# A LOWER MIOCENE HORSE, ANCHITHERIUM AGATENSE (OSBORN).

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SUMMARY.

A description is given of *"Kalobatippus" agatensis,* a long-limber but comparatively short-faced anchitherine horse from the lower Harrison formation (lower Miocene), and a reconstruction attempted. It is suggested that *Kalobatippus* be included in the genus *Anchitherium.*

## INTRODUCTION.

In 1918 Osborn[1] described, as *Kalobatippus agatensis,* a horse from the lower Harrison beds of western Nebraska, the remains consisting of the jaws and a partial skeleton. It was clearly a member of the anchitheriine group of structurally conservative but comparatively large horses, and because of its long limbs was placed in the genus *Kalobatippus,* the type species of which is a long-limber anchitherline from the Upper John Day formation of Oregon.[2] Since that time, a number of specimens of the lower Harrison form have come to light in the collections of the Field Museum of Natural History and Walker Museum of the University of Chicago, which permit of a fuller description.

## DESCRIPTION.

*Material.* Apart from the type and one other specimen in the American Museum of Natural History, the following specimens are known to me:

Walker Museum 1455. Left half of skull, jaws, nearly complete scapula and forelimb, partial hind limb, several vertebræ. One mile south of Van Tassell, Wyoming.

Field Museum 12147. Skull and jaws, nearly complete limbs and girdles, several vertebræ. Rawhide Buttes, Wyoming.

FM 12324. Lower jaws, most of hind limb, a number of vertebræ. Rawhide Buttes.

[1] Memoirs, Amer. Mus. Nat. Hist., n. s. vol. 2, pt. 1, 71-72, 1918.

[2] Osborn, in Cope—Matthew, "Plates of Tertiary Mammals and Permian Vertebrates," Amer. Mus. Nat. Hist. Monograph series No. 2, plate CVIII, 1915.

FM 12289. Scapula, part of manus, hind limb, vertebræ. Rawhide Buttes.

FM 12093. Dentition (poor), femur, tibia. Rawhide Creek, Wyoming.

FM 12280. Jaws, Rawhide Creek.

FM 12042. Dentition, Rawhide Buttes.

Fig. 1. *Anchitherium agatense.* Skull, FM 12147 (incisor region from WM 1455). Jaw, WM 1455 (the region of $p_1$ and the tip of the ascending ramus from FM 12147). x 1/3.

*Skull.* This was previously unknown. The combined lachrymal and malar fossæ are moderately shallow. The orbit has its anterior border over the anterior margin of $m^2$, with a facio-cranial index of 51, in marked contrast to *K. præstans,* the genoholotype. The orbit is not enclosed behind. The basilar length of FM 12147, with allowance for slight imperfections anteriorly, is 308 mm., the vertex length 359 mm. WM 1455 agrees closely with FM 12147 in size and all essential characters, although an imperfection in the cranial region of the former prevents the taking of comparative measurements. (Fig. 1.)

*Jaw.* Described, in the main, by Osborn. The angular region is well rounded as in some species of *Miohippus* and *Hypohippus equinus,* and in contrast with *Parahippus.* The coronoid is quite long, as in *H. equinus.*

*Dentition.* Measurements are given in Table I; there is a variation of about 5% in known specimens. The upper dentition as seen in the side view of the skull is that of a considerably worn set; in comparatively unworn teeth (as WM 1455) the height of the crowns is comparable to that in *Anchi-*

