MEGAHIPPUSS AND HYPOHIPPUSS
(PERISSODACTYLA, MAMMALIA)
FROM THE ESMERALDA FORMATION OF NEVADA

by

J. E. Mawby
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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 metab flexids and the entoflexids of P\(_3\) through M\(_3\). Heavy labial
cingula are present on all the lower cheek teeth. In the molars, the 
metastyloid 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 
metastyloid is about 1 mm. lower than the metaconid in the unworn 
M3, 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 metastyloid, especially in early stages of 
wear. P4 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 P4.

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, \( \text{I}_1 \) was not found, but \( \text{I}_2 \) and \( \text{I}_3 \) are 
large and scoop-shaped. \( \text{I}_2 \) 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. 
\( \text{I}_3 \) is essentially a smaller duplicate of \( \text{I}_2 \), 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.

\( \text{P}_1 \) (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.
P² and P³ 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 P³. P³ has a small crochet near the flexure of the metaloph, as do P³ and P⁴ in the type of _M. matthewi_. P² also has a crochet, but it is weaker and more laterally placed than in P³. 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.

P⁴ 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 P³.

A medial half of one of the molars probably is part of M¹. This fragment has a lingual cingulum nearly as strong as those of the premolars, and a cingular cuspule larger than that on P² or P³. In the type of _M. matthewi_, the lingual cingulum of M¹ 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 M³, 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 P²-M¹ 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 P2, slightly weaker on P3, and discontinuous on P4. In M. matthewi the cingulum is continuous and strong on P2-4, but discontinuous across the protocone and hypocone of M1. 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 P2-4 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 HYPOHIPPUSS 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 dp2-4. 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 dP², 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 dP² 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.

ACKNOWLEDGEMENTS

Field work and research for the study of which this article forms a part, were supported by the University of California Museum of Paleontology. Portions of the work were done during the tenure of a National Science Foundation Graduate Fellowship. This study was carried out under the guidance of the late Dr. R. A. Stirton, to whom I am deeply indebted.

Figure 1 was drawn by Owen J. Poe; figure 2 by Mrs. Augusta Lucas.
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<th>M. matthewi</th>
<th>M. mckennai</th>
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<tr>
<td></td>
<td>cf. matthewi</td>
<td>cast of type</td>
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<tr>
<td>width</td>
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<td>$I^3$, length</td>
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<td>length (2)</td>
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<tr>
<td>width (3)</td>
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<td></td>
<td>38.2</td>
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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.

<table>
<thead>
<tr>
<th></th>
<th>M. cf. matthewi</th>
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<td></td>
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<td>UCMP 28841</td>
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<tr>
<td></td>
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<td>$l_1$, length</td>
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<td>18.7 mm.</td>
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<tr>
<td>width</td>
<td>28</td>
<td>24.5</td>
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<td>16.3</td>
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<tr>
<td>width</td>
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<td>21.1</td>
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<td>$p_2$, length</td>
<td>31.5</td>
<td>29.1</td>
</tr>
<tr>
<td>width</td>
<td>20</td>
<td>20.7</td>
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<td>$p_3$, length</td>
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<td>31.7</td>
</tr>
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<td>width</td>
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<td>$p_4$, length</td>
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<tr>
<td>width</td>
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<td>width</td>
<td>22.5, 22.5</td>
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<tr>
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<td>$p_2$–$p_4$, length</td>
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<td>92</td>
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*a* - approximate dimension
Figure 1. Megahippus cf. M. matthewi. UCMP 59271. Right ramus of mandible with P² - M² in place, M³ erupting.
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


