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The genus *Equus* in North America - The Pleistocene species

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ABSTRACT – The North American species of Equus *of Irvingtonian and Rancholabrean age, which were summarily reviewed by the present author in 1995, are described in detail. They are:* Equus ferus, *widespread in the Pleistocene of Eurasia and well represented in the high latitudes of North America during the latest Pleistocene, but possibly also present in central North America since the earlier Irvingtonian; the related, large sized* Equus niobrarensis *and the smaller* Equus lambei, *possibly a subspecies of the latter; the stilt-legged* Equus semiplicatus *and* Equus francisci, *which betray affinities with Old World hemiones; the short legged* Equus fraternus *and* Equus conversidens, *with complicately wrinkled enamel in their teeth, closely related with the species of South America; the large, highly derived* Equus mexicanus, *of more uncertain affinities; and the stoutly built* Equus excelsus *and* Equus occidentalis, *all three endemic to North America. Their geographical and stratigraphical ranges are discussed. Species are distinguished by their size and by the characters of their skulls, dentitions and limb bones. The paper closes with a summary review of the New and Old World species of* Equus.

RIASSUNTO – Le specie pleistoceniche nordamericane di Equus, *descritte sommariamente dall'autore nel 1995, sono illustrate ampiamente. Esse sono:* Equus ferus, *largamente diffuso nel Pleistocene dell'Eurasia e presente anche nelle alte latitudini dell'Alaska, ma possibilmente diffuso anche nelle medie latitudini fino dal Pleistocene medio, e gli affini* Equus niobrarensis, *di grande statura, e il piccolo* Equus lambei, *forse una sottospecie del precedente, limitati all'America settentrionale;* Equus semiplicatus *e* Equus francisci, *dagli arti snelli, affini agli emioni del Vecchio Mondo;* Equus fraternus *e* Equus conversidens, *dagli arti brevi, provvisti di denti a smalto complicato, imparentati con i cavalli dell'America meridionale; il grande, altamente specializzato* Equus mexicanus, *limitato all'America settentrionale, e gli ugualmente endemici* Equus excelsus *e* Equus occidentalis, *dalle forme robuste. Le distribuzioni geografiche e stratigrafiche di ciascuna specie sono discusse. Le varie specie sono distinte dalla statura e dai caratteri del cranio, della dentatura e degli arti.*
Lo studio si conclude con una sintesi delle specie di Equus *del Nuovo e del Vecchio Mondo.*

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FOREWORD

In 1993 the present writer, jointly with Dr. M.R. Voorhies of Nebraska University, published a description of the Blancan (Pliocene) species of *Equus* in North America. Their paper was followed shortly later by a study of the late T. Downs and G.I. Miller (1994) on Late Blancan and Early Irvingtonian equids from the Anza Borrego Desert of southern California, and the following year by a short account of the present author (1995) on the Irvingtonian and Rancholabrean species, which will be given here a more detailed description.

The author regrets that the present work is inevitably suffering from restrictions due to distance of his working place from Northern America. In the general dearth of synthetic reviews of the American equidae he hopes nevertheless to have given a valuable contribution in the field of their taxonomy and evolution.

A comprehensive paper on the species of *Equus* from Northern America was published by Gidley in 1901. Subsequent papers are numerous but describe isolated species or groups of few species. Substantial additions were made by Savage (1951) and W.E. Miller (1971, 1980). Brief accounts were given by Kurtén and Anderson (1980) in a book dedicated to the Pleistocene fauna of North America; a review by Winans (1989) dealt with groups of related species and was commented by the present writer in his paper of 1995.

It is intended here to give descriptions, as far as possible detailed, of middle and late Irvingtonian and Rancholabrean species documented by significant fossils. Altogether the record is rich. There are nine, or possibly ten valid species represented by skulls and limb bones, some by more or less complete skeletons. More fragmental specimens - parts of skulls, teeth, limb bones - may possibly represent other species in addition to those described here, but their remains are as yet too poor to warrant their recognition as valid taxa. They are briefly commented on at the end of this study.

The author also wishes to express his gratitude to all colleagues and friends who assisted and provided help: the late Dr. T. Downs, Dr. W. Dalquest, the colleagues of the Vertebrate Palaeontology Department of the American Museum of Natural History of New York, of the Smithsonian Institution of Washington, D.C., of the Florida State Museum at Gainesville, of the Texas Memorial Museum at Austin, of the Nebraska State Museum at Lincoln, of the Los Angeles County and Page Museums, of the University of California Museum

at Berkeley, and also to two anonymous referees for their valuable comments.

The following abbreviations were used to designate collections of fossils:

AMNH - American Museum of Natural History, New York, Vertebrate Paleontology Department

F:AM - Frick Collection in the AMNH

FC - Fauna Cedazo, Mooser Private Collection, Ciudad de México

FSM - Florida State Museum, Gainesville

IGCU - Instituto de Geologia, Universidad Autónoma, Ciudad de México

LACM - Los Angeles County Natural History and Page Museums

TMM - Texas Memorial Musuem, Austin

UCMP - University of California Museum of Paleontology, Berkeley

UNSM - University of Nebraska State Museum, Lincoln

USNM - United States Natural History Museum, Washington, D.C.

PRELIMINARY REMARKS

Equid species of late Irvingtonian and Rancholabrean age are characterized by an evolutionary radiation dating from about 1 Ma, the beginnings of which are not fully clear but whose developments may be followed in its general outline. Five lineages with nine, or possibly ten species may be recognised. Three of them are endemic to the Western Hemisphere, the others include representatives of, or species closely related to, those who dispersed into the Old World during the Middle Pleistocene, as had been done in the late Pliocene by the descendants of the American *Equus simplicidens*: the Chinese *Equus sanmeniensis* Teilhard and Piveteau, the European *Equus livenzovensis* Bajgusheva (Azzaroli, 1982, 1990). *Equus stenonis* Cocchi, widespread in the Old World, was also present in Northern America (Azzaroli and Voorhies, 1993).

In former papers the present writer adopted the latin name *Equus caballus* L. for the species represented by domestic and by wild, Pleistocene and Holocene specimens. Gentry *et al.* (1996) proposed the adoption of the name *Equus ferus* Boddaert 1765 for wild horses and the Commission on Zoological Nomenclature has accepted their proposal that Linnean names based on domesticated animals be not applied to wild forms. The specific name *E. przewalskii* Poljakov is not mentioned in the paper by Gentry *et al.* It is not clear whether this taxon should be considered a valid species (Frechkop, 1965) or a subspecies of *E. ferus*.

Equus ferus is well represented in the late Pleistocene or Holocene of Alaska: the Frick collection in the AMNH harbours a rich sample of skulls and limb bones. Its occurrence in other parts of Northern America is discussed in the present study. A close relative of *Equus ferus* is the recently extinct *Equus niobrarensis* Hay, which is known only from Northern America. The small-sized *Equus lambei* Hay shows close relationships with the latter, of which it may represent a subspecies.

Equids characterized by a small head, light build and slender, elongated limbs reminiscent of Old World hemiones, are *Equus semiplicatus* Cope and the smaller and somewhat aberrant *Equus francisci* Hay.

Equus fraternus Hay and *Equus conversidens* Owen are short limbed species with complicated enamel foldings in their teeth and are closely related to Southern American horses, while the large *Equus mexicanus* Hibbard is of more problematic affinity.

This is also the case for the heavily built *Equus excelsus* Leidy and *Equus occidentalis* Merriam (not to be confused with its ill defined homonym, *E. occidentalis* Leidy; see later for discussion).

The fossil and living Old World equids are briefly discussed at the end of this paper.

Measurements were taken according to the tables proposed by Von den Driesch (1976). Owing to the rather uniform pattern of equid skulls and postcranials only the most significant measurements were reported; other measurements, if needed, may be taken from the figures. Contrary to a common practice, only the vertex and the condylobasal length of skulls, which is also their physiological length, were taken. The widely used basal length is inspired to a practice followed in human osteology but is less significant in the case of animals with an elongated skull.

Measurements of dentitions were taken at grinding surfaces.

DESCRIPTION OF SPECIES

Equus ferus Boddaert 1785 - Pl. 1, fig. 1,2; Pl. 2, figs. 1-3

Synonyms: *Equus niobrarensis alaskae* Hay
Equus laurentius Hay

Remains of this species are common in the late Pleistocene-Holocene peat deposits of Alaska, where they are represented by skulls and postcranial bones. They are medium-sized animals: the condylobasal length of the skull F:AM 71163, ♂, from Fairbanks, is 558 mm, the vertex length 565 mm; the same lengths of the skull F:AM 60013, ♂, are 496 and 519 mm; in the skull F:AM 60011, ♂, from Elephant Point, they are 516 and 541 mm; in F:AM 60009, ♂, from Cripple Creek, 515 and 533 mm respectively. The only peculiarity to be pointed out is the occasional occurrence of upper cheek teeth with elongated protocones extending very little in front of the "pedicle" and mainly developed posteriorly to it (Pl. 2, fig. 3). The ectoflexids of the lower molars are consistently deep, except occasionally in M/3, in which they may be moderately deep (Pl. 2, fig. 2).

The length of the tooth rows of the jaw F:AM 60235-1, ♂, is 169 mm, of the jaw F:AM 71463, ♂, 159 mm.

Equus niobrarensis alaskae was based on a nearly complete male skull from Tofty, central Alaska. The narial notch is not visible because the specimen is damaged. The skull is rather shallow, the malar ridge is short and straight, and in its features and average proportions the skull does not differ from *Equus ferus*. Its length from prosthion to akrokranion is 518 mm.

Equus laurentius was based on a male skull found near Lawrence, Kansas, and has been the object of debate: Hay considered it to belong to a wild animal while other authors have suggested that it may represent a domestic horse. Be this as it may, the shape of the skull indicates that the specimen belongs to either Linné's *Equus caballus* or to Boddaert's *Equus ferus*.

Quinn (1957) recorded *"Equus caballus"* from the Pleistocene of Texas on the basis of some teeth and limb bones, but his fossils are not adequate for a reliable specific identification. The same may be said of some cheek teeth from the late Pleistocene of Mexico described by Mooser (1959) and attributed in part to *Equus caballus caballus* and in part to *Equus caballus laurentius*. These fossils are characteristic because of the deep ectoflexids of their lower molars. Later Mooser and Dalquest (1975) more cautiously referred them to *Equus* cf. *caballus*. In any case the fossil occurrence of this species in the southern United States and in Mexico remains questionable.

In the middle latitudes some fragmental remains of Irvingtonian and Rancholabrean age may possibly belong to *E. ferus*, or at least appear to be related to it.

UCMP 58180/V-6007 is a partial skull of a very old specimen with the right tooth row preserved. The praemaxillaries, nasals, part of the frontals and the left maxillary are missing. The remaining parts of the skull are indistinguishable from *Equus ferus*; the lack of downward deflection of the masseteric ridge distinguishes it from *Equus niobrarensis*. The specimen comes from the Rancholabrean of Antioch, Contra Costa Co., California.

UCMP 32879/V-3605 (Pl. 1, fig. 1a-d) is a partial skull of an old animal from Irvington, California. It conforms with *Equus ferus* and differs from *Equus niobrarensis* in the shallower rostrum, the shallower narial notch, which does not extend backwards beyond the anterior pillars of P2/, and the lack of the downward deflection of the malar ridge.

UCMP 33521/V-3107 (Pl. 1, fig. 2) is a lower tooth row of Rancholabrean age from Puerto Creek, Stanislaus Co., California. Its size and the deep ectoflexids of the molars relate it to *Equus ferus*.

A more intriguing specimen is UNSM 93078, ♂, (Pl. 2, fig. 1a-c): the right portion of a mandible with the incisors, the canines and the right row of cheek teeth. It belongs to an animal of large size about 10 years old and comes from the early Irvingtonian Red Cloud Formation, in the Ferry gravel pit, Nebraska. The length of the specimen from the condyle to the incisors is 543 mm, the length of the tooth row (grinding surface) is 188 mm The cheek teeth differ from those of *Equus niobrarensis* in the length of its molars relative to the praemolars and in their deep ectoflexids. The specimen was collected with a fragmental jaw, UNSM 93082, with equally deep ectoflexids in its molars, and with two metatarsal cannons, UNSM 93080, with a total length of 295 mm and UNSM 93081, with a length of 293 mm, and a first phalange of medium size. While the bones of the limbs are not indicative, the shape of the dentitions, in particular the deep ectoflexids of the molars, may indicate that these fossils are possibly the earliest representatives of *Equus ferus* in North America.

Equus niobrarensis Hay 1913a - Pl. 3, fig. 1,2; Pl. 4, fig. 1,2; Pl. 5, fig. 1; Pl. 6, fig. 1; Pl. 7, fig. 1

Synonym: *Equus hatcheri* Hay 1915
non: *Equus niobrarensis alaskae* Hay 1913

This species was based on a skull with mandible from the late Irvingtonian Sheridan Beds in the valley of the Niobrara river near Hay Springs, Nebraska. The skull has been extensively restored. *Equus hatcheri* was based on another skull, also with mandible, from the same locality, which was badly distorted by an unskilled restoration; it does not differ from the holotype in any significant feature.

Authors have interpreted the name *niobrarensis* in different ways. Savage (1951) considered it a possible synnym of *Equus scotti* (= *Equus excelsus* in the present paper) and so did Khan (1970), while Dalquest (1969), Hibbard (1970) and Lundelius (1972) considered it valid. Dalquest and Lundelius stated that this species is smaller than *Equus scotti* but their remarks were based on cheek teeth, which in *Equus niobrarensis* are rather small, especially so the molars. The skull of *Equus niobrarensis* equals in size the largest skulls of *Equus ferus*; it is more elongated than that of *Equus excelsus* and of a more slender build. As in these species, there are no facial fossae. The Late Pleistocene (Sangamonian) equid from Fort Qu'Appelle, Saskatchewan, Canada, referred to *Equus scotti* by Khan (1970) actually belongs to *Equus niobrarensis*. It is represented by a fine skull, other fragmental skulls, jaws and many limb bones.

This species is represented by several skulls and postcranial bones from various sites in the Sheridan Beds of the Niobrara valley: Hay Springs, Gordon, Rushville and Angus, where it is associated with *Equus excelsus, Equus fraternus* and *Equus semiplicatus*. Its range extends from southern Canada to the southern United States and possibly Mexico. The problem of sorting out limb bones of *Equus niobrarensis* from those of *Equus excelsus* will be discussed in connection with the description of the latter species.

The type skulls of *Equus niobrarensis* and *Equus hatcheri* are of restricted interest because of the extensive restorations they underwent. There are some more or less damaged skulls in the collections from Hay Springs in the AMNH and F:AM but the best preserved specimens are in UNSM: three nearly complete skulls from Gordon and one, with mandible, from Hay Springs, the locality of the type of the species.

UNSM 5980, ♂, (Pl. 3, fig. 1a,b; Pl. 4, fig. 1a,b) is a perfect skull of a stallion about 15 years old, from Gordon. The angle between the face and the braincase is widely open, the narial notch extends as far as the posterior lobe of P2/, the masseteric ridge is elongated and bends downward in its rostral portion. The posterior palatine foramina are placed opposite the distal ends of the M3/s. The

condylobasal length is 597 mm, the length of the tooth row at the grinding surface 177 mm, the breadth of the incisors 77 mm.

UNSM 5981, ♂, from Gordon, is the skull of an older specimen and is slightly damaged. The condylobasal length is about 565 mm, the length of the tooth row 165 mm The left first praemolar is preserved.

UNSM 5982, ♂, also from Gordon (Pl. 5) is a skull of about the age of UNSM 5980 and is somewhat damaged. The length from prosthion to akrocranion is 605 mm, the condylobasal length 573 mm, the tooth row 178 mm on the right side and 180 on the left.

UNSM 9417, ♂, also from Gordon (Pl. 3, fig. 2a, b; Pl. 4, fig. 2) is a partial jaw of an animal about 5 years old. The cup of I/3 is partially open, the ectoflexid of M/1 is rather deep, the others are shallow.

UNSM 1346, ♂, from Hay Springs, is the skull, with mandible, of a colt about 3 years of age (Pls. 6, 7). The canines are erupting, the three left milk teeth and two permanent molars are preserved; on the right side the anterior milk praemolar has been lost and the germ of the permanent praemolar is erupting. The alveolus of a first praemolar is clearly visible. The second molars are erupting and the third molars have not yet erupted. In spite of its young age this is the largest specimen, with a condylobasal length of about 615 mm; the measurement is approximate because the incisival region is damaged.

In SMNH 1515/8305, ♀, the skull from Fort Qu'Appelle, the length from prosthion to akrokranion is 583 mm.

The skull of *Equus niobrarensis* is elongated, with a deep, narrow snout and a widely open facial angle (somewhat deformed in the skull from Fort Qu'Appelle). It is more slender in build than the skull of *Equus excelsus*, the snout is narrower, the praemaxillaries are less massive. The upper profile bulges slightly over the parietals and is straight along the forehead and the nasals, as in *Equus ferus*; the narial notch is deeper and extends to above the posterior half of P2/. The masseteric ridge is long and descends ventrally at its rostral end. The posterior palatine foramina are placed opposite the M3/s, as in *Equus ferus*. The cheek teeth are relatively small, with medio-laterally compressed, antero-posteriorly elongated protocones and a richly plicated enamel. As Hay pointed out, the praemolars are large relative to the molars.

The jaw is also of slender build, the medio-laterally compressed rami have sharp upper margins in the diastemata; the row of incisors is narrow, the teeth have well developed cups, frequently open in the third incisors. The ectoflexids as a rule are shallow in M/1 and M/2, somewhat deeper in M/3, and never come into contact with the linguaflexids. The metaconids and metastylids are antero-posteriorly elongated, medio-laterally compressed.

A jaw of *Equus niobrarensis*, F:AM 116971, from a roadcut south of Dalhart, Texas (late Irvingtonian ?), is associated with many remains of *Equus semiplicatus*.