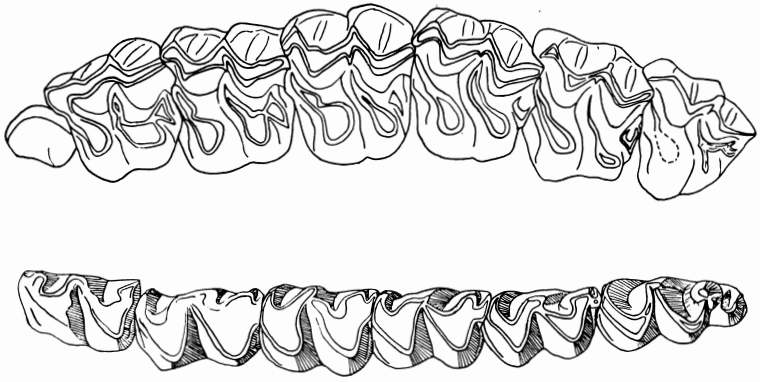

Fig. 2. *Anchitherium agatense.* Dentition, WM 1455. x 4/5.

*therium aurelianense.* In WM 1455 the metaloph is not united to the ectoloph; in the other specimens, somewhat more worn, this union has taken place. The external ribs are prominent. Molar 3 is reduced in the specimen illustrated, less so in other specimens. The teeth are somewhat more crested than in *K. præstans.* The internal cingulum is absent. The incisor row is not so broadly rounded as in *K. præstans* or *Parahippus.* There is practically no diastema between the upper incisors and canine. The upper premolars are broad as compared with those of *K. præstans;* Osborn has noted a similar condition in the lower premolars. In FM 12147 and

TABLE I.

Tooth Measurements, *Anchitherium agatense.*

| | WM1455 | FM12042 | FM12280 | FM12147 | FM12324 | Type |
|---|---|---|---|---|---|---|
| $p^1-m^3$ | 125 | 135 | — | 126 | — | — |
| $p^2-m^3$ | 115 | 120 | 121 | 112 | — | — |
| $p_1-m_3$ | — | 137 | — | 132 | 130 | — |
| $p_2-m_3$ | 125 | 127 | 126 | 122 | 124 | 128 |

TABLE II.

Limb Measurements, *Anchitherium agatense.*

| | WM1455 | FM12147 | FM12324 | FM12289 | FM12093 | Type |
|---|---|---|---|---|---|---|
| scapula, length | — | — | — | 255 | — | 249 |
| humerus, length | 211 | — | — | — | — | 217 |
| radius, length | 251 | 283 | — | — | — | — |
| mtc. III. length | 198.5* | 209 | 215 | 211 | — | 225 |
| width, halfway | 20.5 | 24.5 | 22.5 | — | — | 20 |
| 1 phal., l., side | 29 | 33 | — | — | — | 41 |
| width, halfway | 21.5 | 27 | — | — | — | 25 |
| 2 phal., l., side | 19.5 | — | — | — | — | — |
| width, halfway | 23 | — | — | — | — | — |
| femur, length | — | — | — | — | 336 | — |
| tibia, length | — | — | — | 335 | — | — |
| mts. III, length | — | 242 | 242 | 246 | — | 252 |
| width, halfway | — | 24.5 | 23 | 23 | — | 20 |
| 1 phal., l., side | 32 | 36 | 31 | 27 | — | 39 |
| width, halfway | 22.5 | 29 | 29 | 30 | — | 22.5 |
| 2 phal., l., side | 20 | 22 | — | — | — | 30 |
| width, halfway | 23 | 28.5 | — | — | — | — |

*Shaft incomplete; length exceeds 200 mm., at least.

FM 12042 the "parastyle" of $p^2$ is somewhat larger and more distinct than in the specimen figured. In FM 12147 there is a cingulum cusp on $m^3$ internal to the hypocone; this is not present in other specimens.

