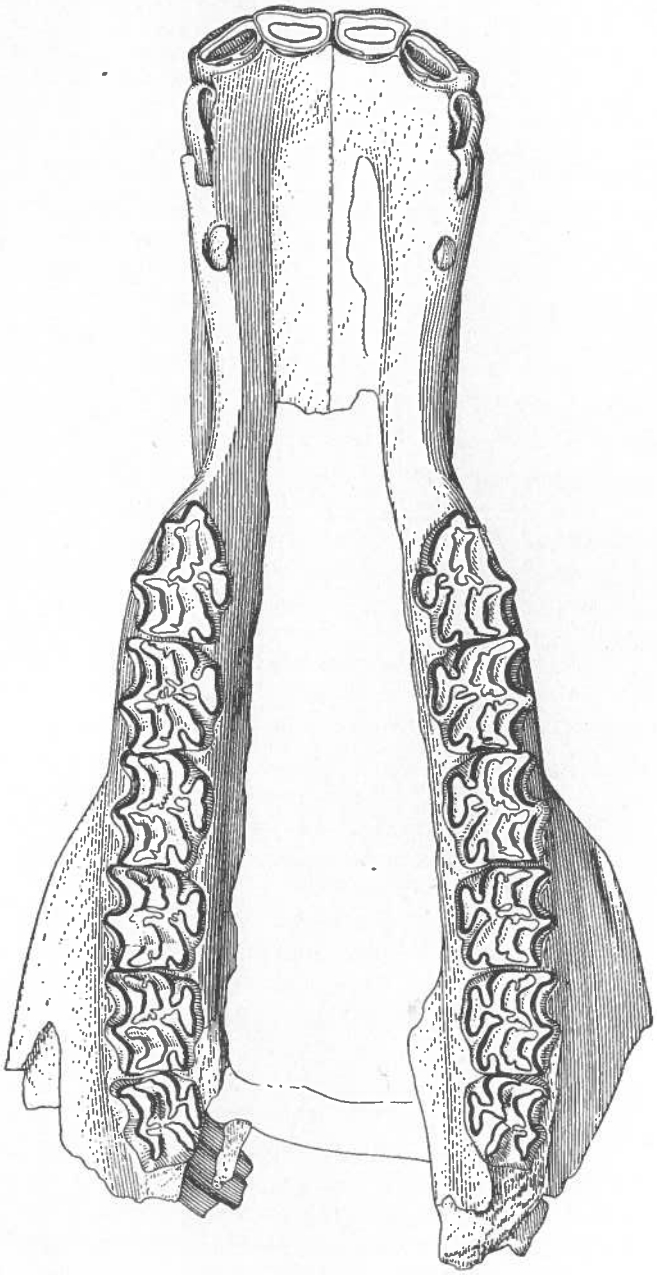

Fig. 13. *Equus* cf. *caballus*, occlusal view of palate with complete dentition, U.C.M.P. no. 38571, loc. V3604. × ½.

Stirton (1939*d*, p
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Description.—N
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VARIATIO

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P^4	
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Protocones incr
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Order PERISSODACTYLA

Equus cf. *caballus* Linnaeus, horse

(Figs. 13, 14, 15, 16)

Stirton (1939*d*, pp. 294–298) noted the occurrence of the genus *Equus* in the Irvington fauna and described a broken skull, part of a lower jaw, a lower cheek tooth, and a cannon bone. This previous description of the Irvington horse can now be supplemented. A palate, maxillary fragments, many lower jaws (juvenile to old age), an abundance of dissociated upper and lower teeth, cannon bones, phalanges, vertebrae, carpals, and tarsals have been obtained. The complete palate, U.C.M.P. no. 38571, is from a young adult and shows characters which were somewhat obscure in the old-age skull described by Stirton.

Description.—No trace of P^1 in materials collected; P^3 widest of cheek-tooth series in young adult (about 27 mm.), P^4 widest in old adult (27.6 mm., Stirton)

VARIATION IN GREATEST TRANSVERSE DIAMETER OF UPPER CHEEK TEETH

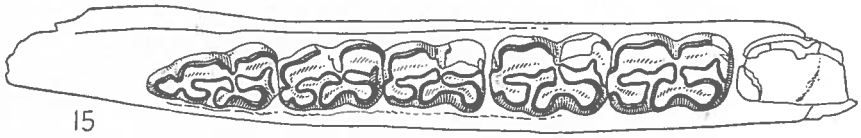
	38571	38716	38573	32879
P^2	25.4	....	25.2	24.4
P^3	27.2	....	25.8	25.2
P^4	25.3	....	27.8	27.7
M^1	26.7	25.0	26.5	26.0
M^2	24.8	24.3	....	25.7
M^3	22.4	22.7	....	22.5
Estimated age	Young adult	Mature	Late mature	Old age

and in late maturity; height of crown in young adult measured on mid-vertical line along external surface, P^2 = 67 mm., P^3 = 79 mm., P^4 = 86 mm., M^1 indeterminable but about same as P^4, M^2 = 94 mm., M^3 = 92 mm.

Protocones increase in transverse diameter from young adulthood to old age, relatively large and long, but triangular to ovoid on P^2; faint to moderately strong lingual groove usually present on protocones but may be absent on posterior premolars and third molar in early stage of wear, this groove directly opposite isthmus from protocone to protoselene on all specimens studied; lingual groove usually much fainter than on type teeth of *E. occidentalis* Leidy; heel of protocone strong on all teeth except P^2; isthmus remains narrow (except in old age) and of consistent width in a single cheek-tooth series; postprotoconal valley narrow in all stages of wear, extends almost to center of tooth in P^3 of young adult, but not deeply extended in all other teeth (different stages of wear were examined); pli caballin absent on all molars studied and on all premolars from maturity to old age inclusive, but only 3 mm. outpocketing of enamel border on P^2 to P^4 of a young adult; hypoconal groove open to base of tooth; fossettes with relatively simple enamel borders as in *E. excelsus* Leidy, *E. occidentalis* Leidy, and in contrast to strongly plicated borders in *E. pectinatus* Cope, *E. leidyi* Hay, *E. yunnanensis* Colbert, and other proposed species; parastyle and mesostyle relatively rounded with wear, mesostyle somewhat V-shaped in young adult.

