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## On the Equid genera *Dinohippus* Quinn 1955 and *Pliohippus* Marsh 1874

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SUMMARY — Distinction between *Dinohippus* and *Pliohippus* rests mainly on characters of the skull and dentition, which are discussed in detail. *Pliohippus* has its latest representative in *P. bakeri* n.sp., from the late Hemphillian Coffee Ranch local fauna of Texas. This species differs from older representatives of the genus by its shallow facial pits.

*Dinohippus* is well represented in the Late Hemphillian of the central and southern U.S. by *D. leidyanus* and in northern Mexico by the somewhat younger, but still Hemphillian *D. mexicanus*. Both species were originally included in the genus *Pliohippus*. *D. leidyanus* is considered to be ancestral to *Equus*, possibly through the more poorly known *D. mexicanus*.

RIASSUNTO — [Osservazioni sui generi *Dinohippus* Quinn 1955 e *Pliohippus* Marsh 1874 (Equidae)] — La distinzione tra *Dinohippus* e *Pliohippus* è basata essenzialmente sui caratteri del cranio e della dentatura, che sono discussi in dettaglio. *Pliohippus* ha l'ultimo rappresentante in *P. bakeri* n.sp., del Miocene superiore della fauna locale del Coffee Ranch, Texas. Questa specie differisce dai rappresentanti più antichi di *Pliohippus* per le fosse facciali poco profonde.

*Dinohippus* è bene rappresentato nel Miocene superiore degli Stati Uniti centrali e meridionali da *D. leidyanus*, e nel Messico settentrionale da *D. mexicanus*, del Pliocene inferiore. Entrambe le specie erano state in origine riferite a *Pliohippus*. *D. leidyanus* è considerato l'antenato di *Equus*, possibilmente attraverso il meno noto *D. mexicanus*.

### LATE HEMPHILLIAN EQUIDAE

The greatest differentiation of equids in North America took place in the Clarendonian. Webb (1983) listed 12 equid genera at this time, 3 browsers and 9 grazers and all provided with tridactyl limbs. By the early Hemphillian the browsing genera had disappeared and in the late Hemphillian, still according to Webb, the number of genera had dwindled to four: two, *Neohipparion* and *Nannippus*, with tridactyl limbs; the other two, *Astrohippus* and *Dinohippus*, monodactyl. Two more genera should however be added to the late Hemphillian list: *Onohippidion* (Mac Fadden & Skinner 1979) and *Pliohippus*; the latter survived from the early Hemphillian with slight modifications and seems to have retained tridactyl limbs in some of its species (see below). Of these three genera only *Dinohippus* comes into consideration as a direct ancestor to *Equus*, the others are ruled out by their diverging apomorphies.

### DISTINCTION BETWEEN *DINOHIPPIUS* AND *PLIOHIPPIUS*

Quinn (1955) proposed *Pliohippus leidyanus* Osborn 1918 as the type species of his new genus *Dinohippus*. The type specimen is an articulated skeleton of a subadult female from the late Hemphillian Snake Creek

Fm. of Sioux County, Nebraska. Quinn included in *Dinohippus* also *Pliohippus interpolatus* Cope 1893, the type of which comes from the Clarendon Fm. of Mulberry Canyon, Texas, and his new species *Dinohippus subvenus*, stated to be the oldest species of the genus, from the late Barstovian Lapara Creek local fauna of Texas.

*Dinohippus subvenus* was based on some isolated teeth and a right ramus, *Pliohippus interpolatus* on two isolated upper cheek teeth. Both species are inadequately defined. Matthew & Stirton (1930) referred to *Pliohippus interpolatus* a perfect skull and several dentitions and limb bones from the late Hemphillian Coffee Ranch local fauna of Texas. Their attributions were accepted by Quinn but are erroneous: the Coffee Ranch skull does not conform to the types of *Pliohippus interpolatus* and the whole sample referred to this species actually consists of two different species and genera: one of these is *Dinohippus leidyanus*, the other a somewhat aberrant species of *Pliohippus*.

A careful examination of the type species of *Dinohippus* reveals that Quinn's definition of this genus needs some amendment. The praeorbital pits are well developed in the type species, although they are not large and merge into the lateral surface of the face with rounded margins; they are never pocketed. The malar



pit is practically lacking, although the surface of the cheek is faintly depressed below the praeorbital pit. The buccinator fossette is deep. In the upper cheek teeth the postprotoconal valley is open throughout the crown length of all teeth and this feature distinguishes the dentition of *Dinohippus* from those of *Pliohippus* and *Protohippus*. The hypoconal groove is variously developed, it may either be large or very small and as a rule tends to be reduced and even disappear in much worn teeth.

The fauna of the Coffee Ranch is rich and Matthew and Stirton recorded in it four species of equids: *Pliohippus interpolatus* Cope, *Protohippus ansae* n.sp. (now *Astrohippus ansae*), *Hipparion* (*Neohipparion*) *eurystyle* Cope and *Hipparion* (*Nannippus*) *lenticulare* (Cope). As a matter of fact the attribution of the first species to *Pliohippus interpolatus* is incorrect: *interpolatus* is a doubtful species but does not seem to belong to *Pliohippus* because of its permanently open postprotoconal groove. Part of the Coffee Ranch sample belongs indeed to *Pliohippus*, but to a new and somewhat aberrant species; and part of the sample belongs to *Dinohippus leidymanus*. So far the Coffee Ranch fauna provides the latest record of the genus *Pliohippus*: its age has been determined as 5.9 Ma by Lindsay *et al.* (1984).

