Art. XXXVI.—*An Early Pliocene One-Toed Horse, Pliohippus lullianus, sp. nov.*; by Edward L. Troxell.

Contents.

I Introduction.

Ninety years ago the first fossil horse was discovered in America, but not until 1856, when Dr. J. W. Leidy described the type of *Protohippus perditus*, did the presence of a race of extinct horses especially attract the attention of anyone. For the last half century the interest in these animals has been steadily growing and in very recent years expeditions have been sent out for the single purpose of securing their skeletons.

The discovery last summer of a skeleton in the Early Pliocene, with but one toe on each foot, yet allied to the protohippine horses which are known to be mostly tridactyl, furnishes a new type of more than ordinary importance. The species is described at this time as a matter of expediency, under the genus *Pliohippus* Marsh, in order not to encroach upon Professor Osborn's revision of the horses which is about to be published.

It gives me pleasure to name the new species in honor of Professor Richard S. Lull of Yale. *Pliohippus lullianus*, then, sp. nov. is the chief subject of this paper.

The list of those who contributed to the success of the summer's expedition or who have aided in the preparation of this article is even longer than can be recorded here. The Rev. A. B. Clark of Rosebud took an interest in my work and directed me to the region where the specimen was found. Professors E. C. Case, H. H. Bartlett and Dr. F. E. Robbins, of Michigan University, have examined my manuscript and their kindly criticisms have been invaluable. Dr. W. D. Matthew and

Professor Lull have generously helped me in many ways, especially in the beginning of the work. Professors Schuchert and Osborn very kindly allowed me to study the material in their respective museums.

II *Pliohippus lullianus* sp. nov.

The specimen here described was the skeleton of a young colt about ten months old. The milk teeth are all visible and some are slightly worn; the first permanent true molar is well formed and about ready to be cut—it has, however, no apparent cement. The loose epiphyses and the incompletely ossified bones also attest the immaturity of the individual.

Vestigial teeth.—The canine teeth of both the upper and lower series are scarcely so large as the lead of a pencil, diameter 1·3^{mm}, but are about 7^{mm} in length. In life it is quite probable that they did not appear above the gum, but lay along the alveolar border and, of course, were not functional. The first deciduous molar, commonly called the wolf tooth, in the upper jaw is large, 17^{mm} antero-posteriorly, and in a later stage of wear might have been functional. The corresponding tooth in the lower jaw, like the canines, is vestigial; it measures 1·5^{mm} in diameter and standing erect in front of the larger tooth, protrudes 2^{mm} from the bone. The length, root and all, is about 7^{mm}. This tooth is not quite so large as one from a small skull of *Mesohippus;* the latter has a distinct crown, while in the former the diameter is uniform throughout.

Permanent molars.—Two uncut, permanent molars were secured, one upper and one lower. Although the upper molar is broken, it shows well certain characters which will be diagnostic of the species. The crown in its present development is less than 40^{mm} long; it is slightly curved antero-posteriorly, but the pronounced transverse curve of the horses' teeth of that period is not conspicuous; however, since the tooth is not fully formed this observation may be of less importance.

The diameter of the tooth at the crown, measured over the styles, is 30^{mm}; 1^{cm} lower it is 27^{mm} and here the width across mesostyle and protocone is 25^{mm}. With still further wear the longitudinal diameter would become less than the transverse. The lakes are broad and very simple in pattern; the horns are quite long and smoothly curved, while the enamel in places is very thick. The protocone, which does not extend anterior to its junction with the protoconule, is very long (10^{mm}), but rather narrow transversely (5^{mm}). The sides are parallel for quite a distance, making it unlike the round or oval cone of *Protohippus.* There is a sharp, thin fold, the plicaballum, between the protocone and the metaconule, which is commonly

seen in *Equus* but not in *Asinus*. The parastyle is broad, nearly 4^{mm}, and has two sharp corners; the mesostyle is sharp but not prominent, while the metastyle is merely the rounded corner of the tooth.