Remains of the dentition and parts of a skeleton, F:AM 116140, come from an early Irvingtonian site at Arkalon, Seward Co., Kansas, and are also associated with *Equus semiplicatus*. If identifications are correct this is the oldest record of *Equus niobrarensis*. Hibbard *et al.* (1978) recorded this species from the late Irvingtonian Kanopolis fauna of Kansas and Lundelius (1972) reported it from the Gray Sand at the archaeological site of Blackwater Draw, New Mexico.

The skull TMM 30967-401, from the Ingleside fauna of Texas, described as *Equus complicatus* by Lundelius (1972), also seems to belong to *Equus niobrarensis*: it has a narrow rostrum, is elongated and the posterior palatine foramina are in a caudal position.

A partial skull from the Rancholabrean of Aguascalientes, central Mexico, FC 709, may also belong to this species. The dentition was figured by Mooser and Dalquest (1975, fig. 8) under the name *Equus calobatus*, which may be an error, or a misprint. Fig. 7 of the same paper represents a skull which the caption states also to be of *Equus calobatus*, but this is again a misprint (Dalquest, personal communication). Dalquest kindly supplied photographs of this skull and jaw. The skull consists of the muzzle, with a slender snout and a deep narial notch (its depth was possibly exaggerated in the restoration) and seems to conform well to Hay's species; the dentition is in agreement with this interpretation.

Equus niobrarensis displays some relationship with *Equus ferus*, from which however it differs in several details. The skull is narrow and deep, the narial notch more extended caudally, although it is never very deep, the masseteric ridge is longer and curved donward at its rostral end. The ectoflexids of M/1 and M/2 are shallow, and so occasionally are the ectoflexids of M/3, which in any case are never very deep. The molars are relatively small in comparison with the praemolars. In general proportions the skull is more slender and elongated than that of *Equus ferus*.

The body size is large. The humeri from Fort Qu'Appelle range in length from 288 to 237 mm, the radii from 348 to 318 mm, the metacarpal cannons (13 specimens) from 260 to 222 mm; the lengths of two femurs are 437 to 383 mm, of two tibiae 375 and 374 mm, the metatarsals (9 specimens) range from 295 to 266 mm Assuming that body proportions were similar to those of *Equus ferus*, the height of the skeleton at the withers ranged between 140 and 155 cm. The limbs are strong but rather slender.

Equus niobrarensis is distinguished from its nearest ally, *E. ferus*, by a somewhat deeper slull, generally a more open facial angle, the elongated masseteric ridges bending downwards at their rostral extremities, the deeper narial notch, the rather small molars relative to the praemolars and their shallow ectoflexids.

Equus lambei Hay 1917
(*Equus niobrarensis lambei* ?)

This species was based on a perfect male skull with mandible, USNM 8226, from the late Pleistocene of Gold Run Creek, Klondike, Yukon Territory. It is much smaller than *Equus niobraren-*

sis, with a relatively short snout - a natural effect of scaling - and a less marked downward bend of the masseteric ridge, also an effect of the reduced size. It may possibly represent a local, small sized subspecies of *Equus niobrarensis*, which it resembles in general shape, in the deep narial notch, the anterior downward bend of the masseteric ridge and in the shallow ectoflexids of the lower molars. The length of the skull from prosthion to akrocranion is 493 mm

Equus semiplicatus Cope 1893 - Pl. 8, figs. 1-3; Pl. 9, fig. 1,2; Pl. 10, fig. 1,2

Synonyms: *Equus calobatus* Troxell 1915
Onager altidens Quinn 1957

This species was named by Cope on some teeth from the Irvingtonian of Rock Creek, Texas. Gidley (1901) referred to it a skull from southeastern Texas, "practically the same locality as the type specimen of *E. semiplicatus*, and from the same locality from which two of the paratypes were collected". The skull, AMNH 8600, had previously been referred to *Equus excelsus* by Cope, although "it does differ in both size and general characters from Leidy's type of *Equus excelsus*" (Gidley, 1901). No limb bones of this species were described by either Cope or Gidley, but from the same site as the skull comes a metatarsal cannon, AMNH 116510, of large size and very slender proportions: the length is 319 mm, the proximal breadth 45 mm, the distal breadth 38 mm.

Troxell (1915) reported on other fossils from the Rock Creek: some very slender limb bones, an atlas and a sacrum, and proposed for them the new name *Equus (Asinus) calobatus*. A metacarpal cannon from his collection is 287 mm long; the proximal breadth 54 mm and the distal breadth 45.5. Hibbard (1953) selected a metatarsal cannon among Troxell's specimens as the lectotype of this species and described some teeth. Quinn (1957) rightly considered *E. calobatus* a junior synonym of *Equus semiplicatus*, which he placed in the genus *Onager*. Skinner (in Skinner and Hibbard, 1972) on the other hand considered Troxell's species valid, referred it to the Old World subgenus *Hemionus* Stehlin and Graziosi and described under the new combination *Equus (Hemionus) calobatus* a juvenile jaw and partial skeleton, F:AM 87459, from Arkalon, Kansas.

Limb bones similar in size and proportions to those from Rock Creek and Arkalon occur in the Sheridan Beds of Nebraska at Gordon, Rushville and Hay Springs, in association with *Equus niobrarensis, Equus excelsus* and *Equus fraternus*.

The richest sample of *Equus semiplicatus* comes from pits along a highway about 10 miles south of Dalhart, Texas. It includes two skulls, several jaws and postcranial bones representing more or less all parts of the skeleton. This collection, in the F:AM, has not been described, nor has, to the author's knowledge, the accompanying fauna. *Equus semiplicatus* forms the largest part of remains of equids but *Equus niobrarensis* is also present (see above).

Equus semiplicatus is characterized by an extremely slender build, with a small skull and slender, greatly elongated limb bones. The dentition is rather small and the enamel of the cheek teeth is poorly plicated; the name of the species was derived from this feature. The lower incisors develop full cups in wear and the molars have consistently shallow ectoflexids.

The limb bones are unusually slender. Radii from near Dalhart range in length between 321 and 304 mm, their proximal breadth from 68 to 61 mm, the distal breadth from 69 to 63.5 mm; the metacarpal cannons range in length from 255 to 244 mm, their proximal breadth between 46 and 45 mm, the distal breadth about 40 mm. A femur is 335 mm long, its proximal breadth 107 mm, its distal breadth 83 mm Tibiae range in length from 329 to 319 mm, their proximal breadth between 89 and 80 mm, their distal breadth between 64.5 and 59.5 mm. The length of the metatarsals ranges between 347 and 319 mm (Lundelius and Stevens, 1970, fig. 3), with proximal breadths around 43 mm and distal breadths around 39 mm. The metatarsal cannon from Rock Creek AMNH 116510, mentioned above, is 319 mm long, with a proximal breadth of 45 mm and a distal breadth of 38 mm. The measurements of the juvenile specimen from Arkalon, Seward Co., Kansas, are: physiological length of the humerus about 255 mm, with the proximal epiphysis not fused; the total length of the metacarpal cannon 282 mm; the femur, physiological length, 340 mm (the proximal epiphyses are not fused); the total length of the tibia is 353 mm, the metatarsal 324 mm One of the largest specimens comes from Rock Creek: TMM 41286-1 is a cast of a metatarsal with a total length of 342 mm, proximal breadth 49 mm, distal breadth 43 mm.

Only three fairly well preserved skulls are known, although none is in a really perfect state.

AMNH 8600 (Pl. 10, fig. 2) is the skull described by Gidley, from a female aged 6-7 years. Of the incisors only a I2/ is preserved and is damaged. The specimen is crushed in the frontal region and lacks the occipital portion, the left zygomatic arch and the corresponding postorbital process.

F:AM 116156 (Pl. 8, fig. 1; Pl. 9, fig. 1), from near Dalhart, Texas, also belongs to a female about 6 years old. The parietals, the supraoccipital and the right zygomatic arch are missing.

F:AM 116158 (Pl. 10, fig. 1), from the same locality, is another skull of a female about six years old and lacks all the braincase, part of the right orbit and the hinder portion of the palate. Its facial portion is better preserved than in the other two skulls.

As compared with other Pleistocene species the skull of *Equus semiplicatus* is small. The condylobasal length of F:AM 116156 is 470 mm There is a small, but distinct praeorbital pit well in front of the orbit and the narial notch extends over the anterior lobe of P2/. The basicranium is rather strongly deflected relative to the face, but it is not easy to tell how far this feature is due to deformation. The vomer extends backwards well beyond the pterygoids, a feature this species shares with Old World hemiones and asses. The orbits are large and rounded. The postorbital process of F:AM 116156

projects laterally as in living hemiones. Behind it the zygomatic arch is directed towards the sagittal plane; the greatest breadth of the skull corresponds to the postorbital processes. The position of the posterior palatine foramina is variable, they lie either opposite the third molar of just in front of it.

F:AM 116158 shows similarity to this skull, only the praeorbital pit is fainter, although clearly recognizable. The postorbital process projects laterally.

The skull of AMNH 8600 is also similar to these but with some differences. The posterior palatine foramina lie opposite the M2/s. The postorbital processes project laterally but behind them the zygomatic arch is somewhat broader; this may be an effect of deformation. The vomer extends posteriorly as in F:AM 116156.

The upper tooth row is characteristic: the enamel pattern is rather simple and the protocones are elongated.

Several jaws from Dalhart belong to *Equus semiplicatus* (Pl. 8, fig. 2, 3; Pl. 9, fig. 2). Their enamel is poorly plicated, the lower molars bear consistently shallow ectoflexids and the incisors show well developed cups.

In the metapodials the volar face is smooth, only occasionally a short and faint ridge 1-2 cm. long is developed over the articular keel.

The proportions of the limb segments are unusual. The metapodials are long in proportion to radius and tibia; no other species shows so extremely elongated metapodials. Among living species the relatively longest metapodials occur in hemiones, but their lengths remain below those of *Equus semiplicatus* (see also Lundelius and Stevens, 1970, fig. 3). In the skeleton from Arkalon, Kansas, AMNH 87695, the metacarpal is 78% the length of the radius, the metatarsal 92% of the tibia. Other proportions of the limb bones are:

Humerus, physiological length/Radius length	70%
Humerus, id. /Metacarpal length	90%
Femur, physiological length/Tibia	96%
Femur, id. /Metatarsal length	104%

These figures cannot be compared directly with ratios of other species as calculated by Willoughby (1974) because this author used total lengths of humeri and femurs, which cannot be measured in the immature Arkalon specimen. However, assuming the total length to be 104% the physiological length (i.e. the minimal length measured on the articular surfaces of the extremities) for the humerus and 110% for the femur, ratios comparable to those of Willoughby may be obtained for AMNH 87495.

	E. semiplicatus F:AM 87495	*E.hemionus* (Willoughby 1974)
Humerus, total length	265	252
Femur, total length	374	339
Humerus/Radius length	73%	82%
Humerus/Metacarpal length	94%	109%
Femur/Tibia length	106%	105%
Femur/Metatarsal length	115%	124%

The humerus and radius are short relative to the metacarpals; femur and tibia in turn are short relative to metatarsals. In *Equus hemionus* the femur/tibia ratio equals the value of *Equus semiplicatus* or even falls slightly below it, but its metapodials are less elongated.

Equus semiplicatus is known from Texas, Kansas and Nebraska Its remains from the Sheridan Beds of Nebraska were referred in part to *Equus (Hemionus) francisci* and in part to *Equus (Hemionus) calobatus* by Howe (1979). This species was also recorded from central Mexico by Mooser and Dalquest (1975) but their attribution does not seem to be based on diagnostic specimens.

The time range of this species is presumably from Middle to Late Irvingtonian. The oldest specimens come from the Rock Creek, the youngest are possibly those from the roadcut south of Dalhart; the age of the latter however has not been established with certainty.

Equus semiplicatus is related to *Equus francisci*, which it resembles in limbs and, to a lesser degree, in the skull. It differs from the latter in its larger size, a deeper narial notch, the retention in female skulls of a faint praeorbital pit, the possession of cups on its lower incisors and the laterally protruding postorbital processes. It resembles more closely *Equus hemionus* in skull and limbs and differs from it only in details: the praeorbital pits, which are lacking in *E. hemionus*; the simpler enamel plication of its cheek teeth, the greater elongation of the distal segments of the limbs. The posterior palatine foramina are in a forward position in *Equus hemionus*, opposite the M2/s; in *Equus semiplicatus* their position seems to be more variable, but only two specimens have been observed, and in a state of preservation which is far from perfect. The peculiar backward extension of the vomer, first observed by Gidley (1901), is shared by *Equus hemionus* and the African ass *Equus africanus*; this is also the case for the laterally protruding postorbital processes. *Equus hemionus* lacks the ridge of the posterior face above the keel of the metapodials; in *Equus semiplicatus* this ridge is present only occasionally and in this case it is shallow and very short; in *Equus africanus* it is well developed.

Equus semiplicatus belongs to the same stock from which Old World hemiones were derived. The oldest record of hemione-like equids in the Old World dates from about 1 Ma, in Central Asia, (Azzaroli, 1983) with *Equus* cf. *altidens* Von Reichenau 1915 (this species is homonym with *Onager altidens* Quinn 1957, which is here considered a junior synonym of *Equus semiplicatus*). The oldest record of *Equus semiplicatus*, from the Rock Creek, is well over 1.2 Ma old (Kurtèn and Anderson, 1980: 23).

The origins of this stock are obscure because of the many gaps in the record. It may perhaps be traced among the small sized, slender limbed equids (*Equus cumminsii* ?) of the late Blancan; see Azzaroli and Voorhies, 1993: 184-185 and Pl. 6, fig. 5.

Equus semiplicatus is a highly distinctive species characterized by a small skull, with a deep muzzle, possibly a marked facial angle, large orbits, and even more by its very slender and elongated limbs.

Equus francisci Hay 1915 - Pl. 11, fig. 1a-d

Synonyms: (?) *Equus tau* Owen 1869
(?) *Equus littoralis* Hay 1913
(?) *Equus achates* Hay and Cook 1930
Equus quinni Slaughter 1962

This species is represented by a satisfactory holotype: a well preserved female skull and some parts of the skeleton, including limb bones. Dalquest (1977) considered *Equus francisci* a junior synonum of *Equus tau.* This may possibly be right, but *Equus tau* was based on an incomplete tooth row which is inadequate to define the species and is not free from ambiguities; so are also the other species names listed above, with the exception of *Equus quinni,* represented by a characteristic metapodial and some teeth, which Dalquest (1979) synonimyzed with *Equus francisci.*

The type comes from the Lissie Formation of Wharton Co., Texas. The species was revised by Lundelius and Stevens (1970), who dated it as Middle Irvingtonian (Yarmouthian). It consists of a partial skeleton: skull, mandible, bones of the hind limb. The skull belongs to a female and is small (condylobasal length 446 mm). It is distinguished by a straight profile, a shallow narial notch, postorbital processes not protruding laterally, a smooth face lacking praeorbital pits, a moderate deflection of the braincase relative to the face. The dentition has a poorly wrinkled enamel. This is not due to age because the animal is only 5-6 years old. The lower incisors lack cups and the molars bear shallow ectoflexids. Lundelius and Stevens (1970) checked Hay's restoration of a supposed metacarpal and found that it belongs to a metatarsal 284 mm long, with a proximal breadth of 39 mm and a distal breadth of 36 mm. It is even more slender than the same bone in the living hemiones.. Three other metatarsals from various sites range from 283 to 295 mm in length. The volar ridge above the keel of the metatarsals is poorly developed and very short. The physiological length of the radius, according to Hay, is 268 mm, the proximal breadth 69 mm, the distal breadth 59 mm.

An incomplete male skull (Pl. 11) with jaw and a slender metatarsal from the late Pleistocene Cedazo fauna of Central Mexico, conforming in size with the type specimens, were referred to *Equus tau* by Mooser and Dalquest (1975), who pointed out the occurrence of a very shallow praeorbital pit in the skull. The specimen was not figured but photographs were kindly supplied to the present writer by Dr. Dalquest. The specimen lacks the braincase and is laterally crushed. Apart from the small praeorbital pit it conforms to the type skull of *E. francisci* in size, in the profile and in dental features. All its teeth are however much worn.

Teeth and limb bones of *Equus francisci* were reported fron a late Palaeolithic settlement at Cueva Quebrada, Texas, by Lundelius (1984).

Equus francisci is related to *Equus semiplicatus* in the features of the limbs and, to a lesser extent, also of the skull and dentition, but differs in several details: the narial notch is shallower, the lower incisors lack the cups and the postorbital processes do not protrude laterally (observations on the type specimen). The upper and lower cheek teeth resemble those of *Equus semiplicatus* in the elongated protocones, the rather simple enamel pattern, the shallow ectoflexids of the lower molars; their size is distinctly smaller.

Like *Equus semiplicatus, Equus francisci* is related to Old World hemiones in general body build but diverges from them more than the former species in the features of its skull and dentition.

Equus fraternus Leidy 1860 - Pl. 12, fig. 1; Pl. 13, figs. 1-4

Synonym: *Equus leidyi* Hay 1913

This species was placed by Cope (1892) in his new subgenus *Tomolabis* because of the lack of cups in its lower molars. This feature is shared by South American species, for which Hoffstetter (1950, 1952) proposed the new subgenus *Amerhippus,* in which he also included the Rancho La Brea equid, *Equus occidentalis* Merriam. The latter species however diverges from the other representatives of Hoffstetter's subgenus in various characters (see later). The lower incisors of *E. francisci* also lack cups (see above).

Cope's name *Tomolabis* was considered valid by Trumler (1961). In the present author's opinion *Equus fraternus,* together with another North American species, *Equus conversidens,* is closely related with South American species. If subgeneric names will be applied *Tomolabis* may perhaps have priority over *Amerhippus,* although when the latter name was proposed *Tomolabis* was already a "forgotten name", having not been used for over 50 years.