The Coffee Ranch *Pliohippus* and *Dinohippus* are of the same size and this may be the reason why they were not separated by Matthew and Stirton: they stated that «there is considerable variation in the size of teeth, ... in the form of the protocone, ... tendency to union between protocone and hypocone, ... development of enamel inflections ...» but failed to notice that the sample is made of two taxa. They ruled out *Pliohippus leidymanus* because «average or normal teeth are larger, higher crowned, with heavier mesostyles, as compared with numerous reported specimens of *leidymanus* ...».

The material figured by these authors is not homogeneous. The jaws UCMP 30204 and 30205 (their Pls. 50 and 51, fig. 1) belong to *Dinohippus leidymanus*: the praemolars are characterized by a wrinkled enamel in their inner folds and by long isthmuses joining the metaconids and metastylids to the outer crescents.

UCMP 30206 (Pl. 51, fig. 2) clearly belongs to another species: the teeth are massive, their enamel is thicker and less convoluted, the isthmuses are short, the metastylids of the molars are very small. The jaw belongs to the same species as the skull UCMP 30200 (Matthew & Stirton, Pls. 45-46). In this skull the praeorbital pit is limited dorsally, caudally and ventrally by a sharp rim and below it a large, although very shallow malar pit is clearly visible. The teeth are more massive than in *Dinohippus leidymanus*, have a thicker enamel with simpler pattern; the protocones of M<sup>1</sup> and M<sup>2</sup> come very close to the hypocones, almost closing the postprotoconal valley.

The Frick Collection in the AMNH contains another large sample of the Coffee Ranch fauna. The jaws may be easily divided between *Dinohippus leidymanus* and *Pliohippus* on the criteria discussed above. A fragmentary skull, AMNH 116164 (Pl. 4, figs. 3-5) belongs to an old mare: the incisors are deeply worn and a trace of the inner enamel can only be seen in I<sup>2</sup>. In all molars and praemolars the protocones are short and the postprotoconal valleys are fully open. The skull AMNH 116172 (Pl. 1, fig. 5; Pl. 2, figs. 1-3) is different. It belongs to a young mare: the incisors have full inner cups and the I<sup>3</sup> have just begun to wear. This corresponds to an age of 5 years in horses. In spite of the young age the protocone of M<sup>1</sup> joins the hypocone; in M<sup>2</sup> only the enamel bands of protocone and hypocone come in contact, closing the lingual outlet of the postprotoconal valley. The praeorbital pit is bordered by a sharp rim dorsally, caudally and rostrally and a broad and very shallow malar pit is present.

The sharply bordered praeorbital pit accompanied by a malar pit characterizes *Pliohippus*, while *Protohippus* resembles *Dinohippus* in facial characters.

In the dentition however *Protohippus* rather recalls *Pliohippus* in the tendency of the protocones of M<sup>1</sup> and M<sup>2</sup>, and occasionally also of P<sup>4</sup>, to join the hypocone in old age.

Matthew and Stirton stated that the limbs of the Coffee Ranch *Pliohippus* are «shorter and considerably heavier than in *P. leidymanus*», but gave no measurements. They figured the bones of fore and hind limbs, except the femur. A metatarsals cannon is ac-

#### EXPLANATION OF PLATE 1

Fig. 1 - AMNH 18972: *Dinohippus leidymanus*, ♂. Late Hemphillian, Snake Creek Fm. at *Aphelops* Draw, Nebraska. Skull, side view.

Fig. 2 - AMNH 87201: *Dinohippus leidymanus*, ♂. Late Hemphillian, Edson Quarry, Kansas. Skull, side view.

Fig. 3 - AMNH 87201: *Dinohippus leidymanus*, ♂. Mandible.