The first true molar of the lower jaw was preserved in good condition, but it had not attained its full development. It is thin, the width being but one-third the antero-posterior diameter (30^{mm}) at the crown; in this respect and also in the great inner extension of the parastylid, it resembles the three-toed horses. In the new species there is no well defined keel or loop antero-exterior to the protoconid. An inconspicuous groove separates the metaconid from the metastylid; it is sharp but not deep and fades out after running slightly more than half the length of the crown. This is like *Protohippus* and results from the narrowness of the metaconid-metastylid column (10^{mm}) and its nearness to the protoconid and hypoconid; the latter are about equal in size. Near the root the entostylid blends into the entoconid and here the longitudinal diameter of the tooth is reduced to 25^{mm}. There is no cement on the tooth.

Skull.—The antero-orbital fossa shows distinctly the lachrymal and malar parts which are commonly seen in Pliocene horses. Although they form a continuous cavity, the two pits are separated by a faint ridge running from the infra-orbital foramen and the posterior border consists of two distinct, overhanging shelves.

The presence of a large depression in this region precludes the possibility of long crowned teeth like those of the modern horse, for both would have to occupy the same space. The exact purpose of this pit is not known, but it is generally thought to have been the seat of a scent gland, which, like the larmier of the deer, was peculiar to animals living in a wooded or hilly country. Presumably, as the horses came to live on the open plains they had less need for such a device to assist in recognizing members of the race, but they had greater need for the long grazing teeth; so that in later generations the pit gave place to the longer crowns, while the increased range of vision in the open country made it no longer necessary to depend on the sense of smell. Even in the life of the individual it is possible that the pit became somewhat obliterated as the lengthening of the skull made room for the incoming molars; we find the lachrymal and malar pits seemingly best developed in young animals. According to Owen (Anat. of Verts. III, pp. 633) the presence of the "maxillary" pit in the antelope is associated with those animals which go in pairs.

It has been suggested that the antero-orbital pit may have marked the insertion of a muscle in an animal with a rather

long proboscis, but this seems very doubtful. In the present specimen the bone is thin and its surface is smooth; generally a place of muscle attachment is rugose, thick and porous. The

FIG. 1.

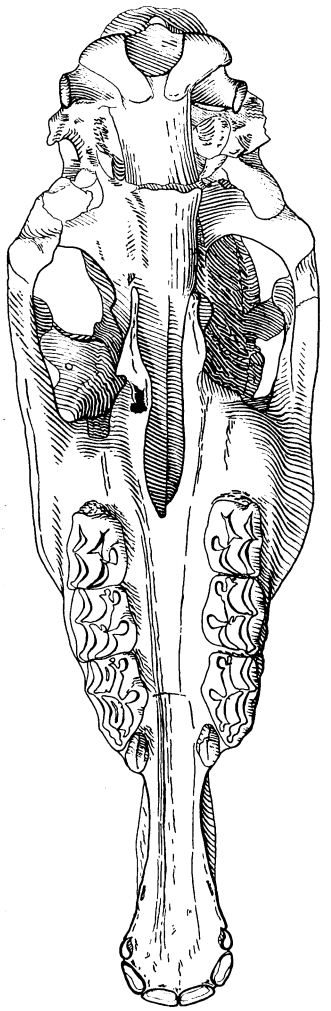

FIG. 1. SKULL. Ventral view. One-third natural size.

FIG. 2.

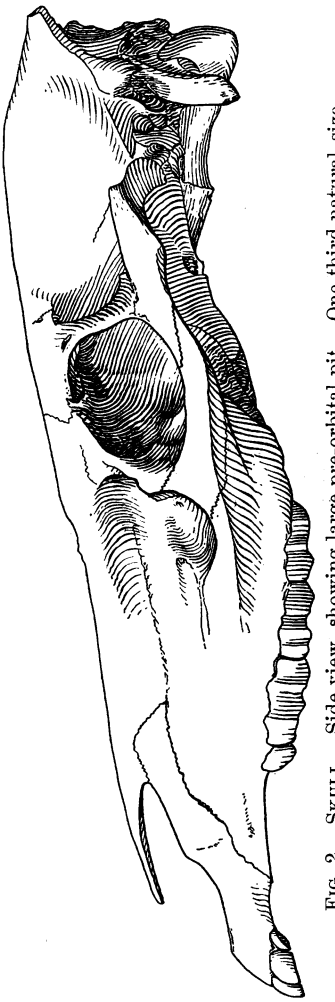

FIG. 2. SKULL. Side view, showing large pre-orbital pit. One-third natural size.

facial pits and narrow muzzle give the skull a very thin appearance above and in front of the molar teeth. In a mature specimen the region in front of the orbit would have been much longer, in order to furnish room for the six permanent molars instead of the three deciduous ones.