Depth of matured lower jaws beneath $P_{\bar{2}}$, 68.5 mm. (no. 32865, measured by Stirton), 70 mm. (no. 38582) to an estimated 80–85 mm. (no. 38573); depth of mature jaws beneath $M_{\bar{3}}$, 108 mm. (no. 38570) to 115 mm. (no. 38573); lower teeth rectangular in appearance due to flattening and frequent emargination of the external borders of protoconid and hypoconid; enamel lines usually simple and unplicated as noted by Stirton, although labial border of entoflexid on specimen

14



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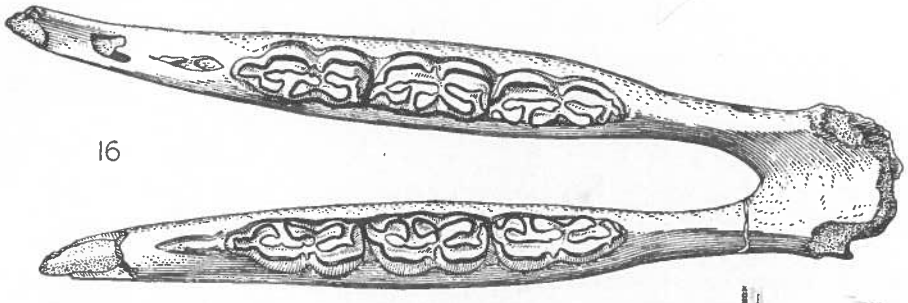

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Fig. 14. *Equus* cf. *caballus*, occlusal view of left lower jaw with $P_{\bar{2}}$ to $M_{\bar{3}}$ inclusive, U.C.M.P. no. 38582, loc. V3604. × ½.

Fig. 15. *Equus* cf. *caballus*, occlusal view of left lower jaw with $P_{\bar{2}}$ to $M_{\bar{3}}$ inclusive, U.C.M.P. no. 38573, loc. V3604. × ½.

Fig. 16. *Equus* cf. *caballus*, occlusal view of mandible with complete deciduous cheek-tooth series, U.C.M.P. no. 38581, loc. V3604. × ½.

no. 38577 is strongly plicate; metaconid rounded and most metastylids with sharp angle to inner corner, configuration of metaconid and metastylid nondistinct from *E. caballus* Linnaeus or from *Equus* of Rancho La Brea; entoconid ovoid to almost square in outline and usually larger than metastylid; no trace of parastylid or hypostylid in any teeth available for study; metaconid and metastylid separated to base of tooth by groove usually U-shaped but approaching V shape on some teeth; hypoflexid extends inward to line of metaflexid and entoflexid on some teeth but not on more than one or two teeth in a given series from one animal; pli caballinid absent or present but not strong when present.

Deciduous upper dentition represented by isolated teeth; evidently with marked extreme in hypsodonty between DP^2 and DP^4, DP^4 approximately one-third higher-crowned than DP^2 at equivalent stage of wear; protocone becomes progressively longer and narrower transversely and with more sharply defined heel from DP^2 to DP^4 as in other species of *Equus;* lingual indentation of protocone progressively broader and deeper from DP^2 to DP^4, may be missing entirely on DP^2; prefossette opens into postprotoconal valley only in very early stage of wear; cross section of parastyle and mesostyle in deciduous premolars relatively longer in anteroposterior dimension and more rectangular in outline than corresponding styles of permanent cheek teeth.

Lower deciduous cheek teeth resemble permanent dentition in simplicity of the enamel lines and general rectangularity of pattern; metastylid more angular in outline than metaconid as in permanent teeth; paralophid and hypoconulid more prominent than in permanent teeth; no trace of parastylid or hypostylid.

Discussion.—The relatively wide, U-shaped valley between the metaconid and metastylid and absence of hypostylid and parastylid in both milk and permanent teeth are the characters of the Irvington horse which make it conform to McGrew's (1944, p. 61) characterization of the caballine horses. It may be concluded that the Irvington horse is not closely akin to the subgenus *Plesippus* Matthew. McGrew's thesis that the plesippine species of North America suffered extinction at the close of Blancan time and that the Pleistocene of North America witnessed an immigration of caballines from Eurasia is judged to be logical after consideration of known evidence. It is noted, however, that the Rancho La Brea horse approaches plesippines in many of its characters.

Is the Irvington horse primitive? What is primitive in species of *Equus?* It is improbable that representatives of *Equus* can be classified as primitive or non-primitive by a system applicable to the entire world. Particularly in the Old World, where *Equus* has been continuously existent since Villafranchian time and has evolved into the caballines, zebras, asses, and half-asses, many of the characters evinced in the earliest forms are still retained by the Recent survivors. In North America certain characters seem to have a chronological implication. It is strongly affirmed, though, that these characters are applied to horse populations or to whatever concept there can be of horse populations as represented by the meager fossil remains; and the dating of a Pleistocene stratum by means of a contained single tooth or a few isolated teeth (particularly upper teeth) is insupportable and often fallacious.