Beside the lack of cups in the lower incisors, South American equids, according to Hofstetter, are characterized by a ventral rotation of the occiput, with a strong deflection of the braincase relative to the face, a broad supraoccipital crest, the vomer joining the palatal processes of the maxillaries well in front of the palatines, a massive jaw and short limbs.

Savage (1951) remarked that *Equus fraternus* "has had a rather complicated nomenclatural history" and concluded considering it a "nomen vanum". The types are few isolated teeth of rather small size and with derived features: elongated protocones, richly plicated enamel. They came from the southeastern United States. On the other hand Cope (1892), Gidley (1901), Hay (1913) and Quinn (1957) considered Leidy's name valid. Cope referred to this species a jaw from the Caloosahatchie River, Florida, in which the first and second incisors bear broadly open cups and the third totally lacks them. This jaw was described and figured by Hay (1913).

Equus fraternus is not restricted to the southern United States, it is also represented in the Sheridan Beds of Nebraska, of late Irvingtonian age, and fragmental remains which may belong to this species were recorded by Churcher (1985) from late Pleistocene (Sangamon) deposits at Medicine Hat, Alberta, Canada. In Florida *Equus fraternus* is com-

mon and is represented by well preserved, although incomplete specimens of Irvingtonian and Rancholabrean age.

A male skull from the Rancholabrean site of Itchetucknee, Florida, F.AM 116143 (Pl. 12, fig. 1a-c; Pl. 13, fig. 3) is one of the most significant fossils. It lacks the incisors, the canines, two cheek teeth, the tips of the nasals and the occiput, but is otherwise perfect and not deformed. It is of rather large size: the total length, in the present condition, is 560 mm and the condylobasal length may have been the same, the vertex length perhaps 575-580 mm The shape of this skull is characteristic: it is elongated, with a tapering snout; the profile is markedly convex from the parietals to mid-length of the nasals and broadly concave over the infraorbital foramina. The braincase is markedly deflected relative to the face. The forehead is also convex transversally and the rather small orbits are placed low. The zygomatic arches are broad and project laterally beyond the postorbital processes. Facial pits are lacking. The teeth are small in proportion to the size of the skull, the protocones of the cheek teeth are elongated and the enamel of the inner fossettes is richly plicated.

A cast of a lower tooth row from El Jobean, Charlotte Co. Florida, (Pl. 13, fig. 4) illustrates an early stage of wear of this species.

A large collection of partial skulls, dentitions and limb bones comes from the Pool Branch site of Florida, of Irvingtonian age.

AMNH 95588, Pl. 13, fig 1a,b, is the cast of the skull of a male 6 years old. It is crushed dorsoventrally and lacks the occipital portion. It resembles the skull F:AM 116143, the tooth enamel is richly plicated.

AMNH 95588A, Pl. 13, fig. 2 is a cast of a lower left dental row, presumably from the same specimen as AMNH 95588. The teeth are small, with a richly plicated enamel and strong "plis caballinids". The ectoflexids of the molars are shallow.

FSM 1143 is the skull of a very old female. It was broken at the diastema and the tip of the snout is preserved as a separate piece; it lacks the canines. The condylobasal length, restored, is about 545-550 mm, slightly less than F:AM 116143. The inner enamel of the cheek teeth has almost completely disappeared as a result of wear, save in the last molars. The bones of the skull roof, although they are crushed, reveal that the forehead was transversally convex.

FSM 11403 is a complete male mandible. The incisors lack the cups, the ectoflexids of the molars are shallow.

FSM 11357 is a right ramus, slightly deformed. The ectoflexid is deep in M/3, less so in M/1 and M/2.

The Florida State Museum collection includes moreover several milk teeth, an axis and a large number of limb bones; these are all of rather small size.

In the Sheridan Beds of Nebraska *Equus fraternus* is not common. It is associated with *Equus semiplicatus, Equus niobrarensis* and *Equus excelsus*. Limb bones are not always easy to separate because their size ranges seem to overlap the lower range of the latter species.

F:AM 116141 is a broken female skull from Hay Springs; AMNH 2738 is a left lower dental row from the same locality, and UNSM 1349 is a female skull, with mandible, six years old.

AMNH 113791 is a cast of a nearly complete female skull about 5 years old, from Iron Bridge locality near Palestine, Texas, of Irvingtonian age.

UCMP possesses a collection of about 80 isolated teeth, and the first and third phalanges from Venice, Sarasota Co., Florida. The teeth are characteristic for their small size and extravagantly plicated enamel. The age is Rancholabrean.

The length of a humerus from Pool Branch, Polk Co., Florida, is 254 mm, the physiological length 245 mm, the proximal breath 85 mm, the distal breadth 75 mm The ranges of two radii from the same site are: greatest length 298 mm, proximal breadths 80 and 74 mm, distal breadths 67 and 65 mm.

The lengths of metacarpals from the same site range between 217 and 214 mm, the proximal breadths between 46 and 44.5 mm, the distal breadths between 44.5 and 42.5.

A femur, also from Pool Branch is 383 mm long, proximal breadth 104 mm, distal breadth 88.5.

A tibia from the same site is 323 mm long, its proximal breadth 97.5, distal breadth 69.5.

The lengths of the metatarsals range between 260 and 255 mm, the proximal breadths between 50 and 44 mm, the distal breadths between 46 and about 43 mm (the last specimen is damaged).

Equus fraternus has a relatively large, elongated skull with small teeth, an undulating profile with a strongly convex forehead, a tapering smout, rather small orbits placed low and short, slender limbs. Its braincase was strongly deflected relative to the face, as is the case in South American horses (Hofstetter, 1952; Azzaroli, 1992). The lower incisors lack the cups, or occasionally have broadly open cups in I/1 and I/2. The ectoflexids of the lower molars as a rule are shallow.

The only close relative to *Equus fraternus* in North America is *Equus conversidens,* which is disntinguished by a smaller skull with a short snout and smaller teeth. Rather surprisingly, the limb bones of these two species appear to be similar in size and proportions.

The partial skeleton from Canyon, Texas, in the Panhandle Historical Museum, referred to *Equus conversidens* by Dalquest and Hughes (1965) is puzzling. The skull equals in size the skulls of *Equus fraternus* from Pool Branch and from the Sheridan Beds of Nebraska. The enamel of its teeth is not particularly plicated, but this may be due to the old age of the specimen.

Some elongated first phalanges from Slaton Quarry, Texas, referred to *Equus conversidens* by the same authors, in their proportions seem rather to belong to *Equus semiplicatus* or to *Equus francisci.*

Equuss conversidens Owen 1869 - Pl. 14

Synonyms: *Equus barcenai* Cope 1884
(?) *Onager zoyatalis* Mooser 1959

This species was based on a palate from the late

the posterior palatine foramina are placed opposite the M3/. The masseteric ridge is of medium length and curves downward rostrally. The supraoccipital ridge is prominent and the occipital region is strongly rotated ventrally.

A largely restored palate of a 7 year-old male from Salt Fork, Brazos River, Stonewell Co., Texas, TMM 31108-82, may possibly be referred to this species. It is of large size, with massive teeth. The age is probably Rancholabrean.

The present author refers to this species a jaw from Barranca del Muerto, Municipio de Tequixquiac, Distrito Zumpango, Mexico, LACM 308/123901 (Pl. 8, fig. 4a-c). The specimen belongs to the late Pleistocene and is nearly complete. The rami are thick and deep, the upper edges of the diastems are bluntly rounded. The ectoflexids of M/1 are rather deep but the others are shallow. The incisors bear cups, which are open lingually in I/3. The age of the specimen is 7-8 years,

The systematic position of *Equus mexicanus* is puzzling. The peculiar features of the profile and of the occipital region have been observed only in species from Southern America, and by the present author in *Equus fraternus* and possibly *Equus conversidens*. Bennett (1980) considered the ventral rotation of the occiput a primitive feature, found in *Dinohippus*. In fact a strong rotation is shown in Osborn's figure of the type skull of *Dinohippus leidyanus* (*Protohippus leidyanus* in the original text: Osborn, 1918, Pl. 30), but the fossil is deformed. Better preserved skulls of the same species, from Nebraska and from Kansas, show backwards sloping paraoccipital processes and lack any trace of ventral rotation of the occiput (Azzaroli, 1988). The peculiarity of *Equus mexicanus*, of the South American species of *Equus* and possibly of the North American *Equus fraternus* and *Equus conversidens* is a derived, not a primitive feature.

Carranza-Castañeda and Miller (1991) gave a summary notice of a skeleton from the Pleistocene deposits of Guanajuato, Mexico, provisionally identified as *E. ?conversidens*. The authors stress the affinities between *E. mexicanus* and their specimen; which is said to be "larger than *E. conversidens* but somewhat smaller than *E. mexicanus*" They remarked the similarities between these two species and concluded that "if future age determinations reveal the new find to be earlier Pleistocene, it could represent a horse with a transitional relationship between *E. mexicanus* and *E. conversidens*". In present writer's view the specimen may perhaps be ascribed to *E. fraternus*, the skull of which had not been described when Carranza and Miller read their paper. The fossil is of interest in as much as it may elucidate possible relationships between *E. fraternus*.-*E. conversidens* and *E. mexicanus*. A full description of the fossil from Guanajuato will be welcome.

Equus excelsus Leidy 1858 - Pl. 16, figs. 1-3; Pl. 17, fig. 1; Pl. 18, figs. 1-4

Synonyms: (?) *Equus major* De Kay 1848
(?) *Equus complicatus* Leidy 1858
(?) *Equus pectinatus* Cope 1899
Equus scotti Gidley 1900
Onager arellanoi Mooser 1959
Onager (Hesperohippus) hibbardi Mooser 1959
Asinus aguascalientensis Mooser 1959

This species was based on an incomplete maxillary, USNM 667, with P4/-M3/, from the Pawnee Loup Branch, Platte River, Nebraska (Pl. 16, fig. 1). The geological horizon is not exactly known but may possibly be late Irvingtonian. The teeth are rather large and the enamel pattern is derived, with narrow, elongated protocones and a richly folded enamel. The posterior palatine foramen is placed opposite M2/.

Gidley considered this species a probable synonym of *Equus complicatus*, which has page priority in Leidy's paper. However *Equus complicatus* was based on a single upper cheek tooth of uncertain age and is considered here a "nomen dubium". Gidley referred to *Equus complicatus* a partial skull from the valley of the Niobrara River in Nebraska, AMNH 2725, and stressed the similarities and differences between this species and his *Equus scotti*. In practice the difference lies in size and in the correlated relative length of the snout; however it does not exceed the range of individual variation (compare Pls. XVIII and XIX in Gidley, 1901) and a complete skull referred to *Equus scotti*, AMNH 10612, forming part of the sample on which Gidley based his species, has a condylobasal length of 586 mm and is of about the same size as the incomplete skull AMNH 2725. *Equus scotti* is therefore considered here a junior synonym of *Equus excelsus*.

This is a species of rather large size, with a heavy skull and massive teeth, with a richly plicated enamel in early stages of wear. The bones of the skull are thick, in particular the praemaxillaries and the mandibular rami; these are bluntly rounded at the upper margins of their diastems. The rostrum is broad. The upper profile of the skull is undulated, the braincase rather strongly deflected from the face, the fronto-parietal region gently convex. The narial notch is not deep, the masseteric ridge is straight. The ectoflexids of the lower molars are either shallow or moderately deep but never penetrate between metaconid and metastylid.

Equus excelsus is represented by skulls and articulated skeletons from the Rock Creek, the type locality of *Equus scotti*, and by some more or less fragmentary skulls, mandibles and postcranials from the Sheridan Beds of the Niobrara valley, Nebraska. Here it is associated with *Equus fraternus*, *Equus semiplicatus* and *Equus niobrarensis*. Separation of skulls and jaws is easy but this is not the case for postcranial bones of *Equus excelsus* and *Equus niobrarensis*. The histogram of a large sample of metatarsals from the Sheridan Beds at Gordon in the UNSM shows an even distribution. The total length of 98 specimens ranges fron 296 to 195 mm; the easily separable metatarsals of *Equus semiplicatus* were not included. The smaller specimens presumably represent *Equus fraternus*, which occurs in the fauna as a minor component. The curve shows two peaks, one (26 specimens) between 275 and 279 mm, the second (also 26 spe-

cimens) between 285 and 289, separated by a low (17 specimens). This may be evidence of the occurrence of two species of different average sizes but with partly overlapping ranges of variation. However the difference between the two peaks is small and the present observation is not fully conclusive.

Gidley figured a skeleton of his *Equus scotti* which includes parts of two individuals and remarked that the skeletons from the Rock Creek display a plumper build than the skeleton of *Equus ferus*: the head is large, the barrel long, the limbs relatively short and stout.

A late Pleistocene skull from Blanco Creek, Bee Co., Texas, TMM 31058-2, associated with human artifacts, may possibly belong to this species. Sellards (1940) referred it to *Equus fraternus* but this identification is untenable: the massive dentition and broad snout are typical of *Equus excelsus*. Moreover, a faint praeorbital pit seems to be present. The skull unfortunately was collected in pieces and was restored, so that some of its features may have been distorted. Its condylobasal length is approximately 515 mm

The following more fragmentary specimens from Irvington, California, are tentatively referred to this species.

UCMP V-3604/38571, a male palate, 4-5 years old. This was described and figured by Savage (1951) as *Equus* cf. *caballus*. The massive praemaxillaries and dentition and the broad snout conform better with *Equus excelsus*.

UCMP V-3604/128286 - A mandibular symphysis of a female 6-7 years old. The ramus is thick, with a blunt upper margin at the diastem, the incisors are broad.

UCMP V-3604/58585 - Two mandibular symphyses.

UCMP V-3604/55366, 38570, 38582, 38731 - Fragmental rami.

Equus excelsus is related to the late Blancan-early Irvingtonian *Equus idahoensis* in its massive build, forward position of the posterior palatine foramina, large dentition, broad snout (Azzaroli and Voorhies, 1993). It is more derived in the elongated protocones, richer enamel plication and in the general lack, or poor development of praeorbital pits. It also appears to be related to *Equus occidentalis* in its plump build, large teeth, broad snout and general body proportions, but differs from it in the richer plication of the tooth enamel, the retention of cups in the lower incisors, and if the restorations are correct also in the stronger deflection of the braincase relative to the snout.

Equus excelsus is a common species in the Irvingtonian. It was also reported, as *Equus scotti*, from Rancholabrean sites (Lundelius *et al.*, 1983) and Mooser and Dalquest (1975) reported it from the late Pleistocene of Aguascalientes, Mexico. However, no unequivocally identifiable skulls nor mandibles were described from Rancholabrean sites.

Equus excelsus is a species of rather heavy build. It is distinguished from other species, in particular from *E. ferus* and *E. niobrarensis*, by the massive bones of its skull, the more anterior position of the posterior palatine foramina and by its massive barrell and rather short limbs. It is distinguished from *E. occidentalis* by the closer facial angle, the more complicated pattern of its teeth and the presence of cups in its lower incisors..

Equus occidentalis Merriam 1913 - Pl. 19, figs. 1-3; Pl. 20, fig. 1; Pl. 21, figs. 1-4
Non: *Equus occidentalis* Leidy 1865

Nomenclature and type

The asphalt pits of Rancho La Brea in California yielded hundreds of bones of a rather large sized and heavily built equid. Merriam (1913) figured a skull and gave a preliminary description of this species, which he referred to *Equus occidentalis*, a species name proposed by Leidy in 1865. Remains of a similar equid occur in the asphalt pits at McKittrick, California, and were also referred to *Equus occidentalis* by Schultz (1938). Savage (1951) and Miller (1971) contended that the Rancho La Brea equid does not conform to Leidy's types of *Equus occidentalis,* few teeth which came from two different sites in California. According to Savage Leidy's species is "of Plesippine affinity" and probably of Blancan age. Rules of nomenclature impose in this case a change of name, but neither Savage nor Miller did this. *Equus merriami,* Merriam's horse, immediately comes to one's mind as appropriate. However the change of a name currently established in literature is disturbing. After Merriam many authors referred the Rancho La Brea equid to *Equus occidentalis* and this name is now deeply rooted in North American literature. Several hundred specimens have been listed and filed in collection catalogues with this name. A proposal to upset a widely estasblished tradition is unlikely to gain general consensus and may cause misunderstanding. It seems wiser for this particular case to waive the rules of nomenclature and keep the name *Equus occidentalis* as amended by Merriam, with the skull figured in his paper as the lectotype. In any case a resolution of the International Commission on Zoological Nomenclature will be welcome.

Description

Equus occidentalis is of late Pleistocene age and is represented in the asphalt pits of Rancho La Brea by a large number of skulls, jaws and postcranials representing all the parts of the skeleton, but owing to the postdepositionsl movements of the asphalt not a single articulated skeleton was found and several skulls were broken, although none appears to have been distorted to any appreciable extent. The same species occurs in the asphalt pits of McKittrick, in the same state of preservation but in smaller number. No other fossils from North America have been referred to this species but two skulls and some bones from Mexico, to be discussed later, may be referred to it.

In spite of the great abundance and good preservation of specimens no full description has been published so far. Merriam (1913) described a skull and a jaw and gave figures, at a small scale. Stock (1963) remarked that the forehead is domed, that

the body is massive and that the terminal phalanges are small. Willoughby (1974) measured a large number of bones and calculated the average proportions of the skeleton. He considered the species to be closely related to *Equus quagga* and *Equus burchelli*, and united these three species in his new subgenus *Quaggoides*, but Eisenmann (1980) contended that the skull proportions do not evidence any close affinity between the Californian and the African species.