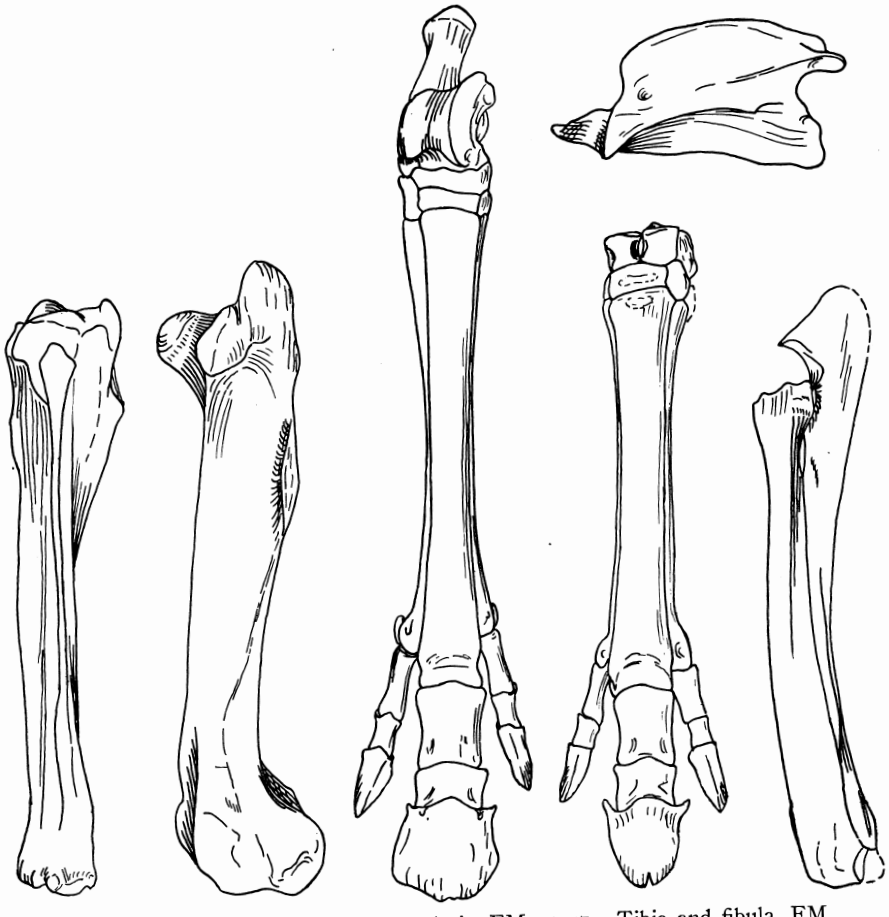

Fig. 3. *Anchitherium agatense.* Axis, FM 12147. Tibia and fibula, FM 12289. Femur, FM 12093 (greater trochanter from WM 1455). Pes, manus, FM 12147. Radius and ulna, WM 1455. All x 1/4.

The lower dentition is present in the type and has been described by Osborn. In Fig. 2 the less worn dentition of WM 1455 is given, and shows the same general features; the entoconulid of $m^3$, however, is not distinct. A minor variant is a tiny cusp between the hypoconulid crest and the entoconid; this cusp is absent in FM 12147 and FM. 12042. In the last mentioned specimens there is no separate entoconulid, but the hypoconulid ridge is strongly recurved internally toward the entoconid.

*Axial skeleton.* The specimens add little to our knowledge here. Atlas and axis, the latter hitherto unfigured, as well as a number of cervicals, are present in WM 1455, FM 12147, and FM 12289. The odontoid is similar to that of *H. equinus,* as described by Scott.[3] A few dorsals and ribs, a series of lumbars and a sacral are preserved, as mentioned under the heading of "Reconstruction." (Fig. 3.)

*Limbs.* These were incompletely known in the type, although the general features were noted by Osborn. In Table II a number of comparative measurements are given.

Scapulæ which agree well with that of the type are present in three specimens. The pelvis is present in FM 12147, but not so well preserved as to merit detailed description. The humeri were found on both sides in WM 1455 and FM 12147, but only one specimen preserves its entire length, and in none is the greater tuberosity present. The femur is complete in length only in FM 12093, with which incomplete specimens from FM 12147 and FM 12324 agree as far as preserved; the greater trochanter is present only in WM 1455. Radius and ulna are complete in both FM 12147 and WM 1455. The two bones are not co-ossified. As Matthew (in mss.) has noted, the radius is flattened on the anterior surface on the proximal half, and antero-internally in the distal half and although slimmer much resembles that of *H. equinus.* A complete tibia and fibula are present in FM 12289; the tibia is shorter in proportion to the metatarsus than in *K. præstans.* The fibula is co-ossified distally with the tibia.