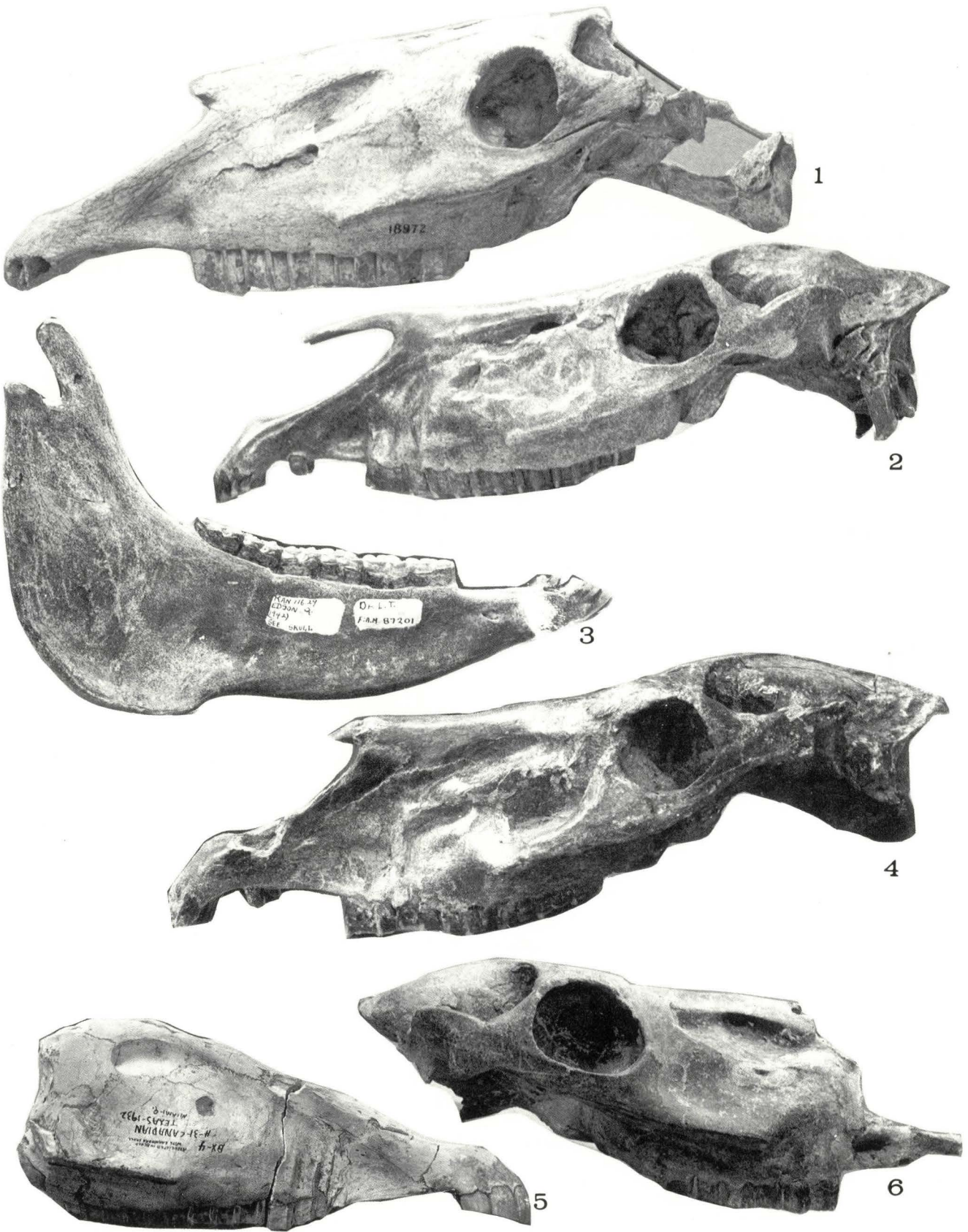
Fig. 4 - AMNH 116129: *Dinohippus leidymanus*, ♂. Late Hemphillian, Edson Quarry, Kansas. Skull (very old), side view.

Fig. 5 - AMNH 116172: *Pliohippus bakeri*, ♀. Late Hemphillian, Coffee Ranch, Texas. Fragmental skull, side view.

Fig. 6 - AMNH 116970: *Dinohippus leidymanus*. Late Hemphillian, Edson Quarry, Kansas. Juvenile partial skull, side view.

All figures 1/3







accompanied by the ends of the lateral metatarsal and by the first phalange of the 4th digit: if the reconstruction is correct this equid had tridactyl limbs, although this does not imply that the lateral digits were necessarily functional.

It is to be expected that if two species are present, their limbs will fall into different size classes, but measurements of 55 metacarpal and 29 metatarsal canons of the UCMP collection failed to give conclusive evidence for this: the two species differ only in their skulls and teeth, and possibly in the retention of lateral digits in one of them. Contrary to the statement of Matthew and Stirton, the sizes of the cannon bones fall in the range of *Dinohippus leidymanus*.

There is little doubt that, in spite of the unusually shallow praeorbital and malar pits of the skulls UCMP 30200 and AMNH 116172, these specimens are closely related to the earlier species grouped under *Pliohippus*. These skulls, and the jaws mentioned above, agree perfectly with the other species of this genus also in dental features. The reduction of the facial fossae is a general trend which set in in equids in the late Miocene and continued into the Pleistocene — with the notable exception of the South American *Onohippidium*. Although the Coffee Ranch fossils conform only imperfectly to the definition of *Pliohippus* as given by Quinn (1955: but the metastylid is usually smaller than the metaconid!) in the characters of the face, creation of a new genus for this species, which clearly represents a final stage of the evolutionary line of *Pliohippus*, is unnecessary and inopportune.

These specimens are therefore included in *Pliohippus*, but the species name *interpolatus* is not applicable to them. The type of this species, an isolated upper molar, belongs to a rather young specimen. The protocone is well separated from the hypocone and the lingual surface of the tooth is marked by a groove in the cement in correspondence of the outlet of the postprotoconal valley, which runs all along the crown to the root. There is no tendency whatsoever of the postprotoconal valley to close and this tooth seems rather to belong to *Dinohippus*, although it is clearly inadequate to define a species. For the *Pliohippus* of Coffee Ranch a new name is needed. I propose the

name *Pliohippus bakeri*, in honour of Mr. Charles Lawrence Baker, who directed the field works of the Rio Bravo Oil Company during which the Coffee Ranch fauna was discovered.

PLIOHIPPIUS BAKERI n.sp.

Pl. 1, fig. 5; Pl. 2, figs. 1-3

*Holotype* — UCMP 30200, complete skull of an adult ♂, referred to *P. interpolatus* by Matthew and Stirton. Fig.: Matthew & Stirton 1930, pls. 45-46.

*Locality* — Coffee Ranch, Miami County, Texas.

*Age* — Late Hemphillian, about 5.9 Ma (Lindsay *et al.*, 1984).

*Hypodigm* — Several more or less fragmental skulls, jaws, teeth, postcranial bones in UCMP and AMNH.

*Definition* — Size large as in *Dinohippus leidymanus*. Praeorbital pit large, shallow, sharply rimmed dorsally, caudally and ventrally, not pocketed; malar pit broad, rounded, much shallower than in the other species of the genus. Teeth massive with thick enamel, not plicated in the inner folds and fossettes; postprotoconal valley of the upper cheek teeth narrow, hypocone strong; protocone joining hypocone in worn M<sup>1</sup> and M<sup>2</sup>; metastylid of lower molars very small; limbs possibly tridactyl.