Equus occidentalis is a species of large size and massive build. The average height at the withers is 147 cm. (Willoughby, 1974; MacFadden,1992, p. 76, gives a height of 150 cm). The length of the barrell, from the shoulder to the ischium is about 157-160 cm: The body is rather plump; the bones of the skull are massive, especially the praemaxillaries and the horizontal rami of the jaw. The angle of deflection between the face and the braincase is widely open. The barrell is massive, the limbs rather plump.

Equus occidentalis shows no affinity to either *Equus quagga* or *Equus burchelli* in its skull. It superficially recalls *Equus burchelli*, which is quite distinct from *Equus quagga* in skull features, in the bulging forehead, with the greatest convexity more or less over the orbits, and in the wavy profile, but differs in the more elongated braincase, the widely open facial angle, the rather small orbits, the narrower zygomatic arches, the slightly deeper, although variable narial notch, the thick praemaxillaries and rami, the massive teeth and the broad rostrum. There is a definite variation in the depth of the narial notch, which may lie on the anterior or on the central part of P2/; in old specimens the tooth row contracts and the angle of the notch may come to lie slightly anterior to P2/. The upper profile as a rule is markedly wavy but in some cases is almost straight, as in the old male skull shown on Pl. 19 fig. 3. The posterior palatine foramina as a rule are in a forward position, opposite to M2/, but this character is subject to variation and occasionally the foramina occur oppposite the anterior lobe of M3/.

The jaw is massive and has blunt, rounded upper edges at the diastems. The dentition is relatively large, the lower incisors are characterized by the lack of cups and the enamel pattern of the cheek teeth is unusually simple for a dentition of this size; plications of the inner fossettes are absent or poorly developed. In the upper cheek teeth protocones are moderately elongated and gently grooved lingually.

An incomplete skull from Comondu, Baja California Sur, Mexico, F:AM 116150, a female jaw, F:AM 116151, possibly of the same individual, and a metacarpal cannon, F:AM 116152, may be referred to this species. Skull and jaw represent a very old specimens and their teeth are much worn. An equally incomplete skull from Chinobampo, Sonora, Mexico, in the AMNH, Frick Collection, not catalogued, may also belong to *Equus occidentalis*. These Mexican specimens are associated with bison and are of Rancholabrean age, like the Californian fossils.

Equus occidentalis shows some affinity with *Equus excelsus* in the general shape of the skull, broad snout, large dentition and in the massive body build. It differs however in the more open facial angle, a much less plicated emamel in its teeth, the lack of cups in the lower incisors and possibly a more elongated braincase, although this feature is not very apparent. The dentition, in spite of its poor complexity, does not seem to be primitive: the teeth are of large size and the protocones of the upper cheek teeth are elongated.

Willoughby (1974) gave the following measurements of *Equus occidentalis*: Skull (2 adult specimens, ♂), length from prosthion to akrokranion, 644 and 613 mm; scapula 362 mm; humerus 314 mm; radius 352 mm; metacarpal cannon 253 mm; femur 437 mm; tibia 388 mm; metatarsal cannon 292 mm.

Doubtful species

Equus crenidens Cope 1884

Cope (1889) based this species on a fragment of a maxillary with three praemolars from the late Pleistocene of Tequixquiac, Mexico. They are characterized by a large size, strongly plicated enamel in the inner fossettes and remarkably short protocones,

Hibbard (1955) was unable to find Cope's type and defined a neotype, a fragment of a maxillary with the right P2/-P3/. He placed this species in the genus *Plesippus* and referred to it a right P4/(?) of another individual and the left P2/-P3/ of a third individual.

The teeth of the right side are all characterized by a richly plicated enamel, but the protocones are short, similar to those of *Equus simplicidens* and *Equus stenonis*; the "plis caballins" are strong. The two left praemolars, which belong to an old individual, have a much simpler enamel pattern, very short protocones and lack any trace of the "plis caballins".

Acconding to Hibbard *Equus crenidens* "exhibits closer relationships to the subgenus *Plesippus* than to the subgenus *Equus* (...) revealed by the small oval protocones, the slightly concave enamel borders between parastyle and mesostyle, and the slight curvature of the molars." A derived feature, not pointed out by Hibbard, is represented by the doubled mesostyles of the neotype; in the other specimens this feature is less marked.

The extremely primitive structure of the protocone is surprising in an equid of late Pleistocene age, but very short procones are also occasionally observed in the living *Equus grévyi*, in which individual variation is great. *Equus crenidens* may possibly be a valid species but is still poorly known.

Equus giganteus Gidley 1901

This species was based on a single tooth from Southwestern Texas. The exact locality and age were not stated. It is characterized by a very large size, the enamel of the inner fossettes is moderately plicated and becomes more complicated 2 cm. above the grinding surface, where the tooth was sectioned. The protocone is very short and the hypocone is prominent.

The teeth of *Equus mexicanus* and *Equus occidentalis* nearly attain the size of this tooth but differ in their elongated protocones and less prominent hypocones. *Equus mexicanus* also differs in its more richly plicated enamel.

Because of its primitive features (short protocone, prominent hypocone) Savage (1951) considered *Equus giganteus* "a valid species, possibly of plesippine affinity". It may perhaps belong to *Equus enormis* (Downs and Miller, 1994) but the holotype is not sufficiently characteristic.

Equus bautistensis Frick 1921

This species is represented by dentitions and limb bones. The types come from the lacustrine deposits of Bautista Creek, Riverside Co., California. The teeth are of rather large size and are derived in their elongated protocones and plicated enamel. Some protocones show a distinct lingual groove. The ectoflexids of the lower molars are shallow. The limbs are of medium size and rather massive.

Although Savage (1951) considered *Equus bautistensis* a valid species, it is very poorly characterized because of the extreme variability of its teeth. The length of the protocones of the upper cheek teeth, the development of the lingual groove, the plications of the inner enamel are subject to such variations that some specimens appear derived in a degree comparable to *Equus ferus* while others display a more primitive pattern reminiscent of *Equus simplicidens* or *Equus idahoensis* (Frick, 1921, folder 2, figs. 1, 2). The same may be said of the linguaflexids of the lower cheek teeth, which may be simply pointed as in zebras or broadly rounded as in caballines (ibid., figs. 19-22). Given the lack of cranial elements *Equus bautistensis* will be considered here a "nomen dubium".

Equus parastylidens Mooser 1959

This species was based on two mandibular fragments from the late Pleistocene of Aguascalientes, Mexico: FC 107, the type, a right ramus with P/2-P/4; FC 677, referred specimen, a right ramus with P/4-M/3. The teeth are of large size and are characterized by the occurrence of well developed parastylids in the third and fourth praemolars; a vestigial parastylid is also said to occur in the first molar. The plication of the enamel is rather simple, the ectoflexids of the lower molars are deep, the linguaflexids broadly rounded. Mooser and Dalquest (1975) proposed for this species the new genus *Parastylidequus*, but this does not solve the problem of its systematic position, which remains indeterminate. This species may possibly have been based on two abnormal specimens provided with parastyles.

CLOSING REMARKS - OUTLINES OF THE EVOLUTION OF *EQUUS*

The list of North American species described in the present paper may not be complete. Some doubtful species have been discussed; there may be others which are known only from poor, fragmental remains. In view of the large number of species recognized it may however be assumed that additional species, if any, should be few.

Species have been distinguished on the ground of their sizes and the morphologies of their skulls, dentitions and limb bones.

Dinohippus is the direct forerunner of *Equus* and the transition between the two genera took place around the end of the Hemphillian and the beginning of the Blancan. It was a gradual process. *Dinohippus leidyanus*, of the late Hemphillian, with a stature of 115-120 cm at the withers, was already a miniature horse. The only remarkable differences in its skeleton, apart from the size, are the lengths of the lateral metapodials of the limbs, which extend to the distal extremity of the central metapodial and terminate with rounded, laterally compressed expansions (Azzaroli, 1988), and to a lesser degree in the moderate lateral expansion of the pelvis. This species was followed towards the end of the Hemphillian by the more poorly represented *D. mexicanus* Lance (MacFadden, 1984).

The oldest record of *Equus* described so far is possibly in the fauna of Las Tunas, Baja California (Miller, 1980). It consists of fragmentary remains: dentitions and limb bones. There are no skulls. Specimens display a rather wide variation in size but fall in the range of *Equus*, and so they were named.

Equus simplicidens, the oldest well documented species, is represented in the U.S. from Texas to Idaho by skulls, limb bones and some skeletons (Azzaroli and Voorhies, 1993). Its skull is an enlarged replica of the skull of *Dinohippus*, with a longer muzzle as an effect of scaling. It was characterized by a rather strong deflection of the braincase relative to the face and by the occurrence of praeorbital and buccinator pits. Its stature at the withers was around 140 cm. This species seems to have been the only forerunner of all subsequent species.

Differentiation began during the later part of the Blancan. Azzaroli and Voorhies gave evidence of the existence, alongside *E. simplicidens*, of at least two species of smaller size, unfortunately represented only by few teeth and limb bones. One of these had slender, elongated metapodials, the other was shorter limbed. They both may have been the forerunners of Pleistocene species. The slender limbed equid may have given origin to *E. semiplicatus* and its relatives, the species with shorter limbs was possibly the forerunner of *E. fraternus, E. conversidens* and their South American relatives. Owing to the scantiness of the record these speculations are however to be taken with care.

Still in the middle Pliocene *Equus* began to disperse to Eurasia. The Chinese *E. sanmeniensis* Teilhard and Piveteau 1930, and *E. livenzovensis* Bajgusheva 1978 from the late Pliocene of Europe are only variants, of larger size, of *E. simplicidens*. In China there was also a smaller sized equid, *E. teilhardi* Eisenmann 1975.

In the later Pliocene species differentiation was more marked. A characteristic, now extinct branch is represented by *E. stenonis* and its descendants. It was distinguished by a skull with an elongated

rostrum and a deep indentation of the narial notch. It retained the rather strong deflection between braincase and rostrum and the facial pits. The size as an average was larger than that of *E. simplicidens*; the posterior palatine foramina, which were placed opposite the M2/s in *E. simplicidens*, were here shifted backwards, opposite the M3/s, as a result of the elongation of the bony palate. The dentition remained largely primitive and was generally characterized by short protocones in its upper cheek teeth, but more elongated protocones appeared sporadically as a result of intraspecific variation (Azzaroli, 1965; Azzaroli and Voorhies, 1993). The range of this species extended from North America to China (Azzaroli, 1982) and throughout Asia to western Europe, as far as Spain (Eisenmann 1980). This lineage survived in North America into the early Irvingtonian with *E. enormis* Downs and Miller, 1994. It survived longer, into the early Middle Pleistocene (Olyorian) of North-Eastern Siberia with *E. verae* (Sher 1971, 1986) and *E. coliemensis* (Lazarev, 1980). Unlike *E. verae,* Lazarev's species is also represented by a damaged skull which shows stenonid features in its elongated rostrum and in the dentition. Lazarev and Tomskaya (1987) pointed out the differences of this species from *E. verae* in the ear region (not figured by Sher), but these may perhaps not exceed individual variations. The same strain survived in Europe, still in the Villafranchian, with *E. stenonis* (the holotype of this species belongs to the early Pleistocene: Azzaroli, 1965), with the smaller *E. stehlini* Azzaroli 1965 and with the large sized *E. bressanus* Boule, and into the early Middle Pleistocene (Galerian) with *E. süssenbornensis* Wüst, with a highly wrinkled enamel in its teeth (Azzaroli, 1990, 1996) It may be pointed out however that the skulls of *E. verae*, *E. bressanus* and *E. süssenbornensis* are not known, and the only skull of *E. coliemensis* is damaged.

The two Indian species of possibly late Pliocene to early Pleistocene age, *E. sivalensis* and *E. namadicus* Falconer and Cautley (Hooijer, 1949, Azzaroli, 1966, 1982) are represented by few skulls. In spite of the somewhat longer protocones of their upper cheek teeth they display the same deep narial notch, the deflected braincase and the facial pits which characterize *E. stenonis,* and are phylogenetically linked to it. Maybe they crossed the Himalayan range following some valley at a time when the mountains were less elevated and the landscape less rugged than it is at present. The appearance of *Equus* in the Indian subcontinent dates from 2.5 My ago (Azzaroli and Napoleone, 1981; Tandon *et al.*, 1984, Ranga Rao *et al.*, 1988), but the stratigraphical position of the extant skulls is not known and the specific identity of the earliest equids in India remains problematic.

The history of later Pleistocene strains is discontinuous and more difficult to trace. The North American Pleistocene radiation was remarkably rich. *Equus simplicidens* may perhaps have given origin, beyond *E. stenonis*, to the sturdy *Equus idahoensis,* although evidence on this score is scanty. This species is represented only by two incomplete skulls. It lived during the final Blancan and the earliest Irvingtonian and is distinguished by a massive build, large teeth with a thick cement cover and with plications that are somewhat intermediate between those of *E. simplicidens* and those of more derived species, and by the occurrence of a small, but distinct praeorbital pit, an unmistakably primitive feature. Its limbs were rather massive (Azzaroli and Voorhies, 1993).

The massive skull and body build of this species suggests that it may possibly have given origin to the heavily built *E. excelsus* and *E. occidentalis*, in which the praeorbital pit was lost. It may perhaps have given origin, independently, to *E. ferus* and *E. niobrarensis*; this assumption however is far from certain, it is based on the observation that no other early Irvingtonian fossils known so far display closer affinities with these two species.

The first appearance of *E. niobrarensis* seems to date from the early Irvingtonian. Dalquest (1967) described two tooth rows from the Slaton local fauna of Texas.. It was common during the later Irvingtonian and survived into the Rancholabrean, where it has been recorded from Fort Qu'Appelle (Khan, 1979) and in the Cedazo fauna of Mexico (Mooser and Dalquest, 1975). Its relative *E. lambei* is of Rancholabrean age.

Equus ferus lived in North America during the Irvingtonian and Rancholabrean. Its first appearance may have been in the Early Irvingtonian Red Cloud Fm., although some doubt remains owing to the incompleteness of the record. It dispersed widely in Eurasia. Several species names have been proposed for horses ranging from Siberia and Mongolia to Western Europe: *E. przewalskii* Poljakov, *E. marxi* Von Reichenau, *E. steinheimensis* Von Reichenau, *E. mosbachensis* Von Reichenau, *E. taubachensis* Freudenberg, *E. simionescui* Radulesco and Samson, *E. nordostensis* Rusanov, *E. orientalis* Rusanov, *E. lenensis* Rusanov. They possibly represent only subspecies of *E. ferus.* The widespread belief that body size of *E. ferus* decreased from the middle to the late Quaternary is not generally valid. Schwarz (1927) in fact described a general reduction in size of European horses from the middle to the late Pleistocene and Lazarev (1980, fig. 45) pointed out a similar decline from the middle Pleistocene *E. nordostensis* to the younger *E. verae,* but in the late Pleistocene of Italy, in the Val di Chiana near Arezzo, Tuscany, and at San Sidero, Lecce province in the South-East of the peninsula, horses of large size are dominant. A male skeleton from San Sidero, compiled from two individuals, measures 154 cm at the withers, i.e. its stature in life was 158-160 cm. The skeletal size of the horses from Dereivka, one of the oldest human settlements with domesticated horses, varied between approximately 137 cm (the majority) to about 145 cm (Bibikova, 1986). The time range of this species in Eurasia extended from little less than 1 Ma (Azzaroli, 1983) to the Holocene.

The later Pleistocene, short limbed species *Equus fraternus* and *Equus conversidens* may possibly have descended from the poorly known, short legged equid of the middle Blancan. The time range of *E. fraternus* extended through the Irvingtonian and Rancholabrean. It also dispersed to South America, where it gave origin to a rich radiation,

singularly uniform in its morphology (Azzaroli, 1992). The first appearance of its descendants in Southern America, at Tarija in Bolivia, has been dated approximately to 700 kyr. (MacFadden and Azzaroli, 1987). In this continent it dispersed widely during the later Pleistocene and Holocene, in the highlands and in the plains and was also recorded from the high latitudes of Southern Chile.

Its close relative *E. conversidens* seems to have been restricted to the later Pleistocene of the southern United States and Mexico.

Equus semiplicatus and *Equus francisci* may have been derived from the middle Blancan species with elongated, slender limbs (? *Equus cumminsii* Cope 1893; see Azzaroli and Voorhies, 1993). It may have given rise in its turn, with the loss of facial pits, to the living Asian hemiones and possibly to the fossil European *E. altidens* Von Reichenau, and perhaps also to *E. hydruntinus* Regalia, although this species differs in the features of its dentition. The first record of hemione-like equids in central Asia dates from about 1 Ma (Azzaroli, 1983). It may be remarked that the skulls of *E. altidens* and *E. hydruntinus* are not known. Both *E. semiplicatus* and hemiones are characterized by a rather small skull. In the American species the rostrum is rather deep, and so it is in hemiones of Central Asia. These species also share the retention of cups in their lower incisors, the slender limbs and the lack, or poor development of a bony ridge above the distal keel on the volar face of their metapodials, a feature which also occurs in *E. hydruntinus*. This ridge is well developed in other living species, including the less slender African asses; it is also present in Pleistocene or Holocene asses of the Middle East. It may be remarked in this context that hemiones have a wide range through central Asia, a range which extended to western Asia until historical rimes. Xenophon relates that onagers were hunted in Syria, and in the second book of the Iliad Homer mentions a tribe from northern Anatolia, the *Henetoi* (= *Veneti*), who bred "half-asses" (Azzaroli, 1985). These have sometimes been interpreted as mules, but Homer speaks of a breed, *"hemionon genos"*, and there cannot be a breed of hybrids.

A peculiarity of the West Indian subspecies *khur* Lesson 1827 lies in its skull, which is similar to that of hemiones of Central Asia except in its muzzle, which tapers towards the snout (Azzaroli, 1966; compare Pls. 16-17 with Pls. 19-20. In this paper the author was misled by the labels of the British Museum of Natural History, which identify, or identified until not long ago as *kiang* two skulls which actually belong to domestic ponies; one of them is, or was, even labelled as the type of this species).

