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by

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ABSTRACT

A specimen from the Esmeralda Formation (Mio-Pliocene) of Nevada provides new information concerning the poorly known anchitheriine horse, Megahippus McGrew. Hypohippus nevadensis Merriam, from the same formation, approaches Megahippus in size, but lacks the characteristic megahippine specialization of the dentition.

INTRODUCTION

The anchitheriine genus Megahippus is perhaps the least well known of the later Tertiary horses. Of the genotypic species, M. matthewi, only a mandible (McGrew, 1938, pp. 315-317), a maxillary fragment, and some questionably referred foot elements (Barbour, 1914) have been adequately described or illustrated. One additional species, M. mckennai, has been described (Tedford and Alf, 1962), based on a crushed skull of an old individual, with heavily worn dentition. Additional specimens of both species are known, but descriptions have not been published.

Specimens collected by the writer provide information on structures not previously recorded adequately, especially the highly specialized upper incisors.

Specimen and locality numbers are those of the University of California Museum of Paleontology, Berkeley.

Order PERISSODACTYLA
Family Equidae
Subfamily Anchitheriinae
Megahippus, cf. M. matthewi (Barbour) 1914

Material: UCMP 59271, parts of cranium and mandibles of a young adult animal: right maxillary with P^{1-3}, part of P^4, fragments of other upper cheek teeth; isolated right I^2 and I^3, probably unerupted; fragments of posterior part of cranium, poorly preserved; parts of both rami of mandible, with P_2-M_3 in place, M_3 partly erupted; isolated left I_1 and right I_2, I_2 unerupted.
Locality: UCMP loc. V-6136, Confusion Quarry. Esmeralda Formation, Mineral County, Nevada. A mile north of north end of Cedar Mountain range, 4 miles northwest of Warrior Mine. Latitude 38° 38' 24" N.; longitude 117° 53' 00" W.
Age: Clarendonian (late Miocene or early Pliocene).
Description: Lower teeth (Fig. 1): Lower incisors are large and heavy, with high lingual cingula enclosing a broad spoon-shaped basin. Strong labial cingula extend up the labial corners of the teeth nearly to the tips. The lower incisors are very similar to those in the mandible (UCMP 28841) of M. matthewi from the Burge fauna of Nebraska, described by McGrew (1938, pp. 315-317, fig. 5). These teeth formed the basis for much of McGrew's diagnosis of the genus Megahippus. Incisors of the Nevada specimen are slightly larger than those of M. matthewi from Burge and have more strongly developed cingula.

Lower cheek teeth are also similar to those of the Burge specimen but are slightly larger (Table 1) and higher crowned. P_4 has a well developed lingual cingulum, interrupted lingual to the entoconid. There are suggestions of a lingual cingulum at the bases of the cusps of P_3 and P_4, but not on the molars. However, strong cingular structures are developed across the lower parts of the lingual openings of the metaflexids and the entoflexids of P_3 through M_3. Heavy labial

cingula are present on all the lower cheek teeth. In the molars, the metastylid and metaconid are separated at their tips by a faint groove extending 2-3 mm. down the lingual side of the tooth. A similar condition appears in the unerupted premolars of an unpublished specimen of M. matthewi from Nebraska (UCMP 29559). The metastylid is about 1 mm. lower than the metaconid in the unworn M_3, and the same difference appears to have been present in the other molars. The premolars differ from the molars in a pronounced posterior extension of the metastylid, especially in early stages of wear. P_4 is the largest of the lower cheek teeth in all dimensions. There is a regular and gradual decrease in size of the other cheek teeth, both anterior and posterior to P_4.