Example. Character of the protocone.—In the North American Blancan to late Pleistocene species respectively, there is a general tendency, except in P^2, for the protocone to become relatively more elongate, relatively thinner transversely, and for its long axis to become aligned more nearly parallel to the anteroposterior diameter of the tooth. Also, the protocones of the premolars are relatively shorter in comparison to those of the molars in the Blancan species which tend to have elongate molar protocones. Notable exceptions to these tendencies occur; some of the Blancan plesippines have long axes of protocones aligned parallel. (See J. R. Schultz, 1936, fig. 1.) The alignment of the protocone cannot be measured accurately; accordingly, the conclusion above is purely a matter of personal judgment.

A series of histograms showing anteroposterior diameters of protocones of adult upper teeth is shown on fig. 17. All the available upper cheek teeth were used except P^2. No more than one series of P^3–M^3 from one animal was measured, so

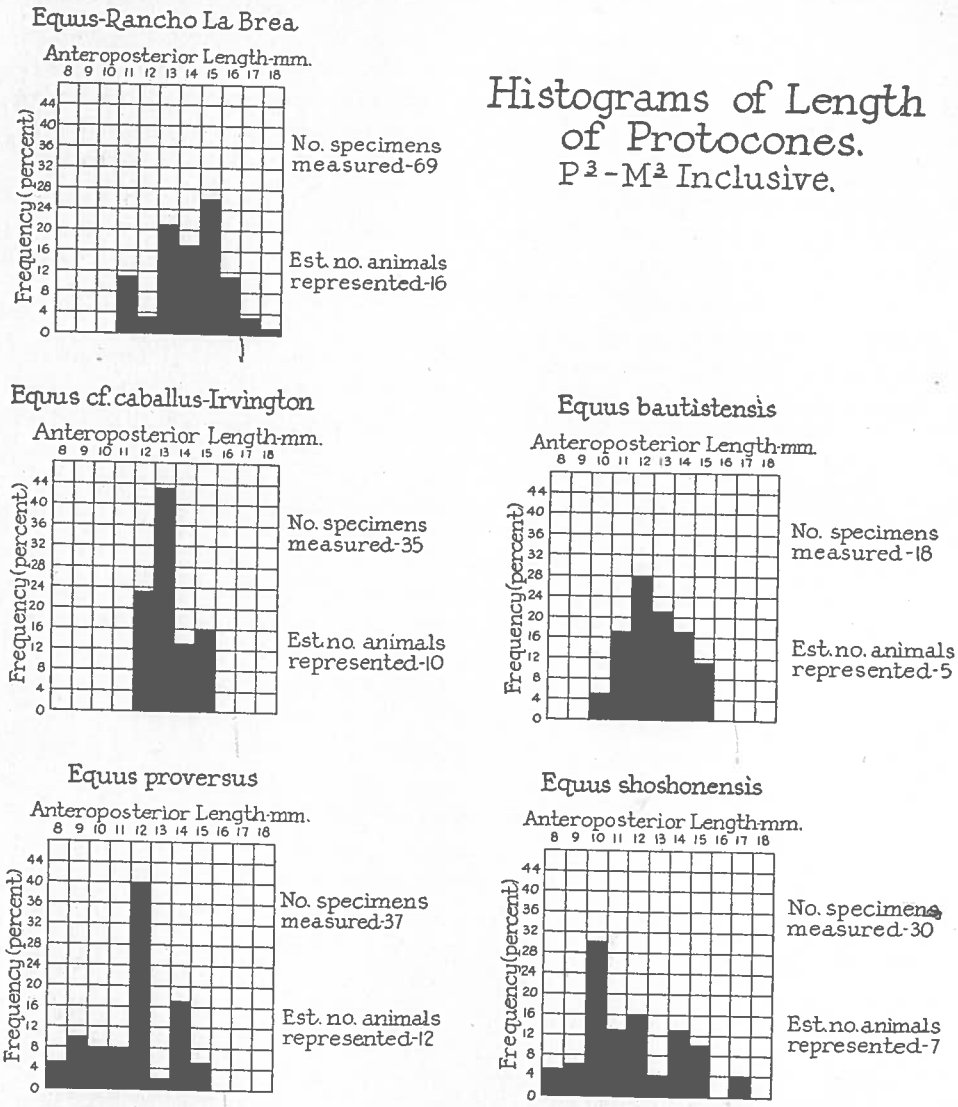

Fig. 17. Histograms of length of protocones in certain species of *Equus*. Lengths taken from P^2 to M^3 inclusive.

far as could be determined. The extremes of variation of the anteroposterior length of the protocone of a given cheek tooth were never farther apart than 2 mm. from the time the tooth is first worn to a normal occlusal surface until extreme old age. Since this variation with wear is relatively slight, teeth of all stages of wear through maturity were used. No attempt is made to establish the arithmetic mean or standard deviation in the manner suggested by Simpson and Roe (1939), but certain

interesting relationships are shown. Complete overlap by all the species in protocone lengths from 11.6 to 15.5, with all but *E. shoshonensis* having predominant numbers of protocones in this range, is evident. The two Blancan species probably have a wider range of variation than any of the later species, particularly in Blancan forms which tend to have elongate molar protocones. Note that in *E. shoshonensis* the variation extremes almost equal the entire range of variation of all the other species, lacking only 2 mm. This chart shows that a protocone between 9.6 and 17.5 mm. in anteroposterior diameter has no time-evolutionary significance.

The horse from Irvington belongs in a group with *E. lambei* Hay, *E. niobrarensis alaskae* Hay, and the horse which Tscherski (1892*a*) described from Liakhof Island, Siberia, as *E. caballus* Linnaeus. To this group I apply the designation *Equus* cf. *caballus*.