The history of asses is poorly known. An ass-like equid, *E.graziosii*, is represented by a skull, several jaws and few postcranial bones in the late Pleistocene of eastern Tuscany, central Italy (Azzaroli, 1979).

The first appearance of *Equus* in Africa dates from approximately 2 My B.P. At this time a species with a large head, reminiscent of the present day *E. grevyi* Oustalet 1882, was dominant. It was called *E. capensis* by Broom in 1909 on the basis of a fragmental lower dentition from Yzerplaats, Maitland district, Cape province, and *E. olduwayensis* by Hopwood in 1937 on a jaw from the Olduvai gorge. The fossils described by Hopwood were stored in München and were destroyed during the second World War. A partly restored male skull referred to *E. capensis* from Elandsfontein in the Cape province was figured by Churcher (1986). Much better preserved is a fine skull of a female about 2-3 years old from Koobi Fora. Eisenmann (1983) based on it the new species *E. koobiforensis*, which may possibly be conspecific with the taxa mentioned above; in the figures given by Eisenmann it can hardly be distinguished from the skull of *E. grévyi.* This specimen is damaged in its rostral portion: the right praemaxillary and the anterior part of the nasal bones are missing, the occipital crest and the auditory ducts are also damaged. The angle between the rostrum and the braincase is widely open, differentiating this skull from those of *E. simplicidens* nd *E. sanmeniensis*. The left maxillary preserves the second and third milk teeth and the third molars are beginning to erupt. The size is large: the basilar length is 577 mm; the condylobasal length and the length from akrocranion to prosthion are not given. The teeth were not figured in detail, but other dentitions from the same area were figured. Two tooth rows and seven isolated cheek teeth referred to the same species are similar to those of *E. capensis* and *E. olduvaiensis*; they also recall the dentition of *E. stenonis* and show moderately elongated protocones, which also occur occasionally in *E. grévyi*. Metapodials referable to this species were not found at Koobi Fora. The skull comes from the *Notochoerus scotti* zone, referred to the terminal Pliocene (Harris, 1983).

Skulls and postcranial bones reveal the widespread occurrence in Africa of a species of large size, closely similar to the present day *E. grevyi*, which is now reduced to a small area extending from Kenya to Ethiopia (Churcher, 1993; this species has also been recorded from the valley of the Awash river in central Ethiopia). The other species, *E. zebra* L., *E. burchelli* Gray 1825 and maybe *E. quagga* Gmelin 1788 are scantily represented in deposits of the late Pleistocene. Contrary to a widespread belief, *E. quagga* is markedly different in its features from both *E. zebra* and *E. burchelli* (Azzaroli and Stanyon, 1991).

A more puzzling fossil is a metatarsal cannon of small size and very slender proportions fom Olduvai Bed 2, which Churcher (1982) interpreted as a possible ancestor of living asses. Fossil skulls referable to asses have not been described from either Africa or Asia.

In spite of their rather uniform size and body build equids displayed a remarkable capacity of expansion. They invaded all continents, except Australia, and their species became adapted to extreme conditions, from arid deserts, with asses and hemiones, to tropical bush and savannahs inhabited by zebras, the high plateaus of the Andes and Tibet, the temperate belts and the extremely cold climates of Northern Siberia and of Southern Chile. Only the most rugged mountains and dense forests remained outside their living areas.

PLATE 1

Fig. 1 - *Equus ferus.* Skull. UCMP 32879/V-3605. Irvington, Calif., 1/3.
Fig. 2 - Id., lower tooth row. UCMP 33521/V-3107 - Rancholabrean, Puerto Creek, Stanislaus Co., Calif., nat. size.

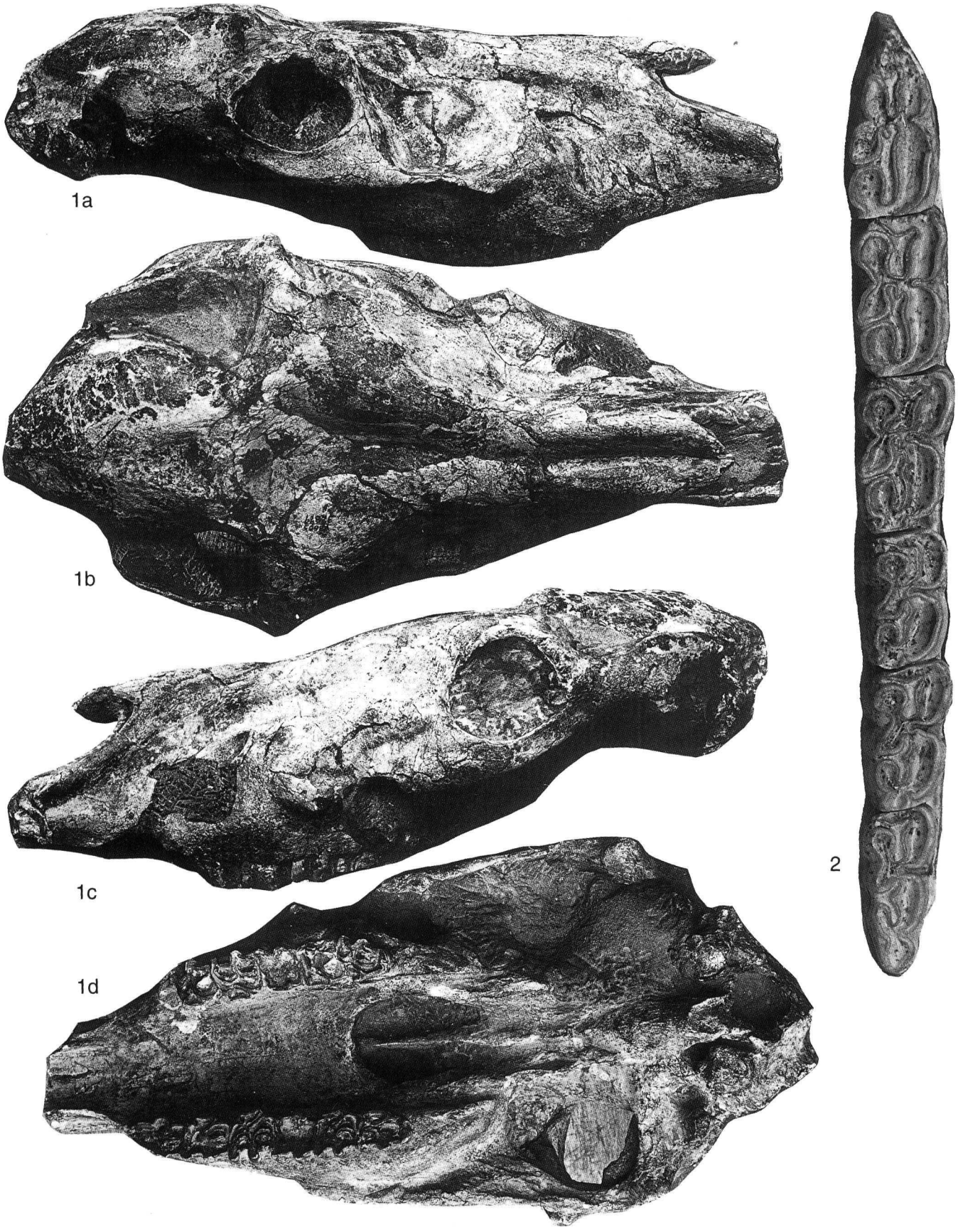

1a
1b
1c
1d
2

PLATE 2

Fig. 1a-c - *Equus ferus (?)*, ♂, UNSM 93078. Lower jaw, 1/3, and details of incisors and cheek teeth, nat. size. Ferry Gravel Pit, Red Cloud Fm., Nebraska, early Irvingtonian.
Fig. 2a,b - Id., ♂. Left lower and upper cheek teeth, F:AM 60009. Fairbanks, Cripple Creek, Alaska.

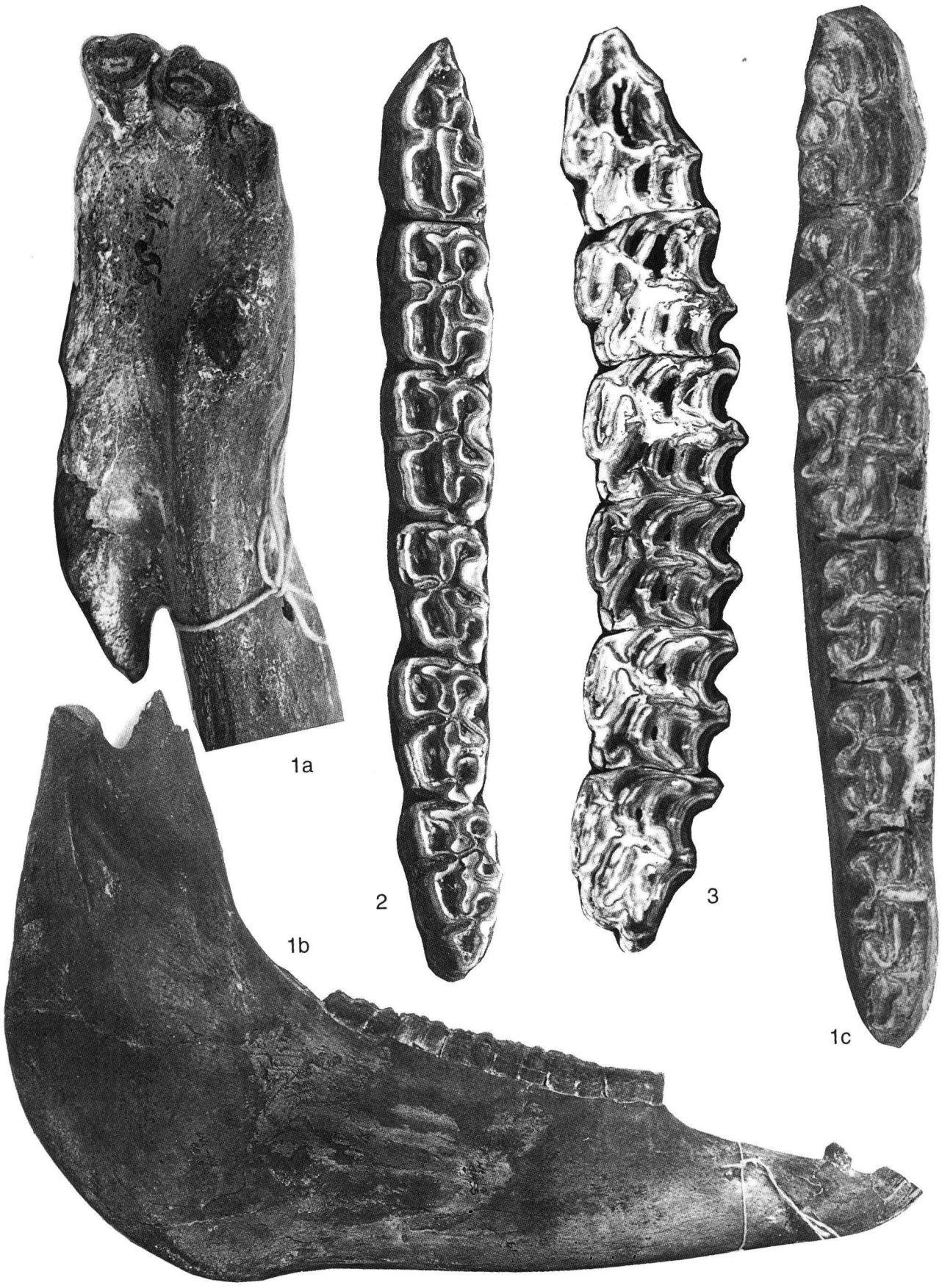

1a
2
3
1b
1c

PLATE 3

Fig. 1a,b - *Equus niobrarensis*, ♂, UNSM 5980. Late Irvingtonian, Sheridan Beds, Gordon, Nebraska. Skull, 1/3, and left cheek teeth, nat. size.
Fig. 2a,b - Id., ♂, UNSM 9417. Gordon, Sheridan Beds, Nebraska. Lower jaw, 1/3, and incisors, nat. size.

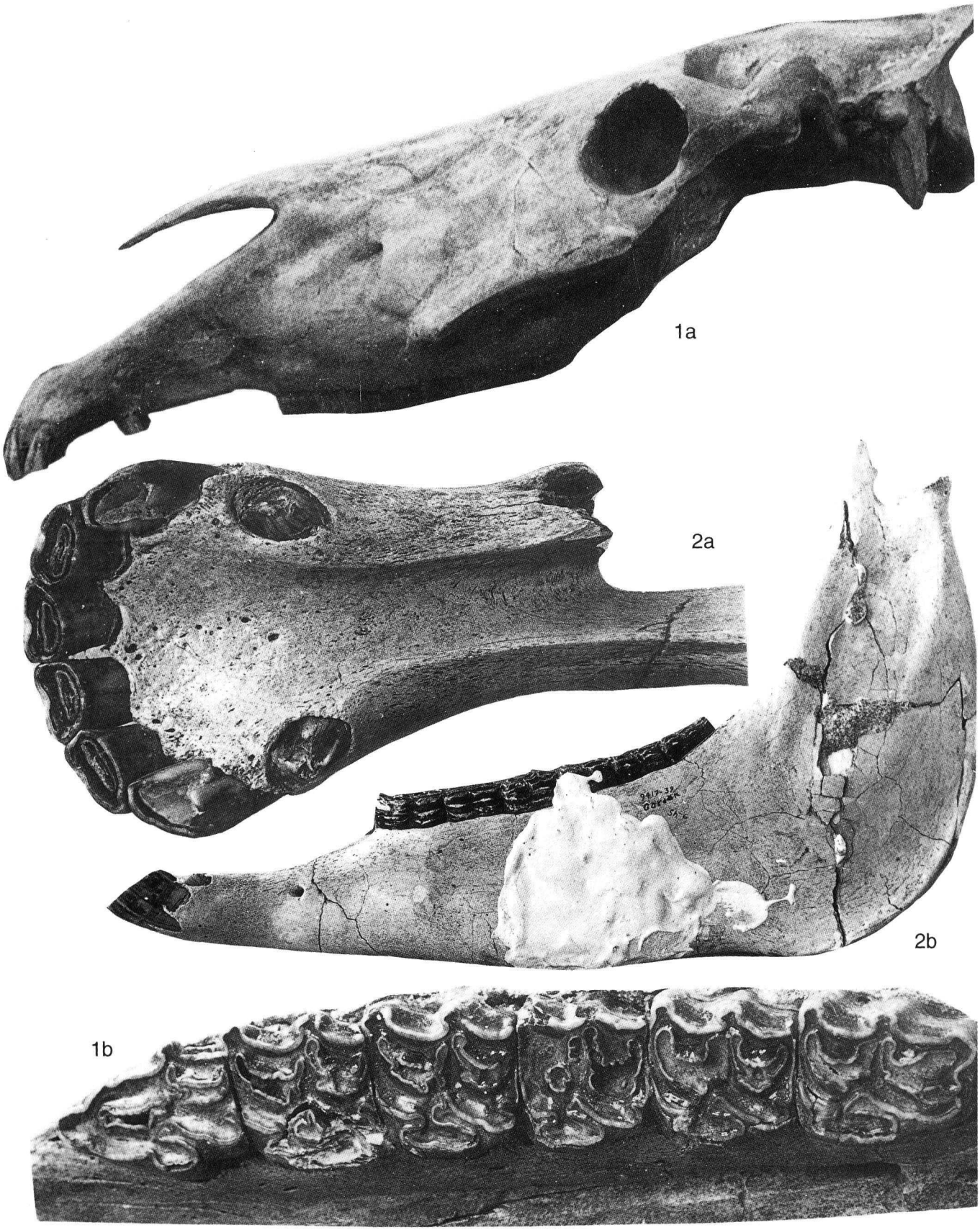

1a
2a
2b
1b

PLATE 4

Fig. 1a,b - *Equus niobrarensis*, ♂. UNSM 5980, Sheridan Beds, Gordon. Skull, upper and lower views, 1/3.
Fif. 2 - Id., ♂. UNSM 9417, Gordon, Saheridan Beds, Nebraska. Lower tooth row, nat. size.


1a
1b
2

PLATE 5

Fig. 1a-c - *Equus niobrarensis*, ♂. UNSM 5982, Sheridan Beds, Gordon, Skull, 1/3.