THE GENUS *DINOHIPPUS* QUINN 1955

*DINOHIPPUS LEIDYANUS* (Osborn) 1918

The type, AMNH 17224

Osborn figured and summarily described the skull of the type specimen of his *Pliohippus leidymanus* but gave no measurements and did not describe the skeleton. The specimen is a subadult female from the late Hemphillian Snake Creek, Sioux County, Nebraska. The third upper and lower incisors are not yet fully erupted and the third molars have just begun to wear. The skull is complete but distorted. The praeorbital pit is rather small and deep, with rounded

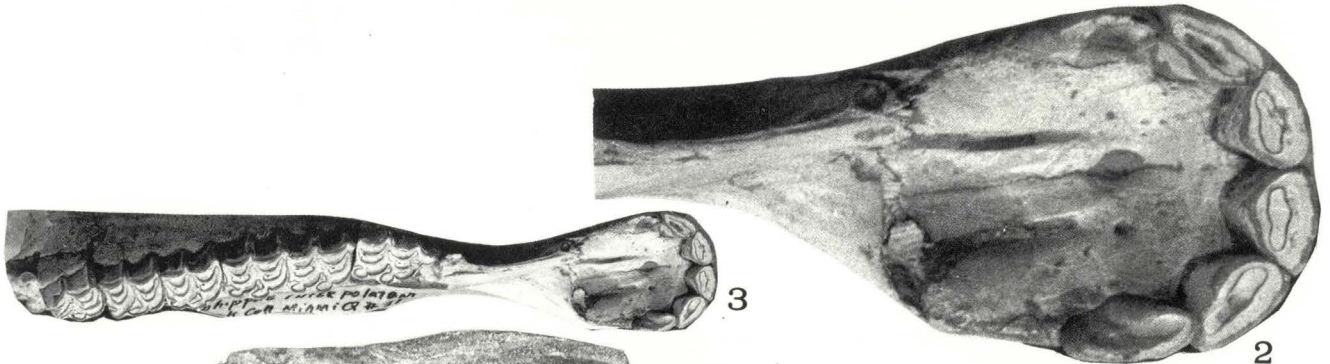
#### EXPLANATION OF PLATE 2

- Fig. 1 - AMNH 116172: *Pliohippus bakeri*, ♀. Late Hemphillian, Coffee Ranch, Texas. Right upper tooth row, 1/1.  
 Fig. 2 - AMNH 116172: *Pliohippus bakeri*, ♀. Late Hemphillian, Coffee Ranch, Texas. Rostrum with incisors and rudimentary canines. 1/1  
 Fig. 3 - AMNH 116172: *Pliohippus bakeri*, ♀. Late Hemphillian, Coffee Ranch, Texas. Fragmental skull, palatal view. 1/3.  
 Fig. 4 - AMNH 87201: *Dinohippus leidymanus*, ♂. Late Hemphillian, Edson Quarry, Kansas. Skull, palatal view, 1/3.  
 Fig. 5 - AMNH 87201: *Dinohippus leidymanus*, ♂. Late Hemphillian, Edson Quarry, Kansas. Skull, upper view.  
 Fig. 6 - AMNH 116970: *Dinohippus leidymanus*. Late Hemphillian, Edson Quarry, Kansas. Pd<sup>3</sup> - M<sup>1</sup>, 1/1.





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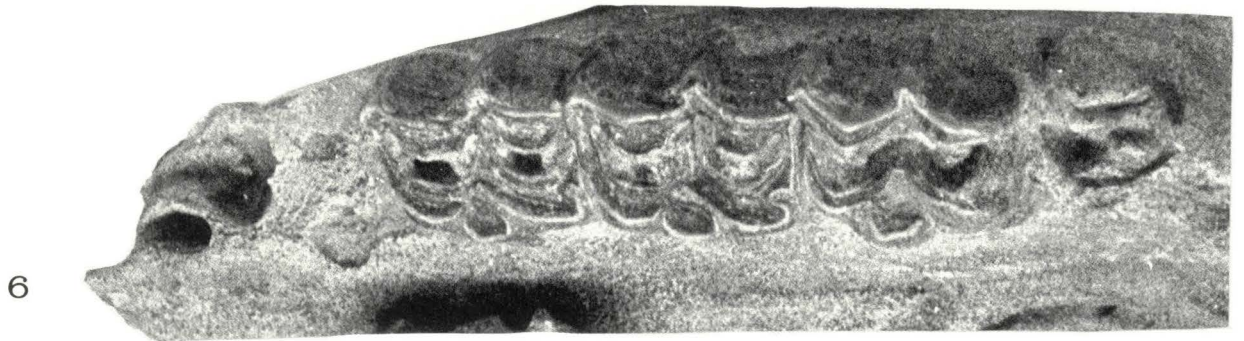
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4



5



6



TABLE I — Measurements of the skull and upper dentition

	1	2	22a	23	24
<i>Dinobippus leidymanus</i>					
AMNH 17224	495	435	154	68	86
AMNH 18972	—	444	153	72	80
AMNH 87201	429	409	149	69	82
AMNH 116129	445	424	141	69	79
AMNH 116132	—	—	149	69	82
AMNH 116133	—	—	166	77	95
AMNH 116136	—	470	147	68	81
AMNH 116164	—	—	160	76	88
<i>Dinobippus mexicanus</i>					
LACM/CIT					
max.	—	—	165	74	92
min.	—	—	145	66	87
<i>Pliobippus bakeri</i>					
UCMP 30200	473	442	169	81	91
AMNH 116172	—	—	158	73	90

AMNH 17224 - Holotype, subadult female, articulated skeleton (skull distorted). Late Hemphillian, Snake Creek, Sioux Co., Nebraska.