Upper teeth (Fig. 2): Barbour (1914a, p. 171) mentions "strong incisors" with the holotype of M. matthewi, but unfortunately these teeth have never been described or figured. Upper incisors in the holotype of M. mckennai Tedford and Alf (1962) are present but heavily worn. The two upper incisors preserved in the Cedar Mountain specimen show that these teeth in Megahippus are as unique as the lowers (Fig. 2a). Unfortunately, I^1 was not found, but I^2 and I^3 are large and scoop-shaped. I^2 bears a deep basin, which is bounded labially by the high, sharp edge of the tooth. Lingually and posteriorly the basin is bounded by a pair of high crests, which meet in a broad V. There is a short, heavy lingual cingulum at the base of the lingual crest; the posterior crest arises at the edge of the tooth. There is a labial cingulum, most pronounced at the anterior edge of the tooth. I^3 is essentially a smaller duplicate of I^2, except that the posterior crest is weaker, and bears a fold or cuspule on its basinward face. The lingual crest is faintly serrated. Incisors of M. mckennai appear to have been similar, but much smaller, and with very weak labial cingula.

P^1 (Fig. 2b) is similar in form to the corresponding tooth of Hypohippus. It differs mainly in the presence of a strong lingual cingulum and a weaker anterolabial cingulum.

P^2 and P^3 closely resemble corresponding teeth in the type of M. matthewi. The state of wear is nearly equivalent in the two specimens. Lingual cingula are stronger in the Nevada specimen, and the shelf anterior to the protocone is broader, especially on P^3. P^3 has a small crochet near the flexure of the metaloph, as do P^3 and P^4 in the type of M. matthewi. P^2 also has a crochet, but it is weaker and more laterally placed than in P^3. There is a second spur of enamel jutting anteromedially from the metaloph near its junction with the hypocone. As in the type of M. matthewi each tooth has a large cuspule on the cingulum anteromedial to the hypocone.

P^4 is represented by a fragment including the anterior half of the protocone and most of the protoloph. An isolated ectoloph and part of a hypocone probably also belong to this tooth. None of these fragments shows any significant difference from P^3.

A medial half of one of the molars probably is part of M^1. This fragment has a lingual cingulum nearly as strong as those of the premolars, and a cingular cuspule larger than that on P^2 or on P^3. In the type of M. matthewi, the lingual cingulum of M^1 does not extend across the protocone or the hypocone. Other fragments suggest that all upper molars of the Nevada Megahippus had well developed lingual cingula. One fragment, apparently of the left M^3, shows a very large cingular cuspule that is more than half the size of the hypocone.

Skull: Structures that can be identified are similar to those of Hypohippus, but are much larger.

Discussion: The type of the genus Megahippus McGrew (1938) was Hypohippus matthewi Barbour (1914). The type material of Barbour's species, from Devil's Gulch, Brown County, Nebraska, included "the right maxilla with four perfect teeth, and the left, with three, together with strong incisors. In addition, scattered lower teeth, numerous limb bones, and several nearly complete feet were found and referred to this species." (Barbour, 1914, p. 171). Only the right maxillary fragment with P^2-M^1 and a forefoot, later referred by Osborn

(1918, p. 210) to "a species of Merychippus," were described and illustrated. McGrew's generic diagnosis was based primarily on the referred mandible from the Burge fauna. Its most distinctive features were the short, upturned symphysis and greatly enlarged, procumbent incisors.

Megahippus mckennai Tedford and Alf (1962) from Barstow provides a link in time, in size, and in structure, between M. matthewi and its unknown ancestor in or near the lineage of Hypohippus. Megahippus mckennai, M. matthewi from Nebraska, and the Nevada Megahippus form a structural series, although not a perfectly graded one. The Nevada form is about 5% larger than M. matthewi, which in turn is about 25% larger than M. mckennai (Table 1). In M. mckennai, the lingual cingulum is strong on P^2, slightly weaker on P^3, and discontinuous on P^4. In M. matthewi the cingulum is continuous and strong on P^{2-4}, but discontinuous across the protocone and hypocone of M^1. In the Nevada Megahippus the cingulum is as strong on at least one (and probably on all) of the upper molars as on the premolars. M. mckennai lacks the cingular cuspule anterolingual to the hypocone, which is present in the Nevada specimen and on P^{2-4} of M. matthewi.

Crochets appear on various upper cheek teeth of all specimens of Megahippus, as they do in advanced species of Hypohippus. This was evidently a variable character, with no taxonomic significance in the Hypohippus-Megahippus branch of the anchitheriine horses.