EVALUATION OF PROPOSED SPECIES OF EQUUS

An attempt to compare the Irvington horse to the proposed species of caballine *Equus* in North America is an almost hopeless task. Stirton (1939*d*, p. 395) has aptly summarized the obstacles which are inherent in this problem. A beginning student of speciation in *Equus* is completely overwhelmed by the multitude of presumably diagnostic species characters which have been used; he is even more confused to find that most of the proposed distinctions collapse into minor variations within a species when a large number of specimens are available from one locality. So many of the species names now carried in the literature are superfluous that an evaluation is demanded.

Any appraisal of fossil species of *Equus* in North America must be grounded on Gidley's excellent study (1901*a*). Some of his observations are erroneous in the light of present data; but his method of approach to the variation dilemma and his general treatment of species at that time were certainly a tribute to the author.

Hay's discussion (1915*a*, pp. 549–568) and review of the European species and subspecies merit praise also. Many of his conclusions are indeed perspicacious and judicial. Hay questioned the advisability of using the various kinds of present-day *Equus caballus* for comparison with fossil forms, since the present caballine has been so greatly affected by domestication and controlled breeding. He further recommended that the various skull and dental indices should first be tested on unmixed and undomesticated species. Of particular interest were Hay's conclusions:

> Not all species can be distinguished by craniometrical methods. . . . Not too much dependence should be placed in any one measurement or in any single index. . . . all other characters ought to be considered in coming to a conclusion. . . . It is difficult to say which measurements and which indices are of the most importance. . . . In the application of these to special cases sometimes one index may be of special value; in other cases another index may be decisive.

One difference has often been emphasized in support of a species distinction when the similarities could be even more important. The species diagnoses have often been nothing more than characterizations of the genus. A notorious example is the presentation of relative size of the cheek teeth and complexity of the enamel folding of their fossettes as the diagnosis. So many of the species have proved to be "moderately large with moderate complications of the enamel" that there is no

longer any diagnostic or descriptive value in such a statement. Lurking among the maze of irrelevant descriptions and comparisons are the really important criteria with which lineages within this puzzling genus are to be compounded. At any time the recognition of a truly consistent difference may be more important than a multitude of similarities, particularly if any acceptable history of speciation or subspeciation is to be divulged.

It seems practical that if Pleistocene caballine materials in North America are ever to be employed with any certainty in stratigraphic problems, a very strict appraisal of the types is necessitated. Only when types are accompanied by sufficient materials to give at least some indication of infraspecific variation can there be a justification for the proposal of a new species among the equines. No objective comparisons may ever be formulated when reference of a specimen from one locality to a species from another locality is based on disparate material.

If one follows these tenets he is forced to utilize only four to eight Pleistocene caballine species names in North America. Such a drastic revision will not be universally accepted. This is true in part because of the lack of complete objectivity and conclusiveness on the part of the reviser, and in part because of established usage of poorly founded names.

Equus achates Hay and Cook (1930) was described from an upper molar collected near Frederick, Oklahoma. Species distinction was made because the writers knew of "no described molar so high, slender, and strongly curved." The diameters of the tooth place it in the size group of *E. tau* Owen. Although the tooth is indeed long as compared to many teeth which have been referred to other species, I believe that its relative length is not excessive. The photograph of the lateral view of this tooth permits no further comparisons. The species *E. achates* will be regarded as a *nomen vanum*.[5]

Equus calobatus Troxell (1915*a*) was established on an assembly of thin limb bones from Rock Creek, Texas. Troxell showed by various indices that *E. calobatus* possessed a slenderer cannon bone than specimens of *E. asinus* Frisch, *E. caballus*, and *E. scotti* Gidley. Troxell's conclusion that this is a very slender-limbed horse is acceptable, but a separate taxonomic category based on these limb elements was not warranted, since comparisons could not be made with species which had been described previously from Rock Creek. Cope (1893*a*), for example, based his species *E. semiplicatus* on material from Rock Creek. It seems much more logical that the equid remains from this locality, with the exception of *E. scotti* Gidley, should pertain to only one species. I regard *E. calobatus* as a *nomen vanum*.

Equus francisi Hay (1915*a*) is based on a skull and parts of a skeleton from the Lissie formation of Wharton County, Texas. Hay indicates that this horse is of the size and general character of *E. tau* Owen, but gave it a separate name because, unlike *E. tau*, the last premolar and the anterior two molars are wider than long.

[5] *Nomen vanum* is the term proposed by Simpson (1945, p. 27). This phrase bears the general implication of the word "indeterminate," which was used by many earlier writers. Simpson (1947, p. 31) has added further explanation of his use of this term: "There are, as it happens, some names . . . the validity of which can hardly be judged one way or the other at present. Such names are not now known to be valid, and they cannot be applied to any specimens other than the type or syntypes. . . . It would be misleading to list these names and to use them on the same basis as names of reasonably established status . . . they are not technically homonyms, synonyms, or *nomina nuda*, and they maintain a standing in nomenclature although they have none in zoölogy."