AMNH 18972 - Adult male, damaged skull; Late Hemphillian, Snake Creek, Sioux Co., Nebraska.

AMNH 87201 - Adult male skull and jaw; Late Hemphillian, Edson Quarry, Kansas.

AMNH 116129 - Old male skull, same loc.

AMNH 116132 - Adult palate, same loc.

AMNH 116133 - Young palate, 4-5 yrs. old, same loc.

AMNH 116136 - Very old male skull; Late Hemphillian, Grey's Ranch Quarry, Wikieup, Arizona.

AMNH 116164 - Fragmental male skull; Late Hemphillian, Coffee Ranch, Texas.

LACM/CIT - Specimens from Yapòmera, Chihuahua, Mexico; Latest Hemphillian. Measurements after Lance 1950, modified.

UCMP 30200 - Holotype, Late Hemphillian, Coffee Ranch, Texas.

AMNH 116172 - Partial female skull, same locality.

margins. It extends caudally to the anterior tip of the lachrymal and becomes indistinct rostrally of the infraorbital foramen. The vomer extends posteriorly shortly behind the pterygoids. Osborn's figures need little comment but attention may be drawn on few details. The enamel of the inner folds of the lower praemolars is richly plicated and metaconids and metastylids are attached to long and slender isthmuses. The narial notch appears to be rather deep, its posterior angle overlies the anterior pillar of P<sup>3</sup>; the specimen is however deformed, the left praemaxillary has been compressed dorso-ventrally and rotated, shifting caudally its upper end. On the right side of the skull (not shown in Osborn's figures) the angle of the narial notch overlies the posterior lobe of P<sup>2</sup>. The basicranium and occipital condyles, with the paraoccipital processes,

are also distorted and appear rotated clockwise in the restoration given by Osborn.

The skeleton is now mounted in an exhibit hall of the AMNH and is not accessible for detailed observation. From measurements taken on the lateral sides of the limb bones of a mounted cast I have calculated the approximate total lengths of the main bones (see table of measurements). It may be remarked that in all living equids the first phalange of the hand exceeds in length that of the foot; the reverse is the case in the mounted skeleton of *Dinobippus leidymanus*. Have the phalanges been mounted in the wrong place? The lateral metapodials extend the full length of the cannon and reach the proximal margin of the trochlea in the manus; in the pes they end about 1 cm above the trochlea. They thin out distally, are slightly expanded dorso-ventrally and are laterally flattened at their lower ends. There is no trace of articular surfaces for the phalanges and the bones are too thin to support functional lateral digits. The hoof phalanges are rounded anteriorly in the manus, subtriangular with a rounded tip in the pes and retain a trace of the central cleft that characterizes primitive equids.

The height at the withers of the live animal may be evaluated somewhere between 1200 and 1250 cm.

#### Snake Creek - Additional specimens

Pl. 1, fig. 1; Pl. 3, fig. 1; Pl. 4, figs. 1, 2

An adult male skull, AMNH 18972, and a jaw, AMNH 18973, possibly of the same individual, come from the Upper Snake Creek Beds at *Aphelops* Draw, Nebraska, the same formation as the type skeleton, and were described by Matthew (1924) and by Azzaroli (1982). The skull lacks the roof of the braincase but is not deformed to any great extent; it is somewhat larger than the type. The praeorbital pit is well

TABLE II — Measurements of the lower cheek teeth.

	6a	7	8
<i>Dinobippus leidymanus</i>			
AMNH 17224	154	76	83
AMNH 18973	153	72	80
AMNH 116165	161		
AMNH 116189	159	76	80
AMNH 87201	145	71	77
AMNH 116130	157	75	84
AMNH 116131	164	76	86

AMNH 17224 - See Table I.

AMNH 18973 - Same locality, possibly same individual as 18972: see Table I.

AMNH 116165 and 116189: Coffe Ranch, Texas.

AMNH 87201 - See Table I.

AMNH 116130, 116131: Edson Quarry, Kansas.

TABLE III — Measurements of the limb bones.

<i>Dinohippus leidyanus</i>	AMNH 17224	AMNH 116134	AMNH 116135			
Scapula HS	273					
Humerus GLI	245					
« GLC	218					
Radius GL	278	262	274			
« Bp		61	66			
« SD		31				
« BD		58	61			
« BFd			46.5			
II Metac. GL			165			
III Letac. GL	210	190	206			
« Bp		36.5	38			
« SD		24.5	25			
« Bd		37	37			
I Phal. GL	60	66	66			
« Bp		40	40.5			
« Bd		33	33			
III Phal. GL		51	55.5			
« GB		52.5	56.5			
« BF		37.5	35			
<i>Dinohippus leidyanus</i>	AMNH 17224	AMNH 87204	AMNH 87208	AMNH 87209	AMNH 87112	AMNH 87211
Femur GL	312					
« GLC	284					291
« Bp						94
« SD						32
« Bd						74
Tibia GL	300	311	309			
« Bp		78.5	74			
« SD		33	33			
« Bd		57.5	54			
Calcaneus GL		93	91	89.5		
Astragalus GH		51	47.5	48.5		
« GB		48	42.5	46		
« BFd		38.5	38	38		
II Metat. GL		176	177		176	
III Metat. GL	240	232	223	221	225	
« Bp		39	35	38	35.5	
« SD		24	22	23.5	24	
« Bd		31.5	34	38	36	
IV Metat. GL			179		182	
I Phalange GL	62	61.5	62	62.5		
« Bp		39	37	40		
« Bd		32	30	32		
III Phalange GL		49	44	48		
« GB		55	53.5	48.5		
« BF		33	32	31		

AMNH 17224: Holotype, see Tab I. Measurements approximate.