The antero-orbital pit is of little value as a means of identifying the species, the genus, or even the sub-family, for it seems to be a variable feature depending on age or sex. We find both portions well developed in *Protohippus* and *Merychippus*

FIG. 3.

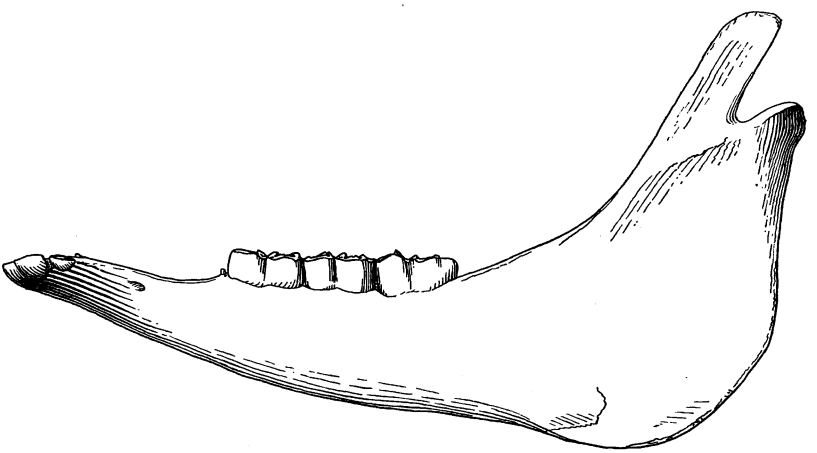

FIG. 3. RAMUS. Side view. One-third natural size.

FIG. 4.

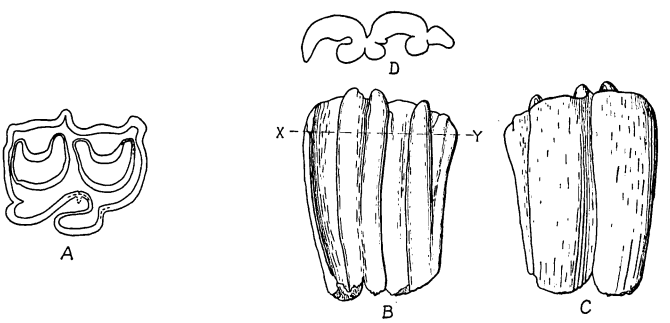

FIG. 4 PERMANENT MOLARS. Two-thirds natural size.

A, a section 1cm from the crown of first true, upper molar. B and C, inner and outer side views of first true, lower molar. D, a section on line, X–Y, of B.

and the lachrymal pit is even conspicuous in some of the Anchitherinae, especially in that aberrant form, *Hypohippus*.

On its lower border the ramus has a single large curve in front of the angle; it is like that of *Asinus* and *Hippanion*

rather than *Equus*, but in the present specimen it may be a character of youth. In the atlas the anterior notch is not closed to form a foramen, in which respect it resembles the more primitive forms. Likewise the intra-vertebral foramen in the axis is not inclosed, showing that it is either primitive or immature.

Fore limb.—The bones of the limb are very slender. In length the cannon bone nearly equals that of *Equus scotti*, but

FIG. 5.

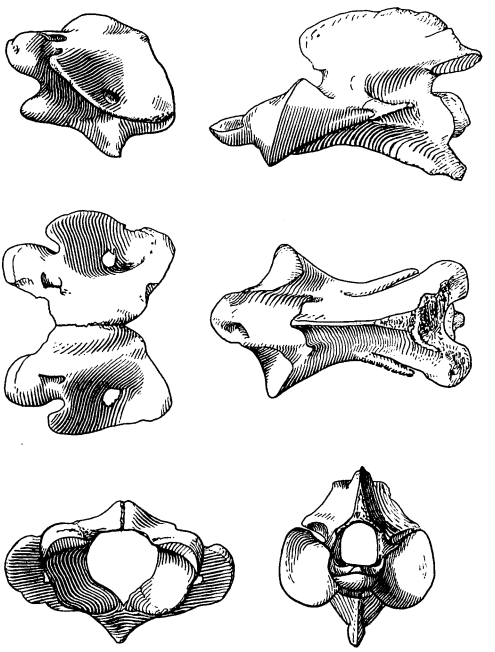

FIG. 5. ATLAS AND AXIS. Lateral, dorsal and anterior views. One-third natural size.

the width is scarcely more than half as great. The distance from the hoof to the elbow, which constitutes about half the height of a horse, in the new species is 23 inches; therefore the whole height is approximately 3 feet and 10 inches. Since the scapula and humerus are not so long relatively, this dimension may be less.