Hay made no statement regarding the stage of wear of *E. francisi* teeth compared to the type of *E. tau;* but in a later publication (1917*f*, p. 439) he mentions that it is known "as the upper teeth are worn down the fore-and-aft length of the crown diminishes more rapidly than the width." Gidley (1901*a*, p. 99) had previously pointed out this characteristic. The teeth in a series of zebra skulls in the Museum of Paleontology, University of California, were examined to see if variations in the ratio of length to width of crown occur in specimens at about the same stage of wear. It was found that ratios in the same stage of wear were quite constant but that there is apparently a marked change in this ratio between early adult and mid-adult levels. A young adult specimen exhibits proportions not unlike *E. tau,* whereas a middle-aged adult specimen is like *E. francisi.* I believe, therefore, that Hay's species *E. francisi* should be referred to *E. tau.*

Hay stated that it was possible that this Texas horse actually belongs with *E. tau* but said that there were certain features which appear to mark the animal as being more primitive than Owen's species. He did not, however, designate the characters which were considered primitive. The characters of *E. tau* and *E. "francisi"* (= *E. tau*) suggest that this species might be a Blancan plesippine with a uniquely advanced protocone, or that it is a somewhat divergent Pleistocene caballine with characters in the lower dentition which approach Blancan plesippines. It is of interest to see that Gromova (1946, pp. 347–350) has found isolated upper and lower cheek teeth of a large horse in "latest Pleistocene" of Samarkand. Gromova named this horse *E. valeriani.* The proposed distinction of this species is its combination of a typical stenonian (hippotigrine or plesippine) metaconid-metastylid column with an elongate protocone. *E. valeriani* would seem to be, then, a structural annectant between stenonines and caballines persisting until a late time. The occurrence of a structural annectant between plesippines and caballines in North America, as is suggested by *E. tau,* might be interpreted as evidence that the containing deposit was either late Blancan or early to middle Pleistocene were it not for contradictory data such as Gromova has presented. Such evidence also opposes the generic separation of the zebras and horses and supports the contention that these two groups did not arise independently from different species of *Pliohippus.*

Equus holmesi Hay (1920*b*) was based on four upper cheek teeth from the Pleistocene of northeastern Oklahoma. The species diagnosis states (p. 119): "Teeth large. Enamel of fossettes with only medium complication; styles unusually broad." Hay stated that these teeth are the same size as *E. scotti* Gidley. He thought *E. scotti* was probably synonymous with *E. complicatus* Leidy. These teeth resemble figured specimens of both *E. scotti* and *E. complicatus. E. holmesi* Hay is a *nomen vanum.*

Equus jubatus Hay (1927*d*) was described from four well-worn associated upper cheek teeth collected at Cameron, Texas. These teeth, like an old individual (U.C.M.P. no. 38572) from the Irvington fauna, show relatively thick enamel. They could be referred to any Pleistocene species of equivalent size. *E. jubatus* is a *nomen vanum.*

Equus leidyi Hay (1913*b*) was based on an upper molar from Peace Creek, Florida. Hay gave as characterization of the species: ". . . teeth of medium size, the length of the grinding surface of the first molar being about 25 mm., the width

about 24 mm., excluding the cement. Enamel surrounding the lakes rather strongly folded. Type tooth moderately curved."

This tooth and other teeth which Hay has referred to this species greatly resemble teeth which have been referred to *E. complicatus* Leidy, *E. holmesi* Hay (*nomen vanum*), and other proposed species. I regard *E. leidyi* as a *nomen vanum*.

Equus littoralis Hay (1913*b*) is based on an upper cheek tooth, also from Peace Creek, Florida. The enamel pattern is like that in the *E. complicatus–E. fraternus* Leidy group, but the tooth is small enough to compare with *E. tau*. This may be logically regarded as a small individual of the probable one species represented at Peace Creek. *E. littoralis* is a *nomen vanum* so far as this study is concerned.

Equus nevadanus Hay (1927*d*) is based on an upper cheek-tooth series from Manhattan, Nevada. Comparisons were made only with *E. laurentius* Hay. This could be one of several previously described species of moderate size. *E. nevadanus* will be regarded as a *nomen vanum*.

Hippotherium princeps Leidy (1890*a*) was formulated from a large upper cheek tooth found at Peace Creek, Florida. It is of the size of some of the larger species of *Equus*. Uniquely, the protocone is separated from the protoselene in a fashion resembling *Neohipparion*, even though the tooth has been abraded to a flat occlusal surface. Hay (1902*a*) thought this tooth belonged with *E. complicatus*. It has an anomalous enamel pattern, and the species is indeterminate. *H. princeps* is a *nomen vanum*.

Equus occidentalis Leidy (1865*c*) was based on an upper cheek tooth from the "Pleistocene auriferous gravels" in Tuolumne County, California, and two upper cheek teeth from an asphalt bed near Buena Vista Lake in Kern County, California. The latter locality is now usually called Asphalto. These teeth are all characterized by a simple and somewhat rectilinear enamel pattern and a broad lingual groove on the protocone. It is impossible to get topotypes of the Tuolumne County specimen, because the exact locality was never specified; it may or may not be Pleistocene in age. Stirton (oral communication, 1948) has called to my attention that topotypal lower cheek teeth from Asphalto bear the plesippine V-shaped groove between the metaconid and metastylid. Merriam (1913*f*) referred the abundant horse material from Rancho La Brea to *E. occidentalis*. Although there is remarkable identity in characters between the Rancho La Brea horse and the types of *E. occidentalis*, the La Brea horse is a true caballine (this is demonstrated by the character of its deciduous dentition) and must be referred to some other species. *E. occidentalis* is believed to be a valid species of plesippine affinity. It is singularly advanced over *E. simplicidens* (Cope), *E. shoshonensis* (Gidley), *E. francescana* Frick, *E. idahoensis* Merriam, and *E. proversus* (Merriam) in its development of a wide and prominent lingual groove on the protocone. The Blancan age assignment for this species is supported by the recovery of *Ischyrosmilus* and *Borophagus* from Asphalto. In a doctoral thesis for the University of Oklahoma, which is to be published posthumously, C. S. Johnston referred the *Equus* from the Cita Canyon fauna (Blancan) to *E. occidentalis*. Johnston came to this conclusion when the characters of the topotypes of *E. occidentalis* were pointed out to him by Stirton in an oral communication.