AMNH 116134: Edson Quarry, Kansas, left fore limb.

AMNH 116135: Id., left fore limb.

AMNH 17224: Holotype, see Tab. I. Measurements approximate.

AMNH 87204: Edson Quarry, Kansas, right hind limb.

AMNH 87208: Id., right hind limb.

AMNH 87209: Id., right hind limb.

AMNH 87212: Id., left hind metatarsals.

AMNH 87211: Id., right femur.



developed, proportionally larger than in the type (about  $80 \times 30$  mm) and the buccinator fossette is deep. There is no malar pit. The posterior angle of the narial notch overlies the central pillar of  $P^2$ . The cheek teeth display the same pattern as the type; the incisors were lost.

The Edson Quarry sample

Pl. 1, figs. 2, 3, 4, 6; Pl. 2, figs. 4, 5, 6; Pl. 3, fig. 2.

The geology of the Edson Quarry site, Sherman County, Kansas, was recently described by Harrison (1983), who studied the carnivores and gave a list of the fauna, which belongs to the Ogallala Fm. and has been referred to the late Hemphillian. There are no radiometric or palaeomagnetic dates at present. Harrison's list includes three equid species: *Dinobippus interpolatus*, *Hipparion eurystyle* and *Nannhippus* sp.

*Dinobippus* is represented in the AMNH, Frick Collection, by a large number of well preserved specimens. In the collection they have been labelled *Dinobippus leidymanus*. The fossils closely resemble the Snake Creek specimens, with minor differences that seem to be due to a rather high individual variability.

Two fine adult skulls are of slightly smaller size than the Snake Creek skulls and show a simpler enamel pattern in the inner fossettes of their cheek teeth; on the other hand the limb bones are of variable size and the largest equal or even exceed the size of the type.

The male skull AMNH 87201, with jaw, is comparatively small. The inner enamel of the cheek teeth is not plicated. The praeorbital pit is somewhat crushed; there is no malar pit but the lateral surface of the cheek has been slightly compressed by deformation in the area between the praeorbital pit and the malar ridge. The occiput is well preserved and shows no trace of the distortion seen in the type skull. The facial angle, between the axis of the face and the axis of the braincase, is rather close,  $26^\circ$ .

A very old male, AMNH 116129, is slightly larger. The praeorbital pit is well preserved, with its rounded margins; below it the bone has been crushed, simulating a malar pit. In both skulls the angle of the narial notch overlies the central pillar of  $P^2$ .

Two juvenile skulls differ from the adult skulls in a significant way. AMNH 116968 is a fragmentary skull

with complete deciduous dentition; AMNH 116970 is better preserved in the facial part; it has the deciduous  $Pd^3$  and  $Pd^4$  and the permanent  $M^1$  in wear. In both specimens the praeorbital pit is about 4 mm deep; it is more elongated than in the adult skulls and overlaps the anterior portion of the lachrymal; moreover, it is bordered dorsally and caudally by a sharp, but shallow rim, which becomes more prominent on the nasal bones; the ventral margin of the pit is more rounded and the anterior termination is indistinct. The floor of the pit is complicated by a shallow, broadly elongated bulge, rounded in profile, running from dorsal to ventral and dividing the pit into two unequal parts, the posterior being about  $1/3$  the length of the anterior. The pit does not resemble the homologous pit of *Pliobippus*, which is more extended dorsoventrally, is uniformly concave and is bordered by a much sharper rim. There is no true malar pit but the cheek area is slightly depressed. The features of these skulls may possibly offer a clue to trace the ancestry of *Dinobippus*.

The limb bones are well preserved. The lateral metapodials terminate shortly above the trochlea of the metacarpal cannon in AMNH 116135 and are distally flattened. In the metatarsal cannon AMNH 87208 they terminate about 25 mm above the trochlea and are similar to the lateral metacarpals in shape. The astragali are higher than broad and their articular facets for the cuboid protrude distinctly beyond the navicular facet.

Altogether the Edson sample appears slightly more primitive than the specimens from Snake Creek and Coffee Ranch because of their uniformly simple enamel pattern of the cheek teeth, the frequent occurrence of very short protocones and the often rudimentary or even absent hypoconal groove. These differences however do not seem to warrant a separation at species level.

Oklahoma

The Frick Collection includes a large number of fossils: skulls, dentitions and postcranials from the Guymon area, Texas County, Oklahoma, referred to the late Hemphillian. *Dinobippus leidymanus* is represented by a large number of specimens; unfor-

#### EXPLANATION OF PLATE 3

Fig. 1 - AMNH 18792: *Dinobippus leidymanus*, ♂. Late Hemphillian, Snake Creek Fm. at *Aphelops* Draw, Nebraska. Detail of the face.

Fig. 2 - AMNH 116970: *Dinobippus leidymanus*. Late Hemphillian, Edson Quarry, Kansas. Juvenile skull, detail of the face.

Fig. 3 - *Dinobippus mexicanus*. Latest Hemphillian, Yepòmera, Chihuahua, Mexico. Subadult skull, detail of the face.

Figures enlarged, not to scale.





tunately fossils are badly crushed and do not add substantial information.