The tarsus and portions of manus and pes were known in the type. Large portions of both the manus and pes are present in WM 1455 and FM 12147, and the pes in addition in FM 12324 and FM 12289. This permits us to figure these parts in their entirety. All specimens agree well in structural features. In proportions, however, there is considerable variation, as is seen in Tables II and III. The metapodials are considerably slender in the type than in FM 12147, while FM 12324, WM 12289, and WM 1455 are intermediate in this respect. There appears to be comparatively little difference between the specimens in the length of the metapodials as compared with the length of the tooth row.

Of the carpus, only the magnum was previously known; the present specimens exhibit all the elements except the trapezoid. The carpals are comparable to those of the European *Anchi-*

[3] Trans. Amer. Phil. Soc., n. s. 19, 94-122, 1896.

*therium,* or *Hypohippus.* The presence of a fifth metacarpal is indicated by a facet of moderate size.

*Species.* As mentioned above, there are dental variations in the material, and a considerable variation in limb proportions. However, recent studies, such as those of Matthew on the Snake Creek fauna, tend to show that wide variations may occur within the limits of a single species of horse. The dental differences are of minor nature; intergrades are found in the limb types; and it is probable that we have to deal here with but a single species, *"Kalobatippus" agatensis.*

## RESTORATION.

Although no single individual is complete enough for a satisfactory mount, the complete anatomy is now known, with the exception of portions of the vertebræ and ribs. For the purpose of restoration (Fig. 4) FM 12147 has been used as a base. This possesses the skull and nearly complete limbs. The incomplete humerus, femur, and tibia have been completed from WM 1455, FM 12093, and FM 12289, respectively.

The axial skeleton is admittedly a composite. The axis and third cervical are present in the specimen used; the other cervicals are present in the type and most of them in WM 1455 and FM 12289 as well. The dorsal region is very poorly known in material available to me. The specimen used has two anterior dorsals with a length of centrum of 32 and 30 mm.; WM 1455 possesses two anterior dorsals with lengths of 30 and 25+. Of more posterior dorsals, FM 12289 possesses three, nearly in sequence, with lengths of 40, 45, and 45 mm., and FM 12147 has two, with lengths of 44 and 50 mm. There is a fair amount of rib material, but it is for the most part fragmentary. FM 12289 retains a fragment of the last dorsal, followed by five lumbars, with lengths of 52, 56, 52, and 54 mm. for the first four. Then there appears to be one vertebra missing, following which the last lumbar (length 34 mm.) is found attached to the first sacral. The remainder of the sacrum and the tail are lacking.

## DISCUSSION.

*Anchitheriine Horses.* From the above description it is obvious that *"Kalobatippus" agatensis* differs from the genoholotype, *K. præstans,* in many respects. A consideration of

the characteristics of anchitheriine horses leads to the conclusion that the genus *Kalobatippus* cannot be clearly separated from *Anchitherium* and that its members should be placed in the latter genus.

The Anchitheriinæ (excluding for our purposes *Mesohippus* and *Miohippus*, as being ancestral to the protohippines as well