Equus fraternus Leidy (1860*b*).—This proposed species has had a complicated nomenclatural history. It was described by Leidy from material obtained near Charleston, South Carolina; but the name was a *nomen nudum,* since Leidy gave no precise description and designated no type. Cope (1896*h,* p. 467) chose to validate the species under Leidy's authorship and selected a tooth from Leidy's material to be the type. Gidley (1901*a,* p. 111) believed that the tooth Cope selected was not described by Leidy at all; so Gidley chose another tooth as Leidy's type. Hay (1913*b,* pp. 569–570) refuted Gidley's correction and reaffirmed Cope's selection of the type. These revisers indicated that *E. fraternus* is separable from *E. complicatus* Leidy only by a slight size difference. *E. fraternus* is the smaller of the two species in the descriptions of these writers, but the larger teeth of *E. fraternus* are indistinguishable from *E. complicatus.* There seems to be no adequate data for a differentiation. I believe that all the teeth from this locality should be referred to one species. *E. fraternus* will be employed only as a *nomen vanum.*

Equus complicatus Leidy (1858*c*) was based on a second upper molar. Paratypes were two posterior upper molars. The specimens were collected near Natchez, Mississippi. It would indeed be fortunate if this name could be retained for practical use, since this is the first proposed fossil *Equus* species from North America and many other subsequently described species are probably referable to this category. As Gidley (1901*a,* pp. 109–110) pointed out, however, *E. complicatus* itself is imperfectly characterized except in size. Although many teeth from different localities have been referred to it, there is no assurance in regard to such reference. The type indicates that *E. complicatus* was of medium to large size and with moderate to strong plication of the enamel borders of the fossettes, but these characters are certainly not unique in *Equus. E. complicatus* will be treated as a *nomen vanum.*

Equus excelsus Leidy (1858*e*) is a fragmentary right maxilla with P^4 to M^3. The specimen was collected somewhere along the Pawnee Loup branch of the Platte River in Nebraska. It is a moderately large horse. Although Hay (1913*b,* p. 592) continued to distinguish this species from *E. niobrarensis* Hay and other species on small differences in enamel configuration, Gidley (1901*a,* p. 113) thought that the species could not be clearly defined. Again, as with *E. complicatus* Leidy (*nomen vanum*) there seems to be no possibility of finding topotypes. *E. excelsus* will be set aside as a *nomen vanum* in this study.

Equus semiplicatus Cope (1893*a*) is an upper molar from Rock Creek, Texas. This specimen is insufficient for the construction of definitive species characters. It is known, though, that much topotypal material has been collected. In view of this fact, it seems possible that eventually this species may be established satisfactorily. It will be treated as a *nomen vanum* at this time. Cope's designation of the teeth from San Diego, Texas, as paratypes is not acceptable. So far as the referred skull and teeth are concerned, this seems to be a medium-sized *Equus* with simple tooth pattern.

Equus tau Owen (1870*b*) is an upper cheek-tooth series, lacking P^2, from the Valley of Mexico. It is characterized by the very small size of the teeth. Owen gave the relatively long anteroposterior diameter of the premolars as a character, but this diameter has been shown to vary markedly with wear of the teeth and probably

COMPARISON OF SPECIES OF EQUUS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
	E. hatcheri	*E. niobrarensis*	*E. scotti*[a]	Extreme of variation between *E. hatcheri* and *E. niobrarensis*	Extreme of variation between either *E. hatcheri* or *E. niobrarensis* and *E. scotti*	*E. przevalskii*, 5216, Salensky[b]	*E. przevalskii*, 512, Tscherski[b]	Extreme of variation in 9 skulls of *E. przevalskii*[b]	*E. grevyi*, U.S.N.M. 163338[b]	*E. grevyi*, U.S.N.M. 182026[b]	Extreme of variation in 8 skulls of *E. grevyi*[b]	Extreme of variation in 8 small domestic horses[b]	Extreme of variation in 8 large domestic horses[b]	Extreme of variation in all 16 domestic horses[b]
Basal length	552	530	530[c]	22.0	22.0	495	440	55	557	525	33	26	49	159
Cephalic index	42.6	45.3	43.5	2.7	1.8	42.2	42.6	2.5	37.7	39.0	3.1	3.9	4.7	7.0
Craniocephalic index	35.3	34.3	37.8	1.0	3.5	34.1	34.1	2.3	34.1	36.2	2.5	1.8	4.6	6.1
Faciocephalic index	74.8	75.3	77.5	0.5	2.7	76.2	76.1	2.6	76.8	77.7	2.1	5.3	4.6	7.7
Vertex length	615	582	610[c]	33.0	28.0	547	488	62	627	595	42	36	59	164
Ratio: Length of upper premolars to length of cheek-tooth series	51.3	54.2	55	2.9	3.0									

[a] Measurements taken from young adult skull of *E. scotti*, U.C.M.P. no. 10608.
[b] Taken from Hay (1915*a*).
[c] Approximate measurement to within 5 mm.

is not diagnostic. No other fossil species described in North America has been demonstrated to grade completely into the *E. tau* teeth on the basis of size, except *E. "francisi"* Hay (synonym of *E. tau* in this paper).

Equus pectinatus Cope (1899*a*) was based on nine upper premolars and molars probably from one animal. These were collected in cave deposits at Port Kennedy, Pennsylvania. The species was distinguished by its relatively small protocones and by the complicated enamel plication of the lakes. The teeth indicate that it is a large horse. I prefer to regard *E. pectinatus* as a valid category until it can be demonstrated that previously named species include the range of characters it portrays. This associated series of teeth at least shows what may be expected in variation of pattern and proportion between teeth in the same animal.