#### Arizona

Pl. 4, fig. 6

*Dinohippus leidymanus* has been identified in two localities: in the Redington Quarry and Old Cabin Quarry, Quiburis Fm. near Redington, and in the Big Sandy Fm. at Grey's Ranch Quarry, Wikeup.

The Wikeup fauna has been dated to the later part of palaeomagnetic Epoch 5; approximately between 5.5 and 5.7 Ma, by Lindsay *et al.*, 1984; at Quiburis faunas are reported by the same authors in two distinct levels, one in the upper normal interval of Epoch 5 (i.e. synchronous with Wikeup), the other in the lower normal interval (approximately 5.8-6.0 Ma).

The Quiburis fauna is characterized by the joint occurrence of *Dinohippus leidymanus* and *Pliohippus* (possibly *P. bakeri*). The Wikeup fauna contains *Onohippidium galushai* as a dominant element among equids and in smaller number *Dinohippus leidymanus*. An extremely old male skull, AMNH 116136, gives evidence that even at this stage of wear the postprotoconal valley remained fully open in the upper molars (Pl. 4, fig. 6).

#### California

May and Repenning (1982) dated the Mt. Eden fauna of the San Timoteo Badlands, southern California, to somewhere between 5.4 and 5.0 Ma: the fauna therefore belongs to the late Hemphillian, but not to the latest phases of this stage. Unfortunately equid remains are fragmentary, mostly isolated teeth and few limb bones. Frick (1921) distinguished two equid species, *Pliohippus osborni* and *Pliohippus edensis*. The former appears to be somewhat more advanced in the anterior elongation of the protocones of the upper cheek teeth. The hypoconal groove is very capriciously developed: in *osborni* it may be very deep, or shallow, or totally lacking; in *edensis* it is shallow or absent; in two specimens figured by Frick it is completely closed.

The enamel of the inner fossettes is not plicated. The limb bones, the most significant of which are a tibia, a metatarsal cannon and a first phalange, are similar to the bones from Edson Quarry.

Lance (1950) expressed the opinion that *P. edensis* may be a synonym of *P. osborni*. The significant fact is however that the most typical features of *Pliohippus* do not appear in the Mt. Eden sample, which belongs to *Dinohippus* and compares well with the sample from Edson Quarry in the characters of the teeth and limbs. Here *Pliohippus osborni* and *Pliohippus edensis* are tentatively synonymized with *Dinohippus leidymanus*. Lance was right in assuming that the Mt. Eden equid was possibly ancestral to his *Pliohippus mexicanus*.

#### DINOHIPPIUS MEXICANUS (Lance) 1950

This species was described as *Pliohippus mexicanus* by Lance (1950). The original description was supplemented by a new description of the skull characters by Mac Fadden (1984).

*Dinohippus mexicanus* comes from the latest Hemphillian of Yepòmera, Chihuahua, Mexico. May and Repenning (1982) date it to about 4.8 Ma while Lindsay *et al.*, (1984) correlate it with the Sidufjall normal magnetic episode (4.32-4.47 Ma).