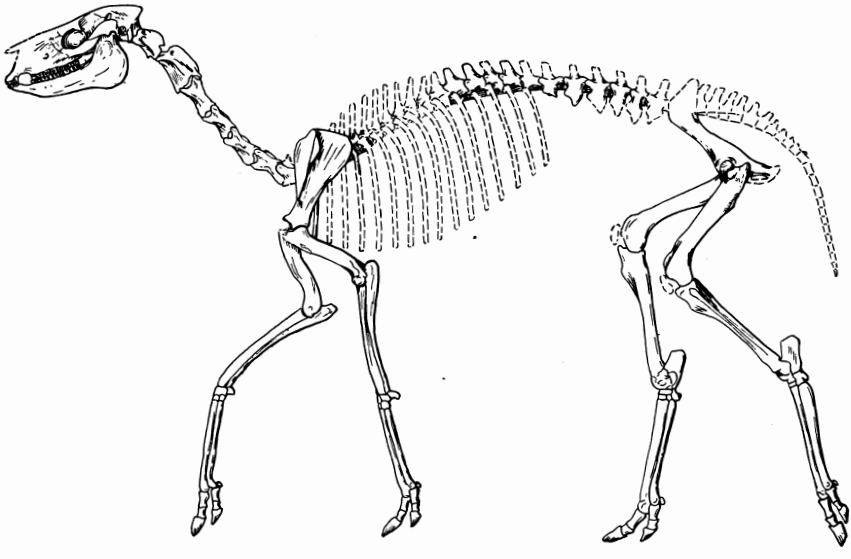

Fig. 4. Restoration of *Anchitherium agatense*. Mainly after FM 12147 (see text). x 1/12.

as to the forms here considered) constitute a Miocene side branch of the Equidæ; they include *Anchitherium* proper, of Europe, *Hypohippus* of North America and China, *Kalobatippus præstans, K. gracilis* (a fragment of uncertain horizon, not further considered) and *"Kalobatippus" agatensis. Archæohippus* usually has been placed here, but a recent, and as yet undescribed, find by the American Museum of Natural History shows that this genus belongs elsewhere.

*Common characteristics.* These forms have been described as "forest horses," which have increased in size with a retention of primitive structures. They were apparently browsers, as indicated by the (usually) brachyodont teeth and the development of a simple lophoid pattern differing little from that of *Miohippus;* the crochet and other complications found in

TABLE III.

Anchitheriine limb ratios.

| | "*K.*" *agatensis* type | WM 1455 | FM 12147 | FM 12324 | "*K.*" *præstans* | *Hypohippus* | *Anchitherium aurelianense* |
|---|---|---|---|---|---|---|---|
| Mtc. III index | 9 | 10* | 12 | 11 | — | 12 | 12 |
| Mts. III index | 8 | — | 10 | 10 | 8 | — | 13 |
| $\frac{p^2-m^3}{Mtc.\ III}$ | — | 58* | 54 | — | — | 66–69 | 62 |
| $\frac{p_2-m_3}{Mtc.\ III}$ | 57 | 63* | 58 | 56 | — | 73–74 | 65 |
| $\frac{p^2-m^3}{Mts.\ III}$ | — | — | 46 | — | 48 | 59 | 59 |
| $\frac{p_2-m_3}{Mts.\ III}$ | 51 | — | 51 | 50 | 52 | 65 | 61 |
| $\frac{1st\ phal.}{Mtc.\ III}$ | 18 | 15 | 16 | — | — | 20–22 | 19 |
| $\frac{1st\ phal.}{Mts.\ III}$ | 15 | — | 15 | 13 | — | 19–22 | 15 |
| $\frac{2nd\ phal.}{Mts.\ III}$ | — | — | 9 | — | 10 | 12–14 | 11 |

*Shaft incomplete; figures should be lower than those given.

the protohippines are absent; the metastylid is not generally separated. There is a tendency toward the reduction of the posterior molars. The orbit remains unenclosed. The feet are persistently digitigrade, with the retention of functional lateral digits; the lateral metapodials are (as far as known) little reduced, and have flattened shafts as contrasted with the protohippines; the phalanges are short and broad. The third metatarsal articulates with both mesocuneiform and cuboid.