Equus giganteus Gidley (1901*a*) is based on a single upper cheek tooth from southwest Texas. It was distinguished by its very great size and relatively small fossettes. No individuals of other species of *Equus* have yet been described which attain the size of this tooth. In general appearance *E. giganteus* is not unlike certain teeth seen in *E. scotti, E. shoshonensis,* or *E. idahoensis.* It seems possible that this tooth might represent an unusually large individual of *E. scotti.* Among the teeth in the University of California collection, the plesippine from the Wichman fauna of Nevada, the large caballine from Fossil Lake, Oregon, and the large horse from Rancho La Brea and McKittrick most nearly attain the size of *E. giganteus.* I believe that *E. giganteus* is a valid species, possibly of plesippine affinity.

Equus niobrarensis Hay (1913*b*) and *Equus hatcheri* Hay (1915*a*).—*E. niobrarensis* was based on a complete skull (broken and restored to shape); *E. hatcheri* was based on a complete skull and lower jaw. Both types were collected from the Hay Springs quarry near Grayson, Nebraska. Hay very carefully compared *E. hatcheri* to *E. niobrarensis* and found that *E. hatcheri* had a longer and narrower skull, a shorter and broader face, and a straighter dorsal profile of skull. Irrespective of the differences which Hay itemized, the two types may be referred to the same species. The variation shown is due to a possible difference in sex between the two types, or is attributable to individual variation. *E. niobrarensis,* the smaller skull, has no canines; whereas *E. hatcheri,* the larger, has canines. This is not conclusive datum, but it suggests that *E. hatcheri* may have been male, and *E. niobrarensis* female. It seems necessary to compare the variation between the two specimens with the variation exhibited in nondomesticated strains of Recent equids. To do this, tables presented by Hay (1915*a*) may be used. (See the accompanying table.) It is believed that this tabulation demonstrates how practical conclusions can be formulated from Hay's data which are directly opposed to Hay's own conclusions. All linear measurements are in millimeters, and all measurements and indices are based on adult skulls. *E. hatcheri, E. niobrarensis,* and *E. scotti* are compared with two skulls of *E. przevalskii* and with two skulls of *E. grevyi* which were selected on account of extreme in basilar length. The fossil skulls are also compared to a series of skulls of *E. przevalskii, E. grevyi,* and a series of large and small domestic horses.

In the table it can be seen that the extremes of variation in indices and lengths are usually found in the domestic horses, even when these domestics are divided into groups of similar size. This supports Hay's conclusion (1915*a*, p. 552) that it

° Approximate measurement to within 5 mm.

is inadvisable to use present-day *E. caballus* Linnaeus for comparison with fossil forms, since the domestic horse has been greatly affected by controlled breeding. Column 4 of this chart shows that (1) the difference in basal length between *E. hatcheri* and *E. niobrarensis* can be less than this difference within *E. przevalskii, E. grevyi,* and the domestic horse; (2) the difference in cephalic index between *E. hatcheri* and *E. niobrarensis* is greater than in the represented individuals of *E. przevalskii,* but can be less than with *E. grevyi* and the domestic horse; (3) the difference in craniocephalic and faciocephalic indices between *E. hatcheri* and *E. niobrarensis* can be much less than within any of the compared species; (4) the difference in vertex length can be less than within the compared species. In only one comparison out of ten, then, does a difference in index or length between *E. niobrarensis* and *E. hatcheri* exceed the difference that may be demonstrated among individuals within one Recent wild species. To be sure, this analysis does not attempt to put greater or lesser weight upon any given index or length; nor does it appraise the fact that differences in indices may or may not represent greater physical variation than do the differences in linear measurements. Is the cephalic index more important than the craniocephalic index or the faciocephalic index? If the cephalic index is most important in this example, will it be most important in comparisons of other species of *Equus?* I cannot even attempt to answer such questions. It seems, however, that by sheer weight of numbers of differences which are less extreme than within one compared species, there is no justification for a specific separation between the two Hay Springs horses on the basis of skull characters.

Hay (1915*a*, pp. 531–533) pointed out differences between the individual teeth of *E. hatcheri* and *E. niobrarensis: E. hatcheri* with all teeth longer anteroposteriorly, wider transversely, different in configuration of parastyle of P^3 and P^4, lacks distinct lingual groove of protocone. He did not, however, give any of these differences any particular weight in the speciation: "It is probable that not all of the differences observed among these horses will prove to be of specific importance, but it seems to be proper to note them in order that the important character may in due time be discovered." In referring to the shape of parastyles of P^3 and P^4, Hay states, "Probably in each species there is in this character a good deal of individual variation." It is here concluded that the differences in dentition are no more severe than the previously reviewed differences in skull characters and that all may be easily contained in the realm of individual variation.

Certain possibilities of error in the figures of the chart should not be disregarded. Considerable tolerance must be allowed when evaluating the linear measurements, even though these lengths were presumably all made by the same man. For example, the vertex length is specified as the distance from the incisive border to the middle of the occipital crest. Was this length measured along the line of curvature of the dorsal profile or was it measured as the straight-line distance between the two points? If either the incisive border or the middle of the occipital crest is incomplete, as it often is, what method was used in the estimation of vertex length? Such questions must, for the most part, remain unanswered for the student of horse skulls. Simpson and Roe (1939) have clearly outlined some of the uncertainties of interpretation of measurements which now exist in the literature.

