3, humerus, U.S.N.M. no. 13795; 4, humerus, U.S.N.M. no. 13814; 5, tibia and fibula, U.S.N.M. no. 13795; 6, tibia and fibula, U.S.N.M. no. 13791; 7, radius and ulna, U.S.N.M. no. 13795; 8, radius and ulna, U.S.N.M. no. 13791. Views of humerus are posterior; all others are anterior. All about one-sixth natural size. Hagerman lake beds, upper Pliocene, Idaho.



PLESIPPUS SHOSHONENSIS.

Limb bones: 1, Femur, U.S.N.M. no. 13795; 2, femur, U.S.N.M. 13815; 3, humerus, U.S.N.M. no. 13795; 4, humerus, U.S.N.M. 13814; 5, tibia and fibula, U.S.N.M. no. 13795; 6, tibia and fibula, U.S.N.M. no. 13791; 7, radius and ulna, U.S.N.M. no. 13795; 8, radius and ulna, U.S.N.M. no. 13791. All lateral views All about one-sixth natural size. Hagerman lake beds, upper Pliocene, Idaho.