Differences between the Nevada Megahippus and described specimens of M. matthewi from the Great Plains may merit specific separation. However, it seems advisable to refrain from naming another species until more information is available concerning the range of variation of M. matthewi.

The specimen from Cedar Mountain is the first record of Megahippus from the Great Basin. Megahippus mckennai is recorded only from the Barstow Formation in the Mojave Desert of California. James (1963) lists but has not yet described specimens of Megahippus

in Clarendonian faunas of the Cuyama Valley Badlands of California. Megahippus matthewi has been reported only in the Devil's Gulch (Barbour, 1914) and Burge assemblages (McGrew, 1938), and possibly at Big Spring Canyon, South Dakota (Gregory, 1942).

AFFINITIES OF HYPOHIPPUS NEVADENSIS

Presence of Megahippus in the Clarendonian assemblage from the Cedar Mountain area raises a question about the relationships of Hypohippus nevadensis Merriam (1913, pp. 420-427). This species was based on a specimen from UCMP loc. 1980, on the east side of Cedar Mountain, a few miles southeast of locality V-6136, and in beds of approximately the same age as those at V-6137. The type specimen (UCMP 21056) includes several parts of the skeleton, including the partly articulated limbs, but the part of most importance in characterizing the species is a maxillary fragment with dP^{2-4}. These teeth are larger but similar to the milk teeth of Hypohippus affinis, and the metaloph does not connect with the ectoloph. Merriam considered the disconnection of the metaloph to be of sufficient value for establishment of a new subgenus, Drymohippus.

Only a few additional specimens referable to Hypohippus have been collected in the Cedar Mountain area. These include a tooth fragment, an astragalus, and a questionably referred metacarpal. They may represent H. nevadensis but are not directly comparable with the juvenile type specimen.

If the type specimen of Hypohippus nevadensis and the Megahippus from Cedar Mountain (UCMP 59271) were juvenile and adult individuals respectively of the same species, and if UCMP 59271 were conclusively referable to Megahippus matthewi (Barbour), the specific name M. matthewi might be a synonym of H. nevadensis, and the generic name Megahippus McGrew (1938) would be synonymous with Drymohippus Merriam (1913). The two Nevada specimens do not appear, however, to be of the same species.

Stock (1926) described two anchitheriine horse specimens from the Esmeralda Formation in Fish Lake Valley (UCMP loc. 2804), fifty miles south of Cedar Mountain. One was a skull fragment with dP^2-M^1. Stock recognized differences in the deciduous teeth but referred this specimen to Hypohippus nevadensis because of the similarity in size and because the M^1 showed "characteristics which at least might be expected in M^1 of the type of Hypohippus (Drymohippus) nevadensis." (1926, p. 64). The other specimen was a right mandible, which he also referred to H. nevadensis, apparently on the basis of its large size.

The deciduous premolars of the right side of the Fish Lake Valley skull fragment (UCMP 27116) and portions of the maxillary bone were removed to reveal the permanent P^{2-4}, in order to determine relationships of Hypohippus nevadensis with Megahippus. These teeth, like the M^1, are large, only slightly smaller than those of Megahippus matthewi. However, they lack the characteristic lingual cingulum of Megahippus premolars. A weak cingulum on the lingual base of the protocone of P^2 is only slightly more pronounced than the similar faint cingulum on some premolars of a skull of Hypohippus affinis (UCMP 28840).

Although the mandible (UCMP 27117) also rivals M. matthewi in size, or at least in length of the cheek tooth series, the relatively shallow ramus and relatively long diastema indicate that it is a large Hypohippus, rather than a Megahippus. The presence of an alveolus for P_1 also supports this identification, if McGrew is correct in believing that absence of this tooth is characteristic of the genus Megahippus. Unfortunately the Cedar Mountain specimen of Megahippus casts no light on this point.