It is important to note that the distal segments, especially the cannon bones, are long, suiting the animal to greater speed, and here may be seen evidence that the race had changed its

habitat. Slenderness and lightness in general are cursorial adaptations to the needs of the individual; for instance, where food and water are scarce the animal has to go farther to satisfy its wants. Moreover, life in the open country was imperilled by preying animals and the little horses had less opportunity to hide and dodge about among bushes or over hilly country; to offset this disadvantage they had to be able to outdistance any pursuers.

Aside from the actual rate of speed, the long-limbed animals seem to be better suited to long continued effort. The slenderness of the cannon bone sometimes goes beyond the point of fitness for speed; the Arab, which is probably our swiftest horse, has only a moderate speed index: 7·26; on the other hand the ass, with a higher index: 8·68, is noted for its endurance but not for its actual speed. It is equally true that where food is scarce nature has to economise, hence the slender, small-boned type is better suited to the environment where less material is available for building up the frame.

As a matter of fact the limbs of *Pliohippus lullianus* are not out of harmony with the general build; it stands three feet and ten inches, while an ordinary horse may be five feet high. The linear dimension of the former is $\frac{3}{4}$ that of the latter; if all the proportions are the same the relative weights would be as the cubes of 3 and 4, that is as 27 and 64; the larger horse would weigh over twice as much and would therefore need greater strength of limb. However, the present specimen, being a colt, does not show the development of the adult, so it is quite probable that later the bones would have increased considerably in diameter, while changing only slightly in length.

Radius and ulna.—A unique feature in this one-toed horse is the complete ulna, separate throughout from the radius. As in the modern horse, the proximal and distal portions serve as part of the articulations; unlike it, the middle portion is not fused to the radius but lies along its posterior surface, a mere remnant of a former functional member.

The shaft of the ulna in its smallest part is 2^{mm} wide and a little more than half as thick. The distal epiphysis is a long segment ($3{\cdot}4^{mm}$) which joins the shaft well above the epiphysis of the radius and conforms to the contour of the latter. The radius is quite slender through its middle portion, but the ends are large; the junction planes of the epiphyses mark the largest parts. The form would change somewhat with age as the shaft fills out to correspond to the heavier joints.

Metacarpals.—The especial character which distinguishes this specimen is its monodactyly. It has commonly been predicted that one-toed specimens of the Protohippinae would be

Measurements of the Radius.

Shaft ant-post	17mm
Proximal and ant-post	33
Distal end ant-post	40
Shaft transverse	24
Proximal end transverse	58
Distal end transverse	56
Length	263

FIG. 6.

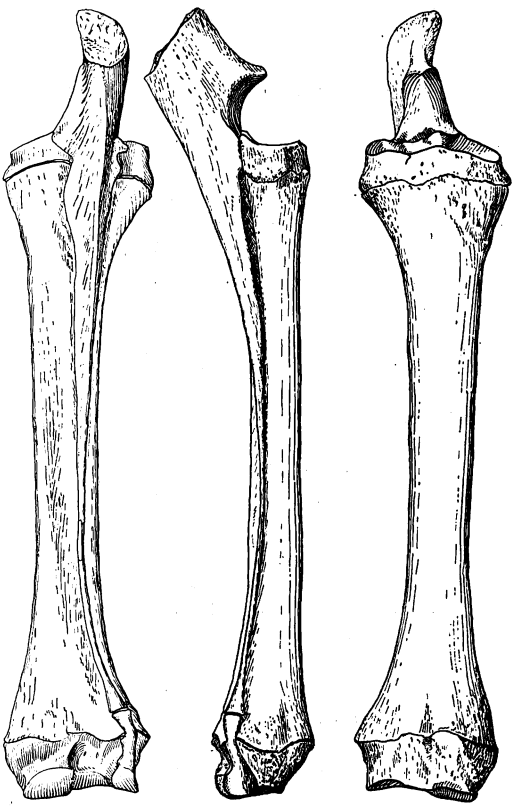

FIG. 6. RADIUS AND ULNA. Rear, side and front views. One-third natural size.

found, but no positive evidence of this feature has, heretofore, been presented.