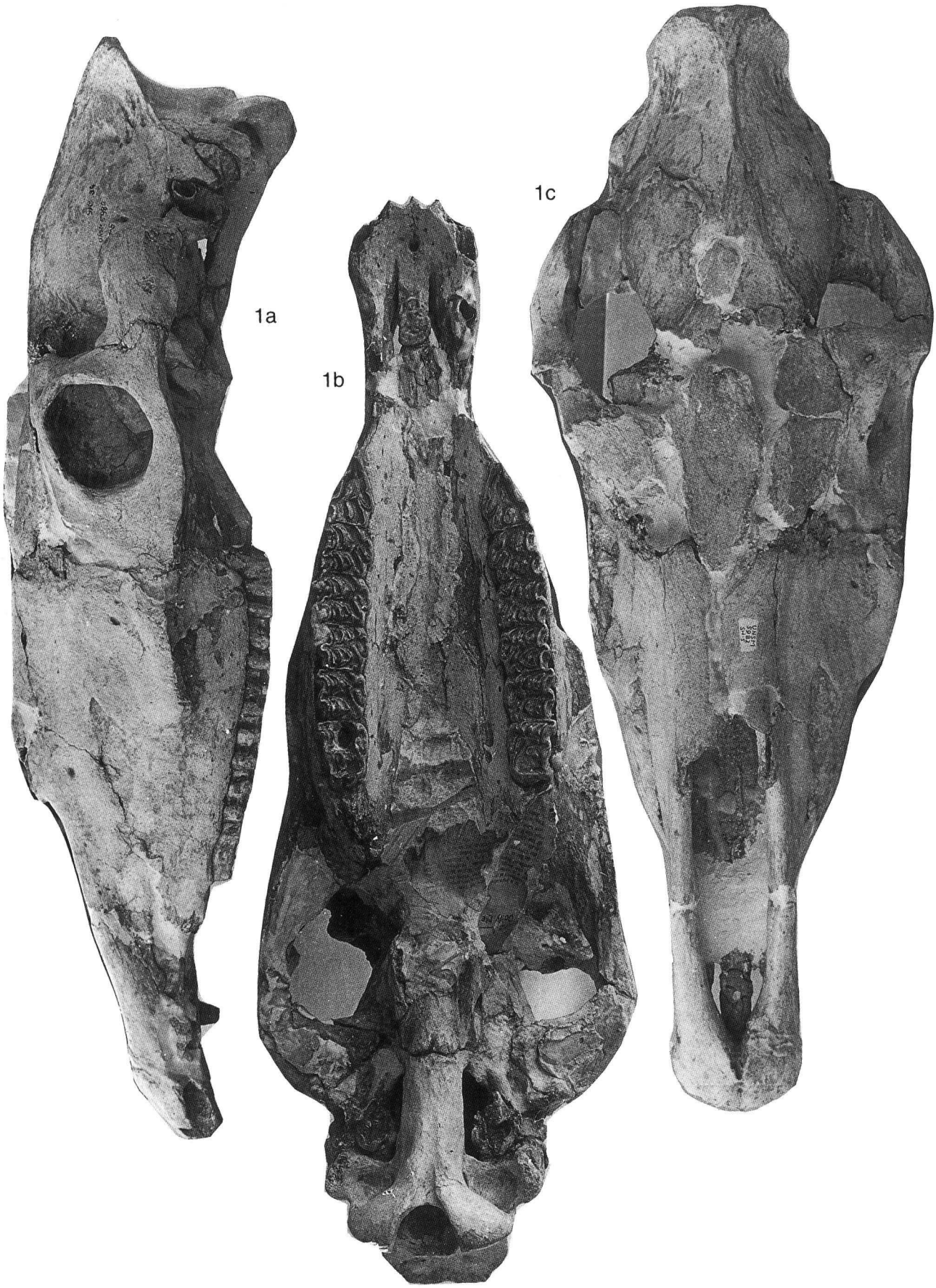

1a
1b
1c

PLATE 6

Figs. 1a-c - *Equus niobrarensis*. ♂, juv. UNSM 1346, Sheridan Beds, Hay Springs. Skull, 1/3.


1a
1b
1c
1346

PLATE 7

Fig. 1 - *Equus niobrarensis,* juv., UNSM 1346 - Palate, nat. size, jaw, 1/3, and lower cheek teeth, nat. size.

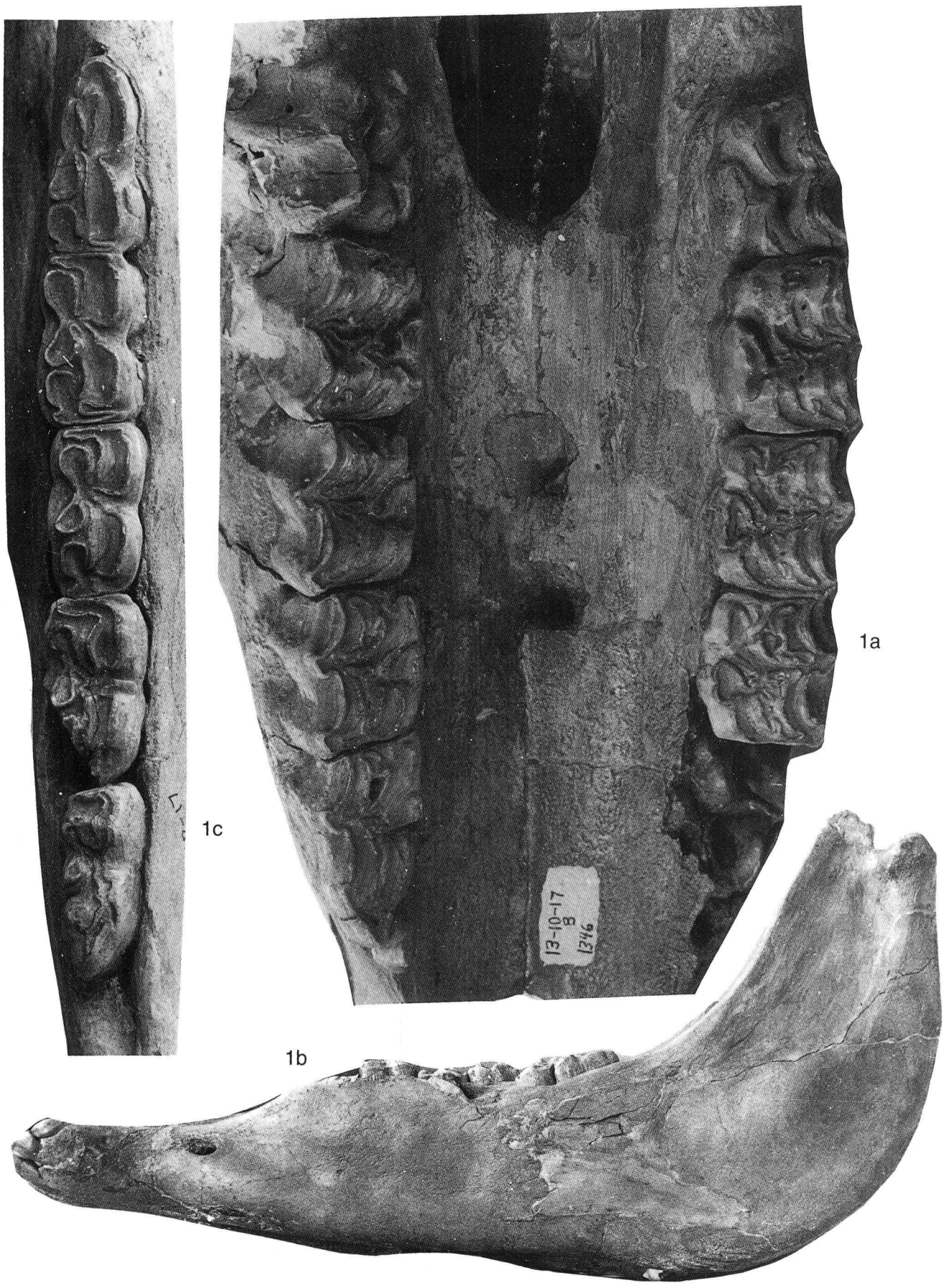

1a
1c
1b

PLATE 8

Fig. 1 - *Equus semiplicatus,* F:AM 116156, ♀. Near Dalhart, Texas, ?Late Irvingtonian. Upper cheek teeth, nat. size.
Fig. 2 - Id., F:AM 116506, lower cheek teeth, nat. size.
Fig. 3 - Id., F:AM 116159, lower cheek teeth, nat. size.
Fig. 4a-c - *Equus mexicanus,* LACM 306/123911, lower jaw, 1/3, and dentition, nat. size. Barranca del Muerto, Mexico, late Pleis

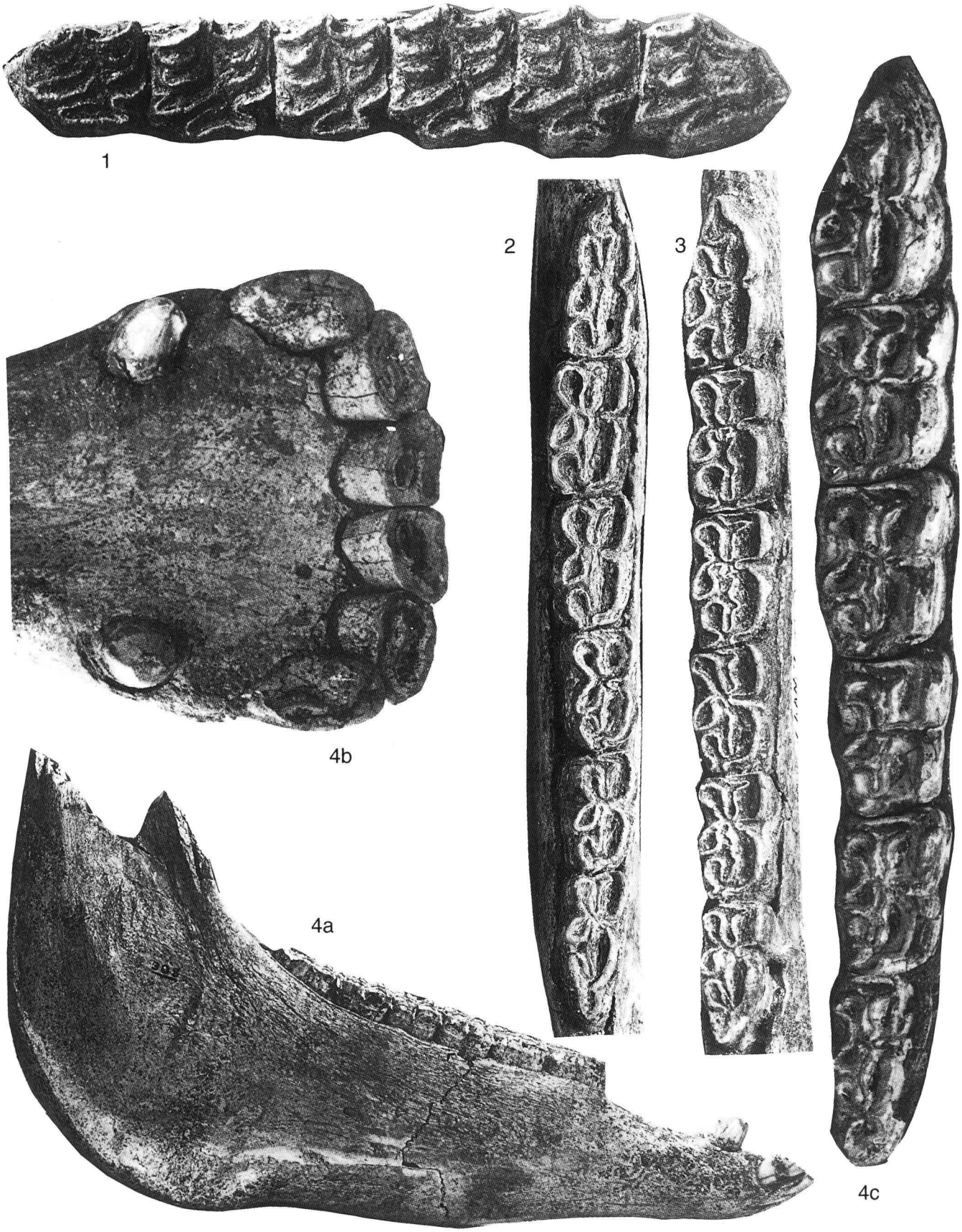

1
2
3
4b
4a
4c

PLATE 9

Fig. 1a-c - *Equus semiplicatus*, ♀, F:AM 116156, skull, 1/3. Near Dalhart, Texas, ?late Irvingtonian.
Fig. 2a,b - Id., ♀, F:AM 116159, lower jaw, 1/3, and incisors, nat. size.

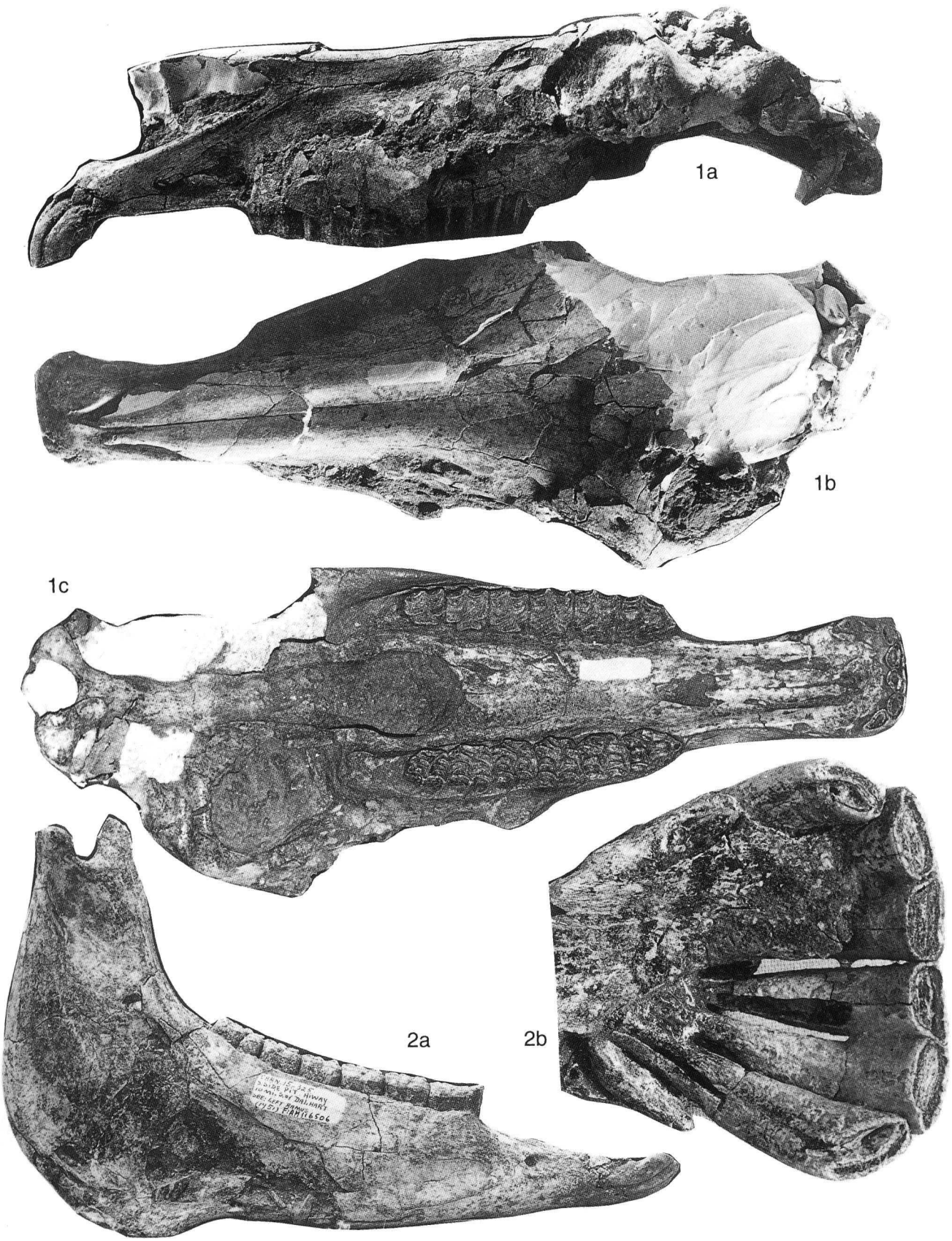

1a
1b
1c
2a
2b

PLATE 10

Fig. 1 - *Equus semiplicatus*, ♀, F:AM 116158. Near Dalhart, Texas, ?late Irvingtonian. Skull, 1/3.
Fig. 2a-d - Id., AMNH 8600, ♀. Rock Creek, Texas, Irvingtonian. Skull, 1/3.

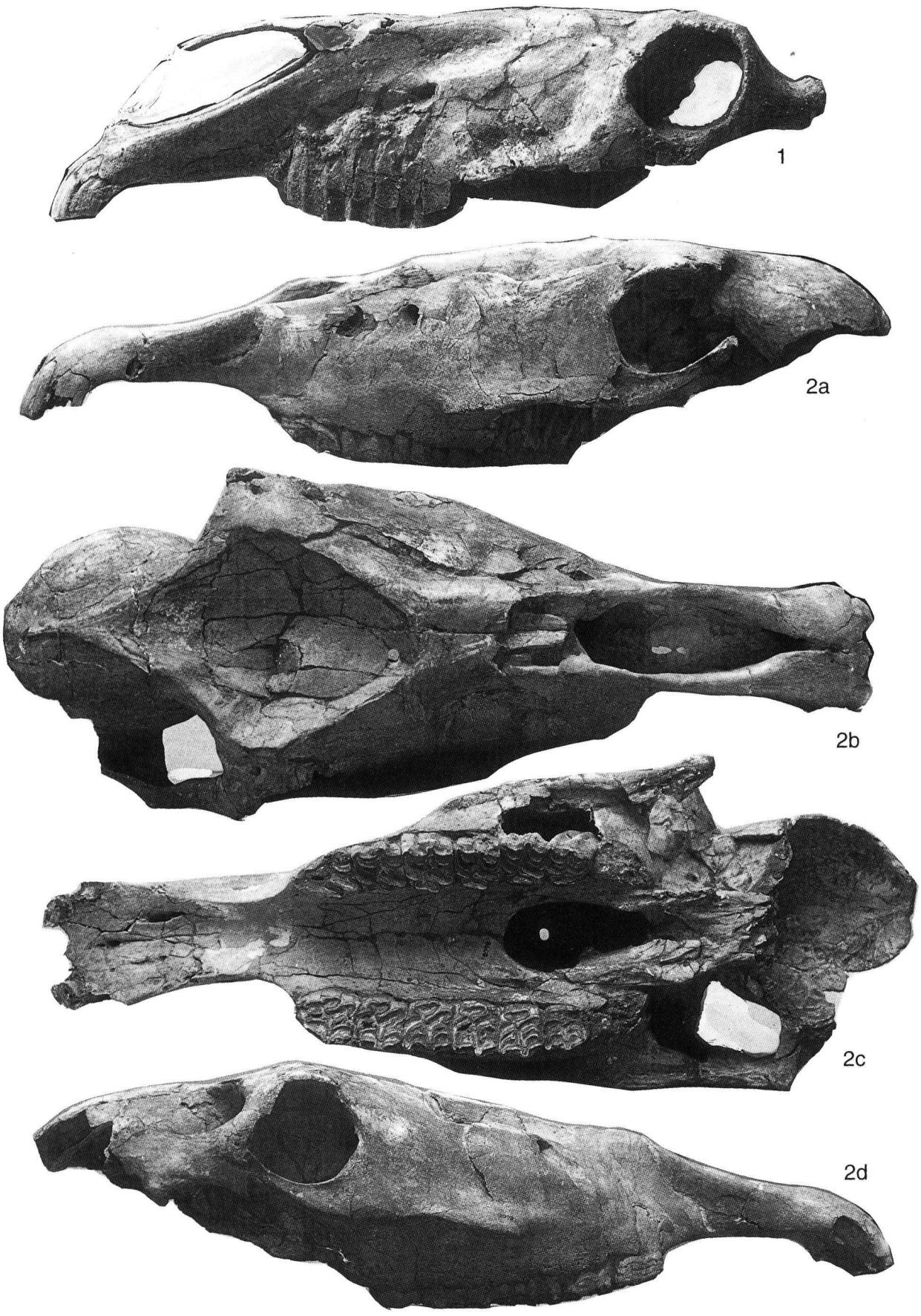

1
2a
2b
2c
2d

PLATE 11

Fig. 1a-d - *Equus francisci*, ♂. Skull. Fauna Cedazo, Central Mexico, late Pleistocene. Total length of specimen 305 mm. Photo kindly supplied by dr. W. Dalquest.