The anchitheriine horse in the Fish Lake Valley fauna is a large species of Hypohippus, but a question may remain about its assignment to H. nevadensis. As Stock recognized, there are significant differences between the deciduous dentition from Fish Lake Valley and that from Cedar Mountain. Chief among these is the good connection between

the metaloph and ectoloph in deciduous premolars of the Fish Lake Valley specimen. This specimen also lacks the strong lingual cingulum on dP^2, which is present in the Cedar Mountain specimen. The milk teeth of the Fish Lake Valley horse are longer anteroposteriorly than those of the type specimen of H. nevadensis, and appear somewhat narrower, which may be the result of crushing.

There is no sure evidence relating H. nevadensis to Megahippus. Although large for Hypohippus, the H. nevadensis milk dentition is smaller than would be expected for the Nevada Megahippus. The cingulum on dP^2 may suggest affinity with Megahippus, but this is not convincing. Until more evidence is found at least two species of large anchitheriine horses in the Clarendonian of west-central Nevada are recognized: Megahippus cf. matthewi, of UCMP loc. V-6136 and Hypohippus nevadensis, Merriam's type specimen, from UCMP loc. 1980. The Fish Lake Valley Hypohippus may represent a third species or may be referable to Hypohippus nevadensis.

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Figure 1 was drawn by Owen J. Poe; figure 2 by Mrs. Augusta Lucas.

TABLE 1

COMPARATIVE MEASUREMENTS OF UPPER TEETH OF MEGAHIPPUS

	Megahippus cf. matthewi UCMP 59271	M. matthewi cast of type	M. mckennai Tedford & Alf, 1962
I^2, length	19.5 mm.		12.6 mm.
width	20.3		a 13.5
I^3, length	12.5		
width	16.7		
P^1, length	21		17.8
width	19		12.1
P^2, length (1)	38	35	
length (2)	33	31.5	23.1
width (3)	39	35.7	29.7
P^3, length (1)	a 38	36.8	
length (2)	37	33.5	26.4
width (3)	a 45	39.9	35.3
P^4, length (1)	a 38	38	
length (2)		34	27.4
width (3)		38.5	38.2

a - approximate dimension
(1) length along ectoloph
(2) length across protoconule-hypostyle
(3) width at base of crown

TABLE 2

COMPARATIVE MEASUREMENTS OF LOWER TEETH OF *MEGAHIPPUS*.

	M. cf. *matthewi* UCMP 59271		*M. matthewi* UCMP 28841
	right	left	
I_1, length		20.4 mm.	18.7 mm.
width		28	24.5
I_2, length	17.6		16.3
width	24		21.1
P_2, length	31.5		29.1
width	20		20.7
P_3, length	35	34.5	31.7
width	24.5	24	24.7
P_4, length	36	a 35	32.5
width	26	a 26	25.0
M_1, length	34.5	a 35	31.3
width	24	23.5	24.8
M_2, length	34	a 33	29.6
width	22.5	22.5	23.5
M_3, length	a 33	a 33	31
width		a 19	19.0
P_2- P_4, length	101		92