The splints, Metacarpals II and IV, unlike those of *Equus* extend the lengths of the cannon bone, but like those of the modern horse they bear no digits on the ends. These slender

bones are large proximally, but at once decreasing in size they run at a uniform diameter to the middle; in the next fourth of the distance they decrease to a width of about 3^{mm} and a thickness of less than 1·5^{mm}. The distal ends are enlarged to

FIG. 7.

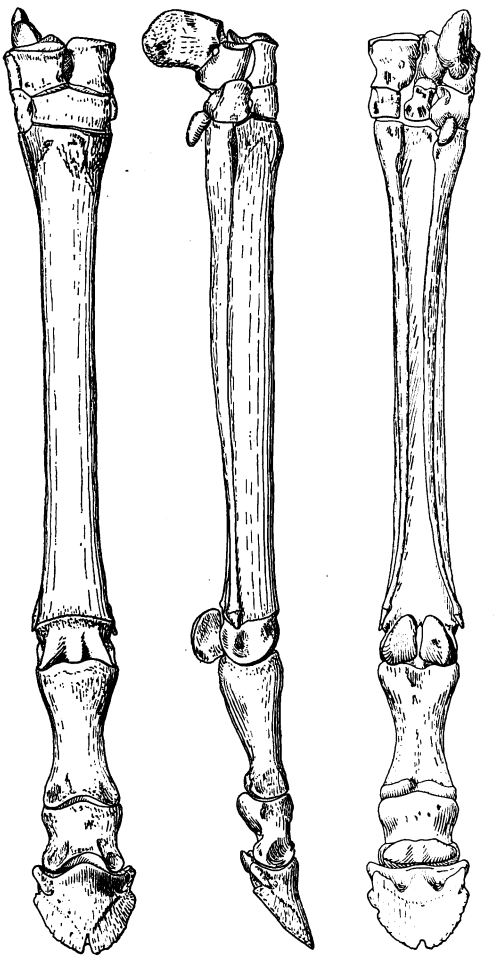

FIG. 7. RIGHT MANUS. Front, side and back views. One-third natural size.

receive the pointed epiphyses, the larger one of which measures 6^{mm} in length. They show no evidence of articular facets; in fact their very sharp ends eliminate the possibility of their ever having borne phalanges.

Metacarpal IV has a diameter greater by 1·5^{mm} than that of II. This difference in size is the character upon which Marsh sought to found *Pliohippus gracilis*, but the species has been ruled out (Lull, Gidley) and the feature upon which it had been established is considered of little importance except as it signifies the unsymmetrical reduction of the foot. The dissymmetry of the foot is also shown by the presence of a small nodule of bone representing the fifth metacarpal; while on the other side the remnant of metacarpal I is not even positively known in the earliest forms of *Eohippus*, showing that the first digit was much more progressive in its reduction. The vestigial metacarpal V has two articular facets joining it with the unciform and metacarpal IV. It harps back to the period of *Eohippus*, when for the last time the front foot bore the phalanges of a fourth toe.

Third phalanx.—The hoof of *Pliohippus lullianus* is very flat, especially in comparison with that of *Equus scotti* or *E. caballus*. The angle of the front slope in the new type is about 27½° and in this respect approaches that of *Mesohippus:* about 22½°. In *Equus* this angle measures over 45°. The feet have a different structure as a result: in *P. lullianus* and the earlier genera the second phalanx hangs on the back of the hoof with no part of the articular surface horizontal, while in the modern genus a part of the weight transmitted falls directly upon the hoof bone, a device better suited to the greater weight. The cleft in the anterior border of the ungue of the new type is a very primitive feature, one not found in *Equus* but common in the earlier forms.