*Variations.* There are a number of features in which variation may be found within the group. It is upon these that generic differences must be based. The limbs exhibit the greatest range of variation; comparative measurements are given in Table III.[4] *Hypohippus* and *Anchitherium* proper

[4] No associated skeleton of the European *Anchitherium* has been described; the ratios given are derived from the average of unassociated elements described by Kovalevsky and Filhol, and hence can only be regarded as approximates, although the bones are those of animals from one locality and presumably adults of one species.

are quite conservative, although it is quite probable that "advanced" species of both will show a considerable variation from primitive conditions when better known. *K. præstans* and *agatensis*, on the other hand, while retaining short phalanges and probably a primitive digitigrade gait, have elongate metapodials. It is to be noted, however, that similar

TABLE IV.

Variations in Anchitheriine Skulls and Dentitions.

| | *"K." praestans* | *"K." agatensis* | *Anchitherium* | *Hypohippus* |
|---|---|---|---|---|
| Position of anterior border of orbit | posterior border $m^3$ | anterior border $m^2$ | anterior border $m^2$ | anterior border $m^2$ |
| Lachrymal and malar fossae | shallow | shallow | moderately deep | variable |
| Molar crowns | brachyodont | brachyodont | brachyodont | variable |
| Comparative degree of cresting of molars | 1 | 2 | 4 | 3 |
| Comparative degree of reduction of $m^3/_3$ | 1 | 2 | 3 | 3 |
| Internal cingulum | absent | absent | present | variable |
| Incisor row broadly rounded | yes | no | no | no |
| External ribbing of upper molars | present | present | obsolete | absent |

differences in *Mesohippus* and *Miohippus* are not regarded as of generic value.

Eight recognized variable features of the skull and dentition are listed in Table IV. Of these only one, the position of the anterior border of the orbit, is worthy of serious consideration in the formation of a generic diagnosis. The remainder are of small value, and almost all can be shown to be variable within the limits of a genus in the forms listed or in other genera of Oligocene and Miocene horses.

*"Kalobatippus."* Fifteen characters were listed by Osborn (1918 p. 69) after Matthew, as definitive of this genus (as regards the skull these were necessarily based upon *K. præstans*). Of the fifteen, six (Nos. 1, 3, 8, 13, 14, 15) are general anchitheriine characters, noted in a previous section.

Five (Nos. 2, 4, 6, 7, 9) are not true, or only partially true, of *"Kalobatippus" agatensis;* these relate to the position of the orbit (radically different in the two forms) and to dental characteristics (given in the table) by which the Harrison form, at least, cannot be clearly separated from *Anchitherium* proper. Several others (Nos. 5, 10, 11) relate to the absence of the internal cingulum and the shallowness of the combined lachrymal and malar fossæ. These are common characters, but characters of little value.

Only one important feature is common to both forms (Osborn's No. 12), the presence of long metapodials and short phalanges. But, as previously mentioned, even this is not considered as a criterion of generic difference in *Miohippus* and *Mesohippus.*

Thus nothing remains by which *"Kalobatippus"* may be separated from *Anchitherium* except the length of the metapodials. As regards the genoholotype alone, the posterior shifting of the orbit is a second feature; but even with this addition the differences are not marked. It would seem advisable to return to a broader generic concept and include the members of *"Kalobatippus"* in *Anchitherium.* Except for the elongation of the limbs *"K." agatensis* would be a suitable ancestor for the entire group.

*Hypohippus.* This genus is also very difficult to separate from *Anchitherium* on the basis of the better known species, *H. equinus* and *H. osborni.* However, as pointed out to the writer by Dr. Matthew, the genoholotype and other imperfectly known later Miocene forms are "advanced" in dentition and perhaps in the limb skeleton as well. When these species are better known it seems probable that they will furnish characters of generic value, and that the more familiar forms may be considered as marginal species.

I am indebted to Dr. E. S. Riggs for the privilege of studying the material in the Field Museum, and to Dr. W. D. Matthew for advice and for the use of pertinent portions of his unpublished studies on Oligocene and Miocene horses, from which, as stated by Osborn, the latter's descriptions of the species mentioned were largely drawn.

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