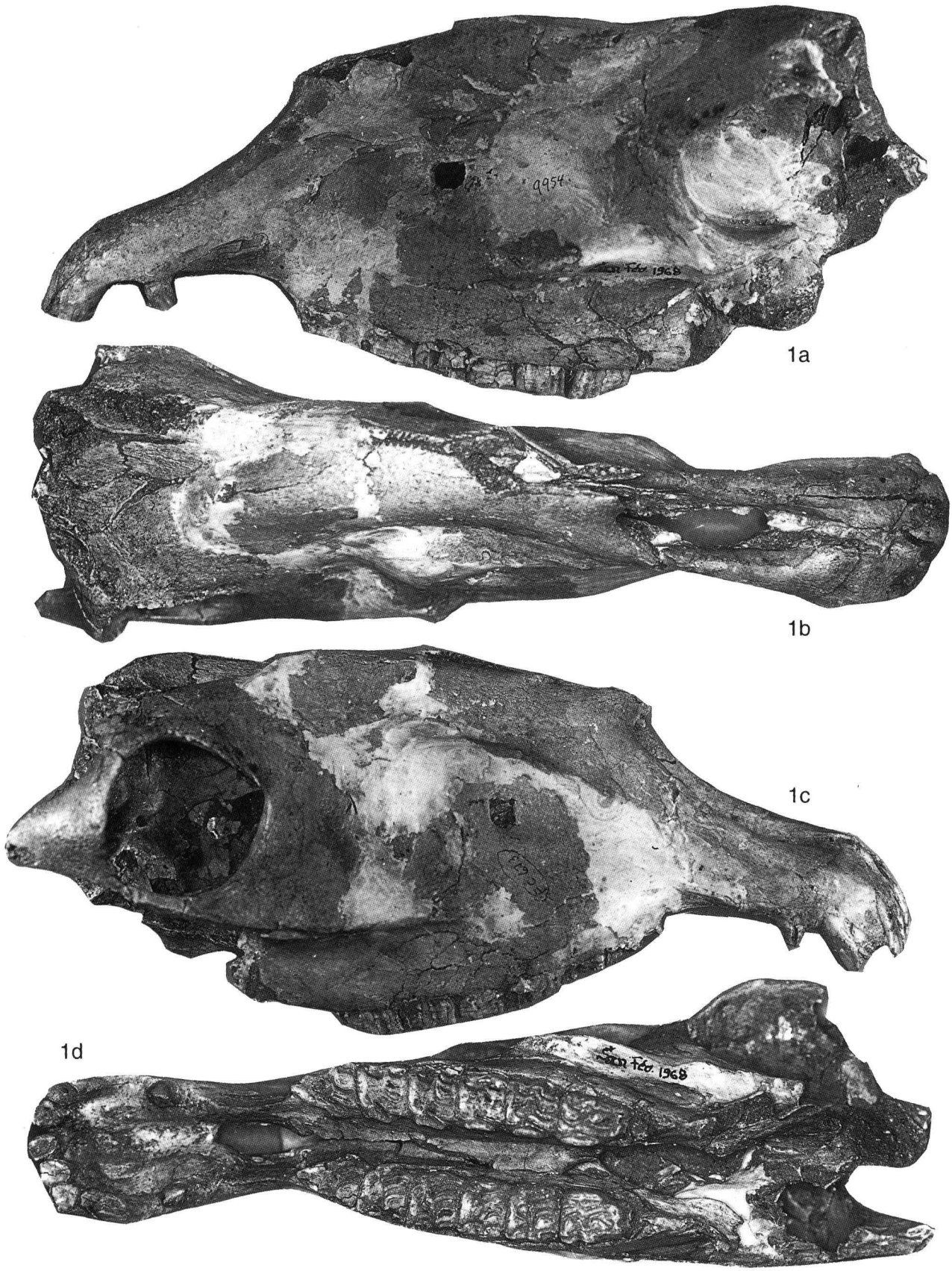

1a
1b
1c
1d

PLATE 12

Fig. 1a-c - *Equus fraternus*, ♂, F:AM 116143. Rancholabrean, Itchetucknee, Florida. Skull, 1/3.

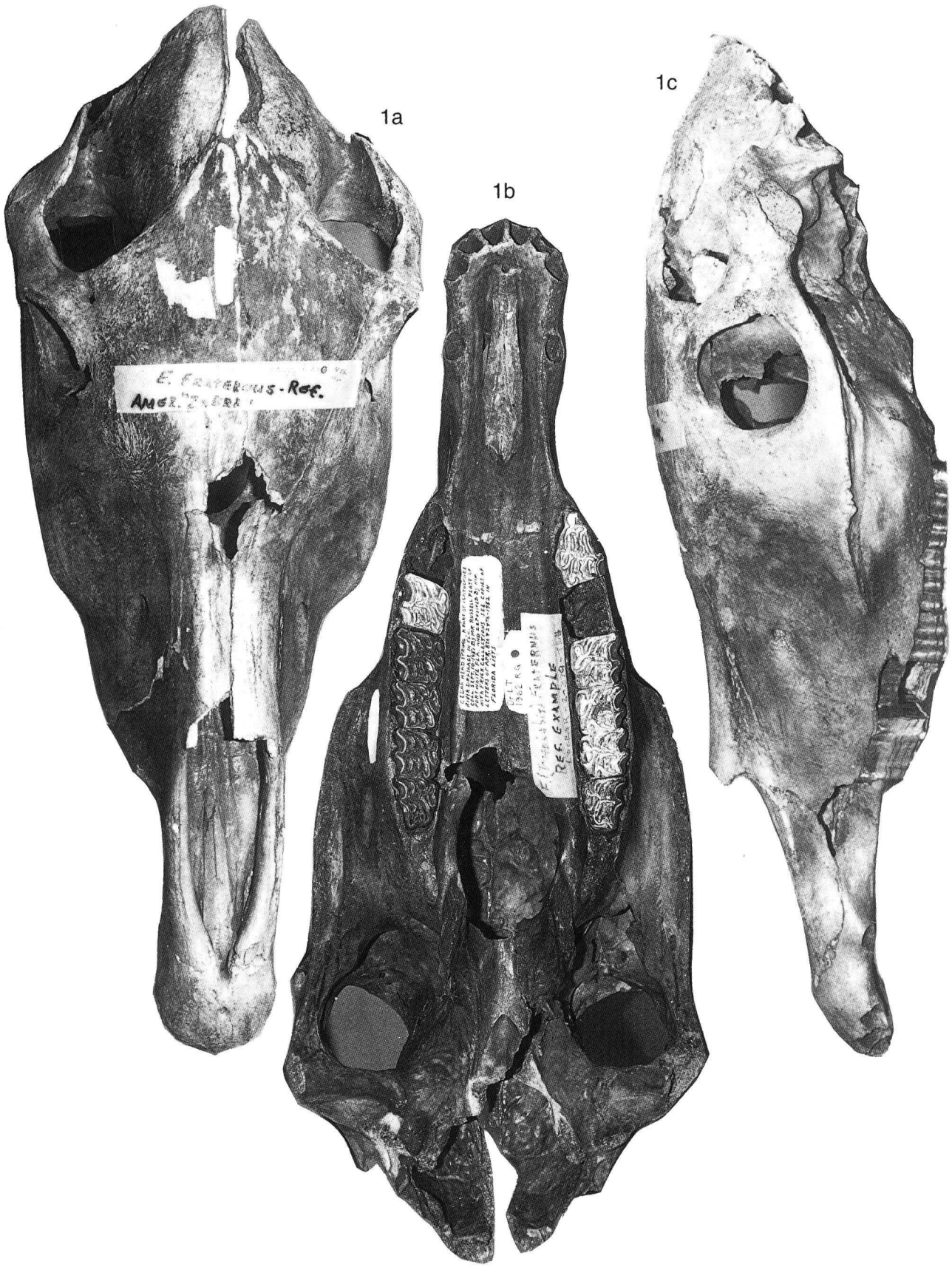

1a
1b
1c
REF. EXAMPLE

PLATE 13

Fig. 1a,b - *Equus fraternus*, ♂ (cast), AMNH 95588 Irvingtonian, Pool Branch, Florida, Skull, 1/3 and cheek teeth, nat. size.
Fig. 2 - Id., (cast), AMNH 95588a. Irvingtonian, Pool Branch, Florida. Left lower cheek teeth, nat. size.
Fig. 3 - Id., F:AM 116143. Rancholabrean, Itchetucknee, Florida, right upper cheek teeth, nat. size.
Fig. 4 - Id., F:AM 104964. Irvingtonian, Cast of a right lower tooth row. El Jobean, Charlotte Co., Florida. nat. size.

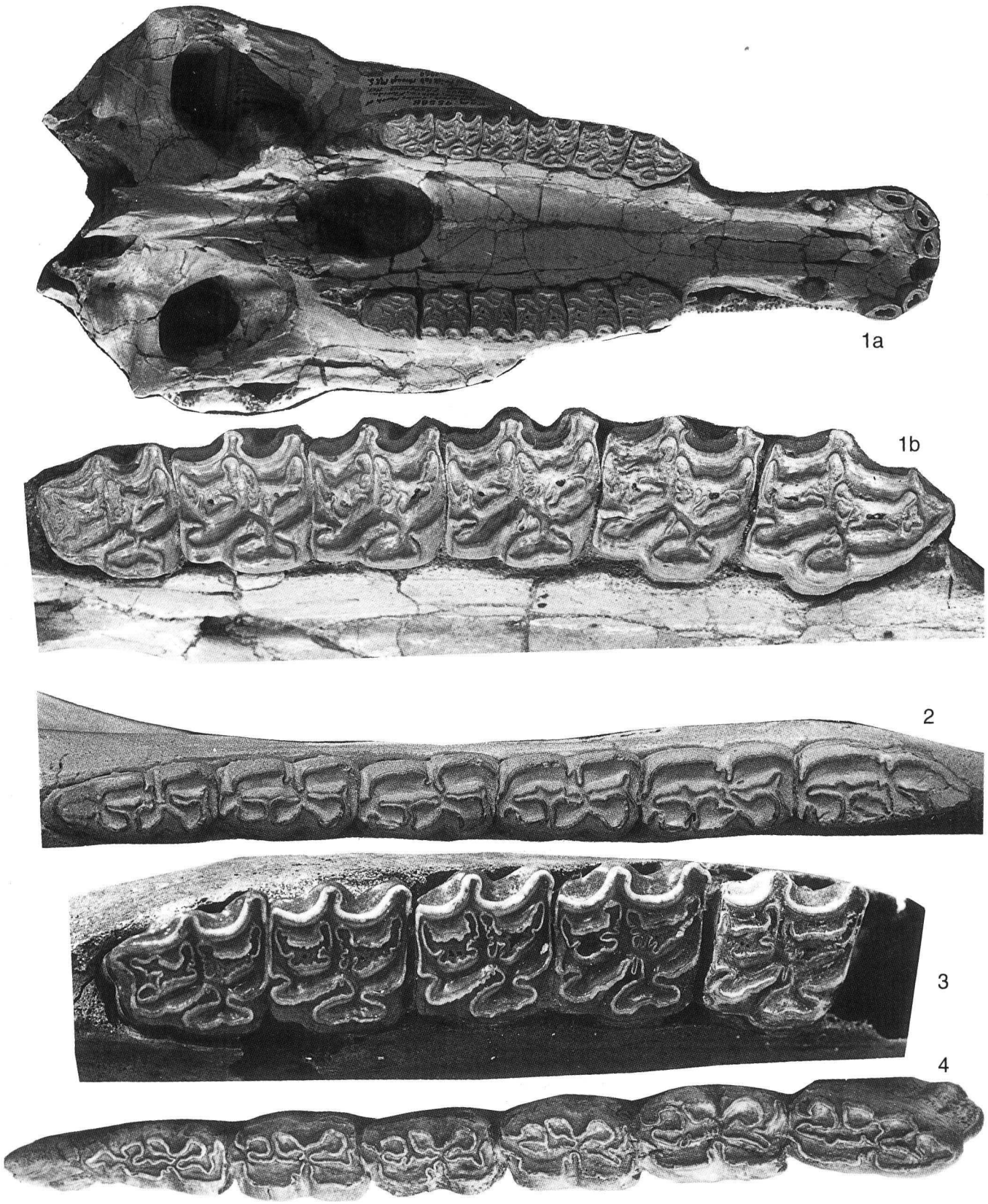

1a
1b
2
3
4

PLATE 14

Fig. 1a-c - *Equus conversidens*, ♂. LACM 308/123900, fragmental skull, 1/3, and palate, nat. size. Barranca del Muerto near Tequ
Central Mexico, late Pleistocene.

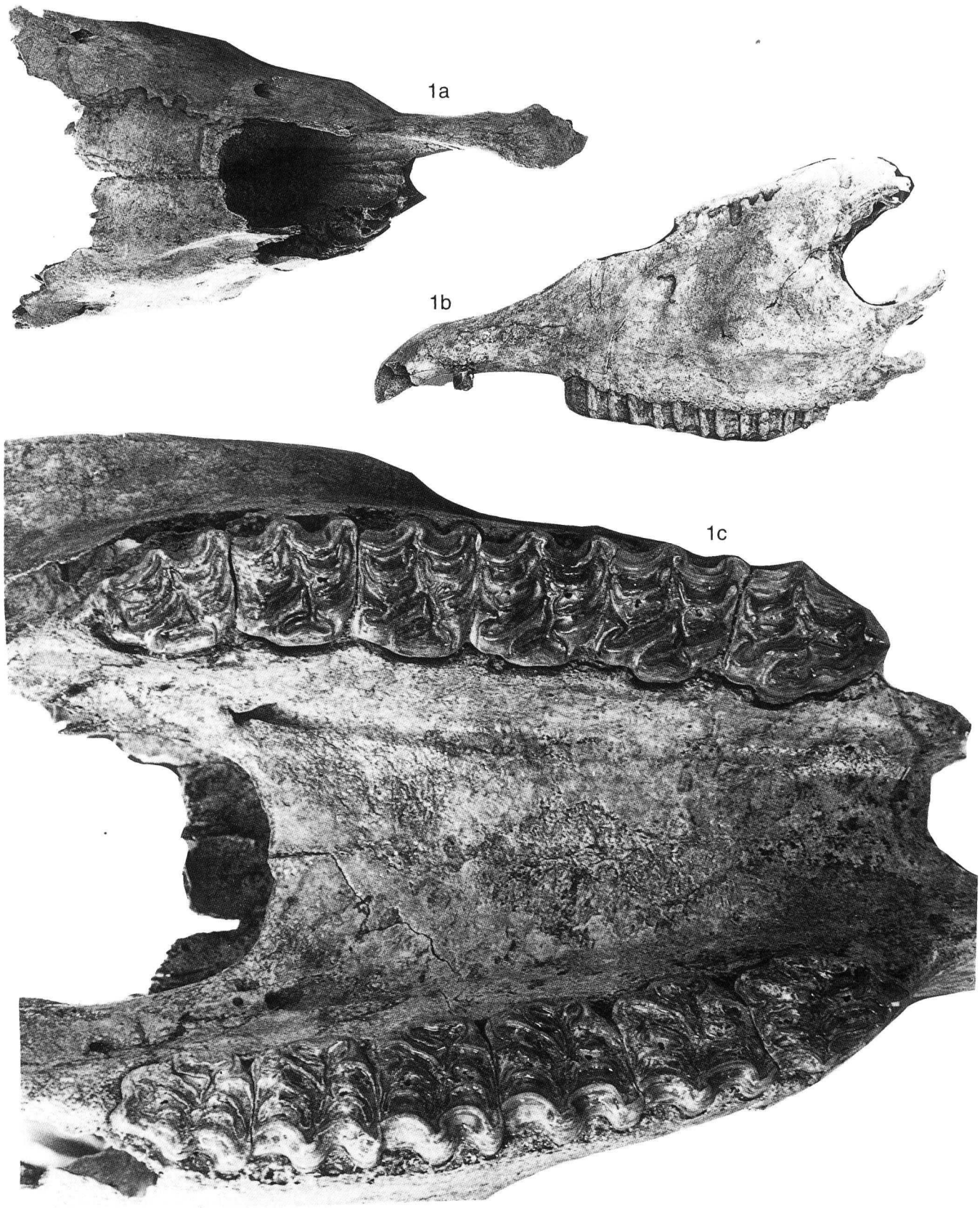

1a
1b
1c

PLATE 15

Fig. 1a,b - *Equus mexicanus,* ♂. Tequixquiac, central Mexico, late Pleistocene. Cast of the type skull described by Hibbard. AMNH. 1/3.