A cursory examination led to the conclusion that these two Nebraska horses greatly resemble *Equus scotti* Gidley. Hay made no comparisons of *E. niobrarensis* and *E. hatcheri* with the previously described *E. scotti*. Column 3 of the table[6] on page 248 shows that *E. scotti* (1) is in the general length of skull range of the Hay Springs horses, (2) is intermediate in cephalic index between *E. niobrarensis* and *E. hatcheri*, and (3) has a greater craniocephalic index than either of the Nebraska horses. Whether the index differences balance, underbalance, or overbalance the index and linear measurement similarities is purely a matter of personal interpretation. I feel that the general similarity in dentition, particularly between *E. hatcheri* and *E. scotti*, together with the skull similarities, is sufficient to throw *E. niobrarensis* and *E. hatcheri* into synonymy with *E. scotti*, with no more than a racial difference separating the Texas horse from the Nebraska forms. This conclusion is based purely on the published evidence; a detailed study of the skeletal topotypal material from the Hay Springs quarries in comparison with the numerous *E. scotti* skeletons may prove that the Nebraska horses differed in body proportions from the huge-skulled, medium-build Texas horse.

Equus scotti Gidley (1900*a*) was described from a nearly complete skeleton, including skull and lower jaws, from Rock Creek, Texas. *E. scotti* might represent the same species as *E. complicatus* Leidy (*nomen vanum*) and has been referred to that proposed species (Hay, 1920*b*). Since the type of *E. complicatus* (*nomen vanum*) is indeterminate and its referred materials (see, for example, Gidley, 1901*a*, Pl. XVIII) cannot qualify as topotypes, *E. scotti* remains a valid species.

Equus bautistensis Frick (1921*a*) was based on three associated upper premolars and referred topotypal upper and lower cheek teeth, incisors, and limb elements collected near Valle Vista, California. All except two of the sixteen lower cheek teeth, including two incomplete cheek-tooth series in jaw fragments, differ from the Irvington horse and others by the asymmetrical U-shaped groove between the metaconid and metastylid. This groove approaches a V shape in several specimens and is close to the pattern seen in some teeth of *E. simplicidens* and *E. shoshonensis* of the Blancan. This character, therefore, might be regarded as primitive. Approximately ten of the eighteen upper cheek teeth of *E. bautistensis* are larger than any of the uppers which have been collected at Irvington. This suggests a probable mean size difference between the two horse populations. A consistent mean size difference, together with a difference in an enamel character, could represent either species distinction or infraspecific distinction so far as the criteria of neozoölogical speciation are concerned. Because of the appearance of the possibly primitive character in the lower cheek teeth, I prefer to treat *E. bautistensis* as a valid species.

Equus pacificus Leidy (1868*d*) was a large P^3 from Martinez, California. Leidy stated that the tooth was not different from the Recent horse on its triturating surface and that it showed a more complex folding of the enamel borders of the fossettes than *E. excelsus* Leidy (*nomen vanum*). Gidley (1901*a*, pp. 116–117) thought the large horse from Fossil Lake, Oregon, belonged with this species. No

[6] The measurements and indices given in the chart for *E. scotti* were taken from the skull of a young adult, U.C.M.P. no. 10608. Gidley (1901*a*) gave no measurements for the type of *E. scotti*.

one can say that Gidley's reference is wrong, yet the type tooth bears no definitive characters. Leidy's type is not considered determinate, and *E. pacificus* will be utilized only as a *nomen vanum*.

Equus laurentius Hay (1913*b*) was proposed on the basis of a remarkably well-preserved skull and mandible found on a sand bar of the Kansas River near Lawrence, Kansas. Hay compared this specimen with *E. caballus*, *E. niobrarensis* (synonym of *E. scotti* in this paper), and *E. excelsus* Leidy (*nomen vanum*). Matthew (1926*c*, p. 180) made a parenthetical statement in the bibliography accompanying his paper that *E. laurentius* was based on a Recent skull which was mistakenly supposed by the author to be of Pleistocene age. Hay (1927*a*) offered a rebuttal to Matthew's comment and reaffirmed that the type was actually a fossil. Hay at this time compared *E. laurentius* to an Arizona "Indian Pony" but could find differences only in the postprotoconal valleys and in the fossettes. I shall regard *E. laurentius* as a synonym of *E. caballus*. It seems likely that this was a feral horse, trapped in river quicksand and subsequently permineralized in a relatively short time.

Equus lambei Hay (1917*f*) was established from a complete skull and lower jaw from Gold Run Creek, Klondike region, Yukon Territory. The specimen is among the smaller, broad-skulled horses; the teeth appear to be unusually broad, with simple enamel lines and long protocones. The upper cheek teeth are similar to many of the teeth of the Irvington horse. Although this species was differentiated from *E. caballus*, there are no justifiable criteria for this distinction when the range of variation of a Recent wild species is compared. I believe that this specimen should be identified as *E.* cf. *caballus* on the basis of its type material.

I conclude that there are not more than seven species names of caballine *Equus* in the late Cenozoic of North America which should be given zoölogical usage at this time. These species are:

Equus pectinatus Cope—Port Kennedy, Pennsylvania
E. scotti Gidley—Rock Creek, Texas
E. bautistensis Frick—Valle Vista, California
E. tau Owen (this may be a plesippine)—Valley of Mexico
E. giganteus Gidley (this may be a plesippine)—Southwestern Texas
E. cf. *caballus* Linnaeus
The Rancho La Brea–McKittrick horse (probably a distinct species)

Order ARTIODACTYLA

Tayassuidae, peccary

(Fig. 18, *a*, *b*)

Maxillary fragment containing base of left upper canine tooth, U.C.M.P. no. 38533; possibly referable to *Platygonus* LeConte because of its large size and particularly because of large upper canine tooth; *Mylohyus* reported to have weakly developed upper canine; much larger than a specimen of *Platygonus leptorhinus* Williston, U.C.M.P. no. 26639; deep indentation of palate to accommodate tip of lower canine,