a - approximate dimension

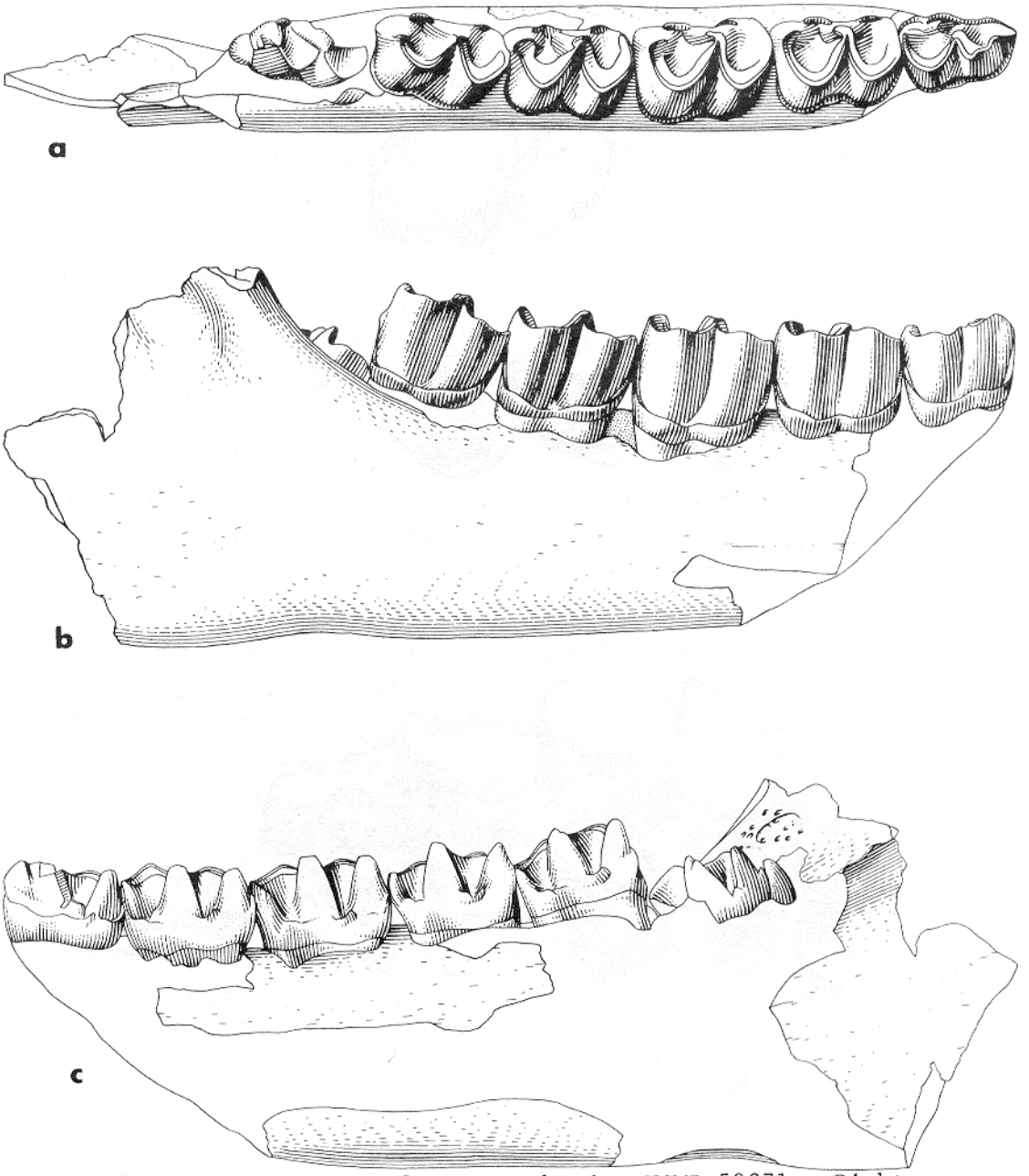

Figure 1. Megahippus cf. M. matthewi. UCMP 59271. Right ramus of mandible with P^2 - M^2 in place, M^3 erupting. a. Occlusal view. b. Lateral view. c. Lingual view. X 1/2.