Measurements in millimeters :—

Cannon bone	*Asinus*	*P. lullianus* ratio %		*E. scotti* ratio %	
Width distal	35·8	*84*	30	*52*	57·7
Diameter of keel, ant-post.	27·8	*94*	26	*61*	42·7
Shaft transverse	22·0	*86*	19	*46*	41·0
Proximal width	38·5	*88*	34	*59*	57·3
Proximal ant-post.	25·3	*99*	25	*60*	41·5
Length	191·0	*115*	219	*90*	244·0
Speed index	8·68		11·53		5·95

First phalanx	*P. lullianus*
Proximal width	32
Distal width	29
Shaft width	19
Proximal, ant-post.	25
Shaft, ant-post.	12
Length	56

Second phalanx	*P. lullianus*
Proximal width	31
Proximal, ant-post.	20
Length	26
Third phalanx, hoof	
Altitude	20
Width	40
Length	36

Comparative measurements of types: *P. lullianus* nov. *P. pernix* Marsh

		ratio %	
Ant-post. diameter of wolf tooth	16	*81*	13
Ant-post. diam. of first upper true molar	27	*81*	22
Ant-post. diam. of second deciduous molar	36	*86*	
" " " " premolar			31
Extent of four upper deciduous molars	107	*82*	
" " " " premolars			88
Extent of three lower deciduous molars	89	*83*	
" " " " premolars			74
Length of radius	263	*96*	253
Width of proximal end	59	*83*	49
Width of articulation, distal	44	*81*	40
Length of cannon bone	219	*86*	189
Length of first phalanx	56	*98*	55
Length of second phalanx	26	*96*	25
Length of hoof bone	36	*106*	38
Width of hoof	40	*125*	50
Length of skull	380	*108*	410

III. *Geology of the Oak Creek Formation.*

The skeleton of the new type was found in the eastern part of the Rosebud Indian Reservation, near the town of Mission, South Dakota. This Reservation, at least the western part in the Miocene formation of the valley of the Little White River, has long been a favorite hunting ground for specimens of extinct animals.

The region east of Mission is slightly rolling but a very fertile farming country. Because it is so productive of vegetation, it was generally considered an unprofitable place to hunt for fossils, for only at infrequent intervals along the crests of the hills is the bed rock of the later formations well exposed. Most of this land has been allotted to the Indians, whose present peaceful life is in great contrast to that of the time of Marsh and the other early explorers.

A table land, whose northern escarpment extends in a direct line for quite a distance and rises about 200 feet above the valley floor, forms a divide between the Keyapaha and the valley of Oak Creek. In nearly every direction the flat topped hills can be seen, all apparently conforming in height.

Few geologists have visited this area, but one, A. B. Reagan,* while carrying on his missionary work among the Indians, paid much attention to the earth formations and collected many

* Albert B. Reagan, American Geologist, vol. xxxvi, pp. 229, 1905.

fossils. He identified and described the Miocene formation, but in the region east of his district he erroneously assumed that the rocks were of Cretaceous age; the fact is that a later formation exists there and the fauna indicates the Early Pliocene.

The rock is entirely of sandstone and most of it is very fine-grained. The variety of the grains, their rounded form and the absence of larger components, suggest the probable eolian origin of the formation, although the sand was shifted and finally deposited by running water. The lower strata are much harder because the grains are much more firmly cemented together; the rock of the main quarry, on the other hand, is not so compact, but is soft enough to be cut with a knife. Under the microscope the cementing substance, which in this case is calcium carbonate, has a filmy appearance and incompletely fills the open spaces between the grains of sand. Where the sandstone is very indurated it stands out in bold cliffs, and bowlders of considerable erosional resistance cover the slopes. The alternate harder and softer areas give rise to differential weathering and in some places result in deep natural caves. That this formation was built up by a stream is quite certain, for the sand, the irregularity of the bedding planes, the discontinuous layers, the water-worn bones and the posture of the complete skeleton, all show this.

In one of the canyons there appeared to be an irregular line marking the boundary of an unconformity and at the bottom of the *P. lullianus* quarry itself, there was a floor of hard sandstone only a few inches beneath the complete skeleton. There was also other vertebrate material, consisting mostly of teeth and small bones, resting on this floor or only an inch or two above it. The peculiar association of this fragmentary material, most of which was water worn, with the complete skeleton, suggests the secondary deposition of these broken parts along with the original deposit of the whole skeleton. The same torrent which washed out and broke up the other bones, once buried, may have engulfed the colt which is now the type of the new species. There is a strong probability that this less consolidated formation is a channel deposit, resting upon and within the Upper Miocene or Earliest Pliocene, but itself of later age, for we frequently find patches of a later formation occupying the old valley of some prehistoric river. Since the Pliocene is commonly considered a period of uplift and also of semi-arid conditions, there would be few streams and no great amount of stream action; we, therefore, consider this one of the rare deposits representing the period.