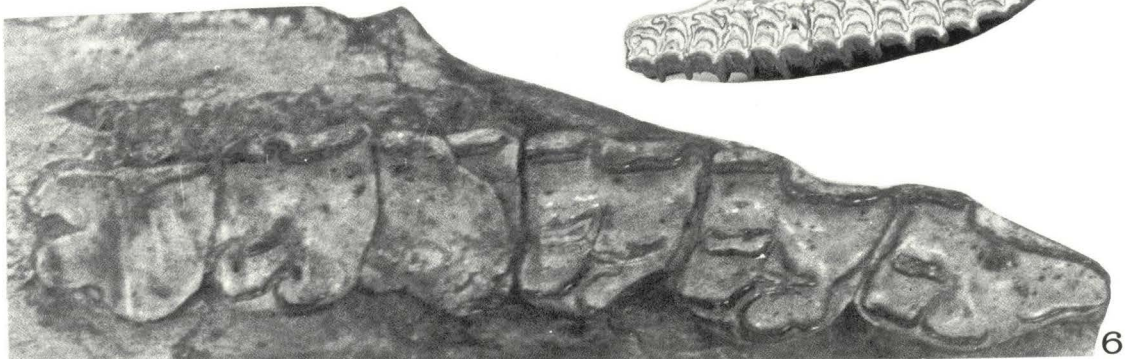
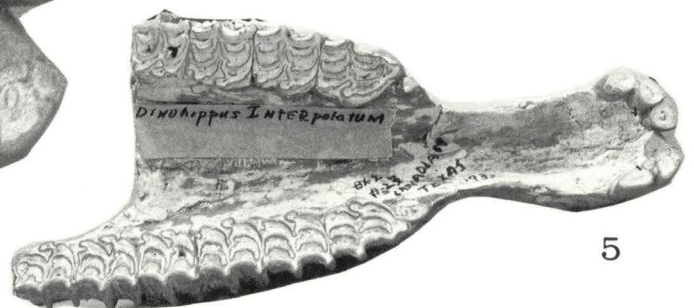
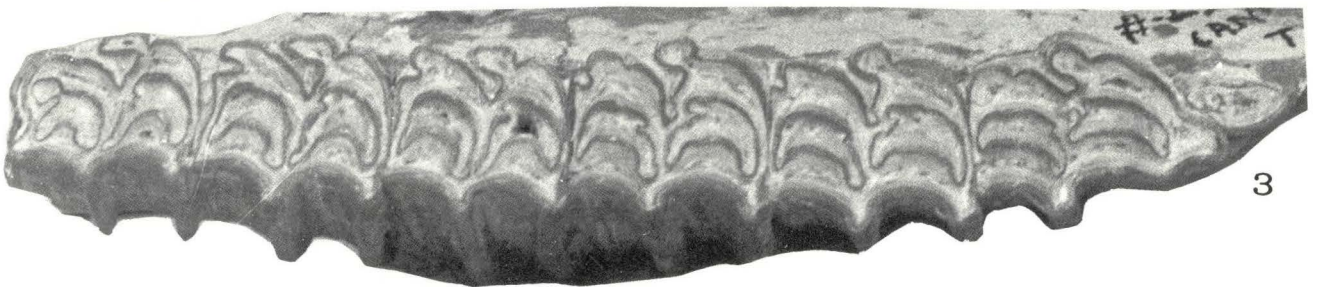
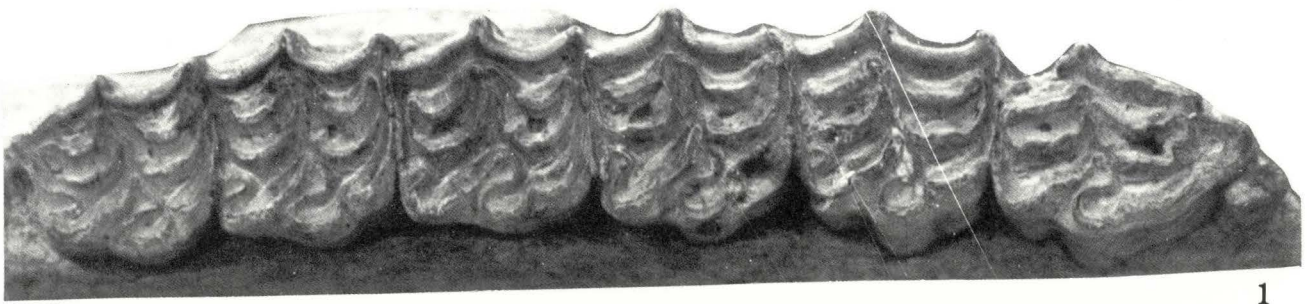
Lance reported the occurrence of four equids in this fauna: *Pliohippus (Pliohippus) mexicanus* n.sp., *Pliohippus (Astrohippus) stocki* n.sp., *Nannippus* cf. *minor* and *Neohipparion* cf. *phosphorum*. The former two species are monodactyl, the others tridactyl. Only the first three species were described. *Astrohippus stocki* is easily distinguished by its small size, simple enamel pattern of the cheek teeth and a complicated system of facial pits (Mac Fadden 1984). *Pliohippus* (now *Dinohippus*) *mexicanus* was considered by Lance to be ancestral to *Plesippus* and, through this, to *Equus*; Quinn (1955) on the other hand included it in *Asinus* and considered it ancestral to asses and hemiones.

The material is very rich but unfortunately includes only few fragments of skulls. The dentitions are closely similar to those of *Dinohippus leidymanus*; some specimens of upper cheek teeth appear rather advanced.

#### EXPLANATION OF PLATE 4

- Fig. 1 - AMNH 18792: *Dinohippus leidymanus*, ♂. Late Hemphillian, Snake Creek Fm. at *Aphelops* Draw, Nebraska. Right upper tooth row, 1/1.  
 Fig. 2 - AMNH 18793: *Dinohippus leidymanus*, ♂. Same locality as AMNH 18792. Right lower tooth row, 1/1.  
 Fig. 3 - AMNH 116164: *Dinohippus leidymanus*, ♀. Late Hemphillian, Coffee Ranch, Texas. Left upper tooth row, 1/1.  
 Fig. 4 - AMNH 116164: *Dinohippus leidymanus*, ♀. Rostrum with incisors and rudimentary canines. 1/1.  
 Fig. 5 - AMNH 116164: *Dinohippus leidymanus*, ♀. Fragmental skull, palatal view, 1/3.  
 Fig. 6 - AMNH 116136: *Dinohippus leidymanus*, ♂. Late Hemphillian, Grey's Ranch Quarry, Wikeup, Arizona. Right upper tooth row, very old; 1/1. Note fully open postprotoconal valley in M<sup>2</sup>.







ed in the richly plicated enamel of the inner fossettes (Lance 1950, fig. 4a, b, d, h). A fragment of a subadult skull ( $M^3$  not yet erupted), LACM/CIT 275/3723, shows a praeorbital pit similar to that of the adult specimens of *Dinohippus leidymanus*, although its dorsal rim is somewhat sharper (Pl. 3, fig. 3). There is no malar pit (Mac Fadden 1984).

Lance gave only summary measurements of the limb bones: average lengths, ranges of variation, standard deviations. Sizes conform well with *Dinohippus leidymanus*.

At the present state of knowledge *Dinohippus mexicanus* may be considered a somewhat progressive descendant of *D. leidymanus*, from which it seems to differ very little. Pending further information, one cannot escape the impression that evolution of *Dinohippus* proceeded very slowly in the time interval between 6 and 4 Ma.

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#### NOTE

The following abbreviations were used in the text:

AMNH: American Museum of Natural History, New York, Department of Vertebrate Palaeontology.

LACM and LACM/CIT: Los Angeles County Museum, Department of Vertebrate Palaeontology.

UCMP: University of California Museum of Palaeontology, Berkeley.

In the tables of measurements, codes conform with: «A Guide to the Measurements of Animal Bones from Archaeological Sites», by Angela Von del Driesch – Harvard University, Peabody Museum of Archaeology and Ethnology, Bulletin 1, 1976.

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