Fig. 2 - *(?)Equus occidentalis.* F:AM 116150, Skull. Comondu, Baja California, Mexico. 1/3.


1a
1b
2

PLATE 16

Fig. 1a,b - *Equus excelsus*, holotype, ♀. USNM 667. Pawnee Loup Branch, Platte River, Nebraska, late Irvingtonian, skull (1/2) and de
tion, nat. size.
Fig. 2 - Id., UNSM 5978, ♂. Sheridan Beds, late Irvingtonian. Upper dentition, nat. size.
Fig. 3 - Id., AMNH 10612, ♀. Irvingtonian. Rock Creek Beds, Briscoe Co., Texas. Skull with mandible, 1/3.

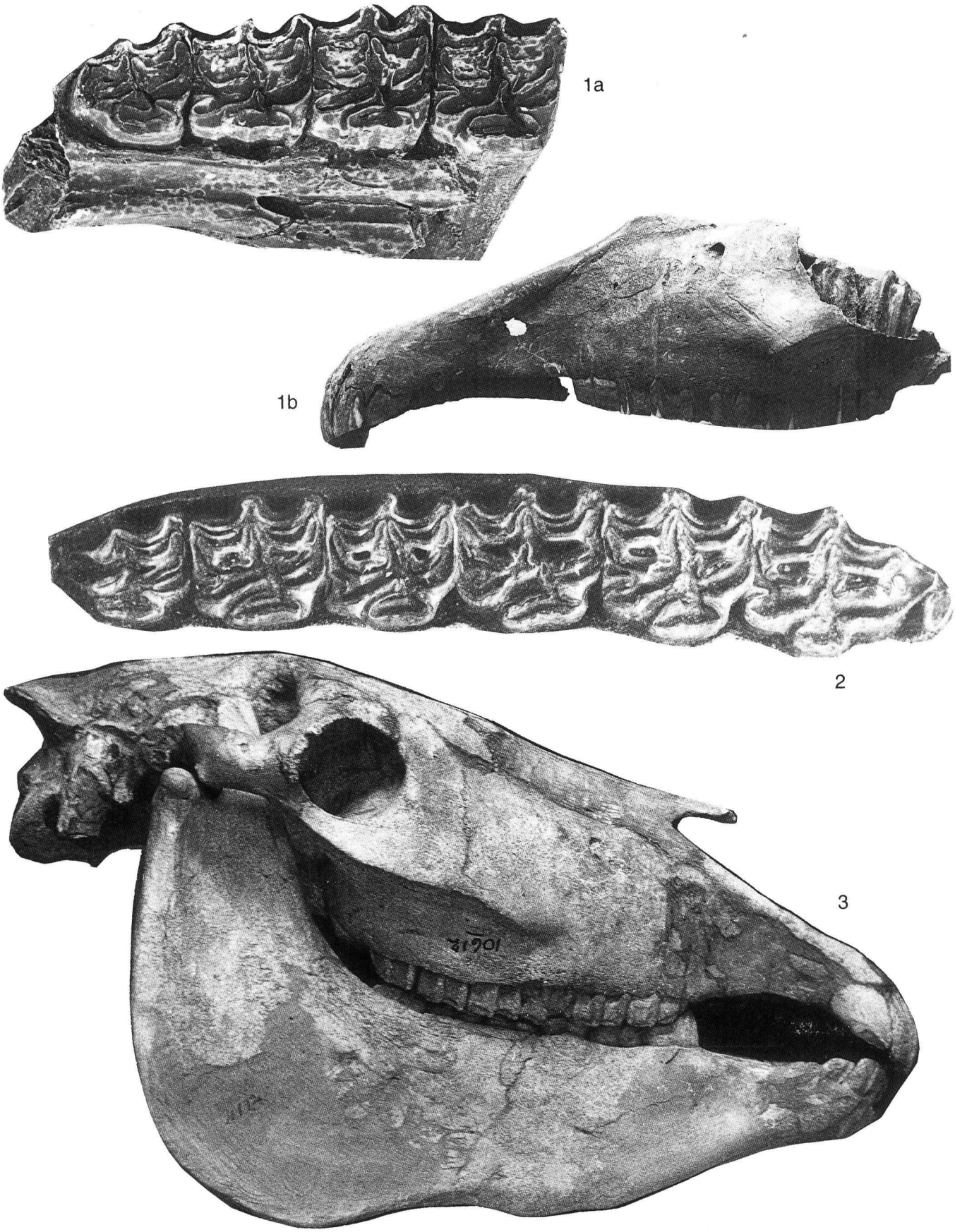

1a
1b
2
3

PLATE 17

Fig. 1a-c - *Equus excelsus*, ♂. Skull, about 4 years old. UNSM 5978, 1/3. Sheridan Beds, late Irvingtonian.


1a
1b
1c

PLATE 18

Fig. 1a,b - *Equus excelsus*, ♂, AMNH 2725, upper dentition, nat. size. Hay Springs, Sheridan Beds, late Irvingtonian. Specimen described by Gidley, 1901: 132-133.
Fig. 3a,b - Id., ♂, lower dentition. AMNH 116142, Hay Springs, Sheridan Beds, Nebraska, late Irvingtonian.

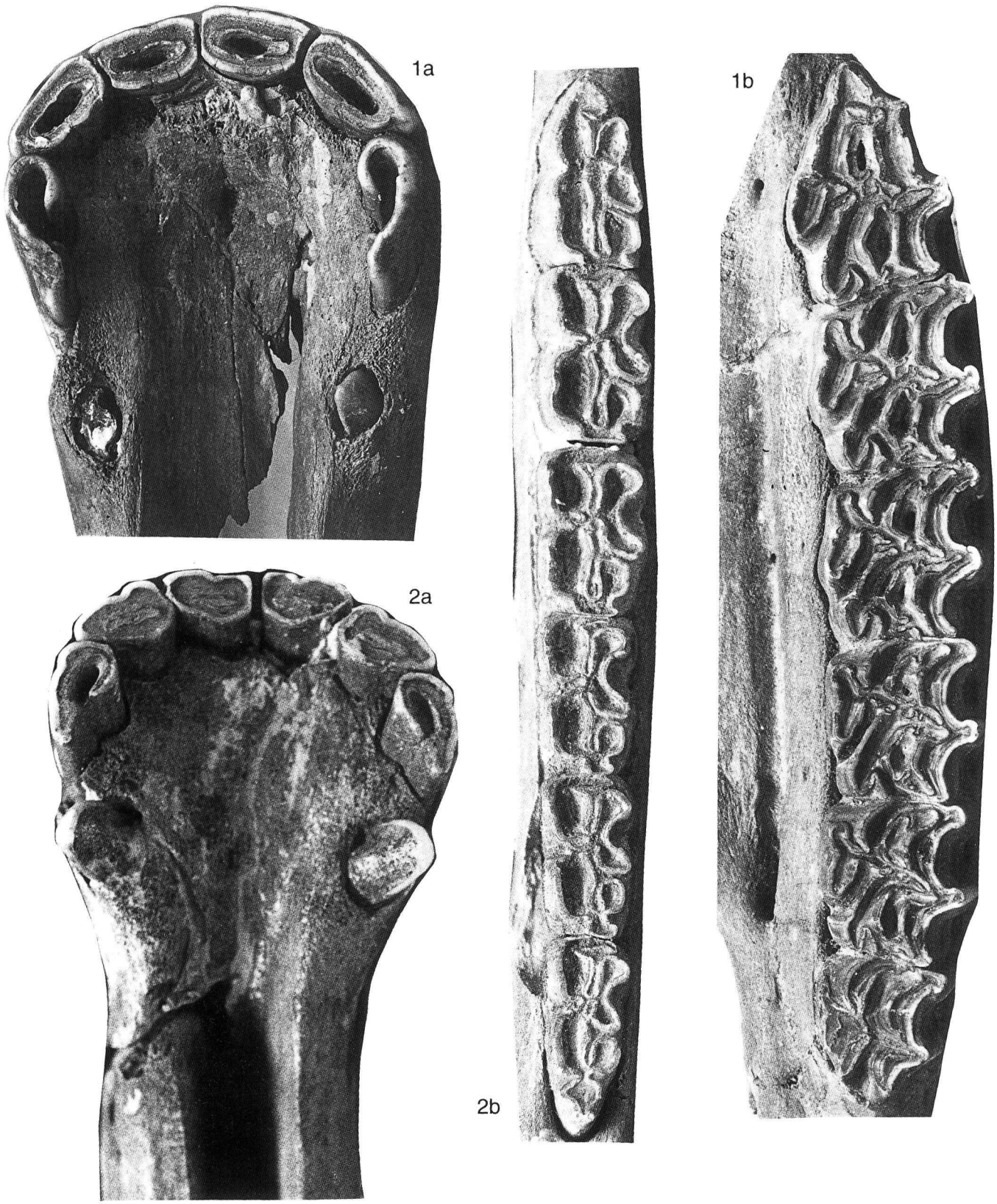

1a
1b
2a
2b

PLATE 19

Fig. 1 - *Equus occidentalis*, ♂. UCMP 2051/114901. Skull figured by Merriam, 1913. Rancho La Brea, proposed as type of the species.
Fig. 2 - Id., ♂, UCMP 2051/19833, Rancho La Brea. Skull.
Fig. 3 - Id., ♂, LACM, Page Inst. 4/A-5,15/3500-6, Rancho La Brea. Skull with lower jaw.
All figures 1/3.

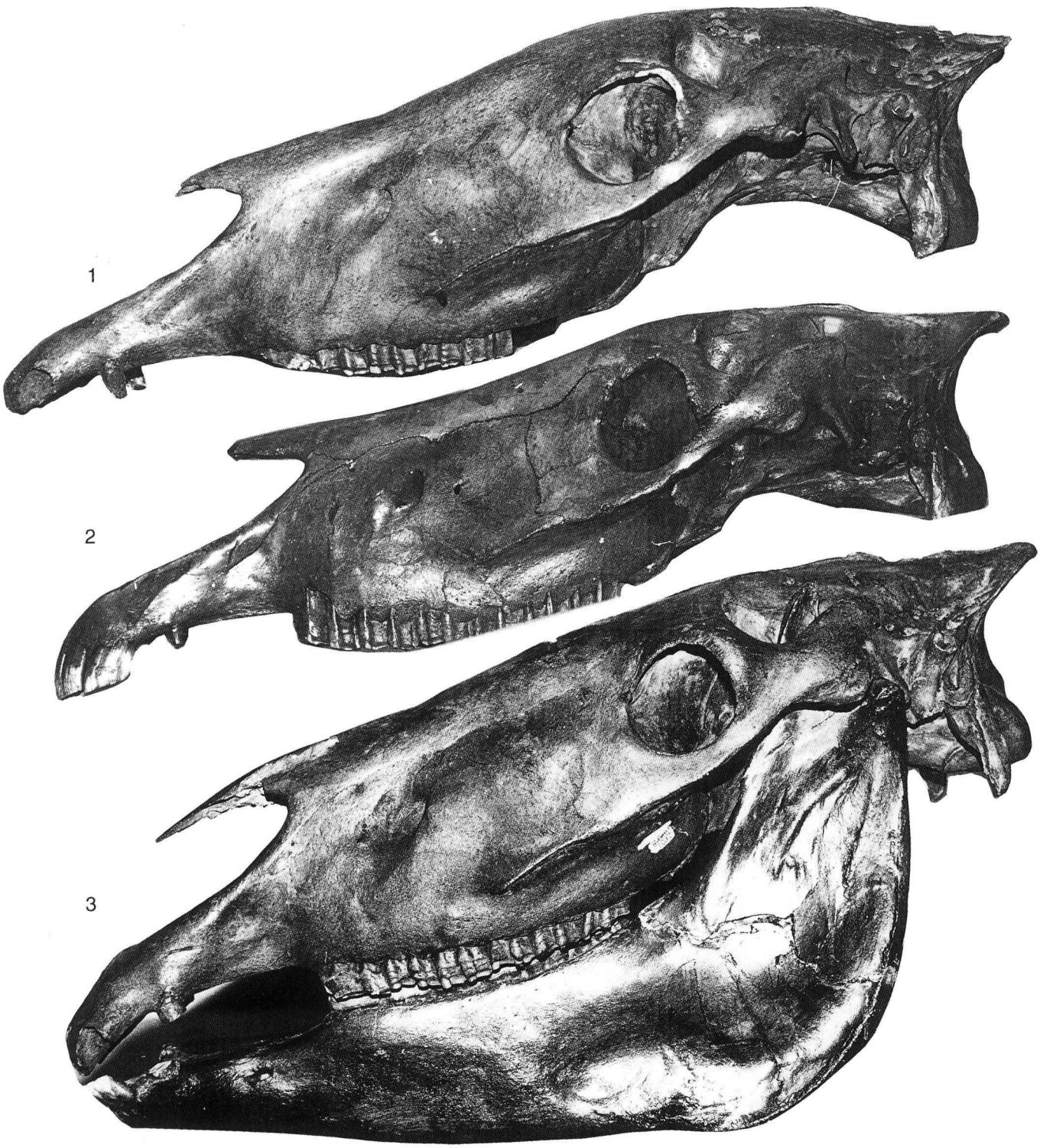
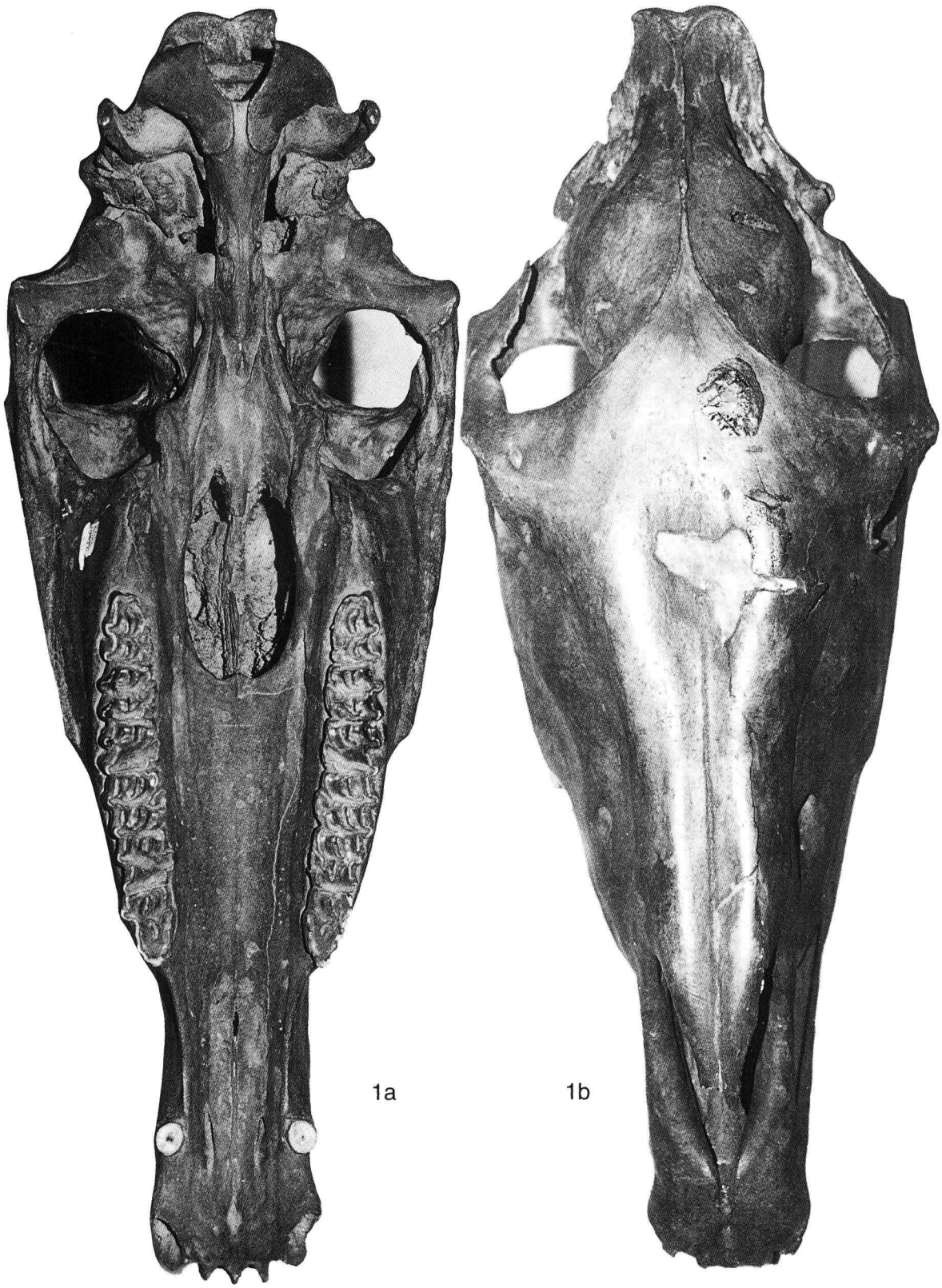

1
2
3

PLATE 20

Fig. 1 - *Equus occidentalis*, ♂, LACM, Page Inst. 4/A-5,15/3500-6. Rancho La Brea. Skull, 1/3.



1a

1b

PLATE 21

Fig. 1 - *Equus occidentalis,* UCMP 2051/114901, row of cheek teeth, nat. size. Rancho La Brea.
Fig. 2 - Id., ♂. LACM, Page Institution 4 D-2,10, 3500-7. Upper incisors.
Fig. 3 - Id., ♂. LACM HC 14557-0. Lower incisors.
Fig. 4 - Id., LACM, Page Institution, 4 D-2,10 3501. Lower tooth row.


1
2
3
4

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