Associated fauna.—Rhinoceroses are represented by fragments in the quarry and by more complete bones in the neigh-

boring outcrops. They are abundant in the Lower Pliocene but in all probability soon became extinct. At this time they seem to have reached their maximum size and are probably best known by the specimens, from Long Island, Kansas; *Teleoceras fossiger* (Cope) seems very close to the variety with short stout limbs represented in the Oak Creek locality.

Ivory from the main quarry, together with parts of tusks and skeletal material from near-by places, shows the presence of a very large proboscidian in the fauna. It may represent any one of several types of Mastodon, which in the Early Pliocene reached a very great size.

An incomplete skeleton of *Merycodus* sp. was found an eighth of a mile away and about seventy-five feet lower than the stratum bearing the horse skeleton. This genus is well known in the Miocene and Lower Pliocene and is rather common. There is a general resemblance in all these forms except that some are almost twice the size of others. The present specimen is one of the largest known to the writer and is, therefore, assumed to be a very late form. It is more than a third larger than the type of *M. necatus sabulonis* of Matthew and Cook* and is twice the size of their smallest specimen: *Merycodus* sp. indesc.; it is also 1/7 larger than the type of *M. osborni* (Matthew). Merriam reports† *Merycodus* from the California Pliocene or Late Miocene, and in size the specimen from the Tejon Hills is quite equal to that from South Dakota.

The absence of *Merycodus* in the Blanco of Texas is taken as an evidence that the formation is distinctly more advanced than most Pliocene deposits. Scott says "these peculiar hypsodont deer persisted even in the Older Pleistocene," but most authors do not credit them with such a long existence. Osborn reports this animal mostly in the Lower Pliocene and it seems quite probable that this was near the close of their career.

The single molar tooth of a grazing camel gives no trustworthy evidence as to the definite age of the formation, for these camels are very abundant in the Upper Miocene and continue on until the Pleistocene.

In this single locality three-toed horses of the *Protohippus* and *Hipparion* type were found, in addition to the new species. Of the true *Protohippus* both large and small species were represented. Three miles from the main quarry, an almost complete specimen was found which resembles *Protohippus placidus*, especially in its size. The association of feet

* Matthew, W. D., Cook, H. J., Bull. Am. Mus. Nat. Hist., vol. xxvi, pp. 412, 1909.

† Merriam, J. C., Univ. Cal. Publ., Bull. Dept. Geol., vol. viii, No. 13, pp. 287, 1915.

and teeth render it of unusual value for comparative study. *P. placidus* is usually found in the Miocene, and this small horse, without the malar pit and with semi-functional lateral toes, shows characters seemingly too primitive for the Pliocene period.

The fauna of this Oak Creek formation corresponds closely with that of the Snake Creek Beds of Western Nebraska; the latter, though resembling the Republican River Beds of Western Kansas, show a more modernized type of animal life and are considered by Matthew and Cook to be intermediate between the Blanco of Texas and the Upper Miocene. The Oak Creek formation, while in some respects like the Etchegoin of California, Middle Pliocene, is not so far advanced and in all probability belongs to the Early Pliocene.

IV. *General Conclusions.*

Pliohippus lullianus, the earliest one-toed horse now known, is here made the type of a new species. It is tentatively assigned to *Pliohippus* Marsh, awaiting the final settlement of the status of that genus, which, founded upon an imperfect specimen, has been alternately accepted and rejected.

Observations by Merriam, Osborn, Lull and others, point to the protohippine horses as the group from which the modern race was derived, and it is probable that *Pliohippus lullianus* sp. nov. was near if not directly in the ancestral line. Through its unique characters it seems to offer the connecting link between its three-toed ancestors and the monodactylous *Equus*.

The fauna indicates that the age of the beds, from which the new type came, is Early Pliocene, a period of grass-covered plains. Because the climate was semi-arid and there was little stream action, the deposits of that period are rare and at the present time are nearly always hidden beneath the luxuriant vegetation of the region.