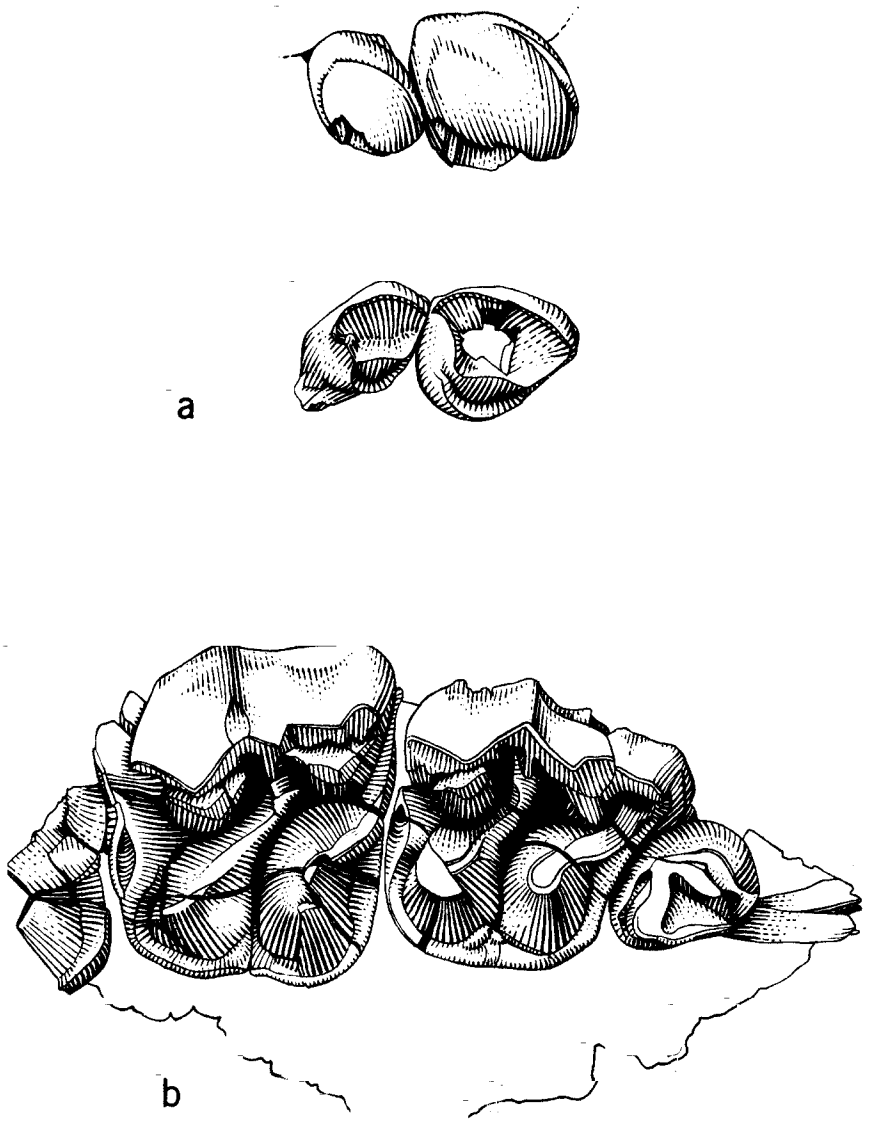

Figure 2. Megahippus cf. M. matthewi. UCMP 59271. a. Right I^2 and I^3. Above, lateral view; below, occlusal view. b. Fragment of right maxilla with P^{1-3}, part of P^4. X 1.

REFERENCES CITED

Barbour, E. H. 1914. A new fossil horse, Hypohippus matthewi. Nebraska Geol. Bull. 4: 169-173.

Gregory, J. T. 1942. Pliocene vertebrates from Big Spring Canyon, South Dakota. Univ. California Publ. Geol. Sci. 26: 307-446.

James, Gideon T. 1963. Paleontology and non-marine stratigraphy of the Cuyama Valley Badlands, California. Part I. Geology, faunal interpretations, and systematic descriptions of Chiroptera, Insectivora, and Rodentia. Univ. California Publ. Geol. Sci. 45: iv + 171 pp.

McGrew, P. O. 1938. The Burge Fauna: a lower Pliocene mammalian assemblage from Nebraska. Univ. California Publ. Bull. Dept. Geol. Sci. 24: 309-328.

Merriam, J. C. 1913. New anchitheriine horses from the Tertiary of the Great Basin area. Univ. California Publ. Bull. Dept. Geol. 7: 419-434.

Osborne, H. F. 1918. Equidae of the Oligocene, Miocene, and Pliocene of North America: iconographic type revision. Amer. Mus. Nat. Hist., Memoirs, n.s., 2: 1-330.

Stock, Chester. 1926. Anchitheriine horses from the Fish Lake Valley region, Nevada. Univ. California Publ. Bull. Dept. Geol. 16: 61-68.

Tedford, R. H. and R. M. Alf. 1962. A new Megahippus from the Barstow Formation, San Bernardino County, California. Southern California Acad. Sci. Bull. 61: 113-122.